On the systematic and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China

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With 7 figures and 4 tables

Abstract

A reassessment of the systematic relationships of pterosaurs from the Lower Cretaceous Yixian Formation of Liaoning Province, China, shows that *Dendrorhynchoides* should be reassigned to the Anurognathidae ("Rhamphorhynchoidea") and that *Eosipterus* possibly belongs within Ctenochasmatidae (Pterodactyloidea). These pterosaurs formed an integral part of a diverse community that inhabited lowland terrestrial environments in the region of northeast China in the Early Cretaceous. A new compilation of data for the Lower Cretaceous hints at a broad differentiation between pterosaurs that lived in continental habitats (anurognathids, ctenochasmatoids, dsungaripteroids) and those that frequented marine environments (ornithocheiroids). Moreover, there is evidence of further differentiation within continental habitats, between pterosaurs living in lowland and coastal regions (anurognathids, ctenochasmatoids) and those living in more inland environments (dsungaripteroids). The temporal and geographical range extensions for high rank taxa that are implied by the Yixian pterosaurs further emphasise the incompleteness and unevenness of the pterosaur fossil record and its unreliability for biostratigraphic zonation.

Key words: Pterosaur, Lower Cretaceous, Jehol Group, China, Anurognathidae, Ctenochasmatidae.

Zusammenfassung

Eine Neubewertung der systematischen Stellung der Flugsaurier von der unterkretazischen Yixian-Formation der Provinz Liaoning, China, zeigt, dass *Dendrorhynchoides* den Anurognathiden („Rhamphorhynchoidea") zugeordnet werden kann und dass *Eosipterus* vermutlich zu den Ctenochasmatiden (Pterodactyloidea) gehört. Diese beiden Flugsaurier bilden einen integralen Bestandteil einer diversen Fauna, die in der Unteren Kreide ein terrestrisches Flachland-Ökosystem im Nordosten Chinas bewohnte. Fasst man die für die Untere Kreide verfügbaren Daten zusammen, so zeigt sich eine weitgehende Differenzierung zwischen Flugsauriern, die überwiegend in kontinentalen Ökosystemen lebten (Anurognathidae, Ctenochasmatoidea, Dsungaripteroidea) und jenen, die auch oft in marinen Bereichen auftreten (Ornithocheiroidea). Darüber hinaus gibt es auch Hinweise auf eine Differenzierung innerhalb der kontinentalen Habitate, zwischen Pterosauriern, die sich in den Ebenen und küstennahen Bereichen aufhielten (Anurognathidae, Ctenochasmatoidea) und den Bewohnern von mehr küstenfernen Ökosystemen (Dsungaripteroidea). Die von den Taxa der Yixian-Formation angezeigte Erweiterung der stratigraphischen und geographischen Reichweite für Taxa höheren Ranges unterstreichen die Unvollständigkeit und Unausgewogenheit des Fossilberichtes der Flugsaurier und seine Unzulänglichkeit für biostratigraphische Zonierungen.

Schlüsselwörter: Pterosaurier, Unter Kreide, Jehol Gruppe, China, Anurognathidae, Ctenochasmatidae.

Introduction

Pterosaurs, Mesozoic flying reptiles, have a relatively modest fossil record compared to most other vertebrate groups (Benton 1993). The record is also highly uneven: only about 30 species, from the 100 or so currently recognised (Wellnhofer 1991a), are known from relatively complete skeletons and most of these have been re-covered from just a handful of fossil lagerstätten scattered across a 140 million year interval, ranging from the Late Triassic to the end of the Cretaceous (e.g. Unwin 2000). The rest of the pterosaur fossil record consists, largely, of isolated and fragmentary remains that, with the exception of jaw fragments, are difficult to identify or assign, except at very general taxonomic levels. Thus, while much progress has been made

recently in understanding pterosaur anatomy, functional morphology and phylogeny (e.g. Padian 1988, Wellnhofer 1991a, Unwin 1999), the evolutionary history of the group remains comparatively poorly known.

The Lower Cretaceous pterosaur fossil record (Fig. 1, Tab. 1) reflects the general situation, although at a somewhat finer scale. The latter half (Aptian + Albian) of this 45 million year long interval contains three pterosaur lagerstätten, each of which has yielded a number of taxa and, in two cases (the Crato Formation and the Santana Formation), exceptionally well preserved remains associated with soft tissues (Martill & Unwin 1989, Martill et al. 1990, Kellner 1997, Martill & Frey 1998). By contrast, the first half of the Lower Cretaceous, the Neocomian (= Berriasian to Barremian) has a much poorer record that is dominated by fragmentary remains (Tab. 1). Until recently, relatively well preserved, associated remains had only been reported from the Tsagaantsav Svita of Western Mongolia (Bakhurina 1982, 1983, 1984, 1986, 1993), the Tugulu group of Xinjiang, China (Young 1964, 1973) and the Vectis Formation of the Isle-of-Wight, England (Hooley 1913). Now, however, a new Lower Cretaceous pterosaur locality has been found in western Liaoning Province, northeast China (Ji Shu'an et al. 1999).

The Jehol Group of western Liaoning Province consists of a thick sequence of Lower Cretaceous fluvial and lacustrine sediments, interca-

lated with lavas and tuffs (see Wang et al. 1998, 1999 and refs therein). The lower part of the sequence has been assigned to the Yixian Formation while the upper part is referred to the Jiufotang Formation (Wang et al. 1998, 1999). Some workers (Ji Qiang et al. 2000) have suggested further subdivision of the Jehol Group, assigning the lower part of the Yixian Formation to a separate unit, the Chaomidianzi Formation, a proposal that we have not adopted here. The Yixian Formation has produced an exceptionally rich and well preserved Early Cretaceous terrestrial biota that includes a diverse palaeoflora, gastropods, bivalves, ostracods, conchostracans, insects, shrimps, fishes, frogs, turtles, lizards, non-avian dinosaurs, birds, mammals and pterosaurs (see Wang et al. [1998, 1999], Barrett [2000] and Chiappe et al. [1999] for principal references on the fauna and flora of this biota).

There has been considerable debate concerning the age of the Yixian Formation, with some workers supporting a Late Jurassic date while others argue for an Early Cretaceous age (see Barrett [2000] for a detailed review of this problem). Recently, Swisher et al. (1999), have provided some well founded radiometric dates of 124.6 ± 0.1 Ma for the Yixian Formation (see also Wang et al. 1999), which indicate that this unit is Barremian. This result is supported by the presence of taxa such as psittacosaurs and angiosperms that are currently known only from the Lower Cretaceous (Xu & Wang 1998, Taylor

			Europe	Asia	North + South America	Australasia
Lower Cretaceous		Alb	**Cambridge Greensand, England** *Anhanguera, Coloborhynchus, Lonchodectes, Ornithocheirus, 'Ornithostoma'*	**Züünbayan Svita, Khuren-Dukh, Mongolia** *Coloborhynchus*	**Paw Paw Fm., Texas, USA** *Coloborhynchus*	**Toolebuc Fm., Australia** *Anhanguera*
					Lagarcito Fm., San Luis, Argentina *Pterodaustro*	
		Apt			**Santana Fm., Araripe, Brazil** *Anhanguera, Brasileodactylus, 'Tropeognathus', Cearadactylus, Tapejara, Tupuxuara*	
					Crato Fm., Araripe, Brazil *Tapejara, Arthurdactylus. ?Azhdarchidae*	
	Neocomian	Bar	**Vectis Fm., Isle-of-Wight, England** *'Ornithodesmus'*	**Yixian Formation** *Dendrorhynchoides, Eosipterus, Pterodactyloidea genus a*		
		Hau				
		Val	**Hastings Beds, Sussex, England** *Coloborhynchus, ?Lonchodectes*			
		Ber	**Purbeck Limestone Fm., England** *Gnathosaurus, Plataleorhynchus, Ornithocheiridae, Purbeckopus*	**Tsagaantsav Svita, Tatal, Mongolia** *Dsungaripteridae*		

Fig. 1. Stratigraphic and geographic distribution of the main Lower Cretaceous pterosaur localities. Abbreviations: **Alb**, Albian; **Apt**, Aptian; **Bar**, Barremian; **Ber**, Berriasian; **Fm**, Formation; **Hau**, Hauterivian; **Val**, Valanginian

& Hickey 1996). Thus, for the present, we accept a late Neocomian (Barremian) age for the Yixian Formation.

Three pterosaurs have been recovered so far from the Yixian Formation (Ji & Ji 1997, 1998, Ji Shu'an et al. 1999, Lü & Wang 2000; Tab. 1; Figs 2, 3). The first pterosaur to be reported, *Eosipterus yangi* (Ji & Ji 1997), consists of an incomplete, but partially articulated postcranial skeleton (Fig. 3). Initially, this pterosaur was identified as a pterodactyloid (Ji & Ji 1997), but was not assigned to a particular family. More recently, a morphometric comparison led Ji Shu'an et al. (1999) to suggest that *Eosipterus* is probably synonymous with *Pterodactylus*, a pterosaur that has been reported from the Late Jurassic of East Africa and a number of localities in Western Europe (Wellnhofer 1991a), although it can only be reliably identified from the Solnhofen Limestone of Bavaria and Late Jurassic flaggy limestones of Nusplingen in Württemburg (Unwin & Heinrich 1999, Unwin unpub. data). There are, however, two difficulties with the results of Ji Shu'an et al.'s morphometric study. First, the technique employed (Principal Components Analysis) does not distinguish between primitive and derived characters and is a phenetic, rather than a phylogenetic approach (e.g. Ridley 1986). It is possible, therefore, that the apparent similarity between *Eosipterus* and *Pterodactylus* reflects a preponderance of comparisons within the analysis that are common to many basal pterodactyloids (i.e. plesiomorphic within the Pterodactyloidea). Moreover, these plesiomorphies may be masking synapomorphies that unite *Eosipterus* with taxa other than *Pterodactylus*. A second problem with the analysis is that it includes only four pterodactyloids, all from the Late Jurassic of western Europe. It is possible that *Eosipterus* might be more closely related to other Jurassic pterodactyloids, or even Cretaceous taxa (as we argue below), but these potential relationships are not tested in the study by Ji Shu'an et al. (1999).

In 1998 a second pterosaur from the Yixian Formation, represented by a complete and fully articulated skeleton (Fig. 2), was described under the name *Dendrorhynchus* by Ji and Ji, although the name was subsequently found to be preoccupied and was replaced with *Dendrorhynchoides* (Ji Shu'an et al. 1999). This pterosaur was identified as a "rhamphorhynchoid" (Ji & Ji 1998), and assigned to the Rhamphorhynchidae, an important family that seems to have been present throughout much of the Jurassic (Wellnhofer 1991a). A morphometric analysis carried out by

Ji Shu'an et al. (1999) appears to support this assignment, with *Dendrorhynchoides* occupying a position close to, though not within, a cluster of individuals representing *Rhamphorhynchus*, a well known Late Jurassic pterosaur that has been reported from a number of European localities (Wellnhofer 1991a).

The assignment of *Dendrorhynchoides* to the Rhamphorhynchidae has recently been thrown into serious doubt, however, because it has been reported by Friend (2000) and confirmed by one of us (LJ) that the supposedly long tail of this pterosaur was not originally associated with the rest of the skeleton and consists of parts of a theropod tail that were set into the slab after its initial collection. The remaining caudal vertebrae of *Dendrorhynchoides* form a rather short tail, a character that does not support a close relationship with *Rhamphorhynchus* or other rhamphorhynchids, all of which have a long tail (Wellnhofer 1978, 1991a). In addition, the morphometric analysis suffers from the same problems as those noted for *Eosipterus*. It is a phenetic approach, as already mentioned, and not only does it omit all Cretaceous taxa, it also excludes a number of well known non-pterodactyloids including forms from the Late Triassic *(Preondactylus, Peteinosaurus, Eudimorphodon)*, Early Jurassic *(Dimorphodon)* and even the Late Jurassic *(Anurognathus* and *Batrachognathus)*.

A third specimen from the Yixian Formation, currently under study by one of us (LJ), consists of a partial skeleton associated with some soft tissue preservation (Lü & Wang 2000). Preliminary comparisons indicate that it does not belong to either of the two taxa named and described so far.

The problems concerning the systematic relationships of the Yixian pterosaurs also bear upon the debate concerning the age of the Yixian Formation. Ji Shu'an et al. (1999) argued in favour of a Late Jurassic date for this unit on the basis of supposed similarities between the Liaoning pterosaurs and Late Jurassic forms from Europe. Other have cited their work in support of a Late Jurassic age (Chiappe et al. 1999), though Barrett (2000) has pointed out some difficulties with the assumptions underlying the use of the Yixian pterosaurs for dating.

In this paper we present the results of a reassessment of the phylogenetic relationships of *Eosipterus* and *Dendrorhynchoides*, consider the significance of these results for our understanding of pterosaur diversity and evolutionary history in the Early Cretaceous and comment on the use of pterosaurs for stratigraphic dating. The term

"Rhamphorhynchoidea", and its derivatives, denotes a paraphyletic taxon, which is indicated herein by placing the name in double quotation marks. We prefer the more neutral term non-pterodactyloid, and restrict use of the term "Rhamphorhynchoidea" to a historic context, for example when referring to opinions published in earlier works. Where there is some doubt regarding the validity of a taxonomic name this is shown by enclosing it in single quotation marks, except in the case of 'Ornithodesmus', which is a valid taxon awaiting a replacement name (Howse & Milner 1993).

Institutional abbreviations

BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburgh, USA; FHSM, Fort Hays State Museum (= Sternberg Memorial Museum), Fort Hays State University, Hays, Kansas, USA; GMV, National Geological Museum of China, Beijing, China; GSM, Geological Survey Museum, Keyworth, England; GPIB, Geologisch-Paläontologisches Institut der Universität Bonn, Germany; GPIH, Geologisch-Paläontologisches Institut der Universität Heidelberg, Germany; IMCF, Iwaki Coal and Fossil Museum, Iwaki, Japan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MB, Museum für Naturkunde, Berlin, Germany; MCSNB, Museo Civico di Storia Naturale, Bergamo, Italy; MFSN, Museo Friulano di Storia Naturale, Udine, Italy; MNHN, Museum National d'Histoire Naturelle, Paris, France; MT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; NSM, National Science Museum, Tokyo, Japan; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; PVL, Paleontología de Vertebrados, Instituto-Fundación Miguel Lillo, Universidad Nacional de Tucumán, Argentina; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TM, Teyler Museum, Haarlem, Holland; TMM, Texas Memorial Museum, Austin, Texas, USA; UB, Katedra Geologie a Paleontologie, University of Brunn, Czech Republic; UNSM, University of Nebraska State Museum, Lincoln, Nebraska, USA; ZMNH, Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China.

Systematic review

Pterosauria Kaup, 1834
"Rhamphorhynchoidea" Plieninger, 1901
Anurognathidae Kuhn, 1937
Dendrorhynchoides (= *Dendrorhynchus* Ji & Ji, 1998 [preoccupied]) Ji, Ji & Padian 1999
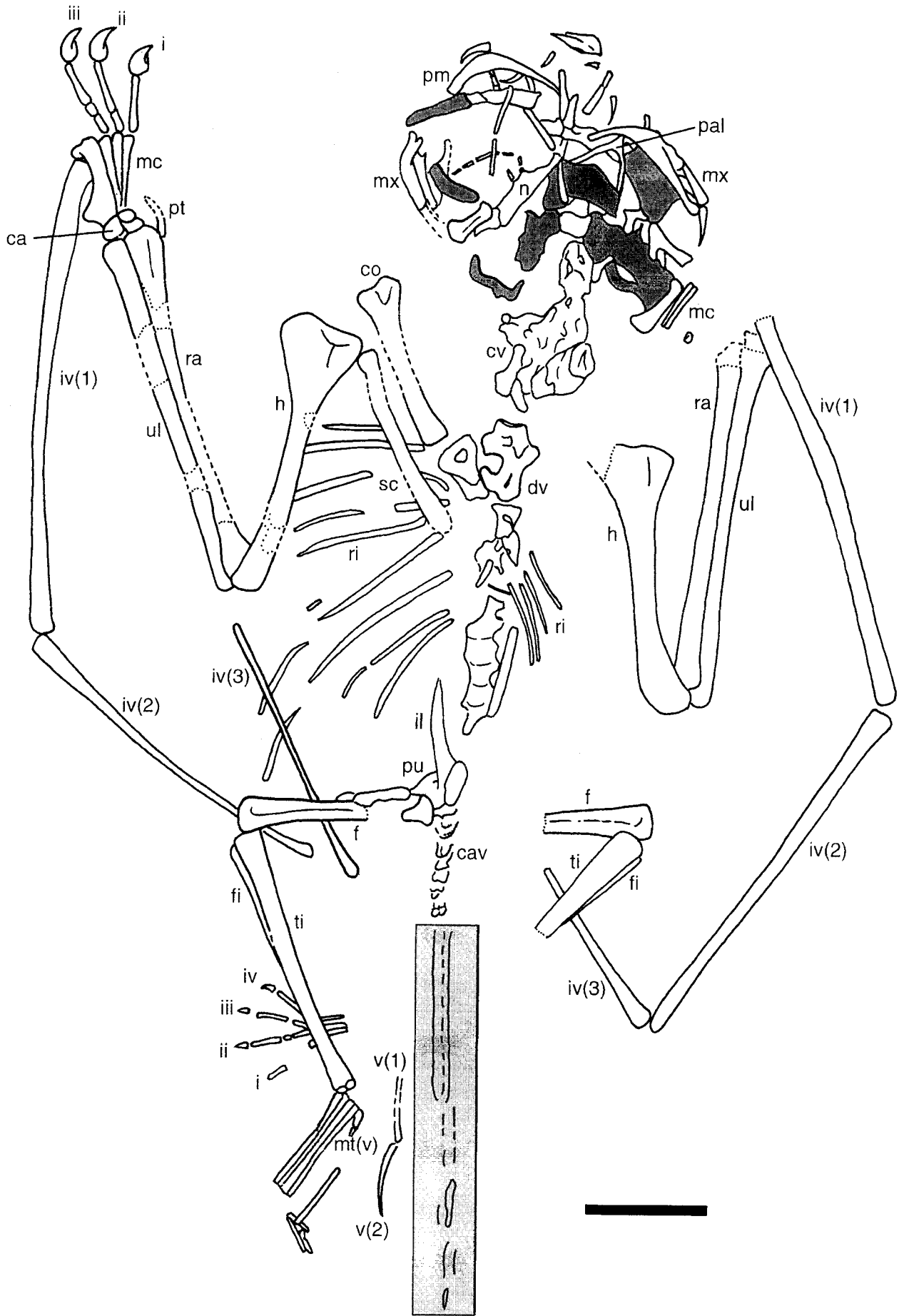*Dendrorhynchoides curvidentatus* (Ji & Ji, 1998)
Fig. 2

This taxon is represented by a single specimen (GMV 2128) collected from the Yixian Formation at the locality of Zhangjiagou (Wang et al.

1999) in the Sihetun region, south of Beipiao City, in western Liaoning Province, China (Ji & Ji 1998). The skeleton (Fig. 2) appears to have been complete and almost fully articulated, though parts of some elements, such as the right femur and right tibia, do not seem to be preserved on the main slab. The skull is somewhat disarticulated, possibly as a result of displacement of bones during compaction of this three dimensional structure. Similarly, the bones of the pectoral girdle also appear to have undergone some displacement. The preservation of the skeleton, and its current disposition, is remarkably similar to that observed in specimens from other pterosaur lagerstätten, most notably *Rhamphorhynchus* from the Solnhofen Limestone (e.g. Wellnhofer 1975a: pl. 35, fig. 1) and *Sordes* from the Karabastau Formation (e.g. Sharov 1971: pl. 4).

A general description of the skeleton, principal measurements and figures of the specimen have been given by Ji & Ji (1998). An illustration of the skeleton, indicating the principal elements, including some of the skull bones, is shown in Figure 2. *Dendrorhynchoides curvidentatus* was a relatively small pterosaur with an estimated wing span of between 0.4 and 0.5 m.

A problematic aspect of GMV 2128 is the tail. The basal section, which is clearly preserved in contact with the sacrum, consists of six, short, stubby, naturally articulated caudals (Ji & Ji 1998). The third to sixth caudals are of similar size, but a little shorter and a little narrower than the first and second caudals. This section is followed by a short gap, then a series of long, slender caudals that are wrapped in a sheath of highly elongate zygapophyses and chevrons (Ji & Ji 1998: fig. 1). Recently, however, Zhou, quoted in Friend (2000), has suggested that the section consisting of the elongate caudals was added subsequent to the fossil discovery and does not belong to *D. curvidentatus*. If this is correct then, originally, *D. curvidentatus* had a short, slightly tapering tail about 15–20 mm long and consisting of at least six and possibly up to eight small caudals that formed a pygostyle-like structure, as found in anurognathids and pterodactyloids.

We agree with Zhou for the following reasons: (1) in all long-tailed pterosaurs early caudals do not show a decline in size caudally, but are either of similar dimensions, or show a slight size increase (Wellnhofer 1978, 1991a). Moreover, by the fifth or sixth caudal the marked elongation typical of later vertebrae is clearly evident and the sixth caudal is usually at least twice as long as it is wide. By contrast, in *D. curvidentatus* the

early caudals exhibit a decrease in size and the fifth and sixth elements are short and stubby. (2) An individual involved in the collection and preparation of GMV 2128 admitted to Wang Xiao-lin (see Wang et al. 1999) that the elongate section of the tail had been added to the fossil subsequent to its discovery. As Chiappe et al. (1999) note, forgery has also been detected in a number of other fossils collected from the Yixian Formation.

Dendrorhynchoides is undoubtedly a member of the Pterosauria as it shows eight unambiguous apomorphies of this taxon:

(1) coracoid elongate and at least 0.75 × length of scapula;

(2) medial carpal-pteroid complex in the wrist;

(3) highly enlarged wing-metacarpal that forms part of the wing spar;

(4) hyperelongated fourth manual digit;

(5) forelimb at least 2 × length of hind limb;

(6) metatarsals i—iv highly elongate, slender and of subequal length;

(7) pedal digit five composed of two elongate phalanges;

(8) penultimate phalanges of both manus and pes elongate.

Dendrorhynchoides appears to lie outside the Pterodactyloidea because it exhibits the primitive condition for all three unambiguous apomorphies of the Pterodactyloidea that can be scored for this pterosaur.

(1) Elongation of the wing (fourth) metacarpal. All pterodactyloids exhibit the derived state for this character wherein the wing-metacarpal always attains at least 0.9 × the length of the humerus. *Dendrorhynchoides* and other non-pterodactyloids exhibit the primitive state wherein the wing-metacarpal reaches less than 0.9 × the length of the humerus (in *Dendrorhynchoides* the wing-metacarpal is only 0.33 × the length of the humerus).

(2) Reduction of the fifth pedal digit. Pterodactyloids are characterised by the derived condition in which phalange two is lost and phalange one is reduced to a small nubbin of bone or is absent. Non-pterodactyloids, including *Dendrorhynchoides* exhibit the primitive condition, in which the fifth pedal digit

retains two elongate phalanges (Wellnhofer 1978).

(3) Elongation of the pteroid. Pterodactyloids are characterised by an elongate, slender pteroid. *Dendrorhynchoides*, and other non-pterodactyloids, exhibit the primitive condition in which the pteroid is a short, stubby structure.

Ji & Ji (1998) cited the presence of a long tail in support of their assignment of *Dendrorhynchoides* to the "Rhamphorhynchoidea", but, as discussed above, this character is no longer valid for this taxon. The presence of a short tail in *Dendrorhynchoides* could be used to argue in support of a relationship with the Pterodactyloidea, because one of the characters that diagnoses the Pterodactyloidea is strong reduction of the tail to a relatively short, pygostyle-like structure (e.g. Bennett 1994). However, a short tail also occurs in the Anurognathidae (Döderlein 1923, Riabinin 1948, Wellnhofer 1975a, Bakhurina 1988), thus it does not provide unequivocal support for the assignment of *Dendrorhynchoides* to the Pterodactyloidea, a hypothesis of relationships that, in any case, would directly conflict with other character distributions discussed earlier.

The position of *Dendrorhynchoides* within "Rhamphorhynchoidea" can also be pinned down fairly precisely. *Dendrorhynchoides* exhibits two clear cut apomorphies of the clade Anurognathidae + Campylognathoididae + Rhamphorhynchidae + Pterodactyloidea (Fig. 4):

(1) Forelimb length more than 2.5 × hind limb length. The basal pterosaurs *Preondactylus* and the Dimorphodontidae exhibit the primitive condition in which the forelimb is less than 2.5 × the hind limb length.

(2) Ulna longer than the tibia. The basal pterosaurs *Preondactylus* and the Dimorphodontidae exhibit the primitive condition in which the ulna is shorter than the tibia (Tab. 2).

By contrast, *Dendrorhynchoides* exhibits the primitive condition for a character that supports the clade Campylognathoididae + Rhamphorhynchidae + Pterodactyloidea (Fig. 4):

(1) Skull elongate with a long, low, preorbital region: *Dendrorhynchoides* exhibits the primitive condition with a skull that appears to

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Fig. 2. *Dendrorhynchoides curvidentatus* (Ji & Ji, 1998), holotype (GMV 2128) in dorsal view. Elements located within the shaded rectangle do not appear to form part of the holotype skeleton (see text for details). Abbreviations: **ca**, carpus; **cv**, cervical vertebrae; **cav**, caudal vertebrae; **co**, coracoid; **dv**, dorsal vertebrae; **f**, femur; **fi**, fibula; **h**, humerus; **i, ii, iii, iv**, digits one to four; **il**, ilium; **mc**, metacarpal; **mt**, metatarsal; **mx**, maxilla; **n**, nasal; **pal**, palatine; **pm**, premaxilla; **pt**, pteroid; **pu**, pubis; **ra**, radius; **ri**, rib; **sc**, scapula; **ti**, tibia; **ul**, ulna; **v**, pedal digit five. Scale bar = 10 mm

Table 1

Compilation of data for the body fossil record and ichnological record of Lower Cretaceous pterosaurs. Data was collected from the literature published up to March 2000. Previous taxonomic assignments were reassessed: the identifications listed here are resolved to the lowest possible taxonomic rank within the limits of current understanding of pterosaur phylogeny.

Body fossil record

Locality and horizon	Age	Depositional setting	Taxon	Material	Principal references
Purbeck Limestone Formation, Dorset, England	Berriasian	marginal marine	*Gnathosaurus macrurus*	mandibular symphysis	Howse & Milner 1995
			Plataleorhynchus streptophorodon	incomplete rostrum	
			Ornithocheiridae	mandibular symphysis	
			Pterodactyloidea	teeth and isolated post-cranial bones	
Couches-Rouges, Eastern High Atlas Mountains, Anoual, Morocco	Berriasian	deltaic	Pterosauria	teeth	Sigogneau-Russell et al. 1998
Cornet, Oradea, Romania	Berriasian	karst landscape	?Dsungaripteroidea	numerous isolated incomplete bones	Benton et al. 1997, Jurcsák & Popa 1983
Villar del Río, Soria, Spain	?Berriasian		Pterosauria	3 wing-finger phalanges	Fuentes Vidarte & Meijide Calvo 1996
Tsagaantsav Svita, Tatal, Mongolia	Berriasian-Valanginian	lacustrine	Dsungaripteridae	extensive series of cranial and postcranial remains	Bakhurina 1982, 1983, 1986, 1993
Okurodani Fm., Kobudani Valley, Shokawa, Gifu Prefecture, Japan	Berriasian-Valanginian	floodplain	Dsungaripteridae	wing-phalange	Unwin et al. 1996, Evans et al. 1998
			Pterodactyloidea indet. (non Dsungaripteridae)	tooth	Evans et al. 1998
Kuwajima Fm., Kuwajima, Shiramine, Ishikawa Prefecture, Japan	Berriasian-Valanginian	flood plain-swamp	Ornithocheiridae	tooth	Hiroshige et al. in press
			Gnathosaurinae	teeth	
			?Dsungaripteroidea	tooth	
Hastings Beds, Sussex, England	Valanginian	fluvio-deltaic	*Coloborhynchus clavirostris* ?*Lonchodectes sagittirostris*	anterior end of rostrum parts of left and right mandibles	Owen 1874
			Pterodactyloidea	30+ isolated, incomplete limb bones	Mantell 1827
Engelbostel, Hannover, Germany	Hauterivian	marine	Ornithocheiridae	fragment of mandibular symphysis, fragments of wing bones	Wild 1990
Calcaire a Spatangues, Attancourt, Wassy, Haute-Marne, France	Hauterivian	marine	Pterosauria	ulna	Buffetaut & Wellnhofer 1983
Corrales del Pelejón-2, Galve, Teruel, Spain	Hauterivian		?Dsungaripteroidea	wing-finger phalange	Cañudo et al. 1997
La Amarga Formation, Arroyo La Amarga, Neuquén, Argentina	Hauterivian-Barremian	coastal plain	Pterodactyloidea	femur	Montanelli 1987

Body fossil record

Locality and horizon	Age	Depositional setting	Taxon	Material	Principal references
Yixian Formation, Sihetun, Liaoning Province, China	Barremian	lacustrine	*Dendrorhynchoides curvidentatus*	complete articulated skeleton	Ji & Ji 1998, Ji et al. 1999
			Eosipterus yangi	incomplete postcranial skeleton	Ji & Ji 1997, Ji et al. 1999
			Pterodactyloidea genus a	incomplete postcranial skeleton	Lü et al. in press
Artoles Formation, Vallipón, Teruel, Spain	Barremian	marginal marine	Pterodactyloidea	teeth	Ruiz-Omenaca et al. 1998
Colladico Blanco, Galve, Teruel, Spain	Barremian		Pterosauria	isolated teeth, limb bones	Krebs 1985, Sanz et al. 1990
Pterocerien marls, Serra Tiago dos Velhos, Extremadura, Portugal	Barremian		?Ornithocheiroidea	cervical vertebra	Galton 1994
Vectis Formation, Isle of Wight, England	Barremian	lagoonal-marginal marine	'Ornithodesmus' latidens	at least two incomplete skeletons, with skull material	Hooley 1913
			Ornithocheiroidea	one incomplete skeleton and various isolated, incomplete bones	this paper
Crato Formation, Araripe, Ceara, Brazil	Aptian	lagoon	*Arthurdactylus conandoylei*	almost complete postcranial skeleton	Frey & Martill 1994
			Tapejara imperator	skull with soft tissues	Campos & Kellner 1997
			Tapejara sp.	two skulls with soft tissues	Martill & Frey 1998
			?Azhdarchidae	partial forelimb	Martill & Frey 1998, 1999
Santana Formation, Araripe, Ceara, Brazil	Aptian	marginal marine	*Anhanguera santanae*	6+ skulls, some associated with postcranial remains	Wellnhofer 1985, 1991c
			Anhanguera blittersdorffi	skull	Campos & Kellner 1985
			'Tropeognathus' mesembrinus	skull + mandibles	Wellnhofer 1987
			'Tropeognathus' robustus	incomplete mandibular symphysis	Wellnhofer 1987
			Brasileodactylus araripensis	incomplete mandibular symphysis	Kellner 1984
			Tapejara wellnhoferi	4+ skulls, some associated with postcranial remains	Kellner 1989, Wellnhofer 1991b, Wellnhofer 1991
			Tapuxuara longicristatus	3 skulls, some associated with postcranial remains	Kellner & Campos 1988
			Tapuxuara leonardii	jaw fragment	Kellner & Campos 1994
			Cearadactylus atrox	incomplete skull + mandibles	Leonardi & Borgomanero 1985
			Ornithocheiridae	numerous postcranial remains	Wellnhofer 1985, 1991b, 1991c

Table 1 (continued)

Body fossil record

Locality and horizon	Age	Depositional setting	Taxon	Material	Principal references
Chinshan Formation, Laiyang, Shandong Province, China	Aptian	floodplain	?Dsungaripteridae	fragmentary limb bones	Young 1958, 1964
Elrhaz Formation, Gadoufaoua, Ténéré Desert, Agadez, Niger	Aptian	fluvial	?Azhdarchidae	limb bones	Sereno et al. 1998
Glen Rose Formation, Glen Rose, Somervell County, Texas	Aptian-Albian	shallow marine	?Azhdarchidae	humerus	Murry et al. 1991
Otway Group, Dinosaur Cove East, Australia	Aptian-Albian	fluvial-lacustrine	Pterosauria	limb bone	Rich & Rich 1989
Antlers Formation, Forestburg, Montague County, Texas, USA	Aptian-Albian	terrestrial	?Pterosauria	bone fragments	Zangerl & Denison 1950
Hudspeth Formation, Mitchell Quadrangle, Wheeler County, Oregon, USA	Albian	marine	?Azhdarchoidea	humerus, vertebrae, other bone fragment	Gilmore 1928
Le Gaty, Troyes, Aube, France	Albian	marine	Ornithocheiroidea	cervical vertebra	Buffetaut et al. 1989
Upper Greensand, Isle of Wight, England	Albian	shallow marine	Ornithocheirus	jaw fragment	Unwin unpublished data
Gault, Louppy-le-Chateau, La Meuse, France	Albian	shallow marine	Pterosauria	vertebra	Sauvage 1882
Toolebuc Formation, Hamilton Hotel, Queensland, Australia	Albian	marine	Anhanguera ?cuvieri	jaw fragment, scapulocoracoid, vertebra, pelvis	Molnar & Thulborn 1980, Molnar 1987
Lagarcito Formation, Quebrada de Hualtarán, San Luis, Argentina	Albian	lacustrine	Pterodaustro guinazui	numerous remains including some complete skeletons with skulls	Bonaparte 1970, Sanchez 1973, Chiappe et al. 1995, 1998a, 1998b
Mowry Shale, Teigen, Montana, USA	Albian	marine	Ornithocheiroidea	humerus	Bennett 1989
Züünbayan Svita, Khüren-Dukh, Mongolia	Albian	lacustrine	Coloborhynchus	skull and most of postcranial skeleton	Bakhurina & Unwin 1995, Unwin & Bakhurina in press
Klaudzin Formation, Klaudzin, Fergana, Kirghizia	Albian	freshwater deposits	Pterosauria	distal end of femur	Nesov 1990
Khodzhakul Formation, Khodzhakul, south west Kizylkum, Uzbekistan	Albian	deltaic-marginal marine	Pterosauria	bone fragments	Nesov 1990
Tlayúa limestones, Tepexi de Rodríguez, Puebla, Mexico	Albian	closed lagoon	Ornithocheiroidea	10 isolated postcranial remains	Cabral-Perdomo & Applegate 1994
Paw Paw Formation, Tarrant County Texas,	Albian		Coloborhynchus	jaw fragment	Lee 1994
Gault, Folkestone, Kent, England	Albian	shallow marine	Lonchodectes platysomus	incomplete mandibular symphysis	Unwin unpublished data
			Pterodactyloidea	isolated limb bones	

Body fossil record

Locality and horizon	Age	Depositional setting	Taxon	Material	Principal references
Chenini Formation, Tataouine region, Tunisia	Albian	fluvial	Ornithocheiridae	tooth	Benton et al. 2000
Chulec Formation, Huallanca, Huanuco, Peru	?Albian	marine	Ornithocheiroidea	incomplete humerus	Bennett 1989
Kobiaki, Tambov district, Russia	Albian-Cenomanian	marine	?Pterosauria	ramus of lower jaw	Bazhanov & Yeremin 1977
Sekmenev Formation, Lebedinsky Quarry, Belgorod, Russia	Albian-Cenomanian	shallow marine	Pterosauria	fragmentary limb bones	Nesov 1990
Cambridge Greensand, England	reworked fossils of Albian age	shallow marine	Ornithocheirus simus	fragments of upper and lower jaws	Owen 1859, 1861, Seeley 1869, 1870, 1871, 1881, 1891, 1901. Hooley 1914
			Ornithocheirus sp.	incomplete mandibular symphysis	
			Coloborhynchus sedgwickii	fragments of upper and lower jaws	
			Coloborhynchus capito	fragments of upper and lower jaws	
			Anhanguera cuvieri	fragments of upper and lower jaws	
			Anhanguera fittoni	fragments of upper and lower jaws	
			Ornithocheiridae gen. et sp. indet.	numerous fragmentary postcranial remains	
			Lonchodectes compressirostris	fragmentary rostrum	
			Lonchodectes microdon	fragments of upper and lower jaws	
			Lonchodectes platysomus	fragmentary rostra	
			Lonchodectes machaerorhynchus	incomplete mandibular symphysis	
			Lonchodectes sp. indet.	60+ fragmentary postcranial remains	
			'Ornithostoma sedgwicki'	jaw fragment	
Quebrada La Carreta, Segunda Región, Antofagasta, Chile	Early Cretaceous	estuarine-coastal environment	Domeykodactylus ceciliae	part of mandibular symphysis and fragment of skull	Casamiquela & Chong Diaz 1978, Martill et al. 2000
Tugulu Group, Urhe, Junggar Basin, Xinjiang China	Early Cretaceous	lacustrine-fluvial	Noripterus complicidens	incomplete skeleton	Young 1973
			Dsungaripterus weii	numerous skulls and postcranial elements	Young 1964, 1973

Table 1 (continued)

Body fossil record

Locality and horizon	Age	Depositional setting	Taxon	Material	Principal references
Ejinhoro Formation, Muhuaxiao Village, Ordos, Inner Mongolia	Early Cretaceous	fluvial	Pterosauria		Dong 1993
Luohangdong Formation, Zhidan Group, Laolongfhuoze, Inner Mongolia	Early Cretaceous	terrestrial, ?aeolian	Pterosauria	bone fragments	Brinkman &Peng 1993, Russell & Dong 1993
Quebrada Monardes Formation, Atacama Region, Chile	Early Cretaceous	flood plain	Pterosauria	bone fragments	Bell & Padian 1995
La Cruz Formation, Quebrada Larga, Hualtarán, San Luis, Argentina	Early Cretaceous	fluvial	*Puntanipterus globosus*	1 vertebra and 3 limb bones	Bonaparte & Sanchez 1975

Track fossil record

Locality and horizon	Age	Depositional setting	Taxon	Material	Principal references
Purbeck Beds, Langton Matravers, Dorset, England	Berriasian	inter-tidal or supra-tidal flats	*Purbeckopus*	prints	Ensom 1984, Wright et al. 1997
Cameros Basin, Santa Cruz de Yanguas, northern Spain	Berriasian	fluvial-lacustrine	cf. *Pteraichnus*	trackway	Moratalla 1993, Lockley et al. 1995
Villar del Río, Soria, Spain	?Berriasian		pterosaur	prints	Meijide Calvo & Fuentes Vidarte 1999
La Huergina Limestones Formation, Las Hoyas, Cuenca, Spain	Barremian	lacustrine	pterosaur	tracks	Fregenal-Martínez & Moratalla 1995, Lockley et al. 1995, Moratalla et al. 1995
Potomac Group, Maryland, USA	Aptian	flood plain	pterosaur	tracks	Kranz 1998
Lower Glen Rose Limestone, Seco Creek, Medina County, Texas, USA	Albian	coastal	?pterosaur	irregular scratches made by three clawed digits	Stricklin & Amsbury 1974, Langston 1974
Rio Limay Formation, Lake Ezequiel Ramos Mexia, Neuquén, Argentina	Albian	flood plain	'*Pteraichnus*'	pterosaur tracks	Calvo & Moratalla 1998, Calvo 1999
Los Cayos, Spain	Early Cretaceous		pterosaur	isolated prints	Moratalla 1993, Lockley et al. 1995

Table 2

Metric data for the DSV and principal elements of the fore and hind limbs of non-pterodactyloid pterosaurs. * = estimate, + = minimum length. Abbreviations: **DSV**, dorsal+sacral vertebrae; **fem**, femur; **hum**, humerus; **mc**, metacarpal; **mt**, metatarsal; **tib**, tibia; **ul**, ulna; **wph**, wing-phalange.

Taxon	Specimen	DSV	hum	ul	mc4	wph1	wph2	wph3	wph4	fem	tib	mt3
Preondactylus buffarinii	MFSN 1770	56	32	42	14.3	35.5	39	39	28	32.5	44	16
Dimorphodontidae												
Peteinosaurus zambellii	MCSNB 3359	82	38.5	48	17	43	43	46.5	34.8	37	49	17.5
Dimorphodon macronyx	GSM 1546	133.8*	79	102	34*	84	93	104.6	84	76	105	
Anurognathidae												
Anurognathus ammoni	BSP 1922 I 42	46	32	45	11	58				27	39	18
Batrachognathus volans	PIN 13		46	49.5+						30.8	41	21.8
Dendrorhynchoides curvidentatus	GMV 2128	38*	27.8	35.5	9.3	44.5	35.6			19*	26.7	12.1
Campylognathoididae												
Eudimorphodon ranzii	MCSNB 2888	103	47	65	29	80+				41	50+	
Eudimorphodon rosenfeldi	MFSN 1797		40.5	55	21	64	58.2	63.2	51.5	37	54.2	21
Campylognathoides liasicus	CM 11424		50.3	60.3	23	93.3	96	84.5	69.6	37.6	47.4	21.6
Rhamphorhynchidae												
Sordes pilosus	PIN 2585/3	75.6	43.1	69.1	16.5	50.5	53	53.8	33.9	36	49.6	14.8
Scaphognathus crassirostris	GPIB 1304	110	53.5	94	27	70	75			55		
Dorygnathus banthensis	MB 1905.15	121.6	62.9	106.2	31.8	79	92.3	93	82.5	53.2	70	29.1
'*Rhamphorhynchus longicaudus*'	TM 6924	47.5	16.5	26.7	10	37	31.8	28.9	32.4	12.5	15.5	9
'*Rhamphorhynchus intermedius*'	UB E554	57	21.8	37.5	13.7	53.8	49.4	43.5	47	17	22	12.8
Rhamphorhynchus muensteri	SMF R 4128	107	38	66	21	114.5	114	106.5	101	33	48.5	
'*Rhamphorhynchus gemmingi*'	GPIH MYE.13	114	43	68	20	113	108.5	98.5	102	30	44	28.8
'*Rhamphorhynchus longiceps*'	MT	136	64.5	96	35	149				45.5	64	34

have been short and with a relatively short, high preorbital region as in other basal non-pterodactyloids (see below).

In addition, *Dendrorhynchoides* also exhibits the primitive condition for a character that supports the clade Rhamphorhynchidae + Pterodactyloidea:

(1) Metatarsal iv markedly shorter than metatarsals i–iii. *Dendrorhynchoides* and other basal non-pterodactyloids (*Preondactylus*, Dimorphodontidae, Anurognathidae) exhibit the primitive condition wherein metatarsals i–iv are of almost the same length.

Ji & Ji (1998) assigned *Dendrorhynchoides* to the Rhamphorhynchidae, but it lacks apomorphies that define this taxon (e.g., deltopectoral crest of humerus with constricted base and tongue-like distal expansion; ulna longer than any other fore or hind limb element) or the Rhamphorhynchinae (e.g., tips of mandibles fused into long prow-like symphysis that, together with large fang-like teeth, forms a fish grab; rear edge of wing-phalanges deeply grooved).

Dendrorhynchoides and *Rhamphorhynchus* share two putative apomorphies (although other members of the Rhamphorhynchidae exhibit the primitive condition for these characters):

(1) Wing-phalange one longer than ulna. Most non-pterodactyloids exhibit the primitive

condition where the ulna is longer than the wing-phalange one.

(2) Wing-phalange two longer than ulna. Again, most non-pterodactyloids exhibit the primitive condition where the ulna is longer than wing-phalange two.

However, the derived state of character 1 also occurs in *Eudimorphodon*, *Campylognathoides* and *Anurognathus* (Tab. 2) and the derived state of character 2 also occurs in *Campylognathoides* (Tab. 2). In view of the homoplasy exhibited by both characters they must be considered as providing only weak support for the pairing of *Dendrorhynchoides* and *Rhamphorhynchus*, a relationship that would also require at least seven reversals to the primitive character state in *Dendrorhynchoides*.

In summary, comparison of *Dendrorhynchoides* with characters that support principal nodes within the Pterosauria indicates a position at node (a) in the cladogram shown in Figure 4. This suggests a possible relationship with the Anurognathidae and comparison of the two taxa reveals that they share at least four clear cut apomorphies:

(1) Presence of a very short, broad, lightly constructed skull with large cranial openings. All other pterosaurs, even dimorphodontids, have relatively longer, taller and narrower skulls. Anurognathids and *Dendrorhynchoides* have

an extremely unusual skull in which the principal bones form a slender frame of thin, fine bars and rods of bone surrounding large cranial vacuities. Many skull bones have a highly distinctive shape quite unlike that seen in other pterosaurs. Thus, the fused premaxillae have the form of an inverted "T" with the left and right maxillary processes diverging at an angle somewhat greater than 90, rather than less than 45, as in other pterosaurs. In addition, the maxilla is "L" shaped with a very short premaxillary process, and the palatine is reduced to a very slender "Y" shaped bone, the stem of which contacted the maxilla on its medial surface. These features are present in *Anurognathus* (Wellnhofer 1975a: fig. 38) and *Batrachognathus* (Riabinin 1948: fig. 1) and are also clearly evident in *Dendrorhynchoides* (Fig. 2). Indeed, the anurognathid skull presents a large complex of derived characters that are diagnostic of this clade, though they have yet to be documented in detail.

(2) The combined length of the dorsal + sacral vertebrae (= DSV) is of almost the same length as the ulna (Tab. 2). In pterosaurs other than anurognathids and *Dendrorhynchoides* the DSV is always substantially

longer than the ulna (Fig. 5), which, as outgroup comparison with other diapsids shows, is the primitive condition. Anurognathids are unusual in that the DSV is remarkably short, principally because of the relatively low number of dorsal vertebrae (12, compared to 14–16 in *Rhamphorhynchus*) and their relative shortness.

(3) Sub-symmetric, angular profile of the proximal end of the humerus in dorsal view. In anurognathids and *Dendrorhynchoides* the deltopectoral and medial crests on the proximal end of the humerus are of similar size and shape, with a broad base and straight, angular outline. These, and the practically flat proximal surface of the caput humeri give the humerus a highly distinctive profile that is unlike that found in other pterosaurs, where, for example, the deltopectoral crest is always considerably larger than the medial crest (Wellnhofer 1978: fig. 10). The humerus of *Dendrorhynchoides* (Fig. 3) is similar to that of *Anurognathus* (Wellnhofer 1975a: fig. 37) and *Batrachognathus* (Riabinin 1948: fig. 1), but is not quite so symmetrical, and the deltopectoral crest is directed a little more proximally than in other anurognathids.

Table 3

Metric data for the principal elements of the fore and hind limbs of pterodactyloid pterosaurs. * = estimate, + = minimum length. Abbreviations as for Table 2.

Taxon	Specimen	hum	ul	mc4	wph1	wph2	wph3	wph4	fem	tib	mt3
Ornithocheiroids											
Arthurdactylus conandoylei	SMK 1132 PAL	230	312	227	445	402	312	275	190	234	60
Anhanguera santanae	NSM PV 19892	257	384	257	462*	387*	270*	225*	236	283*	59
Pteranodon	Bennett 1991	250	344	548	615	499	346	194	250	328	
Nyctosaurus gracilis	UNSM 2/85	94	142	255*	308	245	122		85	120	38
Ctenochasmatoids											
Cycnorhamphus suevicus	MT	65.5	87	108	141	115.2	85	77.5	77	122	30
Cycnorhamphus canjuersensis	MNHN			85+	155	134	94	67+	101	138	35
Pterodactylus antiquus	BSP AS I 739	31.5	47	35	48.5	44.2	37	28.5	34.7	48.3	19
Pterodactylus kochi	BSP 1937 I 18	29	39	27.5	38.5	36.5	32.5	27	28.5	38.5	14.5
Pterodactylus micronyx	BSP 1911 I 31	25	31	40	46	28.5	19.5	17.7	29	40.5	8.7
Pterodactylus longicollum	SMNS	78	104	130	160	109	77.5	65	99	149	30
'Pterodactylus' elegans	BSP 1867 II 1	15	18.2	16.5	19.5	17.8	14.3	12.8	12.3	17.6	5.6
Ctenochasma gracile	BSP 1935 I 24	38.5	52.5	35	66	57			35	55	21
Pterodaustro guinazui	PVL 3860	80	102	78	116	112	86	69	60	90	50
Eosipterus yangi	GMV 2117	34+	95	73	96	95	80	73	60	96	38.5
Dsungaripteroids											
Germanodactylus rhamphastinus	BSP 1977 XIX 1	51	76	58	75	69.5	58.5	40.4	53	80.4	25.8
Germanodactylus cristatus	BSP 1892 IV 1	56	75	66	84	77.5	65.5	55	56.5	87.5	24
Noripterus complicidens	IVPPP 64043-3	76	104	142	174	124	44.5+		87	160	32
Azhdarchoids											
Tupuxuara longicristatus	IMCF 1052	234	291	359	505	301	208		298	398	88.2
Zheijiangopterus linhaiensis	ZMNH M1323	137	234	336	322	220			222	265	
Quetzalcoatlus sp.	TMM 42422	250	358	620	602	305	156	39		604	

(4) The combined length of the caudal vertebrae is shorter than either the cervical or dorsal series. By contrast to all other non-pterodactyloids, which have a caudal series that is longer than either the cervical or dorsal series (and often longer than the two combined), in anurognathids, the tail is reduced to a remarkably short, pygostyle-like structure (e.g. Riabinin 1948, Döderlein 1923: fig. 4). This is similar to the condition in pterodactyloids, but is presumably the result of homoplasy since the Rhamphorhynchidae, members of which have long tails, appear to be more closely related to the Pterodactyloidea than the Anurognathidae (Unwin 1995; Fig. 4). Dendrorhynchoides appears to have a tail that is of the same shape and proportions as those of anurognathids.

In addition to the apomorphies discussed above, the skeletal morphology of Dendrorhynchoides is remarkably similar to that of Anurognathus and Batrachognathus in many other respects, including its relative dimensions (Tab. 2). The following characters are putative synapomorphies uniting Dendrorhynchoides and anurognathids:

(1) Short, conical, sharp-pointed, widely spaced teeth with slightly recurved tips showing little size variation along the jaw. Teeth with a similar morphology occur in some species of Pterodactylus, but are usually more closely spaced and do not have recurved tips.

(2) Wing-phalange one longer than the combined length of the ulna + wing-metacarpal. In all other non-pterodactyloids, with the exception of Rhamphorhynchus and Campylog-

Table 4

Classification, to the generic level, of all pterosaur taxa referred to in the text, Tables 1–3 and in Figures 1 and 4–7. The interrogative mark indicates that there is some ambiguity regarding the position of a particular taxon within the next higher rank taxon

Preondactylus
unnamed plesion 1
  Dimorphodontidae
    Dimorphodon
    Peteinosaurus
  unnamed plesion 2
    Anurognathidae
      Anurognathus
      Batrachognathus
      Dendrorhynchoides
    unnamed plesion 3
      Campylognathoididae
        Campylognathoides
        Eudimorphodon
      unnamed plesion 4
        Rhamphorhynchidae
          Rhamphorhynchinae
            Dorygnathus
            Rhamphorhynchus
          Scaphognathinae
            Scaphognathus
            Sordes
        Pterodactyloidea
          ?'Ornithostoma'
          ?'Puntanipterus'
          Ornithocheiroidea
            ?Nyctosaurus
            'Ornithodesmus'
              Ornithocheiridae
                Anhanguera
                Arthurdactylus
                Brasileodactylus
                Coloborhynchus
                Ornithocheirus
                'Tropeognathus'
             Pteranodontidae
               Pteranodon
          unnamed plesion 5
            Ctenochasmatoidea

Ctenochasmatoidea
  Pterodactylidae
    Pterodactylus
    Cycnorhamphus
  Ctenochasmatidae
    Ctenochasmatinae
      Ctenochasma
      ?Eosipterus
      Pterodaustro
    Gnathosaurinae
      Cearadactylus
      Gnathosaurus
      Huanhepterus
      Plataleorhynchus
  ?Lonchodectidae
    Lonchodectes
  unnamed plesion 6
    Dsungaripteroidea
      Germanodactylidae
        Germanodactylus
      Dsungaripteridae
        Domeykodactylus
        Dsungaripterus
        Noripterus
    Azhdarchoidea
      Tapejaridae
        Tapejara
        Tupuxuara
      Azhdarchidae
        Zhejiangopterus
        Quetzalcoatlus

nathoides, wing-phalange one is shorter than the ulna + wing-metacarpal (Tab. 2). Basal members of the Rhamphorhynchidae and Campylognathoididae exhibit the primitive condition for this character suggesting that the derived condition was independently attained in anurognathids and the other two families.

(3) Wing-phalange two longer than the ulna. This character is only known for *Dendrorhynchoides* among anurognathids, because a complete wing-phalange two is not preserved in specimens of *Batrachognathus* and *Anurognathus* – thus while it is a putative anurognathid apomorphy, more complete material of other taxa is needed to confirm this. In all other pterosaurs, with the exception of *Rhamphorhynchus*, the ulna is longer than wing-phalange two (Tab. 2). More basal members of the Rhamphorhynchidae exhibit the primitive condition, thus the derived state is presumably homoplastic for *Rhamphorhynchus* and anurognathids.

In summary, *Dendrorhynchoides* and anurognathids are united by four unique characters (one of which is a character complex consisting of at least three characters) and this relationship is supported by a further three putative apomorphies. In addition, these taxa also appear to have a very similar general morphology and proportions (Tab. 2). By contrast, *Dendrorhynchoides* does not share any derived characters in common with other non-pterodactyloid taxa, the sole exception being *Rhamphorhynchus*, and in this case character optimisation is ambiguous. In the face of such overwhelming evidence we have no doubt in assigning *Dendrorhynchoides* to the Anurognathidae (Tab. 4).

Pterodactyloidea Plieninger, 1901
Ctenochasmatoidea Kuhn, 1967
?Ctenochasmatidae Nopcsa, 1928
***Eosipterus* Ji & Ji, 1997**
***Eosipterus yangi* Ji & Ji, 1997**

Fig. 3

The holotype and only known specimen of *Eosipterus* (GMV 2117) was collected from lacustrine sediments in the upper part of the Hengdaozi Member of the Yixian Formation at the locality of Tuanshangou (Wang et al. 1999), in the Sihetun region, south of Beipiao City, in western Liaoning Province, China (Ji & Ji 1997). The specimen consists of an incomplete skeleton in-

cluding almost complete right fore and hind limbs, partial left fore and hind limbs, gastralia, and parts of the pelvis (Fig. 3). The skeleton is, for the most part, naturally articulated, although the left wing appears to have undergone some disruption. The current disposition of the fore and hind limbs is similar to that observed, for example, in pterodactyloids from the Solnhofen Limestone (Wellnhofer 1970). A brief description together with measurements of the principal limb bones and illustrations was given by Ji & Ji (1997), and a sketch of the skeleton is reproduced here (Fig. 3). GMV 2117 represents a relatively small pterodactyloid with a wingspan of about 1.25 m, although, as Ji Shu'an et al. (1999) note, the absence of fusion of some elements suggests that it had not reached adulthood.

The single specimen of *Eosipterus* is far less complete than that of *Dendrorhynchoides* and lacks a skull, cervical vertebrae, or well preserved humerus, all of which are important for determining the systematic relationships of pterosaurs (Wellnhofer 1970, 1975a, 1978, Howse 1986, Padian 1984, Unwin & Lü 1997). The main source of evidence regarding the relationships of *Eosipterus* consists of comparative lengths of the major limb bones. This type of data is often of taxonomic significance, and has frequently been used in systematic studies of pterosaurs (e.g. Wellnhofer 1970, 1975a, Wild 1978, 1984, 1993, Padian 1980), but is not without problems. Ontogenetic variation, for example, can be quite marked in some pterosaurs (Bennett 1995, 1996), but this variable has yet to be fully incorporated into morphometric analyses.

Previous studies (Ji & Ji 1997, Ji Shu'an et al. 1999) have consistently identified *Eosipterus* as a pterodactyloid and this is supported by the presence of two unambiguous apomorphies of the Pterodactyloidea:

(1) The wing-metacarpal is more than 1.5 × the length of the third metatarsal (in *Eosipterus* this ratio = 1.9). In non-pterodactyloids the wing-metacarpal reaches, at most, 1.3 × the length of the third metatarsal, but is usually shorter than the latter element.

(2) The fifth pedal digit is highly reduced and represented by just a single, short nubbin of bone. In non-pterodactyloids the fifth toe is composed of two elongate phalanges (see above).

Pterodactyloids can be subdivided into four major clades: the Ornithocheiroidea, Ctenochasmatoidea, Dsungaripteroidea and Azhdarchoidea (Unwin 1995, Unwin & Lü 1997; Fig. 4). In so
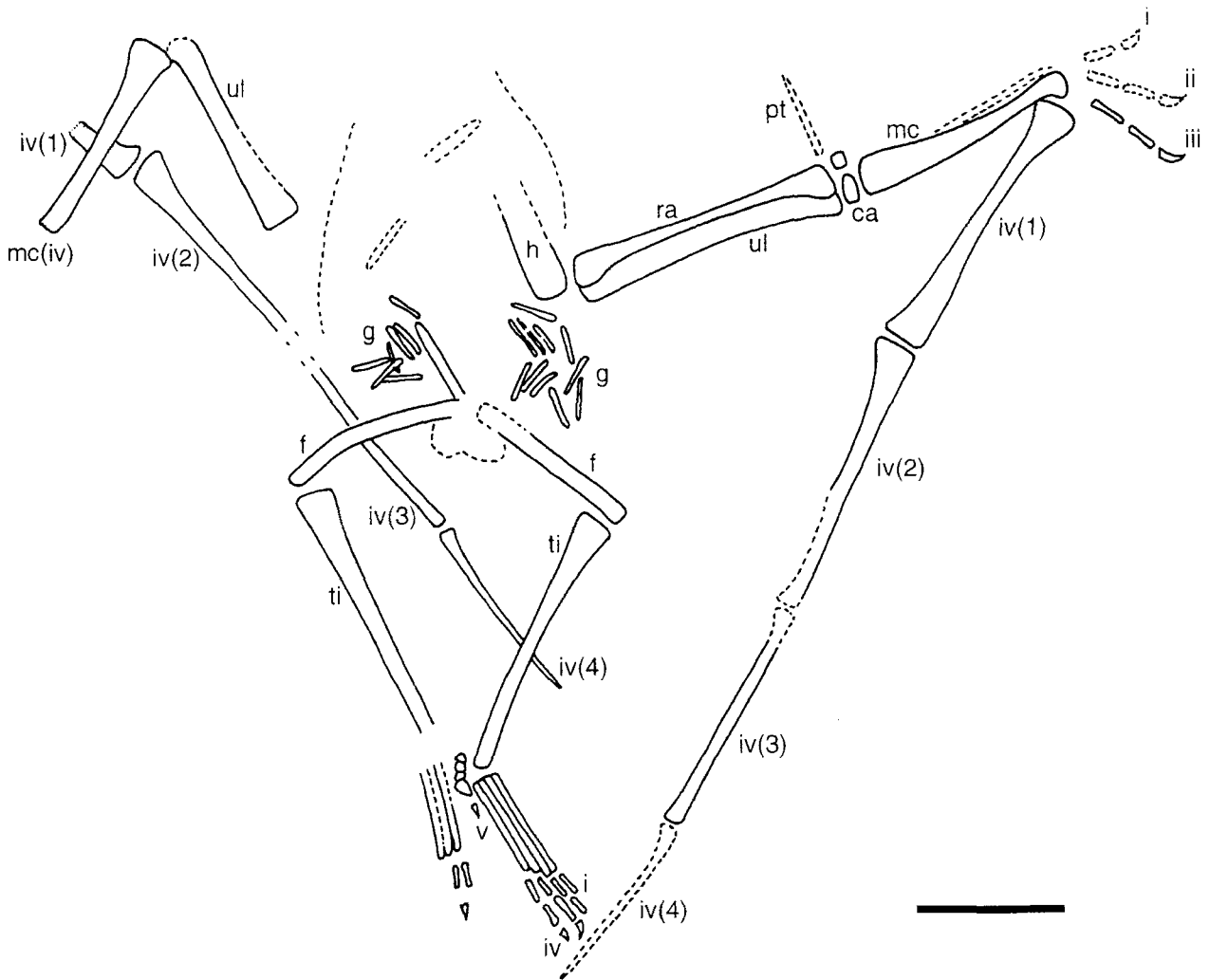
Fig. 3. *Eosipterus yangi* Ji & Ji. 1997. holotype (GMV 2117) in dorsal view.
Abbreviations as for Figure 2. except: **g.** gastralia. Scale bar = 50 mm

far as comparisons can be made. *Eosipterus* exhibits the primitive condition for postcranial apomorphies of ornithocheiroids. dsungaripteroids and azhdarchoids (see Unwin 1995. Unwin & Lü
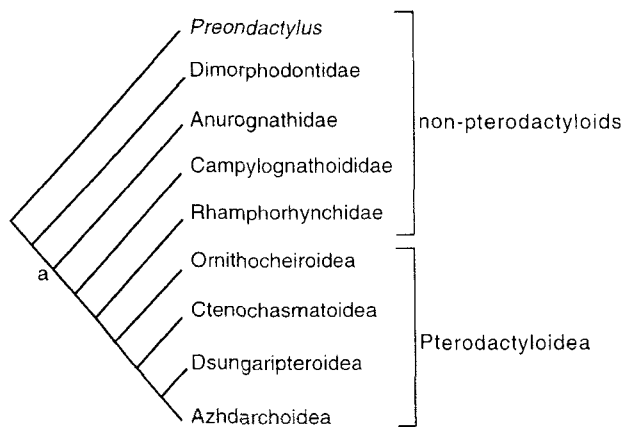

Fig. 4. Hypothesis of phylogenetic relationships of the main clades of pterosaur. After Unwin (1995) and Unwin & Lü (1997)
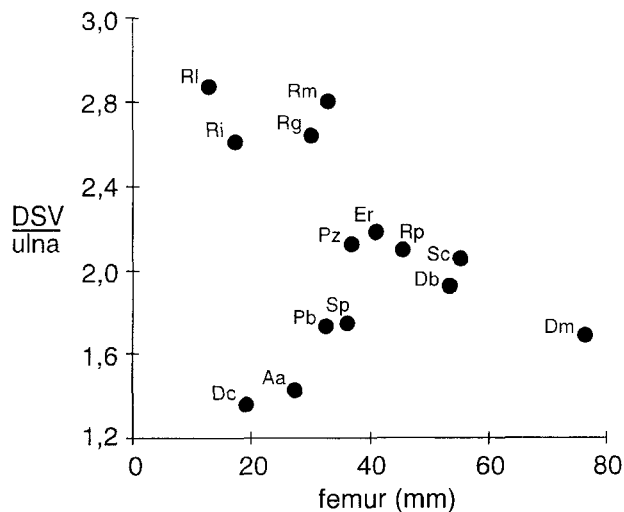
1997). It does, however, have a relatively long third metatarsal, a character that is typical of some ctenochasmatoids (Fig. 6a). Moreover, in its general proportions *Eosipterus* also compares well with ctenochasmatoids, as shown by the results of the morphometric analysis carried out by Ji Shu'an et al. (1999), which grouped *Eosipterus* with *Pterodactylus* — a basal member of the Ctenochasmatoidea.

The Ctenochasmatoidea comprise a series of Late Jurassic and Early Cretaceous taxa. Basal members of the clade include *Pterodactylus* and *Cycnorhamphus*, traditionally placed in the Pterodactylidae (e.g. Wellnhofer 1978), although this taxon is probably paraphyletic as some species appear to be more closely related to the Ctenochasmatidae than to other members of the Pterodactylidae. The Ctenochasmatidae, characterised by remarkably elongate jaws and large numbers of teeth that form a filtering apparatus (e.g. Wellnhofer 1970), consists of two clades: the

Fig. 5. Comparison of the relative lengths of the DSV (dorsal + sacral vertebrae) to the ulna, plotted against femur length, for non-pterodactyloid pterosaurs. Comparing the DSV with other limb bones results in the same basic distribution of points. Bennett (1995) and Unwin (1995) have argued that the five species of *Rhamphorhynchus* indicated here represent a single species. Four species do indeed cluster separately and show little variation, other than in size, but, by contrast, *Rhamphorhynchus longiceps* has a relatively long ulna and plots within the main cluster of points. Abbreviations: **Aa**, *Anurognathus ammoni*; **Db**, *Dorygnathus banthensis*; **Dc**, *Dendrorhynchoides* curvidentatus; **Dm**, *Dimorphodon macronyx*; **Er**, *Eudimorphodon ranzii*; **Pb**, *Preondactylus buffarinii*; **Pz**, *Peteinosaurus zambellii*; **Rg**, *'Rhamphorhynchus gemmingi'*; **Ri** *'Rhamphorhynchus intermedius'*; **Rl**, *'Rhamphorhynchus longicaudus'*; **Rm**, *Rhamphorhynchus muensteri*; **Rp**, *'Rhamphorhynchus longiceps'*; **Sc**, *Scaphognathus crassirostris*; **Sp**, *Sordes pilosus*

gnathosaurines comprising *Gnathosaurus, Plataleorhynchus, Huanhepterus* and *Cearadactylus*; and the ctenochasmatines, comprising *Ctenochasma* and *Pterodaustro*.

In the absence of skull material it is difficult to resolve the relationships of *Eosipterus* to other ctenochasmatoids. We note, however, that *Eosipterus* is of very similar size and proportions to *Pterodaustro* (Tab. 3). Moreover, in some respects, such as the relative length of the femur to the ulna (Fig. 6b) or to the wing-phalange two, and the length of the third metatarsal compared to the wing-phalange one, or the tibia (Fig. 6a), *Eosipterus* exhibits proportions that, among ctenochasmatoids, are most similar to those of *Pterodaustro* and *Ctenochasma*.

In summary, there is some evidence to suggest that *Eosipterus* is a ctenochasmatoid and probably belongs within the Ctenochasmatidae rather than sharing a close relationship with *Pterodactylus*. However, confirmation of this assignment must await the discovery of more complete material of *Eosipterus*.

Discussion

Palaeoecology of Lower Cretaceous pterosaurs

The vast majority of pterosaur remains have been recovered from marginal marine or marine

Fig. 6. Comparison of the third metatarsal to the tibia, plotted against femur length (a) and of the femur to the ulna, plotted against length of wing-phalange one (b) for 18 species of pterodactyloid pterosaurs. Symbols: triangle = ornithocheiroids, circle = ctenochasmatoids, square = dsungaripteroids, diamond = azhdarchoids. In (b) ctenochasmatines are indicated by filled circles. Note that the location of *'Pterodactylus elegans'* is consistent with Bennett's contention (1996) that individuals assigned to this species are juveniles of *Ctenochasma elegans*. Abbreviations: **Ey**, *Eosipterus yangi*, **Cg**, *Ctenochasma gracile*, **Pe**, *'Pterodactylus elegans'*, **Pg**, *Pterodaustro guinazui*. The dispersion of points in plot (b) provides some further support for the systematic arrangement utilised in this paper: for example, azhdarchoids have a very low ulna/femur ratio, while ornithocheiroids and ctenochasmatines have relatively high ratios

deposits and, as is well known. records from continental sediments are rare and generally fragmentary (Wellnhofer 1991a, Bell & Padian 1995, Bakhurina & Unwin 1996). The fossil assemblage from the Yixian Formation thus provides a useful source for new insights into the palaeoecology of pterosaurs in terrestrial ecosystems.

With regard to the specific palaeoecologies of the Yixian pterosaurs, it seems likely that *Dendrorhynchoides*, which has a skull morphology remarkably similar to that of other anurognathids, was a small, aerial insectivore. This inference is based on the occurrence. in anurognathids, of relatively small, widely spaced peg-like teeth. which seem well suited for gripping and puncturing the chitinous exoskeletons of insects (Döderlein 1923, Wellnhofer 1975b). In addition, the jaws of anurognathids had a relatively large gape, that was further extended by a fringe of "hair-like" structures (Bakhurina & Unwin 1995), in a fashion analogous to that of some caprimulgiforms such as *Podargus* and *Caprimulgus*, which also hawk for insects (Tyne & Berger 1976). That potential prey items were abundantly available is demonstrated by the large and diverse insect fauna that has also been recovered from the Yixian deposits (Lin 1998). It may also be significant that the other three deposits that have yielded anurognathids (Bakhar Formation, Bakhar. central Mongolia; Karabastau Formation, Karatau. Kazakhstan and the Solnhofen Limestones. southern Germany) have also yielded large insect faunas.

The palaeoecology of *Eosipterus* is far less certain. Assuming that it was a ctenochasmatine it seems likely that this pterosaur had elongate jaws with numerous, long fine teeth that functioned as a sieve or filtering device. It has recently been shown that pterodactyloid pterosaurs had a reasonably effective quadrupedal stance and gait (Bennett 1997, Unwin 1997, 1999. Henderson & Unwin 1999, Unwin & Henderson 1999). thus *Eosipterus* may be envisioned proceeding on stilt-like fore and hind limbs through streams and along the shallow margins of lakes and rivers sieving for small, soft-bodied crustaceans. the aquatic larvae of insects, other invertebrates and perhaps even fish fry. Again. suitable prey items are known from sediments of the Jehol Group: Chen (1988) has described a diverse freshwater invertebrate fauna, and fish that lived and presumably reproduced in the ancient Liaoning lakes have also been reported (Jin et al. 1995, Jin 1996).

We emphasise. therefore. that the putative palaeoecologies proposed for the Yixian pterosaurs

are consistent with what is known of the co-occurring invertebrate and vertebrate fauna. This supports the idea that these pterosaurs inhabited the Sihetun lakes region and formed an integral part of this Lower Cretaceous terrestrial ecosystem. rather than representing accidental occurrences of individuals displaced from elsewhere by unusual conditions. for example, storms, volcanic activity or disrupted migration patterns.

A new compilation of the Lower Cretaceous pterosaur fossil record, including the taxa from Liaoning (Tab. 1) indicates that, for this interval, pterosaurs are now known from more than 20 localities that represent fully terrestrial settings. Moreover. these localities are widely distributed across three continents, and represent a range of palaeoenvironments from shallow, fresh-brackish water, inland lakes with low diversity faunas and floras (e.g. Tsagaantsav Svita, Tatal, western Mongolia: Bakhurina 1983, 1984, 1986), to well vegetated lowland areas with large and diverse invertebrate and vertebrate communities (e.g. Yixian beds, Liaoning: Barrett 2000 and refs therein). This reinforces the idea that pterosaurs were a typical, if not particularly diverse, component of Lower Cretaceous terrestrial ecosystems. Consequently, their absence from many Lower Cretaceous vertebrate localities can probably be attributed to taphonomic bias rather than true absence. This interpretation is supported by the discovery of pterosaur tracks at localities such as Las Hoyas (Fregenal-Martínez & Moratalla 1995, Lockley et al. 1995) that have yielded a diverse terrestrial fauna, but, as yet. no skeletal remains of pterosaurs (Meléndez 1995).

Comparison of the Yixian pterosaurs with assemblages from other Lower Cretaceous localities (Tab. 1) provides an important new insight into pterosaur palaeoecology during this interval. Similar sedimentologic/biotic associations to those of the Yixian Formation are rare, but a new fossil biota. from the Kuwajima Formation of Shiramine, Ishikawa Prefecture, Japan (Manabe et al. 2000, Hiroshige et al. 2000), forms one possible example. The Kuwajima Formation consists of fluviatile and swamp sediments of Early Cretaceous (Berriasian) age that have yielded a diverse freshwater assemblage (Evans et al. 1998, Manabe et al. 2000, Hiroshige et al. 2000). Pterosaurs are only known from teeth, most of which represent a medium to large sized ctenochasmatoid. though dsungaripterid and ornithocheirid teeth have also been identified. The Lagarcito Formation of Argentina, currently dated as Low-
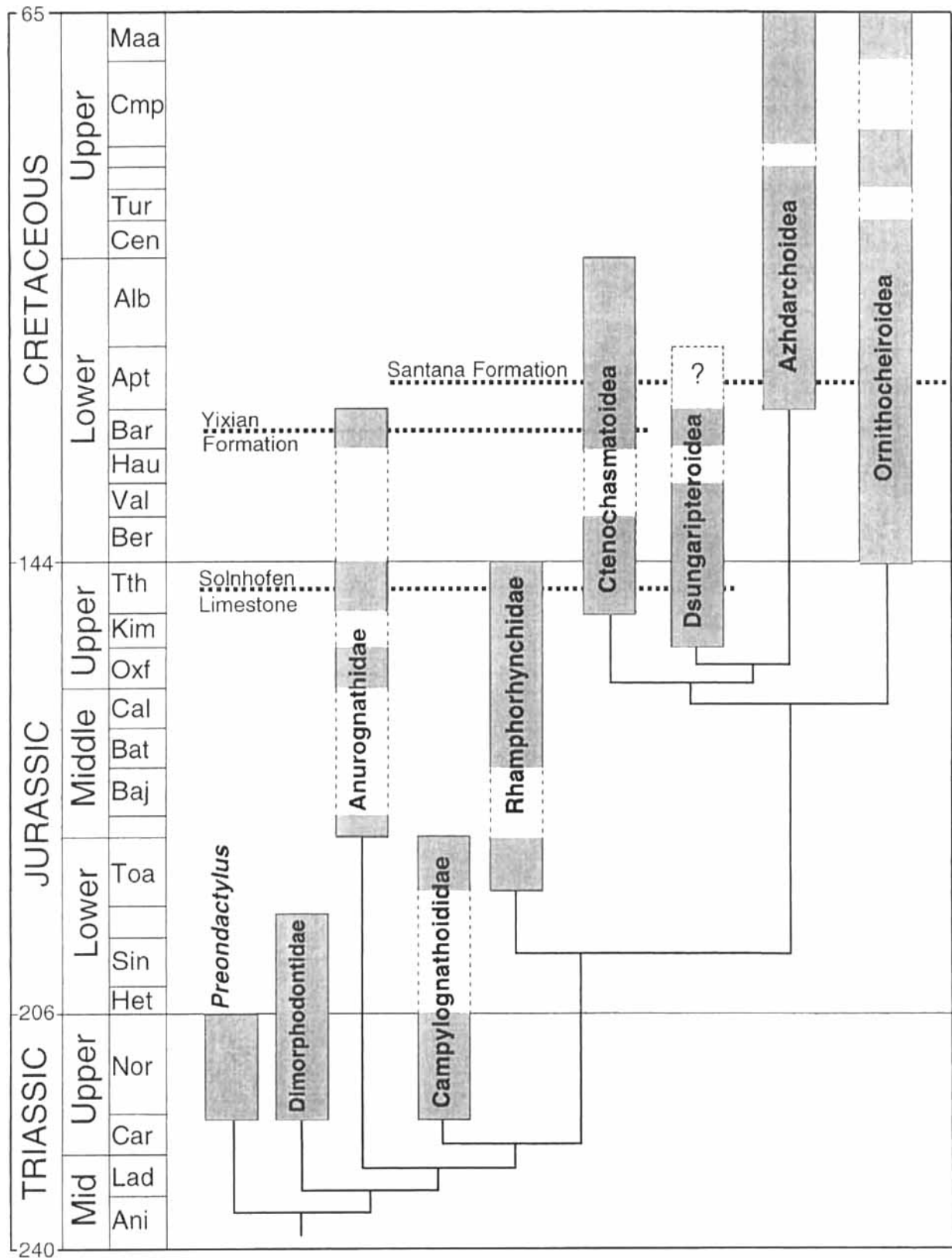
Fig. 7. Stratigraphic range of main pterosaur clades. Tree topology follows that shown in Figure 4. Stage length based on Geological Society of America Timescale 1999. Fossil record data compiled from literature published up to March 2000. Each column represents the known extent of a particular lineage with blank sections indicating gaps in the fossil record. The age of most records can only be resolved, at best, to the stage level, thus the entire stage is shown as represented if any records fall within the stage.

Abbreviations: **Alb**, Albian; **Ani**, Anisian; **Apt**, Aptian; **Baj**, Bajocian; **Bar**, Barremian; **Bat**, Bathonian; **Ber**, Berriasian; **Cal**, Callovian; **Car**, Carnian; **Cen**, Cenomanian; **Cmp**, Campanian; **Hau**, Hauterivian, **Het**, Hettangian; **Kim**, Kimmeridgian; **Lad**, Ladinian; **Maa**, Maastrichtian; **Nor**, Norian; **Oxf**, Oxfordian, **Sin**, Sinemurian; **Toa**, Toarcian; **Tth**, Tithonian; **Tur**, Turonian; **Val**, Valanginian

er Cretaceous (Albian) is also broadly analogous with the Yixian Formation in that it also represents a large. shallow, freshwater lake that has yielded fish. conchostracans, plants and a cteno-chasmatine. *Pterodaustro* (Chiappe et al. 1995, 1998a, b).

In sharp contrast. other continental localities have produced strikingly different pterosaur assemblages. For example. shallow, fresh-brackish water lake sediments in western Mongolia and China, that were deposited in semi-arid. or arid conditions, have produced low diversity biotas dominated by, or in some cases consisting solely of a single species of dsungaripterid pterosaur, often represented by large numbers of remains (Young 1964, 1973, Bakhurina 1982, 1986, 1993, Dong 1992).

Pterosaurs from marginal marine or fully marine settings are different again from those found in continental environments. Pterosaur assemblages from deposits such as the Santana Formation of Brazil (Wellnhofer 1991b), the Toolebuc Formation of Australia (Molnar & Thulborn 1980, Molnar 1987) and the Paw Paw Formation of Texas (Lee 1994) are dominated by, or consist entirely of ornithocheirids, medium to very large pterosaurs specialised in aerial piscivory (Wellnhofer 1991a).

In summary, this brief analysis of the palaeoenvironmental distribution of Lower Cretaceous pterosaurs suggests that two broad palaeoecological distinctions can be made: first. between pterosaurs inhabiting marine and continental environments, and second, within continental environments, between lowland communities such as the Liaoning assemblage, and more specialised inland ecosystems such as the dsungaripterid dominated assemblages of western China and Mongolia. The apparent palaeoecological and systematic diversity of Lower Cretaceous pterosaur is in distinct contrast to the situation in the latest Cretaceous (Campanian-Maastrichtian) wherein continental and marine assemblages are dominated by just a single family of pterosaurs. the Azhdarchidae.

Evolutionary significance of the Yixian pterosaurs

The Yixian pterosaurs also contribute significantly to our understanding of the evolutionary history of pterosaurs. As mentioned above, the Lower Cretaceous fossil record is patchy, with a distinct gap between the better represented basal Cretaceous and late Early Cretaceous assem-

blages (Fig. 1). The Yixian taxa provide the first substantial evidence of pterosaurs from the late Neocomian.

The occurrence of a ctenochasmatine in the mid Lower Cretaceous is not unexpected. The clade is known to have survived until the late Early Cretaceous (Fig. 7) because of the presence of *Pterodaustro* in the Albian Lagarcito Formation (Chiappe et al. 1998a). Teeth of ctenochasmatines have been reported from the basal Cretaceous (Berriasian) of Japan (Hiroshige et al. 2000), but, if correctly identified, *Eosipterus* currently represents the youngest record for this clade in Eurasia.

The presence of an anurognathid seems, at first glance, to be rather surprising, particularly as it indicates that non-pterodactyloids, long thought to have become extinct at the end of the Jurassic (e.g. Padian 1998) actually persisted into the Early Cretaceous. Until now, anurognathids had only been reported from the Jurassic, although some cladistic analyses (e.g. Unwin 1995) imply that the clade first appeared in the Late Triassic (Fig. 7). Anurognathids have a very patchy fossil record, however, which is almost certainly directly related to their occupation of continental habitats. A range extension of 20 million years is not, therefore, so surprising, especially as this is the first Neocomian locality to produce well preserved, reasonably complete, associated remains of small pterosaurs. Combining this new evidence for the fossil record of anurognathids with the predicted range of the clade based on cladistic analysis, suggests that this clade may have persisted for more than 80 million years. Moreover, the remarkable similarity of *Batrachognathus, Anurognathus* and *Dendrorhynchoides* suggests that there was little modification of anurognathid skeletal anatomy over an interval of at least 25 million years.

There are a number of possible explanations for the apparent absence of non-pterodactyloids from the Lower Cretaceous:

(1) Partial extinction. The apparent extinction may be in some part real, in that perhaps only anurognathids persisted into the Lower Cretaceous while the other two main Late Jurassic non-pterodactyloid lineages, the rhamphorhynchines and the scaphognathines, had become extinct by the end of the Jurassic.

(2) Taphonomic bias. Deposits such as the Solnhofen Limestone, that yield well preserved associated remains of small vertebrates and that have also been intensively exploited are

rare in the Neocomian. The Yixian Formation and associated units form the first example from this interval that can be considered, in taphonomic respects and sheer numbers of fossils recovered, as comparable to the Solnhofen Limestone. That they have yielded a non-pterodactyloid only serves to emphasise the patchiness of the pterosaur fossil record.

(3) Taxonomic and systematic biases. Anurognathids must have been present in the Berriasian-Hauterivian interval, and other clades of non-pterodactyloids may also have existed at this time, but the majority of remains recovered from the Neocomian, so far, are highly fragmentary (Tab. 1). Few isolated bones can be reliably identified as non-pterodactyloid (exceptions are the maxilla, caudal vertebrae, wing-metacarpal and [in rhamphorhynchines] the wing-phalanges) while other remains, even though they might be non-pterodactyloid, may have been assigned to the Pterodactyloidea on the grounds that non-pterodactyloids are "known" to have become extinct at the end of the Jurassic. Thus fossil remains of non-pterodactyloids may already be present in museum collections, but remain unidentified and perhaps unidentifiable.

Luo (1999) has suggested, on the basis of the occurrence in the Yixian Formation of "rhamphorhynchoid" pterosaurs, compsognathid theropod dinosaurs and primitive mammals, that, in the Early Cretaceous, eastern Asia was a refugium for typically Late Jurassic taxa. This idea has been challenged by Manabe et al. (2000) who argue that new fossil finds suggest that the historical biogeography of this region may have been much more complex than previously thought.

Three aspects of the Yixian pterosaur assemblage also contradict the idea of a refugium. First, as noted above, pterosaurs have a patchy and highly biased fossil record. In their case, arguments for a refugium depend upon the absence of fossils, rather than a dense, continuous, and widely distributed sequence of fossils that show, for example, that in the Early Cretaceous relict forms similar to those from the Late Jurassic are restricted to eastern Asia. Second, while *Dendrorhynchoides* could be argued to be a relict, *Eosipterus* could not, because other ctenochasmatoids are known from the Lower Cretaceous and have also been reported from outside Asia (Tab. 1). Third, pterosaurs were highly mo

bile, with few if any restrictions on their dispersal, thus it seems unlikely that they would have been confined to refugia.

Pterosaurs as stratigraphic indicators

Ji & Ji (1998) and Ji Shu'an et al. (1999) argued that the similarity of the Yixian pterosaurs to the Late Jurassic forms *Pterodactylus* and *Rhamphorhynchus* supported the idea that the Yixian Formation is Late Jurassic in age.

There are two difficulties with this argument. The first concerns the identity of the Yixian pterosaurs. We have shown, above, that *Dendrorhynchoides* is an anurognathid pterosaur. This clade is certainly known from the Late Jurassic and probably originated in the Late Triassic. Thus the presence of this taxon in the Yixian Formation could be taken as evidence in favour of a Jurassic rather than Cretaceous age for this unit. By contrast, *Eosipterus* probably belongs to the Ctenochasmatoidea (a clade that is known to have existed in the Late Jurassic and Early Cretaceous), and appears to be most closely related to *Pterodaustro*, a form that is currently known only from the Albian (Chiappe 1998a). Thus, if pterosaurs were to be employed for dating purposes, the Yixian taxa could be used to support either a Late Jurassic or an Early Cretaceous age.

The second difficulty is more general and more serious. Fossils selected as candidates for dating purposes must satisfy three basic criteria. They should be: (1) distinct and easily recognisable; (2) common, and with a wide horizontal distribution; and (3) have a clear, well defined and short vertical range (Clarkson 1986). Pterosaurs do not satisfy any of these criteria. Unless critical parts of the skeletal anatomy are preserved (specifically the skull, or at least a substantial portion of the jaws and dentition) it is difficult to assign specimens to particular genera or species. The Yixian pterosaurs provide a good example of this — the skull of *Dendrorhynchoides* clearly demonstrates that it is an anurognathid, while the headless remains of *Eosipterus* are difficult to assign, even at the superfamily level. The pterosaur fossil record is dominated by fragmentary remains few of which can be assigned to a particular taxon. Moreover, fossil remains of pterosaurs are rare and, with a few exceptions, most genera and species are known only from a single locality (cf. Wellnhofer 1978, 1991a). At present, it is doubtful whether a reliable strati-

graphic range can be specified for any clade, irrespective of its rank. The only conclusion that can be drawn from these observations is that pterosaurs are highly unreliable as indicators of stratigraphic age and it seems unlikely that this situation will improve in the near future.

Acknowledgements

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