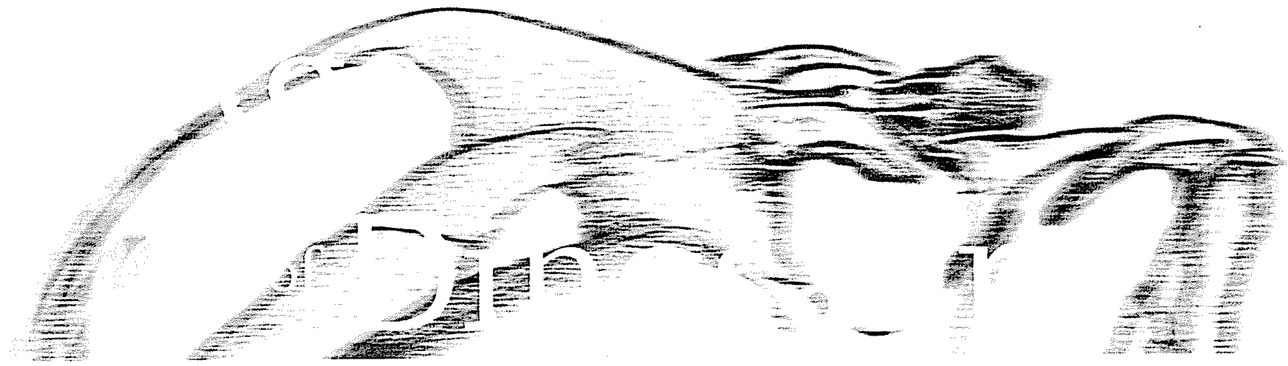
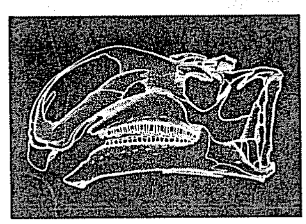


in Russia and Mongolia



Michael J. Benton,
Mikhail A. Shishkin,
David M. Unwin
Evgenii N. Kurochkin

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
10 Stamford Road, Oakleigh, VIC 3166, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2000

Printed in the United Kingdom at the University Press, Cambridge

Typeface Monotype Janson 9.75/13pt. *System* QuarkXPress® [SE]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

The age of dinosaurs in Russia and Mongolia / edited by Michael J.
Benton . . . [et al.].
p. cm.
Includes bibliographical references.
ISBN 0 521 55476 4
1. Dinosaurs – Russia (Federation) 2. Dinosaurs – Mongolia.
I. Benton, M.J. (Michael J.)
QE862.D5A287 2000
567.9′0947–dc21 99-16743 CIP

ISBN 0 521 55476 4 hardback

Character and dating of the Cretaceous formations of Mongolia

Lower Cretaceous

Tsagaantsav (Berriasian–Valanginian)

The oldest horizon of the Cretaceous of Mongolia, the Tsagaantsav, occurs in nearly all regions of Mongolia, but most widely in the centre and south of the country. It is represented by conglomerates (below), sandstones, clays, limestones, marls, in some places with layers of volcanics and tuffs up to 700–800 m and more thick (Figure 14.1). Basic volcanics, and rarely acid volcanics, and tuffs are characteristic of the Tsagaantsav Gorizont in South-east, Central, and North-east Mongolia, but not in the west or north (Shuvalov, 1975a,b, 1982). Sections of the Tsagaantsav Gorizont of the Sangiin Dalai Nuur depression have been given by Devyatkin *et al.* (1975) and Bakhurina (1983).

Dinosaurs are rare in the Tsagaantsav Gorizont. The westernmost dinosaur locality is the Sangiin Dalai Nuur depression, south of Hirgis Nuur lake, where, according to Bakhurina (1983), remains of the dinosaur *Psittacosaurus*, numerous pterosaurs *Dsungaripterus weii* and *D. parvus*, the tooth of a carnivorous dinosaur, the scapula and rib of a large dinosaur, and the jaw of a paramacellodid lizard have been found (Bakhurina, 1983; Bakhurina and Unwin, 1995). The psittacosaurs here are among the oldest known, being generally characteristic of the Aptian–Albian (Shuvalov, 1982; Sereno, 1990). To the north, from the mountain Bayan Ovoo Uul, in many-coloured sandstones, siltstones and clays dated as lower Gurvanereen Svita (Khosbayar, 1972), remains of molluscs and ostracods, characteristic of the Tsagaantsav Gorizont, have also been collected (Devyatkin *et al.*, 1975).

In the region of the Gurvan Ereen range, deposits of the lower part of the Gurvanereen Svita (included in the Tsagaantsav Gorizont) are observed with a thickness of more than 150–200 m (Devyatkin *et al.*, 1975). They are represented mostly by clays, siltstones and sandstones, mainly grey in colour, and lying on red-coloured coarse sediments of Late Jurassic age (Kimmeridgian–Tithonian). Here, and south of Darvi Sum, numerous ostracods and conchostracans characteristic of the Tsagaantsav Gorizont have been found, as well as remains of the primitive chondrostean fish *Stichopterus* sp., characteristic of the lower part of the Early Cretaceous (Yakovlev, 1986). Devyatkin *et al.* (1975) report corixid heteropteran insects similar to *Baissocorixa jacijewski* Popov from the Lower Cretaceous of Transbaikalia, Siberia, and higher in the section, numerous coprolites, probably of dinosaurs.

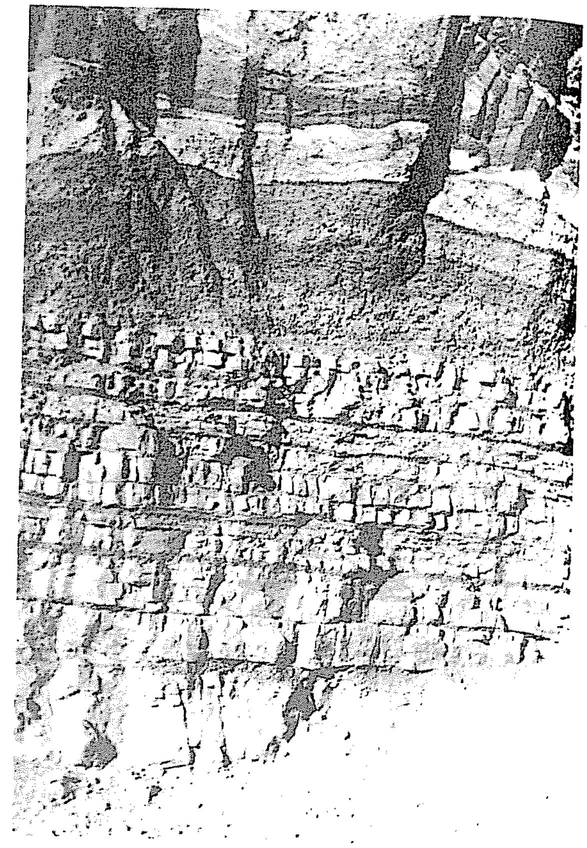


Figure 14.1. Intercalation of clays and marls near the mountain Öndör Ukhaa (north-west part of Gobi Altai). Öndörukhaa Svita, Tsagaantsav Gorizont. (Photo by V.F. Shuvalov.)

In Central Mongolia, in the Öndörukhaa Svita

(Shuvalov, 1975a), remains of dinosaurs are also very rare. They have been found near Tsogtovoo Sum. Sections of the svita were given by Florentsov and Solonenko (1963) and Shuvalov (1975a, 1982, 1987). Among molluscs, most characteristic for this svita are representatives of *Arguniella*, as well as *Limnocyrena kwichowensis* (Grab.), *L. wangshibensis* (Grab.) and others (Martinson, 1975; Shuvalov, 1975a). Numerous ostracods (*Cypridea trita* Lüb., *C.priva* Lüb., *C. remota* Lüb.) and conchostracans (*Brachigrapta kansuensis* (*Chi*), *Bairdestheria halobiformis* Kob. et Kus., and others) are characteristic of the Tsagaantsav Gorizont of Mongolia and of the Early Cretaceous of China and Transbaikalia (Shuvalov, 1975a; Shuvalov and Stepanov, 1970).

The same formation occurs in the south-east of the Gobi Altai, south of Khangai, in particular in the lower part of the Ondaisair Svita of the Tsagaantsav Gorizont, in North Gobi and other places (Shuvalov, 1975a). In South Trans-Altai and East Gobi, the composition of the Tsagaantsav Gorizont is in general similar to Central Mongolia. But, in some places there are thick horizons of tuffs of acid volcanics, which contain zeolites (mainly clinoptilolite, containing more than 20%), especially in the East and South Gobi: on Tüshleg Mountain, near Tsagaan Tsav well, north of the Khanbogd Sum, and in other places. In Central Mongolia, north of the ridge Tariat Uul (Gobi Altai), silts of the Öndörukhaa Svita (or Tevsh Svita) contain 14.81–15.81% of phosphide (Florentsov and Solonenko, 1963). Tsagaantsav deposits in North-east and East Mongolia have a similar content. Here deposits of the Tsagaantsav Svita were included in the Choibalsan series by Nagibina and Badamgarav (1975). The volcanics of the Tsagaantsav Svita have been described by Frikh-Khar and Luchitskaya (1978). In North Mongolia, deposits of the Tsagaantsav Svita are known in the basin of the Uilgan river, where the remains of molluscs have been found, but volcanics are absent.

The Tsagaantsav Svita is dated as Berriasian–Valanginian on the basis of numerous finds of fossils, and K–Ar and Rb–Sr dating of the volcanics (119–141 Myr) (Devyatkin *et al.* 1990; Solov'ev *et al.*, 1977; Verzilin, 1979a; Shuvalov, 1987, 1994). See also Table 14.2.

Shinekhudag Gorizont (Hauterivian–Barremian)

This widely distributed horizon includes the Shinekhudag, Andaikhudag, the upper part of Altanuul, and other svitas (Table 14.1). The Shinekhudag Svita occurs in Central and South-east Mongolia, but it is not known yet in North Mongolia. The unit is composed everywhere of sandstones, argillites, marls and clays together with bituminous shales ('fish shales'), which are the most characteristic facies of these deposits (Figure 14.2). The first deposits were described by Berkey and Morris (1927) from south of Khangai (near the Andai Khudag well) area as a member of the Ondaisair Formation. Detailed descriptions of the deposits were given by Marinov (1957), Vasil'ev *et al.* (1959), and Shuvalov (1975a).

Remains of dinosaurs in Shinekhudag deposits are extremely rare. South of Khangai the Americans found remains of *Protiguanodon mongoliensis* and *Psittacosaurus mongoliensis*. However, everywhere in the Shinekhudag sequences there are ostracods, conchostracans, fishes and molluscs (Devyatkin *et al.*, 1990; Shuvalov, 1975a; Martinson and Shuvalov, 1973; Shuvalov, 1980). Fishes are represented mostly by *Lycoptera fragilis* Huss., but not by *L. middendorfii* Müll., as at Andai Khudag (Berkey and Morris, 1927). The latter form, judging by its most frequent occurrence, is characteristic of the Tsagaantsav Gorizont (Martinson, 1975; Shuvalov, 1975a). Other fossils from Khangai include the insects *Indasia reisi* Cockerell, *Ephemeropsis trisetalis* Eich., and others, and numerous insects were also collected from the Andaikhudag Svita of the Andai Khudag well region. Here, remains of dinosaurs also occur in higher (Aptian–Albian) horizons of the Lower Cretaceous (Khulsangol Svita) (Shuvalov, 1975a).

In West Mongolia, sections of the upper part of the Gurvanereen Svita (Khosbayar, 1972) can be observed to the south-west of Darvi Sum and near Myangat Sum. In Central Mongolia, deposits of the Andaikhudag Svita, belonging to the same horizon, 21

Pterosaurs from Russia, Middle Asia and Mongolia

DAVID M. UNWIN AND NATASHA N. BAKHURINA

Introduction

Russia, Middle Asia and Mongolia form a large territory representing more than one sixth of the Earth's entire continental surface. Mesozoic deposits are widely distributed across this land mass and have yielded important and occasionally extensive remains of pterosaurs ranging in age from Middle Jurassic to latest Cretaceous (Bakhurina and Unwin, 1995a; Unwin *et al.*, 1997). The record is highly uneven, however, with most remains recovered from just a few localities often separated by large temporal gaps (Figure 21.1). This reflects the general situation with regard to the global pterosaur fossil record and is primarily a result of the relative fragility of the remains of these animals, which thus require exceptional conditions for their preservation.

Pterosaurs were first recognized at the end of the eighteenth century, from Late Jurassic deposits in Bavaria (Wellnhofer, 1991a), but were not reported in Russia and Middle Asia until the early twentieth century and in Mongolia only during the 1980s. At the time of writing (1999) pterosaurs have been recovered from five localities in Russia, about 12 in Middle Asia (mainly in Kazakhstan and Uzbekistan) and three in Mongolia (Bakhurina and Unwin, 1995a; Unwin *et al.*, 1997). At least seven species, each in a separate genus and representing at least five families of pterosaurs, have so far been reported (Bakhurina and Unwin, 1995a; Unwin *et al.*, 1997). Five of the seven species are known from reasonably complete skeletons, while the two remaining taxa, and all other records of pterosaurs, are based on isolated and often incomplete bones.

Despite their rarity, Russian and Asian pterosaurs are important for two reasons. First, many of the fossil remains have been collected from sequences that were deposited within a continental setting (Bakhurina and Unwin, 1995a, 1996). This is in contrast to much of the rest of the pterosaur record, which has generally been recovered from marginal marine or marine sediments (Wellnhofer, 1978, 1991a). Thus, although they are sparse, the Russian and Asian records provide important evidence of the evolutionary history of pterosaurs in continental environments. Second, some of the remains recovered, most notably those of *Sordes* and *Batrachognathus* from Karatau and the dsungaripterid from Mongolia, are exceptionally well preserved and provide unique insights into aspects of the anatomy, functional morphology and ecology of this group (Sharov, 1971; Bakhurina, 1986, 1988, 1989, Bakhurina and Unwin, 1992; Bakhurina, 1993; Unwin *et al.*, 1993; Unwin and Bakhurina, 1994; Bakhurina and Unwin, 1995a, 1995b, 1995c, 1995d, 1996, 1997; Unwin and Bakhurina, 1997; Unwin *et al.*, 1997).

Dedication

This chapter is dedicated to the late Dr Valerii Yu. Reshetov whose life was devoted to the JSMPE and to collections.

History of discovery

Russia

The first unequivocal pterosaur fossil to be found in Russia, the posterior half of a cervical vertebra of an

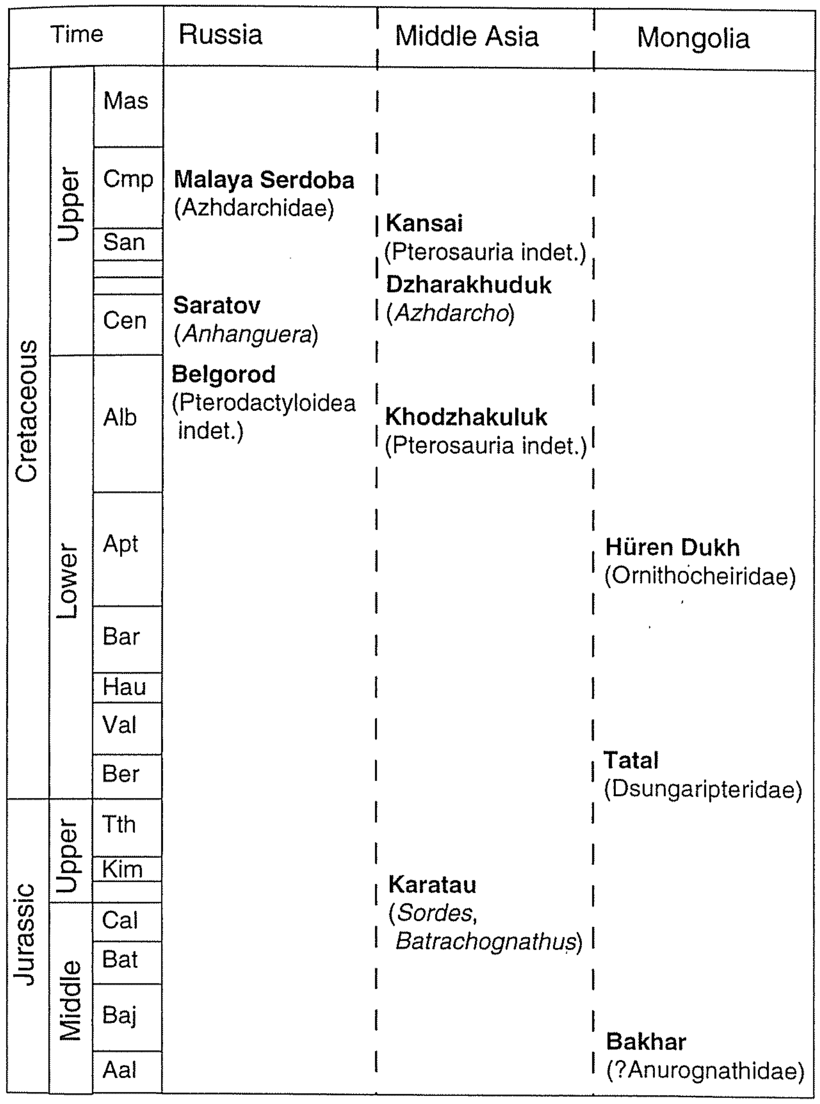


Figure 21.1. Stratigraphic distribution of important pterosaur localities (shown in bold) and taxa (in parentheses) from Russia, Middle Asia and Mongolia.

azhdarchid from Late Cretaceous marine sediments of the Volga region (Figure 21.2, site 1) was collected in 1911 by the geologist V.G. Khimenkov. Further isolated remains have occasionally been found in this region (listed in Bakhurina and Unwin, 1995a), but, with the exception of a short section of a mandibular symphysis (Khozatskii, 1995) they add little to our knowledge of early Late Cretaceous pterosaurs. Elsewhere in Russia, a single incomplete humerus was recovered from the Late Jurassic of the Volga region and in the 1980s Nesov and associates found a few fragmentary remains in late Early to early Late Cretaceous deposits near Gubkin city in the Belgorod district (Nesov *et al.*, 1986).

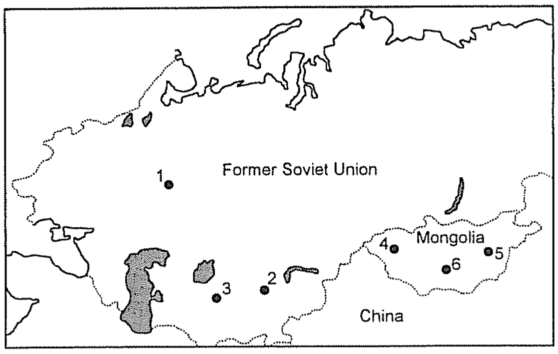


Figure 21.2. Geographic distribution of the main pterosaur localities in Russia, Middle Asia and Mongolia. (1) Lysaya Gora, (2) Karatau, (3) Dzharakhuduk, (4) Tatal, (5) Hüren Dukh, (6) Bakhar. Solid line = coastline, dotted line = international boundary.

Middle Asia

The first discovery of pterosaurs in Middle Asia, a thin slab bearing a semi-complete skeleton from the Late Jurassic of Karatau, Kazakhstan (Figure 21.2, site 2), was made in 1933 by M.A. Vedenyapin and later described as *Batrachognathus volans* (Ryabinin, 1948). Twenty years later a second specimen of *Batrachognathus* and a new taxon, *Sordes pilosus*, exhibiting evidence of soft tissues (Sharov, 1971; Unwin and Bakhurina, 1994; Bakhurina and Unwin, 1995a, 1995b, 1995c, 1995d, 1997) was found in the same sediments by A.G. Sharov, while searching for fossil insects.

The most recent discoveries of pterosaurs in Middle Asia were made by the late L.A. Nesov and a team from the University of St. Petersburg. Fragmentary, but well preserved remains of the Late Cretaceous pterosaur *Azhdarcho* were recovered during a series of expeditions to the locality of Dzharakhuduk in the Kyzylkum desert, Uzbekistan (Figure 21.2, site 3), in the late 1970s, the 1980s and the early 1990s (Nesov, 1984, 1989, 1990). A few additional remains were recovered from this locality by a joint Western-Russian-Kazakh expedition in 1997 (Archibald *et al.*, 1998). Nesov's team also found fragmentary remains of pterosaurs at other sites in the late Early and Late Cretaceous of the Middle Asian republics (see Bakhurina and Unwin, 1995a).

Mongolia

The first discovery of Mongolian pterosaurs, a few fragmentary, but three-dimensional bones, from Early Cretaceous strata in the region of Khovd in Western Mongolia was made in 1970 by V.F. Shuvalov and P. Khosbayar. These remains were only identified as pterosaurian some ten years later (Merkulova, 1980), and subsequently described under the name of '*Dsungaripterus parvus*' (Bakhurina, 1982). In the early 1980s JSMPE (Joint Soviet–Mongolian Palaeontological Expedition) expeditions led by N. Bakhurina located the horizon in the Tatal region of the Sangiin Dalai Nuur depression (Figure 21.2, site 4), from which the original material had been collected, and recovered much additional material, including some remarkably complete and well preserved skulls and lower jaws (Bakhurina, 1983, 1984, 1986, 1989, 1993; Bakhurina and Unwin, 1995a). A third expedition to this locality in 1988, led by B. Namsrai and A. Perle, recovered the associated remains of a relatively small dsungaripterid (Perle, pers. comm. 1993).

In addition to the material found at Tatal in 1981–2, a JSMPE expedition led by P. Narmandakh collected the remains of a large pterodactyloid from the late Early Cretaceous fossil locality of Hüren Dukh (Figure 21.2 site 5) in central Mongolia (Bakhurina, 1989; Bakhurina and Unwin, 1995a) and a JSMPE team led by the palaeoentomologist A.G. Ponomarenko recovered the fragmentary remains of a small pterosaur from the Middle Jurassic locality of Bakhar in central Mongolia (Figure 21.2, site 6) while searching for fossil insects (Bakhurina, 1989; Bakhurina and Unwin, 1995a).

Institutional abbreviations

GIN, Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar; JSMPE, Joint Soviet Mongolian Palaeontological Expedition; MMNH, Mongolian Museum of Natural History, Ulaanbaatar; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow; TsNIGRI Central Institut of Geological Exploration, St. Petersburg; ZIN,

Figure 21.3. The holotype (PIN 52–2) of *Batrachognathus volans*, Ryabinin, 1948, from the Karabastau Formation of Karatau, Kazakhstan.

Collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Systematic review

Order Pterosauria Kaup, 1834
Family Anurognathidae Kuhn, 1937
Genus *Batrachognathus* Ryabinin, 1948

Type and only known species. Batrachognathus volans, Ryabinin, 1948.

Diagnosis. Batrachognathus is distinguished from *Anurognathus*, the only other genus in the Anurognathidae, by the greater number of teeth (at least 11, compared with 8 in *Anurognathus*), marked recurving of the tips of the teeth (straight in *Anurognathus*), and relatively short hind limbs (1.5–1.6 times the length of the humerus compared to >2.0 times the length of the humerus in *Anurognathus*) (Ryabinin, 1948; Bakhurina, 1988).

Batrachognathus volans, Ryabinin, 1948

Holotype. PIN 52–2, a well preserved skull and semi-complete postcranial skeleton (Ryabinin, 1948, pl. 1; fig. 8; Figure 21.3). Aulie, near Mikhailovka, Karatau ridge, Chimkent region, Kazakhstan. Karabastau Svita, Upper Jurassic (Oxfordian/Kimmeridgian: Doludenko and Orlovskaya [1976]).

Referred material. PIN 2585/4a. A heavily crushed skull and semi-complete postcranial skeleton associated with some evidence of soft tissues recovered from the holotype locality (Bakhurina and Unwin, 1995a, 1995b). This specimen lies adjacent to the holotype of *Sordes pilosus* on the same bedding plane: the only example, so far as we are aware, wherein representatives of two different genera of pterosaurs are preserved in direct association.

Diagnosis. As for the genus.

Comments. Batrachognathus was a relatively small pterosaur, about 0.75 m in wingspan and with a reconstructed skull length of 48 mm. The skull was short, broad and deep, but very lightly constructed, possibly kinetic, and with a large orbit (Bakhurina, 1988). The presence of short, peg-like, piercing teeth and the possibility of a large gape suggest an insectivorous diet, as has also been proposed for *Anurognathus* (Döderlein, 1923; Wellnhofer, 1975) and this is at least consistent with the very large numbers of fossil insects found in the Karabastau deposits (Sharov, 1968).

Bakhar anurognathid Bakhurina and Unwin, 1995a
Material. JSMPE (PIN), fragmentary wing bones of one individual. Bakhar, Bayanhongor Aimag, Central Mongolia. Bakhar Svita, Middle Jurassic (?Aalenian/Bajocian [Shuvalov, 1982]) (Bakhurina, 1989; Bakhurina and Unwin, 1995a, fig. 2).
Comment. This small, possibly juvenile, individual has an estimated wingspan of only 0.3–0.4 m. It shows some similarity to anurognathid pterosaurs, especially with respect to the morphology of the humerus, but further work is required to substantiate this systematic assignment.

Family Rhamphorhynchidae Seeley, 1870
Genus *Sordes* Sharov, 1971
Type and only known species. Sordes pilosus, Sharov, 1971
Diagnosis. Sharov (1971) cited numerous characters that supposedly differentiated *Sordes* from other pterosaurs, but many of these are not restricted to this taxon. Apomorphies that distinguish *Sordes* from other rhamphorhynchids include: only seven teeth per side in the upper jaw; and a pes digit four in which phalanx 4 exceeds the combined length of phalanges 1–3.
Comment. Sordes shows some similarity to the Late Jurassic form *Scaphognathus* and the clade that they form, the Scaphognathinae, appears to belong within the Rhamphorhynchidae (see Bakhurina and Unwin, 1995a, for discussion). This view has been challenged by Kellner (1996) who suggests that *Sordes* is a relatively primitive form that occupies a basal position within Pterosauria. Evidence in support of this hypothesis has yet to be published, however, and as *Sordes* exhibits a series of characters including: a skull that is more than three times longer than it is deep; orbit larger than preorbital and nasal openings; premaxillae that separate the frontals anteriorly; a short metatarsal four; a mandibular symphysis; and loss of size dimorphism in the mandibular dentition, all of which unite *Sordes* with derived 'rhamphorhynchoids' (Unwin, 1995), we see no reason to adopt Kellner's proposal.

Sordes pilosus Sharov, 1971
Holotype. PIN 2585/3, almost complete skeleton with evidence of various types of soft tissues (Sharov, 1971, pl. 4; Bakhurina and Unwin, 1995a, 1995b; Unwin and Bakhurina, 1994). Aulie, near Mikhailovka, Karatau ridge, Chimkent region, Kazakhstan. Karabastau Svita, Upper Jurassic (Oxfordian/Kimmeridgian: Doludenko and Orlovskaya [1976]).
Referred material. Remains of another seven individuals (Sharov, 1971, pls 4, 5; Bakhurina, 1986, p. 33; Bakhurina and Unwin, 1995a, 1995b, 1995c, 1995d; Ivakhnenko and Korabel'nikov, 1987, figs. 261, 262; Unwin and Bakhurina, 1994, 1997; Figure 21.4).
Diagnosis. As for the genus.
Comments. Sordes was a medium-sized pterosaur with a wingspan of about 0.6 m and a skull length, in the holotype, of 80 mm. Remains of *Sordes* provide some of the best available evidence regarding wing-shape in pterosaurs. They show that the main wing membrane (cheiropatagium) was attached to the forelimb and to the hind limb as far as the ankle, and the presence of a cruropatagium stretched between the hind limbs and supported along its rear edge by the elongate fifth toes (Bakhurina and Unwin, 1995a; Unwin and Bakhurina, 1994). Other types of fossilized soft tissues include remains of the integument, which bear 'hair-like' structures in some regions, a tail flap, claw sheaths and foot webs (Sharov, 1971; Bakhurina and Unwin, 1992, 1995a, 1995b, 1995c, 1995d; Unwin *et al.*, 1993; Unwin and Bakhurina, 1994).

Suborder Pterodactyloidea Plieninger, 1901
Family Ornithocheiridae Seeley, 1870
'*Ornithocheirus* (?) sp.'
Material. ZIN PNT-S50–1, section of the mandibular symphysis lacking the rostral termination (Khozatskii,

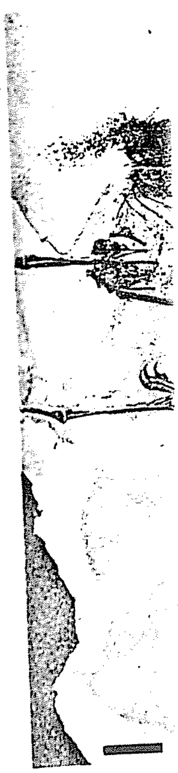


Figure 21.4. Th
Sharov, 1971, fro
Kazakhstan. Scal

1995, fig. 2; Bal
Lysaya Gora,
trict, in the so
1953). Upper (
Comments. Th
large-sized pt
3–4 m. Alth
number of fe
taining relati
with a prono
developed ri
(*Ornithocheiri*
assignment t
accepted he
species = *Ori*
are straight i

Figure 21.4. The paratype (PIN 2470/1) of *Sordes pilosus* Sharov, 1971, from the Karabastau Formation of Karatau, Kazakhstan. Scale bar = 20 mm.

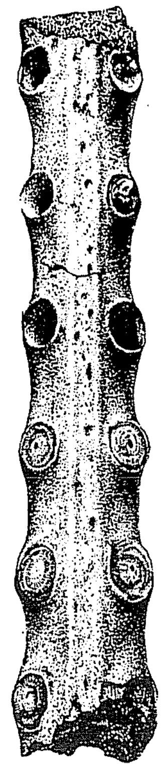


Figure 21.5. Section of the mandibular symphysis, in palatal view, of an ornithocheirid, cf. *Anhanguera* (ZIN.PNT-S50–1) from the early Late Cretaceous of Lysaya Gora, Saratov district, Russia. As preserved, the specimen is 90 mm in total length.

1995, fig. 2; Bakhurina and Unwin, 1995a; Figure 21.5). Lysaya Gora, near Proletarskii village, Saratov district, in the south European part of Russia (Glikman, 1953). Upper Cretaceous (Cenomanian).

Comments. The jaw fragment represents a medium to large-sized pterosaur with an estimated wingspan of 3–4 m. Although incomplete, the jaw exhibits a number of features, such as a rostral expansion containing relatively large teeth and an occlusal surface with a pronounced midline channel flanked by well developed ridges, that are typical of ornithocheirids (*Ornithocheirus* + *Anhanguera* + *Coloborhynchus*), and its assignment to this family by Khozatskii (1995) is accepted here. However, in *Ornithocheirus* (type species = *Ornithocheirus simus* Seeley, 1869) the jaws are straight in lateral view, rather than curved upward anteriorly as in the Russian specimen. Curvature of the lower jaw does occur in another ornithocheirid, *Anhanguera*, and the Russian specimen is also similar in other respects to fossil remains assigned to species of *Anhanguera* from the Santana Formation of Brazil (e.g. Wellnhofer 1991b). Unfortunately, the incompleteness of the Saratov specimen prevents detailed comparisons, thus, for the present, we refer it to cf. *Anhanguera.*

Hüren Dukh ornithocheirid Bakhurina and Unwin, 1995a

Material. MMNH 100/30, rostral end of the upper jaw, almost complete lower jaw and most of the postcranial skeleton (Bakhurina, 1989; Bakhurina and

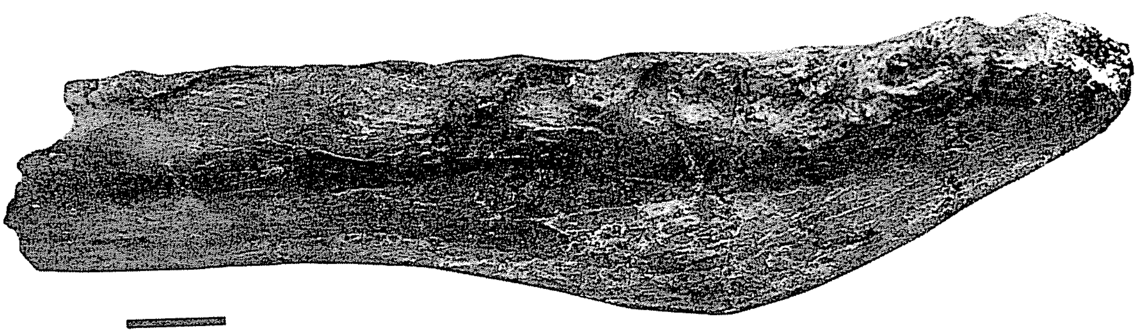


Figure 21.6. Anterior end of the mandibular symphysis, in right lateral view, of a large ornithocheirid from the late Early Cretaceous of Hüren Dukh, Mongolia. Scale bar = 10 mm.

Unwin, 1995a, fig. 12; Figure 21.6). Hüren Dukh, 60 km south west of Choir, middle Gobi region of Central Mongolia. Züünbayan Formation, Lower Cretaceous (Aptian–Albian) (Shuvalov, 1974).

Comments. The remains, amongst the most complete for a large Cretaceous pterosaur and a rare example of cranial and postcranial material preserved in association, represent a pterodactyloid of about 5.5 m in wingspan. This pterosaur exhibits a number of diagnostic features of the Ornithocheiridae (e.g. expanded jaw tips bearing three pairs of large, fang-like teeth, saggital bony crests located at the rostral ends of the jaws) and undoubtedly belongs in this family. Amongst ornithocheirids, the Hüren Dukh form shows closest similarity to species of *Anhanguera* and *Coloborhynchus*, but until the systematic status of these and other ornithocheirid genera has been reviewed we prefer not to assign the Mongolian ornithocheirid to any particular genus (Bakhurina and Unwin, 1995a).

Family Dsungaripteridae Young, 1964

'*Dsungaripterus parvus*' Bakhurina, 1982

Holotype. PIN 3953, fragments of the fore and hind limb bones of a single individual. Seventy kilometres north-north-east of lake Khar Us Nuur, Khovd Aimag, Western Mongolia. Tsagaantsav Svita, basal Early Cretaceous.

Referred material. Remains of at least 45 individuals, including juveniles (Figure 21.7) and GIN 100/31, a complete skull and low jaw (Ivakhnenko and Korabel'nikov, 1987, fig. 264; Wellnhofer, 1991a, p. 120) recovered from Tatal, Sangiin Dalai Nuur depression, Khovd Aimag, Western Mongolia. Upper part of the Tsagaantsav Svita (?Beriassian–Valanginian [Shuvalov and Trusova, 1976; Shuvalov, 1982]) (Bakhurina, 1983, 1984, 1986, 1993; Bakhurina and Unwin, 1995a, figs. 10, 11).

Comments. In 1982 Bakhurina established a new species of pterosaur, '*Dsungaripterus parvus*', on the basis of material (PIN 3953) recovered by Shuvalov and Khosbayar from western Mongolia in the 1970s. Further remains, collected by Bakhurina in the early 1980s. and including well preserved skull material (Bakhurina and Unwin, 1995a), were referred to this taxon and it was assigned to a new genus, '*Phobetor*' (Bakhurina, 1986), a name that we now know to be preoccupied (Bakhurina and Unwin, 1995a). Characters of the skull clearly distinguish the Tatal pterosaur from other pterodactyloids (Bakhurina, 1986; Bakhurina and Unwin, 1995a), but the holotype material (PIN 3953) appears to be indistinguishable from the corresponding bones of *Dsungaripterus* and *Noripterus*, and the validity of the name '*D. parvus*' seems doubtful.

The one complete skull is 360 mm in length and probably represents an individual of 2–2.5 m in wingspan. Most of the material collected appears to represent individuals of a similar size, though remains of specimens with estimated wingspans ranging from 1 to 4 m are present in the collections.

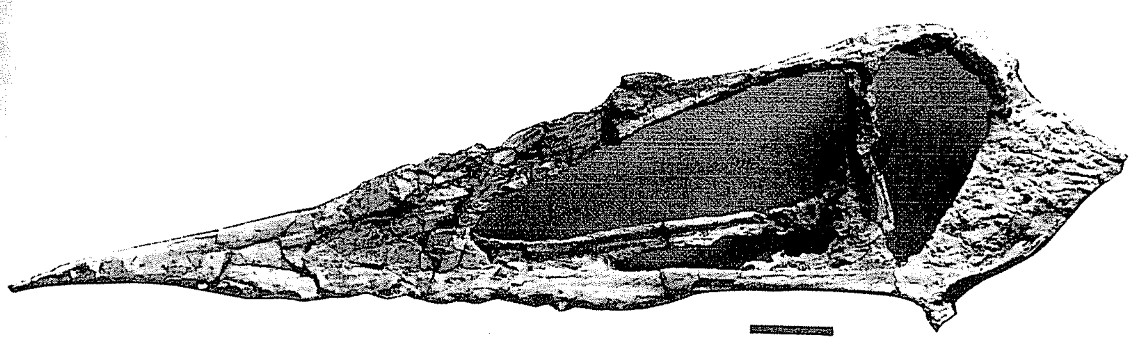


Figure 21.7. Skull remains, in left lateral view, of a juvenile dsungaripterid (MMNH) from the early Early Cretaceous of Tatal, Western Mongolia. Scale bar = 10 mm.

Family Azhdarchidae Nesov, 1984

Genus *Azhdarcho* Nesov, 1984

Type species. *Azhdarcho lancicollis* Nesov, 1984.

Diagnosis. According to Nesov 1984, p. 39, 'Spinous process in middle of tubular cervical vertebrae has the form of a weak crest, which is not approached by the lateral crests.' It is not clear that this feature distinguishes *Azhdarcho* from other pterosaurs and further work on the taxonomic status of this pterosaur is needed.

Azhdarcho lancicollis Nesov 1984

Holotype. TsNIGRI, LU-N 1/11915, anterior part of a mid-series cervical (Nesov, 1984, pl. 7, fig. 2). Dzharakhuduk (= Dzhyrakhuduk, Itemir, Beleuta), Navoi district of the Bukhara region, Uzbekistan. Lower and middle part of the Beleuta Svita, variously referred to by Nesov as the Taikarshin Beds (Nesov, 1981, 1984), or the Bissekty Svita (Nesov, 1990), Upper Cretaceous (Coniacian: Nesov and Roček, 1993; Archibald *et al.*, 1998).

Referred material. More than 40 fragmentary, disarticulated, but otherwise well-preserved bones representing parts of the jaws, vertebrae, pectoral and pelvic girdles and the fore and hind limbs (Nesov, 1984, pl. 7, figs. 1–11 and 13; 1986, pl. 2, fig. 1; Nesov and Yarkov, 1989, pl. 2, figs. 2–8; Bakhurina & Unwin, 1995a, fig. 13; Figure 21.8).

Diagnosis. Same as for the genus.

Comments. *Azhdarcho* exhibits derived features such as the T-shaped cross-section of the second wing-phalanx, which unites it and other taxa, principally *Quetzalcoatlus* and *Zhejiangopterus*, in the family Azhdarchidae (Unwin and Lü, 1997). However, the remains of *Azhdarcho* have yet to be described in detail and its relationships to other azhdarchids are unclear.

Azhdarcho has been referred to as a giant pterosaur (Nesov and Roček, 1993), but most individuals are likely to have been only about 3–4 m in wingspan, although rare remains indicate the presence of animals with wingspans of up to 5–6 m. One or two tiny elements appear to represent very small individuals, perhaps less than 1 m in wingspan (Nesov, 1991).

Azhdarchidae genus and sp. indet.

Material. Posterior half of an elongate cervical vertebra (Bogolyubov, 1914; Bakhurina and Unwin, 1995a, fig. 14) from marine sediments near the village of Malaya Serdoba in what was the province of Saratov (now Penza district), Volga region, Russia. Late Cretaceous: Coniacian?–Santonian (Nesov, 1990) or possibly early Campanian in age (Glazunova, 1972).

Comments. The vertebra, now lost (Bakhurina and Unwin, 1995a), which represents an animal with an estimated wing span of about 3–4 m, is similar to the highly elongate, mid-series cervicals of *Quetzalcoatlus* and *Azhdarcho*, and there seem few grounds to doubt its assignment to Azhdarchidae (Nesov and Yarkov, 1989; Bakhurina and Unwin, 1995a). This specimen was made the holotype of '*Ornithostoma orientalis*' by

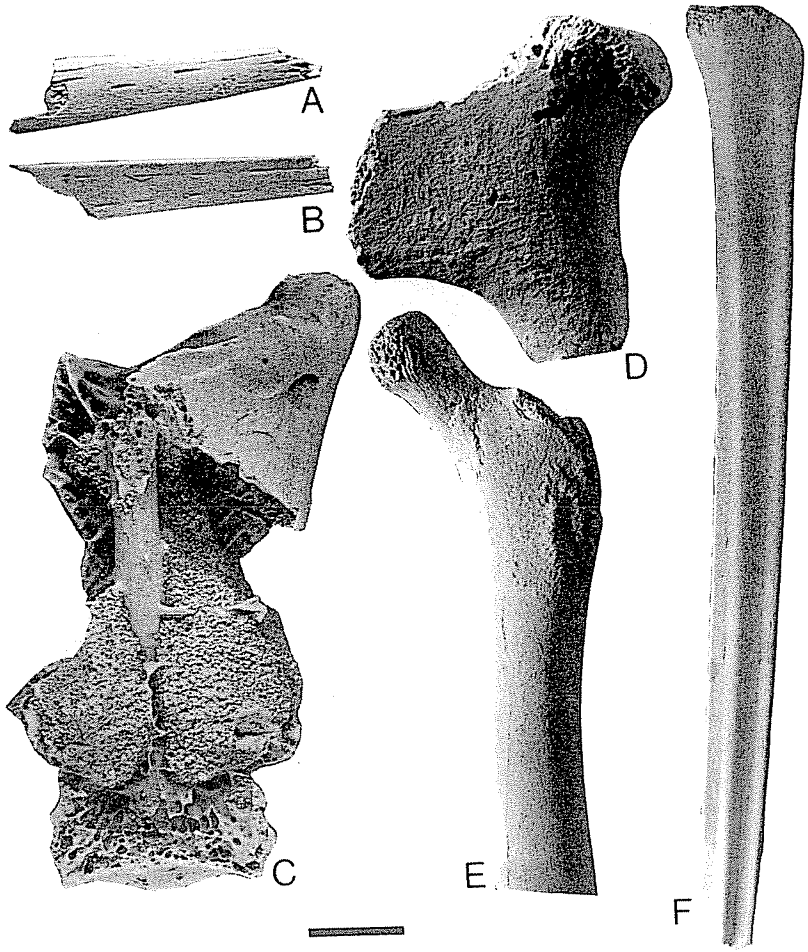


Figure 21.8. Fragmentary remains of *Azhdarcho lancicollis*, Nesov 1984, from the mid–Late Cretaceous of Dzharakhuduk, Uzbekistan. Section of mandibular symphysis in (A) right lateral and (B) occlusal view. Sixth (or possibly seventh) cervical in (C) dorsal view showing the ossified neural canal supported by fine bony trabeculae. Proximal end of left humerus in (D) dorsal view. Left femur in (E) anterior view. Left wing phalanx ii in (F) ventral view showing diagnostic longitudinal ventral ridge. Scale bar = 10 mm.

Bogolyubov (1914), but as it exhibits no features by which it can be distinguished from other azhdarchids the name must be considered a *nomen dubium*.

Pterosauria indet.

Indeterminate remains of pterosaurs have been reported from the Middle Jurassic Balabansai Formation of Northern Fergana in Kirgizstan (Nesov, 1990; Nesov *et al.*, 1987) and the Upper Jurassic of the Volga region of Russia (Khozatskii and Yur'ev, 1964). Fragmentary, indeterminate remains of pterosaurs have also been recovered from Early Cretaceous sediments at Klaudzin (= Kilodzhun) in the south-east part of the Fergana Valley, Kirgizstan, and at Khodzhakul and Scheikhdzheili, on the western part of the Sultanuvais ridge, in the south west Kyzylkum, Karakalpakia, Uzbekistan (Nesov *et al.*, 1987; Nesov, 1989, 1990).

Further indetermi
also been reported fi
ities of Shakh-Shak
Dzhusaly uplift in
north-east Aral re
1990) and from the
and Kyzylpilial in th
west part of the Fer
1990).

Single pterosaur
Nesov (1990) from
Azizbeck region
Bazhanov and
Cenomanian beds
Kirsanov area of T
collected a few poo
late Early Cretace
near Gubkin city
(Nesov *et al.*, 1986;
mentary indetermi
lected from Late
European part of
Gora, near Prol
(Glikman, 1953),
west of Polunino
Volgograd district
1990).

Pterosaurs from t
Mongolia span a
the known temp
and represent mo
main clades (Fig
the general signi
considering them
saur evolutionary

Pre-Middle Ju
from the FSU o
they were prese
since Late Trias
well known fr
(Wellnhofer, 19
been few barrier

Further indeterminate remains of pterosaurs have also been reported from the Upper Cretaceous localities of Shakh-Shakh, Baibishe and Buroinak on the Dzhusaly uplift in the Kyzyl-Orda district of the north-east Aral region, Kazakhstan (Nesov, 1984, 1990) and from the localities of Kansai, Zamuratscho and Kyzylpilial in the Kyzylbulag district of the north west part of the Fergana Valley, Tadzhikistan (Nesov, 1990).

Single pterosaur bones have been reported by Nesov (1990) from the Turonian of Khidzorut, in the Azizbeck region of Southern Armenia and by Bazhanov and Yeremin (1977) from Albian–Cenomanian beds near Kobyaki village, in the Kirsanov area of Tambov district, Russia. Nesov also collected a few poorly preserved pterosaur bones from late Early Cretaceous sediments exposed in quarries near Gubkin city in the Belgorod district of Russia (Nesov *et al.*, 1986; Nesov, 1990). Finally, a few fragmentary indeterminate remains have also been collected from Late Cretaceous horizons in the south European part of Russia at the locality of Lysaya Gora, near Proletarskii village, Saratov district (Glikman, 1953), and from Luchiskina gorge, south west of Polunino village in the Dubovskii area of the Volgograd district (Nesov and Yarkov, 1989; Nesov, 1990).

Discussion

Pterosaurs from the former Soviet Union (FSU) and Mongolia span a considerable portion (110 Myr) of the known temporal range for this group (160 Myr) and represent more than half (five out of nine) of the main clades (Figure 21.9). We can gain some idea of the general significance of the taxa listed above by considering them within the general context of pterosaur evolutionary history.

Pre-Middle Jurassic pterosaurs are so far unknown from the FSU or Mongolia, though we suspect that they were present in this region during this interval since Late Triassic and Early Jurassic pterosaurs are well known from the western half of Eurasia (Wellnhofer, 1991a) and there would appear to have been few barriers to their early dispersal eastwards.

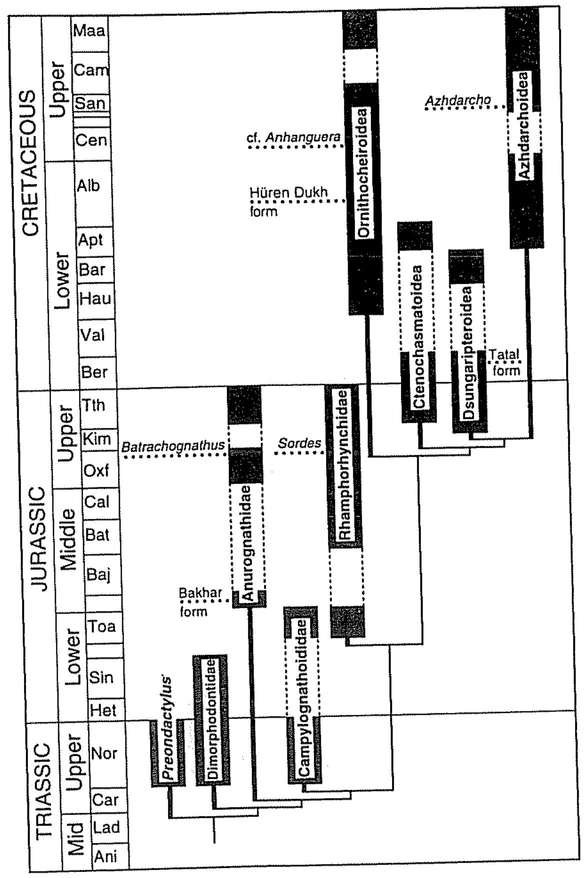


Figure 21.9. The stratigraphic distribution of major clades of pterosaur indicating the approximate position of important taxa from Russia, Middle Asia and Mongolia. The 'tree' used here is based on a synthesis of recent cladistic analyses of pterosaur relationships (see Unwin and Lü, 1997) and data on the stratigraphic distribution of taxa (from Wellnhofer, 1991a, updated to 1998) assigned to each of the nine major clades. Boxes with a solid boundary and black fill indicate the known fossil record, resolved to Stage level, for a particular clade; a dashed boundary represents an inferred record. Note that even if there is only a single record for a particular stage (e.g. *Anurognathus ammoni*) the taxon is assumed to span the entire stage length. Thick vertical lines indicate the maximum likely extension, backward in time, of particular clades, as inferred from the hypothesis of relationships proposed by Unwin (1995). Abbreviations: Alb, Albian; Ani, Anisian; Apt, Aptian; Bar, Barremian; Baj, Bajocian; Bat, Bathonian; Ber, Berriasian; Cal, Callovian; Cam, Campanian; Car, Carnian; Cen, Cenomanian; Hau, Hauterivian, Het, Hettangian; Kim, Kimmeridgian; Lad, Ladinian; Maa, Maastrichtian; Nor, Norian; Oxf, Oxfordian; San, Santonian; Sin, Sinemurian; Toa, Toarcian; Tth, Tithonian; Val, Valanginian.

Anurognathids, small to medium-sized, highly specialized, possibly insectivorous pterosaurs may have first appeared in the Late Triassic or Early Jurassic (Figure 21.9). The Mongolian and Kazakh records are important because, so far, they provide the only evidence to substantiate the predicted longevity of this clade. In addition, their recovery from continental deposits suggests that this group lived in terrestrial habitats and that the single specimen of *Anurognathus ammoni* found in the Solnhofen beds may represent an 'accidental' occurrence.

A similar situation might also pertain for *Sordes*, currently the only rhamphorhynchid known from the FSU or Mongolia. Examples of *Sordes* nearest known relative, *Scaphognathus*, are also exceptionally rare in the Solnhofen Plattenkalke (3 out of 300+ individuals [R. Kemp, pers comm., 1998]), though *Sordes* itself is relatively common in the Karatau deposits (8 out of 10 individuals recovered so far). By contrast, virtually all records of Jurassic rhamphorhynchines (*Dorygnathus* + *Rhamphocephalus* + *Nesodactylus* + *Rhamphorhynchus*) have been found in marginal marine or marine deposits. We hypothesize that rhamphorhynchines were aerial piscivores that lived predominantly in coastal environments, while scaphognathines (*Sordes* + *Scaphognathus*) inhabited continental environments and fed on fish caught in lakes and rivers. Notably, the dentition of scaphognathines is not specialized in the same way as that of rhamphorhynchines and it may be that their diet was not entirely confined to fish.

Ornithocheiroids (*Nyctosaurus* + '*Ornithodesmus*' + Ornithocheiridae + Pteranodontidae) have a good fossil record, for pterosaurs, and are known to have persisted from early in the Early Cretaceous through to the end of this period, though the group probably first arose in the Late Jurassic (Figure 21.9). These medium- to large-sized pterosaurs have been recovered from all continents, except Antarctica, and seem to have been efficient fliers (Bramwell and Whitfield, 1974). The Russian occurrence is of interest because it represents one of the youngest records for the Ornithocheiridae. This family is also known from the Cenomanian of England (Wellnhofer, 1978), but there are no reliable records from younger deposits. The Mongolian ornithocheirid is surprising because, unlike other fossil records for this family, virtually all of which have been found in marginal or fully marine deposits, this individual was recovered from a large, shallow, freshwater lake, located hundreds of kilometres from the nearest coastline. It is not clear, however, if this represents an 'accidental' occurrence, a migrant, or a resident (Bakhurina and Unwin, 1995a).

Dsungaripteroids (Germanodactylidae + Dsungaripteridae) are best known from the Early Cretaceous of Asia (Unwin *et al.*, 1997), and have also been reported from the Early Cretaceous of South America (Martill and Frey, pers comm., 1997) and the Late Jurassic of Europe (Buffetaut *et al.*, 1998) and East Africa (Galton, 1980; Unwin and Heinrich, 1999). The Tatal dsungaripterid is of particular interest because in some respects, for example, size, morphology and geological age, it forms an almost perfect intermediate between early dsungaripteroids such as *Germanodactylus* and the most derived taxon, *Dsungaripterus*. However, *Normannognathus* from the Late Jurassic of France, recently described by Buffetaut *et al.* (1998), does not fit comfortably within this sequence and suggests that dsungaripteroid evolutionary history may be more complex than previously thought.

The Azhdarchidae was first recognized by Nesov in the mid-1980s following his discovery of *Azhdarcho* which, until recently, was also the oldest certain record for this family. Cladistic analysis suggests that azhdarchids appeared before the end of the Early Cretaceous (Figure 21.9) and this seems to be supported by a report of a fossil remain from the Early Cretaceous Crato Formation of Brazil that exhibits at least one diagnostic azhdarchid feature (Martill and Frey, 1998). Following a string of new discoveries during the last ten years and reassignment of some previously described taxa, such as *Quetzalcoatlus* and *Arambourgiania*, to the Azhdarchidae, this family, now known from North and South America, Europe, Africa, Asia and possibly Australia (Unwin and Lü, 1997) appears to have been the most widespread and taxonomically diverse clade of Late Cretaceous pterosaurs.

We are gratefu
specimens:
Ulaanbaatar;
Ulaanbaatar; a
Petersburg. We
(Berlin) for ass
(Bristol), E. Fr
and P. Wellnh
ments on earli
edges the Roya
Sciences, Univ

Archibald, J.D., S
D.J., Tsar
Veretennik
the Cretace
imentology
Kyzylkum
S.G., Kirkl
Middle Cr
Museum of
Bakhurina, N.N
Cretaceous
4: 104–108.
—1983. [Early C
Mongolia.]
Paleontologi
—1984. [On the
saurs in t
western M
Ispytatelei P
—1986. [Flying
—1988. [On t
Batrachogna
Jurassic b
Obshchestva
132.
—1989. Flying
on morpho
pterosaurs.
Mongolian
17–18, Mos

Acknowledgements

We are grateful to the following for allowing access to specimens: A. Perle, Technical University, Ulaanbaatar; R. Barsbold, Geological Institute, Ulaanbaatar; and the late L. Nesov, University of St. Petersburg. We thank S. Powell (Bristol) and W. Harre (Berlin) for assisting with the figures and M.J. Benton (Bristol), E. Frey (Karlsruhe), D. Martill (Portsmouth) and P. Wellnhofer (Munich) for their helpful comments on earlier drafts of the MS. D.M.U. acknowledges the Royal Society and the Department of Earth Sciences, University of Bristol for their support.

References

Archibald, J.D., Sues, H.-D., Averianov, A.O., King, C., Ward, D.J., Tsaruk, O.A., Danilov, I.G., Rezvyi, A.S., Veretennikov, B.G. and Khodjaev, A. 1998. Precis of the Cretaceous paleontology, biostratigraphy and sedimentology at Dzharakuduk (Turonian?-Santonian), Kyzylkum Desert, Uzbekistan, pp. 21–27 in Lucas, S.G., Kirkland, J.I. and Estep, J.W. (eds.), *Lower and Middle Cretaceous terrestrial ecosystems. New Mexico Museum of Natural History and Science, Bulletin* 14.

Bakhurina, N.N., 1982. [A pterodactyl from the Lower Cretaceous of Mongolia.] *Palaeontologicheskii Zhurnal*, 4: 104–108.

—1983. [Early Cretaceous pterosaur localities in western Mongolia.] *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii* 24: 126–129.

—1984. [On the discovery of numerous remains of pterosaurs in the Early Cretaceous locality of Tatal, western Mongolia.] *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii* 59 (3): 130.

—1986. [Flying reptiles.] *Priroda* (1986), 7: 27–36.

—1988. [On the first rhamphorhynchoid from Asia: *Batrachognathus volans* Ryabinin 1948, from Upper Jurassic beds of Karatau.] *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii* 63 (5): 132.

—1989. Flying reptiles from Mongolia: new information on morphology, systematics and palaeogeography of pterosaurs. *Basic research results of the Joint Soviet-Mongolian Palaeontological Expedition*, 1969–1988: 17–18, Moscow: Akademiya Nauk.

—1993. Early Cretaceous pterosaurs from western Mongolia and the evolutionary history of the Dsungaripteroidea. *Journal of Vertebrate Paleontology* 13 (Suppl. to 3): 24A.

—and Unwin, D M. 1992. *Sordes pilosus* and the function of the fifth toe in pterosaurs. *Journal of Vertebrate Paleontology* 12 (Suppl. to 3): 18A.

—and— 1995a. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. *Historical Biology* 10: 197–245.

—and— 1995b. Taphonomy of pterosaurs from the Upper Jurassic lacustrine lithographic limestones of Karatau, Kazakhstan. *II International Symposium on Lithographic Limestones*, Lleida-Cuenca, Spain, Ediciones de la Universidad Autónoma de Madrid, 19–21.

—and— 1995c. A preliminary report on the evidence for 'hair' in *Sordes pilosus*, an Upper Jurassic pterosaur from Middle Asia, pp. 79–82, in Sun, A. and Wang Y. (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*. Short Papers. China Ocean Press: Beijing.

—and— 1995d. The evidence for 'hair' in *Sordes* and other pterosaurs. *Journal of Vertebrate Paleontology* 15 (Suppl. to nb. 3): 17A.

—and— 1996. Pterosaurs from continental environments. *Journal of Vertebrate Paleontology* 16 (Suppl. to nb. 3): 20A.

—and—1997 Pterosaur 'hair'. *Journal of Morphology* 232: 231.

Bazhanov, V.S. and Yeremin, A.V. 1977. [The first discovery of remains of reptiles in the Cretaceous beds of the Tambov district], pp. 20–21 in Darevskii, I.S. (ed.), *Problemy Gerpetologii* 4 (1977). Leningrad: Nauka Press.

Bogolyubov, N.N. 1914. [On the vertebra of a pterodactyl from the Upper Cretaceous beds of Saratoff Province.] *Ezhegodnik po Geologii i Mineralogii Rossii* 16: 1–7.

Bramwell, C.D. and Whitfield, G.R. 1974. Biomechanics of *Pteranodon*. *Philosophical Transactions of the Royal Society of London* B 267, 503–581.

Buffetaut, E., Lepage, J.-J. and Lepage G. 1998. A new pterodactyloid pterosaur from the Kimmeridgian of the Cap de la Hève (Normandy, France). *Geological Magazine* 135: 719–722.

Döderlein, L. 1923. *Anurognathus Ammoni* ein neuer Flugsaurier. *Sitzungs-berichte der Bayerischen Akademie* *der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung* 117–164.

Doludenko, M.P. and Orlovskaya, E.R. 1976. Jurassic floras of the Karatau ridge, southern Kazakhstan. *Palaeontology* 19: 627–640.

Galton, P.M. 1980. Avian-like tibiotarsi of pterodactyloids (Reptilia: Pterosauria) from the Upper Jurassic of East Africa. *Paläontologische Zeitschrift* 54: 331–342.

Glazunova, A.E. 1972. [*Palaeontological basis for the stratigraphic subdivision of Cretaceous deposits in the Volga region*], 144 pp. Leningrad: Nedra Press.

Glikman, L.C. 1953. [Late Cretaceous vertebrates from the region of Saratov.] *Scientific Reports of Saratov State University* 38: 51–54.

Ivakhnenko, M.F. and Korabel'nikov, V.A. 1987. [*Life of the past world*], 253 pp. Moscow: Prosveshchenie Press.

Kaup, J. 1834. Versuch einer Einteilung der Säugetiere. *Isis*. 315pp. Jena.

Kellner, A.W.A. 1996. Pterosaur phylogeny. *Journal of Vertebrate Paleontology* 16 (Suppl. to nb. 3): 45A.

Khozatskii, L.I. 1995. [Pterosaur from the Cenomanian (Late Cretaceous) of Saratov.] *Vestnik Sankt-Peterburgskogo Universiteta, Seriya 3, Biologiya* 2 (2): 115–116.

—and Yur'ev, K.B. 1964. [Pterosauria], pp. 589–603 in Orlov, U.A. (ed.), *Osnovy Palaeontologii*. Moscow: Izdatel'stvo Nauka.

Kuhn, O. 1937. *Die fossilen Reptilien*. 121 pp. Berlin.

Martill, D.M. and Frey, E. 1998. A new pterosaur Lagerstatte in N.E. Brazil (Crato Formation: Aptian, Lower Cretaceous): preliminary observations. *Oryctos* 1: 79–85.

Merkulova, N.N. 1980. [The first discovery of pterosaurs in Mongolia.] *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii* 1980: 103–104.

Nesov, L.A. 1981. [Flying reptiles from the late Cretaceous of Kyzylkum.] *Paleontologicheskii Zhurnal* **1981** (4): 98–104.

—1984. [Upper Cretaceous pterosaurs and birds from Central Asia.] *Paleontologicheskii Zhurnal*, **1984** (1): 47–57.

—1989. [New discoveries of remains of dinosaurs, crocodiles and flying reptiles from the late Mesozoic of the USSR]. *Abstracts of the Seventh All Union Herpetological Conference, Kiev*: 173–174. Kiev: Naukova Dumka.

—1990. [Flying reptiles of the Jurassic and Cretaceous of the USSR and the significance of their remains for the reconstruction of paleogeographic conditions.] *Vestnik Leningradskogo Universiteta, Seriya 7, Geologiya, Geografiya* 1990, 4 (28): 3–10.

—1991. [Giant flying reptiles of the family Azhdarchidae: I. Morphology and systematics]. *Vestnik Leningradskogo Universiteta, Seriya 7, Geologiya, Geografiya* 1991, 2 (14): 14–23.

—, Kaznyshkina, L.F. and Cherepanov, G.O. 1987. [Dinosaurs, crocodiles and other archosaurs from the late Mesozoic of Central Asia and their place in ecosystems]. *Abstracts of the thirty third session of the All-Union Paleontological Society, Leningrad*: 46–47.

—, Mertinene, R.A., Golovneva, L.B., Potapova, O.P., Sablin, M.B., Abramov, A.B., Bugaenko, D.V., Nalbandyan, L.A. and Nazarkin, M.V. 1986. [New discoveries of remains of ancient organisms in the Belgorod and Kursk districts], pp 124–131 in *Comprehensive study of biogeocoenoses of oak woods of forest steppe*. Leningrad: Leningrad University Press.

—and Roček, Z. 1993. Cretaceous anurans from central Asia. *Palaeontographica, Abteilung A* 226: 1–54.

—and Yarkov, A.A. 1989. [New birds from the Cretaceous and Palaeogene of the USSR and some remarks on the origin and evolution of the Class Aves], pp. 78–97 in Potapov, R.L. (ed.) [*Faunistic and ecological studies of Eurasian birds*], *Trudy Zoologicheskogo Instituta AN SSSR* **197**.

Plieninger, F. 1901. Beiträge zur Kenntnis der Flugsaurier. *Paleontographica* 48: 65–90.

Ryabinin, A.N. 1948. [Remarks on a flying reptile from the Jurassic of the Karatau.] *Trudy Paleontologicheskogo Instituta AN SSSR* 15: 86–93.

Seeley, H.G. 1869. Index to the fossil remains of Aves, Ornithosauria and Reptilia in the Woodwardian Museum, Cambridge. *Proceedings of the Cambridge Philosophical Society* 3: 1–169.

—1870. *The Ornithosauria: An elementary study of the bones of Pterodactyles*. 130 pp. Cambridge.

Sharov, A.G. 1968. [*Jurassic insects from Karatau*], 252 pp. Moscow: Nauka Press.

—1971. [New flying reptiles from the Mesozoic of Kazakhstan and Kirgizstan.] *Trudy Paleontologicheskogo Instituta AN SSSR* 130: 104–113.

Shuvalov, V.F. 1974. [On the geological structure and age of the fossil localities Höövör and Hüren Dukh], pp. 296–304 in *Mesozoic and Cenozoic faunas and biostratigraphy of Mongolia. Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii* 1.

—1982. [Palaeogeography and historical development of

Mongolian
Cretaceous
Mezozoiskie
Nauka.
—and Trusova, I
position of
tracans of M
of Mongol.
Paleontologi
Unwin, D.M. 19
analysis of
pp 69–72
Symposium
Short Pape
—and Bakhuri
nature of t
62–64.
—and— 1997.
for unders
Journal of
—, Bakhurina, N
1997. Pt
Palaeontolog

Mongolian lake systems in the Jurassic and Cretaceous], pp. 18–80 in Martinson, G.G. (ed.), *Mezozoiskie Ozernye Basseiny Mongolii.* Leningrad: Nauka.

—and Trusova, E.K. 1976. [New data on the stratigraphical position of late Jurasic and early Cretaceous conchostracans of Mongolia.] In *Paleontology and biostratigraphy of Mongolia, Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii* 3: 236–264.

Unwin, D.M. 1995. Preliminary results of a phylogenetic analysis of the Pterosauria (Diapsida: Archosauria), pp 69–72 in Sun, A. and Wang Y. (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota.* Short Papers. China Ocean Press: Beijing.

—and Bakhurina, N.N. 1994. *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature* 371: 62–64.

—and— 1997. The significance of soft tissue preservation for understanding the palaeobiology of pterosaurs. *Journal of Morphology* 232: 332.

—, Bakhurina, N.N., Lockley, M.G., Manabe, M. and Lü, J. 1997. Pterosaurs from Asia. *Journal of the Palaeontological Society of Korea* 2: 43–65.

Unwin, D.M. and Heinrich, W.-D. 1999. On a pterosaur jaw from the Upper Jurassic of Tendaguru (Tanzania). *Mitteilungen Museum für Naturkunde Berlin, Geowissenschaftlichen Reihe* 2: 121–134.

—and Lü, J. 1997. On *Zhejiangopterus* and the relationships of pterodactyloid pterosaurs. *Historical Biology* 12: 199–210.

—, Martill, D.M. and Bakhurina, N.N. 1993. The structure of the wing membrane in pterosaurs. *Journal of Vertebrate Paleontology* 13 (Suppl. to 3): 61A.

Wellnhofer, P. 1975. Die Rhamphorhynchoidea der Oberjura-Plattenkalke Süddeutschlands. II: Systematische Beschreibung. *Palaeontographica*, A 148: 132–186.

—1978. *Handbuch der Paläoherpetologie.* Teil 19, *Pterosauria.* Stuttgart: Gustav Fischer Verlag.

—1991a. *The Illustrated Encyclopedia of Pterosaurs*, 192 pp. London: Salamander Books.

—1991b. Santana Formation pterosaurs, pp. 351–370 in Maisey, J.G. (ed.), *Santana Fossils.* Neptune City: T.F.H. Publications.

Young, C.C. 1964. On a new pterosaurian from Sinkiang, China. *Vertebrata PalAsiatica* 8: 221–255.