Paleontological Journal, Vol. 38, No. 4, 2004, pp. 426–436. Translated from Paleontologicheskii Zhurnal, No. 4, 2004, pp. 73–83.

New Data on Cretaceous Flying Reptiles (Pterosauria) from Russia, Kazakhstan, and Kyrgyzstan

A. O. Averianov

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia
e-mail: sasha@AA1923.spb.edu

Received December 10, 2002

Abstract—New and previously unpublished finds of pterosaurian bones are described from the Cretaceous of Russia, Kazakhstan, and Kyrgyzstan. The following taxa are determined: Pterodactyloidea indet. (distal fragment of femur; Kylodzhun locality, Kyrgyzstan; Albian); a very large Pterodactyloidea indet. (distal fragment of a second wing phalanx; Pavlovsk, Voronezh Region; Cenomanian); Ornithocheiridae indet. (distal fragment of the fourth metacarpal; Lebedinskii Quarry, Belgorod Region; Albian–Cenomanian; fragmentary maxilla; Sinen'kie locality, Saratov Region; Lower Cenomanian; fragmentary pelvis, femur, and sacral vertebrae from the same animal; Saratov, Russia; Cenomanian); and Azhdarchidae gen. et sp. indet. (jugal and a fragmentary cervical vertebra; Shakh-Shakh locality, Kazakhstan; Santonian–Campanian).

Key words: Pterosauria, Pterodactyloidea, Ornithocheiridae, Azhdarchidae, Cretaceous, Russia, Kazakhstan, Kyrgyzstan.

INTRODUCTION

Flying reptiles—or pterosaurs—are extremely scarce in the paleontological record. These animal have been registered in only three dozens of localities in the former Soviet Union (Nessov, 1990; Bakhurina and Unwin, 1995; Unwin and Bakhurina, 2000; Averianov *et al.*, 2003). Only two localities (Late Jurassic Karatau in Kazakhstan and Late Cretaceous Dzharakuduk in Uzbekistan) have yielded relatively well-preserved and abundant pterosaurs. In other localities, they are extremely rare and fragmentary. They are usually represented only by characteristic fragments of hollow thin-walled tubular bones, which provide evidence of the presence of flying reptiles in early ecosystems but are unsuitable for determination of their taxonomic position. At the same time, significant progress in our knowledge of pterosaurian anatomy and systematics has recently been achieved, which allows us to identify fragmentary remains of flying reptiles (even fragmentary epiphyses of limb bones and isolated vertebrae are commonly identifiable). New and previously unpublished pterosaur specimens from the Cretaceous of Russia, Kazakhstan, and Kyrgyzstan are described in this paper.

In addition to the specimens described in this paper, certain other pterosaurian bones have recently been discovered in Russia and the Commonwealth of Independent States (CIS). Thus, Yarkov (personal communication, 2001) found a tooth of a large pterosaur, presumably belonging to ornithocheirids, in the Cenomanian of the Volgograd Region. In 1995, A.V. Panteleev and I found the distal end of a femur (?) of a large pterosaur (specimen ZIN PH, no. 11/43) in the Albian–Cenomanian gray marine sand of the Belyi Kolodets Quarry near the village of Strelitsa in the Voronezh Region. These sands contain a large phosphoritic layer, which encloses fossil wood. Other fossils arerestricted to an isolated tooth plate of a chimaera. The pterosaurian bone was found in a piece of phosphorite, so its open anterior surface is strongly damaged, while the posterior surface has not yet been prepared. Isolated teeth of the pterosaur Ornithocheiridae indet. were also discovered in the Lower Cretaceous localities of Russia (Mogoito and Shestakovo) and Uzbekistan (Khodzhakul and Sheikhdzheili) (Averianov *et al.*, 2003).

The specimens examined are currently housed at the Paleoherpetological Collection of the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (ZIN PH and ZIN PHT) and at the Chernyshev Central Research Geological Museum, St. Petersburg (TsNIGR).

DESCRIPTIONS

Kylodzhun locality. This locality (= Klaudzin) is confined to the upper part of the Alamyshik Formation, which outcrops along the Sarykungoi Creek near the village of Sary Bulak in the Osh Region of Kyrgyzstan (southeastern Fergana). The vertebrate assemblage from Kylodzhun includes the osteichthyes cf. *Furo* sp. and Actinopterygii indet. (large form); the amphibian? Labyrinthodontia? indet. (tooth with folded dentin); the turtles *Kirgizemys exaratus, Ferganemys verzilini*, and *"Trionyx" kyrgyzensis*; and the crocodiles Crocodilia

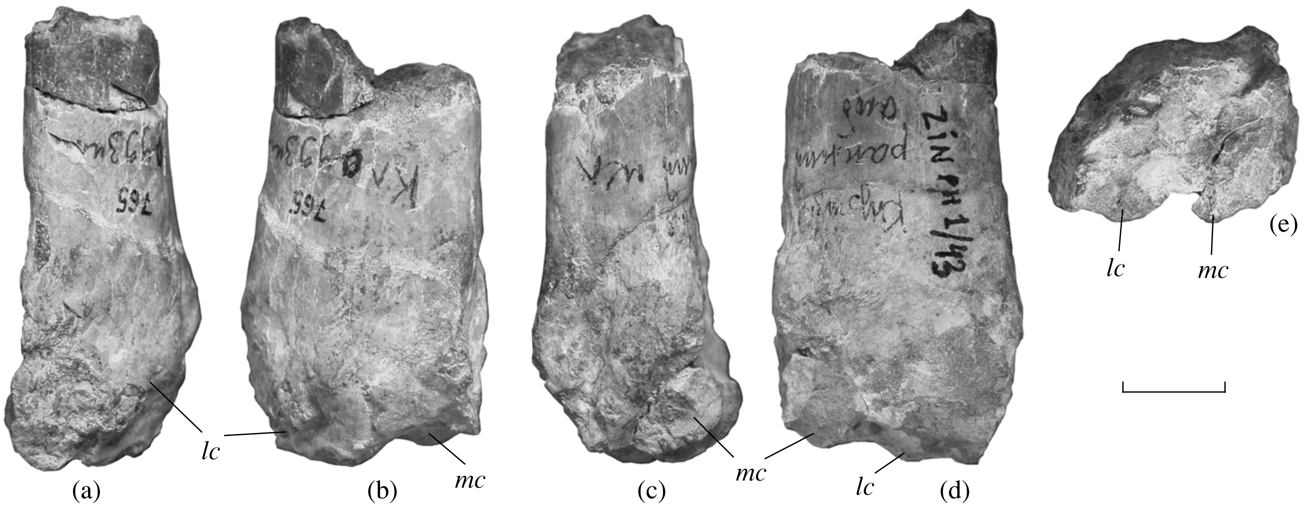

Fig. 1. Pterodactyloidea indet., specimen ZIN PH, no. 1/43, distal fragment of the right femur: (a) lateral, (b) anterior, (c) medial, and (d) posterior views, (e) view of the distal end; Kylodzhun locality, Kyrgyzstan; Lower Cretaceous (Albian). Designations: (*lc*) lateral condyle and (*mc*) medial condyle. Scale bar, 1 cm.

indet. It is tentatively dated as the Early–Middle Albian (Nessov, 1997, and references in this work). The pterosaur from Kylodzhun is represented by the distal end of the right femur (specimen ZIN PH, no. 1/43; Fig. 1) of a relatively large animal tentatively referred to as Ornithocheiridae? (Nessov, 1997).

The distal epiphysis of the bone (maximal width is 21.5 mm) is only slightly wider than the diaphysis. The most prominent distinctive feature of this specimen is the strongly oblique medial and lateral condyles, the ridges of which are positioned at an angle of 23° and 37°, respectively, to the parasagittal plane. The medial condyle projects anteriorly to a greater extent than the lateral condyle. The condyles are separated from each other by a shallow intercondylar sulcus, the posterior part of which forms a deeper fossa shaped into a transversely expanded oval. The poorly pronounced popliteal depression adjoins the condyles posteriorly. It is dorsally bordered by transverse traces of the flexors bending the tibiotarsus in the knee joint.

Specimen ZIN PH, no. 1/43 does not belong to the family Ornithocheiridae; although this family displays the oblique condyles, the ridges of these condyles and the intercondylar sulcus are only slightly developed, and a deep transverse fossa is absent from the posterior end of the intercondylar sulcus (Kellner and Tomida, 2000, text-figs. 52e, 52f). Apparently, this fossa has not been described in pterosaurs; however, it was probably present in the Pteranodontidae (Williston, 1903, pl. 44, fig. 4; Bennett, 2001, text-fig. 107B) and Dsungaripteridae (Bukharina, 1982, text-fig. 1v). The fossa is well-pronounced in the azhdarchid *Azhdarcho lancicollis* Nessov, 1994 (six specimens housed at the ZIN PH). The ligament of a flexor of the pes digits (musculus flexores digitorum) could originate from this fossa. The bone from Kylodzhun differs from that of these groups: the lateral epicondyle of pteranodontids is usually developed to a much greater extent than in specimen ZIN PH, no. 1/43; in dsungaripterids, the distal epiphysis is wider than the diaphysis (Young, 1964, text-fig. 7B; Bakhurina, 1982, text-figs. 1v and 1w); in dsungaripterids and azhdarchids, the ridges of the condyles are almost parallel to the sagittal plane rather than oblique. In addition, the distal femoral epiphysis of the pterosaur from Kylodzhun is flattened to a lesser degree than that of azhdarchids. Based on the above, it is impossible to determine specimen ZIN PH, no. 1/43 more closely than Pterodactyloidea indet.

Pavlovsk locality. The distal fragment of the left (?) second (?) phalanx of the fourth (wing) digit (specimen ZIN PH, no. 2/43, Fig. 2) was found by A.V. Broushkin in 1997 (or 1998) in the lower part of the Cenomanian sandstone in the Shkurlatov Granite Quarry (vicinity of the town of Pavlovsk, Voronezh Region) and transferred to the museum by A.S. Rezvyi. The specimen was accompanied by ichthyosaurian bones.

The fragment preserved is 54 mm long. The bone is oval (18 × 10 mm) in cross section; its long axis is subhorizontal, and the dorsal surface is more convex than the ventral. The posterior edge of the bone is straight, while the anterior edge is slightly concave. The distal condyle is triangular (possibly, it was damaged by rounding and weathering) and considerably curved dorsally, and its height (12.5 mm) is larger than the ventrodorsal diameter of the diaphysis. Two large pneumatic foramina are present anterior to the distal condyle; the dorsal foramen is located closer to the anterior edge of the bone, while the double ventral foramen is located more distally and closer to the posterior edge of the bone. Both foramina open in well-developed depressions. The

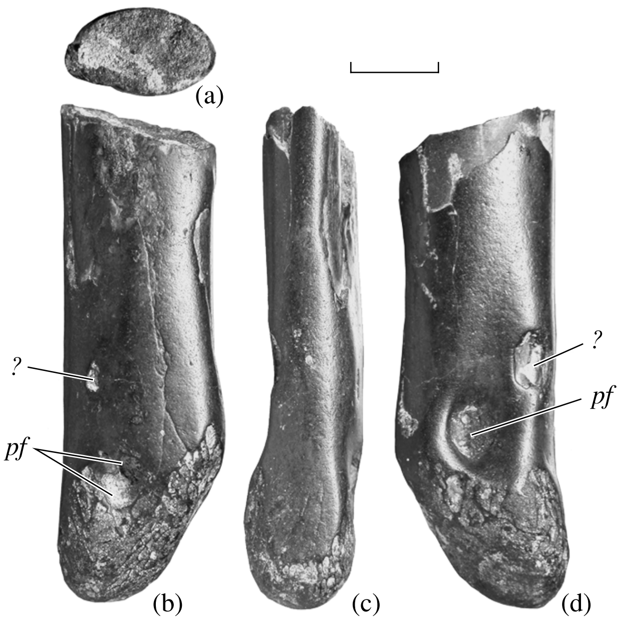

Fig. 2. Pterodactyloidea indet., specimen ZIN PH, no. 2/43, distal fragment of the left (?) second (?) phalanx of the fourth (wing) digit: (a) cross section; (b) ventral, (c) posterior, and (d) dorsal view; Shkurlat Quarry, Voronezh Region, Russia; Upper Cretaceous (Cenomanian). Designations: (*pf*) pneumatic foramen and (*?*) damaged bone. Scale bar, 1 cm.

bone of the diaphysis is very thin (about 0.3 mm thick) and slightly thickened along the posterior edge.

Judging by the oval cross section of the diaphysis, this phalanx belongs to a very large nonazhdarchid pterodactyl (in the majority of rhamphorhynchs, wing phalanges have a deep notch in the posterior edge; in azhdarchids, wing phalanges II and III are T-shaped in cross section and have thicker walls). The second and third phalanges of the fourth digit of large pterodactyls are very similar in morphology and differ only in dimensions and slenderness, i.e., parameters that change considerably in the course of ontogeny (Bennett, 2001). The distal end of the first phalanx is proportionally wider in all pterodactyls. Taking into account the large absolute dimensions and relative narrowness of this fragment, it most likely belongs to the second phalanx. The unique feature of this specimen is the presence of two large pneumatic foramina—dorsal and ventral. The wing phalanges of dsungaripterids are also suboval in cross section, but less pneumatized and more thick-walled. The strongly pneumatic thin-walled wing phalanges are characteristic of giant ornithocheirids and pteranodontids. However, the section of the second and third phalanges of ornithocheirids is subtriangular rather than oval and the distal pneumatic foramina have not been described in this group (Kellner and Tomida, 2000). The wing phalanges of the pteranodontids *Pteranodon* spp. are oval in cross section, but only one small ventral pneumatic foramen is present on the distal end of phalanges II and III (Bennett, 2001, text-fig. 99B). Thus, it is impossible to determine specimen ZIN PH, no. 2/43 more accurately than as Pterodactyloidea indet. It most likely belongs to a new, very large flying reptile.

Lebedinskii Quarry. A thick bed of greenish gray and yellow marine sand with one or two interbeds of large phosphorites, which mark the periods of maximal marine bioproductivity in conditions of upwelling, outcrops in the great iron ore Lebedinskii and Stoilenskii quarries (Kursk Magnetic Anomaly, Belgorod Region, near the towns of Gubkin and Staryi Oskol, respectively). The sand is referred to the Albian–Cenomanian and contains various and abundant chondrichthyans and osteichthyes; common remains of marine saurians (ichthyosaurs *Platypterygius* sp., plesiosaurs Elasmosauridae indet., and giant pliosaurs *Polyptychodon* sp.), marine turtles *Teguliscapha rossica* (Protostegidae: Chelospharginae), and Dermochelyidae indet.; possibly, brackish and freshwater turtles ?Macrobaenidae indet.; and scarce dinosaurs Theropoda indet. and Hadrosauroidea indet. (Nessov *et al.*, 1988; Nessov, 1995, 1997; Averianov, 2002; Arkhangelsky and Averianov, 2003; see also references in these studies). Pterosaurian remains are rather common in the Lebedinskii and Stoilenskii quarries; however, they are extremely poorly preserved and represented by small fragments of the long thin-walled tubular bones of large animals. Only two satisfactory preserved specimens were found during the period of the collecting since 1980 (both in the Lebedinskii Quarry). The first bone, found in 1985 by L.A. Nessov and students at Leningrad (now St. Petersburg) State University, is "a fragment of a wing phalanx 18 cm in length and 1.8 cm in diameter" (Nessov *et al.*, 1988, p. 130). Unfortunately, it is unknown where the specimen is currently housed.

The second bone fragment was found by L.A. Nessov and A.O. Averianov in 1987 and originally identified as "a tibiotarsus… of a large pterosaur" (Nessov, 1990, p. 8). Subsequently, this specimen was determined to be a metacarpal of the fourth (wing) digit (Bakhurina and Unwin, 1995). Only the dorsal and, partially, anterior and posterior walls of the distal part, including less than half of the bone width (specimen ZIN PH, no. 3/43, Fig. 3), are preserved. The bone was relatively large; the preserved fragment is 11.8 cm long and the reconstructed anteroposterior diameter of the dorsal condyle is about 22–23 mm. The diaphysis is hollow and oval in cross section. The wall of the diaphysis along the anterodorsal edge is approximately two or three times thicker than in other parts. The diaphysis slightly narrows toward the proximal end, where it is slightly anteroposteriorly constricted. The anterior surface of the diaphysis is flattened. The dorsal condyle sharply expands in the anteroposterior direction, and its distal end is slightly blunted. The articular facet for the first phalanx is inclined inward at an angle of approximately 60°. A small area is observed on the ventral side; this is probably the base of a rounded ridge between the dorsal and ventral condyles. On the inner side, the proximal diaphysis has a tubular bone structure, with relatively large cavities between bony bars.

The preserved part is almost identical in structure to metacarpal 4 of the ornithocheirids *Anhanguera piscator* Kellner et Tomida, 2000 and *A. araripensis* (Wellnhofer, 1985) (Wellnhofer, 1991, text-fig. 39; Kellner and Tomida, 2000, text-fig. 42). In the pteranodontids *Pteranodon* spp., the dorsal condyle of metacarpal 4 projects above the bone diaphysis to a much greater extent, and a rounded crest between the dorsal and ventral condyles is absent (Bennett, 2001, text-figs. 87–89). The distal end of metacarpal 4 of the dsungaripterid *Dsungaripterus weii* Young, 1964 is curved dorsally and has a dorsal condyle that considerably projects beyond the diaphysis (Young, 1964, text-fig. 4C). The dorsal condyle of the azhdarchid *Azhdarcho lancicollis* Nessov, 1984 (collection ZIN PH) displays somewhat different proportions; in particular, it is more rectangular. Specimen ZIN PH 3/43 can confidently be assigned to the family Ornithocheiridae and identified as Ornithocheiridae indet.

Sinen'kie locality. I and A.V. Panteleev found a small fragment of the pterosaurian maxilla (specimen ZIN PH, no. 6/43, Fig. 4) in 1995 in yellow phosphorite sand exposed in a small quarry near the village of Sinen'kie south of the city of Saratov (Saratov Region). The sand contains diverse fauna of Early Cenomanian chondrichthyans and osteichthyes, while tetrapods are represented by a fragmentary pterosaurian bone as well as an ichthyosaurian vertebra and the fragmentary teeth of plesiosaurs.

The fragment of the right maxilla (specimen ZIN PH, no. 6/43, Fig. 4) contains two oval alveoli (each is approximately 7.5 × 5.0 mm in diameter), whose long axes are located at an angle of 30° to the longitudinal jaw axis. The space between these alveoli is 6.5 mm. The alveolar margin of the bone is curved from the lateral surface at an angle of about 140°. The medial surface of the bone abruptly ascends dorsally at an angle of about 85° to the alveolar margin. The raised medial portion (*longitudinal crest*, according to Fastnacht, 2001) of the bone indicates the presence of a significant depression between the alveolar edge and the palatal (median) ridge (Fig. 4d), or between the opposite alveolar edges (*depressus medianus ventralis*, after Fastnacht, 2001); this corroborates the assignment of this fragment to the maxilla.

Specimen ZIN PH, no. 6/43 belongs to a large toothed pterosaur, whose taxonomic position cannot be determined on the basis of this fragment. Only two groups of large toothed pterosaurs are known in the Late Cretaceous: Ornithocheiridae and Lonchodectidae (Fastnacht, 2001; Unwin, 2001). This fragment could belong to any of them. However, taking into account the presence of an ornithocheirid (see below) in the Cenomanian of Saratov, specimen ZIN PH, no. 6/43 more likely belongs to an ornithocheirid; therefore, it is tentatively determined as ?Ornithocheiridae indet.

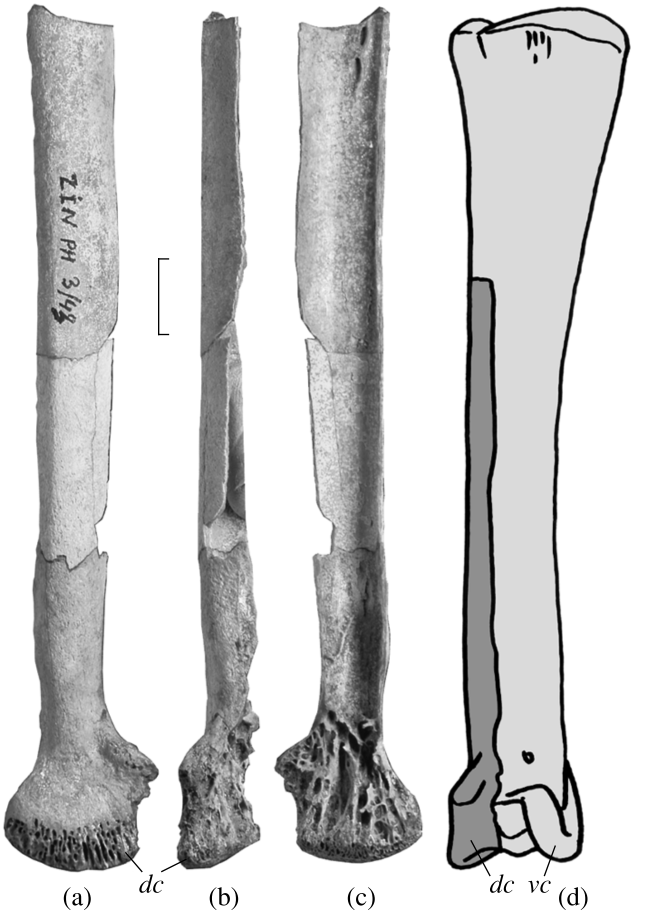

Fig. 3. Ornithocheiridae indet., specimen ZIN PH, no. 3/43, distal fragment of the left metacarpal of the fourth (wing) digit: (a) dorsal, (b) posterior views, (c) internal surface and (d) reconstruction of metacarpal 4, based on *Anhanguera piscator* (Kellner and Tomida, 2000, text-fig. 42d; dark gray color shows preserved fragment), posterior view; Lebedinskii Quarry, Belgorod Region, Russia; Lower–Upper Cretaceous (Albian–Cenomanian). Designations: (*dc*) dorsal condyle and (*vc*) ventral condyle. Scale bar, 1 cm (for a–c).

Saratov locality. The Cenomanian yellow and gray coastal marine phosphatic sands are exposed in several natural outcrops and artificial quarries in Saratov and the adjacent area. They yielded a rich assemblage of chondrichthyans and osteichthyes and rather scarce tetrapods, such as the ichthyosaurs ?*Platypterygius* sp., the plesiosaurs Polycotylidae indet. and Elasmosauridae indet., and marine turtles Chelospharginae indet. or Chelonioidea indet., which existed in conditions of upwelling (Glikman, 1953; Nessov, 1997; Pervushov *et al.*, 1999; Averianov, 2002; see also the references in these studies). Glikman found pterosaurian remains in one such quarry late in the 1940s. Glikman (1953) indicated Lysaya Gora Hill near Saratov as the locality. L.A. Nessov believed that these specimens were found in a quarry near the village of Proletarskii (not far from Lysaya Gora). Gabdullin *et al.* (2002) proposed that they may have come from the Kozlovskii Sand Quarry

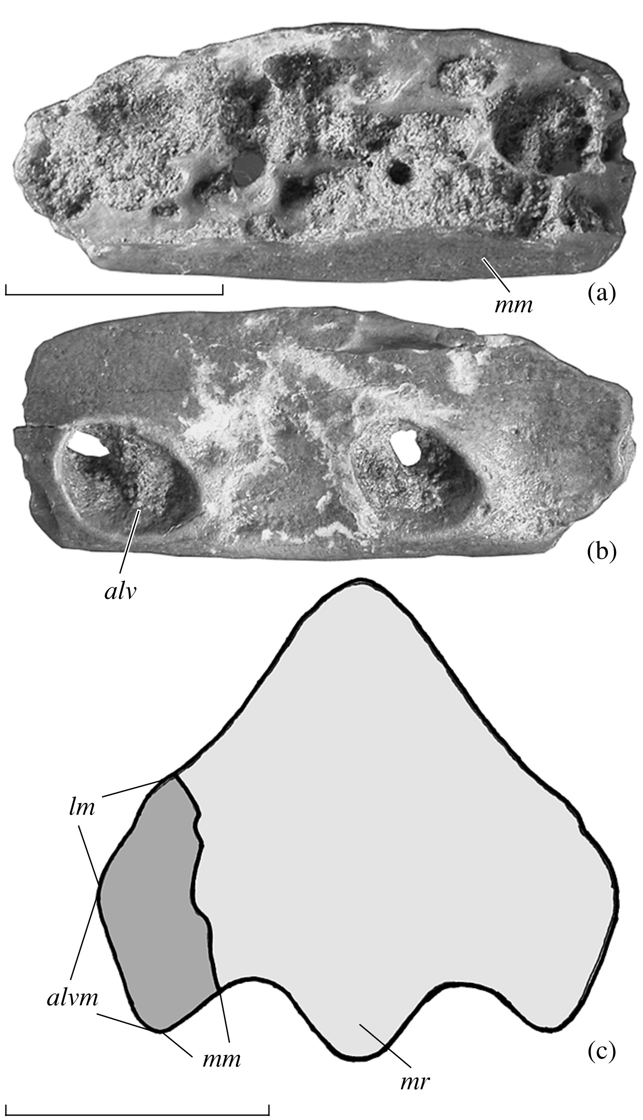

Fig. 4. ?Ornithocheiridae indet., specimen ZIN PH, no. 6/43, fragment of the right maxilla: (a) inner surface, (b) lateral view, and (c) reconstructed cross section of the maxilla, dark gray color shows the preserved fragment; Sinen'kie locality, Saratov Region, Russia; Upper Cretaceous (Cenomanian). Designations: (*alv*) alveolus, (*alvm*) alveolar margin, (*lm*) lateral margin, (*mm*) medial margin, and (*mr*) median ridge. Scale bar, 1 cm.

(School 38). The indication on a finding of a pterosaurian jaw near the village of Uvek, situated south of Saratov (Nessov, 1990), is obviously erroneous. In fact, this jaw comes from Saratov.

The first pterosaur from Saratov (specimen ZIN PHT, no. S50-1; Khozatskii 1995, text-figs. a–e; Unwin and Bakhurina, 2000, text-fig. 21.5) was originally determined as a fragmentary upper jaw of the ornithocheirid *Ornithocheirus* (?) sp. Subsequently, Bakhurina and Unwin (Bakhurina and Unwin, 1995; Unwin and Bakhurina, 2000) showed that, in actuality, this fragment is a lower jaw fragment, including the region of the mandibular symphysis; in addition, it is more similar to the genus *Anhanguera* of the same family and, consequently, can be determined as cf. *Anhanguera* sp.

The second specimen was described as "a fragmentary skeleton of a small thrush-sized pterodactyl" (Glikman, 1953, p. 54), "a wing fragment of a pterodactyl" (Nessov, 1990, p. 8; Bakhurina and Unwin, 1995, p. 232), or even as "a complete skeleton of a relatively small (thrush-sized) pterosaur" (Gabdullin *et al.*, 2002, p. 195). In actual fact, the specimens in question include fragments of the left ilium, pubis, femur, and three centra of the sacral vertebrae of a juvenile large pterosaur (specimen ZIN PH, nos. 8a–8c, 8e–8g/43, Figs. 5, 6). In addition, a relatively long tubular bone (specimen ZIN PH, no. 8d/43) with one preserved epiphysis was found. Nessov probably identified this bone as a wing phalanx. At the same time, it is not inconceivable that this bone is the proximal end of a tibiotarsus. However, it considerably differs from the known tibiotarsi and wing phalanges of large pterodactyls in the shape of the epiphysis, although these differences are possibly attributable to the juvenile ontogenetic stage of this animal.

The pelvis is represented by fragments of nonfused ilium and pubis in the region of the acetabulum and a number of smaller fragments, which are impossible to determine. The fragmentary ilium (Figs. 5g, 5h) retains the base of the anterior process and the entire iliac portion. The true articular facet for the femur occupies only the posterior half of the acetabulum. The ventral triangular area for contact with the anterior end of the pubis is present anterior to this facet. A well-pronounced fossa, which probably contained the rib of the second sacral vertebra, is observed on the internal surface opposite the acetabulum. The pubis is only represented by the proximal end, whose anterior edge for articulation with the ilium is broken off (Fig. 5h). The proximal end of the bone is transversely expanded, while the distal region is considerably flattened. The articular surface of the femur occupies the preserved proximal margin of the pubis almost entirely. This surface is relatively deeply concave. The large obturator foramen, which is not closed posteriorly by the pubis, is developed ventrally and posterior to the acetabulum. The ischium only slightly contributed to the formation of the acetabulum.

The centra of the sacral vertebrae (Figs. 5a–5f) are slightly procelous, and they were neither fused with the neural arches nor merged with each other in the synsacrum. The centrum of the larger and more anterior vertebra (specimen ZIN PH, no. 8f/43) is smooth ventrally. The ventral side of two other vertebrae has two slightly expressed longitudinal ridges that border the median groove; such a structure is characteristic of the middle sacral vertebrae. Sacral vertebrae are not fused in the synsacrum even in relatively large ornithocheirids (Kellner and Tomida, 2000).

The proximal fragment of the femur (Fig. 6) is slightly curved in the frontal plane, and the diaphysis is curved medially in the middle of this fragment. The neck of the femur is relatively long and slender; in the anterior view, it is positioned at an angle of about 25° to the long axis of the diaphysis, while, in *Anhanguera* and *Pteranodon*, these angles are 28° and 35°, respectively (Kellner and Tomida, 2000; Bennett, 2001). The proximal end of the femoral head is oval, while the posteromedial edge is slightly flattened. The greater trochanter is shaped into a wide but only slightly developed crest, which is continued distally by a narrower and relatively long crest. A poorly pronounced crest of the inner trochanter is present on the posterior surface of the bone medially and opposite to the distal third of the preserved part of the crest of the greater trochanter. Two longitudinally extended fossae for attachment of the ligaments of the iliofemoralis internus muscle are present in place of the lesser trochanter and somewhat distally along the anterolateral edge of the bone. The diaphysis of the bone is almost cylindrical in cross section, and its walls are uniform in thickness (about 0.4 mm).

The described fragments of the pelvis and femur are similar to those of adult ornithocheirid *Anhanguera* (Wellnhofer, 1988, 1991; Kellner and Tomida, 2000) and differ in their dimensions being approximately half as large, the posteriorly open obturator foramen, the articular facet for the femur that is limited to the posterior part of the iliac portion of the acetabulum, the relatively longer and more slender neck of the femur, the poorly pronounced lesser trochanter, and the narrower pubis. All these characteristics can be regarded as juvenile features. The pelvis and femur of other large pterosaurs differ to a much greater degree (Young, 1964; Nessov, 1991; Bennett, 2001). In particular, pteranodontids and azhdarchids have a relatively large pneumatic foramen in the intertrochanteric fossa of the femur; this foramen is completely absent in ornithocheirids and specimen ZIN PH, no. 8/43. The synapomorphy for Ornithocheiroidea is the angle between the neck and diaphysis of the femur, which exceeds 150° (ca. 155° in specimen ZIN PH, no. 8/43) (Unwin and Lü, 1997). This allows us to determine this specimen as Ornithocheiridae indet.

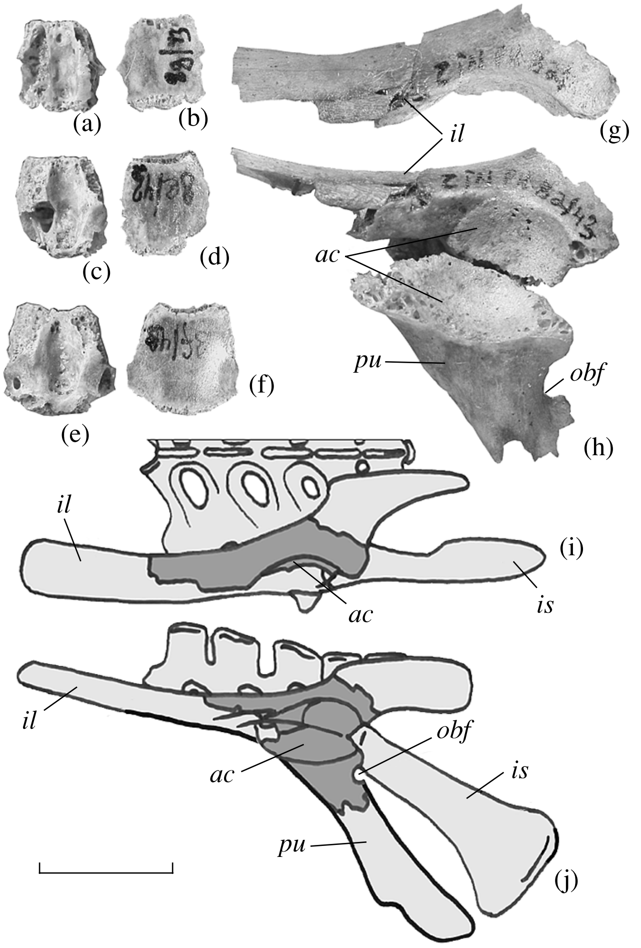

Fig. 5. Ornithocheiridae indet., sacral vertebrae: (a–e) specimen ZIN PH, no. 8e-g/43: (a, c, d) dorsal and (b, d, f) ventral views; (g) left ilium, specimen ZIN PH, no. 8a/43, dorsal view; (h) ilium and left pubis, specimen ZIN PH, no. 8b/43, lateral view; (i) reconstructed pelvis dorsal and (j) lateral views (dark gray shows preserved fragments); Lysaya Gora locality, Saratov, Russia; Upper Cretaceous (Cenomanian). Designations: (*ac*) acetabulum, (*il*) ilium, (*is*) ischium, (*obf*) obturator foramen, and (*pu*) pubis. Scale bar, 1 cm.

Shakh-Shakh locality. The Shakh-Shakh locality in Kazakhstan (90 km northeast of Dzhusaly Station, Kyzyl-Orda Region) is noted for its rich assemblage of Late Cretaceous vertebrates. The red beds of the Bostobin Formation, which most likely belong to the Santonian–Lower Campanian, are widespread in the adjacent areas of the Shakh-Shakh and Baibolat stows (Nessov, 1995, 1997). The Shakh-Shakh locality has mainly yielded large-sized vertebrates, which were collected from the ground's surface or during excavation, while the Baibolat locality (including Zhalmauz) yielded small vertebrates that were washed out of the rock with the use of sieves. This accounted for certain differences in the faunal assemblages from these localities, which are confined to the same level of the Bostobe Formation (Nessov, 1997). The following vertebrates were registered in Shakh-Shakh -Baibolat: the chondrichthyans *Polyacrodus* sp. cf. *P. brabanticus, Hybodus kansaiensis*, Hybodontoidea indet., and *Parapalaeobates glickmani*; the osteichthyes Acipenseridae? indet., *Amia* sp. cf. *A. limosa*, Aspidorhynchifores? indet., *"Diplomystus"* sp., Ichthyodectiformes indet., and Actinopterygii indet.; the amphibian Scapherpetontidae indet.; the turtles *Anatolemys maximus, Anatolemys* sp., *Adocus foveatus* (= *Basilemys* sp.), *Shachemys baibolatica, Lindholmemys* sp. cf. *L. gravis, ?Axestemys riabinini*, and *Paraplastomenus riabinini* (junior synonym of *"Trionyx" zakhidovi*); the lizards Lacertilia indet.; the crocodiles *?Kansajsuchus* sp., *Turanosuchus aralensis*, and Crocodilia indet.; the dinosaurs Sauropoda indet., Tyrannosauridae indet., Ornithomimi-

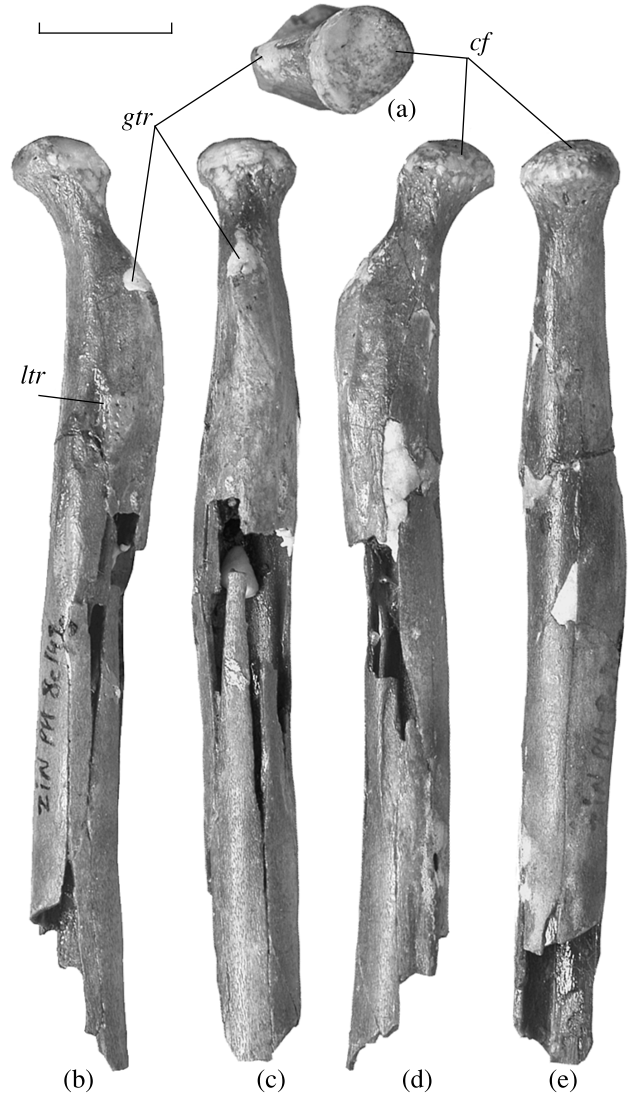

Fig. 6. Ornithocheiridae indet., specimen ZIN PH, no. 8c/43, proximal fragment of the left femur: (a) view from the proximal end, (b) anterior, (c) dorsal, (d) posterior, and (e) ventral views; Lysaya Gora locality, Saratov, Russia; Upper Cretaceous, Cenomanian. Designations: (*cf*) femoral head, (*gtr*) greater trochanter, and (*ltr*) lesser trochanter. Scale bar, 1 cm.

dae indet., Troodontidae indet., Dromaeosauridae? indet. (or Therizinosauridae? indet.), Ankylosauridae indet., and *Aralosaurus tuberiferus*; and the mammals *Beleutinus orlovi* and Mammalia indet. (Nessov, 1995, 1997 and references in these works).

The previously known pterosaurs from Shakh-Shakh include the lateral part of a skull and other cranial fragments (Nessov, 1984, pl. 8, fig. 13; 1990; 1997, pl. 15, fig. 13), which have not been determined, and only the first of these fragments has been depicted, without description. This fragment, previously determined as a jugal (Bakhurina and Unwin, 1995), is referred here to the family Azhdarchidae. In addition, among the turtles from Shakh-Shakh that are currently housed at the Zoological Institute of the Russian Academy of Sciences (material that was studied by L.I. Khozatskii), the author has found a fragmentary cervical vertebra of a pterosaur that most likely belongs to Azhdarchidae as well (described below).

The fragmentary right jugal (specimen TsNIGR, no. 41/11915, Figs. 7d, 7e) comes from outcrop KAD-7, located on the southern slope of a range 5–7 km northwest of the Baibolat Spring, near the boundaries of the Shakh-Shakh and Baibolat stows (middle beds of the Bostobin Formation; collected by L.A. Nessov in 1980). The posterior part of the maxillary process and the base of the lacrimal process are preserved. The maxillary process is long, narrow, and subrectangular in cross section at its base; distally, it becomes oval in section. The area for the jugal process of the maxilla lies ventrally. The jugal process probably reached the base of the maxillary process and did not fuse with it. A thick subvertical crest, limiting anteriorly and ventrally a deep lateral depression, is observed at the base of the lacrimal process. The lateral and medial surfaces of the bone are flat. The bone is relatively thick-walled (the walls are 1.8 mm thick) and filled with spongy tissue.

The lacrimal process of the jugal of ornithocheirids, pteranodontids, and dsungaripterids (Unwin and Bakhurina, 2000, text-fig. 21.7; Kellner and Tomida, 2000; Bennett, 2001) also has a lateral depression and a ventral ridge bordering it; however, the configuration of these structures substantially differs from that in specimen TsNIGR, no. 41/11915. In these taxa, the ventral ridge is a continuation of the dorsal edges of the maxillary and postorbital processes, and the lacrimal process entirely curves medially from the plane of the jugal. In specimen TsNIGR, no. 41/11915, the lacrimal and maxillary processes are located in the same plane, while the ventral ridge is not connected with the dorsal edge of the latter and has a different, almost vertical, orientation. The structure of the jugal (specimen no. TsNIGR 41/11915) is more similar to that in azhdarchids, which are characterized, among other things, by a very short and massive lacrimal process (Figs. 7a, 7b; Kellner and Langston, 1996; Unwin and Lü, 1997). This allows us to determine this specimen as Azhdarchidae indet.

The fragmentary cervical vertebra (specimen ZIN PH, no. 9/43, field no. Sh-548, Fig. 8) was found in Shakh-Shakh (more precise data not available; apparently, collected by A.K. Rozhdestvensky). Only an anterior fragment of the vertebra, 23 mm long (along the midline), is preserved. A part of the right side and the apex of the neural arch are damaged. Nevertheless, it is evident that the neural arch was very low and contained only one foramen at the proximal end—the foramen of the cerebrospinal canal. This foramen is rather small and shaped like a vertically extended oval; it seems to have entirely occupied the space between the dorsal edge of the neural arch and the cotyle. The lateral

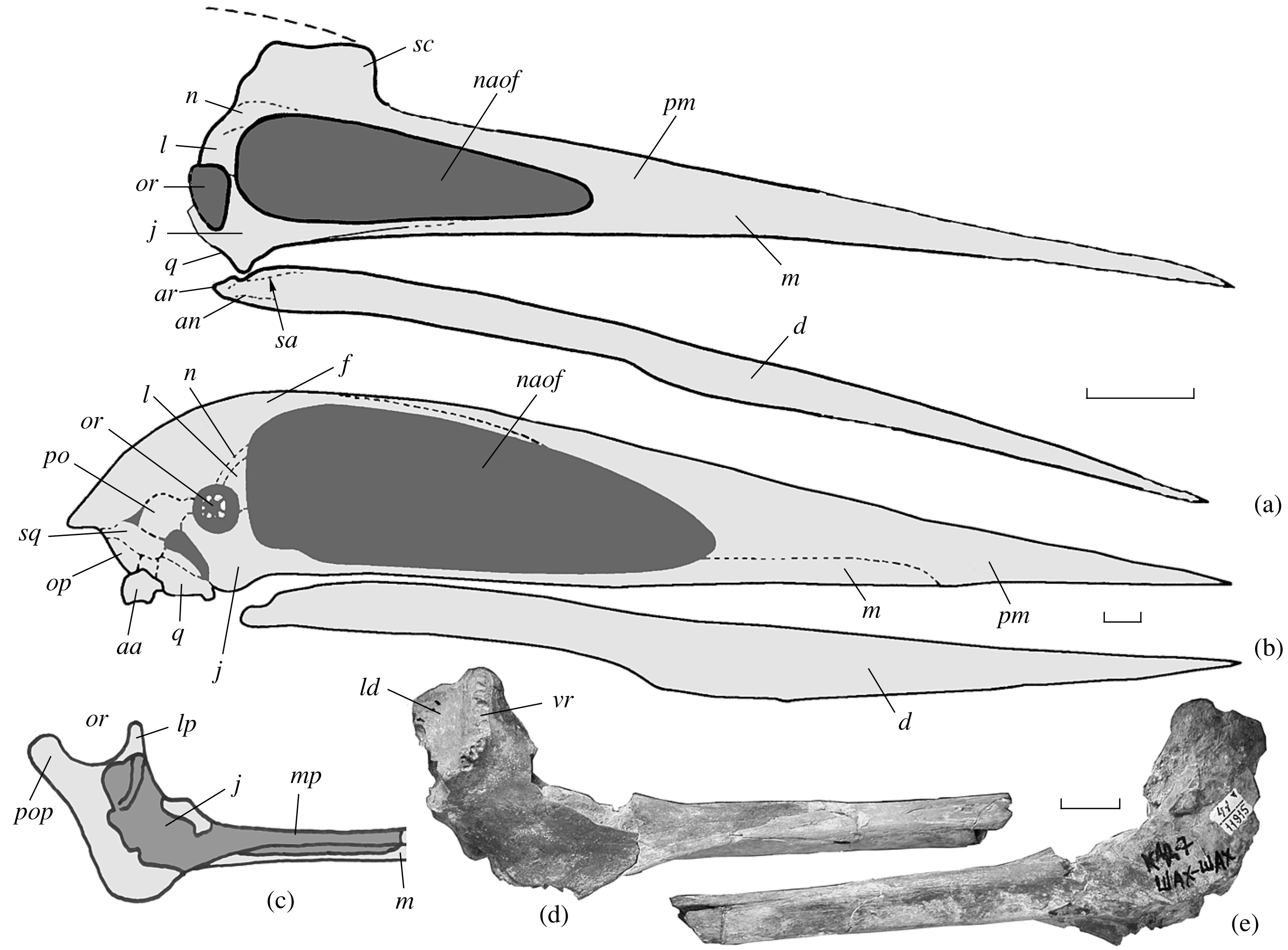

Fig. 7. Azhdarchidae: (a) skull of *Quetzalcoatlus* sp., lateral view (after Kellner and Langston, 1996, text-fig. 7) and (b) *Zhejiangopterus linhaiensis* (after Unwin and Lü, 1997, text-fig. 1), lateral view; (c–e) Azhdarchidae indet., specimen no. TsNIGR 41/11915, fragmentary right jugal: (d) lateral and (e) medial views, and (c) reconstructed bone (dark gray shows preserved fragments); Shakh-Shakh locality, Kazakhstan; Upper Cretaceous, Santonian–Campanian. Designations: (*aa*) atlas–axis, (*an*) angular, (*ar*) articular, (*d*) dentary, (*f*) frontal, (*j*) jugal, (*l*) lacrimal, (*ld*) lateral depression, (*lp*) lacrimal process, (*m*) maxilla, (*mp*) maxillary process, (*n*) nasal, (*naof*) fused nasoantorbital fenestra, (*op*) opisthotic, (*or*) orbit, (*pm*) premaxilla, (*po*) postorbital, (*pop*) postorbital process, (*q*) quadrate, (*sa*) surangular, (*sc*) sagittal crest, (*sq*) squamosal, and (*vr*) ventral ridge. Scale bar, (a) 10 cm and (b, d, e) 1 cm.

pneumatic foramina are absent, only a very small and shallow fossa lies in their place (Fig. 8a). The cotyle is transversely extended, heart-shaped, and strongly concave. The hypapophysis is relatively large; however, it is only slightly detached, and the crista sagittalis ventralis is undeveloped. The carina parasagittalis is a clear lateral crest extending along the border of the ventral and dorsal surfaces of the vertebra. The parapophysis and diapophysis are only slightly detached (the latter is broken off); the space between them is occupied by a deep sulcus that extends caudally on the ventral surface of the vertebra. Frey and Martill (1996) mistook this sulcus for a part of the damaged pneumatic foramen. The prezygapophysis is broken off; however, the preserved fragment suggests that it was relatively small and positioned somewhat ventrally just lateral to the diapophysis. Specimen ZIN PH, no. 9/43 is identified as a middle cervical vertebra on the basis of the shape and relative height of the cotyle, the height of the neural arch, and the extent to which the para- and diapophysis and groove between them are developed. This is most likely cervical vertebra 5 or 6, which belong to the longest cervical vertebrae of azhdarchids. This specimen belonged to a juvenile. It is very similar morphologically to vertebrae of *Azhdarcho lancicollis* (collection ZIN PH) and differs only in the absence of the terminal pneumatic foramina, the lower neural arch, and, probably, the relatively smaller size of the prezygapophysis. Specimen ZIN PH, no. 9/43 differs from the pteranodontid cervical vertebrae in the absence of the

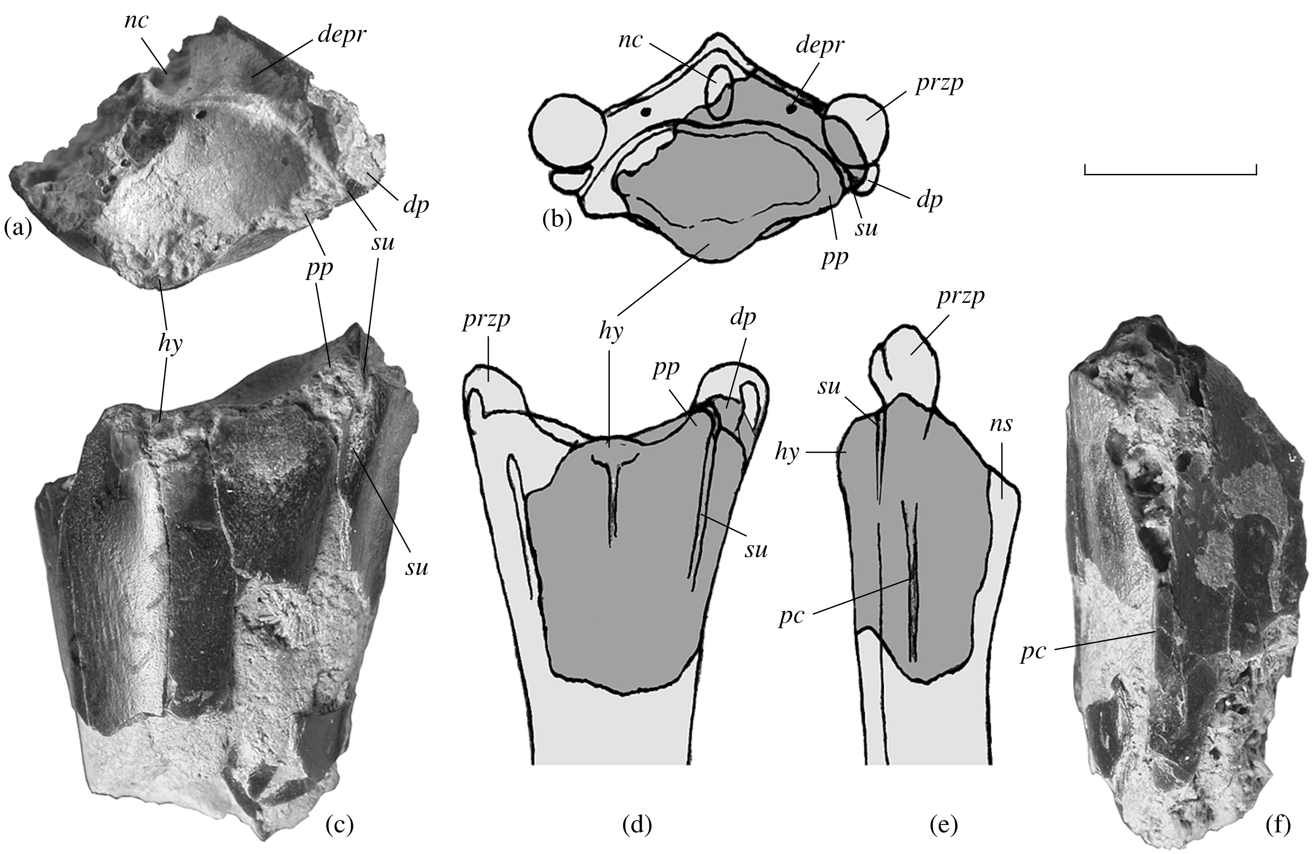

Fig. 8. Azhdarchidae gen. et sp. indet., specimen ZIN PH, no. 9/43, (a, c, f) anterior fragment of cervical vertebrae 5 and 6 and (b, d, e) their reconstructions: (a, b) anterior end, (c, d) ventral, and (e, f) lateral views (dark gray color shows preserved fragments); Shakh-Shakh locality, Kazakhstan; Upper Cretaceous, Santonian–Campanian. Designation: (*depr*) fossa located in place of pneumatic foramen of other azhdarchids, (*dp*) diapophysis, (*hy*) hypapophysis, (*nc*) cerebrospinal canal, (*ns*) neural spine, (*pc*) parasagittal carina, (*pp*) parapophysis, (*przp*) prezygapophysis, and (*su*) sulcus between the parapophysis and diapophysis. Scale bar, 1 cm (for a, c, f).

preexapophyses; it differs from ornithocheirids in the substantially lower neural arch, relatively smaller foramen of the cerebrospinal canal (common feature with *Azhdarcho*), and the absence of the pneumatic foramina at the edges of the cerebrospinal canal (Baird and Galton, 1981; Howse, 1986; Bennett, 2001).

The terminal pneumatic foramina of the middle cervical vertebrae were gradually reduced in the course of azhdarchid evolution. Three such foramina are present in the Lower Cretaceous *Tupuxuara leonardii* Kellner et Campos, 1994 and Turonian *Azhdarcho lancicollis.* The foramen that lay above the spinal canal disappears in the Campanian *Bogolubovia orientalis* (Bogolubov, 1914) and the Maastrichtian *Quetzalqoatlus northropi* Lawson, 1975 and *Arambourgiania philadelphiae* (Arambourg, 1959). Nessov (1991, p. 19) proposed that the disappearance of the terminal pneumatic foramina in late azhdarchids is a derived and specialized feature. Based on this feature and the general reduction of the neural arch, specimen ZIN PH, no. 9/43 is considered to be one of the most advanced azhdarchids. It is hardly probable that these features were associated with the juvenile stage of the individual, since the cervical vertebrae of *A. lancicollis* of approximately the same size (collection ZIN PH) have three well-developed pneumatic foramina. The specimen from Shakh-Shakh most likely belongs to a new azhdarchid taxon and can now be determined as Azhdarchidae gen. et sp. indet.

DISCUSSION

The material described in the present study confirms a wide and almost cosmopolitan distribution of the giant toothed flying reptiles Ornithocheiridae in the Albian–Cenomanian (Kellner and Tomida, 2000; Unwin, 2001; Averianov *et al.*, 2003). To date, only cf. *Anhanguera* sp. has been confidently identified (by a fragment of the lower jaw) in European Russia. Three ornithocheirid genera are known from Brazil and England: *Anhanguera* Campos et Kellner, 1985, *Criorhynchus* Owen, 1874 (= *Tropeognathus* Wellnhofer, 1987), and *Coloborhynchus* Owen, 1874. The third genus was also found in North America (Lee, 1994; Fastnacht, 2001; Unwin, 2001). These giants could make long-distance transoceanic migrations, as was reconstructed in the BBC popular science film *Walks with Dinosaurs*, using *Ornithocheirus* as an example. One such migration path probably passed over the epeiric sea of the Russian Platform. The coastal areas of this sea, which were enriched with biogens due to a rise of deep cold waters (upwelling), were occupied by a diverse community of fishes and marine reptiles, which had a great deal in common with the assemblage from the Cambridge Greensand in England. The fact that finds of pterosaurs are much scarcer in the Russian Platform than in England (see Unwin, 2001) is attributable to the greater distance between Russian localities and the coastline and insufficient collection of the material. The finding of a juvenile ornithocheirid in Saratov suggests that the islands and coastline of the Russian epeiric sea was included in the reproductive area of these reptiles.

Very large pterodactyloids, which have yet to be determined, existed in the middle of the Cretaceous in the Voronezh Region (Pavlovsk) and Kyrgyzstan (Kylodzhun). These reptiles display a number of unique features, which suggests that they belong to new taxa.

Thus, new data on the presumable change in the composition of pterosaurs in the Upper Cretaceous of western Asia have come to light. The Turonian *Azhdarcho lancicollis*,[1] which has well-developed terminal pneumatic foramina in the cervical vertebrae, was replaced in the Santonian by a new and more advanced azhdarchid taxon, in which these foramina were reduced. Nessov (1997, p. 131) marked the presence of *Azhdarcho* sp. nov. in the Early Santonian Kansai locality in Tajikistan. These data are most likely based on a fragment of wing phalanx 2 or 3 from the Kansai locality (specimen ZIN PH, no. 10/43), which is T-shaped in cross section and has a rounded convex dorsal surface (in *A. lancicollis*, this surface is flat or slightly concave). It is not improbable that the same giant flying reptile, Azhdarchidae gen. et sp. indet., occurred in the Santonian of the northeastern Aral Region and Fergana. Judging by the jugal structure, the skull of this new pterosaur was not inferior to *Hatzegopteryx thambema* Buffetaut *et al.*, 2002, a recently established azhdarchid from the Maastrichtian of Romania (Buffetaut *et al.*, 2002).

The finds of recent years demonstrate that pterosaurian bones are much more abundant in the Cretaceous of Russia and the Commonwealth of Independent States than considered before. Although such specimens are usually fragmentary, detailed examination of their morphology can substantially enlarge our knowledge of the diversity and distribution of pterosaurs in this area. Thus, it would be useful to organize regular searches for flying reptiles in the Mesozoic of our country.

ACKNOWLEDGMENTS

I am grateful to A.S. Rezvyi for the transfer of a bone of Pterodactyloidea indet. to the ZIN (specimen ZIN PH, no. 2/43) and to A.V. Panteleev for his assistance in the expedition in 1995. Field work of the author in central Russia in 1995 was supported by the Russian Foundation for Basic Research (project no. 95-05-14186); in Uzbekistan in 1997–2002, by the American National Science Foundation (project nos. EAR-9804771 and EAR-0207004); and by the National Geographical Society (project no. 6281-98). This study was also supported by the Foundation for Compassionate Benefit of Domestic Sciences.

REFERENCES

1. M. S. Arkhangelsky and A. O. Averianov, "On the Find of a Primitive Duckbilled Dinosaur (Ornithischia, Hadrosauroidea) in the Cretaceous of the Belgorod Region," Paleontol. Zh., No. 1, 60–63 (2003) [Paleontol. J., No. 1, 58–61 (2003)].
2. A. O. Averianov, "Review of Mesozoic and Cenozoic Sea Turtles from the Former USSR," Russ. J. Herpetol. **9** (2), 137–154 (2002).
3. A. O. Averianov, S. V. Leshchinskii, P. P. Skuchas, and A. S. Rezvyi, "Pterosaurian Teeth from the Lower Cretaceous of Russia and Uzbekistan," Sovrem. Gerpetol. **2**, 5–11 (2003).
4. D. Baird and P. M. Galton, "Pterosaur Bones from the Upper Cretaceous of Delaware," J. Vertebr. Paleontol. **1** (1), 67–71 (1981).
5. N. N. Bakhurina, "A Pterodactyl from the Lower Cretaceous of Mongolia," Paleontol. Zh., No. 4, 104–108 (1982).
6. N. N. Bakhurina and D. M. Unwin, "A Survey of Pterosaurs from the Jurassic and Cretaceous of the Former Soviet Union and Mongolia," Histor. Biol. **10** (1), 197–245 (1995).
7. S. Ch. Bennett, "The Osteology and Functional Morphology of the Late Cretaceous Pterosaur *Pteranodon*: Part 1. General Description and Osteology," Paläontogr., Abt. A **260** (1-6), 1–112 (2001).
8. E. Buffetaut, D. Grigorescu, and Z. Csiki, "A New Giant Pterosaur with a Robust Skull from the Latest Cretaceous of Romania," Naturwissenschaften **89** (4), 180–184 (2002).
9. M. Fastnacht, "First Record of *Coloborhynchus* (Pterosauria) from the Santana Formation (Lower Cretaceous) of the Chapada do Araripe, Brazil," Paläontol. Z. **75** (1), 23–36 (2001).

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[1] Nessov (1990, 1991, 1997, and others) referred the Bissekty Formation of the central Kyzyl Kum Desert, which yielded *A. lancicollis*, to the Upper Turonian–Coniacian. According to the most up-to-date unpublished data provided by the International Uzbekistan–Russian–Britain–American–Canadian Paleontological Expedition, which investigated the central Kyzyl Kum Desert from 1998 to 2002, the Bissekty Formation and part of the overlying marine Aitym Formation are assigned to the Upper Turonian. Unwin and Bakhurina (2000, p. 427) mistook the Dzharakuduk locality (where *A. lancicollis* was found) for the Itemir and Beleuta localities, where pterosaurs have not been registered, and the latter of which is situated in Kazakhstan instead of Uzbekistan. They also mistakenly referred the beds with *A. lancicollis* to the Beleuta Formation, which occurs in central Kazakhstan (Lobacheva, 1979) rather than the Kyzyl Kum. In addition, these researchers (Unwin and Bakhurina, 2000, p. 422) mistakenly called the above-mentioned international expedition the Western–Russian–Kazakhstan Expedition.

10. E. Frey and D. M. Martill, "A Reappraisal of *Arambourgiania* (Pterosauria, Pterodactyloidea): One of the World's Largest Flying Animals," Neues Jahrb. Geol. Paläontol. Abh. **199** (2), 221–247 (1996).
11. R. R. Gabdullin, I. V. Il'ina, E. V. Popov, *et al.*, *In Searching for Extinct Worlds* (Nauchnaya Kniga, Saratov, 2002) [in Russian].
12. L. S. Glikman, "Upper Cretaceous Vertebrates from the Vicinity of Saratov: Preliminary Study," Uchen. Zap. Saratov. Gos. Univ. **38**, 51–54 (1953).
13. S. C. B. Howse, "On the Cervical Vertebrae of the Pterodactyloidea (Reptilia: Archosauria)," Zool. J. Linnean Soc. **88** (4), 307–328 (1986).
14. A. W. A. Kellner and W. Langston, Jr., "Cranial Remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous Sediments of Big Bend National Park, Texas," J. Vertebr. Paleontol. **16** (2), 222–231 (1996).
15. A. W. A. Kellner and Y. Tomida, "Description of a New Species of Anhangueridae (Pterodactyloidea) with Comments on the Pterosaur Fauna from the Santana Formation (Aptian–Albian), Northeastern Brazil," Nat. Sci. Mus. Monogr., No. 17, 1–135 (2000).
16. L. I. Khozatskii, "A Pterosaur from the Cenomanian (Late Cretaceous) of Saratov," Vestn. St.-Peterb. Univ., Ser. 3 **2** (10), 115–117 (1995).
17. Y.-N. Lee, "The Early Cretaceous Pterodactyloid Pterosaur *Coloborhynchus* from North America," Palaeontology **37** (4), 755–763 (1994).
18. S. V. Lobacheva, "Beleuta Formation," in *Stratigraphic Dictionary of the USSR: Triassic, Jurassic, and Cretaceous*, Ed. by V. N. Vereshchagin (Nedra, Leningrad, 1979), p. 58 [in Russian].
19. L. A. Nessov, "Pterosaurs and Birds from the Late Cretaceous of Central Asia," Paleontol. Zh., No. 1, 47–57 (1984).
20. L. A. Nessov, "Flying Reptiles from the Jurassic and Cretaceous of the USSR and Significance of Their Remains for Reconstruction of Paleogeographic Conditions," Vestn. Leningr. Univ., Ser. 7, No. 4 (28), 3–10 (1990).
21. L. A. Nessov, "Giant Flying Reptiles of the Family Azhdarchidae: 1. Morphology and Systematics," Vestn. Leningr. Univ., Ser. 7, No. 2 (14), 14–23 (1991).
22. L. A. Nessov, *Dinosaurs from Northern Eurasia: New Data on the Composition of Assemblages, Ecology, and Paleobiogeography* (S.-Peterb. Gos. Univ., St. Petersburg, 1995) [in Russian].
23. L. A. Nessov, *Nonmarine Vertebrates from the Cretaceous of Northern Eurasia* (S.-Peterb. Gos. Univ., St. Petersburg, 1997) [in Russian].
24. L. A. Nessov, R. A. Mertinene, L. B. Golovneva, *et al.*, "New Finds of Remains of Early Organisms in the Belgorod and Kursk Regions," in *Complex Studies of Biogeocenoses in Forest–Steppe Oak Forests (1986)* (Leningr. Gos. Univ., Leningrad, 1988), pp. 124–131 [in Russian].
25. E. M. Pervushov, M. S. Arkhangelsky, and A. V. Ivanov, *Catalogue of Fossil Localities of Marine Reptiles in Jurassic and Cretaceous Sediments of the Lower Volga Region* (Kolledzh, Saratov, 1999) [in Russian].
26. D. M. Unwin, "An Overview of the Pterosaur Assemblage from the Cambridge Greensand (Cretaceous) of Eastern England," Mitt. Mus. Natur. Berl. Geowiss. Reiche. **4**, 189–221 (2001).
27. D. M. Unwin and N. N. Bakhurina, "Pterosaurs from Russia, Middle Asia and Mongolia," in *The Age of Dinosaurs in Russia and Mongolia*, Ed. by M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (Cambridge Univ. Press., Cambridge, 2000), pp. 420–433.
28. D. M. Unwin and L. Lü, "On *Zhejiangopterus* and the Relationships of Pterodactyloid Pterosaurs," Histor. Biol. **12**, 199–210 (1997).
29. P. Wellnhofer, "Terrestrial Locomotion in Pterosaurs," Hist. Biol. **1** (1), 3–16 (1988).
30. P. Wellnhofer, "Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien," Paläontogr. Abt. A **215** (1–3), 43–101 (1991).
31. S. W. Williston, "On the Osteology of *Nyctosaurus* (*Nyctodactylus*), with Notes on American Pterosaurs," Field Columbian Mus. Publ., Geol. Ser. **2** (3), 125–163 (1903).
32. C. C. Young, "On a New Pterosaurian from Sinkiang, China," Vertebr. Palasiat. **8** (3), 221–255 (1964).