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New Records of Azhdarchids (Pterosauria, Azhdarchidae) from the Late Cretaceous of Russia, Kazakhstan, and Central Asia

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Abstract—A review of 12 azhdarchid localities in Russia, Kazakhstan, Uzbekistan, and Tajikistan is given. New records of unidentifiable azhdarchids from the Khodzhakul (Cenomanian), Tyul'keli (Turonian–Coniacian), Kansai (Santonian), Malaya Serdoba, and Beloe Ozero (Campanian) localities and a new taxon, *Aralazhdarcho bostobensis* gen. et sp. nov. (Shakh-Shakh, Santonian–Campanian), are described.

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Key words: Azhdarchidae, Pterosauria, Late Cretaceous, Russia, Kazakhstan, Central Asia.

INTRODUCTION

The monophyletic group Azhdarchidae comprises the most advanced toothless long-necked pterosaurs with the wing span ranging from 1.6 to 12 m and more, which occur in the fossil record from the Aptian (Martill and Frey, 1999; Lü and Ji, 2005) to the end of the Maastrichtian (see review in Averianov et al., 2005). The first azhdarchid bones found were from our country (Bogolubov, 1914) and this group was formally established by Nessov (1984) based on material from the Soviet Union. In the present study, new and previously unpublished finds of azhdarchids from Russia and adjacent countries are described, and all localities yielding azhdarchids in this region are listed.

The following abbreviations are used: (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow; (SGU) Saratov State University; (TsNIGR Museum) Chernyshev Central Research Geological Museum, St. Petersburg; (URBAC) Uzbek–Russian–British–American–Canadian International Paleontological Expedition; (ZIN) Zoological Institute of the Russian Academy of Sciences, St. Petersburg; and (ZIN PH or ZIN PHT) paleoherpetological collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

AZHDARCHID LOCALITIES IN THE FORMER SOVIET UNION, AND DESCRIPTION OF NEW FINDS

(1) **Khodzhakul**, a series of steep slopes north of the dry Lake Khodzhakul, southwestern Kyzyl Kum, Karakalpakistan, Uzbekistan. Sands of the lower or middle part of the Khodzhakul Formation, Lower Cenomanian. Material: a small edentulous jaw fragment (ZIN PH, no. 61/44); proximal fragment of the left coracoid of a young animal (ZIN PH, no. 80/44); fragmentary wing phalanx 2 or 3 (ZIN PH, no. 55/44); and proximal end of a proximal pedal phalanx (ZIN PH, no. 44/44) of Azhdarchidae indet.; collected by L.A. Nessov from 1980 to 1985. Unwin et al. (1997) believe that pterosaurian specimens from the Khodzhakul Formation do not show diagnostic characters of azhdarchids. However, the fragment of the proximal pedal phalanx from this locality (ZIN PH, no. 44/44) is almost identical to that of *Azhdarcho lancicollis* from Dzharakuduk. In addition, the fragments of edentulous jaw and wing phalanx 2 or 3, with a longitudinal crest on the ventral side, undoubtedly belong to an azhdarchid.

The coracoid (Pl. 8, fig. 1) is not fused with the scapula, belongs to a young animal. It has a relatively short procoracoid, a narrow glenoid, and three small pneumatic foramina in the depression between the procoracoid and glenoid. The dorsal side shows a well-outlined imprint of the coracoid head of the triceps muscle. The anterior margin of the coracoid forms a convex coracoid flange covered ventrally with an extensive imprint of the supracoracoid muscle. Such a flange occupying more than half the length of the bone is a diagnostic character of Azhdarchidae (Unwin, 2003, p. 181). In the specimen from Khodzhakul, the coracoid flange is developed to the same extent as in *Azhdarcho lancicollis* from the Turonian of Uzbekistan (collection ZIN PH, no. 44) and in *Montanazhdarcho minor* Padian et al., 1995 from the Campanian of the United States (McGowen et al., 2002, text-fig. 3C), while it is substantially weaker than in *Quetzalcoatlus* sp. from the Maastrichtian of the United States (Frey et al., 2003, text-fig. 1b).

(2) **Sheikhdzheili**, northern area of the Sheikhdzheili Ridge, southwestern Kyzyl Kum, Karakalpakistan, Uzbekistan. Sands of the upper part of the

Khodzhakul Formation, Lower Cenomanian. Material: a fragmentary edentulous rostrum or symphysis of the dentaries of a young individual (ZIN PH, no. 40/44) and the proximal end of a rib (ZIN PH, no. 81/44; Nessov, 1997, pl. 20, fig. 3) of Azhdarchidae indet.; collected by L.A. Nessov in 1980 to 1985. Nessov (1990, 1997) indicated that the articular surface of the rib from Sheikhdzheili is similar to that of Senonian azhdarchids.

(3) **Dzharakuduk 2** (= Dzhara-Khuduk = Dzhyrakuduk = Bissekty). Steep slopes near the borehole near Dzharakuduk and wells of Kul'beke and Bissekty, 30 km southwest of the village of Mynbulak, central Kyzyl Kum, Navoi District, Uzbekistan. Sands of the Bissekty Formation, Middle–Upper Turonian. Material: hundreds of bones and fragments of cranial and postcranial bones of *Azhdarcho lancicollis* Nessov, 1984 (TsNIGR Museum, nos. 11915 and 12454; and ZIN PH, no. 44; Nessov, 1984, pl. 7, figs. 1–11; 1986, pl. 2, fig. 1; 1988, pl. 1, fig. 1; Nessov and Yarkov, 1989, pl. 2, figs. 2–8; Bakhurina and Unwin, 1995, text-fig. 13; Nessov, 1995, pl. 1, fig. 18; 1997, pl. 14, figs. 1–13, 15, pl. 15, figs. 1–5, 7–12, 14–17, pl. 16, figs. 1, 2; Unwin and Bakhurina, 2000, text-fig. 21.8; Averianov and Atabekyan, 2005, text-figs. 2f–2j). Nessov (1990, 1991b, 1991c, 1997, etc.) assigned the Bissekty Formation to the Upper Turonian–Coniacian. According to the recent data of the International Paleontological URBAC expedition, which worked in the central Kyzyl Kum from 1997 to 2004, these beds are referred to the Middle–Upper Turonian; collected by L.A. Nessov from 1979 to 1994 and by the URBAC Expedition from 1997 to 2004.

(4) **Zenge Kurgan 3**. Right bank of the Amu Darya River between the villages of Bezergen and Kulatau, Khorezm District, Uzbekistan. Conglomerate of the Bissekty (?) Formation, Turonian. Material: edentulous jaw fragment of Azhdarchidae indet. (ZIN PH, no. 82/44); collected by the URBAC expedition in 2004.

(5) **Khidzorut**. The upper part of an unnamed ravine near the village of Khidzorut, Armenia. Marine beds with the ammonite *Reesidites minimus*, which is characteristic of the *Subprionocyclus neptuni* Zone (Upper Turonian). Material: distal end of the radius of Azhdarchidae indet. (TsNIGR Museum, no. 1/12671; Averianov and Atabekyan, 2005, text-figs. 2a–2e); collected by A.A. Atabekyan, 1986.

(6) **Tyul'keli**. Kankazgan, area west of Tyul'keli Hill, 80–85 km north of the Dzhusaly station, northeastern Aral Region, Kyzylorda Region, Kazakhstan. Middle part of the Zhirkindek Formation, Upper Turonian–Coniacian. Material: dorsal vertebra of Azhdarchidae indet. (ZIN PH, no. 54/43) and a poorly preserved distal fragment of the radius (?) (ZIN PH, no. 38/43) of Azhdarchidae? indet. In addition, Nessov (1997) recorded cf. Azhdarchidae and unidentifiable pterosaurians in this locality. The material was collected by L.A. Nessov in 1982.

The free (nonfused into the notarium) dorsal vertebra (Fig. 1) is procelous, with a deep V-shaped dorsal incisure on the anterior and posterior articular surfaces of the centrum. The width of articular surfaces of the centrum exceeds its height. The ventral surface of the centrum is circular in cross section. The spinal canal is relatively narrow, triangular in anterior view and somewhat larger and more rounded in posterior view. The neural arch is in the anterior part of the vertebra, the prezygapophyses are widely spaced and project anteriorly beyond the line of the anterior intercentral articular surface. The articular facets of the prezygapophyses are circular, directed at an angle of about 45° to the sagittal plane. The articular facets of the postzygapophyses are ovate (the long axis is dorsoventrally oriented). At the base of the right postzygapophysis, the neural arch has a pitlike depression; however, in contrast to *Pteranodon* (see Bennett, 2001), a pneumatic foramen is absent. The transverse processes are mostly broken off; judging from the base, they were directed dorsolaterally. The neural spine (only its base is preserved) was very short anteroposteriorly. Deep interspinous recesses are located anterior and posterior to the neural spine. The floor of the posterior interspinous recess is formed of a bony bridge connecting the bases of the postzygapophyses.

The dorsal vertebra from the Tyul'keli locality is similar in size and structure to that of *Azhdarcho lancicollis* from the Turonian of Dzharakuduk (Kyzyl Kum, Uzbekistan; ZIN PH, no. 44); the similar stratigraphic and geographical positions of the two localities suggest that they belong to the same or closely related azhdarchid species.

(7) **Kansai**. Residual mountains of Cretaceous deposits near the Kyzylbulak spring near the village of Kansai, northwestern Fergana Depression, Khodzhent Region, Tajikistan. Upper strata of the Yalovach Formation, Lower Santonian. Material: fragment of wing phalanx 2 or 3 of Azhdarchidae indet. (ZIN PH, no. 10/43, Pl. 8, fig. 2); collected by L.A. Nessov in 1981. Nessov (1997) reported *Azhdarcho* sp. nov. in this locality. This identification is probably based on the T-shaped section and rounded convex dorsal surface of the wing phalanx fragment from Kansai (Pl. 8, fig. 2c). In *A. lancicollis*, the dorsal surface of these phalanges is flat, or even slightly concave. Another specimen from Kansai, which may belong to an azhdarchid, is considered in the section *Discussion*.

(8) **Shakh-Shakh**. A fissure near Shakh-Shakh and Baibolat, 5–7 km from the well of Baibolat, 90 km northeast of the Dzhusaly station, northeastern Aral Region, Kyzylorda Region, Kazakhstan. Middle part of the Bostobe Formation, Santonian–Lower Campanian. Material: fragments of cranial and postcranial bones of *Aralazhdarcho bostobensis* gen. et sp. nov. (see description below); collected by A.K. Rozhdestvensky in the late 1950s and by L.A. Nessov in 1980 and 1982.

(9) **Malaya Serdoba**. Vicinity of the village of Malaya Serdoba, Penza Region, Russia. Rybushka For-

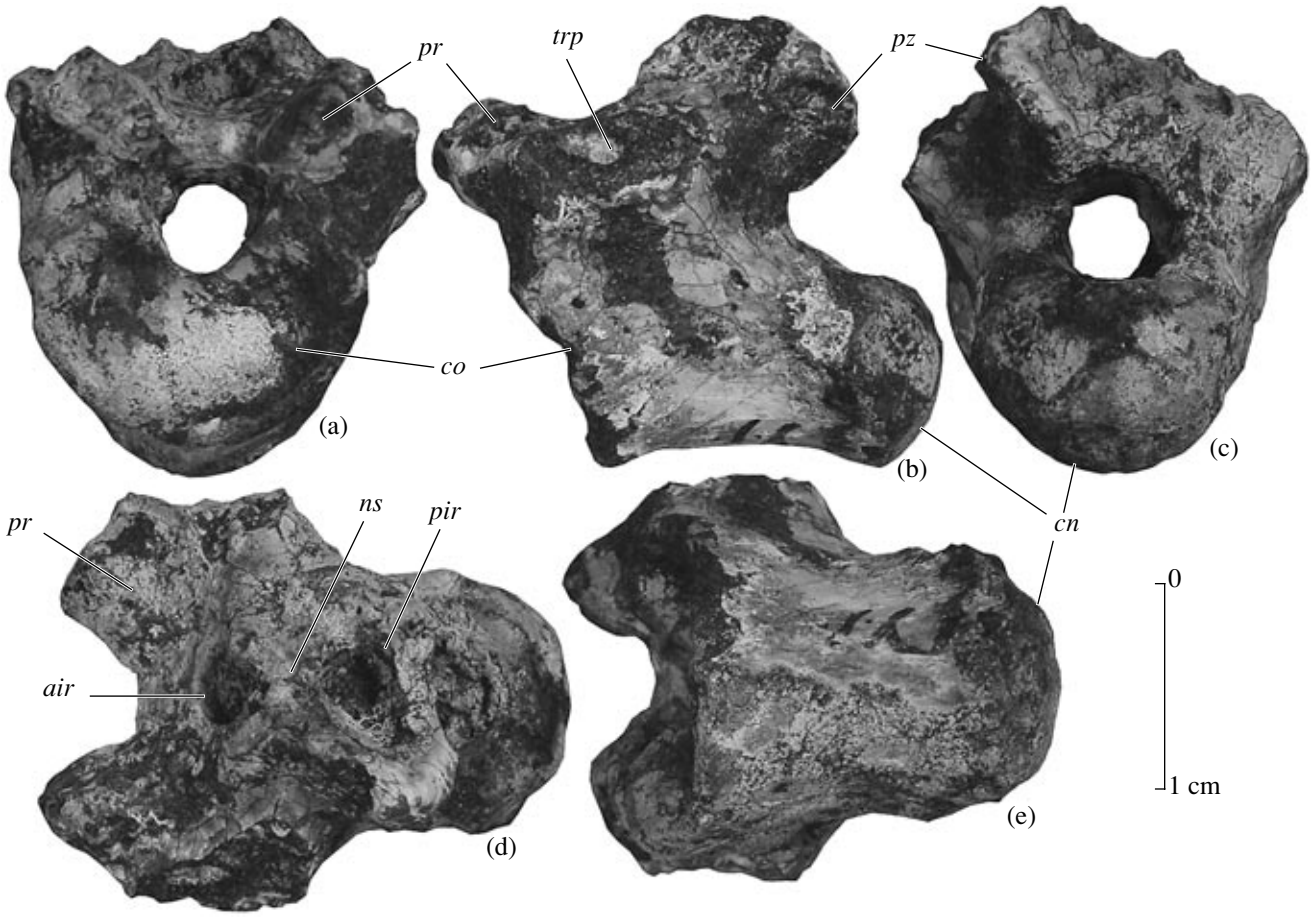

Fig. 1. Specimen ZIN PH, no. 54/43, dorsal vertebra of Azhdarchidae indet. from the Tyul'keli locality (Kazakhstan, Zhirkindek Formation, Turonian–Coniacian): (a) anterior, (b) lateral, (c) posterior, (d) dorsal, and (e) ventral views. Designations: (*air*) anterior interspinous recess, (*cn*) posterior intercentral articular surface, (*co*) anterior intercentral articular surface, (*ns*) neural spine, (*pir*) posterior interspinous recess, (*pr*) prezygapophysis, (*pz*) postzygapophysis, and (*trp*) transverse process.

mation, Lower Campanian. Material: posterior fragment of a midcervical vertebra of the azhdarchid *Bogolubovia orientalis* (Bogolubov, 1914) (see Bogolubov, 1914, text-figs. 1, 2; Bakhurina and Unwin, 1995, text-fig. 14; in the original description, the depository was not indicated; the specimen is probably lost); an edentulous jaw fragment (ZIN PH, no. 48/43); and the distal end of left metacarpal 4 (ZIN PH, no. 49/43) of Azhdarchidae indet.; collected by V.G. Khimenkov in 1911 and by G.N. Uspensky and I.A. Shumilkin in 1998.

The edentulous jaw fragment (Pl. 8, fig. 3) belonged to a rather large individual, judging from the little curvature of the preserved part of the lateral wall.

The distal fragment of metacarpal 4, with a strongly damaged distal ginglymoid joint, is preserved (Pl. 8, fig. 4). The joint fragment preserved is similar in structure to that of *Azhdarcho*. The anterior side has a slitlike depression, with a pneumatic foramen in the center, between and somewhat proximal to the ventral and dorsal condyles (closer to the dorsal condyle). A similar depression, but lacking a pneumatic foramen, is observed on the posterior side of the bone. The diaphysis of the bone is ovate in cross section.

(10) **Beloe Ozero**. A gully near the village of Beloe Ozero, Saratov Region, Russia. Rybushka Formation, Lower Campanian. Material: small edentulous jaw fragment (ZIN PH, no. 14/43); fragments of right (ZIN PH, no. 52/43) and left (ZIN PH, no. 53/43) coracoids; and the proximal end of the left first phalanx of the fourth (wing) digit (ZIN PH, no. 47/43) of Azhdarchidae indet.; collected by A.V. Panteleev and E.V. Popov in 2003 and 2005.

The proximal end of phalanx 1–4 (Pl. 8, fig. 5) is widened strongly anteroposteriorly and flattened dorsoventrally. A large extensor tendon process, which is an ossified tendon of the extensor digiti 4 muscle, is located near the middle, slightly closer to the anterior margin. The suture between this process and the phalanx is indiscernible, that is, the bone belongs to an adult. The anterior surface of the extensor tendon process has at least one small pneumatic foramen (another foramen could have been located somewhat dorsally, in a damaged area). The extensor tendon process is sepa-


Plate 8
1a
tr
1b
2a
2b
2c
3a
3b
3c
sf
g
1c
pf
pr
1d
pr
sco
cf
1e
dco
ep
5a
vcn
pf
4a
dcn
4b
dcn
4c
ep
vco
msc
ep
pf
dco
5b
5c
msc
5d
vcn
4e
ep
pf
5e
vcn
4d

rated by a deep groove from an extensive tubercle on the anteroventral end of the phalanx. A narrow, elongated, concave dorsal cotyle, articulated with the dorsal condyle of metacarpal 4, is located posterior to the extensor tendon process. A small pneumatic foramen is located near the proximal end of this depression (it is also present in *Azhdarcho*). The posterior process of the phalanx is broken off. A shorter and more abruptly directed ventral cotyle, which articulated with the ventral condyle of metacarpal 4, is located ventral to the extensor tendon process. Distal to the cotyles, the posterior surface of the bone is damaged (this area could have contained a large pneumatic foramen, which is recorded in *Azhdarcho*). Well-pronounced wrinkled areas are observed on the ventral side of the bone, marking the origin of muscles connecting the phalanx to the metacarpal. The distal end of the phalanx is ovate–subtriangular in cross section.

(11) **Shyrokii Karamysh**. A gully near the village of Shyrokii Karamysh, Saratov Region, Russia. Phosphorite conglomerate of the Rybushka Formation, Lower Campanian. Material: almost complete toothless symphysis of dentaries; cervical vertebrae 3 and 9; posterior part of the notarium, composed of four vertebrae; and fragmentary femur of Azhdarchidae indet.; collected by M.A. Grigor'ev, A.L. Gorbunov-Gusev, and A.N. Gurenko in 2004 and 2005. This material will be described in other publication.

(12) **Saratov 2**. A trench of the pipeline near the tram stop "Sed'maya dachnaya" in the western area of Saratov, Saratov Region, Russia. Pudovkino Formation, Upper Campanian. Material: distal end of the radius of Azhdarchidae indet. (SGU, no. 104a/35; Averianov et al., 2005, text-fig. 2). Collected by V.B. Sel'tser in 1986.

SYSTEMATIC PALEONTOLOGY

Order Pterosauria

Suborder Pterodactyloidei

Superfamily Azhdarchoidea Nessov, 1984

Family Azhdarchidae Nessov, 1984

Genus *Aralazhdarcho* Averianov, gen. nov.

Etymology. From the Aral Sea and the genus *Azhdarcho* Nessov, 1984.

Type species. *Aralazhdarcho bostobensis* sp. nov.

Diagnosis. Pneumatic foramina on sides of spinal canal of midcervical vertebrae reduced to small superficial fossae on anterior side. Ventral side of atlas–axis convex. Proximal articular surface of phalanx 2 of wing digit 4 relatively high.

Species composition. Type species.

Comparison. The new genus differs from *Azhdarcho* Nessov, 1984 from the Turonian of Uzbekistan, *Bogolubovia* Nessov, 1989 from the Campanian of Russia, *Quetzalcoatlus* Lawson, 1975 from the Maastrichtian of the United States, and *Arambourgiania* Nessov, 1987 from the Maastrichtian of Jordan in the reduced lateral pneumatic foramina of the midcervical vertebrae. In addition, it differs from *Azhdarcho* in the convex (rather than concave) ventral side of the centrum of the atlas–axis and in the relatively high (dorsoventrally) proximal articular surface of phalanx 2 of wing digit 4 (the height-to-width ratio is 59% versus 46–48% in *Azhdarcho*).

Remarks. It is impossible to compare the new genus with *Eoazhdarcho* Lü et Ji, 2005 (Aptian of China), *Bennettazhia* Nessov, 1991 (Albian of the United States), *Montanazhdarcho* Padian et al., 1995 (Campanian of the United States), and *Hatzegopteryx* Buffetaut et al., 2002 (Maastrichtian of Romania) because of incommensurable material. The lateral pneumatic foramina have not been recorded in cervical vertebrae of *Phosphatodraco* Pereda Suberbiola et al., 2003 from the Maastrichtian of Morocco (Pereda Suberbiola et al., 2003). However, this may result from incomplete preservation of the only specimen of *Phosphatodraco*. *Zhejiangopterus* Cai et Wei, 1994 from the Campanian of China is represented by a number of relatively complete skeletons (Cai and Wei, 1994; Unwin and Lü, 1997); however, unsatisfactory preservation of the bones and the absence of a detailed description precludes comparison with the new taxon from Kazakhstan.

***Aralazhdarcho bostobensis* Averianov, sp. nov.**

Plate 9, figs. 1–5

Pterosauria gen. indet: Nessov, 1984, p. 50, pl. 7, fig. 13.

Pterosauria indet.: Nessov, 1997, p. 110, pl. 15, fig. 13.

Azhdarchidae gen. et sp. indet.: Averianov, 2004, pp. 79–82, text-figs. 7c–7e and 8.

Explanation of Plate 8

Figs. 1–5. Azhdarchidae indet. from the Lower Cenomanian of Uzbekistan: (1) Khodzhakul Formation, Khodzhakul, Lower Santonian of Tajikistan; (2) Yalovach Formation, Kansai and Lower Campanian (Rybushka Formation) of the Middle Volga Region, Russia; (3, 4) Malaya Serdoba, Penza Region; and (5) Beloe Ozero locality, Saratov Region: (1) ZIN PH, no. 80/44, proximal fragment of the left coracoid of a young animal, ×1.95: (1a) dorsal, (1b) posterior, (1c) proximal end, (1d) ventral, and (1e) anterior, with the upside down, views; (2) ZIN PH, no. 10/43, fragment of phalanx 2 or 3 of wing digit 4, ×1.65: (2a) dorsal view, (2b) ventral view, and (2c) cross section; (3) ZIN PH, no. 48/43, edentulous jaw fragment, ×1.45: (3a) inner, (3b) dorsal or ventral, and (3c) lateral views; (4) ZIN PH, no. 49/43, distal fragment of left metacarpal 4, ×1.17: (4a) anterior, (4b) dorsal, (4c) distal, (4d) posterior, and (4e) ventral views; and (5) ZIN PH, no. 47/43, proximal fragment of left phalanx 1 of wing digit 4, ×0.87: (5a) proximal, (5b) dorsal, (5c) posterior, (5d) ventral, and (5e) anterior, with the proximal end directed to the right, views. Designations: (*cf*) coracoid flange, (*dcn*) dorsal condyle, (*dco*) dorsal cotyle, (*ep*) extensor tendon process, (*g*) glenoid, (*msc*) imprints of muscles, (*pf*) pneumatic foramen, (*pr*) procoracoid; (*sf*) facet for the scapula; (*sco*) imprint of the supracoracoideus muscle, (*tr*) imprint of the coracoid head of the triceps muscle, (*vcn*) ventral condyle; and (*vco*) ventral cotyle.


Plate 9
pf
pex
1a
1b
1c
pex
2a
1d
pex
4a
2b
3a
2d
2c
3b
gt
pf
5a
gt
lt
gt
it
4b
4c
5b
5c
5d
5e

Etymology. From the Bostobe Formation.

Holotype. ZIN PH, no. 9/43, anterior fragment of cervical vertebra 5–6. Kazakhstan, Kyzylorda Region, 90 km northeast of the Dzhusaly station, Shakh-Shakh locality; Upper Cretaceous, Santonian–Lower Campanian, Bostobe Formation.

Description. The jugal and cervical vertebra 5–6 (holotype) were described in a previous publication (Averianov, 2004).

The atlas–axis complex (Pl. 9, fig. 1) is represented by the centrum of the epistropheus. The posterior condyle is flattened dorsoventrally. The longitudinal groove at the floor of the spinal canal is poorly pronounced. The postexapophyses are well developed, directed posterolaterally. A large pneumatic foramen is located on the lateral surface. The ventral side is convex (in *Azhdarcho*, it is concave).

The centrum of the procelous posterior dorsal vertebra (Pl. 9, fig. 2) is wide and relatively low, with a transversely and anterodorsally concave ventral surface. The transverse process is hollow and almost horizontal; its anterior margin is at the level of the anterior articular surface, the posterior margin begins slightly anterior to the posterior articular surface.

The distal end of the scapula (Pl. 9, fig. 3) is relatively long anteroposteriorly and flattened dorsoventrally. The height reaches the maximum at the anterior margin and gradually decreases posteriorly. The anterior margin is sharp. The articular surface for the notarium is saddle-shaped, convex dorsoventrally and slightly concave anteroposteriorly.

The proximal end of wing phalanx 2 (Pl. 9, fig. 4), with a longitudinal ventral crest, is almost identical to that of *Azhdarcho*, but its proximal articular surface expands dorsoventrally to a much greater extent.

The femur (Pl. 9, fig. 5) is hollow and thin-walled, with a large slitlike pneumatic foramen in the proximal end, dorsal to the base of the femoral neck and posterior to the greater trochanter. The greater trochanter is well developed, looks like a dome-shaped proximally directed tubercle. Distal to the greater trochanter, the anterior surface of the bone is distinctly concave. The proximal end of the posterodorsal margin of the bone has a distinct internal trochanter, with a wrinkled surface for the puboischiofemoralis externus muscle. Just ventral to the internal trochanter, the bone has a narrow longitudinal groove, which is less pronounced than in *Azhdarcho*. Distal to this groove, the posteroventral margin of the bone has a superficial longitudinal groove, which was probably the origin of the tendon of the femorotibialis muscle. This groove is also less developed than in the bones of approximately the same size of *Azhdarcho*. The lesser trochanter is a wrinkled prominence on the proximal end of the anterodorsal margin of the bone (it provided attachment for the iliofemoralis internus muscle). The lesser trochanter occupies a relatively large area, but is less pronounced than in *Azhdarcho*. The distal end of the diaphysis is circular in cross section.

Material. In addition to the holotype, the type locality has yielded a jugal (TsNIGR Museum, no. 41/11915); edentulous jaw fragment (ZIN PH, no. 37/43); atlas–axis centrum (ZIN PH, no. 44/43); posterior dorsal vertebral centrum (ZIN PH, no. 46/43); distal fragment of the scapula (ZIN PH, no. 45/43); proximal end of left phalanx 2 of the fourth (wing) digit (ZIN PH, no. 16/43); and proximal end of the left femur, with the neck and head broken off (ZIN PH, no. 43/43).

Remarks. The dorsal vertebrae and sacrum of azhdarchids are poorly known. The sacrum of *Azhdarcho* has not been found; the specimen identified by Nessov (1991a, p. 21) as a sacrum of *Azhdarcho* is in fact a synsacrum of an oviraptorosaur from Dzharakuduk (ZIN PH, no. 802/16). The material of *Azhdarcho* includes fragments of dorsoventrally flattened vertebral centra, which are similar to the above-described posterior dorsal vertebra of *Aralazhdarcho bostobensis* gen. et sp. nov. The substantially flattened posterior dorsal ("lumbar") vertebrae of *Azhdarcho* and *Aralazhdarcho* gen. nov. suggest that they had a wide sacrum (this probably concerns all azhdarchids), in contrast to, for example, *Pteranodon* spp., the centra of sacral and posterior dorsal vertebrae of which were as wide as and as high as the centra of the middle dorsal vertebrae (Bennett, 2001).

The extraordinarily long (compared to Ornithocheiroidea) distal articular surface of the scapula, which was articulated with the notarium, was also recorded in *Quetzalcoatlus* and *Tupuxuara* Kellner et Campos, 1988 from the Aptian–Albian of Brazil, a sister taxon of Azhdarchidae (Kellner and Hasegawa, 1993). This character is probably an additional synapomorphy of the clade Neoazhdarchia (Unwin, 2003).

Explanation of Plate 9

Figs. 1–5. *Aralazhdarcho bostobensis* sp. nov. from the Bostobe Formation (Santonian–Lower Campanian) of the Shakh-Shakh locality, Kyzylorda Region, Kazakhstan: (1) ZIN PH, no. 44/43, posterior fragment of the atlas–axis centrum: (1a) dorsal, (1b) lateral, (1c) ventral, and (1d) posterior views, ×1.75; (2) ZIN PH, no. 46/43, centrum of posterior dorsal vertebra: (2a) anterior, (2b) ventral, (2c) posterior, and (2d) lateral views, ×1.65; (3) ZIN PH, no. 45/43 (outcrop KAD-7, 1980), distal fragment of the scapula, ×1.75: (3a) distal and (3b) dorsal or ventral views; (4) ZIN PH, no. 16/43, proximal fragment of left phalanx 2 of wing digit 4, ×1.75: (4a) proximal, (4b) ventral, and (4c) dorsal views; and (5) ZIN PH, no. 43/43, proximal fragment of the left femur, ×1.75: (5a) proximal, (5b) posterior, (5c) ventral, (5d) anterior, and (5e) dorsal views. Designations: (*gt*) greater trochanter; (*it*) internal trochanter; (*lt*) lesser trochanter; (*pex*) postexapophysis; and (*pf*) pneumatic foramen.

DISCUSSION

New azhdarchid material from the former Soviet Union shows a wider diversity of this group in this region than was previously thought. The taxonomic position of azhdarchids from the Cenomanian of Karakalpakistan remains uncertain. However, taking into account the identity of known remains of the Cenomanian azhdarchids to respective bones of *Azhdarcho* and the continuity of faunas of dinosaurs and other vertebrates of the Cenomanian and Turonian of the Kyzyl Kum, it is possible to assume that, in the Cenomanian, representatives of the genus *Azhdarcho* occurred there. Edentulous azhdarchids of the Cenomanian of Central Asia coexisted with toothed ornithocheirids (Averianov, 2007); in the post-Cenomanian beds of this region, reliable ornithocheirids have not been found. The vertebrate fauna of the Early Santonian of Tajikistan (Kansai), particularly, turtles, dinosaurs, and mammals, is closely similar to the Turonian fauna of the Kyzyl Kum. However, the only identifiable bone of azhdarchid from Kansai (wing phalanx fragment) differs in morphology from *Azhdarcho* from the Turonian of Kyzyl Kum (see above). In addition to this specimen, the material collected by Nessov includes the proximal end of a humerus of an azhdarchid (ZIN PH, no. 50/43). This specimen was not supplied with a label or code of the locality on the bone (almost all vertebrate bones from the Kyzyl Kum collected by Nessov have such a code). In addition, in places, the bone retains red sandstone similar to that of Kansai and not typical for localities in the Kyzyl Kum. Nessov told me about a pterosaurian humerus from Kansai; however, such a find is not recorded in his field notes for 1981 and 1984. Specimen ZIN PH, no. 50/43 is identical in structure to the humeri of *Azhdarcho* from Dzharakuduk and suggests the presence of this genus in Kansai, if the bone actually comes from this locality.

Aralazhdarcho gen. nov. from the Santonian–Campanian of Kazakhstan substantially differs from *Azhdarcho* in the reduced pneumatic foramina on the sides of the spinal canal; in this character, it is the most advanced taxon of the family. The range of this genus was probably restricted to the southern latitudes, since to the north, at the latitude of the modern Volga Region, azhdarchids were represented at that time by the genus *Bogolubovia*, with normally developed lateral pneumatic foramina in the midcervical vertebrae.

New azhdarchid records from the coastal–marine beds of the Campanian of the Volga Region are evidence that these pterosaurians were common along the adjacent coastal line. Piscivorous azhdarchids probably formed large colonies within the zones of shelf upwelling, like extant marine birds (such as gannets, frigate birds, pelicans; see also Nessov, 1990, 1991a, 1991b; Bell and Padian, 1995). Assuming that all records belonged to the same taxon (genus *Bogolubovia*), this clearly differs from *Azhdarcho* in the longer rostrum and structural details of the third and midcervical vertebrae and the radius (Averianov et al., 2005).

To date, giant Maastrichtian azhdarchids reaching 12 m in wing span have not been recorded in Russia. *Hatzegopteryx* from the Maastrichtian of Romania (Buffetaut et al., 2002, 2003) is the closest geographically. The bones of giant Maastrichtian azhdarchids may occur in the continental beds of this stage in the Far East, or in the coastal–marine beds of the Volga Region.

In the previous study (Averianov et al., 2005), the extreme scarcity of azhdarchids in the marine Campanian beds of the Middle Volga Region was noted (two specimens during 100 years). During the past 1.5 years after the submission of this paper to the Paleontological Journal, six identifiable azhdarchid bones from the Campanian of the Saratov and Penza regions were recorded. This changes the prediction of the development of our knowledge of Russian azhdarchids from pessimistic to optimistic.

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