

A New Late Cretaceous Azhdarchid (Pterosauria, Azhdarchidae) from the Volga Region

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Abstract—A new azhdarchid genus and species, *Volgadraco bogolubovi* gen. et sp. nov., is described based on an anterior fragment of the mandibular symphysis (mandibular beak) and some postcranial elements from the Rybushka Formation (Upper Cretaceous, Lower Campanian) of the Shirokii Karamysh 2 locality, Saratov Region. The new taxon is intermediate in size and vascularization of the mandibular beak between medium-sized Turonian–Santonian azhdarchids (*Azhdarcho*, *Bakonydraco*) and the giant Maastrichtian azhdarchid *Quetzalcoatlus*.

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INTRODUCTION

Several localities of Campanian vertebrates, containing azhdarchid pterosaurs and hesperornithid birds, have recently been discovered in the Volga Region near Saratov (Fig. 1; Panteleyev et al., 2004; Averianov et al., 2005; Averianov, 2007). It is noteworthy that, in the localities with hesperornithids (Karyakino in the Saratov Region and Rychkovo in the Volgograd Region; the last locality was described by Nesson and Yarkov (1993) and Yarkov and Nesson (2000)), pterosaurs are extremely infrequent and represented by indeterminate fragments of large tubular bones. On the contrary, in the localities with identifiable azhdarchid bones (Malaya Serdoba, Shirokii Karamysh 2, Beloe Lake, Saratov 2), hesperornithid bones have not yet been recorded. The difference in occurrence of azhdarchids and hesperornithids is probably attributable to different paleoenvironments and competitive relationships between the two groups of specialized ichthyophagous vertebrates. In the present study, pterosaur bones from the Shirokii Karamysh 2 locality of the Saratov Region, which were collected in 2004 and 2005 by the Saratov amateur collectors M.A. Grigor'ev, A.L. Gorbunov-Gusev, and A.N. Gurenko and assigned to a new azhdarchid taxon, are described.

Abbreviations: (SGU) Saratov State University, Saratov, Russia; (ZIN PH) paleoherpetological collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

GEOLOGICAL AND TAPHONOMIC CHARACTERISTICS OF THE SHIROKII KARAMYSH 2 LOCALITY

The Shirokii Karamysh 2 locality is situated in the upper part of the Lisii gully north of the village of Shirokii Karamysh at the road to the village of Uritskoe (Lysogorskii District, Saratov Region). This is the second gully from the northern boundary of the village, the upper part of which cuts a slope of erosion terrace.

The gully opens the following section of Upper Cretaceous deposits, described downward the section:

K₂ Cmp₂, Bed 1. Greenish gray, glauconitic quartz, inequigranular sandstone, spotty because of nonuniform siliceous cement, solid, furrowed by surface weathering. The horizon gradually passes into the underlying strata, with the transition marked by a projection of denser sandstones in the slope of the gully. The lower surface is uneven. Thickness, up to 0.5 m.

K₂ Cmp_{1–2}, Bed 2. Phosphorite horizon: the upper part is composed of bright green, quartz–glauconitic, strongly bioturbated sand, with phosphorites up to 0.5–1 cm in size, regularly scattered and slightly accumulated in the roof. In the lower part, phosphorites are dark brown, black, sabulous, and angular and black, more rounded. Phosphorites and phosphorite accumulations are abundant. In places, phosphorite inclusions are widely spaced; in some sites (up to 1.5–2.5 m in size), they are accumulated, smaller in size, 1–1.5 cm in diameter. The grayish yellow and grayish brown aleuritic inclusions are more rounded, with signs of bioerosion, more widely spaced and mostly smaller in size. The lower surface is uneven, pitted and nest-shaped.

The accumulations of phosphorite inclusions at the lower boundary are up to 0.1 m thick. This layer contained isolated, frequently well-preserved specimens of marine reptiles (Elasmosauridae indet., Polycotylidae indet., *Prognathodon* sp., and ?*Clidastes* sp.). Pterosaur bones come from this layer. Thickness, 0.4–0.5 m.

K_2 Cmp₁, Bed 3. Dirty green, nonuniformly colored, quartz–glauconitic sand, strongly bioturbated; burrows up to 1.5–5 cm in diameter extend to a depth of 0.5–0.6 m from the roof. This layer contains small, isolated subovate aleuritic inclusions, strongly rounded and, sometimes, positioned vertically (up to 2 cm in diameter). Near the roof, narrow (1–2 mm in diameter) and short (up to 1–3 cm) burrows are sporadically distributed. Below, the sand is uniformly grayish green, medium-grained; signs of bioturbidites are almost absent, which explains the abundance of poorly phosphatized biogenic remains preserved in these strata. Fossils are mostly represented by fish scales, which are accumulated in nests and lower parts of decapod burrows (in the upper part of the horizon); coprolites, buried subautochthonously (scattered at a distance of 1 m); fish vertebrae; teeth and dental plates of cartilaginous fish; and small phosphate mollusk shells, buried in different positions.

At 1.3–1.5 m below the roof of sand, there is a layer containing infrequent, variously oriented aleuritic pellets and shingles, rare nests (up to 0.1 m in diameter) of accumulated phosphate pellets. Below this level, faunal remains are scarce. Visible thickness, 1.9 m.

Vertebrates occur in the phosphorite horizon. The bones are dirty yellow, strongly phosphatized, very dense, slightly rounded, exposed to bioerosion, diversely oriented. Tetrapods were buried within an active sublittoral zone, under conditions of general immersion of the territory; this provided rather extensive accumulation of terrigenous material, psammitic and aleuritic matter. As a result of movements within the sublittoral and supralittoral zones, a sandy–pebble beach was formed from time to time, where large elements of the substrate were phosphorite pellets, vertebral centers, and other reptile bones. The subsidence, short-term of exposure on the surface, and the rapid fossilization (phosphatization) provided good primary preservation of many bones. In some cases, long, narrow bones and vertebral centers in natural articulation with neural spines are preserved, while large vertebral centers of plesiosaurs are usually most rounded and damaged. The presence within a locality of some bones undoubtedly belonging to the same individual (vertebral centers, teeth of fish, etc.) suggests slight scattering of dead bodies and body fragments, in particular, primary burial not influenced by active hydrodynamic factors.

In general, the burial of marine and subcontinental vertebrates in Bed 2 should be classified as synchronous, tabular, nonuniformly scattered.

A distinctive feature of this locality is the fact that, during the short period of the formation of the phospho-

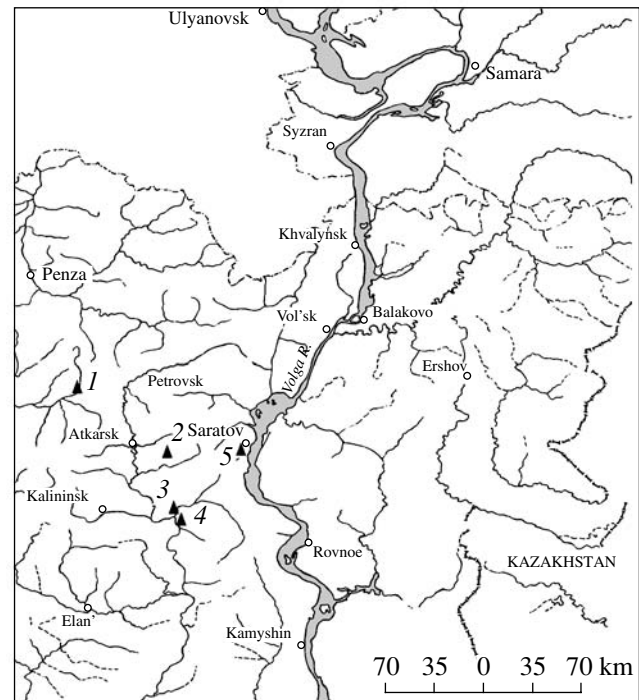


Fig. 1. Localities of pterosaurs and birds in the Campanian of the Saratov and Penza regions: (1) Malaya Serdoba, (2) Karyakino, (3) Shirokii Karamysh, (4) Beloe Lake, and (5) Saratov.

rite horizon, erosion had a minor effect on underlying sands rich in invertebrate and vertebrate remains (see description of Bed 3). The development of diverse digging organisms, which resulted in almost complete disappearance of biogenic inclusions in the upper part of the early deposits, resulted in the stratification and preservation of autochthonous and subautochthonous burials of vertebrates and mollusks. As is usually observed in the majority of localities with similar stratification, the upper part of Bed 3 is eroded and elements of this bed occur in the overlying phosphorite horizon. These results of comparative analysis of a number of relatively synchronous localities (Campanian units) suggest a relatively low position (hypsothetic) of the area of the Shirokii Karamysh 2 locality in the time of the formation of terrigenous deposits and, in particular, of the phosphorite horizon.

The distribution of pterosaurs and birds (hesperornithids) in the Late Cretaceous of the southeastern European paleobiogeographic region was connected with the history of the formation and arrangement of subflat islands of archipelagoes and banks in this region. Within a relatively shallow area between the Voronezh Region on the west and an extensive marine basin in the Recent Caspian Region, local positive elements reflecting a block structure of the base and composing complex systems in the shape of swells were formed for a long time. Changes in both the geodynamic mode and the level of basins in this area had an effect on the man-

ifestation of these positive structures on the bottom of the basin, including a series of archipelagoes.

Pterosaur and avian records occur mostly in the area of the former banks and islands in the southern and central parts of the right bank of the Volga Region and have not yet been recorded to the north of the latitude of the town of Serdobsk (Penza Region).

The Shirokii Karamysh 2 locality is a series of sites of this type in the middle zone on the right bank of the Volga Region, which differs from sites in the adjacent area in the more abundant vertebrate specimens; this is accounted for by concurrence of a number of factors:

(1) The presence of many islands in a large part of the right bank of the Volga Region (from the latitude of Volgograd to the latitude of Saratov), which allowed sublatitudinal and submeridional migration of pterosaurs and birds.

(2) Long-term existence of many islands, including elevations (Uritskoe and Shirokii Karamysh), a slope of which retained the locality under study.

(3) The wide zone of the sublittoral and supralittoral, the gently sloping shore, and warmed water provided abundant food.

(4) Currents in the basin and seasonal movements of water masses developed within certain periods stable routes of migration of marine organisms between islands. This provided habitats and migration patterns of pterosaurs and birds within the coastal zone near the migration routes of fish and other marine organisms.

SYSTEMATIC PALEONTOLOGY

Superorder Pterosauria

Order Pterodactylida

Superfamily Azhdarchoidea Nesson, 1984

Family Azhdarchidae Nesson, 1984

Genus *Volgadraco* Averianov,
Arkhangelsky et Pervushov, gen. nov.

E t y m o l o g y. From the Volga River and the Latin *draco* (dragon).

T y p e s p e c i e s. *Volgadraco bogolubovi* sp. nov.

D i a g n o s i s. Mandibular beak long, with slightly convex lateral outline of dorsal margin. Dorsal surface of mandibular beak concave between sharpened lateral edges. Vascularization of mandibular beak reduced to three irregular foramina on each side. Cervical vertebra 3 with anteriorly high neural arch, large central pneumatic foramen above spinal canal on anterior side, and with series of small pneumatic foramina in lateral surface. Cervical vertebra 9 with large hypapophysis and large slitlike depression on lateral surface of neural arch just anterior to postzygapophysis. Last vertebra of notarium with slitlike, dorsoventrally compressed foramen of spinal canal. Lesser trochanter of femur weakly developed.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. The new genus differs from *Azhdarcho* Nesson, 1984 from the Turonian of Uzbekistan in the longer mandibular beak, with the less convex lateral outline of the dorsal margin; in the fewer foramina for blood vessels in the mandibular beak; the higher neural arch of cervical vertebra 3 on the anterior side, the large central pneumatic foramen above the spinal canal and a series of small pneumatic foramina on the lateral surface of this vertebra; in the larger hypapophysis and the greater volume of the slitlike depression on the lateral surface of the neural arch just anterior to the postzygapophysis of cervical vertebra 9; and in the weaker developed lesser trochanter of the femur.

It differs from *Eoazhdarcho* Lü et Ji, 2005 from the Aptian of China in the longer mandibular beak.

It differs from *Bennettazhia* Nesson, 1991 from the Albian of the United States in the slitlike, dorsoventrally compressed foramen of the spinal canal of the last thoracic vertebra of the notarium.

It differs from *Bakonydraco* Ösi, Weishampel et Jianu, 2005 from the Santonian of Hungary in the longer and less massive mandibular beak with a convex lateral outline of the dorsal margin (in *Bakonydraco*, this margin is posteriorly concave and anteriorly convex) and the fewer slitlike foramina for blood vessels in the mandibular beak.

It differs from *Aralazhdarcho* Averianov, 2007 from the Santonian–Campanian of Kazakhstan in the less developed lesser trochanter of the femur.

It differs from *Zhejiangopterus* Cai et Wei, 1994 from the Campanian of China in the convex rather than concave lateral structure of the dorsal margin and the concave rather than flat dorsal surface of the mandibular beak.

It differs from *Phosphatodraco* Pereda Suberbiola et al., 2003 from the Maastrichtian of Morocco in the larger foramen of the spinal canal on cervical vertebra 9.

It differs from *Quetzalcoatlus* Lawson, 1975 from the Maastrichtian of the United States in the shorter and more massive mandibular beak; the concave rather than flat dorsal surface of the mandibular beak; the presence of slitlike foramina for blood vessels in the mandibular beak; the better developed hypapophysis of cervical vertebra 9; and in the presence of a large slitlike depression on the lateral surface of the neural arch of this vertebra just anterior to the postzygapophysis.

R e m a r k s. It is impossible to compare the new genus with *Montanazhdarcho* Padian et al., 1995 (Campanian of the United States), *Bogolubovia* Nesson, 1989 (Campanian of Russia), *Arambourgiania* Nesson, 1987 (Maastrichtian of Jordan), and *Hatzegopteryx* Buffetaut et al., 2002 (Maastrichtian of Romania) because of incomparability of available material.

It is not improbable that the genus described is a junior synonym of *Bogolubovia* Nesson, 1989, which is represented by a fragment of a middle cervical vertebra and, probably, by some other bones from the Rybushka

Formation near the village of Malaya Serdoba in the Penza Region (Bogolyubov, 1914; Averianov, 2007). Bakhurina and Unwin (1995) and Unwin and Bakhurina (2000) designated this taxon as a nomen dubium; we tentatively adhere to this point of view and, hence, describe the new azhdarchid from the Campanian of the Volga Region based on the better identifiable material. If more complete skeletal material combining characters of *Bogolubovia* and *Volgadraco* gen. nov. are found, the first name should be restored according to the principle of priority and the second name should be regarded as a junior subjective synonym. At the same time, it is possible that several azhdarchid genera existed in the Campanian of the Volga Region.

The assignment of isolated and noncomparable skeletal elements from one locality to the same taxon is always tentative, because it is impossible to exclude the presence of two or more closely related taxa in the same assemblage. To overcome this obstacle a new taxon is sometimes based only on the holotype, while other skeletal elements are not included in the same taxon. For example, *Bakonydraco galaczi* Ösi, Weishampel et Jianu, 2005 from the Santonian of Hungary is only based on the holotype (lower jaw), whereas accompanying postcranial azhdarchid bones from this locality are determined as Azhdarchidae indet. (Ösi et al., 2005). However, from the taxonomic point of view, this conclusion means the presence of two azhdarchid taxa in the assemblage, *Bakonydraco galaczi* and Azhdarchidae indet. We are inclined to assign all specimens of a medium-sized azhdarchid from the Shirokii Karamysh 2 locality to the same taxon, *Volgadraco bogolubovi* sp. nov., until the presence of other azhdarchid taxa in this assemblage is shown with certainty.

Volgadraco bogolubovi Averianov, Arkhangelsky et Pervushov, sp. nov.

Plates 5 and 6

Azhdarchidae indet.: Averianov, 2007, p. 76.

E t y m o l o g y. The species is named in honor of N.N. Bogolyubov, who described the first pterosaur from Russia, which was the first representative of the family Azhdarchidae known to science (Bogolyubov, 1914).

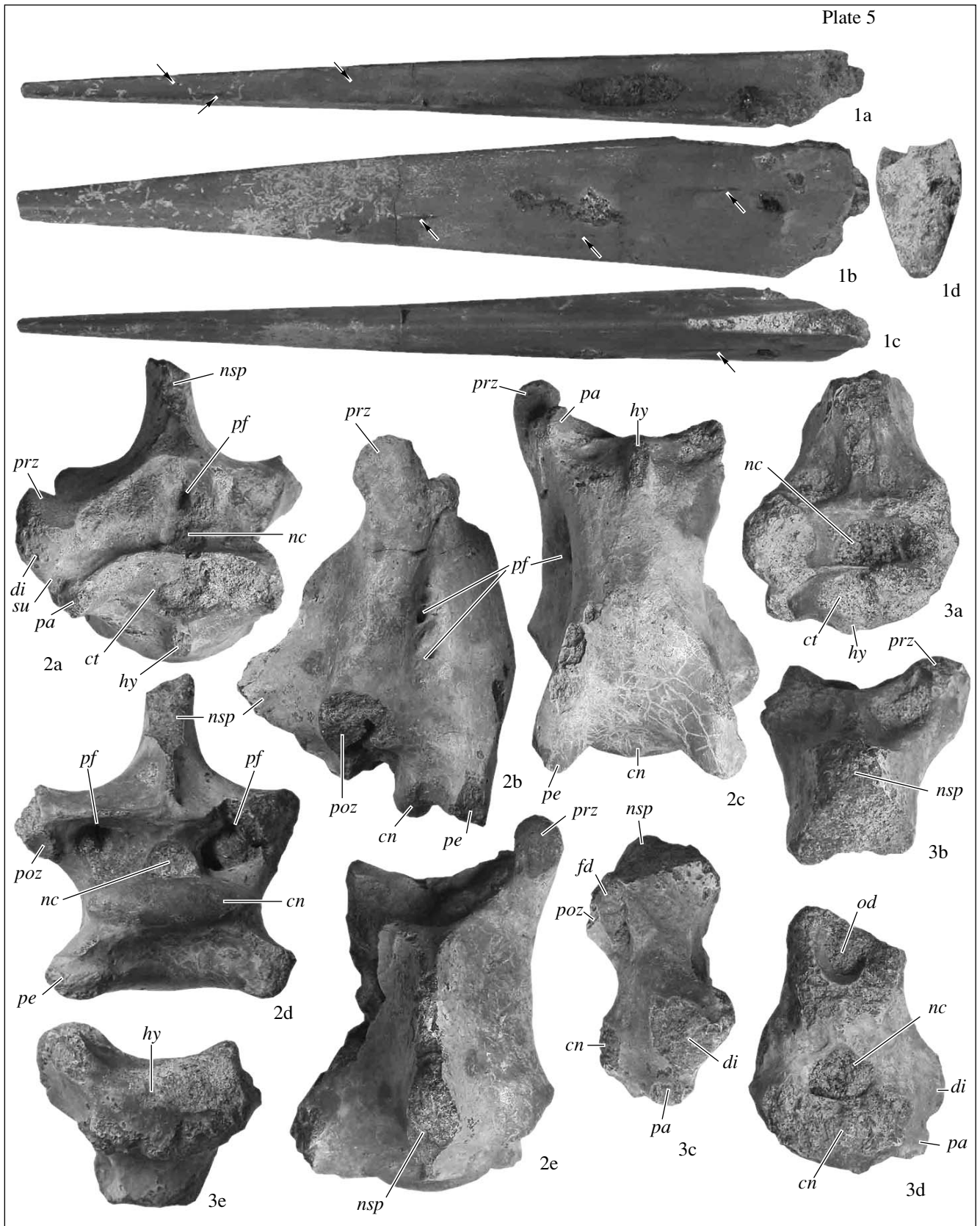
H o l o t y p e. SGU, no. 46/104a, anterior part of the lower jaw symphysis (mandibular beak); Russia, Saratov Region, Shirokii Karamysh 2 locality; Upper Cretaceous, Lower Campanian, phosphorite conglomerate of the Rybushka Formation.

D e s c r i p t i o n. The mandibular beak (holotype, Pl. 5, fig. 1) is triangular in lateral, dorsal, and ventral views. The dorsal and ventral surfaces are positioned at an angle of approximately 13° and the lateral surfaces are at an angle of approximately 4°, forming a pointed end of the beak (the tip of which is broken off). In lateral view, the outline of the dorsal surface is slightly convex, almost straight. On the dorsal surface, the lateral margins form sharp elevated margins, with a slightly concave area between them. The lateral sur-

faces of the beak are convex in the dorsal part and almost straight in the ventral part; converge ventrally at an angle of approximately 37°, forming a sharp ventral crest along the entire beak. In the anterior part, the beak is almost rhomboidal in cross section, with lateral keels near the midheight of the beak. The ventral margin is straight in lateral view. A few slitlike foramina for blood vessels (three on each lateral and dorsal sides) are arranged irregularly.

The third cervical vertebra is almost completely preserved (specimen SGU, no. 47/104a; Pl. 5, fig. 2). The vertebral center is relatively short; its length is only 2.4 times as great as the minimum diameter at the center. The lateral sides of the vertebral center are concave, so that, in ventral view, it is in the shape of a sand-glass. The ventral side of the vertebral center is strongly convex in the central part. The anterior side has a short crest of the hypapophysis. The posterior part of the ventral surface of the vertebral center is flat; laterally, it is limited by weak crests extending from the postexapophyses to the center of the ventral surface. The anterior articular depression of the vertebral center is wide and relatively low, it is three times as wide as high. The dorsal surface of the depression is convex, with a small concavity at the center. The ventral surface is divided by the hypapophysis into two concave parts. The ventrally curved lateral margins of the anterior articular depression correspond to rudimentary parapophyses separated by a wide groove from rudimentary diapophyses on the neural arch. The posterior condyle of the vertebral center is ovate, compressed strongly dorsoventrally, 3.6 times as wide as high. The ventral margin of the condyle is at a distance from the ventral margin of the vertebral center that is greater than the condyle height. This interval is occupied by a shallow depression restricted on the sides by the crests extending from the condyle to the postexapophyses. The postexapophyses are stout, ventrolaterally oriented. The lateral sides of the vertebra have a series of small irregular depressions (four on the right and three on the left) at the boundary between the neural arch and the center. Some depressions (two on the right and, probably, one on the left) contain small pneumatic foramina. Dorsally, a prominent crest extends along the entire neural arch, connecting the prezygapophysis and the postzygapophysis (it corresponds to the parasagittal carina of succeeding cervical vertebrae). This crest is positioned at an angle of approximately 15° to the anteroposterior axis of the vertebral center. Anteriorly, the neural arch is relatively high, higher than the anterior articular depression. The spinal canal is very small, rounded in cross section. The oval pneumatic foramen, which is only slightly smaller than the spinal canal, is positioned somewhat dorsally. On each side of the foramina described, there is an extensive triangular depression, which is restricted ventrally by the vertebral center and dorsolaterally by sharp crests extending from the prezygapophyses to the base of the neural spine. This region is either damaged (on the left side) or covered

Plate 5



with phosphorite (on the right); therefore, it remains uncertain whether or not the lateral pneumatic canals, which have foramina on the posterior side of the neural arch, open here. The prezygapophysis is massive, with a convex ovate articular surface oriented dorsally and slightly anteriorly. On the posterior side of the neural arch, the foramen of the spinal canal is larger than on the anterior side. This foramen is ovate, except for the ventral border, which is straight and coincides with the dorsal border of the posterior condyle. On the sides and somewhat dorsally, there are large foramina of the lateral pneumatic canals. The dorsal (central) pneumatic foramen is absent from the posterior side. A massive horizontal crest passes above the foramina, connecting the postzygapophyses. The central vertical crest, which forms the posterior margin of the neural spine, is located more dorsally. The postzygapophyses are mostly damaged. The articular surface of the postzygapophysis (partially preserved on the left side) is concave, oriented ventrally and slightly posteriorly. The neural spine is relatively high; its base occupies the entire extent of the neural arch. The maximum height of the neural spine is probably close to the posterior margin, in line with the base of the postzygapophyseal processes. At the same point, the neural spine shows the maximum width, which is almost three times as wide as near the anterior margin.

The ninth (last) cervical vertebra (specimen SGU, no. 48/104a; Pl. 5, fig. 3) is also almost completely preserved. The vertebra is high and very short anteroposteriorly. On the vertebral center, the anterior articular surface is strongly concave and the posterior condyle is strongly convex. The hypapophysis is well developed, approximately to the same extent as in the third cervical vertebra (in cervical vertebra 9 of *Azhdarcho* and *Quetzalcoatlus*, it is strongly reduced). The surface of the posterior condyle is damaged; the concave lateral surfaces of this condyle, if present, were probably developed to a much lesser extent than in *Azhdarcho* and *Quetzalcoatlus*. The ventral surface of the vertebral center is slightly convex (in *Azhdarcho* and *Quetzalcoatlus*, it is flat). The foramen of the spinal canal is relatively large, ovate, its ventral border is straight anteriorly and convex posteriorly. The lateral pneumatic foramina were probably present anteriorly (this area of the vertebra is covered with phosphorites). The neural arch is high, with a longitudinal central crest located anteriorly. A pair of transverse depressions extend

between this crest and prezygapophyses (*Azhdarcho* and *Quetzalcoatlus* lack similar depressions). The articular surfaces of the prezygapophyses and postzygapophyses are not preserved. On the lateral surface of the vertebra at the boundary between the vertebral center and neural arch, there is the base of a massive diapophysis (most of the process is broken off), which is divided by a wide groove of a relatively small parapophysis. A large slitlike depression is located just anterior to the base of the postzygapophysis (in *Azhdarcho*, this depression is very small; in *Quetzalcoatlus*, it is absent). A very large ovate, dorsoventrally extended depression is located above the postzygapophyses. The same depression is present in cervical vertebra 9 of *Quetzalcoatlus*, *Phosphatodraco*, and *Pteranodon* (Bennett, 2001, text-fig. 42B; Pereda Suberbiola et al., 2003, text-fig. 3e); the structure of this region in *Azhdarcho* is not known. The neural spine is not preserved; its base is short and wide, located close to the center of the neural arch.

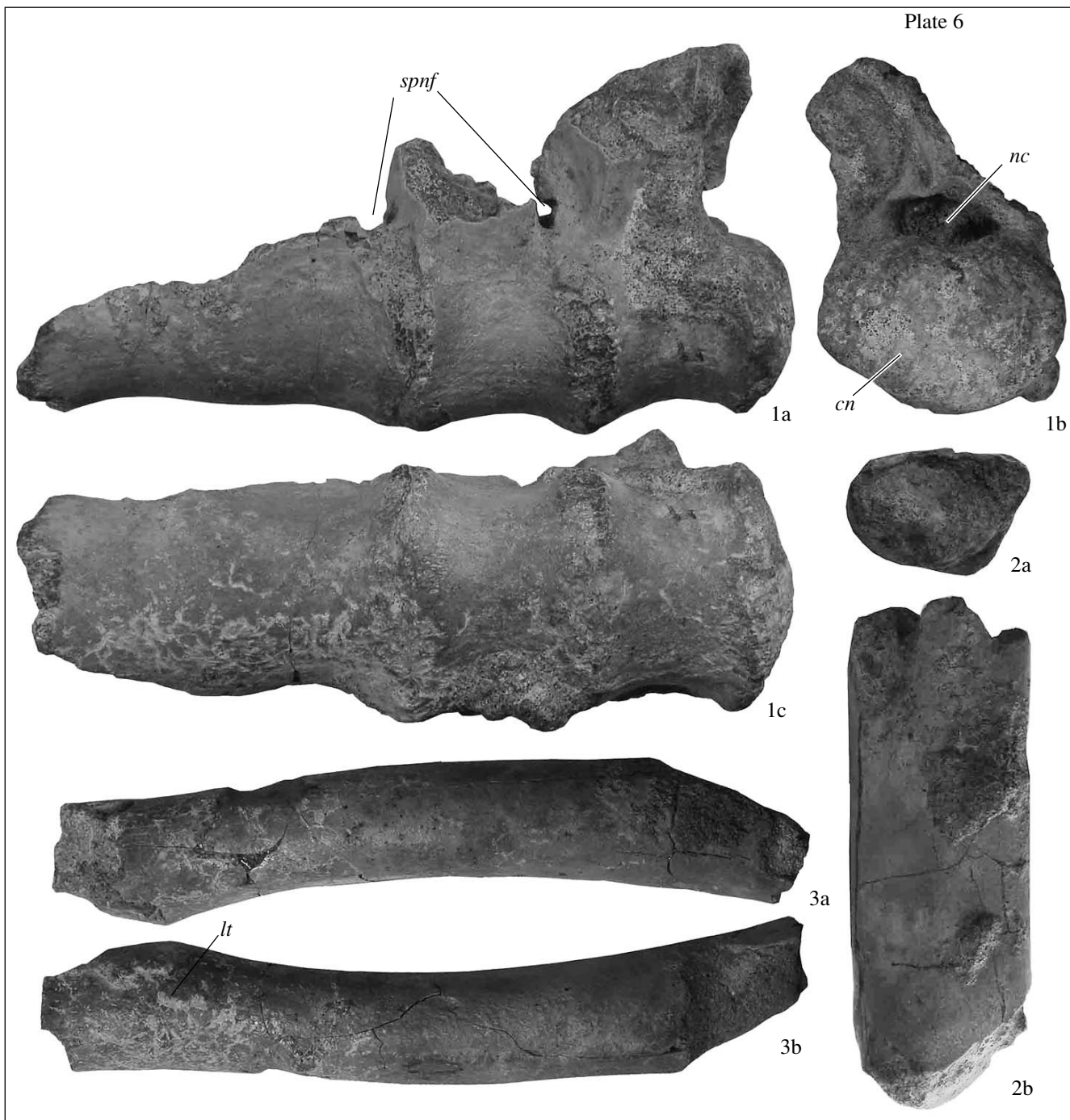
The material includes a posterior fragment of the notarium, consisting of four fused dorsal vertebrae (specimen SGU, no. 49/104a; Pl. 6, fig. 1). In this fragment, the suture between the first and second vertebral centers is hardly discernible. The ventral side of the vertebral center is more concave in two posterior vertebrae than in two anterior vertebrae. The posterior condyle of the center of the last vertebra is strongly convex, ovate (the transverse diameter exceeds the height). The dorsal border of the condyle is concave, forming the bottom of the spinal canal. The foramen of the spinal canal is slitlike, compressed dorsoventrally to a greater extent than in *Azhdarcho* (in *Bennettazhia*, it is ovate and higher).

A fragment of a long tubular bone (specimen SGU, no. 50/104a; Pl. 6, fig. 2) is most likely a part of the diaphysis of the first phalanx of the wing (fourth) digit. The diaphysis is ovate in cross section; the anteroposterior diameter is 1.6 times as long as the dorsoventral diameter (in *Azhdarcho lancicollis*, specimen ZIN PH, no. 37/44, it is two times as long). The anteroposterior diameter is uniform throughout the fragment preserved; this is evidence that the bone was long.

The femur (specimen SGU, no. 50/104a; Pl. 6, fig. 3) is only represented by the diaphysis. The bone is hollow, thin-walled and relatively large; the total length was probably at least 17 or 18 cm. The diaphysis is strongly curved in the frontal plane. This curvature is

Explanation of Plate 5

Figs. 1–3. The pterosaur *Volgadraco bogolubovi* sp. nov. from the Rybushka Formation (Lower Campanian) of the Shirokii Karamysh 2 locality, Saratov Region, Russia: (1) holotype SGU, no. 46/104a, anterior part of the mandibular beak: (1a) dorsal, (1b) lateral, (1c) ventral, and (1d) proximal views, $\times 1.30$; arrows indicate slitlike foramina for blood vessels; (2) SGU, no. 47/104a, cervical vertebra 3: (2a) anterior, (2b) lateral, (2c) ventral, (2d) posterior, and (2e) dorsal views, $\times 0.69$; (3) SGU, no. 48/104a, cervical vertebra 9: (3a) anterior, (3b) dorsal, (3c) lateral, (3d) posterior, and (3e) ventral views, $\times 1.10$. Designations: (cn) posterior condyles of the vertebral center, (ct) anterior articular depression of the vertebral center, (di) diapophysis, (fd) slitlike depression, (hy) hypapophysis, (nc) foramen of the spinal canal, (nsp) neural spine, (od) oval depression, (pa) parapophysis, (pe) postexapophysis, (pf) pneumatic foramen, (poz) postzygapophysis, (prz) prezygapophysis, and (su) sulcus between the parapophysis and diapophysis.



Explanation of Plate 6

Figs. 1–3. The pterosaur *Volgadraco bogolubovi* sp. nov. from the Rybushka Formation (Lower Campanian) of the Shirokii Karamysh 2 locality, Saratov Region, Russia: (1) SGU, no. 49/104a, posterior part of the notarium, consisting of four thoracic vertebrae: (1a) lateral, (1b) posterior, and (1c) ventral views $\times 1.50$; (2) SGU, no. 51/104a, fragment of the presumably first right phalanx of the wing digit: (2a) proximal (?) view and (2b) dorsal or ventral view, $\times 1.28$; (3) SGU, no. 50/104a, left femur fragment: (3a) posterior and (3b) anterior views, $\times 0.95$. Designations: (*cn*) posterior condyles of the vertebral center, (*lt*) small trochanter, (*nc*) foramen of the spinal canal, and (*spnf*) foramen of the spinal nerve.

much more pronounced than in the femoral diaphysis of giant *Quetzalcoatlus* sp. from the Campanian of Alberta, Canada (Currie and Russell, 1982, text-fig. 1) and approximately equal to that of the significantly

smaller *Azhdarcho lancicollis* (specimen ZIN PH, no. 44). The diaphysis is ovate in cross section. The proximal end is broken off at the base of the greater trochanter. A very small rough area of the lesser trochanter

for the iliofemoralis internus muscle is located on the anterior side, near the proximal margin preserved, closer to the dorsal margin. The lesser trochanter is much weaker than in *Azhdarcho* and *Aralazhdarcho* (Averianov, 2007).

Remarks. The symphysis of the dentaries of azhdarchids, which is up to 60% of the lower jaw length, consists of two distinctly differentiated parts, the anterior mandibular beak and the posterior part. These parts are connected by a sutural articulation (synostosis) and probably completely fused only in old animals. Judging from the presence and abundance of large foramina for blood vessels in the anterior part and complete absence of similar foramina in the posterior part of the symphysis, only the mandibular beak was covered by horny tissue. Isolated mandibular beaks of *Azhdarcho lancicollis* relatively frequently occur in fluvial deposits of the Bissekty Formation (Turonian) of Uzbekistan (Nessov, 1984, pl. 7, figs. 10, 11; Nessov, 1997, pl. 15, figs. 1–5). The relative length and shape of the mandibular beak of azhdarchids vary widely (Fig. 2); this is probably connected with different feeding modes, the study of which lies ahead. The shortest and most massive mandibular beak is characteristic of *Bakonydraco*, the longest and most slender beak is in *Quetzalcoatlus*. The lateral outline of the dorsal margin of the beak is concave in *Zhejiangopterus* and partially (posteriorly) in *Bakonydraco*. In *Azhdarcho* and *Quetzalcoatlus*, it is convex. The shape of the mandibular beak of *Volgadraco* gen. nov. is most similar to that of *Azhdarcho* and differs in the less convex, almost straight dorsal margin in lateral view.

The number of foramina for blood vessels in the mandibular beak probably decreased in the evolution of azhdarchids. Turonian *Azhdarcho*, Santonian *Bakonydraco*, and Azhdarchidae indet. from the Campanian of Spain have many large foramina arranged in two rows on the dorsal side and on each lateral side (Nessov, 1984, pl. 7, figs. 10, 11; Nessov, 1997, pl. 15, figs. 1–5; Buffetaut, 1999, text-fig. 1a; Ösi et al., 2005, text-fig. 2). In Maastrichtian *Quetzalcoatlus*, these foramina have not been described (Kellner and Langston, 1996); apparently, this taxon lacks these foramina. *Volgadraco* gen. nov. has three relatively small foramina in each of three sides of the beak, i.e., it is intermediate between the two extreme variants. The reduction of vascularization of the azhdarchid beak was probably connected with increasing ceratinization of the horn cover. Apparently, the foramina considered provided passage not only for blood vessels but also for sensitive fibers of the mandibular ramus of cranial nerve VII (facial nerve); thus, the horn beak of early azhdarchids possessed certain tactile sensitivity, which was important for feeding. The reduction of these foramina could have been connected with changes in feeding strategy.

The Cenomanian beds of Morocco has yielded three fragments of the jaw symphysis of toothless pterosaurs, which are determined as an anterior end of the premax-

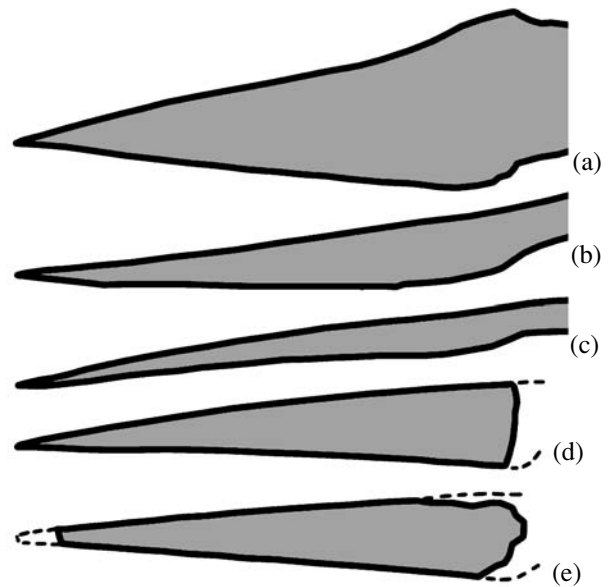


Fig. 2. The shape of the mandibular beak of the lower jaw in representatives of the family Azhdarchidae: (a) *Bakonydraco* (after Ösi et al., 2005); (b) *Zhejiangopterus* (after Unwin, Lü, 1997); (c) *Quetzalcoatlus* (after Kellner and Langston, 1996); (d) *Azhdarcho* (based on specimen ZIN PH, no. 85/44); and (e) *Volgadraco* gen. nov. The specimens are shown on different scales, such that the mandibular beaks are approximately equal in length.

illa (upper jaw beak) of Pteranodontidae (?), anterior end of the premaxilla of Azhdarchidae (?), and an anterior fragment of the mandibular symphysis of Tapejaridae (Wellnhofer and Buffetaut, 1999, text-figs. 2, 4, 5). In our opinion, the three fragments belong to one azhdarchid taxon; these are a mandibular beak, an upper jaw beak, and a more posterior fragment of the premaxilla, with an anterior fragment of the cranial crest. The Cenomanian azhdarchid from Morocco has fewer vascular foramina in the mandibular beak, the lateral foramina form only one (dorsal) row and dorsal foramina are only present in the anterior part of the beak. However, the extent of vascularization of the mandibular beak of this taxon is higher than in *Volgadraco* gen. nov.

The incomplete cervical vertebra of a pterosaur from the Campanian of Delaware, United States, that was referred to Ornithocheiridae (Baird and Galton, 1981, text-fig. 2), is almost identical to specimen SGU, no. 47/104a and could have been cervical vertebra 3 of an azhdarchid. As in *Volgadraco* gen. nov., this specimen has a small lateral pneumatic foramen.

Material. In addition to the holotype, the type locality has yielded cervical vertebra 3 (SGU, no. 47/104a), cervical vertebra 9 (SGU, no. 48/104a), posterior part of the notarium consisting of four vertebrae (SGU, no. 49/104a), a fragment of the presumable first right phalanx of the wing digit (SGU, no. 51/104a), and a fragment of the left femur (SGU, no. 50/104a).

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