


A large pteranodontid pterosaur from the Late Cretaceous of Eastern Europe

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Original Article

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Abstract

The Campanian Beloe Ozero locality within the Rybushka Formation in Saratov Province, Russia, is one of the richest and most diverse Upper Cretaceous pterosaur localities in Europe. It produces identifiable remains of Pteranodontidae indet. and Azhdarchidae indet., as well as bones which can be attributed to either of these groups. The pteranodontid specimens from the Beloe Ozero locality described in this paper include a cervical III, distal scapula, humerus deltopectoral crest, proximal syncarpal, preaxial carpal and complete femur. Based on the femur and proximal syncarpal, the wingspan estimate for the Beloe Ozero pteranodontid varies from 5.2 to 6.5 m. *Volgadraco bogolubovi*, known from the neighbouring Shyrokii Karamysh locality of the same formation and attributed previously to the Azhdarchidae, is more likely pteranodontid than azhdarchid. The other putative records of the Pteranodontidae in the Late Cretaceous of North America, Europe and Asia are discussed. Pteranodontid pterosaurs had a much wider distribution on the northern continents in the Late Cretaceous than previously thought.

1. Introduction

Pteranodontid pterosaurs are best known from the Upper Cretaceous (Coniacian–Campanian) Niobrara and Pierre Shale formations of Kansas, USA, where they are represented by two species of the iconic toothless pterosaur *Pteranodon* (Marsh, 1871, 1872, 1876, 1884; Williston, 1891, 1892, 1893, 1895, 1896, 1897; Eaton, 1903, 1904, 1908, 1910; Wiman, 1920; Miller, 1971, 1972; Mateer, 1975; Schoch, 1984; Bennett, 1987, 1992, 1993, 1994, 2001a, 2018; Witton, 2010). *Tethydraco regalis* from the Maastrichtian of Morocco is the only other taxon referable to the Pteranodontidae (Longrich *et al.*, 2018). Putative records of the Pteranodontidae were reported from the Albian Mowry Shale of Montana, USA (Bennett, 1989), the Albian (?) Chulec Formation of Peru (Bennett, 1989), the Santonian–Campanian Yezo Group of Hokkaido, Japan (Obata *et al.*, 1972; Kellner *et al.*, 2016), the Campanian Selma Formation of Alabama, USA (Bennett, 1994), and the Campanian Merchantville Formation of Delaware, USA (Baird & Galton, 1981; Bennett, 1994).

The first pterosaur bone found in Russia, the posterior fragment of a middle cervical vertebra, was found in the Campanian Rybushka Formation at Malaya Serdoba in Penza Province and described as a new species, *Ornithostoma orientalis* (Bogolyubov, 1914). At that time, *Ornithostoma* was considered a senior subjective synonym of *Pteranodon* (Williston, 1895, 1896, 1897). Now *Ornithostoma* is established as a valid taxon of non-azhdarchid azhdarchoids (Averianov, 2012). Later it was assumed that the vertebra from Malaya Serdoba belonged to an azhdarchid pterosaur, and the species ‘*Ornithostoma*’ *orientalis* was erected to a new genus, *Bogolubovia* (Nesov & Yarkov, 1989). Here, more than 100 years after the discovery of *Pteranodon* in the Late Cretaceous of Russia was announced, we describe several pterosaur specimens from the same Campanian Rybushka Formation that are attributable to the Pteranodontidae. These specimens come from the Beloe Ozero locality in Saratov Province, which is now the biggest pterosaur locality in Russia. All previously described pterosaur specimens from the Beloe Ozero locality were referred to the Azhdarchidae (Averianov, 2007; Averianov & Panteleyev, 2009; Averianov & Popov, 2014; Averianov *et al.*, 2016). Some of these and newly collected specimens are now referred to the Pteranodontidae and described in this paper. *Volgadraco bogolubovi*, described from the Rybushka Formation at the Shyrokii Karamysh locality and initially referred to Azhdarchidae (Averianov *et al.*, 2008), is reassigned here to the Pteranodontidae. *Bogolubovia orientalis* might also be a pteranodontid. We also review other putative records of the Pteranodontidae worldwide.

2. Materials and methods

The first pterosaur bones from the Beloe Ozero locality were collected by EV Popov in 2003. In 2017–19, large-scale excavations at this locality were conducted by Saratov State Technical University under licence SRT 01881 PD. Most pterosaur bones described in this paper were found during these excavations. All pterosaur specimens from Beloe Ozero are housed in the Zoological Institute, Russian Academy of Sciences, in Saint Petersburg (collection ZIN PH 43). The anatomical nomenclature generally follows that in Averianov (2010). For description and measurements, the wing bones are oriented in flight position.

2.a. Geological setting

The locality Beloe Ozero is situated in the Lysogorskii District of Saratov Province, 78 km SW of Saratov city (Fig. 1). The locality is a natural outcrop of Upper Cretaceous sediments, which are exposed on the right side of the Golyi Ravine, extending from the village of Beloe Ozero, in a SE direction to a distance of c. 4 km. The Upper Cretaceous deposits at Beloe Ozero are attributed to the Rybushka Formation of a local stratigraphic scale.

The Rybushka Formation has yielded belemnites (*Belemnelloca-max mammillatus*, *Belemnitella mucronata*), ammonites (*Hoplitoplacenticeras* sp.), bivalves (*Oxytoma psilomonica*, *O. tenuicostata*, *Cataceramus balticus*, *C. regularis*), and foraminifera of the regional zone *Brotzenella monterelensis* and subzone *Cibicidoides aktulagayensis*. The Rybushka Formation also produced teeth and bones of bony fishes (Acipenseridae, Enchodontidae), shark teeth (*Cretolamna appendiculata*, *Squalicorax kaupi*, *Pseudocorax laevis*, *Archaeolamna kopingsensis*, *Eostriatolamia* sp., *Heterodontus* sp., *Squatina hasei*, *Squatirhina* sp.), and dental plates of chimaeras (*Ischyodus bifurcatus*, *Amylodon karamysh*, *Edaphodon* sp., *Elasmodus* sp.). Rare bones of reptiles (plesiosaurs, mosasaurs, sea turtles, pterosaurs) and birds (*Hesperornis*) are also known from this formation (Averianov *et al.*, 2005, 2016; Olfieriev & Alekseev, 2005; Arkhangelsky *et al.*, 2007; Averianov, 2008; Seltser & Ivanov, 2010; Averianov & Popov, 2014; Grigoriev *et al.*, 2015; Zelenkov *et al.*, 2017; Danilov *et al.*, 2018; Zverkov *et al.*, 2018).

Within the locality, facial changes of the layers and their thickness are recorded. Deposits of the Rybushka Formation are represented here by five layers (description from bottom to top).

Layer 1. Green-grey, quartz–glauconitic, medium-grained sand. Some levels are strongly compacted to the state of loose sandstone. In the layer are very rarely found light brown, rounded phosphorites up to 1 cm in size. In places, the layer is stained brown with iron hydroxide. Rare weakly phosphatized bones of marine reptiles and fish are found in levels of loose sandstone. The apparent thickness of the layer is c. 13 m.

Layer 2. Phosphorite horizon. Brown and dark brown, poorly sabulous, irregularly shaped phosphorite nodules up to 3.5 cm in size. Along the strike, phosphorite inclusions are distributed non-uniformly, forming in places lenticular aggregations or, on the contrary, wedging out. In some sites, the horizon is non-uniformly stained with brownish-red spots of iron hydroxide. Rare silicified dolomite pebbles up to 8 cm in size are found in the layer. The horizon is cemented in places. Cementing material – ferruginous and psammitic components. The lower surface of the layer is uneven and pit-like. Numerous teeth and vertebrae of sharks, fin spikes and dental plates of chimaeras, remains of a large sturgeon and salmoniform fishes, bones and teeth of reptiles, and numerous shark coprolites reaching lengths of up to 8 cm are found in the layer. Layer thickness up to 0.2 m.

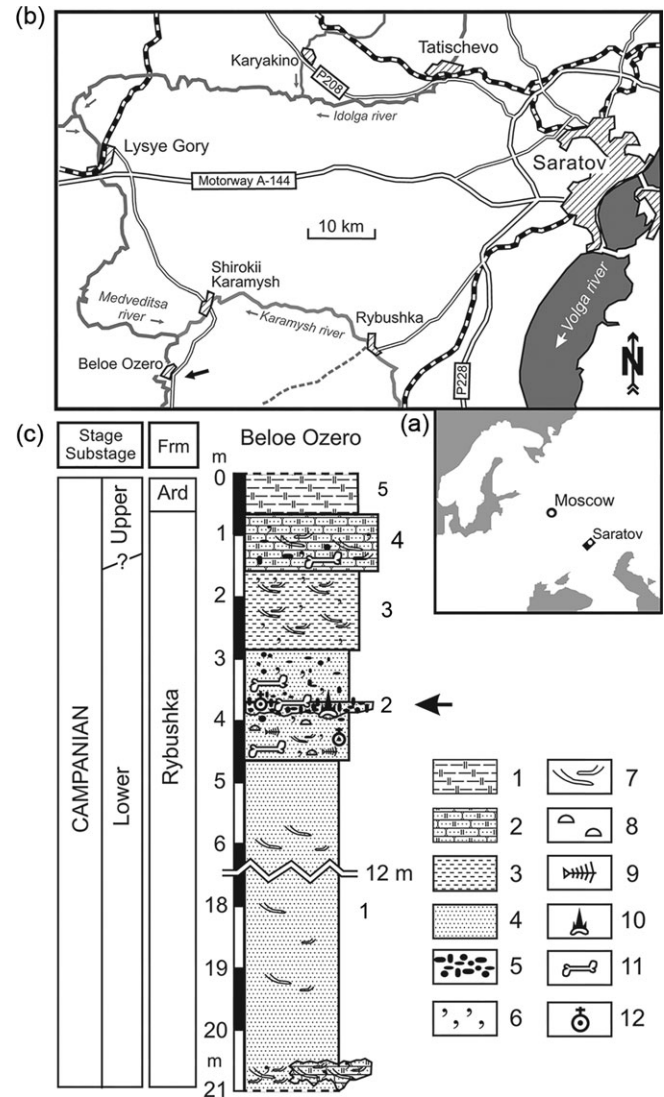


Fig. 1. Geographic position and geological section of Beloe Ozero locality. (a) Map of Eastern Europe showing position of the inset (b). (b) Map of vicinity of Saratov city, with Beloe Ozero locality indicated by arrow. (c) Geological section at Beloe Ozero locality. The fossil-bearing level is indicated by arrow. Legend to the section: (1) siliceous clay, (2) siliceous sandstone, (3) silty sand, (4) inequigranular sand, (5) phosphorite nodules, (6) glauconite, (7) bioturbation, (8) thin-walled shells of linguliform brachiopods, (9) scales and bones of small teleostean fishes, including those in (?) decapod burrows, (10) chondrichthyan (sharks and chimaeroids) remains, (11) marine tetrapod remains; (12) pterosaur remains. Abbreviation: Ard, Ardym Formation. Modified after Zverkov *et al.* (2018).

Layer 3. Green-grey, quartz–glauconitic, medium-grained sand. Over the entire layer, dark brown phosphorite inclusions up to 2 cm in size and ferriferous inclusions up to 10 cm in size are regularly scattered. Rare, weakly phosphatized bones of marine reptiles and fish are found at the base of the layer. The thickness of the layer is c. 1.5 m.

Layer 4. Green-grey, quartz–glauconitic, calcareous, fine-grained sandstone. Subhorizontally oriented moulds of crustacean burrows occur at the base of the layer. The contact with the underlying layer is gradual. Rare weakly phosphatized bones of marine reptiles and fish come across in the layer. The thickness of the layer is c. 1.2 m.

Layer 5. Dark grey with light grey areas clayey silicite, with a small admixture of quartz–glauconitic fine-grained sand. Contact with the underlying layer is prominent. The thickness of the layer is c. 1 m.

The thalweg of the ravine is composed of varying degrees of rounded sandstone fragments and sand. It contains abundant moulds of crustacean burrows, teeth and coprolites of fishes, and less frequent reptile bones.

All the specimens described in the paper were collected in the headwaters of the ravine, in the abandoned quarry for the extraction of flint and sandstone. The bones come from the phosphorite horizon (layer 2).

2.b. Institutional abbreviations

FHSM: Fort Hays State Museum, Fort Hays State University, Hays, Kansas, USA.

HMG: Hobetsu Museum, Hobetsu, Hokkaido, Japan.

LINHM: Long Island Natural History Museum, New York, USA.

MTM: Hungarian Natural History Museum, Budapest, Hungary.

NHMUK: Natural History Museum, London, United Kingdom.

NSM PV: National Science Museum, Tokyo, Japan.

PU: Museum of Natural History, Princeton University, New Jersey, USA.

TMM: Texas Memorial Museum, Austin, Texas, USA.

TMP: Royal Tyrell Museum of Paleontology, Drumheller, Canada.

USNM: United States National Museum, Washington, USA.

ZIN PH: Palaeoherpological collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

3. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Pteranodontidae Marsh, 1876

Pteranodontidae indet.

Figs 2–7

Azhdarchidae indet.: Averianov & Popov (2014: fig. 2).

3.a. Material

ZIN PH 64/43, middle cervical vertebra. ZIN PH 55/43, free dorsal vertebra. ZIN PH 72/43, left scapula distal fragment. ZIN PH 75/43, right deltopectoral crest; ZIN PH 74/43, right proximal syncarpal. ZIN PH 76/43, left preaxial carpal. ZIN PH 66/43, left femur.

3.b. Description

In the middle cervical vertebra ZIN PH 64/43, the cotyle is pentagonal, with a straight dorsal margin and a ventral angle extending onto the very large hypapophysis (Fig. 2). The cotyle width is almost twice its height. The preexapophyses are not preserved. The missing prezygapophyses were placed mostly lateral to the cotyle. On the ventral centrum surface, there is a short ridge extending posteriorly from the hypapophysis. Lateral to the hypapophysis there is a paired pneumatic foramen close to the anterior margin of the centrum. The ventral centrum surface lateral to the midline is flat or slightly concave. The neural arch (excluding the unknown neural spine) is low anteriorly and very high posteriorly, with the postzygapophyses placed higher than the prezygapophyses (missing). There is a relatively large oval-shaped pneumatic foramen on the lateral side of the neural arch anteroventral to the postzygapophysis. The neural canal is almost round; its

anterior and posterior openings are similar in size. On the posterior side, the pneumatic foramina lateral to the neural canal are relatively large, almost half the size of the neural canal. They are oval-shaped. The left lateral pneumatic foramen is oriented horizontally, while the right one is almost vertical. The posterior opening of the neural canal extends dorsal to the left lateral pneumatic foramen, but it is ventral to the dorsal margin of the right lateral pneumatic foramen. The posterior opening of the neural canal and lateral pneumatic foramina are situated in a flat triangular area facing posteroventrally. This area is limited dorsally by a faint ridge which extends laterally towards the postzygapophysis. Above this triangular area and dorsal to the posterior opening of the neural canal, there is a small concave area delimited laterally by a vertical ridge. The postzygapophysis is almost round, slightly concave and faces posterolaterally. The epiphysis projects posterolaterally. It has a bump on its posterior side. The neural arch length is 35.1 mm; the minimum width of the neural arch is 28.2 mm.

The free dorsal vertebra ZIN PH 55/43 is described in Averianov & Popov (2014: pp. 327–8, fig. 2).

The scapular distal fragment ZIN PH 72/43 is flattened dorsoventrally (Fig. 3). Its distal part is somewhat twisted to the proximal part. The distalmost part of the scapular blade has a triangular cross-section, with a flat dorsal side and a longitudinal ridge on the ventral side. The anterior margin of the scapula is thick. Posterior to the median ventral ridge, the depth of the scapula steadily decreases and the posterior end is very thin. In dorsal/ventral view the scapula widens proximally. At the beginning of the proximal widening on the dorsal surface, there is a distinct longitudinal depression. At the anteroproximal end of the preserved fragment, there is a large bump-like scapular tubercle. In the middle of the anteroventral margin of the scapular blade, there is a cleft-like longitudinal depression. There is a prominent longitudinal muscle scar proximal to this depression. There is also an oblique muscle scar on the ventral side of the scapular blade. The supraneural plate articulation is set at an angle to the scapular blade. The scapular blade needs to be oriented dorsomedially to have the supraneural articulation surface vertical. The supraneural plate articulation surface is D-shaped, with flat dorsal margin and convex ventral margin. The articulation surface is slightly convex.

The deltopectoral crest ZIN PH 75/43 belongs to a large specimen. The deltopectoral crest is relatively short, deflecting ventrally and distally at its anterior end (Fig. 4). The proximal margin is convex, converging towards the anterior end. The distal margin is concave. The proximal margin is very thin at the humeral shaft but distinctly increases in thickness towards the anterior end. The anterior end is occupied by the flattened area facing anterodorsally. This flattened area apparently served for the insertion of *m. pectoralis* (Bennett, 2003: fig. 3). The thickness of the distal margin is more constant. On the ventral side, there is a prominent short ridge for the attachment of *m. deltoideus scapularis* (Bennett, 2003: fig. 3).

The proximal syncarpal ZIN PH 74/43 is trapezoidal in the proximal/distal view (Fig. 5). In the centre of the proximal side, there is a large, round and deeply concave circular fovea for articulating with the tubercle of the ulna. Anterodorsal and anteroventral to this fovea there are two elongated and less concave articular surfaces. The dorsal facet is for the dorsal articulating facet of the ulna, and the ventral facet is for the dorsal articulation surface of the radius. The dorsal facets for the ulna and the fovea are confluent, while the ventral facet for the radius is separated from both surfaces by a high ridge. The ventral facet continues posteriorly into a smaller articulation surface apparently for the ventral part of the ulna. The two surfaces are partially separated dorsally by

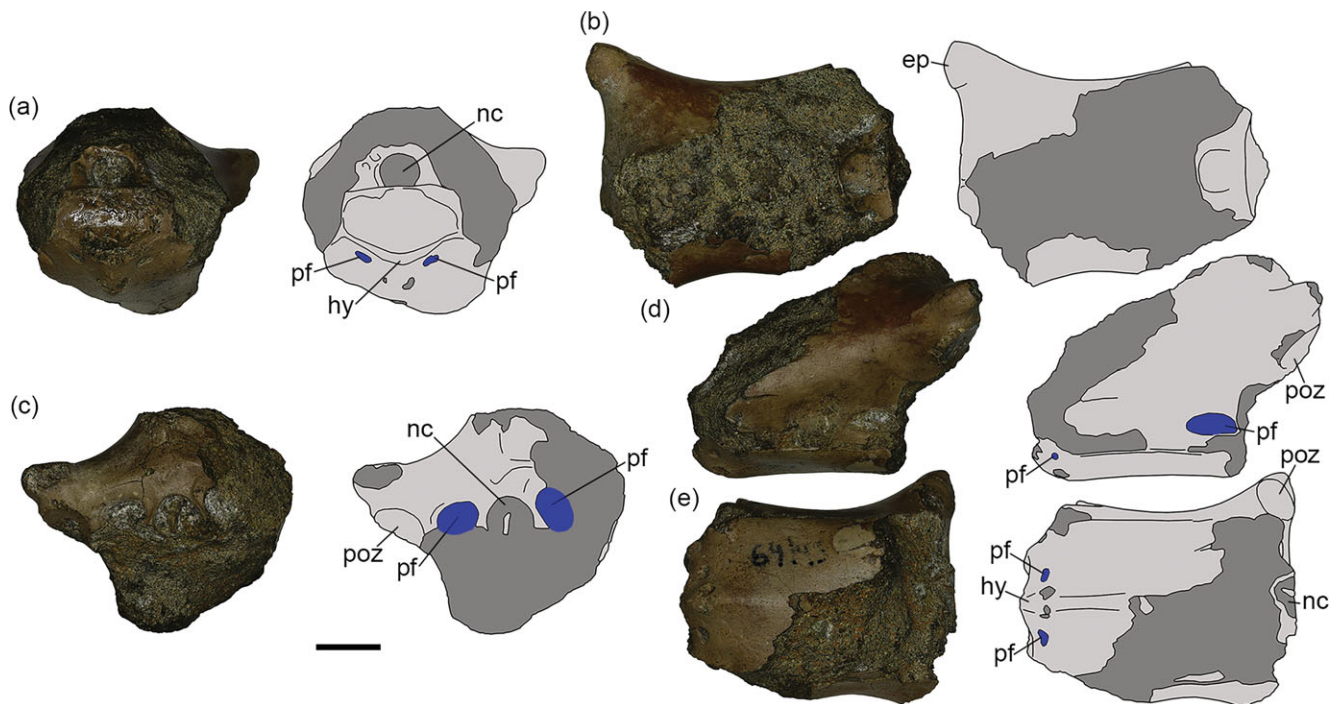


Fig. 2. (Colour online) Pteranodontidae indet., ZIN PH 64/43, incomplete cervical 3, in anterior (a), dorsal (b), posterior (c), lateral (d) and ventral (e) views. Photographs and explanatory drawings. Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Upper Cretaceous (Campanian). Abbreviations: ep, epiphysis; hy, hypapophysis; nc, neural canal; pf, pneumatic foramen; poz, postzygapophysis. Scale bar equals 10 mm.

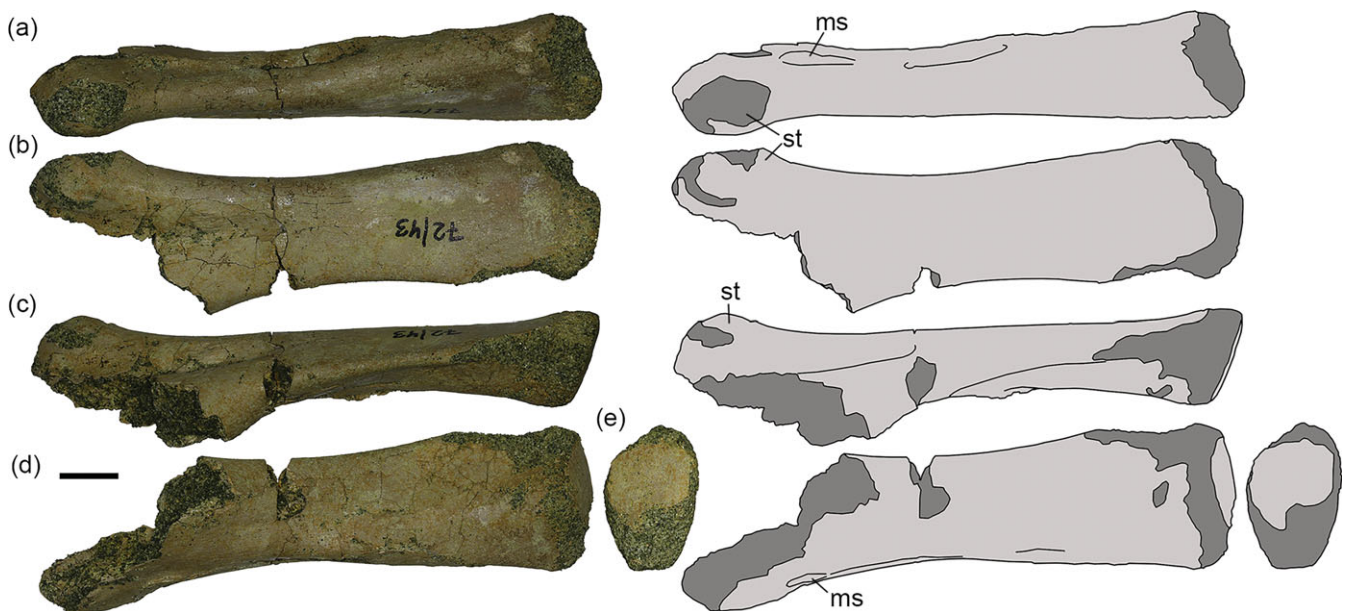


Fig. 3. (Colour online) Pteranodontidae indet., ZIN PH 72/43, distal fragment of right scapula, in anterior (a), dorsal (b), posterior (c), ventral (d) and distal (e) views. Photographs and explanatory drawings. Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Upper Cretaceous (Campanian). Abbreviations: ms, muscle scar; st, scapular tubercle. Scale bar equals 10 mm.

the fovea, and between them and the fovea there is a small pneumatic foramen. Posterior to the fovea and dorsal to the ventral ulna facet there is a round distinct flat eminence: the tuberculum articulating with the fovea on the distal surface of the ulna. Posterior to the dorsal part of the dorsal facet there is a prominent ridge directing posteroventrally and ending in the flexor tendon process. This ridge forms the most elevated surface of the proximal side of

the proximal syncarpal. It is separated from the fovea by a flat area. The distal side of the bone is largely occupied by the intersyncarpal articulation facet which is separated by an oblique ridge into larger posterior and smaller anterior parts. This ridge is oriented antero-dorsally–posteroventrally and consists of two portions separated by a sulcus. The larger dorsal portion is part of the rim surrounding the whole anterior intersyncarpal facet. The smaller ventral portion

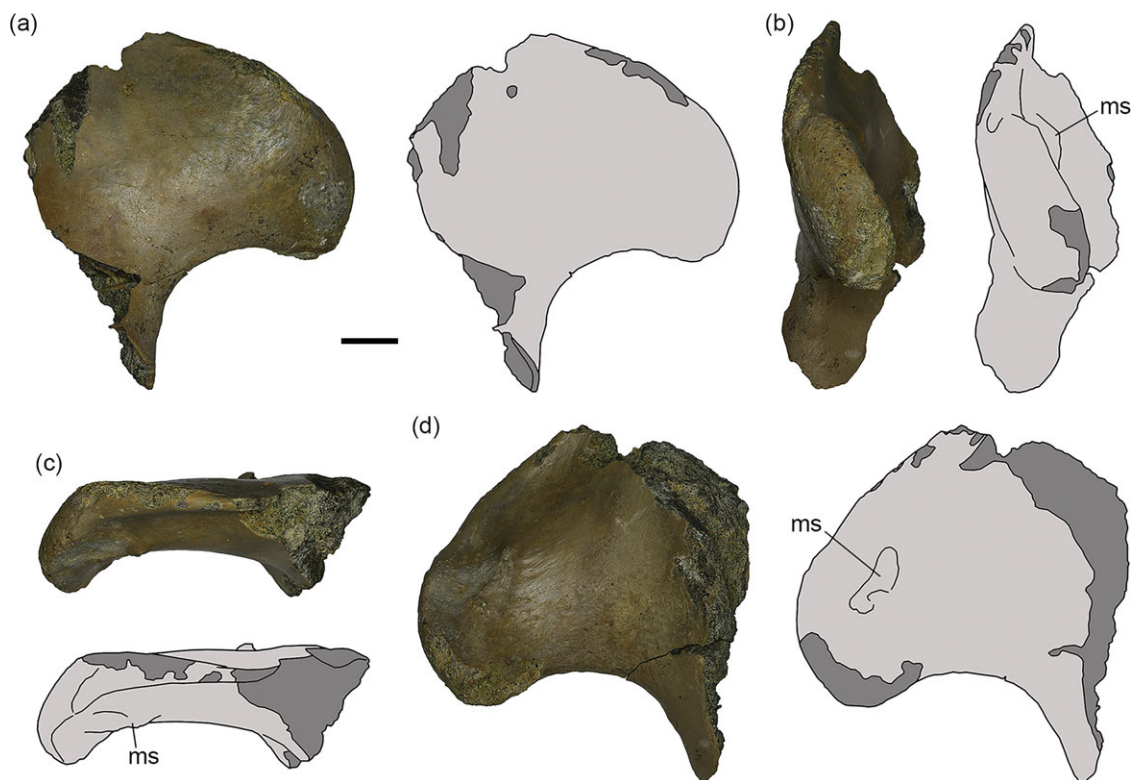


Fig. 4. (Colour online) Pteranodontidae indet., ZIN PH 75/43, deltopectoral crest of right humerus, in dorsal (a), anterior (b), proximal (c) and ventral (d) views. Photographs and explanatory drawings. Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Upper Cretaceous (Campanian). Abbreviations: ms, muscle scar. Scale bar equals 10 mm.

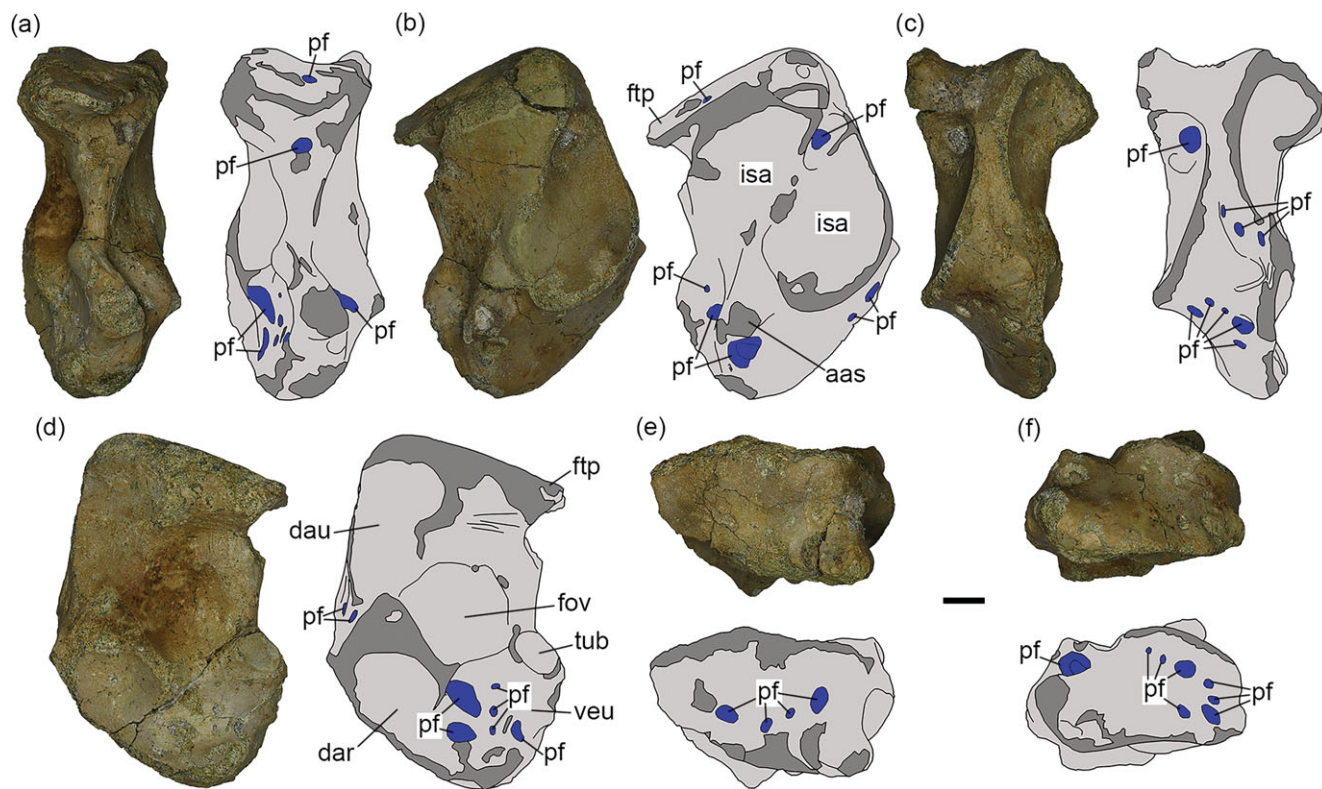


Fig. 5. (Colour online) Pteranodontidae indet., ZIN PH 74/43, right proximal syncarpal, in anterior (a), distal (b), posterior (c), proximal (d), dorsal (e) and ventral (f) views. Photographs and explanatory drawings. Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Upper Cretaceous (Campanian). Abbreviations: aas, accessory articulation surface; dar, articulation surface for radius; dau, facet for dorsal articulation surface of ulna; fov, fovea, facet for ulnar tuberculum; ftp, flexor tendon process; isa, intersyncarpal articulation surface; pf, pneumatic foramen; tub, tuberculum for the ulnar fovea; veu, facet for ventral articulation surface of ulna. Scale bar equals 10 mm.

is a short ridge forming a prominent tubercle at the end. Dorsal and ventral to this tubercle there are two large pneumatic foramina (the dorsal one is somewhat larger and oval). The dorsal portion of the ridge separating the intersynsarpal articulation surfaces terminates anteriorly in a much larger tubercle. Ventral to this tubercle, on the dorsal margin of the anterior intersynsarpal articulation surface, there is a large round pneumatic foramen. The anterior intersynsarpal articulation surface is teardrop-shaped, with a rounded ventral margin and converging dorsally anterior and posterior margins. A prominent subhorizontal ridge bordering the posterior intersynsarpal articulation surface dorsally divides in its posterior part into two ridges. The ventral ridge extends posteroventrally and borders the posterior intersynsarpal articulation surface for some distance (there is no ridge along its short posterior margin). The dorsal ridge extends posterodorsally onto the flexor tendon process. Between the two ridges, there is a deep posteriorly widening groove. Within this groove, close to the ventral ridge, there is a large pneumatic foramen. The anterior and posterior sides of the proximal syncarpal are very narrow. The dorsal side of the proximal syncarpal is more or less flat. The larger ventral side of the proximal syncarpal is convex anteroposteriorly and concave proximodistally. There are four pneumatic foramina of different sizes in the anterior half of this ventral side. The ventral side is bordered by a slight ridge from the anterior side of the bone. The anteroposterior diameter 60.4 mm; dorsoventral height 83.7 mm.

The preaxial carpal ZIN PH 76/43 is complete, with some bone surface eroded on the ventral surface (Fig. 6). The bone is triangular in dorsal/ventral view, with the anterior end deflecting distally. The proximal margin is convex and the distal margin is concave. Most of the posterior surface is occupied by an oval-shaped concave articulation surface for the preaxial carpal process of distal syncarpal. The proximodistal diameter of this surface is about twice its dorsoventral height. There is also a short distal process on the posterior side of the bone. On the ventral side, there is a large pneumatic foramen adjacent to the articulation surface and subdivided by bony septa. There are also several slit-like small pneumatic foramina along the distal bone margin on the ventral surface. The anterior half of the bone dorsal surface is occupied by the elongated concavity of the terminal process. This surface is separated from the rest of the bone by a groove on the proximal side. The poorly defined facet for the pteroid is at the distal margin of the ventral surface. The preserved dorsal surface is flat. The anteroposterior diameter 22.7 mm; mediolateral width 13.5 mm; dorsoventral height 33.4 mm.

ZIN PH 66/43 is an almost complete femur; only a small piece of the diaphysis near the distal end is missing (Fig. 7). The femoral head is globular, with a round articulation surface. It is placed on a relatively long neck which is similar in width to the head anteroposteriorly but distinctly narrower mediolaterally. The neck is oriented at an angle of 39° to the longitudinal axis of the diaphysis proximal portion. The greater trochanter is relatively low. On the posterior side between the greater trochanter and the femoral neck, there is intertrochanteric depression with a large pneumatic foramen in the centre. This depression is bordered laterally by a prominent crest that is connected with the greater trochanter dorsally. The lateral side of the diaphysis adjacent to this crest is depressed.

There is a prominent rugosity along the anterolateral margin of the diaphysis distal to the greater trochanter ('lesser trochanter' for insertion of *m. iliofemoralis internus*). On the anterior side of the diaphysis, medial and parallel to this rugosity, there is a linear muscle scar which extends further distally on the diaphysis.

The diaphysis is sigmoidal in both anterior–posterior and medial–lateral views. The diaphysis in the middle has a slightly convex anteromedial side and a more convex opposite side. The diaphysis widens distally where it has a triangular cross-section with a flat anterior side. There is a prominent longitudinal muscle scar along the posteromedial margin of the middle diaphysis. The mediolaterally narrowest point of the diaphysis is situated well dorsal to its middle height.

The distal epiphysis is asymmetrical in distal view, with the medial condyle extending more anteriorly and the lateral condyle extending more laterally and posteriorly. Both condyles are separated anteriorly and distally by a very shallow intercondylar sulcus. There is a round depression within the intercondylar sulcus in the middle of the distal epiphysis. There are three small pneumatic foramina within this depression. Posteriorly the two condyles are separated by two depressions with a longitudinal ridge between them. The popliteal fossa is very shallow and poorly defined. On the medial condyle near the anterior end, there is a small circular depression. The articulation surface of the medial condyle is convex distally and concave posteriorly. The articulation surface of the lateral condyle is flat distally and posteriorly. On the lateral surface of the lateral condyle, there is a short crest, which is oriented anteroposteriorly. The total length 238 mm; proximal anteroposterior diameter 15.5 mm; proximal width 32.2 mm; distal anteroposterior diameter 30.9 mm; distal width 40.0 mm.

3.c. Comparison

Cervical ZIN PH 64/43 is similar in proportions to the cervical 3 of *Pteranodon* (Bennett, 2001a: fig. 33B), but has a more posterior position of the lateral pneumatic foramen and relatively higher postzygapophysis, which more closely match the condition of more elongated middle cervicals of *Pteranodon* (Bennett, 2001a: fig. 37B). In *Pteranodon* the postaxial cervical vertebrae have a pair of pneumatic foramina lateral to the neural canal and a median pneumatic foramen above the neural canal on both anterior and posterior sides of the neural arch (Bennett, 2001a: p. 43). On the posterior side of the neural arch in the axis of *Pteranodon*, the lateral pneumatic foramina are small and placed mostly dorsal to the neural canal, and the median pneumatic foramen is absent (Bennett, 2001a: figs 34B, 35B). In ZIN PH 64/43, one lateral pneumatic foramen extends dorsally to the neural canal and the median pneumatic foramen is absent.

ZIN PH 64/43 is similar to the cervical 3 in the pteranodontid *Volgadraco* (Averianov *et al.*, 2008: pl. 5, fig. 2) by general proportions (short and wide), by straight dorsal margin of the cotyle, by large hypapophysis, by postzygapophyses placed on the neural arch higher than the prezygapophyses, and by a pneumatic foramen on the lateral side of the neural arch. It differs by pits on the ventral centrum side lateral to the hypapophysis, by smaller pneumatic foramina lateral to the posterior opening of the neural canal (larger than the neural canal in *Volgadraco*), by a much weaker and more oblique ridge above the posterior opening of the neural foramen and collateral pneumatic foramina, and by lack of a strong vertical ridge dorsal to the posterior opening of the neural canal.

A pteranodontid cervical HMG 1052 from the Campanian Hakobuchi Group at Enbetsu, Hokkaido, Japan (Chitoku, 1996: figs 2–4), is very similar to ZIN PH 64/43 in short and wide proportions, postzygapophysis placed higher than the prezygapophyses, pneumatic foramen on the lateral side of the neural arch, shape of the anterior and posterior openings of the neural canal, and size

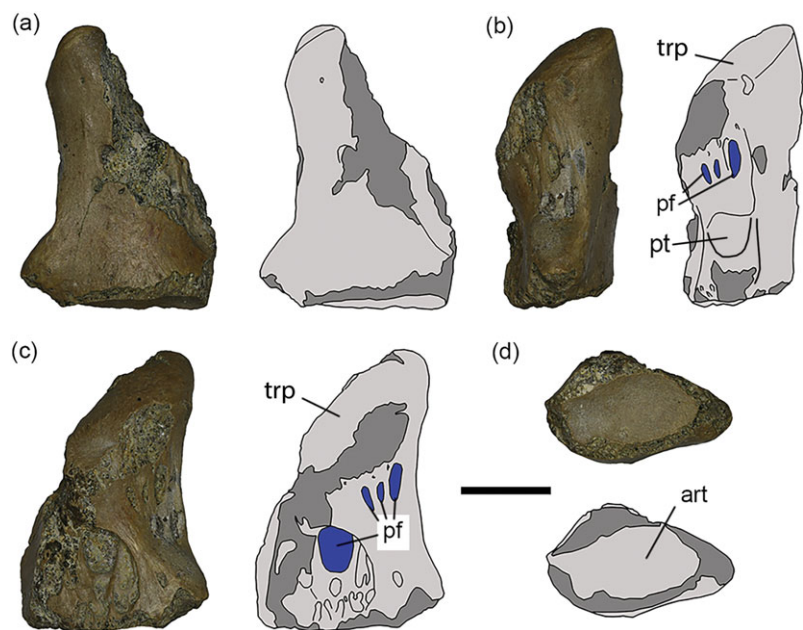


Fig. 6. (Colour online) Pteranodontidae indet., ZIN PH 76/43, left preaxial carpal, in dorsal (a), distal (b), ventral (c) and posterior (d) views. Photographs and explanatory drawings. Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Upper Cretaceous (Campanian). Abbreviations: art, articulation surface for preaxial carpal process of distal syncarpal; pf, pneumatic foramen; pt, facet for pteroid; trp, terminal process. Scale bar equals 10 mm.

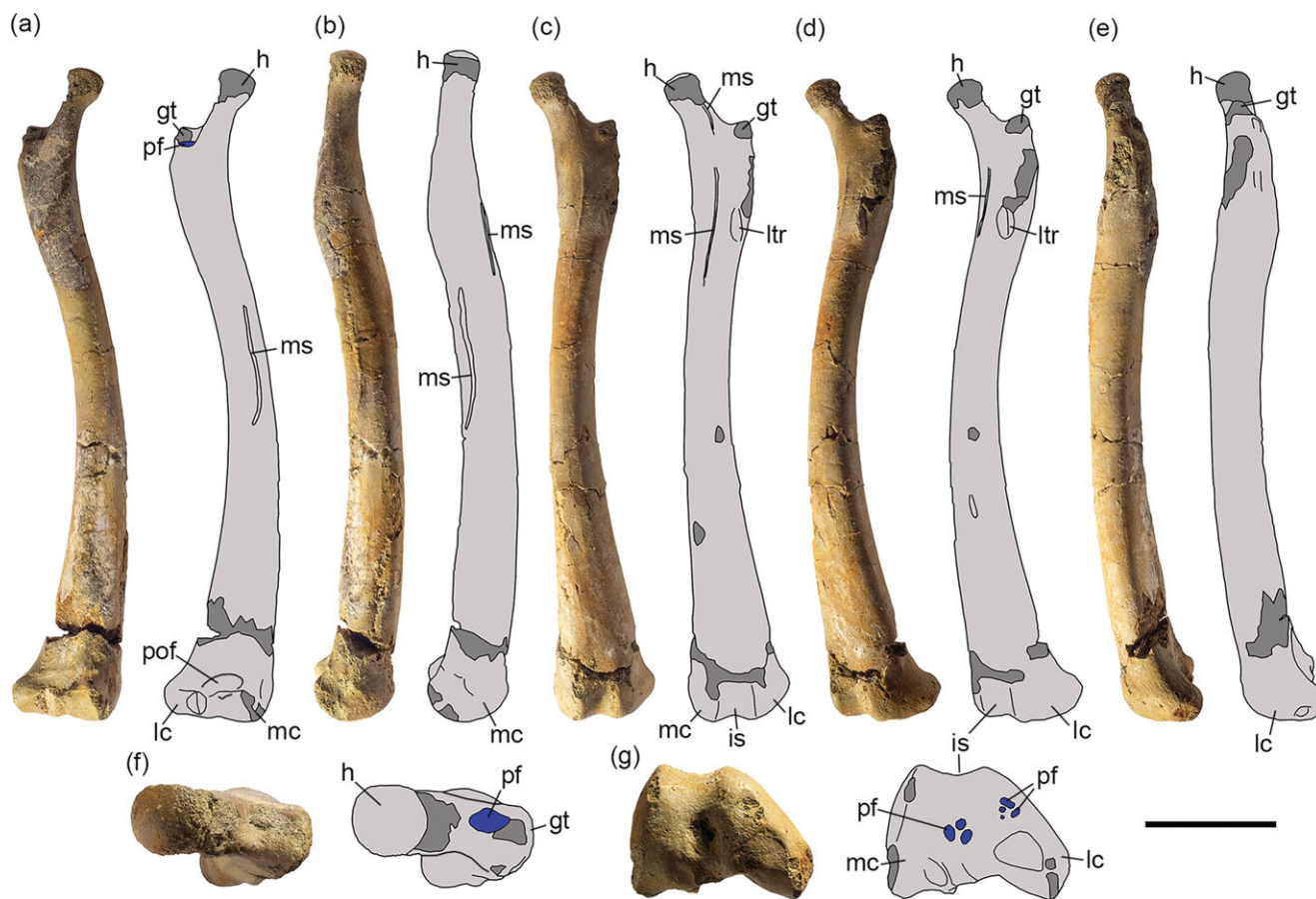


Fig. 7. (Colour online) Pteranodontidae indet., ZIN PH 66/43, left femur, in posterior (a), medial (b), anterior (c), anterolateral (d), lateral (e), proximal (f) and distal (g) views. Photographs and explanatory drawings. Beloe Ozero, Saratov Province, Russia; Rybushka Formation, Upper Cretaceous (Campanian). Abbreviations: gt, greater trochanter; h, femoral head, is, intercondylar sulcus; lc, lateral condyle; ltr, lesser trochanter; mc, medial condyle; ms, muscle scar; pf, pneumatic foramen; pof, popliteal fossa. Scale bar equals 50 mm (for (a)–(e)). (f) and (g) are not to scale.

and relative position of the pneumatic foramina lateral to the posterior opening of the neural canal.

A pteranodontid middle cervical vertebra PU 21820 from the Campanian Merchantville Formation at Marshalltown, Delaware, USA (Baird & Galton, 1981: fig. 2; Bennett, 1994), is relatively longer than ZIN PH 64/43 but similarly wide. It likely had a similarly large hypapophysis which is mostly destroyed. The hypapophysis continues posteriorly into a median ridge, as in ZIN PH 64/43. The dorsal side of the cotyle is convex (straight in ZIN PH 64/43). There is a pneumatic foramen on the lateral side of the neural arch, as in ZIN PH 64/43.

The middle cervical vertebra NHMUK R16479a, b from the Coniacian Chalk Formation at Hope Point, England, United Kingdom (Martill *et al.*, 2008: figs 3–6), was identified initially as belonging to a non-azhdarchid azhdarchoid. This specimen is very similar to ZIN PH 64/43 in proportions (short and wide), in having a large hypapophysis extending posteriorly into a median ridge, a pneumatic foramen on the lateral side of the neural arch, and lateral pneumatic foramina at the level of the middle height of the posterior opening of the neural canal. NHMUK R16479a, b differs from ZIN PH 64/43 by a concave dorsal margin of the cotyle.

In the azhdarchid *Azhdarcho*, there is no cervical vertebra that would match ZIN PH 64/43 in proportions (Averianov, 2010). This specimen differs additionally from the postaxial vertebrae of Azhdarchidae by the presence of the pneumatic foramen on the lateral side of the centrum.

An elongated middle cervical vertebra LINHM 014 of an azhdarchid from the Cenomanian Kem Kem beds of Morocco (Rodrigues *et al.*, 2011: fig. 4) is likely a cervical 4. It is much longer and narrower than ZIN PH 64/43, with a lower neural arch. It is similar to ZIN PH 64/43 in having a paired pneumatic foramen on the ventral centrum side lateral to the hypapophysis, although in the specimen from Beloe Ozero the foramen is smaller. This foramen has not been recorded in other pterodactyloids and its systematic value is unclear.

The free dorsal vertebra ZIN PH 55/43 was differentiated from the dorsal vertebrae in *Pteranodon* by transversely wider centrum, presence of hypapophysis, and the larger pneumatic foramen at the base of the prezygapophysis. However, all these characters are present in a three-dimensionally preserved free dorsal vertebra USNM 11642 of *Pteranodon longiceps* from the Niobrara Formation, Kansas, USA (personal observation by A.A.). These two specimens are nearly identical. In ZIN PH 55/43 there is a slit-like foramen on the dorsal side of the centrum. This foramen is characteristic of the free dorsal vertebrae of *Pteranodon* (Bennett, 2001a: p. 51). This foramen is slit-like in ZIN PH 55/43 but round in USNM 11642. In *Azhdarcho* there is a large depression that occupies most or all of the ventral floor of the neural canal (ZIN PH collection). Averianov & Popov (2014) noted that ZIN PH 55/43 is almost identical to the posterior centrum surface of the notarium fragment of *Volgadraco bogolubovi* from the Rybushka Formation of the Shyrokii Karamysh locality (Averianov *et al.*, 2008: pl. 6, fig. 1b) and concluded that this specimen likely belongs to *V. bogolubovi*. This conclusion is followed here, taking into account that *Volgadraco* is reassigned here to the Pteranodontidae.

The distal fragment of scapula ZIN PH 72/43 is similar in proportions to the scapula of an adult specimen of *Pteranodon*, including the position of the scapular tubercle and the orientation of the articulation facet for the notarium (Bennett, 2001a: fig. 65). Distal scapula morphology is poorly known in the Azhdarchidae.

Padian (1984) and Bennett (1989) considered the form of the deltopectoral crest of the humerus to be diagnostic for the Pteranodontidae. Because of the flattened preservation of most *Pteranodon* specimens, these authors referred to the condition of three-dimensionally preserved proximal humerus fragment USNM 13804 from the Turonian Eagle Ford Group in Texas, USA (Gilmore, 1935; Bennett, 1989: fig. 2, 1–5; 1994). However, this specimen is a non-istiodyctid ornithocheiroid rather than a pteranodontid (Andres & Myers, 2013). Unwin (2003) considered humerus with warped deltopectoral crest a synapomorphy for the Ornithocheiroidea. The deltopectoral crest ZIN PH 75/43 is markedly different from that crest in the Azhdarchidae. In azhdarchids, the deltopectoral crest is much longer and has subparallel proximal and distal margins for most of its length (Lawson, 1975: fig. 1b, c; Buffetaut *et al.*, 2003: fig. 6; Averianov, 2010: fig. 23G, H; Hone *et al.*, 2019: fig. 2).

ZIN PH 74/43 is the largest proximal syncarpal known for the Pterosauria. The shape of the proximal syncarpal and distribution of the articulations surfaces is quite variable in the Pterodactyloidea (Fig. 8a). ZIN PH 74/43 matches closely in proportions the proximal syncarpal of *Pteranodon* (Fig. 8b). It differs from the proximal syncarpal in *Pteranodon* mostly by the relatively larger fovea. In ornithocheirids, the dorsal portion of the proximal syncarpal is distinctly narrower and the flexor tendon process is less prominent (Fig. 8c–f). In the Dsungaripteridae the flexor tendon process is further reduced, the fovea is larger, the radius and ventral ulna articulation surfaces are merged and there are no pneumatic foramina (Fig. 8g). The proximal syncarpal of azhdarchids is similar to that bone in the Dsungaripteridae but has a large pneumatic foramen ventral to the fovea (Fig. 8h).

The preaxial carpal ZIN PH 76/43 is generally similar to that bone in *Pteranodon* (Bennett, 2001a: fig. 81). The preaxial carpal is unknown for the Azhdarchidae. ZIN PH 183/44, identified previously as a preaxial carpal of *Azhdarcho* (Averianov, 2010: fig. 29), is an ulna fragment.

The femur ZIN PH 66/43 is similar to that bone in *Pteranodon* (Bennett, 2001a: fig. 107) in having asymmetrical distal condyles. It differs by more pronounced sigmoidal curvature of the bone, lack of internal trochanter, and distribution of muscle scars. ZIN PH 66/43 is almost identical to the distal femur fragment NSM PV15005 of Pteranodontidae indet. from the Santonian–Campanian Yezo Group in Hokkaido, Japan (Kellner *et al.*, 2016: fig. 4A). It differs by slightly deeper round depression with pneumatic foramen in the centre of the intercondylar sulcus.

ZIN PH 66/43 differs from the femur in *Azhdarcho* (Averianov, 2010: fig. 34) by lack of the internal trochanter and by asymmetrical distal diaphysis, with the lateral condyle extending more laterally and posteriorly. A distal femur fragment TMP 91.36.616 from the Campanian Provincial Park Formation at Dinosaur Provincial Park, Alberta, Canada (Godfrey & Currie, 2005: fig. 16.10 B–D), is similar to that of *Azhdarcho* in having symmetrical distal condyles of roughly similar size but differs in the distal end more expanded anteroposteriorly than mediolaterally. Femora of *Azhdarcho* and TMP 91.36.616 differ from ZIN PH 66/43 by more distinct popliteal fossa.

ZIN PH 66/43 differs from the proximal femur in *Quetzalcoatlus* (TMM 42422–27) by femoral head less expanded mediolaterally, femoral neck relatively longer and gracile, and by the pneumatic foramen on the posterior side placed more

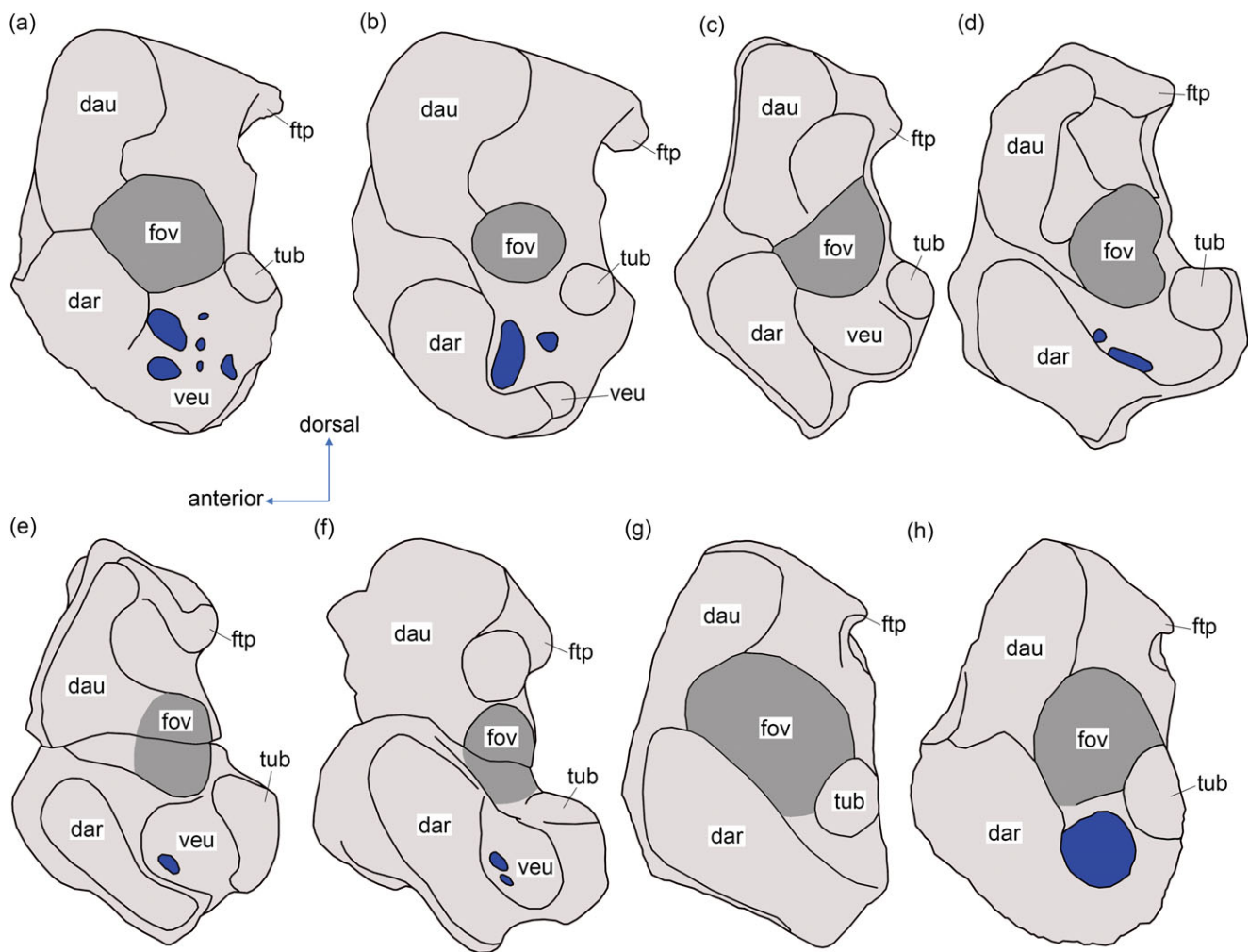


Fig. 8. (Colour online) Right proximal syncarpal in proximal view. (a) Pteranodontidae indet., ZIN PH 74/43. (b) *Pteranodon* sp., after Bennett (2001a: fig. 79C), flipped horizontally. (c) *Santanadactylus pricei*, after Wellnhofer (1991: fig. 29d). (d) *Santanadactylus araripensis*, after Wellnhofer (1985: fig. 11f). (e) *Anhanguera santanae*, after Wellnhofer (1985: fig. 38f). (f) *Anhanguera piscator*, after Kellner & Tomida (2000: fig. 36b). (g) *Dsungaripterus weii*, PIN 3953/1, flipped horizontally. (h) *Azhdarcho lancicollis*, ZIN PH 94/44. Abbreviations: dar, articulation surface for radius; dau, facet for dorsal articulation surface of ulna; fov, fovea, facet for ulnar tuberculum; ftp, flexor tendon process; tub, tuberculum for ulnar fovea; veu, facet for ventral articulation surface of ulna. Not to scale.

proximally and having a round shape (cleft-like in *Quetzalcoatlus*). The femur of *Cryodrakon* (Godfrey & Currie, 2005: fig. 16.10A) is similar to *Azhdarcho* and ZIN PH 66/43 in proportions of the proximal end and similar position of the proximal pneumatic foramen.

The distal femur of *Quetzalcoatlus* (TMM 41544-27) is nearly symmetrical in distal view, but, in contrast to *Azhdarcho*, the medial condyle is distinctly larger than the lateral condyle (both condyles are of nearly the same size in *Azhdarcho*). In this respect, the femur of *Quetzalcoatlus* is markedly different from ZIN PH 66/43, where the distal end is asymmetrical and the lateral condyle is distinctly larger than the ventral condyle.

The bone fragment MTM V2010.99.1 from the Santonian Csehbanaya Formation at Inarkut Mine, Hungary, identified initially as a possible distal end of wing metacarpal of Pterodactyloidea indet. (Ősi *et al.*, 2011: fig. 3C–E), is a right femur distal fragment. It is similar to ZIN PH 66/43 in having an asymmetrical distal end, with distal condyle extending laterally. A pterosaur femur with a similarly asymmetrical distal end is known also from the Albian Alamyshik Formation at Kylodzhun, Kyrgyzstan (Averianov, 2004: fig. 1).

4. Discussion

At least two pterodactyloid taxa are present in the Campanian Rybushka Formation at the Beloe Ozero locality: Azhdarchidae and Pteranodontidae. This makes Beloe Ozero the most diverse pterosaur assemblage for the Late Cretaceous of Europe. The bones of the Pteranodontidae are described in this paper. The free dorsal vertebra ZIN PH 55/43, referred previously to the Azhdarchidae (Averianov & Popov, 2014), is attributed here to the Pteranodontidae. The uncontested specimens of the Azhdarchidae are coracoid fragments (Averianov & Panteleyev, 2009) and undescribed ilium postacetabular process (ZIN PH 73/43). There are some pterosaur bones from the Beloe Ozero locality that cannot currently be attributed to either the Pteranodontidae or Azhdarchidae: edentulous jaw fragment, scapulocoracoid fragment with glenoid, humerus proximal fragments, wing metacarpal distal fragments, and wing phalanx 1 proximal fragments. Some of these fragments were referred previously to the Azhdarchidae (Averianov, 2007; Averianov *et al.*, 2016); the other specimens are undescribed. The most intriguing findings are the scapulocoracoid fragment with flat glenoid (ZIN PH 71/43) and fragments



Fig. 9. (Colour online) Hypothetical reconstruction of a pteranodontid from the Campanian Rybushka Formation of Saratov Province, Russia, by Andrey Atuchin.

of the humerus with a convex head (ZIN PH 59/43 and others) that fit this glenoid surface. These specimens differ significantly from the morphology of the scapulocoracoid and humerus known previously for the Pteranodontidae and Azhdarchidae.

Volgadraco bogolubovi from the Rybushka Formation at Shyrokii Karamysh locality in Saratov Province, Russia, is based on edentulous rostrum fragment, cervical vertebrae 3 and 9 and posterior notarium fragment (Averianov *et al.*, 2008). The rostrum fragment (holotype) is consistent in morphology with either the Pteranodontidae or Azhdarchidae. The cervical 3 differs from the third cervical in *Azhdarcho* by proportions (short and wide), high neural arch, and pneumatic foramen on the lateral centrum side. In these characters and overall proportions, it is very close to the cervical 3 in *Pteranodon* (Bennett, 2001a: fig. 33B). The cervical 9 of *V. bogolubovi* is also very similar to that vertebra in *Pteranodon* (Bennett, 2001a: figs 42–43) in proportions and in having the large depression on the lateral side posterior to the prezygapophysis. As was noted above, the morphology of notarium is also consistent with that bone in *Pteranodon*. Based on these similarities, *Volgadraco* is referred here to the Pteranodontidae (Fig. 9). Previously, this taxon was recovered as a pteranodontoid in a phylogenetic analysis presented by Longrich *et al.* (2018). The Beloe Ozero pteranodontid might well be the same taxon as *Volgadraco bogolubovi*, but currently there are no overlapping skeletal elements between the Beloe Ozero and Shyrokii Karamysh localities to prove this.

Bogolubovia orientalis from the Rybushka Formation at Malaya Serdoba locality in Penza Province, Russia, is known from a single specimen, a posterior fragment of the cervical vertebra

(Bogolyubov, 1914; Nesov & Yarkov, 1989; Bakhurina & Unwin, 1995). The morphology of the posterior side of the cervical vertebrae is poorly known for the Pteranodontidae (Bennett, 2001a). The holotype of *B. orientalis* is similar to the cervical 3 of *V. bogolubovi* by spindle-like condyle, high postexapophyses, large neural canal, large pneumatic foramina lateral to the neural canal, lack of the median pneumatic foramen dorsal to the neural canal and strong horizontal ridge dorsal to the neural canal and side pneumatic foramina. It is possible that the holotype of *B. orientalis* belongs to the Pteranodontidae, as was initially suggested (Bogolyubov, 1914), and even to *V. bogolubovi*. This question can be solved after the discovery of complete pterosaur cervical vertebrae from the Malaya Serdoba locality and other localities of the Rybushka Formation. Additional pterosaur specimens from the Malaya Serdoba locality, an edentulous jaw fragment and wing metacarpal distal fragment (Averianov, 2007), cannot be distinguished between the Pteranodontidae and Azhdarchidae.

The Late Cretaceous Pteranodontidae with a single genus *Pteranodon* was long considered to be endemic for North America. *Tethydraco* from the Maastrichtian of Morocco is the second pteranodontid genus described so far (Longrich *et al.*, 2018). Pteranodontidae indet. were also known previously from the Santonian–Campanian of Japan (Obata *et al.*, 1972; Kellner *et al.*, 2016). The other putative records of Pteranodontidae are briefly discussed below.

The middle cervical PU 21820 from the Campanian Merchantville Formation at Marshalltown, Delaware, USA (Baird & Galton, 1981: fig. 2), is similar to middle cervicals of *Pteranodon* and differs from those in the Azhdarchidae by

proportions (relatively short and wide) and presence of a pneumatic foramen on the lateral side of the centrum. It likely belongs to a pteranodontid or even to *Pteranodon* as was previously suggested (Bennett, 1994).

The cervical HMG 1052 from the Campanian Hakobuchi Group at Enbetsu, Hokkaido, Japan (Chitoku, 1996: figs 2–4), is very similar to ZIN PH 64/43 from Beloe Ozero in short and wide proportions, lateral pneumatic foramen on centrum, and size and position of the pneumatic foramina lateral to the posterior opening of the neural canal. By these characters, this specimen is also similar to *Pteranodon* and likely belongs to the Pteranodontidae. This group was present in the Late Cretaceous of Hokkaido as it is known by material from another locality (Kellner *et al.*, 2016).

A short and wide middle cervical NHMUK R16479a, b with lateral pneumatic foramen on the centrum from the Coniacian Chalk Formation at Hope Point, England, United Kingdom (Martill *et al.*, 2008: figs 3–6), also can be attributed to the Pteranodontidae.

The distal femur fragment MTM V2010.99.1 from the Santonian Csehbanaya Formation at Inarkut mine, Hungary (Ősi *et al.*, 2011: fig. 3C–E), has an asymmetrical distal end with distal condyle extending laterally. A similar morphology is present in a distal femur fragment ZIN PH 1/43 from the Albian Alamyshik Formation at Kылodzһun, Kyrgyzstan (Averianov, 2004: fig. 1). This morphology is found in the Ornithocheiridae, *Pteranodon* and *Nyctosaurus* (Williston, 1903: pl. 43, figs 3, 10). Ornithocheiridae, however, are not known in the fossil record after the Cenomanian–Turonian faunal turnover (Averianov, 2014). While the femur from Kyrgyzstan can still belong to the Ornithocheiridae, the femur from Hungary is more likely attributable to the Pteranodontidae.

The pteranodontid pterosaur from the Beloe Ozero locality was quite a large pterodactyloid. The femur is somewhat smaller than the pteranodontid femur NSM PV15005 from the Santonian–Campanian of Japan (Kellner *et al.*, 2016): the distal femur width is 40.0 and 46.2 mm in the Russian and Japan specimens, respectively. The Japanese pteranodontid with an estimated wingspan of 6.8 m was considered the largest flying reptile from Asia (Kellner *et al.*, 2016). Using the data on the distal femur width from the cited paper, the wingspan of the Beloe Ozero pteranodontid would be 6.31 m. *Pteranodon* sp. FHSM 184 from the Niobrara Formation of Kansas, USA, with a wingspan of 6.1 m, has femur length 278 mm (Bennett, 2001b: tab. 10). By comparison with this specimen, the Beloe Ozero pteranodontid with a femur length of 238 mm would have a wingspan of 5.22 m. The measurements of the proximal syncarpal are available for the two large specimens of an ornithocheiroid *Anhanguera* with a wingspan of 4.15 and 5.00 m (Wellnhofer, 1991; Kellner & Tomida, 2000). Based on these measurements, the proximal syncarpal ZIN PH 74/43 from Beloe Ozero belongs to an individual with a wingspan of 6.48 m.

Identification of the Pteranodontidae in the Campanian Beloe Ozero locality in Saratov Province, Russia, is in line with the previous finding of North American vertebrate taxa in this locality, which include the chelonoid sea turtle Protostegidae indet. close to *Protostega gigas* (Danilov *et al.*, 2018) and the mosasaurid *Clidastes propython* (Grigoriev *et al.*, 2015). The other localities within the Rybushka Formation also produce remains of hesperornithiform birds (Zelenkov *et al.*, 2017). These data, together with the recent identification of the Pteranodontidae in the Santonian–Campanian of Japan (Kellner *et al.*, 2016 and this report), suggest a much more pronounced cosmopolitanism of the Late Cretaceous pterosaurs in the northern continents than was previously thought.

Conflict of interest. Authors declare no competing interests.

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