Two bone fragments of ornithocheiroid pterosaurs from the Cenomanian of Volgograd Region, southern Russia

ALEXANDER O. AVERIANOV, EVGENY N. KUROCHKIN, EVGENY M. PERVUSHOV,
and ALEXEI V. IVANOV

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Two pterosaur bone fragments, a distal humerus and a distal femur, from the upper Cenomanian of the Volgograd Region in the Don River basin of southern Russia are reported. Although fragmentary, these bones come from mature individuals and are exceptionally well and three-dimensionally preserved, allowing a detailed description of their anatomy. Both specimens can be referred to a middle-sized ornithocheiroid pterosaur with a reconstructed wingspan of about 4 m. The humerus shows affinities with *Istiodactylus* from the Barremian of England, whereas the femur fragment is not identifiable beyond Ornithocheiroidea indet.

Key words: Pterosauria, Ornithocheiroidea, Cretaceous, Cenomanian, Russia.

Alexander O. Averianov [sasha@AA1923.spb.edu], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034 Saint Petersburg, Russia;
Evgeny N. Kurochkin [enkur@paleo.ru], Paleontological Institute, Russian Academy of Sciences, Profsouznaya ul. 123, 117868 Moscow GSP-7, Russia;
Evgeny M. Pervushov [pervusch@san.ru], Saratov State University, Astrakhanskaya ul. 83, 410026 Saratov, Russia;
Alexei V. Ivanov [niig@sgu.ssu.runnet.ru], Scientific Research Institute of Geology, Saratov State University, Bol'shaya Kazach'ya ul. 120, 410012 Saratov, Russia.

Introduction

Pterosaurs reached their maximum taxonomic diversity and geographic distribution in the mid-Cretaceous (Barremian to Cenomanian) time, when four major pterodactyloid clades coexisted (Unwin 2003). Recent discoveries in European Russia, Siberia, Transbaikalia, Kyrgyzstan, and Uzbekistan confirmed that pterosaurs were widely distributed in this part of Eurasia in the mid-Cretaceous. The majority of records are represented by fragmentary remains, sometimes by isolated teeth only (Averianov et al. 2003; Averianov 2004). In European Russia, six mid-Cretaceous localities that yielded pterosaur remains are so far known (Fig. 1):

(1) Lebedinskii and Stoilenskii ore quarries near Gubkin and Staryi Oskol cities, respectively, Belgorod Region. White, yellow, and gray sand with phosphorite of Sekmenovsk, or Paramonov and Polpino formations, Albian–Cenomanian. Several bone fragments of a large pterosaur including a wing phalanx fragment (now lost) and wing metacarpal fragment (ZIN PH 3/43). The latter was identified as Ornithocheiroidea indet. (Glickman et al. 1987; Nessov et al. 1988; Nessov 1990; Bakhurina and Unwin 1995; Unwin and Bakhurina 2000; Unwin et al. 2000; Averianov 2004). The vertebrate fauna from this assemblage is very similar to that from the British Cambridge Greensand (see Unwin 2001 for review).

(2) Strelitsa, Voronezh Region. Gray sand with phosphorite, Albian–Cenomanian. Fragment of a large tubular bone (femur?, ZIN PH 11/43; Averianov 2004).

(3) Kobyaki, Tambov Region. Sand, lower Cenomanian. Bone fragment, possibly from the lower jaw (Bazhanov and Eremin 1977; Nessov 1990; Bakhurina and Unwin 1995; Unwin and Bakhurina 2000; Unwin et al. 2000).

(4) Sinen'kie, Saratov Region. Yellow sands with phosphorite, lower Cenomanian. A rostrum fragment of ?Ornithocheiridae indet. (ZIN PH 6/43) and several limb bone fragments (Averianov 2004).

(5) Saratov, Saratov Region. Yellow sand with phosphorite, upper Cenomanian. Mandibular symphysis of cf. *Coloborhynchus* sp. (ZIN PHT-S50-1) and a partial skeleton of a juvenile ornithocheiroid pterosaur, including fragments of ilium, pubis, femur, tibia (?), and sacral centra (ZIN PH 8/43; Glickman 1953; Khosatzky and Yur'ev 1964; Nessov 1990, 1997; Bakhurina and Unwin 1995; Khosatzky 1995; Pervushov et al. 1999; Unwin and Bakhurina 2000; Averianov 2004).

(6) Pavlovsk, Voronezh Region. Cenomanian. Distal end of a second (?) wing phalanx of a large pterodactyloid pterosaur (ZIN PH 2/43; Averianov 2004).

Additionally, a tooth of an ornithocheirid pterosaur was found by Alexander A. Yarkov in an unspecified Cenomanian

Fig. 1. Map of southern European Russia and adjacent territories showing mid-Cretaceous pterosaur localities in Russia: 1, Lebedinskii and Stoilenskii quarries; 2, Strelitsa; 3, Kobyaki; 4, Sinen'kie; 5, Saratov; 6, Pavlovsk; 7, Melovatka 3.

locality in the Volgograd Region (personal communication to the first author 2002).

Here we report the discovery of two pterosaur bones in yellow sand with phosphorite outcropping along Medveditsa River bank 3.5 km east to Melovatka village on the North of Volgograd Region (Fig. 1; locality Melovatka 3 of Pervushov et al. 1999). The fossiliferous horizon is rich in marine invertebrates (mostly bivalves), shark teeth, chimaeroid tooth plates, and remains of osteichthyan fishes (Pervushov et al. 1999 and subsequent collections). More rare remains of marine reptiles (ichthyosaurs, elasmosaurid and pliosaurid plesiosaurs, and sea turtles) and a unique partial avian brain endocast were also found there. A partial pterosaur femur was found in Melovatka 3 by E.M. Pervushov and A.V. Ivanov in 1993, and a partial humerus by E.N. Kurochkin in 2003. These bones are described herein.

Institutional abbreviations.—BMNH, Natural History Museum, London; NSM PV, Division of Vertebrate Paleontology, National Science Museum, Tokyo; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; RGM, National Natuurhistorisch Museum, Leiden; ZIN PH, Paleoherpetological collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Ornithocheiroidea Seeley, 1891

Ornithocheiroidea indet.

Figs. 2, 3.

Locality and horizon: Melovatka 3, Volgograd Region, Russia; phosphorite horizon, upper Cenomanian, Upper Cretaceous.

Material.—PIN 5028-3, distal end of a left humerus. PIN 5028-1, distal end of a left femur.

Description

Humerus (PIN 5028-3).—The epiphysis is fused to the bone and fully ossified, so this specimen belongs to an adult animal. The distal end is expanded compared with the shaft and has a triangular outline in distal view. The posterior [medial] side is projecting somewhat distal than the anterior [lateral] side. The capitulum, articulating with the radius, is more than twice the size of the trochlea that forms the articulation with the ulna. The capitulum and trochlea are oval-shaped and extend on both ventral and distal surfaces of the humerus. The long axis of the trochlea is almost parallel to the distal bone plane. The long axis of the capitulum is oriented at an angle ~45° to this plane. The most proximal point of the capitulum on the ventral side continues into a distinct but short ridge. Just posterior to this point there is an oval-shaped pneumatic foramen. Another slit-like pneumatic foramen on the ventral bone side is located along the anterior edge of the proximal end of the capitulum. Anterior to the latter foramen, there is a depression, which also apparently included a pneumatic foramen. This depression is pierced now by postmortem bone breakage opening into the medullary cavity. Anteriorly and dorsally, the capitulum borders a large and flat articulation area, which continues anteroventrally into the ectepicondyle. The ectepicondyle projects ventrally almost up to the level of the capitulum. It connects on the ventral side to the prominent longitudinal ridge extending along the anteroventral border of the bone. A large circular pneumatic foramen is present on the distal side dorsal to and between the capitulum and trochlea. Posterior to this foramen and directly dorsal to the trochlea, there is a distinct subconical ulnar tubercle articulating to the corresponding depression on ulna and possibly serving as a stop to limit extension of the elbow (Bennett 2001). Between the trochlea and this tubercle a short groove (= "valley for the ulnar ridge" of Hooley 1913: pl. 39: 3) can be seen. The posteriormost extremity of the distal side is formed by a tubercle-like entepicondyle, which is similar in size but somewhat higher than the subconical tubercle. On the posterior side the entepiconyle connects with a distinct longitudinal ridge extending along the posteroventral bone edge. Ventrally and parallel to this ridge there is a second, more prominent ridge, connecting distally with the posteroventral corner of the trochlea. The area between these two ridges is rugose and served for attachment of carpus and digits extensors (Bennett 2003). Muscle scars are also present on the anterior side of the humerus. The maximum width of the distal humerus end is 41.7 mm.

Femur (PIN 5028-1).—The distal epiphysis is fully ossified. The shaft is oval in cross section with a mediolaterally oriented longer axis. The bone wall is ~0.7–0.8 mm thick in the diaphysis. The shaft widens slightly towards the distal end, more on lateral side. On the anterior side of the shaft there are two parallel ridges leading to the medial and lateral condyles. The medial and lateral condyles are almost symmetrical, ex-

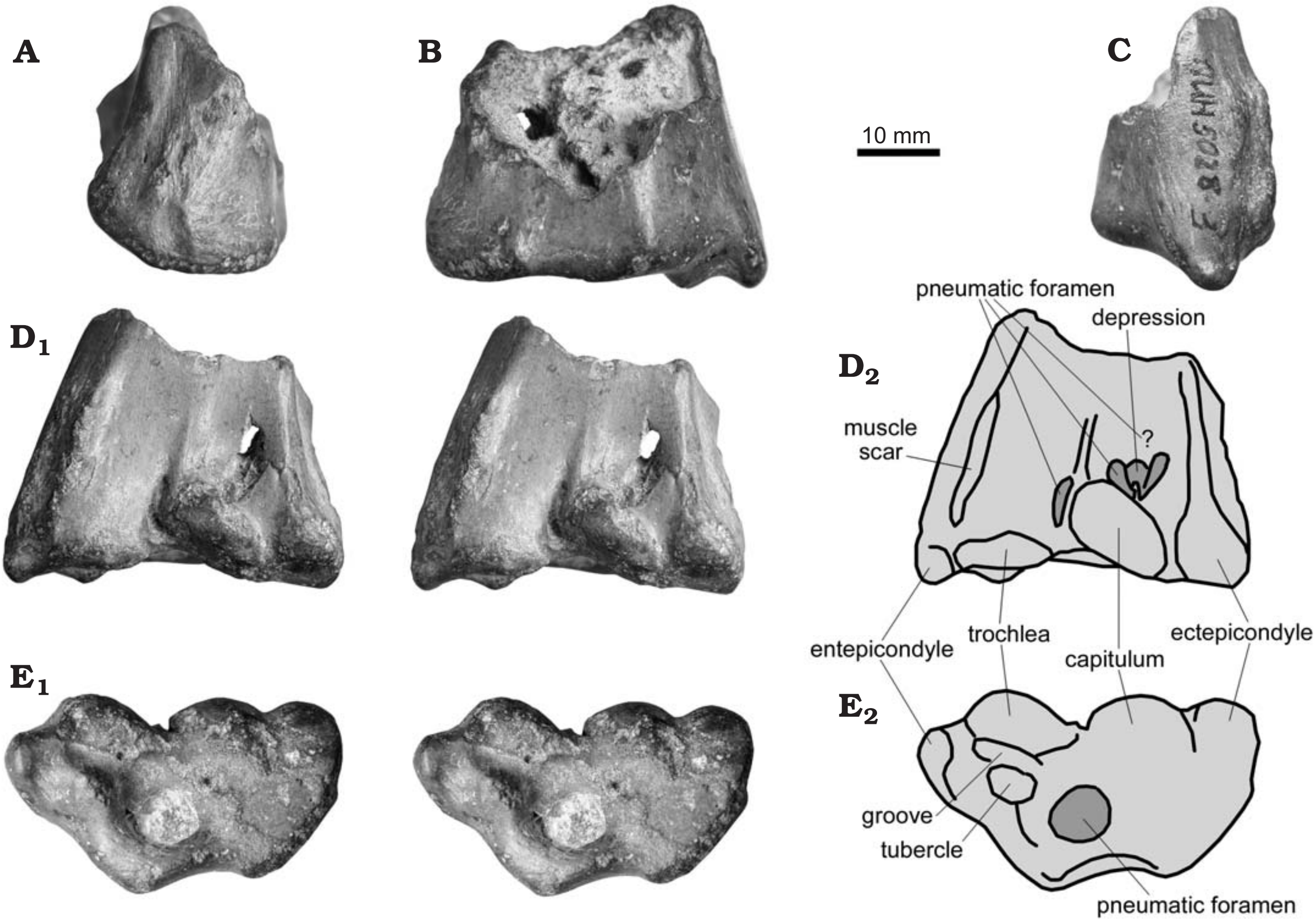

Fig. 2. Ornithocheiroidea indet. PIN 5028-3, left humerus distal end. Melovatka 3, Volgograd Region, Russia; Upper Cretaceous, upper Cenomanian; in anterior (**A**), dorsal (**B**), posterior (**C**), ventral (**D**), and distal (**E**) views. D_1 and E_1 are stereo-photographs with explanatory drawings (D_2, E_2). The oval opening seen in right upper corner of the stereo-photograph in Fig. D_1 is a postmortem bone breakage and therefore it is not shown in explanatory drawing.

cept the posterolateral edge of the lateral condyle projects more than that of the medial condyle. On the distal side there is a ridge delimiting the anterior and medial borders of the intercondylar sulcus. The medial and lateral epicondyles are small tubercles. Posterior to the epicondyles there is a small depression, deeper on the medial side. The maximum width of the femur distal end is 20.3 mm.

Discussion

The humerus PIN 5028-3 can be referred to the Ornithocheiroidea based on the occurrence of a triangular outline of the distal end of the humerus, an apomorphy of this clade (Unwin 2003). This triangularity, however, is less pronounced than in other ornithocheiroids, where both anterodorsal and posterodorsal sides are roughly equal in length (e.g., Hooley 1913: pl. 39: 3; Wellnhofer 1985: figs. 8f, 22f; Kellner and Tomida 2000: fig. 32c, d; Veldmeijer 2002: fig. 2C). This lesser triangularity may be an ontogenetically controlled character, as PIN 5028-3 belongs to an adult individual. The largest ornithocheirid humerus described, that of *Coloborhynchus spielbergi* Veldmeijer, 2003, clearly belongs to an adult, possibly an older individual and has very flattened trapezoid shape of the distal end outline (Veldmeijer 2003: fig. 15F, pl. 10F).

PIN 5028-3 is distinctly not D-shaped in distal outline as are humeri of azhdarchids (collection ZIN PH) or dsungaripterids (Young 1964: fig. 4E). In contrast with PIN 5028-3, in *Azhdarcho lancicollis* Nessov, 1984 the ulnar tubercle is located at the level between the capitulum and trochlea and there is a large pneumatic foramen between this tubercle and the entepicondyle (Nessov 1986: fig. 2-1b; Bakhurina and Unwin 1995: fig. 13g).

There are numerous ornithocheiroid distal humeri described and figured from the Albian Cambridge Greensand in England and the Albian Santana Formation in Brazil, but the majority of them belong to immature individuals with unfused or incompletely ossified epiphysis, which makes comparison of PIN 5028-3 with these specimens difficult. PIN 5028-3 is very similar to an adult humerus from the Cambridge Greensand (Seeley 1870: pl. 4: 13) and with the humerus of

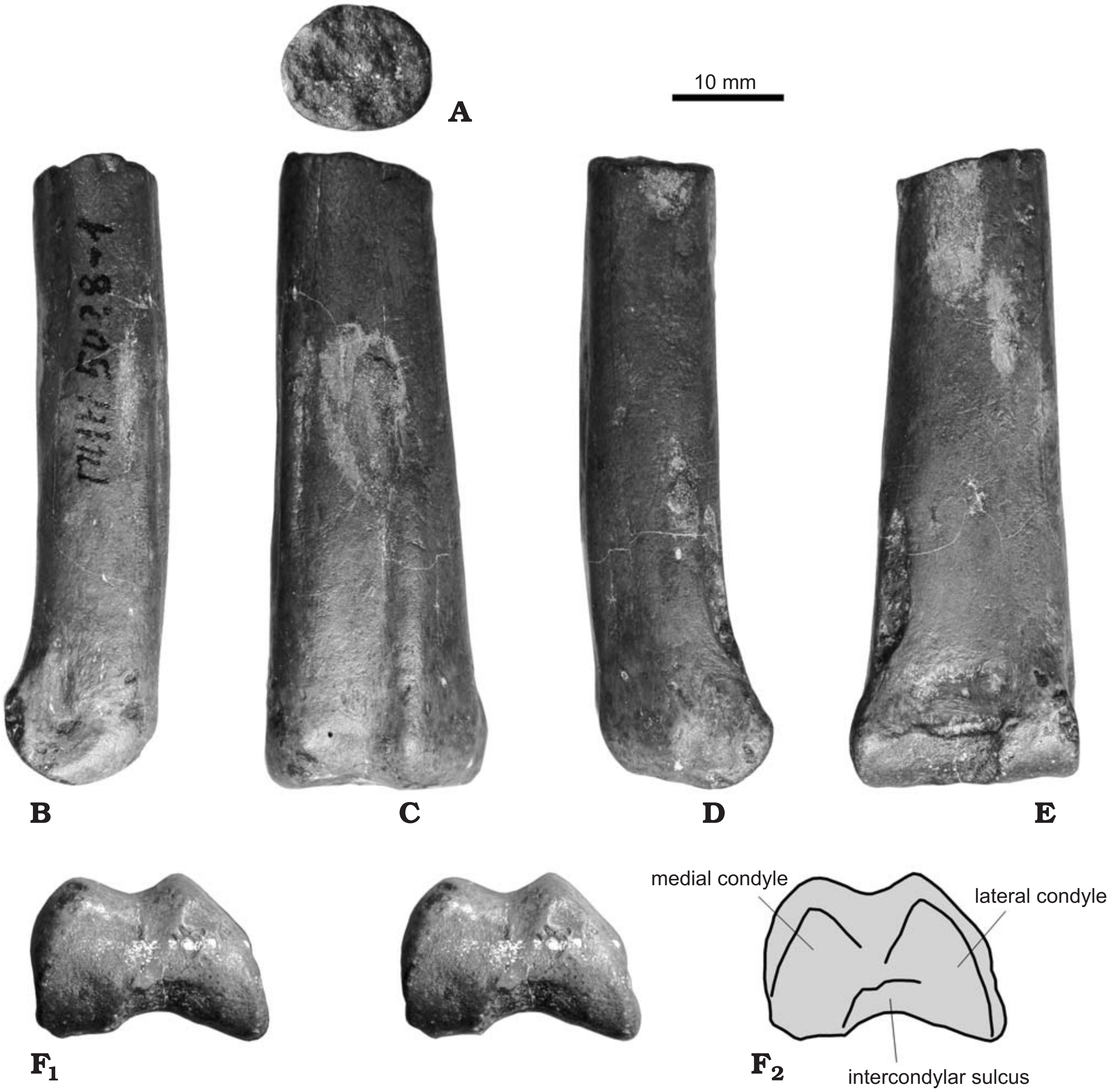

Fig. 3. Ornithocheiroidea indet. PIN 5028-1, left femur distal end. Melovatka 3, Volgograd Region, Russia; Upper Cretaceous, upper Cenomanian. Cross-section of the diaphysis (**A**), medial view (**B**), anterior view (**C**), lateral view (**D**), posterior view (**E**), and distal view (**F**). F_1 is a stereo-photograph with explanatory drawing (F_2).

Istiodactylus latidens (Seeley, 1901) from the Barremian of England (Hooley 1913: pl. 39: 3). Both *Istiodactylus* and PIN 5028-3 have a distinct groove between the ulnar tubercle and trochlea. This groove was found to be characteristic for the group A of distal ends of humeri of Cambridge Greensand ornithocheiroids (Hooley 1914: 543), which Hooley (1914: 547) allied to *Istiodactylus*. Indeed, PIN 5028-3 is almost identical with *Istiodactylus*, and differs from the latter only by a less triangular distal end outline, a relatively larger entepicondyle, and a slightly smaller circular pneumatic foramen on the distal end. In "*Santanadactylus pricei*" Wellnhofer, 1985 the groove between the trochlea and ulnar tubercle is also present, but the ulnar tubercle is more anterior in position. Additionally, there is a small pneumatic foramen between this tubercle and the entepicondyle, and the entepicondyle is not as prominent as in PIN 5028-3 (Wellnhofer 1985: fig. 22f). Concluding, among ornithocheiroids the humerus PIN 5028-3 closely resembles the humerus of *Istiodactylus* and may belong to a related taxon. *Istiodactylus* belongs to the Istiodactylidae [= "Ornithodesmidae"], which are previously considered to be monotypic and restricted to the Barremian Vectis Formation of the Isle of Wight, England (Hooley 1913;

Table 1. Humerus maximum distal width (X), femur maximum distal width (Y), and reconstructed wingspan (Z) in selected ornithocheiroid pterosaurs.

Taxon, specimen	X [mm]	Y [mm]	Z [m]	Reference
Istiodactylus latidens, BMNH R3877	64.0		5.00	Hooley 1913
*Coloborhynchus robustus**, NSM PV 19892	71.0	24.0	5.00	Kellner and Tomida 2000
Coloborhynchus spielbergi, RGM 401880	83.0	35.0	5.90	Veldmeijer 2003
Ornithocheiroidea indet., PIN 5028-3	41.7		3.73	this paper
Ornithocheiroidea indet., PIN 5028-1		20.3	4.70	this paper

* Originally described as *Anhanguera piscator*, immature specimen; synonymy is according to Unwin (2003).

Howse et al. 2001). A second genus of the Istiodactylidae, however, was recently announced from the Barremian Yixian Formation of Liaoning Province, China (Andres and Ji 2003). The Melovatka 3 pterosaur is situated geographically between these two records of the Istiodactylidae and may be within the range of the family.

A unique feature of PIN 5028-3 is the presence of two pneumatic foramina and a depression around the capitulum on the ventral side of the humerus. The posterior of these pneumatic foramina is characteristic for *Pteranodon* (Bennett 2001: figs. 69A, 70B, 74A) and *Azhdarcho* (collection ZIN PH). Occurrence of the anterior pneumatic foramen has not been described for *Istiodactylus* or other ornithocheiroids and is absent in *Pteranodon* and *Azhdarcho*. It is not clear, however, if the absence of this foramen in non-pteranodontid ornithocheiroids is a real character, or an artifact of preservation, ontogenetic immaturity, or inadequate description.

The femur PIN 5028-1 resembles ornithocheirid femora from the Cambridge Greensand (Seeley 1870: pl. 8: 5, 6, 10–12) and the outline of the distal end is similar to that in an immature specimen of *Coloborhynchus robustus* (Wellnhofer, 1987) from the Santana Formation in Brazil (Kellner and Tomida 2000: fig. 52e, f). The femur of *Pteranodon* (Bennett 2001: fig. 107) has also a similar asymmetrical distal end. However, in this taxon the extension of the lateral side of the distal end is formed by an enlarged lateral epicondyle. In PIN 5028-1 the lateral epicondyle is very small and the lateral condyle is extended. In dsungaripterids the femur shaft is more curved in the anteroposterior plane than in PIN 5028-1 and the distal end is more widely expanded compared with the diaphysis (Young 1964: figs. 6A, 7B; Bakhurina 1982: fig. 1h, c). In *Azhdarcho* (collection ZIN PH) the medial and lateral condyles are more symmetrical with more pronounced condylar ridges. Concluding, PIN 5028-1 is most similar with the femora of ornithocheiroid pterosaurs and safely can be referred to Ornithocheiroidea indet.

In PIN 5028-1, *Pteranodon*, *Dsungaripterus*, *Azhdarcho*, and an unidentified large pterodactyloid from the Albian of Kyrgyzstan (Averianov 2004: fig. 1d) there is a similar pit on the intercondylar sulcus delimited anteriorly by the transverse ridge. This pit may serve as an attachment area for the ligament of digits flexor. According to Bennett (2001), some tibiotarsus and/or pes flexors could originate in such a shallow "popliteal" fossa on the posterior side of the femur proximal to the condyles. Whereas in *Pteranodon* minor muscle scars are present in this fossa, in PIN 5028-1 this area is only slightly depressed and bears no distinct muscle scars. Only some small foramina are visible, probably for blood vessels associated with the muscle ligaments.

It is difficult to estimate the wingspan of a pterosaur based on isolated bone fragments alone, especially when sufficient comparative data from complete skeletons is lacking (Table 1). However, a rough estimate can be made. Based on three specimens for which distal humerus width (X) and wingspan (Z) are known, the regression between these two parameters is the following:

$$Z = 1.64 + 0.05X,$$

Pearson correlation coefficient $r = 0.93$, not significant at $p < 0.05$.

This equation would give a wingspan estimate of 3.73 m for PIN 5028-3. There are only two specimens of ornithocheiroids for which distal femur width (Y) and wingspan (Z) are known (Table 1), so the Pearson correlation coefficient cannot be computed in this case. However, the regression equation:

$$Z = 3.036 + 0.082Y$$

would give a wingspan estimate of 4.70 m for PIN 5028-1. Taking into account uncertainty of these equations, the Melovatka 3 pterosaur wingspan could be roughly estimated as around 4 m.

Attribution of both PIN specimens 5028-1 and 5028-3 to Ornithocheiroidea indet, their provenance from the same locality and horizon, and similar size, indicate that they may belong to the single taxon. However, this cannot be unambiguously demonstrated now. As both Melovatka 3 pterosaur specimens belong to mature individuals, this taxon would have been middle-sized by pterodactyloid standards.

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