The First Discovery of Pterosaurs from the Upper Cretaceous of Mongolia

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Cervical vertebrae of azhdarchid pterosaurs were discovered in two Upper Cretaceous (Baynshire Suite) dinosaur localities, Bayshin Tsav and Burkhant, in the Gobi Desert. These are the first discoveries of pterosaur remains in the Upper Cretaceous of Mongolia. The Burkhant specimen includes a nearly complete atlas-axis complex, which has rarely been described in this clade of pterosaurs. Although all elements comprising this complex are fused together, a wing-like atlas neural arch is still discernable. The postzygapophyseal facet of the axis is long anteroposteriorly and convex dorsally, and would likely have allowed a fairly large range of dorsoventral flexion at the axis-third cervical joint unlike in other well-known ornithocheiroids such as *Pteranodon* and *Anhanguera*. Both Mongolian localities represent inland, terrestrial environments, which were apparently not typical habitats of pterosaurs, thus adding further evidence for the ubiquity of Azhdarchidae during the Late Cretaceous.

Key words: Pterosauria, Azhdarchidae, Late Cretaceous, Gobi Desert, Mongolia.

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Introduction

Pterosaur remains in Mongolia are very scarce. In the 1970's and 1980's, remains of many individuals of the dsungaripterid "*Phobetor*" *parvus* (generic name preoccupied) including a complete skull were found from the Lower Cretaceous in Tatal of the Sangiin Dala Nuur depression (Khovd Aimag) by the Joint Soviet-Mongolian Paleontological Expedition (Bakhurina and Unwin 1995; also see Unwin and Bakhurina 2000 for further discussion of the taxonomic status of this pterosaur). Later, pterodactyloid remains were discovered by the same Joint Expedition in Khuren Dukh in Central Gobi Aimag (upper Lower Cretaceous), and were referred to Ornithocheiridae (Bakhurina and Unwin 1995). In addition, a fragmentary, small-sized anurognathid pterosaur was found from the middle Jurassic beds of Bakhar in Bayankhongol Aimag of central Mongolia (Bakhurina and Unwin 1995). Most recently, a cervical vertebra of a tapejaroid (sensu Kellner 2003) pterosaur was discovered at the Lower Cretaceous Öösh locality by the Joint Mongolian-American Expedition (Andres and Norell 2005). To date, however, no pterosaur remains have been discovered in the Upper Cretaceous in the Mongolian territory (Fig. 1).

We here describe pterosaur remains from the Baynshire Suite (early Late Cretaceous) in Burkhant and Bayshin Tsav in the eastern region of the Gobi Desert (Jerzykiewicz and Russell 1991; Hicks et al. 1999). These remains were found during field seasons from 1993 to 2004 of the Hayashibara Museum of Natural Sciences-Mongolian Paleontological Center Joint Paleontological Expedition, and mark the first discoveries of pterosaurs from the Upper Cretaceous in Mongolia. These remains can be assigned to Azhdarchidae Nessov, 1984, and provide new data on stratigraphic and geographic distribution of pterosaurs in the Late Cretaceous.

Measurement method on these cervical vertebrae is shown in Fig. 2, with measurements reported in Table 1.

Institutional abbreviations.—FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MPC, Mongolian Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; NSM-PV, Division of Vertebrate Paleontology, National Museum of Nature and Science (formerly National Science Museum), Tokyo, Japan; TMM, Texas Memorial Museum, University of Texas at Austin, Austin, Texas, USA; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Geological setting

Bayshin Tsav.—This locality is situated 95 km southeast of Manlai Somon and 64 km northeast of Khan Bogd Somon in the eastern part of Southern Gobi Aimag (Fig. 1). This locality

Fig. 1. Geographic distribution of pterosaur localities in Mongolia. 1, Burkhant (Upper Cretaceous, Eastern Gobi Aimag); 2, Bayshin Tsav (Upper Crertaceous, Southern Gobi Aimag); 3, Khuren Dukh (Lower Cretaceous, Central Gobi Aimag); 4, Tatal (Lower Cretaceous, Khovd Aimag); 5, Bakhar (Upper Jurassic–Lower Cretaceous, Bayankhongor Aimag); 6, Öösh (Lower Cretaceous, Övörkhangai Aimag).

is best known for occurrences of three therizinosauroid theropods: *Enigmosaurus mongoliensis*, *Erlikosaurus andrewsi*, and *Segnosaurus galbinensis* (Perle 1979, 1981; Barsbold and Perle 1983). In addition, several other dinosaur taxa have been found from this locality, including the ornithomimid *Garudimimus brevipes*, indeterminate small (dromaeosaurid?) and large theropods, and an indeterminate primitive hadrosaur (Barsbold 1981; Watabe et al. 2000). Remains of turtles are also abundant.

A pterosaur cervical vertebra was found in a bone bed in the northwestern part of this locality. The outcrops in this area consist of alternating thin layers of fining-upward units (from coarse sands to mud) intercalated by many layers of yellowish brown to reddish brown, coarse-grained sandstone and fine-grained conglomerate, probably representing point bar deposits. The bone bed is one of the bluish white, fine- to coarse-grained sandstone layers that alternate with gray mudstone layers, containing isolated bones and teeth of hadrosaurs and small theropods that were transported and accumulated by an ancient stream.

The sediments of this locality have been assigned to the lower Upper Cretaceous Baynshire Suite by Shuvalov and Chikhikvadze (1975) and Ivakhnenko and Kurzanov (1988). Paleomagnetic analyses by Hicks et al. (1999) gave the Baynshire Suite the chronological range of the Cenomanian to Santonian, providing an age constraint for the pterosaur specimens from Bayshin Tsav and Burkhant (see below) described here.

Burkhant.—Horizontal, fossiliferous beds form small outcrops in this locality, which is located in Eastern Gobi Aimag, 69 km and 22 km southwest of the towns of Saynshand and Dzunbayan, respectively (Fig. 1). The new pterosaur specimen consisting of four associated cervicals was found in situ in a bluish white siltstone layer in 1995.

The sediment consists of reddish brown, fine- to medium-grained sandstone intercalated by thin layers of gray to reddish brown mudstone. In hard sandstone layers, there are many trough cross-stratifications showing direction of an ancient stream. The paleocurrent indicated by these cross-stratifications is roughly parallel to the strike of gently tilted beds of sandstone and mudstone. The beds containing vertebrate fossils are interpreted as point bar deposits of a meandering river. Other vertebrate remains found from the same locality include associated skeletal elements of a sauropod (Watabe et al. 2000), dromaeosaurid *Achillobator giganticus* (Perle et al. 1999), and several turtle taxa. The age of the fossiliferous beds is not yet clearly determined. Based on the similar lithology and geographic proximity, however, these beds have been correlated with the Upper Cretaceous Baynshire Suite in Khongil Tsav, 11 km north of the locality, and Bayn Shire, 9 km southeast of the locality (Perle et al. 1999).

Systematic paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Azhdarchidae Nessov, 1984

Bayshin Tsav azhdarchid

Figs. 3, 4.

Material.—MPC-Nd 100/303, an isolated middle cervical vertebra with the posterior end missing from Bayshin Tsav, east of Southern Gobi Aimag, Mongolia, Bayn Shire Suite, early Late Cretaceous (Cenomanian–Santonian).

Description

The specimen is fairly well-preserved although the posterior end of the element including the postzygapophyses and posterior articular surface of the centrum is missing. The vertebra is greatly elongated anteroposteriorly. The preserved portion of the centrum is about 5.6 times as long as the minimum width of the vertebra at its mid-length, and the total length of the preserved portion of the vertebra including prezygapophyses is about 3.1 times as long as the maximum width across the prezygapophyses. There is no recognizable suture line between the neural arch and centrum, which together form a tube-like main body of the vertebra. No pneumatic foramen is present on its lateral aspect. On the anterior aspect of the neural arch, however, there is a pneumatic foramen lying lateral to the neural canal on each side. The neural spine is ridge-like and very low along most part of the neural arch. However, the height of the neural spine, as well as the width of its base, increases at the posterior end. Only the base of the neural spine is preserved on the anterior end of the neural arch, but it is wider than that in the middle to posterior parts, suggesting that the neural spine would also have increased its height at this end.

The prezygapophyseal pedicle is short and extends slightly dorsally as well as anteriorly from the neural arch. The articular facet of the prezygapophysis lies well lateral to

Table 1. Measurements on the cervical vertebrae from the two localities. Measurement lines are shown in Fig. 2.

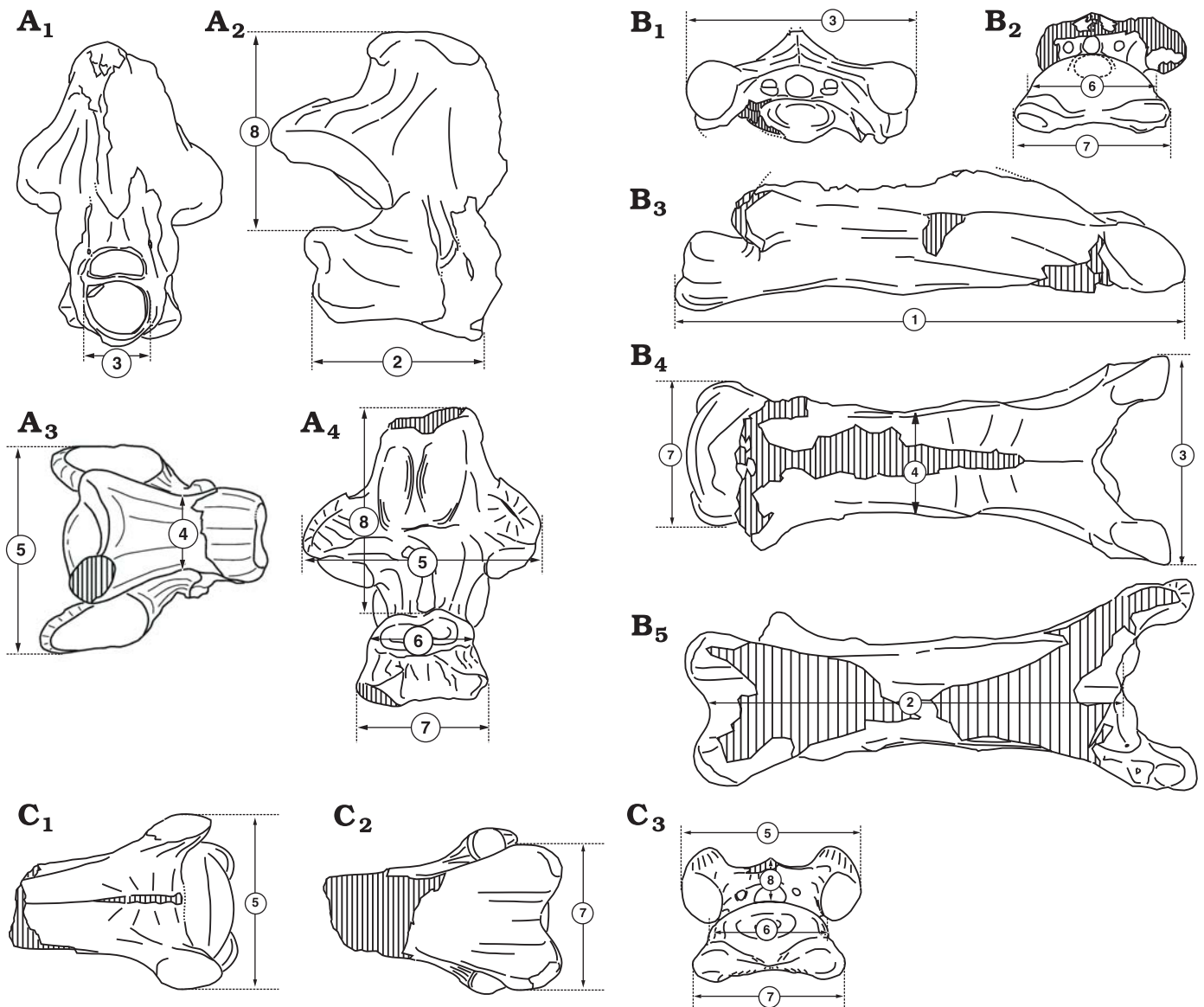| Locality	Specimen No.	Position	1	2	3	4	5	6	7	8
Burkhant	MPC-Nd 100/302	atlas-axis	–	26.0	9.8	10.9	34.1	16.0	19.8	31.9
Burkhant	MPC-Nd 100/302	3rd	90.6	73.1	38.5	18.2	27.7	19.3	–	–
Burkhant	MPC-Nd 100/302	middle cervical	–	–	–	–	31.1	24.3	37.9	11.7
Bayshin Tsav	MPC-Nd 100/303	middle cervical	77+	66+	25.0	12.4	–	–	–	–

Fig. 2. Measurement system for cervical vertebrae. **A**. Atlas-axis complex in anterior (A_1), right lateral (A_2), ventral (A_3), and posterior (A_4) views. **B**. 3rd cervical in anterior (B_1), posterior (B_2), right lateral (B_3), dorsal (B_4), and ventral (B_5) views. **C**. Posterior part of a middle cervical in dorsal (C_1), ventral (C_2), and posterior (C_3) views. Specific measurements are as follows: 1, total length; 2, length of centrum; 3, width of anterior part; 4, width of middle point of centrum; 5, width of posterior part with postzygapophyses; 6, width of posterior part of centrum; 7, width including postexapophyses; 8, height of neural arch on posterior part.

the neural canal, and is elongated anteroposteriorly with its long axis almost parallel to that of the neural arch. The dorsally-convex facet faces mainly dorsally and only slightly medially. A longitudinal ridge extends posteriorly from the dorsolateral edge of the prezygapophyseal pedicle, but disappears at about one third of the preserved portion of the neural arch from its anterior end. The neural arch is slightly concave medial to this ridge. The ventral edge of the prezygapophyseal pedicle forms a distinct keel, which is connected medially to the anterior articular surface of the centrum by a bridge of bone and together forms a short, longitudinal canal that was regarded as a transverse foramen (vertebrocostal ca-
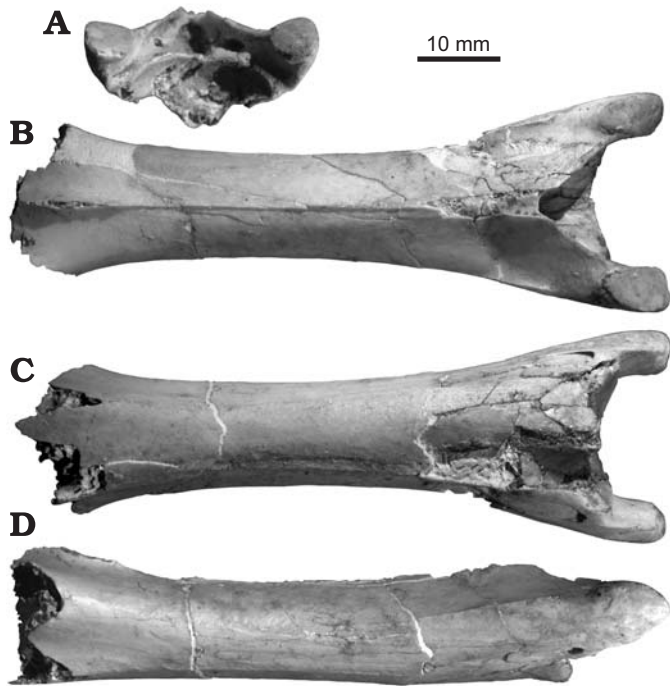
Fig. 3. Middle cervical vertebra of Bayshin Tsav azhdarchid (MPC-Nd 100/303) from the Upper Cretaceous of Southern Gobi Aimag, in anterior (**A**), dorsal (**B**), ventral (**C**), and right lateral (**D**) views.
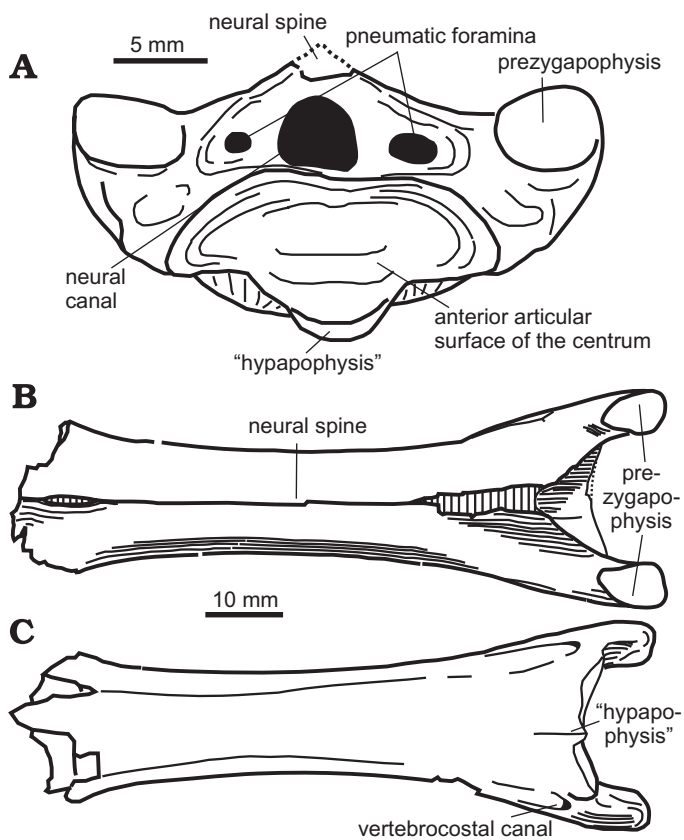

Fig. 4. Explanatory drawings of the Bayshin Tsav azhdarchid (MPC-Nd 100/303) from the Upper Cretaceous of Southern Gobi Aimag, in anterior (**A**), dorsal (**B**), and ventral (**C**) views.

nal) in azhdarchid cervicals by Martill et al. (1998), Godfrey and Currie (2005), and Henderson and Peterson (2006). This canal has a slit-like opening anteriorly and continues posteriorly into a shallow trough that is bounded dorsally by a ridge extending from the ventral edge of the prezygapophysis and ventrally by another short ridge on the centrum. Posterior to the latter ridge appears to lie another, much longer ridge on the ventrolateral aspect of the centrum, dividing this element into the lateral and ventral surfaces.

The anterior articular surface of the centrum forms a mediolaterally broad and strongly concave cotyle. This articular surface extends ventrally onto the so-called "hypapophysis", or a median projection of the centrum.

Burkhant azhdarchid
Figs. 5–10.

Material.—MPC-Nd 100/302, four associated cervical vertebrae (nearly complete atlas-axis complex, probable third cervical with most of the postzygapophyses missing, and posterior part of a middle cervical) from Burkhant, west of Eastern Gobi Aimag, Mongolia; Bayn Shire Suite, early Late Cretaceous (Cenomanian–Santonian).

Description

Atlas-axis.—The right and left neural arches as well as the intercentrum of the atlas are fused together, leaving no distinct sutures. These fused atlas elements are in turn fused posteriorly with the axis although a suture line between these two vertebrae is still visible as illustrated in Fig. 6. In addition, an intervertebral foramen marks the boundary between these two vertebrae. Dorsal to this foramen, each atlas neural arch has a small, spur-like process and then expands further dorsally to form a large, wing-like process. The latter process extends posterodorsally but does not appear to contact the contralateral counterpart. It attaches to the anteroventral end of the axis neural arch as in most pterosaurs (e.g., Wellnhofer 1970, 1975, 1991a) other than *Pteranodon*, in which Bennett (2001) described an unusual condition of the atlas neural arch not extending dorsally beyond the level of the floor of the neural canal and thus not contacting the axis neural arch. The neural canal is mediolaterally wide in anterior view, and the condyloid fossa lying ventral to it is cup-shaped, with the atlas intercentrum apparently comprising most of its periphery.

The axis is nearly complete except for the left surface and dorsal tip of the neural spine. In front of each postzygapophysis on the neural arch lies an anteroventrally-extending, shelf-like diapophysis that overlies a lateral concavity on the centrum described below. The neural spine is tall and appears triangular with the apex directed anteriorly in dorsal view. The posterior surface of the neural spine is a broad concavity that is bounded laterally by laminae connecting the dorsal tip of the neural spine with each postzygapophysis. This concavity, bounded ventrally by a horizontal ridge that demarcates it from the roof of the neural canal, is divided into a pair of depressions by a vertical, median
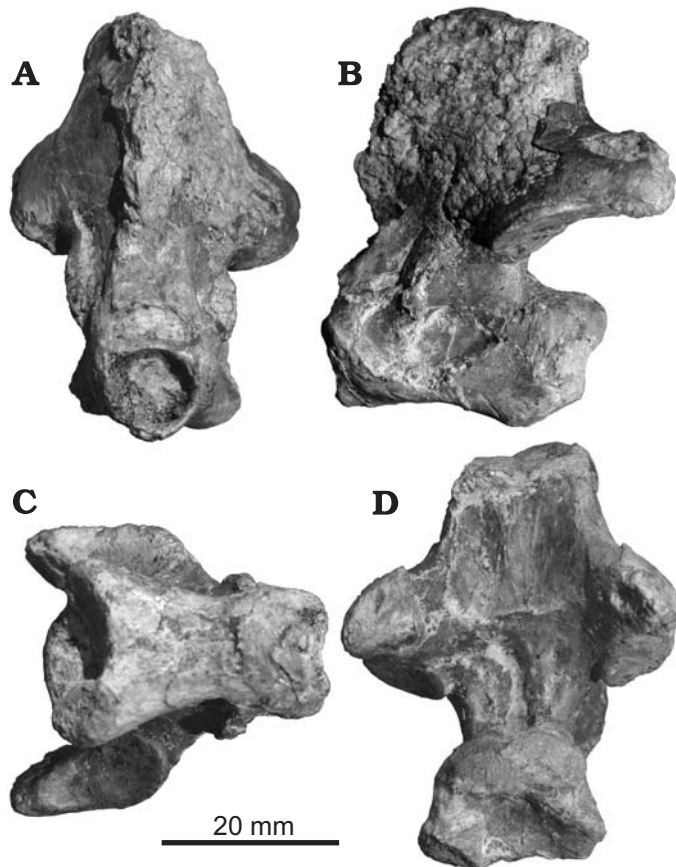
Fig. 5. Atlas-axis complex of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag, in anterior (**A**), left lateral (**B**), ventral (**C**), and posterior (**D**) views.

ridge that likely represents the attachment site of the interspinal ligament. Ventral to this horizontal ridge and between the neural canal and each postzygapophysis lies a small foramen. This may be a pneumatic feature although it is much smaller than the one described in *Pteranodon* (Bennett 2001).

The postzygapophyseal facet is anteroposteriorly long and teardrop-shaped with the attenuating end directed posteriorly. It is curved longitudinally with a dorsal convexity, and faces mainly ventrally with only very slight posterior and lateral inclinations. On the lateral surface of the left postzygapophysis, a shallow groove extends longitudinally and demarcates an area that is probably for the attachment of the zygapophyseal capsule. An epiphysis (Tuberculum der Postzygapophyse of Wellnhofer 1991a) overhangs the posterior end of the postzygapophyseal facet. A small, crest-like process lies on the dorsal aspect of each epiphysis while a distinct scar is present on its medial aspect. Bennett (2001) described a similar scar on the postzygapophysis in *Pteranodon*.

There is no clear separation between the axis intercentrum and centrum as in *Pteranodon* (Bennett 2001) and *Anhanguera santanae* (Wellnhofer 1991a). It is noteworthy, however, that Kellner and Tomida (2000) described separate elements, which potentially represent the axis intercentrum, lying posterior to the atlas intercentrum in *Anhanguera piscator*.

The axis centrum increases the width posteriorly to terminate as a condyle abutted ventrolaterally by a pair of postexapophyses, between which is a deep concavity. The condyle is more than twice as wide as high. Its articular surface extends ventrolaterally onto the dorsolateral aspect of the postexapophysis. The lateral surface of the centrum is slightly concave, but lacks a pneumatic foramen.

Third cervical vertebra.—A nearly complete middle-series cervical is found in association, but not articulated, with the atlas-axis complex. The maximum width between the right and left prezygapophyses (= distance between their lateral margins) of this vertebra is slightly larger than that of the postzygapophyses of the axis, and these two vertebrae can almost perfectly articulate with each other. Accordingly, this vertebra is here considered as the third cervical of the same individual. This vertebra is fairly elongated longitudinally; the ratio of the length of the centrum to the minimum width of the vertebra at the mid-length is about 4.4 while the ratio between the total length of the vertebra (= distance between the anterior tip of the prezygapophysis and the posterior end of the postexapophysis) to the maximum width across the
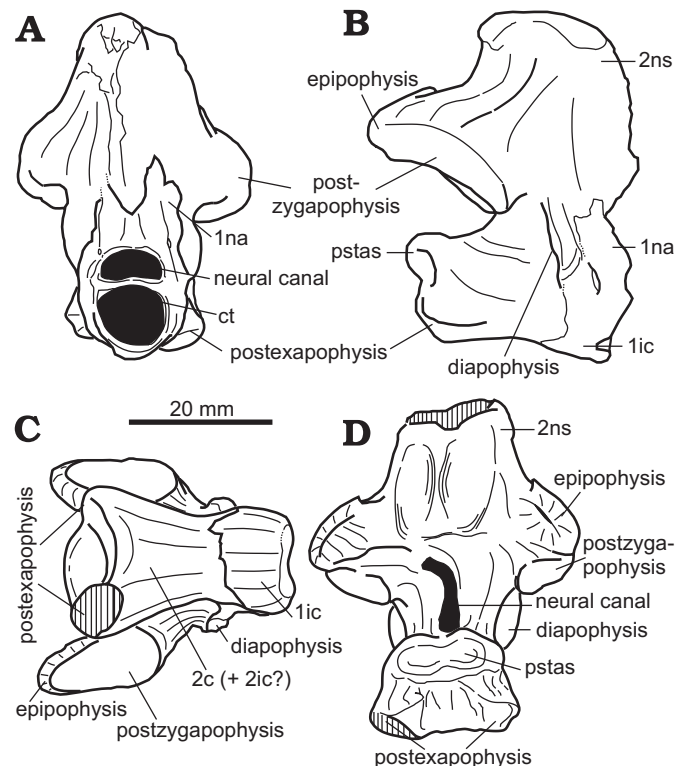

Fig. 6. Explanatory drawings of the atlas-axis complex of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag, in anterior (**A**), right lateral (**B**), ventral (**C**), and posterior (**D**) views. Areas shaded with vertical lines are broken and missing. Abbreviations: 1ic and 1na, intercentrum and neural arch of the atlas, respectively; 2c, 2ic, and 2ns, centrum, intercentrum, and neural spine of the axis, respectively; ct, cotyle of the atlas for articulation with the occipital condyle (condyloid fossa); pstas, posterior articular surface of the centrum.
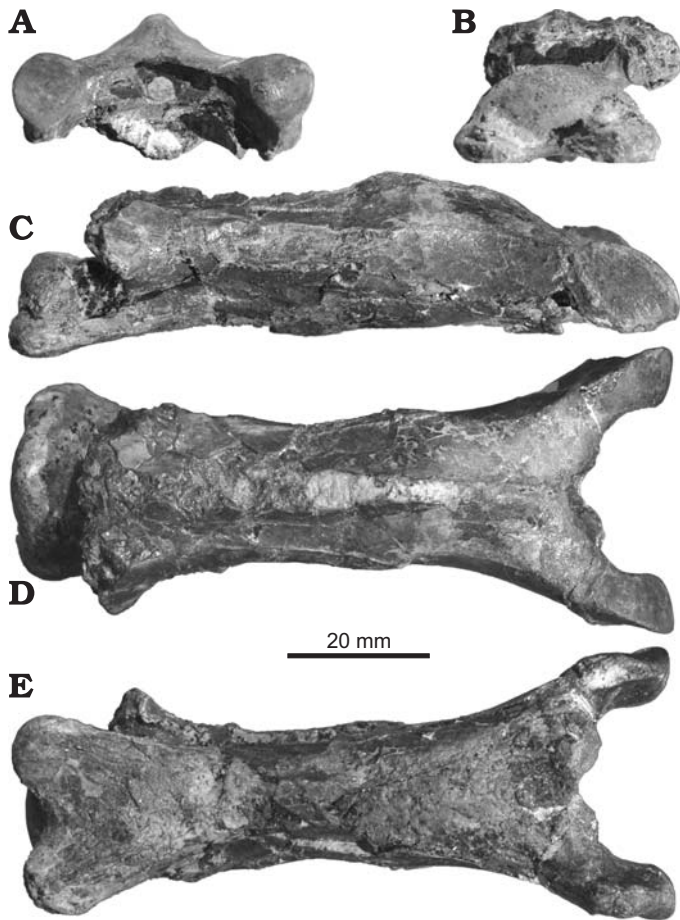
http://app.pan.pl/acta54/app54-231.pdf

Fig. 7. Third cervical vertebra of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag, in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views.

bears a large, mound-like tubercle on its ventral edge, followed posteroventrally by a small tubercle and a round prominence lateral to it. From the large tubercle extends a short ridge posterodorsally toward the dorsolateral corner of the prezygapophyseal facet on the lateral surface of the pedicle. The small tubercle may represent a diapophysis for rib articulation based on its position although it does not bear a clear articular surface. As mentioned above, the postzygapophyses are mostly missing in this specimen. The only preserved part, anterior half of the right postzygapophysis, shows that its articular facet faces posteroventrally.

The neural arch bears two longitudinal ridges on each side. One of them arises from the dorsolateral corner of the prezygapophyseal facet to extend posteriorly, dividing the neural arch into the dorsal and lateral surfaces, but does not reach the
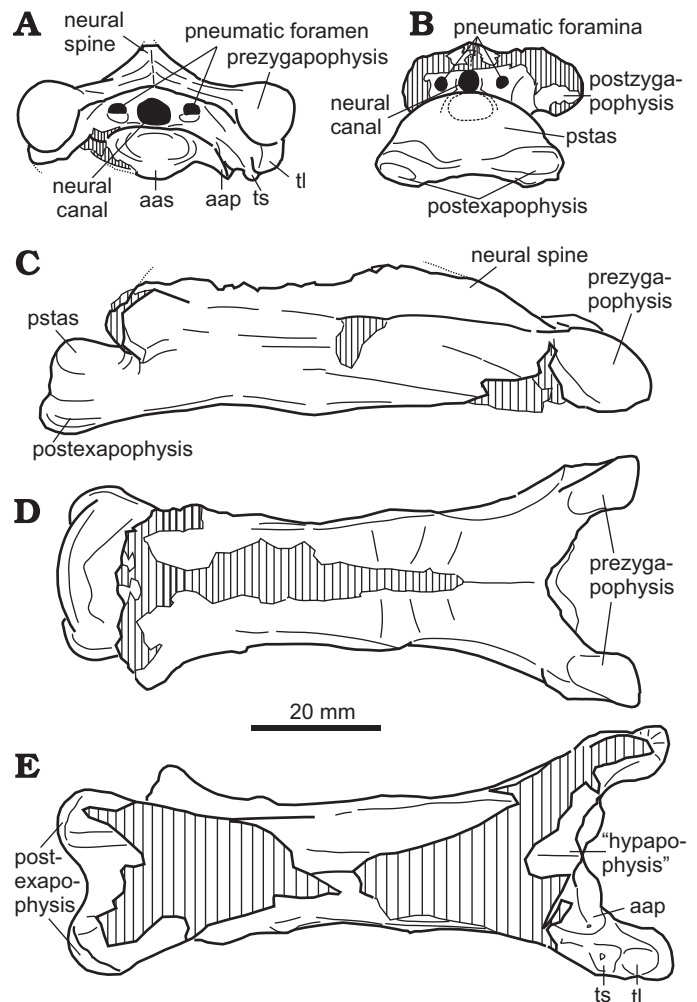

Fig. 8. Explanatory drawings of the third cervical vertebra of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag, in anterior (**A**), posterior (**B**), right lateral (**C**), dorsal (**D**), and ventral (**E**) views. Areas shaded with vertical lines are broken and missing. Abbreviations: aap, accessory articular process (preexapophysis); aas, anterior articular surface of the centrum; pstas, posterior articular surface of the centrum; tl and ts, large and small tubercles on the prezygapophyseal pedicle, respectively.

prezygapophyses is about 2.4. It lacks the left postzygapophysis, posterior half of the right postzygapophysis, and most part of the neural spine. The cortical bone layer is also mostly missing from the ventral surface of the centrum.

The anterior half of the neural arch is vaulted, producing a bulbous appearance and continuing dorsally to the neural spine rather smoothly. The base of the neural spine is preserved and becomes wider posteriorly, suggesting the neural spine itself would have been fairly well-developed and increased its height toward the middle to posterior parts of the neural arch. On both the anterior and posterior ends of the neural arch, a pneumatic foramen flanks the neural canal on each side. In addition, there appears to be another, median foramen lying dorsal to the neural canal on the posterior end.

From the anterolateral corner of the neural arch extends the prezygapophyseal pedicle anterolaterally and slightly ventrally, making its articular facets lie well lateral to the neural canal. The articular facet is longitudinally elongated with its long axis being almost parallel to that of the neural arch. It is curved parallel to the longitudinal axis, producing a dorsally-convex surface that faces anterodorsally with almost no medial inclination. The prezygapophyseal pedicle

Fig. 9. Fragmentary middle cervical vertebra of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag, in dorsal (**A**), ventral (**B**), left lateral (**C**), and posterior (**D**) views.

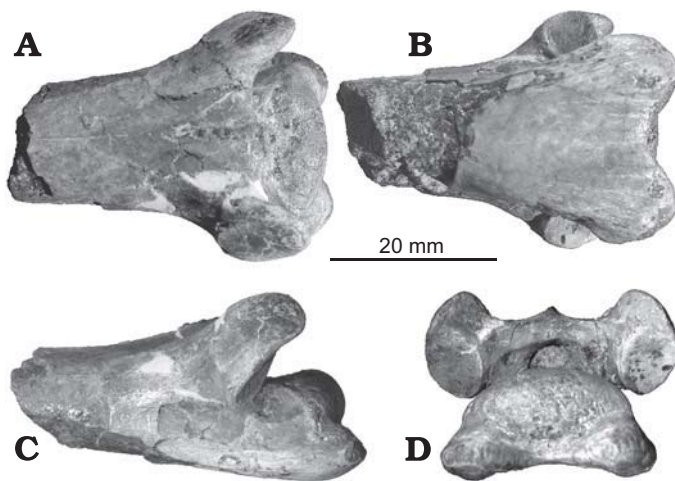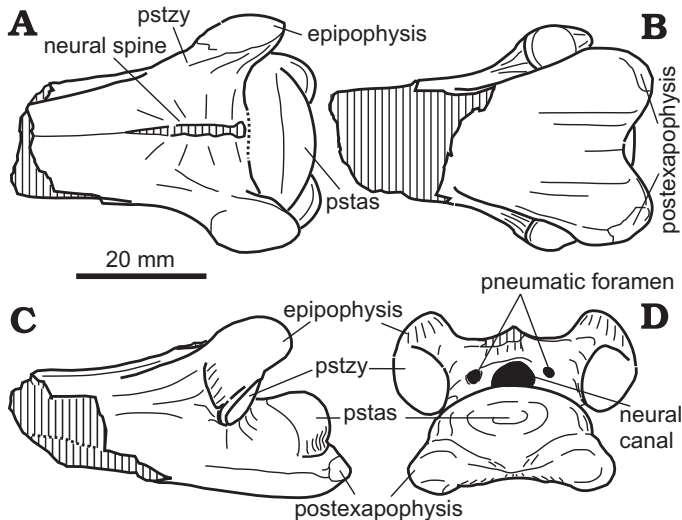Fig. 10. Explanatory drawings of a fragmentary middle cervical vertebra of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag, in dorsal (**A**), ventral (**B**), left lateral (**C**), and posterior (**D**) views. Areas shaded with vertical lines are broken and missing. Abbreviations: pstas, posterior articular surface of the centrum; pstzy, postzygapophysis.

postzygapophysis. The second ridge lies more ventrally, arising from the lateral surface of the prezygapophyseal pedicle dorsal to the round prominence mentioned above and extending posterodorsally. This ridge disappears at about the half way through the neural arch from its anterior end.

The centrum is strongly procoelous and is longer than the neural arch, with the posterior condyle and postexapophyses extending posteriorly beyond the level of the posterior end of the neural arch. At the anterior end, the centrum bears a median "hypapophysis" onto which the articular surface of the centrum extends ventrally as in the Bayshin Tsav specimen described above. In addition, at around the

middle portion of the centrum lies another, median ventral projection. There is no pneumatic foramen on the lateral aspect of the centrum. Instead, it bears a longitudinal ridge that is similar to those on the neural arch described above and disappears at about the half way through the centrum from its anterior end.

The anterior articular surface of the centrum forms a cotyle, which is about twice as wide as high. A lip-like, accessory articular process is preserved lateral to the cotyle on the left side. It is appropriate to call this process the pre-exapophysis (e.g., Howse 1986) although Bennett (2001) dismissed this name. A kink divides the articular facet of this process into the dorsal and ventral surfaces. The dorsal surface is continuous medially with the cotyle and faces anteromedially and would have articulated with the ventrolateral part of the posterior condyle of the axis centrum. The ventral surface, on the other hand, faces mainly ventromedially and would have articulated with the dorsolateral aspect of the postexapophysis of the axis.

The posterior articular surface of the centrum forms a condyle, and is about 2.8 times as wide as high. Ventrolateral to this condyle lies a postexapophysis on each side. The dorsal aspects of the postexapophyses, as well as the concave area between them, form articular surfaces continuous with the condyle of the centrum.

Fragmentary posterior part of a cervical vertebra.—A posterior part of another cervical vertebra was found with the atlas-axis complex and the third cervical, presumably derived from the same individual. The epipophysis is well-developed and crest-like, overhanging the postzygapophyseal facet that faces posteroventrally. Medial to the postzygapophysis lies a pneumatic foramen on each side of the neural canal, but a median dorsal foramen is absent unlike in the third cervical. Within the preserved portion, the ridge-like neural spine becomes higher and slightly wider toward the posterior end of the neural arch. The posterior condyle of the centrum is more than twice as wide as high. Its articular surface continues onto the dorsal aspect of the postexapophysis. The postexapophysis bears a scar on the ventrolateral aspect, which Bennett (2001) interpreted as a muscle attachment in *Pteranodon*. The ventral surface of the centrum is slightly concave between the postexapophyses, and bears several longitudinal ridges or striations. The broken anterior end reveals that an ossified neural canal is absent as in some, but not all, azhdarchids (Currie and Russell 1982; Company et al. 1999).

Discussion

Phylogenetic affinities

Phylogenetic affinities of the described specimens are here assessed based on phylogenetic distributional patterns of cervical characters revealed in analyses of pterosaurian relationships by Kellner (2003) and Unwin (2003). More recent

phylogenetic analyses by Kellner (2004) and Wang et al. (2005), both of which were based on modified and expanded versions of the data matrix used by Kellner (2003), recovered essentially the same phylogenetic distributional patterns of cervical characters as revealed by the latter study.

Bayshin Tsav azhdarchid.—Four of six cervical characters used by Kellner (2003) can be coded for the Bayshin Tsav specimen. First, the cervical rib is apparently lacking although a bony bridge enclosing the vertebrocostal canal ventro-laterally might represent a very reduced rib fused to the verte-bra as proposed for azhdarchid cervicals from Alberta by Godfrey and Currie (2005). Kellner (2003) identified this characteristic (state 1 of character 46) as a synapomorphy of Pterodactyloidea (clade stemming from the most recent com-mon ancestor of *Pterodactylus* and *Quetzalcoatlus*).

Three other character states observed in this specimen fur-ther specify its phylogenetic affinity within Pterodactyloidea. First, the Bayshin Tsav cervical is extremely elongated. This characteristic has been considered as a principal diagnostic feature of Azhdarchidae (e.g., Nessov 1984; Padian 1984, 1986; Bennett 1994). Kellner (2003) indeed found this (state 2 of character 45) as characterizing the clade Azhdarchidae (Kellner [2003: 125] defined Azhdarchidae as a stem-based clade of "all pterosaurs closer [sic] related to *Quetzalcoatlus* sp. than to any other pterosaur [sic]". A literal interpretation of this definition, however, would imply that *Quetzalcoatlus* sp. and its recovered sister taxon are the only member of Azhdar-chidae. As he apparently intended to designate this clade as a sister group of Tapejaridae, this clade should have been de-fined as a stem-based clade consisting of all pterosaurs more closely related to *Quetzalcoatlus* sp. than to *Tapejara* or *Tupu-xuara*). Elongation of middle cervicals was also found to char-acterize the clade Archaeopterodactyloidea by Kellner (2003). Although Kellner (2003) distinguished "elongated" cervicals in Archaeopterodactyloidea as "not to the same degree as azhdarchids", he did not provide a quantitative criterion for differentiating the "extreme elongation" in Azhdarchidae from mere "elongation" in Archaeopterodactyloidea. Bennett (1994) and Unwin and Lü (1997) specified "extreme elonga-tion" of middle cervicals observed in Azhdarchidae as the length being equal to, or greater than, five times as long as the width. These studies, however, did not describe how this ratio was calculated, i.e., how the length and width were measured. Unwin (2003), on the other hand, used the length and mini-mum width of the centrum to assess the degree of elongation, and found that the length-to-width ratio of middle cervicals measured in this way being at least 4 characterizes both Euctenochasmatia (including *Pterodactylus*, Lonchodectidae, and Ctenochasmatidae in his analysis) and Azhdarchidae. As described above, the ratio of the length to width of the pre-served portion of the centrum is approximately 5.6 in the Bayshin Tsav specimen, and thus satisfies the criterion used by Bennett (1994) and Unwin and Lü (1997) for "extreme elongation" in Azhdarchidae. In contrast, other studies such as Frey and Martill (1996) and Pereda Suberbiola et al. (2003)

used the ratio between the total length of the vertebra and max-imum transverse distance across the prezygapophyses to as-sess the degree of elongation. This ratio in the preserved por-tion of the Bayshin Tsav specimen is only 3.1. As shown by Frey and Martill (1996) and Pereda Suberbiola et al. (2003), however, this ratio does not necessarily exceed 5 in all azhdar-chid middle cervicals.

Second, the Bayshin Tsav specimen possesses an ex-tremely reduced neural spine (state 3 of character 47), which is also an azhdarchid synapomorphy recovered by Kellner (2003). As described above, the neural spine of this specimen is ridge-like, very low or almost absent in the middle, but in-creases its height on the anterior and posterior ends of the neural arch. Such a "double peak" neural spine is commonly present in azhdarchid middle cervicals including *Azhdarcho longicollis* (Nessov 1984), *Quetzalcoatlus* sp. (Howse 1986), and other forms (e.g., Pereda Suberbiola et al. 2003; Godfrey and Currie 2005; Ösi et al. 2005; Henderson and Peterson 2006). This morphology is in contrast to that of the cervical neural spines in other forms with elongated cervicals such as *Pterodactylus antiquus* (Wellnhofer 1970), ctenochasmatids (Broili 1936), and lonchodectids (Unwin 1991). In these pterosaurs, the neural spine on each post-axial cervical is lamina-like with its height almost constant throughout the entire length of the neural arch.

Third, the Bayshin Tsav specimen lacks a lateral pneu-matic foramen on the centrum (state 0 of character 44). Ac-cording to Kellner (2003), Azhdarchidae is characterized by reversal to this pterosaur plesiomorphy within Ornithocheiro-idea. Therefore, all the observable characters in this specimen are congruent with its placement in the stem-based Azhdar-chidae sensu Kellner (2003).

Three cervical characters used in Unwin's (2003) data matrix are practically the same as those employed by Kellner (2003). First, strong reduction or absence of the cer-vical rib (state 1 of character 26) places the specimen in Pterodactyloidea. The two other character states observed in the Bayshin Tsav specimen, a low neural arch bearing a low neural spine (state 1 of character 52) and elongation of the vertebra (state 1 of character 53), occur twice within Pterodactyloidea in Unwin's (2003) tree: first on the line to Euctenochasmatia and second on the line to Azhdarchidae as mentioned above. Therefore, these character states alone do not determine which clade this specimen belongs to. Unwin (2003), however, proposed detailed characteristics with which the apparently same character states can be dis-tinguished between these two clades. He pointed out that the neural arch is "entirely confluent with the vertebral centrum, forming a single, tubular structure" (Unwin 2003: 167) in Azhdarchidae while these two elements "remains distinct" in some ctenochasmatids. The former condition in Azhdarchidae is probably due to the lack of prominent pro-cesses or laminae (such as the one connecting the pre- and postzygapophyses) that project laterally from the neural arch. The Bayshin Tsav specimen lacks such laminae, and the neural arch and centrum are confluent to produce a

round cross-section, thus conforming to this condition. Therefore, this characteristic suggests the placement of this specimen on the line to Azhdarchidae. It is noteworthy, however, that Unwin (2003) defined Azhdarchidae as a node-based clade consisting of the most recent common ancestor of *Azhdarcho longicollis* and *Quetzalcoatlus northropi* and all its descendants. In a strict sense, therefore, characters discussed here alone would not confidently place this specimen within this node-based Azhdarchidae sensu Unwin (2003).

In addition to characters used for phylogenetic analyses described above, the Bayshin Tsav specimen has a shallow trough extending posteriorly from the vertebrocostal canal on the anterior end of the centrum. Such a trough or sulcus is commonly present in azhdarchid cervicals (e.g., Currie and Russell 1982; Frey and Martill 1996; Kellner and Mader 1996; Martill et al. 1998; Pereda Suberbiola et al. 2003), further supporting the azhdarchid affinity of this specimen.

Burkhant azhdarchid.—One of the cervical characters used by Kellner (2003), presence or strong reduction/absence of cervical ribs, cannot coded decisively for the Burkhant specimen as possibilities that ribs were originally present but have been detached from the specimen cannot be completely ruled out considering that the putative third cervical of this specimen possess a possible diapophysis as described above. Five other characters, however, can be coded for this specimen (assuming the all elements belong to a single individual), and distribution of these characters on Kellner's (2003) phylogenetic hypothesis allows a rather robust inference on the phylogenetic affinity of this specimen. First, the fusion of the atlas and axis (state 1 of character 42) and presence of postexapophyses (state 1 of character 43) place this specimen in Dsungaripteroidea, which is defined by Kellner (2003) as a node-based clade consisting of the most recent common ancestor of *Quetzalcoatlus* and *Nyctosaurus* and its all descendants. As is the case with Bayshin Tsav specimen, the Burkhant specimen is characterized by an extremely reduced neural spine (observed in the fragmentary, posterior part of a cervical) and absence of a lateral pneumatic foramen on the centrum (observed in the putative third cervical). Within Dsungaripteroidea, these characteristics occur only in Azhdarchidae, thus strongly supporting the placement of this specimen in the latter clade.

One characteristic that might potentially contradict the above inference is the shape of the neural spine of the putative third cervical. As described above, the morphology of the base of the neural spine preserved in this vertebra suggests that the neural spine would have been fairly well-developed, unlike a very low, ridge-like neural spine typically present in azhdarchid middle cervicals. Kellner (1996, 2003), however, mentioned that the third cervical in *Quetzalcoatlus* sp. has a well-developed neural spine unlike those of the fourth through sixth cervicals. We examined casts (FMNH PR1081 and TMM uncatalogued specimen) of putative third

cervicals of *Quetzalcoatlus* sp., TMM 41544-16 and TMM 42422-24, and confirmed that these vertebrae indeed bear laminar-like, well-developed neural spines. Therefore, the possible presence of a high neural spine in the Burkhant third cervical is still consistent with the azhdarchid affinity of this specimen proposed here.

As mentioned above, another azhdarchid synapomorphy is the extreme elongation of the middle cervical vertebrae. In the putative third cervical of the Burkhant specimen, the ratio of the length of the centrum to the minimum width of the vertebra is about 4.4 while the ratio between the total length of the vertebra to the maximum width across the prezygapophyses is about 2.4 as described above. Even the former ratio, therefore, does not satisfy the criterion for "extremely elongated" cervicals used by Bennett (1994) and Unwin and Lü (1997). As Pereda Suberbiola et al. (2003) pointed out, however, the length-to-width ratio of middle cervical vertebrae varies greatly within a cervical series of a single taxon, as well as among taxa, in Azhdarchidae. In *Quetzalcoatlus* sp., the only azhdarchid taxon for which a complete cervical series is known, a putative third cervical has the lowest ratio of the total vertebral length to the maximum width across the prezygapophyses (approximately 3.2) among middle cervicals examined by Frey and Martill (1996). Furthermore, Ösi et al. (2005) recently reported that this ratio is approximately 2 in an azhdarchid middle cervical vertebra from Hungary. Therefore, the apparently small length-to-width ratio of the putative third cervical of the Burkhant specimen still falls within the variation of azhdarchid cervicals. Therefore, all the characters used by Kellner (2003) observable in the Burkhant specimen are congruent with its placement in his stem-based Azhdarchidae.

Among three cervical characters in Unwin's (2003) data matrix, on the other hand, two characters can be coded for this specimen: middle cervicals elongated (observed in the putative third cervical) and their neural arch being depressed and bearing a low neural spine (observed in the fragmentary element). As mentioned above, these two character states were found as synapomorphies of Euctenochasmatia as well as those of Azhdarchidae by Unwin (2003). However, as is the case with the Bayshin Tsav specimen, the putative third cervical of the Burkhant specimen apparently lacks laminae that project laterally from the neural arch, and accordingly its neural arch appears to be confluent with the vertebral centrum (although diagenetic breakages along the lateral sides obscure the morphology in these regions to some extent). This characteristic therefore suggests that the specimen belongs to the node-based Azhdarchidae sensu Unwin (2003) or its stem lineage, which is congruent with the result based on Kellner's (2003) characters.

In addition to the above characters, the putative third cervical of the Burkhant specimen possesses a large tubercle on the ventral aspect of the prezygapophyseal pedicle. Such a tubercle is present in an azhdarchid from Spain (Company et al. 1999) as well as in *Phosphatodraco mauritanicus* (Pereda Suberbiola et al. 2003). Although the phylogenetic distribu-

tion of this character has not been examined in a cladistic context, its presence may nevertheless further support the azhdarchid affinity of the Burkhant specimen.

The Burkhant specimen is significant in that it includes a nearly complete, three-dimensionally preserved atlas-axis complex. Among azhdarchids, this complex has been described only briefly in *Zhejiangopterus* (Cai and Wei 1994; Unwin and Lü 1997) and *Azhdarcho* (Nessov 1984). Therefore, the present description of the Burkhant specimen provides the most detailed information on the atlas-axis complex currently available for Azhdarchidae, thus contributing to a better understanding of the anatomy of this clade of pterosaurs (note, however, that this complex of *Quetzalcoatlus* sp. has also been discovered and is now being described together with other postcranial elements: Wann Langston Jr., personal communication 2005). For example, the teardrop-shaped axis postzygapophyseal facet that is anteroposteriorly long and curved dorsally may be unique to Azhdarchidae within Ornithocheiroidea sensu Bennett (1994) and Kellner (2003): the axis postzygapophyseal facet in other well-known ornithocheiroids such as *Pteranodon* (e.g., YPM 1175: see also Bennett 2001) and *Anhanguera* (e.g., NSM-PV 19892: see also Wellnhofer 1991a; Kellner and Tomida 2000) is roughly circular and anteroposteriorly short. In addition to a potential phylogenetic significance, this shape of the postzygapophyseal facet, together with a similarly elongated and anteroposteriorly curved prezygapophyseal facet of the third cervical, would have allowed a fairly large range of dorsoventral flexion at this joint. Assuming that these zygapophyseal facets can slide with each other up to the point where only a half of each area overlaps, as postulated by Stevens and Parrish (1999) as the maximal possible displacement between zygapophyses (without considering effects of the surrounding soft tissues), the axis-third cervical joint of the Burkhant specimen would have allowed an arc of about 45° of dorsoventral motion (Fig. 11). Such a range of mobility would probably not have been possible with anteroposteriorly short zygapophyseal facets observed in *Pteranodon* and *Anhanguera*, suggesting possible differences in functions of the neck between these ornithocheiroids and the Burkhant azhdarchid.

Biogeography and ecology

Most of the Late Cretaceous pterosaur remains that have been found in Inner and East Asia (except for highly fragmentary, indeterminate pterosaurs) belong to Azhdarchidae (e.g., Bakhurina and Unwin 1995; Unwin and Lü 1997; Ikegami et al. 2000; Sues and Averianov 2004). This, in fact, simply reflects the global trend of this clade becoming dominant toward the end of this epoch (e.g., Unwin 2003, 2006). The presence of azhdarchids in the Gobi Desert described here, therefore, is consistent with this trend.

Like many other pterosaur remains, those of many azhdarchids were found in lacustrine (e.g., Padian 1984),
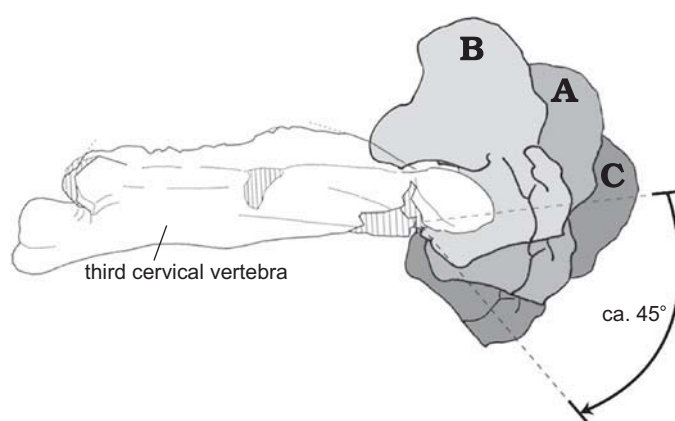

Fig. 11. Dorsoventral mobility at the axis-third cervical joint of the Burkhant azhdarchid (MPC-Nd 100/302) from the Upper Cretaceous of Eastern Gobi Aimag. The "neutral" position with the greatest overlap of the zygapophyseal facets (**A**) and the "maximum" dorsal (**B**) and ventral (**C**) flexions with only a half of each facet overlapping are shown in right lateral view. An arc of about 45° of motion would have been possible at this joint.

coastal (e.g., Bakhurina and Unwin 1995), and marine facies (e.g., Frey and Martill 1996; Pereda Suberbiola et al. 2003). *Quetzalcoatlus* from North America, however, was found in sediments of an inland, fluvial system that was located about 400 km from the nearest coastal line at that time (Lawson 1975; Langston 1981). The Gobi Desert was a mid-continental area situated far from the ocean coastal line of Eurasia in the Late Cretaceous, as it is today (e.g., Jerzykiewicz 2000). Accordingly, the present discovery adds further evidence that some members of Azhdarchidae lived in inland environments, which were apparently not typical habitats of pterosaurs (e.g., Wellnhofer 1991b), reflecting the ubiquitous presence of this clade of pterosaurs in the Late Cretaceous world.

Acknowledgements

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