First evidence of azhdarchid pterosaurs from the Late Cretaceous of Hungary

ATTILA ŐSI, DAVID B. WEISHAMPEL, and CORALIA M. JIANU

New remains of an azhdarchid pterosaur were discovered from the Upper Cretaceous (Santonian) Csehbánya Formation at the Iharkút vertebrate locality in the Bakony Mountains, western Hungary. Among the isolated bones, consisting principally of 21 symphyseal jaw fragments, four cervical vertebrae, a right radius, and some fragmentary limb bones, is a complete articulated mandible that represents one of the best-preserved mandibular material of any presently known azhdarchid pterosaur. The complete edentulous jaw, referred to *Bakonydraco galaczi* gen. et sp. nov. posesses several features diagnostic for azhdarchids which prove that *Bakonydraco* belongs to this group. The cervical vertebrae exhibit azhdarchid features and consequently are referred to as Azhdarchidae indet. The discovery of these fossils helps to understand the construction of the azhdarchid mandible and provides new insight for studying the feeding style of the edentulous azhdarchid pterosaurs.

Key words: Pterosauria, Azhdarchidae, mandible, cervical vertebrae, Cretaceous, Hungary.

Attila Ősi [hungaros@freemail.hu], Department of Palaeontology, Eötvös Loránd University, Budapest, 1117, Hungary; David B. Weishampel [dweisham@mail.jhmi.edu], Center for Functional Anatomy and Evolution, Johns Hopkins University, Baltimore, 21205, USA;
Coralia M. Jianu [coralia.jianu@xnet.ro], Muzeul Civilizației Dacice şi Romane Deva, Deva, 2700, Romania.

Introduction

The systematics of Azhdarchidae Nessov, 1984 (emend. Padian 1986) are among the problematic questions of the pterosaur paleontology, because the material is mostly fragmentary and in most cases poorly preserved. Thus far, the only characters used to diagnose Azhdarchidae are characters of the cervical vertebrae (Frey and Martill 1996; Kellner 2003) because the cervicals are the most often preserved elements of the azhdarchid skeleton. However, it has been noted (Frey and Martill 1996: 244) that the "validity of a family based solely on characters of the cervical vertebrae" is doubtful. Beyond the features of the cervicals, Unwin (2003) mentioned several cranial and non-cervical postcranial characters to diagnose Azhdarchidae; unfortunately, few of these features are well enough preserved among the described taxa that their validity has yet to be determined. Only *Azhdarcho lancicollis* Nessov, 1984 from the Turonian–Coniacian of Uzbekistan (Nessov 1984; Bakhurina and Unwin 1995; Unwin and Bakhurina 2000), *Zhejiangopterus linhaiensis* Cai and Wei, 1994 from the Campanian of China (Unwin and Lü 1997), *Quetzalcoatlus* sp. from the Maastrichtian of North America (Kellner and Langston 1996), *Hatzegopteryx thambema* Buffetaut, Grigorescu, and Csiki, 2002 from the Maastrichtian of Romania (Buffetaut et al. 2003), and *Montanazhdarcho minor* Padian, Ricqlès, and Horner, 1995 from the Campanian of Montana (see McGowen et al. 2002) are represented by at least some reasonably well-preserved cranial and postcranial material. Other taxa in Azhdarchidae, such as

Arambourgiania philadelphiae (Arambourg, 1959) from the Maastrichtian of Jordan (Frey and Martill 1996; Martill et al. 1998), *Quetzalcoatlus northopi* Lawson, 1975 from the Maastrichtian of Texas, and *Phosphatodraco mauritanicus* Pereda Suberbiola, Bardet, Jouve, Iarochéne, Bouya, and Amaghzaz, 2003 from the Maastrichtian of Morocco were described on the basis of postcranial remains only.

During field work from 2000 to 2004 at the recently documented Late Cretaceous (Santonian) Iharkút vertebrate locality (Bakony Mountains, western Hungary; Fig. 1; Ősi et al. 2003; Ősi 2004a, b, in press), several pterosaur specimens were discovered among other vertebrate fossils (such as lepisosteid and pycnodontiform fishes, albanerpetonid amphibians, varanoid lizards, bothremydid turtles, alligatoroid, hsiosuchian? and heterodont eusuchian crocodiles, as well as non-avian theropod, ornithopod and nodosaurid dinosaurs, and enantiornithine birds). All are isolated and most of them are fragmentary. Fortunately, however, a complete lower jaw documents the existence of a new azhdarchid pterosaur in western Hungary. It is one of the best preserved azhdarchid mandibles hitherto known. This and other discoveries (including 21 rostral jaw fragments) represents one of the richest assemblages of azhdarchid pterosaur remains in Europe. Furthermore these are the oldest azhdarchid remains from the continent.

Institutional abbreviation.—MTM, Magyar Természettudományi Múzeum (Hungarian Natural History Museum), Budapest, Hungary.

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Geological setting

The vertebrate locality is situated in an open-pit bauxite mine near the villages of Iharkút and Németbánya, in the northern part of the Bakony Mountains, in western Hungary (Fig. 1). The fossiliferous layer occurs in the Upper Cretaceous Cseh-bánya Formation, which is a fluvial, flood-plain unit consist-ing mainly of variegated clays, paleosols and silt with sand and sandstone layers (Jocha-Edelényi and Császár 1997; Ősi et al. 2003). Palynological studies by Knauer and Siegl-Farkas (1992) indicate a Santonian age for the Csehbánya Formation. The underlying unit is the Upper Cretaceous (pre-Santonian) Halimba Bauxite Formation, which was de-posited in very deep (sometimes 80 m) karstic holes of the Upper Triassic Hauptdolomit Formation. The thickness of the Csehbánya Formation at the Iharkút locality is nearly 50 m and is only partially covered by the Middle Eocene Iharkút Conglomerate Formation.

 The fossil bones are usually isolated and represent a very diverse fauna composed of lepisosteid and pycnodontiform fishes, albanerpetontid amphibians, turtles, varanoid lizards, crocodilians, non-avian theropod, ornithopod and nodosaurid dinosaurs, enantiornithine birds, and azhdarchid pterosaurs. These bones were periodically transported by running water, and subsequently deposited in fossil pockets, similar to the condition reported from other terrestrial vertebrate localities in Europe (Grigorescu 1983; Weishampel et al. 1991; Buffetaut and Le Loeuff 1991; Astibia et al. 1999).

Taxonomy

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Azhdarchoidea Unwin, 1992
Azhdarchidae Nessov, 1984 (emend. Padian 1986)
Genus *Bakonydraco* nov.

Type species: *Bakonydraco galaczi* described below.

Etymology: The generic name derives from name of the Bakony Moun-tains where the locality is situated and from the Latin *draco* = dragon.

Diagnosis.—As for the species.

Bakonydraco galaczi sp. nov.

Holotype: MTM Gyn/3, nearly complete mandible (Fig. 2).

Etymology: In honour of professor and adviser András Galácz who helped us in the Iharkút Research Program.

Type locality: Iharkút, Veszprém County, Bakony Mountains, Trans-danubian Range, western Hungary.

Type horizon: Csehbánya Formation, Upper Cretaceous (Santonian; Knauer and Siegl-Farkas 1992).

Paratypes: MTM Gyn/4, 21 symphyseal fragments of the dentary.

Diagnosis.—Medium-sized azhdarchid pterodactyloid ptero-saur (estimated wing span 3.5 m) that differs from other pterodactyloids in having edentulous, triangular mandible (in
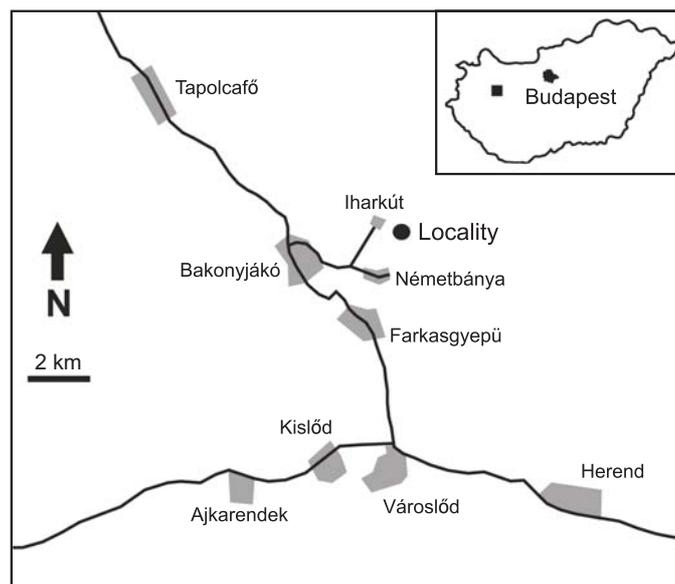

Fig. 1. Locality map showing the site where the pterosaur remains were found.

dorsal view), which has a strong, pointed, laterally com-pressed anterior half of the symphysis. The anterior half of the symphysis bears slit-like foramina on its slightly concave dor-sal surface. The laterally deep profile of the symphysis and the dorsal surface of the anterior half of the symphysis which curves posterodorsally, ending in a transverse ridge posteri-orly clearly distinguish *Bakonydraco* from *Azhdarcho* and from *Zhejiangopterus*. The new taxon differs from *Quetzal-coatlus* in having a different, undivided glenoid fossa.

Description

Mandible (Fig. 2).—The fused symphysis of the 29-cm-long edentulous mandibular rami (MTM Gyn/3) extends approxi-mately 50% of the length of rami and forms a long, pointed ventral mandibular crest. The symphyseal part of the mandi-ble is separated into two parts by a transverse ridge (Fig. 2A, B, E, F). The anterior half of the symphysis is a strong promi-nent beak (Fig. 2E, F) whose dorsal surface curves postero-dorsally and ends in the transverse ridge posteriorly. The maximum height of the symphysis is near the level of this transverse ridge. The dorsal surface of the beak is slightly concave transversely with a very weak median ridge that rises posteriorly. Parallel with the sharp margin this dorsal surface bears 20 slit-like foramina in two rows. In addition, small foramina are visible on the lateral surfaces of the beak of the symphysis. The sizes of these foramina are similar to the sizes of those situated on the dorsal surface of the beak.

 Along the sagittal surface of the left lower jaw (Fig. 3; MTM Gyn/4) are two channels that extend logitudinally. The ventral channel is two times thinner than the dorsal one. It starts on the posteroventral end of the fragmentary lower jaw (MTM Gyn/4) and merges anteriorly with the dorsal channel. The dorsal channel tends to be wider anteriorly and runs al-
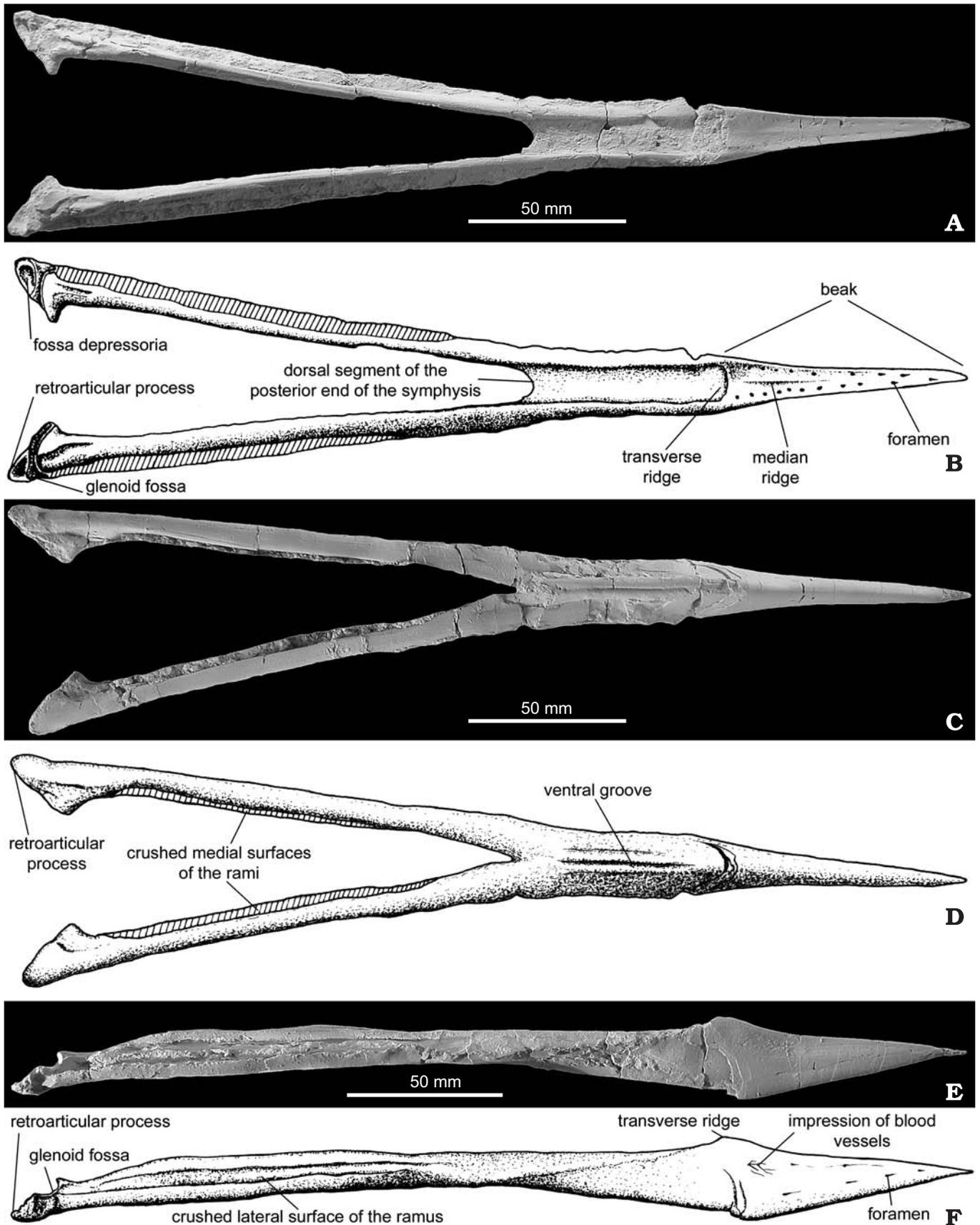
Fig. 2. *Bakonydraco galaczi* gen. et sp. nov. MTM Gyn/3, Iharkút, Bakony Mts., Hungary, Csehbánya Formation, Santonian (Upper Cretaceous). Mandible in dorsal (**A**, **B**), ventral (**C**, **D**), and lateral (**E**, **F**) views.
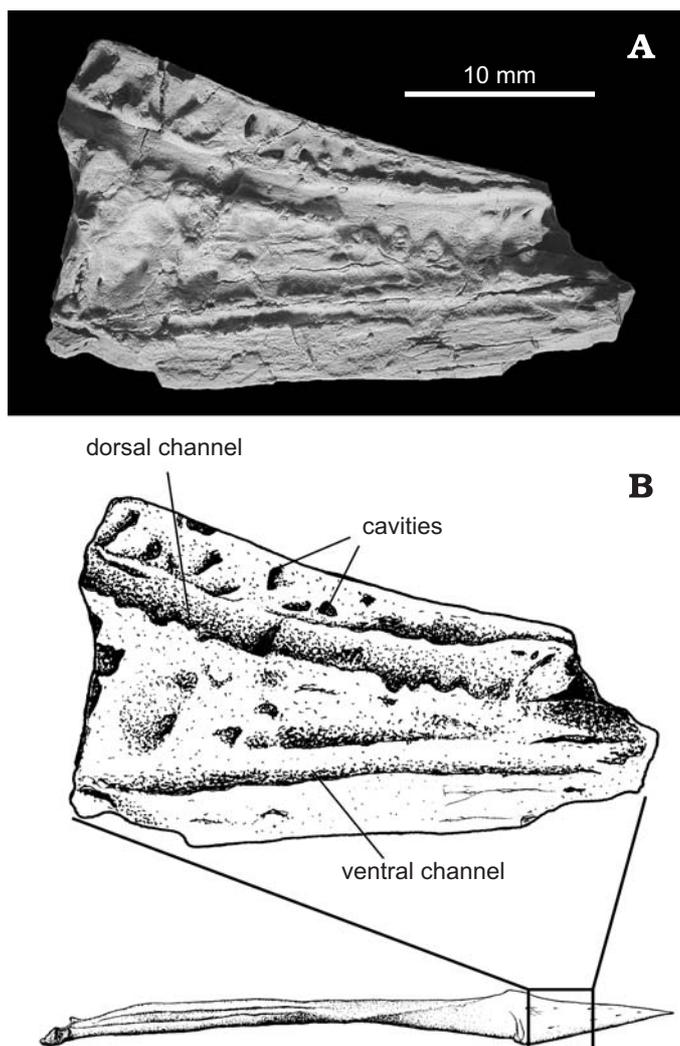
dorsal channel

cavities

ventral channel

Fig. 3. *Bakonydraco galaczi* gen. et sp. nov. MTM Gyn/4, Iharkút, Bakony Mts., Hungary, Csehbánya Formation, Santonian (Upper Cretaceous). Detail of the internal structure of the anterior beak of the lower jaw, photograph (**A**) and explanatory drawing (**B**).

most parallel with the dorsal surface of the beak, reaching the tip of the jaw (MTM Gyn/4). Small cavities and grooves of different sizes are situated between these two channels. The internal structure of the anterior half of the symphysis is filled with cavities that contact the dorsal surface of the symphysis via small foramina.

The ventral border of the ventral mandibular crest is not sharp but rounded anteriorly. A strong groove extends longitudinally on the posterior half of the ventral side of the symphysis. The ventral keel of the beak is straight and is broken only slightly at the tip. Posteriorly the symphysis ends in dorsal and ventral segments. A cavity opens posteriorly between these two segments. The anterior extent of this cavity inside the symphysis is unknown. The ventral segment of the symphysis extends more posteriorly (approximately 5 mm) than the thin, laminated, dorsal segment.

The postsymphyseal rami have rounded dorsal and ventral edges. Due to slight dorsoventral compression, the lateral

and medial walls of the rami are crushed and no sutures between the dentary and the other bones of the mandible are visible.

In posterodorsal view the glenoid fossa is mediolaterally enlarged and S-shaped but is not separated into lateral and medial cotyles. In lateral view the anterior edge of the glenoid fossa lies approximately 5 mm dorsally above the level of the posterior one. In dorsal view the medial part of the glenoid fossa is narrow and inclined anteromedially while its width is doubled laterally. Due to the crushed medial wall of the ramus the adductor fossa is not visible.

Directly posterior to the glenoid fossa, a large, roughly circular depression forms the complete dorsal part of the retroarticular process. This depression is probably the fossa depressoria for the attachment of the M. depressor mandibulae (Wellnhofer 1980).

Azhdarchidae indet. postcranial remains (Figs. 4–6).— Several postcranial remains (cervical vertebrae, limb bones) were also referred to Azhdarchidae. Because all were isolated, they can not be reffered to any taxon with certainty. There is no direct evidence that these remains belong to *Bakonydraco galaczi*, but there are no other azhdarchids yet known in the Iharkút fauna.

Cervical vertebrae (Figs. 4, 5).—Four cervical vertebrae were found as isolated fragments. They are compressed dorsoventrally. In all cases the neural arch is confluent with the centrum. The centrum is hollow and tube-like.

The longest though incomplete cervical (MTM Gyn/448) is 110 mm as preserved and estimated to have been approximately 116 mm long (Fig. 4A). The estimated length (from the end of the postexapophysis to the anterior end of the prezygapophysis) to width ratio (between the prezygapophyses) is 3.3. The elongate prezygapophyses diverge anteriorly with slightly convex oval articular surfaces anterodorsally. The prezygapophysial tubercles emerge from the concave medial faces of the prezygapophyses. The procoelous centrum has a transversely ovoid cotyle that is almost three times wider than high. The anterior end of the hypapophysis is crushed.

A longitudinal sulcus is present on the left side of the ventral surface close to the base of the prezygapophyses. The neural spine is only a low ridge that is slightly higher (no more than 2 mm) anteriorly and posteriorly. The ventral and ventrolateral faces of the centrum are not compressed but here the bony wall is fragmentary. Based on the preserved parts, the middle part of the ventral face of the centrum appears to be semicircular in cross-section. Although the dorsal and dorsolateral faces are mostly compressed, they are flatter than the ventral face. Thus the complete cross-section of the middle section of the centrum was probably subcircular but slightly wider than high. There is no evidence for pneumatic foramina on the preserved part of the bony wall of the centrum. On a small preserved part of the left lateral side of the centrum, a very weak ridge runs anteroposteriorly, parallel with the neural ridge. The postzygapophyses are crushed and missing. The condyle is damaged.
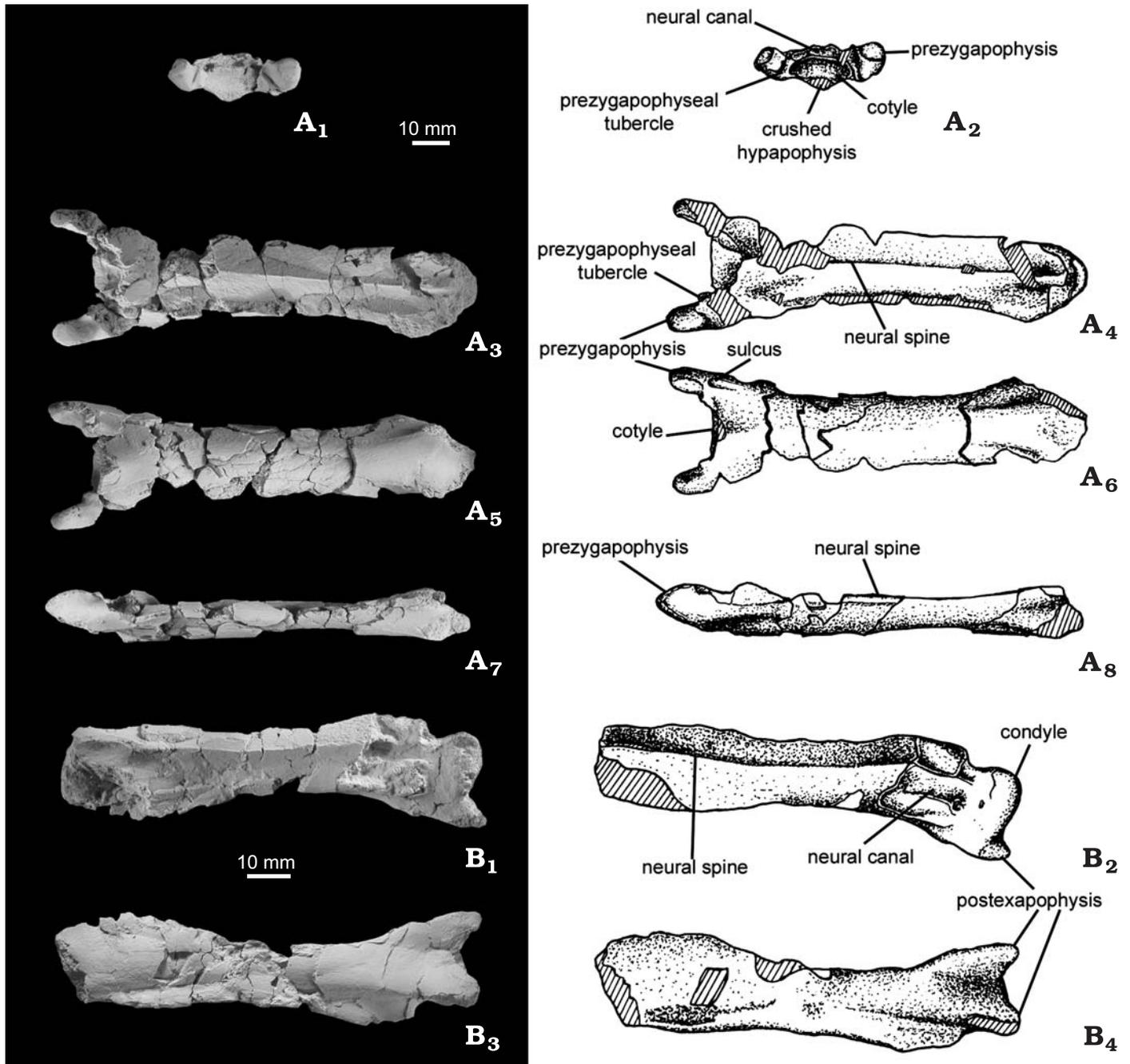
Fig. 4. Azhdarchidae indet. cervical vertebrae, Iharkút, Bakony Mts., Hungary, Csehbánya Formation, Santonian (Upper Cretaceous). **A**. MTM Gyn/448 in anterior (A_1, A_2), dorsal (A_3, A_4), ventral (A_5, A_6), and lateral (A_7, A_8) views. **B**. MTM Gyn/449 in dorsal (B_1, B_2) and ventral (B_3, B_4) views.

The second specimen of cervical vertebrae (MTM Gyn/449) is 99 mm long as preserved, with an estimated length of about 115 mm. Its estimated L/W ratio equals that of MTM Gyn/448 (Fig. 4B). The anterior end is completely damaged, although the anterior end of the low, crest-like neural spine is still visible. Posteriorly the neural spine forms a slight ridge. The pre- and postzygapophyses and the hypapophysis are missing. The condyle of the centrum is slightly damaged, but has a transversely wide oval shape. The postexapophyses, although terminally damaged, pro-ject posteriorly and slightly laterally. Due to the crushed wall of the centrum, its cross-section can only be estimated to be similar to that of MTM Gyn/448.

The third specimen (MTM Gyn/450) is the best preserved of the cervicals and only slighly compressed dorsoventrally (Fig. 5A). Its length as preserved is 77 mm and its estimated length was approximately 79 mm. The estimated L/W is approximately 2.0. Only the lateral and dorsal parts of the left prezygapophysis and a small portion of the left lateral corner of the cotyle are preserved at the anterior end of the vertebra.
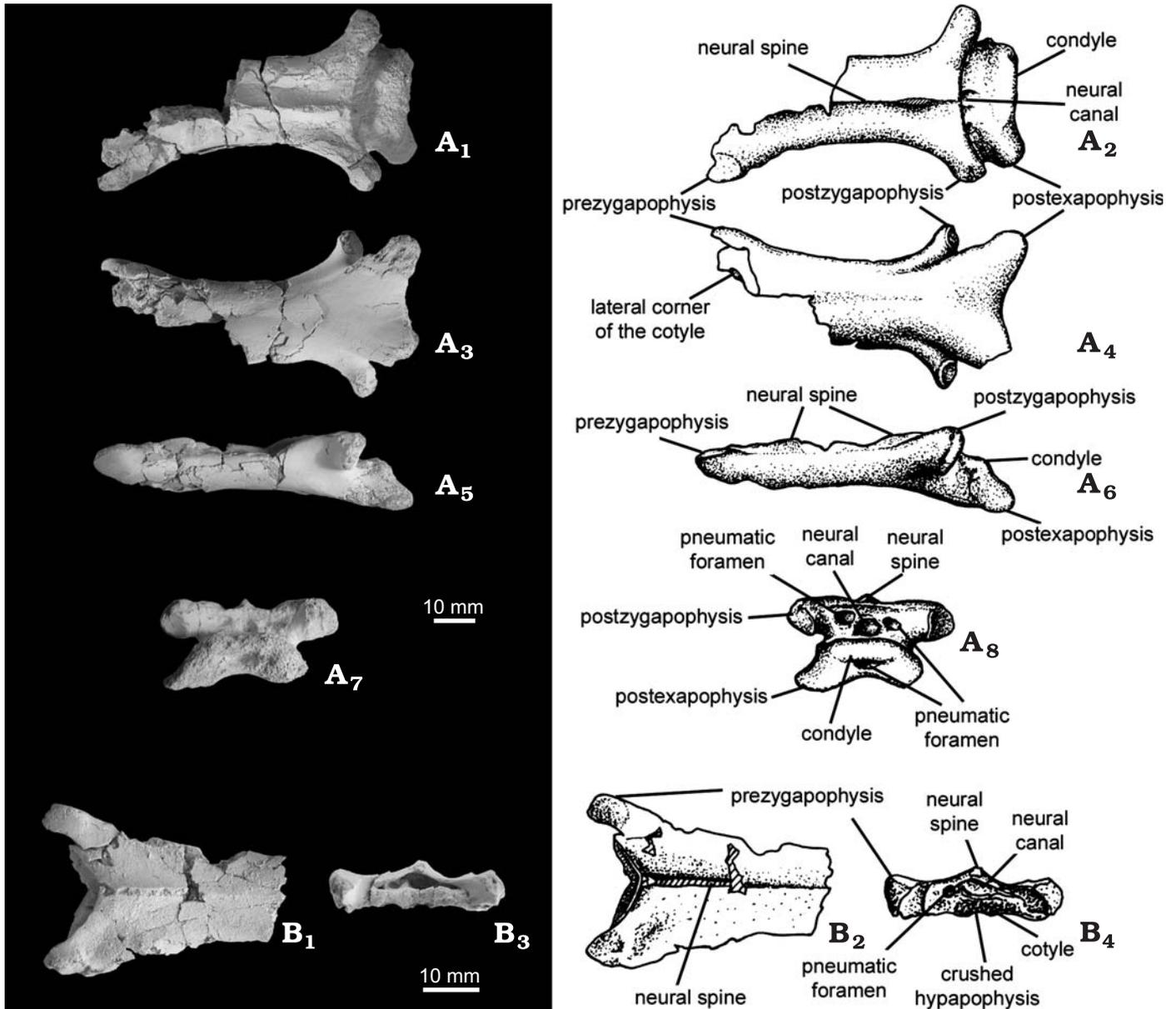
Fig. 5. Azhdarchidae indet. cervical vertebrae, Iharkút, Bakony Mts., Hungary, Csehbánya Formation, Santonian (Upper Cretaceous). **A**. MTM Gyn/450 in dorsal (A_1, A_2), ventral (A_3, A_4), lateral (A_5, A_6), and posterior (A_7, A_8) views. **B**. MTM Gyn/451 in dorsal (B_1, B_2) and anterior (B_3, B_4) views.

The prezygapophyis is almost two times shorter and one and a half times wider than that of the above mentioned longer cervicals (MTM Gyn/448, MTM Gyn/449). The neural spine is higher than in the case of MTM Gyn/448 and MTM Gyn/449. Anteriorly the neural spine is not completely preserved but the height of the left dorsolateral region of the vertebra indicates that the neural spine here was the highest (Fig. 5A_5, A_6). Posteriorly the neural spine is lower and almost disappears after the middle section of the vertebra. The height of the neural spine increases again posteriorly but never reaches the assumed height of the anterior part. There is no evidence for any pneumatic foramina on the lateral sides of the centrum. The postzygapophyses are strongly divergent. Their articular surfaces are directed posteroventally at an angle of 60° against

the horizontal plane. The wide condyle is a little worn. A deep oval depression is present ventral to the condyle. Only the completely preserved left postexapophysis, is directed posterolaterally parallel to the left postzygapophysis in dorsal view. The right postexapophysis is crushed. Two small ovoid cavities are situated lateral to the neural canal. These could be the pneumatic foramina. It is unclear if they continue parallel to the neural canal into the medullar cavity. The middle part of the centum is transversely oval.

The fourth specimen (MTM Gyn/451) is represented by an anterior fragment (Fig. 5B). The procoelous centrum is dorsoventrally compressed. The visible anterior part of the neural spine is very low, similar to those of MTM Gyn/448, MTM Gyn/449, but damaged at the top, and nearly absent on
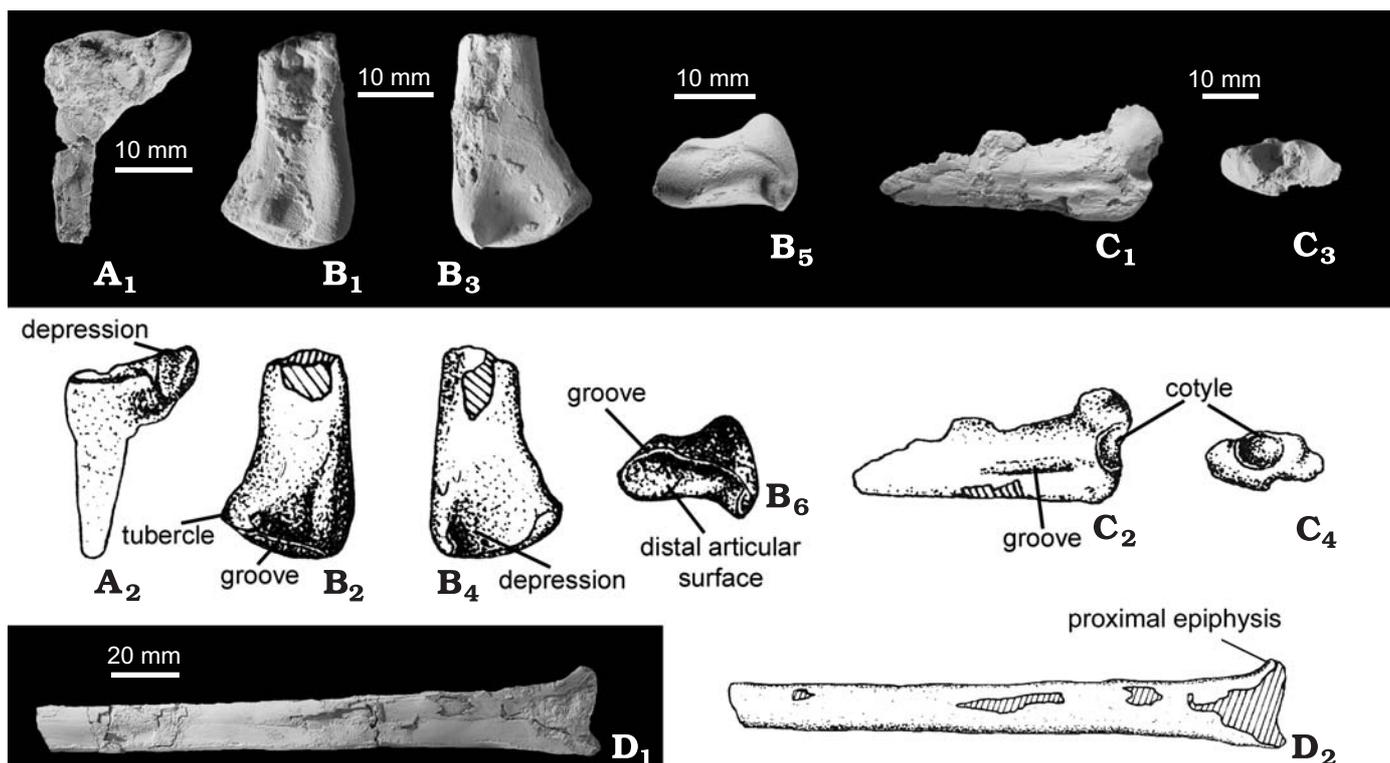
Fig. 6. Azhdarchide indet. wing bones, Iharkút, Bakony Mts., Hungary, Csehbánya Formation, Santonian (Upper Cretaceous). **A**. MTM Gyn/452 proximal end of a right radius in ?anterior (A_1, A_2) view. **B**. MTM Gyn/452 distal end of a right radius in posterior (B_1, B_2), anterior (B_3, B_4), and distal (B_5, B_6) views. **C**. MTM Gyn/453 second? phalanx? of the wing finger in ventral (C_1, C_2) and proximal (C_3, C_4) views. **D**. MTM V.2002.04 proximal half of a first phalanx of the wing finger in ?dorsal view.

the posterior preserved part of the cervical. The hypapophysis is crushed. Although the vertebra is strongly compressed, two small, separated foramina are visible on both lateral sides of the neural canal. They are approximately two times smaller than the opening of the neural canal. The circular cross-section of the neural canal is slightly visible only on the crushed posterior end of the vertebra inside the cylindrical centrum. The prezygapophysial tubercles are discernable on the medial face of the prezygapophyses. There is no evidence for a median pneumatic foramen above the neural canal. Shallow sulci exist on the ventral surface of the vertebra close to the base of the prezygapophyses.

Wing bones (Fig. 6).—Among the five fragmentary pterosaur limb bones discovered at Iharkút, two are undeterminable. The third specimen is a crushed, but complete right radius (MTM Gyn/452, Fig. 6A, B). Most of the diaphysis is completely compacted but preserved (not figured in this paper). A part of the proximal articular surface is crushed, while the distal articulation is well preserved. The distal articular surface is separated by a groove from the anterodistal part of the epiphysis. The ventral tubercle is well developed. The distal part of the radius is wide and robust, ending dorsally in a pointed process posterodistally. The fifth specimen probably represents the proximal end of the second or third phalanx of the wing finger (MTM Gyn/453, Fig. 6C) because in ventral view a groove runs parallel to the shaft of the bone,

which is present on the second and third phalanges of the wing finger of Azhdarchidae (Unwin 2003). A deep, subcircular cotyle is situated on the proximal end of the bone.

The last specimen is the proximal half of a first phalanx of the wing finger (length: 165 mm, MTM V.2002.04, Fig. 6D). Its proximal articular surface is damaged. Whether or not it comes from an azhdarchid pterosaur is uncertain. Should it prove to be, then this phalanx would have come from a pterosaur with a wing span of about 3.3 m (based on calculations by Buffetaut et al. 1996). This would be an estimated wing span like in *Bakonydraco* (3.5–4 m) the wing span estimation of which based on the length of the mandible.

Comparison of the mandible

Given that the nature of diagnostic support for Azhdarchidae consists mainly of postcranial characters (Nessov 1984; Padian 1986; Kellner 2003; Unwin 2003), the position of *Bakonydraco* within this group is difficult to prove. However, four members of the group can be used for a comparison with *Bakonydraco* based on cranial material. The North American *Quetzalcoatlus* is represented by several more or less complete lower jaws (Kellner and Langston 1996). *Montanazhdarcho* from Montana includes fragmentary pieces of an edentulous mandible (Padian et al. 1995; McGowen et al. 2002). *Zhejiangopterus* from China has a nearly complete

but mediolaterally crushed mandible (Cai and Wei 1994; Unwin and Lü 1997). Furthermore some short sections of jaws referred to *Azhdarcho* from Uzbekistan (Nessov 1984; Bakhurina and Unwin 1995) and Spain (Buffetaut 1999) provide further opportunity for comparison.

The dentary of *Quetzalcoatlus* is at least three times longer and has a proportionally longer symphysis than that of *Bakonydraco* (Kellner and Langston 1996). *Zhejiangopterus* has a shorter mandible with a proportionally longer and lower mandibular crest compared to the Hungarian specimen (Cai and Wei 1994). The fragmentary material, which probably includes the symphysis of *Azhdarcho lancicollis* described by Nessov (1984: pl. 7: 10, 11) and the jaw fragment from Spain identified as cf. *Azhdarcho* sp. (Buffetaut 1999: fig. 1a) are very similar to the symphyseal part of the Hungarian mandible. The lack of teeth and the slit-like foramina in two rows on the dorsal surface of the anterior part of the symphysis are common features of the jaw fragments of *Azhdarcho* and of *Bakonydraco* (Nessov 1984; Bakhurina and Unwin 1995). In both taxa this part of the jaw was probably covered by a rhamphotheca which was well supplied by blood vessels and nerves. Similar foramina are present on the tip of the premaxilla of *Thalassodromeus sethi*, a tapejarid from the Early Cretaceous of Brazil (Kellner and Campos 2002), suggesting that not only the tip of the mandible but also that of the premaxilla probably possessed foramina in both *Azhdarcho* and *Bakonydraco*.

The Hungarian mandible has a distinctly deeper profile in lateral view than that of *Azhdarcho* (Alexander Averianov, personal communication to A.Ő. 2004; Unwin and Bakhurina 2000). Furthermore *Azhdarcho* lacks the posterodorsal curvature of the dorsal surface of the anterior part of the symphysis seen on the Hungarian specimen, although the *Azhdarcho* material is very fragmentary (see Unwin and Bakhurina 2000: fig. 21.8a, b).

The divergent mandibular rami of *Bakonydraco* are more similar to those of *Tapejara*, a tapejarid azhdarchoid from the Lower Cretaceous of Brazil (Kellner 1990; Unwin 1992). Moreover the slightly concave dorsal surface with sharp lateral edges at the tip of the symphysis is similar in both *Bakonydraco* and *Tapejara* (Wellnhofer and Kellner 1991). The mandible of *Sinopterus* (a tapejarid from the Early Cretaceous of western Liaoning) is shorter, but proportionally similar to that of *Bakonydraco* (Wang and Zhou 2003). The *Sinopterus* mandible lacks a transverse ridge and the posterodorsal curvature on the dorsal surface of the anterior part of the symphysis in contrast with that of *Bakonydraco*. *Zhejiangopterus* and *Quetzalcoatlus* also differ from *Bakonydraco* in having a flat dorsal surface of the symphysis (Unwin and Lü 1997; Kellner and Langston 1996). The jaw fragments of *Montanazhdarcho* are probably from the anterior part of the mandible; they bear a ventral groove (McGowen et al. 2002) which is also present on the posteroventral part of the symphysis of *Bakonydraco*. In addition, the mandible of *Tapejara* bears a more prominent bony ventral crest on the symphyseal area compared with that of *Bakonydraco*. A sim-

ilar posterodorsal inclination of the dorsal surface of the anterior part of the symphysis that ends in a ridge posteriorly is also known in *Tapejara* but in this taxon, this ridge is blunt. In *Quetzalcoatlus* the dorsal segment of the posterior end of the symphysis is longer than ventrally (see Kellner and Langston 1996), in contrast to *Bakonydraco* which has a 5 mm longer ventral segment. The shape of the unseparated glenoid fossa and the large depression (probably fossa depressoria; Wellnhofer 1980) on the dorsal side of the articular clearly distinguish *Bakonydraco* from *Quetzalcoatlus*.

Compared with the length of the Hungarian mandible to those of *Quetzalcoatlus* and *Zhejiangopterus*, the estimated wing span of *Bakonydraco* was about 3.5–4 m. As such it was a medium-sized pterosaur, similar to most individuals of *Azhdarcho* (wing span 3–4 m; Bakhurina and Unwin 1995) and *Zhejiangopterus* (wing span 3.5 m; Unwin and Lü 1997).

The majority of features presented here (such as the narrow, pointed anterior end of the symphysis, the lack of teeth, the low mandibular crest, the slit-like foramina in two rows dorsally on the symphysis, as well as the cavity at the posterior end of the symphysis which was also mentioned in *Quetzalcoatlus* Kellner and Langston 1996) appear to be possibly diagnostic for the crania of Azhdarchidae and prove that *Bakonydraco* belongs to this group. Nevertheless, based on comparable azhdarchid material, some features of *Bakonydraco* (the profile of the mandibular crest laterally; the shape of the undivided glenoid fossa) indicate that *Bakonydraco* has its own suite of cranial apomorphies. In addition, the posterodorsal inclination of the dorsal surface of the anterior part of the symphysis and the relatively deep profile of the mandible (compared with those of *Quetzalcoatlus*, *Zhejiangopterus* and *Azhdarcho*) are interpreted as convergences with tapejarids. These cranial features might be aligned with the mode of feeding (Eberhardt Frey, personal communication to A.Ő. 2005).

Comparison of the postcranial remains

Apart from *Hatzegopteryx*, all azhdarchid genera are represented by cervical vertebrae although the only azhdarchid taxon with a complete series of cervicals is *Quetzalcoatlus* sp. (Kellner 2003). In addition, several isolated azhdarchid cervicals (mostly fragments) are documented from different regions of the world (see Currie and Russel 1982; Buffetaut et al. 1996; Company et al. 1999; Buffetaut 2001). The four cervical vertebrae (Figs. 4, 5) from Iharkút show a disparity in length. They differ from the peculiar cervical of *Arambourgiania* in having a slightly transverse, oval centrum and they lack two additional dorsal carinae lateral to the neural spine (Frey and Martill 1996; Martill et al. 1998). The two longest vertebrae (MTM Gyn/448, MTM Gyn/449; Fig. 4A, B) with an estimated L/W ratio of 3.3 probably come from the middle (fourth to sixth) of the cervical series. They have a similar L/W ratio like the cervical vertebra referred to cf. *Azhdarcho* by Buffetaut (1999: fig. 1b, c). They share at least two diagnostic features of Azhdarchidae: elongation of the

vertebral body and presence of a low or vestigial neural spine (Nessov 1984; Padian 1984, 1986; Howse 1986; Wellnhofer 1991; Padian et al. 1995; Kellner 2003) although these features are mentioned also in ctenochasmatids and lonchodectids (Howse 1986; Unwin, 2003). The well-preserved specimen (MTM Gyn/448, Fig. 5A) and an other fragmentary cervical (MTM Gyn/451; Fig. 5B) have a sulcus on the ventral side, close to the base of the prezygapophysis, similar to the cervicals of *Azhdarcho* and *Phosphatodraco*. MTM Gyn/448 has a prezygapophysial tubercle (medial process, Pereda Suberbiola et al. 2003), similar to *Phosphatodraco* and to the azhdarchid cervicals from Spain (Company et al. 1999; Pereda Suberbiola et al. 2003).

The confluence of the neural arch with the centrum is characteristic for all the cervicals from the Iharkút locality. Contrast with the above mentioned characters, up to now this feature and the T-shaped cross-section of wing phalanges 2 and 3 seem to be the only clear postcranial character which distinguish azhdarchids from all other known pterosaurs (Unwin 2003; Eberhardt Frey, personal communication to A.Ő. 2005). Because of the preservation, the cervicals lack the pneumatic foramina laterally on the vertebra (probably a secondarily lost feature in azhdarchids, Kellner 2003). However, pneumatic foramina are recognizable lateral to the neural canal on the shortest specimen (MTM Gyn/450; Fig. 5A). Based on the complete or nearly complete azhdarchid cervical series of *Quetzalcoatlus*, *Zhejiangopterus*, and *Phosphatodraco* this cervical (MTM Gyn/450) with an estimated L/W ratio of two could be an anterior (third) or posterior (seventh to ninth) element of the series (Kellner and Langston 1996; Unwin and Lü 1997; Pereda Suberbiola et al. 2003). The presence of three air canals above the neural canal on the anterior end of the cervical vertebra of *Azhdarcho* mentioned by Nessov (1984) is uncertain (Kellner 2003). Similar cavities on the Hungarian vertebrae (MTM Gyn/448, MTM Gyn/451) are present lateral to the neural canal both on the anterior and posterior (MTM Gyn/450) ends, but there is no evidence for the median pneumatic foramen above the neural canal, mentioned by Nessov (1984). We suggest that these lateral cavities are pneumatic foramina similar to the azhdarchid cervicals from the Upper Cretaceous of La Solana (Spain), Cruzy (France), to those of *Azhdarcho*, to *Arambourgiania* from the Maastrichtian of Jordan and to those of *Tapejara*, Brazil (Company et al. 1999; Buffetaut 2001; Frey and Martill 1996; Martill et al. 1998; Wellnhofer and Kellner 1991).

In cross-section, the middle part of two cervicals (MTM Gyn/450, MTM Gyn/451) exhibits only a single, thin bony ring dorsomedially inside the centrum. This must be the neural canal ("tuba vertebralis"; Martill et al. 1998). If this is correct, then the neural canal is ossified throughout its length similar to *Arambourgiania*. A unique feature of one of the Iharkút cervicals (MTM Gyn/450) is the presence of a median cavity ventral to the condyle of the centrum (Fig. $5A_7$, A_8). It is almost twice as wide as high. A similar, although wider cavity is present in *Tapejara* (Wellnhofer and Kellner 1991). This cavity probably also represents a pneumatic foramen.

Comparison of the Hungarian vertebrae with other azhdarchid cervicals suggests a wing span of about 3–3.5 m for the Hungarian azhdarchid. This is the same interpretation that was deduced from estimation based on the mandible (see above). The longest cervicals (MTM Gyn/448, MTM Gyn/449) are similar in absolute length or slightly shorter than those of the mid-cervicals of *Zhejiangopterus* (Unwin and Lü 1997). An anterior cervical fragment from Cruzy, southern France (Buffetaut 2001), has nearly the same size as the fragmentary cervical from Iharkút (MTM Gyn/451). Based on this cervical the estimated wingspan of the Cruzy pterosaur is estimated to be 3 m, which corresponds to the estimate in the case of the Hungarian pterosaur.

Compared the right radius (Fig. 6A, B) from Iharút with that of other azhdarchids the ratio between the total length of radius and the width of the distal end is approximately 7. This ratio is about 8.5 in *Quetzalcoatlus* sp. (Wellnhofer 1991) and 7.8 in another azhdarchid specimen from Montana (Padian and Smith 1992). In distal view the Hungarian radius is very similar to the distal part of the radius of *Azhdarcho* (Nessov 1984: pl. 7: 8; Bakhurina and Unwin 1995) in having a similarly shaped articular surface and a robust and well-developed dorsal side of the distal end. Dorsally the posterodistal process is more pointed in the Hungarian azhdarchid than in *Azhdarcho*.

Discussion

The Late Cretaceous (Santonian) pterosaur material presented here represents the first discovery of pterosaurs from Hungary. All of the remains (one complete mandible, 21 anterior symphyseal jaw fragments, 4 fragmentary cervical vertebrae, one right radius, one partial first phalanx and one partial second or third phalanx of the fourth digit and two undeterminable limb bones) come from the same outcrop at Iharkút. Because all of the pterosaur fossils were isolated, it remains ambiguous whether or not the mandible and the cervical vertebrae originate from the same taxon. The mandible described here as *Bakonydraco galaczi* gen. et sp. nov. and the cervicals bear features diagnostic for azhdarchids, suggesting a single azhdarchid taxon. Furthermore the estimate for the wing span of the animal based on cervicals (3–3.5 m) and on the mandible (3.5–4 m) are similar. The Hungarian cervicals (Figs. 4, 5) which are of azhdarchid construction are probably the cervicals of *Bakonydraco* because the presence of two different azhdarchid pterosaur taxa in one and the same locality appears highly unlikely. The pointed and laterally compressed symphyseal tip with a double row slit-like foramina on the slightly concave dorsal surface of the symphyseal region; as well as the posterodorsal curvature of the dorsal surface of the anterior half of the symphysis that terminates posteriorly in a transverse ridge are unique to the Hungarian mandible, while the vertebrae are almost identical with those of other known azhdarchids. The median pneumatic foramen situated ventral to the condyle of the centrum

(Fig. 5A$_7$, A$_8$) is the single feature of the Hungarian cervicals which distinguish them from other azhdarchid cervicals. On the best preserved cervical (MTM Gyn/450; Fig. 5A) from Iharkút, the articular surfaces of the pre- and postzygapophyses are not parallel. While the articular surface of the prezygapophysis faces nearly dorsally, the postzygapohyses face posteroventrally, similar to the azhdarchid cervicals from Valencia and to those of *Phosphatodraco* (Company et al. 1999; Pereda-Suberbiola et al. 2003). Moreover the posteriorly elongated postexapophyses prevent the downward bending of the vertebral series. These features indicate a rather rigid neck of the Hungarian azhdarchid. Because *Bakonydraco galaczi* is an azhdarchid, it must have had a long neck formed of elongate cervicals which was certainly not very flexible.

The features of *Bakonydraco* provide intriguing information on pterosaur feeding habits. Based on the long, pointed, edentulous mandible with a relatively low mandibular crest, it is likely that this azhdarchid was piscivorous (see Wellnhofer and Kellner 1991), and was able to use its jaws to grab small fishes out of the water. The pointed, laterally compressed tip of the mandible and the relatively wide and slightly concave dorsal surface of the anterior part of the symphysis support this hypothesis. However, skimming as was proposed for *Rhamphorhynchus* (Abel 1912; Wellnhofer 1980) and for *Thalassodromeus sethi* (Kellner and Campos 2002) was certainly not an option for *Bakonydraco* and probably for all azhdarchids because of their narrow, elongate and straight mandibular rami, and their long, rigid neck (Eberhardt Frey, personal communication to A.Ő. 2004).

Another possible feeding option of *Bakonydraco* could be frugivory. The concave, dorsal surface and pointed tip of the symphysis (Fig. 2A, B) looks similar to that of *Tapejara*. In *Tapejara* only the concave tips of the dentary and premaxilla were in contact when the jaws were closed. Thus the resulting oval gap "would have made a perfect tool for picking and plucking fleshy fruits" (Wellnhofer and Kellner 1991: 103). The relatively large wing span (3–4 m) of *Bakonydraco* (estimated wing span in *Tapejara*: 1.5 m, Wellnhofer and Kellner 1991) probably hindered the easy quadrupedal climbing in trees and thus the frugivorous habit of *Bakonydraco* might have been restricted on trees with spacious foliage and/or while walking around among shrubs and trees.

The structure of the mandible of *Bakonydraco* indicates several feeding habits, thus a diverse diet with primarily small, aquatic food items is the most probable for the Hungarian pterosaur.

The well-preserved Hungarian pterosaur remains are particularly important for documenting the diversity, geographic distribution, and stratigraphic occurrence of azhdarchid pterosaurs in Europe. They further confirm the hypothesis that azhdarchids had become the dominant pterosaurs during the Late Cretaceous not only in central Asia and North America but also in Europe (Buffetaut 1999).

Conclusion

Evidence of azhdarchid pterosaur remains in the Late Cretaceous (Santonian) of Iharkút (Bakony Mountains, western Hungary) is provided by a complete mandible, moreover isolated specimens of 21 symphyseal fragments of the dentary, cervical vertebrae and limb bones. The edentulous mandible and the symphyseal fragments are described as a new taxon, *Bakonydraco galaczi* and the postcranial material referred here to the Azhdarchidae. The mandible of *Bakonydraco* clearly differs from that of *Quetzalcoatlus* in having an unseparated glenoid fossa and a depression (probably fossa depressoria) on the dorsal side of the articular. The anterior half of the symphysis closely resembles the jaw fragments of *Azhdarcho*, but the posterodorsal inclination of the dorsal surface of the anterior part of the symphysis and the relatively deep profile of the mandible of *Bakonydraco* distinguish the two taxa. The cervical vertebrae possess several azhdarchid features (e.g., low or vestigial neural spines, neural canal confluent with the centrum), the best preserved specimen (MTM Gyn/450) has a foramen ventral to the condyle (probably a ventral median pneumatic foramen) which is a unique character of the Hungarian azhdarchid vertebra. These remains represent the first discovery of pterosaurs from Hungary and suggest that from the Santonian azhdarchids were the dominant pterosaurs in Europe.

Acknowledgements

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