New pterosaurian remains from the Late Cretaceous (Santonian) of Hungary (Iharkút, Csehbánya Formation)

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Abstract – The Late Cretaceous (Santonian) continental vertebrate locality of Iharkút, western Hungary has provided numerous azhdarchid pterosaur remains including the recently described, *Bakonydraco galaczi*. Since the first report of these fossils, additional remains have been discovered that improve considerably our knowledge of some aspects of the anatomy of azhdarchid pterosaurs. New cranial material described here indicates an edentulous, non-crested premaxillary rostrum in *Bakonydraco* similar to that of *Quetzalcoatlus* and reveals that this rostrum was considerably thinner and more lightly built than the relatively massive, pointed mandibular symphysis. In addition, the contact surface of the upper and lower jaws of *Bakonydraco* at least in the symphyseal region was more similar to *Tapejara wellnhoferi* than to other azdarchids: the contact is irregular and the premaxilla does not fit closely the rostral part of the mandible. Among the postcranial material the atlas–axis complex possessing lateral pneumatic foramina is of great importance because it further supports the notion of interspecific variability of vertebral pneumaticity among pterosaurs.

We describe new azhdarchid pterosaur remains from the Late Cretaceous of Hungary.

1. Introduction

Remains of azhdarchid pterosaurs are among the rarest vertebrate fossils, nevertheless they inform us about some of the largest known flying creatures in the history of life. Although most of this record consists of incomplete material (Witton and Naish, 2008), it indicates a cosmopolitan occurrence of the group (Fig. 1, Barrett et al., 2008). Only two genera (*Quetzalcoatlus* and *Zhejiangopterus*) are represented by abundant (several individuals in each genus) and relatively well preserved cranial and mandibular material (Kellner and Langston, 1996; Cai and Wei, 1994; Unwin and Lü, 1997). Other azhdarchid genera such as *Hatzegopteryx* (fragmentary occipital region and quadrate, humerus, Buffetaut et al., 2002; 2003), *Azhdarcho* (lower jaw tips, premaxilla fragments, premaxilla–nasal fragment, fragmentary quadrates, Nessov, 1984; Buffetaut, 1999, Averianov 2010), *Bakonydraco* (complete lower jaw, symphyseal tips, Ősi et al., 2005; premaxilla [described here]), *Alanqa* (lower jaw tip, Ibrahim et al., 2010), *Volgadraco* (lower jaw tip, Averianov et al., 2008), *Aralazhdraco*, (jugal, Averianov, 2004; 2007) and *Montanazhdarcho* (lower jaw tip, wing bones, vertebrae, Padian et al., 1995; McGowen et al., 2002) possess only scanty and fragmentary cranial remains, thus comparative work on most of them has proven to be quite difficult. *Eoazhdarcho* from the Early Cretaceous of China was originally referred to the Azhdarchidae (Lü and Ji 2005) but recent cladistic analyses indicated its more basal position within the Azhdarchoidea (Lü et al. 2008, Witton and Naish 2008). Besides the material described at generic level, some additional lower jaw tips have been referred to Azhdarchidae (Wellnhofer and Buffetaut, 1999; Averianov et al., 2008).

Regarding postcranial material, isolated or sometimes associated cervical vertebrae are among the most frequently found diagnostic elements (see e.g. Lawson, 1975; Currie and Russell, 1982; Nessov, 1984; Frey and Martill, 1996; Company et al., 1999; 2001; Buffetaut, 1999; 2001; Buffetaut et al., 1997; Kellner, 2003; Pereda Suberbiola et al., 2003; Godfrey and Currie, 2005; Ősi et al., 2005; Henderson and Peterson, 2006; Averianov et al., 2008; Vremir et al., 2009; Watabe et al., 2009). In addition, isolated remains of part of the notarium, pectoral girdles and limb elements have been described from various Cretaceous localities (for an overview see Barrett et al., 2008).

In the first report on Hungarian pterosaurs Ősi et al. (2005) described a complete mandible (MTM Gyn/3) and 21 symphyseal fragments of *Bakonydraco galaczi*, and some isolated postcranial elements referred to as Azhdarchidae indet., including four cervicals (MTM Gyn/448–451), a fragmentary right radius (MTM Gyn/452), a second phalanx of the wing finger (MTM Gyn/453, reinterpreted here as the distal end of an ulna?), and the proximal half of a first phalanx of the wing finger (MTM V.2002.04).Here, we describe additional pterosaur remains from the Late Cretaceous (Santonian) of Iharkút, western Hungary that, although fragmentary and isolated, improve our knowledge of this poorly known group of pterosaurs. All pterosaur material has been collected from the Upper Cretaceous Csehbánya (Santonian) Formation (for a detailed geological setting see Ősi and Mindszenty, 2009). The material is housed in the Hungarian Natural History Museum in Budapest.

Institutional Abbreviations— **BSPG**, Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany; **MPC**, Mongolian Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **MTM**, Magyar Természettudományi Múzeum (Hungarian Natural History Museum), Budapest, Hungary; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

2. Systematic Palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Azhdarchoidea Nessov, 1984

Azhdarchidae Nessov, 1984 (emend. Padian 1986)

Bakonydraco Ősi, Weishampel et Jianu, 2005

Bakonydraco galaczi Ősi, Weishampel et Jianu, 2005

Holotype: MTM 2007.110.1 (originally Gyn/3 in Ősi et al., 2005), nearly complete mandible.

Paratype: MTM 2007.111.1 (originally Gyn/4 in Ősi et al., 2005), 21 symphyseal fragments of the dentary.

Referred material: fragmentary premaxilla (MTM V 2010.80.1.), 22 symphyseal fragments of the dentary (MTM V 2010.74.1–22.).

Description and comparisons

Premaxilla. The pointed, edentulous premaxilla (Fig. 2A–C) with a preserved anteroposterior length of 114 mm is triangular in cross section with a more or less flat ventral (occlusal) surface. Opposing premaxillae are fused at the midline and no suture can be observed between them. The premaxilla can be easily distinguished from the beak-like edentulous mandibular symphysis on the basis of the following features: 1) the lateral edges of the premaxilla are not as sharp as those of the lower jaw tips, especially in its anterior part; 2) the dorsal margin of the premaxilla is keeled (but not crested) and not rounded as the ventral margin of the mandibular tips; 3) the angle between the dorsal and ventral margins of the premaxillary anterior tip is 10° (Fig. 2A, B) in contrast to the 15° angle of the mandibular tip; 4) the internal structure of the premaxillary rostrum is distinct from that of the mandibuar tip in having a single, median channel with an oval or drop-shaped cross section (for details of the inner structure of the mandibular tip see Ősi et al., 2005:fig. 3); 5) the occlusal surface of the premaxilla bears approximately six pairs of small and elongate slit-like foramina in two rows

(Fig. 2C) in contrast to the 10 pairs present in the mandible. Small nutritive foramina are also seen on the lateral surfaces of the premaxilla, similarly to *Azhdarcho* (Averianov 2010). The ventral surface bears a very shallow median ridge resembling that seen on the dorsal surface of mandibular tip., A similar shallow, median ridge is also present in *Azhdarcho* (Averianov 2010). There is no indication of a sagittal crest on the dorsal part of the premaxilla. The preserved part of the dorsal margin is straight, similar to *Quetzalcoatlus* (Kellner and Langston, 1996) and *Zhejiangopterus* (Cai and Wei, 1994) and contrary to *Tapejara* (Wellnhofer and Kellner, 1991). Posteriorly, the premaxilla is crushed thus the position of the anterior margin of the nasoantorbital fenestra is ambiguous. In dorsal aspect, the rostrum of the azhdarchoid *Lacusovagus magnificens* anterior to the nasoantorbital fenestra (Witton, 2008) appears to be wider lateromedially than in *Bakonydraco*.

Azhdarchidae indet.

Referred material: atlas–axis complex (MTM V 2010.82.1.), posterior part of a mid-cervical vertebra (MTM V 2010.81.1.), glenoid region of a scapulocoracoid (MTM V 2010.79.1.); distal fragment of a humerus (MTM V 2010.77.1.), distal fragments of two ulnae (MTM V 2010.78.1. and MTM V 2010.75.1.=Gyn/453); ?third or ?fourth wing phalanx (MTM V 2010.83.1.); proximal tibia fragment (MTM V 2010.76.1.).

In addition, four cervical vertebrae (MTM V 2010.100.1.=Gyn/448 in Ősi et al., 2005, MTM V.01.51.=Gyn/449, MTM V 2010.101.1.=Gyn/450, MTM V. 2003.21.=Gyn/451) a right radius (MTM V 2010.102.1.=Gyn/452), and the proximal half of a first wing finger phalanx (MTM V.2002.04.) were assigned to Azhdarchidae by Ősi et al. (2005),but are not considered here.

Remarks: Except for the posterior part of a mid-cervical vertebra (MTM V 2010.81.1.), none of the elements listed above possesses diagnostic features of the Azhdarchidae (Kellner, 2003; Unwin, 2003), thus they are assigned to this lineage on the basis of comparison with other specimens referred to azhdarchids.

Description and comparisons

Atlas–axis complex. The atlas and the axis are strongly fused but a weak suture can be observed between their centra on the left lateral side (Fig. 2D). The neural arch is broken. Anteriorly the deep, circular cotylus has a distinct margin and it is oriented anteroventrally at an angle of 57° against the ventral surface of the centrum. The ventral suface of the complex is flat posteriorly and slightly convex anteriorly. The massive and divergent postexapophyses have a posteroventral orientation (Fig. 2D, E) and are almost twice as high dorsoventrally as wide lateromedially. Only a small part of the original articular surface of the condyle is preserved which indicates a wider than high, oval condyle, similarly to that of *Anhanguera* (Wellnhofer, 1991), *Pteranodon* (Howse, 1986), and azhdarchids such as *Azhdarcho* (Nessov, 1984), *Aralazhdarcho* (Averianov, 2007) and the Mongolian azhdarchid "Burkhant specimen" (MPC-Nd 100/302, Watabe et al., 2009). Laterally the centrum of the axis possesses one pair of pneumatic foramina (3 mm in diameter, Fig. 2D) similarly to that of the Central Asian azhdarchids (Nessov, 1984; Averianov, 2007) but in contrast to the Mongolian azhdarchid MPC-Nd 100/302 (Watabe et al., 2009). This foramen presumably opens into the centrum.

Mid-cervical vertebra. The posterior half of a mid-series cervical (MTM V 2010.81.1.) is slightly compressed dorsoventrally due to compaction. Most of its features including its position in the cervical series appear to be identical with those described in MTM V 2010.101.1. (Ősi et al., 2005). The estimated length/width ratio is approximately 2.0 similarly to MTM V 2010.101.1. However, this specimen bears the best preserved condyle among the cervicals from Iharkút, and is 2.5 times wider than high. A possible intraspecific or ontogenetic difference appears in the dimensions of the oval depression below the condyle.

On the new specimen this depression is as deep as on MTM V 2010.101.1. (Ősi et al., 2005:fig. 5).

Scapulocoracoid. MTM V 2010.79.1. is a partial left scapulocoracoid (Fig. 2G–I) preserving only the most robust area immediately around the glenoid. This specimen is slightly compressed and it is very similar to a scapulocoracoid fragment (TMP 81.16.182) from the Late Cretaceous of Canada (Godfrey and Currie, 2005: fig. 16.6A). The scapula and the coracoid are completely fused and no suture can be seen. The glenoid is saddle-shaped and is bordered anteriorly by the robust coracoid tubercle (Fig. 2G) and towards the scapula by a shallow ridge that is slightly eroded. Similarly to TMP 81.16.182, the glenoid extends more anteriorly on the dorsal than on the ventral side. In this dorsal part a pneumatic foramen invades the coracoid (Fig. 2I) as in the coracoids of TMP 81.16.182 (Godfrey and Currie, 2005) and of *Montanazhdarcho* (McGowen et al., 2002). The medial side of the glenoid area is crushed but this dorsoventrally wide surface appears to have been slightly concave. Only a 1.5 cm long piece is preserved from the scapula that is more extensive lateromedially than dorsomedially.

Humerus. The distal fragment of a right humerus (MTM V 2010.77.1.) has preserved only a short segment of the partial diaphysis and the medial part of the distal epiphysis (Fig. 2J–L). The humerus is characterized by a complex distal articulation similar to the smaller, fragmentary humeri described by Godfrey and Currie (2005:fig. 16.6F, G) from the Late Cretaceous of Canada. The medial condyle has a well developed, rounded and obliquely oriented surface ventrally and partly distally (Fig. 2K). It is separated from the slightly eroded medial epicondyle by a 3 mm wide shallow ridge.

Ulna. Of the two fragmentary ulnae (MTM V 2010.78.1. and MTM V 2010.75.1.=Gyn/453) MTM V 2010.75.1. has been referred to as the proximal end of the second or third phalanx of the wing finger by Ősi et al. (2005). Here, we reassess this element and consider it as a distal part of the right ulna based on the presence of the fovea carpalis (Bennett, 2001) and a slightly eroded but remarkable tubercle dorsally. MTM V 2010.78.1. is a left and more complete one (Fig. 2M–P) possessing a relatively well preserved distal epiphysis. The dorsal condyle is well developed but is slightly eroded posterodorsally and anteriorly. A wide and slightly concave ridge separates this condyle from the tubercle (Fig. 2N, P). The tubercle is slightly eroded but must have been quite pronounced as in *Pteranodon* (Bennett, 2001) and *Santanadactylus* (Wellnhofer, 1985). It borders the deeply concave and circular fovea carpalis dorsally (Fig. 2N, P). Posteriorly, proximal to the tubercle no pneumatic foramen occurs in contrast to the condition in *Pteranodon*, *Santanadactylus*, and *Montanazhdarcho* (Wellnhofer, 1985; Bennett, 2001; McGowen et al., 2002). On the posterior surface of both ulnae a shallow groove is present proximodistally just below the fovea carpalis.

Tibia. The proximal end of a left tibia (MTM V 2010.76.1., Fig. 2Q–S) is compressed anteroposteriorly. The proximal articular surface is slightly concave anteroposteriorly (Fig. 2S), similar to that of *Pteranodon* (Bennett, 2001). In anterior view, a deep groove is present (Fig. 2Q) between the shallow cnemial crest of the tibia and the lateral process for the attachment of the fibula (Fig. 2R). Possibly, this lateral process is the co-ossified fibula. This groove continues distally becoming progressively shallower.

Pterodactyloidea indet.

Referred material: Left articular region of a lower jaw (MTM V 2010.98.1.), metacarpal IV (MTM V 2010.99.1.).

Description and comparisons:

Mandible. The posterior end of the mandible (MTM V 2010.98.1., Fig. 3A, B) is compressed lateromedially due to diagenetic events. It has a well developed glenoid which appears not to be as wide lateromedially as that of *Bakonydraco*. Due to its preservation, however, the exact lateromedial width and also the presence or absence of an intercotylar ridge as seen in *Quetzalcoatlus* (Kellner and Langston, 1996) or in *Pteranodon* (Bennett, 2001) are unclear (Fig. 3B). The anterior margin of the deep glenoid is high (Fig. 3A) indicating the articulation of a steeply inclined quadrate corresponding to the general condition in pterodactyloids. The ventral side of the jaw fragment is straight and rounded lateromedially. The retroarticular process is short; a fossa depressoria is not recognizable in contrast to *Bakonydraco*. Due to its fragmentary nature, it is not clear whether this specimen belongs to an azdarchid or rather represents a non-azhdarchid pterosaur.

Metacarpal IV. A possible distal end of a fourth metacarpal (MTM V 2010.99.1., Fig. 3C–E) is strongly compressed dorsoventrally. The diaphysis is flattened and the condyles are slightly rotated relative to their original plane. In the intercondylar groove a rounded crest can be observed (Fig. 3C, E) that is not present in azhdarchids but a similar structure has been reported in *Santanadactylus* (Wellnhofer, 1985:fig. 21; Wellnhofer, 1991:fig. 30). Proximal to the intercondylar groove a small depression is present but no pneumatic foramen can be observed as is the case in *Pteranodon* (Bennett, 2001). The anterior surface of the epiphysis is strongly compressed so the presence of a pneumatic foramen as seen on the azdarchid wing metacarpal described by Godfrey and Currie (2005) is ambiguous. The dorsal condyle is in a better condition than the ventral one and it is not as developed and crest-like as that on the azhdarchid metacarpal illustrated by Godfrey and Currie (2005:fig. 16.9). The ventral condyle appears to have had a ventrally oriented knob-like process. The dorsal condyle of *Pteranodon* (Bennett, 2001:fig. 89) differs from that of the Hungarian specimen because it has a massive condyle with a wide articular surface.

Wing phalangx. The distalmost part of a third or fourth phalanx (MTM V 2010.83.1.) of the wing finger is missing. The anteroposteriorly slightly bowed bone is needle-like, appears to be pointed distally and is widest at its proximal epiphysis. Its cross section is not T-shaped but rather oval with a more keeled anterior edge. Here, the proximal articular surface is shallow, circular and concave and is bordered anteriorly by a thicker bony margin probably for the attachment of ligaments of the interphalangeal joint.

3. Discussion

3.1 *The rostrum of* Bakonydraco

Although azhdarchid remains have been reported from various localities and indicate a more or less cosmopolitan occurrence of the group at least during the Late Cretaceous (Barrett et al., 2008), cranial material is extremely rare (Witton and Naish, 2008). Thus, the cranial remains of *Bakonydraco* are of significance because the complete lower jaw (holotype, Ősi et al., 2005) along with the premaxilla (MTM V 2010.80.1.) described herein improve our knowledge of the rostral portions of the cranium and mandible of azhdarchid pterosaurs (Fig. 4). Wellnhofer and Buffetaut (1999) described a pointed premaxilla (BSPG 1993 IX 338) from the Kem Kem beds of Morocco and referred to it as a member of Pteranodontidae. Ibrahim et al. (2010) reinterpreted this bone as an azhdarchid and assigned it to *Alanqa*. The latter authors may be right, however, this rostral part of pteranodontids and azhdarchids shows numerous common features, thus, until more complete specimens are described, we regard the taxonomic position of this specimen as doubtful. Otherwise, some unpublished postcranial material from this horizon further supports the presence of pteranodontids (Buffetaut, in prep.), thus the coexistence of pteranodontids and azhdarchids in this area seems to be valid. Besides the North American *Quetzalcoatlus* and the Chinese *Zhejiangopterus*, *Azhdarcho* (Averianov 2010) and *Bakonydraco* are the only azhdarchid pterosaurs in which the rostral region of both the upper and lower jaws is known.

Reconstruction of the rostral region (i.e. matching the premaxillary fragment with the mandible, Fig. 4) in *Bakonydraco*, however, raises some interesting questions. The ventral surface of the premaxilla is straight (at least on the 114 mm long preserved part) as in *Quetzalcoatlus* (Kellner and Langston, 1996), *Zhejiangopterus* (Cai and Wei, 1994) and the azhdarchoid *Lacusovagus* from the Early Cretaceous of Brazil (Witton, 2008), and not concave as in tapejarids (i.e. "rostral end [of the skull] downturned" used as a diagnostic character by Kellner and Campos, 2007). The mandibular symphysis of *Bakonydraco*, however, has an anteroposteriorly concave occlusal surface that is followed by a transverse ridge seen both on the holotype and on various isolated symphyseal fragments. This feature does not occur in any other known azhdarchid mandibles (Averianov et al., 2008:fig. 2) where the occlusal surface, including the symphyseal region, remains straight along the entire length of the mandibular rami. A similar transverse ridge, although with different dimensions dorsally, is more characteristic of tapejarids (e.g. in different species of *Tapejara*, *Tupandactylus, Sinopterus*, Lü et al., 2007; Fig. 4). On the other hand, concerning the interpretation of the actual shape and possible functional mechanism of the pterosaurian jaws, the presence of a keratinous rhamphotheca should always be taken into account. Direct (soft part preservation, Frey et al., 2003a) and indirect (nutritive foramina on the surface of the jaws, Buffetaut, 1999; Ősi et al., 2005) evidence of such a keratinous covering has led Frey et al. (2003b) to conclude that this feature was probably present in all edentulous pterosaurs, including *Bakonydraco* where the surface of both the premaxillary fragment and the rostral portion of the mandible has numerous openings interpreted as nutritive foramina. Thus, what is questionable is probably not the presence of a rhamphotheca in *Bakonydraco*, but rather its exact shape and extent. For example, the thickness and structure of the cutting-edge of the keratinous covering on the occlusal surface or its extent beyond the bony tip anteriorly are practically unknown in *Bakonydraco* and most other azhdarchoid taxa (in all azhdarchids and most tapejarids, e.g. *Tapejara wellnhoferi, Tupandactylus imperator*). These are exactly those features that would contribute to our knowledge of the functional aspects of jaw mechanics and possible feeding strategy of these animals, similarly to birds with a highly developed rhamphotheca (Fig. 5). Based on the available cranial material it appears that the contact surface of the jaws of *Bakonydraco* was more similar to that of *Tapejara wellnhoferi* than to those of other azhdarchids, in the manner of an irregular contact (Fig. 4) where the premaxilla is not the exact counterpart of the mandible rostrally. By contrast, in other azhdarchids there is an apparently extensive and uninterrupted contact present along most of the dorsal edge of the mandible. This conspicuous diversity in form and structure of the rostrum may be related to different feeding strategies adopted by different toothless pterosaurs. They could have equally been “stork- or ground hornbill-like generalists foraging for small animals and carrion” (Witton and Naish, 2008) or frugivores (Wellnhofer and Kellner, 1991; Ősi et al., 2005).

3.2 *Remarks on vertebral pneumaticity*

The presence or absence of a pneumatic foramen on a cervical vertebra does not necessarily reflect taxonomical differences. Based on a newly described specimen of *Rhamphorhynchus muensteri*, Ősi and Prondvai (2009) pointed out that as in extant birds (Hogg, 1984) the occurrence of pneumatic foramina is characterized by both inter- and intraspecific variability. The atlas–axis complex described here as well as the atlas–axis complexes from Central Asia (Nessov, 1984; Averianov, 2007) possess a lateral pneumatic foramen in contrast to the apneumatic Mongolian azhdarchid specimen MPC-Nd 100/302 (Watabe et al. 2009).

4. Conclusions

The new Santonian pterosaur material from Hungary described here has on the one hand answered some open questions, on the other raised some new ones. With the rostral part of the previously unknown premaxilla of *Bakonydraco galaczi* it is clear that the upper jaw of the Hungarian azhdarchid was similar in shape to that of other azdarchids. However, owing to the structure of the lower jaw which is so different from the general azhdarchid condition and more resembles that of tapejarids, the occlusion of the jaws appears to be imperfect with pronounced gaps being present between the occluding surfaces. This construction makes functional interpretations of jaw mechanics and thus feeding habits very difficult; at the same time it gives rise to different interpretations of the functional relevance of a keratinous rhamphotheca.

The preserved parts of the mid cervical vertebra, scapulocoracoid, humerus, ulnae, wing phalanx and tibia all assigned to Azhdarchidae have provided new information on morphological attributes thus expanding our general knowledge of azhdarchid anatomy. The comparison of the state of pneumaticity of the atlas–axis complex among azhdarchids has confirmed the notion of interspecific variability in this feature at family level. The morphological differences between the articular region of the indeterminate Pterodactyloidea mandible and that of *Bakonydraco galaczi* and the peculiar metacarpal IV which shows a mixture of characteristics of different pterosaur clades raises the question of whether pterosaurs were represented by more than one family, the Azhdarchidae, in this area during the Santonian.

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Figure captions:

Figure 1. Geographic distribution of azhdarchid pterosaur remains (data from Barrett et al., 2008).

Figure 2. Azhdarchid pterosaur remains from the Upper Cretaceous (Santonian) Csehbánya Formation, Iharkút, western Hungary. A, premaxillary rostrum of *Bakonydraco galaczi* (MTM V 2010.80.1.) in right lateral, B, left lateral, C, occlusal views. D, Azhdarchidae indet. atlas–axis complex (MTM V 2010.82.1.) in left lateral, E, ventral, F, anterior views. G, partial left scapulocoracoid (MTM V 2010.79.1.) in lateral, H, ventral, I, dorsal views. J, distal fragment of a right humerus (MTM V 2010.77.1.) in posterior, K, ventral, L, distal views. M, distal fragment of a left ulna (MTM V 2010.78.1.) in dorsal, N, posterior, O, ventral, P, distal views. Q, proximal end of a left tibia (MTM V 2010.76.1.) in anterior, R, lateral, S, proximal

views. Abbreviations: aso, articular surface for occipital condyle; cc, cnemial crest; ct, coracoid tubercle; dc, dorsal condyle; fc, fovea carpalis; fo, foramen; g, groove; gl, glenoid; lpf, lateral process for the fibula; mc, medial condyle, pex, postexapophysis; pf, pneumatic foramen; r, ridge; s, suture; sc, scapula; t, tubercle; vsnc, ventral surface of the neural canal

Figure 3. Pterodactyloidea indet. remains from the Upper Cretaceous (Santonian) Csehbánya Formation, Iharkút, western Hungary. A, posterior end of a left mandible (MTM V 2010.98.1.) lateral, B, dorsal views. C, distal end of a fourth metacarpal? (MTM V 2010.99.1.) in posterior, D, dorsal, E, distal views. Abbreviations: dc, dorsal condyle; gl, glenoid; ig, internal groove; rp, retroarticular process; vc, ventral condyle

Figure 4. Anterior part of the rostrum and mandible in edentulous pterosaurs. Scale bars equal 5 cm.

Figure 5. The rhamphotheca and its attachment area in *Ramphastos sulfuratrus*. A, *Ramphastos sulfuratrus* skull without horny rhamphotheca, B, *Ramphastos sulfuratrus* skull with rhamphotheca. Note the serrated lateral margin of the horny rhamphotheca. Courtesy of Natural History Musum, London. Photo taken by Joanne H. Cooper.