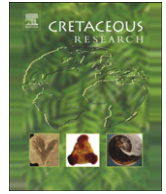




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Non-avian theropod dinosaurs from the early late cretaceous of central Europe

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ABSTRACT

Quantitative and qualitative analyses of isolated teeth and postcranial elements of non-avian theropod dinosaurs from the Upper Cretaceous (Santonian) Csehbánya Formation, Iharkút (western Hungary) indicate that these remains represent multiple dinosaur groups. Based on comparative and statistical analyses, 58 teeth and tooth fragments are identified as belonging to medium-sized basal tetanuran theropods that may have represented the top-predator of the terrestrial Iharkút ecosystem. These teeth are almost identical with the two '*Megalosaurus pannoniensis*' teeth from the lower Campanian of Muthmannsdorf (Austria) and show a notable similarity to teeth of the Middle Jurassic *M. bucklandii* and the Lower Cretaceous '*M. dunkeri*' from England. A single pedal ungual phalanx is interpreted as the oldest European occurrence of Late Cretaceous abelisaurids, as suggested by a ventral groove and bifurcated grooves laterally bordering a convex, triangular area. Small-bodied paravian theropods are found to be the best represented group in Iharkút, including teeth, caudal vertebrae, a metacarpal III, manual phalanges, and a fragmentary left tibia. A particularly notable paravian remain is a complete left scapulocoracoid possessing a unique pneumatic foramen ventral to the coracoid foramen. This specimen is assigned to *Pneumatoraptor fodori* n. g. et sp. Finally, numerous postcranial elements of Theropoda indet. were recovered, including a fragmentary sacrum that offers new insights into the sacral pneumaticity of theropods. The presence of these theropods in the Santonian Iharkút ecosystem provides the first evidence that during the early Late Cretaceous the Mediterranean archipelago was inhabited by both Gondwanan and Euramerican members of theropod dinosaurs. Consistent with data available for other archosaurian taxa, the close relationship of the basal tetanuran teeth with much older forms suggests that the Iharkút area may have functioned as a refugium in the early Late Cretaceous Mediterranean archipelago.

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1. Introduction

The Cretaceous fossil record of terrestrial vertebrates is discontinuous in Europe, with most fossil occurrences concentrated in two time intervals: the Early Cretaceous and the youngest part of the Cretaceous (late Campanian to Maastrichtian) (Weishampel et al., 2004). The dearth of early Late Cretaceous records of terrestrial vertebrates masks the evolutionary and faunal successions that took place throughout the Cretaceous across islandic landscape of the European archipelago

The Early Cretaceous fossil record offers a detailed documentation of diverse vertebrate taxa, with clear faunal links to vertebrate associations of both other Euramerican regions (especially

North America) as well as Gondwanan landmasses. These Early Cretaceous faunas are represented by fossils of the Wealden Supergroup and its equivalents in Belgium, England, France, Germany, Portugal, and Spain (Martill and Naish, 2001; Weishampel et al., 2004; Sánchez-Hernández et al., 2007). In contrast, the Late Cretaceous fossil record is affected by an almost 20 myr long gap between the Cenomanian to early Campanian, thus, providing a limited record of faunal associations that dominated ecosystems of this long and evolutionarily important time interval.

The European fossil record of the early Late Cretaceous theropod dinosaurs is even more limited due, most likely, to poor preservation of their usually fragile and hollow bones. Until recently, the Cenomanian record of non-avian theropods was documented by teeth and a few isolated, fragmentary bones documented from a few localities in France (Buffetaut et al., 1991; Buffetaut, 1994; Buffetaut and Pouit, 1994) and western Russia (Rozhdestvensky, 1973). Most of this material was identified as Theropoda indet.

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Recently, on the basis of isolated teeth, carcharodontosaurs, dromaeosaurids, and troodontids have been reported from western France (Vullo et al., 2007; Vullo and Neraudeau, 2008). Furthermore, theropod footprints have been described from Spain (Cuenca-Bescós et al., 1999) and Croatia (Dalla Vecchia, 2001). From the Turonian to the Coniacian, the theropod record is almost non-existent. Only Buffetaut et al. (1991) mentioned some material from Turonian deposits. Until the discovery of the Iharkút locality in western Hungary (see below), the Santonian theropod record was also extremely poorly known, with data limited to terrestrial vertebrate occurrences in shallow marine sedimentary rocks of Belgium (Dollo 1903; Le Loeuff and Buffetaut, 1991) and France (Buffetaut and Pouit, 1994). Early Campanian fossils were reported from Scania, Sweden (Persson, 1959), France (Buffetaut et al., 1991; 1997), eastern Austria (Seeley, 1881), Slovenia (Debeljak et al., 1999), and possibly from Borod (Nagybáród) in western Romania (Nopcsa, 1902; Csiki and Grigorescu, 1998, these latter specimens appear to be lost).

Due to the relatively higher number of Late Campanian–Maastrichtian localities, the abundance and diversity of theropods from this time interval are also higher (Pereda-Suberbiola, 2009). The main localities of Portugal, Spain, France, and western Romania provided evidence for presence of abelisauroids (Buffetaut et al., 1988; Astibia et al., 1990; Le Loeuff and Buffetaut, 1991), tetanurans (Casanovas-Cladellas et al., 1988; Csiki and Grigorescu, 1998; Prieto-Marquez et al., 2000), dromaeosaurids (Antunes and Sigogneau-Russell, 1991, 1992; Le Loeuff et al., 1992; Weishampel and Jianu, 1996; Csiki and Grigorescu, 1998; Le Loeuff and Buffetaut, 1998; Antunes and Mateus, 2003; Ősi and Főzy, 2007), troodontids (Grigorescu et al., 1999; Codrea et al., 2002), ornithomimosaur (Pereda-Suberbiola et al., 2000; Canudo and Ruiz-Omeñaca, 2003), and alvarezsaurids (Naish and Dyke, 2004; Kessler et al., 2005).

Throughout the Late Cretaceous of Europe, the dominant terrestrial faunal assemblages vary across time and regions. Only for the Campano–Maastrichtian, sufficient data are available to provide a tentative picture of dinosaur (and mostly other vertebrate) faunas of that time. The Campano–Maastrichtian record clearly indicates a mixed fauna consisting of both Euramerican (e.g. nodosaurid ankylosaurs, dromaeosaurids) and Gondwanan (e.g. bothremydid turtles, sebecosuchian crocodylians, abelisaurid theropods) components (Le Loeuff, 1991; Ősi and Rabi, 2006). However, the spotty nature of the pre-Campanian fossil record hinders a more complete understanding on the origin and evolution of the Cretaceous European vertebrate faunas before the Campanian. Consequently, the theropod material discovered in the Santonian of Iharkút represents a particularly important source of data.

The aim of the present study is to discuss the systematics of the Hungarian theropods discovered recently in the Santonian Cseh-bánya Formation in Iharkút (western Hungary). Given that the material is dominated by isolated teeth, the traditional qualitative systematics has been augmented here with an array of statistical analyses based on univariate, bivariate, and multivariate evaluations of morphometric data. In addition, the documented fossils have been also used to provide new data regarding the continental paleobiogeography of the Late Cretaceous European archipelago.

Institutional Abbreviations—**IGM**, Mongolian Institute of Geology, Ulan Bataar; **MTM**, Hungarian Natural History Museum, Budapest; **NHM**, Natural History Museum, London, UK; **PIUW**, Paläontologisches Institut, Universität Vienna, Vienna; **OUMNH**, Oxford University Museum of Natural History, Oxford.

2. Material and methods

The material described here was collected during the field work conducted between 2001 and 2008 at the Iharkút locality, Bakony

Mountains, western Hungary. All the bones and teeth represent isolated specimens and were recovered from a sedimentary breccia layer that represents the richest bone-yielding horizon within the Santonian (Knauer and Siegl-Farkas, 1992; Mártonné Szalai, 2005) fluvial Cseh-bánya Formation (for geological details see Makádi et al., 2006; Tuba et al., 2006; Ősi and Mindszenty, 2009). Specimens were prepared mechanically in the technical labs of the Department of Paleontology, Eötvös Loránd University and the Hungarian Natural History Museum. The bones are well preserved, rich in pyrite and organic material, and black in color.

The theropod teeth were analyzed and compared using both descriptive morphological characters as well as quantitative morphometric techniques. The latter approach, detailed in the next section, was based on numerical parameters developed recently for theropod teeth by Smith et al. (2005).

2.1. Analytical methods

The primary analytical motivation is to summarize variation in theropod tooth morphology and examine this variation in the context of pre-existing taxonomic classifications. In addition to the two groups of Hungarian theropod teeth (basal Tetanurae, Paraves indet.), the parameters of two teeth from the lower Campanian of Austria (*Megalosaurus pannoniensis*) and three teeth of *Megalosaurus dunkeri* from the Lower Cretaceous of England were merged with the dataset reported by Smith et al. (2005). To evaluate new data in the context of preexisting data, a combination of univariate, bivariate and multivariate methods is employed here. Univariate and bivariate methods include standard parametric (e.g., ANOVA) and non-parametric (e.g., Kruskal-Wallis test) statistical methods. In addition to ANOVA, the Tukey's test, which allows for simultaneous pairwise comparisons of all possible pairs of taxa, was also carried out. Multivariate methods include a series of exploratory and confirmatory approaches selected to maximize inherent strengths (and also minimize inherent weaknesses) of the analyzed data.

In the case of multivariate methods, a diverse array of techniques has been employed to fully explore the data. These methods are partly redundant, but differ somewhat in terms of assumptions, goals, and analytical efficiency. Some require substantial restrictions (due to missing values or inadequacy of variables), while others offer an all-inclusive opportunity to explore the entire dataset, but typically provide analytical results that are less powerful statistically and more ambiguous in terms of morphometric interpretations.

Because tooth morphology is best captured by a mixture of variables of various types, the standard landmark methods used currently in most morphometric studies (e.g., Zelditch et al., 2004) are not applicable here. In addition, because this study builds on a major recent study by Smith et al. (2005), it necessarily requires comparable (non-landmark) data. The multivariate approaches used below includes a series of approaches often used in non-landmark morphometric studies. These include the following sequence of analyses:

1. Principal component analysis (PCA), based on log-transformed linear dimensions, represents the “traditional morphometric approach”, which restricts data to linear-dimension variables and excludes observations with missing values, but provides data that can be readily explored in terms of morphometric interpretations.
2. Non-metric multidimensional scaling (MDS) allows for an all-inclusive analysis of all variables and observations, but is much more difficult to interpret in morphometric context. This approach is also somewhat redundant with PCA, but offers an opportunity to evaluate more variables and more observations simultaneously.

All analyses were performed using SAS/STAT procedures (e.g., PROC ANOVA, PROC NPAR1WAY, PROC PRINCOMP, PROC MDS) as well as custom-designed SAS/IML codes. All statistical tests assumed the significance level of $\alpha=0.05$.

The systematics used in this study follows primarily Holtz (1994) and Turner et al. (2007). Specimens are housed in the Hungarian Natural History Museum (MTM).

3. Systematic paleontology

Dinosauria Owen, 1842
Saurischia Seeley, 1889
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Tetanurae indet.

Referred material: 58 isolated teeth and tooth fragments from Iharkút: V.01.54, V.01.30, V.01.20, V.2003.04–08, V 2008.36.1–V 2008.36.51. Two fragmentary teeth from Muthmannsdorf, eastern Austria (PIUW uncatalogued specimens).

Locality: Iharkút, Bakony Mountains, western Hungary; Muthmannsdorf, eastern Austria.

Age and horizon: Late Cretaceous, Santonian, Csehbánya Formation; early Campanian Gosau beds, Coal-bearing Complex, Gosau Group (Grünbach Syncline).

3.1. Description and comparisons

From the 58 isolated specimens, 27 have an almost complete crown, and they seem to represent the whole, morphologically

heterodont tooth row. The assemblage is represented by rostral but more frequently posterior teeth.

3.1.1. Rostral teeth

As in the rostralmost teeth of several other theropod groups (e.g. coelophysoids, Tykosky and Rowe, 2004, basal tetanurans, Holtz et al., 2004), the supposed rostral teeth from Iharkút (Fig. 1A–C) have a lenticular, almost circular basal cross-section, as reflected by a high (0.7–0.8; see supplementary data) crown base ratio (CBR=crown base width [CBW]:crown base length [CWL]; Smith et al., 2005). Their crown curves only slightly distally (crown angle [CA] is high, 63° in V 2008.36.6 and 70° in V.2003.05) being in contrast with the posterior, transversely more flattened teeth that show a slight lingual curvature. As usual in theropods, the base of the crown is not constricted. These teeth show bands of growth along both the labial and lingual surfaces but these bands are not as strong as those on the more posterior teeth.

Both mesial and distal carinae are present and they are completely serrated. In cross-section the carinae, especially the mesial one, are not in the saggital plane of the crown instead, the mesial carina is lingually displaced and the distal one passes labially. Similar asymmetrical configuration of the carinae (Fig. 1B–C) has been described in numerous theropod groups (Currie et al., 1990; Holtz et al., 2004; Smith et al., 2005). The mesial carina does not extend along the complete crown (Fig. 1C) being restricted to about the apical half or two-third of it. In contrast to the more frequent posterior teeth, in no case the distal carina of these rostral teeth reaches the base of the crown, but rather it ends basally approximately at the two-thirds or four-fifths of the crown. The denticle-free anterior margin is rounded basally and completely devoid of any trace of carina. Distal denticles are larger than the anterior ones.

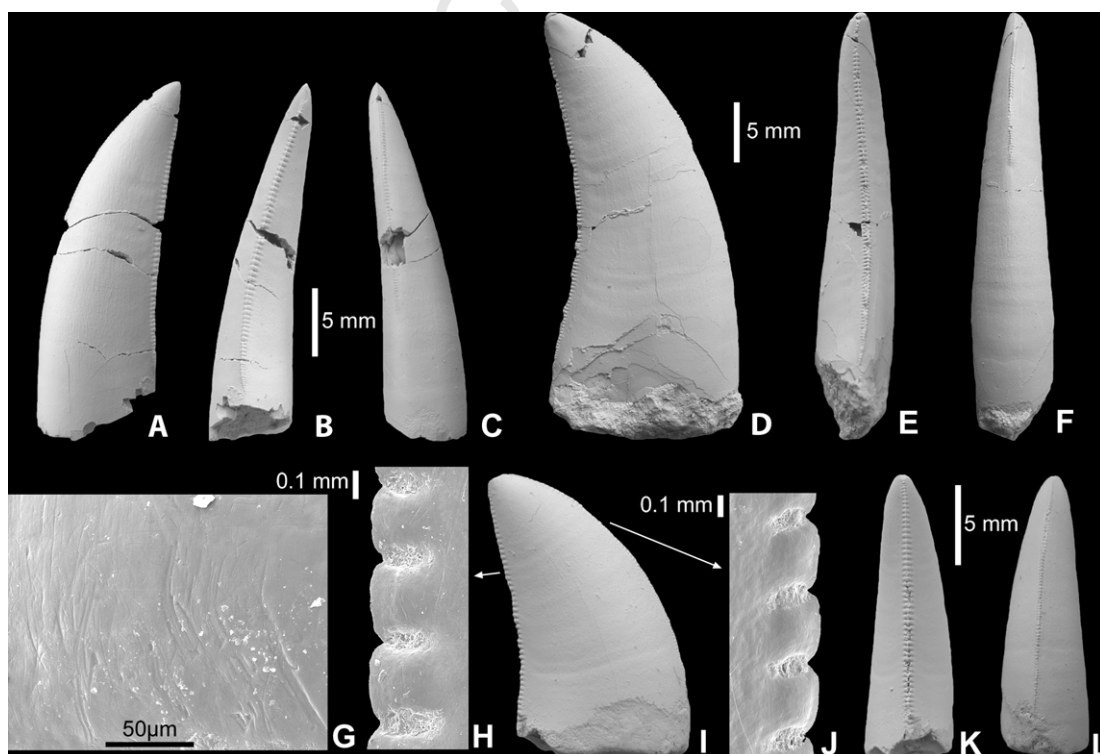


Fig. 1. Isolated teeth of basal tetanuran theropods from the Santonian Csehbánya Formation, Iharkút, western Hungary. A, rostral tooth (MTM V 2008.36.6.) in lateral, B, distal, C, mesial views. D, posterior tooth (MTM V.01.54) in lateral, E, distal, F, mesial views. G, microwear features on a denticle of MTM V 2008.36.30. Note that the cutting margin of the denticle is on the left and scratches are roughly parallel with this margin. H, distal serration of MTM V 2008.36.30. I, posterior tooth (MTM V 2008.36.30.) in lateral view. J, mesial serration of MTM V 2008.36.30. K, MTM V 2008.36.30. in distal, L, and mesial views.

The average serration density on the mesial carina (MAVG) is of 22–24 denticles in 5 mm, whereas the distal carina (DAVG) bears 17 denticles in 5 mm. The number of denticles in both carinae is usually higher both basally and apically than in the mid-section (see supplementary data) because close to the crown base and apex smaller denticles are present. Denticles are neither symmetrical nor as hooked as those of troodontids (Currie, 1987), but instead slightly square-shaped similar to *Dromaeosaurus albertensis* (Currie et al., 1990). They are chisel-like and the apex is oriented apically. Blood-grooves are visible between the individual denticles.

3.1.2. Posterior teeth

Labiolingually flattened, distally curved teeth are more frequent probably representing most probably the teeth more posterior than those described above (Fig. 1D–L). They have mesiodistally elongated, tear-shaped cross-section with lower (0.4–0.6) crown base ratios compared to the rostral teeth (see supplementary data). The crown curves only distally with a crown angle ranging between 56° and 60° that appears to be a characteristic feature of these basal tetanuran teeth (see statistical analyses below). Bands of growth or enamel wrinkles are frequent and well-developed along the labial and lingual surfaces, similarly to the teeth of *Megalosaurus* (Brusatte et al., 2007; Fig. 1D, I). The serrated distal carina always reaches the base of the crown. The mesial carina, however, generally continues only about half or one-third of the way down the crown. Basally, the starting point of the serrated mesial carina is abrupt and forms a small step in the tooth profile. Features of the denticles described for the rostral teeth are almost identical with those of the posterior teeth. The MAVG on the mesial carina is 20–21, the DAVG varies between 14–19.

Currie et al. (1990) remarked the presence of strong blood grooves in most Laurasian theropod teeth (e.g. *Allosaurus*, *Tyrannosauridae*, *Dromaeosauridae*) a feature absent in the Hungarian specimens. Wear facets have been detected on both the apical region and along the mesial and distal carinae of the teeth (Fig. 1G). Apical wear is usually an oval-shaped, rounded surface with developed dentine exposure. Spalled and irregular surfaces, similar to those in tyrannosaurids (Schubert and Ungar, 2005) occur on two teeth (MTM V2008.36.7., V.2003.06.). Scratches are usually heavy and heterogeneously oriented. These spalled surfaces are more rounded apically than basally. Besides scratches, heavy pits are also frequent. Tooth wear along the carinae is usually not as heavy as that of the apical region. Here, the dentine is usually not exposed

and wear patterns can be observed on the enamel surface. Micro-wear features are represented by dominantly short and heavy scratches (Fig. 1G) that are generally parallel to the edge of the denticle, but longer scratches (max. 1–2 mm) also occur oriented in an acute angle relative to the carinae. Besides scratches, deep, rectangular pits also occur. Tanke and Currie (2000) elaborated a classification of theropod tooth wear marks. From the five types recognized by these authors, the studied material is in concordance with their type 1 tooth wear, showing basically an oval shape in the apex of the labial face. As they noted, this feature could be related to puncture-shaped perforation of bone periostium.

One of the two fragmentary theropod teeth (Fig. 2A) from the lower Campanian of Muthmannsdorf (estern Austria) was originally described and figured by Seeley (1881:plate 27, Fig 21–22) as '*Megalosaurus pannoniensis*'. This rather complete tooth is slightly crushed distally at its base but has well-preserved, serrated mesial and distal carinae. In general, the Austrian teeth are almost identical with the above described, posterior basal tetanuran teeth from Iharkút in having a mesial carina that ends approximately at two-third of the crown, with also showing similarly well-developed bands of growth and distal curvature of the crown (CA=60°). Other variables measured in these teeth are also very similar to those of the Iharkút teeth (see supplementary data).

Other theropod teeth from Europe particularly similar to these basal tetanuran teeth from Iharkút and Muthmannsdorf are the single erupted tooth in the lectotype dentary of *Megalosaurus bucklandii* (OUMNH J.13505) from the Middle Jurassic (Benson et al., 2008:423) and the isolated teeth of '*Megalosaurus dunkeri*' (e.g. NHM R15909, R210, R1997, Fig. 2B–E; see the result of the statistical analysis below) from the Lower Cretaceous (Wealden) of England, the latter being considered as a nomen dubium by Holtz et al. (2004). In addition, the Middle Jurassic "megalosaurid" *Dubreuillosaurus valesdunensis* (Allain, 2002) from northwestern France possesses similar teeth. The general shape of the crown, the crown base length/width, the crown curvature, the morphology of the carinae (especially the development pattern of the mesial carina) are all features shared by these Jurassic and Early Cretaceous forms of basal tetanurans from Europe and the Late Cretaceous tetanurans from Iharkút and Muthmannsdorf.

Abelisauroida Bonaparte, 1991
Abelisauridae Bonaparte et Novas, 1985
Abelisauridae indet.

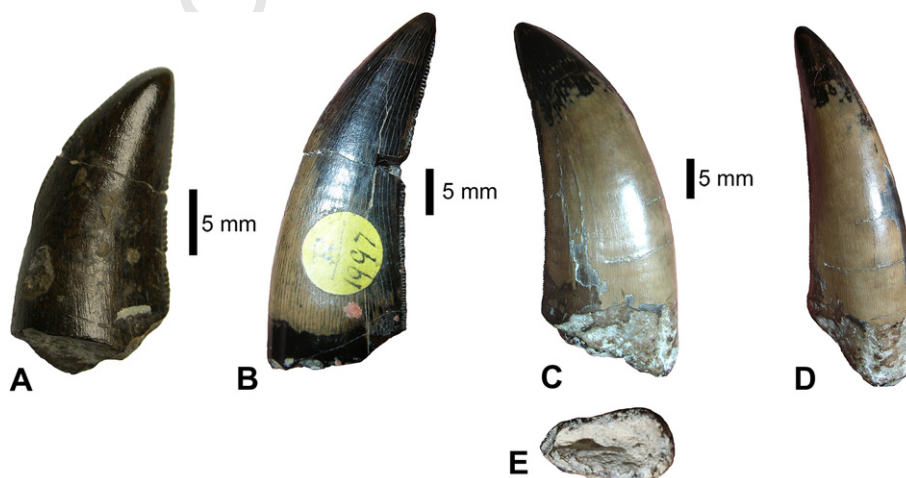


Fig. 2. Basal tetanuran teeth. A, '*Megalosaurus pannoniensis*' (PIUW uncatalogued) from Muthmannsdorf, eastern Austria. B, '*Megalosaurus dunkeri*' (NHM R 1997) from the Lower Cretaceous of England (Wealden). C, '*Megalosaurus dunkeri*' (NHM R 15909) from the Lower Cretaceous of England (Wealden) in lateral; D, anteromedial; E, basal views.

Referred material: MTM V 2008.43.1.

Locality: Iharkút, Bakony Mountains, western Hungary.

Age and horizon: Late Cretaceous, Santonian, Csehbánya Formation.

3.2. Description and comparisons

A single, well-preserved pedal ungual phalanx (Fig. 3) is 14 mm long, but its distal tip is missing indicating an original total length of around 16 mm. The pointed, slightly curved claw has a convex dorsal surface. The articular surface is circular in proximal view and has a shallow dorsoventrally oriented ridge dividing the articular surface into two cotyles. The claw bears a shallow groove on its ventral surface (Fig. 3D) and bifurcated grooves laterally bordering a convex, triangular area (Fig. 3A, C). These features are characteristic for the Abelisauridae (Novas and Bandyopadhyay, 2001:147). Novas (1997) mentioned bifurcated grooves in the alvarezsaurid *Patagonykus*, but later indicated that their bifurcation is located more proximally (Novas and Bandyopadhyay, 2001). This triangular surface is bordered proximally by a different, third groove that separates this area from the lateral margin of proximal end as it also occurs in *Masiakasaurus* (Sampson et al., 2001). In dorsal view, the medial part of the margin of the proximal articular surface is pointed extending proximally over the articular surface. Proximoventrally, no flexor tuber is present.

The surface of the bone is not smooth but ornamented by numerous small pores. Comparison of the pedal ungual from Iharkút with other theropod ungual phalanges clearly points to abelisaurid affinities. The Hungarian specimen differs from unguals of other theropod groups in having the above mentioned characteristic features on its ventral and lateral sides. In addition, the general form and curvature of the bone is also much more similar to the unguals of various abelisaurid forms (Novas and Bandyopadhyay, 2001; Sampson et al., 2001; Novas et al., 2005; Carrano, 2007).

Maniraptora Gauthier, 1986

Paraves Sereno, 1997 sensu Holtz and Osmólska (2004)

Pneumatoraptor gen. nov.

Type species: *Pneumatoraptor fodori* described below.

Etymology: Genus name refers to the pneumatic construction of the scapulocoracoid.

Diagnosis: as for the species.

Pneumatoraptor fodori sp. nov.

Holotype: MTM V.2008.38.1., nearly complete, left scapulocoracoid (Fig. 4).

Etymology: Named after Géza Fodor †, who provided a generous support during the early stages of the Iharkút field works.

Locality: Iharkút, Bakony Mountains, western Hungary.

Age and horizon: Late Cretaceous, Santonian, Csehbánya Formation.

Diagnosis: *Pneumatoraptor fodori* can be diagnosed on the basis of a large, circular pneumatic foramen ventral to the coracoid foramen (2 mm in diameter) that opens towards the coracoid tubercle and is also in connection with the hollow scapular blade (Fig. 4C, D).

3.3. Description and comparisons

3.3.1. Scapulocoracoid

The scapular blade is narrow and proximally it is almost circular in cross-section. In dorsal view, the scapular blade thins distal to the glenoid and its distal end is a strongly flattened lamina with an approximate thickness of 0.5 mm. In lateral view, the scapular blade widens slightly distal to the glenoid (Fig. 4A). The suture between the scapula and coracoid is indistinct referring to a skeletally mature animal. The bone along with other paravian postcranial remains indicate that the Iharkút paravian theropod was a small-bodied animal, about three times smaller than the Late Cretaceous *Velociraptor* (Norell and Makovicky, 1999) and 1.2–1.5 times smaller than the Barremian *Sinornithosaurus* (Xu et al., 2001). The scapulocoracoid is L-shaped, a paravian synapomorphy defined by Turner et al. (2007).

Although the dorsal edge of the acromion process is eroded, it is well-developed and anteroposteriorly more elongated than that in *Velociraptor* (Norell and Makovicky, 1999:Fig. 4b). The deeply concave glenoid fossa is oriented laterally and slightly ventrally, similarly to *Velociraptor*. The coracoid displays a flexure of approximately 70° between its glenoid portion and the ventral coracoid blade. This reverse flexure of the distal part of the coracoid is also present in *Buitreraptor* (Makovicky et al., 2005) and *Sinornithosaurus* (Xu et al., 1999) but not in a so prominent extent as on the Iharkút specimen (Fig. 4A–C). The coracoid tubercle occupies this flexure anterolaterally, but it is a rounded knob rather than a prominent boss as in *Bambiraptor* (Burnham et al., 2000) or in *Buitreraptor* (Makovicky et al., 2005). The ventral coracoid blade widens lateromedially as in various

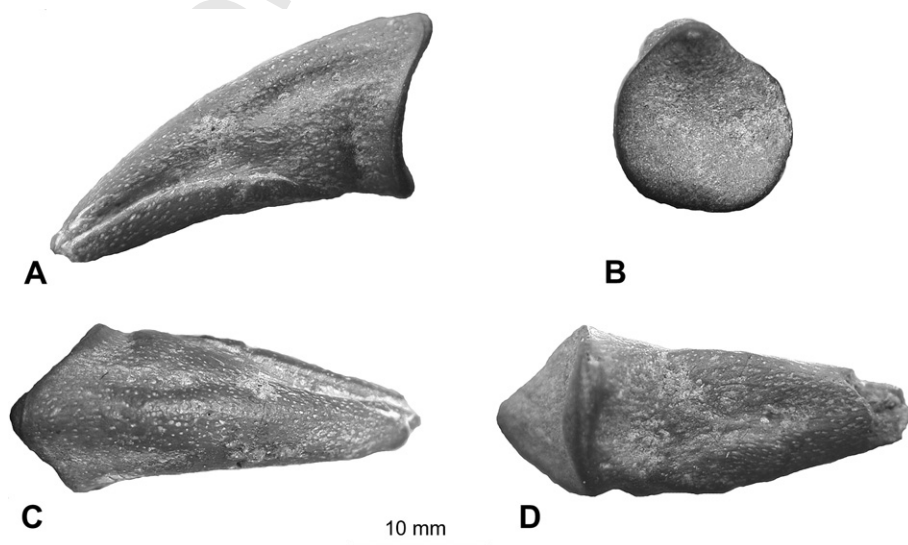


Fig. 3. Abelisaurid pedal ungual phalanx (MTM V 2008.43.1.) from the Santonian Csehbánya Formation, Iharkút, western Hungary. A, lateral, B, proximal, C, dorsal, D, ventral views.

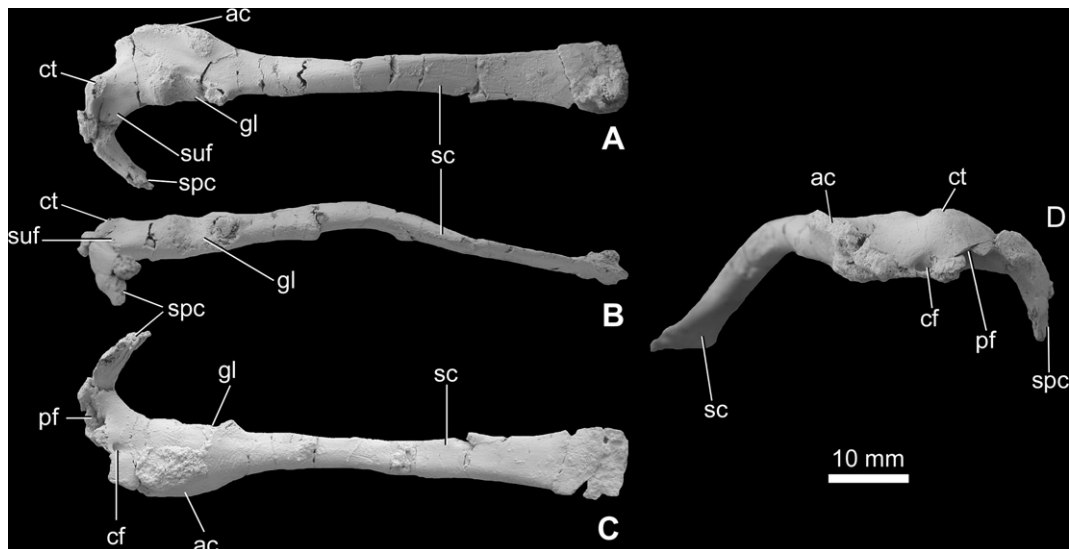


Fig. 4. *Pneumatoraptor fodori* n. g. et n. sp. holotype, left scapulocoracoid (MTM V 2008.38.1.) from the Santonian Cseh anya Formation, Ihark ut, western Hungary in A, lateral; B, ventral; C, medial; D, anterior views. Abbreviations: **ac**, acromion process; **cf**, coracoid foramen; **ct**, coracoid tubercle; **gl**, glenoid; **pf**, pneumatic foramen; **sc**, scapula; **spc**, sternal process of coracoid; **suf**, subglenoid fossa.

dromaeosaurids. The thin, medial side of the coracoid is eroded, as commonly occurs in dromaeosaurids, e.g. *Velociraptor* (IGM 100/986) and *Buitreraptor* (Makovicky et al., 2005; A. Turner pers. comm.). The distal end of the coracoid blade is damaged thus the facet for the sternum is not recognizable. No trace of the supra-coracoid fenestra, described in *Sinornithosaurus* (Xu et al., 1999), can be observed. At the anteromedial part of the coracoid flexure a small coracoid foramen is present that is bordered dorsally by the anterior part of the acromion process and laterally by the coracoid tubercle. As in *Deinonychus* (Ostrom, 1974:3), the tract of the coracoid foramen forms an almost anteroposteriorly oriented canal (Fig. 4C, D) in contrast with the dorsoventrally oriented canal described in *Velociraptor* (Norell and Makovicky, 1999). The medial margin of the coracoid is slightly crushed. The characteristic subglenoid fossa is well-defined as in most dromaeosaurids (Norell and Makovicky, 1999, 2004). In medial view, ventral to the coracoid foramen a deep and rounded pneumatic foramen (2 mm in diameter) that probably entered also the scapular blade, opens towards the coracoid tubercle (Fig. 4C, D). This hypothesis is supported by the hollow condition of the scapular blade observed in cross-section during preparation. This feature distinguishes clearly the Ihark ut specimen from the scapulocoracoid known in other paravians. *Pneumatoraptor fodori* therefore provides additional evidence for the presence of clavicular air sacs in non-avian tetanurans (see Wedel, 2009), and perhaps shows that they were present throughout paravians.

Paraves indet.

Referred material: isolated teeth: V.01.215, V.01.231, V.2000.35, V 2008.37.1–V 2008.37.10., V.2000.02–V.2000.06.; three isolated distal caudal vertebrae V 2009.46.1–3., one metacarpal V 2009.45.1., three ungual phalanges V 2008.40.1–3., phalanges V 2008.42.1–2., proximal half of a left tibia V 2008.31.1.

Locality: Ihark ut, Bakony Mountains, western Hungary.

Age and horizon: Late Cretaceous, Santonian, Cseh anya Formation.

Remarks. All the following material referred to Paraves may represent the remains of *Pneumatoraptor fodori* n. gen. et n. sp., a dromaeosaurid-like theropod dinosaur. However, as most of these bones do not preserve features optimised by phylogenetic analysis

as paravian synapomorphies (e.g. Turner et al., 2007) they are referred to this clade on a comparative basis.

3.4. Description and comparisons

3.4.1. Teeth

Six isolated teeth referred to three different morphotypes within the Theropoda have been described by Ősi (2004). 12 additional isolated teeth have been discovered subsequently showing great similarity to the earlier described ones; nevertheless, some additional comments can be added here. The small (max. height 8 mm), distally curved teeth have an oval to flattened cross-section (see MTM V 2007.37.4, Fig. 5D). Basally their labial and lingual surfaces are slightly concave (Fig. 5A–D). The strong labiolingually compressed crown indicates a low crown base ratio (0.38–0.54). Crown angle is high ranging from 56° to 69° similarly to that found in *Deinonychus* or *Dromaeosaurus* (Smith et al., 2005:appendix A). In contrast to the basal tetanuran teeth from Ihark ut, the crown base of the higher and more elongate teeth is slightly constricted distally. It is interesting to note that the paravian tooth MTM V.01.231 (Fig. 5B) shows striae as in southern unenlagiine dromaeosaurids (Makovicky et al., 2005).

Average serration density on the mesial carina is of 18–20 denticles in 2 mm (following Smith et al., 2005), whereas the distal carina bears 14–17 denticles in 2 mm. As in the basal tetanuran teeth from Ihark ut and most theropod teeth, the number of denticles on both carinae are usually higher both basally and apically compared to the mid-section (see supplementary data). Denticles are slightly rounded and both the mesial and distal ones resemble those of *Richardoestesia gilmorei* (Currie et al., 1990). The statistical analysis based on the various parameters derived from the teeth resulted in a great similarity of these small teeth with those of *Bambiraptor feinbergi* (see below).

3.4.2. Caudal vertebrae

Three, elongated distal caudals (MTM V 2009.46.1–3.; Fig. 5E–I) were identified as belonging to paravians on the basis of a distinct lateral ridge on the vertebral body and the elongated zygapophyses (A. Turner pers. comm.). They are slightly amphicoelous and the

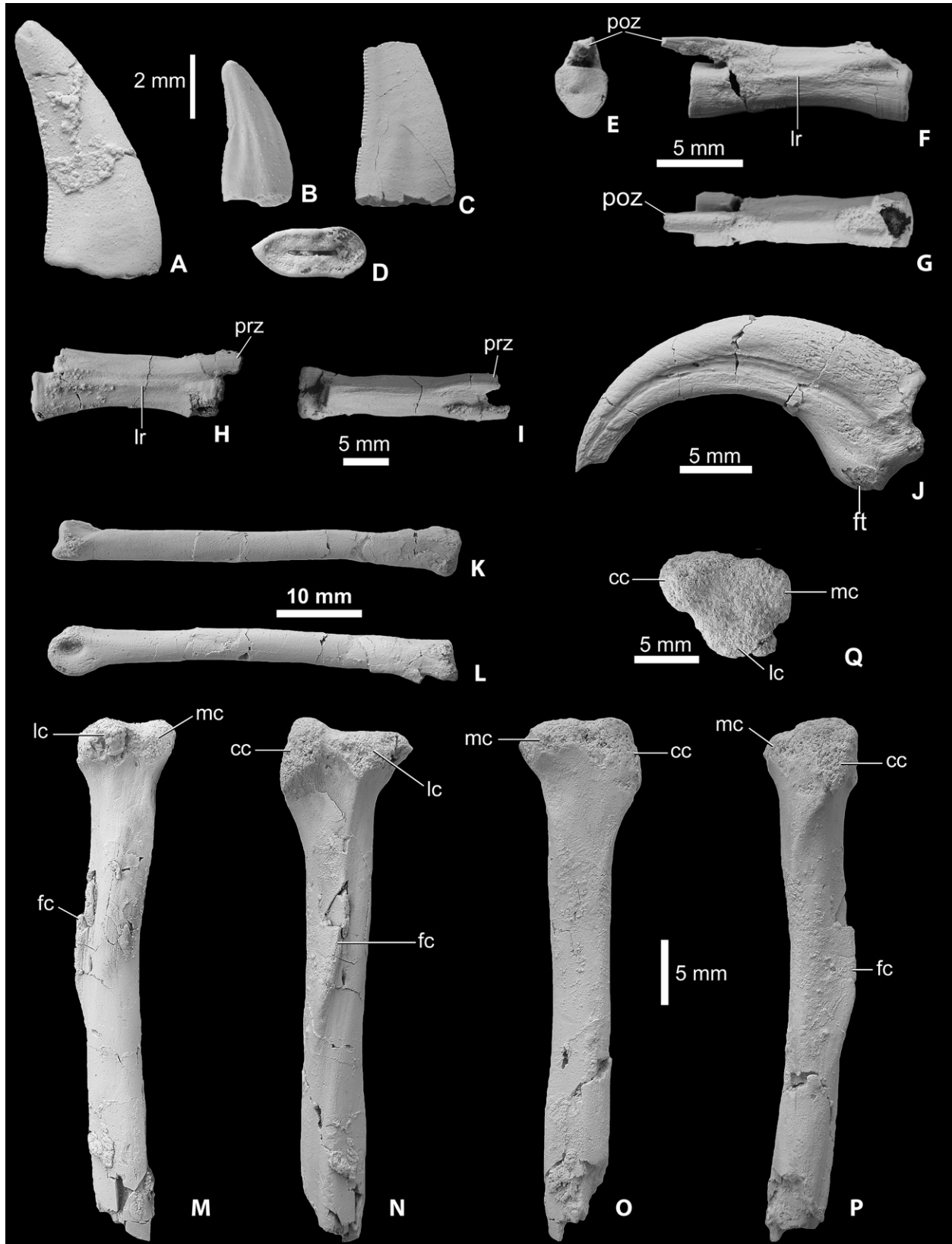
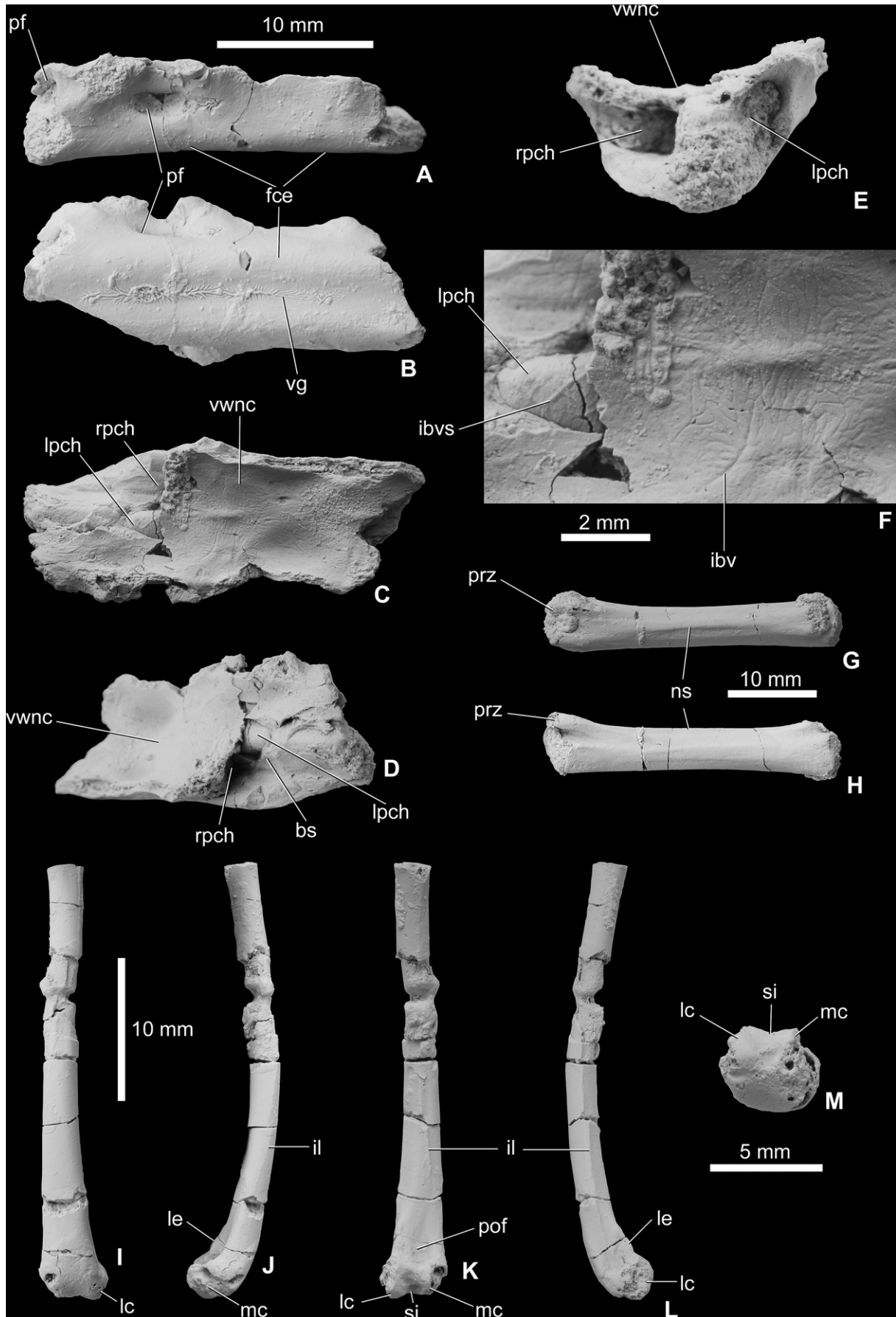


Fig. 5. Paraves indet. remains from the Santonian Csehbánya Formation, Iharkút, western Hungary. A–C, paravian teeth in lateral view (from left to right: MTM V 2007.37.4, V.01.231, V 2007.37.1.). D, cross-section of the base of MTM V 2007.37.4. E, caudal vertebra in posterior; F, lateral; G, dorsal views; H, distal caudal vertebra in lateral; I, dorsal views; J, manual ungual phalanx in lateral view; K, metacarpal III of the left? manus in dorsal, L, lateral views. M, left fragmentary tibia in posterior; N, lateral; O, medial; P, anterior; Q, proximal views. Abbreviations: **cc**, cnemial crest; **fc**, fibular crest; **ft**, flexor tubercle; **lc**, lateral condyle; **lr**, lateral ridge; **mc**, medial condyle; **poz**, postzygapophysis; **prz**, prezygapophysis;



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articular facet of the vertebral body is heart-shaped. The neural arch is low and the neural spine is ridge-like.

3.4.3. Metacarpal

A complete limb element has been identified as metacarpal III of the left manus (MTM V 2009.45.1.; Fig. 5K–L). It is very slender, similar to that of *Deinonychus* (Ostrom, 1969) and *Velociraptor* (Norell and Makovicky, 1999). The diaphysis is straight in dorsal view and slightly bowed in lateral view. Proximally, the epiphysis is slightly compressed mediolaterally and its proximal surface is finely concave. No proximoventrally oriented process on this epiphysis can be seen in contrast to *Deinonychus* but similar to *Velociraptor* (Norell and Makovicky, 2004). The ventral side of the diaphysis is flat and bordered by fine ridges both medially and laterally. The distal epiphysis is gently medially oriented. The two condyles of the distal epiphysis are separated by a shallow groove.

3.4.4. Phalanges

Numerous phalanges have been discovered in Iharkút. Among them, three strongly curved unguals can be referred unambiguously to paravian theropods. The best preserved and largest specimen is considered a manual ungual (MTM V 2008.40.1., Fig. 5J) because its dorsal edge arches higher than the dorsally highest point of the articular facet when the latter is held vertically (Sues, 1978; Senter, 2007). It is strongly compressed lateromedially and bears a prominent flexor tubercle with a rugose surface as it is usually seen in dromaeosaurids. It strongly resembles the manual unguals of *Velociraptor* (Norell and Makovicky, 1999:Fig. 9), that of the digit II in *Saurornitholestes* (Sues, 1978:plate 5A), and those of *Deinonychus* (Ostrom, 1969:Fig. 63). The latter ones, however, possess a stronger curvature compared with the Iharkút ungual. Deep grooves can be observed both laterally and medially. The lateral edge is flat and the dorsal edge is rounded and bears a rough surface proximally. All of these features are also present in a different, fragmentary ungual (MTM V 2008.40.2.) whose articular region is missing, and could be either manual or pedal ungual. The third specimen (MTM V 2008.40.3.) is complete but shows a slightly different morphology compared to the other unguals. It is the smallest specimen, being not as strongly curved with the articular region relatively higher than that of the most complete ungual. Moreover, it does not bear a deep groove laterally and medially as it can be observed on the strongly curved claws. The largest specimen of these unguals suggests a much larger animal (only 1.5 times smaller than *Velociraptor*) than the aforementioned, adult scapulocoracoid referred to *Pneumatoraptor*, and thus indicates a wide range of body size for the Iharkút paravian theropods.

Two non-ungual phalanges (MTM V 2008.42.1–2.) closely resemble the penultimate phalanx of digit II of the manus of *Saurornitholestes* (Sues, 1978:plate 4B/3) and that of the digit III of *Velociraptor* (Norell and Makovicky, 1999:Fig. 9). One of these is strongly compressed dorsoventrally. The other one is well-preserved and possesses well-defined interphalangeal articulation surfaces. The proximal articular facet is markedly divided into two cotyles by a ridge for the precise reception of the first phalanx. The slightly asymmetrical distal articular facet consists of two well-developed condyles that are separated by a deep groove proximally and ventrally. In dorsal view, the condyles are fused to form a single bridge over the subcircular fossae. These fossae are deep on each

side of the distal articular end. In lateral view, the condyles extend slightly further back ventrally than dorsally.

3.4.5. Tibia

A proximal part of a left tibia (MTM V 2008.31.1.; Fig. 5M–Q) can also be referred to paravian theropods. Its shaft is slightly bowed in the mediolateral plane. Distally, it has a subtriangular cross-section, and proximally it is expanded and bears a well-developed single cnemial crest. Compared to the cnemial crest, the lateral and medial condyles are smaller and the posterior side of the medial condyle is slightly damaged. The distal extension of the cnemial crest is more developed than that in *Velociraptor* (Norell and Makovicky, 1999:Fig. 11B). The bone can be unambiguously distinguished from the tibia of abelisauroid theropods based on the lack of the pronounced anterior extension of the cnemial crest (Carrano, 2007). It further differs from the tibia of basal tetanurans because the cnemial crest does not curve laterally towards the lateral condyle and also because the tibial shaft does not turn broader mediolaterally than anteroposteriorly (Holtz et al., 2004). Between the cnemial crest and the lateral condyle a developed groove is present (Fig. 5N). In proximal view (Fig. 5Q), the proximal epiphysis of the tibia is much wider mediolaterally than anteroposteriorly, compared to that of *Velociraptor* (Norell and Makovicky, 1999) or *Achillobator* (Perle et al., 1999). The fibular crest is placed proximally and continues into a ridge towards the lateral condyle. Although the distal part of the tibia is not preserved, the fibular crest appears to be longer than that of *Velociraptor* (Norell and Makovicky, 1999:Fig. 11a).

Theropoda indet.

Referred material: fragmentary sacrum MTM V 2009.48.1., six isolated caudals MTM V 2009.47.1–6., left distal femur MTM V 2009.49.1.

Locality: Iharkút, Bakony Mountains, western Hungary.

Age and horizon: Late Cretaceous, Santonian, Csehbánya Formation.

3.5. Description and comparisons

3.5.1. Sacrum

Despite its fragmentary nature, the preserved anterior part of a sacrum (MTM V 2009.48.1., Fig. 6A–F) composed by two and a half, completely fused vertebrae provides information on the morphology of its pneumatic system. The neural arch is completely missing thus the ventral wall of the neural canal can be well observed (Fig. 6C). This surface is highly ornamented by the impression of the fine network of blood vessels (Fig. 6F). The anteriormost part of the sacrum is missing and thus it starts at the posterior end of the probably first sacral. In this centrum the posterior margin of the left pneumatic foramen can be identified (Fig. 6A). This foramen opens into the left pneumatic canal that extends parallel to the sagittal plane (Fig. 6C). This pneumatic canal is roughly quadrangular or suboval in cross-section and it is filled by calcified sediment (Fig. 6F). This left canal is separated by a thin bony septum from the right one that has a similar in morphology. Posteriorly these canals become thinner and they seem to end or become very thin after the third or fourth centra (not completely clear due to the fragmentary nature of the specimen). The second

Fig. 6. Theropoda indet. remains from the Santonian Csehbánya Formation, Iharkút, western Hungary. A, fragmentary sacrum in lateral; B, ventral; C, dorsal; oblique (anterolateral); E, anterior views. F, details of the surface of the ventral wall of the neural canal and the pneumatic channels; G, distal caudal vertebra in dorsal; H, lateral views. I, fragmentary left femur in anterior; J, medial; K, posterior; L, lateral; M, distal views. Abbreviations: **bs**, bony septum; **fce**, fused vertebral centra; **ibv**, impression of blood vessels; **ibvs**, positive impression of blood vessels on the infilled sediment; **il**, intermuscular line; **lc**, lateral condyle; **le**, lateral epicondyle; **lpch**, left pneumatic channel; **mc**, medial condyle; **pf**, pneumatic foramen; **pof**, popliteal fossa; **prz**, prezygapophysis; **rpch**, right pneumatic channel; **si**, sulcus intercondylaris; **vg**, ventral groove; **vwnc**, ventral wall of the neural canal.

centrum is also pierced by a pneumatic foramen on both sides, connected as well to the pneumatic canals of the corresponding sides (Fig. 6A, B). Similarly to birds, this pneumatic system was probably invaded by the abdominal air-sac diverticula (O'Connor and Claessens, 2005). The pneumatized body of the vertebral centra in this sacrum is in contrast to the sacrum of *Majungatholus atopus*, where pneumaticity is restricted only to neural arches (O'Connor and Claessens, 2005), but similar to other theropods with pneumatization in the vertebral centra (Harris, 1998; O'Connor, 2006).

3.5.2. Caudals

Six isolated caudals (MTM V 2009.47.1–6; Fig. 6G, H) can be referred to Theropoda indet. on the basis of their following features. They strongly elongated with

slightly amphicoelous centra. All of them possess strongly hollow centra but no pneumatic foramen can be observed neither on the neural arch nor on the centra. The neural arch is low with a ridge-like neural spine. In the smaller, rod-like, more distal vertebrae the neural spine is not present. In contrast to the paravian vertebrae described above, these specimens do not bear a distinct lateral ridge on their centra.

3.5.3. Femur

The distal part of a left femur (MTM V 2009.49.1., Fig. 6I–M) represents one of the smallest theropods from Iharkút and it is perhaps from a subadult animal. This bone retains an original, subcircular cross-section although at the proximal end of the preserved shaft is slightly wider lateromedially than anteroposteriorly. Intermuscular lines on the shaft of this specimen can be observed (Fig. 6J–L) as frequently seen on various bird femora. In lateral view, the shaft is slightly anteriorly bowed and it is more slender compared to that of *Velociraptor* (Norell and Makovicky, 1999). Both the lateral and medial condyles are damaged and only their medial and lateral parts can be studied, respectively. The lateral epicondyle is present continuously along the lateral margin of the lateral condyle. Medially from this ridge a shallow popliteal fossa is present. The lateral condyle projects more distally than the medial one. In distal view, the intercondylar sulcus is well developed extending anteriorly up to a transverse ridge that connects the posterior ridge of the medial and lateral condyles.

4. Statistical analysis of the teeth

4.1. Univariate and bivariate analyses

Consistently with analyses presented previously by Smith et al. (2005: Figs. 12–13), out of all morphometric measurements collected from the teeth, the crown angle (CA) is the most useful to compare the basal tetanuran teeth with those of other theropod taxa. The mean within-taxon CA (Fig. 7) shows statistically significant variation across dinosaur genera, as indicated consistently by both non-parametric (Kruskal-Wallis, chi-square=292.1, $p < 0.0001$) and parametric (ANOVA, $F = 199.9$, $p < 0.0001$) tests. The Tukey's Studentized Range Test, which allows for pairwise comparisons of means while controlling for the Type I experimentwise error rate, suggests that all genera differ significantly from many other genera. However, for most of the taxa some comparisons are insignificant (i.e., nearly all genera have CA means similar to at least some other genera). The fact that some genera are indistinguishable from one another is also obvious visually.

Following Smith et al. (2005), bivariate analyses (Fig. 8) were performed using five variables: crown height (CH), crown angle (CA), average distal serration density (DAVG), crown basal width (CBW), and crown basal length (CBL). In every case, the original bivariate plots of Smith et al. (2005: Fig. 9) show a distinct gap

between the *Allosaurus–Majungatholus* and *Dromaeosaurus–Deinonychus* groups. Except for the plot of CBL versus CH, the Hungarian basal Tetanurae teeth fill this gap and plot in a well-defined area distinct from all the other analysed theropod teeth. The teeth of '*Megalosaurus dunkeri*' are always close to the Hungarian teeth, further demonstrating their similarities (Fig. 8). The more complete theropod tooth from Austria also yield values of the key morphometric parameters (e.g. CBL: 10 mm, CA: 60°) that are also very similar to those measured for the Hungarian basal tetanuran teeth (see Figs. 2, 8).

The ratios of CBW versus CBL and CH versus CBL show that the paravian teeth from Hungary are close to the teeth of *Bambiraptor* and *Deinonychus* (Fig. 8A, D). The ratios of DAVG versus CBL and CA versus CBL, however, separate the Hungarian paravian teeth from those of other groups. The high value of the number of denticles on the distal carina is characteristic for these teeth. Comparably numerous denticles were also observed in *Richardoestesia gilmorei*, which is not included in the analysis presented here (see Ősi, 2004).

4.2. Multivariate analyses

Only four linear variables without missing values were available for the traditional morphometric approach: CBL, CBW, CH, and AL. Principal Component Analysis based on variance-covariance matrix was performed for log-transformed values of those four variables (Fig. 9A). The results are typical for what is expected for data consisting of linear dimensions with substantial size variation. PC1 explains an overwhelming proportion of variance in the data (98.2%) and all four variables are highly and positively correlated with PC1 ($r > 0.98$ in all four cases). This pattern indicates that PC1 is a robust proxy for size of teeth: the high PC1 scores represent teeth that are large (all four linear dimensions have high values when PC1 score is high). It is important to remember that PC1, when computed from linear size-correlative dimensions, approximates an allometric, and not an isometric, size vector (see Jolicoeur, 1963; Kowalewski et al., 1997; and references therein). That is, it may also contain some growth-related shape variation. The statistical interpretation of this axis as reflecting primarily size is consistent with the taxonomic gradient observed along PC1 (Fig. 1): teeth of the smallest taxa (*Bambiraptor*–Hungarian paravian teeth) are located to the left and teeth of increasingly larger taxa are progressively shifted to the right end of the PC1 axis. Good separation of teeth along PC1 is thus primarily reflecting size differences.

The basal tetanuran teeth from Iharkút plot along PC1 between *Majungatholus–Allosaurus* and *Dromaeosaurus*, reflecting the fact that these Hungarian teeth are medium-sized relative to the other analysed theropod teeth. It is noteworthy also that the Hungarian paravian teeth plot together with those of *Bambiraptor*, forming jointly a distinct cluster on the ordination plot. The non-metric multidimensional scaling (MDS), despite the inclusion of additional variables that could not be applied in PCA, does not result in an improved separation of the theropod taxa (Fig. 9B). The patterns are generally similar to those of PCA, although the distribution of taxa along the first axis (Dim 1) is reversed relative to PC1 patterns – an analytical artifact of different scaling algorithms commonly observed when comparing these two types of ordinations (e.g., Huntley et al., 2006).

5. Palaeobiogeographical implications

Isolated remains of non-avian theropod dinosaurs indicate the appearance of at least three different taxa (basal Tetanurae, Abelisauridae, Paraves indet.) in the Santonian Iharkút ecosystem (Bakony Mountains, Transdanubian Central Range, western Hungary).

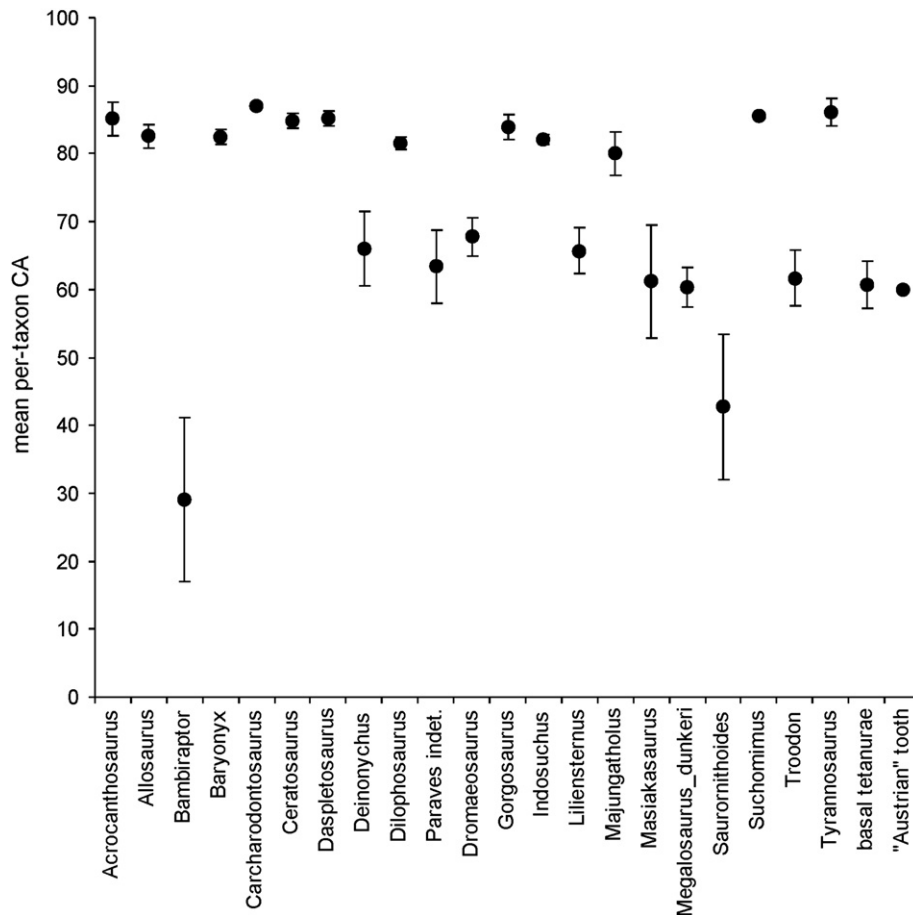


Fig. 7. Between-taxon comparisons of the shape variable, crown angle (CA) used in the two-way ANOVA. Dataset is composed of 20 theropod taxa taken from Smith et al. (2005) and four new taxa (basal Tetanuræ and Paraves indet. from the Santonian of Iharkút, Hungary; *Megalosaurus 'dunkeri'* from the Wealden, England; and the "Austrian tooth"=*Megalosaurus pannoniensis* from the lower Campanian of Muthmannsdorf, Austria).

Such an assemblage, with these three taxa co-occurring jointly at a single site, has not been reported previously for the theropod fauna at any other single Late Cretaceous locality in Europe. However, separate occurrences of one or two of these three taxa have been reported from Late Cretaceous units of similar age, including sites in northern Spain (Campanian?; Pereda Suberbiola, 1999) and southern Morocco (Cenomanian; Buffetaut, 1989; Russell, 1996).

Among basal tetanurans, remains of "Megalosauridae indet." are known from the Campanian of northern Spain (Casasnovas-Cladellas et al., 1988; Canudo and Ruiz-Omeñaca, 2003) and from the lower Campanian of eastern Austria (Seeley, 1881). A pedal ungual is known from the Santonian of Belgium (Dollo, 1903), but its systematic position is uncertain (Le Loeuff and Buffetaut, 1991).

The two fragmentary teeth from Austria (early Campanian) are identical to the basal tetanuran teeth from Iharkút suggesting the existence of a single basal tetanuran taxon in the northern part of the Apulian microplate (positioned between Africa and Europe), at least during the Santonian–early Campanian time interval (Figs. 10 and 11A). This is further supported by the vicinity of the two areas in the time interval considered, as reconstructed on the basis of the post-Campanian tectonic history of the region. In the Santonian, the eastern Alps (i.e. the Muthmannsdorf area) and the Transdanubian Central Range (i.e. the Bakony Mountains including the Iharkút area) were much closer to each other than today, but a roughly eastward continental movement of numerous blocks of the Alcapan terrane starting from the late Eocene to Oligocene resulted in a 60–

100 km divergence of this terrane (Kázmér and Kovács, 1985; Csontos and Vörös, 2004). Later in the Miocene, as a "consequence of the progressive termination of subduction roll-back along the arc" of the Carpathians, tensional stresses in the Pannonian Basin resulted in a south-southeastward movement of the Transdanubian Range (Fodor et al., 1999:295), increasing the distance between the two areas.

The great similarity of the basal tetanuran teeth from Central Europe to the teeth of stratigraphically much older *Megalosaurus bucklandii* from the Middle Jurassic (Benson et al., 2008) and '*M. dunkeri*' from the Lower Cretaceous of southern England is intriguing. Indeed, the Iharkút theropods appear to be "anachronistic relative to their chronostratigraphic position", as was noted previously for the Late Cretaceous Hațeg fauna located in the same region (western Romania; Csiki and Grigorescu, 2007:8). However, the basal tetanurans are not the only group in the Late Cretaceous of Europe that shows close relationship with much older forms. For example, the closest relative of the basal eusuchian crocodylian *Iharkutosuchus makadii* is *Hylaeochampsia vectiana* from the Barremian of the Isle of Wight (Ősi et al., 2007). Similarly, phylogenetic analysis of the nodosaurid ankylosaur, *Hungarosaurus tormai* (together with *Struthiosaurus* spp.), indicated that the European Late Cretaceous ankylosaurs are more primitive than their Early to mid-Cretaceous relatives from North America (Pereda-Suberbiola and Galton, 2001; Ősi, 2005; Ősi and Makádi, 2009).

These data suggest a very early separation of numerous European taxa from the typical (Middle Jurassic–Early Cretaceous)

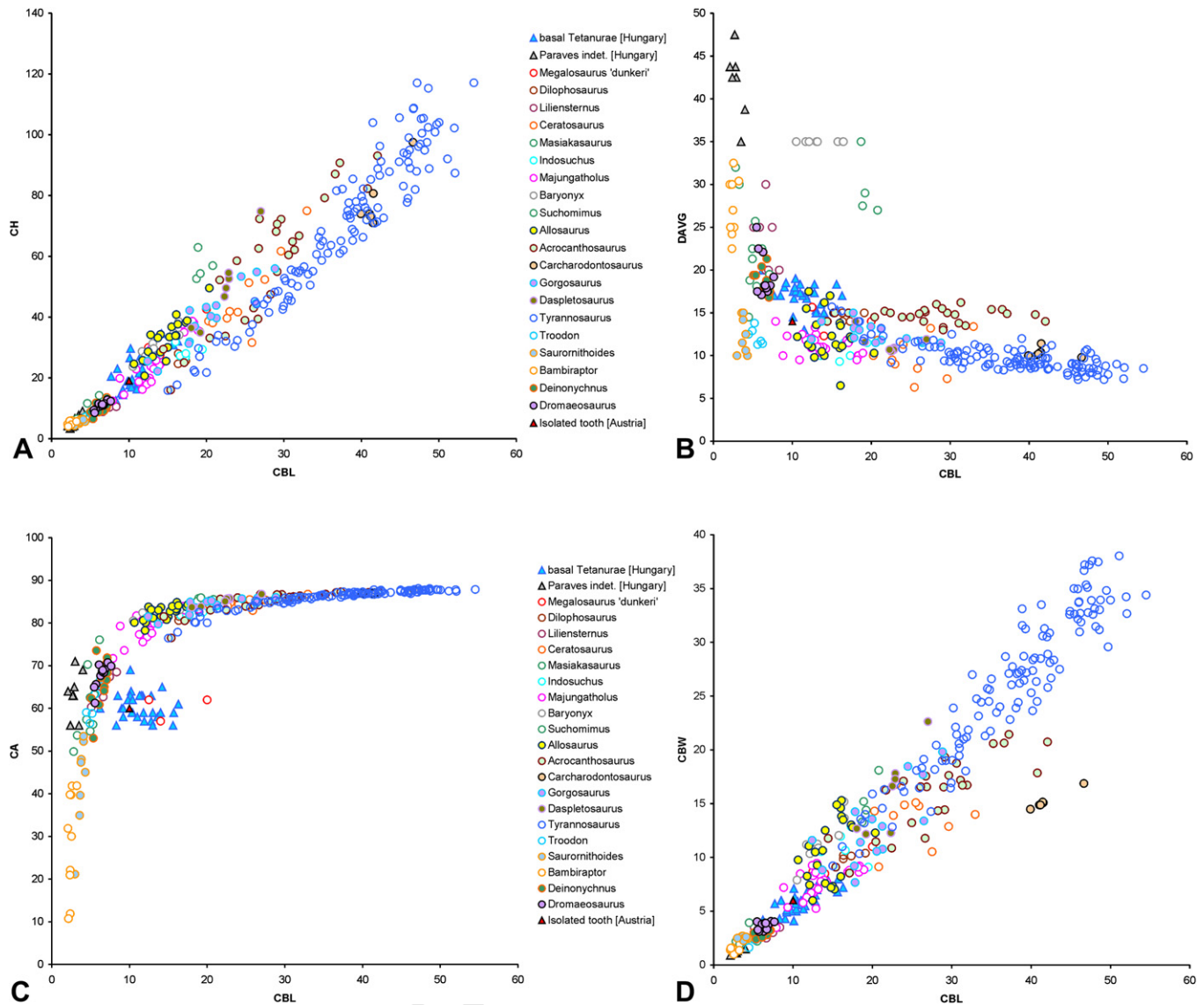


Fig. 8. Plots of CBL versus CH (A), CBL versus DAVG (B), CBL versus CA (C), and CBL versus CBW (D) for the 20 theropod taxa taken from Smith et al. (2005) and four new taxa (basal Tetanurae and Paraves indet. from the Santonian of Iharkút, Hungary; '*Megalosaurus dunkeri*' from the Wealden, England; and an "isolated tooth [Austria]"=*Megalosaurus pannoniensis*' from the lower Campanian of Muthmannsdorf, Austria).

Euramerican Faunal Province. The isolated habitats of the Mediterranean archipelago, separated at least from the Early Cretaceous, could have affected the evolutionary history of various (sometimes probably locally confined) ecosystems. For example, small-bodied taxa existed in isolated environments of Europe already in the Cenomanian (Dalla Vecchia, 2003; Fejfar et al., 2005; Vullo et al., 2007; Fig. 11). The Santonian Iharkút fauna, the hadrosaurids discovered at the Adriatic–Dinaric Carbonate Platform (Dalla Vecchia, 2002, but see Dalla Vecchia, 2008), the early Campanian Muthmannsdorf fauna, and the Maastrichtian 'Hațeg Island' fauna of western Romania all show primitive and endemic features (Nopcsa, 1902, 1923; Weishampel et al., 1991; Jianu and Weishampel, 1999; Csiki and Grigorescu, 2007; Fig. 11). All these data suggest also that, at some point in time, this area may have further fragmented into isolated island habitats (but see Jianu and Boekschoten, 1999), which may have functioned as refugia in the Late Cretaceous Mediterranean archipelago.

Besides the primitive and probably endemic characters of at least some archosaurian taxa in the Late Cretaceous Mediterranean

archipelago, the presence of some Gondwana-related faunal elements (e.g. bothremydid turtles, abelisauroids) in Europe (Allain and Pereda Suberbiola, 2003; Buffetaut, 1989; Buffetaut and Le Loeuff, 1991; Le Loeuff, 1991; Le Loeuff and Buffetaut, 1991) is further supported by the Hungarian theropod record. Abelisauroids have been described from the Albian of France (*Genusaurus sisteronensis* Accarie et al., 1995, but see Carrano and Sampson, 2008), from the Santonian of Hungary (in this paper), and Campano–Maastrichtian sediments of France (Buffetaut et al., 1988; Buffetaut, 1989; Le Loeuff and Buffetaut, 1991; Allain and Pereda Suberbiola, 2003) and Spain (Astibia et al., 1990) (Fig. 10).

In addition to the abelisauroid material, remains of the sebecosuchian crocodylian, *Doratodon* (Ősi and Rabi, 2006; Rabi, 2009), also of Gondwanan origin, were reported from Muthmannsdorf (Buffetaut, 1979), the Hațeg Basin (Grigorescu et al., 1999), and Spain (Company et al., 2005). These taxa further strengthen the paleobiogeographic argument that besides Euramerican taxa (e.g. eusuchian crocodylians, nodosaurid ankylosaurs, dromaeosaurid theropods), the Mediterranean archipelago was also inhabited by

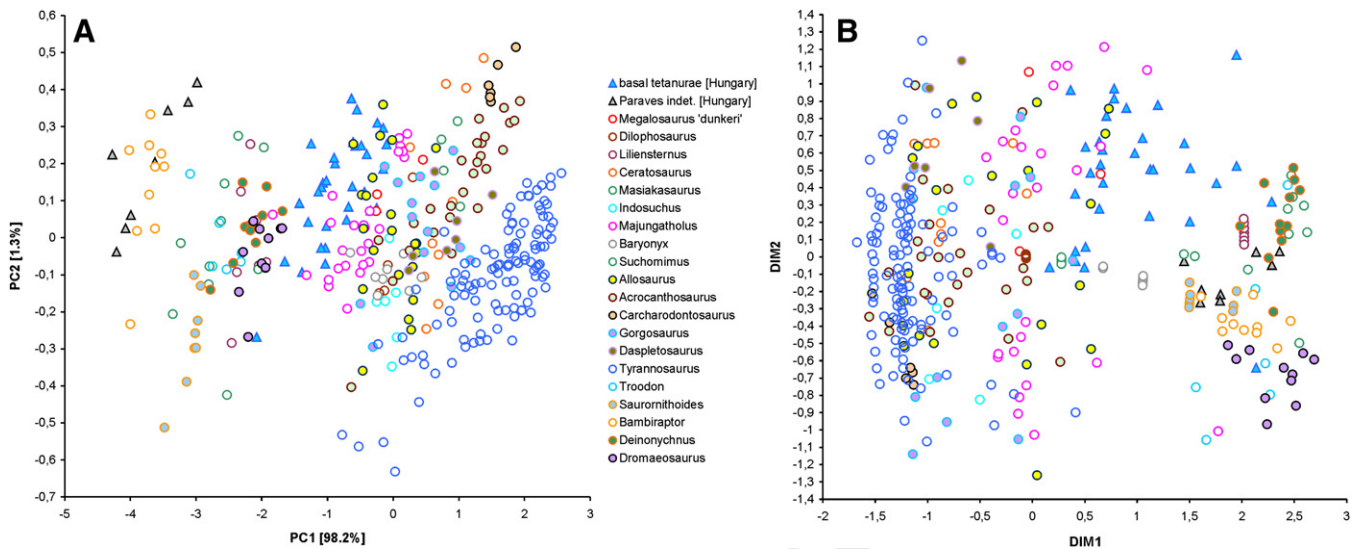


Fig. 9. Results of multivariate analyses. **A**, Principal component ordination of teeth plotted in the coordinate systems of PC1 and PC2 with symbols indicating taxonomic identity of teeth. Data restricted to log-transformed values of four linear dimensions. **B**, Non-metric multidimensional scaling ordination of teeth plotted in the coordinate systems of dim1 and dim2 with symbols indicating taxonomic identity of teeth. Data includes all morphological variables and all specimens (see text and supplementary data for additional details).

Gondwanan forms. The age of the Iharékút locality indicates that these taxa existed in the region certainly already by the Santonian. Carcharodontosaurids (but also titanosaurs and rebbachisaurids), however, coexisted with Euramerican forms in Europe (or at least in Iberia) already from the Aptian (Canudo and Ruiz-Omeña, 2003) to the Cenomanian (Vullo et al., 2007; Figs. 10, 11). This would indicate two interchange events between Africa and Europe, as was suggested by Le Loeuff (1991). However, the dispersal of different faunal elements among the larger landmasses (Africa, Ibero-Armorican landmass) and islands could have been much more complex spatially and temporally, and our recent interpretations are hampered by the generally poor fossil record of the early Late Cretaceous time interval in Europe, as was already suggested by Wilson and Sereno (1998). In addition, Buffetaut (1989) noted that the occurrence of Gondwanan faunal elements in the Late Cretaceous of Europe does not need to record interchange events during the Late Cretaceous. Indeed, except for some very poorly preserved material, almost nothing is known about the terrestrial fauna of the European archipelago from the Turonian–Coniacian time intervals

(Fig. 11). Thus, for example, abelisauroids (similarly to dromaeosaurids and troodontids) may have been present in this region throughout the entire Cretaceous (or at least from the Albian, based on *Genusaurus sisteronensis* Accarie et al., 1995, but see Carrano and Sampson, 2008). It is noteworthy here that the Gondwanan faunal elements are known from northern Africa from both the Cenomanian and the Maastrichtian sedimentary rocks (Russell, 1996; Buffetaut, 2005; Figs. 10, 11); the absence of those taxa in the unrepresented time intervals of both Africa and Europe may simply suggest that they have not been unearthed yet. If faunal interchange events really existed between Africa and southern Europe during the Late Cretaceous then these events should have happened via crossing seaways and/or by island hopping because paleogeographic data do not indicate any direct land connection between the two areas. Taking this into account, at least three possible dispersal routes can be suggested (Fig. 11): (1) between northwestern Africa and Iberia (Buffetaut, 1989), (2) across the Apulian microplate via island hopping (Gheerbrant, 1987), and/or (3) from northeastern Africa towards the islands of the subduction zone of the Tethys Ocean along the southwestern Asiatic margin. The latter may have formed elevated arches (land bridges) that supported the faunal dispersal routes from eastwards used by hadrosaurids, as suggested by Dalla Vecchia (2002). As of today, however, the fossil record of terrestrial vertebrates from the Late Cretaceous of Africa and Europe is too scarce to provide conclusive answer as to the importance of dispersal events and vicariance as possible scenarios determining the faunal composition of the Mediterranean region during the Cretaceous.

Nevertheless, remains of basal tetanurans, abelisaurids, and paravians in the Santonian Iharékút vertebrate assemblage clearly indicate the presence of these groups in the Apulian archipelago well before the Campano–Maastrichtian theropod faunas documented in the most important European localities of France, Spain, Romania, and Austria. Similar to the fauna documented from these geochronologically younger sites, the theropod groups from Iharékút also represent a complex ecosystem with mixed Gondwanan and Euramerican faunal elements, reflecting a biogeographical *status quo* that may have persisted throughout the entire Late Cretaceous.

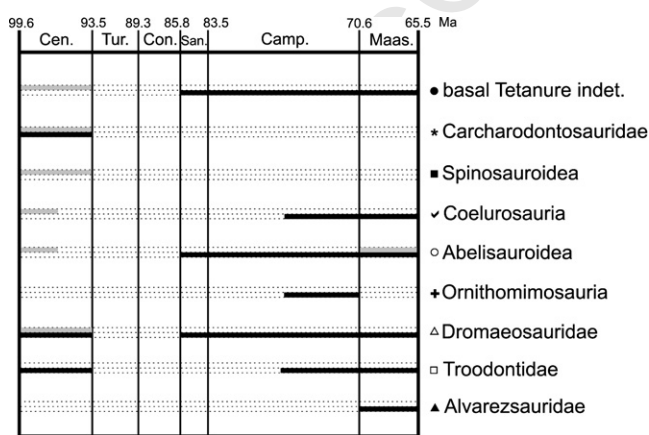


Fig. 10. Stratigraphical distribution of different non-avian theropod taxa during the Late Cretaceous in Europe (with black) and in northern Africa (with grey). Data are based on the references listed in Fig. 11.



Fig. 11. Late Cretaceous non-avian theropod localities in Europe and northern Africa. A, map showing the location of the main Late Cretaceous non-avian theropod dinosaur localities in Europe and northern Africa with the discovered groups indicated by symbols: **France:** 1, Charentes (Vullo et al., 2007); 2, Le Haute-Garonne (Laurent et al., 1999, 2002); 3, Aude Valley (Laurent et al., 2001); 4, Villeveyrac, Cruzy (Buffetaut et al., 1986, 1999, Buffetaut and Le Loeuff, 1991); 5, Serviers, Champ-Garimond (Buffetaut et al., 1986); 6, Roques-Hautes (Le Loeuff et al., 1992; Le Loeuff and Buffetaut, 1998; Allain and Taquet, 2000); 7, Beausset Syncline (Le Loeuff and Buffetaut, 1991); 8, Fox Amphoux (Le Loeuff et al., 1992). **Spain:** 9, Laño (Pereda Suberbiola, 1999, Pereda-Suberbiola et al., 2000); 10, Arén (Torices et al., 2004, Weishampel et al., 2004); 11, Tremp (Casanovas-Cladellas et al., 1988, López-Martínez et al., 2001). **Portugal:** 12–13, Viso, Aveiro, Taveiro (Antunes and Sigogneau-Russell, 1991, Antunes and Mateus, 2003). **Netherlands and Belgium:** 14, Dutch and Belgian Limburg (Buffetaut and Le Loeuff, 1991). **Austria:** 15, Muthmannsdorf (Seeley, 1881). **Hungary:** 16, lharkút (in this paper). **Slovenia:** 17, Kozina (Debeljak et al., 1999). **Romania:** 18, Borod (Nagybárd) (Csiki and Grigorescu, 1998); 19, Hațeg Basin (Csiki and Grigorescu, 1998, 2003). **Morocco:** 20, Ouled Abdoun Basin (Buffetaut, 2005); 21, Kem Kem region (Sereno et al., 1996); 22, Tafilalt (Kem Kem region) (Buffetaut, 1989, Russell, 1996). **Egypt:** 23, Bahariya Oasis (Rauhut, 1995). B, Paleogeographic map of the Mediterranean region during the Late Cretaceous with the suggested position of non-avian theropod localities. Paleogeographic map is based on the paleogeographic map made by Ron Blakey (<http://jan.ucc.nau.edu>). Arrows refer to possible routes of faunal interchange between Africa and Europe during the Cretaceous. Black box indicates that part of Europe shown in detail on Fig. 6A. Lands marked in light brown, shallow seas in light blue and deep seas in dark blue.

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References

- Accarie, H., Beaudoin, B., Dejax, J., Fries, G., Michard, J.-G., Taquet, P., 1995. Découverte d'un Dinosaurien théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes de Haute-Provence, France) et extension au Crétacé inférieur de la lignée cérorosaurienne. *Comptes Rendus de l'Académie des Sciences Paris, série Ila* 320, 327–334.
- Allain, R., 2002. Discovery of megalosaur (Dinosauria, Theropoda) in the middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology* 22, 548–563.
- Allain, R., Taquet, P., 2000. A new genus of Dromaeosauridae (Dinosauria, Theropoda) from the Upper Cretaceous of France. *Journal of Vertebrate Paleontology* 20, 404–407.
- Allain, R., Pereda Suberbiola, X., 2003. Dinosaurs of France. *Comptes Rendus Palevol* 2, 27–44.
- Antunes, M.T., Sigogneau-Russell, D., 1991. Nouvelles données sur les dinosaures du Crétacé supérieur du Portugal. *Comptes Rendus de l'Académie des Sciences Paris, sér 2 (313)*, 113–119.
- Antunes, M.T., Sigogneau-Russell, D., 1992. La faune de petits dinosaures du Crétacé terminal portugais. *Comunicações dos Serviços Geológicos de Portugal* 78 (1), 49–62.
- Antunes, M.T., Mateus, O., 2003. Dinosaurs of Portugal. *Comptes Rendus Palevol* 2, 77–95.
- Astibia, H., Buffetaut, E., Buscalioni, A.D., Cappelletta, H., Corral, C., Estes, R., Garcia-Garmilla, F., Jaeger, J.J., Jiménez-Fuentes, E., Le Loeuff, J., Mazin, J.M., Orue-Etxebarria, X., Pereda-Suberbiola, J., Powell, J.E., Rage, J.C., Rodríguez-Lazaro, J., Sanz, J.L., Tong, H., 1990. The fossil vertebrates from the Lano (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. *Terra Nova* 2, 460–466.
- Benson, R., Barrett, P.M., Powell, H.P., Norman, D.B., 2008. The taxonomic status of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Middle Jurassic Oxfordshire, UK. *Palaeontology* 51, 419–424.
- Brusatte, S.L., Benson, R.B.J., Carr, T.D., Williamson, T.E., Sereno, P.C., 2007. The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology* 27, 1052–1056.
- Buffetaut, E., 1979. Revision der Crocodylia (Reptilia) aus der Gosau-Schichten (Ober-Kreide) von Österreich. *Beiträge zur Paläontologie von Österreich* 6, 89–105.
- Buffetaut, E., 1989. Archosaurian reptiles with Gondwanan affinities in the Upper Cretaceous of Europe. *Terra-Nova* 1, 69–74.
- Buffetaut, E., 1994. An investigation based on the French record. *Berliner Geowissenschaftliche Abhandlungen* 13, 125–133.
- Buffetaut, E., 2005. First theropod dinosaur from the Maastrichtian phosphates of Morocco. *Kaupia. Darmstädter Beiträge zur Naturgeschichte* 14, 3–8.
- Buffetaut, E., Le Loeuff, J., 1991. Late Cretaceous dinosaur faunas of Europe: some correlation problems. *Cretaceous Research* 12, 159–176.
- Buffetaut, E., Pouit, D., 1994. Restes de dinosaures et de crocodyliens dans le Crétacé supérieur du centre-ouest de la France. *Comptes Rendus de l'Académie des Sciences Paris, sér 2 (319)*, 253–259.
- Buffetaut, E., Marandat, B., Sigé, B., 1986. Découverte de dents de Deinonychosaures (Saurischia, Theropoda) dans le Crétacé supérieur du Sud de la France. *Comptes Rendus de l'Académie des Sciences Paris, sér 2 (319)*, 1393–1396.
- Buffetaut, E., Mechin, P., Mechin-Salesy, A., 1988. Un dinosaure Théropode d'affinités gondwaniennes dans le Crétacé supérieur Provence. *Comptes Rendus de l'Académie des Sciences Paris, sér 2 (306)*, 153–158.
- Buffetaut, E., Cuny, G., Le Loeuff, J., 1991. French dinosaurs: The best record in Europe? *Modern Geology* 16, 17–42.
- Buffetaut, E., Le Loeuff, J., Cavin, L., Duffaud, S., Gheerbrant, E., Laurent, Y., Martin, M., Rage, J.-C., Tong, H.-Y., Vasse, D., 1997. Late Cretaceous non-marine vertebrates from southern France: A review of recent finds. *Géobios* 20, 101–108.
- Buffetaut, E., Le Loeuff, J., Tong, H.-Y., Duffaud, S., Cavin, L., Garcia, G., Ward, D., 1999. Un nouveau gisement de vertébrés du Crétacé supérieur à Cruzy (Hérault, Sud de la France). *Comptes Rendus de l'Académie des Sciences Paris, sér 2 (328)*, 203–208.
- Burnham, D.A., Derstler, K.L., Currie, P.J., Bakker, R.T., Zhou, Z., Ostrom, J.H., 2000. Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. 13. University of Kansas Paleontological Contributions, New Series, 1–14.
- Canudo, J.I., Ruiz-Omeñaca, J.I., 2003. Los restos directos de dinosaurios terópodos (excluyendo Aves) en España. *Ciencias de la Tierra. Dinosaurios y otros reptiles mesozoicos de España* 26, 347–373.
- Carrano, M.T., 2007. The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology Memoir* 8, 163–179.
- Carrano, M.T., Sampson, S.D., 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 6, 183–236.
- Casanovas-Cladellas, M.L., Santafé-Llopis, J.V., Sanz, J.L., 1988. La primera resta fósil d'un Terópode (Saurischia, Dinosauria) en el Crétacé superior de la Conca de Tremp (Lleida, España). *Paleontologia I Evolució* 22, 77–81.
- Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroit, P., Van Itterbeeck, J., 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Hateg Basin (Romania). *Comptes Rendus Palevol* 1, 173–180.
- Company, J., Pereda Suberbiola, X., Ruiz-Omeñaca, J.I., Buscalioni, A.D., 2005. A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *Journal of Vertebrate Paleontology* 25, 343–353.
- Csiki, Z., Grigorescu, D., 1998. Small theropods from the Late Cretaceous of the Hateg Basin (western Romania) – An unexpected diversity at the top of the food chain. *Oryctos* 1, 87–104.
- Csiki, Z., Grigorescu, D., 2003. Theropod dinosaurs of the Hateg Basin – are they more diverse than thought? Abstract Volume of the 4th National symposium of Paleontology, Cluj-Napoca, p. 17.
- Csiki, Z., Grigorescu, D., 2007. The dinosaur island – new interpretation of the Hateg Basin vertebrate fauna after 110 years. *Sargatia* 20, 5–26.
- Csontos, L., Vörös, A., 2004. Mesozoic plate tectonic reconstruction of the Carpathian region. *Palaeoclimatology, Palaeoecology, Palaeogeography* 210, 1–56.
- Cuenca-Bescós, G., Amo, O., Barco, J.L., Canudo, J.I., Royo-Torres, R., Ruiz-Omeñaca, J.I., 1999. Dinosaurios de Aragón. *Zubia* 17, 235–257.
- Currie, P.J., 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 7, 72–81.
- Currie, P.J., Rigby Jr., J.K., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Currie, P.J., Carpenter, K. (Eds.), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge, pp. 107–125.
- Dalla Vecchia, F.M., 2001. Atlas of the ichnofossils exposed in the late Cenomanian (Cretaceous) track site of San Lorenzo di Daila/Lovrecica (Istria, Croatia). *Natura Nascosta* 23, 24–35.
- Dalla Vecchia, F.M., 2002. Cretaceous dinosaurs in the Adriatic-Dinaric carbonate platform (Italy and Croatia): paleoenvironmental implications and paleogeographical hypotheses. *Memoire della Società Geologica Italiana* 57, 89–100.
- Dalla Vecchia, F.M., 2003. Observations on the presence of plant-eating dinosaurs in an oceanic carbonate platform. *Natura Nascosta* 27, 14–27.
- Dalla Vecchia, F., 2008. I dinosauri del Villaggio del Pescatore (Trieste): qualche aggiornamento. *Atti Museo Civico di Storia Naturale di Trieste* 53, 111–130.
- Debeljak, I., Kosir, A., Otonicar, B., 1999. A preliminary note on dinosaur and non-dinosaurian reptiles from the Upper Cretaceous carbonate platform succession at Kozina (SW Slovenia). *Razprave IV. Razreda Sazu* 40, 3–25.
- Dollo, L., 1903. Les dinosauriens de la Belgique. *Comptes Rendus de l'Académie des Sciences Paris, sér 2 (136)*, 565–567.
- Fejfar, O., Košťák, M., Kvaček, J., Mazuch, M., Moučka, M., 2005. First Cenomanian dinosaur from Central Europe (Czech Republic). *Acta Palaeontologica Polonica* 50, 295–300.
- Fodor, L., Csontos, L., Bada, G., Györfi, I., Benkovics, L., 1999. Tertiary tectonic evolution of the Pannonian basin system and neighbouring orogens: a new synthesis of alaeostress data. In: Durand, G., Jolwet, L., Horváth, F., Serrante, M. (Eds.), *The Mediterranean Basins: Tertiary Extension within the Alpine Orogen*, 156. Geological Society, London, Special Publication, pp. 295–334.
- Gheerbrant, F., 1987. Les Vertébrés continentaux de l'Adrar Mgorn (Maroc, Paléocène); une dispersion de mammifères; transtéthysienne aux environs de la limite Mésozoïque/Cénozoïque? *Geodinamica Acta* 1, pp. 233–216.
- Grigorescu, D., Venczel, M., Csiki, Z., Limborea, R., 1999. New latest Cretaceous microvertebrate fossil assemblages from the Hateg Basin (Romania). In: Jagt, J.W.M., Lambers, P.H., Mulder, E.W.A., Schulp, A.S. (Eds.), *Proceedings of the Third European Workshop on Vertebrate Paleontology. Geologie en Mijnbouw*, 78, pp. 301–314.
- Harris, J.D., 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin* 13, 1–75.
- Holtz Jr., T.R., 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Vertebrate Paleontology* 68, 1100–1117.
- Holtz, T.R., Molnar, R.E., Currie, P.J., 2004. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley, California, pp. 71–110.
- Huntley, J.W., Xiao, S., Kowalewski, M., 2006. 1.3 Billion years of archtarch history: An empirical morphospace approach. *Precambrian Research* 144, 52–68.
- Jianu, C.-M., Boekschoten, G.J., 1999. The Hateg – island or outpost? In: Reumer, J.W.F., De Vos, J. (Eds.), *Elephants have a snorkel! Papers in honour of Paul Y. Sondaar*. Denisia 7, pp. 195–198.
- Jianu, C.-M., Weishampel, D.B., 1999. The smallest of the largest: A new look at possible dwarfing in saurpoid dinosaurs. In: Jagt, J.W.M., Lambers, P.H., Mulder, E.W.A., Schulp, A.S. (Eds.), (eds.), *Proceedings of the Third European Workshop on Vertebrate Paleontology*, 78. *Geologie en Mijnbouw*, pp. 335–343.

- Jolicoeur, P., 1963. The degree of generality of robustness in *Martes Americana*. *Growth* 27, 1–27.
- Kázmér, M., Kovács, S., 1985. Permian-Paleogene Paleogeography along the Eastern part of the Insubric-Periadriatic Lineament system: Evidence for continental escape of the Bakony-Drauzug Unit. *Acta Geologica Hungarica* 28, 71–84.
- Kessler, J., Grigorescu, D., Csiki, Z., 2005. *Elopteryx* revisited – A new bird-like specimen from the Maastrichtian of the Hațeg Basin (Romania). *Acta Paleontologica Romaniaica* 5, 249–258.
- Knauer, J., Siegl-Farkas, Á., 1992. Palynostratigraphic position of the Senonian beds overlying the Upper Cretaceous bauxite formations of the Bakony Mts. Annual Report of the Hungarian Geological Institute of 1990, 463–471 (Hungarian 463–469; English 469–471.).
- Kowalewski, M., Dyreson, E., Marcot, J., Vargas, J., Flessa, K., Hallman, D., 1997. Phentic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottida*. *Paleobiology* 23, 444–469.
- Laurent, Y., Cavin, L., Bilotte, M., 1999. Découverte d'un gisement à vertébrés dans le Maastrichtien supérieur des Petites-Pyrénées. *Comptes Rendus de l'Académie des Sciences Paris, sér 2* (328), 781–787.
- Laurent, Y., Le Loeuff, J., Bilotte, M., Buffetaut, E., Odin, G.S., 2001. Campanian-Maastrichtian continental-marine connection in the Aquitaine-Pyrénées-Provence area (S France). In: Odin, G.S. (Ed.), *The Campanian-Maastrichtian Stage Boundary, Characterisation at Tercis les Bains (France) and Correlation with Europe and other Continents*. *Developments in Palaeontology and Stratigraphy* 19, pp. 657–665.
- Laurent, Y., Bilotte, M., Le Loeuff, J., 2002. Late Maastrichtian continental vertebrates from southwestern France: correlation with marine fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 187, 121–135.
- Le Loeuff, J., 1991. The Campanian-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Research* 12, 93–114.
- Le Loeuff, J., Buffetaut, E., 1991. *Tarascosaurus salluvicus* nov. gen., nov. sp., dinosaur theropode du Crétacé supérieur du Sud de la France. *Geobios* 24, 585–594.
- Le Loeuff, J., Buffetaut, E., 1998. A new dromaeosaurid theropod from the Upper Cretaceous of southern France. *Oryctos* 1, 105–112.
- Le Loeuff, J., Buffetaut, E., Mechin, P., Mechin-Saleusy, A., 1992. The first record of dromaeosaurid dinosaurs (Saurischia, Theropoda) in the Maastrichtian of southern Europe: Palaeobiogeographical implications. *Bulletin de la Société Géologie du France* 163, 337–343.
- López-Martínez, N., Canudo, J.L., Ardévól, L., Pereda Suberbiola, L., Orue-Etxebarria, X., Cuenca-Bescós, G., Ruiz-Omeñaca, J.L., Murelaga, X., Feist, M., 2001. New dinosaur sites correlated with upper Maastrichtian pelagic deposits in the Spanish Pyrenees: implications for the dinosaur extinction pattern in Europe. *Cretaceous Research* 22, 41–61.
- Makádi, L., Botfalvai, G., Ősi, A., 2006. The Late Cretaceous continental vertebrate fauna from the Bakony Mountains I: fishes, amphibians, turtles, squamates. *Földtani Közönlöny* 136, 487–502. In Hungarian.
- Makovicky, P., Apesteguía, S., Agnolin, F., 2005. The earliest dromaeosaurid theropod from South America. *Nature* 473, 1007–1011.
- Martill, D.M., Naish, D., 2001. *Dinosaurs of the Isle of Wight*. Dorset Press, Dorchester, 433 pp.
- Mártonné Szalai E., 2005. Paleomagnetic studies at Iharkút. Unpublished manuscript, ELTE Department of Applied Geology. (In Hungarian).
- Naish, D., Dyke, G., 2004. *Heptasteornis* was no ornithomimid, troodontid, dromaeosaurid or owl: the first alvarezsaurid (Dinosauria: Theropoda) from Europe. *Neues Jahrbuch für Geologie und Paleontologie Monatshefte* 2004, 385–401.
- Nopcsa, F., 1902. Mathematisch-Naturwissenschaftliche Klasse. *Notizen über cretatische Dinosaurier*, 111. Akademie der Wissenschaften, Wien. 93–114.
- Nopcsa, F., 1923. On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallobiotium*). *Quarterly Journal of the Geological Society of London* 79, 100–116.
- Norell, M.A., Makovicky, P., 1999. Important features of the dromaeosaurid skeleton II: information from a newly collected specimens. *American Museum Novitates* 3282, 1–5.
- Norell, M.A., Makovicky, P., 2004. Dromaeosauridae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley, California, pp. 196–209.
- Novas, F.E., 1997. *Abelisauridae*. In: Currie, P.J., Padian, K. (Eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego, pp. 1–2.
- Novas, F.E., Bandyopadhyay, S., 2001. *Abelisaurid* pedal unguals from the Late Cretaceous of India. *Vllth International Symposium on Mesozoic Terrestrial Ecosystems, Asociación Paleontológica Argentina. Publicación Especial* 7, 145–149.
- Novas, F.E., Dalla Vecchia, F., Pais, D.F., 2005. Theropod unguals from the Late Cretaceous (Cenomanian) of Morocco, Africa. *Revista Museo Argentino ciencias Naturales n.s* 7, 167–175.
- O'Connor, P., 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology* 267, 1199–1226.
- O'Connor, P.M., Claessens, L.P.A.M., 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436, 253–256.
- Ostrom, J.H., 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History* 30, 1–165.
- Ostrom, J.H., 1974. The pectoral girdle and forelimb function of *Deinonychus* (Reptilia: Saurischia): A correction. *Postilla* 165, 1–11.
- Ősi, A., 2004. The first dinosaur remains from the Upper Cretaceous of Hungary (Csehbánya Formation, Bakony Mts). *Geobios* 37 (6), 749–753.
- Ősi, A., 2005. *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology* 25, 370–383.
- Ősi, A., Rabi, M., 2006. Egy késő-kréta kontinentális gerinces fauna a Bakonyböl: krokodilok, dinoszauruszok, pteroszauruszok és madarak. *Földtani Közönlöny* 136, 503–526.
- Ősi, A., Fözy, I., 2007. A maniraptoran (Theropoda, Dinosauria) sacrum from the Upper Cretaceous of the Hațeg Basin (Romania) – in search of the lost pterosaurs of Baron Franz Nopcsa. *Neues Jahrbuch für Geologie und Paleontologie* 246, 173–181.
- Ősi, A., Makádi, L., 2009. New remains of *Hungarosaurus tormai* (Ankylosauria, Dinosauria) from the Upper Cretaceous of Hungary: skeletal reconstruction and body mass estimation. *Paläontologische Zeitschrift* 83, 227–245.
- Ősi, A., Mindszenty, A., 2009. Iharkút, Dinosaur-bearing alluvial complex of the Csehbánya Formation. In: Babinszky, E. (Ed.), *Cretaceous sediments of the Transdanubian Range*. Field guide of the geological excursion organized by the Sedimentological Subcommittee of the Hungarian Academy of Sciences and the Hungarian Geological Society, pp. 51–63.
- Ősi, A., Clark, J.M., Weishampel, D.B., 2007. First report on a new basal eusuchian crocodyliform with multi-cusped teeth from the Upper Cretaceous (Santonian) of Hungary. *Neues Jahrbuch für Geologie und Paleontologie* 243, 169–177.
- Pereda Suberbiola, X., 1999. Las faunas finicretácicas de dinosaurios ibéricos. *Zubia* 17, 259–279.
- Pereda-Suberbiola, X., 2009. Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review. *Bulletin de la Société géologique France* 180, 57–71.
- Pereda-Suberbiola, X., Galton, P., 2001. Reappraisal of the nodosaurid ankylosaur *Struthiosaurus austriacus* Bunzel from the Upper Cretaceous Gosau Beds of Austria. In: Carpenter, K. (Ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, Indiana, pp. 173–210.
- Pereda-Suberbiola, X., Astibia, H., Murelaga, X., Elorza, J.J., Gómez-Alday, J.J., 2000. Taphonomy of the Late Cretaceous dinosaur-bearing beds of the Laño Quarry (Iberian Peninsula). *Palaeogeography, Palaeoclimatology, Palaeoecology* 157, 247–275.
- Perle, A., Norell, M.A., Clark, J.M., 1999. A new maniraptoran theropod – *Achillobator giganticus* (Dromaeosauridae) – from the Upper Cretaceous of Burkhan, Mongolia. *Ulaanbaatar: Geology Department, National University of Mongolia*, pp. 1–106.
- Persson, P.O., 1959. Reptiles from the Senonian (U. Cret.) of Scania (S. Sweden). *Arkiv för Mineralogi och Geologi* 2, 431–478.
- Prieto-Marquez, A., Gaete, R., Galobart, A., Ardevol, L., 2000. A *Richardostesia*-like theropod tooth from the Late Cretaceous foredeep, south-central Pyrenees, Spain. *Ecolae Geologica Helvetica* 93, 497–501.
- Rabi, M., 2009. Presence of sebecosuchian crocodyliforms in the Late Cretaceous of Europe. In: Godefroit, P., Lambert, O. (Eds.), *Tribute to Charles Darwin and Bernissart Iguanodons: New perspectives on Vertebrate Evolution and Early Cretaceous Ecosystems*. Belgium, Brussels, p. 83.
- Rauhut, O.W.M., 1995. Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Bahariasaurus* Stromer 1934, 16. *Berliner Geowissenschaftliche Abhandlungen*, E, pp. 357–375.
- Rozhdetsvensky, A.K., 1973. The study of Cretaceous reptiles in Russia. *Paleontologiskij Zhurnal* 1973, 90–99. In Russian.
- Russell, D.A., 1996. Isolated dinosaur bones from the Middle Cretaceous of the Tafilalet, Morocco. *Bull. Bulletin de la Société Géologie du France, sér 4*. C 18, 349–402.
- Sampson, S.D., Carrano, M.T., Forster, C.A., 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* 409, 504–506.
- Sánchez-Hernández, B., Benton, M.J., Naish, D., 2007. Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 249, 180–215.
- Schubert, B.W., Ungar, P.S., 2005. Wear facets and enamel spalling in tyrannosaurid dinosaurs. *Acta Paleontologica Polonica* 50, 93–99.
- Seeley, H.G., 1881. The reptile fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. *Quarterly Journal of the Geological Society London* 37, 620–702.
- Senter, P., 2007. A method for distinguishing dromaeosaurid manual unguals from pedal "sickle claws". *Bulletin of the Gunma Museum of Natural History* 11, 1–6.
- Serenó, P.C., Duthell, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P., Sidor, C.A., Varricchio, D.J., Wilson, J.F., 1996. Predatory dinosaurs from the Sahara. *Science* 272, 986–991.
- Smith, J.B., Vann, D.R., Dodson, P., 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *Anatomical Record A* 285, 699–736.
- Sues, H.-D., 1978. A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta, Canada. *Zoological Journal of the Linnean Society* 62, 381–400.
- Tanke, D.H., Currie, P.J., 2000. Head-biting behavior in theropod dinosaurs: paleopathological evidence. In: Pérez-Moreno, B.P., Holtz Jr., T.R., Sanz, J.L., Moratalla, J.J. (Eds.), *Aspects of Theropod Paleobiology*, 15. *Gaia*, pp. 167–184.
- Torices, A., Ruiz-Omeñaca, J.L., Canudo, J.L., López-Martínez, N., 2004. Nuevos datos sobre los dinosaurios terópodos (Saurischia: Theropoda) del Crétacé superior de los Pirineos Sur-Centrales (Huesca y Lleida). *Geo-Temas* 6, 71–74.

- 2061 Tuba, Gy., Kiss, P., Pósfai, M., Mindszenty, A., 2006. Preliminary data on the
2062 diagenesis of Cretaceous Dinosaur bones from the Bakony Mts, Hungary.
2063 *Földtani Közlöny* 136, 1–24. In Hungarian.
- 2064 Turner, A.H., Pol, D., Clarke, J.A., Erickson, G.M., Norell, M.A., 2007. A Basal Dro-
2065 maosaurid and Size Evolution Preceding Avian Flight. *Science* 317, 1378–1381.
- 2066 Tykosky, R.S., Rowe, T., 2004. Ceratosauria. In: Weishampel, D.B., Dodson, P.,
2067 Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley,
2068 California, pp. 47–70.
- 2069 Vullo, R., Neraudeau, D., 2008. Cenomanian vertebrate assemblages from south-
2070 western France: a new insight into the European mid-Cretaceous continental
2071 fauna. *Cretaceous Research* 29, 930–935.
- 2072 Vullo, R., Neraudeau, D., Lenglet, T., 2007. Dinosaur teeth from the Cenomanian of
2073 Charentes, western France: evidence for a mixed Laurasian–Gondwanan
2074 assemblage. *Journal of Vertebrate Paleontology* 27, 931–943.
- 2075 Wedel, M.J., 2009. Evidence for bird-like air sacs in saurischian dinosaurs. *Journal of
Experimental Zoology* 311A, 611–628.
- Weishampel, D.B., Jianu, C.M., 1996. New theropod dinosaur material from the
Hațeg Basin (Late Cretaceous, western Romania). *Neues Jahrbuch für Geologie
und Paläontologie, Abhandlungen* 200, 387–404.
- Weishampel, D.B., Grigorescu, D., Norman, D.B., 1991. The dinosaurs of Transylvania. *National Geographic Research and Exploration*, 196–215.
- Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X., Sahni, A.,
Gomani, E.M., Noto, C.R., 2004. Dinosaur distribution. In: Weishampel, D.B.,
Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*. University of California Press,
Berkeley, California, pp. 517–606.
- Wilson, J.A., Sereno, P.C., 1998. Early evolution and higher-level phylogeny of the
sauropod dinosaurs. *Memoir Society of Vertebrate Paleontology* 5, 1–68.
- Xu, X., Wang, X.-L., Wu, X.-C., 1999. A dromaeosaurid dinosaur with a filamentous
integument from the Yixian Formation of China. *Nature* 401, 262–266.
- Zelditch, M.L., Swiderski, D.L., Sheets, H.D., Fink, W.L., 2004. *Geometric Morpho-
metrics for Biologists: A Primer*. Elsevier Academic Press, San Diego, p. 441.

Appendix. Supplementary data

Supplementary data associated with this article can be found in the online
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