

**Additional non-avian theropod and bird remains from the early Late
Cretaceous (Santonian) of Hungary and a review of the European
abelisauroid record**

*Restes supplémentaires de théropodes non-aviens et d'oiseaux du Crétacé supérieur
(Santonien) de Hongrie et revue des abelisauroïdes européens.*

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RH: Theropods from Hungary

Abstract – Hitherto unpublished remains of non-avian and avian theropods from the Late Cretaceous (Formation Csehbánya, Santonian) Iharkút locality (western Hungary) are described. Non-avian theropod remains include an abelisaurid femur, which confirms the presence of this theropod family at Iharkút, and a metacarpal and a tibiotarsus from a paravian which may belong to *Pneumatoraptor fodori*, previously described from Iharkút. Birds are represented by two femora which clearly belong to enantiornithines, possibly to *Bauxitornis*, previously described from Iharkút. The abelisauroid record from the Cretaceous of Europe is reviewed.

Keywords: Abelisauridae, Paraves, Enantiornithes, Late Cretaceous; Hungary

Résumé - Des restes inédits de théropodes non-aviens et aviens du gisement Crétacé supérieur (Formation Csehbánya, Santonien) d'Iharkút (Ouest de la Hongrie) sont décrits. Les restes de théropodes non-aviens comprennent un fémur d'abelisauridé, qui confirme la présence de cette famille de théropodes à Iharkút, et un métacarpien et un tibiotarse d'un paravian qui appartient peut-être à *Pneumatoraptor fodori*, déjà décrit à Iharkút. Les oiseaux sont représentés par deux fémurs qui appartiennent clairement à des enantiornithes, peut-être à *Bauxitornis*, déjà signalé à Iharkút. Les abelisauroïdes signalés dans le Crétacé d'Europe sont passés en revue.

Mots-clés : Abelisauridae, Paraves, Enantiornithes, Crétacé supérieur, Hongrie.

Introduction

Late Cretaceous theropod dinosaur remains (including birds) are poorly known in Europe and most of the collected material is represented by isolated and fragmentary bones and teeth (Buffetaut and Le Loeuff 1991, Weishampel et al. 2004, Pereda-Suberbiola 2009). Although these remains apparently indicate a great diversity of non-avian theropod dinosaurs in the European archipelago (including abelisauroids, basal tetanurans, carcharodontosaurs, dromaeosaurs, troodontids, ornithomimosaurids, and alvarezsaurids, see Ósi et al. 2010 for a review), most specimens cannot be determined beyond family level. Up to the present, a single species referred to Abelisauridae, *Tarascosaurus salluvicus* Le Loeuff and Buffetaut, 1991, and four species of dromaeosaurid or dromaeosaur-like paravians such as *Variraptor mechinorum* Le Loeuff and Buffetaut, 1998 (see also Chanthasit & Buffetaut, 2009), *Pyroraptor olympius* Allain and Taquet, 2000, *Pneumatoraptor fodori* Ósi, Apesteguía and Kowalewski, 2010, and *Balaur bondoc* Csiki, Vremir, Brusatte and Norell, 2010 have been described from the Late Cretaceous of Europe. Most of these species are based on disarticulated or isolated material, and only *Balaur* from western Romania was established on the basis of well preserved, articulated postcranial remains (Csiki et al. 2010).

Concerning birds of the European Late Cretaceous, fossils are even more scanty than in the case of non-avian theropods and except for some associated bones in marine sediments (Dyke et al. 2002) the material is actually represented by isolated postcranial remains (Dyke and Ósi 2010). Only three taxa, a giant ground bird *Gargantuavis philoinos* Buffetaut and Le Loeuff, 1998 and two enantiornithine *Martinavis cruzyensis* Walker, Buffetaut and Dyke, 2007 and *Bauxitornis mindszentyae* Dyke and Ósi, 2010 have been identified at species level. Most of the additional, isolated bird bones were mainly referred to enantiornithine (Buffetaut 1998;

Buffetaut et al. 2000, Dyke et al. 2008, Ósi 2008) and ornithurine (Dyke et al. 2002, Dyke et al. 2008, Wang et al. 2010) birds. Furthermore, an isolated feather from Upper Cretaceous of Slovenia has to be mentioned (Buffetaut et al. 2002).

In this paper, we provide a detailed comparative description of five isolated but well preserved theropod bones from the Santonian of Iharkút, western Hungary. Three of them are from non-avian theropods, among which a right femur is the second representative of the poorly represented family Abelisauridae from this area. Along with a fragmentary humerus and the tarsometatarsus of *Bauxitornis* (Dyke and Ósi 2010), two complete enantiornithine femora further represent large-sized birds in the Iharkút ecosystem and highlight the diverse morphologies present in Late Cretaceous birds.

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

Geological and taphonomical setting

The five specimens described in this study are from the same stratigraphical unit of the Csehbánya Formation that contained 95% of the vertebrate remains found in Iharkút. These bone yielding units are about 3 m thick, lenticular beds made up by coarse pebbly sand and organic rich silt and clay, interpreted as a shallow channel or pond filled up by episodic muddy debris flows, silt and sand. Deposition of the Csehbánya Formation began in the Santonian (Occullopollis- Complexiopollis-zone, Knauer and Siegl-Farkas 1992). This stratigraphic position was approved also by paleomagnetic measurements carried out by Szalai (2005).

Ninty percent of the bones from Iharkút including the five specimens discussed here represent isolated elements that were found together with the remains of other vertebrate groups (e.g. fishes, pterosaurs, crocodiles etc.) in a rather chaotic arrangement. Thus it is unknown if two

or more elements from the same taxon represent a single individual or not.

The material can be regarded as fragmentary, because 78% of the bones exhibit some kind of postmortem fracture. The data retrieved from the breakage angles suggests that the majority of the breaks occurred after the fossilization of the bones, which also suggests rapid burial and deposition shortly after the initiation of diagenetic processes (Ősi et al. in press).

Have both enanthionothine femora found together?

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.

Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1985

Abelisauridae indet.

Referred material: right fragmentary femur (MTM PAL 2011.17).

Locality: Iharkút, Bakony Mountains, western Hungary.

Age and horizon: Late Cretaceous, Santonian, Csehbánya Formation (Knauer and Siegl-

Farkas 1992, Szalai 2005, Ósi and Mindszenty 2009).

Description and comparisons

The right femur (MTM PAL 2011.17, Fig. 1) is slightly compacted latero-medially, the dorsal margin and the antero-medial end of the femoral head, and the distal articular head are missing. The preserved length of the bone is 15.3 cm. The hollow shaft is relatively straight in anterior and posterior views and not as sigmoid as seen in *Berberosaurus* (Allain et al. 2007, Fig. 2N–P) but it is bowed in medial and lateral views. Among others (see below) the general shape of the bone strongly resembles the femur of *Genusaurus* from the Early Cretaceous of France (Accarie et al. 1995, Fig. 2A–D). The proximal half of the bone including most details of the proximal end is well preserved. The preserved part of the femoral head is oriented antero-medially (approximately 45°) but because the end of the femoral head is missing, it cannot be determined whether it was angled slightly ventrally as in various ceratosaurians, whether this end was rather oriented horizontally. The proximal part of the femur becomes narrower postero-laterally toward the greater trochanter (Fig. 1C) as in other non-tetanuran theropods (Carrano et al. 2002). The greater trochanter is confluent with the femoral head, its posterior margin is straight and it has a very shallow, crest-like lateral margin. The greater and lesser trochanters are separated by a notch that continues in a very shallow, anterodorsally–posteroventrally oriented groove (Hutchinson 2001). Ventral to the greater trochanter an extended trochanteric shelf is present. The laterally or slightly posterolaterally facing trochanteric shelf has a rugose surface of which the expanded anterior portion is the lesser trochanter (Hutchinson 2001). The lesser trochanter is actually a huge process on the lateral surface of the proximal end of the bone. In lateral view, it has a rectangular shape with a dorsal tip and a rounded anterior margin.

The lesser trochanter of the Hungarian femur is much larger relative to the size of the proximal end than those of *Berberosaurus* (Allain et al. 2007), *Genusaurus* (Accarie et al. 1995, pers. obs.), *Ceratosaurus* (Madsen and Welles 2000, Fig. 2H–J) or *Masiakasaurus* (Carrano et al. 2002, Fig. 2Q–T) but comparable in size with that of *Carnotaurus* (Bonaparte et al. 1990 Fig. W–Z). It is a dorsoventrally high and anteroposteriorly wide flange and not as pointed and process-like as in *Tarascosaurus* (Le Loeuff and Buffetaut 1991, Fig. 2E–G). The orientation of this trochanter is not perpendicular to the axis of the femoral head as seen in basal tetanurans (Currie and Zhao 1993, Allain 2002, Holtz et al. 2004) but it projects anteriorly-anteromedially, being nearly parallel with the axis of the femoral head, much as in *Taracosaurus*, *Genusaurus* or other ceratosaurians (e.g. some abelisauroid femora from India, Huene and Matley 1933: pl. XVI, fig. 9a). The dorsalmost point of the lesser trochanter reaches the level of the half of the greater trochanter. Anteriorly, this trochanter is flattened and crest-like. No accessory trochanter (Makovicky and Sues 1998) is present at the distal base of the lesser trochanter. At the level of its ventralmost point the developed fourth trochanter starts on the posteromedial side of the femoral shaft. It is a rounded crest and more pronounced than that of *Genusaurus* and similar in relative size to that of *Berberosaurus* (Allain et al. 2007), *Xenotarsosaurus* (Martinez et al. 1986, Fig. 2K–M) and *Ceratosaurus* (Madsen and Welles 2000). Ventrally it continues onto the posteromedial margin of the shaft. No intermuscular lines, which frequently occur in more derived theropods, can be observed on the Hungarian femur.

Based on the length/width ratio of the femur it appears that its distal part was broken directly above the distal end. No medial crest as in *Masiakasaurus* (Carrano et al. 2002) or ridge as in *Xenotarsosaurus* (Martinez et al. 1986) was present distally on the Hungarian femur.

To sum up, based on character 132 of Carrano and Sampson (2008) on the morphology of anterolateral muscle attachments on the proximal part of the femur, the Hungarian femur is

definitely from a ceratosaurian theropod because a well developed lesser trochanter is present and the trochanteric shelf is reduced to a discrete rugosity, the insertion for *M. iliofemoralis*. Compared to various ceratosaurian and abelisauroid femora, the following features support the abelisaurid affinities of the Hungarian femur (MTM PAL 2011.17) and distinguish it from basal tetanuran femora: 1) the femoral head faces antero-medially, 2) the femoral head becomes narrower postero-laterally toward the greater trochanter, 3) the lesser trochanter projects anteriorly-anteromedially and is not perpendicular to the proximal femur but almost parallel with the axis of the femoral head.

Maniraptora Gauthier, 1986

Paraves Sereno, 1997 sensu Holtz and Osmólska (2004)

Paraves indet.

Referred material: one right tibiotarsus (MTM PAL 2011.18) and one metacarpal III of the left? manus (MTM PAL 2011.19).

Locality: Iharkút, Bakony Mountains, western Hungary.

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

Remarks. The following material referred to Paraves may represent the remains of *Pneumatoraptor fodori* a dromaeosaurid-like theropod dinosaur previously described from Iharkút on the basis of a scapulocoracoid (Ósi et al. 2010). However, as 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.

Description and comparisons

Metacarpal. A complete limb element (MTM V 2009.45.1.) has been described by Ósi et al. (2010) as metacarpal III of the left? manus. An additional, complete specimen (MTM PAL 2011.19) bearing all the features recognized on the earlier specimen has been discovered, its proximal end is, however, complete in contrast to that of MTM V 2009.45.1. The proximal end is dorsoventrally higher than its mediolateral width and the proximal articular facet is subtriangular and concave. While the dorsal margin is compressed and ridge-like, the ventral part is wide and concave, bordered lateromedially by a faint ridge. This ventral part of the proximal end is relatively wider than that of *Deinonychus* (Ostrom 1969).

Tibiotarsus. A proximal part of a left tibia (MTM V 2008.31.1.; Ósi et al. 2010:fig. 5M–Q) has been referred to paravian theropods. Here we list only those features that were unknown or unambiguous from the former specimen, The new specimen is a right tibiotarsus (MTM PAL 2011.18, Fig. 3) and it was broken into two parts, but only a small (approximately 3–5 mm long) missing piece of the shaft prevents them from fitting together. Distally, the shaft is crushed due to compaction but the articular ends are three-dimensionally preserved. The proximal end is in a much better condition than on the earlier specimen and along with the developed distal end they indicate a mature animal in spite of the fact that this specimen is 1.5 smaller than the former one. The smooth proximal surface is concave, especially between the lateral condyle and the cnemial crest. Proximally the cnemial crest merges with the medial rim of the proximal articular surface. The lateral condyle is larger than the medial one (Fig. 3F, H) and it has a circular, posteriorly facing articular facet. This new specimen reveals a thin but deep groove between the two condyles. At the broken, distal end of the proximal part of the bone where the fibular crest is still present, it has a drop-shaped cross-section. More distally, it has a subtriangular or subcircular cross-section that becomes oval and directly above the distal end it is anteroposteriorly flattened. Ósi et al. (2010) supposed that the fibular crest appears to be longer than that of *Velociraptor*. This very elongate and thin specimen

disproves this statement and indicates a relatively shorter fibular crest compared to that of *Velociraptor* (Norell and Makovicky 1999). Most of the distal end is formed by the astragalus that has a wide and proximally elongate ascending process. This process is twice longer proximally than the articular part of the astragalus, but its proximal end is missing. Lateromedially, this ascending process reaches the margins of the tibia thus their sutural contact can be well observed, although these sutures are not as marked as in *Velociraptor* (Norell and Makovicky 1999:Fig. 11B, D). The distal, pin-like tip of the fibula is preserved and it is fused with the proximal part of the calcaneum in contrast to *Velociraptor*. In contrast to *Deinonychus* (Ostrom 1969), no suture can be seen on the articular surface between the calcaneum and astragalus. In anterior view, proximal to the calcaneum a small protuberance is preserved on the ascending process of the astragalus. The distal articular surfaces slightly differ from those of *Velociraptor* (Norell and Makovicky 1999:Fig. 11A, 12) in having a lateromedially wider articular facet of the calcaneum and a slightly smaller, rather crest-like articular facet for the astragalus. No intermuscular lines are present on the shaft.

Aves Linnaeus, 1758

Ornithothoraces Chiappe and Calvo, 1994

Enantiornithes Walker, 1981

Enantiornithes indet.

Referred material: one complete (MTM PAL 2011.20) and one fragmentary femur (MTM PAL 2011.21).

Locality: Iharkút, Bakony Mountains, western Hungary.

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

Description and comparisons

Two almost complete right femora are referred to enantiornithines (Fig. 4). Concerning the preserved anatomical features they are almost identical. The longer (8.9 cm) and slightly more robust one is exceptionally preserved. The other one is broken into two pieces and the tip of the distal end is eroded. In anterior and posterior views, the shaft is straight and in medial and lateral views it is slightly bowed anteriorly. The femoral head is cylindrical in medial view. The distinct neck connecting the femoral head with the rest of the proximal part of the femur is constricted anteroposteriorly and it is not as elongate as in some Argentinian El Brete specimens (PVL 4037, Chiappe and Walker 2002:Fig. 11.12A–D), notably *Martinavis* (Walker & Dyke 2009). A small foramen is present on the posteroventral surface of this neck. This foramen is much closer to the femoral head on the shorter specimen. Lateral to this neck a low, but massive, proximally convex, trochanteric crest is present as in other enantiornithines. On the lateral side, more distal than the lower level of the femoral head, a prominent, step-like posterior trochanter is present. This trochanter is slightly eroded on the less complete specimen. Three intermuscular lines occur on the surface of the shaft on both specimens. One of them starts from a proximodistally elongate foramen on the medial side of the bone, just at the distal end of the medial arch connecting the shaft with the femoral head. This line continues distally and ends just proximal to the posterior surface of the medial condyle. The second one starts one cm distal to the posterior trochanter on the posterior side and ends laterally just above the lateral epicondyle. The third, main intermuscular line is on the anterior surface and starts from the proximal head and ends just beyond the midpoint of the diaphysis. Intermuscular lines on the shorter, less robust specimen are not as prominent as on the larger specimen. Both the medial and lateral condyles of the distal articular head are well developed on the longer specimen. The medial one is cylindrical with a five mm wide

articular surface on the posterior side. The lateral condyle is not as rounded as the medial one and proximally it continues as a prominent ridge that also borders the shallow popliteal fossa laterally. Lateral to the lateral condyle a massive and crest-like lateral epicondyle is present. A deep groove occurs between the lateral and medial condyles on the posterior and posteroventral surface of the distal end. Approximately two cm proximally from the distal end on the lateral surface of the shaft a four mm long, marked muscle scar is present.

Besides the size difference, these four times larger femora differ from the small femur described by Ósi (2008:fig. 2) in having a less prominent trochanteric crest. The Hungarian enantiornithine femora described here strongly resemble the femur from the Late Cretaceous of Cruzy (southern France) described by Buffetaut (1998) both in size and morphology. The main difference is the orientation of the femoral neck and head. Whereas in the Hungarian specimens this part is perpendicular to the long axis of the bone, on the French specimen the neck is oriented slightly proximally. Large enantiornithines, comparable in size with the femora discussed above, have been described on the basis of a tarsometatarsus and referred to the avisaurid *Bauxitornis mindszentyae* (Dyke and Ósi 2010). The new remains possibly belong to *Bauxitornis* but to support this hypothesis, further, more complete material is needed.

The abelisauroid record of Europe

Abelisauroid material is very scanty in Europe, but already sufficient to unambiguously indicate the presence of this dominantly Gondwanan group on the continent. In stratigraphical order, the earliest occurrence of the group is *Genusaurus* from the Albian of France (Accarie et al. 1995). Carrano and Sampson (2008) tentatively referred this taxon to the Noasauridae. This genus is represented by pelvic and hind limb elements including the left femur with a total length of approximately 39 cm. Based on comparison of the femora of

Genusaurus and *Carnotaurus* (femur length 103 cm, body length approximately 7–8 m, Bonaparte et al. 1990), the estimated length of *Genusaurus* was around 3–4 m.

After the occurrence of the Albian *Genusaurus*, a huge gap is present up to the Santonian assemblage of Hungary, a general feature of the Cenomanian to Coniacian European continental vertebrate record (Le Loeuff 1991, Pereda-Suberbiola 2009, but see Buffetaut et al., 1991, Vullo and Neraudeau 2008).

The Santonian material from Hungary consists of two isolated bones. The first specimen is a small, 1.3 cm long, pedal ungual phalanx (MTM V 2008.43.1.) characterized by a shallow groove on its ventral surface and bifurcated grooves laterally bordering a convex, triangular area (Ösi et al. 2010). The right femur (MTM PAL 2011.17), described here, is the second specimen of the group from the Santonian western Tethyan archipelago. Both specimens correspond to relatively small animals and the length of the femur (15.3 cm, incomplete) is comparable to that of *Masiakasaurus* (16–20 cm) from the Late Cretaceous of Madagascar, indicating a body length of 1.8 m (Carrano et al. 2002) for both genera.

The Campanian abelisaurid record of Europe is represented by the fragmentary *Tarascosaurus* (Le Loeuff and Buffetaut, 1991). This taxon is known by a proximal half of a left femur and two dorsal and one caudal vertebrae. Based on the femur, the estimated length of this abelisaur is about 3–4 m, comparable to that of *Genusaurus*. A well-preserved tibia was published from the Upper Campanian of La Boucharde, southern France (Allain and Pereda-Suberbiola 2003) and was later referred to Abelisauridae (Carrano and Sampson 2008). Furthermore, Buffetaut et al. (1999) referred some teeth from the Late Campanian (or Early Maastrichtian) of Cruzy (Hérault, southern France) to Abelisauridae.

Concerning the material from Maastrichtian deposits, Buffetaut et al. (1988) and Buffetaut (1989) described a right maxilla from the continental Early Maastrichtian of Fox-Amphoux (Var, southern France) as belonging to an abelisaurid (this was the first report of this family

from Europe). Carrano and Sampson (2008) regarded this bone as either abelisaurid or caracharodontosaurid, but in view of the confirmed presence of abelisaurids in deposits of comparable age in that area (Tortosa et al. 2010), which have yielded no evidence of caracharodontosaurids, an attribution to Abelisauridae appears more likely.

Two fragmentary femora with possible abelisaurid affinities have been mentioned from the Maastrichtian of northern Spain (Astibia et al. 1990, Astibia et al. 1999) but no further details about these bones are available.

The latest report on new European abelisaurid material is by Tortosa et al. (2010) from the Late Cretaceous of southern France. This relatively abundant material contains both well-preserved cranial and postcranial material that unambiguously support its taxonomic status as an abelisaurid (Tortosa et al., 2010). A more precise assessment of the phylogenetic position of this abelisaurid will have to wait for a detailed description, which is in progress.

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References

- Accarie H., Beaudoin B., Dejax J., Fries G., Michard J.-G., Taquet P. (1995). Découverte d'un Dinosauré 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 cératosaurienne, *Compte Rendus de l'Académie des Sciences Paris, série IIA*. 320: 327-334.
- Allain R., Pereda Suberbiola X. (2003). Dinosaurs of France, *Comptes Rendus Palevol*. 2: 27–44.
- 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., Tykoski R., Aquesbi N., Jalil N-E., Monbaron M., Russell D., Taquet P. (2007). An Abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the Radiation of Ceratosaurs, *Journal of Vertebrate Paleontology*. 27: 610-624.
- 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.
- Astibia H., Buffetaut E., Buscalioni A.D., Cappetta 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.
- Astibia H., Murelaga X., Pereda-Suberbiola X., Elorza J.J., Gomez-Alday J.J. (1999). Taphonomy and palaeoecology of the Upper Cretaceous continental vertebrate-bearing beds of the Laño quarry (Iberian Peninsula), *Estudios del Museo de Ciencias Naturales de Alava*. 14 (Num. Espec.1): 43–104.
- Bonaparte J.F. (1991). The Gondwanian theropod families Abelisauridae and Noosauridae, *Historical Biology*. 5(1): 1-25.
- Bonaparte J.F. (1996). Cretaceous tetrapods of Argentina, *Münchener Geowissenschaften Abhandlungen*. 30: 73-130.
- Bonaparte J.F., Novas F.E. (1985). *Abelisaurus comahuensis*, n.g., n.sp., Carnosauria del Crétacico Tardío de Patagonia [*Abelisaurus comahuensis*, n.gen., n.sp., Carnosauria from the Late Cretaceous of Patagonia], *Ameghiniana*. 21(2-4): 259-265.
- Bonaparte, J.F., Novas, F., Coria R. (1990). *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia, *Contributions in Science Natural History Museum of Los Angeles County*. 416: 1-41.
- Buffetaut E. (1989). Archosaurian reptiles with Gondwanan affinities in the Upper Cretaceous of Europe, *Terra-Nova*. 1: 69–74.
- Buffetaut E. (1998). First evidence of enantiornithine birds from the upper Cretaceous of Europe: postcranial bones from Cruzy (Hérault, France), *Oryctos*. 1: 127-130.
- Buffetaut E., Le Loeuff J. (1991). Late Cretaceous dinosaur faunas of Europe: some correlation problems, *Cretaceous Research*. 12: 159–176.
- Buffetaut E., Le Loeuff J. (1998). A new giant ground bird from the Upper Cretaceous of southern France, *Journal of Geological Society, London*. 155: 1-4.

- Buffetaut E., Mechin P., Mechin-Salessy A. (1988). Un dinosaure Théropode d'affinités gondwaniennes dans le Crétacé supérieur Provence, *Comptes Rendus d'la Academie Scinces 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., 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 d'la Academie Scinces Paris*, sér. 2. 328: 203–208.
- Buffetaut E., Mechin P., Mechin Salessy A. (2000). An archaic bird from the Upper Cretaceous of Provence (southern France), *Comptes Rendus de l'Academie de Sciences, Paris, Sciences de la Terre et des planètes*. 331: 557-561.
- Buffetaut E., Jurkovšek B., Jurkovšek T.K. (2002). A fossil feather from the Upper Cretaceous of Kras (Slovenia), *Comptes Rendus Palevol*. 1: 705-710.
- Carrano M.T., Sampson S.D. (2008). The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 6, 183-236.
- Carrano M.T., Sampson S.D., Forster C.A. (2002). The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar, *Journal of Vertebrate Paleontology*. 22(3): 510-534.
- Chanthasit P., Buffetaut, E. (2009). New data on the Dromaeosauridae (Dinosauria: Theropoda) from the Late Cretaceous of southern France, *Bulletin de la Société géologique de France*. 180: 145-154.
- Chiappe L., Calvo J.O. (1994). *Nequenornis volans*, a new Late Cretaceous bird (Enantiornithes: Avisauridae) from Patagonia, Argentina, *Journal of Vertebrate Paleontology*. 14: 230-246.
- Chiappe L., Walker A. (2002). Skeletal Morphology and Systematics of the Cretaceous

- Euenantiornithes (Ornithothoraces: Enantiornithes). In L. M. Chiappe, L. Witmer (eds) *Mesozoic birds: above the heads of dinosaurs*. University of California Press, Berkeley: 240-267.
- Csiki Z., Vremir M., Brusatte S.L., Norell M.A. (2010). An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania, *Proceedings of the National Academy of Sciences of the United States of America*. 107 (35): 15357–15361.
- Currie P.J., Zhao X.-J. (1993). A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China, *Canadian Journal of Earth Sciences*. 30: 2037-2081.
- Dyke G., Dortangs R.W., Jagt J.W.M., Mulder E.W.A., Schulp A.S., Chiappe L.M. (2002). Europe's last Mesozoic bird, *Naturwissenschaften*. 89: 408–411.
- Dyke G., Schulp A.S., Jagt J.W.M. (2008). Bird remains from the Maastrichtian type area (Late Cretaceous), *Geologie en Mijnbouw*. 87: 353–358.
- Dyke G., Ósi A. (2010). Late Cretaceous birds from Hungary: implications for avian biogeography at the close of the Mesozoic, *Geological Journal*. 45: 434-444.
- Gauthier J.A. (1986). Saurischian monophyly and the origin of birds. In K. Padian (ed.) *The Origin of Birds and the Evolution of Flight*. *Memoirs of the California Academy of Sciences*, 8: 1-55.
- Holtz T.R. JR. (1994). The phylogenetic position of the Tyrannosauridae: implications for theropod systematics, *Journal of Vertebrate Paleontology*. 68: 1100–1117.
- Holtz T.R. Jr., Molnar R.E., Currie P.J. (2004). Basal Tetanurae. In D.B. Weishampel, P. Dodson H. Osmólska (eds.) *The Dinosauria*. Second Edition. University of California Press: 71–110.
- Holtz T.R., Osmólska, H. (2004). Saurischia. In D.B. Weishampel, P. Dodson H. Osmólska (eds.) *The Dinosauria*. Second Edition. University of California Press: 21-24,

- von Huene, F., Matley C.A. (1933). The Cretaceous Saurischia and Ornithischia of the Central Provinces of India, *Palaeontologica Indica* (New Series), Memoirs of the Geological Survey of India. 21(1): 1-74.
- Hutchinson J.R. (2001). The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes), *Zoological Journal of the Linnean Society*. 131: 169–197.
- Knauer J., Siegl-Farkas Á. (1992). Palynostatigraphic position of the Senonian beds overlying the Upper Cretaceous bauxite formations of the Bakony Mountains, *Annual Report of the Hungarica Geological Institute of 1990*. p. 463–471.
- Le Loeuff J. (1991). The Campano-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., dinosaure théropode 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.
- Linnaeus C. (1758). *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tomus I. Laurentii Salvii, Holmiae (Stockholm) 823 pp.
- Madsen J.H., Welles S.P. (2000). *Ceratosaurus* (Dinosauria, Theropoda): A Revised Osteology. Utah Geological Survey, Miscellaneous Publication pp. 1–80.
- Makovicky P., Hans-Dieter, S. (1998). Anatomy and phylogentic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana, *American Museum Novitates*. 3420: 1-27.
- Marsh O.C. (1881). Principal characters of American Jurassic dinosaurs. Part V., *The American Journal of Science and Arts*, series 3. 21: 417-423.

- Martínez R.D., Giménez O., Rodríguez J., Bochaty G. (1986). *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina [*Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), a new Theropoda from the Bajo Barreal Formation, Chubut, Argentina], IV Congreso Argentino de Paleontología y Bioestratigrafía. 1: 23-31.
- 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.
- 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.
- Owen R. (1842). Report on British fossil reptiles, part II, Report of the British Association for the Advancement of Science. 11: 60-204.
- Ósi A. (2008). Enantiornithine bird remains from the Late Cretaceous of Hungary, Oryctos. 7: 55–60.
- Ósi A., Apesteguía S., Kowalewski M. (2010). Non-avian theropod dinosaurs from the early Late Cretaceous of Central Europe, Cretaceous Research. 31: 304-320.
- Ósi A. Mindszenty A. (2009). Iharkút, Dinosaur-bearing alluvial complex of the Csehbánya Formation. In E. Babinszki (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: 51–63.
- Pereda-Suberbiola X. (2009). Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review, Bulletin d'la Société géologique France. 180: 57–71.
- Seeley H.G. (1888). On the classification of the fossil animals commonly named Dinosauria, Proceedings of the Royal Society of London. 43: 165-171
- Sereno P.C. (1997). The origin and evolution of dinosaurs, Annual Review of Earth and

- Planetary Sciences. 25: 435-489.
- Szalai E. (2005). Paleomágneses vizsgálatok Iharkúton. Eötvös University, Department of Physical and Applied Geology, manuscript.
- Tortosa T., Buffetaut E., Dutour Y., Cheylan G. (2010). Abelisaur remains from Provence (Southeastern France): phylogenetic and paleobiogeographic implications, Abstract volume, 8th EAVP meeting, Aix-en-Provence. p. 82.
- Turner A.H., Pol D., Clarke J.A., Erickson G.M., Norell M.A. (2007). A Basal Dromaeosaurid and Size Evolution Preceding Avian Flight, *Science*. 317: 1378–1381.
- Vullo R., Neraudeau D. (2008). Cenomanian vertebrate assemblages from southwestern France: a new insight into the European mid-Cretaceous continental fauna, *Cretaceous Research*. 29: 930–935.
- Walker C.A. (1981). New subclass of birds from the Cretaceous of South America, *Nature*. 292: 51-53.
- Walker C.A., Buffetaut E., Dyke G. (2007). Large euenantiornithine birds from the Cretaceous of southern France, North America and Argentina, *Geological Magazine*. 144: 977-986.
- Walker C.A., Dyke G. (2009). Enantiornithine birds from the Late Cretaceous of El Brete (Argentina), *Irish Journal of Earth Sciences*. 27: 15-62.
- Wang, X., Csiki, Z., Ósi, A., and Dyke, G. (2010). The first definitive record of a fossil bird from the upper Cretaceous (Maastrichtian), Hațeg Basin, Romania, *Journal of Vertebrate Paleontology*. 31: 227–230.
- Weishampel D.B., Barrett P.M., Coria R.A., Le Loeuff J., Xu X., Zhao X., Sahni A., Goman E.M., Noto C.R. (2004). Dinosaur distribution. In D.B. Weishampel, P. Dodson, H.Osmólska (eds) *The Dinosauria*. University of California Press, Berkeley, California: 517–606.

Figure captions:

Figure 1. Abelisaurid right femur (MTM PAL 2011.17) from the Santonian Csehánya Formation, Iharkút, western Hungary. A, posteromedial, B, lateral, C, proximal, D, medial, E, anterior views. Abbreviations: **fh**, femoral head; **gt**, greater trochanter; **lt**, lesser trochanter; **ts**, trochanteric shelf; **4t**, fourth trochanter.

Figure 1. Fémur droit d'abelisauridé (MTM PAL 2011.17) de la Formation Csehánya (Santonien), Iharkút, Ouest de la Hongrie. Vues posteromédiale (A), latérale (B), proximale (C), médiale (D) et antérieure (E). Abréviations : **fh**, tête du fémur ; **gt**, grand trochanter ; **lt**, petit trochanter ; **ts**, plateau trochantérien ; **4t**, quatrième trochanter.

Figure 2. Comparison of ceratosaurian femora. A–D, *Genusaurus* from the Albian of France. A, anterolateral, B, posteromedial, C, anterior, D, proximal views. E–G, *Tarascosaurus salluvicus* from the Campanian of southern France. E, medial, F, lateral, G, proximal views. H–J, *Ceratosaurus dentisulcatus* from the Late Jurassic of the United States (after Madsen and Welles 2000). H, anterior, I, lateral, J, medial views. K–M, *Xenotarsosaurus bonapartei* from the Cenomanian–Turonian of Argentina (after Martínez et al. 1986). K, anterior, L, medial, M, posterior views. N–P, *Berberosaurus liassicus* from the Early Jurassic of Morocco

(redrawn from Allain et al. 2007). N, anterior O, medial P, lateral views. Q–T, *Masiakasaurus knopfleri* from the Campanian–Maastrichtian of Madagascar (redrawn from Carrano et al. 2002). Q, anterior, R, lateral, S, medial, T, proximal views. U–V, *Ligabueino andesi* from the Barremian of Argentina (after Bonaparte 1996). U, anterior, V, posterior views. W–Z, *Carnotaurus sasteri* from the Maastrichtian of Argentina (after Bonaparte et al. 1990). W, anterior, X, lateral, Y, posterior, Z, medial views.

Figure 2. Comparaison de fémurs de cératosaures. A–D, *Genusaurus* de l’Albien de France. Vues anterolatérale (A), posteromédiale (B), antérieure (C), proximale (D). E–G, *Tarascosaurus salluvicus* du Campanien du Sud de la France. Vues médiale (E), latérale (F), proximale (G). H–J, *Ceratosaurus dentisulcatus* du Jurassique supérieur des Etats-Unis (d’après Madsen et Welles 2000). Vues anérieure (H), latérale (I), médiale (J). K–M, *Xenotarsosaurus bonapartei* du Cénomaniens–Turonien d’Argentine (d’après Martínez et al. 1986). Vues antérieure (K) médiale (L) et postérieure (M). N–P, *Berberosaurus liassicus* du Jurassique inférieur du Maroc (redessiné d’après Allain et al. 2007). Vues antérieure (N), médiale (O), latérale (P). Q–T, *Masiakasaurus knopfleri* du Campanien–Maastrichtien de Madagascar (redessiné d’après Carrano et al. 2002). Vues antérieure (Q), latérale (R), médiale (S), proximale (T). U–V, *Ligabueino andesi* du Barrémien d’Argentine (d’après Bonaparte 1996). Vues antérieure (U) et postérieure. W–Z, *Carnotaurus sasteri* du Maastrichtien d’Argentine (d’après Bonaparte et al. 1990). Vues antérieure (W), latérale (X), postérieure (Y) et médiale (Z).

Figure 3. Paraves indet. right tibia (MTM PAL 2011.18) from the Santonian Csehbánya Formation, Iharkút, western Hungary. A, anterior, B, lateral; C, posterior; D, medial, E,

proximal views. Details of the distal end in F, anterior, G, lateral, H, distal views.

Abbreviations: **apas**, ascending process of astragalus; **as**, astragalus; **ca**, calcaneum; **cc**, cnemial crest; **dfi**, distal end of the fibula; **fc**, fibular crest; **g**, groove; **lc**, lateral condyle; **mc**, medial condyle.

Figure 3. Tibia droit de *Paraves* indet. (MTM PAL 2011.18) de la Formation Csehbánya (Santonien), Iharkút, Ouest de la Hongrie. Vues antérieure (A), latérale (B), postérieure (C) médiale (D) et proximale (E). Détails de l'extrémité distale en vues antérieure (F), latérale (G) et distale (H). Abréviations: **apas**, processus ascendant de l'astragale; **as**, astragale; **ca**, calcaneum; **cc**, crête cnémienne; **dfi**, extrémité distale de la fibula; **fc**, crête fibulaire; **g**, sillon; **lc**, condyle latéral; **mc**, condyle médial.

Figure 4. *Enantiornithes* indet. right femora (larger: MTM PAL 2011.20, smaller: MTM PAL 2011.21) from the Santonian Csehbánya Formation, Iharkút, western Hungary. A–B, posterior, C–D, medial, E–F, anterior, G–H, lateral, I, proximal, J, distal views. Abbreviations: **f**, foramen; **fh**, femoral head; **g**, groove; **il**, intermuscular lines; **lc**, lateral condyle; **lec**, lateral epicondyle; **mc**, medial condyle; **ms**, muscle scar; **pt**, posterior trochanter; **r**, ridge; **tc**, trochanteric crest.

Figure 4. Fémurs droits d'*Enantiornithes* indet. (le plus grand: MTM PAL 2011.20, le plus petit: MTM PAL 2011.21) de la Formation Csehbánya, Iharkút, Ouest de la Hongrie. Vues postérieures (A-B), médiales (C-D), antérieures (E-F), latérales (G-H), proximale (I), distale (J). Abréviations : **f**, foramen ; **fh**, tête du fémur ; **g**, sillon ; **il**, lignes intermusculaires ; **lc**, condyle latéral ; **lec**, épicondyle latéral ; **mc**, condyle médial ; **ms**, insertion musculaire ; **pt**, trochanter postérieur ; **r**, crête ; **tc**, crête trochantérienne.