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Latest Cretaceous hadrosauroid (Dinosauria: Ornithopoda) remains from Bulgaria

Restes d'hadrosauroïdes (Dinosauria : Ornithopoda) du Crétacé terminal de Bulgarie

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ABSTRACT

Disarticulated dinosaur bones have been discovered in a fossiliferous lens in the Labirinta Cave, southwest of the town of Cherven Bryag, in NW Bulgaria. This cave is formed within marine limestones belonging to the Kajlâka Formation of Latest Cretaceous age. Associated fossils and Sr isotopy suggest that the fossiliferous sediments belong to the uppermost part of the Upper Maastrichtian. The dinosaur bones discovered in this lens include the distal portion of a left femur, a right tibia, the proximal part of a right fibula, a left metatarsal II, the second or third phalanx of a left pedal digit IV, the proximal end of a second metacarpal, and a caudal centrum. All the bones undoubtedly belong to ornithopod dinosaurs and more accurately to representatives of the hadrosauroid clade. All belong to small-sized individuals, although it cannot be assessed whether they belong to juveniles or small-sized adults, pending histological analyses. Hadrosauroid remains have already been discovered in Late Maastrichtian marine sediments from western, central and eastern Europe, reflecting the abundance of these dinosaurs in correlative continental deposits. Indeed, hadrosauroids were apparently the dominating herbivorous dinosaurs in Eurasia by Late Maastrichtian time.

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RÉSUMÉ

Des ossements isolés de dinosaures ont été découverts dans une lentille fossilifère de la Grotte de Labirinta, au sud-est de la ville de Cherven Bryag, dans le Nord-Ouest de la Bulgarie. Cette grotte s'est formée dans des calcaires marins appartenant à la Formation de Kajlâka, d'âge Crétacé terminal. Des fossiles associés et l'isotopie Sr suggèrent que les sédiments fossilifères appartiennent à la partie terminale du Maastrichtien supérieur. Les ossements de dinosaures découverts dans cette lentille comprennent la portion distale d'un fémur gauche, un tibia droit, la partie proximale d'une fibula droite, un second métatarsien gauche, la deuxième ou troisième phalange d'un quatrième orteil gauche, l'extrémité proximale d'un second métacarpien et un centrum caudal. Tous les ossements appartiennent sans aucun doute à des dinosaures ornithopodes et, plus particulièrement, à des représentants du clade des hadrosauroïdes. Tous appartiennent à de petits individus, mais, en l'absence de

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données histologiques, il n'est pas possible de savoir s'ils appartiennent à des juvéniles ou à des adultes de petite taille. Des restes d'hadrosauroïdes ont déjà été découverts dans des sédiments marins en Europe occidentale, centrale et orientale, reflétant l'abondance de ces dinosaures dans des formations continentales du même âge. En effet, les hadrosauroïdes étaient apparemment les dinosaures herbivores dominants en Eurasie au Maastrichtien supérieur.

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1. Introduction

Non-avian dinosaurs were unknown in Bulgaria until recently when Mateus et al. (2010) reported the discovery of a fragmentary left humerus possibly belonging to an ornithomimosaur, from the Upper Maastrichtian of Vratsa district (NW Bulgaria). Because this bone was obviously redeposited in marine sediments, this first discovery provoked our interest to look in closer detail into previous vertebrate findings in correlative marine sediments, which were considered to belong to marine reptiles, but were never investigated in detail and officially published. These vertebrate remains were collected in the summer of 1985. from a cave called Labirinta in Vratsa district, NW Bulgaria. From this locality, Jagt et al. (2006) briefly described the fragmentary lower jaw of a mosasaurine squamate, Mosasaurus cf. hoffmanni, with two teeth preserved in situ and mentioned the presence of possible other marine reptiles. However, closer examination revealed that most of the remaining fragmentary bones collected from the Labirinta Cave belong in fact to hadrosauroid dinosaurs. Here we provide the detailed description of these dinosaurian bones. The description of the remaining marine reptile fragments will be provided in another paper by a different set of authors.

2. Geological setting and taphonomy

The dinosaurian material described in the present paper was collected from the Labirinta Cave during a paleontological expedition in 1985. This cave is situated southwest of the town of Cherven Bryag, between the villages of Drashan and Breste, in NW Bulgaria (Fig. 1). The history of the expedition and the details of the geographical and geological setting are provided by Jagt et al. (2006). All the bones belong to individuals of small size, but in the absence of histological analysis, it cannot be known whether they are juveniles of a large species or adults of a small species. The fossil bones were collected from the cave wall at two sites (see Fig. 2 in Jagt et al. (2006)): all accessible fossil material was collected, albeit rather chaotically without documenting the exact position of specimens taken from the rock. The material from the two sites was subsequently mixed and transferred to the collections of the National Museum of Natural History Sofia. Therefore, it cannot be decided now whether all the dinosaur bones described in the present article come from a single site, whether they were mixed together with mosasaur bones, and of course whether they belong to a single specimen or several individuals.

The Labirinta Cave is formed within limestones belonging to the Kajlâka Formation of Latest Cretaceous age (see

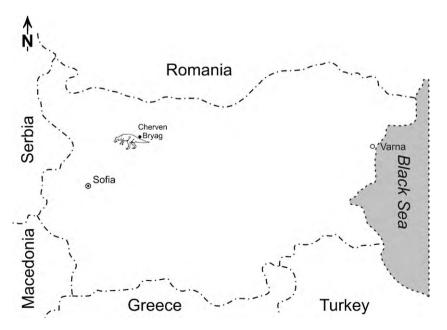


Fig. 1. Map showing the location of the Labirinta Cave (NW Bulgaria).

Fig. 1. Carte montrant l'emplacement de la Grotte Labirinta (Nord-Ouest de la Bulgarie).

Fig. 2 in Jagt et al. (2006)). The limestones of this formation are often karstified and numerous sinkholes and small caves are formed in the study area. In some places, the limestones contain organodetritic lenses, sometimes including vertebrate remains. The rock that enclosed the vertebrate material from the Labirinta Cave is a light grey, strongly recrystallised and slightly sandy limestone, containing Mnoxihydroxide dendrites. Jagt et al. (2006) suggested that the fossiliferous rocks are form the highest unit of the Kajlâka Formation, overlying the 'quarry-type' limestones (the so-called 'Vratsa' stone: see description of correlative section see in Jolkičev (1982), p. 18, Fig. 7; topmost unit 10). The morphology of the lamniform shark tooth Squalicorax pristodontus (Agassiz, 1843), together with the occurrence of the pachydiscid ammonite Anapachydiscus (Menuites) cf. terminus in the 'quarry-type' limestones of the Kajlâka Formation at the nearby village of Varbeshnitsa (see Jolkičev (2006), Fig. 5E), confirm that the limestones are Late Maastrichtian in age and even probably belong to the latest part of the Late Maastrichtian (Jagt et al., 2006).

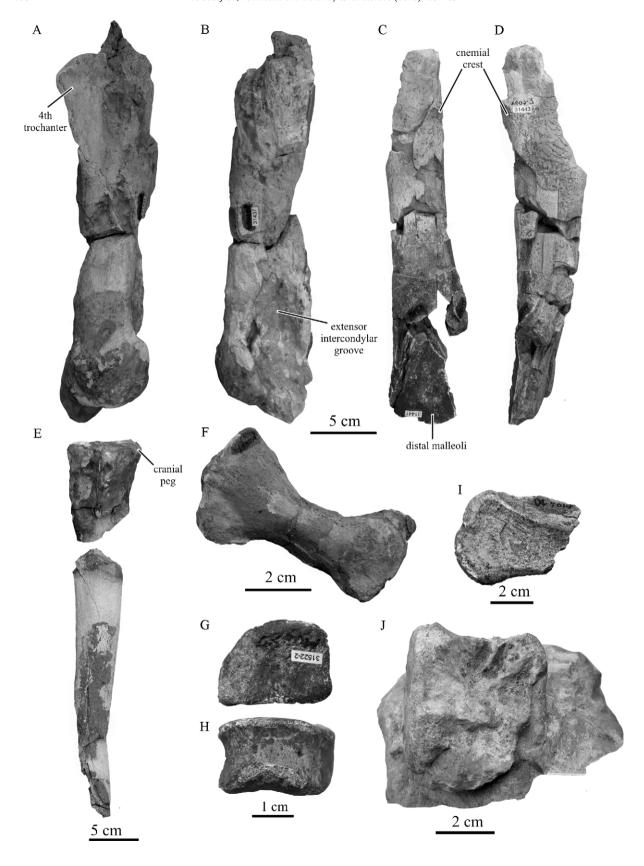
A portion of the left humerus of a possible ornithomimosaur was recently discovered in a nearby sinkhole, some 200 m east from the Labirinta Cave (Mateus et al., 2010). The bone was collected from the same level of marine limestones of the Kajlâka Formation. Because the occurrence of this bone of a terrestrial vertebrate within marine limestones suggested redeposition, the authors Mateus et al. (2010) performed several geochemical analyses to study the taphonomy of the bone and to check the age of the host marine limestones. Rare earth element (REE) and Sr isotope analyses were conducted and an age of between 66 Ma and 63 Ma was calculated for the marine limestones of the Kajlâka Formation, according to McArthur and Howarth (2004). For comparison, a bone found in situ in the Labirinta Cave (NMNHS F-31438¹ = sample 8 see in Mateus et al. (2010), Fig. 3 and Table 1) was included in these analyses. At that time, this bone was thought to pertain to a marine reptile. NMNHS F-31438 (Fig. 2, E) showed distinct REE pattern with bell-shaped mid-heavy REE and negative Ce anomaly. The comparative marine limestone samples (samples 6, 7, and 9 in Mateus et al. (2010)) exhibited REE patterns similar to each other and to sample 8, suggesting that NMNHS F-31438 was likely fossilised in these marine carbonates. However, this bone exhibited elevated ⁸⁷Sr/⁸⁶Sr ratio (0.70835), compared to the local limestone samples. Mateus et al. (2010) speculated that due to its very high Sr content, the bone did not completely equilibrate with the host marine carbonates during diagenesis. As a result, the elevated ⁸⁷ Sr/⁸⁶ Sr signal in NMNHS F-31438 suggested that this animal either did not have an exclusively marine diet or that the bone was from a terrestrial animal that lived near the ancient marine basin. Below we show that this bone probably belongs to a hadrosauroid dinosaur, not to a marine reptile. Thus the geochemical results of Mateus et al. (2010) helped us to understand the taphonomy of NMNHS F-31438: they suggest that it belongs to a terrestrial animal, although buried and fossilised in marine sediments.

3. Description of the material

NMNHS F-31437 (Fig. 2, A-B) is the distal portion of a left femur with typical hadrosauroid morphology. The femoral shaft is robust and quadrangular in cross-section. The fourth trochanter forms a prominent, thin, curved, and triangular process at midshaft along the posteromedial side of the femur. Its entire medial side is deeply excavated by a large insertion area for a powerful M. caudi-femoralis longus. According to Norman (2002), this morphology of the fourth trochanter is synapomorphic for Hadrosauridae and Bactrosaurus johnsoni, from the Upper Cretaceous of Inner Mongolia. It can also be observed in Telmatosaurus transsylvanicus, from the Maastrichtian of the Hateg Basin in Romania (Weishampel et al., 1993; P.G., pers. obs.). It means that a fourth trochanter forming a curved, laterally compressed eminence, as observed in NMNHS F-31437, would in fact be a synapomorphy for Hadrosauroidea (sensu Godefroit et al., 2008; Sues and Averianov, 2009): Bactrosaurus, Telmatosaurus, Hadrosauridae, their most common ancestor and all descendants. The medial distal condule is partially preserved in NMNHS 31437. The extensor intercondular groove forms an extended triangular depressed area on the anterior side of the distal femur. It is surrounded by well-developed crests extending from the distal condyles along the anteromedial and anterolateral margins of the distal femur. Complete, the bone measured about 40 cm. According to Horner et al. (2000), this femur length corresponds to late juvenile individuals in the hadrosaurid Maiasaura peeblesorum (0-1 year old), about 3.5 m long. However, it cannot be excluded that this femur belonged to a small fully-grown individual. Indeed, all the hadrosauroids discovered so far in Late Cretaceous sites of Europe are small-sized and probably did not exceed 6 m in length (Dalla Vecchia, 2009; Laurent, 2003; Pereda Suberbiola et al., 2009; Wellnhofer, 1994). Histological data are unfortunately not available for the dinosaur material from Labirinta Cave and, in the current state of our knowledge, it is not possible to assess whether these bones belong to immature or fully-grown individuals.

NMNHS F-31441/31443 (Fig. 2, C and D) can be identified as the right tibia of a hadrosauroid dinosaur. The proximal and distal articular surfaces are broken off, but the estimated length of the bone probably comprised between 35 and 40 cm; this size also corresponds to that of NMNHS F-31437 and it cannot be excluded that it belongs to the same individual. The base of the cnemial crest is preserved. Transverse widening of the cnemial crest was apparently progressive, extending on the proximal part of the tibial shaft, as usually observed in Hadrosauridae, but also in more basal forms such as Probactrosaurus, Bactrosaurus, and Telmatosaurus (Godefroit et al., 1998; Taquet, 1976). In more basal Iguanodontia, transverse widening of the cnemial crest is quite proximal, as observed in Camptosaurus, Iguanodon and Mantellisaurus (Godefroit et al., 1998; Taquet, 1976). The medial side of the proximal tibia is perfectly flat. In medial view, the anterior border of the tibia is regularly bowed. Because of the development of the cnemial crest, the proximal part of the tibia is anteroposteriorly widened and mediolaterally compressed. Because of the development of the distal malleoli, the distal part of the

¹ NMNHS = National Museum of Natural History, Sofia, Bugaria.



bone progressively widens mediolaterally and compresses anteroposteriorly.

Although it is incomplete and it does not display any true diagnostic character, NMNHS F-31438 (Fig. 2. E) is clearly reminiscent of the proximal part of a right hadrosauroid fibula. With an estimated length probably comprised between 35 and 40 cm, its size is compatible with NMNHS F-31437 and NMNHS F-31441/31443. The bone is perfectly straight and mediolaterally flattened and its anteroposterior diameter progressively lessens distally. Although it is eroded, the presumed anteroproximal corner of the bone looks expanded, forming an anterior peg as usually observed on hadrosauroid fibulae. The lateral side of the fibula is smoothly convex anteroposteriorly along its whole height. Its medial side is, on the other hand, occupied by an elongated, triangular and deeply excavated surface. It bears elongated vertical striations for ligamentous contact with the tibia.

NMNHS F-11899 (Fig. 2, F) displays the typical morphology of a left metatarsal II of a hadrosauroid dinosaur. Its general size also suggests that it belonged to a rather small individual. Its medial surface is smoothly convex, whereas its lateral side is clearly concave where it was intimately attached to metatarsal III. Its proximal end is laterally compressed and anteroposteriorly well expanded. Both its anterior and posterior edges form lips that overhang the shaft below. The proximal articular surface is rounded. Distally, the shaft is contracted and laterally compressed. About the middle of the shaft, the dorsolateral border of metatarsal II forms a rather prominent lip-like projection that reinforced attachment with metatarsal III. Beneath the lip, the shaft of metatarsal II slightly diverges medially from metatarsal III. The distal articular end is regularly convex planto-dorsally and faces obliquely inwards. A very shallow intercondylar groove probably acted like a pulley to guide the flexor tendon.

NMNHS F-31522-2 (Fig. 2, G-H) closely resembles the left second or third phalanx of the fourth toe of a hadrosauroid. Again, this element is of small size. This is a shortened block-like element with a slightly concave proximal articular surface and a convex, saddle-like distal surface. The distal surface is slightly less expanded than the proximal one and the trochlea is better developed ventrally than dorsally. Between both articular surfaces, the dorsal medial and lateral sides are depressed and roughened. The dorsal surface is irregularly pierced by half-dozen nutritive foramina. The medial side is vertical whereas the lateral is more oblique, so that the phalanx looks very asymmetrical in dorsal view. The plantar side is flattened and scarred for insertion of flexor tendons.

NMNHS F-31517 (Fig. 2, I) is tentatively interpreted as the proximal end of a hadrosauroid second metacarpal. The bone is mediolaterally compressed, with a medial surface that is regularly convex anteroposteriorly and a concave lateral surface that bears elongated striations marking the attachment of powerful ligaments that held the adjacent metapodials together. The proximal articular surface is regularly rounded and roughened by a cartilaginous cap.

NMNHS F-31530 (Fig. 2, J) is interpreted as a hadrosauroid caudal centrum. Because it is not fused to the neural arch, it belonged to a juvenile individual. The centrum is roughly cubic in shape, being slightly wider and long and high. The articulation facets with the neural arch form kidney-shaped and much roughened surfaces on the dorsal side of the centrum and surround the narrow floor of the neural canal. Both proximal and distal articular surfaces are slightly concave. The lateral sides are only slightly depressed. One haemapophyseal facet can be observed on the only exposed ventral corner.

4. Discussion

Although it is very fragmentary, most of the vertebrate material accumulated in the fossiliferous lens from the Labirinta Cave undoubtedly belongs to ornithopod dinosaurs and more accurately to representatives of the hadrosauroid clade. The presence of dinosaur bones in Upper Cretaceous marine deposits is a well-known phenomenon. Horner (1979) published a revised census of dinosaur specimens from marine Upper Cretaceous sediments in North America. This checklist revealed a relative abundance of hadrosaurines (noncrested hadrosaurids) and nodosaurs (armoured dinosaurs), groups that may have inhabited marginal marine environments. He also noticed that approximately one-half of the hadrosaur specimens from marine sediments in North America belong to juvenile individuals. The overrepresentation of juveniles in marine sediments can easily be explained from a taphonomic point of view. Indeed, the presence of dinosaurs in marine deposits is not the result of a local catastrophic event, but rather results from the accumulation of animals dead in different places and in different times. Such accumulations usually display ideal attritional age-frequency profiles (Lyman, 1994): in this case, age-class abundances reflect the number of animals dying from one class to the next, showing peaks corresponding to ages where mortality rates are the highest, among the very young and, to a lesser extent, the very old. The resulting death profile of the fossil assemblage is therefore completely different from the age profile of the living population and younger individuals are overrepresented (Lyman, 1994). However, as explained

Fig. 2. Hadrosauroidea indet. from Labirinta Cave (NW Bulgaria). **A-B**: distal part of left femur (NMNHS F-31437) in medial (**A**) and anterior (**B**) views. **C-D**: right tibia (NMNHS F-31441/31443) in anterior (**C**) and medial (**D**) views. **E**: right fibula (NMNHS F-31438) in lateral view. **F**: left metatarsal II (NMNHS F-11899) in medial view. **G-H**: left second or third phalanx of toe digit IV (NMNHS F-31522-2) in proximal (**G**) and dorsal (**H**) views. **I**: proximal end of ?second metacarpal (NMNHS F-31517) in lateral view. **J**: caudal centrum (NMNHS F-31530) in dorsal view.

Fig. 2. Hadrosauroidea indet. de la Grotte Labirinta (Nord-Ouest de la Bulgarie). **A-B**: partie distale d'un fémur gauche (NMNHS F-31437) en vues médiale (**A**) et antérieure (**B**). **C-D**: tibia droit (NMNHS F-31441/31443) en vues antérieure (**C**) et médiale (**D**). **E**: fibula droite (NMNHS F-31438) en vue latérale. **F**: métatarsien Il gauche (NMNHS F-11899) en vue médiale. **G-H**: deuxième ou troisième phalange gauche du quatrième orteil (NMNHS F-31522-2) en vues proximale (**G**) et dorsale (**H**). **I**: extrémité proximale d'un ?second métacarpien (NMNHS F-31517) en vue latérale. **J**: centrum caudal (NMNHS F-31530) en vue dorsale.

above, it is impossible to determine how many individuals are represented in Labirinta Cave and if the small size of the bones reflects the presence of juveniles or of adults of small species.

As previously discussed by Buffetaut (1994), the occurrence of dinosaur remains in marine deposits does not necessarily indicate that these animals lived close to the place of deposition of these sediments. Isolated and waterworn dinosaur remains are frequently found in littoral or fluvio-marine deposits, in which they are part of a detritic component that may have travelled over a long distance in non-marine environments. Studies of the gradual decay of floating mammal carcasses have shown that carcasses bloated by putrefaction gases can drift for more than one month before what is left of them finally settles to the bottom, after having lost a large part of their bony elements (Schäfer, 1962). Thus, portions of the skeleton can be transported over long distances (reaching hundreds or even thousands of kilometres) by marine currents, as it is the case of the Oxford Clay dinosaur remains (Martill, 1988). Most parts of the present north-western Bulgarian territory during the latest Maastrichtian were covered by a shallow epicontinental sea. Close to the south of the described locality was the landmass separating the Tethyan Ocean and the North European epicontinental sea. It is quite probable that hadrosauroids, other dinosaurs and other terrestrial animals inhabited this landmass (Mateus et al., 2010).

In Europe, hadrosauroid remains have already been described from various Late Maastrichtian marine deposits. Since the end of the nineteenth century, many isolated hadrosaur bones and teeth were discovered in the Maastricht Formation, in the Maastrichtian type-area (southern Limburg, The Netherlands) and adjacent areas in Belgium. Orthomerus dolloi was based on scattered postcranial material from the Maastricht area (Seeley, 1883), but this taxon can be regarded as a nomen dubium (Brinkmann, 1988; Horner et al., 2004; Mulder et al., 2005). Disarticulated hadrosauroid bones and teeth are regularly described from this area (Buffetaut et al., 1985; Jagt et al., 2003; Mulder et al., 2005; Mulder et al., 1997; Weishampel et al., 1999). Although dinosaurs are very abundant in the Maastrichtian of southern France, the vast majority of the discoveries are from continental deposits (Allain and Pereda Suberbiola, 2003). Few discoveries of hadrosaurid remains have been made in marine deposits of Late Maastrichtian age in Department of Haute-Garonne, including a dentary fragment from the Jadet Calcarenites of Le Jadet (Paris and Taquet, 1973) and finely preserved postcranial material from littoral deposits in Lestaillats (Laurent, 2003; Laurent et al., 1999). In central Europe, juvenile hadrosauroid bones, including a caudal neural arch, a very fragmentary scapula, a femur, a metatarsal IV, and two phalanges, were collected in the shallow marine Late Maastrichtian Gerhartsreiter Schichten of southern Bavaria (Wellnhofer, 1994). Hadrosaur limb bones referred to Orthomerus weberi were collected in 1934 from Late Maastrichtian marine deposits at Mt. Besh-Kosh on the Crimean peninsula (Riabinin, 1945). These remains are not diagnostic beyond Hadrosauroidea gen. et sp. indet. (Horner et al., 2004).

The relative abundance of hadrosauroid remains from Late Maastrichtian marine deposits in Europe reflects their

abundance in correlative continental deposits (Buffetaut, 1994). Although Ceratopsidae (horned dinosaurs) dominate most terrestrial ecosystems in North America and Hadrosauridae usually represent a minor component of these faunas (Lehman, 1987), Hadrosauridae are the dominant herbivorous in Late Maastrichtian continental deposits from far eastern Asia. Hadrosaurid remains represent more than 90 percent of the dinosaur bones discovered in the Late Maastrichtian of NE China and Far Eastern Russia and at least seven hadrosaurid genera are represented in this area (Godefroit et al., 2008). This is apparently also the case in western Europe. Hadrosauroid dinosaurs are rather abundant and appear well diversified in Late Maastrichtian deposits from the Iberian Peninsula. The basal lambeosaurine Arenysaurus ardevoli was recently described from the Late Maastrichtian of Aren (Huesca, South-central Pyrenees, Spain; (Pereda Suberbiola et al., 2009)), and at least three other different hadrosauroid taxa are known from the Upper Maastrichtian formations of Spain, though they are indeterminate at the genus and species level (López-Martínez et al., 2001; Pereda Suberbiola et al., 2009). The age of the basal lambeosaurine Pararhabdodon isonensis (including Koutalisaurus kohlerorum; (Prieto-Márquez and Wagner, 2009)) is uncertain: Early Maastrichtian to early Late Maastrichtian (López-Martínez et al., 2001). Most of the dinosaur bones discovered in the Late Maastrichtian Auzas Marls formation of the Petites Pyrénées (SW France) also belongs to hadrosauroids (Laurent, 2003; Laurent et al., 2002). Therefore, the discoveries within both continental and marine deposits indicate that hadrosauroids were the dominant herbivorous dinosaurs in Europe by Late Maastrichtian times. Hadrosauroids were abundant and apparently still well diversified in Europe just before the Cretaceous-Paleocene extinction of all non-avian dinosaurs.

5. Conclusions

We report the second case of unambiguous findings of non-avian dinosaur remains from Bulgaria following the first record reported by Mateus et al. (2010). The described collection from the uppermost Maastrichtian of NW Bulgaria includes the distal portion of a left femur, a right tibia, the proximal part of a right fibula, a left metatarsal II, the second or third phalanx of a left pedal digit IV, the proximal end of a second metacarpal, and a caudal centrum. All the bones are undoubtedly ascribed to ornithopod dinosaurs and more precisely to representatives of the hadrosauroid clade. Unlike previous unpublished opinions of several Bulgarian geologists that dinosaurs are unlikely to be found in Bulgaria because of the predominant marine environments during Mesozoic times, we have shown that dinosaur remains in Bulgaria were in fact found about 25 years ago, but were not correctly identified.

The occurrences of dinosaur bones in Upper Cretaceous marine deposits are not unusual. The new records from Bulgaria add new information for the palaeobiogeography of hadrosauroids. The discoveries within both continental and marine deposits indicate that hadrosauroids were the dominant herbivorous dinosaurs in Europe by Late Maastrichtian time. They were abundant and well diversified

in Europe just before the Cretaceous-Paleocene Extinction Event.

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