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TELMATOSAURUS AND THE OTHER HADROSAURIDS OF THE CRETACEOUS EUROPEAN ARCHIPELAGO. AN OVERVIEW.

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Abstract - Telmatosaurus is considered the best known European hadrosaurid. It is represented by a skull with lower jaw and scattered skeletal elements collected from unknown levels of four thick lithostratigraphic units of Transylvania (Romania). Several parts of the skeleton still remain unknown. Once considered one of the last dinosaurs despite to its primitiveness, it has been demonstrated that it lived during Early Maastrichtian, ranging at maximum to the beginning of the Late Maastrichtian. All the other hadrosaurid record of Europe is briefly reviewed in order to have a panoramic view of what we know about those dinosaurs living in the European Archipelago (Anglo-Irish, Ibero-Occitan, Renish-Bohemian, Australpine, Adriatic, Transylvanian and Crimean Islands) during the Late Campanian-latest Maastrichtian interval. That record consists only of scattered bones, vertebral strings, or at best small portions of disarticulated skeletons. It generally represent small-sized individuals and show features considered primitive for the group, both possibly a consequence of insularity. A comparison with the nearly complete and articulated hadrosaurid skeletons from the Campanian-Maastrichtian of the western North American continent and Asia is limited by this incompleteness. Therefore we do not really know how European hadrosaurids differed in body morphology from their better known American and Asiatic relatives.

Introduction

The Transylvanian Baron Ferenc NOPCSA (1900) described a new "trachodontid" dinosaur from the continental beds of Transylvania based on a nearly complete skull with mandible (now at The Natural History Museum, London, BMNH R3386; Figs. 6-15). The specimen was brought to him by his sister Ilona in 1895. She (or the local peasants who gave her the specimen) had discovered it close to the Baron Nopcsa family estate of Sâcel, near the village of Szentpéterfalva (now Sâmpetru) along the Sibişel valley of the Hateg depression in the Southern Carpathians, Hunyad (now Hunedoara) county of Transylvania (Fig. 1). At that time Transylvania was a Hungarian territory of the Austro-Hungarian Empire, but now is a part of the Republic of Romania.

Nopcsa originally named it *Limnosaurus transsylvanicus*, but that name resulted preoccupied by a crocodyliform described by O. C. Marsh in 1872. Thus the Transylvanian Baron changed it in *Telmatosaurus* (NOPCSA, 1903). Later (1915) NOPCSA considered *Telmatosaurus* as a younger synonym of *Orthomerus* based on the comparison of the femora. *Orthomerus* was a genus created by SEELEY (1883) based on a few hadrosaurid bones (referred to O. dolloi) from the Maastrichtian of Limburg (The Netherlands). *Orthomerus* is based on undiagnostic material and is now considered a *nomen dubium* (BRINKMANN, 1988; WEISHAMPEL & HORNER, 1990; HORNER *et al.*, 2004). There is no evidence supporting a generic affinity



Fig. 1 - Latest Cretaceous continental units of Transylvania (from THERRIEN, 2005, modified). A) Outcrops of Cretaceous rocks in the Hateg and Transylvanian basins; asterisk indicates the zones where dinosaur remains have been found. B) Geodynamic-paleogeographic units of Romania and location of the area of figure A. C) Geology of the Hateg Basin.

with the Transylvanian hadrosaurids. WEISHAMPEL & HORNER (1990), as also all the more recent papers on the subject, have retained the name *Telmatosaurus*.

Telmatosaurus is considered the best known European hadrosaurid (WEISHAMPEL *et al.*, 1993) and the only European hadrosaurid species to be reputed valid by HORNER *et al.* (2004) as they do not mention the recently named *Pararhabdodon isonensis* (CASANOVAS *et al.*, 1993, 1999a) from Spain and possibly southern France, in their list of valid hadrosaurid species.

Institutional abbreviations: ACKK = Ivan Rakovec Institute of Paleontology ZRC SAZU, Ljubljana, Slovenia; BMNH = The Natural History Museum (former British Museum of Natural History), London; FGGUB = Facultatea de Geologie și Geofizica, Universitatea București, Bucharest; IPFUB = Institut für Paläontologie der Freien Universität, Berlin; IPS = Institut de Paleontologia Dr. M. Crusafont, Sabadell, Barcelona; IRScNB = Institut Royal des Sciences Naturelles de Belgique, Brussels; MAFI = Magyar Allami Földtani Intézet, Budapest, MCDRD = Muzeul Civilizației Dacice și Romane Deva, Deva (Romania); MDE = Musée des Dinosaures, Esperaza (France); MGUV = Museo de Geologia, Universidad de Valencia (Spain); MPZ = Museo Paleontólogico, Universidad de Zaragoza (Spain); NHMM = Natuurhistorisch Museum Maastricht (RD = R.W. Dortangs collection), Maastricht (The Netherlands); SNMMS = Südostbayerischen Naturkunde- und Mammut-Museum, Siegdorf 8Germany).

Geographic provenance of *Telmatosaurus*

Bone remains attributed to *Telmatosaurus* have been reported from Transylvania (NOPCSA, 1900; WEISHAMPEL *et al.*, 1991, 1993; THERRIEN, 2005), southern France (WEISHAMPEL *et al.*, 1991, LE LOEUFF *et al.*, 1993, LE LOEUFF & BUFFETAUT, 1994), Spain (BRINKMANN, 1988) and Limburg (MULDER, 1984), but this wide geographic distribution is dubious (CASANOVAS *et al.*, 1999b; PEREDA SUPERBIOLA, 1999). Specimens from France, Spain and Limburg cannot be reliably attributed to the genus and only those from Romania were finally referred to it (WEISHAMPEL *et al.*, 2004).

According to THERRIEN (2005) *Telmatosaurus transsylvanicus* occurs in the Sâmpetru Formation (former Sîmpetru, before a recent change in the writing of Romanian language) cropping out mainly along the Sibişel River in the Haţeg Basin (Hunedoara county, Transylvania), in the Densuş-Ciula Formation also cropping out in the Haţeg Basin, in the "Pui beds" (near the village of Pui, along the Bărbat River, 15 km SE of the Sibişel valley), and in the "Red Continental Strata" of the south-western Transylvanian Basin, Alba Iulia County (Fig. 1).

Geological and paleoenvironmental remarks of the *Telmatosaurus*-bearing beds

The latest Cretaceous continental units of Transylvania represent the deposition in an intramontane basin. Although they are lithologically different from each other, they were considered contemporaneous based on the similar faunal and floral assemblages found in the respective fossil-bearing horizons (see THERRIEN, 2005).

The Sâmpetru Formation crops out in the central part of the Hateg Basin (Fig. 1). The whole formation is nearly 2500 m thick (WEISHAMPEL *et al.*, 1991; THERRIEN, 2005). A 1000-m thick section is exposed along the Sibişel valley (THERRIEN, 2005), the uppermost 200 m of which are devoid of dinosaur remains. The unit is divided into a lower and an upper, unnamed members. Red clay is common in the lower member whereas the upper one is characterized by conglomerates and a marked lack of red clay. The upper member is barren, whereas the lower member has historically been the one that yielded the highest number of dinosaur bones of all the latest Cretaceous continental units of

Transylvania, mainly along the Sibişel valley. The formation crops out also along the Râul Mare creek, where mainly vertebrate microremains were collected.

According to WEISHAMPEL *et al.* (1991, p. 201) the Sâmpetru Formation originated from deposition of clastic sediments (including volcanic ash and sand) in a braided river "probably developed in the lower parts of an alluvial fan system" that, following THERRIEN *et al.* (2002) evolved finally into a better-drained floodplain. For THERRIEN (2005) it originated by braided streams and to a lesser extent by meandering rivers, in a mosaic of wetlands and moderately-drained floodplains. Unlike the case of the other dinosaur-bearing units, the environment was unstable and constantly changing. The sandstone composition shows that the source of the clasts was to the (present day) south (THERRIEN, 2005).

Densuş-Ciula Formation crops out in the north-western part of the Hateg Basin along the margin of the Poiana Ruscă Mountains. It is nearly 4000 m thick (WEISHAMPEL *et al.*, 1991; THERRIEN, 2005) and is divided into a lower, a middle and an upper member. The lower member is characterized by coarse volcanoclastics (also lava flows, THERRIEN *et al.*, 2002), the middle member is made of finer sediment poor in volcanoclastics and fossiliferous, the upper member lacks both volcanoclastics and fossils. Red mudstone is common in the middle and upper members, as also thick sandstone beds. The formation was deposited in a low-sinuosity fluvial system, by "alluvial fans and braided streams, interspersed with pulses of volcanic activity" (THERRIEN, 2005, p. 19). The middle member represents the deposition in well-drained floodplains with local areas of impeded drainage. The sandstone is compositionally distinct from that of the Sâmpetru Formation, clasts coming from a different, NW source (THERRIEN, 2005). Dinosaur remains occur only in the middle member. Fossils are found close to the villages of Vălioara and Tuştea.

The "Pui beds" (Bărbat Formation of THERRIEN, 2005), cropping out along the Bărbat River in the south-eastern part of the Haţeg Basin, were "traditionally" considered as part of the Sâmpetru Formation, but since they deposited under different paleoenvironmental conditions, they have been distinguished by THERRIEN (2005). They formed in moderately -to well-drained floodplains more distal than those of the Sâmpetru Formation, crossed by meandering rivers. Red mudstone is the prevailing lithology. The source of the clasts was similar to that of the Sâmpetru Formation (THERRIEN, 2005).

"Red Continental Strata" (sensu THERRIEN, 2005), known also as "Vinţu de Jos strata", occur in the Transylvanian Basin 60 km NE of the Haţeg Basin, and are possibly 2500 m thick. Red mudstone is the prevailing lithology and conglomerates representing channel deposits also occur. They were deposited in moderately -to well-drained floodplains crossed by meandering rivers (THERRIEN, 2005). The sandstone is compositionally distinct from that of the Sâmpetru Formation, clasts coming from a different, northern source (THERRIEN, 2005).

The area where Transylvanian dinosaurs lived was subject to volcanic activity due to local subduction of oceanic crust (THERRIEN, 2005), although no subducing oceanic crust was present in the zone according to the Late Maastrichtian paleogeographic map of PHILIP *et al.* (2000; here Fig. 4).

Palynomorph associations from the sites of Pui, Totești-Baraj and Nalaț-Vlad (Sâmpetru Formation) as well as in the stratotypes of the Densuș-Ciula Formation and Sâmpetru Formation, suggest the presence of an open vegetation in a subtropical paleoclimate where briophytes and ferns prevailed (with freshwater ferns in the floodplain ponds), while angiosperms were disperse and gymnosperms rare (VAN ITTERBEECK *et al.*, 2005). The lower member of the Densuș-Ciula Formation yielded a rich macroflora including ferns, palms (*Palmophyllum longirachis*) and dicotyledon angiosperms (GRIGORESCU *et al.*, 1994).

The paleosols of the "Red Continental Strata", "Pui beds" and Densuş-Ciula Formation are indicative of a paleoclimate with low, seasonal precipitations (<1000 mm/year) and low mean annual temperatures (11.5-11.7°C) (THERRIEN, 2005). They are sensibly lower than those indicated by the paleoflora found in the "Red Continental Strata" and other coeval continental units of Romania (1350-2500 mm/year; $22^{\circ}-24^{\circ}$ C; *ibidem*). THERRIEN (2005) considers as valid the paleosol indication, at least for what regards the precipitations; the discrepancies are supposed to reflect a strong seasonality of precipitation, with most of the rainfall concentrated only in part of the year. The climate was monsoonal, sub humid with alternating wet and dry periods similar to the one of present day India (*ibidem*). According to BOJAR *et al.* (2005), the changes in oxygen and carbon isotopes toward the top of the Sâmpetru Formation section along the Sibişel valley is indicative of a transition from a semi-arid towards a more humid, perhaps cooler, climate.

Age of the Telmatosaurus-bearing beds

For a long time *Telmatosaurus* and the associate dinosaur fauna were considered among the latest dinosaurs (WEISHAMPEL *et al.*, 1991, 1993; GRIGORESCU, 1992; GRIGORESCU & CSIKI, 2002), probably because NOPCSA (e.g., 1915) had reputed them as "Danian" and the Danian stage was then considered the last one of the Cretaceous Period after the Maastrichtian stage. HORNER *et al.* (2004), who report the genus only from the Sâmpetru Formation, still consider it as Late Maastrichtian in age.

Actually, until recent times the age of the dinosaur fossil-bearing beds of Transylvania was based on scarce evidence and nothing was done in the 80ies and 90ies to solve the problem. An Early Maastrichtian age possibly ranging up to the early Late Maastrichtian is supported in recent papers (LÓPEZ-MARTINEZ *et al.*, 2001; PANAIOTU & PANAIOTU, 2002; BOJAR *et al.*, 2005; VAN ITTERBEECK *et al.*, 2005; THERRIEN, 2005).

The age of the Sâmpetru Formation was initially considered Late Cretaceous in age based on a freshwater gastropod fauna and the palynomorphs association (WEISHAMPEL *et al.*, 1991), which are similar to those found in the Densuş-Ciula Formation (e.g., THERRIEN *et al.*, 2002). The middle member of the latter contains the Maastrichtian gastropods *Bauxia bulimoides*, *Gastrobulimus munieri*, *Rognacia abreviata* and *Akaja* cf. *gregaria* (BOJAR *et al.*, 2005). The palynomorph *Pseudopapillopollis praesubhercynicus* occurring in the same member was reputed an index species for the Maastrichtian (GRIGORESCU *et al.*, 1994; BOJAR *et al.*,

2005). For WEISHAMPEL *et al.* (1991, p. 201) the "upper portion of the subjacent strata is Early Maastrichtian in age; accordingly, the basal age of the Sâmpetru Formation is probably Late Maastrichtian". The last 200 m of the section lack dinosaur remains and overlaying rocks contain Paleogene (THERRIEN *et al.*, 2002, p. 34) or Paleocene (THERRIEN *et al.*, 2002, p. 37) bivalves and gastropods; that suggested a post-Cretaceous age for the upper part of the formation along the Sibişel valley.

The Densuş-Ciula Formation overlies with angular unconformity a *flysch* unit once supposed to be of Campanian-Early Maastrichtian age. WEISHAMPEL *et al.*, 1991 (p. 202) believed that the "upper part of the lower member of the Desuş-Ciula Formation may correlate with those of the top of the Sâmpetru Formation".

The Tuştea site in the uppermost part of the middle member of the Densuş-Ciula Formation, was supposed to be close to the K/T boundary by GRIGORESCU (1993) because the upper member is devoid of dinosaur remains.

The first doubt about the reliability of those datings was estabilished by LÓPEZ MARTÍNEZ *et al.* (2001). According to them, the benthic foraminifer *Lepidorbitoides minor* – on which was based the dating of the marine (*flysch*) beds underlying the continental formations - is no longer considered a Maastrichtian marker, but is Late Campanian in age. Furthermore, the palynomorph *Pseudopapillopollis praesubhercynicus* is not reliable to dating purposes because the stratigraphic ranges of single palynomorph taxa at the Cretaceous/Tertiary transition in the Tethys area are scarcely known.

THERRIEN *et al.* (2002, p. 34) concluded on paleomagnetic basis that "if the K/T boundary is located in the upper part of the section [of Sâmpetru Formation in the Sibişel valley] the basal most deposits may be as old as early to middle Maastrichtian". They mean that the basal 175 m of the estimated 800 m thick section with dinosaur bones are Early to middle Maastrichtian in age because they formed during an interval of reverse polarity (identified as the magnetochron C31r; Fig. 2), but the remaining 625 m were not sampled for magnetostratigraphical analyses in 2000-2001 field work by those authors, thus they supposed that the K/T boundary could be reached in the upper part of the unit.

Paleomagnetic studies by PANAIOTU & PANAIOTU (2002) on 14 sites along the Sibişel valley filled the gap, showing that the Sâmpetru Formation was deposited entirely during a long interval of reverse polarity (C31r), excluding the lowermost site that formed during normal polarity of the magnetic field (representing the C32n3; Fig. 2). The same results were reached by BOJAR *et al.* (2005). The age of the whole Sâmpetru Formation therefore ranges from the Early Maastrichtian and possibly the early Late Maastrichtian (Fig. 2), as "middle" Maastrichtian is not a formal geochronological subdivision. Also the middle member of the Densuş-Ciula Formation was deposited during a long interval of reverse polarity (PANAIOTU & PANAIOTU, 2002).

Palynomorph associations found in the sites of Pui, Totești-Baraj and Nalaţ-Vlad (the latter two representing sections of the Sâmpetru Formation) are very similar to those occurring in the stratotypes of Densuş-Ciula Formation and Sâmpetru Formation and are indicative of a Maastrichtian age (VAN ITTERBEECK *et al.*,



Fig. 2 - Latest Cretaceous magnetostratigraphical scale correlated to the geochronological/chronostratigra phical global scale from GRADSTEIN & OGG (2004). The magnetic polarities found in the French Rognacian and Romanian Sâmpetru Formation (from VAN ITTERBEECK et al., 2005) and their correspondent position in the magnetostratigraphic scale are also reported.

2005). Correlations with palynoflores from the lower Rognacian of southern France, lower Garumnian of Spain and the Gulpen Formation (Lixhe and Lanaye Members; see Fig. 23) of the Maastrichtian stratotype in The Netherlands, suggest a dating around the Early/Late Maastrichtian boundary for the Transylvanian sites (VAN ITTERBEECK *et al.*, 2005). This is in agreement with the paleomagnetic data. The main result of those new datings is that *Telmatosaurus* is slightly younger that previously supposed, and does not represent one of the latest dinosaurs.

Regarding the problem of the dating of dinosaur-bearing beds, I must emphasize that also in rocks derived from sediments deposited in prevailing marine settings and rich in microfossils useful for biostratigraphic purposes, errors occur. The site of the Villaggio del Pescatore (Trieste, NE Italy), with remains of derived iguanodontians (possibly basal hadrosaurids; DALLA VECCHIA & BUFFETAUT, 2006) was for a long time considered as late Santonian in age (TARLAO *et al.*, 1994; DALLA VECCHIA, 2001, 2003; DAL SASSO, 2001; NICOSIA *et al.*, 2005) or more vaguely Santonian-Campanian (ARBULLA *et al.*, 2006), but it is most probably younger than previously supposed and work is in progress to define better its age.

No data in the past were collected (or, if collected, they were never published) about the exact stratigraphic position of the levels bearing *Telmatosaurus* bones in the dinosaur-bearing sections of the different units. Furthermore, we do not know whether hadrosaurid specimens are found in preferential facies (i.e., paleosols, overbank or channel deposits, proximal or distal facies with respect to the source of the sediment) and whether they were strictly associated (i.e., in the same bed) with other dinosaur taxa and which ones. Therefore, we do not know, for example,

whether *Telmatosaurus* and the similarly-sized ornithopod *Zalmoxes* were really sympatric.

It is not even clear from literature (e.g., WEISHAMPEL *et al.*, 1993) how many and which referred specimens come from respectively the Sâmpetru Formation, the "Pui Beds", the Densuş-Ciula Formation, and the "Red Continental Strata". According to HORNER *et al.* (2004) and WEISHAMPEL *et al.* (2004) *Telmatosaurus* is found only in the Sâmpetru Formation of the Sibişel valley, but both NOPCSA (1915) and WEISHAMPEL *et al.* (1993) report the presence of the taxon in the Vălioara site of the Densuş-Ciula Formation. According to NOPCSA (1915) the first femur and some caudal vertebrae of *Telmatosaurus* were found at Vălioara. WEISHAMPEL *et al.* (1993) and GRIGORESCU *et al.* (1994) report hatchlings and eggs attributed to *Telmatosaurus* from the Tuştea site of the Densuş-Ciula Formation. THERRIEN (2005) after an exhaustive bibliographic research reports the species from all the units.

Paleogeographic occurrence of Telmatosaurus

The eustatic sea level increase that began in Albian times and reached its maximum in Late Cenomanian/Turonian times (HAQ *et al.*, 1987) made the present day southern, western, central and eastern Europe an Archipelago of relatively small islands. Northern Europe (from Fennoscandia to the Uralian Range) was a larger emergent landmass, whereas to the south there was the enormous Afro-Arabian continent, divided into two parts by a narrow seaway connecting the western Tethys with the southern Atlantic Ocean (Figs 3-5). The western most of the two parts was the smaller. Also tectonic movements due mainly to the opening of the southern Atlantic Ocean, the consequent Afro-Arabian rotation and drifting and the final collision against the Euro-Asiatic continent, contributed to create emergent areas in the Archipelago. The opening of a small Mediterranean Ocean between Afro-Arabia and the Apulian Microplate (see Fig. 4), also produced local effects in a very complex geodynamic framework.

The paleogeographic reconstructions of the western Tethys between the Fennoscandian Shield and the Afro-Arabian continent by different authors are only partly in agreement to each other. According to WEISHAMPEL et al. (1991) Telmatosaurus lived on a small island with a surface of only 7500 km², based on the paleogeographic map by DERCOURT et al. (1986). The paleogeographic map by BUSCALIONI et al. (1999) also indicates the island was small (Fig. 3). Updated palaeoenvironmental/paleogeographic maps were published subsequently (DERCOURT et al., 1993, 2000) and on the basis of such maps I surmised that the Hateg Basin occurred in a relatively large emergent land including the AustroAlpine domain to the west and the Eastern Dacides to the east (PHILIP et al., 2000; Fig. 4), that I called "Austro-Transylvanian Island" (DALLA VECCHIA, 2003). According to other recent paleogeographic reconstructions (e.g., THERRIEN, 2005; Fig. 5) this is not correct. The Hateg Basin occurred in the zone of collision of three microplates: Apulia, Rhodope and Moesia. More precisely, it was situated on a long strip of land separated from the Apulian "Austro-Transylvanian Island" (better renamed Austroalpine Island), but rather close to it, and part of the Rhodope microplate (see Fig. 5 below). According to PHILIP *et al.* (2000) this narrow land continued to the east for hundreds of kilometres, including parts of the present day Turkey (Fig. 4). A separate identity of the Transylvanian land is evident in the schematic paleogeographic reconstruction of western Tethys about 69 million years ago by ODIN & LAMAURELLE (2001, fig. 2; here Fig. 5 above).

The paleogeographic reconstructions published by BUSCALIONI *et al.* (1999), PHILIP *et al.* (2000), and ODIN & LAMAURELLE (2001) differs also in other aspects. For example, the Irish and Anglo-Scottish lands are united or not in a single Anglo-Irish island, and the Renish-Bohemian island is sometimes united to the



Fig. 3 - Maastrichtian paleogeography of Europe, showing the islands of the European Archipelago. General latest Cretaceous paleogeography after BUSCALIONI *et. al.* (1999) based on TYSON & FUNNELL (1987). <u>Abbreviations</u>: AA = Australpine island, C = Crimean Island, IB = Ibero-Occitan Island, IR = Irish Island, RB = Renish-Bohemian Island, SE = Anglo-Scottish Island, T = Transylvanian Island.

Ibero-Occitan (or Ibero-Armorican) island to form a larger Ibero-Bohemian island (see Figs. 3-5).

The Sâmpetru Formation was deposited south of the European Platform at tropical paleolatitudes of $21^{\circ}N\pm9$; the paleolatitude obtained in the Densuş-Ciula Formation is similar ($27^{\circ}N\pm5$) according to the confidence limits of the method



Fig. 4 - Maastrichtian paleogeography of Europe, showing the islands of the European Archipelago. Late Maastrichtian paleogeography from PHILIP *et al* (2000). <u>Abbreviations</u>: A = Apulia Carbonate Platform (southern Italy), Aa = Australpine (mainly Austria, Switzerland, S Germany), AA = Anti-Atlas (Morocco), ACP = Apennine Carbonate Platform (central and southern Italy), AD = Adriatic-Dinaric Carbonate Platform (mainly NE Italy, S Slovenia and Croatia), <math>Am = Armorican Massif (France), Bm = Bohemian Massif (Czech Republic), <math>Ca = Calabria (southern Italy), ED = Eastern Dacides (Romania), G = Gavrovo (Greece), Gh = Grampian High = (Scotland), Ibm = Iberian Massif (Spain), Im = Irish Massif (Ireland), Mc = Massif Centrale (France), Md = Munzur Dag (Turkey), Rh = Rhodope (Romania and neighbour SW countries), Rm = Renish Massif (Germany), Us = Ukrainian Shield (Ukraina), Wm = Welsh Massif (Wales). ACP, Aa, ED, AD, G, A are part of the Apulian Microplate.





Fig. 5 - Maastrichtian paleogeography of Europe, showing the islands of the European Archipelago. Above: Early-Late Maastrichtian paleogeography from ODIN & LAMAURELLE (2001, modified). Below: Geodynamic-paleogeographic units during the latest Cretaceous collision, with the asterisk marking the position of the Hateg and Transylvanian intramontane basins, according to THERRIEN (2005, modified). Abbreviations: AA = Austroalpine Island, AD = Adriatic Island, AI = Anglo-Irish Island, AP = Apulian Island, C = Crimean Island, IB = Ibero-Bohemian Island (Ibero Occitan+Renish-Bohemian), Mo = Moesia, $\mathbf{Rh} = \mathbf{Rhodope}, \mathbf{T} = \mathbf{Transylvanian}$ Island.

(PANAIOTU & PANAIOTU, 2002). This recent datum does not fit perfectly with the paleogeographic reconstructions of figures 4-5. During Tertiary times the region moved to the north and rotated 80° clockwise (*ibidem*).

The collision among microcontinents began during the Albian in the Carpathian area, causing the formation of an orogen; during the Early Maastrichtian the compression that had produced the orogen ceased and the following collapse caused the formation of extensional basins, filled by continental or marine sediments according to their position with respect to the sea-level (THERRIEN, 2005). "Red Continental Strata", "Pui beds", Densuş-Ciula Formation, and Sâmpetru Formation all originated in a continental, intramontane, extensional basin.

Taphonomy of *Telmatosaurus* remains

Skeletal elements of *Telmatosaurus*, as those of most other vertebrates from the latest Cretaceous continental units of Transylvania, were found scattered and isolated. The only occurrence of articulated elements, other than the holotype skull and lower jaws, is represented by a string of four cervical vertebrae (BMNH R3841), three sacral vertebrae with two sacral ribs (BMNH R4911), and some other articulated vertebrae.

Generally speaking (no data are available specifically to hadrosaurid remains), bones in Sâmpetru Formation and Densuş-Ciula Formation are reported as "disarticulated, rarely articulated, occasionally associated" (THERRIEN, 2005, p. 34); those from the "Pui beds" are "disarticulated, rarely articulated,", articulated remains coming from fine-grained overbank deposits; those from the "Red Continental Strata" are "disarticulated, occasionally associated" (associated ankylosaurian bones were recently recovered; *ibidem*).

Bones from the Sâmpetru Formation were preserved in floodplain depressions (lenses of sand), channel deposits and paleosols. They are concentrated in "pockets" by hydraulic processes on wet floodplains. Those in the other three units often represent attritional mortality assemblages preserved in dry paleosol profiles (THERRIEN, 2005, p. 16). Bones from Densuş-Ciula Formation were found in paleosols and splay deposits and suffered a limited hydraulic transport. Those from the "Red Continental Strata" and the "Pui beds" were found in paleosols and channel deposits (*ibidem*).

As far as I observed during the 1997 fieldwork season at the Sibişel valley sites of the Sâmpetru Formation and in the collections of the Museul Civilizației Dacice și Romane of Deva, hadrosaurid remains are not common at all in the Sâmpetru Formation. They appear to be outnumbered by bones of titanosaurian sauropods and *Zalmoxes*. Also, isolated teeth of theropods, crocodiles and *Zalmoxes* were collected, but no hadrosaurid teeth.

Associated vertebrates

According to the list of THERRIEN (2005), some vertebrate taxa are common to all four units. Besides *Telmatosaurus transsylvanicus*, those are the rhabdodontid iguanodontians *Zalmoxes robustus* and *Z. shqiperorum* (the latter dubitatively

reported in the "Pui beds"), the titanosaurid sauropod *Magyarosaurus dacus* (absent in the main outcrop of the "Pui beds"), and the chelonian *Kallokibotion bajazidi*. The nodosaurid *Struthiosaurus transsylvanicus* was found only in the Sâmpetru Formation and in the "Red Continental Strata".

Theropod remains occurs in all four, but are indeterminate in the "Red Continental Strata" and referred to just a velociraptorine and a troodontid-like in Densuş-Ciula Formation and "Pui beds". They appear much more diversified in the Sâmpetru Formation, although based on teeth and few scattered bones: a possible neoceratosaur abelisaurid (the only medium-sized theropod taxon in the sample), Euronychodon sp., Paronychodon sp., Richardoestesia sp., a velociraptorine closely related to Saurornitholestes, the tetanuran or maniraptoran Bradycneme draculae, the troodontid or pygostylian avialae Elopteryx nopcsai, the Heptasteornis possible alvarezsaurid andrewsi. and an indeterminate enantiornithine.

A large indeterminate crocodylian occurs in the "Red Continental Strata", whereas Densuş-Ciula Formation yielded remains of *Doratodon* sp. and *Allodaposuchus precedens* (bulky teeth are also mentioned for the Vălioara site). *Allodaposuchus precedens* is the only crocodyliform reported from the "Pui beds" and the Sâmpetru Formation.

Pterosaurs occur in the Densuș-Ciula Formation (the giant *Hatzegopteryx thambema*) and in the Sâmpetru Formation (cf. *Ornithodesmus* sp.).

Anuran amphibians are reported mainly from the Densuş-Ciula Formation (*Eodiscoglossus* sp., *Hatzegobatrachus grigorescui*, and *Paralatonia transsylvanica*). *Eodiscoglossus* sp. occurs also in the "Pui beds", whereas anuran remains are only doubtfully present in the Sâmpetru Formation. Albanerpetonid amphibians are also found in Densuş-Ciula Formation (*Albanerpeton* sp., *Celtedens* sp.) and in the "Pui beds" (*Albanerpeton* cf. *inexpectatum*). Only an indeterminate albanerpetonid taxon is reported from the Sâmpetru Formation.

Two unnamed scincomorph lizards occur in the Densuş-Ciula Formation sample, two indeterminate scincomorphs are reported in the Sâmpetru Formation. The "Pui beds" show an higher squamate diversity, with a possible anguimorph, the teiid *Paraglyphanodon* sp., and the paramacellodids *Becklesius* sp. and *B*. aff. *hoffstetteri*.

The multituberculate mammals *?Paracimexomys dacicus* (= *Barbatodon transsylvanicus*), *Hainina* sp. and an indeterminate kogaiononid are reported in the Densuş-Ciula Formation. The Sâmpetru Formation yielded *Kogaionon ungureanui*, *Kogaionon* n. sp., an indeterminate kogaiononid, *Barbatodon* n. sp., and an indeterminate taxon. The "Pui beds" contains *?Paracimexomys dacicus* (= *Barbatodon transsylvanicus*) and an indeterminate taxon.

Two dinosaur nests (three clutches) with eggs of *Megaoolithus* type were found in the Densuş-Ciula Formation. Discretispherulitic, prolatospherulitic, prismatic, ratite and geckonoid eggshell types occurs in the "Pui beds". Eleven dinosaur nests with *Megaoolithus* cf. *siruguei* egg type occur in the Sâmpetru Formation with also prismatic (theropod?) and geckonoid eggshells. Finally, several kinds of fishes, among which *Lepisosteus*, are recorded in the microremains from the Densuş-Ciula Formation, indeterminate acipenseriformes and characids occurs in the "Pui beds", no fish are reported from the Sâmpetru Formation.

I think that the material is in need of a revision, both for the provenance and the systematic attribution. I suspect that *Magyarosaurus dacus* is a "basket-taxon" for all sauropod bones found in the continental latest Cretaceous of Transylvania, as there is no modern diagnosis for it. The same situation may apply to *Telmatosaurus transsylvanicus* (see below).

The vertebrate associations from the different units are not exactly the same, as may be expected because of the different environment of deposition, mainly between the Sâmpetru Formation and the others.

Telmatosaurus skeleton: what we know and what we do not know

Although the Transylvanian hadrosaurid is reported as the best known among European hadrosaurid taxa (WEISHAMPEL *et al.*, 1993), the knowledge of its skeleton is far from complete.

The diagnosis of the species given in WEISHAMPEL *et al.* (1993, p. 362) is: "a hadrosaurid dinosaur....of small body size (a dwarf?), having a large caudal ectopterygoidal shelf, an isosceles triangle-shaped rostral process of the jugal, a relatively long post-metotic braincase, relatively large basipterygoid processes, a relatively large scar for *m*[*usculus*] *protractor pterygoideus* on the lateral aspect of the basisphenoid, a well-developed channel for the palatine branch of the facial nerve that also accommodated the median cerebral vein, absence of a diastema between the predentary and dentary dentition, and slightly bowed femur".

Six of nine diagnostic characters are in the skull, one in the lower jaw, one in a hind limb bone and one regarding the overall body size. Four of the six skull characters refer to the braincase. It is evident that defined in this way *Telmatosaurus transsylvanicus* can be compared only with other taxa represented by a complete, uncrushed skull, mainly when the braincase is well-preserved. This is not the case of any of the European hadrosaurids, as we will see below. Small body size (*Telmatosaurus* was considered ~5 m long and 500 kg in weight; WEISHAMPEL *et al.*, 1991) is common among hadrosaurids of the European Archipelago (see below), possibly because of insular dwarfism. The features of the braincase defined as "relatively long" and "relatively large" are somewhat ambiguous because these terms do not clearly refer to a standard.

The skull and mandible of *Telmatosaurus* are nearly completely known thanks to the nearly entire, although somewhat crushed dorsally, cranial specimen BMNH R3386 and several other disarticulated remains. They are described in NOPCSA (1900) and WEISHAMPEL *et al.* (1993) (Figs 6-15). NOPCSA (1900) figured also the endocast of the brain (Fig. 11). The missing parts are the posterior portion of the jugal and the quadratojugal, the postorbital process of the squamosal and the squamosal process of the postorbital, the prefrontals and the predentary (Fig. 15). Most of the nasals seem to be present in the holotype, but they may be too crushed to be reconstructed (see WEISHAMPEL *et al.*, 1993, fig. 1).

Maxillary teeth are high and narrow (mean tooth width = 4 mm), with a strong median carina and no secondary ridges, with relatively large denticles along the margins but without marginal ridges reaching them (WEISHAMPEL *et al.*, 1991,





Fig. 7 - The skull of *Telmatosaurus transsylvanicus* (holotype, BMNH R3386) in dorsal view. From NOPCSA (1900). Abbreviations like in figure 6 with the addition of exoc = exoccipital.



Fig. 8 - The skull of *Telmatosaurus transsylvanicus* (holotype, BMNH R3386) in ventral view. From NOPCSA (1900). Abbreviations like in figures 6-7 with the addition of **boc** = basioccipital, **bpp** = basipterygoid processes, **ec** = ectopterygoid, **pl** = palatine, **pt** = pterygoid, **qc** = quadrate distal condyle.



Fig. 9 - The skull of *Telmatosaurus transsylvanicus* (holotype, BMNH R3386). From NOPCSA (1900). A) Posterior view; B) Particular of the basicranium in ventral view. Abbreviations like in figures 6-8 with the addition of **bsf** = basisphenoid, **fm** = *foramen magnum* and **soc** = supraoccipital.



Fig. 10 - Quadrates of *Telmatosaurus transsylvanicus*. **A1-2**) Right element from the holotype (BMNH R3386), anterior view (A1), lateral view (A2), from NOPCSA (1900). **B**) Right quadrate (FGGUB 1005), lateral view, from WEISHAMPEL *et al.* (1993). Abbreviations: **ptf** = pterygoid flange, **qc** = quadrate distal condyle.



Fig. 11 - Cast of the brain of *Telmatosaurus transsylvanicus* (taken from the holotype, BMNH R3386). <u>Abbreviations</u>: V-XII = cranial nerves V-XII, **crb** = cerebellum **hy** = hypophysis. From NOPCSA (1900).



Fig. 12 - Maxillae of *Telmatosaurus transsylvanicus*. A1-2) holotype (BMNH R3386), A1) left maxilla, medial view; A2) posterior/caudal view; B) left maxilla (FGGUB 1010), lateral view. <u>Abbreviations</u>: dpr = dorsal process, ecs = ectopterygoid shelf, for = neurovascular foramina, mth = maxillary teeth. A from NOPCSA (1900), B from WEISHAMPEL *et al.* (1993).



Fig. 13 - Lower jaws of *Telmatosaurus transsylvanicus*. **A-B1-2**) holotype (BMNH R3386), **A**) left lower jaw ramus, medial view; **B1**) right lower jaw ramus, lateral view; **B2**) right lower jaw ramus, medial view. **C**) Right dentary (BMNH R3401), medial view. <u>Abbreviations</u>: **a** = angular, **alv** = alveoli, **ar** = articular, **cop** = coronoid process, **d** = dentary, **pop** = postarticular (retroarticular) process, **sa** = surangular, **sy** = mandibular symphysis. A-B from NOPCSA (1900); C from WEISHAMPEL *et al.* (1993).



Fig. 14 - Teeth of *Telmatosaurus transsylvanicus*. **A-B-D**) holotype (BMNH R3386). **A1**) teeth from the right lower jaw, buccal-occlusal view; **A2**) particular of A1; **B**) teeth from the left lower jaw ramus, lingual view; **C**) single tooth (FGGUB [5]) from the left dentary (right for Weishampel *et al.*, 1993), lingual view; **D1-4**) maxillary teeth, buccal (**D1**), mesiodistal (**D2**), occlusal (**D3**) view, mesiodistal denticles, magnified (**D4**). A-B and D from NOPCSA (1900), C from WEISHAMPEL *et al.* (1993).



Fig. 15 - Skull of *Telmatosaurus transsylvanicus*, reconstruction by WEISHAMPEL *et al.* (1993, modified). A1) Lateral; A2) dorsal, B) posterior view, based on NOPCSA (1900, pl IV, fig. 1). The missing, unknown or unidentifiable parts are in black. <u>Abbreviations</u> like in figures 6-8 with the addition of **ang** = angular, **pd** = predentary, **prf** = prefrontal, **ltf** = lower temporal fenestra, **nf** = narial fenestra, **of** = orbital fenestra, **qj** = quadratojugal, **utf** = upper temporal fenestra.



Fig. 16 - Vertebrae of *Telmatosaurus transsylvanicus*. A) axis and articulated cervical vertebrae 3-5 (BMNH R3841), right lateral view; B) last cervical and first dorsal vertebrae (BMNH R3841), left lateral view; C) partial sacrum (BMNH R4911), ventral view; D) proximal caudal vertebra (BMNH R4973), right lateral view. From WEISHAMPEL *et al.* (1993). <u>Abbreviations</u>: **ax** = axis, **cr** = cervical rib, **nc** = notch at the base of the neural spine, **ns** = neural spine, **poz** = postzygapophysis, **prz** = prezygapophysis, **sr** = sacral rib, **tp** = transverse process (caudal rib or pleurapophysis).

1993; Fig. 14D). Although not mentioned in the diagnosis, the dentary teeth are peculiar. They are wider than the maxillary teeth (mean tooth width = 8 mm), the crown is slightly recurved distally with a pointed apex, has a shallower primary ridge (slightly offset mesially) and sometimes a faint, mesial secondary ridge (Fig. 14B-C); margins are denticulate with each mesial denticle reached by a thin ridge apparently starting from the mesial secondary ridge (Fig. 14C).

Postcranial elements were described in NOPCSA (1915) and WEISHAMPEL *et al.* (1993) (Figs 16-19). We do not know the number of the vertebral elements, nor the total one or that of each segment of the vertebral column. WEISHAMPEL *et al.* (1993) did not figure or describe the middle and posterior dorsal vertebrae, if existing in the apodygm (unfortunately WEISHAMPEL *et al.*, 1993, report only the inventory numbers of the referred material, without specifying the corresponding



Fig. 17 - Forelimb and shoulder girdle bones of *Telmatosaurus transsylvanicus*. A) Left scapula (FGGUB [4]), lateral view; B) incomplete right coracoid (BMNH R3843), lateral view; C1-2) left humerus (MAFI Ob. 3126), medial (C1) and cranial view (C2); D) right ulna (MAFI Ob. 3124), lateral view. From WEISHAMPEL *et al.* (1993), modified. <u>Abbreviations</u>: **acr** = "acromion" process, **corf** = coracoid foramen, **dp** = deltopectoral crest.

skeletal element). NOPCSA (1915) described the centra of caudal vertebrae "almost as long as high, therefore not elongate", but the proximal caudal figured in WEISHAMPEL *et al.*, 1993 (here Fig. 16D), has a centrum decidedly longer than high. This could be apomorphic of *Telmatosaurus*, as well as the "notch" at the posterior base of the neural spine just above the postzygapophysis, in a way that the basal part of the spine is narrower than the upper part (Fig. 16D) (but see DALLA VECCHIA, 2001). The neural spine appears somewhat bent posteriorly (i.e., the anterior margin is concave and the posterior convex; Fig. 16D). If this is not



Fig. 18 - Hind limb bones of *Telmatosaurus transsylvanicus*. A) Left femur (MAFI v.10338), cranial view. B-C) Hind limb bones of hatchlings; B1-3) distal part of a right femur (FGGUB 248), lateral (B1), anterior/cranial (B2), and ventral/distal (B3) view; C) proximal part of a left tibia (FGGUB 250), lateral view. From WEISHAMPEL *et al.* (1993), modified. <u>Abbreviations</u>: **4tr** = fourth trochanter, **caig** = caudal intercondylar groove, **cp** = caput femuris, **crig** = cranial intercondylar groove, **gtr** = greater trochanter; **lcdy** = lateral condyle, **mcdy** = medial condyle.

affected by incomplete preservation of the specimen BMNH R4973 of figure 16D, it could also be peculiar of *Telmatosaurus*.

Oddly, no ossified tendon remains have been reported from the fossiliferous beds (they are common hadrosaurid evidence, for example, in the Late Maastrichtian Hell Creek Formation of Wyoming and Montana). The bones of the manus are practically unknown, as also the radius. No sternal plates are referred to the taxon and the coracoid is only partially preserved (Fig. 17B). The scapula is incomplete at the glenoid and possibly at the distal termination of the scapular blade, which appears to flare distally (Fig. 17A). Neither ilium nor pubis was ever described and the only ischium referred to *Telmatosaurus* was destroyed at the Museum of Budapest in 1938 (WEISHAMPEL *et al.*, 1993). The fibula in unknown and the tibia was reconstructed on the basis of several fragmentary tibiae. Of course, no articulated hind and forefoot was ever discovered, thus proportions as also the shape of some phalanges (e.g., ungual ones) are unknown. We ignore also the proportions among hind limb elements (e.g., the ratio femur/tibia lengths).



Fig. 19 - *Telmatosaurus transsylvanicus*. The skeletal parts (supposed to be) known according to WEISHAMPEL *et al.* (1993), in black. The basis for the postcranial skeleton is that of *Edmontosaurus*, from WELLNHOFER (1994), modified.

Following the sentence "due to the high neurapophyses and long hemapophyses, the tail cross-section of the living animal was laterally compressed (NOPCSA, 1915, Tab. II. fig. 2-4)" Nopcsa had or thought to have found hemapophyses of *Telmatosaurus*. This is also the case of the dorsal ribs, described in NOPCSA (1915). Furthermore, slender metatarsalia and metacarpalia, as also phalanges are mentioned in the same paper. The three metatarsals are described as "closely pressed together" and "much more slender than *Iguanodon*", the distal phalanges are reported as "hoof-shaped". However, none of those skeletal elements are mentioned by WEISHAMPEL *et al.* (1993). The femur is described in NOPCSA (1915) as "straight; the fourth trochanter is a widely extending, wing-like crest that



Fig. 20 - The phylogenetic position of *Telmatosaurus* in the Hadrosauridae cladogram by HORNER *et al.* (2004) (above) and in the Iguanodontia cladogram by NORMAN (2004) (below).

projects horizontally and not pendantly"; it is bowed according to WEISHAMPEL et al. (1993).

The very thick sedimentary sequences that yielded the bones attributed to *Telmatosaurus* could preserve the mixed or stratigraphically separated remains of more than a single hadrosaurid taxon. This appears to be the case of scattered remains from Maastrichtian localities of Spain, that are considered as belonging to at least two different hadrosaurid taxa:

- *Pararhabdodon isonensis* occurs with an indeterminate, but more basal hadrosaurid in the Arén Formation of Sant Romà d'Abella site (Spain) (see below);

- An indeterminate Euhadrosauria and a different, although indeterminate, Hadrosauridae are found in the Tremp Formation of the Huesca Province (see below).

Also isolated teeth in the Maastrichtian Maastricht Formation of Limburg suggest the presence of more than one taxon (see below).

Therefore, only the skull material, in particular the holotype BMNH R3386, can be reliably attributed to *Telmatosaurus*. Postcranial bones were all found scattered and not associated with skull remains, thus they could theoretically belong to another hadrosaurid taxon, although this is not necessary the case.

The coronoid process of the holotype lower jaws (Fig.13A-B) is bent forward, whereas that of the right mandibular ramus of figure 13C is straight. If this character has a systematic meaning, they could belong to two different taxa.

WEISHAMPEL et al. (1993) considered as belonging to a same taxon an array of disarticulated and scattered hadrosaurid bones coming from different levels of a 800 m-thick fossiliferous section (and even from different possibly lithostratigraphic units that cannot be lithostratigraphically correlated to each other; THERRIEN, 2005) because that was supposed to be the opinion of Ferenc Nopcsa. In fact, they wrote: "referral of these postcranial elements [all the hypodigm excluding the cranial bones] to T. transsylvanicus is based principally on Nopcsa's personal account of their association (through notes, museum acquisition records, and publications)" (p. 362). Actually, there is no direct evidence that the postcranials were associated, at least partly, with the holotype. The description of the skull and lower jaws was presented by Nopcsa in 1899 and published in 1900. According to NOPCSA (1915) the dorsal vertebrae were not well-known up to that date and the first femur was found after 1900 and in a locality (Vălioara) different from that of the holotype (on the basis of that femur and of others found later near Sâmpetru, Nopcsa abandoned the name Telmatosaurus for Orthomerus). This evidently indicates that the apodygm is made of scattered bones not associated with the holotype, that they were gathered together by Nopcsa simply because they are "hadrosaurid" in aspect and size and under the assumption that the continental Maastrichtian of Transylvania preserves only one hadrosaurid species.

In fact, some specimens referred to *Telmatosaurus* in WEISHAMPEL *et al.* (1993) were proved later to belong to *Zalmoxes robustus* (WEISHAMPEL *et al.*, 2003). They were originally considered hadrosaurid elements probably because of their

size. They are BMNH R.3401 (only some of the premaxilla, maxilla, partial braincase, quadrate, dentary identified by this number were formerly referred to the hadrosaurid), R.3809 (humerus, tibia, ischia, vertebrae, sacrum), R.3828 (frontal), MCDRD 66 (femur), 70 (femur), FGGUB R.1000 (humerus), R.1016-1021 (only some of the vertebrae identified by this number were formerly referred to the hadrosaurid), R.1024 (sacrum), R.1025-1026 (sacral vertebrae), R.1027-1032 (only some of the vertebrae identified by this number were formerly referred to the hadrosaurid), R.1040 (scapula), MAFI Ob. 3079 (femur).

The two nests (3 clutches) found at the Tuştea site of Densuş-Ciula Formation contain eggs, hatchling and adult skeletal elements. Because of the presence of hatchling and adult hadrosaurid bones in the sample (see Fig. 18B-C), the nests were initially supposed to be built by hadrosaurids (e.g., GRIGORESCU *et al.*, 1994). This appears now less probable, as the subsphaerical eggs, lying in nearly linear rows, are of the megaloolithid type that is generally attributed to sauropods (THERRIEN, 2005).

Other European hadrosaurid dinosaurs

Bone remains of hadrosaurid dinosaurs are reported from several European localities dated to the Late Campanian-Maastrichtian, a time-span of about 9-10 million-years (GRADSTEIN & OGG, 2004). However, unlike the coeval specimens from North America and, to a lesser extent, Asia, all those remains are disarticulated or represent at best a small articulated portion of the skeleton (mainly strings of vertebrae).

The following list of specimens and sitessites is based on WEISHAMPEL *et al.* (2004) and is organized according to the Maastrichtian paleogeography (cfr. Fig. 3-5). The biostratigraphic correlation of sites from different continental basins is a problem that has only been partly solved in recent times (see, for example, LÓPEZ MARTÍNEZ *et al.*, 2001). When contrasting dates exist for a same site, the alternative dating is reported in parentheses.

ENGLAND (Anglo-Irish, Anglo-Scottish or just English Island, Figs. 3-5)

<u>Hadrosauridae indet. (= *Trachodon cantabrigensis*), Cambridge Greensand, Late Albian reworked into the Cenomanian, Cambridgeshire.</u>

"Trachodon cantabrigensis" is represented by a single dentary tooth (BMNH R. 496, Fig. 21), with denticulate mesiodistal margins and a single and prominent median ridge. Although the crown is rather mesiodistally wide in comparison to its height, like in iguanodontid teeth and unlike typical hadrosaurid teeth, the absence of secondary ridges favoured the identification as a hadrosaurid tooth, determination that is reported in WEISHAMPEL *et al.* (2004, p. 558). However it must kept on mind that the specimen has been reworked.

Hadrosauridae indet. (= Iguanodon hillii of NEWTON, 1892; Orthomerus hillii of NOPCSA, 1915), Lower Chalk, Early Cenomanian, Hertfordshire.

The specimen is a single and partial maxillary tooth described by NEWTON (1892). HEAD (1998, p. 737) labels it as "indistinguishable from primitive iguanodontian morphology". However, WEISHAMPEL *et al.* (2004) list it as Hadrosauridae indet..



Fig. 21 - The tooth of "*Trachodon cantabrigensis*" (BMNH R. 496) from the Late Albian of Cambridgeshire (England). A) Lingual, and B) mesiodistal view. From LYDEKKER (1888).

The two teeth from England appear to be the only purported pre-Late Campanian hadrosaurid remains in Europe. If they were actual hadrosaurid teeth, it would imply the presence of hadrosaurids as early as the beginning of the Cenomanian (~99-96 million years ago). However, their morphology is somewhat ambiguous and without any additional remains of those iguanodontians, they are a rather tenuous evidence of the existence of Albian-Cenomanian hadrosaurids in the Anglo-Irish Island (see HEADS, 1998). No other hadrosaurid remains are reported from England. WEISHAMPEL *et al.* (2004) list other two Cenomanian dinosaurbearing "localities" in England and none Late Albian in age, nine Albian and eight Cenomanian in France, one Aptian-Cenomanian in Portugal, and one Cenomanian in the Czech Republic. No hadrosaurid remains are reported from those "localities", but the sample is small and fragmentary. Actually, there is a serious problem of dinosaur sampling and dating in the Albian-Cenomanian of Europe.

BELGIUM & THE NETHERLANDS (specimens possibly coming from the Renish-Bohemian Island or the enlarged Ibero-Bohemian one; Figs. 3-5)

Hadrosauridae indet. (including *Orthomerus dolloi*) and Euhadrosauria, Maastricht Formation, Late Maastrichtian, Limburg (The Netherlands).

Orthomerus dolloi was based by SEELEY (1883) on a complete right femur with "imperfect" extremities (BMNH 42955, 50 cm long; Fig. 22A1-3), the distal extremity of another right one (BMNH 42956, Fig. 22A4), a left tibia (BMNH 42954, Fig. 22B) and an incomplete metatarsal (BMNH 42957) collected in the Maastricht area, probably from the marine Maastricht Formation, but from an unknown level (WEISHAMPEL *et al.*, 1999). Although WEISHAMPEL *et al.*, (1999)



Fig. 22 - The hadrosaurid "*Orthomerus dolloi*" from the Late Maastrichtian of the Maastricht area, Limburg (The Netherlands). **A1-4**) Right femur (BMNH 42955), posterior/caudal (**A1**), medial (**A2**), proximal (**A3**) and distal (**A4**) view; **B1-4**) left tibia (BMNH 42954), lateral (**B1**), posterior/caudal (**B2**), proximal (**B3**) and distal (**B4**; BMNH 42956) view. **C)** Proximal caudal vertebra, right lateral view. A-B from SEELEY (1883), C from LYDEKKER (1888). <u>Abbreviations</u>: like in figure 16 and 30.



Fig. 23 - Hadrosaurid teeth from the Maastrichtian of Limburg (The Netherlands and Belgium). **A1-3**) hadrosaurid maxillary tooth (NHMM 1999012) from Ankerpoort-Marnebel quarry, Belgium, buccal (**A1**), occlusal (**A2**) and mesiodistal (**A3**) view; **B1-3**) hadrosaurid maxillary tooth (NHMM 1997274) from Sibbe near Valkenburg, The Netherlands, buccal (**B1**), occlusal (**B2**) and mesiodistal (**B3**) view; **C1-3**) ?Euhadrosaurid dentary tooth (NHMM RD 214) from Blom quarry, The Netherlands, buccal (**C1**), occlusal (**C2**) and mesiodistal (**C3**) view; **D**) stratigraphy of the Gulpen and Maastricht Formations, with the position of the hadrosaurid remains (asterisks), and the position of the Gulpen Formation in the magnetostratigraphic scale. From WEISHAMPEL *et al.* (1999), modified.

do not list it in the *Orthomerus* material, a proximal caudal vertebra, with a centrum higher than long and a narrow and posteriorly inclined neural spine (Fig. 22C) was also found (see LYDEKKER, 1888). No teeth, skull bones and girdle elements are known for it. According to BRINKMANN (1988), WEISHAMPEL & HORNER (1990), HORNER *et al.* (2004) the specimens are not diagnostic at the generic and specific level, thus *O. dolloi* should be considered a *nomen dubium*.

A caudal vertebra (IRScNB) from the Maastricht area and a second one (Ubaghs collection) from an unknown level of the Maastricht Formation were

reported by DOLLO (1883). UBAGHS (1893; cited in WEISHAMPEL *et al.* [1999], but the paper is not listed in the references) reported a tooth from the higher part of the Maastricht Formation of the Maastricht area, and one from the Maastricht Formation of the Kunrade area (both in the Ubaghs collection).

MULDER (1984) attributed some scattered hadrosaurid remains (MND K 21.04.003, distal part of a femur; MND K 21.04.004, a fragment of a left tibia; MND K 21.04.005, the proximal end of a left fibula) to *Telmatosaurus dolloi*, considering invalid the genus *Orthomerus* but valid the species "O". *dolloi*. Specimens came from the base of the Meerssen Member of the Maastricht Formation, Ankerpoort-Curfs quarry, Geulhem.

BUFFETAUT *et al.* (1985) reported a proximal fragment of a right lower jaw (NHMM 198027) from Ankerpoort-'t Rooth quarry near Bemelen, possibly from the Nekum Member. They attributed it to *Orthomerus dolloi*, probably because it was the only available name for a hadrosaurid in that part of the world.

WEISHAMPEL *et al.* (1999) described a (?right) maxillary tooth (NHMM 1997274; Fig. 23B) from the Sibbe quarry near Valkemburg aan de Geul perhaps coming from the lower Emael Member; a (?left) dentary tooth (NHMM RD 214; Fig. 23C) from Blom Quarry, Berg en Terblijt, coming from the base of the Nekum Member; the fragmentary ?right humerus (TM 11253) of a ?non-lambeosaurine hadrosaurid from St. Pietersberg (Maastricht), coming from an unknown level of the Maastricht Formation.

Hadrosauridae indet., Maastricht Formation and possibly Gulpen Formation, Late Maastrichtian, Liège, Limburg (Belgium).

BUFFETAUT *et al.* (1985) reported a proximal fragment of a left ulna Garcet collection from the Ankerpoort-Marnebel quarry near Eben-Emael, possibly coming from the Emael/Nekum members. They reported also a phalanx from Pach-Lowe (Eben-Emael), from the Maastricht or Gulpen Formation. Bones were attributed to *Orthomerus dolloi* (probably because it was the only available name for a hadrosaurid in that part of the world).

A left metatarsal III (NHMM 1996001) from the Ankerpoort-Marnebel quarry near Eben-Emael, in the Emael Member of the Maastricht Formation, is described by MULDER *et al.* (1997).

A right maxillary tooth (NHMM 1999012; Fig. 23A) from the Ankerpoort-Marnebel quarry near Eben-Emael opened in the lower Gronsveld Member is described by WEISHAMPEL *et al.* (1999). The prominent median ridge is straight, but is slightly offset and angled distally (this suggests a provenance from the mesial portion of the dentition, according to WEISHAMPEL *et al.*, 1999). It is mistakenly reported as having a height/width ratio = 0.34 (WEISHAMPEL *et al.*, 1999), probably meaning that the estimated height/mesiodistal width ratio of the crown is 3.4. A right metatarsal III (NHMM RD 241) from the CBR-Romontbos quarry near Eben-Emael, coming from the Valkemburg Member, is also described by WEISHAMPEL *et al.* (1999).

FRANCE & SPAIN (Ibero-Occitan or Ibero-Armorican Island, Figs. 3-5)

Hadrosauridae indet., Calcarinites du Jadet Formation (a unit of marine origin), Late Maastrichtian, Département de Haute-Garonne (France).

A fragment of a left dentary (MNHN) found near Saint-Martory was considered by PARIS & TAQUET (1973) to belong to an animal very close to *Telmatosaurus transsylvanicus* (LAURENT *et al.*, 1997).

Hadrosauridae indet., "Lestaillats Marls" (below the "Marnes d'Auzas"), Late Maastrichtian (probable age greater than Early Maastrichtian according to LÓPEZ-MARTINEZ *et al.*, 2001), Petites-Pyrénées, Département de Haute-Garonne (France).

The sites of Lestaillats and Jadet have yielded scattered remains of indeterminate hadrosaurids.

Hadrosauridae indet., basal part of the "Marnes d'Auzas", Late Maastrichtian (Late Campanian to early Late Maastrichtian according to LÓPEZ-MARTINEZ *et al.*, 2001), Petites-Pyrénées, Département de Haute-Garonne (France).

The sites of Peyrecave A and B, Tricouté 1 and 2, and Auzas have all yielded scattered remains of indeterminate hadrosaurids. According to COMPANY *et al.* (1998) a tooth (MDE-Ma1-01, Fig. 24) from Tricouté resembles those from La Solana (Valencia, Spain; Fig. 26A3).



Fig. 24- Dentary tooth (MDE-Ma1-01) from the site of Tricouté (France). From COMPANY *et al.* (1998).

10 mm

Hadrosauridae indet., "Marnes d'Auzas", Late Maastrichtian (mid-late Late Maastrichtian according to LOPEZ-MARTINEZ *et al.*, 2001), Le Plantaurel, Département de Ariège (France).

The Mérigon site yielded remains of indeterminate hadrosaurids.

Hadrosauridae indet., Marnes Rouges de Roquelongue Formation, Late Maastrichtian (mid Late Maastrichtian according to LOPEZ-MARTINEZ *et al.*, 2001), Département de l'Aude (France).



Fig. 25 - The hadrosaurid remains (*Pararhabdodon* sp.) from the Maastrichtian Le Bexen (eastern Corbières, Aude, southern France). A1-3) Right maxillary (MDE-Fo1-11), lateral (A1), medial (A2), and dorsal (A3) views; B1-3) right dentary (MDE-Fo1-10), medial (B1), posterior (B2), and dorsal (B3) views; C1-3) teeth (MDE-Fo1-12, 14, 16) (C1, dentary tooth); D1-4) shaft fragment of a right femur (MDE-Fo2-01), anterior (D1), lateral (D2), posterior (D3), medial (D4) views; E1-2) right humerus (MDE-Fo1-18), anterior (E1), and posterior (E2) view. After LAURENT *et al.* (1997), modified. <u>Abbreviations</u>: 4tr = fourth trochanter, avp = antero-ventral process, dc = denticles, dp = deltopectoral crest, Mc = Meckelian canal, pac = proximal articular condyle of the humerus, smf = supra-meckelian foramen, sr = secondary ridges.

LAURENT et al. (1997) described several scattered hadrosaurid bones found in the site of Le Bexen near Fontjoncouse, Corbierès orientales. They consist in a partial right maxilla (MDE-Fo1-11; Fig. 25A), a right lower jaw (MDE-Fo1-10; Fig. 25B) 21 cm long, two fragments of a right (MDE-Fo1-01), and a left (MDE-Fo1-03) lower jaw, three teeth (MDE-Fo1-12, 14, 16; Fig. 25C), six cervical centra (MDE-Fo1-4, 5, 17, 22-23, 114), three sacral centra (MDE-Fo1-21, 52-53), three proximal caudal centra (MDE-Fo1-64, 97, 136), and about 30 posterior caudal centra, a right humerus (MDE-Fo1-18; Fig. 25E), a fragmentary left radius (MDE-Fo1-45), three partial right femora (MDE-Fo1-01, 19, 148; Fig. 25D), and three (two left, one right; MDE-Fo1-139, 143, 115) incomplete tibiae. The remains were originally reported as belonging to Telmatosaurus transsylvanicus (LE LOEUFF & BUFFETAUT, 1994). Later LAURENT et al. (1997) and LÓPEZ-MARTINEZ et al. (2001) reported them as *Pararhabdodon* sp. (LAURENT et al., 1997, referred them provisionally). However, WEISHAMPEL et al. (2004) list them as Hadrosauridae indet., considering them not diagnostic to the genus level (or simply they do no recognize *Pararhabdodon* as a valid taxon). They represent small-sized individuals (cfr. Fig. 25) and LAURENT et al. (1997) considered them as belonging to juveniles.

The maxilla differs from that of *Telmatosaurus* because has a well-developed lateral process in the posterior part of the preserved portion (LAURENT *et al.*, 1997, p. 413). The maxilla is unknown in "*Orthomerus*" *dolloi* and that of *Pararhabdodon isonensis* seems to be different (see Fig. 28A-B). The main axis of the supra-Meckelian canal (appearing in caudal view as an elliptical foramen, see Fig. 25B2) in the lower jaw is oriented obliquely (45° with respect to the medial, alveolar surface, see Fig. 25B2), while in *Telmatosaurus* it is vertical; furthermore, the position and shape of the alveolar furrows is slightly different (LAURENT *et al.*, 1997). The deltopectoral crest of the humerus is more developed than that of *Telmatosaurus* (see Figs 17C and 25E) and similar to that of *Pararhabdodon* (Fig. 28F) (LAURENT *et al.*, 1997). Femora resemble those of "*Orthomerus*" *dolloi (ibidem*) (Fig. 22A) and differ from those with a slightly bowed diaphysis of *Telmatosaurus* (Fig. 18A). The centra of the three proximal caudals are higher than long, unlike those of *Telmatosaurus*.

Euhadrosauria indet., uppermost member of the Sierra Perenchiza Formation, Campanian-Maastrichtian, between Carlet and Tous, Provincia de Valencia (Spain).

La Solana site near the village of Carlet has yield an incomplete left lower jaw with teeth (MGUV 2200, most of the dentary, 18.2 cm long), an isolated dentary tooth like those in the mandibula (MGUV 2201), several isolated teeth (also maxillary teeth, MGUV 2232-33), fragmentary ribs, several incomplete vertebral centra, the proximal part of a left humerus and a portion of the shaft of a right femur (COMPANY *et al.*, 1998).

Twenty-nine tooth positions are present in lower jaw; based on the drawing of the specimen (here Fig. 26A), there seems to be two functional teeth and no more than two replacement teeth (possibly just one) for each tooth position. They are lanceolate, based on the drawing (here Fig. 26A1 and A3), height/mesiodistal



Fig. 26 - Remains of Euhadrosauria indet. from the Campanian-Maastrichtian La Solana site, Provincia de Valencia (Spain). A1-2) left dentary (MGUV 2200), medial (A1), and lateral (A2) views, A3) dentary tooth (MGUV 2200) with a magnification of the marginal denticulation; B1-3) right maxillary tooth (MGUV 2233), distal (B1), buccal with magnification of the marginal papillae (B2), mesial (B3), and occlusal (B4) view. From COMPANY *et al.* (1998), modified. <u>Abbreviations</u>: **alv** = alveoli, **cop** = coronoid process, **Mc** = Meckelian canal, **mf** = mental foramina, **tb** = teeth battery.





width ratio of the crown is 3.36, have a sharp median carina and a faint, mesial, secondary ridge; the apex of the crown is not recurved distally and the mesiodistal margins have very small marginal denticles without marginal ridges (Fig. 26A3). The main axis of the cross-section of the supra-Meckelian canal (cf. Fig. 25B2) is oriented obliquely unlike *Telmatosaurus*.

There are two larger, maxillary teeth in the sample; one nearly complete (Fig. 26B) has an elongate crown with a prominent median carina offset distally (according to COMPANY *et al.*, 1998; see Fig. 26B4). Two parallel, short, secondary ridges occur at the mesiobasal region; the mesiodistal margins of the crown are raised and have papillae.

COMPANY *et al.* (1998) underline the resemblance of the lower jaw teeth to an isolated tooth (Fig. 24) found in the French site of Tricouté. They differ from those of *Telmatosaurus* having a straight apex, mesial denticles without secondary ridges and a raised mesiodistal margin. The maxillary teeth differ from those of *Telmatosaurus* because they have raised margins and papillae instead of denticles.

Hadrosauridae indet., Unit S3U1 according to WEISHAMPEL *et al.* (2004) (actually, unnamed unit), probably Late Campanian (based on palynomorphs, NUÑEZ-BETELU, 1999; and local geology, PEREDA SUPERBIOLA *et al.*, 2003), Vitoria-Gasteiz, Treviño, Provincia de Burgos (Basque Country, Spain).

The <u>Laño</u> quarry site yielded a rich vertebrate association with, among the others, titanosaurid sauropods (*Lirainosaurus*), nodosaurids (*Struthiosaurus*) and rhabdodontid ornithopods (*Rhabdodon*). Among crocodiles worthy of note is the peculiar alligatoroid *Acynodon iberocitanus*, short-snouted and with characteristic spatulated and tribodont teeth (BUSCALIONI *et al.*, 1999). Another species, *A*.



Fig. 28 - *Pararhabdodon isonensis*, from the Maastrichtian Sant Romà d'Abella site, Provincia de Lleida (Catalogna, Spain). A1-2) left maxilla (IPS SRA-23), lateral view (A1), and drawing (A2); B1-2) right maxilla (IPS SRA-22), medial view (B1) and drawing (B2); C1-2) right lower jaw (IPS SRA-27), medial view (C1) and drawing (C2); D1-2) cervical vertebra (IPS SRA-23, holotype), anterior (D1), left lateral (D2), view; E) proximal caudal vertebra, right lateral view; F) left humerus (IPS SRA-15), anterior view; G) right ischium (IPS SRA-26), distal end in lateral view.

H) Left ischium (IPFUB; without the distal end) in medial view of a presumed lambeosaurine from the Morò (Moror) site (Maastrichtian, Provincia de Lleida). From CASANOVAS *et al.* (1999), modified; E from a photograph kindly given by Xabier Pereda Superbiola.

<u>Abbreviations</u>: \mathbf{a} = acetabulum, \mathbf{alv} = alveoli, \mathbf{ap} = alveolar parapet, \mathbf{cop} = coronoid process, \mathbf{dp} = deltopectoral crest, \mathbf{ecf} = ectopterygoid facet, \mathbf{f} = foramen, \mathbf{js} = surface for the jugal, \mathbf{ib} = ischial booth, \mathbf{ip} = iliac peduncle, \mathbf{Mc} = Meckelian canal, \mathbf{ns} = neural spine, \mathbf{op} = obturator process, \mathbf{pds} = surface for the predentary, \mathbf{pms} = surface for the premaxilla, \mathbf{poz} = postzygapophysis, \mathbf{pp} = pubic peduncle, \mathbf{prz} = prezygapophysis, \mathbf{ptp} = pterygoid process, \mathbf{sf} = "special" foramina, \mathbf{tp} = transverse process.

lopezi, is reported from the Late Campanian-Maastrichtian Quintanilla del Coco site of the Burgos province, separated by slightly different teeth morphology. *Acynodon* is reported also from the Late Campanian-Maastrichtian Fox-Amphoux site (Provence, France). Bulky teeth somewhat similar to those of this genus occur also in other latest Cretaceous sites of Europe as Fons (France), the Gosau Formation of Muthmannsdorf (Austria), Vălioara in Transylvania (BUSCALIONI *et al.*, 1999) and other with hadrosaurid remains reported below.

The only hadrosaurid remain in Laño is a single, partial, maxillary tooth crown (MCNA 10510) found by screen-washing (PEREDA-SUPERBIOLA & SANZ, 1999; PEREDA SUPERBIOLA *et al.*, 2003). The median ridge is relatively low; there are neither secondary ridges nor denticulate margins.

Hadrosauridae indet. (= *Orthomerus* sp.), and *Pararhabdodon isonensis*, Arén Formation (Tremp Formation according to CASANOVAS *et al.*, 1999a, b), latest Campanian to Maastrichtian according to the different sites (see below), Conca de Tremp (Tremp Syncline), Provincia de Lleida (Catalonia, Spain).

The <u>Els Nerets/Vilamitjana 1</u> site is within the Maastrichtian Tremp Formation according to CASANOVAS *et al.* (1999b), in the uppermost interval of the Aren 2 sequence and dated to the latest Campanian according to LÓPEZ-MARTINEZ *et al.* (2001). Two femora (IPS N- 21 and N3, Fig. 27; a right one is nearly complete) and several caudal vertebrae (IPS N-1, 3, 5-8, 13, 21), belonging to a slender built hadrosaurid unlike *Pararhabdodon* were collected in the site (CASANOVAS *et al.*, 1999a; PEREDA SUPERBIOLA *et al.*, 2003). Unlike *Pararhabdodon* the neural spine of the anterior caudal vertebrae is low and vertical (but unfortunately it was never figured). The slender femur is grooved longitudinally; unlike other European hadrosaurids the distal condyles have an open anterior/cranial canal and a

relatively shallow posterior/caudal intercondylar groove (Fig. 27) (PEREDA SUPERBIOLA *et al.*, 2003).

The <u>Morò (Moror)</u> site (southern part of Tremp Syncline) is referred to the Arén Formation (it is within the Tremp Formation according to CASANOVAS *et al.*, 1999b) and according to LÓPEZ-MARTINEZ *et al.* (2001) cannot be younger than early Late Maastrichtian and older than Late Campanian on biostratigraphic basis; it is probably Early Maastrichtian in age. Two partial ischia (IPFUB; Fig. 28H) and a fragment of maxilla were found in this site (BRINKMANN, 1984; LÓPEZ-MARTINEZ *et al.*, 2001). The ischia are referred to a lambeosaurine by CASANOVAS *et al.* (1999a) because of their robustness, the nearly closed obturator process and the large public and iliac pedicels/processes.

The <u>Barcedana</u> site also yielded scattered hadrosaurid remains and has a similar age as the Morò (Moror) site (LÓPEZ-MARTINEZ *et al.*, 2001).

The <u>Sant Romà d'Abella</u> site (Barranco de la Llau de Doba) near Isona, occurs 70 m below limestones dated as Late Maastrichtian (LOPEZ-MARTINEZ *et al.*, 2001). CASANOVAS *et al.* (1987) described there some remains that they considered similar to those of the primitive iguanodontian *Rhabdodon*. Later, new material showed that the bones belong to a new, *incertae sedis*, iguanodontian taxon that was named *Pararhabdodon isonensis* (CASANOVAS *et al.*, 1993). LAURENT *et al.* (1997) considered *Pararhabdodon isonensis* as a hadrosaurid. CASANOVAS *et al.* (1999a) redescribed *Pararhabdodon isonensis* (Fig. 28A-G) as a lambeosaurine hadrosaurid on the basis of the possession of 1) a medial maxillary shelf, 2) rounded, truncated maxilla-jugal contact, 3) angular and long deltopectoral crest of the humerus.

The relationship to the crested hadrosaurids was later questioned by HEAD (2001, p. 394-395) because the jugal is not known in *Pararhabdodon*, the angular deltopectoral crest occurs "primitively in iguanodontians" and the teeth number is lower than in hadrosaurines or lambeosaurines "suggesting that *Pararhabdodon* may be basal with respect to both". Thus *Pararhabdodon* could be more basal than Euhadrosauria, like *Telmatosaurus*.

The fossil material consists of skull remains (two, left and right, maxillae with at least 35 teeth positions; Fig. 28A-B), four cervical vertebrae (with no traces of a neural spine, like *Telmatosaurus* according to NOPCSA, 1915) (Fig. 28D), two dorsal vertebrae, rib fragments, four fragmentary vertebrae, a complete sacrum (8 co-ossified vertebrae with tall neural spines), a proximal caudal vertebra with a centrum decidedly higher than long and without the notch at the posterior base of the neural spine (Fig. 28E), a left humerus (Fig. 28F) with a prominent, although broken, deltopectoral crest, an ulna, the distal part of a right ischium (Fig. 28G). All bones come from the same stratigraphic level and outcrop; they were found scattered over a surface of 10 square meters and were assigned to a single individual, about six-meters long (PEREDA SUPERBIOLA *et al.*, 2003). The holotype is a cervical vertebra (IPS SRA-23, Fig. 28D).

The <u>Sant Romà d'Abella site II</u> is close Sant Romà d'Abella site and has the same age (PEREDA SUPERBIOLA *et al.*, 2003). It yielded 14, poorly preserved, caudal vertebral centra (IPS SRA 2-6, 9-10, 14 and SRA II-1, 3-6, 9) belonging to an

indeterminate hadrosaurid (PEREDA SUPERBIOLA *et al.*, 2003). Near this site, a right, toothless lower jaw (IPS SRA 27; Fig. 28C) was found, provisionally attributed to *Pararhabdodon isonensis* ("there is no direct evidence allowing the attribution to *Pararhabdodon*", PEREDA SUPERBIOLA *et al.*, 2003, p. 378). It has 35 tooth positions, a relatively long diastema and a coronoid process projecting caudally that is possibly an artifact (CASANOVAS *et al.*, 1999a).

Resuming, *Telmatosaurus* differs from *Pararhabdodon* (considering the lower jaw from Sant Romà d'Abella II as belonging to this latter taxon) in having a small (or not existent) diastema between the predentary and first dentary tooth, only 30 tooth positions in the lower jaw, relatively low neural spines in dorsal and caudal vertebrae, a ridge along the ventral surface of the sacrum and gracile humerus and ulna (CASANOVAS *et al.*, 1999a).

Because no teeth are present in the sample from Sant Romà d'Abella, comparison with isolated teeth from other Spanish and French localities is not possible.

Autapomorphies of *Pararhabdodon isonensis* are: 1) 35 tooth families in the lower jaw and maxilla (considering also the lower jaw from Sant Romà d'Abella II, which could belong to another taxon), 1) very well-developed postzygapophyses in the cervical vertebrae, 2) neural spines of posterior sacral vertebrae are very high (height/anteroposterior length ratio = 6.3), 3) bowed shaft of the ulna, 4) distal extremity of the booted ischium projecting posteroventrally forms an angle of 120° with the longitudinal axis of the diaphysis (CASANOVAS *et al.*, 1999a; PEREDA SUPERBIOLA *et al.*, 2003).

HORNER *et al.* (2004) completely omitted this taxon in their systematic list of Hadrosauridae, possibly because of the dubious attribution of the lower jaw.

The <u>Abella de la Conca</u> site yielded a fragment of a maxilla and an incomplete, gracile femur (IPS TG-2) belonging to a slender built hadrosaurid unlike *Pararhabdodon* (CASANOVAS *et al.*, 1999a; PEREDA SUPERBIOLA *et al.*, 2003). The site is within the Late Maastrichtian Tremp Formation according to CASANOVAS *et al.* (1999b) and is not mentioned in LÓPEZ-MARTINEZ *et al.* (2001).

Euhadrosauria indet., Tremp Formation ("Garumnian"), Late Maastrichtian, Serra del Montsec, Conca d'Ager (Ager Syncline), Provincia de Lleida (Catalonia, Spain).

The Fontllonga site occurs in the highest part of Chron C30n (latest Maastrichtian), 15 m below the occurrence of C29r and 18 m below Paleocene beds (LÓPEZ-MARTINEZ *et al.*, 2001).

A partial left lower jaw with teeth (IPS; most of the dentary, 28 cm long) was found in this site. It is more derived than that of *Telmatosaurus*, but lacks some characters diagnosing the clade Hadrosaurinae + Lambeosaurinae and is considered as belonging to a primitive Euhadrosaurian (CASANOVAS *et al.*, 1999b). The attribution to Euhadrosauria is based on the following characters: 1) dentary teeth not recurved distally, 2) narrow dentary crowns, 3) denticles along the crown margins not supported by subsidiary ridges (CASANOVAS *et al.*, 1999b), all

features that simply distinguish its teeth from those of *Telmatosaurus*. The main axis of the transverse section of the supra-Meckelian canal is oriented obliquely (CASANOVAS *et al.*, 1999b) like in the hadrosaurid from Le Bexen (cf. Fig. 25B2) and unlike *Telmatosaurus*. There are at least 30-31 tooth positions and four successional teeth, two of which functional (i.e., there are only two replacement teeth for each position), at least in the caudal portion of the battery (*ibidem*). The height/mesiodistal width ratio of the crowns is about 2.7; a secondary ridge occurs mesially to the prominent medial carina that is linear and slightly displaced distally (*ibidem*). The secondary ridge can be bifid at the basal part of the crown edge and there is sometimes a shallow, distal, secondary ridge (*ibidem*). The crown margins do not show papillae or denticles, but this has been suggested to be due to the close interlocking of the teeth (*ibidem*).

According to PEREDA SUPERBIOLA *et al.* (2003), it just belong to a basal hadrosaurid different from *Telmatosaurus* because of crowns with a prominent median ridge, a mesial secondary ridge, and a coronoid process perpendicular to the longitudinal axis of the lower jaw; those features exclude its belonging to "the clade formed by Hadrosaurinae and Lambeosaurinae" (p. 380).

The locality of Norets de Tremp, near Talaran, yielded a posterior caudal vertebra (MNCN 4688) (PEREDA SUPERBIOLA *et al.*, 2003).

Euhadrosauria indet. and Hadrosauridae indet., Tremp Formation, latest Maastrichtian, Conca de Tremp (Tremp Syncline), Provincia de Huesca (Catalonia, Spain).

Remains attributed to Hadrosauridae indet. have been collected in the Blasi 1b and Blasi 3-5 sites, whereas those listed as Euhadrosauria indet. were found at Blasi 1 and 2 (LÓPEZ-MARTINEZ *et al.*, 2001). They all correlate with marine deposits of the same basin which represent the last planctonic foraminiferal Zone of the Late Cretaceous (*A. mayaroensis* Zone) and are of latest Maastrichtian age (*ibidem*).

The material was only partly described and preliminary. The Blasi 1 euhadrosaurian is represented by skull bones (MPZ 99/666-667, left jugal, fragmentary left maxilla with teeth) and a nearly complete left lower jaw (MPZ 99/665, the whole dentary, 33 cm long, with most of the dental battery, and a right surangular, MPZ 99/664) (Fig. 29A). They are supposed to belong to a single individual. Each maxillary tooth position has at least two replacement teeth and one or two functional teeth. Teeth have a prominent medial carina and the mesiodistal margins have small papillae (possibly not in all teeth). The anterior part of the mandible is deflected ventrally and there is a diastema (although not very long, about the length of 5-6 dentary teeth) between the surface for the predentary and the first mandibular tooth. The coronoid process is inclined anteriorly (forming an angle of 75° with the long axis of the mandible) with a concave anterior margin. The anteroventral part of the symphysial region is pierced by a large foramen. There are 33 tooth positions, with two functional teeth and up to three replacement teeth.



Fig. 29 - The hadrosaurid remains from the uppermost Maastrichtian of Blasi, Huesca Province (Spain). A) Euhadrosaurian skull (MPZ 99/666-667) and lower jaw (MPZ 99/664-665) elements from Blasi 1 site. B) Hadrosaurid postcranials probably belonging to a single individual from Blasi 3 site. C1-4) Teeth from Blasi 2 site; left dentary tooth (MPZ 99/668; C1) in lingual view; right maxillary tooth (MPZ 99/670; C2) in buccal view; shed maxillary tooth (MPZ 99/669; C3) in occlusal view; shed maxillary tooth (MPZ 99/671; C4) in occlusal view. From LóPEZ-MARTINEZ *et al.* (2001), modified.

<u>Abbreviations</u>: **cop** = coronoid process, **cv** = caudal vertebra, **d** = dentary, **hm** = hemapophysis (chevron), **j** = jugal, **mx** = maxilla, **rf** = fragmentary rib, **sa** = surangular, **v** = vertebrae.

(but those of the ends that are slightly curved distally) and height/mesiodistal width ratio of the crowns (in the anterior positions) is about 3.5.

This specimen differs from *Telmatosaurus* because: 1) the jugal is shorter and more expanded anteriorly (rostrally), 2) dentary teeth are narrower, not recurved distally (but with exceptions) and with a single, prominent carina. It is considered more derived than Telmatosaurus and the indeterminate euhadrosaurians from Fontllonga and La Solana by LÓPEZ-MARTINEZ et al. (2001, p. 47) because 1) it has a coronoid process inclined rostrally (but compare Fig. 13B and Fig. 29A), 2) a median single carina on the dentary teeth, 3) secondary ridges on the crowns are absent. Therefore, they consider it a Euhadrosauria (possibly a new taxon) inside the clade Hadrosaurinae + Lambeosaurinae, with a mosaic of both lambeosaurine (flat and dorsoventrally expanded rostral process and the height of the postorbital process of jugal; very high dentary crowns) and hadrosaurine (shallow caudal process of jugal and its scalloped ventral margin) features (LÓPEZ-MARTINEZ et al., 2001). It differs from Pararhabdodon in having a shorter mandibular diastema (*ibidem*), and, possibly, a differently oriented coronoid process (but see p. 43). The skull was very short and high (much shorter than that of Telmatosaurus) according the bone assembling of figure 29A.

Blasi 2 and 3 have yielded isolated teeth; dentary teeth (with smooth enamel and without papillae) are like those from Blasi 1, maxillary teeth (with rough enamel and with papillae) have a more prominent median carina as usual (Fig. 29C).

Button-like teeth similar to the distal teeth of the crocodile *Acynodon* and referred to *Acynodon* sp. (LÓPEZ-MARTINEZ *et al.*, 2001) have been found at Blasi 2.

Hadrosaurid postcranials probably belonging to a single individual (caudal vertebrae, chevrons, other vertebrae, rib fragments) have been found in Blasi 3 (Fig. 29B) and are not described in detail by LÓPEZ-MARTINEZ *et al.* (2001). Cervical vertebrae were also collected in the Blasi sites and are not figured in LÓPEZ-MARTINEZ *et al.* (2001). The centra of the proximal caudal vertebrae are apparently higher than long, unlike those of *Telmatosaurus* (LÓPEZ-MARTINEZ *et al.*, 2001; Fig. 29B), with tall, anteroposteriorly narrow and caudally angled neural spines like in *Pararhabdodon*. Chevrons are not described, but appear to be long rods not booted distally (LÓPEZ-MARTINEZ *et al.*, 2001; Fig. 29B). Appendicular bones from Blasi sites include an incomplete humerus, a femur, a proximal fragment of an ulna, the distal end part of a tibia, a metatarsal III and a phalanx, that are not figured in LÓPEZ-MARTINEZ *et al.* (2001). The humerus is slender, with a "modestly developed, angular, deltopectoral crest" (LÓPEZ-MARTINEZ *et al.*, 2001, p. 47); the femur, without the distal condyles, is 73 cm long (total animal body length estimated in 6 m by LÓPEZ-MARTINEZ *et al.*, 2001) and is straight.

Many specimens from several sites in the surroundings of Isona, Vall' d'Ager and the locality of Peguera are still undescribed (PEREDA SUPERBIOLA *et al.* 2003).



Fig. 30 - The hadrosaurid remains (SNMMS, no numbers available) from the Upper Maastrichtian of Bavaria (southern Germany). A1-6) The right femur; posterior/caudal (A1), medial (A2), anterior/cranial (A3), lateral (A4), proximal (A5) and distal (A6) view; **B**) the neural arch of a proximal caudal vertebra, left side; **C**) the remains collected (black), the postcranial skeleton is that of *Edmontosaurus*, the skull that of *Telmatosaurus*. Abbreviations: 4tr = fourth trochanter, **caig** = caudal intercondylar groove, **cf** = caput femuris, **crig** = cranial intercondylar groove, **gtr** = greater trochanter, **lcdy** = lateral condyle, **ltr** = lesser (anterior) trochanter, **mcdy** = medial condyle. From WELLNHOFER (1994), modified.



Fig. 31 - Hadrosaurid teeth from the Maastrichtian of Kozina site, south-western Slovenia. **A1**) ?Maxillary tooth (ACKK-D8/20), **A2**) particular of the denticulate margin of ACKK-D8/20, **B**) another tooth (ACKK-D8/121), wider and possibly from the dentary. From DEBELJAK *et al.* (2002).

GERMANY (hadrosaurid possibly living in the Australpine Island, Figs. 3-5)

Hadrosauridae indet., Gerhartsreiter Schichten (a flysch unit representing a deep marine depositionary environment), Late Maastrichtian (Late Campanian-early Late Maastrichtian according to LÓPEZ-MARTINEZ *et al.*, 2001), southern Bavaria.

The sample is made of bones from the right hind limb (femur, metatarsal IV, two phalanges), a possibly caudal centrum, a fragment of a left scapula and a caudal neural arch (WELLNHOFER, 1994; Fig. 30). Remains belong to a single animal only 2 m long. The original specimens are at the Südostbayerischen Naturkunde- und Mammut-Museum Siegdorf (Germany).

SLOVENIA (Adriatic Island, Figs. 3-5)

Hadrosauridae indet., possibly from deposits time-corresponding to the lower Liburnian Beds, Maastrichtian, Karst (Kras), Kozina, SW Slovenia (DEBELJAK *et al.*, 1999; 2002).

Remains were preserved inside a paleokarst fissure formed inside the Santonianlower Campanian Lipica Formation and filled by light limestone fragments from the Lipica Formation and dark limestone fragments from the Maastrichtian-

Paleocene Liburnian Beds (DEBELJAK *et al.*, 1999). Therefore I consider them as Maastrichtian in age.

Hadrosaurids are represented by few teeth (at least two teeth- ACKK-D8/20 and ACKK-D8/121, but probably more, being them "the most frequent ornithopod at Kozina locality"; see DEBELJAK *et al.*, 2002). One is small, narrow and with a single, prominent median ridge (Fig. 31A1), and is probably a maxillary tooth. The mesiodistal margins are denticulate (DEBELJAK *et al.*, 2002) (see Fig. 31A). The second tooth is larger and mesiodistally wider (Fig. 31B) and possibly is a dentary tooth.

Other teeth were attributed to the "Iguanodontidae family" and to "an unidentified ornithopod" (DEBELJAK *et al.*, 2002, p. 197). Some teeth are similar to those of the Late Campanian-Maastrichtian alligatoroid *Acynodon*, although not identical to those of the Spanish *Acynodon* species (DEBELJAK *et al.*, 2002).

Possible hadrosaurids were also found in the close site of the Villaggio del Pescatore site (Duino, Trieste, Friuli Venezia Giulia Region, NE Italy) (e.g., DALLA VECCHIA, 2001, 2002). The study of the material and its dating is in progress (DALLA VECCHIA & BUFFETAUT, 2006). The site yielded also remains of *Acynodon* (BUFFETAUT & DELFINO, 2006).

SOUTHERN ITALY (Apulian Island, Fig. 5)

Ichnotaxon Apulosauripus fredericianus, Calcare di Altamura (Santonian), Puglia Region, Bari Province, former De Lucia quarry near Altamura.

Apulosauripus fredericianus is an ichnotaxon based on two trackways attributed to small-sized (5 m long) hadrosaurids (NICOSIA *et al.*, 1999). Because of the age (Santonian) and above all because of the footprint morphology, I do not think that those trackways can be indisputably attributed to hadrosaurids. Actually, they could belong to a more basal iguanodontian. *Craspelodon* represents a Santonian iguanodontian from Belgium and rhabdodontids were common in the Campanian-Maastrichtian of the European Archipelago and present in the Santonian of Hungary. Furthermore, it cannot be discharged that *Apulosauripus fredericianus* was produced by an ankylosaurian track maker, as it was supposed for hundreds of other footprints in the same site.

UKRAINE (Crimean Island, Figs. 3-5)

Hadrosauridae indet. (= Orthomerus weberi), unnamed unit, Maastrichtian (possibly latest Maastrichtian, according to LÓPEZ-MARTINEZ et al., 2001), near Sebastopol, Crimea (RIABININ, 1945).

The sample is made of hadrosaurid fragmentary hind limb bones, including a femur. No recent description exists for this material.

Conclusions

The European hadrosaurid record has increased sensibly in the last 15 years as has the information about the dating of the rocks containing the fossils. Also, the knowledge of the systematic position of the hadrosaurids living in different islands or on the same island in different times is limited. Excluding *Telmatosaurus*, that is considered in the most recent phylogenetic analyses as the most basal hadrosaurid (Fig. 20), the phylogenetic position of the other European hadrosaurids is unknown, or debated (e.g., *Pararhabdodon*).

Telmatosaurus is reputed as the best known European hadrosaurid, but is based on a sample of scattered bones found in different sites, in diverse lithostratigraphic units deposited in different environmental contexts, and with a thickness of thousand meters probably representing the deposition during some million years. If we consider as plausible the presence in the Maastrichtian of Transylvania of more than one hadrosaurid taxa (as was done, for example, in some more or less coeval sites of Spain) there is not a strong support of the fact that the postcranial material, or at least all of it, belong to the same taxon as the holotype skull. Some important parts of the postcranial skeleton of *Telmatosaurus* are unknown (e.g., hands, feet, pelvic girdle) as well as some cranial elements (e.g., predentary, quadratojugal, posterior part of the jugal).

The Late Campanian-Maastrichtian hadrosaurids from North America are known by a much higher number of skeletal remains, including "mummified" specimens with skin cast. Particularly rich is the Late Campanian Dinosaur Park Formation of Alberta (Canada) with *Brachylophosaurus*, *Gryposaurus*, *Prosaurolophus*, *Corythosaurus*, *Lambeosaurus* and *Parasaurolophus*. The 60 m-thick Formation (representing about two million years) is subdivided into two or three faunal zones yielding different hadrosaurid taxa (RYAN & EVANS, 2005). The hadrosaurids of the Dinosaur Park Formation have limited stratigraphic ranges and most species are found only in the zone of deposition of the formation (RYAN & EVANS, 2005), i.e. they do not have a wide geographic distribution.

The Early Maastrichtian Horseshoe Canyon Formation of Alberta yielded *Edmontosaurus, Saurolophus* and *Hypacrosaurus.* The Late Maastrichtian Scollard (Alberta), Hell Creek (Montana, North Dakota) and Lance (Wyoming, South Dakota) Formations contain abundant remains of *Edmontosaurus.*

All those dinosaurs lived along the eastern margin of the north to south elongated, western North American continent.

We can hypothesize that also European hadrosaurid taxa had limited stratigraphic ranges, limited geographic distribution and, at least in largest islands, more sympatric genera, like their North American relatives.

Some North American hadrosaurid genera are represented by at least one complete skull and articulated postcranial skeleton (*Parasaurolophus*, *Saurolophus*, *Gryposaurus*), others by skull and most of the articulated skeleton (e.g., *Corythosaurus*, *Edmontosaurus*). Thus we know very well their head morphology and the shape and proportions of the postcranium (limbs, tail, etc.). The same cannot be said for European hadrosaurids, even in the better case of *Telmatosaurus*.

Despite their apparent spreading in the European Archipelago during Late Campanian-Maastrichtian times and relative abundance in the fossil record, the relationships, history and even the actual body morphology of European hadrosaurids remain mysterious.

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References

ARBULLA D., COTZA F., CUCCHI F., DALLA VECCHIA F.M., DE GIUSTO A., FLORA O., MASETTI D., PALCI A., PITTAU P., PUGLIESE N., STENNI B., TARLAO A., TUNIS G. & ZINI L. (2006) – Escursione nel Carso Triestino, in Slovenia e Croazia. 8 giugno. Stop 1. La successione Santoniano-Campaniana del Villaggio del Pescatore (Carso Triestino) nel quale sono stati rinvenuti i resti di dinosauro. In: MELIS R., ROMANO R. & FONDA G., Guida alle escursioni/excursions guide, Società Paleontologica Italiana - Giornate di Paleontologia 2006, pp. 20-27, EUT Edizioni Università di Trieste, Trieste.

BOJAR A.-V., GRIGORESCU D., OTTNER F. & CSIKI Z. (2005) - Palaeoenvironmental interpretation of dinosaur- and mammal-bearing continental Maastrichtian deposits, Hateg basin, Romania. Geol. Quart., v. 49(2), pp. 205-222, Warszawa.

BRINKMANN W. (1984) - Erster Nachweis eines Hadrosauriers (Ornithischia) aus dem unteren Garumnium (Maastrichtium) des Beckens von Tremp (Provinz Lérida, Spanien). Paläont. Zeitschr., v. 58, pp. 295-305.

BRINKMANN W. (1988) - Zur Fundgeschicte un Systematik der Ornithopoden (Ornitischia, Reptilia) aus der ober-Kreide von Europe. Documenta Naturae, v. 45, pp. 1-157.

BUFFETAUT E., MEIJER A.W.F., TAQUET P. & WOUTERS G. (1985) - New remains of hadrosaurid dinosaurs (Reptilia, Ornitischia) from the Maastrichtian of Dutch and Belgian Limburg. Rev. Palébiol., v. 4(1), pp. 65-70, Genève.

BUFFETAUT E. & DELFINO M. (2006) - A preliminary description of the crocodylian remains from the Late Cretaceous of Villaggio del Pescatore (northeastern Italy). In FONDA G., MELIS R. & ROMANO R. (eds), Giornate di Paleontologia 2006 - Trieste, Riassunti/Abstracts, p. 33, Trieste.

BUSCALIONI A., ORTEGA F. & VASSE D. (1999) - *The Upper Cretaceous crocodilian* assemblage from Laño (northcentral Spain): implications in the knowledge of the finicretaceous European faunas. Est. Mus. Cienc. Nat. de Alava, v. 14 (num. espec. 1), pp. 213-233, Alava.

CASANOVAS M.L., SANTAFÉ J. V. & ISIDRO A. (1993) - Pararhabdodon isonense *n. gen. n. sp. (Dinosauria). Estudio morfológico, radio-tomográfico y consideraciones biomecánicas.* Paleontologia y Evolució, v. 26-27, pp. 121-131.

CASANOVAS M.L., PEREDA SUPERBIOLA X., SANTAFE J.V. & WEISHAMPEL D.B. (1999a) - *First lambeosaurine hadrosaurid from Europe: paleobiogeographical implications*. Geol. Mag., v. 136(2), pp. 205-211.

CASANOVAS M.L., PEREDA SUPERBIOLA X., SANTAFE J.V. & WEISHAMPEL D.B. (1999b) - A primitive euhadrosaurian dinosaur from the uppermost Cretaceous of the Ager syncline (southern Pyrenees, Catalonia). Geologie en Mijnbouw, v. 78, pp. 345-356.

COMPANY J., GALOBART A. & GAETE R. (1998) - First data on the hadrosaurid dinosaurs (Ornitischia, Dinosauria) from the Upper Cretaceous of Valencia, Spain. Oryctos, v. 1, pp. 121-126.

DALLA VECCHIA F.M. (2001) - Terrestrial ecosystems on the Mesozoic peri-adriatic carbonate platforms: the vertebrate evidence. Proceedings VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires, September 26th-October 1st, 1999, Asociación Paleontológica Argentina, Publ. Esp., v. 7, pp. 77-83, Buenos Aires.

DALLA VECCHIA F.M. (2002) - Cretaceous dinosaurs in the Adriatic-Dinaric carbonate platform (Italy and Croatia): paleoenvironmental implications and paleogeographical hypotheses. Mem. Soc. Geol. It., v. 57(2002), pp. 89-100, Rome.

DALLA VECCHIA F.M. (2003) - *I dinosauri nani dell'Arcipelago europeo*. Le Scienze, v. 423, pp. 86-94, Rome.

DALLA VECCHIA F.M. & BUFFETAUT E. (2006) - *I dinosauri del Villaggio del Pescatore* (*Trieste*): *potenzialità e problemi*. In: FONDA G., MELIS R. & ROMANO R. (eds), Giornate di Paleontologia 2006 - Trieste, Riassunti/Abstracts, p. 26, Trieste.

DAL SASSO C. (2001) - Dinosauri italiani. Marsilio, Venice, pp. 256.

DEBELJAK I., KOŠIR A. & OTONICAR B. (1999) - A preliminary note on dinosaurs and nondinosaurian reptiles from the Upper Cretaceous carbonate platform succession at Kozina (SW Slovenia). Razprave IV. Razreda Sazu, v. XL(1), pp. 3-25, Ljubljana.

DEBELJAK I., KOŠIR A., BUFFETAUT E. & OTONICAR B. (2002) - *The Late Cretaceous dinosaurs and crocodiles of Kozina (SW Slovenia). Mem. Soc. Geol. It.*, v. 57, pp. 193-201, Rome.

DERCOURT J., RICOU, L. E. & VRIELYNCK, B. (eds.) (1993). Atlas Tethys Palaeoenvironmental Maps. Gauthier Villars, Paris, 307 p., 14 maps.

DERCOURT J., ZONENSHAIN L.P., RICOU L.E. et al. (1986) – Geological evolution of the Tethys Belt from the Atlantic to the Pamirs since the Lias. Tectonophysics, v. 123, pp. 241-315.

DERCOURT J., GAETANI M., VRIELYNCK B., BARRIER E., BIJU-DUVAL B., BRUNET M.F., CADET J. P., CRASQUIN S. & SANDULESCU M.(eds.) (2000) - *Atlas Peri-Tethys, Palaeogeographical Maps.* Explanatory notes, I-XX + 269 pp., and 24 maps. Paris, CCGM/CGMW.

DOLLO L. (1883) - Note sur les restes de dinosauriens recontrés dans le Crétace supérieur de la Belgique. Bull. Mus. Roy. Hist. Nat. Belg., v. 2, pp. 205-221, Bruxelles.

GRADSTEIN F. M. & OGG J.G. (2004) – *Geologic Time Scale 2004 – why, how, and where the next!* Lethaia, v. 37, pp. 175-181, Oslo.

GRIGORESCU D. (1992) - Nonmarine cretaceous formations of Romania. In: MATEER N. & PEN-JI C. (eds), Aspects of non-marine Cretaceous geology, pp. 142-164, China Ocean Press, Beijing.

GRIGORESCU D. (1993) - The latest Cretaceous dinosaur eggs and embryos from the Hațeg Basin - Romania. Rev. Paléobiol., sp. v. 7, pp. 95-99, Genève.

GRIGORESCU D. & CSIKI Z. (2002) - *Excursion field guide*. The 7th European Workshop of Vertebrate Paleontology - Sibiu (Romania), pp. 47-49.

GRIGORESCU D., WEISHAMPEL D.B., NORMAN D.B., SECLAMEN M., RUSU M., BALTRES A. & TEODORESCU V. (1994) - Late Maastrichtian dinosaur eggs from the Hateg Basin (Romania). In: CARPENTER K., HIRSCH K.F. & HORNER J.R. (eds), Dinosaur eggs and babies, pp. 75-87, Cambridge University Press, New York.

HAQ B.U., HARDENBOL H. & VAIL P.R. (1987) - Chronology of fluctuating sea-level since the Triassic. Science, v. 235, pp. 1156-1167.

HEAD J.J. (1998) - A new species of basal hadrosaurid (Dinosauria, Ornithischia) from the Cenomanian of Texas. Journ. Vert. Pal., v. 18(4), pp. 718-738, Lawrence.

HEAD J.J. (2001) - A reanalysis of the phylogenetic position of Eolambia caroljonesa (Dinosauria, Iguanodontia). Journ. Vert. Pal., v. 21(2), pp. 392-396, Lawrence.

HORNER J.R., WEISHAMPEL D.B. & FORSTER C.A. (2004) – *Hadrosauridae*. In: WEISHAMPEL D. B., DODSON P. & OSMÓLSKA H. (eds), *The Dinosauria – Second Edition*. pp. 438-463 University of California Press, Berkeley and Los Angeles.

LAURENT Y., LE LOEUFF J. & BUFFETAUT E. (1997) - Les Hadrosauridae (Dinosauria, Ornithopoda) du Maastrichtien supérieur des Corbières orientales (Aude, France). Rev. Paléobiol., v.16(2), pp. 411-423, Genève.

LE LOEUFF J., BUFFETAUT E., MARTIN M., MARTIN V. & TONG H. (1993) - Découverte d'Hadrosauridae (Dinosauria, Ornithischia) dans le Maastrichtien des Corbières (Aude, France). C.R. Acad. Sci. Paris, v. 316(2), pp. 1023-1029, Paris.

LE LOEUFF J. & BUFFETAUT E. (1994) - *Gli ultimi dinosauri della Francia del sud*. In: LIGABUE G. (Ed), *Il tempo dei dinosauri*, Quaderni de Le Scienze, n. 76, pp. 43-51, Milano. LÓPEZ-MARTÍNEZ N., CANUDO J.I., ARDÈVOL LL., PEREDA SUPERBIOLA X., ORUE-EXTEBARRIA X., CUENCA-BESCÓS G., RUIZ-OMEÑACA J. I., 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*. Cret. Res., v. 22, pp. 41-61.

MULDER E.W.A. (1984) - Resten van Telmatosaurus (Ornitischia, Hadrosauridae) uit het Boven-Krijt van Zuid-Limburg. Grondb. Hamer, v. 38, pp. 108-115.

MULDER E.W.A., KUYPERS M.M.M., JAGT J.W.M. & PEETERS H.H.G. (1997) - A new late Maastrichtian hadrosaurid dinosaur record from northeast Belgium. N. Jb. Geol. Paläont. Mh., v. 6, pp. 339-347, Stuttgart.

NEWTON E.T. (1892) - Note on an iguandont tooth from the Lower Chalk ("Totternhoe Stone"), near Hitchin. Geol. Mag., v. 9, pp. 49-50.

NICOSIA U., MARINO M., MARIOTTI N., MURARO C., PANIGUTTI S., PETTI F. M. & SACCHI E. (1999) - *The Late Cretaceous dinosaur tracksite near Altamura (Bari, southern Italy). II* - Apulosauripus federicianus *new ichnogen. and new ichnosp.*. Geologica Romana, v. 35, pp. 237-247, Rome.

NICOSIA U., AVANZINI M., BERBERA C., CONTI M.A., DALLA VECCHIA F.M. and other 15 coauthors in alphabetic order (2005) - *I vertebrati continentali del Paleozoico e Mesozoico*. In: BONFIGLIO L. (ed.), *Paleontologia dei Vertebrati in Italia*, Memorie del Museo Civico di Storia Naturale di Verona, serie 2, Sez. Scienze della Terra, 6, pp. 41-66, Verona.

NOPCSA F. (1900) – Dinosaurierreste aus Siebenbürgen (Schädel von Limnosaurus transsylvanicus nov. gen. et spec.). Denkschriften der königlichen Akademie der Wissenschaften, Wien, v. 68: 555-591, Wien.

NOPCSA F. (1903) – Telmatosaurus, *new name for the dinosaur* Limnosaurus. Geol. Mag. (s. 4), v. 10, pp. 94-95.

NOPCSA F. (1915) - Die Dinosaurier der siebenbürgischen Landesteile Ungarns. Mitteil. Jb. K. Ungar. Geol. Reichsanst., v. 23, pp. 1-24.

NUÑEZ-BETELU K. (1999) - Preliminary palynological assessment of the vertebrate-rich Laño beds; age and paleoenvironment. Est. Mus. Cienc. Nat. de Alava, v. 14 (num. espec. 1), pp. 37-42, Alava.

ODIN G. S. & LAMAURELLE M.A. (2001) - The global Campanian-Maastrichtian stage boundary. Episodes, v. 24(4), pp. 229-238

PANAIOTU C. & PANAIOTU C. (2002) – *Palaeomagnetic studies*. In: The 7th European Workshop of Vertebrate Palaeontology. Abstract volume, Excursion Field Guide, p. 59, Sibiu.

PARIS J.P. & TAQUET PH. (1973) - Découverte d'un fragment de dentaire d'Hadrosaurien (Reptile Dinosaurien) dans le Crétacé supérieur des Petites Pyrénées (Haute-Garonne). Bull. Mus. Natl. Hist. Nat. Paris, v. 130, pp. 17-27, Paris.

PEREDA-SUPERBIOLA X. (1999) - Las faunas finicretácicas de dinosaurios ibéricos. Zubia, v. 17, pp. 259-279.

PEREDA-SUPERBIOLA X., RUIZ OMEÑACA J.I. & COMPANY J. (2003) - Los dinosaurios hadrosaurios del registro ibérico. Descripción de nuevo material del Cretacico superior de Laño (Condado de Treviño). In: PÉREZ-LORENTE F. (ed.), Dinosaurios y otros reptiles mesozoicos en España, pp. 375-388, Ediciones Insituto de Estudios Riojanos, Logroño.

PEREDA-SUPERBIOLA X. & SANZ J.L. (1999) - *The ornithopod dinosaur* Rhabdodon *from the Upper Cretaceous of Laño (Iberian Peninsula)*. Est. Mus. Cienc. Nat. de Alava, v. 14 (num. espec. 1), pp. 257-272, Alava.

PHILIP J., FLOQUET M., PLATEL J. P., BERGERAT F., SANDULESCU M., BARABOSHKIN E., AMON E. O., POISSON A., GUIRAUD R., VASLET D., LE NINDRE Y., ZIEGLER M., BOUAZIZ S. & GUEZOU J. C. (2000) - *Map 16. - Late Maastrichtian (69.5-65 Ma)*. In : DERCOURT J., GAETANI M., VRIELYNCK B., BARRIER E., BIJU-DUVAL B., BRUNET M.F., CADET J.P., CRASQUIN S. & SANDULESCU M. (eds.), Atlas Peri-Tethys, Palaeogeographical Maps, CCGM/CGMW, Paris.

RIABININ A.N. (1945) - *Dinosaurian remains from the Upper Cretaceous of Crimea* [in Russian with English summary]. Vsesoy. Nauch.-Issledov. Geol. Inst. Matl.Paleont. Strat., v. 4, pp. 4-10.

RYAN M. J. & EVANS D.C. (2005) – Ornithischian dinosaurs. In: CURRIE P.J. & KOPPELHUS E.. B. (eds), Dinosaur Provincial Park – A spectacular ancient ecosystem revealed, pp. 312-348, Indiana University Press, Bloomington & Indianapolis.

SEELEY H.G. (1883) - On the dinosaurs from the Maastricht beds. Q.J.Geol. Soc. London, v. 39, pp. 246-253, London.

TARLAO A., TENTOR M., TUNIS G. & VENTURINI S. (1994) - Evidenze di una fase tettonica nel Senoniano inferiore dell'area del Villaggio del Pescatore (Trieste). Gortania-Atti Mus. Friul. St. Nat., v. 15(1993), pp. 23-34, Udine.

THERRIEN F. (2005) – Palaeoenvironment of the latest Cretaceous (Maastrichtian) dinosaurs of Romania: insights from fluvial deposits and paleosols of the Transylvanian and Hateg basins. Palaeogeog., Palaeoclim., Palaeoecol., v. 218, pp.15-56, Amsterdam.

THERRIEN F., JIANU C.-M., SCARLAT B., WEISHAMPEL D.B., KING J.W. (2002) – Paleoenvironment reconstruction of latest Cretaceous dinosaur-bearing formations of Romania: preliminary results. Sargetia, v. 19, pp. 33-59, Deva.

TYSON R.V. & FUNNELL B.M. (1987) - *European Cretaceous shorelines, stage by stage*. Palaeogeogr. Palaeoclimatol. Palaeoecol., v. 59, p. 69-91, Amsterdam.

VAN ITTERBEECK J., MARCHEVICH V.S. & CODREA V. (2005) - Palynostratigraphy of the Maastrichtian dinosaur - and mammal sites of the Râul Mare and Barbat Valleys (Hateg Basin, Romania). Geol. Carpathica, v. 56(2), pp. 137-147.

WEISHAMPEL D.B., BARRETT P.M., CORIA R.A., LE LOEUFF J., XING X., XIJIN Z., SAHNI A., GOMANI E.M.P. & NOTO C.R. (2004) - *Dinosaur distribution*. In Weishampel D. B., Dodson P. & Osmólska H. (eds), The Dinosauria – Second Edition, pp. 517-606, University of California Press, Berkeley and Los Angeles.

WEISHAMPEL D.B., GRIGORESCU D. & NORMAN D.B. (1991) - *The dinosaurs of Transylvania: island biogeography in the Late Cretaceous*. National Geographic Research and Exploration, n. 7, pp. 68-87.

WEISHAMPEL D.B. & HORNER J.R. (1990) - *Hadrosauridae*. In: WEISHAMPEL D.B., DODSON P., OSMÓLSKA H. (eds), *The Dinosauria*, University of California Press, pp. 534-561, Berkeley.

WEISHAMPEL D.B., JANU C.-M., CSIKI Z. & NORMAN D.B. (2003) - Osteology and phylogeny of Zalmoxes (n.g.), an unusual Euornithopod dinosaur from the latest Cretaceous. Journ. Syst.Palaeont., v. 1(2), pp. 65-123, London.

WEISHAMPEL D.B., MULDER E.W.A., DORTANGS R. W., JAGT J.W.M., JANU C.-M., KUYPERS M.M.M., PEETERS H.H.G. & SCHULP A.S. (1999) - *Dinosaur remains from the type Maastrichtian: an update*. Geologie en Mijnbouw, v. 78, pp. 357-365.

WEISHAMPEL D.B., NORMAN D.B. & GRIGORESCU D. (1993) - Telmatosaurus transsylvanicus from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. Palaeontology, v. 36, pp. 361-385, London.

WELLNHOFER P. (1994) - Ein Dinosaurier (Hadrosauridae) aus der Oberkreide (Maastricht, Helvetikum-Zone) des bayerischen Alpenvorlandes. Mitt. Bayer. Staatsslg. Paläont. hist. Geol., v. 34, pp. 221-238, Munich.

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