

Ontogenetic development of *Telmatosaurus transsylvanicus* (Ornithischia: Hadrosauria) from the Maastrichtian of the Hațeg Basin, Romania — evidence from the limb bones

Dan GRIGORESCU¹ & Zoltan CSIKI²

¹Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, e-mail: dangrig@geo.edu.ro; ²Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, e-mail: dinozoli@geo.edu.ro

Abstract — Hatchling remains of the hadrosaur *Telmatosaurus transsylvanicus* were found associated with megaloolithid eggs in the Tuștea nesting site, Hațeg Basin, Romania. Despite the small sample size, these remains yield the first data concerning the early post-natal ontogenetic development of this basal hadrosaur; the analyzed limb bones (humerus, ulna, femur, tibia) provide evidence of the morphological, as well as allometric size and proportion changes occurring during growth in the appendicular skeleton of *Telmatosaurus*.

Keywords — Hadrosauridae, *Telmatosaurus*, hatchlings, ontogeny, Hațeg Basin, Maastrichtian

Introduction

Telmatosaurus transsylvanicus is the only dinosaur species from the Maastrichtian faunal assemblage of the Hațeg Basin represented by a complete ontogenetic scale, from embryos and hatchlings to. The bone remains of adults and subadults of *Telmatosaurus* are commonly encountered in “fossiliferous pockets” within the continental deposits of the Hațeg Basin, while the embryos and hatchlings were found associated with clutches of megaloolithid eggs in the only known incubation horizon from Tuștea (Grigorescu et al., 1994; Grigorescu, 2003, 2006).

The Tuștea nesting site is, however, unique in the European Late Cretaceous in that the nests are associated within the same horizon with skeletal remains of baby dinosaurs. After rare and isolated hatchling bone fragments were found accidentally shortly after the discovery of the eggs (see Weishampel et al., 1993), the large-scale excavations taking part in the last several years at the nesting site revealed the presence of a large number of such baby dinosaur remains (during the 2005 field season only, associated remains of three individuals and several isolated finds were recovered).

The purpose of the present contribution is to shortly introduce these embryo and hatchling bones, referable to the duck-billed *Telmatosaurus transsylvanicus* and to discuss their significance in the understanding of the early ontogenetic development of the taxon. Due to the limitations of the available material, only limb bones will be addressed, although other skeletal remains are also known (see below).

Institutional abbreviations — BMNH: Natural History Museum (former British Museum of Natural History), London, UK; FGGUB: Laboratory of

Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; MAFI: Magyar Állami Földtani Intézet, Budapest, Hungary.

Geological setting

The Upper Cretaceous continental deposits of the Hațeg area (Southern Carpathians, Romania) accumulated in a subsiding intermontane basin formed following the main thrusting phase of the Laramian tectogenesis (Willingshofer et al., 2001). The molasse-type deposits are distributed along the northwestern and central parts of the basin, and include a wide range of siliciclastic rocks, from conglomerates to mudstones. Two largely synchronous lithostratigraphic units are recognized, the Sânpetru and the Densuș-Ciula formations. These were deposited in an environment dominated by fluvial processes; both channel and floodplain deposits are well represented, these later being subjected to extensive periods of pedogenesis (Grigorescu, 1992). Sedimentological and geochemical studies show that the deposits accumulated under a warm subhumid, subtropical climate, with seasonal rainfall (e.g. Therrien, 2005; Bojar et al., 2005). Although age constraints are poor, these suggest a Maastrichtian age for the continental deposits (see Grigorescu & Csiki, 2002).

Vertebrate remains, representing all major groups, occur throughout the outcropping area of the continental deposits, either as isolated remains or in larger politaxic bone accumulations. Besides skeletal remains, dinosaur eggs were also discovered in several nesting sites (Grigorescu et al., 1994; Codrea et al., 2002); the most important nesting site, in the Oltoane Hill near Tuștea locality, yielded not only egg clutches, but remains of baby dinosaurs as well.

The Tuștea nesting site is located in the (unnamed)

middle member of the Densuş-Ciula Formation, in a succession of grey-greenish matrix-supported conglomerates and coarse sandstones and pedogenetically modified red, micaceous silty mudstones (see Grigorescu & Csiki, 2002; Therrien, 2005; Bojar et al., 2005). The extensive nesting horizon occurs in a red mudstone body, closely associated with a calcret horizon in the upper part of the bed. Sedimentological, geochemical and taphonomical study of the nesting horizon shows it was a well-drained distal floodplain area marked by extensive periods of subaerial exposure and pedogenetic processes. Available data suggest that all nests discovered are distributed in a single horizon; the baby dinosaur bones, here described, were found in the same level, sometimes closely associated with the nests. As these remains are referable without doubt to the hadrosaur *Telmatosaurus transylvanicus* (e.g. Weishampel et al., 1993; Grigorescu, 2006), this taxon is considered the egg-layer responsible for the nests as well (see below).

***Telmatosaurus* and the „Tuştea puzzle”**

Telmatosaurus transylvanicus was the first dinosaur described by Nopcsa from the Hateg Basin, initially under the genus name *Limnosaurus* (Nopcsa 1900), but renamed afterwards as *Telmatosaurus* (Nopcsa 1903). Its skeletal remains, mostly disarticulated and coming from both young and adult individuals are commonly found either isolated or within the politaxic “fossiliferous pockets”, in the Maastrichtian continental deposits of the Hateg Basin. Although reported previously from the French and Spanish Uppermost Cretaceous as well, its presence in Western Europe was infirmed by recent studies (Laurent, 1996).

Telmatosaurus was reviewed by Weishampel et al. (1993); their phylogenetic analysis has placed it as the basalmost hadrosaur, which lacked several apomorphic features of the other, more derived members of Hadrosauridae. The most recent comprehensive review of the clade also supports this basal position of the taxon within the Hadrosauridae (Horner et al., 2004), position that contrasts with its late stratigraphic occurrence. It has been also suggested that the relatively small size of *Telmatosaurus* represents a case of insular dwarfing (Weishampel et al., 1993). Both of these facts are related to the conditions in which *Telmatosaurus transylvanicus* lived for several millions of years, on an island of the North Tethys Ocean, being geographically isolated from all other hadrosaurids.

More recently, bone remains of embryos and hatchlings of *Telmatosaurus* were also found, closely associated to clutches of megaloolithid eggs from the Tuştea nesting site, in the north-western part of the basin (Grigorescu et al., 1994). The association of hadrosaurid bones with megaloolithid type of eggs, that are now quasi-unanimously assigned to sauropod dinosaurs (Chiappe et al., 1998) was presented at the 2nd and 3rd international symposia on “Dinosaur eggs and babies” from Montpellier, France and Plaza Huincul, Argentina (Grigorescu, 2003, 2006) as the “Tuştea puzzle”, a new subject of controversy among scientists. All available evidence from this nesting site suggests that (at least) the megaloolithid eggs from Tuştea were laid by hadrosaurids and not titanosaurian sauropods.

The embryonic and hatchling remains of *Telmatosaurus transylvanicus* from Tuştea include mostly disarticulated bones: fragmentary skull and dentary elements, vertebral centra and limb bones. However, associated and even articulated skeletal elements were also found, including partial skeletons. Among the baby remains, the limb bones are better preserved and more frequently encountered. Even the rather small number of limb bones elements we dispose do not allow a detailed statistical analysis, they are sufficiently indicative for identify the most important ontogenetic changes that occur during maturation.

The hatchling limb bones

The hatchling appendicular elements found at Tuştea include the scapula, humerus, ulna, radius, femur, tibia, fibula and metatarsals. Of these, only the humeri, ulnae, femora and tibiae occur in several specimens belonging to different sized individuals and are complete enough in order to be observed and measured accurately; in cases of incompletely preserved specimens the length was estimated using comparison with complete specimens of similar dimensions. In order to identify possible allometric changes during ontogeny, large-sized specimens (corresponding to individuals that presumably were either adults or approaching adulthood) were also measured; availability of adult specimens, however, restricted the range of skeletal elements used in this study, since e.g. no complete radius of adult *Telmatosaurus* is known.

Finally, a total of 17 baby dinosaur appendicular elements were used in this study: 2 humeri, 3 ulnae, 6 femora and 6 tibiae; adult elements measured for comparison include 1 humerus, 2 ulnae, 3 femora and 3 tibiae (see Tab.1).

Humerus — (Pl. 1, figs. 1 A, B). Four baby humeri are available for study, out of which 2 can be accurately measured. From the sample two specimens (FGGUB R.1852.1, 3) are from a smaller-sized individual; the other two are somewhat larger. The general shape of the baby humerus is reminiscent to the adult one, except that the articular faces are less

well defined and the deltopectoral crest is less prominent (especially so in FGGUB R.1852). Although size difference is not significant between the two humeri measured, important changes can be observed between the two: while the smaller one shows poorly defined (distal) articular condyles and a rugose, unfinished bone texture, the larger specimen

Element	Spec. no.	L	PW	DW	MW	1	Ontogenetic status
Humerus							
left	MAFI Ob.3126	227.83	58.04	53.73	32.73	98.01	Adult
left	FGGUB R.1980.1	28.58	8.34	6.22	3.38	11.16	Hatchling (H8)
left	FGGUB R.1852.1	23.04*	6.38	5.04	2.99	-	Newborn? (H5)
Ulna							
right	MAFI Ob.3124	327.83	57.9	32.81	32.04	-	Adult
left	FGGUB R.1282	297.62	48.8	37.08	25.45	-	Adult
right	FGGUB R.1851.2	36.11	6.12	5.25	2.74	-	Hatchling (H4)
left	FGGUB R.1980.2	27.51	5.08	4.55	2.2	-	Hatchling (H8)
left	FGGUB R.1850.2	14.42**	5.57	-	2.32	-	Hatchling (H6)
right	FGGUB R.1852.2	11.27**	4.74	-	2.13	-	Newborn? (H5)
Femur							
left	BMNH R.4914	430.02	103.88*	112.69	62.53	230.35	Adult
right	MAFI v.10338	377.33	101.92	100.82	55.65	189.29	Adult
left	MAFI Ob.3128	270.56	87.54	71.21	40.28	137.93	Small dult
right	FGGUB R.248	50.27	-	11.56	6.07	-	Hatchling (H1)
left	FGGUB R.1850.1	48.11	12.31	11.22	6.93	24.98	Hatchling (H6)
left	FGGUB R.1980.3	46.12*	-	9.48	5.2	25.39	Hatchling (H8)
right	FGGUB R.1980.4	43.63*	-	9.39	5.45	23.73	Hatchling (H8)
right	FGGUB R.1981.1	43.3	-	-	4.92	24.39	Hatchling (H9)
right	FGGUB R.1852.3	35.38	-	6	4	-	Newborn? (H5)
Tibia							
left	FGGUB R.0002	448.38*	-	116	50.62	-	Adult
left	FGGUB R.0001	428.83	174.16	113*	50.77	-	Adult
right	MAFI Ob.3129a	408.87*	-	83.51	38.55	-	Adult
right	FGGUB R.1853	63.4	17.73	16.65	5.9	-	Large baby (H)
left	FGGUB R.246+250	41.5*	10.77	8.92	3.85	-	Hatchling (H1)
right	FGGUB R.1982.1	41.05*	-	12.03	3.68	-	Hatchling (H10)
left	FGGUB R.1851.1	38.72	10.53	10.37	3.81	-	Hatchling (H4)
right	FGGUB R.1979	35.78	10.9	8.97	3.73	-	Hatchling (H7)
left	FGGUB R.1852.4	33.6*	-	7.38	3.06	-	Newborn? (H5)

Table 1 — Measurements of selected *Telmatosaurus* limb bones. * – estimated measurements; ** – dimensions as preserved; H1 to H10 refer to different individuals, represented by associated material as identified in the field. 1 – additional measurements: deltopectoral crest length, in humerus, distance of 4th trochanter from proximal end, in femur

has clearly defined articular condyles reminiscent in shape of those of the adults, and the bone surface seems smoother.

Ulna — (Pl. 1, figs. 2, A - D). Two complete and several fragmentary baby ulnae were found; these are both in shape and in proportions comparable to those of the adults. The only observable trends are a

slight allometric increase in the robustness of the ulna (measured here as the ratio of minimal shaft width to length) and a decrease of the proximal width to minimal width ratio.

Femur — (Pl. 1, figs. 3. A-D). One complete and four almost complete baby femora are known, together with several fragments, ranging from about

35 to slightly more than 50 mm in length. The smallest femur belongs to a presumed newborn specimen (H5), and shows the same coarse surface texture and poorly defined articular surfaces as the associated humerus. As size increase, the ossification of the distal articular end augments, so that around 46 mm length the condyles are clearly individualized and start to contact each other in the midline cranially, enclosing the cranial intercondylar groove that is becoming tunnel-like as in adults. Although the trend is not consistent, it appears to be a slight allometric increase in the robustness of the bone (measured as the minimal shaft width to length ratio), conversely to the situation reported in *Hypacrosaurus stebingeri* by Horner & Currie (1994). The distal end (as shown by the distal width to length ratio) is also relatively larger in larger specimens. The width of the distal end seems to increase more rapidly than the minimal width during growth, but this is probably related to the advancement of the ossification of the distal end. The proximal end of the bone looks more unfinished, probably bearing during life an extensive cartilaginous cap, as was suggested for *Hypacrosaurus stebingeri* (Horner & Currie, 1994); apparently strengthening of the knee joint occurred earlier in ontogeny than that of the hip joint. Interestingly, the position of the 4th trochanter along the shaft seems to present a proximal shift with increasing size.

Tibia — (Pl. 1, figs. 4. A-C). The tibia is the best represented element from the studied sample; four complete or almost complete specimens are known, along with several fragmentary remains. It also shows the largest size variation, from newborn (approx. 33.6 mm) to large baby (63.4 mm). No allometric size or proportional changes are evident in the sample. During ontogeny, the size and degree of cranio-lateral projection of the cnemial crest increases. The distal articular end appears to be better ossified than the proximal one; this process is apparently finished by late baby ontogenetic stage (exemplified by FGGUB R.1853), in which the distal articular face is already smooth, well formed.

Limb element ratios — As in several instances the baby *Telmatosaurus* bones belong to the same individual, their relative proportions can also be assessed. Unfortunately, no similar data is available for the adults, so that allometric proportion changes are impossible to document. The data can be compared, however, to those available for other hadrosaurs, as tabulated by Brett-Surman (1989).

The ulna/humerus ratio is 0.96 in FGGUB R.1980, an average baby specimen from the sample; this contrasts with values recorded in hadrosaurids, where

the ulna is longer than the humerus, but is larger than in adult non-hadrosauroid ankylopollexians. In the hatchlings of *Hypacrosaurus stebingeri* this value is similar to that seen in adult hadrosaurids (Horner & Currie, 1994). Two possibilities can be envisaged. If this ratio has similar values in adult *Telmatosaurus* and in other hadrosaurids, then the ulna must show positive allometric growth pattern relative to the humerus. Conversely, this ratio in adults might be more similar to those seen in more basal iguanodontoids, and in this case the baby ratio here reported is characteristic for *Telmatosaurus*; interestingly, a juvenile specimen of *Eolambia carolinjonesa*, a basal hadrosauroid, is also reported to have an ulna “nearly as long as the humerus” (Kirkland, 1998).

The humerus/femur ratio is 0.65 in FGGUB R.1852 and 0.62 in FGGUB R.1980, close to the highest values of the variation range known in hadrosaurids, as reported by Brett-Surman (1989); apparently, it changes ontogenetically through the relative lengthening of the femur (but see below, Conclusions).

The tibia is shorter than the femur, as usually in hadrosaurids (tibia/femur ratio is estimated to 0.95 in FGGUB R.1852). This ratio is slightly higher than most values reported for hadrosaurids by Brett-Surman (1989); it is, however, comparable to those seen in embryonic and nestling specimens of *Hypacrosaurus stebingeri* (Horner & Currie, 1994). It is possible that during ontogeny the ratio decreased (through the relative lengthening of the femur, similar to the condition reported in *Tenontosaurus*, Forster, 1985), so that in adult specimens it became comparable to that known in other hadrosaurids.

Conclusions

Ontogenetic data are here reported for the first time for the early development of the basal hadrosaurid *Telmatosaurus transsylvanicus*, from the Maastrichtian of the Hațeg Basin, Romania, based on material found associated with megaloolithid eggs in the Tuștea nesting site. Despite the limited number of the specimens available for the study, some conclusions can be drawn:

1. there are no major morphological or proportion changes from the early ontogenetic stages documented by the studied material and the adult stage;

2. the most important morphological changes are evidenced by the humerus (increase of the deltopectoral crest robustness) and tibia (development of a larger cnemial crest); on the femur, the cranial intercondylar canal is enclosed during ontogeny through

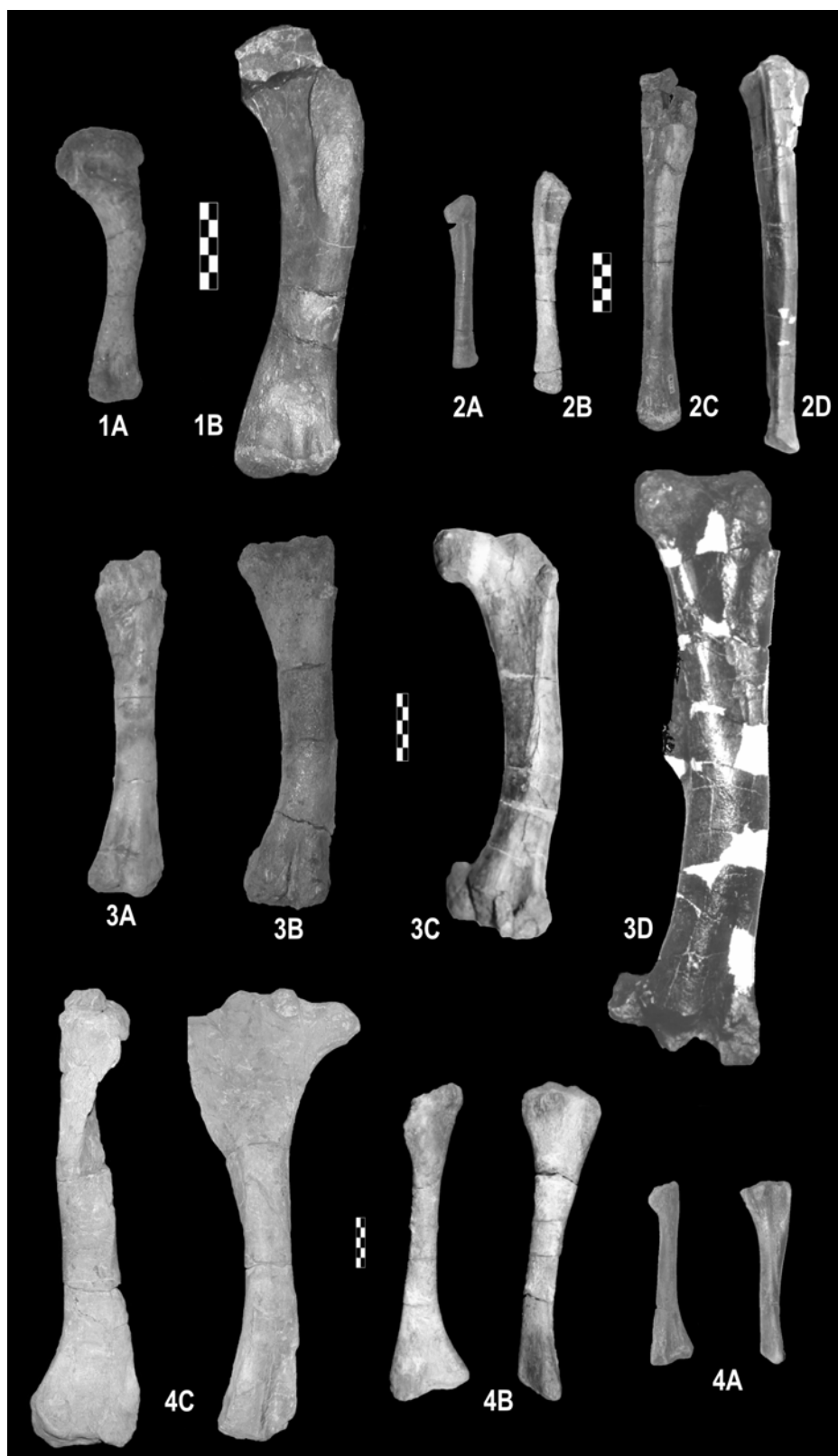


Plate 1 — *Telmatosaurus transsylvanicus* limb bones from the Maastrichtian of the Hăţeg Basin, Romania. 1. Humeri. A – left humerus of hatchling (FGGUB R.1980.1) and B – left humerus of adult (MAFI Ob.3126), both in cranial view. 2. Ulnae. A – left ulna of hatchling (FGGUB R.1980.2), B – right ulna of hatchling (FGGUB R.1852.1), C – right ulna of adult (FGGUB R.1282) and D – left ulna of adult (MAFI Ob.3124), all in cranio-lateral view. 3. Femora. A – left femur of hatchling (FGGUB R.1980.3), B – left femur of hatchling (FGGUB R.1850.1), C – left femur of young adult (MAFI Ob.3128) and D – left femur of adult (BMNH R.4914), all in cranial view. 4. Tibiae. A – right tibia of hatchling (FGGUB R.1979), B – right tibia of large hatchling (FGGUB R.1853) and C – left tibia of adult (FGGUB R.0001), all in cranial (left) and lateral (right) view. Scale bar represents 5 cm for figs. 1B, 2C, D, 3C, D and 4C, and 1 cm for figs. 1A, 2A, B, 3A, B and 4A, B.

the strong cranial development of the articular condyles;

3. ossification at the articular ends of the limb bones is incipient during the early stages of post-natal development and develops later, as reported in *Maiaasaura* (Horner & Weishampel, 1988); ossification proceeds at different rates between the different bones and even between different ends of the same bone;

4. allometric changes during growth are present in the ulna and the femur, both bones becoming increasingly robust (in terms of minimal shaft width/length ratio) with increasing size;

5. ratios of the different limb bones are for the first time documented in *Telmatosaurus*; in some aspects (such as the ulna-to-humerus ratio) *Telmatosaurus* seems to depart from other hadrosaurids and is closer to more basal iguanodontoids; in the absence of data from adult specimens, it is unclear whether this represents a juvenile condition modified afterwards during ontogeny or it represents a genuine feature of the taxon, corresponding probably to its basal position within the Hadrosauridae;

6. the presence of different growth stages in the same hatchling bone accumulations suggests a high growth rate during early post-natal development.

The main drawback of the above conclusions sits in the limited size of the analyzed sample; small sample size can suggest “patterns” that will be blurred when larger number of specimens becomes available. Moreover, the overall ontogenetic sample used is heavily biased towards the two ends of the size spectrum, the juveniles and small adults missing altogether. Whether this is due to chance preservation, a taphonomic bias or a paleobiological bias (juveniles and small adults migrating and living most of their lives outside the Hațeg Basin) is unknown. Regardless the reasons lying behind this preservation pattern, one should be aware that small sample size and missing crucial ontogenetic information make the above conclusions preliminary and potentially modified by subsequent discoveries.

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