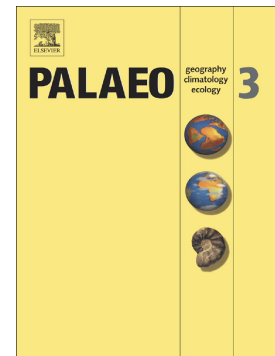


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Taphonomical and palaeoecological investigation of the late cretaceous (Maastrichtian) Tuştea vertebrate assemblage (Romania; Haţeg Basin) - insights into a unique dinosaur nesting locality

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TAPHONOMICAL AND PALAEOECOLOGICAL INVESTIGATION OF THE LATE  
CRETACEOUS (MAASTRICHTIAN) TUȘTEA VERTEBRATE ASSEMBLAGE  
(ROMANIA; HAȚEG BASIN) - INSIGHTS INTO A UNIQUE DINOSAUR NESTING

LOCALITY

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Keywords: vertebrate taphonomy; nesting site; dinosaur eggs; dinosaur hatchlings; Late Cretaceous; Romania

## Abstract

The Tuştea vertebrate locality, at Oltoane Hill (northwestern part of the Haţeg Basin, Romania), has provided a rich and diverse assemblage of Late Cretaceous (Maastrichtian) continental vertebrates. More than 800 vertebrate fossils were recovered from this locality; the isolated and associated remains represent 21 different taxa including amphibians, turtles, lizards, snakes, crocodyliforms, pterosaurs, dinosaurs and mammals. The local assemblage is overwhelmingly dominated by dinosaurs, with the rhabdodontid *Zalmoxes* as the most abundant taxon. The bonebeds that yielded this fossil material occur in a stacked series of mudstone/calcrete units belonging to the middle member of the Densuş-Ciula Formation. The taphonomical investigations suggest that the Tuştea assemblage is made up of attritionally accumulated politaxic remains and that it is a parautochthonous assemblage with no evidence for significant bone transport or reworking.

According to the synthesis of all available field data two outstanding fossiliferous levels can be identified within the Tuştea locality, where *Megaloolithus* eggs and hadrosauroid hatchling material are preserved together, recognized here as two superposed nesting grounds. Such co-occurrence was considered controversial, since there is a long-standing and quasi-general consensus that eggs of the *Megaloolithus* oogenus were laid by titanosaurian sauropods. We present several alternative scenarios to account for the co-occurrence of *Telmatosaurus* hatchling remains and megaloolithid eggs in the nesting horizons and explore these alternative hypotheses by weighing the arguments supporting or contradicting them. The burden of evidence derived from our sedimentological, taphonomical and palaeoecological investigations at Tuştea is still in favor of the autochthony of the hatchlings, preserved within their own nesting grounds, whereas there is no such support for a titanosaurian origin of the Tuştea megaloolithid eggs.

Keywords: vertebrate taphonomy; nesting site; dinosaur eggs; dinosaur hatchlings; Late Cretaceous; Romania

## 1. INTRODUCTION

The Oltoane Hill, near Tuştea village (Fig. 1), in the northwestern part of the Haţeg Basin represents the place where the first dinosaur eggs from Romania were discovered in 1988 (Grigorescu et al., 1990). This discovery came after a century-long history of palaeontological studies in the Haţeg area that established its importance for the continental Late Cretaceous of Europe and worldwide (Grigorescu, 2010a; Csiki-Sava et al., 2015). The fossiliferous lithological succession exposed at Oltoane Hill was unearthed by a landslide that took place in the late 1980s (Fig. 1C). The discovery of dinosaur eggs in the vertical exposure created by the landslide soon highlighted the importance of this new vertebrate-bearing site, and in order to gain better accessibility for conducting large-scale excavations, starting with 1994 arrangements were made to transform the vertical outcrop into a horizontal platform, more suitable for systematic quarrying.

Subsequent to this levelling effort, intensive excavations were conducted at the Tuştea site more or less annually until 2011, and during the 23-year long period of collecting, the locality (see below) yielded a large number of vertebrate fossils, including hatchlings and embryonic remains of the hadrosauroid *Telmatosaurus transsylvanicus*, closely associated with megaloolithid eggs generally considered to belong to titanosaurian sauropods – an unusual co-occurrence quoted after 2000 as the “Tuştea puzzle” (e.g., Grigorescu, 2010b). The dinosaur eggs and perinatals are associated at Tuştea with a large number of other vertebrates: frogs, albanerpetontids, lizards (including geckoid eggshells), snakes, turtles, crocodyliforms, pterosaurs, diverse dinosaurs (theropods, including the aberrant dromeosaurid *Balaur*, titanosaurian sauropods, rhabdodontid and hadrosauroid ornithopods), and

multituberculate mammals (Csiki and Grigorescu, 2000; Grigorescu and Csiki, 2002; Buffetaut et al., 2003; Weishampel et al., 2003; Dalla Vecchia, 2006; Martin et al., 2010; Csiki et al., 2010a,b; Grigorescu et al., 2010; Vasile and Csiki, 2010; Csiki-Sava et al., 2012, 2016; Brusatte et al., 2013; Vasile et al., 2013; Venczel et al., 2015). The Tuștea locality is also the type locality of two newly erected taxa, the madtsoiid snake *Nidophis insularis* (Vasile et al., 2013) and the advanced neosuchian crocodyliform *Sabresuchus* ('*Theriosuchus*') *sympiestodon* (Martin et al., 2010; Tennant et al., 2016). The presence of such a rich faunal assemblage (Table 1) and the interesting association of dinosaur eggs and neonates promoted Tuștea as one of the outstanding Late Cretaceous continental fossiliferous sites, not only in Romania, but also throughout Europe.

Although taphonomical characters and genetic models for the Tuștea vertebrate assemblage have been discussed preliminarily in several previous contributions (Grigorescu and Csiki, 2002; Csiki et al., 2010a; Vasile and Csiki, 2010; Martin et al., 2010; Venczel et al., 2015), a thorough taphonomical investigation of the Tuștea locality was yet to be made. The present study aims to supplement this shortcoming, and focuses on the detailed taphonomical study of this important vertebrate locality and its fossil content, with emphasize on the macrovertebrate and particularly on the dinosaur egg-hatchling assemblages, in order to gain a more profound understanding of the sedimentary and biotic conditions and processes that controlled the genesis of this unique Maastrichtian fossil locality.

## 2. MATERIAL AND METHODS OF INVESTIGATION

As mentioned above, discovery of the fossiliferous nature of the Tuștea section (Fig. 2) was first followed by excavation of the eggs exposed in the still quasi-vertical section starting from 1988 (nest 1 in Fig. 3), and then by the fortuitous identification of hatchling remains associated with the second sample of eggs (nests 2 and 3; Fig. 3) between 1992–1994 (Grigorescu et al., 1990, 1994). In order to mitigate the serious disadvantages of a vertical

outcrop with limited accessibility to the fossiliferous level, a horizontal platform was later created by bulldozer-aided mechanical removal of the upper mudstone-conglomerate overburden, and this allowed a more extensive and rigorous excavation of the site starting from 1997. Since then, a 180m<sup>2</sup> area of the quarry was excavated, on a maximum depth that varies between 3.5–4 m (between 1997 and 2000) and only about 2–2.5 m (until 2011); this reduction in excavation depth was the by-product of the natural erosion and of the previous excavations, both of which filled up and covered over time with fallen debris the deeper levels of the succession.

During the excavation, pick-axes and/or an electrically driven pick-hammer were employed to remove the conglomeratic-sandy channel deposit (Fig. 2A-C) in order to reach the fossiliferous mudstones, and then mechanically dislodge blocks from the mudstone layers to check them for possible presence of macrovertebrate remains. Furthermore, several microvertebrate fossils were recovered by bulk screen washing of mudstone from different parts of the fossil quarry using 0.75 mm and 2 mm mesh size sieves (Vasile and Csiki, 2010)

During the 23-year period of excavation, a number of 18 dinosaur nests, 83 hadrosauroid hatchling remains (indicating a minimum number of 5 individuals), over 400 other macrovertebrate remains, and over 200 microvertebrate remains were recovered, representing at least 21 taxa (Table 1 and see below). This assemblage stands as one of the largest samples of vertebrate remains derived from one single locality from the Transylvanian uppermost Cretaceous, and probably ranks among the richest ones in Europe (Csiki-Sava et al., 2015). During excavation, the position of the different vertebrate remains in the lithological succession was recorded as exactly as possible (see below) in all instances when this could be achieved; such positional data include horizontal coordinates, depth, as well as (especially in case of elongated skeletal elements and/or those deviating sensibly from the horizontal) the azimuth and plunge. Further distributional data recorded in the field included

approximate size, skeletal and taxonomical identity (whenever recognizable in the field), lithology yielding the remains, possible association or articulation with other remains, and relationships with the calcrete levels. During excavation, other data recorded were the eventual presence of invertebrates, burrows (including their orientation), mottles and rootlets.

Virtually all vertebrate remains excavated from the Tuștea locality are currently curated as part of the collection of the Laboratory of Paleontology, from the Faculty of Geology and Geophysics, University of Bucharest, and are accessioned here under LPB (FGGUB) numbers. To our knowledge, a very small number of vertebrate remains originating from Tuștea are also present in the collections of the Muzeul Civilizației Dacice și Romane in Deva (Hunedoara County, Romania), but these specimens were inaccessible and thus not considered in the present study.

During the taphonomic investigation carried out, macrovertebrate and microvertebrate remains were further examined in the laboratory in order to determine the osteologic and taxonomic identity of each. In addition, any modification feature of the bone surfaces (for instance weathering, abrasion, breakage pattern, etc.) was carefully documented for the macrovertebrates. Data such as position, taxonomic and skeletal identity, shape, state of preservation, and taphonomic modifications observed on the specimens were summarized in a comprehensive taphonomic observation file (“Tuștea taphonomic dataset” files; See Supplementary Information 1 and 2). In order to gather as much of the taphonomic information about the fossil remains as possible, we followed the methodology described by Behrensmeyer (1991), Pereda Suberbiola et al. (2000) and Botfalvai et al. (2015).

Detailed excavation maps are currently available only for the nesting horizons (Fig. 3), and they include solely the position of the different egg clutches and of the nestling remains, because the accessibility of the bonebed did not allow the continuous employment of precise quarrying methods throughout the 23-year excavation period, and the *in situ*

recorded localisation data are either not available or is not yet possible to assemble for the largest part of the skeletal elements.

Basic taphonomic observations from the Tuştea locality were documented previously by Grigorescu and Csiki (2002), Csiki et al. (2010a), Grigorescu et al. (2010), Martin et al. (2010) and Venczel et al. (2015), whereas a preliminary palaeoecological analysis of the microvertebrate fossil assemblage recovered from the Tuştea locality was conducted by Vasile and Csiki (2010).

### 3. GEOLOGICAL SETTING

The Haţeg Basin represents an early Alpine collapse basin located within the ranges of the western Southern Carpathians, in central-western Romania (Fig. 1). It was shaped through localised gravitational collapse of a complex 'mid'- to Late Cretaceous nappe stack during a post-tectonic relaxation phase, subsequent to the major nappe emplacement that built the large-scale structure of the Southern Carpathians during the latest Cretaceous Laramidian (or Second Getic) orogenic phase (Săndulescu, 1984; Bojar et al., 1998; Willingshofer et al., 2001). In this newly formed basin, the basal part of the sedimentary infill is represented by molasse-type, mainly siliciclastic uppermost Cretaceous (Maastrichtian) continental deposits that are distributed over large areas in the northwestern part of the basin, and more patchily in its central-eastern parts (Csiki-Sava et al., 2016). Their age is rather loosely constrained as Maastrichtian based on magnetostratigraphy (Panaiotu and Panaiotu, 2010; Panaiotu et al., 2011), palynostratigraphy (Antonescu et al., 1983; Van Itterbeeck et al., 2005; Csiki et al., 2008) and radiometric dating (Bojar et al., 2011), as well as by their superposition on top of micropalaeontologically dated Campanian marine beds (Dincă et al., 1972; Grigorescu and Melinte, 2002; Melinte-Dobrinescu, 2010).



These Maastrichtian continental deposits were traditionally included into two, largely synchronous lithostratigraphic units, the Densuș-Ciula Formation in the northwest, and the Sînpetru Formation in the central-eastern outcrop areas (Grigorescu, 1992), although recently acquired data suggest that their lithostratigraphy might be more complex (e.g., Therrien, 2005; Ciobănete et al., 2011; Csiki-Sava et al., 2016). In the northwestern part of the basin, deposits of the Densuș-Ciula Formation are characterized by intermixing of siliciclastic, terrigenous sediments with volcanoclastic material and even tuff interbeds (e.g., Nopcsa, 1905; Grigorescu, 1992; Bârzoi and Ţeclăman, 2010; Csiki-Sava et al., 2016). These mixed detritic-volcanoclastic deposits are well developed in the westernmost part of the basin, near Răchitova and Densuș, where they were separated as the lower subunit (member) of the formation. More to the east, the mixed deposits are covered by the deposits of the informal middle and upper members of the Densuș-Ciula Formation, characterized by the presence of a lesser amount of volcanogenic material, usually interspersed within, or even reworked into, the dominantly terrigenous deposits.

Overall, deposits of the Densuș-Ciula Formation are interpreted to have been deposited within the confines of alluvial fan and braided river depositional systems (Csiki-Sava et al., 2016) fed by rivers that drained the metamorphic terrains of the Getic-Supragetic nappe pile bordering the basin to the north and north-west (Bojar et al., 2010a). These alluvial systems developed on an island, part of the Late Cretaceous European Archipelago fringing the northern margin of the Mesozoic Neo-Tethyan – Alpine Tethyan realm (Benton et al., 2010; Csiki-Sava et al., 2015). Both palaeomagnetic (Panaiotu and Panaiotu, 2010), palaeobotanic (Van Itterbeeck et al., 2005; Csiki et al., 2008; May Lindfors et al., 2010; Popa et al., 2014) and paleosol (Therrien, 2005) data suggest that this island was in the subtropical zone during the Maastrichtian, under a seasonally variable, partly semi-arid climate.

### 3.1 Stratigraphic position and depositional setting of the Tuştea locality

The Tuştea nesting locality belongs to the middle member of the Densuş-Ciula Formation (Grigorescu, 1992; Bojar et al., 2005; Therrien, 2005), which was deposited farther to the east from, and later than the peak activity of, the volcanic eruption centres that represented the distinctive feature of the northwestern Haţeg Basin area. The local succession is interpreted to have formed within an alluvial fan setting with braided streams (Therrien, 2005). Based on its stratigraphic position, it appears that the Tuştea locality can be dated loosely as early late Maastrichtian in age (Csiki-Sava et al., 2016).

The local succession at the Tuştea vertebrate locality (Fig. 2) is dominated by a 6 m thick bed of greenish-grey, cross-bedded, matrix-supported conglomerates and coarse sandstones, underlain by a thick body of massive, red silty micaceous and bioturbated mudstones (Fig. 2A; Grigorescu et al., 1994; Grigorescu and Csiki, 2002; Bojar et al., 2005; Therrien, 2005). The conglomerates and sandstones (Fig. 2B-C) are topped by a second level of reddish calcareous mudstones grading into greenish, gleyed mudstones, covered on their turn by recent soil (Fig. 2D). The conglomerate bed includes pebble- to rarely cobble-sized, altered andesitic clasts, diverse metaclasts (quartzites, amphibolites) and, locally, red mudstone rip-up clasts reminiscent of the underlying fossiliferous mudstones (Fig. 2B). All of these clasts float in a sandy-silty matrix, whereas the red mudstones show sedimentary features such as the presence of several discontinuous calcrete horizons, slickensides and vertical to sub-horizontal burrows.

The thick conglomerate layer was studied preliminarily by Therrien (2005), who noted features such as cobble to pebble grain size, presence of large- to small-scale trough, as well as large-scale tabular cross-stratification, a minimal-relief erosional contact with the underlying red mudstones, and slight variability in palaeocurrent orientation. Based on these

features, he concluded that the depositional system of the conglomerate bed consisted of distal gravelly and sandy braided streams. Palaeocurrent direction measurements for the conglomerate layer indicate a unique direction of palaeoflow to the south-east (Therrien, 2005). Only very few indeterminate bone fragments (LPB (FGGUB) R.1841, R.1962) were found in this coarse channel deposit.

By far the largest part of the vertebrate fossils, as well as the eggs were discovered in the lower part of the Tuştea section, which consists of alternating levels of pedogenetically-modified red-coloured mudstones with calcareous concentrations and dark red massive silty mudstone deposits (Fig. 2). The main grain size of the paleosols is silty, and they show prominent pedogenic features such as well-developed vertical roots and burrows, blocky structures (peds), as well as the presence of calcic (Bk) horizons formed by diffuse to well-differentiated carbonate nodules (Bojar et al., 2005; Therrien, 2005). The main clay component is smectite (montmorillonite; Bojar et al., 2005; Therrien, 2005).

The main vertebrate-bearing mudstone situated below the conglomerate layer can be divided into two main parts (named hereon Unit 1 and Unit 2) separated by a light greenish sandstone layer (Fig. 2). This sandstone (ranging in thickness from 10 to 20 cm and extending over more than 15 meters in width laterally) is interpreted as a sheet-splay deposit based on its high width/thickness ratio, fine sandstone grain size, and limited incision (see also Therrien, 2005). Therrien (2005) reported that the sheet-splay sandstone (a conglomeratic lithic arenite) passes laterally into a carbonate-cemented layer; we cannot confirm his observation based on our field notes, but it does not contradict the interpretation of this bed as a splay deposit spread onto the floodplain. Mudstone-dominated Unit 1 is positioned below the sandstone sheet-splay and includes three mudstone (MO4, MO5, MO6) and two calcrete (C4 and C5) horizons, whereas Unit 2, located above the sandstone layer,

contains three main (MO1, MO2, MO3) and one minor (MO4a) mudstone and three calcrete (C1, C2, C3) horizons (Figs. 2, 4).

Vertebrate remains were collected from virtually all of these horizons (both mudstones and calcretes; Fig. 2) in the section and were mapped corresponding to their horizons (see Supplementary Data 2). Unit 1 yielded a lesser amount of vertebrate material (mostly turtle - *Kallokibotion* - plate elements and *Zalmoxes* remains) than Unit 2 (Table 2), but this bias might be due largely to the more reduced accessibility of the deposits belonging to Unit 1, excavated mainly in the first few years following the creation of the horizontal platform, after which excavation proceeded exclusively within the deposits of Unit 2 lying above the sheet-splay sandstone (Figs. 2, 4). Vertebrate remains tend to be found throughout the red mudstone body, whereas the dinosaur eggs and nests are restricted almost exclusively to only two horizons (C1 and C2 *nesting horizons*; see below) within the upper mudstone body (Unit 2; Figs. 2, 4). It is worth noting, however, that isolated megaloolithid eggshell fragments were also discovered in 1994 in red silty mudstone deposits belonging to Unit 1, when a vertical exploration trench was cut into the fallen sandy-muddy debris to expose more completely the local succession in the still vertical outcrop. Although no further eggshells were recovered from Unit 1 after systematic digs started on the horizontal platform, the presence of these isolated eggshells suggests that the lower mudstone unit might potentially hold more complete egg remains yet to be discovered.

The presence of calcic horizons (stage 3 type according to Wright and Tucker, 1991 and Wright and Marriott, 1996; Fig. 2A) inside the well-developed paleosol section (Unit 1+ Unit 2) of the Tuștea locality indicates a limited sediment supply and low floodplain aggradation rate during paleosol formation (Wright and Marriot, 1996; Therrien, 2005; Armenteros and Huerta, 2006). The presence of vertical root traces and calcrete horizons in the Tuștea site also suggests that the water table was limited to the lower part of the soil

section, and thus the meteoric water evaporated before reaching the water table (Wright and Tucker, 1991; Therrien, 2005).

Based on the cyclic recurrence of calcrete levels, the red fossiliferous mudstones of Tuştea preserve composite paleosol profiles, in which the residence time of the soil was long enough to allow development of differentiated soil horizons. However, the thickness of sediment increments deposited during high flood events was larger than that of an individual paleosol horizon, which led to the stacking of successive paleosol profiles in the Tuştea succession (Wright and Marriott, 1996; Kraus, 1999; Therrien, 2005). Moreover, the paleosol horizons at Tuştea show incomplete profiles where the “A horizon” is not represented, most probably because this soil horizon was overprinted by the pedogenic features of a second paleosol that developed on top of it (see also Therrien, 2005). The composite paleosol profile with calcrete horizons (at a Stage 3 of development) indicates a depositional environment where sedimentation rates were usually low, but significant amounts of fresh sediment were deposited periodically during peak flood events (e.g., Wright and Marriott, 1996). Development of successive calcrete profiles as those present in the Tuştea succession requires discrete periods of higher-magnitude aggradation, when the amount of accumulated increments was large enough to bury the existing soil surface (Tandon et al., 1998). These peak flood events, when clastic sedimentation took place, occurred during more humid periods, whereas the calcrete levels would have developed during drier periods.

The depositional processes and environmental conditions that contributed to the genesis of the fossil vertebrate locality of Tuştea (i.e., units 1 and 2) can be summarized - based partly on previous sedimentological investigations (Therrien, 2005; Bojar et al., 2005) - according to the following scenario (Fig. 4B): (1) The mudstones and siltstones were deposited on the elevated parts of the floodplain by ephemeral flood events, forming sheet-splay deposits. These sheet flows were episodic in the area, thus the active sediment transport

and accumulation took place only during, or shortly after, high precipitation intensity (e.g., Daniels, 2003). (2) After the deposition of fine-grained sediment on the distal floodplains, pedogenic processes started to develop within this soft substratum, creating a highly bioturbated soil. The pedogenic processes took place under oxidizing, alkaline conditions, as indicated by the red colour and micritic carbonate texture seen in the Tuştea paleosol sequences (Khadkikar et al., 2000; Bojar et al., 2005; Retallack, 2008). Such conditions also promoted the complete destruction of any existing plant material. (3) Evapotranspiration exceeded precipitation during the drier periods of the subhumid climate that characterized the Tuştea locality sedimentation (Therrien, 2005; Bojar et al., 2005, 2010b) and thus the meteoric water evaporated before reaching the watertable, which resulted in the precipitation of dissolved carbonates forming the calcic ( $B_k$ ) horizons at the Tuştea site (e.g., Wright and Tucker, 1991; Wright and Marriott, 1996; Khadkikar et al., 2000). (4) These circumstances created a thick pedogenically-modified red mudstone with secondary carbonate precipitation that formed calcic horizons situated around the average depth of rainfall or soil water percolation (Wright and Marriott, 1996; Therrien, 2005; Retallack, 2008), depth which, in the case of the Tuştea site, was up to 40 cm deep according to Bojar et al. (2010b). The well-developed geochemical trends (reported by Therrien, 2005) and the presence of well-defined calcrete horizons in the section suggest that pedogenesis was uninterrupted by the addition of new material to the paleosol profile, thus indicating a prolonged period of pedogenesis between two higher-magnitude aggradation events. (5) On rare occasions, during the higher-magnitude flooding events, the thickness of the deposited increment exceeded the thickness of the previously-developed soil horizon, so a new soil profile developed on the top of the former one (e.g., Tandon et al., 1998; Armenteros and Huerta, 2006; Lucas et al., 2010). After the new sediment deposition, the above-mentioned pedogenic and geochemical processes restarted in the newly formed soft substrate and led to the genesis of another

calcrete horizon above the older one, marking the development of the new soil (Fig. 4B). This succession of sedimentological processes was repeated several times during the formation of the Tuştea succession, resulting in a stacked series of mudstone/calcrete units (Fig. 4A).

### 3.2. Dinosaur eggs, nests and hatchlings at Tuştea

The identification of dinosaur eggs at Tuştea (Figs. 3, 5), the first ones to be reported from the Cretaceous of central and eastern Europe (Grigorescu et al., 1990), followed by that of nesting structures and dinosaur hatchling remains (Grigorescu et al., 1994), highlights the uniqueness of this vertebrate locality.

#### 3.2.1 The nesting horizons

Despite several subsequent discoveries of dinosaur eggs and nests in different parts of the Transylvanian area (e.g., Codrea et al., 2002; Smith et al., 2002; Grigorescu and Csiki, 2008; Grigorescu et al., 2010; Grellet-Tinner et al., 2012; Barta et al., 2015; Fig. 1B), the first-to-be-identified Tuştea nesting site still remains unique in the Upper Cretaceous of Romania and even Europe in that a rich assemblage of macrovertebrate remains (both as isolated and associated skeletal elements), including *Telmatosaurus* hatchling bones, was discovered together with well-preserved egg clutches (e.g., Grigorescu et al., 1994, 2010; Grigorescu and Csiki, 2002; Martin et al., 2010; Venczel et al., 2015). Despite being the subject of a long-term research program and of several publications (see Grigorescu, 2010a, 2016.), the precise meaning of the terms ‘nesting horizon’, ‘nesting locality’ and ‘nesting site’ (used as roughly synonymous expressions when referring to Tuştea) remains somewhat confuse as they were employed in different manners in previous publications: while Therrien

(2005), Martin et al. (2010) or Csiki-Sava et al. (2012) interpreted the term ‘nesting horizon’ to refer to the entirety of Unit 2 of the Tuştea site as defined here (Figs. 2, 4), Grigorescu and Csiki (2002), Grigorescu (2010b), Grigorescu et al. (2010) or Venczel et al. (2015) identified only one particular layer of Unit 2 as the nesting horizon at Tuştea.

To further complicate this issue, Grigorescu et al. (2010) explicitly recognized the presence of only one level with dinosaur eggs and nests at Tuştea, whereas Bojar et al. (2005: Fig. 2) hinted at the possibility, but without presenting any supportive evidence for this interpretation, that dinosaur eggs are present at two different levels within Unit 2. It was further unclear whether the eggshell samples analysed by Bojar et al. (2005), and collected mainly as isolated elements, belong to (and mark) actual nest locations and horizons, or were simply scattered elements throughout the succession of Unit 2.

In order to clarify these controversial issues, we take here a two-fold approach: first, we define unambiguously the semantics of terms such as ‘Tuştea (nesting) site’, ‘Tuştea (nesting) locality’ and ‘Tuştea (nesting) horizon’, and second, we investigate in detail the number and position of the dinosaur nest-bearing levels within the Tuştea succession using existing detailed field notes, photos and observations.

In accordance with the definition suggested by Csiki-Sava et al. (2016: p. 685), we propose to use the term ‘Tuştea (nesting) locality’ specifically to refer to the local sedimentary unit that hosts the dinosaur eggs and nests (and associated vertebrate remains), exposed in the Tuştea (Oltoane Hill) section, that is, especially Unit 2 and probably also extending to Unit 1 as defined in this study, pending certain identification of eggs or nest structures in the latter. The more comprehensive term ‘Tuştea (nesting) site’ should be used to refer to the entire succession exposed in the eastern face of Oltoane Hill, north of Tuştea village (precise locality data: 45°36’25.4” N 22°50’53.1”E), that is, the succession including units 1 and 2, as well as the conglomerate-sandstone body overlying the ‘nesting locality’



itself and the uppermost mudstone body that covers in turn the coarse-grained channel deposits, grading from red to green in colour (Fig. 2). According to these definitions, the Tuştea site hosts the important Tuştea nesting locality but also further vertebrate localities, represented by the two isolated bone occurrences within the basal part of channel deposits overlying Unit 2 (see above). Finally, we here define the ‘*nesting horizon*’ as a particular, spatially well-constrained level within the Tuştea nesting locality where eggs and especially nest structures were discovered, eventually also associated with hatchling remains (Fig. 2), and thus this term should not be used to encompass the entire thickness of the Tuştea locality bonebed (Fig. 4).

Furthermore, in order to address the issue of precisely identifying the position of the nesting horizon(s), we have closely re-evaluated all the available field data from the Tuştea vertebrate locality, collected between 1988 and 2011. Unfortunately, due to the excavation methods (see above) and the different exposure type of the fossiliferous units (first a vertical outcrop, then a horizontal platform), as well as to the activity of excavation teams with different field expertise during this 23-year long period, part of the exact location data for the recovered elements (macrovertebrate elements, microvertebrate remains, eggshells, eggs, nests) is missing. Moreover, since no reliable marker levels are present and traceable throughout the lateral extent of the Tuştea quarry, vertical position of the fossil remains could only be recorded roughly, as their depth relative to (= below) the conglomerate/mudstone contact and double-checked whenever possible by their relationships to the laterally traced calcrete horizons. This method provided a crude estimate for the vertical position of many of the fossil remains, given the uneven, erosional nature of the conglomerate/mudstone contact, but the low (<15 cm) topographic relief of the contact combined with the secondary depth control using the calcrete levels make these estimates still usable.

Despite all these difficulties, we have amassed enough reliable location data recording the spatial distribution of the fossil remains (especially eggs, nests and hatchlings) both horizontally and vertically within the fossiliferous beds to ascertain the existence of two different nesting horizons within Unit 2, i.e., two well-separated, vertically restricted levels where eggshells, eggs and nest structures were found associated with hatchling bones, besides other vertebrate remains (Figs. 2 and 3). Note, however, that these two nesting horizons identified here should not be confused with the two ‘closely superposed levels’ reported by Grigorescu et al. (1994: p. 77) based on the position of the earliest discovered eggs, ‘levels’ that in fact correspond to overlapping eggs that belong to the same nest, as documented in nest structures subsequently excavated on the horizontal platform (see Grigorescu et al., 2010). Instead, the two nesting levels we identify here are well individualized, widely spaced vertically, associated with different calcrete levels, and separated by a thick (~30–40 cm) mudstone interval devoid of discrete calcrete levels or nest structures (see below). It is worth stressing, nonetheless, that the eggs preserved in these different nesting horizons from Tușteea locality represent the same morphotype, and can be referred to *Megaloolithus* cf. *siruguei* (Grigorescu, 2016).

The *lower nesting horizon*, revealed by the first eggs and nests identified in 1988–1989, is located on average ~50–60 cm below the conglomerate-mudstone contact and is closely associated with a calcrete horizon (C2 level in this study; Figs. 2, 4A, 5A); it corresponds to the nesting horizon identified and marked as such in several previous publications (e.g., Grigorescu and Csiki, 2002; Grigorescu et al., 2010). In this nesting horizon, the megaloolithid eggs and *Telmatosaurus* hatchling remains were found near the boundary between the C2 calcrete and MO2 mudstone horizons (Table 2), with the bottom half of the eggs close to/lodged in the C2 horizon, and the MO2 mudstone covering the eggs.

The *upper nesting horizon*, first found (but not recognized as such) in 2002, is situated at most ~20–30 cm below the conglomerate-mudstone contact, and is closely related to the C1 calcrete horizon (Figs. 2, 4A, 5B). Here, the eggs and the *Telmatosaurus* hatchling remains were found distributed at the boundary between the C1 calcrete and the MO1 mudstone horizons, with the bottom of the eggs close to/lying in the C1 calcrete horizon, and the MO1 mudstone covering the eggs.

There is a clearly recognizable spatial pattern in the distribution of the nests between the two horizons (Fig. 3). Nests belonging to the lower nesting horizon (C2 level) are distributed across a rather large, ~130 m<sup>2</sup> area, covering the entire southern and central sectors of the quarried surface, although with a relatively extensive ‘barren’ (i.e., devoid of nests or eggs, while macrovertebrate remains have been recovered here) area in its central part (Fig. 3). This barren area does not represent the result of an excavation bias, because the entire quarry area had been excavated with the same methods, and to the same depth; instead, it appears to represent a genuine pattern of original areal distribution of the nests, although the factors controlling this non-random distribution remain unknown. Meanwhile, nests belonging to the upper nesting (C1 level) horizon are restricted to the northern-northwestern corner of the quarry surface, covering a surface of only about 25 m<sup>2</sup>, although hatchling remains associated with this nesting horizon were also found well outside this area (i.e., hatchling occurrence no. 5 in Fig. 3). This quasi-completely non-overlapping spatial distribution between nests belonging to the lower and upper nesting horizons, respectively, with a roughly east-west trending line separating the distribution areas of the nests in the two horizons does not appear to represent an excavation bias, as excavation depth in the north-western corner of the quarry reached the calcrete level C3 and below, that is, extended below the level of the second, lower nesting horizon.

Ten variable-sized egg clusters (possible nest structures: nests no. 1–4, 10–12 and 15–17 in Fig. 3) were identified in the lower nesting horizon, some of these obviously partially preserved, with only 2–4 eggs. As some of these smaller egg concentrations (e.g., nests 15 and 16) are widely separated from other clusters, they most probably represent distinct nests, despite the low number of eggs they contain. The lower horizon hosts the largest nest structure discovered at Tuştea (nest no. 17), with 14 eggs; this cluster also yielded the holotype of the madtsoiid snake *Nidophis insularis* (Vasile et al., 2013), whose partially articulated remains were discovered associated with the nest. In total, 71 eggs were discovered in the lower nesting horizon, most of these within the nests themselves (e.g., Fig. 5E); however, this figure also includes one almost complete, unhatched egg (IsE in Fig. 3) found isolated and separated by about 45–50 cm from the nearest cluster (nest 11).

Despite its significantly smaller egg-bearing area, the upper nesting horizon hosts 7 nest-like clusters (nests no. 5–9, 13 and 14 in Fig. 3). The nests preserved here are smaller on average (Fig. 5F), with the largest cluster formed by 10 eggs (nest no. 7). Although one relatively large nest of this horizon (nest 13), removed from the field in plaster jacket, still remains unprepared and thus with uncertain egg count, based on a preliminary *in situ* assessment it does not appear to contain more eggs than nest 7. In total, a minimum number of 39 eggs were identified until now in this nesting horizon, a figure that might increase once the preparation of the remaining jacketed nest will be completed. Finally, there is a recently recovered nest structure containing 2 eggs (nest 18) that was removed from the field in a salvage excavation under difficult field conditions, and thus its position (i.e., depth and relationships to calcrete levels) cannot be ascertained.

Dinosaur hatchling remains are associated with eggs and nests in both nesting horizons (Figs. 3 and 5D). In the nest-richer lower horizon and its surroundings, these are relatively rare and more poorly preserved, whereas they are represented by more complete

and sometimes articulated material in and around the upper nesting horizon. Most of the recovered hatchling remains have good position data on record, which allows positioning them rather precisely within the quarry (Fig. 3 – position of the hatchling remains marked by stars). Usually each of these locations preserves hatchling remains belonging to only one distinct individual based on commensurate size of, and lack of overlapping between, the skeletal elements recovered. One intriguing exception to this pattern might be represented by location 5, where partially articulated incomplete skeletons of potentially 2 (or maybe even 3) distinct individuals (H3/1, H3/2, H5) have been discovered; definitively establishing the number of individuals here is hampered by the fact that skeletal overlap was not observed between the different sets of articulated remains. Remarkably, this hatchling location is also the one lying farthest away from nest structures from within the same horizon. The hatchling remains display a wide spectrum of preservation (from articulated to isolated material) and size categories, suggesting that neonates of different ontogenetic developmental stages are preserved in the nesting locality; ontogenetic developmental diversity can be documented for both nesting horizons (see Grigorescu, 1993, 2010b; Grigorescu et al., 1994, 2010; Grigorescu and Csiki, 2006).

Two areas yielded hatchling elements in the lower nesting horizon, concentrated in its east-central and west-central areas, respectively (Fig. 3). In the first of these areas, hatchling remains are represented only by a few incomplete hindlimb elements (Weishampel et al., 1991, 1993; Grigorescu, 1993; Grigorescu et al., 1994), restricted to the proximity of nests 1 and 3, and discovered in the original, still vertical outcrop conditions. However, neither their state of preservation nor their rarity can be explained by such admittedly adverse outcrop conditions, since even during the second quarrying stage after 1997, hatchling elements remained rare in the lower nesting horizon. The second area of hatchling occurrence in this horizon is concentrated around nest no. 17, and it yielded a few better preserved neonate

skeletal elements, including a partly articulated partial hindlimb (Fig. 5D). Nevertheless, these remains remain restricted in skeletal diversity, and include mainly robust and more preservation-prone hindlimb elements (femora, tibiae). Occasionally, hatchling bones probably related to the lower nesting horizon show a wider range of vertical dispersion, being found slightly above the nesting horizon itself, in its red mudstone (MO2) covering (e.g., the femur LPB [FGGUB] R.2319).

The upper nesting horizon proved to be richer in hatchling remains, and these are occasionally scattered more widely, lying several meters apart from the nearest nest structures (e.g., hatchlings from location 5). Nevertheless, hatchling remains recovered from the upper nesting horizon are remarkable in two respects: some of these were found closely associated, sometimes even inside the nests (hatchling locations 4 and 6; see also Grigorescu, 2010b), and preserve more complete specimens, including individuals with cranial and dental remains associated with postcrania (e.g., hatchling location 6, with hatchling H6; Grigorescu et al., 2010: Fig. 8) and others represented by articulated partial skeletons (hatchling location 5, with hatchlings H3/1, H3/2, H5; see also Grigorescu, 2010b: Fig. 4; Grigorescu et al., 2010: Fig. 8G; Venczel et al., 2015: Fig. 2E).

### 3.2.2 Eggs and eggshells

The eggs, found in the red mudstones underlying the coarse-grained channel deposits (i.e., Unit 2 as defined here; Fig. 5), were identified previously as *Megaloolithus cf. siruguei* (Grigorescu, 2010b; Grigorescu et al., 2010) and may in fact be definitively referable to that oogenus (Grigorescu, 2016), a common and widespread ootaxon in the Maastrichtian beds of western Europe (France, Spain; e.g., Garcia and Vianey-Liaud, 2001; Sellés et al., 2013). These eggs are characterized by a subspherical shape, with a larger diameter varying between

14–16 cm, a mean eggshell thickness of 2.30 mm, an outer surface covered by closely packed tubercles (compactituberculate ornamentation), a discretispherulitic microstructure, and a tubocanaliculate pore pattern (Grigorescu et al., 1994, 2010; Grigorescu, 2010b, 2016). They are usually arranged in closely spaced aggregations that were recognized as nests or clutches and described in some detail by Grigorescu et al. (2010: Fig. 6; an updated version of the original nest map, with the nests distributed into the two distinct nesting horizons, is presented in Fig.3); such nests might contain up to 14 eggs, but very often they preserve fewer than this maximum number of eggs (Figs. 3, 5E, F). Also, most eggs are preserved hatched, with only their lower halves more or less intact (Fig. 5C), and there are only a very few instances when quasi-complete (thus assumedly unhatched) eggs were discovered at Tuştea (Grigorescu et al., 1990, 1994, 2010). Besides the eggs arranged in nest structures, isolated eggshells also occur dispersed in the nesting locality, although their largest concentrations are usually present around or in close proximity to the nests.

Dinosaur hatchling bones are occasionally associated with eggs and nests, discovered mainly nearby (less than 50 cm apart) or even inside the nests (see above). Exceptionally, a few very poorly ossified and indeterminate (?embryonic) remains together with a well-preserved, diagnostic hadrosauroid dentary tooth have been found in the sedimentary fill of a broken and eroded egg belonging to nest 9 (Fig. 3; Grigorescu, 2010b, 2016; Grigorescu et al., 2010). As noted above, these hatchling remains are represented by often very well preserved cranial, dental, axial and appendicular elements, found both isolated and in association (occasionally even in life-time articulated position; Fig. 5D). Alternatively, hatchling remains also occur without being closely associated with nests, or, more rarely, even scattered in the sediments separating the nesting horizons (Figs. 2, 3). Remarkably, all diagnostic hatchling bones can be identified unambiguously as belonging to hadrosauroids, and were referred conservatively to the derived non-hadrosauroid hadrosauroid *Telmatosaurus*

*transsylvanicus* (e.g., Weishampel et al., 1991, 1993; Grigorescu, 1993, 2010b; Grigorescu et al., 1994, 2010; Grigorescu and Csiki, 2006), the only nominal hadrosauroid taxon recognized so far from the Transylvanian area.

Megaloolithid eggs are customarily considered to have been laid by titanosaurian sauropods (e.g., Mikhailov, 1997; Horner, 2000; Chiappe et al., 2005; García et al., 2015), a hypothesis that is supported by perinatal titanosaurian remains discovered associated with different megaloolithid ootaxa in Argentina (Chiappe et al., 1998, 2001, 2003, 2005) and India (Wilson et al., 2010). Accordingly, the Tuştea eggs were also referred to titanosaurian sauropods by Grigorescu et al. (1990), as well. Under such circumstances, the significance of the later recognized, unique field association between *Megaloolithus* cf. *siruguei* eggs and *Telmatosaurus* hatchlings has been considered highly controversial (e.g., Grigorescu, 2010b; Grigorescu et al., 2010; Weishampel and Jianu, 2011; Sellés, 2012), considered either to reflect the true biological identity of the egg-layers, or to be a simple taphonomic artefact. More recently, there appears to be a growing consensus that considers the presence of marked differences between *Megaloolithus siruguei* and definitively titanosaurian megaloolithid ootaxa such as *Megaloolithus patagonicus* (e.g., Jackson et al., 2008; Grellet-Tinner et al., 2012; Bravo and Gaete, 2015). It is thus possible that the Tuştea eggs might indeed belong to hadrosauroids, i.e., the *Megaloolithes* cf. *siruguei* eggs and hadrosauroid (possibly *Telmatosaurus*) hatchling remains associated in the Tuştea nesting locality represent the same taxon (Grigorescu, 2016, and see below).

#### 4. FOSSIL ASSEMBLAGE DATA AND TAXONOMIC ABUNDANCES

At least 21 taxa have been recognized from Tuştea (Table 1), including frogs, albanerpetontids, snakes, lizards, turtles, crocodyliforms, dinosaurs (theropods, ornithopods,



sauropods), pterosaurs and multituberculates, besides the dinosaur egg clutches (e.g., Grigorescu and Csiki 2002; Buffetaut et al., 2003; Weishampel et al., 2003; Grigorescu, 2005; Dalla Vecchia, 2006; Csiki et al., 2010a,b; Grigorescu et al., 2010a; Martin et al., 2010; Vasile and Csiki, 2010; Csiki-Sava et al., 2012; Venczel et al., 2015 and references therein). Presently the fossil vertebrate collection catalogue of the Laboratory of Paleontology, Department of Geology, University of Bucharest (LPB [FGGUB]) records 87 isolated teeth and 651 bones/bone fragments excavated at Tuştea, alongside 18 dinosaur nests, as well as over 200 different microvertebrate elements (see Supplementary information 2). From these, the palaeoecological signal of the microvertebrate component have been investigated in detail by Vasile and Csiki (2010), and thus our survey focuses on the taphonomic and palaeoecologic signal offered by the macrovertebrates (including here the hatchling dinosaur remains) and secondarily by the dinosaur nests and eggs (recently reviewed in detail by Grigorescu, 2016.).

#### 4.1 Number of identified specimens (NISP) and diversity data

*Method:* The NISP value includes the number of bones, teeth and fragments in the Tuştea vertebrate assemblage that were taxonomically identified at least at order level (Badgley, 1986a,b; Lyman, 2008).

*Results:* Of the vertebrate remains taken into account, 608 specimens were identified osteologically and taxonomically (NISP = 608). The taxonomic abundances based on NISP show that remains of the madtsoiid snake *Nidophis* and of the stem-testudine turtle *Kallokibotion* represent the most commonly identified elements in the Tuştea assemblage (Table 3). The dinosaur remains make up about 44% of the Tuştea collection (Fig. 6A), with the rhabdodontid ornithopod *Zalmoxes* being the most abundant taxon (Fig. 6B).

Crocodyliforms are the third most common group (about 3% NISP), whereas the amounts of fossil specimens assigned to other taxa (amphibians, lizards, pterosaurs and mammals) are approximately equal (each about 0.5–1% of NISP; Fig. 6A).

Approximately 50% of the identified dinosaur remains belong to *Zalmoxes*, with the hadrosauroid *Telmatosaurus* ranking as the second most common taxon (about 41% of dinosaur NISP) from Tuștea; theropods and sauropods are far less well represented (Fig. 6B). Dinosaurs also form the most diverse higher-level taxonomic grouping (with possibly nine different taxa; Table 1) in the Tuștea assemblage. Meanwhile, presumably aquatic or semiaquatic taxa (anurans, *Albanerpeton*, the crocodyliform *Allodaposuchus*, or the dortokid turtles) are only subordinately represented, with about 5%, according to the NISP. Most of the vertebrate fossils (93% of the NISP) were discovered in Unit 2 of the Tuștea succession, and here the C2 horizon is the richest one in fossils (Table 2).

*Comments:* The taxonomic diversity recorded according to the NISP is higher in the different horizons of Unit 2 (MO1, C1, MO2, C2, MO3, or C3) than in the lower part of the Tuștea section (levels MO4b, C4, MO5, C5), but this might come partly as a consequence of the fact that the excavation was focused on the upper part (Unit 2) of the locality, and fewer specimens were collected from the lower Unit 1, especially in the later part of the quarrying period (see above). The MO3 horizon contains only turtle plate fragments, but otherwise the vertebrate assemblages recorded in other horizons of Unit 2 do not show significant changes in diversity: remains of all major vertebrate groups represented in this locality (turtles, crocodyliforms and dinosaurs) were present in all horizons (Table 2). Except for MO3, *Zalmoxes* remains are present in all horizons, whereas *Telmatosaurus* hatchling fossils are restricted to only three horizons (C1, MO2 and C2). Titanosaurians represent the rarest dinosaur taxon in the assemblage, with specimens found only in the MO1 horizon (Table 2). This abundance spectrum stands in stark contrast with that reported for the entire Hațeg Basin

by Csiki et al. (2010a), in which titanosaurs are ranked close second only to *Zalmoxes* in abundance, while *Telmatosaurus* and the theropods are approximately equally well represented, both being less common even than the advanced neosuchian *Allodaposuchus*. These differences in abundance rank might suggest some degree of habitat preference and habitat selectivity in *Telmatosaurus* for the environments represented by the Tuştea locality, that is, for the relatively drier, better drained floodplains reconstructed here according to the local sedimentology and paleosols (Bojar et al., 2005; Therrien, 2005) as well as to the palaeoecological signal derived from microvertebrates (Vasile and Csiki, 2010).

The unprecedentedly high NISP abundance of the snake remains in the Tuştea assemblage represents an overestimation of the original abundance of *Nidophis*, because this material includes 168 rib and vertebral elements (Table 3) that most likely belong to only one individual (Vasile and Csiki, 2010; Venczel et al., 2015). To a lesser extent, the high abundance of *Kallokibotion* represents another overestimation, due to the high preservation potential and easily diagnosable nature of the specimens (mainly plates), although the widespread presence of this taxon throughout the Tuştea succession suggests that at least several different individuals are certainly represented.

#### 4.2 Minimum number of individuals (MNI)

*Methods:* During the calculation of MNI, we first determined the minimum number of elements (MNE) for each taxon based on its referred skeletal elements, and then the greatest MNE value was defined as the MNI value for that taxon (White, 1953; Badgley, 1986a; Lyman, 1994; Moore and Norman, 2009; Botfalvai et al., 2015). The advantage of this method is that it minimizes the chance of the same element to be counted twice, but tends to ignore factors such as age and size of the individuals represented (Ringrose, 1993).

This calculation method was used separately for each individual horizon (MO1, C1, MO2, C2, MO3, C3 etc.), and thus MNI values for each taxon were defined for all horizons (Table 2). The successive mudstone/calcrete horizons reflect recurring depositional and pedogenic processes (see above and Fig. 4), indicating that the bones associated with different calcrete horizons were incorporated in the succession at different times (see Fig. 4B), and represent distinct individuals. Thus, for example, bones found at levels C1 (e.g., left femur LPB [FGGUB] R.1981) and C2 (e.g., right femur LPB [FGGUB] R.0248) most certainly do not belong to the same hadrosauroid hatchling individual due to the relatively long time span separating the development of two calcrete horizons. However, remains from the mudstone horizons might overlap with those from certain other mudstone or calcrete horizons (based on Fig. 4B), because there are no indications as to how many separate flooding/accretion events deposited the sediments from which one particular paleosol developed. Furthermore, the “A” horizons of the successive paleosol levels are completely missing through the Tuştea section (Therrien, 2005), so the boundaries between two successive pedogenetic sequences remain untraceable, with the “A” horizon of one particular paleosol overprinted by pedogenic features of the second paleosol that developed on top of it (Therrien, 2005). Based on the above-mentioned considerations, the MNI values associated with the different horizons cannot be considered as definitive, because the pedogenetic processes operating at the Tuştea site (Fig. 4B) made it potentially possible that skeletal elements belonging to the same individual were included in different paleosol horizons. For example, sediments from horizons MO6, C5 and the lower part of MO5 may have been all deposited during a single flood event (see Fig. 4B), so different bones in these different horizons might conceivably belong to only one individual, scattered during the flooding event throughout the deposited sediment column. In order to mitigate the effects of such mixing instances, we also examined the possibility of potential skeletal element matches between

specimens recorded from different succeeding horizons, aiming to estimate more realistic MNI values for each taxon.

*Results:* Based on the MNI calculation, at least 35 different vertebrate individuals were detected in the Tuştea assemblage (Table 3). The taxonomic abundances estimated based on MNI show that dinosaurs are still the most abundant group in the Tuştea assemblage (about 57% of MNI; Fig. 6C), dominated by *Zalmoxes* and the *Telmatosaurus* hatchlings (Fig. 6D). Turtles and crocodyliforms form the second most common groups (about 12–15% MNI), whereas all other taxa (anurans, albanerpetontids, lizards, snakes, pterosaurs, and mammals) are only represented by one individual each, based on the MNI calculations (Fig. 6C).

*Comments:* The distribution of MNI-derived taxonomic abundances shows a somewhat similar distribution to the one indicated by NISP (Fig. 6). Sedimentological and taphonomical investigations of the Tuştea locality suggest that the bones were deposited in a floodplain environment, where bone transport was probably not significant, based on the large hydraulic disparity between the majority of the bones and the enclosing sediment (Behrensmeyer, 1975; Gangloff and Fiorillo, 2009) as well as other taphonomical characters (see below). The co-occurrence of these circumstances – quiet floodplain environment characterized by fine-grained sediments, and the presence of several associated or articulated skeletal parts (e.g., Martin et al., 2010; Venczel et al., 2015) – documents the presence of a taphocoenosis where the probability of skeletal association is higher than normal (Badgley, 1986a; Lyman, 2008). Accordingly, the MNI-based frequency calculation may represent a more appropriate method to estimate realistic taxon frequencies and abundances in the Tuştea vertebrate assemblage (Badgley, 1986b).

It is conceivable that the MNI value estimated in the case of hadrosauroid hatchling material (MNI=5) is underrepresented, because associated hatchling remains discovered from

the C1 and C2 levels might represent different individuals, despite their commensurate size and lack of overlap between the skeletal elements recovered, features that form the basis of MNI calculations. This is also probable in the case of other vertebrate groups recorded at Tuştea, whose different remains occur in distinct levels of the locality. Nevertheless, applying a unitary method of MNI calculation for all the taxa discovered from Tuştea (see above) is essential, because this is the most important assumption in assessing taxon abundances in the fossil material (Lyman, 2008).

### 4.3 Skeletal representation and preservation mode in the Tuştea locality

Many of the bones analysed from our Tuştea sample (over 60%) are disarticulated, although well-preserved, associated (about 37% of the sample), or, more rarely, articulated (about 2%) skeletal parts were also discovered at this locality (Figs. 7, 8).

The associated remains (vertebrae and ribs) of the madtsoiid snake *Nidophis* were discovered in close association with a megaloolithid egg clutch (nest no. 17) from the C2 horizon; taphonomic and sedimentologic evidence suggests that this snake individual was buried autochthonously inside the nest, with at least a partially articulated skeleton (Venczel et al., 2015). Small-sized, disarticulated but associated skull elements of the derived neosuchian crocodyliform *Sabresuchus* (*'Theriosuchus'*) *sympiestodon* (Martin et al., 2010) were found in the MO2 level, about 30 cm below the conglomerate/mudstone contact.

But probably the most emblematic (and significant) associated and/or articulated remains from the Tuştea locality are the *Telmatosaurus* hatchlings (Grigorescu, 2010b; Grigorescu et al., 2010) that originate from the C1 and C2 horizons, associated with *in situ* egg material in what we interpreted here as superposed nesting horizons (see above). This co-occurrence between *Telmatosaurus* hatchlings and megaloolithid eggs was cited as key

evidence to support that the *Megaloolithus* cf. *siruguei* eggs from Tuştea were probably laid by the hadrosauroid *Telmatosaurus* (Grigorescu, 1993, 2005, 2010b; Weishampel et al., 1993; Grigorescu et al., 1994, 2010). The hatchling remains (NISP=70; MNI=5) mainly consist of elongated hindlimb bones, more rarely of vertebrae and a few skull elements; these are often preserved in association or even in articulated position close to each other (Figs. 5D, 8G), in the C1 and C2 nesting horizons (Grigorescu et al., 2010; see also above). In addition, associated skull remains of a *Telmatosaurus* adult or subadult are also known from the C2 level, including fragments of the dentary, maxilla, surangular and quadrate (LPB [FGGUB] R.1587–1589). Overall, this material indicates that at least the lower nesting horizon (C2 level) preserves several age groups of *Telmatosaurus*.

Unlike the non-hatchling *Telmatosaurus*, *Zalmoxes* is represented in the Tuştea assemblage by several partial skeletons (associated/articulated skull or appendicular elements; Fig. 8A, F, H), which were discovered at different levels (C3, MO2, C5). All these skeletons appear to represent subadult to adult specimens (Benton et al., 2010; Prondvai, 2014). Titanosaurian caudal vertebrae, haemaphysae and an articulated sacrum-iliac complex were found in the MO1 level, about 20 cm above the upper nesting horizon (C1); these specimens possibly represent an associated material and show that, albeit rare, titanosaurs were also present at the Tuştea locality (Csiki-Sava et al., 2012). Finally, associated forelimb elements (humerus, ulna, metacarpals, manual phalanges) of a theropod dinosaur, referred to the dromaeosaurid *Balaur* (Brusatte et al., 2013; LPB [FGGUB] R.1580–1585) were also discovered in the MO1 horizon.

Based on taphonomical characters and bone size differences, the associated or articulated bone material from Tuştea supports the presence of at least 14 partial skeletons at this locality, represented by a madtsoiid snake (*Nidophis*), an advanced neosuchiancrocodyliform (*Sabresuchus*), and numerous dinosaurs – *Zalmoxes*,

*Telmatosaurus*, *Balaur* and an indeterminate titanosaurian (e.g., Martin et al., 2010; Csiki et al., 2010b; Grigorescu et al., 2010; Csiki-Sava et al., 2012; Brusatte et al., 2013; Venczel et al., 2015).

All Voorhies Groups are represented in the Tuştea assemblage, with elements belonging to Groups I (69%; ribs and vertebrae) and II (20%; limb bones) being dominant, while skull and mandible elements (Group III) make up only about 11% of the macrovertebrate sample (Fig. 9). Elements of the axial skeleton (mostly vertebrae) are the most abundant remains (about 31% NISP) in the bone assemblage, followed by plate-like turtle shell fragments and by appendicular skeletal elements. The appendicular elements are the ones most frequently preserved in associated or articulated position (about 50% of the associated specimens), followed by cranial elements (30%; Fig. 8F, H) and vertebrae (20%). Bones are usually lying more or less along the bedding plane, but there is no sign of preferential orientation of the long bones (Grigorescu and Csiki, 2002); nevertheless, obliquely or even vertically oriented specimens are also present, mostly in the mudstone levels (see Venczel et al., 2015: Fig. 2C).

#### 4.3.1 Calculation of recovery rate and total skeletal completeness

*Method:* The recovery rate indicates the percentage (relative proportion) of a given element in the population of MNI (Holtz and Barberena, 1994; Gangloff and Fiorillo, 2010). Recovery rate of different skeletal elements (limb bones and vertebrae; n=110; Table 4) was calculated in the Tuştea assemblage using the following equation:

$$RR (\%) = [(n \times FR) / MNI] \times 100, \text{ where}$$

RR (%) represents the recovery rate;

n, the number of elements in the collection;



FR, the factor of representativeness (a function of the number a specific bone is present in a complete skeleton); and

MNI, the minimum number of individuals.

Obviously, the value of FR is 0.5 in the case of the paired limb bones, such as the femur or the humerus, because there are two femora or humeri in each individual skeleton. Comparatively, elements such as vertebrae have very low FR values, since the number of these elements in the skeleton is high. Unfortunately, no complete skeletons are known for any of the taxa represented at Tuştea, so the exact number of vertebrae of these animals remains unknown. Based on published data, we estimate the number of vertebrae as being 87 for hadrosauroids, 78 for basal iguanodontians (i.e., *Zalmoxes*), 82 for titanosaurians, and 73 for theropods (Weishampel et al., 2004; Britt et al., 2009; Gangloff and Fiorillo, 2010; Botfalvai et al., 2015). In our analyses, we used a calculated arithmetic mean for  $FR_{\text{vertebrae}}$  which is 0.012. Calculation of skeletal completeness was done only for dinosaurs, as the other major taxa represented at Tuştea (turtles, crocodyliforms, pterosaurs, let alone the microvertebrate amphibians, squamates and mammals) do not offer enough data (i.e., skeletal elements) for this method to be implemented.

A calculation of total skeletal completeness (%TC) was also conducted on five dinosaurian categories (i.e., *Zalmoxes*, adult and hatchling *Telmatosaurus*, titanosaurian, and *Balaur*; Table 5), using the following equation (Shotwell, 1955; Lyman, 1994; Britt et al., 2009; Botfalvai et al., 2015):

$$\%TC = (\sum A_t \times 100) / (\sum E_t \times MNI), \text{ where}$$

$\%TC_t$  represents the percentage of total skeletal completeness of taxon t;

$\sum A_t$ , the actual number of skeletal elements from Tuştea referred to taxon t;

$\sum E_t$ , the expected number of elements in a complete skeleton of taxon t; and

MNI, the minimum number of individuals.

*Results:* The limb bones have a much higher recovery rate (average  $RR_{\text{limb}}=25\%$ ) than the vertebrae (average  $RR_{\text{vertebrae}}=3\%$ ), for most taxa except for the titanosaur material where limb bones are absent (Table 4). The limb bone recovery rate is highest in the case of the *Telmatosaurus* hatchlings and the *Zalmoxes* remains (Table 4). The total skeletal completeness of the five dinosaur categories considered varies from 2% (non-hatchling *Telmatosaurus* remains) to 6% (titanosaurs, *Telmatosaurus* hatchlings), whereas *Zalmoxes* presents about 5% of the expected elements (Table 5).

*Comments:* Paradoxically, in the dinosaur assemblage from Tuştea the vertebrae show a lower recovery rate than the limb bones (Table 4), which is a surprising result given that normally there is a reverse ratio between these indices, corresponding to the number of elements in each of these two categories in a complete skeleton, i.e., the preservation rate of vertebrae should be statistically higher than that of limb bones, simply because one dinosaur skeleton has only two femora but more than 80 vertebrae (e.g., Gangloff and Fiorillo, 2010). Accordingly, the large number of vertebrae in a skeleton should increase their chance of preservation, even though they are smaller in size and more vulnerable to physical or chemical destructive effects (Holtz and Barberena, 1994; Gangloff and Fiorillo, 2010). The observed lower recovery rate of vertebrae at Tuştea might be a by-product of any combination of the following factors: (1) small, fragmentary vertebrae might have been overlooked during excavation, whereas even fragmentary limb bones would have been collected preferentially due to their easily available anatomical and taxonomical significance (e.g., Holtz and Barberena, 1994); (2) vertebrae are more sensitive to destructive environmental effects (temperature fluctuations, weathering, etc.) than are limb bones, since vertebrae are more porous, less dense, and are thus more rapidly degraded on the soil surface (Behrensmeyer, 1975); (3) there are several lines of evidence showing that the relatively small and porous vertebrae can be transported much easier than the heavier and more

compact limb bones by water currents, and thus the vertebrae of disarticulated skeletons can be scattered over a larger area causing a depletion in these skeletal elements when compared to limb bones that are not easily transported (e.g. Voorhies, 1969; Dodson, 1973; Behrensmeyer, 1975; Fiorillo, 1991; Holz and Barberena, 1994; Lucas et al., 2010).

The very low values of total skeletal completeness for the five dinosaur groups considered indicate that only a small portion of the original skeletons was preserved and/or collected from the Tuştea locality (e.g., Britt et al., 2009; Botfalvai et al., 2015). The very low values of total skeletal completeness (Table 5) are not unexpected in an environment that is characterized by low sedimentation rates, because large part of the carcasses can be destroyed on the soil surface within a relatively short time interval (i.e., a few years) due to biological, chemical and/or physical destructive agents (e.g., Behrensmeyer, 1978, 1982; Bown and Kraus, 1981; Evans et al., 2015). Indeed, Behrensmeyer (1982) mentioned that only about 5% of the total yearly bone contribution would be actually buried into a temporarily stable land subsurface characterized by a low sedimentation rate, as was also reconstructed for the Tuştea palaeoenvironment (see above).

Alternatively, it is also conceivable that the relatively low percentage of total skeletal completeness indicates transportation of the disarticulated skeletal parts by fluvial action before burial, large portions of the individual skeleton being winnowed during such transportation (e.g., Britt et al., 2009; Lucas et al., 2010). However, the apparent lack of preferred orientation of long bones, the quiet floodplain palaeoenvironment suggested by the fine-grained sediments with several calcrete horizons, the presence of associated skeletal parts, and above all the observed taphonomical characters (see below) convergently indicate that the bone material was deposited without significant fluvial transport, and thus such a sorting mechanism did not play a significant role during bone deposition.

#### 4.3.2 Bone representation by size

*Method:* The bones and bone fragments from the sample were divided into three size categories (small: <5 cm; medium: 5–10 cm; large: 10–50 cm) according to their maximum dimension. We also estimated a maximum length for the incomplete bones for their pre-breakage state (based on Weishampel et al., 1993, 2003; Dalla Vecchia, 2006) and grouped them into the same size categories as the complete ones. Furthermore, we checked whether any one of these size categories is frequently underrepresented relative to its expected value, based on their frequency distribution in the skeletons of the different taxa present in the sample. In order to decide which size category of skeletal elements is over- or underrepresented in the assemblage, we used the approach of Britt et al. (2009): an element is overrepresented in the fossil sample if its  $\%R_T$  (recovered element percentage of a certain skeletal element belonging to taxon  $t$ ) exceeds the  $\%TC_t$  (percentage of total skeletal completeness of taxon  $t$ ) in the dataset (Table 5). Calculation of size bias was not done for the microvertebrate assemblage (amphibians, squamates and mammals), because these remains were collected using a markedly different method (screen-washing from limited amounts of sediment; Vasile and Csiki, 2010), and most probably underwent very different sorting processes during their accumulation.

*Results:* Maximum bone dimension varies between 0.3 cm and 36 cm in the Tuştea vertebrate assemblage (see Supplementary Information 2). About 73% of the sample is represented by elements smaller than 5 cm, and only 8% of the bones are larger than 10 cm in maximum dimension (Fig. 10A). About half of the bones were smaller than 5 cm even in their original, pre-breakage state, whereas the frequencies of medium-sized (5–10 cm) and large (10–50 cm) bones have similar values (about 20%; Fig. 10B). Most size categories are significantly underrepresented compared with the expected value based on total skeletal

completeness calculated in Table 5 - about 75% of the observed material shows a %R value that is lower than its corresponding %TC. However, the elements of the large size category (maximum dimension of the complete or reconstructed element between 10–50 cm) are frequently overrepresented in the Tuştea assemblage (for about 40% of the large bones, %R exceeds %TC, based on Table 5), regardless of their taxonomic status (Fig. 10C).

*Comments:* Overwhelmingly, the maximum dimension of both the complete and of the reconstructed skeletal elements is less than 10 cm, which suggests that the dominance of small bones in the Tuştea assemblage is not entirely the result of *in situ* fragmentation and destruction of (previously) larger bones (Fig 10B). To the contrary, the dominance of small elements in the Tuştea bone assemblage indicates that relatively small bones (<10 cm) accumulated and were buried from the start in greater numbers than larger ones, probably because the skeletons of the taxa represented in the Tuştea sample contained greater amounts of small (less than 10 cm) bones than larger (> 10 cm) ones – at least in part also as a consequence of their life-time small, often dwarfed body sizes (e.g., Csiki and Grigorescu, 1998; Weishampel et al., 1993, 2003; Jianu and Weishampel, 1999; Benton et al., 2010; Stein et al., 2010).

However, when comparing the frequencies of size categories represented in the Tuştea sample with their expected values in a complete skeleton of the different taxa, the distribution of size categories indicates that elements of the large-size category are frequently (about 40% of these) overrepresented whereas the small and medium-sized (<10 cm) elements are even more frequently underrepresented (about 70%) in the Tuştea assemblage, regardless of their taxonomic status (Fig. 10C). The underrepresentation of smaller bones is not unexpected, because there are evidences for taphonomic size bias against small-bodied taxa in most vertebrate assemblages (e.g., Behrensmeyer et al., 1979; Behrensmeyer, 1991; Oindo et al., 2001; Britt et al., 2009; Brown et al., 2013; Evans et al., 2013). The low

sediment accumulation rate that characterized the Tuştea locality was not favourable for the preservation of the smaller bones, because these can be destroyed faster while exposed on the soil surface than are the larger ones (Behrensmeyer, 1978; Behrensmeyer et al., 1979; Brown et al., 2013), resulting in their underrepresentation compared to their expected frequency value. On the other hand, the underrepresentation of smaller bones theoretically could indicate that these skeletal parts were winnowed from the assemblage by weak water currents, but such a scenario is less well supported by the available sedimentological and taphonomical evidence (see below).

## 5. TAPHONOMIC FEATURES OF THE BONE ASSEMBLAGE

Bones and teeth are exposed post-mortem to a wide variety of physical, chemical or biological destructive agents and processes that all leave modifications on the bones surface (Fig. 8). Different processes result in different types of modification on the bones, and these modifications are process-specific, distinguishable from each other based on recent field observations and experimental studies. Thus, bone modifications offer important information about the origins of bonebed assemblages, and play a critical role in a more profound understanding of their taphonomical history (e.g., Haynes, 1988; Behrensmeyer, 1991; Lyman, 1994; Fiorillo et al., 2000; Gates, 2005; Eberth et al., 2007; Mukherjee and Ray, 2012; Bertog et al., 2014; Smith et al., 2015).

### 5.1 Abrasion and weathering

*Method:* Abrasion is an indicator of the interaction between sediment particles and bones, interaction that leads to physical grinding and polishing of the edges and/or surface of

vertebrate fossils (Behrensmeyer, 1982, 1991; Fernández-Jalvo and Andrews, 2003; Thompson et al., 2011). We examined the bones from our sample for such modifications, and divided them into two categories: 1) unabraded bones; and 2) abraded bones. Weathering, on the other hand, is an indicator of the physical-chemical interaction between temperature fluctuations, moisture and/or other natural destructive agents and the bone surface, and therefore indirectly indicates the period of surface exposure of bones before burial (Behrensmeyer, 1978, 1991; Lyman and Fox, 1989). Based on our assessments of their weathering stage, we divided the macrovertebrate remains from the Tuştea assemblage into two basic categories: 1) unweathered bones; and 2) weathered bones. Teeth and microvertebrate remains (amphibians, squamates and mammals) were excluded from these analyses because of their strikingly different taphonomical history and/or resilience to abrasion and weathering (Dodson, 1973; Behrensmeyer et al., 1979; Argast et al., 1987).

*Results:* About 80% of the studied sample shows no evidence of abrasion (Fig. 8A, C, F, H, I), and only 20% of the specimens were abraded to some extent (Fig. 11A). Similarly, the vast majority of the bones (93%) present no evidence of more than minor weathering, with only 7% of the specimens showing flaking associated with cracks (Figs. 10A, B, 11B). The material referred to *Kallokibotion* shows the highest abrasion rate (about 20% of the elements referred to this taxon are abraded), whereas the *Telmatosaurus* hatchling remains were quasi-completely unabraded and unweathered (Figs. 5D, 8G; see Supplementary Information 2). The amount of weathered bones was less than 10% in each of the taxa considered.

*Comments:* The observed low abrasion rate probably indicates that interaction between sediment particles and bones was not significant (e.g., Fernández-Jalvo and Andrews, 2003). The high frequency of unabraded bones and the apparent lack of preferred orientation of long bones (Grigorescu and Csiki, 2002) both suggest that fluvial transport of

the bone material into the site was not substantial before and during its burial. The low incidence rate of weathering, together with the presence of several associated and articulated partial skeletons, suggest that most of the bones in the assemblage were buried relatively rapidly after death (probably within 1–2 years; Behrensmeyer, 1978) and were not exposed to significant destructive physical and/or chemical agents and processes on the surface or within the soil zone. The low rates of both abrasion and weathering lend support to the idea that the Tuştea death assemblage was probably buried in its living environment, with a minimum of physical post-mortem disturbance, and thus it represents a largely (par)autochthonous assemblage (e.g., Johnson, 1960; Kidwell et al., 1986; Behrensmeyer, 1991). This pattern stands in stark contrast with the very advanced weathering and (especially) abrasion presented by the very few vertebrate elements recovered from the overlying fluvial conglomerate-sandstone (Fig. 8D), in accordance with the entirely different sedimentary setting and processes reconstructed for this unit.

## 5.2 Fracture patterns of skeletal elements

*Methods:* We have also surveyed the macrovertebrate material from Tuştea (except the turtle plate elements) for breakage/fracture incidence and pattern. We distinguished two categories of fracture in the Tuştea “long bone” assemblage (e.g. limb bones): 1) “pre-fossilization” breakage, with a fracture surface that is highly uneven and oriented mainly oblique or parallel to the longitudinal axis of the element (Fig. 8B, C, E); and 2) “fossildiagenetic” breakage, with a smooth and transverse fracture surface oriented quasi-perpendicular to the long axis of the bone (Fig. 8A; Haynes, 1983; Pereda-Suberbiola et al., 2000; Ryan et al., 2001; Britt et al., 2009; Gangloff and Fiorillo, 2010). The presence or absence of epiphyses on limb bones was also recorded, and bones were grouped accordingly



into the following categories: 1) both epiphyses present (Fig. 8A), 2) only one epiphysis present, and 3) both epiphyses missing (Fig. 8B, C, E).

*Results:* Most bones in the assemblage were broken, and only about 20% of the material is quasi-complete (unbroken; Figs. 8A, F, I, 12A). About 36% of the limb bones are complete (Figs. 8A, 12B), and here frequency of the two different fracture types (“pre-fossilization” and “fossildiagenetic”) was found to be almost equal (30%). About 80% of the limb bones preserve the epiphysis on at least one end (Fig. 12C).

*Comments:* The distribution of bones with fossildiagenetic breakage type is probably strongly biased in the Tuştea assemblage, because 64% of the bones with smooth transverse breakage are represented by the *Telmatosaurus* hatchling limb bone material (Fig. 5D), whereas the biostratigraphic breakage is considerably more common in other skeletal elements (i.e., non-hatchling remains; Fig. 8B, C, E). The high frequency of the transverse breakage type in the hatchling limb bone material at the Tuştea locality is largely due to the small and more fragile nature of the fossilized hatchling bones, that can be easily broken during the excavation or in the preparation phase, thus increasing the number of fossildiagenetic breakage types in the collection (Fig. 5D; see Grigorescu et al., 2010: Fig. 8E).

The high number of broken bones (80% of the material) suggests that the fossil assemblage suffered significant mechanical fragmentation before burial (Fig. 12A). This stands in apparent stark contrast with our previous observations that suggest very low to no amounts of weathering (that is, absence of significant subaerial fragmentation through cracking and flaking) and of abrasion (that is, lack of transport, a process that is usually instrumental in skeletal dispersal and bone scattering, and one that can also contribute to fragmenting the bones). Since no important physical or chemical agents appear to be responsible for the high fragmentation rate observed, biological agents like trampling were probably a significant destructive factor.

Trampling might have caused high degrees of skeletal fragmentation in the vertebrate remains from Tuştea, because the low sedimentation rate and the protracted pedogenesis hindered a very rapid burial of the bones (e.g., Bojar et al., 2005; Therrien 2005), and thus most skeletal parts were exposed to trampling by other organisms that passed through the floodplain (e.g., Haynes, 1983; Olsen and Shipman, 1988; Gates, 2005; Britt et al., 2009; Domínguez-Rodrigo et al., 2009; Evans et al., 2015). Occasionally, bones were discovered embedded in vertical position (see Venczel et al., 2015: Fig. 2C), and these are usually interpreted as being pressed into the still soft substrate due to trampling by other animals (e.g., Mathews et al., 2009). In other instances, fragments of the same skeletal element were found closely associated but displaced at an angle and with irregular, jagged transverse breakage surfaces that match each other loosely, suggesting the presence of *in-situ* preburial fragmentation most probably induced by a biotic agent (Csiki et al., 2010a). Nevertheless, we were unable to identify direct evidence for trampling (in the form of shallow, sub-parallel grooves on the surface of bones; e.g., Fiorillo, 1989) in the Tuştea vertebrate material, but trampling may have been nevertheless occurred at the site without leaving direct record because of the quasi-absence of sand in the substrate (e.g., Fiorillo et al., 2000).

Rare occurrences of tooth marks on disarticulated elements (Fig. 8I) and the number of shed theropod and crocodyliform teeth suggest that bone breakage and fragmentation may have, in part, also resulted from scavenging (e.g., Barrett and Rayfield, 2006; Jennings and Hasiotis, 2006; Hone et al., 2010; Botfalvai et al., 2014; Evans et al., 2015). However, carnivore activity probably did not play a significant role in the fragmentation of the Tuştea vertebrate remains, just as in the case of other Mesozoic vertebrate assemblages, because theropod teeth were appropriate for cutting flesh (Fiorillo, 1991; Ryan et al., 2001; Farlow and Holtz, 2002; D'Amore and Blumenschine, 2009) while there is only very scanty evidence that they could also crush and fragment bones (Chin et al., 1998; Hone and Rauhut, 2010).

Nevertheless, it must be emphasized that despite the high fragmentation rate of the Tuştea vertebrate assemblage, remarkable preservation of even very fragile bones is often recorded (e.g., rhabdodontid skull bones with delicate processes or paper-thin ridges; Fig. 8F, H; see also Venczel et al., 2015: Fig. 2B).

## 6. DISCUSSION

The Tuştea locality can be classified as a succession of high diversity, multitaxic (multidominant) microfossil bonebeds, because it has yielded remains of 21 vertebrate taxa (Table 1), a figure that accounts for 60% of the known formational palaeobiodiversity (Therrien et al., 2005; Benton et al., 2010; Csiki-Sava et al., 2016), and because 80% of the identifiable specimens (NISP) are smaller than 5 cm in maximum dimension (Wood et al., 1988; Eberth et al., 2007). Furthermore, according to the definition given by Behrensmeyer et al. (1979), about 50% of the specimens identified in the Tuştea assemblage (cumulative NISP of amphibians, squamates, *Telmatosaurus* hatchlings, and kogaionids) can be interpreted as microvertebrates, because their estimated body weight was less than 1 kg.

### 6.1 Taxon distribution and palaeoecological significance

Dinosaur bones are the most abundant elements at the Tuştea locality, both in the micro- (Vasile and Csiki, 2010) and the macrofossil assemblages (NISP=61% and MNI=64%, respectively), indicating that remains of terrestrial animals dominate the local fossil assemblage. However, the presence of aquatic and/or semiaquatic taxa (e.g., amphibians, *Allodaposuchus*) suggests that aquatic habitats were also present near the site when and where the Tuştea taphocoenosis accumulated and was eventually entombed.

Sedimentological data concurrently suggest that the Tuştea depositional area was situated on the floodplain, an environment subjected to frequent flooding (Bojar et al., 2005, 2010b; Therrien, 2005). These periodic floods, which brought onto the floodplain the fine-grained sediments that form today the fossiliferous mudstone units, may have also delivered/brought remains of aquatic or semiaquatic animals and deposited them alongside the terrestrial ones. The most frequent skeletal elements, beside those pertaining to dinosaurs, are *Kallokibotion* shell fragments, but, unfortunately, the precise ecological preferences (more aquatic or more terrestrial) of this primitive turtle remain poorly understood (Rabi et al., 2013).

Three higher-level taxa of dinosaurs dominate the vertebrate assemblage - ornithopods, theropods and sauropods. Of these, ornithopod elements (belonging to both the rhabdodontid *Zalmoxes* and the hadrosauroid *Telmatosaurus*) form more than 90% of the identified dinosaur remains, and represent 75% of the detectable dinosaur individuals based on our MNI calculation (Fig. 6B, D).

*Zalmoxes* is the most abundant dinosaur taxon in the Tuştea assemblage, representing about half of dinosaur NISP (Fig. 6B). It was also discovered in the largest number of different horizons (=bonebeds) in the locality (C1-C3, C5, MO1-MO2, MO4; Table 2), and is represented by isolated, associated (e.g., LPB [FGGUB] R.1629 and R.1591, *Zalmoxes* basioccipital and exoccipital, respectively; Fig. 8G), and even articulated (LPB [FGGUB] R.1616, Fig. 8F; LPB [FGGUB] R.1608 – Venczel et al., 2015: Fig. 2F) remains.

*Telmatosaurus* is the second most abundant dinosaur in the Tuştea collection (Fig. 6B), and is remarkable in that it includes both hatchling and non-hatchling material (Weishampel et al., 1993; Grigorescu and Csiki, 2006; Grigorescu, 2010b; Grigorescu et al., 2010). By far the largest part of the *Telmatosaurus* material is represented by hatchling skeletons (Table 3). Only about 24% of the *Telmatosaurus* NISP is derived from non-hatchling (adult/subadult) individuals, while the ratio of hatchling and non-hatchling

individuals is about 2:1, based on the MNI calculation; this contrast between NISP and MNI values illustrates the largely associated/articulated nature of the hatchling elements, compared to the mainly isolated non-hatchling hadrosauroid remains. Most hatchling remains are restricted to the two calcrete horizons (C1 and C2; Fig. 2 and Table 2) marking the nesting horizons identified here, where they were usually found associated with egg clutches (see above), whereas only a few limb bones (e.g., the isolated femur LPB [FGGUB] R.2319 and tibia LPB [FGGUB] R.2378) were discovered in the MO2 horizon, although only about 10 cm above the C2 level and thus still closely associated with the lower nesting horizon. On the other hand, the remains of adult/subadult *Telmatosaurus* individuals originate from several different bonebed levels of the Tuştea locality (C2-C4, MO1-MO2), and while on occasion they were discovered in the same layer (C2) with the hatchling bones (e.g., LPB [FGGUB] R.1586–1590; Table 2), these are also present at levels not closely associated with the nesting horizons.

The presence of non-hatchling *Telmatosaurus* remains in different paleosol horizons suggests that this taxon was constantly present in the floodplain area during the genesis of the Tuştea succession. Meanwhile, the *Telmatosaurus* hatchling material is restricted largely to the two bonebed levels also identified as nesting horizons, indicating their limited and apparently non-random occurrence during the same time period. The co-occurrence of different age classes of *Telmatosaurus* associated with the lower nesting horizon (C2 level), including several different ontogenetic stages of the perinatals themselves (Grigorescu and Csiki, 2006; Grigorescu, 2010b) suggests that various groups of *Telmatosaurus* were present in the same habitat, closely associated with the nesting ground (see below).

Titanosaurian sauropods are represented by only one individual based on MNI calculation (Table 3), and its associated material was found in the MO1 horizon (~20 cm above the C1 nesting horizon; Table 2). This occurrence shows that despite earlier comments

suggesting the contrary (Grigorescu, 2010b; Grigorescu et al., 2010), titanosaurs were also present in the palaeoenvironments represented by the Tuştea nesting locality (Csiki-Sava et al., 2012). The rarity of titanosaurian material and its restricted occurrence in only one horizon of the Tuştea locality (MO1) suggests that titanosaurs were probably members of a community living in different habitats, but on rare occasions they entered the nesting area itself, even if not precisely during active incubation periods. Identification of titanosaurs at Tuştea potentially has a great significance, because there is a quasi-general consensus that the *Megaloolithus* oogenus reported from this locality by Grigorescu(2010b, 2016) and Grigorescu et al. (2010) belongs to titanosaurian dinosaurs (see below).

Three to four (but possibly only as few as two) taxa of theropod dinosaurs were detected in the Tuştea collection, mainly based on isolated teeth, although postcranial elements were also discovered at this locality. These include the associated forelimb material of the dromaeosaurid *Balaur* (Brusatte et al., 2013; also interpreted as a possible aberrant flightless bird, Cau et al., 2015) from the MO1 horizon (Table 2), as well as a proximal limb bone fragment that was very tentatively referred to *Elopteryx* based primarily on the peculiar wrinkled surface texture of the bone (Andrews, 1913; Le Loeuff et al., 1992), a feature that, however, was also reported later to occur in *Balaur* (Csiki et al., 2010b; Brusatte et al., 2013). It is thus conceivable that the velociraptorine teeth (e.g., LPB [FGGUB] R.1429), the forelimb referred to *Balaur* and the hindlimb fragment referred tentatively to *Elopteryx* in fact represent the same taxon, one that is morphologically close to the dromaeosaurid paravialians. The well-preserved and associated theropod forelimb material indicates its parautochthonous nature in the Tuştea assemblage, because the lightly built limb bones of theropods can be quickly destroyed or become unrecognizable due to weathering, long-term transport or reworking (White et al., 1998; Eberth et al., 2010).

To conclude, it appears likely that the above-mentioned taxon assemblage reflects closely the composition of the local life assemblage (palaeobiocoenosis), especially since the Tuştea taphocoenosis represents a paleosol concentration that apparently resulted from attritional mortalities instead of being a mass death assemblage (Behrensmeyer, 1982), and include mainly autochthonous-parautochthonous elements. It is known that paleosol-related taphocoenoses offer a material that is more appropriate for palaeoecological reconstructions than those taphocoenoses where the fossil remains were concentrated by fluvial transport (e.g., Bown and Kraus, 1981; Behrensmeyer, 1982; see also below).

## **6.2 Discussion and interpretation of taphonomic features of the Tuştea assemblage**

Many bones (over 60%) from the Tuştea taphocoenosis are disarticulated, and it can be thus interpreted as accumulation of isolated and dispersed remains (e.g., Hill and Behrensmeyer, 1984; Behrensmeyer, 1991; McNamara et al., 2012). However, it should be mentioned that due to the excavation methods employed during the 23 years of quarrying, several skeletal elements were collected without precise bone-mapping and thus there is a chance that association of skeletal elements remained undetectable in many cases. In our analyses, we followed the conservative approach of Badgley (1986a), who considered that as long as there is no positive evidence for the probability of skeletal association among the vertebrate remains, all elements should be regarded as separate and isolated skeletal parts. Nevertheless, the sedimentological (well-drained floodplain environment) and taphonomical (limited transport) characters of the Tuştea locality suggest that the number of associated skeletal parts is probably underestimated in the available sample, due to collecting bias. The simultaneous presence of isolated bones and associated partial skeletons in the Tuştea

assemblage shows that degree of decomposition and skeletal scattering recorded in this thanatocoenosis was not homogenous, and at least part of the recovered skeletal material was buried while still in partial articulation – a distinct possibility given the attritional nature of the accumulation that preceded the periodic flooding events and subsequent burial.

Most bones show little to no sign of weathering and abrasion, but a very high percentage of them are broken (Figs. 11, 12). The low abrasion rate and the apparent lack of preferred orientation in long bones (Grigorescu and Csiki, 2002) indicate that fluvial transport of the bone material was not significant. The reduced weathering, together with the presence of an important proportion of associated and articulated material, suggests that a large part of the bone assemblage was buried rapidly after death (within 1-2 years; Behrensmeyer, 1978). Meanwhile, a high fragmentation rate (the majority of the bones are broken), together with the very low values of skeletal completeness (ranging from 2% to 6% in the five dinosaur groups considered; Table 5), which demonstrate that a large proportion of the skeletons are missing, suggest that biological agents promoting carcass destruction and/or scattering were present and very active.

The sedimentological data (presence of well-drained, red coloured paleosols) and the overall rarity of aquatic-semiaquatic taxa (see also Vasile and Csiki, 2010) indicate that the palaeoenvironment in which these carcasses originally accumulated and decayed was relatively dry, well-drained and subaerially exposed for long periods of time. In such circumstances, the carcasses started breaking down immediately after death (Davis and Briggs, 1998; Carter et al., 2007). Additionally scavengers, both vertebrate (e.g., theropods and crocodyliforms) and invertebrate (e.g., insect larvae), could have contributed to a rapid decomposition, disarticulation and scattering of the vertebrate carcasses (Weigelt, 1989; Hill and Behrensmeyer, 1984; Oliver and Graham, 1994; Davis and Briggs, 1998; Brand et al., 2003; Carter et al., 2007; Cameron and Oxenham, 2012). Indeed, taphonomical investigation



of the Tuştea assemblage pointed out a high degree of biostratinomic modifications, including intense carcass disarticulation, high incidence of biostratinomic breakage, presence of tooth-marked elements documenting predation or scavenger activity (Csiki et al., 2010a; Fig. 8D), all these associated with a minimum amount of abrasion.

Taken together, these biostratinomic modification features and the sedimentological evidence (low sedimentation rate, long-term subaerial exposure and pedogenesis) indicate that carcasses were exposed for a time period to biological, physical and (less intensively) chemical destructive effects on the floodplain, where they rotted, were scavenged and trampled. Under such a scenario, a large proportion of the skeletons can be destroyed during small amounts of time spent on the soil surface, without any reworking or fluvial transport (e.g., Dodson et al., 1980; Evans et al., 2015). Furthermore, bone burial and preservation in such floodplain environments is not always dependant on annual flooding and active sediment build-up, because insect and root activity or clay shrinkage operates even in a non-aggrading situation, resulting in significant bone burial within the soil, especially in the case of the smaller-sized skeletal elements (Bown and Kraus, 1981; Behrensmeyer, 1982).

The fluvial transport of the vertebrates at Tuştea was not significant, as shown by the absence of significant abrasion and lack of evidence for preferential orientation of long bones (Grigorescu and Csiki, 2002). Furthermore, the sedimentary matrix of the bonebeds is fine-grained, dominated by the mud and silt fraction (Bojar et al., 2005), somost of the bones from the Tuştea assemblage are not in hydraulic equilibrium with the energy of the current that deposited these sediments (Behrensmeyer, 1975; Fiorillo et al., 2010; Gangloff and Fiorillo, 2010). However, the presence of aquatic taxa, poor geochemical differentiation of the pedogenic horizons (Therrien, 2005), and geochemical evidence regarding the presence of an early successional ground vegetation at the Tuştea locality (Grigorescu and Csiki, 2002) suggest that it was situated not far from the active channel, in an area where sediment

accumulation could have occurred through crevasse splay deposits. The periodical flooding events covered and buried the bones lying on the surface with sediments, and may have had sufficient energy to allow a short-distance transport of low-density bones. Such a transport is also suggested by the observation that in the dinosaur assemblage vertebrae have lower recovery rates (average  $RR_{\text{vertebra}}$  is ~3%; Table 4) than the limb bone group (average  $RR_{\text{limb}}$  is ~25%), consistent with the idea that the easiest-transported elements of the disarticulated skeletons were scattered and eventually completely removed, probably at least in part by fluvial action (Holz and Barberena, 1994; Gangloff and Fiorillo, 2010; Lucas et al., 2010). There is evidence showing that the relatively small and porous vertebrae can be transported by water current much easier than the heavier and more compact limb bones, and thus the vertebrae of disarticulated skeletons can be dispersed over a large area, causing a relative loss of these elements when compared to limb bones which are not easily transported (e.g. Voorhies, 1969; Dodson, 1973; Behrensmeyer, 1975; Dodson et al., 1980; Fiorillo, 1991; Holz and Barberena, 1994). We note that according to Holz and Barberena (1994) the large number of vertebrae present in a skeleton increases the chance of their preservation even though they are smaller in size and more vulnerable to the activity of physical or chemical destructive agents. The preservation rate of vertebrae should be expected thus to be statistically higher than it is for limb bones (e.g., Gangloff and Fiorillo, 2010). The Tuştea assemblage shows a reverse distribution of these values, as limb bones (femur, tibia, fibula, humerus, radius and ulna) have a higher recovery rate than the vertebrae, and such a counter-intuitive distribution raises the possibility that the low-density bones were sorted out and removed from the thanatocoenosis by transport, during periodic intense rainfall events.

Nevertheless, it should be taken into account that several other causes (collecting bias, higher sensitivity of vertebrae to temperature fluctuations and weathering compared to limb bones, etc.) can lead to the relative underrepresentation of vertebrae in a thanatocoenosis, and

that fluvial sorting represents but one of the possible explanations. Furthermore, there is no other sedimentological or taphonomical evidence to suggest significant bone-by-bone transport at the Tuştea locality (no preferred orientation of long bones, very limited abrasion, lack of hydraulic equivalence between the bones and the enclosing sediment), and it is merely the low recovery rate of the vertebrae that suggests the action of a bone-sorting mechanism in the genesis of the local taphocoenosis. Accordingly, we consider the low recovery rate of vertebrae an important taphonomic characteristic which raises the possibility of some degree of bone sorting, but a significant degree of bone transport, especially through fluvial processes, can be excluded based on other sedimentological and taphonomical features.

The depositional model of the Tuştea vertebrate taphocoenosis can be summarized as follows: the Tuştea site was situated on a well-drained floodplain near the active channel, so that sediment accumulation was possible rather frequently through crevasse splay deposition (Therrien, 2005). The main sedimentation mechanism on the floodplain was the transport of finer-grained material (clay/silt and fine sand) during flooding events, sediments that periodically covered the carcasses lying on the floodplain, in different stages of decay and scattering. The sedimentological, geochemical and palaeopedological investigations suggest that the local palaeoenvironment was characterized by a subtropical climate (mean annual temperature of  $\sim 14^{\circ}\text{C}$ ; Bojar et al., 2010b) with alternating dry and wet seasons, the later ones also corresponding to the time of the periodic, but not necessarily annual, floods. In between two successive flooding events, the newly laid sediments started to undergo pedogenetic processes; meanwhile, the attritionally accumulated remains (resulting from the “everyday death” within the biocoenosis) have been subjected to decomposition, scavenging and disarticulation on the soil surface. During rainy seasons with heavy precipitation, channel deposits, coarser crevasse splay sands and especially thick sheets of sandy-muddy sediments were blanketed over the surface of the floodplain, when the raising floodwaters overstepped

the river banks. The generally fine-grained sediments indicate a low-energy environment, in which significant bone transport is not assumed to have taken place, although the low representativeness of vertebrae may suggest that selective transport and eventually removal of bones was occasionally possible during such severe flooding events.

The Tuştea assemblage corresponds to the taphonomic mode of ‘overbank assemblage’ (Bown and Kraus, 1981) because it is characterized by the presence of disarticulated and partially articulated vertebrate elements which have been exposed to biological, physical or chemical destructive effects prior to burial, accumulated within the overbank deposits of a fluvial system (e.g., Behrensmeyer, 1982; Behrensmeyer and Hook, 1992; Riga and Astini, 2007). The occurrence patterns of the fossil remains from the Tuştea locality allow distinction between two main taphonomic categories: one, including remains exposed for a long period of time, and another, with rapidly buried carcasses. The vertebrate remains that experienced long-term exposure are represented by isolated bone material, disarticulated mainly by biotic action, since weathering on the bone surface is limited and significant bone transport cannot be documented. On the other hand, the well-preserved associated and articulated material (including here most of the *Telmatosaurus* hatchling remains as well; see below) represents those carcasses buried rapidly after death during peak flood events.

The vertebrate accumulation from the Tuştea locality represents a parautochthonous assemblage; all available evidence suggests that the skeletal material was accumulated on an extensive well-drained floodplain characterized by low-energy conditions, with no evidence for significant bone transport or reworking. Accordingly, the Tuştea vertebrate assemblage is composed mainly of parautochthonous taxa that were buried in their habitat with only minimal disturbance, i.e., no transport of their remains other than within their original environment (Johnson, 1960; Kidwell et al., 1986). The largest part of the Tuştea assemblage

is made up of attritionally accumulated polytaxic remains, as the fossil material consists of bones that belong to individuals representing multiple taxa and different ontogenetic stages, and which accumulated over a long period of time as the result of ‘normal’, within-habitat background mortality (e.g., Behrensmeyer, 1982; Holz and Barberena, 1994; Lyman, 1994; Kidwell and Flessa, 1996).

## 7. THE PUZZLE OF THE TUȘTEA DINOSAUR EGGS - INSIGHTS FROM DEPOSITIONAL ENVIRONMENT AND TAPHONOMY

As outlined above, according to the synthesis of all available field data there are two outstanding fossiliferous levels within the Tuștea locality – associated largely with the calcrete levels C1 and C2 –, where eggs and hatchling material are preserved together (Table 2). Grigorescu et al. (2010) suggested that the co-occurrence of *Telmatosaurus* hatchling remains and *Megaloolithus* eggs documents the presence of a hadrosauroid nesting ground at Tuștea. Based on our newly assembled data, both egg-bearing levels identified at Tuștea share the spectacular feature of co-occurrence between hatchling remains and egg clutches closely associated within roughly the same horizon, so the Tuștea locality might represent a dinosaur nesting site with a more complex history, one where fragile hadrosauroid hatchling bones and megaloolithid eggs/nests were buried and preserved together *in situ* recurrently, at least at two different moments.

However, there is a long-standing and quasi-general consensus that eggs of the *Megaloolithus* oogenus were laid by titanosaurian sauropods (e.g., Buffetaut and Le Loeuff, 1994; Sahni and Khosla, 1994; Mohabey, 1996; Chiappe et al., 1998, 2003, 2005; Grellet-Tinner et al., 2006; Salgado et al., 2007; Vila et al., 2010a, b; Wilson et al., 2010; García et al., 2015), and the Tuștea locality stood as the single, outstanding occurrence of this oogenus

with indications that some megaloolithid eggs were laid by hadrosauroids (Grigorescu et al., 1994, 2010; Grigorescu, 2010b).

To address this still ongoing controversy, we discuss separately in this sub-chapter the results of our taphonomical investigations of the Tuştea nesting horizons, then formulate and preliminarily assess – on sedimentological and taphonomical grounds – three alternative hypotheses that could explain the co-occurrence of megaloolithid eggs and *Telmatosaurus* hatchling material in these horizons. In parallel, a more detailed investigation of the Tuştea dinosaur eggs and nests, and of their affinities, was published by one of the authors (Grigorescu, 2016).

## 7.1 Taphonomical investigation of nesting horizons

### 7.1.1 Taphonomy of the egg clutches

Two levels of the Tuştea locality (associated with the calcrete horizons C1 and C2; see above) yielded several egg clutches (Figs. 3, 5A, B). These clutches consist mainly of the lower halves of the eggs, all showing concave-up horizontal orientation (Fig. 5C). This position indicates that the eggs were most probably preserved and buried *in situ*, in their original positions, since material transported and deposited by water would favour concave-down orientations over those that are concave-up, as being more stable in fluid flow conditions (Hayward et al., 2000, 2011; Imai et al., 2015). Trampling can probably be excluded as a significant fragmentation agent in the case of the eggshell and egg accumulations of Tuştea, because this mechanism also creates concave-down rather than concave-up orientation, and would have led to a more advanced destruction of the eggs themselves. It can be thus hypothesized that the eggshell- and egg-bearing levels at Tuştea

represent actual nesting grounds where eggs and nests experienced little or no trampling or other type of disturbance prior to burial (Hayward et al., 2000, 2011).

Furthermore, there are other lines of evidence that indicate that the eggs were preserved in their original position, thus excluding their transport (Grigorescu et al., 2010; Grigorescu, 2016): (1) the eggs are grouped closely within the excavated clusters (Figs. 3, 5E, F), with occasional overlapping between the different incomplete lower halves; (2) the position of the clusters is more or less parallel with the bedding plane (Fig. 5A), with the convex lower halves of eggs oriented downwards (Fig. 5C); and (3) the eggs were preserved in relatively low-energy floodplain environments (contra Grellet-Tinner et al., 2012: p. 2), where the transport of the eggs is highly unlikely. The cyclic occurrence of flooding events at the Tuştea site (see above) greatly enhanced the chances of egg preservation, covering them with fine-grained deposits of crevasse splays spilling out onto the floodplain, and thus contributing to the *in situ* preservation of the original nest structures (e.g., Horner, 1994).

These taphonomical and sedimentological features that characterize both egg-bearing levels support the idea that the eggs were buried *in situ*, which is consistent with the hypothesis that the egg material from Tuştea documents the presence of two nesting grounds (Figs. 2, 4). The occurrence of several clutches in what appears to represent one short timespan (as marked by the calcrete levels), and within a relatively small area, further suggests that the egg-laying dinosaurs were nesting in a colony.

Moreover, the lower nesting horizon with its egg clutches, associated with calcrete level C2, represent a discrete and relatively short time interval, whereas the C1 calcrete and the associated upper nesting horizon clearly belong to a younger time interval, subsequent to that represented by level C2 (see Fig. 4). This clearly indicates that the eggs/nests associated with calcrete levels C1 and C2, respectively, were laid and buried during two different time intervals (i.e., two different nesting seasons) separated by at least one flooding event and a

period of protracted pedogenesis. The fact that identical megaloolithid eggs and clutches occur associated with two different calcrete levels (thus represent distinct, successive time intervals) suggests that members of the same egg-laying taxon returned to the same nesting area on at least two occasions, a pattern of multi-year repeated usage of the same nesting area described previously as “nest site fidelity” (e.g., Horner, 1982, 2000; Moratalla and Powell, 1994; Mohabey, 1996; Chiappe et al., 2003, 2005; Garcia et al., 2003; Grellet-Tinner and Fiorelli, 2010; Reisz et al., 2012). Discovery of isolated eggshell fragments below the crevasse-splay sandstone in 1994 would represent another argument to support the scenario of multiple re-utilisation of the same nesting area, but further support in this respect, through discovery of eggs, nests and eventually hatchling remains in this lowermost egg-bearing level, is required.

The absence of eggs and egg clutches between these two calcrete horizons (C1 and C2; or for that matter, elsewhere in the Tuştea section), although suggestive, does not necessarily indicate the absence of a further nesting horizon(s) located in between (i.e., within horizon MO2). This is because the carbonate leaching zone of the paleosols resting above the Bk (calcrete) horizon inhibits the preservation of eggshell material (e.g., Retallack, 1984). Accordingly, although the presence of further nesting grounds at Tuştea, inclusively between the C1 and C2 levels, is theoretically possible, positive evidence for these – in the form of eggshells – will probably be difficult to produce due to the carbonate dissolution in these non-calcareous sections of the paleosol succession (e.g., Sahni and Khosla, 1994).

The discovery of a few *Telmatosaurus* hatchling limb bones (e.g., LPB [FGGUB] R.2319 and R.2378) in the MO2 horizon, about 10 cm above the C2 nesting horizon, may point to the presence of another nesting ground situated above (and subsequent to) the one associated with the C2 calcrete, one where the eggshell material was dissolved, while the more resilient bones were preserved. Alternatively, however, these small isolated bones could



have been mobilised during the flash-flood event, uplifted and mixed within the silty-muddy sediment that covered the C2 nesting horizon. It is noteworthy in this respect that no associated/articulated hatchling remains were recovered from within the MO2 horizon, nor from another part of the Tuştea locality except the nesting horizons associated with the C1 and C2 calcretes.

#### 7.1.2 Taphonomy of the *Telmatosaurus* hatchling remains

The *Telmatosaurus* hatchling remains that represent the main basis of the enigmatic “Tuştea puzzle” (Grigorescu, 2010b) may have had a somewhat different taphonomical history compared with the remaining of the Tuştea assemblage, based on our investigation. Although some of the hatchling remains consist of more or less completely preserved, but isolated bones, these are represented more commonly by associated, well-preserved material, as well as by at least four incomplete skeletons found in life-time articulated position (Grigorescu, 2010b; Grigorescu et al., 2010): LPB (FGGUB) R.1852, that includes an articulated ribcage associated with other skeletal elements; LPB (FGGUB) R.2087, that includes articulated scapula, humerus and dorsal vertebrae (see Grigorescu et al., 2010: Fig. 8G); LPB (FGGUB) R.2088, that consists of an incomplete pelvic girdle articulated with femur and tibia (see Grigorescu, 2010b: Fig. 4); and LPB (FGGUB) unnumbered, hindlimb with partial femur and articulated tibia and distal fibula (Fig. 5D). Most of the *Telmatosaurus* hatchling material was discovered in the close vicinity of (less than 1 m apart), or even within the clutches (Grigorescu, 2010b; Grigorescu et al., 2010; Fig. 3), although in a few instances isolated or even articulated remains were found meters away from the nearest nests (e.g., LPB [FGGUB] R.1852, LPB [FGGUB] R.2087 – see above).

The *Telmatosaurus* hatchling assemblage includes elements from every major part of the skeleton, but the most frequently found and best preserved elements are the limb bones, whereas the skull elements are fragmentary and often indeterminate. Vertebrae and ribs are rare-to-common elements in the hatchling material, and even tooth-bearing dentary fragments and isolated teeth, particularly diagnostic of *Telmatosaurus*, were also discovered (e.g., Grigorescu, 2010b). Study of these remains indicates that they represent ontogenetic developmental stages ranging from near-term embryos to early-to-late hatchlings (Grigorescu and Csiki, 2006; Benton et al., 2010; Grigorescu et al., 2010), and thus document the simultaneous presence of individuals with different body sizes and representing different age classes in the *Telmatosaurus* hatchling material. Despite the relatively wide size range of the limb bones (suggesting the presence of babies of different sizes in the nesting ground), these size differences do not represent a long time interval, and it is probable that these different sized neonates hatched during the same breeding season, followed by a rather rapid early ontogenetic development, as already suggested for hadrosauroids (e.g., Horner and Weishampel, 1988; Horner et al., 2000; Grigorescu and Csiki, 2006; Woodward et al., 2015).

The good preservation state, as well as the common associated or articulated nature of most *Telmatosaurus* hatchling remains (Fig. 8G) demonstrate that the small partial carcasses were buried a relatively short time after death, especially since bones of hatchling or early juvenile individuals, when left exposed on the surface, can be destroyed rapidly and easily by different physical, chemical or biological agents (e.g., Behrensmeyer, 1978; Behrensmeyer et al., 1979; Horner and Makela, 1979; Brown et al., 2013). The low percentage values of skeletal completeness and the disarticulation of many skeletal parts indicate that decay processes already affected the small bodies before their final burial, as scattering of the skeletal elements becomes possible once most of the digestible soft tissues have been removed (Toots, 1965; Syme and Salisbury, 2014).

Reliable estimates of the duration of decay and disarticulation processes are difficult in the case of dinosaur remains because these processes largely depend on the nature of skin, body size, and environmental conditions (Brand et al., 2003), factors which are usually poorly constrained (but see Venczel et al., 2015, for estimates concerning the body size of the Tuştea *Telmatosaurus* hatchlings). However, information derived from experimental taphonomy shows that small-bodied lizards (of a body size roughly comparable to that of a small neonate *Telmatosaurus*) become completely disarticulated within six months under water, and at most within one year in terrestrial environment, through bacterial and invertebrate scavenging (Brand et al., 2003). Based on this empirical observation we estimate that the articulated hatchling skeletal remains must have been buried within one year after death, at the latest. A very short nesting period – of only 1 to 2 months - is reported for the more derived hadrosauroid *Maiasaura* by Horner et al. (2000); if *Telmatosaurus* had a similarly fast early ontogenetic development rate, the different hatchling skeletons would have been subaerially exposed for a comparable amount of time, at most, before their entombment, which concurs with our assessment concerning their short-term surface residence and rapid burial.

As already discussed, the largest part of the hatchling remains was discovered in the two nesting horizons associated with the C1 and C2 calcrete levels, and were often closely associated with the eggs and nests (Fig. 3). The hatchling material of the C1 calcrete level is dominantly associated or articulated, whereas the C2 horizon includes a single partial skeleton (LPB [FGGUB] unnumbered; Fig. 5D). A few isolated limb bones were also found in the MO2 horizon, ~10 cm above the C2 nesting horizon (see above).

The C1 nesting horizon yielded several *Telmatosaurus* hatchling remains, some grouped close to each other as associated or articulated skeletons (location 5 in Fig. 3; Fig. 8G), and representing at least four individuals based on MNI calculation. The four

*Telmatosaurus* hatchling skeletons preserved in a localized area (about 160 m<sup>2</sup>) and in the same horizon (C1 *nesting horizon*; Table. 2), as well as their homogenous taphonomic features (well-preserved, often associated material) raise the possibility that these animals were buried very shortly after death (at most within one year; see above), and approximately at the same time. The roughly uniform bone preservation patterns seen in this assemblage (almost complete absence of surface modifications such as weathering or abrasion; most of the epiphyses well preserved, even if incompletely ossified) also indicate that hatchling bone accumulation occurred over a short period of time. Should this vertebrate material have accumulated over a longer time interval, a wide range of different taphonomical modifications would be expected, especially in this case of small-sized and poorly ossified hatchling remains (e.g., Behrensmeyer, 1978; Fiorillo et al., 2010).

The C2 *nesting horizon* includes several egg clutches and hatchling remains, but only one case of associated hatchling material from this level was recorded (Fig. 5D). The hatchling remains are, again, well preserved (not abraded and not weathered), which also indicates rapid burial after death.

## **7.2 Hypothetical taphonomical histories of the *Telmatosaurus* hatchling remains in the megaloolithid nesting grounds of Tuştea**

Based on the taphonomical and sedimentological investigations of the Tuştea locality, several potential alternative scenarios can be outlined to account for the co-occurrence of *Telmatosaurus* hatchling remains and megaloolithid eggs in the nesting horizons (the ‘Tuştea puzzle’). In the following, we will explore these alternative hypotheses and weigh the arguments supporting or contradicting them.

7.2.1 **Scenario 1:** The *Telmatosaurus* hatchling assemblage was transported post-mortem into a titanosaur nesting site by fluvial currents, and thus the connection seen *in-situ* between *Telmatosaurus* hatchlings (indicating it as possible egg-layer) and the *Megaloolithus cf. siruguei* eggs is only apparent, being a simple by-product of a taphonomic accident (e.g., Weishampel and Jianu, 2011: p.57–58)

*Hypothesis:* The rapid burial of the hatchling remains, as was detected through taphonomical investigations (see above) does not exclude the idea that the *Telmatosaurus* hatchling carcasses may have been transported into the megaloolithid nesting ground before their final burial (based on Brand et al., 2003; Syme and Salisbury, 2014). For example, in order to explain the presence and good articulation state of the *Telmatosaurus* hatchlings at Tuştea, it can be hypothesized that these died somewhere in the wider Tuştea area during or shortly before a flooding event, and that their carcasses were transported as floating bodies into the nesting ground where they were finally deposited. Dinosaur nests were probably built in elevated parts of the floodplain, above and far enough from the active rivers so as to escape submergence during minor flooding (e.g., Carpenter, 1982). Thus, stranding of the hatchling carcasses inside the nesting ground might not have been accidental, as water depth and velocity, and thus its hydraulic capacity, decreased at these higher-lying areas of the floodplain, allowing for the accumulation of the transported carcasses. After their stranding, the carcasses started to decay, followed by a more or less advanced disarticulation on the soil surface of the nesting ground until their burial. The hatchling bones could have been thus buried during the following flooding event able to bring enough sediment to cover both the eggs and the bones lying around. Most of the eggs were buried *in situ* (as discussed above), especially those still within the original nests, partly because they were probably laid in

shallow depressions on the distal floodplain, which prevented their removal from their original setting.

*Testing the hypothesis:* It was already suggested that floating carcasses can be transported even by wind-driven ripples across the water surface (Sander, 1987; Wood et al., 1988; Weigelt, 1989), without the involvement of true fluvial processes, and therefore the perceived lack of hydraulic equivalence between sediment particles and hatchling bones becomes irrelevant in such cases. During peak flooding events, even the distal reaches of the floodplain can be covered by water, and the small-sized *Telmatosaurus* hatchling carcasses could have been easily transported by weak ripple currents across the surface of such extended water bodies into a different location than that where they lived and eventually died.

Accordingly, post-mortem transport of *Telmatosaurus* hatchling carcasses into titanosaur nesting ground is theoretically possible. We note, however, several problematic issues connected to this hypothesis:

- (1) It must be emphasized that such a transport mechanism would not function in the case of other, non-perinatal dinosaur individuals that were also found in the nesting horizons, and thus the presence of non-hatchling associated dinosaurian skeletal material from Tuştea cannot be accounted for by the ‘floating carcass’ scenario. This is because the depth of the water column in the distal, more elevated, parts of the floodplain can reach only a few centimetres (about 5–15 cm; Allen, 1965; Miall, 1996) even during flooding events, and thus it cannot support the drift of larger floating dinosaur carcasses this far, unlike the case of smaller carcasses such as the *Telmatosaurus* hatchlings.
- (2) In the case of the best-documented titanosaur nesting ground, that from Auca Mahuevo in Patagonia, Argentina, Chiappe et al. (2005) reported that remains of embryonic (prenatal) and (rare) adult titanosaurs have been collected from the

different megaloolithid nesting horizons containing eggs provisionally referred to *Megaloolithus patagonicus*. Skeletal remains of large-sized abelisaurid theropods (including the derived carnosaurin *Aucasaurus* – Coria et al., 2002) were also discovered in the local section, but not precisely in either one of the identified nesting horizons. Nevertheless, no remains of titanosaur hatchlings or early juveniles have been found in the egg-bearing horizons, nor in other parts of the local succession. In the titanosaur nesting locality described from Dholi Dungri in Gujarat, India, Wilson et al. (2010) reported the *in-situ* co-occurrence between several articulated skeletons of the large-sized madtsoiid *Sanajeh*, eggs referred to *Megaloolithus dhoridungriensis*, and one indeterminate titanosaur hatchling. This represents a unique case of egg-vertebrate field association described from India, and also the only known circumstance when titanosaur hatchlings have been found besides megaloolithid eggs. This stands in stark contrast with the rich record of reported co-occurrences between hadrosauroid eggs, nests and perinatal individuals representing a wide range of ontogenetic stages, from embryos to large hatchlings (e.g., Horner, 1982, 1994, 1999; Horner and Currie, 1994; Dewaele et al., 2015) – a pattern of field association strongly reminiscent of that reported here from the Tuştea nesting horizons.

- (3) All of the associated/articulated hadrosauroid hatchling material from Tuştea was found in the two nesting horizons associated with calcrete levels C1 and C2, often in close proximity of the *Megaloolithus* eggs and nests (Fig. 3), while such remains are completely absent from other horizons of the Tuştea locality. Such a preferential, exclusive and recurrent co-distribution suggests a probable close relationship between the eggs and hatchlings (see Scenario 3, below) rather than

an accidental by-product of a group of floating carcasses being washed into a dinosaur nesting ground.

- (4) It is difficult to conceive that (a) flotation of hatchling carcasses (scenario of Hypothesis 1) only occurs when dinosaur eggs are present on the emerged part of the floodplain; and (b) such a random coincidence as that implied by Scenario 1 happened recurrently (at least) twice, identically, during the genesis of the Tuştea locality succession. Again, the most parsimonious explanation suggests genuine association between eggs and hatchlings, rather than accidental co-occurrence.
- (5) Furthermore, eggs that are now recorded as occurring together with the hatchling remains within the same horizon must have been laid subsequent to the first flooding event that brought the hatchling carcasses (otherwise the eggs themselves would have been damaged and covered by sediments), and on top of the newly formed paleosol, which means that either (a) each ‘nesting horizon’ identified in this study actually represents the superposition of two temporally and vertically closely associated nesting grounds, one into which the hatchlings have been washed in, and one developed after their deposition but before their final burial; or (b) instead of the hatchlings being brought into the nesting ground as floating carcasses, the presumed egg-layer titanosaurs (e.g., Chiappe et al., 1998; Salgado et al., 2007; Wilson et al., 2010; Weishampel and Jianu, 2011) actually constructed their nests in an area already littered with hatchling remains of *Telmatosaurus*. If the first one of these alternatives remains a possibility, although one that does not appear to be supported by field observations, the second alternative completely reverses the “Tuştea paradox”, making the chance co-occurrence of megaloolithid eggs and *Telmatosaurus* hatchlings even less probable. Furthermore, the hatchling remains could not have been present at the



site, buried or not, before nest building, since they were found in few instances, well preserved, inside or closely associated with the nests themselves (Fig. 3) and in such a case they would have been probably destroyed by trampling by the egg-laying animals, instead of being found still in articulation, despite their fragile nature.

- (6) Finally, it should be emphasized that even if the Tuştea megaloolithid eggs were laid by titanosaurian sauropods as suggested previously for eggs of this oofamily (e.g., Sahni and Khosla, 1994; Chiappe et al., 1998, 2003; Salgado et al., 2007), the hadrosauroids must have nested roughly at the same time and in the same general area of the Tuştea site, close to the titanosaur nesting ground from Oltoane, because the *Telmatosaurus* hatchlings could not have been transported by wind-generated ripples for long distances, exceeding several hundred meters (see Scenario 2).

**7.2.2 Scenario 2:** Both the titanosaurian sauropods and the hadrosauroid *Telmatosaurus* laid their eggs in the same palaeoenvironment, roughly synchronously, and spatially close to each other, and the *Telmatosaurus* hatchlings visited occasionally the titanosaur nesting ground, where they were buried together with the titanosaur eggs during flooding events

*Hypothesis:* There is evidence showing that different taxa of birds or reptiles (turtles and crocodiles) can lay their eggs in the same nesting colony, sharing roughly the same space during the same time period (Horner, 1994; Hayward et al., 2000; Srivastava et al., 2015). Thus, it is also conceivable that two different herbivorous dinosaurs might have nested

roughly synchronously and close to each other in the same general habitat. In this case, the ‘Tuştea puzzle’ represents a paradox no more - the megaloolithid eggs were indeed laid by titanosaurs, whereas the *Telmatosaurus* hatchlings were just occasional visitors of the titanosaur nesting site from Tuştea.

*Testing the hypothesis:* The absence of titanosaurian skeletal material in either of the nesting horizons of Tuştea does not represent strong evidence to contradict the hypothesis that titanosaurs laid the megaloolithid eggs from this locality (contra Grigorescu et al., 2010). The absence of hatchling or juvenile sauropod remains in the locality can be due to taphonomical (e.g., delayed moment of sediment accumulation relative to titanosaur hatching period) and/or biological (the sauropod hatchlings quickly left the nesting area after they hatched) circumstances. Recent discoveries have shown that titanosaur remains, although rare, are present in the Oltoane Hill area, and even strictly in the Tuştea locality as well (Csiki-Sava et al., 2012), although not precisely in the same horizon as the megaloolithid eggs.

This pattern of exclusive distribution of titanosaur eggs vs. skeletal remains is not unprecedented. The available fossil record shows that despite the abundance of titanosaur eggs and nesting horizons reported from different parts of the world (see, e.g., Carpenter and Alf, 1994; Carpenter et al., 1994; Carpenter, 1999; Weishampel et al., 2004), the remains of adult individuals are extremely rare in the egg-bearing layers, perhaps because titanosaurs, like modern crocodylians, did not spend time caring for their egg clutches or hatchlings (e.g., Gelles-Tinner et al., 2006). Even more strikingly, despite the abundance of titanosaur eggs, some even with embryos inside, in the Late Cretaceous Auca Mahuevo nesting site from Patagonia, no remains of hatchlings and early juveniles have been discovered in this locality (Chiappe et al., 2005) that might also indicate that neonate titanosaurs probably left their nesting area soon after hatching from the eggs. On the other hand, hadrosauroid hatchlings

often remained close to their respective nests in crèche-like aggregations after they hatched (e.g., Horner and Makela, 1979; Horner, 1982; Varricchio and Horner, 1993; Horner and Currie, 1994), and thus might have been still around their nesting area in Tuştea when flooding occurred.

Several lines of reasoning can support the possibility of temporal and spatial proximity of titanosaurian and hadrosauroid nesting grounds. Nesting areas should be sought, and selected, for certain reasons, such as protection of the nests and hatchlings against natural hazards and/or predators and scavengers, as well as availability of food resources for the nesting animals and the would-be hatchlings. If for some reasons the well-drained floodplains of the Tuştea site satisfied such conditions for the taxon laying the *Megaloolithus cf. siruguei* eggs, it would have been potentially suitable for another nesting animal with largely similar ecological requirements (i.e., herbivorous diet) as well. Selecting similar palaeoenvironments for nesting would be also expected as it appears that both titanosaurs and hadrosauroids had roughly similar nesting strategies, characterized by: colonial nesting; moderate-sized (10–22 cm in maximum diameter, but usually ranging between 12–16 cm) subspherical eggs laid in clutches that are only very diffusely organised, sometimes with two partly overlapping levels of eggs; and clutches covered most probably by dirt and/or vegetation mounds (e.g., Horner, 2000; Grellet-Tinner et al., 2006). Furthermore, both of these taxa (or eggs referred to them) appear to have had rather wide environmental flexibility in nesting site selection (e.g., Horner, 1982, 1999; López-Martínez et al., 2000; Fanti and Miyashita, 2009; Sellés, 2012; García et al., 2015). All of these characteristics were already noted in the case of the megaloolithid eggs from the Haţeg Basin (Grigorescu et al., 2010). Finally, Grellet-Tinner et al. (2012) noted the co-occurrence of two different egg morphotypes in the Râul Mare sites of Toteşti and Nălaţ-Vad, sites characterized by similar lithology and depositional environments (e.g., Van Itterbeeck et al., 2004), which suggests that at least two different egg-laying

dinosaur taxa from the Hațeg Basin were able to successfully and repeatedly exploit the same palaeoenvironments as nesting ground.

Food resource availability was probably a key factor in nesting site selection, but also in timing of the nesting activity and especially hatching of the eggs. Just as in the case of modern animals, hatching must have been naturally ‘scheduled’ to occur when food availability (i.e., lush vegetation) was also guaranteed, and this most probably occurred during the wet season in the Hațeg Basin – a time period that would have benefited both titanosaurs and hadrosauroids. Such a timing for egg-laying and hatching provided the necessary food resources for the nesting animals and their new-born babies, while also creating the opportunity for roughly synchronous nesting activity of the different taxa. Accidentally, temporal coincidence between hatching season and beginning of the wet season probably also created the circumstances for the fortuitous preservation of the nesting grounds and hatchlings. This is because peak flooding episodes – like those that promoted sediment accumulation in the floodplain and the covering of the vertebrate remains present there - were most probable to occur during the beginning of the wet, rainy season.

Near-synchronous hatching of different taxa, some of them with altricial, nest-bound and gregarious babies as already suggested for hadrosauroids (e.g., Horner and Weishampel, 1988; Weishampel et al., 1993; Horner, 2000; Horner et al., 2000), others with precocial and nidifugous ones, as was suggested for titanosaurs (e.g., Chiappe et al., 2005; Grellet-Tinner et al., 2006), occupying nearby nesting grounds would have allowed the hadrosauroid hatchlings to venture into the neighbouring nesting grounds already vacated by the titanosaurs, and to get buried there together with the titanosaur nest remains once floods started. However, there are several lines of evidence that question the above summarized hypothetical scenario, besides further potential problems discussed under scenarios 1 and 3:

(1) Despite the large number of nesting sites reported worldwide (Horner, 1982, 1999; Mohabey, 1996; Carpenter et al., 1994; Sahni and Khosla, 1994; Carpenter, 1999; Chiappe et al., 2005; Grellet-Tinner et al., 2006; Salgado et al., 2007; Jackson et al., 2008; Vila et al., 2010a; Sellés et al., 2013; García et al., 2015 and references therein), there is no paleontological evidence to suggest that titanosaurs and hadrosauroids (or for that matter, any other large-sized dinosaurs) used the same (or closely neighbouring) location(s) as (quasi-)common nesting grounds (e.g., Horner, 2000). An exceptional co-occurrence between perinatal specimens of the oviraptorid *Citipati* and an indeterminate dromaeosaurid has been interpreted either to suggest predator-prey relationship (with the embryonic dromaeosaurids as prey items) or, alternatively, as an example of nest parasitism by Norell et al. (1994), but even the latter possibility does not document large-scale nesting ground sharing between the two taxa. An isolated occurrence of a crocodyliform nest within an Indian titanosaur nesting ground has been reported by Srivastava et al. (2015), but again, this occurrence appears to represent an isolated case of common egg-laying by dimensionally, ecologically and habitually markedly different taxa, rather than extensive and recurrent usage of adjoining nesting grounds by ecologically roughly similar, large-bodied species. The available fossil record does not support the idea of closely adjoining nesting grounds used by different dinosaur taxa, such as proposed in the case of the Tuştea locality under Scenario 2.

(2) Different bird taxa are known to nest together in the same colony (e.g., on islands), in part because due to their aerial habit they can access more easily and forage for food in distant areas, and thus potential limitations to food resources around the nesting ground do not pose an essential problem (e.g., Hayward et al.,

2000). However, in the case of large-bodied herbivorous dinosaurs, proximity of available food resources to the nesting area was an essential factor. Heightened food requirements were probably in part mitigated by the appropriate timing of the hatching period to coincide with the onset of the wet season (see above). Nevertheless, concurrent nesting and hatching by two large-bodied and gregarious herbivorous taxa in the same area would have still depleted severely the vegetation of the Tuştea area. Food resource partitioning is known to lessen competitive pressure and thus allow the sympatric presence of contemporaneous large-bodied herbivores in dinosaur-dominated ecosystems (e.g., Gomani, 2005; Henderson, 2010; Lyson and Longrich, 2011; Mallon and Anderson, 2013; Mallon et al., 2013; Barrett, 2014). However, even if resource partitioning through separate dietary preferences was probably present between titanosaurs and hadrosauroids (as hinted at by their distinctive and markedly different dietary adaptations such as dentition structure or feeding height; e.g., Weishampel and Norman, 1989; Barrett, 2014), quasi-overlap of their nesting areas, and the resulting requirements for a diversified and abundant vegetal food source available nearby, would have been even more difficult to accommodate in a floodplain area where palaeoenvironmental reconstructions suggest soil development under mainly semi-arid conditions, and thus most probably with only a sparse and not very diversified vegetation cover.

7.2.3 **Scenario 3:** The co-occurrence of *Telmatosaurus* hatchlings and *Megaloolithus* eggs at Tuştea supports the presence of a genuine hadrosauroid nesting ground with megaloolithid eggs, where the hadrosauroid perinatal individuals remained close to their respective nests after hatching, and were buried *in situ* together with the remnants of the nests (e.g., Grigorescu, 2010b; Grigorescu et al., 2010).

*Hypothesis:* The neonate hadrosauroids remained in close proximity to their respective nests after hatching, or returned to the nesting site frequently. Either of these alternatives is conformable with the presence of extended parental care that has already been suggested for altricial hadrosauroids (e.g., Horner and Makela, 1979; Horner, 1982; Grigorescu et al., 2010). The eggs and hatchling remains were buried *in situ* in the nesting ground during a flooding event that covered them with fine-grained crevasse splay deposits spilling out into the floodplain.

*Testing the hypothesis:* There are several lines of evidence that suggest a close causal connection between the hatchlings and the eggs at the Tuştea locality, already cited by Grigorescu (2010b) and Grigorescu et al. (2010): (1) the position of the hatchling remains in the succession coincides rather closely with the egg-bearing horizon(s); (2) most of the hatchling remains appear closely associated with the egg clusters, being located within 1 m or less of a nest, and, in few instances, the neonate bones were discovered inside a nest (Fig. 3); and (3) with the exception of a few isolated limb bones that were excavated from horizon MO2 slightly above calcrete level C2, the remaining *Telmatosaurus* hatchling elements, and all of the associated or articulated ones, were discovered exclusively in the egg-bearing horizons (Table 2), while these are completely absent from other parts of the local section.

Furthermore, the reconstructed sizes of the Tuştea eggs and hatchlings appear largely matched in size. The volume of the eggs, roughly 14 cm x 16 cm in diameter, was reconstructed to range from 1000 to 1350 cm<sup>3</sup> by Grigorescu (2016). Meanwhile, the *Telmatosaurus* hatchlings have femoral lengths varying between 35 and 50 mm (Grigorescu and Csiki, 2006), with one small (very early) hatchling individual being estimated to about 25 cm in body length by Venczel et al. (2015). Both of these values are significantly smaller than those reported in the derived lambeosaurine hadrosaur *Hypacrosaurus stebingeri*, whose eggs had 18 to 22 cm in diameter, with a volume of up to 3900 cm<sup>3</sup> (Horner, 1999; Horner and Currie, 1994), corresponding to embryos that had femoral lengths varying between 62 and 84 mm, respectively early hatchlings with femora ranging from 170 to 235 mm in length, and a body size of up to 1.6 m (Horner and Currie, 1994; Bailleul et al., 2012). Nonetheless, the absolute and relative dimensions of the Tuştea eggs and hatchlings are largely similar to those reported in the brachylophosaurin hadrosaur *Maiasaura peeblesorum*, with egg diameter of 12 cm and volume of 900 cm<sup>3</sup>, corresponding to embryos with 35-40 cm long femora and early hatchlings of about 45 cm estimated body length (Horner, 1999). Comparable proportions with those documented in the positively associated *Maiasaura* eggs and hatchlings suggest that the Tuştea eggs and hatchlings are indeed commensurate. Furthermore, if their conspecificity is upheld (as also advocated by Grigorescu et al., 1994, 2010; Grigorescu, 2010, 2016), then it appears that *Telmatosaurus* was closer in its reproductive strategy to *Maiasaura* (relatively smaller eggs and, correspondingly, smaller hatchlings, and possibly also smaller clutch size) than to *Hypacrosaurus*. In this respect it is probably also worth noting that whereas *Maiasaura* hatchlings have been discovered in and near nest-like structures, somewhat reminiscent of the Tuştea occurrence discussed here, this is not the case for *Hypacrosaurus* (Horner, 1999).



According to the field data assembled for this study and to our sedimentological and taphonomical survey, two distinct levels of the Tuştea locality include several hatchling remains and egg clutches close to each other, and are thus interpreted as two nesting grounds where fragile hatchling bones and eggs representing the same taxon were buried and preserved *in situ*. It was already suggested that the chance of preservation for hatchling remains is relatively high in their nesting areas. This is because here the baby skeletal elements are very abundant as a consequence of high mortality rates during the hatching period, resulting from intrinsic causes such as disease, abandonment, trampling or siblicide (e.g., Horner, 1994; Rogers and Kidwell, 2007; Brinkman et al., 2007; Woodward et al., 2015). Horner (1994) even suggested that most, if not all, baby dinosaur mortality occurred in the nesting areas, since baby dinosaur remains are extremely rare in the fossil record except in nesting grounds or accumulations reworked directly from these. The *Telmatosaurus* hatchling assemblage of the C2 horizon from Tuştea includes at least four individuals based on the MNI calculation, and their taphonomic features (see above) suggest that these individuals were contemporaries as far as can be ascertained, i.e., they lived, died and were buried together within a relatively short (weeks to months long) period – such a scenario is consistent with the idea that they remained in a group around the nesting ground after hatching.

The most common scenario proposed for the genesis of monodominant (including hatchling-dominated) hadrosauroid assemblages relies on the idea of the existence of some degree of social interactivity such as gregarious behaviour and parental care in this dinosaur clade (e.g., Horner and Makela, 1979; Horner, 1982, 1994, 1997; Varricchio and Horner, 1993; Lauters et al., 2008). There is also a growing body of evidence indicating that juvenile hadrosauroids remained in the vicinity of the nest after they hatched, and joined the adult community only when they reached about half of the adult body size (Horner and Makela,

1979; Horner, 1982, 1994, 1997, 1999; Horner and Currie, 1994; Carpenter, 1999; Lauters et al., 2008; Dewaele et al., 2015; Woodward et al., 2015). Horner and Makela (1979) and Horner (1982, 1994, 1997) also suggested that altricial perinatal hadrosauroids were fed by their parents while remaining in the nesting area, a type of social interaction that also contributes to the common occurrence (and thus potentially relatively high preservation rate) of hadrosauroid juvenile material in their nesting locations.

Under such circumstances, the co-occurrence of *Telmatosaurus* hatchlings and (supposedly) *Telmatosaurus*-laid *Megaloolithus* cf. *siruguei* eggs within the same nesting horizon(s) at Tuştea does not form an exception, but instead conforms to the pattern already described for several other hadrosauroids.

However, even if the above-cited cases offer a reliable parallel for the co-occurrence of *Telmatosaurus* hatchling remains with its eggs and eventually with remains of adults in the nesting horizons of Tuştea, they definitively fail to explain the presence of the *Zalmoxes*, *Hatzegopteryx* or *Kallokibotion* remains in the same nesting horizon(s) (Table 2). Indeed, the uniqueness of the Tuştea locality, under the assumption of scenario 3, consists in that it yielded not an exclusive co-occurrence between hadrosauroid eggs and hatchlings (eventually associated with shed theropod teeth), a taphocoenosis that appears to represent the rule in the case of hadrosauroid nesting grounds (e.g., Horner, 1994), but instead a rich politaxic assemblage of diverse dinosaur, as well as other macro- and microvertebrate remains associated with these eggs and hatchlings.

To conclude, based on the taphonomical, sedimentological and palaeoecological considerations discussed throughout this contribution, it seems reasonable to assume that the *Megaloolithus* eggs and the *Telmatosaurus* hatchling material belong the same taxon, and that they together document the presence of nesting colonies (Weishampel et al., 1991, 1993;

Grigorescu et al., 1994, 2010; Grigorescu, 2010b, 2016). There are some points, however, that potentially question such a relationship:

- (1) There is a wide consensus that the *Megaloolithus* oogenus belongs exclusively to titanosaurian sauropods (e.g., Buffetaut and Le Loeuff, 1994; Sahni and Khosla, 1994; Mohabey, 1996; Chiappe et al., 1998, 2001, 2003, 2005; Horner, 2000; Salgado et al., 2007; Jackson et al., 2008; Wilson et al., 2010; Sellés et al., 2013; García et al., 2015). Furthermore, reports of megaloolithid eggs that include *in ovo* titanosaur embryos from the Early Cretaceous locality of Algui Ulaan Tsav in Mongolia (Grellet-Tinner et al., 2011) and the Late Cretaceous localities of Auca Mahuevo in Patagonia, Argentina (Chiappe et al., 1998, 2005), as well as that of the co-occurrence of one titanosaur hatchling and megaloolithid eggs at Dholi Dungri in India (Wilson et al., 2010), allow confident association of certain megaloolithid eggshell types with titanosaurs. Currently, the Tuştea locality represents the only known co-occurrence of this oogenus with hadrosauroid hatchling remains, and was cited previously in support of the idea that megaloolithid eggs might have been also laid by hadrosauroids (e.g., Grigorescu et al., 1994, 2010), although this inference is still seen as controversial (Weishampel and Jianu, 2011).

It should be noted nonetheless, that despite the fact that *Megaloolithus* eggs from northern Spain, southern France or India are being commonly attributed to titanosaurian sauropods (Buffetaut and Le Loeuff, 1994; Mohabey, 1996), there is no direct proof to support this referral (e.g., Sander et al., 1998; López-Martínez et al., 2000). Recently it has been also suggested that in western Europe, *Megaloolithus siruguei* (the very same oospecies to which the Tuştea eggs were tentatively referred to) can possibly be associated with hadrosauroids instead of

titanosaurs (Bravo and Gaete, 2015); indeed, Kohring (1989) already suggested, again without positive evidence to support his claim, that megaloolithid eggs from the Spanish site of Basturs might belong to hadrosauroids.

Even in the Hațeg area, Grellet-Tinner et al. (2012) pointed out the presence of two different types of macroscopically similar ‘megaloolithid’ egg morphologies, one reported from Totești and considered to be related to the titanosaur-laid Patagonian megaloolithid eggs, and a second type, to which the Tuștea eggs belong, referred to a second, distinct, but not specified egg-layer. Although these observations do not exclude definitively the titanosaurian affinities of *Megaloolithus* cf. *siruguei* from Tuștea, they are reminiscent of the situation reported from northern Spain by Bravo and Gaete (2015) and do allow for the distinct possibility that the Tuștea eggs were laid by a different, non-titanosaurian taxon.

- (2) The typical hadrosauroid nesting grounds are characterized by high abundance of perinatal skeletal remains associated with eggs/eggshells, and quasi-absence of adult remains, as well as that of other vertebrates (e.g., Horner, 1994), whereas the nesting horizons recognized at Tuștea include remains of several taxa represented by different ontogenetic stages, and not exclusively hatchling skeletal elements (Table 2). Besides the *Telmatosaurus* hatchlings, associated skeletal material of adult/subadult *Telmatosaurus* (LPB [FGGUB] R.1586–R.1590) and of the madtsoiid snake *Nidophis* (LPB [FGGUB] v.574; Venczel et al., 2015), as well as isolated bones and teeth of the rhabdodontid *Zalmoxes*, several *Kallokibotion* plate fragments, and isolated shed teeth of the theropod *Richardoestesia* were also discovered in the pedogenic calcrete levels C1 and C2 that mark the two nesting horizons (Table 2).

Hayward et al. (2000) noted that the nesting sites of modern gull colonies contain bones from other birds besides those of the adult and juvenile gulls, and the latter are interpreted as remains of the gulls' prey, being thus brought into the site by the nesting animals. Indeed, in somewhat rarer occurrences, skeletal remains of prey animals were described from dinosaur nesting sites, as well (e.g., Norell et al., 1994; Varricchio et al., 2002), associated with those of the autochthonous hatchlings and eggs. Such an explanation, however, cannot be cited to explain 'exotic' (i.e., non-hadrosauroid) vertebrate remains in the Tuştea nesting horizons, since both potential egg-layers (hadrosauroids in scenario 3, or titanosaurs in scenarios 1 and 2) had a purely herbivorous diet.

Vertebrate remains reported previously from dinosaur nesting grounds (whether discovered *in situ*, or else parautochthonously concentrated), other than perinatal individuals and eggs or else remains of prey brought into the site to feed the babies (e.g., Norell et al., 1994; Varricchio et al., 2002), include common shed teeth of small theropods and, occasionally, scarce remains of crocodyliforms, turtles or microvertebrates (e.g., Horner, 1994; Horner and Currie, 1994; Kirkland, 1994; Ryan et al., 1998; Fanti and Miyashita, 2009). Shed small theropod teeth, and more rarely squamate (snake and lizard) bones or mammal teeth, have been reported to occur parautochthonously in dinosaur nesting sites (e.g., Horner, 1994), so their occurrence is not entirely surprising in the Tuştea nesting horizons either. Theropod teeth are considered to belong to predators that habitually raided the nesting grounds and hunted small-sized hatchlings (e.g., Carpenter, 1982; Ryan et al., 1998; Horner, 1994; Fanti and Miyashita, 2009), as are the remains of large madtsoiid snakes (Wilson et al., 2010) or that of terrestrially adapted, cursorial crocodyliforms (Kirkland, 1994). Meanwhile, small-sized squamates and

mammals may have used the nesting area as hiding place and as an occasional foraging area (e.g., Venczel et al., 2015). Interestingly, lizard remains appear to be associated occasionally with dinosaur nesting grounds in North America (Horner, 1994), and are common in a microvertebrate assemblage that was parautochthonously concentrated from a nearby hadrosauroid nesting locality (Fanti and Miyashita, 2009); lizard remains, together with those of snakes and terrestrial crocodyliforms, are also present in and around the Tuştea nesting grounds (Martin et al., 2010; Vasile and Csiki, 2010; Vasile et al., 2013).

More unexpected is the presence of different skeletal parts of larger animals that represent diverse taxa – including ones that differ from the suspected egg-layer – and age classes, in the very same level inferred to represent the nesting horizon. To our knowledge, there is no reported dinosaur nesting ground worldwide where eggs, nests and hatchlings of a particular taxon are preserved together, in same horizon, with bones of other non-prey dinosaur taxa (compare with, e.g., Horner, 1994; Sahni and Khosla 1994; Mohabey, 1996; Sahni, 1997; López-Martínez et al., 2000; Chiappe et al., 2005; Sellés et al., 2013).

This exceptional co-occurrence that characterizes the Tuştea locality could be explained by hypothesizing that the exotic skeletal material was collected from different parts of the floodplain and transported/concentrated through fluvial action, i.e., these remains are parautochthonous to possibly allochthonous in origin, and do not belong to individuals that died and got buried *in situ* in the proximity of the nesting area. An allochthonous origin of these skeletal elements, however, remains poorly supported by the available taphonomical and sedimentological data. Even if smaller bone fragments and isolated teeth, more hydraulically compatible with the sediments, could have been transported by the

same periodic floods that brought fine-grained sediment and covered the eggs and hatchling skeletons, this scenario does not apply to the larger elements from the taphocoenosis. Transport of large, isolated dinosaur bones (e.g., a 12 cm long *Zalmoxes* fibula) by fluvial processes is unlikely, because such elements are not hydraulically equivalent to the enclosing silty/muddy sediments (Behrensmeyer, 1975; Fiorillo et al., 2010; Gangloff and Fiorillo, 2010); convergently, taphonomical characteristics recorded at Tuştea also contradict the idea of long-term transportation of large bones (see above). Movement as floating carcasses can also be excluded in the case of larger, adult dinosaurs, because the assumed water depths in these distal reaches of the floodplain would not allow the drifting of large-sized carcasses.

Another conceivable explanation could be that these larger skeletal elements representing 'exotic' taxa were already buried on the floodplain before the settlement of the nesting colony, and the nesting dinosaurs simply dug their nests into the bone-bearing soft sediment. Such a scenario, however, still has to account for the results of our taphonomical analysis, results that (a) show that larger-sized dinosaur bones tend to co-occur with the egg clusters at roughly the same stratigraphic levels; and (b) strongly suggest that, regardless of the exact horizon they are coming from (nesting ground or simple paleosol), the skeletal remains show the same general set of taphonomic modifications, one that suggests lack of significant transport and (par)autochthonous, *in situ* burial of the remains. Together, these observations support the continuous and autochthonous presence of at least certain taxa such as *Zalmoxes* and *Kallokibotion* throughout the time interval represented by different horizons separated in the Tuştea locality section, that is, their presence in the local palaeoenvironment regardless whether it

represented the site of dinosaur nesting or not. Such a continuous presence of other taxa in the nesting area, even if not precisely during the nesting seasons themselves, further underlines the uniqueness of the Tuştea nesting locality.

### 7.3 Conclusions of the depositional circumstances of the nesting locality

Based on the results of our sedimentological, taphonomical and palaeoecological investigations of the Tuştea nesting horizons, the assessment of three alternative scenarios to explain to co-occurrence of megaloolithid eggs and hadrosauroid hatchling remains led us to conclude that the burden of evidence is still in favour of the autochthony of the hatchlings preserved within their own nesting ground. This conclusion is supported by the following lines of evidence:

1) There are several observational data from Tuştea (e.g., the stratigraphic position of the associated hatchling remains that coincides strictly with the egg-bearing horizons; autochthony and good preservation state of these remains) that, together with the available fossil record which suggests that the chance of preservation for hatchling remains is relatively high in the nesting areas, whereas baby dinosaur remains are extremely rare away from their nests, support a close causal connection between the presence and distribution of the hadrosauroid hatchlings and the megaloolithid eggs at this locality. Meanwhile, we note an obvious lack of local taphonomic and sedimentologic evidences that would support and explain the large-scale introduction of hatchling *Telmatosaurus* specimens (either pre- or post-mortem) into a foreign (presumably titanosaurian) nesting ground.

2) It is difficult to conceive that the introduction of *Telmatosaurus* hatchling carcasses (scenarios of Hypotheses 1 and 2) only occurred when titanosaurian eggs were present on the



emerged part of the floodplain, and that this random coincidence happened recurrently (at least) twice during the genesis of the Tuştea locality.

3) The taphonomical features of the Tuştea nesting horizons, most prominently the occurrence of several articulated and associated partial skeletons of hatchling hadrosauroids found in close association with egg clutches, show similarities with other reported cases of hadrosauroid nesting-hatching grounds (e.g., Horner, 1982; Horner and Currie, 1994; Dewaele et al., 2015). These same features are markedly different from those reported from titanosaurian nesting places, where there is a unique case when titanosaur hatchling material has been found besides megaloolithid eggs (Wilson et al., 2010).

Based on the above-listed arguments, we conclude that the *Telmatosaurus* hatchling remains and the megaloolithid eggs from Tuştea-Oltoane were buried *in-situ* within genuine hadrosauroid nesting grounds by fine sediments brought during higher-magnitude flood events, rather than to consider this locality a titanosaurian nesting area into which the hadrosauroid hatchling material was drifted accidentally by fluvial transport or arrived in the form of occasionally visiting *Telmatosaurus* babies.

We acknowledge that there is still a wide consensus that relates *Megaloolithus*-type eggs exclusively to titanosaurian sauropods, and the well-documented titanosaurian origin of at least some megaloolithid eggs (e.g., Chiappe et al., 1998, 2005; Wilson et al., 2010; Grellet-Tinner et al., 2011) represents the frequently cited ‘key evidence’ against the idea that the Tuştea eggs were laid by the hadrosauroid *Telmatosaurus*. However, we note here that:

- until 1998, when the first *in ovo* titanosaur embryos were found in megaloolithid eggs from Auca Mahuevo (Chiappe et al., 1998), titanosaur affinities of megaloolithid eggs were based on the coincidental occurrence of titanosaur remains in/around *Megaloolithus* nesting sites from the Upper Cretaceous of southern France (co-occurrence first noticed by Matheron in 1869, fide Buffetaut and Le Loeuff, 1994) and of India (Sahni et al., 1994).

There is still little positive evidence, if any except than circumstantial ones, to link all types of megaloolithid eggs exclusively to titanosaur sauropods as was advocated by, e.g., Mikhailov (1997; but see Hirsch, 1994) and followed in many recent studies (e.g., Garcia et al., 2006; Sellés, 2012). This situation is most aptly summarized by Vila et al. (2009: p. 42): „Nowadays, and especially after the discovery of *in ovo* titanosaur embryos in megaloolithid eggs at Auca Mahuevo (Argentina), most of the specialists assume that eggs of this oofamily correspond to titanosaurs.” (our underline).

- although the presence of *in ovo* embryonic remains is generally considered as sole and definitive proof of the taxonomic identity of fossil eggs or eggshells, there are several previously reported instances when occurrence of *ex ovo* hatchling and embryonic remains alongside eggs or even in parautochthonously concentrated eggshell accumulations was deemed sufficient to refer these remains (eggs and babies) to the same taxon (e.g., Bonaparte and Vince, 1979; Wilson et al., 2010; Reisz et al., 2013). Such inferences were also used to genetically link enantiornithin skeletal remains and ratite-type eggshells in a coquina-like accumulation from the uppermost Cretaceous of the Tansylvanian Basin that was interpreted as a reworked bird nesting colony by Dyke et al. (2012).

- finally, as we have already noted, important differences in egg morphology and microstructure as well as nesting behaviour were already reported between definitive titanosaur-related megaloolithid eggs/eggshells (e.g., *Megaloolithus patagonicus*) and other oospecies referred to this oogenus (including *Megaloolithus siruguei*; Jackson, 2007; Jackson et al., 2008; Grellet-Tinner et al., 2012; Bravo and Gaete, 2015). Convergenly, cladistic analyses of dinosaur ootaxa relationships (e.g., Garcia et al., 2006; Grigorescu et al., 2010; Bravo and Gaete, 2015) suggest possible non-monophyly of *Megaloolithus*, and reveal close relationships between certain species of this oogenus and spheroolithid eggs usually linked to hadrosauroids based on *in ovo* embryos and associated hatchlings (e.g., Horner and Currie,

1994; Horner, 1999; Dewaele et al., 2015). Altogether, these data suggest the possibility that certain megaloolithid eggs were not laid by titanosaurs, but instead by hadrosauroids (see also Bravo and Gaete, 2015), especially since true spheroolithid eggs, although present (Sellés et al., 2014), are relatively rare in the latest Cretaceous European fossil record, contrary to the common, diverse and widespread presence of contemporaneous hadrosauroids (e.g., Prieto-Márquez et al., 2013; Cruzado-Caballero et al., 2014; Dalla Vecchia, 2014; Blanco et al., 2015; Csiki-Sava et al., 2015).

Despite the fact that none of the above considerations support directly our assertion that the megaloolithid eggs from Tuștea were laid by hadrosauroids, they represent evidence that is concordant with our conclusions based on the detailed taphonomical and sedimentological investigations of the Tuștea locality, i.e., that hadrosauroid hatchlings and hadrosauroid-laid megaloolithid eggs are both autochthonously buried here in what were genuine hadrosauroid nesting grounds.

Nevertheless, there is an unexpected taphonomical feature of the Tuștea nesting horizons that significantly distinguishes these from other hadrosauroid (or for that matter, dinosaurian) nesting sites. These nesting horizons did not yield quasi-exclusively hatchling skeletal elements, associated with the nests, but also include remains of several ‘exotic’ taxa represented by different ontogenetic stages, whereas typical hadrosauroid nesting grounds are characterized by high abundance of perinatal skeletal remains associated with eggs/eggshells, and quasi-absence of adult remains, as well as that of other vertebrates (e.g., Horner, 1994). This exceptional co-occurrence that characterizes the Tuștea locality is difficult to explain for the moment, as transport of non-hatchling, often large-sized macrovertebrate remains into the area of the Tuștea locality is poorly supported by the available taphonomical and sedimentological data.

As a conceivable alternative explanation to this unusual occurrence, we suggest that larger skeletal elements of these ‘exotic’ taxa might have been already buried on the floodplain before the settlement of the nesting colony, and the nesting dinosaurs simply dug their nests into the bone-bearing soft sediment. Nevertheless, the common presence of different vertebrate remains throughout the time of deposition of the Tuştea section should be regarded as a consequence of quasi-continuous and habitual occupation of the local palaeoenvironment, chosen occasionally as preferred nesting site by hadrosauroids, by a diverse vertebrate assemblage that included hadrosauroids, but also other dinosaurs (the rhabdodontid *Zalmoxes*, at the least, but most probably also the predatory theropods), alongside turtles, crocodyliforms, squamates and mammals.

## 8. CONCLUSIONS

The co-occurrence of common hadrosauroid hatchling remains with megaloolithid eggs and nests in the latest Cretaceous Tuştea-Oltoane vertebrate site, in the northwestern Haţeg Basin, represents one very intriguing fossil association and one that, being rather controversial (e.g., Weishampel and Jianu, 2011; Sellés, 2012; Sellés et al., 2014), is a provoking palaeontological enigma, often dubbed the ‘Tuştea puzzle’ (e.g., Grigorescu, 2010b). In order to more fully understand the genetic conditions of this unique fossil locality (the only one known from the European Upper Cretaceous where dinosaur eggs and hatchling remains are preserved together), a detailed taphonomic investigation of the site was carried out by synthesizing a large amount of field and laboratory data gathered during a 23-year long period of excavations. Our thorough sedimentological and taphonomical analysis of the Tuştea-Oltoane dinosaur nesting site led to the following results:

- 1) The Tuştea locality can be classified as a succession of high-diversity, multitaxic (multidominant) microfossil bonebeds, because it has yielded remains of 21

vertebrate taxa, a figure that represents 60% of the known formational biodiversity, and because 80% of the identifiable specimens (NISP) are smaller than 5 cm in maximum dimension.

- 2) The taphonomical investigations pointed out that most vertebrate remains show little to no sign of weathering and abrasion, but a very high percentage of them are broken. The apparent lack of preferred orientation of long bones and the limited abrasion indicate that fluvial transport of the bone material was not significant, which, together with the reduced amount of weathering and the presence of an important proportion of associated and articulated skeletons, suggests that the largest part of the bone assemblage from any of the recognized fossil-bearing levels was fragmented *in situ* and buried relatively rapidly after death.
- 3) The occurrence patterns of the taphonomic characteristics presented by the fossil remains from Tuştea allow distinction between two main taphonomic categories:
  - a) vertebrate remains that experienced longer-term exposure and are represented by isolated bone material, disarticulated mainly by biotic actions; and b) well-preserved, associated and articulated material (including here most of the *Telmatosaurus* hatchling remains) that represents carcasses buried rapidly after death, during peak flood events.
- 4) The Tuştea taphocoenosis is dominated overwhelmingly by dinosaurs (with a minimum of 20 individuals that represent at least 9 taxa). These are associated with other land-bound taxa such as squamates, mammals, and terrestrially adapted crocodyliforms (*Sabresuchus*) and possibly turtles (*Kallokibotion*), indicating that remains of terrestrial animals form the core the local fossil assemblage. However, the presence of aquatic and/or semiaquatic taxa (e.g., amphibians, *Allodaposuchus*) suggests that aquatic habitats were also present nearby the site.

- 5) Despite Tuştea representing the nesting area of another taxon, *Zalmoxes* is the most abundant dinosaur taxon in the local assemblage, based on both MNI and NISP calculations; it is seconded in abundance by the turtle *Kallokibotion*. The second most abundant dinosaur taxon is *Telmatosaurus*, while theropods and titanosaurs are far less well represented. The available sedimentological-taphonomical evidence suggests that the area of the nesting grounds represented in the same time the natural living habitat of other, non-egg-layer ('exotic') taxa.
- 6) Contrary to previous assumptions, we show here based on the synthesis of all available field data that there are two outstanding fossiliferous levels within the Tuştea locality, where *Megaloolithus* eggs and hadrosauroid (probably *Telmatosaurus*) hatchling remains are preserved together. The taphonomical and sedimentological features of both of these egg-bearing levels are comparable, and they support the idea that the eggs were buried here *in situ*, thus document the presence of two distinct, superposed nesting grounds. The fact that identical megaloolithid eggs and clutches occur associated with two different calcrete levels (i.e., represent distinct, successive time intervals) shows that members of the same egg-laying taxon (as we document here, the hadrosauroid *Telmatosaurus*) returned to the same nesting area on at least two occasions, a pattern of multi-year and repeated usage of the same nesting area by the same taxon defined as 'nest site fidelity'.
- 7) Based on our sedimentological, taphonomical and palaeoecological investigations, we provide further supporting evidence for the 'Tuştea puzzle', i.e., for the hypothesis that the hatchling *Telmatosaurus* material from the Tuştea nesting horizons represent autochthonous remains, that most probably they represent the egg-laying taxon, and that they were buried *in-situ* within their nesting grounds by

recurrent high-intensity flood events that took place most probably towards the end of the nesting season.

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### FIGURE CAPTIONS

**Figure 1.** **A.** Location of the Hațeg Basin (**HB**), in the western part of Romania. **B.** Simplified geological map of the Hațeg Basin, with the main dinosaur nesting localities. 1 – Crystalline basement, 2 – pre-Maastrichtian sedimentary cover (mainly marine), 3 – Maastrichtian continental deposits: a – volcanoclastic lower member of the Densuș-Ciula Formation, b – fossiliferous terrigenous middle–upper members of the Densuș-Ciula Formation, c – Sînpetru Formation and tentatively referred deposits, 4 – Cenozoic sedimentary deposits, 5 – nesting localities (Tuștea underlined in bold). **C.** The Tuștea dinosaur quarry, showing the local succession as revealed after the leveling of the horizontal platform (1998): I – lower red mudstone-calcrete unit (Unit 1, as defined in this study), II – sheet-splay sandstone, III – upper red mudstone-calcrete unit (Unit 2, as defined in this study), IV – massive to cross-bedded coarse fluvial conglomerates and sandstones, and V – uppermost red and grey-green mudstone unit.

**Figure 2.** Schematic stratigraphic section of the Tuștea site showing the main sedimentological and lithofacies details. **A.** Paleosol section at Tuștea showing the C1 calcrete horizon and the contact between Unit 1 paleosol and overlying conglomerates. **B.** Detail of the conglomerates, with included red mudstone rip-up clasts. **C.** Detail of the thick conglomerate layer with large-scale tabular cross-stratification. **D.** Conglomerates topped by a second bed of reddish calcareous mudstones grading into greenish, gleyed mudstones.

**Figure 3.** Detailed nest map of the Tuștea locality (completed and updated from Grigorescu et al., 2010), showing the location of the nests from the lower (in red) and upper (in green) nesting levels, with indication of their relative depth below the conglomerate/mudstone erosional contact; code following registration number of certain nests corresponds to figure number in Grigorescu et al. (2010). **IsE** represents an isolated, complete egg (see Grigorescu, 2010b: Fig. 3.1), found outside of the egg clusters (nests). Blue stars mark the position of the

hatchling remains, with indication of their relative depth below the conglomerate/mudstone erosional contact.

**Figure 4.** Detailed scheme of the Tuştea bonebeds showing the different sedimentological units and their fossil content. **A.** Successive paleosol horizon–related bonebeds at the Tuştea vertebrate locality. **B.** Flow-chart illustrating the action of pedogenic processes generating the bonebeds at Tuştea; different colours indicate the successive amounts of fresh sediment depositions during periodic peak flooding events.

**Figure 5.** Dinosaur eggs, nests and hatchlings from the Tuştea locality. **A.** *In situ* nest no. 10 (**N10**; LPB [FGGUB] R.1866) from the lower nesting horizon; arrows point to the position of the upper (C1) and lower (C2) calcrete levels that mark the two nesting horizons; brush (20 cm long) for scale. **B.** *In situ* nests no. 8 (**N8**; LPB [FGGUB] R.2148) and 9 (**N9**; LPB [FGGUB] R.2151) from the upper nesting horizon; arrow marks the conglomerate (**congl**)-mudstone (**MO1**) contact. **C.** Detail of two *in situ* hatched megaloolithid eggs (nest no. 4) showing their lifetime, concave-up orientation; lens cap (5 cm) for scale. **D.** *Telmatosaurus transsylvanicus*, *in situ* articulated partial hatchling skeleton (LPB [FGGUB] uncatalogued; hatchling no. 12 in Fig. 3): incomplete left hindlimb with partial femur (**Fe**) and articulated tibia (**Ti**) and distal fibula (**Fi**); tape measure for scale. **E.** Megaloolithid nest no. 11 (LPB [FGGUB] R.2146) from the lower nesting horizon. **F.** Megaloolithid nest no. 14 (LPB [FGGUB] R.2150) from the upper nesting horizon.

**Figure 6.** Relative abundances of vertebrate taxa in the Tuştea assemblage. **A.** NISP distribution of the main vertebrate groups. **B.** NISP distribution of dinosaur taxa. **C.** MNI distribution of the main vertebrate groups. **D.** MNI distribution of dinosaur taxa.

**Figure 7.** Distribution of the different skeletal preservation states in the Tuştea vertebrate assemblage.

**Figure 8.** Macrovertebrate remains from Tuștea, illustrating taphonomic features discussed in the text. **A.** *Zalmoxes shqiperorum*, left femur (LPB [FGGUB] R.1608) from level C5 in cranial (**A1**), lateral (**A2**) and caudal (**A3**) views; complete and well-preserved hindlimb element from an articulated partial skeleton (see Venczel et al., 2015: Fig. 2F) without signs of weathering and abrasion, and showing post-burial cracks and fractures. **B.** *Telmatosaurus transsylvanicus*, right femur (LPB [FGGUB] R.1702) from level C3 in posterior view, an incomplete hindlimb element showing advanced weathering (crisscrossing cracks filled with matrix) and pre-burial damage (breakage) at the epiphyseal parts. **C.** *Zalmoxes* sp., right tibia (LPB [FGGUB] R.2188) from level MO1 in cranial (**C1**) and caudal (**C2**) views, an incomplete, but unweathered and unabraded element missing both epiphyses and showing complex pre-burial breakage at both ends. **D.** Rounded bone pebble (LPB [FGGUB] R.1962) from the overlying fluvial conglomerates-coarse sandstones (Unit IV in Fig. 1C) in external (**D1**) and internal (**D2**) views; highly abraded and weathered element showing complete removal of the periosteum. **E.** Ornithopoda indet. (?*Zalmoxes*), left tibia (LPB [FGGUB] R.1694) from level C4 in cranial (**E1**) and caudal (**E2**) views; it shows complex pre-burial breakage, being completely split longitudinally in caudal view (yellow dotted line marks the boundary between wall of diaphysis and exposed medullary cavity). **F.** *Zalmoxes* sp., articulated left frontal-postorbital complex (LPB [FGGUB] R.1616) from level C3 in dorsal (**F1**) and ventral (**F2**) views (rostral part up); it shows shiny, non-weathered bone surface, a well-preserved prefrontal process on the frontal (*fr*), respectively posterior and ventral (jugal) processes on the postorbital (*po*), as well as clearly marked sutural ridges for the braincase on its ventral surface. **G.** *Telmatosaurus transsylvanicus*, articulated partial skeleton (LPB [FGGUB] R.2087) from level C1; neonate specimen with humerus (*hu*), scapula (*sc*) and dorsal vertebrae (*dv*) close to life-time articular position, the otherwise quasi-complete, well-preserved bones showing an unfinished surface texture that suggests a very early ontogenetic



stage. **H.** *Zalmoxes* sp., basioccipital (**bo**; LPB [FGGUB] R.1629) and left exoccipital-opisthotic (**eo**; LPB [FGGUB] R.1591) from level C3 in articulation, in caudal (**H1**) and oblique dorso-medial (**H2**) views; the two well-preserved, unworn specimens were found in different years in the same area of the quarry, yet their perfect fit suggests that they belong to the disarticulated skull of one individual. **I.** *Zalmoxes* sp., anterior-mid caudal vertebra (LPB [FGGUB] R.1770) in left lateral view, a well-preserved, non-weathered and non-abraded but slightly damaged (tip of neural spine) isolated element from level C3, showing paired toothmarks (**tm**) probably inflicted by the crocodyliform *Allodaposuchus*. Scale bar represents 5 cm for A, B; 2 cm for C; 1 cm for D–I.

**Figure 9.** Relative abundance of the skeletal elements in the Tuştea vertebrate assemblage.

**Figure 10.** Bone representation by size in the Tuştea vertebrate assemblage. **A.** Size distribution of the bones based on the maximum dimension of bones and bone fragments. **B.** Size distribution based on the maximum dimension of the complete and reconstructed skeletal elements. **C.** The percentages of the different size categories that are over- and underrepresented compared to their expected number in the fossil material. The expected numbers of observed elements are calculated from data in Table 5.

**Figure 11.** Distribution of abrasion (**A**) and weathering stages (**B**) in the Tuştea vertebrate assemblage.

**Figure 12.** **A.** Bone breakage distribution in the Tuştea assemblage. **B.** Distribution of breakage types in the limb bone assemblage. **C.** Presence or absence of epiphyses in limb bones.

## TABLE CAPTIONS

**Table 1.** Synthetic faunal list of the Late Cretaceous vertebrate fauna from the Haţeg Basin (based mainly on Csiki-Sava et al., 2016 and references listed therein).

**Table 2.** Distribution of the fossil material (including vertebrate and egg remains) among the different bonebed levels of the Tuştea locality: C1–C5 – calcrete horizons, MO1–MO5 – pedogenetically-modified red mudstone horizons, NISP – Number of Identified Specimens, MNI – Minimum Number of Individuals. \*The MNI values shown here are not equivalent with the MNI calculation in the text, since MNI values associated with the different horizons (as presented in this table) cannot be considered as definitive (see discussion in text, 4.2). \*\*Depth of occurrence of this isolated eggshell, relative to the crevasse splay, not known with certainty (see text, 7.1.1.).

**Table 3.** NISP and MNI values as well as fragmentation rate associated with taxa in the Tuştea vertebrate locality.

**Table 4.** Recovery rate of the different skeletal elements in the dinosaur assemblage of Tuştea locality.

**Table 5.** Skeletal completeness data in the Tuştea vertebrate assemblage: %TC– represents the percentage of total skeletal completeness; A – the actual number of skeletal elements recorded from Tuştea; E – the expected number of elements in a complete skeleton; %R – recovered element percentage of a certain skeletal element.

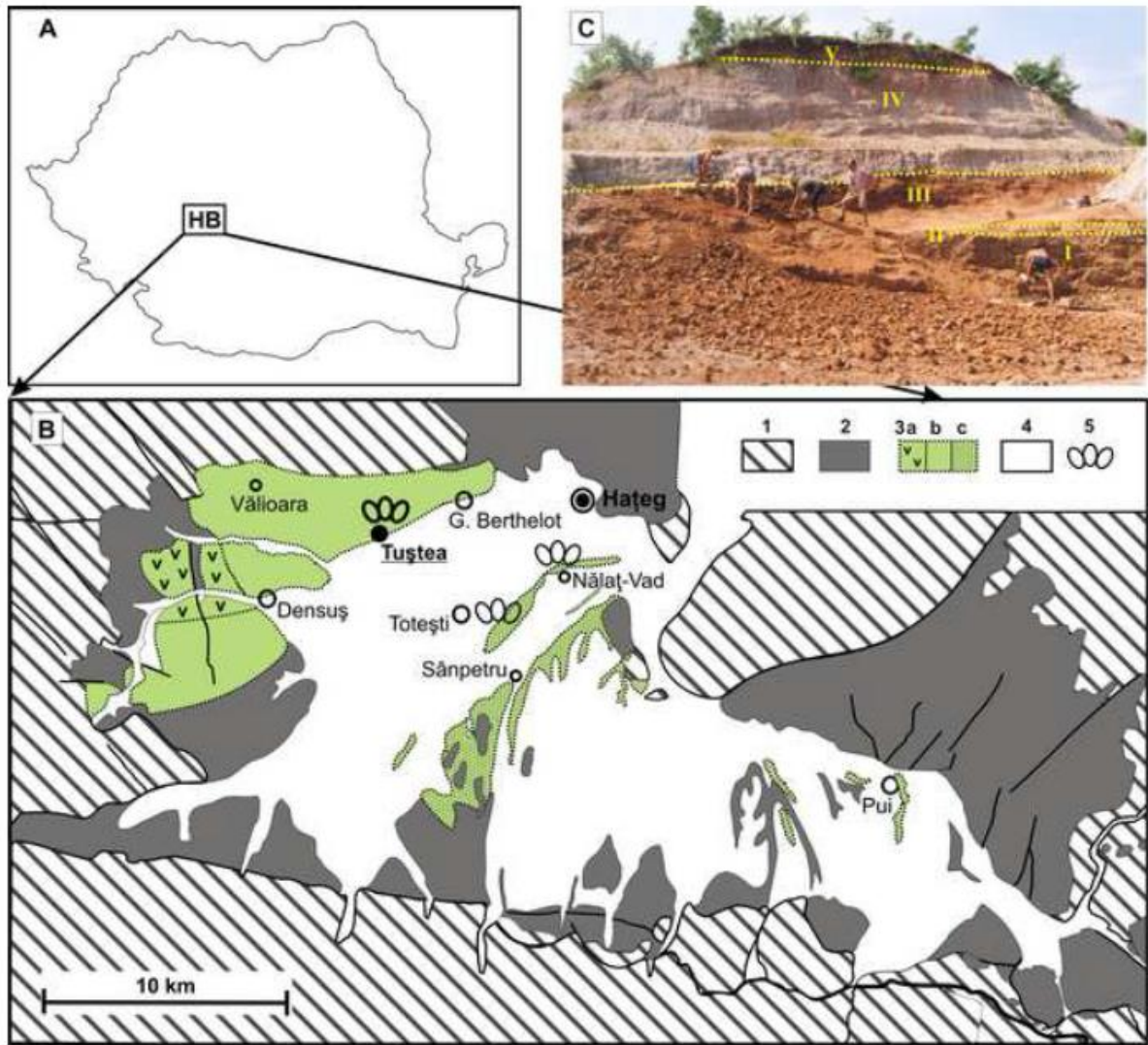


Fig. 1





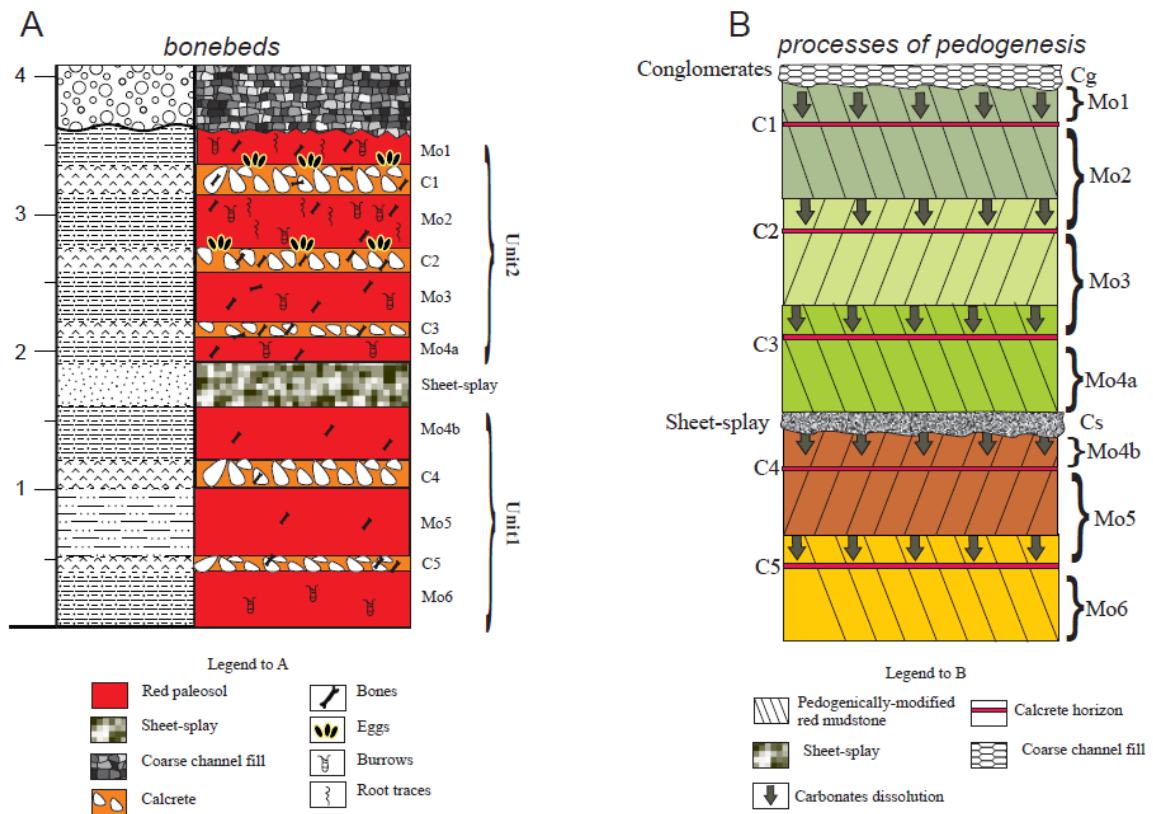


Fig. 4

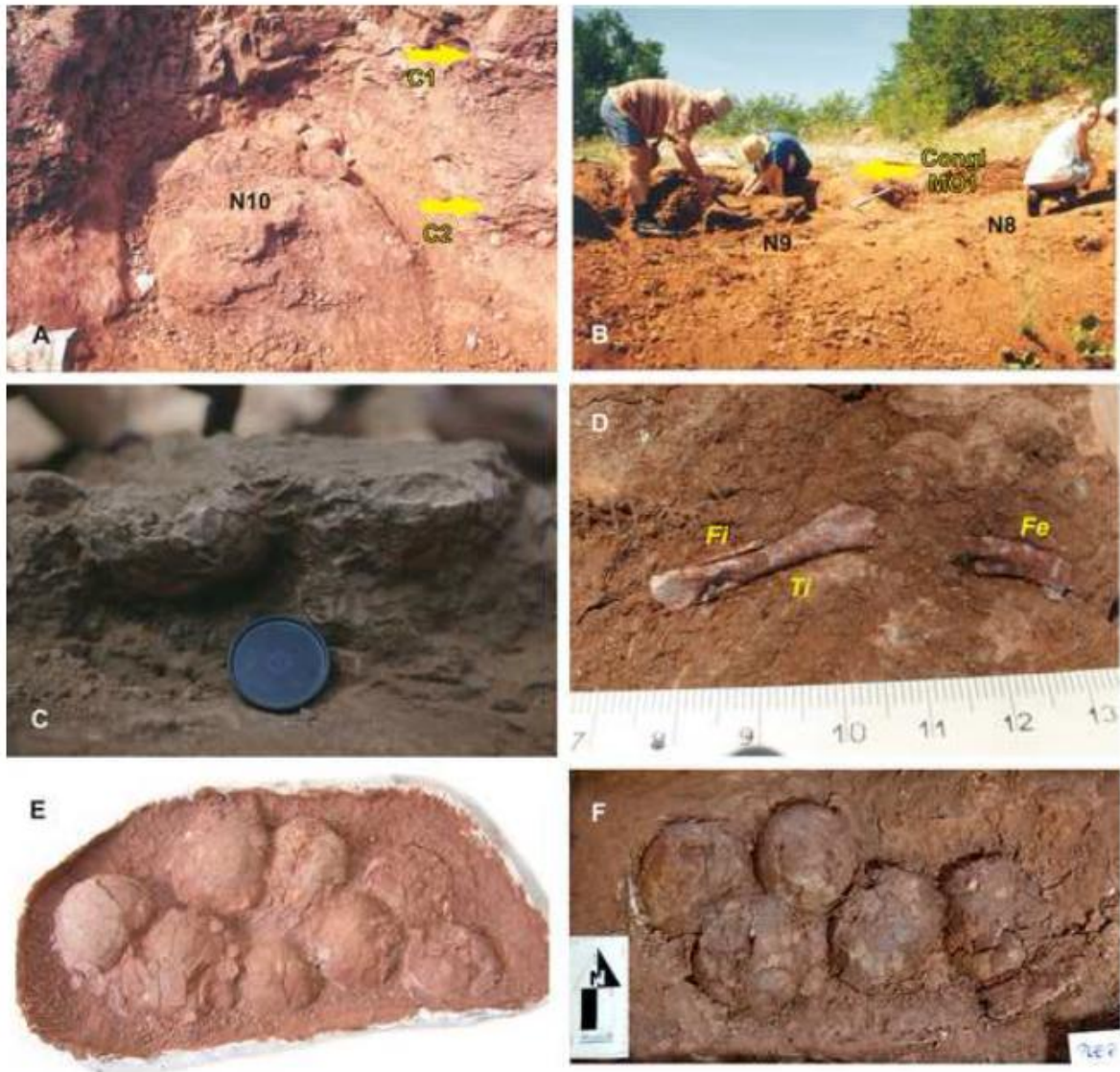


Fig. 5

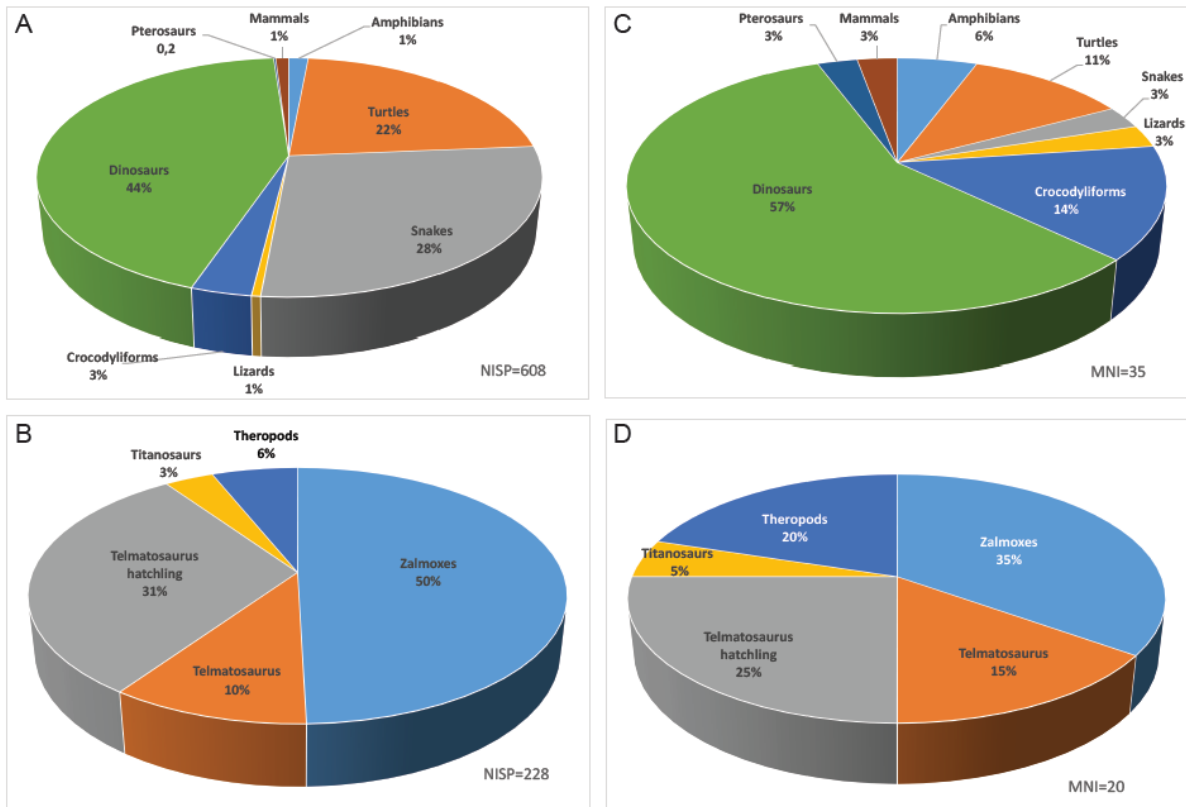


Fig. 6



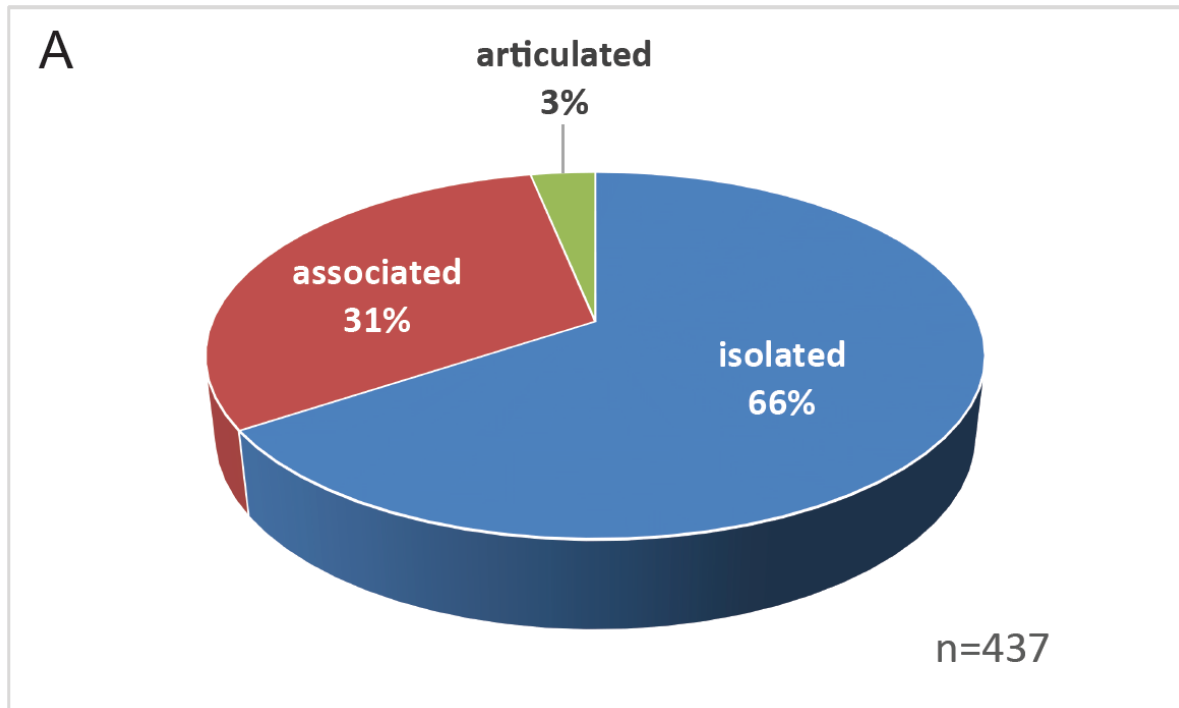


Fig. 7

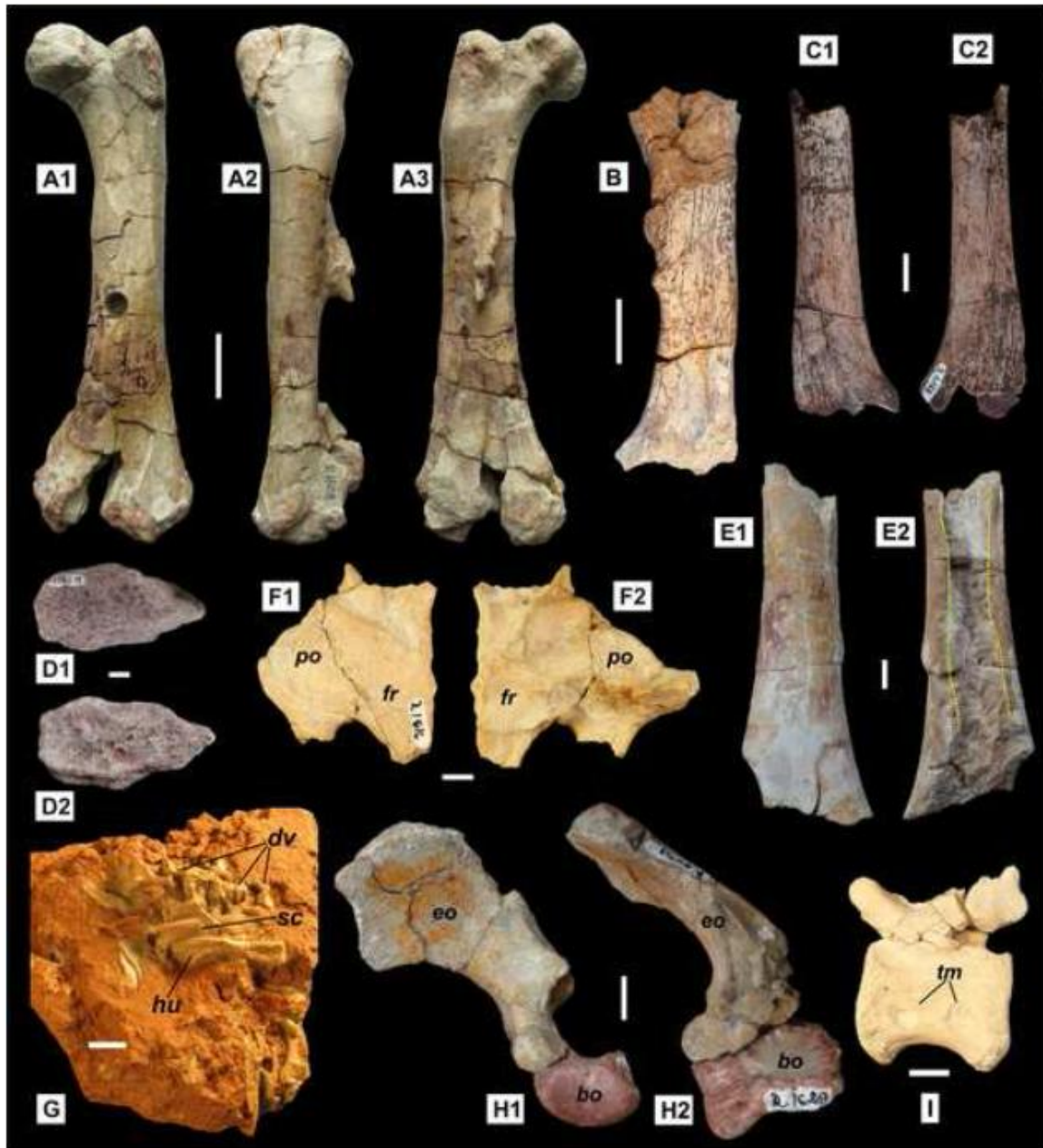


Fig. 8

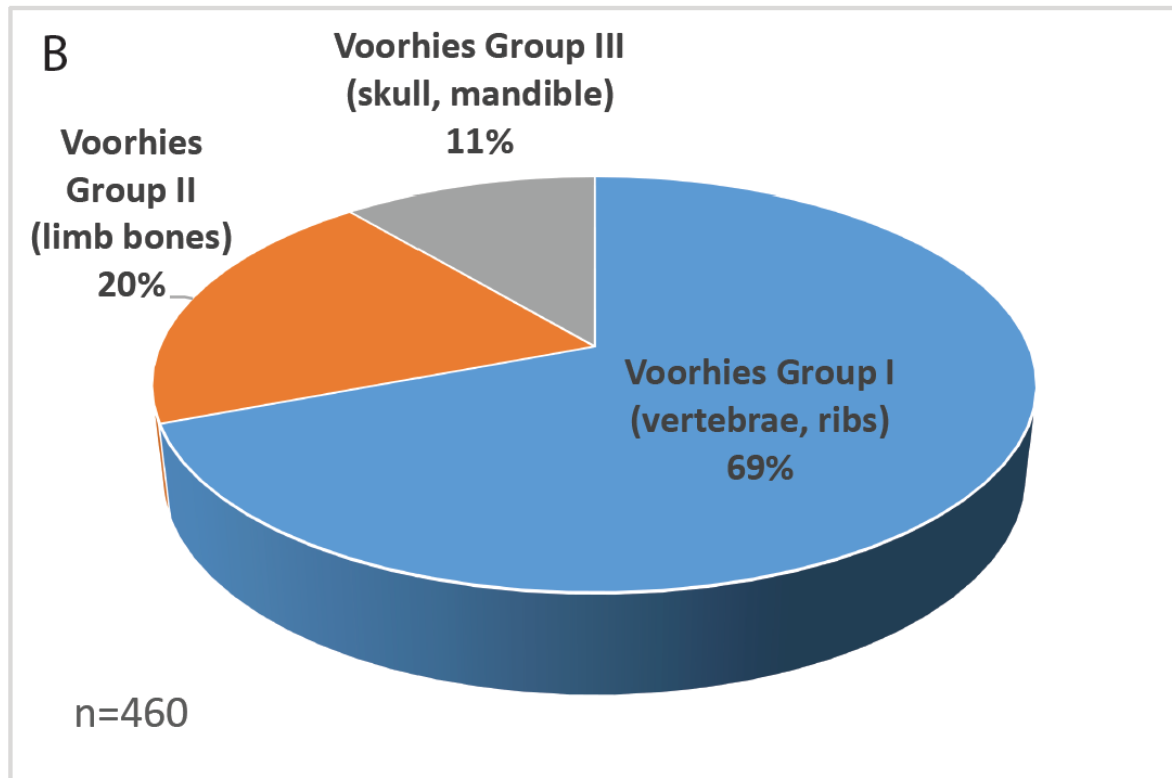


Fig. 9

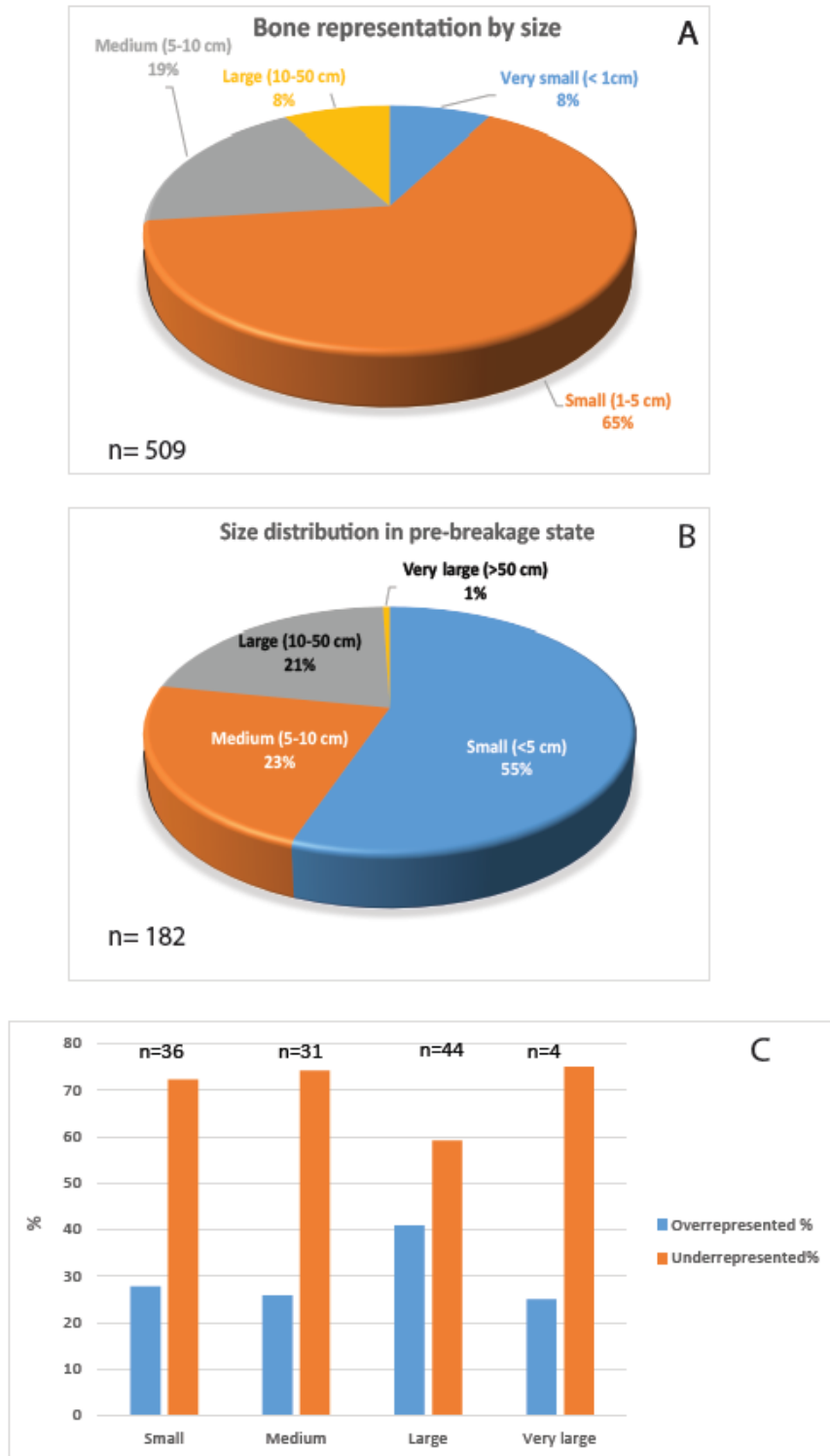


Fig. 10

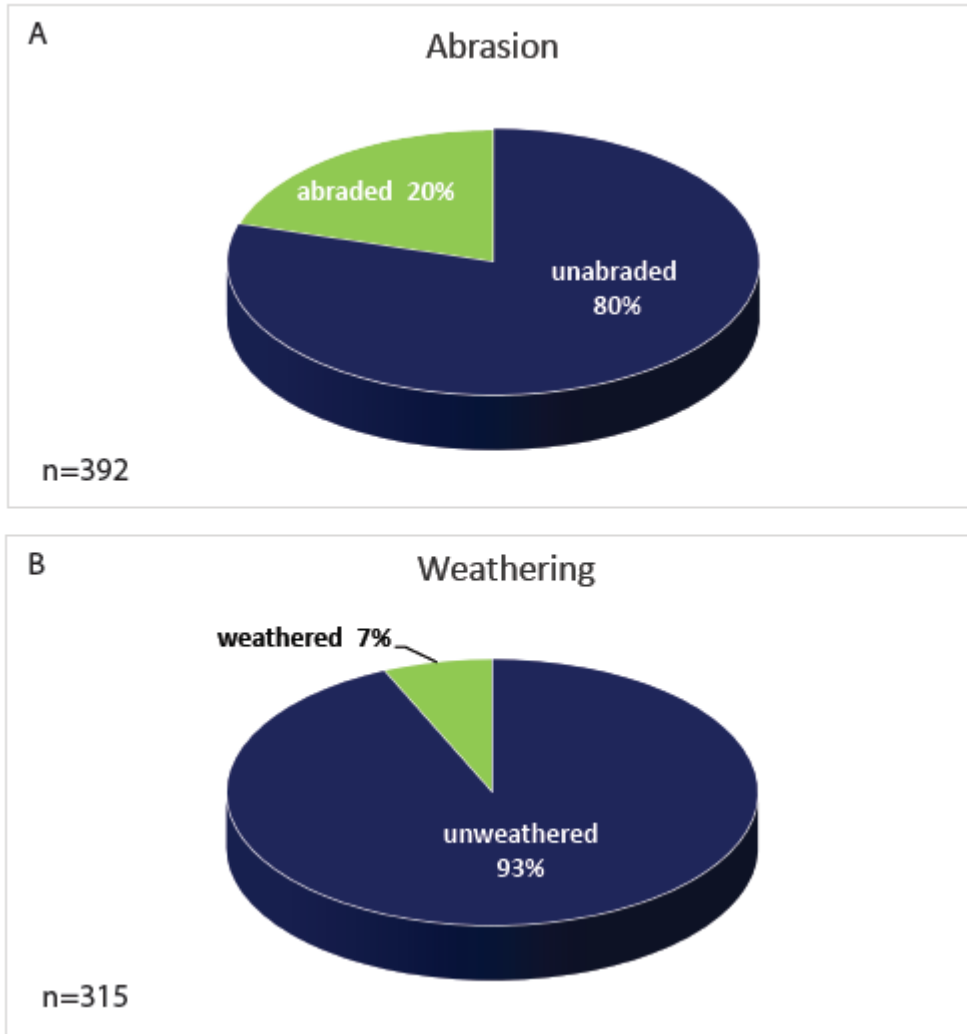


Fig. 11

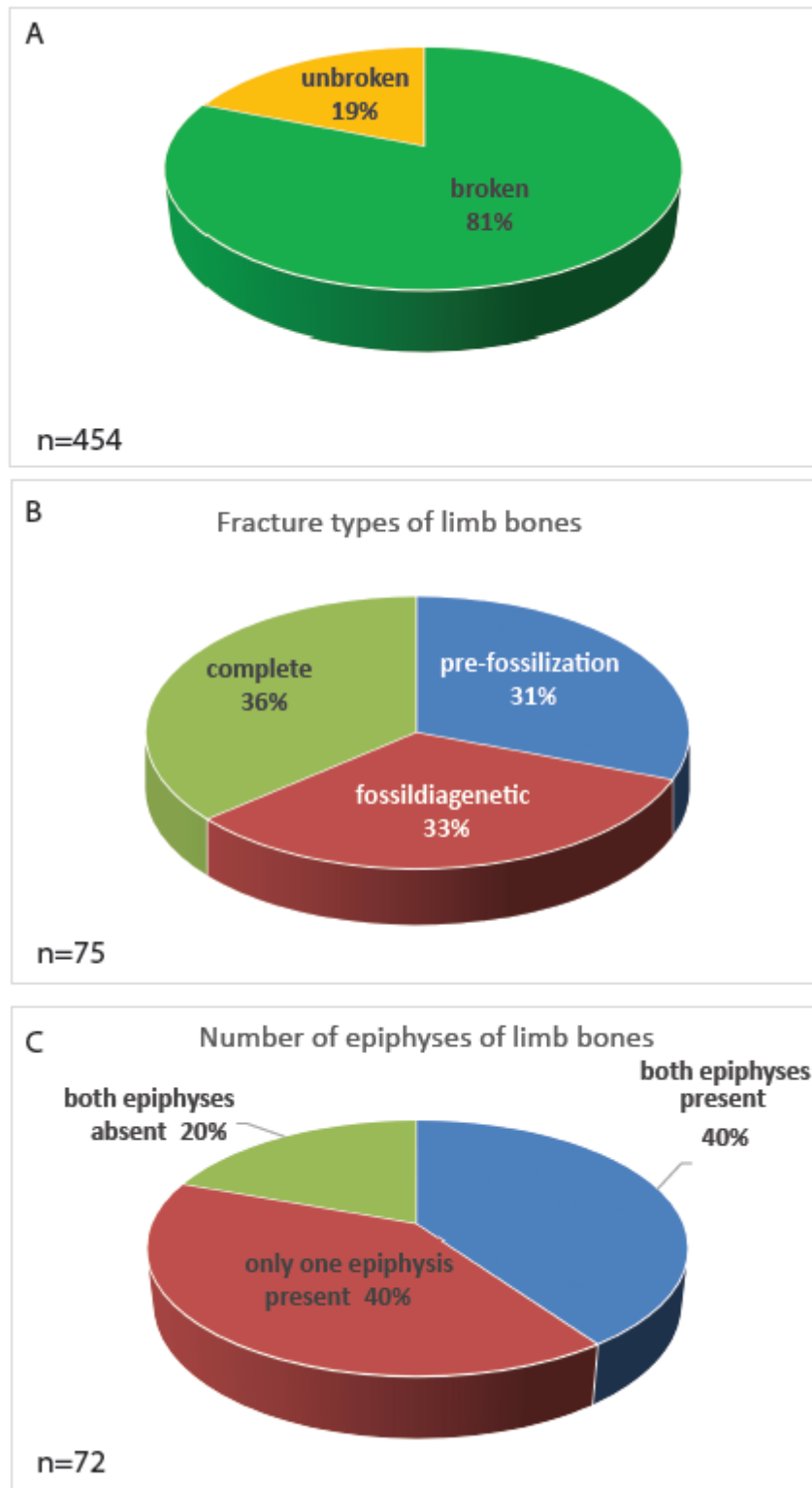


Fig. 12

Table 1

Taxon		Densuş -Ciula Fm.	'Pui beds ,	Râul Mare valley	Sîmpetru Formation	Tuştea site
Fish	<i>Acipenseriformes</i>		X			
	<i>Atractosteus</i> sp.	X				
	<i>Lepisosteus</i> sp	X				
	Characiformes		X			
Amphibian s	<i>Hatzegobatrachus grigorescui</i>	X				
	<i>Paralatonia transylvanica</i>	X	X			
	cf. <i>Eodiscoglossus</i>		X			
	cf. <i>Bakonybatrachus</i>	X				
	Pelobatidae	X				
	Indeterminate anurans	X	X	X	X	X
	<i>Albanerpeton</i>	X	X	X	X	X
Turtles	<i>Kallokibotion</i> sp.	X	X	X	X	X
	Dortokidae indet.	X	X			X
Squamates	<i>Bicuspidon hatzegiensis</i>		X			
	<i>Barbatteius vremiri</i>		X			
	<i>Becklesius nopcsai</i>	X	X			
	<i>B. cf. B. hoffstetteri</i>		X			
	? <i>Slavoia</i> sp.	X				
	? <i>Contogenys</i> sp.			X		
	? <i>Paracontogenys</i> sp.		X			
	Indeterminate lizards	X	X	X	X	X
	Madtsoiidae		X			
	<i>Nidophis insularis</i>	X				X
Crocodiles	<i>Doratodon</i> sp.	X	X		X	X
	<i>Sabresuchus</i> ( <i>Theriosuchus</i> ) <i>sympiestodon</i>	X	X		X	X
	<i>Allodaposuchus precedens</i>	X	X	X	X	X
	<i>Acynodon</i>	X	X		X	X
Pterosaurs	<i>Hatzegopteryx thambemā</i>	X				X
	Azdarchidae indet	X	X	X	X	
Dinosaurs	<i>Struthiosaurus transylvanicus</i>	X		X	X	
	<i>Telmatosaurus transsylvanicus</i>	X	X	X	X	X
	<i>Zalmoxes robustus</i>	X			X	X
	<i>Zalmoxes shqiperorum</i>	X	X	X	X	X
	<i>Zalmoxes</i> sp.	X	X	X	X	X
	<i>Magyarosaurus dacus</i>	X				
	" <i>Magyarosaurus</i> " <i>hungaricus</i>	X			X	

	<i>Paludititan nalatzensis</i>			X		
	Titanosauria indet.	X	X	X	X	X
	Dromeosauridae indet.	X	X	X	X	X
	<i>Balaur bondoc</i>	X				X
	<i>Elopteryx nopsai</i>	X		X	X	X
	Troodontidae indet.			X		
	<i>Richardoestesia</i> sp.	X	X	X		X
	<i>Euronychodon</i> sp.	X		X	X	
	<i>Paronychodon</i> sp.			X		
Birds	Ornithurae indet.	X				
	Enantiornithes indet.			X		
Mammals	<i>Barbatodon transylvanicus</i>		X			
	<i>Barbatodon</i> sp.		X	X		
	<i>Kogaionon unguoreanui</i>				X	
	<i>Kogaionon</i> sp.			X		
	<i>Hainina</i> sp.	X				
	Kogaionidae indet.	X			X	X



Table 2

Layer	Taxa	Skeletal remains	Hatchling material	Eggs	NIS P	Taxon/MNI/horizon*
<b>Conglomerates</b>	unidentified	unidentified	no	no	2	unidentified
<b>MO1</b>	<i>Kallokibotion</i> ; <i>Sabresuchus</i> (' <i>Theriosuchus</i> '); <i>Allodaposuchus</i> ; <i>Zalmoxes</i> ; Titanosauria; <i>Balaur</i> <i>Kallokibotion</i>	vertebrae; ribs; limbs; teeth; sacral region; plates; skull fragments	no	no	46	<i>Kallokibotion</i> =1; <i>Allodaposuchus</i> =1; ; <i>Sabresuchus</i> (' <i>Theriosuchus</i> ')=1; ; <i>Zalmoxes</i> =1; <i>Telmatosaurus</i> =1; Titanosauria=1; <i>Balaur</i> =1
<b>C1</b>	<i>Allodaposuchus</i> ; <i>Zalmoxes</i> ; <i>Telmatosaurus</i> ; Theropoda <i>Kallokibotion</i> ; ; <i>Dortokidae</i> ; <i>Nidophis</i> ; <i>Sabresuchus</i> (' <i>Theriosuchus</i> '); <i>Allodaposuchus</i> ; <i>Zalmoxes</i> ; <i>Telmatosaurus</i> ; Theropoda	vertebrae; ribs; limbs; teeth; plates	<b>yes</b> (R.1786; R.1851; R.1852; R.1979-1982; R.2087-2088)	<b>yes</b> (R.1867; ; R.2145; R.2150; R.2156)	62	<i>Kallokibotion</i> =1; <i>Allodaposuchus</i> =1; ; Theropoda=1; <i>Zalmoxes</i> =1; hatchling- <i>Telmatosaurus</i> =4
<b>MO2</b>	<i>Kallokibotion</i> ; ; <i>Nidophis</i> ; <i>Sabresuchus</i> (' <i>Theriosuchus</i> '); <i>Allodaposuchus</i> ; <i>Zalmoxes</i> ; <i>Telmatosaurus</i> ; Theropoda	vertebrae; ribs; limbs; teeth; scapula; sacral region; plates; dentaries; skull fragments	<b>yes</b> (R.2319; R.2378)	no	52	<i>Kallokibotion</i> =1; <i>Dortokidae</i> =1; <i>Nidophis</i> =1; <i>Allodaposuchus</i> =1; ; <i>Sabresuchus</i> (' <i>Theriosuchus</i> ')=1; ; Theropoda=1; <i>Zalmoxes</i> =2; <i>Telmatosaurus</i> =1; hatchling- <i>Telmatosaurus</i> =1
<b>C2</b>	<i>Kallokibotion</i> ; ; <i>Nidophis</i> ; <i>Zalmoxes</i> ; <i>Telmatosaurus</i> ; <i>Hatzegopteryx</i>	vertebrae; ribs; limbs; teeth; plates; dentaries; skull and mandibular fragments	<b>yes</b> (R.0245-0250)	<b>yes</b> (R.2123-2127)	200	<i>Kallokibotion</i> =1; <i>Nidophis</i> =1; <i>Zalmoxes</i> =1; <i>Telmatosaurus</i> =1; hatchling- <i>Telmatosaurus</i> =1; <i>Hatzegopteryx</i> =1
<b>MO3</b>	<i>Kallokibotion</i> ; ; <i>Dortokidae</i>	ribs; metacarpals; plates	no	no	10	<i>Kallokibotion</i> =1; <i>Dortokidae</i> =1

<b>C3</b>	<i>Kallokibotion</i> ; <i>Acynodon</i> ; <i>Allodaposuchus</i> ; <i>Zalmoxes</i> ; <i>Telmatosaurus</i>	vertebrae; ribs; limbs, teeth; sacral region; plates; skull fragments	no	no	48	<i>Kallokibotion</i> =1; <i>Allodaposuchus</i> =1; ; <i>Acynodon</i> =1; <i>Zalmoxes</i> =2; <i>Telmatosaurus</i> =1
<b>MO4b</b>	<i>Zalmoxes</i>	tooth; vertebrae	no	no	2	<i>Zalmoxes</i> =1
<b>C4</b>	<i>Kallokibotion</i> ; <i>Telmatosaurus</i>	limbs; vertebrae; plates	no	**egg fragments ?	5	<i>Telmatosaurus</i> =1; <i>Kallokibotion</i> =1
<b>MO5</b>	Ornithopoda <i>Kallokibotion</i>	pubis; plates	no	no	2	<i>Kallokibotion</i> =1
<b>C5</b>	<i>Kallokibotion</i> ; <i>Zalmoxes</i>	vertebrae; limbs; teeth; plates; dentaries; skull and mandibular fragments	no	**egg fragments ?	18	<i>Kallokibotion</i> =1; <i>Zalmoxes</i> =1

Table 3

Taxon	NISP	NISP%	MNI	MNI%	Fragmentation rate
Anurans	6	1.0	1	3	6
<i>Albanerpeton</i>	3	0.5	1	3	3
<i>Kallokibotion</i>	130	21.4	3	9	43
Dortokidae	5	0.8	1	3	5
<i>Nidophis</i>	169	27.8	1	3	169
Lizards	3	0.5	1	3	3
<i>Allodaposuchus</i>	12	2.0	2	6	6
<i>Sabresuchus</i> (' <i>Theriosuchus</i> ')	5	0.8	2	6	3
<i>Acynodon</i>	3	0.5	1	3	3
Ornithopoda indet.	37	6.1	0	0	
<i>Zalmoxes</i>	113	18.6	7	20	16
<i>Telmatosaurus</i>	23	3.8	3	9	8
<i>Telmatosaurus</i> hatchling	70	11.5	5	14	14
Titanosauria	8	1.3	1	3	8
Theropoda (including <i>Balaur</i> )	14	2.3	4	11	4
<i>Hatzegopteryx</i>	1	0.2	1	3	1
Kogaionidae	6	1.0	1	3	6
<i>Total</i>	<i>608</i>	<i>100</i>	<i>35</i>	<i>100</i>	<i>288.1</i>

Table 4

Taxon	Vertebrae	Femur	Humerus	Radius	Tibia	Ulna	Fibula	M NI
<i>Zalmoxes</i>	25	2	1	1	6	2	6	7
<i>Telmatosaurus</i>	4	2	0	0	1	0	1	3
<i>Telmatosaurus</i> hatchling	14	11	6	0	12	4	2	5
Titanosauria	7	0	0	0	0	0	0	1
Theropoda (including <i>Balaur</i> )	0	1	1	0	0	1	0	4
<b>Total</b>	<b>50</b>	<b>16</b>	<b>8</b>	<b>1</b>	<b>19</b>	<b>7</b>	<b>9</b>	<b>20</b>

Taxon	Vertebrae %	Femur %	Humerus %	Radius %	Tibia %	Ulna %	Fibula %	M NI
<i>Zalmoxes</i>	4.6	14.3	7.1	7.1	42.9	14.3	42.9	7
<i>Telmatosaurus</i>	1.5	33.3	0.0	0.0	16.7	0.0	16.7	3
<i>Telmatosaurus</i> hatchling	3.1	110.0	60.0	0.0	120.0	40.0	20.0	5
Titanosauria	8.4	0	0	0	0	0	0	1
Theropoda (including <i>Balaur</i> )	0.0	12.5	12.5	0	0	12.5	0	4

Arithmetic mean of RR\_limb bones % = 25

Arithmetic mean of RR\_vertebrae % = 3

Table 5

MNI	<i>Zalmoxes</i>				<i>Teilmatosaurus</i> (adult)				<i>Teilmatosaurus</i> (hatchling)				Titanosauria				<i>Balaur</i>			
	A	E	%R	Size category	A	E	%R	Size category	A	E	%R	Size category	A	E	%R	Size category	A	E	%R	Size category
<i>Skull</i>																				
complete or partial cranial	0	1	0	3	1	0	3	1	0	1	0	1	0	1	0	3	1	0	2	2
quadratum	1	2	7	3	1	2	17	2	2	0	1	0	2	0	3	2	0	0	1	1
frontal	3	2	21	2	2	0	2	2	0	1	0	2	0	3	2	0	0	1	1	1
jugal	2	2	14	3	2	0	3	2	0	1	0	2	0	3	2	0	0	1	1	1
maxilla	1	2	7	3	1	2	17	3	2	0	1	0	2	0	3	2	0	0	2	2
dentary	3	2	21	3	2	2	33	3	2	2	20	1	0	2	0	3	2	0	2	2
surangular	2	2	14	2	1	2	17	2	2	0	1	0	2	0	3	2	0	0	1	1
<i>Vertebrae</i>																				
cervical	0	11	0	2	13	0	2	13	0	1	0	12	0	3	10	0	0	1	1	1
dorsal	2	17	2	2	16	0	2	14	16	18	1	0	12	0	3	13	0	1	1	1
caudal	19	44	6	2	4	49	3	2	49	0	1	3	53	6	3	49	0	1	1	1
sacrum	3	6	7	2	9	0	1	9	0	1	5	5	100	2	1	0	0	1	1	1
<i>Girdle and limb</i>																				
scapula	1	2	7	3	2	0	3	2	2	20	1	1	2	50	3	2	0	2	2	2
coracoid	0	2	0	2	2	0	2	2	0	1	0	2	0	3	2	0	0	1	1	1
humerus	1	2	7	3	2	0	3	6	2	60	1	0	2	0	4	2	0	2	2	2
ulna	2	2	14	3	2	0	3	4	2	40	1	0	2	0	3	2	0	2	2	2
radius	1	2	7	3	2	0	3	2	0	1	0	2	0	3	2	0	0	2	2	2
metacarpal or metatarsal	0	14	0	2	8	0	2	1	8	3	1	0	20	0	2	1	16	6	1	1
phalanges	1	22	1	1	48	0	1	48	0	1	0	36	0	2	4	36	11	1	1	1
ilium	0	2	0	3	2	0	3	2	0	1	1	2	50	4	2	0	0	2	2	2
ischium	0	2	0	3	2	0	3	2	0	1	0	2	0	4	2	0	0	2	2	2
femur	2	2	14	3	2	2	33	3	11	2	110	1	0	2	0	4	2	0	2	2
tibia	6	2	43	3	1	2	17	3	12	2	120	1	0	2	0	3	2	0	2	2
fibula	6	2	43	3	1	2	17	3	2	2	20	1	0	2	0	3	2	0	2	2
$\Sigma$ A	56				13			54			10				5					
$\Sigma$ E	147				176			176			171				158					
%TC		5			2			6			6				3.2					

Size categories:	1;	small: <5 cm;
	2;	medium: 5-10 cm
	3;	large: 10-50 cm

## Highlights

- Megaloolithid eggs and hadrosauroid hatchlings co-occur at Tuştea nesting site
- A detailed taphonomic investigation was conducted to address this ‘Tuştea puzzle’
- The assemblage is parautochthonous, dominated by dinosaurs, but not hadrosauroids
- Two distinct levels contain *Megaloolithus* eggs-*Telmatosaurus* hatchlings association
- Results suggest that Tuştea dinosaur eggs and hatchlings belong to the same taxon