COMPARATIVE PALEOECOLOGICAL ANALYSIS OF SOME MICROVERTEBRATE FOSSIL ASSEMBLAGES FROM THE HAŢEG BASIN, ROMANIA

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Abstract. This paper presents a preliminary quantitative analysis of some of the most important Maastrichtian microvertebrate assemblages from the Haţeg Basin, documenting the relative abundance of the identified taxa and discussing the palaeoecological significance of the differences derived from the current samples. The different abundance of the taxonomic groups, as well as the different abundance of taxa as grouped based on their diet and habitat point to significant between the studied assemblages, that appears to be closely related to the distance each local palaeoenvironment was placed from the river course (i.e. proximal vs. distal).

Keywords: microvertebrates, Maastrichtian, Haţeg Basin.

Rezumat. Analiza paleoecologică comparativă a unor asociaţii de microvertebrate fosile din Bazinul Haţeg, România. Lucrarea prezintă o analiză cantitativă preliminară a unora dintre cele mai importante asociaţii de microvertebrate maastrichtiene din Bazinul Haţeg, documentând abundenţa relativă a diferiţilor taxoni identificaţi şi discutând semnificaţia paleo-ecologică arătată de eşantioanele colectate până în prezent. Abundenţa diferită a grupurilor taxonomice, ca şi abundenţa diferită a taxonilor în funcţie de modul de hrănire şi de habitatul acestora, sugerează diferenţe între asociaţiile studiate, ce apar strâns legate de distanţa la care fiecare paleomediu de viaţă local se găsea faţă de cursul râului (proximal sau distal).

Cuvinte cheie: microvertebrate, Maastrichtian, Bazinul Haţeg.

INTRODUCTION

The uppermost Cretaceous continental deposits of the Haţeg Basin have yielded abundant vertebrate remains giving important information on the taxonomic diversity of the local palaeocommunity, as well as on that of the European Cretaceous vertebrates. The pioneer of fossil vertebrate research in the Haţeg Basin was Franz Nopcsa, who tirelessly collected and described reptilian remains from these deposits. By the abrupt end of Nopcsa's life the faunal list of the Haţeg Basin included representatives of crocodilians, chelonians, sauropods, ankylosaurs, ornithopods, and pterosaurs, all known exclusively from macroscopic remains, mostly found in the „Sânpetru Sandstone" facies, along the Sibişel valley (NOPCSA, 1923).

After a long break, the research on the Cretaceous dinosaur-bearing fauna from the Haţeg Basin was revitalized in the late 1970's by teams led by Dan Grigorescu from the University of Bucharest, Laboratory of Palaeontology and Ioan Groza from the Deva County Museum, and the ongoing research studies have contributed ever since to the better understanding of the palaeontology, palaeoecology, palaeobiogeography, sedimentology and taphonomy of the Haţeg Basin (see review by GRIGORESCU, 2005). Two lithostratigraphical units have been separated in the area: the Densuş-Ciula Formation, comprising three unnamed members of which only the middle one has yielded vertebrate fossil remains, mainly from fine-grained floodplain deposits, and the Sânpetru Formation, without any defined sub-units, that includes Nopcsa's "Sânpetru Sandstone" facies and the fine-grained red deposits cropping out along the Bărbat River, at Pui (GRIGORESCU & ANASTASIU, 1990). The specimens collected from the two formations consist of macrofaunal remains, as well as of microvertebrates, the latter unknown to Nopcsa. The microvertebrate discoveries completed the faunal list with fishes, anurans, albanerpetontids, lizards, snakes, crocodilians, theropods and multituberculate mammals, some of these being represented by new taxa (e.g., RĂDULESCU & SAMSON, 1996, 1997; GRIGORESCU et al., 1999; CODREA et al., 2002; SMITH et al., 2002; VENCZEL & CSIKI, 2003; FOLIE & CODREA, 2005).

Most of the microvertebrate remains have been found in the fine-grained, either bright red-, or drab-coloured deposits corresponding to well-, respectively to poorly drained sectors of a floodplain. The discovery of microvertebrates led to a better understanding on the palaeoecology and palaeobiogeography of the latest Cretaceous faunas from the Haţeg Basin (e.g. CSIKI & GRIGORESCU, 2007).

MATERIAL AND METHODS

The specimens included in this study are represented by anatomically identifiable isolated remains, most of them recovered by bulk screen washing of the sediment, using 0.75 mm and a 2 mm mesh size sieves; the recovered bone fragments and teeth range from 0.75 mm to over 1 cm in size. Teeth and bone fragments hand-picked from the same sites that yielded the screen-washed material, 1 - 4 cm in size, have also been included. The microvertebrate bonebeds being usually attritional accumulations, the remains are represented dominantly by isolated elements. As such, in this study they have been counted as separate individuals (the "number of identifiable remains" counting method; see BADGLEY, 1986; FOSTER, 2001, 2003), with two notable exceptions. Around 50 snake vertebrae and rib fragments, and respectively 7 hadrosaur hatchling vertebrae found at the Tuştea nesting site are considered to derive from the same individual, and have been tallied accordingly as single specimens. This is based on their spatial proximity, commensurate size, similar preservation style, as well as lack of other microvertebrate remains in their surroundings

and the general taphonomical assessment of the site that suggests a dominantly autochthonous–parautochthonous assemblage with little spatial averaging (GRIGORESCU & CSIKI, 2000).

Fishes are rare and represented by comparable amounts of teeth, vertebrae and scales, assigned to characids and lepisosteids (e.g. GRIGORESCU et al., 1999). The frog remains are numerous, being dominated by limb bone fragments (radioulnae, tibiofibulae, humeri or phalanges), followed by a fair amount of vertebrae, while the taxonomically diagnostic elements, such as the ilia or the maxillae/dentaries/prearticulars are the rarest. The albanerpetontid material mostly consists in toothed maxillae and dentaries, the limb bones (especially humeri fragments) and vertebrae occurring in lower percentages. The rarest albanerpetontid bones recovered so far are the frontal bones fragments (GRIGORESCU et al., 1999; FOLIE & CODREA, 2005), a very diagnostic element within the genus *Albanerpeton* (e.g. GARDNER, 2002). The lizard remains are dominated by maxilla/dentary fragments, suggesting a great variety of taxa (over 10; CSIKI, 2005), of which only a few have been determined tentatively (FOLIE & CODREA, 2005).

Lizard vertebrae are also present, although in a significantly lower percentage. Snakes are represented by a single vertebra at Budurone, and by the above-mentioned associated vertebrae and rib fragments found at Tuştea; although snake remains have been previously reported from Pui (FOLIE & CODREA, 2005), the present study takes into account only the remains curated at the University of Bucharest, in the Laboratory of Palaeontology collections. The considered crocodilian material consists exclusively of isolated teeth, assigned to four taxa, as detailed below. Except for the hatchling vertebrae association mentioned above, the ornithopods are only represented by teeth fragments, as are the sauropods, pterosaurs and multituberculates.

Bird remains are restricted to very few fragmentary limb bones; while isolated teeth make up the largest part of the theropod material, besides markedly fewer phalanges (especially unguals). Four microvertebrate-yielding sites have been taken into account (Fig. 1), covering both of the above-mentioned lithostratigraphic units, sites that yielded the largest part of the microvertebrate remains housed in the collections of the University of Bucharest Laboratory of Palaeontology. Two of the sites, Fântânele 1 and Budurone, are located in gray-green and gray-blue mudstones, the depositional environment inferred from the sedimentological data being that of a poorly drained distal floodplain channel or pond (CSIKI et al., 2008), while the other two, Tuştea and Pui, consist of red mudstones with pedogenetic calcrete levels, interpreted to have deposited in a well-drained floodplain, with temporarily dry periods when soil levels have formed (GRIGORESCU & CSIKI, 2002; BOJAR et al., 2005; THERRIEN, 2005; THERRIEN et al., 2009).

During the last 15 years, large quantities of fossiliferous sediments were processed from these sites, although these differ due mainly to richness of the individual sites, accessibility and spatial extent of the fossiliferous sedimentary body; accordingly, the processed quantities represent about 3,400 kg from Fântânele 1, 1,200 kg Budurone, but only about 600 kg from Tuştea and only an amount as small as 250 kg from Pui, where surface collecting was more important. In order to assess the palaeoecology and palaeoenvironment of the local communities preserved within these sites based on the microvertebrate fossil record, raw specimen counts have been used to calculate taxonomic abundances, as well as abundance of palaeoecological guilds including taxa separated by diet and by habitat. The relative abundance has been detailed within some of the vertebrate groups, where the recovered material allowed a detailed taxonomic identification (i.e. at the generic level), namely among the crocodilians, the theropods and the ornithopods.

Figure 1.The position of the four microvertebrate sites from the Haţeg Basin discussed in this paper (Google Earth satellite imagery).
Figura 1. Poziţia celor patru situri de microvertebrate din Bazinul Haţeg discutate în această lucrare (imagine satelitară Google Earth).

RESULTS AND DISCUSSIONS

The relative taxonomic abundance tally for each site shows the presence of diverse local microvertebrate assemblages, comprising remains belonging to several higher-level taxa (see Fig. 2); it is worth noting that certain taxa are rather rare, and are occurring only in some of the sites. Remains belonging to fishes, frogs, albanerpetontids, lizards, snakes, crocodilians, ornithopods, sauropods, theropods, birds, pterosaurs, and multituberculate mammals have been identified in this analysis; a further group of remains (indet. = taxonomically indeterminate) was also used, to include those remains that are identifiable anatomically, but not taxonomically, because of their fragmentary nature. The most commonly identified groups are the anurans, albanerpetontids, lizards, crocodilians, ornithopods, theropods and multituberculates, which appear, although in sensibly different percentages, within each of the four sites considered.

The faunal assemblages of Budurone and Fântânele 1 are dominated by frogs and albanerpetontids, the only definitively terrestrial animals that reach relatively high abundances being the lizards. This suggests the existence of an aquatic habitat, where the small aquatic and amphibious vertebrates would thrive. The dominance of aquatic taxa is even more obvious for the Budurone assemblage, where terrestrial vertebrates common in the other sites (such as ornithopods, theropods, multituberculates) are virtually absent, suggesting they were only seldom visitors of these local paleoenvironments. Even the top of the food chain appears here to be dominated by crocodilians (mainly semi-aquatic animals), while other, definitively terrestrial predators, such as theropods or snakes, are rare.

By contrast, the relative taxonomic abundance figures from Tuştea and Pui are similar to one another, while being different from those seen at Budurone and Fântânele 1: this pattern is matched by the lithofacial affinities of the sites. The terrestrial animals are much better represented, the ornithopods reaching here the highest observed abundances within the sites considered in this study. The crocodilians are still present, suggesting a near-water environment, but the theropods and multituberculate mammals rise in abundance. While the crocodilians and lizards are present in the Pui and Tuştea assemblages with almost equal relative percentages, the frogs and albanerpetontids are more abundant at Pui, gaining ground compared to the ornithopods and theropods that dominate the Tuştea assemblage.

It can be suggested that this difference could be related to the distance from the river within the floodplain, the Tuştea environment being more distal, located farther from the water course than the one from Pui, as it contains only a small amount of semi-aquatic vertebrates, and being obviously dominated by terrestrial vertebrates, such as the ornithopods, mammals and lizards, as well as the dromaeosaurids. This hypothesis must be checked in the future by sedimentological studies, as well as by expanding the sample of microvertebrate bonebeds.

A plot showing the relative abundance of vertebrates based on their habitat preferences (Fig. 3) appears to support the conclusions drawn from the taxonomic abundance data.

The aquatic vertebrates are very rare overall in the Haţeg Basin, being represented only by a few teeth and scales collected from the Budurone microvertebrate fossil site. The paucity of fish remains is most probably caused in part by their fragility, as most of the recent aquatic habitats host significant fish populations in their local assemblages, and fishes are frequently found in Late Cretaceous continental ecosystems as well (e.g. BRINKMAN et al., 2004). Nevertheless, the ganoid scales of lepisosteids are resistant elements and should occur in larger numbers, had the fishes been present commonly in the local ecosystems. Their rarity suggests thus that fishes were rare in the local community, although explanation of this unusual situation appears to be elusive for the moment.

Therefore, the guilds of semi-aquatic (frogs, albanerpetontids, and some crocodilians) and terrestrial (ornithopods, sauropods, theropods, birds, snakes, mammals, and pterosaurs, also including certain crocodilians – e.g. KARL et al., 2006) taxa were used as proxies to assess the degree of water-dependency of the local assemblages derived from the four sites under scrutiny. The plotted data (Fig. 3) show similarities between the habitat preference patterns emphasized by the vertebrates from Fântânele 1 and Budurone, the semi-aquatic animals being more abundant than the terrestrial ones, by a ratio higher than 2/1. The situation is different at Pui, where the semi-aquatic vertebrates are still more abundant than the terrestrial ones, but only marginally so, showing that the environment must have been a dryer, but still near-river one, where the two groups of animals lived in comparable relative abundances. That is not the case for Tuştea locality, dominated by terrestrial vertebrates that are more than twice as abundant as the semi-aquatic ones, suggesting a more distal, better drained part of the floodplain.

The local foodchains must be also tightly connected to the palaeoenvironment of the local assemblages; we checked whether this is upheld by using a taxon breakdown by dietary guilds (Fig. 4). For the two water-dominated environments from Fântânele 1 and Budurone, the invertivores, represented by frogs, albanerpetontids and lizards, make up the largest part of the vertebrate diversity. Herbivores are rare and less abundant than carnivores, and therefore they could not have sustained the local ecosystem if it had not been for the invertivores, that were the primary prey items of the crocodilians and, possibly of some of the theropods. The assemblage from Pui is also dominated by invertivores, but not by a large margin. The herbivores are also fairly well represented here, while the number of theropods is increased too, probably in relation to the higher abundance of the potential prey taxa. An even more typical terrestrial diet-based assemblage can be seen at Tuştea, where the herbivores (mostly ornithopods) are the most abundant taxa, representing the food source for the theropods and the crocodilians (regardless the semi-aquatic or terrestrial habitat of the latter). The omnivorous mammals, present in low numbers at the other sites, are also relatively more abundant at Tuştea, where a more distal, dry environment is suggested by the sedimentological data (THERRIEN, 2005), but also by the previously reported taxonomic and habitat preference abundance figures.

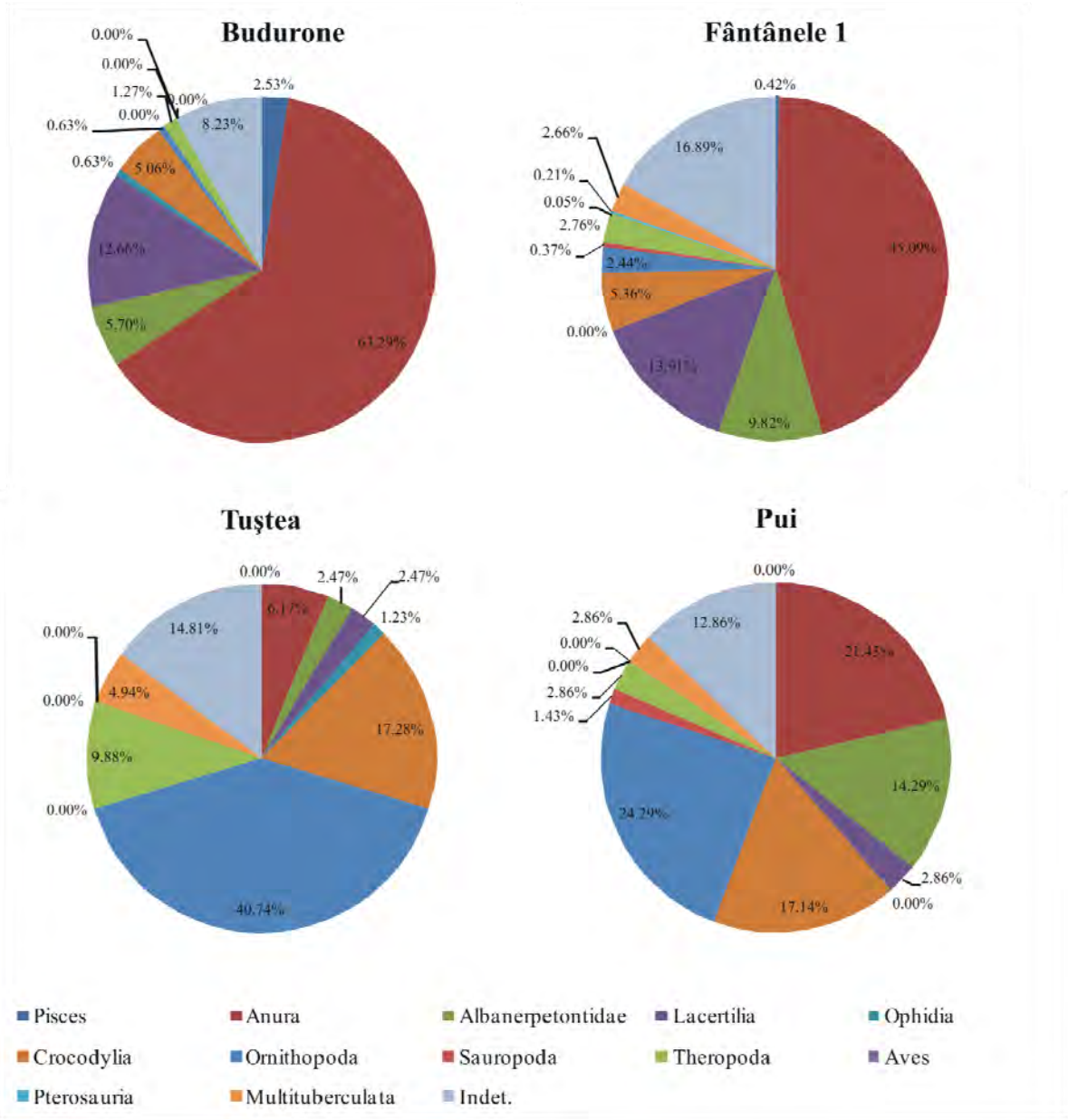

Figure 2. Relative taxonomic abundance in the studied microvertebrate assemblages from the Haţeg Basin.Taxonomic groups from the legend appear on the charts clockwise, starting from its top.
Figura 2. Abundenţa taxonomică relativă pentru asociaţiile de microvertebrate din Bazinul Haţeg. Grupurile taxonomice din legendă apar pe grafic în sens orar, începând din partea de sus a acestuia.

Wherever the data offered by the fossil record allowed it, genera-level breakdown was also accomplished within the vertebrate groups discussed above, and the relative abundance of the different genera within their higher-level taxa has been studied as well. This detailed study was possible only for the crocodilians, theropods and ornithopods.

The crocodilians are represented mostly by isolated teeth belonging to four genera: *Allodaposuchus*, a middle-sized semi-aquatic generalized carnivore (DELFINO et al., 2008); *Acynodon*, a small-to-medium-sized semi-aquatic specialized durophagous carnivore or omnivore (MARTIN et al., 2006, DELFINO et al., 2008a); *Doratodon*, a small-sized terrestrial carnivore (MARTIN et al., 2006, submitted) and a newly reported taxon (MARTIN et al., submitted) referred to *Theriosuchus*, a terrestrial omnivore (e.g., KARL et al., 2006). The relative abundances of these genera do not show

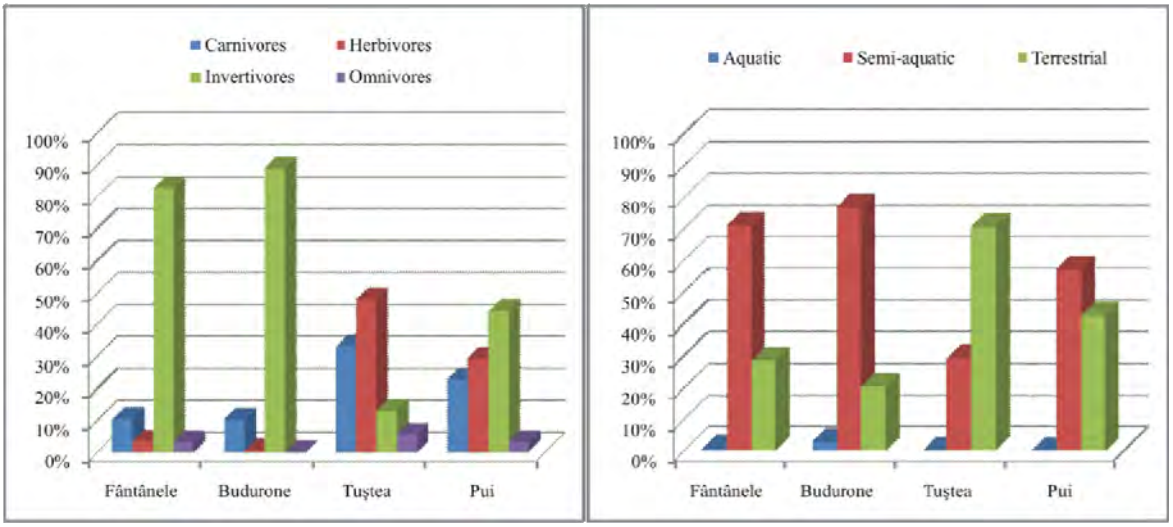

Figure 3. Relative abundance of microvertebrates from the Haţeg Basin based on their diet.
Figura 3. Abundenţa relativă a microvertebratelor din Bazinul Haţeg pe baza dietei acestora.
Figure 4. Relative abundance of microvertebrates from the Haţeg Basin based on their habitat.
Figura 4. Abundenţa relativă a microvertebratelor din Bazinul Haţeg pe baza habitatului acestora.

a clear connection to the environment. *Allodaposuchus* is by far the most abundant at all of the four sites; it is accompanied by all the other three crocodilians at Fântânele 1, while by only one other crocodilian taxon at Budurone, Tuştea and Pui: *Theriosuchus*, *Acynodon*, and *Doratodon*, respectively. This could be the result of a strong competition between the crocodiles, the local food source not supporting such a variety. However, the apparent absence of different crocodilian genera might also be linked to the reduced amount of data from the respective sites, since the overall number of collected microvertebrate remains is much higher at Fântânele 1 (1,883 specimens), than at Budurone (158 specimens), Tuştea (81 specimens) and Pui (70 specimens).

Three types of theropods have been identified based on their teeth morphology: *Euronychodon*, *Richardoestesia* and indeterminate dromeosaurids. As in the case of the crocodilians, the highest theropod diversity is reached at Fântânele 1, where all the theropods are represented, with dromeosaurids and *Euronychodon* being slightly more abundant than *Richardoestesia*. The only theropod found at Budurone is *Euronychodon*, as are the dromeosaurids at Pui; the dromesaurids also dominate among the theropods from Tuştea, followed by *Richardoestesia*. Again, as in the case of the crocodilians, this absence of one theropod from a site or another might be caused by a taphonomical and/or recovery bias in these last three sites. The presence of *Richardoestesia* might indicate once more the river proximity of all these sites, the dental morphology of this maniraptoran theropod suggesting it was a fish-eater (BASZIO, 1997).

The ornithopods are represented by isolated teeth fragments, assigned to the euornithopod *Zalmoxes*, with two recognized species, *Z. robustus* and *Z. shqiperorum* (WEISHAMPEL et al., 2003), and respectively to the hadrosaurid *Telmatosaurus transylvanicus*; the two genera make up the largest part of herbivorous dinosaur remains found at the microvertebrate sites, along with a few teeth questionably assigned to the sauropods. *Zalmoxes* is more abundant in all the four sites discussed (Fig. 5). The relative abundance of *Zalmoxes* and *Telmatosaurus* is remarkably similar for three of the four sites, suggesting a rather constant relative abundance for the entire basin. However, at species level breakdown, an even more balanced distribution might have been present, since the two species of *Zalmoxes* cannot be separated based on their dental morphology (WEISHAMPEL et al., 2003). Assuming the two species had a fairly similar abundance, the three ornithopod species would have a very well balanced distribution throughout the basin. The data from Budurone are not reliable, since the entire ornithopod material is represented by a single *Zalmoxes* tooth fragment that is probably of parautochthonous origin (CSIKI et al., 2008).

CONCLUSIONS

The comparative study of the most important microvertebrate assemblages from the Maastrichtian of the Haţeg Basin offer interesting insights on the differences between the local habitats.

Two of the four sites taken into account, Budurone and Fântânele 1, suggest a water-bound environment, typical for the floodplain ponds, poorly drained floodplains and abandoned river channels. The microvertebrate remains collected from these sites show a dominance of the semi-aquatic vertebrates, such as frogs, albanerpetontids and crocodilians. As a consequence, the invertivore lower vertebrates are abundant, the carnivores being best represented by the semi-aquatic crocodile *Allodaposuchus*, followed by other, more specialized crocodilians, such as the durophagous *Acynodon*, and by rare theropods among which some, like *Richardoestesia*, probably fed mainly on fish. The conclusions based on quantitative information derived from microvertebrates support the sedimentological data,

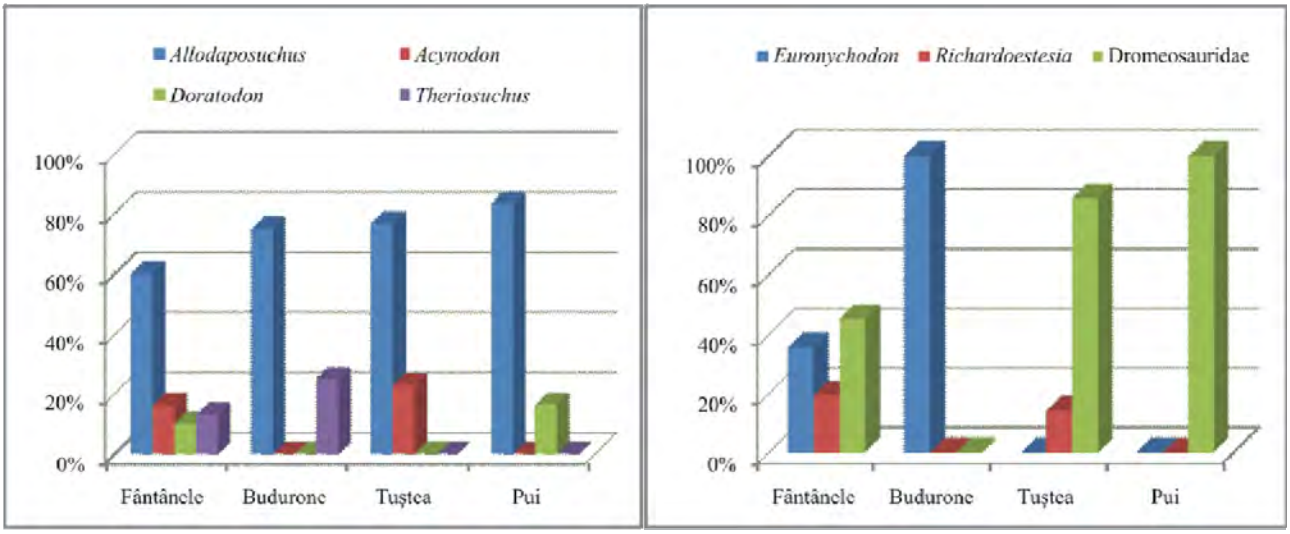

Figure 5. Relative abundance of the crocodilian taxa in the microvertebrate assemblages from the Haţeg Basin.
Figura 5.Abundenţa relativă a taxonilor de crocodilieni în asociaţiile de microvertebrate din Bazinul Haţeg.
Figure 6. Relative abundance of the theropod taxa in the microvertebrate assemblages from the Haţeg Basin.
Figura 6. Abundenţa relativă a taxonilor de theropode în asociaţiile de microvertebrate din Bazinul Haţeg.

as the fossiliferous rocks are dark coloured fines, due to the presence of ferrous iron, present in rocks deposited in poorly drained channels or ponds.

The other two sites, Tuştea and Pui, suggest a distal floodplain environment where the terrestrial and the semi-aquatic vertebrates lived together, with the terrestrial ones dominating in abundance. The herbivore dinosaurs are by far the most important, followed by theropods and crocodilians, both terrestrial and semi-aquatic. The semi-aquatic invertivores lose ground, and the multituberculate mammals occur in higher numbers. Dromeosaurids, efficient killers of the herbivorous dinosaurs, are the most abundant theropods in these sites, followed at the top of the food chain by *Allodaposuchus*, the most abundant of crocodilians. The dominance of terrestrial vertebrates is more obvious for the Tuştea assemblage, where the terrestrial vertebrates are more than twice as many than the semi-aquatic ones. The sedimentological study of the ferric iron-bearing red mudstones with pedogenetic calcrete levels supports this conclusion.

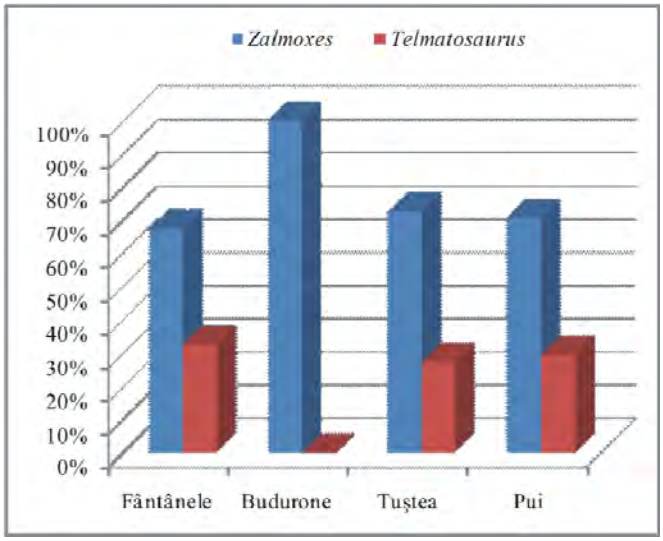

Figure 7. Relative abundance of the ornithopod taxa in the microvertebrate assemblages from the Haţeg Basin.
Figura 7. Abundenţa relativă a taxonilor de ornithopode în asociaţiile de microvertebrate din Bazinul Haţeg.

The raw specimen counts cannot identically reflect the original composition of the assemblage, but the larger the data sets, the closer the two images are. Plotting several different types of data (taxonomic abundance, abundance by diet or habitat preference guilds) may show how representative the data are, in the case of correlative results. Although the data presented here support the difference between the four microvertebrate assemblages, the information can (and will be) further refined by continuing the sampling at Budurone, Pui and Tuştea, the data from Fântânele 1, based on a data set comprising 1,883 specimens, being the most reliable.

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