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TAPHONOMIC AND PALAEOECOLOGIC INVESTIGATIONS OF THE LATE CRETACEOUS (SANTONIAN) IHARKÚT VERTEBRATE ASSEMBLAGE (BAKONY MTS, NORTHWESTERN HUNGARY)

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Abstract

The Iharkút vertebrate locality, an open-pit mine in the Bakony Mountains (western Hungary), has provided a rich and diverse assemblage of Late Cretaceous (Santonian) continental vertebrates. The isolated and associated remains represent 31 different taxa including fish, amphibians, turtles, lizards, pterosaurs, crocodilians, non-avian dinosaurs and birds. Sedimentologic investigations suggest that the Iharkút depositional environment was represented by the floodplain of a very low-gradient river. The 10-50 cm thick bonebed of site SZ-6, is the most important fossiliferous layer in the open-pit mine and analysis of this site indicates alternating energy conditions during the bone accumulation, which resulted in fossils of different states of preservation being deposited together. The vertebrate assemblage of site SZ-6 includes three main different subsets with widely different taphonomic history. The characteristics and the preservation mode (high rate of abrasion and the spherical shape) of the "bone pebbles" suggest that this type of the isolated bones was more exposed to abrasion and probably the remains were transported from farther away than the other isolated bones. The second group includes 88% of the Iharkút collection, containing most of the identified isolated bones and teeth, and represents polytypic attritional remains transported and deposited by high density flow during ephemeral flood events. Meanwhile the monospecific ankylosaur skeletal material from Iharkút site SZ-6 may represent a mass death assemblage because seven skeletons of *Hungarosaurus* were discovered from an area of approximately 400 m^2 and in many cases close to each other in the same layer. The Iharkút vertebrate assemblage is dominated by bones of aquatic/semi-aquatic animals, while the number of terrestrial animal remains is subordinate. The taphonomic analysis of the ankylosaur material from Iharkút locality further strengthens the previously suggested hypothesis that some of the ankylosaurs preferred wetland habitats (e.g. areas along fluvial

systems) while the other two herbivorous dinosaur groups from Iharkút (ornithopods and ceratopsians) were probably living in distal habitats.

1. INTRODUCTION

Vertebrate taphonomy is a relatively young discipline within paleontological investigations and initially has been focused on Tertiary mammal assemblages (e.g. Voorhies, 1969; Shotwell, 1955; Behrensmeyer, 1975; Shipman, 1981; Badgley, 1986a,b; Weigelt, 1989; Badgley et al., 1995; see also Behrensmeyer et al., 2000 and references therein), and there were only a limited number of researches which expanded the taphonomic investigations for vertebrate assemblages of Mesozoic sites (Dodson, 1971; Dodson et al., 1980; Wood et al., 1988). In the last three decades, many taphonomic investigations were published related to Mesozoic dinosaur sites of North America (e.g. Rogers, 1990; Fiorillo, 1991; Varricchio and Horner, 1992;, Schwartz and Gillette, 1994; Varricchio, 1995; Carpenter, 1998; White et al., 1998; Ryan et al., 2001; Jennings and Hasiotis, 2006; Britt et al., 2009; see also Eberth et al., 2007a and references therein), while only a few studies have been focusing on the Mesozoic dinosaur assemblages of Europe (e.g. Grigorescu, 1983; Norman, 1987; Sander, 1992; Cook, 1995; Benton et al., 1997; Posmosanu and Cook, 2000; Pereda Suberbiola et al., 2000; Therrien, 2005; Csiki et al., 2008, 2010; Baele et al., 2012; see also Eberth et al. 2007a and references therein).

Iharkút is a Late Cretaceous (Santonian) vertebrate-bearing locality in the Bakony Mountains of western Hungary (Fig. 1A), where productive and continuous excavations have been carried in the last thirteen years (Ősi et al., 2012b). Field work resulted in a very rich and diversified assemblage of continental animals (i.e. fish, amphibians, turtles, mosasaurs, lizards, pterosaurs, crocodilians, dinosaurs including birds). The large amount of available data made necessary a detailed taphonomic evaluation of the vertebrate remains from the

Iharkút locality. Approximately 9234 complete and fragmentary bones and 2259 teeth of at least 31 different taxa have been collected from Iharkút. This abundance and diversity of fossil taxa plays a significant role in the understanding of the history of European Late Cretaceous continental vertebrate faunas. Furthermore, due to the palaeogeographic position (on the Apulian microplate within the western Tethyan archipelago) and the Santonian age of the locality fills an important gap in the Late Cretaceous record of continental vertebrates in Europe. Several taxonomic, palaeobiologic and palaeobiogeographic investigations have been published to demonstrate the diversity and faunalistic relationships of the Iharkút vertebrates (e.g. Ősi, 2005; Ősi et al., 2005; Ősi and Makádi, 2009; Ősi et al., 2010a,b; Rabi et al., 2011; Szentesi and Venczel, 2012; Makádi et al., 2012; Ősi et al., 2012a,b; Makádi, 2013a,b). Taphonomic and palaeoecologic studies of the locality are, however, quite underrepresented.

The aim of the present work is to review the taphonomic features of Iharkút vertebrate assemblage and to interpret the sedimentologic characteristics of the lithofacies units in order to determine the depositional model of vertebrate fossils. After discussing the geological and sedimentologic aspects of the locality, we provide an overview of the relative abundance of vertebrate groups and review the modifications on both the isolated and the associated/articulated skeletal remains. Finally, we discuss the sedimentologic, taphonomic and palaeoecological significance of the locality and its fauna, and determine the possible accumulation circumstances of the isolated bone assemblages and also the skeletal material.

2. GEOLOGICAL SETTING

The Iharkút locality is situated on an uplifted Mesozoic block of the North Bakony area in the Transdanubian Range (TR). In Late Mesozoic times the TR was part of the northern segment of the Apulian microplate between Africa and Europe (e.g. Channell et al., 1979; D'Argenio and Mindszenty, 1991, 1992). Until after Late Cretaceous times it shared the history of the

Eastern Alps (Oberhauser and Bauer, 1980; Mindszenty et al., 1987). Its Triassic carbonate platforms were drowned in the Early Jurassic when the opening of the Neotethys resulted in lithospheric extension. In early Cretaceous times extension changed for compression the TR - sitting on the northern tip of the Periadriatic margin – soon became involved in the deformation of the Austro-Alpine domain. Thrusting nape movements and the related uplift resulted in intense erosion and subaerial exposure in this area. In Late Cretaceous times bauxite deposits formed in those sectors of the exposed carbonate terrains where local topography provided for relative isolation from coarse-grained clastics. Progressing deformation resulted in differential subsidence of the previously uplifted areas and bauxites became covered by clastic sediments eroded from the hinterland (Wagreich, 1988; Willingshofer et al., 1999). Based on the striking geological similarity of the TR and the Southern Alps, Kázmér and Kovács (1985) proposed that in its present position the TR was an "escaped" block having been originally situated in the Alps somewhere in the vicinity of the present day Drauzug, between the depositional environments of the Northern Calcareous Alps (Austria) and the Southern Alps (Italy). They suggested that the reason for the eastward escape was large-scale right-lateral displacement along the Periadriatic lineament in early Cenozoic times resulted by the convergence of the African and European plates. Cretaceous bauxites of Austria occurring right below the basal layers of the Late Cretaceous Gosau sedimentary complex are strikingly similar to Cretaceous bauxites of Hungary supporting the original juxtaposition of the two areas and corroborating the idea of Kázmér and Kovács (1985).

Though differences between the history of the TR and the Northern Calcareous Alps became more pronounced only in Tertiary times, subtle differences between the subsidence histories of the two areas were obvious already as early as in Late Cretaceous times. Bauxites in the NCA became covered already in Turonian times (Siegl-Farkas and Wagreich, 1996)

and accelerated subsidence resulted in the accumulation of thousands of meters of the clastic Gosau sedimentary complex there, whereas in the TR bauxites remained exposed until after the early Santonian. Subsidence began later and was much slower here with the thickness of the Late Cretaceous cover never exceeding 1000 meters (Haas, 2001).

The Cenozoic story of the TR consists of flexural deformation in early Palaeogene times followed by repeated events of strike-slip faulting at various scales and of various geodynamic controls. In the Miocene, as a result of overall, extension related subsidence of the wider surroundings, also the TR became partly submerged. This was the time of the establishment of the Pannonian basin, a Neogene structure formed as a result of large scale extension and attenuation of the lithosphere in the areas surrounded by the Carpathians (Royden and Horváth, 1988). In latest Cenozoic times compression resumed and basin inversion began. Erosion of the uplifting sectors (like the TR) resulted in exhumation of the Mesozoic and Cenozoic basement. Iharkút is one of those uplifted blocks where a typical Mesozoic- Cenozoic succession with a major regional unconformity and the related bauxites between the eroded surface of Late Triassic dolomites and their Late Cretaceous and Cenozoic cover are exposed at the actual surface.

2.1. Local geology

The oldest rocks in the Iharkút open-pit mine are Upper Triassic shallow marine dolomites (Main Dolomite Formation) the irregular karstified surface of which was filled by bauxite (Nagytárkány Bauxite Formation) during the Upper Cretaceous (pre-Santonian) as a result of subaerial exposure (Gellai et al., 1985) (Figs. 1B and C). Bauxite and dolomite are unconformably overlain by the Late Cretaceous Csehbánya Formation, which is rich in both plant and vertebrate fossils. The Csehbánya Formation is a typical alluvial, flood-plain unit consisting mainly of fine-grained siltstones and mudstones with several paleosol horizons and

crosscut by shallow channel fill sandstones (Tuba et al., 2006; Ősi and Mindszenty, 2009; Botfalvai et al., 2012).

Higher up in the stratigraphic sequence Middle Eocene (Lutetian) conglomerates and limestones unconformably cover the Csehbánya Formation. The youngest deposit exposed in the open-pit mine is Pleistocene loess which forms a discontinuous blanket over most of the area (Fig. 1C).

2.2. Lithofacies and depositional environment of the Csehbánya Formation

The Csehbánya Formation at the Iharkút locality is built up mainly by overbank fines (about 80% of all the alluvial complex). Sandstones and conglomerates are subordinate in the exposed section. The absence of desiccation cracks, the subordinate amount of secondary (pedogenic) carbonate accumulation and the floral association (subtropical floodplain forest vegetation; Bodor et al., 2012) show that the climate was dominantly humid, however, with occasional flash-flood like episodes suggesting some seasonality (Ősi and Mindszenty, 2009). The deposition of the Csehbánya Formation started in the Santonian (*Oculopollis-Complexiopollis* Zone; Siegl-Farkas, 1991) confirmed also by palaeomagnetic studies (Szalai, 2005).

The age of bonebed at site SZ-6 was examined by palynological methods and resulted in a more accurate age showing that the age of the bone accumulations (Bodor and Baranyi, 2012) is equivalent to the Santonian *Oculopollis zaklinskaiae–Tetracolporopollenites* (*Brecolpites*) *globosus* Zone.

2.2.1. Floodplain deposits

Description: The fine siltstones and mudstones are organized into more-or-less regular, meter- to two-meter thick, paleosol-capped alluvial cycles interrupted by occasional

shallow (2 to 3 m deep 30 to 60 m wide) fine-grained sandstone bodies and thin (0.5 to 1 m) fine-grained sheet sandstones. The abundance and depth of such cross-cutting channel forming sandstone-bodies and sandstone-blankets increase upwards. Coarse sandstones and/or conglomerates are rare, the latter always restricted to the channel-forming sandstone bodies. Tabular- or through cross-bedding is likewise rare. There are no desiccation cracks, and even secondary carbonate accumulation is not apparent (observable in thin sections only) in the paleosols, however, smaller or larger ripped-up clayclasts are abundant at the base of some of the channels. Three major types of paleosols could be distinguished: (a) reddish, slightly calcareous, moderately developed, well-drained 30 to 100 cm thick paleosols with vertical root traces (and burial-gley features), situated – as a rule – in the lower part of the open-pit (b) thick (> 100 cm), however, weakly developed, pale, yellowish paleosols with purple to violet coloured gleyed spots and abundant root-mottles, predominant in the upper section of the open pit (Fig. 1C), (c) > 100 cm thick, pale yellowish to grey very weakly developed paleosols with tiny irregular root traces. On top of the channel fills (e.g. site SZ-6), and at the lower segment of the open pit such as site SZ-7-8 (see below) fine-grained dark grey siltstone layers are abundant

Interpretation: The discrete well-drained reddish paleosol horizons encountered exclusively in the lower 20 meters of the exposed cover sequence are products of subaerial exposure in a relatively high-level floodplain environment. Most paleosols, however, abound in hydromorphic features (gley-spots) and thus point to either occasional or - particularly in the upper part of the exposed thickness – permanent water-logging which may be interpreted as a low-level flood-plain position for the sedimentary environment. They are also mostly aggradational (i.e. "cumulate" sensu Wright and Marriott (1996)) reflecting an alluvial sedimentary regime keeping pace with the steady subsidence of the area. The fine-grained dark-grey (organic rich) layers occurring also in these upper levels, particularly on top of the

coarser-grained channel-forming sandstone bodies are interpreted as flood-plain ponds and/or abandoned channels (Tuba et al., 2006; Ősi and Mindszenty, 2009).

2.2.2. Channel-filling deposits

Description: Channel-fill deposits can be divided into at least three lithotypes in the Iharkút open-pit mine based on their lithofacies, geometry and palaeontology.

The first group includes lenticular sandstone ribbons max. 2 to 3 m thick and 30 to 60 m wide. They are the most frequent fluvial units exposed in the open-pit (Fig. 1C) and predominantly composed of fine- to medium-grained sandstone, although smaller or larger ripped-up clayclasts (0.3-2 cm in diameter) of the floodplain-fines are also abundant at the base of some of the channels (e.g. SZ-1 and SZ-6 sites; Figs. 2 and 3). Grain size decreases upwards and bioturbation (root traces) occasionally appears at the top of these channel bodies. The lower surface of these beds is clearly erosional, cutting into the floodplain deposits. Point bar accretion is absent and cross-bedding is very rare in the channel fills. They contain plant debris and bone fragments occasionally in large quantities (e.g. SZ-1 and SZ-6 sites), but coarse sandstone and conglomerates are rare (Ősi and Mindszenty, 2009). These types of channel sandstones are typically isolated from one another laterally. The lenticular sandstone bodies have a homogeneous texture because both tabular and through cross-bedding is very rare.

The second group consists of tabular sandstone bodies with flat, non-erosional base. Their thickness is usually limited to a few meters (0.5–1.5 m) and they are more extensive laterally than the sandstone bodies of the first group. The tabular sandstone bodies are more frequent in the upper part of the exposed thickness. They predominantly consist of finer grained sandstones than the lenticular sandstones, and contain only scattered plant debris, while the bones are generally missing (in the studied strata). Fining-upward trends are

common and the top of the sheets is grading into pedogenically modified siltstone. Tabular or through cross-bedding and ripped-up clayclasts are very rare.

The third group includes conglomerates and sandstone channel fills restricted mainly to the uppermost part of the exposed thickness. The lower surface of such beds is clearly erosional, they cut into the floodplain deposits. The conglomerate horizons are often interrupted by sandstone, and this alternation repeatedly appears in the conglomerate filling sequences. Lateral accretion was present, since cross-bedding is discernible in the channel fills. The presence of this type of fluvial sediment is very limited in the open pit mine (only two occurrences recorded) and bones and plant debris are completely absent from these channel fills.

Interpretations: Since the lenticular sandstone bodies, occurring at various topographic levels, are clearly isolated from each other they can be interpreted as anastomosing river deposits (Makaske, 2001; Roberts, 2007; Ősi and Mindszenty, 2009). Furthermore, the low width/depth ratios, the relatively homogenous internal texture (infrequent cross-bedding), and the grain size ranges (from coarse clayclasts to fine sand; Fig. 3) are also characteristic features of the anastomosing rivers (Makaske, 2001). The tabular sandstone sheets may be interpreted as crevasse-splay deposits or sheet splays which are likewise commonly associated with anastomosing river systems (Miall, 1996; Makaske, 2001; Makaske et al., 2002; Roberts, 2007). The term anastomosing is identified here by the presence of multiple, vertically aggraded sandstone ribbons (Eberth and Miall, 1991), which can be interpreted as "interconnected channels that enclose floodbasins" (Makaske, 2001:149). The characters of the lenticular channels (stable banks, multiple-story bodies) and the abundant crevasse-splay deposits observed in the Iharkút open-cast mine might suggest that seasonal flooding and substantial vertical aggradation of the floodplain were common

250 indicating high rate of sediment accumulation (i.e. high rate of subsidence, see also above)
251 (Roberts, 2007) for the Csehbánya Formation.
252
253 **2.3. Description of the depositional environment of the bonebeds in the Iharkút mine**
254 Three different stratigraphic units of the Csehbánya Formation contain bones in
255 Iharkút, these are exposed in 8 different sites (SZ-1–SZ-8) within the open-pit mine. The SZ-1
256 site is in the northern part of the mine and a few hundred poorly preserved fossils have been
257 collected from here. The sites SZ-2–SZ-6, corresponding to the localities that yielded six
258 *Hungarosaurus* skeletons and most of the isolated bones used in this study, are
259 stratigraphically equivalent and relatively close to each other, so the name SZ-6 is here
260 applied for all of these sites (see Ősi et al., 2014 for the position of site Sz-6 at Iharkút mine).
261 Sites SZ-7-8 are two outcrops of a dark grey, silt and clay bed rich in organic matter that
262 contains coalified plant remains and a rich assemblage of microvertebrates. Though bones can
263 be found essentially all over the area of the open-pit mine, bone accumulation is most
264 significant in the sites SZ-1, SZ-6 and SZ-7-8 (Figs. 2–4). However, the taphonomic
265 investigations were restricted only to the material collected from the site SZ-6, because the
266 amount of material from site SZ-1 is not sufficient for detailed investigations (amounting less
267 than the 1% of the entire Iharkút assemblage), while the remains from sites SZ-7-8 are limited
268 for microvertebrates which have different taphonomic history (Dodson, 1973; and see later in
269 this text). Nevertheless, we felt it necessary to describe the other bonebeds in the Iharkút
270 mine, as well, because their presentation contributes to our understanding of the bone
271 depositional modes in the locality. We use the term bonebed as "relative concentration of
272 vertebrate hardparts preserved in a localized area or stratigraphically limited sedimentary unit
273 and derived from more than one individual" (Eberth et al., 2007a:3).
274

2.3.1. Site SZ-1

Description: The site SZ-1, situated in the northern part of the open-pit, was the first exposure where vertebrate remains were found and the area was recognized as a potential Cretaceous vertebrate locality (Ősi, 2004). The bonebed of site SZ-1 is a 20 to 30 cm thick yellow sandstone which contains bone fragments, teeth, plant debris, and ripped up clayclasts at the base of the bonebed (Fig. 2). The base of this layer is erosional, it cuts into the underlying yellow clay stone layer. The bones can be found in the basal breccia as well as in the immediately overlying medium-grained sandstone layer. The grain size of the sequence is fining upward and it is homogeneous in texture, neither tabular or through cross-bedding nor lateral accretion were detected at this site. The vertebrate remains found at this site are less than the 1% of the whole Iharkút assemblage.

Interpretations: Section SZ-1 can be characterized first by increasing energy conditions, followed by energy decrease after the accumulation of the bonebed (Fig 2). The site was interpreted as a ribbon channel, because the lateral erosion was limited and width/depth ratios are low (Botfalvai et al., 2012).

2.3.2. Site SZ-6

Description: The site SZ-6 is the most important bone accumulation in the Iharkút locality because of the high abundance of vertebrate remains; approximately 80% of the complete specimens were discovered here. Most of the vertebrate fossils were recovered from an approximately 3 m thick sequence of beds made up of coarse-grained, sandstone and organic-rich siltstone (Fig 3). The basal surface of the sequence is clearly erosional, it cuts into the underlying green-clay stone layer. The lowest bonebed in SZ-6 is a 10 to 50 cm thick basal breccia composed of grey sandstone, siltstone, clayclasts, pebbles and plant debris (Fig. 3A) that occasionally contains complete or, more frequently, fragmentary bones. The basal

breccia presents a clear tendency of fining upwards. This sequence with poorly sorted coarse sandstone breccia overlain by finely laminated siltstone is repeated several times (Fig. 3B) resulting in a stacked series of fining upward units. The clayclasts in the basal breccia are poorly sorted varying between 0.3 to 2 cm in diameter and occasionally even with a few cm-sized dolomite pebbles scattered among the clayclasts. This most important fossiliferous layer is covered by a sandstone bed also containing scarce remains of vertebrate fossils. The uppermost bed of this succession is a 30 to 50 cm thick, laminated, greyish siltstone which contains plant debris, fewer bones but yielded incomplete skeletons of *Hungarosaurus* (see below). Vertebrate fossils are common in the coarse-grained, poorly sorted deposits of the lower part of sequence SZ-6, while they are only rarely encountered in the upper laminated deposit.

Interpretation: The basal erosional surface of the sequence, together with the overlying smaller or larger ripped-up clayclasts of floodplain origin indicate high–energy conditions associated with rapid flooding events resulting in the efficient reworking of the material from the interfluve areas (Tuba et al., 2006; Ősi and Mindszenty, 2009). The depositional environment was probably that of a high density (flash) flow because: (1) The transported sediment is poorly sorted, clasts ranging from few cm-sized dolomite pebbles to medium-grain sand often with several meters long tree trunks deposited together within the basal breccia layer (Ősi and Mindszenty, 2009). (2) Absence of unidirectional, hydraulic-flow-generated sedimentary structure, but occurrences of the clay laminas sign that the massive sedimentary fabric of this deposits is primary and not the results of bioturbations or other postdepositional events (such as Eberth et al., 2006). (3) The highest bone concentration occurs at the base of the unite (basal breccia layer) and are poorly sorted (see below at the taphonomic section). (4) The bones and tree trunks show little evidence of preferred orientation and some elements have very high dip angles (such as Eberth et al., 2006). Energy

conditions at site SZ-6 were, however, not constant because deposition of the basal breccia was interrupted several times by that of quiet water deposits (silty-sandstone and clay) particularly during the deposition of the lower part of the succession (Fig. 3B). The depositional environment characterized by these alternating energy conditions provided for the accumulation of bones of highly different states of preservation in the same bed (isolated, associated and even articulated skeletal remains were found together in the basal breccia horizon; see below). The fining upward sequence covering the basal important fossiliferous layer indicates reductions in flow velocity, either when the channels were abandoned or possibly at the end of the flood events (Botfalvai et al., 2012). Site SZ-6 is interpreted as one of the abandoned channels formed during these (ephemeral) flood events (Ősi and Mindszenty, 2009). Incised and subsequently suddenly abandoned channels are common structures associated with anastomosing systems in low-level floodplain environments, because they can be created by the process of avulsion as the river compensates for the aggradation or plugging of individual channels during the flood events (Behrensmeyer, 1988; Smith et al., 1989; Eberth and Miall, 1991; Aslan and Behrensmeyer, 1996; Miall, 1996; Makaske, 2001; Makaske et al., 2002; Roberts, 2007).

2.3.3. SZ-7-8 site

Description: The bonebed of the SZ-7-8 site is a 10 to 20 cm thick, dark grey, siltstone and clay bed rich in organic matter (Fig. 4), containing mainly larger fragments of coalified tree trunks and twigs, plant meso- and microfossils, microvertebrates and rarely larger fragmentary bones. Furthermore, 1 to 3 mm sized amber fragments and a large number of pyritized mollusc shells have been also collected. This bonebed consists mainly of skeletal elements of fish, albanerpetontids, anurans, turtles, squamates, crocodilians and dinosaurs

(Szentesi and Venczel, 2010, 2012; Ősi et al., 2012b). The microfossil bonebed is sandwiched between two medium grained sandstone layers (Fig. 4).

Interpretation: The presence of hydromorphic paleosol horizons above and below the sequences (Fig. 4) may indicate that the studied area was part of the low-level floodplain characterized by overall hydromorphy. Furthermore, the fossiliferous layers also show clear signs of hydromorphy and low energy conditions indicating that these were probably a small-scale stagnant pools of the floodplain filled up by organic-rich sediments (Botfalvai et al., 2012; Ősi et al., 2012b). They are typical microfossil bonebeds sensu Eberth et al. (2007a), because these are concentrated deposits of bones of several individuals in a stratigraphically well-limited sedimentary units within which the dimension of the bioclasts (bones and teeth) does not exceed 5 cm.

3. METHOD OF INVESTIGATION

All fossil remains from Iharkút are housed in the collection of the Hungarian Natural History Museum (MTM) in Budapest. The examined material was collected from 2000 to 2012. Iharkút, as a Late Cretaceous continental vertebrate site, was discovered in 2000 and ever since then annually a two or three weeks long field work has taken place at the locality. The first excavations started at the site SZ-1, then from 2003 fieldwork continued at site SZ-6.

Furthermore, several tons of sediment has been collected from sites SZ-6 and SZ-7-8 for screenwashing, from which 20% was the potentially fossiliferous fraction. Three mesh sizes were used for screenwashing, of which the 1 mm size proved to be the most favourable for the extraction of microvertebrates.

Basic taphonomic investigations began in 2008 when careful documentation of the taphonomic features started both at the excavation sites and on the previously collected

material. Taphonomic investigations were confined to the entire macrofossil material (following Behrensmeyer et al. (1979), macrofossil assemblages consisting of bones of animals whose body weight was over 1 kg). However, investigation of taxon diversity was also extended to include those taxa which were known exclusively from microvertebrate assemblages, (e.g. amphibians and small squamates), because the presence of these taxa provided important information about the studied palaeocommunities.

During the taphonomic investigation each bone was examined to determine its osteological and taxonomic identity wherever it was possible. In addition, any taphonomic modification feature of the bone surfaces (i.e., weathering, abrasion, breakage pattern, etc.) was documented. Bone morphology, state of preservation and the deformations observed on the specimens have been summarized in Supplementary Information 1. We have followed mostly the methods described by Pereda Suberbiola et al. (2000) in order to gather all the taphonomic information about the fossil remains. Pereda Suberbiola et al. (2000) built a useful database using previous works (e.g. Behrensmeyer, 1978, 1991) that includes the most important quantitative and qualitative taphonomic features of the fossil material. Furthermore, we extended the database of Pereda Suberbiola et al. (2000) with additional characters (e.g. maximum dimension of bones after the fragmentation, number of epiphyseal regions of limb bones, and presence of pyrite crust on the bone surface).Data were collected in the "Iharkút taphonomic dataset" file (See Supplementary Information 2) that includes all characters of the examined bones.

4. TAXONOMIC COMPOSITION

In general, the Santonian Iharkút vertebrate fauna shows a composition basically similar at family level to other Late Cretaceous continental vertebrate faunas of Europe (see

399 e.g. Buffetaut and Le Loeuff, 1991; Allain and Pereda Suberbiola, 2003; Weishampel et al.,
400 2010). Nevertheless, at generic and species level, numerous differences have been
401 documented (Ősi et al., 2012b), which, among other factors, further support the insular
402 evolution of the Iharkút continental fauna within the European archipelago (Ősi et al., 2012b).
403 The isolated and associated remains represent 31 different taxa including fish,
404 amphibians, turtles, lizards, pterosaurs, crocodilians, non-avian dinosaurs and birds (detailed
405 taxon list of the Iharkút fauna, see Table 1).
406
407 **5. VERTEBRATE MATERIAL OF IHARKÚT**
408
409 Currently the complete vertebrate material collected from the Csehbánya Formation at
410 Iharkút contains 9222 bone and bone fragments and 2271 isolated teeth based on "Iharkút
411 taphonomic dataset" (see Supplementary Information 2 and Table 2). Of these vertebrate
412 remains, 7475 items (isolated macro- and microvertebrates, teeth and bones, associated and
413 articulated skeletal elements) were identified osteologically and taxonomically. 9099 bones
414 and fragments were discovered at site SZ-6 from an approximately 400 m^2 area excavated
415 during the last ten years, and indicate that the bonebed has a concentration of close to 23
416 bones (fragments)/m^2 at site SZ-6 (based on "Iharkút taphonomic dataset"). This is a
417 relatively high bone concentration compared with the bonebeds of various dinosaur sites (e.g.
418 Fiorillo, 1991; Varricchio, 1995; Pereda Suberbiola et al., 2000; Gates, 2005; Britt et al.,
419 2009; Fiorillo et al., 2010).
420
421 **5.1. Isolated bones**

We follow the interpretation of Badgley (1986a) considering that as long as there is no evidence for the probability of association among the vertebrate remains, all of the elements should be regarded as separated and isolated elements.

Most of the bones discovered in the bonebeds of the Iharkút locality are isolated specimens. The high number of disarticulated and isolated bones suggests the presence of dispersal processes during the accumulation of vertebrate remains (Hill, 1979; Hill and Behrensmeyer, 1984; Coard and Dennell, 1995; McNamara et al., 2012). The isolated bone assemblages can be divided into four different groups (Fig. 5 A-D), these subsets have widely different taphonomic histories (Table 2).

- The first subset is built up of the highly abraded, small-sized, rounded "bone pebbles" which are unidentified taxonomically and/or anatomically (Fig. 5A).

-The second group consists of well- and medium-preserved, identified isolated bone elements, and represents one of the most important taphonomic subjects (Fig. 5B).

-The third subset contains "complex", co-ossified skeletal elements such as skulls, mandibles (Fig. 5C and D), as well as the synsacra of ankylosaurs and a rhabdodontid dinosaur. These are not considered here as partial skeletons (contra Csiki et al., 2012), because they can be regarded as a single ossified unit in the original skeleton and therefore can be preserved together in many cases (Hill, 1979; Hill and Behrensmeyer, 1984; Dodson 1971). As, for instance, the limb elements are connected along a joint surface (easily separable) and hence the preservation of association of those elements is limited, thus they are considered as a partial skeleton if found in associated position. These "complex" isolated skeletal elements (Fig. 5C and D) are rare in the assemblages and their occurrence is confined to the layers of the SZ-6 site. Separation of this category within the isolated bones group is justifiable, because completely preserved skulls and mandibles are very rare (usually only separated parts of these bones are found, e.g. frontal, articular, dentary, etc.) and they are

confined to just a few taxa (*Foxemys*, *Iharkutosuchus*, *Hungarosaurus*, *Mochlodon*, *Bakonydraco*). Furthermore, the taphonomic history of "complex" isolated skeletal elements may be different from that of the separated elements of the skull and mandibles (Boaz and Behrensmeyer, 1976). The fourth subset in this category consists of the isolated teeth. Distinction of tooth remains from the other groups of isolated bones is reasonable, because the dispersal potential of teeth is probably different from that of the bones at the same current velocity, therefore the mode of accumulation of teeth is different from that of other fossils (Behrensmeyer, 1975; Fiorillo, 1991). Furthermore, the resistance of teeth against the abrasion is different from that of other fossils, because the enamel-coated teeth are more durable in transport environments than bones (Argast et al., 1987).

5.2. Associated and articulated bone assemblages

The disarticulated but associated skeletal elements are rarer than the isolated bones, and it seems that these are limited to only certain horizons of SZ-6 site and only to one taxon (Table 2 and Fig. 5E). All of the six associated skeletons belong to *Hungarosaurus* (Ankylosaur) and were discovered at SZ-6 site (Ősi, 2005; Ősi and Makádi, 2009).

There is only one *Hungarosaurus* skeleton in the collection from Iharkút which is preserved in an articulated position (Table 2; Fig 5F). It was found in the basal breccia of the SZ-6 site. This skeletal segment includes both ilia, ischia, the co-ossified synsacrum region with the ossified ribs in articulation. All elements were preserved in their original anatomical position, thus the partial skeleton is regarded as articulated (Badgley, 1986a).

5.3. Microvertebrate assemblages

According to Behrensmeyer et al. (1979) microvertebrate assemblages consist of bones of animals whose body weight was <1kg (Table 2). All of the microvertebrate elements are isolated bones from the SZ-7-8 and the SZ-6 sites and most of them were collected by screenwashing (Szentesi and Venczel, 2010, 2012; Makádi, 2013a,b). We refer to microfossil remains only where necessary; the detailed taphonomic investigation of the microfossil assemblage is not the subject of the present paper, because they have a different taphonomic history (Dodson, 1973; Behrensmeyer, 1991; Pereda Suberbiola et al., 2000).

5.4. Discussion

The wide range of taphonomic modes (isolated, associated and articulated preservation) represented within the same vertebrate-bearing lithofacies units suggests that there were variations regarding both the bone sources and the transportation histories of the individual bones at site SZ-6 in the Iharkút mine. The isolated vertebrate elements (all of the four subsets) represent a multispecific (or multitaxic/multidominant) assemblage (Behrensmeyer, 2007; Eberth et al., 2007a), while the other two main preservation modes, associated and articulated skeletal material, are restricted to only one taxon (*Hungarosaurus*), indicating a significantly different taphonomic (and palaeoecological) history for these ankylosaur remains.

6. FOSSIL ASSEMBLAGE DATA AND TAXONOMIC ABUNDANCES

Many archaeological and paleontological investigations employed estimates of abundances of taxa in mammalian (e.g. Shotwell, 1955; Gilinsky and Bennington, 1994; Lyman, 1994a,b; Badgley, 1986a,b) and reptilian (e.g. Fiorillo, 1991; Varricchio, 1995; White et al., 1998; Pereda Suberbiola et al., 2000; Eberth et al., 2007b; Britt et al., 2009,) assemblages. This kind of taphonomic investigations are of crucial importance to deduce ecological conclusions.

6.1. Number of identified specimens (NISP)

Method: The number of identified specimens is the most popular and simplest measure of taxonomic abundances and therefore it is commonly used by palaeontologists (e.g. Varricchio, 1995; Pereda Suberbiola et al., 2000; Alberdi et al., 2001; Britt et al., 2009; Cannon, 2012). The NISP value includes the number of bones, teeth and fragments which were taxonomically identified as skeletal elements at least at order level (Lyman, 2008) in the Iharkút vertebrate assemblages This method has not been used on the associated and articulated skeletal elements because they are proven as being separate individuals, unlike the isolated bones (see below).

Result: The total NISP value of the Iharkút remains was 6871 based on isolated bones and teeth (including macro- and microvertebrates). The $NISP_i$ (where $_i$ signifies a particular taxon) was determined for each taxon in order to estimate the frequency differences among taxa in the studied material (Table 3). The taxon diversity calculation based on NISP shows that turtle and dinosaur remains represent more than half of the identified elements (Fig. 6A). Crocodilians are the third most common group while the amount of fossils of *Pannoniasaurus* and fish are about approximately equal in the Iharkút assemblages. The amphibian taxa represent about 4% of the NISP of the Iharkút collection (Fig. 6A).

Comments: Our results show that taxa with a high number of resistant and frequent osteoderms (ankylosaurs, turtles) are the most abundant in the assemblage (Table 3). This fact may distort rates of frequency of taxa because taxa with osteoderms will be overrepresented compared to other forms. This problem was also observed by several authors, namely that NISP varies intertaxonomically, because different taxa may have different number of bones and teeth (White, 1953; Ringrose, 1993; Lyman, 2008; Britt et al., 2009; Moor and Norman, 2009; Domingo et al., 2013). Furthermore , the fragmentation increases the NISP value (for a while) because fragmentation creates more pieces from one bone and therefore the fragmentation rate of the bone assemblage significantly affects the NISP value (the fragmentation rate is calculable if $NISP_i$ is divided by MNI_i, where $_i$ signifies a particular taxon; Cannon, 2012). The vertebrate remains of Iharkút also show relationship between NISP and bone fragmentation (Table 3).

6.2. Minimum number of individuals (MNI)

Various methods are used to determine the minimum number of individuals (MNI) in vertebrate assemblages and different assessments can introduce problems when several assemblages are compared by their MNI (Horton, 1984; Turner and Fieller, 1985; Pereda Suberbiola et al., 2000; Domingo et al., 2013). Therefore we discuss the details of the calculation process of minimum number of individuals which was applied here for the Iharkút vertebrate remains.

Method: During the calculation of MNI, at first we determined the minimum number of elements (MNE) for the most common skeletal elements of a taxon, then the greatest MNE value was defined as an MNI value for that taxon (White, 1953; Badgley, 1986a; Lyman, 1994b; Moor and Norman, 2009). The MNE value is represented by a minimum number of a

546 particular skeletal element of a taxon, for example, the left femur, left dentary, or the skull
547 (Grayson and Frey, 2004; Lyman, 2004a, 2008). The MNE value was determined only for the
548 accurately definable skeletal parts of all taxa. In cases when accurate anatomical position of
549 the element was not determinable (e.g. ribs, vertebrae, limb bone fragments), the MNE value
550 could not be calculated. The MNI values for each taxa were defined by the most frequent
551 diagnostic skeletal part whose accurate anatomic position (e.g. left or right side of the body)
552 was well defined. The advantage of this method is that it minimizes the chance of the same
553 element being counted twice, which is the principle of MNI and MNE (Ringrose, 1993).
554 However, this method ignores age (e.g. juvenile or adult) and size factors and this bias
555 potentially increases or decreases the MNI value for a particular taxon. Furthermore we
556 considered the six associated and one articulated skeletal remains as different seven
557 individuals in the Iharkút remains during the MNI calculation (Table 3).

558 *Result:* A minimum of 218 individuals including fish, amphibians, reptiles and birds
559 were identified in the Iharkút vertebrate assemblage (Table 3). The taxon diversity calculation
560 based on MNI shows that pterosaurs, amphibians and fish are the most abundant taxa in the
561 Iharkút assemblage while dinosaurs and turtles are rarer (Table 3 and Fig. 6B).

562 *Comments:* The MNI values show different distribution of taxonomic abundances
563 from that was indicated by NISP. Taxa whose bones are rare in the observed material show
564 relatively high MNI value, while taxa which have rich bone remains in the Iharkút assemblage
565 were underrepresented by MNI. The difference is explained by correlation between MNI and
566 NISP (Lyman, 2008):

567 (1) Fragmentation increases the NISP value of a taxon but the MNI does not increase
568 with NISP because the MNI depends on the anatomical and taxonomical features of elements
569 and not the number of bone fragments (Turner and Fieller, 1985; Ringrose, 1993). As Lyman

570 (2008:46) concluded “MNI values exaggerate the importance of rarely represented taxa, or
571 taxa represented by low NISP values”.
572 (2) Material representing certain rare taxa includes a large number of bones, all of
573 which are defined as single individuals. For instance, pterosaurian remains contain 58
574 symphyseal regions of the mandible representing 58 different individuals (Ősi et al., 2005;
575 Prondvai et al., 2014), thus the MNI_{pt} is 58. On the other hand, turtle material includes a lot of
576 indeterminable shell fragments (which increase NISP value), but does not represent disparate
577 individuals (MNI is low). These problems of calculation of MNI introduce several biases and
578 these should be considered when making comparison of taxonomic abundances of fragmented
579 assemblages (Moor and Norman, 2009).
580
581 **6.3. Skeletal representation**
582
583 The abundance of skeletal elements in a given vertebrate assemblage can be measured
584 (White, 1953; Shotwell, 1955; Grayson, 1978; Badgley, 1986a,b;, Spencer et al., 2003; Britt
585 et al., 2009; Mannion and Upchurch, 2010; Domingo et al., 2013). The determination of
586 abundance of skeletal elements has significance in deciding, for instance, whether the bones
587 of ankylosaurs are more abundant than the bones of other dinosaur taxa either because the
588 former taxon was originally more abundant in the ecosystem, or there were some agents or
589 processes of fossil accumulation (e.g. the differing durabilities of bone material, differences in
590 the pre- or postdepositional taphonomic history of the vertebrate remains) which simply
591 collected more elements of ankylosaurs than those of other dinosaur taxa (Behrensmeyer,
592 1975; Kidwell, 2001; Fernández-Yalvo and Andrews, 2003; Lyman 2008).
593
594 *6.3.1. Skeletal completeness*

We used the measure of Shotwell (1955) of relative skeletal completeness in order to decide which taxa were members of a community living in proximity to the site of deposition (and therefore are expected to have died often near it) and which taxa lived in more distant communities (Shotwell, 1955; Grayson, 1978; Lyman 1994b). The basic assumption is that taxa from a distant community are expected to show limited percentage of skeletal completeness because they have lesser probabilities for complete skeletal preservation (because of carnivore activity, transportation etc.) than the skeletons of those taxa which lived closer to the site of deposition (Shotwell, 1955; Dodson, 1971).

Method: We used the following equation for this calculation (Shotwell, 1955; Lyman, 2004b; Britt et al., 2009):

$$\%R_i = (A_i \times 100) / (E_i \times MNI)$$

$$\%TC = (\sum A_t \times 100) / (\sum E_t \times MNI)$$

$\%R_i$: percentage of relative proportion of element i in population of MNI

A_i: actual number of element i in the collection

E_i: expected number of element i in a complete skeleton per individual

MNI: minimum number of individuals

$\%TC_t$: percentage of total skeletal completeness of taxon t

$\sum A_t$: actual number of skeletal elements of taxon t

$\sum E_t$: expected number of elements in a complete skeleton of taxon t

The calculation of skeletal completeness per taxa was restricted to the isolated bone assemblage of sit SZ-6. The calculation of skeletal representations was not done on the

620 microfossil assemblage (amphibians and small lizards) because they may have a different
621 taphonomic history. In addition, calculations of skeletal completeness of fish and
622 *Ajkaceratops* cannot be performed due to limited available information, since the expected
623 number of elements in their complete skeleton is unknown.

624 *Results*: The total skeletal completeness of the counted eight groups (turtles,
625 mosasauroids, crocodilians, pterosaurs, ankylosaurs, rhabdodontid ornithopods, non-avian
626 theropods and avialans) range from 0.47% to 30% (Table 4). Among dinosaurs, ankylosaurs
627 and theropods show higher skeletal completeness than rhabdodontid ornithopods.

628 *Comments*: Relatively high percentage of the skeletal completeness of the site SZ-6
629 vertebrate assemblage (most taxa show over 10% of skeletal completeness) may suggest that
630 the sorting effects were not significant before bone accumulation and that a large proportion
631 of the individual skeletons was deposited together in a particular place (Table 4).

632

633 *6.3.2. Bone representation by size*

634

635 There is evidence for taphonomic size bias against the small-bodied taxa in most
636 vertebrate assemblages (Behrensmeyer et al., 1979; Behrensmeyer, 1991; Rogers et al., 2001;
637 Britt et al., 2009; Brown et al., 2013; Evans et al., 2013). Thus it is essential to investigate this
638 kind of biases during the palaeoecological analysis.

639 *Method*: At first, we divided the bones of the SZ-6 assemblage into three size
640 categories according to their dimension at pre-breakage state (small: <5 cm; medium: 5-10
641 cm; large: 10-50 cm) and then we observed which size category is frequently overrepresented
642 relative to its expected value (that element was overrepresented where $\%R_i$ exceeds $\%TC_t$ in
643 the dataset of Table 4 based on Britt et al., 2009). The calculation of size bias was not done on
644 the microvertebrates assemblage (remains of amphibians, small lizards), teeth of sauropsids,

and associated and articulated skeletons because these preservational categories have a different collecting method and taphonomic history (e.g. Coard and Dennell, 1994; Blob and Fiorillo, 1996).

Results: The elements of medium and large size categories are frequently overrepresented (about 40%) while elements of small size are even more frequently underrepresented (about 90%), regardless of taxonomic status (Fig. 7) at SZ-6 assemblage. This distribution indicates a direct correlation between bone size and abundance.

Comments: There are several explanations for commonly observed bias against small-bodied taxa, for instance, biological and physical degradation; biases of collection and taxonomy or fragmentation rate of the bone assemblage (Behrensmeyer et al., 1979; Behrensmeyer, 1991; Benton, 2008; Britt et al., 2009; Mannion and Upchurch, 2010; Brown et al., 2013; Evans et al., 2013). In the SZ-6 assemblage probably the collecting method contributed to the bias because the field methods are not favourable for small bones. The small bones and fragments are more difficult to recognize and collect than larger ones during excavation. The detected taphonomic size sorting may be caused by collecting bias, and may not be the consequence of transportation sorting. However, the size biases should be considered during the investigation of taxon diversity, because small-bodied taxa are underrepresented in the SZ-6 assemblage.

6.3.3. Specimen shape sorting

The shape of bones appears to be an important factor when studying bone deposition after fluvial transport, because the theoretical dispersal potential of fossils depends on the bone shape besides its size and density (Behrensmeyer, 1975). The bones became shape

669 sorted during transport because spherical and rod-like fossils are transported earlier and easier
670 than disc- and blade-shaped bones (Frostick and Reid, 1983).

671 *Method*: At first we measured all three axes of bones of SZ-6 assemblage, which are
672 referred to as length, width and thickness, regardless of the anatomical orientation of the
673 measured bone (number of measured bones was 2475). Following the empirical model of
674 Frostick and Reid (1983) we used the ratios of the measured axes (D2/D3; D3/D2 that
675 allowed dividing our specimens into four subcategories: sphere, rod, disc and blade shapes.
676 The microfossil assemblage was excluded from this part of the analysis because their different
677 size and shape sorting may distort the evaluation of the studied bone assemblage (Blob and
678 Fiorillo, 1996). Furthermore, we compared the occurrence of shape categories of bones in the
679 SZ-6 vertebrate assemblage with the ideal relative occurrence of elements in a complete
680 skeleton per taxon (Table 4) in order to observe which shape category is frequently
681 underrepresented relative to its expected value (Britt et al., 2009).

682 *Results:* The disc- and blade-like elements are the most common specimens (about
683 80%) in the SZ-6 assemblage while the comparatively mobile shape categories of bones
684 (spherical and rod-like shape) are far less frequent (Fig. 8). However, when comparing the
685 frequencies of isolated bones shape categories with their expected values in a complete
686 skeleton of taxon (based on Table 4), the distribution of shape categories was random (Table
687 5). The later approach can be regarded more realistic, because it includes a value of reference
688 (expected value of bones per shape category) and it indicates only which shape categories are
689 over- or underrepresented in the SZ- 6 assemblage in Iharkút locality.

690 *Comments*: There is no strong evidence for shape sorting in the SZ-6 assemblage,
691 because the over- or underrepresentation of shape categories in the fossil material was random
692 when compared to their occurrence in a complete skeleton. This fact suggests that the Iharkút
693 taphocoenose was not a typical fluvially transported assemblage; rather elements were

transported for a short time or by high density (or energy) flows (e.g. Rogers, 2005; Britt et al., 2009). It also conceivable that there were multiple sources of bone input (e.g. Aslan and Behrensmeyer, 1996) and thus these were transported and sorted in different ways.

6.4. Discussion

The Iharkút vertebrate assemblage is fragmented and highly dispersed, therefore the assessment of taxon diversity is complicated.

The use of the NISP method would be reasonable for the analysis of taxon distribution in the Iharkút vertebrate collection because the material is very fragmented, dispersed, transported and the possibility of association is zero (following Badgley, 1986b) for most taxa (excepting ankylosaur remains). However, the pattern of NISP distribution in the Iharkút assemblage is unexpected when compared with that seen in modern ecosystems which tend to have a higher abundance of fish and amphibians (or other small-bodied taxa) compared to larger-bodied reptiles or mammals (Oindo et al., 2001). The NISP index profile of the Iharkút assemblage differs from modern ecosystems from fluvial environments because the remains of terrestrial animals (e.g. dinosaurs) are more frequent than those of aquatic form (e.g. amphibians or fish) despite the fact that the depositional area was a typical alluvial, floodplain palaeoenvironment. It is important to note that there is a taphonomic bias against the small bodied animals in the SZ-6 vertebrate assemblage. Small-sized fossils are more frequently underrepresented than the larger size categories and this may contribute to the fact that amphibians, fish or small lizards show lower frequency in the NISP calculation.

On the contrary, the MNI profile of the Iharkút vertebrate assemblage shows a distribution similar to that seen in modern ecosystems. In this case small-bodied taxa (e.g. fish, amphibians, lizards) are relatively more frequent than large-bodied taxa (e.g. dinosaurs).

719 Furthermore there are several characters of the SZ-6 vertebrate assemblage that
720 suggest that this site acted as a ”trapping place” for the bones.
721 (1) 9099 bones and fragments (and 2271 teeth) were discovered from an
722 approximately 400 m^2 area, showing densities ranging up to 23 specimens/m^2. The relatively
723 high fossil density (Fiorillo et al., 2010) in site SZ-6 of Iharkút may be interpreted as sign of a
724 preferred bone accumulation place where the fossils could have been deposited and
725 concentrated through the attritional processes.
726 (2) There is no strong evidence for shape sorting which would refer to transport
727 conditions (Aslan and Behrensmeyer, 1996). The absence of shape sorting in the SZ-6
728 remains may suggest that the distance and/or time of transportation was not too long and it
729 raises the possibility that several elements from the same individual accumulated together in
730 the same horizon (Behrensmeyer, 1991; Badgley, 1986a,b).
731 (3) The presence of a limited number of associated and even articulated ankylosaur
732 skeletons in the same horizons as the isolated bones may indicate that dispersion was not
733 always very significant during bone accumulation.
734 (4) The relatively high skeletal representation for many taxa may suggest that a large
735 proportion of their skeletons was deposited together in a particular place and sorting was not
736 significant before bone accumulation.
737 Due to the above listed arguments, we suggest that the place of site SZ-6 was a
738 trapping place for bones rather than a slowly filling up depositional area, thus the calculation
739 of taxon distribution by MNI is more realistic (Badgley, 1986a,b) in the case of the SZ-6
740 assemblage in Iharkút locality.
741
742

7. TAPHONOMIC FEATURES OF THE BONE ASSEMBLAGE OF SITE SZ-6, IHARKÚT LOCALITY

Many physical, chemical or biological destructive agents conspire during the deposition of a bone assemblage which result in different damages on the bone surface; these different types of modifications are diagnostic and distinguishable from each other (based on the experimental studies) thus they play a critical role in a better understanding of the taphonomic history (Behrensmeyer, 1991; Lyman, 1994a).

7.1. Taphonomic features of the isolated bone assemblage at site SZ-6 from Iharkút locality

The majority of the Iharkút vertebrate assemblage consists of isolated bones, which suggest a different taphonomic history from that of the associated or articulated skeletal materials (Coard and Dennell, 1995) and suggest presence of dispersal processes before burial.

7.1.1. Abrasion features on isolated bones

The investigation of bone abrasion refers to the physical erosion of the surface of bones before the final burial (Behrensmeyer, 1991; Fernández-Jalvo and Andrews, 2003). Abrasion is an indicator of the interaction between sediment particles and bones, therefore can be used indirectly for estimating the distance bones were transported (Behrensmeyer, 1982; Aslan and Behrensmeyer, 1996; Zeigler, 2003). However, many observations in natural conditions pointed out that the abrasion of bones does not always correlate with transportation

768 (Behrensmeyer 1982, Aslan and Behrensmeyer 1996). In addition, there are other
769 taphonomic processes or agents (e.g. trampling, chewing) that generate similar damage on the
770 edges or external surfaces of bones (Behrensmeyer et al, 1986; Britt et al., 2009; Domínguez-
771 Rodrigo et al., 2009).

772 *Methods:* We examined alterations related to physical grinding and polishing on the
773 edges and/or surface of vertebrate fossils in the SZ-6 assemblage and divided the fossils into
774 two categories (1: unabraded bone; 2: abraded bone). The bone pebbles and microvertebrates
775 were excluded from this part of the analysis because their different "transportation history"
776 distorts the evaluation of the identified bones assemblage (see above).

777 *Results*: 2603 isolated bones were observed to detect abrasion. About 60% of the
778 examined isolated bones are abraded (Fig. 9A). The bones of terrestrial animals show some
779 evidence of abrasion in greater proportion than those of aquatic or semiaquatic taxa (Fig. 9B)
780 and smaller-sized bones are more frequently abraded than larger ones (Fig. 9C). The
781 ankylosaurs show the highest degree of abrasion in the vertebrate material of the site SZ-6
782 (Fig. 9D).

783 *Comments*: The relatively high percentage of abraded bones indicates that more than
784 half of the site SZ-6 material was exposed to physical impacts before final burial. This does
785 not imply that most fossils from Iharkút were long-term transported, because empirical
786 experiments have shown that bones can travel many kilometres without evidence for abrasion
787 (Behrensmeyer, 1982, 1991; Aslan and Behrensmeyer, 1996). The high density flow (which
788 played a significant role in the bone accumulation at the SZ-6 site of Iharkút mine) probably
789 caused significant impact on the bone surfaces when the bones came in contact with the
790 moving sediment particles. This presumably highly energetic (but short-term) process could
791 have grinded the edges and/or surface of the transported bones. The fact that small-sized
792 bones are more frequently abraded than larger ones can be explained that there is evidence

that small bones weather more rapidly than large ones (Behrensmeyer, 1978) and weathered bones become strongly rounded after a short period of abrasion more easily than fresh bones (Fernández-Jalvo and Andrews, 2003). The fossils of terrestrial animals show higher rate of abrasion than the bones of aquatic or semiaquatic animals, which might be also related to different weathering stages of the bones before abrasion (Behrensmeyer, 1975; Fernández-Jalvo and Andrews, 2003). The ankylosaur remains are more abraded compared to the bones of other dinosaur taxa. This suggests some differences in their habitats. Ankylosaurs might have been members of the floodplain channel environment so their bones had more probability for fluvial abrasion. Effect of trampling was also detected both in the skeletal and the isolated bone material (*in situ* breakage type; Fig.10) suggesting that abrasion partly resulted from trampling (Conybeare and Haynes, 1984; Behrensmeyer et al., 1986; Britt et al., 2009).

7.1.2. Weathering on isolated bones

Weathering is the result of the effects of physical and chemical agents during which the organic and inorganic components of bones got separated from each other or have been destroyed in situ on the surface or within the soil zone (Behrensmeyer, 1978; Lyman and Fox, 1989).

Methods: We attempted to divide the fossils of site SZ-6 into two categories: 1) unweathered bones; 2) weathered bones. The bone pebbles (and microvertebrates) were excluded from this part of the analysis.

Results: Presence or absence of weathering on the bone surface could be observed only in the case of 15% of the identified isolated bones because in the other cases abrasion or pyrite crust development on the bone surfaces made this type of observation impossible.

About 6% of the observed material showed flaking associated with cracks due to weathering (Fig. 11A). The turtle and ankylosaur remains are more highly weathered than bones of other taxa in the site Sz-6 assemblage (Fig. 11B).

Comments: Observation of weathering on bone surfaces in the SZ-6 remain cannot be considered of full value due to the following reasons: (1) the Iharkút vertebrate assemblage is highly abraded. The flaking resulted from weathering presumably developed on the bone surface sooner than the abrasion and thus the latter process might have overwritten characteristics of weathering in many cases (Lyman and Fox, 1989). (2) In other cases pyrite crust covers the bone surface and masks the traces of modification. (3) bones of fish, reptiles and birds are different from the mammals in weathering features (Behrensmeyer, 1978) and therefore the direct comparison of Mesozoic non-mammalian fossil assemblages with the weathering stages of Behrensmeyer (1978) is questionable (e.g. Ryan et al., 2001; Britt et al., 2009; Csiki et al., 2010). For these reasons it can be stated that evaluation of the weathering characteristics is strongly limited in the SZ-6 assemblages and therefore the utility of this method for palaeoecological interpretations is also limited

.

7.1.3. Frequencies of breakage types in isolated bone assemblage

The type of break on a fossil bone provides information whether the specimen was fresh or already "fossilized" or mineralized when it got broken. Patterns of breakage in fossil accumulations are of great importance for understanding the different agents (trampling, carnivore gnawing, fluvial transport etc.) acting during the deposition of a vertebrate assemblage (Haynes, 1983; Todd and Rapson, 1988; Ryan et al., 2001).

Methods: We distinguish oblique, longitudinal and smooth transverse fracture categories in the site SZ-6 assemblage (see Supplementary data 1) Furthermore the presence or absence of

843 epiphyses of limb bones was documented separately in this remains. The bone pebbles and
844 microvertebrates were excluded from this part of the analysis.

845 *Results*: 88% of the site SZ-6 vertebrate assemblage is broken indicating a high
846 fragmentation rate (Fig.12A). About 64% of the fractures have indeterminate origin; 18% of
847 the broken bones show different types of "pre-fossilization" fracture (oblique and
848 longitudinal) while only 3% of the fracture was created in the fossildiagenetic phase. There is
849 no significant difference in the distribution of breakage types between the assemblages of
850 aquatic/semiaquatic and terrestrial taxa (Fig. 12B). About 71% of the limb bones preserve the
851 epiphysis at least one end (Fig. 12C).

852 *Comments*: There are three main groups of destructive factors which can cause
853 significant but varying degrees of fractures in a bone assemblage. These are carnivore and/or
854 scavenger effects, trampling, and transportation (Haynes, 1983; Fiorillo, 1991; Jennings and
855 Hasiotis, 1996; Domínguez-Rodrigo et al., 2009; Noto et al., 2012). In Cenozoic vertebrate
856 remains the high degree of fragmentation of the bone material can be caused by mammalian
857 carnivores because their teeth are suited for crushing bones (Fiorillo, 1991; Spencer et al.,
858 2003; Faith and Behrensmeyer, 2006; Faith et al., 2007). Nevertheless, such fragmentation is
859 subordinate in dinosaurs-dominated ecosystems, because the teeth of theropods were
860 appropriate for cutting meat (Fiorillo, 1991; Ryan et al., 2001; Farlow and Holtz, 2002;
861 D'Amore and Blumenschine, 2012) and there is only a limited evidence that they could crush
862 bones (Chin et al., 1998; Hone and Rauhut, 2009). The *Allodaposuchus*-like crocodiles with
863 conical teeth might have crushed bones, when they try to place the food item in the most
864 adequate position for swallowing (Noto et al., 2012; Botfalvai et al., 2014). However the role
865 of crocodiles in fragmentation of SZ-6 bone assemblage could be limited because the
866 crocodiles attempt to swallow large parts of the carcasses and thus the fragmentation is
867 minimal when carcasses are consumed by crocodiles (Njau and Blumenschine, 2006) The

freshwater mosasaur *Pannoniasaurus*, a potential top predator known from the locality, has slender, pointed and slightly distally curved teeth; a tooth morphology that, in contrast to conical teeth, is considered to be inadequate for crushing bone (Botfalvai et al., 2014). Based on the foregoing list, carnivore activity did not play a (significant) role in the fragmentation of Iharkút vertebrate remains just as in other Mesozoic bone assemblages.

Bone fracturing by trampling is a significant and frequent agent in terrestrial bone assemblages (Haynes, 1983; Villa and Courtin, 1983; Olsen and Shipman, 1988; Gates, 2005; Britt et al., 2009; Domínguez-Rodrigo et al., 2009). The *in situ* breakage may be interpreted as resulting from trampling (Gates, 2005; Britt et al., 2009), and such fracture type occurs in a few cases in the isolated (Fig. 10) and associated material (e.g. MTM V.152.1.) of the SZ-6 assemblage. Only 3% of ribs show longitudinal splintering, which type of fracture that is otherwise common in a trampled material (Haynes, 1983). The results of our investigation suggest that the presence of a trampling agent is detectable in the Iharkút material, but it may not be sufficient to explain the high fragmentation rate of isolated bones.

If most of the bones were transported by a high density (energy) flow (hypothesis supported by sedimentologic studies in the basal breccia at site SZ-6) then bones could suffer fragmentation on contact with the substrate or other transported materials. Some authors questioned the possibility of bone breakage during fluvial transport, because the bones become rounded and abraded rather than broken or fractured when transported in water (Behrensmeyer, 1975; Holz and Barberena, 1994). However, the action of high density flow may suggest a more significant destructive impact for the bones which could result in higher fragmentation rate in the fossil assemblage. High energy and density flow can transport large-sized tree trunks and other sediment particles which can produce significant physical impact for the transported bones when these collide with each other (Lancaster and Hayes, 2003; Britt et al., 2009). The basal breccia of site SZ-6 contains larger-sized tree trunks (e.g. an 8 m

893 long Araucariaceae trunk was discovered in close proximity <2 m of the 4th partial ankylosaur
894 skeleton) and highly fragmented bones which were all transported together. Simultaneous
895 presence of the two groups with high current velocity may induce fractures in the transported
896 bone assemblage.
897 The high proportion of oblique and longitudinal fractures indicates that most bones
898 were fresh, collagen-rich elements when broken (Haynes, 1983; Pereda Suberbiola et al.,
899 2000). The low ratio of the fossildiagenetic fracture type may suggest that: (1) sediment
900 reworking within the channel was limited (Behrensmeyer, 1982; Badgley, 1986b; Aslan and
901 Behrensmeyer, 1996); (2) the site suffered no post-burial disturbance.
902
903 *7.1.4. Other surface marks*
904
905 Pyrite crusts on the bone surface (Fig. 5E) are observed in min. 4% of the Iharkút
906 macroscopic vertebrate material (this parameter was observed after the preparation of the
907 bones).
908 There are few tooth-marked turtle plates and one *Iharkutosuchus* skull fragment in the
909 Iharkút vertebrate material (Botfalvai et al., 2014). These tooth marks are bowl-shaped
910 depressions and are often bisected pits which are characteristic of the crocodile gnawing
911 (Njau and Blumenschine, 2009; Boyd et al., 2013). There is no evidence of theropod feeding
912 traces in the vertebrate material of from the site SZ-6 (Botfalvai et al., 2014).
913
914
915 **7.2. Taphonomic features of the skeletal material from the Iharkút locality**
916

There are six associated and one articulated skeletons identified as *Hungarosaurus tormai* (Ősi and Makádi, 2009). These were classified in three subcategories; (1) associated incomplete skeleton which includes at least two different major segments of the skeleton (Csiki et al., 2010), (2) associated partial skeleton which includes only one segment of the skeleton (Heinrich, 1999; Csiki et al., 2010), (3) articulated partial skeleton which includes one segment of the skeleton where the skeletal elements are in contact and retained their original anatomical position (Badgley, 1986a). The more detailed description of the taphonomic features and stratigraphic position of skeletal remains from Iharkút is described in Supplementary data 3.

7.2.1. Associated incomplete skeletons

Material: 1st, 2nd, 3rd and 5th skeletons (MTM V.152; MTM 2007.26; MTM 2007.24; MTM 2007.25). They included different parts of the bodies (Figs. 5E and 13-14) which belong to different disarticulation sequences (based on empirical observations by Hill, 1979; Hill and Behrensmeyer, 1984; Cameron and Oxham, 2012; Cambra-Moo and Buscalioni, 2003).

Taphonomic interpretations: The 1st and 3rd skeletons are limited in the number of the bones preserved which does not allow a precise reconstruction of their detailed taphonomic history (see Supplementary data 3). Furthermore the 1st skeleton was discovered in a sandstone block, found separately in an overburden dump and probably was moved from other parts of the skeleton, thus it is not known how much and what kind of other parts of skeleton were preserved in the original associated skeleton.

Resistant elements of the 2nd (holotype) skeleton of *Hungarosaurus*, such as the synsacrum or skull, can only be broken through significant mechanical effects; however, their

942 scattering was limited, being the bones found close to each other (Fig. 13). These two factors
943 (significant mechanical impact and limited dispersion) suggest that trampling (and perhaps
944 scavenging) was in large part responsible for the destruction of the 2nd ankylosaur skeleton.
945 Trampling is indeed often the main destruction agent in the soft substrate of abandoned
946 channel environments (Behrensmeyer, 1988; Capaldo and Peters, 1995). The enclosing
947 sediment (siltstone with plant fragments which were deposited on the coarse grained
948 sandstone) indicates reduced current velocities which made the stranding of the corpse
949 possible. The carcases have been subsequently exposed to biological and mechanical agents
950 (e.g. decay, trampling, scavenging) during the disarticulation. The skeletal material contains
951 both the earliest disarticulating (cervical vertebrate, ribs, osteoderms) and most resistant
952 elements (limbs and lumbar vertebrate) (Cambra-Moo and Buscalioni, 2003) together within a
953 48 m^2 area, which may indicate that disarticulation of the skeleton began after the final
954 deposition of the corpse. There is no evidence for (longer term) transportation of the skeletal
955 elements from a primary accumulation place to the final one. The elements of the 2nd skeleton
956 of *Hungarosaurus* have been dispersed by weak currents after accumulation and
957 disarticulation, which currents could spread the bones over a restricted area (Fig. 13).

958 The enclosing sediment (coarse sandstone), composition (several parts of the body are
959 represented in the material; Fig. 14C) and taphonomic features of the 5th ankylosaur skeleton
960 (see Supplementary data 3) indicate that the corpse floated with the currents to the site when
961 soft tissue and ligaments still kept parts of the body together. When the transportation of the
962 carcass stopped and skeletal degradation was started by biological agents (decay, scavenging),
963 the currents were occasionally still sufficient to move parts of the body and thus progressively
964 dissociated the skeletal elements to arrange them in a disarticulated but associated position.
965 Skull elements were not found in the 5th ankylosaur skeleton material, but the mandibles

966 remained with the deposited elements which is not an uncommon phenomenon (Tooth, 1965;
967 Dodson, 1971; Weigelt, 1989:85; Holz and Barberena, 1994; Capaldo and Peters, 1995).
968 *7.2.2. Associated partial skeletons*
969
970 *Material:* 4th and 7th *Hungarosaurus* skeletons (MTM 2007.23, MTM PAL.2013.57.1)
971 including the elements of the hip region in associated position (Fig. 14B).
972 *Comments*: Elements of the hip region (pelvic girdle and synsacrum) of ankylosaurs
973 are much more resistant to physical effects (e.g. transportation) than other skeletal parts,
974 because these are usually co-ossified, hence they are often preserved in articulated or
975 associated position (e.g. Pereda Suberbiola et al., 2000), despite of the high energy
976 transportation.
977 The pelvic girdle elements were in an articulated position when they got deposited on
978 the bottom of the channel. This assumption is based on the model of random scattering
979 described by Hill (1979) saying that the probability of dispersion of disarticulated bones of
980 individual "A" is always higher than the probability of disarticulated bones of individual "A"
981 concentrated together in the same space. Presumably, the elements of the deposited pelvic
982 girdle suffered damage from biological agents, because several skeletal elements were broken
983 in the biostratonomic phase (oblique fracture type).
984
985 *7.2.3. Articulated partial skeleton*
986 *Material:* 6th skeleton (MTM PAL.2013.58.1) composed of the complete hip region
987 including pelvic elements and the sacral region, but not the sacral armour elements (Fig. 5F).
988 *Comments*: The original skeleton presumably began to become decomposed by
989 biological and physical effects and the parts of the skeleton were separated from each other.
990 The hip region is a resistant part of the body and its density and size might have been greater

than the other segments of the skeleton, consequently it was transported to a different place from the other bones. Furthermore, the hip region might have remained articulated far longer than the other parts of the body because its elements were ossified. It is plausible, that these parts of the ankylosaur skeleton might have been dispersed with different rate than the other parts by water action (Nasti, 2005), because the hydraulic transport potential of articulated remains is often greater than that of the disarticulated bones (Coard and Dennell, 1995). This assumption may explain the frequency of the pelvic and sacral regions among the associated material of the SZ-6 assemblage.

7.3. Discussion and interpretation of taphonomic features of Iharkút bones material

On the basis of taphonomic investigations performed on the vertebrate material of site SZ-6 it is suggested that the assemblage consists of three different taphonomic fractions.

The first fraction includes unidentifiable bone pebbles which were transported for a long time with the bed-load sediment of ancient streams from the background area. The high rate of abrasion and the spherical shape of these elements indicate that they were reworked many times and exposed to channel bottom processes for a long time, during which they suffered significant physical impact and destruction before the final burial (Behrensmeyer, 1988; Wood et al., 1988).

The second group includes about 88% of the Iharkút collection, containing most of the identified isolated bones and teeth. Most of these isolated bones were abraded and fractured (Figs. 9 and 12). The isolated bones were exposed to physical and/or biological destruction in the preburial phase. Trample-induced breakage (*in situ* breakage type; Fig. 10) is detectable in the isolated bone material, however, fractures observed in the bones were also formed during

1016 transportation by high density flows, since there is evidence for large-sized tree trunks
1017 transported alongside the bones; occasional collision between these trunks and the transported
1018 bones could have also resulted in bone fractures in the Iharkút material. Skeletal
1019 representation (bones of different size, density and shape were deposited in the same horizon),
1020 abrasion stages and fragmentation ratio vary among terrestrial and aquatic/semiaquatic taxa
1021 which may imply that this fraction of the Iharkút collection represents polytypic attritional
1022 remains of isolated and dispersed elements which were deposited by fluvial processes
1023 (Kidwell et al., 1986; Holz and Barberena, 1994; Kahlke and Gaudzinski, 2005). The high
1024 skeletal completeness of nodosaurids ankylosaurs suggests that they were members of the
1025 floodplain channel environment and their bones have more probability for concentration by
1026 fluvial action (Table 4).

1027 The third fraction includes the associated and articulated bone assemblages, which
1028 have a different taphonomic history from that of the isolated bones. All the
1029 associated/articulated skeletons are from ankylosaurs and this fact further supports that
1030 ankylosaurs lived close to the place of final bone accumulation. The associated skeletal
1031 material shows high fragmentation rate (see Supplementary data 3). The greater proportion of
1032 fractures was created by a trampling agent (*in situ* breakage) after the deposition. The
1033 extremely high frequency of ankylosaur hip regions preserved in the Iharkút locality suggests
1034 that this represented the most resistant part of the body. The pelvic girdle elements of
1035 ankylosaurs were originally co-ossified, hence they could have remained far longer in
1036 articulated position compared to the other parts of the body.

1037 The low completeness values of the skeletons in the Iharkút collection may indicate
1038 that the carcasses were exposed to subaerial or subaqueous destructive processes and then
1039 they were transported by fluvial action during which parts of the skeleton were dispersed
1040 before final burial (Holtz and Barberena, 1994; Davis and Briggs, 1998; Brand et al., 2003;

1041 Cameron and Oxenham, 2012; Syme and Salisbury, 2014). Decay processes affecting the
1042 carcasses preceded scattering of the skeleton (which was generated by fluvial action during
1043 short term transportation), because currents can only disarticulate the corpse after the most
1044 digestible tissues have been removed (Tooth, 1965; Syme and Salisbury, 2014). Furthermore,
1045 scavengers might have been also significant agent in disarticulation or degradation of the
1046 studied skeletons, because empirical studies have documented that vertebrate (e.g. crocodiles)
1047 and invertebrate (e.g. gastropods, insect larvae) scavengers have primary role in the
1048 degradation of carcasses (Weigelt, 1989:13; Hill and Behrensmeyer, 1984; Oliver and
1049 Graham, 1994; Davis and Briggs, 1998; Brand et al., 2003; Carter et al., 2007; Cameron and
1050 Oxenham, 2012; Syme and Salisbury, 2014). Real estimation of decay and disarticulation
1051 period is not possible in the case of dinosaur remains because these processes largely depend
1052 on the nature of skin, body size and environmental conditions (Brand et al., 2003), factors
1053 which are poorly known.

1054 The most conspicuous feature of the skeletal materials from Iharkút is that these are
1055 confined to only one taxon (*Hungarosaurus*) thus representing a monospecific assemblage.
1056 This fact has a number of possible explanations:

1057 (1) The skeletal structure of ankylosaurs was favourable for articulated preservation
1058 (e.g. because many elements were co-ossified) thus their elements could remain in a strongly
1059 associated position far longer during transportation or exposure to subaerial destructions than
1060 the skeletal parts of other taxa. However, this possibility can be probably discarded in the case
1061 of the *Hungarosaurus* skeletal material from Iharkút, because in the sites of the Dinosaur Park
1062 Formation (Upper Cretaceous, Dinosaur Provincial Park, Alberta, Canada) the number of
1063 articulated ankylosaur skeletons is subordinate when compared to that of hadrosaurs and
1064 ceratopsians (Wood et al., 1988). This comparison is probably relevant, because in many
1065 cases the taphonomic characters documented in the Dinosaur Park Formation are very similar

to those from the Iharkút sites if one considers the deposition or transportation of the carcasses. At first the carcasses floated downstream as bloated carcasses in the Dinosaur Park Formation, as it was also suggested in some Iharkút skeletons (2nd and 5th skeletons). Second, incomplete preservation of skeletons also occurs in the Dinosaur Park Formation (as a result of longer periods of exposure; Wood et al., 1988), as it was demonstrated in case of ankylosaurian skeletal material from Iharkút. Third, the two most common dinosaur groups of the Dinosaur Park Formation, the ornithopods (hadrosaurs) and ceratopsians, are also known from the Iharkút sites (Ősi et al., 2010b, 2012b) but their fossils are very rare and their skeletons have not yet been discovered. Furthermore, Dodson (1971) also mentioned that in the Dinosaur Park Formation the number of ankylosaur skeletons is also significantly less common than those of ornithopods and ceratopsians, which confirms that the skeletal structure of ankylosaurs was not more favourable for articulated preservation than that of other dinosaur taxa (ornithopods, ceratopsians and theropods) from the Iharkút locality.

(2) Ankylosaurs lived in a habitat close to the site of deposition, consequently the probability of articulated preservation was higher than for other taxa, because their bones were transported for a shorter period. This habitat preference (which was demonstrated by the measure of relative skeletal completeness in the isolated bone assemblage by Shotwell (1955)) definitely played a significant role in the associated and articulated preservations of ankylosaur bone material in the Iharkút sites. However, it is unlikely that only the ankylosaurs were members of a proximal community and all the other taxa lived in more distal habitat(s). For instance, *Iharkutosuchus* remains include numerous unabraded skulls with in situ teeth (Ősi, 2008a) which may indicate that the *Iharkutosuchus* material was not transported from distant areas, but instead these animals died close to the site of final deposition (e.g. Behrensmeyer, 1982, 1988; Aslan and Behrensmeyer, 1996). The skull of *Iharkutosuchus* is flattened and rather disc-like, a morphology which could have lowered transport rates (based

on empirical observations) compared to spherical or rod-like fossils (Frostick and Reid, 1983). The presence of numerous disc-shaped and heavier (high density) bones in the *Iharkutosuchus* material probably indicates that this crocodile was also member of the proximal habitat community as it was concluded in ankylosaurs; nonetheless, skeletons of *Iharkutosuchus* are yet to be discovered. Although the suggested habitat of ankylosaurs, close to the place of deposition might have played a significant role in the relatively common articulated and associated preservation of their bones in the Iharkút sites; this is, however, not considered to be a sufficient explanation for the occurrence of a monospecific assemblage of associated/articulated ankylosaur skeletons in the Iharkút locality.

(3) The monospecific skeletal material of Iharkút may represent a mass death assemblage (see e.g. Wood et al., 1988; Sander, 1992; Varricchio and Horner, 1992; Henrici and Fiorillo, 1993; Coria, 1994; Holz and Barberena, 1994; Schwartz and Gillette, 1994; Ryan et al., 2001; Lucas et al., 2010; Mukherjee and Ray, 2012). A mass death assemblage includes remains of animals (possibly member of a herd or group of animals) that died over a brief time span due to a single agent of death (Haynes, 1988). It is often very complicated to distinguish mass mortality from mass accumulation in terrestrial and/or fluvial environments, because many agents can create individual rich mass accumulation of fossils by reworking, transporting and concentrating attritional assemblages (e.g. scavenger and carnivore effect or fluvial transportation), and these occurrences are easily confused with mass mortality assemblages (Turnbull and Martill, 1988; Haynes, 1988; Capaldo and Peters, 1995, Lucas et al., 2010). Mass mortality events can be caused by natural events such as drought (Shipman, 1975; Conybeare and Haynes, 1984; Rogers, 1990; Varricchio and Horner, 1992; Schwartz and Gillette, 1994; Fiorillo et al., 2000; Gates, 2005; Mukherjee and Ray, 2012), high density debris flows (Turnbull and Martill, 1988,; Rogers 2005), volcanic or gas eruptions (Rogers et al., 2001; Baele et al., 2012), poisoning or infections (Varricchio and Horner, 1992;

1116 Varricchio, 1995; Henrici and Fiorillo, 1993), trapping (Eberth et al., 2010; Domingo et al.,
1117 2013), miring in soft ground (Sander, 1992; Spencer et al., 2003; Varricchio et al., 2008;
1118 Eberth et al., 2010) and drowning during the high-flood events (Wood et al., 1988; Fiorillo,
1119 1991, Capaldo and Peters 1995, Ryan et al. 2001, Kahlke and Gaudzinski 2005, Gangloff and
1120 Fiorillo 2010).

1121 The taxonomic exclusiveness and relatively high frequency of the ankylosaur
1122 skeletons preserved in a localized area (about 400 m^2), as well as their similar taphonomic
1123 features raise the possibility that several individuals of one species were killed in one place
1124 and over a brief time span. The hypothesis of mass mortality of the Iharkút ankylosaurs is
1125 supported by the following observations: six associated and one articulated *Hungarosaurus*
1126 skeletons were discovered from an area of approximately 400 m^2 and in many cases the
1127 skeletons were found close to each other in the same layer (e.g. 2^{nd}-3^{rd} and 6^{th}-7^{th} ankylosaur
1128 skeletons, respectively). The associated skeletal material from Iharkút has almost uniform
1129 taphonomic features (e.g. limited abrasion, absence of weathering, often complete epiphyses)
1130 which may also suggest mass mortality. The enclosing layer shows sign of rapid deposition
1131 (clay clasts and sand with plant fragments, poorly sorted sediment), which is a sedimentologic
1132 criterion of a mass-death assemblage (Turnbull and Martill, 1988).

1133 The question of whether the *Hungarosaurus* mass assemblage is a result of
1134 catastrophic (nonselective) or noncatastrophic (selective) mass mortality (Conybeare and
1135 Haynes, 1984, Turnbull and Martill, 1988; Varricchio and Horner, 1992; Henrici and Fiorillo,
1136 1993; Lyman, 1994a:118; Heinrich, 1999; Ryan et al., 2001; Kahlke and Gaudznski, 2005;
1137 Baele et al., 2012; Mukherjee and Ray, 2012) is difficult to answer, because the number of
1138 specimens (only seven carcasses) is limited for estimating a U-shaped or L-shaped age profile
1139 of the Iharkút skeletal material. The skeletal material from Iharkút is most probably composed
1140 of both adult and subadult individuals, but this hypothesis is supported only partly by accurate

1141 bone histological examinations (Company and Ősi, 2012). Several studies documented that
1142 rich bone accumulation of dinosaurs (e.g. ceratopsids) could have been the results of mass
1143 death events of herds that occurred when the herd attempted to cross the flooded river (Wood
1144 et al., 1988; Fiorillo, 1991; Ryan et al., 2001; Gangloff and Fiorillo, 2010). We suggest that
1145 the cause of death of the Iharkút ankylosaurs was also probably drowning when the herd
1146 attempted to cross the flooded river, as supported by the following arguments: drowning is a
1147 frequent cause of death in terrestrial animals with herding lifestyle (Weigelt, 1989; Capaldo
1148 and Peters, 1995; Ryan et al., 2001; Rogers and Kidwell, 2007; Gangloff and Fiorillo, 2010),
1149 documented in the fossil record by several authors (Turnbull and Martill, 1988; Wood et al.,
1150 1988; Fiorillo, 1991; Kahlke and Gaudzinski, 2005). Sediments of periodic heavy flooding
1151 events were detected in Iharkút locality since the basal breccia of the site SZ-6 (which
1152 contains most of the ankylosaur skeletons) was deposited during a high density flow (see
1153 above, the sedimentologic settings). As it was pointed out based on trackways, ankylosaurs
1154 preferred herding lifestyle (McCrea et al., 2001) and the structure of their body (large and
1155 heavy osteoderms on the body) might have been unfavourable for swimming across the
1156 flooded river.

1157 There are no evidences for other possible causes of death, but this does not mean that
1158 other causes can be excluded conclusively. Drought as another common cause of mass-death
1159 events could not have been detected at the locality because there are no sedimentologic
1160 evidences for periodic drought (such as mud cracks or evaporites etc.) and the flora suggests a
1161 subtropical, moist climate (Bodor et al., 2012). Furthermore, the faunal composition and
1162 taphonomic observations (most of the skeletons are preserved in disarticulated position, small
1163 number of juvenile individuals) clearly against this hypothesis (Shipman, 1975; Rogers, 1990;
1164 Varricchio and Horner, 1992; Schwartz and Gillette, 1994; Gates, 2005). There are not
1165 taphonomic evidences for miring in the soft ground such as articulated preservation, strongly

recovered neck, *in situ* death and skeleton pose (Sander, 1992; Eberth et al., 2010). Disease or poisoning, as possible causes of mass-death events, are theoretically possible (Varricchio, 1995; Henrici and Fiorillo, 1993; Baele et al., 2012), but detection of these agents is difficult, and there is no evidence that modern diseases (e.g. botulism) were already present in the Cretaceous (Henrici and Fiorillo, 1993; Gates, 2005). Furthermore, this hypothesis may not explain the monospecific features of the skeletal assemblages. Forest fire is often associated with catastrophic death events (Sander, 1987; Zeigler, 2003) but fire not necessarily threatens the life of large-bodied animals significantly, because most of them can easily escape from the endangered area (Lawrence, 1966; Singer et al., 1989). Fire-related mass death further seems improbable, because fusinite and fossil charcoal are only sparsely present in the sediments; only the remains of seeds and fruits were coalified, while fusinite was not detected in these plant fossils (Bodor and Baranyi, 2012). The existence of monospecific skeletal material in a layer deposited under high energy conditions raises the possibility that all or some of these ankylosaurs were killed by an instantaneous event when they attempted to cross the flooded river. The carcasses of the drowned animals drifted downstream by flotation until the current velocity decreased and/or water column become too shallow. The deposited carcasses were exposed to destructive processes (decay, trampling, scavenging) during which the bodies disarticulated and certain parts of the skeletons were destroyed or scattered. The mass deposited carcasses represent an important food source for the scavengers which can cause a notable reduction of the skeletons (Capaldo and Peters, 1995; Spencer et al., 2003; Carter et al., 2007). Furthermore, an empirical examination showed that commonly about 70-80% of the bone material of mass vertebrate assemblages becomes destroyed within 1-2 years by physical and biological destructive processes (Capaldo and Peters, 1995). Thus the low percentages of skeletal completeness documented in the ankylosaur skeletal material from Iharkút are not considered an unusual phenomenon.

On the other hand, it cannot be excluded that these *Hungarosaurus* individuals died in unknown death event(s) or through normal, attritional mortality in the background area and their corpses were afterwards collected during the (ephemeral) flood events and deposited into the studied area. We do not have unequivocal evidence for the cause of death but we have presented a possible scenario for the death and accumulation of seven *Hungarosaurus* individuals providing a monospecific assemblage of skeletons in the SZ-6 site of the Iharkút locality.

8. PALAEOECOLOGICAL CONSIDERATIONS

The vertebrate assemblage of Iharkút originated from multiple bone sources, because attritional (isolated bones) and most probably mass killed assemblages (associated and articulated skeletal materials) are found together in the same layer, and these do not show significant evidence for sorting by size and/or shape. This kind of vertebrate assemblages from over extended periods (Behrensmeyer, 1982; Aslan and Behrensmeyer, 1996) are probably represent the result of long-term time average. Thus we estimated the duration of time averaging represented in the SZ-6 assemblage, because without it accurate palaeoecological investigations cannot be achieved (Behrensmeyer, 1982; Kidwell and Flessa, 1996; Martin, 1999:220).

The length of time represented by fluvial bone assemblages can be related to influences of rates of sedimentation and sediment reworking as well as the preservation of bones in floodplain sediments and soils (Aslan and Behrensmeyer, 1996). The rate of sedimentation at site SZ-6 was probably rapid, because the channel fill formed during ephemeral flood events as a result of high density (flash) flows. The presence of frequent sandstone ribbon and poorly developed paleosols in the Iharkút locality probably also

indicates relatively rapid sediment accumulation (Aslan and Behrensmeyer, 1996; Martin 1999:221). Sediment reworking appears to be restricted; absence of point bar accretion and the rarity of cross-bedding in the channel fills indicate that lateral accretion of the channels was limited in the Iharkút locality. These conditions were not favourable for the preservation of bones in the floodplain sediments of Iharkút because "rapid sediment accumulation inhabits paleosol development and favours low density of bones in the floodplain deposit" (Aslan and Behrensmeyer, 1996:419). The Iharkút locality is thus generally characterized by conditions of rapid sedimentation and limited sediment reworking as well as predominant presence of poorly developed, hydromorphic paleosols. These conditions minimize the duration of time averaging (based on empirical observations, amounting time intervals of about 10^1–10^2 years) represented in the channel-related bone assemblages (based on Aslan and Behrensmeyer, 1996). The sedimentologic and taphonomic investigations suggest that the vertebrate sample of site SZ-6 represents an assemblage of animals that lived approximately at the same time in and around the ancient fluvial system and thus the palaeoecological interpretation of the Iharkút fauna can be regarded as well supported based on the available fossil material. Nevertheless, we have to keep in mind that the fossils from Iharkút reflect only a fraction of the total diversity present in this area during the Santonian, a circumstance that is true for every fossil site (Behrensmeyer, 1991; Behrensmeyer et al., 2000; Pereda Suberbiola et al., 2000; Lyman, 2008:23).

The Iharkút vertebrate assemblage is composed of aquatic, semi-aquatic and terrestrial vertebrates. Macrofossils are dominated by bones of aquatic and semi-aquatic animals while bones of terrestrial animals are subordinate. The estimated body size of the taxa represented ranges from less than 1 kg (amphibians and fish) up to 650 kg (*Hungarosaurus tormai*; based on Ősi and Makádi, 2009), while dinosaurs with larger body size (e.g. sauropods) appear to be absent in the Iharkút vertebrate fauna. The taphonomic examinations show that both the

parautochthonous and allochthonous faunal elements are present together in the fossil assemblage; the definition of parautochthonous and allochthonous faunal elements follows Kidwell et al. (1986).

Besides gars (lepisosteiforms), the freshwater fish fauna from Iharkút is unique in having two different pycnodontiforms, a group of fish with massively built crushing dentition in their jaw apparatus, and were previously reported mainly from marine environments (Kocsis et al. 2009). The fish material is probably a parautochthonous element of the SZ-6 assemblage because several well preserved mandibular with *in situ* teeth were discovered (Ősi et al., 2012b) and the fish remains destroyed easily during the long term transportation (Smith et al., 1988). The relatively small number of amphibian bones in the Iharkút material represents a relatively diverse group including both allocaudatans and anurans. The anuran fauna is mainly dominated by *Hungarobatrachus* characterized by both good swimming and jumping abilities in the freshwater habitat (Venczel and Szentesi, 2012).

The aquatic bothremydids are the most common turtle taxa in the Iharkút locality (the material includes skulls, jaws, limb bones and numerous plates), while the freshwater dortokids and the terrestrial *Kallokibotion* are quite rare in the fauna, and their fossils are limited only to plate elements. Bothremydid turtles were thus probably present in large numbers in the fluvial system close to the site of deposition, while the other turtle taxa might belong to a more distal habitat. The four different crocodiles provide a very rich fossil material representing about 14% of the total Iharkút vertebrate material. *Iharkutosuchus makadii* was probably a member of a community living in proximity to the site of deposition because its remains include several unabraded (disc-like) skulls with teeth (Ősi 2008a) which may indicate that the material of *Iharkutosuchus* was not transported from distant areas. The other, terrestrial (*Doratodon* and a *Theriosuchus*-like form) and semi-aquatic (*Allodaposuchus*-related taxon) crocodiles cannot be examined from this point of view,

because taxonomical examinations of their postcranial elements is yet not completed (Rabi, pers. comm.).

The freshwater mosasaur *Pannoniasaurus inexpectatus* is probably a parautochthonous element of the SZ-6 assemblage because diverse remains of several individuals (skull and mandibular elements, teeth, vertebrae, ribs, pectoral and pelvic girdle elements of different ontogenetic stages) were discovered in the same layer and most of the bones are well preserved (unabraded, unweathered and complete). These mosasaurs were the largest known aquatic predators in this palaeoenvironment (Makádi et al., 2012). Besides mosasaurs, the squamates are also represented by seven small- to medium-sized taxa of lizards, most probably all terrestrial animals. The terrestrial macrofauna is dominated by herbivorous dinosaurs such as ankylosaurs, ornithopods and ceratopsians, the ankylosaurs being considered by far the dominant element of the Iharkút material (their fossils amount to 83% of the total dinosaur assemblage). The carnivorous dinosaurs are represented by three different taxa, but their frequency is subordinate compared to herbivores. The proportion of herbivorous and carnivorous dinosaurs is about 6:1 based on MNI calculations, while 90% of the isolated dinosaur bone assemblage belongs to the herbivores (Table 3). The presence of the associated and articulated skeletal remains of *Hungarosaurus* indicates that this ankylosaur is a parautochthonous element of the local community. Furthermore, the relatively high percentage of the skeletal completeness of isolated bones of *Hungarosaurus* also indicates that ankylosaurs lived in a community closer to the site of deposition. The taphonomic analysis of the ankylosaur material from Iharkút further strengthens the previously proposed hypothesis (Horner, 1979; Lee, 1996; McCrea et al., 2001) that ankylosaurs preferred wetland habitats such as fluvial systems and coastal regions. The other two taxa of herbivorous dinosaurs (ornithopods and ceratopsians) are significantly less common than the ankylosaurs as they constitute only 6% of the known dinosaur fauna. They

were probably members of a community living in the distal, drier habitats, also characterized by different vegetation (Bodor, pers. comm.). The remains of three different theropods (a large-bodied basal tetanuran, a small-bodied abelisaurid and the small-bodied paravian, *Pneumatoraptor fodori*, including several teeth and bones, suggest that they were parautochthonous rather than allochthonous faunal elements. A few lightly built limb bones, most probably referable to non-avian theropods, have been quickly destroyed or became unrecognizable during sediment reworking or long term transportation (White et al., 1998; Eberth et al., 2010), thus the well-preserved bone material of theropods may indicate their parautochthonous status in the SZ-6 assemblage. Furthermore, the calculation of the skeletal completeness of isolated theropod bones ranks these in the second position after the *Hungarosaurus* material, which also indicates their proximal habitat.

Two types of enantiornithine birds were identified on the basis of a few complete and several fragmentary limb bones (Ősi, 2008b; Dyke and Ősi, 2010; Ősi and Buffetaut, 2011), but their lifestyles have not been determined yet.

The unusually large number of pterosaur mandibular symphyses along with various postcranial elements indicates at least 58 individuals (Table 3). These pterosaurs probably were members of the proximal habitat community and preferred wetland environments, because we also found a relatively large number of fragmentary pterosaur bones (e.g. Ősi et al., 2005) which (like the similarly thin-walled theropods bones) can be easily destroyed during sediment reworking or long term transportation.

9. CONCLUSIONS

The sedimentologic investigations of the Santonian Csehbánya Formation at Iharkút pointed out that the depositional environment was probably represented by the floodplain of a

very low-gradient river system, based on the predominance of fine overbank deposits, abundance of hydromorphic paleosols as well as the presence of shallow channel deposits and fine sandstone sheets. The multiple storied, vertically aggraded shallow sandstone ribbons with low width/depth ratios, and their relatively homogeneous texture suggest that the channels were created by low sinuosity rivers which can be interpreted as an anastomosing river system. The bonebed of site SZ-6, being the most important fossiliferous layer in the Iharkút locality, indicates alternating energy conditions during bone accumulation which resulted in fossils of different states of preservation being deposited into the same layer. The deposits of site SZ-6 are interpreted as those of an abandoned channel which was formed during (ephemeral) flood events. The vertebrate material from site SZ-6 represents a channel-fill assemblage based on the following sedimentary and taphonomic attributes: (1) the site represents a channel with mixed fill (sand-clay clast deposits alternated with fine-grained siltstone-clay sediments) which indicates gradual abandonment during bone deposition; (2) there is no strong evidence for shape or size sorting; (3) the rich micro- and macrofossil assemblages from the same layer represent a wide range of body sizes in the Iharkút fauna; (4) the preservation stage of fossils varies with in same layers (ranging from highly abraded "bone pebbles" to unabraded skulls with teeth); (5) associated incomplete and partial skeletal material and very fragile bones (e.g. complete mandible of *Bakonydraco galaczi*) were found in the basal section of the SZ-6 site, and these preservation modes contradict the scenario of accumulation during sustained active flow. Based on the listed features we consider that the assemblage of site SZ-6 was deposited when the extensive and sustained active flow already abandoned the channel, that resulting in a sudden deposition and accumulation of the transported bones and skeletal parts due to the reduction of current velocity. The bones are significantly concentrated into the basal breccia layer of site SZ-6 which implies that they were accumulated during the initial filling stages of the channel (based on Behrensmeyer

1988), but the presence of associated skeletal remains in the same layer indicates that the current velocity suddenly decreased after the cutting stages of the channel development.

The isolated bone assemblage from site SZ-6 was deposited through attritional processes within the abandoned channel: the bone pebbles were transported for a long time with the bed-load sediments of the ancient streams from the background area while other isolated bones (e.g. unabraded skulls of *Iharkutosuchus* with *in situ* teeth, bones of pterosaurs and birds) were probably only transported for a short time or by sporadic flows during rainfall. We further consider that the monospecific skeleton assemblage of the SZ-6 site probably represents the end product of a mass-death event of herding ankylosaurs because: (1) six associated and one articulated *Hungarosaurus* skeletons were discovered from an area of approximately 400 m^2 and in many instances the skeletons were found close to each other in the same layer; (2) they show similar taphonomic features; (3) the bone-bearing layer suggests rapid deposition, which is a sedimentologic criterion of a mass-killed assemblage. The existence of this monospecific *Hungarosaurus* skeletal material in a layer deposited under high energy conditions raises the possibility that they were killed instantaneously, possibly when they attempted to cross the flooding river. The carcasses of the drowned animals drifted downstream by flotation until the current velocity decreased and they accumulated. The deposited carcasses were exposed to destructive processes (decay, trampling, scavenging) during which the bodies were disarticulated and certain parts of the skeletons were destroyed or transported to different places.

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Figure captions

Figure 1. Map and simplified stratigraphy of the Iharkút locality. A. Location map of the Iharkút vertebrate locality. B. Time/space relations of the Senonian formations in the Bakony Mountains, western Hungary modified from Haas et al. (1992). C. Schematic section of the Iharkút open-pit mine after Ősi and Mindszenty (2009).

Figure 2. Schematic stratigraphic section of the site SZ-1 showing the main palaeoenvironments and lithofacies associations.

Figure 3. Schematic stratigraphic section of the site SZ-6 showing the main palaeoenvironments and lithofacies associations (A) and basal breccia of site SZ-6 (B).

Figure 4. Schematic stratigraphic section of the sites SZ-7-8 showing the main palaeoenvironments and lithofacies associations.

Figure 5. Bonebed of site SZ-6 and aspect of different preservation of Iharkút vertebrate assemblage. A. bone pebbles. B. Well preserved isolated *Pannoniasaurus* vertebra. C. Well preserved skull of the *Iharkutosuchus makadii* ("complex" skeletal element). D. Well preserved pterosaur mandible in the enclosing sediment at site SZ-6 (left) and after the preparation (right). E. Associated incomplete *Hungarosaurus* skeleton (MTM V.152). F. Articulated *Hungarosaurus* partial skeleton (MTM PAL.2013.58.1). G. Turtle plate fragments with pyrite crust.

Figure 6. Relative abundances of vertebrate taxa in Iharkút. A. NISP distribution is calculated from only the isolated bones material of Iharkút mine. B. MNI distribution includes the macro- and microfossils and skeletal elements of *Hungarosaurus tormai*.

Figure 7. The percentages of small (<5 cm), medium (5–10 cm) and big (10–50 cm) elements that are over- and underrepresented compared to their expected number in the fossils material. The expected numbers of observed elements are calculated from data of Table 4.

Figure 8. Shape sorting of the Iharkút bone assemblage based on the method of Frostick and Reid (1983).

Figure 9. Abrasion stages of isolated bones from the site SZ-6, Iharkút without bone pebbles and microvertebrates. A. Distribution of abrasion in the vertebrate assemblage. B. Abrasion stages of bones between aquatic/semiaquatic and terrestrial taxa. C. Abrasion stages among different bone sized. D. Abrasion stages of bones among the main sauropsid taxa.

Figure 10. *In situ* breakage. Turtle limb bone in anterior, A. and medial, B. views.

Figure 11. Weathering stages of bones from the site SZ-6 Iharkút, (only 15% of the identified isolated bones, see text). A. Distribution of weathering stages in the SZ-6 vertebrate assemblage. B. Weathering profiles limited to the isolated bone of SZ-6 assemblage.

Figure 12. Breakage distribution of bones in the SZ-6assemblage. A. distribution of breakage types. B. Breakage stages of bones compared between aquatic/semiaquatic and terrestrial taxa. C. Presence or absence of epiphyses on limb bones in the Iharkút material.

Figure 13. Quarry map of the 2nd (holotype) skeleton of *Hungarosaurus tormai* (meaning of the numbers see in Supplementary Information 2).

Figure 14. Quarry maps of *Hungarosaurus tormai* skeletons of from the Iharkút locality (meaning of the numbers see in Supplementary Information 2). A. 3rd *Hungarosaurus* skeletal material. B. 4th *Hungarosaurus* skeletal material. C. 5th *Hungarosaurus* skeletal material.

Table 1. List of the Late Cretaceous vertebrate fauna from Iharkút.

Table 2. Classification of the taphonomic modes in the Iharkút bone assemblage based on taphonomic dataset (See Supplementary Information 2).The characters of the table were separated after Csiki et al. (2010).

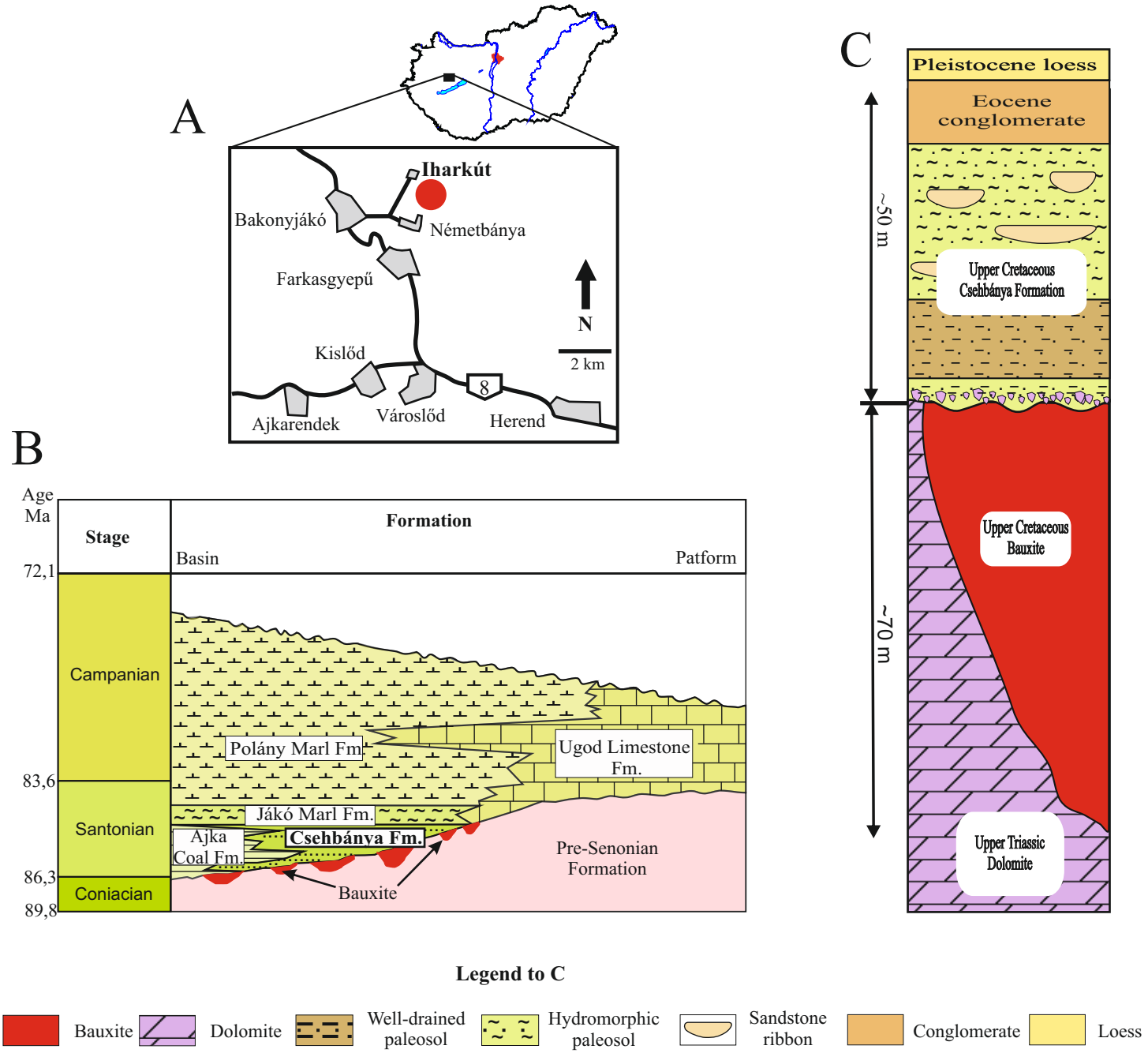
Table 3. NISP and MNI values as well as fragmentation rate associated with taxa in the Iharkút vertebrate locality (the NISP and fragmentation rate are calculated from only the isolated bones material).

Table 4. Skeletal completeness data in the Iharkút vertebrate assemblage. The MNI is calculated from the isolated bones material of site SZ-6. Size and shape category see subchapter of 6.3.2 and 6.3.3 and their figures and tables. *Only turtle plate fragments which were identified as part of a carapax or plastron. **The crocodyliform vertebrae were not separated as cervical, dorsal or caudal vertebrate in this table, because there is not enough information about the expected number of these elements in the original skeleton as well as due to the impossibility of distinguishing the vertebrae of different crocodyliform taxa.

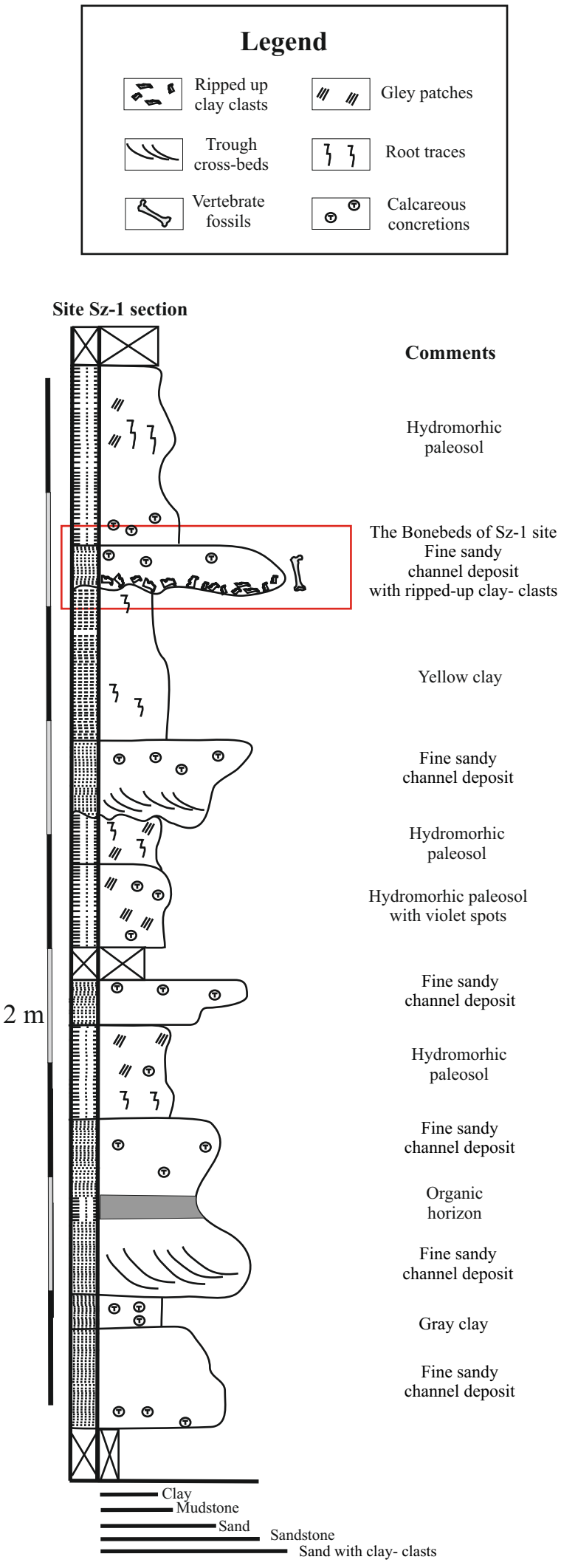
%R_i: percentage of relative proportion of element i in population of MNI; **A_i**: actual number of element i in the collection; **E_i**: expected number of element i in a complete skeleton per individual; **MNI**: minimum number of individuals; **%TC_t**: percentage of total skeletal completeness of taxon t; $\sum$ **A_t**: actual number of skeletal elements of taxon t; $\sum$ **E_t**: expected number of elements in a complete skeleton of taxon t

Table 5. Shape sorting data of isolated bones for six sauropsid taxa associated with their expected values at SZ-6 assemblage. Expected number of elements was adopted from Table 4. The easily moveable shape categories are spherical and rod-like fossils, while hardly moveable are disc- and blade-like bones based on empirical observations of Frostick and Reid (1983).

Figure

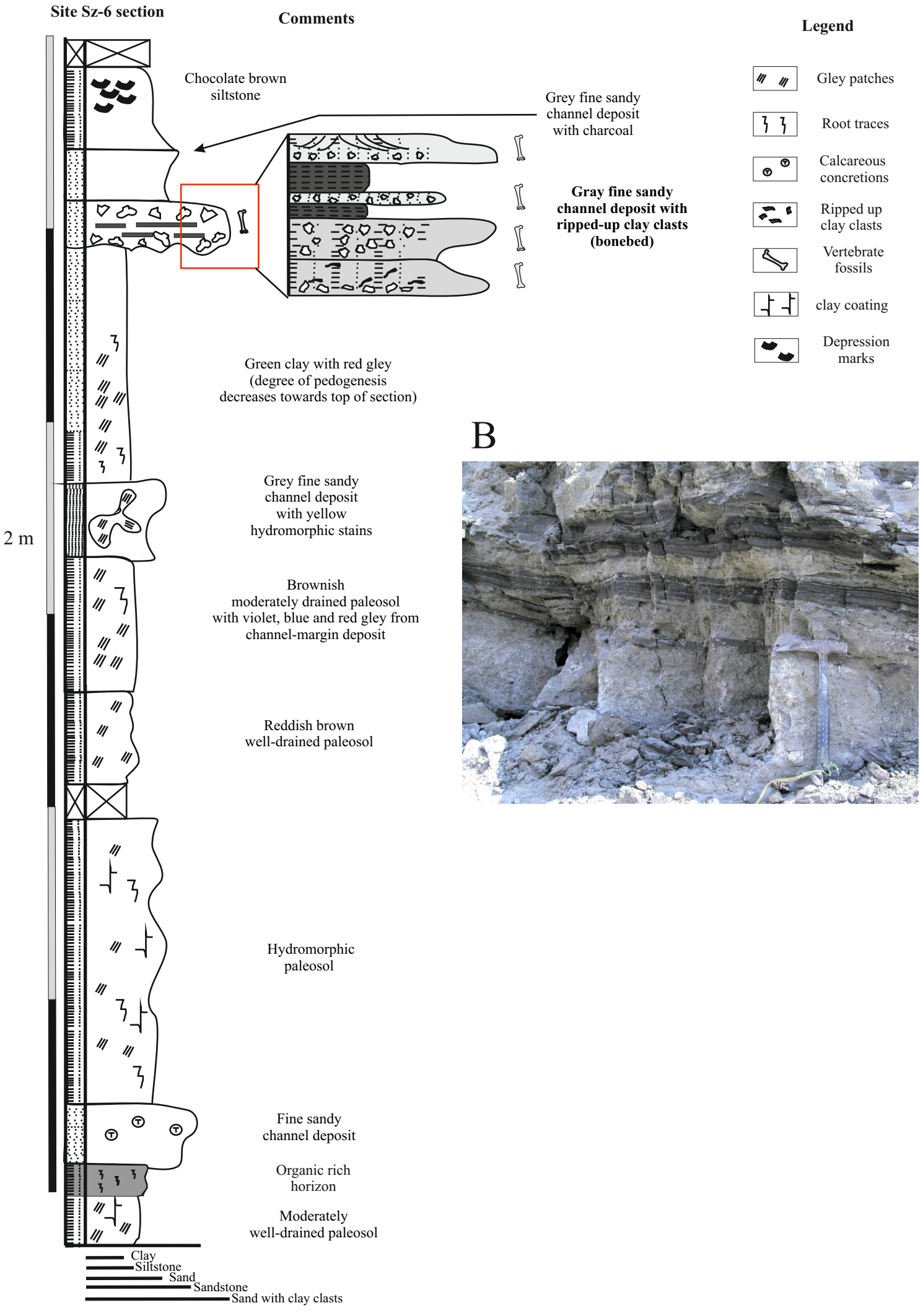

A
Iharkút
Bakonyjákó
Németbánya
Farkasgyepű
N
2 km
Kislőd
8
Ajkarendek
Városlőd
Herend
B
Age
Ma
Stage
Formation
Basin
Patform
72,1
Campanian
83,6
Santonian
86,3
Coniacian
89,8
Polány Marl Fm.
Ugod Limestone
Fm.
Jákó Marl Fm.
Ajka
Coal Fm.
Csehbánya Fm.
Pre-Senonian
Formation
Bauxite
C
Pleistocene loess
Eocene
conglomerate
~50 m
Upper Cretaceous
Csehbánya Formation
Upper Cretaceous
Bauxite
~70 m
Upper Triassic
Dolomite
Legend to C
Bauxite
Dolomite
Well-drained
paleosol
Hydromorphic
paleosol
Sandstone
ribbon
Conglomerate
Loess

Figure


Legend
Ripped up clay clasts
Gley patches
Trough cross-beds
Root traces
Vertebrate fossils
Calcareous concretions
Site Sz-1 section
Comments
Hydromorhic paleosol
The Bonebeds of Sz-1 site
Fine sandy channel deposit with ripped-up clay- clasts
Yellow clay
Fine sandy channel deposit
Hydromorhic paleosol
Hydromorhic paleosol with violet spots
Fine sandy channel deposit
2 m
Hydromorhic paleosol
Fine sandy channel deposit
Organic horizon
Fine sandy channel deposit
Gray clay
Fine sandy channel deposit
Clay
Mudstone
Sand
Sandstone
Sand with clay- clasts

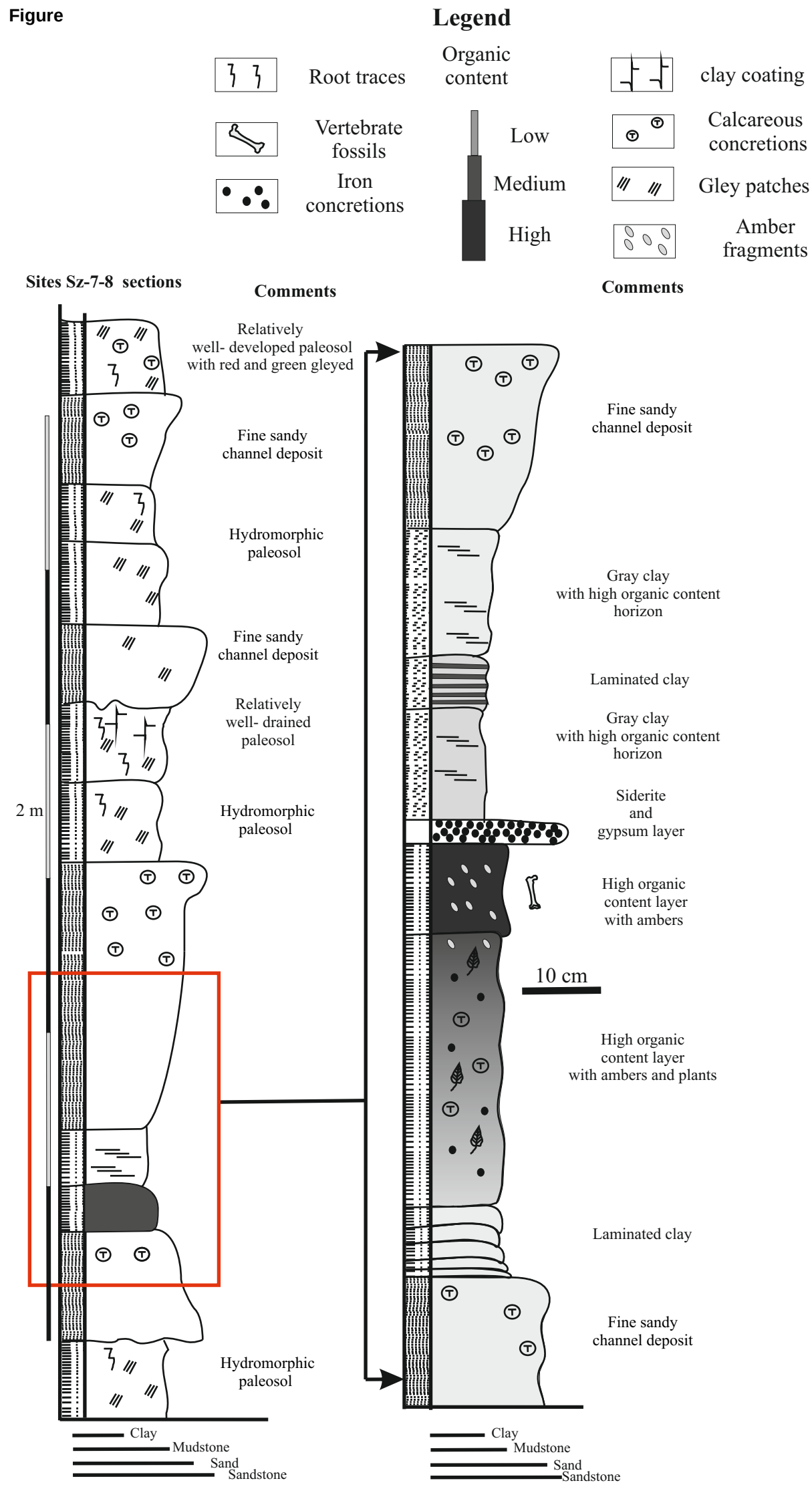
Figure

A

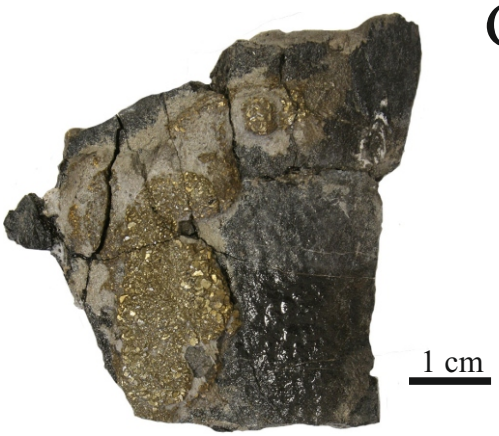

Site Sz-6 section
Comments
Legend
Chocolate brown siltstone
Grey fine sandy channel deposit with charcoal
Gray fine sandy channel deposit with ripped-up clay clasts (bonebed)
Gley patches
Root traces
Calcareous concretions
Ripped up clay clasts
Vertebrate fossils
clay coating
Depression marks
Green clay with red gley (degree of pedogenesis decreases towards top of section)
2 m
Grey fine sandy channel deposit with yellow hydromorphic stains
Brownish moderately drained paleosol with violet, blue and red gley from channel-margin deposit
Reddish brown well-drained paleosol
Hydromorphic paleosol
Fine sandy channel deposit
Organic rich horizon
Moderately well-drained paleosol
Clay
Siltstone
Sand
Sandstone
Sand with clay clasts

B

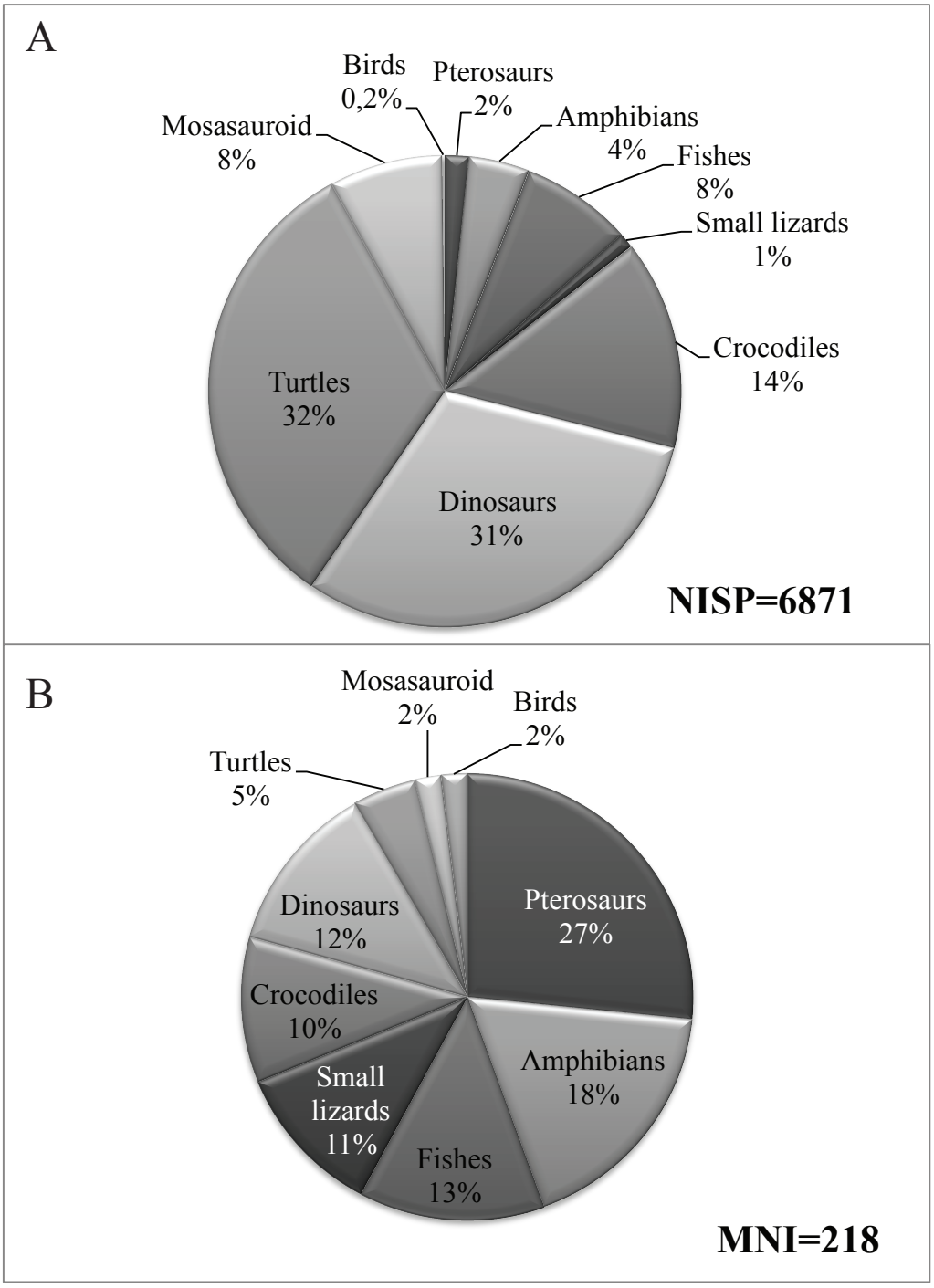
Figure


Legend
Root traces
Organic content
clay coating
Vertebrate fossils
Low
Calcareous concretions
Iron concretions
Medium
Gley patches
High
Amber fragments
Sites Sz-7-8 sections
Comments
Comments
Relatively well- developed paleosol with red and green gleyed
Fine sandy channel deposit
Hydromorphic paleosol
Fine sandy channel deposit
Relatively well- drained paleosol
Hydromorphic paleosol
2 m
Hydromorphic paleosol
Fine sandy channel deposit
Gray clay with high organic content horizon
Laminated clay
Gray clay with high organic content horizon
Siderite and gypsum layer
High organic content layer with ambers
10 cm
High organic content layer with ambers and plants
Laminated clay
Fine sandy channel deposit
Clay
Mudstone
Sand
Sandstone
Clay
Mudstone
Sand
Sandstone

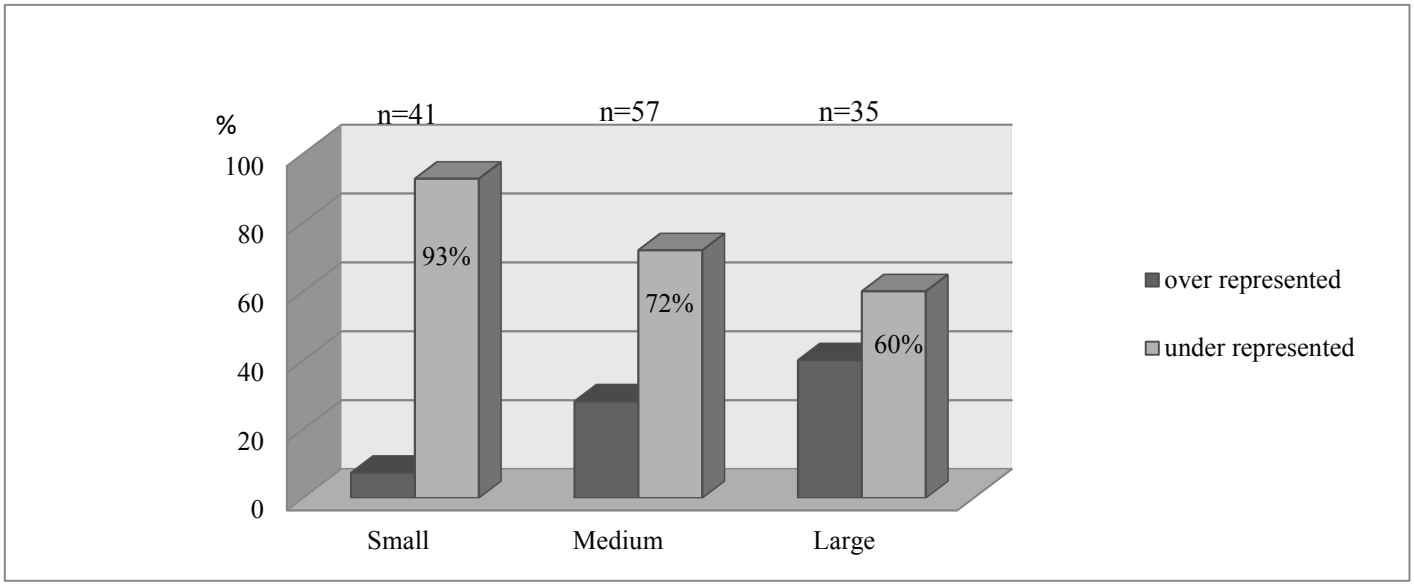
Figure



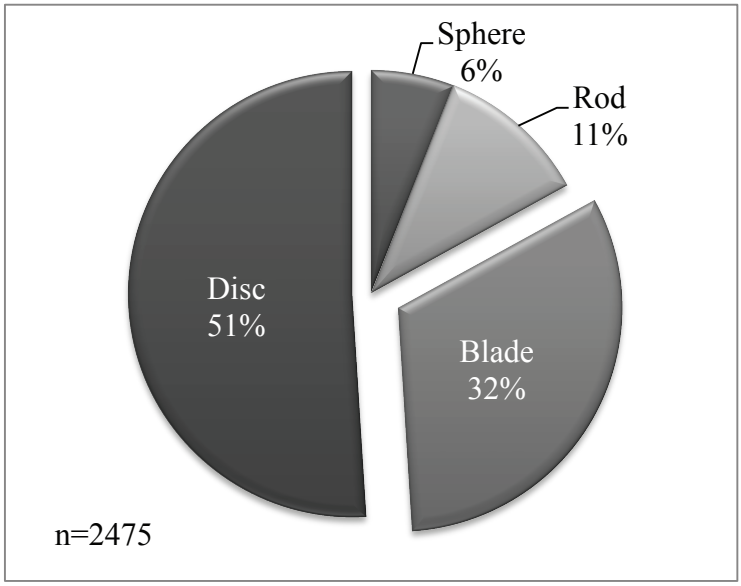
Figure


A
Birds
0,2%
Pterosaurs
2%
Mosasauroid
8%
Amphibians
4%
Fishes
8%
Small lizards
1%
Crocodiles
14%
Turtles
32%
Dinosaurs
31%
NISP=6871
B
Mosasauroid
2%
Birds
2%
Turtles
5%
Pterosaurs
27%
Dinosaurs
12%
Crocodiles
10%
Amphibians
18%
Small
lizards
11%
Fishes
13%
MNI=218

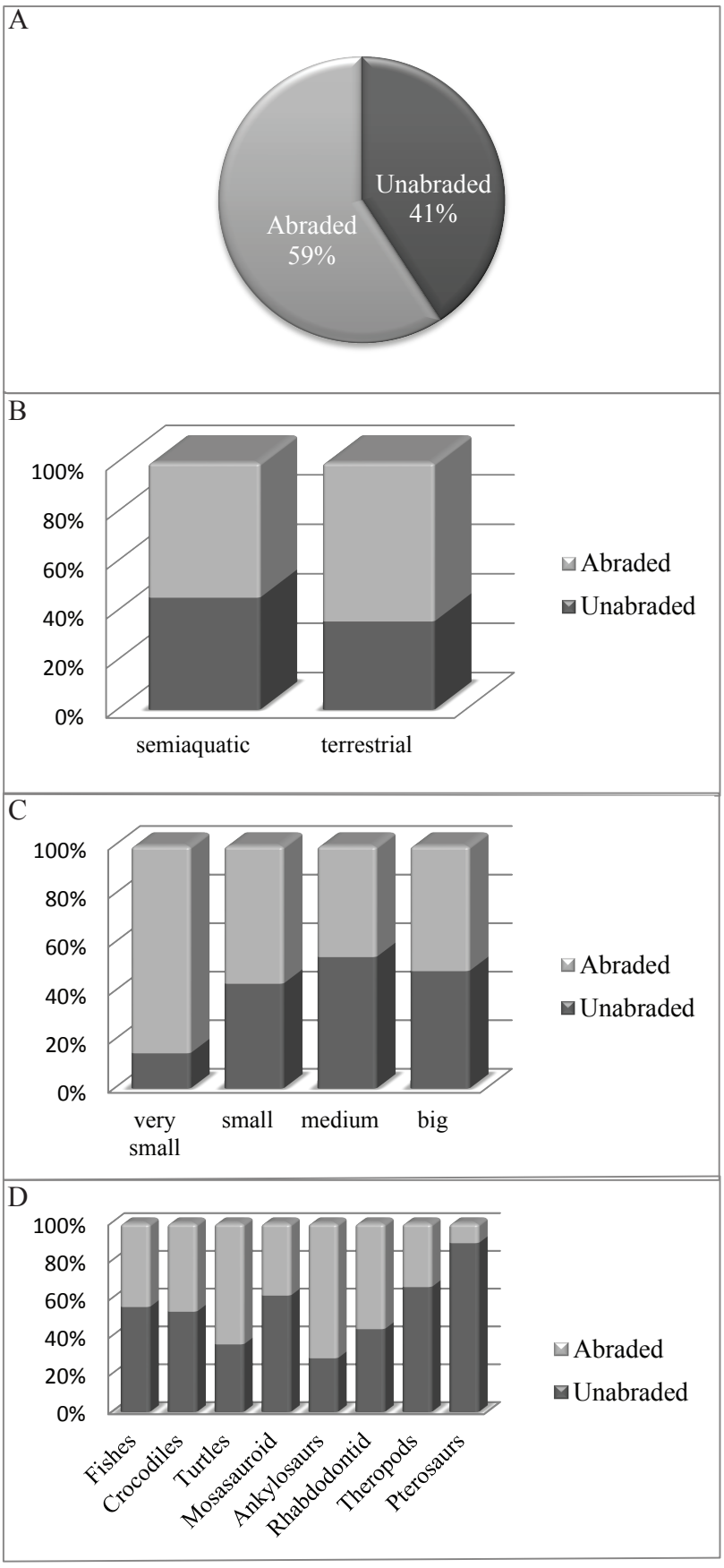
Figure


%
100
80
60
40
20
0
n=41
n=57
n=35
93%
72%
60%
Small
Medium
Large
over represented
under represented

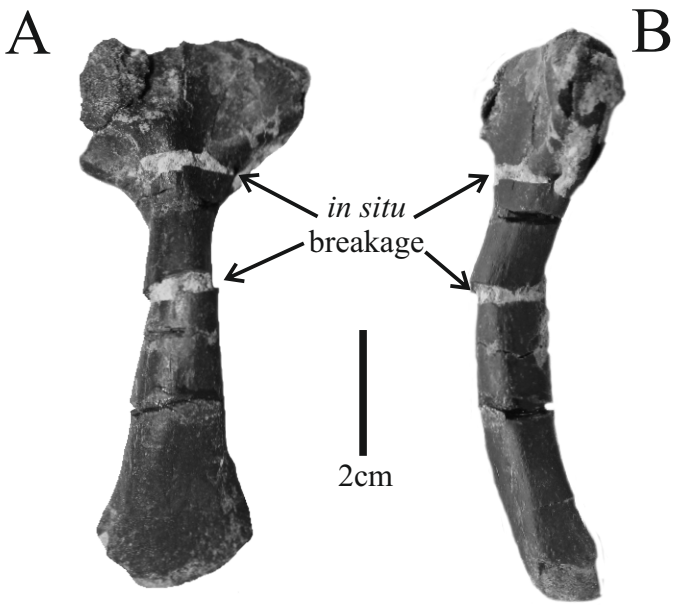
Figure



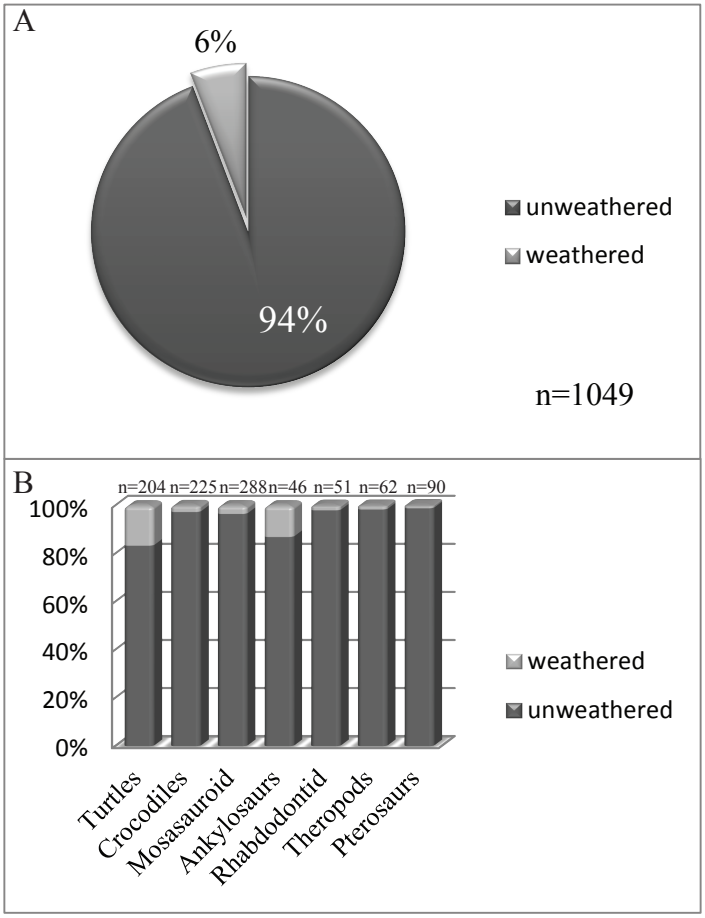
Figure


A
Unabraded
41%
Abraded
59%
B
100%
80%
60%
40%
20%
0%
semiaquatic
terrestrial
Abraded
Unabraded
C
100%
80%
60%
40%
20%
0%
very small
small
medium
big
Abraded
Unabraded
D
100%
80%
60%
40%
20%
0%
Fishes
Crocodiles
Turtles
Mosasauroid
Ankylosaurs
Rhabdodontid
Theropods
Pterosaurs
Abraded
Unabraded

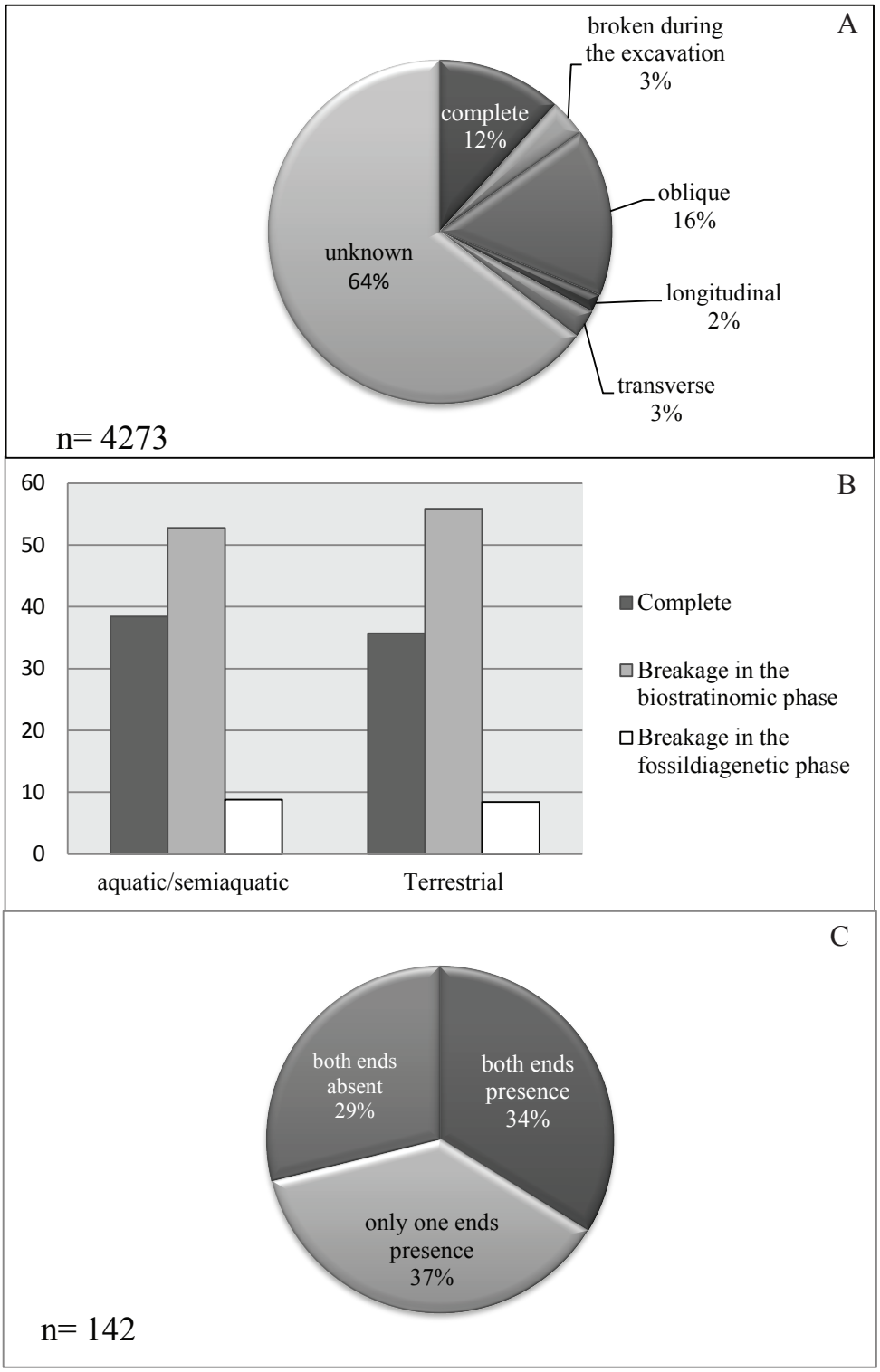
Figure



Figure


A
6%
94%
unweathered
weathered
n=1049
B
n=204 n=225 n=288 n=46 n=51 n=62 n=90
100%
80%
60%
40%
20%
0%
Turtles
Crocodiles
Mosasauroid
Ankylosaurs
Rhabdodontid
Theropods
Pterosaurs
weathered
unweathered

Figure


A
broken during the excavation 3%
complete 12%
oblique 16%
unknown 64%
longitudinal 2%
transverse 3%
n= 4273
B
60
50
40
30
20
10
0
aquatic/semiaquatic
Terrestrial
Complete
Breakage in the biostratinomic phase
Breakage in the fossildiagenetic phase
C
both ends absent 29%
both ends presence 34%
only one ends presence 37%
n= 142

Figure

N

edge of the excavated area

Szál-3

Legend

Skull elements

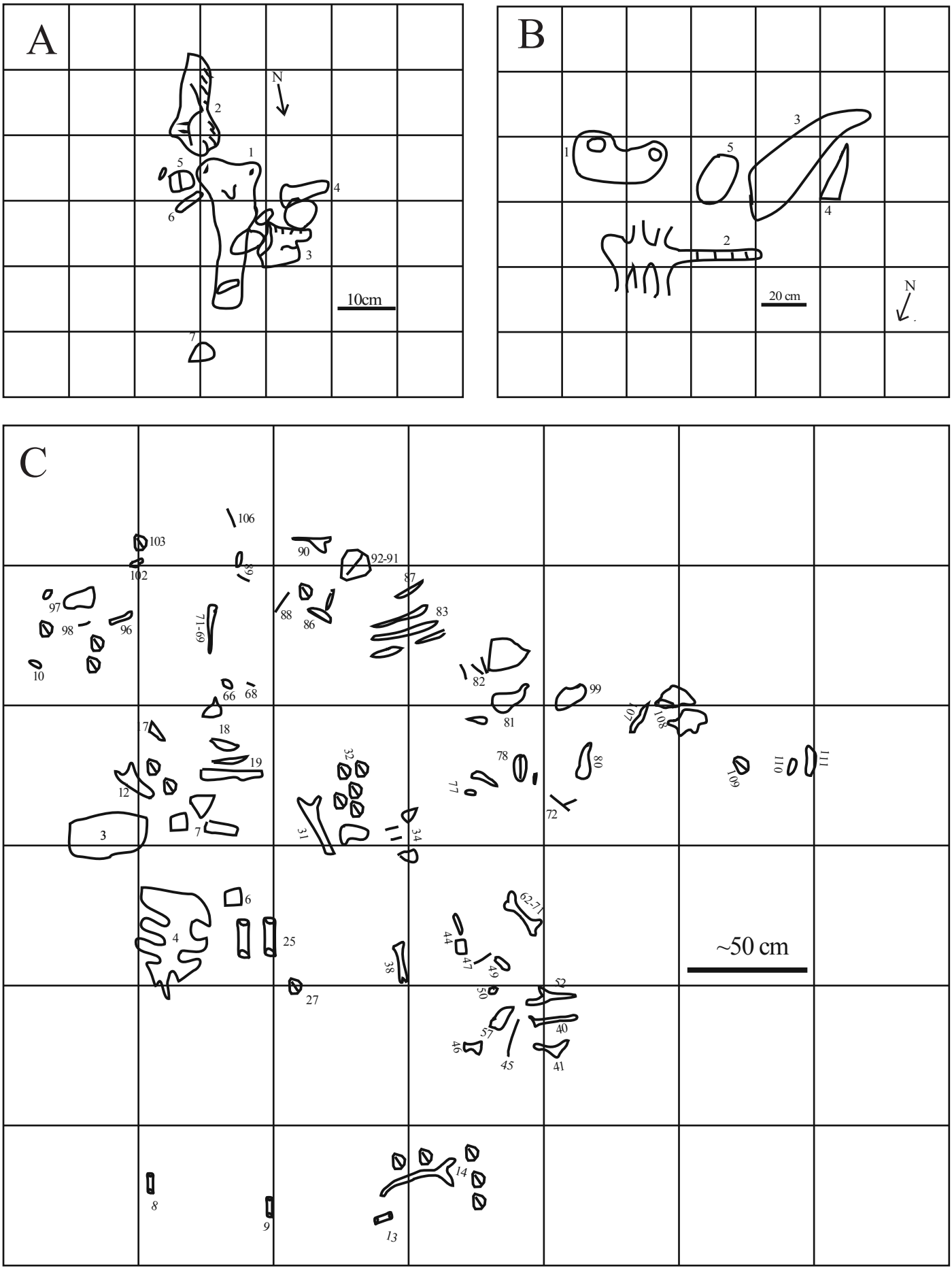
Sacrum elements

N

edge of the mine

50 cm

Figure



Table

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Taxon		Material	References
Fish	Pycnodontiformes indet. 1.	predentaries, vomer, teeth	Ősi et al., 2012b
	Pycnodontiformes indet. 2.	predentaries, vomer, teeth	
	Atractosteus sp.	jaw fragments, teeth, scales, vertebrae	Ősi et al., 2012b
Amphibians	*Hungarobatrachus szukacsi*	pelvic elements	Szentesi and Venczel, 2010
	Bakonybatrachus fedori	pelvic elements	Szentesi and Venczel, 2012
	Palaeobatrachidae indet.	postcranial remains	Szentesi, 2010
	Pelobatidae indet.	postcranial remains	Szentesi Z., pers. comm.
	Albanerpeton sp.	cranial and mandible elements	Szentesi et al., 2013
Turtles	*Foxemys trabanti*	complete and partial skulls, mandibles, vertebrae, pectoral and pelvic girdle elements, limb bones, plastron and carapax fragments	Rabi et al., 2011
	Kallokibotion sp.	shell fragments	Ősi et al., 2012b
	Dortokidae indet.	shell fragments	Ősi et al., 2012b
Squamates	*Pannoniasaurus inexpectatus*	cranial and mandibular elements, teeth, vertebrae, ribs, pelvic girdle elements, limb bones	Makádi et al., 2012
	Bicuspidon aff. *hatzegiensis*	fragmentary mandibles, maxillae	Makádi, 2006
	Pelsochamops infrequens	fragmentary dentary, dentary fragments	Makádi, 2013a
	Distrodon rhomboideus	dentaries, maxilla	Makádi, 2013b
	Scincomorpha indet. 1	fragmentary mandible	Makádi L., pers comm.
	Scincomorpha indet. 2	fragmentary dentary	Makádi L., pers comm.
	Scincomorpha indet. 3	fragmentary dentary	Makádi L., pers comm.
	Scincomorpha indet. 4	fragmentary dentary	Makádi L., pers comm.
	Doratodon sp.	teeth, jaw fragment	Ősi et al., 2012b
	?Theriosuchus sp.	teeth, cranial elements	Rabi M., pers comm.
	?Allodaposuchus sp.	teeth, jaw fragments, cranial elements	Rabi M., pers comm.

Crocodiles	*Iharkutosuchus makadii*	complete and partial skulls, mandibles, various cranial elements, teeth	Ősi et al., 2007; Ősi, 2008a; Ősi and Weishampel, 2009
	Bakonydraco galaczi	premaxilla, complete mandible, 56 mandibular symphyses	Ősi et al., 2005; Ősi et al., 2011
Pterosaurs	Azhdarchidae indet.	cervical vertebrae, pelvic girdle elements, limb bones	Ősi et al., 2005 and 2011
	Pterodactyloidea indet.	3 mandibular symphyses	Prondvai E., pers comm.
Dinosaurs (including birds)	Tetanurae indet.	teeth	Ősi et al., 2010a
	Abelisauridae indet.	limb bones	Ősi et al., 2010a, Ősi and Buffetaut, 2011
	Pneumatoraptor fodori	scapulocoracoid	Ősi et al., 2010a
	Paraves indet.	teeth, caudals, limb bones	Ősi et al., 2010a, Ősi and Buffetaut, 2011
	Bauxitornis mindszentyae	tarsometatarsus	Ősi, 2008b, Dyke and Ősi, 2011
	Enantiornithes indet.	limb bones	Ősi, 2008b, Dyke and Ősi, 2011
	Hungarosaurus tormai	6 associated and 1 articulated partial skeletons, associated and isolated cranial and mandibular elements, teeth, vertebrae, ribs, pectoral and pelvic girdle elements, limb bones, osteoderms	Ősi, 2005, Ősi and Makádi, 2009
	cf. *Struthiosaurus* sp.	humerus	Ősi and Prondvai, 2013
	Mochlodon vorosi	cranial and mandibular elements, teeth, vertebrae, pectoral and pelvic girdle elements, limb bones	Ősi et al., 2012a
	Ajkaceratops kozmai	cranial and mandibular elements	Ősi et al., 2010b

Table

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code	Taphonomic modes	Description	Number of elements in the dataset (2013)	Taxonomic composition	Taphonomic features	Interpretation	Lithological situation and site
1	*Isolated bones*						
1.1	bone pebbles	Small-sized, high abraded bone fragments	4018 specimens	Taxonomically and/or anatomically unidentified	Highly abraded and fragmented	Interpreted as coarse-grained particles of the bed-load of the ancient stream. These are common bone preservation forms in the channel-lag deposit (Behrensmeyer 1988)	Ubiquitous elements, but are very common in the basal breccia of the SZ-6 site
1.2	"single" isolated bone elements	Well- and medium-preserved isolated bone elements which are defined as a single element in each skeleton (e.g. scapula, femur, humerus etc.)	4225 specimens	High diversity assemblages, all taxa are represented within	Usually well-preserved, often broken and abraded but rarely weathered	Short-distance transported bones	Ubiquitous elements, but are very common in the layers of the SZ-6 site
1.3	"complex" isolated skeletal elements	Skeletal elements which are preserved as ossified multiple bones (e.g. skull, mandible, synsacrum of ankylosaurs)	9 mandibular, 10 skulls, 9 anklosaur sacral regions and 1 rhabdodontid sacral region	Lower diversity assemblages, turtles (*Foxemys*), crocodiles (*Iharkutosuchus*), dinosaurs (*Hungarosaurus*, *Mochlodon*), and pterosaurs (*Bakonydraco galaczi*) are represented in this group	Usually well-preserved, sometimes broken and abraded	Not or short-distance transported bones	Rare elements in the assemblages, occurrence is confined to the layers of the SZ-6 site
1.4	Teeth	Well- and medium-preserved isolated tooth elements	2259 specimens	High diversity assemblages	Usually well-preserved	The mode of accumulation of teeth is different than that of the bones (Behrensmeyer, 1975; Argast et al., 1987; Fiorillo, 1991)	Ubiquitous elements in all of the bone beds of the Iharkút site
2	*Microfossils*	Well- and medium-preserved isolated bone elements, representing animals whose body weight was <1kg (Behrensmeyer et al., 1979)	358 specimens	High diversity assemblages, almost every taxon of the macrofauna as well as frogs, small lizards and Albanerpetontidae are represented in this group	Well-preserved but fragmentary assemblages. The teeth are usually missing from the dentary, premaxilla or maxilla	Most of the microfossils were transported for a short time before accumulation	Most of them were obtained by screen-washing from SZ7-8 and SZ-6 site
3	*Associated skeletal elements*	Bones and teeth which are isolated and separated from each other but belong to the same skeleton (Lyman, 1994a)	595 specimens of six individuals	Ankylosaurs	Well-preserved but fragmentary assemblages. There is evidence for occurrences of in situ brakeage by trampling	Size and taphonomic features of these bones remain indicated that they were not transported with the sediment clasts or isolated elements. Instead, these assemblages accumulated at the site by carcass floating or during a subsequent event	They were discovered from the SZ-6 site
4	*Articulated skeleton*	Elements of the skeleton found in the same anatomical position as in the living organism (Badgley, 1986a)	Hip region of one individual	Ankylosaurs	There is evidence for occurrences of in situ brakeage by trampling	This assemblage accumulated at the site by carcass floating or during a subsequent event	It was discovered in the basal breccia of SZ-6 site
	Total elements in the Iharkút dataset (See supplementary information 2)		**11493**				

Table

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Taxa	NISP	NISP%	MNI	MNI%	Fragmentation rate
Pycnodontiformes indet.	327	4,76	28	12,84	11,68
Atractosteus sp.	199	2,90	1	0,46	199,00
Anurans	194	2,82	10	4,59	19,40
Albanerpeton sp.	92	1,34	29	13,30	3,17
Turtles	2 233	32,50	10	4,59	223,30
Allodaposuchus -like crocodile	392	5,71	5	2,29	78,40
Iharkutosuchus makadii	241	3,51	7	3,21	34,43
Doratodon sp.	176	2,56	1	0,46	176,00
Unidentified post-cranial elements of crocodile	181	2,63	10	4,59	18,10
Pannoniasaurus inexpectatus	532	7,74	4	1,83	133,00
small-sized lizards	71	1,03	24	11,01	2,96
Ankylosaurs (isolated bones)	1 764	25,67	9	4,13	196,00
Ankylosaurs (skeletal elements)	-	-	7	3,21	-
Mochlodon vorosi	138	2,01	5	2,29	27,60
Theropods	198	2,88	3	1,38	66,00
Ajkaceratops kozmai	6	0,09	3	1,38	2,00
Pterosaurs	113	1,64	58	26,61	1,95
Birds	14	0,20	4	1,83	3,50
Total	**6 871**	**100,00**	**218**	**100,00**	**1 196,49**

Table

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	Turtles					Mosasauroid					Crocodiles					Nodosaurids					Rhabdodontid					Theropods					Pterosaurs					Aves				
	10					**4**					**23**					**9**					**5**					**3**					57					4				
Element	A	E	%R	size category	shape category	A	E	%R	size category	shape category	A	E	%R	size category	shape category	A	E	%R	size category	shape category	A	E	%R	size category	shape category	A	E	%R	size category	shape category	A	E	%R	size category	shape category	A	E	%R	size category	shape category
Skull																																							
full or partial cranial	4	1	40		2	1	0	1	0		2	6	1	26	3	3	1	1	11	3	1	0	1	0	3	1	0	1	0	2	1	0	1	0			0	1	0		
quadratum	1	2	5		1	2	5	2	63	2	2	0	2	0	1	2	1	2	6	2	2	3	2	30	2	2	0	2	0	1	2	0	2	0			0	2	0		
dentale	4	2	20		2	4	4	2	50	3	2	19	2	41	3	4	4	2	22	3	4	8	2	80	3	4	0	2	0	3	4	2	2	2	3		0	0	0		
teeth	0	0	0				176	180	24		2	719	72				703	84	93		2	76	40	38		2	128	60	71		4	0	0	0							
Vertebrae																																									
cervical	1	7	1		1	2	24	7	86	2	1						16	10	18	3	1	3	7	9	2	1	1	10	3	1	1	5	7	1	3		0	9	0		
dorsal	2	10	2		1	2	75	20	94	2	1	**115	72	7	1	1	11	16	8	3	1	6	16	8	2	1	2	13	5	1	1	0	7	0			0	6	0		
caudal	0	24	0		1	2	26	75	9	2	1						42	40	12	3	2	4	40	2	1	2	6	49	4	1	2						0				
sacral or sacrum	0	1	0		1	2	2	2	25	2	1						9	1	100	3	2	1	1	20	3	2	0	1	0	1	2	0	1	0			0				
Girdle and limb																																									
scapula	0	0	0				1	2	13	3	3	2	2	4	2	4	2	2	11	3	4	0	2	0	3	4	1	2	17	2	4	1	2	1	2		0	2	0		
coracoid	4	2	20		2	4	0	2	0	2	4	0	2	0	2	4	0	2	0	2	4	3	2	30	3	4	0	2	0	2	4	0	2	0			0	2	0		
humerus	0	2	0		2	2	2	2	25	1	3	5	2	11	3	2	1	2	6	3	2	2	2	20	3	2	0	2	0	2	2	1	2	1	1		2	2	25		2
ulna	0	2	0		2	2	0	2	0	2	2	0	2	0	1	2	0	2	0	2	2	1	2	10	3	2	0	2	0	2	2	2	2	2	1		0	2	0		2
radius	0	2	0		2	2	0	2	0	2	2	2	2	4	1	2	1	2	6	2	2	1	2	10	3	2	0	2	0	2	2	1	2	1	2		0	2	0		2
metacarpal or metatarsal	0	20	0		1	2	0	36	0	2	3	0	20	0	1	3	7	16	5	2	2	0	14	0	3	2	3	16	6	1	2	2	16	0	2		1	4	6		2
phalanges	0	56	0		1	2	0	64	0	1	2	0	52	0	1	2	1	40	0	2	2	3	22	3	2	2	14	36	13	1	2	2	8	0	3		0				
ilium	0	2	0		1	2	4	2	50	2	4	0	2	0	2	3	3	2	17	3	3	0	2	0	2	3	0	2	0	2	3	0	2	0			0	2	0		
ischium	0	2	0		1	4	0	2	0	2	3	6	2	13	2	3	6	2	33	3	4	0	2	0	2	4	0	2	0	2	4	0	2	0			0	2	0		
femur	9	2	45		2	2	0	2	0	1	2	13	2	28	2	2	0	2	0	3	2	4	2	40	3	2	5	2	83	3	2	0	2	0	2		8	2	100		2
tibia	0	2	0		2	2	0	2	0	1	2	0	2	0	1	2	0	2	0	3	2	2	2	20	3	2	1	2	17	1	2	1	2	1	2		0	2	0		2
fibula	3	2	15		2	2	0	2	0	1	2	0	2	0	1	2	1	2	6	3	2	0	2	0	2	2	0	2	0	1	2	0	2	0	1		0	2	0		1
horn or claw	0	20	0		1	4	0	0	0			0	18	0	1	4	10	16	7	1	2	0	17	0	1	2	5	14	12	1	4										
osteoderms/plate	*168	58	29			3	0	0	0								728	332	24		3	0	0				0	0	0			0	0	0			0	0	0		
∑A	196						319					887					1547					117					166					17					11				
∑ E		219						409					259					580					182					224					64					42			
%IC			18						19					16					30					13					25					0,47					7		
Fragmentation rate	39,2						79,75					38,57					171,89					23,40					55,33					0,30					2,75			
Number of species	4						1					4					2					1					3					3					2			

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

Shape categories:	1;	sphere-like
	2;	rod-like
	3;	disc-like
	4;	blade-like

Table

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Taxa	Transportable feature	Actual number of elements in the collection	Expected number of elements in the collection	Percentage of actual number of elements	Percentage of excepted number of elements	Representation
Turtles	easier	20	122	16	100	under
	delayed	176	76	232	100	over
Crocodiles	easier	135	508	27	100	under
	delayed	33	180	18	100	under
Mosasauroid	easier	312	276	113	100	over
	delayed	7	35	20	100	under
Nodosaurids	easier	804	643	125	100	over
	delayed	743	923	80	100	under
Rhabdodontid	easier	106	86	123	100	over
	delayed	3	8	38	100	under
Theropods	easier	32	19	168	100	ovre
	delayed	134	60	223	100	over

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