TAPHONOMY AND GEOCHEMISTRY OF A VERTEBRATE MICROREMAINS ASSEMBLAGE FROM THE EARLY TRIASSIC FISSURE DEPOSITS AT CZATKOWICE 1, SOUTHERN POLAND

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Surface morphology and trace element geochemistry of the bone assemblage from the Early Triassic fissure deposits of the Czatkowice 1 locality near Kraków, Poland, suggest that bones were reworked (probably from ephemeral water bodies) and transported into the nearby cave systems *post mortem*. Geochemical analyses indicate the influence of aeolian conditions during concentration of the Czatkowice assemblage, and show that the assemblage is relatively mixed (averaged) when compared to similar Triassic cave deposits.

Key words: Taphonomy, Triassic, karst deposits, microvertebrates, Rare Earth Elements (REE), geochemistry.

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INTRODUCTION

The processes that contribute to the formation of fossil assemblages are complex. Detailed sedimentological and taphonomic analyses are often needed to determine the extent of time averaging and mixing suffered during the formation of a faunal assemblage, and therefore its ecological significance. Historical archived collections are the main primary source for palaeontological investigations, but these collections consist of bones that have already been excavated and curated, in some cases without full recognition of the importance of detailed taphonomic and sedimentological analysis. Site practicalities may make detailed contextural investigations impossible. In such circumstances it is necessary to develop techniques that may be applied to isolated bones, in the absence of coherent sedimentological data.

Techniques that relate the surface morphology of bones to their *post mortem* history are well established (see for example Behrensmeyer, 1975, 1978, 1982; Fiorillo 1988). Recently these techniques have been augmented by methods based on the geochemical composition of fossil bones. As these characters are intrinsic to the bones themselves, they may be investigated after excavation and curation. The primary aim of this study is to construct a taphonomic history for a microvertebrate assemblage from karst deposits of southern Poland, where primary sedimentological data are missing, using a combination of "classical" physical taphonomic indices and geochemical techniques.

Paszkowski and Wieczorek (1982) report ten fissures (Fig. 1) discovered in the Carboniferous limestone at Czatkowice quarry, near Krzeszowice, Kraków Uplands in 1978. The fissures contain Mesozoic sediments of various ages, some of which preserve vertebrate material. The most important of these fissure fillings is Czatkowice 1, a funnel-shaped karst form, that yielded a diverse Early Triassic microvertebrate assemblage (Paszkowski and Wieczorek 1982; Paszkowski 2009). The vertebrate remains were extracted from the bone-bearing breccias using acetic acid. Most of the bone material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, and in the Museum of the Earth, Polish Academy of Sciences, Warsaw.

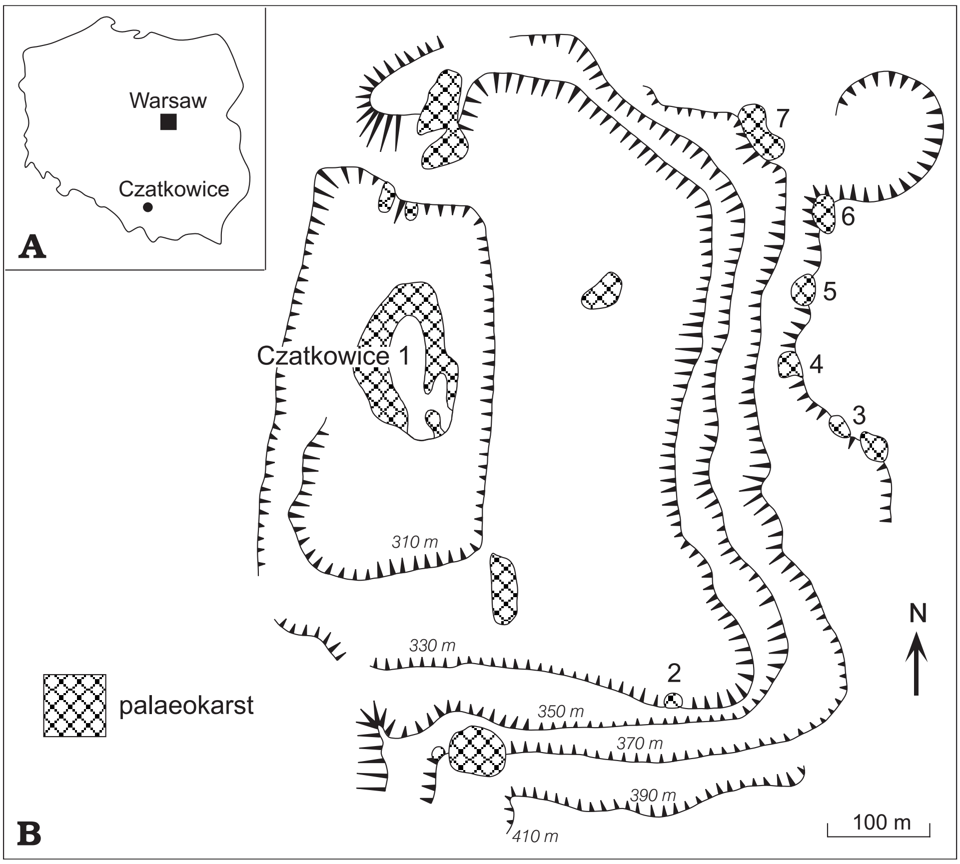

Fig. 1. **A**. Location of the Czatkowice quarry in Poland. **B**. Mesozoic fissures in the Czatkowice quarry (modified from Paszkowski and Wieczorek 1982); numbers refer to fossil karst lacalities.

The Czatkowice 1 fauna (Borsuk-Białynicka *et al.* 1999) is dominated by a small (approximately 1 m long) archosauriform predatory reptile *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003, 2009a; Borsuk-Białynicka and Sennikov 2009). Other taxa include a prolacertiform grade reptile (Borsuk-Białynicka and Evans 2009b), lepidosauromorphs (Evans and Borsuk-Białynicka 2009a; Evans 2009), procolophonids (Borsuk-Białynicka and Lubka 2009) and temnospondyl amphibians (Shishkin and Sulej 2009) as well as rare fish and an extremely rare salientian *Czatkobatrachus polonicus* (Evans and Borsuk-Białynicka 1998; Evans and Borsuk-Białynicka 2009b). These animals are considered to have inhabited an area of arid or semi-arid desert with shallow ephemeral water bodies (Gradziński *et al.* 1979; Gradziński 1992; Gradziński and Uchman 1994; Paszkowski 2009).

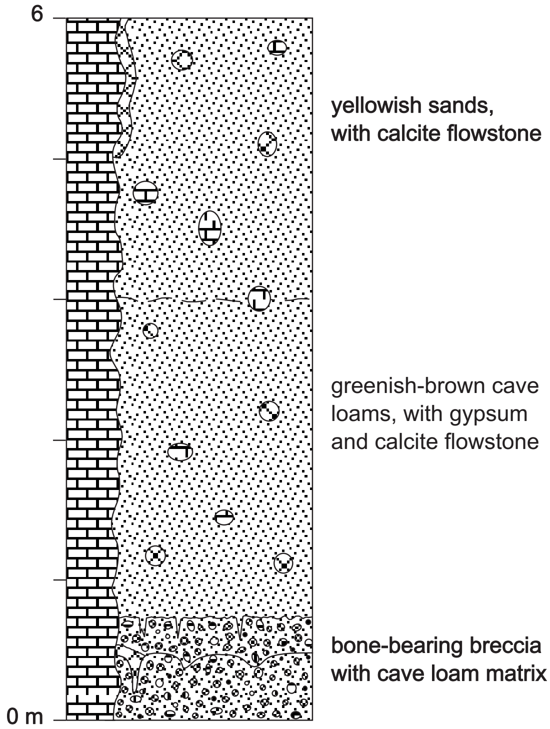

Fig. 2. Sketch of the sediment infilling the Czatkowice 1 fissure (information taken from Paszkowski and Wieczorek 1982).

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GEOLOGICAL SETTING

Czatkowice 1 is the largest of several karst fissures cut into the Early Carboniferous (Tournaisian to Mid Viséan) limestone (Paszkowski and Wieczorek 1982; Paszkowski 2009) of the Dębnik Massif (southern Poland). Sedimentary data relating to Czatkowice 1 are scanty (Paszkowski and Wieczorek 1982; Paszkowski 2009). The karst form described was a small fragment of a cave, approximately 6 m in depth (exact dimensions not given), the upper part of the walls and the roof of which were decribed as "pockmarked", and supported a 0.2 to 0.3 m thick flowstone deposit. The cave sediments were divided into two (Fig. 2). The lower sediments reached a thickness of 4 m, were coloured green-brown and contained intercalations of gypsum and calcite flowstones; fragments of limestone and calcite were present throughout the sediments. These were overlain by approximately 2 m of yellow sandy sediments (Paszkowski and Wieczorek 1982; Paszkowski 2009).

A variety of fragments of the bone-bearing sediments from Czatkowice 1 have been studied in hand specimen, polished section and thin section. The sediments are yellowish, creamy-yellow, or dark ochre in colour. According to Paszkowski and Wieczorek (1982, p. 35), the lowest part of the cave was filled with bone breccia layers. Most of the specimens examined show no evidence of sedimentary structures; the sediments tend to be poorly sorted with large clasts of bone, lithics and nodules, and often contain large patches of crystalline calcite cement (Table 1).

Table 1. Summary of the physical characteristics of the hand specimens of Czatkowice 1 fissure-fill sediments.

Sample	Colour	Grain size	Matrix/Cement	Texture	Clast types
Cz 1	creamy-yellow, darker grey when fresh, dendritic magnetite on surface		clay-grade matrix and crystalline calcite cement	subangular grains	quartz; rare opaques
Cz 2	mottled pale creamy-brown and pale creamy-white with patches of ochreous material	fine sand to coarse sand	well-cemented with crystalline calcite	poorly-sorted	quartz, bones; rare opaques and mica
Cz 5	pale creamy-white, surfaces darker yellow	fine sand	crystalline calcite cements (possibly two phases)		quartz; rare opaques, mica and bones
Cz 7	ochreous with dark speckles on surface (magnetite?)	very fine sand or silt		possible parallel orientation of the bones, matrix supported, sediment poorly sorted	bones, quartz, lithics
Cz 18	pale creamy-yellow, with darker grey clasts, giving a speckled appearance	very fine sand with rare larger clasts	calcite cement	poorly sorted	quartz, lithics, bone
Cz 19	pale cream, ochreous when weathered	very fine sand, with clasts up to 15 mm diameter	very fine-grained matrix and crystalline calcite cement	very poorly-sorted, graded and parallel bedding, possible geopetal structure, possible parallel orientation of the bones, veins of calcite	quartz, lithics, bones; rare mica and opaques
Cz 23	pale creamy-yellow, with small patches of ocreous sediment	coarse sand and larger clasts	very well cemented by crystalline calcite	bones randomly scattered throughout the sediment, moderately well-sorted	quartz, bones, lithics
Cz 24	dark ochre, with brownish sediment adhering to the surface	coarse sand	silty matrix, with crystalline calcite cement	possible weak parallel bedding	very little bone, ? quartz

Recent studies have tied the Czatkowice 1 vertebrate assemblage into the terrestrial vertebrate sequence for Eastern Europe (Shishkin *et al*. 2000). The presence of tooth plates of the dipnoan *Gnathorhiza* and the characteristics of the teeth of the procolophonids suggests that the assemblage should be placed within the early to late Olenekian time frame (Borsuk-Białynicka *et al*. 2003). The temnospondyl remains from Czatkowice 1 deposits support an earliest Late Olenekian age (Shishkin and Sulej 2009).

METHODS

PHYSICAL TAPHONOMY

Behrensmeyer (1978) designed a classification scheme for the weathering of mammal bones in the tropical grassland environments of Africa. Following this work, Fiorillo (1988) adapted Behrensmeyer's (1978) scheme for use with fossil material (simplifying the classification to take into account the loss of resolution seen in fossil material when compared to recent bones) and produced a similar scheme for the classification of abraded bones (Table 2). Cook (1995a, b) further modified the schemes to take into account the extreme levels of abrasion frequently observed in the fossil record.

Additional information may be gained from an analysis of the nature of the fractures (Table 3) and breakage surfaces of the bone:

Spiral fractures: Bones that break relatively soon *post mortem*, while the collagen is still intact, break with a characteristic spiral or jagged fracture. In this case the growth of the fracture is controlled by the tensile strength of the collagen fibres. Such fractures are caused by predation, scavenging and trampling (especially associated with large animals), but are rarely caused during transport (Cook 1995b).

Parallel fractures: Fractures running parallel to the length of the bone are commonly associated with weathering damage (such as changes in relative humidity and temperature) to bone before permineralisation (Behrenesmeyer 1978).

Table 2. Taphonomic parameters used to describe the vertebrate material preserved at Czatkowice 1 (Fiorillo 1988; Cook 1995a, b).

Abrasion stage	Characteristics
Stage 0	Very angular: the bone is fresh and unabraded. Processes and bone edges are well-defined.
Stage 1	Subangular: the bone edges and processes are slightly abraded and polished.
Stage 2	Subrounded: the bone edges are well-rounded, processes are still recognisable. Moderate abrasion.
Stage 3	Rounded: edges show a high degree of rounding. Processes are remnant or absent. Heavily abraded.
Stage 4	Extremely rounded: bones often show a high degree of sphericity. Extremely abraded.

Transverse fractures: After collagen has degraded, the bone loses its tensile strength and typically breaks with a clean fracture, perpendicular to the length of the bone.

Conchoidal fractures: After significant mineralisation, the bone loses most of the internal porosity and conchoidal fractures may develop (Fiorillo 1988).

It is also productive to consider vertebrate fossils as sedimentary particles. Grain size and grain shape analysis of bone fragments can help to shed light on the sedimentary regime, and particularly on the energy levels of the transport agent (Martin 1999). Voorhies (1969) classified bones according to their susceptibility to transport in fluvial environments (simulated in a flume tank).

Voorhies Group I: Bones that are easily removed by currents by processes of flotation and saltation, for example ribs and vertebrae.

Voorhies Group II: Bones that move more slowly, moving by traction along the river bed, comprise long bones and metapodials.

Voorhies Group III: Includes the skull and mandible: bones which move very slowly.

Certain bones appear in more than one Voorhies Group, for example the ulna and scapula appear in both Groups I and II. It has been suggested that Group I bones can be moved by normal flow rates, and that Groups II and III material can only be moved during flood events (Behrensmeyer 1975).

At the time of acid preparation the blocks of sediment were numbered consecutively; these numbers bear no relation to the sedimentological context of the blocks. One sample from the Czatkowice 1 fissure infill, designated Cz 24, was analysed before the identifiable and well-preserved bones had been removed, and may be regarded as an unbiased cross-section of the remains preserved in sediment block Cz 24.

Most of the Czatkowice 1 samples have been sorted into various taxonomic groups, therefore it was not possible to complete an unbiased quantitative analysis of the complete collection. Small blocks of unprepared sediment were used to provide an unbiased bone sample: any bones visible on the surface of the blocks were also categorised according to their taphonomic characteristics.

However, it should be kept in mind that the Czatkowice 1 samples differ from the reference material used to construct the various “classic” taphonomic classification schemes which were based on the degradation behaviour of large (>50 kg) mammalian carcasses. The Polish fossils described here are mostly reptilian microremains.

GEOCHEMICAL TAPHONOMY

During fossilisation bone mineral changes from carbonate hydroxyapatite (dahllite), to carbonate fluorapatite (francolite). Many trace elements are taken up from pore waters by the bone during recrystallisation, and are incorporated into the apatite lattice via adsorptive substitution for Ca^{2+} ions. Consequently, a fossil bone contains a record of the trace element composition of the pore waters at the site of burial (Trueman and Tuross 2002). After early diagenetic recrystallisation the trace element signal is essentially stable. Further ionic exchange must occur by solid-state diffusion, which is a very slow process at low temperatures. The trace element content of fossil bone may therefore be used to reconstruct some aspects of the burial environment and *post mortem* history of a single bone.

The variation in trace element compositions of bones within a single accumulation is a function of the variation in original burial environments and the rate of introduction of bones into the deposit (Trueman 1999). Therefore, the amount of trace element variation seen in fossil bones from two assemblages can be

Table 3. Results of the physical taphonomy analysis of the Czatkowice 1 fissure-fill vertebrate samples. P, present; VC, very common; C, common. * vertebrate samples consisting of well-preserved, identifiable remains.

Sample	Sample type	Abrasion Index		Grain size (mm)			Grain shape							Fractures							
		Range	Most common	Max.	Min.	Average	Conical (teeth)	Blade	Rod	Disc	Cuboid	Flattened cone	Misc	Straight, fresh	Oblique, fresh	Parallel, fresh	Jagged, fresh	Straight, abraded	Oblique, abraded	Parallel, abraded	Jagged, abraded
Cz 1	Sorted sample	0-1 to 3	1-2 to 2	12	1	5 to 6	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 2	Hand specimen	0-1 to 1-2	0-1	9	4	5.5	0	1	4	0	1	0	0	2	0	1	0	1	0	0	0
Cz 2	Sorted sample	0-1 to 3	1-2 to 2	19	1	7 to 8	–	–	–	–	–	–	–	VC	–	–	–	–	–	–	–
Cz 3	Sorted sample	–	1-2	–	–	–	–	–	–	–	–	–	–	VC	–	P	P	–	P	P	P
Cz 4	Hand specimen	1 to 2	1-2	18	1.5	6.99	0	6	17	0	5	0	6	22	0	1	1	8	0	3	3
Cz 4	Sorted sample	1 to 2	1-2	15	1	5 to 10	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 5	Sorted sample	0-1 to 1-2	1 to 1-2	25	3	5 to 10	–	–	–	–	–	–	–	VC	–	–	–	–	–	–	–
Cz 6-7	Sorted sample	1 to 2	1-2	10	1	5	P	–	–	–	–	–	–	VC	–	P	P	–	P	P	P
Cz 7	Sorted sample	1 to 2-3	1-2	18	1	4	–	–	–	–	–	–	–	VC	P	–	P	P	P	–	P
Cz 7*	Sorted sample	0-1 to 1-2	0-1	6.5	2	4.3	–	–	–	–	–	–	–	5	0	0	0	0	0	0	2
Cz 7b	Hand specimen	0-1 to 2	1-2	15	1.5	5.57	0	17	18	0	1	0	1	17	0	3	11	3	0	0	0
Cz 11	Sorted sample	–	1-2	20	1	4 to 6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 12	Sorted sample	0-1 to 3	1-2	17	1	4 to 5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 13	Sorted sample	0-1 to 3	1-2	10	1	4 to 6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 14*	Sorted sample	0-1 to 2	0-1 to 1-2	–	–	–	P	–	–	–	–	–	P	–	–	–	–	–	–	–	–
Cz 14	Sorted sample	–	1-2	17	1	~ 5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 16	Sorted sample	1 to 2	–	14	1	~ 5	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 17	Sorted sample	0-1 to 1-2	1 to 1-2	20	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cz 18	Hand specimen	0 to 1	0-1	26	6	13	–	2	4	–	1	–	–	–	–	–	–	–	–	–	–
Cz 18	Sorted sample	0 to 2	1-2 to 2	15	1	~ 7	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 19	Hand specimen	1 to 2-3	2	4	1.5	7.92	0	16	25	0	0	0	2	13	3	1	0	20	2	1	1
Cz 19	Sorted sample	1 to 3-4	1-2 to 2	10	1	~ 5	–	–	–	–	–	–	–	VC	–	–	–	C	–	–	–
Cz 24	Hand specimen	0-1 to 2	0-1 & 2	9	2	4.5	0	4	2	0	0	0	0	3	0	1	0	0	0	0	0
Cz 24	Unbiased sample	0 to 2-3	1-2	10	1.2	4.41	19	38	45	0	34	82	69	155	5	15	13	45	20	15	35
Cz 26	Sorted sample	0-1 to 2	1-2	10	1.5	4.5	1	6	14	0	3	0	2	28	3	6	4	4	3	4	7

used as a proxy for the relative amounts of time and space averaging suffered by those assemblages, provided that they are matched in terms of their general sedimentary setting (Trueman *et al*. 2003).

Previous work (Trueman and Benton 1997; Trueman 1999; Staron *et al*. 2001; Patrick *et al*. 2002; Trueman *et al*. 2003) has shown that the rare earth elements (REE) are ideal for geochemical taphonomic studies as they are present in low concentrations in life, but are rapidly incorporated into bone after death. Fossil bone commonly contains concentrations of REE more than four orders of magnitude greater than those found in fresh bone (Wright *et al.* 1984; Chenery *et al*. 1996; Trueman and Tuross 2002). The REE are fractionated from one another during weathering and sedimentary transport, and thus the relative abundances of REE found in natural waters and minerals are potentially sensitive to small changes in depositional environment or recrystallisation behaviour (Dupré *et al*. 1996; Sholkovitz *et al.* 1990; Denys *et al*. 1996). The REE composition of fossil bones is therefore governed by the REE composition of the pore waters at the site of burial, and can be used as a natural tag indicating the early depositional locality. All bones from a single depositional locality will share a common REE signal (Trueman and Tuross 2002; Trueman *et al*. 2003).

REE concentrations in eleven bones from the Czatkowice 1 locality were determined by ICP-MS analysis (Table 4). Values were obtained on a VG Plasmaquad II ICP-MS at the University of Bristol, Department of Earth Sciences. A detailed description of the procedure for sample preparation and methods are given in Trueman (1999). Briefly, the samples were washed and any adhering sediment was removed. The cleaned bones were crushed to a powder in an agate pestle and mortar and dried overnight. Approximately 0.1 g of sample was accurately weighed and digested on a hot plate with HNO_3. Solutions were evaporated to dryness and redissolved in 1% HNO_3. Final solutions were made up to 100 ml (resulting in a total dilution of 1000 times) together with an internal standard of 100 ppb Re and Ru. Analytical precision and accuracy were monitored with reference to international standards, errors (2s) were within 10% of certified values. Analytical detection limited (3* blank standard deviation) were less than 0.5 ppb.

RESULTS

PHYSICAL TAPHONOMY

All of the bones from the Czatkowice 1 fissure sediments are disarticulated, and most (approximately 99% of the sample) are incomplete. Most of the bone fragments recovered from the cave sediments are white, pale yellow or orange in colour, with occasional dark coloured heavily abraded shark teeth reworked from the Carboniferous Limestones enclosing the Mesozoic fissure-fill. Similar reworked teeth are found in the Triassic cave sediments of the Cromhall fissures, south west England.

Shape analysis: The bone fragments are typically small with a maximum length of approximately 30 mm, but most are considerably smaller: between 5 and 7 mm long. All of the main categories of bone fragment shape (based in part on the sediment particle classification scheme of Zingg 1935), except disc, are present within the Czatkowice 1 collection. In samples Cz 24 and Cz 26 the most commonly occurring vertebrate clast shapes are rods, blades, flattened cones and “miscellaneous” (bones with an irregular shape which does not really fit into the other categories).

Fractures: Few bones show longitudinal cracks (cracks orientated parallel to the major axis of the bone or to the principle direction of collagen fibres), but some of the archosaur tooth crowns have such cracks running from the tooth tip to the root. The most commonly occurring breaks preserved in the samples are transverse or straight fractures. Jagged and parallel fractures are present, but uncommon. The vast majority of the skeletal elements have been broken at some point in their *post mortem* history. From observations of the acid digestion process it is clear that most (at least 60%) of the breakage (but not the disarticulation) is produced during preparation. Many bones show evidence of multiple breakage events. Such bones have been broken and then abraded, producing smoothed or rounded breakage surfaces, and broken again at a later stage, producing sharp, fresh surfaces.

Weathering: A few bones show signs of *in situ* weathering (producing cracks parallel to the bone fibres), including the archosaur teeth described above.

Abrasion: The abrasion (degree of rounding) of the bones is low; most have abrasion damage characteristic of stage 1 to 2 (Fiorillo1988; Cook 1995a, b), although a few specimens show more extreme abrasion.

There is little or no difference between the taphonomic characteristics of the indeterminate and identified material. Analysis of an unsorted unbiased sample (Cz 24) confirms the observations of the biased samples (samples where the identifiable material has been isolated). A total of 268 fragments of bone from Cz 24 were described. None of the specimens show any definite evidence for weathering. The bone fragments display a range of abrasion states, ranging from stage 0 (fresh bones with no sign of abrasion) to stage 2–3 (moderate levels of abrasion). Most of the bones (54.5% of the sample) show abrasion-related modifications characteristic of stage 1–2 (slight abrasion). Several types of fracture were identified from bones of the Cz 24 sample. Of these, the most common were fresh (unabraded) straight fractures. Such damage is typified by a very smooth breakage surface, which generally (but not always) cuts across the long axis of the bone tissue at an angle of 90°. Less common, but still occurring in significant numbers, are abraded straight fractures. Parallel (or longitudinal) fractures and jagged breakages are present in small numbers, and have both fresh and abraded surfaces. In many cases a bone will show more than one kind of fracture.

There does not appear to be any difference in the preservational characteristics of the different taxa. Only terrestrial taxa have been identified from Cz 24 (procolophonids, archosaurs and small reptiles); the aquatic and semiaquatic creatures (fish, temnospondyls, and protofrogs) known from other samples in the Czatkowice 1 fissure are absent from the Cz 24 sample.

GEOCHEMICAL TAPHONOMY

Total rare earth elements (REE) concentrations range from 600 to 7 000 ppm (Table 4). These are a function of both the REE concentrations in the bone, and the relative amounts of apatite and other authigenic minerals in the sample. As REE are concentrated strongly in the apatite, other authigenic minerals do not significantly alter the relative concentrations of the REE in the sample, but effectively dilute the REE concentrations overall. However, the total REE concentrations measured in these bones are similar to those recorded in fossil bone samples from other terrestrial environments (*e.g.*, Denys *et al*. 1996; Hubert *et al*. 1996; Trueman 1999; Samoilov and Benjamini 2001).

REE data from sedimentary rocks and natural waters are commonly reported relative to an average shale value, which approximates the average REE composition in the crust. Several shale composite values are used, and in this study all REE values are reported normalised to Post Archean Average Shale (PAAS) values (Taylor and MacClennan 1985). The shale-normalised REE concentrations in fossil bones from Czatkowice show distinct convex-upward patterns, with relatively high concentrations of intermediate or middle REEs, and higher concentrations of the light REE compared to the heavy REE. These patterns are generally expressed as inter-element ratios (*e.g.*, Sm/La, Dy/Yb, La/Yb). Bones from Czatkowice 1 all yield Sm/La,

Table 4. REE, U and Th concentrations (ppm) in bones from the Czatkowice assemblage.

	CZ 6-7L	CZ 6-7LC	CZ 17 LC	CZ 33	CZ 2VB	CZ 23 LB	CZ 23 LC	CZ 2 (13) L	CZ 6-7LB	CZ 17	CZ 2V
La	285.69	226.65	257.65	436.74	98.29	429.07	137.37	116.89	773.97	517.62	117.51
Ce	924.15	965.15	1078.20	1415.54	247.95	1909.23	541.96	456.87	3186.46	1609.76	469.33
Pr	115.34	112.75	121.35	150.62	30.14	205.49	59.27	51.19	367.50	183.31	48.50
Nd	465.91	453.43	473.46	574.67	115.98	783.70	227.43	197.29	1521.93	699.84	190.27
Sm	100.43	101.95	110.10	133.12	26.79	176.87	51.52	45.76	335.67	160.06	45.64
Eu	21.54	20.56	19.39	22.09	4.48	31.60	9.34	8.02	67.60	26.33	7.41
Gd	114.79	106.66	104.09	136.02	30.85	178.09	53.45	44.82	347.22	163.33	46.07
Tb	14.31	13.25	13.14	16.84	4.08	23.20	6.92	5.71	41.99	19.61	5.78
Dy	78.80	69.47	72.19	92.89	24.77	122.93	37.16	30.68	218.85	103.88	30.25
Ho	13.44	10.85	11.82	16.25	4.80	19.33	6.10	4.87	34.47	16.50	4.82
Er	32.08	23.89	28.26	39.72	13.17	47.09	15.17	11.48	77.41	40.46	11.14
Tm	3.74	2.36	3.20	4.77	1.73	5.14	1.74	1.28	7.91	4.49	1.17
Yb	18.09	10.36	14.14	21.15	8.38	21.15	7.56	5.92	33.32	19.74	5.10
Lu	2.62	1.30	2.09	3.21	1.25	3.02	1.08	0.76	4.57	2.94	0.69
Th	8.87	6.61	8.33	9.31	9.51	28.27	14.66	10.21	19.22	17.54	14.43
U	33.57	30.88	31.30	37.59	5.04	57.71	10.75	10.95	115.16	52.55	11.33

Dy/Yb, and La/Yb ratios >1. Uniquely amongst the REE, Ce may be present as a tetravalent ion in oxidising conditions. As Ce^{4+} behaves rather differently to Ce^{3+}, Ce anomalies are frequently developed in oxidising environments. The Ce anomaly is simply the ratio between the measured value of Ce and the expected value derived from either linear interpolation between Ce and Pr, or by linear extrapolation from Nd and Pr. All samples from Czatkowice 1 display a positive Ce anomaly, although the size of this anomaly varies within the sample tested. In addition to the REE, concentrations of U and Th were also determined in bones from Czatkowice 1. In the Czatkowice 1 sample, U/Th ratios range from 0.5 to 6.

INTERPRETATION

PHYSICAL TAPHONOMY

The taphonomic characteristics of the various Czatkowice 1 samples (biased and unbiased) provide limited evidence for the depositional history of the Czatkowice 1 cave accumulation. The scarcity of weathering damage (parallel cracks or splintering of the surface of the bones) suggests several possible histories: (1) that the bones were not subjected to any prolonged episodes of subaerial exposure and were rapidly buried or transported into the cave system before any surface modification could take place; (2) that complete carcasses were washed into the cave systems. The second option is less probable, because of the lack of articulated elements within the assemblage. The longitudinal cracks seen in some archosaur teeth may be a product of mechanisms other than weathering (*e.g.*, damage during life, chemical changes during diagenesis, or damage caused by the processes of fossil recovery, extraction and preparation).

The wide range of abrasion states displayed by the Czatkowice 1 fossils are typical of an assemblage that has accumulated over an extended period of time. Accumulations that are a product of catastrophic process tend to have a limited range of abrasion states as all the bones have a virtually identical taphonomic history. The assemblage preserved in the Czatkowice 1 fissure typically displays slight abrasion, most likely reflecting low levels of fluvial transport. In an arid or semi-arid environment with ephemeral water bodies wave action is unlikely to have played a significant part in the modification of the vertebrate debris. Multiple phases of reworking of terrestrial and lacustrine sediments during flash floods is to be expected. However, in such an arid environment it is reasonable to expect that bones could also have been abraded by air-borne sand.

The presence of several types of fracture hints at a complex taphonomic pathway. The presence of straight fractures suggests that a portion of the bone sample underwent some degree of diagenetic alteration, involving the loss of collagen and/or recrystallisation, and was then broken and transported or reworked before final deposition. The proportion of the biased and unbiased samples showing evidence for permineralisation and subsequent abrasion is similar (33% of bones in the biased samples compared with 37.8% of the bones from the unbiased sample). In the case of the Czatkowice 1 material, the parallel fractures were probably caused during the acid preparation of the sediment blocks, as there is no other evidence of the *in situ* weathering of the material. The Cz 24 sample has examples of fresh and abraded spiral or jagged fractures, suggesting that bones in the assemblage were broken by predators and/or scavengers before diagenesis.

The generally small size of the vertebrate fossils preserved in the Czatkowice 1 assemblage suggests that the bones were transported and deposited in a relatively low-energy environment. The limited size range of the bones indicates winnowing or hydrodynamic sorting. The bones described as blades, rods, cuboids and flattened cones are all classified as Voorhies Group I skeletal elements (Voorhies1969). Flume tank experiments with a range of mammalian skeletal elements (Voorhies 1969; Korth 1979) indicate that these bones are rapidly and easily moved by river currents. It is likely that reptilian bones displaying similar shapes would also be easily transported.

The evidence from the physical taphonomic characteristics of the Czatkowice 1 assemblage suggests that the material was either incorporated into the sediment or transported into the ephemeral water bodies or cave system soon after death, thus protecting the bones from *in situ* weathering damage. The generally low levels of abrasion suggest that the assemblage was not subject to transport over any great distance, although aeolian processes may have been important. However, abrasion experiments (Cook 1995b) imply that the degree of abrasion observed on a bone cannot be related directly to the distance travelled. Very large transport distances are required to produce mild levels of abrasion on fresh bones, whereas bone that had previously been buried for approximately 100 years was rapidly abraded. Therefore it is likely that the majority of abrasion seen on bone is a result of reworking and static abrasion. This suggests that many of the Czatkowice 1 bones were subject to at least one phase of reworking. It is difficult to calculate the relative timing of these events. The fact that some of the bones have abraded fractures associated with post-mineralisation breakage would suggest that reworking, at least for part of the assemblage, took place after diagenesis. Other bones display features consistent with breakage of unmineralised tissue, followed by transport and/or reworking.

GEOCHEMICAL TAPHONOMY

The relative abundances of the rare earth elements (REE) developed in fossil bones are principally controlled by the distribution of REE in pore waters, which are in turn controlled by REE weathering and transport mechanisms. Broadly speaking, in environments where the bulk of the REE are transported into sediments associated with particle surfaces, fossil bones will inherit a shale normalised REE pattern characterised by La/Yb ratios >1, and commonly middle REE enrichment. This pattern is most frequently seen in bones from estuarine and coastal marine environments where light REE are scavenged from solution during particle flocculation and settling. In most terrestrial settings the heavy REE apparently form more stable dissolved complexes than the light REE, and consequently the light REE may be more effectively immobilised through adsorption onto particle surfaces. This process results in pore waters with a relatively high proportion of exchangeable heavy REEs with respect to the initial REE source. Bones from most terrestrial settings are consequently characterised by shale normalised La/Yb ratios <1. Bones recovered from soils typically have slightly higher La/Yb ratios than bones from associated fluvial sediments (Trueman 1999). Bones from the Czatkowice 1 assemblage plot in the field of REE space characterized by bones from coastal marine and estuarine environments (Fig. 3). This is evidently inconsistent with their true palaeogeographic setting. However, the Czatkowice 1 assemblage shares its position in REE space with bones recovered from the Cretaceous Djadhokta Formation (Samoilov *et al*. 2001), an environment characterised by extensive local dune fields. This association points strongly to the influence of particle-surface associated transport of REE in aeolian settings, and therefore confirms a significant role for wind-blown dust in the Czatkowice palaeoenvironment.

As discussed earlier, the comparative behaviour of Ce and the adjacent REE can potentially indicate redox conditions during fossilisation. All bones from the Czatkowice assemblage display positive Ce anomalies, suggesting that Ce was present in oxidised form, and was preferentially incorporated into the apatite lattice compared to other trivalent light REE. Ce^{4+} is a smaller ion than Ce^{3+}, similar to the heavy REE. Thus, increasing positive Ce anomalies should correlate with increasing heavy REE enrichment. In fact, the Ce anomaly shows no significant relationship with either La/Yb ratios, or Dy/Yb values. This suggests that the development of Ce anomalies cannot be explained simply by considerations of ion radius (although charge considerations may be important), and thus variations in the extent of the Ce anomaly within the Czatkowice assemblage may reflect real differences in the transport chemistry of Ce^{4+} compared to trivalent REEs in the environment, and therefore derivation of bones from different burial settings.

The variation in trace element chemistry of fossil bones from a single assemblage can also be used as a taphonomic characteristic for a particular assemblage. Bone samples from the Czatkowice assemblage show considerable variation in their REE patterns, particularly in terms of the relative abundance of light REE (*e.g.*, La), and heavy REEs (*e.g.*, Yb). To test the significance of this variation, the assemblage must be compared to another assemblage from a similar sedimentary setting, preferably using similar bones, with a contrasting taphonomic history. We compared the geochemistry of the Czatkowice 1 assemblage to bones from Cromhall Quarry, a Triassic fissure-fill deposit from the south-west of England containing an abundant and diverse small reptile fauna (Fraser and Walken 1983; Fraser 1994; Blessed 1998). The geological setting for the Cromhall deposit is broadly similar to that proposed for Czatkowice 1 (*i.e.*, fissure fills developed in Carboniferous limestone proximal to extensive aeolian Triassic red bed sedimentation). The fissure system at Cromhall, however, was developed in a coastal setting, presumably with some influence of marine waters. The vertebrate-bearing Triassic sediments within the Cromhall fissures are capped by Rhaetic sediments containing abundant marine fossils. REE concentrations in bones from a several blocks of sediment from the

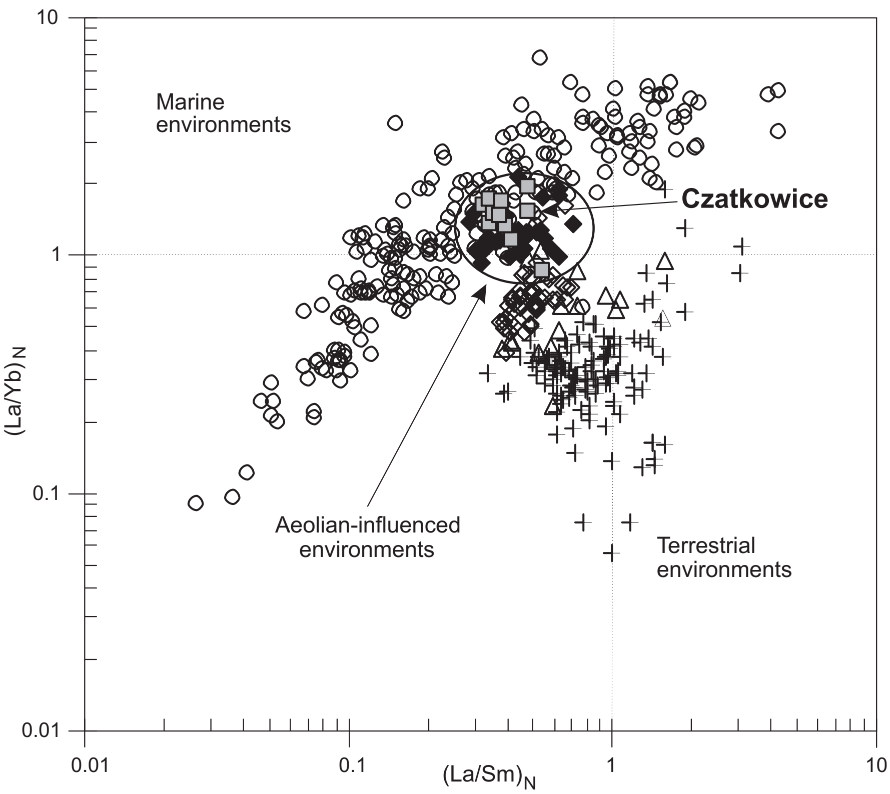

Fig. 3. Shale-normalised ratios of REE concentrations in bones from a variety of depositional settings. Open circles, coastal shelf marine environments (6 localities); open triangles, deep marine environments (4 localities); open diamonds, single estuarine setting; crosses, terrestrial fluvial settings (22 localities); closed symbols, bones from terrestrial localities with aeolian influence (3 localities). Note that broad environmental settings are well-separated in REE-space, and that aeolian influenced localities are distinct from other terrestrial settings. Bones from Czatkowice (filled squares) have similar REE compositions to bones from other aeolian influenced localities. Data taken from Blessed (1998); Elderfield and Pagett (1986); Girard and Albarède (1996); Grandjean-Lécuyer *et al*. (1993); Laenen *et al* (1997); Samoilov *et al*. (2001); Trueman, 1997; and Wright *et al.* (1984).

Cromhall fissure-fill were determined at the University of Bristol using the same analytical equipment and methods (Blessed 1998).

The variation in shale normalised La/Yb ratios in both assemblages was compared using an F-Test (the values were first transformed using common logarithms to ensure normal distributions and thus validate parametric statistical testing methods). Using the F-Test, the variance of REE patterns in bones from the Czatkowice 1 assemblage is not significantly different from the Cromhall Triassic assemblage (as long as the assumption of equivalence in geochemical environments is correct). However, the Cromhall assemblage is mixed, including reworked Carboniferous shark teeth, and stratigraphically younger Rhaetian shark teeth. If these allochthonous elements are removed, then the Cromhall assemblage is significantly less varied than the Czatkowice assemblage. Variation in La/Sm ratios accounts for almost all difference between the two populations (ANOVA (La/Sm values) $F = 4.66$, $p = 0.04$).

The relatively high levels of variation in geochemical composition of bones from Czatkowice 1 suggests that this assemblage contains bones from a range of local depositional environments. Furthermore, these bones must have remained in these separate horizons long enough to inherit distinct geochemical signals before being reworked and introduced into the cave deposit. The absolute time required to produce these separate geochemical signals is linked to the rate of bone recrystallisation, which is poorly known and varies with the depositional environment. However, recent attempts at modelling rates of recrystallisation of bone suggest that fossil bones are recrystallised within 103–104 years (Trueman and Tuross 2002). Therefore, this suggests time averaging over at least 100 year time scale in the Czatkowice 1 deposit. It should be noted, however, that it is possible that trace metals are adsorbed rapidly onto bone crystal surfaces or associated organics, and are introduced into the apatite lattice from this adsorbed reservoir. If so, the amount of time needed to develop the varied trace element signals seen in bones from the Czatkowice assemblage (and thus the minimum time averaging) would be much less. These interpretations are consistent with the relatively complex behaviour of the Ce anomaly discussed above.

Based on the inter-element REE ratios, Ce anomalies, and U/Th ratios, three bones can be identified as distinctly different from the main sample, Cz 33, Cz 17, and particularly, Cz 2 VB. This suggests that these bones were derived from distinctly different depositional environments, compared to the rest of the bones. As all the bones analysed were indeterminate fragments, no palaeoecological inferences may be drawn from this geochemical evidence.

CONCLUSIONS

The excavation and sampling techniques necessarily employed at Czatkowice 1 have led to the loss of almost all detailed sedimentological and stratigraphic information, and preparation and curation has further resulted in a taxonomically and taphonomically biased assemblage — both situations are common to many important historical vertebrate collections. Such loss of information places significant constraints on the palaeobiological and palaeoenvironmental inferences that can be obtained from the collection.

Some sedimentological and taphonomic information can, however, be derived retrospectively through physical and chemical characterisation of the curated bone assemblage. The physical characteristics of bones from the Czatkowice 1 cave suggest an attritional, winnowed assemblage that experienced limited fluvial-lacustrine transport and multiple cycles of reworking. The absence of cracking and flaking of the outer layers of the bone tissue suggests that the bulk of the material was buried rapidly, either in the aeolian-lacustrine sediments or within the cave complex. The presence of abraded post-mineralisation fractures, however, suggests that some bones were mobilised after significant periods of burial. After burial the bones were subjected to chemical changes and associated mineral deposition, for example the bone cavities are frequently infilled with crystalline calcite and dendritic manganese growths cover many bone surfaces.

The geochemical characteristics of the bones support these observations, suggesting a significant aeolian influence on the early diagenetic environment, and derivation of bone remains from a variety of different early burial settings. It is likely that the vertebrate remains were sourced from a small-scale depocentre, possibly an ephemeral water body or channel bank. In addition, interpretations concerning the relative degree of time and space averaging represented in the Czatkowice fissure deposit can be made through comparison of the chemical variation of bones from the Czatkowice 1 cave with other, similar fissure deposits. These studies suggest that the Czatkowice 1 deposits represent relatively large spans of time and/or varied depositional settings.

Inevitably, the strength of such interpretations is limited by the lack of sedimentological and stratigraphic information available, however the combination of independent sources of taphonomic information adds some weight to the reliability of the interpretations. Similar techniques could be applied to historical collections where supporting palaeoenvironmental data are missing, and localities are inaccessible or lost.

REFERENCES

Behrensmeyer, A.K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology* **146**, 473–578.

Behrensmeyer, A.K. 1978. Taphonomic and ecological information from bone weathering. *Paleobiology* **4**, 150–162.

Behrensmeyer, A.K. 1982. Time resolution in fluvial vertebrate assemblages. *Paleobiology* **8**, 211–227.

Blessed, B. 1998. *The Taphonomy of the Cromhall Palaeokarst Deposits*. 129 pp. Unpublished MSc thesis, University of Bristol.

Borsuk-Białynicka, M. and Evans S.E. 2003. A basal archosauriform from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **48**, 649–652.

Borsuk-Białynicka, M. and Evans, S.E. 2009a. Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. *Palaeontologia Polonica* **65**, 235–281.

Borsuk-Białynicka, M. and Evans, S.E. 2009b. A long-necked archosauromorph from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 203–234.

Borsuk-Białynicka, M. and Lubka, M. 2009. Procolophonids from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 107–144.

Borsuk-Białynicka, M. and Sennikov, A.G. 2009. Archosauriform postcranial remains from the Early Triassic karst deposits of southern Poland. *Palaeontologica Polonica* **65**, 283–328.

Borsuk-Białynicka, M., Cook, E., Evans, S.E., and Maryańska, T. 1999. A microvertebrate assemblage from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **44**, 167–188.

Borsuk-Białynicka, M., Maryańska, T., and Shishkin, M.A. 2003. New data on the age of the bone breccia from the locality Czatkowice 1 (Cracow Upland, Poland). *Acta Palaeontologica Polonica* **48**, 153–155.

Chenery, S., Williams, T., Elliott, T.A., Forey, P., and Werdelin, L. 1996. Determination of rare earth elements in biological and mineral apatite by EPMA and LAMP-ICP-MS. *Microchemica Acta* (Supplement) **13**, 259–269.

Cook, E. 1995a. Taphonomy of two non-marine Lower Cretaceous bone accumulations from south-eastern England. *Palaeogeography, Palaeoclimatology, Palaeoecology* **116**, 263–270.

Cook, E. 1995b. *Sedimentology and Taphonomy of Wealden (Lower Cretaceous) Bone Accumulations*. 272 pp. Unpublished PhD thesis, University of Bristol.

Denys, C., Williams, C. T., Dauphn, Y., Andrews, P., and Fernandez-Jalvo, Y. 1996. Diagenetical changes in Pleistocene small mammal bones from Olduvai Bed-1. *Palaeogeography, Palaeoclimatology, Palaeoecology* **126**, 121–134.

Dupré, B., Gaillardet, J., Rousseau, D., and Allegre, C. J. 1996. Major and trace elements of river-bourne material: The Congo Basin. *Geochimica et Cosmochimica Acta* **60**, 1301–1321.

Elderfield, H. and Pagett, R. 1986. Rare earth elements in icthyoliths: variaitons with redox conditions and depositional environment. *The Science of the Total Environment* **49**, 175–197.

Evans, S.E. 2009. An early kuehneosaurid reptile (Reptilia: Diapsida) from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 145–178.

Evans, S.E. and Borsuk-Białynicka, M. 1998. A stem-frog from the Early Triassic of Poland. *Acta Paleontologica Polonica* **43**, 573–580.

Evans, S.E. and Borsuk-Białynicka, M. 2009a. A small lepidosauromorph reptile from the Early Triassic of Poland. *Palaeontologia Polonica* **65**, 179–202.

Evans, S.E. and Borsuk-Białynicka, M. 2009b. The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontologica Polonica* **65**, 79–105.

Fiorillo, A.R. 1988. Taphonomy of Hazard Homestead Quarry (Ongalla Group), Hitchcock County, Nebraska. *Contributions to Geology, University of Wyoming* **26**, 57–97.

Fraser, N.C. 1994. Assemblages of small tetrapods from British Late Triassic fissure deposits. *In*: N.C. Fraser and H.-D. Sues (eds) *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 214–226. Cambridge University Press, Cambridge.

Fraser N.C. and Walkden, G.M. 1983. The ecology of a Late Triassic reptile assemblage from Gloucestershire, England. *Palaeogeography, Palaeoclimatology, Palaeoecology* **42**, 341–365.

Girard, C. and Albarè, F. de 1996. Trace elements in conodont phosphates from the Frasnian/Famennian boundary. *Paleogeography, Palaeoclimatology, Palaeoecology* **126**, 195–209.

Gradziński, R. 1992. Deep blowout depressions in the aeolian Tumlin Sandstone (Lower Triassic) of the Holy Cross Mountains, central Poland. *Sedimentary Geology* **81**, 231–242.

Gradziński, R., Gagol, J., and Ślączka, A. 1979. The Tumlin Sandstone (Holy Cross Mountains, central Poland): Lower Triassic deposits of aeolian dunes and interdune areas. *Acta Geologica Polonica* **29**, 151–175.

Gradziński, R. and Uchman, A. 1994. Trace fossils from interdune deposits — an example from the Lower Triassic aeolian Tumlin Sandstone, central Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* **108**, 121–138.

Grandjean-Lécuyer, P., Feist, R., and Albarède, F. 1993. Rare earth elements in old biogenic apatites. *Geochimica et Cosmochimica Acta* **57**, 2507–2514.

Hubert, J.F., Panish, P.T., Chure, D.J., and Prostak, K.S. 1996. Chemistry, microstructure, petrology, and diagenetic model for Jurassic dinosaur bones, Dinosaur National Monument, Utah. *Journal of Sedimentary Research* **66**, 531–547.

Korth, W.W. 1979. Taphonomy of microvertebrate fossil assemblages. *Annals of the Carnegie Museum* **48**, 235–285.

Laenen, B., Hertogen, J., and Vandenberghe, N. 1997. The variation of the trace-element content of fossil biogenic apatite through eustatic sea-level cycles. *Palaeogeography, Palaeoclimatology, Palaeoecology* **132**, 325–342.

Martin, R.E. 1999. *Taphonomy: A Process Approach.* 508 pp. Cambridge University Press, Cambridge.

Paszkowski, M. 2009. The Early Triassic karst of Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 7–16.

Paszkowski, M. and Wieczorek, J. 1982. Fossil karst with Mesozoic bone breccia in Czatkowice (Cracow Upland, Poland). *Kras i Speleologia* **3**, 32–39.

Patrick, D., Martin, J.E., Paris, D.C., and Grandstaff, D.E. 2002. Rare earth element signatures of fossil vertebrates compared with lithostratigraphic subdivisions of the Upper Cretaceous Pierre Shale, South Dakota. *Proceedings of the South Dakota Academy of Sciences* **81**, 161–179.

Samoilov, V.S., Benjamini, Ch., and Smirnova, E.V. 2001. Early stabilization of trace elements in reptile bone remains as an indicator of Masstrichtian–Late Paleocene climatic changes: evidence form the Naran Bulak locality, the Gobi Desert (South Mongolia). *Sedimentary Geology* **143**, 15–39.

Shishkin, M.A. and Sulej, T. 2009. Temnospondyl amphibians of the Czatkowice 1 tetrapod assemblage. *Palaeontologia Polonica* **65**, 31–77.

Shishkin, M.A., Ochev, V.G. Lozovskii, V.R., and Novikov, I.V. 2000. Tetrapod biostratigraphy of the Triassic of Eastern Europe. *In*: M.J. Benton, M.A. Shishkin, D. Unwin, and E.N. Kurochkin (eds) *The Age of Dinosaurs in Russia and Mongolia*, 120–139. Cambridge University Press, Cambridge.

Sholkovitz, E.R., Landing, W.M., and Lewis, B.L. 1994. Ocean particle chemistry — the fractionation of rare-earth elements between suspended particles and seawater. *Geochimica et Cosmochimica Acta* **58**, 1567–1579.

Staron, R., Grandstaff, B., Gallagher, W., and Grandstaff, D.E. 2001. REE signals in vertebrate fossils from Sewel, NJ: Implications for the location of the K-T boundary. *Palaios* **16**, 255–265.

Taylor, S.R. and McLennan, S.M. 1985. *The Continental Crust: Its Composition and Evolution: An Examination of the Geochemical Record Preserved in Sedimentary Rocks*. 312 pp. Blackwell Scientific, Oxford.

Trueman, C.N. 1997. *Rare earth element taphonomy of vertebrate assemblages*. Unpublished PhD thesis, University of Bristol.

Trueman, C.N. 1999. Rare earth element geochemistry and taphonomy of terrestrial vertebrate assemblages. *Palaios* **14**, 555–556.

Trueman, C.N. and Benton, M.J. 1997. A geochemical method to trace the taphonomic history of reworked bones in sedimentary settings. *Geology* **27**, 263–265.

Trueman, C.N. and Tuross, N. 2002. Trace elements in recent and fossil bone apatite. *In*: M.J. Kohn, J. Rakovan, and J.M. Hughes (eds) Phosphate: Geochemical, Geobiological and Materials Importance. *Reviews in Mineralogy and Geochemistry* **48**, 489–522.

Trueman, C.N., Benton, M.J., and Palmer, M.R. 2003. Geolchemical taphonomy of shallow marine vertebrate assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* **197**, 151–169.

Voorhies, M.R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *University of Wyoming Contributions to Geology Special Paper* **1**, 1–69.

Wright, J., Seymour, R.S., and Shaw, H.F. 1984. REE and Nd isotopes in conodont apatite: variations with geological age and depositional environment. *In*: D.L. Clark (ed.) Conodont Biofacies and Provincialism. *Geological Society of America Special Papers* **196**, 325–340.

Zingg, T. 1935. Beitrage zur Schotter analyse. *Schweizerische Mineralogische und Petrographische Mitteilungen* **15**, 39–140.