

Palaeoenvironments of vertebrates on the southern shore of Tethys: The nonmarine Early Cretaceous of Tunisia

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Abstract

Through the Late Jurassic and Early Cretaceous, the southern shore of the Tethys Ocean migrated north and south over short distances. These vicissitudes are documented in the ‘continental intercalaire’, a long series of mainly non-marine sediments deposited across North Africa. A combined taxonomic, physical and chemical taphonomic study provides independent lines of evidence for reconstruction of palaeoenvironments within this marginal marine setting.

The Douiret, Chenini and Oum ed Diab formations from the Tataouine basin of southern Tunisia span the later part of the Early Cretaceous. Microvertebrates from four sites in these formations show different modes of physical abrasion, time averaging, and mixing, based on a taphonomic analysis using a combination of physical and chemical methods. The taxonomic composition of each assemblage, and trends in rare earth element (REE) compositions of bones, from each locality were used as independent lines of evidence to indicate differences in early depositional environments. The Jebel Boulouha assemblage (Douiret Formation) is interpreted as a terrestrial carbonate-rich environment with relatively little mixing. The Touil el Mra assemblage (Oum ed Diab Formation) suggests a marginal marine environment with some mixing of previously interred bones. The Oued el Khil assemblage (Chenini Formation) and the Oum ed Diab assemblage (Oum Ed Diab Formation) are more equivocal, suggesting mixed freshwater and marine influences. Interpreting salinity in marginal marine settings is difficult, and best attempted from multiple, independent lines of evidence. We suggest that REE geochemistry can contribute to palaeoenvironmental reconstruction when used in combination with other, independent physical, palaeontological and /or geochemical methods.

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1. Introduction

The Late Jurassic and Early Cretaceous sedimentary successions of North Africa show evidence of many

minor cycles of transgression and regression as the southern margin of the Tethys Ocean moved north and south. These were important times palaeogeographically, as the North Atlantic Ocean continued to open, as the South Atlantic Ocean began to open, and as land connections between Africa and Europe, perhaps across the Iberian Peninsula, waxed and waned.

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This story is told in a long sequence of sediments termed loosely the ‘continental intercalaire’ (Lapparent, 1960) that are found across North Africa both north and south of the Sahara Desert. These successions range in age from Mid Jurassic to Mid Cretaceous, and they are largely non-marine, but with occasional minor marine transgressions, some consisting of limestones with ammonites, before the major worldwide late Cenomanian transgression. The ‘continental intercalaire’ has produced rich vertebrate remains from a dozen countries, from Morocco to Egypt, and from Sudan to Niger, and especially from Tunisia (Bouaziz et al., 1988; Benton et al., 2000; Cuny et al., 2004).

Hitherto, the sedimentary interpretation of many of the formations of the ‘continental intercalaire’ has been disputed, whether they were entirely non-marine or partially or fully marine (Lefranc and Guiraud, 1990). Geologists have cited evidence from sedimentary structures and fossils, but many of these are equivocal: for example, the discovery of shark fossils has been said to indicate that the deposits were marine, but several of these Mesozoic shark groups were almost certainly freshwater (Cuny et al., 2004). Without clear indications of depositional environment at a local level, it has proved

hard to interpret the palaeogeography of southern Tethys.

Here, we present information from three formations that span the Aptian/Albian interval. Classic taxonomic and physical sedimentological parameters are presented, but these are then cross-tested using novel geochemical techniques. The aim of this paper is twofold: to demonstrate the value of rare earth elements in ancient bones and teeth in identifying time averaging and mixing, and in distinguishing marine and freshwater settings of ancient vertebrate deposits; and to use the new data to document some of the movements of the southern shore of Tethys in the Early Cretaceous.

2. Geological setting

The Late Jurassic and Early Cretaceous sediments of southern Tunisia were deposited during the filling of the Tataouine Basin, part of a major subsiding platform (Busson, 1967). The main vertebrate-bearing units are located on the Dahar plateau, which extends from the margin of the Saharan ergs in the west to the Jeffara plain in the east (Fig. 1). These Mesozoic rocks form a cliff line that runs for around 300 km from north to south through

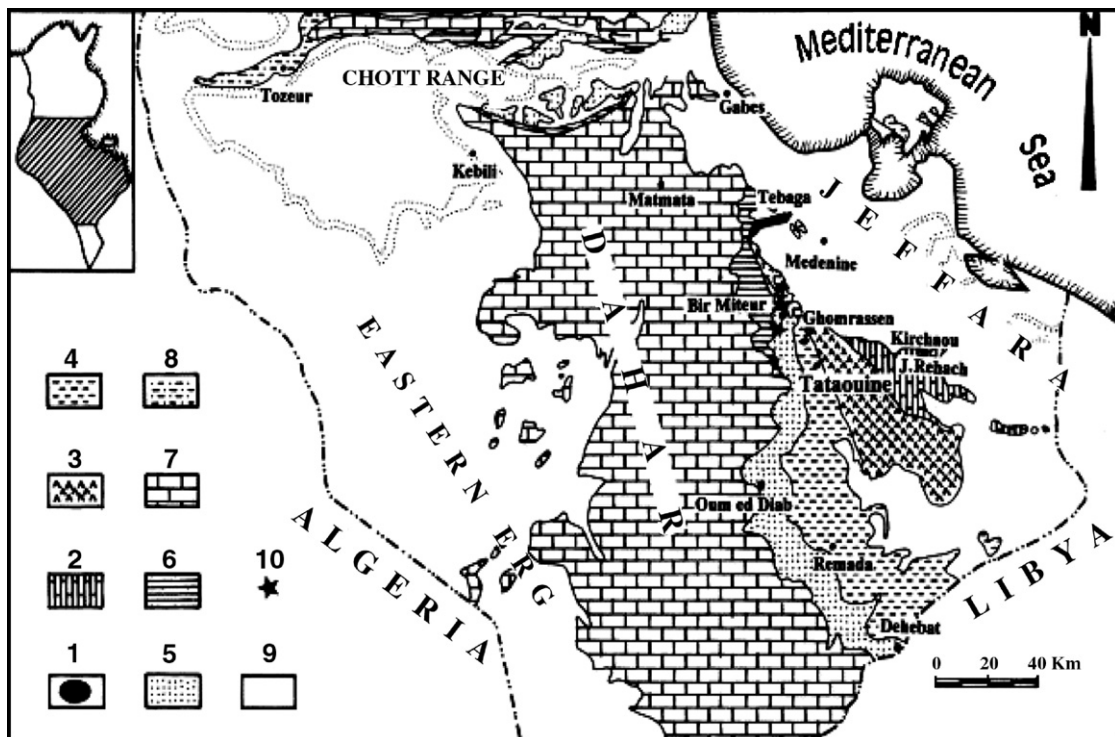


Fig. 1. Outline geological map, showing the area of study in southern Tunisia. Outlined are the major geomorphological regions, the Jeffara coastal plain, the Dahar plateau, and the Saharan Erg Oriental. The inset map shows the location of southern Tunisia. Stratigraphic units: 1. Permian; 2. Triassic; 3. Lias; 4. Dogger; 5. Malm-Neocomian; 6. Vraconian (mid-late Albian); 7. Late Cretaceous; 8. Mio-Pliocene; 9. Pliocene-Quaternary; 10. dinosaur sites. (modified from Zarbout et al., 1994; Benton et al., 2000).

southern Tunisia and then curves to run from west to east into westernmost Libya. The Late Jurassic to Early Cretaceous succession is best seen in the cliff line since the Dahar plateau to the west sits on the overlying Late Cretaceous limestones, and the base of the cliffs sits faulted against Cenozoic rocks of the Jeffara plain to the east.

The Late Jurassic and Early Cretaceous succession (Fig. 2) is divided into three groups and eight formations. The latest Jurassic and Early Cretaceous are represented by two groups, the Asfer Group (Bir Miteur, Boulouha, and Douiret formations) and the Ain el Guettar Group (Chenini and Oum ed Diab formations).

The Asfer Group varies from a maximum thickness of 220 m in the south at Merbah el Asfer to just a few metres in the north. The Bir Miteur Formation, at the base of this group, is a 70 m thick unit of late Oxfordian to Kimmeridgian age. The formation consists of alternating

green shales, gypsum, silts, sands and dolomites, indicating lagoonal conditions (Benton et al., 2000). Overlying this is a marginal marine carbonate sequence, the Boulouha Formation, reaching a maximum thickness of 80 m, and ranging from Tithonian to Neocomian in age. Finally, the uppermost Douiret Formation consists mainly of mudstones, and has been dated as early Aptian (Ben Ismaïl, 1991). Rocks of the Merbah el Asfer Group therefore represent deposition in a shallow, marginal marine setting.

We sampled one locality from the Douiret Formation, Jebel Boulouha. Here, intercalations of fine sand, sandy mudstone, and dolomite are overlain by a thick bed of green clay. The vertebrate remains are preserved at the base of each sandy unit, especially the two nearest the base, where abundant fish and reptile fossils were obtained. Fine bands of gypsum occur here and there,

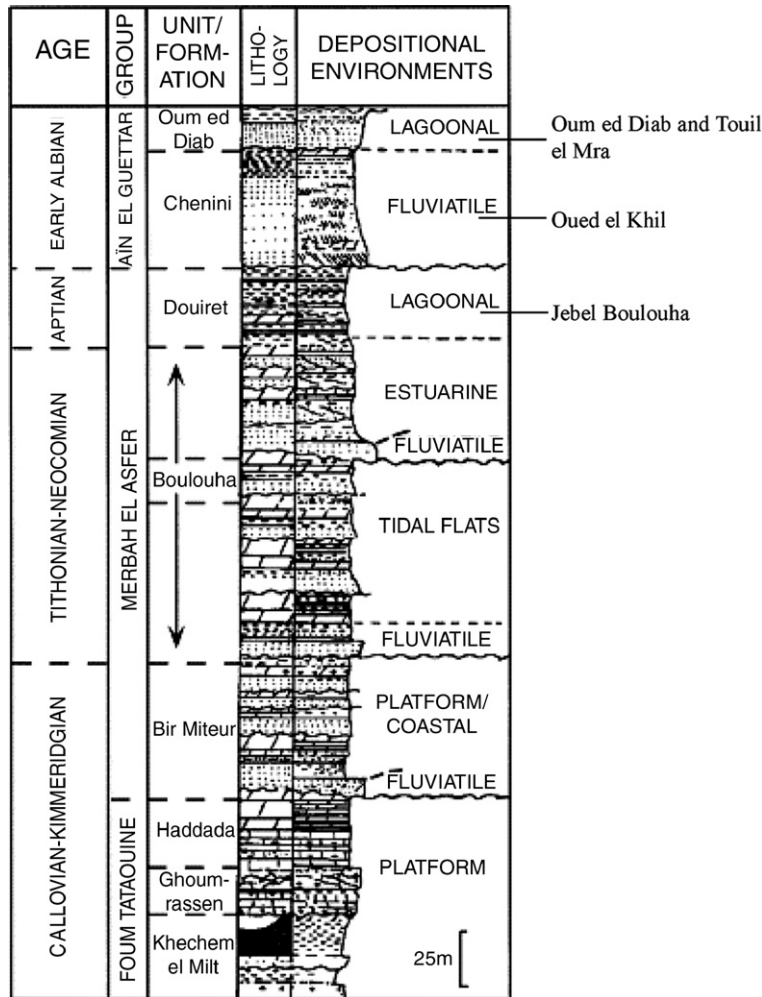


Fig. 2. Simplified stratigraphy of the Late Jurassic to latest Early Cretaceous succession on the Dahar plateau in southern Tunisia. The horizons of the four sampled bonebeds are indicated. (Modified from Zarbout et al., 1994; Benton et al., 2000).

and fossilised logs are invested with gypsum. The base of the locality, marking the base of the Formation, is marked by a regional discordance, characterised by a conglomeratic unit containing fossil wood and vertebrate debris.

The Chenini Formation (50 m thick), the lower division of the Aïn el Guettar Group (Fig. 2), consists mainly of coarse sandstones, but also includes interspersed conglomerates, breccias, and mudstones, which contain varied fossil plant material. It is, however, the coarse sandstones that are of relevance to this study, as these yield numerous fish, turtle, crocodile and dinosaur remains (Benton et al., 2000). The Oued el Khil locality was sampled. The sedimentology here consists of cross-bedded, buff-coloured and yellowish sandstones, containing large quartz grains, and showing in places breccias and conglomerates. The basal conglomerate unit, indurated and cemented by iron oxide, contains wood fragments, isolated bones and teeth, and coarse quartz grains. At the base of the sands is a prominent channel 3 m wide and 1 m deep, part of a larger sand body 20 m wide and 4–5 m deep. Within the channel are coarse lags, consisting of gravels, with abundant flattened clay clasts and rarer wood and bone fragments. The cross bedding and other sedimentary structures suggest deposition of the sands in fluvial point bars (Benton et al., 2000).

The overlying Oum ed Diab Formation (25 m thick) is marked by a transition to alternating shales and sands, which are dated as Albian to Cenomanian (Bouaziz et al., 1988). The Radouane Member of this formation represents a major Cenomanian transgression. A carbonate-rich sandy offshore bar marks this event, yielding various marine taxa, such as ammonites, *Lepidotes* and pycnodonts.

Two localities in the Oum ed Diab Formation were sampled, Touil el Mra and Oum ed Diab. This formation is a series of fine, micaceous sands, marked at the base by a clay layer, in places conglomeratic, resting on an erosive surface, and rich in debris of vertebrates. At Touil el Mra, the basal unit consists of 3 m of deep red, unconsolidated coarse sandstone, with numerous channels containing cross bedding and with coarse basal lags. The lags are composed of mudstone and sandstone clasts, with abundant bones and teeth. Above the basal beds are repeated units of grey, poorly consolidated, cross-bedded coarse sandstones.

In summary, fossil material for this study was collected from four localities, spanning the Douiret (Jebel Boulouha north side), Chenini (Oued el Khil) and Oum ed Diab (Touil el Mra, Oum ed Diab) formations. These formations were interpreted as mixed marine/freshwater, non-marine, and freshwater respectively, based on sedimentology and fossil content. For example, Benton et al.

(2000) interpreted the Oued el Khil deposits of the Chenini Formation as fluvial, based on observations of channel and bar deposits in the field.

Study of the fossil sharks by Cuny et al. (2004) confirms some of these views, but provides sharp disagreement on the Chenini Formation. The Douiret Formation is characterised by a dominance of sharks, and of these, the hybodont *Priohybodus* is thought to be restricted to freshwater environments, while the ray *Rhinobatos* is considered mainly marine. The Douiret Formation is therefore interpreted to represent marginal marine deposition, possibly within a large delta. The overlying Chenini Formation produces a typically marine shark assemblage, implying shallow marine conditions (Cuny et al., 2004). The overlying Oum ed Diab Formation, sampled at the Touil el Mra and Oum ed Diab sites, was interpreted as a freshwater environment, because of the terrestrially-derived fossils and the absence of unequivocal obligate marine faunal remains. The current study aims to resolve the contrasting interpretations derived from sedimentological and palaeontological evidence.

3. Physical taphonomy

3.1. Previous work

Palaeoecologists commonly use physical abrasion of bones and teeth as evidence for transport (Fiorillo, 1988; Lyman, 1994). Such methods are notoriously difficult to apply as many variables other than duration and distance of travel affect the degree of abrasion suffered by bone. For example, experiments documenting the effect of transport on bones and teeth show that the physical status of bone upon introduction to the transport system largely determines its response to abrasion (Argast et al., 1987; Cook, 1995).

Despite problems associated with interpreting abrasion as a direct measure of transport, indices of abrasion

Table 1
Taphonomic characteristics of abraded bone material (modified from Fiorillo, 1988; Cook, 1995)

Stage 0	Very angular: the bone (or tooth) is fresh and unabraded. Processes and bone edges well defined and sharp. (little or no abrasion.)
Stage 1	Subangular: the bone edges and processes are slightly abraded and polished.
Stage 2	Subrounded: bone edges well rounded, processes recognizable. (Moderate abrasion.)
Stage 3	Rounded: edges show a high degree of rounding, processes generally remnant.
Stage 4	Extremely rounded. (extreme abrasion.)

provide a useful insight into the transport history of vertebrate assemblages. Cook (1995) modified the abrasion index of Fiorillo (1988) in which physical abrasion can be quantified by analysing the surface characteristics of bones or teeth (Table 1). Variations in abrasion stage of specimens from a single deposit can indicate *time averaging*, where material has accumulated over a long span of time. *Mixing*, in other words, the occurrence of material

in one deposit that has undergone a range of different transport histories, originating from more than one source environment, might also be indicated.

3.2. Methods

Microvertebrate-bearing sediment was collected from four localities, Jebel Boulouha, Oued el Khil,

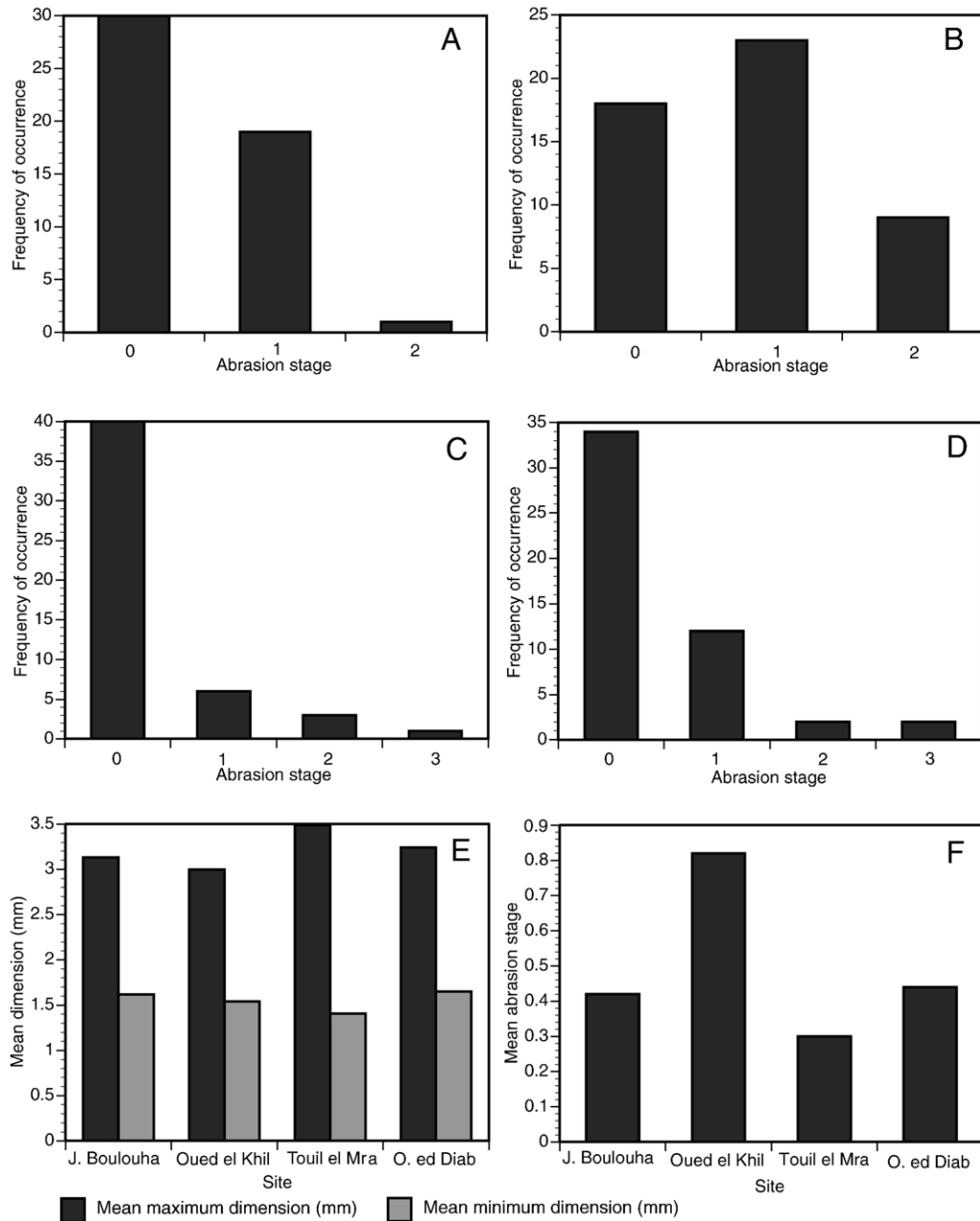


Fig. 3. Results of abrasion analysis for all four sites. A–D, Recorded abrasion stages for specimens from Jebel Boulouha (A), Oued el Khil (B), Touil el Mra (C), and Oum ed Diab (D). E, Median magnitudes of maximum and minimum specimen dimensions for each site. F, Median abrasion stage for each site.

Touil el Mra, and Oum ed Diab. The material was largely disaggregated. The clay fraction was removed in the field by washing and large sandstone and limestone fragments were removed by hand picking. Approximately 25 kg of the sand-sized concentrate was brought back to the laboratory for picking. Under the microscope, sand grains, small concretions, and wood fragments were discarded, and rare small gastropods and vertebrate fossils were retained. The vertebrate fossils (~ 1–3 mm diameter) consisted of bone fragments, teeth, and fish scales. The teeth were grouped on the basis of their morphology in order to aid later taxonomic classification.

Fifty specimens from each locality were analysed for signs of abrasion. These were chosen so that the taxonomic diversity of samples from a particular site would roughly match that of the site as a whole. The 50–55 specimens were as follows: Jebel Boulouha (44 bone fragments, 1 fish vertebra, 5 teeth, 4 shells), Oued el Khil (44 bone fragments, 4 teeth, 2 shells), Touil el Mra (30 bone fragments, 10 fish vertebrae, 6 teeth, 4 shells), and Oum ed Diab (32 bone fragments, 18 teeth). The teeth were almost exclusively those of *Lepidotes*, with one or two caturid teeth as well; among the bony fish teeth, only about 5% remain unidentified. Taphonomic analysis involved recording the maximum and minimum dimensions of each specimen, and its abrasion stage (Table 1), and comparisons between localities were made by comparing histograms.

3.3. Results

The abrasion analysis (Fig. 3) shows considerable variation in physical abrasion stages between sites. The Jebel Boulouha material (Fig. 3A) was mainly assigned to abrasion stages 0 and 1, with only one of the 50 specimens being sufficiently rounded to fall into abrasion stage 2. Oued el Khil, on the other hand (Fig. 3B) shows a more even distribution of abrasion stages 0, 1, and 2, indicating a higher median level of abrasion for the site (Fig. 3F). The Touil el Mra and Oum ed Diab samples, both from the Oum ed Diab Formation, have similar abrasion profiles (Fig. 3C, D), with the majority of the sample falling in abrasion stage 0, and diminishing quantities in abrasion stages 1–3. Note, however, that the median abrasion stages differ (Fig. 3F), with the latter locality showing more of the material at higher abrasion stages than the former. Sample sizes are too small ($n < 5$) for statistical testing of distinctness of distributions.

These differences in abrasion profiles between the localities (Fig. 3A–D) are not associated with differ-

ences in the size of material: the mean specimen sizes and the maximum specimen sizes are nearly identical from site to site (Fig. 3E).

4. Taxonomic diversity

4.1. Methods

The picked fossil material was also used for taxonomic analysis. Non-descript lumps of bone and bone fragments were set aside. Small bivalve and gastropod shells were counted. The identifiable vertebrate material consisted of isolated fish scales and fish vertebrae, as well as teeth of fishes and tetrapods. The teeth of sharks in particular are identifiable to genus and species in many cases (Cuny et al., 2004), while teeth of certain actinopterygians, such as *Lepidotes* and caturids, are robust and readily identifiable. Reptile teeth were much rarer, and these could be separated into those of crocodylians, and others that might be ascribed to any of a number of reptilian groups. Some fragments of crocodylian scutes were also observed.

4.2. Results

All localities share some common features of the relative abundance of different vertebrate fossils. Actinopterygian remains are most abundant at all sites with hybodonts, neoselachians, reptiles and invertebrates being notably less numerous (Fig. 4A). Of the fish specimens (Fig. 4B), *Lepidotes* teeth are by far the most abundant, especially from Oum ed Diab.

There are also major differences in faunal composition among the four localities (Fig. 4C–F), and this is supported by the Kolmogorov–Smirnov tests between all pairs of data: all distributions differ, Oued el Khil and Oum ed Diab the most. Jebel Boulouha (Fig. 4C) shows the widest variety of taxonomic groups, whereas the remaining three sites display a clearly lower fossil diversity. There are also more subtle differences between sites. For example, at Oued el Khil (Fig. 4D) there is a roughly equal abundance of *Lepidotes* and caturid remains, in contrast to the dominance of *Lepidotes* at the other sites.

Perhaps the most obvious discrepancy between sites, however, exists in the proportions of *Lepidotes* teeth of differing morphology. The Jebel Boulouha sample contains a large proportion of the fish's elongate pharyngeal teeth, while Touil el Mra, Oued el Khil and Oum ed Diab are dominated by domed *Lepidotes* oral teeth. Furthermore, Jebel Boulouha and Oum ed Diab yield a large number of fragmented *Lepidotes*

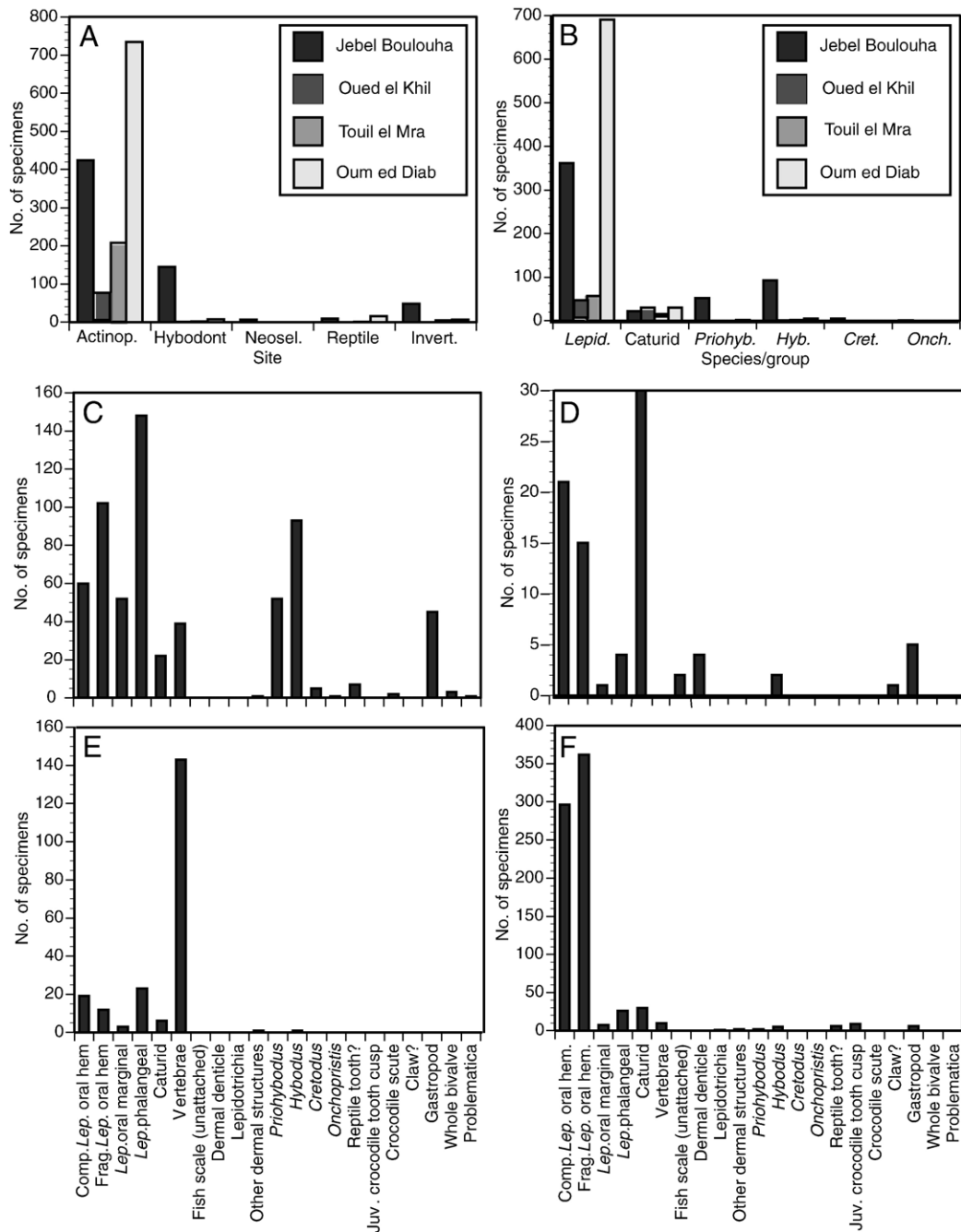


Fig. 4. Results of taxonomic analysis. A, Abundance of major taxonomic groups from all four sites. B, Abundance of major groups of actinopterygians (bony fishes) from all four sites. C–F, Abundance of all taxonomic divisions from Jebel Boulouha (C), Oued el Khil (D), Touil el Mra (E), and Oum ed Diab (F).

teeth, and these are not seen at the other sites. The absence of other *Lepidoties* elements is quite commonplace — the bones of the skull and skeleton are so much more delicate than the pebble-like teeth that they are readily ground up either during transport, or during preparation.

5. Chemical taphonomy

5.1. Previous work

Bone is composed of nanocrystals of calcium phosphate intimately associated with a protein matrix largely

constructed from collagen. The small size of bone crystallites ($\sim 20 \times 40 \times 5$ nm, Weiner and Price, 1986) results in a high surface area/mass ratio and thus metals dissolved in circulating pore waters are readily sorbed onto bone crystallite surfaces. Bone crystallites have a high affinity for trace elements such as the rare earth elements (REE) (Koeppenkastrop and DeCarlo, 1992; Reynard et al., 1999) and bone acquires REE in direct proportion to their abundances in the surrounding pore waters (e.g. Bernat, 1975; Wright et al., 1984; Trueman and Benton, 1997; Staron et al., 2001; Trueman and Tuross, 2002; Trueman et al., 2003a; Lécuyer et al., 2004; Metzger et al., 2004; Trueman et al., 2004).

The collagenous matrix in bone is readily hydrolysed in aqueous environments, and thus in order to survive into deep time, micron-scale pore spaces originally occupied by collagen must be filled with authigenic apatite. 'Fossilisation' of bone is essentially growth of secondary apatite into intra-crystalline pore spaces, and is complete when intra-crystalline porosity is closed. At this point, the bone is closed to further circulation of pore waters and uptake of metals from the depositional environment effectively ceases. Estimates of the time scale of recrystallisation are on the order of 10^3 – 10^5 years (e.g. Trueman and Tuross, 2002).

Rare earth elements are relatively heavy elements, ranging from lanthanum, with atomic number 57, to lutetium, with atomic number 71. The ionic radius of REE ions decreases smoothly with atomic number (the so-called lanthanide contraction), and this leads to trends in the behaviour across the REE series. Subtle geochemical processes produce fractionations across the REE series, and alter the relative abundance of each of the REE. The REE pattern of natural waters is largely controlled by exchange of REE between particle surfaces and dissolved complexes. Because of the lanthanide contraction, stability constants for REE, particularly $\text{Ln}(\text{CO}_3)_n$ complexes, increase with atomic number, so that HREE form more stable complexes, which in turn leads to light rare earth elements being preferentially adsorbed onto surfaces and HREE being preferentially retained in solution (Sholkovitz et al., 1992).

In surface waters, REE are typically held as complexes with a number of ligands, the most important of which in environments conducive to survival of bone are carbonate, organic (humate and fluvate) and phosphate species (e.g. Johannesson et al., 1996; Tang and Johannesson, 2003). In waters with $\text{pH} > 7$, or with high concentrations of dissolved carbonate, most REE will be held as carbonate complexes (e.g. Johannesson et al., 1996). Stability constants for REE carbonato

(REECO_3^+) and dicarbonato ($\text{REE}(\text{CO}_3)_2^-$) complexes show large differences across the REE series (Lee and Byrne, 1993; Johannesson et al., 1996), so fractionation of LREE from HREE is enhanced in high-pH waters. In circumneutral waters, or in waters with high dissolved organic content, a significant proportion of the REE will be bound to organic matter either as colloidal particles or as organic coatings on inorganic particles (e.g. Dupré et al., 1999; Tang and Johannesson, 2003). REE previously sorbed on to particle surfaces may be released to solution following reduction of metal oxide coatings or decomposition of organic particles or particle coatings. As LREE are preferentially removed during sorption, release of these sorbed REE leads to LREE enrichment in pore fluids (e.g. Sholkovitz et al., 1992).

The relative abundance and availability of REE ions in the pore water is thus influenced by pH, ionic strength and particle surface chemistry. The REE composition of ground waters may evolve along flow paths or through time through progressive removal of dissolved REE via sorption or release of sorped REE into solution. The resulting differences in REE patterns will be imparted to bones undergoing diagenetic recrystallisation (Sholkovitz et al., 1992; Johannesson et al., 1996; Trueman and Tuross, 2002; Martin et al., 2005).

The REE composition of fossil bones can indicate two taphonomic parameters: source environment and mixing (Trueman, 1999; Trueman et al., 2003a; Metzger et al., 2004; Patrick et al., 2004; Martin et al., 2005). The relative abundances of REE within bones (the REE pattern) can be compared to modern pore waters from known environments to infer aspects of the microenvironment of burial (e.g. Henderson et al., 1983; Metzger et al., 2004; Patrick et al., 2004; Martin et al., 2005). The degree of mixing within a deposit can be determined from variation in REE signatures among specimens of bones and teeth in a sample. Deposits with low levels of mixing display relatively homogeneous REE patterns, because the bones were all buried in similar environments (Trueman et al., 2003a; 2005; Metzger et al., 2004). On the other hand, mixed assemblages are more likely to contain bones that exhibit a wide variation of REE patterns if the bones are from many different original burial environments. Time averaging can be implied by REE signatures, but is harder to prove. A rapidly accumulated attritional assemblage (i.e. low time averaging) is likely to show uniform REE patterns, while slow accumulation (i.e. high time averaging) is likely to show increased variation in REE as the likelihood of variation in the REE composition of early depositional environments increases with longer accumulation times.

5.2. Methods

Thirty fragments selected at random from each of the four sites were analysed for bulk REE compositions. These 120 bone fragments were individually crushed into fine powders using an agate pestle and mortar, and reacted with 1 ml of sodium acetate solution buffered to pH 5 with acetic acid to remove diagenetic calcite. The supernatant was removed and discarded, and the resulting powder dried and dissolved in 1 ml of 3 M HNO₃. 0.5 ml of the resulting solution was removed and made up to 10 ml with distilled water and internal standards (Re, Ru) were added. Where necessary, samples were diluted further to ensure measured concentrations were within the linear range of the calibration. Analysis was performed on a VG/Thermo PlasmaQuad 3 ICP-MS at the University of Bristol. Instrument tuning limited the formation of oxides, although corrections for LREE oxide interferences on the HREE were applied. Analytical precision, including uncertainty in calibration curves, is typically 2–3% (95% confidence limits).

5.3. Results

Mean total REE concentrations in bones from Jebel Boulouha, Oum ed Diab, Oued el Khil, and Touil el Mra are 57, 70, 128, and 60 µg/g respectively. These values are relatively low compared to those of bones recovered from terrestrial sequences (e.g. Trueman, 1999; Metzger et al., 2004), but are well within the range previously reported for fossil bone (e.g. Trueman and Tuross, 2002). The total concentration of REE within fossil bone is controlled by the relative rates of recrystallisation of bone apatite, the rate of supply of REE via groundwater and the concentration and availability of REE within groundwater. It is difficult to demonstrate a single cause for the relatively low concentrations seen in bones from each of the four horizons sampled in this project, but the microvertebrate remains sampled in this study are relatively small. Small bones are typified by thin cortex and it is possible that the low concentrations seen reflect relatively rapid rates of recrystallisation.

The Post-Archean Australian Shale (PAAS, Taylor and McLennan, 1985) normalised concentrations of

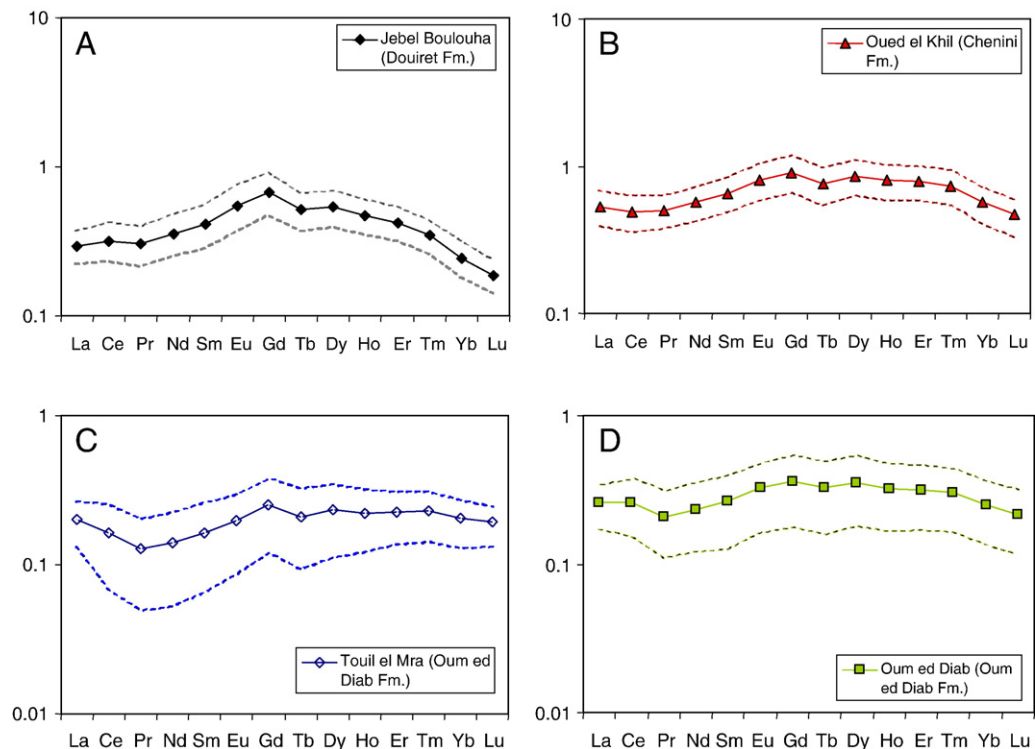


Fig. 5. Mean rare earth element (REE) bulk composition for bone samples from each of the four sites: Jebel Boulouha (Douiret Formation) (A), Oued el Khil (Chenini Formation) (B), Touil el Mra (Oum ed Diab Formation) (C), and Oum ed Diab (Oum ed Diab Formation) (D). REE compositions are shown normalised to the Post-Archean Australian Shale standard. Dotted lines bracket one standard deviation above and below the mean.

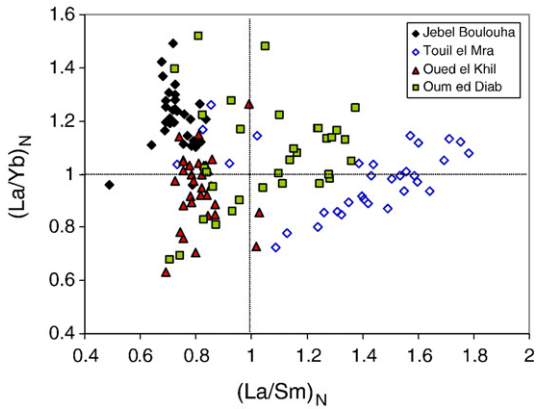


Fig. 6. Comparison of relative light (La), light middle (Sm) and heavy (Yb) REE abundances in bones from Jebel Boulouha (Douiret Formation), Oued el Khil (Chenini Formation), Touil el Mra (Oum ed Diab Formation), and Oum ed Diab (Oum ed Diab Formation). Subscript (N) indicates shale (PAAS) normalised values.

REEs in bones from Jebel Boulouha (Douiret Formation; Fig. 5) are typified by relatively high concentrations of mid mass REEs (Nd–Tm) and relative depletion in HREE. Samples from Oued el Khil (Chenini Formation; Fig. 5) are similar to those from Jebel Boulouha, but with less pronounced depletion in HREE. Samples from the Oum ed Diab Formation (Fig. 5) are distinguished by relatively flat REE patterns with slight enrichment of mid mass REE and in some cases a pronounced Ce anomaly. Bones from each of the four sites differ in their REE compositions and can be relatively well separated in a simple bivariate plot (Fig. 6).

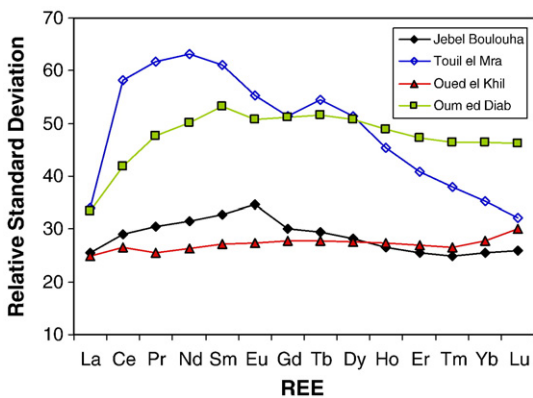


Fig. 7. Relative standard deviation [(Standard deviation/mean) * 100%] of bulk REE composition in bones from Jebel Boulouha (Douiret Formation), Oued el Khil (Chenini Formation), Touil el Mra (Oum ed Diab Formation), and Oum ed Diab (Oum ed Diab Formation). Note greater total variance in REE compositions of bones from the Oum ed Diab Formation and increased variance in light middle REE particularly in bones from the Touil el Mra locality.

Table 2
Matrix of between-group *F* values for REE compositions for the four localities

	Jebel Boulouha	Oum ed Diab	Oued el Khil	Touil el Mra
Jebel Boulouha	0.00			
Oum ed Diab	304.75	0.00		
Oued el Khil	268.24	60.47	0.00	
Touil el Mra	315.72	29.57	66.02	0.00

Bones from Jebel Boulouha exhibits high La/Yb_N ratios and low values of La/Sm_N , whereas most bones from Touil el Mra show the opposite. Bones from Oued el Khil and Oum ed Diab display intermediate values. The within-group variance in REE composition for these ratios also shows significant differences among the four sampled localities (Table 4). Expressed as standard deviations from the mean signatures (Fig. 7), Bones from the Touil el Mra and Oum ed Diab localities in the Oum ed Diab Formation display highly varied LREE compositions, whereas those from Jebel Boulouha and Oued el Khil show relatively consistent signatures. This is supported by the distribution seen in REE values (Fig. 6).

Multivariate analysis of variance (MANOVA) indicates that location significantly affects REE composition of bones (Wilk’s Lambda $F=640$; $DF=16, 345$; $P<0.001$). The between-groups variance matrix indicates that the localities Touil el Mra and Oum ed Diab are the most similar in terms of their REE compositions (Table 2; Figs. 6 and 7).

Jackknifed discriminant analysis was used (Table 3) to assess the degree to which bones from each locality could be distinguished on the basis of their REE compositions (Shale normalised (REE_N) REE ratios $La/Sm_N, La/Yb_N, Dy/Yb_N, Ce/Ce^*$ were used in the classification matrix to avoid effects of absolute concentration). Total classification success was 93%.

In summary, the mean bulk compositions of samples all differ among the four sites (Fig. 6), clearly indicating

Table 3
Jackknifed discriminant analysis classification matrix (samples in row categories classified into columns) for assignment of samples to the correct localities

	Jebel Boulouha	Oum ed Diab	Oued el Khil	Touil el Mra	%correct
Jebel Boulouha	30	0	0	0	100
Oum ed Diab	0	27	2	1	90
Oued el Khil	0	0	29	1	97
Touil el Mra	0	3	2	25	83
Total	30	30	33	27	93

Table 4

Within-group variance table for selected REE ratios from all four localities

	La/Sm	La/Yb	Tb/Yb	Ce/Ce*
Jebel Boulouha	0.004	0.012	0.020	0.001
Oum ed Diab	0.040	0.036	0.038	0.010
Oued el Khil	0.006	0.015	0.015	0.006
Touil el Mra	0.079	0.014	0.046	0.019

significant differences in early diagenetic pore water chemistry among these four environments. The two locations in the Oum ed Diab Formation, Touil el Mra and Oum ed Diab, show the most similar REE compositions, with relatively flat REE signatures, while the REE signatures from Jebel Boulouha and Oued el Khil are enriched in mid-heavy REE with diminishing proportions of the heavier REEs.

6. Discussion

6.1. Taphonomic processes

Combination of the physical, taxonomic, and chemical analyses allows the four sites to be distinguished, and points to major differences in burial conditions through time. These are outlined below, site by site. Time and space averaging is suggested by high levels of abrasion and possibly by the faunal content. Differing levels of variation in REE patterns in bones between sites suggest differences in the number of primary depositional sources, and thus also indicates variation in the extent of mixing. High levels of abrasion coupled with high variance in REE compositions thus implies a temporally and spatially mixed deposit, whereas high levels of abrasion with relatively low levels of REE variation implies time averaging from a limited range of depositional environments.

6.1.1. Jebel Boulouha (Douiret Formation)

The Jebel Boulouha microvertebrates appear to form an attritional time-averaged assemblage, based on the relative abundance of specimens assigned to abrasion stages 1 and 2 (Fig. 3A). This is consistent with the taxonomic mix, with abundant actinopterygian and shark remains, as well as relatively abundant gastropods (Fig. 4C). REE compositions of bones from Jebel Boulouha are relatively consistent, showing relatively low variance which is equally distributed between the REE (Figs. 5 and 7, Table 4), indicating averaging from a limited range of early depositional environments.

6.2. Oued el Khil (Chenini Formation)

The physical and taxonomic results from Oued el Khil also indicate considerable transport of some material, but low levels of mixing. Specimens from the site show the most uniform distribution of abrasion stages (Fig. 3B), suggesting sourcing from a broad range of distances. The specimens are taxonomically diverse (Fig. 4D), including the usual abundant actinopterygian teeth and scales, as well as some gastropods.

The chemical results (Figs. 5–7) suggest that these physical features are a result of time averaging rather than mixing: the REE signatures are all similar, suggesting a single burial environment as the source of most material. Indeed, while mixing is not indicated, time averaging at Oued el Khil may have been more extreme than at any of the other three sites, judging from the wide range of abrasion stages (Fig. 3B).

6.2.1. Touil el Mra (Oum ed Diab Formation)

The Touil el Mra results indicate high levels of mixing and time averaging. The presence of a small number of subrounded and rounded specimens (abrasion stages 2 and 3; Fig. 3C) implies mixing. The taxonomic profile (Fig. 4E) is apparently contradictory in this regard, however, showing a concentration of fish vertebrae, and low abundances of other bony fish remains.

High levels of mixing are borne out by the REE results (Figs. 5–7), which display relatively high variance (Table 4). REE signatures in bones from Touil el Mra can be divided into two groups (Figs. 6 and 7), implying at least two different initial burial environments. The discrepancy between taphonomic and taxonomic results could be explained by taphonomic bias in favour of fish remains derived from a variety of original sources.

6.2.2. Oum ed Diab (Oum ed Diab Formation)

The Oum ed Diab material also suggests some mixing and time averaging. The small number of rounded specimens (Fig. 3D) suggests a mixture of transport regimes. The taxonomic mix, however, is extremely skewed, with little other than *Lepidotes* teeth recorded (Fig. 4F). The breakage of dome-shaped *Lepidotes* teeth indicates that some fossils in the assemblage were transported by high-energy currents, but the site has also yielded delicate *Hybodus* teeth, as well as cephalic and dorsal fin spines (Cuny et al., 2004). There is therefore no differential sorting of hybodont remains (one cephalic and one dorsal fin spine for around 100 teeth corresponds roughly to what would be expected from a single half

individual). These fossils are therefore likely to have different origins. The REE compositions of bones from Oum ed Diab display relatively high variance (Table 4), implying sourcing from a range of initial depositional environments and thus averaging from a relatively complex regional setting.

6.3. Palaeoenvironment and palaeoecology

Compared to a global dataset of REE compositions in fossil bones, samples measured in the current study display intermediate La/Yb_N ratios, relatively enriched in LREE compared to many (but not all) bones from terrestrial environments, and relatively depleted in LREE compared to bones from marginal marine (but not open marine) environments. La/Sm_N and La/Yb_N ratios effectively split bone samples into two groups; samples from the Douiret and Chenini formations (Jebel Boulouha and Oued el Khil) describe a trend of changing La/Yb_N ratios, with little variation in La/Sm_N. Samples from the Oum ed Diab Formation (Touil el Mra and to a lesser extent Oum ed Diab) show greater variation in La/Sm_N ratios (Fig. 6).

The REE patterns in samples from the Douiret and Chenini formations are best explained by recrystallisation of bones in contact with carbonate-rich, high pH groundwaters whose REE patterns evolved towards greater HREE-enrichment via preferential removal of LREE during sorption onto particle surfaces. This is similar to patterns previously reported in bones from alkaline lake sediments (Martin et al., 2005), clay pan sediments (Trueman et al., 2005) and palaeosol sediments (Trueman and Tuross, 2002). By contrast, samples from the Oum ed Diab Formation are relatively scattered, but bones from both the Touil el Mra and Oum ed Diab localities show trends towards increasing enrichment of La over both HREE and MREE. Light REE are preferentially sorbed onto particle surfaces, so the high La/Yb values seen in bones from the Oum ed Diab Formation are best explained by release of REE from light REE-enriched particles to local pore waters and subsequent immobilisation in recrystallising bones. This pattern is similar to trends seen in bones from some coastal and shelf marine settings (Trueman et al., 2003b).

These interpretations suggest that bones from the Douiret Formation and to a lesser extent the Chenini Formation recrystallised in contact with groundwaters where REE were actively removed via sorption onto particle surfaces, and by analogy with modern waters, in terrestrial or marginal marine settings. Bones from both localities in the Oum ed Diab Formation display

trends of increasing LREE enrichment, suggesting recrystallisation in shallow marine settings where REE may be supplied by release from particle surfaces. Interestingly, whereas samples from the Douiret and Chenini formations form discrete groups, samples from Oud ed Diab Formation are relatively mixed, including samples that cannot be distinguished from the Douiret and Chenini formations (e.g. Fig. 6). It is tempting to suggest that the Oum ed Diab Formation assemblages were formed in coastal marine settings and include bones previously fossilised in the terrestrial and marginal marine environments of the Douiret and Chenini formations.

These observations from geochemistry support previous determinations from palaeoenvironmental studies, some of them controversial. Jebel Boulouha had previously been identified as a dominantly freshwater site based on the relative abundance of teeth of the hybodont shark *Priohybodus* (Fig. 4C), a form that was mainly restricted to freshwater conditions (Cuny et al., 2004). The presence of reptile remains at this site, including seven possible teeth and two crocodile scutes, also implies a fluvial influence.

The palaeoenvironmental interpretation of the Chenini Formation, as represented by Oued el Khil, has been equivocal. Bouaziz et al. (1988) argued that the site was marginal, with marine influence indicated by the shark teeth and by putative herring-bone cross-bedding in the sandstones. Benton et al. (2000), on the other hand, argued that the sharks could very well be freshwater, and that the cross-bedding was all related to channels. They interpreted the site as entirely continental. Larger fossils from Oued el Khil seemed to confirm this: they include great logs, as well as abundant dinosaur and crocodylian remains, as well as rarer turtle carapace fragments and a single pterosaur tooth (Bouaziz et al., 1988; Benton et al., 2000). The pterosaur is not indicative of the environment, but the dinosaurs, including abundant teeth and other elements of the characteristic North African theropods *Spinosaurus* and *Carcharodontosaurus*, as well as a medium-sized sauropod and an iguanodontid, were clearly land-livers. The crocodylian remains had been assigned to marine genera, but evidence is unclear. A single putative plesiosaur vertebra is housed in the museum of the Geological Survey of Tunisia — if correctly identified, this is an unequivocal marine animal. According to Lefranc and Guiraud (1990), the Oued el Khil locality was situated in the delta of a large south-to-north flowing river system on the southern margin of Tethys. The dominance of actinopterygian remains at this site (Fig. 4D) suggests a shallow marine provenance, while the dubious reptile claw fragment may have come from upstream.

On balance, then, Oued el Khil, and perhaps most of the Chenini Formation, was deposited in river channels in a distal deltaic region, where marine fishes, plesiosaurs, and possibly marine crocodylians, mixed with rarer freshwater forms. The dinosaur bones and teeth must have been washed in from further inland, although note that these occur in a bed some 1 m below the lens with microvertebrates, and this might represent enough time for a modest transgression.

The Oum ed Diab Formation shows mixed conditions: samples from Oum ed Diab are similar taxonomically to those from Oued el Khil, perhaps reflecting mixed freshwater and marine influences, whereas those from Touil el Mra suggest greater marine influence. The dominance of actinopterygian remains at Touil el Mra (Fig. 4E) supports this interpretation, as does the recent discovery of teeth of the nearshore marine shark *Cretodus* at Oum ed Diab by A. Cobbett. The Oum ed Diab and Touil el Mra localities also display high variance in REE patterns, consistent with high rates of mixing in coastal marine attritional deposits.

The palaeosalinity of the successive formations through the Early Cretaceous of North Africa could be further assessed by a study of strontium and oxygen isotopes in the bone. Oxygen isotope values representative of local rainwater can be determined through chemical analysis of fossil bone (Amiot et al., 2004). This approach is based on the assumption that vertebrates ingested local water, that oxygen isotopes in the rainwater equilibrated in the bone, and that bone either reflects the isotopic composition of early diagenetic pore waters, or retains a pristine biogenic signal.

7. Conclusions

Physical, taxonomic, and geochemical analysis of material from four study sites in the Early Cretaceous of Tunisia indicates these conclusions:

- The Douiret Formation (Aptian; Jebel Boulouha) was deposited in essentially freshwater conditions. The succeeding Chenini Formation (early Early Albian; Oued el Khil) shows evidence for modest transgression. The Oum ed Diab Formation (late Early Aptian) shows a continuation of mixed conditions (Oum ed Diab), and then more fully marine conditions (Touil el Mra).
- Material from the Oum ed Diab Formation is significantly more time and space averaged than from the other two formations.

Previous work has established that REE analysis is a viable method for deducing time averaging and/or

mixing within fossil deposits, and for gaining some hints about specific environmental regimes (e.g. Trueman et al., 2003a, b; Lécuyer et al., 2004; Metzger et al., 2004; Martin et al., 2005). Interpreting REE patterns in fossil bones to recover specific palaeoenvironmental information is complex as the REE composition of groundwaters is controlled by many competing processes. In this study we interpret trends in REE values in populations of bones from single localities to infer evolutionary pathways in groundwaters. Conclusions based on such information are speculative and should be evaluated in the context of independent supporting information. The present study has combined these new geochemical methods with well-established palaeontological and abrasion analysis to interpret of the burial and depositional sites of some differing bone beds. Future studies should compare information from REE analyses with other geochemical environmental proxies (e.g. isotopic composition of Sr and O) together with detailed sedimentological and palaeontological evidence.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2006.07.015](https://doi.org/10.1016/j.palaeo.2006.07.015).

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