Isotopes and Environments of the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates

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While the focus of research on terrestrial fossil vertebrates continues to be morphological and taxonomic, palaeoecological reconstructions have become an established component of site analyses. Embedding faunal evolution within the framework of evolving habitats provides a means of assessing the adaptive significance of morphological and behavioural changes documented in the fossil record. Reconstructing the context of faunal assemblages also provides an opportunity to address one of the central debates in evolutionary theory—the extent to which evolution is driven by perturbations in the physical environment versus biotic interactions. Compilations of site-specific palaeoenvironmental interpretations can ultimately be used to develop detailed regional and global phytogeographic maps of the past and allow us to evaluate how patterns of mammalian evolutionary radiation and intercontinental dispersal are influenced by vegetational changes.

Although it is generally acknowledged that palaeoecological reconstructions are central in understanding evolutionary processes, establishing a detailed and accurate environmental context for fossil assemblages remains problematic. To a large extent, this difficulty is related to the fragmentary nature of the known fossil record, in space and time. Presented with isolated fragments of a modern terrestrial ecosystem such as a random assortment of surface-collected bones, an incomplete assessment of lithofacies, and possibly a leaf or wood specimen, even neocologists would find it difficult unequivocally to identify the habitat from which the collection was made. Generalisations could be made concerning the temperate or tropical nature of the assemblage and habitat-specific faunal elements might provide further insight, but typically a spectrum of habitats could potentially contribute similar elements. Many animals and plants, and in some cases entire communities, tolerate a wide array of environmental circumstances depending on ecological pressures and can occur in variable settings. Animals with extensive ranging patterns, migratory or daily, typically traverse a number of habitats and it is often difficult to associate them with any single discrete vegetational background. The resolution of the reconstruction improves as the size of the sample set increases, especially if the assumption can be made that the components represent an association of interacting organisms (a community) rather than a fortuitous association of fossil taxa. Uncertainties in interpreting data from modern environments occur in spite of the wealth of detailed data documenting ecological aspects of habitats found today. Interpretation of fossil material typically relies on the assumption that modern habitats can provide a template for palaeohabitat reconstructions. This uniformitarian approach may not in all cases be valid as it is possible that no modern analogues exist for specific ecosystems in the past.

Palaeontologists, working with fragments of palaeoecosystems, face the daunting task of reconstructing the interplay of environment, ecology, and evolution while simultaneously defining each of these parameters. Many different approaches have
been taken in reconstructions of terrestrial palaeoenvironments, including an assessment of lithofacies, ecomorphology (Kappelman, 1991; Plummer and Bishop, 1994), palaeocommunity reconstructions (Andrews et al., 1979; Andrews, 1996), indicator species, palaeobotanical evidence, and inferences based on the global climatic record documented in marine cores. Despite the innovative and circumstantial nature of these analyses, taphonomic and interpretive biases are inherent in deciphering the fossil record and it has become increasingly clear that accurate and high-resolution reconstructions need to draw from as many lines of evidence as possible. Within the past decade, stable isotopic analyses of palaeosol components and fossil herbivore enamel have been used to help constrain interpretations of the vegetational physiognomy of palaeohabitats as well as dietary items available for herbivore foraging.

**ISOTOPIC VARIATION AND PHOTOSYNTHETIC PATHWAYS**

The underlying premise for reconstructing palaeovegetation by isotopic analyses of palaeosol carbonates and tooth enamel is that terrestrial plants using different photosynthetic pathways under varying environmental conditions can be differentiated on the basis of the relative abundance of two naturally occurring stable isotopes of carbon, $^{12}$C and $^{13}$C (Farquhar et al., 1989). Plants assimilate carbon from the atmospheric CO$_2$ reservoir by one of three photosynthetic pathways. These pathways, typically referred to as C$_3$ (Calvin–Benson), C$_4$ (Hatch–Slack or Kranz), and CAM (crassulacean acid metabolism), represent adaptations to different atmospheric and climatic conditions. In general, carbon incorporated into the organic matrix of vegetation during photosynthesis is significantly depleted in the heavy isotope ($^{13}$C) relative to atmospheric CO$_2$, which currently has an isotopic composition ($\delta^{13}$C) of $-7.8$ per mil ($\%$) (Keeling et al., 1989). C$_3$ plants are most depleted whereas plants endowed with the C$_4$ metabolic pathway are least depleted. Plants that fix CO$_2$ by CAM display intermediate values overlapping the range of both C$_3$ and C$_4$ flora. Essentially all of the isotopic separation or fractionation during plant metabolism is associated with initial phases of carbon fixation involving the uptake of CO$_2$ into the tissue and subsequent conversion into organic compounds (Craig, 1953; Park and Epstein, 1961; Smith and Epstein, 1971; Farquhar et al., 1982; O’Leary, 1981). Distribution of carbon isotopes among C$_3$, C$_4$, and CAM plants is related to a difference in the isotopic fractionation associated with the activity of RuBPC in all plants and PEPC activity in C$_4$ and CAM plants.

C$_3$ plants dominate terrestrial environments and account for approximately 85% of all plant species, including almost all trees, shrubs, and high-latitude/altitude grasses preferring wet, cool growing seasons. C$_3$ flora has a mean $\delta^{13}$C value of $-27.1 \pm 2.0\%$ (O’Leary, 1988) with a range extending from $-22$ to $-38\%$, reflecting genetic and environmental factors (fig. 25.1). Environmental influences affecting the $\delta^{13}$C of C$_3$ plants include water stress, nutrient availability, light intensity, CO$_2$ partial pressure, and temperature (Farquhar et al., 1982; Toft et al., 1989; Tieszen, 1991). Overall, the $\delta^{13}$C value of C$_3$ plants tends to be most positive in open, arid, and hot habitats and most negative in cool, moist, and forested environments. In closed-canopy understories, where free exchange with atmospheric CO$_2$ is restricted, CO$_2$ can become substantially depleted, resulting in even more negative values (Sternberg et al., 1989; van der Merwe and Medina, 1989). As altitude increases, the partial pressure of CO$_2$ decreases, resulting in increased CO$_2$ uptake by plants and more positive $\delta^{13}$C values for C$_3$ plants (Tieszen et al., 1979; Körner et al., 1988) with differences of up to 2.6% in individual species (Körner et al., 1988). These environmental factors, coupled with genetic differences, result in substantial variations in stable carbon isotopes that need to be considered when attempting to estimate relative proportions of C$_3$ and C$_4$ plants in the past either by analysing preserved organic matter or proxies for palaeovegetation.

C$_4$ physiology is linked almost exclusively to monocots, especially grasses and sedges growing in
hot, arid habitats. A mean $^{13}$C value of $-13.1 \pm 1.2\%$ has been calculated for $C_4$ plants (O’Leary, 1988) with a range of $-9$ to $-15\%$ (fig. 25.1), or about half that of $C_3$ plants. The $C_4$ photosynthetic pathway represents a modification of the $C_3$ mechanism and is considered to have evolved independently at least 26 times (Peisker, 1986) as a response to either depressed atmospheric CO$_2$ levels relative to O$_2$ or to water-stressed environments (Woodward, 1990; Ehleringer, 1991). The CO$_2$ concentrating mechanism of $C_4$ plants increases the carbon-fixing efficiency during photosynthesis and $C_4$ vegetation generally tolerates higher temperatures, drier conditions, and lower atmospheric pCO$_2$ levels than $C_3$ species. $C_4$ photosynthesis, however, is energetically more costly (Salisbury and Ross, 1985) and $C_4$ vegetation is outcompeted by $C_3$ plants at temperatures below 25 °C and at higher pCO$_2$ levels.

Crassulacean acid metabolism (CAM) has evolved independently in many succulent plants
including the cacti (Cactaceae) and stonecrops (Crassulaceae). Like C₄ plants, they utilise both the C₃ and C₄ pathways but CAM plants differentially utilise the two pathways depending on environmental conditions, which results in δ¹³C values that span the range of values covered by C₃ and C₄ plants (Deines, 1980; O'Leary, 1981). Under high light intensity or high temperatures, CAM vegetation has C₄-like values whereas under environmental conditions such as low light intensity, cold temperatures, or long days, it has C₃-like values. Although CAM plants can endure extremely xeric conditions their ability to take in and fix CO₂ is severely limited. In general, therefore, they compete poorly with C₃ and C₄ plants under less-extreme conditions. Generalised habitat reconstructions based on assumed ecological preferences of fossil fauna recovered from the Baynunah Formation suggest that it is highly unlikely that CAM plants comprised a significant component of the biomass during Baynunah times.

As the C₃ and C₄ photosynthetic pathways are associated with different environmental conditions and plant physiognomy, documenting relative proportions of C₃ and C₄ vegetation by isotopic analyses is a useful tool in palaeoenvironmental reconstructions. Specifically, the link between C₄ metabolism and grasses provides a means of differentiating open woodland/grassland landscapes from forested ecosystems in the past. In general, an increase in the proportion of C₄ grasses can be interpreted as representing a decrease in canopy cover. While a C₄ carbon signal implies arid grasslands, a C₃ value can reflect a variety of habitats, ranging from lowland rainforest to arid bushland, which limits the resolving power of a C₃ isotopic signal in reconstructing vegetation. The key to using this relationship is developing a means of retrieving an intact record of the relative proportions of C₃ and C₄ vegetation in the fossil record. As it turns out, several approaches can be used to recover this isotopic record, including isotopic analyses of preserved organic matter, of palaeosol carbonate formed in isotopic equilibrium with palaeovegetation, and of carbon incorporated within fossil bone or enamel—a reflection of available dietary plants.

**Palaeosols and Pedogenic Carbonates in the Baynunah Formation**

Theoretical models and studies of modern soils have established a correlation between the stable carbon and oxygen isotopic composition of soil components and prevailing climatic and ecological conditions (Cerling, 1984; Amundson et al., 1987; Quade et al., 1989; Kelly et al., 1991). In general, the carbon isotopic composition of soil CO₂ and of soil carbonate precipitated in equilibrium with soil CO₂ is controlled by the proportion of surface vegetation utilising the C₃ or C₄ photosynthetic pathway. When CaCO₃ precipitates, its stable carbon and oxygen isotope ratios are determined by that of HCO₃⁻. The total amount of dissolved carbon in the soil solution, however, is relatively small and it has been demonstrated experimentally that when CO₂ gas is present, the gas phase controls the isotopic composition of the CO₃²⁻ and in turn that of the precipitating carbonate (Bottinga, 1968). Soil CO₂ is a function of mixing from two isotopically distinct sources, biologically respired CO₂ and atmospheric CO₂ (Amundson et al., 1989: Quade et al., 1989). Biologically respired CO₂ refers to CO₂ derived from microbial oxidation of soil organic matter and root respiration. The carbon isotopic composition of biologically derived CO₂ reflects the proportion of C₃ versus C₄ biomass in the local ecosystem and averages about −27‰ when the plant cover is C₃ dominated to about −13‰ when the vegetation is predominantly C₄ grasses (Deines, 1980). At respiration rates typical for temperate and subtropical ecosystems during the growing season (8 mmol/m² per hour) (Singh and Gupta, 1977), the carbon isotopic composition of the soil atmosphere is overwhelmingly a function of respired plant CO₂ and closely reflects the C₃/C₄ plant ratio. In arid or semi-arid climates where plant activity is greatly reduced, the soil CO₂ incorporates a larger atmospheric input resulting in more positive δ¹³C values for soil CO₂. In addition to the input of atmospheric and biologically respired CO₂, the isotopic composition
of soil CO₂ and, ultimately, pedogenic carbonate is a function of several factors and processes, which include soil porosity, soil temperature, mean production depth of soil CO₂, absolute pressure, and the depth within a soil profile (Cerling, 1984). As a result of ¹³C enrichment due to fractionation during gaseous diffusion and carbonate precipitation, pedogenic carbonates forming at 35°C and 15°C are enriched by about 14% and 15.5%, respectively, relative to biologically respired CO₂ (Dorr and Munnich, 1980; Friedman and O’Neil, 1977).

**Baynunah Palaeosols**

Interbedded within fluvial and floodplain sediments of the Baynunah Formation are a number of palaeosol horizons, which are most conspicuous within the upper portion of the succession. Palaeosols were in general not well developed and in some cases difficult to unequivocally differentiate from fine-grained floodplain facies. Only horizons clearly displaying several pedogenic features were sampled. Criteria for the recognition of palaeosols include destruction of primary bedding resulting in a hacky outcrop weathering pattern, bioturbation, slickensides, root or burrow motting, carbonate nodule concentrations, and gradational boundaries with underlying lithology. Organic-rich A-horizons were not observed; the palaeosols typically consist of grey or reddish carbonate-leached Bt-horizons ranging from 30 cm to over 2 metres thick. Poorly developed coarse- to medium-grained palaeosols were also evident towards the middle of the formation, suggesting development on aeolian sands. Pedogenic carbonate nodules were associated with a limited number of palaeosol horizons and typically occurred near the base of the palaeosol profile. Nodules were sampled at depths of more than 40 cm in the soil profile to minimise potential mixing of isotopically heavy atmospheric CO₂ with biologically respired CO₂ during carbonate precipitation (Cerling et al., 1989). The carbon isotopic signature of soil organic matter also reflects local plant cover, and analysis of the preserved organic residue in palaeosols can constitute a test of the state of preservation of the original ecological signal in the palaeosol components (Cerling et al., 1989). Preliminary attempts to isolate organic matter from Baynunah palaeosols have been unsuccessful, presumably due to oxidation of the original organic residue.

A prominent feature of some palaeosols are complexes of root casts comprised of celestine (Whybrow and McClure, 1981). Originally described by Glennie and Evamy (1968), these root-like structures were interpreted as having been formed in a wadi environment within a desert. Whybrow and McClure (1981) subsequently suggested that these root structures might represent fossilised mangrove roots, indicating a more tropical rather than arid climatic regime for the region. More recent interpretations of these structures (P. J. Whybrow, personal communication) have cast doubt on a mangrove origin and microscopic examination of root casts has instead revealed morphology with affinities to the family Leguminosae, which includes lianas, laburnums, and acacias (Whybrow et al., 1990).

**Methods and Materials**

Pedogenic carbonate nodules were rinsed in double-distilled water (ddH₂O) to remove adhering detrital material, soaked in 0.1M HCl for 30 seconds to dissolve potentially contaminating diagenetic surficial CaCO₃, rinsed twice more in ddH₂O, and dried in an air convection oven at 75°C. Nodules were then pulverised to less than 0.5 mm in an agate mortar, which was carefully cleaned with ddH₂O and 0.1M HCl between samples to avoid cross-contamination. Crushed nodules were baked under vacuum at 475°C for 1 hour (8-hour cool down) to eliminate any organic matter. Carbon within the nodules was then converted to CO₂ by reacting the powder with 100% H₃PO₄ in individual evacuated reaction vessels overnight at 25°C in a constant temperature waterbath. The CO₂ released was manually collected by cryogenic distillation on a glass vacuum line in 6 mm ampules, which were then analysed on a Finnigan MAT 251 isotope ratio mass spectrometer.
Differences in the carbon isotopic composition of substances are expressed as $\delta^{13}C$ values, which give the per mil deviation of the $^{13}C / ^{12}C$ ratio of a sample relative to that of the conventional Pee Dee Belemnite carbonate standard (PDB), which has a $^{13}C / ^{12}C$ value of 88.99. Positive values of $\delta^{13}C$ indicate an enrichment of heavy carbon ($^{13}C$) in the sample relative to the standard whereas negative readings stand for its depletion. The $\delta^{13}C$ ratio is defined by the following equation:

$$\delta^{13}C (\%o) = \left[ \frac{^{13}C / ^{12}C}_{\text{sample}} \right] - 1 \times 1000$$

Analysis of an internal standard in conjunction with carbonate nodule samples yielded a standard deviation of $\pm 0.03\%o$ ($n = 20$). Replicate analysis of four samples resulted in a standard deviation of $\pm 0.06\%o$. Overall analytical precision is better than $0.1\%o$.

**Results and Interpretation**

Isotopic analyses of 15 palaeosol carbonate nodules collected from four fossil localities—Hamra (site H5), Shuwaihat, Kihal (site K1), and Jebel Barakah—in the Bayunah Formation indicate an average $\delta^{13}C$ of $-5.5\%o$ with a range of $-9.0$ to $-2.2\%o$ (table 25.1 and fig. 25.2). With the possible exception of three samples from the locality of Hamra (with $\delta^{13}C$ values of $-8.6$ to $-9.0\%o$), nodular $\delta^{13}C$ values indicate formation in soils in which biologically respired CO$_2$ was derived from both C$_3$ and C$_4$ vegetation. Although it is impossible unequivocally to correlate palaeosol horizons between the different localities, all samples were collected from palaeosol profiles intercalated within fluvial/floodplain facies of the upper Bayunah Formation, less than 15 metres stratigraphically below the gypsum-bearing cap-rock facies. The extent to which these horizons are correlative depends on whether the cap-rock at the various localities reflects primary...

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<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Locality</th>
<th>Site no.</th>
<th>Sample</th>
<th>$\delta^{13}C (%o)$</th>
<th>$\delta^{18}O (%o)$</th>
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<tr>
<td>AD 636a</td>
<td>Jebel Barakah</td>
<td>JB2</td>
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</tr>
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deposition in a contemporaneous late Miocene sabkha environment or instead reflects a secondary diagenetic feature (Ditchfield, 1999—Chapter 7).

Reconstructions of the Bayunahah habitat based on these data depend on assumptions about how the $\delta^{13}$C variation is partitioned within the sequence. At each locality, except Shuwaihat, carbonates were collected from palaeosol horizons at different stratigraphic levels in the local sections. Although there are distinctive differences in $\delta^{13}$C values vertically in the section at each locality (table 25.1), there is no consistent trend towards enrichment or depletion of $\delta^{13}$C values, reflecting an increase or decrease in $C_4$ vegetation, respectively, through time, moving upsection at the various localities. At Khial, for example, the $\delta^{13}$C value of the youngest measured palaeosol carbonate is 2.5% more positive than that of an underlying palaeosol whereas at Hamra, the younger palaeosol has carbonates depleted by over 5% relative to an older horizon (table 25.1 and fig. 25.3).

In addition to sampling vertically, at the locality of Hamra, two palaeosol horizons were sampled laterally to assess local heterogeneity in $C_3$ and $C_4$ vegetation at each level (fig. 25.3). Carbonates from the upper soil profile (H12) range from $-9.0\%$ to $-5.9\%$, indicating a grassy woodland type of environment in which $C_3$ and $C_4$ vegetation was unevenly distributed across the landscape. The lower palaeosol sampled at Hamra yielded carbonates with more positive $\delta^{13}$C values, indicating a significantly greater $C_4$ component (and more open environment) although only two carbonate nodules were analysed.

Other than closed canopy forest or open grasslands, isotopic analyses of modern vegetation and soil carbonates/organic matter (Tiezen, 1991; Kingston, 1992; Handley et al., 1994; Kingston et al., 1994; Sikes, 1994) indicate that many tropical habitats are isotopically heterogeneous, which reflects localised variation in $C_3/C_4$ vegetation related to differences in drainage, bedrock, topography, and rainfall. Fluvial/flood plain lithofacies associated with the Bayunahah palaeosols indicate that soils formed near a river system that may have supported a mosaic environment ranging from more forested conditions along the river levee to more open woodland/grasslands on adjacent
floodplains. Evidence for vegetational heterogeneity in the Hamra palaeosol horizon also has potentially important implications for interpreting the vertical variation in the succession. Rather than reflecting vegetational change between the palaeosol levels, these differences may in fact reflect sampling of different microhabitats within a persisting mosaic landscape. A shifting of ecotones associated with lateral migration of the river system within the floodplain could result in a riverine woodland gallery being superimposed over a more open floodplain environment, as implied by the palaeosols at Hamra. Such a scenario does not require invoking a widespread transformation from wooded grassland to more forested vegetation in the relatively short interval of time represented by sediments intercalated between the palaeosols at Hamra as well as the other localities sampled.

Although isotopic values suggest a grassy woodland-type environment, the specifics of the environment remain unknown. Ascribing specific percentages of C3 and C4 biomass for the different δ13C values is problematic because the final isotopic composition of pedogenic carbonate is ultimately a function of the isotopic composition of vegetation, which varies significantly for both C3 and C4 vegetation. An attempt to estimate the relative contribution by C3 and C4 vegetation for the average isotopic composition of pedogenic carbonate from the Baynunah sequence, ~5.5%, illustrates the difficulties. Assuming an average δ13C of −23‰ and −13‰ for C3 and C4 plants, respectively, and a 15% CO2-CaCO3 phase transformation fractionation (Cerling, 1984), a −5.5‰ value indicates that 75% of the biomass was C3. This percentage, however, drops to about 50% if C3 and C4 vegetation had instead average δ13C values of −28‰ and −12‰, respectively. Temperature-sensitive fractionation factors during carbonate precipitation (Dienes et al., 1974; Friedman and O’Neil, 1977) and assumptions regarding a correction factor for pre-industrial δ13C values of atmospheric CO2 (Marino and McElroy, 1991) can add another 2–3‰ of uncertainty when interpreting the δ13C of soil carbonates as a proxy for vegetation. Despite these limi-
lations, the link between a C₄ signal and tropical open-habitat grasses provides valuable clues to the physiognomic types of tropical plant paleocommunities and the extent to which they were dominated by C₃ or C₄ biomass.

**ISOTOPIC ANALYSIS OF FOSSIL ENAMEL AND PALEODIETARY RECONSTRUCTIONS**

A corroborative approach to palaeosol carbonate analysis in documenting relative proportions of C₃ and C₄ vegetation in the past is an analysis of the isotopic signature of carbon incorporated into the inorganic fraction of fossil tooth enamel. It has been well established that the carbon isotopic composition of modern herbivore tissue, including bone and teeth, is directly related to the Δ¹³C value of the primary photosynthesising plants in the food chain (DeNiro and Epstein, 1978; Tieszen et al., 1983; Ambrose and DeNiro, 1986). Because of physiological fractionation effects, the enamel of mammalian herbivores is consistently enriched by about 12.5% relative to diet in terrestrial ecosystems (Krueger and Sullivan, 1984). The relationship between the carbon isotopic composition of body tissue and diet was initially exploited primarily to address archaeological issues such as the introduction of maize, a C₄ domesticate, into previously C₃-dominated New World agricultural economies (Vogel and van der Merwe, 1977; van der Merwe and Vogel, 1978; Schoeninger and Moore, 1992). In almost all of these studies, isotopic analysis focused on collagen, the major constituent of the organic phase of bone. Hydrolysis and dissolution of collagen during fossilisation, however, limits its use to the past few thousand years and in extending these techniques to fossil assemblages, isotopic analysis has concentrated on the mineral portion of bone and teeth. Application of isotopic analyses to fossil specimens has been controversial, primarily due to the difficulty in assessing diagenetic alteration and differential offsets in diet-tissue Δ¹³C related to trophic-level effects (Sullivan and Krueger, 1981, 1983; Schoeninger and DeNiro, 1982, 1983; Krueger and Sullivan, 1984). Studies have shown that bone apatite is an isotopically unreliable substrate, even for relatively young specimens (5000–10 000 years old), and palaeodietary reconstructions have instead relied on analysis of carbonate occluded within the mineral phase of enamel. Enamel, like the inorganic portion of bone, is a highly substituted, nonstoichiometric hydroxyapatite containing primarily calcium, phosphate, and hydroxide ions (Ca₁₀(PO₄)₆(OH)₂) (Eanes, 1979). Carbonate substitutes for both phosphate and hydroxide ions in several positions within the crystal lattice and constitutes between 2 and 4% of the apatite by weight (Brudevold and Søremark, 1967; Rey et al., 1991). Enamel apatite differs significantly from bone apatite in that it is more crystalline, less porous, denser, and has substantially less organic matrix than bone apatite. These features limit potential pathways for infiltration of calcite and minimise the effects of ionic and isotopic exchange during fossilisation (Lee-Thorp, 1989; Glimcher et al., 1991). In addition, the larger crystal size of enamel apatite, relative to bone apatite, provides less surface area per unit weight, which dramatically reduces reactivity. These attributes have led to the recognition of enamel apatite as a much more suitable substrate than bone apatite for dietary reconstructions.

Isotopic analyses of an extensive suite of fossil taxa collected from various South African archaeological and fossil sites (Lee-Thorp, 1989; Lee-Thorp et al., 1989a) provide empirical support for the use of fossil enamel carbonate as a proxy for the relative proportions of C₃ and C₄ components in the diet. Fossil grazers (C₄-dominated diet), browsers (C₃-dominated diet), and mixed or intermediate feeders (combination of C₃ and C₄ diet), distinguished on the basis of microwear analyses, cranial and dental morphology, and taxonomic affinity to extant ungulate species, consistently yielded Δ¹³C values that reflected the expected dietary signal. Ericson et al. (1981) determined the Δ¹³C value of enamel apatite from Pliocene herbivore fossils dating to 2 million years ago and reconstructed diets based on isotopic analysis that are in accord with those inferred by analogy to closely related modern taxa. Application of isotopic
analyses to fossil enamel strictly for palaeodietary interpretation has been limited, however (Ericson et al., 1981; Lee-Thorp et al., 1989b), and instead its use has been primarily for palaeoecological reconstruction (Thackeray et al., 1990; Kingston, 1992; Quade et al., 1992; Wang et al., 1993; Kingston et al., 1994; MacFadden et al., 1994; Morgan et al., 1994; Quade et al., 1994; Quade et al., 1995).

Methods

Factors controlling the isotopic alteration of biogenic hydroxyapatite are poorly understood. Successful isotopic analysis of enamel apatite for palaeodietary reconstruction depends on the extent to which biogenic structural carbonate is segregated from diagenetic carbonate. In general, the strategy is to digest any organic material associated with the apatite using one of a variety of oxidants such as sodium hypochlorite (NaOCl), hydrogen peroxide (H2O2), or hydrazine (NH2NH2) (Koch et al., 1989; Lee-Thorp and van der Merwe, 1991) and to remove any secondary carbonate by dissolution in acetic acid (CH3COOH), hydrochloric acid (HCl), or triammonium citrate ((NH4)3C6H5O7) (Hassan et al., 1977; Sillen, 1986; Lee-Thorp and van der Merwe, 1991). Presumably the more exchangeable carbonates (bicarbonates) associated with the hydration layer, exogenous carbonate such as calcite, and structural apatite close to crystal surfaces or along dislocations that has experienced significant incorporation of secondary carbonate will dissolve during acid treatment, leaving biogenic structural carbonates. Although X-ray diffractometry and infrared spectroscopy provide a means of monitoring the presence of a diagenetic calcite phase or the degree of apatite recrystallisation, there are no methods for distinguishing between structural biogenic and structural diagenetic carbonate. Different pretreatments can have profound effects on the mineralogy and isotopic composition of the remaining apatite (Lee-Thorp and van der Merwe, 1991). In this study, the basic methodology outlined by Lee-Thorp (1989) has been followed with a few modifications.

Enamel was carefully cleaned of adhering matrix, dentine, and weathering rinds with a high-speed dremel drilling tool and then ground in an agate mortar. Powdered enamel (50–130 mg) was reacted for 24 hours with 2% NaOHCl in 50 ml plastic centrifuge tubes and then rinsed to a pH of 7 by centrifugation with ddH2O. The residue was treated with 0.1M CH3COOH for 16 hours under a weak vacuum, rinsed to neutrality by centrifugation with ddH2O, and freeze-dried. The dried samples (30–100 mg) were reacted with 100% phosphoric acid (H3PO4) at 90°C in sealed borosilicate reaction tubes for 48 hours. The liberated carbon dioxide was cleaned and separated cryogenically and then analysed on a MAT-Finnegan 251 mass spectrometer. Precision was ± 0.11‰ for δ13C ratios of four replicate pairs of fossil enamel. A laboratory standard analysed with the enamel samples yielded a standard deviation of ± 0.07‰ (n = 5). Based on these data, overall analytical precision was better than 0.2‰.

Results and Interpretation

Stable carbon isotope data from 33 specimens from at least 10 herbivore species representing 5 families is presented in table 25.2 and in figure 25.4. δ13C values, ranging from -10.4 to + 0.9‰ suggest that although both C3 and C4 plants were available as dietary sources, most of the taxa analysed either relied on a mixed C3/C4 diet or were exclusively grazers consuming C4 grasses. Only several specimens (Giraffidace gen. et sp. indet., one of the Tragoparvus cyanicus samples, and possibly some of the Hipparion samples) yielded 13C-depleted values (less than 8‰) consistent with a predominantly browsing (C3) foraging strategy.

Based on dental and postcranial morphology, the Bayunahipparion material is attributed to two species (Eisenmann and Whybrow, 1999— Chapter 19), a small to middle-sized hipparion representing a new species (Hipparion abudhabiense), and a middle-sized to large Hipparion sp. Eisenmann notes that although H. abudhabiense had a relatively short and broad muzzle—suggesting grazing rather than browsing habits—it also retains primitive characters, which are interpreted as poor adaptations to abrasive foods such as C4 grasses.
<table>
<thead>
<tr>
<th>Sample no.</th>
<th>AUH or BMNH* no.</th>
<th>Tooth</th>
<th>Material</th>
<th>Genus and species</th>
<th>Family</th>
<th>Site no.</th>
<th>$\delta^{13}$C(‰)</th>
<th>$\delta^{18}$C(‰)</th>
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</thead>
<tbody>
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<td>M49464*</td>
<td>Fragment</td>
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<td>-2.62</td>
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<td>46</td>
<td>Fragment</td>
<td>Enamel</td>
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<td>H5</td>
<td>-3.61</td>
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</tr>
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<td>Material</td>
<td>Genus and species</td>
<td>Family</td>
<td>Site no.</td>
<td>δ¹³C(‰)</td>
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<td>231a</td>
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<td>Enamel</td>
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<td>Equidae</td>
<td>H5</td>
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<td>-3.84</td>
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<td>Enamel</td>
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<td>Enamel</td>
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<td>Equidae</td>
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<td>-7.26</td>
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<td>Enamel</td>
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<td>-4.94</td>
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<tr>
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<td>Giraffidae</td>
<td>R2</td>
<td>-2.69</td>
<td>1.92</td>
</tr>
</tbody>
</table>

Locality abbreviations: B, Jebel Barakah; S, Shuwaihat; H, Hamra; JD, Jebel Dhanna; R, Ras Dubay’ah; K, Kihal; TH, Thu- mayriyah.
Isotopic analyses of enamel attributed to *H. abudhabiense* indicates a wide range of food sources in the diet, ranging from exclusively C₄ grasses to predominantly C₃ plants (more than 80% C₃). Three specimens yielded isotopic values consistent with dedicated grazing (δ¹³C more than −1‰) while the remaining specimens indicate mixed grazing and browsing strategies with an emphasis on grazing. The range of isotopic values for the larger hippo- parion species (−7.4 to −0.4‰) is indistinguishable from that of *H. abudhabiense* and also indicates an intermediate grazing strategy.

The isotopic signature of enamel fragments of giraffid species from the Baynunah succession (Gentry, 1999b—Chapter 22)—Giraffidae gen. et sp. indet., and *?Braamatherium* sp.—appear to indicate ecological partitioning. Two specimens of *Braamatherium* sp. from the locality of Ras Dubay’ah yielded δ¹³C<sub>enamel</sub> values of −1.6‰ and −2.6‰, indicating a dietary intake in the range of −16 to −14‰, which is essentially a pure C₄ diet. A third enamel fragment from the same locality had a value of −5.6‰, suggesting a mixed C₃/C₄ diet. These data suggest that, unlike both extant members of the Giraffidae (which are specialised browsers), the foraging strategy of the extinct Baynunah giraffid was dominated by grazing. While these results are in general at odds with conventional assumptions regarding the foraging behaviour of giraffids, a grazing strategy has been suggested for Miocene giraffids. Hamilton (1973) characterised members of the family Sivatheriidae as having short necks and limbs and suggests that they “fed near the ground and grazing forms may have developed”. Meladze (1964) hypothesised that the sivatheriids were adapted to life in the savannah. Based on pre-maxillary shape analysis and quantitative analysis of tooth microwear, Solounias et al. (1988) suggested that the Miocene giraffid *Samotherium boissieri* had dietary adaptations most similar to committed grazers and could have occupied a grazing niche. Of nine late Miocene herbivore species analysed from Samos, Greece (Quade et al., 1994), *Samotherium boissieri* had the most enriched values in δ¹³C (−5.4‰), which was interpreted to indicate that it preferred moisture-stressed C₃ plants, possibly C₃ grasses, or had a C₄ component in its diet. Isotopic analyses of fossil giraffid enamel apatite derived from other sequences, *Samotherium* sp. from the late Miocene of Kemiškitepe, Turkey (Bocherens et al., 1994), *Giraffokeryx punjabiensis* and *Braamatherium megacephalum* from middle–late Miocene
strata of the Siwalik sequence in Pakistan (Morgan et al., 1994), Pliocene *Giraffa camelopardalis* from Makapansgat, South Africa (Lee-Thorp and van der Merwe, 1987), and *Giraffa gracilis* from the Pliocene Shungura Formation of Ethiopia (Ericson et al., 1981), yield δ13C values between -9.8 to -13.2‰, implying that these forms were all obligate browsers. The δ13C enamel value of the other Baynunah giraffid analysed, Giraffidae gen. et sp. indet., reflects a C3 diet indicative of a dedicated browser. Isotopic variation in the enamel of the two different giraffids collected from the same locality also provides evidence that diagenetic overprinting is not a factor in the isotopic signal in Baynunah fossil enamel as δ13C enamel Values would be expected to converge rather than yield such contrasting values.

Enamel from an elephantid (*Stegostetrabelodon* sp.) (n = 3; see Tassy, 1999—Chapter 18) and hippopotamus (*Hexaprotodon aff. sahlbenensis* (n = 3; see Gentry, 1999a—Chapter 21) analysed from the Baynunah sequence indicates a strong dietary reliance on C4 grasses. For both of these taxa, two samples plot within or very close to the δ13C range of an exclusive C4 grazer, while one specimen for each suggests a more diverse, mixed C3/C4 diet. The bovid enamel reflects diverse foraging strategies ranging from committed browsing for *Tragopornax* sp. to a grazing habit for *Pachyportax latidens*.

**Conclusions**

Stable carbon isotopic values of palaeosol carbonate collected from the upper Baynunah Formation record the presence of C3 and, to a lesser extent, C4 vegetation at the time during which the soils formed. Lateral variability in the δ13C of pedogenic carbonate collected from the locality of Hamra implies a heterogeneous environment. None of the palaeosol carbonates analysed yielded δ13C values indicative of open C4 grassland. Vertical variability in the isotopic composition of palaeosol carbonates from local sections could reflect shifts in the relative proportions of C3 and C4 vegetation through time but this variation most likely represents an artifact of insufficient lateral sampling. If C3 and C4 are heterogeneous in the landscape, randomly selected palaeosol carbonates would reflect microhabitats within a mosaic environment rather than provide an overall estimate of vegetation in a region. Without extensive lateral sampling, apparent shifts in the δ13C of pedogenic carbonate through a local section could simply reflect variable sampling of different microhabitats within similar ecosystems. Palaeosols sampled at the various fossil localities were all less than 15 metres stratigraphically below the cap-rock. If the cap-rock unit is correlative between the localities then the palaeosol levels are roughly penecontemporaneous. As it is unlikely that there were significant changes in habitat during this interval, it is not unreasonable to pool the data from the various levels at the different localities to interpret the data from the upper Baynunah Formation. The range of δ13C values represented by a compilation of Baynunah palaeosol carbonate analyses is most consistent with a grassy woodland ecosystem.

Unlike isotopic analyses of palaeosol components that directly reflect aspects of palaeovegetation, analyses of fossil herbivore enamel as a proxy of vegetation must be interpreted through a series of filters as there is no definitive correlation between diet and habitat. In general, browsers inhabit forested ecosystems, grazers more open woodland and grassland habitats, and mixed feeders are ecotonal. There are modern grazing ruminants, however, that inhabit forests and browsers occur in open grasslands. In addition to dietary selection by animals, competitive exclusion, migration, and immigration present confounding factors that need to be carefully considered in translating palaeodietsignals into palaeoenvironmental reconstructions. The strategy in reconstructions of the Baynunah environment based on the isotopic composition of herbivore enamel involves sampling a wide range of taxa that would incorporate both grazing and browsing feeding strategies and potentially reflect relative proportions of C3 and C4 vegetation in the habitat. While an analysis of 34 specimens representing five herbivore families indicates that both C3 and C4 plants were available for
consumption, there appears to be a heavy reliance on C₄ grasses with a number of specimens from various taxa falling within the isotopic niche occupied by committed grazers. Only a few specimens plotted within the range of obligate browsers. Of the specimens indicating a mixed grazing and browsing strategy, most of the isotopic values suggest a major C₄ component. These data would appear to imply a more open environment than that reflected by the paleosol carbonates.

In contrasting environmental reconstructions of the Baynunah habitats based on the paleosol and enamel isotopic datasets, it should be noted that the two types of data reflect different spatiotemporal aspects of the ecosystem. Paleosol carbonates typically form over hundreds or even thousands of years and thus preserve a paleoenvironmental record averaged over an interval spanning many generations of plants. Lateral migration of CO₂ in soil profiles is limited and the δ¹³C of pedogenic carbonate is controlled by the local plant cover in an area of less than 10 m². Unlike the mineral portion of bone, which is in a constant state of flux during an organism’s life span, carbonate is incorporated into the apatite crystal lattice during vertebrate tooth formation only and remains sequestered from subsequent physiological activity during life. As such, the carbon in enamel apatite records the diet for a relatively brief interval of time relative to the formation of paleosol carbonate. In addition, as noted earlier, herbivores can have extensive ranging patterns and the diet may reflect vegetation sampled from a variety of habitats over a large area. In reconciling the enamel and paleosol isotopic profiles from the Baynunah Formation two scenarios seem most plausible. Possibly, the herbivore population, dominated by grazers and intermediate feeders, were selectively grazing on C₄ grasses within a regionally extensive grassy woodland environment. Alternatively, and more likely, the environment was heterogeneous and the paleosol carbonates sampled formed in more wooded environments flanking a river system while many of the herbivores grazed in more open grasslands or wooded grasslands distal to the fluvial environments represented by the Baynunah sediments.

ACKNOWLEDGEMENTS

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