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Distinguishing the diets of coexisting fossil theridomyid and glirid rodents using carbon isotopes☆

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Abstract

Carbon isotope analyses were conducted on the teeth of four species of rodents and associated plant fossils from the Late Eocene–Early Oligocene Solent Group of the Hampshire Basin, UK. Results indicate that there is no detectable difference in the overall mean $\delta^{13}C$ values between permanent cheek teeth of the two species of theridomyid, *Thalerimys fordi* and *Isoptychus* sp. This accords with their very similar teeth that indicate comparable diets. However, the teeth of the two species of glirid (dormouse), *Glamys priscus* and *Glamys fordi*, have distinctly more negative mean $\delta^{13}C$ values than those of either *T. fordi* or *Isoptychus* sp., with which they co-existed. This indicates that both glirids had diets significantly different from those of the theridomyids. This dietary distinction is consistent in all three levels studied spanning at least 3 million years. Carbon isotope analysis of associated plant fossils combined with independent evidence from dental morphology and gnaw marks on *Stratiotes* seeds shows that seeds of the open water, free-floating aquatic plant *Stratiotes* formed a significant proportion of the diet of *G. priscus* and by inference that of *G. fordi*. In contrast calculated dietary $\delta^{13}C$ values of *T. fordi* and *Isoptychus* sp. overlap the $\delta^{13}C$ values of marginal freshwater aquatic plant seeds and thick-walled plant tissues. This evidence, combined with independent taphonomic and palaeoecological information, suggests that these theridomyids and glirids foraged in close association with large water bodies. This supports the use of tooth enamel from these rodents as a proxy for freshwater oxygen isotope values, in palaeoclimate reconstruction.

Keywords: Apatite; Carbon isotopes; Teeth; Micro-mammals; Diet; Palaeoclimate

1. Introduction

The $\delta^{13}C$ isotope ratio in the carbonate component of mammalian enamel bioapatite has become accepted as a proxy for palaeodietary reconstruction (e.g., Lee-Thorp and Van Der Merwe, 1987; Quade et al., 1992; MacFadden and Cerling, 1996; Koch et al., 1998; MacFadden et al., 1999) and palaeoclimate reconstruction (Rogers and Wang, 2002; Blondel et

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al., 1997; Koch et al., 1995). Palaeodietary studies are important in reconstructing the ecology and climate of past environments (Cerling and Harris, 1999). This is because the interpretation of enamel phosphate oxygen values in palaeoclimate reconstruction relies upon the judgment that drinking water formed a large proportion of an ancient mammal's oxygen intake. With large mammals this is likely to be the case, but less reliably so with small mammals (Bryant and Froelich, 1995). Using a new analytical technique (Lindars et al., 2001), Grimes et al. (2003) proposed the use of rodents in palaeoclimate studies, and it is important to be able to demonstrate a strong link between their drinking water and depositional environment.

Grimes et al. (2003) chose the Solent Group, Hampshire Basin (UK), for their test study. This succession was deposited across a key interval of global climate change (the Late Eocene–Early Oligocene greenhouse–icehouse transition), as documented in the

Table 1.
Sequence of principal lithostratigraphic units of the Solent Group, western Isle of Wight, UK

Geochronology	Age (Ma)	Formation	Member	Sampled mammal taxa	Sampled plant fossils
Early Oligocene (Rupelian)	33.7	Bouldnor	Cranmore		
			Hamstead	*Isoptychus* sp. *Glamys fordi*	
			Bembridge Marls		
Late Eocene (Priabonian)					
		Bembridge Limestone			
		Headon Hill	**Osborne**	*T. fordi* *Isoptychus* sp. *G. priscus*	*Caricoidea* *Strationtes* *Brasenia* Thick walled tissue
			Fishbourne		
			Laccy's Farm		
			Cliff End		
			Hatherwood		
			Linstone Chine		
			Colwell Bay		
	37.0		**Totland Bay**	*Thalerimys fordi* *Glamys priscus*	

Absolute ages are in Ma (Berggren et al., 1995). Sampled members are shown in bold.

marine proxy isotope record (Zachos et al., 2001). Here, we report $\delta^{13}C$ results from the carbonate component of tooth enamel, dentine and whole tooth samples from four rodent species from the Solent Group, namely *Thalerimys fordi*, *Isoptychus* sp., *Glamys priscus* and *Glamys fordi*. In addition, we also report $\delta^{13}C$ results from the analysis of whole samples of aquatic plant seeds (*Stratiotes*, *Brasenia* and *Caricoidea*) and unidentified, charcoalified, thick-walled plant tissues. There are three aims in this study: Firstly, to ascertain if carbon isotope analyses enable discrimination between the diets of coexisting plant-eating rodents; secondly, to attempt to relate rodent diet to both the coexisting flora and the local foraging habitat; and, thirdly, to determine whether dietary and behavioural evidence confirms the suitability of using rodent tooth enamel in palaeoclimate reconstruction (Grimes et al., 2003).

2. Sample location and materials

Three levels from the Late Eocene (Priabonian) to Early Oligocene (Rupelian) Solent Group, Isle of Wight, UK, were targeted. These are from the Totland Bay and Osborne Members of the Headon Hill Formation (Late Eocene) and from the Hamstead Member of the Bouldnor Formation (Early Oligocene) (Table 1).

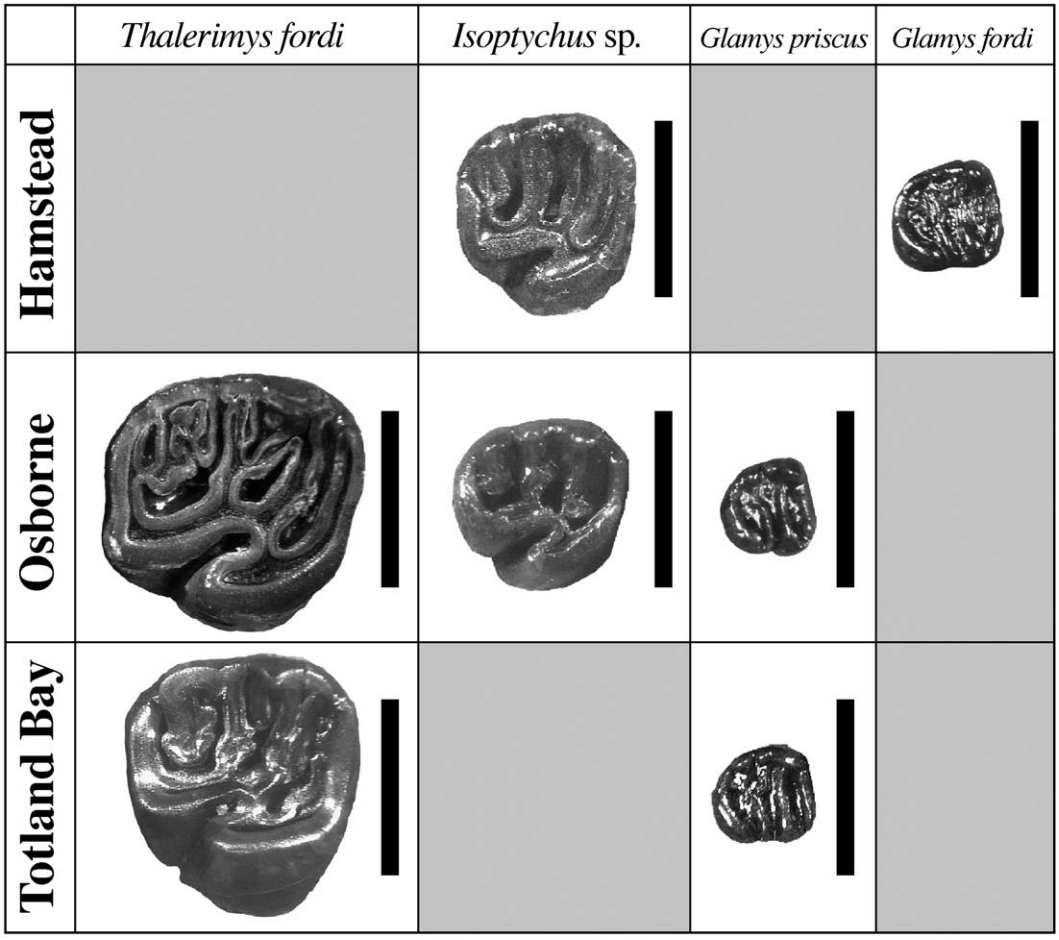

Fig. 1. Representative reflected light images of crown views of upper right third molars of the theridomyid rodents *Thalerimys fordi*, *Isoptychus* sp., and lower right third molars of the glirid rodents *Glamys priscus* and *Glamys fordi* used in this study. The scale bar in all the images = 2 mm.

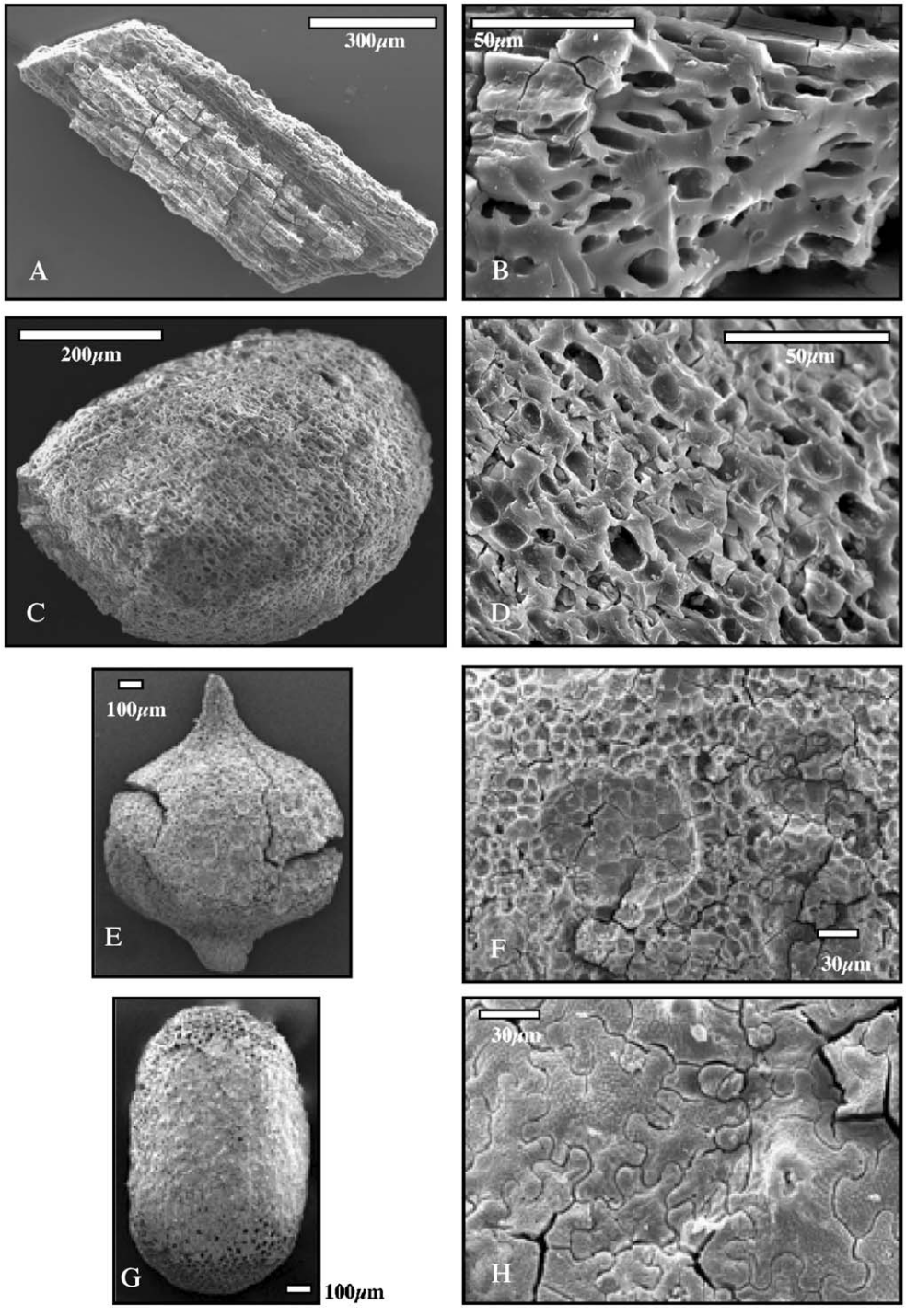

Fig. 2. Representative scanning electron microscope images of plant fossils (A, B) elongate thick-walled plant tissue, (C, D) rounded thick-walled plant tissue, (E, F) *Caricoidea* endocarp wall and (G, H) *Brasenia* seed coat.

The sampled unit in the Totland Bay Member is from Headon Hill and located near the top of the member in a clay within the How Ledge Limestone. This clay is dominated by freshwater pulmonate gastropods, suggestive of a shallow lake or paludal environment. The Osborne Member was sampled at Newtown about 8 m below the top. The unit is a shelly clay lens within a sequence of dominantly colour-mottled clays with mudcrack horizons and occasional bonebeds, suggestive of the overbank environment of a floodplain. The sampled level in the Hamstead Member is at Bouldnor Cliff. It is about 18 m above the base and comprises bone-rich pockets within a sequence of mainly colour-mottled clays. Like the Osborne Member, these suggest a floodplain overbank environment.

Teeth were collected from all three levels. *Thalerimys fordi* and *Isoptychus* sp. belong to the extinct European family Theridomyidae. The systematics of the Solent Group theridomyids has been treated in detail by Bosma and Insole (1972) and Bosma (1974). Some changes to the generic assignment have been made by Tobien (1972) and Vianey-Liaud (1979). *Glamys priscus* and *Glamys fordi* are extinct members of the modern family Gliridae (Dormice) (see Bosma and de Bruijn, 1979 and Vianey-Liaud, 1994 for systematic coverage). A species of *Glamys* and either *T. fordi* or *Isoptychus* sp. occur in all three levels, but the two theridomyids co-occur in sufficient abundance for sampling only in the Osborne Member (Table 1; Fig. 1). Bulk sediment samples were collected from each of the three levels. After screenwashing in the laboratory, individual teeth were picked from the resultant residues. The cheek teeth used in this study (Fig. 1) comprise first and second molars (undifferentiated in theridomyids as M1/2, but distinguished in glirids M1, M2), third molars (M3), fourth premolars (P4) and deciduous fourth premolars (DP4). Only teeth that showed no obvious sign of corrosion, as a result of possible ingestion by predators or scavengers, or of abrasion, from fluvial transport, were used.

Plant fossils (Fig. 2) were also studied from the Osborne Member, where all three rodent genera co-occur. Seeds (term used herein for simplicity to include both seed coats and endocarp walls) were collected from the closest possible horizon to that containing the mammals. This seed-bearing horizon is 2.7 m higher in the succession and is judged to be close temporally to the mammals because of suspected high sedimentation rates in this member. The seed assemblage contains three freshwater aquatic plant genera, *Stratiotes* (Hydrocharitaceae), *Brasenia* (Nympheaceae s.l.) and *Caricoidea* (Cyperaceae) (see Appendix A for details of material).

The only plant fossils found co-occurring with the mammals were small (<1676 μm) pieces of unidentified, charcoalified, thick-walled tissues (Fig. 2A–D) (see Appendix A). Angular, elongate shapes (Fig. 2A) suggest little transport whilst rounded less-elongate shapes (Fig. 2B) might indicate transport from a more distant site of growth. Therefore, each was analysed separately.

3. Methodology

Of all the mineralised biogenic apatite phases (bone, dentine and enamel), enamel has been shown to be the most resistant to diagenetic alteration of the primary carbon isotope signature (Lee-Thorp and Van Der Merwe, 1987; Quade et al., 1992; Koch et al., 1992; Morgan et al., 1994; Wang and Cerling, 1994; Bocherens et al., 1996). However, bone apatite and by inference tooth dentine can nevertheless under favourable circumstances also retain its primary carbon isotope signature (Lee-Thorp, 1997).

Enamel was separated from dentine by the hand picking of fractured samples of *Thalerimys fordi* and *Isoptychus* sp. teeth from the Osborne Member, and *T. fordi* teeth from the Totland Bay Member. In the case of the Osborne Member, the dentine from the *T. fordi* and *Isoptychus* sp. M1/2, M3 and P4 samples was also retained after enamel separation for analysis and comparison with enamel $\delta^{13}C$ values. However, with the *Isoptychus* sp. tooth samples from the Hamstead Member, only dentine was available for carbon isotope analysis (the enamel had been used in another study). In the case of the *Glamys* teeth from all three members, their size (<1 mm) made separation of enamel from dentine difficult and time consuming. Therefore, enamel was handpicked from the combined fractured remains of four upper left M3s for only one analysis of *Glamys priscus*. For all the remaining *Glamys* teeth, single or combined whole tooth analyses were conducted.

The aim of the present study was to target tooth carbonate carbon only, to determine the entire, inte-

grated diet (Ambrose and Norr, 1993) of the rodents. Therefore, all tooth samples (enamel, dentine and whole teeth) were heated to 400 °C, prior to analysis to remove any organic matter from the mineralised biogenic apatite. This pre-treatment method has been shown in step-heating experiments by Lindars et al. (2001) to remove organic carbon with no evidence for the removal of the carbonate carbon. Furthermore, Holden et al. (1995) showed that heating bone material had no effect on its crystalline structure up to 400 °C. Recrystallisation only occurred at 600 °C where the bone material either retained its original rod shaped morphology or changed to tabular or equidimensional shapes.

The carbon isotope analysis of the carbonate (CO_3^{2-}) component of the theridomyid enamel and dentine from the M1/2s, M3s and P4s was conducted using a Micromass Isoprime continuous flow mass spectrometer. Details of the technique can be found in Grimes et al. (2003). In-run analysis of an internal lab carbonate standard (RHBNC) gave a $\delta^{13}C$ value of 3.38 ± 0.30‰ (VPDB) (known value 3.25‰ VPDB). In-run analysis of the international carbonate NBS-19 standard, for offset calculations, gave a $\delta^{13}C$ value of $+2.01 \pm 0.04$ ‰ (VPDB) (known value + 1.96‰ VPDB). Owing to the small sample masses of the handpicked enamel and dentine samples (~ 2 mg on average), replicate analyses could not be conducted. Therefore, the error on the individual $\delta^{13}C$ analyses is assumed to be the same as that on the internal lab standard ($\delta^{13}C = \pm 0.30$‰), rather than the international NBS-19 standard, as the former had the larger error range.

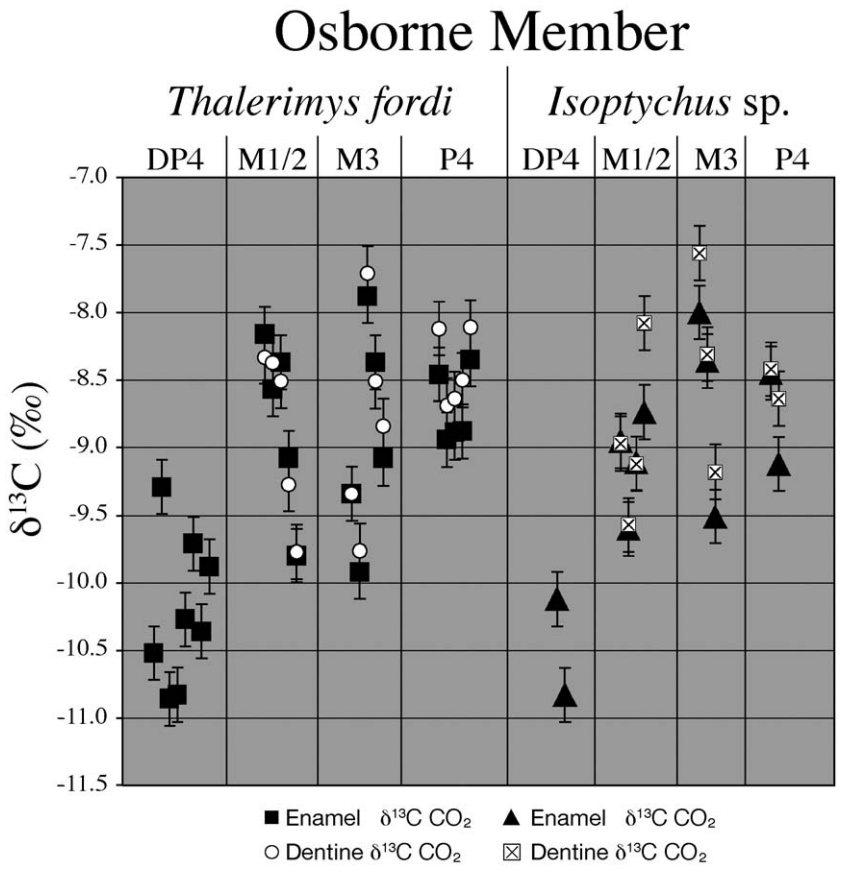

Fig. 3. Plot of enamel and dentine $\delta^{13}C$ values against tooth type for *Thalerimys fordi* and *Isoptychus* sp. cheek teeth from the Osborne Member. Data for this figure is available in an online electronic supplementary file.

Where sample masses were approximately 1 mg or less, analysis by acid digestion and continuous flow mass spectrometry was considered to be inappropriate. Therefore, the single combined enamel sample and the whole tooth samples of the *Glamys*, the enamel from *Thalerimys fordi* and *Isoptychus* sp. deciduous fourth premolars (DP4) and the plant fossils were analysed using a reduced carbon isotope technique. Details of this EA-IRMS technique can be found in Grassineau et al. (2001). After every 10 samples, a blank was run and then immediately afterwards one of four isotopic standards, to flush the system and check the calibration. For the calibration of the results two international standards, NBS 21 graphite ($\delta^{13}C$ of -28.16‰ (VPDB)) and IAEA-CO9 barium carbonate ($\delta^{13}C$ of -47.10‰ (VPDB)), and two internal standards, RHBNC calcite ($\delta^{13}C$ of 3.25‰ (VPDB)) and GF graphite ($\delta^{13}C$ of -23.95‰ (VPDB)) were used. Values obtained during this study were; NBS 21 $\delta^{13}C = -28.18 \pm 0.07$‰ (VPDB); IAEA-CO9 $\delta^{13}C = -47.00 \pm 0.03$‰ (VPDB); RHBNC $\delta^{13}C = 3.30 \pm 0.11$‰ (VPDB); GF $\delta^{13}C = -24.05 \pm 0.12$‰ (VPDB). Owing to the small sample masses of the handpicked samples replicate analyses could not be conducted. Therefore, the error on individual $\delta^{13}C$ analyses is taken to be the same as the largest reproducibility on the standards (± 0.13‰).

Two different techniques (acid digestion and a reduced carbon isotope technique) were used in this study to obtain carbon isotope values. However, the same internal isotope standard (RHBNC) was used with both techniques and gave similar values (acid

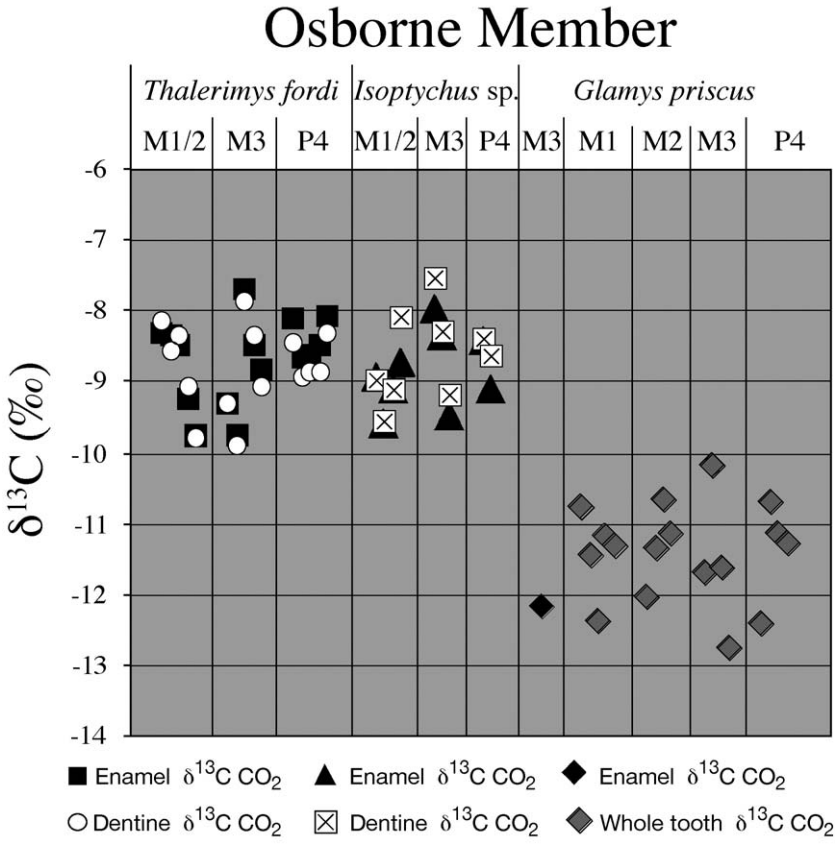

Fig. 4. Plot of enamel, dentine and whole tooth $\delta^{13}C$ values against tooth type for *Thalerimys fordi*, *Isoptychus* sp. and *Glamys priscus* permanent cheek teeth from the Osborne Member. Data for this figure is available in an online electronic supplementary file.

digestion RHBNC = δ^{13}C of 3.38 ± 0.30 ‰ (VPDB) and reduced carbon, RHBNC = δ^{13}C of 3.250 ± 0.11 ‰ (VPDB)). It would have been preferable to use a biogenic apatite carbonate carbon standard but there is no such standard available at present.

4. Results

4.1. The δ^{13}C results from tooth samples

Fig. 3 shows the δ^{13}C results from the analyses of the *Thalerimys fordi* and *Isoptychus* sp. and *Glamys priscus* cheek teeth from the Osborne Member. The δ^{13}C values for the enamel and dentine from all of the *T. fordi* (15) and six of nine *Isoptychus* sp. permanent cheek teeth (M1/2, M3, P4) plot within error of each other (± 0.3) (Fig. 3). There appear to be no significant differences in the δ^{13}C values of the enamel of the permanent cheek teeth between *T. fordi* (mean = – 8.76 ± 0.72 ‰) and *Isoptychus* sp. (mean = – 8.98 ± 0.91 ‰) or between the different permanent cheek teeth of either taxon from the Osborne Member (Fig. 3). In contrast, the enamel samples from the DP4s of these taxa both have more negative δ^{13}C values than the permanent cheek teeth (Fig. 3). DP4s of *Glamys* were too rare to analyse. Like the theridomyids, the respective permanent cheek teeth of *G. priscus* showed no distinguishable differences in their δ^{13}C values (Fig. 4). The enamel and whole tooth samples of *G. priscus* (mean = – 11.46 ± 0.69 ‰) have significantly more negative δ^{13}C values than do

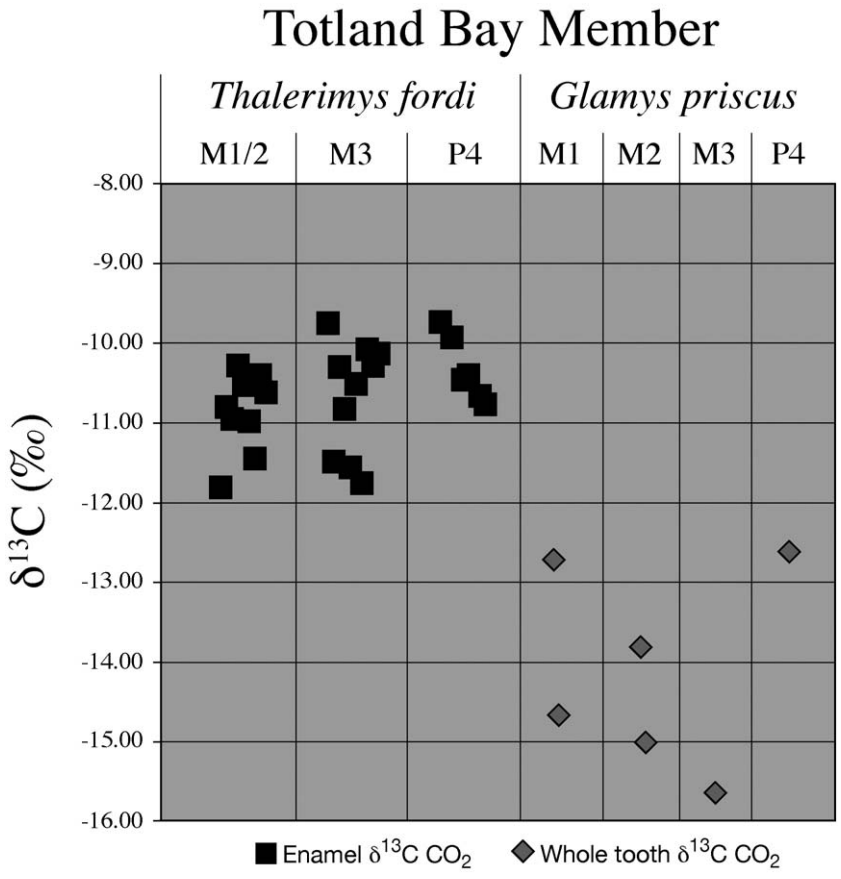

Fig. 5. Plot of enamel and whole tooth δ^{13}C values against tooth type for *Thalerimys fordi* and *Glamys priscus* permanent cheek teeth from the Totland Bay Member. Data for this figure is available in an online electronic supplementary file.

the enamel samples of permanent cheek teeth of co-occurring *T. fordi* and *Isoptychus* sp. (Fig. 4). The enamel (mean = − 12.16 ± 0.3 ‰) and whole tooth samples (mean = − 11.46 ± 0.69 ‰) of *G. priscus* plot within error of each other (Fig. 4).

The $\delta^{13}C$ results from the analysis of the theridomyid enamel and *Glamys* whole tooth samples of permanent cheek teeth from both the Totland Bay and Hamstead Members show that there is no distinguishable difference in the $\delta^{13}C$ results with respect to tooth type (Figs. 5 and 6). However, the *Glamys* whole tooth samples have more negative $\delta^{13}C$ values (mean = − 14.07 ± 1.23 ‰ in the Totland Bay Member − 11.56 ± 0.53 ‰) in the Hamstead Member) than the theridomyid samples (mean = − 10.67 ± 0.59 ‰ in the Totland Bay Member and − 9.11 ± 0.36 ‰ in the Hamstead Member). The degree of $\delta^{13}C$ offset (3.40 ‰ in the Totland Bay Member and 2.63 ‰ in the Hamstead Member) between the *Glamys* and theridomyid $\delta^{13}C$ mean values from both levels are similar to that observed between the same taxa in the Osborne Member (2.70 ‰).

4.2. The $\delta^{13}C$ results from plant fossils and extrapolation to whole tissue counterparts

The $\delta^{13}C$ results from the analysis of the plant fossils from the Osborne Member show that the two categories of unidentified, charcoalified, thick-walled plant tissues have indistinguishable $\delta^{13}C$ values (elongate mean = − 21.32 ± 0.44 ‰, rounded mean = − 21.87 ± 0.54 ‰) (Fig. 7). These results imply either isotopic homogeneity of this plant material irrespective of the potential growth site (rounded specimens may have been transported or reworked) or, more likely, no difference in the sources of the elongate and rounded specimens. The aquatic seed samples, however, not only have more negative $\delta^{13}C$ values than the thick-walled tissues, but they also have progressively more negative $\delta^{13}C$ values (Fig. 7) in the sequence: *Caricoidea* (mean = − 22.44 ± 1.45 ‰), *Brasenia* (mean = − 24.01 ± 1.15 ‰), *Stratiotes* (mean = − 25.53 ± 0.50 ‰). A comparable difference in $\delta^{13}C$ values between *Stratiotes* and *Brasenia* seeds from the

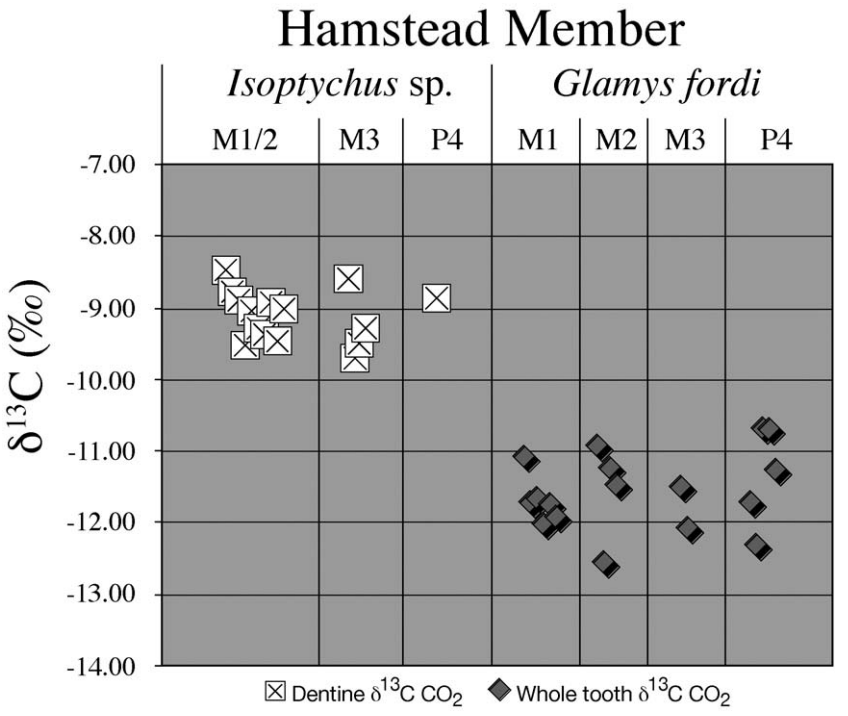

Fig. 6. Plot of dentine and whole tooth $\delta^{13}C$ values against tooth type for *Isoptychus* sp. and *Glamys fordi* permanent cheek teeth from the Hamstead Member. Data for this figure is available in an online electronic supplementary file.

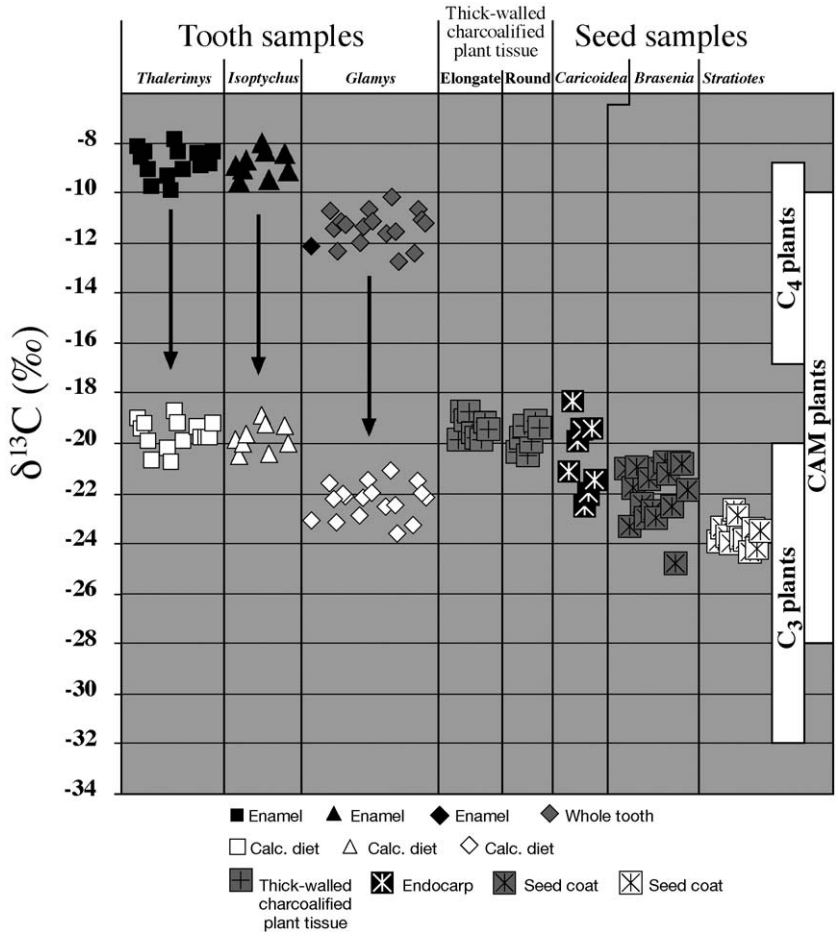

Fig. 7. Plot of enamel and dentine $\delta^{13}C$ values for rodent genera *Thalerimys*, *Isoptychus* and *Glamys* and the $\delta^{13}C$ values for the unidentified, charcoalified, thick-walled plant tissues and the aquatic seed samples (*Caricoidea*, *Brasenia* and *Stratiotes*) from the Osborne Member. The data points below the bold arrows represent the calculated dietary value for each rodent genus, assuming a 9.9‰ fractionation and a 1‰ offset between laboratory and field based studies (see Section 4 for full explanation). The $\delta^{13}C$ values for plants represent original whole tissues, the measured values having been corrected by +2‰ to account for either chemical alteration or charcoalification processes involving loss of cellulose (see Section 4.2. for a full explanation).

Bembridge Limestone Formation was reported by Hooker et al. (1995).

Chemical analyses of Solent Group plant fossils (including *Stratiotes* and *Brasenia*) have shown that original lignin–cellulose complexes have undergone chemical alteration with loss of cellulose components resulting in a composition of modified lignin (Van Bergen et al., 1996, 2000; Hooker et al., 1995). Based upon modern studies by Benner et al. (1987), their measured $\delta^{13}C$ values are therefore likely to be approximately 2‰ more negative than their original lignin–cellulose whole tissue counterparts.

The thick-walled plant tissues on the other hand have been charcoalified, a process which has been shown to result in the preferential removal of cellulose from woody tissue, the amount depending upon the temperature and time over which the pyrolysis occurred (Jones, 1991). The preferential removal of the isotopically heavier cellulose carbon results in charcoalified tissues having between 0.4‰ and 2‰ more negative $\delta^{13}C$ values than their original whole tissue counterparts (Jones, 1991; Jones and Chaloner, 1991; Jones et al., 1993; Schleser et al., 1999; Poole et al., 2002).

Whole tissue values are used in Fig. 7, which provide an overview of results used for dietary interpretations.

4.3. Calculations of dietary intake

Laboratory studies on rodents have indicated a similar degree of fractionation between rodent bone carbonate $\delta^{13}C$ and the $\delta^{13}C$ of a C_3 only diet (between +9.5‰ and +9.7‰ (DeNiro and Epstein, 1978); between +9.5‰ and +10.3‰ (Ambrose and Norr, 1993)). It is likely that late Eocene–early Oligocene vegetation was composed of C_3 plants (Bocherens et al., 1994). Therefore, as there are no laboratory-based studies using rodent tooth enamel, an average fractionation value of +9.9‰ for bone has been used to calculate the $\delta^{13}C$ value of the food ingested by *Thalerimys fordi* and *Isoptychus* sp. and *Glamys priscus* from the Osborne Member. This results in a mean $\delta^{13}C$ value of -18.71 ± 0.58‰ for *T. fordi*, 18.77 ± 0.53‰ for *Isoptychus* sp. and -21.32 ± 0.68‰ for *G. priscus*, for their ingested food. (The DP4s of *T. fordi* and *Isoptychus* sp. were not included in the calculation as they are considered to be pre-weaning teeth, see Section 5.2). However, it is generally accepted that laboratory based dietary studies typically underestimate the degree of fractionation between bone $\delta^{13}C$ and food $\delta^{13}C$ (Koch, 1998). Metages et al. (1990) attributed this difference of approximately +1‰ between laboratory and field-based studies to food quality and the extent of fermentation during digestion. The calculated $\delta^{13}C$ values for the mammals' ingested food, taking account of all these fractionations, are shown in Fig. 7, which forms the basis for subsequent dietary interpretations.

5. Discussion

5.1. Diagenesis

The use of carbon isotopes in palaeodiet reconstruction studies has become generally accepted. Field (Krueger and Sullivan, 1984; Lee-Thorp, 1989; Lee-Thorp et al., 1989) and laboratory studies (Ambrose and Norr, 1993; Tiezsen and Fagre, 1993) have shown that bone and tooth collagen carbon isotope values are directly related to dietary protein values. On the other hand, carbon isotopes in the carbonate component of biogenic apatite reflect the isotopic value of the entire integrated diet (Ambrose and Norr, 1993). However, the carbonate carbon (CO_3^{2-}) in both tooth enamel and dentine is susceptible to diagenetic alteration. The degree to which diagenetic alteration of the carbonate carbon is likely to occur is, however, subject to debate. For example, Lee-Thorp and Van der Merwe (1987) and Quade et al. (1992) reported small shifts of ~ 2‰ in the $\delta^{13}C$ of enamel carbonate towards that of the co-occurring sedimentary carbonate. However, Wang and Cerling (1994), on the basis of the modelled process of water/biomineral interactions, indicated that the CO_3^{2} component of biogenic apatite retained an original $\delta^{13}C$ signal in a closed system and open system with either very low porosity, or with low temperature and very low water/biomineral ratios.

The results from this study show that with respect to the Osborne Member, there is no significant difference in the $\delta^{13}C$ values between *Thalerimys fordi* and *Isoptychus* sp. permanent cheek tooth dentine and enamel (Fig. 3). As the carbonate carbon isotopes in both enamel and dentine would have originally precipitated in equilibrium with each other, this would indicate that either the carbon isotopes in both phases are unaltered or that both have been altered and equilibriated. Circumstantial evidence would, however, favour the former case. For example, the Osborne Member is a sequence of clays with low porosity. In addition, it presently has minimal overburden and shows no evidence of having been deeply buried. Therefore, using Wang and Cerling (1994) classifications, the Osborne Member could be considered as either a closed system, or an open system with very low porosity, which has experienced a low temperature gradient and low water/biomineral ratios. This would suggest that the $\delta^{13}C$ values in the *T. fordi*, *Isoptychus* sp. and *Glamys priscus* dentine and enamel have been little altered by diagenesis.

In view of the similarity of lithologies and geological context, carbonate carbon isotopes within the enamel and dentine from the Totland Bay and Hamstead Members can also be considered to have experienced little diagenetic alteration. Therefore, the comparison of $\delta^{13}C$ values from dentine, enamel and whole tooth samples one with another, both within and between individual levels, can be regarded as reliable.

5.2. Suckling and weaning

Studies of modern plant-eating, carnivorous, hibernating and non-hibernating mammals (e.g., Jenkins et al., 2001; Balaisse et al., 2001; Polischuk et al., 2001) indicate that mothers' milk can have a $\delta^{13}C$ value of between 0.8‰ and 2.1‰ lower than that of their diet. Even though there are no reported data for rodent species, it can be expected that they would display a similar degree of depletion. In Fig. 3 (Osborne Member), the enamel of *Thalerimys fordi* and *Isoptychus* sp. DP4s has more negative $\delta^{13}C$ values than those of their permanent cheek teeth. The degree of offset between the mean of the DP4 enamel and the combined mean of the M1/2, M3 and P4 enamel is 1.46‰ for *T. fordi* and 1.50‰ for *Isoptychus* sp. These values are within the range 0.8–2.1‰, reported by, among others, Jenkins et al. (2001), Balaisse et al. (2001) and Polischuk et al. (2001) in lactation studies of a range of modern mammals. Therefore, we can conclude that for *T. fordi* and *Isoptychus* sp. weaning most likely occurred before the mineralization of the first molar (M1). Furthermore, it can be argued that all cheek teeth apart from the DP4s are suitable for use in palaeodiet and palaeoclimate reconstruction.

5.3. Distinguishing theridomyid and glirid diets

In the Osborne Member, there is no significant difference between *Thalerimys fordi* and *Isoptychus* sp. in the overall mean $\delta^{13}C$ values of their permanent cheek teeth (Fig. 4). However, the permanent cheek teeth of the co-existing *Glamys priscus* have a distinctly lower mean $\delta^{13}C$ value (Fig. 4). This distinction between theridomyids and glirids is repeated in the Totland Bay Member and in the Hamstead Member. This indicates that the theridomyids had similar diets to one another but that co-existing glirids had a significantly different diet. This dietary distinction is maintained through the Late Eocene (Totland Bay Member) to the Early Oligocene (Hamstead Member).

5.4. Causes of isotopic differences in the plant fossils

The $\delta^{13}C$ results from the analysis of three different types of aquatic plant seeds from the Osborne Member show increasingly negative values in the sequence: *Caricoidea*, *Brasenia*, *Stratiotes*. A comparable difference in $\delta^{13}C$ values between *Stratiotes* and *Brasenia* seeds was reported by Hooker et al. (1995). This increasingly negative trend in the aquatic seed samples most likely reflects their different living environments. For example, the *Stratiotes* plant is free floating, whereas *Brasenia* is an open water rhizomatous plant with surface floating leaves and *Caricoidea* a fully rooted marginal plant. Therefore, the increasingly negative trend in the $\delta^{13}C$ values of their seeds may reflect the level of "water stress" and stomatal conductance experienced by each plant (see Farquhar et al., 1989 for explanation). It should also be noted that plants can also source some of their carbon directly from the water or soil in which they live. Total Dissolved Inorganic Carbon (ΣDIC) can range widely, but is generally depleted in ^{13}C with respect to associated terrestrial vegetation (Fry and Sherr, 1984). However, soil is considered to be generally more enriched in ^{13}C than associated vegetation (Cerling, 1984; Cerling et al., 1989). These two reasons combined could explain why with respect to the seeds, *Stratiotes*, the most aquatic of the three plants, has the most negative $\delta^{13}C$ values, whereas *Caricoidea*, a fully rooted marginal plant, has the most positive $\delta^{13}C$ values.

5.5. Evidence for diet and foraging behaviour of the rodents from their morphology

The theridomyids and glirids discussed here have distinctly different cheek teeth, with implications for different diets when modern dental analogues are considered.

5.5.1. Thalerimys fordi and Isoptychus sp.

The cheek teeth of these closely related genera are semihypsodont, the uppers unilaterally so, with strong, transverse to oblique lophs, which soon wear to expose dentine bordered by sharp enamel ridges (Fig. 1; Bosma, 1974; Bosma and Insole, 1972). *Thalerimys fordi* and *Isoptychus* sp. differs from *Isoptychus* sp. only in being slightly larger and having additional minor crests. Many modern rodents have lophodont cheek teeth, but few are really close in morphology or crown height to those of *Thalerimys* and *Isoptychus*. The closest dental analogues of *Thalerimys* and *Isoptychus* are *Thryonomys*, the cane rats of Africa, and *Erethizon*, the North American Porcupine. They differ mainly in being two to three times larger and *Thryon-*

omys has one fewer transverse lophs (Collinson and Hooker, 1987, Fig. 10.4c–d; Stehlin and Schaub, 1951, Figs. 40, 144, 348, 451). Both feed on a wide variety of plants. *Thryonomys* mainly eats the stems of grasses and to a lesser extent fruits and bark (Kingdon, 1997; Nowak, 1999). *Erethizon* feeds on the foliage of many different kinds of trees and herbs, including that of wetland plants (Chapman and Feldmaner, 1982). *Thryonomys* feeds entirely on the ground, whilst *Erethizon* feeds both on the ground and in the trees. Despite the variety of plants taken, the diets of both modern genera are dominated by leaves. Isolated ankle bones, which, by sample association and relative abundance, almost certainly represent those of *T. fordi* and *Isoptychus* sp., indicate foraging on the ground for these two genera (J.J. Hooker, personal observation). This is supported by the ground dwelling habits interpreted for the closely related theridomyid *Pseudoltinomys*, which is known from a complete articulated skeleton (Schmidt-Kittler and Storch, 1985).

5.5.2. Glamys

The cheek teeth of *Glamys* are very low crowned. They are dominated by three or four main cusps joined by strong but low transverse ridges, some irregular and branching; the ridges are separated by shallow valleys (Fig. 1; Bosma and de Bruijn, 1979, as genus *Gliravus*). Wear rarely proceeds further than exposing cusp tip dentine, so that alternating enamel and dentine ridges like those of theridomyids are not formed. *Glamys fordi* differs from *Glamys priscus* in being slightly larger and having extra minor cresting. Both are much smaller than the theridomyids (Fig. 1). Of modern glirids, *Dryomys* (forest dormice) has cheek teeth closest in morphology to those of *Glamys* (Van Der Meulen and De Bruijn, 1982, Fig. 3; Stehlin and Schaub, 1951, Figs. 201, 516). The diet of *Dryomys* is dominantly fruits, seeds and buds, plus arthropods and small vertebrates (Nowak, 1999), which it acquires by foraging in the trees. It is possible that the irregular and extra cresting in *Glamys*, which is lacking in *Dryomys* and other modern genera, is indicative of a greater fruit and seed component in the diet. The diet of *Glamys* is thus very different from that inferred for theridomyids by their modern analogues. Ankle bones attributed to *Glamys* suggest a scansorial mode of life, with foraging both in trees and on the ground, much as another modern glirid *Eliomys* (Collinson and Hooker, 2000).

5.6. Relating glirid and theridomyid diets to the co-existing flora

Results from the Osborne Member show that the calculated $\delta^{13}C$ values for the diet of the glirid *G. priscus* overlap with those of the sampled *Stratiotes* seeds (Fig. 7). These results are consistent with direct dietary evidence, in the form of gnawed *Stratiotes* seeds (Collinson and Hooker, 2000), and indirect evidence from dental analogy and inferred foraging behaviour (Section 5.5.2). In combination these results provide near conclusive evidence that the diet of *Glamys* included seeds of the free-floating open water aquatic plant *Stratiotes*. The $\delta^{13}C$ values of *Brasenia* seeds also overlap with the calculated dietary values for *Glamys*, but the values for thick-walled plant tissues do not. This indicates that *G. priscus* could also have consumed other seeds but probably not a wide range of other plant tissues. This is also consistent with indirect evidence based on dental morphology (Section 5.5.2) for a diet dominated by seeds.

The theridomyids *Thalerimys fordi* and *Isoptychus* sp. have more positive calculated dietary $\delta^{13}C$ values than *Glamys priscus* indicating a diet not dominated by aquatic seeds (Fig. 7). The calculated dietary $\delta^{13}C$ values for *T. fordi* and *Isoptychus* sp. partly overlap the *Caricoidea* $\delta^{13}C$ values and totally overlap the values for the thick-walled plant tissues. These results suggest that their diet encompassed a range of plant tissues including marginal aquatic plants. These suggestions are consistent with evidence from dental analogues and foraging behaviour (Section 5.5.1), which suggest ground foraging with a diet not dominated by seeds.

5.7. Relating diet to the local foraging habitat and application to palaeoclimate reconstruction

Thalerimys fordi and *Isoptychus* sp. probably included marginal aquatic plants as part of their diet (Section 5.6). This provides additional evidence in support of earlier conclusions (Grimes et al., 2003) that these rodents were closely associated with large water bodies from which they most likely drank while foraging. This is an important conclusion with respect to the use of these rodent species in palaeoclimate studies because the use of phosphate $\delta^{18}O$ values from any mammal tooth enamel relies upon the judgement that the mammals obtained the majority of their water

intake from drinking and not from their food. Our results show that the fossil glirids had an unequivocal association with water. However, glirid teeth are far smaller than those of theridomyids (Fig. 1). This makes the separation of enamel for phosphate oxygen isotope analysis much more difficult, and means that it requires a much larger number of tooth samples, four teeth needing to be combined to produce sufficient enamel for one analysis. Together, these difficulties currently prevent the use of glirid teeth for palaeoclimate reconstruction in the Solent Group.

6. Conclusions

Carbon isotope analyses have been undertaken on teeth from four species of rodent and associated plant fossils from the Late Eocene to Early Oligocene Solent Group, Hampshire Basin, UK. The fact that there is no difference between the $\delta^{13}C$ values of enamel and dentine, combined with the geological context, suggests that there has been no significant diagenetic alteration of the carbonate carbon isotopes. Therefore, the $\delta^{13}C$ values from dentine, enamel and whole tooth samples can all be reliably compared.

The negative offset (Fig. 3) in the $\delta^{13}C$ values between the DP4 versus permanent cheek tooth enamel in *Thalerimys* and *Isoptychus* suggests that mineralization of DP4 was influenced by the mother's milk during suckling and implies that weaning occurred before the mineralization of the first molar (M1). One can therefore rely on isotope values from permanent cheek teeth but not DP4 for palaeodietary or palaeoclimate reconstruction using these taxa.

There is no significant difference between co-occurring *Thalerimys fordi* and *Isoptychus* sp., in the overall mean $\delta^{13}C$ values of their permanent cheek teeth suggesting that these theridomyids, had similar diets. The *Glamys* species (*Glamys priscus* or *G. fordi*) that co-occur with the theridomyids have distinctly more negative mean $\delta^{13}C$ values for their permanent cheek teeth showing that glirids and theridomyids had significantly different diets. This dietary distinction is maintained through the Late Eocene to Early Oligocene (Totland Bay to Hamstead Members).

The carbon isotope values of associated plant fossils, combined with independent evidence of gnaw marks on *Stratiotes* seeds (Collinson and Hooker, 2000) show that seeds of the aquatic plant *Stratiotes* formed a significant proportion of the diet of *Glamys priscus* and by inference that of *Glamys fordi*. This conclusion is consistent with dental morphology and with osteological evidence for foraging behaviour. The calculated dietary $\delta^{13}C$ values of the theridomyids overlap the *Caricoidea* $\delta^{13}C$ values as well as those of the thick-walled plant tissues. Combined with evidence from dental analogy and bone morphology this suggests that the theridomyids foraged on the ground feeding on a range of plant material, which probably included marginal aquatic plants.

The inferred diet and foraging behaviour of the theridomyids support other evidence (Grimes et al., 2003) of a close association between these rodents and large water bodies, which, by implication, they used for drinking. This further validates the use of their isotope values in palaeoclimate reconstruction.

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Appendix A. Diagnostic features of the plant material from the Osborne member

Stratiotes is represented by fragments of seed coats. These were identified using characteristic surface cell anatomy which was comparable to that illustrated for well-preserved specimens by Collinson and Hooker (2000) and Hooker et al. (1995). Fossil *Stratiotes* is interpreted as a free-floating, open water aquatic plant (water soldier) based on many lines of evidence documented by Collinson and Hooker

(2000). *Brasenia* is represented by fragments and by almost complete seed coats (Fig. 2G) although all lacked the diagnostic operculum that is shed on germination. The specimens were identified by characteristic micropapillate digitate surface cells, which lack long hair-like papillae but sometimes possess a single large central tubercle (Fig. 2H) (Collinson, 1980). Fossil *Brasenia* is interpreted as an open water, rooted rhizomatous aquatic plant (small-leaved water lily) on the basis of nearest living relatives and facies associations (Collinson, 1980, 1983; Collinson et al., 1993). *Caricoidea* is represented by half endocarps (Fig. 2E) and endocarp fragments. Portions used for analysis were identified by the characteristic urn-shape with a basal neck and apical prolongation (Fig. 2E) (Collinson, 1983) combined with distinctive surface pitting (Fig. 2F), which is likely to be a specific feature. Fossil *Caricoidea* (an extinct genus) is interpreted as a rooted, emergent marginal aquatic plant (sedge) on the basis of nearest living relatives and facies associations (Collinson, 1983).

The unidentified thick-walled tissues were brittle and shiny, with homogenised cell walls and three-dimensional cellular preservation (Fig. 2B, D). All these features are characteristic of charcoalified material (Jones, 1991). These thick-walled tissues are not wood as their constituent cells are not in rows, are relatively equiaxial and lack characteristic wood pitting (Fig. 2A–D). They probably represent sclerenchymatous supporting tissues and their radial (as opposed to bilateral) organisation suggests derivation from an axial system (e.g., stems). These fossils may represent terrestrial plants as such thick-walled tissues are relatively uncommon in aquatics. However, we cannot rule out an aquatic derivation. The fact that these tissues are charcoalified argues against a derivation from open water plants or the submerged parts of aquatic plants but does not exclude derivation from marginal aquatics or marsh plants.

References

Ambrose, S.H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J., Grupe, G. (Eds.), Prehistoric Human Bone, Archaeology at the Molecular Level. Springer-Verlag, Berlin, pp. 1–37.

Balaisse, M., Bocherens, H., Mariotti, A., Ambrose, S.H., 2001. Detection of dietary changes by intra-tooth carbon and nitrogen isotopic analysis: an experimental study of dentine collagen of cattle (*Bostaurus*). Journal of Archaeological Science 28, 235–245.

Benner, R., Fogel, M.L., Sprague, E.K., Hodson, R.E., 1987. Depletion of 13C in lignin and its implications for stable carbon isotope studies. Nature 329, 708–710.

Berggren, W.A., Kent, D.V., Swisher III, C.C., Aubry, M.P., 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren, W.A., Kent, D.V., Aubry, M.-P., Hardenbol, J. (Eds.), Geochronology, Time Scales and Global Stratigraphic Correlation. Special Publication-SEPM (Society for Sedimentary Geology), vol. 54, pp. 129–212.

Blondel, C., Bocherens, H., Mariotti, A., 1997. Stable carbon and oxygen isotope ratios in ungulate teeth from the French Eocene and Oligocene localities. Bulletin of the Geological Society of France 168, 775–781.

Bocherens, H., Friis, E.M., Mariotti, A., Pedersen, K.J., 1994. Carbon isotopic abundances in Mesozoic and Cenozoic fossil plants: palaeoecological implications. Lethaia 26, 347–358.

Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.J., 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammal enamel from African Pleistocene hominid sites: implications for the preservation of paleoclimatic signals. Palaios 11, 306–318.

Bosma, A.A., 1974. Rodent biostratigraphy of the Eocene–Oligocene transitional strata of the Isle of Wight. Utrecht Micropaleontological Bulletins 1, 1–128.

Bosma, A.A., de Bruijn, H., 1979. Eocene and Oligocene Gliridae (Rodentia, Mammalia) from the Isle of Wight, England: Part 1. The *Gliravus priscus–Gliravus fordi* lineage. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 84, 367–384.

Bosma, A.A., Insole, A.N., 1972. Theridomyidae (Rodentia Mammalia) from the Osborne Beds (Late Eocene), Isle of Wight, England. Proceedings Koninklijke Nederlandse Akademie van Westenschappen 75, 133–144.

Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica Acta 59, 4523–4537.

Cerling, T.E., 1984. The stable isotopic composition of modern soil carbonate and its relationship to climate. Earth and Planetary Science Letters 71, 229–240.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363.

Cerling, T.E., Quade, J., Wang, Y., Bowman, J.R., 1989. Carbon isotopes in soil and paleosoils as ecology and paleocology indicators. Nature 341, 138–139.

Chapman, J.A, Feldmaner, G.A., 1982. Wild Mammals of North America, Biology, Management and Economics. Johns Hopkins Univ. Press, Baltimore. 1147 pp.

Collinson, M.E., 1980. Recent and Tertiary seeds of the Nymphaeaceae s.l. with a revision of *Brasenia ovula* (Brongn.) Reid & Chandler, Annals of Botany 46, 603–632.

Collinson, M.E., 1983. Palaeofloristic assemblages and palaeoecol-

ogy of the Lower Oligocene Bembridge Marls, Hamstead Ledge, Isle of Wight. Botanical Journal of the Linnean Society 86, 177–225.

Collinson, M.E., Hooker, J.J., 1987. Vegetational and mammalian faunal changes in the Early Tertiary of southern England. In: Friis, E.M., Chaloner, W.G., Crane, P.R. (Eds.), The Origins of Angiosperms and Their Biological Consequences. Cambridge Univ. Press, Cambridge, pp. 259–304.

Collinson, M.E., Hooker, J.J., 2000. Gnaw marks on Eocene seeds: evidence for early rodent behaviour. Palaeogeography, Palaeoecology, Palaeoclimatology 157, 127–149.

Collinson, M.E., Singer, R.L., Hooker, J.J., 1993. Vegetational change in the latest Eocene of southern England. In: Planderová, E., Konzálová, M., Kvacek, Z., Sitár, V., Snopková, P., Suballyová, D. (Eds.), Paleofloristic and Paleoclimatic Changes during Cretaceous and Tertiary. Konferencie. Sympozia. Seminare. Dionyz Stur Institute of Geology, Bratislava, pp. 81–87. pls XX–XXV.

DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 45, 341–351.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40, 503–537.

Fry, B., Sherr, E.B., 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions to Marine Science 27, 13–47.

Grassineau, N.V., Mattey, D.P., Lowry, D., 2001. Sulfur isotope analysis of sulphide and sulfate minerals by continuous flow-isotope ratio mass spectrometry. Analytical Chemistry 73, 220–225.

Grimes, S.T., Mattey, D.P., Hooker, J.J., Collinson, M.E., 2003. Paleogene palaeoclimate reconstruction using oxygen isotopes from land and freshwater organisms: the use of multiple palaeoproxies. Geochimica et Cosmochimica Acta 67, 4033–4047.

Holden, J.L., Clement, J.G., Phakey, P.P., 1995. Age and temperature related changes to the ultrastructure and composition of human bone material. Journal of Bone and Material Research 10, 1400–1409.

Hooker, J.J., Collinson, M.E., Van Bergen, P.F., Singer, R.L., De Leeuw, J.W., Jones, T.P., 1995. Reconstruction of land and freshwater palaeoenvironments near the Eocene–Oligocene boundary, southern England. Journal of the Geological Society (London) 152, 449–468.

Jenkins, S.G., Partridge, S.T., Stephenson, T.R., Farley, S.D., Robbins, C.T., 2001. Nitrogen and carbon fractionation between mothers, neonates, and nursing offspring. Oecologia 129, 336–341.

Jones, T.P., 1991. The nature, origin and recognition of fusian. PhD thesis, University of London, 2 volumes (unpublished).

Jones, T.P., Chaloner, W.G., 1991. Fossil charcoal, its recognition and palaeoatmospheric significance. Palaeogeography, Palaeoecology, Palaeoclimatology 97, 39–50.

Jones, T.P., Scott, A.C., Mattey, D.P., 1993. Investigations of "fusain transition fossils" from the Lower Carboniferous: comparisons with modern partially charred wood. International Journal of Coal Geology 22, 37–59.

Kingdon, J., 1997. The Kingdon Field Guide to African Mammals. Academic Press, London. 464 pp.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annual Reviews in Earth and Planetary Science 26, 573–613.

Koch, P.L., Zachos, J.C., Gingerich, P.D., 1992. Correlations between isotope records in marine and continental carbon reservoirs near the Palaeocene/Eocene boundary. Nature 358, 319–322.

Koch, P.L., Zachos, J.C., Dettman, D.L., 1995. Stable isotope stratigraphy and paleoclimatology of the Paleogene Bighorn Basin (Wyoming, USA). Palaeogeography, Palaeoclimatology, Palaeoecology 115, 61–89.

Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America: Part 1. Florida. Chemical Geology 152, 119–138.

Krueger, H.W., Sullivan, C.H., 1984. Model for carbon isotope fractionation between diet and bone. In: Turnland, J.F., Johnson, P.E. (Eds.), Stable Isotopes in Nutrition. ACS Symposium Series, vol. 258. American Chemical Society, Washington, pp. 205–222.

Lee-Thorp, J.A., 1989. Stable carbon isotopes in deep time. The diets of fossil fauna and homonids. PhD thesis, University of Cape Town (unpublished).

Lee-Thorp, J.A., 1997. Perservation of biogenic carbon isotope signals in Plio-Pleistocene bone and tooth material. In: Ambrose, S., Katzenberg, K.A. (Eds.), Close to the Bone: Biogeochemistry and Palaeodietary Analysis. Plenum Press, London, pp. 89–116.

Lee-Thorp, J.A., Van Der Merwe, N.J., 1987. Carbon isotope analysis of fossil bone apatite. South African Journal of Science 83, 712–715.

Lee-Thorp, J.A., Sealy, J.C., Van Der Merwe, N.J., 1989. Stable carbon isotope ration difference between bone collagen and bone apatite and their relationship to diet. Journal of Archaeological Science 16, 585–599.

Lindars, E.S., Grimes, S.T., Mattey, D.P., Collinson, M.E., Hooker, J.J., Jones, T.P., 2001. Phosphate $\delta^{18}O$ determination of modern rodent teeth by direct laser fluorination: an appraisal of methodology and potential application to palaeoclimate reconstruction. Geochimica et Cosmochimica Acta 65, 2535–2548.

MacFadden, B.J., Cerling, T.E., 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10-million-year sequence from the Neogene of Florida. Journal of Vertebrate Paleontology 16, 103–115.

MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology and extinction of 5-million-year-old horses from Florida. Science 283, 824–827.

Metages, C., Kempe, K., Schmidt, H.L., 1990. Dependence of the carbon-isotope contents of breath carbon dioxide, milk, serum and rumen fermentation products on the $\delta^{13}C$ value of food in dairy cows. British Journal of Nutrition 63, 187–196.

Morgan, M.E., Kingston, J.D., Marino, B.D., 1994. Carbon isotopic evidence for the emergence of C4 plants in the Neogene from Pakistan and Kenya. Nature 367, 162–165.

Nowak, R.M., 1999. Walker's Mammals of the World, Sixth edition, vols. 1 and 2. The Johns Hopkins Univ. Press, Baltimore. 1936 pp.

Polischuk, S.C., Hobson, K.A., Ramsay, M.A., 2001. Use of stable carbon and nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology 79, 499–511.

Poole, I., Braadbaarta, F., Boon, J.J., Van Bergen, P.F., 2002. Stable carbon isotope changes during artificial charring of propagules. Organic Geochemistry 33, 1675–1681.

Quade, J., Cerling, T.E., Barry, J.C., Morgan, M.E., Pilbeam, D.R., Chivas, A.R., Lee-Thorp, J.A., Van Der Merwe, N.J., 1992. A 16-Ma record of palaeodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. Chemical Geology 94, 183–192.

Rogers, K.L., Wang, Y., 2002. Stable isotopes in Pocket Gopher teeth as evidence of a Late Matuyama climate shift in the southern Rocky Mountains. Quaternary Research 57, 200–207.

Schleser, G.H., Frielingsdorf, J., Blair, A., 1999. Carbon isotope behaviour in wood and cellulose during artificial aging. Chemical Geology 158, 121–130.

Schmidt-Kittler, N., Storch, G., 1985. Ein vollständiges Theridomyiden-Skelett (Mammalia: Rodentia) mit Rennmaus-Anpassungen aus dem Oligozän von Céreste, S-Frankreich. Senckenbergiana. Lethaia 66, 89–109.

Stehlin, H.G., Schaub, S., 1951. Die Trigonodonite der simplicidentaten Nager. Schweizerische Palaeontologische Abhandlungen 67, 1–35.

Tiezsen, L.L., Fagre, T., 1993. Effects of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite and soft tissue. In: Lambert, J.B., Grupe, G. (Eds.), Molecular Archaeology of Prehistoric Bone. Springer-Verlag, Berlin, pp. 123–135.

Tobien, H., 1972. Mikromammalier aus dem alttertiären Melanienton von Nordlessen. Teil 2: Rodentia, Biostratigraphie, Biostratinomie. Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 100, 7–40.

Van Bergen, P.F., Collinson, M.E., De Leeuw, J.W., 1996. Characterisation of the insoluble constituents of propagule walls of fossil and extant water lilies: implications for the fossil record. Ancient Biomolecules 1, 55–81.

Van Bergen, P.F., Collinson, M.E., Stankiewicz, B.A., 2000. The importance of molecular palaeobotany. Acta Palaeobotanica 2, 653–657.

Van Der Meulen, A.J., De Bruijn, H., 1982. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece): Part 2. The Gliridae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Palaeontology 85, 485–524.

Vianey-Liaud, M., 1979. Evolution des rongeurs à l'Oligocène en Europe occidentale. Palaeontographica 166, 136–236.

Vianey-Liaud, M., 1994. La radiation des Gliridae (Rodentia) à l'Eocène supérieur en Europe Occidentale, et sa descendance Oligocène. Münchner Geowissenschaftliche Abhandlungen 26, 117–160.

Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 281–289.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.