Comparative dietary evaluations of an extinct giraffid (*Sivatherium hendeyi*) (Mammalia, Giraffidae, Sivatheriinae) from Langebaanweg, South Africa (early Pliocene)

Tamara A. FRANZ-ODENDAAL
Department of Zoology, University of Cape Town,
Rondebosch, 7700, Cape Town (South Africa)
Current address: Department of Biology, Dalhousie University,
1355 Oxford Street, Halifax, B3H 4J1 (Canada)
tfranzod@dal.ca

Nikos SOLOUNIAS
Department of Anatomy, New York College of Osteopathic Medicine,
Old Westbury, NY 11568-8000 (USA)
nsolouni@nyit.edu

Franz-Odendaal T. A. & Solounias N. 2004. — Comparative dietary evaluations of an extinct giraffid (*Sivatherium hendeyi*) (Mammalia, Giraffidae, Sivatheriinae) from Langebaanweg, South Africa (early Pliocene). *Geodiversitas* 26 (4) : 675-685.

ABSTRACT
The dietary preference of *Sivatherium hendeyi* (Harris, 1976), an extinct giraffid from the early Pliocene of South Africa, was investigated by applying three dietary reconstruction tools – hypsodonty, mesowear and microwear. The hypsodonty index for *S. hendeyi* is 1.51 ± 0.06, which is within the brachyodont category as in most ruminant browsers. The mesowear signature of *S. hendeyi* is most similar to the mixed feeders (the seasonal mixed feeders). Microwear investigations also support a mixed diet for *S. hendeyi*. Taken together, results indicate that the dietary preference of this extinct giraffid is most similar to that of seasonal mixed feeders and show no similarities with grazers. The slight differences in the type of mixed feeding are discussed and highlight the constraints of each method for the interpretation of diets of fossil herbivores. The importance of the results in terms of the evolution of dietary strategies amongst African Sivatheriinae are also discussed.

KEY WORDS
Mammalia,
Giraffidae,
Sivatheriinae,
South Africa,
microwear,
mesowear,
paleodiet.

RÉSUMÉ
*Caractérisations comparatives de l'alimentation d'un giraffidé éteint (*Sivatherium hendeyi*) (Mammalia, Giraffidae, Sivatheriinae) de Langebaanweg, Afrique du Sud (Pliocène inférieur).*
Les préférences alimentaires de *Sivatherium hendeyi* (Harris, 1976), un giraffidé éteint du Pliocène inférieur d'Afrique du Sud, ont été étudiées en appliquant trois outils de reconstitution du régime alimentaire : hypsondontie, méso-usure (mesowear) et micro-traces d'usures (microwear). L'indice d'hypsodontie pour *S. hendeyi* est de 1,51 ± 0,06. Cet indice le place dans la catégorie des ruminants herbivores brachyodontes. Le type de méso-usure observé pour *S. hendeyi* est similaire à celui des espèces ayant une alimentation mixte (mixte saisonnière). L'analyse des micro-traces d'usure confirme aussi une stratégie de type alimentation mixte pour *S. hendeyi*. Considérés simultanément, les résultats indiquent que la préférence alimentaire de ce giraffidé éteint est assez similaire à celle des espèces ayant une alimentation mixte saisonnière et ne montre aucune similarité avec les paisseurs. Les légères différences dans le type d'alimentation mixte sont discutées et soulignent les contraintes de chaque méthode pour l'interprétation de l'alimentation des herbivores fossiles. L'importance de ces résultats en terme d'évolution des stratégies alimentaires parmi les Sivatheriinae africains est également discutée.

MOTS CLÉS
Mammalia,
Giraffidae,
Sivatheriinae,
Afrique du Sud,
micro-traces,
méso-usure,
paléorégime.

INTRODUCTION

The dietary preference of an early Pliocene giraffid, *Sivatherium hendeyi* (Giraffidae Gray, 1821, Sivatheriinae Zittel, 1993), is investigated by means of three dietary reconstruction tools – hypsodonty index, mesowear and microwear. The determination from unworn teeth (used for hypsodonty index) provides a broad indication of diet, with more pronounced hypsodonty indicating a larger wear (attrition and abrasion). The mesowear method is based on a combined evaluation of the relative amounts of attritive and abrasive wear on occlusal dental enamel and gives a reasonably good estimation of the diet of an animal throughout its life. Microwear investigations are also applied to provide insight of the "last" meals of the animal prior to death.
The diet of fossil Giraffidae was until recently thought to be similar to that of extant giraffes (i.e. that they were committed browsers). In other words, all Giraffidae were described traditionally as browsers. Such notion changed when Solounias *et al.* (1988) showed that the extinct giraffid *Samotherium boissieri* Major, 1888 from the Miocene of Samos (Greece) was a mixed feeder-grazer. Solounias and co-workers (Solounias *et al.* 1988, 2000; Solounias & Moelleken 1993) showed, using tooth microwear analyses and premaxillary shape, that the diets of fossil Giraffidae are highly heterogeneous. For example, the Sivatheriinae *Bramatherium megacephalum* (Lydekker, 1878) and *Sivatherium giganteum* Falconer & Cautley, 1835 were probably grazers. Of the two Sivatheriinae *s.l.*, *Giraffokeryx punjabensis* Pilgrim, 1910, was a mixed feeder whereas "*Palaeotragus*" *primaevus* Churcher, 1970 was a browser. The Sivatheriinae, *Helladotherium duvemoyi* Gaudry, 1860, was also a browser. Among the Giraffinae and Palaeotraginae Pilgrim, 1911 there are also browsing, grazing and mixed feeding taxa. In addition, Solounias & Semprebon (2002) found that the okapi (*Okapia johnstoni* (Sclater, 1901)), the

second and rare extant species of Giraffidae, is not a browser but a fruit-dominated browser while the giraffe (*Giraffa camelopardalis* (Linnaeus, 1758)) can be redefined as a leaf-dominated browser. Such dietary data suggest that giraffid grazing was taking place before the expansion of C_4 grasslands. Some giraffids were mixed feeders around 6 to 8 My ago (Cerling *et al.* 1997), and as such, they were feeding on C_3 grasses, which are dominant in wooded environments (in open meadows and near the margins of water). Since, Harris & Cerling (1998), report that African sivatheres became grazers during the late Pliocene, when the C_4 expansion took place, we were interested to investigate the diet of the South African sivathere *S. hendeyi*.

The dietary preferences of *S. hendeyi* are not only important to help elucidate dental defects such as enamel hypoplasia, which are particularly abundant in this animal (Franz-Odendaal *et al.* 2003, 2004), but also because it should provide clarity on the evolution of the diets of African Sivatheriinae, especially in Southern Africa where no data are currently available. None of these methods have previously been applied to any of the fauna of Langebaanweg. Previous dietary interpretations of herbivores from this locality were largely based on general comparisons with extant animals (e.g., by Hendey 1976, 1981, 1983, 1984). Using this approach, Hendey assumed that the short-necked giraffid, *S. hendeyi*, was a browser similar to extant giraffes. In the last 20 years, however, several methods have been developed for determining the diets of extinct mammals. Stable isotope analysis were unable to determine the diet of *S. hendeyi* and other herbivores because of a strong C_3 dominant signature at Langebaanweg which could be grazing on C_3 grasses or browsing (Franz-Odendaal *et al.* 2002).

ABBREVIATIONS

HI	hypsodonty index;
m2	mandibular second molar;
M2	maxillary second molar;
PQL	Palaeontology Quaternary Langebaanweg collection;
SAM	South African Museum, Cape Town.

MATERIAL AND METHODS

S. hendeyi teeth from the Pelletal Phosphate Member at Langebaanweg (18°9'E, 32°58'S), South Africa, housed at the South African Museum, Iziko Museums of Cape Town, were examined. The HI was determined based on the measurements of two completely unworn m3s. The HI for *S. hendeyi* was determined according to Janis (1988) where HI = unworn m3 height/m3 width. Thirty M2 and 30 m2 were selected for mesowear analyses according to Fortelius & Solounias (2000). The mesowear method determines average diet based on two variables – cusp relief and cusp shape. Both variables were determined by direct observation and the percentage of teeth with high/low cusps and sharp/round/blunt cusps was calculated for the species. These variables were then plotted against HI, as recommended by Fortelius & Solounias (2000). The new light microscope method for examining microwear scar topography established by Solounias & Semprebon (2002) was applied to 52 lower third molars (Appendix A). Clear epoxy casts were first made and then examined for microwear scarring. The average number of pits and scratches per cast was calculated, as recommended by Solounias & Semprebon (2002), and used to obtain an average for the species. Pits were also classified as small or large and scratches were qualitatively scored by determining whether 1) only fine scratches were present; 2) only coarse scratches were present; or 3) whether a mixture of fine and coarse scratches were present within the counting area (see Solounias & Semprebon 2002 for details). The presence of cross scratches and gouges was also noted. Statistical analyses were performed using Statistica (version 6.0).

RESULTS

HYPSODONTY INDEX

S. hendeyi is brachyodont. However, it is slightly more hypsodont than the giraffe. The published HI for the extant giraffe, *G. camelopardalis*, is 1.2 (Janis 1988). The HI for *S. hendeyi* determined

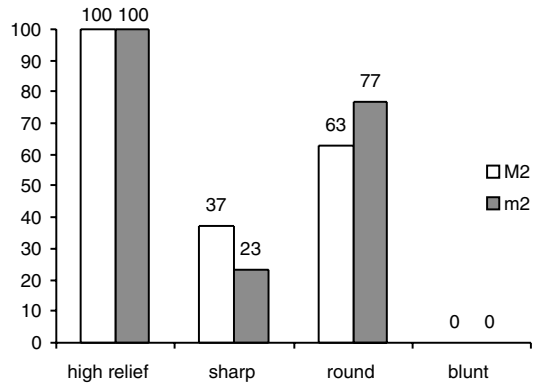

FIG. 1. — Mesowear cusp relief and cusp shape for *S. hendeyi* (Harris, 1976) lower (m2) and upper (M2) molars. Cusp relief (100% high) and cusp shape (sharp and round) are shown. No blunt teeth or teeth with low relief were observed.

here is 1.51 ± 0.06 (n = 2). By including nine slightly worn m3s, a recalculation of HI gives 1.33 ± 0.1 (n = 11). HI is used here primarily to evaluate mesowear results and to compare it to extant giraffids (*Giraffa camelopardalis* and *Okapia johnstoni*). Since there is no difference in the mesowear results obtained when using 1.3 or 1.5 as the HI, the HI of 1.3 is used for *S. hendeyi* in all graphical representations. Accession numbers as well as crown height and width measurements are given in Appendix B.

MESOWEAR ANALYSIS

The mesowear of *S. hendeyi* is similar to both browsers and mixed feeders (browsers such as the gerenuk (*Litocranius walleri* (Brooke, 1879)) and mixed feeders such as the lama (*Lama glama* (Linnaeus, 1758)) and other mixed feeders). The raw data for each mesowear variable for each second molar is provided in Appendix C and D and the absolute and relative scorings for upper and lower teeth are provided in Table 1. The average occlusal relief for upper teeth is very similar to that in lower teeth with all *S. hendeyi* teeth having high relief. In terms of cusp shape, maxillary teeth have 63% round cusps, 37% sharp cusps and no blunt cusps, whereas mandibular teeth have slightly more rounded (77%) and fewer sharp (23%) cusps than upper teeth (Fig. 1). No blunt cusps were observed in the either dental sample. Mesowear results for *S. hendeyi* were plotted against mesowear variables obtained by Fortelius & Solounias (2000) for 64 extant ungulate species in Figure 2. Bivariate plots, for the three dietary classes (browsers, grazers, mixed feeders), of percentage high occlusal relief against HI indicates that *S. hendeyi* falls within the range for browsers and mixed feeders. *S. hendeyi* is not similar to grazers (no blunt cusps). The same result is obtained when cusp shape is plotted against HI (Fig. 3). That is, no similarities with grazers were found.

MICROWEAR ANALYSIS

The microwear shows that *S. hendeyi* was a mixed feeder. Examination of individual microwear scoring for each specimen shows that approximately half of the teeth have microwear similar to that of browsers and the other half similar to that of grazers. This is a bimodal distribution of microwear as in mixed feeders (Solounias & Semprebon 2002). Average values for each microwear variable are given in Table 2. Average number of pits and scratches for *S. hendeyi* are 20.5% and 15.8% respectively, per unit area. The range of pit counts per tooth was 3.5 to 73.

TABLE 1. — Absolute and relative mesowear scorings of *S. hendeyi* (Harris, 1976) upper (M2) and lower (m2) second molars following the scoring convention of Fortelius & Solounias (2000). Percentages of high, low, sharp, round and blunt cusps were calculated for each dental sample. Abbreviation: **n**, number of specimens.

	Counts						Percentages				
		Cusp relief		Cusp shape			Cusp relief		Cusp shape		
	n	Low	High	Sharp	Round	Blunt	% Low	% High	% Sharp	% Round	% Blunt
M2	30	0	30	11	19	0	0	100	37	63	0
m2	30	0	30	7	23	0	0	100	23	77	0

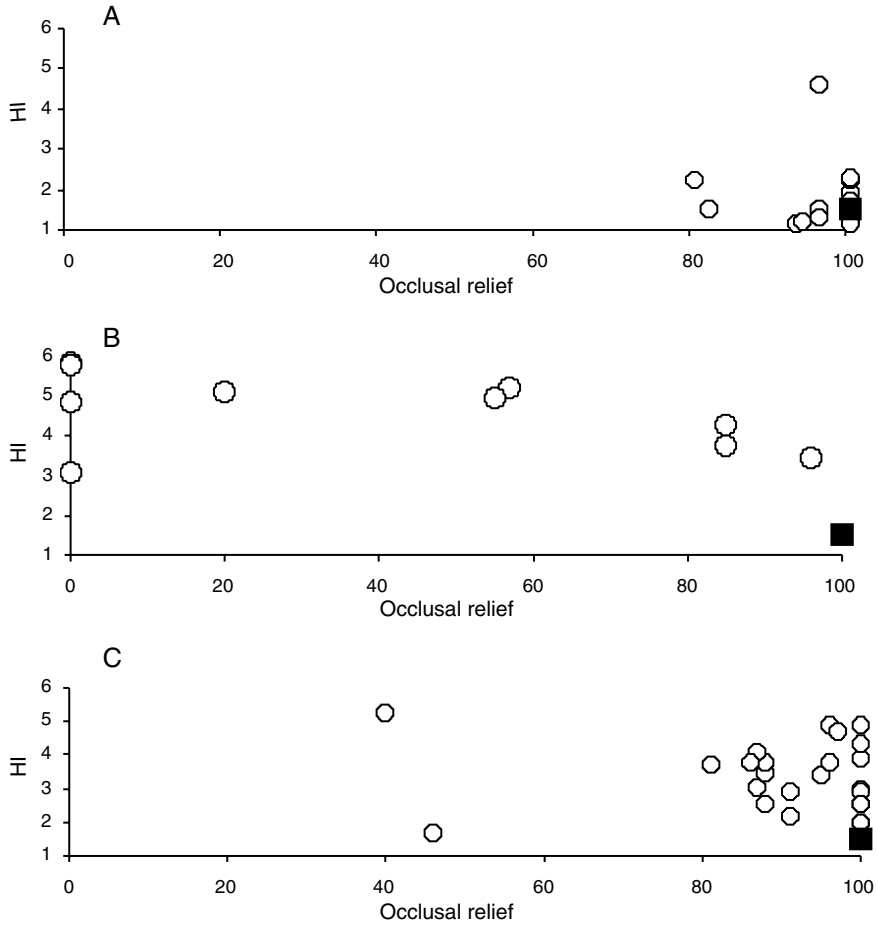

FIG. 2. — Bivariate plots of percentage high occlusal relief against hypsodonty index (HI); **A**, browsers; **B**, grazers; **C**, mixed feeders. Data from Fortelius & Solounias (2000) (○) and *S. hendeyi* (■) (Harris 1976).

Average scratch counts were slightly more variable ranging from 4 to 38. In *S. hendeyi* large pits were present in 48.1% of teeth. The average pit and scratch counts for browsing phase is 19.4 pits and 10.9 scratches, compared to 22.1 pits and 23 scratches for the grazing phase.

Microwear data were compared to data obtained by Solounias & Semprebon (2002) for 50 extant ungulate species (Fig. 4). Taking both average pits and average scratch counts into account, *S. hendeyi* falls on the browser side of a division between traditional grazers (more than 17 scratches) and traditional browsers (less than 17 scratches) (Fig. 4) (see Discussion below).

DISCUSSION

HYPSODONTY INDEX

The HI for *S. hendeyi* (1.51) falls within the category of brachyodont as defined by both Janis (1988) and Fortelius & Solounias (2000). The tooth morphology is similar to that of other brachyodont species. Using Janis' (1988) interpretations of hypsodonty, *S. hendeyi* also falls within the range for mixed feeders in closed habitats, and all types of browsers (regular, selective and high-level). In addition the HI of *S. hendeyi* is most similar to the average for selective browsers (1.5 ± 0.08). By comparing the HI of *S. hendeyi* to the published

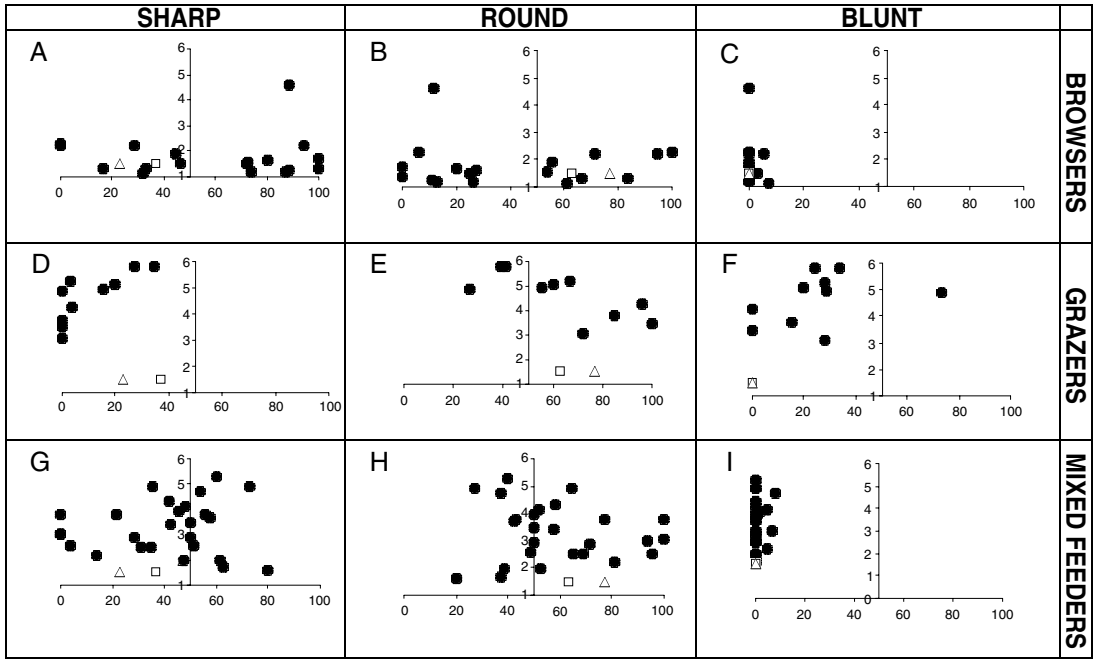

FIG. 3. — Mesowear analyses of cusp shape in *S. hendeyi* (Harris, 1976). *S. hendeyi* data for lower (□) and upper (△) teeth are plotted against 64 ungulate species (●) from Fortelius & Solounias (2000); **A**-**C** browsers; **D**-**F**, grazers; **G**-**I**, mixed feeders. In all graphs, y-axis represents hypsodonty index and x-axis represents one of the three mesowear variables (percentage sharp cusps in A, D, G; percentage round cusps in B, E, H, and percentage blunt cusps in C, F and I).

HI of 127 species of living ungulates (Janis 1988), *S. hendeyi* HI is most similar to that of two cervids, *Capreolus capreolus* (Linnaeus, 1758) (roe deer) and *Blastocerus dichotomus* Wagner, 1844 (marsh deer) (Janis 1988). These two animals were classified by Janis (1988) as mixed feeders in closed habitats. However, both of these animals have body weights of less than 150 kg, which is significantly smaller than that estimated for *S. hendeyi*. Janis (1988) suggests that HI of fossil taxa should be compared to animals of similar body size. However there are very few living ungulates with body masses equivalent to that of *S. hendeyi*. *S. hendeyi* with its robust metapodials is estimated to have been heavier than *G. camelopardalis* (*c.* 1075 kg) and more similar to the living rhinoceroses (see Janis 1988). The published HIs of these animals are 1.59 for *Rhinoceros unicornis* Linnaeus, 1758, 1.72 for *R. sondaicus* Desmarest, 1822, 2.24 for *Diceros bicornis* Linnaeus, 1758 and 1.2 for *G. camelopardalis* (see Janis 1988). The extant giraffe is a high-level browser whereas the rhinoceroses are mixed feeders in closed habitats.

MESOWEAR

Although cusp relief in the extant giraffe, *G. camelopardalis*, and *S. hendeyi* are similar, cusp shape differs markedly. In terms of numbers, *G. camelopardalis* has 74% sharp cusps and 26% round cusps compared to the less marked pattern in *S. hendeyi* (63% sharp, 37% round) (Fortelius & Solounias 2000). Bivariate plots of mesowear variables indicate that *S. hendeyi* had a different diet from those of the extant giraffes. The sivathere appears to be most similar to mixed feeders. No evidence for pure grazing was found.

MICROWEAR

Solounias & Semprebon (2002: table 2) presented five types of diets ranging from extreme

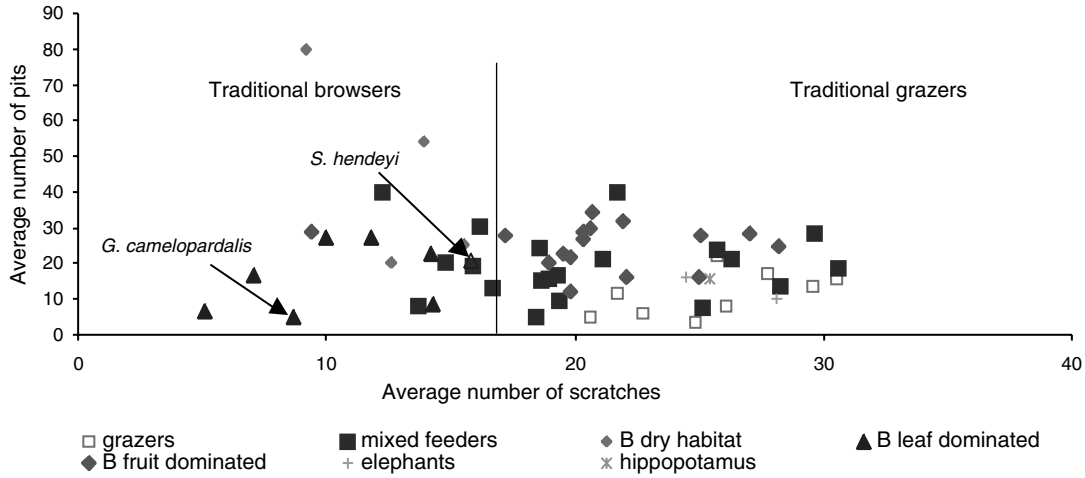

FIG. 4. — Microwear data for *S. hendeyi* (Harris, 1976) (△) compared to extant ungulates (from Solounias & Semprebon 2002). Browsers in dry, leaf-dominated and fruit-dominated habitats are shown.

TABLE 2. — Microwear data for *S. hendeyi* (Harris, 1976). Average number of pits and scratches are reported. The percentage of large pits (LP), cross-scratches (CS), gouges (GOU), fine, coarse and mixed scratch textures are also reported. Abbreviation: **n**, number of specimens.

n	Pits	Scratches	LP	CS	GOU	Fine	Coarse	Mixed
52	20.5	15.8	48.1	67.3	48.1	54.9	11.8	33.3

browsing to extreme grazing. The four columns in between the two extremes have been termed the transitional browsing-grazing group. The bimodal microwear pattern of *S. hendeyi* is similar to the mixed feeders of column 2 and in particular to *Gazella granti* Brooke, 1872 (Grant's gazelle), *Tragelaphus scriptus* (Pallas, 1766) (bush buck) and other seasonal-regional mixed feeders (Solounias & Semprebon 2002: table 2). Microwear shows similarities with *Tragelaphus scriptus* (19.1% pits, 15.8% scratches) and *Gazella granti* (20.5% pits, 14.7% scratches). Solounias & Semprebon (2002: table 2, column 2) includes additional dietary categories to the mixed feeders; such as fruit-browsers and leaf browsers. Comparison of *S. hendeyi* to the leaf-dominated browser *Odocoileus hermionus* (Rafinesque, 1817) (22.7% pits, 14.2% scratches) is of interest. Solounias & Semprebon (2002) also show that seasonal and regional mixed feeders show a greater dispersion of scratch numbers and a higher number of pits on average than typically seen in grazers. *S. hendeyi* has a wide range of scratch counts (from 1 to 34 per counting area) and a high number of pits (up to 70) indicating greatest similarity to the seasonal mixed feeders.

Microwear can also distinguish browsing from grazing based on scratch textures (widths of scratches). Solounias & Semprebon (2002) suggest that grazers have more coarse scratches and browsers and mixed feeders have more fine scratches. *S. hendeyi* teeth have all three scratch textures (fine, coarse and mixed), however coarse scratches are the least prevalent (Table 2) illustrating that *S. hendeyi* was more similar to browsers and mixed feeders.

In summary, microwear data seems to indicate that *S. hendeyi* was probably a seasonal mixed feeder – it browsed about 50% of the time and grazed about 50% of the time on grasses that do

not form many wide scratches. It must be noted that Solounias & Semprebon's (2002) analysis correctly classified all extant browsers in their database but only 38% of mixed feeders. The correct classification is less reliable for mixed feeders because of the very nature of what it means to be a mixed feeder. Mixed feeders incorporate a relatively high percentage of browse in their diet and may therefore be misclassified as browsers. Since both microwear counts and scratch textures suggest mixed feeding, this is probably the likely diet of *S. hendeyi* in Southern Africa.

CONCLUSION

All three dietary assessments of the African sivathere, *S. hendeyi* from the early Pliocene, indicate that this animal was not a grazer and is best categorized as being a mixed feeder. Mesowear, which incorporates HI, indicates that *S. hendeyi* is most similar to abrasion-dominated seasonal mixed feeders. Microwear data also classifies *S. hendeyi* as a mixed feeder but more likely an attrition-dominated mixed feeder. *S. hendeyi* was clearly not an exclusive browser or grazer. Some possible reasons for the differences in abrasion and attrition within the mixed feeding category are outlined below.

The Langebaanweg assemblage represents a number of populations or cohorts of animals that accumulated over 0.5 My (Hendey 1981, 1984) and it is therefore highly likely that animals died at different times of the year and hence had diets that varied seasonally. This could account for the large differences in scratch and pit counts for individual *S. hendeyi* teeth. Alternatively, a transition in overall diet was made, possibly relating to the changing environmental conditions (Franz-Odendaal *et al*. 2003, 2004). The microwear dietary evaluation may be slightly less accurate than the mesowear one, which incorporates HI, and which gives average diet for the species (over geological time) rather than scoring individual "last" meals and averaging them out (as is the case with the microwear method).

Another source of complexity is that the southwestern region of South Africa is dominated by a unique fynbos vegetation. Fynbos is an evergreen species-rich sclerophyllous macchia vegetation unique to the Western Cape, South Africa. Scott (1995) showed that fynbos was beginning to establish itself during the period of deposition of the Pelletal Phosphate Member at Langebaanweg *c.* 5 My ago. The microwear features that this vegetation would cause are not known, and therefore interpretations of what is causing the observed gouges, cross scratches, large pits, coarse scratches etc. in *S. hendeyi* is not clear. Determining the wear features that fynbos produces is not easily accomplished as few extant ungulates live in the fynbos areas of South Africa today.

Acknowledgements

We would like to thank the staff of the SAM for access to the Langebaanweg material. We are grateful to The National Research Foundation (South Africa) and the University of Cape Town (South Africa) for funding this study. We also thank Thomas Kaiser (Greifswald University, Germany) for discussions, Floret Rivals (New York College of Osteopathic Medicine, USA) for the French translation, and Mikael Fortelius (University of Helsinki, Finland) and Raymond L. Bernor (Howard University, USA) for their valuable comments on our manuscript.

REFERENCES

CERLING T. E., HARRIS J. M., MACFADDEN B. J., LEAKEY M. G., QUADE J., EISENMANN V. & EHLERINGER J. R. 1997. — Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 152-157.

FORTELIUS M. & SOLOUNIAS N. 2000. — Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstruction paleodiets. *American Museum Novitates* 3301: 1-36.

FRANZ-ODENDAAL T. A., LEE-THORP J. A. & CHINSAMY A. 2002. — New evidence for the lack of C_4 grassland expansions during the Early

Pliocene at Langebaanweg, South Africa. *Paleobiology* 28: 378-388.

FRANZ-ODENDAAL T. A., LEE-THORP J. A. & CHINSAMY A. 2003. — Insights from stable light isotopes on enamel defects and weaning in Pliocene herbivores. *Journal of Bioscience* 28: 101-109.

FRANZ-ODENDAAL T. A., CHINSAMY A. & LEE-THORP J. A. 2004. — High prevalence of enamel hypoplasia in an Early Pliocene giraffid (*Sivatherium hendeyi*) assemblage. *Journal of Vertebrate Paleontology* 24 (1): 235-244.

HARRIS J. M. & CERLING T. E. 1998. — Isotopic changes in the diet of Giraffids. *Journal of Vertebrate Paleontology* 18, Supplement to 3: 49A.

HENDEY Q. B. 1976. — The Pliocene fossil occurrences in "E" quarry, Langebaanweg, South Africa. *Annals of the South African Museum* 69: 215-247.

HENDEY Q. B. 1981. — Palaeoecology of the Late Tertiary fossil occurrences in "E" quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum* 84: 1-104.

HENDEY Q. B. 1983. — Palaeoenvironmental implications of the Late Tertiary vertebrate fauna of the fynbos region. *South African National Science Programmes Report* 75: 100-116.

HENDEY Q. B. 1984. — Southern African Late Tertiary vertebrates, *in* KLEIN R. G. (ed.), *Southern African Prehistory and Paleoenvironments*. A.A. Balkema, Rotterdam: 81-106.

JANIS C. M. 1988. — An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference, *in* RUSSEL D. E., SANATORO J. P. & SIGOGNEAU-RUSSEL D. (eds), Teeth Revisited. Proceedings of the VIIth International Symposium on Dental Morphology, Paris, May 1986. *Mémoires du Muséum national d'Histoire naturelle*, sér. C, Sciences de la Terre 53: 367-387.

SCOTT L. 1995. — Pollen evidence for vegetational and climatic change in southern Africa during the Neogene and Quaternary, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New York: 65-76.

SOLOUNIAS N. & MOELLEKEN S. M. C. 1993. — Determination of dietary adaptations of some extinct ruminants determined by premaxillary shape. *Journal of Mammology* 74 (4): 1059-1071.

SOLOUNIAS N. & SEMPREBON G. 2002. — Advances in the recontruction of ungulate ecomorphology and application to early fossil equids. *American Museum Novitates* 3366: 1-49.

SOLOUNIAS N., TEAFORD M. & WALKER A. 1988. — Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology* 14: 287-300.

SOLOUNIAS N., MCGRAW W. S., HAYEK L. & WERDELIN L. 2000. — The Paleodiet of Giraffidae, *in* VRBA E. S. & SCHALLER G. B. (eds), *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics, and Conservation*. Yale University Press, New Haven, Connecticut: 84-95.

Submitted on 6 November 2003;
accepted on 16 April 2004.

APPENDIX A

Accession numbers of mandibular m3s of *Sivatherium hendeyi* (Harris, 1976) used for microwear analysis. Abbreviations: **SAM**, South African Museum, Cape Town; **PQL**, Palaeontology Quaternary Langebaanweg collection.

Accession number	Accession number	Accession number	Accession number
SAM PQL 43964	SAM PQL 44024	SAM PQL 62737/2	SAM PQL 62737/27
SAM PQL 43966	SAM PQL 44034	SAM PQL 62737/4	SAM PQL 62737/28
SAM PQL 43976	SAM PQL 44945	SAM PQL 62737/5	SAM PQL 62737/32
SAM PQL 43994	SAM PQL 44948	SAM PQL 62737/11	SAM PQL 62737/34
SAM PQL 43995	SAM PQL 44950	SAM PQL 62737/12	SAM PQL 62737/36
SAM PQL 43999	SAM PQL 44952	SAM PQL 62737/15	SAM PQL 62737/36
SAM PQL 44003	SAM PQL 44956	SAM PQL 62737/16	SAM PQL 62737/39
SAM PQL 44004	SAM PQL 44959	SAM PQL 62737/19	SAM PQL 62737/43
SAM PQL 44008	SAM PQL 44970	SAM PQL 62737/22	SAM PQL 62737/44
SAM PQL 44011	SAM PQL 44971	SAM PQL 62737/23	SAM PQL 62737/45
SAM PQL 44012	SAM PQL 44972	SAM PQL 62737/24	SAM PQL 62737/49
SAM PQL 44020	SAM PQL 44976	SAM PQL 62737/25	SAM PQL 62737/50
SAM PQL 44021	SAM PQL 44977	SAM PQL 62737/26	SAM PQL 62738/38

APPENDIX B

Specimens used to calculate the hypsodonty index of *Sivatherium hendeyi* (Harris, 1976). Abbreviations: **SAM**, South African Museum, Cape Town; **PQL**, Palaeontology Quaternary Langebaanweg collection.

Accession number	Crown height (mm)	Width (mm)	Hypsodonty index
SAM PQL 62732/33, unworn	46.89	30.33	1.55
SAM PQL 62733/63, unworn	43.50	29.72	1.46
SAM PQL 62733/11	39.18	32.10	1.22
SAM PQL 62732/12	42.10	35.08	1.20
SAM PQL 62733/20	40.63	30.28	1.34
SAM PQL 62732/26	47.88	36.03	1.33
SAM PQL 62732/28	47.52	31.28	1.52
SAM PQL 62732/42	45.70	36.52	1.25
SAM PQL 62733/43	44.78	35.42	1.26
SAM PQL 62732/45	45.26	35.87	1.26
SAM PQL 62732/49	40.04	32.83	1.22

APPENDIX C

Raw mesowear data of *Sivatherium hendeyi* (Harris, 1976) lower second molars. Cusp shape is described as round (R), sharp (S) and blunt (B). Occlusal relief is described as high (H) or low (L) depending on how high the cusps rise above the valley between them. Abbreviations: **SAM**, South African Museum, Cape Town; **PQL**, Palaeontology Quaternary Langebaanweg collection.

Accession number	Cusp shape	Occlusal relief	Accession number	Cusp shape	Occlusal relief
SAM PQL 43967	R	H	SAM PQL 44917	R	H
SAM PQL 43976	S	H	SAM PQL 44968	R	H
SAM PQL 43997	R	H	SAM PQL 44978	S	H
SAM PQL 44001	R	H	SAM PQL 44970	R	H
SAM PQL 44004	R	H	SAM PQL 44967	S	H
SAM PQL 44008	R	H	SAM PQL 44966	R	H
SAM PQL 44024	R	H	SAM PQL 44985	R	H
SAM PQL 43994	S	H	SAM PQL 45167	S	H
SAM PQL 43978	R	H	SAM PQL 44032	R	H
SAM PQL 43889	S	H	SAM PQL 44021	R	H
SAM PQL 44895	R	H	SAM PQL 43995	R	H
SAM PQL 44956	R	H	SAM PQL 43959	R	H
SAM PQL 44943	R	H	SAM PQL 44028	R	H
SAM PQL 44957	R	H	SAM PQL 43992	S	H
SAM PQL 44921	R	H	SAM PQL 44035	R	H

APPENDIX D

Raw mesowear data of *Sivatherium hendeyi* (Harris, 1976) upper second molars. Cusp shape is described as round (R), sharp (S) and blunt (B). Occlusal relief is described as high (H) or low (L) depending on how high the cusps rise above the valley between them. Abbreviations: **SAM**, South African Museum, Cape Town; **PQL**, Palaeontology Quaternary Langebaanweg collection.

Accession number	Cusp shape	Occlusal relief	Accession number	Cusp shape	Occlusal relief
SAM PQL 44658	S	H	SAM PQL 44743	S	H
SAM PQL 44659	S	H	SAM PQL 44745	R	H
SAM PQL 44661	R	H	SAM PQL 44759	R	H
SAM PQL 44663	R	H	SAM PQL 44760	R	H
SAM PQL 44668	S	H	SAM PQL 44740	R	H
SAM PQL 44665	R	H	SAM PQL 44761	S	H
SAM PQL 44660	S	H	SAM PQL 44739	S	H
SAM PQL 44664	R	H	SAM PQL 44734	R	H
SAM PQL 44674	R	H	SAM PQL 44736	S	H
SAM PQL 44671	S	H	SAM PQL 44937	S	H
SAM PQL 44672	R	H	SAM PQL 44729	S	H
SAM PQL 44673	R	H	SAM PQL 44731	R	H
SAM PQL 44670	R	H	SAM PQL 44723	R	H
SAM PQL 44751	R	H	SAM PQL 44752	R	H
SAM PQL 44755	R	H	SAM PQL 44758	R	H