Variability in Plio-Pleistocene climates, habitats, and ungulate biomass in southern Africa

J. Francis Thackeray and S. Reynolds

Vrba,[1] and de Monecal and Bloemendal[2] have emphasised the importance of climatic change, particularly temperature, in the context of evolution on the African continent within the past 5 million years. There is no doubt that long-term changes in climate would have affected African habitats, which in turn would have affected the distribution and abundance of populations of various mammalian taxa, including ungulates and hominids. In this study we explore relationships between oxygen isotope ratios (as determined from Shackleton's[3] analysis of foraminifera from deep-sea cores), and estimates of ungulate biomass as determined from faunal assemblages from Plio-Pleistocene sites in southern Africa, using an approach outlined previously.[4] We go further to assess temporal variability in ungulate biomass in terms of changes in habitat, gene pools and hominid evolution.

Damuth[5] has previously shown a general relationship between mean adult body weight and population density of mammalian taxa. The relationship has been used in conjunction with data on modern African ungulates to obtain ungulate biomass for areas in sub-Saharan Africa.[4] Estimates of mean adult body mass of any mammalian species is a requirement if the same relationship is to be applied to faunal assemblages from palaeontological sites of known age. For purposes of this study, we have obtained the following general equation for estimating mean adult body mass (MAB) from first lower molar dimensions (M_1), based on collections of extant mammalian species represented in collections at the Transvaal Museum:

$$\text{Log MAB} = 3.442 \log M_1 - 2.263 \quad (r = 0.91)$$

We have used this relationship, in combination with faunal data from Plio-Pleistocene sites in the interior of southern Africa,[6] to estimate ungulate biomass for particular assemblages of ungulate taxa for which age estimates are available. Included in this analysis are assemblages from Sterkfontein (Members 4 and 5), Swartkrans (Members 1, 2 and 3), Kromdraai A, Kromdraai B (Member 3), Makapansgat, Plovers Lake, Cornelia, Florisbad, Equus Cave and the Cave of Hearths. The estimates of ungulate biomass (UB) for inland South African assemblages were obtained using the approach described by Thackeray[4] for modern fauna from sub-Saharan environments. The results were then compared to pene-contemporaneous oxygen isotope ratios obtained from Plio-Pleistocene deep-sea cores,[3] averaging isotope data within intervals of *circa* 100 000 years.

The following relationship was obtained:

$$\text{UB} = 25.8\ \delta\ ^{18}\text{O} - 72.9, \quad (r = 0.75)$$

where UB refers to ungulate biomass predicted for past environments in the interior of southern Africa (including the Sterkfontein valley), in units of kilograms per hectare (kg ha^{-1}). This equation was then used to assess ungulate biomass variability for southern African palaeoenvironments, based on Shackleton's high resolution oxygen isotope record from deep-sea cores (ODP sites 677 and 846). Results are shown in Fig. 1.

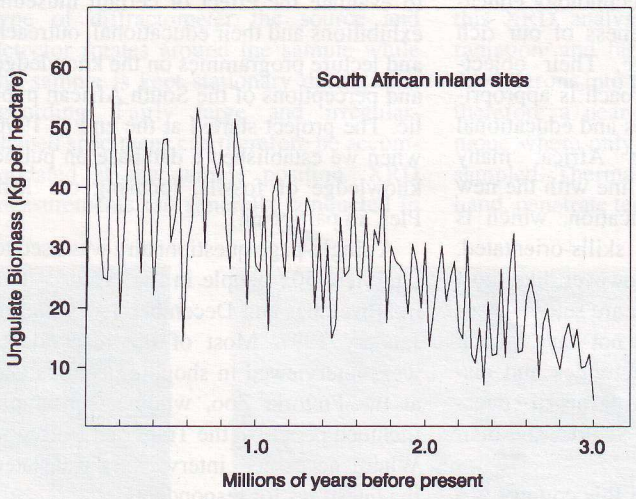

Fig. 1. Estimated ungulate biomass (kg per hectare) for interior regions of southern Africa including the Sterkfontein valley, South Africa. Relatively low ungulate biomass values can be associated with a relatively high degree of woodland and forest cover, during periods between 3 and 2 million years ago, as opposed to higher ungulate biomass values for later intervals, associated with a greater degree of mixed grassland savanna. Such fluctuations in ungulate biomass at intervals of less than 100 000 years imply episodes of expansion of woodland and forest habitats (in warm, moist intervals), followed by contraction and fragmentation of such habitats during cooler intervals, allowing for gene flow between certain populations (including hominids). Episodic gene flow may have contributed to the perpetuation of lineages.

Two observations can be made, using modern ungulate biomass estimates and present-day African habitats as a frame of reference,[4] for assessing *relative* changes in ungulate biomass in the interior regions of South Africa:

1) Relatively low ungulate biomass estimates are obtained for the period between 3 and 2 million years ago (Myr), associated with limited temporal variability in biomass.

2) Higher biomass estimates are obtained within the period between 2 and 1 Myr, associated with an increased degree of temporal variability in biomass.

3) Yet higher ungulate biomass estimates are obtained for the period since 1 Myr, associated with a still greater degree of temporal variability.

From the study of ungulate biomass in modern African habitats,[4] it was evident that low biomass estimates can be associated with woodland and forest environments; higher ungulate biomass estimates can be associated with mixed woodland savanna habitats. The low ungulate biomass estimates for the interior regions of southern Africa between 3 and 2 Myr can be interpreted in terms of a greater degree of woodland and forest, as compared to modern environments in the same area. Higher ungulate biomass estimates for later periods, associated with a greater degree of temporal variability in biomass, can be interpreted in terms of a greater degree of mixed grassland savanna and a greater temporal variability in habitats, at intervals of less than 100 000 years.

We infer that woodland habitats can have expanded and contracted within intervals of less than 100 000 years, in response to global changes in climate (primarily temperature), associated with Milankovitch cycles within the last 3 million years. Today woodland habitats in parts of subequatorial Africa separate Serengeti grasslands in East Africa from grasslands on the highveld of South Africa. How-

ever, episodic cold or cool intervals, occurring at intervals of 100 000 years or less, would have led to repeated episodes of fragmentation of woodland habitats, allowing for episodic gene flow to occur between populations of various taxa (e.g. wildebeest) that would otherwise have been separated by woodland, as is the case today for East African and South African populations of blue wildebeest, *Connochaetes taurinus*, a single species separated today by Miombo woodland. We suggest that episodic expansion and contraction of woodland habitats (occurring at intervals of less than 100 000 years) were of such short duration that speciation 'events' would not always be expected as a result of habitat fragmentation linked to climatic change over the African continent; instead, high genetic variability may have been maintained within lineages, such that boundaries between species and genera (hominid or ungulate) may be especially difficult to recognise.

We recommend that hominid fossils from sites in East and South Africa be studied without necessarily attempting to 'pigeon-hole' particular fossils into one or other taxon, recognising that boundaries between taxa may be blurred on account of episodic expansion and contraction of habitats, associated with repeated episodes of gene flow between populations of taxa that were only temporally isolated by habitat changes.

This research has been supported by a grant from the Foundation for Research Development.

1. Vrba E.S. (1995). On the connections between paleoclimate and evolution. In *Paleoclimate and Evolution, with Emphasis on Human Origins*, eds E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, pp. 24–48. Yale University Press, New Haven.
2. De Menocal P.B. and Bloemendal J. (1995). Plio-Pleistocene climatic variabilty in subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach. In *Paleoclimate and Evolution, with Emphasis on Human Origins*, eds E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, pp. 262–288. Yale University Press, New Haven.
3. Shackleton N.J. (1995). New data on the evolution of Pliocene climatic variability. In *Paleoclimate and Evolution, with Emphasis on Human Origins*, eds E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, pp. 242–248. Yale University Press, New Haven.
4. Thackeray J.F. (1995). Exploring ungulate diversity, biomass, and climate in modern and past environments. In *Paleoclimate and Evolution, with Emphasis on Human Origins*, eds E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, pp. 479–482. Yale University Press, New Haven.
5. Damuth J. (1981). Population density and body size in mammals. *Nature* **290**, 699–700.
6. Smithers R.H.N. (1983). *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.

The authors are in the Department of Palaeontology and Palaeoenvironmental Studies, Transvaal Museum, P.O. Box 413, Pretoria, 0001 South Africa.

Evaluating public awareness of 'Mrs Ples' and palaeontological heritage

J.F. Thackeray and Kathryn Mathers

Museums in South Africa are positioned to play a fundamental and vital role in improving science and technology education, and raising awareness of our rich palaeontological heritage. Their object-centred educational approach is appropriate for people of all ages and educational achievement. In South Africa, many museums are already in line with the new approach to school education, which is multidisciplinary and skills-orientated. Museum programmes, however, like most educational programmes, are seldom evaluated. At present we do not have a clear idea of the impact of activities and displays at our museums, in terms of educational value, attitudes of visitors and their perception of a subject.

Palaeoanthropology in this country is a field that has not been well covered in school curricula, and only tentatively addressed by many museums. The Transvaal Museum is promoting public awareness of South Africa's palaeontological heritage in 1997, the year in which the 50th anniversary of the discovery of 'Mrs Ples' is celebrated. This offers an opportunity to evaluate knowledge before and after publicity associated with exhibitions, including the display of the original 'Mrs Ples', during the month of April, at the Transvaal Museum in Pretoria and then at the Science Festival in Grahamstown.

We have launched a long-term project to evaluate the effect of certain museum exhibitions and their educational, outreach and lecture programmes on the knowledge and perceptions of the South African public. The project started at the end of 1996 when we established a database on public knowledge of fossils, focusing on 'Mrs Ples' in particular.

A single-page questionnaire was used to interview 502 people in the Pretoria area in November and December 1996, and in January 1997. Most of the respondents were interviewed in shopping centres and at the Pretoria Zoo, while a subsample included people at the Transvaal Museum. Where necessary, interviewers translated the questions for respondents.

The majority of respondents (approximately 60%) were African language speakers, about 20% were Afrikaans speakers, and another 20% spoke English. Most of the respondents (about 80%) were between the ages of 18 and 45 years. Approximately 10% were younger than 18, and almost 10% were older than 45 years.

Professionals and students account for almost 50% of the metropolitan sample; the other 50% include individuals in service, clerical and production industries, as well as housewives and schoolchildren (each comprising about 10% of the sample, respectively). People in the technical professions (2%) and retired individuals are under-represented. The sample is therefore not representative of the South African population, but is a good cross section of a metropolitan community.

Results are presented first for the metropolitan sample, excluding individuals visiting the Transvaal Museum. Only 13.3% of this sample said they had heard of 'Mrs Ples', and a slightly higher proportion (18.0%) had heard of australopithecines. A yet larger proportion of the sample (45%) knew about fossils. Surprisingly, given the lack of knowledge about australopithecines and 'Mrs Ples', many respondents in the metropolitan sample have visited Sterkfontein (31%), and the majority had visited a museum (80%), including the Transvaal Museum (67%).

In a separate study in January 1997, visitors to the Transvaal Museum were asked the same set of questions. Sixty-five per cent of the respondents indicated that they were aware of 'Mrs Ples' after they had gone through the 'Genesis II' hall featuring exhibitions of australopithecines.

Recent efforts to promote an awareness of 'Mrs Ples' through publicity in newspapers, a YouthLink programme (EcoLink '97) run at the Transvaal Museum, and

J.F. Thackeray is in the Department of Palaeontology and Palaeoenvironmental Studies, Transvaal Museum; Kathryn Mathers is in the Department of Anthropology and Archaeology, University of South Africa.