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Palaeogeography, Palaeoclimatology, Palaeoecology 221 (2005) 153–174

PALAEO

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Diets of modern and late Miocene hippopotamids: Evidence from carbon isotope composition and micro-wear of tooth enamel

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Received 17 September 2004; received in revised form 20 January 2005

Abstract

Carbon isotope composition and micro-wear analyses of tooth enamel were used to reconstruct the diet of late Miocene hippopotamids unearthed in the Toros-Ménalla area, Chad, contemporary to the oldest known hominids. A large sample of wild modern *Hippopotamus amphibius* from various locations in Africa was also analysed for comparison. Isotopic analyses showed that the modern hippo, reputedly a strict grazer, has a more varied diet than usually thought, including a significant amount of C_3 plants in closed to moderately open environments. Enamel formed before weaning was on average 3‰ depleted in ^{13}C compared to post-weaning enamel, a pattern that could be partially explained by milk consumption. The observed micro-wear pattern of the modern hippo differs from that of other modern ungulates. We explain the very abundant fine scratches and small pits found on these hippo teeth by the preference for fresh short grasses with low silicon content. The diet of the late Miocene hippopotamid was probably close to that of the modern *Hip. amphibius*, but included a larger amount of C_3 plants. This contradicts previous palaeoecological findings based on relative hypsodonty degree and indicates that the modern feeding behaviour of large hippos was already developed at the end of the Miocene, when C_4 grass exploitation by large ungulates became much more frequent in Africa. Finally, it also indicates that C_4 grasses were a significant component in late Miocene environments of Central Africa.

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Keywords: Palaeodiet; Hippopotamidae; Tooth enamel; Carbon stable isotopes; Dental micro-wear; Late Miocene; Chad; Africa

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0031-0182/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2005.02.010

1. Introduction

Fossil mammals are a major source of data for reconstructing late Neogene environments of Africa. However, many taxa are not or rarely considered for that purpose, although they may be of great palaeoecological significance. The fossil hippopotamids fall into this scheme. A recent work stresses the potential value of these mammals for palaeoenvironmental studies in Asia (Jablonski, 2003). This should also apply to African hippopotamids, which are among the most common mammals found in the late Neogene deposits of this continent (Coryndon, 1978; Harris et al., 1988; Harris, 1991; Faure, 1994; Harrison, 1997; Brunet and M.P.F.T., 2000; Alemseged, 2003; Weston, 2003). Moreover, the extant common hippo, *Hippopotamus amphibius*, is a keystone species of the lakes, rivers, and their surroundings in Sub-Saharan Africa (Kingdon, 1979; Eltringham, 1999). This semi-aquatic mammal directly and significantly influences different components of aquatic and peri-aquatic ecosystems. The trails of the modern common hippo modify the substrates of these ecosystems at both local and regional levels, inducing localized sedimentological structures (Deocampo, 2002) and shaping the geomorphology of hydrographical networks (McCarthy et al., 1998). Under water, hippos affect trophic inputs (Verheyen, 1954; Kingdon, 1979; Grey and Harper, 2002), water stratification (Wolanski and Gereta, 1999) and nutrient suspension (Verheyen, 1954). Above all, because of their conservative habitat, large size and grazing preferences, the common hippos play a dramatic role in the composition and regeneration of wetland terrestrial vegetation, with great consequences for the other herbivores (Laws, 1968a; Field, 1970; Lock, 1972; Olivier and Laurie, 1974; Kingdon, 1979; Eltringham, 1999).

Despite these promising characteristics, a full integration of fossil hippos in the study of African palaeoenvironments still requires major advances in the knowledge of their ecology and diet. Reconstruction of fossil hippo diets has often been based on superficial observations of the cranio-dental morphology. Grazing or browsing diets have been assessed by using the degree of hypsodonty of the cheek teeth, the morphology of the anterior dentition (Coryndon, 1977; Gèze, 1985), and general morphological comparisons with the modern species (Coryndon, 1967). The resulting assumptions are rather inaccurate. On one hand, the hypsodonty degree is weakly variable in hippos, being quite low even in the extant grazer *Hippopotamus amphibius* (Janis, 1988), and moreover can be misleading for diet recognition (Solounias et al., 1988; MacFadden et al., 1999). On the other hand, the anterior teeth of the Hippopotamidae take an insignificant part in the feeding process. Their morphology is mostly constrained by intraspecific competition, as part of a cranial morphology heavily specialized for biting (Herring, 1975; Kingdon, 1979). Unfortunately, these adaptations are likely to preclude correct identifications of many of the morphological features associated to grazing or browsing that were recognized and used for other ungulates (Solounias and Dawson-Saunders, 1988; Solounias et al., 1988; Janis, 1995). Until now, the most reliable data on fossil hippo diet have been provided by carbon isotope analyses in tooth enamel (Morgan et al., 1994; Bocherens et al., 1996; Kingston, 1999; Zazzo et al., 2000; Franz-Odendaal et al., 2002; Cerling et al., 2003b; Schoeninger et al., 2003). The work of Cerling et al. (2003b) is the most significant, being based on a large sample of late Miocene/basal Pliocene hippopotamids from one locality, Lothagam (Turkana basin, Kenya).

This study is an attempt to characterize the diet of a Miocene hippopotamid from Toros-Ménalla (Central Africa, Chad) combining carbon isotope and dental micro-wear analyses. Results obtained on the fossils were compared with those obtained on a large sample of living *Hippopotamus amphibius*.

2. The Toros-Ménalla fossiliferous area

The Toros-Ménalla (TM) area is located just above 16°N and between 17°E and 18°E, in the Djurab erg, i.e. the most southern extension of the Sahara in Northern Chad. The monotonously flat substrate of TM is composed of aeolian and perilacustrine sandstones, and lacustrine deposits (Vignaud et al., 2002). Those sediments are patchily covered by active aeolian sands and sand dunes that isolate outcrops. Between 1997 and today, the Mission Paléoanthropologique Franco-Tchadienne (MPFT) collected more than 10,000 fossil vertebrates in these outcrops. The hippos studied here were found in association with a fauna typically including suids (*Nyanzachoerus syrticus*), anthracotheriids (*Libycosaurus*), and proboscideans (*Anancus kenyensis* and *Loxodonta* sp.aff. 'Lukeino stage'). A biochronological correlation was established between this fauna and that of the Nawata formation at Lothagam, Kenya, the best match being with the lower member of this formation (Vignaud et al., 2002), dated between 7.4 Ma and 6.5 Ma (McDougall and Feibel, 2003). TM appears to be a unique window into the late Miocene of central Africa, as well as into late Miocene human evolution. Indeed, this area produced a complete hominid skull and other remains classified as *Sahelantropus tchadensis* (Brunet et al., 2002).

The faunal assemblages indicate that different habitats co-occurred at TM: grassland, wooded savannah, and gallery forest (Vignaud et al., 2002). Taxa related to fresh water are particularly frequent. Among them, hippopotamids constitute about 25% of the TM fossil remains. With Lothagam, this is the best record of the family in the late Miocene. A few of the remains indicate a small-sized undetermined hippopotamid, but most of the fossils were attributed to a new species of the genus *Hexaprotodon*, noted here *Hex*. nov. sp. "TM" (Vignaud et al., 2002). This species is slightly smaller than *Hippopotamus amphibius*.

3. Samples

For the purpose of comparison, modern hippos from different regions of Africa were sampled in

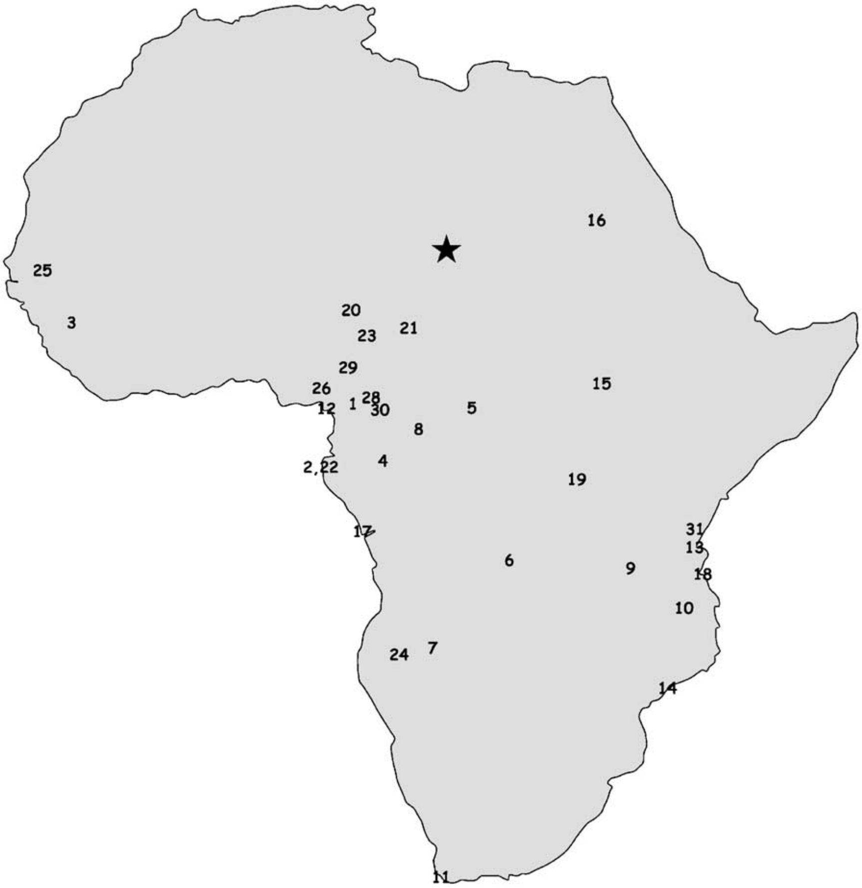

Fig. 1. Geographical distribution in Africa of analysed samples of Hippopotamidae. Numbers refer to locality numbers (LN) listed in Table 1 and Appendix A. Star: Toros-Ménalla (TM), Chad.

Table 1

Specimens of modern *Hippopotamus amphibius*: samples, locations, environments, and results of their carbon stable isotope analysis (δ^{13}C corrected according to values of recent changes atmospheric CO_2 composition given by Francey et al., 1999) and of their tooth micro-wear analysis

Specimen	W	Locality	LN	Environment	Corrected δ^{13}C	Ns	Nls	Np	Nlp
1077-08	0	Cameroon, Bafia	1	closed	−5.4	–	–	–	–
1885-671	–	Gabon, Cap Lopez	2	closed	−10.9	48	0	28	0
1885-672	–	Gabon, Cap Lopez	2	closed	−0.5	28	0	82	2
1895-431	–	Guinea	3	intermediate	−3.9	53	1	18	0
1911-351	–	Congo	4	closed	−6.5	26	1	20	0
1926-144	–	Congo	4	closed	−4.7	31	0	27	1
1959-131	–	Central African Republic	5	intermediate	0.6	37	0	48	0
23	0	DRC, River Lubilash	6	intermediate	−0.3	–	–	–	–
235	1	Angola, River Cubango	7	intermediate	−3.0	–	–	–	–
32131	1	Cameroon, River Sangha	8	closed	−3.6	–	–	–	–
32132	1	Cameroon, River Sangha	8	closed	0.3	–	–	–	–
33800	1	Tanzania, between Lake Malawi and Songea	9	intermediate	−2.1	–	–	–	–
35448	1	Tanzania, River Ruvuma	10	intermediate	−3.2	–	–	–	–
401-67	1	South Africa, C. Good Hope	11	open	−3.4	–	–	–	–
41825	1	Cameroun, Douala	12	closed	−2.4	–	–	–	–
42706	1	Tanzania, River Wami	13	intermediate	−2.5	–	–	–	–
42707	1	Tanzania, River Wami	13	intermediate	−1.7	–	–	–	–
43132	1	Mozambique, Quelimane	14	intermediate	−0.5	–	–	–	–
43587	0	Tanzania, River Ruvuma	10	intermediate	0.4	–	–	–	–
44088	1	Soudan, Nil bleu, Kenisa	15	closed	0.4	–	–	–	–
481	0	Soudan, Dunqulah	16	closed	0.9	–	–	–	–
482	1	DRC, Banana	17	intermediate	−0.6	–	–	–	–
483	1	Tanzania, Kiwindji	18	intermediate	−4.9	–	–	–	–
5553	1	DRC, Kivu, River Rwindi	19	open	−1.3	56	0	6	1
6088	1	DRC, Kivu, River Rwindi	19	open	0.5	51	4	46	0
6089	1	DRC, Kivu, River Rwindi	19	open	0.4	46	3	30	1
6090	1	DRC, Kivu, River Rwindi	19	open	−2.4	65	1	75	0
6092	1	DRC, Kivu, River Rwindi	19	open	−0.9	55	4	70	0
6093	0	DRC, Kivu, River Rwindi	19	open	−0.3	–	–	–	–
6094	0	DRC, Kivu, River Rwindi	19	open	1.0	57	0	43	0
6095	1	DRC, Kivu, River Rwindi	19	open	−0.3	55	1	51	8
6096	1	DRC, Kivu, River Rwindi	19	open	−0.4	70	1	42	0
6097	1	DRC, Kivu, River Rwindi	19	open	0.0	46	1	14	5
6098	0	DRC, Kivu, River Rwindi	19	open	−1.1	50	1	49	2
6100	1	DRC, Kivu, River Rwindi	19	open	−1.5	76	0	34	0
6101	1	DRC, Kivu, River Rwindi	19	open	−4	36	0	70	1
6102	–	DRC, Kivu, River Rwindi	19	open	−1.1	57	2	18	2
6103	–	DRC, Kivu, River Rwindi	19	open	−4.4	52	1	15	1
6104	1	DRC, Kivu, River Rwindi	19	open	0.9	33	0	85	0
6105	1	DRC, Kivu, River Rwindi	19	open	−4.8	36	2	44	0
6106	1	DRC, Kivu, River Rwindi	19	open	−3.8	59	0	33	1
6426	1	Nigeria, Katamma	20	intermediate	−1.8	–	–	–	–
6427	1	Chad, Katoua	21	open	−2.5	–	–	–	–
843-76	1	Mozambique, Quelimane	14	intermediate	−6.5	–	–	–	–
843-77	1	Mozambique, Quelimane	14	intermediate	−1.2	–	–	–	–
847-100	1	Gabon, River Ogooué	22	closed	−4.5	–	–	–	–
847-99	1	Gabon, River Ogooué	22	closed	−2.3	–	–	–	–
865-18	1	Gabon, River Ogooué	22	closed	−4.0	–	–	–	–
865-18	0	Gabon, River Ogooué	22	closed	−3.1	–	–	–	–
91275	1	Cameroon, northern/Nigeria, Eastern	23	intermediate	−3.7	–	–	–	–
91326	1	Angola, Ovamboland, River Cunene	24	intermediate	−2.6	–	–	–	–

Table 1 (*continued*)

Specimen	W	Locality	LN	Environment	Corrected δ^{13}C	Ns	Nls	Np	Nlp
A2219	–	Senegal	25	intermediate	−3.5	48	1	53	0
Abon	1	Cameroon, River Cross	26	closed	−1.4	–	–	–	–
Br1	0	Cameroon	27	closed	−3.0	–	–	–	–
Cun1	1	Angola, River Cunene	24	intermediate	−5.4	–	–	–	–
Cun2	0	Angola, River Cunene	24	intermediate	−10.9	–	–	–	–
Dong1	1	Cameroon, Donga	28	closed	−0.5	–	–	–	–
Dong2	0	Cameroon, Donga	28	closed	−3.9	–	–	–	–
Dong3	1	Cameroon, Donga	28	closed	−6.5	–	–	–	–
Dong4	1	Cameroon, Donga	28	closed	−4.7	–	–	–	–
Dong5	1	Cameroon, Donga	28	closed	0.6	–	–	–	–
Maig1	1	Cameroon, Banyo	29	closed	−0.3	–	–	–	–
Sato1	1	Cameroon, Kap	30	closed	−3.0	–	–	–	–
Usam1	1	Tanzania, Mounts Usambara	31	intermediate	−3.6	–	–	–	–
TM009-01-050	–	Chad, Toros-Ménalla, late Miocene	TM	–	−5.6	–	–	–	–
TM009-01-051	–	Chad, Toros-Ménalla, late Miocene	TM	–	−4.8	–	–	–	–
TM009-01-192	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.4	–	–	–	–
TM009-01-259	–	Chad, Toros-Ménalla, late Miocene	TM	–	−2.9	–	–	–	–
TM009-01-363	–	Chad, Toros-Ménalla, late Miocene	TM	–	−6.9	–	–	–	–
TM016	–	Chad, Toros-Ménalla, late Miocene	TM	–	0.2	–	–	–	–
TM050-00-002	–	Chad, Toros-Ménalla, late Miocene	TM	–	−4.7	–	–	–	–
TM069-98-002	1	Chad, Toros-Ménalla, late Miocene	TM	–	−9.3	35	0	125	3
TM074	–	Chad, Toros-Ménalla, late Miocene	TM	–	−5.0	–	–	–	–
TM074-99	1	Chad, Toros-Ménalla, late Miocene	TM	–	−2.0	21	1	21	1
TM082-99-004	–	Chad, Toros-Ménalla, late Miocene	TM	–	–	26	0	36	0
TM115-00-126	–	Chad, Toros-Ménalla, late Miocene	TM	–	–	39	1	51	1
TM177-01-033	1	Chad, Toros-Ménalla, late Miocene	TM	–	0.8	20	0	33	3
TM207-01-005	–	Chad, Toros-Ménalla, late Miocene	TM	–	−5.0	–	–	–	–
TM241-01-009	–	Chad, Toros-Ménalla, late Miocene	TM	–	−4.3	–	–	–	–
TM242-01-029	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.0	–	–	–	–
TM242-01-030	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.5	–	–	–	–
TM242-01-032	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.1	–	–	–	–
TM242-01-035	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.4	–	–	–	–
TM243-01-012	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.3	–	–	–	–
TM258-01-050	1	Chad, Toros-Ménalla, late Miocene	TM	–	−3.1	5	0	37	8
TM259-01	0	Chad, Toros-Ménalla, late Miocene	TM	–	−6.9	27	0	88	0
TM259-01-008	–	Chad, Toros-Ménalla, late Miocene	TM	–	−3.6	13	0	32	0
TM259-01-026	–	Chad, Toros-Ménalla, late Miocene	TM	–	1.4	–	–	–	–
TM259-02-001	0	Chad, Toros-Ménalla, late Miocene	TM	–	−4.1	22	0	23	0
TM293-01-030	1	Chad, Toros-Ménalla, late Miocene	TM	–	−2.8	–	–	–	–
TM315-01-004	1	Chad, Toros-Ménalla, late Miocene	TM	–	−4.2	–	–	–	–
TM337-01-001	1	Chad, Toros-Ménalla, late Miocene	TM	–	1.0	25	3	66	4

(W) enamel sample formed before or after weaning (0 or 1 respectively); (LN) locality numbers of Fig. 1; (Ns) number of scratches; (Nls) number of large scratches; (Np) number of pits; (Nlp) number of large pits.

several European collections (Fig. 1, Table 1, Appendix A). These specimens all belong to *Hippopotamus amphibius*, for which diet is acceptably known, and for which it was possible to constitute a large reference group of wild specimens. On the basis of the vegetation distribution in Africa described by White (1983), compared to the works of Mayaux et al. (2004) and Rattray (1960), the vegetation types were listed for the location of each sampled specimen (Appendix A). According to the dominant vegetation type, specimens were attributed for comparison purpose to three categories describing the general features of the environment: closed, intermediate, open (Table 1, Appendix B). Each specimen was aged according to the groups defined by Laws (1968b) on the basis of lower tooth wear and eruption, except for four fully adult specimens with no mandible (Appendix A). Fifty-three modern individuals were selected for isotopic analyses, including both sexes and all age groups. All types of permanent teeth were included, as well as some deciduous teeth, so that nearly the entire duration of enamel formation was represented. A total of 24 modern individuals were selected for micro-wear analysis, 17 of them from the River Rwindi valley, south of Lake Edward in the Democratic Republic of Congo. All teeth used in this analysis were M2; the mesial lobe of the paracone and the distal lobe of the protoconid being the area of interest (Merceron et al., 2004a,b).

Fossil samples were taken from different locations in the TM area. They include fragmentary teeth as well as more complete cranio-dental remains (Appendix A). Most of the sampled specimens were identified as *Hex.* nov. sp. "TM". The remaining unidentified samples likely belong to this species as well, according to the proportion of cranio-dental specimens attributed to this species at TM (more than 99.5% of identified specimens). Data were generally insufficient for accurate ageing. Enamel fragments from 26 specimens were collected for analysis of their carbon isotopic content, which was shown to be unaffected by diagenesis in the late Miocene deposits from the Toros-Ménalla area (Zazzo, 2001). Because the TM area is subject to frequent sand storms, weathering of fossils is a concern in performing micro-wear analysis. Only 10 specimens were adequately preserved to assess micro-wear. Therefore, micro-wear results from fossil specimens must be considered with caution.

4. Methods

4.1. Carbon isotope analysis

Dietary reconstruction using carbon isotopes is based on the premise that the δ^{13}C value of ingested food is recorded into biogenic apatite with an enrichment of about 14‰ (Cerling et al., 1997). In subtropical to tropical environments, plants rely primarily on two photosynthetic pathways that fractionate carbon to different degrees. Trees, shrubs and high-altitude grasses use the C_3 photosynthetic cycle ($\delta^{13}C=-25.0$‰, on average), whereas low-altitude grasses use the C_4 photosynthetic cycle ($\delta^{13}C=-12.1$‰, on average). Based on these δ^{13}C values, and the enrichment in biogenic apatite, ranges of C_4 plant proportion in diet can be calculated using a two end-member mixing model (Cerling et al., 2003a).

The analyses were performed as follows. A small volume of enamel was cut from each tooth using a tungsten drill and ground with a mortar and pestle. Care was taken to avoid collecting any underlying dentine. Powder enamel was first soaked in 2–3% NaOCl for 4–5 h to remove any organic contaminant, and then treated with 1 M acetic acid–Ca acetate buffer for 20 h to remove exogenous carbonate. About 15–20 mg of powder was reacted in vacuum with 100% H_3PO_4 at 50 °C for 5 h to release CO_2. The carbon dioxide was purified by cryogeny under vacuum and introduced to a VG Sira 9 mass spectrometer to measure carbon isotope ratios. Analytical precision for carbon isotopic analyses is ± 0.1‰ (1σ), determined by replicate analyses of an internal bioapatite standard. Isotopic measurements were normalized to daily analyses of the international standard NBS-19. δ^{13}C analyses are reported in the permil notation relative to V-PDB. Based on data from Francey et al. (1999), a correction was applied to δ^{13}C obtained on modern specimens in order to take account of the recent changes of atmospheric CO_2 composition (Table 1).

4.2. Micro-wear analysis

Microscopic observation of the surface of mammal dental enamel has shown that the form and number of microscopic marks resulting from feeding are well correlated with diet (Walker et al., 1978). This method has been successfully applied to both living and fossil ungulates (Solounias and Dawson-Saunders, 1988; Solounias et al., 1988; Solounias and Moelleken, 1992a,b; Blondel, 1996). Until recently, the enamel surface was observed by using SEM. However, a recent work proposed a modified methodology using optic microscopy at moderate magnification (Solounias and Semprebon, 2002). This method has proved to be consistent and more logistically convenient, even more slow with slight adaptations (Merceron, 2003; Merceron et al., 2004a,b). The protocol, equipment and material employed here were strictly identical to those used by Merceron et al. (2004a,b). M2/ and M/2 teeth were analyzed, most exhibiting an intermediate stage of wear. The wear facets studied were localized on the paracone mesial lobe and the protoconid distal lobe, which are in contact during the occlusion phase of chewing. Organic remains, sediments, and protective coats (glues, varnishes) were removed prior to moulding. Moulds were made with a polyvinylsiloxane based material (Coltene President Microsystem®). Replicas were then obtained using a transparent epoxy resin. The replicated wear facets were observed at low magnification (30×) and digitalized. Areas of 0.09 mm^2 (=90,000 μm^2) were delimited on the digital pictures, and data acquisition was performed in these areas using Optimas v.6.5.2 by one observer (J.-R. B.). Following Grine (1986) and Solounias and Semprebon (2002), the observed marks were classified as scratches (at least four time longer than wide), or pits (more or less circular). Data included the number of scratches (Ns), the number of wide scratches (wider than 15 μm), the number of pits (Np) and of large pits (wider than 15 μm). Several indices were used to present the results: the percentage of pits (%p), calculated as following: %p = 100 × Np/(Np + Ns); the percentage of individuals with more than two wide scratches (%ws); the percentage of individuals with more than four large pits (%lp) (Merceron et al., 2004a,b).

5. Results

5.1. Carbon isotope analysis

δ^{13}C values of modern samples of *Hippopotamus amphibius* are indicative of a dominant C_4 feeder with a significant C_3 component in its diet (Fig. 2). Only one marginal individual from southern Democratic Republic of Congo (DRC) approached an exclusive C_3 diet ($\delta^{13}C = -10.9$‰; see Fig. 2). A normality test (Shapiro–Wilk's $W = 0.93$, $p = 0.004$) indicated a non-normal distribution of the sample values, confirmed by visual observation of a multimodal distribution. Two factors of δ^{13}C variations in the sample were identified: environment at location and age. First, specimens sampled in open environments (Table 1, Fig. 2) present an average δ^{13}C

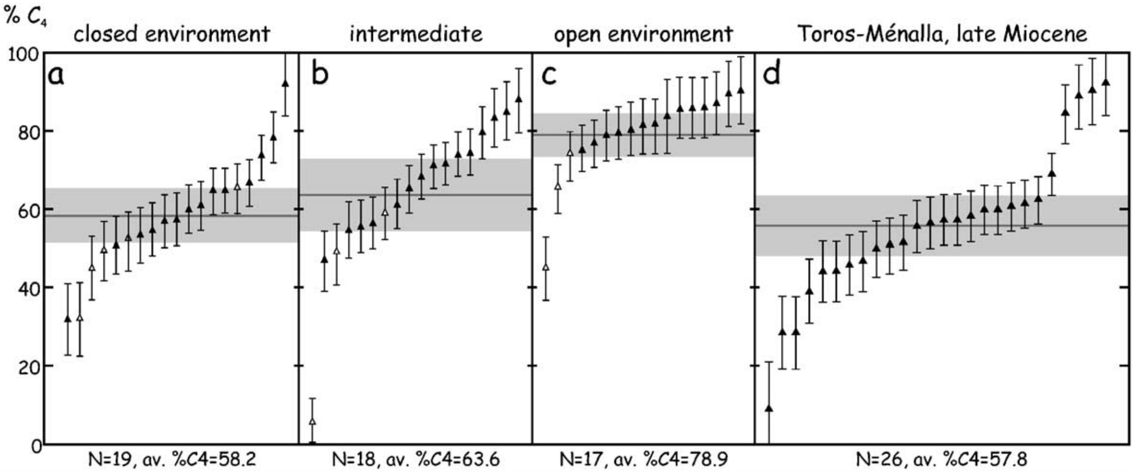

Fig. 2. Comparison of estimated % of C_4 plant in the diet of analysed specimens of modern *Hippopotamus amphibius* (a, b, c) and of late Miocene hippopotamids from Toros-Ménalla, Chad (d). Values were computed using a two endmember mixing model (Cerling et al., 2003a,b). Average (triangles) and uncertainty (whiskers) are plotted for each specimen. Form modern hippos, open and filled triangles are used to differentiate pre- and post-weaning samples, respectively. Sample size (N) and average C_4 contribution in diet are given for each category (closed, intermediate, and open environments, and fossil group). Solid lines and shaded areas represent the average C4 contribution in diet and its confidence interval ($\alpha = 0.05$), respectively.

Table 2
Results of micro-wear analyses performed on *Hippopotamus amphibius* and the late Miocene hippopotamids from Toros-Ménalla, Chad, and comparison with previous studies

Taxa	N	Ns	%ws	Np	%lp	%p
Hip. amphibius	**24**	**48.8 ± 5.5**	**12.5**	**41.7 ± 9.5**	**8.3**	**43.7 ± 6.8**
C_4 dominant	**18**	**52.7 ± 5.6**	**16.7**	**43.2 ± 11.1**	**11.1**	**42.6 ± 8.1**
C_3 and C_3/C_4	**6**	**37.2 ± 11.7**	**0.0**	**37.2 ± 25.6**	**0.0**	**47.2 ± 17.7**
***Hex*. n. sp. ‘TM’**	**10**	**23.3 ± 7.0**	**10.0**	**51.2 ± 23.7**	**10.0**	**66.4 ± 9.1**
Grazers (6 sp.)[a]	6–28	20.3–29.8	0–53	8.4–16.3	29–95	27.2–37.1
Grazers (9 sp.)[b]	5–27	–	–	–	–	12.5–46.4
Browsers (6 sp.)[a]	8–50	15.1–24.4	0–62	25.5–55.8	0–36	56.1–69.4
Browsers (19 sp.)[b]	3–44	–	–	–	–	50.2–79.5
Mixed 1 (2 sp.)[a]	18–19	18.3–24.9	18–16	22.0–24.3	83–58	45.1–56.2
Mixed 1 (12 sp.)[b]	6–43	–	–	–	–	21.1–76.5
Mixed 2 (4 sp.)[b]	9–28	–	–	–	–	23.1–48.9

Samples analysed in this study (in bold): averages and 95% confidence intervals are given for Ns, %ws, Np, %lp, %p.

Comparative data: number of studied species indicated between brackets; ranges for N are ranges of individual sample size for each species; ranges for Ns, %ws, Np, %lp, %p are ranges of species averages; absence of comparative data results from the different surface size and resolution used in the latter study.

(Mixed 1) seasonnal or regional mixed feeders; (Mixed 2) are meal-by-meal mixed feeders (see Solounias and Semprebon, 2002).

[a] Data from Merceron et al. (2004a).

[b] Data from Solounias and Semprebon (2002).

($\delta^{13}C = -0.6‰$) significantly higher than that of specimens from intermediate ($\delta^{13}C = -2.6‰$) and closed ($\delta^{13}C = -3.3‰$) environments (Anovas results: *df*: 1,33; $F = 8.42$; $p = 0.007$ and *df*: 1,34; $F = 65.00$; $p < 10^{-3}$, respectively). No significant differences were observed between specimens from

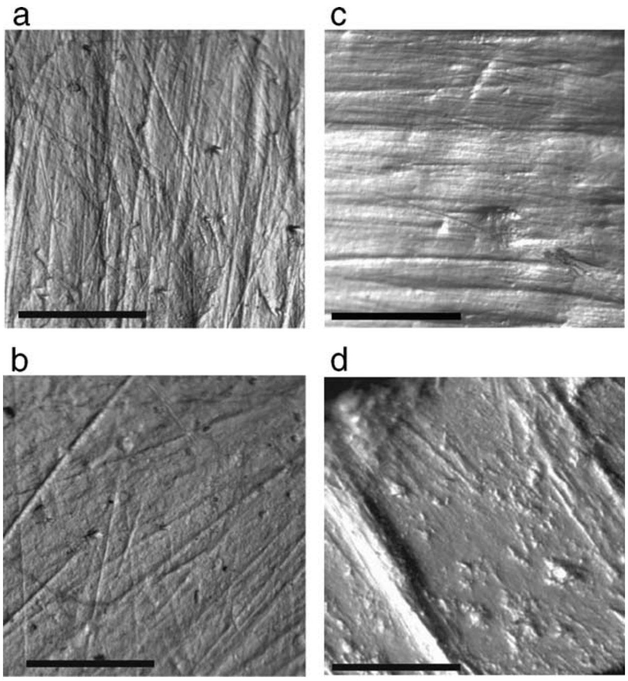

Fig. 3. Digital pictures of enamel surfaces of hippopotamids and other ungulates. (a) *Hippopotamus amphibius*; (b) late Miocene hippopotamid from Toros-Ménalla, Chad; (c) *Equus burchelli*, a grazer; (d) *Rangifer tarandus*, a browser. Scale bars are 300 μm.

the two latter environments (*df*: 1,35; $F=0.67$; $p=0.409$). The distribution of $\delta^{13}C$ values of the modern group is also correlated to the age of tooth formation. Indeed, two distinct groups were identified according to whether teeth were formed before or after weaning. In *Hip. amphibius*, weaning starts after 6 months, and is generally completed between 10 and 12 months (Laws and Clough, 1966; Eltringham, 1999), that is between age groups 2 and 3 (Laws, 1968b). According to this work and to direct observations by one of us (J.-R. B.), pre-weaning enamel includes that of deciduous premolars, M1s, and incisors and canines of 12 month calves at the oldest (these teeth are ever-growing). The germs of P2–4 and M2–3 develop later than 12 months, while pre-weaning canine and incisor enamel likely disappears after this age. Pre-weaning samples ($N=11$) had an average $\delta^{13}C$ of -4.5‰, while post-weaning teeth ($N=43$) had a significantly different average $\delta^{13}C$ of -1.6‰ ($p<10^{-3}$ for *t*-test, Mann–Whitney *U*-test, and Kolmogorov–Smirnov two sample test). This pattern was also observed within groups made according to the environment type (Fig. 2). When pre-weaning samples were discarded, the Shapiro–Wilk's *W* test indicated normal distribution. Moreover, the largest population sample (from the Rwindi Valley, DRC) show the same pattern of variations in relation with weaning age and a restricted range of variations when pre-weaning samples are not considered ($-0.9<\delta^{13}C<1.0$; $N=12$). Finally, altitude was not a significant factor on the observed $\delta^{13}C$ values, because most specimens from known localities were sampled below the limit (ca. 2000 m) above which the proportion of C_3 grasses increases significantly (Tieszen et al., 1979).

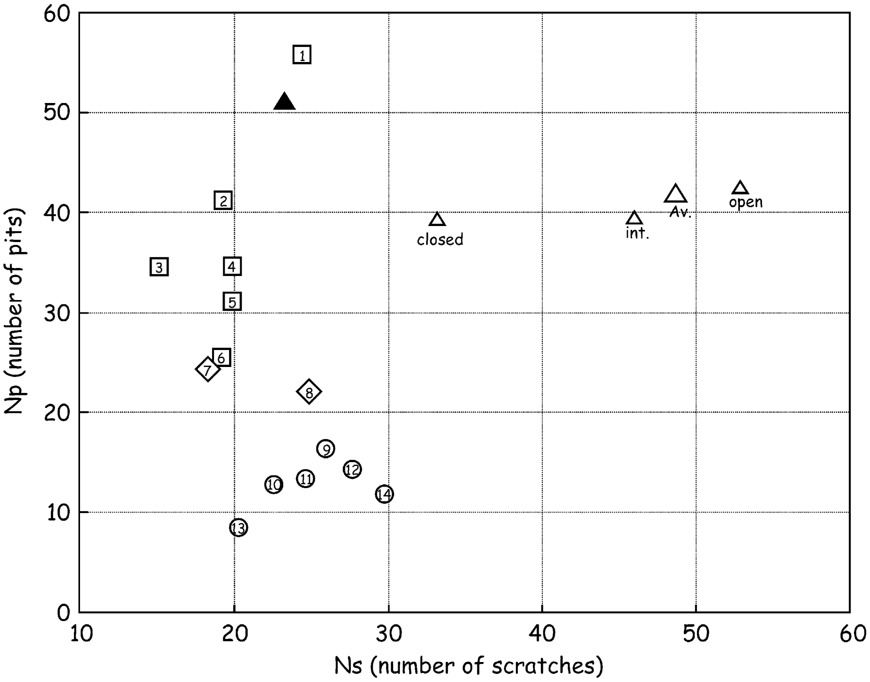

Fig. 4. Scatterplot of number of scratches and number of pits of studied hippopotamids and of other ungulates. (△) *Hippopotamus amphibius*; (Av.) average for the whole sample ($N=24$); (closed) average for closed environment specimens ($N=4$); (int.) average for intermediate environment specimens ($N=3$); (open) average for open environment specimens ($N=17$); (▲) late Miocene hippopotamids from Toros-Ménalla; (◇) mixed feeder ungulates; (○) browser ungulates; (□) grazer ungulates; (1) *Rangifer tarandus*; (2) *Gazella soemmerringi*; (3) *Litocranius walleri*; (4) *Cephalophus sylvicultor*; (5) *Odocoileus virginianus*; (7) *Tragelaphus scriptus*; (8) *Aepyceros melampus*; (9) *Alcelaphus buselaphus*; (10) *Damaliscus lunatus*; (11) *Syncerus caffer*; (12) *Hippotragus niger*; (13) *Equus burchelli*; (14) *Equus przewalskii*.

$\delta^{13}C$ values of fossil hippos from Toros-Ménalla indicate they were mostly mixed C_3/C_4 feeders (Fig. 2). The average $\delta^{13}C$ value ($\delta^{13}C = -3.5‰$) was lower than that of *Hippopotamus amphibius*, but this difference appeared to be moderately significant (*df*: 1,78; $F=5.62$; $p=0.02$). In fact, the fossil group showed values similar to those of *Hip. amphibius* from closed and intermediate environments (*df*: 1,43; $F=0.17$; $p=0.685$ and *df*: 1,42; $F=1.33$; $p=0.255$, respectively), and differ significantly only from open environment *Hip. amphibius* (*df*: 1,41; $F=20.34$; $p<10^{-3}$; see also Fig. 2). Due to the difficulty of accurately aging most fossil specimens, it was not possible to perform meaningful comparisons between pre-weaning and post-weaning samples.

5.2. Micro-wear analysis

To our knowledge, this is the first time that micro-wear analysis was performed on hippopotamids. For this reason, results (Table 2, Figs. 3 and 4) were compared to those obtained on other extant ungulates by Merceron et al. (2004a) and, to a lesser extent (because of some differences in methodology), to the results of Solounias and Semprebon (2002). For *Hippopotamus amphibius*, the most striking feature is the very high quantity of observed scratches (Ns; Table 2; Figs. 3a and 4). Scratches are usually more frequent in grazers than in browsers (Solounias and Semprebon, 2002; Merceron et al., 2004a), but for this modern hippo, the Ns average is well above that of grazers analysed by Merceron et al. (2004a) and on a larger area by Solounias and Semprebon (2002). The number of pits (Np) is also high, falling in the range observed by Merceron et al. (2004a) for the browsers (Table 2; Fig. 4) and higher than the Np obtained on a larger area by Solounias and Semprebon (2002) for grazers. The percentage of pits (%p) appeared intermediary between the values obtained by Merceron et al. (2004a) for grazers and browsers. It generally corresponds to the range observed for mixed feeders (Table 2). It must also be noted that wide scratches and pits have a low frequency (Table 2; Fig. 3a). In summary, these results are not readily interpretable when compared to other ungulates. A tentative interpretation is given below in the discussion.

The Ns was much lower in the fossil than in the modern species, and the Np slightly higher (Table 2; Figs. 3b and 4). Accordingly, the %p is higher than in *Hippopotamus amphibius*, and fits the range given by Merceron et al. (2004a,b) for browsers. Otherwise, the scratches here are also fine, and large pits have a low frequency (Table 2; Fig. 3b).

6. Discussion

6.1. Hippopotamus amphibius

6.1.1. Carbon isotopes

The modern common hippos are classically known as grazers that feed at night on grasses nearby waters where they spend the daytime. Most observers noted a strong preference for short green grasses (Bere, 1959, Verheyen, 1954; Field, 1970; Olivier and Laurie, 1974; Mackie, 1976; Scotcher et al., 1978; Kingdon, 1979; Clemens and Maloiy, 1982; Eltringham, 1999). Direct identification of eaten species determined by stomach content or faecal analyses (Field, 1970; Scotcher et al., 1978) indicated that most ingested plants were C_4 grasses (pathways are listed by Watson and Dallwitz, 1992). However, in this study, average $\delta^{13}C$ values measured in hippo teeth correspond to a significant proportion (27% to 40%) of C_3 ingested plants, principally in individuals found in closed or intermediate environments (Fig. 2). It must be noted that most above cited diet studies were realized on *Hippopotamus amphibius* from eastern and southern Africa, whereas our study included 37% of specimens from central and western Africa, where closed environments and C_3 vegetation are more frequent. Two hypotheses can be formulated to explain these differences between hippo from different environmental contexts. One explanation could be related to a lack of food selection. Although common hippos are selective in their diet, they are not able to select plants species by species while cropping (Mackie, 1976; Scotcher et al., 1978; Eltringham, 1999). This must be related to their cranio-mandibular anatomy, and particularly their enlarged muzzle, which cannot allow precise control over the cropped items. Rather, they choose assemblages where their favourite species are well represented, then graze whole patches. As a consequence, C_3 grasses, herbs and sedges possibly mixed with C_4 grasses may be ingested (Eltringham, 1999). Therefore, in areas where these plants are mixed in greater quantity with grasses, they would be included in the diet to a greater extent. Another possible explanation would be to consider that hippos are more versatile in their diet than is generally thought. In fact, most authors recorded intentional consumption of C_3 plants, but in most cases claimed this to be insignificant. However, some C_3 plants can be added in substantial quantities to the diet on an irregular basis, including aquatic and wetland plants (Mugangu and Hunter, 1992) and fruits (Ansell, 1965). More regular variations in hippo diet were observed on a seasonal basis in Natal, South Africa (Scotcher et al., 1978), but also in northern Central African Republic (Barber et al., 1980), where woodlands are foraged during the wet season. It is noteworthy that such woodland foraging is strongly avoided in localities of eastern and southern Africa (Olivier and Laurie, 1974; O'Connor and Campbell, 1986). Although these latter reports were mainly concerned with different grass assemblages, *Hip. amphibius* would probably be better depicted as an opportunistic grazer, rather than a strict one. Given this flexibility, a wider range of feeding behaviour can reasonably be suggested to explain the results obtained here. This is supported by the variations in $\delta^{13}C$ values measured along the length of a hippo canine from Kenya (Passey and Cerling, 2002). Finally, it must be noted that unintentional and active inclusions of C_3 plants are not mutually exclusive, and the observed values could result from both activities.

Large differences in average $\delta^{13}C$ values are observed between pre- and post-weaning individuals. Differences can be as high as 5.7‰ between pre-weaning and post-weaning enamel measured in a given individual (specimen 865-18, see Appendix A). Cerling et al. (2003b) obtained similarly a very low $\delta^{13}C$ value (−13.7‰) for a calf sampled in Lake Baringo, Kenya. A first possible explanation for this shift resides in the carbon isotope value of the milk ingested before weaning. Milk lipids are 5‰ depleted in ^{13}C compared to carbohydrates and proteins (DeNiro and Epstein, 1978), thus bioapatite synthesized before weaning may have lower $\delta^{13}C$ values than bioapatite synthesized after weaning. The magnitude of this effect depends on the lipid content of the consumed milk. Unfortunately, published hippo milk content analyses are rare and contradictory. Gray (1959) and Phillis (1976) reported low milk fat content of 3.4% and 4.5%, respectively, whereas Widdowson (1981) reported a much higher fat content of 17.2%. Simple mass balance calculations indicate that the magnitude of the pre-weaning signal cannot account for more than a 1‰ ^{13}C depletion. Alternatively, Olivier and Laurie (1974) reported frequent consumption of adult male faeces which is probably ^{13}C depleted relatively to the ingested food (Grey and Harper, 2002). However, the approximate 2‰ depletion estimated by Grey and Harper (2002) and the faeces consumption frequency are not sufficient to explain the results obtained in the present study. Another possibility is that pre-weaning juveniles or lactating females include more C_3 plants in their diet, but there is no report of such a difference, although Field (1970) examined stomach contents of many individuals including juveniles. On the contrary, Verheyen (1954) observed that calves are interested early in short grasses, and that grazing starts after 4 to 6 months, i.e. 4 to 6 months prior to weaning. Therefore, in absence of detailed milk analyses, including the evolution of fat content during lactating periods, the observed difference between pre-weaning and post-weaning $\delta^{13}C$ can for now only partially (up to 1/3) be attributed to milk consumption.

6.1.2. *Micro-wear*

Scratches on enamel are thought to be principally caused by grass silicon phytoliths. Thus, a high number of scratches (Ns) on occlusal tooth enamel is correlated with a grazing diet (Solounias and Moelleken, 1992a,b; MacFadden et al., 1999; Solounias and Semprebon, 2002; Merceron, 2003; Merceron et al., 2004a). The results obtained here (Ns very high: Table 2; Fig. 4) seem to agree overall with the common hippo diet reported in literature (Field, 1970; Mackie, 1976; Scotcher et al., 1978; Eltringham, 1999). However, in detail they differ quantitatively and qualitatively from what would be expected from a grazer feeding exclusively on C_4 plants. Solounias and Semprebon (2002) and Merceron et al. (2004a,b) noted that regular grazing causes an enamel abrasion so intense that it induces an underestimation of the number of scratches and pits by 'overscarring' the enamel surface. This lead Solounias and Semprebon (2002) and Merceron et al. (2004a) to observe some grazer taxa exhibiting a smaller number of scratches than some non-grazers. This phenomenon is likely to be more frequent in C_4 grazers. Indeed, phytoliths, more frequent in C_4 grasses than in C_3 grasses (Lanning and Eleuterius, 1989; McNaughton et al., 1985; Runge, 1999), cause also larger scratches (Solounias and Semprebon, 2002; Merceron et al., 2004a), this amplifying the 'overscarring' artefact. For those reasons, the high number of recorded scratches seen in *Hippopotamus amphibius*, most of them fine (Fig. 3a), would be expected from a C_3 grazer rather than from a C_4 grazer. Accordingly, in the comparative sample (Fig. 4), the highest number of scratches recorded by Merceron et al. (2004a) is that of *Equus przewalskii*, a C_3 grazer. However, according to what is known from African grasses and hippo diet, C_3 grasses probably may have not contributed decisively to the observed micro-wear pattern. An alternative interpretation is proposed here: that the number and thinness of scratches in *Hip. amphibius* are related to consumption of short green C_4 grasses. Phytolith concentration in grasses varies according to many parameters, including grazing pressure and development stages, but does not follow a simple pattern. Regarding the former parameter, McNaughton et al. (1985) found a higher silica deposition in heavily grazed grasses, but Cid et al. (1989) thought that higher silica contents were correlated to general conditions of grazed areas rather than grazing itself. Results obtained by Bañuelos and Obeso (2000) showed that relatively frequent grazing probably favours silica deposition, but that a high herbivore pressure (clipping every 7 days) reduces it. Regarding development of grasses, it was shown that cell silicification does not occur in their early stages of growth (Sangster and Parry, 1969; Sangster, 1970, 1977). Therefore, the material usually foraged by *Hip. amphibius* is likely to contain a relatively small amount of phytoliths. Indeed, common hippos mostly graze on green sprouting leaves of grasses, a selection reinforced by their incapacity to cut coarse grasses with their tusklike incisors (Field, 1970; Olivier and Laurie, 1974; Mackie, 1976; Scotcher et al., 1978; Eltringham, 1999). They actively maintain short grasses by exerting a high grazing pressure on the pastures (Laws, 1968a; Field, 1970; Lock, 1972; Olivier and Laurie, 1974; Eltringham, 1999). Moreover, the ingested phytoliths, especially in early stages of growth, could be on average smaller than in more mature leaves. Thus, hippo tooth abrasion should be less intense, and enamel surfaces should be moderately marked by less frequent and thinner scratches than in other C_4 grazers (Fig. 3). In these conditions, the Ns can be more accurately assessed. Finally, although the relatively small sample size calls for some caution, the smaller value of Ns in closed environment specimens (Table 2) support the results obtained on carbon isotopes, fewer scratches being expected for a diet that includes less C_4 grasses relative to other plants.

Although the number of pits (Np) is probably less reliable than the Ns to assess diet (Solounias and Semprebon, 2002), it is correlated to the consumption of C_3 plants pits are potentially caused by hard object like fruit seeds and lignified parts of trees and bushes. For *Hippopotamus amphibius*, the Np is similar to that of browser taxa (Table 2; Fig. 4). In fact, since the isotopic data indicated a more mixed diet in common hippos from closed and intermediate environments, a higher number of pits should be found in such specimens. However, those analysed here gave a Np somewhat smaller than in specimens from open environments (Table 2; Fig. 4). This lead us to attribute the high Np to other factors. First, Np could be related to a relatively weak abrasion by chewing short grass fresh leaves. In the same way as scratches, pits would be more accurately counted on an enamel surface not saturated by wide scratches. A second factor, considered here as preponderant, is the presence of grit in the eaten food. Indeed, the grazing method of *Hip. amphibius* favours the inclusion of soil particles in the food: short plants are grasped by their leathery lips and pulled out by a swing of the head (Field, 1970; Eltringham, 1999). Accordingly, Clemens and Maloiy (1982) found a particularly high content of mineral material in hippo gut. Important pitting was related by Solounias and Semprebon (2002) to grit. Other ungulates that take food close to the ground show high Np compared to the other taxa of their respective guild (Table 2; Fig. 4): this is the case for *Rangifer tarandus* (a browser) and *Alcelaphus buselaphus* (a grazer). Merceron et al. (2004a) also suggested a similar interpretation for *Gazella soemmerringi* inhabiting the arid shrublands of Ethiopian highlands.

6.2. Hexaprotodon nov. sp. 'TM'

The δ^{13}C values of TM hippopotamids, widely spread from pure C_3 to pure C_4 values, fit better the versatile diet of *Hippopotamus amphibius* from closed and intermediate environments (Fig. 2). Compared to the micro-wear analysis of the extant species, the higher Np and smaller Ns (inducing a higher %p; Table 2) would also imply a diet incorporating more C_3 plants. Nevertheless, this very high Np should be, again, linked to the abundance of grit in the food. The fossils were unearthed in a peri-lacustrine facies, intermediate between lacustrine and aeolian facies, that was related to wet ecosystems prograding on aeolian sand dunes (Vignaud et al., 2002). Consequently, the high Np observed on the late Miocene hippopotamids from TM is probably related to ingested food covered with abundant grit from the sandy substratum and, possibly, with grit blown from the nearby desert. The association of this high Np with the same qualitative aspects of the enamel surface seen in *Hip. amphibius*, i.e. few coarse scratches and large pits (Fig. 3b), can be therefore related to a similar consumption of fresh sprouting leaves on a vegetation close to the ground. According to its δ^{13}C values, the TM hippopotamids foraged on more heterogeneous lawns (including C_4 and C_3 plants both in significant proportions) than those exploited by the extant *Hip. amphibius*, and/or had a somewhat more diversified feeding behaviour. In any case, the diet proposed here for those fossil hippos was most probably that of a herbivore preferentially grazing on short vegetation including C_3 grasses and plants, but possibly more opportunistic than *Hip. amphibius*. It is important to note that the TM hippopotamids are identical to other Mio-Pliocene species in exhibiting low-crowned molars relative to that of *Hip. amphibius*: for the lower molars, the average hypsodonty indices [$h = 100 \times$ (crown height)/(crown maximal width)] are 105 for *Hex.* nov. sp. 'TM' and 140 for *Hip. amphibius*. This difference was used in some previous works to depict Mio-Pliocene hippos as browsers in close environments (Coryndon, 1967, 1977; Gèze, 1985). Again, the results obtained in this study show the limits of such simple general assessments.

The δ^{13}C values of the Chadian fossils are overall similar to those obtained by Cerling et al. (2003b) for the hippopotamids (most probably *Hex. harvardi*) analysed from the late Miocene Nawata Formation at Lothagam, Kenya ($N = 45$; av. $\delta^{13}C = -3.6‰$ not significantly different from that of TM hippopotamids: *df*: 1,69, $F = 5.10^{-3}$, $p = 0.94$). This indicates that contemporary hippopotamids from TM and Lothagam had similar diets regarding overall C_4 and C_3 plant intakes, and maybe shared feeding behaviours. Five other analyses of late Miocene–early Pliocene mammals included hippopotamids and were based on more limited samples. Late Miocene and early Pliocene hippopotamids from Arabia and eastern Africa show wide diet ranges compatible with those observed for TM and Lothagam hippopotamids (Morgan et al., 1994; Kingston, 1999; Schoeninger et al., 2003). In the study of Zazzo et al. (2000) on early to middle Pliocene hippopotamids from Chad (Brunet et al., 1995, 1998; Boisserie et al., 2003), the observed shift toward a more exclusive C_4 diet is possibly related to more open and arid environments developing during the Pliocene in Chad (Zazzo et al., 2000; Geraads et al., 2001; Boisserie et al., 2003), although the small sample size calls for caution. On the contrary, the diet of early Pliocene hippopotamids from Langebaanweg (Franz-Odendaal et al., 2002) is clearly dominated by C_3 plants (possibly grasses). These results speak for diversity among Mio-Pliocene hippo diets. In any case, late Miocene hippopotamids, at the time they became abundant in the central and eastern African ecosystems, relied heavily on C_4 plants in their diet. This corresponds well to the expansion of C_4 plant diets documented between 8.5 Ma and 6.5 Ma (Jacobs et al., 1999; Leakey et al., 1996; Cerling et al., 1997, 1998, 2003b). Given the frequency of hippopotamid remains at Toros-Ménalla, this study also testifies that C_4 grasses were a major component of the vegetation of Toros-Ménalla during the late Miocene, at least in the environments inhabited by hippos, i.e. wetlands and riparian lands.

7. Conclusion

The results obtained here strongly support the need to refer to large modern samples when studying palaeodiets with these methods, even when the diet of modern representatives is thought to be well known. In this case, the use of a single population of *Hippopotamus amphibius* could have greatly exaggerated the differences between the diet of modern and fossil hippopotamids. Regarding micro-wear analysis alone, sampling was not totally satisfying for *Hip. amphibius* from closed and intermediate environments, and additional analyses are required for a better assessment of intra-specific dietary variations that may have further implications for fossil species. Also, in future studies of fossil samples, accurate information on the biologic age of enamel sampled for carbon isotope analysis should no longer be neglected. Concerning the ^{13}C depletion observed in pre-weaning enamel of *Hip. amphibius*, a better understanding, notably of its exact timing, should come from intra-individual sequential sampling, notably on the ever-growing canines that would provide a continuous record in time.

The results obtained here on the late Miocene Chadian hippopotamids indicate that combined carbon isotope and micro-wear analyses may turn fossil hippos into powerful tools for reconstructing the evolution of African wet environments. These tools should apply even better in the Rift Valley, where the fossil record of the Hippopotamidae is much more complete, almost continuous from 9–8 Ma to present. The intra-basin diversity observed in eastern Africa, where two or three species are often found in the same deposits, could also find a coherent explanation in relation with different diets.

Because of their feeding behaviour and their concentration in small areas, common hippos influence local floras, strongly favouring their preferred food (Field, 1970; Eltringham, 1999). The early adaptation of hippos to C_4 grass foraging, confirmed in this study, is not only contemporaneous with the extension of C_4 diets in large mammals in Africa, but also corresponds to first records of the Hippopotamidae as the dominant continental semi-aquatic large mammal in the African fauna, a niche previously occupied by the Anthracotheriidae. This could suggests a co-evolution between C_4 grasses and hippos, maybe explaining how hippos came to dominate this niche. More extensive combined palaeoecological data can be used to test this and other similar hypotheses, and could as well have important insights on hippo evolution.

Acknowledgements

The fossils studied here were found by the MPFT, notably supported by: in Chad, Université de N'Djaména and CNAR; in France, Université de Poitiers, CNRS, Ministère des Affaires Etrangères. We owe great tribute for all the members of the MPFT, and to G. Florent and C. Noël. We gratefully thank the staffs of the institutions who generously authorized sampling and moulding of specimens from their collections: CNAR, Ndjamena; Forschunginstitut und Naturmuseum Senkenberg, Frankfort; Muséum d'Histoire Naturelle, Bern; Muséum d'Histoire Naturelle de la Ville de Genève, Geneva; Museum für Naturkunde, Berlin; Muséum National d'Histoire Naturelle, Paris; Musée Royal d'Afrique Centrale, Tervuren. The isotopic analyses were performed as part of A. Z.'s PhD thesis at the Lab. Biogéochimie Isotopique, Univ. Paris 6. We thank D. Billiou (LBI, UPMC) and J.-F. Saliège (LODYC, UPMC) for technical assistance during isotopic analyses. Access to collections of modern ungulates for the micro-wear comparative database was kindly provided by M. Tranier, M. Robineau, J. Cuisin, and G. Pothet (MNHN, Paris), G. Storch and J. Anger (FNS, Frankfort), M. Moerike (SMN, Stuttgart), G. Van Leer (ONCFS, Chizé), J.-M. Angibault (IBGM, INRA, Toulouse). We thank also P. Voisin (SIMIS, Poitiers). We are gratefully indebted to E. Agrilla (UC Berkeley), J. Grey (MPIL, Plön), F.C. Howell (UC Berkeley) and K. Dietrich for their precious help. J.-R. Boisserie expresses his most grateful thanks to M. Balasse (MNHN, Paris) for her beloved help and advice. The comments and advice from two reviewers (B.H. Passey and an anonymous one) deeply improved the manuscript of this paper. This research was partially funded by post-doctoral fellowships to J.-R. B. from the Fondation Fyssen, the MAE (Programme Lavoisier), and the NSF (RHOI).

Appendix A

Details and results for sampled specimens of *Hippopotamus amphibius* and of late Miocene hippopotamids from Toros-Ménalla, Chad

Specimen	Sampled teeth	n. c. δ^{13}C	Age	Date	LN	Coordinates (lat.–long.)	Altitude (m)	Vegetation
1077-08[1]	C 1/	−5.4	3	1947	1	04°45′N, 11°14′E	200	closed to degraded evergreen lowland forest
1885-671[2]	–	–	11	1885	2	0°39′N, 8°42′E	10	closed to degraded evergreen lowland forest
1885-672[2]	–	–	11	1885	2	0°39′N, 8°42′E	10	closed to degraded evergreen lowland forest
1895-431[2]	–	–	a	1895	3	inaccurate location	<1750	degraded evergreen lowland forest to deciduous woodland
1911-351[2]	–	–	10	1911	4	inaccurate location	<900	closed to degraded evergreen lowland forest, swamp forest
1926-144[2]	–	–	13	1926	4	inaccurate location	<900	closed to degraded evergreen lowland forest, swamp forest
1959-131[2]	–	–	a	1959	5	inaccurate location	<1400	closed to degraded evergreen lowland forest to deciduous woodland
23[3]	C /1	−11.3	3	1934	6	06°42′S, 24°11′E–10°2′S, 24′9°E	500–800	deciduous woodland
235[3]	P 2/	−0.5	8	unknown	7	17°36′S, 18°37′E–15°44′S, 17°27′E	1060–1140	mosaic forest/savanna, deciduous woodland, closed grassland
32131[4]	C /1	−4.1	10	1904	8	01°39′N, 16°4′E–2°42′N, 16°5′E	300–320	closed evergreen lowland forest, swamp forest
32132[4]	P 3/	−6.7	11	1904	8	01°39′N, 16°4′E–2°42′N, 16°5′E	300–320	closed evergreen lowland forest, swamp forest
33800[4]	P 3/	−4.8	12	1860–1920	9	10°41′S, 35°38′E–10°46′S, 34°49′E	500–2000	deciduous woodland
35448[5]	P /2	0.5	12	1894	10	11°36′S, 35°24′E–10°29′S, 40°29′E	<830	mosaic forest/savanna, deciduous woodland
401–67[1]	C 1/	−0.3	9	1847	11	34°22′S, 18°29′E	<1000	open deciduous shrubland
41825[4]	P 3/	−3.2	12	1900–1920	12	04°1′N, 9°41′S	10	closed evergreen lowland forest
42706[4]	M 3/	−3.6	13	1884	13	06°9′S, 38°50′E–6°46′s, 37°6′E	<2000	mosaic forest/savanna, deciduous woodland
42707[4]	C /1	0.2	12	1884	13	06°9′S, 38°50′E–6°46′s, 37°6′E	<2000	mosaic forest/savanna, deciduous woodland
43132[4]	M /2	−2.2	12	1860–1920	14	17°53′S, 37°53E	<10	mosaic forest/savanna

(continued on next page)

Appendix A (*continued*)

Specimen	Sampled teeth	n. c. δ^{13}C	Age	Date	LN	Coordinates (lat.–long.)	Altitude (m)	Vegetation
43587[4]	M 1/	−3.3	12	1860–1920	10	11°43′S, 36°18′E–11°25′S, 38°29′E	150–500	mosaic forest/savanna, deciduous woodland
44088[4]	M 3/	−3.6	13	1912	15	06°50′N, 31°8′E	400	open grassland
481[5]	I /2	−2.4	3	1825	16	19°10′N, 30°29′E	260	sparse grassland
482[5]	M 3/	−2.5	8	unknown	17	06°1′S, 12°24E	0	mosaic forest/savanna
483[5]	M 2/	−1.9	12	1903	18	8°45′S, 39°25′E	0	mosaic forest/savanna
5553[6]	M 2/	−0.7	12	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6088[6]	P /2	0.2	16	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6089[6]	C 1/	0.2	16	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6090[6]	C 1/	0.6	14	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6092[6]	C 1/	−0.8	11	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6093[6]	D 4/	−5.3	4	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6094[6]	M 1/	−1.5	5	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6095[6]	C 1/	0.2	2	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6096[6]	C 1/	0.1	10	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6097[6]	–	–	18	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6098[6]	M /1	−2.6	11	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6100[6]	C 1/	−1.1	11	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6101[6]	P 3/	−0.5	15	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6102[6]	–	–	9	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6103[6]	–	–	12	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6104[6]	C 1/	0.8	11	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6105[6]	P 4/	−0.5	13	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6106[6]	M 2/	−0.6	11	ca. 1920	19	0°37′S, 29°10′E–1°0′S, 29°22′E	900–1100	closed grassland
6426[6]	M /3	−0.1	20	1911	20	12°33′N, 10°56′E	350	deciduous woodland
6427[6]	C /1	−1.3	15	1910–1911	21	11°11′N, 15°20′E	300	closed grassland
843-76[1]	C 1/	−1.5	15	1929	14	17°53′S, 37°53E	<10	mosaic forest/savanna
843-77[1]	M 3/	−4.0	10	1929	14	17°53′S, 37°53E	<10	mosaic forest/savanna
847-100[1]	P /3	−1.1	8	1931	22	0°43′S, 8°56′E–1°2′S, 9°5′E	<10	degraded evergreen lowland forest
847–99[1]	M 3/, M /3	−4.4	16	1931	22	0°43′S, 8°56′E–1°2′S, 9°5′E	<10	degraded evergreen lowland forest
865–18[1]	C1/, P/3	0.9	10	1940	22	0°43′S, 8°56′E–1°2′S, 9°5′E	<10	degraded evergreen lowland forest

Appendix A (*continued*)

Specimen	Sampled teeth	n. c. δ^{13}C	Age	Date	LN	Coordinates (lat.–long.)	Altitude (m)	Vegetation
865–18[1]	D4/	−4.8	10	1940	22	0°43′S, 8°56′E–1°2′S, 9°5′E	<10	degraded evergreen lowland forest
91275[4]	P 2/	−3.9	11	1860–1920	23	inaccurate location	<4000	degraded evergreen lowland forest to deciduous woodland
91326[4]	C 1/	−1.9	14	1860–1920	24	17°23′S, 14°13′E–16°45′S, 14°58′E	1000–1800	deciduous woodland
A2219[2]	–	–	13	unknown	25	inaccurate location	<500	degraded evergreen lowland forest, deciduous woodland, deciduous shrubland with sparse trees
Abon[4]	C 1/	−2.7	13	1901	26	05°49′N, 8°51′E–5°4′N, 9°45′E	150–2000	closed evergreen lowland forest
Br1[4]	M /1	−6.6	16	1860–1920	27	inaccurate location	<4000	closed to degraded evergreen lowland forest, deciduous woodland
Cun1[4]	C 1/	−1.5	8	1904	24	13°38′S, 16°3′E–17°23′S, 14°13′E	1000–1800	mosaic forest/savanna, deciduous woodland, open deciduous shrubland
Cun2[4]	M /1	−4.6	15	1904	24	13°38′S, 16°3′E–17°23′S, 14°13′E	1000–1800	mosaic forest/savanna, deciduous woodland, open deciduous shrubland
Dong1[4]	C 1/, M 3/	−2.5	15	1913	28	04°46N, 11°48′E	610	closed to degraded evergreen lowland forest
Dong2[4]	M 1/	−4.2	14	1913	28	04°46N, 11°48′E	610	closed to degraded evergreen lowland forest
Dong3[4]	P 2/	−3.4	7	1913	28	04°46N, 11°48′E	610	closed to degraded evergreen lowland forest
Dong4[4]	M 3/	−3.9	14	1913	28	04°46N, 11°48′E	610	closed to degraded evergreen lowland forest
Dong5[4]	P 3/	−2.8	12	1913	28	04°46N, 11°48′E	610	closed to degraded evergreen lowland forest
Maig1[4]	P 3/	−3.6	14	1860–1920	29	06°45′N, 11°50′E	1200	degraded evergreen lowland forest
Sato1[4]	C 1/	−1.6	17	1914	30	04°25′N, 13°1′E	710	closed evergreen lowland forest
Usam1[4]	M 2/	−3.1	11	1860–1920	31	05°9′S, 38°27′E–4°26′S, 38°12′E	300–1500	montane forest, mosaic forest/savanna, deciduous shrubland with sparse trees, open grassland with sparse shrub

(continued on next page)

Appendix A (*continued*)

Specimen	Sampled teeth	n. c. δ^{13}C	Age	Date	LN	Coordinates (lat.–long.)	Altitude (m)	Vegetation
TM009-01-050[7]	M	−5.6	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM009-01-051[7]	M	−4.8	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM009-01-192[7]	C 1/	−3.4	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM009-01-259[7]	C 1/	−2.9	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM009-01-363[7]	P or M	−6.9	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM016[7]	P	0.2	–	1997–2002	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM050-00-002[7]	M	−4.7	–	2000	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM069-98-002[7]	C /1	−9.3	–	1998	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM074[7]	M	−5.0	–	1997–2002	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM074-99[7]	C 1/	−2.0	–	1999	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM082-99-004[7]	–	–	–	1999	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM115-00-126[7]	–	–	–	2000	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM177-01-033[7]	M 2/	0.8	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM207-01-005[7]	C 1/	−5.0	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM241-01-009[7]	C /1	−4.3	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM242-01-029[7]	C 1/	−3.0	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM242-01-030[7]	C 1/	−3.5	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM242-01-032[7]	C /1	−3.1	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM242-01-035[7]	M	−3.4	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM243-01-012[7]	C 1/	−3.3	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM258-01-050[7]	M 2/	−3.1	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM259-01[7]	M 1/	−6.9	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM259-01-008[7]	M	−3.6	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM259-01-026[7]	C /1	1.4	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM259-02-001[7]	M 1/	−4.1	–	2002	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM293-01-030[7]	M /3	−2.8	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation

Appendix A (*continued*)

Specimen	Sampled teeth	n. c. $\delta^{13}C$	Age	Date	LN	Coordinates (lat.–long.)	Altitude (m)	Vegetation
TM315-01-004[7]	M /3	−4.2	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation
TM337-01-001[7]	C /1	1.0	–	2001	TM	17°00′N, 15°30′E–17°00′N, 18°30′E	280–430	late Miocene vegetation

The sampled teeth and non-corrected (n. c.) $\delta^{13}C$ are indicated for carbon isotope analyses. Ages are age groups defined by Laws (1968b), whereas dates are those of acquisition by the institution. For each locality (referenced by the locality number (LN); see Fig. 1 and Table 1), the dominant types of vegetation were mostly determined from White (1983). Altitudes are approximates.

Housing institutions: [1]Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland; [2]Muséum National d'Histoire Naturelle, Paris, France; [3]Muséum d'Histoire Naturelle, Bern, Switzerland; [4]Museum für Naturkunde, Berlin, Germany; [5]Forschunginstitut und Naturmuseum Senkenberg, Frankfurt-am-Main, Germany; [6]Musée Royal d'Afrique Centrale, Tervuren, Belgium; [7]Centre National d'Appui à la Recherche, Ndjamena, Chad.

Appendix B

Vegetation grouping in three environmental categories used for data comparisons (vegetation types and average tree cover percentages are from Mayaux et al., 2004)

Closed environment		Intermediate environment		Open environment	
Dominant vegetation	Tree cover %	Dominant vegetation	Tree cover %	Dominant vegetation	Tree cover %
Swamp forest	78.7 ± 8.96	Mosaic forest/savanna	43.1 ± 11.8	Open deciduous shrubland	13.7 ± 10.1
Closed evergreen lowland forest	68.8 ± 17.4	Closed deciduous forest	35.2 ± 13.4	Closed grassland	9.58 ± 9.31
Submontane forest	66.9 ± 18.5	Mangrove	33.0 ± 21.0	Open grassland with sparse shrubs	2.96 ± 4.32
Montane forest	57.6 ± 19.0	Deciduous woodland	28.1 ± 11.1	Open grassland	0.87 ± 1.97
Degraded evergreen lowland forest	49.0 ± 20.2	Deciduous shrubland with sparse trees	20.3 ± 9.00	Sparse grassland	0.14 ± 0.57
		Swamp bushland and grassland	18.5 ± 13.9		

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