

Environmental and climatic evolution of the Namib Desert since the Middle Miocene: the contribution of carbon isotope ratios in ratite eggshells

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Received 21 July 2002; accepted 27 August 2002

Communicated by Jean Dercourt

Abstract – Carbon isotope ratios of ratite eggshells were measured in samples without diagenetic alterations. Temporal evolution (Miocene to Recent) of this ratio is related to the diet of the birds, which reflects a fluctuation in the percentage of C₃ and C₄ plants in the Namib ecosystem. The palaeoclimatic implications are discussed. *To cite this article: L. Segalen et al., C. R. Geoscience 334 (2002) 917–924.*

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ratites / CO₂ / carbone 13 / palaeoclimate / Namibia / Neogene

Résumé – Évolution environnementale et climatique du désert de Namib depuis le Miocène moyen : contribution des rapports isotopiques du carbone des coquilles d'œufs de ratites. Le rapport isotopique du carbone a été mesuré sur des coquilles d'œufs de ratites de Namibie, dépourvues d'altérations diagénétiques. L'évolution de ce rapport (du Miocène à l'Actuel) est reliée au régime alimentaire des oiseaux, qui reflète une fluctuation du pourcentage de plantes en C₃ et C₄ dans l'écosystème du Namib. Les implications paléoclimatiques sont discutées. *Pour citer cet article : L. Segalen et al., C. R. Geoscience 334 (2002) 917–924.*

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Version abrégée

1. Introduction

Les éolianites affleurant en fenêtre au sein de l'erg du désert de Namibie contiennent des restes de mammifères et des œufs de ratites [21, 27–30]. Le $\delta^{13}\text{C}$ a été mesuré sur ces coquilles, pour déterminer si la biosphère continentale a enregistré les changements climatiques des derniers millions d'années, liés à la formation du Namib.

2. Le carbone 13 dans la biosphère continentale

Les $\delta^{13}\text{C}$ varient de $-26,5\text{‰}$ pour les plantes dites en C₃ à $-12,5\text{‰}$ pour celles en C₄. Par rapport aux plantes en C₃, la photosynthèse de type C₄ présente un meilleur rendement pour les basses pressions de CO₂ [6]. La teneur en CO₂ de l'atmosphère est donc un facteur au moins aussi important que l'humidité ou la température pour le développement des plantes en C₄ [6, 22].

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3. Le rapport isotopique du carbone dans les coquilles d'œufs de ratites

Le $\delta^{13}\text{C}$ des coquilles des autruches actuelles présentent un enrichissement de 16,2‰ par rapport à celui de l'alimentation [34]. Pour les fossiles, nous considérons que leur physiologie n'a pas changé depuis le Miocène. Le $\delta^{13}\text{C}$ de leur nourriture est fonction des proportions consommées de plantes en C_3 et en C_4 [13]. En tenant compte de la variabilité ($\pm 3\%$) des $\delta^{13}\text{C}$ de chaque type de plantes (lié à l'aridité, aux précipitations [7, 9–11]), on peut donc calculer le pourcentage de chaque type consommé par individu : [% de plantes en C_3] = $[(-\delta^{13}\text{C}_{\text{coq}} + 3,7)/14] \times 100$ et [% de plantes en C_4] = $[1 - (-\delta^{13}\text{C}_{\text{coq}} + 3,7)/14] \times 100$. Ces relations ont été vérifiées en élevages à nourriture contrôlée [34] ; toutefois, dans leur milieu naturel, ces animaux présentent une préférence pour les plantes en C_3 [12], qui introduit un biais dans la reconstitution des paléoenvironnements.

4. Résultats isotopiques

Les fluctuations du $\delta^{13}\text{C}$ (Tableau 1 et Fig. 2) ont été établies pour les 20 derniers millions d'années (l'âge des coquilles de type Aepyornithoïde d'Elisabethfeld est estimé à 19–20 Ma par les mammifères). Le $\delta^{13}\text{C}$ moyen est de $-8,6\%$ au Miocène inférieur. Au Miocène moyen, il augmente d'abord légèrement ($-8,25\%$ dans la biozone à *Namornis oshanaï*, 15–16 Ma), puis chute en deux étapes : (1) vers 15 Ma, il diminue de $-1,31\%$ entre les biozones à *N. oshanaï* et à *D. corbetti*, où le $\delta^{13}\text{C}$ moyen est alors de $-9,56\%$, puis reste ensuite stable ($-9,51\%$) durant la biozone à *D. spaggiarii* (12–14 Ma) ; (2) vers 12 Ma, une nouvelle diminution de $-1,25\%$ survient entre les biozones à *D. spaggiarii* (12–14 Ma) et à *D. wardi* (10–12 Ma), où le $\delta^{13}\text{C}$ moyen atteint $-10,76\%$. Durant le début du Miocène supérieur, le $\delta^{13}\text{C}$ se stabilise ($-10,89\%$ dans la biozone à *D. laini*, 8–10 Ma), puis diminue légèrement, pour atteindre $-11,26\%$ dans la biozone à *S. karingarabensis* (Miocène supérieur–Pliocène basal, 8–5 Ma). Durant la biozone à *S. daberansensis* (2–5 Ma), le $\delta^{13}\text{C}$ remonte de près de 1‰, pour atteindre une valeur de $-10,23\%$ au cours du Pliocène. Enfin, les œufs actuels (*S. camelus*) présentent un $\delta^{13}\text{C}$ de $-5,62\%$.

5. Discussions

5.1. Des plantes en C_4 présentes en Namibie dès le Miocène inférieur ?

Pour chaque période, il est possible de déterminer un $\delta^{13}\text{C}$ théorique des coquilles, qui tienne compte à la fois du régime alimentaire et de la variabilité du $\delta^{13}\text{C}$ des plantes [11] :

$$\begin{aligned} \delta^{13}\text{C}_{\text{coquille}} = & (\delta^{13}\text{C}[\text{CO}_2] - \delta^{13}\text{C}[\text{CO}_2]_0) \\ & - (0,02 \times ([\text{CO}_2] - [\text{CO}_2]_0)) \\ & - (0,033 \times (\text{Précip} - \text{Précip}_0)) \\ & + \delta^{13}\text{C}_{\text{plante C}_{30}} + 16,2 \end{aligned}$$

avec $[\text{CO}_2]_0 = 280$ ppmv, $\delta^{13}\text{C}[\text{CO}_2]_0 = -6,5\%$ et $\delta^{13}\text{C}_{\text{plante C}_{30}} = -26\%$ (valeurs pour les temps préindustriels), $\text{Précip}_0 = 50$ mm (pluviométrie annuelle pour le désert du Namib). Les concentrations en CO_2 atmosphérique pour le Miocène proviennent de l'étude de Pagani [16]. Les précipitations sont estimées à partir des données environnementales déduites des études paléontologiques et sédimentologiques établies au cours du Miocène et de la répartition actuelle des précipitations en Namibie. Pour les autruches actuelles, cette méthode indique un régime composé à 60–65% de plantes en C_3 . Compte tenu des préférences des autruches pour ces plantes, cette estimation est en accord avec la répartition des plantes de type C_3 dans l'écosystème namibien (30% de la flore [26]). Les valeurs isotopiques mesurées sur les espèces du Miocène inférieur impliquent, même en tenant compte de la variabilité isotopique des plantes sources, la présence de plantes C_4 dans la nourriture. Ceci est en accord avec la découverte de Chloridoïdæ (proches des graminées en C_4) au Kenya vers 14 Ma [25] et avec les données isotopiques sur les dents de Rhinocerotidés et de Proboscidiens impliquant des plantes en C_4 vers 15,3 Ma [15].

5.2. Conséquences paléoclimatiques

Si la concentration du CO_2 atmosphérique est, à long terme, le paramètre majeur pour le développement des plantes en C_4 , les conditions climatiques (température et régime de pluies durant la phase de croissance [26]) jouent également un rôle.

5.2.1. Au Miocène inférieur–moyen

Les données paléontologiques de Namibie [19] indiquent, pour le Miocène basal, un climat subtropical, plus chaud et plus humide qu'actuellement. Ces conditions perdurent au moins jusqu'à 17 Ma [20]. Au Miocène moyen se produit une aridification de la zone côtière [33], qui se marque par les premiers dépôts éoliens (biozone à *N. oshanaï*, 15–16 Ma) à Awasisib.

5.2.2. Du Miocène supérieur à l'Actuel

Le $\delta^{13}\text{C}$ des coquilles augmente de 1‰ au cours du Miocène supérieur et du Pliocène, puis de près de 4,5‰ entre le Pliocène et l'Actuel (Fig. 2). Malgré une préférence pour les plantes en C_3 [12], le $\delta^{13}\text{C}$ moyen des œufs des autruches actuelles correspond à un régime composé seulement à 60–65% de ces plantes. Par contre, nos données suggèrent une présence plus importante de plantes en C_3 au Miocène supérieur. Le Pliocène apparaît donc comme une période charnière, où les plantes en C_4 prennent alors une place prépondérante dans certains écosystèmes continentaux [3, 15, 23, 24].

Après d'importantes fluctuations au cours du Quaternaire [14], les concentrations actuelles du CO_2 dans l'atmosphère (350 ppmv) sont proches de celles du Miocène supérieur (320 ppmv). Comme le climat, au niveau du Namib, était moins aride qu'actuellement (traces de racines et développement de paléosols à Awasisib), la température et les régimes des pluies paraissent être les principaux fac-

teurs responsables de l'augmentation des plantes en C₄ dans le système désertique, entre le Miocène supérieur et l'Actuel.

6. Conclusions

L'évolution du $\delta^{13}\text{C}$ des coquilles met en évidence une modification du régime alimentaire des ratites, indiquant

une variation du pourcentage relatif des plantes en C₃ et en C₄ dans l'écosystème du Namib. Les faibles concentrations en CO₂ atmosphérique au Miocène inférieur semblent être le paramètre majeur expliquant la présence de plantes C₄ dans le milieu. Durant le Miocène moyen et terminal, les conditions régionales de température et de précipitations exercent ensuite un effet de plus en plus important sur la composition de l'écosystème namibien.

1. Introduction

It is classically thought that the causes of the coastal deserts (Namibia and Chile–Peru) are: (1) the development of the Antarctic Ice Sheet, which reinforced the high pressure belt under the Tropic of Capricorn, (2) the installation of cold currents along the western coasts of continents (i.e., Benguela Current) and (3) the associated upwellings. In Namibia, ancient aeolanites have yielded ratite eggshells and fossil mammals, leading to a biostratigraphic scale from ca 20 Ma to Present [21, 27–30] (calibrated by radiometric dates on volcanic rocks interlayered between fossiliferous beds of similar East African fauna [17, 18]). This preliminary study aims at verifying whether the ratite eggshell $\delta^{13}\text{C}$ could have recorded the Neogene climatic changes responsible for the formation of the Namib Desert.

2. Carbon-13 in the continental biosphere

Photosynthesis presents two basic biochemical cycles: the Calvin cycle alone is present in C₃ plants, while C₄ plants use the Hatch–Slack cycle. These two categories of processes lead to very different $\delta^{13}\text{C}$: -12.5‰ ($\pm 3\text{‰}$) in C₄ plants and -26.5‰ ($\pm 3\text{‰}$) in C₃ type. The variability is in relation with climatic factors as humidity, precipitations, temperatures, or light intensity [7–10]. The C₄ photosynthetic process permits the concentration of the amount of intracellular CO₂ by a factor of 10 to 20 times in the Kranz cell as compared to the quantity of CO₂ present in the mesophyllian cell [5]. Therefore, C₄ photosynthesis has a better efficiency when the atmospheric pressure of CO₂ is low. In contrast, when the pressure of CO₂ increases, the photosynthetic cycle in C₃ plants is improved [6, 22].

3. Carbon isotopic ratios in ratite eggshells

The egg cycle is relatively short (about 24 h). During the shell synthesis, the amount of Ca²⁺ in the

blood increases. Specialised cells secrete the organic components that permit the precipitation of calcium ions, associated with carbonate ions (derived from metabolic CO₂), to form the eggshell [31]. The $\delta^{13}\text{C}$ eggshell is related to the diet of the birds [34]. The ostrich eggshells present enrichment in ¹³C relative to their diet:

$$\delta^{13}\text{C}_{\text{eggshell}} = \delta^{13}\text{C}_{\text{diet}} + 16.2 \quad (1)$$

For the fossils species, we assume that metabolic processes are unchanged since the Miocene. Being herbivores, the isotope ratios of their food is a function of the mixture between a diet composed of 100% of C₃ plants, on the one hand, and of 100% of C₄ plants, on the other hand [13]:

$$\delta^{13}\text{C}_{\text{diet}} = X(-26.5) + (1 - X)(-12.5) \quad (2)$$

where X and $(1 - X)$ are the percentage of C₃ and C₄ consumed.

From Eqs. (1) and (2), we can deduce the percentage of C₃ or C₄ plants in the diet:

$$\begin{aligned} [\% \text{C}_3 \text{ plants}] &= [(-\delta^{13}\text{C}_{\text{eggshell}} + 3.7)/14] \times 100 \\ [\% \text{C}_4 \text{ plants}] &= [1 - (-\delta^{13}\text{C}_{\text{eggshell}} + 3.7)/14] \times 100 \end{aligned} \quad (3)$$

Isotopic record reliability has been verified for domestic ostriches by experiments with controlled amounts of C₃ and C₄ plant diets [34]. However, in wild environment, these animals prefer C₃ plants [12]. Thus, in ecosystems with 25 to 75% of C₃ plants (South Africa), the eggshell $\delta^{13}\text{C}$ correspond to a rate of 70 to 100% of the C₃ plants ingested. Hence, dietary choice by the animals introduces a bias in the reconstruction of palaeoenvironments.

4. Choice and preparation of material

Fossil eggs were collected in the central and southern Namib Desert (Fig. 1): Karingarab, GP Pan and Rooilepel, all close to Oranjemund, Elisabethfeld, to the south of Lüderitz, and Awasib and Haiber Hill, both in the Namib–Naukluft Park.

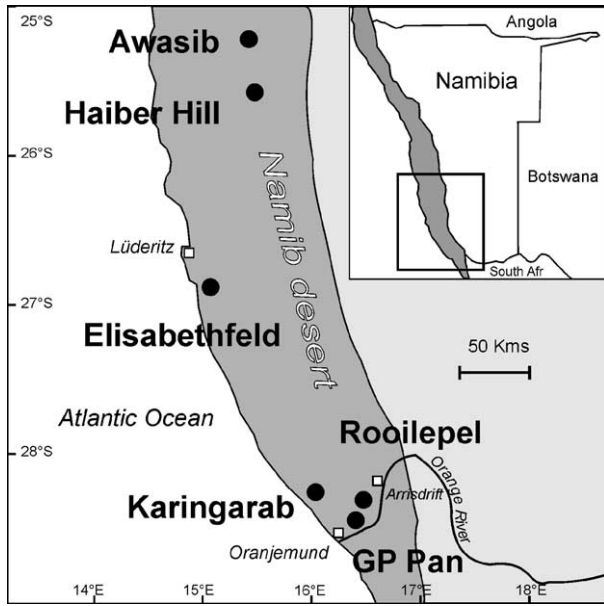


Figure 1. Location of fossiliferous sites: Karingarab: (28° 11' 41.8'' S/ 16° 21' 12.0'' E), GP Pan (28° 29' 96.8'' S/ 16° 32' 28.2'' E), Rooilepel (28° 17' 99.6'' S/ 16° 35' 53.1'' E), Elisabethfeld (26° 58' 58.5'' S/ 15° 53' 9'' E), Awasib (site I: 25° 18' 28.7'' S/ 15° 38' 43.6'' E; site II: 25° 22' 48.4'' S/ 15° 34' 42.1'' E) and Haiber Hill (site I: 25° 37' 14.5'' S/ 15° 39' 34.9'' E; site II: 25° 40' 16.9'' S/ 15° 39' 68.5'' E).

Figure 1. Localisation des sites fossilifères : Karingarab : (28° 11' 41.8'' S/ 16° 21' 12.0'' E), GP Pan (28° 29' 96.8'' S/ 16° 32' 28.2'' E), Rooilepel (28° 17' 99.6'' S/ 16° 35' 53.1'' E), Elisabethfeld (26° 58' 58.5'' S/ 15° 53' 9'' E), Awasib (site I : 25° 18' 28.7'' S/ 15° 38' 43.6'' E; site II : 25° 22' 48.4'' S/ 15° 34' 42.1'' E) et Haiber Hill (site I : 25° 37' 14.5'' S/ 15° 39' 34.9'' E; site II : 25° 40' 16.9'' S/ 15° 39' 68.5'' E).

Related to diagenetic alterations [4], the external and internal surfaces eggshells (low-magnesian calcite), which often present a bright cathodoluminescence, were cleaned by abrasion and then treated by ultrasound. Samples were extracted from the thickest parts of the shell (not eroded by the wind) and away from the pore complexes (which tend to be recrystallised). Comparison with previous ostrich eggshell data from Dauphin et al. [4] shows that the chosen sampling technique eliminates up to 95% of the diagenetic and allochthonous sediments. Isotope ratios were measured on a SIRA9/VG602 spectrometer. The analytical precision for carbon is of about 0.05‰.

5. Isotopic results

From isotopic values obtained for each eggshell species at the various sites (Table 1), it is possible to draw the $\delta^{13}\text{C}$ fluctuation curve from 20 Ma up to present times (Fig. 2). Isotopic fluctuations are validated by the Student test (Table 1). The oldest eggshells (Aepyornithoidea type) from Elisabethfeld

Table 1. Eggshell carbon isotopic ratios from the different studied sites.

Tableau 1. $\delta^{13}\text{C}$ des coquilles de ratites pour l'ensemble des sites étudiés.

Species	$\delta^{13}\text{C}$ (per mill)	Test de Student
<i>Struthio camelus</i> (Modern) n = 22	mean = -5,22 max. = -3,26 min. = -8,08	} $T_{30} = 10.19$ ddl=30, $\alpha = 0.05$ $t = 2.04$
<i>Struthio daberassensis</i> (2-5 Ma) n = 11	mean = -10,23 max. = -8,41 min. = -11,34	
<i>Struthio karingarabensis</i> (5-8 Ma) n = 8	mean = -11,26 max. = -9,88 min. = -12,59	} $T_{17} = 2.66$ ddl=17, $\alpha = 0.05$ $t = 2.11$
<i>Diamantornis laini</i> (8-10 Ma) n = 19	mean = -10,89 max. = -8,77 min. = -12,40	
<i>Diamantornis wardi</i> (10-12 Ma) n = 56	mean = -10,76 max. = -8,77 min. = -12,89	} $T_{28} = 1.21$ ddl=28, $\alpha = 0.05$ $t = 2.05$
<i>Diamantornis spaggiarii</i> (12-14 Ma) n = 17	mean = -9,52 max. = -8,00 min. = -11,02	
<i>Diamantornis corbetti</i> (14-15 Ma) n = 29	mean = -9,56 max. = -7,54 min. = -11,47	} $T_{75} = 0.52$ ddl=75, $\alpha = 0.05$ $t = 1.96$
<i>Namornis oshanai</i> (15-16 Ma) n = 15	mean = -8,25 max. = -6,80 min. = -10,72	
<i>Aepyornithoid</i> (18-20 Ma) n = 2	mean = -8,6 max. = -8,29 min. = -8,91	} $T_{70} = 4.65$ ddl=70, $\alpha = 0.05$ $t = 1.96$
		} $T_{44} = 0.13$ ddl=44, $\alpha = 0.05$ $t = 1.96$
		} $T_{42} = 3.92$ ddl=42, $\alpha = 0.05$ $t = 1.96$
		} $T_{15} = 0.41$ ddl=15, $\alpha = 0.05$ $t = 2.13$

are dated around 19–20 Ma (mammalian biochronology). The mean $\delta^{13}\text{C}$ during the Early Miocene is -8.6‰ (Fig. 2). At the base of the Middle Miocene, it increases slightly (0.35‰) to reach -8.25‰ in the *Namornis oshanai* biozone (ca 16–15 Ma). During the Middle Miocene, the curve shows an important negative excursion by two steps. The first one occurs at ca 15 Ma, when the mean $\delta^{13}\text{C}$ drops by -1.31‰ between the *N. oshanai* and *D. corbetti* biozones ($\delta^{13}\text{C} = -9.56\text{‰}$). Then it remains stable ($\delta^{13}\text{C} = -9.51\text{‰}$) during the *D. spaggiarii* zone (14–12 Ma). The second drop occurs at about 12 Ma (a diminution of -1.25‰) occurs between the *D. spaggiarii* and *D. wardi* zones (12–10 Ma), where the $\delta^{13}\text{C}$ value reaches -10.76‰ . The student test (Table 1) shows that the two Miocene $\delta^{13}\text{C}$ drops are signif-

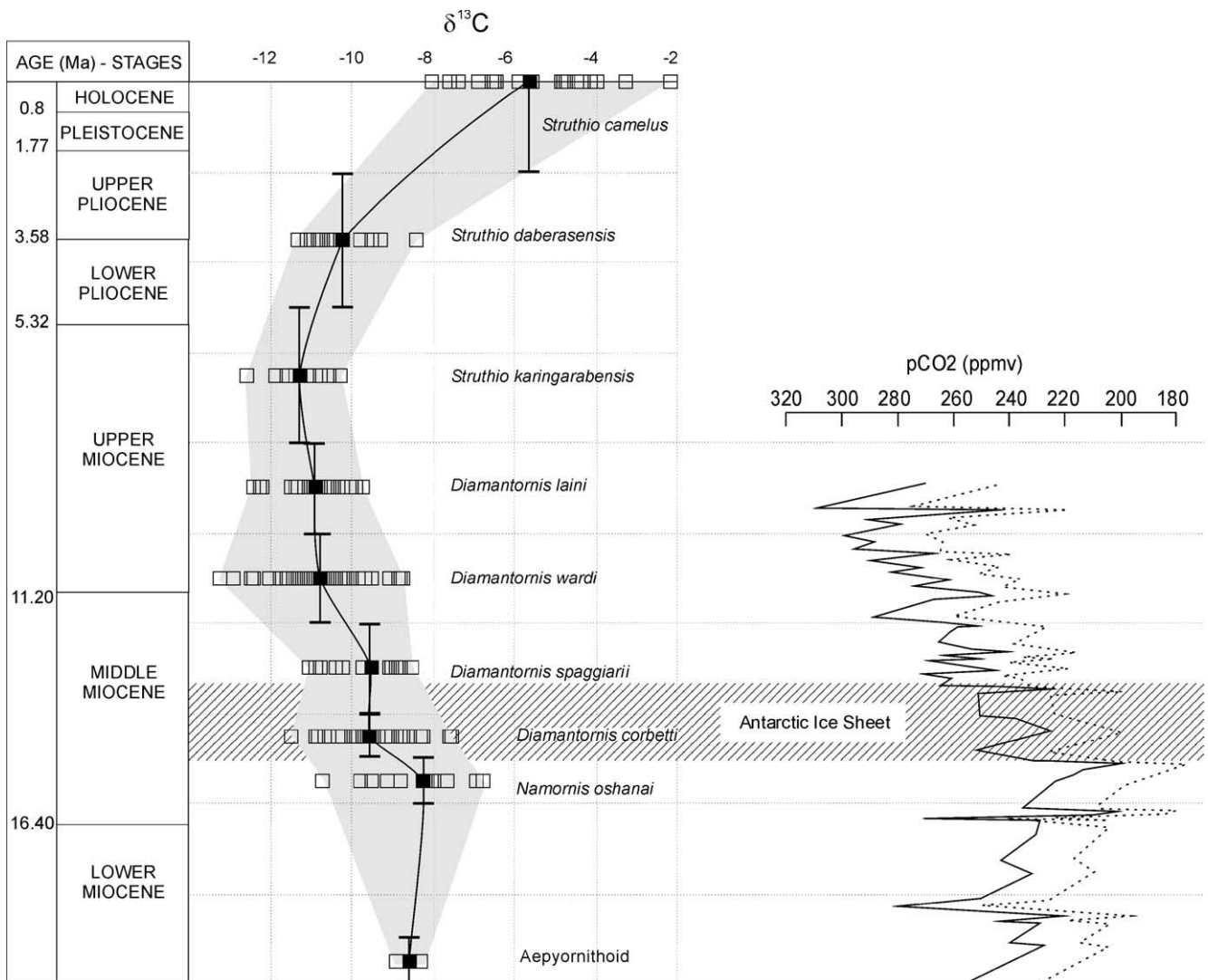


Figure 2. Ratite eggshell $\delta^{13}\text{C}$ evolution during the Neogene and Quaternary. Correlation with atmospheric CO_2 concentration estimates during the Miocene in the southern hemisphere. Modified from Pagani [16]. Time scale from Berggren and Cande [1, 2].

Figure 2. Variations au cours du Néogène et du Quaternaire du $\delta^{13}\text{C}$ des coquilles de ratites. Corrélation avec les variations du CO_2 atmosphérique durant le Miocène dans l'hémisphère sud. Modifié d'après Pagani [16]. Échelle de temps d'après Berggren et Cande [1, 2].

icant ($t = 3.92$, $\alpha = 0.05$ and $t = 4.65$, $\alpha = 0.05$). During the early part of the Late Miocene, the mean $\delta^{13}\text{C}$ remains reasonably stable, around -10.89‰ , in the *D. laini* biozone. It diminishes slightly (-0.37‰) to reach -11.26‰ during the *S. karingarabensis* biozone (Latest Miocene to Basal Pliocene; 8–5 Ma). During the *S. daberassensis* biozone (5–2 Ma), the $\delta^{13}\text{C}$ increases nearly of 1‰ to reach -10.23‰ during the Pliocene. Finally, the mean $\delta^{13}\text{C}$ obtained from modern ostrich eggs (*S. camelus*) is -5.62‰ . Due to climatic differences between north and south outcrop localities, the variability of $\delta^{13}\text{C}$ could be relatively large ($\pm 3\text{‰}$) for the modern Namibian eggshells. Student tests (Table 1) valid the $\delta^{13}\text{C}$ positive evolution from Pliocene to Recent ($t = 2.66$, $\alpha = 0.05$ and $t = 10.19$, $\alpha = 0.05$).

6. Discussion

6.1. C_4 plants in Namibia ecosystems during the Early and Middle Miocene?

The evolution of eggshell $\delta^{13}\text{C}$ could be interpreted in term of C_3/C_4 diet evolution from Eq. (3). Taking into account the $\delta^{13}\text{C}$ variability of plant ($\pm 3\text{‰}$), the diet of Early and Middle Miocene species (20–14 Ma), is made of 65 to 100% of C_3 plants (most probable value 85%). The diminution of the $\delta^{13}\text{C}$ occurring between 14 and 12 Ma leads to a 75 to 100% contribution of C_3 plants (probable value: 95%). C_3 plants reach 85 to 100% between 12 and 5 Ma (probable value: 100%). For modern Namibian ratites, a large proportion of C_4 plants should be

present in the food diet to explain the eggshell $\delta^{13}\text{C}$. C_3 plants represent only between 45 and 85% (probable value 65%) of the diet. This estimation is in accordance with the modern Namibian ecosystem composition (30% of C_3 plants [26]), in relation with the ostriches' dietary preference for C_3 plants [12].

Numerous studies have shown that environmental parameters can influence the value of the $\delta^{13}\text{C}$ of plants: aridity increases the $\delta^{13}\text{C}$ value in C_3 plants (0.33‰ per 100 mm decrease in precipitation, [32]). An increase of 100 ppm in atmospheric CO_2 concentrations leads to a decrease of 2‰ in plant $\delta^{13}\text{C}$; the $\delta^{13}\text{C}$ of atmospheric CO_2 has also an impact [9]. In spite of these relationships, we should test if $\delta^{13}\text{C}$ fluctuations in the Upper Tertiary could be explained by climatic variations without diet composition fluctuations. For this, we can use the equation proposed by Hatté and Antoine [11]:

$$\begin{aligned} \delta^{13}\text{C}_{\text{egg}} = & (\delta^{13}\text{C}[\text{CO}_2] - \delta^{13}\text{C}[\text{CO}_2]_0) \\ & - (0.02 \times ([\text{CO}_2] - [\text{CO}_2]_0)) \\ & - (0.033 \times (\text{Precip} - \text{Precip}_0)) \\ & + \delta^{13}\text{C}_{\text{C}_3\text{plant } 0} + 16.2 \end{aligned} \quad (4)$$

Pre-industrial period parameters could be $[\text{CO}_2]_0 = 280$ ppmv, $\delta^{13}\text{C}_{\text{C}_3\text{plant } 0} = -26$ ‰, $\delta^{13}\text{C}[\text{CO}_2]_0 = -6.5$ ‰ and $\text{Precip}_0 = 50$ mm (mean value for the Namib desert). During the Neogene, in the absence of data, we have used the $\delta^{13}\text{C}$ of pre-industrial period as $\delta^{13}\text{C}[\text{CO}_2]$. The Miocene atmospheric CO_2 concentrations during the Miocene could be estimated on the basis of Pagani data [16]. From the beginning of Early Miocene (24 Ma) to Middle Miocene (16–15 Ma), the concentration has first diminished by 110 ppmv, before increasing after 15–14 Ma (220 ppmv, Fig. 2). Related to the installation of the East Antarctic Ice Sheet (as recorded by an excursion of +1‰ in planktonic foraminifera $\delta^{18}\text{O}$ at about 14 Ma), this increase continues until 10 Ma (280 ppmv). Nowadays, in Namibia, annual precipitation means are comprised between 150–400 mm in grassland savannah regions and between 100–150 mm in semi-arid regions; they are lower than 50 mm in arid areas.

From Eq. (4), we can calculate a theoretical eggshell $\delta^{13}\text{C}$ for different rates of precipitations (Table 2). For modern Namibian species, the use of Eq. (4) (Table 2) confirms that with the actual rate of precipitation (<50 mm), the eggshell $\delta^{13}\text{C}$ could not correspond to a 100% C_3 diet. A participation of C_4 plant of the order of 40% is needed (see above).

Results are compatible with a 100% C_3 diet during the Upper and Middle Miocene, if the precipitation were lesser than 50 mm in the first case and comprised between 50 and 100 mm in the second one. These precipitation estimations agree with sedimentological and palaeontological data.

Studies from Elisabethfeld [19] and Arrisdrift [20] show that, during Early Miocene, the climate was more humid and warmer than it is today. During Middle Miocene, an important climatic change occurred in the southern hemisphere. The installation of the East Antarctic Ice Sheet comes along with important modifications in oceanic circulation patterns [34]. In Namibia, these changes correspond to the development of arid conditions [33], as indicated by the first occurrences of aeolianites during the *Namornis oshanai* biozone at Awasiib. This aridification of the southwestern Africa coastal zone confirms the passage from a warm, humid weather to a drier climate during the Early to Middle Miocene transition.

For the Early Miocene species, the eggshells $\delta^{13}\text{C}$ values are only compatible with a diet composed of 100% of C_3 plants, if the precipitations are lower than 50 mm. This is incompatible with the palaeontological and sedimentological data, which indicate a wetter climate during this period. For precipitations in the range 200–250 mm, the theoretical $\delta^{13}\text{C}$ (Eq. (4)) is similar to the measured $\delta^{13}\text{C}$, only if we admit a large participation of C_4 plants in the diet of these birds. This value (about 40%) is undoubtedly too high, but proves a presence of C_4 plants in the Early Miocene ecosystem. This development of C_4 plants could be related to the weak atmospheric CO_2 concentrations (Fig. 2). Previous studies have documented C_4 plant occurrences during the Early–Middle Miocene in some peculiar environments. Their presence is recorded in the $\delta^{13}\text{C}$ of Rhinocerotidae and Proboscidea teeth from the Tugen Hills (Kenya) at 15.3 Ma [15]. The site of Fort Ternan (14 Ma) has also yielded C_4 Graminae (Chloridoidae), indicating the existence of open forest ecosystems, with a dominance of grasses [25]. The rarefaction of C_4 plants in the ecosystem during Middle and Upper Miocene could reflect an increase in the atmospheric CO_2 concentration.

6.2. Late Miocene to Present Namibian climate evolution

The eggshell $\delta^{13}\text{C}$ increases by 1‰ during the Late Miocene and Pliocene and by 4.5‰ from the Pliocene to the present day (Fig. 2). Despite the ostriches' preference for C_3 plants [12], the modern Namibian $\delta^{13}\text{C}$ eggshell corresponds to a diet comprising only 65% C_3 plants (cf. above). In contrast, the $\delta^{13}\text{C}$ value suggests a greater presence of this plant type in the diet during the Late Miocene. Namib data confirms, therefore, that apart from changes related to regional climatic fluctuations, the Pliocene was a crucial period in the development and ecology of C_4 plants in the continental biosphere. It was at this epoch that they became preponderant in some ecosystems [3, 15, 23, 24].

Table 2. Calculation of the $\delta^{13}\text{C}$ of ratite eggshells, for a given diet, according to different precipitation rates. Bold numbers correspond to the compatible values for the diet suggested.

Tableau 2. Calcul du $\delta^{13}\text{C}$ des coquilles de ratites, pour un régime donné, en fonction de différents taux de précipitation. Les chiffres en gras correspondent aux valeurs compatibles pour le régime proposé.

Modern; $[\text{CO}_2] = 320$ ppmv			Upper Miocene (10 Ma); $[\text{CO}_2] = 290$ ppmv	
Precip. (mm)	Diet = 60% C_3 & 40% C_4	$\delta^{13}\text{C}$ eggshell (per mill)	Diet = 100% C_3	$\delta^{13}\text{C}$ eggshell (per mill)
0			–24.55	–8.35
50	–22.2	–5.5	–26.2	–10
100			–27.85	–11.65
150			–29.5	–13.3
200			–31.15	–14.95
250			–32.8	–16.6
300			–34.45	–18.25
350			–36.1	–19.9
400			–37.75	–21.55
Middle Miocene (15 Ma); $[\text{CO}_2] = 220$ ppmv				
Precip. (mm)	Diet = 100% C_3	$\delta^{13}\text{C}$ eggshell (per mill)	Diet = 85% C_3 & 15% C_4	$\delta^{13}\text{C}$ eggshell (per mill)
0	–23.15	–6.95	–21.05	–4.85
50	–24.8	–8.6	–22.7	–6.5
100	–26.45	–10.25	–24.35	–8.15
150	–28.1	–11.9	–26	–9.8
200	–29.75	–13.55	–27.65	–11.45
250	–31.4	–15.2	–29.3	–13.1
300	–33.05	–16.85	–30.95	–14.75
350	–34.7	–18.5	–32.6	–16.4
400	–36.35	–20.15	–34.25	–18.05
Lower Miocene (18 Ma); $\text{CO}_2 = 240$ ppmv				
Precip. (mm)	Diet = 100% C_3	$\delta^{13}\text{C}$ eggshell (per mill)	Diet = 60% C_3 & 40% C_4	$\delta^{13}\text{C}$ eggshell (per mill)
0	–23.55	–7.35	–17.95	–1.75
50	–25.2	–9	–19.6	–3.4
100	–26.85	–10.65	–21.25	–5.05
150	–28.5	–12.3	–22.9	–6.7
200	–30.15	–13.95	–24.55	–8.35
250	–31.8	–15.6	–26.2	–10
300	–33.45	–17.25	–27.85	–11.65
350	–35.1	–18.9	–29.5	–13.3
400	–36.75	–20.55	–31.15	–14.95

After important fluctuations during the Holocene [14], the Modern (320 ppmv) and Late Miocene (280 ppmv), atmospheric CO_2 concentrations are now close together. From Late Miocene to Present, the CO_2 concentrations do not seem to be the main control of the C_3/C_4 plant ratio in the Namibian desert ecosystem. Abundant roots and incipient palaeosols in Awasib aeolianites show that Upper Miocene was a less arid period than Present. The temperature and rainfall patterns seem to control the increase of the C_4 plants in the Namib Desert ecosystem between Late Miocene and today.

7. Conclusions

This preliminary study of Namibian $\delta^{13}\text{C}$ eggshell has shown changes in the ratite diet from Miocene to Present and has suggested the presence of C_4 plants during Early Miocene. The low concentration of the atmospheric CO_2 (around 230 ppmv) during this period seems to be the main control parameter of C_4 plants occurrence. During the Middle to Late Miocene, regional conditions of temperature and precipitation play an increasingly significant role in the Namibian ecosystem composition.

Acknowledgements. This work was supported by the Geological Survey of Namibia, the Namdeb Diamond Corporation (Pty) Ltd, the National Monuments Council of the Republic of Namibia, the France Embassy in Namibia, the MNHN, the UPMC of Paris, the CNRS (ECLIPSE) and the IFP (France). We thank Nathalie Labourdette for analytical assistance.

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