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THE LAND SNAIL *LIMICOLARIA KAMBEUL CHUDEAUI* GERMAIN IN THE ETHIOPIAN RIFT VALLEY: HABITAT, ECOLOGY AND SHELL ISOTOPE GEOCHEMISTRY

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ABSTRACT: The land snail *Limicolaria kambeul chudeaui* Germain was collected from the margins of Lake Tilo, a small caldera in the Ethiopian Rift Valley. Although fossil specimens of this subspecies have been used in palaeoclimatic reconstruction, there have been no previous reports of living examples. Here we describe the local habitat, climate and some aspects of ecology and isotopic variation within the snail shell. If isotope data can be obtained for fossil shells, this may provide a high-resolution record of-past seasonal climate variability.

Key words/phrases: Ethiopia, isotope geochemistry, Lake Tilo, *Limicolaria kambeul chudeaui* Germain, snail

INTRODUCTION

Live specimens of the land snail *Limicolaria kambeul chudeaui* Germain (Achatinidae: Pulmonata) (Fig. 1) were collected in January 1997 from the margins of Lake Tilo (7°03′N, 38°06′E; altitude 1540 m), a small crater lake in the

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Ethiopian Rift Valley (Fig. 2). The snails were identified by comparison with specimens held in the Natural History Museum, London (F. Naggs personal communication). *Limicolaria kambeul* is today widespread in sub-Saharan Africa (Haynes and Mead, 1987), but there are no previous reports of living specimens of the subspecies *chudeaui*. Fossil examples have been collected in a narrow band north of 15°N latitude and between 17°W and 35°E longitude in Senegal, Mauritania, Mali, Niger, Chad and the Sudan. Here we report on the snails' habitat, the local climate, some aspects of ecology, and details of the isotopic composition of the shell. If isotope data were obtained from a stratigraphical sequence of fossil shells, then these could provide a long-term high resolution record of seasonal climatic variation in north tropical Africa.

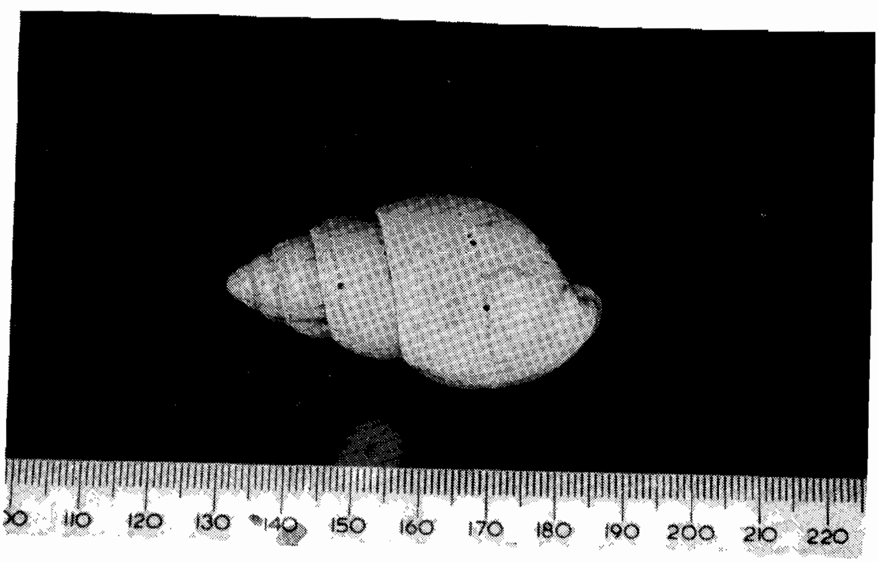

Fig. 1. ***Limicolaria kambeul chudeaui.*** The holes represent the sample sites (from the study by Leng *et al.* (1998)) at *ca* 1.5 mm intervals along the whorls of the shell. Scale in mm.

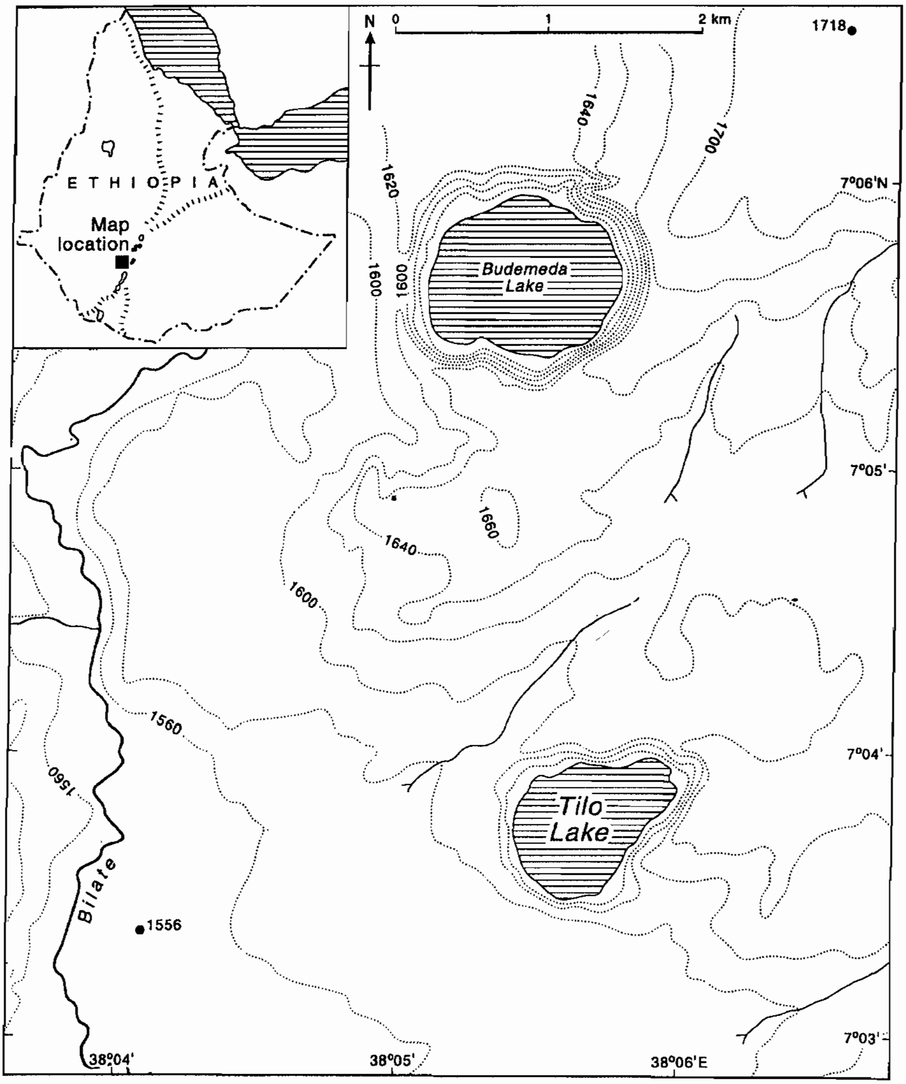

Fig. 2. Location map of Lake Tilo in the Ethiopian Rift Valley.

HABITAT AND ECOLOGY

Living snails collected in January 1997 were aestivating, buried a few centimetres below the soil surface around plants of the spiky succulent *Aloe*, and thus protected from excessive heat and predators. A thin, white, calcareous epiphragm entirely covered the shell apertures; a 1 mm long slit in the epiphragm allows gaseous exchange. The snails apparently remain in this dormant condition until roused by the onset of spring rains. Empty shells were found scattered on the soil surface, and in sections exposed by gullies. The vegetation on the steep crater walls around Lake Tilo consists of scattered trees of *Acacia*, *Combretum molle, Cordia ovalis* and a well-grazed ground-cover dominated by the labiate *Hypoestes forskoalii*. The shrub *Seena didimobotryia* is common; other plants include the herbs *Datura stramonium, Argimone mexicana, Kalanchoe lanceolata, Solanum incanum, Justicia hetrocarpa, Boerhavia erecta, Drimia altissima, Leucas abyssinica, L. martinicensi, Pluchea ovalis, Asparagus flagellaris, Sansevieria* spp., and *Dombeya* sp. These are dominantly C3- photosynthetic plants, many of which are widespread in moist tropical regions. Most of the surrounding area is densely cultivated by subsistence farmers, who grow both tef (*Eragrostis tef*) and maize, which are both C4 plants. Until about fifty years ago, the area was savanna grassland according to local sources. The carbon isotope composition of *Limicolaria* shells indicates that the snails have a diet based dominantly on C3 plants (Leng *et al.*, 1998). They also ingest inorganic carbonate which must be pedogenic in origin, because the volcanic rocks of the locality are non-calcareous.

CLIMATE

Temperature, rainfall, and evapotranspiration data for Awassa, 40 km to the east of Lake Tilo, are shown in Fig. 3. The region experiences two periods of rainfall annually (Griffiths, 1972). In March to May, the dry season is broken by the "Little Rains" that result from south-easterly airflow from the Indian Ocean. From June to October heavy monsoonal rainfall accompanies incursion by air masses of Atlantic origin. Awassa receives in excess of 900 mm of rain per year which is consistent with the description of the habitat of *Limicolaria* as forest or savanna with moderately high rainfall (Haynes and Mead, 1987). The dry season occurs between November and February. There are large diurnal variations in temperature and small seasonal changes.

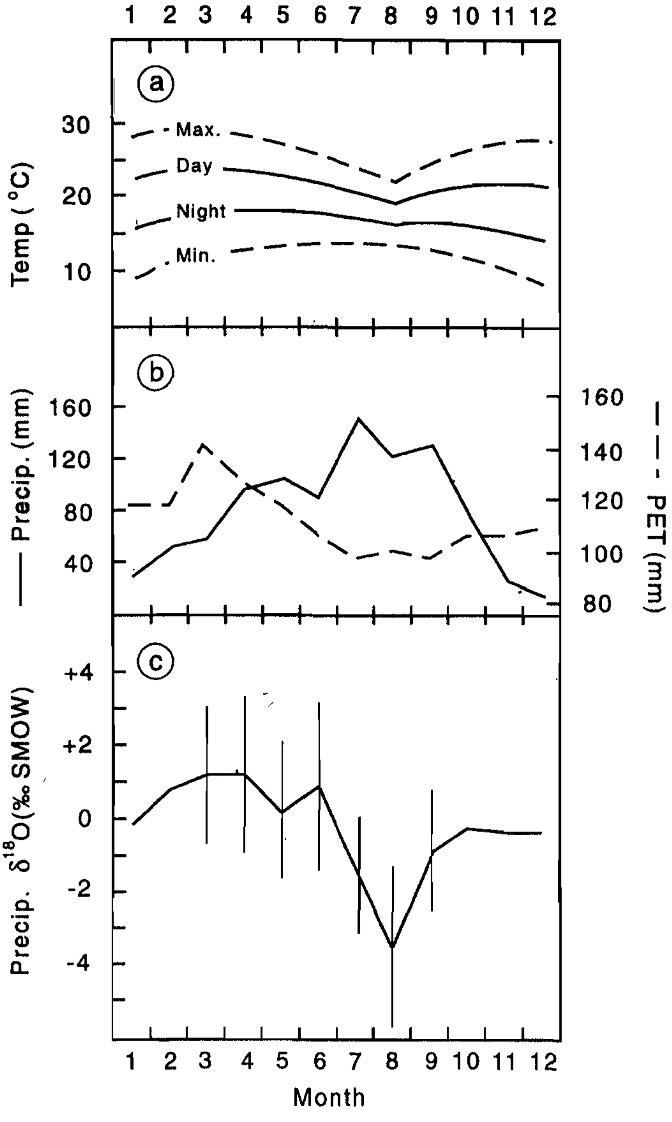

Fig. 3. Mean monthly climate parameters of precipitation. (a) maximum and minimum diurnal temperatures, and average day-time and night-time temperatures at Awassa (FAO, 1984); (b) precipitation and potential evapotranspiration (PET) at Awassa (FAO, 1984), (c) $\delta^{18}O$ values of precipitation at Addis Ababa, with ± 1 S.D. bars for the wetter months (non-weighted average of monthly values for the 13 years during 1969-1992 where at least 80% of the total precipitation was analyzed, from IAEA data).

SHELL DESCRIPTION

The shells are marked by transverse pale and dark brown streaks, typically 0.5 to 1 mm wide. Occasionally several streaks merge to form a thick band, although they also occur as very thin (<0.1 mm) fine bands, especially towards the apex of the shell. The juveniles have thin, almost transparent shells, the bands being more pronounced on the younger, larger whorls as the snail increases in size. Similar markings have been described in *Limicolaria martensiana* (Owen, 1964) where it is thought to be a form of camouflage against predation; banded snails are more difficult to detect in areas of bright sunshine and thick vegetation.

The shells are also ribbed, except on the apical protoconch. The ribs may represent lines formed as a result of growth interruptions. In thin section the central layer of the shell is composed of optically continuous, columnar crystals of aragonite aligned normal to the shell surface and the growth direction. Each crystal is *ca* 200 μm wide and 400 μm long, and probably represents a single growth event. As the snails appear to be opportunistic feeders, these growth events may not occur at regular intervals, but merely in response to food supply.

The 30 live specimens and 22 empty shells collected span a range of sizes. There is a linear relationship between maximum length and width of the shells (Fig. 4), reflecting their regular form and growth pattern. All the shells examined have apparent breakage lines across the whorls, up to a maximum of eight in the larger specimens, although some of the smaller snails have only one or two. It seems likely that these are a result of damage to the shell aperture margin during burial prior to aestivation. If so, the number of these discontinuities may bear some relationship to age, although not all shells have such features. Eight discontinuities in the larger specimens is consistent with an estimated life span of up to ten years for *Limicolaria* (Haynes and Mead, 1987).

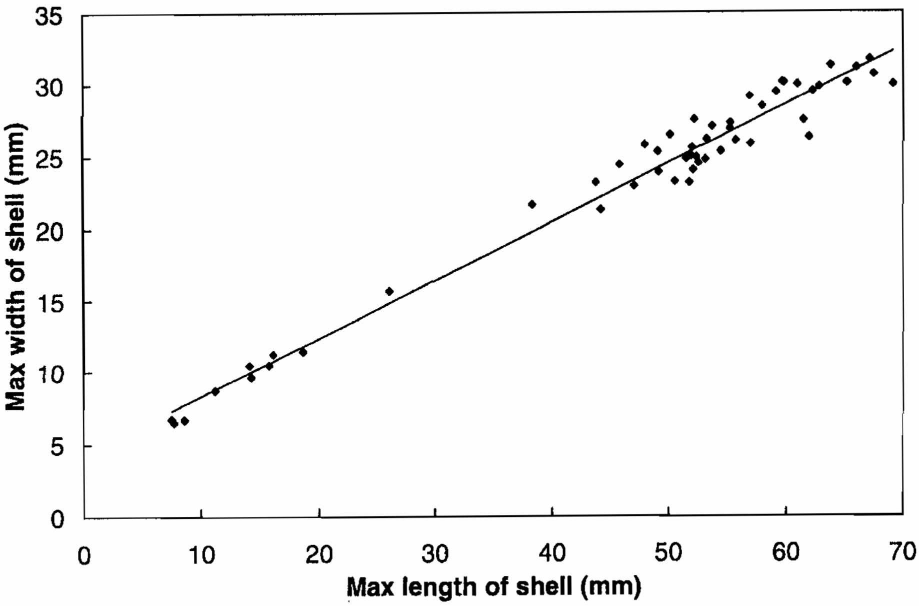

Fig. 4. Maximum length vs width of the shells of *Limicolaria* collected from around Tilo.

ISOTOPIC COMPOSITION OF THE SNAIL SHELL

Isotopic analysis of carbonate samples taken at close intervals along the axis of an empty shell has revealed a pattern of variation which may result from seasonal changes in the $\delta^{18}O$ value of rainfall (Leng *et al.*, 1998). A plot of $\delta^{13}C$ and $\delta^{18}O$ values (Fig. 5) along the length of the whorl has three features which support this conclusion. First, the shape of the shell $\delta^{18}O$ cycles is consistent with seasonal changes in the amount and $\delta^{18}O$ values of rainfall (Fig. 3c). Second, the amplitude of the shell $\delta^{18}O$ cycles, a maximum of 8‰, can be accounted for by the magnitude of the seasonal cycle in rainfall $\delta^{18}O$ coupled with temperature/evaporative effects. Third, the number of shell $\delta^{18}O$ cycles ($\sim$10) is approximately consistent with the estimated lifespan of *Limicolaria*. Generally constant $\delta^{13}C$ values suggest unvarying diet (dominated by C3 plants), environmental CO_2 influence, and metabolism throughout the snail's life, except for one interval of large variations in both $\delta^{13}C$ and $\delta^{18}O$ that may be related to the onset of reproductive activity.

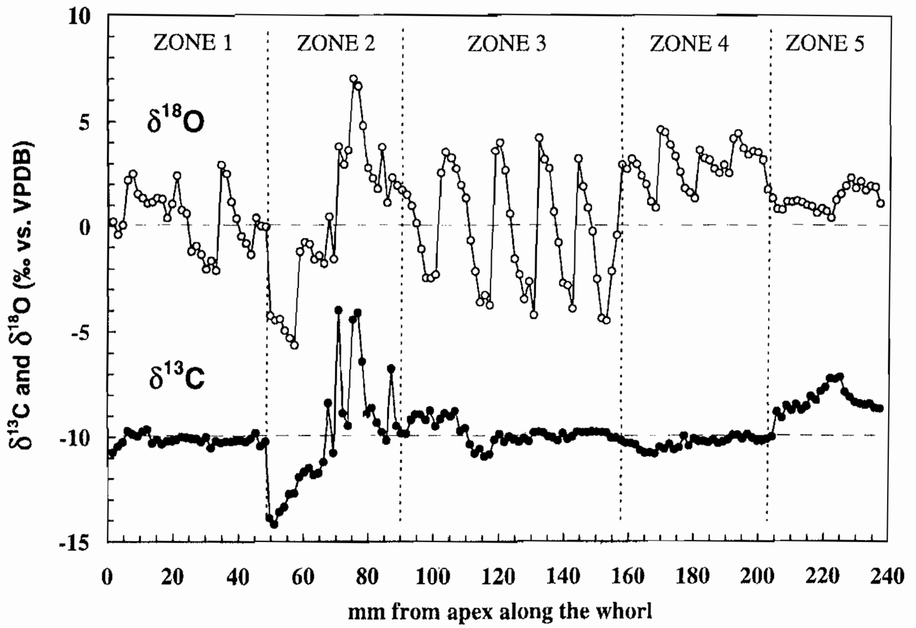

Fig. 5. **$\delta^{13}C$ and $\delta^{18}O$ values plotted at intervals of 1.5 mm along the spiral of the whorl, against distance from the apex to the aperture (from Leng *et al.* (1988)).**

This interpretation of the shell isotope variation is currently under investigation by monitoring living specimens in a controlled laboratory environment, and by measuring the isotopic composition of the snails' diet. Aestivation of the live snails was interrupted by an increase in relative humidity, when the snails emerged by pushing or breaking through the epiphragm. The snails are kept in plastic plant propagators, at a constant temperature of 20° C (±2° C) and at a relative humidity of approximately 90%. They are fed on dry ground oats (breakfast cereal), deionised water and cuttlefish bone, the carbon and oxygen isotopic composition of which are closely monitored. Shell growth immediately resumed, even in the largest specimens, confirming shell growth throughout life, a feature common to members of the superfamily Achatinidae (Mead, 1979). The amount of growth is variable between individuals: one snail grew 10 mm during the first month, while others grew less than 1 mm. Although the amount of food intake cannot easily be measured, the snails most commonly observed on the cuttlefish bone appear to be growing most rapidly, suggesting a link between the amount of calcium carbonate ingested and shell growth.

If the interpretation of the isotopic composition of the shell is correct then *Limicolaria*, which are widely distributed as Late Quaternary fossils throughout north tropical Africa, represents a powerful tool for the determinations of past inter-annual variations in rainfall, one of the key features of monsoonal climatic variability. If repeated for a sequence of shells through a stratigraphic sequence, this would provide a long-term high-resolution record of seasonal climatic variation. The approach should also allow discrimination of the relative importance of different rainfall sources, and provide a record of changes in the relative influence of Indian and Atlantic air masses from differences in their $\delta^{18}O$ values. Variations in $\delta^{13}C$ values between shells of different ages may provide a proxy-record of the changing abundances of C3 and C4 plants in the snails' habitat, which is itself related to climate.

SUMMARY

The land snail *Limicolaria kambeul chudeaui* occurs around the shores of Lake Tilo, in the Ethiopian Rift Valley. There are no previous reports of living specimens of this subspecies. Its occurrence may be significant in that previous studies have used fossil occurrences of this subspecies as a palaeoclimatic indicator (Haynes and Mead, 1987), despite the fact that details of the ecology and habitat have only been known from related subspecies. Current laboratory investigations aim to test the link between $\delta^{13}C$ and $\delta^{18}O$ values of the diet, rainfall and shell carbonate.

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