

This is a repository copy of *Notes on Pleistocene and Recent non-marine Mollusca from Zambia*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/220744/>

Version: Published Version

Article:

Baldreki, Chloe, Barham, Lawrence, Simms, Michael J. et al. (2 more authors) (2024)
Notes on Pleistocene and Recent non-marine Mollusca from Zambia. *Journal of Conchology*. pp. 382-395. ISSN 2755-3531

<https://doi.org/10.61733/jconch/4532>

Reuse

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here:

<https://creativecommons.org/licenses/>

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

Notes on Pleistocene and Recent non-marine Mollusca from Zambia

CHLOË BALDREKI¹, LAWRENCE BARHAM², MICHAEL J. SIMMS³,
KIRSTY E.H. PENKMAN¹ & TOM S. WHITE⁴

¹ Department of Chemistry, University of York, UK

² Department of Archaeology, Classics and Egyptology, University of Liverpool, UK

³ Department of Natural Sciences, National Museums Northern Ireland, UK

⁴ Principal Curator, Non-Insect Invertebrates, Natural History Museum, London, UK

Corresponding author: C. Baldreki (chloe.baldreki@york.ac.uk)

Abstract. Pleistocene and Recent non-marine molluscan faunas from Zambia, and from South-Central Africa more generally, are relatively poorly understood. Many extant species have been reported only from single localities, often the type localities from which they were first described, and their distributions and ecological preferences are unknown. Fossil assemblages have seldom been documented in any detail, partly because early archaeological investigations often disregarded non-marine molluscs as invasive elements of the fossil record. Here, we present new data from the late Middle to Late Pleistocene Palaeolake Kafue lacustrine sequence, situated in the landscape below the archaeological site of Twin Rivers Kopje, Zambia, where non-marine mollusc shells are preserved in cemented carbonate-rich sediments. The composition of this fauna, its palaeoecological significance, and relevance to the archaeological and hydrological records of the Lake Kafue Basin are discussed. We also briefly review the molluscan fauna of Zambia as a basis for future research in the region. Type specimens of *Achatina craveni* E.A. Smith, 1881, *A. morrelli* Preston, 1905, *A. morrelli* var. *kafuensis* Melvill & Ponsonby, 1907, and *A. tavaresiana* Morelet, 1866 are illustrated.

Key words. Land snails, palaeoenvironments, South-Central Africa, taxonomy

ZooBank identifier. urn:lsid:zoobank.org:pub:09A03202-921E-4BF3-ABE0-61CF25F39C36

DOI. <https://doi.org/10.61733/jconch/4532>

INTRODUCTION

The use of fossil non-marine mollusc assemblages as part of multi-disciplinary reconstructions of past environments and climates has a long pedigree, but their potential in this regard varies dramatically around the world depending on local preservation conditions and traditions of research. Pleistocene molluscs have long been a staple of Quaternary research in temperate regions with predominantly calcareous bedrock (such as parts of North-West Europe), but in other parts of the world they have been largely unresearched (cf. White *et al.* 2017). This is the case for the South-Central Africa region, which encompasses present day Zambia and adjacent areas of bordering countries (Angola, Namibia, Botswana, Zimbabwe, Mozambique, Malawi, Tanzania and Democratic Republic of the Congo (DRC); Fig. 1). Although the Pleistocene remains understudied, earlier (Neogene, Pliocene) sequences in East Africa have been documented and represent a potentially useful source of

comparative data (e.g. Verdcourt 1987; Pickford 1995; Tattersfield 2011; Tattersfield *et al.* 2024).

Archaeological sites in Zambia range in age from ~1.1 million years old (Barham *et al.* 2011) to the historic present (Fletcher *et al.* 2022). The region has preserved the earliest evidence to date of a wooden structure, dated to >476 ka (Barham *et al.* 2023), and the transition from Early to Middle Stone Age tool technologies is recorded in the north and south of the country (Duller *et al.* 2015; Richter *et al.* 2022). Twin Rivers Kopje has also preserved evidence of pigment use associated with Middle Pleistocene deposits (Barham 2002). The famous hominin cranium recovered from Kabwe (Broken Hill), attributed to *Homo heidelbergensis/rhodesiensis*; *Homo bodoensis* (Woodward 1921; Stringer 2012; Roksandic *et al.* 2022), has also been dated to the Middle Pleistocene (~300 ka, Grün *et al.* 2020). However, the relationship between these important changes apparent in the archaeological and fossil records and the regional

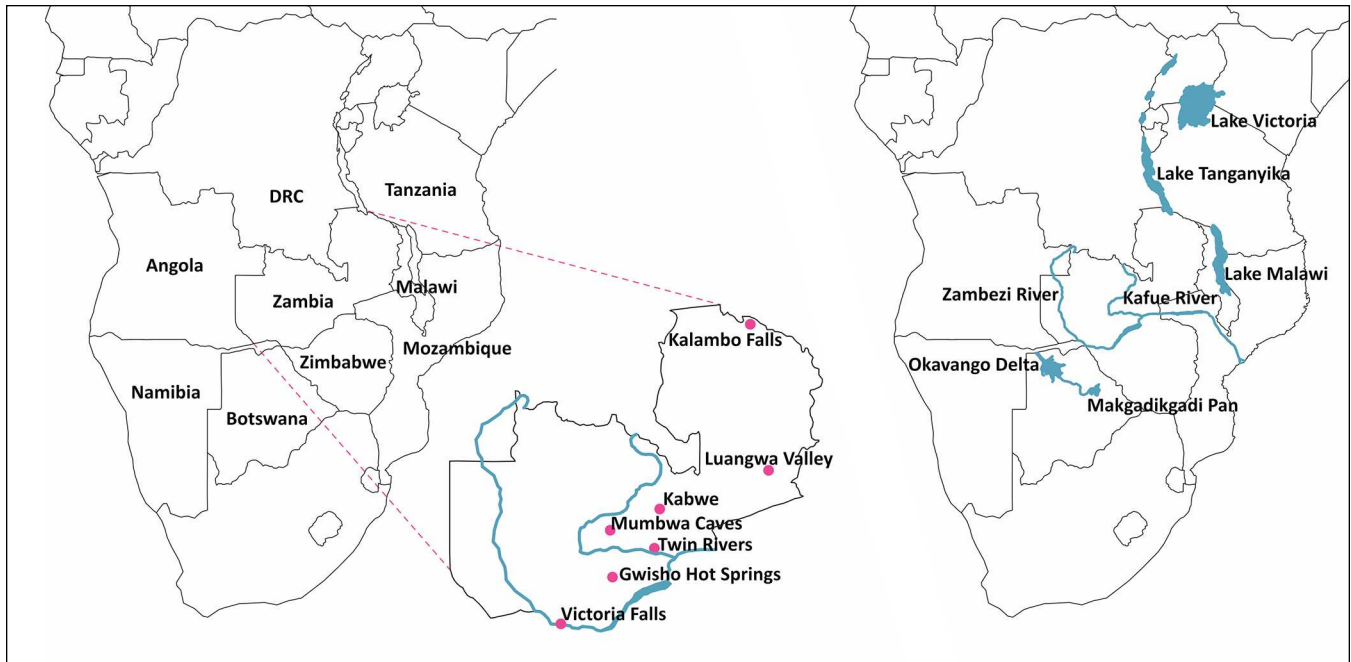


Figure 1. Left: Map of southern Africa highlighting the South-Central African region; Centre: Map of Zambia highlighting relevant archaeological sites; Right: Map of southern Africa highlighting current major water bodies.

climatic record are difficult to assess given the small number of well-stratified sites with reliable chronological data.

With the exception of malacological studies focusing on biomedical topics, particularly the transmission of schistosomiasis (e.g. Wright 1956; Richards 1970; Brown & Rollinson 1996; Stensgaard *et al.* 2019), little attention has been given to the taxonomic study of Pleistocene or Recent non-marine Mollusca in Zambia; the most extensive studies have focused on the endemic aquatic faunas in major lakes on or close to the Zambian border, such as Lake Malawi (Genner *et al.* 2007) and Lake Tanganyika (Michel *et al.* 2004). The most recent checklist summarising the land-snail fauna of Zambia was compiled over 35 years ago (van Bruggen 1988; see also van Bruggen 1993), and this review included fewer than 45 localities scattered across a country with an area of more than 750,000 km². Although the faunas of neighbouring countries have been studied and reviewed in more detail (e.g. van Bruggen & Meredith 1984; van Bruggen 2008; Herbert & Kilburn 2004; Verdcourt 2004; Seddon *et al.* 2005), a similar paucity of modern records is apparent for the majority of neighbouring central southern African countries, with little development in the way of regional distribution maps for common terrestrial species, making it difficult to infer their ecological tolerances. Additional obstacles to their study arise from the recent colonial history of sub-Saharan Africa, with international borders and nomenclature having changed significantly since the

first research on regional molluscan faunas was undertaken at the end of the 19th century, requiring care when interpreting earlier publications and labels associated with museum specimens (e.g. Fig. 2).

Early malacological syntheses for central and southern Africa were compiled by Pilsbry (1919), who reviewed the terrestrial Mollusca collected by the American Museum Congo Expedition (1909–1915), and Connolly (1939), whose work was focussed on South Africa and the Cape. German malacologists also contributed some early records from eastern Africa (e.g. Thiele 1911). Zambia, formerly known as Northern Rhodesia, falls between these three regions but was neglected in terms of malacological research. Indeed, van Bruggen (1988) was able to find only a handful

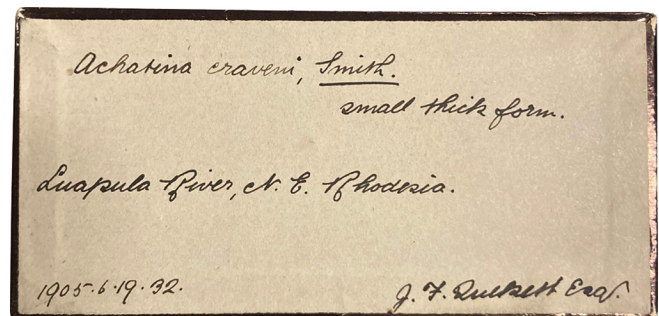


Figure 2. Original label for a specimen of *Achatina craveni* E.A. Smith, 1881 (NHMUK 1905.6.9.32) from the Luapula River, N. E. Rhodesia (now Zambia).

of papers on Zambian molluscs, of which only one (Germain 1920) specifically focussed on “Rhodésie septentrionale” [Northern Rhodesia]. Other more localised records include the southern part of Lake Tanganyika (Bourguignat 1885), relevant parts of British Central Africa (Smith 1893), a single new species from the Zambezi River (Preston 1905), and a small collection made in North-Eastern Rhodesia (Melvill & Standen 1907).

A related issue stems from the tendency to assess molluscan faunas in terms of modern geopolitical boundaries, compiling checklists for individual countries rather than for broader regions defined using environmental criteria. This is difficult to avoid, as the focus of this paper on Zambia demonstrates, but is worth acknowledging. The presence or absence of species in such lists might therefore be predicated entirely on the amount of effort focussed on a particular country (or region, such as a national park), and is unlikely to represent an accurate record of its distribution across a wider region. Checklists are also often compiled uncritically from published records or museum specimens, some of which may date to the early 19th century. Verification of these records can be impossible unless the original specimens can be examined, and the precision of the locality data must be taken at face value. As a result of the sporadic study in this region, and more broadly across Africa, it is not uncommon to encounter numerous *taxa inquirenda* and synonymised names; this is particularly true of Achatinidae, a group that contains a plethora of old names that are often difficult to match to specimens. Caution is therefore required in using them for any comparative analysis. Nonetheless, the most comprehensive published checklist for Zambia (van Bruggen 1988) provides a useful starting point for species that could potentially be preserved in late Middle and Late Pleistocene archaeological and palaeoenvironmental contexts in this region.

Similar issues are evident when it comes to palaeontological studies of Pleistocene molluscan material from Zambia and neighbouring countries. These have often been focussed on marine or estuarine sequences (e.g. Sessa *et al.* 2013; Kilburn & Tankard 1975; Langejans *et al.* 2017) or records from large lake basins (e.g. Cooper *et al.* 1989; van Damme & Gautier 2013), with few detailed records from fluvial or other non-marine habitats. Herbert (2010) mentioned “subfossil” shells from localities in South Africa and Namibia that were tentatively identified as *Vertigo anti-vertigo* (Draparnaud, 1801) and *Zonitoides nitidus* (O.F. Müller, 1773), although these records remain enigmatic. Many archaeological publications have emphasised the use of molluscs as food (e.g. Thackeray 1988; Taylor *et al.*

2011; Taylor 2014) or decoration (e.g. Fagan & van Noten 1971; Phillipson 1976; Bouzouggar *et al.* 2007; Miller *et al.* 2018), rather than their potential to elucidate past environments (cf. Faulkner *et al.* 2021). Shells have been used for dating with mixed success (see examples in Grine 2016), with well-documented limitations in using shell biomineral for radiocarbon and electron spin resonance (ESR) dating techniques (e.g. Pigati *et al.* 2010, 2013; Philippsen 2013; Douka 2017; Duval *et al.* 2020). The fossil record for the South-Central African region is extremely sparse, and mollusc fossils have probably been encountered more often than has been documented.

Part of this lack of study is probably due to long-standing traditions of research, with Mollusca either not recorded or retained. Quarrying in the 1920s at Kabwe (Broken Hill) led to the discovery of well-preserved hominin fossils and significant fossil mammal assemblages (most notably micromammals), but there were no reported molluscan assemblages (Avery 2003), suggesting either that these fossils were not preserved or that they were not deemed sufficiently important to sample. Another reason for the apparent reticence to use molluscan data gleaned from archaeological sequences is a common misconception that land snails are an intrusive part of the fossil record. Numerous archaeological papers refer to the “burrowing” habit of giant African land-snail species, often dismissing potential data from these fossils as being unreliable due to potential bioturbation (e.g. Biittner *et al.* 2017). Whilst it is true that most large snail species seek shelter from high temperatures by burying themselves in loose surface sediment or amongst damp leaf litter, they have no capacity to tunnel deeply into well-consolidated sedimentary sequences in the same way obligate burrowing animals, such as rabbits and hares, can (e.g. Fowler *et al.* 2004; Robbins *et al.* 2008; Pelletier *et al.* 2017). Therefore, they should not be disregarded for this reason. There are few (if any) terrestrial snail taxa that actively burrow in the subsoil, although members of the genera *Cecilioides* and *Coilostele* exploit cracks and root hollows to significant depths and have consequently been routinely excluded in interpretations of Pleistocene land-snail faunas for decades (e.g. Evans 1972).

Non-marine molluscs can act as excellent palaeoenvironmental markers, with taxa inhabiting environments ranging from freshwater bodies, marshes and fens, and vegetated terrestrial habitats. Recording their presence can provide valuable climatic and ecological information, especially in areas where the palaeoenvironmental record is scant, providing evidence for climatic oscillations, one suggested driver of mammalian (including hominin) evolution (e.g. Chan *et al.*

2019; Tattersfield *et al.* 2024). Several recent archaeological excavations have recognised the benefits of including analyses of molluscan assemblages, in addition to macro- and micro-mammals, to provide palaeoenvironmental context. One of the most detailed long records to include Pleistocene non-marine Mollusca is from Panga-ya-Saidi, Kenya (Ship-ton *et al.* 2018; Rowson *et al.* 2024), where well-preserved molluscan assemblages excavated from a long sequence within a rock shelter provide a record of local environmental change spanning the last ~60,000 years.

In this paper we therefore summarise the Pleistocene terrestrial record from Zambia and neighbouring parts of South-Central Africa and provide an initial regional context for fossil assemblages obtained from sediments at the base of the archaeological site at Twin Rivers Kopje associated with Palaeolake Kafue.

MATERIALS AND METHODS

Palaeolake Kafue near Twin Rivers Kopje, Zambia

Sedimentary successions associated with Palaeolake Kafue have yielded some of the only late Middle – Late Pleistocene molluscan assemblages documented from Zambia, although the precise dating remains somewhat problematic (see Baldreki *et al.* 2024 for further discussion). Two calcareous lacustrine sequences containing fossil non-marine Mollusca were found directly below (Site 1; Fig. 3), and within 16 km (Site 19; Fig. 3), of the archaeological site of Twin Rivers Kopje in Zambia, ~30 km southwest of Lusaka (Fig. 1). The succession of clays, limestones, and sands are interpreted as evidence of a fluctuating sequence of lacustrine and terrestrial deposits reflecting palaeolake expansion and contraction. At its maximum extent, the lake is estimated to have covered 17,000 km², making it comparable in size to present day Lake Nyanza [Victoria] (Simms & Davies 2000).

The non-marine Mollusca from Site 1 were briefly documented by Simms (Simms & Davies 2000), although only one terrestrial snail was identified to species level (*Achatina tavaresiana* Morelet 1866 [as *A. tavaresiense*]). The fauna from Site 1 also included specimens identified as belonging to the genus *Vertigo*. This genus has a predominantly Holarctic distribution across North America, Central and East Asia, and Europe (cf. Adam 1954 for African records), but it has now been shown that some African taxa (e.g. *Afripupa* Pilsbry & C.M. Cooke 1920) are synonymous with *Vertigo* (Nekola & Coles 2016; Nekola *et al.* 2018). All other identifications were to family level and included the aquatic fami-

lies Lymnaeidae and Planorbidae and the terrestrial groups Succineidae, Euconulidae, “Subulinidae”, and Achatinidae. None of the fossil shells were figured, and the original specimens identified from Site 1 have been lost (P. Davies pers. comm.), meaning that the identities of the specimens (in particular those identified as *A. tavaresiana* and *Vertigo* sp.) cannot be independently confirmed.

All the material identified as part of this study was recovered from fossiliferous calcareous sediments at Site 19. The internal stratigraphic position of the molluscs within the chalky limestone was not recorded and the assemblage is therefore best considered as a single time-equivalent population (although this may span a considerable time window). These sediments may correlate with the palaeosols of Beds 3–6 at Site 1, which indicate a significant retreat of the lake shoreline from its highstand position at Site 1. The Site 19 mollusc assemblage is, therefore, inferred to be somewhat older than the Site 1 assemblages that were recovered from calcareous sediments above Bed 6, as discussed by Simms & Davies (2000). See Baldreki *et al.* (2024) for further site relationship interpretations.

Extraction Methodology

The blocks of sediment containing molluscan remains from Site 19 were heavily indurated and cemented and were essentially very young limestone. This presented a significant challenge to the extraction of thin non-marine mollusc shells, since they were resistant to most of the standard methods of disaggregating stubborn sediment, and they could not be treated with acids due to the likelihood of shell damage. The blocks were soaked in water and disaggregation was manually encouraged. Some samples were treated with anionic surfactant (household dish soap) in an attempt to improve sediment breakdown, but this proved of limited use. Loosened sediment was sieved with a 300 µm mesh, rinsed with water and left to air dry for ~24 hours. Mollusc shells (whole and fragments) were collected with tweezers and the remaining sediment blocks were placed back in water to soak. The soaking, sieving and mollusc collection was repeated multiple times, but the assemblages were hard won.

RESULTS

Identification of fossil shells

The new shell materials were extracted from heavily cemented calcareous sediments from Site 19 (Fig. 3), some of which was used as the basis for assessment of the suit-

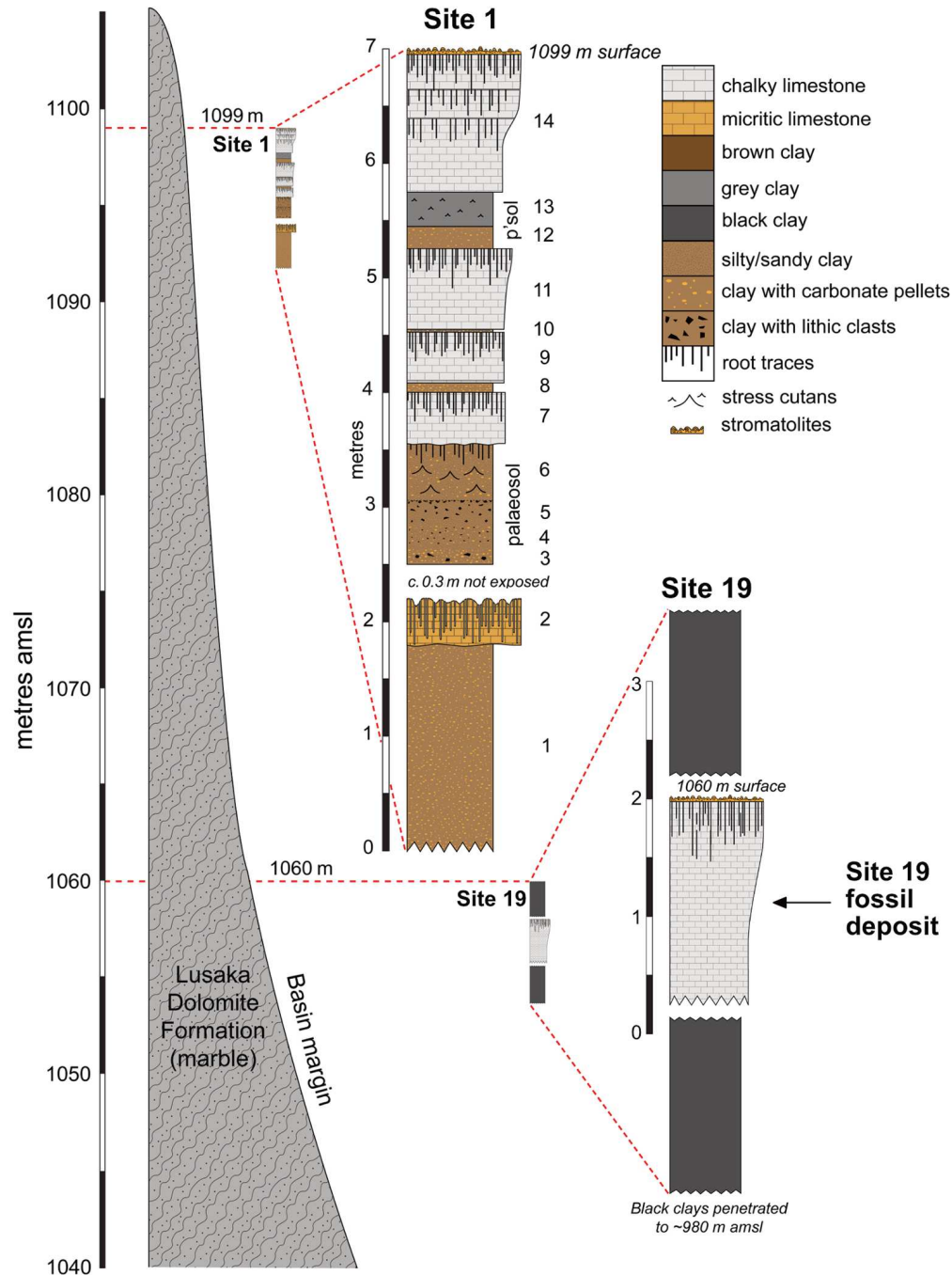


Figure 3. Palaeolake Kafue, excavation site sequences.

ability of achatinid shell for amino acid geochronology (Baldreki *et al.* 2024). The only taxon identified to species level in published records from the site is *Achatina tavarasiana* (Simms & Davies 2000; Fig. 4). The shell characters of Achatininae are notoriously labile, and even fresh specimens can be difficult to identify with certainty. However, the distributions of *Achatina*, which is restricted to West Africa, and *Lissachatina*, which is restricted to East Africa

(Fontanilla 2010), strongly suggest that identification of the Lake Kafue shells as *Achatina* is incorrect (F. Naggs pers. comm.). Molecular data clarifying the genetic and biogeographical distributions of Achatininae is forthcoming (Fontanilla *et al.* in press).

The taxonomic positioning of species within Achatinidae is complex, and whilst several studies have attempted to identify and discuss classifications for the subgenera, this

has not yet been fully resolved. In his revision of the genus *Achatina*, Bequaert (1950) placed *A. tavaresiana* in the subgenus *Achatina* (*Achatina*). This was distinguished from his new subgenus *Lissachatina* on the basis of microsculpture on the nepionic whorls. In *Achatina* these are covered with “granulations in closely set, regular, spiral and vertical rows”, but in *Lissachatina* they are smooth (cf. Bequaert 1950: 12–13 and 49). This dichotomy appeared to separate the western and central African species with sculptured apices as *Achatina*, from the eastern African taxa with smooth apices as *Lissachatina*. However, Mead (1991, 1995) subsequently noted that these sculptural differences were unreliable, and so added additional shell characters and, for some species, features of the genital anatomy (in particular the penial sheath) to further refine the distinction between *Achatina* and *Lissachatina*.

Mead (1991) also noted an emerging tendency to identify achatinid species on the basis of weaker morphological characters, such as shell sculpture, if the locality of the

specimen was well documented. This highlights an obvious and inherent problem for fossil material, such as the specimens from Palaeolake Kafue, in that species distributions may have been different in the past. Confident identification of fossil achatinid shells is especially problematic given that the shells are often worn (e.g. Fig. 4) and anatomical details of the soft body are unavailable to the taxonomist. Zambia is therefore an interesting place to attempt to identify fossil achatinid specimens, since it is situated at the interface between the “eastern” and “western” biogeographical provinces first proposed by Bequaert (1950). The Zambian fossil record could therefore potentially provide evidence for the expansion and contraction of the ranges of *Achatina* and *Lissachatina* species as a response to Quaternary climate change. However, in the absence of full molecular analyses, these systematic issues remain problematic, and we therefore assign only provisional identities to the fossil shells from sediments associated with Palaeolake Kafue.

Additional problems arise from misidentification of

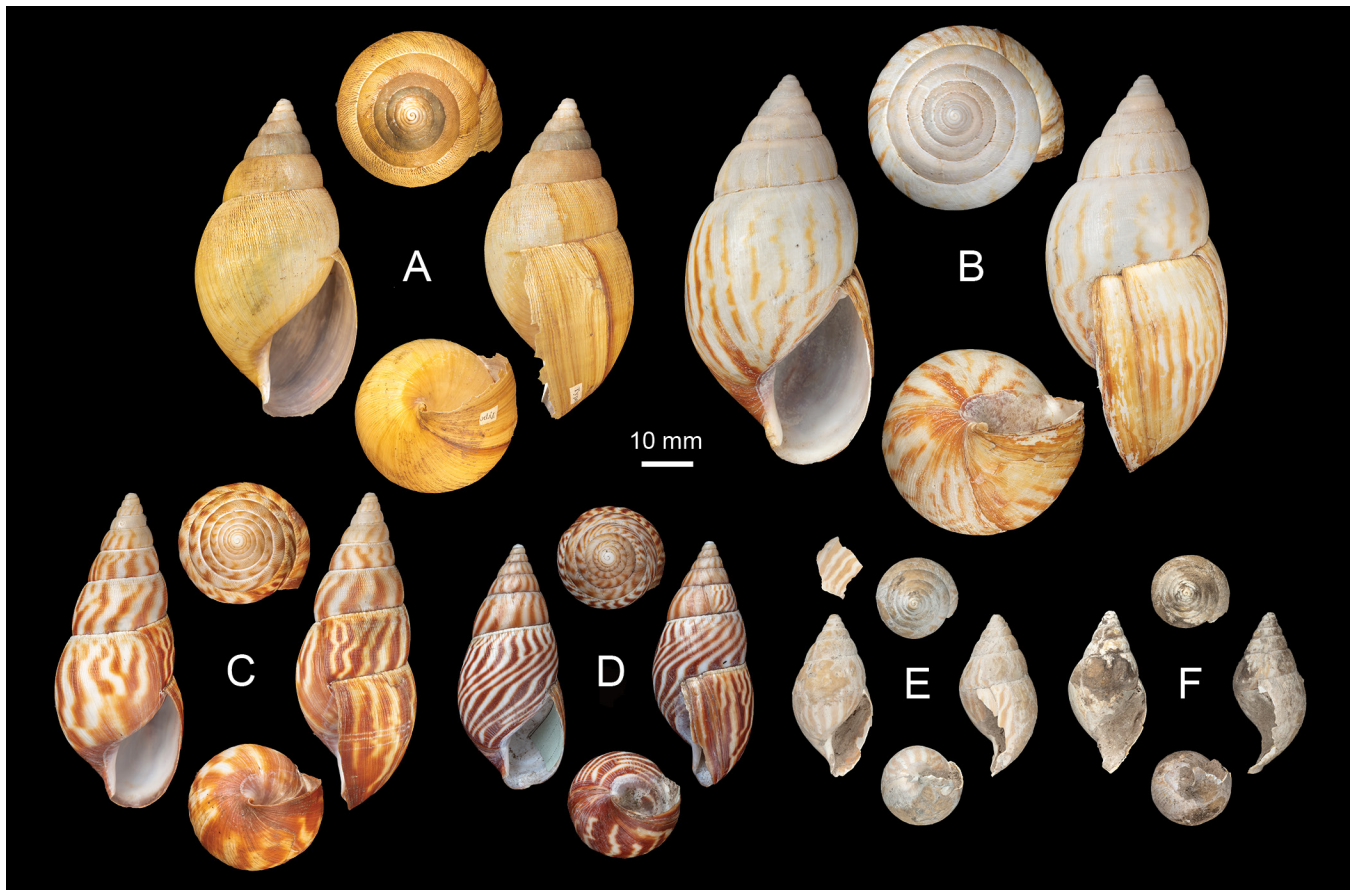


Figure 4. A, *Achatina tavaresiana* Morelet, 1866 (syntype, NHMUK 1893.2.3.151). B, *Achatina craveni* E.A. Smith, 1881 (syntype, NHMUK 1880.12.22.2). C, *Achatina morrelli* Preston, 1905 (NHMUK 1907.11.21.89) D, *Achatina morrelli* var. *kafuensis* Melvill & Ponsoby, 1907 (syntype, NHMUK 1905.6.19.25). E, F, Palaeolake Kafue fossils: (E) PK.S19.4 (ZM.LV.AR.9888); (F) PK.S19.3 (ZM.LV.AR.9887).

material and failure to consult type specimens when making taxonomic judgements. The type specimens of *A. tavaresiana* and *A. craveni* E.A. Smith, 1881, both of which have been examined for this work (Fig. 4), are clearly conchologically distinct. *Achatina tavaresiana* exhibits granulose sculpture on its nepionic whorls that would place it in the subgenus *Achatina* (*sensu* Bequaert 1950), but also the “half-domed” apex characteristic of *Lissachatina* (*sensu* Mead 1995), which illustrates the contradictory nature of the published evidence. *Achatina craveni* has a smooth, fully rounded apex, which would place it in either *Lissachatina sensu* Bequaert or *Achatina sensu* Mead. MolluscaBase currently places both species in *Achatina* (MolluscaBase Eds 2024), although the authority for this is unclear; Brown and Evans (2021) figured a specimen as “*Cochlitoma tavaresiana* (Morelet, 1866)” but provided no further details for this generic placement. The placement of *A. tavaresiana* in *Lissachatina* by Bequaert (1950) appears to have been overruled by Mead (1995), who moved it back to *Achatina* on the basis of the form of the apex. In his checklist of Zambian land snails, van Bruggen (1988) listed only *L. craveni* as part of the Recent Zambian fauna, also noting its distinctness from *A. tavaresiana*. In contrast, Crowley & Pain (1964) had suggested that the two species are synonymous. In the absence of molecular data, these problems remain unresolved (Fontanilla *et al.* in press).

A further taxonomic issue relates to another species recorded in Zambia, *Achatina morrelli* Preston, 1905, which was listed as a synonym of *A. capelloi* Furtado, 1886 by Bequaert (1950: 49) and placed in the subgenus *Lissachatina*. Brown and Evans (2021: 63) preferred instead to retain *A. morrelli* as a distinct species of *Achatina*, noting that shells they had examined and identified as this taxon were clearly different to *L. capelloi*. However, examination of the type of *A. morrelli* (NHMUK 1907.11.21.89; Fig. 4) shows that it is clearly a *Lissachatina*, and it superficially resembles the type of *A. capelloi* figured by Furtado (1886). The type of *A. capelloi* has not been located, so its generic position remains provisional, but the synonymy proposed by Bequaert (1950) appears sound. Brown & Evans (2021) provided two unnumbered figures of shells labelled as “*A. morrelli*”, which are a closer match to *A. morrelli kafuensis* Melvill & Standen (1907), but the distinctness of this Zambian taxon remains unclear until its taxonomic position can be confirmed.

Additional species identified in the Pleistocene assemblage include several juvenile specimens of *Afroguppya rumrutiensis* (Preston 1911) (Fig. 5B), a tropical East African species with a range extending from Kenya, through

Tanzania, Malawi, Zambia, Zimbabwe, and Mozambique (de Winter & van Bruggen 1992; Herbert & Kilburn 2004), although the conspecificity of specimens collected across this large area requires confirmation. Van Bruggen (1988) noted that this species has been recorded primarily in East Africa, but he acknowledged the possibility of it being found further west in central Africa. It has been recorded living in Zambia at only a single locality, the Chowo forest on the eastern border with Malawi (van Bruggen 1988), so the Pleistocene record from the Palaeolake Kafue site appears to be the westernmost record of this species yet reported. Although the fossil specimens are all juvenile or broken shells, the distinctive microsculpture characteristic of *A. rumrutiensis* can clearly be seen on the upper whorls (Fig. 5C). In South Africa this species has been recorded in leaf litter, under stones, and amongst vegetation in a range of habitats including forest and thicket, and it is evidently tolerant of somewhat drier conditions (Herbert & Kilburn 2004).

A single shell identified as *Vertigo* sp. (Fig. 5G) is potentially significant, although the nature of the sediments mean that the shell’s mouth cannot be cleared to allow identification to species level. It is possible that it is *V. antivertigo*, which has been reported as an enigmatic “subfossil” in South Africa and Namibia (Herbert 2010) and could therefore be the same species identified to genus level by Davies (in Simms & Davies 2000). However, it is also possible that it represents *V. congoensis garambae* Adam, 1954 or *V. bisulcata* (Jickeli 1873). The environmental implications of this specimen therefore remains unclear. Two specimens of *Helicarion cf. issangoensis* Thiele, 1911 were also identified from the Site 19 Palaeolake Kafue (Fig. 5F). The type locality “Issango Ferry” refers to the ferry that crossed the Semiliki (formerly Issango) River during the latter part of the expedition to the African interior undertaken by Franz Stuhlmann in 1891 (Thiele 1911). This species was not recorded in the checklist of land-snail species compiled by van Bruggen (1988). The only other record of a species from the genus in Zambia was *Helicarion nyassanus* var. *excellens* (Melvill & Standen 1907), but this has not been recorded since the early 20th century. It is possible that these taxa are conspecific, but a revision of southern African *Helicarion* is beyond the scope of this paper. Several specimens of *Ceciloides* sp. were also recovered. Members of this burrowing genus are routinely excluded from Pleistocene palaeoenvironmental reconstructions (cf. Evans 1972) because their burrowing habit makes them a rare example of a non-marine mollusc that could be invasive to an archaeological or geological context. These shells probably entered the fossil

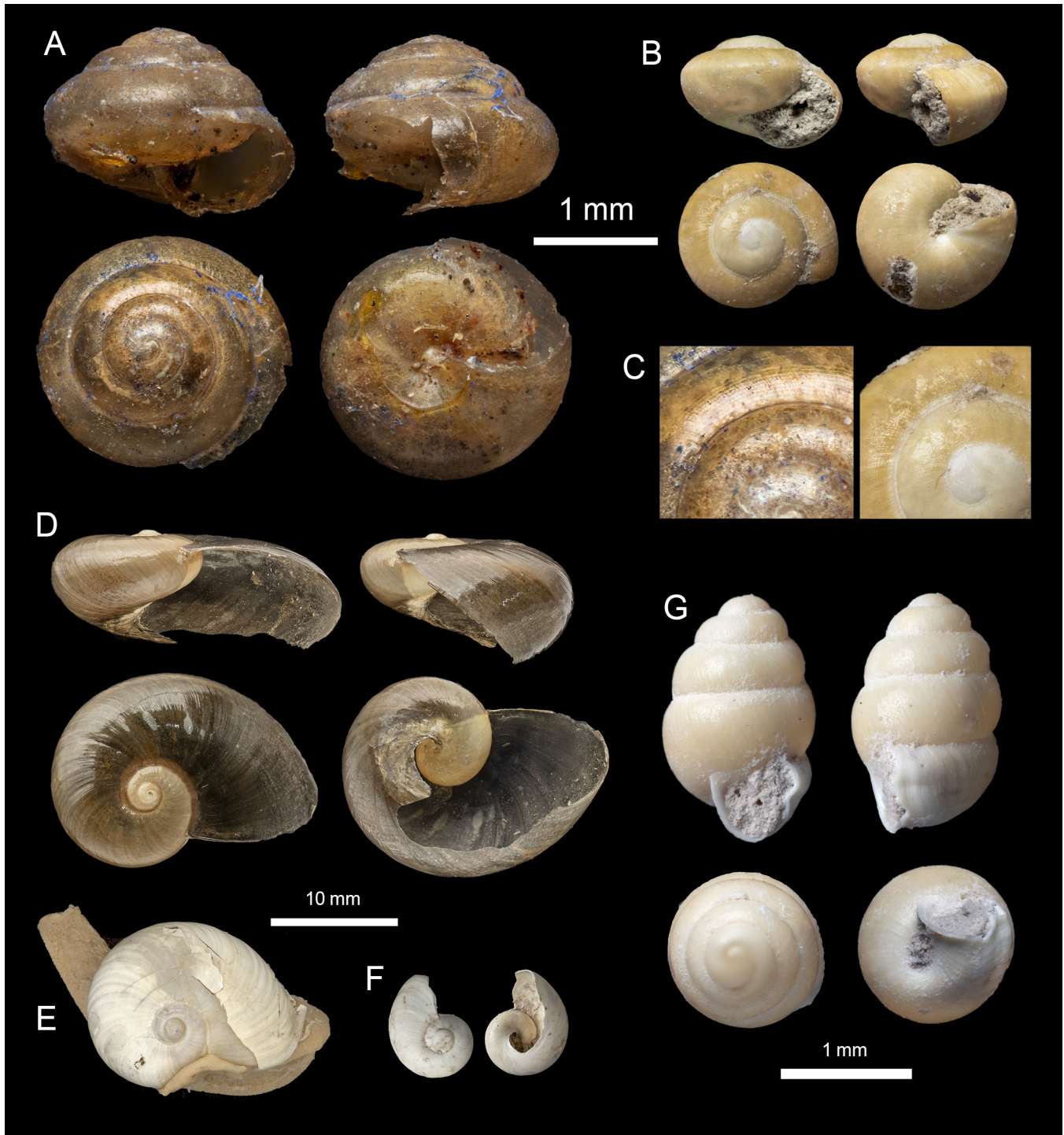


Figure 5. A–C, *Afroguppya rumrutiensis* (Preston, 1911): (A) NHMUK 20210195, Mount Kinangop, Abedare Range, Kenya; (B) Palaeolake Kafue fossil specimen PK.S19.26; (C) comparison of shell microsculpture on apical whorls. D–F, *Helicarion issangoensis* Thiele, 1911: (D) NHMUK 1937.12.30.1420; (E) syntype, ZMB/Moll-109970; (F) Palaeolake Kafue fossil specimen PK.S19.7. G, *Vertigo* sp. Palaeolake Kafue fossil specimen.

record via the numerous root holes and fissures evident in the sediments, but whether they are contemporaneous with the other material is unclear. Van Bruggen (1988) listed *C.*

gokweanus (O. Boettger 1870) as the only species recorded from Zambia but also noted that the Afrotropical *Ceciliooides* are poorly known.

Palaeoenvironmental implications

Despite the small size and low species diversity of the molluscan fauna derived from the Palaeolake Kafue Site 19 sediments, some general inferences about the local environment can be made. It is difficult to characterise the vegetation precisely, although the *Helicarion* is a potential indicator of shade/tree cover. The *Vertigo* specimen (Fig. 5G) could be associated with woodland (e.g. *V. bisulcata* (Jickeli 1873); see Tattersfield *et al.* 2024) or, if an identification as *Vertigo antivertigo* can be confirmed, rather wetter environments. However, the assemblage provides a general impression of a vegetated environment proximal to a large body of water and is wholly in keeping with the interpretation of the sediments representing a lake margin (Simms & Davies 2000). Two freshwater taxa were identified, although the specimens were fragmentary juvenile shells that could not be identified with confidence to species level; five specimens represented Planorbidae and three represented Lymnaeidae. The most common shells represented were Succineidae, with over 40 countable specimens recovered; these were again mostly juvenile shells that could not be identified to species level. In northern Europe, this family is strongly associated with marshy habitats close to bodies of water. However, this is not the case in sub-Saharan Africa, where succineids can be found in places that are (at least seasonally) remarkably dry, such as grasslands on the southern Serengeti (Tattersfield *et al.* 2024). Pickford (1995) considered African Succineidae to be characteristic of “seasonally waterlogged ground, even in semi-arid to arid country”. Nevertheless, given the proximity of Site 19 to Palaeolake Kafue, it seems clear that waterlogged conditions were at least seasonally available. The most common terrestrial species represented was *Afropuppa rumrutiensis* (Preston 1912), with 26 countable specimens identified. This species has a generally east African distribution, with records from South Africa (KwaZulu Natal), Zimbabwe, Malawi, Tanzania, and Kenya (van Bruggen 1988; de Winter & van Bruggen 1992), although van Bruggen (1988) noted the possibility that it might occur further west. The record from this assemblage represents the first Pleistocene record of the species in Zambia. This species was also recorded in relatively low numbers at the Late Pleistocene cave site of Panga ya Saidi, Kenya, where much richer faunas have been recovered from a sequence spanning a period of ~80,000 years (Rowson *et al.* 2024). It says much about current knowledge of African non-marine Mollusca that even a comparatively rich sequence like Panga ya Saidi was difficult to interpret due to the limited knowledge of the habitat preferences of extant species (Rowson *et al.* 2024).

DISCUSSION

The South-Central African region’s current ecology, reflective of its topography, is diverse. Zambia contains tropical deciduous woodlands across its high central plateau, which grade to dryland savannah on the margins of the Kalahari basin. Several major river systems (e.g. Kafue and Zambezi rivers; Fig. 1) and lakes (Bangweulu, Mweru, and Tanganyika; Fig. 1) are present in Zambia, and large wetlands occur seasonally in much of the north of the country. Today the Twin Rivers Kopje overlooks the Kafue River floodplain to the south-east and the Lusaka dolomite plateau to the north-west, giving rise to a mixed grassland–woodland habitat typical of these ecozones, but during the Middle Pleistocene it would have overlooked a vast lake (Clark & Brown 2001; Barham *et al.* 2000).

The Zambian non-marine molluscan fauna is poorly known. The checklist compiled by van Bruggen (1988) included 56 terrestrial taxa; of these, 25 were reported for the first time, and most of these new records were from the Chowo Forest, an area on the Zambia–Malawi border that had recently been subject of an intensive survey. Few other areas of Zambia have been similarly investigated for terrestrial molluscs, and those that have are usually on the borders with neighbouring countries where surveys have been carried out (e.g. Smith 1893; Muratov 2010). Some of the localities included by Smith (1893) are now in eastern Zambia, including the western part of the Nyika Plateau, hence the inclusion by van Bruggen (1988) of some of the taxa recorded in his checklist of the Zambian terrestrial fauna. This collection bias is likely to be the reason why many widely distributed families such as Maizaniidae, Veronicellidae, and Ariophantidae are not represented in published checklists for Zambia. It is notable that *Helicarion* (*Gymnarion*) *issangoensis*, recorded at Palaeolake Kafue Site 19, is a member of the last-mentioned group, and this represents its first record in Zambia.

Molluscan assemblages have also only rarely been reported from archaeological sites in Zambia. Apart from the sequences associated with Palaeolake Kafue, only one gastropod species was reported from the Twin Rivers archaeological site (G block; Barham 2000), whilst in the Luangwa Valley only a brief mention of the recovery of land-snail artefacts amongst other organic material was reported from late Holocene deposits (Fletcher *et al.* 2022). At the site of Mumbwa Caves in central Zambia, mollusc fragments were reported with human remains (Dart & Del Grande 1931) and from early Holocene deposits, but these were not described in detail (Barham 2000). A more detailed account of the Mollusca preserved at the mid-Holocene site of Gwisho

Hot Springs was provided by Fagan and van Noten (1971), which identified several taxa to species level (e.g. *Achatina schinziana* Mousson, 1888, *Aspatharia sinuata* (E. von Martens 1883), *Burtoa nilotica* (L. Pfeiffer 1861), *Lanistes ellipticus* E. von Martens 1866) as well as fragments representing the unionid genus *Cafferia* C.T. Simpson 1990; however, the discussion was focused on their use as food and decoration rather than their palaeoecological potential. Similarly, at the Later Stone Age archaeological sites of Kalemba, Thandwe, and Makwe, *Achatina* shells were discussed with reference to beads and decoration, but not in terms of any paleoenvironmental implications (Phillipson 1976).

In general terms, climate oscillations across Africa during the Pleistocene are less well understood than those of middle to high latitudes in the northern hemisphere, where glacial and interglacial phases dominate the record (Maslin *et al.* 2014). In Africa, regional arid-humid fluctuations occurred as a result of a complex combination of environmental factors, such as ice-sheet volume in the northern hemisphere, global sea-surface temperatures, precipitation volume and patterns, and trade winds (Demenocal *et al.* 1993; Weij *et al.* 2024). These fluctuations happened asynchronously across different regions (Blome *et al.* 2012) and would have resulted in expansion, contraction, and alteration of habitats dependent on locality. In Zambia, evidence for phases of lake expansion and contraction in the latter part of the Middle Pleistocene for Palaeolake Kafue has been previously reported (Simms & Davies 2000).

The taxa identified here from recent studies of Pleistocene sediments associated with Palaeolake Kafue show evidence of varied climatic conditions, including wetter conditions than the present prevailing climate. More catholic terrestrial taxa, such as *Achatina* sp. and *Afrotropis rumrutiensis*, were found alongside taxa that potentially indicate wetter environments, such as *Vertigo* sp. and *Succinea* sp., and obligate freshwater taxa such as *Planorbis* sp. These findings, whilst not currently providing much insight into changes in the local climate and environment through time, nevertheless represent an important datapoint for future regional studies of the Zambian Pleistocene malacofauna.

CONCLUSIONS

Zambia lies at a central crossroads between major biogeographical provinces in central southern Africa and its extant and fossil molluscan faunas are potentially critical to understanding changing distributions of species in response to climate change during at least the last half million years. The Pleistocene non-marine molluscan assemblage extracted

from sediments preserved at Palaeolake Kafue in southern Zambia included freshwater taxa (Lymnaeidae and Planorbidae), species indicative of vegetation at the lake-margin (Succineidae), and terrestrial species, some of which represent the first records in the Zambian Pleistocene record (*Afrotropis rumrutiensis* and *Helicarion issangoensis*). Although the assemblage is not large enough to make significant claims about past climatic and environmental conditions, it represents an important record for continued research in this area. This study also provides the first record of *Helicarion issangoensis* from Zambia and highlights the need for detailed studies of both Recent faunas (through ecological surveys and examination of museum collections) and the Pleistocene fossil record in under-researched regions such as South-Central Africa.

ACKNOWLEDGEMENTS

This research was supported through the ACCE DTP by the Natural Environment Research Council [NE/S00713X/1]. Fieldwork in Zambia was funded by the National Geographic Society [GEFNE38-12]. We would like to thank Constance Mulenga and Clare Mateke at the Livingstone Museum, Zambia for providing curatorial assistance. Photographs of specimens included in Figures 4 and 5 were taken by Kevin Webb, Natural History Museum Publishing and Image Resources, © Trustees of the Natural History Museum, London. Christine Zorn (Museum für Naturkunde, Berlin) kindly provided the image of the type of *Helicarion issangoensis* Thiele, 1911.

For the purpose of open access, the author has applied a Creative Commons Attribution (CC BY) licence to any Author-Accepted Manuscript version arising from this submission.

REFERENCES

- ADAM W. 1954. *Études sur les mollusques de l'Afrique centrale et des régions voisines 1. Vertiginidae et Valloniidae. Volume Jubilaire Victor Van Straelen. Tome II.* Institut Royal d'Histoire Naturelle de Belgique, Brussels, pp. 725–817.
- EVERY DM. 2003. Early and Middle Pleistocene environments and hominid biogeography; micromammalian evidence from Kabwe, Twin Rivers and Mumbwa Caves in central Zambia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **189** (1–2): 55–69. doi: 10.1016/S0031-0182(02)00593-X
- BALDREKI C, BURNHAM A, CONTI M, WHEELER L, SIMMS MJ, BARHAM L, WHITE TS, PENKMAN KEH. 2024. Investigating the potential of African land snail shells (Gastropoda: Achatininae) for amino acid geochronology. *Quaternary Geochronology* **79**: 101473. doi: 10.1016/j.quageo.2023.101473

- BARHAM LS. 2000. *The Middle Stone Age of Zambia, South Central Africa*. Western Academic & Specialist Press, Liverpool, 303 pp.
- BARHAM L. 2002. Systematic pigment use in the Middle Pleistocene of south-central Africa. *Current Anthropology* **43** (1): 181–190. doi: 10.1086/338292
- BARHAM L. 2011. Clarifying some fundamental errors in Herries' "A Chronological Perspective on the Acheulian and Its Transition to the Middle Stone Age in Southern Africa: The Question of the Fauresmith". *International Journal of Evolutionary Biology* **2012**: 230156. doi: 10.1155/2012/230156
- BARHAM L, SIMMS MJ, GILMOUR M, DEBENHAM N. 2000. Chapter 10. Twin Rivers, excavation and behavioural record. Pp. 165–216 in: Barham L (Ed.) *The Middle Stone Age of Zambia, South Central Africa*. Western Academic & Specialist Press, Liverpool.
- BARHAM L, DULLER GAT, CANDY I, SCOTT C, CARTWRIGHT CR, PETERSON JR, KABUCKU C, CHAPOT MS, MELIA F, ROTS V, GEORGE N, TAIPALE N, GETHIN P, NKOMBWE P. 2023. Evidence for the earliest structural use of wood at least 476,000 years ago. *Nature* **622**: 107–111. doi: 10.1038/s41586-023-06557-9
- BEQUAERT JC. 1950. Studies in the Achatininae, a group of African land snails. *Bulletin of the Museum of Comparative Zoology at Harvard College* **105** (1): 1–216.
- BIITNER KM, SAWCHUK EA, MILLER JM, WERNER JJ, BUSHOZI PM, WILLOUGHBY PR. 2017. Excavations at Mlambalasi Rockshelter: a Terminal Pleistocene to Recent Iron Age record in Southern Tanzania. *African Archaeological Review* **34**: 275–295. doi: 10.1007/s10437-017-9253-3
- BLOME MW, COHEN AS, TRYON CA, BROOKS AS, RUSSELL J. 2012. The environmental context for the origins of modern human diversity: a synthesis of regional variability in African climate 150,000–30,000 years ago. *Journal of Human Evolution* **62** (5): 563–592. doi: 10.1016/j.jhevol.2012.01.011
- BOURGUIGNAT, JR. 1885. *Notice Prodomique sur les Mollusques Terrestres et Fluviatiles recueilles par M. Victor Giraud dans la Région Méridionale du Lac Tanganika*. Tremblay, Paris, 110 pp. doi: 10.5962/bhl.title.12882
- BOUZOUGGAR A, BARTON N, VANHAEREN M, D'ERRICO F, COLLCUTT S, HIGHAM T, HODGE E, PARFITT S, RHODES E, SCHWENNINGER J-L, STRINGER C, TURNER E, WARD S, MOUTMIR A, STAMBOULI A. 2007. 82,000 year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 9964–9969. doi: 10.1073/pnas.0703877104
- BROWN DS, ROLLINSON D. 1996. Aquatic snails of the *Bulinus africanus* group in Zambia identified according to morphometry and enzymes. *Hydrobiologia* **324**: 163–77. doi: 10.1007/bf00018178
- BROWN K, EVANS M. 2021. *The Achatinid Landshells of Southern Africa*. ConchBooks, Harxheim, 138 pp.
- CHAN EK, TIMMERMANN A, BALDI BF, MOORE AE, LYONS RJ, LEE SS, KALSBECK AM, PETERSEN DC, RAUTENBACH H, FÖRTSCH HE, BORNMAN MS. 2019. Human origins in a southern African palaeo-wetland and first migrations. *Nature* **575** (7781): 185–189. doi: 10.1038/s41586-019-1714-1
- CLARK JD, BROWN KS. 2001. The Twin Rivers Kopje, Zambia: stratigraphy, fauna, and artefact assemblages from the 1954 and 1956 Excavations. *Journal of Archaeological Science* **28** (3): 305–330. doi: 10.1006/jasc.2000.0563
- CONNOLLY MW. 1939. *A Monographic Survey of South African Non-marine Mollusca*. Trustees of the South African Museum, Cape Town, 660 pp.
- COOPER JAG, KILBURN RN, KYLE R. 1989. A Late Pleistocene molluscan assemblage from Lake Nhlange, Zululand, and its palaeoenvironmental implications. *South African Journal of Geology* **92** (2): 73–83.
- CROWLEY TE, PAIN T. 1964. *Achatina (Lissachatina) tavaresiana* Morelet; its synonymy and distribution. *Revue de Zoologie et de Botanique Africaines* **64** (1–2): 121–131.
- DART RA, GRANDE, N DEL. 1931. The ancient iron-smelting cavern at Mumbwa. *Transactions of the Royal Society of South Africa* **19**: 379–427.
- DEMENOCAL PB, RUDDIMAN WF, POKRAS EM. 1993. Influences of high-and low-latitude processes on African terrestrial climate: Pleistocene eolian records from equatorial Atlantic Ocean Drilling Program site 663. *Paleoceanography* **8** (2): 209–242. doi: 10.1029/93pa02688
- DE WINTER AJ, VAN BRUGGEN AC. 1992. Systematic position and distribution of the African land snails *Afropunctum seminium* (Morelet) and '*Guppya rumrutiensis* (Preston) (Mollusca, Gastropoda Pulmonata: Euconulidae), with the description of two new taxa. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **95** (4): 515–533.
- DOUKA, K. 2017. Radiocarbon dating of marine and terrestrial shell. Pages 381–399 in: Allen MJ (Ed.) *Molluscs in Archaeology: Methods, Approaches and Applications*. Oxbow Books, Oxford.
- DULLER GAT, TOOTH S, BARHAM L, TSUKAMOTO S. 2015. New investigations at Kalambo Falls, Zambia: Luminescence chronology, site formation, and archaeological significance. *Journal of Human Evolution* **85**: 111–125. doi: 10.1016/j.jhevol.2015.05.003
- DUVAL M, ARNOLD LJ, RIXHON G. 2020. Electron spin resonance (ESR) dating in Quaternary studies: evolution, recent advances and applications. *Quaternary International* **556**: 1–10. doi: 10.1016/j.quaint.2020.07.044
- EVANS JG. 1972. *Land Snails in Archaeology*. Seminar Press, London and New York, 436 pp.
- FAGAN BM, VAN NOTEN FL. 1971. *The Hunter Gatherers of Gwisho*. Musée Royal de l'Afrique Centrale, Tervuren, 228 pp.
- FAULKNER P, MILLER JM, QUINTANA MORALES EM, CROWTHER A, SHIPTON C, NDIEMA E, BOIVIN N, PETRAGLIA M. 2021. 67,000 years of coastal engagement at Panga ya Saidi, eastern Africa. *PLoS ONE* **16** (8): e0256761. doi: 10.1371/journal.pone.0256761

- FLETCHER R, BARHAM L, DULLER G, JAIN M. 2022. Nothing set in stone: Chaines operatoires of later stone age sequences from the Luangwa valley and Muchinga Escarpment, Zambia. *South African Archaeological Bulletin* **77** (217): 89–114.
- FONTANILLA IKC. 2010. *Achatina (Lissachatina) fulica* Bowdich: its molecular phylogeny, genetic variation in global populations, and its possible role in the spread of the rat lungworm *Angiostrongylus cantonensis* (Chen). Unpublished Ph.D. thesis, University of Nottingham.
- FONTANILLA IKC, NAGGS F, TANG, C, HERBERT DG, WADE, CM. In press. Radiation of giant snails across sub-Saharan Africa: the molecular phylogenetic evidence. *Molecular Phylogenetics and Evolution*.
- FOWLER KD, GREENFIELD HJ, VAN SCHALKWYK LO. 2004. The effects of burrowing activity on archaeological sites: Ndonondwane, South Africa. *Geoarchaeology* **19** (5): 441–470. doi: 10.1002/gea.20005
- FURTADO A. 1886. Coquilles terrestres et fluviatiles de l'exploration Africaine de M.M. Capello et Ivens (1884–1885). *Journal de Conchyliologie* **34** (2): 138–152.
- GENNER MJ, TODD JA, MICHEL E, ERPENBECK D, JIMOH A, JOYCE DA, PIECHOCKI A, POINTIER JP. 2007. Amassing diversity in an ancient lake: evolution of a morphologically diverse parthenogenetic gastropod assemblage in Lake Malawi. *Molecular Ecology* **16** (3): 517–530. doi: 10.1111/j.1365-294x.2006.03171.x
- GERMAIN, L. 1920. Contributions a la Faune Malacologique de l'Afrique équatoriale LX. Sur quelques mollusques de la Rhodésie septentrionale. *Bulletin du Muséum National d'Histoire Naturelle* **26**: 239–244.
- GRINE FE. 2016. The Late Quaternary hominins of Africa: the skeletal evidence from MIS 6–2. Pp. 232–281 in: Jones SC, Steward BA (Eds) *Africa from MIS 6–2*. Springer, Dordrecht.
- GRÜN R, PIKE A, MCDERMOTT F, EGGINS S, MORTIMER G, AUBERT M, KINSLEY L, JOANNES-BOYAU R, RUMSEY M, DENYS C, BRINK J. 2020. Dating the skull from Broken Hill, Zambia, and its position in human evolution. *Nature* **580** (7803): 372–375. doi: 10.1038/s41586-020-2165-4
- HERBERT D. 2010. *The introduced terrestrial Mollusca of South Africa*. SANBI Biodiversity Series 15. South African National Biodiversity Institute, Pretoria, 108 pp.
- HERBERT D, KILBURN R, 2004. *Field Guide to the Land Snails and Slugs of Eastern South Africa*. Natal Museum, Pietermaritzburg, 336 pp.
- KILBURN RN, TANKARD AJ. 1975. Pleistocene molluscs from the west and south coasts of the Cape Province, South Africa. *Annals of the South African Museum* **67** (6): 183–226.
- LANGEJANS GH, DUSSELDORP, GL, THACKERAY JF, 2017. Pleistocene molluscs from Klasies River (South Africa): Reconstructing the local coastal environment. *Quaternary International* **427**: 59–84. doi: 10.1016/j.quaint.2016.01.013
- MASLIN MA, BRIERLEY CM, MILNER AM, SHULTZ S, TRAUTH MH, WILSON KE. 2014. East African climate pulses and early human evolution. *Quaternary Science Reviews* **101**: 1–17. doi: 10.1016/j.quascirev.2014.06.012
- MEAD AR. 1991. Anatomical criteria in the systematics of the Achatinidae (Pulmonata). In: Meier-Brook C (Ed.) *Proceedings of the 10th International Malacological Congress*, Tübingen, 549–553.
- MEAD AR. 1995. Anatomical studies reveal new phylogenetic interpretations in *Lissachatina* (Pulmonata: Achatinidae). *Journal of Molluscan Studies* **61** (2): 257–273. doi: 10.1093/mollus/61.2.257
- MELVILL JC, STANDEN R. 1907. Notes on a collection of terrestrial and fluviatile Mollusca, made in North-Eastern Rhodesia, during 1905, by Mr. Sheffield A. Neave, M.A., B.Sc. *Memoirs and Proceedings of the Manchester Literary & Philosophical Society* **51** (4): 1–16.
- MICHEL EL, TODD JA, CLEARY DF, KINGMA IR, COHEN AS, GENNER MJ. 2004. Scales of endemism: challenges for conservation and incentives for evolutionary studies in a gastropod species flock from Lake Tanganyika. *Journal of Conchology, Special Publication* **3**: 155–72.
- MILLER JM, SAWCHUK EA, REEDMAN AL, WILLOUGHBY PR. 2018. Land snail shell beads in the sub-Saharan archaeological record: when, where, and why? *African Archaeological Review* **35**: 347–378. doi: 10.1007/s10437-018-9305-3
- MURATOV IV. 2010. Terrestrial molluscs of Cabo Delgado and adjacent inland areas of north-eastern Mozambique. *African Invertebrates* **51** (2): 255–288.
- NEKOLA JC, COLES BF. 2016. Supraspecific taxonomy in the Vertiginidae (Gastropoda, Stylommatophora). *Journal of Molluscan Studies* **82** (1): 208–212. doi: 10.1093/mollus/eyv034
- NEKOLA JC, CHIBA S, COLES BS, DROST CA, VON PROSCHWITZ T, HORSÁK M. 2018. A phylogenetic overview of the genus *Vertigo* O.F. Müller, 1773 (Gastropoda: Pulmonata: Pupillidae: Vertiginidae). *Malacologia* **62** (1): 21–161. doi: 10.4002/040.062.0104
- PELLETIER M, ROYER A, HOLLIDAY TW, DISCAMPS E, MADELAINE S, MAUREILLE B. 2017. Rabbits in the grave! Consequences of bioturbation on the Neandertal “burial” at Regourdou (Montignac-sur-Vézère, Dordogne). *Journal of Human Evolution* **110**: 1–17. doi: 10.1016/j.jhevol.2017.04.001
- PHILIPPSEN B. 2013. The freshwater reservoir effect in radiocarbon dating. *Heritage Science* **1**: 24. doi: 10.1186/2050-7445-1-24
- PHILLIPSON DW. 1976. *The Prehistory of Eastern Zambia*. British Institute in Eastern Africa, Nairobi, 229 pp.
- PICKFORD M. 1995. Fossil land snails of East Africa and their palaeoecological significance. *Journal of African Earth Sciences* **20** (3-4): 167–226.
- PIGATI JS, RECH JA, NEKOLA JC. 2010. Radiocarbon dating of small terrestrial gastropod shells in North America. *Quaternary Geochronology* **5** (5): 519–532. doi: 10.1016/j.quageo.2010.01.001
- PIGATI JS, MCGEEHIN JP, MUHS DR, BETTIS III, EA. 2013. Radiocarbon dating late Quaternary loess deposits using small terrestrial gastropod shells. *Quaternary Science Reviews* **76**:

- 114–128. doi: 10.1016/j.quascirev.2013.05.013
- PILSBRY HA. 1919. A review of the land mollusks of the Belgian Congo: chiefly based on the collections of the American Museum Congo Expedition, 1909–1915. *Bulletin of the American Museum of Natural History* **40** (1): 1–370.
- PRESTON HB. 1905. Description of a new *Achatina* from the Zambesi. *Proceedings of the Malacological Society of London* **6** (4): 244. doi: 10.1093/oxfordjournals.mollus.a066084
- RICHARDS CS. 1970. Genetics of a molluscan vector of schistosomiasis. *Nature* **227** (5260): 806–810. doi: 10.1038/227806a0
- RICHTER M, TSUKAMOTO S, CHAPOT MS, DULLER GAT, BARMHAM LS. 2022. Electron spin resonance dating of quartz from archaeological sites at Victoria Falls, Zambia. *Quaternary Geochronology* **72**: 101345. doi: 10.1016/j.quageo.2022.101345
- ROBBINS LH, CAMPBELL AC, MURPHY ML, BROOK GA, LIANG F, SKAGGS SA, SRIVASTAVA P, MABUSE AA, BADENHORST S. 2008. Recent archaeological research at Toteng, Botswana: early domesticated livestock in the Kalahari. *Journal of African Archaeology* **6** (1): 131–149.
- ROKSANDIC M, RADOVIĆ P, WU XJ, BAE CJ. 2022. Resolving the “muddle in the middle”: the case for *Homo bodoensis* sp. nov. *Evolutionary Anthropology: Issues, News, and Reviews* **31** (1): 20–29. doi: 10.1002/evan.21929
- ROWSON B, LAW M, MILLER JM, WHITE T, SHIPTON C, CROWTHER A, NDIEMA E, PETRAGLIA M, BOIVIN N. 2024. A Quaternary sequence of terrestrial molluscs from East Africa: a record of diversity, stability, and abundance since Marine Isotope Stage 5 (78,000 BP). *Archiv für Molluskenkunde* **153** (1): 61–86. doi: 10.1127/arch.moll/153/061-086
- SEDDON MB, TATTERSFIELD P, HERBERT DG, ROWSON B, LANGE CN, NGEREZA C, WARUI CM. 2005. Diversity of African forest mollusc faunas: what we have learned since Solem (1984). *Records of the Western Australian Museum Supplement* **68**: 103–113.
- SESSA JA, CALLAPEZ PM, DINIS PA, HENDY AJ. 2013. Paleoenvironmental and paleobiogeographical implications of a Middle Pleistocene mollusc assemblage from the marine terraces of Baía das Pipas, southwest Angola. *Journal of Paleontology* **87** (6): 1016–1040. doi: 10.1666/12-119
- SHIPTON C, ROBERTS P, ARCHER W, ARMITAGE SJ, BITA C, BLINKHORN J, COURTNEY-MUSTAPHI C, CROWTHER A, CURTIS R, ERRICO FD, DOUKA K, FAULKNER P, GROUCUTT H, HELM R, HERRIES AIR, JEMBE S, KOURAMPAS N, LEE-THORPE J, MARCHANT R, MERCADER J, MARTI AP, PRENDERGAST ME, ROWSON B, TENGAZA A, TIBESASA R, WHITE TS, PETRAGLIA MD, BOIVIN N. 2018. 78,000-year-old record of Middle and Later Stone Age innovation in an East African tropical forest. *Nature Communications* **9** (1): 1832. doi: 10.1038/s41467-018-04057-3
- SIMMS MJ, DAVIES P. 2000. Appendix 7. Preliminary report on the sediments and molluscs of Lake Patrick. Pp. 275–280 in: Barham LS (Ed.) *The Middle Stone Age of Zambia, South Central Africa*. Western Academic & Specialist Press, Liverpool.
- SMITH EA. 1893. On a collection of land and freshwater shells transmitted by Mr. H.H. Johnston C.B. from British Central Africa. *Proceedings of the Zoological Society of London* **1893**: 632–641.
- STENSGAARD AS, VOUNATSOU P, SENGUPTA ME, UTZINGER J. 2019. Schistosomes, snails and climate change: current trends and future expectations. *Acta Tropica* **190**: 257–68. doi: 10.1016/j.actatropica.2018.09.013
- STRINGER C. 2012. The status of *Homo heidelbergensis* (Schoetensack 1908). *Evolutionary Anthropology: Issues, News, and Reviews* **21** (3): 101–107. doi: 10.1002/evan.21311
- TATTERSFIELD P. 2011. Gastropoda. Pp. 567–587 in Harrison T. (Ed.) *Paleontology and Geology of Laetoli: Human Evolution in Context: Volume 2: Fossil Hominins and the Associated Fauna*. Springer, Dordrecht.
- TATTERSFIELD P, ROWSON B, NGEREZA CF, HARRISON T. 2024. Laetoli, Tanzania: Extant terrestrial mollusc faunas shed new light on climate and palaeoecology at a Pliocene hominin site. *PLoS ONE* **19** (5): e0302435. doi: 10.1371/journal.pone.0302435
- TAYLOR VK, BARTON RNE, BELL M, BOUZOUGGAR A, COLLICUTT S, BLACK S, HOGUE JT. 2011. The Epipalaeolithic (Iberomaurusian) at Grotte des Pigeons (Taforal), Morocco: a preliminary study of the land Mollusca. *Quaternary International* **244** (1): 5–14. doi: 10.1016/j.quaint.2011.04.041
- TAYLOR VK. 2014. Land snail middens in the Late Pleistocene and early Holocene in North Africa: a case study from Taforal (Grotte des Pigeons), Morocco. Unpublished Ph.D. thesis, University of Reading.
- THACKERAY JF. 1988. Molluscan fauna from Klasies River, South Africa. *South African Archaeological Bulletin* **43**: 27–32. doi: 10.2307/3887610
- THIELE J. 1911. Mollusken der deutschen Zentral-Afrika-Expedition. *Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika-Expedition, 1907–1908. Band III, Zoologie I*. Klinkhardt & Biermann, Leipzig, 175–214.
- VAN BRUGGEN AC. 1988. A record of the genus *Cerastua* (Mollusca, Gastropoda, Pulmonata: Enidae) from Zambia, with a preliminary list of the terrestrial molluscs of that country. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C: Biological and Medical Sciences* **91**: 1–17.
- VAN BRUGGEN AC. 1993. *Cerastua* in the south revisited, a new taxon in Malawi and Zambia (Mollusca, Gastropoda, Pulmonata: Enidae). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C: Biological and Medical Sciences* **96**: 143–149.
- VAN BRUGGEN AC. 2008. New studies on the land molluscs of Malawi, a second interim progress report. Prolegomena for a new checklist. *Basteria* **72** (4–6): 353–368.
- VAN BRUGGEN AC, MEREDITH HM. 1984. A preliminary analysis of the land molluscs of Malawi. Pp. 156–171 in: Solem A, van Bruggen AC (Eds) *World-wide Snails: Biogeographical Studies on Non-marine Mollusca*. E.J. Brill / W. Backhuys, Leiden.
- VAN DAMME D, GAUTIER A. 2013. Lacustrine mollusc radiations in the Lake Malawi Basin: experiments in a natural laboratory

- for evolution. *Biogeosciences* **10** (9): 5767–5778. doi: 10.5194/bg-10-5767-2013
- VERDCOURT B. 1987. Mollusca from the Laetolil and Upper Ndolanya Beds. Pp. 438–450 in: Leakey MD, Harris JM (Eds). *Laetoli: a Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford.
- VERDCOURT B. 2004. New and little known species of terrestrial Mollusca from East Africa and Congo (Kinshasa). *Annales Historico-naturales Musei Nationalis Hungarici* **96**: 299–315.
- WEIJ R, SNIDERMAN JK, WOODHEAD JD, HELLSTROM JC, BROWN JR, DRYSDALE RN, REED E, BOURNE S, GORDON J. 2024. Elevated Southern Hemisphere moisture availability during glacial periods. *Nature* **626** (7998): 319–326. doi: 10.1038/s41586-023-06989-3
- WHITE TS, BRIDGLAND DR, LIMONDIN-LOZOUET N, SCHREVE DC. Fossils from Quaternary fluvial archives: sources of biostratigraphical, biogeographical and palaeoclimatic evidence. *Quaternary Science Reviews* **166**: 150–176. doi: 10.1016/j.quascirev.2017.04.016
- WOODWARD AS. 1921. A new cave man from Rhodesia, South Africa. *Nature* **108** (2716): 371–372. doi: 10.1038/108371a0
- WRIGHT CA. 1956. A note on the ecology of some Molluscan intermediate hosts of African schistosomiasis. *Annals of Tropical Medicine & Parasitology* **50** (4): 346–349. doi: 10.1080/00034983.1956.11685775
- Manuscript received: 22 May 2024
Revised manuscript accepted: 18 October 2024
Editor: Robert Forsyth