



## Quaternary ostracodes and molluscs from the Rukwa Basin (Tanzania) and their evolutionary and paleobiogeographic implications



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### ABSTRACT

Much of the spectacular biodiversity of the African Great Lakes is endemic to single lake basins so that the margins of these basins or their lakes coincide with biogeographic boundaries. Longstanding debate surrounds the evolution of these endemic species, the stability of bioprovinces, and the exchange of faunas between them over geologic time as the rift developed. Because these debates are currently unsettled, we are uncertain of how much existing distribution patterns are determined by modern hydrological barriers versus reflecting past history. This study reports on late Quaternary fossils from the Rukwa Basin and integrates geological and paleoecological data to explore faunal exchange between freshwater bioprovinces, in particular with Lake Tanganyika. Lake Rukwa's water level showed large fluctuations over the last 25 ky, and for most of this period the lake contained large habitat diversity, with different species assemblages and taphonomic controls along its northern and southern shores. Comparison of fossil and modern invertebrate assemblages suggests faunal persistence through the Last Glacial Maximum, but with an extirpation event that occurred in the last 5 ky. Some of the molluscs and ostracodes studied here are closely related to taxa (or part of clades) that are currently endemic to Lake Tanganyika, but others testify to wider and perhaps older faunal exchanges between the Rukwa bioprovince and those of Lake Malawi and the Upper Congo (in particular Lake Mweru). The Rukwa Basin has a long history of rifting and lacustrine conditions and, at least temporarily, its ecosystems appear to have functioned as satellites to Lake Tanganyika in which intralacustrine speciation occurred. Paleontological studies of the Rukwa faunas are particularly relevant because of the basin's important role in the late Cenozoic biogeography of tropical Africa, and because many of the molecular traces potentially revealing this history would have been erased in the late Holocene extirpation.

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### 1. Introduction

The Great Lakes of East Africa are well-known centers of lacustrine biodiversity, a consequence of their size, age and environmental variability (Coulter, 1991; Turner et al., 2001; Schultheiß et al., 2009; Wagner et al., 2012). Some of these lakes, such as Lakes Malawi, Tanganyika and Victoria, house hundreds of species of endemic fish,

invertebrates and algae, many of which are restricted in distribution to a single lake or basin. Frequently, a very strong differentiation exists between the fauna and flora of a long-lived lake proper with biota from the immediate surrounding waterbodies (marginal streams, rivers, marshes, and satellite lakes). The lakes' margins appear to form biogeographic "barriers" between intralacustrine taxa and those occupying the surrounding waters. It is commonly hypothesized that the differences in ecological interactions within and outside these lakes are nearly insurmountable to the attempting colonizers in both directions (Andrusov, 1902; Cohen and Johnson, 1987; Martens, 1994; Michel, 1994), likely because the environmental conditions within long-lived lakes are very different from those of the surrounding waterbodies (Kozhov, 1963). Possibilities for colonization may furthermore be

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limited if the ecospace that is to be colonized is already occupied by other, well-adapted taxa (West et al., 1991). However, despite more than a century of debate (i.e., since Andrusov, 1902), these hypotheses have not been adequately tested and the conspicuous biogeographic pattern remains controversial and poorly understood, partly because there are occasional examples of supposed long-lived lake “endemics” that have colonized surrounding waterbodies (e.g., Wouters and Martens, 1994; Takhteev, 2000; Schelly et al., 2003; Schelly and Stiasny, 2004; MacDonald et al., 2005; Salzburger et al., 2005; Schultheiß et al., 2009; Sturmhuber et al., 2010). These examples suggest a certain permeability of these ancient lakes' margins as existing biogeographic boundaries. Moreover, this permeability likely varied over the lakes' histories, e.g., during climatic cycles of moisture and aridity and tectonic alterations to watershed boundaries, which could dramatically alter the bathymetric configuration of the basins. Such variations in the permeability of biogeographic boundaries related to climate cycles have been documented for paleolakes in the Turkana Basin (Van Bocxlaer et al., 2008). However, the permeability of biogeographic boundaries is usually very difficult to study through time because ancient lakes and their surrounding waterbodies have a very different potential for fossil preservation. Additionally, adequate testing of hypotheses on the origin of biogeographic boundaries of long-lived lakes requires the study of a diversity of taxa, with independent colonizations across biogeographic boundaries.

Lake Tanganyika and its neighbor, Lake Rukwa (100 km to the southeast of Lake Tanganyika), provide a promising setting to study biogeographic patterns and affinities across a diverse range of taxa, several of which are preserved in the fossil record. This potential in no small part relates to the long history of aquatic ecosystems in the Tanganyika and Rukwa Basins, as demonstrated by extensive sediment archives (e.g., Cohen et al., 1993; Morley and Wescott, 1999; Morley et al., 1999). However, in contrast to the biota of Lake Tanganyika, Rukwa's fauna and flora remain largely unstudied aside from an extensive investigation of the ichthyofauna (Seegers, 1996). A thorough investigation of the Lake Rukwa biota is warranted to obtain insight into how the bioprovince of Lake Rukwa interacted with that of Lake Tanganyika and other African bioprovinces during the Neogene (Seegers, 1996; Cotterill and De Wit, 2011).

Here we summarize the Quaternary paleohydrological and geological history of the Rukwa Basin. Our purpose is to redress the lack of studies on the fauna of the basin, by reviewing the scattered paleontological information available and by reporting on new fossil and modern finds from the Rukwa Basin. In doing so, we aim to start filling the void that the Rukwa Basin represents in our current understanding of the historical biogeography of Africa.

### 1.1. Quaternary geology and paleohydrology of the Rukwa Basin

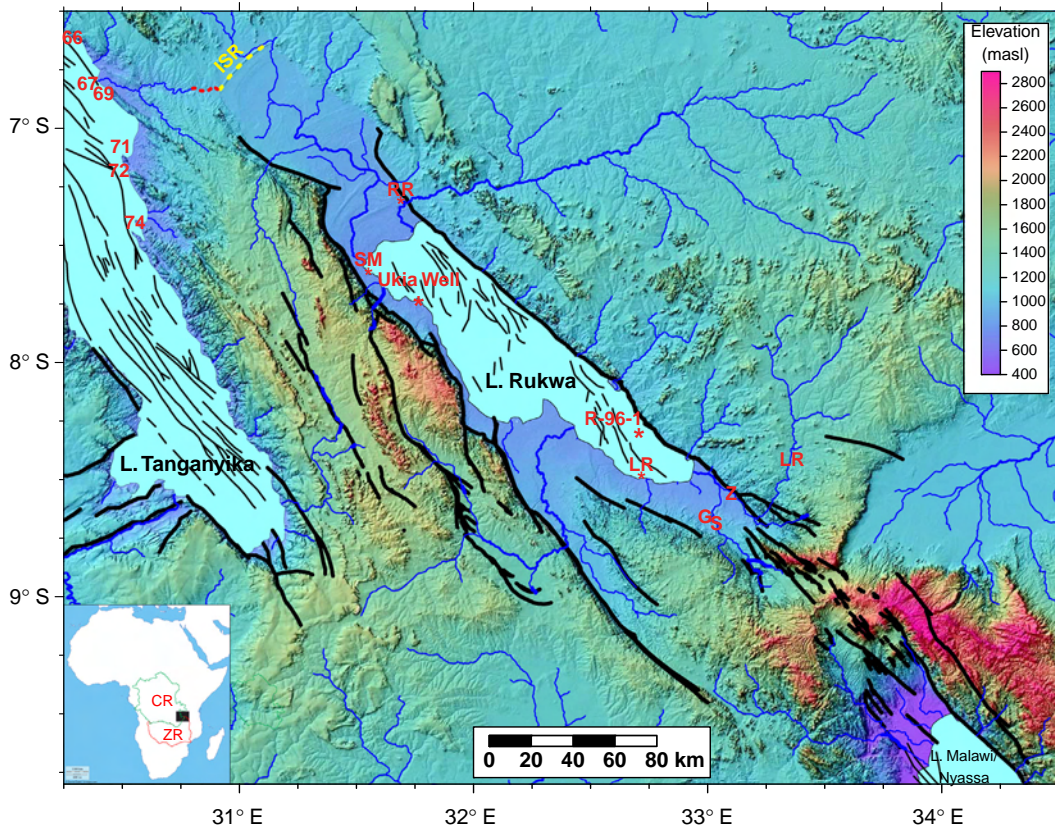
The paleolimnological history of the Rukwa Basin and its hydrographical connections provide useful constraints on biogeographic hypotheses for East African freshwaters. Lake Rukwa is currently a shallow (maximum depth 14 m in 1996; Thevenon et al., 2002), moderately saline/alkaline ( $\sim 1200 \mu\text{S cm}^{-1}$ , pH 8–9; Seegers, 1996), closed-basin lake, with predominantly muddy shorelines (Fig. 1). The lake's surface elevation is  $\sim 802$  m asl (early 2012; as it was in 1977–1978 [Delvaux et al., 1998]), but this varies considerably interannually, as illustrated by a drop of over four meters between 1998 (an El Niño year) and 2007 ([http://www.pecad.fas.usda.gov/cropeplorer/global\\_reservoir](http://www.pecad.fas.usda.gov/cropeplorer/global_reservoir)). Currently the lake receives about 1000 mm/yr precipitation, mostly during the Austral summer (December–April) although precipitation is highly variable from year to year (Thevenon et al., 2002). The region's variable climate makes Lake Rukwa highly susceptible to lake-level fluctuations, which strongly affected the lake's ecosystems over the Quaternary (Talbot and Livingstone, 1989; Delvaux et al., 1998).

We use the term “Paleolake Rukwa” to collectively refer to Pleistocene/early Holocene lacustrine phases of the Rukwa Basin's history.

The paleolimnological history of Paleolake Rukwa has been studied using sediment cores, outcrops and geophysical methods. Palynological data from drill cores, coupled with seismic-reflection data, demonstrate that the Rukwa Rift Basin formed in the late Tertiary with a strong structural imprint from Permian–Triassic (Karoo) rifting (Morley et al., 1999). A thick sequence of lake deposits (up to 2 km in places) is evident from borehole and seismic-reflection data. Biostratigraphic (palynological) data suggest that lakes were present, at least intermittently, in the Rukwa Basin back to the Miocene (Morley and Wescott, 1999; Morley et al., 1999), and the basin itself may date from the late Oligocene (Roberts et al., 2012). Parts of this lacustrine sequence are exposed in outcrops along the basin flanks, especially south of the modern lake along the Lupa and Zira River valleys (Grantham, 1932), and near Galula (Grove, 1983), along the Rungwa River north of the modern lake (Stockley, 1938), and in some newly discovered outcrops, both north and south of the modern lake, which we report here.

The late Quaternary history of Paleolake Rukwa is known from several cores collected from the modern lake as well as geomorphic studies of high-stand lacustrine and alluvial terraces. Livingstone and Richardson collected a 23.1 m core from the southern marginal region of the lake in 1960 (8°30'S, 32°40'E, labeled “LR” on Fig. 1), from which Haberyan (1987) described the diatoms of the past  $\sim 13$  ky ( $^{14}\text{C}$  yr). In 1996, a 12.8 m core, spanning  $\sim 22$  cal ky was retrieved from the deepest part of the lake (southern region,  $\sim 14$  m; Thevenon et al., 2002; Barker et al., 2002; Vincens et al., 2005; “R-96-1” on Fig. 1). This last core indicates that the lake's depocenter experienced relatively shallow nearshore environments during the cool, dry conditions of the Last Glacial Maximum (LGM), but the lake does not appear to have completely desiccated (Barker et al., 2002; Vincens et al., 2005). Water depths remained relatively shallow until  $\sim 13.5$  cal ka BP, after which the lake level rose dramatically. Core data suggest deep lake conditions during the terminal Pleistocene into the early Holocene (Barker et al., 2002). After  $\sim 7.0$  cal ka BP the surroundings became more arid and lake level dropped. During the period from  $\sim 4.4$  to 4.2 cal ka BP, much lower levels and more saline conditions prevailed (Haberyan, 1987) and various sedimentological indicators from both cores indicate that the lake was very shallow and saline at times between 4.4 and 3.0 cal ka BP. The Livingstone lake-margin core contains desiccation surfaces during this time, but the depocenter core does not indicate complete disappearance of the lake (Talbot and Livingstone, 1989; Thevenon et al., 2002). A composite lake-level curve based on terrace elevations and covering the past  $\sim 22$  ka was presented by Delvaux and Williamson (2008).

Quaternary deposits representing high lake stands around the Rukwa Basin were first documented in the mid-20th Century (Grantham, 1932; Stockley, 1938; Spence, 1954). McConnell (1950) described the remarkable Ilyandi Sand Ridge (“ISR” on Fig. 1), an arcuate feature extending for over 40 km across the northern portion of the Rukwa Basin and which lies between 980 and 998 m asl. McConnell interpreted this to be an Eolian ridge or spit formed by southeast trade winds blowing across the paleolake. The spit's basal elevation marks the water level at which Lake Rukwa reached open conditions, with an outlet (the modern Nkamba and lower Ifume River) flowing through the Karema Depression into Lake Tanganyika (Figs. 1, 2 and 3). Delvaux et al. (1998) and Delvaux and Williamson (2008) agreed with this interpretation and also reported the existence of a series of lower-elevation terraces, representing later, lower shorelines within the Rukwa Basin. A number of  $^{14}\text{C}$  ages on lake beds, lake terraces and fan-delta terraces confirm that the high-stand deposits are of latest Pleistocene to early Holocene age (Table 1, Clark et al., 1970; Grove, 1983; Delvaux et al., 1998; Delvaux and Williamson, 2008). Most of these  $^{14}\text{C}$  dates were obtained from freshwater mollusc shells (Table 1), but several of these samples appear to be no longer available for malacological study. Our new data is broadly consistent with the lake-level curve of Delvaux and Williamson (2008).



**Fig. 1.** Shuttle Radar Topography Mission (SRTM) Digital Elevation Model of the Lake Rukwa region, with surrounding lakes and sampling localities discussed in the text. SM = mollusk death assemblage sampling site at fishing village of Iranga; S = Songwe measured section, G = sampling site 3 km south of Galula Mission station; Z = Sampling locality at bridge crossing of the Zira River, LR = Lupa River, RR = Rungwa River. Dotted yellow line (ISR) is the Ilyandi Sand Ridge and dotted red line to the west of that is the early Holocene Nkamba and lower Ifume River outlet channel to Lake Tanganyika. LR and R-96-1 refer to sediment-core sites collected by Livingstone and Richardson in 1960 (see Haberyan, 1987), and the French core collected in 1996 (described by Thevenon et al., 2002) respectively. Numbers in Lake Tanganyika refer to 86-RJ sampling stations discussed in Fig. 9. Inset map shows location of main map (black rectangle) and Zambezi (ZR) and Congo River (CR) drainage basins. Base map produced using MICRODEM©. SRTM processing based on Jarvis et al. (2008). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

## 2. Material and methods

### 2.1. Historical and new collections

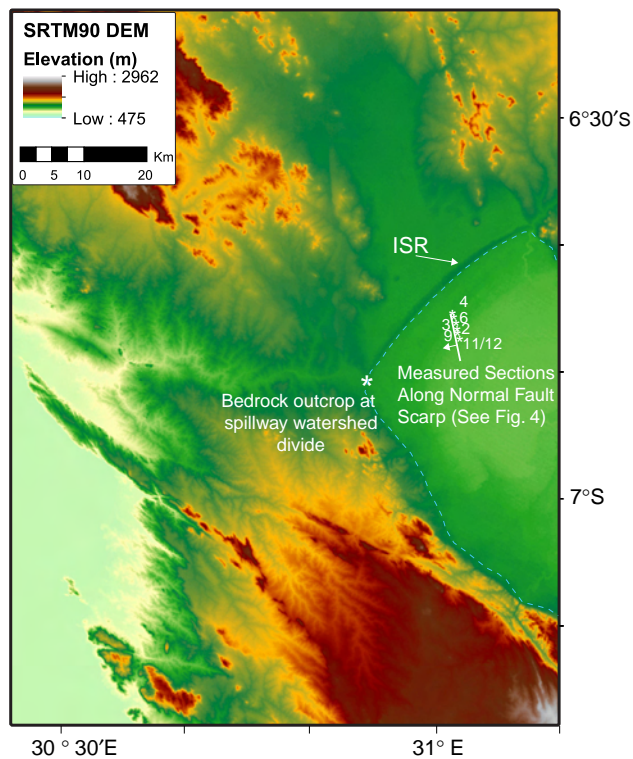
The most abundant faunal remains in deposits of the Rukwa Basin are freshwater ostracodes and molluscs. Fortunately, these remains often allow species-level identification. No earlier investigations have been made on fossil ostracodes from the Rukwa Basin, but several fossil mollusc collections were made prior to our study and are revised here.

Fossil molluscs were first described from the Paleolake Rukwa lake beds north of the modern lake by Smith (1906). In 1938, Stockley collected more samples from cliffs of the Rungwa River; this fauna was described by Cox (1939). Haynes, Clark and Grove (Clark et al., 1970; Haynes et al., 1971; Grove, 1983) collected material near the village of Galula, south of the present lake in the Songwe River valley (Fig. 1) and obtained several radiocarbon dates on freshwater shells (Table 1). Additionally, some samples from a well site near Ukia were reported by McConnell (1950). These samples are problematic because their stratigraphic position is unclear and the borehole is currently submerged in the lake, preventing us from reexamining it. Hence, we report the samples here for completeness, but will leave them largely undiscussed. All of these historical collections are housed in the Department of Earth Sciences (ex-Dept of Palaeontology), Natural History Museum, London (institutional coden NHMUK). Although sediment samples associated with the historic mollusc fossils were usually not collected, some shells contained sediment, which we extracted and screened for ostracode remains.

In 2006, we (A.C., J.T. and H.N.) prospected parts of the Rukwa Basin and discovered a series of newly exposed paleolake outcrops, some of which contained previously unsampled, fossiliferous beds. Some of these outcrops are exposed along a small fault escarpment (orientation ~N13W) located just south of the Ilyandi Sand Ridge (Kervyn et al., 2006). In 2008–2011, we (D.D.) investigated the late Pleistocene–Holocene lacustrine deposits of the Songwe River Valley south of the modern lake. These are geographically close to the Galula section that was previously sampled by Grove (1983). We report on the molluscs and ostracodes of these newly discovered outcrops here.

The modern fauna of Lake Rukwa is, with the exception of fish (Seegers, 1996), poorly sampled and studied. Aside from some small collections described by Lindroth (1953), little prior work has been done on the modern ostracodes. For molluscs, there seem to have been no focused collecting expeditions and only the unionid bivalve fauna has been synthesized from museum specimens (Graf and Cummings, 2011). Beyond unionids we found only a few references to the extant freshwater malacofauna of the Lake Rukwa Basin. Some modern gastropod material was mentioned by Cox (1939) and Mandahl-Barth (1957), but beyond these we know of no reference to the gastropod fauna of Lake Rukwa, not even in Brown's detailed accounts of the freshwater gastropods of Africa (1980, 1994).

Two of the four sediment-surface samples we collected from modern Lake Rukwa yielded ostracode valves. Ostracode samples from the current study are kept at the Laboratory of Paleolimnology, Department of Geosciences, University of Arizona. In addition, we sampled the molluscs from two sediment-surface death assemblages at the shore of the



**Fig. 2.** Digital Elevation Model of the northern portion of the Rukwa Basin, showing the highstand Paleolake Rukwa (light blue dashed outline), the Ilyandi Sand Ridge (ISR), the outlet channel, and new sampling localities of the northern Rukwa Basin. Base map produced using ArcGIS©. SRTM processing based on [Jarvis et al. \(2008\)](#). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lake (location labeled SM on [Fig. 1](#)) to augment existing records of its extant malacofauna and to enable direct comparison to the taphonomic setting of the fossil assemblages. New collections of fossil and modern molluscs will be deposited at the Natural History Museum, London, except for the material collected by Delvaux (sample codes starting with DD), which will be deposited at the Royal Museum for Central Africa (Tervuren).

## 2.2. Stratigraphy

The records from the northern and southern part of the Rukwa Basin present notably different lithofacies. Because the stratigraphic relationship between deposits in the north and south remains ambiguous, we present the stratigraphy and our results by geographic subregion.

### 2.2.1. Northern Rukwa Basin

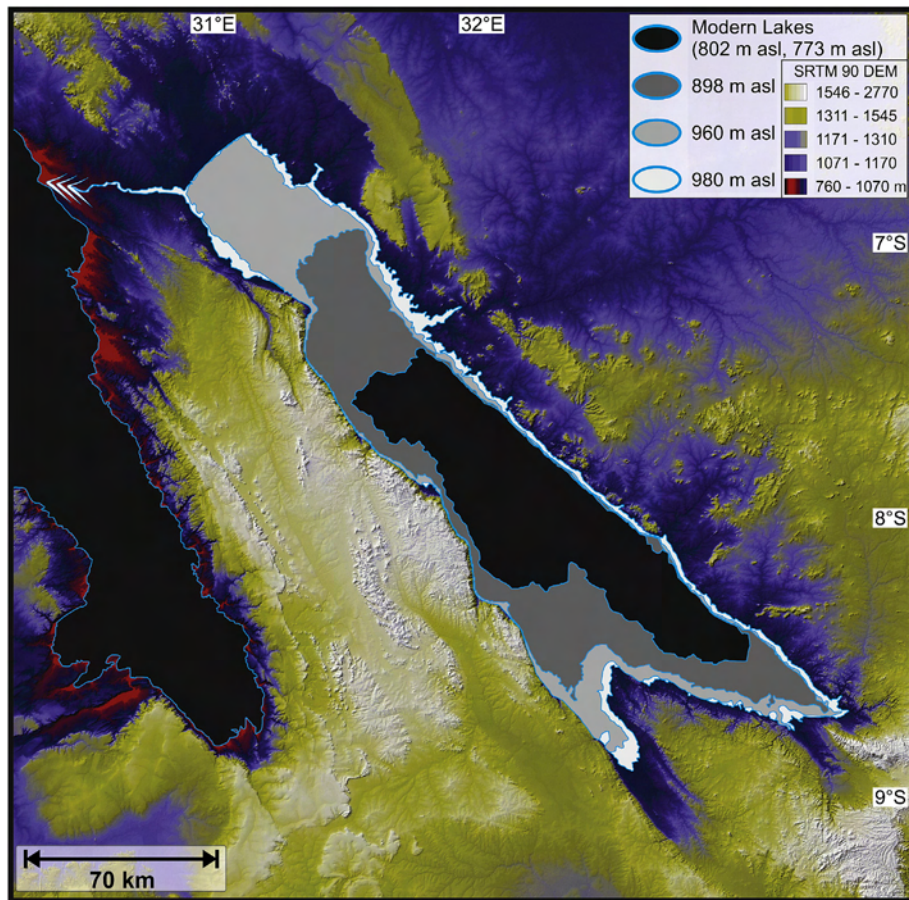
**2.2.1.1. Rungwa River section.** This section was first described by [Stockley \(1938\)](#), who reported the sequence exposed at Rungwa River to be at least 180 ft (55 m thick) and described the mollusc-bearing unit as “a sandy bed five feet [1.5 m] thick within... shales”, and “sands and clays overlying diatomaceous shales”. We ([A.C., J.T., H.N.](#)) revisited the Rungwa River section locality area (easternmost bluff at 7°19.2'S, 31°42.62'E) (RR on [Fig. 1](#)), where we observed a well-exposed and thick sequence of diatomite (26 m exposed) with an intercalated ~2 m thick, poorly sorted pebble bed in a matrix of coarse sand at 846 m asl. Field observations indicated that the pebble bed becomes finer in a downstream direction. This unit may correlate with the horizon sampled by [Stockley](#) based on its position immediately above the diatomites and because there were no other siliciclastic units observed in the section. This correlation is also supported by the characteristics

of the sediments (an unlithified gritty fine sand) present within the mollusc shells collected by [Stockley](#). This section has not yet been dated.

**2.2.1.2. Ilyandi sand ridge.** Shallow exposures of 1 to 2 m of sediments that stratigraphically underlie the Ilyandi Sand Ridge are present at several locations along the eastern footwall of a fault scarp ([Figs. 2, 4, 5](#); Samples jt-06-04-03 through -07, jt-06-09-01 through -08, jt-06-12-02 through -07 and jt-06-14-02). This fault escarpment probably results from recent earthquakes and is consistent in orientation with the regional fault-strike orientations documented by [Delvaux et al. \(1998\)](#) and [Kervyn et al. \(2006\)](#). From north to south the fault crosscuts a series of recessional shoreline terraces (at least 10 are visible on satellite imagery between the northern and southernmost outcrops studied). From their elevation range (925–945 m asl) we infer that these terraces formed after the lake receded from its maximum elevation of >976 m asl (outlet threshold; our measured elevation of the highest exposed bedrock channel, marked on [Fig. 2](#), thus actual lake maximum elevation is estimated at ~980 m asl). Terrace elevations decline systematically towards the south and the modern lake ([Fig. 4](#)). Dates of  $8510 \pm 60$  and  $8290 \pm 80$  cal yr. BP were obtained on mollusc shells from a somewhat higher (and presumably older) terrace at 960 m asl ([Table 1](#)). A minimum age for the lake-terrace deposits is provided by a calibrated date of  $5540 \pm 50$  cal yr BP on a land snail (*Burtoa nilotica*; [Table 1](#)) from section 3 (sample jt-06-04-06) collected from dark-gray to brown sandy silts (see *in-situ* shell in [Fig. 5B](#)). The degree to which the older, recessional terrace lime-gravels that outcrop in this area (discussed below) might influence these dates is unknown. However, these carbonates do not appear to make up a major portion of the substrate within the watershed. The dark sandy silts are poorly exposed, but probably represent a middle Holocene paleosol or marsh deposit overlying the lake-terrace beds. At section 9 ([Fig. 4](#)), where these deposits are well exposed, a clear unconformity separates rhizolith-bearing silts (root mats) from the underlying lake beds.

Beneath the thin cover of modern vertisols, locally referred to as *mbuga* soils, and the middle Holocene paleosols mentioned above are deposits that form recessional terrace paleoshorelines. These consist of lime-gravels, sands and silts, displaying varying degrees of induration ([Fig. 5A, C, D](#)). At most localities examined, these lake-terrace deposits are richly fossiliferous, containing molluscs, ostracodes and rarer fish teeth and bones. Both the sedimentology and fossil assemblages indicate that they accumulated under shallow (littoral) conditions, consistent with their geomorphic expression as probable beach or shoreline terraces. At section 9, the lake deposits coarsen upward from basal silts (slightly offshore), to shelly gravels and low-angle cross-stratified sands, typical of lacustrine-beach deposits. Some of the sandy beach deposits display probable beach rock development ([Fig. 5A, C](#)), which is highly reminiscent of that occurring in the vadose zone of the shores of Lake Tanganyika today ([Cohen and Thouin, 1987](#)). [Delvaux and Williamson's \(2008\)](#) lake-level reconstructions suggest that all of the lacustrine units are probably of a similar early to middle Holocene age (>5500 cal yr BP). Most of these units contain transported assemblages of dominantly lacustrine molluscs, either scattered or concentrated in thin shell beds ([Fig. 5](#)). All of the sampled outcrops appear to have been deposited in very similar environments, with minor differences in the time of deposition, even though some differences in size-sorting and abrasion may be present. Most of the lacustrine shells are moderately to heavily abraded, probably through wave action on a sandy and pebbly shoreline (e.g., [McGlue et al., 2009](#)), and bivalves are always disarticulated.

**2.2.1.3. Ukia well site.** [McConnell \(1950\)](#) listed a collection of molluscs and associated sediment obtained from a borehole near Ukia (7°45'S, 31°48'E), a site currently submerged in Lake Rukwa on its northwestern side ([Fig. 1](#)). The sample was reported to have been obtained from a depth of about 30 ft (~9 m) ([McConnell, 1950](#)), but specimen labels at the NHM (London) suggest it was obtained from depths of 10–15 ft



**Fig. 3.** SRTM Digital Elevation Model of the extent of modern and Paleolake Rukwa at various lake level elevations. The 898 m asl level represents the lake at the time of the late Pleistocene (~22 cal ka BP) Songwe measured section (Table 1 and Fig. 6). The 980 m asl level is the overflow elevation occurring in the latest Pleistocene-earliest Holocene (~13.5 cal ka BP and possibly later). Outlet channel of the Nkamba and Ifume Rivers is shown to Lake Tanganyika (the elevation of Lake Tanganyika at that time is unknown). The 960 m asl level represents dated early Holocene (~8300–8500 cal yr. BP) shoreline fossiliferous terraces south of the Ilyandi Ridge. The modern lake elevations for Lakes Rukwa and Tanganyika are also shown. SRTM processing based on Jarvis et al. (2008).

(3–5 m). In any case, the material was collected from ‘superficial deposits’ consisting of ‘thick series of gravels, sands and clays of recent origin’ that lie above the paleo-lake beds (McConnell, 1950). However, the precise stratigraphic position and age remain unknown.

### 2.2.2. Southern Rukwa Basin

**2.2.2.1. Zira Bridge.** Late Pleistocene and early Holocene lacustrine deposits are also well exposed south of modern Lake Rukwa. We (D.D.) discovered another exposure of late Pleistocene lacustrine deposits at Zira Bridge (“Z” on Fig. 1), approximately 14 km from the Songwe River site discussed below. At this location a thin (~2 m) sequence of colluvial deposits sits on the fault basement of the footwall of the Lupa fault scarp along the left bank of the Zira River. These colluvial deposits are interbedded with thin and mollusc-rich lacustrine sediments (fossil sample DD738/2011). This transgressive horizon has been  $^{14}\text{C}$  dated to  $22,990 \pm 280$  cal yr BP (Table 1).

**2.2.2.2. Songwe River Valley.** One of the best exposures in the south is a ~49 m thick section of mixed lacustrine, fluvio-lacustrine and fluvial deposits exposed along the Songwe River Valley (S on Fig. 1, and Figs. 6 and 7) (Delvaux, unpublished data). These sediments, currently lying between 865 and 914 m asl, record relatively deep-lake conditions (~60–120 m deep) prior to the latest Pleistocene low-stand event. They indicate an interval of alternating shallow lacustrine and fluvio-deltaic deposition, which started before ~29 cal ka BP, followed by an interval of fluvial deposition and a rapid lacustrine transgression

dated to  $22,010 \pm 320$  cal yr BP from fossil shell material (Table 1). The transgression is marked by a prominent unconformity and shell lag, which yielded some of the fossil material discussed below (Samples DD736/2008-10, DD736/2009-17, DD736/2011). Above these late Pleistocene lake beds there is an apparent hiatus or condensed interval of fluvial deposits.

**2.2.2.3. Galula.** Grove (1983) collected molluscs from Holocene deposits in 1977 at two localities. One site lies ~3 km south of the Galula mission station, in a gullied escarpment exposure of lake beds about 10 m thick at about 860 m asl ( $8^{\circ}37'S$ ,  $33^{\circ}1'E$ , radiocarbon sample SR-1408, labeled G on Fig. 1). This exposure is a thin sandy horizon, which has been radiometrically dated to  $7270 \pm 60$  cal yr BP (Table 1). A second Holocene deposit lies in close proximity to the Songwe Pleistocene deposits described above, ~8 km southwest of the Galula mission station ( $8^{\circ}39'S$ ,  $33^{\circ}02'E$ , sample A-945, Table 1; “S” on Fig. 1). This site was revisited by one of us in 2008 (D.D., radiocarbon sample DD734/2008-21, Table 1). Holocene sediments from this site are indicative of shallow-water lacustrine and fluvio-deltaic conditions.

### 2.3. Ostracodes

Of the 15 bulk-sediment samples studied from the Ilyandi Sand Ridge sites in the north (Figs. 2 and 4), 14 yielded fossil ostracodes. No ostracodes were obtained from the small amounts of matrix we extracted from the interior of museum specimens of molluscs from the Rungwa River section. Some samples from the Songwe River valley

**Table 1**  
Radiocarbon dates relevant to this study. (1) Ages calibrated using CalPal® online, using the CalPal\_2007\_Hulu calibration curve. Rounding off of ages and standard errors following Stuiver and Polach (1977). Potential hard-water effects for dates based on aquatic shells from the Paleolake Rukwa, and limestone effects on terrestrial molluscs (and hence the appropriate corrections) are unknown. \* Conventional <sup>14</sup>C age determination. \*\* AMS <sup>14</sup>C age determination. † Potential old carbonate contamination. Laboratories where samples were analyzed (refer to Sample numbers): A and AA = University of Arizona; SRR = Scottish Universities Research and Reactor Centre; DD738/2009-1 and 2011, DD736/2009-17, and DD734/2008-21 at the Radiocarbon Laboratory, Silesian University of Technology; Muze, Kat-T1-17 and Kat-T1-3 at the R.J. Aan de Graaff laboratorium, Utrecht University.

Sample number	Location	Material	C-14 age (BP)	δ <sup>13</sup> C	Calibrated age (years BP) ± 2σ <sup>(1)</sup>	References
DD738/ 2009-1 & 2011	Bridge over the Zira river against the Lupa fault scarp; 8° 32.16'N, 33° 5.64'E, 91 m asl	<i>Lavigeria</i> sp., shell	19,220 ± 60**	Indet.	22,990 ± 280	This report (D. Delvaux analysis)
DD736/ 2009-17	Songwe measured section, in a deep gully; 8° 38.62'S, 33° 01.8'E, 898 m asl	<i>Coelatura</i> cf. <i>ujujiensis</i>	18,360 ± 60**	Indet.	22,010 ± 320	This report (D. Delvaux analysis)
A-945	S. of Galula, ~60 m above modern lake level; 8°39'S, 33°02'E, 925 m asl	<i>Etheria elliptica</i> (bivalve) shell in mudstone overlain by nodular carbonates near top of 41 m section on fluvio-lacustrine sediments	9740 ± 140*	— 2.45‰	11,070 ± 200	Clark et al. (1970)
Muze	High lake stand fan delta terrace (1000 m asl; terrestrial sample from above actual paleolake elevation) near Muze	Charcoal	9620 ± 100 **	Indet.	10,960 ± 160	Delvaux et al. (1998)
A-944	8 km S. of Galula, ~60 m above modern lake level"; 8°42'S, 33°02'E	Unidentified bivalve shell	8060 ± 120*	— 1.36‰	8950 ± 190	Grove (1983)
DD734/2008-21	Same outcrop as A-945, 8°39'S, 33°02'E, 925 m asl	Unidentified bivalve shell	8030 ± 30 **	Indet.	8910 ± 90	This report (D. Delvaux analysis)
Kat-T1-17	Katavi, Trench 1, 6°43.05'S, 31°1.34'E, 960 m asl	Indet. mollusc shell	7720 ± 60 **	−2.5	8510 ± 60	This report (D. Delvaux analysis, collected by F. Kervyn)
Kat-T1-3	Katavi, Trench 1, 6°43.05'S, 31°1.34'E, 960 m asl	Indet. mollusc shell	7480 ± 80 **	−4.4	8290 ± 80	This report (D. Delvaux analysis, collected by F. Kervyn)
SRR-1408	~3 km SW of Galula Mission Station in gullied escarpment above Songwe R., 8°37'S 33°01'E, ~860masl	<i>Lavigeria</i> sp. shell	6340 ± 50 *	— 1.8‰	7270 ± 60	Grove (1983)
AA91461	Marsh/Paleosol deposits in upper part of Section 3, 6°46.59'S, 31°02.36'E, 938 m asl	<i>Burtoa nilotica</i> (land snail) shell (sample voucher NHMUK QG 5611)	4800 ± 40 **	— 8.8‰	5540 ± 50†	This report (U Arizona analysis)

in the south also yielded ostracode material (i.e., Grove's Galula sample SRR-1408; DD618, DD736/2008, DD736/2011, DD930-1 and DD738/2011). Additional ostracode material was obtained from sediment removed from mollusc shells from the borehole sample at Ukia and two surface-sediment samples from modern Lake Rukwa.

Ostracode samples were prepared from bulk samples using standard freeze-thaw techniques for disaggregation (modified from Forester, 1991, following Palacios-Fest et al., 2005), and wet-sieved with a 63-µm screen. Whenever possible, we counted 300 valves to determine species proportions; experience has shown that this number is adequate to recover all or most species present in freshwater ostracode samples with diversities similar to ours. However, in nine of the bulk samples ostracodes were rare and less than 300 valves were present (Supplemental Documents Table 1). Additionally, we counted 100 valves, if available, to determine taphonomic characteristics of the assemblages (% whole carapaces, % adult valves, % broken valves, and % with CaCO<sub>3</sub> coatings, oxidation stains or reduction stains).

## 2.4. Molluscs

We collected 38 fossil mollusc samples from 17 outcrops. Most of these are bulk samples, but a limited set of mollusc samples consists of hand-picked material. Some outcrops are very rich in mollusc material (more weight in molluscs than in other sediment). Quantitative samples were made from the outcrops we sampled ourselves, but because the sampling methods of historical samples are often unknown and dependent on the specific purpose of collecting, we restrict our

analysis to qualitative comparisons. This allows us to include all historical fossil collections that have been previously listed or discussed (see Section 2.1). Bulk samples were wet-sieved using test sieves of 2 mm and 500 µm mesh. Molluscs, ostracodes and fish bones were isolated from these samples. The mollusc material was studied using the relevant literature (e.g., Cox, 1939; Brown, 1994) and directly compared to type and other reference material when necessary. A summary of the collections is provided in Supplemental Documents Table 2. Given the limited nature of the collections, the exploratory nature of our study, and the goals of the current paper, which can be addressed with information at the genus level, we refrain here from a formal systematic revision of the species involved. However, we do provide descriptive notes.

## 3. Ostracode and mollusc faunas

### 3.1. Ostracodes

#### 3.1.1. Recent ostracodes

Our modern samples of northern Lake Rukwa sediments yielded a very depauperate fauna (*Limnocythere michaelsoni* and rare *Potamocypris* sp.) typical of large, shallow, alkaline African lakes. An earlier study by Lindroth (1953) reported the presence of the following taxa *Cypris bouvieri*, *Hemicypris* (*Cyprinotus*) *fossulatus*(?), *Hemicypris* (*Cyprinotus*) *fülleborni*, *Cypridoposis newtoni*, and *L. michaelsoni*. Of these, *C. bouvieri* and *H. fülleborni* appear to be endemic to Lake Rukwa, whereas the other three taxa occur in other alkaline-saline lakes in East Africa,

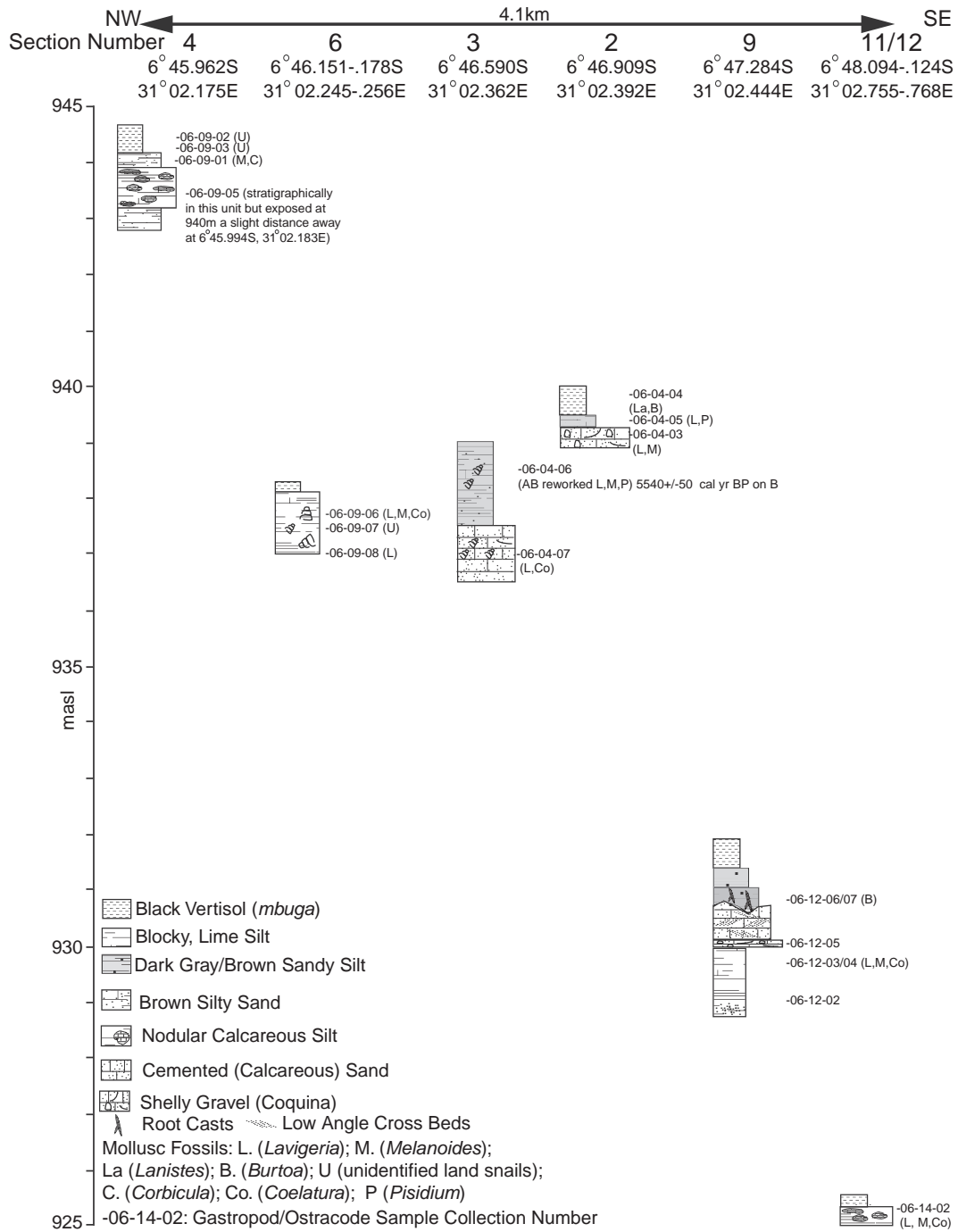


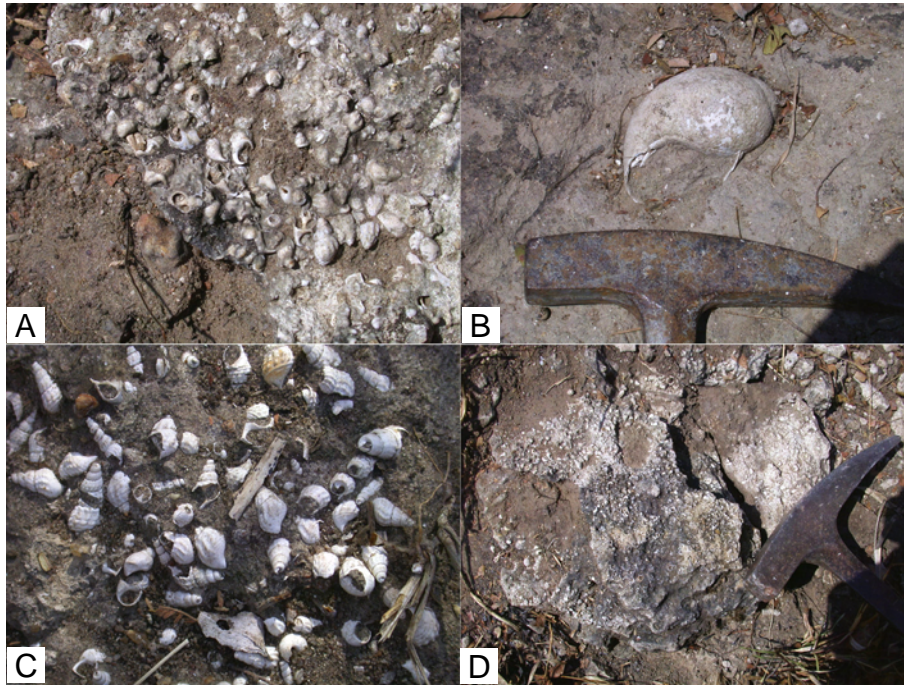
Fig. 4. Measured sections and sample locations discussed in the text. All sections are plotted against current elevation above sea level. Note Sections 11/12 are essentially identical in stratigraphy, with Section 12 lying ~80 m southeast of Section 11.

notably Lake Turkana (Cohen, 1986), whose benthic habitats and water chemistry are similar to those of Lake Rukwa.

3.1.2. Fossils from the northern Rukwa Basin

Fossil ostracode samples from the Ilyandi Sand Ridge area are moderately diverse (7 or 8 species in all samples for which 300 valves were counted) and generally well-preserved. The fauna in this area is typical of what might be found today along the margins of a large tropical African lake with abundant fringing macrophytes. With few exceptions, the faunas are dominated by a species of *Cyprideis*, which appears to be either very similar or identical to the Tanganyikan “endemic” *Cyprideis mastai* (Figs. 8 and 9; Wouters and Martens, 1994). *Sclerocypris jenkinae*

and *L. michaelsoni*, both widespread, tropical African species, are also common in most samples, as are unidentified species of *Cypridopsis* and *Potamocypris*. The cosmopolitan species *Darwinula stevensoni*, and unidentified species of *Zonocypris* and *Gomphocythere* occur more sporadically. The *Gomphocythere* species is almost certainly new. It bears some similarity to *Gomphocythere downingi* from Lake Tanganyika, especially in the presence of well-developed ventro-lateral alae on both valves (Park and Martens, 2001), particularly in the males (Fig. 9). However, the females of this species are quite distinct from *G. downingi*, because they have a highly inflated and swollen posterior brood pouch area. A large proportion of the Ilyandi Sand Ridge area ostracode fossils are unbroken (mean 57.0 ± 29.1% 1σ, n = 17), adult



**Fig. 5.** Outcrop photos from the Ilyandi Ridge fossil sites. A. Cemented *Lavigeria* shelly gravel (beach accumulation) from Section 3 (sample jt-06-04-07). Field of view ~10 cm across. B. *Burtoa nilotica* land snail in dark gray/brown sandy silts from Section 3 that was used for dating (sample jt-06-04-06; AA91461 in Table 1). C. *Melanoides* shelly lime silt from Section 6 (sample jt-06-09-06). Field of view ~16 cm across. D. Cemented *Lavigeria* gravel (beach rock?) from Section 3 (sample horizon jt-06-04-07). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

carapaces (mean  $42.8 \pm 16.8\%$   $1\sigma$ ), fairly typical of littoral assemblages of large African lakes. Many display calcium carbonate coatings (mean  $70.0 \pm 42.8\%$   $1\sigma$ ), common for littoral accumulations in  $\text{CaCO}_3$  supersaturated lakes, whereas only a few possess reduction ( $0.6 \pm 1.4\%$   $1\sigma$ ) or oxidation ( $0.7 \pm 3.2\%$   $1\sigma$ ) staining.

The Ukia sample is almost entirely composed of *L. michaelsoni*, with small numbers of *Hemicypris kliei* and a second, unidentified *Hemicypris* species. This may be *H. fülleborni* or *H. fossilatus*, both of which were found by Lindroth (1953) in the modern lake, along with *L. michaelsoni*. The Ukia sample was almost entirely composed of broken uncoated juvenile valves.

### 3.1.3. Fossils from the southern Rukwa Basin

The samples from the Songwe River Valley and Zira Bridge sections are very different from the samples of the northern part of the Rukwa Basin. However, the Songwe and Zira samples pre-date the late Pleistocene Paleolake Rukwa low-stand and are hence older than the early Holocene material from Galula (=SRR-1408, Table 1). Samples from the south are considerably more diverse (e.g., 11 species in the Galula sample) than those from the north and have similar compositions (i.e., the early Holocene Galula sample is more similar to the nearby late Pleistocene Songwe and Zira material than it is to the northern Rukwa early Holocene material). In addition to containing most of the species found at the sites in the north (including the *Hemicypris* species from Ukia), the southern samples also contained an undescribed *Sclerocypris* and two genera, here-to-fore only known from Lake Tanganyika, *Romecytheridea* (*R. ampla*) and *Tanganyikacypridopsis*. The *Tanganyikacypridopsis* species is almost certainly new, although it bears some similarities to *T. depressa* (Fig. 9 and Martens, 1985). Samples from the Songwe River Valley and from Galula contain exactly the same taxa with affinities to Lake Tanganyika “endemics”.

A relatively high proportion of intact adult carapaces in the Galula sample (85% unbroken, 43% carapaces) suggests a similar mechanical depositional setting as the one that created the assemblages in the north of the basin. However, the absence of  $\text{CaCO}_3$  coatings and the common (85%) oxidation staining of the carapaces from the early

Holocene Galula material suggest a different geochemical depositional environment at Galula compared to those from early Holocene deposits in the north of the basin. At the nearby but older Songwe sites, the ostracode fossils display variable proportions of adults and variable but generally high proportions of broken valves. The three Songwe and Zira Bridge samples with ostracodes were uncoated. Like the Galula sample, two of the Songwe samples that lacked  $\text{CaCO}_3$  coatings did possess Fe-oxide coatings, suggesting they may have been deposited in a similar carbonate undersaturated and oxidized environment as Galula (quite different from what is observed in the northern samples).

It is somewhat surprising that the southern faunal samples from both Songwe and Galula contain more species with Tanganyika affinities than those from the north, because the sites in the north are in closer proximity to the Paleolake Rukwa outlet channel to Lake Tanganyika. Furthermore, although *Romecytheridea* and *Tanganyikacypridopsis* are currently only known from Lake Tanganyika, we do not know their phylogeographic history. It is possible that these genera are quite old and have a more widespread history than their current endemism in Lake Tanganyika would suggest, potentially consistent with Schön and Martens' (2011) interpretations of the phylogeny of *Romecytheridea* based on molecular genetic data.

## 3.2. Molluscs

### 3.2.1. Recent molluscs

Graf and Cummings (2011) report four unionid species from the Rukwa Basin based on museum collections: *Coelatura mossambicensis*, *Chambardia bourguignati*, *Chambardia wahlbergi*, and *Etheria elliptica*. C.K. Ricardo collected *Bulinus forskalii* and *Biomphalaria pfeifferi* (taxonomy updated herein) from the shores of Lake Rukwa (Cox, 1939), and Mandahl-Barth (1957) has referred to the occurrence of probable *Bulinus africanus* in the basin. Our modern samples were obtained as death assemblages from the northwest shoreline of Lake Rukwa at the fishing village of Iranga ( $7^\circ 37.4'S$ ,  $31^\circ 34.5'E$ ; SM on Fig. 1). The first, sample jt-06-16-01, consists of small, dead gastropod shells obtained from shoreline drift near a small stream entering the lake from a



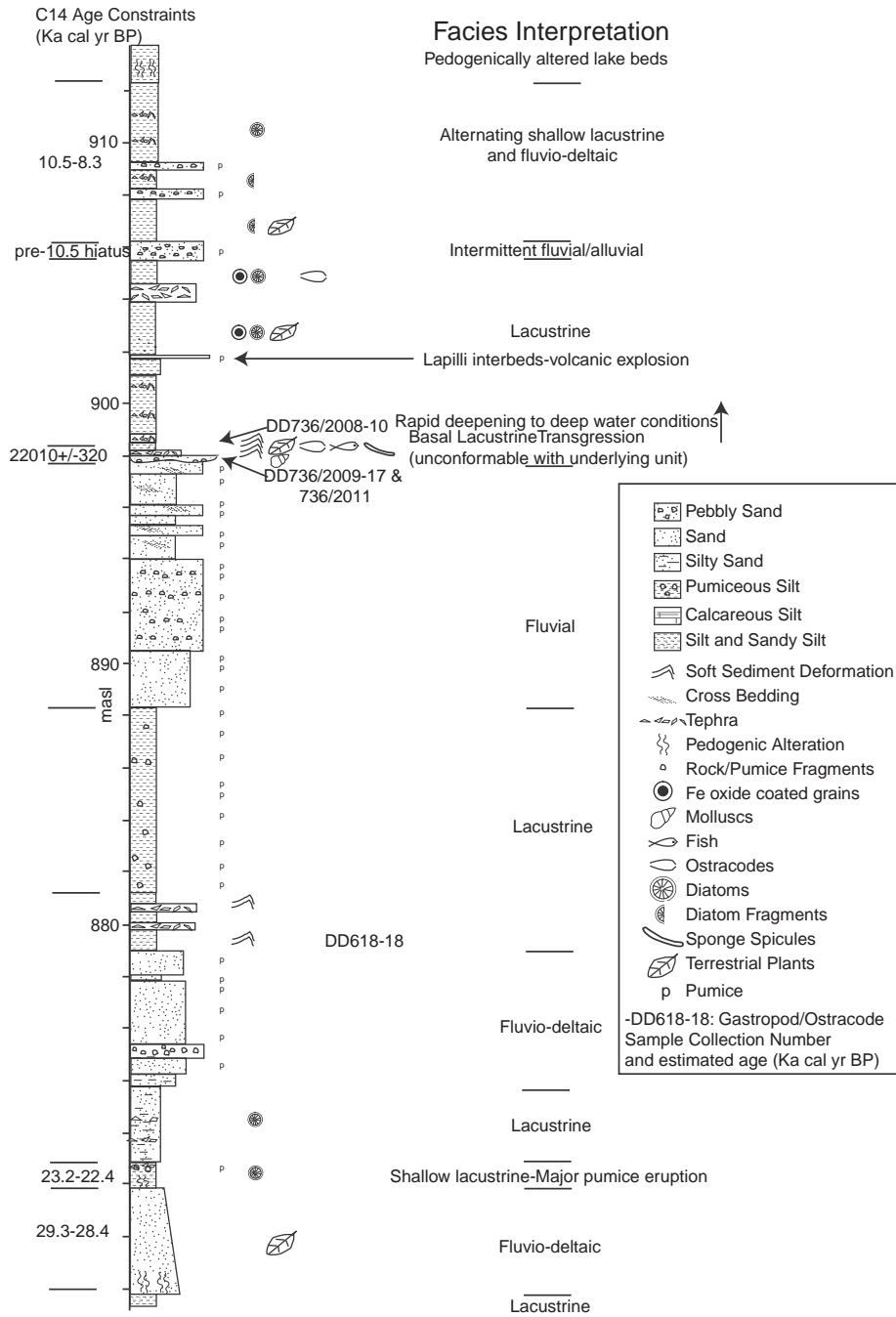


Fig. 6. Songwe River outcrop stratigraphy.

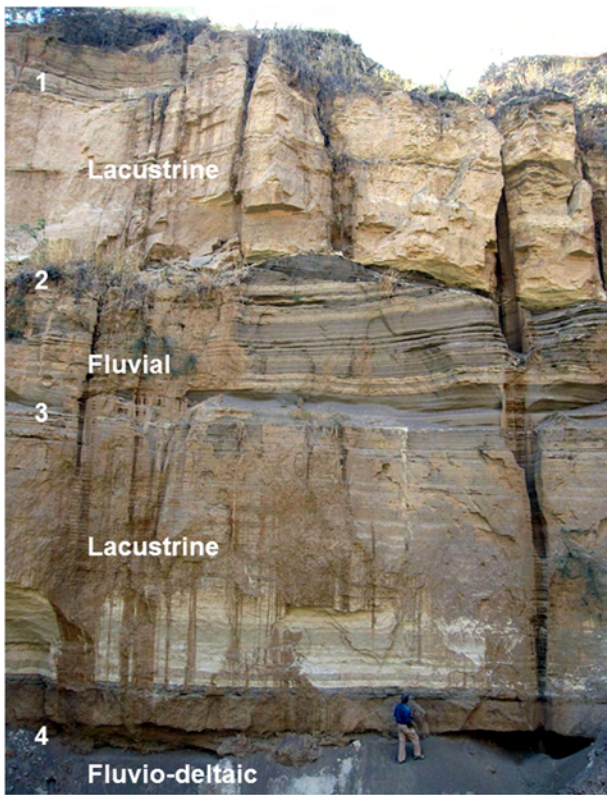
marginal reedy marsh area. This minimally transported assemblage consists entirely of pulmonate snails, overwhelmingly dominated by planorbids, and a few unidentified land snails. The most frequent taxa are *Biomphalaria angulosa* (Fig. 12, C) and *Bulinus globosus* (Fig. 12, D). Other planorbids present, which were not recorded from our Paleolake Rukwa samples, include *Ceratophallus natalensis?* (Fig. 12, I) and *Lentorbis junodi?* (Fig. 12, H). *Bulinus forskalii*, *Lymnaea natalensis* and *Biomphalaria pfeifferi* are also present. All these species are indicative of marshy conditions (Brown, 1994), which is consistent with the lake-side marsh habitat drained by small streams from which they were obtained. Our current record of *B. angulosa* (based on empty shells only) extends the species' known range in south-central Tanzania and Malawi (Appleton et al., 2010) to the northwest.

The second sample, jt-06-16-02, in contrast, was obtained from within Lake Rukwa at the edge of a reed stand growing in fine mud

and left exposed by the falling water level. The assemblage consists of mostly articulated, recently dead specimens of the unionoid *Chambardia wahlbergi* (Fig. 12, B) and a single valve of the unionoid *Mutela dubia* (Fig. 12, A), which was not reported by Graf and Cummings (2011) from the Rukwa Basin, and hence represents a new record. The ampullariids *Pila ovata* (Fig. 12, E) and *Lanistes ovum* are also present. Taken together, the small modern samples contain eight (potentially nine) species (Supplemental Documents Table 2), which are not known from our Paleolake Rukwa samples but which are widely distributed species in tropical Africa today.

### 3.2.2. Fossil molluscs

The late Pleistocene to middle Holocene (~25.0–5.0 ka) mollusc fauna of the Rukwa Basin includes numerous species. At least 7 unionoid bivalves, 3 sphaeriid bivalves, 7 pulmonate taxa (excluding at least 5

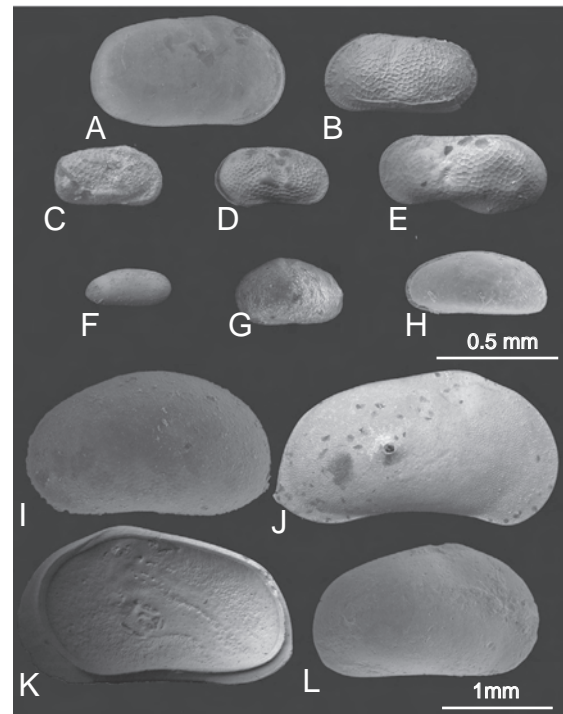


**Fig. 7.** Songwe River outcrop photo. Numbers refer to the following key stratigraphic horizons indicated on Fig. 6: 1 = pre-10.5 cal ka hiatus; 2 = sampling horizon DD 736/2009-17 (22,010 ± 320 cal yr BP); 3 = 888 m asl; 4 = sampling horizon DD 618-18. Key paleoenvironmental transitions inferred from the stratigraphy within the section are also indicated.

land snails), and 20–28 caenogastropods were obtained (Supplemental Documents Table 2). A representative selection is illustrated by region in Figs. 10 and 11. The modern fauna adds 3 unionids, 5 pulmonates and 1 caenogastropod to this list (Fig. 12). As with the ostracodes, mollusc samples from different periods and localities within the Rukwa Basin show substantial differences as to their composition, and regional differences in preservation and taphonomy have been observed as well. For this reason, we will discuss the material first by region and second by age.

**3.2.2.1. Fossil molluscs from the northern Rukwa Basin.** Lacustrine shells from the northern part of the Rukwa Basin (Figs. 5 and 10) are generally abraded and broken and appear to have been rolled in the surf zone of the lake prior to deposition in shoreline deposits. Consequently, it is possible that smaller and thinner shells have been lost or are underrepresented in these nearshore faunas compared to collections from the south of the basin (Fig. 12). Shells are frequently covered with a thin carbonate crust, as in recent alkaline or hardwater lakes.

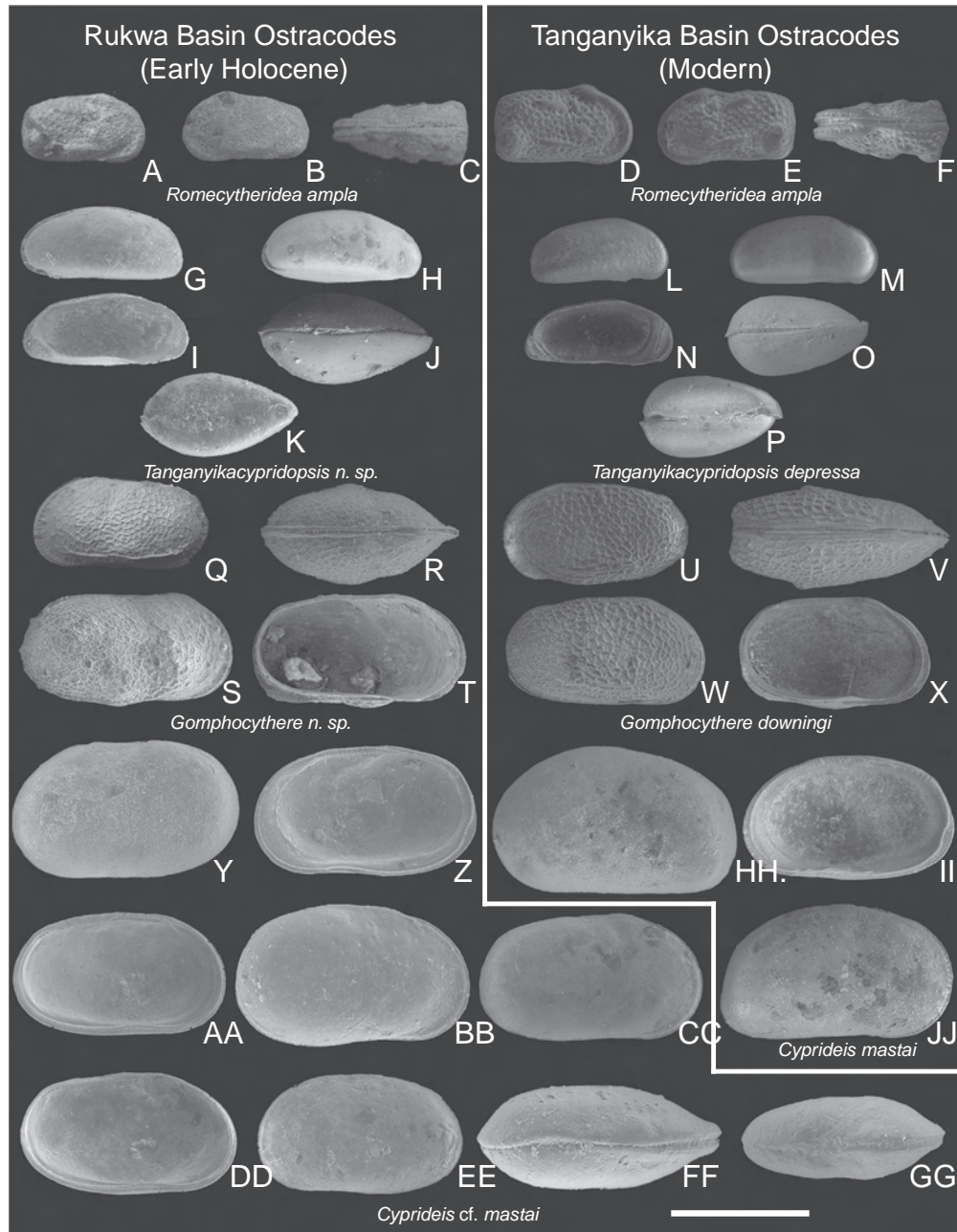
The first significant collection made was from the Rungwa River section. The fossil molluscs of this section have been described and figured by Cox (1939) and are reexamined here. Cox (1939) erected three new *Edgaria* species from this sample, a cerithioid snail genus that is currently synonymized with *Lavigeria* (West et al., 2003). Cox's material largely consists of broken and moderately to heavily abraded shells. We have reexamined these specimens for the first time since their description and have preliminarily grouped the specimens into two taxa, but given the wide variation present in both teleoconch and larval shell morphology, each may comprise more than a single species. These are *L. rukwaensis* (here including Cox's *L. cingulata*) and the more strongly costulate *L. stockleyi* (Fig. 10, T–V). Other caenogastropods in this assemblage, beyond the numerically dominant *Lavigeria*, are some



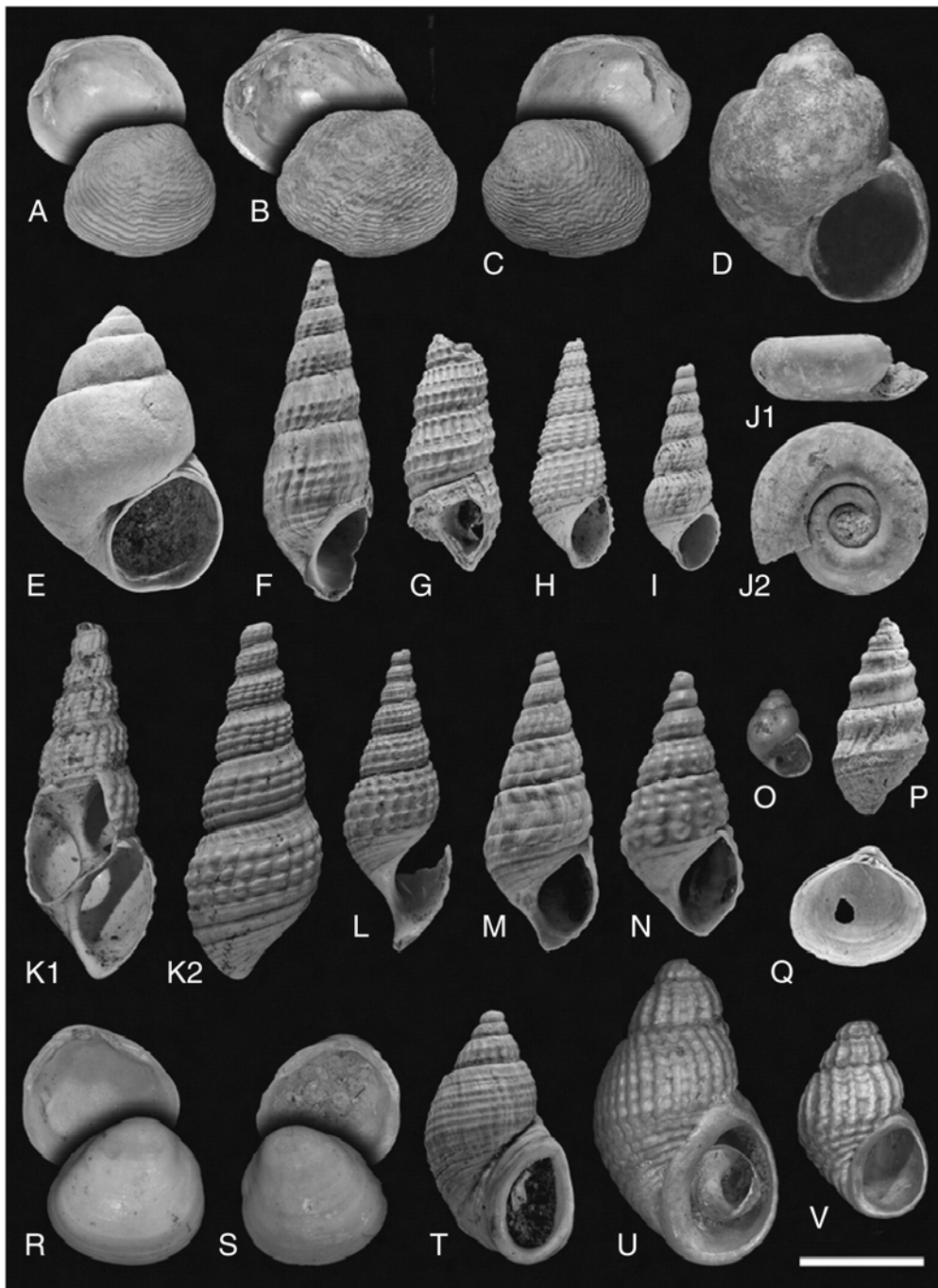
**Fig. 8.** Fossil (Holocene) and modern ostracodes from the Lake Rukwa Basin. Upper scale bar (500 µm) for specimens A–I. Lower scale bar (1 mm) for specimens J–L. A. *Cyprideis* n. sp. RV male exterior Ilyandi Ridge area, sample ac-06-15-01; B. *Gomphocythere* n. sp. male exterior lateral view LV Galula area; C. *Romecytheridea ampla* female exterior lateral view RV, Galula area.; D. *Limnocythere michaelsoni* female exterior lateral view RV, Modern Lake Rukwa Sample 4; E. *Limnocythere michaelsoni* male exterior lateral view LV Galula; F. *Darwinula stevensoni* exterior lateral view LV Galula area; G. *Cypridopsis* sp. exterior lateral view LV, Ilyandi Sand Ridge area sample ac-06-04-04; H. *Tanganyikacypridopsis* sp. exterior lateral view RV, Galula area; I. *Hemicypsis kliei* exterior lateral view LV, Galula area; J. *Sclerocypris* n. sp. exterior lateral view RV, Galula area; K. *Sclerocypris jenkiniae* interior view RV, sample ac-06-04-05; L. *Sclerocypris jenkiniae* interior RV, Ilyandi Sand Ridge area sample ac-06-12-07.

viviparids that Cox identified to the genera *Viviparus* and *Neothauma*, *Melanoides* specimens that Cox assigned to *Melanoides tuberculata* and a single specimen of a *Gabbiella* species that Cox assigned to a taxon now known as *G. humerosa* (sp. 1; Fig. 10, O), but in light of our new collections from the south appears more likely to represent a new species.

Our taxonomic attributions differ from those of Cox in several respects, which reflect the major advances in our knowledge of recent and fossil malacofaunas of the East African rift lakes since Cox's study. To us, the two viviparid specimens of Cox do not belong to separate genera, and very likely represent an adult and a juvenile specimen of a single *Bellamyia* species (cf. *foai* of Cox; Fig. 10, D), that resembles the extant *B. jeffreysi* from Lake Malawi in shell shape but has a lower spire. From Rungwa we distinguish three morphs of *Melanoides* (two are illustrated in Fig. 10, I & K), which are likely to represent distinct parthenogenetic lineages. Only one of these morphs likely belongs to the clade we here refer to as African indigenous *M. tuberculata* (Fig. 10, K), in light of recent work on the genus (e.g., Genner et al., 2004, 2007). Cox's *Coelatura rukwaensis* is the single unionid bivalve present (Fig. 10, A–C). Cox also figured several pulmonates: *Bulinus* cf. *truncatus* (three small specimens Cox referred to *Isidora coulboisi*; see Brown (1994) and references therein for details of synonymy), and three land snails, *Succinea badia*, *Limicolaria martensiana* and a *Tropidophora* species. The caenogastropods and the unionid bivalve from this assemblage are poorly preserved and strongly worn, whereas the thin-shelled pulmonates are much better preserved. The collection represents an aggregation from various sources; the littoral-lacustrine molluscs have been extensively rolled before they were apparently washed onto a beach, whereas land and marsh snails appear to have been buried much faster into seemingly the same



**Fig. 9.** Comparison of Rukwa Basin Holocene fossils with conspecific or closely related species from Lake Tanganyika. Tanganyika sample localities are shown in Fig. 1, except for 85-AC-27, which is located in southern Burundi, at the north end of the lake. A. *Romecytheridea ampla* female RV exterior RV, Galula; B. *Romecytheridea ampla* female? LV, Galula; C. *Romecytheridea ampla* carapace dorsal view, Galula; D. *Romecytheridea ampla* female RV of carapace, Lake Tanganyika, 86-RJ-72 (7°10'S, 30°31'E, 12.25 m water depth); E. *Romecytheridea ampla* female LV of carapace, Lake Tanganyika, 86-RJ-72 (7°10'S, 30°31'E, 12.25 m water depth); F. *Romecytheridea ampla* female dorsal carapace view, Lake Tanganyika, 86-RJ-72 (7°10'S, 30°31'E, 12.25 m water depth); G. *Tanganyikacypridopsis* sp. RV exterior, Galula; H. *Tanganyikacypridopsis* sp. LV tilted to show ventral side, Galula; I. *Tanganyikacypridopsis* sp. LV interior, Galula; J. *Tanganyikacypridopsis* sp. dorsal carapace, Galula; K. *Tanganyikacypridopsis* sp. Ventral carapace view, Galula; L. *Tanganyikacypridopsis depressa* RV exterior, Lake Tanganyika, 86-RJ-74 (7°27'S, 30°35'E, 30.5 m water depth); M. *Tanganyikacypridopsis depressa* RV exterior, Lake Tanganyika, 86-RJ-66 (6°33'S, 30°12'E, 24.5 m water depth); N. *Tanganyikacypridopsis depressa* LV interior, Lake Tanganyika, 86-RJ-66 (6°33'S, 30°12'E, 24.5 m water depth); O. *Tanganyikacypridopsis depressa* dorsal carapace view, Lake Tanganyika, 86-RJ-66 (6°33'S, 30°12'E, 24.5 m water depth); P. *Tanganyikacypridopsis depressa* ventral carapace view, Lake Tanganyika, 86-RJ-66 (6°33'S, 30°12'E, 24.5 m water depth); Q. *Gomphocythere* n. sp. male LV, Galula; R. *Gomphocythere* n. sp. male dorsal carapace, Galula; S. *Gomphocythere* n. sp. female exterior RV, Galula; T. *Gomphocythere* n. sp. female interior LV, Galula; U. *Gomphocythere downingi* male LV exterior, Lake Tanganyika, 86-RJ-67 6 (6°46'S, 30°23'E, 3 m water depth) V. *Gomphocythere downingi* female dorsal carapace, Lake Tanganyika, 86-RJ-71 (7°02'S, 30°31'E, 80 m water depth) X. *Gomphocythere downingi* female LV interior, Lake Tanganyika, 85-AC-27 (4°17'S, 29°57'E, 40 m water depth); Y. *Cyprideis* cf. *mastai* female LV exterior, Ilyandi Sand Ridge area, sample ac-06-15-01; Z. *Cyprideis* cf. *mastai* RV female interior, Ilyandi Sand Ridge area, sample ac-06-15-01; AA. *Cyprideis* cf. *mastai* LV interior, Ilyandi Sand Ridge area, sample ac-06-15-01; BB. *Cyprideis* cf. *mastai* female RV exterior, Ilyandi Sand Ridge area, sample ac-06-15-01; CC. *Cyprideis* cf. *mastai* exterior RV, Ilyandi Sand Ridge area, sample ac-06-15-01; DD. *Cyprideis* cf. *mastai* male LV interior, Ilyandi Sand Ridge area, sample ac-06-15-01; EE. *Cyprideis* cf. *mastai* male LV exterior, Ilyandi Sand Ridge area, sample ac-06-15-01; FF. *Cyprideis* cf. *mastai* dorsal carapace female, Galula; GG. *Cyprideis* cf. *mastai* dorsal carapace male, Ilyandi Sand Ridge area, sample ac-06-15-01; HH. *Cyprideis mastai* male LV, Lake Tanganyika, 86-RJ-7 (5°13'S, 29°50'E, 2 m water depth); II. *Cyprideis mastai* male RV interior, Lake Tanganyika, 86-RJ-7 (5°13'S, 29°50'E, 2 m water depth); JJ. *Cyprideis mastai* male RV exterior, Lake Tanganyika, 86-RJ-69 (6°50'S, 30°25'E, 9.25 m water depth). Scale bar: 500  $\mu$ m.



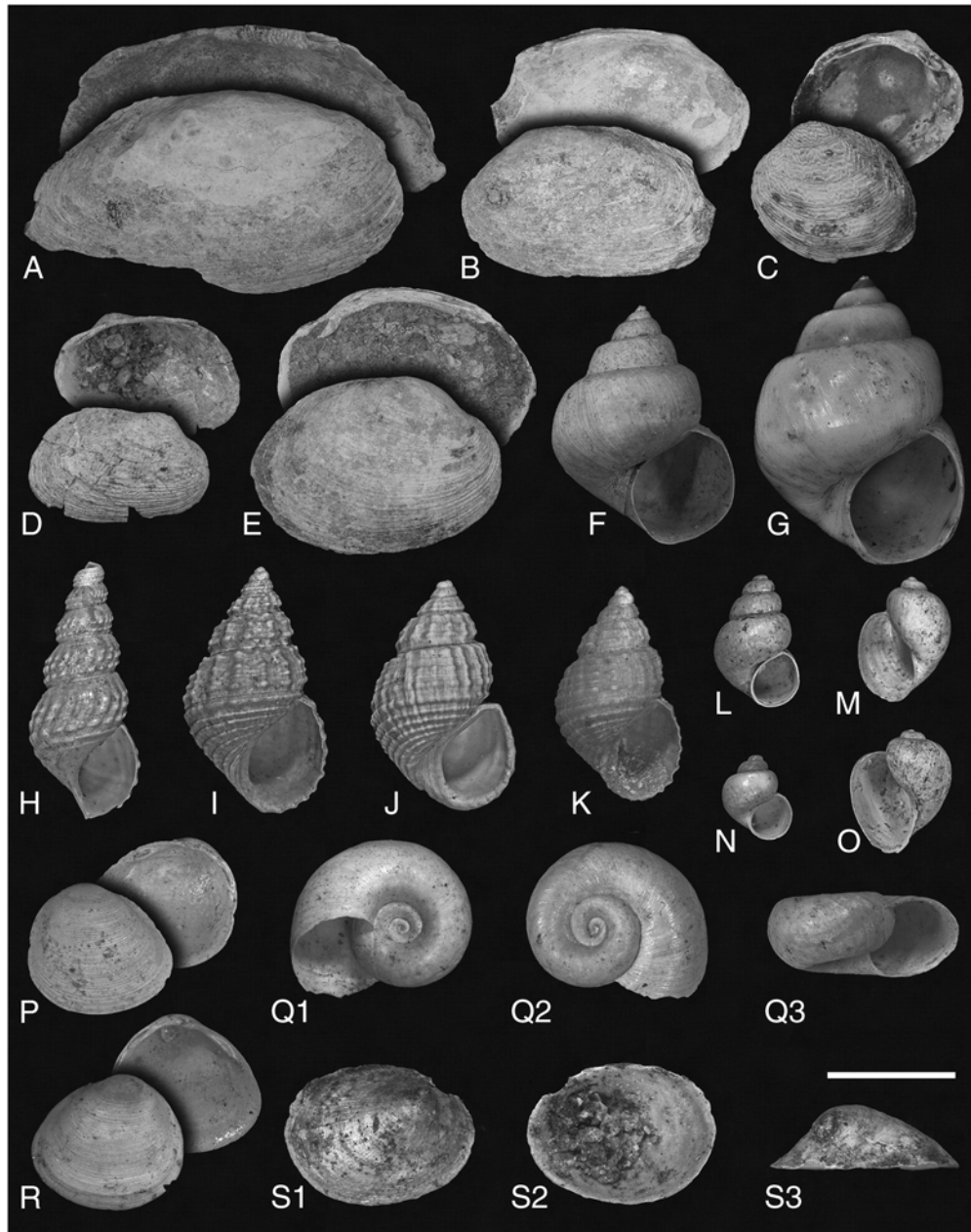
**Fig. 10.** Fossil molluscs from the Northern Rukwa Basin. (All specimen registration numbers are prefixed by NHMUK). A–C. *Coelatura rukwaensis* (jt-06-12-01; QB 1276–1278); D. *Bellamyia* sp. (cf. *foai* by Cox; G.64636); E. *Bellamyia* cf. *kalingwisensis* (Smith; G.17529); F. *Melanooides* morph L (aff. *mweruensis*) (jt-06-09-08; QG 5596); G. *Melanooides* morph F (aff. *imitatrix*) (jt-06-09-06; QG 5597); H. *Melanooides* morph A (jt-06-04-03; QG 5595); I. *Melanooides* morph D (Rungwa River, Cox, 1939; QG 5598); J. *Biomphalaria pfeifferi* (jt-06-12-07; QG 5607); K. *Melanooides tuberculata* (indigenous African) morph E (Rungwa River, Cox, 1939; QG 5599); L. *Melanooides tuberculata* (indigenous African) morph I (jt-06-09-01; QG 5600); M. *Melanooides* morph M (jt-06-14-01; QG 5601); N. *Melanooides* morph K (jt-06-09-08; QG 5602); O. *Gabbiella* sp. 1 (jt-06-09-08; QG 5608); P. *Melanooides* morph with inflated shoulder (jt-06-04-03; QG 5603); Q. *Corbicula* cf. *fluminalis* (jt-06-12-01; QB 1279); R. & S. *Pisidium* cf. *giraudi* (jt-06-12-04; QB 1280, 1281); T. *Lavigeria rukwaensis* (jt-06-12-01; QG 5604); U. & V. *Lavigeria stockleyi* (jt-06-09-08; QG 5605, 5606). Scale bar: 2 cm for A–C; 1 cm for D–J, P, Q; 5 mm for K–O, T–V; 2 mm for R & S.

death assemblage. Without rediscovery of the exact outcrop from which Stockley collected, the precise depositional setting of this fauna and whether or not the pulmonates were buried simultaneously with the littoral species remains unclear.

At the Ilyandi Sand Ridge, fossil molluscs were collected from 14 discontinuous outcrops exposed over a distance of ~6 km. These mollusc assemblages, in particular those of samples jt-06-04-03 and jt-06-09-07/8, show great similarities with the assemblages from the Rungwa River section in taphonomy and faunal composition (they share ten

taxa). The aquatic mollusc fauna is fairly rich and comprises a total of ~17 species as well as more than 12 distinct morphs of *Melanooides*; some are illustrated in Fig. 10, F–I, K–N. Shells of *Lavigeria rukwaensis*, *L. stockleyi*, *Melanooides* morphs, and the unionoid *Coelatura rukwaensis* are the most visible components of most assemblages, but the small *Pisidium* cf. *giraudi* (Fig. 10, R and S) may also be common.

We have followed standardized usage (e.g., Genner et al., 2007) in referring to distinct morphological groups of *Melanooides* as morphs. One of the morphs present appears to fall within the African indigenous

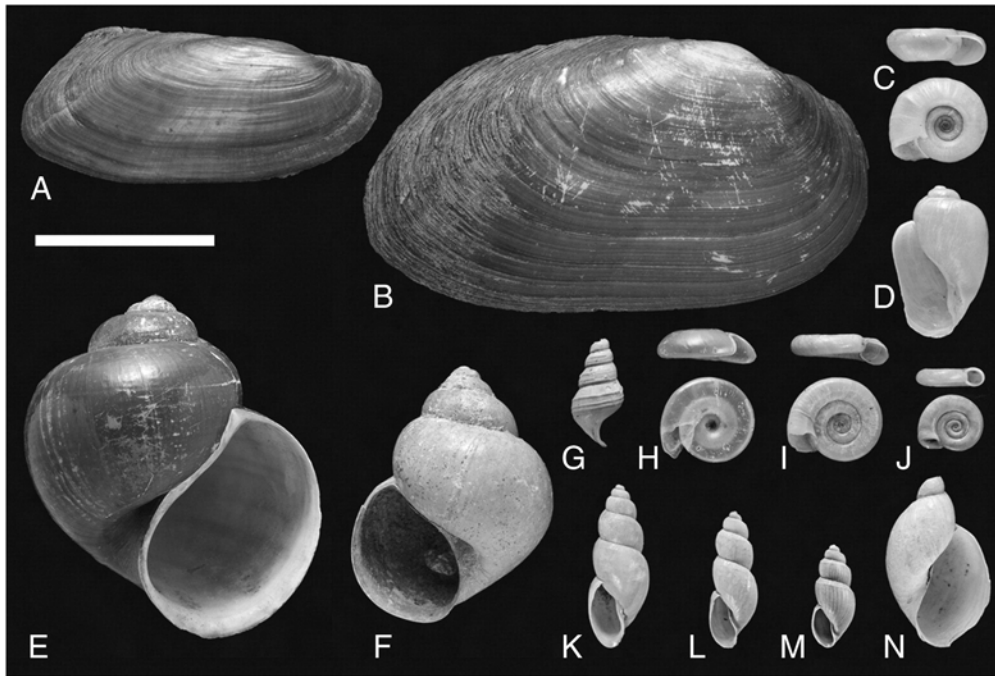


**Fig. 11.** Fossil molluscs from the Southern Rukwa Basin. A. *Iridina spekkii* (DD734/2008); B. *Chambardia* sp. (DD734/2008); C. *Coelatura* cf. *rukwaensis*/cf. *ujijiensis* (DD736/2009); D. *Coelatura* cf. *mossambicensis* (DD738/2011b); E. *Coelatura* cf. *horei* (DD734/2008); F. *Bellamya* cf. *capillata* (DD738/2011b); G. *Bellamya* sp. 2 (Grove Galula, sample #1; NHMUK QG 5609); H. *Melanoides tuberculata* (indigenous African) morph J (DD738/2011b); I–K. *Lavigeria* sp. 1. (DD738/2011b); L. *Gabbiella* sp. 3 (DD738/2011); M. *Bulinus* cf. *truncatus* (DD738/2011b); N. *Gabbiella* sp. 2 (DD738/2011); O. *Bulinus* cf. *truncatus* (DD738/2011); P. & R. *Pisidium* cf. *giraudi* (DD738/2011b); Q. *Biomphalaria* cf. *pfeifferi* (DD738/2011b); S. *Ferrissia* sp. (DD738/2011b). Scale bar: 3 cm for A & B; 2 cm for C–E; 1 cm for F & G; 5 mm for H–O, Q; 2 mm for P, R, S.

*M. tuberculata*-clade (morph E; see Genner et al., 2007), and two are morphologically most similar to species found living in Lake Mweru and the Upper Congo River, although we consider the Rukwa taxa to be specifically distinct. We refer to them as *M.* morph L (Fig. 10, F) – which is closest to *M. mweruensis* – and *M.* morph F (Fig. 10, G) – which is closest to *M. imitatrix*. Other morphs are not easily placed within known living groups and include specimens with highly inflated shoulders producing an overall morphology that appears to be unique to these deposits (Fig. 10, P). Some of these morphs almost certainly represent separate species. A few morphs have only been obtained from a single outcrop, whereas others are represented at several sampling localities. A *Gabbiella* species occurs rarely and appears to be identical to the Rungwa River taxon figured by Cox as *G. humerosa*. Overall this species falls morphologically at the edge of the range of the low-spired *Gabbiella*

we obtained in the southern part of the Rukwa Basin and it appears to be closely related to it. Among the bivalves, *Coelatura rukwaensis* is the only unionid present. The *Pisidium* cf. *giraudi* specimens from the Ilyandi Sand Ridge (Fig. 10, R and S) are much more inflated than the specimens from the south and lack the concentric ridges of the latter (Fig. 11, P and R). Specimens of *Corbicula* cf. *fluminalis* are rare (Fig. 10, Q).

Overall, the taphonomic settings in the deposits at the Ilyandi Sand Ridge are very similar to those in the Rungwa River section. The aforementioned lacustrine taxa are usually accompanied by much smaller numbers of conspicuously better preserved specimens of terrestrial and marsh snails. These include *L. ovum*, *Biomphalaria* cf. *pfeifferi*, *B. forskalii*, *Bulinus* cf. *truncatus*, *L. natalensis* and, rarely, small land snails, like *Pseudopeas* sp. and *Succinea* sp. or a subset of these depending on the outcrop. We interpret these as minimally transported



**Fig. 12.** Modern molluscs from the Rukwa Basin and some material from the Ukia well. (All specimen registration numbers are prefixed by NHMUK). A. *Mutela dubia* (jt-06-16-02; 20130359); B. *Chambardia wahlbergi* (jt-06-16-02; 20130360/1); C. *Biomphalaria angulosa* (jt-06-16-01; 20130361/1); D. *Bulinus globosus* (jt-06-16-01; 20130362/1); E. *Pila ovata* (jt-06-16-02; 201303603); F. *Lanistes ovum* (from mbuga soil; jt-06-04-04; QG 5610); G. *Cleopatra mweruensis* (from Ukia well; G.66848); H. *Lentorbis junodi*? (jt-06-16-01; 20130364/1); I. *Ceratophallus natalensis*? (jt-06-16-01; 20130365/1); J. *Afrogyrus coretus* (from Ukia well; G.66850); K–M. *Bulinus forskalii* (from Ukia well; G.66828–G.66830); N. *Lymnaea natalensis* (jt-06-16-01; 20130366). Scale bar: 3 cm for A, B, E, F; 2 cm for C & D; 1 cm for G–N.

shells washed onto the shoreline from the land or neighboring marshy habitats. Taphonomically, very similar mixtures of highly abraded lacustrine molluscs mixed with well-preserved riverine or terrestrial molluscs are commonly found on sandy beaches of Lake Tanganyika today (McGlue et al., 2009).

Organic-rich silts with caliche nodules overlie the lacustrine sediments and rest on an unconformity. They contain rare, large specimens of *B. pfeifferi* (Fig. 10, J) and common, thin-shelled but very well preserved, large land snails (*B. nilotica* [Fig. 5B], *L. martensiana*, *Tropidophora* sp. and a variety of smaller taxa) that tend to be scattered throughout the sediment. These silts frequently contain scattered specimens or size-sorted 'nests' of very abraded lacustrine taxa, including *Lavigeria*, *Melanoides*, *Coelatura*, and *Pisidium* that appear to have been transported into what we interpret as a marshy depositional environment.

The small collection reported by Smith (1906) was obtained from "a cliff or ridge, about six feet [2 m] high, in the northwest of the Rukwa Valley", and is mainly of historical value. It consists of a worn specimen of a conical, high-spined species of *Bellamya* (*Bellamya* cf. *kalingwisensis*) that has a body whorl with a flat-sided profile (Fig. 10, E), a shell of *L. ovum*, two valves of *Corbicula* sp. and some indeterminate fragmentary unionoids preserved in pebbly carbonate-cemented sand. The fragments of *Melania* referred to by Smith (i.e. *Melanoides*) are no longer in this collection.

For completeness we also report on the mollusc collection from the Ukia well site (Fig. 12), which was originally identified by W. Adam (McConnell, 1950). We have checked the identifications and updated the nomenclature. The sample is distinct from those reported above by the overwhelming abundance of freshwater pulmonates. The small aquatic *B. forskalii* (Fig. 12, K–M) is numerically dominant, but the land snails *Succinea* sp. (*badia* of Cox, 1939 and Adam) and *Pseudopeas* sp. are also common. Other aquatic pulmonates are rare and include *Bulinus* cf. *truncatus* and *Afrogyrus coretus* (Fig. 12, J). Some caenogastropods occur in the sample as well: *L. ovum* and the seemingly correctly identified *Cleopatra mweruensis* (Fig. 12, F–G), which is represented by two worn and broken shells; this is the only occurrence of *Cleopatra* known from the Rukwa Basin. Also present is a taxon we questionably refer to

as *Gabbiella*? sp. 4, which was previously unidentified and absent from McConnell's (1950) list. The cerithioid taxa *Lavigeria* and *Melanoides* are absent from the fauna and so are bivalves. The small and thin-shelled snails preserved in this assemblage show no sign of having been transported. The presence of *B. forskalii*, *A. coretus* and the land snail *Succinea* indicates that the deposit was likely formed in a marginal and possibly seasonal pool or in swampy backwater that was rich in aquatic vegetation (Brown, 1994; Verdcourt, 2007).

**3.2.2.2. Fossil molluscs from the southern Rukwa Basin.** The oldest mollusc outcrop in the southern part of the Rukwa Basin is preserved at Zira Bridge (DD738; Table 1 and Fig. 1) and contains 11 or 12 species of gastropods and bivalves. With a date of  $22,990 \pm 280$  cal yr BP, it predates the ~15 ka lowstand of Paleolake Rukwa. Its caenogastropods comprise *Bellamya* cf. *capillata* (Fig. 11, F), of which the penultimate whorl has a remarkably angulated shoulder compared to the more rounded shoulders of more apical whorls and the body whorl; an undescribed *Lavigeria* species (sp. 1; Fig. 11, I–K); rare African indigenous *M. tuberculata* morph J; (Fig. 11, H); and two *Gabbiella* species, a common smaller one (sp. 2; Fig. 11, N) and a rare larger species that has a much higher spire (sp. 3; Fig. 11, L). The pulmonates include a common *Biomphalaria* species with rapidly expanding whorls and a strongly downward deflected adult aperture that we refer to as *B. cf. pfeifferi* (Fig. 11, Q), and which also occurs rarely in the northern outcrops. Also present are *Bulinus* cf. *truncatus* (Fig. 11, M and O) and a much rarer *Ferrissia* species (Fig. 11, S). Two unionoids are present as well: the large, unsculptured and thick-walled *Coelatura* cf. *horei* (Fig. 11, E) and a more fragile, sculptured and elongated *C. cf. mossambicensis*-like species (Fig. 11, D). Furthermore *Pisidium* cf. *giraudi* with concentric ridges is common (Fig. 11, P and R). This assemblage suggests deposition in a shallow-water setting that captured faunal elements from a sandy to muddy substrate benthic community (mainly consisting of caenogastropods and unionoids), as well as smaller and more fragile species (pulmonates) that had a cryptic, plant-dwelling lifestyle inhabiting aquatic vegetation in calm waters.

The outcrop at the Songwe–Galula gully ( $22,010 \pm 320$  cal yr BP; DD736) is slightly younger than that at Zira Bridge, but at 14 km distance is geographically close. However, mollusc material is much more scarce here and the most abundant taxon is the strongly ornamented *Coelatura* cf. *rukwaensis*/cf. *ujijiensis* (Fig. 11, C), which is less elongate, has a less strongly developed anterior side and an umbo that is less dorsally protruded than *C. cf. mossambicensis* from Zira Bridge. The shell is also thicker, has a more strongly developed hinge and a coarser and more uniform sculpture that extends over the complete surface of the shell. Whereas the sculpture in *C. cf. mossambicensis* consists of strong zigzags with two rows of somewhat stronger developed nodules, the sculpture in *C. cf. rukwaensis*/cf. *ujijiensis* has weaker zigzags with thickened ridges following the growth lines; there are no rows of stronger developed tubercles, and, though potentially just environmental variation, specimens from these deposits show periods of reduced growth. The material is regularly more elongate and more angulated at the posterior end of the hinge plate than *C. rukwaensis*; it also has a sharper, more protruded umbo and, hence, in general shape resembles *C. ujijiensis*, although the illustrated specimen (Fig. 11, C) displays affinities to *C. rukwaensis* better. Other molluscs, all smaller than the abovementioned *Coelatura* species, are poorly preserved, but the abraded material indicates the presence of *Lavigeria*, *Melanoides*, *Bulinus*, *Corbicula*, and *Pisidium*. Whereas *Corbicula* is absent from the Zira Bridge samples, it appears to have been common here.

Another fossiliferous outcrop with an early Holocene age occurs in the Songwe–Galula gully ( $8910 \pm 90$  cal yr BP; DD734). Only large bivalves have been sampled from this outcrop; potentially the absence of smaller species is due to the hand-picked nature of the material. *Iridina spekkii*, *Etheria elliptica*, *Coelatura* cf. *horei*, and a worn valve of a *Chambardia* species are present. More and better-preserved material is required to identify the *Chambardia* find. The corrosion and abrasion of these thick-shelled species and the large grain sizes of the sediment suggests a high-energy environment, so that the absence of smaller species alternatively may be the result of taphonomic bias; recollection is required to determine which causal factor applies.

Our final sample from the south of the Rukwa Basin was collected by one of us (Grove, 1983) at the site ~3 km southwest of Galula and dated to  $7270 \pm 60$  cal yr BP. It has been examined by Brown (1994) and Mandahl-Barth (1957), who recorded a total of 12 species. These comprise *Pisidium* cf. *giraudi*, an unidentifiable planorbid, a few juvenile *Bulinus* cf. *truncatus*, the two *Gabbiella* species recorded at Zira Bridge, isolated calcareous opercula attributable to *Gabbiella*, the undescribed *Lavigeria* species also found in other deposits of the south (Fig. 11, I–K), the African indigenous *M. tuberculata* morph J that was mentioned earlier (Fig. 11, H), and two *Bellamya* species. The first small and broad *Bellamya* species (*Bellamya* sp. 1) has strongly inflated whorls that lack a shoulder but have deeply inset sutures; it also has a large aperture. Overall the shell has a regularly conical spire; it resembles *B. capillata* though is unlikely to be conspecific. *Bellamya* sp. 2 (Fig. 11, G) is larger and has 5.5 whorls that are strongly inflated like in the first species. However, in comparison to this first species they have a more strongly developed shoulder and overall the shell has a cyrtocoid shape. Mandahl-Barth (1957) added three bivalves (unionids?) to the list, which he appears to have retained for further study and we were unable to locate these specimens.

The material from the southern part of the Rukwa Basin is generally much better preserved than that from the north (compare Figs. 10 and 11). The preserved deposits of the south are suggestive of a low-energy environment and minimal post-mortem transport. They were likely formed in calm, shallow-lacustrine environments that were rich in vegetation, with open patches of sandy substrates. The higher energy conditions of the north end of the lake are consistent with both predicted prevailing wind patterns and the development of the Ilyandi Sand Ridge. The exclusively lacustrine nature of the southern deposits is corroborated by the absence of land snails, which were frequently obtained from deposits in the north.

## 4. Discussion

### 4.1. Comparison of faunal assemblages from the Rukwa Basin

Our samples indicate that the Rukwa Basin should be viewed as having two regions, north and south, that differ in lithofacies (as mentioned above) and consistent with earlier interpretations by Delvaux et al. (1998) and Delvaux and Williamson (2008), taphonomy and faunal assemblages. Mollusc fossils from the southern region are much better preserved than those from the northern region (compare preservation in Figs. 10 and 11). The northern shores of Paleolake Rukwa would likely have had strong wave reworking because of southeasterly prevailing winds running the length of the lake, which could explain the preservational difference. Also, carbonate coatings are much more common on fossils from the northern region than on those from the south, which indicates different calcium carbonate saturation conditions in the two regions.

Taxonomic species richness is considerably greater in our collections of ostracodes and molluscs from the southern region than from those in the north. The ostracode genera *Romecytheridea* and *Tanganyikacypridopsis* are present in the south but not in the north. Freshwater mollusc communities are also richer in the south, including at least six bivalves, *Coelatura* cf. *mossambicensis*, *Coelatura* cf. *rukwaensis*/cf. *ujijiensis*, *Coelatura* cf. *horei*, *I. spekkii*, *Chambardia* sp., *Etheria elliptica*, a new *Lavigeria* species, and three *Bellamya* species that do not occur in the north. Samples from the south also contain a much richer freshwater-pulmonate community. The only exception is a wide array of *Melanoides* morphs that occurs in the north but not in the south. Differences among the samples within each region (north and south) are smaller, both for ostracodes and molluscs. For example, ten of the twelve freshwater molluscs reported by Cox (1939) from the Rungwa River section also occur in samples from the Ilyandi Sand Ridge (jt-06-09-07/8). This includes the co-occurrence of the same *Melanoides* morphs, which moreover suggests that these deposits are of similar age, given the propensity and rapidity with which sympatric *M. tuberculata* morphs may generate new morphs (Samadi et al., 1999). The differences among samples in the south are generally more pronounced than among those in the north, which probably relates to the larger timespan covered by deposits from the south. The differences between assemblages from the two regions may additionally be influenced by differences in the time of deposition, but perhaps mainly by differences in the depositional environments and nearby habitats. The most obvious difference in depositional environment is indicated by the presence of land snails and swamp molluscs in the northern but not in the southern deposits.

Paleolake Rukwa assemblages of Late Pleistocene (~22 cal ka BP) and early Holocene (~10–5 cal ka BP) ages are very similar in composition, at least at the genus level. This suggests that the fauna persisted in Paleolake Rukwa through a lowstand in the terminal Pleistocene (~15–13 cal ka BP), a period of considerable environmental stress, when Paleolake Rukwa was reduced to a depth and area similar to today. Some new elements with affinities to extant endemic taxa in Lake Tanganyika appear in younger deposits (9.0–8.8 cal ka BP), e.g., *I. spekkii* and *Coelatura* cf. *horei*. This implies that some faunal exchange may have occurred intermittently, potentially in a period when very high lake levels were observed in the Rukwa Basin (particularly between ~13.5 and 9.0 cal ka BP; Thevenon et al., 2002; Vincens et al., 2005; Delvaux and Williamson, 2008). Thus, the fauna suggests that there may have been more faunal persistence through the LGM in the Rukwa Basin than previously assumed. The alternative scenario that the molluscs and ostracodes were eradicated during an intermittent lowstand and that the lake was recolonized by very similar faunal assemblages is unlikely given the diverse nature of the faunal affinities we discuss below.

The strongest contrast in faunal assemblages over time is the one obtained upon comparing fossil samples (both for ostracodes and

molluscs, from both the north and the south) with the extant fauna. Fossil samples are considerably more diverse than modern samples for ostracodes and caenogastropod molluscs. The exception to this is the sample from the Ukia well site. This undated sample is faunistically similar to the extant fauna, suggesting that it may represent (sub)recent (i.e., late Holocene) material. The ostracode community in modern samples is almost entirely composed of the cosmopolitan *L. michaelsoni* and lacks the numerous taxa found in the fossil samples. The modern aquatic mollusc communities mainly consist of pulmonate gastropods (e.g., *B. forskalii*) and unionid bivalves (*Chambardia* and *Mutela*) that have not been found (except for one fossil *Chambardia* valve from the southern Rukwa Basin) as fossils.

None of the fossil caenogastropods (*Bellamyia*, *Lavigeria*, *Melanoides*, *Gabbiella*) has been recorded in the modern Rukwa fauna and the few caenogastropods that currently occur in the basin are ampulariids, which can aestivate during dry periods. These differences could be partially explained by the limited sampling of the modern fauna. However, more differences exist in the pulmonate gastropod community and it remains noteworthy that the modern community consists entirely of widespread taxa (although some of these are in need of taxonomic revision). An overall comparison of the characteristics of the modern community with those of the fossil assemblages from the Rukwa Basin strongly suggests faunal discontinuity since the middle Holocene (after the youngest paleontological sample; ~5.5 cal ka BP). This is corroborated by the suggestion of an extreme drawdown of Paleolake Rukwa between 4.4 and 3.0 cal ka BP (Talbot and Livingstone, 1989; Thevenon et al., 2002), after which the shallow and moderately saline current lake originated.

#### 4.2. Evidence of intralacustrine evolution in the Rukwa Basin

The fossil assemblages sampled in the Rukwa Basin contain a number of taxa that appear to be endemic to the basin. Cox (1939) described four new species, three belonging to *Lavigeria* (two of which we tentatively lumped together, pending detailed reexamination) and one to *Coelatura*. None of these was subsequently found outside the Rukwa Basin, in spite of extensive malacological surveys on Lake Tanganyika, its tributaries, and detailed study of many large and new collections of *Lavigeria* species from Lake Tanganyika (E.M., J.T.). The new material we report on here reveals several other undescribed taxa, some of which are closely related to species that are currently endemic to Lake Tanganyika (as we point out below). Candidates for new species among the molluscs belong to the genera *Lavigeria*, *Bellamyia*, *Melanoides* (though the parthenogenetic nature of this genus complicates species recognition), and *Gabbiella*. Among the ostracodes there are new species of *Sclerocypris* and *Hemicypris*, which do not show Tanganyikan affinities, and possibly also in the genera *Cyprideis*, *Romecytheridea*, *Tanganyikacypridopsis*, and *Gomphocythere*, which include Tanganyikan endemics. Like the taxa described by Cox (1939), some of these new species were probably confined to the Rukwa Basin. Expanded sampling in the Rukwa Basin is needed to provide more accurate insights into the temporal and geographical occurrence and the succession of faunas in the basin before we can engage in detailed formal descriptions of new taxa.

Whereas some of the new ostracode species are very similar to congeners in Lake Tanganyika, and may be derived from immigrants that colonized the Rukwa Basin, the mollusc material reported here of *Lavigeria*, *Bellamyia* and *Melanoides* strongly suggests that diversification has also occurred within intralacustrine environments in the Rukwa Basin. This suggests that the Rukwa Basin was not merely a sink for arriving immigrants. It is noteworthy that our fossil assemblages cover a long period (~23 to 5.5 cal ka), creating promising possibilities for time-series analyses of faunal succession and evolution over an interval that spans major phases of environmental change, e.g., the Pleistocene–Holocene transition.

#### 4.3. Faunal affinities and biogeography

##### 4.3.1. Lake Tanganyika

Cox (1939) already recognized that some of the fossil molluscs from the Rukwa Basin (herein reassigned to *Lavigeria*) are part of a clade that was up to then considered to be endemic to Lake Tanganyika. We report more examples of molluscs from the Rukwa Basin that up to now have been considered to be endemic to Lake Tanganyika (e.g., *Coelatura* cf. *horei*; *I. spekii*) and have made the first examination of such faunal affinities for ostracodes. Ostracode fossils belonging to several unrelated species also show strong affinities to extant Tanganyikan endemics. We demonstrate important similarities in fossil *Cyprideis* and *Gomphocythere* specimens from the Rukwa Basin to Lake Tanganyika endemics and discovered the presence of *Romecytheridea* and *Tanganyikacypridopsis*, genera previously only known from Lake Tanganyika, in the Rukwa Basin. Surprisingly, the fossil assemblages with the closest taxonomic ties to the modern fauna of Lake Tanganyika were collected from the southern Rukwa Basin, hence furthest away from Lake Tanganyika and possible hydrographical connections. However, this may have more to do with specific local paleoecological conditions at the time of deposition than with biogeography, and it is premature to interpret this finding as significant given the limited material available.

Some of the ostracode and mollusc taxa from the Rukwa Basin are very similar to endemics of Lake Tanganyika, but it is also noteworthy that some of these appear to have undergone intralacustrine diversification in the Rukwa Basin (see section above). Hence, some parts of the lacustrine ecosystem in the Rukwa Basin may have acted both as a source and a sink for the biological diversity of Lake Tanganyika. The long history of lacustrine environments in the Rukwa Basin (Morley and Wescott, 1999; Morley et al., 1999; Roberts et al., 2012) only increases the significance of organismal evolution in the Rukwa Basin for understanding the development of biological diversity in Lake Tanganyika and elsewhere in tropical Africa.

##### 4.3.2. Other biogeographical affinities

Some taxa in the Rukwa faunas have affinities with other bioprovinces in tropical Africa (beyond Lake Tanganyika). All of the modern and many of the fossil Rukwa ostracodes are broadly distributed in tropical Africa and typically occupy (mostly) shallow, mildly alkaline lakes and ponds. The exception to this pattern (beyond the aforementioned taxa with affinities to Tanganyikan endemics) is *H. kliei*, which was found in the Ukia well, at Galula and as an isolated individual in the northern Rukwa Basin deposits. This benthic (crawling) ostracode was previously only known from the saline and alkaline Lake Turkana (Kenya) where it lives in shallow (<3.5 m), mostly vegetated areas and embayments (Cohen, 1986).

Like the ostracodes, some fossil molluscs from the Rukwa Basin are closely related to taxa that do not currently occur in Lake Tanganyika (nor have they been recorded in its fossil record). Examples include *Bellamyia* and *Gabbiella* species, the *Melanoides* morphs, *Coelatura* cf. *mossambicensis*, *Corbicula* cf. *fluminalis*, and several pulmonates. Some of these taxa may have widespread distributions (e.g., some pulmonates), whereas others (*Bellamyia* and *Melanoides*) share morphological features with taxa that currently inhabit the Malawi Basin (Zambezi drainage) and the Mweru Basin (Congo drainage). These possible paleobiogeographic relationships have yet to be validated with detailed systematic study, but they are concordant with the results of biogeographic analyses of several fishes (e.g., Roberts, 1975; Seegers, 1996). The Rukwa Basin lies at the triple junction of three ichthyological provinces: the Malawi/Zambezi drainage; Lake Tanganyika; and the rivers of the East Coast of Africa (Roberts, 1975). In an extensive study, Seegers (1996) concluded that the fish fauna of the Rukwa Basin shares affinities with all three bioprovinces, testifying to the interconnectivity of these watersheds through time. In contrast to the molluscs and fish, the fossil ostracodes of the Rukwa Basin have no apparent direct relationships



with the fauna of Lake Malawi, the Zambezi or eastern coastal regions, but ostracode collections from the latter two regions remain very sparse.

Biogeographic scenarios of faunal exchange are only speculative without detailed information on geological events and their impact on hydrographical connections on the one hand and a wide spatial sampling, a robust phylogeny and an adequate fossil record (e.g., to date phylogenies so that geological events and phylogenies can be independently dated and correlated) on the other. A single reported case (to our knowledge) allows an integrated approach and demonstrates the biogeographical relevance of rifting and tectonic changes in the larger Rukwa region. This is the case of *Lanistes* gastropods and the development of the Rungwe Volcanic Province (RVP), which separates the southern Rukwa Basin from the Lake Malawi Rift. The development of the RVP disrupted paleohydrographical connections of the Rukwa region and areas to the north from those to the south of the RVP. The period over which the RVP developed (oldest volcanism ~7.25 Ma; Ebinger et al., 1989) coincides with molecular clock estimations on the divergence in the sister pair ((Malawian *Lanistes* + *Lanistes ellipticus*), *Lanistes purpureus*) (Schultheiß et al., 2009). The ancestral *Lanistes* lineage occupied a large hydrographically connected area, but development of the RVP and associated drainage reversals caused hydrographic disruptions. As *Lanistes* requires hydrographic connections for dispersal (e.g., Van Bocxlaer et al., 2011), the hydrographic disruption seems to have confined part of the ancestral *Lanistes* lineage to more southern regions (Lake Malawi and the Zambezi) and the other part to more northern regions (extending to Zanzibar). This presumably caused allopatric divergence leading to the sister group relationship documented by Schultheiß et al. (2009).

The cladogenesis in *Lanistes* and the mixed zoogeographic relationships of the fish from Lake Rukwa as reported in Seegers (1996) indicate that the larger Rukwa region has been of major importance in East African aquatic biogeography. Only a handful of studies actually report samples from the Rukwa Basin itself, so that this region has been a biogeographic *terra incognita* on the African map. However, additional neontological studies are unlikely to shed much light on the role of Lake Rukwa in shaping the history of aquatic biodiversity in the region because of the near desiccation of Paleolake Rukwa between ~4.4 and 3.0 cal ka BP, and with that, the extirpation of much of the aquatic fauna. This renders the fossil assemblages in the Rukwa Basin invaluable to our understanding of the biogeography of this part of tropical Africa.

#### 4.4. Dispersal mechanisms

The Rukwa Basin fauna includes elements that share affinities with the endemic fauna of Lake Tanganyika, and elsewhere in Africa like the Lake Mweru area. Furthermore, intralacustrine evolution appears to have taken place in the Rukwa Basin. Interestingly, the phases showing evidence for intralacustrine evolution appear to coincide with periods during which the Rukwa fauna shared conspicuous affinities with the fauna of Lake Tanganyika. Through its history the faunal affinities of taxa in the Rukwa Basin have changed, and these alterations suggest that a variety of mechanisms were responsible for dispersal of faunal elements to and from the Rukwa Basin. Moreover it suggests that the relative importance of each of these mechanisms has varied over time. Two main categories of dispersal mechanisms exist for freshwater biota, i.e., mechanisms that depend on the existence of freshwater connections, and those that do not.

Although Paleolake Rukwa periodically overspilled into the Tanganyika Basin via the Nkamba/Ifume Rivers, there is no evidence that Lakes Tanganyika and Rukwa would ever have been united into one single lake. Precambrian structural highs separate the two lakes and no sedimentary deposits or geological structures exist in support of a surface-level connection (i.e., a single megalake; e.g., Rosendahl, 1988; Morley and Wescott, 1999; Morley et al., 1999). High lake-stand terraces and other lake deposits indicate that on multiple occasions during the

Quaternary, and as recently as the early Holocene, Lake Rukwa was a deep (>200 m), dilute, Ca-rich and, along its shoreline, wave-swept rift lake, not unlike modern Lake Tanganyika (Delvaux et al., 1998). At its maximum highstand, water from Lake Rukwa overflowed into Lake Tanganyika through the Karema Gap (McConnell, 1950; outlet channel, Figs. 2 and 3). During these intervals, ostracodes and molluscs may have dispersed via the river connecting the two basins, either under their own power or transported passively by fish. The latter scenario is particularly likely for unionid bivalves, because they have a larval stage that is parasitic on fish (Graf and Cummings, 2006). However, other organisms may occasionally be transported by fish too (e.g., through consumption and live excretion; see Vinyard, 1979; Brown, 2007). This dispersal scenario is perhaps supported by the occurrence of a number of extant fish species that are restricted to the Rukwa–Tanganyika area, but occur in both lakes (Ricardo, 1936; Seegers, 1996). In any case, faunal dispersal under this scenario suggests that the permeability of the biogeographic boundary between both bioprovinces increased at least temporarily since the late Pleistocene. The habitats provided by the river that connected both lakes would have been substantially different from those existing in both lakes. Overcoming these differences would have been difficult. Species of Lake Tanganyika's extant endemic fauna are rarely found in the lake's surrounding rivers, most likely because of the strong physicochemical and biological contrasts between the two types of waterbodies. Most influent streams entering Lake Tanganyika have high suspended-sediment loads (inimical to the Lake's invertebrate fauna, see Cohen et al., 2005) and are dilute in Ca and carbonate plus bicarbonate, which is unfavorable for the heavily calcified molluscs and ostracodes endemic to Lake Tanganyika today. However, based on the paleochemistry of Paleolake Rukwa and the low suspended-solids loads typical of outflow rivers from lakes, the Paleolake Rukwa outflow was probably a clear water stream with a Ca-rich water chemistry (not too dissimilar to Lake Tanganyika). In such a circumstance, the river's compositional contrast with Lake Tanganyika waters would have been minimized. In fact, the environmental conditions at the Paleolake Rukwa outlet may have been closely analogous to the modern Lukuga River outlet of Lake Tanganyika itself, where a clear water, Ca-rich river hosts a remarkable fish fauna of numerous Tanganyikan "endemic" fish species as much as 100 km downstream of the lake's outlet, species which are unknown in any of the numerous low-salinity influent streams nearby (Kulander and Roberts, 2011).

The second scenario is that of dispersal in the absence of freshwater connections. Whereas some aquatic organisms may, at least over short distances, disperse actively outside the water, freshwater ostracodes of the genera reported here and molluscs are not able to do so over distances beyond perhaps a few meters. Hence they rely on passive zoochoric dispersal, e.g., via waterfowl, if no aquatic connections exist. Passive transport of propagules by waterfowl, internally or externally, has long been known as a mechanism of dispersal for aquatic macroinvertebrates between waterbodies that lack hydrographic connections (Lyell, 1832; Boag, 1985; Green and Figuerola, 2005; Van Bocxlaer et al., 2011). Zoochoric dispersal via waterfowl would result in a faunal composition that is biased towards opportunistic wide-spread taxa, which were potentially obtained from multiple source areas. The extant fauna of the Rukwa Basin consists of taxa, such as pulmonates, that are much more prone to zoochoric dispersal in the absence of freshwater connections than the species recorded in the fossil assemblages.

The current fauna is likely to have colonized the Rukwa Basin after the near desiccation of Paleolake Rukwa between 4.4 and 3.0 cal ka BP. Because lake levels were generally low in the Rukwa Basin since that period, very few opportunities for dispersal via freshwater connections would have existed. Hence, the extant fauna is dominated by: (1) taxa that are able to disperse zoochorically over long distances out of the water (pulmonate snails, veneroid mussels, and limnocytherid ostracodes); (2) taxa that can aestivate in the absence of water (ampullarid snails, some unionid bivalves, limnocytherid ostracodes);

or (3) taxa that have increased dispersal possibilities via their mobile fish hosts (unionid bivalves). Since the early Holocene, no hydrographic connection has existed between Lake Tanganyika and Lake Rukwa, and it is important to note that Tanganyikan taxa with relatively poor “out-of-water” dispersal capabilities have apparently been absent from Lake Rukwa since the salinization of the lake at its maximum during the late Holocene drawdown (e.g., *Lavigeria*, *Coelatura* and *Iridina*). Furthermore, two of the ostracode taxa, *Gomphocythere* and *C. mastai*, live in sublittoral habitats on soft substrates (Wouters and Martens, 1994; Wouters and Martens, 1999; Park and Martens, 2001). Hence, beyond their biology being poorly adapted for dispersal outside the water, their opportunities for interactions with waterfowl seem limited to non-existent. Beyond the taxa with Tanganyikan affinities, some other taxa preserved in the fossil assemblages of the Rukwa Basin, e.g., *Bellamyia*, are also poorly adapted to dispersal in the absence of hydrographic connections. Their presence in fossil assemblages in the Rukwa Basin may reflect shifts in headwater boundaries or alternatively, and perhaps less likely, their long-lasting persistence within the basin.

#### 4.5. Conclusions

The material reported on in this paper comprises all mollusc and ostracode samples currently known from the Rukwa Basin, and although the collections are limited, especially for the extant molluscs and ostracodes, these collections shed new light on East African aquatic biogeography.

Our samples offer an important faunal time-series spread over the last 25 cal ky, a period with extensive climatic fluctuations (Haberyan, 1987; Barker et al., 2002; Thevenon et al., 2002; Vincens et al., 2005) over which the biological history of the Rukwa Basin is currently poorly known. Studying fossil ostracode and mollusc assemblages from the northern and southern regions of the Rukwa Basin revealed notable differences in taphonomy, depositional environments and faunal composition. Within each region, the fossil assemblages are much more similar than compared to those of different regions. However, the largest faunal differences are observed upon comparing the diverse ostracode and mollusc faunas of the fossil assemblages with the extant fauna. These observations suggest faunal continuity during low lake-level phases in the terminal Pleistocene (~15.0–13.5 ka; Thevenon et al., 2002; Delvaux and Williamson, 2008), but that faunal extirpation occurred in a later desiccation event between ~4.4 and 3.0 cal ka BP (Talbot and Livingstone, 1989). A number of the fossil ostracode and mollusc taxa reported on here have not yet been described and may be endemic to the Rukwa Basin, like the four mollusc species that Cox (1939) described. The close resemblance of some species to their congeners within the basin, compared to relatives outside is highly suggestive of intralacustrine speciation having taken place within the Rukwa Basin. Several ostracodes and molluscs from the Rukwa Basin, including some that may have had intralacustrine origins, show biogeographic affinities to extant endemics of Lake Tanganyika, but others are more closely related to the fauna of other bioprovinces in tropical Africa. The latter is particularly true for the modern fauna of Lake Rukwa. The predominant mode of dispersal to and from the Rukwa Basin may have varied over time. Hydrographical connections that left geomorphologic evidence (Fig. 2) may have allowed the dispersal of fossil ostracodes and molluscs between the Tanganyika and Rukwa Basins, and this scenario can likewise apply to other fossil taxa that have more widespread congeners. However, the modern fauna appears to derive mainly from an accumulation of taxa that were dispersed in the absence of hydrographic connections.

Specifying the role that the Rukwa Basin played in the late Cenozoic biogeography of tropical Africa remains a challenge given (1) the long history of rifting and lacustrine conditions in the Rukwa Basin (Morley and Wescott, 1999; Morley et al., 1999; Roberts et al., 2012); (2) the potential existence over substantial periods of ecosystems in the Rukwa Basin that functioned as satellites (with intermittent faunal

exchange) to Lake Tanganyika and in which intralacustrine evolution appears to have occurred; and (3) the multitude of geological, environmental and climatological changes associated with the complex rifting in the Rukwa region. However, currently available data on fish and invertebrates clearly indicates that the Rukwa Basin has strongly affected the aquatic biogeography of tropical Africa. Unfortunately, many of the molecular traces of this history were probably erased from the modern fauna during Paleolake Rukwa's drawdown between 4.4 and 3.0 cal ka. Hence, paleontological studies of Rukwa faunas are essential to reveal the role of the Rukwa Basin in the biogeography of tropical Africa and to enhance our knowledge on how rift development affected faunal evolution in the southern part of the East African Rift. More extensive sampling in the basin, and a subsequent increase in resolution, may eventually allow us to unravel faunal interactions between the Rukwa Basin and its surroundings, yielding improved insight into potential phases of intralacustrine evolution in Lake Rukwa. This will help structure our understanding of East African freshwater evolution in general.

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