Archiv für Molluskenkunde | 153 (1) | 61–86 | Frankfurt am Main | 22 March 2024

A Quaternary sequence of terrestrial molluscs from East Africa: a record of diversity, stability, and abundance since Marine Isotope Stage 5 (78,000 BP)

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Abstract. A Quaternary sequence of subfossil terrestrial molluscs from tropical Kenya is described and discussed. It preserves a remarkably complete fauna of the Indian Ocean coastal forest from the surroundings of Panga ya Saidi cave, a site featuring repeated human occupation extending back at least 78,000 years. Mollusc diversity, composition, and abundance are very similar to extant faunas of the coastal forest. They vary relatively little over the period studied (chiefly a 50,000-year sequence from MIS 5 to the start of MIS 2) apart from a short-lived decrease in the dominance of "forest-only" species around 45,800 BP. The fauna of the most recently preserved layers (MIS 1) is likewise similar. Most of the 72 snail (and slug) species found are still extant at the coast, including some narrow-range endemics, but 8 species are now more western in their known distribution. The native African status of *Kaliella barrakporensis* and 2 other snail species with Asian type localities are confirmed, as is the previously disputed occurrence of native Helicoidea at the coast. Two new subfossil species were identified and are described as *Maizania meteor* sp. n. (Maizaniidae) and *Juventigulella saidii* sp. n. (Streptaxidae). No major habitat or faunistic shifts are observed, confirming previous evidence for long-term ecological continuity at the site. The data are the first of their kind from coastal East Africa and provide a new independent proxy of the environmental context to the archaeological sequence, as well as a reference point for future studies of terrestrial molluscs in the region.

Key words. Pleistocene, Kenya, forest, snails, palaeoecology, Panga ya Saidi

ZooBank registration. urn:lsid:zoobank.org:pub:2C283720-1170-46CA-A7EA-56D14C03D911

DOI. https://doi.org/10.1127/arch.moll/153/061-086

Introduction

The terrestrial malacofauna of sub-Saharan Africa remains incompletely described and recorded, though it has lived alongside humans throughout our evolutionary history. Africa has the world's oldest archaeological record, spanning the entire Quaternary period to 2.6 mya, and even back into the Pliocene in Kenya (Harmand et al. 2015). Land snails may thus be found among hominin tools as well as hominin remains. In East Africa, studies record the exploitation of large Achatinidae ("giant African land snails") by humans as food, tools, or sources of shell material from the Pleistocene, throughout the Holocene, and into the present (e.g. Shipton et al. 2016, Walz 2017, Miller et al. 2018, Faulkner et al. 2019). Indeed, shell carbonates from the achatinids *Achatina*, *Burtoa*, and *Limicolaria* have proven useful for the radiocarbon dating of archaeological deposits in the region (e.g. Tryon et al. 2012, Cohen et al. 2013, Eren et al. 2014). Prior to such chronometric dating methods, the similarity of such fossils to extant species had even been considered a disadvantage when attempting to gauge the age of deposits on the basis of shell morphology (Newton 1914, as quoted by Adam 1959: 133).

Owen (1963, 1966) published on the colour polymorphism preserved in Pleistocene *Limicolaria* from Uganda. However, observations on archaeological Achatinidae relate to only a few (<10) East African species of terrestrial mollusc, out of a fauna of over 1200 documented species (Verdcourt 2006). Quaternary or Holocene

E. Schweizerbart'sche Verlagsbuchhandlung and Senckenberg Gesellschaft für Naturforschung ISSN 1869-0963, eISSN 2367-0622

records of the vast majority of species are cursory, despite their potentially being informative ecologically and biogeographically. Published records consist only of short lists of 5–10 snails from Holocene and Pleistocene sites in Kenya (Connolly 1931, Pickford 1995, a few records by Verdcourt 2006). The situation is not dissimilar in southern Africa (e.g. Connolly 1939, Frankel 1964, Davies 1982), and led van Bruggen (1969: 101) to generalise that "the fossil record for Southern African terrestrial molluscs is exceedingly poor and in fact almost non-existent". It is slightly better on Aldabra (van Bruggen 1975) and the Mascarenes (Griffiths & Florens 2006). The state of knowledge contrasts with that of freshwater molluscs, for which Quaternary and Cenozoic faunas and stratigraphies have been documented in detail for Rift Valley lakes (e.g. Adam 1959, Brown 1994, Cohen et al. 2013) and other basin systems (e.g. the Kalahari; Mocke et al. 2016). Even the Cenozoic terrestrial molluscs of East Africa, parts of which are now well described in association with Miocene and Pliocene hominid sites (e.g. Verdcourt 1963, 1987, Pickford 1995, Tattersfield 2011), are better known than later subfossil faunas.

Yet, as shown by their use in dating, Quaternary terrestrial molluscs are preserved in suitable environments in East Africa. Anecdotal evidence suggests that when smaller terrestrial snails are encountered during archaeological fieldwork they are frequently overlooked, unexamined, misidentified as juveniles, or (sometimes advisedly) discounted as fossorial or accidental interlopers (e.g. Walz 2017). Isolated land-snail finds from larger studies of freshwater molluscs or other faunal groups may be similarly disregarded. It is also possible, as throughout the world, that some empty shells encountered at the soil surface in depositional, base-rich environments are in fact Holocene subfossils but not described as such. Terrestrial snails (as well as the internal "slug plates" of Urocyclidae, which can fossilise well) are potentially very useful in the reconstruction of local palaeoenvironments and past distributions. However, this requires that the stratigraphic context of samples is secure, ideally that it is dated, and that it relates to an extant fauna that is well documented enough for comparisons to be made.

Here we report the malacological data arising from an extraordinary sequence excavated from a limestone solution cave in coastal Kenya. The Panga ya Saidi sequence preserves a rich and apparently complete terrestrial malacofauna as far back as Marine Isotope Stage (**MIS**) 5 approximately 78,000 years ago. Interdisciplinary results, including archaeological details of the near-continuous use of the cave by humans, were reported by Shipton et al. (2018). The raw species counts of terrestrial molluscs have already contributed to the palaeoenvironmental reconstruction of the site as being vegetated with forest or woodland throughout this period, during which the site is modelled as having consistently received >1000 mm average annual rainfall (Shipton et al. 2018).

The details of the records are also of faunistic significance. The cave lies on an ecotone between lowland tropical forest (the Coastal Forests Region of Endemism; Burgess & Clarke 2000) and the drier habitats of the Kenyan interior. Forests typically support a higher abundance, diversity, and endemism of molluscs in East Africa, while savannah (a mosaic of woodland, bushland, and grassland) supports a smaller suite of ancient and distinctive specialists (Verdcourt 1972, 2000). Studies in coastal Kenya have examined the habitat preferences of the snail fauna in wooded environments at Arabuko-Sokoke National Park (Lange & Mwinzi 2003) and at Shimba Hills National Reserve (Ndalila 2011). Some species showed strong preferences for (or against) forest habitats, but many were present in at least small numbers in a range of shaded habitat types. There is pronounced narrow-range endemism among the terrestrial molluscs of the coastal forests (e.g. Tattersfield 1998a, Verdcourt 2000, Rowson et al. 2010). However, the non-endemic taxa occur along the coastal strip from Somalia to South Africa or range into the highlands of East Africa, and a few are even recorded on other continents. The material studied is therefore relevant to places and habitats further afield. Our hope is that this publication will help stimulate closer examination of Quaternary and terrestrial malacofaunas in East Africa.

Materials and Methods

Site details and stratigraphy

The site of Panga ya Saidi (PYS) (Fig. 1; 03°40′41.4″S, 039°44′09.4″E) is a karstic limestone cave located around 15 km inland from the Nyali Coast of southern Kenya. It is a large, multi-storey, partially unroofed cave complex. It sits at approximately 150 m a.s.l. on the east-facing escarpment of an outcrop of the Kambe Limestone known as the Dzitsoni Uplands (Helm et al. 2012). These hills run parallel to the coast within a narrow band of Zanzibar–Inhambane vegetation that stretches along the eastern coast of Africa from Somalia through to Mozambique (Shipton et al. 2018). As well as lying within the coastal forest, with its unique biome, PYS is located near the junction of several other environments, including savanna grasslands to the west, lowland tropical forests to the east, and mangrove swamplands at the coast. Multi-proxy palaeoenvironmental reconstructions suggest the area around PYS remained relatively stable throughout the Late Pleistocene and into the Holocene (Roberts et al. 2020, Prendergast et al. 2023).

Archaeological material from PYS shows pulses of human presence at the cave over the past 78,000 years. Nineteen layers have been documented in the 3.5 m sequence, with dates published in detail elsewhere (e.g. Shipton et al. 2018, 2021, Martinón-Torres et al. 2021). More than 20 radiometric dates from the excavated sequence, featuring Bayesian-modelled radiocarbon and luminescence age estimates, indicate that PYS witnessed human activity in each of the last 5 Marine Isotope Stages.

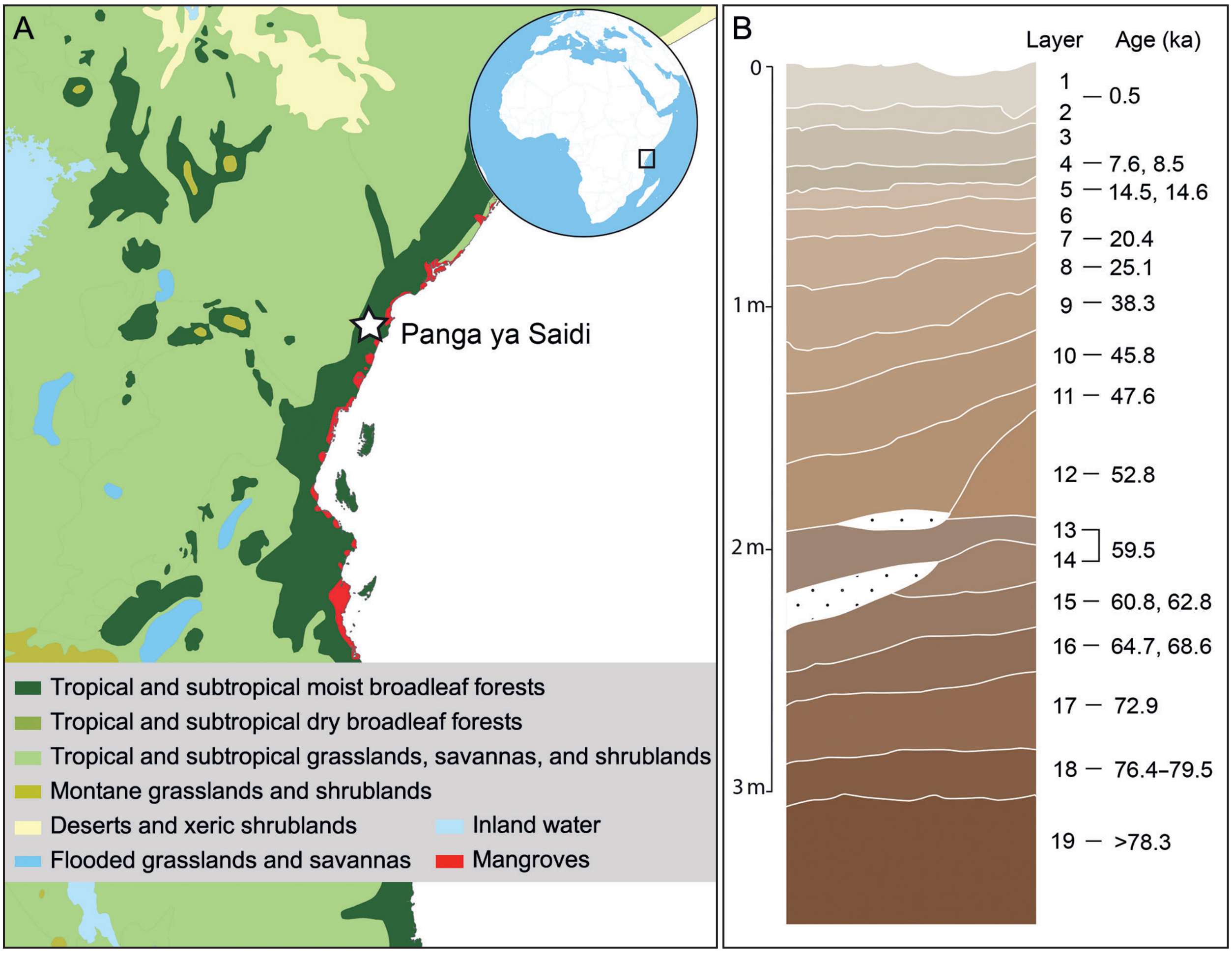

Figure 1. Environmental setting and PYS stratigraphic section. **A.** The location of PYS in the tropical moist forest of coastal East Africa, situated in the Ditzoni upland, southeastern Kenya. **B.** The stratigraphic sequence of PYS showing the layers and published ages. For simplicity, age estimates are shown as the median of the highest Bayesian-posterior-density age range.

Malacological material

The terrestrial molluscs in the present study were recovered from Trench 4 at Panga ya Saidi. Bulk sediment samples were collected from all stratigraphic features and deposits for fine-mesh flotation and wet-sieving to recover archaeobotanical, zooarchaeological, and palaeoenvironmental samples. Where possible, a minimum sample volume of 60 l per context was maintained, with smaller contexts (<60 l) sampled in their entirety, and double samples taken for contexts of particular interest (120 l).

Sediments were processed manually by bucket flotation. A small subsample of sediment (3–4 l) was added to a 10 l bucket and mixed by hand with clean water from the ocean (pre-sieved to remove contaminants). The water and suspended particles were then poured into a 0.3 mm mesh bag to collect charred plant remains and other light organics. This process was repeated until charred remains were no longer visible within the sediment or the floating fraction (usually 5–8 repetitions). Floating fractions were air-dried in the flotation bags and, once dry, were transferred to clean plastic sample bags for storage. Molluscs were extracted from flotation samples from the layers of the site dating to the Last Glacial Maximum (MIS 2) and earlier as far back as MIS 5 (Layers 8–19), as well as the upper 2 layers (Layers 1 & 2) for a recent reference sample.

The shell material is in an excellent state of preservation. Some shells in the uppermost layers even preserve a glassy periostracum (though without hairs or spines) and weak traces of colour bands. Those in lower layers generally show more grey-brown mineral encrustation and infilling or are stained red-brown by the soil. Larger Achatinidae are typically fragmented, apparently by natural breakage. Urocyclid slug plates are thick and infilled by mineral deposits. Juvenile shells are present for most species (including Achatinidae), indicating local reproduction. The taxonomic diversity matches that of the fauna of the coastal forest, the only notable absences being Veronicellidae (which lack an internal shell) and species that are considered to be modern introductions. The fauna is entirely terrestrial, strongly supporting its local origin. The snails are likely to have fallen or been washed into the cave from its immediate surroundings, not transported over longer distances by rivers or floods. The assemblage is very unlikely to have been intentionally assembled by humans or hoarding predators such as mongoose, which typically accumulate only larger shells. Marine molluscs at PYS comprise 37 taxonomic categories, which in contrast were introduced by the cave's human occupants for economic and symbolic purposes and include only shells of a larger size (Shipton et al. 2018, d'Errico et al. 2020, Faulkner et al. 2021).

Flotation samples were sieved through 5 mm, 2 mm, and 0.5 mm sieves, and all mollusc specimens were picked under magnification, sorted into morphospecies, and counted (minimum number of individuals). Species were identified by the first author with reference to the primary literature, collections at the National Museum of Wales, Cardiff, UK (**NMW**), and photographs of other type specimens. It was possible to identify most species with confidence, but others only as "cf." or "sp." where uncertainty remains or the material was too scanty. Two species are here described as new, while 1–3 smaller "subulinid" morphospecies ("*Opeas*" spp.) were treated in aggregate to avoid overinterpretation of these common, but taxonomically poorly defined, small snails (e.g. Rowson et al. 2010; Gittenberger & van Bruggen 2013). Distributional data largely follow Verdcourt (2006, and his unpublished additions), with habitat data from various publications dealing with the molluscs of the coastal forests (e.g. Tattersfield 1998a, Verdcourt 2000, Lange & Mwinzi 2003, Herbert & Kilburn 2004, Rowson 2007a, Muratov 2010, Rowson et al. 2010, Ndalila 2011, Gittenberger & van Bruggen 2013). Nomenclature follows MolluscaBase (MolluscaBase Eds 2023). Authorities for all species names are given in Table 1.

Photographs of examples of all subfossil species are provided (Figs 3–11, arranged by family). The vast majority of the material (98% of specimens, including all species found only as singletons) is available for future studies at the National Museum of Kenya, Nairobi (**NMK**) (site code PYS13), with 401 representative voucher specimens (2%) at NMW (accession number NMW.Z.2014.016).

Analysis

Mollusc data for Layers 17–19 (contexts 423A, 422A, and 420E), and the 2 contexts in Layer 10 (414 and 414C) were pooled owing to the low number of specimens in each. Layers 7 and 8 were represented by a single context (412 "ASH") that had already been pooled because only a very small portion of Layer 7 was excavated in Trench 4. Two small, late contexts were excluded from the analysis on the grounds that they could be intrusions: an animal burrow beneath layer 2 (409), and a hearth between Layers 2 and 1 (406). These yielded 99 and 191 mollusc specimens respectively. All these species were also present in Layers 1, 2, or 7–8, with the exception of *Rhachistia picturata*. This taxon was excluded from analyses because it was present only in the excluded layers.

Relative abundances of each species were calculated as percentages of all shells in each layer and displayed in C2 v. 1.5 (Juggins 2007). To obtain an estimated species richness for each layer, given that the numbers of shells found were unequal, individual rarefaction was conducted in PAST v. 3.14 (Hammer et al. 2001). Brillouin and Shannon diversity indices were also calculated in PAST. The Brillouin index is widely used in stratigraphy, whereas the Shannon index is conventional in surveys of the extant East African snail fauna.

As the ecology (and taxonomy) of this fauna is little known, and subfossil records are so few, there is no existing framework for interpretation of its stratigraphy (unlike in Europe and North Africa, for example). Care was therefore taken not to over-interpret the results. To obtain a measure of the community's habitat preference, based on the very limited ecological data available, species were assigned to 2 habitat groupings as either "forest-only" or "forest-rarely/never" based on the relevant literature, particularly Verdcourt (2000), Lange & Mwinzi (2003), and Ndalila (2011) (Table 1). This was done as strictly as possible, meaning that many species could not be assigned to either category.

Results

Richness and abundance

In total, from flotation of 960 l of sediment, the excavation of Trench 4 at Panga ya Saidi yielded 16,757 specimens of terrestrial molluscs, belonging to 72 morphospecies. The biostratigraphy, using relative abundance, is summarised in Figure 2. The species recorded are listed in Table 1 with existing habitat details. The number of individuals recorded is given in Table 2, with the details of each layer and diversity indices given in Table 3.

The number of individuals per layer varied substantially, from 221 to 5,668 (mean 1,372), and the number of species varied from 25 to 54 (mean 33). Following rarefaction to the number of individuals (221) in the smallest sample (Layer 13), the estimated number of species per layer was between 23 and 38 throughout the sequence (see Fig. 2 and supplementary fig. 22 in Shipton et al. 2018). When rarified to 221 individuals, the largest sample (Layer 9) is slightly less diverse (23.8 species) than the smallest (Layer 13). Most layers were therefore highly diverse, even when accounting for the varying number of individuals found, and this pattern was maintained throughout the sequence.

Values of the Shannon index ranged from 2.1 (Layer 13) to 3.2 (Layer 10). These were the same layers in which the minimum and maximum Brillouin index values were found. The differences between the 2 indices were small. Most species were of rare occurrence, contributing less than 5% of the shells in each layer, whereas the 10 most abundant species in total accounted for 13,342 shells (81% of all individuals). Species making up at least 10% of the shells in at least 1 layer were *Juventigulella habibui*, *Dadagulella radius radius*, *Subulina intermedia*, *Opeas* sp./spp., *Trachycystis lamellifera*, and urocyclid slugs. Both

Table 1. Terrestrial mollusc species found as subfossils in the Panga ya Saidi sequence, taxonomic authorities, habitat data from the literature, and habitat groupings.

Identification (classification follows MOLLUSCABASE EDS 2023)		Known habitat and distribution				Habitat-group assignation
Family	**Species**	**Coastal Kenya and Tanzania (VERDCOURT 2000)**	**Arabuko-Sokoke National Park, coastal Kenya (LANGE & MWINZI 2003): MF = mixed forest; BW = *Brachystegia* woodland; CT = *Cynometra* thicket**	**Shimba Hills National Reserve, coastal Kenya (NDALILA 2011): forest, scrub, plantation**	**Distribution (all sources)**	
Cyclophoridae	*Cyathopoma azaniense* Verdcourt, 1978				Extant at coast	Unassigned
Hydrocenidae	*Hydrocena tanzaniensis* Verdcourt, 2004				Now inland	Forest-only
Maizaniidae	*Maizania volkensi* (E. von Martens, 1895)				Extant at coast	Forest-only
	Maizania meteor new species				?	Unassigned
	Maizania wahlbergi (Benson, 1852)	Forest	Preferred MF	As *M. hildebrandti*; forest and scrub	Extant at coast	Unassigned
Pomatiidae	*Tropidophora* (*Otopoma*) *letourneuxi* (Bourguignat, 1887)	Coastal scrub, etc., plantations	MF only	Not in forest, only plantation	Extant at coast	Unassigned
Ferussaciidae	*Cecilioides callipleplum* (Connolly, 1923)	“Dry areas”			Extant at coast	Forest-rarely/never
Achatinidae	*Achatina* (*Lissachatina*) *albopicta* E.A. Smith, 1878	Bushland to forest	Preferred BW	Prefers forest, though in both	Extant at coast	Unassigned
	Curvella caloraphe Preston, 1910	Forest		Forest only	Extant at coast	Forest-only
	Curvella pertranslucens Preston, 1910	Bushland to forest			Extant at coast	Unassigned
	Ischnoglessula gracillima (Pilsbry, 1919)				?	Forest-only
	Kempioconcha boivini (Morelet, 1860)	Forest to bushland	Preferred BW	Prefers forest, though in both	Extant at coast	Unassigned
	Kempioconcha ingloria Connolly, 1923	Bushland	Preferred BW	Prefers forest, though in both	Extant at coast	Unassigned
	Kempioconcha terrulenta (Morelet, 1883)				Now western	Forest-only
	Pseudopeas igembiense Connolly, 1923	Forest		Prefers scrub	Extant at coast	Unassigned
	Subulina mrimensis Verdcourt, 1979	Forest	CT only		Extant at coast	Unassigned
	Subulina sp. “very slender”				?	Unassigned
	Subulina intermedia (Taylor, 1877)				Extant at coast	Unassigned
	“Opeas” sp./spp.				Extant at coast	Unassigned
	“Subulinidae” sp. juv., “singleton”				?	Unassigned
	Subulona ordinaria (Preston, 1910)	(Not listed but other spp. forest)			Extant at coast	Unassigned
Cerastidae	*Gittenedouardia conulina* (E. von Martens, 1869)	Bushland to forest			Extant at coast	Unassigned
	Gittenedouardia alycaeoides Verdcourt, 1957	Forest	MF only	Forest only	Extant at coast	Forest-only
	Rhachidina chiradzuluensis (E.A. Smith, 1899)	(Not listed but other spp. bushland)	Preferred BW	Equal forest and scrub	Extant at coast	Unassigned
	Rhachistia picturata (Morelet, 1889)	Bushland to forest	MF only	Forest only	Extant at coast	Unassigned

Table 1. Continued.

Identification (classification follows MOLLUSCABASE EDS 2023)		Known habitat and distribution				Habitat-group assignation
Family	**Species**	**Coastal Kenya and Tanzania (VERDCOURT 2000)**	**Arabuko-Sokoke National Park, coastal Kenya (LANGE & MWINZI 2003): MF = mixed forest; BW = *Brachystegia* woodland; CT = *Cynometra* thicket**	**Shimba Hills National Reserve, coastal Kenya (NDALILA 2011): forest, scrub, plantation**	**Distribution (all sources)**	
Endodontidae	*Endodonta kempi* (Connolly, 1925)		Avoided BW		Extant at coast	Unassigned
	Afroguppya rumrutiensis (Preston, 1911)				?	Unassigned
Ariophantidae	*Microcystina rowsoni* Gittenberger & van Bruggen, 2013				Extant at coast	Forest-only
Charopidae	*Psichion ariel* (Preston, 1910)	Forest		Forest only	Extant at coast	Unassigned
	Trachycystis iredalei Preston, 1912				Now inland	Unassigned
Punctidae	*Trachycystis lamellifera* (E.A. Smith, 1903)				Now inland	Unassigned
	Punctum ugandanum (E.A. Smith, 1903)				?	Unassigned
Chronidae	*Kaliella barrakporensis* (L. Pfeiffer, 1852)				Extant at coast	Unassigned
Helicarionidae	*Sitala jenynsi* (L. Pfeiffer, 1845)	Open areas, scrub, woodland, plantations			Extant at coast	Forest-rarely/never
Urocyclidae	Urocyclid slug sp./spp.	All urocyclid slugs listed as “forest”			Extant at coast	Unassigned
	Thapsia curvatula (E. von Martens, 1897)			As *T. curvatula*; prefers forest	Extant at coast	Forest-only
	Thapsia insulsa (Preston, 1910)				Extant at coast	Forest-rarely/never
	Trochonanina shimbiensis (Preston, 1910)	Forest		Prefers forest, though in both	Extant at coast	Unassigned
	Trochonanina sp. “not *shimbiensis*”	Bushland/forest	Avoided MF (if correctly identified)	Prefers scrub, though in both	Extant at coast	Unassigned
	Trochozonites sp.	Forest		Equal forest and scrub	Extant at coast	Unassigned
Hygromiidae	*Halolimnohelix gaziensis* (Preston, 1911)	“Must be an identification error!”			?	Forest-only
Vertiginidae	*Vertigo bisulcata* (Jickeli, 1873)	Bushland	MF only		Extant at coast	Unassigned
	Afripupa misaliensis (Gittenberger & van Bruggen, 2013)				Extant at coast	Forest-rarely/never
Gastrocoptidae	*Gastrocopta klunzingeri* (Jickeli, 1874)	Bushland			Extant at coast	Forest-rarely/never
Vertiginidae	*Insulipupa malayana* (Issel, 1874)	Bushland			Extant at coast	Forest-rarely/never
Valloniidae	*Pupisoma misaliensis* Gittenberger & van Bruggen, 2013		MF only		Extant at coast	Unassigned
	Salpingoma harpula (Reinhardt, 1886)				Extant at coast	Unassigned
Truncatellinidae	*Truncatellina ninagongonis* (Pilsbry, 1935)				Now western	Forest-only
Streptaxidae	*Dadagulella radius browni* (van Bruggen, 1969)				Now southern	Unassigned

Table 1. Continued.

Identification (classification follows MOLLUSCABASE EDS 2023)		Known habitat and distribution				Habitat-group assignation
Family	**Species**	**Coastal Kenya and Tanzania (VERDCOURT 2000)**	**Arabuko-Sokoke National Park, coastal Kenya (LANGE & MWINZI 2003): MF = mixed forest; BW = *Brachystegia* woodland; CT = *Cynometra* thicket**	**Shimba Hills National Reserve, coastal Kenya (NDALILA 2011): forest, scrub, plantation**	**Distribution (all sources)**	
Streptaxidae, continued	*Dadagulella conoidea* (Verdcourt, 1996)	Forest (*G. rondoensis*)			Now southern	Forest-only
	Dadagulella radius radius (Preston, 1910)	Woodland/forest	Avoided CT	Scrub only	Extant at coast	Unassigned
	Edentulina affinis (*ovoidea auct.*) C.R. Boettger, 1913			Forest only	Extant at coast	Forest-only
	Edentulina obesa obesa (J.W. Taylor, 1877)	Bushland to forest, even rocky grassland	CT only		Extant at coast	Unassigned
	Gonaxis denticulatus (Dorhn, 1878)	Bushland to forest	Preferred BW		Extant at coast	Unassigned
	Gonospira expatriata (Preston, 1910)	Woodland/forest			Extant at coast	Unassigned
	Gulella tomlini (Preston, 1911)				Now inland	Unassigned
	Gulella prestoni Connolly, 1922				Now inland	Forest-only
	Gulella gwendolinae gwendolinae (Preston, 1910)	Bushland to forest	MF only		Extant at coast	Unassigned
	Gulella jod (Preston, 1910)	?Forest			Extant at coast	Forest-only
	Gulella tracheia Rowson, 2007b				Now southern	Forest-only
	Gulella marionae (Preston, 1910)	Forest	(*G. foveolata* preferred CT)		Extant at coast	Forest-only
	Gulella sp. “large, smooth”				?	Unassigned
	Gulella carea (Preston, 1913)	?			Extant at coast?	Unassigned
	Gulella streptostelopsis van Bruggen, 2007				Extant at coast?	Forest-only
	Gulella (Pliciguella) vicina (E.A. Smith, 1899)	Bushland, woodland?		Prefers scrub	Extant at coast	Unassigned
	Juventigulella habibui (Tattersfield, 1998b)				Extant at coast?	Unassigned
	Juventigulella saidii new species				?	Forest-only
	Juventigulella peakei continentalis (van Bruggen, 1975)				Extant at coast	Forest-only
	Ptychotrema sp. “smooth”				Now inland	Unassigned
	Ptychotrema (Parennea) sperabile (Preston, 1910)	?Forest			Extant at coast	Forest-only
	Ptychotrema sp. “not *sperabile*”				?	Forest-only
	Tayloria quadrilateralis (Preston, 1910)	Generally bushland to forest	??Preferred BW	Prefers forest, though in both	Extant at coast	Unassigned

Table 2. Number of individual terrestrial molluscs found in each layer in the Panga ya Saidi sequence, with totals. For layer details see Table 3.

Species	**Individuals recorded from each layer**														**Total specimens**	
	17–19	**16**	**15**	**14**	**13**	**12**	**11**	**10**	**9**	**7–8**	**Excluded**	**2**	**Excluded**	**1**	**Including excluded samples & taxa**	**Without exclusions**
C. azaniense		3	2	8	2			32	14	21				1	83	83
H. tanzaniensis				1	2		5	1	33	49		1			92	92
M. volkensi	8	6	11	14	2	8	27	19	160	180	2	4		1	442	440
M. meteor	2	3	5			2	1	1			1	22	8	13	58	49
M. wahlbergi									1						1	1
T. letourneuxi		1	4	21	14	31	26	41	31	88		17	7	21	302	295
A. (L.) albopicta	23	3	3	6	6	4	3	7	27	13	2	13	6	23	139	131
C. callipleplum								5	1						6	6
C. caloraphe	6	5	10	6	1		1	20	20	23		12	4	2	110	106
C. pertranslucens										4		5	1	4	14	13
I. gracillima	4	1	2	6	1	6	10		41	100		1		1	173	173
K. boivini	16	4	10	6	1	2	10	31	60	75	6	22	30	36	309	273
K. ingloria								4		3		3		8	18	18
K. terrulenta	3		3	4	1										11	11
P. igembiense	1	4	5	3	1	1		6	1	1					23	23
S. mrimensis								2							2	2
Subulina sp. "very slender"	2	3	1	4	2		1	1	7	3	1				25	24
S. intermedia	45	2	5	3	3	1	5	5	4	7	1	17	3	7	108	104
"Opeas" sp./spp.	55	50	87	57	100	60	63	156	454	482	26	280	62	297	2,229	2,141
Subulinid sp. juv., "singleton"	1														1	1
S. ordinaria	1							1	1	8					11	11
G. conulina	1							10		2					13	13
G. alycaeoides	1		3	1			1		12	10					28	28
R. chiradzuluensis									19	12		17	8	16	72	64
R. picturata											2		2		4	0
E. kempi	9	7	6	11	3	7	12	33	43	78	1	7		7	224	223
A. rumrutiensis								1	7	7		1			16	16
M. rowsoni							1	14	3	3	2	18	2	13	56	52
T. ariel		1	1	3		1	3	3	18	14	1				45	44
T. iredalei	7	5	2	8	1		2	6	80	72	2	3			188	186
T. lamellifera	27	14	7	6	6	7	54	66	1,403	1,118	16	39	2	45	2,810	2,792
P. ugandanum	6	2	24		1	8	23	32	441	304		3			844	844
K. barrakporensis	2	2	2	14	1			19	14	19	1			6	80	79
Urocyclid slug sp./spp.	2		64	5	9	46		105	9	119	1	36	12	8	416	403
S. jenynsi												1			1	1
T. curvatula	5	1	2	4		1	2	5	19	14		2		4	59	59
T. insulsa									3						3	3
T. shimbiensis	1		1	1		1		14	10	12	1	11	6	13	71	64
T. sp. "not *shimbiensis*"			1												1	1
Trochozonites sp.										1					1	1
H. gaziensis									1						1	1

Table 2. Continued.

Species	Individuals recorded from each layer														Total specimens	
	17–19	**16**	**15**	**14**	**13**	**12**	**11**	**10**	**9**	**7–8**	Excluded	**2**	Excluded	**1**	Including excluded samples & taxa	**Without exclusions**
V. bisulcata	14	2	11	26	2	1	5	18	102	68	6	10	1	21	287	280
A. misaliensis								10							10	10
G. klunzingeri								8	1	1		2			12	12
I. malayana								4				1		1	6	6
P. misaliensis	2		3					1	21	2	1	4		3	37	36
S. harpula	1			1		1			1	4					8	8
T. ninagongonis	8	4	4	1		3	6	12	306	59		1		1	405	405
D. radius browni	8	3	3	3				4					1		22	21
D. conoidea	2	2	2	2		14	12	6	96	117		3		4	260	260
D. radius radius	44	56	88	138	13	49	79	52	552	501	6	31	2	26	1,637	1,629
E. affinis (*ovoidea* auct.)	1				1				1	6	1	1		5	16	15
E. obesa obesa				1	5		2	1	3			1	3		16	13
G. denticulatus								26		9	1	8		4	48	47
G. expatriata	19	12	18	14		16	22	31	88	120	5	40	8	28	421	408
G. tomlini	2			3			5	4	19	26		1			60	60
G. prestoni				1				7	3	3		2		2	18	18
G. gwendolinae gwendolinae	4	8	4	10	8			14		7	2	13	4	14	88	82
G. jod	2	1	6	4				10	6	14		4		2	49	49
G. tracheia			1	2					7	6					16	16
G. marionae						3			4						7	7
Gulella sp. “large, smooth”										5					5	5
G. carea	4		1					1	2	7		2			17	17
G. streptostelopsis	1			2		3	1	1	14	6		2		4	34	34
G. (*P.*) *vicina*										2					2	2
J. habibui	58	105	128	96	34	104	72	83	1,471	1,616	9	118	15	100	4,009	3,985
J. saidii								20							20	20
J. peakei continentalis	12	17	13	17		3	3	14	33	16	2	3			133	131
Ptychotrema sp. “smooth”	1		1	1											3	3
P. (*P.*) *sperabile*								1		2					3	3
Ptych. sp. “not *sperabile*”						1									1	1
T. quadrilateralis		2						1	1	1		1	4	2	12	8
Total	**411**	**329**	**544**	**514**	**220**	**384**	**457**	**969**	**5,668**	**5,440**	**99**	**783**	**191**	**743**	**16,752**	**16,462**

richness and evenness were therefore consistently high and varied relatively little throughout the sequence.

Some turnover of species between layers was evident. The number of layers in which each species occurred varied from 1 to 12 (mean 6.5). Thirteen species (19%) occurred only in a single layer, while 10 (14%) occurred in all 12 layers. There were 5 “early” species that appeared only in Layer 11 or earlier (*Kempioconcha terrulenta*; a “subulinid” singleton; *Trochonanina* sp. not *shimbiensis*; *Ptychotrema* sp. smooth, *Ptychotrema* sp. not *sperabile*). There were 21 “late” species that only appear in Layer 11 or later. Five of these appear only in Layer 7–8 or later (*Sitala jenynsi*, *Trochozonites* sp., *Halolimnohelix gaziensis*, *Gulella vicina*, and *Gulella* sp. large, smooth). However, it was not easy to identify large changes in community composition in the sequence. There was instead some alteration between the most abundant taxa, with *Opeas* sp./spp. moderately dominating in the middle and end of the sequence, and *J. habibui*, *D. radius radius*, and *T. lamellifera* dominating

Table 3. Layer details (after Shipton et al. 2018) and diversity summaries for terrestrial molluscs in the Panga ya Saidi sequence.

Layer number	Start depth (m)	Floated fraction volume (l)	Median Bayesian date (BP)	Marine Isotope Stage	Original context number	Total individuals (*n*)	Species richness (*S*)	Rarified richness (*N* = 220)	Shannon index (*H*)	Brillouin index
1	0.20	60	450	1	402	743	35	33.3	2.4	2.3
Excluded	—	—	—	1	406 (hearth)	191	22	—	—	—
2	0.26	60	—	1	407	783	43	27.5	2.6	2.5
Excluded	—	—	—	1	409 (burrow/ root hole	99	25	—	—	—
7–8	0.98	120	25,128	2	412 “ASH”	5,440	53	29.9	2.4	2.4
9	1.28	60	38,300	3	413A	5,668	50	31.8	2.4	2.3
10	1.42	60	45,775	3	414–414C (pooled)	969	51	25.0	3.2	3.1
11	1.58	60	47,612	3	415B	457	29	22.9	2.6	2.5
12	—	60	52,837	3	416B	384	27	24.5	2.4	2.3
13	1.78	60	59,500	4	417	220	25	37.7	2.1	1.9
14	1.84	60	59,500	4	418	514	39	23.8	2.7	2.5
15	1.98	60	64,560	4	419	544	38	26.0	2.6	2.5
16	—	60	68,575	4	420A	329	30	30.1	2.4	2.2
17–19	2.06	180	79,525–76,350	5a	17–19 (pooled)	411	40	27.3	3.0	2.8

at other times. The urocyclid slugs were unusual in making up over 10% of individuals in some layers but being absent from others.

Habitat preferences

Twenty species (29% of the total) were classed strictly as forest-only and 6 species (9%) as forest-rarely/never, the rest being unassigned. The forest-only taxa accounted for 36% of individuals overall. The relative abundance of forest-only taxa was high throughout the sequence, ranging from 43% in Layer 16 to 17% in Layer 1 and 20% in Layer 2. Each of the sets of taxa that are listed above as occurring only in the early or late parts of the sequence included species classified as forest-only, so despite some turnover, forest-only species were always present.

In contrast, the forest-rarely/never taxa accounted for less than 1% of all individuals overall. Their relative abundance reached only 15% in Layer 10, less than 1% in Layers 2 and 1, and was close to zero in all other layers. Perhaps notably, some other species also showed their highest relative abundances in Layer 10. These include 1 species in the forest-only group (*Gulella jod*) and 4 species in the unassigned group (*Cyathopoma azaniense*, *Gittenedouardia conulina*, *Gonaxis denticulatus*, and *Juventigulella saidii*). Overall, therefore, the sequence was dominated by forest-only and unassigned species throughout, with only 1, moderate reduction in dominance in Layer 10.

Faunistic composition and noteworthy occurrences

The fauna throughout the sequence is unmistakeably similar to extant native faunas of coastal forest in East Africa, including those at Arabuko-Sokoke (Lange & Mwinzi 2003) and the Shimba Hills (Ndalila 2011). The taxonomic make-up at the family and genus level is typical for the region, with Streptaxidae the dominant family in terms of species richness (24 species, 34% of the total). The majority of these species are endemic to the Indian Ocean coastal strip (the Zanzibar–Inhambane mosaic), or to small parts of it, and are still extant today. The excavation provides the first record of several other taxa from beyond their type localities, for instance *Dadagulella conoidea*, *Gulella carea*, and *G. marionae*. The streptaxid *Gonospira expatriata*, abundant throughout the sequence, has always been enigmatic. Described by Preston (1910) from the Shimba Hills (though not found by Ndalila 2011), it has also been collected at Malindi (Verdcourt 2006) but apparently never found alive.

Eight taxa were, however, recorded for the first time from the coast, having previously been noted only from the highlands to the west. These include *Hydrocena tanzaniensis*, *Punctum ugandanum*, *Trachycystis iredalei*, *T. lamellifera*, and *Gulella tomlini*. *Truncatellina ninagongonis* (which was referred to as *T.* cf. *obesa* by Shipton et al. 2018) is the first species of its genus found near the coast and was previously known no closer than Kakamega Forest in western Kenya (Tattersfield 1995). It is

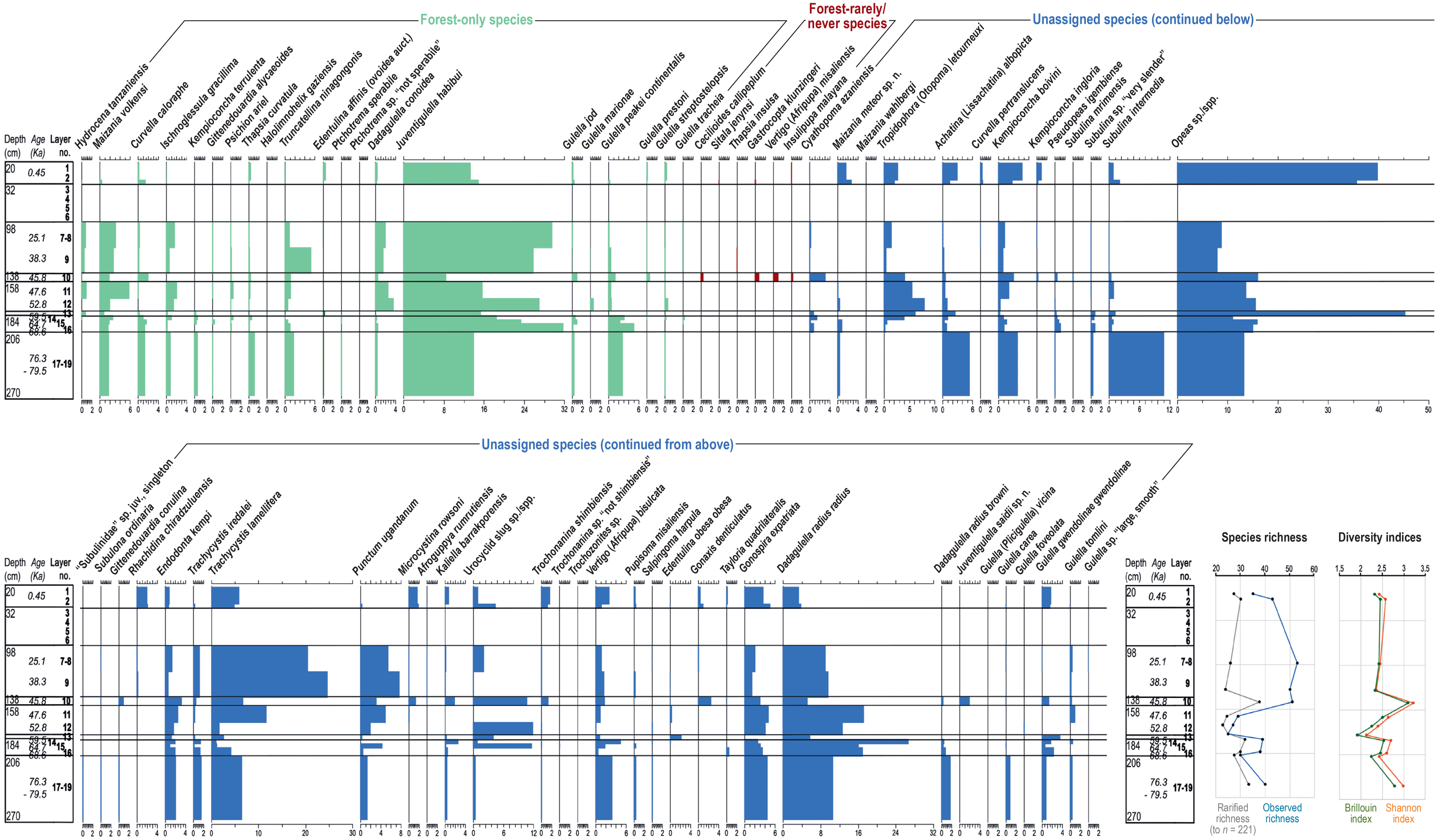

Figure 2. Biostratigraphy of terrestrial molluscs at Panga ya Saidi, showing each species' percentage contribution to the total individuals in each layer. Species are assigned to habitat groups (or left unassigned) following Table 1. Species richness and diversity indexes for each layer are shown at the bottom right.

present in low numbers almost throughout the sequence, peaking in relative abundance in Layer 9 where 306 individuals were found. Similarly, the Central African forest genus *Ischnoglessula* is also newly recorded from the coast. It has not previously been recorded east of Kakamega and the Isuria Escarpment of the Kenyan Rift Valley, and the species *I. gracillima* no further east than Uganda (Verdcourt 1967, 2006). Meanwhile, *Kempioconcha terrulenta* and the genus *Ptychotrema* are taxa with Central or West African affinities that are very scarce at the coast. Indeed Verdcourt (1972, 2000) strongly doubted the veracity of Preston's (1911) description of a *Halolimnohelix* from Gazi near the Shimba Hills, and even that any member of the Helicoidea could occur at the coast. Nonetheless, the specimen from Layer 9 shows that the genus did live locally, at least late in the Panga ya Saidi sequence. There is, thus, evidence for forest connections to the west in both the early and late parts of the sequence that do not exist today. In contrast, as far as is known, none of the taxa recovered are any more than 250 km beyond their present ranges to the north or south (several extend to KwaZulu-Natal in South Africa). The distinctive streptaxid genus *Raffraya* (usually considered a subgenus of *Streptostele*), now common at the coast, is apparently absent from the sequence.

The dated layers also supply pre-Holocene minimum ages for the African occurrence of 3 widespread species described from Asian type localities: *Kaliella barrakporensis*, *Insulipupa malayana*, and *Salpingoma* (formerly *Pupisoma*) *harpula*. This indicates that they are part of the native African fauna. Two of the streptaxid species, *Gulella gwendolinae* and *Juventigulella peakei*, are also recorded from Aldabra, in the Indian Ocean, as subfossils (van Bruggen 1975).

One additional species, *Rhachistia picturata* (not in Fig. 2) was recovered as 2 individuals from each of the late instrusion contexts 409 and 406, which were excluded from the analysis (Table 2). It is another coastal species of forest and bushland, identified at the Arabuko Sokoke forest to the north (Verdcourt 2000, Lange & Mwinzi 2003).

Typical subfossil examples of each species are shown in Figures 3–11.

Descriptions of new taxa

Superfamily Cyclophoroidea J.E. Gray, 1847

Family Maizaniidae Tielecke, 1940

Genus *Maizania* Bourguignat, 1890

Type species by monotypy: *M. olivacea* Bourguignat, 1890.

Subgenus *Micromaizania* van Bruggen, 1983

Type species by subsequent designation: *Cyclophorus volkensi* E. von Martens, 1895. The name *Micromaizania* was first used by Verdcourt (1964) who did not designate a type species, so authorship is attributed to van Bruggen (1983).

Maizania (*Micromaizania*) *meteor* new species

Figure 3F, G

ZooBank registration. urn:lsid:zoobank.org:act:59A840FE-8036-4136-83C3-EA696C7D96CE

Holotype. NMK.PYS13: Layer 2/407, Panga ya Saidi cave (−03.679, 039.736), Kilifi County, Kenya (excavated 2013).

Paratypes. Site data as holotype, total 48 shells. NMK. PYS13: Layers 17–19/423A/422A/420E (2 shells), Layer 16/420A (3 shells), Layer 15/419 (5 shells), Layer 12/416B (2 shells), Layer 11/415B (1 shell), Layer 10/414-414C (1 shell), Layer 2/407 (19 shells), Layer 1/402 (12 shells). NMW.Z.2014.016.00001: Layer 2/407 (2 shells). NMW.Z.2014.016.00002: Layer 1/402 (1 shell).

Etymology. From Greek *meteoros*, a meteorite. A noun used in apposition for the species' detached peristome and spiral sculpture, the shell recalling a shooting star.

Diagnosis. A small to medium-sized *Maizania* with clear spiral apical sculpture and a detached last whorl in most large individuals. The spiral apical sculpture allows juveniles to be distinguished from sympatric *Maizania* species, which have smooth apical whorls.

Description. Shell small to medium-sized (6.55–8.20 mm maximum diameter × 4.15–5.00 mm high), low-spired, with a wide, perspective umbilicus. Whorls 3½–4½, tumid, and loosely coiled; last ½ whorl fully detached in most large individuals. Aperture nearly circular, moderately enlarged (c. 35% of shell diameter). Spire little exserted. Protoconch (1½ whorls) clearly sculptured with fine, parallel spiral grooves. Remaining whorls (teleoconch) sculptured with very fine, silky radial wrinkles. Shell unpatterned, opaque; form and colour of periostracum unknown.

Distribution. Pleistocene and Holocene deposits in Panga ya Saidi cave, coastal Kenya.

Remarks. This species appears to be unique in having spiral apical sculpture and a detached last whorl. Neither feature was given by Verdcourt (1964) in his revision of all 15 nominal species of East African *Maizania*, or by Varga (1976) in his description of *M. pocsi* Varga, 1976 from eastern Tanzania. The new species is intermediate in size and relative aperture size between the other 2 *Maizania* species in the Panga ya Saidi sequence, *M. volkensi* and *M. wahlbergi* (Benson, 1852). The present species *M. meteor* is attributed to *M.* (*Micromaizania*), an eastern African subgenus extending to Malawi and eastern DR Congo (Verdcourt 1964, van Bruggen 1983). *Maizania* (*Micromaizania*) *scalarioidea* van Bruggen, 1983 from Malawi reaches 6.2 mm in diameter and has a smooth protoconch, but is strongly scalariform, a feature van Bruggen (1983) considered unique in Maizaniidae at the time. *Maizania* (*Micromaizania*) *kazibae* Adam, 1987 is another species with a detached body whorl but

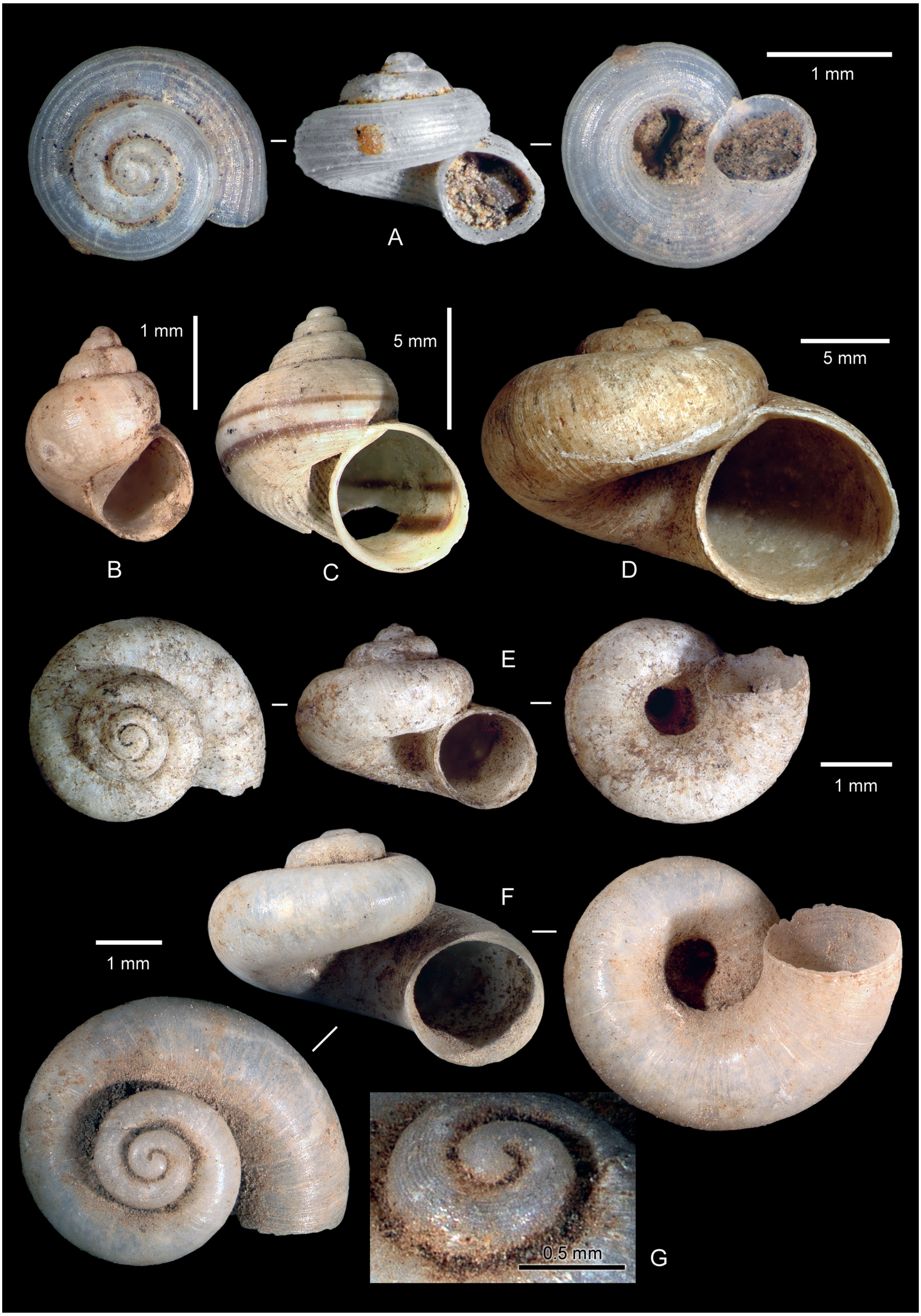

Figure 3. Panga ya Saidi subfossils: operculates. **A.** *Cyathopoma azaniense*, NMW.Z.2014.016.0004. **B.** *Hydrocena tanzaniensis*, NMW.Z.2014.016.0005. **C.** *Tropidophora letourneuxi*, NMW.Z.2014.016.0008. **D.** *Maizania wahlbergi*, NMK.PYS13. **E.** *Maizania volkensi*, NMW.Z.2014.016.0007. **F.** *Maizania meteor* sp. n., holotype, NMK.PYS13. **G.** *M. meteor*, spiral apical sculpture of holotype, enlarged.

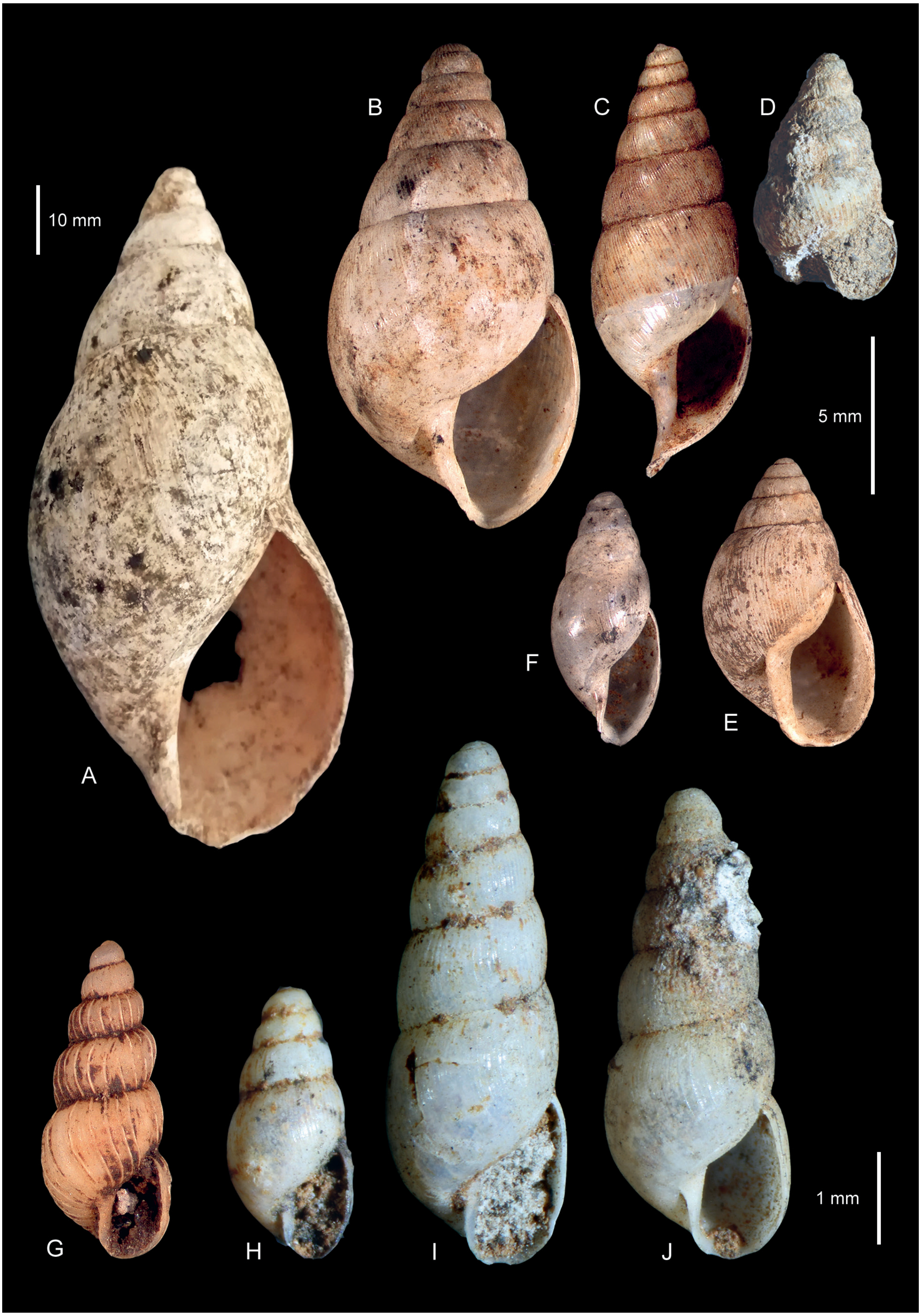

Figure 4. Panga ya Saidi subfossils: Achatinidae. **A.** *Achatina* (*Lissachatina*) *albopicta*, NMW.Z.2014.016.00010. **B.** *Kempioconcha boivini*, NMW.Z.2014.016.00016. **C.** *Kempioconcha ingloria*, NMW.Z.2014.016.00017. **D.** *Kempioconcha terrulenta*, NMW.Z.2014.016.00018. **E.** *Curvella calorhaphe*, NMW.Z.2014.016.00012. **F.** *Curvella pertranslucens*, NMW.Z.2014.016.00013. **G.** *Pseudopeas igembiense*, NMW.Z.2014.016.00019. **H–J.** “*Opeas*” sp./spp. (3 shells from same context), NMW.Z.2014.016.00023.

a smooth protoconch. It occurs from eastern DR Congo to Uganda (Adam 1987, Verdcourt 1995). Whilst detached whorls are found as a rare, spontaneous aberration in many snail species, spiral apical sculpture does not vary nearly as much. In the Maizaniidae it seems to be a western character. Van Bruggen (1982) revised the West and Central African genus *Maizaniella*, creating a subgenus *Maizaniella* (*Spirulozania*) for the 5 species with spiral sculpture. All of these are 4.9 mm or less in diameter and all have strong radial as well as spiral sculpture. The presence of 2 rare character states in *M.* (*M.*) *meteor* supports the hypothesis that it is a distinct species, perhaps with a western affinity.

Superfamily Streptaxoidea J.E. Gray, 1860

Family Streptaxidae J.E. Gray, 1860

Genus *Juventigulella* Tattersfield, 1998b

Type species by original designation: *Gulella* (*J.*) *habibui* Tattersfield, 1998b.

Juventigulella saidii new species

Figure 11F

ZooBank registration. urn:lsid:zoobank.org:act:E77B73DC-9D63-4CF2-8880-C4334F42AD14

Holotype. NMK.PYS13: Layer 10/414, Panga ya Saidi cave (−03.679, 039.736), Kilifi County, Kenya (excavated 2013).

Paratypes. Site and layer data as holotype; total 19 shells. NMK.PYS13 (15 shells). NMW.Z.2014.016.00003 (4 shells).

Etymology. A noun in the genitive case, after Saidi, the person for whom Panga ya Saidi is named.

Diagnosis. A *Juventigulella* with a relatively tall and narrow shell, spiral apical sculpture, fine close-set radial ribs, and an open aperture with 3-fold dentition.

Description. Shell small (1.53–1.60 maximum diameter × 2.00–2.10 mm high), ovate-subconical, with a narrow, deep umbilicus. Whorls 4½–5, tumid, last whorl appreciably narrower than preceding one, leading to an ovate-subconical shape. Protoconch (1½ whorls) irregularly granular, with distinct spiral threads, apparently worn away in some places. Remaining whorls (teleoconch) sculptured throughout with fine, slightly oblique, very close-set radial ribs (c. 21 visible on apertural half of last whorl). Aperture little constricted, only barely downturned. Apertural dentition: (1) a strong, v-shaped parietal tooth; (2) a strong, knob-like baso-palatal tooth; (3) a strong, peg-like columellar tooth. All 3 teeth are set only shallowly behind the peristome. Juvenile shells lack a parietal lamella or other apertural dentition. Shell colourless, translucent or opaque.

Distribution. Pleistocene deposits in Panga ya Saidi cave, coastal Kenya.

Remarks. The genus *Juventigulella* is here considered to include *J. habibui* (Tattersfield, 1998b), *J. amboniensis* (Tattersfield, 1998b), *J. spinosa* (Tattersfield, 1998b), *J. ngerezae* (Rowson, 2007b), *J. kimbozae* (Verdcourt, 2004), *J. peakei* (van Bruggen, 1975), and *J. cryptophora* (Morelet, 1881). This accords with the classification in Mollusca Base (MolluscaBase Eds 2023). Three of the species are known only from Tanzania (Tattersfield 1998b). As well as the new species, 3 have now been recorded in Kenya: *J. spinosa* in the Taita Hills (Lange et al. 1998), *J. habibui* at Panga ya Saidi, and *J. peakei*. The last is the most widespread species, ranging from western Kenya to South Africa and Aldabra (van Bruggen 1975, Pickford 1995, Herbert & Kilburn 2004). It is very similar to *J. cryptophora*, which is found on the Comoros. The affinities of *Gulella lacuna* (Preston, 1911) from central Kenya remain unknown—it might also be a *Juventigulella*. Among all these species, the new species *J. saidii* is most similar to *J. ngerezae*, described from forest in Tanzania's Ukaguru Mountains. *Juventigulella saidi* differs from *J. ngerezae* in having a more ovoid shape, stronger dentition, and the much finer and more closely set radial sculpture. The comparisons made by Rowson (2007b) between *J. ngerezae* and the other species thus largely also apply to *J. saidii*. The new species is clearly distinct from the 2 others in the Panga ya Saidi sequence, *J. peakei* and *J. habibui* (Fig. 11). All 3 are numerous in Layer 10, but, while the others occur throughout the sequence, *J. saidii* is restricted to a single layer. It may therefore have had different habitat requirements that were only transiently satisfied at Panga ya Saidi, a hypothesis that could be addressed if living populations are found.

Discussion

The quantity and diversity of terrestrial molluscs recovered at Panga ya Saidi is extraordinary, especially given that the total sediment volume examined at the site was only 960 l. It provides the first detailed record of its kind from coastal East Africa and highlights the value of applying flotation to archaeological sites in the region, including Late Pleistocene and Holocene cave sites, where such recovery methods are rarely used. It also demonstrates, more broadly, the utility of archaeobotanical recovery methods for the study of other non-cultural proxies like terrestrial molluscs.

The total fauna of 72 terrestrial mollusc species is very diverse, resembling the total fauna (70 species) recorded for Kakamega Forest, a large complex of moist forest in western Kenya at an elevation of 1500 m (Tattersfield 1996, Lange & Maes 2003). Moreover the mean number of species in an individual layer (38.5) and even the minimum for a layer (25) resemble the total faunas found in surveys of protected areas nearby, including Arabuko

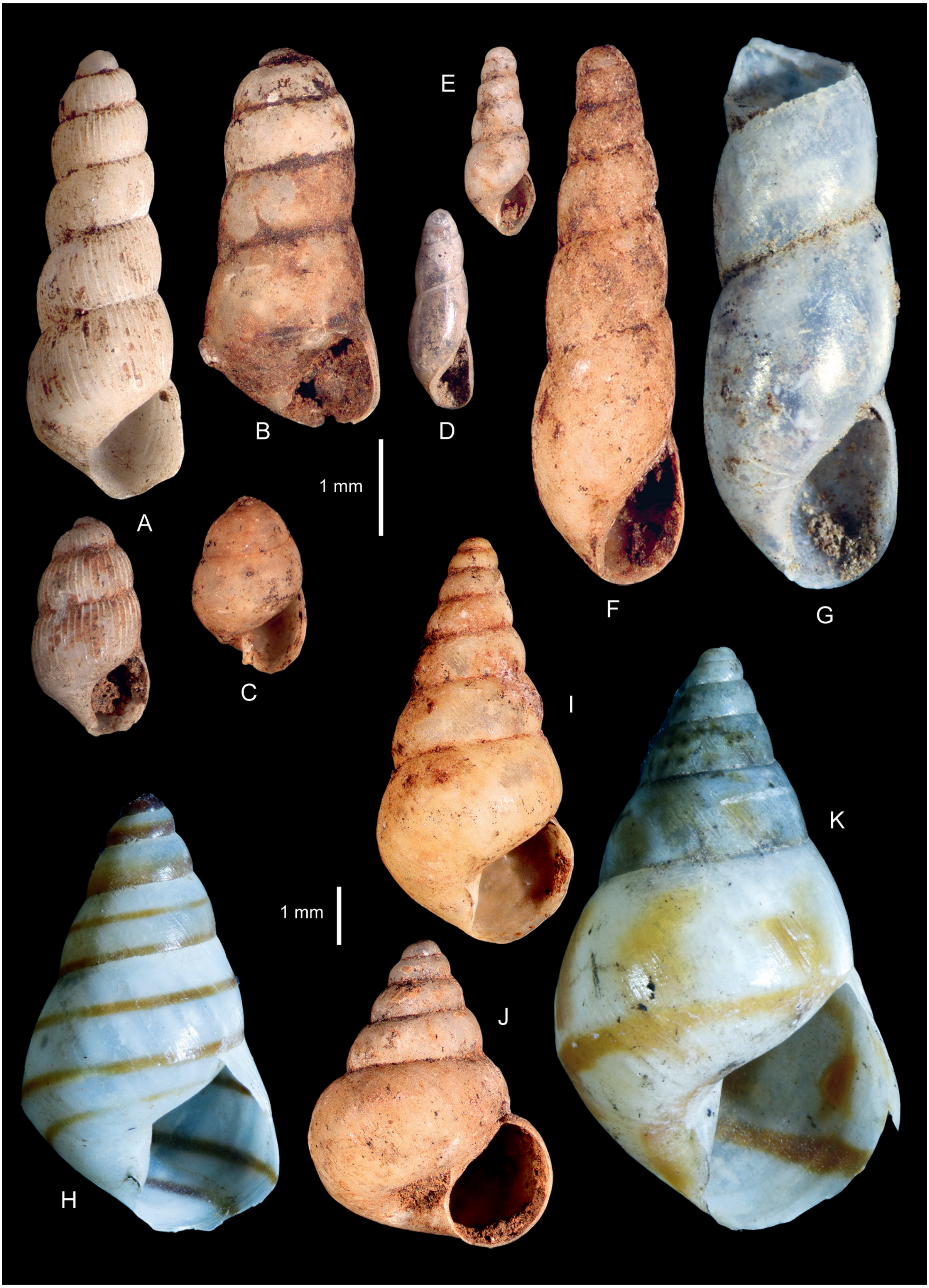

Figure 5. Panga ya Saidi subfossils: Achatinidae, Ferussaciidae and Cerastidae. **A.** *Ischnoglessula gracillima*, subadult and juvenile, NMW.Z.2014.016.00014. **B.** *Subulona ordinaria*, NMW.Z.2014.016.00024. **C.** "Subulinid singleton juv.", NMK.PYS13. **D.** *Cecilioides callipeplum*, NMW.Z.2014.016.00011. **E.** *Subulina* sp. "very slender", NMW.Z.2014.016.00021. **F.** *Subulina intermedia*, NMW.Z.2014.016.00022. **G.** *Subulina mrimensis*, NMW.Z.2014.016.00020. **H.** *Rhachidina chiradzuluensis*, NMW.Z.2014.016.00027. **I.** *Gittenedouardia conulina*, NMW.Z.2014.016.00025. **J.** *Gittenedouardia alycaeoides*, NMW.Z.2014.016.00026. **K.** *Rhachistia picturata*, NMW.Z.2014.016.00029. A–G are at a different scale to H–K.

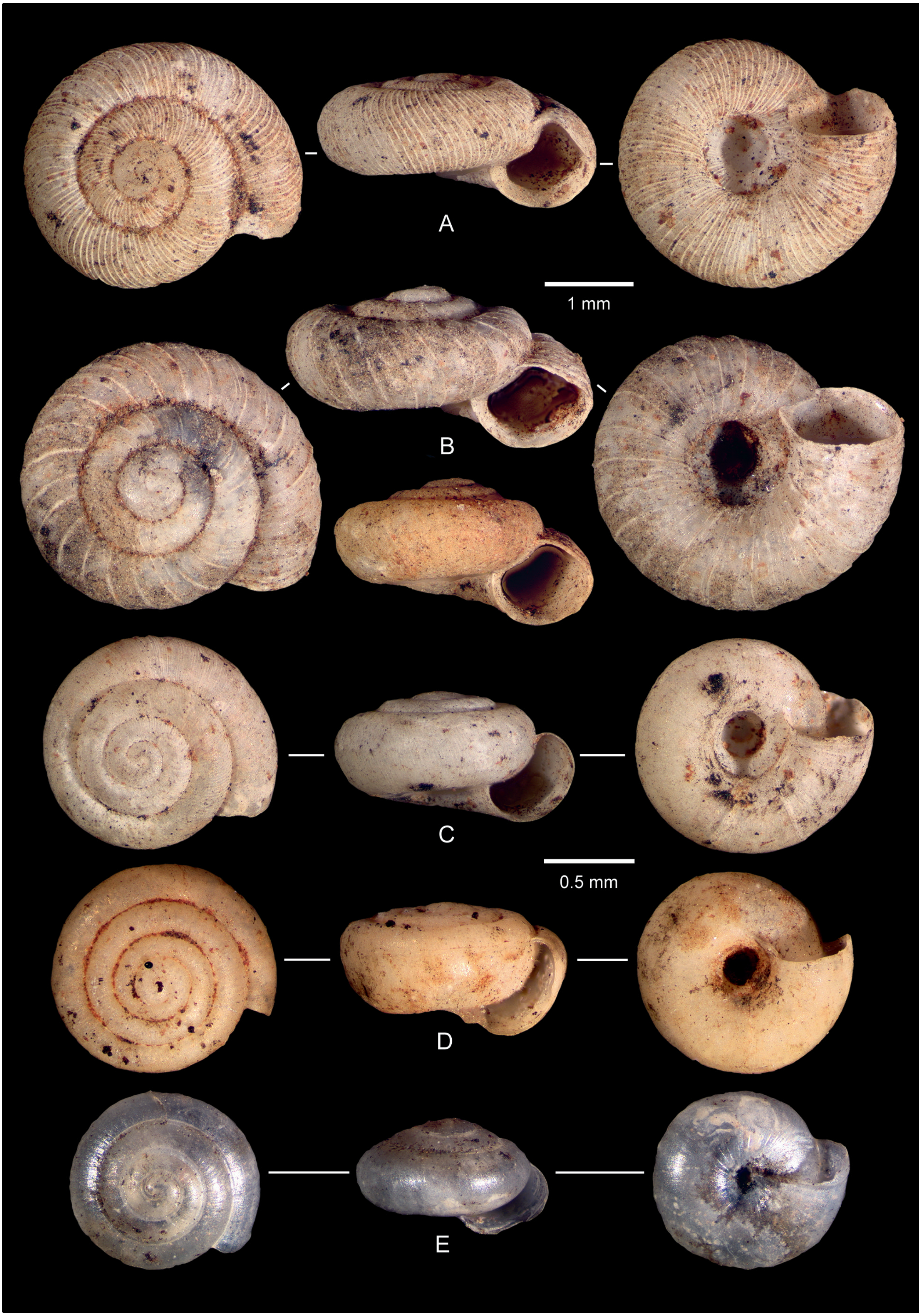

Figure 6. Panga ya Saidi subfossils: Charopidae, Endodontidae, Punctidae and Ariophantidae. **A**. *Trachycystis iredalei*, NMW.Z.2014.016.00034. **B.** *Trachycystis lamellifera* (a large shell with a more typically sized one below), NMW.Z.2014.016.00034. **C.** *Punctum ugandanum*, NMW.Z.2014.016.00036. **D.** *Endodonta kempi*, NMW.Z.2014.016.00030. **E.** *Microcystina rowsoni*, NMW.Z.2014.016.00032.

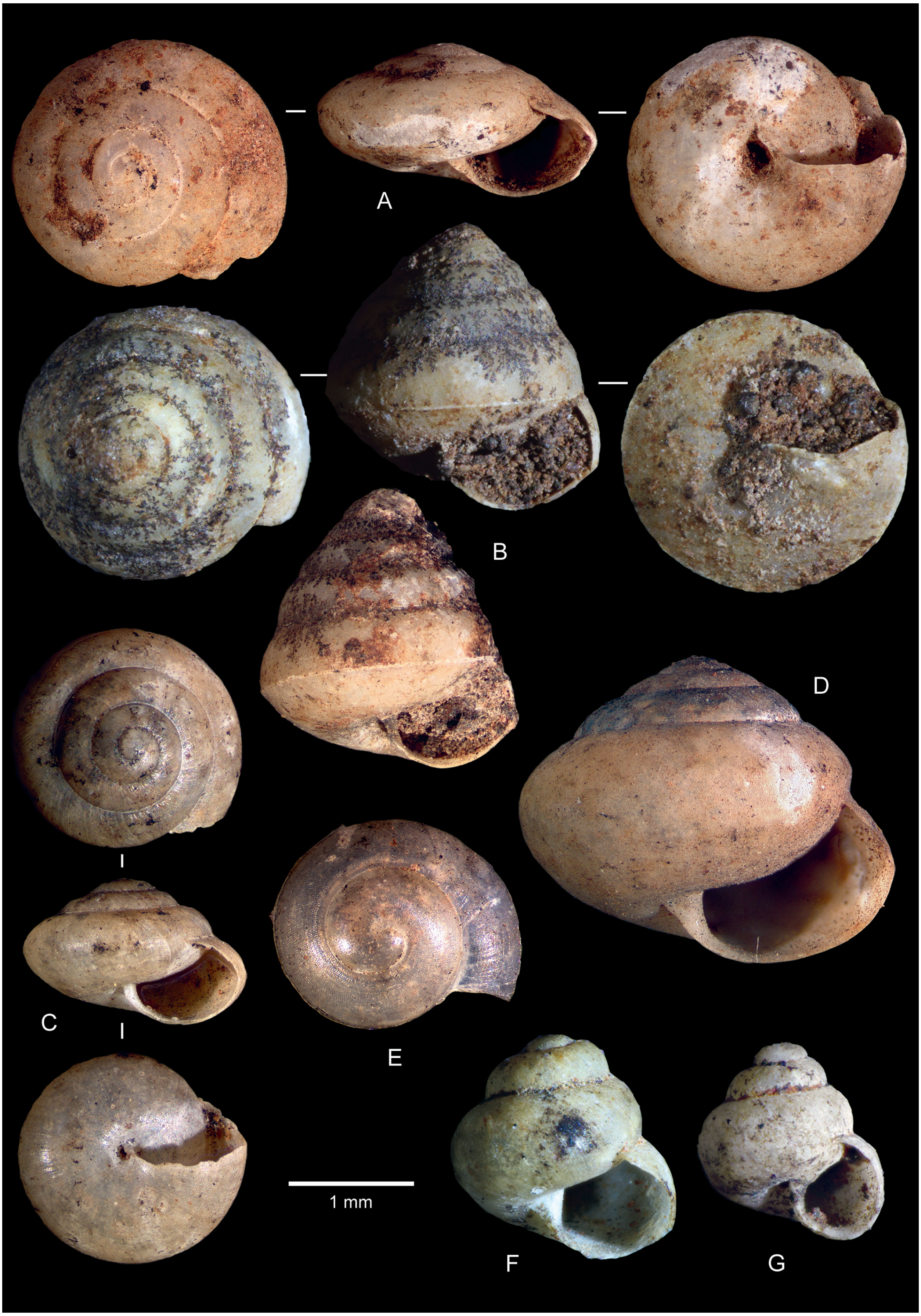

Figure 7. Panga ya Saidi subfossils: Urocyclidae, Chronidae, Euconulidae, Charopidae, Helicarionidae, and Valloniidae. **A.** *Thapsia insulsa*, NMW.Z.2014.016.00040. **B.** *Kaliella barrakporensis* (2 shells), NMW.Z.2014.016.00037. **C.** *Afroguppya rumrutiensis*, NMW.Z.2014.016.00031. **D.** *Psichion ariel*, NMW.Z.2014.016.00033. **E.** *Sitala jenynsi* (apex/juvenile shell only), NMK.PYS13. **F.** *Pupisoma misaliensis*, NMW.Z.2014.016.00046. **G.** *Salpingoma harpula*, NMW.Z.2014.016.00047.

Figure 8. Panga ya Saidi subfossils: Urocyclidae and Hygromiidae. **A.** *Thapsia curvatula*, NMW.Z.2014.016.00039. **B.** *Trochonanina shimbiensis*, NMW.Z.2014.016.00041. **C.** *Trochozonites* sp., NMK.PYS13. **D.** Urocyclid slug sp. (plate), NMW.Z.2014.016.00038. **E.** *Halolimnohelix gaziensis*, NMK.PYS13.

Sokoke Forest (25 species; Lange & Mwinzi 2003), Shimba Hills National Reserve (28 species; Ndalila 2011), and Ngezi Forest on Pemba Island, Tanzania (27 species, with 49 from the island as a whole; Rowson et al. 2010). The Shannon diversity index values for each layer is highly comparable to those given by Tattersfield (1998a) for a range of coastal forests in Tanzania. This indicates a very high completeness of preservation at Panga ya Saidi, both in individual layers and as a whole.

The high diversity and similarity to extant forest communities also supports this being a fauna dependent upon the complex microhabitats and biogenic input provided by the surrounding vegetation, and not simply the shade provided by the cave itself. Lange (2003) found that canopy cover, litter abundance, dead-wood abundance, and tree size (diameter at breast height) all influenced the diversity and abundance of snails in the forest complex at Arabuko Sokoke. Likewise, the diversity of other animal and plant species preserved at Panga ya Saidi far exceeds what could be supported by the cave itself (Shipton et al. 2018).

The overall pattern of community diversity and composition throughout the sequence is one of only minor change, and only gradual species turnover. This accords with stable-isotope data from mammal teeth excavated at PYS, indicating long-term environmental continuity in the area (Roberts et al. 2020). The East African coastal forest is well known for its long-term relative climatic stability during the Pleistocene, due to the effect of the Indian Ocean (Burgess & Clarke 2000, Shipton et al. 2018). As a whole, the bioata of the coastal forest predates the Pleistocene, partly explaining the persistence of Central or West African mollusc elements such as *Ptychotrema*, and now *Truncatellina*, indicating ancient connections to the interior (Burgess & Clarke 2000, Verdcourt 2000). The newly observed presence of the inland taxa *Hydrocena tanzaniensis*, *Maizania volkensi*, *Trachycystis iredalei*, *T. lamellifera*, and *Punctum ugandanum* suggests that the last of these forest links may only recently have been broken, as does confirmation of *Halolimnohelix* at the coast, at least during MIS 3. A few species now have a slightly more southern distribution (e.g. *Dadagulella conoidea*), but there is little evidence of substantial north–south shifts along the coastal strip.

The importance of forest to molluscs in East Africa is well known (Verdcourt 2000), yet many of these species also live in other habitats, which may in some cases be more optimal, as shown by the abundances given by Lange & Mwinzi (2003) and Ndalila (2011) for different habitats. Nevertheless, 20 (29%) of the mollusc species at Panga ya Saidi were classified as forest-only species, which have previously been recorded only from forest habitat. This includes large, reliably identified species for which this preference can be judged with most confidence, in both the early and late parts of the sequence (e.g. *Ischnoglessula gracillima*, *Kempioconcha terrulenta*, *Gittenedouardia alycaeoides*, and *Edentulina affinis*). This suggests that forest persisted locally throughout the entire period covered by the sequence.

The subtleties in the snail record suggest only minor or local changes in the fauna. In particular, an alteration in the relative abundance of forest-only and forest-rarely/never species in Layer 10 (in MIS 3, roughly 45,800 BP) and, to a lesser extent, in Layers 2 and 1 (<1000 BP) could indicate a local degradation or reduction of forest cover, shade, or rainfall. Isotopic evidence shows an increased consumption of C4 plants by prey species in Layers 10–12, an increase in the proportion of phytoliths from palms relative to woody plants, and larger bovids (hartebeest, topi, and wildebeest) rather than small ones (suni, duiker, and dikdik) (Shipton et al. 2018, Roberts et al. 2020, Prendergast et al. 2023). This could indicate a general reduction in local forest cover at this point in the sequence. The relatively high abundances of other, unassigned species in Layer 10 (e.g. *Gittenedouardia conulina*, *Gonaxis denticulatus*, and the new species *Juventigulella saidii*, which was not found in any other layer) suggest that these too may have responded to the putative forest reduction. Layer 10 shows a distinctive signature in the stone-tool technology, having very little evidence for simple bipolar technology, which is otherwise common in the sequence, but abundant evidence for complex Levallois technology (Shipton et al. 2021). All sources, including the molluscs, suggest a subsequent reversal to the previous, more wooded situation by the time of Layer 9 (38,300 BP). In marked contrast to Layer 10, Layer 9 has frequent evidence for bipolar stone knapping technology and no evidence for Levallois (Shipton et al. 2021). Layer 9 is also the only layer to feature bone-point technology at the site (d'Errico et al. 2020), possibly an innovative adaptation to the altered environment from Layer 10.

The second change in the relative abundance of forest-only and forest-rarely/never molluscs, seen in the most recent Layers 2 and 1, is highly likely to relate to deforestation during the last 1000 years, as a result of the arrival and spread of agricultural populations (Shipton et al. 2013, Crowther et al. 2018, Marchant et al. 2018). The late occurrence of *Rhachistia picturata* (excluded from analysis but present between the later layers) may indicate a relatively recent arrival of this species in the region. *Kempioconcha boivini*, *Opeas* sp./spp., and *Gulella gwendolinae* are relatively numerous in Layers 2 and 1. Several other species present in the final layer have not been found in the extant fauna at the coast (or at least not found alive, in the case of *G. expatriata*). Some may have been overlooked, but it is possible that others are already locally extinct as a result of forest loss during the historical era.

The mollusc sequence as a whole presents a remarkably complete picture of a rich fauna of the coastal forest throughout a long period of relative stability. The extent to which habitat changes can be detected is limited, due to the limited knowledge about the modern fauna's habitat preferences. A comparable fossil land-snail sequence from the Niah Caves, Sarawak, was discussed by Nekola et al. (2019). Like Panga ya Saidi, Niah is a cave complex with a comparable history of human occupation,

Figure 9. Panga ya Saidi subfossils: Streptaxidae. **A.** *Gonaxis quadrilateralis* (juvenile), NMW.Z.2014.016.00070. **B.** *Edentulina obesa obesa*, NMW.Z.2014.016.00053. **C.** *Gonospira expatriata* (2 shells, showing length variation), NMW.Z.2014.016.00055. **D.** *Gonaxis denticulatus*, NMW.Z.2014.016.00054. **E.** *Gulella (Plicigulella) vicina*, NMW.Z.2014.016.00065. **F.** *Ptychotrema* sp. (not *P. sperabile*), NMW.Z.2014.016.00069. **G**. *Ptychotrema sperabile*, NMW.Z.2014.016.00068. **H.** *Gulella foveolata*, NMK.PYS13. **I.** *Gulella tomlini*, NMW.Z.2014.016.00056. **J.** *Gulella marionae*, NMW.Z.2014.016.00061. **K.** *Gulella* sp. “large, smooth” (spire only), NMW.Z.2014.016.00062. A is at a different scale to B–K.

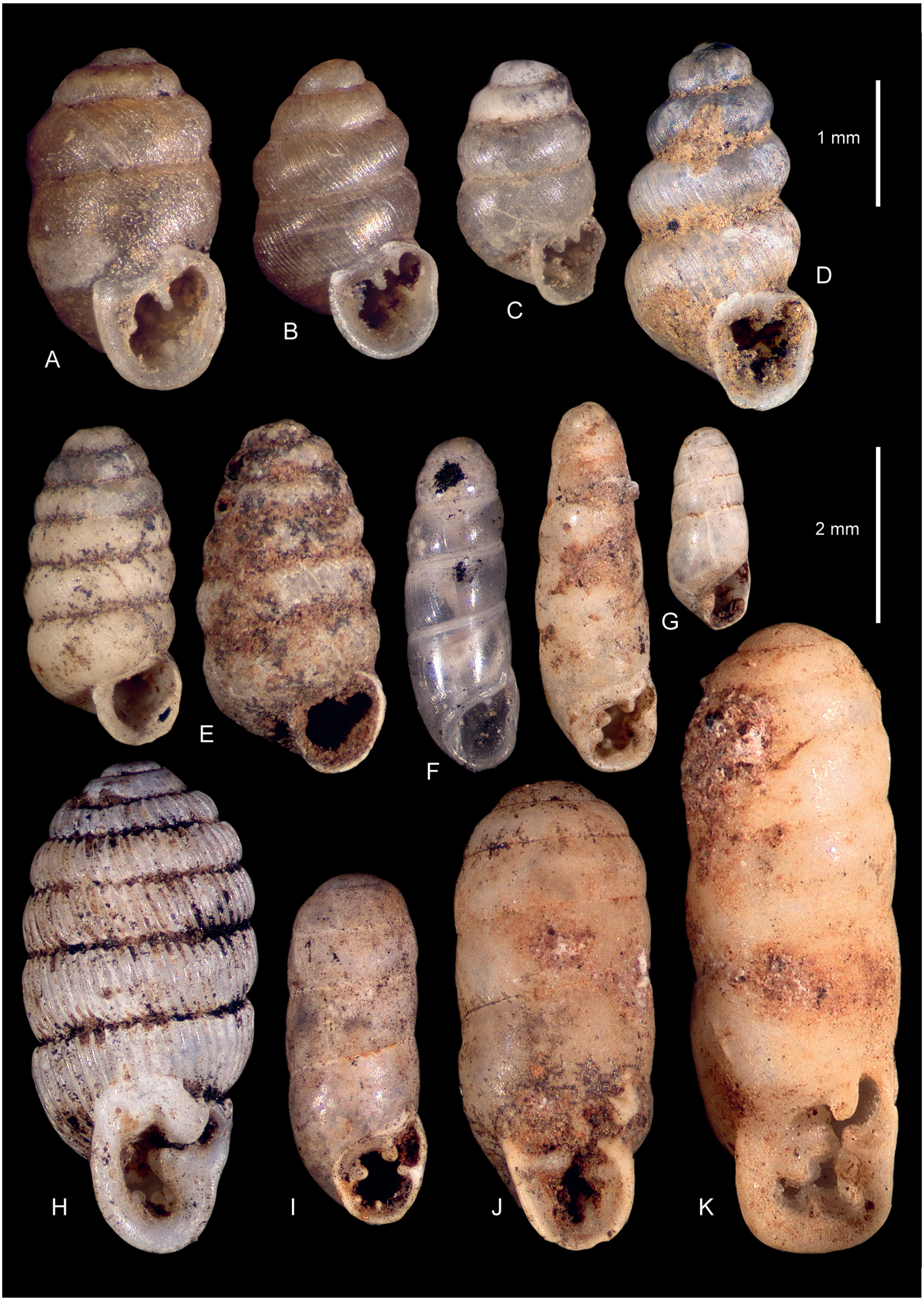

Figure 10. Panga ya Saidi subfossils: Vertiginidae, Gastrocoptidae, Truncatellinidae, and Streptaxidae. **A.** *Insulipupa malayana*, NMW.Z.2014.016.00045. **B.** *Vertigo bisulcata*, NMW.Z.2014.016.00042. **C.** *Afripupa misaliensis*, NMW.Z.2014.016.00043. **D.** *Gastrocopta klunzingeri*, NMW.Z.2014.016.00044. **E.** *Truncatellina ninagongonis*, NMW.Z.2014.016.00048. **F.** *Gulella streptostelopsis*, NMW.Z.2014.016.00064. **G.** *Gulella carea*, NMW.Z.2014.016.00063. **H.** *Gulella prestoni*, NMW.Z.2014.016.00057. **I.** *Gulella jod*, NMW.Z.2014.016.00059. **J.** *Gulella tracheia*, NMW.Z.2014.016.00060. **K.** *Gulella gwendolinae gwendolinae*, NMW.Z.2014.016.00058.

Figure 11. Panga ya Saidi subfossils: Streptaxidae. **A.** *Dadagulella conoidea*, NMW.Z.2014.016.00050. **B.** *Dadagulella radius radius*, NMW.Z.2014.016.00051. **C**. *Dadagulella radius browni*, NMW.Z.2014.016.00049. **D.** *Juventigulella peakei continentalis*, NMW.Z.2014.016.00067. **E.** *Juventigulella habibui*, NMW.Z.2014.016.00066. **F.** *Juventigulella saidii* sp. n., 3 views of holotype, NMK.PYS13.

situated amidst forest in the wet tropics (Barker & Farr 2016). At Niah, relative continuity in the mollusc fauna was considered to reflect both long-term habitat stability and biogeographical stasis in species ranges. This was contrasted with the changes shown by land-snail faunas in temperate regions (Nekola et al. 2019). The data from Panga ya Saidi suggest that the same pattern may be exhibited in tropical Africa. Nonetheless, the present data do indicate some range changes, and they highlight the value of studies of terrestrial molluscs for further exploring environmental and cultural interactions in East Africa. The present study also demonstrates the value of sediment flotation for obtaining records of terrestrial molluscs in these preservation circumstances. The exceptionally well-preserved assemblage at Panga ya Saidi contributes to ongoing reconstructions of the regional palaeofauna, but also we hope it will encourage further palaeoecological and ecological studies of terrestrial molluscs in the region.

Acknowledgements

This research was conducted as part of the Sealinks Project, funded by grants to NB from the European Research Council (no. 206148) and the Max Planck Society. We thank James Blinkhorn for his work on the excavation and Ruth Tibesasa for conducting the flotation. We are grateful to Sarah Foster and Seren Thomas for assistance with snail counts and photography. Dai Herbert confirmed the identification of *Endodonta kempi*. We thank John Hutchinson and 2 anonymous referees for comments that improved the manuscript.

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Manuscript submitted 1 August 2023
Revised manuscript accepted 19 November 2023