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Paleoecological insights from fossil freshwater mollusks of the Kanapoi  
Formation (Omo-Turkana Basin, Kenya)

Bert Van Bocxlaer<sup>a,b,\*</sup>

<sup>a</sup>Limnology Unit, Department of Biology, Ghent University, B-9000 Ghent, Belgium.

<sup>b</sup>CNRS, Univ. Lille, UMR 8198 – Evolution, Ecology, Paleontology, F-59000 Lille, France

\*Corresponding author. Address: UMR 8198 – Evolution, Ecology, Paleontology; Lille University –  
Science and Technology, Cité Scientifique – Bât. SN5, F-59655 Villeneuve d'Ascq cedex, France; E-  
mail: bert.van-bocxlaer@univ-lille1.fr; tel: +33 3 20 43 40 15.

**Running Title:** Fossil freshwater mollusks from Kanapoi



## Abstract

The Early Pliocene Kanapoi Formation of the Omo-Turkana Basin consists of two fluvial/deltaic sedimentary sequences with an intermediate lacustrine sequence that was deposited in Paleolake Lonyumun, the earliest large lake in the basin. Overall, the geology and vertebrate paleontology of the Kanapoi Formation are well studied, but its freshwater mollusks, despite being a major component of the benthic ecosystem, have not been subjected to in-depth study. Here I present the first treatment of these mollusks, which have been retrieved mainly from the lacustrine but also from the upper fluvial sediments, with a focus on paleoecological implications. Overall, the freshwater mollusk fauna is reasonably diverse and contains the gastropods *Bellamya* (Viviparidae), *Melanoides* (Thiaridae), *Cleopatra* (Paludomidae) and *Gabbiella* (Bithyniidae), as well as the unionoid bivalves *Coelatura*, *Pseudobovaria* (Unionidae), *Aspatharia*, *Iridina* (Iridinidae) and *Etheria* (Etheriidae). Material is typically recrystallized, lithified and its taphonomy suggests deposition in a system with intermediate energy, such as a beach, with post-depositional deformation and abrasion. The mollusk assemblage is indicative of perennial, fresh and well-oxygenated waters in the Kanapoi region. It suggests that Paleolake Lonyumun had largely open shores with limited vegetation and that swampy or ephemeral backwaters were rare. Overall, these findings support earlier paleoecological interpretations based on the fish assemblage of Paleolake Lonyumun at Kanapoi. Moreover, mollusk assemblages from this lake are very similar across the Omo-Turkana Basin (Nachukui, Usno, Mursi and Koobi Fora Formations) suggesting that the lacustrine paleoecological conditions found in the Kanapoi Formation existed throughout the basin.

**Keywords:** freshwater gastropods; freshwater bivalves; taphonomy; paleoecology; East African Rift System



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## Introduction

The Kanapoi Formation provides a unique insight into Early Pliocene environments in the southern Omo-Turkana Basin, including into the terrestrial and aquatic faunas of the region at that time (e.g., Harris et al., 2003; Stewart, 2003; Werdelin, 2003). Here I provide an overview of freshwater mollusks from the Kanapoi Formation, with a focus on their paleoenvironmental implications. Treatment of these mollusks is warranted here because unlike the geological setting and vertebrate remains of the Kanapoi Formation (e.g., Harris and Leakey, 2003), they have not been subjected to detailed studies before. Moreover, they arguably are an important component of the aquatic ecosystem, as evidenced by various shell assemblages, *Etheria* bioherms of up to 1 m in thickness (Feibel, 2003a), and the associated rich fauna of medium to large molluscivorous fishes (Stewart, 2003). Sediments of the Kanapoi Formation have a composite thickness of ~60 m, and they have been deposited during two fluvial/deltaic phases of the Kerio River system, with an intervening lacustrine phase (Fig. 1) (Feibel, 2003a). Three tuffs occur in the formation, i.e., the lower and upper pumiceous airfall tuffs and the vitric Kanapoi tuff. These tuffs have been dated to  $4.195 \pm 0.033$  Ma,  $4.147 \pm 0.019$  Ma and  $4.108 \pm 0.029$  Ma, respectively (McDougall and Brown, 2008). The Kanapoi Formation is capped by the Kalokwanya Basalt (Feibel, 2003a), which has been dated to ~3.4 Ma (Leakey et al., 1995), although its reversed magnetic polarity (Powers, 1980) is inconsistent with this age (McDougall and Brown, 2008). Most of the fossil remains of the Kanapoi Formation have been obtained from deposits between the lower pumiceous tuff and the Kanapoi tuff, including remains of *Australopithecus anamensis* Leakey, 1995 (Leakey et al., 1995; Leakey et al., 1998; Ward et al., 2013). Freshwater mollusks have only been obtained from sediments above the upper pumiceous tuff: some mollusk material derives from the



upper fluvial phase, but most is obtained from strata that were deposited during the lacustrine phase, i.e., in stratigraphic proximity to the Kanapoi tuff. These lacustrine sediments also contain ostracodes and plant fragments, and were deposited in Paleolake Lonyumun, the earliest extensive lacustrine interval in the Omo-Turkana Basin (Fig. 1) (Feibel, 1997, 2003a, 2011). Evidence of this paleolake is recorded throughout the whole Omo-Turkana Basin: from the Usno and Mursi Formations along the Omo River in the North (de Heinzelin, 1983), from the Lonyumun Member of the Nachukui Formation in West Turkana (Harris et al., 1988), from the Murungori Member of the same formation at Lothagam (Feibel, 2003b), from the Kanapoi Formation in Southwest Turkana (Feibel, 2003a), and from the Lonyumun Member of the Koobi Fora Formation in East Turkana (Brown and Feibel, 1991; Feibel et al., 1991). The Omo, Kerio and Turkwell Rivers were the main sources of inflow for Paleolake Lonyumun, and the lake is presumed to have been hydrologically open, with the Turkana River in the Southeast as outflow (Feibel, 2011). Paleolake Lonyumun appears to have been extensive but shallow and probably persisted for about 100 ka (Feibel, 2011). Below, I first introduce the mollusk fauna of the Kanapoi Formation, and subsequently I discuss its paleoenvironmental implications.

## Material and methods.

Remains of freshwater mollusks from the Kanapoi Formation have been collected during the Harvard University expeditions led by B. Patterson from 1964 to 1968, during expeditions by D. W. Powers in 1972, by C. S. Feibel in 1995 and 1996, and during fieldwork in 2014 led by C. W. Ward and F. K. Manthi. I here report on all of this material, ~925 specimens, however, as most material is preserved in lithified blocks of sediment future disaggregation may yield more specimens. Material is reported with original processing numbers for the first two expeditions (e.g., DVD KP6501L, with



DVD indicating Dirk Van Damme, who assigned the processing number, KP65 indicating the Kanapoi 1965 collecting event, 01 the sample number in that collecting event, and L the stratigraphic position. For this material two stratigraphic positions, i.e., lower [L] and upper [U] are possible, representing lacustrine and fluvial/deltaic environments, respectively. Other material is indicated with fieldcodes, e.g., CSF K96-5643 with CSF indicating Craig S. Feibel [collector], K96 representing Kenya 1996 and 5643 the sample number; KAP14-001 represents sample 001 from fieldwork at Kanapoi in 2014. Material will be deposited in museum collections after formal taxonomic treatment. Furthermore, some scattered Late Pleistocene-Holocene mollusk-bearing sediments occur at Kanapoi, but as these do not belong to the Kanapoi Formation this material is not treated here—they contain *Melanoides* cf. *tuberculata* (Müller, 1774) and *Iridina turkanica* Van Bocslaer and Van Damme, 2009.

Overall, the preservation of mollusks at Kanapoi is moderate to poor, certainly in comparison to those of the Nachukui, Koobi Fora and Shungura Formations, which relates to corrosion of specimens, recrystallization and abrasion. Much of the abrasion has occurred after deposition of material as part of the processes that have resulted in lithified shell beds: bivalves regularly are fragmented but the fragments are usually still in place, whereas flattened gastropod shells also evidence the great pressures associated with sediment compaction and potentially tectonic processes to which assemblages have been exposed. Additionally, shells may be dissolved, leaving mainly imprints of the external shell and internal molds. Similar processes are observed in other shell beds in the Turkana Basin of the same age, however, to varying degrees. For example, several shell beds in the Nachukui Formation have not been exposed to the same pressures as those experienced at Kanapoi, resulting in better preservation and less aggregation, so that in situ collecting is easier. As a



result of its preservation, mollusk material from the Kanapoi Formation is typically collected as shell-  
enclosing sediment blocks, or as weathered, surface-picked specimens.

Here, I describe the freshwater mollusk fauna from the Kanapoi Formation up to genus level and  
provide comments on specific attributes in the context of the current literature. Some of the included  
species are likely new to science, but I refrain from formal species-level description here for several  
reasons: First, my main focus here is on paleoenvironmental implications, which can be inferred at  
genus level, rather than on mollusk taxonomy. Second, descriptions ideally are complemented with  
objective morphometric comparisons and detailed diagnoses that allow distinguishing between  
closely related species that have been obtained from other regions in the Omo-Turkana Basin and  
other periods, which would detract from a strong focus on the Kanapoi Formation. Finally, for some  
taxa more typical and better preserved material is found elsewhere, and I consider it warranted that  
the type material is as complete as possible regarding diagnostic features. Nevertheless, as the  
mollusk fauna of the Kanapoi Formation is poorly known, I provide concise treatments and  
schematic reconstructions to allow identification of material in the field and to make  
paleoenvironmental interpretations more traceable and reproducible. However, I first investigate the  
effect of sample size upon the sampled genus-level diversity as a measure of how reliable we can  
expect paleoenvironmental interpretations to be. I performed individual-based rarefaction at the  
genus level with all abundance data pooled into a single reference sample. Assumptions and  
requirements for rarefaction are indicated in the discussion. Rarefaction was performed in R version  
3.2.1 (R Core Team, 2015) using the package iNEXT (Chao et al., 2014; Hsieh et al., 2016) and in  
EstimateS version 9.1.0 (Colwell et al., 2012; Colwell, 2013). Calculations were performed with  
variance estimators that are conditional or unconditional on the sampling data to calculate 95 %  
confidence intervals (CIs). Use of the conditional variance estimator allows examining expectancies



for samples that are considerably smaller than the observed ‘reference’ sample, but it results in increasingly narrow confidence intervals when the size of the estimated sample approaches that of the reference sample. As the reference sample represents a random sample from an unknown ecological community/assemblage, we can use the unconditional variance estimator to examine how reliable the sample represents the total assemblage, and to calculate extrapolated species richness estimates (Colwell et al. 2012). Finally, I calculated Chao1 as a non-parametric estimator of asymptotic richness.

## Results

### *Systematic Paleontology*

Viviparidae Gray, 1847

Bellamyinae Rohrbach, 1937

*Bellamyia* Jousseume, 1886

**Remarks.** A single species of *Bellamyia* appears to occur in the Kanapoi Formation (Fig. 2A), and it is morphologically very similar to material that has been referred to by Fuchs (1939: 269) as *Bellamyia unicolor* var. *rudolfianus* from deposits at Gaza waterhole (Alia Bay area, East Turkana), the Losidok (Lothidok) Hills (West Turkana) and from northwest of Labur (Northwest Turkana). However, the currently accepted concept of *Bellamyia unicolor* (Olivier, 1804), described from extant material from Alexandria, Egypt (Brown, 1994) appears to contain multiple phylogenetic lineages, like is the case for *B. capillata* (Frauenfeld, 1865) (Schultheiß et al., 2014; Sengupta et al., 2009), and as such it is in need of revision. The specimens of the Kanapoi Formation attain a size up to 30 mm and display a basal ridge surrounding the umbilicus. They likely belong to a species that is new to science, and that was abundant in Paleolake Lonyumun.





**Material examined:** CSF K95-5487 (23 specimens); CSF K95-5557 (12 specimens); CSF K96-5643 (4 specimens, 3 fragments); DVD KP6502L (10 fragmentary molds in a block); DVD KP6504L, KP6506L (3 internal molds); DVD KP6601L (15 internal molds, 1 recrystallized juvenile shell and 9 fragmentary shells); DVD KP6602L (19 internal molds, 12 fragmentary internal molds); DVD KP6601L, 6602L, 6604L, 7202L (4 specimens, somewhat deformed, 1 external mold, 1 fragment); DVD KP7201L (4 deformed fragments); DVD KP7203L (4 fragments, 9 internal molds, 1 external mold); DVD KP7205L (28 internal molds, 1 external mold, 3 fragments); DVD KP7206L (2 fragments); KAP14-001 (1 specimen); KAP14-002 (1 specimen); KAP14-003 (1 specimen); KAP14-004 (1 deformed specimen); KAP14-005 (3 specimen, 2 internal molds, 1 fragment). Other material of the same species is known from the Mursi Formation, the Nachukui Formation at Lothagam, and the Koobi Fora Formation.

Paludomidae Stoliczka, 1868

Cleopatrinae Pilsbry & Bequaert, 1927

*Cleopatra* Troschel, 1856

**Remarks.** A single species of *Cleopatra* appears to occur in the Kanapoi Formation (Fig. 2B), although dimorphism seems to exist in some samples, with a rare, small and often poorly preserved morph besides the typical form. I tentatively consider this small morph to be a variant of the same species. The typical form is very similar to the *Cleopatra* species described by Roger (1944) from the Omo Valley (between Kalam and Bourillé) as *C. arambourgi*, and also to material from Kubi Algi (the Lonyumun Member of the Koobi Fora Formation) that Williamson (1979, 1981), perhaps following Fuchs (1939), referred to the extant species *Cleopatra ferruginea* (Lea and Lea, 1850). However, as the



type locality of *C. ferruginea* is Zanzibar (Brown, 1994), substantial differences exist in geographical and temporal occurrence with material from the Kanapoi Formation. Moreover, growth patterns differ somewhat between both species, with *C. arambourgi* growing more in width early on, and later in length, resulting in a wider apical angle in juveniles than adults, whereas the apical angle in *C. ferruginea* remains more constant through life. As such, I consider it unlikely that *C. arambourgi* is conspecific with *C. ferruginea*. *Cleopatra* sp. A of Van Damme and Gautier (1972) from the Omo Valley is also conspecific with *C. arambourgi*.

**Material examined:** CSF K96-5643 (~70 shells); DVD KP6502L (14 specimens, 17 fragments); DVD KP6505U (16 specimens in blocks); DVD KP6601L (15 specimens, 1 fragment, 1 external mold); DVD KP6601L, 6602L, 6604L, 7202L (2 specimens); DVD KP6605L (3 specimens); DVD KP7201L (3 internal molds); DVD KP7203L (16 internal molds, 1 external mold); DVD KP7205L (~95 internal molds in blocks); DVD KP7206L (7 fragments); KAP14-004 (1 fragment); KAP14-005 (33 specimens, 1 fragment). Material is also known from East Turkana, the Omo Valley and the Lothidok area.

Thiaridae Gill, 1871

*Melanoides* Olivier, 1804

Williamson (1979, 1981) considered all *Melanoides* specimens from the lower part of the Koobi Fora Formation and Holocene Beds in the Turkana Basin to be *Melanoides tuberculata*, and he specifically referred material from the Kanapoi Formation to belong to *Melanoides tuberculata* as well. Earlier, Van Damme and Gautier (1972) considered *Melanoides* from the Mursi Formation of the Omo-Turkana Basin to be a new subspecies of *Melanoides tuberculata*. A difficulty with the identification of *Melanoides*



is that several species appear to be morphologically very variable, perhaps because of parthenogenetic reproduction, and, furthermore, that polyploid lineages exist (Jacob, 1957; Samadi et al., 1999, 2000). Moreover, recent molecular work indicates that a number of different species with similar shell morphological features are likely aggregated under *M. tuberculata*, including a native African as well as an invasive oriental lineage (Genner et al., 2004; Van Bocxlaer et al., 2015). The material from the Kanapoi Formation is morphologically variable, but most specimens are ornamented with strong, often nodular ribs, a subsutural cord and other spiral cords at the base, as well as fainter spiral lines in between (Fig. 2C). The ribs are more widely spaced than those of *M. reticosta* (von Martens, 1882), and the set of ornamentation displayed by *Melanoides* from the Kanapoi Formation is not observed in extant populations of *M. tuberculata* (Van Bocxlaer et al., 2015). As such, I consider it more likely that the *Melanoides* species of the Kanapoi Formation represents a separate species, but more in-depth morphometric work is required to confirm this issue.

**Material examined:** CSF K96-5643 (~60 relatively well preserved specimens); DVD KP6501L (48 specimens in blocks); DVD KP6503L (1 specimen); DVD KP6601L (1 specimen); DVD KP6605L (~105 specimens in blocks); KAP14-005 (53 isolated specimens and more specimens in blocks of sediment). In-depth work on other faunas is required to establish the geographical extent of this taxon.

Bithyniidae Gray, 1857

*Gabbiella* Mandahl-Barth, 1968

**Remarks.** Some evidence of the presence of Bithyniidae has been found in the Kanapoi Formation, consisting of one shell, an inner core, and several opercula. As the preservation is poor, identification



at the genus level is somewhat tentative, but supported by the strongly calcified opercula and a specimen resembling *Gabbiella* in contemporaneous deposits of the Mursi Formation (DVD MU6801). It is somewhat surprising that this taxon is mainly known from opercula in the Kanapoi Formation, because *Gabbiella* typically has a relatively thick shell, so that preservation bias is not a likely cause for its absence. It is possible that the taxon was rare in general, or largely restricted to specific microhabitats, e.g., associated with aquatic plants, that may have been underrepresented in the Kanapoi Formation.

**Material examined:** CSF K96-5640 (~5 opercula); DVD KP6502L (1 specimen, identification tentative); DVD KP6601L (1 inner core and 2 opercula). As mentioned, the taxon also occurs in the Mursi Formation.

Unionidae Rafinesque, 1820

Coelaturinae Modell, 1942

*Coelatura* Conrad, 1853

**Remarks.** I reported earlier that two *Coelatura* species appear to be present in the Kanapoi Formation, i.e., *C. aegyptiaca* (Cailliaud, 1827) and *C. bakeri* (Adams, 1866), although these identifications were reported as tentative (Van Bocxlaer, 2011). Both taxa are very variable in shell shape in the extant fauna (Mandahl-Barth, 1954, 1988), and in fossil deposits from the Turkana Basin, as evidenced from shell shape data based on elliptic Fourier analysis (Van Bocxlaer, 2011). However, *C. aegyptiaca* specimens have a posterior wing and more prominent angulations at the anterior and posterior sides of the dorsal margin than *C. bakeri*, which typically is more elongate (Mandahl-Barth, 1954, 1988). The morphotype resembling *C. aegyptiaca* is represented in Fig. 2E.



Typical *C. bakeri* specimens display zigzag sculpture on the umbo, whereas *C. aegyptiaca* bears tubercles (Van Bocxlaer, 2011). Two issues affect identification of *Coelatura* specimens from the Kanapoi Formation: most specimens are preserved as fragments and, second, umbonal sculpture is difficult to discern on most specimens of the Kanapoi Formation, perhaps because of recrystallization of the material. Nevertheless, specimens with features of each taxon, including umbonal sculpture, have been obtained from the Kanapoi Formation, suggesting that both were present. Additional, better-preserved material from the Kanapoi Formation and molecular work on extant representatives of both species may elucidate the current ambiguity.

**Material examined:** (identifications are tentative) *C. aegyptiaca*: CSF K96-5643 (5 doublets, some more valves and fragments); DVD-KP6606L (mold of 1 doublet, 10 internal molds of valves, 6 fragmentary valves); KAP14-005 (1 valve); *C. bakeri*: DVD KP6501L (2 doublets, 1 valve); DVD KP6503L (5 fragmentary valves); DVD-KP6601L/6602L/KP6604L/7202L (1 doublet, 3 imprints); DVD-KP6605L (5 doublets, 19 fragmentary valves); KAP14-005 (1 doublet); *Coelatura* sp. indet.: DVD KP6501L (2 fragmentary valves, 2 external molds); DVD-KP6503L (1 valve, 2 external molds); DVD KP6602L (2 fragmentary valves); DVD-KP6605L (37 fragmentary valves); DVD KP6606L (2 valves); KAP14-005 (18 fragmentary valves). *Coelatura aegyptiaca* and *C. bakeri* occur in various regions of the Turkana Basin, including in the Nachukui Formation at Lothagam and West Turkana, the Mursi Formation, the Koobi Fora Formation and the Shungura Formation, and in various periods, notably in Paleolakes Lonyumun and Lorenyang (Van Bocxlaer, 2011).

Unionidae with uncertain subfamily position

*Pseudobovaria* Adam, 1957



**Remarks.** Several features, including the hinge, indicate that the extinct genus *Pseudobovaria* belongs to Unionidae, however, its attribution at the subfamily level is uncertain. Morphologically, representatives of the genus compare well to the North American genera *Obovaria* Rafinesque, 1819, and *Pleurobema* Rafinesque, 1819, which belong to the subfamily Amblesminae Rafinesque, 1820. Extant representatives of this subfamily are deeply split molecularly, and geographically distant from African taxa (Whelan et al., 2011), suggesting that remarkable convergence is the most likely cause of similarity. Also Gonideinae Ortmann, 1916, to which Van Damme and Pickford (2010) attributed *Pseudobovaria*, is deeply split from Coelaturinae Modell, 1942 (Whelan et al., 2011), and given that good arguments for any subfamily attribution are lacking, I consider the genus' position within Unionidae currently uncertain. In any case, the few *Pseudobovaria* valves that have been obtained from the Kanapoi Formation differ morphologically from previously described *Pseudobovaria* species in that they are more elongate, with valves and hinges that are less strongly calcified (Fig. 2D). As such they likely represent a new species. Better preserved material has been obtained from the Nachukui Formation near Kalokol. Van Damme and Gautier (1972) also obtained material of this taxon from the Mursi and Usno Formations, but at the time they considered it to belong to *Nyassunio* Haas, 1936.

**Material examined:** DVD KP6502L (1 specimen); DVD KP6601L (17 specimens in blocks, some being fragmentary). Finds at other localities are indicated in the remarks.

Iridinidae Swainson, 1840

Aspathariinae Modell, 1942

*Aspatharia* Bourguignat, 1885



**Remarks.** Some material that can be attributed to *Aspatharia* has been obtained from the Kanapoi Formation, but it is not well preserved. However, at least part of the fragments that have been obtained display conspicuous radial ridges on the posterior-dorsal surface of the shell, linking the material with better preserved specimens from the Mursi Formation. This material has been assigned to *A. cf. rugifera* (Dunker, 1858) (Van Bocxlaer and Van Damme, 2009). More and better preserved material, as well as insights into the phylogenetic relationships between extant *Aspatharia* species, may elucidate the affinities of the material better in the future. In any case, *A. rugifera* is currently confined to West African rivers (Mandahl-Barth, 1988).

**Material examined:** DVD KP 6603L (1 internal mold, fragments of 6 doublets, 1 fragmentary valve with the typical ornamentation on the posterior side); KP 6504L (1 fragment of a doublet); KP6501L (fragments of ?*Aspatharia*). More material of this taxon has been obtained from the Mursi Formation.

Iridininae Swainson, 1840

*Iridina* Lamarck, 1819

**Remarks.** Much material from the Kanapoi Formation belonging to Iridininae is fragmentary, but at least part of the material can be clearly assigned to *Iridina subelongata* Gautier, 1965 (Van Bocxlaer and Van Damme, 2009). Some other fragments do not display a denticulate hinge, which may have resulted from corrosion or abrasion. As Van Bocxlaer and Van Damme (2009) indicated, it is possible that a second iridinine species occurs in the Kanapoi Formation, but no sufficiently well-preserved material exists to confirm this hypothesis.





**Material examined:** CSF K96-5643 (3 doublets, fragmentary valves of *Iridina* sp. indet); CSF K95-5487 (fragments of *Iridina* sp. indet); DVD-KP 6503L (1 doublet); 6605L (fragments of 4 doublets and 1 single valve); 6606L (5 fragmentary external molds); 7204L (fragmentary molds); all of these samples, except for 6605L contain additional unidentifiable *Iridina* fragments and/or internal molds; KAP14-005 (fragments of *Iridina*, possibly of *I. subelongata*). More material has been obtained from the Mursi, Usno, Nachukui, Koobi Fora and Shungura Formations.

Etheriidae Deshayes, 1832

*Etheria* Lamarck, 1807

**Remarks.** *Etheria* has been considered to be monospecific in the latest systematic treatments of extant African freshwater mollusks (Mandahl-Barth, 1988; Daget, 1998; Graf and Cummings, 2007), and in this context Van Damme and I attributed all *Etheria* specimens obtained from the Turkana Basin to *Etheria elliptica* Lamarck, 1807 (Van Bocxlaer and Van Damme, 2009). Recent work (Elderkin et al., 2016), however, indicates deep phylogenetic splits between populations of *Etheria*, suggesting that some of the other described species, e.g., by Lamarck (1807), may actually be valid. As *Etheria* has very limited diagnostic shell-morphological features at the species level (Mandahl-Barth, 1988) it will be a challenge to clear up the existing taxonomic confusion. As such, the Turkana Basin may have, over time, been home to several *Etheria* species, but for now, I am unable to revise our previous assignment as knowledge on the extant *Etheria* fauna remains too fragmentary. I have not had an opportunity to investigate *Etheria* specimens from Kanapoi, but Feibel (2003a) identified a reef of *Etheria* in his section CSF 96-12, directly on top of the Kanapoi Tuff. The lack of samples may relate to the practical difficulties to sample a bioherm. The reconstruction provided here (Fig. 2H) is based on a contemporary specimen from the Lothagam area of the Nachukui Formation.





### Rarefaction

As mentioned, all the examined material was pooled into a single sample for individual-based rarefaction. For *Etheria* five specimens were included to cover the existing reports on its presence in the Kanapoi Formation, resulting in a total sample size of  $n = 931$ . The accumulation curve reaches an asymptote well before the total number of individuals sampled, and the associated 95 % CIs are narrow, even upon using the unconditional variance estimator and at sample sizes approximating the total size of the reference sample (Fig. 3). Non-parametric asymptotic richness (Chao1; mean and 95 % CI) converges to the generic richness in our reference sample ( $n = 9$ ).

## Discussion

Rarefaction has a number of requirements that may be difficult to meet in a paleontological context (e.g., standardized sampling of lithified shell assemblages), and it makes a number of assumptions (e.g., random distribution of individuals in environments), which may be affected by taphonomic processes (see e.g., Foote, 1992; Gotelli and Colwell, 2001). As such, results are to be interpreted with care. Nevertheless, chances that the number of genera sampled underestimates the true but unknown diversity significantly are small if our collective, historic sampling of freshwater mollusks is representative of all existing shell beds in the Kanapoi Formation. Note that the seeming sufficiency of the collected material for reliable paleoecological interpretations does not contradict the need of more and better preserved material for species-level taxonomy.

I have made some comments on the preservation of mollusk specimens already, but discuss taphonomic aspects related to depositional environments in more detail here. Shells from the Kanapoi Formation have typically been rolled somewhat before they were deposited, resulting



regularly in the abrasion of early whorls and the aperture in gastropods, and sometimes in the separation of both valves in bivalves. However, the abrasion taking place before deposition remains overall limited and doublets are still commonly obtained in bivalves. Overall this indicates a depositional environment with intermediate water energy, much like is the case for beach deposits in other African Great Lakes. I have not observed indications that would suggest long distance transportation, except perhaps the difference in abundance between bithyniid opercula and shells. The taxa recovered from the Kanapoi Formation are medium to large (longest axis ~1.0 cm or larger) and rather strongly calcified, indicating that smaller and more fragile taxa, such as some heterobranchs, may have been present, especially in fluvial deposits, but not preserved due to preservation bias. Perhaps the rarity of bithyniid shells is caused by this factor, but *Gabbiella* is typically rather thick-walled. Furthermore, the presence of even smaller, but chemically more resistant calcareous bithyniid opercula indicates that size alone is no major driver of any preservation bias. Aragonite dissolution does not provide a straightforward explanation for the absence of certain taxa neither. Overall the effects of dissolution vary between sampling sites of Paleolake Lonyumun, but even in the Mursi Formation, which is heavily affected by dissolution, a *Gabbiella* shell (our results) and two genera of Sphaeriidae Deshayes, 1855 with very fragile shells were preserved (Van Damme and Gautier, 1972). Furthermore, most assemblages of the Kanapoi Formation show limited evidence for dissolution, e.g., the fragile, aragonitic early teleoconchs of *Melanoides* are occasionally preserved. Variation in preservation potential may vary between habitats (e.g., sites with more vegetation may create more acidic depositional environments due to decaying plant material), but a specimen of the heterobranch *Bulinus* Müller, 1781 is known from the Nachukui Formation at Lothagam, indicating, together with the observations in the Mursi Formation, that there are no basin-wide factors that have eliminated the chances for the preservation of fragile specimens in



deposits of Paleolake Lonyumun. Most thin-shelled heterobranchs typically adopt a cryptic lifestyle within vegetation, where they are better protected against predators (Brown, 1994). None of the freshwater mollusk taxa present in the Kanapoi Formation prefers this type of habitat, which may indicate the overall limited occurrence of vegetation-rich habitats in Paleolake Lonyumun at Kanapoi. This finding is corroborated by the fish assemblages of the Kanapoi Formation, which are rare in herbivores (Stewart, 2003). Note that the remains of such herbivorous fish would not be affected by any of the abovementioned potential sources of preservation bias for mollusks.

In general, the freshwater mollusk fauna of the Kanapoi Formation is with ~10 species modestly to reasonably diverse. In genus-level composition the fauna is very similar to the modern mollusk fauna of the southern waters of Lake Chad, apart from the fact that a diversity of (small, fragile) heterobranchs have been recorded from the surroundings of this lake (Lévêque and Saint-Jean, 1979; Brown, 1994). Lake Chad lacks the extinct *Pseudobovaria*, but contains the similar-sized corbiculid bivalve *Corbicula* von Mühlfeld, 1811. *Corbicula* appears to have been absent from Paleolake Lonyumun, but it is present in later paleolakes in the Turkana Basin (e.g., Van Bocxlaer et al., 2008; Williamson, 1981). Not unlike in Lake Chad, mollusks reached great biomass in Paleolake Lonyumun, as evidenced from the deposition in a mollusk packstone of up to 1 m in thickness. The gastropods *Cleopatra*, *Melanooides* and *Bellamya* are the most abundant taxa, representing ~32, 29 and 19 % of the recovered specimens, respectively. The substantial molluscan biomass in Paleolake Lonyumun is also corroborated by the presence of a diverse community of medium to large molluscivore fishes (Stewart, 2003). Substantial diversity in unionoids, which have a fish-parasitizing larval stage, is furthermore congruent with substantial fish diversity.



The mollusk assemblage indicates the presence of year-round waters, with open sandy shorelines, and some aquatic macrophytes. Reed fringes and swampy areas, as regularly associated with deltaic conditions, were likely restricted at Kanapoi during the lacustrine phase—several of the occurring mollusk taxa do not tolerate desiccation or oxygen stress, avoid marginal reed mats, and most of the occurring taxa are typically restricted to perennial waterbodies (*Bellamya*, *Gabiella*, and unionoids) (Brown, 1994; Van Bocxlaer et al., 2011). Moreover, some of these taxa, e.g., *Bellamya*, have a limited tolerance for brackish/saline conditions (Lévêque, 1972) indicating that Paleolake Lonyumun was substantially less saline than the current Lake Turkana. The freshwater mollusks of the Kanapoi Formation therefore indicate well-oxygenated, freshwater conditions, which is also suggested by the associated fish assemblage (Stewart, 2003). Furthermore, amphibious snails that are adapted to swamp-like and seasonally desiccating habitats, e.g., the ampullariids *Pila* Röding, 1798 and (to somewhat lesser extent) *Lanistes* Montfort, 1810, are absent, not only from the Kanapoi Formation, but also from most other contemporaneous deposits of Paleolake Lonyumun. The general absence of ampullariids indicates that the lake, despite presumably being shallow (Feibel, 1997), had substantial stretches of open water, probably not unlike Lake Victoria today, and that shallow, densely vegetated and potentially seasonally desiccating lagoons were rare. Some *Lanistes* and *Bulinus* specimens have been obtained from the Nachukui Formation at Lothagam, but their exact age is somewhat uncertain. Nevertheless, the occurrence of amphibious snails at Lothagam is again congruent with the fish community, which unlike that at Kanapoi, includes species that are regularly associated with vegetated, shallow backwaters or bays, i.e., *Protopterus* Owen, 1839, *Polypterus* Geoffroy Saint-Hilaire, 1802 and *Heterotis* Ruppell, 1829 (Stewart, 2003). As such, both the fish and mollusk communities suggest that lacustrine environments at Kanapoi were substantially different from those at Lothagam. The contrast in habitats is perhaps most eloquently indicated by comparing



the mollusk fauna obtained from lacustrine and fluvial/deltaic deposits of the Kanapoi Formation (Table 1), although in all fairness, fluvial mollusk-bearing deposits are much rarer and likely still underrepresented in current samples of the Kanapoi Formation. In any case, it is probably not a coincidence that only *Cleopatra*, which is more tolerant to a number of stressors than *Bellamya* and unionoid bivalves (Brown, 1994; Van Bocxlaer et al., 2011), was obtained from fluvial/deltaic deposits. Although the sediments of the Kanapoi Formation provide the oldest record of fluvial sediments deposited by the Kerio River, and although most of the terrestrial vertebrates may have been deposited in the paleoenvironment of a deltaic tongue that extended into the subsequently expanding Palaeolake Lonyumun (Feibel, 2003a), most of the freshwater mollusks have been deposited in a fully lacustrine context rather than in a fluvial/deltaic environment.

Exploratory comparisons of the freshwater mollusk fauna of the Kanapoi Formation to mollusk faunas that have been deposited in other parts of the Turkana Basin during the existence of Paleolake Lonyumun indicate overall great faunal resemblance across regions (see also systematic paleontology). This resemblance indicates that the lake was indeed large, but that faunal connectivity between its various regions was nevertheless good. If this finding remains standing after more in-depth morphometric comparisons, it suggests that the lake was too short-lived for intra-lacustrine speciation and the emergence of regional endemism. Our understanding of the Early Pliocene freshwater mollusk faunas of Africa is too limited to make strong predictions as to the biogeographic origin of the molluscan assemblage of the Kanapoi Formation. However, some similarities exist with the fauna of the Albertine Basin, where *Iridina subelongata* and *Pseudobovaria* occurred since the Miocene (Van Damme and Pickford, 2010). Moreover, the hydrographic catchment of the Albertine Basin extended substantially further eastward in the Early Pliocene than it does currently (Salzburger



et al., 2014). The occurrence of *A. cf. rugifera* in the Turkana Basin may also highlight a stronger connectivity between East and West African faunas in the Early Pliocene. Care needs to be taken with this interpretation as the Early Pliocene freshwater mollusk fauna of North Africa, and the hydrographic connections of the Omo River, are poorly known. Nevertheless, progressive rift formation and the associated emergence of long-lasting waters in the Early Pliocene Turkana Basin have attracted diverse terrestrial and aquatic faunas. The Kanapoi Formation provides, among the first places, testimony to the start of a strongly interlinked succession of terrestrial and aquatic faunal diversity in the Omo-Turkana Basin as climate and environments changed through time.

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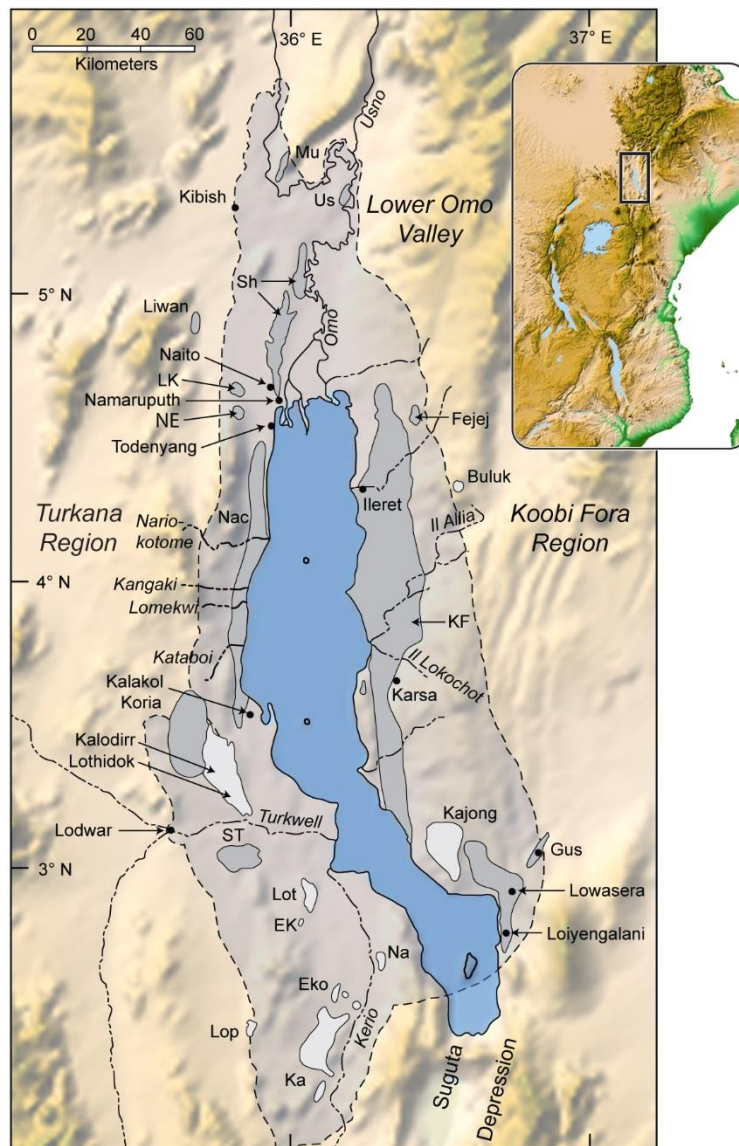


**Table 1.** Comparison between the mollusk fauna derived from lacustrine and fluvial/deltaic deposits of the Kanapoi Formation. Note however that fluvial/deltaic mollusk-bearing deposits are substantially less abundant than lacustrine ones, and therefore underrepresented. A = absent; P = present.

<b>Taxa</b>	<b>Lac.</b>	<b>Fluv./Delt.</b>
<b>Gastropoda</b>		
<i>Bellamyia</i>	P	A
<i>Cleopatra</i>	P	P
<i>Melanoides</i>	P	A
<i>Gabbiella</i>	P	A
<b>Bivalvia</b>		
<i>Coelatura</i>	P	A
<i>Pseudobovaria</i>	P	A
<i>Aspatharia</i>	P	A
<i>Iridina</i>	P	A
<i>Etheria</i>	P	A



## Figures.

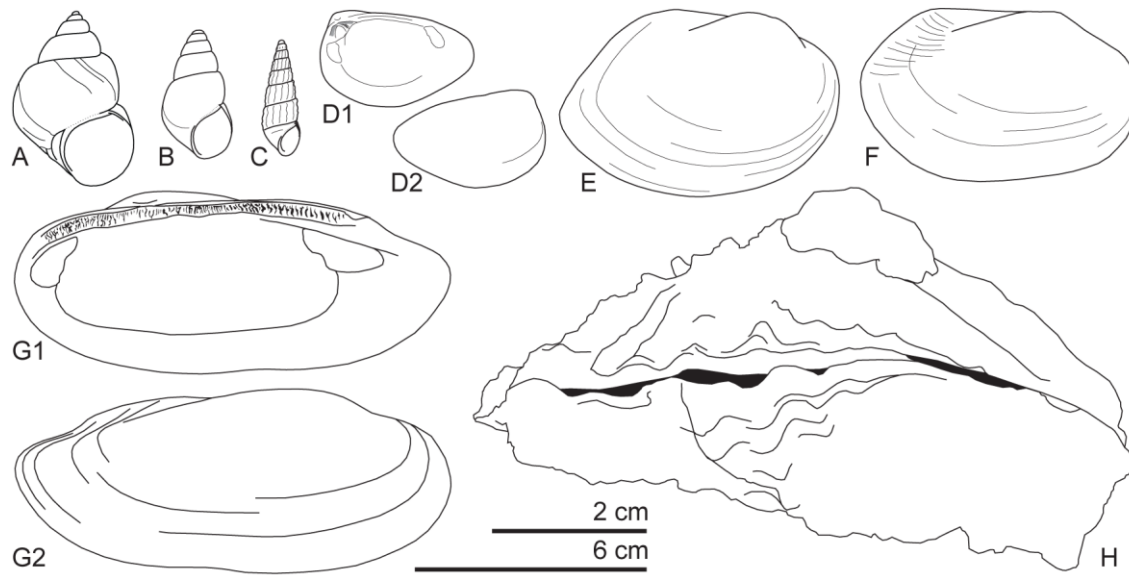


**Figure 1.** Topographic representation of the East African Rift System and the Omo-Turkana Basin, with major areas of exposure of Neogene sediments indicated in gray (light gray areas in the South are Mio-Pliocene localities, darker grey areas in the north indicate exposures belonging to the Omo Group). Lake Turkana is indicated in blue and the approximate extent of Paleolake Lonyumun at ~4.1 Ma ago, in which the lacustrine deposits of the Kanapoi Formation (southwestern Omo-

Turkana Basin) were deposited, with a dashed line. Although the Kanapoi Formation is geographically restricted and although it captures a relatively short period in the history of the basin, studies of its deposits have been exceptionally informative as to the geology of the basin as well as biological and hominin cultural evolution. Abbreviations: KF = Koobi Fora Formation (Fm.); LK = Loruth Kaado Fm.; Lop = deposits at Loperot; Lot = Lothagam area of Nachukui Fm.; Mu = Mursi Fm.; Na = deposits at Nakoret; Nac = Nachukui Fm., NE = Nayiena Epul Fm.; Sh = Shungura Fm.; ST = deposits at South Turkwell; US = Usno Fm. Map compiled from topographic data of Amante and Eakins (2009) with data from Brown and Feibel (1991) and Feibel (2011).

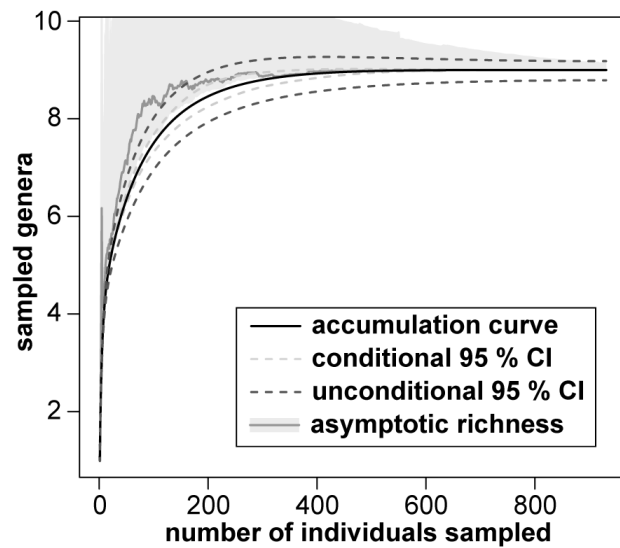






**Figure 2.** Freshwater mollusks of the Kanapoi Formation. A) *Bellamya*, B) *Cleopatra*, C) *Melanoides*, D) *Pseudobovaria*, E) *Coelatura*, F) *Aspatharia*, G) *Iridina*, H) *Etheria* (ventral view). Scale bar of 2 cm for A-E, that of 6 cm for F-H.





**Figure 3.** Individual-based rarefaction at the genus level with all fossil freshwater mollusk finds of the Kanapoi Formation pooled into a single reference sample. The rarefaction curve reaches a plateau well before the total number of individuals sampled ( $n = 931$ ), and assuming that the reference sample is representative of the total diversity of shell assemblages in the Kanapoi Formation, our material likely approaches the real but unknown genus-level diversity of freshwater mollusks in the formation. This interpretation is supported by the narrow confidence interval based on the unconditional variance at the total sample size and the convergence of the asymptotic richness to the accumulation curve for large samples. 95 % confidence intervals on the rarefaction curve based on conditional or unconditional variance estimators are indicated with dashed lines, the 95 % confidence interval on asymptotic richness as a grayscale polygone.