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► **To cite this version:**

Bert Van Bocxlaer. Paleoecological insights from fossil freshwater mollusks of the Kanapoi Formation (Omo-Turkana Basin, Kenya). *Journal of Human Evolution*, 2020, 140, pp.102341. 10.1016/j.jhevol.2017.05.008 . hal-02323652

HAL Id: hal-02323652

<https://hal.science/hal-02323652>

Submitted on 18 Aug 2020

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

3

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5

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11

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



13 **Abstract**

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

33

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

35 System



36 Introduction

37 The Kanapoi Formation provides a unique insight into Early Pliocene environments in the southern
38 Omo-Turkana Basin, including into the terrestrial and aquatic faunas of the region at that time (e.g.,
39 Harris et al., 2003; Stewart, 2003; Werdelin, 2003). Here I provide an overview of freshwater
40 mollusks from the Kanapoi Formation, with a focus on their paleoenvironmental implications.
41 Treatment of these mollusks is warranted here because unlike the geological setting and vertebrate
42 remains of the Kanapoi Formation (e.g., Harris and Leakey, 2003), they have not been subjected to
43 detailed studies before. Moreover, they arguably are an important component of the aquatic
44 ecosystem, as evidenced by various shell assemblages, *Etheria* bioherms of up to 1 m in thickness
45 (Feibel, 2003a), and the associated rich fauna of medium to large molluscivorous fishes (Stewart,
46 2003).

47 Sediments of the Kanapoi Formation have a composite thickness of ~60 m, and they have been
48 deposited during two fluvial/deltaic phases of the Kerio River system, with an intervening lacustrine
49 phase (Fig. 1) (Feibel, 2003a). Three tuffs occur in the formation, i.e., the lower and upper
50 pumiceous airfall tuffs and the vitric Kanapoi tuff. These tuffs have been dated to 4.195 ± 0.033 Ma,
51 4.147 ± 0.019 Ma and 4.108 ± 0.029 Ma, respectively (McDougall and Brown, 2008). The Kanapoi
52 Formation is capped by the Kalokwanya Basalt (Feibel, 2003a), which has been dated to ~3.4 Ma
53 (Leakey et al., 1995), although its reversed magnetic polarity (Powers, 1980) is inconsistent with this
54 age (McDougall and Brown, 2008).

55 Most of the fossil remains of the Kanapoi Formation have been obtained from deposits between the
56 lower pumiceous tuff and the Kanapoi tuff, including remains of *Australopithecus anamensis* Leakey,
57 1995 (Leakey et al., 1995; Leakey et al., 1998; Ward et al., 2013). Freshwater mollusks have only been
58 obtained from sediments above the upper pumiceous tuff: some mollusk material derives from the



59 upper fluvial phase, but most is obtained from strata that were deposited during the lacustrine phase,
60 i.e., in stratigraphic proximity to the Kanapoi tuff. These lacustrine sediments also contain ostracodes
61 and plant fragments, and were deposited in Paleolake Lonyumun, the earliest extensive lacustrine
62 interval in the Omo-Turkana Basin (Fig. 1) (Feibel, 1997, 2003a, 2011). Evidence of this paleolake is
63 recorded throughout the whole Omo-Turkana Basin: from the Usno and Mursi Formations along
64 the Omo River in the North (de Heinzelin, 1983), from the Lonyumun Member of the Nachukui
65 Formation in West Turkana (Harris et al., 1988), from the Murungori Member of the same
66 formation at Lothagam (Feibel, 2003b), from the Kanapoi Formation in Southwest Turkana (Feibel,
67 2003a), and from the Lonyumun Member of the Koobi Fora Formation in East Turkana (Brown and
68 Feibel, 1991; Feibel et al., 1991). The Omo, Kerio and Turkwell Rivers were the main sources of
69 inflow for Paleolake Lonyumun, and the lake is presumed to have been hydrologically open, with the
70 Turkana River in the Southeast as outflow (Feibel, 2011). Paleolake Lonyumun appears to have been
71 extensive but shallow and probably persisted for about 100 ka (Feibel, 2011). Below, I first introduce
72 the mollusk fauna of the Kanapoi Formation, and subsequently I discuss its paleoenvironmental
73 implications.

74

75 **Material and methods.**

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

4



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

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



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

106 Here, I describe the freshwater mollusk fauna from the Kanapoi Formation up to genus level and
107 provide comments on specific attributes in the context of the current literature. Some of the included
108 species are likely new to science, but I refrain from formal species-level description here for several
109 reasons: First, my main focus here is on paleoenvironmental implications, which can be inferred at
110 genus level, rather than on mollusk taxonomy. Second, descriptions ideally are complemented with
111 objective morphometric comparisons and detailed diagnoses that allow distinguishing between
112 closely related species that have been obtained from other regions in the Omo-Turkana Basin and
113 other periods, which would detract from a strong focus on the Kanapoi Formation. Finally, for some
114 taxa more typical and better preserved material is found elsewhere, and I consider it warranted that
115 the type material is as complete as possible regarding diagnostic features. Nevertheless, as the
116 mollusk fauna of the Kanapoi Formation is poorly known, I provide concise treatments and
117 schematic reconstructions to allow identification of material in the field and to make
118 paleoenvironmental interpretations more traceable and reproducible. However, I first investigate the
119 effect of sample size upon the sampled genus-level diversity as a measure of how reliable we can
120 expect paleoenvironmental interpretations to be. I performed individual-based rarefaction at the
121 genus level with all abundance data pooled into a single reference sample. Assumptions and
122 requirements for rarefaction are indicated in the discussion. Rarefaction was performed in R version
123 3.2.1 (R Core Team, 2015) using the package iNEXT (Chao et al., 2014; Hsieh et al., 2016) and in
124 EstimateS version 9.1.0 (Colwell et al., 2012; Colwell, 2013). Calculations were performed with
125 variance estimators that are conditional or unconditional on the sampling data to calculate 95 %
126 confidence intervals (CIs). Use of the conditional variance estimator allows examining expectancies



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

134

135 **Results**

136 *Systematic Paleontology*

137 Viviparidae Gray, 1847

138 Bellamyinae Rohrbach, 1937

139 *Bellamyia* Jousseume, 1886

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



150
151 **Material examined:** CSF K95-5487 (23 specimens); CSF K95-5557 (12 specimens); CSF K96-5643
152 (4 specimens, 3 fragments); DVD KP6502L (10 fragmentary molds in a block); DVD KP6504L,
153 KP6506L (3 internal molds); DVD KP6601L (15 internal molds, 1 recrystallized juvenile shell and 9
154 fragmentary shells); DVD KP6602L (19 internal molds, 12 fragmentary internal molds); DVD
155 KP6601L, 6602L, 6604L, 7202L (4 specimens, somewhat deformed, 1 external mold, 1 fragment);
156 DVD KP7201L (4 deformed fragments); DVD KP7203L (4 fragments, 9 internal molds, 1 external
157 mold); DVD KP7205L (28 internal molds, 1 external mold, 3 fragments); DVD KP7206L (2
158 fragments); KAP14-001 (1 specimen); KAP14-002 (1 specimen); KAP14-003 (1 specimen); KAP14-
159 004 (1 deformed specimen); KAP14-005 (3 specimen, 2 internal molds, 1 fragment). Other material
160 of the same species is known from the Mursi Formation, the Nachukui Formation at Lothagam, and
161 the Koobi Fora Formation.

162

163 Paludomidae Stoliczka, 1868

164 Cleopatrinae Pilsbry & Bequaert, 1927

165 *Cleopatra* Troschel, 1856

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

8



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

180
181 **Material examined:** CSF K96-5643 (~70 shells); DVD KP6502L (14 specimens, 17 fragments);
182 DVD KP6505U (16 specimens in blocks); DVD KP6601L (15 specimens, 1 fragment, 1 external
183 mold); DVD KP6601L, 6602L, 6604L, 7202L (2 specimens); DVD KP6605L (3 specimens); DVD
184 KP7201L (3 internal molds); DVD KP7203L (16 internal molds, 1 external mold); DVD KP7205L
185 (~95 internal molds in blocks); DVD KP7206L (7 fragments); KAP14-004 (1 fragment); KAP14-005
186 (33 specimens, 1 fragment). Material is also known from East Turkana, the Omo Valley and the
187 Lothidok area.

188
189 Thiaridae Gill, 1871
190 *Melanooides* Olivier, 1804
191 Williamson (1979, 1981) considered all *Melanooides* specimens from the lower part of the Koobi Fora
192 Formation and Holocene Beds in the Turkana Basin to be *Melanooides tuberculata*, and he specifically
193 referred material from the Kanapoi Formation to belong to *Melanooides tuberculata* as well. Earlier, Van
194 Damme and Gautier (1972) considered *Melanooides* from the Mursi Formation of the Omo-Turkana
195 Basin to be a new subspecies of *Melanooides tuberculata*. A difficulty with the identification of *Melanooides*



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

208
209 **Material examined:** CSF K96-5643 (~60 relatively well preserved specimens); DVD KP6501L (48
210 specimens in blocks); DVD KP6503L (1 specimen); DVD KP6601L (1 specimen); DVD KP6605L
211 (~105 specimens in blocks); KAP14-005 (53 isolated specimens and more specimens in blocks of
212 sediment). In-depth work on other faunas is required to establish the geographical extent of this
213 taxon.

214
215 Bithyniidae Gray, 1857

216 *Gabbiella* Mandahl-Barth, 1968

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



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

226
227 **Material examined:** CSF K96-5640 (~5 opercula); DVD KP6502L (1 specimen, identification
228 tentative); DVD KP6601L (1 inner core and 2 opercula). As mentioned, the taxon also occurs in the
229 Mursi Formation.

230
231 Unionidae Rafinesque, 1820

232 Coelaturinae Modell, 1942

233 *Coelatura* Conrad, 1853

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



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

250
251 **Material examined:** (identifications are tentative) *C. aegyptiaca*: CSF K96-5643 (5 doublets, some
252 more valves and fragments); DVD-KP6606L (mold of 1 doublet, 10 internal molds of valves, 6
253 fragmentary valves); KAP14-005 (1 valve); *C. bakeri*: DVD KP6501L (2 doublets, 1 valve); DVD
254 KP6503L (5 fragmentary valves); DVD-KP6601L/6602L/KP6604L/7202L (1 doublet, 3 imprints);
255 DVD-KP6605L (5 doublets, 19 fragmentary valves); KAP14-005 (1 doublet); *Coelatura* sp. indet.:
256 DVD KP6501L (2 fragmentary valves, 2 external molds); DVD-KP6503L (1 valve, 2 external
257 molds); DVD KP6602L (2 fragmentary valves); DVD-KP6605L (37 fragmentary valves); DVD
258 KP6606L (2 valves); KAP14-005 (18 fragmentary valves). *Coelatura aegyptiaca* and *C. bakeri* occur in
259 various regions of the Turkana Basin, including in the Nachukui Formation at Lothagam and West
260 Turkana, the Mursi Formation, the Koobi Fora Formation and the Shungura Formation, and in
261 various periods, notably in Paleolakes Lonyumun and Lorenyang (Van Bocxlaer, 2011).

262

263 Unionidae with uncertain subfamily position

264 *Pseudobovaria* Adam, 1957



265 **Remarks.** Several features, including the hinge, indicate that the extinct genus *Pseudobovaria* belongs
266 to Unionidae, however, its attribution at the subfamily level is uncertain. Morphologically,
267 representatives of the genus compare well to the North American genera *Obovaria* Rafinesque, 1819,
268 and *Pleurobema* Rafinesque, 1819, which belong to the subfamily Amblemineae Rafinesque, 1820.
269 Extant representatives of this subfamily are deeply split molecularly, and geographically distant from
270 African taxa (Whelan et al., 2011), suggesting that remarkable convergence is the most likely cause of
271 similarity. Also Gonideinae Ortmann, 1916, to which Van Damme and Pickford (2010) attributed
272 *Pseudobovaria*, is deeply split from Coelaturinae Modell, 1942 (Whelan et al., 2011), and given that
273 good arguments for any subfamily attribution are lacking, I consider the genus' position within
274 Unionidae currently uncertain. In any case, the few *Pseudobovaria* valves that have been obtained from
275 the Kanapoi Formation differ morphologically from previously described *Pseudobovaria* species in that
276 they are more elongate, with valves and hinges that are less strongly calcified (Fig. 2D). As such they
277 likely represent a new species. Better preserved material has been obtained from the Nachukui
278 Formation near Kalokol. Van Damme and Gautier (1972) also obtained material of this taxon from
279 the Mursi and Usno Formations, but at the time they considered it to belong to *Nyassunio* Haas,
280 1936.

281
282 **Material examined:** DVD KP6502L (1 specimen); DVD KP6601L (17 specimens in blocks, some
283 being fragmentary). Finds at other localities are indicated in the remarks.

284
285 Iridinidae Swainson, 1840
286 Aspathariinae Modell, 1942
287 *Aspatharia* Bourguignat, 1885



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

296
297 **Material examined:** DVD KP 6603L (1 internal mold, fragments of 6 doublets, 1 fragmentary valve
298 with the typical ornamentation on the posterior side); KP 6504L (1 fragment of a doublet); KP6501L
299 (fragments of ?*Aspatharia*). More material of this taxon has been obtained from the Mursi Formation.

300
301 Iridininae Swainson, 1840

302 *Iridina* Lamarck, 1819

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

309



310 **Material examined:** CSF K96-5643 (3 doublets, fragmentary valves of *Iridina* sp. indet); CSF K95-
311 5487 (fragments of *Iridina* sp. indet); DVD-KP 6503L (1 doublet); 6605L (fragments of 4 doublets
312 and 1 single valve); 6606L (5 fragmentary external molds); 7204L (fragmentary molds); all of these
313 samples, except for 6605L contain additional unidentifiable *Iridina* fragments and/or internal molds;
314 KAP14-005 (fragments of *Iridina*, possibly of *I. subelongata*). More material has been obtained from
315 the Mursi, Usno, Nachukui, Koobi Fora and Shungura Formations.

316

317 Etheriidae Deshayes, 1832

318 *Etheria* Lamarck, 1807

319 **Remarks.** *Etheria* has been considered to be monospecific in the latest systematic treatments of
320 extant African freshwater mollusks (Mandahl-Barth, 1988; Daget, 1998; Graf and Cummings, 2007),
321 and in this context Van Damme and I attributed all *Etheria* specimens obtained from the Turkana
322 Basin to *Etheria elliptica* Lamarck, 1807 (Van Bocxlaer and Van Damme, 2009). Recent work
323 (Elderkin et al., 2016), however, indicates deep phylogenetic splits between populations of *Etheria*,
324 suggesting that some of the other described species, e.g., by Lamarck (1807), may actually be valid.
325 As *Etheria* has very limited diagnostic shell-morphological features at the species level (Mandahl-
326 Barth, 1988) it will be a challenge to clear up the existing taxonomic confusion. As such, the Turkana
327 Basin may have, over time, been home to several *Etheria* species, but for now, I am unable to revise
328 our previous assignment as knowledge on the extant *Etheria* fauna remains too fragmentary. I have
329 not had an opportunity to investigate *Etheria* specimens from Kanapoi, but Feibel (2003a) identified
330 a reef of *Etheria* in his section CSF 96-12, directly on top of the Kanapoi Tuff. The lack of samples
331 may relate to the practical difficulties to sample a bioherm. The reconstruction provided here (Fig.
332 2H) is based on a contemporary specimen from the Lothagam area of the Nachukui Formation.



333
334 *Rarefaction*
335 As mentioned, all the examined material was pooled into a single sample for individual-based
336 rarefaction. For *Etheria* five specimens were included to cover the existing reports on its presence in
337 the Kanapoi Formation, resulting in a total sample size of $n = 931$. The accumulation curve reaches
338 an asymptote well before the total number of individuals sampled, and the associated 95 % CIs are
339 narrow, even upon using the unconditional variance estimator and at sample sizes approximating the
340 total size of the reference sample (Fig. 3). Non-parametric asymptotic richness (Chao1; mean and 95
341 % CI) converges to the generic richness in our reference sample ($n = 9$).

342
343 **Discussion**
344 Rarefaction has a number of requirements that may be difficult to meet in a paleontological context
345 (e.g., standardized sampling of lithified shell assemblages), and it makes a number of assumptions
346 (e.g., random distribution of individuals in environments), which may be affected by taphonomic
347 processes (see e.g., Foote, 1992; Gotelli and Colwell, 2001). As such, results are to be interpreted
348 with care. Nevertheless, chances that the number of genera sampled underestimates the true but
349 unknown diversity significantly are small if our collective, historic sampling of freshwater mollusks is
350 representative of all existing shell beds in the Kanapoi Formation. Note that the seeming sufficiency
351 of the collected material for reliable paleoecological interpretations does not contradict the need of
352 more and better preserved material for species-level taxonomy.

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



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



379 deposits of Paleolake Lonyumun. Most thin-shelled heterobranchs typically adopt a cryptic lifestyle
380 within vegetation, where they are better protected against predators (Brown, 1994). None of the
381 freshwater mollusk taxa present in the Kanapoi Formation prefers this type of habitat, which may
382 indicate the overall limited occurrence of vegetation-rich habitats in Paleolake Lonyumun at
383 Kanapoi. This finding is corroborated by the fish assemblages of the Kanapoi Formation, which are
384 rare in herbivores (Stewart, 2003). Note that the remains of such herbivorous fish would not be
385 affected by any of the abovementioned potential sources of preservation bias for mollusks.
386
387 In general, the freshwater mollusk fauna of the Kanapoi Formation is with ~10 species modestly to
388 reasonably diverse. In genus-level composition the fauna is very similar to the modern mollusk fauna
389 of the southern waters of Lake Chad, apart from the fact that a diversity of (small, fragile)
390 heterobranchs have been recorded from the surroundings of this lake (Lévêque and Saint-Jean, 1979;
391 Brown, 1994). Lake Chad lacks the extinct *Pseudobovaria*, but contains the similar-sized corbiculid
392 bivalve *Corbicula* von Mühlfeld, 1811. *Corbicula* appears to have been absent from Paleolake
393 Lonyumun, but it is present in later paleolakes in the Turkana Basin (e.g., Van Bocxlaer et al., 2008;
394 Williamson, 1981). Not unlike in Lake Chad, mollusks reached great biomass in Paleolake
395 Lonyumun, as evidenced from the deposition in a mollusk packstone of up to 1 m in thickness. The
396 gastropods *Cleopatra*, *Melanooides* and *Bellamyia* are the most abundant taxa, representing ~32, 29 and 19
397 % of the recovered specimens, respectively. The substantial molluscan biomass in Paleolake
398 Lonyumun is also corroborated by the presence of a diverse community of medium to large
399 molluscivore fishes (Stewart, 2003). Substantial diversity in unionoids, which have a fish-parasitizing
400 larval stage, is furthermore congruent with substantial fish diversity.



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



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

434
435 Exploratory comparisons of the freshwater mollusk fauna of the Kanapoi Formation to mollusk
436 faunas that have been deposited in other parts of the Turkana Basin during the existence of
437 Paleolake Lonyumun indicate overall great faunal resemblance across regions (see also systematic
438 paleontology). This resemblance indicates that the lake was indeed large, but that faunal connectivity
439 between its various regions was nevertheless good. If this finding remains standing after more in-
440 depth morphometric comparisons, it suggests that the lake was too short-lived for intra-lacustrine
441 speciation and the emergence of regional endemism. Our understanding of the Early Pliocene
442 freshwater mollusk faunas of Africa is too limited to make strong predictions as to the biogeographic
443 origin of the molluscan assemblage of the Kanapoi Formation. However, some similarities exist with
444 the fauna of the Albertine Basin, where *Iridina subelongata* and *Pseudobovaria* occurred since the
445 Miocene (Van Damme and Pickford, 2010). Moreover, the hydrographic catchment of the Albertine
446 Basin extended substantially further eastward in the Early Pliocene than it does currently (Salzburger



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

455

456 **Acknowledgements**

457 Kanapoi fieldwork in 2014 was supported by NSF BCS-1231749 (to C. V. Ward and F. K. Manthi),
458 by NSF BCS-1231675 (to J. M. Plavcan and P. S. Ungar), the Wenner Gren Foundation and the
459 University of Missouri Research Board. I thank C. V. Ward and F. K. Manthi for their invitation to
460 participate to this research, and their support along the way, F. H. Brown, C. S. Feibel and F. K.
461 Manthi for samples from Kanapoi and other regions in the Turkana Basin, and F. H. Brown for
462 insights in the field. Research was funded by a postdoctoral Fellowship of the Flanders Research
463 Foundation. I am not aware of any conflict of interest as to this paper.

464

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

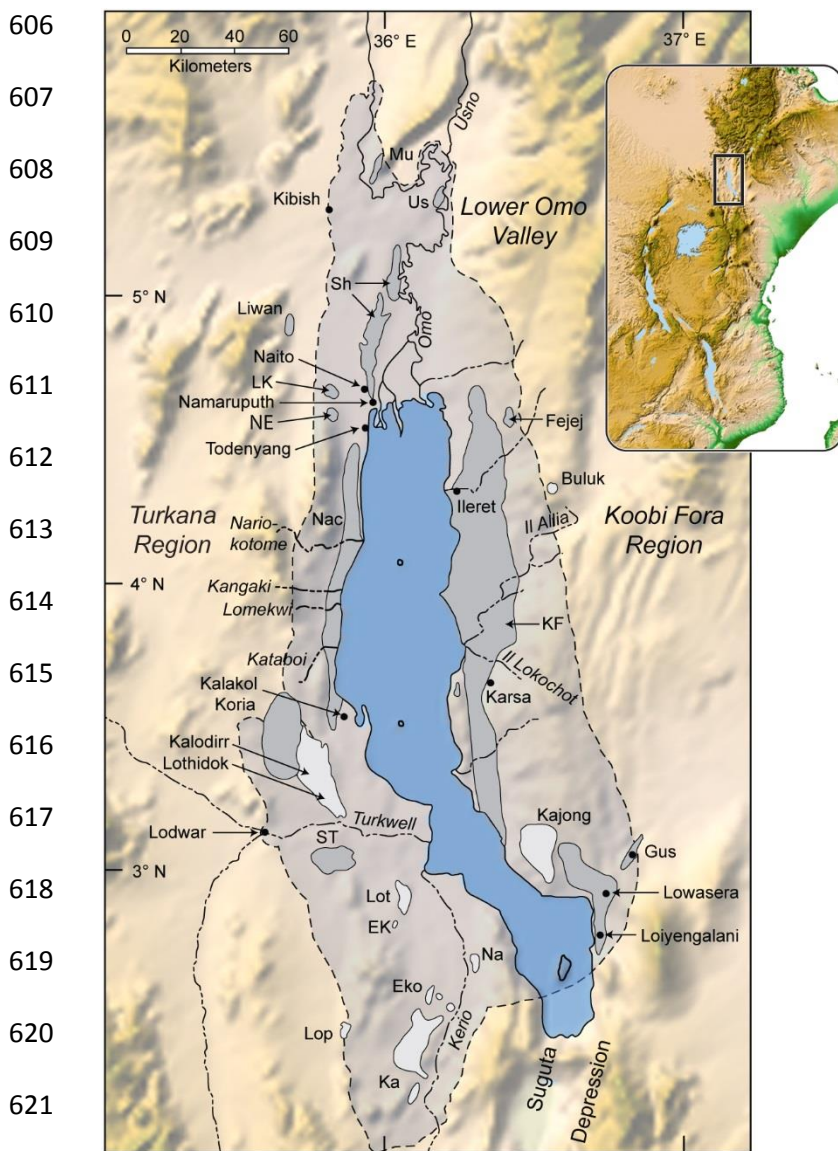
Taxa	Lac.	Fluv./Delt.
Gastropoda		
<i>Bellamyia</i>	P	A
<i>Cleopatra</i>	P	P
<i>Melanoides</i>	P	A
<i>Gabbiella</i>	P	A
Bivalvia		
<i>Coelatura</i>	P	A
<i>Pseudobovaria</i>	P	A
<i>Aspatharia</i>	P	A
<i>Iridina</i>	P	A
<i>Etheria</i>	P	A

603

604



605 **Figures.**

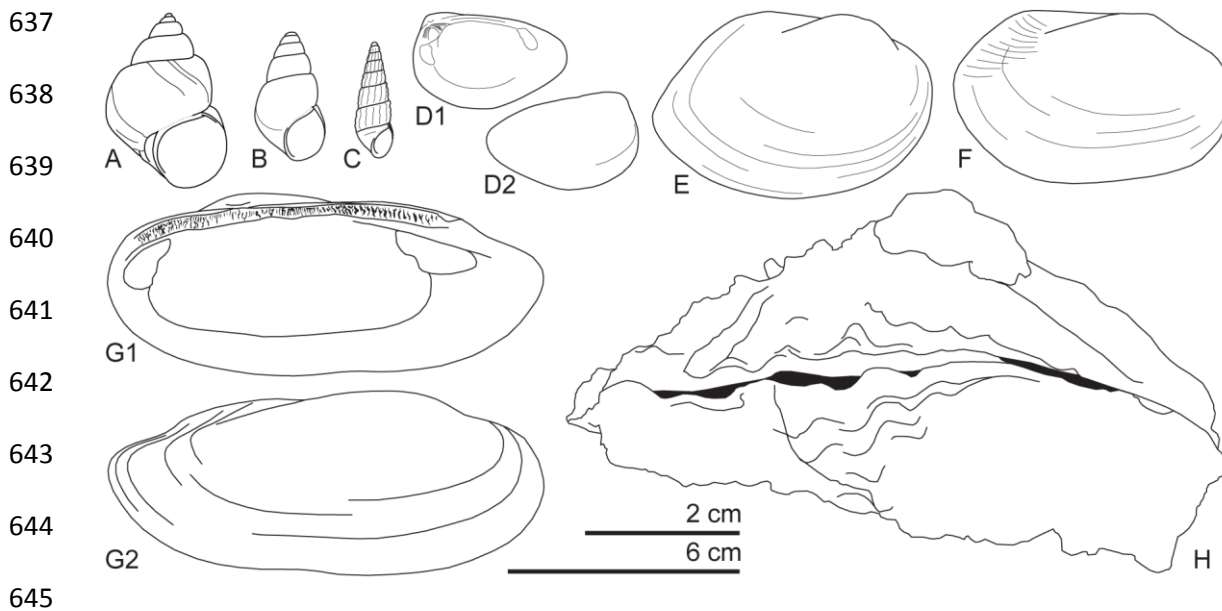


623 **Figure 1.** Topographic representation of the East African Rift System and the Omo-Turkana Basin,
624 with major areas of exposure of Neogene sediments indicated in gray (light gray areas in the South
625 are Mio-Pliocene localities, darker grey areas in the north indicate exposures belonging to the Omo
626 Group). Lake Turkana is indicated in blue and the approximate extent of Paleolake Lonyumun at
627 ~4.1 Ma ago, in which the lacustrine deposits of the Kanapoi Formation (southwestern Omo-



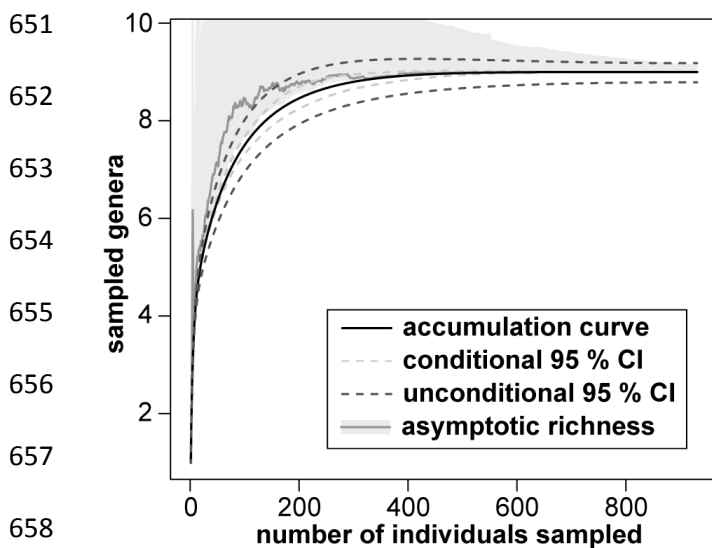
628 Turkana Basin) were deposited, with a dashed line. Although the Kanapoi Formation is
629 geographically restricted and although it captures a relatively short period in the history of the basin,
630 studies of its deposits have been exceptionally informative as to the geology of the basin as well as
631 biological and hominin cultural evolution. Abbreviations: KF = Koobi Fora Formation (Fm.); LK =
632 Loruth Kaado Fm.; Lop = deposits at Loperot; Lot = Lothagam area of Nachukui Fm.; Mu =
633 Mursi Fm.; Na = deposits at Nakoret; Nac = Nachukui Fm., NE = Nayiena Epul Fm.; Sh =
634 Shungura Fm.; ST = deposits at South Turkwell; US = Usno Fm. Map compiled from topographic
635 data of Amante and Eakins (2009) with data from Brown and Feibel (1991) and Feibel (2011).
636





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

649
650



659 **Figure 3.** Individual-based rarefaction at the genus level with all fossil freshwater mollusk finds of
660 the Kanapoi Formation pooled into a single reference sample. The rarefaction curve reaches a
661 plateau well before the total number of individuals sampled ($n = 931$), and assuming that the
662 reference sample is representative of the total diversity of shell assemblages in the Kanapoi
663 Formation, our material likely approaches the real but unknown genus-level diversity of freshwater
664 mollusks in the formation. This interpretation is supported by the narrow confidence interval based
665 on the unconditional variance at the total sample size and the convergence of the asymptotic
666 richness to the accumulation curve for large samples. 95 % confidence intervals on the rarefaction
667 curve based on conditional or unconditional variance estimators are indicated with dashed lines, the
668 95 % confidence interval on asymptotic richness as a grayscale polygone.

669

