

GRADUAL VERSUS PUNCTUATED EQUILIBRIUM EVOLUTION IN THE TURKANA BASIN MOLLUSCS: EVOLUTIONARY EVENTS OR BIOLOGICAL INVASIONS?

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A running controversy in evolutionary thought was Eldredge and Gould's punctuated equilibrium model, which proposes long periods of morphological stasis interspersed with rapid bursts of dramatic evolutionary change. One of the earliest and most iconic pieces of research in support of punctuated equilibrium is the work of Williamson on the Plio-Pleistocene molluscs of the Turkana Basin. Williamson claimed to have found firm evidence for three episodes of rapid evolutionary change separated by long periods of stasis in a high-resolution sequence. Most of the discussions following this report centered on the topics of (eco)phenotypy versus genotypy and the possible presence of preservational and temporal artifacts. The debate proved inconclusive, leaving Williamson's reports as one of the empirical foundations of the paradigm of punctuated equilibrium. Here we conclusively show Williamson's original interpretations to be highly flawed. The supposed rapid bursts of punctuated evolutionary change represent artifacts resulting from the invasion of extrabasinal faunal elements in the Turkana palaeolakes during wet phases well known from elsewhere in Africa.

KEY WORDS: Biogeography, Kenya, palaeobiology, palaeohydrology, Plio-Pleistocene, stratigraphy.

The punctuated equilibrium model of evolution (Eldredge and Gould 1972; Gould and Eldredge 1977) initially generated considerable debate. A search for well-documented examples of speciation in the fossil record followed. Although most published reports showed little evidence (Benton and Pearson 2001), several detailed studies are now available that appear to support this model (Jackson and Cheetham 1999). Williamson (1979, 1981a) studied the Plio-Pleistocene molluscs of the Koobi Fora Formation of Turkana Basin in northern Kenya (Fig. 1). He attracted the attention of the scientific audience reporting these molluscs to be "prima facie" evidence for the punctuated equilibrium mode of evolution. Several other case studies, for example, on Neogene

bryozoans (Jackson and Cheetham 1999) and Palaeozoic trilobites (Eldredge and Gould 1972), are at present also considered prominent palaeontological documentation of the punctuated equilibrium model. These latter two and other examples (Erwin and Anstey 1995), however, are not derived from fossil records with as high resolution as the Turkana Basin molluscs, or discuss less significant, at best subspecific, morphological changes. The evidence Williamson compiled consisted of an ultrafine resolution palaeontological record of 92 sequential faunas, documenting a ~3.3 Ma time frame. These sequential faunas were interpreted as three pulses of rapid evolutionary change interrupting long-lasting periods of stasis. The evolutionary pulses would have been caused

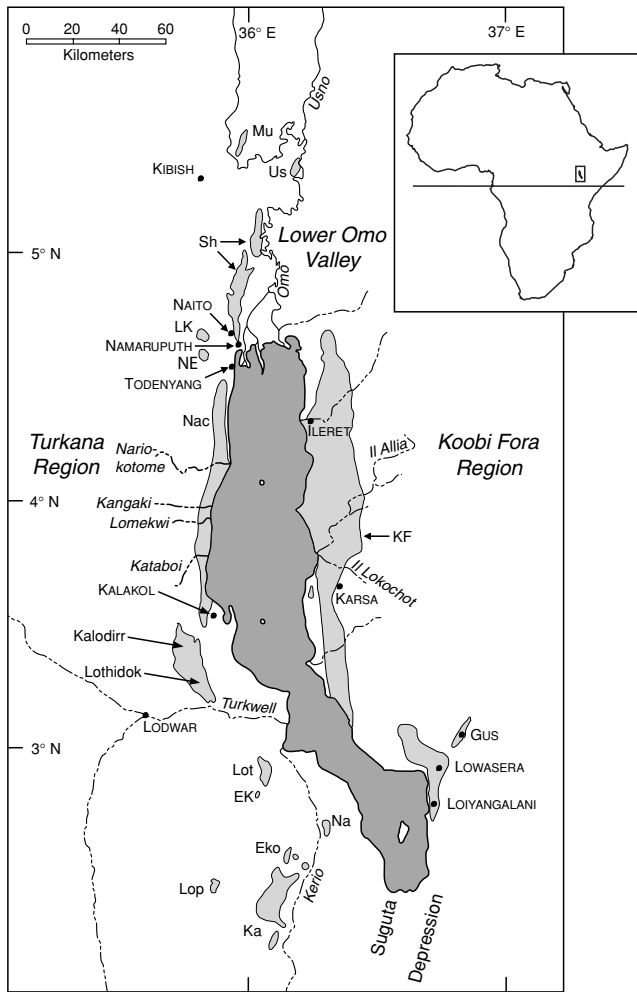


Figure 1. The Turkana Basin, with the modern lake indicated in dark gray and the areas of fossiliferous Pliocene and Early Pleistocene freshwater deposits in light gray. Williamson (1979, 1981a) studied molluscs of a limited part of the Koobi Fora Formation (KF) at East Turkana. Other collections come from EK (Eshoa Kakuron-gori), Eko (Ekora Fm.), Ka (Kanapoi Fm.), LK (Loruth Kaado Fm.), Lop (Loperot), Lot (Lothagam Area of Nachukui Fm.), Mu (Mursi Fm.), Na (Nakoret), Nac (Nachukui Fm.), NE (Nayiena Epul Fm.), Sh (Shungura Fm.), US (Usno Fm.) as well as deposits in the Kalodirr and Loiyangalani areas. Late Pleistocene–Holocene deposits occur scattered around the basin and are not indicated on this map. Figure compiled from Brown and Feibel (1991); Feibel (1993); Leakey et al. (1996).

by ecological stress due to the shrinking of the lake in drier periods, leading to severe decimation of molluscan populations and to genetic drift in the small surviving populations, followed by rapid evolutionary change. Williamson claimed to have proven unambiguously that all lineages of both sexual and asexual molluscan taxa showed an evolutionary pattern conforming to the punctuated equilibrium model, with no gradualistic morphological changes occurring. The subsequent discussion focused on the general problems raised by the punctuated equilibrium paradigm.

Were the observed morphological changes ecophenotypical rather than genetic (Boucot 1982; Mayr 1982; Kat and Davis 1983; Fryer et al. 1983)? How could evolutionary changes occur simultaneously in sexually and asexually reproducing or clonal lineages (Mayr 1982)? How can morphological stasis be explained (Charlesworth and Lande 1982)? How imperfect was the fossil record due to sampling time scales (Ginzburg and Rost 1982) with chronological gaps in the sequence possibly masking gradual changes (Lindsay 1982; Cohen and Schwartz 1983)? In this debate, limited attention was paid to the general stratigraphic and paleoenvironmental context in which Williamson had fitted his reported events. This helped Williamson to counter his critics, and although his reports were placed in perspective, his three evolutionary pulses are still cited by modern evolutionary textbooks (e.g., Kemp 1999; Benton 2003).

Of the three phases of evolutionary change interrupting the longer lasting periods of stasis initially reported by Williamson (Fig. 2; part C), two are very brief. The third is more diffuse and does not really resemble the two other events, as already observed by Williamson's critics (Boucot 1982). In fact, the third event represents a modest adaptive radiation occurring in the relatively long-lived upper Burgi palolake (see Fig. 2) and fits the concept of gradual, intralacustrine evolution (P. G. Williamson, pers. comm. 1990). Therefore it will not be discussed further here. The first rapid wholesale faunal transformation was named the Suregei Isolate (SI), after the associated Suregei Tuff, a stratigraphic term no longer in use following stratigraphic revisions of the Koobi Fora Formation (Brown and Feibel 1986). The SI fauna is now stratigraphically placed near the Burgi Tuff, dated to 2.68 ± 0.06 Ma (Brown and Feibel 1986; Feibel et al. 1989). The second rapid transformation was termed the Guomde Isolate (GI), after the Guomde Formation, which is also abandoned in modern stratigraphy (Brown and Feibel 1986). The typical GI fauna is presently situated in the Chari Member of the Koobi Fora Formation and is stratigraphically associated with the Silbo Tuff, dated to 0.75 ± 0.02 Ma (McDougall and Brown 2006).

Material and Methods

In the Turkana Basin, Neogene sediments accumulated in thick deposits (> 2 km aggregate thickness), with volcanic ash (tuff) beds occurring throughout the sequence. Over half a century of extensive fieldwork has been performed all over the Turkana Basin, addressing various geological and paleobiological aspects, mainly in the light of hominid evolution. Since Williamson (1981a) presented his evolutionary considerations, the number of stratigraphic units for which numerical ages are available has increased considerably (McDougall 1981, 1985; Feibel et al. 1989; McDougall and Feibel 1999; McDougall and Brown 2006), and earlier views of lithostratigraphy, paleohydrology, and paleoenvironmental setting

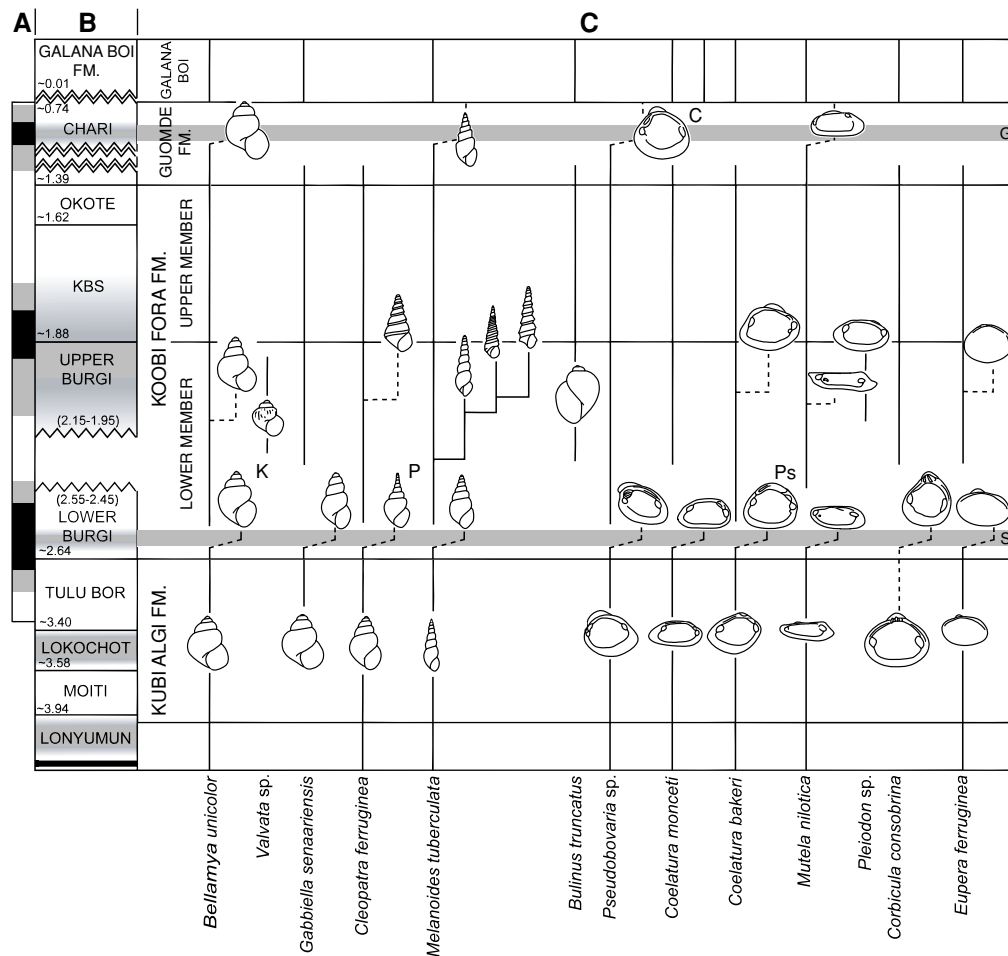


Figure 2. Morphological changes in the Pliocene–Holocene Turkana Basin malacofauna. (A) Known East African wet phases during the period of 3.0–0.7 Ma ago (Trauth et al. 2005); white: arid; gray: relatively wet; black: markedly wet. (B) Modern, revised lithostratigraphic column of East Turkana, with the recognized Plio-Pleistocene lacustrine phases (gray) (Brown and Feibel 1986, 1991). Sedimentary gaps are indicated with zigzag lines. (C) Williamson's (1981a) original stratigraphical framework and his faunal sequence; gray rectangles indicate the two events of supposed punctuated change. Suregei Isolate fauna indicated with SI; the Guomde Isolate fauna with GI; abbreviations near the shells indicate taxonomic misidentifications on generic level: K: *Kaya*, P: *Potadoma*, C: *Coelatura*, Ps: *Pseudodiplodon*. Molluscs not depicted to scale. Modified after Williamson (1981a).

in the basin have been drastically revised (e.g., Brown and Feibel 1986, 1991; Feibel 2003a, b; Brown et al. 2006). This body of new data is used here to update the older mollusc collections, whereas extensive fieldwork by several parties, including the first and third author, also yielded additional molluscan material from more than 150 stratigraphically controlled assemblages with a very broad geographical range covering the complete Turkana Basin (Fig. 1), and increasing Williamson's (1979, 1981a) original resolution.

Equally important are the taxonomic revisions of the modern African malacofauna (Mandahl-Barth 1988; Brown 1994) as well as the studies on the Late Cenozoic freshwater molluscs collected during the 1990s in the nearby Albertine Basin (Van Damme and Pickford 1994, 1995, 1999, 2003; Van Damme et al., unpubl. ms.), the Manonga Basin (Van Damme and Gautier 1997), and other regions in central Africa. These studies allow us to place the Turkana

molluscs into a broader context and to study intrabasinal events by comparison with the extrabasinal environment and biota. The Turkana Basin mollusc collections were studied qualitatively and by traditional and geometric morphometrics. Detailed analyses of the paleobiology of the extensive molluscan collections from the Turkana Basin and their geological and ecological contexts will be presented in specialized journals.

Results

THE TURKANA BASIN MOLLUSCS REVISED

The real problems with Williamson's work concern the paleoenvironmental reconstructions, the stratigraphy and dating, and the reconstruction of ancestor-descendant relationships.

Paleohydrology and paleoenvironment

In the 1980s, paleoenvironmental reconstructions proposed that the Turkana Basin had been occupied by a single long-lived lake that underwent marked water level oscillations (Cerling 1979; Cerling et al. 1979; Williamson 1981a, 1985). During most of its existence salinity was low and conditions similar to those in the modern, alkaline Lake Turkana, were rare (Cerling 1979). More recent paleoenvironmental studies conclusively indicate that the dominant aquatic ecosystem during the Plio-Pleistocene, that is for 85% of that time, was riverine, alternating with more- or less-extensive lacustrine phases (Brown and Feibel 1991). The fluvial phases correspond with the long intervals of stasis reported by Williamson (1981a), whereas the lacustrine phases correspond with his punctuational events (Fig. 2). As a result of climatic changes, general humid phases created lacustrine conditions that were not only recorded in the Turkana Basin (Brown and Feibel 1991), but also synchronously in other East African basins (Trauth et al. 2005).

Stratigraphy and dating

Already in 1982, it had become evident that errors had occurred in the lithostratigraphic framework. Williamson (1982) recognized that the stratigraphy of the Late Cenozoic deposits of East Turkana needed to be revised and introduced limited corrections claiming his general evolutionary considerations not to be affected. His original work was based on a composite stratigraphic column (Williamson 1981a). This column was compiled by the physical correlation of tuffs that crop out in different areas, and that were poorly dated at that time (Oldroyd 1987), in combination with biostratigraphic, and hence circular inferences based on the malacofauna. The ensuing application of new dating techniques and chemical analyses of tephra (e.g., Brown and Cerling 1982; McDougall 1985) enabled comparison of the age and chemical composition of tuffs and allowed more extensive revisions of the Turkana Basin stratigraphy (Brown and Feibel 1986; Oldroyd 1987; Feibel et al. 1989). These revisions of the stratigraphic framework indicated that several tuff layers in different geographical areas had been incorrectly dated and miscorrelated. Moreover, these studies indicated the existence of disconformities in the depositional sequence, and the erroneous correlation of several of Williamson's faunas. Figure 2 illustrates the modern stratigraphy, with ages based on radiometrically datable volcanic tuffs; it also combines the modern stratigraphical insights with Williamson's faunal sequences.

Reconstruction of ancestor-descendant relationships

Williamson (1979, 1981a) studied only the molluscan faunas of the Koobi Fora Formation (Fig. 1) and did not present a complete species-level taxonomy, except for the limited taxonomic efforts in his Ph.D. dissertation (Williamson 1979; Fryer et al. 1983).

The present insights in African freshwater malacology indicate that, although Williamson's morphometric data remain essentially valid, major errors in his taxonomy have resulted in the establishment of erroneous ancestor-descendant relationships and therefore pseudo-lineages and evolutionary punctuations. For example, the material of the SI fauna assigned to *Bellamya* (Jousseume 1886) in fact is representative of the genus *Kaya* (Van Damme and Pickford 1999) (Figs. 3 and 4). Also, representatives of *Potadoma* (Swainson 1840) are mistaken for *Cleopatra* (Troschel 1856)

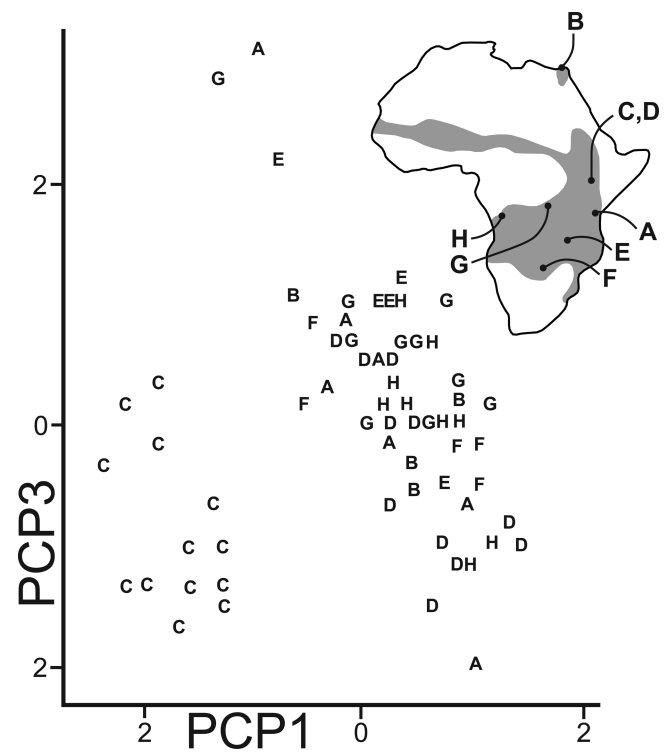


Figure 3. Morphometric principal component analysis of viviparid snails by Williamson (1983) in reply to Kat and Davis (1983), who suggested that the morphological changes at the SI level were of ecophenotypic origin. Williamson included, apart from his Turkana Basin *Bellamya unicolor* (D) and the supposed SI *Bellamya* (C), other specimens of *B. unicolor* (B; Nile Valley) and *B. capillata* (A, E–H; subequatorial Africa), the two modern widely distributed African *Bellamya* species, in his morphometric analyses. The map indicates in gray the combined distribution of *B. unicolor* and *B. capillata*, and A–H the localities of populations of which specimens are included in the analysis. One of Williamson's conclusions was that the SI "*Bellamya*" is quite distinct from all other included *Bellamya* specimens. This is not surprising: the SI "*Bellamya*" in fact belongs to *Kaya* (Van Damme and Pickford 1999), an extinct African viviparid genus originally described from the Late Miocene in the Lake Albert-Edward region (Van Damme and Pickford 1999). The graph thus shows a separation that is not ecophenotypic as suggested by Kat and Davis (1983), nor specific as suggested by Williamson (1983) but intergeneric. Modified after Williamson (1983).

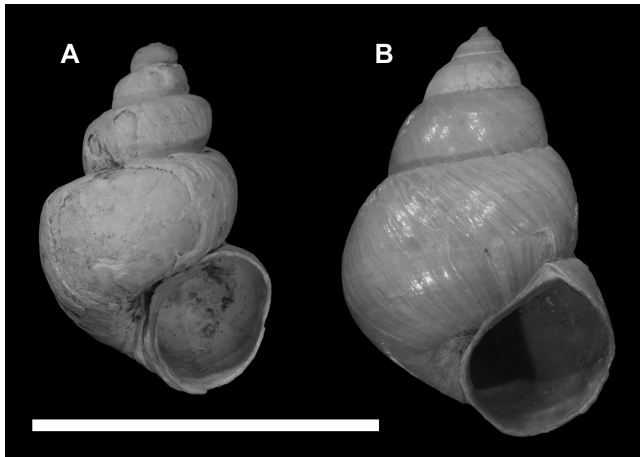


Figure 4. Evidence for misidentifications on the generic level. While Williamson's taxonomy (1979) was based on geometric morphometry of adult shells, the present revision is based on a combination of diagnostic characters of the protoconch and the adult shell. (A) *Kaya* sp. from the Koobi Fora Formation at the SI (lower Burgi Member), displaying a strongly curved periphery and deep sutures. This morph was described by Williamson (1979, 1981a) as a new *Bellamya* species. (B) *Bellamya* sp. from the Koobi Fora Formation (upper Burgi Member). Both specimens have a well-preserved protoconch that can be well distinguished from apertural view. Scale bar 30 mm.

(Fig. 5), perhaps because of their misleading morphological convergence in lacustrine environments, without intermediate shapes being documented in the Koobi Fora Formation. Generic identification using protoconch morphology in well-preserved, non-decolate shells is unambiguous for *Kaya* and *Bellamya* as well as *Potadoma* and *Cleopatra* (Fig. 6). The diagnostic value of the protoconch in the taxonomy of freshwater molluscs has been demonstrated by several studies (Brown 1994; Van Damme and Pickford 1999). Mistakes were also made in case of the bivalves. The so-called *Pseudobovaria* (Adam 1957) specimens in the GI fauna in fact belong to the genus *Coelatura* (Conrad 1853) whereas the SI *Coelatura* can morphologically not be distinguished from the extinct genus *Pseudodiplodon* (Adam 1957) (Fig. 7). Considering these taxonomic updates, Table 1 shows the earliest known occurrences in the central East African fossil record of the genera involved at the SI punctuation. Members of Williamson's (1981a) ancestral lineages, *Bellamya*, *Cleopatra*, and *Coelatura*, are present in the Turkana Basin in the Early Pliocene, ~4.2 Ma, and the so-called SI descendants, *Kaya*, *Potadoma*, and *Pseudodiplodon* occur elsewhere in African deposits before or synchronous with the SI period. This proves that the SI fauna did not develop in situ in the Turkana Basin. Ancestor–descendant relationships and the taxonomy on the specific level are similarly flawed. As will be demonstrated in more-detailed accounts to be published later, several of the supposed continuous lineages of

Williamson, for example, that of *Mutela nilotica*, consist of forms in the upper sequence that are not direct descendants from those lower in the sequence (Fig. 8).

Discussion

New evidence indicates that Williamson's work is flawed, but not primarily because of the original objections that the punctuations result from ecophenotypical changes and/or from gaps in the sampling record. Although genetic distinctiveness cannot directly be evaluated by the study of fossil shell remains, we can exclude that the supposed punctuated morphological changes are mainly ecophenotypical in origin. New and morphologically identical assemblages of both SI- and GI-associated faunas have been discovered in the northern, western, and southern parts of the Turkana Basin in a broader chronostratigraphic framework than reported before (Harris et al. 1988). These new finds show that the SI and GI faunas were living in variable ecological conditions in time and space, indicating that their morphological characteristics are genetically based. The argument of punctuations being time scale artifacts (Ginzburg and Rost 1982) is part of the general discussion on the punctuated equilibrium model, but is in this case irrelevant due to the high resolution of the record.

THE ROLE OF BIOLOGICAL INVASIONS

On the basis of the foregoing results we claim that the observed morphological punctuations at the SI and GI time frame need no evolutionary explanation. The observed sudden faunal changes reflect biological invasions and changes from fluvial to lacustrine conditions, which induced fluvial molluscs to adapt to lacustrine conditions, a process documented in Figure 5. Before the SI time frame, a typical East African freshwater malacofauna, found in Tanzania, Kenya, and Uganda thrived in the Turkana Basin, containing *Bellamya*, *Cleopatra*, and *Coelatura* (Table 1). During the SI time frame, ~2.6 Ma ago, *Potadoma*, *Kaya*, *Corbicula*, and several other molluscs invaded the Turkana Basin. Fossil evidence also suggests an invasion by freshwater sponges of the genus *Potamophloios* (Brien 1970) shortly before the SI period. These sponges, represented by their spicules, are unknown from other periods in the Turkana Basin sequence and at present occur only in the Congo Basin and Zambia (Manconi and Pronzato 2002). Changes in the molluscan communities moreover suggest that the SI invasions were not restricted to the Turkana Basin, as some immigrants, for example *Corbicula* and *Pseudodiplodon*, also invaded the Albertine Basin in the same period (Van Damme et al., unpubl. ms.). *Potadoma* and *Kaya* need hydrographical connections for dispersal and thus suggest fluvial connections between East Africa and regions more to the west at the time. *Corbicula*, an Asian invader (Korniushin 2004), may have been brought in by waterbirds. Williamson (1985) reported limited evidence in

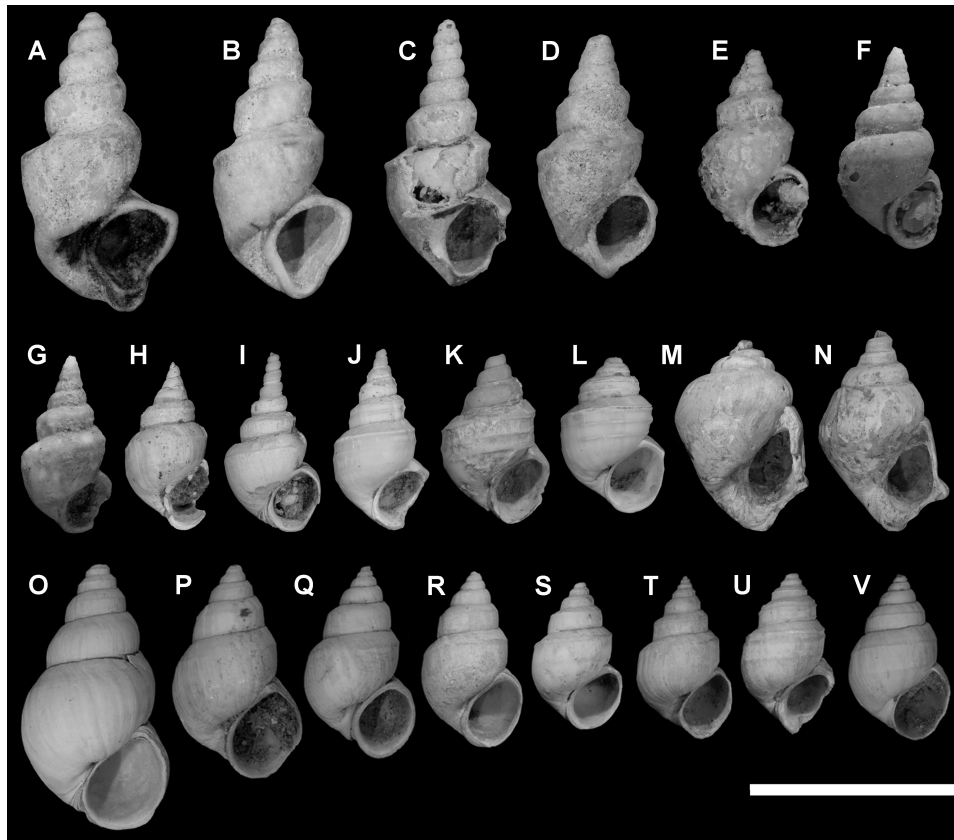


Figure 5. Gradual changes in shell morphology at the shift from fluvial to lacustrine habitats. The upper and middle lines show representatives of the genus *Potadoma*, the lower line representatives of *Cleopatra*. (A) typical riverine *Potadoma lomekwiensis* (Williamson 1985) from West Turkana. (B–D) morphological variations of riverine *P. lomekwiensis*, with (C) displaying an attenuated spire. (A–D) derived from beds deposited in high energy channel environments. (E–G) *Potadoma* specimens derived from moderate energy beach environments at Loiyangalani. (H–L) lacustrine *Potadoma* specimens, deposited in low energy environments. (I) the SI morph, described by Williamson (1979, 1981a) as *Cleopatra*. This SI *Potadoma* morph is the only one occurring in deposits of the Koobi Fora Formation. (M–N) *Potadoma* shells of moderate energy environments in the Albertine Basin, also showing the spires (partly broken off) to have been attenuated. (O–P) deltaic-lacustrine *Cleopatra* specimens from the upper Burgi Member of the Koobi Fora Formation. (Q–V) are lacustrine-adapted *Cleopatra* specimens derived from the KBS Member of the Koobi Fora Formation; some of these lacustrine *Cleopatra* specimens have a morphology that is convergent to that of the lacustrine *Potadoma* specimens (I–L). Changes in shell morphology in *Potadoma* occurred gradually as indicated by the numerous intermediate shapes shown in (A–L). Scale bar 20 mm.

support of an early Plio-Pleistocene rainforest expansion in East Africa, mainly substantiated by the spread of anacardiacean trees and the arrival of *Potadoma* in the Turkana Basin. The event was dated to ~3.34 Ma ago, but revisions of the stratigraphical context (see results) suggest an SI time frame.

Molluscan invasions also coincide with the so-called evolutionary pulsation at ~1.9 Ma, during the upper Burgi wet phase, when *Bellamyia* and *Cleopatra*, absent from the lower Burgi Member, reappear in the fossil record. A nonmolluscan invader of the upper Burgi wet phase is the well-reported example of the stingray *Dasyatis africana* (Feibel 1993). Although fish remains generally do not allow subgeneric identification, and thus detailed information on faunal changes, the fossil remains of this stingray, that adapted to the freshwater environment, are very distinctive. As

Feibel (1993) noted, the lacustrine molluscs and the stingray became extinct during the early Chari Member. As such the GI fauna is part of another wave of invasion, taking place at ~1.1 Ma.

Biological invasions explain why morphological changes are simultaneously observed in all molluscan lineages, and obviate an evolutionary explanation for the parallelism in sexually and asexually reproducing lineages, a problem raised by Mayr (1982). Moreover, it explains why these changes are sudden. Modern invasions by alien species show that a few decades are sufficient for the establishment of newcomers (Pointier et al. 1998). In the invasion-hypothesis, riverine habitats play an important role as evolutionary reservoirs as on average these are more stable and predictable over time and space than lacustrine ones (Marten et al. 2006). From these fluvial reservoirs populations can colonize

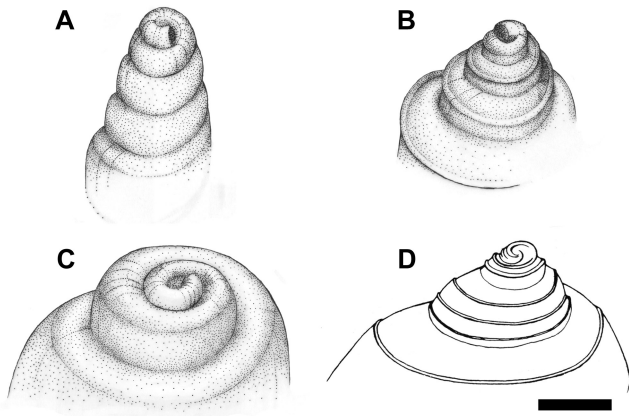


Figure 6. Protoconchs of (A) *Potadoma*, (B) *Cleopatra*, (C) *Kaya*, (D) *Bellamyia*. The elongated protoconch of the SI *Potadoma* is initially larger than that of *Cleopatra*, but increases slowly in size coiling rapidly down the spiral axis, whereas that of *Cleopatra* increases rapidly in size, creating a pyramidal, carinated appearance. The large, inflated and almost planispiral protoconch of the SI *Kaya* sp. is markedly different from the carinated protoconch of *Bellamyia*. (D after Brown 1994). Scale bar 1 mm.

developing lakes. The colonizing riverine-adapted species are no longer subject to the restraints of their original fluvial environments, and encounter a whole array of new, lentic econiches allowing more morphological disparity. Saturation of habitat occupation by the invader and changes of biota interactions can increase selec-

tive pressure, toning down intraspecific morphological disparity. At saturation, coherent lacustrine-adapted morphotypes may arise. At the same time, habitat separation can allow for genetic isolation, leading to parapatric and/or sympatric speciation and high interspecific morphological disparity. Figure 5 shows the gradual morphological change from a fluvial to a lacustrine morph in Turkana Basin *Potadoma* and *Cleopatra*. Williamson's (1981a) intervals of elevated phenotypic variation, preceding the punctuations, correspond with phases directly subsequent to the invasion of the lentic econiches. During this invasion process, the restraints of the original fluvial environments are removed and initially more morphological disparity is displayed. In the Turkana Basin, the short duration of the wet phases (~10–50 ka) limited genetic isolation and the magnitude of subsequent evolutionary change.

Williamson's long periods of stasis conform to periods of aridification in the basin. During the shift of lacustrine environments toward fluvio-paludal conditions, the original lacustrine-adapted fauna becomes slowly impoverished and finally only eurytopic organisms able to stand increasing instability may enter and take over. Such an aridification occurred during the middle and upper KBS Member and the Okote Member. Molluscan assemblages gradually impoverish upwards in the Okote Member and the mollusc community was extinguished during the early Chari period (Feibel 1993). Continuity of molluscan lineages during the punctuational events, and possibly also during the

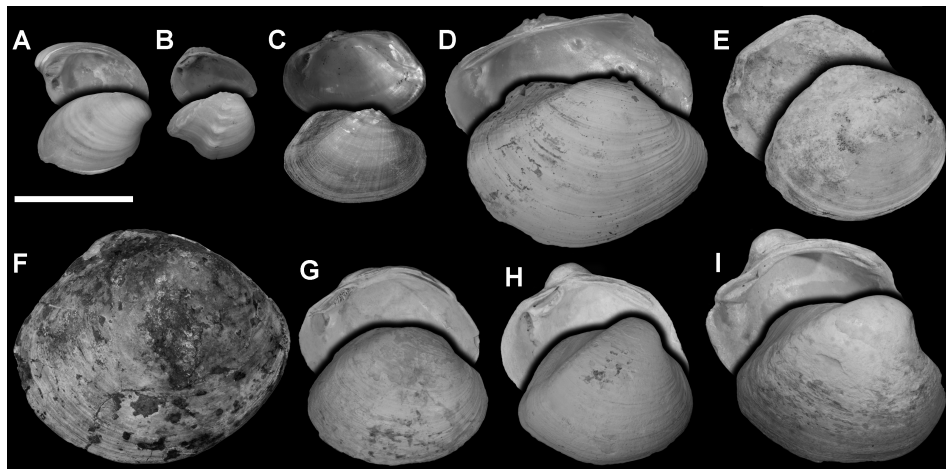


Figure 7. Right valves of some African bivalves. (A) Adult SI *Pseudobovaria*, with a curved, massive hinge that in the right valve has a central, triangular cardinal, in between two depressions, almost perpendicular to the length axis of the hinge; the unsculptured umbo is very acentral. (B) Adult upper Burgi Member *Pseudobovaria* with less-developed hinge, a less acentral umbo and sculpture covering the complete shell. (C) Modern, subadult *Coelatura aegyptiaca* from the Nile, with umbonal sculpture nonhomologous to *Pseudobovaria*, a straighter hinge plate with weakly developed pseudocardinals, almost parallel to the length axis of the hinge and a more central umbo. (D) Adult *C. aegyptiaca*-like specimen from the upper Burgi Member, cooccurring with shell (B). (E) Adult, laterally flattened SI *Pseudodiplodon* specimen, with large interspace on the hinge below the umbo. (F) Holotype of *Pseudodiplodon sengae* (Adam 1957; Late Pliocene Albertine Basin), strongly resembling the late Pliocene shell E of the SI. (G) *Coelatura* from the Shungura Formation, Member L of the Omo Basin, rounded and with a centralized umbo. (H and I) Adult variants of the GI *Coelatura* assigned by Williamson (1981a) to *Pseudobovaria*. Scale bar 20 mm.

Table 1. First known occurrence in the fossil record of central East African regions of the genera involved in the SI morphological punctuation. The genera *Kaya*, *Potadoma* and *Pseudodiplodon*, as assigned here, were recovered only from the Albertine and Turkana Basin, whereas the other genera were also recovered from other regions in central East Africa, supporting their wide occurrence during the Early Pliocene. Ages, provided in Ma, show that representatives of Williamson's (1981a) so-called descending lineages occur in the Albertine Basin before or during the SI period. Data were obtained from (1) Van Damme and Pickford (1999); (2) Van Damme and Pickford (2003); (3) this study; (4) Van Damme and Gautier (1997); (5) De Groeve (2005) and (6) Van Damme et al. (unpubl. ms.).

Genus	Occurrence	Time frame	Age	Source
<i>Kaya</i>	Albertine Basin	Late Miocene	~7.5	1,2
<i>Kaya</i>	Turkana Basin	Late Pliocene	~2.6	3
<i>Bellamyia</i>	Albertine Basin	Late Pliocene	~2.3	1,2
<i>Bellamyia</i>	Turkana Basin	Early Pliocene	~4.2	1,3
<i>Bellamyia</i>	Manonga Basin	Late Miocene	7.0–5.5	4
<i>Bellamyia</i>	Tugen Hills-Kenya	Middle Miocene	~12.0	5
<i>Potadoma</i>	Albertine Basin	Early Pliocene	~5.0	2
<i>Potadoma</i>	Turkana Basin	Late Pliocene	~2.6	3
<i>Cleopatra</i>	Albertine Basin	Middle Miocene	~12.0	2
<i>Cleopatra</i>	Turkana Basin	Early Pliocene	~4.2	2,3
<i>Cleopatra</i>	Manonga Basin	Late Miocene	7.0–5.5	4
<i>Cleopatra</i>	Karunga-Kenya	Early Miocene	~17.5	2
<i>Pseudodiplodon</i>	Albertine Basin	Late Pliocene	~2.6	6
<i>Pseudodiplodon</i>	Turkana Basin	Late Pliocene	~2.6	3
<i>Coelatura</i>	Albertine Basin	Late Miocene	~7.0	6
<i>Coelatura</i>	Turkana Basin	Early Pliocene	~4.2	3
<i>Coelatura</i>	Tugen Hills-Kenya	Early Pliocene	~5.0	5,6

periods of stasis is no longer supported. Williamson (1981a) actually compared evolutionary tempo and mode of organisms in two completely different environmental settings, namely in fluvial (stasis) and lacustrine (punctuation) environments. The molluscs of these different environments are documented with different sampling resolutions. They were merged in pseudo-lineages whose pattern of morphological changes corresponds to that of punctuated equilibrium evolution. The more limited morphological changes in the periods of so-called stasis were evaluated by direct comparison to the morphological changes at the punctuations in Williamson's (1981a) analyses. However, since Williamson's (1981a) reconstruction of ancestor-descendant relationships at the punctuational events is no longer supported, the degree of morphological disparity during periods of so-called stasis was erroneously documented. Figure 8 shows the results of a morphometric analysis in the absence of direct comparison to the morphologies at the SI and GI punctuations, and suggests Williamson's (1981a) *M. nilotica* lineage to consist of several morphological clusters, belonging to at least three separate lineages. Exhaustive quantitative documentation of the morphological changes during the phases of so-called stasis falls beyond the scope of the present article, and will be provided as part of forthcoming taxonomic studies.

The argument of Williamson (1981b) that conventional neo-Darwinism failed to predict the widespread long-term morpho-

logical stasis is no longer based on empirical observations in the Turkana Basin molluscs. That morphological stasis due to developmental constraints or homeostasis would pose real problems for Neo-Darwinism, as suggested by Williamson (1981b) was theoretically countered by Charlesworth and Lande (1982). We here indicate that new observations in the Turkana Basin molluscs, in the light of revisions in paleohydrology, paleoenvironmental reconstructions, stratigraphy, dating and molluscan taxonomy, do not document stasis in the sense proposed by Williamson (1981a).

Conclusions

Although punctuated equilibrium may be an important mode of evolution, the observation of punctuations in the fossil record does not necessarily require an evolutionary explanation. Williamson (1981a) and his critics (Boucot 1982; Mayr 1982; Kat and Davis 1983; Fryer et al. 1983) focused primarily on rapid evolutionary changes as explanations for the observed punctuations in the Turkana Basin molluscan faunas. Such unilateral thinking sustained the Turkana Basin molluscs as prima facie evidence for punctuated equilibrium for 25 years. Other examples of punctuated equilibrium evolution in the fossil record may be similarly biased. Our work stresses the importance of integrating geological, climatological, hydrogeographical, ecological, and taxonomical data to evaluate observed punctuations.

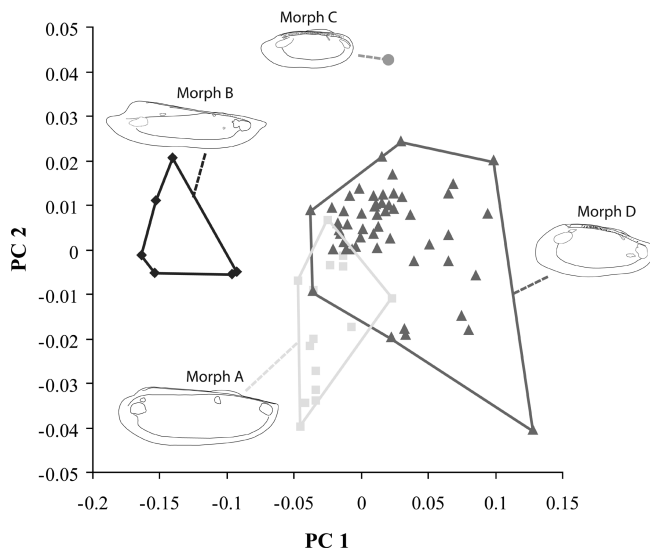


Figure 8. Principal Component Analysis following an Elliptic Fourier Analysis of some representatives of Williamson's (1981a) *M. nilotica* lineage. In the upper Burgi and KBS Members morph A and morph C occur together. Morph B is a lacustrine-adapted descendant of morph A that evolved in situ and illustrates the modest adaptive radiation occurring in the relatively long-lived upper Burgi paleolake. Morph C was recovered also from older and younger deposits in the Turkana Basin and from other regions, for example, the Albertine Basin (Van Damme et al., unpubl. ms.). It is about half the size of morphs A and B, and is not directly related to these two species nor to morph D, that is also not directly related to morphs A and B as will be discussed in detailed accounts. Morph D occurs only in the Late Pleistocene–Holocene. At least three separate lineages, that is that of morphs A and B, that of morph C and that of morph D were lumped by Williamson (1979, 1981a) in *M. nilotica*. The analysis does not support morphological stasis within the so-called *M. nilotica* lineage because it consists of several unrelated morphs with minor overlap.

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