Palaeobiology and evolution of the late Cenozoic freshwater molluscs of the East African Rift

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The first chapter presents a historical overview of research on African freshwater molluscs, introducing the main genera that compose the freshwater molluscan community of most African ecosystems. It demonstrates the requirement of accurate information on the palaeoenvironments where freshwater molluscs lived and their palaeobiogeography to obtain insight into patterns and processes of diversification.

Chapter 2 discusses the fact that morphological disparity and taxonomic diversity are not always correlated, resulting often in the need for additional biological information, apart from the morphological information preserved in fossil molluscs, to evaluate evolutionary changes in the phenotype. The chapter also lines out how interpretations based on morphospace occupation were made. Chapter 3 reviews some commonly used morphometric techniques to study morphological variation in the individuals of natural populations. Moreover, it compares the applicability of the introduced techniques for gastropod shells with various degrees of complexity based on machine-learning approaches to biological discrimination.

Some of the following chapters (4, 5, 6 and 8) make use of the in chapter 3 presented morphometric techniques. Chapter 4 presents a study that re-examines the only sequence of fossil freshwater molluscs in the East African Rift of which evolutionary phenotypic changes had been rigorously analysed prior to my PhD. The phenotypic changes in these molluscs preserved in the Plio-Pleistocene Turkana Basin had been considered, despite critics, good evidence in support of the paradigm of punctuated equilibria. With the aid of multidisciplinary data including absolute dating, a synthesis of our palaeoenvironmental and stratigraphical re-examination and a taxonomic revision of the freshwater molluscs from the Turkana Basin and elsewhere, I demonstrate that the faunal changes represent invasions after faunal decimations rather than *in situ* evolutionary changes according to the model of punctuated equilibria.

Chapter 5 and 6 elaborate on the new findings reported in chapter 4 via the study of some Turkana bivalves belonging to the families of Etheriidae, Iridinidae and Unionidae. I present their taxonomy, palaeobiology and evolution to demonstrate that in the earlier analyses some taxa were linked in pseudo-stationary lineages, whereas some other taxa were linked in pseudo-punctuations because of erroneous interpretation of ancestor descendant relationships. Returning to the points raised in chapter 2, chapters 4 to 6 emphasise 'taxonomic diversity', although it cannot be entirely separated from 'morphological disparity' and some aspects of phenotypic disparity are addressed as well.

In chapters 7 and 8 molecular and morphological variation between the individuals of natural populations constitute the data presented. These chapters deal respectively with the freshwater gastropod genera *Lanistes* and *Bellamya* in the Malawi Basin. The reason why much research was devoted to the Malawi Basin molluscs is that direct descendants of some of the fossil ancestors studied live at present in Lake Malawi and can hence be studied with the full range of methods in modern ecology and genetics. Hence, many issues introduced in chapter 2 are more straightforward to deal with for the case of the Malawi molluscs than for the Turkana and Albertine molluscs this PhD is concerned with.

Chapter 7 provides a molecular study of the extant *Lanistes* representatives in the Malawi Basin that integrates information on fossil finds of this genus. The study illustrates that endemism in the Malawi Basin is not confined to the lake proper, but to the Malawi Rift and that the onset of the extant molecular diversification dates back to the Middle or Late Pleistocene, long after deposition of the Plio-Pleistocene *Lanistes* fossils in the basin.

Chapter 8 documents a 3.1-5.4 times morphospace expansion since the middle Holocene in *Bellamya* gastropods in the Malawi Basin. Whereas the increase in morphological disparity appears spectacular from the palaeontological viewpoint, examination of the changes from generation to generation suggest that phenotypic change in other taxa occurs regularly with a similar or higher rate, and that the phenotypic changes in *Bellamya* are thus quite common from the neontological perspective.

Finally, chapter 9 compares the differences in the natural history of caenogastropods in the Turkana, Malawi and Albertine basins. The caenogastropods of the Albertine Basin are markedly more diverse and show a greater disparity than those in the Malawi Basin, which in turn display a greater diversity and disparity than those in the Turkana Basin. Two factors, namely ecosystem stability and ecological opportunities, are introduced to allow comparison. Without sufficient environmental stability, selective pressures may be periodically intense, but their direction changes frequently over time so that divergence is normally reversed before the speciation process is completed. Without ecological opportunities, selection pressures are so similar that they do not cause populations to diverge, and only more passive restrictions on gene flow may exist. Different combinations of both factors allow to explain the differences in the evolutionary trajectories observed in the three basins, but more data are required to allow more precise comparisons.