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Conchological differentiation in an ongoing radiation of *Lanistes* gastropods from ancient Lake Malawi: how adaptive is shell morphology?

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Lake Malawi is an ancient, deep lake situated at the southern end of the western branch of the East African Rift System (EARS). Like other extant lakes in the EARS and several paleolakes that occupied rift basins in the EARS before, Lake Malawi provides habitats for an extraordinary diversity of freshwater biota ranging from vertebrates, like the adaptive radiations in cichlid fish (e.g. Kocher, 2004), to the phytoplankton communities that provide nutrients to the benthic and pelagic ecosystems (e.g. Van Bocxlaer et al., 2012 and references therein). Major environmental changes in the Malawi Basin since the Middle Pleistocene, including fluctuations in the water level of Lake Malawi, are recognized in the sediments of drill cores and are considered to be a driving force for organismal evolution (Cohen et al., 2007), including the diversification of ampullarid gastropods of the genus *Lanistes* (Schultheiß et al., 2009). In the latest revisions of the *Lanistes* from the Malawi Basin (Mandahl-Barth, 1972; Berthold, 1990) five species (*L. ellipticus* Martens, 1866, *L. ovum* Troschel, 1845, *L. solidus* Smith, 1877; *L. nyassanus* Dohrn, 1865 and *L. nasutus* Mandahl-Barth, 1972) were recognized mainly based on anatomical traits and shell morphology, but further revision is required (Schultheiß et al., 2009). In any case, the extant *Lanistes* fauna of the Malawi Basin is a monophyletic, endemic clade (Schultheiß et al., 2009). The onset of molecular diversification in this clade is much younger (~0.6 Ma) than the first *Lanistes* fossils recorded in the basin, which are preserved in Unit 3A of the Chiwondo Beds (~3.75-1.80 Ma; Kullmer, 2008). However, the mechanisms of this young diversification event are poorly understood, as is the relation between molecular diversity and disparity in shell morphology. In this study we aim to get a better insight into the heritability of shell morphology.

In order to evaluate the heritability of morphological variation, we collected living specimens of three *Lanistes* morphospecies ('*L. ovum*', '*L. solidus*' and '*L. nyassanus*') from the South of Lake Malawi and transferred these to the Research Unit Palaeontology of Ghent University for a Common Garden Experiment. These three morphospecies are regularly found in micro-sympatry along the southern shores of Lake Malawi. In a Common Garden Experiment live-collected specimens are transferred from their natural habitats to a 'standardized' habitat in which offspring generations are raised. Biological traits of the offspring populations can then be compared to those of the parent populations and across morphospecies. In total 122 of the specimens collected alive from Lake Malawi were used for the experiment and each of these individuals was assigned to a morphospecies based on shell morphology. In addition to the Common Garden Experiment, a hybridization experiment was designed to study the reproductive compatibility of two of the morphospecies (*L. nyassanus* and *L. ovum*, which differ considerably in shell morphology). Beyond aspects of mating behavior, this second experiment can provide insight into the potential for hybridization and gene flow between the morphospecies, i.e. it may allow evaluating the applicability of the biological species concept (Mayr, 1942) to these *Lanistes*. Following the guidelines of Van Bocxlaer & Schultheiß (2010), we used a semi-landmark geometric morphometric approach to document and compare shell shapes between the various populations in the Common Garden Experiment. Shells were photographed in apertural view after which we digitized 11 landmarks and 4 open curves of semi-landmarks (20, 40, 20 and 15 semi-landmarks, respectively). After exploration, 44 semi-landmarks were redefined as helper points and excluded from subsequent analyses. Detailed procedures and software information are reported by Van Bocxlaer & Schultheiß (2010). This dataset was subjected to Procrustes superimpositioning and semi-landmarks were slid along the curves using the Procrustes distance criterion (perpendicular projection; Sheets, 2008). The resulting partial Procrustes superimposition coordinates were subjected to ordination and statistical analyses in PAST (Hammer et al., 2001). Patterns of morphospace occupation were studied with principal component analysis. A canonical variates analysis and a multivariate analysis of variance (MANOVA) were performed to make statistical comparisons among parent-offspring couples and between morphospecies. MANOVA allowed evaluating whether the diverse groups have equal multivariate means.

In total, 242 first generation (F1) juveniles were bred in the Common Garden Experiment. Substantial differences were observed in fecundity between morphospecies and replicate experiments. Fecundity appears to be inversely proportional to the parent population size. Consistent shifts in morphospace occupation from the parent generation to the F1 generation were obtained in replicate experiments for the same morphospecies, suggesting that our study design was robust. Except for *L. nyassanus*, the parent and F1 offspring groups of each experiment were significantly different. However, the respective morphospecies underwent different shifts in morphospace occupation from the parent to the offspring generation. Statistical tests demonstrated that the morphological differences between two morphospecies pairs (*L. nyassanus*-*L. solidus*; *L. nyassanus*-*L. ovum*) remained in the F1 generation whereas the difference in the third morphospecies pair (*L. solidus*-*L. ovum*) disappeared at F1. Our results indicate that much of the morphological disparity in the *Lanistes* morphospecies from the South of Lake Malawi relates to inherited differences even though gene-flow between these morphospecies may occur. This suggests that some isolation by adaptation has occurred in these *Lanistes* morphospecies. However, plastic responses to environmental differences also add to the variability in shell shapes observed in the *Lanistes* from the South of Lake Malawi. The hybrid experiment indicated that, at least in the lab, hybridization between live-collected *L. ovum* and *L. nyassanus* is possible and a handful hybrid parent couples produced 419 viable F1 hybrids, although hybrid parent couples differed in reproductive success. It remains yet to be documented how the morphology of F1 hybrids relates to that of the parents, and how variable the offspring of a single couple is. In some tanks copulation has been observed between F1 hybrids (brothers-sisters), and in four tanks egg clusters were produced. Some of these eggs did not grow and appear to have been sterile, but a limited number of eggs hatched. The viability of these juveniles remains to be documented, but the observations in any case suggest that some F1 hybrids are fertile and capable of reproduction with other F1 hybrids. Currently we are still working on the F1 hybrids, after which we hope to design an F2 hybrid experiment.

References.

Berthold, T., 1990. Phylogenetic relationships, adaptations and biogeographic origin of the Ampullariidae (Mollusca, Gastropoda) endemic to Lake Malawi, Africa. Verhandlungen des Naturwissenschaftliches Vereins in Hamburg, (NF) 31/32, 47-84.

Cohen, A.S., Stone, J.R., Beuning, K.R.M., Park, L.E., Reinthal, P.N., Dettman, D., Scholz, C.A., Johnson, T.C., King, J.W., Talbot, M.R., Brown, E.T. & Ivory, S.J., 2007. Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. Proceedings of the National Academy of Sciences, 104, 16422-16427.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1), 9pp.

Kocher T.D., 2004. Adaptive evolution and explosive speciation: the cichlid fish model. Nature Reviews Genetics 5, 288-298.

Kullmer, O., 2008. The fossil Suidae from the Plio-Pleistocene Chiwondo Beds of northern Malawi, Africa. Journal of Vertebrate Paleontology, 28, 208-216.

Mandahl-Barth, G., 1972. The Freshwater Mollusca of Lake Malawi. Revue de Zoologie et du Botanique Africaines, 86, 257-289.

Mayr, E., 1942. Systematics and the origin of species. Columbia University Press, New York.

Schultheiß, R., Van Bocxlaer, B., Wilke, T. & Albrecht, C., 2009. Old fossils-young species: evolutionary history of an endemic gastropod assemblage in Lake Malawi. Proceedings of the Royal Society London B – Biological Sciences, 276, 2837-2846.

Sheets, H. D., 2008. IMP: integrated morphometrics package. Department of Physics, Canisius College, Buffalo, N.Y.

Van Bocxlaer, B. & Schultheiß, R., 2010. Comparison of morphometric techniques for shapes with few homologous landmarks based on machine-learning approaches to biological discrimination. Paleobiology, 36, 497-515.

Van Bocxlaer, B., Schultheiß, R., Plisnier, P.-D. & Albrecht, C., 2012. Does the decline of gastropods in deep water herald ecosystem change in Lakes Malawi and Tanganyika? Freshwater Biology, 57, 1733-1744.

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