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Interactive comment on “Lacustrine mollusc radiations in the Malawi Basin: experiments in a natural laboratory for evolution” by D. Van Damme and A. Gautier

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Reply to J. Heller comments dd February 2013. Prof Dr. Heller expresses the wish for future research concerning the following topics:

â– General patterns of endemism in lacustrine African freshwater groups. R. The pattern here described for L. Malawi, with the clear majority of endemism occurring in prosobranchs and significantly less in pulmonates and bivalves, appears indeed to be a general one. This is in our opinion partly due to the fact that in the two last groups, the capacity of passive dispersal is considerable higher, as well for pulmonates (i.e. via birds, insects, etc.) as for bivalves (via fish through ectoparasitic larvae or also

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via birds, etc. for smaller bivalves, Sphaeriidae, Corbiculidae). But this is a partial explanation. How in the parthenogenetic prosobranch genus *Melanoides*, also spread via birds, an endemic clade could evolve in L. Malawi and in the Congo Basin, remains an unsolved question.

â“ The extent of niche stability in Lake Malawi in time should be investigated, namely were lacustrine niches of the palaeo-lake Chiwondo broadly similar to those of the Modern Lake Malawi?. R. This is indeed a possibility, but the restricted amount of fossil material available (3 or 4 drawers only, mainly *Bellamya* specimens), the restricted region from which fossil material originates (Chiwondo area only), the poor fossilisation and the mechanical selection taking place during deposition, are all factors greatly hampering the palaeo-environmental reconstruction. For example, were *Bellamya* species the dominant group in Palaeolake Chiwondo or is their marked abundance the result of mechanical selection?

The fact that a sizable amount of the Chiwondo species have been listed as morphological similar (cf) to extant Malawi species, has an historical reason, as the first identifications date from the time when it was generally accepted that a continuity existed in the lacustrine malacofauna since Pliocene times. Therefore the fossils, though often badly preserved, were linked to Modern Malawi morphs. Genner et al. (2007) already pointed out the close relationship between Malawi and non-Malawi taxa and hence the inherent fallacy in trying to link the Chiwondo fossils with Modern Malawi morphs (see our remarks on Malawi *Melanoides* and *Bellamya*). As to the subsidiary question if the Modern *Melanoides* species occur along the whole lake, the answer is equivocal. Some appear to be strongly localized, but large parts of the lake, except for the shallow southern part, are inadequately sampled due to the rocky bottoms.

â“ It would be challenging to study whether in the Modern fauna all the fifteen species (of endemic *Melanoides* and *Bellamya*) differ in their habitats; and then to extrapolate the conclusions to the fossil fauna. R. We fully agree.

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The referee has brought to our attention that the reference list is incomplete. Following references were indeed overlooked:

Cohen, A., S. Todd, J., McGlue, M., Michel, E., Nkotagu, H and Grove, A.T.: Paleobiogeographic connections between the African Rift Lakes: an example from the Lake Rukwa Basin and implications for the intralacustrine dispersal of species flocks. In: African Lakes and Paleolakes: Processes, Paleoenvironments, and Paleoclimate, GSA Denver Annual Meeting (31 October –3 November 2010), Abstracts with Programs, 42 (5), 405, 2010.

Schrenk, F., Bromage, T.G., Gorthner, A. and Sandrock, O: Paleoecology of the Malawi Rift: vertebrate and invertebrate faunal contexts of the Chiwondo Beds, Lake Malawi. *J. Hum. Evol.*, 28, 59-70, 1995.

Van Bocxlaer, B., Salenbien, W., Praet, N. and Verniers, J.: Stratigraphy and paleoenvironments of the early to middle Holocene Chipalamawamba Beds (Malawi Basin, Africa). *Biogeoscience* 9, 4497-4512, 2012.

In addition the reference of Gautier, unpublished manuscript, 1975 in the text (p. 18521) needs to be Gautier, unpublished manuscript, 1968.

Replies to the original two anonymous referees' comments (December 2012) 1. Reply to the comments of Referee 1 Comment 1. The MS is a slightly biased in respect to which general ideas and postulates are accepted, and which are ignored. In particular with respect to generalizations on the origin and evolution of the Lake Tanganyika fauna. It does not fully incorporate / discuss alternative suggestions on the age of radiations in that lake. But this is only a minor aspect in this discussion paper, I assume. Reply 1. The referee is correct. The whole issue of possible alternatives is not discussed for the reason that most of the possible alternative scenarios available, predate the findings on the age estimates recently forwarded for e.g., plathytelphusid crabs. Many old concepts have become invalid in the light of these new findings. Though it certainly would be interesting to write a paper on the evolution on evolutionary views of

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the Tanganyika fauna, we feel this would not fit in the present paper. Comment 2. The first paragraph of the discussion reads odd. The text states "... number of molluscan species in all African lakes was decimated. In Lake Malawi none of the endemic thiarid genera survived this reduction..." when he actually means that the number of recognized species-taxa was reduced due to changed views on species concepts. Should be formulated in a clear manner. Reply 2. This comment has been addressed, the text was altered. Comment 3. In general, it might be interesting to incorporate latest findings on radiations of other lake organisms in the discussion of lacustrine speciation in rift lakes - in particular when generalizing findings. Reply 3. Latest findings of most radiations in organisms in other African lakes have been included. Admittedly we did avoid some of the cichlid debates because – lacking fossil material for calibrating molecular clocks, the estimates proposed vary widely and seem to depend on assumptions. 2. Reply to the comments of Referee 2 Comment 1: It seems somewhat odd that Author presents Introduction, Materials & Methods, Discussion and Conclusion sections; yet he does not present a separate section for the Results. Reply 1: The captions have been altered. This is an overview article and using the traditional captions was indeed not the best way to divide the text. Comment 2. For the benefit of readers not closely involved in Lake Malawi mollusks a separate Results section, containing both the fossil and Modern faunas (at species level) should and must be presented. A simple table or two would be just fine. This is important because much of the literature on the Malawi fossil species is not easily accessible on the internet. Reply 2. A table has been provided but we would prefer to leave it to the editor to make the final decision if this benefits the article, considering that the Chiwondo fossils have not been officially described. Hence such a preliminary species list consists of names such as *Bellamyia cf mweruensis* which just reflect superficial morphological similarities and names such as *Coelatura* sp. A. Comment 3: "Mayrian optimism...the equivalence to 'standard' or BSC species of the 8 remaining *Melanoides* species is considered debatable. For these morphospecies are asexual clones and are presently ranged in what Genner and Von Gersdorff & Sørensen call the '*Melanoides polymorpha*-complex'". Please be

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fair to Mayr: in defining the BSC (Biological Species Concept) he always stated very clearly that one difficulty with this concept is that of what-is-a-species in parthenogenetic groups. There is no a-priori reason to consider the four *Melanoides* polymorpha clones as less diverse than four species in a sexually-reproducing genus. Reply 3: We know Mayer's works quite well and he did indeed point out very clearly the difficulties mentioned. But since Mayer, there has been a tendency among some biologists to raise the BSC-concept to a special level. We therefore just use a quote made by the malacologists (Michel , Genner and Todd) working on these Malawi molluscs to show that some specialists consider this matter debatable. The reason these authors probably made this comment is because the clones are genetically almost inseparable. In addition, the Lake Malawi *Melanoides* shell morphs – on which the modern taxonomy of the clones is based- are quite unstable. The morphs that occurred in Mid-Holocene times are not the same as the morphs recently found in the lake and even the morphs collected c. 50 years ago are different. In addition, modern authors do not agree on the different Malawi *Melanoides* species that can be morphologically discerned and I must admit that, if one must arrange a few hundred Malawi specimens according to the different recognized 'species' this appears to be extremely difficult, because of the many intermediate forms that exist between the type species. Comment 4: "Diversification is not spectacular and neither are niche partitioning and occupation. Most Malawi species are restricted to the shallow littoral zone with sandy substrate (above 20m) and only a few are found in the deep sublittoral (i.e. between 50 and 100m). But at such depths their occurrence is sporadic and the only two species, *Lanistes natus* and *Bellamya ecclesi*, that possess morphological adaptations for live at greater depths, are represented by a few rare and highly localized populations. On a vertical gradient only a small part of the total range (~ 30m in a lake with a maximum depth of 700m) has hence been successfully colonized and even in the shallow sublittoral, densities and diversity are low on rocky bottoms, i.e. the dominant substrate in Lake Malawi." 1. Morphological adaptations for life in deep water are relevant and should be fully spelled out, in this paper. 2. Without presenting data on vertical distribution

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in the lake of food, oxygen and other environmental factors, the fact that mollusks do not extend into deep water is not evidence of lack of diversification – environmental conditions in deep waters may be beyond the ability of any mollusk. 3. Could author present data as to whether mollusks reach down to vast depths in any other African lake of similar conditions? Reply 4. As to (1), the morphological adaptations are described in the corrected version. As to (2), the fact that molluscs do not extend into deep water is indeed no evidence of lack of diversification. We never did claim that and to be certain, the last sentence quoted was omitted. As to (3) our article cites evidence from species occurring in deeper water in Lake Tanganyika. Species in e.g., the Caspian Sea and Lake Baikal also penetrate to greater depths. But the whole point of our argument is to show that the molluscs in the few deep tropical lakes known have not evolved any physiological adaptations that enables them to live in hypoxic or anoxic conditions, contrarily to e.g. some groups of marine bivalves such as Thyasiridae. The only known African true abyssal species is possibly the Late Miocene Iridina (Pleiodon) adami found in situ in abyssal clays of Palaeo-Lake Obweruka and suggested to be a chemosymbiont by Seilacher (1990) because of the presence of a long funnel anteriorly and hence of a worm-like foot. Other recent and fossil freshwater bivalves have been cited as being probably chemosymbiotic and hence the statement of the referee concerning inability is debatable. Comment 5: Of the four Chiwondo beds only one contains mollusks. Author claims "that these Chiwondo lacustrine endemics are ancestral to the present ones is highly unlikely". However, from Chiwondo Author mentions "Bellamya cf. robertsoni, which is morphologically similar to the present day L. Malawi B. robertsoni but smaller". The Chiwondo Bellamya cf. robertsoni could very well be ancestral to Modern B. robertsoni. Author claims that "The morphological likeness between Modern (e.g., Bellamya robertsoni) and Pliocene (e.g., Bellamya cf robertsoni) morphs does not imply direct parentage". This could be right; but so too could be the opposite. Bellamya robertsoni being an endemic species, it stands to reason that it has evolved only once. If so, then from where did the Modern Bellamya robertsoni come? Reply 5: African Viviparidae are reproducing similar morphs in dif-

ferent lakes (as is stated in the text). It is a well-known example of convergence. The phenomenon is also quite common in time, i.e., molluscs repeating the same morphs over and over again. As paleontologists and ecologists we are convinced that the primary arguments to consider continuity of a lineage through time, is evidence of the continuity of suitable environmental conditions or of the presence of adaptations in a certain group, that would enable them to survive extreme conditions. Morphological similarities, on the contrary, do not form a convincing argument. *Bellamyia* and actually all viviparids are stenotopic. They are unable to survive even relatively moderate increases in salinity and are unable to aestivate. The vast amount of evidence on severe salinity crises in the Malawi Basin definitely excludes continuity in viviparid lineages. Bourguinat noted that the Malawi viviparids (only two were known in his time) wore a striking similarity to Chinese species. This is indeed true. Does it infer that the Modern *B. robertsoni* comes from China? We also cite Schultheiss et al and Van Boxclaeer who, studying the recent Malawi *Bellamyia*, concluded that this is a very young clade. Comment 6. Similarly Author claims that *Melanoides nodicincta* described from Chiwondo actually "belongs to the *M. nodicincta*-*M. mweruensis*-*M. anomala* species-group, occurring in the southeastern African region". Again, this does not refute a claim that the Modern *nodicincta* could have descended from the *M. nodicincta*-*M. mweruensis*-*M. anomala* species-group. Reply 6: true, and therefore we do write that taxa which can stand higher salinity, such as *Melanoides* and *Gabiella*, or that can aestivate, such as *Lanistes*, may have survived the Pleistocene salinity crises. Comment 7. This is all the more so as Author claims that "It is safe to conclude that during terminal Pliocene times the Chiwondo lake fauna did already consist for an important part of the same ubiquitous and basin endemic taxa that occur in the present lake." This statement contradicts Authors previous statement "that these Chiwondo lacustrine endemics are ancestral to the present ones is highly unlikely". Reply 7. In the whole article we stress the point that in the Lake Malawi Basin which presently includes the Ruhuhu River Basin, the Malawi Lake Basin and the Shire River Basin, quite a few basin endemics occur and seem to have persisted possible since Early or Late Pliocene times. This in contrast

to the lake endemics which evolved in the freshwater lakes itself that existed briefly in the basin, namely Palaeo-Lake Chiwondo that only existed during Late Pliocene times and Modern Lake Malawi that seems to have been a freshwater ecosystem since Late Pleistocene or possibly only since Holocene times. We do understand the confusion that arises when speaking about the Lake Malawi Basin, which is an hydrological term that includes not only the lake but the whole drainage. Perhaps it would be better to speak of the Malawi Basin. Comment 8. With the claim that the Modern fauna is not descended from the Chiwondo fauna, times of origin are of central importance in this paper. It would be of interest to the reader to know whether-or-not any of the references Author reviews offer any dates, for any of the Modern lineages. Reply 8. Different authors do offer different dates or remain vague about the issue. We do state why one of the the date forwarded by Genner (4 Ma) is erroneous in our opinion and we do cite Schultheiss et al who propose a Pleistocene age for the Modern *Bellamya* and *Lanistes* clades. Comment 9. A minor point: The aim of this research is described in Author's sentence "The present paper is essentially a critical review of the fossil material cited above and the published literature on the modern and fossil Lake Malawi malacofauna in the light of . . ." In view of the trend taken by the paper itself, may I suggest to consider a slightly different aim: "This paper presents the faunal history of the Lake Malawi molluscs, in the light. . ." Reply 9. We do not have a problem of altering the sentence but the sentence proposed by the referee suggests that the history of the Modern Lake Malawi molluscs is threatened only in this article which is not the case. Comment 10. As another minor point, Author may perhaps wish to consider a slight rephrasing of the title: Lacustrine mollusk radiations in the Malawi Basin: experiments in a natural laboratory for evolution? Reply 10. The title was altered, but we leave it to the editor to make the final choice. Style: Comment: The style is not always crystal clear and a quick rigorous style brush-up should perhaps be considered. As a few examples: "both groups consisted not exclusively of lake endemics, as was formerly assumed, but of in-lake endemics sensu stricto + one or two paludal/fluvial species endemic to the Malawi Basin." – I do not understand this sentence, the difference between "lake endemics"

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and "in-lake endemics" is not clear to me. Reply: In-lake endemics is the general term used for species that evolved within the lake ecosystem. The sentence has been altered for clarification Comment: "Diversification is not spectacular and hence are niche partitioning and occupation neither." Altered in: Diversification is not spectacular and hence niche partitioning and occupation are neither." Comment: "morphological adaptations for live at greater depths". OK, corrected Comment: "But generally is the Chiwondo littoral malacofauna surprisingly similar in diversity and composition to the Early Holocene fauna" OK, altered Comment: "The composition of the faunal community around the time of the Pliocene/Pliocene boundary was hence..." OK, omitted Comment: "Though significant lake level drops did occur during the Pleistocene (~435m level drop during the early Late Pleistocene mega-drought, the Tanganyikan freshwater system hence did not crash and the lake acted...".OK, altered

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