ANALYSIS OF BODY SHAPES AMONG *BARBUS TRIMACULATUS, BARBUS PALUDINOSUS* AND *BARBUS JACKSONII* (ACTINOPTERYGII: CYPRINIDAE) FROM MALAGARASI AND PANGANI RIVER BASINS BASED ON GEOMETRIC MORPHOMETRIC METHOD

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ABSTRACT

This study analyzed variability in body shapes among the small Barbus species of the family Cyprinidae currently occurring in the Malagarasi and Pangani River basins years after uplift of the east African topology. Fish specimens were collected from Songati, Muumbara and Nyamagoma within the Malagarasi River basin; Hale and Pangani fall located on Pangani River. It was found that although the landmarks were placed at the same anatomical regions, significant body shapes variations existed. The relative warps analysis for Barbus trimaculatus and Barbus jacksonii populations from Malagarasi and Pangani wetlands revealed intra-locality variations as for populations from other African countries. The Tanzanian B. trimaculatus overlapped with B. jacksonii from Kenya and Mozambique suggesting that the two species could be the same. The populations of B. jacksonii and B. trimaculatus from Tanzania and Mozambique overlapped only at some few points suggesting significant morphoshape variability. The Zambian B. trimaculatus maintained their own cluster even when compared to specimens of the same species from Malawi, Mozambique, Kenya and Tanzania, hence could be considered a separate species yet to be described.

Keywords: Morphoshape, *Barbus* species, geometric morphometric.

INTRODUCTION

Phenotypic plasticity implies the degree of variations of expressions of genotypes with respect to environmental changes (Thompson 1991). Phenotypic variations are commonly influenced by a range of environmental conditions that among others include temperature, salinity, radiation, dissolved oxygen, water depth and current flow (O'Reilly and Horn 2004). Studies of morphological character variations are still critical in order to explicate patterns observed in phenotypic and genetic character variations among fish populations (Beheregaray and Levy 2000).

Despite the geohistorical relationships between the Malagarasi and Pangani River systems, little is known on the morphological relationships among their aquatic biota (Ndaro and Nkotagu 2004). Species widely distributed in these heterogeneous environments are expected to exhibit genetic and/or phenotypic characters isolation. Among fishes, the likelihood of such character variations increases if the species has limited powers of dispersal (Planes 1998), as is the case for the cyprinid barbs of the Malagarasi and Pangani River systems. In addition, a number of fish species that occur in widely dispersed localities have disjunct populations and several have been shown to exhibit high morphological, ecological, behavioural, phylogenetic and molecular divergence (Huang and Bernardi 2001).

High morphological divergence is reported among and within tribes of cichlids from Lake Tanganyika (O'Reilly and Horn 2004). Furthermore, there has been convergence in eco-morphological traits and colouration patterns between distantly and closely related groups (Rüber *et al*. 1999). Being close to Lake Tanganyika, the cyprinid barbs of the Malagarasi system are likely to behave the same. It is therefore important to quantitatively describe differences in body shapes that exist between cyprinid barbs of the Malagarasi and Pangani River systems.

Geometric morphometric (GMMs) is a landmark based technique that explicitly retains information on spatial covariation (Rohlf and Marcus 1993). The technique is effective in capturing meaningful information about the shapes of organisms. Furthermore, due to its statistically comparable shape variables, it is possible to reconstruct a hypothetical shape of a common ancestor and visualize changes and transformations that distinguish two or more body shapes. The technique is strong enough to analyze external morphology and shape differences among organisms (Roth and Mercer 2000).

According to Stankiewicz and de Wit (2006), prior to uplifting of the East African topology, the Congo and Malagarasi Rivers drained to the east into the Indian Ocean, as does the present Pangani River. These changes on the geometry of the River basins considerably affected the aquatic flora and fauna on their distribution, diversity and local speciation. Based on this accord therefore, it is envisaged that the changes in the flowmetry of the East African Rivers might have influenced the genetic diversity and even the morphology of the small barbs currently occurring in Malagarasi and Pangani Rivers. Henceforth, the current study examined and compared the body shapes variability among the small *Barbus* spp. of the family Cyprinidae from Malagarasi and Pangani River basins based on Geometric Morphometric analysis.

MATERIALS AND METHODS

Study area

The study was conducted in Pangani and Malagarasi River basins. The Malagarasi basin is located in the North Western side of Tanzania (Figure 1A). Samples were collected from Lakes Sagara and Nyamagoma within the Malagarasi-Muyovozi Wetland systems. The lakes are located 200 km North East of Lake Tanganyika. The sites were chosen due to the fact that they are located in the Malagarasi-Muyovozi Ramsar site which is the first Ramsar site in Africa since 2000 (Ndaro and Nkotagu 2004). Secondly, the Malagarasi River is one of the potential fish biodiversity hotspots in Africa (Ndaro and Nkotagu 2004, Tamatamah, *pers.com*). Also, the areas have high abundance of *Barbus* spp., and are accessible from Nguruka ward (31°2´E, 5°7´S) (Ndaro and Nkotagu 2004). On the other hand, the Pangani basin is located in the North Eastern Tanzania between latitudes 3°03´S and 5°59´S and longitudes 36°23´E and 39°13´E with an area of about 53,600 km² (Figure 1 B). The basin is composed of five river sub-catchments, namely the Pangani, Zigi, Umba, Mkulumuzi and Msangazi with main rivers draining to the Indian Ocean. Natural lakes in the basin are Chala, Jipe, Duluti, Manga and Karamba. Nyumba ya Mungu, Mabayani and Kalimawe Dams are manmade reservoirs. Major uses of water are domestic, irrigation, industries, hydropower, livestock, fisheries, recreation and transportation (Mwandosya 2009).

Sampling sites

Specimens were collected from various sites (Figure 1 A and B) at Songati, Muumbara and Nyamagoma within the Malagarasi River basin; Hale and Pangani fall located on Pangani River. The sites were chosen based on accessibility, samples availability and a distance of at least 10 km apart to justify for hypothesized reproductive isolation of the analyzed species.

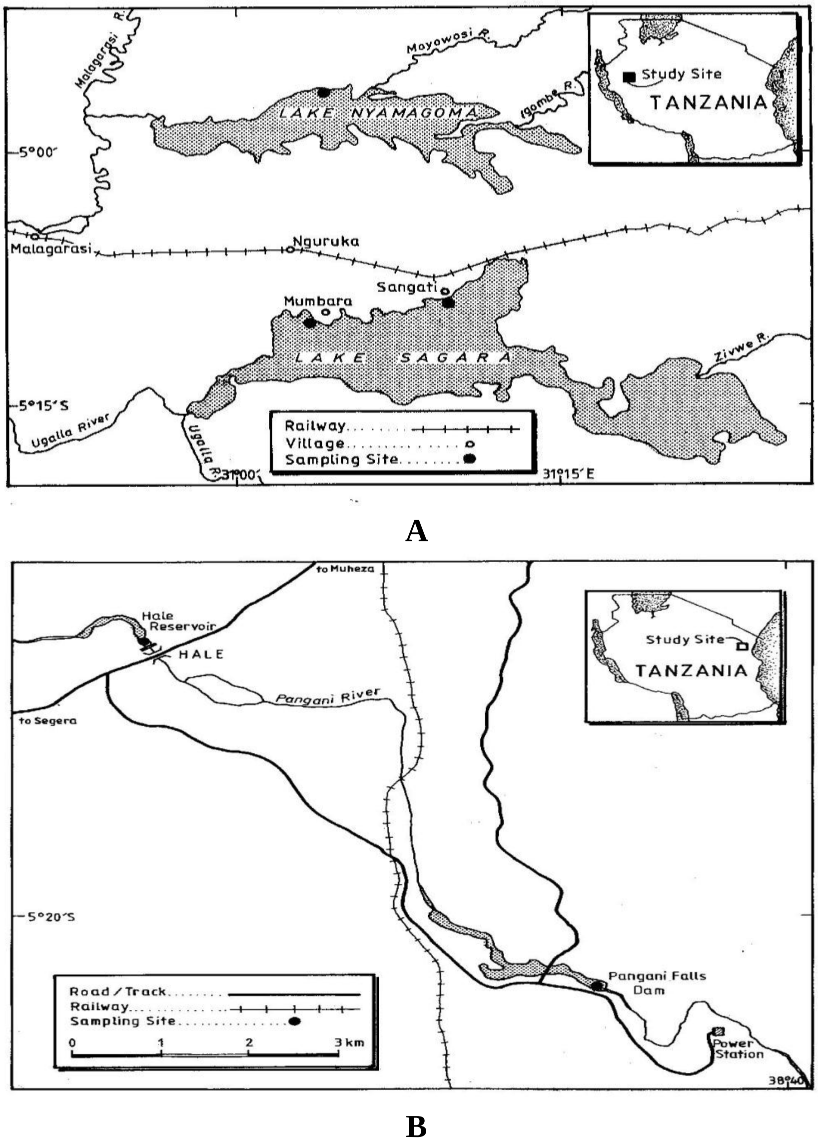

Figure 1: A: Map of Tanzania describing the sampling points on Malagarasi River basin. **B**: Map of Tanzania describing sampling points on Pangani River basin.

Collection of fish samples

Gillnets ranging between 5 cm and 25 cm mesh size were used to increase the possibility of catching a wide range of small barbs. The obtained specimens had different body sizes, ages and other samples were purchased from local fishers. The specimens were stored in zip-lock bags with 80% ethanol and placed in the bucket for easy carrying. In the laboratory, specimens were cleaned in 10% ethanol and further stored in bottles with 70% ethanol until processed. Specimens from other African countries used in this study were obtained from the South African Institute for Aquatic Biodiversity (SAIAB) fish collection.

Specimen identification

The collected fish specimens were identified on field following the available keys such as (Eccles 1992, Witte and Van Densen 1992, and Skelton 2001). The identification of samples was further confirmed by a fish taxonomist (Denis Tweddle) at SAIAB fish collection.

Fish specimen preparation for photographing

Ethanol fixed specimens were recovered, rinsed in fresh water and bloated prior to photographing.

A digital camera (Canon Power Shot A2200 with 14.1 mega pixels) was mounted on a tripod stand and levelled with bubble water level assuring that no formations of perspective deformations. The proper setting and connection of the camera and the computer were done aiming at obtaining best quality photographs.

Photographing of the fish specimens

The bloated specimens were then fixed on a Petri dish by using special glue and situated parallel to the surface. Each specimen was then photographed following remote shooting instructions. Four photographs were taken per each specimen to assure quality. The photographed specimens were renamed and stored in the folders created for further analysis. The quality of the photographs was assessed in terms of orientation, resolution and clarity for further processing and analysis (Rohlf 1996). The poor photographs were discarded.

Determination of landmarks on the fish photographs

Fourteen homologous landmarks were determined basing on the potential variations suggested by the conventional morphometric measurements. Homologous landmarks were put on each photograph, then renamed and saved (Plate1). The numbers of landmarks were decided based on the sample size and each specimen was characterized by a landmark configuration. The landmarks were then linked using the *tpsUtil* program as described by (Rohlf 2004).

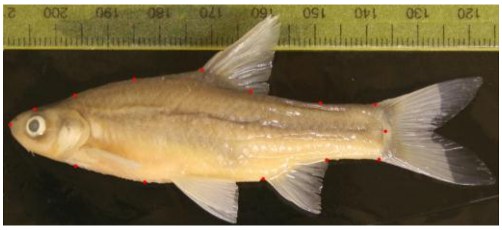

Plate 1: Landmarks on a photo of *B. paludinosus* after digitizing.

Consensus image

The program file tpsSuper was used to digitize photographs to create the consensus image (Rohlf 2004). All the landmarks were compared and finally clearly seen with similar shape of the digitized points on the fish body photograph (Figures 2a and 2b).

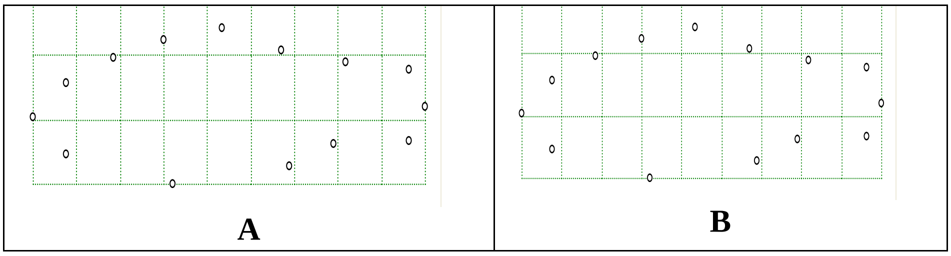

Figure 2 (A): Consensus body shape for *B. jacksonii*. **(B):** Consensus body shape for *B. paludinosus.*

Aligning the data from the linked files

The program file tpsRelw (Rohlf 2004) was used to align the data from the linked files. The input data option allowed to select the original file with homologous landmarks obtained in *tpsDig* program. The consensus, partial warps and relative warps were computed. The results obtained were saved until further analysis.

Consensus configuration within landmarks

The non-shape variations (translation, scaling and rotation) were removed by Generalized Procrustes Analysis (GPA) so that only the differences related to shape remained. GPA based on the simple idea of overlaying the images of two or more specimens so that the homologous landmarks match as closely as possible, with a subsequent translation, rotation and scaling of every object's points to the centroid size (the square root of the sum of square distances from each landmark to the specimen's centroid). Finally, the centroid size was obtained for each specimen. Consensus (mean) configuration, uniform and non-uniform components of shape were computed. The program was allowed to view different reports on landmark links, variances for aligned specimens and Eigen values for each principal (Rohlf 2004).

Relative warps scores

The non-uniform shape component is represented by Partial Warp Scores matrix (the new set of shape variables together with the uniform component). These components were treated as multivariate data representing shapes, and were used in conventional multivariate analyses. Relative Warp Analysis (a Principal Component Analysis of partial warps) was performed to identify the main tendencies of non-uniform shape variation (Baylac *et al*. 2003, Adams *et al*. 2004, Rohlf 2004).

Statistical data analysis

The statistical analysis was done using a Paleontological Statistics Software Package (PAST) (version 10.0). The fish shape data were tested for allometry (if the shape was influenced by size) by using multiple regression tpsRegr. The centroid size was used to test for all uniform and non-uniform measures (Rohlf 2004). The data showed allometry behaviour so they were transformed by importing relative warps uniform components and centroid size from Excel program into PAST. The scatter plot and regression analysis were performed to get the linear equation. The regression equation was then used to calculate the relative warps residues used in the final analysis. The analysis of species population differentiation at both low and high scale was done by using Multivariate analysis of variance (MANOVA).

RESULTS

Body shape for *Barbus paludinosus*

Regression analysis showed that body shape in *Barbus paludinosus* specimens was influenced by their respective size, (percent unexplained = 90.41%) and Generalized Goodall F-test (F = 7.26, df = 4, P > 0.001). Most of the shape points (centroid size) concentrated to the red line (Figure 3) implying that size influenced the body shape in *B. paludinosus.*

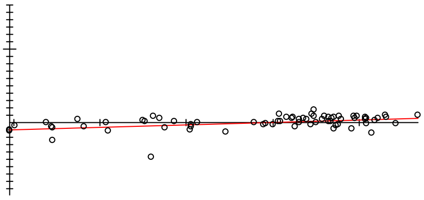

Figure 3: The scatter plot of shape against size indicating the influence of size to the shape of *B. paludinosus*.

Relative warps for *B. paludinosus*

The singular values of relative warps were tested to see if they were sufficient for interpreting the variations in body shapes. The results indicated that cumulative values for the first four singular values were more than 50% and hence sufficient to interpret shape variations. Henceforth, multivariate analysis of the relative warps along the RW1 in *Barbus paludinosus* showed significant differences (percent unexplained = 90.41%, F = 7.26, df = 24, P < 0.001). According to Figure 4, some specimens from Pangani, Muumbara and Songati overlapped at the central point (grey cycle) indicating similar body shapes, while most of the specimens from either of the localities showed large variations in body shapes. The Hale reservoir population was distinct from those of Malagarasi and Pangani Rivers except few which showed body shape similarity with Pangani fall population.

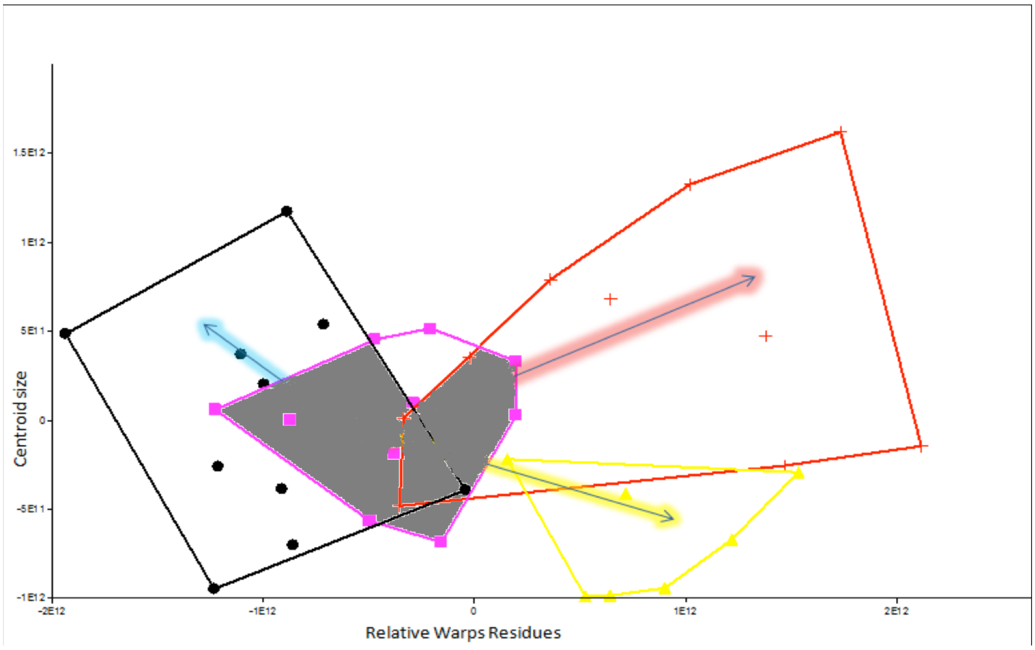

Figure 4: Results of the relative warps analyses for the populations of *B. paludinosus* under MANOVA analysis Tanzania populations from Malagarasi and Pangani River basins. (a) The points represent individual specimens; (b) the polygons represent sampled stations (red = Pangani falls, black = Muumbara, yellow = Hale reservoir, and pink = Songati).

The multivariate analysis of the relative warps along the RW1 axis (relative warp axis one) in the *B. trimaculatus*, *B. jacksonii and B. paludinosus* from five sampling stations (Tanzanian populations) and other samples from Malawi, Mozambique, Zambia, Congo DRC and Kenya showed that individuals were variable in terms of body shapes even those from the same locality (intra-locality variations), inter-localities and among populations of other countries (Figure 5). *B. paludinosus* from Congo DRC were more variable in terms of body shape when compared to those from other countries.

The body shapes for *Barbus trimaculatus* and *Barbus jacksonii*

The relative warps matrix data for body shape showed allometry (percent unexplained= 79.9% and the Generalized Goodall F-test (F = 16.37, df = 2 and $p < 0.001$) for *B. jacksonii* and *B. trimaculatus*. Most of the shape points (centroid size) concentrated to the red line (Figure 6) implying that size influenced the body shapes of the two species.

Relative warps for *B. trimaculatus* and *B. jacksonii*

The percentages of variance for the first singular values were 34.1%, 19.4%, 9.4% and 8.6%, with cumulative percentage of more than 50%. Hence the relative warps were sufficient to interpret the body shape variations among *B. trimaculatus* and *B. jacksonii* populations. Based on this context, most specimens of *B. trimaculatus* from Malawi, Mozambique and Tanzania were classified as being one and the same in terms of body shapes. Nevertheless, specimens of the same species from Zambia formed their own independent cluster. In addition, the morphoshape was unable to fully distinguish *B. jacksonii* (from Kenya and Malagarasi, Tanzania) from *B. trimaculatus* (Figure 7).

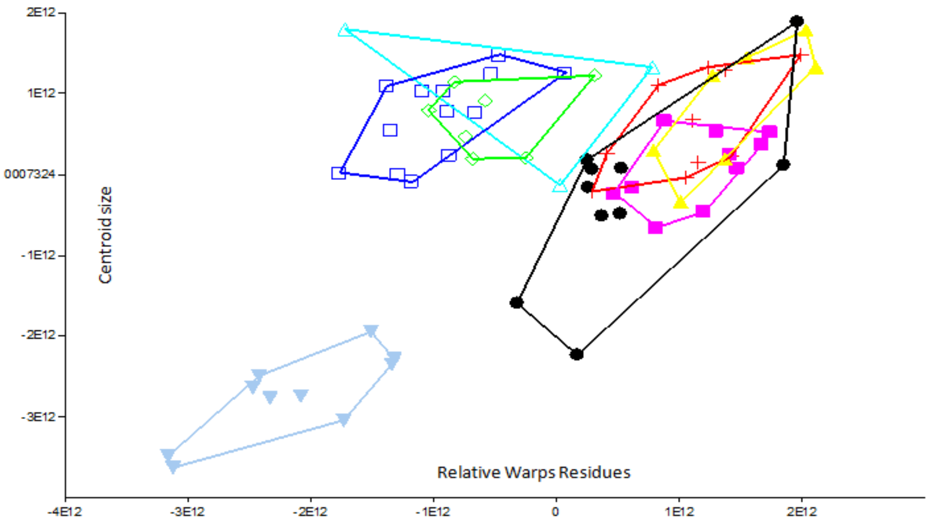

Figure 5: Comparison of *Barbus* spp. from Tanzania (Malagarasi and Pangani Rivers), DR Congo, Kenya, Malawi, Zambia and Mozambique populations (red = Pangani falls, black = Muumbara, yellow = Hale reservoir, pink = Songati, Blue = Malawi, pale blue = Zambia, green = Mozambique and aqua = DR Congo).

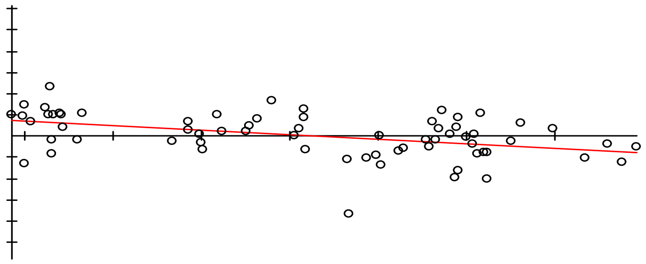

Figure 6: The scatter plot of shape against size for *B. trimaculatus and B. jacksonii*.

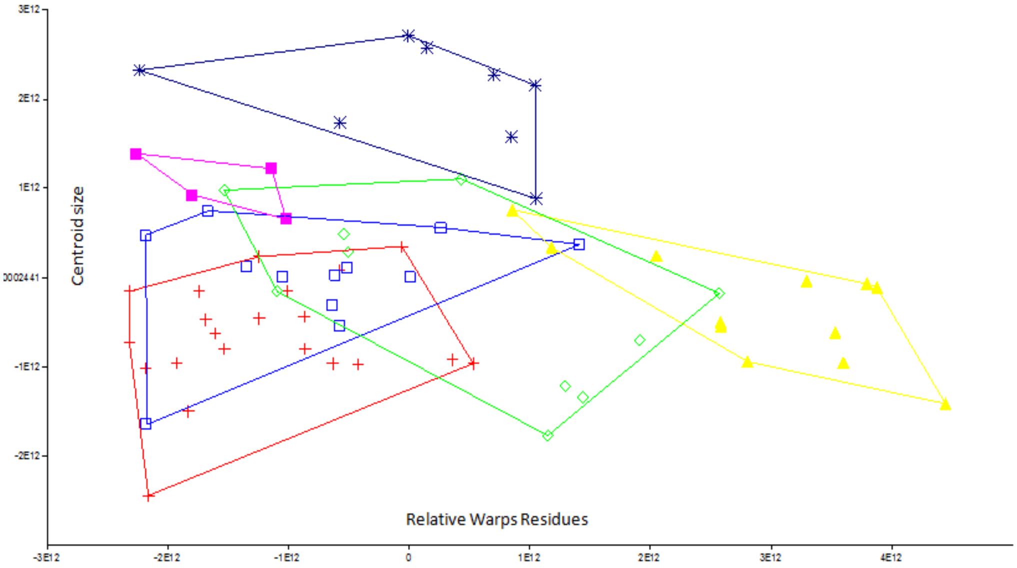

Figure 7: Relative warps analyses for the populations of *B. trimaculatus* and *B. jacksonii*: red = *B. jacksonii* (Kenya), blue = *B. trimaculatus* (Tanzania), pink = *B. jacksonii* (Tanzania), dark-blue = *B. trimaculatus* (Zambia), yellow = *B. trimaculatus* (Malawi), and green = *B. trimaculatus* (Mozambique).

DISCUSSION

The findings of the present study revealed that *Barbus* spp. from Malagarasi and Pangani River basins are morphologically related (Figures 3 and 4). However, significant intra and inter-locality body shape variations in *B. paludinosus* populations from the two wetlands were noted (Figure 4). According to Figure 4, individuals of *B. paludinosus* in the grey cycle probably represent the ancestral shape and those outside the cycle radiated into their respective direction and their morphoshapes modified to suit the new habitat conditions. Previous studies have shown that body-form is often correlated with diet/foraging behaviour (Winemiller *et al.* 1995) and trophic morphology (Ruber and Adams 2001). However, despite marked differences in morphology, the Mumbara and Songati populations (from the Malagarasi ecosystem) were not found to differ significantly in size and body shape. This may be explained by the fact that, may be because the two populations are sharing more or less the same Malagarasi ecosystem, the effects of which are not apparent in external forms. Similar explanation possibly suits the populations of *B. paludinosus* that radiated to Pangani and Hale ecosystem. Nevertheless, the morphoshape for the Pangani population deviated significantly from that of similar population occurring at Hale (Figure 1B). These two populations are geographically separated by manmade hydropower dams, which most likely could have led to differentiation of the body forms in the two *B. paludinosus* population as supported by the molecular study (Mwita 2013).

The results of the relative warps analysis (Figure 5) for *B. trimaculatus* and *B. jacksonii* populations from Malagarasi and Pangani wetlands in Tanzania revealed intra-locality variations as did individuals in populations from different countries. This can be justified by reproductive mutations, which in the long run bring about changes in the body morphology (Carroll *et al*. 2005). The *B. trimaculatus* from Malagarasi, Tanzania separated from *B. jacksonii* from Pangani River basin, though there was a narrow overlap of morphological characters between the two related species. Body-form in fishes may result from environmental (Robinson and Parsons 2002), genetic (Toline and Baker 1997) or a combination of inputs (Robinson and Wilson 1996). There are several possible explanations for differences in body-form variability between *B. trimaculatus* and *B. jacksonii*; choosing between them hinges mainly on the issue of how genotype and environment combine to result in the body-form phenotype.

The population of *B. trimaculatus* from Tanzania overlapped with *B. jacksonii* from Kenya and Mozambique; they showed close morphological relationship and left aside the populations of *B. trimaculatus* from the rest of the countries investigated (Figure 7). The populations of *B. jacksonii* did not show morphoshape similarity to populations of *B. trimaculatus* except at some few points of overlap for the Tanzanian and Mozambique populations (Figure 7). The body shape similarities between *B. trimaculatus* and *B. jacksonii* suggested here is supported by the molecular evidence (Mwita 2013). The morphoshape variations observed may also have resulted from genetic divergence due to spatial separation. Since spatial distance between populations may lead to genetic divergence and ultimately phenotypic variations (Ashrafi *et al*. 2006). This further implies that some of the *Barbus* spp. in different localities might belong to different biological species, even though there was no concrete evidence to support this hypothesis. If body-form in these two species is primarily under genetic control (i.e. different genotypes produce different phenotypes), it may be that the specific genes involved differ between *B. trimaculatus* and *B. jacksonii*.

West-Eberhard (1986) pointed out that not all morphometric variations should be attributed solely to genetic differences; environmental influences could also impact fish morphology. Such environmental influences on morphology could lead to the definition of phenotypic stocks characterized by differences that are exclusively environmentally induced (Swan and Foote 1999). Temporal differences in sampling could also be sources of morphological variability in the case old materials are studied. This however, was not the case for the current study because only fresh specimens were employed except for the few old materials that were obtained from the SAIAB fish collection.

The morphoshape variations among *Barbus* of the same species could also reflect adaptations to different functions though there is paucity of information with regard to this relation (Schaack and Chapman 2003).

The position of fins, eyes, mouths, head depth and caudal peduncle depth for instance, are used to discriminate between congeneric species of *B. trimaculatus* and *B. jacksonii* (Schaack and Chapman 2004). Likewise, roughness of scale surfaces has been studied from the viewpoint of hydrodynamics (Sudo *et al*. 2002). Thus, shape variations possibly arise from adaptations to varying hydrodynamic conditions and future studies may combine biomechanical analyses and change the approach to the study of form-function relationships.

Although the landmarks were placed at the same anatomical regions of the body of the fish, some variations existed within the region in each fish and eventually there were considerable variations over the whole fish (Ibanez *et al*. 2007). This approach however is useful in discriminating closely related species that are otherwise difficult to distinguish, between fish of hybrid origins and conspecifics in polyploidy populations (Martins *et al*. 1998, Ribeiro *et al*. 2003, and Mahenge 2009).

CONCLUSIONS

The geometric morphometric results indicated that *B. jacksonii* and *B. paludinosus* from Pangani and Malagarasi wetlands have distinct body morphology. The *B. paludinosus* populations from Pangani River are related due to gene pool connectivity and distinct from those of Malagarasi wetlands. Furthermore, *B. trimaculatus* from Malagarasi separated from *B. jacksonii* from Pangani River basin although there was a narrow overlap of the morphological characteristics between the two closely related species. There is a large morphoshape relationship among the *Barbus* spp. of the countries in the Central, Eastern and Southern Africa. The Zambian *B. trimaculatus* maintained their own cluster even when compared to specimens of the same species from other countries and hence, could be considered a separate species yet to be described.

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