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Ecology and speciation of the ostracod clade (*Gomphocythere*) in a tropical lake system, Lake Tanganyika, East Africa

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Introduction

Speciation in the East African lakes is remarkable, with many endemic species flocks, each consisting of 10s to 100s of species of vertebrate and invertebrate aquatic organisms. Lake Tanganyika, in particular, supports one of the most diverse faunas of any lake system on Earth. The origin of the Tanganyikan cichlid fish and gastropod flocks has been attributed to divergence of populations caused by the creation of physical barriers to dispersal such as the formation of separate lakes or habitat fragmentation within a single lake during major lake level falls (FRYER & ILES 1972, BROWN & MANDAHL-BARTH 1987, RIBBINK 1991, MICHEL et al. 1992, STURMBAUER & MEYER 1992, COULTER 1994, SULTMANN et al. 1995, VERHEYEN et al. 1996, MAYER et al. 1998). Similar mechanisms may have been important in the history of the diverse ostracod (small, bivalved crustaceans) fauna of Tanganyika and are the focus of this study.

Lake Tanganyikan environment

Lake Tanganyika is situated in the western branch of the East African Rift Valley with a latitude between 3° and 9° S. It is the deepest of the African rift lakes (1470 m). It is long (~650 km) and narrow (~80 km maximum width) and divided into eight tectonically formed sub-basins (three bathymetric basins) that are expressions of linked, asymmetrical half-grabens (HABERYAN & HECKY 1987, SCHOLZ & ROSENDAHL 1988, TIERCELIN & MONDEGUER 1991). The tectonic activity producing these geometries also produces patchy distributions of rock and sand substrates that dramatically alternate along the shore, providing a wide variety of habitats and the potential for niche subdivision. The substrates vary in character from silt, sand, and shell lags to stromatolites and rocks. The geologic history and resultant sedimentation patterns may be important to ostracod speciation because distribution patterns of species according to substrate and depth often have corresponding morphological innovations.

Problem to be addressed

The purpose of our study was to examine the relationships between speciation and ecology within the ostracod genus *Gomphocythere*. Specifically, we investigated how the distributions of individual species and corresponding morphologies are correlated with ecological variables, such as substrate and depth tolerances. In turn, we examined these correlates to elucidate and develop hypotheses of speciation mechanisms within the *Gomphocythere* clade.

Methods

Ecological distribution data of *Gomphocythere* species from Lake Tanganyika were extracted from a database of ostracod occurrences from Lake Tanganyika, compiled by COHEN et al. 1985–1995, including the Belgian Hydrobiological expedition of 1946–1947 and expeditions of COHEN et al. in 1986, 1989 and 1992 and MARTENS et al. in 1990 and 1992. Substrate and depth data were used as well as *Gomphocythere* abundance data from each sample site ($n = 128$ sites). Our database was constructed from counts of 350 valves of adult ostracods randomly chosen from grab samples. For each site, we calculated the proportion of the total fauna made up by each *Gomphocythere* species.

Results

Substrates

The presence/absence of *Gomphocythere* species in each substrate is summarized in Fig. 1. From these distributions, it appears that some species are more abundant in specific substrates than others. Some substrates have not been extensively sampled because they are relatively rare compared to the other samples and grab samples were not uniform for each site. However, the counts of ostracods from these individual samples were uniform ($n = 350$) and random-

Taxa	Substrate Presence									
	PLA	SIL	SIS	SAN	SHS	SHL	SSS	MSR	RKS	
<i>G. alata</i>	X	X	X	X	X	X	X	X	X	X
<i>G. coheni</i>	X	X	X	X	X	○	X	X	X	X
<i>G. cristata</i>	○	X	X	X	X	○	○	X	X	X
<i>G. curta</i>	○	○	X	X	X	○	○	X	○	○
<i>G. downingi</i>	X	X	X	X	X	X	X	X	X	○
<i>G. lenis</i>	○	○	○	X	○	○	○	○	○	X
<i>G. simplex</i>	○	○	○	X	○	○	○	○	○	X
<i>G. wilsoni</i>	X	X	X	X	X	○	○	○	X	X
<i>G. woutersi</i>	○	X	○	X	X	○	○	X	○	○

PLA= Plants
 SIL= Silt
 SIS= Silt/Sand
 SAN= Sand
 SHS= Shells/Sand
 SHL= Shells
 SSS= Shells/Sand/Strom.
 MSR= Mixed Rx/Sand
 RKS= Rocks

Fig. 1. Substrate preferences for the nine species of *Gomphocythere* found in Lake Tanganyika. X marks presence and O marks absence. Substrates are classified as indicated.

ized. From these data, several patterns emerge and are summarized in Figs. 2 and 3.

Depth

Depth range data for *Gomphocythere* species show that some species have broad ranges and others narrow ranges (Fig. 4). In all groups examined, distributions of the relative abundance of individual species with respect to the

total ostracod fauna for that depth range often spans a broad range of depths (just as in the substrate distribution), but there are specific depths at which each species is most abundant. More importantly, just as with substrate, depth affinities appear to differ among those members of closely related species (i.e. subclades). For example, *G. alata* and *G. cristata* are found at all depths up to 50 m, but the two species reach their maximum abundances at slightly different depths (20–29 m vs. 40–49 m, respectively).

Gomphocythere n. sp. downingi and *G. n. sp. wilsoni* show different depth affinities. *G. lenis* and *G. simplex* occur in very shallow depths and have the narrowest of all depth tolerances. *Gomphocythere curta*, which is distributed in many different substrates, is also distributed at many different depths, but is particularly abundant in waters between 20 and 29 m.

When looking at individual subclades, each species can be found in greatest abundance at narrow depth ranges that are different from sister species within that subclade. This is consistent with the substrate distribution data and also with the concept of niche segregation or specialization for *Gomphocythere* species. Whereas the expected pattern might be one that has an entire subclade with a specific sub-

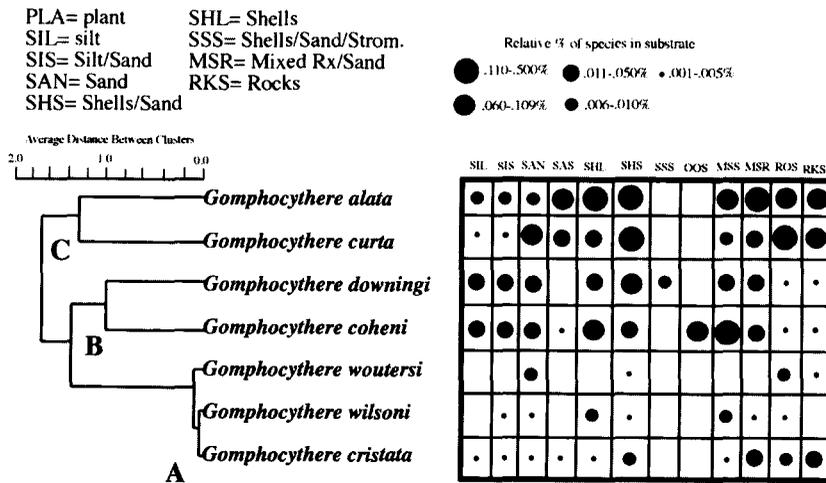


Fig. 2. R-mode cluster analysis of species grouped according to substrate distribution. Black circles indicate the relative abundance of each species with respect to the total ostracod fauna for that sample in each substrate. Clusters are indicated by the letters: A, B, C.

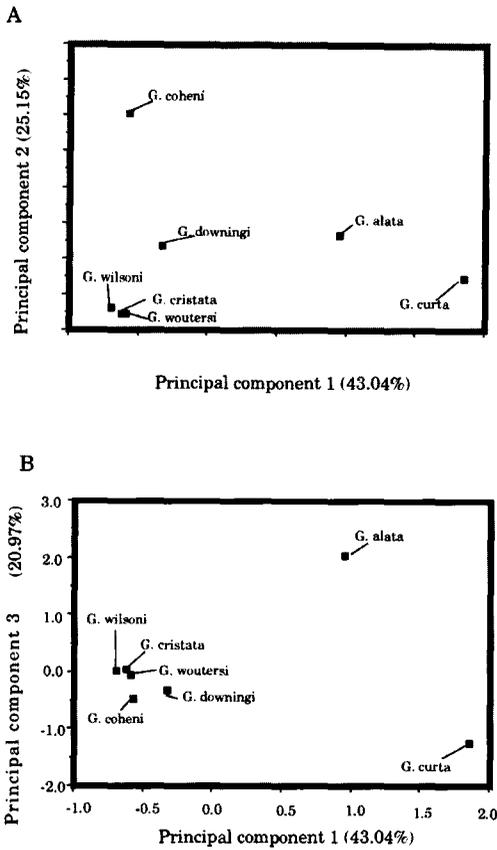


Fig. 3. Principal component ordination of species distribution according to substrate affinities. Species are labeled. A) PC1 versus PC2; B) PC1 versus PC3. Each point represents a species. Principal Component 1 contains 43.04% of the variation, Principal Component 2 contains 25.15% of the variation and Principal Component 3 contains 20.97% of the variation.

Taxa	DEPTHS (m)								
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90
<i>G. alata</i>	X	X	X	X	X	X	X	X	X
<i>G. coheni</i>	X	X	X	X	X	X	X	X	X
<i>G. cristata</i>	X	X	X	X	X	X	X	X	X
<i>G. curta</i>	X	X	X	O	O	O	O	O	O
<i>G. downingi</i>	X	X	X	X	X	X	X	X	X
<i>G. lenis</i>	X	O	O	O	O	O	O	O	O
<i>G. simplex</i>	X	X	O	O	O	O	O	O	O
<i>G. wilsoni</i>	X	X	X	X	X	X	X	X	X
<i>G. woutersi</i>	X	X	O	O	O	O	O	O	O

Fig. 4. Depth preferences for the nine species of *Gomphocythere* found in Lake Tanganyika. X marks presence and O marks absence. Depths are arbitrarily divided into 10-m increments. Note the rarer species have the most limited depth ranges.

strate or depth affinity, this pattern, instead, shows niche partitioning within the subclade. The patterns of independent character acquisition are consistent with the substrate and depth distributions.

Discussion

Biogeographic distribution of *Gomphocythere* species throughout Africa demonstrates that closely related species are found in geographically distant lake systems. Within Lake Tanganyika, the lack of phylogenetic constraint on substrate and depth distribution across the *Gomphocythere* phylogeny, including within subclades, appears consistent with the homoplastic distribution of many independent character states for individual species.

Gomphocythere species have been demonstrated to have affinities for certain substrates and depths. Physical barriers have been shown to occur in the lake basin throughout the basin's history (COULTER 1991). Niche specificity or partitioning in a substrate range could be the result of competitive exclusion between species after sympatric speciation, or allopatric speciation over very short niche space distances within the same subclade for dominance in that habitat.

In addition, species occurring at the base of some of the subclades appear to be generalists, whereas other species have specific substrates in which they are most abundant. For example, the generalist *Gomphocythere curta* occurs in many different substrates, while *G. n. sp. downingi* and *G. n. sp. wilsoni* are more narrowly distributed to specific substrates. These distributions indicate that there may be adaptations for certain types of substrates that are shared by all members of a subclade and that individual autapomorphies defining species have likely been derived from associations with specific substrates and corresponding micro-environments.

The pattern of depth distributions, like the pattern of substrate distributions within subclades, suggests partitioning of the environment according to individual species' affinities and may also connote possible mechanisms described above for substrates between species

that occupy similar niche spaces. In addition, it is significant to note that the species that are most abundant at all depths are situated at the base of certain subclades, indicating that these species are most broadly distributed and most abundant, with the most generalized (plesiomorphic) morphologies.

Fluctuation in lake levels

Lake level fluctuations have had a profound effect on speciation of the endemic faunas of the Tanganyikan trough (ROSSITER 1995, SULTMANN et al. 1995, VERHEYEN et al. 1996, and MAYER et al. 1998). Low lake levels isolate populations into separate water bodies, with different evolutionary pressures (or enough time for random mutations) such that the populations would be reproductively isolated. When the lake level rose again, the two (or more) newly evolved species would become sympatric. This theory is also compatible with the concept of allopatric speciation. Through the repeated connection and isolation, there would be opportunities for invasions and also for extinctions of species, which would open up possible new niche space for these invading species to occupy.

The implications for paleoecological interpretations for *Gomphocythere* and other ostracod species in the fossil record in Lake Tanganyika highlights the strong correlation between substrate and ostracod lifestyle, including specific morphologies and faunal abundances. In some cases, in substrates of equal grain size, such as mixed rock and sand and mixed rock and stromatolite, the faunal components are similar but there is a switch in the dominant species from one to another, suggesting niche partitioning within these habitats. Such observations concerning *Gomphocythere* species in current habitats should provide guidance when interpreting environmental and faunal change as represented in lake cores, and may provide future testable hypotheses.

Conclusions

Gomphocythere species differ in their environmental affinities in Lake Tanganyika, as defined by their relative abundances in the various substrates and

depths recorded along the lake margin. Members of the various subclades within the phylogeny are present in similar substrates, but species show some specificity in substrate and depth distributions suggesting niche partitioning.

In addition, certain morphologies are correlated with ecological variables. These ecologically correlated morphologies are linked to these habitat affinities and distributional patterns and represent major morphological innovations in these groups, some of which are recurrent in various species.

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References

- BROWN, D. S. & MANDAHL-BARTH, G., 1987: Living molluscs of Lake Tanganyika: a revised and annotated list. – *J. Conchol.* 32: 305–327.
- COULTER, G. W., 1991: *Lake Tanganyika and its Life*. – Oxford University Press, London.
- COULTER, G. W., 1994: Lake Tanganyika. – In: MARTENS, K., GODDEERIS, B. & COULTER, G., (eds): *Speciation in Ancient Lakes*: 13–18. – *Arch. Hydrobiol.*, Stuttgart.
- FRYER, G. & ILES, T. D., 1972: *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution*. – Oliver and Boyd: Edinburgh. 641 pp.
- HABERYAN, K. A. & HECKY, R. E., 1987: The late Pleistocene and Holocene stratigraphy and paleolimnology of Lakes Kivu and Tanganyika. – *Palaeogeog. Palaeoclim. Palaeoecol.* 61: 169–197.
- MAYER, W. E., TICHY, H. & KLEIN, J., 1998: Phylogeny of African cichlid fishes as revealed by molecular markers. – *Heredity* 80: 702–714.
- MICHEL, E., COHEN, A. S., WEST, K., JOHNSTON, M. R. & KAT, P. W., 1992: Large African lakes as natural laboratories for evolution: examples from the endemic gastropod fauna of Lake Tanganyika. – *Mitt. Int. Ver. Theor. Angew. Limnol.* 23: 85–99.
- RIBBINK, A. J., 1991: Distribution and ecology of the cichlids of the African Great Lakes. – In: KEENLEYSIDE, M. H. A. (ed.): *Cichlid Fishes, Fishes and Fisheries Series*: 2: 36–59. – Chapman and Hall, London.
- ROSSITER, A., 1995: The cichlid fish assemblages of Lake Tanganyika: ecology, behaviour and evolution of its species flocks. – *Adv. Ecol. Res.* 26: 187–252.
- SCHOLZ, C. A. & ROSENDAHL, B. R., 1988: Low lake stands in

- Lake Malawi and Tanganyika, East Africa, delineated with multi-fold seismic data. – *Science* **240**: 1645–1648.
- STURMBAUER, C. & MEYER, A., 1992: Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. – *Nature* **358**: 578–581.
- SULTMANN, H., MAYER, W. E., FIGUEROA, F., TICHY, H. & KLEIN, J., 1995: Phylogenetic analysis of cichlid fishes using nuclear-DNA markers. – *Mol. Biol. Evol.* **12**: 1033–1047.
- TIERCELIN, J.-J. & MONDEGUER, A., 1991: The geology of the Tanganyika trough. – In: COULTER, G. (ed.): *Tanganyika and its Life*: 7–48. – Oxford University Press, London.
- VERHEYEN, E., RUBER, L., SNOEKS, J. & MEYER, A., 1996: Mitochondrial phylogeography of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. – *Phil. Trans. R. Soc. London, Ser. B* **351**: 797–805.
- Authors' addresses:
- L. E. PARK*, Department of Geology, University of Akron, Akron, OH 44325-4101, U.S.A. Tel.: +1 330-972-7633, Fax: +1 330-972-7611.
E-mail: lepark@uakron.edu
- A. S. COHEN, Department of Geosciences, University of Arizona, Tucson, AZ 85721, U.S.A.
- K. MARTENS, Royal Belgian Institute of Natural Sciences, 29 Vautierstraat, 1000 Brussels, Belgium.
- *Author to whom correspondence should be addressed.