

NEWS AND VIEWS

PERSPECTIVE

Ongoing ecological divergence in an emerging genomic model

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Much of Earth's biodiversity has arisen through adaptive radiation. Important avenues of phenotypic divergence during this process include the evolution of body size and life history (Schluter 2000). Extensive adaptive radiations of cichlid fishes have occurred in the Great Lakes of Africa, giving rise to behaviours that are remarkably sophisticated and diverse across species. In Tanganyikan shell-brooding cichlids of the tribe Lamprologini, tremendous intraspecific variation in body size accompanies complex breeding systems and use of empty snail shells to hide from predators and rear offspring. A study by Takahashi *et al.* (2009) in this issue of *Molecular Ecology* reveals the first case of genetic divergence between dwarf and normal-sized morphs of the same nominal lamprologine species, *Telmatochromis temporalis*. Patterns of population structure suggest that the dwarf, shell-dwelling morph of *T. temporalis* might have arisen from the normal, rock-dwelling morph independently in more than one region of the lake, and that pairs of morphs at different sites may represent different stages early in the process of ecological speciation. The findings of Takahashi *et al.* are important first steps towards understanding the evolution of these intriguing morphs, yet many questions remain unanswered about the mating system, gene flow, plasticity and selection. Despite these limitations, descriptive work like theirs takes on much significance in African cichlids due to forthcoming resources for comparative genomics.

Keywords: body size, genomic resources, habitat preference, lamprologine cichlids, mating system, stages of divergence

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Eastern Africa is the theatre of several extraordinary radiations of cichlid species flocks, each of which is endemic to a single lake. Together, on the order of 1500 or more cichlid species inhabit Lakes Malawi, Victoria and

Tanganyika, composing a textbook model for comparative studies of speciation and adaptive radiation (Kocher 2004). Sexual selection on male displays is thought to be the primary selective mechanism of phenotypic divergence in contemporary populations of haplochromine cichlids in Lakes Malawi and Victoria, although lately this view has broadened somewhat to include important ecological influences as well. Presently, the best understood case of cichlid speciation involves the red and blue colour forms of *Pundamilia* in Lake Victoria (Seehausen 2009). The work of Takahashi *et al.* now suggests that genetic and morphological divergence might be occurring in a lineage of lamprologine cichlids in Lake Tanganyika primarily due to predator-driven natural selection rather than sexual selection.

Predation is an important facet of cichlid evolution (e.g. Heg *et al.* 2004). In Lake Malawi, for example, size-dependent use of rocky substrates varying in degree of protective cover suggests that predation influences habitat preference of a rock-dwelling cichlid (Markert & Arnegard 2007). In addition to rocky shoreline, expansive beds of empty snail shells resist erosion in Lake Tanganyika, offering cover to small cichlids (Fig. 1). Predation risk in Lake Tanganyika is thought to be particularly high over open sand, where hiding places are scarce (Konings 1998).

Takahashi's team convincingly demonstrates the presence of morphologically differentiated normal and dwarf forms of *T. temporalis* at neighbouring sites (Nkumbula Island and Wonzye Point) and at a site 80 km away (Chibwensolo). The normal morph lives among rocks as adults, whereas the dwarf morph inhabits shell beds. Additional sites without shell beds lack the dwarf morph. The authors show that all females and most males of the normal morph are nearly twice the body length of the dwarf morph at sexual maturity. Given the tight match between body size and crevice size in the preferred habitats, Takahashi *et al.* infer that predation on size-mismatched fish is the selection pressure underlying divergence, although selection has not yet been measured directly in these populations.

The development of adaptive radiation theory has already benefited from many examples of divergence in fish body size in north-temperate, postglacial settings with fewer competing species compared with Lake Tanganyika. Pairs of large and small fish ecotypes have diverged independently within high latitude lakes around the globe (e.g. threespine stickleback and lake whitefish). In these cases, frequency-dependent competition for different food resources has selected for large and small forms adapted to feeding in nearshore and offshore food webs, respectively (Schluter 2000). This is quite different from the selective mechanism proposed by Takahashi *et al.* (2009), although differing predation regimes between postglacial

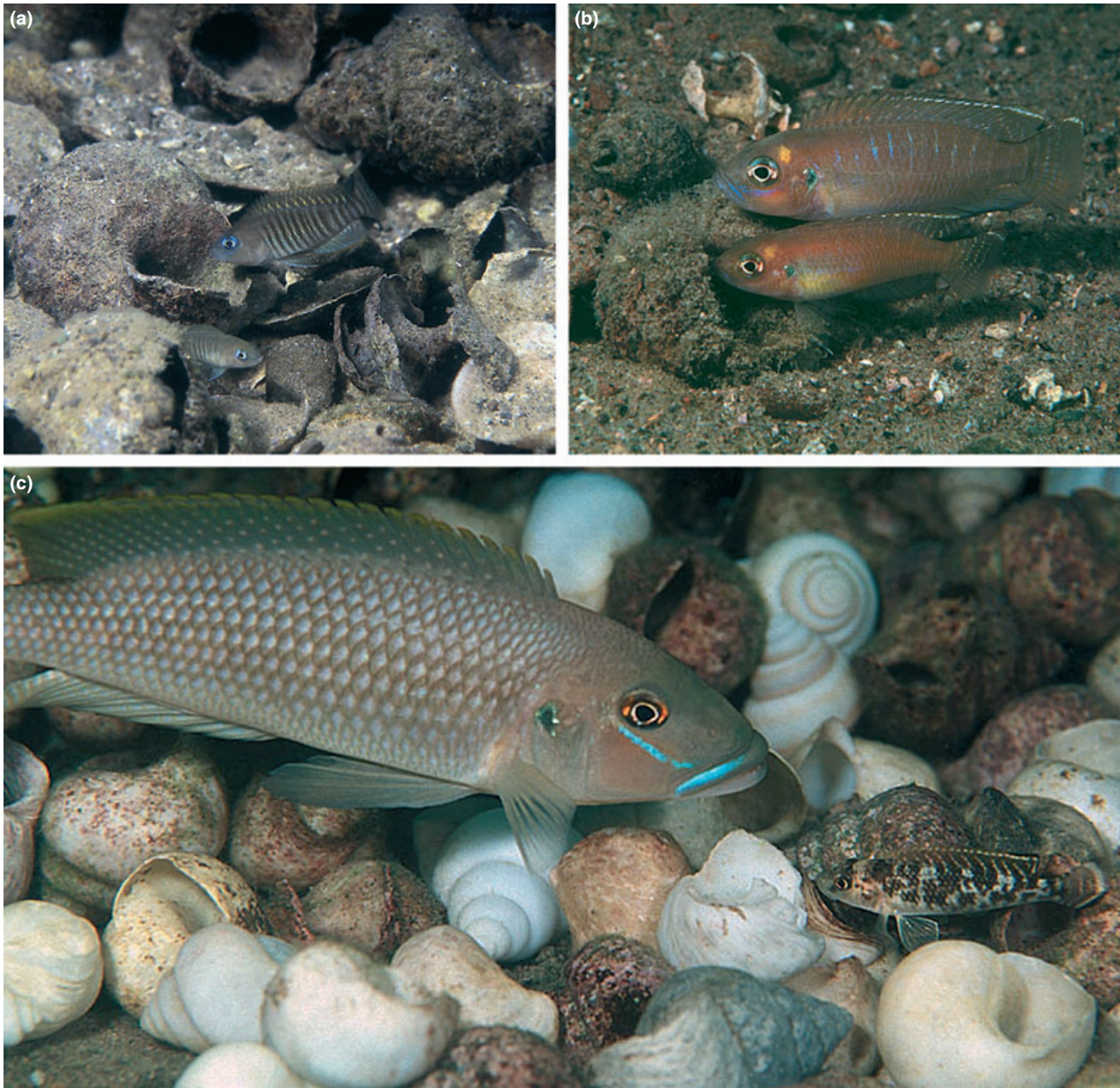


Fig. 1 Shell-brooding cichlids of Lake Tanganyika, Africa (photos by Ad Konings). (a) *Neolamprologus multifasciatus*, a facultative shell brooder thought to be the smallest cichlid species in the world (male above, female below; photo taken at Mbita Island, Zambia). (b) *Neolamprologus brevis* at Chaitika, Zambia (male above, female below). (c) *Lamprologus callipterus* at Kipili, Tanzania (male left, female right). Territorial males of *L. callipterus* transport large snail shells over long distances and accumulate them into sizeable nests that are used by other shell-brooding cichlids at the sand-rock interface (Sato & Gashagaza 1997).

lake habitats might also contribute secondarily to divergence in some species pairs (Marchinko 2009).

Investigating variation at eight microsatellite loci, Takahashi *et al.* (2009) demonstrate levels of nuclear genetic differentiation between normal and dwarf populations in the Nkumbula–Wonzye area that are similar to those found between diverging red and blue *Pundamilia* species (Seehausen *et al.* 2008). It is unlikely that Takahashi *et al.* would have detected such a pattern if it were based solely

on predatory selection acting directly on genes involved in predator avoidance in a single population of interbreeding ecomorphs. Instead, their finding suggests evidence of genetic isolation between morphs that is more widespread in the nuclear genome.

One form of such isolation—geographical isolation due to philopatry (i.e. site fidelity)—is common in rock-dwelling cichlids (Wagner & McCune 2009). In a case of extreme philopatry, a stretch of sand only 35 m wide acts as a

barrier to dispersal for a Malawi cichlid (Rico & Turner 2002). Additional fine-scale study of population structure in the *T. temporalis* complex using a broad array of nuclear loci is warranted. At present, Takahashi *et al.* describe *adjacent* rocky shoreline and shell beds and a noteworthy overlap in the distributions of normal and dwarf morphs, without mentioning any barriers between habitat types at Nkumbula-Wonzye (see also Fig. 11-4 of Sato & Gashagaza 1997). In fact, where geographical isolation is mentioned (Chibwensolo), the authors report essentially no genetic differentiation between morphs. These observations suggest that a second form of isolation—some degree of reproductive isolation—may be more important than fine-scale geography in structuring populations of co-occurring morphs at Nkumbula-Wonzye. Potential mechanisms of partial reproductive isolation include divergent, predator-driven habitat preferences and/or size-based assortative mating, although additional studies are needed to test these possibilities.

The current evidence offered by Takahashi's team raises the intriguing possibility that normal and dwarf morphs of *T. temporalis* are currently diverging in the Nkumbula-Wonzye region through the process of ecological speciation. Given the authors' description of overlap in the distributions of morphs in this region, future work on this system should consider the possibility that significant gene flow has occurred during the earliest stages of within-site divergence. Sympatric speciation theory becomes relevant whenever selection must overcome strong gene flow during speciation. Disruptive natural selection on ecological traits (e.g. in *T. temporalis*) and sexual selection by female preferences for extreme displays may have very different consequences for the likelihood of speciation under strong gene flow, as well as the expected genetic architectures of trait differences when sympatric speciation is detected (Arnégard & Kondrashov 2004).

Takahashi *et al.* find much deeper genetic divergence between geographically distant populations of the same morph than between co-occurring morphs. The authors conclude that the descendant morph—they argue the dwarf morph—arose independently in different regions of the lake. Although this is certainly one possible explanation, gene flow between co-occurring morphs could also have generated the observed pattern of genetic variation given only a single lake-wide origin of the dwarf morph. In either case, the authors appear to have detected populations of *T. temporalis* at different stages of divergence (e.g. the stage at Chibwensolo appears to be a dimorphism in morphology and habitat preference preceding obvious genetic divergence). Even if the genetic divergence they describe between co-occurring morphs in the Nkumbula-Wonzye region is not associated with completed speciation, multiple populations at different stages of divergence are still valuable for investigating mechanisms that drive or impede speciation (Nosil *et al.* 2009).

While predation may play the most fundamental role in divergence in *T. temporalis*, breeding systems also influence the evolution of body size in lamprologine cichlids. Social hierarchies are exquisitely organized by size in many

lamprologines (Heg *et al.* 2005). One shell-brooder, *Lamprologus callipterus*, exhibits the most extreme sexual size dimorphism in the animal kingdom in the direction of larger males (Taborsky 2001; Fig. 1c). In *T. temporalis*, a 'piracy' tactic of taking control of nests and females through aggression (without providing paternal care) has been described in males larger than the normal morph (Mboko & Kohda 1999). More importantly, some mature, normal morph males of *T. temporalis* are small—like dwarf males—and engage in 'sneak mating' behaviour (Kato *et al.* 2005; Takahashi *et al.* 2009). These observations raise questions. Are 'sneaker' males a source of gene flow between the diverging morphs described by Takahashi *et al.* at some sites? Does plasticity of growth affect stage of divergence between the morphs? Taborsky (2001) showed that wild-caught, dwarf sneaker males of *L. callipterus* exhibit no further growth in the laboratory, yet Konings (1998) mentioned retained potential for growth in other shell-brooding species. Regardless of the specific answers, future studies of divergence in *T. temporalis* should certainly consider the importance of mating system in addition to predation.

Understanding the genetic basis of speciation in different contexts is an exciting new frontier in evolutionary biology (e.g. Rogers & Bernatchez 2007). The Broad Institute is currently constructing a complete genome sequence for the tilapiine cichlid, *Oreochromis niloticus*, and low density genome sequencing projects are being pursued in three haplochromine species (N.H.G.R.I. 2009). When completed, these resources will facilitate comparative genetic investigations of behavioural evolution (Hofmann 2003) and adaptive radiation (Kocher 2004) in an unrivalled number of closely related vertebrate species. Thus, natural history, behavioural ecology and descriptive population genetics take on renewed significance in the cichlid 'supermodel' for evolutionary genetics. Such efforts help to identify interesting and potentially informative phenotypes and populations, and they continue to be needed in the under-explored cichlid system. The new case of genetic and ecological divergence in *T. temporalis* holds promise for offering insights into questions about selective mechanisms of adaptive radiation. Moreover, *T. temporalis* exhibits divergence in body size (and probably several other features of life history), as well as shell-brooding behaviours, which are traits of interest for future studies aimed at dissecting the genetic underpinnings of adaptive phenotypic evolution.

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References

- Arnégard ME, Kondrashov AS (2004) Sympatric speciation by sexual selection alone is unlikely. *Evolution*, **58**, 222–237.

- Heg D, Bachar Z, Brouwer L, Taborsky M (2004) Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **271**, 2367–2374.
- Heg D, Bachar Z, Taborsky M (2005) Cooperative breeding and group structure in the Lake Tanganyika cichlid *Neolamprologus savoyi*. *Ethology*, **111**, 1017–1043.
- Hofmann HA (2003) Functional genomics of neural and behavioral plasticity. *Journal of Neurobiology*, **54**, 272–282.
- Katoh R, Munehara H, Kohda M (2005) Alternative male mating tactics of the substrate brooding cichlid *Telmatochromis temporalis* in Lake Tanganyika. *Zoological Science*, **22**, 555–561.
- Kocher TD (2004) Adaptive evolution and explosive speciation: the cichlid fish model. *Nature Reviews Genetics*, **5**, 288–298.
- Konings A (1998) *Tanganyika Cichlids in their Natural Habitat*. Cichlid Press, El Paso, Texas.
- Marchinko KB (2009) Predation's role in repeated phenotypic and genetic divergence of armor in threespine stickleback. *Evolution*, **63**, 127–138.
- Markert JA, Arnegard ME (2007) Size-dependent use of territorial space by a rock-dwelling cichlid fish. *Oecologia*, **154**, 611–621.
- Mboko SK, Kohda M (1999) Piracy mating by large males in a monogamous substrate-breeding cichlid in Lake Tanganyika. *Journal of Ethology*, **17**, 51–55.
- N.H.G.R.I., National Human Genome Research Institute (2009) *Online List of the Statuses of Approved Sequencing Targets*. National Institutes of Health, Bethesda, Maryland. Available from <http://www.genome.gov/10002154>.
- Nosil P, Harmon LJ, Seehausen O (2009) Ecological explanations for (incomplete) speciation. *Trends in Ecology & Evolution*, **24**, 145–156.
- Rico C, Turner GF (2002) Extreme microallopatric divergence in a cichlid species from Lake Malawi. *Molecular Ecology*, **11**, 1585–1590.
- Rogers SM, Bernatchez L (2007) The genetic architecture of ecological speciation and the association with signatures of selection in natural lake whitefish (*Coregonus* sp. Salmonidae) species pairs. *Molecular Biology and Evolution*, **24**, 1423–1438.
- Sato T, Gashagaza MM (1997) Shell-brooding cichlid fishes of Lake Tanganyika: their habitats and mating systems. In: *Fish Communities in Lake Tanganyika* (eds Kawanabe H, Hori M, Nagoshi M), pp. 221–240. Kyoto University Press, Kyoto.
- Schluter D (2000) *The Ecology of Adaptive Radiation*. Oxford University Press, New York.
- Seehausen O (2009) Progressive levels of trait divergence along a 'speciation transect' in the Lake Victoria cichlid fish *Pundamilia*. In: *Speciation and Patterns of Diversity* (eds Butlin R, Bridle J, Schluter D), pp. 155–176. Cambridge University Press, Cambridge.
- Seehausen O, Terai Y, Magalhaes IS *et al.* (2008) Speciation through sensory drive in cichlid fish. *Nature*, **455**, 620–626.
- Taborsky M (2001) The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *The Journal of Heredity*, **92**, 100–110.
- Takahashi T, Watanabe K, Munehara H, Rüber L, Hori M (2009) Evidence for divergent natural selection of a Lake Tanganyika cichlid inferred from repeated radiations in body size. *Molecular Ecology*, **18**, 3110–3119.
- Wagner CE, McCune AR (2009) Contrasting patterns of spatial genetic structure in sympatric rock-dwelling cichlid fishes. *Evolution*, **63**, 1312–1326.

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