# What big lips are good for: on the adaptive function of repeatedly evolved hypertrophied lips of cichlid fishes

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Linking phenotypic traits to an adaptive ecological function is a major goal of evolutionary biology. However, this task is challenging and has been accomplished in only a handful of species and ecological model systems. The repeatedly evolved adaptive radiations of cichlid fishes are composed of an enormously diverse set of species that differ in trophic morphology, body shape, coloration, and behaviour. Ecological guilds of species with conspicuously hypertrophied lips have evolved in parallel in all major cichlid radiations and are characterized by large lips and pointed and narrow heads. In the present study, we experimentally tested the adaptive significance of this set of conspicuous traits by comparing the success of hypertrophied-lipped and closely-related thin-lipped endemic Lake Victoria cichlids in a novel foraging assay. The hypertrophied-lipped species (*Haplochromis chilotes*) was clearly more successful in exploiting food resources from narrow crevices and the observed difference in foraging success increased more at narrower angles. Furthermore, pronounced differences in exploratory behaviour between the species suggest that the evolution of hypertrophied-lipped species involved the co-evolution of a suite of traits that include foraging behaviour. The repeated evolution of hypertrophied-lip morphology in conjunction with a narrow and pointed head shape in cichlids represents an evolutionary innovation that facilitates foraging in rocky crevices, thus allowing access to a novel niche. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 448–455.

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## INTRODUCTION

Deciphering the ecological functions of apparently adaptive morphologies has been a major goal in biology ever since Darwin. Adaptations to explore different niches ease competition between diverging populations (Pfennig & Pfennig, 2012) and are fundamental to the current theory of ecological speciation (Via, 2009; Nosil, 2012). However, distinguishing particular morphological traits as potential adaptations and confirming that they actually are adaptations is not trivial. The famous 'Spandrels' paper by Gould & Lewontin (1979) highlighted the need for empirical tests over telling 'just-so stories', and emphasized that non-adaptation should comprise the null-hypothesis to be refuted when analyzing the presumed adaptive value of a phenotypic trait. Certain evolutionary phenomena such as character displacement and convergent evolution suggest an adaptive function for the traits under consideration because it is assumed that they arose as a result from a response to similar selection pressures (Losos, 2010; Elmer & Meyer, 2011). However, correlations between an environmental factor and a trait value and a pattern of convergent evolution are not sufficient evidence for adaptive functions (Endler (1986; Losos (2011). Often, those responses might be constrained by genetic and/or developmental biases (Elmer & Meyer, 2011). Convergence and parallelism are not restricted to single traits but might affect different

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apparently unlinked characters, including those that influence trophic, morphological, and behavioural traits as a consequence of pleiotropy and/or natural selection (Johnson, Revell & Losos, 2010; Montaña & Winemiller, 2013; Elmer *et al*., 2014).

The African cichlid adaptive radiations are considered among the most diverse and fastest speciating of all vertebrates (Near *et al*., 2013). Competition for food might be the major driver of divergence in trophic specialization and, consequently, for speciation (Losos, 2010). Cichlid species that occupy similar niches in different lakes often exhibit parallelism in many traits, including swimming performance, foraging, coloration, and behaviour (Henning & Meyer, 2014). A conspicuous trophic trait that has evolved repeatedly in different adaptive radiations is lip hypertrophy (Stiassny & Meyer, 1999; Burress, 2014). Species with hypertrophied lips are not particularly common, although each of the great lakes in Africa contains at least one endemic species with these characteristic lips: *Cheilochromis euchilus*, *Placidochromis milomo*, *Melanochromis labrosus*, *Eclectochromis ornatus*, *Otopharynx pachycheilus*, all from Lake Malaŵi, *Lobochilotes labiatus* from Lake Tanganyika, and *Haplochromis chilotes* from Lake Victoria (Colombo *et al*., 2013). Also in the Neotropics, cichlids with hypertrophied lips occur in lake (*Amphilophus labiatus*) and river (*Crenicichla tendybaguassu*) habitats (Burress *et al*., 2013; Colombo *et al*., 2013). In other teleosts, such as barbs (Cyprinidae) of Lake Tana, Ethiopia (de Graaf *et al*., 2008) and sailfin silverside fishes (Telmatherinidae) of Malili lakes, Indonesia (Herder, Schwarzer & Jobst Pfaender, 2006), hypertrophied-lipped species exist as well.

Despite the evidence that hypertrophied lips evolved convergently and are associated with diet and foraging mode, the fitness implications of this phenotype in cichlids have not been investigated and the factors promoting its evolution remain unknown (Oliver & Arnegard, 2010). Yet, this knowledge is necessary to conclude that a phenotype is adaptive (Endler, 1986). Several hypotheses have been proposed to explain the ecological significance of hypertrophied lips. For example, that they serve as a seal allowing the fish to suck prey out of crevices (Ribbink *et al*., 1983), as a bumper that reduces mechanical stress during foraging in a habitat of sharp rocks (Greenwood, 1974), or as an increased surface area for accommodating taste-buds (Arnegard & Snoeks, 2001). However, none of these hypotheses has been tested experimentally and the exact function(s) of hypertrophied lips in cichlids remain uncertain (Manousaki *et al*., 2013). It should be pointed out that a slender and shallower body and an elongated (pointed) and more narrow head have been noted as

covariant phenotypic traits that go along with hypertrophied lips (Manousaki *et al*., 2013). This combination of traits consisting of a pointed head and hypertrophied lips might therefore jointly serve the same ecological function. Cichlids with this ecomorphology are associated with a specialization on rock-oriented foraging (see also Supporting Information, Video Clip S1) and a shift in diet towards an increased proportion of invertebrates such as insects, small crustaceans and larvae, as demonstrated in several different lineages of cichlids (Elmer *et al*., 2010; Colombo *et al*., 2013; Manousaki *et al*., 2013; Burress, 2014).

Because behaviour is a key-link between ecology and morphology, similar animal 'personalities' might be common to hypertrophied-lipped cichlids (Johnson *et al*., 2010). An animal personality is a behavioural correlation across a range of situations (Sih, Bell & Johnson, 2004). For example, risk-taking male fish not only tend to be aggressive and active in competition with other male fish of the same species, but also tend to be more active in the presence of predators (Sih *et al*., 2004). In African cichlids, as well as in zebrafish, aggressive behaviour is negatively correlated with habitat complexity (Basquill & Grant, 1998; Danley, 2011). Therefore, the specialization of foraging in complex rocky habitats might also have consequences on the aggression and risk-taking behaviour (Danley, 2011). Possibly, a rocky habitat for feeding might also harbour more predators and hence select for more cautious behaviour.

Hypertrophied lips and the associated changes in head morphology might be regarded as an evolutionary innovation that increases the adaptive potential to utilize new resources and a new trophic niche (Oliver & Arnegard, 2010; Manousaki *et al*., 2013; Burress, 2014; Machado-Schiaffino, Henning & Meyer, 2014). In the present study, we investigate the joint functions of hypertrophied lips and a more pointed head by describing morphological and behavioural differences between two species of the Lake Victoria species-flock, *H. chilotes* (hypertrophied-lipped) and *Haplochromis nyererei* (thin-lipped). The effect of the trophic morphology on foraging is investigated by using a novel assay that measures the performance across crevices with different angles (i.e. varied degrees of access). We aimed specifically to test the hypothesis that cichlids with more pointed heads and hypertrophied lips have an increased ability to obtain prey from more narrow crevices.

## MATERIAL AND METHODS

### STUDY SPECIES

Foraging experiments were conducted using hypertrophied- (*H. chilotes*) and thin-lipped
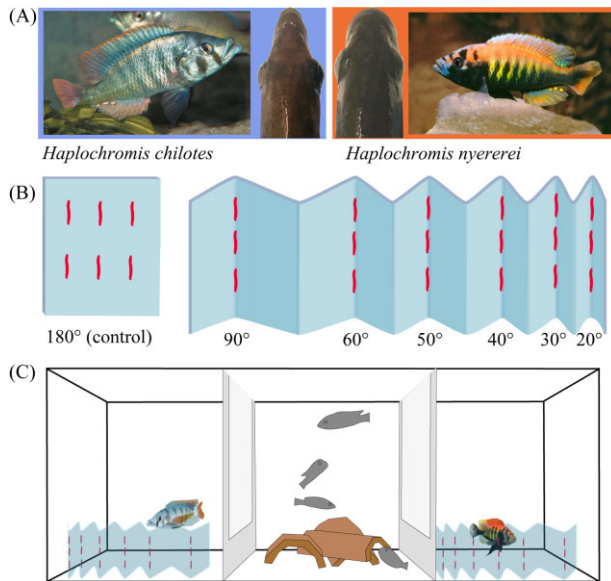
**Figure 1.** Specimens and experimental set-up. A, haplochromine cichlid species used in the present study photographed from the lateral and dorsal views. The photographs of *Haplochromis chilotes* and *Haplochromis nyererei* from lateral view were kindly provided by Erwin Schraml and Ad Konings, respectively. B, acrylic glass structures with attached mosquito larvae used for the assessment of foraging performance. C, experimental set-up shown with test fish and the acrylic glass structure in lateral compartments and untested fish (for social acclimation) in the mid-compartment.

(*H. nyererei*) species of the endemic Lake Victoria haplochromine cichlid fish radiation. Stocks of both species have been maintained for over 10 years at the Animal Research Facility of the University of Konstanz under identical feeding and housing conditions. Under these conditions, both species continued to exhibit consistent morphological differences in lip and head morphology (Figs 1A, 2C, D). The small difference in standard length between *H. chilotes* (mean 95.2 mm, SD 7 mm) and *H. nyererei* (mean 81.8 mm, SD 6.2 mm) did not affect substantially the comparability of both species.

## FORAGING EXPERIMENT

To test for differences in foraging performance, three mosquito larvae of similar size were fixed by drying them at 50 °C for 5 min to each groove of a series of decreasing angles of an acrylic glass structure (Fig. 1B). In an additional control experiment, six attached mosquito larvae were also fixed to an acrylic glass plane to exclude general differences in foraging that are unrelated to crevices (e.g. scraping). No

detachment of mosquito larvae was observed, even after leaving the structure for 24 h in the water. The experimental tank (60 × 120 × 50 cm) was divided into three compartments, with the central one holding non-experimental fish for the duration of the whole experiment to induce calmer and more natural behaviour (Fig. 1C). Experimental fish were starved for 3 days prior to the experiment. Fish were acclimatized overnight to the experimental tank and tested on the next day around 12.00 h. The experiment started with the placement of the acrylic glass structure in to the experimental portion of the tank and behaviour was recorded with a video camera (see Supporting information, Video Clips S2 and S3). The experiment lasted 90 min. A total of 13 fish per species and per set-up (angular and plane acrylic glass) were tested. For each angle, the number of successful and unsuccessful attacks was counted. An attack was considered successful if the mosquito larva was removed from the acrylic glass. For the statistical analysis, the success rate (ratio of successful and total attempts) was calculated and analyzed by means of a Kruskal–Wallis test in R, version 3.0.0, followed by Bonferroni correction (R Core Team, 2012).

## MEASUREMENT OF BOLDNESS

Preliminary observations of the behaviour of both species when presented with novel objects suggested the existence of behavioural differences in boldness between *H. chilotes* and *H. nyererei*. This difference in boldness was quantified in this experiment by recording the latency to first feeding attempt (Schürch & Heg, 2010) on the novel object, namely the angular acrylic glass structure.

## MORPHOLOGICAL DIFFERENTIATION

Morphological measurements were taken from fish anaesthetized with 0.02% Tricaine (MS-222) using standardized photographs taken from the dorsal and left lateral views. The area of the protruded lip normalized by body-area was measured using IMAGEJ (Fig. 2B) (Rasband, 1997). This measurement is known to reflect differences in lip size (Machado-Schiaffino *et al*., 2014).

For the assessment of head shape from dorsal view, three landmarks and 10 semi-landmarks were digitized. A more detailed description of the geometric morphometrics procedure is provided in the Supporting information (Appendix S1). First, the allometric effects were removed from shape using a pooled within-group regression with the Procrustes coordinates as dependent variables and standard length as independent variable. A covariance matrix
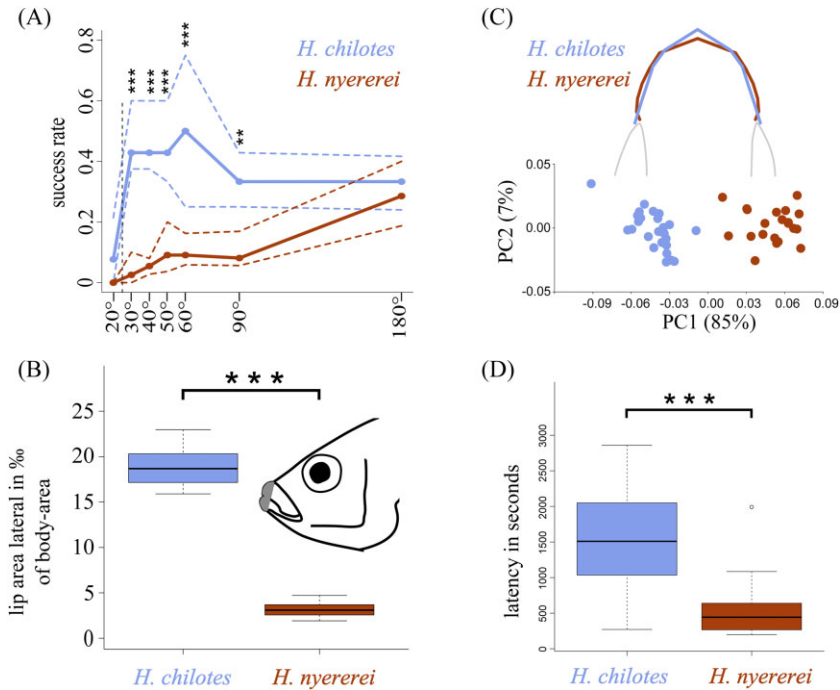
**Figure 2.** Morphological and behavioural differences between *Haplochromis chilotes* (blue) and *Haplochromis nyererei* (red). A, results of foraging experiment: circles represent the median at every angle and are connected by lines. The dashed lines represent the first and third quartile values at every tested angle. B, differences in lip area: the measurement was taken as shown by the grey area and was normalized by the body area. C, dorsal view of the head shape (excluding the lips): represented is the median head shape of each species according to the first principal component (PC). The grey lines represent the eyes of the fish, which were not part of the analysis. D, results of boldness measurements (statistical significance at $**P < 0.01$ and $***P < 0.001$ after Bonferroni correction, respectively).

was generated with the regression residuals to perform a principal component analysis. Multivariate analyses were conducted in MORPHOJ, version 1.05f (Klingenberg, 2011).

## RESULTS AND DISCUSSION

In the present study, the differences in foraging performance between two cichlid species from Lake Victoria, *H. chilotes* (hypertrophied-lipped, pointed head) and *H. nyererei* (thin-lipped, blunt head), were tested using a novel assay. In addition to the morphological differences (lips and head shape), both species exhibited clear differences in foraging performance and exploratory behaviour. The hypertrophied-lipped species was more successful foraging in crevices and the difference in success increased at more narrow angles.

The results show that hypertrophied-lipped cichlids probably evolved to exploit food resources in narrow crevices and suggest that the difference in performance is related to a suite of morphological adaptations in lip and head morphology. The behavioural

difference that was found might represent an additional adaptation that probably evolved as a consequence of a new foraging mode.

### ENHANCED FORAGING PERFORMANCE OF *H. CHILOTES*

Hypertrophied lips together with an elongated head evolved repeatedly in parallel adaptive radiations of cichlids (Colombo *et al.*, 2013). The way that this trophic morphology contributes to increased fitness is unknown. In the wild, species with hypertrophic lips are observed to forage mainly in rock crevices (Kohda *et al.*, 2008). In the present study, foraging performance in crevices was investigated experimentally under laboratory conditions (Fig. 1; see also Supporting information, Table S1). In our experiments, it is not possible to separate the effects of the hypertrophied lips from head shape; however, we consider that these traits serve the same ecological function. Pronounced differences in foraging performance were found between hypertrophied-lipped *H. chilotes* and thin-lipped *H. nyererei* (Fig. 2A, Table 1). Other

**Table 1.** Increased differences in success rate between *Haplochromis chilotes* and *Haplochromis nyererei* with decreasing angles

|  | 30° | 40° | 50° | 60° | 90° | 180° |
|---|---|---|---|---|---|---|
| Differences in mean | 0.434 | 0.427 | 0.293 | 0.351 | 0.247 | 0.007 |
| *P*-value | $3.14 \times 10^{-5}$ | $1.42 \times 10^{-5}$ | $7.62 \times 10^{-4}$ | $1.19 \times 10^{-4}$ | $3.27 \times 10^{-4}$ | 0.75 |

*P*-values were calculated by means of a Kruskal–Wallis test.

factors such as the latency to start feeding or standard length did not have a significant effect on the foraging score (data not shown). At every angle that was tested, the difference in foraging efficiency between the species was highly significant. Interestingly, no difference in foraging performance between the two species was detected when feeding on a plane surface (Table 1). Differences in means increased with decreasing angles, except at 60° where the difference was slightly elevated compared to 50°. The increase of the differences in mean foraging success between species with decreasing angle is significant (regression analysis: $P < 0.001$, $r^2 = 0.93$). This suggests that *H. chilotes* copes significantly better with the decrease in crevice angles than does *H. nyererei*. Only three (all of them were *H. chilotes*) out of 26 individuals tested were able to successfully forage at the narrowest crevice (angle 20°); hence, these measurements were excluded from further statistical analysis. Nevertheless, this shows that some *H. chilotes* individuals can successfully forage in narrower crevices despite being generally larger. *Haplochromis chilotes* performed slightly worse in broader angles, in comparison with the narrow ones (Fig. 2A). These results suggest that the advantage of this trophic morphology increases at the expense of the ability to forage on a plane and at larger angles in what might consist in a trade-off (Meyer, 1989). Karel Liem, the late cichlid functional morphologist, used to call cichlids 'jack of all trades, master of none' (Liem, 1973). He appeared to imply that there is no cost to 'normal' feeding on any substrates for feeding specialists that cichlids with hypertrophied lips most certainly are. In our experience from years of observations in Africa and Central America, we regard cichlids to be opportunistic feeders in times of over-abundance of a particular prey but, at 'ecological crunch times', their specializations pay off and they will seasonally feed only on certain prey items that only they can exploit, whereas they will be less efficient or completely unable to feed on others (Meyer, 1990). There certainly are trade-offs in feeding performance and specialization (Meyer, 1989). Apart from previous hypotheses about the function of hypertrophied lips of cichlids (Greenwood, 1974; Ribbink *et al.*, 1983; Arnegard & Snoeks, 2001), the present study high-lights additional aspects of adaptation such as reaching prey in crevices that is not available to other species without the suit of adaptations, such as the hypertrophied lips and the pointed head.

## HYPERTROPHIED LIPS AND POINTED HEADS FACILITATE FORAGING IN CREVICES

Hypertrophied lips are the most evident trait of *H. chilotes*, being six times greater than the mean lip size of *H. nyererei* ($P < 0.001$) (Fig. 2B). Hypertrophied-lipped cichlids share other morphological traits such as an elongated and pointed head that might have evolved in concert with lips to increase foraging ability in crevices (Manousaki *et al.*, 2013). Clear differences in head shape between both species were captured by the first principal component ($P < 0.001$) (Fig. 2C). The head of *H. chilotes* is much more pointed compared to that of *H. nyererei*. These differences in head shape agree with the notion that narrower heads allow better access to food resources in narrower crevices: a putative co-adaptation with hypertrophied lips.

The correlation between head and lip traits observed in many species might either result from conserved genetic correlations and/or be the product of similar selection pressures (Elmer & Meyer, 2011). These possibilities should be further investigated by analyzing the segregation of both traits in genetic crosses (as is under way in our laboratory). Genetic correlations between traits might constrain the number of available evolutionary paths leading to adaptations (Schluter, 2000). It would be interesting to extend the present study and uncouple the effects of the lips from those of the pointed head. This could be achieved by testing the foraging performance of: (1) wild-caught specimens with variation in these traits; (2) other species with different lip sizes and head shapes; or (3) an $F_2$ hybrid population that segregates for both traits.

Another character that might play a role in feeding in crevices is the degree to which the jaws can be protruded (Hulsey, Hollingsworth & Holzman, 2010). A high protrudability would tend to increase suction force and would also confer an advantage to reach prey in rock crevices (Wainwright *et al.*, 2001). In the

present study, no data concerning the jaw morphology was assessed, although we have carried out crosses of these two species, the results of which we plan to report elsewhere. However, a more conical head shape, as also found for cichlid species with hypertrophied lips, is typically associated with increased suction force (Liem, 1993). The thin-lipped species, exhibits a long ascending arm of the premaxilla and a small angle between the ascending arm and the dentigerous arm, a jaw morphology known to be associated with high suction force, which was also confirmed experimentally (Bouton *et al*., 1998). More research on the jaw morphology would be needed to determine its precise effects on feeding efficiency in narrow crevices.

## Exploratory behaviour might be explained by foraging mode

The focus of the present study was to test for foraging advantages of hypertrophied-lipped fish in crevices, although additional behavioural differences became obvious during the performance trials. These are likely to have a genetic basis since all fish were housed and fed the same way. *H. chilotes* approached the novel object and started to feed on mosquito larvae much later than *H. nyererei* ($P < 0.001$) (Fig. 2D). Also, the lateral stripes in *H. chilotes* were very conspicuous during the foraging trials and can be interpreted as a signal of an agonistic motivational status (Baerends, Wanders & Vodegel, 1985). Despite being constitutive in some piscivorous species, lateral stripes are transient in most haplochromine cichlids and their intensity is known to reveal their motivational status (Henning *et al*., 2014). Marked lateral stripes are associated with reduced aggression and an increased propensity for fleeing (Henning *et al*., 2014). Aggression and boldness are often correlated behaviours and contribute to a common behavioural syndrome that has been described as proactive or risk-taking behaviour (Sih *et al*., 2004). Hence, the reactive or risk-averse behaviour of *H. chilotes* might be an adaptation to its complex rocky habitat. However, behavioural differences cannot be explained by habitat complexity alone because *H. chilotes* and *H. nyererei* both appear to prefer rocky habitats (Seehausen & Bouton, 1998). Risk-taking species are commonly superficial explorers and risk-averse species such as *H. chilotes* are commonly thorough explorers (Wolf *et al*., 2007). Possibly, the adaptations to foraging in rock crevices favoured thorough explorers that need more time to find foraging locations. These hypotheses merit future investigation in natural and laboratory settings and might provide more complete insights into the trophic morphology of hypertrophied-lipped cichlids.

In conclusion, we found strong evidence that the morphology of *H. chilotes*, consisting of hypertrophied lips and more pointed heads, is an adaptation to foraging in crevices. We note that the function investigated (i.e. mechanical access to crevices) and the additional proposed functions (e.g. mechanical protection or sensorial) of hypertrophied lips are not mutually exclusive. It appears that a suite of morphological and behavioural traits evolved in concert with lip hypertrophy, including a pointed head morphology and putatively risk-averse behaviour. These traits might either be genetically linked and/or a result of pleiotropic effects, or might be the consequence of directional selection.

## REFERENCES

**Arnegard ME, Snoeks J. 2001.** New three-spotted cichlid species with hypertrophied lips (Teleostei: Cichlidae) from the deep waters of Lake Malawi/Nyasa, Africa. *Copeia* **2001:** 705–717.

**Baerends GP, Wanders J, Vodegel R. 1985.** The relationship between marking patterns and motivational state in the pre-spawning behaviour of the cichlid fish *Chromidotilapia guentheri* (Sauvage). *Netherlands Journal of Zoology* **36:** 88–116.

**Basquill SP, Grant JW. 1998.** An increase in habitat complexity reduces aggression and monopolization of food by zebra fish (*Danio rerio*). *Canadian Journal of Zoology* **76:** 770–772.

**Bouton N, Van Os N, Witte F. 1998.** Feeding performance of Lake Victoria rock cichlids: testing predictions from morphology. *Journal of Fish Biology* **53:** 118–127.

**Burress ED. 2014.** Cichlid fishes as models of ecological diversification: patterns, mechanisms, and consequences. *Hydrobiologia*: 1–21.

**Burress ED, Duarte A, Serra WS, Loueiro M, Gangloff MM, Siefferman L. 2013.** Functional diversification within a predatory species flock. *PLoS ONE* **8:** e80929.

**Colombo M, Diepeveen ET, Muschick M, Santos ME, Indermaur A, Boileau N, Barluenga M, Salzburger W.**

**2013.** The ecological and genetic basis of convergent thick-lipped phenotypes in cichlid fishes. *Molecular Ecology* **22:** 670–684.

**Danley PD. 2011.** Aggression in closely related Malawi cichlids varies inversely with habitat complexity. *Environmental Biology of Fishes* **92:** 275–284.

**Elmer KR, Fan S, Kusche H, Spreitzer ML, Kautt AF, Franchini P, Meyer A. 2014.** Parallel evolution of Nicaraguan crater lake cichlid fishes via non-parallel routes. *Nature Communications* **5:** 5168.

**Elmer KR, Lehtonen TK, Kautt AF, Harrod C, Meyer A. 2010.** Rapid sympatric ecological differentiation of crater lake cichlid fishes within historic times. *BMC Biology* **8:** 60.

**Elmer KR, Meyer A. 2011.** Adaptation in the age of ecological genomics: insights from parallelism and convergence. *Trends in Ecology & Evolution* **26:** 298–306.

**Endler JA. 1986.** *Natural selection in the wild*. Princeton, NJ: Princeton University Press.

**Gould SJ, Lewontin RC. 1979.** The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London Series B, Biological Sciences* **205:** 581–598.

**de Graaf M, Dejen E, Osse JW, Sibbing FA. 2008.** Adaptive radiation of Lake Tana's (Ethiopia) *Labeobarbus* species flock (Pisces, Cyprinidae). *Marine and Freshwater Research* **59:** 391–407.

**Greenwood PH. 1974.** *The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock*. London: British Museum (Natural History).

**Henning F, Lee HJ, Franchini P, Meyer A. 2014.** Genetic mapping of horizontal stripes in Lake Victoria cichlid fishes: benefits and pitfalls of using RAD markers for dense linkage mapping. *Molecular Ecology* **23:** 5224–5240.

**Henning F, Meyer A. 2014.** The evolutionary genomics of cichlid fishes: explosive speciation and adaptation in the postgenomic era. *Annual Review of Genomics and Human Genetics* **15:** 417–441.

**Herder F, Schwarzer J, Jobst Pfaender RK. 2006.** Preliminary checklist of sailfin silversides (Teleostei: Telmatherinidae) in the Malili Lakes of Sulawesi (Indonesia), with a synopsis of systematics and threats. *Verhandlungen der Gesellschaft für Ichthyologie* **5:** 139–163.

**Hulsey CD, Hollingsworth PR, Holzman R. 2010.** Co-evolution of the premaxilla and jaw protrusion in cichlid fishes (Heroine: Cichlidae). *Biological Journal of the Linnean Society* **100:** 619–629.

**Johnson MA, Revell LJ, Losos JB. 2010.** Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution* **64:** 1151–1159.

**Klingenberg CP. 2011.** MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources* **11:** 353–357.

**Kohda M, J-y S, Awata S, Gomagano D, Takeyama T, Hori M, Heg D. 2008.** Niche differentiation depends on body size in a cichlid fish: a model system of a community structured according to size regularities. *Journal of Animal Ecology* **77:** 859–868.

**Konings A. 2008.** *Malawi cichlids – feeding behavior*. El Paso, TX: Cichlid Press: ISBN 978-1-932892-06-2.

**Liem KF. 1973.** Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Biology* **22:** 425–441.

**Liem KF. 1993.** Ecomorphology of the teleostean skull. *The Skull* **3:** 422–452.

**Losos JB. 2010.** Adaptive radiation, ecological opportunity, and evolutionary determinism. American Society of Naturalists E. O. Wilson award address. *American Naturalist* **175:** 623–639.

**Losos JB. 2011.** Convergence, adaptation, and constraint. *Evolution* **65:** 1827–1840.

**Machado-Schiaffino G, Henning F, Meyer A. 2014.** Species-specific differences in adaptive phenotypic plasticity in an ecologically relevant trophic trait: hypertrophic lips in Midas cichlid fishes. *Evolution* **68:** 2086–2091.

**Manousaki T, Hull PM, Kusche H, Machado-Schiaffino G, Franchini P, Harrod C, Elmer KR, Meyer A. 2013.** Parsing parallel evolution: ecological divergence and differential gene expression in the adaptive radiations of thick-lipped Midas cichlid fishes from Nicaragua. *Molecular Ecology* **22:** 650–669.

**Meyer A. 1989.** Cost of morphological specialization: feeding performance of the two morphs in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*. *Oecologia* **80:** 431–436.

**Meyer A. 1990.** Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: alternative adaptations and ontogenetic changes in shape. *Journal of Zoology* **221:** 237–260.

**Montaña CG, Winemiller KO. 2013.** Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. *Biological Journal of the Linnean Society* **109:** 146–164.

**Near TJ, Dornburg A, Eytan RI, Keck BP, Smith WL, Kuhn KL, Moore JA, Price SA, Burbrink FT, Friedman M. 2013.** Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of the National Academy of Sciences of the United States of America* **110:** 12738–12743.

**Nosil P. 2012.** *Ecological speciation*. Oxford: Oxford University Press.

**Oliver MK, Arnegard ME. 2010.** A new genus for *Melanochromis labrosus*, a problematic Lake Malawi cichlid with hypertrophied lips (Teleostei: Cichlidae). *Ichthyological Exploration of Freshwaters* **21:** 209–232.

**Pfennig DW, Pfennig KS. 2012.** *Evolution's wedge: competition and the origins of diversity*. Berkeley, CA: University of California Press.

**R Core Team. 2012.** R: a language and environment for statistical computing.

**Rasband WS. 1997.** *ImageJ*. Bethesda, MD: US National Institutes of Health.

**Ribbink AJ, Marsh BA, Marsh AC, Ribbink AC, Sharp BJ. 1983.** A preliminary survey of the cichlid fishes of rocky

habitats in Lake Malawi. *South African Journal of Zoology* **18:** 149–310.

**Schluter D. 2000.** *The ecology of adaptive radiation*. Oxford: Oxford University Press.

**Schürch R, Heg D. 2010.** Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behavioral Ecology* **21:** 588–598.

**Seehausen O, Bouton N. 1998.** The community of rock-dwelling cichlids in Lake Victoria. *Bonner Zoologische Beitrage* **47:** 301–312.

**Sih A, Bell A, Johnson JC. 2004.** Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19:** 372–378.

**Stiassny MLJ, Meyer A. 1999.** Cichlids of the Rift lakes. *Scientific American* **280:** 64–69.

**Via S. 2009.** Natural selection in action during speciation. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 9939–9946.

**Wainwright PC, Ferry-Graham LA, Waltzek TB, Carroll AM, Hulsey CD, Grubich JR. 2001.** Evaluating the use of ram and suction during prey capture by cichlid fishes. *Journal of Experimental Biology* **204:** 3039–3051.

**Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007.** Life-history trade-offs favour the evolution of animal personalities. *Nature* **447:** 581–584.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Head shape measurement.
**Video Clip S1.** Ad Konings' *Placidochromis milomo*.
**Video Clip S2.** Chilotes experimental.
**Video Clip S3.** Nyererei experimental.
**Table S1.** Foraging results.