Hydrobiologia
DOI 10.1007/s10750-014-1960-z

ADVANCES IN CICHLID RESEARCH

Review Paper

Cichlid fishes as models of ecological diversification: patterns, mechanisms, and consequences

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Received: 24 January 2014 / Accepted: 21 June 2014

Abstract Cichlid fishes are hypothesized to encompass several independent adaptive radiations that display increased diversification rates and impressive ecological heterogeneity. Here, I review major ecological patterns associated with the evolutionary history of cichlids, with particular focus on comparison of Afrotropical and Neotropical lineages. Specifically, I present major patterns of ecological diversification, potential mechanisms that may promote ecological diversification, and possible consequences of ecological diversification. Evolutionary convergence and specialization of ecological (e.g., diet), behavioral (e.g., benthic sifting), and morphological traits (e.g., oral dentition) characterize adaptive patterns that transcend continents. Craniofacial mechanics, the pharyngeal jaw apparatus, phenotypic plasticity, and hybridization may have facilitated diversification of cichlid fishes by generating functional, morphological, and/or genetic diversity. The benthic–pelagic axis has been an important source of divergence during adaptive radiation. Additionally, there are several discrepancies between Afrotropical and Neotropical lineages, such as the relative frequency of herbivorous species, the importance of hybridization in generating diversity, the relative frequency of dentition types, and relationships between dental organization and ecological function. Emphasis on contrasts between Neotropical and Afrotropical lineages improves characterization of patterns at a broader level of organization and indicates that the genetic basis, functional capacity, and ecological opportunity for many traits may be conserved across lineages.

Keywords Adaptive radiation · Cichlidae · Evolution · Niche · Speciation

Introduction

Cichlid fishes are model organisms in evolutionary biology and have been particularly fundamental in developing our understanding of adaptive radiations and speciation among vertebrates. Cichlids are one of the most diverse lineages of freshwater fishes with more than 1,600 species (McMahan et al., 2013). Cichlids are conventionally purported to have arose via Gondwanan vicariance during the early Cretaceous (ca. 135 Ma). However, recent fossil-calibrated molecular analyses place the origin of Cichlidae in the late Cretaceous (ca. 96–67 Ma; McMahan et al., 2013) or Paleocene (ca. 65–57 Ma; Friedman et al., 2013).

Guest editors: S. Koblmüller, R. C. Albertson, M. J. Genner, K. M. Sefc & T. Takahashi / Advances in Cichlid Research: Behavior, Ecology and Evolutionary Biology

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These dates significantly postdate the tectonic fragmentation of Gondwana and have led to novel hypotheses about the role of dispersal in explaining extant cichlid distributions and diversity (Rícan et al., 2013; Friedman et al., 2013). Thus, the evolutionary history of Cichlidae is complex and has produced similarly complex ecological patterns that warrant broadscale synthesis. This review aims to characterize cichlid fishes as models for ecological diversification by summarizing broad patterns revealed in prior literature such as instances of resource partitioning, omnivory, convergence, and ecological novelty. I will specifically address convergence in ecology, behavior, and morphology using the examples of diet, benthic sifting, oral dentition, and hypertrophied lips. Secondly, I will present potential mechanisms that may promote ecological diversification such as hybridization, cranial and jaw mechanics, the pharyngeal apparatus, and phenotypic plasticity. Then, I will discuss some evolutionary consequences of these patterns such as ecological speciation and adaptive radiation. Lastly, I will posit future directions that present fruitful research opportunities regarding the evolution and ecology of cichlid fishes. Historically, comparisons within physically analogous contexts (i.e., among the East African Great Lakes) have been commonplace. Herein, I will focus largely on comparison between Afrotropical and Neotropical cichlid lineages, with respect to the aforementioned topics, to better elucidate ecological patterns at a broader level of organization. Species names used herein are updated in accordance with current taxonomy when appropriate and thus may not match those used in the publications referenced.

Patterns

Resource partitioning

Resource partitioning is an accommodative process such that it facilitates coexistence among competing organisms, a prerequisite for coevolution (Connell, 1980). Competition is a well-known source of disruptive selection (e.g., favoring extreme values of traits) and may promote speciation in cichlids (Seehausen & Schluter, 2004). For example, size-dependent competition drives divergence among rock- and shell-dwelling ecotypes of Afrotropical *Telmatochromis temporalis* (Winkelmann et al., 2014). Resource partitioning provides a means for increased fitness associated with ecological divergence and subsequent divergence of additional traits such as morphology, color pattern, or body size (Kocher, 2004).

Resource partitioning is common among cichlids in Lakes Tanganyika, Malawi, and Victoria (Goldschmidt et al., 1990; Sturmbauer et al., 1992; Genner et al., 1999). For example, there is considerable ecological diversification among cichlids of Lakes Malawi and Tanganyika that are prominently grazing lineages (Kocher, 2004; Muschick et al., 2012). These lineages have diversified considerably within this general ecological role, encompassing numerous distinct niches. For example, cichlid grazers may partition themselves by foraging on habitat-specific communities of benthic algae, diatoms, or macrophytes, or based on substrate type, or substrate slope (Sturmbauer et al., 1992; Genner et al., 1999). Likewise, zooplanktivorous cichlids in Lake Victoria segregate themselves according to water depth and prey size, and vary considerably in their degree of omnivory (Goldschmidt et al., 1990). Carnivorous species may also partition food resources according to prey size, microhabitat, or prey type (Montaña & Winemiller, 2009; Burress et al., 2013a). Isotopic and dietary analyses of Afrotropical (Bootsma et al., 1996; Campbell et al., 2003; Muschick et al., 2012) and Neotropical (Winemiller et al., 2011; Cochran-Biederman & Winemiller, 2013; Burress et al., 2013a; Montaña & Winemiller, 2013) cichlid assemblages also reveal diversification in resource utilization among large groups of species. Food resource and microhabitat partitioning may be coupled (Barluenga et al., 2006; Montaña & Winemiller, 2009) or decoupled (Goldschmidt et al., 1990; Burress et al., 2013b). Habitat–food resource relationships may also be complex, such as when species are only loosely associated with habitat-specific resources or utilize resources from multiple habitats (Bootsma et al., 1996).

Examples of resource partitioning are also highly associated with morphological or physiological adaptations that permit varied degrees of resource specialization. For example, intestine length is often associated with trophic position and food quality (Wagner et al., 2009) because herbivorous species must overcome high fractions of carbon-rich molecules that are difficult to digest relative to nitrogenrich animal material (Rudnick & Resh, 2005). Specific enzyme activity is also associated with different diets. For example, laminarinase activity is significantly higher in detritivorous than algivorous species (Sturmbauer et al., 1992). Resource partitioning is an important evolutionary outcome of competition, such that species must co-occur sustainably to coevolve (Connell, 1980). Thus, resource partitioning has many evolutionary implications including disruptive selection, morphological and ecological diversification, and specialization.

Omnivory

Consuming fractions of animal and plant matter (e.g., omnivory) is ubiquitous among cichlids in Neotropical and Afrotropical ecosystems (Winemiller et al., 1995; López-Fernández et al., 2012) and even characterizes entire lineages (Geophagini; López-Fernández et al., 2012, 2014). Omnivory is usually considered generalized (i.e., non-specialized), such that it is often associated with an opportunistic foraging strategy (Gerking, 1994). For example, species with highly specialized morphology (e.g., dentition) and physiology (e.g., specific enzyme activity) associated with herbivory will opportunistically exploit benthic invertebrates (*Eretmodus*; Sturmbauer et al., 1992; Rüber et al., 1999) or pelagic invertebrates (*Pseudotropheus*; Genner et al., 1999). The fact that many distinct, perhaps specialized, forms can be co-opted for general or opportunistic foraging (e.g., Liem's Paradox; Liem, 1980) may in part explain the ubiquity of omnivory among cichlids. Omnivory is often considered an adaptive response to variable and unpredictable resource availability (Winemiller, 1989; Jepsen & Winemiller, 2002), which is consistent with the complex biogeographic history associated with many cichlid lineages (Piálek et al., 2012; Rícan et al., 2013).

Omnivory is complex because an organism feeds at multiple trophic levels and thus faces diverse physiological demands such as highly variable food quality (i.e., nutrient content and digestibility; Rudnick & Resh, 2005). For example, omnivores must balance functional demands associated with capturing evasive prey (Hulsey & De León, 2005) with maintenance of specific enzymes necessary for digestion of plant material (Sturmbauer et al., 1992). There are also anatomical discrepancies associated with consumption of plant or animal matter such as intestine length (Wagner et al., 2009) that are likely to result in inefficiencies when an organism consumes prey that it is ill-equipped to digest. Omnivory is thought to evolve in response to low nutrient availability (Diehl, 2003), which is consistent with the tropical distribution of cichlids (i.e., warmer conditions increase consumer nutrient limitation; reviewed in González-Bergonzoni et al., 2012). Thus, the ubiquity of omnivory among cichlids may be largely an adaptive response to environmental conditions throughout their evolutionary history and therefore may also represent an ancestral condition.

Convergent and replicate evolution

Convergence infers that natural selection has independently selected similar traits and thus provides strong evidence for their adaptive quality (Losos, 2011; Elmer & Meyer, 2011). Therefore, such traits may be associated with increased fitness and/or positive selection. Here, I present examples of convergence in form, function, and behavior, and briefly address cases of ecological novelty (i.e., lack of converging traits).

Ecological guild

There are numerous examples of convergence of general body form and function among cichlids (Fig. 1). Winemiller et al. (1995) described numerous trophic roles that are shared among fluvial cichlids in Central and South American and African lineages (listed, respectively) including piscivores (e.g., *Parachromis*, *Cichla*, *Serranochromis*), epibenthic generalists (e.g., *Astatheros*, *Aequidens*, *Pharyngochromis*), vegetation-dwelling insectivores (e.g., *Archocentrus*, *Mesonauta*, *Sargochromis*), epibenthic detritivore/algivores (e.g., *Paraneetroplus*, *Satanoperca*, *Coptodon*), and sifter/diggers (e.g., *Astatheros*, *Geophagus*, *Sargochromis*). Additionally, there are examples of convergence between lake- and river-dwelling cichlids. For example, zooplanktivores and epibenthic algae scrapers are ubiquitous among Afrotropical cichlid lineages in the East African Great Lakes such as Tanganyikan algae scraping *Tropheus* (Sturmbauer et al., 1992) and *Eretmodus* (Rüber et al., 1999), Malawian algae scraping *Labeotropheus* (Genner et al., 1999), and Victorian zooplankton feeding

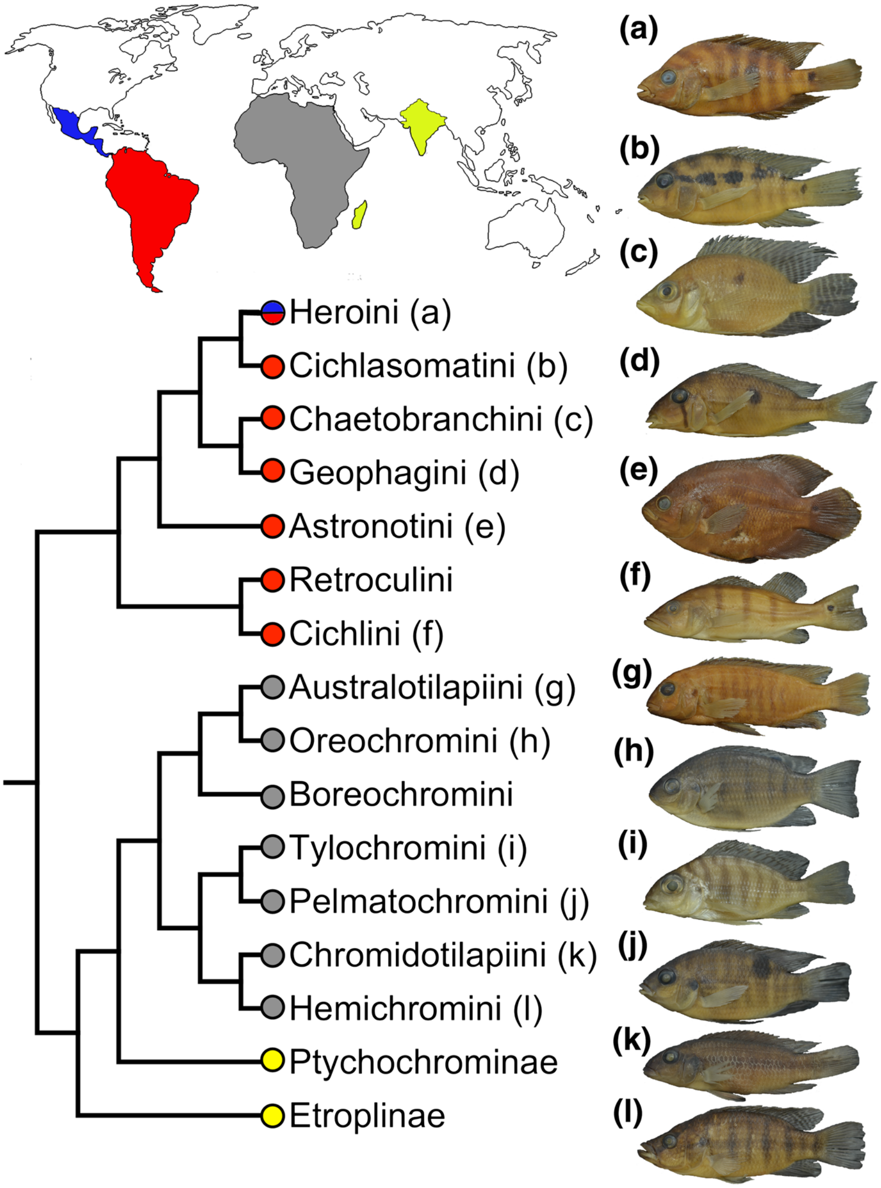


Fig. 1 Representatives associated with the major cichlid lineages depicting a relatively conserved ovoid ecomorphology (phylogenetic relationships adapted from McMahan et al., 2013): (**a**) *Amphilophus citrinellus*, (**b**) *Bujuquina eurhinus*, (**c**) *Chaetobranchus flavescens*, (**d**) *Geophagus taeniopareius*, (**e**), *Astronotus ocellatus*, (**f**) *Cichla ocellaris*, (**g**) *Pseudotropheus tropheops*, (**h**) *Sarotherodon* sp., (**i**) *Tylochromis lateralis*, (**j**) *Pelmatochromis buettikoferi*, (**k**) *Pelvicachromis humilis*, (**l**) *Hemichromis elongatus*. All images are specimens accessioned in the Auburn University Museum of Natural History (AUM) and were photographed by the author

Haplochromis (Goldschmidt et al., 1990). Although rare, these trophic modes are also found among lotic (i.e., riverine) Neotropical lineages: *Chaetobranchus flavescens* (zooplanktivorous) and *Neetroplus nematoplus* (epibenthic algae scrapers) (Winemiller et al., 1995). Non-scraping algivores, such as those described as pickers or browsers, are also abundant among African lakes and rivers, such as *Tropheops* (Stauffer & Posner, 2006; Albertson, 2008) and *Coptodon*, respectively (Winemiller et al., 1995). This foraging mode is also present in Neotropical cichlids such as *Amatitlania* and *Symphysodon* (Winemiller et al., 1995; Crampton, 2008). In contrast to African lake species, in which algivory (scraping and non-scraping) appears highly associated with rocky surfaces (Sturmbauer et al., 1992; Genner et al., 1999), it may be more associated with Neotropical vegetation-dwelling species (López-Fernández et al., 2013).

Piscivory has evolved independently many times among disparate cichlid lineages, and these groups have converged on multiple morphologies. For example, elongate, tubular-shaped piscivores can be found in South America (*Crenicichla*; Burress et al., 2013b) and Lake Tanganyika (*Lepidolamprologus*; Wagner et al., 2009). Neotropical *Cichla* and *Petenia* and Tanganyikan *Boulengerochromis* represent elongate, laterally compressed piscivores that have independently evolved on three continents (Wagner et al., 2009; López-Fernández et al., 2013). Similar transcontinental patterns are also present for ovoid-shaped *Caquetaia*, *Parachromis*, and *Cyphotilapia* (Winemiller et al., 1995; Wagner et al., 2009). Thus, multiple discrete morphologies have evolved repeatedly in association with piscivory.

Benthic sifting

Benthic sifting is a particularly interesting behavior because it targets prey buried beneath loose sediments and presents several key difficulties. First, it involves bringing a heterogeneous mixture of sediment and food into the mouth that must be separated (e.g., via winnowing) such that food is transported into the esophagus while inorganic material is expelled via the gill openings or mouth (Drucker & Jensen, 1991). This behavior is common among teleost fishes (Sazima, 1986) and has independently evolved among several major cichlid lineages. For example, benthic sifting is ubiquitous among the South American Geophagini, such as *Geophagus*, *Satanoperca*, *Gymnogeophagus*, and *Mikrogeophagus*, among others (López-Fernández et al., 2014). Benthic sifting is less common among Central American cichlids. However, it has independently evolved in *Astatheros* and *Thorichthys* (Winemiller et al., 1995; Cochran-Biederman & Winemiller, 2013). Specialized foraging via benthic sifting has also evolved in numerous lineages of African cichlids that inhabit both river and lake habitats. For example, *Sargochromis* are omnivorous benthic sifters that inhabit rivers (Winemiller et al., 1995; Konan et al., 2011). *Xenotilapia* (Lake Tanganyika) and *Lethrinops* and *Taeniolethrinops* (Lake Malawi) are benthic sifters that inhabit lentic (i.e., lake) habitats (Gysels et al., 1997; Duponchelle et al., 2005). These genera are largely omnivorous (Winemiller et al., 1995; López-Fernández et al., 2012), perhaps reflecting an opportunistic component to benthic sifting. Indeed, the diets of benthic sifters are often diverse mixtures, consisting of fractions of detritus, algae, diatoms, fruits, seeds, insects, crustaceans, and mollusks (Winemiller et al., 1995). Additionally, inadvertent ingestion of inorganic materials such as sand is also common among benthic sifters, indicating some functional inefficiency associated with separating food items from mouthfuls of sediment. Morphological traits that appear to be consistently associated with benthic foraging include a large oral cavity to accommodate mouthfuls of sediment, long snout, and eyes positioned high on the head to facilitate plunging the mouth into the substrate (Sazima, 1986; Winemiller et al., 1995; López-Fernández et al., 2012).

Hypertrophied lips

Several examples of highly specialized morphological adaptations appear in distinct lineages (Fig. 2). Hypertrophied lips have independently evolved in all three East African Great Lakes (Arnegard et al., 2001; Salzburger et al., 2005; Oliver & Arnegard, 2010; Colombo et al., 2012), including: *Haplochromis chilotes* (Lake Victoria), *Lobochilotes labiatus* (Lake Tanganyika), and *Abactochromis labrosus*, *Promelas ornatus*, *Placidochromis milomo*, *Otopharynx pachycheilus*, and *Chilotilapia euchilus* (Lake Malawi). This morphology has also evolved in Central American lakes among numerous populations of *Amphilophus citrinellus* and *A. labiatus* (Elmer et al., 2010a, b; Colombo et al., 2012) as well as two South American riverine lineages: *Gymnogeophagu labiatus* (Reis & Malabarba, 1988) and *Crenicichla tendybaguassu* (Burress et al., 2013b). Hypertrophied lips are associated with grazing rocky surfaces. For example, *Crenicichla tenybaguassu* specializes on rock-clinging invertebrates such as insect larvae (Burress et al., 2013b), and Afrotropical *Lobochilotes labiatus* specializes on snails (Colombo et al., 2012). In contrast, *Amphilophus citrinellus* is a generalist that grazes upon epilithic materials such as insects, crustaceans, and algae (Elmer et al., 2010a, b; Colombo et al., 2012). The specific function of hypertrophied lips remains unknown. Perhaps the most accepted hypothesis posits that they increase suction during foraging by sealing cracks and grooves along rocky surfaces (Barlow & Munsey, 1976; Seehausen, 1996; Konings, 1998; Oliver & Arnegard, 2010). However, additional hypotheses include that they may serve a sensory function by acting as an enlarged substrate for taste buds (Arnegard et al., 2001), mechanoreceptors (Fryer, 1959; Fryer & Iles, 1972), or protection from

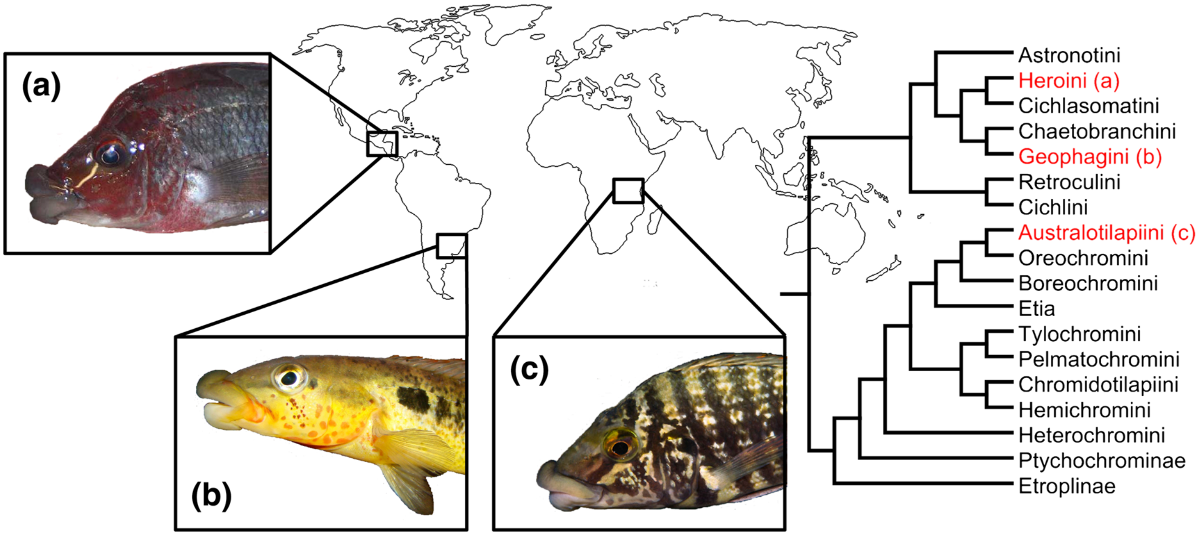


Fig. 2 Illustration showing the independent evolution of hypertrophied lips among **a** Central American *Amphilophus* (Heroini), **b** South American *Crenicichla* (Geophagini), and **c** African *Lobochilotes* (Australotilapiini). Evolutionary relationships are based on McMahan et al. (2013)

mechanical shock (i.e., impact) during foraging on hard rocky surfaces (Greenwood, 1974; Yamaoka, 1997). Furthermore, in addition to evolving independently on three continents, hypertrophied lips appear to have evolved from a large continuum of ancestral states. For example, *Lobochilotes* is part of a largely algivorous lineage (Wagner et al., 2009; Muschick et al., 2012), *Amphilophus* are generally omnivorous (Barluenga et al., 2006; Elmer et al., 2010a; Colombo et al., 2012), and *Crenicichla* are piscivorous (Burress et al., 2013c). Therefore, development of hypertrophied lips may or may not be associated with a shift in diet relative to the ancestral state, but is consistently linked to specialization on rock-oriented foraging. Additionally, plasticity associated with hypertrophied lips may be species-specific, such that plasticity is selected for among incipient thick-lipped species (Machado-Schiaffino et al., 2014). These patterns suggest that the genetic basis, functional capacity, and ecological opportunity for developing hypertrophied lips may be conserved among disparate cichlid lineages (Colombo et al., 2012).

Oral dentition

Cichlid dentition (Fig. 3a) has evolved rapidly and convergently in association with diversification of foraging modes (Rüber et al., 1999; Streelman et al., 2003). Cichlids have multiple rows of teeth on their oral jaws, with similarly shaped teeth within a row, and tooth replacement throughout life (Streelman et al., 2003). Species generally have unicuspid first-generation teeth, regardless of replacement tooth type, and replacement time varies according to feeding ecology (Streelman et al., 2003). Oral dentition is highly conserved among Neotropical cichlids, with most groups possessing unicuspid, conical teeth on the premaxilla and dentary (Casciotta & Arratia, 1993). These teeth may be strongly recurved in some predatory lineages such as *Crenicichla* (Lucena & Kullander, 1992). Bicuspid teeth are also present in some groups such as *Australoheros*, *Hericththys*, and *Cryptoheros* (Casciotta & Arratia, 1993). Perhaps the most extreme Neotropical tooth morphology is that of *Neetroplus nematopus*, which possesses flattened blade-like teeth (Casciotta & Arratia, 1993), associated with scraping algae from rocky surfaces (Winemiller et al., 1995).

In contrast, tooth morphology has been a prominent feature among Afrotropical cichlid radiations, varying among species based on feeding behaviors. Species that utilize suction mechanisms to feed on evasive prey (e.g., predators) possess an elongate jaw and an outer row of unicuspid or bicuspid teeth (Albertson & Kocher, 2006; Streelman & Albertson, 2006). In contrast, species that utilize biting mechanisms to feed

Fig. 3 Tooth-shape **a** diversity among cichlid fishes (top to bottom): tricuspid, bicuspid, conical unicuspid, cylindrical unicuspid, and spatula-shaped unicuspid. Representatives of the ecomorphological diversity **b** among cichlid fishes (top to bottom): *Pterophyllum*, *Symphsodon*, *Crenicichla*, *Paretroplus*, *Cyphotilapia*, *Altolamprologus*, *Xenotilapia*, *Tropheus*

on attached prey (e.g., algae or snails) are often characterized by having a short, robust lower jaw, and an outer row of closely spaced tricuspid teeth (Albertson & Kocher, 2006). Thus, teeth are typically widely spaced and sharply pointed among predators, such as insectivores and zooplanktivores, and comparatively tightly packed among algae scrapers (Streelman et al., 2003). For example, insectivorous *Labidochromis* and zooplanktivorous *Cynotilapia* possess unicuspid teeth, omnivorous *Mylochromis* and *Metriaclima* possess bicuspid teeth, and the algae scraping *Labeotropheus* possess spatulate tricuspid teeth (Streelman et al., 2003; Streelman & Albertson, 2006). The morphology of unicuspid teeth may vary considerably. For example, spatula- (e.g., *Eretmodus*), cylindrical- (e.g., *Spathodus*), and conical-shaped (e.g., *Tanganicodus*) teeth have evolved repeatedly among species in Lake Tanganyika (Rüber et al., 1999). The flattened, spatula shape is associated with herbivory, similar to spatula-shaped tricuspids, and has evolved independently in Lake Tanganyika (e.g., *Eretmodus*), Lake Malawi (e.g., *Labeotropheus*), and Neotropics (e.g., *Neetroplus*) in association with algae scraping (Casciotta & Arratia, 1993; Rüber et al., 1999; Albertson & Kocher, 2006).

There is considerable incongruence between Neotropical and Afrotropical dentition. For example, bicuspid teeth are considered generalized structures among Afrotropical lineages such that they have non-specialized or intermediate function (Greenwood, 1974). However, this tooth morphology is not only rare, but appears specialized in Neotropical lineages, such that the cusps are often hooked, while those of African species are not (Casciotta & Arratia, 1993). Secondly, tricuspid teeth that are ubiquitous among Afrotropical species are not represented in Neotropical species (Casciotta & Arratia, 1993). Lastly, the number of teeth on the premaxilla and dentary vary considerably among trophic modes, but specific patterns do not transcend continental comparisons. For example, the algae scraping species of the East African Great Lakes possess many, tightly spaced teeth in the outer row relative to other guilds (Streelman et al., 2003), but Neotropical piscivores such as *Acaronia*, *Crenicichla*, *Cichla*, and *Petenia* display significantly more teeth in the outer row, and in some instances (i.e., *Crenicichla* and *Cichla*) considerably more rows of teeth compared to other Neotropical guilds (Casciotta & Arratia, 1993). Thus, Afrotropical and Neotropical cichlids differ in the diversity of dentition and in how dentition relates to ecological characteristics. Interestingly, in both cases, the lineages that evolved elevated numbers of teeth encompass groups that display dramatic diversification in terms of species (e.g., many Australotilapiini genera and *Crenicichla*). Perhaps in combination with other factors, such as association with rocky habitats that provide heterogeneous axes to partition resources (e.g., depth and angle) in the case of many Australotilapiini (Sturmbauer et al., 1992; Seehausen & Bouton, 1997; Genner et al., 1999) or fast flowing rocky habitats in the case of *Crenicichla* (Lucena & Kullander, 1992; Burress et al., 2013b), dentition may be an important trait involved in the diversification process.

These patterns indicate many traits that may be adaptive across Neotropical and Afrotropical cichlids, evidenced by their independent selection. For example, both lineages display similar ecological roles (e.g., omnivory), behaviors (e.g., benthic sifting), and morphology (e.g., dentition). This suggests that the genetic basis, mechanistic flexibility, and ecological opportunity for these traits are conserved across many habitats, ecosystems, and lineages. However, there are several instances of discrepancy. For example, the relative abundance of algivores and zooplanktivores, the relative occurrence of dentition types, and the primary foraging substrate associated with algivory differs significantly between Neotropical and Afrotropical cichlids. Potential discrepancies that are difficult to evaluate but seem plausible include higher frequency of omnivory and benthic sifting among Neotropical cichlids.

Ecological novelty

Despite the aforementioned frequency of convergence in both form and function among cichlids, some lineages display unique characteristics. For example, perhaps the most extreme morphological examples are found among the laterally compressed and disk-shaped *Symphysodon*, the laterally compressed and dorso-ventrally exaggerated *Pterophyllum*, or the elongate, tubular *Crenicichla* (Fig. 3b; López-Fernández et al., 2013). Unique functional examples include scale eaters (Takahashi et al., 2007) that exhibit a continuum between left and right handedness, such that individual's jaws are curved to the left or right to facilitate grazing the flanks of prey (Hori, 1993; Kusche et al., 2012). Additionally, frugivory appears to be relatively rare among cichlids, despite the availability of fruit in the habitat, as revealed by co-occurring lineages such as Neotropical anostomids that frequently exploit fruits (de Mérona & Rankin de Mérona, 2004). Epibenthic frugivory is reported in *Tomocichla tuba* and *Astronotus ocellatus* (Winemiller et al., 1995; de Mérona & Rankin de Mérona, 2004), although this has not been corroborated for the latter (López-Fernández et al., 2012). Despite the prevalence of molluskivory in multiple lineages of cichlids (Winemiller et al., 1995), most of those examples pertain to the exploitation of snails; however, *Crenicichla minuano* consumes large fractions of bivalves even when snails are abundant (Burress et al., 2013b). Trophic specialization may arise for several reasons. For example, morphological specialization of the pharyngeal jaws (Burress et al., 2013b) or teeth (Takahashi et al., 2007) may preclude exploitation of a wide range of resources (i.e., generalist feeding). Additionally, ecological opportunity (Mahler et al., 2010; Yoder et al., 2010) and resource-based competition (Mittelbach, 1984, 1988) may also promote specialization.

Here, I have discussed ecological diversification only insofar as observable ecological patterns among cichlid fishes. Many traits exhibit an adaptive nature, evidenced by their independent recruitment by distinct lineages, and these traits include forms, functions, and behaviors. In the following section, I address how these traits and patterns may arise, particularly with regard to generation of morphological, ecological, or genetic diversity, and ultimately, with regard to their association with the processes of speciation and adaptive radiation.

Mechanisms

Hypotheses about the steps involved in adaptive radiation among cichlids suggests that occupation of different macrohabitats precedes functional diversification of feeding structures, after which sexual selection may generate additional phenotypic diversity such as nuptial polymorphisms (Kocher, 2004). In this section, I address factors primarily associated with the first and second step of this hypothesis. Several key innovations among specific lineages of fishes (of which cichlids are part) were fundamental in their proclivity toward adaptive radiation. Some mechanisms that are hypothesized to promote speciation or inflate the rate of speciation, but either do not necessarily have explicit implications in ecological diversification or are already reviewed elsewhere, are not discussed. For example, diversification of nuptial phenotypes (via sexual selection), such as color pattern, is not inherently an ecological phenomenon (Nosil, 2012). However, such phenotypic diversification may be coupled with ecological traits such as specific behaviors (i.e., courting or mate guarding), or have other social implication such as diffusing competition (Seehausen & Schluter, 2004). Here, I present four potential mechanisms that may facilitate the adaptive nature of cichlids: hybridization, craniofacial mechanics, the lower pharyngeal jaw apparatus, and phenotypic plasticity. I then briefly address the genetic basis for these mechanisms.

Hybridization

Increased genetic and phenotypic diversity due to introgressive hybridization may promote rapid speciation (Salzburger et al., 2002; Seehausen, 2004) and ecological specialization (Koblmüller et al., 2007). Transgressive segregation (e.g., when hybrids exhibit extreme or novel phenotypes) is a product of recombination and assortment between alleles associated with various morphological traits such as the length of the lower jaw and maxilla (Parnell et al., 2008). Transgression has been noted in the lateral morphology (Parsons et al., 2011a) and functional mechanisms (simple levers and 4-bar linkages; Parnell et al., 2012) of cichlid skulls. Hybrids also exhibit reduced integration (e.g., covariation among traits), particularly among transgressive individuals (Parsons et al., 2011a). This relaxed trait covariance may facilitate morphological diversification in adaptive radiations (Selz et al., 2014b). Oral jaws appear resistant to transgression, perhaps due evolving under strong directional selection (Albertson & Kocher, 2005). Thus, the genetic architecture of cichlid jaw morphology may be constrained by foraging mechanics. Alternatively, the genetic basis of the cranium may accommodate transgression (Albertson & Kocher, 2005). Additionally, functional transgression may occur at an appreciable frequency, particularly when many forms are linked to a specific function (Parnell et al., 2008). Assortative mating among hybrids may be facilitated by behavioral isolation from parental species, such as new combinations of traits or preferences leading to reproductive isolation (Selz et al., 2014a). Hybridization events can leave long-lasting imprints on genomic architecture. For example, distinct evolutionary histories for different genomic regions can be attributed to past introgression and may lead to novel trait combinations and the origins of species (Keller et al., 2012). Additionally, hybridization provides genetic and phenotypic variation that may assist hybrid organisms in maneuvering across fitness landscapes (Mallet, 2007).

Hybridization may play an important role in adaptive radiation (reviewed in Seehausen, 2004). However, among cichlids, this phenomenon may be limited to the East African Great Lakes (Salzburger et al., 2002; Koblmüller et al., 2007), where adaptive radiations may have arisen from hybrid swarms (Seehausen, 2004). In contrast, hybridization is less documented among Neotropical cichlids. Introgression may have played an important role in the evolutionary history of *Cichla* (Willis et al., 2012) and *Amphilophus* (Geiger et al., 2013). *Crenicichla* are known to hybridize (Lucena & Kullander, 1992); however, this is probably due to extant gene flow among incipient species (Kullander et al., 2010; Piálek et al., 2012). Hybridization among other groups such as *Vieja* (McMahan et al., 2010) and *Herichthys* (León-Romero et al., 2012) has been proposed to explain lineages not sorting in phylogenetic analyses; however, these cases could be explained by lack of phylogenetic signal. The primarily lotic conditions associated with the Neotropics may not facilitate behavioral isolation or ecological opportunity necessary for hybrid sustainability due to frequent ecological disturbance. For example, the heterogeneous environmental conditions such as unpredictable hydrological regimes and resource availability are often associated with Neotropical ecosystems (Winemiller, 1989; Jepsen & Winemiller, 2002). Thus, there may be a large discrepancy in the relative importance of hybridization between Afrotropical and Neotropical adaptive radiations.

Cranial and jaw mechanics

The cichlid skull consists of complex (4-bar linkages) and simple (lower jaw levers) functional systems that have a known genetic basis (Parnell et al., 2012). Most of the observed anatomical variation in the cichlid head is restricted to the preorbital region, implicating the importance of resource exploitation as an agent of selection. The preorbital region evolves relatively independently from other cranial areas, and exhibits similar shape changes among Lakes Tanganyika, Malawi, and Victoria (Parsons et al., 2011b). Specifically, mechanical shifts in jaw function are associated with repeated exploitation of the benthic–pelagic resource axis (Cooper et al., 2010). Additionally, cranial and jaw diversity correlates with lineage age among the East African lakes, such that each lake serves as a snapshot of morphological disparity associated with a progression of adaptive radiation (Cooper et al., 2010).

Mechanistic feeding characteristics are evolutionarily important among predatory lineages because different prey types require different ram distances and velocities during capture (Wainwright et al., 2001). Thus, for species to exploit diverse resources, they must display necessary and sufficient functional diversity. Ram distance is often coupled with both ram velocity and suction distance such that they are positively and negatively correlated in cichlids, respectively (Wainwright et al., 2001; Waltrek & Wainwright, 2003). Many cichlids display high ram velocity when capturing prey, which is hypothesized to increase the capacity and efficiency of capturing motile (i.e., evasive) prey. Jaw protrusibility is also important to many cichlids, particularly those that must utilize ram velocity to catch highly motile prey such as fishes, because the two traits are often correlated (Wainwright et al., 2001). Comparative studies have shown that cichlids utilize different ram velocity, ram distance, and gape when foraging (Wainwright et al., 2001; Higham et al., 2006) and that these traits are generally associated with the degree to which they exploit evasive prey (Hulsey & De León, 2005). Thus, the evolution of the functional capacity for high ram velocity and jaw protrusion may have been necessary to facilitate the trophic diversification apparent in cichlids.

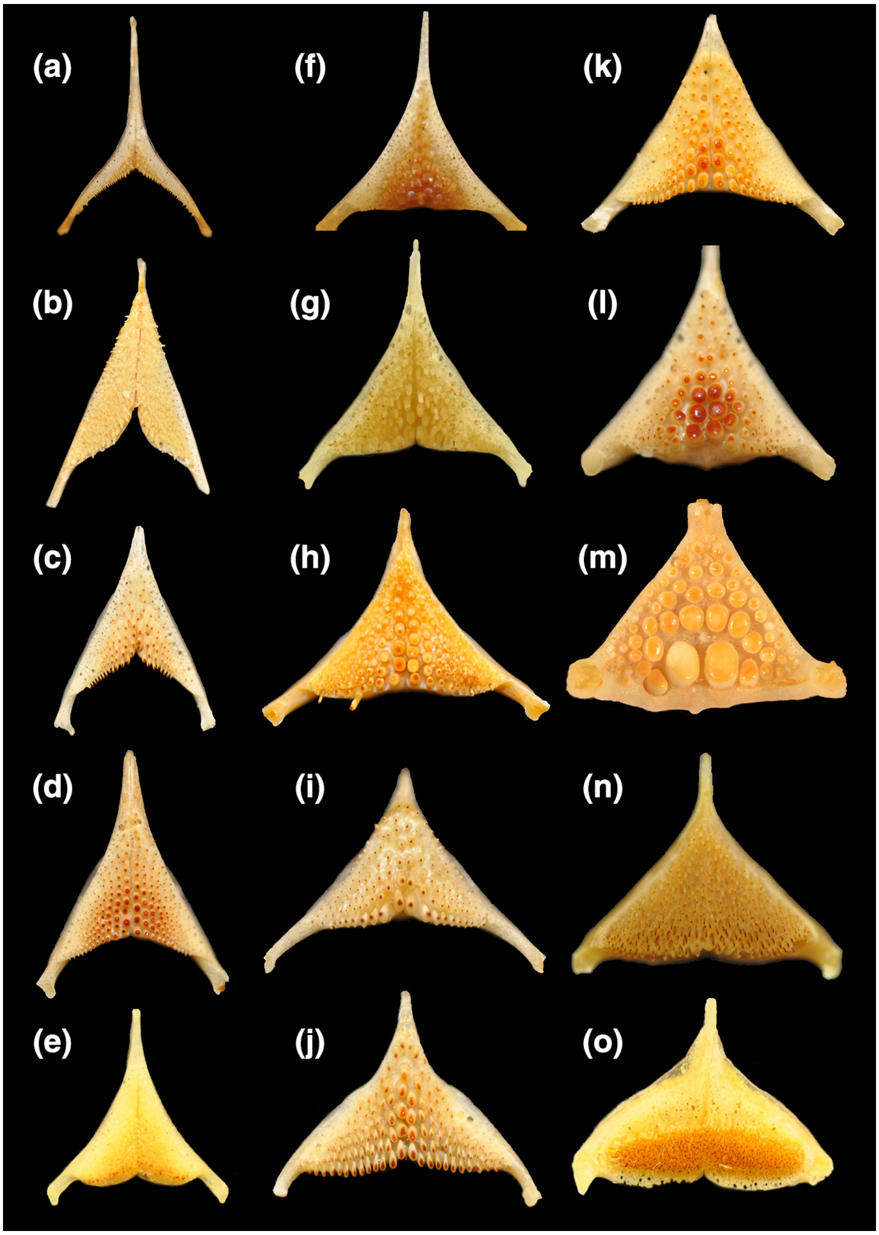
Pharyngeal jaws

The pharyngeal apparatus is hypothesized to increase functional capacity, efficiency, and versatility (Wainwright et al., 2012). Indeed, pharyngognathy occurs within some of the most species-rich and ecologically diverse fish lineages, specifically wrasses (Labridae) and cichlid fishes (Wainwright et al., 2012). Among cichlids, the pharyngeal apparatus consists of two independent upper plates and a single, fused lower plate, all containing various degrees of unicuspid, bicuspid, or molariform dentition (reviewed in Casciotta & Arratia, 1993; Hulsey, 2006). Oral and pharyngeal jaws are developmentally and functionally decoupled (Liem, 1973; Hulsey, 2006), such that oral and pharyngeal jaws are derived from the first and seventh pharyngeal arch, respectively (Fraser et al., 2009), and involved in food acquisition and processing, respectively (Liem, 1973). Pharyngeal jaws likely facilitated evolutionary diversification among cichlids not only by increasing functional capacity, efficiency, and versatility, but also by releasing the oral jaws from many functional demands associated with processing food (Liem, 1973).

The shape and structure of the lower pharyngeal jaw is often highly associated with the dietary characteristics of the species and thus displays considerable variation in shape and dentition (Fig. 4). For example, hypertrophied pharyngeal jaws enable more crushing force (Meyer, 1989) and thereby reduce handling time associated with manipulating hard-shelled prey such as snails (Mittelbach, 1984). Hypertrophied pharyngeal jaws are often associated with difficult-to-crush organisms (e.g., mollusks). During prey processing, structural stress is concentrated along the posterior midline of the pharyngeal jaw (Hulsey et al., 2008), where most dentition specialized for crushing is located. The degree that the pharyngeal bone is reinforced and the size and type of dentition on the bone vary greatly depending on the degree to which a species exploits hard-shelled prey and thus the degree of stress incurred during mastication (Hulsey et al., 2008). For example, species that opportunistically consume snails such as *Paraneetroplus* and *Amphilophus* (Colombo et al., 2012; Cochran-Biederman & Winemiller, 2013) may have only a few enlarged conical teeth (Fig. 4h, k). Snail specialists such as *Thorichthys* (Cochran-Biederman & Winemiller, 2013) possess molariform teeth on a sturdy pharyngeal bone (Fig. 4l). Bivalve specialists must generate considerable crushing force, which requires large molariform teeth and a highly reinforced pharyngeal bone such as those of *Crenicichla minuano* (Fig. 4m; Burress et al., 2013b).

Prey types that do not require crushing force, such as fishes, are often associated with reduced pharyngeal

Fig. 4 Structural diversity of lower pharyngeal jaw among cichlid fishes: *Chaetobranchus flavescens* (**a**, Chaetobranchini), *Cichla temensis* (**b**, Cichlini), *Satanoperca daemon* (**c**, Geophagini), *Geophagus megasema* (**d**, Geophagini), *Pseudotropheus tropheops* (**e**, Australotilapiini), *Tylochromis lateralis* (**f**, Tylochromini), *Haplochromis* sp. (**g**, Australotilapiini), *Paraneetroplus maculaicauda* (**h**, Heroini), *Aequidens diadema* (**i**, Cichlasomatini), *Tomocichla sieboldi* (**j**, Heroini), *Amphilophus citrinellus* (**k**, Heroini), *Thorichthys aureum* (**l**, Heroini), *Crenicichla minuano* (**m**, Geophagini), *Coptodon rendalli* (**n**, Oreochromini), and *Sarotherodon galilaeus* (**o**, Oreochromini). All jaws are from specimens accessioned in the Auburn University Museum of Natural History and were dissected and photographed by the author



jaws that possess conical recurved teeth suitable for grasping and manipulating prey that is consumed whole (Fig. 4b; Hellig et al., 2010; Burress et al., 2013b). These relatively atrophied pharyngeal bones probably precludes these species from exploitation of difficult to manipulate prey items such as mollusks that possess shells that require crushing force (Mittelbach, 1984). Particularly extreme morphological examples can be found among zooplanktivores. For example, Neotropical *Chaetobranchus* (Winemiller, 1989) has a highly reduced lower pharyngeal jaw with elongate lateral processes and keel, and conical teeth (Fig. 4a). Afrotropical *Coptodon* (Bootsma et al., 1996) has a hypertrophied lower pharyngeal jaw with knob-like processes and bristle-like teeth (Fig. 4n). Afrotropical *Halplochromis* (Goldschmidt et al., 1990) displays an intermediate lower pharyngeal jaw and variably sized conical teeth (Fig. 4g). These examples illustrate the diversity of morphologies that can evolve in association with pelagic resources.

Some herbivorous species have relatively well-developed pharyngeal jaws that often possess large conical teeth (Neotropical *Tomocichla*; Fig. 4j). These large teeth may generate the crushing and/or tearing force necessary to efficiently manipulate husks or seeds associated with many fruits. In contrast, the Afrotropical *Pseudotropheus* that specializes in algae scraping (Genner et al., 1999) possesses small conical teeth (Fig. 4e) that likely assist in rupturing algae cells during mastication and thus improves digestibility of this otherwise difficult-to-digest resource (Rudnick & Resh, 2005).

Lastly, pharyngeal jaws are functionally linked to the aforementioned benthic sifting foraging strategy that is ubiquitous among cichlids. For example, sifting species utilize the pharyngeal jaw much like a rake to help separate food from mouthfuls of sediment (Drucker & Jensen, 1991) and thus may be associated with various pharyngeal morphologies depending on the degree of sifting and target prey. For example, omnivorous *Satanoperca* and *Geophagus* utilize sifting as their primary foraging mode (López-Fernández et al., 2014) and have similar pharyngeal morphologies (Fig. 4c, d) compared to opportunistic sifters that are generalist feeders (*Tylochromis*; Fig. 4f), and opportunistic sifters that specialize in another discrete foraging mode (e.g., molluskivorous *Thorichthys*; Fig. 4l).

Phenotypic plasticity

Phenotypic plasticity (i.e., the ability of an organism's phenotype to vary in response to its environment) can play an important role in generating ecological diversity (reviewed in Pfennig et al., 2010) and has been hypothesized to have played an important role in the explosive radiation of cichlid fishes by facilitating adaptation to heterogeneous ecological conditions (Sage & Selander, 1975; Stauffer & Gray, 2004). Laboratory experiments that utilize different food resources to elicit distinct foraging strategies (e.g., suction versus biting) produce different skull and jaw morphologies in both old and new world cichlids (Meyer, 1987; Wimberger, 1991; Stauffer & Gray, 2004). However, phenotypic plasticity may be constrained by ecological properties associated with particular cranial forms (Parsons et al., 2014). Naturally occurring plasticity is also apparent in cichlids, particularly when associated with trophic polymorphisms. For example, *Herichthys minckleyi* has pharyngeal jaws that range from reduced plates possessing papilliform teeth to hypertrophied plates with molariform teeth, representing individuals that specialize on eating soft-bodied invertebrates and snails, respectively (Hulsey et al., 2006). Individual variation in pharyngeal jaw shape (i.e., varied proportions of molariform teeth) is also present in *Amphilophus citrinellus* (Elmer et al., 2010a, b), *Crenicichla minuano* (Lucena & Kullander, 1992; Burress et al., 2013a), and *Astatoreochromis* (Huysseune, 1995; Smits et al., 1996). Pharyngeal polymorphism is also associated with ecological divergence of sister species in Neotropical *Amphilophus* and *Crenicichla* (Barluenga et al., 2006; Burress et al., 2013b) as well as Afrotropical *Tramitichromis* (Kidd et al., 2006), implicating the importance of ecologically based selection in speciation events. Therefore, some intraspecific pharyngeal variation may be associated with genetic polymorphism instead of plasticity (Kornfield & Taylor, 1983). Additionally, ontogenetic diet shifts may also elicit changes in pharyngeal jaw shape. For example, size-structured shifts to piscivory by *Lepidolamprologus elongatus* may be associated with narrowing of the lower pharyngeal jaw (Hellig et al., 2010). Similarly, among species of *Crenicichla*, narrowing and elongation of the pharyngeal jaw is associated with increased exploitation of fishes (Burress et al., 2013b).

Plasticity is also present in soft tissues. For example, intestine length varies based on the C:N ratio of algae among grazing cichlids such that poorer quality (e.g., high C:N) food elicits longer intestines to aid digestion (Wagner et al., 2009). Such plasticity allows individuals to adapt to site-specific food quality. Additionally, the intestine may shorten during periods of reduced or irregular feeding associated with mouthbrooding females (Reinthal, 1989) or when individuals are kept in captivity (Sturmbauer et al., 1992). Another highly variable trait, hypertrophied lips, also displays plasticity such that in unnatural conditions (i.e., captivity) fleshy lips are reduced or lost completely (Barlow & Munsey, 1976; Barlow, 1976). This suggests that some environmental property may be responsible for their development; however, this has not been corroborated in experiments that attempted to elicit the development of hypertrophied lips in cichlids (Muschick et al., 2012).

Phenotypic plasticity has important evolutionary implications because it may allow an initial form of divergence, such as specialization upon different food resources or habitat types (Kocher, 2004), and provides additional variation upon which disruptive selection may act (Martin, 2012). The tendency to mate with like individuals, even at an ecological level, may then facilitate assortative mating and the subsequent development of divergent color patterns (e.g., a progression of the speciation process; Kocher, 2004). Notably, different cichlid lineages exhibit different levels of phenotypic plasticity, suggesting that variation in this trait has a genetic basis, and can evolve (Parsons et al., 2014).

From genes to ecology

There has been much advancement in our understanding of the genetic mechanisms behind ecological innovation (reviewed in Irschick et al., 2013). Specifically, cichlid jaws and teeth have evolved in response to strong, divergent selection linked to several chromosomal regions (Albertson et al., 2003), implicating the importance of pleiotropy in generating trophic diversity. Some studies have found specific genes that regulate the development of cichlid jaw morphology. For example, early expression of *bmp*4 (bone morphogenetic protein 4) may be important in generating evolutionary changes in craniofacial morphology (Albertson & Kocher, 2006). Variability in *bmp*4 expression accounts for more than 30% of phenotypic variation in the opening and closing mechanism of the cichlid lower jaw (Albertson et al., 2005). Differential expression of the hedgehog pathway receptor *patched1* gene caused by different alleles is associated with adaptive variation in the cichlid skull, which is predicted to effect the kinematics of lower jaw rotation and the efficiency of suction feeding (Roberts et al., 2011; Hu & Albertson, 2014). For example, the length of the retroarticular (RA) process is associated with the continuum between suction (short RA) and biting (long RA) feeding modes (Roberts et al., 2011). Allelic variation in Calmodulin (*cam1*) is linked to variation in jaw width, which also has functional implications in biting- versus suction-based foraging modes (Parsons & Albertson, 2009). Signaling via the Wnt pathway is also linked to the appearance of ecologically novel cranial morphologies (Parsons et al., 2014). Similar to craniofacial morphology, there has also been recent insight into the genetic basis of dentition. Tooth regeneration and shape morphogenesis are integrated by a common set of genetic pathways (Fraser et al., 2013). Tooth development is linked to a subset of HOX genes (e.g., *hoxA2b*, *hoxB5b*, *hoxB6b*, and *hoxD4a*) and an ancient regulatory network (e.g., *barx1*, *bmp2*, *bmp4*, *dix2*, *pitx2*, *runx2*, and *shh*; Fraser et al., 2009). Additionally, variation in dentition (i.e., bicuspid vs. tricuspid) is not linked to mutations in *bmp*4 (Streelman & Albertson, 2006), but cichlid teeth are believed to have a simple origin such that shape differences in the first tooth row may be controlled by changes in a small number of genes (Streelman et al., 2003).

Several additional phenomena have recently been linked to genes. Integration (e.g., covariation among traits) has a genetic basis that is distinct from shape, suggesting a complex interaction between integration and shape (Hu et al., 2013). Expression in a large set of genes is linked to phenotypic polymorphism elicited by ecological selection (Gunter et al., 2013). One such trait, hypertrophied lips, is associated with the under-expression of a select suite of genes (Manousaki et al., 2013). Furthermore, several genes linked to the connective tissue that constitute hypertrophied lips are conserved across Neotropical and Afrotropical lineages (Colombo et al., 2012), suggesting that these genes may have been independently recruited to develop this specialized phenotype. Divergent selection on visual systems (e.g., fixed opsin proteins) has also been implicated in generating divergent male breeding coloration via adapting populations to environmental light gradients (Terai et al., 2006).

Here, I have presented several mechanisms hypothesized to facilitate ecological diversification and established their genetic basis. In the next section, I discuss evolutionary implications associated with these mechanisms and the ecological traits they elicit.

Consequences

Ecological speciation

Cichlids provide several prominent examples of ecologically based speciation events or ecological speciation (reviewed in Nosil, 2012). Ecological divergence among sister species that occur in sympatric conditions is a frequent occurrence among Neotropical and Afrotropical cichlids. For example, species pairs of Nicaraguan *Amphilophus* display benthic and pelagic ecotypes that diverge in whole body shape, pharyngeal jaw morphology, and diet (Barluenga et al., 2006; Elmer et al., 2010b). Among these crater lakes, *Amphilophus* species display varied degrees of lineage sorting and ecological divergence depending on lake age (Elmer et al., 2010b; Franchini et al., 2013), such that these lakes serve as a snapshot of the speciation process. The ecological basis for such divergence may be due to individual specialization along the benthic–pelagic resource axis (Kusche et al., 2014). Variation in body elongation and body depth vary predictably with lake depth and littoral area, respectively (Recknagel et al., 2014). Thus, local adaptation and environmental constraints are important during the speciation process. This pairing of benthic–pelagic sister species is also apparent in Afrotropical *Coptodon* (Schliewen et al., 2001) and has occurred multiple times among cichlids in Lake Malawi (Hulsey et al., 2013). In Lake Tanganyika, small- and large-bodied *Telmatochromis temporalis* ecotypes have diverged based on spawning substrate preference, utilizing shell and rocky habitat, respectively (Winkelmann et al., 2014). These studies emphasize the importance of habitat use as a source of disruptive selection. However, habitat utilization is not always the primary agent of selection. In four Nicaraguan lakes, *A. citrinellus* and *A. labiatus* have independently diverged into thick- and thin-lipped ecotypes that display divergence in skull shape, pharyngeal jaw morphology, diet, and isotopic composition (Elmer et al., 2010a; Manousaki et al., 2013). In Lake Tanganyika, *Tramitichromis* sister species pairs often differ in pharyngeal jaw shape and shape of the bowers (e.g., sand mounds) built by males during courtship and nesting (Kidd et al., 2006). These examples suggest that diet-based resource divergence plays an important role in replicate speciation events. Secondly, the ecological similarity of these studies, such as the benthic–pelagic and thick–thin lip axes, suggests that the genetic basis, functional plasticity, and ecological opportunity for these speciation events may be conserved across Neotropical and Afrotropical conditions.

Adaptive radiation

Among fishes, cichlids display comparatively fast diversification rates (Near et al., 2013; Rabosky et al., 2013). Among cichlids, several lineages have been hypothesized to be the result of rapid adaptive radiation (Kocher, 2004; Sturmbauer et al., 2011). For example, Afrotropical pseudocrenilabrine lineages, that encompass the East African Great Lakes, display a rate shift increase in diversification relative to other lineages based on fossil-calibrated analyses (Day et al., 2008; McMahan et al., 2013). These lineages often display significant diversification of whole body morphology (Clabaut et al., 2007; Young et al., 2009), pharyngeal jaw shape, isotopic composition, and diet (Muschick et al., 2012). In lentic environments, these bursts of diversification have often been associated with benthic to pelagic habitat shifts in Lake Malawi (Hulsey et al., 2013) and Lake Tanganyika (Duftner et al., 2005), and correlate with significant cranial modification and adaptation (Cooper et al., 2010). Such successful diversification events are often considered invasions into an open niche that presents ecological opportunity (Mahler et al., 2010; Wagner et al., 2012). Among Neotropical lineages, both the Heroini and Geophagini have been proposed as having undergone adaptive radiation, although with less corroboration (López-Fernández et al., 2010, 2013; McMahan et al., 2013). For example, Geophagini displays characteristics of rapid lineage accumulation (López-Fernández et al., 2010, 2013), but it has also been argued that the comparatively high diversity of this lineage may be explained simply by lineage age (McMahan et al., 2013). Similar to Afrotropical lineages, diversification along a benthic–pelagic gradient has occurred independently among numerous Neotropical lake cichlids (Barluenga et al., 2006; Elmer et al., 2010b; Franchini et al., 2013). Rates of evolution may differ between lineages. For example, Lake Malawi species exhibit a faster rate of evolution in the lower jaw than Central American cichlids and the most rapidly evolving components (i.e., lever systems) of the jaw also differed between the two lineages (Hulsey et al., 2010).

Particular sets of traits that incur evolutionary advantages such as increased fitness, survivorship, or reproductive success may represent adaptive peaks. For example, benthivory among Neotropical cichlids has been suggested as a potential adaptive peak (López-Fernández et al., 2010, 2013; Arbour & López-Fernández, 2013), although recent experimental evidence indicates that benthic sifting may not provide increased efficiency during excavation of food items buried in sediment (López-Fernández et al., 2014), suggesting that the adaptive nature of this behavior may be complex. Morphological innovations often correlate with such bursts in diversification. For example, the epibranchial lobe on the first gill arch among geophagines is hypothesized to have implications in foraging via benthic sifting and mouthbrooding reproductive behavior (López-Fernández et al., 2013) and thus may have contributed to the diversification of that lineage (Arbour & López-Fernández, 2013). Piscivory is another potential adaptive peak among fishes (Collar et al., 2009). Among Neotropical cichlids, piscivory has largely coevolved with elongate body forms (i.e., *Crenicichla*; López-Fernández et al., 2013; Burress et al., 2013b, c). Indeed, *Crenicichla* are hypothesized to have colonized the predatory, ram feeding adaptive peak early and thus may have precluded other lineages from occupying a similar ecological role (Arbour & López-Fernández, 2013).

Several key innovations likely facilitated the diversification of many cichlid lineages, encompassing phenotypic (e.g., color polymorphism), behavioral (e.g., mouthbrooding), and ecological (e.g., trophic guild) traits (Salzburger et al., 2005). Although morphological, physiological, and behavioral traits often correlate with phylogeny (Wagner et al., 2009; Burress et al., 2013b; Arbour & López-Fernández, 2013), these traits may or may not be predictably coupled. For example, among piscivores (i.e., Neotropical *Crenicichla*) there may be large discrepancies between consumption and assimilation of nutrients (Burress et al., 2013b). This pattern suggests that the evolution of traits (i.e., morphology) that permit the exploitation of certain resources may be decoupled from the physiological ability to efficiently assimilate them. Additionally, coupling between physiology (e.g., intestine length) and behavior (e.g., trophic position) may be linked to the importance of environmental properties such as nutrient availability (Wagner et al., 2009). Thus, the interplay among morphology, physiology, and behavior in respect to adaptive radiation is highly complex such that patterns may be linked to environmental heterogeneity or may be lineage specific. For example, morphology, diet, and physiology (e.g., gut microbial communities) are coupled among Neotropical *Amphilophus* that independently evolve benthic–pelagic species pairs in crater lakes (Barluenga et al., 2006; Elmer et al., 2010a, b; Franchini et al., 2014). These traits are also coupled in Afrotropical crater lakes (Sturmbauer et al., 1992; Genner et al., 1999; Wagner et al., 2009). Thus, I speculate that this discrepancy in trait covariation between lotic and lentic conditions is due to the heterogeneous and unpredictable nature of lotic ecosystems that may result in selection for relaxed covariation among ecological traits, at least as a short-term response (e.g., among incipient species; Burress et al., 2013b).

Future directions and concluding remarks

The future of cichlids as model organisms for evolutionary and ecological research is bright, and several areas are of particular interest and in need of extensive investigation, for example, expanding our understanding of the interplay between genetic and ecological processes and how they relate to the processes of speciation and adaptive radiation. Specifically, utilization of high-throughput molecular techniques to investigate genome-wide patterns and how they relate to ecological processes is of special interest (reviewed in Fan et al., 2012), for example, what changes in genomic architecture precede (i.e., may initiate) or are ongoing during adaptive radiation? Investigation into the number, size, and distribution of genomic regions associated with morphological and ecological diversification is in its infancy, yet is the first step in understanding the genetic basis of adaptive radiation (Irschick et al., 2013). Furthermore, molecular factors that promote and constrain evolution, identification of candidate genes that underlie phenotypic variation and adaptive shifts, and the fate of heterospecific alleles are all fruitful topics that remain poorly understood. Such research would vastly expand our understanding of the genes to phenotype to function linkage and thus clarify questions pertaining to the processes of adaptive radiation and speciation. Numerous recent papers have embarked on this journey (Keller et al., 2012; Recknagel et al., 2013; Franchini et al., 2013). Additionally, high-throughput techniques will help resolve poorly understood evolutionary histories (e.g., Wagner et al., 2013; Ilves & López-Fernández, 2014), which is a common problem among cichlids due to shallow divergence times and complications due to hybridization early in the speciation process (i.e., Píalek et al., 2012).

Cichlids are an ideal model for studying adaptive radiations. Afrotropical and Neotropical lineages are similar in many respects such as (1) common form–function relationships with regard to body shape, oral dentition, and pharyngeal jaws, (2) ubiquity of omnivory and benthic sifting, (3) a central role for craniofacial mechanics, the pharyngeal apparatus, and phenotypic plasticity as mechanisms for generating ecological diversity, and (4) comparable examples of ecological speciation and adaptive radiation, particularly the importance of the benthic–pelagic axis. However, these systems also differ in key aspects of processes and patterns of evolution such as (1) the relative frequency of herbivorous species, (2) the primary foraging substrate associated with algivorous species, (3) the relative importance of hybridization as a source of diversification, and (4) relationships between oral tooth integration, shape, and ecology. Both these lineages provide key components to understanding the interplay between ecology and evolution among cichlids, yet studies on the lineages have largely not been integrated (but see Hulsey et al., 2010). Thus, there would be great benefit from improved integration of both systems in the form of comparative analyses, particularly as we advance into linking the genome to form and function.

Acknowledgments I am grateful to the many researchers cited herein whose work with cichlid fishes was instrumental in constructing this review and fostered my interest in cichlid fishes. Jonathan W. Armbruster provided access to laboratory facilities and equipment. For contributing photos, I am grateful to Ad Konings (*Lobochilotes*, *Cyphotilapia*, *Altolamprologus*, *Xenotilapia*, *Tropheus*), Jeff Rapps (*Amphilophus*, *Symphsodon*), and Oliver Lucanus (*Paretroplus*). Discussions with Pamela B. Hart benefitted this work. Jonathan W. Armbruster, Malorie Hayes, and Milton Tan provided feedback on a draft of this manuscript. Extensive comments from Craig Albertson and two anonymous reviewers improved the content and organization of this manuscript. This work was partially supported by the Jim Smith Endowment Fund and the Guy Jordan Endowment Fund. This paper is Contribution No. 703 of the Auburn University Museum of Natural History.

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