

Evolution in the Fast Lane: Diversity, Ecology, and Speciation of Cichlids in the Lower Congo River



Melanie L. J. Stiassny and S. Elizabeth Alter

Abstract More than 40 years ago in their compendium of fish diversity in the lower Congo River (LCR), T. R. Roberts and D. J. Stewart posed the question, “Why does the LCR harbor so many cichlids?” Here we seek an answer through a synthesis of the last 40+ years of research on cichlid diversity, ecology, and speciation. Our review suggests a key role for the unique geomorphology and hydrology of the river itself and its history of connectivity to other African freshwater ecosystems. In contrast to the river upstream of Pool Malebo, the LCR channel is entirely bedrock, and littoral habitats are mostly rocky and rock-strewn. In situ measurements have recorded dramatic changes in channel topology, fluctuating bed bathymetry, and regions of extreme depth. A combination of high annual discharge, steep elevational decline, and fluctuating channel width and depth result in extraordinarily high-energy flow regimes throughout the LCR. In-stream hydraulics and bathymetry appear to play a key role in isolating cichlid populations and are likely powerful drivers for micro-allopatric isolation and speciation, often over remarkably small geographical scales. Moreover, this hydrologically extreme environment is the evolutionary backdrop for an unusual array of cichlid morphologies, including the only known blind cichlid (*Lamprologus lethops*).

Keywords Congo basin · Geomorphology · Flow dynamics · Diversification · Micro-allopatry

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M. E. Abate, D. L. G. Noakes (eds.), *The Behavior, Ecology and Evolution of Cichlid Fishes*, Fish & Fisheries Series 40, https://doi.org/10.1007/978-94-024-2080-7_4

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1 Introduction

Sprawling across 4370 km of equatorial Africa, from Lake Tanganyika in the east to the mouth of the Atlantic Ocean in the west, the Congo River drains some 3.68 million km², including the largest remaining expanse of intact rainforest on the continent. Zaire, the former name for the Congo River, is said to be a corruption of the word “Nzere,” meaning “*the river that swallows all rivers*”—surely an apt descriptor of this largest of all African river basins. Perhaps not surprisingly, given its complex and extensive drainage network, the Congo basin (CB) harbors an exceptionally rich fish fauna. Estimates of species richness for the CB vary but converge on a number close to 1270 species (Winemiller et al. 2016). However, as numerous new species are discovered each year, that number is likely a significant underestimate. In contrast, cichlid diversity, excluding the hyperdiverse faunas of the Lake Tanganyika basin, is relatively muted. With only around 120 named (if not all formally described) species across the entire basin (Table 1), Congo cichlids conform to a pattern of relative paucity in African rivers compared with their predominance in the lacustrine systems of the continent. However, looking at species distributions and broad-scale patterns of endemism across the CB (Fig. 1), it is evident that cichlid diversity is not evenly partitioned. Remarkably, given an area of less than 2% of the entire basin, the lower Congo (LC), with a representation of 30% of cichlid species present in the entire basin and with 78% of those endemic to the LC, is an obvious outlier (Fig. 1), and clearly a hotspot of cichlid richness and endemism. This is not a novel observation: in their seminal paper on fishes of lower Congo River (LCR), Roberts and Stewart (1976:240) wrote:

Perhaps the most striking aspect of the taxonomic composition of the Zairean rapids fishes is the preponderance of Cichlidae” and that “Such predominance of Cichlidae is a noteworthy contrast to the situation in rich riverine faunas everywhere else in Africa, including low gradient rivers in the Zaire basin, where cichlid species, endemic or not, are always few in number and seldom contribute substantially to the numbers of individuals present.

Roberts and Stewart’s study was published more than four decades ago and since then new surveys and taxonomic revisions, and a number of molecular-based investigations, have revealed even greater diversity (Table 1). These studies have begun to illuminate the complex evolutionary histories of many LCR cichlids as well as of the river itself. However, the question implicitly posed by Roberts and Stewart—why does the LCR harbor so many cichlids?—remains unanswered. In this chapter, we seek to investigate this question through a synthesis of the last 40+ years of research on cichlid diversity, ecology, and speciation, as well as in the context of recent findings that suggest a key role for the unique geomorphology and hydrology of this extraordinary system.

Table 1 List of cichlid species present in the Congo River basin (exclusive of Lake Tanganyika and associated Malagarasi River)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
<i>Chromidotilapia</i>	<i>schoutedeni</i>	Poll and Thys van den Audenaerde, 1967 (see Schwarzer et al. 2015)	CC, UC
<i>Congochromis</i>	<i>sabinae</i>	(Lamboj, 2005)	CC (+LG)
<i>Congochromis</i>	<i>squamiceps</i>	(Boulenger, 1902)	UC
<i>Congochromis</i>	<i>dimidiatus</i>	(Pellegrin, 1900)	CC (+LG)
<i>Congochromis</i>	<i>pugnatus</i>	Stiassny and Schliewen, 2007	UC
<i>Congolapia</i>	<i>bilineata</i>	(Pellegrin, 1900)	CC
<i>Congolapia</i>	<i>crassa</i>	(Pellegrin, 1903)	CC
<i>Congolapia</i>	<i>louna</i>	Dunz, Vreven & Schliewen, 2012	CC
<i>Coptodon</i>	<i>congica</i>	(Poll and Thys van den Audenaerde, 1960) (see Dunz and Schliewen 2013)	CC
<i>Coptodon</i>	<i>rendalli</i>	(Boulenger, 1897) (see Dunz and Schliewen 2013)	ZC, UC, Ka (+SA)
<i>Coptodon</i>	<i>tholloni</i>	(Sauvage, 1884) (see Dunz and Schliewen 2013)	LC, CC (+LG)
<i>Ctenochromis</i>	<i>oligacanthus</i>	(Regan, 1922)	Ub
<i>Ctenonochromis</i>	<i>polli</i>	(Thys van den Audenaerde, 1964)	LC, CC
<i>Cyclopharynx</i>	<i>fwae</i>	Poll, 1948	CC*
<i>Cyclopharynx</i>	<i>schwetzi</i>	Poll, 1948	CC*
<i>Haplochromis</i>	<i>snoeksi*</i>	Wamuini Lunkayilakio and Vreven, 2010	LC
<i>Hemichromis</i>	<i>cerasogaster</i>	(Boulenger, 1899)	CC*
<i>Hemichromis</i>	<i>elongatus</i>	(Guichenot, 1861)	LC, CC, Ka, Ub, UC (+LG +SA)
<i>Hemichromis</i>	<i>lifalili</i>	Loiselle, 1979	CC?
<i>Hemichromis</i>	<i>stellifer</i>	Loiselle, 1979	LC (+LG)
<i>Heterochromis</i>	<i>multidens</i>	(Pellegrin, 1900)	CC
<i>Lamprologus</i>	<i>congoensis</i>	Schilthuis, 1891	CC, Ka
<i>Lamprologus</i>	<i>lethops*</i>	Roberts and Stewart, 1976	LC
<i>Lamprologus</i>	<i>mocquardi</i>	Pellegrin, 1903	CC, Ub, UC
<i>Lamprologus</i>	<i>symoensis</i>	Poll, 1976	UC
<i>Lamprologus</i>	<i>teugelsi*</i>	Schelly and Stiassny, 2004	LC
<i>Lamprologus</i>	<i>tigripictilis*</i>	Schelly and Stiassny, 2004	LC
<i>Lamprologus</i>	<i>tumbanus</i>	Boulenger, 1899	CC*
<i>Lamprologus</i>	<i>werneri*</i>	Poll, 1959	LC
<i>Lamprologus</i>	<i>markerti*</i>	Tougas and Stiassny, 2014	LC
<i>Nanochromis</i>	<i>consortus*</i>	Roberts and Stewart, 1976	LC

(continued)

Table 1 (continued)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
<i>Nanochromis</i>	<i>minor</i>*	Roberts and Stewart, 1976	LC
<i>Nanochromis</i>	<i>nudiceps</i>	(Boulenger, 1899)	Ka
<i>Nanochromis</i>	<i>parilus</i>	Roberts and Stewart, 1976	LC, CC
<i>Nanochromis</i>	<i>splendens</i>*	Roberts and Stewart, 1976	LC
<i>Nanochromis</i>	<i>teugelsi</i>	Lamboj and Schelly, 2006	Ka, CC
<i>Nanochromis</i>	<i>transvestitus</i>	Stewart and Roberts, 1984	Ka*
<i>Nanochromis</i>	<i>wickleri</i>	Schliewen and Stiassny, 2006	Ka*
<i>Nanochromis</i>	<i>sp. "mbandaka"</i>	see Schwarzer et al. (2011)	CC
<i>Nanochromis</i>	<i>sp. "ndongo"</i>	see Schwarzer et al. (2011)	CC
<i>Oreochromis</i>	<i>lepidurus</i>*	(Boulenger, 1899)	LC
<i>Oreochromis</i>	<i>mweruensis</i>	Trewavas, 1983	ZC
<i>Oreochromis</i>	<i>upembae</i>	(Thys van den Audenaerde, 1964)	UC
<i>Oreochromis</i>	<i>salinicola</i>	(Poll 1948)	ZC
<i>Orthochromis</i>	<i>kalungwishiensis</i>	(Greenwood and Kullander, 1994)	ZC
<i>Orthochromis</i>	<i>luongoensis</i>	(Greenwood and Kullander, 1994)	ZC
<i>Orthochromis</i>	<i>polyacanthus</i>	(Boulenger, 1899) (see Salzburger et al. 2005; Schwarzer et al. 2012a)	UC, ZC
<i>Orthochromis</i>	<i>stormsi</i>	(Boulenger, 1902) (see Salzburger et al. 2005; Schwarzer et al. 2012a)	LC, UC, ZC
<i>Orthochromis</i>	<i>torrenticola</i>	(Thys van den Audenaerde, 1963)	ZC
<i>Pelmatochromis</i>	<i>nigrofasciatus</i>	(Pellegrin, 1900)	CC, UC
<i>Pelmatochromis</i>	<i>ocellifer</i>	Boulenger, 1899	CC
<i>Pseudocrenilabrus</i>	<i>nicholsi</i>	(Pellegrin, 1928)	UC
<i>Pseudocrenilabrus</i>	<i>philander</i>	(Weber, 1897)	Ka, UC, ZC (+SA)
<i>Pseudocrenilabrus</i>	<i>philander dispersus</i>	(Trewavas, 1936)	Ka, UC
<i>Pterochromis</i>	<i>congicus</i>	(Boulenger, 1897)	CC
<i>Sargochromis</i>	<i>mellandi</i>	(Boulenger, 1905)	Ka, UC, ZC
<i>Sargochromis</i>	<i>thysi</i>	(Poll, 1967)	Ka
<i>Sarotherodon</i>	<i>galilaeus boulengeri</i>	(Pellegrin, 1903)	LC, CC, Ka
<i>Sarotherodon</i>	<i>nigripinnis</i>	(Guichenot, 1861)	LC (+LG)
<i>Schwetzoichromis</i>	<i>neodon</i>	Poll, 1948	Ka*
<i>Serranochromis</i>	<i>angusticeps</i>	(Boulenger, 1907)	ZC (+ SA)
<i>Serranochromis</i>	<i>macrocephalus</i>	(Boulenger, 1899)	ZC, Ka (+SA)
<i>Serranochromis</i>	<i>jallae</i>	(Boulenger, 1896)	ZC (+SA)

(continued)

Table 1 (continued)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
<i>Serranochromis</i>	<i>spei</i>	Trewavas, 1964	Ka, UC
<i>Serranochromis</i>	<i>stappersi</i>	Trewavas, 1964	ZC (+SA)
<i>Serranochromis</i>	<i>thumbergi</i>	(Castelnau, 1861)	ZC, UC (+SA)
<i>Serranochromis</i>	<i>toddi</i>	(Boulenger, 1905)	Ka
<i>Steatocranus</i>	<i>bleheri</i>	Meyer, 1993	UC
<i>Steatocranus</i>	<i>bleheri</i>	see Schwarzer et al. (2011)	CC
<i>Steatocranus</i>	<i>casuarius</i> *	Poll, 1939	LC
<i>Steatocranus</i>	<i>casuarius</i> “brownpearl”*	see Schwarzer et al. (2011)	LC
<i>Steatocranus</i>	<i>gibbiceps</i> *	Boulenger, 1899	LC
<i>Steatocranus</i>	<i>cf. gibbiceps</i> *	see Schwarzer et al. (2011)	LC
<i>Steatocranus</i>	<i>glaber</i> *	Roberts and Stewart, 1976	LC
<i>Steatocranus</i>	<i>mpozoensis</i> *	Roberts and Stewart, 1976	LC
<i>Steatocranus</i>	<i>rouxi</i>	(Pellegrin, 1928)	Ka
<i>Steatocranus</i>	<i>tinanti</i> *	(Poll, 1939)	LC
<i>Steatocranus</i>	<i>tinanti</i> “ultraslender”*	see Schwarzer et al. (2011)	LC
<i>Steatocranus</i>	<i>tinanti</i> “inga”*	see Schwarzer et al. (2011)	LC
<i>Steatocranus</i>	<i>tinanti</i> “intermediate”*	see Schwarzer et al. (2011)	LC
<i>Steatocranus</i>	<i>ubanguiensis</i>	Roberts and Stewart, 1976	Ub
<i>Steatocranus</i>	<i>sp. “lefini”</i>	see Schwarzer et al. (2011)	CC
<i>Steatocranus</i>	<i>sp. “redeye”</i>	see Schwarzer et al. (2011)	Ka
<i>Steatocranus</i>	<i>sp. “Kwilu”</i>	see Schwarzer et al. (2011)	Ka
<i>Steatocranus</i>	<i>sp. “dwarf”</i>	see Schwarzer et al. (2011)	CC
<i>Steatocranus</i>	<i>sp. “bulkyhead”</i>	see Schwarzer et al. (2011)	CC
<i>Steatocranus</i>	<i>sp. “maluku”</i>	see Schwarzer et al. (2011)	CC
<i>Steatocranus</i>	<i>sp. “mbandaka”</i>	see Schwarzer et al. (2011)	CC
<i>Steatocranus</i>	<i>sp. “kisangani”</i>	see Schwarzer et al. (2011)	UC
<i>Teleogramma</i>	<i>brichardi</i> *	Poll, 1959	LC
<i>Teleogramma</i>	<i>cf. brichardi</i> *	see Alter et al. (2017)	LC
<i>Teleogramma</i>	<i>depressa</i> *	Roberts and Stewart, 1976	LC
<i>Teleogramma</i>	<i>cf. depressa</i> *	see Alter et al. (2017)	LC
<i>Teleogramma</i>	<i>gracile</i> *	Boulenger, 1899	LC
<i>Teleogramma</i>	<i>monogramma</i>	(Pellegrin, 1927)	Ka
<i>Teleogramma</i>	<i>obamaorum</i>	Stiassny and Alter, 2015	CC
<i>Thoracochochromis</i>	<i>bakongo</i> *	(Thys van den Audenaerde, 1964)	LC
<i>Thoracochochromis</i>	<i>brauschi</i>	(Poll and Thys van den Audenaerde, 1965)	CC*
<i>Thoracochochromis</i>	<i>callichromus</i>	(Poll, 1948)	CC*
<i>Thoracochochromis</i>	<i>demeusii</i> *	(Boulenger, 1899)	LC
<i>Thoracochochromis</i>	<i>fasciatus</i> *	(Perugia, 1892)	LC
<i>Thoracochochromis</i>	<i>luluae</i>	(Fowler, 1930)	Ka

(continued)

Table 1 (continued)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
<i>Thoracochromis</i>	<i>moeruensis</i>	(Boulenger, 1899)	ZC
<i>Thoracochromis</i>	<i>schwetzi</i>	(Poll, 1967)	Ka
<i>Thoracochromis</i>	<i>stigmatogenys</i>	(Boulenger, 1913)	Ka, ZC
<i>Tilapia</i>	<i>baloni</i>	Trewavas and Stewart, 1975	ZC
<i>Tilapia</i>	<i>ruweti</i>	(Poll and Thys van den Audenaerde, 1965)	ZC (+SA)
<i>Tilapia</i>	<i>sparrmanii</i>	Smith, 1840	Ka, UC (+SA)
<i>Tylochromis</i>	<i>aristoma</i>	Stiassny, 1989	CC
<i>Tylochromis</i>	<i>bangwelensis</i>	Regan, 1920	ZC
<i>Tylochromis</i>	<i>elongatus</i>	Stiassny, 1989	UC
<i>Tylochromis</i>	<i>labrodon</i>	Regan, 1920	CC, Ub, UC
<i>Tylochromis</i>	<i>lateralis</i>	(Boulenger 1898)	LC, CC, Ka, Ub, UC
<i>Tylochromis</i>	<i>microdon</i>	Regan, 1920	CC*
<i>Tylochromis</i>	<i>mylodon</i>	Regan, 1920	ZC*
<i>Tylochromis</i>	<i>praecox</i> *	Stiassny, 1989	LC
<i>Tylochromis</i>	<i>pulcher</i>	Stiassny, 1989	CC
<i>Tylochromis</i>	<i>regani</i>	Stiassny, 1989	ZC, UC
<i>Tylochromis</i>	<i>robertsi</i>	Stiassny, 1989	Ub, CC, UC
<i>Tylochromis</i>	<i>variabilis</i>	Stiassny, 1989	CC, Ka, Ub, UC

Haplochromine generic assignments follows: Froese, R. and D. Pauly. Editors. 2020. FishBase. World Wide Web electronic publication. www.fishbase.org. Species indicated in bold are present in the LCR and those in bold underscored and marked with an asterisk are endemic to the LCR region. Column on far right indicates broad regional occurrence: LC (lower Congo), CC (central Congo), UC (upper Congo), Ka (Kasai drainage), Ub (Ubangi drainage), ZC (Zambian Congo). (+) Indicates distribution extends beyond the Congo basin: SA (southern Africa), LG (lower Guinea). Asterisks following regional occurrence indicate species restricted to lacustrine habitats. Broad geographical subdivision of the CB is as in Fig. 1

2 Characterization of the LCR: A Geo-hydrological Context for Cichlid Diversification

The important summary of Runge (2008) builds on the authoritative earlier studies of Veach (1935), Robert (1946), and Cahen (1954) to provide an excellent introduction to the physical geography and geomorphology of the present-day Congo basin. A number of recent reviews also provide additional useful information for the basin (O'Loughlin et al. 2013; Alsdorf et al. 2016; Harrison et al. 2016). Of most interest in the present context is the final course of the main stem of the Congo River as it flows out of Pool Malebo en route to the Atlantic some 450 km downstream (LCR, Fig. 2a, b). At the western edge of the CB, a sill formed at the eastern boundary of the Atlantic Rise (Western Escarpment), impeded the flow of the river, backing it up into a shallow lake-like expansion known as Pool Malebo

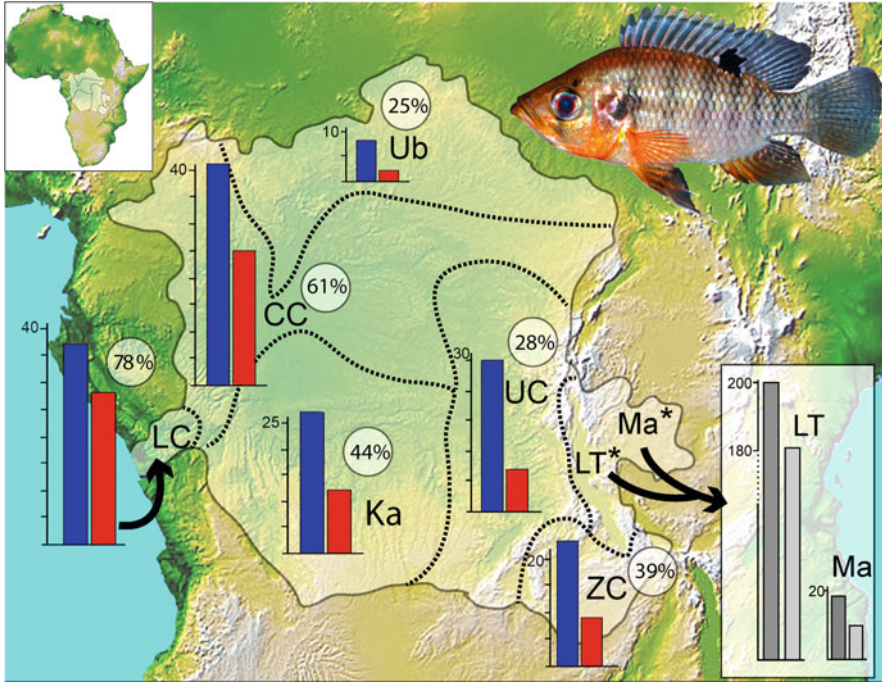


Fig. 1 Cichlids of the Congo Basin. Regionalization of the basin modified after Brooks et al. (2011): LC, lower Congo, CC, central Congo, Ka, Kasai, Ub, Ubangui, UC, upper Congo, ZC, Zambian Congo, LT, Lake Tanganyika, Ma, Malagarasi. Inset bar charts indicate estimates of regional species richness (blue) and endemism (red). Shaded circles indicate percentage endemism (excludes cichlids of LT* and Ma*). Species estimates for LT from Konings (2015), and for Ma from DeVos et al. (2001). Inset photograph of *Pterochromis congicus*, courtesy of P.V. Loiselle

(formerly Stanley Pool). Although the precise origin of the Pool is unclear, most authors consider it to be a remnant of a large, land-locked lake formed in the early Pliocene when repeated uplift of the Atlantic Rise last dammed the outflow of the Congo River (see below, and Runge 2008). Today, near the twin capitals of Kinshasa (Democratic Republic of Congo) and Brazzaville (Republic of Congo), the LCR spills over that rocky sill and plunges down a narrow gorge cut through the Crystal Mountains of the Atlantic Rise. From Pool Malebo, at an elevation of c. 280 m above sea level to the port town of Matadi 350 km downstream, the river drops 270 m in elevation as it flows through series of intermittently narrow (<0.2 km) and wide (>2 km) gorges in a channel that undergoes numerous and often rapid changes in direction, in response to a highly variable bedrock bathymetry. The average rate of discharge from the Pool is $46,200 \text{ m}^3 \text{ s}^{-1}$ (Runge 2008), and this enormous volume of water flows down a rock-strewn, bedrock-constrained channel on a contorted route to the Atlantic.

Based on a combination of geomorphology and geology, Robert (1946) divided the “rapids section” from the Pool to Matadi into three regions of the LCR. The first,

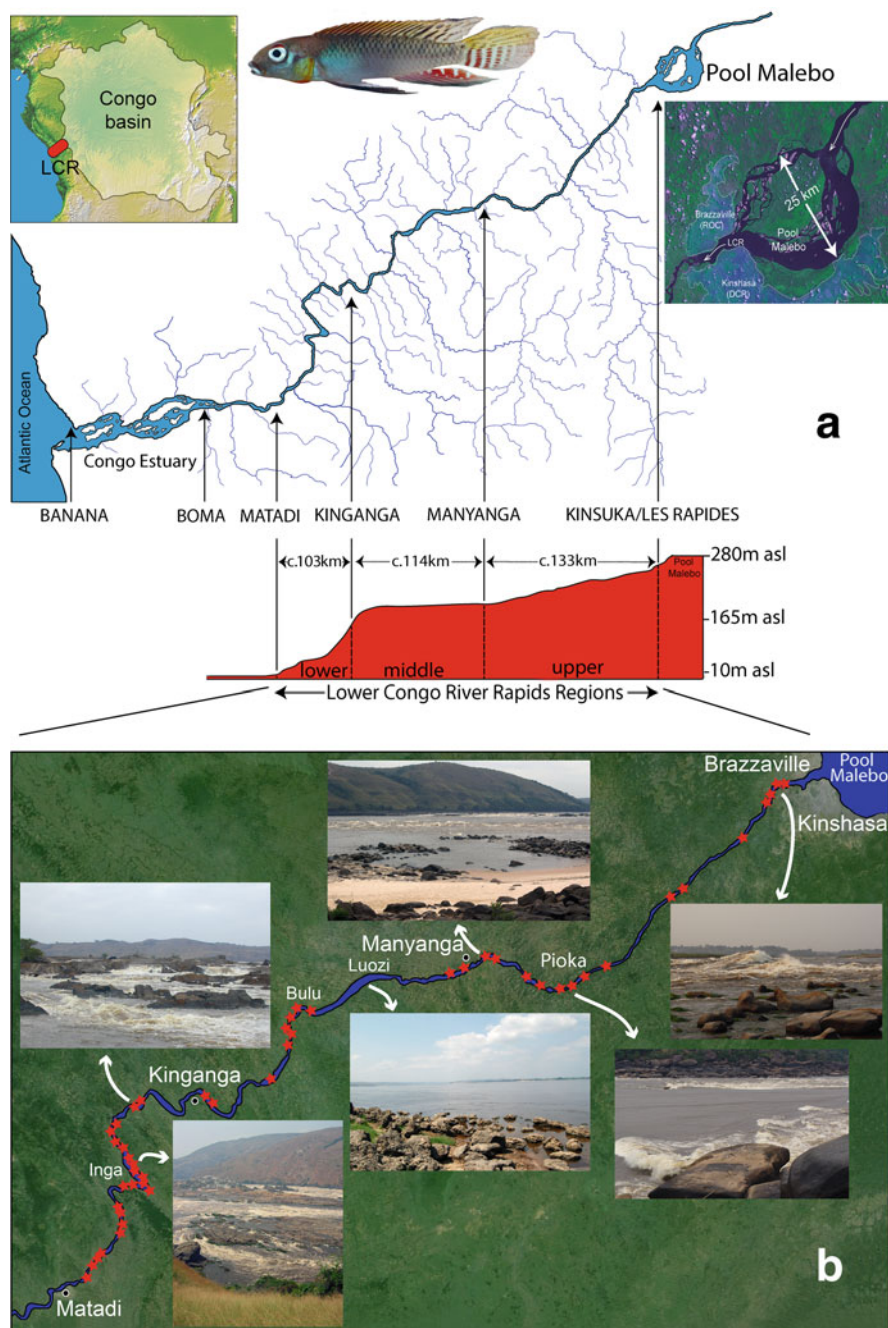


Fig. 2 Location and course of LCR from Pool Malebo to the Atlantic Ocean. (a) Broad regionalization of the LCR and elevation profile modified after Robert (1949). Inset photograph of *Nanochromis splendens*, courtesy of U. Schliewen. (b) Course of LCR "rapids regions" from Pool Malebo to Matadi. Red stars indicate approximate locations of major cross-channel rapids. Inset photographs show water surface and shoreline conditions at sites indicated by white arrows. Photographs courtesy of AMNH

uppermost region stretches 133 km from the Pool to Manyanga, over which the river drops more than 80 m resulting in numerous surface rapids, some of which span the channel. Between Manyanga and Kinganga, the middle (navigable) section spans about 114 km, and here the river is generally wider with a more gradual elevational drop of less than 20 m and few surface rapids, most of which are concentrated around and below the region of Bulu (Fig. 2b). Below Kinganga to Matadi the lower section extends for some 103 km over which the river drops nearly 170 m forming a series of massive rapids and cataracts, including the spectacular 15-km-long Inga Falls (Fig. 2b).

In order to better understand how channel bathymetry and hydraulic conditions within the LCR relate to patterns of fish diversity, hydrologists from the US Geological Survey and American Museum of Natural History (AMNH) conducted a series of in situ measurements. The surveys took place during July 2008 and July–August 2009, at the end of the main dry season and time of lowest water in the LCR. These studies included a series of cross-channel and short longitudinal transects and a 130 km single-line longitudinal bathymetric survey undertaken by a National Geographic Society-sponsored team of white water kayakers with kayaks outfitted with differential GPS and digital echo sounders (Fig. 3b). Short cross-channel transects were conducted from a motorized wooden pirogue with a digital echo sounder and a dGPS unit securely fastened to its hull (Fig. 3a). In addition, flow dynamics at depth and channel bathymetry were investigated using a four-beam acoustic Doppler current profiler (ADCP) in tandem with dGPS and echo sounders deployed from a large motorized wooden pirogue in reaches around Kinshasa, Manyanga, and Bulu (Fig. 4). Detailed methods of ADCP data collection and analysis and a series of preliminary findings are discussed by Oberg et al. (2009) and Jackson et al. (2009).

In marked contrast to the river upstream of Pool Malebo, the LCR channel is entirely bedrock (although some in-channel, alluvial deposits are present), and strong bedrock controls are clearly evident throughout the system. Littoral habitats are almost entirely rocky and rock-strewn (Fig. 2b), with some intermittent sandy, or occasionally grass fringed or muddy, shorelines. In situ measurements recorded dramatic changes in channel topology even over very short distances (Fig. 3a, b), and this highly irregular bed topography appears to have profound effects on flow dynamics even in the absence of rapids. In many stretches of deep, open water, large vortices, boils and suck holes are visible at the surface, formed as deep jets of water traveling at high velocities encounter towering rock columns and canyons. In addition to dramatic changes in bed bathymetry, regions of extreme depth were also recorded. For example, in the Bulu reach (Fig. 4a), ADCP deployment accurately recorded depths of up to 160 m (Fig. 4c), and during the single-line longitudinal bathymetric survey kayakers recorded depths of greater than 220 m (Fig. 3b). While that depth trace is not corrected for pitch and roll of the kayaks, there can be little doubt that the LCR is, in places, among the world's deepest rivers. But perhaps even more striking is the observation that these deep canyons, pools, and trenches are located in close proximity to, and interspersed between, regions of extremely shallow water where massive whitewater rapids span the entire channel (Fig. 2b).

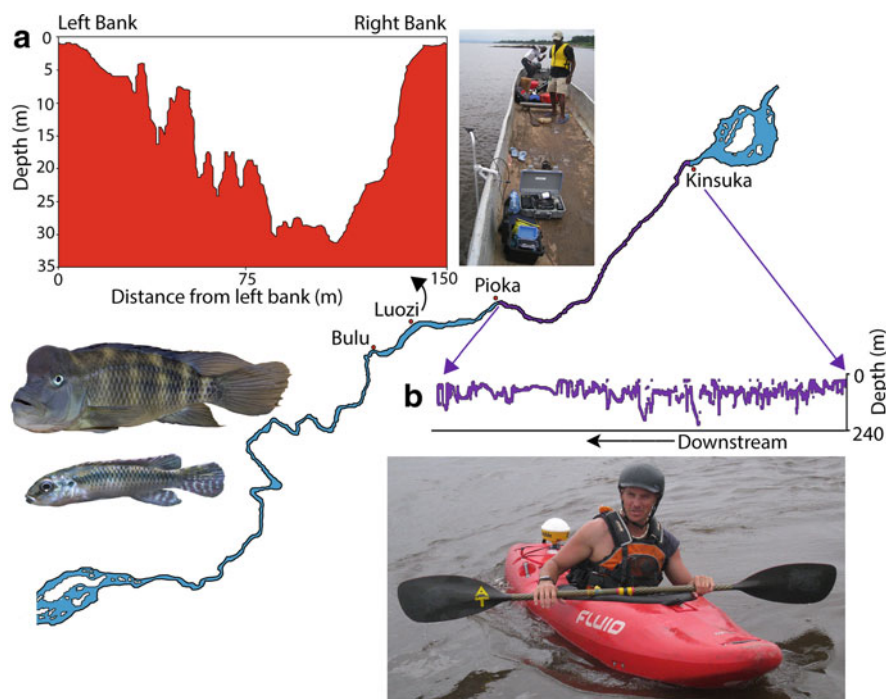


Fig. 3 Bathymetry at sites along the LCR. (a) Cross-channel profile near Luozi with photograph of wooden pirogue from which digital echo sounder and dGPS were deployed during repeated bank to bank transects across the channel. (b) 130 km single-line longitudinal depth trace made by kayakers between Kinsuka and Pioka (trace uncorrected for pitch and roll). Kayaks (inset) were outfitted with base-mounted echo sounders and rear-mounted dGPS receivers. Inset photographs of *Steatocranus casuarius* and *Nanochromis minor*, courtesy of O. Lucanus

The combination of high annual discharge, steep elevational incline, and fluctuating thalweg and channel width result in extremely complex flow regimes throughout much of the LCR. To better record and visualize these hydrological features, the 2008–2009 surveys employed ADCPs linked with dGPS to gather detailed measurements of water velocity profiles, backscatter, and channel depth. Most effort was expended in the Bulu reach (Fig. 4a), as this was the region from which specimens of the enigmatic blind cichlid, *Lamprologus lethops* had been found, suggestive that this region may harbor deepwater habitats (see below). Examination of individual transects and depth-averaged velocities indicate that, in much of the sampled area, coherent bank-to-bank flow structures are entirely absent. For example, a transect made while entering bend 1 at Bulu (Fig. 4b) shows that regions of low flow velocity (blue and green) near the banks are completely isolated from those at the opposite bank by a high shear zone of flow separation vertically spanning the entire water column. A high-velocity downstream core (red) exceeds 4 m/s, while secondary flow structures (arrows) appear as persistent large vortices, and significant recirculation of water flowing *upstream* at the banks with velocities exceeding 2 m/s is recorded. In

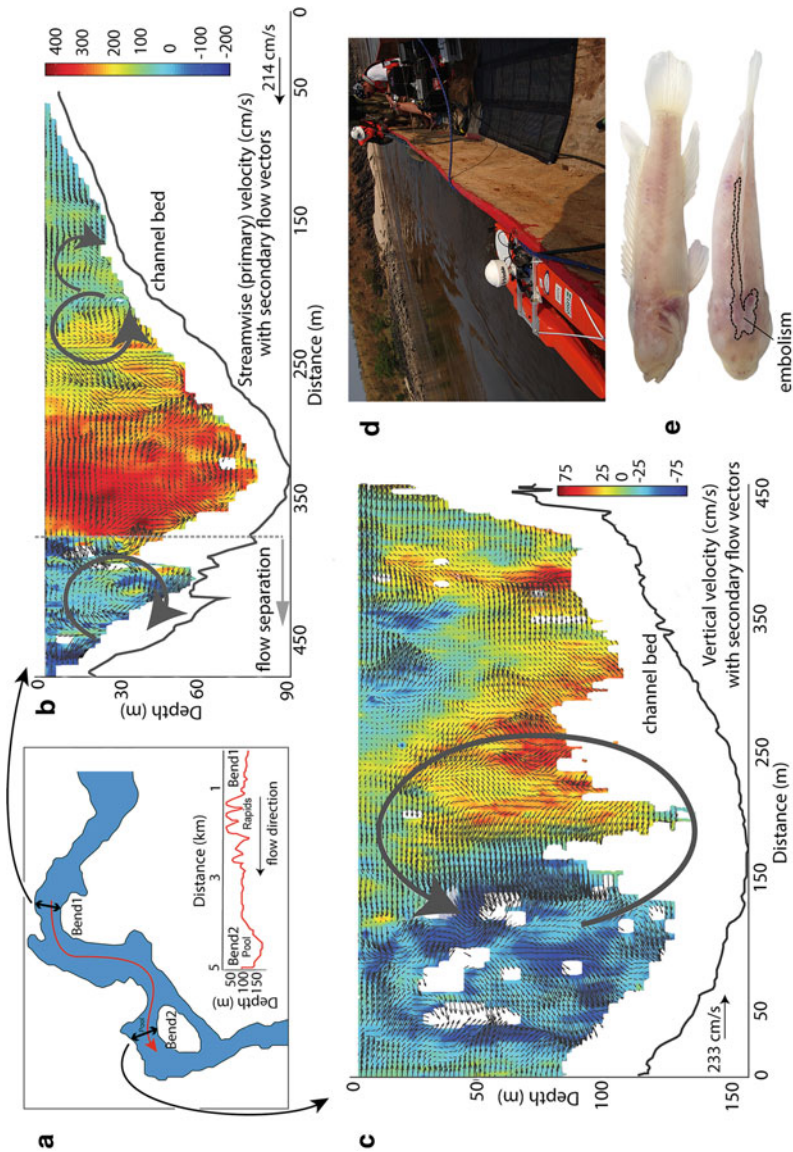


Fig. 4 Flow dynamics and bathymetry at additional sites along the LCR. (a) Map of Bulu reach with sampled sites indicated. (b) ADCP data visualization of primary (colors) and secondary (arrows) velocities of cross-channel section at Bend 1. Interference limits data acquisition near bed (white). (c) ADCP data visualization of vertical (color) and secondary (arrows) at cross-section of “pool” at Bend 2. Interference and intense turbulence limit data acquisition (white) (b, c modified after Jackson et al. 2009). (d) Wooden pirogue with ADCPs and dGPS deployed from a tethered trimaran, a digital echo sounder is located on the pirogue opposite the trimaran. (e) *Lamprologus lethops* (AMNH 248124, 56.2 mm SL), photographed immediately post-mortem. Black outline indicates the surface location of gas bubble embolism

regions of much greater depth (Fig. 4c), coherent vertical structures span the full 160 m depth, and large persistent cells of upwelling (yellow) and downwelling (blue) water coexist with vertical jets (red) that rapidly transport water between the bed and the surface.

3 Geological Context of the LCR

Current understanding of the complex history and manner of formation of the present-day Congo River network is incomplete. However, recent studies synthesizing seismic data (Kadima et al. 2011), and evidence from terrigenous depositional studies, regional geomorphological analyses, and phylogeography provide a compelling reconstruction of the Neogene evolution of the basin (Flügel et al. 2015). In the western CB, sedimentary studies along the coastal zone suggest a protracted history of shifting and intermittent outflow of the CB into the Atlantic. The first capture of a previously endorheic basin is thought to have occurred late in the Cretaceous, near the site of the present-day Ogowe River, with progressive southward migration taking place through to the mid Cenozoic. Although a final consensus has yet to be reached, interpretation of palaeosedimentological data and analyses of present-day river topology indicates that by the mid to late Miocene the main depocenter of sedimentation from the CB was in the vicinity of the Kouilou-Niari River, located to the north of the outflow of the present-day LCR. Although mechanisms are unclear, sediment loading and flexural uplift of the interior basin may have played a role in the migration of the Congo outlet, while tectonic activity associated with Miocene reactivation of the west African orogen appears to have initiated the final capture of the entire CB by the LCR. The formation of the current outlet—the LCR—is likely the result of ongoing tectonic activity causing the reactivation of an antecedent LCR valley (“Bas Congo” aulocogen, Gioan et al. 1989). A single high-energy capture event draining an inland Pliocene lake is now generally considered to have occurred around the Miocene–Pliocene transition, resulting in the formation of the present-day LCR and the remaining Congo River network. While an earlier proto-LCR, persistent as a small Atlantic coastal drainage, likely occupied some unknown extent of the preexisting valley, the current high-energy, high-flow regime of the present-day LCR is recent and was not fully established until sometime between 2 and 5 myr. In addition, studies of terrigenous dust flux from marine sediments indicate cycles of aridity across the African continent over the late Pliocene and Pleistocene, indicating that the LCR may have undergone significant fluctuations in water level with low discharge periods occurring ~2.8, 1.7, and 1 Mya (deMenocal 2004; Takemoto et al. 2015).

Regardless of the precise mechanisms of its origin, the present-day LCR is clearly a highly unusual riverine system. In many respects, it better resembles a high-gradient, headwater mountain stream—albeit one with an extraordinarily large discharge—than the lower reaches of any more typical large tropical river. Its rocky shorelines, heterogeneous bed topology, and extreme hydraulics generate a

complex array of flow regimes and habitats, and these features potentially play a key role in isolating fish populations by inhibiting both cross-channel and upstream–downstream movement. Such features, whether torrential whitewater rapids, deep canyons, or turbulent high-energy in-stream flows, likely present effective barriers for the small-bodied, predominantly lithophilic cichlid fishes so characteristic of the LCR system. Our findings suggest that the river itself may be a powerful driver of micro-allopatric isolation, actively facilitating phenotypic and ecological divergence, often over remarkably small geographical scales, through processes of natural selection, sexual selection, and genetic drift (Alter et al. 2017; Markert et al. 2010; Schwarzer et al. 2011).

4 Living on the Edge: *Lamprologus lethops*

Of all LCR cichlids, none is more intriguing than the so-called “blind cichlid” of Bulu. Described in 1976 by Roberts and Stewart, *Lamprologus lethops*, is the only cichlid that is cryptophthalmic and fully depigmented. Specimens are primarily known from a short stretch of the LCR centered around Bulu, although a few individuals have reportedly been recovered near Luozi less than 20 km upstream, and a single individual was recently found entrained in a circulating current alongside a rocky outcrop at Tadi, some 30 km downstream of Bulu. The highly derived, seemingly troglomorphic morphology of *L. lethops* (Figs. 5a and 6a) is strikingly divergent from that of the sympatric *L. tigrisipictilis* (Figs. 5d and 6b) or other congeners. While *L. tigrisipictilis* is found in large numbers in inshore habitats throughout the region, *L. lethops* is only found dead or moribund at the water surface in a condition of strong positive buoyancy. According to local fishermen, dead or dying *L. lethops* are found entrained among flotsam or wedged under rocks along the shorelines, but source population(s) are unknown. During five field visits totaling approximately 60 days AMNH ichthyologists, aided by local fishermen, recovered over 50 specimens ranging in size from 125.4 mm SL to 32.2 mm SL, but despite intensive efforts found no evidence of surface-dwelling populations, nor any nearby cave systems. In individuals of less than 40 mm SL small, dorsally positioned, optic globes are often clearly visible beneath expansive frontal bones (Fig. 5a), while in all larger specimens the optic globes are not externally visible being deeply recessed under heavily ossified frontals covered by a substantial epaxial musculature that has migrated anteriorly over the entire orbital region. Schobert et al. (2012) provide a detailed comparative ocular anatomy of *L. lethops* and *L. tigrisipictilis* and describe a series of “degenerative” features of the eyes in *L. lethops*. These include greatly foreshortened optic globes, a decreased number of neuronal layers in the retina, and the absence of extraocular muscles and a rete mirabile. Based on these, and other features, Schobert et al. (2012) concluded that the eyes of *L. lethops* are not capable of image formation but may potentially be functional as light-sensing organs. This capability appears most likely in juveniles, in which optic globes are exposed

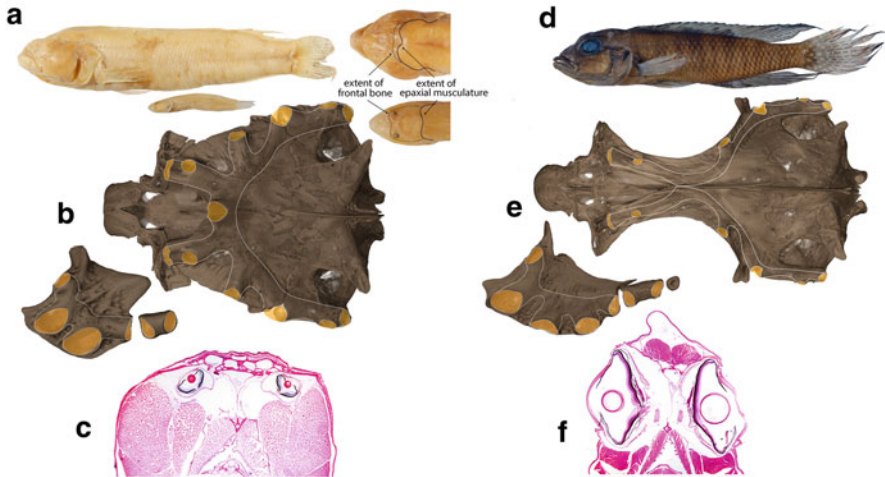


Fig. 5 (a) *Lamprologus lethops* AMNH 247885, 125.4 mm SL and AMNH 251325, 32.2 mm SL, with inset showing extent of epaxial musculature. (b) MicroCT segmentation of neurocranium (dorsal view) and infraorbital series with laterosensory canals and pores highlighted. (c) Transverse section through cranium and eyes (hematoxylin and eosin stained). (d) *L. tigripictilis* (AMNH 247252, 119.5 mm SL). (e) MicroCT segmentation of neurocranium (dorsal view) and infraorbital series with laterosensory canals and pores highlighted. (f) Transverse section through cranium and eyes (hematoxylin and eosin stained)

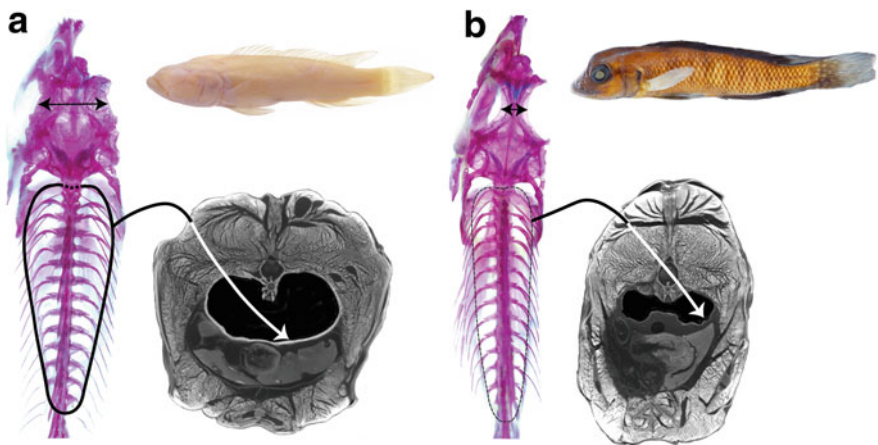


Fig. 6 (a) Cleared and stained *L. lethops* (AMNH 247962) in dorsal view, extent of gas bladder outlined. (b) Cleared and stained *L. tigripictilis* (AMNH 240906) in dorsal view, extent of gas bladder outlined. Both with transverse section through gas bladder (microCT scan after incubation in phosphotungstic acid). Double-headed arrows in (a, b) indicate width of frontal bones over orbit

beneath weakly ossified frontal bones. They also posited that the extreme dorsal positioning of optic globes is suggestive of a benthic lifestyle.

The serendipitous recovery of a single living individual found by fishermen from the shoreline at Bulu in 2007 provided a key observation. That specimen (Fig. 4e) exhibited some endothelial lesions when first retrieved, but was otherwise apparently undamaged. However, within a short time, numerous subcutaneous gas bubbles formed over its head, dorsum, and closer examination revealed numerous gas bubbles accumulated beneath the operculum and over the gills. The fish appeared to be suffering from gas-bubble disease, with resulting symptoms of catastrophic decompression syndrome (CDS) (Bouck 1980; Rummer and Bennett 2005) and died shortly after the onset of symptoms. In the absence of any nearby source of natural or human-mediated supersaturation of water (Weitkamp and Katz 1980), it seemed possible that the observed CDS was the result of the rapid transport of a depth-acclimatized fish to the surface. This was the first, albeit inferential, indication that in addition to rapids there may be deep water in the LCR.

The ADCP data illustrated in Fig. 4 not only reveals the presence of extremely deep water in the region but also suggests a potential mechanism for rapid vertical transport from the benthic zone. The large “pool” at bend 2 (Fig. 4c) is located below a sheer rock face about 3 km downstream of the village of Bulu and is a site where fishermen reported frequently finding dead *L. lethops*. In this pool, hydrologists recorded the presence of vertical jets that rapidly transport water between the deep rocky bed and the surface (Fig. 4c). If individuals of *L. lethops* living at, or close to, the rocky bottom were to become entrained in one of these jets they would be subjected to rapid and likely irreversible, upward transport. Such a scenario would result in their catastrophic decompression and death at the water surface.

While speculative, the supposition that populations of *L. lethops* live at extreme depths in one or more of the canyons in the Tadi–Bulu–Luozi region is supported by several anatomical and genomic singularities of the species when compared to its surface-dwelling congener, *L. tigrisipictilis* (Fig. 5d) and other cichlids. Consistent with reduction of eye size and image formation abilities, *L. lethops* possess markedly inflated laterosensory canals and pores (Fig. 5b), features associated with enhanced sensory acuity in diverse deepwater lineages of lake cichlids (Fryer and Iles 1972; Webb et al. 2014). But perhaps most suggestive of a depth association is the condition of the gas bladder in *L. lethops*. All cichlids are physoclistous and, although efficiently maneuverable within equilibrated depth ranges, are generally highly sensitive to rapid depth/pressure change. Most have limited compensatory abilities with slow equilibration rates—in experimental conditions in the range of just a few meters over 12 h periods (Ribbink and Hill 1979). The typically thin-walled tunica externa of the cichlid gas bladder (e.g., Fig. 6b) apparently contributes to low decompression and pressure equilibration rates and poor ability to rapidly move vertically through the water column. Given the extreme hydraulic conditions potentially exposing benthic fishes to upward transport and rapid decompression, it would be reasonable to anticipate that a reduced, or absent, gas bladder would be adaptive for such a benthic species. While uncommon, gas bladder reduction and loss is known to occur in other LCR cichlids, such as the rapids-adapted genus

Teleogramma (Stiassny and Alter 2015). However, this is not the case in *L. lethops* where, in contrast, the gas bladder is enlarged, encased by a greatly thickened tunica externa, and constrained within a hypertrophied rib cage (Fig. 6a); both attributes that would limit gas bladder expansion. Such a reinforced anatomy would potentially serve to increase the depth range over which *L. lethops* is able to resist positive buoyancy, possibly allowing it to maneuver over and above rocks and crevices, perhaps among pockets of calm or downwelling water. Occasionally, depth equilibrated individuals, or groups of individuals, must be swept out of that “pressure safe” zone above which positive buoyancy would exceed downward swimming abilities, and with an expanding gas bladder, they ascend rapidly to the surface—buoyant and exhibiting symptoms of CDS.

Whether individuals are able to recover from CDS, and/or persist in shallow water habitats has been controversial. We note here that many, but not all, specimens examined have ruptured gas bladders, evident as an anteriorly located tear or hole in the bladder wall. Clearly, such individuals would be unable to recover after ascent, and we suspect that even with intact gas bladders, if untreated, the effects of CDS would either kill the fishes outright or render them vulnerable to predation. However, with intensive human intervention specimens have been revived and a few survived in captivity. Lucanus (2013, p. 8) documents the process as follows:

The fish showed some distress via gas bubbles and were pierced with a needle to relieve the pressure. For the next two weeks the fish lay on their sides and would not eat, in individual aquariums without decor, but eventually recovered. Of all animals caught, eighty percent would die in the first minutes after capture, another fifteen percent in the next day.

In addition to anatomical and physiological evidence, new genomic data support the hypothesis that *L. lethops* lives in a light-free or extremely low-light environment in the LCR. An analysis of genome-wide variation in *L. lethops* shows that, in addition to loss-of-function mutations in many genes related to eye development and pigmentation, disabling mutations also occur in the gene *DDB2*, related to repairing DNA damaged by UV light (Aardema et al. 2020). The loss of a functional spexin gene also suggests that *L. lethops* may have altered appetite or satiety as an adaptation to a low-food environment, a phenomenon also observed in Mexican cavefish (e.g., Riddle et al. 2018).

Clearly much remains to be learned about the ecology, evolutionary history, habitat, and population dynamics of this highly unusual LCR cichlid. Ongoing comparative genomic studies of *L. lethops* and related species, informed by the genomic resources currently available for its sympatric congener *L. tigrisictilis* (Aardema et al. 2020), and the related Lake Tanganyikan species, *Neolamprologus brichardi* (Brawand et al. 2013), will further illuminate aspects of the genetic underpinnings of the unusual anatomy and physiology of *L. lethops*—perhaps the first known example of persistent, hydrology-driven, mortality in a natural system.

5 Molecular Phylogenetics: Patterns of Colonization and Radiation in the LCR

New molecular techniques can yield insights into the diversity and evolutionary histories of cichlid fishes that were difficult or impossible with the methods available to Roberts and Stewart. Numerous LCR cichlid lineages have since been identified with molecular data (Markert et al. 2010; Schwarzer et al. 2011; Alter et al. 2017; see also Table 1) and, in most cases, where subsequent morphological reexamination has been undertaken, these assessments have been corroborated and new species formally described (e.g., Schelly and Stiassny 2004; Wamuini Lunkayilakio and Vreven 2010; Tougas and Stiassny 2014; Stiassny and Alter 2015). As more refined molecular analyses continue to aid in focusing morphological studies, the tally of LCR endemics will undoubtedly rise further (Lowenstein et al. 2011).

Molecular approaches can now also be used to investigate when and how these diversification events occurred, elucidate patterns of hybridization and introgression, the genomic basis of morphological change and evolutionary innovations, and provide enhanced ecological insights through isotopic studies of food webs and dietary specialization. Though such methods hold great potential for a deeper understanding of the evolutionary history of Congo cichlids, to date only a handful of studies have used these tools to resolve phylogenetic relationships among LCR cichlid lineages or estimate patterns and timing of their diversification. Although relatively few compared to the burgeoning number of molecular investigations of African lake cichlids, these studies have utilized a diversity of approaches, including amplified fragment length polymorphisms (AFLPs), Sanger sequencing of mitochondrial and nuclear genes, microsatellite analysis, and genome-wide single nucleotide polymorphism (SNP) based approaches (double-digest restriction-associated DNA sequencing, or ddRAD-Seq). Most recently studies utilizing genome-wide ultraconserved elements (UCEs) have been initiated (Stiassny et al. 2016). For cichlids, these earlier efforts were advanced by the pioneering work of Julia Schwarzer, Ulrich Schliewen, and colleagues, with molecular studies focused on the numerous LCR endemics in the diverse genera *Steatocranus* and *Nanochromis*. Here we review these and other studies, highlighting areas where similar patterns across groups can be identified and common underlying processes invoked.

Recent molecular studies suggest a rather narrow time frame for colonization of the LCR by cichlids and other fishes and support the idea that colonization occurred at least twice in many clades. With calibrated divergence times for endemic LCR clades ranging from several thousand to ~5 Myr, these findings are consistent with the hypothesis that modern flow conditions in the contemporary LCR have been in place no longer than the last several million years (see Sect. 3 above).

Schwarzer et al. (2011) examined diversification patterns and timing of LCR colonization by *Steatocranus* and *Nanochromis*, using AFLPs and the mitochondrial marker, ND2. Their findings are broadly consistent with the estimated age of the LCR (2–5 Myr) and suggest that at least two temporally distinct colonization events

occurred in each genus, followed by in situ diversification. Their phylogenetic reconstruction indicates that endemic LCR species in *Nanochromis* and *Steatocranus* do not comprise single, monophyletic clades, but rather fall into two independent lineages, indicating that the ancestors of these genera arrived in at least two events. Schwarzer et al. (2011) inferred the ages of the two endemic LCR *Nanochromis* clades as 2.67 (1.5–3.9) Myr and 1.6 (0.7–2.5) Myr. Likewise, they identified two clades of *Steatocranus* with age estimates of 4.48 (3.3–5.8) Myr and 0.94 (0.3–1.7) Myr. In addition, in both genera, younger taxa have a distribution limited to the upper and middle LCR, further supporting a hypothesis of two episodes of colonization, since in a single-colonization scenario followed by downstream diversification, the youngest species is expected to be distributed furthest down river.

Results from our own studies using mitochondrial and genome-wide SNP data for the genus *Teleogramma* are broadly consistent with the findings for *Nanochromis* and *Steatocranus* in both timing and spatial patterns. Our data indicate that the oldest mitochondrial lineage found in the LCR, represented by the endemic *T. brichardi*, dates to 4.7 (1.7–7.6) Myr and that the majority of LCR endemic mitochondrial lineages diversified some 0.77 (0.25–1.4) Myr (Alter et al. 2017). Moreover, nuclear SNP data also suggest two episodes of colonization, with *T. gracile* resolved as sister to the other LCR *Teleogramma* species, despite a distribution in the middle of the ranges of these other species (Fig. 7a). Interestingly, a recent study focusing on LCR spiny eels (*Mastacembelus*) found a similar pattern of two independent colonizations and subsequent diversification within a timeframe of ~4 Myr and ~0.5 Myr, respectively (Alter et al. 2015). Such common observations across diverse lineages lend support to the idea that geological, hydrological, and/or ecological conditions facilitated the colonization of the LCR at least twice during the past several million years.

Inferring the biogeographic origins of endemic LCR cichlids is fraught due to undersampling in many of the potential source areas including the Congo basin, but examining the ranges of putative sister taxa provides evidence that the CB and LCR gained and lost connections to several African ecoregions at different times during periods of hydrological reorganization of African river networks. For example, based on a study of the age and potential origins of several chromidotilapiine genera including *Teleogramma*, *Congochromis*, and *Nanochromis*, Schwarzer et al. (2015) propose an ancient connection between the northern CB, the northern part of Lower Guinea, and the Ghanaen–Eburneo region around the late Oligocene/early Miocene. These inferences are based on the ranges of the sister clades to *Congochromis* + *Nanochromis* (including *Chromidotilapia schoutedeni* found in the middle Congo/Lualaba; and *Limbochromis robertsi* found in Ghana). Divergence of these groups in the Oligocene/early Miocene appears to have occurred in allopatry. Biogeographic links between the CB and West Africa/Lower Guinea are also observed in some non-cichlid fishes including *Synodontis* (Day et al. 2013), and *Epiplatys* killifishes (Collier et al. 2009). These patterns provide support for the suggestion, based on sedimentary studies along the Atlantic coastal zone (see

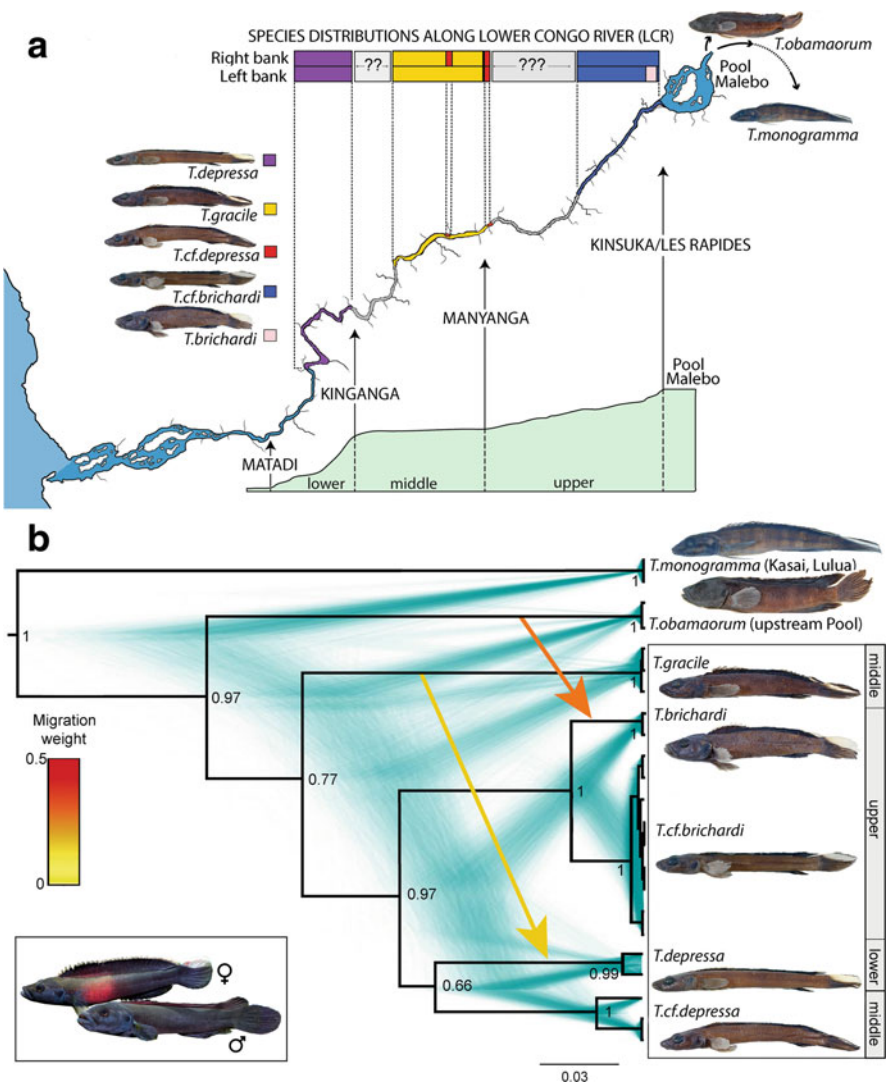


Fig. 7 (a) Distributional ranges of *Teleogramma* species along the LCR color coded and schematically represented by offset colored blocks. Regions where no sampling has been possible indicated in gray. (b) Phylogenetic relationships estimated from 37,826 SNPs using a multispecies coalescent analysis with the SNAPP program (Bryant et al. 2012). Posterior probabilities are indicated at nodes. Underlying tree cloud (in turquoise) indicates the range of tree topologies recovered. Arrows indicate possible introgression events detected based on the discordance between mitochondrial and nuclear phylogenies. Modified after Alter et al. (2017)

above), that the outflow of a proto-Congo may have initially drained west in the region of the present-day Ogowe Valley.

Haplochromines present evidence of another biogeographic connection. The phylogenetic reconstruction of Schwarzer et al. (2012a), which included the LCR species *Thoracochromis fasciatus*, *T. demeusi*, *T. bakongo*, *Haplochromis snoeksi*, *Ctenochromis polli*, and *Orthochromis stormsi* suggests that dynamic watershed rearrangements driven by Neogene tectonism (late Miocene/Pliocene boundary) caused multiple instances of introgression and potential hybrid speciation in this group. Mitochondrial and nuclear data in these taxa indicate ancient connections between Congolian and eastern African drainage systems as well as southern Congo–Zambezi connections (Schwarzer et al. 2012a).

Finally, phylogenetic relationships among lamprologine cichlids suggest a recent biogeographic connection between the LCR and Lake Tanganyika, a finding concordant with the pattern found in a clade of spiny eels (*Mastacembelus*) (Alter et al. 2015; Day et al. 2017) and in the cichlid genus *Oreochromis* (Ford et al. 2019). Although based mainly on mitochondrial data, most molecular studies suggest that riverine lamprologines are nested within the Lake Tanganyika radiation (Clabaut et al. 2005; Day et al. 2007; Schedel et al. 2019). Sturmbauer et al. (2010) used mtDNA and AFLPs to reconstruct the phylogenetic history of Lamprologini and, assuming the most recent connection between the Congo and Lake Tanganyika via the Lukuga River occurred in a window between 1.1 and 3.5 Mya, they estimate the split between riverine and lake lamprologines at ~1.7 Mya. Schedel et al. (2019) identify an mtDNA-based clade of central and lower Congo drainage lamprologines that diverged from Lake Tanganyika lamprologines 4.31–9.49 Mya; their analysis supports seeding of the Congo from Lake Tanganyika. While these studies have used a limited set of markers and very few representatives of riverine lamprologines, a recent analysis utilizing over 270 UCEs (151,727 bp) and including multiple individuals of all Congo River species also strongly supports a nested placement of a wholly riverine clade within the Lake Tanganyika radiation (Stiassny et al. 2016 and in prep.).

Taken together, these studies suggest that cichlid clades from different regions of the African continent gained access to the Congo or proto-Congo, and ultimately the LCR, during several distinct periods of connectivity, with chromidotilapiines arriving first during the Oligocene/early Miocene, followed by a range of haplotilapiines during connections with east African and Zambezi drainages in the late Miocene/Pliocene, and most recently connections between Lake Tanganyika and Congo in the Quaternary (over the last ~1–2 Myr). Even within the relatively older chromidotilapiines, however, the ages of modern LCR endemics appear to be constrained to the last ~5 Myr, consistent with geological evidence suggesting contemporary hydrological conditions in the LCR are not likely to be much older. Additional data from other cichlid clades (Table 1) and fish families with LCR endemics are ongoing and will be essential for a more refined assessment of these biogeographic patterns and scenarios.

6 Biogeographic Divisions Within the LCR

Based on a series of geomorphological and geological features, three main biogeographic divisions have been recognized across the LCR “rapids region” (see above, and Robert 1946); these divisions are characterized not only by differences in habitat and hydrological attributes but also in patterns of local endemism and species assemblages. Not surprisingly, molecular studies have confirmed biogeographic breaks across a number of species, with the most dramatic break on either side (upstream/downstream) of the massive rapids at Inga (Fig. 2). For example, two clades of *Steatocranus* diversified on either side of the rapids roughly 3 Myr: (1) *S.* sp. aff. *tinanti* “Inga” found downstream of rapids versus *S.* cf. *tinanti* found upstream of rapids; (2) *S. glaber* and *S. mpozoensis* found downstream versus *S.* cf. *gibbiceps* found upstream (Schwarzer et al. 2011). Likewise, a split in *Nanochromis* of roughly the same age occurs between *N. consortus* (downstream) and *N. splendens* (upstream) (Schwarzer et al. 2011). In a study of *Lamprologus tigripictilis* sensu lato using microsatellite and mitochondrial markers, strong population structure was observed between populations upstream and downstream of the Inga rapids (Markert et al. 2010), and the downstream populations have since been described as a distinct, narrowly endemic species (Tougas and Stiassny 2014). These patterns are consistent with the “large Inga waterfall hypothesis” proposed by Schwarzer et al. (2011), suggesting that a waterfall once existed at Inga and isolated downstream lineages, followed by erosion of the falls into rapids allowing for subsequent upstream movement.

While no species of *Teleogramma* have been found below Inga, Markert et al. (2010) describe strong population structure across smaller rapids upstream of Inga in *T. depressa*, and Alter et al. (2017) highlight population structuring across the range of *T.* cf. *brichardi*. Moreover, the majority of lineages in *Teleogramma* (*T. brichardi*, *T. obamaorum*, *T. depressa*, *T.* cf. *depressa*, *T. gracile*) and many other LCR endemics (Schwarzer et al. 2011) have narrow geographic distributions broadly corresponding to hydrological features or habitat regions (Fig. 7a). In all, these studies demonstrate that high-energy in-stream flow structure, complex bathymetry, and the presence of numerous cross-channel rapids have likely played a major role in isolating upstream–downstream, and perhaps cross-channel, populations over extremely small geographical scales thus likely contributing to micro-allopatric speciation in several clades. Such hydrological controls are expected to be particularly effective for strongly lithophilic, small-bodied, physoclistous fishes such as the majority of cichlid species found in the LCR.

7 Hybridization and Reticulate Evolution

For many African cichlids, genetic data have revealed evidence of both recent and ancient gene flow across species boundaries (introgressive hybridization) resulting in repeated patterns of reticulate evolution (e.g., Salzburger et al. 2002; Smith et al.

2003; Koblmüller et al. 2007, 2010; Joyce et al. 2011; Schwarzer et al. 2012a, b; Wagner et al. 2013; Keller et al. 2013; Ford et al. 2015; Meyer et al. 2016). Interspecific gene flow has been hypothesized to play a generative role in diversification as well, for example through acquisition of novel traits and generating species of hybrid origin (Seehausen 2004). Hybridization is also evident across several clades of LCR cichlids and has been inferred via discordance between mitochondrial and nuclear phylogenies and other tests in *Steatocranus*, *Teleogramma*, and *Nanochromis*. Earlier work by Schwarzer et al. (2009) using mtDNA and AFLPs showed cytonuclear discordance in the placement of several taxa in both *Steatocranus* and *Nanochromis*. A subsequent analysis by Schwarzer et al. (2012b) confirmed complex patterns of reticulation in *Steatocranus* by detecting conflicting phylogenetic signals. Their data support the hypothesis that the *Steatocranus* radiation represents an evolutionary network rather than a bifurcating tree, with one widespread species (*S. cf. gibbiceps*) serving as a “vector,” connecting geographically distant lineages through gene flow. Similarly, Alter et al. (2017) found conflicting phylogenetic signal in the genus *Teleogramma*, with evidence for ancient but not ongoing introgressive hybridization between certain species (Fig. 7b). While the pattern of hybridization is not as complex as the one inferred for *Steatocranus* by Schwarzer et al. (2012b), it is notable that in both cases introgression appears to have occurred between species found on either side of Pool Malebo.

The apparent preponderance of strong mitonuclear discordance across these, and other, cichlid genera serve to emphasize the dangers of relying solely on mitochondrial genes for phylogenetic reconstruction of cichlids. These studies also demonstrate the potential importance of hybridization as a force shaping evolution and speciation in LCR cichlids, warranting closer study in other key LCR cichlids including those in the genus *Lamprologus*. Ancient hybridization has been postulated for lacustrine species of *Lamprologus* and *Neolamprologus* (see Gante et al. 2016 and references therein), including an instance of total mitochondrial replacement in *N. fasciatus* from *L. callipterus* (Nevado et al. 2009) and mitonuclear discordance in other Tanganikyan species (Koblmüller et al. 2007). Ongoing studies incorporating population-level sampling of all LCR and Congo River lamprologines targeting genome-wide UCEs will likely provide additional insights into potentially complex hybridization patterns in LCR lamprologines.

8 Conclusions and Future Studies

Since the publication of Roberts and Stewart’s monograph in 1976, ongoing research has strengthened their proposition that, unlike the situation in most other African riverine systems, the LCR harbors a richly endemic and hyperdiverse cichlid fauna. We have attempted to summarize many of these new findings, particularly those related to the hydrology and geological history of the LCR, as well as evolutionary patterns revealed by molecular data. Overall, these studies indicate that the extreme hydrology and bathymetry of the river has shaped cichlid diversity

through micro-allopatric processes, augmented by a series of ancient tectonic and hydrological changes that connected the paleo-Congo to various parts of southern, western and eastern Africa during diverse geological eras. With the relatively recent advent of extreme in-stream water velocities of the LCR, as it plunges from Pool Malebo toward the Atlantic, a pattern of downstream serial colonization and differentiation would be expected. However, molecular data indicate that the history of diversification has been more complex, with evidence for multiple episodes of colonization in several clades. Regardless, it is clear that this turbulent, high-energy system has exerted strong selective pressures on endemic cichlid species—most evident in unusual rheophilic morphologies that appear in *Steatocranus*, *Teleogramma*, and *Lamprologus*. The only known blind cichlid, *Lamprologus lethops*, represents the most extreme consequence of these selective pressures, though a deeper understanding of its evolutionary history awaits additional morphological, phylogenetic, and genomic analyses.

While enormous progress has been made in the last four decades in understanding cichlid evolution and ecology in the LCR, the studies summarized here have only scratched the surface of this exceptional system. New techniques in imaging including micro- and Dice-CT, and sophisticated new methods in 2D and 3D morphometrics, hydrological modeling, and next-generation sequencing have enormous potential to expand our knowledge about morphological diversification, and the timing and sources of speciation events, and the intrinsic and extrinsic drivers of those events. Most critically, more biological surveys are urgently needed, particularly in downstream areas such as Bulu, Tadi, and Inga where many of the most narrowly endemic and morphologically distinctive species have been discovered. Such surveys should also integrate geological and hydrological data collection to further our understanding of the physical context of evolutionary and ecological processes. Additional surveys to document the region's aquatic biodiversity have taken on increased urgency in light of the proposed development of a mega-dam (Grand Inga) that threatens to massively impact the flow regime of the LCR (Showers 2011; Oyewo et al. 2018).

Acknowledgments We gratefully acknowledge the numerous colleagues and students who have made significant contributions to the work reported on here. In particular, we recognize the innumerable contributions of our colleagues in the Republic of Congo and the Democratic Republic of Congo. Their participation has been pivotal to the success of this project and represents the future for ichthyological research throughout the region. In particular, we would like to acknowledge our colleagues Victor Mamonekene and Armel Ibala at the Université Marien Ngouabi, Republic of Congo and Raoul Monsembula Iyaba, José Justin Mbimbi Mayi Munene, Tobit Liyandja and Myriam Modima Yoko of the Université de Kinshasa, Democratic Republic of Congo. Without their enthusiastic help and ongoing commitment to documenting and conserving Congo's rich aquatic resources, this work would not have been possible.

For their assistance with collection and exportation permitting we are grateful to the Ministère de la Recherche Scientifique et de l'Innovation Technique, Institut National de Recherche En Sciences Exactes et Naturelles (IRSEN) and Groupe d'Etude et de Recherche sur la Diversité Biologique (GERBID) in the Republic of Congo, and to the Ministère de l'Agriculture et du Développement Rural, Secrétariat Général de l'Agriculture, Pêche et Elevage, Direction des Pêches and the Université de Kinshasa, Cabinet du Recteur, in the Democratic Republic of Congo.

We thank the following institutions and individuals for support for this project over our years of working in the LCR: the US National Science Foundation (DEB-05423540 and DEB-1655227), the AMNH Axelrod Research curatorship, the Carnegie Corporation of New York, a PSC-CUNY Award (jointly funded by The Professional Staff Congress and The City University of New York), and Ms. Janine Luke, a resident of New York City.

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