

Unrecognized and imperilled diversity in an endemic barb (Smiliogastrini, *Enteromius*) from the Fouta Djallon highlands

Ray C. Schmidt^{1,2}  | Megan N. Dillon¹ | Natalie M. Kuhn¹ | Henry L. Bart Jr³ | Frank Pezold⁴

¹Biology Department, Randolph-Macon College, Ashland, Virginia

²Division of Fishes, Smithsonian Research Associate, National Museum of Natural History, Washington, District of Columbia

³Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana

⁴College of Science and Engineering, Texas A&M University – Corpus Christi, Corpus Christi, Texas

Correspondence

Ray C. Schmidt, Biology Department, Randolph-Macon College, Ashland, VA 23005.

Email: rayschmidt@rmc.edu

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Abstract

The Upper Guinean Forests of Guinea, Sierra Leone and Liberia contain high levels of freshwater biodiversity. The Guinean Range and associated Fouta Djallon highlands separate two biogeographical provinces in the region and served as a refuge during past climatic fluctuations. While many species of freshwater fishes are restricted to one biogeographical province or the other, some are reported to occur on both sides of the divide. Here, we examine the molecular and morphological diversity of an endemic small African barb, *Enteromius foutensis*, reported to occur in both provinces. This integrative analysis revealed unrecognized diversity and suggests recent, or ongoing, events that facilitated geodispersal and subsequent divergence in the region. The molecular analysis revealed three divergent and well-supported populations within *E. foutensis*. Accounting for allometric shape variation allowed us to observe diagnostic morphological differences among the populations. *Enteromius foutensis sensu stricto* is restricted to the Little Scarcies drainage in Guinea and northern Sierra Leone. Our study revealed two candidate species distinct from *E. foutensis*. One is likely a narrow endemic restricted to a small area in the Konkouré River basin; the other candidate species inhabits the upper Senegal and Gambie River drainages. How these patterns of diversity compare with other freshwater species from the Fouta Djallon highlands and the conservation status of these candidate species are also discussed.

KEYWORDS

allometric correction, “*Barbus*”, biodiversity, endemism, geodispersal, headwater capture

1 | INTRODUCTION

Freshwater ecosystems are among the most threatened ecosystems globally (Darwall et al., 2018; Harrison et al., 2018). They provide critical ecosystem services and are home to incredible amounts of biodiversity. One of the major threats facing freshwater ecosystems is the lack of baseline knowledge about the environmental health of these areas (Darwall et al., 2018). This lack of basic knowledge hampers efforts to

accurately assess biodiversity prior to development activities (e.g., hydropower, road construction, mineral extraction) and does not allow monitoring of the effects of this development on freshwater biodiversity. One of the regions where baseline information on freshwater biodiversity remains nascent is the Upper Guinean Forests in West Africa.

The freshwater environments of the Upper Guinean Forests in Guinea, Sierra Leone and Liberia in western Africa contain a wealth of biodiversity with many recently discovered

species endemic to individual rivers drainages (Pezold, Schmidt, & Stiassny, 2016; Schmidt, Bart, & Pezold, 2016; Schmidt, Bart, Pezold, & Friel, 2017b). The Guinean Range forms the backbone of forest environments on either side and divides the large drainages flowing to the north and east (e.g., Senegal, Gambie, and Niger Rivers) from smaller drainages flowing west into the Atlantic Ocean. The Fouta Djallon highlands occupy the northern region of the Guinean Range and are characterized by moderate elevation (~1,500 m), forested streams, and many waterfalls. The boundary of the Upper Guinea and Nilo-Sudan biogeographic provinces (Roberts, 1975) bisects the highlands. Some species are restricted to one biogeographic province or the other, but other recognized species are “amphi-guinean,” occurring on both sides of the divide (Daget, 1962). These amphi-guinean taxa presented a challenge to understanding the region's diversity and biogeographic history, but a clearer picture is beginning to emerge from recent studies (Schmidt, 2014; Schmidt et al., 2016; Schmidt & Pezold, 2011).

Initially uplifting in the Jurassic and again in the Miocene, the Fouta Djallon highlands and Guinean Range are proposed to have served as refugia for freshwater species and other organisms (Mayr & O'Hara, 1986; Michel, 1973). These highlands appear to have facilitated speciation through events (e.g., headwater capture) that allowed geodispersal and subsequent divergence from ancestral populations. The geologic history of drainages arising on the Guinean Range is largely unknown, but investigations of phylogeography of taxa from the area are providing insights into the evolution of these drainages. Evidence of geodispersal across the Guinean Range and subsequent speciation is observed in the suckermouth catfishes, amphiliid catfishes and small African barbs (Schmidt, 2014; Schmidt et al., 2016; Schmidt & Pezold, 2011). Integrative studies of fishes from the region resulted in the discovery of nine new species of suckermouth catfishes (Schmidt, Bart, Pezold, et al., 2017b) and many new species of amphiliids that remain to be described. Studies of other nominal fish species from the different rivers and biogeographic provinces of the region are revealing additional diversity. Here, we examine *Enteromius foutensis* purported to be an amphi-guinean species of small African barb endemic to the Fouta Djallon highlands.

The small African barbs are ubiquitous across tropical Africa and quite diverse. With nearly 200 recognized species (Hayes & Armbruster, 2017), recent works suggest that the actual number of species is likely several times greater (Schmidt, Bart, & Nyingi, 2017a; Van Ginneken, Decru, Verheyen, & Snoeks, 2017). Previously recognized as “*Barbus*,” the genus *Enteromius* is now used to accommodate all of the diploid small African barbs that do not fit into other monophyletic genera (Hayes & Armbruster, 2017; Yang et al., 2015). Though recognizing the non-monophyletic *Enteromius* was criticized (Schmidt & Bart,

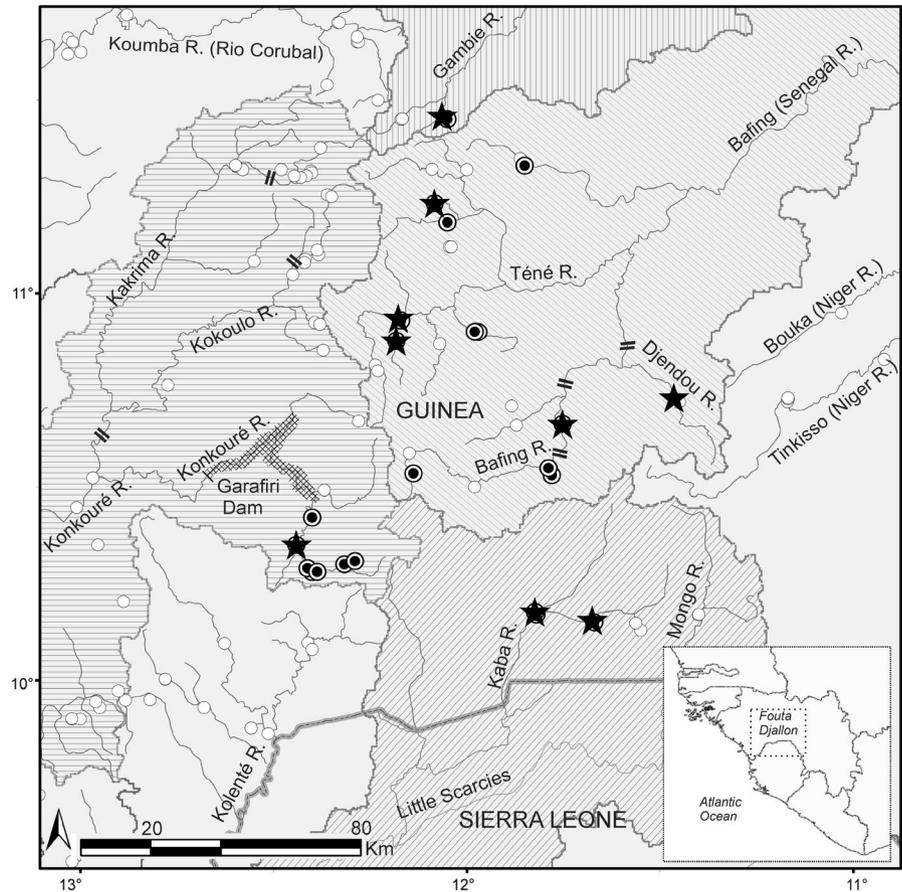
2015), we follow Hayes and Armbruster (2017) and use *Enteromius* to prevent further confusion. *Enteromius foutensis* was described from the Little Scarcies basin and distinguished from other co-occurring species by the lack of pigment along the sides and well-developed cephalic pores (Lévêque, Teugels, & Thys van den Audenaerde, 1988). The species, previously referred to as *Barbus spurelli* (Daget, 1962), is also reported in the Konkouré, Gambie, Senegal, and Niger River drainages (Lévêque et al., 1988). Preliminary studies on the phylogenetic relationships of *Enteromius* from the Upper Guinean Forests revealed genetic divergences among several populations of *E. foutensis* (Schmidt, 2014). The present integrative study was conducted to further explore molecular and morphological variation among populations in the Fouta Djallon highlands. We discovered three distinct populations within *E. foutensis* that likely deserve specific recognition. The molecular and morphological differences observed are discussed along with biogeography, the conservation status of these candidate species, and additional work needed before these candidate species are formally described.

2 | METHODS

The rivers and streams of Guinea, West Africa were sampled extensively during several expeditions in 2003 and 2013. Specimens identified as *E. foutensis* were collected from several localities within the Fouta Djallon highlands and surrounding areas by seine, cast net and electrofisher (Figure 1). Tissue samples dissected from voucher specimens were stored in 95% ethanol and these and other collected specimens were fixed in 10% formalin and preserved in 75% ethanol or 50% isopropyl. Specimens from 2013 collections were deposited in the Tulane University Biodiversity Research Institute (TU), Cornell University Museum of Vertebrates (CUMV) and Auburn University Museum of Natural History (AUM). The material from the 2003 collection is designated by field number and will be catalogued in natural history collections at the completion of subsequent species descriptions.

The molecular analyses included published cytochrome b (cytb) data from other barbs in the area (Hayes & Armbruster, 2017) and newly generated cytb sequences and portions of the nuclear RAG1 marker. Protocols and primers used to amplify genetic markers follow Schmidt, Bart, and Nyingi (2017a). PartitionFinder2 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) was used to determine the best model of evolution for each codon position in the cytb and RAG1 datasets. Phylogenetic analyses were conducted with GARLI 2.0 (Zwickl, 2006) and MrBayes version 3.2 (Ronquist et al., 2012) on the CIPRES Science Portal (Miller, Pfeiffer, & Schwartz, 2010) following parameters from Schmidt, Bart, Pezold, et al. (2017b). Specimens, locality data, voucher

FIGURE 1 Localities where putative *Enteromius foutensis* specimens were collected within the Fouta Djallon highlands and surrounding areas. Black circles indicate localities where specimens were collected, stars indicated localities where genetic material was collected, and empty circles are collection localities where no *E. foutensis* was collected. Important river drainages in this study are filled with different hatching and waterfalls are denoted with two hatch marks



numbers and GenBank accession numbers included in the phylogenetic analyses are listed in Table S1.

Morphological measurements and meristics follow Bamba, Vreven, and Snoeks (2011) and Schmidt, Bart, and Nyingi (2018) with the inclusion of anterior and posterior barbel length. All measurements were collected with digital calipers and recorded to the nearest 0.1 mm. To determine the amount and difference of allometric scaling among groups, we compared the slopes and elevations of reduced major axis (RMA, also referred to as standardized major axis) regression lines in the SMATR package of R (Team, 2013; Warton, Wright, Falster, & Westoby, 2006) following methods detailed in Sidlauskas, Mol, and Vari (2011). Principal component analysis using the covariance matrix of log-transformed data and assessing the correlation between resulting eigenvectors (e.g., PC1 and PC2) and standard length were performed in MYSTAT 12 (SYSTAT Software Inc.). Differences among eigenvectors not correlated with standard length were analysed with ANOVA in SPSS (IBM Corp.).

3 | RESULTS

A well-supported phylogeny inferred by a concatenated analysis of 1,844 characters revealed three distinct populations within *E. foutensis* from the Fouta Djallon highlands (Figure 2).

An alignment of partial cytb (1,116 bp) from 34 specimens was included in the analyses. This included 21 specimens of *E. foutensis* and several published sequences from *E. macrops* and *E. guineensis* from the area. Populations from the Konkouré River are sister to populations from the upper Senegal and Gambie drainages. These two populations are sister to *E. foutensis* from the Little Scarcies drainage. Though well-supported in the Bayesian Inference phylogeny, the above relationships are not well-supported in the Maximum Likelihood analyses. In the resulting phylogeny, the three populations are recovered as a polytomy (Figure 2). The uncorrected cytb p-distance among the three populations is 4.6%–7.1% (Table S2). Nuclear markers were difficult to sequence for *E. foutensis*. Growth hormone intron 2 contained a transposed element (Schmidt, unpublished) and showed no variation among the populations. Partial sequences of RAG1 (728 bp) were produced for each population recovered in the cytb analysis. Uncorrected p-distance of RAG1 among the three populations was 0.3%–0.4% (Table S2). Models of evolution implemented for each codon position in the cytb and RAG1 alignment are provided in Table S3.

The morphological analyses, involving 23 measurements and 9 counts from 137 specimens from the Konkouré, Senegal, Little Scarcies, and including one specimen from the Gambie River drainages, revealed differences among the populations. The scatterplot of PC1 vs. PC2 shows that populations in the

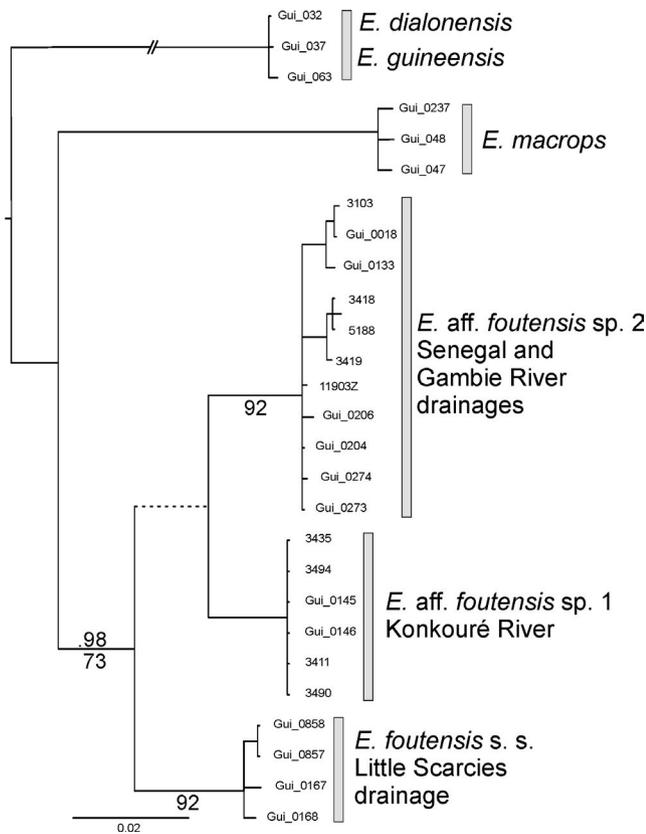


FIGURE 2 Phylogeny inferred from concatenated cytochrome b and RAG1 data from members of the *E. foutensis* complex. Posterior probabilities from Bayesian inference (above) and Bootstrap values from Maximum Likelihood analysis (below). Values above 0.99 and 95 not shown. Dotted branch is unsupported in Maximum Likelihood analysis. Metadata for specimens included in phylogenetic analysis can be found in the supplemental Table 1

Senegal River are largely distinct from the Konkouré, Little Scarcies and Gambie River populations (Figure 3a). There is overlap between populations in the Konkouré River, Little Scarcies and the single specimen from the Gambie River (Figure 3a). Principal component 1 is correlated with standard length (Pearson's correlation = 0.971), and by observing the component loadings associated with PC1 it is clear that this is also an allometric vector that describes variation in shape in addition to variation due to size (Table 1). Barbel lengths and body depth measurements appear to increase at a faster rate than other measurements as specimen increase in standard length (Table 1).

Regressing the PC1 scores against the log-transformed standard lengths reveals that each population displays the same allometric trajectory and there is no difference in slope among the various populations (Figure 3b; p -value = 0.57105). The single specimen from the Gambie River could not be included in the analysis as RMA requires $n \geq 3$ for each group. With similar slopes, we can test for differences of the y-intercepts (i.e., elevation) among the different populations. The elevation was significantly different

TABLE 1 Principal component (PC) loadings from 23 log-transformed linear measurements. Bolded values contributing the most variation along PC2

	PC1	PC2
Per cent variance explained	79.16	10.52
Standard length	0.083	0.017
Predorsal length	0.082	0.013
Head length	0.074	0.019
Preoccipital length	0.073	0.015
Eye diameter	0.072	-0.003
Snout length	0.086	0.003
Preoperculum length	0.075	0.016
Interorbit width	0.063	0.021
Dorsal-fin origin to caudal peduncle	0.086	0.023
Dorsal-fin terminus to caudal peduncle	0.074	0.019
Dorsal-fin base length	0.104	0.024
Dorsal-fin length	0.078	0.012
Prepectoral fin length	0.067	0.027
Prepelvic fin length	0.087	0.020
Preanal fin length	0.084	0.018
Origin of anal fin to caudal peduncle	0.083	0.028
Terminus of anal fin to caudal peduncle	0.090	0.024
Body depth at head	0.088	0.013
Body depth at dorsal fin	0.101	0.070
Body depth at anal fin (terminus)	0.109	0.015
Caudal peduncle depth	0.110	0.016
Anterior barbel length	0.155	-0.110
Posterior barbel length	0.144	-0.085

among the populations, and post hoc tests showing significant differences among all populations except the Senegal and Little Scarcies populations (Table 2).

PC2 is not highly correlated with standard length (Pearson's correlation = 0.177), suggesting that variation observed within this component is a result of differences in shape among populations. Posterior and anterior barbel length and body depth at the dorsal fin have the highest loadings on PC2 (Table 1). The ANOVA on the PC2 scores showed significant differences among the three populations (Table 2). Meristics are largely invariable among the populations except for the number of pored scales in the lateral line. Populations from the Little Scarcies generally have more scales in the lateral line series (21–25) than populations from Gambie, Senegal and Konkouré river drainages (21–23). By plotting the number of pored scales in the lateral line against

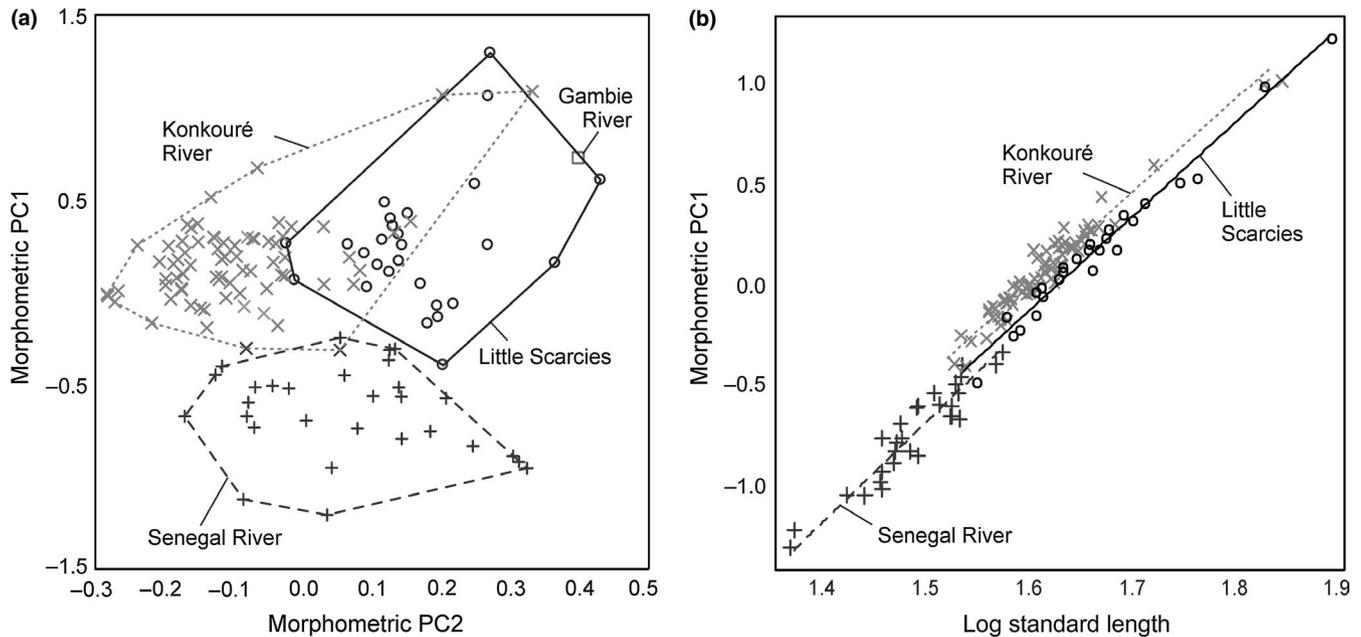


FIGURE 3 Scatterplot of PC1 vs. PC2 from principal component analysis of 23 log-transformed linear measurements from 137 specimens (a). Reduced major axis regression of PC1 from standard morphometrics on log standard length for populations of putative *E. foutensis*, not including the one specimen from the Gambie River drainage (b). Trendlines are shown for each group; slopes of groups are equal (p -value = 0.57105), tests for equivalence of intercept among groups are reported in Table 2

the relative measurement of posterior barbel length, structure is observed among the populations though with some overlap (Figure 4). These characters and those contributing to shape variation on PC1 will aid in diagnosing these distinct populations.

4 | DISCUSSION

4.1 | Molecular and morphological variation among *E. foutensis* populations

The molecular analysis revealed three distinct populations within *E. foutensis*. These three populations are from the Little Scarcies, Konkouré River, and the Senegal and Gambie river drainages (Figure 2). The divergences of cyt b among these populations (4.6%–7.1%) are consistent with

mitochondrial divergences among closely related *Enteromius* species (Mamonekene, Zamba, & Stiasny, 2018; Schmidt et al., 2018; Van Ginneken et al., 2017). As discussed when elevating *E. amboseli* from the widespread East African *E. apleurogramma*, much of the reported interspecific divergence in mitochondrial markers among African barb species is likely overestimated by underestimating the diversity within wide-ranging species complexes, or by recognizing broadly defined morphological species that contain distinct and distantly related taxa (e.g., *E. paludinosus*, Schmidt, Bart, & Nyngi, 2017a; Schmidt et al., 2018).

Though not as straightforward as the molecular analysis, the morphological analyses also suggest at least three distinct populations that correspond to those observed in the molecular analyses. The allometric correction of PC1 reveals that the component contains information on both size and shape, and

TABLE 2 Above the diagonal are the differences in intercept. Bold represents statistically significant p -values following sequential Bonferroni correction at a table-wide alpha value of 0.05. The analysis revealed no difference among the slopes for each population (p -value = 0.57105). Below the diagonal are p -values for post hoc Tukey's pairwise comparisons, with Bonferroni corrections, on principal component two (PC2) scores from linear measurements

	Senegal River	Konkouré River	Little Scarcies
Senegal River	–	0.0000	0.0588
Konkouré River	0.0000	–	0.0000
Little Scarcies	0.0040	0.0000	–

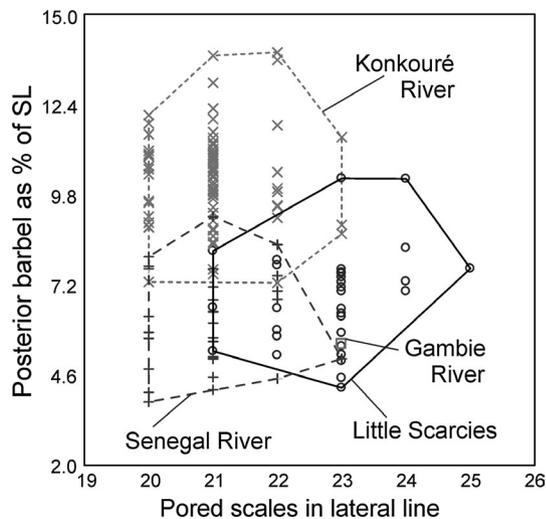


FIGURE 4 Scatterplot of relative posterior barbel length (as % of standard length) vs. the number of pored scales in the lateral line. These measurements and others identified as contributing to shape variation among groups in PC1 and PC2 (Table 1) will aid with diagnosing and describing these populations

including this PC in the analysis assists in distinguishing several of the populations. Within PC2, all three populations are recovered as statistically distinct. Additional specimens from the Gambia River and Niger River drainage are needed to more clearly understand the morphological variation among these populations. Although there is a fair amount of morphological overlap among some of the populations and few characters that clearly diagnose these populations, it is likely that a combination of several morphological characters (e.g., pored lateral line scales, body depth at dorsal fin, posterior barbel length) will diagnose these populations and allow us to formally describe them as new species.

4.2 | Taxonomic implications

Originally described from the Little Scarcies drainage, our results suggest that *E. foutensis* is restricted to this drainage and should be referred to as *E. foutensis sensu stricto*. The population in the Konkouré River drainage and populations in the Senegal and Gambia river drainages should be considered candidate species, which we provisionally refer to as *E. aff. foutensis* sp. 1, and *E. aff. foutensis* sp. 2, respectively. Additional populations from the area need to be examined before these candidate species can be fully diagnosed and formally described. Only one specimen of *E. aff. foutensis* sp. 2 from the Gambia River drainage was collected during the 2013 expedition and included in the molecular and morphological analyses. Additional specimens from the Gambia River drainage have been requested from natural history collections. Study of these specimens will assist us in determining if this population is morphologically similar to the Senegal River population. Populations of *E. aff. foutensis* are

also reported from the Tinkisso River in upper Niger River drainage (Daget, 1962; Lévêque et al., 1988). Expeditions in 2003 only collected a few small specimens in the Niger River drainage, but no tissues were collected from these specimens. Fortunately, there are specimens from this population housed in natural history collections that will be included in future descriptive work.

4.3 | Biogeography of the *E. foutensis* complex

This study further suggests that the evolutionary history of the Fouta Djallon highlands and Guinean Range is more dynamic than previously thought. Rather than being an amphiguinean species (i.e., the same species occurs on both sides of the Guinean Range), *E. foutensis* comprises at least three distinct populations that warrant specific recognition. This general pattern has also been observed in the suckermouth catfishes, mountain catfishes and other species of small African barbs (Schmidt, 2014; Schmidt et al., 2016; Schmidt & Pezold, 2011). Though the geological processes responsible for the transfers are unknown, it is clear that geodispersal across the Fouta Djallon highlands and subsequent divergence is promoting higher levels of diversity within the region than previously recognized. The genetic similarity between the Gambia River and Senegal River drainage populations suggest recent, or ongoing, geodispersal between these two drainages (Figure 2). Evidence of recent geodispersal between these two drainages has also been observed in mountain catfishes and certain barb species (Schmidt, 2014), but not observed in the suckermouth catfishes (Schmidt et al., 2016).

Molecular evidence suggests that several headwater capture events have allowed exchanges of populations of *Amphilius* cf. *grammatophorus* among the upper Konkouré River drainage (Kakrima River), Rio Corubal, Gambia River and Senegal rivers basins (Schmidt, 2014). Evidence of recent faunal exchange among the Gambia, Rio Corubal and Kakrima drainages, but not the Senegal River, was observed in the *Enteromius salessei*, *E. cadenati*, and *E. guineensis* species complexes (Schmidt, 2014). Members of these complexes are in the Senegal River drainage, suggesting older transfer events (e.g., Pliocene) that may have facilitated faunal exchange among drainages. *Chiloglanis* species do not occur in the upper Konkouré River, Rio Corubal or Gambia River drainages, but do occur in the upper reaches of the Senegal River drainage. Recent connections between the Senegal River drainage and the upper Niger River drainage (Tinkisso R.) are evidenced by genetically similar populations of *Chiloglanis waterloti* occurring in both drainages (Schmidt et al., 2016; Schmidt, Bart, Pezold, et al., 2017b). Based on this evidence, we hypothesize that the population of *E. aff. foutensis* in the upper Niger is most similar

to *E. aff. foutensis* sp. 2 in the Senegal River. Lack of fossil evidence from these groups makes it difficult to pinpoint precisely when these populations diverged, but conservative estimates based on molecular divergences suggest that the isolation occurred in the Pleistocene, well after the Guinean Range was formed (Schmidt, 2014; Schmidt et al., 2016).

Seemingly incongruent patterns of divergence among co-occurring species may be a result of how these taxa initially colonized the region. Additionally, understanding the causes of contemporary patterns of species distribution is confounded by past faunal exchanges that did not include the taxa in question (i.e., the species were not present when the headwater capture event took place), or instances where populations are part of the faunal exchange but ultimately go extinct. It is overly simplistic to assume that all co-occurring taxa in an area, each with their own distinct evolutionary histories, will react to vicariant events in the same way (Burridge, Craw, & Waters, 2006). Recent and ongoing headwater capture events are clearly allowing geodispersal and subsequent divergence of many, but not necessarily all, of the groups of fishes that inhabit the Fouta Djallon highlands. This complicated history has promoted diversity within the region, and while the patterns observed among all groups are not exactly congruent, by investigating the phylogeography of different groups of proposed amphi-guinean taxa, a clearer picture of the historical biogeography of the region is beginning to emerge. In the suckermouth catfishes and mountain catfishes, the general pattern is that populations initially colonized the Fouta Djallon highlands from the south through headwater capture events along the eastern and western side of the Guinean Range. Subsequent headwater capture events facilitated transfers across the Guinean Range divide in southeastern Guinea and in the northern drainages (e.g., Gambie, Konkouré, Rio Corubal and Senegal; Schmidt, 2014; Schmidt et al., 2016). The processes through which certain barb species, endemic to the Fouta Djallon highlands, initially colonized the area are still unclear. Ongoing efforts to resolve the phylogenetic relationships of these African barbs at the continental level will allow us to address these questions.

4.4 | Endemism and areas of conservation concern

The diversity revealed in the present study further suggests that freshwater diversity in the Upper Guinean Forests region is underestimated by current taxonomy. The results of this study permit an updated assessment of the conservation status of *E. foutensis* s. s. and the candidate species found in the Konkouré River and the Gambie and Senegal River drainages. *Enteromius aff. foutensis* sp. 1 is restricted to the Konkouré River proper and several small streams upstream of a large impoundment cause by the Garafiri Dam (Figure

1). The environmental assessment of this impoundment, constructed from 1995 to 1999, reported *E. foutensis* from the same areas that our surveys did, and in the area that was to be submerged by the resulting reservoir, but no populations were recorded downstream of the dam (IRD- BCEOM – BRLi, 2003). These populations appeared to be locally abundant in our samples from 2003 and 2013, but their restricted range (~20 km) is cause for conservation concern. Nearly 300 specimens were collected at one locality in the Kombira River in 2013. This small stream with fairly open canopy had a large pool below the bridge drained by two runs with submerged vegetation.

Enteromius aff. foutensis sp. 2 populations from the Senegal and Gambie River drainages are fairly widespread in small and medium streams, though less abundant than populations in the Konkouré River drainage. Genetic diversity (~1%) was observed among *E. aff. foutensis* sp. 2 populations, but does not correspond to geographical variation (Figure 2). Small waterfalls within the upper Senegal River drainage may have contributed to the genetic variation observed by initially isolating and reconnecting populations during Pleistocene climatic variations. More pronounced genetic variation was also observed in another barb species, *E. dialonensis*, within the upper Senegal River drainage (Schmidt, 2014). *Enteromius foutensis* s. s. is recorded from several localities within the Little Scarcies drainage in Guinea (Lévêque et al., 1988; this study). Collections from this drainage usually yielded less than a dozen specimens. It seems that this species might also inhabit small streams and tributaries of the Little Scarcies in Sierra Leone, but sampling in the area is needed to assess the range of this species.

The present study of nominal *Enteromius foutensis* populations from the Fouta Djallon highlands restricts *Enteromius foutensis* s. s. to the Little Scarcies drainage and has revealed the presence of two candidate species in the Konkouré River drainage and in the Gambie and Senegal river drainages. Additional specimens from populations in the Niger and Gambie drainages need to be examined before formally describing these candidate species. The endemism revealed in this study underscores the necessity of re-examining variation in other proposed amphi-guinean species with an integrative molecular and morphological approach. This region holds enormous amounts of mineral wealth and vast hydro-power potential, and projects to exploit these resources are in development. A more accurate depiction of freshwater biodiversity in the region will allow researchers, conservationists and policy makers to incorporate this knowledge into current and future environmental impact assessments.

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MATERIAL EXAMINED

TU 203311:31, 25.2–67.2 mm SL; Konkouré River drainage, Kombira River, Loguin, north of Linsan; 10.35044, –12.4409; 11 Jan 2013; Armbruster, Bart, Hayes, Friel and Schmidt. TU 203323:14, 18.9–78.2 mm SL; Little Scarcies drainage, Kaba River at Berteya; 10.17669, –11.82355; 11 Jan 2013; Armbruster, Bart, Hayes, Friel and Schmidt. TU 203572:2, 40.9–51.5 mm SL; Little Scarcies drainage, Penselli River, near Ourékaba, on N2; 10.15565, –11.6748; 30 Jan 2013; Armbruster, Bart, Hayes, Friel and Schmidt. ABS 45:31, 35.4–58.0 mm SL; Little Scarcies drainage, Kaba River at Kouloundala; 10.10, –11.49; 6 Apr 2003; Samoura and others. FP03-82:64, 15.6–37.5 mm SL; Senegal River drainage, Bafing River at Tolo dam; 10.53448, –12.13813; 19 Jan 2003; Diallo, Fermon and Ballard. FP03-86:150, 34.2–52.6 mm SL; Konkouré River drainage, Karaka River, Tamagaly (road Mamou-Kindia); 10.30787, –12.28930; 19 Jan 2003; Diallo, Fermon and Ballard.

ORCID

Ray C. Schmidt  <https://orcid.org/0000-0002-3106-7908>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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