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Two New Species of Suckermouth Catfishes (Mochokidae: *Chiloglanis*) from Upper Guinean Forest Streams in West Africa

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Suckermouth catfishes of the genus *Chiloglanis* are found throughout tropical Africa. Recent studies highlighted the diversity within this genus remains incompletely documented and nearly 20 new species have been described in the past ten years. Here we describe two new species of *Chiloglanis* from streams in the Upper Guinean Forest. *Chiloglanis fortuitus*, new species, is only known from one specimen collected in the St. John River drainage in Liberia and is readily distinguished from other species of *Chiloglanis* by the number of mandibular teeth and the length of the barbels associated with the oral disc. *Chiloglanis frodobagginsi*, new species, from the upper Niger River was previously considered to be a disjunct population of *C. micropogon*. A combination of several characters diagnoses *C. frodobagginsi*, new species, from topotypic *C. micropogon* in the Lualaba River (Congo River basin) and from Central African populations of *Chiloglanis* cf. *micropogon* in the Benue, Ndian, and Cross River drainages. The biogeographical implications of the recognition of *C. frodobagginsi*, new species, the likelihood of finding additional diversity in the streams of the Upper Guinean Forests, and the taxonomy of *C. micropogon* and *C. batesii* are also discussed.

THERE are currently 63 species of suckermouth catfishes in the genus *Chiloglanis* (Mochokidae) generally associated with flowing waters throughout tropical Africa (Fricke et al., 2022). Several species were described in recent years (Friel and Vigliotta, 2011; Schmidt et al., 2015, 2017; Schmidt and Barrientos, 2019; Kashindye et al., 2021) and many more taxa remain to be formally described (Morris et al., 2016; Chakona et al., 2018; Watson, 2020; Ward, 2021). Though superficially similar in morphology, these species have many informative diagnostic characters associated with their teeth, oral disc morphology, barbels, and spine and fin-ray lengths. Thus, many species originally considered to be widely distributed can clearly be separated into different species by carefully examining these characters.

This research on the Upper Guinean species of *Chiloglanis* started by looking at the morphological and molecular variation within the previously reported widespread species *Chiloglanis occidentalis* in streams of the Upper Guinean Forest. A molecular analysis revealed the presence of distinct lineages/species within *C. occidentalis*, many of which were endemic to individual river basins (Schmidt et al., 2016). These species broadly formed two groups: one group with generally shorter dorsal spines, pectoral spines, and maxillary barbels, and the other with longer dorsal and pectoral spines, and longer maxillary barbels. Within the region, endemic species belonging to both groups co-occur (sympatry) in several drainages in southeastern Guinea, seemingly using different microhabitats. The same study also showed that populations of another species, *C.* aff. *micropogon*, in the upper Niger River drainage in Guinea were genetically distinct from topotypic populations of *C. micropogon* in the Lualaba River (Congo River drainage) with 3.6% divergence in cytochrome *b* and 6.2% divergence in growth hormone intron 2 (Schmidt et al., 2016). In another paper on the diversity of *Chiloglanis* in the Upper Guinean Forests, when examining and selecting the type series for *C. tweddlei*, one specimen clearly stood out morphologically (Schmidt et al., 2017). This specimen superficially resembled members of the group with shorter spines and barbels, but it had more mandibular teeth than any other species of *Chiloglanis* in the region.

The present study aimed to examine the morphological variation among populations of *C. micropogon* and *C.* aff. *micropogon* to determine if the populations in the upper Niger River deserved specific recognition. Further, the unique specimen collected in the St. John River drainage was re-examined and the presence of other specimens of this unique morphotype in ichthyological collections investigated. The results of this study support the recognition of these two populations as distinct species of *Chiloglanis* which are described herein: *C. frodobagginsi*, new species, from the upper Niger River previously identified as *C.* aff. *micropogon*, and *C. fortuitus*, new species, from the St. John River drainage. We also discuss the variation within populations of *C. micropogon* in Central Africa and highlight areas where further collection efforts are needed.

MATERIALS AND METHODS

Specimens of *Chiloglanis* and other taxa were collected during several expeditions in Guinea and Liberia. Three of these

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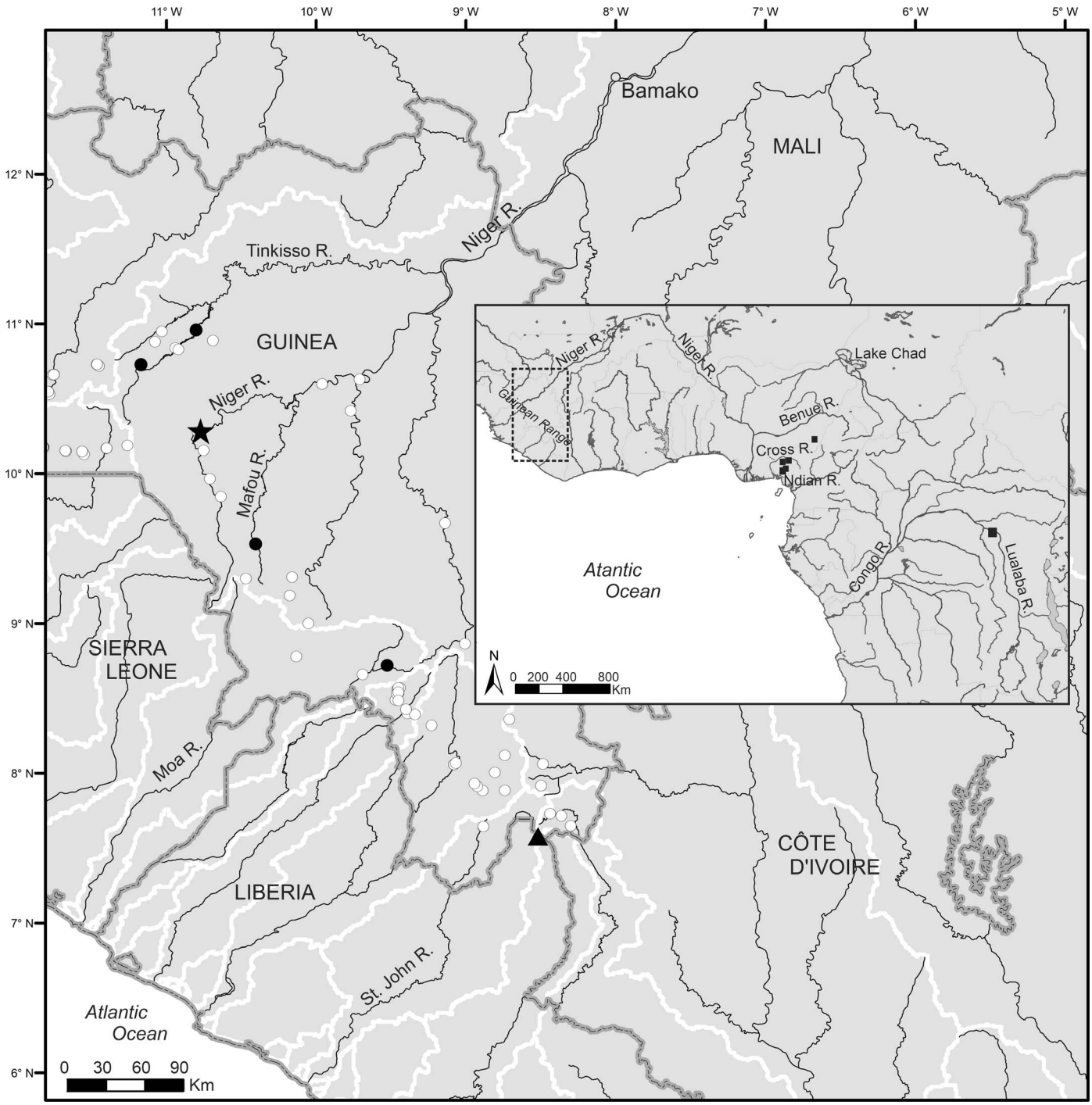

Fig. 1. Localities of species of *Chiloglanis* discussed in this study. Rivers of the Upper Guinean Forests enlarged from outlined region in the inset map of West and Central Africa. River drainages outlined in white lines. White circles are localities where no *Chiloglanis* were collected. Locations of *Chiloglanis frodobagginsi* (black circles), holotype of *C. frodobagginsi* (black star), type locality of *Chiloglanis fortuitus* (black triangle), and comparative *Chiloglanis micropogon* and *Chiloglanis* cf. *micropogon* (black squares).

expeditions occurred during 2003, and the most recent collections took place in 2012 (Liberia) and 2013 (Guinea; Fig. 1). Specimens from these expeditions are cataloged at several institutions with the bulk of the material residing in AMNH, AUM, CUMV, SAIAB, and TU (acronyms according to Sabaj, 2020). Comparative material from the Lualaba River (type locality of *C. micropogon*) and populations of *Chiloglanis* cf. *micropogon* in the Benue River, Cross River, and Ndian River drainages were also included in the analysis. Measurements were taken to 0.1 mm with a digital caliper and a stereo microscope equipped with an ocular micrometer. Morphometric measurements and meristic counts follow Schmidt et al. (2017) modified from Skelton and White (1980) and Friel and Vigliotta (2011). The holotype of *C. micropogon* was examined during a previous study, but a full suite of measurements was not collected. Sex of type

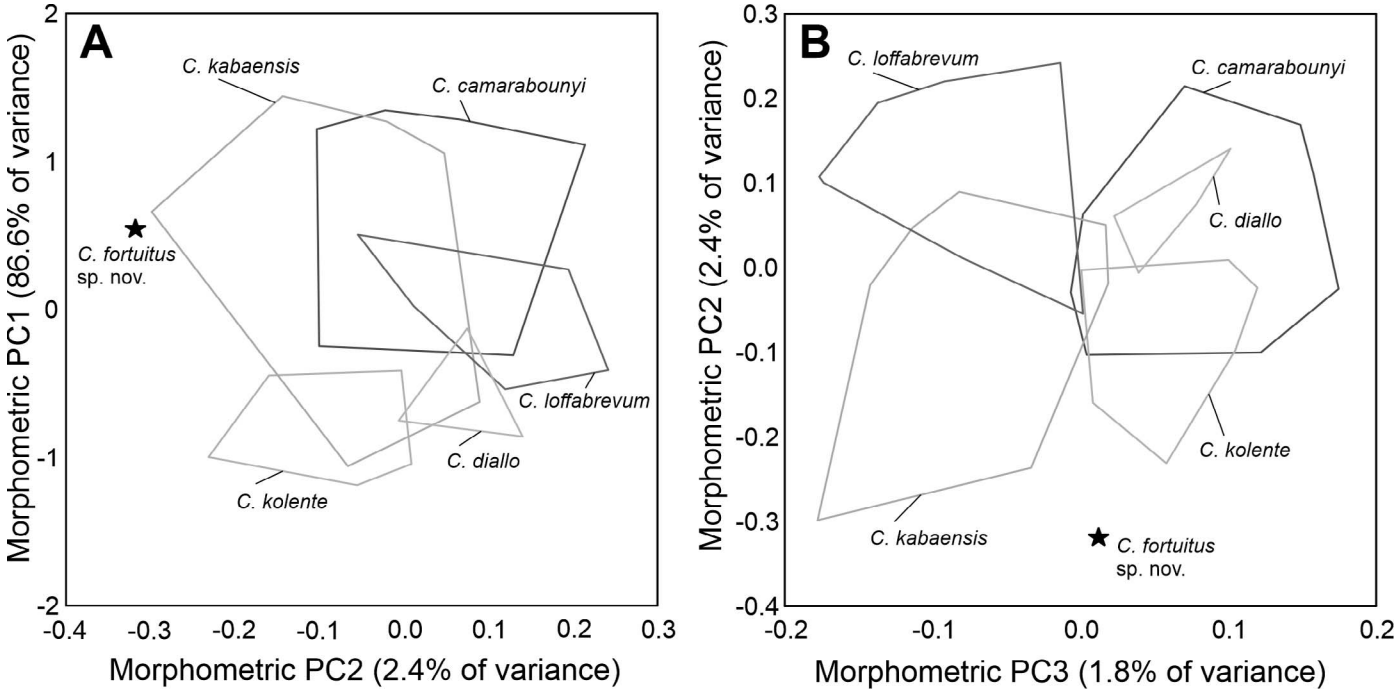

Fig. 2. Plots of PC1 to PC2 (A) and PC2 to PC3 (B) from principal component analysis of 45 log-transformed measurements from 114 specimens of the short-spine taxa from the Upper Guinean Forests. Holotype of *Chiloglanis fortuitus* denoted by star.

specimens was determined by external examination of genital papillae following Friel and Vigliotta (2011). Measurements collected from the unique specimen from the St. John River drainage were included with the measurements from the short-spine taxa obtained in a previous study (Schmidt et al., 2017). A principal component analysis (PCA) using the covariance matrix of log-transformed measurements and descriptive statistics was completed in MYSTAT (SYSTAT Software Inc.). Body shape variation within principal components strongly correlated to size for populations of *C. micropogon* (e.g., PC1) was assessed through reduced-major axis (RMA) regression lines in the SMATR package in R (Warton et al., 2006).

RESULTS

***Morphological comparisons of populations of* Chiloglanis.**—A PCA of 45 morphometric measurements of *C. fortuitus*, new species, and 113 specimens of short-spine taxa shows *C. fortuitus*, new species, as distinct from the other taxa in the region (Fig. 2). Premaxillary tooth length and the length of the maxillary, medial, and lateral mandibular barbels contribute to the variation observed in PC2. These barbels are longer in *C. fortuitus*, new species, than in the other short-spine taxa, although with just one specimen of *C. fortuitus*, new species, it isn't possible to investigate these characters further.

The morphological comparison of *C. frodobagginsi*, new species, and *C. micropogon* included 35 measurements and eight meristics from 50 specimens. Measurements shown to be sexually dimorphic (e.g., fin lengths and length of post-cleithral process) were not included in the analysis (Supplemental Table A; see Data Accessibility). Plots of principal components 1 and 2 clearly separate *C. frodobagginsi*, new species, from *C. micropogon* in the Lualaba River (Fig. 3A). Populations of *Chiloglanis* cf. *micropogon* from the Benue, Ndian, and Cross River drainages are also distinct from topotypic *C. micropogon* and *C. frodobagginsi*, new species. Occipital shield width, mandibular tooth row width, maxillary barbel length, and distance between dorsal and adipose fins contribute to variation observed in PC2 (Supplemental Table B; see Data Accessibility). In plots of PC2 to PC3, populations of *C. micropogon* from the Lualaba River and *C. frodobagginsi*, new species, are still distinct (Fig. 3B). The populations in the Moa River are also largely distinct from Niger River *C. frodobagginsi*, new species (Fig. 3A, B). These two specimens are only 19.4 and 20.1 mm SL so additional specimens from this population are needed to better understand the variation observed.

The first principal component was positively correlated with standard length (Pearson's correlation = 0.99). The RMA regression of PC1 to the log-transformed standard length (not shown) shows that the slopes of populations of *Chiloglanis* cf. *micropogon*, *C. micropogon*, and *C. frodobagginsi*, new species, are equal ($P = 0.14$) and that there is no difference in the elevation (i.e., the y-intercept) for each group ($P = 0.39$). When examining just the population of *C. micropogon* and *C. frodobagginsi*, new species, there is a difference in the elevation between the two ($P = 0.04$). Examining individual measurements and counts does give a sense of how the allometric trajectory of some of these traits differ in *C. frodobagginsi*, new species, and *C. micropogon* (Supplemental Fig. A; see Data Accessibility). The distance between the dorsal fin and adipose fin as a percentage of standard length has equal slopes ($P = 0.164$), but they have significantly different elevations ($P = 0.0036$; Fig. 4A). The number of premaxillary teeth plotted against log-transformed standard length for each species also clearly shows that these two species are distinct (Fig. 4B).

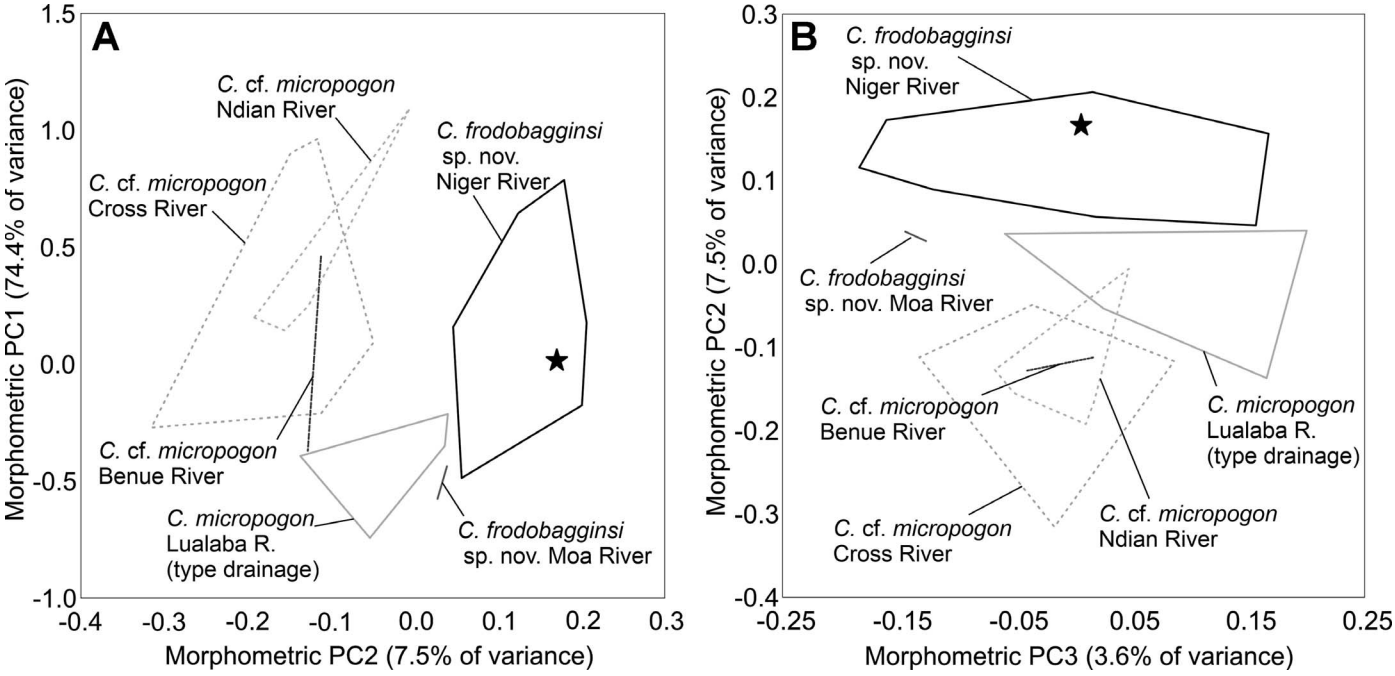

Fig. 3. Plots of PC1 to PC2 from principal component analysis of 35 log-transformed measurements from 47 specimens (A) and PC2 to PC3 (B). The holotype of *Chiloglanis frodobagginsi* is noted by the black star. Refer to Supplemental Table B (see Data Accessibility) for component loading values.

***Chiloglanis fortuitus*, Schmidt, Bragança, and Tweddle, new species**

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Figure 5, Table 1

Holotype.—SAIAB 202292, 35.0 mm SL, Liberia, St. John River drainage, Nimba County, Dayea River, above Yekepa, 7.579333°N, 8.516889°W, D. Tweddle, 30 March 2012.

Diagnosis.—*Chiloglanis fortuitus* is distinguished from all known species of *Chiloglanis*, including all species in the Upper Guinean Forest, except *C. disneyi*, *C. microps*, *C. niger*, and *C. orthodontus*, in having 18 mandibular teeth in the functional row (vs. 6–15 teeth; Table 1). *Chiloglanis fortuitus* is easily distinguished from *C. disneyi*, *C. microps*, and *C. niger* in having longer mandibular barbels whereas these are absent or reduced in the latter species. *Chiloglanis fortuitus* is distinguished from *C. orthodontus* in having a more robust

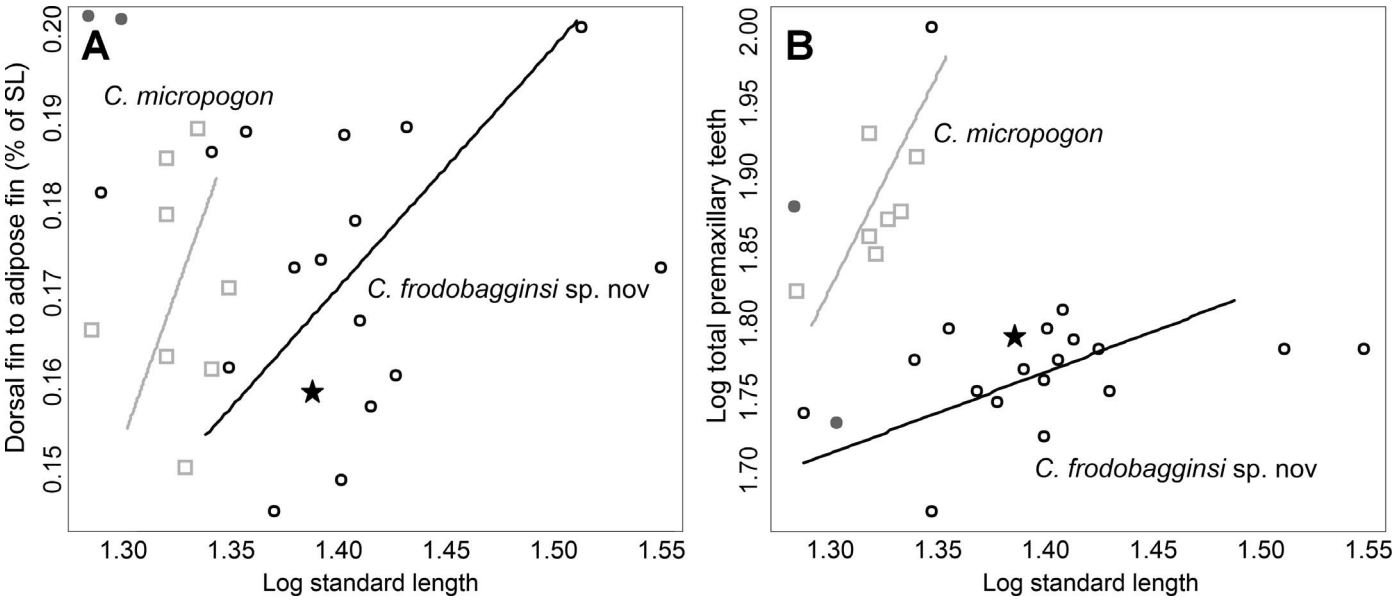

Fig. 4. Reduced-major axis regression of distance from dorsal fin to adipose fin (as a percentage of standard length) on log-transformed standard length (A). Reduced-major axis regression of log-transformed total number of premaxillary teeth on log-transformed standard length (B). *Chiloglanis frodobagginsi* (open circle), *Chiloglanis frodobagginsi* from the Moa River (filled circle), *Chiloglanis micropogon* (open square), and holotype of *C. frodobagginsi* (black star).

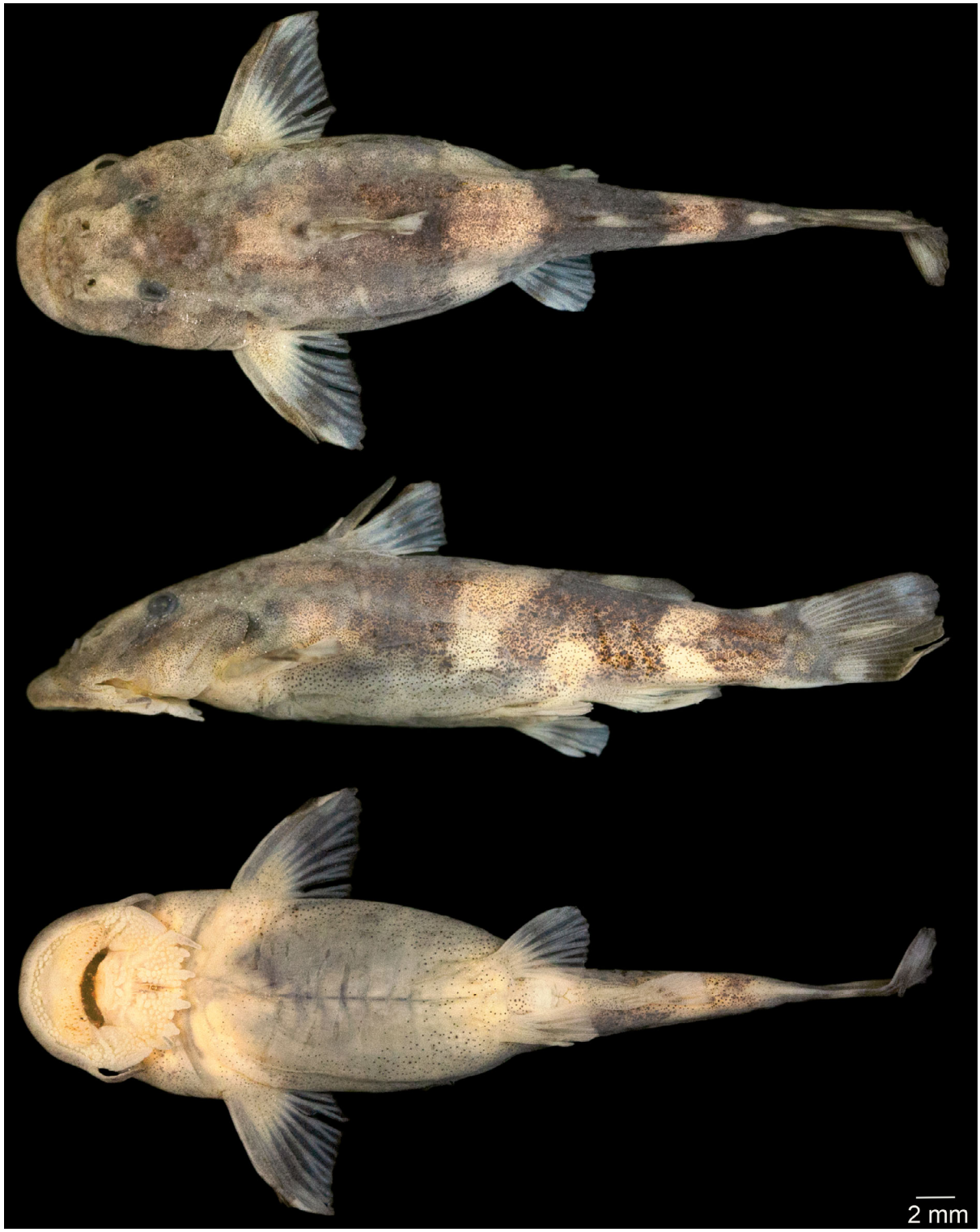

Fig. 5. Dorsal, lateral, and ventral views of the holotype of *Chiloglanis fortuitus*, SAIAB 202292, 35.0 mm SL, Liberia, St. John River drainage, Nimba County, Dayea River, above Yekepa, 7.579333°N, 8.516889°W. Scale bar equals 2 mm. Photographs by P. H. N. Bragança.

oral disc and its length equal to its width versus length much shorter than width (Friel and Vigliotta, 2011). *Chiloglanis fortuitus* is further distinguished from *C. orthodontus* in having a longer dorsal spine (12.8 versus 4.1–7.8 % SL) and shorter maxillary barbels (7.2 versus 9.4–14.8 % SL).

Description.—Morphometric measurements and meristics for holotype summarized in Table 1. Dorsal, lateral, and ventral views (Fig. 5) illustrate body shape, fin shape and placement, oral disc size and shape, and maxillary and mandibular barbel lengths.

Moderate-sized *Chiloglanis*, maximum standard length observed 35.0 mm in one male specimen. Body dorsally depressed anteriorly and laterally compressed posteriorly. Pre-dorsal convex, sloping ventrally towards posterior nares, pre-orbital convex. Post-dorsal body sloping ventrally to-

Table 1. Morphometric measurements and meristics for holotype of *Chiloglanis fortuitus*. Standard length expressed in mm. All other measurements expressed in percent SL.

	Holotype
Morphometrics	
Standard length (mm)	35.0
Head length	32.0
Head depth (maximum)	20.4
Body depth at anus	17.0
Occipital shield width (minimum)	4.3
Prepectoral length	32.0
Predorsal length	43.4
Prepelvic length	62.6
Preanal length	75.7
Eye diameter (horizontal)	4.6
Orbital interspace	7.6
Snout length	22.3
Premaxillary tooth-patch width	13.3
Premaxillary tooth-patch length	3.4
Mandibular tooth row width	4.0
Anterior nares interspace	5.0
Posterior nares interspace	5.0
Maxillary barbel length	7.2
Medial mandibular barbel length	3.0
Lateral mandibular barbel length	5.1
Mouth width	10.3
Oral disc width	21.1
Oral disc length	21.4
Upper lip length	5.3
Lower lip length	9.7
Pectoral-spine length	16.6
Pectoral-fin length	18.3
Width at pectoral-fin insertion	26.6
Length of postcleithral process	11.8
Pelvic-fin length	11.4
Depth at dorsal-fin insertion	23.4
Dorsal-spine length	12.8
Dorsal-fin length (longest ray)	14.3
Dorsal-fin base length	10.7
Dorsal fin to adipose-fin length	18.3
Adipose-fin base length	17.1
Adipose fin to caudal-ped length	12.0
Adipose-fin height	2.9
Anal-fin length (longest ray)	11.4
Anal-fin base length	7.8
Lower caudal-fin lobe length	24.0
Upper caudal-fin lobe length	19.4
Fork length	15.2
Caudal-peduncle depth (maximum)	10.5
Caudal-peduncle length	17.1
Meristics	
Mandibular tooth rows	1
Mandibular tooth count (total)	18
Mandibular tooth count (functional anterior row)	18
Mandibular tooth count (posterior replacement row)	—
Primary premaxillary teeth (total)	72
Pectoral-fin count	I, 7
Pelvic-fin count	i, 6
Dorsal-fin count	II, 4
Anal-fin count	iii, 6
Caudal-fin count	i, 7, 8, i

wards caudal fin. Post-anal profile concave, pre-anal profile horizontal. Small unculiferous tubercles present on body, concentrations of tubercles higher near head. Lateral line complete, arising at level of orbit and sloping ventrally to midlateral alongside of body towards caudal peduncle. Urogenital papillae presumed sexually dimorphic; males with elongated urogenital papilla.

Head depressed. Gill membranes broadly united. Gill openings restricted, opening near pectoral-fin origin to horizontal level of orbit. Occipital-nuchal shield covered and visible through skin. Eye moderate in size, located post mid-head length, horizontal axis longest, without free margins. Anterior and posterior nares equidistant, positioned mid-snout. Naris with raised rims, posterior naris with elongated anterior flap.

Mouth inferior, upper and lower lips united to form oral disc. Oral disc moderate in size, length equaling width and covered in papillae. Barbels in three pairs; maxillary barbel originating from posterolateral region of disc, unbranched, moderate in length, 7% of SL. Lateral and medial mandibular barbels moderate, incorporated into lower lip and positioned on both sides of midline cleft on posterior margin of oral disc. Lateral barbel 5% of SL, less than twice length of medial barbel. Primary maxillary teeth "S" shaped with exposed brown tips. 72 teeth in four scattered rows on ovoid tooth pads. Secondary premaxillary teeth scattered on posterior surface of premaxillae. Tertiary teeth small and needle-like, near midline of dorsal edge of tooth plate. Mandibular teeth in one to two rows, "S" shaped and grouped near midline. Functional (anterior) row with 18 brown-tipped teeth.

Dorsal-fin origin just posterior to anterior third of body. Dorsal fin with small spinelet, spine, and four rays. Dorsal spine moderate to short in length, reaching 13% of SL. Adipose fin medium length, reaching 17% of SL; margin convex with small notch posteriorly. Caudal fin forked with rounded lobes, lower lobe longer than upper lobe, count i, 7, 8, i. Anal-fin origin posterior to origin of adipose fin, margin convex, count iii, 6. Pelvic-fin origin at vertical between dorsal and adipose fins, margin convex, reaching beyond anal-fin origin, count i, 6. Pectoral fin with smooth spine, reaching 16% of SL, count I, 7. Postcleithral process in holotype short and pointed.

Coloration.—Coloration of preserved specimen in Figure 5. In dorsal view, dark brown with mottled areas of medium brown. Lighter areas between nares and orbits, at origin of dorsal fin, at origin and terminus of adipose fin, and at caudal peduncle. In lateral view, specimen with yellow-buff color with overlying medium and dark brown blotches. Dark area more prevalent dorsal to midline, extending ventrally at origins of pelvic and anal fins. Dark brown melanophores scattered across body, more readily visible ventral to midline, prominent on sides of belly. Ventral surface yellow-buff colored with few melanophores scattered near pelvic and anal fins. Oral disc and barbels cream colored.

Pectoral and dorsal spines pigmented distally, rays cream to translucent. Dorsal base of pectoral fin lightly marked by triangular area of dark brown melanophores, band of melanophores at mid-length. Dorsal fin with area of melanophores near base and mid-length. Anal fin with melanophores at base and mid-length. Pelvic fin cream with few melanophores at base and band at mid-length. Adipose fin cream to translucent with dark brown markings from

region just posterior of origin to its posterior third. Caudal fin cream to translucent with dark brown areas near base, mid-length, and distal end on upper and lower lobes; lighter areas forming circular marking on upper and lower lobes.

Etymology.—The specific epithet is "fortuitus," referring to the fortuitous aspect of collecting this one specimen at the type locality. The collector, D. Tweddle, sampled fishes at 36 localities in the upper St. John River drainage in Liberia and collected 69 specimens of *Chiloglanis* at ten of these localities. Additionally, the lot that contained *C. fortuitus* was one of the three lots borrowed by the lead author to aid with the description of *C. tweddlei* (Schmidt et al., 2017). The discovery and formal description of *C. fortuitus* is fortuitous in several aspects.

Distribution.—*Chiloglanis fortuitus* is only known from the type locality in the Dayea River above Yekepa in Nimba County, Liberia (Supplemental Fig. B; see Data Accessibility). The site looked natural, yet it had been severely impacted many years earlier by the iron ore mine upstream. It was fast flowing, of uniform depth with a bottom of gravel with small rocks, with very little natural structure (e.g., woody debris and large boulders) likely due to previous mining activities. It is interesting that this species was not collected at the other ten localities in the region that contained *C. tweddlei*. As with other members of *Chiloglanis* that are found in streams in the Upper Guinea Forests, when two species co-occur within a drainage, they usually utilize different microhabitats (Schmidt et al., 2017). Additional collection efforts in the upper St. John River drainage in Guinea and Liberia may yield additional specimens and populations of *C. fortuitus*.

Remarks.—Species descriptions based on a single specimen are not ideal though in this case it is warranted. This species is morphologically distinct from congeners in the region (Fig. 2), and the number of mandibular teeth and morphology of the oral disc and barbels, characters used in the taxonomy of species of *Chiloglanis*, clearly separate it from all other known species of *Chiloglanis*. In sampling fishes at 36 localities, the collector was only able to get one specimen of *C. fortuitus*. Another lot from the St. John River drainage, USNM 193949, collected in the 1950s, contained 17 specimens all of which were determined to be *C. tweddlei*. This species is seemingly rare within the drainage and we don't know when, or even if, additional specimens of *C. fortuitus* will be collected. Additionally, this area is under intense pressures from the mining industry and all species present face an uncertain future. Indeed, the type specimen was collected in a stream that had previously been disturbed by iron ore mining. Formally describing this species is an important step in recognizing and conserving the freshwater biodiversity in the Upper Guinean Forests.

Chiloglanis fortuitus resembles species of *Chiloglanis* that are in the short-spine group referenced in Schmidt et al. (2016, 2017). The discovery of this new species within the St. John River suggests that additional species of *Chiloglanis*, and other taxa, remain to be discovered and described from the region. This is especially likely for rivers in the region (e.g., Rokel, Jong, Sewa, and Mano) where collections of freshwater taxa are still lacking. While collecting this specimen was fortuitous, depositing the specimen and the others collected during an environmental impact assessment into natural history collections is what allowed this species to be discovered and described. Other new species have been collected and formerly described from similar surveys in the region (Pezold et al., 2016, 2020). We encourage practitioners in this field to continue the practice of depositing specimens collected during assessments in natural history collections so that the specimens will be available to researchers.

Chiloglanis frodobagginsi, Schmidt, Friel, Bart, and Pezold, new species

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Figure 6, Table 2

Chiloglanis batesii.—Paugy and Roberts, 1992 (in part): 502–511; Paugy and Roberts, 2003 (in part): 197–207.

Chiloglanis micropogon.—Daget, 1954 (in part): 307–308; Daget, 1959 (in part): 682–683; Daget, 1962 (in part): 115.

Chiloglanis cf. *micropogon*.—Schmidt et al., 2016: 201–204.

Chiloglanis sp. aff. *micropogon*.—Schmidt et al., 2017: 301–336.

Holotype.—TU 203552, 24.1 mm SL, Guinea, Niger River, North of Faranah, on road N29, 10.28382°N, 10.76925°W, 2013 Guinea expedition team, 29 January 2013.

Paratypes.—AMNH 263794, 4, 23.1–25.7 mm SL, AUM 59751, 8, CUMV 97679, 8, TU 203527, 4, 24.8–25.3 mm SL, Guinea, Niger River drainage, Mafou River, on road N2 ~80 km South of Faranah, 9.53072°N, 10.40199°W, 2013 Guinea expedition team, 28 January 2013; AUM 59554, 19, CUMV 97678, 18, TU 203348, 19, 20.6–24.1 mm SL, FLMNH 249106, 5, 20.0–24.6 mm SL, Guinea, Niger River drainage, Tinkisso River, below Tinkisso Dam, 10.72793°N, 11.16855°W, 2013 Guinea expedition team, 12 January 2013; CUMV 97680, 6, TU 204171, 4, 19.2–24.3 mm SL, collected with holotype; SAIAB 203746, 9, 19.9–23.3 mm SL, USNM 437542, 9, 22.1–38.1 mm SL, Niger River drainage, Tinkisso River, at dam, 10.72°N 11.17°W, B. Samoura and others, 7 April 2003; TU 204157, 1, 20.4 mm SL, Guinea, Niger River drainage, Tinkisso River, at dam, 10.72793°N 11.16855°W, F. Pezold and others, 18 January 2003.

Non-type material examined.—AMNH 264623, 1, 26.3 mm SL, Guinea, Niger River drainage, Tinkisso River, at Toumania, 10.57902°N, 10.47273°W, F. Pezold and others, 16 May 2003; CUMV 98653, 1, 19.4 mm SL, TU 204170, 1, 20.1 mm SL, Guinea, Moa River drainage, Masseni River, about 3 miles north of Konesseridou, 8.7204°N, 9.52436°W, 2013 Guinea expedition team, 26 January 2013; MRAC 2016.029.P.52-63, 12, 20.0–27.0 mm SL, Guinea, Niger River drainage, Tinkisso River, at Bissikrima, 10.83°N, 10.92°W, B. Samoura and others, 8 April 2003; USNM 437545, 5, 22.2–23.5 mm SL, Guinea, Niger River drainage, Niger River, north of Faranah, F. Pezold and others, 26 May 2003.

Diagnosis.—*Chiloglanis frodobagginsi* is distinguished from all known species of *Chiloglanis* in the Upper Guinean Forests, and most of the other described species (except *C. disneyi*, *C. harbinger*, *C. marlieri*, *C. micropogon*, *C. microps*, *C. mongoensis*, and *C. niger*) by the very reduced, or absent, mandibular barbels on the oral disc. *Chiloglanis frodobagginsi* can be distinguished from *C. disneyi*, *C. harbinger*, *C. marlieri*, *C. microps*, *C. mongoensis*, and *C. niger* in having fewer

Fig. 6. Dorsal, lateral, and ventral views of *Chiloglanis frodobagginsi* holotype, TU 203552, 24.1 mm SL, Guinea, Niger River drainage, Niger River, North of Faranah, on road N29, 10.28382°N, 10.76925°W. Scale bar equals 2 mm. Photographs by S. Raredon.

mandibular teeth in one row (10–12 versus 16–20, 26–30, 26–28, 16–18, 28, and 16–20 respectively). *Chiloglanis frodobagginsi* is distinguished from *C. batesii* in having two prominent papillae on the roof of the oral cavity; versus the absence of papillae in *C. batesii*. This species is further distinguished from *C. batesii* in having shorter and more blunt mandibular teeth arranged in bunched rows; versus sharper, more elongate, and disordered mandibular teeth. *Chiloglanis frodobagginsi* also has a fleshy unpapillated ridge posterior to the mandibular teeth versus several large papillae in *C. batesii* (Friel and Vigliotta, 2011).

A unique combination of characters distinguishes *C. frodobagginsi* from the closely related *C. micropogon* and *C.* cf. *micropogon* from Central Africa. As compared to *C. micropogon* from the Lualaba River, *C. frodobagginsi* has a larger eye diameter (4.2–6.5 versus 4.7–5.5 % SL; Supplemen-

Table 2. Morphometric measurements and meristics for *Chiloglanis frodobagginsi* ($n = 22$; holotype and 21 paratypes) and topotypic *Chiloglanis micropogon* ($n = 10$). Standard length expressed in mm. All other measurements expressed in percent SL. Meristic data for holotype are identified by an asterisk (*).

	Chiloglanis frodobagginsi, new species			*Chiloglanis micropogon*	
	Holotype	Range	Mean ± %SD	Range	Mean ± %SD
Morphometrics					
Standard length (mm)	24.1	19.2–38.1		18.6–22.0	
Head length	33.6	30.9–38.1	35.1±1.9	33.2–35.9	34.5±1.0
Head depth (maximum)	17.2	14.1–17.6	16.0±1.0	15.4–17.8	16.3±0.7
Body depth at anus	13.0	12.3–16.0	14.0±0.9	12.9–14.9	14.1±0.7
Occipital shield width (minimum)	3.3	3.0–4.0	3.4±0.3	3.2–3.8	3.6±0.2
Prepectoral length	33.2	30.5–36.7	33.7±1.7	32.8–36.4	34.7±1.2
Predorsal length	43.6	40.8–46.0	43.7±1.6	43.0–47.1	44.7±1.3
Prepelvic length	58.9	56.8–63.5	60.3±1.5	56.8–63.7	59.2±2.0
Preanal length	75.1	71.4–78.5	75.2±1.7	71.0–76.8	73.8±1.7
Eye diameter (horizontal)	6.1	4.2–6.5	5.4±0.6	4.7–5.5	5.1±0.2
Orbital interspace	7.7	6.5–8.7	7.7±0.6	6.7–9.2	7.7±0.7
Snout length	22.8	20.8–24.7	22.4±1.1	20.9–22.3	21.7±0.5
Premaxillary tooth-patch width	19.6	15.6–20.5	18.5±1.1	17.2–19.7	18.4±0.8
Premaxillary tooth-patch length	3.9	3.0–4.3	3.6±0.4	3.2–4.6	3.7±0.4
Mandibular tooth row width	2.2	1.6–2.8	2.1±0.3	2.4–3.1	2.8±0.2
Anterior nares interspace	5.0	4.6–5.6	5.1±0.2	4.7–5.6	5.2±0.3
Posterior nares interspace	5.0	3.2–5.6	4.8±0.5	4.2–5.3	4.7±0.3
Maxillary barbel length	6.0	3.8–7.2	5.9±1.1	3.4–6.5	4.7±0.8
Mouth width	12.2	10.0–12.9	11.5±0.9	11.6–12.9	12.2±0.5
Oral disc width	27.7	22.8–29.4	26.2±1.5	23.9–25.9	25.2±0.7
Oral disc length	22.7	20.6–25.3	23.0±1.3	22.7–34.5	25.0±3.4
Upper lip length	6.1	4.3–7.3	5.8±0.9	5.1–6.4	5.5±0.4
Lower lip length	10.8	9.6–12.5	11.1±0.7	8.7–12.0	10.9±0.9
Pectoral-spine length	14.9	10.6–15.6	13.9±1.3	13.1–17.0	15.2±1.4
Pectoral-fin length	18.7	16.0–18.7	17.5±0.8	16.0–18.9	17.4±0.9
Width at pectoral-fin insertion	27.0	26.2–29.0	27.4±0.9	25.4–29.0	26.8±1.2
Length of postcleithral process	12.7	8.8–14.7	10.8±1.6	10.3–12.1	11.0±0.6
Pelvic-fin length	14.7	11.9–15.0	13.7±0.7	11.0–16.5	13.9±1.5
Depth at dorsal-fin insertion	17.7	12.4–18.5	20.3±1.2	15.2–19.0	16.8±1.1
Dorsal-spine length	11.3	10.2–13.3	11.8±0.9	9.6–12.6	11.0±1.1
Dorsal-fin length (longest ray)	15.5	12.6–16.7	14.7±1.2	12.9–16.5	14.3±1.1
Dorsal-fin base length	12.2	11.4–13.4	12.6±0.5	11.3–13.8	12.4±0.9
Dorsal fin to adipose-fin length	15.8	14.4–21.5	17.3±1.8	14.9–18.8	16.9±1.2
Adipose-fin base length	18.8	14.0–19.6	17.0±1.6	12.9–16.4	15.1±1.0
Adipose fin to caudal-ped length	12.4	11.2–13.6	12.5±0.7	12.2–15.8	13.9±1.0
Adipose-fin height	4.1	2.8–4.9	3.7±0.6	3.1–4.2	3.5±0.4
Anal-fin length (longest ray)	15.5	11.9–15.9	13.7±1.1	12.9–15.9	14.2±0.9
Anal-fin base length	10.0	8.0–10.8	9.5±0.7	9.7–12.7	11.2±1.2
Lower caudal-fin lobe length	27.7	24.0–29.3	26.5±1.3	24.9–29.8	27.7±1.7
Upper caudal-fin lobe length	24.1	21.2–26.0	23.3±1.1	22.7–28.4	25.7±1.9
Fork length	16.9	13.1–17.4	15.2±1.1	13.6–16.2	14.7±0.8
Caudal-peduncle depth (maximum)	10.0	9.2–10.8	10.0±0.4	9.1–10.5	9.8±0.4
Caudal-peduncle length	15.8	13.7–17.1	15.8±1.0	15.4–17.5	16.5±0.7
Meristics					
Mandibular tooth rows		1–2; 1*		1–2	
Mandibular tooth count (total)		10–24; 12*		10–33	
Mandibular tooth count (functional anterior row)		9–13; 12*		10–12	
Mandibular tooth count (posterior replacement row)		8–12		4–11	
Primary premaxillary teeth (total)		36–70; 63*		62–103	
Pectoral-fin count		I, 8(8); I, 9*(14)		I, 8(3); I, 9(7)	
Pelvic-fin count		i, 6*(22)		i, 6(10)	
Dorsal-fin count		II, 5(7); II, 6*(15)		II, 5(1); II, 6(8); II, 7(1)	
Anal-fin count		iii, 5(6); iii, 6*(13); iii, 7(3)		iii, 5(2); iii, 6(7); iii, 7(1)	
Caudal-fin count		i, 7, 8, i*(22)		i, 7, 8, i(10)	

tal Fig. A; see Data Accessibility), longer maxillary barbels (3.8–7.2 versus 3.4–6.5 % SL; Supplemental Fig. A; see Data Accessibility), a narrower mandibular tooth row (1.6–2.8 versus 2.4–3.1 % SL; Supplemental Fig. A; see Data Accessibility), a longer distance between dorsal fin and adipose fin (14.4–21.5 versus 14.9–18.8 % SL; Fig. 4A), and a shorter anal-fin base length (8.0–10.8 versus 9.7–12.7 % SL; Supplemental Fig. A; see Data Accessibility). *Chiloglanis frodobagginsi* is further distinguished from *C. micropogon* in having fewer premaxillary teeth (36–70 versus 62–103) scattered in three rows versus four (Fig. 4B; Table 2). While the ranges of these measurements and counts overlap, these distinctions hold true when comparing similar sized species (Fig. 4; Supplemental Fig. A; see Data Accessibility). Compared to *Chiloglani*s cf. *micropogon* from the Benue, Ndian, and Cross River basins *Chiloglanis frodobagginsi* has a narrower occipital shield (3.0–4.0 versus 4.0–5.4 % SL), a shorter dorsal fin to adipose fin distance (14.5–21.5 versus 19.3–24.2), and a narrower mandibular tooth row (1.6–2.8 versus 1.8–3.2 % SL).

Description.—Morphometric measurements and meristics for holotype and 21 paratypes summarized in Table 2. Dorsal, lateral, and ventral views (Fig. 6) illustrate body shape, fin shape and placement, oral disc size and shape, and maxillary and mandibular barbel lengths.

Small to moderate-sized *Chiloglanis*, maximum standard length 38.1 mm. Body dorsally depressed anteriorly and laterally compressed posteriorly. Pre-dorsal convex, sloping ventrally towards posterior nares, pre-orbital convex, sharply angling towards tip of snout pre-nares. Post-dorsal body sloping ventrally towards caudal fin. Post-anal profile shallowly concave, pre-anal profile horizontal to slightly convex. Small unculiferous tubercles present on body, concentrations of tubercles higher near head. Lateral line complete, arising at dorsal level of orbit and sloping ventrally to midlateral alongside of body towards caudal peduncle. Urogenital papillae sexually dimorphic; males with elongated urogenital papillae, females with reduced papillae, separated from anus by shallow invagination.

Head depressed. Gill membranes broadly united. Gill openings restricted, opening near pectoral-fin origin to horizontal level of mid-orbit. Occipital-nuchal shield covered and visible through skin. Eye moderate in size, located post mid-head length, horizontal axis longest, without free margins. Anterior naris set farther apart than posterior naris, positioned mid-snout. Nares with raised rims, posterior naris with elongated anterior flap.

Mouth inferior, upper and lower lips united to form oral disc. Oral disc moderate in size, slightly wider than long and covered in papillae. Maxillary barbel originating from posterolateral region of disc, unbranched, moderate in length, reaching 7% of SL. Lateral and medial mandibular barbels absent or very reduced. Two prominent papillae on roof of oral cavity. Primary maxillary teeth "S" shaped with exposed brown tips. 36–70 teeth in three scattered rows on ovoid tooth pads. Secondary premaxillary teeth scattered on posterior surface of premaxillae. Tertiary teeth small and needle-like, near midline of dorsal edge of toothplate. Mandibular teeth in one to two rows, curved and bunched near midline. Functional (anterior) row with 12 brown-tipped teeth. Distinct, slightly concave rectangular fleshy ridge posterior to mandibular teeth.

Dorsal-fin origin just posterior to anterior third of body. Dorsal fin with small spinelet, spine, and five to six rays. Dorsal spine medium to short in length, reaching 13% of SL. Adipose fin medium length, reaching 19.6% of SL; margin convex. Caudal fin forked with rounded lobes, lower lobe longer than upper lobe, count i, 7, 8, i, no sexual dimorphism observed in examined specimens. Anal-fin origin posterior to origin of adipose fin, margin convex, count iii, 5–7. Pelvic-fin origin at vertical between dorsal and adipose fin, margins convex, reaching beyond anal-fin origin, count i, 6. Pectoral fin with smooth spine, reaching 15.6% of SL, count I, 8–9. Postcleithral process shorter and bluntly pointed, no sexual dimorphism noted in specimens examined.

Coloration.—Typical coloration of preserved specimens in Figure 6. In dorsal view, specimens medium brown with mottled areas of light brown. Lighter areas on tip of snout anterior to nares, at origin of dorsal fin, at origin and terminus of adipose fin, and on caudal peduncle. White or cream unculiferous tubercles scattered across body, more concentrated near head. In lateral view, specimens with yellow-buff color with overlying medium brown blotches. Dark area more prevalent dorsal to midline, but extending ventrally at origin of pelvic and anal fins. Dark brown melanophores scattered across body, more readily visible ventral to midline, absent on belly. Ventral surface yellow-buff colored with few melanophores scattered near anus and origin of anal fin. Oral disc and barbels cream colored.

Pectoral and dorsal spines pigmented distally and rays cream to translucent. Dorsal base of pectoral fin lightly marked by triangular area of dark brown melanophores, band of melanophores at mid-length. Dorsal fin with area of melanophores near base and mid-length. Anal fin with melanophores at mid-length. Pelvic fin cream with few melanophores at base and band at mid-length. Adipose fin cream to translucent with dark brown markings at origin. Caudal fin cream to translucent with dark brown areas near base and at mid-length.

Etymology.—*Chiloglanis frodobagginsi* is named after another diminutive traveler, Frodo Baggins, a fictional character well known from J. R. R. Tolkien's *The Lord of the Rings* series. Roughly 3,000 miles (4,800 km) separate *C. frodobagginsi* in the upper Niger River drainage and *C. micropogon*, the sister species, found in the Congo River basin. Another seemingly closely related species, *Chiloglanis* cf. *micropogon*, is found in the southern Benue drainage and in several small coastal rivers about 3,000 km from the upper Niger River drainage (e.g., Cross and Ndian Rivers). It is unclear whether these species are descended from a more widespread species, or the result of dispersal from the Congo River basin into the Niger River drainage, via the Benue River, and then up to the headwaters of the Niger River. This was an incredible journey for such a small and seemingly non-vagile fish.

Distribution.—*Chiloglanis frodobagginsi* occurs in the upper Niger River drainage in Guinea and further downstream in the Niger River near Bamako (Fig. 1; Daget, 1959). This species was collected in several tributaries to the Niger River in Guinea and also collected in the upper reaches of the Moa River drainage (Masseni River), a coastal river drainage. Only two specimens were collected in the Moa River drainage and no tissues were retained. Given that most species of

Chiloglanis in the region are restricted to individual river drainages and since the Moa River drainage is on the other (i.e., west) side of the Guinean Range from the Niger River drainage, this population may be a distinct species. For this reason, these specimens were not included in the type material for *C. frodobagginsi*. In the Tinkisso River, *C. frodobagginsi* was collected below the waterfall over small gravel in the middle of the channel. *Chiloglanis waterloti* is also found in the Tinkisso River, but this species is usually associated with woody debris or large rocks.

Remarks.—The affinity between *Chiloglanis frodobagginsi* and *C. micropogon* was first reported in research on fishes in the upper Niger River drainage (Daget, 1954, 1959). The large distance between the populations in the upper Niger River and the Lualaba River (Congo River drainage) warranted further examinations of these specimens (Daget, 1959). Daget sent specimens from the upper Niger River to Max Poll for comparison to those that Poll described as *C. micropogon* from the Congo River drainage (Poll, 1952; Daget, 1959). Poll noted some variation between the different populations, but it wasn't enough to readily distinguish one from the other (Daget, 1959). Daget also noted their diminutive size and rarity relative to the co-occurring specimens of *C. waterloti* (Daget, 1954). Herein we noted another aspect of these specimens that wasn't directly noted: the apparent lack of an elongated upper caudal-fin lobe and an elongate and spatulate postcleithral process in males. An examination of the type specimen of *C. micropogon* and the sketch of the holotype clearly shows an elongated upper caudal-fin lobe (Poll, 1952, fig. 3, page 228). The larger specimens collected in recent expeditions were mostly females, and none of the males collected showed an elongated upper caudal-fin lobe. More specimens of *C. frodobagginsi* are needed to better understand if this species also displays those sexually dimorphic characteristics, or if the lack of sexual differentiation can be a useful trait in distinguishing both species. *Chiloglanis frodobagginsi* is also genetically distinct from *C. micropogon* with a divergence observed of 3.6% in cytochrome *b* and 6.2% in Growth Hormone intron 2 (Schmidt et al., 2016).

Populations of *Chiloglanis* cf. *micropogon* in the Benue, Cross, and Ndian Rivers have only been relatively recently collected (e.g., in the 1970s and 1980s) and were unknown to Daget and Poll at the time of their comparisons of upper Niger and Lualaba River specimens. In examining these specimens, they clearly concur with *C. micropogon*, but also differ in some respects (Fig. 3). Some specimens showed the sexual dimorphism attributed to *C. micropogon* (e.g., an elongated upper caudal-fin lobe and an elongated and spatulate postcleithral process), but most of the specimens examined did not have these traits. Many of these collections and subsequent identifications took place before many of the species in the region were described (Roberts, 1989) and cataloged under superficially similar species names *C. niger* and *C. disneyi*. Additional populations from the Benue and the smaller coastal drainages in Central Africa are needed to fully resolve the relationships within the *C. micropogon* complex.

DISCUSSION

The two new species of *Chiloglanis* described herein provide further evidence that the Upper Guinean Forests support a wealth of biodiversity. *Chiloglanis fortuitus* was collected during an environmental assessment in the upper St. John River drainage in Liberia. This one specimen was serendipitously borrowed when examining type material for the description of the co-occurring *C. tweddlei*. The presence of multiple species within these forested streams suggests many more species remain to be discovered and formally described. Many of the streams that originate on the western slope of the Guinean Range remain relatively unexplored. As anthropogenic pressures increase in the region, it is critical that these rivers are surveyed so that this biodiversity can be documented before it is lost (Lalèyè et al., 2021).

Chiloglanis micropogon was, until recently, considered a synonym of *Chiloglanis batesii* (Roberts, 1989; Friel and Vigliotta, 2011). Roberts considered *C. batesii* to be one of the most widespread species of *Chiloglanis* occurring from the upper Niger River drainage to the Congo River basin, and throughout Central Africa (Roberts, 1989). Friel and Vigliotta (2011) recognized *C. micropogon* as a distinct taxon based on several different characters. Papillae on the roof of the oral cavity are present in *C. micropogon* but absent in *C. batesii*. These papillae are also present in the holotype of *C. frodobagginsi* (Fig. 6). There were also several oral disc characters mentioned (e.g., fleshy ridge posterior to mandibular teeth) that distinguished *C. micropogon* and *C. batesii* (Friel and Vigliotta, 2011). *Chiloglanis batesii* was likely described from Nyong River drainage in southern Cameroon (Boulenger, 1904). Populations of *Chiloglanis*, reported as *C. batesii* or *C. micropogon*, from the Nyong River to the Niger River need to be examined in more detail to determine the distributions of these species. Populations of *Chiloglanis* cf. *micropogon* from the Benue, Ndian, and Cross River basins appear to be distinct from topotypic *C. micropogon*, but additional specimens are needed from the region for confirmation (Fig. 3; Supplemental Table C; see Data Accessibility).

Understanding the diversity of *Chiloglanis* in the region is complicated by the presence of several species that are superficially similar to *C. micropogon* and *C. batesii*, especially smaller individuals. *Chiloglanis niger* also has reduced/absent mandibular barbels and around 12 mandibular teeth. The smaller individuals examined are very similar to *C. micropogon*, but are readily distinguished by the straight, robust mandibular teeth and smaller eye, relative to similar-sized *C. micropogon*. Small specimens of *C. disneyi* can also superficially resemble *C. micropogon*, but this species usually has many more mandibular teeth (16–20 versus 12) and has small mandibular barbels. Most of these species were described around the same time as several major collecting expeditions in the region (Teugels et al., 1992), and many of the specimens were deposited as *Chiloglanis* sp. or incorrectly placed into one of the newly described species. Sexual dimorphism in these species is also seemingly variable. One smaller male specimen of *C.* cf. *micropogon* from the Benue River clearly has an elongate and spatulate postcleithral process and elongated upper caudal-fin lobe. Another specimen, determined to be *C. niger*, has an elongated upper caudal-fin lobe but not an elongate postcleithral process. Another issue is the relative lack of material from the region. Many lots only contain one or a few specimens and some of those are damaged. It seems that many of these fishes are relatively rare (but may be locally abundant) and are often not sampled if electrofishers are not utilized. Examining the

remaining cataloged material from this region should clarify some of these issues, but additional collecting in Cameroon and surrounding areas is also needed.

The biogeographical implications of the close relationship between the Upper Guinean Forest *C. frodobagginsi* and the Congolese *C. micropogon* are also quite interesting. A previous study (Schmidt et al., 2016) appears to offer the first molecular evidence of a recent connection between the fish fauna in the Congo River basin and the Niger River drainage. This past connection was hypothesized based on several presumptive shared taxa that occur within the Congo, Chad, and Niger River drainages (e.g., *Campylomormyrus tamandua*; Lévêque, 1997). Lévêque (1997) hypothesized that fishes from the Congo River first entered the Chad basin and then gained access to the Niger River drainage through the Gauthiot Falls in the upper Benue River. The presence of *Chiloglanis* cf. *micropogon* in the Benue River drainage also supports the hypothesis that this river served as a dispersal corridor for fishes in the region. These fishes could have then spread throughout the Niger River drainage, and subsequent climatic changes may have restricted them to well-watered regions within the watershed. The headwater streams of the Niger River drainage in Guinea have likely served as refugia where forests, and more importantly water, have persisted during climatic fluctuations (Mayr and O'Hara, 1986). Other fishes that are thought to occur within the Congo and Niger drainages should be investigated to see if similar patterns exist.

The presence of *C. frodobagginsi* in the upper Moa River also provides further evidence for headwater capture in the region. The diversity within these forested streams that arise along the Guinean Range has likely been fueled by recurring headwater capture events in the region. This would allow for species to geodisperse (vicariance) into neighboring drainages and diversify. If enough time passes before another headwater capture event, or the headwater capture event is across the Guinean Range versus alongside of it, a second or third species can become established in the system. In the Moa River system, there are three species of *Chiloglanis*, and within the Loffa and St. John River drainages there are two species present (Schmidt et al., 2017). These mechanisms that have probably promoted diversification within *Chiloglanis* have likely also promoted diversification within the mountain catfishes (*Amphilius*) and African small barbs (*Enteromius*; Schmidt and Pezold, 2011; Schmidt, 2014; Schmidt et al., 2019). Similarly, it seems that the diversity in other co-occurring groups of fishes is also vastly underestimated and needs to be investigated further.

MATERIAL EXAMINED

Chiloglanis micropogon: Democratic Republic of the Congo: Congo River drainage: CUMV 97580, 10 of 101, 18.6–22.0 mm SL, Lualaba River, at main portion of Wagenia Falls, 0.49413°N, 25.20701°E; MRAC 91479, holotype, 49 mm SL, Nzokwe River, affluent of Ulindi River, Territory Kabare, 2.92°S, 28.53°E, G. Marlier, 20 May 1949.

Chiloglanis cf. *micropogon*: Nigeria: Benue River drainage: USNM 338276, 2, 21.3–28.0 mm SL, Mayo Santo (Fulani) or River Shuntan, small stream inflow to main river near Gashaka Camp. This eventually drains to the River Taraba which joins the River Benue, 7.3806°N, 11.4736°E. Cameroon: Cross River drainage: USNM 304265, 3, 22.4–26.3 mm SL, collecting points upper tributaries of Munaya, near Baro Village, northern Korup, Bake River below Nere Bifa Falls, 5.833°N, 9.1722°E; USNM 304331, 5, 22.3–36.3 mm SL, Akpa-Yafe System, streams and rivers of southwest Korup, Akpasang River at crossing point nearest end of 'P' (transect), 5.01°N, 8.75°E; Ndian River drainage: USNM 303409, 44, 25.7–27.4 mm SL, streams and rivers of southeast boundary of Korup, main Ndian River at bridge crossing into Korup, 4.9833°N, 8.85°E; USNM 303624, 1, 39.7 mm SL, streams and rivers of southeast boundary of Korup, Owaye River just north of Mana River, Korup 'buffer zone A,' 5.1°N, 8.9833°E.

Chiloglanis niger: Cameroon: Benue River drainage: USNM 280387, 1, 54.7 mm SL, Northwest Province, Fujua, fast flowing stream with rocky bottom, 6.28333°N, 10.28333°E (georeferenced); USNM 338335, 1, 38.9 mm SL, Mayo Dundere, the upper reaches of the Mayo Gashaka/Mayo Korngal. This eventually drains to the River Taraba which joins the River Benue, 7.0306°N, 11.5667°E; USNM 338717, 1, 41.7 mm SL, Mayo Katan, at the crossing point with a dirt road. This stream eventually drains to the River Taraba which joins the River Benue, 7.1639°N, 11.3917°E.

Chiloglanis tweddlei: Liberia: St. John River drainage: SAIAB 188313, 3, Nimba County, Kahn River upstream, 7.589167°N, 8.568611°W; SAIAB 188352, 1, Nimba County, Bold River, 7.50444°N, 8.58944°W; SAIAB 188448, 1, Nimba County, Yiti River, main road, 7.4875°N, 8.615278°W; SAIAB 188466, 3, Nimba County, Dehn River, at Lugbei, 7.608611°N, 8.622778°W; SAIAB 188551, 8, Nimba County, Yiti River, 7.516111°N, 8.704167°W; SAIAB 188582, 10, Nimba County, Yiti River upstream, 7.510278°N, 8.749167°W; SAIAB 188608, 1, Nimba County, Bee River, at Saniquellie, 7.369556°N, 8.697278°W; SAIAB 188639, 3, Nimba County, Tributary of Vellie River, 7.5755°N, 8.657722°W; USNM 193949, 17, Bong County, Gbarngy District, streams and tributary to St. John River.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/i2022067. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License. ZooBank publication urn:lsid:zoobank.org:pub:AA5998FE-9F91-46B2-AB49-B8EDE9B6E4DA.

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