1.5	Phylogeny and biogeography Shield endemic <i>Corymbophar</i> catfishes (Loricariidae)	y of the Brazilian–Guiana nes clade of armoured	$\begin{array}{c} 1.54\\ 1.55\end{array}$
	NATHAN K. LUJAN <sup>1,2*,0</sup> , JONATHAN W. ARM TÚLIO FRANCO TEIXEIRA <sup>4,5</sup> and NATHAN F	BRUSTER <sup>3</sup> , DAVID C. WERNEKE <sup>3</sup> , R. LOVEJOY <sup>2</sup>	1.60
1.10	<sup>1</sup> Department of Ichthyology, American Museum of No <sup>2</sup> Department of Biological Sciences, University of Tor Canada	atural History, New York, NY, 10024, USA conto Scarborough, Toronto, Ontario, M1C 1A4,	
1.15	<sup>3</sup> Department of Biological Sciences, Auburn Universi <sup>4</sup> Programa de Pós-graduação em Biologia de Vertebr Gerais, Belo Horizonte, Minas Gerais, 30535–901, Br <sup>5</sup> Museu de Zoologia da Universidade de São Paulo, S	ity, Auburn, Alabama, 36849, USA ados, Pontifícia Universidade Católica de Minas vazil São Paulo, SP, 04263-000, Brazil	1.65
1.20	Received 28 February 2019; revised 17 May 2019; accepted	for publication 8 August 2019	1.70
1.25	Numerous rivers, interrupted by large waterfalls and externational Highlands. We describe a new armoured catfish genus and rivers, respective tributaries of the Amazon and Essequibo <b>nov.</b> is distinguished by having vermiculations on the abd caudal peduncle. <i>Yaluwak primus</i> gen. & sp. nov. is distinguished and absence of adipose fin an analysis inclusive of these and several related genera the several related genera.	ensive rapids, drain the geologically ancient Guiana Shield two new species endemic to the upper Ireng and Kuribrong basins in western Guyana. <i>Corymbophanes ameliae</i> sp. omen, bands on the caudal fin, the anal fin i,5 and narrow stinguished by having evertible cheek odontodes, a plated d iris operculum. We present a new molecular phylogenetic hat suggests that the <i>Corymbophanes</i> clade ( <i>Araichthys</i> ,	1.75
1.30	Corymbophanes, Cryptancistrus, Guyanancistrus, Hopliam secondary dispersal to the Brazilian Shield. Within the G Yaluwak are consistent with geodispersal between drain relictual distribution cannot be ruled out. ND2 haplotyp ichthyofaunal diversity on the Guiana Shield escarpment to gene flow.	<i>cistrus</i> and <i>Yaluwak</i> ) originated in the Guiana Shield with Guiana Shield, relationships among <i>Corymbophanes</i> and ages via headwater capture, although an uplift-mediated be structure among <i>C. ameliae</i> populations suggests that is shaped not only by inter-, but also intrafluvial barriers	1.85
1.35	KEYWORDS: Amaila Falls – Amazonian Craton – Guia River – sexual dimorphism.	nas – Ireng River – Kuribrong River – Rio Maú – Potaro	
1.40	INTRODUCTION	1908 ichthyofaunal survey of Guyana; an expedition	1.90
1.45	<b>Eigenmann (1909)</b> described the genus and species <i>Corymbophanes andersoni</i> based on a single specimen (FMNH 52675) collected in the upper Potaro River basin above Kaieteur Falls in what was then British Guiana (now Guyana; Fig. 1). Eigenmann's collections above Kaieteur were the culmination of a landmark	in a subsequent monograph (Eigenmann, 1912). Eigenmann (1909) described <i>C. andersoni</i> as being primarily distinguished from other loricariids by lacking an adipose fin and instead having 'a low median ridge extending from the tip of the dorsal to the caudal' and 'no externally visible occipital crest' (Eigenmann, 1912: 5). In 1912, he provided the first illustrations	1.95
1.50	*Corresponding author. E-mail: nklujan@gmail.com [Version of record, published online 21 October 2019; http:// zoobank.org/urn:lsid:zoobank.org:pub:C0ADB1A2-4850-49A4- 9DBC-34CA9F6CB6BC]	of <i>C. andersoni</i> , but otherwise did not expand on his original description, adding only that <i>C. andersoni</i> 'differs from <i>Plecostomus</i> [now <i>Hypostomus</i> ] in trifling characters only' (Eigenmann, 1912: 103). Like	1.100

1

2.25

2.30

2.55

2.56



Figure 1. Distributions of Corymbophanes and Yaluwak specimens examined in this study. OC = Oung Creek.

Hypostomus, Corymbophanes is distinguished from most other members of subfamily Hypostominae by lacking evertible cheek odontodes. Because of this similarity to *Hypostomus* – a genus known to be widespread in South America - Eigenmann hypothesized that *Corymbophanes* may only be 'a local modification of a comparatively recent immigrant to the [Guiana Shield] plateau' (ibid.).

Ninety years after Eigenmann's expedition to the 2.35upper Potaro River, one of us (JWA) participated in an expedition to resample many of the same sites as Eigenmann, with results of this temporal comparison being summarized by Hardman et al. (2002). In addition to collecting five new specimens of 2.40C. andersoni from its type locality at Chenapou Falls (known to Eigenmann in 1908 as Aruataima Falls) in the Potaro River main channel, members of this expedition collected five specimens of a new congener from the nearby Oung Creek (Fig. 1: OC). This new 2.45species, Corymbophanes kaiei Armbruster & Sabaj 2000, differs from *C. andersoni* by having a dark brown abdomen with white vermiculations (vs. mostly white), white vermiculations on the sides (vs. spots) and by having three to four plates beneath the adpressed 2.50

pectoral-fin spine (vs. five; Armbruster et al., 2000). Interpretation of the phylogenetic and biogeographical history of Corymbophanes changed with Armbruster's (2004) morphology-based phylogenetic analysis of the Hypostominae. Armbruster found *Corymbophanes* to be monophyletic, diagnosed by 11 non-unique synapomorphies, and sister to all other members of the Hypostominae, including Hypostomus. Corymbophanes was, therefore, placed 2.85in its own tribe Corymbophanini. This interpretation of the phylogenetic placement of Corymbophanes held until the first comprehensive molecular phylogenetic analysis of Hypostominae (Lujan et al., 2015), which again dramatically changed our understanding of 2.90relationships within this subfamily. Both Lujan et al. (2015) and Fisch-Muller et al. (2018), using different sets of markers, found Corymbophanes to be nested within the Hypostominae tribe Ancistrini and to be well supported as sister to either the Guiana Shield 2.95endemic species Cryptancistrus similis (Fisch-Muller et al., 2018) or the Brazilian Shield endemic genus Hopliancistrus [according to Lujan et al. (2015) who did not examine Cr. similis]. Together, the clade of either *Corymbophanes* + *Hopliancistrus* (Lujan *et al.*, 2015) or 2.100*Hopliancistrus* + (*Corymbophanes* + *Cryptancistrus*) (Fisch-Muller et al., 2018) was sister to the genus *Guyanancistrus*, which is distributed across large lowland rivers of the eastern Guiana Shield in north-eastern Brazil, French Guiana and Suriname 2.105(Cardoso & Montoya-Burgos, 2009; Covain & Fisch-Muller, 2012). Problematically, Corymbophanes lacks the evertible cheek odontode mechanism of most other members of Ancistrini, but that mechanism has likely been reduced or lost at least four times within 2.110Hypostominae (Armbruster, 2004; Lujan et al., 2015). 2.111These taxa formed a largely Guiana Shield-restricted 2.112 clade within which the evertible cheek odontode mechanism is highly variable, being absent in *Corymbophanes*, modified into a three-hooked, anteriorly highly evertible pinching mechanism in

Hopliancistrus and present but unspecialized in

3.5

3.10

3.40

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3.50

3.55

Cryptancistrus and Guyanancistrus.
Corymbophanes was represented in the Lujan et al.
(2015) study by tissue samples that were collected by two of us (NKL, TFT) in a 2011 survey of the upper Kuribrong River basin, a watershed that borders the north-eastern margin of the upper Potaro River basin. Although the Kuribrong is a tributary of the Potaro, these rivers do not coalesce until after they

- have both exited the Guiana Shield escarpment via
  3.15 the respective Amaila and Kaieteur waterfalls (Fig. 1), which are both tall, formidable barriers to fish dispersal. In addition to *Corymbophanes*, our 2011 fieldwork in the upper Kuribrong River yielded a new endemic South American darter species
  3.20 (*Characidium amaila* Lujan et al., 2013) and likely
- 8.20 (Characidium amaila Lujan et al., 2013) and likely new but still undescribed species in the genera Astyanax, Brachyglanis, Chasmocranus, Lebiasina and Trichomycterus (Table 1). Although hydrologically disconnected from the upper Potaro River, the upper
- 3.25Kuribrong populations of Corymbophanes are similar to C. kaiei in both coloration and gross external morphology. Potaro and Kuribrong populations of C. kaiei were, therefore, originally treated as conspecific. However, recent re-examination of these 3.30 specimens, in combination with newly generated DNA sequence data for Potaro River populations of both C. andersoni and C. kaiei, indicate that the Kuribrong River populations represent a new species that is most closely related to C. andersoni. One of the goals of this 3.35 study is to describe this new Kuribrong River species and present evidence for its phylogenetic placement and population structure.

Another goal of this study is to describe and phylogenetically place an enigmatic new loricariid genus and species that was recently discovered in the upper Ireng River (known as the Rio Maú in Brazil) by three of us (JWA, NKL, DCW). The upper Ireng River flows south from the same Pakaraima Mountain range that gives rise to the east-flowing headwaters of the Potaro River. Although the upper Ireng River also has several high waterfalls, the top and bottom of these falls are at much higher elevations (690 m a.s.l. at their top, 624 m a.s.l. at their bottom) than both Amaila and Kaieteur falls (400 m a.s.l. at their top, c. 90 m a.s.l. at their bottom) and the Ireng River descends the elevational range of Amaila and Kaieteur falls (400-90 m a.s.l.) in a series of rapids and waterfalls that are much smaller than either Amaila or Kaieteur. Two specimens of the curious new species were collected above these cataracts, but below the taller waterfalls As part of our description of these two new taxa from the Guiana Shield, we present the first phylogenetic hypothesis for relationships between *Corymbophanes*, the new genus and two other enigmatic, recently described genera: *Cryptancistrus* Fisch-Muller *et al.*, 2018 from the upper Parú de Oeste River near the Suriname-Brazil border (south-eastern Guiana Shield) and *Araichthys* Zawadzki *et al.*, 2016 from the upper Rio Tapajós basin (northern Brazilian Shield, Zawadzki *et al.*, 2016). We also summarize fish endemism and distribution patterns across the upper Ireng, Kuribrong and Potaro River basins.

3.70

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3.65

# MATERIAL AND METHODS

#### **MORPHOMETRICS**

Measurements were made with digital callipers to 3.75the nearest 0.1 mm. Measurements and counts of bilaterally symmetrical features were from the left side of the body when possible; if a feature was damaged on the left side, it was examined on the right side. Measurements followed Boeseman (1968) as modified 3.80 by Armbruster & Page (1996), Armbruster & Hardman (1999) and Armbruster et al. (2000), with the addition of Minimum Caudal Peduncle Width, which was taken from the ventral side between the posterior edges of the last ventral plates at the point where they angle 3.85dorsally. Counts follow Armbruster et al. (2000). Names of skeletal characteristics follow Schaefer (1987) and Geerinckx et al. (2007), and names of plate rows follow Schaefer (1997). Morphometric and meristic data were examined in JMP (v.11.0; SAS Institute, 2013). 3.90

#### MATERIAL EXAMINED

48.3, 48.5 mm SL, plus 1 cleared and stained, CSBD F644,

holotype, 65.6 mm SL, INHS 48583, 2, 26.2, 70.0 mm

SL and FMNH 108246, 1, 47.6 mm SL, Oung Creek,

tributary of Chenapou River, about one hour hike SW of

coordinates 04.97389°, -059.57806° (mouth of Chenapou

River); AUM 62908, 1, not measured, Potaro River at

Ayanganna Old, 05.30181°, -059.89838°; and ROM 89928,

2, 49.0, 108.9 mm SL, Kopinang River at Kopinang Village

landing, schoolhouse rapids, 04.9407°, -059.85882°.

#### Corymbophanes kaiei

GUYANA, Region 8 (Potaro–Siparuni), Potaro River– Essequibo River drainage: AUM 28163, 2, paratypes,

3.100

5.100

3.95

3.105

#### Corymbophanes andersoni

GUYANA, Region 8 (Potaro–Siparuni), Potaro River–Essequibo River drainage: FMNH 52675, holotype,65.5 mm SL, Aruataima Falls, Upper Potaro; AUM28149, 3, 25.6–57.0 mm SL, plus 1 cleared andstained, INHS 49586, 2, 17.3, 64.9 mm SL, topotypes,3.112

3.56 of the upper Ireng.

**Table 1.** Summary of species documented in the upper Ireng River upstream of Orinduik Falls, upper Potaro River upstream of Kaieteur Falls, and upper Kuribrong River upstream of Amaila Falls. Data for the Ireng summarized from recent fieldwork by JWA, NKL, DCW, for the Potaro and Kuribrong summarized from Hardman *et al.* (2002) and field work by JWA, NKL, TFT, DCW

CharaciformesCharacidaeXXXAstyanax bimaculatusXXXAstyanax mutatorXXXAstyanax sp. 'Ireng'XXXBryconops affinisXXXBryconops caudomaculatusXXXHemigrammus bellottiiXXXJupiaba essequibensisXXXMoenkhausia browniXXXMoenkhausia sp. 'Ireng'XXTetragonopterus georgiaeXXCrenuchidaeXXCharacidium boavistaeXXCharacidium crandelliXXPoecilocharax bovalliiXXXXXX
CharacidaeXXAstyanax bimaculatusXXAstyanax mutatorXXAstyanax sp. 'Ireng'XXAstyanax sp. 'Kuribrong'XXBryconops affinisXXBryconops caudomaculatusXXBryconops caudomaculatusXXMenigrammus bellottiiXXJupiaba essequibensisXXMoenkhausia browniXXMoenkhausia cf. oligolepisXXMoenkhausia sp. 'Ireng'XXCrenuchidaeXXCharacidium amailaXXCharacidium n.sp. 'Ireng'XXPoecilocharax bovalliiXXNoenkhaus bovalliiXX
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Bryconos caudomaculatusXBryconos caudomaculatusXHemigrammus bellottiiXJupiaba essequibensisXMoenkhausia browniXXXMoenkhausia cf. oligolepisXMoenkhausia sp. 'Ireng'XTetragonopterus georgiaeXCrenuchidaeXCharacidium amailaXCharacidium crandelliXCharacidium n.sp. 'Ireng'XXX
Hemigrammus bellottiiXJupiaba essequibensisXJupiaba essequibensisXMoenkhausia browniXXMoenkhausia cf. oligolepisXMoenkhausia sp. 'Ireng'XTetragonopterus georgiaeXCrenuchidaeXCharacidium amailaXCharacidium boavistaeXCharacidium n.sp. 'Ireng'XXXPoecilocharax bovalliiXXX<
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Characidium crandelliXCharacidium n.sp. 'Ireng'XPoecilocharax bovalliiXXX
Characidium n.sp. 'Ireng'XPoecilocharax bovalliiXXX
Poecilocharax bovallii X X X
Erythrinidae
Erythrinus erythrinus X X X
Hoplerythrinus unitaeniatus X X X
Hoplias malabaricus X
Lebiasinidae
Lebiasina cf. ardilai X
Pyrrhulina stoli X X X
Siluriformes
Callichthvidae
Callichthys callichthys X X X
Cetopsidae
Helogenes marmoratus X X
Loricariidae
Ancistrus saudades X
Corymbophanes ameliae X
Corymbophanes andersoni X
Corymbophanes kajej X
Harttia n.sp. (Treng' X
Hypostomus hemiurus X X X
Lithorus honallii X
Lithogenes villosus V
Yalunak primus Y
Hentanteridae
Brachvolanis n sn 'Kurihrong' X
Brachyslanie n. sp. Harrolong X
Chaemogranus n sp. 'Kuribrong' V
Chaemocranue n.sp. Ixuitorong A
Chaemocranue n.sp. 1 (hard) A
Rhandia foina V
Rhandia ef auden V
Knamaia ci. quelen X

Taxa	Upper Kuribrong River	Upper Potaro River	Upper Ireng River
Trichomycteridae			
Trichomycterus guianensis		Х	
Trichomycterus cf. guianensis1	X	Х	
Trichomycterus cf. guianensis2		Х	
Trichomycterus conradi			Х
Trichomycterus n.sp. 'long'		Х	
Gymnotiformes			
Gymnotidae			
Gymnotus carapo		Х	Х
Hypopomidae			
Brachyhypopomus beebei		Х	
Hypopomus artedi	X		
Cyprinodontiformes			
Rivulidae			
Rivulus holmiae		Х	
Rivulus waimacui	X		
Rivulus cf. breviceps			Х
Synbranchiformes			
Synbranchidae			
Synbranchus marmoratus	X	Х	Х
Cichliformes			
Cichlidae			
Crenicichla alta	Х	Х	Х
Krobia potaroensis	Х	Х	Х
Nannacara bimaculata	Х		
Total species:	24	32	26
Total endemic species:	10	16	13
% endemic species:	42%	50%	50%
Number shared between Ireng and Potaro:	13		
Number shared between Kuribrong and Potaro:	14		
Number shared between Ireng and Kuribrong:	11		
Number shared between all three:	11		

PHYLOGENY OF CORYMBOPHANES CATFISH CLADE

5.40 Aruataima (Chenapou) Falls, 23.7 km southwest of Menzies Landing, 05.00139°, -059.62583°.

# PHYLOGENETIC TAXON SAMPLING

In addition to both Corymbophanes andersoni and 5.45C. kaiei, we included in our phylogenetic analysis several populations of Corymbophanes from different parts of the Kuribrong River basin, giving us the opportunity to test hypotheses related not only to species relationships, but also population-level 5.50divergence and pathways by which Corymbophanes may have dispersed into and throughout the upper Kuribrong River drainage. The geographic distribution of these samples is illustrated in Figure 1. We also included both specimens of the enigmatic recently 5.55collected species from the upper Ireng River. 5.56

As outgroups, we included representatives of six other genera found to be included in the tribe Ancistrini in the multilocus analysis by Lujan et al. (2015): Ancistrus, Dekeyseria, Guyanancistrus, Hopliancistrus, Lasiancistrus and Pseudolithoxus, plus Cryptancistrus, which was found to be sister to Corymbophanes in a multilocus analysis by Fisch-Muller et al. (2018), and Araichthys, which was found to be sister to *Hopliancistrus* in a phylogenomic analysis by Roxo et al. (2019). To root our trees, we included Lithogenes villosus, which has been found to be either sister to all other Loricariidae based on morphological data (Schaefer, 2003) or part of a basal polytomy with Delturinae based on multilocus analyses (Lujan et al., 2015) and Cteniloricaria platystoma, which is a member of the subfamily Loricariinae that is sister to Hypostominae + Hypoptopomatinae.

5.105

5.110

5.111

5.112

5	5	)	5								
<b>Fable 2.</b> Loci sequenced, vouchgroupings according to family, sur near the type locality	er catalogue	number and tribe. Type	country a specimen'	nd river indicat	draina es that	ge of orig	in for tissue was either	samples a part of the	nalysed in this st type series for a	udy. Taxa are li species or was	sted in indente collected from a
laxa	Tissue #	Type specimen	Type species	# of loci	16S C	ytb NI	02 RAGI	RAG2	Voucher Cat #	Country	Drainage
Loricariidae Lithomeninge											
Lithogenes villosus	T17140	X	X	4	X		Х	X	ROM 95075	Guyana	Potaro
Cteniloricaria platystoma Hypostominae	T06288		X	ъ С	x	X	X	X	ROM 85921	Guyana	Essequibo
Ancistrini				ľ		ļ	ļ			-	τ
Ancistrus clementinae	T13829 01600	X	~	с С	X	×	×	X >	КОМ 93737 т вр 20005	Ecuador Brogil	Guayas Teneiás
Araichthys loro Araichthys loro	01009 81590		< ×		< \x	< ×	< ×	<	LBF 20905 LBP 20905	Brazil	Tanaiós
Corymbophanes ameliae	AUF1486	Χ	1	2		1	1	×	AUM 62704	Guvana	Kuribrong
Corymbophanes ameliae	AUF1561	Χ		5 C	X	Х	Х	Χ	AUM 62741	Guyana	Kuribrong
Corymbophanes ameliae	AUF2101	Х		5	X	Χ			AUM 62732	Guyana	Kuribrong
Corymbophanes ameliae	T12637	Χ		4	X		Χ	Χ	ROM 89856	Guyana	Kuribrong
Corymbophanes ameliae	T12659	X		5 C	X	X	X	X	ROM 89897	Guyana	Kuribrong
Corymbophanes ameliae	T12665	X		ю I	X	X	X	X	ROM 89895	Guyana	Kuribrong
Corymbophanes ameliae	T12666	X		2	×	×	X	X	ROM 89895	Guyana	Kuribrong
Corymbophanes ameliae	T12667	X÷		ر م	X	X÷	X÷	X÷	ROM 89895	Guyana	Kuribrong
Corymbophanes ameliae	T12669	XX		۵. ۲	X	X¥	X	X	ROM 89897	Guyana	Kuribrong
Corymbophanes ameliae	G/.971.T.	XX		4 0	×	× >	X	X	KOM 89897	Guyana	Kuribrong
Corymbophanes ameliae	OCCCT.T.	×		NI	× ×	X >	~	~	KUM 91358	Guyana	Kuribrong
Corymbophanes ameliae	T15561	X X		ດັນ	< >	X	X	X	ROM 91358	Guyana	Kuribrong
Commbonhange amelia	T15573	<b>V</b>		่วน		< >	< >	<b>X</b> X	missing	Guyana	Kurihrong
Corvmhonhanes ameliae	T15574					4 ×	4 ×	* ×	missing	Guyana	Kurihrong
Correntonhanes ameliae	T17360	X		0 4		: ×	1	: ×	ROM 94980	Guyana	Kurihrong
Corvmbonhanes ameliae	T17361	: ×		5 7		* ×			ROM 94980	Guvana	Kuribrong
Corvmbophanes anderson	<i>i</i> AUF4133	×				1			AUM 28149	Guvana	Potaro
Corvmbonhanes kaiei	T12701		X	24	X	Х	Х	Х	ROM 89928	Guvana	Potaro
Corvmhonhanes kaiei	T12702			1.0					ROM 89928	Guyana	Potaro
Cryptancistrus similis	SU07-672	Х	X	4	X	X		Х	MZUSP 117150	) Brazil/Suri-	Parú de
-				,	;		;	;		name	Oeste
Dekeyseria picta Debewseria scanhirhwncha	v 5297			4 4	x x x x		××	x	AUM 44110 ATTM 54309	Venezuela Venezuela	Atabapo Ventuari
Guyanancistrus brevispin	isSU01-121		X	4	X		X	X	MHNG 2621.07	73 French Guiana	Maroni
6.10 6.11 6.11	6.10	6.9	6.9		6.8		6.8	6.7	6.7	6.0	6.6
05 10 11	00	95	90		85		80	75	70	65	60

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7.5		Drainage	Oyapock	Oyapock	Xingu	Tapajos	Marañon	Orinoco	Ireng	Ireng
7.10		Country	0 French Guiana	9 French Guiana	Brazil	Brazil	Peru	Venezuela	Guyana	Guyana
7.15		Voucher Cat #	MHNG 2725.10	MHNG 2722.08	ANSP 193087	AUM 39853	AUM 45548	AUM 57674	CSBD F1722	AUM 67193
7.20		RAG2	X	Х	X	X	X	Χ	X	X
		RAGI	X	X	X	X	X	X	X	x
7.25		ND2						X	X	x
		Cytb	X	Х	X	X	Х	X		
7.30		16S	X	Х	Χ	X	X	Χ	Х	×
		# of s loci	4	4	4	4	4	5	4	4
7.35		Type species				X		X	X	x
7.40		Type specimen							X	X
		Tissue #	: GF99-204	GF99-185	B2167	T9018	P6123	T09376	AUF10277	AUF10303
7.45			ngispinis	ger	p. Xingu	cornis		ris		
7.50	2. Continued		Guyanancistrus lo	Guyanancistrus ni	Hopliancistrus n.s.	Hopliancistrus tric	Lasiancistrus nburgkii	Pseudolithoxus tig	Yaluwak primus	Yaluwak primus
7.55 7.56	Table	Таха	-	-	7	1	schoi	7		

# TISSUE AND DNA SOURCES

Newly generated sequence data (Table 2) were obtained from tissue samples or DNA extracts collected by the 7.60authors or provided by the Academy of Natural Sciences of Drexel University in Philadelphia, PA, USA (ANSP), the Auburn University Museum Fish Collection in Auburn, AL, USA (AUM), the Laboratório de Biologia e Genética de Peixes, Departamento de Morfologia, Instituto de 7.65Biociências. Universidade Estadual Paulista 'Júlio de Mesquita Filho', Campus de Botucatu, São Paulo, Brazil (LBP), the Royal Ontario Museum in Toronto, Canada (ROM), the Muséum d'Histoire Naturelle, Geneva, Switzerland (MHNG) or obtained via the ornamental fish 7.70 trade. Voucher specimens (Table 2) were identified either by direct examination or in collaboration with museum workers at different institutions. Most of the taxa in our analysis were represented in either this or previous analyses by multiple individuals, but Corymbophanes 7.75andersoni was represented in our analysis by only a single degraded tissue collected in 1998. Institutional abbreviations follow Sabaj (2016).

# MOLECULAR MARKERS, DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

7.80

7.85

7.90

Molecular phylogenetic methods followed those of Lujan *et al.* (2015) with the exception that the mitochondrial gene region NADH dehydrogenase 2 (ND2) was added to this analysis and the nuclear gene region MyH6 was not examined in this study. In brief, we amplified and sequenced a fragment of the mitochondrial 16S (538 bp), cytochrome *b* (865 bp) and ND2 (1040 bp) genes, as well as fragments of the nuclear RAG1 (807 bp) and RAG2 (873 bp) genes for a total of 4123 aligned base pairs. Most gene regions were sequenced from most taxa (Table 2), with the exception that only the 16S gene region could be amplified and sequenced from *Corymbophanes andersoni*.

Gene regions were amplified using combinations of previously published primers (Arroyave *et al.*, 2013; Lujan *et al.*, 2015). Whole genomic DNA was extracted from fin or muscle tissues preserved in 95% ethanol following either manufacturer's instructions for the DNeasy Blood & Tissue Kit (Qiagen N.V., Venlo, Netherlands) or standard laboratory protocols for salt extraction followed by ethanol precipitation. Fragment amplifications were performed following the methods of Arroyave *et al.* (2013) and Lujan *et al.* (2015).

Post-PCR clean-up of all loci was achieved by either<br/>running the entire volume of PCR product on a 1%<br/>agarose gel with 0.01% SYBR Safe DNA gel stain (LTI:<br/>Life Technologies Inc., Carlsbad, CA) or by adding<br/>ExoSap-IT (Applied Biosystems Co., Foster City, CA)<br/>and following manufacturer's instructions. For samples<br/>that were gel purified, the band corresponding to the<br/>target locus was cut from the gel and the target PCR7.105

product extracted by centrifuge filtration through the top of a P-200 pipette filter tip in a labelled 1 mL snaptop tube (5 min at 15 000 rpm) followed by precipitation and washing of the DNA to remove salts. Forward and reverse sequencing reactions either followed the manufacturer's recommendations for sequencing on an Applied Biosystems 3730 DNA Analyzer (LTI) at the Royal Ontario Museum or were conducted by staff at The Centre for Applied Genomics at The Hospital for Sick Children (SickKids) in Toronto, ON, Canada.

8.10

#### SEQUENCE ASSEMBLY, ALIGNMENT AND PHYLOGENETIC INFERENCE

Sequence data were assembled, edited, aligned and 8.15 concatenated following the methods of Lujan et al. (2015). PartitionFinder (v.1.1.1, Lanfear et al., 2012) was used to determine codon-position specific models of molecular evolution for each gene under the Bayesian information criterion (BIC). 8.20

For the Bayesian analysis, an HKY model with rate heterogeneity being modelled by a gamma distribution (HKY+G) was determined to be the best model of molecular evolution for third codon positions of ND2 and *Cytb* and first codon positions of RAG1 and RAG2. 8.25 A GTR model with a proportion of invariable sites estimated and with rate heterogeneity being modelled by a gamma distribution (GTR+I+G) was determined to be the best model for 16S and the first codon positions of ND2 and Cvtb. An HKY model with a proportion of 8.30 invariable sites estimated (HKY+I) was determined to be the best model for the second codon positions of ND2 and *Cytb*. A K80 model with a proportion of invariable sites estimated (K80+I) was determined to be the best model for the second codon positions of RAG1 8.35 and RAG2. And a K80 model with rate heterogeneity being modelled by a gamma distribution (K80+G) was determined to be the best model for the third codon positions of RAG1 and RAG2. All data partitions were unlinked with rates free to vary across partitions and 8.40 *Lithogenes villosus* designated as the outgroup.

For the Bayesian analysis, a Markov chain Monte Carlo (MCMC) search of tree space was conducted using MrBayes (v.3.2.3; Ronquist & Huelsenbeck, 2003) programmed to run for 10 million generations using two 8.60 sets of eight chains (one cold, seven hot, with default temperature parameter), sampling every 666 trees with the first 5000 trees (~33%) being discarded as burn-in, thus generating a total of 10 000 trees from which posterior probabilities were calculated. The Bayesian 8.65 search was determined to have reached stationarity when likelihood values of the cold chains began randomly fluctuating within a stable range and when effective sample sizes for all metrics exceeded 2000 as determined by the program TRACER (v.1.6; Rambaut et al., 2007). 8.70

For the maximum likelihood analysis, the concatenated alignment was also partitioned by genes and codon positions, but the same model (GTR+G) was used for all partitions. Maximum likelihood analysis was conducted using RAxML (v.8.0.0; Stamatakis, 2014) run locally, with a 200 generation GTR+G search for a best tree and a 2000 generation GTR+G bootstrap.

# PRESENTATION OF PHYLOGENETIC RESULTS

Complete results of the Bayesian and maximum likelihood analyses are presented as Supporting Information (Figs S1, S2). Manuscript figures were trimmed of select outgroup taxa and were based on results of the Bayesian analysis. Node support 8.85 values from both the Bayesian and maximum likelihood analyses are provided in Table 3. We also provide Bayesian posterior probability (i.e. Bayesian inference = BI) and maximum likelihood (ML) bootstrap support values for each node discussed in the text.

## RESULTS

#### PHYLOGENETIC RELATIONSHIPS

Relationships among previously examined Ancistrini genera differ slightly from those found in previous

8.45 Node BI MLClade Node BI ML Clade 0.521 85 1 11  $\mathbf{2}$ 0.7750 121 100 3 0.90 47 13 1 81 Guvanancistrus 8.105 8.50 1 76 4 0.91 81 14 0.97 C. ameliae 150.92 72 $\mathbf{5}$ 64 0.63 86 16 0.91 64 6 Corymbophanes 7 1 100 17 1 100 Dekeyseria 8 0.6 37 18 0.7 8.110 9 1 97 19 1 99 Ancistrini 8.55 8.111 10 1 100 8.56 8.112

Table 3. Support values for each of the nodes in Figure 2, derived from Bayesian inference (BI) and maximum likelihood (ML) optimality criteria. Numbers in italics indicate BI < 0.90; numbers in bold indicate ML < 60

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8.5

8.75

8.80

8.90

8.100

molecular studies (Covain & Fisch-Muller, 2012; Lujan et al., 2015; Fisch-Muller et al., 2018) primarily in respect to the position of Dekeyseria. Our ML analysis finds weak support (Supporting Information, Fig. S2,

- 9.5ML: 38) for the previously published relationship found by (Lujan et al., 2015) in which Dekeyseria is sister to the clade containing Corymbophanes, Cryptancistrus, Hopliancistrus and Guvanancistrus (plus the previously unexamined new genus presented below), whereas our 9.10 Bayesian analysis finds weak support (Fig. 2, Node 18:
- BI: 0.67) for a never previously recovered relationship in which *Dekevseria* is sister to the clade containing Ancistrus, Lasiancistrus and Pseudolithoxus. This placement of Dekeyseria receives strong additional 9.15 support from an unpublished exon-based phylogenomic dataset currently being analysed by two of us (NKL, JWA). Thus, the emerging picture of large-scale intergeneric relationships within Ancistrini is one in

which the strongly monophyletic (Fig. 2, Node 14: BI: 1, ML: 76) mostly upland, shield-restricted Corymbophanes clade (Araichthys, Cryptancistrus, Corymbophanes, Hopliancistrus, Guyanancistrus and the new genus) is sister to a clade that is more widely distributed across lowland habitats and includes Ancistrus, Dekeyseria, Lasiancistrus and Pseudolithoxus.

9.60

9.65

9.70

9.75

9.110

9.111

9.112

Within the Corymbophanes clade, Guyanancistrus and *Hopliancistrus* are strongly supported as successive sister lineages (Fig. 2: Node 14: BI: 1, ML: 76; Node 11: BI: 1, ML: 85) to a strongly monophyletic clade containing Araichthys, Cryptancistrus, Corymbophanes and the new genus (Fig. 2, Node 9: BI: 1, ML: 97). Unfortunately, relationships among these latter four genera remain weakly supported or unresolved. Corymbophanes is weakly supported as sister to the new genus Yaluwak (Fig. 2, Node 8: BI: 0.59, ML: 37), but relationships between this clade, Araichthys and Cryptancistrus are unresolved.



9.55

9.56

Figure 2. Phylogenetic relationships of taxa within the tribe Ancistrini (Loricariidae: Hypostominae), including the new genus and species Yaluwak primus and new species Corymbophanes ameliae. Relationships based on Bayesian analysis of a 4123 bp alignment consisting of three mitochondrial (16S, Cytb, ND2) and two nuclear loci (RAG1, RAG2; Table 2). Node numbers correspond to Bayesian posterior probability (BI) and maximum likelihood (ML) support values in Table 3; numbers in red indicate BI < 0.90, whereas numbers in italics indicate ML < 60. Green, red and blue colours for Corymbophanes ameliae correspond to those in Figure 3. MC = main channel, Trib = tributary.



	Figure 3. Neighbour-joining network and map describing	Corymbophanes ameliae ND2 haplotype relationships and	10.80
10.25	spatial distributions. Numbers along branches indicate num	per of nucleotide changes between each node. Green, red and	20100
10.20	blue colours show the distribution of Corymbophanes ameli	ae haplotype lineages, corresponding to colours in Figure 2.	
	Black circles on map represent localities where Corymbopha	nes ameliae specimens were collected but not included in the	
	haplotype analysis. Rapids indicated by R1, R3–R5 (rapids 1	, 3–5). See also Lujan <i>et al.</i> (2013; Fig. 7) for a more detailed	
	map showing the distribution of known rapids habitats throu	ghout the upper Kuribrong River basin.	10.85
10.20			10.00
10.30	Corymbophanes species relationships	Holotype: CSBD F1721, ex. ROM 89895, 89.3 mm	

10.35

10.40

10.55

Corymbophanes is strongly supported as monophyletic (Fig. 2, Node 7: BI: 1, ML: 100), with C. kaiei being sister to a weakly supported clade containing C. andersoni and C. ameliae (Fig. 2, Node 6: BI: 0.63, ML: 86), a relationship informed only by the 16S gene region (the only DNA sequence obtained from C. andersoni).

#### TAXONOMIC ACCOUNTS

	CORYMBOPHANES AMELIAE LUJAN ET AL., SP. NOV. [FIGS. 4, 5, 6, TABLES 4, 5].
10.45	urn:lsid:zoobank.org:act:0CF1AEDC-FF34-49D7- A4EE-C917FE53A411
	Corymbophanes kaiei – Lujan <i>et al.</i> , 2015: 278, 281
	[molecular phylogeny, data sent to GenBank]
10.50	Corymbophanes kaiei – Lujan <i>et al.</i> , 2017: 323
	[molecular phylogeny]

CORYMBOPHANES KAIEI - FISCH-MULLER ET AL., 2018: 11, 18

10.56[molecular phylogeny, data from GenBank] SL; GUYANA, Region 8 (Potaro-Siparuni), Kuribrong River, Potaro River-Essequibo River drainage, at rapids ~15 min upstream of upstream Kuribrong 10.90 Camp; 05.33766°, -059.56615°, 454 m a.s.l.; 19-20 March 2011; N. K. Lujan, F. C. T. Lima, T. C. Pessali, T. F. Teixera, P. Bernardo, A. Khan, G. Savory and K. Andrew.

10.95Paratypes: All collections GUYANA, Region 8 (Potaro-Siparuni), Kuribrong River, Potaro River-Essequibo River drainage. AUM 53676, 1, 100.6 mm SL, tributary of Kuribrong River, above Amaila Falls, 05.36637°, -059.54324°, 29 March 2011, B. Noonan; 10.100 AUM 62704, 2, 72.5-99.6 mm SL, Amaila River, at campsite near confluence with Kuribrong, 05.37626°, -059.55114°, 5-6 March 2014, E. A. Liverpool and D. C. Taphorn; AUM 62732, 1, 84.6 mm SL, Amaila River, mouth, 05.37608°, -059.55053°, 8 Mar 2014, 10.105 D.C. Taphorn, E.A. Liverpool and L. Benjamin; AUM 62741, 1, 55.8 mm SL, Amaila River, just upstream from mouth, 05.37608°, -059.55053°, 7-8 March 2014, D. C. Taphorn, J. W. Armbruster, D. C. Werneke, E. A. Liverpool and D. P. Fernandes; MZUSP 110846, 3, 10.110 81.6–88.3 mm SL, same data as holotype; ROM 89856, 10.111 1, 73.6 mm SL, same locality of holotype, 16 March 10.112 2011, N. K. Lujan, F. C. T. Lima, T. C. Pessali and T. F.

Teixera; ROM 89895, 3, 86.4–93.8 mm SL, same data as holotype; ROM 89897, 3, 80.7–92.7 mm SL, same locality as holotype, 20–22 March 2011, T. C. Pessali and T. F. Teixera; ROM 91390, 1, not measured, upper

- 11.5 Kuribrong River at right (south) bank tributary mouth, 05.32438°, -059.57321°, 15–17 October 2011, D. Abraham and N. K. Lujan; ROM 91506, 2, not measured, small right (south) bank tributary of upper Kuribrong upstream upper rapids (rapid 3), 05.33458°,
- 11.10 -059.56738°, 15, 16 and 18 October 2011, D. Abraham and N. K. Lujan; ROM 91402, 1, not measured, upper Kuribrong River at upper rapid (rapid 3), 05.34109°, -059.56474°, 24 October 2011, N.K. Lujan, D. Abraham, D. Stoby, D. Gordon and O. Williams; ROM 94980, 2, 11.15 not measured, rapid 6, tributary of upper Kuribrong, Itabu Creek, 05.29113°, -059.71923°, 28 March 2014, D. C. Taphorn, E. Liverpool, H. Lopéz-Fernández, M. Benjamin and G. Pablo.
- 11.20 Non-types: All collections GUYANA, Region 8 (Potaro-Siparuni), Kuribrong River, Potaro River-Essequibo River drainage. AUM 62801, 1, Kuribrong River, above Amaila Falls in rapid 1, 05.37608°, -59.55053°; AUM 62811, 1, Kuribrong River, at riffle midway between rapid 1 and 2, 1.58 km SSE of Amaila River confluence, 05.36405°, -59.54318°. These specimens are small juveniles whose identity cannot be confirmed.

Diagnosis: Corymbophanes ameliae can be 11.30distinguished from C. andersoni by having dark and light vermiculations on the ventral surface and bands in the caudal fin (vs. white spots on the caudal fin and ventral surface white to grey) and by generally having the anal fin i,5 (vs. i,4; two specimens of C. ameliae 11.35are i,4). Corymbophanes ameliae can be separated from C. kaiei by having a longer head (Fig. 7) that is more rounded (vs. straight), by having a narrow caudal peduncle, visible dorsally by being nearly flat at end and ventrally by having the minimum caudal 11.40peduncle width 10.1-12.2% HL (vs. 12.3-13.0% HL; Fig. 7). Corymbophanes ameliae can be separated from the new genus Yaluwak by lacking hypertrophied cheek odontodes and evertible cheek plates. The only other loricariid with which Corymbophanes ameliae is 11.45sympatric is *Hypostomus hemiurus*, from which it can be distinguished by lacking an adipose fin.

Description: Morphometrics in Table 4; meristics in Table 5. Counts and measurements based on 16
 11.50 specimens. It is a member of subfamily Hypostominae, tribe Ancistrini sensu Lujan et al. (2015). Small to medium-sized loricariids, largest specimen examined 100.6 mm SL. Body narrow, subcylindrical with ventral surface completely flat, dorsal surface flattened from dorsal to adipose origins and tapering

from cleithrum to caudal fin. Head gently sloped to dorsal fin. Parieto-supraoccipital not higher than nuchal region. Dorsal slope decreasing in straight line to insertion of dorsal procurrent caudal-fin rays then ascending to caudal fin. Body depth greatest at origin of dorsal fin. Ventral profile flat to caudal fin. Caudal peduncle almost triangular in cross section: flattened laterally, becoming transversely pointed dorsally and flattened ventrally. Body widest at origin of pectoral fins, narrowest at origin of caudal fin. Snout rounded.

Eye small (orbit diameter  $15.3 \pm 1.0\%$  of head length),dorsal rim of orbit slightly higher than interorbitalspace. Iris operculum absent. Interorbital space withslight, rounded, median hump. Parieto-supraoccipitalstraight posteriorly with no crest. Infraorbitals, frontal,nasal, compound pterotic and parieto-supraoccipitalsupporting odontodes. Preopercle without odontodes.Exposed portion of opercle oval (long axis inanteroventral to posterodorsal angle) covered with11.75

Lips covered with short papillae with circular bases. Lower lip wide, reaching just to, or slightly short of, pectoral girdle; upper lip narrow. Edge of lower lip smooth. Maxillary barbel reaching about half distance to gill opening from base of barbel.

11.80

Median plates 22(1), 23(11) or 24(4). Plates unkeeled, but first three or four plates of mid-ventral series bent to form a slight ridge and ventral plates posterior to pelvic fin with concave dorsal halves forming ventral 11.85ridge; ventral ridge most pronounced posteriorly. Mid-dorsal plate row consisting of just three plates anteriorly; mid-ventral plate row ends ventral to anterior portion of postdorsal ridge; dorsal and median plate rows complete, ventral row beginning 11.90 dorsal to pelvic-fin origin; three caudal peduncle plate rows. Plates on all dorsolateral surfaces of body; ventral surface of head and abdomen naked. Cheek plates not evertible; cheek dontodes slightly longer than average body odontodes present along dorsal-. 11.95adipose-, pelvic-, caudal- and pectoral-fin spines; larger individuals with somewhat larger odontodes at tip of pectoral spine.

Dorsal fin ii,7; dorsal spinelet V-shaped, dorsal-fin 11.100 locking mechanism present, spinelet ranging from covered in skin to just slightly exposed; last ray of dorsal fin almost reaching postdorsal ridge when adpressed. Adipose fin absent, replaced by postdorsal ridge of 12(2), 13(3), 14(3), 15(3), 16(4) or 18(1) median, azygous plates. Caudal fin i,14,i (one specimen i,13,i); 11.105 caudal fin slightly forked, ventral lobe longer than dorsal lobe. Pectoral fin i,6; pectoral-fin spine reaching almost to pelvic fin when adpressed. Pelvic fin i,5; pelvic-fin spine extending almost to anal fin when adpressed. Anal fin i,4(2) or i,5(14); unbranched anal-11.110 11.111 fin ray slightly shorter than first branched ray. 11.112

$\begin{array}{c} 12.55\\ 12.56 \end{array}$	12.50	12.45		12.40		12.35		12.30	12.20	10.05	12.20	12.15	10.15	12.10	19.10	12.5	
Table	4. Morphometric	s of all thr	ee specie	s of <i>Cor</i> y	hqodm	<i>anes</i> a	nd <i>Yaluu</i>	vak primus	6								
		Co	rymbopha Eigenm	thes ander ann 1909	rsoni		Arr	Corymboph nbruster an	anes kaŭ d Sabaj	ei 2000		<i>Corymbop</i> new	<i>hanes an</i> species	neliae		Yaruwak genus, 1	<i>primus</i> new 1ew species
ILM	Measurement	Holotype	N Mean	SD	Min N	Iax ]	Holotype	N Mean	SD	Min	Max Holot	ype N Mea	n SD	Min	Max	Holotype	Paratype
1-20	Standard	65.5	4 58.4	9.1	46.1 6	5.5	65.6	7 62.5	22.5	47.6	108.9 89.3	16 85.5	11.2	55.8	100.6	122.9	103.4
1_10	Dradoreal	43.1	4 43 K	-	49.3 A	α Υ	Percer	nts of stan	dard le	ngth 43-1	44 4 45 9	16 AK A	00	43.0	47.0	59 1	0 77
0T-T	length	40.1	4 40.0	1.1	46.0	0.4	70.0	1.04	0.4	40.1	44.4 40.4	10 40.4	.0.3	40.0	41.0	1.20	44.3
$1-7 \\ 1-12$	Head length Snout-pectoral	34.0 28.1	$\begin{array}{ccc} 4 & 34.3 \\ 4 & 28.9 \end{array}$	0.6 0.6	33.9 3 28.1 2	5.2 9.4	20.2 15.1	$\begin{array}{ccc} 7 & 32.2 \\ 7 & 25.1 \end{array}$	$1.5 \\ 1.7$	30.5 23.1	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	16 32.8 16 24.9	8 0.9 1.1	31.0 22.3	34.8 26.4	39.7 34.2	35.4 27.5
12 - 13	Thorax length	21.0	4 22.5	1.5	21.0  2	4.1	16.5	7 24.7	1.7	22.3	26.7 $25.4$	$16 \ 25.1$	1.0	23.3	26.3	30.6	25.5
12 - 29	Pectoral-spine	23.8	4 23.0	1.0	21.5 2	3.8	14.0	7 22.5	1.6	20.4	24.3 23.2	16 22.5	1.4	19.3	24.2	31.3	26.1
13 - 14	Abdominal	21.5	4 20.8	0.5	20.3 2	1.5	14.9	7 21.7	0.7	20.9	22.7 $23.1$	16 21.9	1.1	19.4	24.4	26.9	22.3
13 - 30	length Pelvic-spine	23.7	4 23.9	1.9	21.4 2	15.9	16.9	7 23.9	1.9	21.9	26.6 19.7	16 21.4	1.1	19.0	22.9	25.1	23.3
14–31	length Anal-fin base	5.1	4 3.7	0.9	3.1 5	.1	3.3	7 4.7	0.5	4.0	5.3 3.8	16 4.5	0.7	3.4	5.5	4.3	3.2
14 - 15	lengtn Postanal length	32.1	4 30.1	1.6	28.2 3	2.1	18.2	7 27.9	1.1	26.1	29.6 27.6	16 28.2	1.9	24.6	32.1	38.8	31.1
14–31	Anal-fin spine length	12.0	4 11.4	1.0	10.0 1	2.2	10.2	7 14.4	1.0	13.0	15.6 14.7	16 14.5	1.5	11.7	17.3	11.4	9.8
15 - 19	Caudal- peduncle	11.0	4 11.2	0.9	10.0 1	2.1	7.7	7 12.3	0.6	11.7	$13.5 \ 13.2$	16 11.5	9.0	10.9	13.4	14.2	10.9
17 - 19	depth Adipose-caudal	28.8	4 28.5	0.7	27.5 2	9.2	18.7	7 28.7	1.6	26.5	31.5 23.6	16 26.3	2.3	23.1	31.6	24.7	22.9
	distance	C I			Ē		, c						Ţ	C E	Ţ		c c
/.T9T	Interdorsal distance	2.7	4 8.3	L.9	6.7 I	0.9	0.0	1 9.4	0.8	X.X	10.7 11.8	16 10.5	L.3	0.1	11.9	20.0	13.6
10 - 16	Dorsal-fin base langth	19.5	4 20.5	1.4	19.3 2	2.1	12.4	7 19.0	0.8	17.7	20.1 18.8	16 18.1	1.4	14.2	20.2	22.2	20.2
10 - 11	Dorsal-spine length	24.0	4 23.2	0.7	22.5 2	4.0	15.1	7 22.9	1.9	19.7	25.0 21.9	16 22.2	1.6	19.1	25.0	I	20.8
	Folded dorsal- fin length	29.3	3 29.3	0.9	28.4 3	0.2	20.0	7 30.1	1.0	29.2	32.0 30.8	16 28.1	1.1	26.7	30.8	32.0	25.7
$7-12 \\ 10-12$	Head depth Dorsal-pectoral depth	16.2 25.4	$\begin{array}{ccc} 4 & 16.7 \\ 4 & 25.0 \end{array}$	$1.2 \\ 0.7$	$\begin{array}{ccc} 15.7 & 1\\ 24.2 & 2\end{array}$	8.5	11.6 18.8	7 18.1 7 28.2	$0.5 \\ 1.1$	$17.4 \\ 26.0$	$\begin{array}{cccc} 18.7 & 19.3 \\ 29.6 & 28.9 \end{array}$	16 17.7 16 28.9	3.1	6.7 25.8	19.9 30.9	21.3 32.3	$17.2 \\ 26.7$
$12.110 \\ 12.111 \\ 12.112$	12.105		12.100	12.95		12.30	19 00	12.85		12.80	12.75		12.70		12.65		12.60

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$13.55 \\ 13.56$	13.50	13.45	10.45		13.40		13.35		13.30		13.25		13.20		13.15		13.10		13.5	
Table :	4. Continued		orvn.	nhonhane	s ander	inos.			Corvmhc	by souther ke	niei			orvmh	sanadao	amelia	an		Yaruwak	nrimus new
			ч <i>с</i> бо Н	Gigenman	n 1909	1100		Aı	mbruste	r and Sab	aj 2000			u u	ew spec.	ies	2		genus, n	ew species
ILM	Measurement	Holotype	N	Mean	SD	Min	Max	Holotype	N Mea	n SD	Min	Max	Holotype .	N N	lean S.	D	lin M	ax F	Iolotype	Paratype
10-13	Dorsal-pelvic	18.6	4	18.6	1.5	16.6	19.8	12.5	7 19.0	) 1.3	17.4	21.1	20.2	16 19	9.9	1.4 1	7.5	23.0	27.2	22.9
10 - 16	Pelvic-dorsal	21.3	4	21.2	1.2	20.0	22.8	14.4	7 22.0	) 1.5	19.2	23.7	22.6	16 2	2.0	1.1 1	9.5	23.6	28.5	23.5
14–16	uepui Dorsal-anal donth	15.1	4	14.0	1.1	12.8	15.1	11.6	7 15.9	1.0	14.5	17.6	16.5	16 1	5.5	1.0 1:	3.1	17.2	19.1	17.1
14 - 17	Adipose-anal	13.3	4	13.6	0.8	12.6	14.4	9.6	7 15.2	0.5	14.6	15.9	16.3	16 1	5.2	1.0 1:	2.9	16.4	20.5	16.1
17 - 20	depth Adipose- hypural	31.1	4	30.5	1.2	28.8	31.6	19.9	7 29.7	, 1.7	27.6	32.0	25.3	16 23	8.0	1.9 2	5.3	31.5	25.7	25.1
14–20	distance Anal-hypural	34.1	4	34.1	1.6	32.0	35.6	21.8	7 30.9	7.3	14.5	35.3	33.5	16 33	3.4	1.9 3	1.3	37.6	37.0	32.6
	anstance Caudal- peduncle	14.0	4	13.6	1.1	12.5	15.0	10.9	7 15.5	1.0	13.9	16.7	17.8	16 1	4.6	1.5 1	1.5	17.8	20.8	18.3
89	width Cleithral width	27.4	4	28.1	2.0	25.8	30.5	17.9	7 27.4	0.9	26.0	28.8	30.5	$16 \ 23$	8.3	1.3 2	5.6	30.5	33.8	30.0
	Min. caudal- peduncal	mn	0	mn	uu	uu	mn	2.6	5 2.9	9 2.0	3.8	4.3	3.7	16	3.5	0.2	3.2	4.0	4.8	4.1
	width							Dowe	nonte of	يما اممط	horth									
5-7	Head-eye	34.5	4	33.8	1.3	32.3	35.1	8.2	7 41.4	1 2.5	39.5	46.1	41.5	16 49	2.0	1.8 33	9.4	45.8	37.9	30.0
4-5	Orbit diameter	11.5	4	12.9	1.8	11.5	15.4	3.5	7 16.8	1.1	14.4	17.9	16.0	16 1	5.4	1.1 1;	3.5	17.4	12.9	13.0
1-4	Snout length	64.6 19 E	4 -	66.6 1 1 1	1.9	64.6 10 E	69.1 15 0	12.3 2.0	7 60.4	1.4	58.1	62.3	61.7	16 6	1.2	2.0 5	9.9	64.6 1 E E	64.7	66.8 12.8
2-4	Lye-nares distance	0.21	4	14.1	<b>I.</b> 4	0.21	10.Y	×.	1 13.5	0.1 0	C.11.	10.8	14.0	1 01	0. <i>.</i> 0	Π.α.Τ.		C.CI	13.2	13.8
1 - 2	Snout-nares	46.6	4	49.0	1.6	46.6	50.4	9.2	7 43.5	2.3	39.3	46.4	47.2	16 4	5.8	3.1 4.	2.5	55.9	45.2	45.7
$2^{-3}$	Internares	10.1	4	10.7	0.6	10.1	11.3	3.2	7 16.9	2.9	14.0	22.0	18.1	16 10	6.0	1.3 1,	4.0	18.1	20.8	11.9
5-6	width Interorbital	33.2	4	34.0	0.6	33.2	34.8	9.0	7 45.2	2.9	41.0	49.9	48.6	16 4	4.4	2.5 39	8.6	48.6	38.1	34.7
	width	1 00	-	0.00	C 7	100		C L		Ţ	00		0 10		0				0.00	
21-22	Month width	63.6	4 4	67.3	4.6	63.6	73.4	0.2 12.2	7 56.8	6.1 6.6	46.4	62.5	62.4	10 19 19	5.2 5.2	3.9 4	t.0	62.4	07.00 68.7	70.1
1-24	Mouth length	60.7	4	62.5	3.1	60.7	67.0	10.2	7 53.0	1.3	50.8	54.4	52.1	16 55	3.6	3.6 4	8.7	6.09	61.0	61.7
25-26	Dentary tooth cup length	22.7	4	23.8	1.8	22.0	25.6	3.3	7 15.7	2.1	13.4	18.6	15.3	16 10	6.8	1.7 1 <sup>.</sup>	4.6	21.0	23.7	24.7
ILM, Inte	sr-Landmark.																			
$13.110 \\ 13.111 \\ 13.112$	13.105		13.100		13.95			13.90	13.85		13.80		13.75		13.70		10.00	13 65		13.60

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# PHYLOGENY OF CORYMBOPHANES CATFISH CLADE

able 5. Meristics o				nbobha	nes and	LUDDAN WAY										
	Co	orymb. Eig	ophanes a	nderson 1909	$\dot{r}$	Arn (	Jorymbop	hanes ka ind Sabaj	iei 2000		Corymbc ne	<i>phanes</i> w speci	amelia¢ es		Yaruu new g	<i>ak primus</i> enus, new pecies
	Holotype	N	Mode 1	Min	Max	Holotype	N Mot	le Min	Max	Holotype	N M	ode	Min	Max	Holotyp	e Paratyp
ateral-line plates	23	4	23 2	23	26	24	7 23	23	24	23	16 23		22	24	25	25
lates under dorsal fin	9	4	8	9	00	9	7 6	9	9	9	16 6		5	9	9	9
iterdorsal plates	က	4	3 1	1	ŝ	ŝ	7 3	3	4	4	16 4		ŝ	5	7	5
dipose-caudal nlates	11	4	11	10	12	11	7 11	10	11	6	16 10		6	11	8	6
lates under folded dorsal fin	6	4	3	6	10	6	7 9	6	10	6	16 9		8	10	6	6
ostanal plates	11	4	11 1	11	12	12	7 11	10	12	12	16 11		10	13	11	11
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lates below folded	œ	4	8	8	10	7	7 7	7	00	7	16 7		9	00	7	80
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eft premaxilary +ooth	0	က	цэ 	56	72	59	7 58	43	59	59	15 48		44	76	77	72
orsal-fin branched	7	4	7 7	7	7	7	7 7	7	7	7	16 7		7	7	7	7
rays	c		, ,		c		, ,	c	c	c	0 0 1		c	c	c	c
ectoral-tin branched ravs	9	4	9	O	9	6	/ 6	9	9	9	16 6		9	9	9	9
elvic-fin branched	5	4	5	10	5	5	7 5	5	5	5	16 5		5	5	5	5
rays nal-fin branched	4	4	4	स	4	ณ	7 5	5 C	5	บ	16 5		4	5	ŝ	4
rays andal-fin	14	4	14	14	14	14	7 14	14	14	14	11 14		13	14	14	14
branched rays			-	-	1	-	-	4	•	-				4		-
ostdorsal azygous plates	16	4	16 1	13	17	15	7 14	13	17	14	16 16		12	18	7	00
-																
14.1 14.1	14 11	14.1		14.		14.	14.		14.	14.'		14.		14.0		14.6

Teeth bicuspid with lateral cusp one-half to threequarters length of medial cusp and lateral cusp half width of medial cusp; 38–70 left dentary teeth (mode 54; one specimen damaged); 44–76 left premaxillary teeth (mode 44; one specimen damaged).

Coloration: Dorsal surface and sides of head and body dark brown to black with small white to cream-colored spots (most spots smaller than 15.10eve size; Figs. 4, 5). Light spots smallest and most tightly spaced on head, becoming slightly larger and more irregularly spaced towards caudal peduncle; combining to form bars and/or vermiculations in some larger specimens. Ventral surface brown 15.15with distinct white vermiculations (light and dark vermiculations of approximately equal width); centre of dark vermiculations often fade towards middle of abdomen. Fin spines and rays tan to cream with dark spots forming bands (interradial membranes 15.20grev to brown): light areas generally narrower than intervening dark bands. Juveniles more uniformly coloured; appear medium to dark brown overall except for faint light spots on head, faint light bands on caudal fin and lightly pigmented abdomen; sides 15.25of body slightly darker midlaterally, forming broad, diffuse, dark brown stripe.

15.5

15.55

15.56

15.30 Sexual dimorphism: Only nuptial male specimen known was found dead in a stream (AUM 53676, 100.6 mm SL, sex determined by examining gonads;

Fig. 4). Specimen has slightly thickened skin over dorsal and lateral surfaces of body and posterior part of head. Skin greatly thickened in circular patch anterior to nares with fleshy area extending over 15.60snout tip. Skin in this patch rugose with greatly elongated odontodes distributed along the periphery of the naked area. Some hypertrophied odontodes in the centre of the circle, but the soft tissue is damaged due to rot. Longest odontodes at anterior 15.65corners of snout with largest much longer than head (38.7 mm long, 116% of head length). Odontodes also considerably longer along back of circle (longest 16.8 mm long, 47.8% of head length). Damage caused by rot means odontodes are loosely held in flesh and 15.70some are pushed inward, making exposed length difficult to ascertain. Pectoral-spine odontodes barely, if any, greater than other specimens. Out of the >40 specimens of *Corymbophanes* that have been deposited in collections, this is the only individual to 15.75show any sign of sexual dimorphism.

Range: Known only from the Kuribrong Riverdrainage upstream of Amaila Falls, and within thisdrainage only from regions adjacent to four rapidshabitats (rapids 1, 3, 4 and 5; Figs. 1, 3).

 15.35
 Isolar

 15.40
 Isolar

 15.45
 Isolar

 15.50
 Isolar

**Figure 4.** Sexually dimorphic male *Corymbophanes ameliae*, AUM 53676, 100.6 mm SL, Guyana, Region 8, tributary of Kuribrong River above Amaila Falls, 05.36637°, -059.54324°, 456 m a.s.l., 29 March 2011. Photos by NKL.

15.85 15.90 15.90 15.95 15.95 15.100 15.105

**Figure 5.** Corymbophanes ameliae paratype, ROM 89897, 80.8 mm SL, Guyana, Region 8 (Potaro-Siparuni), Kuribrong River at rapids ~15 min upstream of upstream Kuribrong Camp, 05.33766°, -059.56615°, 454 m a.s.l., 19–20 March 2011. Photos by NKL.

15.110

15.111

*Etymology:* Named for Amelia, a Patamona Amerindian girl who disappeared near Amaila Falls in the late 19<sup>th</sup> century. The falls are named for her, but her name was misspelled.

16.5

Haplotype diversity: Within Corymbophanes ameliae, ND2 provided the most geographically associated variation (Fig. 3), although Cytb also 16.10exhibited multiple haplotypes that corresponded with geography. 16S was variable but geographically uninformative, and no fixed polymorphisms were observed within the nuclear RAG1 or RAG2 regions. The phylogenetic analysis (Fig. 2, Node 5: BI: 0.97, ML: 64) and ND2 haplotype network (Fig. 3) 16.15 both supported a sister relationship between the C. ameliae population in tributary 4 (rapid 5) and those in the remainder of the upper Kuribrong River watershed (rapids 1–4; see Fig. 3 inset map). Some 16.20population structure was also detected within the upper Kuribrong River main channel, with a few individuals from rapid 1 immediately upstream of Amaila Falls being distinguished from both syntopic individuals and more upstream populations by a single ND2 polymorphism (Fig. 3). 16.25

## YALUWAK LUJAN & ARMBRUSTER, GEN. NOV.

16.30 urn:lsid:zoobank.org:act:62553708-A74C-4695-88A0-76B32F1C0EB4

Type species: Yaluwak primus, sp. nov.

16.35
Diagnosis: Yaluwak can be distinguished from the Hypostominae genera Corymbophanes, Hypostomus and Pterygoplichthys and from all non-Hypostominae loricariids by having a cluster of
16.40 >25 evertible cheek odontodes (vs. cheek odontodes absent or <10); and from all other members of the Hypostominae except some Ancistrus species</li>

(Norman, 1935) and <i>Leptoancistrus</i> by lacking an adipose fin, having instead a low ridge of azygous plates. <i>Yaluwak</i> can be diagnosed from all <i>Ancistrus</i> species and <i>Chaetostoma carrioni</i> by having a	16.60
fully plated snout, from <i>Araichthys loro</i> by having a taller caudal peduncle (10.9, 14.2% SL, vs. $\leq 8\%$ ) and longer tooth rows (23.7, 24.7% HL, vs. 19%) and from <i>Leptoancistrus</i> by lacking cheek odontodes that extend past the cleithrum and having dorsal	16.65
fin il,7 (vs. il,8). <i>Yaluwak</i> is also differentiable from <i>Corymbophanes</i> by its larger maximum body size (122.9 vs. 100.6 mm SL).	16.70
<i>Etymology: Yaluwak</i> is the Patamona Amerindian word for this species (and used generally for larger loricariids). The pronunciation of the 'l' in <i>Yaluwak</i> is a guttural 'lr' sound. Name is treated as masculine.	16.75
Included species: Yaluwak contains only the type species	16.80
YALUWAK PRIMUS LUJAN, ARMBRUSTER & WERNEKE, SP. NOV. [FIG. 8, TABLES 4, 5]	
urn:lsid:zoobank.org:pub:C0ADB1A2-4850-49A4- 9DBC-34CA9F6CB6BC	16.85
<i>Holotype:</i> CSBD F1722, ex. AUM 67193, female, 122.9 mm SL, Guyana, Region 8 (Potaro–Siparuni); 5.08867°, -59.96952°, 634 m a.s.l.; Sukwabi Creek, East Fork, downstream of Wotowanda Falls; 13 January 2016; J. W. Armbruster, N. K. Lujan, D. I. Brooks, D. C. Werneke, P. Peters, R. Daniel, local fishermen; tissue tag:	16.90
	<ul> <li>(Norman, 1935) and Leptoancistrus by lacking an adipose fin, having instead a low ridge of azygous plates. Yaluwak can be diagnosed from all Ancistrus species and Chaetostoma carrioni by having a fully plated snout, from Araichthys loro by having a fully plated snout, from Araichthys loro by having a fully plated snout, from Araichthys loro by having a taller caudal peduncle (10.9, 14.2% SL, vs. ≤8%) and longer tooth rows (23.7, 24.7% HL, vs. 19%) and from Leptoancistrus by lacking cheek odontodes that extend past the cleithrum and having dorsal fin ii, 7 (vs. ii, 8). Yaluwak is also differentiable from Corymbophanes by its larger maximum body size (122.9 vs. 100.6 mm SL).</li> <li>Etymology: Yaluwak is the Patamona Amerindian word for this species (and used generally for larger loricariids). The pronunciation of the T in Yaluwak is a guttural 'hr' sound. Name is treated as masculine.</li> <li>Included species: Yaluwak contains only the type species</li> <li>YALUWAK PRIMUS LUJAN, ARMBRUSTER &amp; WERNEKE, SP. NOV. [FIG. 8, TABLES 4, 5]</li> <li>urn:lsid:zoobank.org:pub:COADB1A2-4850-49A4-9DBC-34CA9F6CB6BC</li> <li>Holotype: CSBD F1722, ex. AUM 67193, female, 122.9 mm SL, Guyana, Region 8 (Potaro–Siparuni); 5.08867°, -59.96952°, 634 m a.s.l.; Sukwabi Creek, East Fork, downstream of Wotowanda Falls; 13 January 2016; J. W. Armbruster, N. K. Lujan, D. I. Brooks, D. C. Werneke, P. Peters, R. Daniel, local fishermen; tissue tag:</li> </ul>

(see summary in: Oliveira *et al.*, 2016), Araichthys loro Zawadzki *et al.*, 2016, Chaetostoma carrioni

*Paratype:* AUM 67193, female, 103.4 mm SL; same data at holotype; tissue tag: AUF10303.

Key to species of <i>Corymbophanes</i>
<ul> <li>1a. Dorsal and lateral body and fins black with white spots, abdomen white to grey; anal fin i,4</li></ul>
caudal peduncle robust, distinctly oval dorsarly at caudal nii, tapering signify along length, inininal caudal peduncle width 12.3–13.0% HL; head more pointed Corymbophanes kaiei, upper Potaro River

Diagnosis: As for genus above.

Description: Morphometrics in Table 4; meristics in Table 5. Counts and measurements based on two 17.5specimens. Member of subfamily Hypostominae, tribe Ancistrini sensu Lujan et al. (2015). Medium-sized loricariids, largest specimen examined 122.9 mm



Figure 6. Corymbophanes ameliae holotype, CSBD F1721, 89.3 mm SL, Guyana, Region 8 (Potaro-Siparuni), Kuribrong River at rapids ~15 min upstream of upstream Kuribrong Camp, 05.33766°, -059.56615°, 454 m a.s.l., 19-20 March 2011. Photos by JWA.

SL female. Body narrow, subcylindrical with ventral surface completely flat, dorsal surface flattened form dorsal to adipose origins and tapering from 17.60cleithrum to caudal fin. Head gently sloped to dorsal fin. Parieto-supraoccipital not higher than nuchal region. Dorsal slope decreasing slightly in a straight line to insertion of dorsal procurrent caudal-fin rays then ascending to caudal fin. Body depth is greatest at the origin of the dorsal fin. Ventral profile flat to 17.65the caudal fin. Caudal peduncle ovoid in cross section: flattened dorsally and ventrally. Body widest at origin of pectoral fins, narrowest at origin of caudal fin. Snout rounded.

17.70Eve small (orbit diameter 12.9, 13.0% of head length), dorsal rim of orbit slightly higher than interorbital space. Iris operculum absent. Interorbital space with slight, rounded, median hump. Parieto-supraoccipital straight posteriorly with no crest. Infraorbitals, frontal, 17.75nasal, compound pterotic and parieto-supraoccipital supporting odontodes. Preopercle without odontodes. Ventral margin of opercle covered with uniformly small odontodes, but dorsal two thirds of opercle covered in skin. 17.80

Lips covered with short papillae with circular bases. Lower lip wide, reaching just to or slightly short of pectoral girdle; upper lip narrow. Edge of lower lip smooth. Maxillary barbel only barbel present, barely free from lip, not reaching to base of evertible cheek plates.

Median plates 25. Plates unkeeled, but first three or four plates of mid-ventral series slightly bent to form slight ridge and ventral plates posterior to anal fin slightly bent to form a weak ridge. Dorsal, mid-dorsal, median and mid-ventral plate rows complete, ventral row beginning with single plate dorsal to pelvic-fin origin

C. ameliae

30

25 HL



17.85

17.90

17.30

17.35

17.40

17.45

17.50

35

30

20

15

40

50

60

70

SL

C. ameliae

kaie

80



Δ

35



110

Minimum Caudal Peduncle Width

3.5

3

2.5

15

C. kaiei

20

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90

100

and then no plates until after pelvic-fin base in holotype and only after pelvic-fin base in paratype; three caudal peduncle plate rows. Plates on all dorsolateral surfaces of body except for a fairly large patch lacking plates between 18.5pterotic and start of median plate row, and relatively large area lacking plates above pectoral-fin base caused by anterior plates of mid-ventral plate rows being shorter than other plates in series; throat and abdomen lacking plates. Ventral plates meet at midventral line on caudal 18.10 peduncle, but plates are covered in thick skin and do not support odontodes. Cheek plates moderately evertible (to ~30° from head); 40, 47 moderately hypertrophied cheek odontodes with none reaching further than exposed portion of opercle. Odontodes slightly longer than 18.15 average body odontodes present along dorsal-, adipose-, pelvic-, caudal- and pectoral-fin spines.

Dorsal fin ii,7; dorsal spinelet V-shaped, dorsal-fin locking mechanism functional, spinelet ranging from covered in skin to just slightly exposed; last ray of dorsal 18.20 fin almost falling far short of postdorsal ridge when adpressed. Adipose fin absent, replaced by postdorsal ridge of seven to eight median, azygous plates. Caudal fin i,14,i; caudal fin almost straight, ventral lobe longer than dorsal lobe. Pectoral fin i,6; pectoral-fin spine 18.25reaching to posterior edge of pelvic-fin spine when adpressed. Pelvic fin i,5; pelvic-fin spine extending almost to anal fin when adpressed, unbranched pelvicfin ray very wide, particularly at base. Anal fin i,3 (holotype) or i.4 (paratype); unbranched anal-fin ray 18.30slightly shorter than first branched ray.

> Teeth bicuspid with cusps almost equal in length; lateral cusp distally pointed and medial cusp wide and flat distally, narrow proximally; 64, 76 left dentary; 42, 77 left premaxillary teeth (smaller specimen with 58 right premaxillary teeth).

Coloration: Light brown mottling on a dark brown base; light and dark mottling combine to form indistinct, alternating light and dark stripes on caudal 18.40peduncle (Fig. 8). Abdomen pale white base throughout with light brown or grey stippling around margins and posterior to pectoral girdle. Ventral surface of oral disk cream-coloured. Fins lighter distally than proximally. Pectoral fin with spots on spine and faint or no spots 18.45 on rays; rays darker than membranes, fin especially dark at base and along spine and first branched ray. Pelvic, dorsal and anal fins with small dark spots on rays and dorsal spine, rays considerably darker than membranes; dorsal fin with black band at distal 18.50edge. Caudal fin with dark spots centred on rays, but combining to form bands proximally; number of bands higher in larger specimen. Iris brick red. Colour in life and in alcohol similar, but distinctions between light and dark areas more subdued. 18.55

*Sexual dimorphism:* Unknown, both specimens female and released eggs on capture.

18.60 Distribution: Yaluwak primus is only known from the uppermost rapids of Sukwabi Creek, an eastern arm of the Ireng River (Brazil: Rio Maú), just below Wotowanda Falls. Other similar habitat exists below 18.65 the nearby Andu Falls and Uluk Tuwuk Falls and it seems likely that the species also occurs there, if not also in similar habitats further downstream. 18.70 *Etymology:* The species epithet *primus* comes from the same Latin word meaning first, foremost, chief or principal and is in reference to the large body size of the species and the fact that it retains the evertible cheek odontodes, likely inherited from the common 18.75ancestor of the Yaluwak/Corymbophanes clade. This species name was also inspired by our indefatigable Patamona guide, Mr Primus Peters, who led the collection effort for this species and assisted in innumerable other ways during our 2016 expedition

18.80

18.112

Taxonomic remarks: Since its original description, the genus Corymbophanes has been primarily 18.85 distinguished by its absence of both evertible cheek odontodes and an adipose fin (Eigenmann, 1909, 1912). Given that Yaluwak primus was at least weakly supported as sister to an otherwise monophyletic Corymbophanes, we faced the decision 18.90 of whether to broaden the existing definition of *Corymbophanes* or recognize the new lineage as a distinct genus. Conservative arguments could be made for either choice. Including a species that retains the plesiomorphic character of evertible 18.95 cheek odontodes in Corymbophanes would reduce the proliferation of loricariid genera. However, erecting a new genus allows the historical definition and strong cladistic diagnosis of Corymbophanes to be retained. Our choice of the latter recognizes Eigenmann's 18.100 original concept of Corymbophanes as being a genus similar to *Hypostomus*, i.e. without cheek odontodes. Also, because of the scarcity of obvious morphological characters diagnosing many Hypostominae genera, we argue that when such diagnostic characters 18.105are available, they should be used to advantage by explicitly linking them to the classification scheme. Lastly, there is high support for the monophyly of Corymbophanes (see below), but relatively weak support for sister group relationship between 18.110 Yaluwak and Corymbophanes and deep divergence 18.111

18.56

18.35

to the upper Ireng River.

between these lineages, which are consistent with our choice to erect a new genus.

The presence and characteristics of an evertible

cheek plate mechanism (e.g. evertibility, number and

19.5

19.10

19.15

19.20

19.25

length of odontodes) have long been taxonomically and phylogenetically important for diagnosing the Hypostominae - the only loricariid subfamily in which this mechanism is present (Armbruster, 2004) - and for distinguishing genera and inferring evolutionary relationships throughout Hypostominae. Although the plesiomorphic absence of an evertible cheek odontode mechanism in Corymbophanes caused the cladistic analysis of Armbruster (2004) to place this genus as sister to all other Hypostominae, the molecular phylogeny presented here indicates that absence of these characters is a reversal. The intermediate cheek plate characteristics in Yaluwak (i.e. short odontodes reaching just to the end of the exposed opercle and not to the exposed dorsal process of the cleithrum) help to illustrate the transitional series leading to a lack of cheek odontodes in Corymbophanes. A similar sequential evolutionary loss of evertible cheek odontodes can be seen in the genus Spectracanthicus, in which S. punctatissimus (Steindachner, 1881) has short cheek odontodes while its congener S. murinus

DISCUSSION

Nijssen & Isbrücker, 1987 has none.

19.30 The discovery and description of Corymbophanes ameliae and Yaluwak primus, and this first taxonomically complete, genus-level phylogenetic analyses of the Corymbophanes clade (Araichthys, 19.35 Corymbophanes, Cryptancistrus, Guyanancistrus, Hopliancistrus and Yaluwak; Fig. 2, Node 14), yield new insights into patterns and processes of fish faunal diversification across the oldest highlands of South America. The Corymbophanes clade is particularly valuable for biogeographical study 19.40 because it has a trans-shield distribution in which Corymbophanes, Guyanancistrus and Yaluwak have distributions restricted to the Guiana Shield uplands and Hopliancistrus and Araichthys are distributed exclusively within the Brazilian Shield. Trans-shield 19.45distributions are a widespread biogeographical pattern seen in many other freshwater fish and invertebrate groups, including many other loricariid clades (Farlowella, Harttia, Hypancistrus, 19.50Hypoptopoma, Leporacanthicus, Peckoltia, Pseudacanthicus, Pseudancistrus, Pseudolithoxus, Rineloricaria and Sturisoma), various non-loricariid fishes (Leptorhamdia, Heptapteridae; Archolaemus, Sternopygidae; Synaptolaemus, Anostomidae; Myloplus, Tometes, Serrasalmidae; Machado et al., 19.55

19.56 2018) and a few invertebrates [the bivalve genus

Rheodreissena, Dreissenidae; Geda et al., 2018; the sponge species Drulia cristata (Weltner, 1895), Metaniidae; Oncosclera spinifera (Bonetto & Ezcurra de Drago, 1973), Potamolepidae; Volkmer-Ribeiro, 2019]. Although an incomplete phylogenetic understanding of many of these taxa hinders robust analyses, comparisons of Corymbophanes clade biogeographical patterns with disparate taxa are needed to test the significance of biogeographical phenomena.

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We found the Brazilian Shield lineages Araichthys and *Hopliancistrus* to be separately nested in the mostly Guiana Shield-distributed Corymbophanes clade, indicating that each of these genera separately 19.70 invaded the Brazilian Shield from Guiana Shield ancestors. Although such a pattern might also be hypothesized to have resulted from vicariant subdivision of a historically contiguous range, the bedrock, rheophilic habitats to which these fishes are restricted are not known to have ever been 19.75contiguous across the sediment-filled valley through which the lower Amazon River now flows (i.e. the Amazon Graben). The geologic distinctiveness of the Amazon Graben, and the restriction of many rheophilic freshwater taxa to upland habitats north 19.80 and south of the graben, suggest that it functions as a semipermeable barrier to dispersal among such habitat specialists. Historical periods of glacial maxima during which lower sea levels promoted the down-cutting and incision of many lower Amazon river channels (Irion 19.85 et al., 1997) may have reduced the role that the graben played in limiting dispersal of rheophilic taxa between shield uplands. Phylogeographic data indicate that the loricariid genera Pseudancistrus (Silva et al., 2014) and Pseudolithoxus (Collins et al., 2018) also contain 19.90 lineages that dispersed south from the Guiana Shield to the Brazilian Shield, and a geologically calibrated time tree for Pseudolithoxus (Collins et al., 2018) suggests that such dispersal occurred during the Pleistocene, when sea levels regularly fluctuated over 19.95 a range of >120 m (Waelbroeck et al., 2002).

Within the Corymbophanes clade, the clade containing Araichthys, Corymbophanes, Cryptancistrus and Yaluwak (Fig. 2, Node 9) is particularly 19.100 interesting, because these lineages are distributed along an approximately latitudinal gradient, ranging from 5.38°N (Corymbophanes) to 13.56°S (Araichthys), with Yaluwak and Cryptancistrus in between at 5.09°N and 1.91°N, respectively. The northern clade of Corymbophanes + Yaluwak branches from the 19.105 shallowest node in this clade (Fig. 2, Node 8), whereas the southern lineages Araichthys and Cryptancistrus branch at the base (Fig. 2, Node 9), suggesting that these four genera radiated from a geographically intermediate ancestor, possibly along the southern 19.110 flanks of the Guiana Shield. Although our poor 19.111 phylogenetic resolution for this clade obscures a more 19.112

precise interpretation of its biogeographical history, there is growing evidence for the southern Guiana Shield slope being a region of north-south dispersal in various fish groups. Guyanancistrus brevispinis 20.5(Heitmans et al., 1983), for example, is hypothesized to have dispersed from the Amazonian versant of the Guiana Shield in Brazil northward into coastal Guiana Shield drainages of French Guiana and Suriname (Cardoso & Montoya-Burgos, 2009; Fisch-20.10Muller et al., 2018). Other fishes that appear to have dispersed north-south across this watershed divide include Corydoras bondi bondi Gosline, 1940 (Nijssen, 1970), Paralithoxus cf. stocki (Nijssen & Isbrücker, 1990) (Lujan et al., 2018) and Tetragonopterus rarus 20.15(Zarske et al., 2004) (Silva et al., 2016). Nijssen (1970) described a number of potential headwater corridors near the only known Cryptancistrus similis locality that might provide a dispersal route for fishes between the north-flowing Courantyne and south-flowing Paru 20.20de Oeste rivers, across the Grens and Acarai mountains, which form the drainage divide. However, a parsimony analysis of endemism in fish communities from across the eastern Guiana Shield by Lemopoulos & Covain (2018) found little support for Nijssen's (1970) corridor 20.25hypothesis. They found instead that the Courantyne and Paru de Oeste rivers share only three fish species and these are either also present in the neighbouring Maroni River to the east (Tetragonopterus rarus and Corydoras baderi Geisler, 1969) or are widespread 20.30in the Guianas [Cyphocharax helleri (Steindachner, 1910)], suggesting that dispersal around the central shield highlands to the east or west is more likely than dispersal across these highlands.

The taxonomic discoveries of this study centre on 20.35the western Guiana Shield highlands, which stretch across western Guyana, southern Venezuela and the northernmost border of Brazil, and comprise a plateau with an average elevation of 200-450 m above sea level (m a.s.l.) and dozens of isolated mountains or 20.40tepuis that range up to >2500 m a.s.l. These highlands formed during at least five phases of geologic uplift, and consequent erosion, beginning before the Late Cretaceous (see review by: Lujan & Armbruster, 2011). The 200-450 m a.s.l. plateau that spans this 20.45region was first uplifted in the Late Oligocene to Early Miocene (~30–15 Mya). Uplifted with this plateau were the upper watersheds of rivers that now drain in all directions, including major right-bank tributaries of the Orinoco River (e.g. Caroni, Caura 20.50and Ventuari), left-bank tributaries of the Negro River (Siapa, Ireng and Uraricoera/Branco) and left-bank tributaries of the Essequibo River (e.g. Kuribrong/ Potaro and Mazaruni/Cuyuni). As a consequence, the lower courses of all these rivers are separated from 20.55their headwaters by tall waterfalls and extensive 20.56rapids. Noteworthy among these barriers are the enormous Kaieteur Falls (Potaro River), Amaila Falls<br/>(Kuribrong River), Salto de Oso (Siapa River), Salto<br/>Para (Caura River), Salto Tencua (Ventuari River) and<br/>a series of significant rapids that isolate the upper<br/>Mazaruni. Each of these waterfalls or rapids marks<br/>the upstream limit of many lowland fish species and<br/>the downstream limit of a wide range of headwater-<br/>endemic species and lineages, with loricariid catfishes<br/>being disproportionately represented among the<br/>headwater endemics (Eigenmann, 1912; Provenzano<br/>et al., 2005; Lujan, 2008; Lujan et al., 2013; Maldonado-<br/>Ocampo et al., 2013; Alofs et al., 2014; Table 1).20.60

Given that Yaluwak is at least weakly supported 20.70 as sister to Corymbophanes (Fig. 2, Node 8: BI: 0.59, ML: 67) and that the respective Ireng and Potaro river headwaters, to which these genera are endemic, share a watershed divide (Fig. 1), two different vicariance scenarios might best explain how the most recent ancestor of Yaluwak and Corymbophanes underwent 20.75allopatric speciation. First, a geodispersal or stream capture process in which a portion of the habitat of the ancestral lineage shifted between the Ireng and Potaro could have occurred. Second, geologic uplift may have disrupted a previously contiguous 20.80 distribution, followed by secondary extinction of ancestral populations occupying intervening river channels below the shield escarpment. A third active dispersal scenario is unlikely, because loricariids are not vagile, significant downstream dispersal barriers 20.85(waterfalls) have likely been present for >20 Myr (Schubert et al., 1986) and headwaters of the Ireng and Potaro have likely been embedded in relatively high-elevation terrain (Fig. 1) for even longer. Timecalibrated phylogenies and phylogeographic data for 20.90 multiple taxa spanning both the upper Ireng and upper Potaro and the upland/lowland divide are needed to help differentiate between these hypotheses, although community-wide species distribution patterns provide some initial insights (Table 1). With 13 species shared 20.95between the upper Ireng and upper Potaro basins, these drainages are only slightly less similar than the upper Potaro and upper Kuribrong basins, which share 14 species (Table 1). Regardless, endemism rates are 20.100 high across all three basins, ranging from 42% in the upper Kuribrong to 50% in the upper Potaro and upper Ireng. Endemism rates in the nearby upper Mazaruni River basin are estimated to be even higher, between 67 and 95% (Alofs et al., 2014).

As with the trans-shield freshwater fauna, endemism rates and phylogenetic patterns among fishes of the western Guiana Shield escarpment indicate that many of the species in this region formed vicariantly in response to the intermittent opening and closing of portals/barriers, both between and within major watersheds. Sharing of species between drainages is at least partly a factor of the length and interdigitation 20.105 20.105 20.105 20.105 20.105 20.105 20.105 20.105 20.105

## PHYLOGENY OF CORYMBOPHANES CATFISH CLADE

of their shared watershed divide. Indeed, slightly higher similarity between the fish faunas of the upper Kuribrong and upper Potaro river basins (Table 1: 14 vs. 11–13 shared species) is consistent with these rivers

21.5 sharing a long watershed divide, the lower portion of which runs across terrain with little relief where modest geologic tilting or extensive sheet flooding might lead to intermittent hydrologic connections (Fig. 1). Such connections may have facilitated the dispersal of fishes between drainages.

of fishes between drainages. Haplotype diversity across *Corymbophanes ameliae* populations within the upper Kuribrong suggests that not only have intermittent portals or barriers between major watersheds shaped diversity in *Corymbophanes*,

other individuals by either three or four mutations

- 21.15 but that diversity is also influenced by barriers to gene flow within these watersheds. A distinctive ND2 haplotype was observed at the mouth of the Amaila River, whereas all individuals sampled from rapids further up the Kuribrong main channel shared a
  21.20 different haplotype (Fig. 3). Also, the tributary 4 (rapid 5) population has a haplotype distinguished from all
- (Fig. 3). Tributary 4 is isolated from the main channel of the upper Kuribrong River by an extensive, densely
  21.25 forested swamp at its mouth, through which the river's discharge slows, disperses and likely loses dissolved oxygen before joining the Kuribrong (NKL pers. obs.).
- Considering that tributary 4 headwaters stretch south-east toward headwaters of Muremure Creek,
  a left-bank tributary of the Potaro River (Figs 1, 3; Lujan *et al.*, 2013), and that these rivers are separated
- by a relatively low-elevation drainage divide, we hypothesize that historical dispersal between the Kuribrong and Potaro river basins occurred via these 21.35tributaries. The next closest tributaries are between the uppermost headwaters of the Kuribrong and Potaro (Figs 1, 3), but these tributaries are smaller and cradled within mountainous terrain producing more formidable barriers to dispersal. Intraspecific 21.40morphometric differences (Lujan et al., 2013, Fig. 8) and an unpublished genomic dataset for Characidium amaila, a South American darter (Crenuchidae) that is codistributed with Corymbophanes ameliae, also describe a phenotypically and genetically distinct 21.45tributary 4 (rapid 5) population, plus additional population structure within the upper Kuribrong main channel (Lujan, unpublished).

We are rapidly approaching an exciting time when combinations of new genomic tools and dense, 21.50 widespread sampling from decades of fieldwork will allow us to generate the well-resolved, broadly comparative datasets needed for a more robust understanding of the hydrologic history and colonization processes that shaped the diverse ichthyofauna of the ancient shields of South America. 21.56 However, such a time is still impeded by a lack of



Figure 8. Holotype of Yaluwak primus, CSBD F1722,<br/>122.9 mm SL, Guyana, Region 8 (Potaro-Siparuni),<br/>5. Sukwabi Creek, East Fork, downstream of Wotowanda<br/>Falls, 05.08867°, -059.96952°, 634 m a.s.l., 13 January<br/>2016.21.80

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collections in many of the most remote areas of these shields. The tremendous element of chance involved in the collections of some taxa in this study – such as *Corymbophanes andersoni*, *Cryptancistrus similis* and *Yaluwak primus*, which are known from a total of only six, one and two individuals respectively – suggests that the range and diversity of the *Corymbophanes* clade may be much greater than what is represented in this study. Our results demonstrate that extensive field exploration and dense taxon sampling remain essential prerequisites to the full phylogenetic understanding of the diverse South American biota.

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SUPPORTING INFORMATION

23.50	Additional Supporting Information may be found in the online version of this article at the publisher's web-site.	23.105
	<b>Figure S1.</b> Complete results of the full Bayesian phylogenetic analysis. <b>Figure S2.</b> Complete results of the full maximum likelihood phylogenetic analysis.	

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