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Morphological and molecular study of the torrent catfishes (Sisoridae: Glyptosterninae) of Bhutan including the description of five new species

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Abstract

Torrent catfishes of the subfamily Glyptosterninae from Bhutan are examined based on morphological and molecular data. Five new species are described: *Creteuchiloglanis bumdelingensis* sp. nov., *Exostoma mangdechhuensis* sp. nov., *Parachiloglanis benjii* sp. nov., *P. dangmechhuensis* sp. nov., and *P. drukyulensis* sp. nov. Molecular data derived from the mitochondrial gene Cyt *b* and the nuclear gene RAG2 recovered relationships within *Parachiloglanis* and the Glyptosterninae. A dichotomous key to the Glyptosterninae of Bhutan is provided.

Keywords: *Creteuchiloglanis*, *Exostoma*, *Parachiloglanis*, Glyptosternoid fishes

Introduction

The term "torrent catfish" refers to siluriform fishes that are specially adapted to high-flow environments, typically in mountainous or hilly regions. Though not a natural group, there are convergent features common to catfishes in high-flow environments, such as a dorsoventrally flattened body, development of a ventral adhesive apparatus, an inferior mouth, frequently with suctioning lips, enlarged and horizontally-inserted paired fins, and small body size. These convergent morphologies are exhibited in catfishes found in high gradient streams of the Andes in South America (*Astroblepus*), the mountains and hills of the African Rift (*Chiloglanis*), and throughout Asia and the Middle East (Sisoridae).

In the higher altitudes of the Himalayas, most torrent catfishes belong to the subfamily Glyptosterninae Gill, 1861. Throughout its history, the genera that make up Glyptosterninae have changed several times. In this paper, the authors refer to Glyptosterninae as the group defined by Ng & Jiang (2015). This group includes the following genera: *Chimarrichthys* Sauvage 1874, *Creteuchiloglanis* Zhou, Li & Thomson 2011, *Exostoma* Blyth 1860, *Glaridoglanis* Norman 1925, *Glyptosternon* McClelland 1842, *Myersglanis* Hora & Silas 1952, *Oreoglanis* Smith 1933, *Parachiloglanis* Wu, He & Chu 1981, *Pareuchiloglanis* Pellegrin 1936, and *Pseudexostoma* Chu 1979. The diversity and ecology of many of the glyptosternine genera are poorly known throughout their Himalayan distribution, and even less is known about their diversity in Bhutan due to historically limited access and little inventory work.

The Sisoridae is becoming a relatively well-studied family, particularly with respect to its better-known genera and in better-sampled regions of Asia. The monophyly of the Sisoridae has been corroborated by many authors using both molecular and morphological approaches (Sullivan *et al.* 2006; Ng 2010; Jiang *et al.* 2011; Ng 2015; Ng & Jiang 2015). However relationships within Glyptosterninae remain unresolved, and there remain a few poorly studied and/or phylogenetically enigmatic genera such as *Parachiloglanis*. Molecular data have previously been lacking for *Parachiloglanis*. Only one molecular study of the Sisoridae has included *Parachiloglanis* (Ng & Jiang 2015). However, when Ng & Jiang (2015) published their work, only two species of *Parachiloglanis* (*P. hodgarti* and *P. bhutanensis*) were known, and only *P. hodgarti* was included in their analysis. We herein analyze sequence

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data for a much more robust sampling of *Parachiloglanis*, representing all known species (including those described herein) of the genus for the mitochondrial gene, Cyt *b*, and the nuclear gene RAG2. We hypothesize that *Parachiloglanis* is a monophyletic group which is much more diverse than previously known and together form a clade sister to the rest of the Glyptosterninae.

Of the glyptosternine genera, *Creteuchiloglanis*, *Exostoma,* and *Parachiloglanis,* are found in Bhutan. In this study we account for two known species and describe five new species of Glyptosterninae.

Methods

Fishes were collected during the monsoon and post-monsoon season in 2013 by flipping large rocks with a seine held immediately downstream. Fishes were collected in compliance with local customs; collecting was not conducted on days or in areas of cultural or religious importance, and was done with the permission of local forest jurisdictions as outlined in the permit from the Royal Government of Bhutan Ministry of Agriculture and Forests letter CoRRB/TCO/D2/1065. Specimens were fixed in 10% formalin for 7–10 days before being rinsed and transferred to 70% ethanol for long-term storage. Tissues were removed from the right pectoral and pelvic fins and placed in 95% ethanol and sent to Saint Louis University, Missouri, USA, for molecular analysis. Type specimens were deposited in the National Biodiversity Centre (NBC) of Bhutan and the California Academy of Sciences (CAS); paratypes were split and deposited in either the Royal University of Bhutan College of Natural Resources Natural History Collection (CNR) in Lobesa, Bhutan, NBC, or CAS. Those specimens deposited in CAS were collected by T. R. Roberts in 1995 and remained in an uncataloged collection at CAS until this work. In the Bhutanese materials examined, for each specimen where no tissue sample was taken, there is a four-digit catalog number, whereas those that had tissue samples taken received a five-digit catalog number (based on the tissue catalog system of the authors). In the case of no tissues, the number following CNR is the lot number, followed by the individual specimen number within the lot (each signified with a corresponding gill tag inserted into the right operculum). In the case of multiple specimens examined from a single lot an underscore followed by a hyphenated number is used to represent which specimens were examined (e.g. CNR 1345_2-6). Those that had tissue samples removed are simply individually cataloged with a five-digit number (e.g. CNR 15022).

Figure 1 illustrates measurements used for analyses in this study. Measurements were taken point to point using digital calipers. Fin rays were counted with a backlit dissecting scope; dorsal- and anal-fin ray counts excluded the short "spinlet" rays *sensu* Thomson & Page (2006). Branched and unbranched rays were counted separately. Meristic counts include: dorsal-fin rays, anal-fin rays, caudal-fin rays, pectoral-fin rays, and pelvic-fin rays.

Other characteristics that were used in morphological analysis were the presence or absence of distinct lateral-line pores (punctate lateral line), caudal-fin shape, dentition, adipose-fin morphology, and coloration. Caudal-fin types are described as semilunate, which consists of a roughly symmetrical caudal fin with upper and lower tips connected by an evenly concave, rounded margin; truncate, which consists of a roughly symmetrical caudal fin with upper and lower tips projecting equally and connected by a vertical margin with no curvature; and emarginate, which is similar to truncate but with a slight concave curvature between the upper and lower tip. Diagnostic traits associated with adipose-fin shape in this analysis include the presence or absence of an anteriorly oriented undercut of the posterior end of the adipose fin, and the joining or lack of joining of the posterior end of the adipose fin with the principal caudal-fin rays (adnate versus not adnate, respectively). Dentition patterns were used to diagnose differences within *Parachiloglanis* (Fig. 2).

DNA was extracted using Qiagen DNeasy tissue extraction kits (Qiagen, USA). One mitochondrial gene, Cyt *b* (cytochrome *b*), and one nuclear gene RAG2 (recombination activating gene two) were amplified for analysis. PCR methods follow Jiang *et al.* (2011). All PCR products were sent to htSEQ High-Throughput Genomics Unit (University of Washington, USA) for purification and sequencing. All sequences used in this study were uploaded to GenBank with reference numbers provided in Table 1. Sequences were aligned and checked for stop codons and errors using MEGA (Tamura *et al.*, 2013).

Maximum Likelihood analysis was conducted using RAxML 7.2.8 (Stamatakis 2006). The number of nonparametric bootstrap replications was set as 1000 with the ML criterion. The best-fit partition model was selected using Partition Finder (Lanfear *et al*. 2012). The following partition schemes were selected: Cyt *b* codon position 1 (GTR+I+G); Cyt *b* codon position 2 (GTR+I+G); Cyt *b* codon position 3 (GTR+I+G); RAG2 codon

position 1 (GTR+G); RAG2 codon position 2 (GTR+ G); RAG2 codon position 3 (GTR+G). Trees were built using Figtree with bootstrap values provided at each node. In-group taxa were mined from GenBank to represent a broader spectrum of genera within the Glyptosterninae including: *Chimarrichthys davidi*, *Creteuchiloglanis kamengensis*, *Exostoma labiatum*, *Oreoglanis macropterus*, *Pseudecheneis sulcata*, and *Pseudexostoma yunnanensis*. The following outgroup taxa were mined from GenBank: *Bagarius yarrelli*, *Ictalurus punctatus*, *Hemibagrus nemurus*, *Gagata cenia*, *Gogangra viridescens*, *Glyptothorax fokiensis*, *Glyptothorax macromaculatus*, *Glyptothorax interspinalus*, and *Pseudecheneis sulcata*.

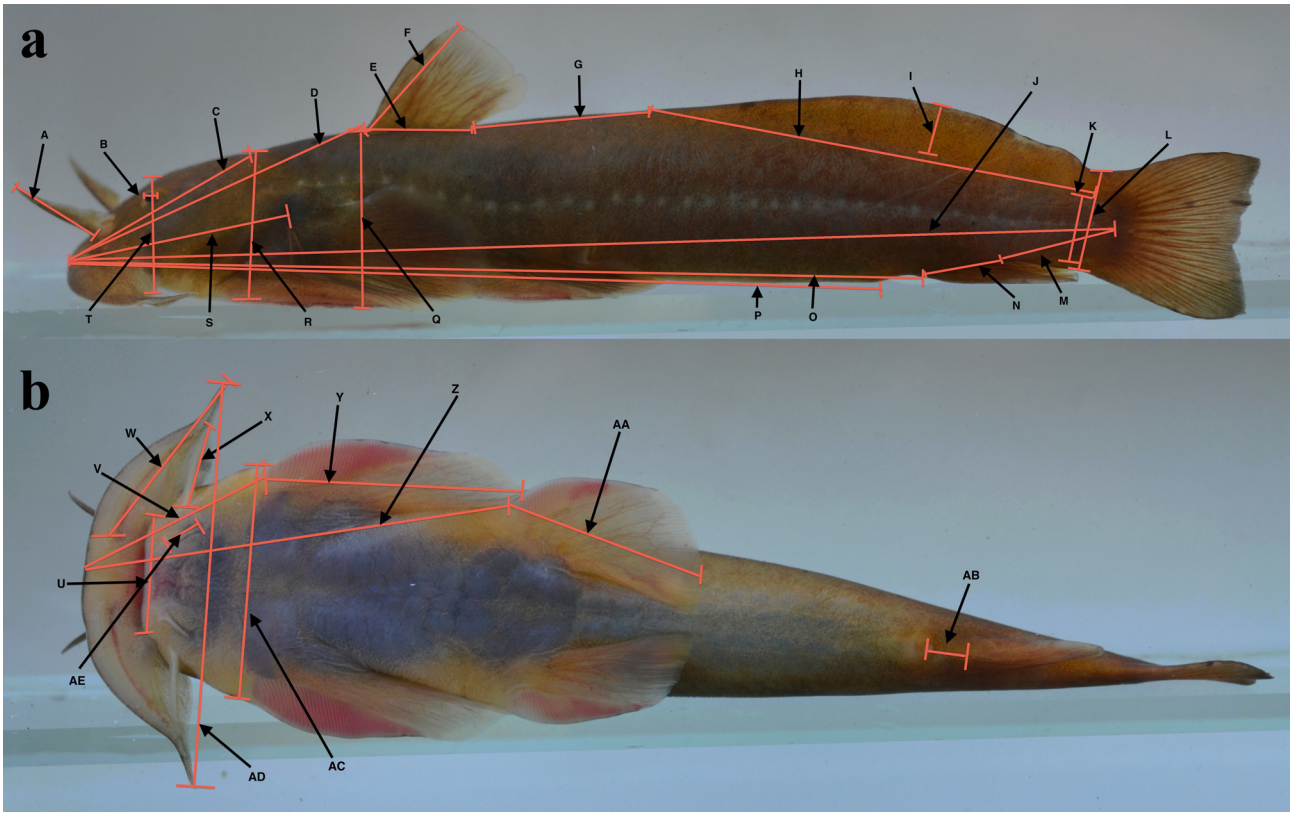

FIGURE 1. Measurements used for morphometric analysis of Glyptosternine catfishes. a) lateral view, b) ventral view. A) nasal barbel length, B) eye width, C) preocciput length, D) predorsal length, E) dorsal-fin base length, F) dorsal-fin height, G) dorsal-adipose length, H) adipose-fin base length, I) adipose fin height, J) standard length, K) caudal-peduncle depth, L) caudal-peduncle depth w/adipose fin, M) caudal-peduncle length, N) anal-fin base length, O) pre-anal length, P) pre-vent length, Q) body depth, R) head depth, S) head length, T) head depth at eye, U) mouth width, V) pre-pectoral length, W) maxillary barbel length, X) outer-mandibular barbel length, Y) pectoral-fin length, Z) pre-pelvic length, AA) pelvic-fin length, AB) vent-anal length, AC) breast width, AD) snout width, AE) inner-mandibular barbel length.

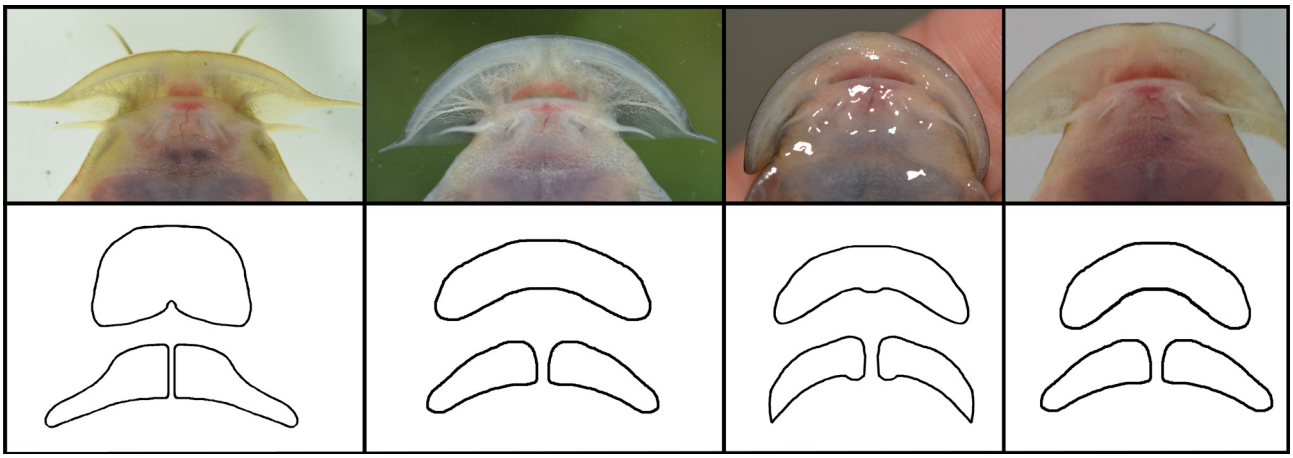

FIGURE 2. Dentition patterns of *Parachiloglanis dangmechhuensis* (a), *Parachiloglais hodgarti* (b), *P. benjii* (c), and *P. drukyulensis* (d).

TABLE 1. GenBank accession numbers for specimens used in the phylogenetic analysis.

Species	Genbank accession number	
	Cyt *b*	RAG2
Bagarius yarrelli	EU490904	DQ492334
Creteuchiloglanis bumdelingensis	MG001351	MG001362
Creteuchiloglanis bumdelingensis	MG001352	MG001363
Creteuchiloglanis kamengensis	DQ192474	DQ192439
Euchiloglanis davidi	DQ192485	DQ192438
Exostoma labiatum	DQ192461	DQ192448
Exostoma mangdechhuensis 15223		MG001364
Exostoma mangdechhuensis 15529		MG001365
Exostoma mangdechhuensis 15222		MG001366
Exostoma mangdechhuensis 15170		MG001367
Exostoma mangdechhuensis 15173		MG001368
Gagata cenia	DQ192468	DQ192432
Glyptothorax fokiensis	HQ593598	HQ593559
Glyptothorax interspinalus	HQ593589	HQ593537
Glyptothorax macromaculatus	HQ593592	HQ593542
Gogangra viridescens	EU490917	DQ508048
Hemibagrus nemurus	AF499600	N020132
Ictalurus punctatus	EU490914	DQ492398
Oreoglanis macropterus	DQ192479	DQ192444
Parachiloglanis benjii 15558		MG001378
Parachiloglanis benjii 15022		MG001379
Parachiloglanis benjii 15010	MG001360	MG001380
Parachiloglanis benjii 15007		MG001381
Parachiloglanis benjii 15006	MG001361	MG001382
Parachiloglanis bhutanensis 15256	MG001359	MG001376
Parachiloglanis bhutanensis 15257	MG001358	MG001377
Parachiloglanis dangmechhuensis 15280	MG001353	MG001370
Parachiloglanis drukyulensis 15538	MG001357	MG001372
Parachiloglanis drukyulensis 15542		MG001373
Parachiloglanis drukyulensis 15539	MG001356	MG001374
Parachiloglanis drukyulensis 15533	-	MG001375
Parachiloglanis hodgarti 15176	MG001354	MG001369
Parachiloglanis hodgarti 15227	MG001355	MG001371
Psuedecheneis sulcatus	DQ192470	DQ192452
Psuedexostoma yunnanensis	DQ192478	DQ192443

Parachiloglanis Wu, He & Chu 1981

Parachiloglanis Wu, He & Chu 1981: 76, 79. Type species: *Glyptosternum hodgarti* Hora 1923, by original designation.

***Parachiloglanis benjii* sp. nov.**
(Figs. 3 & 4)

Holotype. NBC 15558, 83.0 mm SL; Bhutan: Punakha Dzongkhag: Mendegangchhu stream, 27.525413 N, 89.867606 E, R.J. Thoni & D.B. Gurung, August 31, 2013.

Paratypes. CNR 1345_2-6, 5 specimens, 59.0–88.2 mm SL, same data as holotype.

Non-type material. CNR: 15010, 1 specimen, Bhutan: Punakha Dzongkhag: stream crossing 20 meters before Gasa border 1594 m, D.B. Gurung & R.J. Thoni, August 31, 2013; 15004–15007, 4 specimens, Bhutan: Punakha Dzongkhag: confluence of Rimchhu and Mochhu, D.B. Gurung & R.J. Thoni, August 31, 2013; 15016, 1 specimen, 55.9 mm SL; Bhutan: Punakha Dzongkhag: small tributary of Dangchhu, R.J. Thoni & D.B. Gurung, August 31, 2013; 15022, 1 specimen, Bhutan: Wangdue-Phodrang Dzongkhag: upper Dangchhu at roadside with stone wall 20 km from main road past Wangdue, roughly 1800 m, D.B Gurung & R.J. Thoni, September, 2013.

Diagnosis. *Parachiloglanis benjii* is diagnosed by the absence of a post-labial fold, the combination of heterodont dentition in the upper jaw and homodont dentition in the lower jaw, having a posteriorly and widely arched tooth patch with a medial cusp on the upper jaw (Fig. 2), adipose fin adnate, a narrow anterior portion of intestine, the presence of black pigmentation on the caudal-fin margin, caudal fin emarginate, absence of a punctate lateral line, head depth 40.0–43.4% HL, and the absence of a mottled coloration pattern.

Description. Morphometric and meristic data are provided in Table 2. Live coloration and form is presented in Figures 3 and 4. Head dorsoventrally flattened; rising gradually and smoothly from tip of snout to dorsal-fin origin. Body flat or with slight rise from posterior edge of dorsal fin to origin of adipose fin. Dorsal profile sloping gently downward from dorsal-fin origin to caudal base. Ventral profile flat from snout to anal-fin origin; along anal-fin base ventral profile rises slightly; ventral profile flat from posterior to anal fin to caudal base.

FIGURE 3. *Parachiloglanis benjii.* Live specimen. Bhutan: Punakha Dzongkhag: Mendegangchhu stream, August 31, 2013.

Head broad, roughly 1/4 SL, width roughly 4/5 HL. Mouth inferior, with wide gape; roughly 2/5 HL. Maxillary barbels extending outward from base as much as 3/4 HL. Ventral view of mouth and snout bell-shaped due to the posterior membranous flap connecting maxillary barbels to upper jaw. Eye reduced; roughly 1/20 HL; located anterodorsally on head; interorbital width about 1/3 HL.

Mouth inferior; without post-labial fold or thick fleshy lips on either jaw. Teeth forming a thin, arch-shaped patch on upper jaw with homodont dentition; patch broadly arched and posteriorly produced; much wider then deep (Fig. 2); posterior edge with small, medial cusp (Fig. 2). Lower jaw with straight or slightly rounded rigid edge, naked of post-labial fold. Lower jaw with heterodont dentition; formed by two laterally-symmetrical, patches with an anterior row of widely separated sharp teeth and a rough, sandpaper-like pad of densely packed teeth posteriorly; each patch anteroposteriorly narrow and laterally elongate (Fig 2).

FIGURE 4. *Parachiloglanis benjii*. Holotype. NBC 15558, 83.0 mm SL; Bhutan: Punakha Dzongkhag: Mendegangchhu stream.

Dorsal-fin origin located in first third of body; fin short, less than 2/3 body depth; base narrower than height; fin with i,6 rays. Anal fin located in posterior fourth of body; base roughly 1/2 to 3/4 length of dorsal-fin base; fin with i,6 rays. Pectoral fin large, with striations lining thick first ray creating adhesive apparatus; fin length roughly 1/3-1/4 SL. Pelvic fin also with striations lining thick first ray creating adhesive apparatus; fin length roughly 1/5 SL. Caudal fin emarginate; rays 18.

Live coloration. Body olive green to grey in color, but appearing almost translucent. Fins brown, becoming more translucent distally. Ventral surface pale. Caudal fin with faint black margin.

Preserved coloration. Preserved specimens appear almost uniformly brown on all surfaces other than ventral. Ventral surface of body and head pale.

Distribution. This species inhabits the cool, well-oxygenated waters of the upper Punatsangchhu and its tributaries. It was found in tributaries of the Mochhu River at Rimchhu, Tashithang, and two other unnamed streams between Punakha village, Punakha Dzongkhag and Damji, Gasa Dzongkhag. It was found in the Dangchhu River at Samtegang, and Tseshingang in Punakha Dzongkhag. It is presumed to be in the Phochhu as well, however, sampling was not conducted in that river. Individuals were encountered in small order streams and large tributaries of the Punatsangchhu.

Etymology. We take great pleasure in naming this species after a prominent conservationist, Dasho Paljor Jigme Dorji, fondly known in Bhutan as Dasho Benji, who has been a long-standing advocate for the protection of nature in Bhutan.

Ecology. *Parachiloglanis benjii* was found in cold, moderate-to-fast-flowing streams of varying orders, at elevations ranging from 1200–2100 m above sea level, with one anecdotal account of its occurrence in a large river (Punatsangchhu) at an altitude of at least 2500 m (pers. comm., Wangchuk). Like its congeners, it can be found adhering to the bottom side of boulders, preferring areas of riffles and cascades rather than pools. They prefer flat rocks with deep undercut areas instead of those with only small refuge from the current. The streams in which they inhabit are clear, cold-water environments, usually in areas with steep banks and a dense canopy above. *Parachiloglanis benjii* is adapted to high flow environments; having adhesive striations on the leading rays of the paired fins aiding in adhesion to the substrate, as well as a mouth fit for scraping invertebrates from rocks. It is currently known to live in sympatry primarily with *Schizothorax* in higher elevation streams. In the lowest elevation stream where it was encountered, below the village of Metsina, it was found with *Pseudecheneis sulcata* in addition to *Schizothorax*.

Remarks. This species is one of the most common fishes in the middle to high elevation portions of the Punatsangchhu River. It was collected in several streams ranging in size from first to fourth order, and at altitudes from roughly 1000–2300 m. Many specimens were caught, recorded, and released in addition to the voucher specimens examined. There was also anecdotal evidence of *P. benjii* at higher elevations, washing up after floods near the hot springs of Gasa. This fish would have been upstream of the hot springs, which are located at approximately 2500 m in elevation.

Parachiloglanis bhutanensis Thoni & Gurung 2014

(Fig. 5)

Parachiloglanis bhutanensis Thoni & Gurung 2014: 307, figs.1, 4a. Type Locality: Bhutan: Trashigang Dzongkhag: Khalingchhu stream, 100 m above bridge, 27.200435 N, 91.601453 E, Holotype: UF 236349, 101.5 mm SL.

Remarks. This study accounts for a new record of *P. bhutanensis* occurring in Trashiyangtse Dzongkhag in the northeast of Bhutan. Two specimens were collected in the Bumdeling Wildlife Sanctuary, 10 km north of Trashiyangtse Town (27.619616 N, 91.491346 E). They were collected in sympatry with two other glyptosternine species described in this paper, *Creteuchiloglanis bumdelingensis*, and *P. dangmechhuensis*, as well as with a species of *Schizothorax.* All four species were encountered in a small stream roughly 1 m wide and 1/2 m deep. This record offers better distribution data for *P. bhutanensis*, previously only know from two small adjacent streams in Khaling, Trashigang Dzongkhag. This suggests that it occurs throughout the upper Dangmechhu River. Additionally, a population of *P. bhutanensis* was recently discovered in a tributary of the Dangmechhu River in Arunachal Pradesh (personal communication, A. Darshan).

FIGURE 5. *Parachiloglanis bhutanensis.* Holotype. UF 236349, 101.5 mm SL; Bhutan: Trashigang Dzongkhag: Khalingchhu stream, 100 m above bridge east of Khaling Village.

***Parachiloglanis dangmechhuensis* sp. nov.**
(Figs. 6 & 7)

Holotype. CAS 243915, 69.7 mm SL; Bhutan: Mongar Dzongkhag: Lingmethangchhu at confluence with Kurichhu, T.R. Roberts and T. Dhendup, October 5, 1995.

Paratypes. CAS 244033, 13 specimens, 19.9–70.7 mm SL, same data as holotype.

Non-type material. CAS 244039, 13 specimens, 19.8–70.7 mm SL, Bhutan: Trashigang Dzongkhag: Gamrichhu River, 10 km east of Trashigang Town, T. R. Roberts and T. Dhendup, October 7, 1995; CNR 1359_3-5, 3 specimens, 50.6–57.9 mm SL, Bhutan: Trashiyangtse Dzongkhag: Kuktorgangchhu stream near Tshaling, 1776 m elevation, 27.619616 N, 91.491346 E, D.B. Gurung & R.J. Thoni, October 23, 2013; CNR 15280, CNR 1363_8-9, 3 specimens, 52.4–56.1 mm SL, Bhutan: Mongar Dzongkhag: Sherichhu stream at Rusikaka; 940 m elevation, 27.341593 N, 91.359640 E, R.J. Thoni & D.B. Gurung, October 24, 2013.

Diagnosis. *Parachiloglanis dangmechhuensis* is diagnosed by the absence of a post-labial groove, lower lip fold, or any other posteriorly-produced lip-like structure on the lower jaw, a narrow, semi-circular tooth patch on the upper jaw, adipose fin ending with discrete notch, a relatively thickened anterior portion of the intestine, 16 branched pectoral-fin rays, 13–14 branched caudal-fin rays, mouth width 27.6–36.9% HL, caudal peduncle length 7.2–10.6% SL, and the presence of three conspicuous pale spots on the caudal fin.

TABLE 2. Morphometric and meristic data for *Parachiloglanis dangmechhuensis, P. benjii,* and *P. drukyulensis.*

	Parachiloglanis dangmechhuensis					*Parachiloglanis benjii*					*Parachiloglanis drukyulensis*				
Morphometrics	Holotype	min	max	mean	sd	Holotype	min	max	mean	sd	Holotype	min	max	mean	sd
Standard length	69.7	41.3	81.6	61.9	10.2	83.0	55.9	83	69.4	19.1	69.1	48.2	75.2	63.9	9.2
% SL															
Head length	23.4	22.5	26.2	24	0.9	26.0	24	26	25	1.4	25.4	23.1	25.6	24.5	0.8
Predorsal length	31.3	29.9	33.5	31.7	1	33.4	32.5	33.4	33	0.6	34.2	31.1	34.2	33	1
Dorsal-fin base length	9.5	7.9	10.5	9.8	0.7	8.5	8.5	8.9	8.7	0.3	10.0	7.2	10.9	9	1.2
Dorsal-fin height	13.5	11.2	15.5	14.1	1.2	13.3	13.3	15.8	14.5	1.8	15.8	13.4	16.6	15.3	0.9
Dorsal-adipose length	22.2	15.9	26.7	22.4	2.7	26.9	19.8	26.9	23.4	5	22.9	19.6	26.3	23.4	2
Adipose-fin length	33.4	29.2	37.7	34	2.4	34.3	33.8	34.3	34	0.4	35.8	30.6	37.4	34.9	2
Adipose-fin height	5.3	2.3	5.3	3.7	0.7	3.0	3	3.6	3.3	0.4	3.6	2.7	3.9	3.2	0.4
Caudal-peduncle depth	5.8	5.3	6.6	6.1	0.4	6.6	6.6	6.7	6.7	0.1	6.0	5.9	6.8	6.3	0.4
Caudal-peduncle depth w/adipose	5.8	5.3	6.6	6.1	0.4	7.9	7.9	8.2	8.1	0.2	7.1	6.4	8.2	7.4	0.6
Caudal-peduncle length	9.2	7.2	10.6	8.9	1	10.8	10.6	10.8	10.7	0.2	10.0	9.1	14	11.2	1.5
Anal-fin base length	5.6	5	8.4	6.4	0.9	5.3	5.3	8.6	7	2.3	8.3	7.4	9.9	8.4	0.8
Preanal-fin length	82.9	80.5	86.6	83.4	1.6	85.0	82.7	85	83.9	1.7	82.5	80.8	85.6	82.5	1.7
Preanal length	80.9	78.4	84.9	80.9	1.6	81.5	78.9	81.5	80.2	1.9	79.6	77	80.8	78.8	1.4
Body depth	11.7	10.2	14.7	12.3	1.1	12.5	12.1	12.5	12.3	0.3	13.8	10.6	13.8	12.1	1.2
Prepectoral-fin length	16.9	13.8	20.2	16.5	1.4	19.7	18.3	19.7	19	1	19.7	16.5	19.7	18.6	1.2
Pectoral-fin length	21.2	21.2	29.6	25.4	2.2	29.4	29.4	30.5	29.9	0.8	30.4	26.1	30.4	28.1	1.3
Prepelvic-fin length	37.1	34.5	40.9	37.7	1.8	42.0	42	42	42	0	41.6	38.6	42.2	40.7	1.1
Pelvic-fin length	16.7	16.5	20.5	18.2	1.2	20.5	20.5	21.3	20.9	0.6	21.0	18.9	24.3	21.2	1.5
Vent-anal length	2.4	1.3	2.9	2.4	0.4	3.8	2.9	3.8	3.4	0.6	3.1	1.4	4.2	3.2	1

……continued on the next page

TABLE 2. (Continued)

	Parachiloglanis dangmechhuensis					*Parachiloglanis benjii*					*Parachiloglanis drukyulensis*				
Morphometrics	Holotype	min	max	mean	sd	Holotype	min	max	mean	sd	Holotype	min	max	mean	sd
% HL															
Nasal barbel length	39.7	32.6	43.3	36	2.8	25.0	25	33.4	29.2	5.9	32.9	21.1	37.6	31.8	5.2
Eye diameter	7.6	5.2	9.2	7	1.2	3.9	3.9	6.2	5	1.6	4.8	4.8	7.1	5.5	0.7
Preocciput length	88.5	74.6	91.3	83.8	5.1	84.5	84.5	88.8	86.7	3.1	88.9	84.6	96.7	89.7	3.7
Head depth at occiput	40.9	38.3	51.1	42.4	3.7	40.0	40	43.4	41.7	2.4	41.8	33.5	47.8	40.5	5
Head depth at eye	28.8	24	36.7	29.3	3	27.7	27.7	31.4	29.5	2.6	30.5	22.7	33.1	28.7	3.6
Mouth width	30.8	27.6	36.9	32.1	2.7	40.5	40.5	43.6	42.1	2.2	40.8	36.1	44	39.1	2.5
Maxillary barbel length	60.9	60.9	82.1	71.5	6.3	69.7	69.7	76.2	73	4.6	81.4	59.8	85.7	75.3	8.4
Head width	71.9	69	85.9	78.2	5.6	80.6	80.6	87.8	84.2	5.1	84.9	77.7	86.7	83	3.7
Outer mandibular barbel length	25.3	15.3	27.6	23.6	2.8	21.3	21.3	30.3	25.8	6.3	22.3	21.3	31.9	27.5	3.9
Inner mandibular barbel length	11.5	8	14.1	11.8	1.5	9.1	9.1	13.9	11.5	3.4	10.4	7.9	14.5	11.2	2.2
Interorbital width	23.0	21.5	32	25.9	3.1	27.9	27.9	28	27.9	0	29.0	26.7	30.6	28.9	1.2
Meristic counts															
Branched pectoral-fin rays	17		17			15		15			14		14-15		
Branched pelvic-fin rays	6		5			5		5			5		5		
Branched dorsal-fin rays	6		6			6		5-6			6		5-6		
Branched anal-fin rays	6		6			6		6			6		5-6		
Branched caudal-fin rays	14		13-14			14		14-15			14		14-16		

Description. Morphometric and meristic data are provided in Table 2. Live form and coloration are presented in Figures 6 and 7. Head dorsoventrally flattened; rising gradually and smoothly from tip of snout to dorsal-fin origin. Dorsal profile from dorsal-fin origin to adipose-fin origin flat or with slight concave saddle; from adipose-fin origin to caudal base slopes gradually downward. Ventral profile from snout to anal-fin origin flat; along anal-fin base ventral profile rises slightly; from posterior to anal fin to caudal base flat.

Head blunt, length roughly 1/4 SL, width roughly 4/5 HL. Mouth inferior. Maxillary barbels extending outward from base as much as 3/4 HL; ventral view of mouth and snout bell-shaped due to the posterior membrane connecting maxillary barbels to upper jaw. Eye reduced, not subcutaneous in live specimens, almost entirely protruded; in preserved specimens eye appear subcutaneous; located anterodorsally on head. Interorbital distance roughly 1/4 HL.

Mouth inferior; without post-labial fold or thick fleshy lips on either jaw. Tooth patch on upper jaw with homodont dentition; patch exposed and continuous with ventral surface of snout without lip or demarcation; patch semi-circular; acutely rounded on anterior edge; posterior edge slightly concave to straight; extending longer anteroposteriorly than laterally (Fig. 2). Lower jaw with straight or slightly rounded stiff edge, free of any lip fold or post-labial fold. Lower jaw with heterodont dentition; formed by two laterally-symmetrical, patches with an anterior row of widely separated sharp teeth and a rough, sandpaper-like pad of densely packed teeth posteriorly; each patch anteroposteriorly narrow and laterally elongate; patches nearly fused, separated by very narrow gap (Fig 2).

Dorsal-fin origin located in first third of body; fin short, less than 2/3 body depth; base narrower than height; fin with i,6 rays. Anal fin located in posterior fourth of body; base roughly 1/2 length of dorsal-fin base; fin with i,6 rays. Pectoral fin large, with striations lining thickened first ray creating adhesive apparatus; fin length roughly1/4 SL. Pelvic fin also with striations lining thickened first ray creating adhesive apparatus; fin length roughly 1/5 standard length. Caudal fin emarginate; rays 18. Vertebral counts 35(2), 36(9), 37(1).

Live coloration. Body olive green; color fading slightly along sides of body below adipose fin giving way to a slight pinkish hue. Head olive green; opercle with shades of grey and pink on lower half. Venter of body pink, purple, and grey, due largely to translucent, scaleless skin, making visible abdominal musculature; lower intestinal tract visible running posteriorly from between pelvic fins to vent immediately anterior to anal fin.

Dorsal fin olive green and translucent; darkest at the base; becoming very clear distally. Adipose fin olive green, fading from dark along fin base to translucent dorsally. Paired fins olive green on dorsal surface, becoming clearer distally; pale and translucent on ventral side. Caudal fin with three conspicuous pale spots; one on the dorsal portion of the fin base, one on the upper fin lobe, and one on the bottom fin lobe. A thin, lunate, black band extends from the dorsal to the ventral margins of the fin, with its posteriormost arc reaching the posterior margin of the fin along the medial caudal-fin rays. This dark pigmentation arc separates and highlights the two pale spots on the upper and lower caudal-fin lobes. Aside from the three pale spots and black band, caudal fin is largely olive green with brown and red color along the fin rays.

Preserved coloration. In ethanol, specimen exhibits all pigmentation patterns observed above, except that color has faded to brown on body, and pale white on venter.

Distribution. Bhutan; mid to high elevation tributaries of the Dangmechhu River. Specimens collected from Kuktorgangchhu stream in Trashiyangtse, Gamrichhu River Trashigang, Sherichhu River Mongar, and Lingmethangchhu River Mongar.

Etymology. The species epithet *dangmechhuensis* is in reference to the Dangmechhu River where it is known to occur.

Ecology. *Parachiloglanis dangmechhuensis* was found in two relatively different environments. Two streams were moderate-to-fast-flowing streams roughly 6–7 m wide at roughly 900 m in elevation. The two other streams were much colder streams with fast-flowing current, one roughly 1 m wide the other 6 m, both at elevations of above 1700 m. Like many Glyptosternines, it was found adhering to rocks, in riffles and torrents rather than pools. *Parachiloglanis dangmechhuensis* is adapted to high flow environments; having striations on the leading rays of the paired fins aiding in adhesion to the substrate, as well as a mouth fit for scraping invertebrates from rocks. Gut content analysis revealed largely Ephemeroptera and Plecoptera larvae. Females were ripe with fully mature ova at time of collection in Sherichhu (October 24, 2013), suggesting post-monsoon spawn. Ova were large and few in number (<30 per individual) and made up the bulk of all internal tissue, suggesting a large energetic investment. It was found in sympatry with *Creteuchiloglanis*, *Garra, Parachiloglanis, Psilorhynchus, Schistura*, and *Schizothorax.*

Remarks. After the revisionary work of Ng (2015), based on osteology, we find that this species falls within *Parachiloglanis*. However, both molecular and morphological data reveal a large rift between *P. dangmechhuensis* and the remaining species of the genus.

FIGURE 6. *Parachiloglanis dangmechhuensis.* Live specimen. CNR 15280, 52.4 mm SL; Bhutan: Mongar Dzongkhag: Sherichhu stream at Rusikaka

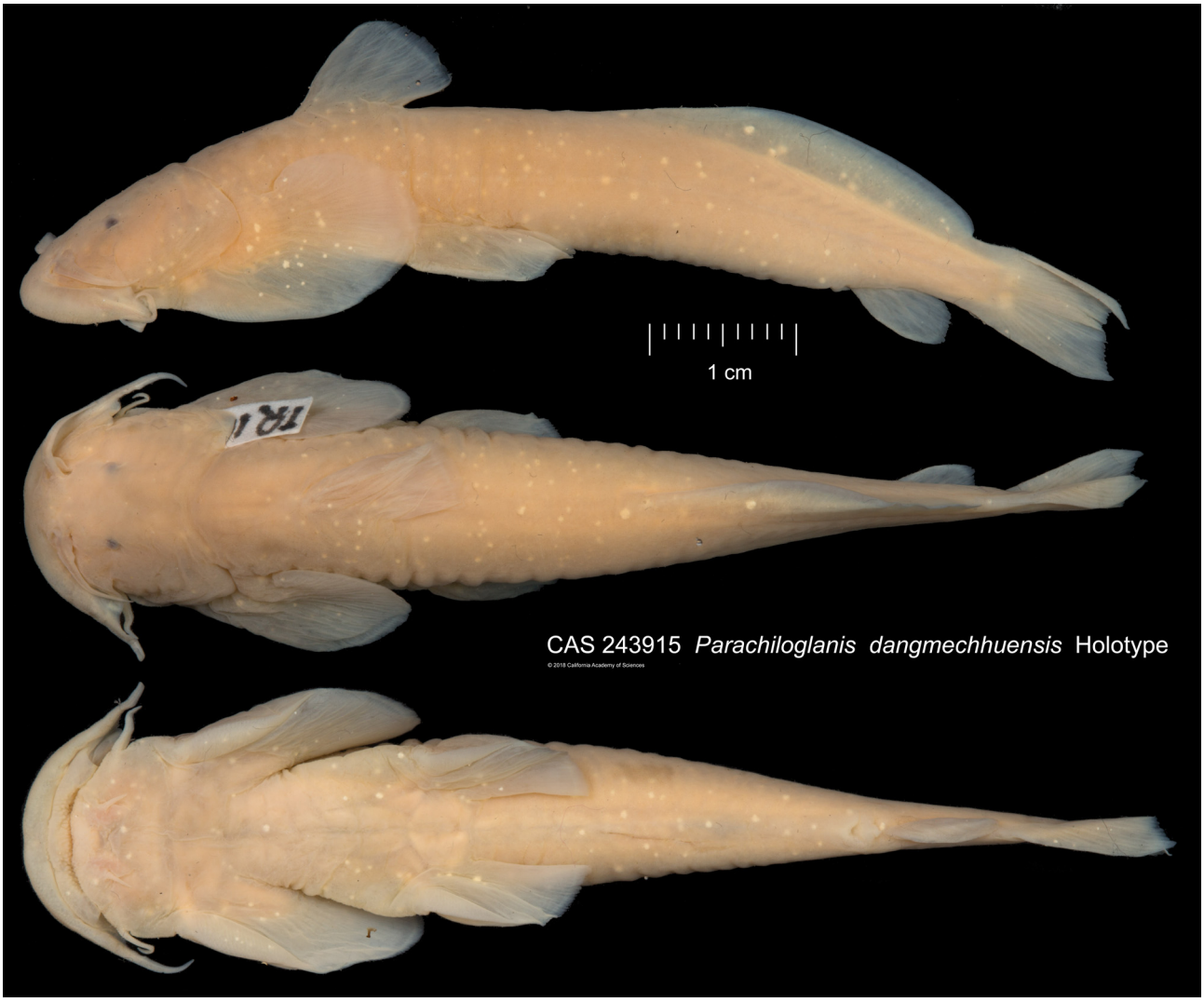

FIGURE 7. *Parachiloglanis dangmechhuensis*. Holotype. CAS 243915, 69.7 mm SL; Bhutan: Mongar Dzongkhag: Lingmethangchhu at confluence with Kurichhu.

***Parachiloglanis drukyulensis* sp. nov.**
(Figs. 8 & 9)

Holotype. NBC 15155, 69.1 mm SL, Bhutan: Sarpang Dzongkhag: Chaplaychhu stream. 27.037270 N, 90.626826 E, R.J. Thoni and D.B. Gurung, September 2013.

Paratypes. CNR 15556, 15532–15534, 15537–15541, 9 specimens, 48.2–74.1 mm SL, same data as holotype.

Non-type material. CNR 15536, 1 specimen, 51.5 mm SL, Bhutan: Sarpang, 3 km north of type locality on Gelephu-Zhemgang Road, R.J. Thoni and D.B. Gurung, September 2013.

Diagnosis. *Parachiloglanis drukyulensis* is diagnosed by the absence of a post-labial fold, and the combination of heterodont dentition in the upper jaw and homodont dentition in the lower jaw, having a posterolaterally arched tooth patch on the upper jaw (Fig. 2), the presence of a mottled pattern covering the entire exposed surface of body, adipose fin adnate with caudal peduncle, the absence of a punctate lateral line, head depth of 33.5–47.8% HL, having a narrow anterior portion of the intestine, and in having a semilunate caudal fin.

Description. Morphometric and meristic data are provided in Table 2. Live form and coloration are presented in Figures 8 and 9. Head dorsoventrally flattened; rising gradually and smoothly from tip of snout to dorsal-fin origin. Dorsal profile flat or with slight concave saddle from dorsal-fin origin to adipose-fin origin; profile slopes gradually downward from adipose-fin origin to caudal base. Ventral profile flat from snout to anal-fin origin; along anal-fin base ventral profile rises slightly; ventral profile flat from posterior to anal fin to caudal base.

Head broad, length roughly 1/4 SL; width roughly 4/5 HL. Mouth inferior with wide gape; roughly 2/5 HL. Maxillary barbels extending outward from base as much as 4/5 HL; Ventral view of mouth and snout bell-shaped due to the posterior membranous flap connecting maxillary barbels to upper jaw. Eye reduced, nearly subcutaneous in preserved specimens; almost entirely protruded in live specimens; located anterodorsally on head. Interorbital distance roughly 2/7 HL.

FIGURE 8. *Parachiloglanis drukyulensis.* Live specimen. Holotype. NBC 15155, 69.1 mm SL; Bhutan: Sarpang Dzongkhag: Chaplaychhu stream.

Mouth inferior; without post-labial fold or thick fleshy lips on either jaw. Teeth forming a thin, arch-shaped patch on upper jaw with homodont dentition; patch exposed and continuous with ventral surface of snout without lip or demarcation; patch broadly arched and posteriorly produced; much wider then deep (Fig. 2). Lower jaw with straight or slightly rounded rigid edge, naked of any post-labial fold. Lower jaw with heterodont dentition; formed by two laterally-symmetrical patches with an anterior row of widely separated sharp teeth and a rough, sandpaper-like pad of densely packed teeth posteriorly; each patch anteroposteriorly narrow and laterally elongate (Fig. 2).

Dorsal-fin origin located in first third of body; fin short, less than 2/3 body depth; base narrower than height; fin with i,6 rays. Anal fin located in posterior fourth of body; base roughly 1/2 to 3/4 length of dorsal-fin base; fin with i,6 rays. Pectoral fin large, with striations lining thick first ray creating adhesive apparatus; fin length roughly 2/7 SL. Pelvic fin also with striations lining thick first ray creating adhesive apparatus; fin length roughly 1/5 SL. Caudal fin semilunate; rays 14 (5), 15(3), 16(1).

FIGURE 9. *Parachiloglanis drukyulensis.* Holotype. NBC 15155, 69.1 mm SL; Bhutan: Sarpang Dzongkhag: Chaplaychhu stream.

Live coloration. From dorsal view heavily mottled in a vibrant rust-red color. Grey base, heavily covered in rust-colored blotches; mottled pattern continuous over entire dorsum and onto dorsum of head, and extending onto

dorsal side of maxillary barbels and connective tissue between maxillary barbels and upper jaw; continuous over adipose fin and caudal peduncle. Dorsal surface of pectoral fins rust-colored; leading ray appearing darker red than rest of fin; clear or white areas between rays; posterior margin of fin without pigment. Dorsal surface of pelvic fin brown to rust-colored; posterior margin of fin with little to no pigmentation. Side of body mottled in rust-red like that of dorsum. Large black spot immediately posterior to opercle below lateral line; spot roughly 1/3 HL. Belly without color; appearing grey or black where dark organs can be seen through skin. Ventrally, surface of paired fins pale, except for leading pectoral rays, which are red, due to muscle tissue, not pigmentation. Immediately posterior to anus brown and mottled coloration continues on ventral surface.

Preserved coloration. In ethanol, specimens exhibit all pigmentation patterns observed above, only color and saturation is greatly reduced. Specimen with pale brown base; mottled pattern appears to be grey.

Etymology. We take great pleasure in naming this species in honor of Bhutan, "the land of the Thunder Dragon", or Drukyul, to celebrate the country's commitment to conservation, sustainable development, and the preservation of nature. This species exhibits the beauty and wonder of its country, and its discovery, amongst other species, is a beacon of the scientific progress that has taken place as a result of this commitment.

Distribution. *Parachiloglanis drukyulensis* is currently known from the Chaplaychhu and a smaller, unnamed stream 2 km north of Chaplaychhu on the Gelephu-Zhemgang road, two small headwater streams of the Jamkhar Khola drainage, in the Brahmaputra basin (Figure 10).

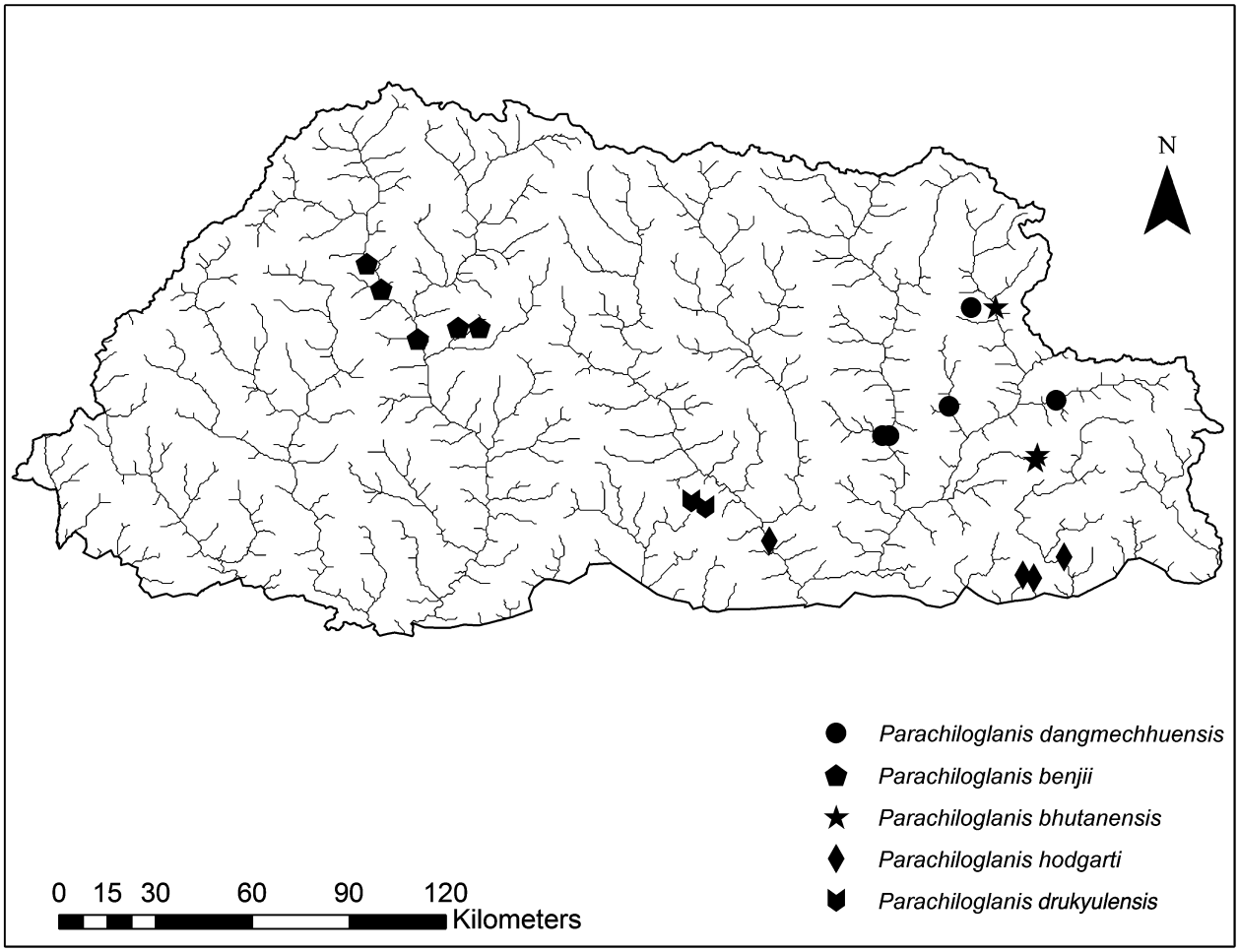

FIGURE 10. Distribution map of the *Parachiloglanis* of Bhutan.

Ecology. *Parachiloglanis drukyulensis* was found in cold, moderate to fast flowing streams. Specimens were collected at elevations ranging from 1550–1800 m above sea level. Like its congeners, it was found adhering to the bottom side of boulders, preferring areas of riffles and cascades rather than pools. They prefer flat rocks with deep undercut areas rather than those with only small refuge from the current. The streams in which they inhabit are

clear, cold-water environments, with steep banks and a dense canopy above. *Parachiloglanis drukyulensis* is adapted to high flow environments; having striations on the leading rays of the paired fins aiding in adhesion to the substrate, as well as an inferior mouth fit for scraping invertebrates from rocks. Gut content analysis was performed on seven specimens. The analysis revealed that they feed almost exclusively on Plecoptera. An analysis of other species collected at this site (*Psilorhynchus* and *Schizothorax*) reveal that alternative prey items were present in the stream, suggesting that either *P. drukyulensis* prefers Plecoptera or feeds in parts of the stream where only Plecoptera exist. It is currently known to live in sympatry with *Schizothorax* sp. and *Psilorhynchus* sp. Both streams where it was found have large waterfalls (>8 m) less than 2 km downstream from their collection sites, suggesting that they may be able to climb nearly vertical wet surfaces.

The 11 specimens collected were exclusively females, despite being collected individually and from different areas within the stream. Females were fully ripe, each with few, but very large, eggs. The mature condition of the eggs suggests that they were ready to spawn. Without further sampling during other seasons, it is not possible to tell whether they only spawn during the post-monsoon autumn months, or multiple times each year.

Parachiloglanis hodgarti **(Hora 1923)**

(Fig. 11)

Glyptosternum hodgarti Hora 1923: 38, pl. 2 (figs. 1–3).

Type Locality: Pharping, Nepal.

Distribution. Found in streams throughout the southern slope of the Himalayan Foothills from Nepal to Yunnan. In Bhutan, *P. hodgarti* was encountered in low elevation, warm-water torrents. It was collected in small tributaries of the Manas, Mangdechhu, and Dangmechhu Rivers, in southern Bhutan. It likely occurs in other rivers throughout the southern parts of the country as well.

Holotype: ZSI F1553/1.

Ecology. *Parachiloglanis hodgarti* was found in a warmer water streams than its congeners, with moderate-to-fast-flowing current ranging from 200–700 m in elevation. Like its congeners, it was found amongst boulder and cobble substrate, preferring areas of riffles and cascades rather than pools. They appear to be found in streams at lower elevation relative to other members of the genus, and often near areas where water temperatures are in transition from that of cool water to warm, usually with a stronger presence of warm water species. *Parachiloglanis hodgarti* is adapted to high flow environments; having striations on the leading rays of the paired fins aiding in adhesion to the substrate and having a mouth fit for scraping invertebrates from rocks. It was found in sympatry with *Aborichthys*, *Barilius*, *Exostoma*, *Garra*, and *Schistura*.

FIGURE 11. *Parachiloglanis hodgarti.* Live specimen. CNR 15227, Bhutan: Samdrup Jongkhar Dzongkhag: Martangchhu.

Remarks. This species continues to be one of great confusion. This is addressed in-depth in the discussion below. The identification of specimens collected in Bhutan was made based on Hora's (1923) original description of *Glyptosternum hodgarti*. Further, this appears to be the same species or very similar to those that exist in Nepal based on comparative specimens deposited at KU and OSUS. These specimens are seemingly interchangeably named *Parachiloglanis hodgarti* and *Myersglanis blythii* despite being the same species.

Because of its occurrence in relatively warmer waters and lower elevations compared to its congeners, it makes

sense that *P. hodgarti* is more likely to have a broader distribution in the Himalayan foothills region, being able to move more freely through warmer downstream reaches than its congeners, which seem to be restricted to colder, more oxygen rich environments.

Exostoma Blyth 1860

Exostoma Blyth 1860: 155. Type species*: Exostoma berdmori* Blyth 1860, by subsequent designation by Bleeker (1862: 13).

Exostoma mangdechhuensis sp. nov.
(Figs. 12 &13)

Exostoma labiatum (McClelland 1842).–Gurung *et al.* 2013.

Holotype. NBC 15222, 71.1 mm SL, Bhutan: Zhemgang Dzongkhag: Nabbey Khola stream at Tingtibi, 803 m elevation, 27.117618 N, 90.673532 E, D.B. Gurung & R.J. Thoni, September 30, 2013.

Paratypes. CNR 15220 and 15223, 2 specimens, 58.9–61.7 mm SL; same data as holotype.

Non-type material. CNR 13351, 15169–15170, 3 specimens, 54.5–68.5 mm SL, Bhutan: Zhemgang, Kiragang stream at Mamung, R.J. Thoni & D.B. Gurung.

Diagnosis. *Exostoma mangdechhuensis* is distinguished from its congeners by the presence of a conspicuous anteriorly-projected notch on the posterior connection of the adipose fin to the caudal peduncle, HL 22.6–24.9% SL, preocciput length of 91.9–102.1% HL, head width 79.7–88.2% HL, mouth width 33.2–39.4% HL, caudal peduncle depth 7.7–8.4% SL, and 11 branched pectoral-fin rays.

Description. Morphometric and meristic data are provided in Table 3. Live form and coloration are presented in Figures 12 and 13. Head dorsoventrally flattened; rising gradually and smoothly from tip of snout to dorsal-fin origin. Dorsal profile from dorsal-fin origin to adipose-fin origin with slight concave saddle; profile from adipose-fin origin to caudal base slopes gradually downward. Ventral profile from snout to vent flat; ventral profile from vent to posterior point of anal-fin base rises slightly; ventral profile from posterior to anal-fin base to caudal-fin base flat.

Head blunt, length roughly 1/4 SL, width roughly 5/6 HL. Mouth inferior. Maxillary barbel extending outward from base as much as HL. Ventral view of mouth and snout bell-shaped due to the posterior membranous flap connecting maxillary barbel to upper jaw. Eye small; 1/10 HL; not subcutaneous in live specimens, entirely protruded; subcutaneous in preserved specimens; located anterodorsally on head; interorbital width roughly 2/7 HL.

Mouth inferior; with thick, fleshy, papillose lips reflected around the mouth; post-labial fold continuous. Tooth patches on upper and lower jaw with homodont dentition and split along midline forming two laterally symmetrical patches on each jaw; upper jaw tooth patch exposed. Upper jaw M-shaped; lower jaw with cleft in middle, with small pit between jaw and post-labial fold. Medial patch of papillae present, anterior to upper lip, and continuous with papillose anterior margin of snout. Anterior margin of snout with minor cleft medially.

Dorsal-fin origin located in second third of body (predorsal length roughly 2/5 SL); fin length slightly greater than body depth at dorsal-fin origin; base narrower than height; fin with i,6 rays. Anal fin located in posterior fourth of body; base roughly 1/2 length of dorsal-fin base; fin rays i,4 (4), i,5 (2). Pectoral fin large, with striations lining thickened first ray creating adhesive apparatus; fin length roughly 1/4 SL. Pelvic fin also with striations lining thickened first ray creating adhesive apparatus; fin length roughly 1/5–1/6 SL. Caudal semilunate; rays 15(1), 16 (5).

Live coloration. Base color of body pale pink to tan. Body sparsely scattered with round gold speckles roughly equal in size to eye; anteriorly much more densely speckled than posteriorly. Head covered densely with gold speckling so that it appears mottled and golden-brown. In some specimens body is much darker. Caudal peduncle free of speckles. Dorsum of entire body darker than sides of body. Entire ventral surface lacking pigmentation. Caudal fin with dark blotch at base; upper and lower lobes of fin with dark pigmentation; medial rays without color.

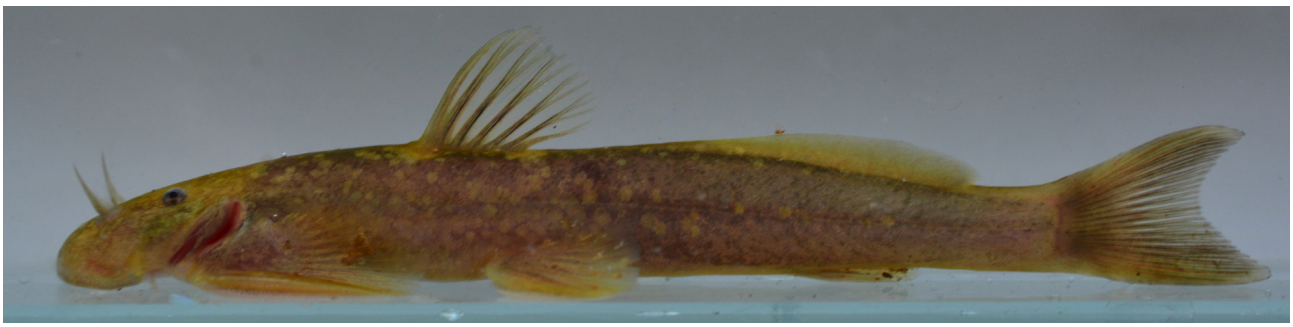

FIGURE 12. *Exostoma mangdechhuensis.* Live specimen. Holotype. NBC 15222, 71.1 mm SL; Bhutan: Zhemgang Dzongkhag: Nabbey Khola stream at Tingtibi.

FIGURE 13. *Exostoma mangdechhuensis.* Holotype. NBC 15222, 71.1 mm SL; Bhutan: Zhemgang Dzongkhag: Nabbey Khola stream at Tingtibi.

TABLE 3. Morphometric and meristic data for *Creteuchiloglanis bumdelingensis* and *Exostoma mangdechhuensis.*

		Creteuchiloglanis bumdelingensis				*Exostoma mangdechhuensis*				
Morphometrics	Holotype	min	max	mean	sd	Holotype	min	max	mean	sd
Standard length	34.2	28.6	39.1	33.4	4.0	71.1	54.5	71.1	62.7	6.1
% SL										
Head length	26.8	23.5	26.8	25.5	1.4	22.6	22.6	24.9	23.8	0.9
Predorsal length	34.9	31.9	38.3	35.4	2.4	39.2	38.9	41.9	40	1.2
Dorsal-fin base length	11.2	7.9	11.8	10.6	1.6	9.6	9.3	10.6	9.8	0.6
Dorsal-fin height	15.3	15.3	18.5	17.6	1.4	17.5	16.2	17.9	17.0	0.7
Dorsal-adipose length	14.3	11.4	14.7	12.9	1.5	18.7	12.5	18.7	16.3	2.6
Adipose-fin length	30.1	29.3	36.3	32.6	3.3	25.6	23.4	29.6	26.4	2.5
Adipose-fin height	3.1	2.7	3.8	3.3	0.4	2.5	2.5	4.4	3.5	0.7
Caudal-peduncle depth	6.4	6.4	7.9	7.1	0.5	8.7	7.7	8.7	7.9	0.4
Caudal-peduncle length	19.6	17.0	19.7	18.6	1.4	20.5	19.0	21.3	20.4	0.8
Anal-fin base length	4.3	4.3	6.9	5.4	1.0	3.5	3.5	5.1	4.3	0.6
Preanal-fin length	72.1	72.1	75.4	73.6	1.3	77.5	73.1	77.5	74.0	1.8
Preanal length	65.1	61.9	65.9	64.6	1.5	68.0	65.4	68.0	66.5	1.1
Body depth	14.6	11.6	17.2	13.8	2.2	11.8	11.3	13.3	12.3	0.8
Prepectoral-fin length	20.5	17.6	21.3	19.2	1.7	17.6	17.6	19.6	18.7	0.7
Pectoral-fin length	26.4	26.4	28.2	27.2	0.7	22.2	22.2	24.3	23.2	0.9
Prepelvic-fin length	40.6	40.3	43.4	41.7	1.5	46.6	45.6	47.5	46.5	0.8
Pelvic-fin length	19.8	18.2	21.6	19.6	1.3	18.7	16.6	19.4	18.5	1.0
Vent-anal length	6.9	6.9	9.9	8.1	1.3	8.0	5.3	8.0	7.1	1.1
% HL										
Nasal barbel length	20.6	17.2	25.6	22.2	3.4	23.1	23.1	30.1	26.3	2.6
Eye diameter	8.5	8.3	12.8	9.9	2.0	9.2	9.2	12.3	10.7	1.2
Preocciput length	95.4	91.5	107.1	98.6	7.5	102.1	91.9	102.1	96.6	4
Head depth at occiput	47.9	43.5	52.1	46.9	3.4	46.5	39	49.5	45.5	3.5
Head depth at eye	32.5	30.7	35.8	33.1	2.5	31.2	31.2	37.8	34.2	2.8
Mouth width	26.2	22.3	27.7	25.5	2.4	39.4	33.2	39.4	36.7	2.3
Maxillary barbel length	93.3	79.3	98.2	87.8	8.0	101.6	91.5	101.6	96.7	3.5
Head width	78.5	78.5	90.5	84.8	5.3	85.3	79.7	88.2	84.7	3.3
Outer mandibular barbel length	20.8	20.8	26.5	23.3	2.2	23.3	17.2	25.7	22	3
Inner mandibular barbel length	14.0	11.2	14.0	12.6	1.3	4.7	4.5	9	6.6	1.9
Interorbital width	27.5	27.5	32.2	29.3	1.7	29.8	26.1	29.8	28.1	1.3
Meristic counts										
Branched pectoral-fin rays	15	15-16				11	11			
Branched pelvic-fin rays	5	5				5	5			
Branched dorsal-fin rays	6	6				6	6			
Branched anal-fin rays	4	4				5	5-Apr			
Branched caudal-fin rays	14	13-15				15	15-16			

Preserved coloration. In ethanol, specimens exhibit all pigmentation patterns observed above, only color and saturation is greatly reduced. Specimen with pale brown base; mottled pattern appears to be grey and fading with time.

Distribution. *Exostoma mangdechhuensis* is known to occur in the Mangdechhu river drainage and several of its tributaries between 200 and 800 m above sea level.

Etymology. The species epithet *mangdechhuensis* is in reference to the Mangdechhu River from which it was collected.

Ecology. *Exostoma mangdechhuensis* was found in moderate-to-fast-flowing streams ranging from roughly 300 to 800 m of elevation. Like many glyptosternines, it was found adhering to rocks, in riffles and torrents rather than pools. *Exostoma mangdechhuensis* is adapted to high flow environments, having striations on the leading rays of the paired fins aiding in adhesion to the substrate and has a mouth with large papillose labial folds for suction and eating invertebrates from rocks. Gut content analysis revealed largely Ephemeroptera and Plecoptera larvae. Sympatric species were often far more abundant than *E. mangdechhuensis* and typically consisted of *Aborichthys, Devario, Garra, Neolissochilus, Schistura,* and *Schizothorax.*

Remarks. This species was collected from many streams throughout the Mangdechhu drainage. In addition to four sites where voucher specimens were collected, it was captured, recorded, and released in other localities along the Mangdechhu River, though never in high densities.

Creteuchiloglanis Zhou, Li & Thomson 2011

Creteuchiloglanis Zhou, Li and Thomson 2011: 227. Type species: *C. longipectoralis* Zhou, Li & Thomson, 2011.

Creteuchiloglanis bumdelingensis sp. nov.

(Figs. 14 & 15)

Holotype. NBC 1359_1, 34.2 mm SL; Bhutan: Trashiyangtse Dzongkhag: Kuktorgangchhu stream near Tshaling in the Bumdeling Wildlife Sanctuary, 1776 m elevation, 27.619616 N, 91.491346 E, R.J. Thoni & D.B. Gurung, October 23, 2013.

Paratypes. CNR 15266 & 1359_2, 2 specimens, 34.1–39.5 mm SL; same data as holotype.

Non-type material. CAS 244035, 2 specimens, 46.4–53.0 mm SL, Bhutan: Trashigang Dzongkhag: Gamrichhu River, 10 km east of Trashigang Town, T.R. Roberts & T. Dhendup, October 7, 1995; CAS 244034, 1 specimen, 30.0 mm SL, Bhutan: Mongar Dzongkhag: Lingmethangchhu at confluence with Kurichhu, T.R. Roberts and T. Dhendup, October 5, 1995; CNR 15281, 1 specimen, 39.1 mm SL, Bhutan: Mongar, Sherichhu stream at Rusikaka, near Moorungdrang, 940 m elevation, 27.341593 N, 91.359640 E, R.J. Thoni and D.B. Gurung, October 24, 2013.

Diagnosis. *Creteuchiloglanis bumdelingensis* can be distinguished from other members of the genus in having a large post-labial fold which extends to or beyond the base of the outer mandibular barbel, caudal peduncle 6.4–7.9% SL, mouth width 22.3–26.2% HL, 15–16 branched pectoral-fin rays, pectoral-fin rays extending beyond pelvic-fin insertion, adipose-fin length 29.3–36.0% SL, and pigmentation differences discussed below.

Description. Morphometric and meristic data are provided in Table 3. Live coloration and form is presented in Figures 14 and 15. Head dorsoventrally flattened; rising gradually and smoothly from tip of snout to dorsal-fin origin. Dorsal profile from dorsal-fin origin to caudal base gradually sloped downward. Inter-dorsal region slightly raised and keeled, forming the anterior portion of the adipose fin. Ventral profile flat from snout to anal-fin origin; along anal-fin base ventral profile rises slightly; ventral profile flat from posterior to anal fin to caudal base.

Head broad, roughly as wide across as long. Tip of snout with prominent cleft (possibly juvenile condition). Eye reduced, nearly subcutaneous; located anterodorsally on head. Mouth inferior. Maxillary barbel extending outward from base as much as 1/2 HL; posterior margin on barbel smooth. Lower lip continuous, though with medial cleft. Upper lip fold absent. Teeth on upper jaw forming oval to slightly arched palate; largely exposed when mouth closed

Dorsal-fin origin located in first third of body; fin short, less than 2/3 body depth; base narrower than height; fin with i,6 rays. Anal fin located in posterior fourth of body; base roughly 1/2 length of dorsal-fin base; fin with i,4 rays. Pectoral fin large, extending beyond pelvic-fin insertion; fin with modified adhesive striations lining thick, spinous first ray; fin length about 1/4 SL; fin rays i,15(2), i,16 (3). Pelvic fin large, with modified first ray; fin rays i,5. Caudal fin truncate; branched rays 13–15.

FIGURE 14. *Creteuchiloglanis bumdelingensis.* Live specimen. Holotype. NBC 1359_1, 34.2 mm SL; Bhutan: Trashiyangtse Dzongkhag: Kuktorgangchhu stream near Tshaling, Bumdeling Wildlife Sanctuary.

Live coloration. Overall body color pale and tan. Dorsum much darker than venter. Faint pink stripe running entire length of lateral line. Body from opercle to anterior to adipose fin origin tan; some melanophores along dorsal ridge immediately anterior to dorsal fin origin. Body posterior to adipose fin origin tan, appearing darker towards caudal base; dark margin along base of adipose fin; dark spot at anal fin insert, mostly present on fin itself, but extends onto body surface. Dark spot below lateral line at vertical with adipose fin origin, roughly the size of caudal peduncle width. Dark band around posteriormost portion of caudal peduncle, but mostly this is found on caudal fin. Underside of body white; translucent around gut. Dorsum of head tan to olive green. Side of head fading from olive at dorsum to pale tan at venter; large pink to red spot suborbitally on operculum. Dorsal fin dark stripe down midline, formed by pigment on midline of rays; membrane without pigmentation. Adipose fin dark along base, with scattered melanophores, except at anterior part of fin, where there is a conspicuous white area; appearing as white spot when viewed dorsally. Caudal fin with dark band at base; dark marginal band

Preserved coloration. Body dark grey; dorsally much darker. Dorsum dark grey from dorsal-fin origin to slightly before anterior edge of adipose-fin base, where there is a pale white spot. Adipose fin dusky; translucent with few scattered melanophores; anteriorly darker. Between dorsum and lateral line uniformly grey. Lateral line dark grey from operculum to caudal peduncle. Slightly below lateral line, uniformly grey; same as above lateral line. Horizontally in line with pelvic-fin insertion to venter from pelvic-fin insertion to caudal-fin base light grey. Head dark grey; dorsally darker. Suborbital region lighter shade of grey. Entire ventral surface pale white, except for venter of caudal peduncle, which is grey like rest of lateral surface of body.

Distribution. Known from three tributaries of the Dangmechhu River; Kuktorgangchhu stream near Tshaling, in the Bumdeling Wildlife Sanctuary, Trashiyangtse, Sherichhu River in Mongar, and Gamrichhu River in Trashigang (Fig. 16). See remarks for further notes on range.

Etymology. The species epithet *bumdelingensis* is in reference to the Bumdeling Wildlife Sanctuary from which it was first collected.

Ecology. *Creteuchiloglanis bumdelingensis* was encountered at both high and mid altitude (1776 m and 940 m) streams. The higher altitude stream was small, roughly 1–2 m in width and with a moderate grade. At this locality it was found in sympatry with *Parachiloglanis dangmechhuensis, P. bhutanensis*, and *Schizothorax* sp. The second locality was a much larger stream, roughly 8 m in diameter with swift current over large boulders and cobble. At this locality, the fish assemblage was one of a more temperate transitional zone, with *Schizothorax, Parachiloglanis, Schistura, Psilorhynchus,* and *Garra. Creteuchiloglanis bumdelingensis* prefers cold to moderately warm water in medium to high flow environments, and was collected in rocky substrate and feeds on benthic invertebrates.

Remarks. This species was first encountered in a small stream in the Bumdeling Wildlife Sanctuary. There was a glyptosternine specimen on display at the Bumdeling Wildlife Sanctuary visitor center, although the specimen was in poor condition and impossible to identify (possibly *C. bumdelingensis*). There were unconfirmed reports by park rangers of this species throughout the park. Sampling was only done at one locality in the park by

the authors due to time constraints, but the species appears to occur in multiple streams in the Dangmechhu drainage. More specimens were encountered in the Sherichhu River, a separate tributary of the Dangmechhu drainage, nearly 800 m lower in elevation.

FIGURE 15. *Creteuchiloglanis bumdelingensis.* Holotype. NBC 1359_1, 34.2 mm SL; Bhutan: Trashiyangtse Dzongkhag: Kuktorgangchhu stream near Tshaling, Bumdeling Wildlife Sanctuary.

Phylogenetic results

Both genes were successfully sequenced for all species with the exception of *Exostoma mangdechhuensis*, which

failed to produce viable Cyt *b* sequences. Due to a large percentage of missing data, the outgroup species *Glyptothorax interspinalus* was removed from the RAG2 analysis. A total of 907 bp were successfully produced for RAG2 for all samples except for those of *C. bumdelingensis*, which both produced 877 bp. A total 1117–1138 bp were successfully produced for Cyt *b* with roughly half of the samples achieving the full 1138 bp. Sequences were trimmed to 877 and 1117 for RAG2 and Cyt *b*, respectively, to avoid using missing data in Partition Finder and Maximum Likelyhood analyses.

The Glyptosterninae of Bhutan fall into two major mitochondrial lineages (Fig. 17a), supporting the monophyly of *Parachiloglanis* and its hypothesized sister relationship to the rest of Glyptosterninae. Within *Parachiloglanis*, *P. dangmechhuensis* is a basal member. *Parachiloglanis benjii* is sister to *P. hodgarti* and together form the sister group to a *P. drukyulensis/P. bhutanensis* clade. Within the remaining Glyptosterninae, *Creteuchiloglanis bumdelingensis* is grouped with its congener *Creteuchiloglanis kamengensis. Creteuchiloglanis* forms a sister group with *Pseudexostoma*, together forming a group that is sister to *Oreoglanis* plus *Chimarrichthys*; *Exostoma* is sister to that entire clade. At the deeper nodes of the tree bootstrap values are too weak to extrapolate reliable relationships.

Nuclear data present similar, yet slightly discordant relationships (Fig. 17b). The RAG2 gene is generally known to be a more conserved gene with a slower mutation rate than Cyt *b*, and is therefore usually used to elucidate larger scale relationships. At the species level, differences were apparent however, yet distances were close in some species, particularly in the *P. drukyulensis* and *P. bhutanensis* clade. In most taxa however, and on a broader scale, relationships were clearer, and had strong bootstrap support. In the RAG2 tree, again, there is a well-supported split between *Parachiloglanis* and remaining Glyptosterninae. Within *Parachiloglanis, P. dangmechhuensis* was basal to the rest of the genus. Within the rest of Glyptosterninae, *Exostoma* was the basal-most genus. *Exostoma mangdechhuensis* falls within the genus. The placement of *Pseudecheneis* remains elusive, as in many studies (Peng 2004; Jiang *et al.* 2011; Ng & Jiang 2015).

Discussion

This study examines the diversity and relationships of the Glyptosterninae known to occur in Bhutan. There are seven species in total, belonging to three genera. Together, the Glyptosterninae of Bhutan inhabit every major river system and can be found in nearly all lotic habitats inhabited by native fishes (exceptions being rivers and streams above 3000 m, where only *Schizothorax*, *Triplophysa,* and non-native *Salmo* have been recorded). In Bhutan, two genera, *Creteuchiloglanis* and *Parachiloglanis*, are found in headwater streams at relatively high elevations (800–3200 m). This appears to be a character highly correlated with endemism across many taxonomic groups, likely due to isolation and physiological adaptive pressures (Hora, 1930; Ma *et al.,* 2015). It makes sense that these genera tend to exhibit greater diversity and have species with narrow ranges in the steep and isolating river gorges of the Himalayas.

Exostoma is differentiated from *Parachiloglanis* in having a post-labial fold and from *Creteuchiloglanis* in that the lower lip fold is continuous with the upper lip fold. *Exostoma* is represented by one species in Bhutan, *E. mangdechhuensis*. Gurung *et al.* (2013) originally identified this species as *E. labiatum*; however, upon inspection of the holotype of *E. labiatum,* the species were found to differ in many respects. Like many of McClelland's species, *E. labiatum* became a catchall species name applied indiscriminately to many members of the genus encountered in northeast India and surrounding areas. *Exostoma labiatum* and *E. tenuicaudata* Tamang, Sinha, & Gurumayam 2015 are the only other species of *Exostoma* known from the Brahmaputra drainage. Other species of *Exostoma* known from northeast India are *E. barakensis* Vishwanath & Joyshree 2007 and *E. sawmteai,* Lalramliana *et al.* 2015. *Exostoma mangdechhuensis* is differentiated from *E. labiatum* by the presence of a conspicuous, anteriorly-projected notch on the posterior terminus of the adipose fin where it joins the caudal peduncle (versus adipose fin adnate with caudal peduncle, or with first procurrent caudal-fin rays), head length 22.6–24.9% SL (versus 21.4% SL), preocciput length of 91.9–102.1% HL (versus 111.2% HL), head width 79.7–88.2% HL (versus 97.9% HL), and 11 branched pectoral-fin rays. *Exostoma mengdechhuensis* differs from *E. tenuicaudata* in having a much deeper and truncated caudal peduncle, with a depth a 7.7–8.7% SL (versus 4.3.6–4.7) and length 19.0–21.3% SL (versus 26.3–28.0), caudal fin semilunate (versus slightly forked), a much smaller plicated adhesive pad anterior to the mouth, and in having wider gaps between this pad and the lateral plicated pads on the lip sulcus. *Exostoma dangmechhuensis* differs from *E. barakensis* by the presence of a conspicuous,

anteriorly-projected notch on the posterior terminus of the adipose fin where it joins the caudal peduncle (versus adipose fin adnate with caudal peduncle, or with first procurrent caudal-fin rays), caudal fin semilunate (versus emarginate), caudal peduncle depth 7.7–8.7% SL (versus 9.5–11.1% SL), and body depth 11.3–13.3% SL (versus 14.0–16.5% SL); from *E. berdmorei* by the presence of a conspicuous, anteriorly-projected notch on the posterior terminus of the adipose fin where it joins the caudal peduncle (versus adipose fin adnate with caudal peduncle, or with first procurrent caudal-fin rays), and 11 (versus 8–10) branched pectoral-fin rays; and from *E. sawmteai* by the presence of a conspicuous, anteriorly-projected notch on the posterior terminus of the adipose fin where it joins the caudal peduncle (versus adipose fin adnate with caudal peduncle, or with first procurrent caudal-fin rays), and 11 (versus 8–10) pectoral-fin rays.

Zhou *et al.* (2011) diagnosed *Creteuchiloglanis* by the presence of an interrupted post-labial fold, broad isthmus, gill openings not extending onto venter, homodont dentition, teeth pointed, tooth patches not extending posterolaterally, and 14–16 pectoral-fin rays. There are three species of *Creteuchiloglanis* in India, all occurring in the Brahmaputra drainage, *C. arunachalensis*, *C. kamengensis*, and *C. payjab*. *Creteuchiloglanis bumdelingensis* differs from *C. kamengensis* and *C. payjab* by having a larger post-labial fold, which extends to or beyond the base of the outer mandibular barbel (versus not extending to the base of the outer mandibular barbel), mouth width 22.3–27.7% HL (versus 34.4% HL and 44.4% HL respectively; ratios extracted from photos of holotypes and were tested for accuracy using photos of *C. bumdelingensis* with known measurement ratios), and pigmentation differences, and from *C. arunachalensis* by having a larger post-labial fold, which extends to or beyond the base of the outer mandibular barbel (versus not extending to the base of the outer mandibular barbel), 15–16 (versus 14) branched pectoral-fin rays, mouth width 22.3–27.7% HL (versus 41.2% HL; ratio extracted from photo of holotype), preanal length 61.9–65.9% SL (versus 77.3% SL), pectoral-fin length 26.4–28.8% SL (versus 23.1% SL), caudal peduncle length 17.0–19.7% SL (versus 16.8% SL), dorsal-adipose distance 11.4–14.7% SL (versus 20.0% SL), nasal barbel length 17.2–25.6% HL (versus 32.4% HL) and caudal-fin pigmentation differences. *Creteuchiloglanis bumdelingensis* bears an ostensibly similar appearance to two species of *Oreoglanis* recently described from northeast India, *O. majusculus* and *O. pangenensis. Creteuchiloglanis bumdelingensis* differs from these two species in having an interrupted (versus continuous) post-labial fold.

Parachiloglanis is shown to have significant diversity throughout Bhutan. With the exception of the recently described *P. bhutanensis,* and those species described above, fishes of this genus are lumped within *P. hodgarti*, a catchall species name. Species of *Parachiloglanis* are small in size, with elongate, dorsoventrally flattened bodies, inferior mouths, homodont dentition forming a crescent shaped pad on the upper jaw and heterodont dentition on the lower jaw, and a series of striations on the leading pectoral- and pelvic-fin rays. This genus is distinguished from other glyptosternines, by the absence (versus presence) of a post-labial groove on the lower jaw, heterodont (versus homodont) dentition, a posteriorly-located vent, occurring immediately anterior to the anal-fin origin, and in osteological characters (Ng 2015). *Parachiloglanis* is reported from Nepal, northeast India, Bhutan, Myanmar, and China. It is likely that, based on our observations from Bhutan, the species diversity of *Parachiloglanis* is much greater than what is currently recognized. This paper continues to explore the diversity of this group, with three additional new species from Bhutan, *P. benjii*, *P. dangmechhuensis*, and *P. drukyulensis*.

Parachiloglanis benjii differs from its congeners in having a posteriorly and widely arched (versus narrow and semi-circular) tooth patch with a posteromedial cusp on the upper dentition pad (Fig. 2), adipose fin adnate with caudal peduncle (versus ending with distinct notch), a narrow (versus thick) anterior portion of intestine, the presence (versus absence) of black pigmentation on the caudal-fin margin, caudal fin emarginate (versus truncate or semilunate), absence (versus presence) of a punctate lateral line, head depth 40.0–43.4%, and the absence (versus presence) of a mottled pattern covering entire exposed surface of body. *Parachiloglanis drukyulensis* can be differentiated from its congeners by the presence (versus absence) of a rusty red-colored mottled pattern covering the entire exposed surface of body. It further differs from *P. bhutanensis* by the absence (versus presence) of 30–40 conspicuous lateral line pores, and a head depth of 33.5–47.8% HL (versus 46.6–59.3% HL), from *P. hodgarti* in having a semilunate (versus truncate) caudal fin, and from *P. benjii* in coloration characters and in having a semilunate (versus truncate) caudal fin, and from *P. dangmechhuensis* in having a wide, posterolaterally arched (versus narrow and semi-circular) tooth patch on the upper jaw, adipose fin adnate with caudal peduncle (versus ending with discrete notch), and by the presence (versus absence) of a mottled pattern covering the body. *Parachiloglanis dangmechhuensis* is differentiated from its congeners in having a narrow, circular to semi-circular tooth patch on the upper jaw, adipose fin ending with discrete notch, a thickened anterior portion of the intestine,

and the presence of three conspicuous pale spots on the caudal fin. *Parachiloglanis dangmechhuensis* has several unique morphological characters amongst its congeners. Head shape, dentition, adipose fin, pectoral-fin ray counts, intestinal morphology, as well as unique caudal fin pigmentation makes this species stand out from the rest of *Parachiloglanis*. Further, molecular data show a large rift between it and the remaining species of *Parachiloglanis* (Figs 17a–b).

Due to its omission from previous works (He 1996; Peng *et al.* 2004; Ng 2006; De Pinna 1996; Jiang *et al.* 2011) and its seemingly interchangeable use with *Myersglanis blythii* (Day 1870) in some collections, it is clear that there is confusion around the validity of *Parachiloglanis* and *Myersglanis*. From a review of the taxonomic history of *Parachiloglanis* and *Myersglanis*, it is evident that *Parachiloglanis* is valid. In the original description of *Myersglanis blythii* (originally *Exostoma blythii*), Day (1870) states that the lips were "thick and reflected around the mouth", a condition that can be seen in his illustration (plate CXVII, fig 2a). Further, Day (1876) specifies that the lower labial fold is uninterrupted. Later, Day (1878) either confused different lots of specimens or overlooked the characters of the mouth of specimens collected from a different locality than the type (Darjeeling hills), stating "sulcus behind lower lip interrupted". Never in his accounts does he state that lips or libial folds were absent. *Parachiloglanis hodgarti*, originally *Glyptosternum hodgarti*, was described by Hora (1923) on the basis that is was "readily distinguished from all others examined by the absence of any labial fold on the lower lip." In this same monograph, Hora also explains that *Glyptosternum blythii* had an inconsistent taxonomic history, discussing the same oversights made by Day (1878) mentioned above. *Myersglanis* was erected by Hora & Silas (1952) to accommodate the unique features of *Exostoma blythii*. In their redescription of the species, the authors point out again that the lower lip fold is continuous. Wu *et al.* (1981) elevated Hora's *Glyptosternum hodgarti* to its own genus, *Parachiloglanis*, based on its markedly different lip morphology from all other members of Glyptosterninae. Elevating *Glyptosternon hodgarti* to *Parachiloglanis* is supported in this study and in others (Ng 2015; Ng & Jiang 2015).

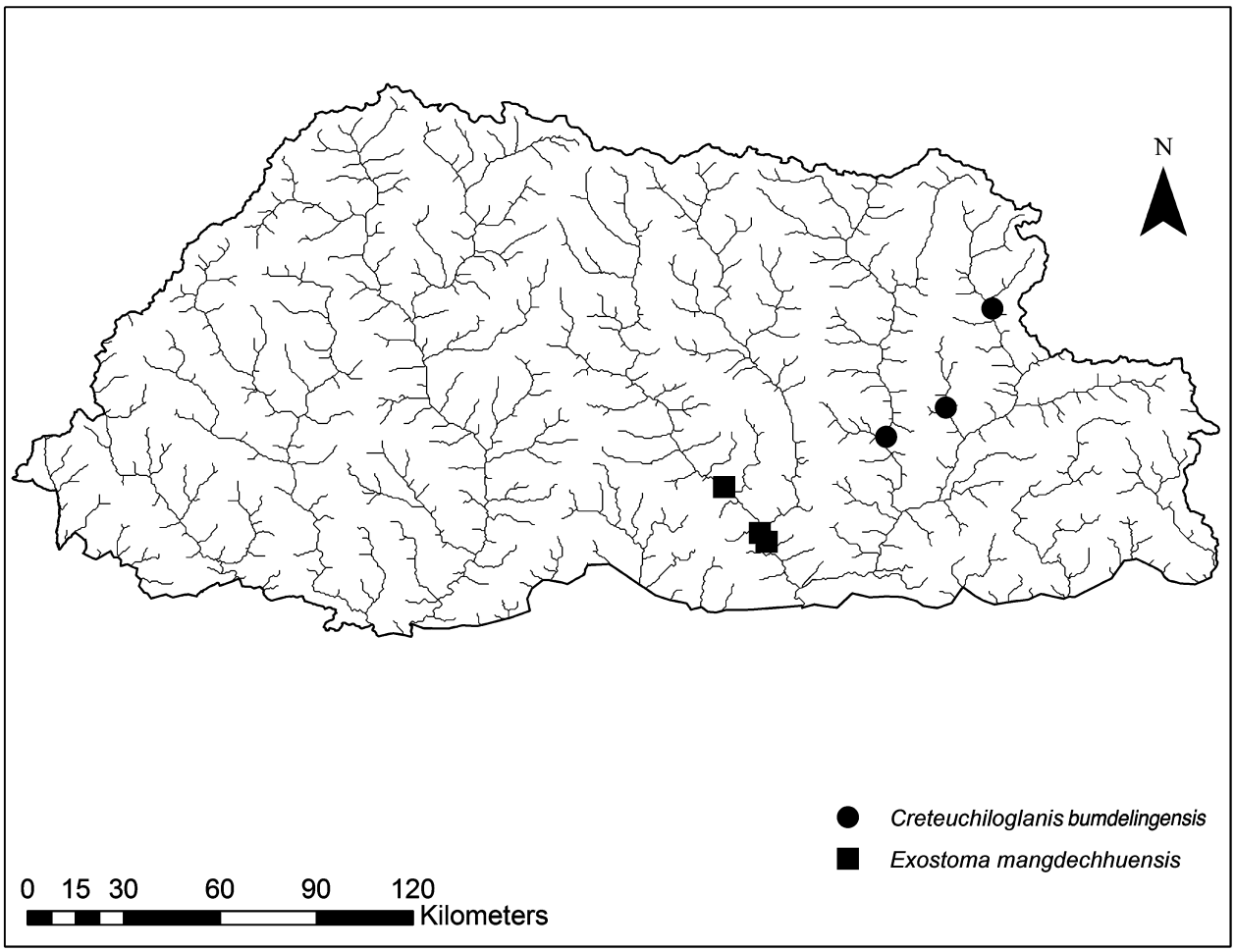

FIGURE 16. Locality map of *Exostoma mangdechhuensis* and *Creteuchiloglanis bumdelingensis* in Bhutan.

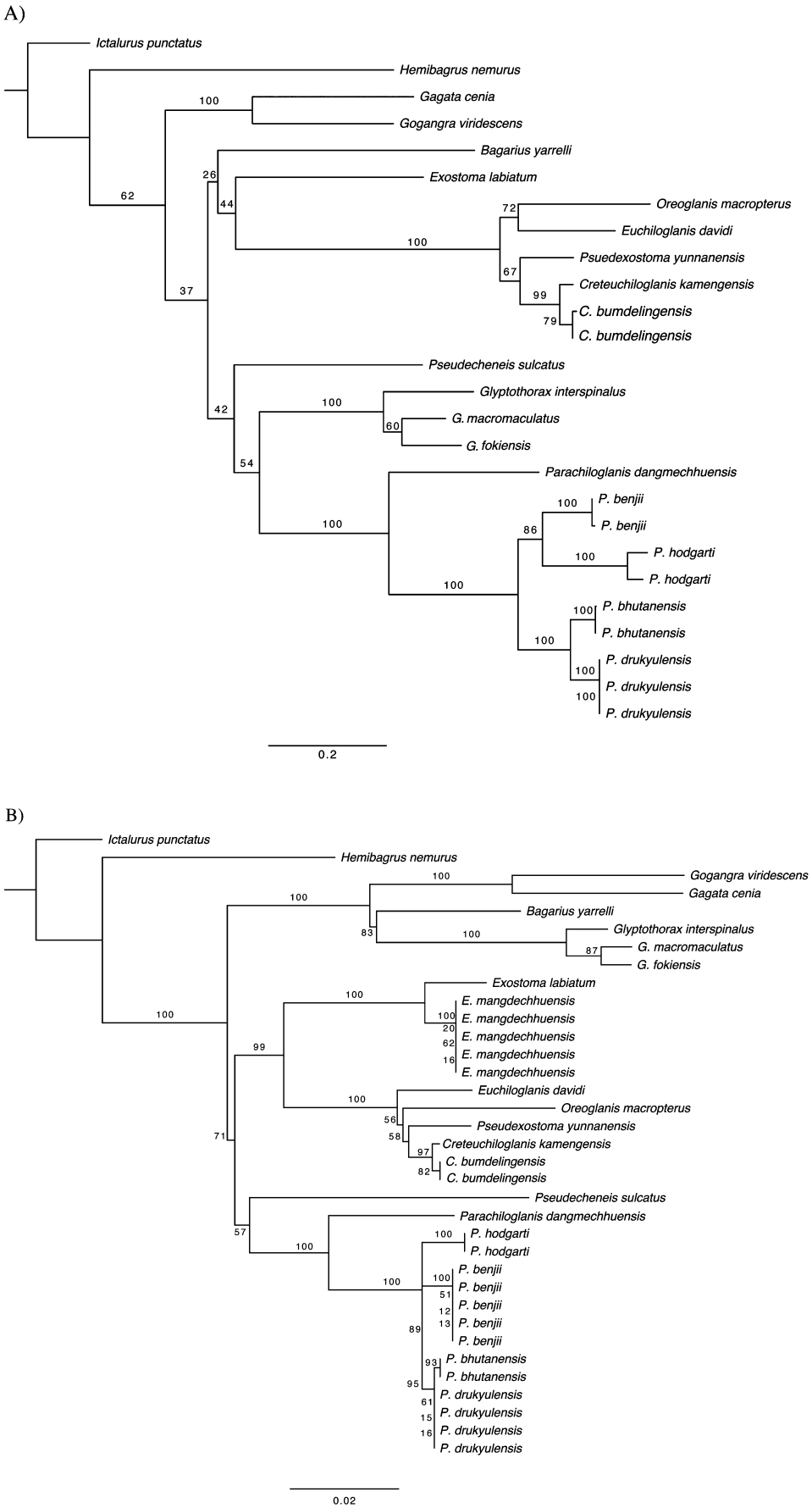

FIGURE 17. Phylogenetic relationships of Glyptosterninae inferred from Maximum Likelihood analysis of gene sequences of RAG2 (a) and Cyt *b* (b). Bootstrap values are provided at each node.

Within this examination of the Glyptosterninae of Bhutan is the addition of the western-most species of *Creteuchiloglanis.* This adds a westward expansion to the known range of the genus to include the Dangmechhu River Drainage in Bhutan; a tributary of the Manas River of the Brahmaputra drainage. This discovery, as well as other recently discovered species of other glyptosternine genera such as *C. payjab*, *Oreoglanis majusculus*, and *O. pangenensis* may offer insight into the biogeographical and geomorphological histories of the major river systems of South Asia. Many of these species appear to be restricted to isolated upstream bodies of water, versus being found commonly throughout entire basins, suggesting that their evolutionary mobility through these systems may have been facilitated by stream capture events in headwaters, rather than by large, basin-scale basin shifts, followed by dispersal throughout the large river systems. Further, the absence of groups such as *Creteuchiloglanis* and *Parachiloglanis* in southern tributaries of the Brahmaputra suggests that the Brahmaputra is, and historically has been, a barrier, rather than a route of dispersal, for these fishes.

Molecular analysis provides strong support for the monophyly of *Parachiloglanis* and for the independence of lineages of all new taxa described herein. There was a consistent and well-supported sister relationship between *Parachiloglanis* and the rest of Glyptosterninae. Due to diminishing bootstrap support at deeper relationships in the Cyt *b* gene tree, less can be inferred about broader relationships. However, the nuclear gene RAG2 is generally more conserved than Cyt *b*, and therefore provides better insight, with better support, into deeper relationships. In *Parachiloglanis*, all species described herein, as well as *P. bhutanensis*, formed well-supported lineages in both gene trees. Both trees show *P. dangmechhuensis* falling out as a basal member of the group, having a deep divergence between it and the remaining species of the genus. Tissues of *Exostoma mangdechhuensis* failed to produce mitochondrial sequences, however, in the RAG2 tree, it fell within its genus with a well-supported separate branch from *E. labiatum. Creteuchiloglanis bumdelingensis* also grouped within its genus with a well-supported separate branch from *C. kamengensis*.

Key to the glyptosterninae of Bhutan

1	Post-labial fold present	2
-	Post-labial fold absent (*Parachiloglanis*)	3
2	Lips thick, reflected around the mouth	*Exostoma mangdechhuensis*
-	Lips not reflected around the mouth, post-labial fold in interrupted	*Creteuchiloglanis bumdelingensis*
3	Tooth patch on upper jaw small and semi-circular	*Parachiloglanis dangmechhuensis*
-	Tooth patch on upper jaw widely arched posteriorly	4
4	Dorsal-fin rays well-defined; fin membrane thin, caudal fin truncate with white spot at base.	*Parachiloglanis hodgarti*
-	Dorsal-fin rays difficult to count; fin membrane thick and leathery	5
5	Lateral line punctate	*Parachiloglanis bhutanensis*
-	Lateral line not punctate	6
6	Body covered in rust colored vermiculation	*Parachiloglanis drukyulensis*
-	Body coloration mostly brownish grey to olive green, caudal fin emarginate	*Parachiloglanis benjii*

Comparative materials examined. *Parachiloglanis hodgarti*: KU: 29046, 3 specimens, 41.5–57.3 mm SL, Nepal: Ghaara River confluence, Edds, D.; 29558, 5 specimens, 48.5–60.8 mm SL; Nepal: Jhungala, Edds, D.; 29231, 3 specimens, 44.5–63.7 mm SL; Nepal: Beni, Edds, D.; 29549, 5 specimens, 39.1–53.2 mm SL, Nepal: Bajura at Kholti, Edds, D; 29045, 5 specimens, 4.5–55.6 mm SL, Nepal: Myagdi at Beg Khola, Edds, D. CNR: 15227 45.1 mm SL, Bhutan: Samdrup Jongkhar Dzongkhag: Marangchhu, Thoni & Gurung; 15176, Bhutan: Zhemgang Dzongkhag: Chirangchhu at sangsiri, Thoni & Gurung; 13551 59.7 mm SL, Bhutan: Samdrup Jongkhar Dzongkhag: 200 m upstream from Dimala bridge, Thoni & Gurung. CAS: 44187, 2 specimens, 51.1–55.4 mm SL, Nepal: Chitawan Valley, headwaters of Rapti R., 1–2 mi. west of Bhimpedi. *Exostoma labiatum*: Holotype, BMNH 1860.3.19.97, 72.7 mm SL, India: Meghalaya: Mishmee Hills. *Pseudecheneis sulcata*: BMNH2005.5.17.5. Holotype, 76.3 mm SL, India, Meghalaya: Kasyah Hills. CAS 230829, China: Yunnan, Small tributary to the Dulong River near Bapo. *Creteuchiloglanis kamengensis*: CAS 226644, 1 specimen, 103.4 mm SL, China: Yunnan: Nujiang, Lushui County; 340 m. section of Wu Zhong River, approx. 20 km from Pianma on rosd to Myanmar; CAS 230831, 1 specimen, China: Yunnan, Small tributary to the Dulong River near Bapo. *Oreoglanis insignis*: CAS: 226060, 3 specimens, 36.2–64.1 mm SL, China: Yunnan: Tengching, Ming Guang River at first bridge on road N of Ming Guang. Elev. 1836 m. *Oreoglani macropterus*: CAS: 226790, 2 specimens, 94.1–133.7

mm SL, China: Yunnan: Nujiang, Xiao Jiang at Gulang Ba Village, close to Gang Fang; 26 km from Pianma; Lushui County. *Pseudecheneis sulcata*: BMNH2005.5.17.5. Holotype, 76.3 mm SL, India, Meghalaya: Kasyah Hills.

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