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A New Species of Snailfish (Cottiformes: Liparidae) Closely Related to *Careproctus melanurus* of the Eastern North Pacific

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A new species, *Careproctus ambustus,* is described from 64 specimens based on evidence from morphological and molecular data. Specimens of *Careproctus ambustus*, new species, have been historically misidentified as the common Blacktail Snailfish, *C. melanurus*. The new species is distinguished from *C. melanurus* by its higher numbers of vertebrae (62–66 vs. 56–62 in *C. melanurus*), dorsal-fin rays (57–63 vs. 53–58), and anal-fin rays (51–55 vs. 46–51), and longer pelvic disc (14.1–21.2 vs. 12.6–20.7 % HL). In addition, the new species differs from *C. melanurus* by seven base pairs within a 492-base-pair region of the cytochrome oxidase *c* subunit 1 region, a 1.4% sequence divergence. *Careproctus ambustus,* new species, is found at depths of 58–1,172 m and ranges from Japan, through Alaska, to the west coast of Vancouver Island, British Columbia, where its distribution overlaps with *C. melanurus*, which ranges from southern Alaska and British Columbia to Baja California.

OVER 400 species of snailfishes are distributed among approximately 30 genera of the family Liparidae (Chernova et al., 2004; Orr et al., 2019). All snailfishes are strictly marine and have been recorded in all oceans in both the Northern and Southern Hemispheres (Stein, 2012; Orr et al., 2015). While more shallow members of the family are bipolar in distribution, liparids are also found at great depths in the tropics, where the undescribed Ethereal Snailfish (Linley et al., 2016) from the Mariana Trench is at 8,178 m the deepest-dwelling vertebrate documented (Kido, 1988; Fujii et al., 2010; Overdick et al., 2014; Linley et al., 2016; Gerringer et al., 2017a, 2017b; JAMSTEC, 2017). Having scaleless gelatinous bodies that are often long and tapered posteriorly to form a slender tail, they are characterized by pelvic fins modified to form a ventral sucking disc, although many exceptions occur in deep-sea and pelagic species in which the disc has been lost (Chernova et al., 2004; Orr et al., 2019).

Careproctus is the most diverse liparid genus, comprising approximately 140 species to date, with new species being described relatively often (e.g., Ji et al., 2012; Orr et al., 2015; Orr, 2016; Fricke et al., 2019) and many undescribed species known (Orr et al., 2019). Members of the genus are found frequently in deeper waters of the continental slope in the Antarctic, Arctic, Atlantic, and Pacific Oceans (Chernova et al., 2004; Orr and Maslenikov, 2007; Ji et al., 2012), with more than 50 species recognized from the North Pacific alone (Nakabo and Kai, 2013; Parin et al., 2014; Orr et al., 2015). Although recent molecular analyses have demonstrated that *Careproctus* is paraphyletic (Duhamel et al., 2010; Shen et al., 2017; Orr et al., 2019), it is characterized morphologically by having a single pair of nostrils, a pelvic disc, fewer pectoral-fin rays than anal-fin rays, pseudobranchs absent, and body coloration uniformly dark or light, often gradually darkening posteriorly when light, and rarely variegated (Kido, 1988; Stein et al., 2001; Orr and Maslenikov, 2007; Ji et al., 2012).

Careproctus melanurus has been considered a widespread species, one of the most common larger snailfishes in the eastern North Pacific, being recorded commonly from the Bering Sea and Aleutian Islands, Alaska, to California (Stein, 1978), as well as in the western North Pacific off the Kuril Islands and Kamchatka (Orlov, 2000; Orlov and Tokranov, 2011), and rarely to Japan (Kido and Shinohara, 1997). It is abundant as well, being one of the most frequently captured liparids in commercial fishing operations at depths of 200 m or more off the North American west coast (Stein, 1978) and noted as the most abundant liparid on the upper slope of both the west coast (Stein et al., 2006) and Bering Sea (Hoff, 2016). A deep-water liparid, it is commonly found at depths of 200 m or more but has also been recorded in shallower waters (Stein, 1978; Stein et al., 2006). Known commonly as the Blacktail Snailfish (Page et al., 2013), this name has been extended in common usage to the many species of *Careproctus* with a similar color pattern, including *C. cypselurus*, *C. furcellus*, and *C. simus*, all significant species in fisheries bycatch in Alaska and the eastern North Pacific. With further reviews and revisionary works on the fauna (e.g., Stein, 1978; Kido, 1988; Mecklenburg et al., 2002), identifications of the several species have been more clearly resolved.

Similarly, widespread species such as *C. melanurus* have been subjected to greater scrutiny, and molecular analyses have revealed differences between northern and southern populations. Gardner et al. (2016) conducted a molecular study attempting to identify snailfish egg masses found in the gill cavities of commercially important species of Alaskan lithodid crabs using sequence data from the mitochondrial

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cytochrome oxidase c subunit I (COI) region. They found several egg masses for which the COI sequence data did not match that of adult voucher specimens of several species of snailfishes, including *C. melanurus*, the species most commonly identified with egg masses found in lithodids of the eastern North Pacific (Parrish, 1972; Peden and Corbett, 1973). While *C. melanurus* was included among the original vouchers, the tissue was from a specimen taken off the Washington coast (UW 115415), and so new sequence data from several specimens of *C. melanurus* collected in Alaska were added. All data of the specimens from Alaska matched the previously unidentified egg clusters and differed by at least 1.4% from vouchers taken off Washington, within the range of other interspecific divergences among closely related species determined in later molecular phylogenetic analyses (Orr et al., 2019).

Using COI and RADseq analyses, Orr et al. (2019) recently recovered two highly supported and reciprocally monophyletic clades within *C. melanurus*. These two clades clearly indicated that the taxon currently known as *C. melanurus* included two distinct species. We herein recognize and describe the new species, based on material collected from Alaska and British Columbia and compared primarily with material of the closely related *Careproctus melanurus* taken from British Columbia to California.

MATERIALS AND METHODS

In addition to sequence data published by Gardner et al. (2016) and other data available in BOLD and GenBank, we obtained new COI sequence data (GenBank accession numbers MN126583–MN126595; Supplemental Table 1; see Data Accessibility). DNA was extracted using the Qiagen DNeasy blood and tissue kit (Qiagen, Inc., Valencia, CA). COI was amplified via polymerase chain reaction (PCR) in 25 μl reactions using the standard protocol for *OneTaq* Hot Start 2X Master Mix with Standard Buffer (New England Biolabs, Ipswich, MA), primers FishF1 and FishR1 (Ward et al., 2005), and about 200 ng genomic DNA template. The thermocycle profile consisted of 2 min at 95°C; 35 cycles of 95°C for 30 sec, 54°C for 45 sec, 72°C for 1 min; and a final cycle of 72°C for 5 min. PCR products were sequenced in both forward and reverse directions with Sanger sequencing using the PCR primers at the Molecular Cloning Laboratories (MCLAB, South San Francisco, CA). Contigs were assembled, checked manually with their chromatograms using Sequencher (2011, version 5.0, Gene Codes Corporation, Ann Arbor, MI), and visually aligned using BioEdit version 7.2.6 (Hall, 1999). Forward and reverse sequences were obtained from all 13 new samples. A fragment of 492 bp was used for analysis after trimming ends with low sequencing quality. Specimens examined with genetic data are indicated with an asterisk in material examined. BOLD sequence identification numbers and GenBank accession numbers are given in Supplemental Table 1 (see Data Accessibility).

Counts, measurements, and descriptive terminology follow Andriashev and Stein (1998), with the exception of the cephalic sensory-pore series, which follows Stein et al. (2001), and pectoral girdle morphology, which follows Orr and Maslenikov (2007). Counts of median-fin rays and vertebrae were taken from radiographs. Counts of teeth were made according to methods of Able and McAllister (1980). Counts of gill rakers were taken from the first gill arch on the right side. The right gill membrane and abdomen in most specimens were cut to examine the branchial and visceral cavities; right pectoral girdles were dissected, cleared, and counter-stained following Potthoff (1984). Lengths are presented as standard length (SL) and proportions as percent SL, unless otherwise indicated as percent total length (TL), head length (HL), orbit length (OL), or caudal length (CL). Fleshy interorbital width is taken at the greatest width including tissue extending dorsally over the eye; bony interorbital width is the narrowest bony width. Suborbital depth to lower jaw is measured from the ventral rim of the orbit to the mandibular articulation. Measurements and counts are presented in species accounts as the range for all material examined followed by the value for the holotype or lectotype in parentheses when intraspecific variation is indicated. Institutional abbreviations are those provided by Sabaj (2020).

Statistical analyses were performed with Statgraphics Centurion XV, ver. 15.2 (StatPoint Technologies Inc., Warrenton, VA), and Spotfire S+ 8.2 (TIBCO Software Inc., Palo Alto, CA). Using the Bonferroni method (Haynes, 2013) to adjust for multiple comparisons, we considered differences significant at $P < 0.025$.

A total of 359 specimens were examined morphologically for meristic and morphometric data or for meristic data only. Among these were 38 specimens for which COI sequence data were available. A reduced data set of 88 specimens, including many of those with sequence data, that had a complete suite of meristic and morphometric character data was used to conduct most univariate and multivariate analyses. Meristic characters and the selected morphometric characters HL, OL, and pelvic-disc length and width were analyzed for all undamaged specimens. Arcsine-transformed morphometric ratios (with SL as denominator) were tested to meet the assumptions of normality and equality of variance required for analysis of covariance (ANCOVA), as well as for significance of interaction with the covariate SL. A Kruskal-Wallis nonparametric test was employed to test for differences in means among all characters that violated ANCOVA assumptions or that were not significant in the ANCOVA. Allometry was evaluated by plotting each measurement divided by head length against SL. Pectoral girdles of 16 specimens were cleared and stained.

A stepwise discriminant function analysis (DFA) was conducted with morphometric and meristic data to establish the relative significance of characters in distinguishing the species and to identify specimens preserved in formalin without tissues available for genetic identification. Morphometric data were standardized by dividing values by SL. Only characters meeting assumptions of multivariate normality and that were statistically significant were analyzed. The robustness of the discriminant function analysis was tested with a leave-one-out cross-validation procedure.

Principal component analyses (PCA) were conducted to visualize differences between the species. The analyses were conducted on the correlation matrix of meristic characters and on the covariance matrix of log-transformed morphometric characters, following Kai et al. (2011a). Differences between species were illustrated by plotting scores of meristic principal component (PC) 1 against PC2 and morphometric PC2 against PC3, the axes that most clearly indicated differences between the species.

RESULTS

Genetics.—Among 13 new sequences and 52 sequences from public databases (Supplemental Table 1; see Data Accessibility), no COI haplotype was shared between *C. ambustus,* new species, and *C. melanurus*. All sequence data from specimens collected in Alaska differed from that of specimens taken south of Alaska, from British Columbia to California, by at least 7 bp in 492 bp (1.4%) and 8 bp in those sequences with 610 bp (1.3%). All eight sites exhibited fixed differences between the two species. All except one putative substitution at the second codon position (converting isoleucine to valine) were third codon position substitutions that did not result in amino acid changes.

Among 57 COI sequences (492 bp in length) of *C. ambustus*, new species, representing 19 adult specimens and embryos from 38 egg clusters (Gardner et al., 2016; Supplemental Table 1; see Data Accessibility), two unique haplotypes were detected. All adults shared the same haplotype, as did 36 embryos. Two embryos from two clusters each differed from all others by 1 bp. Two haplotypes present in nine sequences from adult specimens of *C. melanurus* differed by 1 bp: eight had the common haplotype and one had the uncommon haplotype.

Morphology.—In the dataset of 88 specimens with complete data, mean counts of dorsal-fin rays, anal-fin rays, and caudal vertebrae differed significantly between *C. melanurus* and *C. ambustus*, new species, all being greater in *C. ambustus*, new species (Table 1); median counts of pectoral-fin rays of the lower lobe and principal caudal-fin rays were also significantly different. When the two species are combined, dorsal-fin ray, anal-fin ray, and caudal vertebrae count distributions are clearly bimodal, and a strong latitudinal cline is evident. Each species alone displays a unimodal distribution, and a slight latitudinal cline is evident in each significant meristic character (Table 2). Among morphometric characters, only the length of the pelvic disc when flattened was significantly different in the ANCOVA. Median values for several characters (greatest body depth, suborbital depth to lower jaw, lengths of the pectoral fin and its lower lobe, snout to pelvic disc length, snout to anal fin length, and anus to anal fin length) were significantly different (Table 1). All except anus to anal fin length were greater in the new species (Table 1). All body depth and width measures were allometric, with larger specimens being proportionally deeper and wider in both species.

Plots of PCA scores revealed clear differences between *C. ambustus*, new species, and *C. melanurus* in meristic characters but broad overlap in morphometric characters. In the meristic PCA, all characters were positively loaded on PC1, which explained 44.6% of the total variation, and heavily loaded on the median elements anal-fin rays, dorsal-fin rays, and caudal vertebrae; PC2 explained 16.6% of variation and was heavily loaded on pectoral-fin rays, anterior anal-fin pterygiophores, and caudal-fin rays (Table 3). In the plot of PC1 versus PC2 (Fig. 1A), the clusters representing the two species did not overlap, with nearly all the separation being along the PC1 axis. In the morphometric PCA, all characters were positively loaded on PC1 (the size component; Table 3), which explained 86.1% of the total variation. Among the principal shape components, PC2 explained 7.1% of variation and was heavily loaded on distance from pelvic disc to anus and body depth characters (body depth from dorsal-fin origin to anal-fin origin, body depth at anal-fin origin, and greatest body depth); PC3 explained 1.0% of variation and was heavily loaded on anus to anal-fin origin length, pelvic-disc length, pectoral-fin lower-lobe length, and snout to pelvic disc length (Table 3). In the plot of PC2 versus PC3 (Fig. 1B), the two clusters representing *C. ambustus*, new species, and *C. melanurus* overlapped broadly, with about half of the specimens of both species in the area of overlap. In the plot of meristic PC1 versus morphometric PC2 (not shown), the clusters were clearly distinct along the meristic axis with broad overlap on the morphometric axis.

Following the PCA, a stepwise DFA on a dataset of 28 genetically identified specimens using significantly different and externally available meristic characters produced the following highly significant ($P < 0.00001$) discriminant function:

$$D = -1597.96 - 11.8641 * d + 14.0982 * a + 49.3115 * v$$

where D = the discriminant score of an individual, d = number of dorsal-fin rays, a = number of anal-fin rays, and v = number of vertebrae. The leave-one-out cross-validation procedure correctly classified 100% of individuals. Applying this discriminant function to 234 specimens without genetic data definitively classified all individuals. Individuals with a score >1,500 were classified as *C. ambustus*, new species; those with a score <1,500 were classified as *C. melanurus*.

Systematic account

***Careproctus (Allochir) ambustus*, new species, Orr**

Scorched Snailfish
urn:lsid:zoobank.org:act:BF1517AE-707D-4A19-9E70-9506386F3188
Figures 2–4, Tables 1–3

Careproctus melanurus: Quast and Hall, 1972:28 (in part, Alaska, checklist).—Fedorov, 1973:66 (Bering Sea).—Stein, 1978:16 (in part, Alaska and British Columbia, review).—Allen and Smith, 1988:66 ("blacktail snailfish," in part, Alaska, atlas).—Kido and Shinohara, 1997:127 (Japan).—Orlov, 1998:146 (Kuril Islands, Kamchatka).—Orlov, 2000:189 (Kuril Islands, Kamchatka, western Bering Sea).—Sheiko and Fedorov, 2000:32 (Kamchatka).—Mecklenburg et al., 2002:616 (in part, Alaska, synopsis, illustration, in key).—Chernova et al., 2004:11 (in part, checklist).—Love et al., 2005:102 (in part, Alaska and British Columbia, checklist).—Orlov, 2005:146, tables 2–5 (Kuril Islands).—Knudsen et al., 2007:659, fig. 3 (phylogeny).—Knudsen and Møller, 2008:179 (comparison with *C. kidoi*).—Orlov and Binohlan, 2009:225, table 1 (length–weight relationships, western Bering Sea).—Shinohara et al., 2009:720 (Pacific Japan).—Kai et al., 2011a:353 (compared with *C. notosaikaiensis*).—Kai et al., 2011b:146 (compared with "*Careproctus* sp. 2").—Orlov and Tokranov, 2011:2, fig. 3 (life history, Russia).—Nakabo and Kai, 2013:1211 (in part, Pacific Japan, illustration, in key).—Overdick et al., 2014:132 (eggs).—Parin et al., 2014:322 (and citations within, Russia, checklist).—Orr et al., 2014a:20 (eastern Bering Sea).—Orr et al., 2014b:30, 165 (Gulf of Alaska and Aleutian Islands).—Datsky, 2015:808 (western Bering Sea).—Gardner et al., 2016:648, tables 2–3, figs. 2A, 4, 5, appendix 1 (eggs deposited in crabs, molecular phylogeny).—Kells et al., 2016:212, facing

Table 1. Proportional morphometric and meristic characters of *Careproctus ambustus* and *Careproctus melanurus*. Morphometric data are given in percent standard length and presented as the range, followed by the mean±standard deviation (SD). Significance refers to that determined from the ANCOVA. K-W = significance of Kruskal-Wallis test

	C. ambustus			*C. melanurus*				
	n	Range	Mean±SD	*n*	Range	Mean±SD	Significance	K-W
Standard length	127	90–410	205.5±83.8	185	55–295	176.1±49.3		
%SL								
Head length	101	17.4–29.7	23.9±2.3	163	18.6–28.7	24±1.8		NS
Head width	36	11.5–16.3	13.9±1.0	55	10.6–15.6	13.5±1.0	NS	NS
Greatest body depth	36	18.8–34.2	26.2±4.3	55	16.1–28.1	22.8±2.7	NS	0.0003
Body depth at anal-fin origin	36	17.6–34.5	25.6±4.7	55	14.5–28.9	21.6±3.1	NS	NS
Body depth from anal-fin origin to dorsal-fin origin	36	19.5–37.7	28.2±4.7	55	19.2–32.8	25.3±2.9	NS	NS
Body depth at pelvic fin	36	13.6–19.1	16.6±1.3	55	12.7–20.5	15.7±1.8	NS	NS
Body depth at dorsal-fin origin	36	18.8–33.9	25.1± 3.4	55	16.8–28.1	22.4±2.6	NS	NS
Snout length	36	5.2–9.0	6.9±0.8	55	5.3–10	7.0±1.0	NS	NS
Orbit length	101	4.5–8.7	6.7±1.0	163	4.9–9.3	7.1±0.9	NS	NS
Interorbital width (bony)	36	4.1–6.6	5.4±0.6	55	4.2–6.6	5.3±0.6	NS	NS
Interorbital width (fleshy)	36	9.1–12.9	11.3±0.9	55	8.7–12.8	11±0.9	NS	NS
Suborbital depth to upper jaw	36	2.2–3.8	3.1±0.4	55	1.9–3.8	3.0±0.4	NS	NS
Suborbital depth to lower jaw	36	5.0–7.8	6.6±0.7	55	4.6–7.7	6.2±0.6	NS	<0.002
Mouth width	36	9.4–14.8	11.9±1.4	55	8.7–13.9	11.4±1.2	NS	NS
Maxilla length	36	9.4–13.5	11.1±1.1	55	8.5–13.1	11±1.0	NS	NS
Mandible length	36	9.4–14.3	11.7±1.3	55	9.4–14.3	11.6±1.1	NS	NS
Gill slit length	36	6.1–10.5	8.8±0.9	54	6.1–10.2	8.4±0.9	NS	NS
Pectoral-fin length	36	15–24.1	20.2±2.0	53	14.3–22.5	18.5±1.9	NS	<0.01
Lower lobe of pectoral fin length	35	15.5–24.9	19.7±2.4	53	12.9–20.4	16.7±1.7	NS	<0.0001
Notch ray of pectoral fin length	35	9.0–17.8	12.2±2.2	53	8.2–13.8	10.7±1.3	NS	NS
Predorsal length	36	22.4–31.3	27.2±2.4	55	21.4–31.1	27.1±2.2	NS	NS
Preanal length	36	33.6–46.5	39.3±3.0	55	30.3–45.8	38.8±3.1	NS	NS
Snout to pelvic disc length	36	8.7–12.2	10.7±1.1	55	7.4–13.6	10.2±1.3	NS	<0.02
Snout to anal fin length	36	12.6–19.6	16.1±1.6	55	11.9–18.7	14.9±1.7	NS	<0.001
Pelvic-disc length	101	3.2–6.0	4.4±0.7	163	2.9–5.6	4.0±0.5	<0.0219	
Pelvic-disc width (flattened)	92	2.4–4.6	3.2±0.4	162	2.1–3.9	3.1±0.4	NS	NS
Pelvic-disc width (curled)	83	1.3–3.5	2.4±0.4	150	1.6–3.6	2.4±0.4	NS	NS
Pelvic disc to anus length	36	0.5–2.3	1.3±0.4	55	0.2–2.6	1.1±0.5	NS	NS
Anus to anal fin length	36	16.8–27.1	22.2±2.4	55	17.2–30.1	24.5±3.0	NS	<0.001
Caudal-fin length	36	9.6–17.0	13.1±1.4	51	10.0–15.9	12.9±1.5	NS	NS
Dorsal-fin attachment to caudal fin length	36	6.6–10.8	8.7±1.1	48	6.1–11.6	8.4±1.2	NS	NS
Anal-fin attachment to caudal fin length	36	7.3–11.8	9.2±1.1	48	6.4–11.6	8.8±1.2	NS	NS
Caudal-fin base depth	36	1.2–2.1	1.6±0.2	55	1.2–1.9	1.5±0.2	NS	NS
Nasal tube length	32	0–1.0	0.6±0.2	44	0–1.1	0.5±0.3	NS	NS
Meristics								
Dorsal-fin rays	170	57–63	59.7±1.2	193	53–59	56.4±1.2	<0.00001	
Anal-fin rays	172	51–57	53.1±1.0	197	46–51	49.5±1.1	<0.00001	
Pectoral-fin rays	139	28–35	31.2±1.4	187	28–34	30.7±1.4	NS	NS
Pectoral-fin lower lobe rays	125	7–11	8.2±0.7	178	6–10	7.9±0.7	NS	0.0001
Principal caudal-fin rays	87	10–12	11.2±0.6	135	9–12	11.0±0.6	NS	NS
Precaudal vertebrae	183	9–11	10±0.2	204	9–11	9.9±0.3	NS	NS
Caudal vertebrae	182	51–57	54.2±1.1	203	45–52	50.4±1.1	<0.00001	
Total vertebrae	182	61–67	64.1±1.1	203	55–62	60.3±1.2	<0.00001	
Pterygiophores anterior to haemal spine I	128	1–2	1.1±0.3	195	0–2	1.1±0.3	NS	NS
Tooth count	37	11–27	16.4±4.0	59	10–20	13.7±2.7	NS	NS
Tooth rows	37	23–45	33.7±6.2	59	21–45	31.4±5.4	NS	NS
Gill rakers	45	9–12	10.8±0.8	63	9–13	10.3±0.8	NS	NS
Pleural ribs	155	0–2	0.5±0.6	172	0–2	0.7±0.7	NS	NS

Table 2. Counts of dorsal-fin rays, anal-fin rays, total pectoral-fin rays, rays of lower pectoral-fin lobe, total vertebrae, caudal vertebrae, and gill rakers in *Careproctus ambustus* and *C. melanurus*. Asterisks indicate specimens identified with cytochrome oxidase *c* subunit I (COI) sequence data.

	Dorsal-fin rays											
Region	53	54	55	56	57	58	59	60	61	62	63	*n*
C. ambustus												
Hokkaido, Japan									1			1
Northern Kuril Islands						2	3	2				7
Northern Bering Sea							1	1	1		1*	4
Southern Bering Sea							5	4	2	4	1	16
Western Aleutian Islands					1	1	5	6	2	2*	1	18
Central Aleutian Islands							1	1				2
Eastern Aleutian Islands						3*	6*	4*	2*			15
Northern Gulf of Alaska					1	7*	21*	31*	14*	3	1	78
Southeast Alaska					2	2	8*	4	2	1		19
British Columbia						1	7					8
C. melanurus												
Southeast Alaska				1	1	3	1					6
British Columbia			3	24*	19*	11	3					60
Washington	1			9	10	5						25
Oregon	1*	1	12*	28*	16*	5	3					66
California	2*	4	8	13*	7	2						36

	Anal-fin rays												
	46	47	48	49	50	51	52	53	54	55	56	57	*n*
C. ambustus													
Hokkaido, Japan										1			1
Northern Kuril Islands						1	1	3	2				7
Northern Bering Sea								1	1	2*			4
Southern Bering Sea								3	8	4			15
Western Aleutian Islands							4	4	8*	1	1		18
Central Aleutian Islands								1	1				2
Eastern Aleutian Islands							6*	7*	2				15
Northern Gulf of Alaska						1	21*	33*	20*	3*	1	1	80
Southeast Alaska						1	7	8*	1	2			19
British Columbia							7	1					8
C. melanurus													
Southeast Alaska				2		4							6
British Columbia			3	15*	25*	17*	1						61
Washington			3	8	7	8							26
Oregon	1*		12*	23	25*	7							68
California		2*	13	11*	5	5							36

	Pectoral-fin rays								
	28	29	30	31	32	33	34	35	*n*
C. ambustus									
Hokkaido, Japan		1							1
Northern Kuril Islands									
Northern Bering Sea				2*		2			4
Southern Bering Sea	1	2	5	3	3				14
Western Aleutian Islands	1*	3	1	1			1		7
Central Aleutian Islands		1*							1
Eastern Aleutian Islands			1*	3*	2*	1*	1	1	9
Northern Gulf of Alaska	1	3	8	25*	25*	13*	1*		76
Southeast Alaska		4*	3	7	2		1		17
British Columbia			3	3*		1	1		9
C. melanurus									
Southeast Alaska	2	1	1	2					6
British Columbia		3	14	26*	17	1*			61
Washington	2	2	4	9	6		1		24
Oregon	5*	10	8*	17*	12*	9			61
California	6*	5	6	9*	8		1		35

Table 2. Continued.

Region	Rays of lower pectoral-fin lobe						
	6	7	8	9	10	11	*n*
C. ambustus							
Hokkaido, Japan							
Northern Kuril Islands							
Northern Bering Sea		2	1	1*			4
Southern Bering Sea		3	7				10
Western Aleutian Islands		1	4*	1		1	7
Central Aleutian Islands					1*		1
Eastern Aleutian Islands			6*	2	1		9
Northern Gulf of Alaska		5	41*	14*	2		62
Southeast Alaska		3	8	5*			16
British Columbia			5*	4			9
C. melanurus							
Southeast Alaska	1	1	3	1			6
British Columbia		15*	34*	8	1		58
Washington	1	5	10	7			23
Oregon	2*	12	37*	7	1		59
California		9*	16	5			30

Region	Total vertebrae													
	55	56	57	58	59	60	61	62	63	64	65	66	67	*n*
C. ambustus														
Hokkaido, Japan													1	1
Northern Kuril Islands									1	2	3	1		7
Northern Bering Sea											2	2*		4
Southern Bering Sea									1	1	8	6		16
Western Aleutian Islands									1	7	7*	4		19
Central Aleutian Islands										1	1			2
Eastern Aleutian Islands									3*	8*	4			15
Northern Gulf of Alaska							1	1*	23*	40*	18*	3*	2	88
Southeast Alaska								3	8*	6	2			19
British Columbia								1	7					9
C. melanurus														
Southeast Alaska						2		4						6
British Columbia				1	3	14	28*	16*						62
Washington				2	1	10	9	4						26
Oregon		1*			13*	28*	21*	6						69
California	1		1	3	15	13*	5	2						40

Region	Caudal vertebrae												
	45	47	48	49	50	51	52	53	54	55	56	57	*n*
C. ambustus													
Hokkaido, Japan												1	1
Northern Kuril Islands								1	1	5			7
Northern Bering Sea										2	2		4
Southern Bering Sea								1		9	6		16
Western Aleutian Islands								1	5	9*	4		19
Central Aleutian Islands									1	1			2
Eastern Aleutian Islands								3*	7*	5			15
Northern Gulf of Alaska						1	1*	23*	38*	20*	3*	2*	88
Southeast Alaska							3	8*	6	2			19
British Columbia							1	7					8
C. melanurus													
Southeast Alaska					2		4						6
British Columbia			1	3	13	28*	17*						62
Washington			1	2	8	11	4						26
Oregon		1*		13*	28*	20*	7						70
California	1	1	3*	14	14*	5	2						40

Table 2. Continued.

	Gill rakers					
Region	9	10	11	12	13	*n*
C. ambustus						
Hokkaido, Japan						
Northern Kuril Islands						
Northern Bering Sea			1			1
Southern Bering Sea			5	1		6
Western Aleutian Islands			2*	1		3
Central Aleutian Islands			1*			1
Eastern Aleutian Islands			1*	2		3
Northern Gulf of Alaska		4*	8*	4*		16
Southeast Alaska	1	3	2			6
British Columbia	1	5	2	1		8
C. melanurus						
Southeast Alaska	1	2	1		1	5
British Columbia	1	6	5	1		14
Washington	2	11	5	3		21
Oregon		5*	4*			9
California	4	7*	4			15

illustration (in part, Alaska, field guide).—Shen et al., 2017:S12, table S2, fig. S5–S6 (molecular phylogenetics, "KU28298" = KU28098).—Pietsch and Orr, 2019:802 (in part, northern populations, illustration).

Careproctus sp. cf. *melanurus*: Shen et al., 2017:S14, table S2, fig. S6 (molecular phylogenetics).—Orr et al., 2019:17, table 3, figs. 10, 12, appendix tables 1–2 (molecular phylogenetics).

Holotype.—UW 152101*, 323 mm, ripe male, Aleutian Islands, 51.8402°N, 173.886°W, 330 m depth, F/V *Ocean Explorer*, cruise 2012-01, haul 90, 1 July 2012, J. W. Orr.

Paratypes.—Total of 63 specimens, 97–420 mm. Eastern Bering Sea: UW 158238*, 275 mm, 58.5240°N, 176.1268°W, 677 m depth, F/V *Cape Flattery*, cruise 2016-01, haul 81, 6 July 2016; HUMZ 81828, 1, 54.55°N, 167.65°W, 800 m depth, *Yakushi Maru,* 14 June 1979; HUMZ 81887, 1, 56.18°N, 169.45°W, 530 m depth, *Yakushi Maru,* 17 June 1979; HUMZ 82669, 1, 55.98°N, 170.28°W, 780 m depth, *Yakushi Maru,* 7 July 1979; HUMZ 82670, 1, 55.98°N, 170.28°W, 780 m depth, *Yakushi Maru,* 7 July 1979; HUMZ 82895, 1, 56.02°N, 169.3°W, 610 m depth, *Yakushi Maru,* 18 June 1979; HUMZ 82896, 1, 56.02°N, 169.3°W, 610 m depth, *Yakushi Maru,* 18 June 1979; HUMZ 93335, 1, 56.68°N, 173.27°W, 470 m depth, *Ryoan Maru 31*, 19 August 1981; RBCM 16115, 410 mm, north of Unalaska, 54.95°N, 167.35°W, 377–457 m depth, M/V *Paragon* II, cruise 1978-01, hauls 200–202, 16 August 1978; UW 25177, 385 mm, 55°N, 167°W, 1 October 1981, J. Linville. Aleutian Islands: UW 118920*, 300.6 mm, 53.6345°N, 165.0592°W, 407 m depth, F/V *Pacific Explorer*, cruise 2009-01, haul 15, 28 May 2009, J. W. Orr; UW 150548*, 380 mm, 59.6429°N, 142.7169°W, 446 m depth, F/V *Gladiator*, cruise 2007-01, haul 260, 23 July 2007, J. W. Orr; UW 151029*, 328.1 mm, 52.8380°N, 172.3383°E, 313 m depth, F/V *Sea Storm*, cruise 2010-01, haul 208, 6 August 2010, K. P. Maslenikov; UW 156087*, 4, 97–110 mm, 53.4257°N, 165.797°W, 515 m depth, F/V *Alaska Provider*, cruise 2013-01, haul 11, 1 June 2013, D. Drumm; HUMZ 102016–102018, 3, eastern Aleutians, 53.6°N, 164.85°W, 535 m depth, *Daikichi Maru 37*, 27 July 1984; HUMZ 68500, 1, west of Attu I., 52.97°N, 171°E, 580 m depth, *Tanshu Maru*, 25 June 1977; HUMZ 88391, 1, northeast of Amlia I., 52.33°N, 173.23°W, 600 m depth, *Hatsue Maru*, 15 July 1980; HUMZ 88393, 1, northeast of Amlia I., 52.33°N, 173.23°W, 600 m depth, *Hatsue Maru*, 15 July 1980; HUMZ 88521, 1, off Herbert Is., 52.4°N, 170.37°W, 300 m depth, *Hatsue Maru*, 27 July 1980; HUMZ 88753, 1, east of Agattu Is., 52.3°N, 174.04°E, 418 m depth, *Hatsue Maru 62*, 16 August 1980; HUMZ 88767, 1, off Attu Is., 52.62°N, 172.73°E, 550 m depth, *Hatsue Maru*, 19 August 1980; HUMZ 88768–88770, 3, off Attu Is., 52.58°N, 172.83°E, 412 m depth, *Hatsue Maru*, 19 August 1980; HUMZ 88789–88794, 6, off Attu Is., 52.82°N, 172.2°E, 446 m depth, *Hatsue Maru*, 21 August 1980. Gulf of Alaska: UW 150528*, 270 mm, 59.5680°N, 142.9251°W, 570 m depth, F/V *Gladiator*, cruise 2007-01, haul 259, 23 July 2007, J. W. Orr; UW 151215*, 130 mm, 58.9902°N, 152.6027°W, 148 m depth, F/V *Ocean Explorer*, cruise 2011-01, haul 205, 7 July 2011, J. W. Orr; UW 151242*, 2, 132–135 mm, 55.7310°N, 154.3303°W, 625 m depth, F/V *Ocean Explorer*, cruise 2011-01, haul 206, 8 July 2011; UW 153536*, 260 mm, 58.7803°N, 140.9751°W, 621 m depth, F/V *Northwest Explorer*, cruise 2005-01, haul 261, 22 July 2005, J. W. Orr; UW 154478*, 122 mm, 59.5641°N, 143.0207°W, 501 m depth, F/V *Gladiator*, cruise 2007-01, haul 258, 23 July 2007, J. W. Orr; UW 156553*, 2, 280–350 mm, 55.2214°N, 156.7282°W, 192 m depth, F/V *Cape Flattery*, cruise 2015-01, haul 83, 12 July 2015, M. Zimmermann; UW 156580*, 390 mm, 58.1284, 137.0457 W, 240 m depth, F/V *Sea Storm*, cruise 2015-01, haul 290, 29 July 2015; UW 158236*, 420 mm, 57.7450°N, 149.7851°W, 423 m depth, F/V *Ocean Explorer*, cruise 2017-01, haul 192, 15 July 2017, R. Manning; UW 158237*, 400 mm, 57.0391°N, 151.3205°W, 582 m depth, F/V *Ocean Explorer*, cruise 2017-01, haul 183, 13 July 2017, R. Manning; HUMZ 34423, 1, southeast Alaska, 55.92°N, 135.42°W, 510 m depth, 6 June 1969; SIO 63-536, 2, 265–325 mm, 58°N, 146°W; SIO 91-59, 3, 270–350 mm, 59.2435°N, 146.5842°W, 432 m depth, F/V *Green Hope*, cruise 1990-01, haul 271, 7 September 1990, W. C. Flerx. British Columbia: RBCM 16111, 280 mm, 51.7261°N, 130.6681°W,

Table 3. Factor loadings for principal components (PC) analysis of morphometric and meristic characters of *Careproctus ambustus* and *C. melanurus*.

	PC1	PC2	PC3
Morphometric			
Standard length	0.1724	0.0517	−0.1097
Head length	0.1454	0.0227	0.0646
Head width	0.1796	0.0569	−0.0603
Greatest body depth	0.2406	0.0827	−0.1672
Body depth at anal-fin origin	0.2622	0.0875	−0.2190
Body depth from anal-fin origin to dorsal-fin origin	0.2417	0.0895	−0.2225
Body depth at pelvic fin	0.1740	0.0573	0.1164
Body depth at dorsal-fin origin	0.2232	0.0676	−0.1662
Snout length	0.1322	0.0408	−0.0207
Orbit length	0.1154	0.0133	0.0002
Interorbital width (bony)	0.1868	0.0503	−0.0934
Interorbital width (fleshy)	0.1748	0.0602	−0.1214
Suborbital depth to upper jaw	0.1633	0.0518	0.2375
Suborbital depth to lower jaw	0.1665	0.0243	0.2456
Mouth width	0.1999	0.0805	−0.1605
Maxilla length	0.1417	0.0306	0.0936
Mandible length	0.1429	0.0230	0.0696
Gill slit length	0.1846	0.0414	−0.0917
Pectoral-fin length	0.2019	0.0160	0.1462
Lower lobe of pectoral fin length	0.2005	−0.0264	0.3286
Notch ray of pectoral fin length	0.2111	0.0134	0.1888
Predorsal length	0.1580	0.0461	0.0255
Preanal length	0.1747	0.0164	−0.0514
Snout to pelvic disc length	0.1551	0.0048	0.3149
Snout to anal fin length	0.1582	−0.0567	0.2163
Pelvic-disc length	0.1398	0.0103	0.3374
Pelvic-disc width (flattened)	0.1496	0.0368	0.1599
Pelvic disc to anus length	0.2227	−0.9626	−0.1101
Anus to anal fin length	0.1753	0.0618	−0.3905
Caudal-fin base depth	0.1850	0.0608	−0.0830
Meristic			
Dorsal-fin rays	0.5448	0.1003	−0.0811
Anal-fin rays	0.5518	0.0845	−0.0896
Pectoral-fin rays	0.0833	0.5670	0.5626
Principal caudal-fin rays	0.2551	−0.4946	0.1093
Precaudal vertebrae	0.1006	−0.3527	0.8003
Caudal vertebrae	0.5453	0.1557	−0.0900
Pterygiophores anterior to haemal spine I	0.1385	−0.5177	−0.0910

877 m depth, 19 October 1996; RBCM 16130, 155 mm, Vancouver I., Clayoquot Canyon, 48.9217°N, 126.54°W, 925 m depth, sta. P88-44, 24 November 1976; RBCM 16420 (out of RBCM 16097), 152 mm, off Vancouver I., offshore to west of Nootka Sound, 2003 Tow 30, 49.5316°N, 127.6413°W, 958 m depth, 16 April 2003; RBCM 16421 (out of RBCM 16104), 180 mm, off the west coast of Vancouver I., 49.5675°N, 127.4967°W, 1068 m depth, 9 April 2003; RBCM 16422 (out of RBCM 16127), 220 mm, Vancouver I., west of Nootka Sound, 49.5667°N, 127.4267°W, 931 m depth, 10 March 1999; RBCM 16423 (out of RBCM 16132), 120 mm, Vancouver I., 48.7333°N, 126.4967°W, 550 m depth, 25 February 1988. Russia, northern Kuril Islands: MIMB 38374, 250 mm, 49.3333°N, 155.8667°E, 715 m depth, R/V *Prof. Levanidov*, haul 164, 17 October 2000; MIMB 38375, 291 mm, 49.4°N, 156.0167°E, 630 m depth, *Tora Maru 58*, haul 75, 19 September 1993, D. L. Pitruk; MIMB 38376, 264 mm, 49.9672°N, 156.5855°E, 592 m depth, *Tora Maru 58*, haul 120, 5 October 1993, D. L. Pitruk; MIMB 38377, 268 mm, 49.9672°N, 156.5855°E, 592 m depth, *Tora Maru 58*, haul 120, 5 October 1993, D. L. Pitruk; MIMB 38378, 250 mm, 50.3012°N, 157.0008°E, 550 m depth, *Tora Maru 58*, haul 130, 6 October 1993, D. L. Pitruk; ZIN 56417, 291 mm, 49.4°N, 156.0167°E, 630 m depth, *Tora Maru 58*, haul 75, 19 September 1993, D. L. Pitruk; ZIN 56418, 250 mm, 50.3012°N, 157.0008°E, 550 m depth, *Tora Maru 58*, haul 130, 6 October 1993, D. L. Pitruk.

Additional material examined.—A total of 129 specimens, 90–420 mm (see Supplemental Text A; see Data Accessibility).

Diagnosis.—*Careproctus ambustus* is distinguished from all other North Pacific species of *Careproctus* except *C. melanurus* by the combination of the shape of its pelvic disc, which is oval, longer than wide (vs. round or wider than long in other species of *Careproctus*), shallowly cupped (vs. flat or deeply cupped), and somewhat smaller than the orbit (vs. minute or large); shallowly notched pectoral fin with elongate rays in the lower lobe (vs. deeply notched with elongate or short rays, or shallowly notched with short rays in other species of *Careproctus*); and unique COI haplotypes (Orr et al., 2019). It is further distinguished morphologically from *C. melanurus*, with which it has been historically confused, by its higher vertebral and median fin-ray counts (vertebrae 61–67 vs. 56–62, dorsal-fin rays 57–63 vs. 53–59, anal-fin rays 51–57 vs. 46–52 in *C. melanurus*), in combination with its longer pelvic disc (14.1–21.2 vs. 12.6–20.7 % HL in *C. melanurus*).

Among other species of subgenus *Allochir*, *C. ambustus* is also similar to *C. cypselurus* and *C. colletti*, from which it can be further distinguished by its oval and curled pelvic disc (vs. triangular in *C. cypselurus* and typically triangular in *C. colletti*), pinkish red to red body coloration (vs. purplish pink in *C. cypselurus* and purplish pink to dark purple in *C. colletti*), orientation of the opercular spine, which is angled ventrad and extends well below the lower orbital rim (vs. nearly horizontal and above the lower orbital rim in *C. cypselurus* and *C. colletti*), and dark inner surface of the pectoral fin contrasting strongly with the lighter outer surface (vs. dusky inner surface and typically dark outer surface in *C. cypselurus* and *C. colletti*). It is further distinguished from *C. colletti* by its shallowly notched pectoral fin with a moderately long lower lobe (vs. strongly notched pectoral fin with elongate filamentous rays in the lower lobe in *C. colletti*), higher counts of vertebrae, median fin rays, and pyloric caeca (vertebrae 61–67 vs. 59–65, dorsal-fin rays 57–63 vs. 51–57, anal-fin rays 51–57 vs. 47–52, and pyloric caeca 25–37 vs. 8–13 in *C. colletti*). *Careproctus ambustus* is also similar in body shape and color to *C. furcellus* but can be distinguished by its rounded snout (vs. prominent protruding snout in *C. furcellus*); oval pelvic disk (vs. triangular in *C. furcellus*); and long, slender rays in the lower pectoral-fin lobe (vs. short, fleshy rays in *C. furcellus*), as well as lower vertebral and median fin-ray counts (vertebrae 61–67 vs. 67–71, dorsal-fin rays 57–63 vs. 61–65, and anal-fin rays 51–57 vs. 54–59 in *C. furcellus*). *Careproctus ambustus* is also distinguished from all species within the subgenus, including three undescribed or

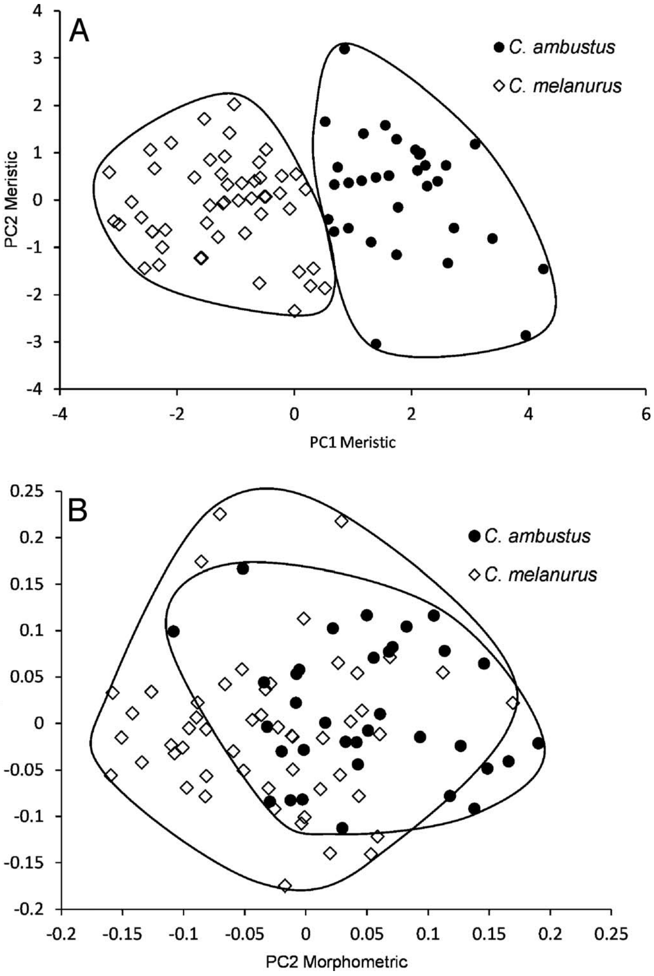

Fig. 1. Plots of principal component scores for (A) meristic and (B) morphometric characters of *Careproctus ambustus*, new species, and *C. melanurus*.

unidentified species (see Orr et al., 2019), by differences in COI sequence data (Orr et al., 2019).

Description.—Body heavy and deep anteriorly, deeper with increasing standard length, tapering slightly posteriorly, moderately compressed; depth at pelvic-disc center 54.4–85.6 (68.4) % HL. Head large, 17.4–29.7 (23.8) % SL, robust, dorsal profile flattened from nape to orbit, rounded to snout. Snout blunt, slightly projecting anterior to lower jaw. Mouth terminal, small, horizontal; upper jaw 41.4–54.3 (43.8) % HL, maxilla extending to mid-orbit, oral cleft extending to anterior rim of orbit; lower jaw 41.4–54.2 (44.7) % HL. Premaxillary tooth plates matching mandibular tooth plates. Premaxillary and mandibular teeth weakly trilobed in 23–45 (35) oblique rows of 11–27 (11) teeth, higher counts in larger specimens, forming moderately wide bands. Diastema absent at symphysis of upper and lower jaws. Orbit 21.7–34.1 (24.1) % HL, dorsal margin below dorsal contour of head, suborbital depth to upper jaw 8.7–16.7 (11.7) % HL, to lower jaw 23.9–33.0 (27.1) % HL; pupil round. Interorbital space broad, fleshy distance 32.8–59.7 (48.2) % HL, bony distance 14.7–27.8 (22.8) % HL, flat to weakly convex. Snout about as long as orbit, 81.7–137.2 (113.0) % OL, 24.3–36.5 (27.2) % HL. Nostril single, at level slightly above midorbit, with well-developed short tube 3.5–14.4 (9.1) % OL.

Pores of cephalic-lateralis system small to moderate size, pore pattern 2-6-7-2, postorbital pore small, possibly absent in some specimens, preoperculomandibular pore 7 smaller than more anterior pores, chin pores paired. Interorbital pore absent.

Gill opening moderate in size, 30.2–45.2 (40.1) % HL, upper margin at or above midorbit, extending ventrally to just above upper pectoral-fin ray. Opercular flap rounded, opercular tip extending well below orbit to cleft or below. Gill rakers 9–12 (11; Tables 1–2), short, blunt.

Dorsal-fin rays 57–63 (60; Tables 1–2), anterior dorsal lobe absent, anterior rays not buried in tissue, tips of more posterior rays not exserted. Anteriormost dorsal-fin pterygiophore inserted between neural spines 3 and 4, rayless or bearing a single small or rudimentary ray (rayless). Predorsal length 22.4–31.3 (29.2) % SL. Anal-fin rays 51–57 (53; Tables 1–2), one or two anal-fin pterygiophores anterior to first haemal spine (one), each bearing a single ray, tips of all rays slightly exserted. Anal-fin origin below vertebrae 11–12 (12), preanal length 33.6–46.5 (38.4) % SL.

Pectoral fin with shallow, nearly indiscernible notch, with 28–35 (29) rays (Tables 1–2). Upper lobe 68.8–108.1 (90.6) % HL, with 19–26 (19) rays extending well beyond anus near or beyond anal-fin origin to the base of ray 4, slightly longer than lower lobe, dorsalmost rays lengthening to rays 8–10, more ventral rays gradually shortening to shortest ray of notch. Lower lobe elongate, 60.3–104.9 (88.7) % HL, with 7–11 rays (10), extending well beyond anus to 70% or more of the distance between the anus and anal-fin origin; uppermost rays gradually lengthening to elongate rays 4–5, ventral rays gradually shortening to ventralmost ray near pectoral symphysis. Tips of rays in upper lobe 0–5 % free of membrane, rays of lower lobe more strongly exserted up to 70% free. Notch shallow, rays in notch slightly more widely spaced than rays of lobes, more widely spaced ventrally. Uppermost pectoral-fin ray level with cleft. Insertion of lowermost pectoral-fin ray below anterior part of orbit.

Proximal pectoral radials four (3 + 1), rounded, thin: radial 1 notched dorsally at scapular fenestra; radials 2 and 3 round, unnotched; radial 4 widely spaced from more dorsal radials, small, round (Fig. 4). Single interradial fenestra extending between scapula and proximal radial 1 an irregular oval. Scapula with robust distally broadened helve; coracoid broadly triangular with narrower helve and upper rib, angled slightly anteriorly. Distal radials present at base of rays 2–25, ventralmost at level of proximal radial 4, dorsalmost ray and more ventral rays articulating directly with the pectoral cartilage or with a separate fibrocartilage pad.

Pelvic disc small, length 14.1–21.2 (18.0) % HL, shorter than orbit, 52.4–87.3 (63.5) % OL, shallowly cupped, oval, curled, nearly round and slightly more elongate when flattened, width when curled 5.1–13.9 (9.1) % HL, when flattened 10.4–17.1 (13.1) % HL, 39.5–100.0 (72.8) % pelvic length, anterior lobe weakly developed, lateral and posterior margin fleshy and curled medially, more anteroposteriorly shortened in larger mature specimens appearing somewhat triangular, distance from snout to pelvic disc 8.7–12.2 (10.7) % SL. Anus at level slightly behind posterior rim of orbit, close behind pelvic disc; distance from pelvic disc to anus 8.8–31.5 (13.3) % HL.

Principal caudal-fin rays 10–12, dorsal procurrent rays 0–2, ventral procurrent rays 0–2 (1–2 + 5–6/5–6 + 0–2) (1 + 6/6 + 0). Caudal fin truncate to rounded, 41.1–66.7 (60.4) % HL.

Fig. 2. (A) *Careproctus ambustus*, new species, UW 152101, 323 mm, holotype, Aleutian Islands, 51.8402°N, 173.886°W, 330 m depth, photographed before fixation and preservation; (B) *Careproctus melanurus*, UW 47264, 205 mm, Oregon, 44.3993°N, 124.8355°W, 447 m depth, photographed before fixation and preservation.

Membrane of posterior dorsal-fin rays attached to caudal fin at slightly shorter distance than anal-fin rays: dorsal-fin rays attached to caudal fin 50.8–87.2 (73.3) % CL; anal-fin rays, 53.7–90.5 (79.3) % CL. Depth at base of caudal fin 5.1–9.4 (7.1) % HL, 7.9–17.3 (17.3) % CL.

Skin thin, flaccid, prickles absent. Pyloric caeca 25–37 (Kido and Shinohara, 1997), length about 54% HL, center-left side of visceral cavity.

Vertebrae 61–67 (64), precaudal 9–11 (10), caudal 51–57 (54; Tables 1–2). Pleural ribs 1, 2, or absent (1), all short and slender, anteriormost smallest, present on vertebrae 9–11 (9).

Coloration.—In life (Fig. 2A), body pink to red, darker posteriorly; the posterior third of dorsal and anal fins darker along margins to entirely black posteriorly; caudal fin black; pectoral fins red to pink laterally, distally with red to dark red margins and dark membranes, dark red or black medially. Peritoneum overall dark, darkly speckled with little space between, or uncommonly pale with more widely scattered speckles; orobranchial cavity black; stomach pale, intestines pale, pyloric caeca pale; urogenital papilla dark or mottled, with light tip, ovipositor white. After preservation, body pale with fins darker posteriorly.

Life history.—Females with a large ovipositor and yolked eggs ranged from 305 to 420 mm (the largest female, UW 154579), and males from 230 to 420 mm (the largest male, RBCM 16115) appeared ripe with large testes. At least two sizes of eggs were present in ripe females: yolked eggs were 3.2–3.8 mm in diameter and white eggs had diameters of 0.5–1.5 mm. All eggs collected in the wild and verified as those of *C. ambustus* have been identified from clusters deposited

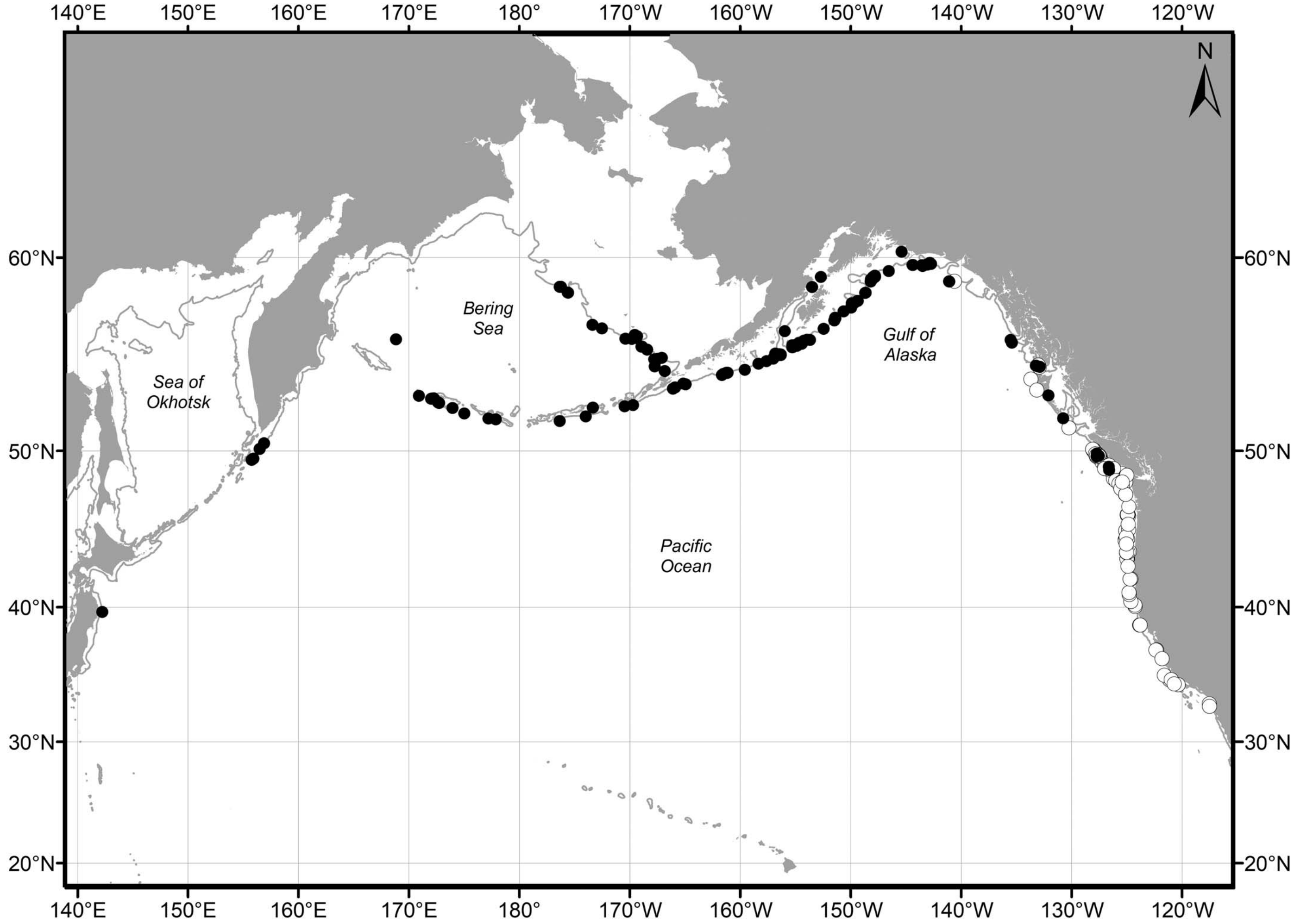

Fig. 3. Distribution of *Careproctus ambustus*, new species (black), and *C. melanurus* (white) in the Bering Sea and North Pacific Ocean based on material examined. Each symbol may represent more than one capture. Bottom contour illustrated is 200 m.

within the lithodid crab *Lithodes aequispinus* (Gardner et al., 2016, as *C. melanurus*). Mean egg sizes in clusters (fixed and preserved in 95% ethanol) collected from crabs in the Aleutian Islands and southeastern Bering Sea ranged from 3.82 to 4.87 mm, with an overall average mean of 4.36 mm (Gardner et al., 2016). Specimens of *C. ambustus* taken in the western Pacific Ocean off Kamchatka and the Kuril Islands have been aged to 10–13 years (Tokranov and Orlov, 2001; Orlov and Tokranov, 2011).

Distribution.—*Careproctus ambustus* is known in the North Pacific Ocean from British Columbia, Alaska, Russia, and Japan (Fig. 3) at depths of 58 to 1,172 m, based on material examined and confirmed field identifications (Tokranov, 2000; Orr et al., 2014a, 2014b; G. R. Hoff, pers. comm., 2016). In the eastern North Pacific, it ranges from British Columbia off central Vancouver Island, throughout the Gulf of Alaska and Aleutian Islands, and into the eastern Bering Sea to at least 60.3°N (Hoff, 2016) and off Cape Navarin in the western Bering Sea (Parin et al., 2014). In the western North Pacific, it ranges from Kamchatka and the Kuril Islands, Russia (Orlov, 1998, 1999, 2001; Sheiko and Fedorov, 2000; Orlov and Tokranov, 2011), to the northwestern coast of Honshu, Japan (Kido and Shinohara, 1997).

Etymology.—The specific epithet of *Careproctus ambustus* is taken from the Latin *ambusti,* meaning "scorched," referring to the black tail that contrasts with the pink to red anterior part of the body.

DISCUSSION

Careproctus melanurus has been considered one of the most common large snailfishes throughout the eastern North Pacific, ranging from Baja California to Japan. With detailed molecular and morphological analysis of specimens from throughout the range of the species (*sensu lato*), we determined that northern and southern populations, overlapping geographically from extreme southeastern Alaska to British Columbia, differ significantly from one another and therefore recognize northern and western populations as the new species *C. ambustus*.

While molecular data and multivariate morphological analyses distinguish the two species, useful diagnostic morphological differences between *C. ambustus* and *C. melanurus* are comparatively slight. As is evident in these two species, counts of median fin rays and vertebrae commonly increase with increasing latitude, a pattern known as Jordan's rule (Jordan, 1892) and generally attributed to the effect of colder temperatures during

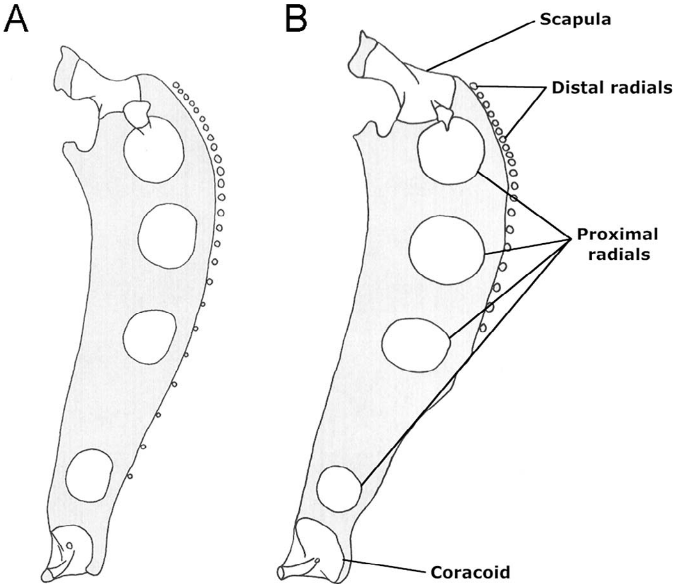

Fig. 4. (A) Right medial view of pectoral girdle of *Careproctus ambustus*, new species, UW 119240, 150 mm; (B) Right medial view of pectoral girdle of *Careproctus melanurus*, UW 47479, 125 mm. Shaded areas represent cartilage.

embryonic development (McDowall, 2008). In contrast to other liparids that release pelagic eggs, many species of *Careproctus* and both *C. ambustus* and *C. melanurus* deposit eggs in lithodid crabs, where they develop until the hatching of demersal, well-developed larvae (Gardner et al., 2016). The limited dispersal of the eggs in the crabs generally restricts their development to the temperature regime in which they were deposited, thus enhancing latitudinal differences in development. Although when the species are treated together, median fin rays and vertebrae exhibit a strong latitudinal cline, the COI sequence divergence between the two species provides clear evidence that they are distinct. A combination of meristic characters can diagnose the two without the need for sequence data, but median fin rays and, obviously, vertebrae are difficult or impossible to count without the aid of radiographs. Field identifications will be difficult, especially for individuals taken in the area of geographic overlap from southeastern Alaska to Vancouver Island.

The two species do not appear to differ in body coloration, both having an anteriorly pink to red head and body, dorsal and anal fins darkening to black posteriorly, with the caudal fin black. The pectoral fin is dark medially. However, a possible chromatic difference may lie in the lateral color of the pectoral fins. While the fin is dark distally in both species, in *C. ambustus* the central part of the pectoral fin is pink to red laterally (Fig. 2A), but white with pink margins in *C. melanurus* (Fig. 2B). Additional observations of color patterns in freshly caught specimens will be necessary to confirm this tentative conclusion.

We examined 16 cleared-and-stained pectoral girdles of *C. ambustus*. Perhaps with the exception of a slight difference in the size of the first interradial fenestra between the scapula and proximal radial 1, differences between all were trivial. For other species, authors have reported significant differences in multiple specimens, specifically in numbers of radials and fenestrae (Chernova, 2006; Knudsen and Møller, 2008), with the suggestion that pectoral girdle morphology may be more plastic than previously supposed. We found no evidence to support this in our material.

In our material, the pectoral girdles of *C. ambustus* differ slightly from *C. melanurus* only in the numbers and ventral extent of the distal radials. In *C. ambustus*, 25 distal radials extend to the fourth proximal radial. In *C. melanurus*, 20 distal radials extend to the third proximal radial. Additional material suitable for examining the distal radials will be required to further assess this putative difference between the species.

The subgenus *Allochir* was erected for *C. melanurus* (Jordan and Evermann, 1896). Based on molecular data, Orr et al. (2019) recovered a highly supported clade containing *C. melanurus, C. ambustus* (=*C.* sp. cf. *melanurus*), *C. colletti, C. cypselurus, C. furcellus*, an undescribed species from British Columbia (Orr, unpubl.), and an unidentified species of *Careproctus (*Rock et al., 2008) from the Southern Hemisphere, allocating all to the subgenus *Allochir* (Fig. 5). The new sequence data included here for *C. ambustus* and *C. melanurus* did not vary from the data used by Orr et al. (2019) and thus confirmed these results. *Careproctus ambustus* is similar to other species of *Allochir* but is easily distinguished by morphological characters, as well as differences in COI sequence data. From all, it can be distinguished by the combination of its pink to red body coloration, oval pelvic disc, and shallowly notched pectoral fin with moderately elongate and emarginate lower rays. In the eastern Bering Sea, *C. ambustus, C. colletti, C. cypselurus,* and *C. furcellus* all broadly overlap both geographically and bathymetrically and are commonly caught in the same hauls over the upper continental slope. Each of these other species has a triangular pelvic disc and most differ in body coloration as well as in the configuration of the lower pectoral-fin rays and lobe. In *C. furcellus*, the body is pink to purple, lower pectoral-fin rays are short and finger-like, and a pectoral-fin notch is absent; in *C. cypselurus,* the body is light to dark grayish pink, rays are moderately elongate, and the fin is shallowly notched; and in *C. colletti*, the body is light to dark purple, several rays are highly elongate and filamentous, and the fin is deeply notched. In addition, meristic differences (Kido, 1988) are useful to distinguish *C. ambustus* from *C. furcellus* and *C. colletti* (vertebrae 67–71, dorsal-fin rays 61–65, anal-fin rays 54–59 in *C. furcellus* and vertebrae 59–65, dorsal-fin rays 51–58, anal-fin rays 47–52 in *C. colletti* vs. vertebrae 61–67, dorsal-fin rays 57–63, anal-fin rays 51–57 in *C. ambustus*). *Careproctus (Caremitra) simus*, another pink blacktailed species in the North Pacific, has often been misidentified in field surveys but is readily distinguished by its pronounced snout, slender body, and counts of dorsal- and anal-fin rays (dorsal-fin rays 54–60, anal-fin rays 47–53 in *C. simus* [Kido, 1985; Mecklenburg et al., 2002] vs. dorsal-fin rays 58–63, anal-fin rays 51–57 in *C. ambustus*).

Among currently recognized species of *Careproctus*, sequence divergences between all species range from 0.2% to 9.1% (Orr et al., 2019), and among species of the subgenus *Allochir*, sequence divergences between members range from 1.4% to 7.7%. *Careproctus ambustus* differs from *C. melanurus* by 1.4% and from all other members of *Allochir* by 3.3–6.9%. A similar pattern of meristic differences correlated with COI sequence differences is evident in other species of eastern North Pacific liparids (Orr et al., 2019). Further work is likely to reveal additional currently unrecognized diversity, as specimens from Alaska and farther west may represent

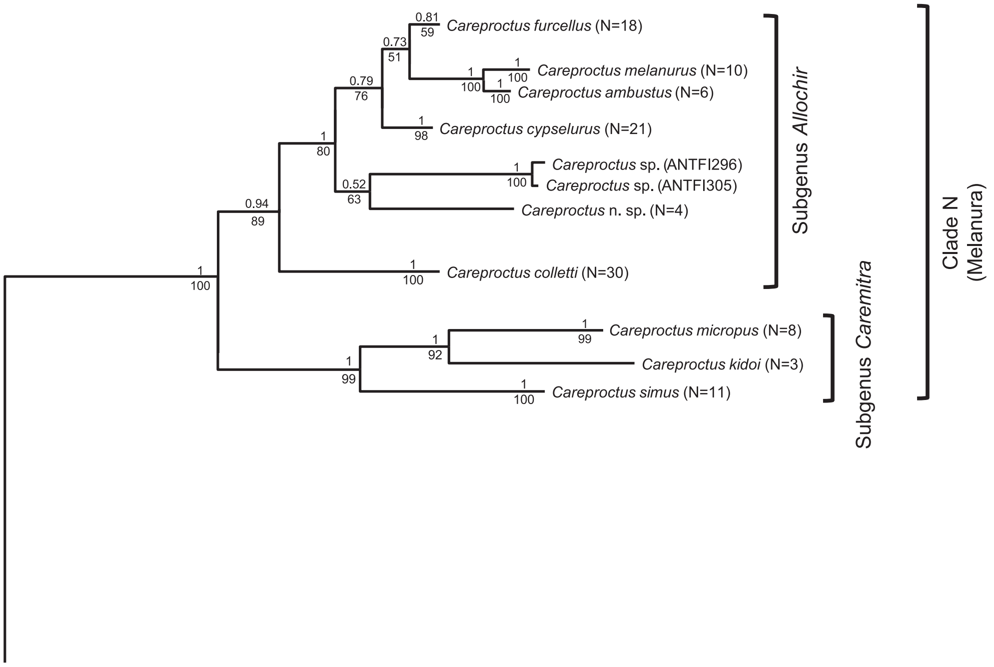

Fig. 5. Phylogeny of the *Careproctus* subgenus *Allochir* after Orr et al. (2019). Majority rule (50%) consensus tree from the Bayesian inference of a 490 bp alignment of 270 cytochrome *c* oxidase subunit one gene (COI) sequences. Nodal values represent Bayesian posterior probabilities and bootstrap values from the maximum likelihood analysis (above and below, respectively). Species names are followed by a catalog number or BOLD "Sequence ID" number when represented by a sequence from a single specimen in our dataset. N indicates number of sequences when multiple sequences support a branch tip. Only unique sequences were subjected to analyses. See Orr et al. (2019) for additional details.

different species from those found farther south along the North American west coast.

The geographic ranges of *C. ambustus* and *C. melanurus* overlap narrowly in extreme southeastern Alaska at the border with British Columbia and farther south along the west coast of Vancouver Island. This region has been recognized as an intermediate or transitional zoogeographic province within the Boreal Eastern Pacific zoogeographic region (Allen and Smith, 1988; Horn et al., 2006; Pietsch and Orr, 2019) between the Oregonian Province to the south and the Aleutian Province to the north. As an indication of this intermediacy, it has been included in the northern part of the Oregonian Province by some (Briggs, 1974, 1995; Horn et al., 2006; Briggs and Bowen, 2012) and in the southern part of the Aleutian Province by others (Peden and Wilson, 1976). Other presumed cognate pairs of species exhibit a similar pattern, overlapping latitudinally in British Columbia. For example, *Lycodes beringi* and *L. diapterus* are northern and southern cognate species in the eastern North Pacific that overlap latitudinally only in British Columbia and northern Washington (Stevenson and Sheiko, 2009).

Depth ranges of *C. ambustus* and *C. melanurus* overlap broadly. *Careproctus ambustus* ranges in depth in our data from 58 to 1,172 m, while in our material *C. melanurus* ranges from 50 m to 1,481 m. Others have reported *C. melanurus* as ranging possibly as deep as 2,453 m, based on individuals tentatively identified as *C. melanurus* (Stein et al., 2006). Deep survey trawling efforts within the last 100 years in Alaska have generally been limited to a few hauls at 1,600 m in the Bering Sea, 1,000 m in the Gulf of Alaska, and 500 m in the Aleutian Islands, unlike off the West Coast where deeper surveys and explorations have been more routinely conducted.

DATA ACCESSIBILITY

Supplemental material, including the full listing of additional and comparative material examined and GenBank and BOLD accession numbers for COI region sequence data, is available at https://www.copeiajournal.org/CI2020008.

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