Zootaxa 4294 (4): 419–435
http://www.mapress.com/j/zt/
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Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4294.4.2
http://zoobank.org/urn:lsid:zoobank.org:pub:151ACA96-34F5-4248-B795-1D9DB5F079FA

Taxonomic clarification of the *Eumicrotremus asperrimus* species complex (Teleostei: Cyclopteridae) in the eastern North Pacific

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Abstract

The *Eumicrotremus asperrimus* species complex includes three nominal species from the eastern North Pacific and Bering Sea: *Eumicrotremus gyrinops* (Garman 1892); *Eumicrotremus muticus* (Gilbert 1896); and *Eumicrotremus phrynoides* Gilbert & Burke 1912. These species have been distinguished from each other primarily on the basis of the strength and coverage of bony tubercles on the head and body. However, several recent genetic studies have cast doubt on the utility of bony tubercles for diagnosing species-level differences among cyclopterids, and a recent genetic study of the *E. asperrimus* species complex indicated that population structure is not correlated with tubercle development. Here we present additional evidence from the mitochondrial COI gene indicating that there is little genetic structure within a sample of specimens from the eastern North Pacific and Bering Sea with a wide range of tubercle development. We also examine several lines of morphological evidence, including meristic and morphometric data and osteology, and conclude that the three nominal species described from the eastern North Pacific represent a single polymorphic species. We present a re-description of *Eumicrotremus gyrinops* (Garman), the oldest of the three nominal species, recognizing the other two nominal species of the *Eumicrotremus asperrimus* species complex described from the eastern North Pacific as junior synonyms. Individuals of this highly polymorphic species may be covered in large bony tubercles, or sparsely covered in small tubercles, or may have no evidence of tubercles at all. There is clear evidence of sexual dimorphism, as males tend to have fewer and smaller tubercles than females, and all large specimens (> 58 mm SL) are females. Both males and smaller females may lack any evidence of tubercles.

Key words: *Eumicrotremus gyrinops*, Alaskan lumpsucker, Cyclopteridae, DNA barcoding, *Lethotremus*, *Cyclopteroides*

Introduction

The *Eumicrotremus asperrimus* species complex, as defined by Kai *et al.* (2015), includes three nominal species from the eastern North Pacific and Bering Sea. The oldest of these is *Cyclopteroides gyrinops* Garman 1892, originally described as a new genus and species on the basis of a single specimen from St. Paul Island in the Bering Sea. Garman (1892:20) distinguished the genus *Cyclopteroides* Garman 1892 from *Eumicrotremus* Gill 1862 and *Cyclopterus* Linnaeus 1758 by the presence of barbels on the chin, the "central, subabdominal" disc (vs. "anterior, subcephalic"), and the minute lateral tubercles. *Lethotremus muticus* Gilbert 1896, also originally described as a new genus and species, was based on three specimens collected from near Unimak Pass in the eastern Aleutian Islands. This new genus was distinguished from *Eumicrotremus* by the "total absence of the bony plates and in the absence of pores on sides of head or body" (Gilbert 1896:449). Finally, *Eumicrotremus phrynoides* Gilbert & Burke 1912, the only one of the three not to warrant a new genus, was described for a single specimen collected on Petrel Bank in the south-central Bering Sea. The tubercles of this species were described as "small and inconspicuous, largely concealed beneath the thick integument, only the rosettes of short spines a little protruding" (Gilbert & Burke 1912:70). Along with their description of *E. phrynoides*, Gilbert & Burke (1912:70) reported two specimens

Accepted by E. Hilton: 24 Apr. 2017; published: 20 Jul. 2017

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of *L. muticus* taken from Petrel Bank, noting that "the only character remaining to distinguish *Lethotremus* Gilbert 1896 [from *Eumicrotremus*] is the total absence of spinous tubercles."

The taxonomy of cyclopterids, particularly *Eumicrotremus* and related genera, has historically been based primarily on the presence, pattern of placement, and morphology of spiny tubercles. However, sexual dimorphism and ontogenetic changes in the number and size of spiny tubercles have been noted by several authors (e.g., Arita 1969; Ueno 1970; Meklenburg *et al.* 2002; Mecklenburg & Sheiko 2003; Byrkjedal *et al.* 2007), and recent genetic studies have shown inconsistencies between tubercle-based species-level taxonomy and patterns of genetic relatedness (Byrkjedal *et al.* 2007; Kai *et al.* 2015; Hatano *et al.* 2015). Thus, it appears that intraspecific variability in tubercle patterns and morphology may be confounding the taxonomy of this group, resulting in taxonomic over-splitting similar to that which has been found in other fish groups (e.g., Steinke *et al.* 2009; Mecklenburg & Anderson 2015). In the most recent cladistic analysis of this family, Oku *et al.* (2017) recognized many cyclopterid genera, including *Lethotremus*, as junior synonyms of *Eumicrotremus*.

Kai *et al.* (2015) investigated genetic variation in members of the *E. asperrimus* species complex from both sides of the Pacific, as well as the Sea of Japan, Sea of Okhotsk, and Bering Sea. Their sequence data resolved two distinct clades within the complex—one represented by specimens from the seas of Japan and Okhotsk (WNP, western North Pacific), the other represented by all material examined from the Bering Sea, Aleutian Islands, and Gulf of Alaska (ENP, eastern North Pacific)—separated from each other by 2.5% sequence divergence. Within each of these clades a broad spectrum of tubercle morphology was observed, ranging from specimens with tubercles completely absent to specimens completely covered with large conical tubercles. Within-group genetic structure did not correspond with tubercle morphology for either the ENP or WNP clades (Kai *et al.* 2015). In fact, there was very little genetic variation within groups, particularly for the ENP. Mecklenburg and Steinke (2015) found similar results in an analysis of COI sequences from material attributed to *Eumicrotremus muticus*, *Eumicrotremus phrynoides*, and *E. asperrimus* from the ENP and suggested (following Mecklenburg & Sheiko 2003) that the group should be synonymized with *E. gyrinops*.

However, most recently Oku *et al.* (2017) examined the phylogenetic relationships of Cyclopteridae based on osteological characters, and included two members of the *E. asperrimus* complex from the ENP (*Eumicrotremus phrynoides* and *E. muticus*) in their character matrix. They found four osteological characters separating these two taxa: number of foramina for nerves on the prootic (TS 2); laminar structure of the urohyal (TS 15); first proximal pterygiophore of the dorsal fin (TS 22); and second preural centrum and haemal spine (TS 27). Oku *et al.* (2017) also included three external characters in their matrix (presence of interorbital pore, anterior dorsal branch of lateral line, and pores above lateral line), but could not evaluate the condition of these characters in *E. muticus* because they had only a single cleared and stained specimen. The objective of this study was to assess the validity of the nominal species of the *E. asperrimus* complex in the ENP, using genetic data and morphology, including examination of type specimens.

Materials and methods

Methods of counting and measuring, as well as tubercle series terminology, follow Ueno (1970). Meristic data were obtained from digital radiographs. Body measurements were made with digital calipers and rounded to the nearest 0.1 mm. Counts and proportions in the text are presented as a range followed by the mean in parentheses. In order to evaluate the osteological characters used in Oku *et al.* (2017), three specimens with tubercles completely absent (UW 49474, 37.4–38.5 mm SL), corresponding with the morphology of *E. muticus*, and three specimens with small tubercles scattered on the head and body (UW 47923, 35.5–37.7 mm SL), corresponding with *E. phrynoides*, were cleared and stained, using the method of Potthoff (1984), and dissected. Osteological observations are restricted to the relevant characters listed in Oku *et al.* (2017). Institutional abbreviations are as listed by Sabaj Pérez (2016).

Tissue samples were obtained from 71 specimens of the *E. asperrimus* species complex, and one specimen of *Eumicrotremus orbis* (Günther 1861) was used as an outgroup (UW 119821). DNA extraction, amplification, and sequencing were described by Kai *et al.* (2015). Genetic distance calculations and neighbor-joining analysis were conducted using MEGA 6.06 (Tamura *et al.* 2013) and the Kimura 2-parameter model. Bootstrap support was calculated using the Willi Hennig Society edition of TNT (Goloboff *et al.* 2003, 2008), with 1000 standard bootstrap replicates of the matrix and the Traditional Search option. For the Bayesian analysis, a test of 24 different

nucleotide substitution models was run in MEGA6.06 (Tamura *et al.* 2013). The model with the greatest log likelihood score was a generalized time reversible (GTR) model with gamma-distributed rate variation across sites and invariant sites (GTR + I + Γ). This model was chosen for the Bayesian analysis, conducted with MrBayes v3.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Posterior probability distributions were generated by running four Markov chains, under the default of three heated chains and one cold. After two million generations, minimum ESS values were greater than 200 for all parameters, and PSRF scores were either 1.000 or 1.001 for all parameters. Sampling frequency was 100 generations. The initial 5,000 samples were discarded as burn-in, and the remaining 15,000 samples were used to estimate tree topology and posterior probabilities.

Distributions of log-transformed meristic characters and arcsine-transformed morphometric ratios were tested to meet assumptions of normality (standardized skew and kurtosis values between -2 and +2) and equality of variances. Characters that did not violate these assumptions were subjected to ANOVA (meristics) or ANCOVA (morphometric ratios, using SL as the covariate) to test for significant differences between sexes and morphotypes (Table 1). All univariate analyses were performed using STATGRAPHICS Centurion XV, Version 15.2.00 (StatPoint Technologies, Inc., Warrenton, VA). Principal component analysis (PCA) was performed on a data set that included only specimens for which all morphometric and meristic data were collected. Raw morphometric data were log-transformed, the covariance matrix was subjected to PCA, and the correlation matrix of raw meristics was subjected to PCA. Differences between the two morphotypes were illustrated by plotting scores of meristic PC1 vs. meristic PC2, morphometric PC2 vs. morphometric PC3, and meristic PC1 vs. morphometric PC2. Factor loadings for principal components are listed in Tables 2 and 3. The PCA was conducted using TIBCO Spotfire S+ (TIBCO Software, Inc., Boston, MA).

Results

DNA Sequencing. Sequence data from the mitochondrial COI (569 bp) and Cyt-*b* (1085 bp) genes were obtained from 47 specimens of the *E. asperrimus* species complex from the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska, as well as 24 specimens from the WNP. The ENP specimens exhibited 38 distinct haplotypes with a maximum sequence divergence of 0.5% (mean divergence 0.2%). The frequency distribution of pairwise differences among the sequences showed a single clear peak (Fig. 1), with a modal pairwise difference of 4 bp (0.2% sequence divergence).

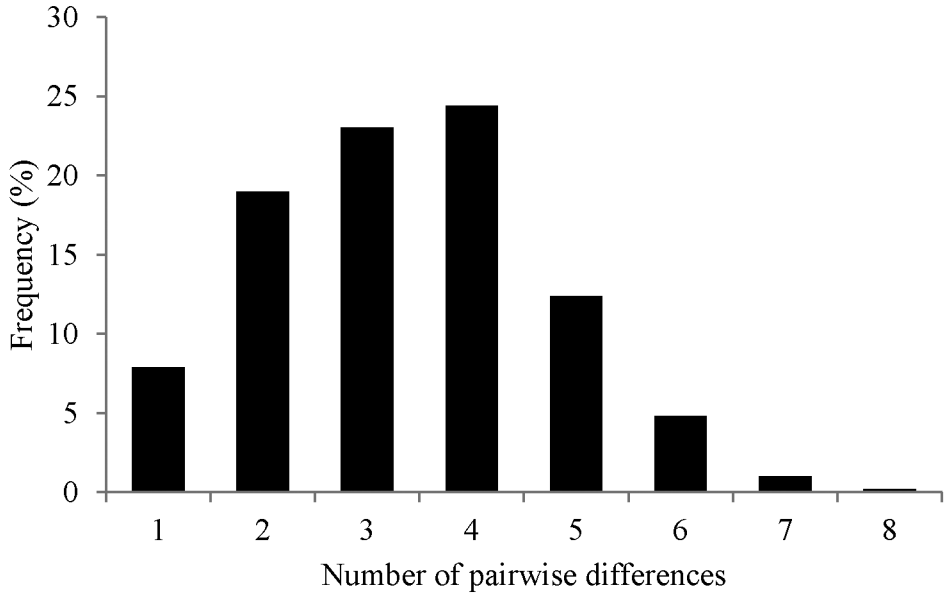

FIGURE 1. Frequency distribution of pairwise sequence differences observed among the 47 specimens of the eastern North Pacific *E. asperrimus* species complex sequenced for this study (concatenated CO1 + Cyt-*b* genes: 1654 bp total).

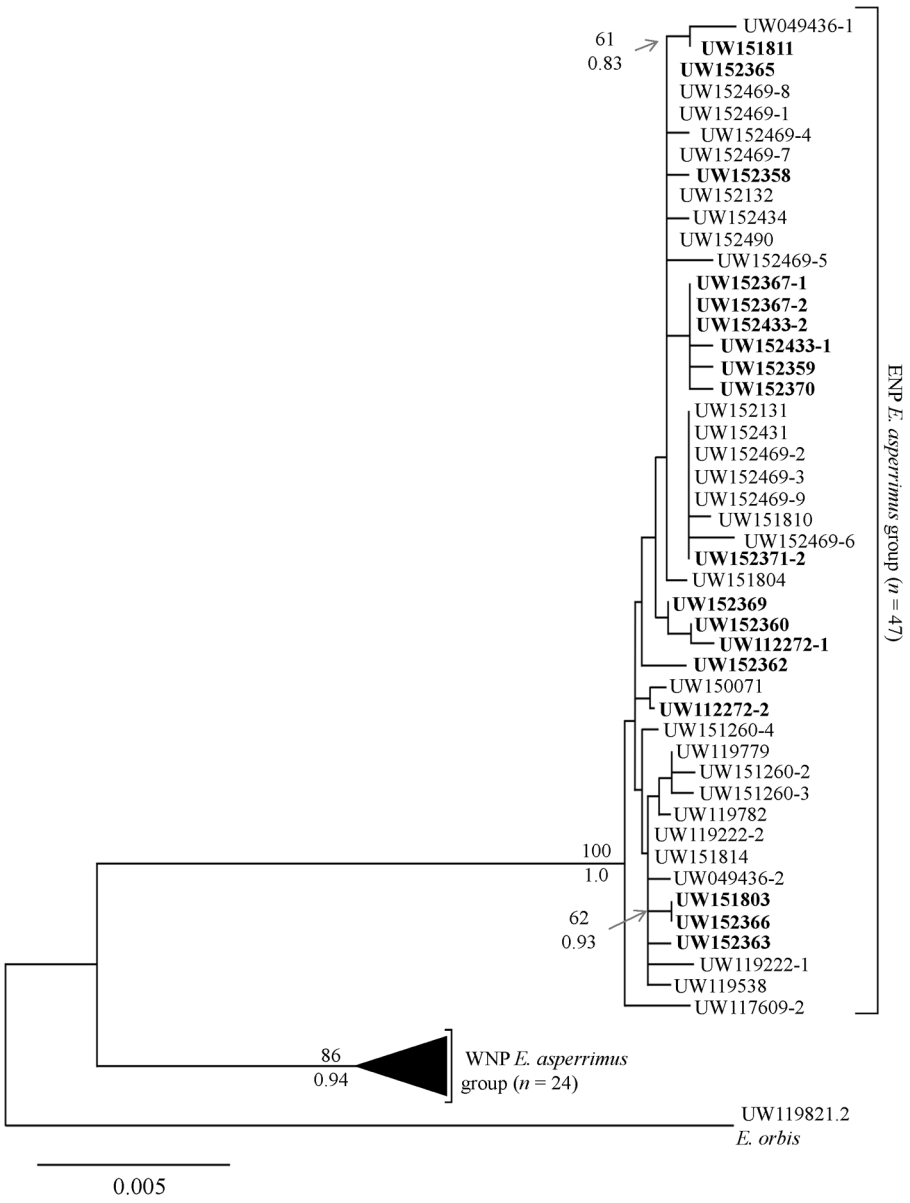

FIGURE 2. Neighbor-joining tree relating specimens of the *E. asperrimus* species complex sequenced for this study, including specimens from the Sea of Japan and Sea of Okhotsk (WNP), and *Eumicrotremus orbis* as an outgroup. Catalog numbers in **BOLD** represent specimens without any evidence of tubercles (*E. muticus* morphotype). Numbers at nodes represent bootstrap support, as a percentage of 1,000 replicates; scale bar represents Kimura 2-parameter distance.

A neighbor-joining tree constructed from the concatenated CO1 and Cyt-*b* sequences (Fig. 2) showed very little structure within the ENP group, with only two nodes supported by >50% bootstrap support. The structure that was present within the ENP group was not correlated with tubercle development. Specimens with no tubercles (e.g., UW151811 and UW151803) were dispersed throughout the tree, among specimens with well-developed tubercles. As reported by Kai *et al.* (2015), ENP and WNP specimens were recovered in two distinctly separate clades with strong bootstrap support and high posterior probabilities.

Tubercle morphology. The specimens examined (n = 235) exhibit a broad range of tubercle morphology and distribution. In many of the specimens (n = 82), tubercles are completely absent. The head and body are completely smooth, without any trace of bony tubercles, spines, or warts. This morphology corresponds to the original description of *E. muticus* (Fig. 3A), and this morphology is hereafter referred to as "naked." The size range of these specimens is 27–52 mm, and the sex ratio is approximately equal (42 M, 40 F). In the remaining specimens (n = 153), tubercles are present in some form, ranging from just a few rudimentary rosettes of spines on the head to several low rounded tubercles distributed on the head and body, to strongly developed conical tubercles covering

the entire head and body. This morphology, in part, corresponds to the original descriptions of *Cyclopteroides gyrinops* and *Eumicrotremus phrynoides* (Figs. 3B, C), and is hereafter referred to as "armored." The size range of these specimens is 27–92 mm, and the sex ratio is heavily female-biased (50 M, 95 F, 8 unsexed). All specimens larger than 58 mm SL (n = 13) are females.

TABLE 1. Meristic and proportional morphometric characters for the armored (*E. gyrinops*) morphotype and the naked ("*E. muticus*") morphotype of *Eumicrotremus gyrinops*, with significant results (p<0.01) from ANCOVA comparisons among sexes and morphotypes. Eg = *E. gyrinops* morphotype; Em = *E. muticus* morphotype.

	E. gyrinops (armored)		"*E. muticus*" (naked)		
	Range (mean)	n	Range (mean)	n	Significance
Males SL	28.6–58.0 (39.2)	50	27.3–43.8 (36.4)	42	
Females SL	26.5–91.9 (50.2)	95	29.0–52.3 (38.0)	40	
Meristics:					
First dorsal-fin spines	6–8 (6.9)	71	6–8 (7.2)	39	
Second dorsal-fin rays	10–12 (10.6)	77	10–12 (10.6)	38	
Anal-fin rays	9–12 (10.1)	77	9–11 (10.1)	39	
Pectoral-fin rays	24–28 (26.1)	73	25–27 (26.2)	38	
Vertebrae	26–30 (28.1)	60	26–29 (27.8)	39	
Percentage of standard length:					
Head length	28.9–43.2 (36.1)	61	32.2–45.1 (38.6)	32	
Body depth	30.0–57.7 (47.7)	61	28.7–51.3 (41.6)	32	Eg>Em
First dorsal-fin base	16.1–28.3 (23.0)	61	17.3–29.9 (24.4)	32	
Second dorsal-fin base	16.2–26.2 (21.6)	61	15.4–25.7 (21.3)	32	
Anal-fin base	13.7–25.4 (18.0)	61	13.9–22.2 (17.9)	32	
Pectoral-fin base	24.8–35.8 (29.5)	61	25.3–33.1 (29.0)	32	
Interdorsal distance	2.1–19.7 (8.6)	61	2.7–10.8 (6.4)	32	
Predorsal length	29.1–47.2 (38.8)	61	33.0–45.1 (38.9)	32	
Snout to vent	57.3–76.6 (65.0)	61	58.3–73.9 (63.7)	32	
Vent to anal-fin origin	10.7–23.6 (16.9)	61	9.7–20.7 (15.2)	32	Em♀>Em♂
Caudal peduncle length	8.5–14.7 (11.6)	61	8.8–14.3 (11.7)	32	
Caudal peduncle depth	8.0–13.0 (9.7)	61	8.9–11.7 (10.1)	32	
Pectoral-fin length	15.6–26.1 (21.1)	61	17.5–26.8 (21.6)	32	
Snout to disc	17.5–35.1 (24.5)	61	19.3–29.8 (24.2)	32	
Disc length (outer)	20.2–30.3 (24.0)	61	20.4–28.5 (23.2)	32	Em♂>Em♀
Disc length (inner)	10.3–16.2 (12.1)	61	9.9–13.9 (12.0)	32	
Disc width (outer)	18.5–29.3 (24.5)	61	18.5–26.7 (23.2)	32	
Disc width (inner)	9.7–17.0 (13.5)	61	11.5–15.9 (13.0)	32	
Disc to vent (outer)	8.5–29.7 (21.2)	61	12.1–31.1 (20.8)	32	
Disc to vent (inner)	11.6–33.2 (25.9)	61	17.7–35.6 (25.1)	32	
Caudal-fin length	22.5–31.9 (26.6)	61	24.1–31.2 (27.0)	32	
Percentage of head length					
Orbit length	32.0–50.8 (40.8)	61	31.5–49.2 (39.5)	32	
Snout length	7.4–25.0 (15.6)	61	12.2–24.3 (16.3)	32	
Postorbital head length	32.8–54.1 (41.7)	61	32.7–53.9 (40.0)	32	
Interorbital width	42.3–78.5 (57.3)	61	40.9–66.1 (51.9)	32	
Mouth width	54.0–93.8 (74.9)	61	50.4–93.9 (70.1)	32	
Anterior internasal width	22.9–36.1 (29.4)	61	20.4–35.7 (27.8)	32	

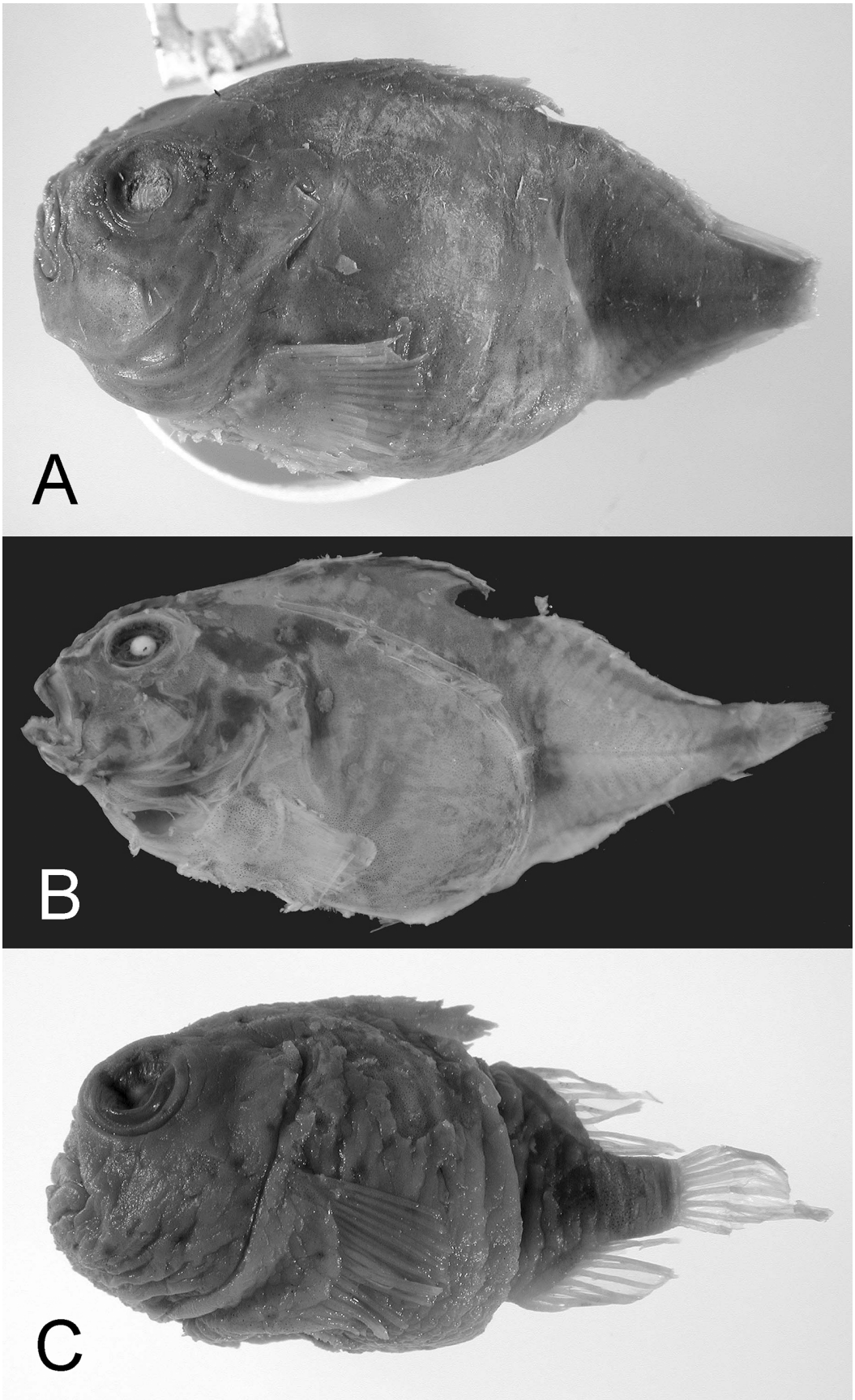

FIGURE 3. Type specimens for nominal species of the eastern North Pacific *Eumicrotremus asperrimus* species complex: (A) *Lethotremus muticus*, lectotype, USNM 53806; (B) *Cyclopteroides gyrinops*, holotype, MCZ 16026; and (C) *Eumicrotremus phrynoides*, holotype, USNM 74378.

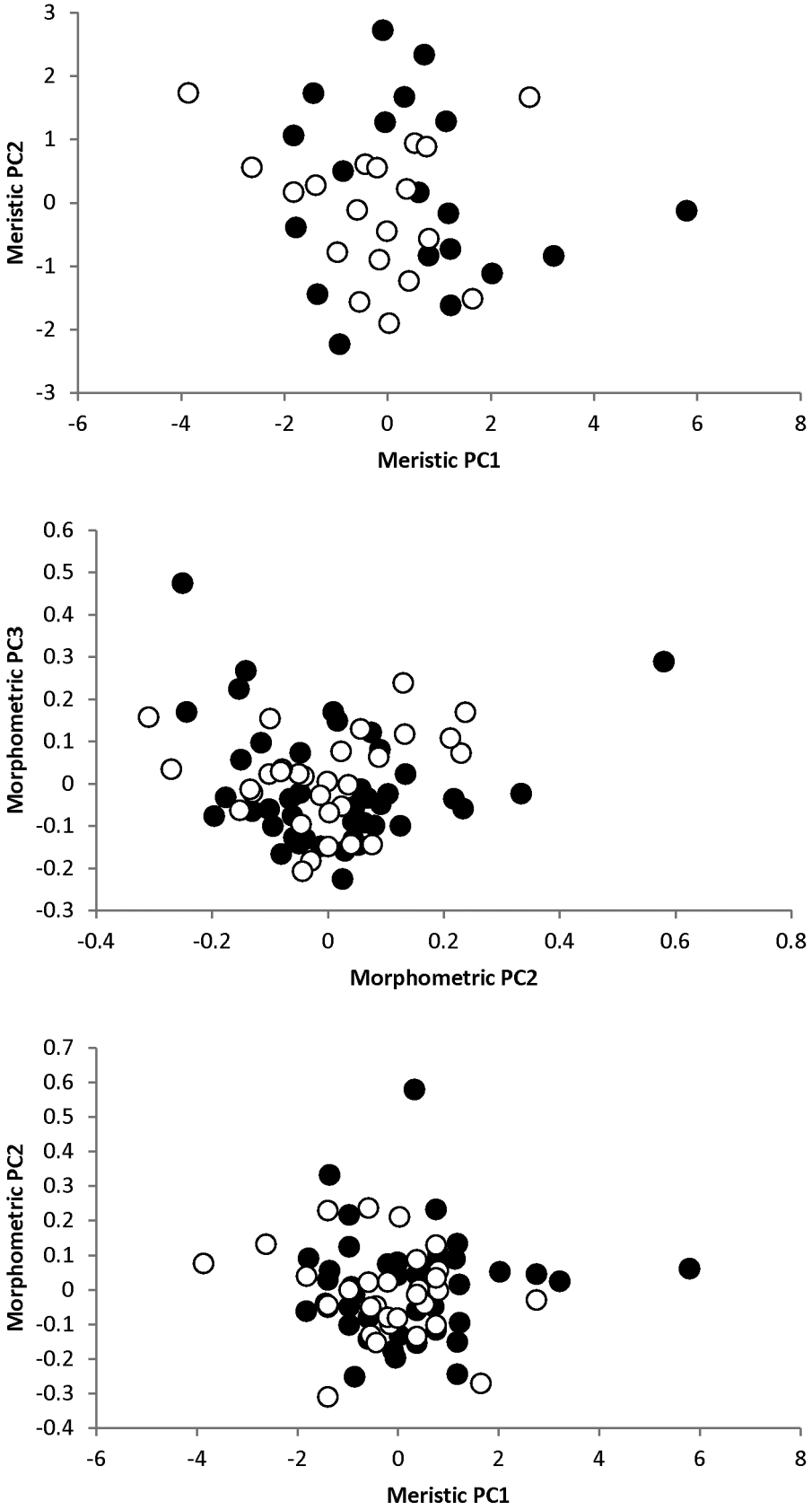

FIGURE 4. Plot of morphometric and meristic principal component scores for armored specimens (black circles) and naked specimens (white circles) of the *E. asperrimus* species complex.

TABLE 2. Factor loadings for principal component analysis (PCA) of meristic characters for the armored (*E. gyrinops*) morphotype (n = 42) and the naked (*E. muticus*) morphotype (n = 30) of *Eumicrotremus gyrinops*.

Character	PC1	PC2
First dorsal-fin spines	0.0238	-0.7820
Second dorsal-fin rays	0.5219	0.1806
Anal-fin rays	0.5604	-0.1283
Pectoral-fin rays	0.2971	0.5138
Vertebrae	0.5697	-0.2744

TABLE 3. Factor loadings for principal component analysis (PCA) of morphometric characters for the armored (*E. gyrinops*) morphotype (n = 42) and the naked (*E. muticus*) morphotype (n = 30) of *Eumicrotremus gyrinops*.

Character	PC1	PC2	PC3
Head length	0.1494	-0.0016	0.1178
Body depth	0.2352	0.0246	0.1039
First dorsal-fin base	0.1635	0.0368	0.0847
Second dorsal-fin base	0.1888	0.0041	0.1287
Anal-fin base	0.1833	0.0393	0.1056
Pectoral-fin base	0.1784	0.0258	0.1010
Interdorsal distance	0.3687	0.5853	-0.5900
Predorsal length	0.1820	-0.0492	0.0498
Snout to vent	0.1991	-0.1391	0.1024
Vent to anal-fin origin	0.2694	-0.1099	-0.1278
Caudal peduncle length	0.1611	0.0583	0.0306
Caudal peduncle depth	0.1578	-0.0554	0.0737
Pectoral-fin length	0.1502	0.0338	0.1109
Snout to disc	0.1863	-0.1001	0.3435
Disc length (outer)	0.1601	0.1006	0.1244
Disc length (inner)	0.1570	0.0203	0.0812
Disc width (outer)	0.1831	0.0956	0.0784
Disc width (inner)	0.1762	0.0910	0.1219
Disc to vent (outer)	0.2339	-0.6025	-0.2971
Disc to vent (inner)	0.2338	-0.4297	-0.2803
Caudal-fin length	0.1604	-0.0150	0.0976
Orbit length	0.1294	-0.0016	0.0702
Snout length	0.1456	-0.0068	-0.3051
Postorbital head length	0.1436	0.1514	0.1464
Interorbital width	0.1946	0.0057	0.1430
Mouth width	0.1707	0.0427	0.2359
Anterior internasal width	0.1710	-0.0278	0.0274

Meristics and morphometrics. Meristic ranges are nearly identical for naked vs. armored specimens, and are consistent with those previously reported (Ueno 1970; Kai *et al.* 2015; Table 1). Because of the clear possibility of sexual dimorphism, morphometrics were tested for significant differences among sexes and among morphotypes (naked vs. armored). The only significant differences among the sexes are in naked specimens, in which vent to anal-fin distance is significantly greater in females than in males (ANCOVA p = 0.0053) and outer disc length is significantly greater in males than in females (ANCOVA p = 0.0008). Among morphotypes, the only significant difference detected is in body depth, measured from the origin of the second dorsal fin to the vent, which is significantly less in naked specimens (ANCOVA p = 0.0003) than in armored specimens. The principal component analysis (Fig. 4) provides no evidence of separation between the two morphotypes, either using meristic or morphometric characters.

Lateralis system. All specimens examined have an extensive cephalic lateralis system, including supraorbital, interorbital, postorbital, suborbital, and operculomandibular canals. The supraorbital canal includes two pores

anterior to the orbit, one anterior to the nostrils and one medial to the internarial space. All examined specimens of the *E. asperrimus* species complex (both ENP and WNP), including the type material for *E. muticus*, have an interorbital canal with a conspicuous median interorbital pore, and occasionally this pore is paired (e.g., two specimens of UW 49474). The postorbital canal includes two pores, one at the junction with the supraorbital and suborbital canals, and one at its posterior terminus near the dorsal margin of the gill slit. In the majority of specimens examined, the suborbital canal opens through two pores, one posteroventral to the orbit and another ventral to the orbit, but usually posterior to midorbit. In rare specimens this canal is represented by only one or three pores. The operculomandibular canal includes four mandibular pores, situated along the ventral surface of the mandible, and one preopercular pore well separated from the closely spaced mandibular series.

Most pores of the cephalic lateralis system open through short barbel-like tubes. However, the apparent length and prominence of these tubes is variable, and at least partially dependent on the condition of the specimen (tubes generally appear longer in dehydrated specimens). Although the tubes associated with the cephalic lateralis pores are often more easily distinguished when they are not surrounded by large tubercles, there is no apparent correlation of tube size with armor development.

The lateral line on the body extends from the posterior pore of the postorbital canal posteriorly in a slightly ventrally directed arch to the caudal peduncle. Although previous authors (e.g., Ueno 1970; Oku *et al.* 2017) have made reference to lateral line "pores", the specimens examined here exhibit no evidence of open pores or lateralis canals posterior to the postorbital canal. The lateral line on the body instead consists of an inconspicuous series of neuromasts running along the longitudinal axis of the body, with one connecting series of neuromasts running dorsomedially in front of the first dorsal fin, and two or three additional neuromasts dorsal to the lateral line near the interdorsal space. These lateral line neuromasts are extremely inconspicuous and covered with mucus in many of the specimens examined, but there is no evidence of a consistent difference between naked specimens and armored specimens.

Osteological characters. Almost all cyclopterids have a single foramen for nerve passage on the prootic; only *Eumicrotremus awae* and *E. muticus* were coded by Oku *et al.* (2017: TS 2) as having two foramina on the prootic. Specimens examined for this study vary in this character. The three specimens of the naked form (UW 49474) have either one closed and one incompletely closed foramen (Fig. 5A) or two closed foramina, and one specimen has one foramen on the left side prootic and two on the right side. The three specimens of the armored form (UW 47923) are more variable. They have a single open foramen (Fig. 5B), a single closed foramen, or one closed and one open foramen, and in two of the three specimens this character differs on the left and right sides.

Cyclopterids vary in the amount of ossification on the urohyal, with some species having a well-developed dorsoventrally oriented laminar structure spanning the processes of the bone, and others having reduced laminar structure or no laminar structure (Oku *et al.* 2017: TS 15). This laminar structure was considered by Oku *et al.* (2017) to be "restricted to dorsal part of lower ridge" in *E. muticus* and "absent" in *E. phrynoides*. All six specimens prepared for this study exhibited some laminar structure associated with the ventral process of the urohyal (Fig. 5C,D). Although the extent of this laminar structure was somewhat variable, it was present in all specimens.

A large proximal radial associated with the anteriormost spine of the first dorsal fin was reported by Oku *et al.* (2017: TS 22) to be present and inserted between the second and third neural spines in all cyclopterids except *Aptocyclus ventricosus* and *Eumicrotremus phrynoides*. In all of the cleared and stained material examined for this study this proximal radial is invariably present and is inserted between the second and third neural spines in all specimens (Fig. 5E,F).

According to Oku *et al.* (2017: TS 27), the haemal spine is fused to the second preural centrum in *Eumicrotremus awae* and *E. muticus*, while the two elements are autogenous in all other cyclopterids. Specimens examined for this study vary in this character as well. The three specimens of the naked form all present a haemal spine clearly autogenous from the second preural centrum, as does one of the three specimens of the armored form (Fig. 5G,H). The other two specimens of the armored form have the haemal spine fused to the second preural centrum.

Discussion. The molecular and morphological data presented here for the ENP members of the *E. asperrimus* species complex provide no clear and consistent evidence to warrant the recognition of more than one species in this region. Analysis of mitochondrial COI and Cyt-*b* sequence data shows no evidence of two or more well-defined clades within this group of specimens, and coding samples by extent of tubercle development (naked vs. armored) does not result in reciprocally monophyletic clades.

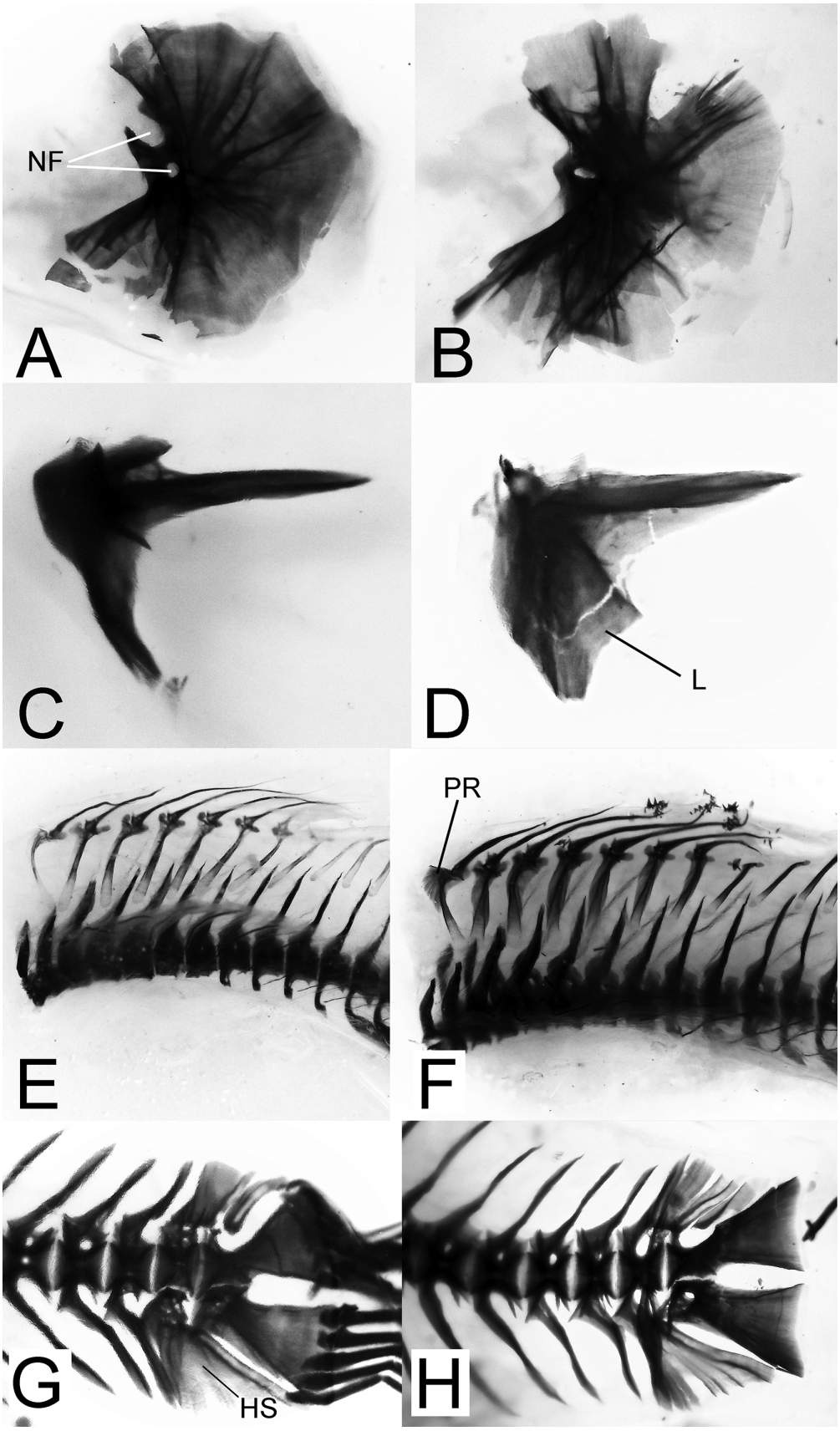

FIGURE 5. Osteological variation in *Eumicrotremus gyrinops*: lateral view of the prootic in (A) UW 49474 and (B) UW 47923; lateral view of the urohyal in (C) UW 49474 and (D) UW 47923; first dorsal fin in (E) UW 49474 and (F) UW 47923; and caudal skeleton in (G) UW 49474 and (H) UW 47923. HS, haemal spine of second preural centrum; L, laminar structure of urohyal; NF, nerve foramen; PR, proximal radial of first dorsal spine.

The DNA sequence data presented here and by Kai *et al.* (2015) indicate that there is a clear genetic gap between the ENP and WNP members of the *E. asperrimus* species complex. Indeed it is unclear at this time how many valid species comprise the WNP *E. asperrimus* species complex, but the findings of Kai *et al.* (2015) and Hatano *et al.* (2015) suggest that a close look at the taxonomy of that group is needed. The variability in tubercle development in WNP specimens is very similar to that reported here for ENP specimens, and a single diagnostic morphological character separating the WNP group from the ENP group has not been identified. The western extent of the distribution of the ENP group is unclear at this time, and a more extensive collection of tissue samples from the western Bering Sea, Commander Islands, and Kuril Islands will probably be required to determine to what extent, if any, the distributions of the two clades overlap.

Variation in tubercle development related to specimen size and sex has confounded the taxonomy of *Eumicrotremus* for over a century. Several previous studies of *Eumicrotremus* (Arita 1969; Byrkjedal *et al.* 2007; Hatano *et al.* 2015; Kai *et al.* 2015) have noted sexual dimorphism in tubercle development, with males generally having fewer and more reduced tubercles than females (but see Voskoboinikova & Chernova 2016). Furthermore, Hatano *et al.* (2015) found that in males of *E. asperrimus* tubercle development is not necessarily ontogenetically unidirectional, and that the relatively well-developed and widespread tubercles of immature males may recede and become completely embedded in the skin as the individual matures. The pattern appears to be similar in the ENP clade of the *E. asperrimus* complex. Smaller specimens of both sexes, up to about 60 mm SL, may show no evidence of tubercles. If tubercles are present at all, these smaller specimens often have only a few small patches of spines concentrated in the occipital and predorsal regions or a sparse scattering of deeply embedded rounded protuberances. Tubercles tend to be larger and more numerous in females than in males, and larger specimens tend to have more extensive tubercle development than smaller specimens. Specimens greater than about 55 mm SL are generally females and all show extensive development of strong conical tubercles, while the largest males (>45 mm SL) often have the tubercles partially or completely covered with skin, or completely absent.

Morphological characters show very little evidence of separation between the two morphotypes examined here. Indeed, skeletal meristic data exhibit little variation within the family Cyclopteridae. Elements of the first dorsal fin, second dorsal fin, anal fin, and pectoral fin, as well as vertebral counts, all vary within narrow ranges for most species, and overlap broadly among species. Gill rakers are reduced and nub-like, and vary little in terms of number or morphology. The only meristic characters that Ueno (1970) used to differentiate taxa were pore counts of the lateral-line and cephalic-lateralis system, which he used to distinguish among some genera, and tubercle counts to distinguish some of the species of *Eumicrotremus*. In the lateralis system we noted some variation in pore counts among the specimens examined, but in many cases the pores and lateral-line neuromasts were difficult to distinguish, and variant pore counts on paired canals were not necessarily equal on the right and left sides of the same specimen. Therefore, we have serious reservations about the taxonomic utility of these counts, at least on the level of closely related species. As noted above, the size, count, and even presence of tubercles is questionable as a taxonomic character.

The recent work on the phylogeny of the Cyclopteridae by Oku *et al.* (2017) has contributed greatly to our understanding of the evolutionary relationships of these fishes. However, at least some of the osteological characters they used exhibit too much intraspecific variability to be useful at the species level. Three of the four characters they coded differently between *E. phrynoides* and *E. muticus* (number of foramina on prootic, laminar structure of the urohyal, and fusion of the second preural centrum and haemal spine) are clearly variable at the intraspecific level, demonstrating variation within the same lot of specimens of similar size, and for the bilateral character even in the same specimen. The fourth character (proximal radial of first dorsal-fin spine) exhibited no variation among the specimens examined for this study. Thus, although *E. phrynoides* and *E. muticus* are clearly separated in the phylogeny presented by Oku *et al.* (2017), we can find no clear osteological evidence that these taxa should be separately recognized, and consider the interpretations of Oku *et al.* (2017) to be the result of limited material.

Finding no consistent morphological characteristics to distinguish the three nominal species of the ENP *E. asperrimus* species complex, and additionally no genetic evidence that two or more distinct clades are present among a large sample of specimens with highly disparate tubercle morphologies, we conclude that this complex represents a single species in the eastern North Pacific and Bering Sea. Thus, *Eumicrotremus phrynoides* Gilbert & Burke 1912 and *Eumicrotremus muticus* (Gilbert 1896) are herein recognized as junior synonyms of *Eumicrotremus gyrinops* (Garman 1892).

This study adds to the growing body of literature indicating that the relative development of tubercles in cyclopterids must be used with caution as a taxonomic character. Tubercle characters should be used to distinguish species and genera only when they are demonstrably consistent across sexes, or are clearly documented for both sexes, and only when ontogenetic tubercle development is considered.

Taxonomic accounts

Eumicrotremus gyrinops (Garman 1892)

Alaskan Lumpsucker
Figs. 3, 5; Table 1

Cyclopteroides gyrinops Garman 1892:37. [Type locality: St. Paul Island, Alaska. Holotype: MCZ 16026.]
Lethotremus muticus Gilbert 1896:449. [Type locality: *Albatross* station 2844, near Unimak Pass, 54 fathoms. Lectotype: USNM 53806; Paralectotypes: CAS-SU 774, CAS-SU 3093, USNM 48614, USNM 59376.]
Eumicrotremus phrynoides Gilbert & Burke 1912:69. [Type locality: *Albatross* station 4779, Petrel Bank, Bering Sea, 54–56 fathoms. Holotype: USNM 74378.]
Cyclopteropsis phrynoides: Soldatov & Lindberg 1930:325. [New combination].
Cyclopterocottus phrynoides: Popov 1930:74. [New combination].
Eumicrotremus gyrinops: Lindberg & Legeza, 1955:423. [New combination].
Eumicrotremus muticus: Oku *et al*., 2017:55. [New combination].

Holotype. MCZ 16026, 38.5 mm, St. Paul Island, Alaska, 56.9°N, 170.4°W.

Diagnosis. A species of *Eumicrotremus* distinguished from all other ENP species of *Eumicrotremus* by the following combination of characters: tubercles, when present, irregularly arranged in interorbital space (vs. four distinct interorbital rows in *E. orbis*); enlarged pair of tubercles absent at origin of second dorsal and anal fin (vs. present in *E. andriashevi*); thick dermal papillae absent (present in *E. barbatus*). *Eumicrotremus gyrinops* is distinguished from members of the WNP *E. asperrimus* species complex (including *E. asperrimus*, *Cyclopteropsis bergi*, and *C. lindbergi*) by higher modal counts of dorsal-fin spines (usually VII vs. usually VI) and lower modal counts of pectoral-fin rays (24–28 vs. 25–30).

Counts and proportions. First dorsal-fin spines VI–VIII; second dorsal-fin rays 10–12 (10.6); anal-fin rays 9–12 (10.1); pectoral-fin rays 24–28 (26.1); vertebrae 10–12 + 15–19 = 26–30 (27.9). Following proportions as percent SL: head length 28.9–45.1 (36.9); body depth 28.7–57.7 (45.6); first dorsal-fin base 16.1–29.9 (23.5); second dorsal-fin base 15.4–26.2 (21.5); anal-fin base 13.7–25.4 (18.0); pectoral-fin base 24.8–35.8 (29.3); interdorsal distance 2.1–7–19.7 (7.9); predorsal length 29.1–47.2 (38.9); snout to vent 57.3–76.6 (64.6); vent to anal-fin origin 9.7–23.6 (16.3); caudal peduncle length 8.5–14.7 (11.6); caudal peduncle depth 8.0–13.0 (9.9); pectoral-fin length 15.6–26.8 (21.3); snout to disc 17.5–35.1 (24.4); disc length (outer) 20.2–30.3 (23.7); disc length (inner) 9.9–16.2 (12.1); disc width (outer) 18.5–29.3 (24.1); disc width (inner) 9.7–17.0 (13.3); disc to vent (outer) 8.5–31.1 (21.1); disc to vent (inner) 11.6–35.6 (25.6); caudal-fin length 22.5–31.9 (26.7). Following proportions as percent HL: orbit length 31.5–50.8 (40.4); snout length 7.4–25 (15.9); postorbital head length 32.7–54.1 (41.2); interorbital width 40.9–78.5 (55.4); mouth width 50.4–93.9 (73.2); anterior internasal width 20.4–36.1 (28.9).

Description. Head and body short, firm, and globose; snout short; cheeks tumid. Interorbital space broad, slightly concave. Eye large, placed high on head, entering dorsal profile. Nostrils with tubes, the anterior short and wide, posterior relatively narrow, approximately same length as anterior. Mouth wide, slightly oblique, posterior margin of maxilla terminating anterior to margin of orbit. Teeth in jaws blunt, conical, arranged in three to five distinct diagonal rows on both premaxilla and dentary, approximately 25–35 teeth in each jaw. Upper and lower pharyngeal teeth present, similar in size and shape to jaw teeth.

Cephalic sensory system consisting of supraorbital, interorbital, postorbital, suborbital, and operculomandibular canals. Supraorbital canal opening through two pores, one anterior to nostrils and one medial to internarial space. Interorbital canal opening through single median pore. Postorbital canal opening anteriorly through a supraorbital pore and posteriorly through a postbranchial pore. Suborbital canal with two pores, anteriormost pore ventral to orbit, posterior pore posteroventral to orbit. Operculomandibular canal with single opercular pore on cheek and four mandibular pores closely spaced along lower jaw. All sensory pores opening through short thick tubes.

Development and distribution of bony tubercles on head and body highly variable. In holotype (38.5 mm SL), tubercles small, low, rounded, embedded in skin, each with several prominent spines; tubercles few and sparsely spaced, forming an indistinct row on either side of spinous dorsal fin, several additional tubercles dispersed along anterior portion of body; head naked. Tubercles generally smaller and fewer in smaller specimens and in males; larger males (45–55 mm SL) with tubercles completely covered by skin, producing wart-like protrusions on body; males and smaller females often without tubercles on head or body; all specimens examined over 58 mm SL (n = 13) completely covered with large tubercles, and all female.

First dorsal fin high, usually not covered with thick skin or tubercles in smaller specimens (including holotype); becoming increasingly embedded in skin and covered with spiny tubercles in larger specimens, particularly in females; fin membranes moderately to heavily pigmented. Second dorsal and anal fins directly opposite each other, nearly equal in length and height, usually without bony tubercles or fleshy papillae; fin membranes translucent, without pigment. Caudal fin truncate; fin membranes translucent, without pigment; rays in some specimens with several faint dark blotches suggesting bands running perpendicular to body axis. Pectoral fins translucent, their bases densely covered with small melanophores; larger specimens usually with several rounded tubercles covering pectoral base. Pelvic disc large, ovate, slightly constricted anteriorly; its length usually slightly greater than its width. Anus approximately midway between posterior margin of pelvic disc and origin of anal fin.

Coloration. Holotype with small melanophores relatively evenly spaced over entire head and body, without conspicuous bands, stripes, or blotches. Additional material in life yellowish-brown to medium brown, generally darker on head and dorsum, often with dark brown to black blotches and vermiculations, particularly on dorsal surface of head and body; becoming lighter posteriorly and generally white or nearly white on ventral surface. Some degree of faint banding usually present on pectoral and all median fins.

Distribution. Specimens examined are from the eastern Bering Sea, Aleutian Islands, and western and central Gulf of Alaska (Fig. 6).

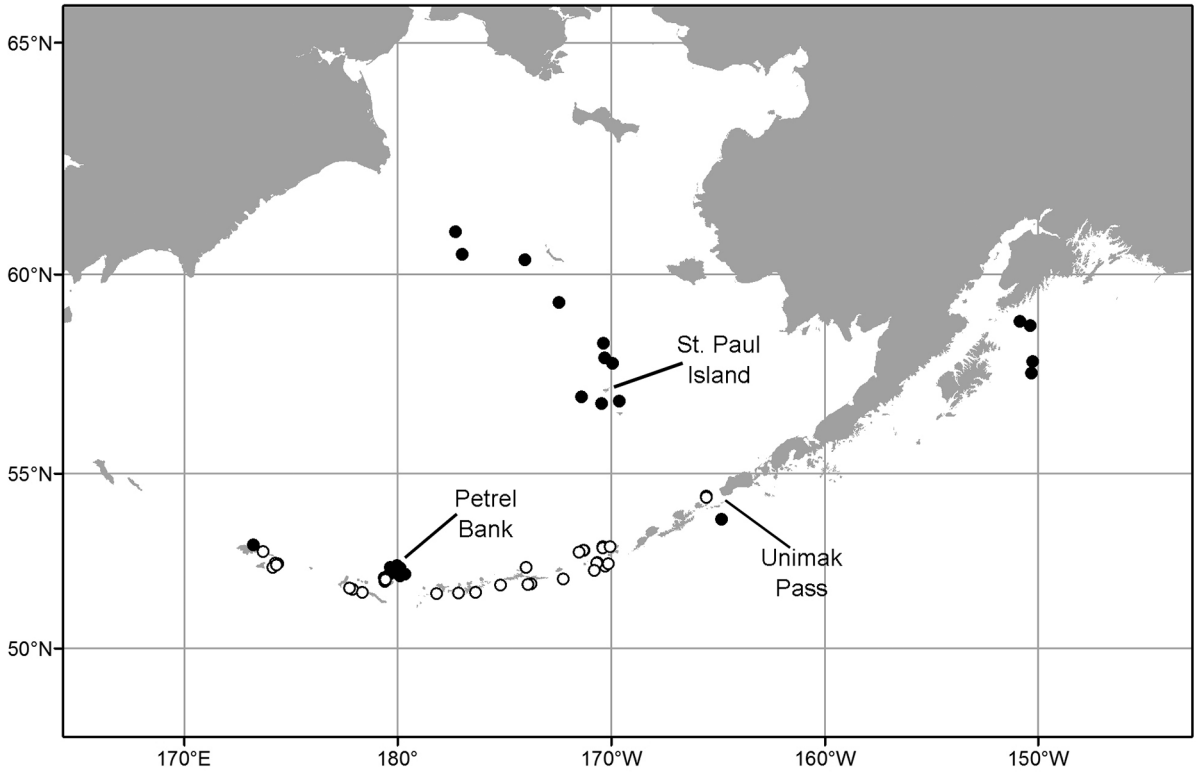

FIGURE 6. Distribution of material examined for *Eumicrotremus gyrinops*. Open circles represent specimens with no evidence of tubercles on the head or body.

Remarks. The holotype of *E. gyrinops* (MCZ 16026) is in poor condition. It has apparently been desiccated and rehydrated at least once. Thus, the tubes associated with the mandibular pores, and to a lesser extent the other

pores as well, appear longer and more prominent than in most other specimens. In addition, its fins are badly damaged, and its internal organs have been removed through a very large incision on the left side of the body.

Material examined. *Eumicrotremus asperrimus* (18 specimens): **Sea of Japan**: FAKU 131263 (GenBank AB917623, 917693), 102 mm female, Kyoto, 36°N, 134.75°E, 320 m; FAKU 131983 (GenBank AB917614, 917684), 40 mm male, 35.881°N, 132.474°E, 240 m; FAKU 132544 (GenBank AB917600, 917670), 59 mm male, 37.758°N, 136.294°E, 342 m; FAKU 132564 (GenBank AB917601, 917671), 58 mm male, 38.026°N, 136.916°E, 330 m; FAKU 132598 (GenBank AB917621, 917691), 34 mm male, Ishikawa, 37.7°N, 136.308°E, 260 m; FAKU 133204 (GenBank AB917615, 917685), 61 mm male, Kyoto, 38.03°N, 135.413°E, 300 m. **Sea of Okhotsk**: FAKU 133231 (GenBank AB917616, 917686), 98 mm female, 45.062°N, 143.068°E; FAKU 133235 (GenBank AB917620, 917690), 52 mm, 44.99°N, 144.115°E, 220 m; FAKU 133279 (GenBank AB917604, 917674), 56 mm female, 44.382°N, 144.341°E, 350 m; FAKU 133280 (GenBank AB917605, 917675), 54 mm female, 44.382°N, 144.341°E, 350 m; FAKU 133281 (GenBank AB917606, 917676), 59 mm female, 44.382°N, 144.342°E; FAKU 133282 (GenBank AB917607, 917677), 60 mm male, 44.382°N, 144.342°E; FAKU 133283 (GenBank AB917608, 917678), 60 mm female, 44.382°N, 144.342°E; FAKU 133284 (GenBank AB917609, 917679), 49 mm male, 44.382°N, 144.341°E, 350 m; FAKU 133285 (GenBank AB917610, 917680), 91 mm female, 44.382°N, 144.342°E; FAKU 133286 (GenBank AB917611, 917681), 56 mm female, 44.382°N, 144.341°E, 350 m; FAKU 134958 (GenBank AB917639, 917709), 59 mm female, 44.78°N, 143.928°E, 170 m; FAKU 134985 (GenBank AB917643, 917713), 56 mm male, 45.46°N, 142.967°E, 117 m.

Eumicrotremus awae: FAKU 134183, 18 mm, Japan, Sagami Bay; FAKU 134725, 18 mm, Japan, Sagami Bay; FAKU 135824, 24 mm, Japan, Sagami Bay; UW 42938, 16 mm, Japan, Sagami Bay, 35.15°N, 139.17°E.

Eumicrotremus bergi (2 specimens): FAKU 132552 (GenBank AB917597, 917667), 59 mm male, Sea of Japan, 38.031°N, 136.778°E, 419 m; FAKU 132557 (GenBank AB917596, 917666), 62 mm male, Sea of Japan, 37.959°N, 137.31°E, 320 m.

Eumicrotremus gyrinops (235 specimens): **Type material**: MCZ 16026, holotype of *Cyclopteroides gyrinops*, 38.5 mm, St. Paul Island, Alaska; USNM 74378, holotype of *Eumicrotremus phrynoides*, Albatross station 4779, Petrel Bank, Bering Sea, 54–56 fm; USNM 53806, lectotype of *Lethotremus muticus*, Albatross station 2844, near Unimak Pass, 54 fm; CAS-SU 774, paralectotype of *Lethotremus muticus*, Albatross station 2844, near Unimak Pass, 54 fm; CAS-SU 3093, USNM 48614, USNM 59376, paralectotypes of *Lethotremus muticus*, Albatross station 3223, Unimak Pass, 39 fm. **Bering Sea** (31 specimens): UW 28373, 85 mm female, 57°0'N, 171°25.02'W, 59 fm; UW 28384, 69 mm female, 60°59.1'N, 177°19.02'W, 130 m; UW 28390, 65 mm female, 60°28.14'N, 177°W, 143 m; UW 119071, 16(29–47 mm males, 27–40 mm females), 56º53'N, 169º39'W, 75 m; UW 119538 (GenBank AB917661, 917731), 92 mm female, 57º59.23'N, 170º20.09'W, 74 m; UW 150056, 82 mm female, 59°19.98'N, 172°28.26'W, 87 m; UW 150057, 51 mm male, 56º50.08'N, 170º26.76'W, 98 m; UW 150071 (GenBank AB917626, 917696), 75 mm female, 54º50.25'N, 169º57.12'W, 71 m; UW 150072, 88 mm female, 60°20.28'N, 174°3.36'W, 90 m; UW 151282, 3(41 mm male, 33–77 mm females), 56°49.57'N, 170°28.07'W, 101 m; UW 151285, 80 mm female, 58°20.58'N, 170°22.32'W, 74 m; UW 151415, 46 mm male, 56°40.32'N, 170°4.44'W, 95 m; UW 152368, 36 mm male, 60°8.88'N, 172°57.12'W, 59 m; UW 155892, 81 mm female, 56°35.22'N, 170°38.22'W, 108 m.

Aleutian Islands (160 specimens): UW 22199, 69 mm, 53°43.98'N, 164°49.98'W, 209 m; UW 28389, 42 mm, 54°24'N, 165°24'W; UW 46659, 32 mm, 51°54.6'N, 176°52.2'W, 211 m; UW 46660, 45 mm, 52°51.53'N, 172°27.52'E, 146 m; UW 46662, 45 mm, 53°1.68'N, 173°12.36'E, 133 m; UW 46664, 5(43–51 mm females), 52°11.04'N, 179°39.84'W, 115 m; UW 46665, 5(44–49 mm females), 51°58.98'N, 179°23.52'E, 139 m; UW 49401, 2(40 mm male, 45 mm female), 52°7.8'N, 179°54.6'W, 112 m; UW 49409, 41 mm male, 52°4.92'N, 179°21.54'E, 306 m; UW 49412, 45 mm male, 52°25.86'N, 179°56.52'E, 163 m; UW 49418, 49 mm male, 52°31.27'N, 174°26.96'E, 182 m; UW 49423, 50 mm female, 52°2.82'N, 179°25.26'E, 143 m; UW 49436 (GenBank AB917625, 917629, 917695, 917699), 2(36–38 mm, males), 52º08.14'N, 179º53.41'W, 121 m; UW 49467, 34 mm male, 52°29.96'N, 170°40.65'W, 208 m; UW 49470, 4(37–52 mm females, 36 mm male), 52°10.86'N, 179°37.02'E, 124 m; UW 49471, 4(41–44 mm males), 52°22.62'N, 179°38.82'E, 245 m; UW 49474, 18(34–38 mm males, 30–40 mm females), 51°39.23'N, 176°22.56'W, 143 m; UW 49504, 61 mm female, 52°2.34'N, 179°24.96'E, 145 m; UW 49577, 5(40–42 mm females), 52°59.42'N, 172°21.95'E, 146 m; UW 49580, 49 mm female, 52°28.15'N, 173°11.34'E, 116 m; UW 49587, 45 mm female, 52°35.6'N, 172°55.38'E, 154 m; UW 111260, 39 mm male, 52°27.91'N, 174°12.6'E, 110 m; UW 111265, 35 mm female, 52°23.82'N, 173°58.72'E, 112 m; UW 111267, 2(34–

41 mm females), 51°39.23'N, 176°22.2'W, 145 m; UW 111280, 52 mm female, 52°52.7'N, 175°12.5'W, 151 m; UW 111288, 62 mm female, 52°25.27'N, 170°16.74'W, 211 m; UW 111300, 47 mm female, 52°21.71'N, 171°16.14'W, 134 m; UW 111309, 40 mm male, 52°21.96'N, 179°54.84'W, 168 m; UW 111310, 35 mm female, 52°29.56'N, 174°22.08'W, 177 m; UW 111311, 7(32–42 mm males, 38–51 mm females), 52°57.72'N, 170°23.82'W, 221 m; UW 111314, 2(49–50 mm females), 52°18.38'N, 175°48.91'E, 235 m; UW 111335, 35 mm male, 52°30.19'N, 174°15.22'W, 102 m; UW 111451, 2(36–44 mm males), 52°29.46'N, 170°8.82'W, 183 m; UW 112040, 35 mm male, 52°22.97'N, 174°8.62'E, 148 m; UW 112041, 41 mm female, 52°26.26'N, 174°17.57'E, 220 m; UW 112272 (GenBank AB917663, 917664, 917733, 917734), 2(32 mm male, 45 mm female), 52º31.20'N, 170º39.25'W, 124 m; UW 117593, 43 mm female, 52°39.45'N, 173°50.48'E, 79 m; UW 151458, 3(35–38 mm males, 33 mm female), 51°2.50'N, 172°15.1'W, 162 m; UW 151803 (GenBank AB917644, 917714), 36 mm male, 51º53.15'N, 173º55.29'W, 136 m; UW 151804 (GenBank AB917645, 917715), 45 mm female, 52º02.56'N, 179º48.44'W, 250 m; UW 151810 (GenBank AB917646, 917716), 43 mm female, 52º49.40'N, 173º41.17'W, 109 m; UW 151811 (GenBank AB917647, 917717), 44 mm female, 52º24.33'N, 170º16.57'W, 213 m; UW 151814 (GenBank AB917648, 917718), 46 mm male, 52º49.42'N, 170º27.32'W, 99 m; UW 152131 (GenBank LC209624, 209640), 49 mm female, 52°35.48'N, 172°55.48'E, 145 m; UW 152132 (GenBank LC209625, 209641), 40 mm male, 52°28.32'N, 173°11.4'E; UW 152138, 2(31 mm male, 33 mm female), 54°22.2'N, 165°32.94'W, 83 m; UW 152355, 3(39–60 mm male, 41 mm female), 52°55.94'N, 170°24.61'W, 222 m; UW 152358 (GenBank LC209626, 209642), 35 mm female, 51°45.04'N, 177°51.7'E, 157 m; UW 152359 (GenBank LC209627, 209643), 3(38 mm male, 37–41 mm females), 51°54.64'N, 173°47.03'W, 118 m; UW 152360 (GenBank LC209628, 209644), 33 mm male, 51°39.08'N, 178°20.06'E, 206 m; UW 152361, 4(36–42 mm males, 33 mm female), 52°29.62'N, 170°23.63'W, 216 m; UW 152362 (GenBank LC209629, 209645), 32 mm male, 52°2.16'N, 179°24.84'E, 150 m; UW 152363 (GenBank LC209630, 209646), 29 mm female, 51°36.96'N, 178°11.28'W, 134 m; UW 152364, 38 mm female, 52°17.28'N, 170°47.58'W, 226 m; UW 152365 (GenBank LC209631, 209647), 35 mm male, 52°49.68'N, 173°41.28'E, 115 m; UW 152366 (GenBank LC209632, 209648), 36 mm male, 51°52.92'N, 173°55.38'W; UW 152367 (GenBank LC209633, 209634, 209649, 209650), 2(37–41 mm males), 52°52.02'N, 171°18.06'W, 204 m; UW 152369 (GenBank LC209635, 209651), 33 mm female, 51°47.28'N, 177°43.56'E, 155 m; UW 152370 (GenBank LC209636, 209652), 3(40–41 mm females), 51°37.98'N, 177°9.96'W, 172 m; UW 152371 (GenBank LC209637, 209653), 2(35–37 mm males), 52°26.88'N, 174°18.66'E, 228 m; UW 152428, 53 mm female, 52°52.28'N, 171°19.06'W, 202 m; UW 152431 (LC209833, 209845), 40 mm female, 52°22.92'N, 174°8.46'E, 155 m; UW 152432, 43 mm female, 52°26.88'N, 174°18.66'E, 228 m; UW 152433 (GenBank LC209638, 209639, 209654, 209655), 2(35–42 mm males), 52°58.62'N, 170°3.72'W, 122 m; UW 152434 (LC209834, 209846), 41 mm male, 52°28.33'N, 173°11.37'E; UW 152438, 2(27–43 mm males), 52°28.59'N, 170°8.7'W, 183 m; UW 152444, 39 mm male, 54°20.65'N, 165°32.94'W, 104 m; UW 152460, 2(38 mm male, 31 mm female), 52°23.18'N, 174°W, 85 m; UW 152466, 2(36 mm male, 46 mm female), 52°48.65'N, 171°31.38'W, 201 m; UW 152469 (LC209835–209843, 209847–209855), 9(37–48 mm females), 52°48.95'N, 173°44.35'E, 111 m; UW 152490 (LC209844, 209856), 42 mm female, 52°24.22'N, 174°15.53'E, 255 m; UW 154964, 9(41 mm male, 36–57 mm females), 52°10.84'N, 179°36.97'E, 127 m; UW 156510, 4(32–38 mm females), 51°47.46'N, 177°40.74'E, 171 m; UW 156512, 37 mm female, 52°28.5'N, 170°44.94'W, 260 m; UW 156511, 2(41–42 mm females), 52°35.28'N, 172°55.72'E, 127 m.

Gulf of Alaska (42 specimens): UW 28386, 2(52–54 mm), 56°N, 157°W, 50 fm; UW 47916, 38 mm female, 58°7.47'N, 151°30.6'W, 157 m; UW 47923, 9(34–39 mm females, 37 mm male), 58°56.46'N, 150°19.02'W, 146 m; UW 47935, 2(39 mm female, 39 mm male), 56°43'N, 152°36.72'W, 97 m; UW 47948, 3(32 mm female, 37–40 mm males), 54°53.85'N, 158°42.48'W, 98 m; UW 116417, 40 mm female, 58°46.32'N, 150°23.58'W, 151 m; UW 117047, 4(34–38 mm males, 36–38 mm females), 54°44.1'N, 158°37.26'W, 104 m; UW 117609 (GenBank AB917634, 917704), 3(41–43 mm females, 38 mm male), 58º15.17'N, 151º24.51'W, 157 m; UW 119222 (GenBank AB917627, 917628, 917697, 917698), 2(32–38 mm females), 57º36.33'N, 150º20.16'W, 130 m; UW 119548, 39 mm male, 55º16.88'N, 157º6.48'W, 94 m; UW 119596, 40 mm male, 57º53.28'N, 150º16.47'W, 158 m; UW 119690, 4(38–41 mm females), 58º53.03'N, 150º52.08'W, 164 m; UW 119706, 60 mm female, 58º54.29'N, 150º36.3'W, 119 m; UW 119779 (GenBank AB917631, 917701), 35 mm male, 58º38.59'N, 150º08.45'W, 121 m; UW 119782 (GenBank AB917632, 917702), 39 mm male, 58º30.48'N, 150º17.52'W, 90 m; UW 151260 (GenBank AB917657, 917658, 917659, 917727, 917728, 917729), 5(31–37 mm males, 35 mm female), 58°54'N, 151°24.96'W, 153 m; UW 154590, 39 mm male, 55°29.21'N, 157°2.82'W, 90 m.

Eumicrotremus lindbergi (4 specimens): FAKU 132535 (GenBank AB917599, 917669), 55 mm male, Sea of Japan, 36.845°N, 136.317°E, 261 m; FAKU 132563 (GenBank AB917598, 917668), 59 mm male, Sea of Japan, 38.026°N, 136.916°E, 330 m; FAKU 134222 (GenBank AB917624, 917694), 53 mm male, Sea of Japan, Shimane, west of Oki I.; FAKU 134862 (GenBank AB917638, 917708), 54 mm male, Sea of Japan, Shimane, 35.6°N, 131.033°E, 180 m.

Eumicrotremus orbis: UW 119821 (GenBank AB917655, 917725), 2(17 mm male, 31 mm female), Salish Sea, San Juan Island, Jackson Beach, 48°31.2'N, 123°W, 2 m.

Acknowledgments

We thank T. W. Pietsch and K. P. Maslenikov (UWFC), T. Nakabo (FAKU), and K. E. Hartel and A. Williston (MCZ) for loans of specimens, and A. Williston for the micro-CT scan of the type specimen. We also thank J. W. Orr (AFSC) and T. W. Pietsch for helpful reviews of the manuscript.

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