

**Descriptions and records of liparid fishes (Scorpaeniformes, Liparidae) from the Mariana Islands**

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**Abstract** Three new bathyal species of *Paraliparis* (Liparidae) are described from Tinian and Anatahan Islands, and from Esmeralda Bank, in the Mariana Islands. All were collected in shrimp traps set at 903-1207 m. Although liparids have been found, described, and studied at hadal depths in the Mariana Trench, the three new species are the first species of the family described from bathyal depths of the Mariana Islands. The existence of three species from collections at three locations in the same archipelago, and their distinctiveness from liparids known from other areas in the western Pacific to the north and south of the Mariana Archipelago, is in accordance with the high degree of endemism in species of *Paraliparis*. Biogeographic and liparid life history factors that influence bathyal fish distributions in the Mariana Archipelago and enhance endemism in *Paraliparis* are discussed.

**Key words** Liparidae • *Paraliparis* • Mariana Archipelago • Bathyal fishes • Biogeography

## **Introduction**

Snailfishes (Liparidae) are most abundant and diverse in temperate and polar regions of the world, and less often reported from subtropical and tropical areas (Chernova et al. 2004). In fact, liparids occur worldwide in waters of suitable temperatures, which, in the tropics, only occur at bathyal and greater depths that are poorly sampled. There are very few records of snailfishes from islands in the tropical and subtropical Pacific Ocean (Stein and Drazen 2014). In the Mariana Islands (Fig. 1), the family is best known from observations and collections of hadal species in the Mariana Trench at 6198-8145 m (Linley et al. 2016). As has been the case at many previously unsampled or inadequately sampled locations, snailfishes are also present in the

Mariana Archipelago at bathyal depths. During the 1980s, NOAA research vessels made ichthyological collections throughout the Mariana Islands. These collections, obtained largely from shrimp traps fished between March of 1981 and January of 1984, captured a surprising number of snailfishes, which were unexamined until recently. These were reported as “Family Cyclopteridae (Liparididae) Unid. Sp.: currently under study by R. Moffitt” by Myers (1988:179) and as “Cyclopteridae (Liparidae of some authors) Unid. Sp.” by Myers and Donaldson (2003:620), but no other information was given. Unfortunately, neither their collection nor their preservation has been kind to these soft-bodied, fragile fishes. However, the condition of some specimens is good enough to allow their description. They include three undescribed species. This paper describes and names those fishes, discusses the characters used to distinguish them, and discusses the zoogeography of Mariana Archipelago bathyal fishes as it pertains to them.

## **Materials and methods**

Specimens were captured during fisheries assessments of deepwater shrimp populations in the Mariana Archipelago (Fig. 1) during 1981-1984 (Moffitt, 1983; Moffitt and Polovina 1987). Those in 1981 were caught during surveys from the commercial fishing vessel *Typhoon* using half-round shrimp traps (91 x 72 x 42 cm) with 1.3 x 2.5 cm or 1.3 x 1.3 cm mesh covered with burlap or canvas (Moffitt 1983). Some traps used near Guam had 1.3 x 1.3 cm wire mesh because of materials availability (unpublished F/V *Typhoon* cruise 81-01 report). Traps were baited with chopped fish, usually skipjack tuna (*Katsuwonus pelamis*). Single strings of three traps each were deployed at each location to target depths of 366, 732, and 1097 m in the

afternoon and retrieved the next morning, having soaked for 16-20 hours. The specimens from 1982-1984 were caught during surveys from the NOAA ship *Townsend Cromwell* in the same depth range using half-round shrimp traps (90 x 65 x 45 cm) with 1.3 x 2.5 cm wire mesh covered with canvas (Moffitt and Polovina 1987). Each trap was baited with three chopped mackerel (*Scomber japonicus*). Four strings of five traps each, 40 m apart, were set at each location in the afternoons and retrieved the following morning for soak times of 15-24 hr. In May 1984 six traps were deployed on each string. In addition, a single pyramidal trap (150 x 150 x 150 cm) was also set at some locations. Traps had entry cones with 10 cm diameter apertures. The sampling effort for all years combined consisted of 2745 individual trap deployments. Liparid specimens were sorted from each catch, fixed in 10% formalin, and preserved in 40-50% isopropyl alcohol or 70% ethanol. Many of the 18 specimens available for our examination had deteriorated from the time of capture before this study began, and only those in the best condition were used for the descriptions herein.

Definitions of counts, measurements, and characters follow Stein et al. (2001), Andriashev (2003), and Stein (2012). Terminology of the epipleurals follows Stein et al. (2001). Museum abbreviations follow Sabaj Perez (2020). Counts of vertebrae, dorsal and anal fin rays, and pre-dorsal- and anal-fin lengths were obtained from radiographs of specimens. Pectoral and caudal fin ray counts were made by direct examination. The right pectoral girdle was removed from each holotype and other specimens as needed, and stained using alizarin red S (Taylor 1967a; b). Whole specimens were temporarily stained with cyanine blue when necessary (Saruwatari et al. 1997). The illustrations are by B. Mundy.

Counts given are from the holotype, followed by the range for all specimens in parentheses. Ratios for proportions are given as percent standard length (SL) and percent head

length (HL) for the holotype first, followed in parentheses by the range for the other specimens.  
Sex and stage of development were determined visually.

We compare our new species with those recorded from the Kyushu-Palau Ridge and other subtropical western North Pacific areas, referred to herein as the region, because those species are the most likely to be collected near the Mariana Islands where our new species are found.

## Results

### *Paraliparis echongpachot* sp. nov.

(Fig. 2, 3; Table 1, 2)

**Holotype.** OS 20118 2/4, TL unknown, SL >228 mm, female, 14°58.99' N, 145°10.84' E, west side of Esmeralda Bank west of Tinian Island, Commonwealth of the Northern Mariana Islands, commercial fishing vessel *Typhoon*, Cruise Typhoon 81-01, stn. 110, shrimp trap, 1207 m, 20 March 1981.

**Paratypes.** OS 20118 1/4 sex unknown, SL >210 mm, 3/4 sex unknown, SL>140 mm, 4/4 female, SL >160mm, all collected with holotype.

**Diagnosis.** Mouth oblique, large. Pectoral fin rays 22-23, dorsal-most ray level with bottom edge of orbit or below. Snout-anus 140% HL or more. Epipleurals long, equal in length to 3-4 abdominal vertebrae. Intestines and pyloric caeca gray.

109 **Description.** Counts and measurements are shown in Tables 1 and 2. Head length as % SL  
110 unknown, estimated as at most about 1/5 SL; dorsal profile straight, sloping gradually to blunt  
111 snout. Snout short, not protruding much beyond upper lip, about 1/4 HL. Nostrils single, at about  
112 level of upper half of orbit, nares badly damaged. Orbit large, about 1/4 HL, eye diameter 1/5-1/6  
113 HL. Interorbital broad, flat. Mouth oblique, its angle about 20° to horizontal. Lower jaw  
114 included, upper jaw reaching posteriorly to below rear margin of orbit. Teeth small, stout  
115 canines, arranged in about 46 oblique curved rows of up to 15 teeth each, inner teeth slightly  
116 largest, gradually increasing in size from outside to inside, forming a band in each jaw. A clear  
117 symphyseal diastema present in upper and lower jaws, wider and deeper in upper jaw than in  
118 lower. Gill opening length unknown, opercle pointing ventrally, curved posteriorly, its tip almost  
119 horizontal. Cephalic pores unknown, all missing.

120 Pectoral fin divided into upper and lower lobes, a distinct but relatively shallow notch  
121 present between them. Dorsal-most pectoral fin ray on horizontal below orbit but well above  
122 posterior corner of mouth. Rays 22-23 (13-16+4-6+3-4), notch rays gradually becoming much  
123 more widely spaced ventrally, but not clearly distinct from upper or lower lobe rays. Upper fin  
124 lobe reaching about 2/3 distance to posterior end of body cavity; lower lobe about half length of  
125 upper lobe. Radials of right pectoral fin girdle in three specimens (including holotype) 5  
126 (1+1+1+1+1) (Fig. 3a), and in OS 20118 1/4, 4 (3+1) (Fig. 3b). Scapula a broad horizontal V with  
127 two forward facing limbs and ventral notch opposite that in R1; coracoid with long helve.  
128 Radials and scapula highly variable: 20118 1/4 with 4 (3+1) unnotched radials, unnotched  
129 scapula; 20118 3/4 with 5 unnotched radials, unnotched scapula; and 20118 4/4 with 5  
130 unnotched radials, notched scapula.

Body deepest at posterior of abdomen, probably tapering evenly to end (caudal and several vertebrae missing). Predorsal-fin length about 1.2-1.5 times HL, preanal-fin length about 1.8-2.1 times HL. First dorsal pterygiophore between vertebrae 3-4. Anal fin origin between vertebrae 10-11. Epipleurals present, longest equal in length to 3-4 abdominal vertebrae. Caudal fin and last few vertebrae lost. Pyloric caeca 5-6, short to very long in each individual; longest caecum extends dorsally along stomach wall. Stomach large, thick walled.

**Color of preserved specimens.** In alcohol, only skin remnants remaining, sufficient to show body color was dense dark brown to black. Peritoneum brownish black, mouth and gill cavity brown, stomach pale, intestines and caeca gray or greenish.

**Distribution.** Known from four specimens collected by a shrimp trap at 1207 m at the west side of Esmeralda Bank to the west of Tinian Island, Commonwealth of the Northern Mariana Islands.

**Comparisons.** Of the three previously described liparid species known from the region and the three additional species described herein, only *P. echongpachot* and *P. mandibularis* have an oblique mouth. However, the mouth angle in the latter is greater than that in *P. echangpachot*. In addition, *P. echongpachot* differs from *P. mandibularis* in having fewer pectoral fin rays (22-23 vs 27-30), a shorter snout (23-24 vs 27-35% HL), and different body color (dark brown vs pale; Kai et al. 2020). In addition, although the number of radials (5) in three of the four specimens of *P. echongpachot* is anomalous for liparids (Orr et al. 2019), the consistency of that number suggests that it may be normal for the species, in which case it would be unique in the family.

The pectoral girdle structure of any future specimens should be carefully examined for that character.

**Etymology.** *Echongpachot* from the Chamorro language of the Mariana Islands, "crooked mouth".

***Paraliparis marianae* sp. nov.**

(Fig. 4, 5, 6; Table 1, 2)

**Holotype.** OS 20115 2/2, TL 185, SL 172 mm, female, 15.0723° N, 145.5221° E, Tinian Island, Commonwealth of the Northern Mariana Islands, R/V *Townsend Cromwell*, Cruise TC 82-02, shrimp trap, stn. 138, 903 m, 15 May 1982. Paratype. OS 20115 1/2, TL 142, SL 128 mm, female, collected with holotype.

**Diagnosis.** Mouth horizontal, lower jaw slightly included. Nostril not tubular. Chin pores paired, in a well-defined pit; other cephalic pores with thickened rims. Opercle pointing posterodorsally at an angle of about 45°. Pectoral fin rays 22-23, upper pectoral fin lobe 1 1/3 times length of lower lobe; upper pectoral fin ray on horizontal between middle and upper edge of orbit. Caudal fin of nine rays. Epipleurals moderately long, twice as long as an abdominal vertebra. Intestines pale, pyloric caeca pale or dark gray. No longitudinal dark peritoneal stripe but two parallel interrupted pale dashed lines extending from either side of anus to rear of peritoneum (Fig. 6).

**Description.** Counts and measurements are shown in Tables 1 and 2. Head small, about 1/5 SL, broad, its dorsal profile evenly convex to blunt snout. Snout high, slightly protruding above



176 mouth. Nostrils single, small, with poorly developed thickened rim, on horizontal through middle  
177 of eye. Mouth horizontal, almost terminal, upper jaw reaching posteriorly to below rear of orbit;  
178 lower jaw tooth band  $1/3$ - $1/2$  width of upper. Teeth small, bluntly conical canines, forming a  
179 moderately wide band of about 35 obliquely curved rows of up to nine teeth each, outermost  
180 smallest, a clear symphyseal gap present in upper jaw, a narrow gap present at symphysis of  
181 lower jaw. Eye small,  $1/4$  to  $1/5$  HL. Dorsal rim of orbit well below dorsal profile of head. Gill  
182 opening short, completely above pectoral fin; opercle lunate, its tip above and anterior to base of  
183 dorsal pectoral fin ray and pointing posterodorsally at an angle of about  $45^\circ$ . Gill flap broad and  
184 bluntly pointed. Chin pores paired, opening in a broad, laterally oriented oblong pit, its posterior  
185 margin poorly defined; other cephalic pores moderately large, with cartilaginous rims; pore  
186 formula unknown owing to damage.

187         Pectoral fin uppermost ray on level between upper margin of orbit and mid-pupil. Fin  
188 clearly divided into two lobes, notch only moderately deep. Rays 22-23 (13-15+5-6+3-4),  
189 rudimentary rays absent, notch rays much more widely spaced than upper and lower rays. Upper  
190 lobe almost reaching posterior end of abdomen or above first anal fin ray,  $2/3$  to  $4/5$  HL; lower  
191 lobe about  $3/4$  upper lobe length. Radials 4 (3+1) rounded, unnotched (Fig. 5); scapula a broad  
192 horizontal V, barely notched anteriorly; coracoid moderately long, its helve broadly supported by  
193 webbing.

194         Body deep, compressed, its deepest point over mid-abdomen. Vertebrae 66-69 (10+56-  
195 59), epipleurals present, about as long as two vertebrae. Predorsal-fin length 1.2 HL, first dorsal  
196 pterygiophore unusually far anterior, between vertebrae 1-2 or 2-3; preanal-fin length about 1.9  
197 HL, first anal fin pterygiophore between vertebrae 11-12; caudal region elongate, narrow. Dorsal  
198 and anal fins of even depth posterior to anteriormost rays. Preanus length less than  $1/5$  SL,

below rear edge of pectoral fin base; abdomen deep, relatively short. Pyloric caeca 5-6, large, thin-walled, distributed around ventral surface of stomach, not just on one side. Two rows of pale dashes present, one on each side of ventral midline, less obvious in (larger) holotype. Caudal fin of 9 (1+4/4) rays, hypural fused completely. Skin thin, loose, suggesting thick layer of extracellular matrix (Eastman et al. 1994) in life.

**Color of preserved specimens.** Mostly skinned. In alcohol, remnants of translucent brown skin remaining on body, paler posteriorly. Oral and branchial cavities pale, peritoneum dark brown. Stomach and intestines pale, caeca pale or gray. Pale dashes on either side of the ventral midline, contrasting with the externally brown abdominal cavity.

**Distribution.** Known from two specimens collected in a shrimp trap at 903 m off Tinian Island, Commonwealth of Northern Mariana Islands.

**Comparisons.** *Paraliparis marianae* differs distinctly from all species compared here in having two parallel dashed lines on either side of the ventral midline (Fig. 6). It differs further from *P. echongpachot* and *P. mandibularis* in having a horizontal, not oblique, mouth. See below for its differences from *P. kadadakaleguak*. It differs from *P. atramentatus* in having more vertebrae (V 66-69 vs 57-58), many more dorsal and anal fin rays (D 62-65 vs 52-53, A 54-56 vs 46), nostril lacking a tube or strongly thickened rim (vs having a short tube), chin pores close in a pit or with a skin fold (vs chin pores widely separated), color of the branchial cavity (pale vs black or dusky) and several other morphometric characters. It differs from *P. meridionalis* in having chin pores in a pit (vs chin pores close but not in a pit), in lacking a nasal tube (vs having a short tube), and a deeper body (21-23 vs 15-19% SL). It differs from *P. hawaiiensis* in its chin pores

222 paired in a shallow pit or with a skin fold (vs touching in a deep pit), a longer head (19-21 vs  
223 16% SL), smaller eye (21-22 vs 29% HL), more anterior anus position (anus-anal fin 99-113 vs  
224 158% HL) and shorter predorsal fin length (120-126 vs 160% HL).

225

226 **Etymology.** Named after the archipelago to which it is indigenous, the Mariana Islands.

227

228 ***Paraliparis kadadakaleguak* sp. nov.**

229 (Fig. 7, 8; Table 1, 2)

230 **Holotype.** OS 20114 2/3, TL 143, SL 135 mm, female, 16°20.2' N, 145°44.9' E, Anatahan  
231 Island, Commonwealth of the Northern Mariana Islands, R/V *Townsend Cromwell*, Cruise TC  
232 82-02, shrimp trap, stn. 50, string 4, 1006 m, 28 April 1982.

233

234 **Diagnosis.** Mouth horizontal, lower jaw included. Nostril tubular, short. Chin pores paired, in a  
235 pit. Opercle strongly curved dorsally. Pectoral fin rays 26, upper pectoral fin ray about on level  
236 with mid orbit; upper and lower pectoral fin lobes of about equal length. Caudal fin of eight rays.  
237 Epipleurals less than twice length of an abdominal vertebra. Intestines pale, pyloric caeca dark  
238 gray. Longitudinal dark peritoneal stripe present.

239

240 **Description.** Counts and measurements are shown in Tables 1 and 2. Head small, less than  
241 1/5 SL, dorsal profile flat from behind orbit to snout, sloping gradually ventrally to rounded,  
242 blunt snout. Snout protruding slightly anterior to mouth. Nostrils single, short and tubular, on  
243 horizontal through middle of orbit. Mouth horizontal, small, lower jaw included; oral cleft  
244 extending to below mid-orbit, maxilla extending to below rear edge of orbit. Teeth small, blunt

245 canines, arranged in about 30 oblique curved rows of up to 8 or 9 teeth each; a narrow  
246 symphyseal gap present in upper jaw, a similar gap at symphysis of lower jaw but including a  
247 few teeth. Teeth in both jaws forming moderately narrow bands. Eye moderately large, orbit  
248 greater than  $\frac{1}{3}$  HL, dorsal margin of orbit close to profile of head. Opercular flaps both  
249 damaged, gill opening apparently entirely above pectoral fin; opercle a narrow broadly lunate  
250 spine pointing dorsally at about  $30^\circ$ . Pore counts 2-7- $\geq$ 5-1; chin pores small, paired, individually  
251 distinct, close together, surrounded by an oval skin fold. Other pores larger, their rims thickened  
252 and paler than surrounding skin.

253 Pectoral-fin upper ray about on horizontal through mid orbit; fin divided into two lobes  
254 by moderately deep notch. Fin rays 26 (17+5+4) in both fins, notch rays much more widely  
255 spaced than those in upper and lower lobes. Upper and lower lobes similar in length, lower lobe  
256 narrow, its rays largely free. Upper lobe reaching posteriorly to about  $\frac{3}{4}$  of abdomen length,  
257 lower lobe to about half abdomen length. Radials four (3+1) (Fig. 8), more or less round, R1, R2  
258 notched dorsally and ventrally, R3 notched dorsally only, R4 unnotched; scapula a wide  
259 horizontal V deeply notched anteriorly, coracoid blade short, helve long.

260 Body slender, tapering gradually and evenly to caudal. Vertebrae 67 (10+57). Predorsal  
261 length about  $\frac{1}{4}$  SL, preanal length  $\frac{2}{5}$  SL. Epipleurals shorter than two abdominal vertebrae.  
262 First dorsal pterygiophore between vertebrae 3-4 (damaged, possibly farther anterior), first anal  
263 fin ray between vertebrae 11-12. Abdomen short, swollen with eggs; anus below posteriormost  
264 edge of preopercle. Stomach large, thick-walled. Pyloric caeca 5, mostly ventral to stomach; one  
265 caecum very long, extending dorsally along side of stomach. Hypural fused distally; in  
266 radiograph, suture visible near base. Caudal fin rays 8 (4/4), extending well behind ends of  
267 terminal dorsal and anal fin rays. Skin thin, translucent, badly damaged.

**Color of preserved specimen.** In alcohol, skin brown, mouth dusky, tongue pale, gill cavity brownish, peritoneum dark brown, stomach pale, intestines pale, caeca gray.

**Distribution.** Known from one specimen collected in a shrimp trap at 1006 m off Anatahan Island, Commonwealth of Northern Mariana Islands.

**Comparisons.** *P. kadadakaleguak* differs distinctly from its regionally occurring congeners. It is similar to *P. marianae* in its horizontal mouth and general proportions, but differs in having more pectoral fin rays (26 vs 22-23), fewer caudal rays (8 vs 9), shorter head (18 vs 19-21% SL), closer chin pores (3 vs 5% HL), and a more slender body (101 vs 114% HL). It differs from *P. atramentatus* in number of vertebrae (67 vs 57-58), number of dorsal and anal fin rays (62 vs 52-53; 55 vs 46), in pyloric caeca color (dark gray vs pale), wider head (15% SL vs 10% SL), and other characters. It differs from *P. hawaiiensis* in number of pectoral fin rays (26 vs 20-21), chin pores (in a shallow pit or skin fold vs touching in a deep pit), snout-anus distance (15 vs 19% SL), mandible-anus distance (69 vs 96% HL), predorsal fin length (139 vs 160% HL) and other characters. Finally, it differs from *P. meridionalis* in number of pectoral fin rays (26 vs 22-23), chin pores (in a shallow pit with a skin fold vs not in a pit, skin fold absent), mandible-anus distance (69 vs 82-90% HL), pyloric caeca color (dark gray vs pale), and peritoneum color (dark brown vs black).

**Etymology.** *Kadadakaleguak* from the Chamorro language of the Mariana Islands, *kadada'* *kaleguak* "short rib bone".

## Discussion

## Biogeography

The bathydemersal fish fauna of the Mariana Archipelago is poorly known. Myers (1988) and Myers and Donaldson (2003) listed only 26 deepwater species from the Mariana Archipelago. Of those 26, only 11 are found at depths (800-1300 m) bracketing those where the new species were collected (903-1207 m). One of those 11 species was an unidentified liparid. That record was based on the specimens described as three new species herein. There are 19 additional unpublished records of fish species at 800-1300 m in the region, from remotely-operated video surveys by the NOAA ship *Okeanos Explorer*. It is unlikely that these species represent a significant proportion of the actual deep-water ichthyofauna in this poorly studied region. Lack of information about the distributions of these deep-water species and absence of phylogeographic analyses prohibit robust faunal level biogeographic inferences.

The new liparid species described herein are considered to be Mariana Archipelago endemics. Their biogeographic affinities are unclear, and their sister taxa are unknown. Investigators have repeatedly concluded that the genus *Paraliparis* is paraphyletic (Kido 1988; Knudsen et al. 2007, Steinke et al. 2009, Orr et al. 2019; Kai et al. 2020). Nevertheless, some hypotheses can still be generated from basic biogeographic patterns. The Marianas are included in a West Pacific or Indo-West Pacific Province (Zezina 1997; Briggs and Bowen 2012; Watling et al. 2013; Bowen et al. 2016). Based on the presence and absence of shallower-living coral-reef fish species, the Marianas are most similar to the central and western South Pacific island groups of Tonga, Tuvalu, Samoa, Fiji, and Vanuatu, and then to the Marshall and Caroline Islands (Kulbicki et al. 2013).

Habitat characteristics (including substrate, oxygen concentration, and food availability) exert a strong influence on the biogeography of fishes in the Marianas Archipelago (Myers 1988, 1999; Myers and Donaldson 2003). The steep island slopes and distance from continental shelves and rises limit the availability of low-gradient sediment habitats. The proximity of the Mariana Archipelago near and somewhat north of the western part of an oxygen-limited ( $\leq 60 \mu\text{mol kg}^{-1}$  or  $1.5 \text{ mL L}^{-1} \text{ O}_2$ ) zone may also affect deep-water fish communities in the region (Suntsov and Domokos 2013; Gallo and Levin 2016). Food availability, which is strongly dependent on surface primary productivity, may affect bathyal fish biogeography and community structure in the Marianas (Carney 2005; Drazen and Sutton 2017). The Marianas are in the oligotrophic North Pacific gyre, which has low to very low primary productivity compared to areas near continents or along the equator in the Pacific (Suntsov and Domokos 2013; Gove et al. 2016), and the Island Mass Effect that enhances primary productivity is low to moderate ( $<25\%$ ) compared to the Hawaiian Islands (Gove et al. 2016). Therefore, bathyal food availability in the region probably restricts deep-water fish distributions. We suggest that the West Pacific province of Watling et al. (2013) most likely characterizes the biogeographic affinities of the new species described above.

Geologic history strongly influenced the biogeography of Mariana fishes (Myers 1988, 1999; Myers and Donaldson 2003). The Marianas are part of the Izu-Bonin-Mariana arc where the Philippine tectonic plate meets and is subducted below the Pacific Plate at the Mariana Trench (Riegl et al. 2008). The Kyushu-Palau Ridge to the west (the closest locality to the Marianas where liparids are known) is an older arc formed on the Philippine Plate (Riegl et al. 2008; Ishizuka et al. 2018) and the Mariana Island arc began its formation as part of that ridge

(Myers 1988). The West Mariana Ridge formed at 20-5 ma, but the emergent Mariana Islands formed from about 43 ma (Riegl et al. 2008).

The oldest parts of the Izu-Bonin-Mariana arc and the Mariana Archipelago are younger than the only available estimate of age of divergence of the Liparidae from the Cottidae and similar to the estimated age of divergence of *Paraliparis* from *Liparis* (Near et al. 2012). However, those age estimates are based on only a few cottoid taxa, and that phylogenetic analysis was not intended to resolve phylogenies at the genus or even family level. There are no estimates of cladal divergence or lineage coalescence times in the more detailed examinations of liparid phylogenies (Kido 1988; Knudsen et al. 2007; Smith and Busby 2014; Orr et al. 2019) that can help with determining the biogeographic origins of liparids in the Mariana Islands.

Larval dispersal can influence the biogeography of marine fishes (e.g., Barlow 1981; Mora et al. 2003), most notably for the limited ranges of marine teleosts without a larval stage or with short larval durations (Weersing and Toonen 2009; Luiz et al. 2013), but little is known about the early life history of bathyal liparid species. Shallow-water liparids have smaller eggs than deeper-living species (Stein 1980) and often have planktonic larvae found in the mixed layer or upper thermocline (Able et al. 1986; Ambrose 1996; Plaza-Pasten et al. 2002; Matarese et al. 2003; Sokolovskii and Sokolovskaya 2003), although some shallow-living species have demersal larvae (Marliave and Peden 1999). Deeper species hatch at a larger size than shallow-water species, and have direct development without a distinct larval phase (Able et al. 1984, 1986; Kido and Kitagawa 1986; Matarese et al. 1989; Ambrose 1996; Takami and Fukui 2011). Juvenile deep-water liparids are rare in collections; most have been captured with nets fishing below the thermocline, often near the sea floor, instead of in shallower plankton tows (Able et al. 1986; Kido and Kitagawa 1986; Matarese et al. 1989; Ambrose 1996; Takami and Fukui 2011).



Stein (1980: 697) suggested for deep-water liparids that “The young probably take up benthic residence and habits very soon or immediately after hatching.” In contrast, Gerringer et al. (2018) presented evidence for ontogenetic vertical migration of a hadal species. It seems likely that juvenile deep-water liparids that move up into the water column remain below the thermocline and strong surface currents, as suggested for other bathyal benthic and benthopelagic species by Merrett and Haedrich (1997). The large size, direct development, and putative limited dispersal ability of deeper liparid species may contribute to the restricted ranges and high endemism of most of these species, particularly at insular and seamount locations.

The origins of the shallow-water Marianas fish fauna are to its south and west (Myers 1999). Although surface currents in the region generally flow from east to west, in the path of or influenced by the North Equatorial Current, there is also a strong influence of the north-easterly flowing southern branch of the Subtropical Counter Current from the Luzon Strait in the Philippines to the Northern Mariana Islands (Myers 1988). Most Mariana shallow-water fish species occur to the south and west around continental islands (Myers 1999). However, current directions vary with depth in the region (Reid 1997; Suntsov and Domokos 2013), and at depths where our new species were collected, general flows are from the southwest to northeast, from the Philippines through the Marianas. East to west currents do not dominate below the 500 dbar level (Reid 1997). Equatorial flows separate the Northern and Southern Hemisphere currents in the Pacific and are barriers to cross-equatorial dispersal of organisms.

#### **The utility of pectoral girdle morphology as a taxonomic character for liparids**

Pectoral girdle radial number, shape, position, and presence/absence of notches are now widely used as characters for identification since Andriashev et al. (1977) and Andriashev (1986,

2003) described and discussed their putative taxonomic utility. However, accumulating evidence of the variability and plasticity of radial morphology casts doubt on the reliability of this character. At present, we know of 25 species in three genera (Table 3) in which so-called "abnormal" or variable radial patterns have been described. These include odd patterns, odd numbers, odd positions, and variability of these characters within species and even between both sides of a single individual. Of these 25 exemplars more than one pectoral girdle has been examined in 20 species, although in some species both girdles from one individual have been studied rather than one girdle from each of two individuals (Table 3). The loss of radials and reduction of other pectoral fin characters such as fin rays and notched radials is a characteristic of more derived liparid species, which generally occur at greater depths than more basal species, especially those of *Liparis*, in which the skeletal elements tend to be better developed (Kido 1988; Orr et al. 2019). The Liparidae is a fast-evolving family (Orr et al. 2019) that includes a number of what can be termed "species flocks" (Stein et al. 2001). Thus, such variability is not surprising in characters that are being lost in such a broad spectrum of species living at depths from 300 to 7500 m, and may be widespread in deep sea snailfishes below the continental shelf. Furthermore, the functional effects (e.g., swimming and prey detection using the pectoral fins) of such structural variability are unknown. Further study of pectoral girdle morphological variability within (rather than between) common species of *Liparis* (a genus limited to shallow waters), *Careproctus* (occurring at intermediate depths), and *Paraliparis* (generally at bathyal and abyssal depths), would be useful in explaining evolutionary patterns of liparid morphology (Andriashev 2003; Orr et al. 2019).

As not only the most widely distributed family of marine fishes, but also a rapidly evolving complex group of great morphological variability, snailfishes provide a unique

405 opportunity to clarify how speciation occurs both geographically and bathymetrically. New  
406 methods of analysis make previously impossible studies possible, and we look forward to future  
407 clarification and description of these important (and interesting) processes.

408

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596

Table 1. Morphological characters, counts, and morphometric ratios for three new liparid species from the Mariana Islands. A = anal fin, bd = body depth, C = caudal fin, D = dorsal fin, F = female, go = gill opening, H = holotype, HL = head length, HW = head width, imm = immature, L = left, LLW = distance between the bases of the lowest right and lowest left pectoral fin rays, mand = mandible, LPL = lower pectoral fin lobe length, OS = Oregon State University Ichthyology Collection, P = pectoral fin, Par = paratype, pc = pyloric caeca, pmax = premaxilla length, PreA = preanal-fin, PreD = predorsal-fin, R = right, SL = standard length (mm), sn = snout, TL = total length (mm), UPL = upper pectoral fin lobe length, V and Vert = vertebrae.

	OS20114 2/3	OS20115 2/2	OS20115 1/2	OS20118 2/4	OS20118 1/4	OS20118 3/4	OS20118 4/4
	<i>kadadakaleguak</i> H	<i>marianae</i> H	<i>marianae</i> Par	<i>echongpachot</i> H	<i>echongpachot</i> Par	<i>echongpachot</i> Par	<i>echongpachot</i> Par
Mouth angle	horizontal	horizontal	horizontal	oblique	oblique	oblique	oblique
SL	135	172	128	>228	>210	>140	>160
TL	143	185	142				
Sex	F	F	F	imm F or spent	?	?	
Vert	67 (10+57)	69 (10+59)	66 (10+56)	>62 (8+>54)	65 (79+>56)	>65 (11+>54)	>69 (9+>60)
D	62	65	62	>61	>63	>59	>55
D insertion	V 3-4?	V 1-2 or 2-3		V 3-4			
A	55	56	54	>54	>55	>53	>47
A insertion	V 11-12	V 11-12	V 10-11?	V 10-11			
C	8 (4/4)	9 (1+4/4)	9 (5/4)				
P	L26(17/5/4) R26(17/5/4)	L22(13/6/3) R23(14/5/4)		L22(15/4/3) R23(16/4/3)	L22(13/5/4) R22(14/5/3)		L23(14/6/3) R23 (14/5/4)
pyloric caeca	5	6	5 1 long on right side	□ 3 long on L side	□ 4	5 possibly 6, 1 very long	>3, very long
chin pores	pit/skin fold	pit/skin fold	pit/skin fold				
radials	4 (3+1, 3 notched)	4 (3+1)	?	5 (1+1+1+1+1, 3 notched)	4 (3+1)	5 (1+1+1+1+1)	5 (1+1+1+1+1)
body color	translucent brown	translucent brown	translucent brown	dark brown	dark brown	dark brown	black
branchial color	brownish	pale	pale	brown		brown	dusky black
mouth color	dusky, pale tongue	pale	pale	dusky brown	blackish dusky		dusky, tongue pale
peritoneum color	dark brown	dark brown	dark brown	black-brown	dark brown/black	brown-black	dark brown-black
stomach color	pale	pale	pale	pale	pale	pale	pale
intestine color	pale	pale	dark gray and pale	grayish	greenish gray		green-grey
pc color	dark gray	pale	dark gray	grayish	apparently gray	gray green	green-grey
HL/SL	18.1	20.6	19.1				
HW/SL	14.8	15.8	14.2				
bd/SL	18.3	23.4	20.8				
eye/SL		74.4	4.3				
orbit/SL	6.7	7.2	6.2				
interorbital	8.9						
snout/SL	4.4	4.7	4.9				
pmax/SL	10.0	11.3	9.5				
mandible/SL	8.7	10.5	8.7				
go/SL	above P?	3.7	2.8				
mand-anus/SL	12.6	14.5	10.3				
sn-anus/SL	15.2	18.0	13.5				
UPL/SL	10.7	13.9	15.9				
LPL/SL	10.4	10.7	11.9				
PreD/SL	25.2	24.7	24.1				
PreA/SL	39.6	38.5	35.5				
anus-A/SL	23.2	20.5	21.7				
chin pores/SL	0.5	1.1	1.1				
LLW/SL	3.2	4.6					
HW/HL	81.6	76.8	74.3				
bd/HL	100.8	113.6	108.6	ca 86			
eye/HL		21.2	22.4	ca 16	ca 20		

orbit/HL	37.1	35.0	32.2	ca 26			25.9
interorbital	49.0						
snout/HL	24.5	22.9	25.7	24.2			23.4
pmax/HL	55.1	54.8	49.8	49.4	ca 48	54.3	47.7
mandible/HL	48.2	51.1	45.3	43.7	ca 46	53.7	46.3
go/HL	above P?	17.8	14.7				
mand-anus/HL	69.4	70.6	53.9	66.3			
sn-anus/HL	84.1	87.6	70.6				
UPL/HL	58.8	67.8	83.3	50.0	ca 52		~54
LPL/HL	57.1	52.2	62.4	□31.6			41.0
PreD/HL	138.8	120.1	126.1	130.0	~135	149.6	~114
PreA/HL	218.0	187.0	185.7	211.0	~184		~194
anus-A/HL	127.8	99.4	113.5	141.4			
chin pores/HL	2.8	5.4	5.7				
LLW/HL	17.6	22.6	20.4				~10
LPL/UPL	97.2	77.1	75.0				~75

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604

Table 2. Selected counts and ratio ranges for Mariana liparid specimens and comparison species. Blanks represent unavailable data. § Indicates values calculated from HL ratios. Abbreviations are defined in Table 1.

Character	<i>P. kadadakeleguak</i>	<i>P. marianae</i>	<i>P. echongpachot</i>	<i>P. atramentatus</i>	<i>P. hawaiiensis</i>	<i>P. mandibularis</i>	<i>P. meridionalis</i>
Data source	This paper	This paper	This paper	Kido, 1988	Stein & Drazen, 2014	Kai et al., 2020	Kido, 1985
Mouth angle	horizontal	horizontal	oblique	horizontal	horizontal	strongly oblique	Horizontal
SL (mm)	135	128-172	>140->228	69-71	132-ca 141	104-128	127-149
Vert	67	66-69	>62->69	57-58	68-69	63-66	66-68
D	62	62-65	>63	52-53	62	58-61	60-62
A	55	54-56	>55	46	55	52-54	54-56
C	8 (4/4)	9 (1+4/4 or 5/4)		8	7	6	8
P	L 26 (17/5/4) R 26 (17/5/4)	L 22 (13/6/3) R 23 (14/5/4, 15/5/3)	L 22-23 (13-15/4-6/3-4) R 22-23 (14-16/4-5/3-4)	ca. 22-26	L 20-21 (13-14/3/4) R 20 (13-14/3/3-4)	27-30	21-23 (14-16/4/3)
Chin pores	pit/skin fold	pit/skin fold		widely separated	touching, in a pit	widely separated	close, not in a pit
Radials	4 (3+1, 3 notched)	4 (3+1)	4 (3+1) or 5 (1+1+1+1+1), R3 notched or not		3 (2+0+1)	4 (1+1+1+1)	
Body color	translucent brown	translucent brown	dark brown or black	black or dusky	translucent brown	pale, fins dusky	dusky
Branchial color	brownish	pale	brown or dusky black	black or dusky	dusky	pale dotted	dusky
Mouth color	dusky, pale tongue	pale	dusky brown or blackish, pale tongue	dusky	dusky	pale dotted	dusky
Peritoneum color	dark brown	dark brown	black-brown	black	black or dusky	black	black
Pyloric caeca color	dark gray	pale or dark gray	grayish or greenish	pale	pale	pale	pale
HL/SL	18.1	19.1-20.6		18.7	16.3	18.0-20.7	17.4-18.8
HW/SL	14.8	14.2-15.8		10.3	12.4	9.0	9.3-9.9
Eye/SL		4.3-4.4			4.8		4.5-5.7§
Orbit/SL	6.7	6.2-7.2			5.6	4.4-6.0	
Snout/SL	4.4	4.7-4.9			4.2	5.6-6.9	4.5-5.2§
Upper jaw/SL	10.0	9.5-11.3			8.3	9.7-11.1	8.1-8.7§
Lower jaw/SL	8.7	8.7-10.5			6.4		7.8-8.6§
Gill opening/SL	above pectoral fin?	2.8-3.7		above pectoral fin	above pectoral fin	6.9-10.5	2.7-3.8§ short, above pectoral fin
Mandible-anus/SL	12.6	10.3-14.5			15.6		14.8-15.9§
Snout-anus/SL	15.2	13.5-18.0			19.2	12.0-18.8	15.2-17.0§
UPL/SL	10.7	13.9-15.9			13.6	21.6-26.0	12.4-13.2§
LPL/SL	10.4	10.7-11.9			12.6	13.8-15.9	10.3-12.2§
Predorsal L/SL	25.2	24.1-24.7			26.0	19.7-23.7	
Preanal fin L/SL	39.6	35.5-38.5			39.0	31.8-36.1	
HW/HL	81.6	74.3-76.8			76.3		
Eye/HL		21.2-22.4	ca 16-ca 20	28.0	29.3	27.5	26.1-30.6
Orbit/HL	37.1	32.2-35.0	25.9-ca 26		34.4	23.2-29.0	
Snout/HL	24.5	22.9-25.7	23.4-24.2	28.8	25.6	27.4-34.6	25.6-29.6
Upper jaw/HL	55.1	49.8-54.8	47.4-54.3	43.9	51.2	51.8-56.3	46.2-48.2
Lower jaw/HL	48.2	45.3-51.1	43.7-53.7	41.7	39.5	47.3	44.7-47.6
Gill opening/HL	above P?	14.7-17.8		16.7 above pectoral fin		34.7-51.9 64.0	15.8-21.0 82.1-90.1
Mandible-anus/HL	69.4	53.9-70.6	66.3		95.8		
Snout-anus/HL	84.1	70.6-87.6			117.7		84.7-96.9
UPL/HL	58.8	67.8-83.3	50.0-ca 55		83.7		68.7-73.9
LPL/HL	57.1	52.2-62.4	Ca 32-41.0	56.7	77.7		58.4-67.7
Predorsal fin L/HL	138.8	120.1-126.1	Ca 114-149.6		159.5		
Preanal fin L/HL	218.0	185.7-187.0	Ca 184-211.0		239.5		
Anus-anal fin/HL	127.8	99.4-113.5	141.4				

Table 3. Liparid species known to have a variable number of pectoral girdle radials or other anomalies. Source cited is not necessarily original describer of the species, but rather the author of the data used below.

Species	Source	Girdles	Individuals	Radial number and arrangement
<i>Careproctus continentalis</i>	Andriashev & Prirodina, 1990: 11	6	5	3 (2+0+1), 2 (0+1+0+1), 1 (0+0+0+1)
<i>Careproctus guillemi</i>	Matallanas, 1998: 383		1	3 (1+0+2)
<i>Careproctus kidoi</i>	Knudsen & Moller, 2008: 179	15		usually 4 (3+1), but 5 (4+1), 3 (2+1), 2 (1+0+1)
<i>Careproctus patagonicus</i>	Matallanas & Pequeno, 2000: 520	1	1	1 (0+0+0+1), perforated
<i>Careproctus roseofuscus</i>	Kido, 1988: 149	2		3 (2+1+0) L, 4 (1+1+1+1) R
<i>Careproctus vladibeckeri</i>	Andriashev & Stein, 1998: 54	2	2	2 (1+0+0+1)
<i>Notoliparis stewarti</i>	Stein, 2016: 912		5	3 (2+0+1), 4 (1+1+1+1), or 5 (1+1+1+1+1)
<i>Paraliparis anarthractae</i>	Stein & Tompkins, 1989: 1	1	1	R1, R2 smaller than R4
<i>Paraliparis antarcticus</i>	Andriashev, 2003: 232	17	14	4 (3+1), 3 (2+0+1) in holotype
<i>Paraliparis australis</i>	Andriashev, 2003: 240	3		3? 4 (1+1+1+1) L, 2 (2+0+0) R
<i>Paraliparis charcoti</i>	Chernova, 2006: S13		4	5 (1+1+1+1+1) or usually 3 (2+0+1)
<i>Paraliparis devriesi</i>	Andriashev, 2003: 267	14		10 2 or 4, also 2 (0+1+0+1)
<i>Paraliparis echangpachot</i>	Stein & Mundy, (this paper)	4	4	5 (1+1+1+1+1), 4 (3+1)
<i>Paraliparis garmani</i>	Kido, 1988: 149		2	1 3 L, 5 R radials
<i>Paraliparis hureaui</i>	Matallanas, 1999: 1021	1		1 4 (3+1), R3, R4 D-shaped at girdle rear edge
<i>Paraliparis incognita</i>	Andriashev, 2003: 294	9		7? 3 radials except one fry with 4 radials
<i>Paraliparis kocki</i>	Chernova, 2006: S3		3	3 radials 4 (3+1), 3 (2+1), 5 (4+1)
<i>Paraliparis mawsoni</i>	Andriashev, 2003: 315	4		4 holotype 4 (3+1), two others 3 (2+0+1)
<i>Paraliparis neelovi</i>	Duhamel et al., 2010: 326	3		3 4 (3+1), 3 (2+0+1)
<i>Paraliparis operculosus</i>	Duhamel et al., 2010: 327	2	2	4 (3+1), 3 (2+0+1)
<i>Paraliparis regina</i>	Andriashev & Chernova, 2010: 378	4		4 4 (3+1), 3 (2+0+1)
<i>Paraliparis stehmanni</i>	Stein, 2012: 99		2	2 4 (3+1), 5 (1+1+1+1+1)
<i>Paraliparis terraenovae</i>	Andriashev, 2003: 382	7	7	3 with anomalous radials
<i>Paraliparis trilobodon</i>	Andriashev, 2003: 365	10	8	4 (3+1), 3 (2+0+1)
<i>Paraliparis voroninorum</i>	Stein, 2012: 107		1	1 either 4 (3+1) or 3 (2+0+1)



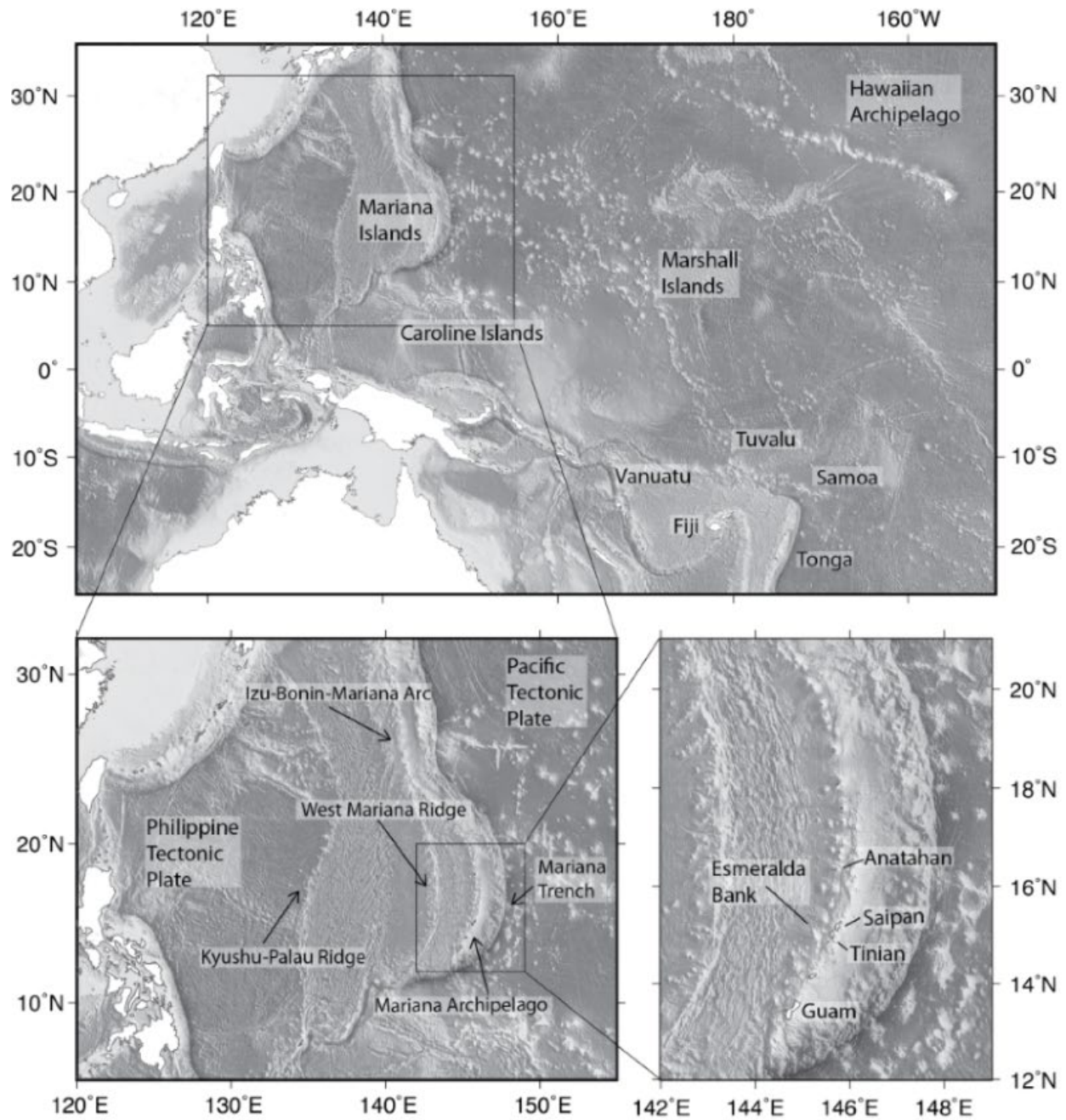


Fig. 1

Fig. 1. Geographic features and locations specified in this paper: a) the location of the Mariana Islands and other island groups in the western Pacific; b) the position of the Mariana

Archipelago relative to geologic features pertinent to its origin; c) the collection localities of the new species described in this paper (Anatahan, Esmeralda Bank, and Tinian).

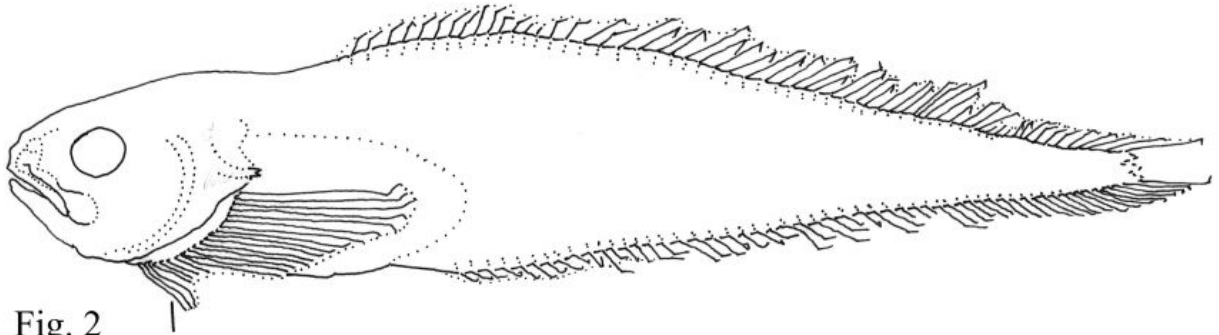


Fig. 2

Fig. 2. The female holotype of *Paraliparis echongpachot*, OS 20118 2/4, SL > 228 mm, 14°58.99' N, 145°10.84' E, west side of Esmeralda Bank west of Tinian Island, 1207 m. The total length and standard length of this specimen could not be measured because the posterior tip of the tail was missing.

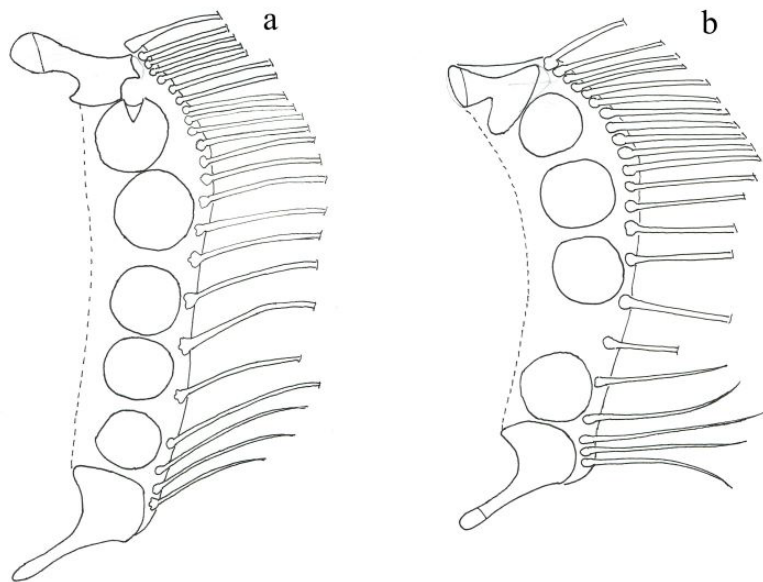


Fig. 3

Fig. 3. Pectoral girdles of *Paraliparis echongpachot* after dissection and clearing and staining, showing the proximal parts of the fin rays, the shape of the scapula (upper), the shape of the

654 coracoids (lower), and variation in the number and shapes of the pectoral-fin radials. (a)  
655 holotype, OS 20118 2/4, (b) paratype, OS 20118 1/4.

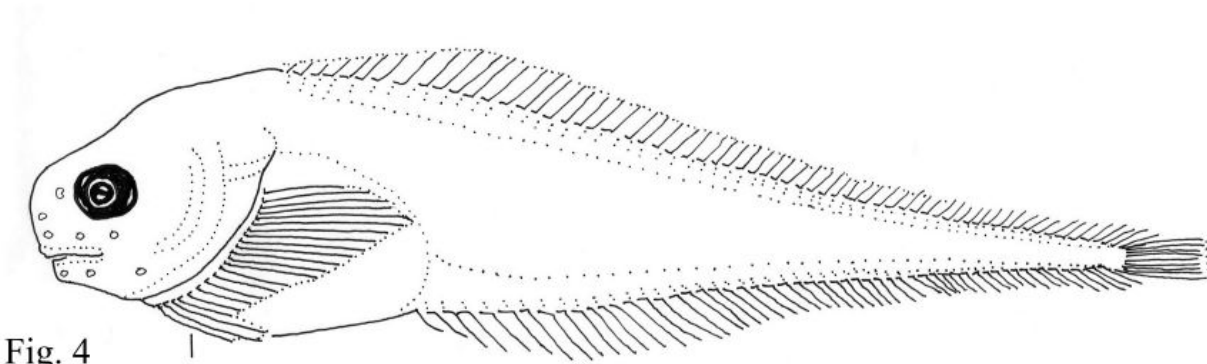


Fig. 4

656  
657 Fig. 4. Female holotype of *Paraliparis marianae*, OS 20115 2/2, TL 185, SL 172 mm, 15.0723°  
658 N, 145.5221° E, Tinian Island, Commonwealth of the Northern Mariana Islands, 903 m.

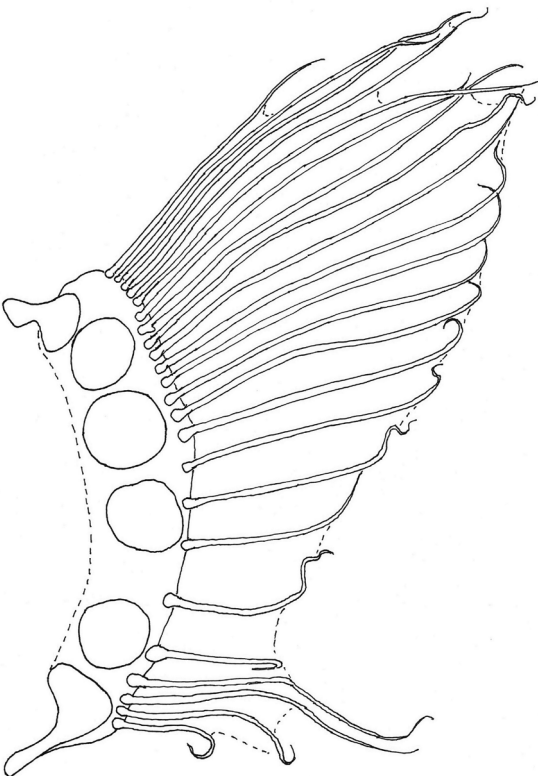


Fig. 5

Fig. 5. Pectoral girdle of the female holotype of *Paraliparis marianae* after dissection and clearing and staining, showing fin rays, the shape of the scapula (upper), the shape of the coracoids (lower), and variation in the number and shapes of the pectoral-fin radials.



Fig. 6. Photograph of ventral abdomen of paratype of *Paraliparis marianae*, OS 20115, TL 142, SL 128 mm, collected with holotype, showing pale parallel dashed lines on either side of ventral midline. A green dot marks each dash.

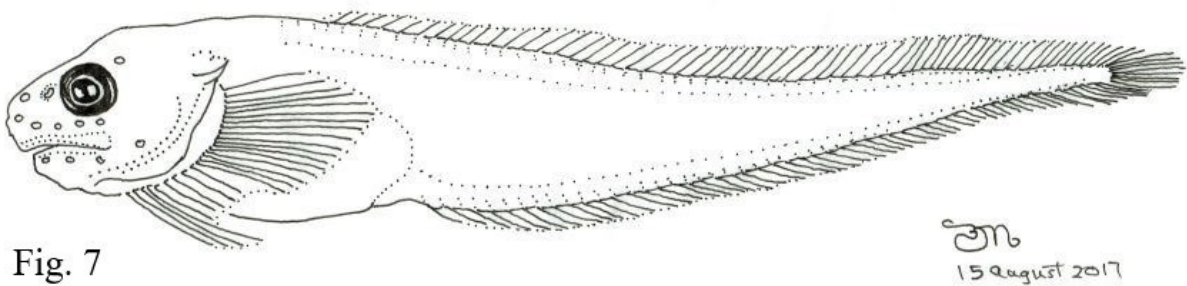


Fig. 7. Female holotype of *Paraliparis kadadakaleguak*, OS 20114 2/3, TL 143, SL 135 mm, 16°20.2' N, 145°44.9' E, Anatahan Island, Commonwealth of the Northern Mariana Islands, 1006 m.

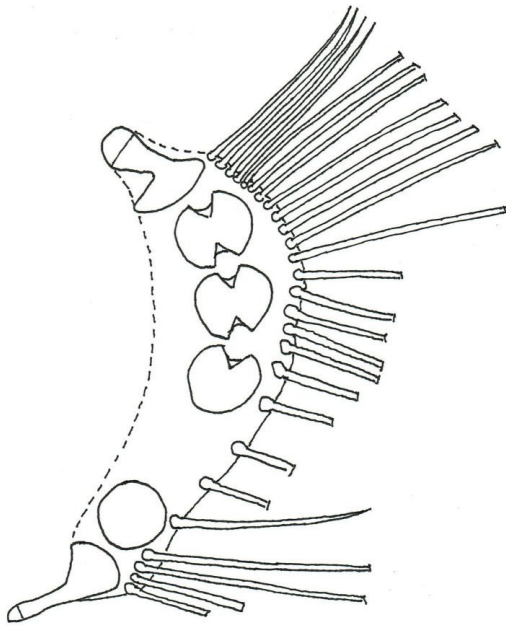


Fig. 8

Fig. 8. Pectoral girdle of the female holotype of *Paraliparis kadadakaleguak* after dissection and clearing and staining, showing the proximal parts of the fin rays, the shape of the scapula (upper), the shape of the coracoids (lower), and variation in the number and shapes of the pectoral-fin radials.