Revision of the Tubenose Poacher Genus *Pallasina* Cramer (Perciformes: Cottoidei: Agonidae)

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ABSTRACT

Species of the tubenose poacher genus *Pallasina* Cramer are assessed following examination of over 450 specimens from throughout the Pacific Rim, from the coast of California to the Chukchi Sea and Sea of Japan. The results presented here, including both morphological and mitochondrial DNA data sets, indicate that three species of *Pallasina* occur in the North Pacific and surrounding seas. *Pallasina aix* Starks is found in the eastern North Pacific from California to southeast Alaska, and in the Salish Sea. It has the shortest barbel of the three species, and a unique haplotype in the mitochondrial COI region. *Pallasina barbata* Steindachner is the most widespread species, ranging from the Gulf of Alaska to the Chukchi Sea and west to northern Japan. It is distinguished by having a moderate barbel length, and can be separated from the other two species using a variety of meristic characters. *Pallasina eryngia* Jordan and Richardson is found only in the central and northern Japanese Archipelago, and is a relatively deep-water species. It is distinguished by having a long barbel, as well as relatively high counts of vertebrae and dermal plates. This study presents redescriptions of all three species, and a key to their identification.

The agonid genus *Pallasina* Cramer, commonly known as tubenose poachers, contains three described species: *Pallasina barbata* (Steindachner, 1876); *P. aix* Starks, 1896; and *P. eryngia* Jordan and Richardson, 1907. Steindachner (1876) described the type species, as *Siphagonus barbatus*, based on specimens from the northern Bering Sea, Hakodate, and Nangasaki [sic], Japan. Cramer (in Jordan and Starks, 1895:815) established the genus *Pallasina* for this species, distinguishing it from *Brachyopsis* Gill, 1861, and by extension its junior synonym *Siphagonus* Steindachner, 1876, by the "long, *Syngnathus*-like body, and by the presence of a long barbel at the chin." Starks (1896) described *Pallasina aix* from specimens collected in Puget Sound, distinguishing it from *P. barbata* by the shorter barbel, the arrangement of prepelvic plates, and the narrower space between the abdominal ridges. The description of the third species, *Pallasina eryngia*, was based on a single specimen from the Sea of Japan, near Echigo (Jordan and Richardson, 1907). It was distinguished from *P. barbata* by its more slender body, longer barbel, and fewer pectoral fin rays.

Pallasina aix has been considered by most authors to be either a subspecies (Gilbert and Burke, 1912; Schultz, 1936; Barraclough, 1952; Hubbs et al., 1979; McAllister, 1990) or a junior synonym (Kanayama, 1991; Mecklenburg et al., 2002; Sheiko and Mecklenburg, 2004; Pietsch and Orr, 2015, 2019) of *P. barbata*. Although it has been widely recognized that specimens from the Salish Sea generally differ from more northern and western specimens in having a shorter (and less variable) barbel length, lower pectoral fin-ray count, and fewer median prepelvic plates, most previous authors have not considered these differences enough to warrant species status. However, Starks (1911) examined over 60 specimens from the San Juan Islands in Puget Sound, and considered *P. aix* to be distinct from *P. barbata* due to its larger eye (5% of length vs. 3.5% of length), less variable mandibular barbel length, and typically two median prepelvic plates.

Jordan et al. (1930) recognized both *P. barbata* and *P. aix*, stating, with regard to the type material of *P. barbata*, that "the locality of Nagasaki also mentioned is impossible" (Jordan et al., 1930:394), presumably because they thought the range of the species did not extend south beyond Hokkaido.

The status of *Pallasina eryngia* is somewhat less controversial. Although some authors have maintained its validity (Freeman, 1951; Kanayama, 1984; Lindberg and Krasyukova, 1987), most authors have considered it a junior synonym of *P. barbata* (e.g., Kanayama, 1991; Mecklenburg et al., 2002; Sheiko and Mecklenburg, 2004; Parin et al., 2014; Pietsch and Orr, 2015, 2019). Those who have considered *P. eryngia* a valid species have distinguished it from *P. barbata* by having a longer chin barbel.

Recently, molecular data have provided new insight into this taxonomic problem. Mecklenburg et al. (2016) examined mitochondrial COI gene sequences in several specimens of *Pallasina* from Alaskan waters, as well as three specimens from the Salish Sea. They found two haplotypes, differing by 2% sequence divergence, with one haplotype shared by all of the specimens from Alaska and the other shared by all three specimens from the Salish Sea. As they pointed out, this evidence suggests that *P. aix* and *P. barbata* are both valid species. No comparative sequence data for specimens of *P. eryngia* from Japan were previously available. Here we confirm the validity and redescribe all three species of the genus *Pallasina* on the basis of morphological and mitochondrial sequence data. We also document the distribution of all species and provide a key to their identification.

MATERIALS AND METHODS

Morphology.—Measurements and counts follow Kanayama (1991), including definitions of dermal plate series. Additional plate series are defined as follows: cheek plates, defined as the number of plates in the single antero-posterior row below the eye; pelvic-anal plates, defined as the number of paired ventrolateral plates between the base of the pelvic fin and the origin of the anal fin (a subset of the ventrolateral row); and prepelvic plates, defined as the pattern of plates on the ventral midline anterior to the pelvic base, anterior to posterior, where "1" indicates a single plate on the midline and "2" indicates a pair of plates straddling the midline (Fig. 1). Standard length (SL) is used throughout. Vertebral counts were determined using digital radiographs. Body measurements were made with digital calipers, and rounded to the nearest 0.1 mm. Institutional abbreviations are as listed at https://asih.org/standard-symbolic-codes. Meristic data are summarized in Tables 1 and 2; morphometric data are summarized in Table 3.

Distributions of meristic characters and arcsine-transformed morphometric ratios were tested to meet assumptions of normality using the Shapiro-Wilk normality test (shapiro.test in R) and Levene's test for homogeneity of variance (leveneTest in R); characters that did not violate these assumptions were subjected to ANOVA (meristics) or ANCOVA (morphometric ratios) to test for significant differences between species. Characters that did not meet the assumptions of normality or equality of variance were tested for significant differences among species means using the non-parametric Kruskal-Wallis test (kruskal.test in R). For characters in which a significant difference among species was indicated, pairwise t-tests were performed to determine which species means were significantly different (Table 3). All univariate analyses were performed in R, Version 3.6.1. Principal component analysis (PCA) was performed on a data set comprising only specimens for which all morphometric and meristic data were collected. Log-transformed morphometric data and raw meristic data were subjected to PCA using the "prcomp" command in the "stats" package in R. Differences between the species 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 4 and 5. All differences were considered significant at the 0.01 level, after Bonferroni correction for multiple tests. A linear discriminant function analysis (DFA) using the "lda" function in R was conducted with morphometric and meristic data to establish the relative significance of characters in distinguishing the species. Morphometric data were standardized by dividing values by SL or HL, and the variable loadings for the discriminant functions are listed in Table 6. The robustness of the DFA was tested with a leave-one-out cross-validation procedure conducted in R.

DNA Sequencing.—Total DNA was extracted from muscle tissue preserved in 99.5% ethanol, using the Wizard Genomic DNA Purification Kit (Promega Inc.), according to the manufacturer's protocols. The partial COI gene was amplified using the primers designed by Folmer et al. (1994) (LCO1490: 5'- GGT CAA CAA ATC ATA AAG ATA TTG G -3'; HCO2198: 5'- TAA ACT TCA GGG TGA CCA AAA AAT CA -3'). The PCR proceeded for 30 cycles, with denaturation at 94 °C for 15 sec, annealing at 45 °C for 15 sec and extension at 72°C for 30 sec, using the KAPA2G Robust PCR Kit (KAPA Biosystems). The PCR products were purified with ExoSAP-It (USB Corporation) enzyme. Automated sequencing was performed for both directions, using the BigDye terminator sequencing kit (Applied Biosystems), and analyzed on a model 310 Sequencer (Applied Biosystems). All sequences determined here have been deposited in DDBJ under Accession numbers LC491581–LC491585.

RESULTS

Morphology.—For nearly all meristic characters that exhibited interspecific variation, the range for *P. barbata* was intermediate between that of *P. aix* and *P. eryngia* (Tables 1–3). Vertebral counts were useful for distinguishing *P. aix* and *P. barbata* from *P. eryngia* (Table 1), but the distributions of vertebral counts for *P. aix* and *P. barbata* were very similar. The mean dorsal spine count was significantly higher for *P. aix* than for the other two species, mean anal-fin ray count was significantly lower for *P. eryngia* than for the other two species, and the modal pectoral-fin ray count for *P. barbata* was 12, while in the other two species the modal count was 11 (Tables 1, 3). Frequency distributions overlapped substantially for all dermal plate series (Table 2), but the mean plate counts differed significantly among all species for nearly all plate series (Table 3), and the ranges for *P. aix* were completely distinct from those of *P. eryngia* for many of the series. *Pallasina aix* was the only one of the three species that typically had five rows of prepelvic plates (typically six or seven in the other species), and *P. eryngia* was the only species that typically had 15 or 16 pelvic-anal plates (Table 2). The pattern of variation in all these series of dermal plates was the same, with *P. aix* having the fewest plates, *P. eryngia* having the most, and *P. barbata* intermediate between the two.

When meristics were combined in a multivariate PCA, the first principal component explained 76.3% of the total variation and was loaded most heavily on dorsolateral and ventrolateral plates (Table 4). The second principal component explained 8.7% of the total variation and was most heavily loaded on mid-ventral plates, followed by mid-dorsal and infralateral plates (Table 4). A plot of meristic PC1 vs. meristic PC2 (Fig. 2A) shows some separation among the three species along the PC1 axis, with *P. aix* and *P. eryngia* completely separated from each other, although both species overlap to some degree with *P. barbata*. The PC2 axis provided very little additional separation among the species.

Morphometric characters were generally less useful than meristics for distinguishing among species of *Pallasina* (Table 3). The exception to this was barbel length (Fig. 3). The barbel was long (49–157 % HL) in *P. eryngia*, shorter but highly variable in *P. barbata* (2–58 % HL), and very short in *P. aix* (<10% HL). Some of the other significantly different morphometrics (first dorsal-fin base length, anal-fin base length, pectoral-fin base length) appeared to be related to differences in fin ray counts, with higher mean fin ray counts correlated with longer fin base lengths. *Pallasina aix* had the shortest, deepest caudal peduncle, while *P. eryngia* had a significantly longer, shallower caudal peduncle, again with *P. barbata* falling in between. In general, *P. eryngia* had a more slender body than the other two species, with body width and depth being significantly less than in either *P. aix* or *P. barbata*.

In the morphometric PCA, the first principal component (the size component) explained 73.6% of the total variation. The two primary shape components (morphometric PC2 and PC3) explained 13.4% and 4.6% of the total variation, respectively. Morphometric PC2 was most heavily loaded on interdorsal distance, followed distantly by pelvic fin to anus distance, while PC3 was most heavily loaded on pelvic fin to anus distance and pelvic fin length (Table 5). A plot of morphometric PC2 vs. morphometric PC3 shows little separation among any of the species on either axis (Fig. 2B). A plot of meristic PC1 vs. morphometric PC2, combining the most explanatory shape components of both data sets, shows distinct clusters for each of the three species (Fig. 2C), although *P. aix* and *P. eryngia* are the only species pair that shows no overlap.

In the DFA, both discriminant functions were significant (Wilks' lambda; $P<0.0001$). All specimens of *P. eryngia* were distinguished from specimens of *P. barbata* and *P. aix* on the first discriminant axis, while the clusters of specimens of *P. barbata* and *P. aix* narrowly overlapped on the second axis (Fig. 4). The discriminant function analysis correctly classified 97.2% of the specimens, with three specimens of *P. aix* misclassified as *P. barbata*. The cross-validation procedure correctly classified 93.5% of the specimens; three specimens of *P. aix* were misclassified as *P. barbata*, three specimens of *P. barbata* were misclassified as *P. aix*, and one specimen of *P. eryngia* was classified as *P. aix*. Discriminant function 1 was heavily loaded on snout-to-anus length, snout length, predorsal length, anal-fin base length, head length, and caudal peduncle length; discriminant function 2, on head length, predorsal length, maxilla length, snout-to-anus length, pectoral-fin length, and caudal peduncle length (Table 6).

DNA Sequencing.— Sequence data from the mitochondrial COI (580 bp) gene were obtained for 14 specimens of *Pallasina* (nine sequences from BOLD, and the other five generated for this study). These specimens exhibited three distinct haplotypes (Table 6), with a maximum sequence divergence of 2% (12/580 bp); all putative substitutions were third codon position substitutions that did not result in translational changes. The most common haplotype (nine of 14 specimens) was shared by specimens collected from widespread localities, including the Gulf of Alaska, Chukchi Sea, Sea of Okhotsk, and Sea of Japan (Fig. 5). The second haplotype (two of 14 specimens) differed from the common haplotype by a single base pair, and was shared by two of the four specimens collected from the Sea of Japan. The third haplotype (three of 14 specimens) differed from the most common haplotype by 12 bp, and was shared by all three specimens collected from the Salish Sea.

Genus *Pallasina* Cramer 1895

Pallasina Cramer in Jordan and Starks, 1895:815. Type species: *Siphagonus barbatus* Steindachner 1876, by original designation.

***Diagnosis*.**— Species of the genus *Pallasina* differ from all other members of the family Agonidae in having the following combination of character states: two dorsal fins; gill membranes free from isthmus; lower jaw projecting anteriorly beyond upper; snout elongate, tubelike; barbel at anterior tip of lower jaw; first dorsal-fin spines IV–IX; and pectoral fin rays 10–13.

***Remarks*.**— Jordan and Starks (1895) used several generic names for the first time, including *Pallasina*. Although these genera are not explicitly listed as “n. gen.” unless they accompany the description of a new species, a statement in the introductory text of that paper clearly indicates that *Pallasina* and several other generic names “are here used for the first time” (p. 787).

***Pallasina aix* Starks, 1896**

Southern Tubenose Poacher

Figures 6A, 7A; Tables 1–3

Pallasina aix Starks, 1896:558. (Type locality: near Port Ludlow, Washington, Salish Sea. Holotype: CAS SU5040).

***Diagnosis*.**—A species of the genus *Pallasina* distinguished from its congeners by having a short chin barbel (< 10% HL in 84 of 84 specimens), and a unique COI haplotype (Haplotype 1 in Table 6). It is further distinguished from *P. barbata* by the combination of fewer pectoral fin rays (usually 11 vs. usually 12 in *P. barbata*) and fewer prepelvic plates (usually 5 rows vs. usually 6–7 in *P. barbata*); and from *P. eryngia* by the combination of fewer predorsal plates (10–12 vs. 12–15 in *P. eryngia*), dorsolateral plates (31–37 vs. 40–45 in *P. eryngia*), lateral line plates (44–

49 vs. 49–54 in *P. eryngia*), pelvic-anal plates (12–15 vs. 14–16 in *P. eryngia*), and vertebrae (43–48 vs. 48–52 in *P. eryngia*), as well as in several morphometrics.

***Counts and Proportions*.**—See Tables 1–3.

***Description*.**—Body elongate, nearly cylindrical, deepest near pectoral-fin base and tapering posteriorly to caudal peduncle, completely encased in dermal plates. Head elongate, conical, with narrow, protracted snout; single row of dermal plates on cheek. Mouth slightly upturned, positioned well anterior to orbit; lower jaw projecting beyond upper, with very short barbel extending anteriorly from dentary symphysis. Jaw teeth small, short, villiform, in 3–4 indistinct rows along most of premaxilla, expanding slightly near premaxillary symphysis, in 2–3 indistinct rows along most of dentary, expanding to 4–5 rows near dentary symphysis. Vomer with chevron-shaped patch of small teeth, interrupted along midline, with approximately 10–20 teeth on each side; palatine with approximately 5–15 small teeth arranged in single row. Eye round, its length 1/3 to 1/2 snout length; interorbital space narrow, distinctly concave, approximately half orbit diameter. Preopercular spines short, simple; first spine moderately pointed, extending posteriorly from posterior margin of preopercle on level of ventral margin of orbit; second spine shorter, more rounded, extending posteroventrally from preopercle; third spine present as small, rounded protuberance extending ventrally from preopercle. Upper opercular margin with strong posterior lobe; gill membranes free from narrow isthmus. Gill rakers short, rounded, rugose, 0–1 rakers on upper arch, 10–15 on lower arch.

Dermal plates organized into several longitudinal series on body (Table 2). Dorsolateral row (31–37 plates) extending bilaterally along dorsal surface of body from postoccipital region to caudal peduncle, merging posteriorly to form a single medial mid-dorsal row (7–13 plates), extending along dorsal midline to caudal fin. Supralateral row (31–35 plates) on lateral surface of body between dorsolateral row and lateral line, originating slightly anterior to first dorsal fin and extending to caudal fin. Lateral line row (44–49 plates) extending full length of lateral line, from upper opercular margin to caudal fin. Infralateral row (40–44 plates) on lateral surface of body ventral to lateral line, originating near pectoral-fin base and extending to caudal fin. Ventrolateral row (26–35 plates) extending bilaterally on ventral surface of body from pelvic-fin origin to caudal peduncle, merging posteriorly to form a single medial mid-ventral row (5–11 plates), extending along ventral midline to caudal fin. Prepelvic and prepectoral regions completely covered with dermal plates; 5 or 6 transverse rows of prepelvic plates, most commonly in a 1,2,1,1,2 pattern.

First dorsal fin short, rounded, originating well posterior to pelvic and pectoral fin origin, consisting of VI–IX flexible spines. Second dorsal fin short, rounded, consisting of 6–8 unbranched rays, separated from first dorsal fin by small gap. Anal fin longer than dorsal fins, originating approximately under posterior insertion of first dorsal fin, consisting of 10–12 unbranched rays. First dorsal-, second dorsal-, and anal-fin elements slightly exserted. Caudal peduncle elongate, narrow, its length 15–20 times its depth; caudal fin rounded. Pectoral fin broad, rounded, its dorsal insertion approximately even with middle of orbit, consisting of 11–13 rays; upper pectoral rays longest. Pelvic fins short, narrow, their bases touching on ventral midline. Anus immediately posterior to pelvic-fin bases. Lateral line originating near dorsal margin of opercle, slightly curving ventrally along body, and extending to caudal fin; lateral line canal opening through a single pore on each plate.

Coloration.—Dark, densely packed, brown to black chromatophores on dorsal surface of head and cheeks, extending ventrally to ventral margin of orbit; ventral surface of head and branchiostegal membranes unpigmented; chin barbel and lower jaw heavily pigmented. Dark, densely packed, brown to black chromatophores on dorsal and upper lateral surfaces of body, extending ventrally to middle of pectoral fin base; ventral surface of body unpigmented anteriorly, with scattered dark chromatophores near anterior anal fin base, becoming denser along anal fin; entire body surface heavily pigmented posterior to anal fin base. First and second dorsal fins with dark chromatophores sparsely arranged on membranes, more densely packed along spines and rays, and denser near distal margin; anal fin with sparsely arranged chromatophores along rays, membranes unpigmented; caudal fin heavily pigmented on both rays and membranes. Pectoral fin heavily pigmented with chromatophores arranged on dorsal-most rays, becoming less dense along ventral rays, membranes unpigmented; pelvic fins unpigmented, or sparsely pigmented distally along rays.

Distribution.—All specimens examined were collected in the eastern North Pacific, from California to southeast Alaska, and in the Salish Sea (Fig. 5). Specimens examined here were generally collected in shallow water, ranging from the intertidal zone to 63 m.

Pallasina barbata **(Steindachner, 1876)**

Tubenose Poacher

Japanese name: yagi-uo

Figures 6B, 7B; Tables 1–3

Siphagonus barbatus Steindachner, 1876:188 (Type locality: Bering Sea; Hakodate and Nagasaki, Japan. Syntypes, 2: NMW 12103, NMW 19835).

Diagnosis.—A species of the genus *Pallasina* distinguished from its congeners by having a moderate chin barbel (length 10–50 % HL in 77 of 86 specimens). It can further be distinguished from *P. aix* by COI haplotype (Haplotype 2 in Table 6), as well as a combination of relatively high counts of pectoral-fin rays (usually 12 vs. usually 11 in *P. aix*) and prepelvic plates (usually 6 rows vs. usually 5 rows in *P. aix*); and from *P. eryngia* by having a combination of fewer predorsal plates (11–13 vs. 12–15 in *P. eryngia*), dorsolateral plates (33–43 vs. 40–45 in *P. eryngia*), lateral line plates (45–52 vs. 49–54 in *P. eryngia*), pelvic-anal plates (12–15 vs. 14–16 in *P. eryngia*), and vertebrae (42–50 vs. 48–52 in *P. eryngia*), as well as several morphometric characters.

Counts and Proportions.—See Tables 1–3.

Description.—Body elongate, nearly cylindrical, deepest near pectoral-fin base and tapering posteriorly to caudal peduncle, completely encased in dermal plates. Head elongate, conical, with narrow, protracted snout; single row of dermal plates on cheek. Mouth slightly upturned, positioned well anterior to orbit; lower jaw projecting beyond upper, with short to long barbel extending anteriorly from dentary symphysis. Jaw teeth small, short, villiform, in 3–4 indistinct rows along most of premaxilla, expanding slightly near premaxillary symphysis, in 2–3 indistinct rows along most of dentary, expanding to 4–5 rows near dentary symphysis. Vomer with chevron-shaped patch of small teeth, interrupted along midline, with approximately 10–20 teeth on each side; palatine with approximately 5–15 small teeth arranged in single row. Eye round, its length 1/3 to 1/2 snout length; interorbital space narrow, distinctly concave, approximately half orbit diameter. Preopercular spines short, simple; first spine moderately pointed, extending posteriorly from posterior margin of preopercle on level of ventral margin of orbit; second spine shorter, more rounded, extending posteroventrally from preopercle; third spine present as small, rounded protuberance extending ventrally from preopercle. Upper opercular margin with strong posterior lobe; gill membranes free from narrow isthmus. Gill rakers short, rounded, rugose, 0–1 rakers on upper arch, 10–14 on lower arch.

Dermal plates organized into several longitudinal series on body (Table 2). Dorsolateral row (33–43 plates) extending bilaterally along dorsal surface of body from postoccipital region to caudal peduncle, merging posteriorly to form a single medial mid-dorsal row (6–13 plates), extending along dorsal midline to caudal fin. Supralateral row (32–38 plates) on lateral surface of body between dorsolateral row and lateral line, originating slightly anterior to first dorsal fin and extending to caudal fin. Lateral line row (45–52 plates) extending full length of lateral line, from upper opercular margin to caudal fin. Infralateral row (40–47 plates) on lateral surface of body ventral to lateral line, originating near pectoral-fin base and extending to caudal fin. Ventrolateral row (30–40 plates) extending bilaterally on ventral surface of body from pelvic-fin origin to caudal peduncle, merging posteriorly to form a single medial mid-ventral row (4–11 plates), extending along ventral midline to caudal fin. Prepelvic and prepectoral regions completely covered with dermal plates; 4–7 transverse rows of prepelvic plates, most commonly in a 1,2,1,1,1,2 pattern.

First dorsal fin short, rounded, originating well posterior to pelvic and pectoral fin origin, consisting of V–VIII flexible spines. Second dorsal fin short, rounded, consisting of 5–9 unbranched rays, separated from first dorsal fin by small gap. Anal fin longer than dorsal fins, originating approximately under posterior insertion of first dorsal fin, consisting of 9–13 unbranched rays. First dorsal-, second dorsal-, and anal-fin elements slightly exserted. Caudal peduncle elongate, narrow, its length 15–20 times its depth; caudal fin rounded. Pectoral fin broad, rounded, its dorsal insertion approximately even with middle of orbit, consisting of 10–13 rays; upper pectoral rays longest. Pelvic fins short, narrow, their bases touching on ventral midline. Anus immediately posterior to pelvic bases. Lateral line originating near dorsal margin of opercle, slightly curving ventrally along body, and extending to caudal fin; lateral line plates each opening through single pore.

Coloration.—No consistent coloration differences were detected among species of *Pallasina* – see description of *P. aix*.

Distribution.—Specimens examined were collected in the North Pacific from the Gulf of Alaska to Hakodate Bay in Japan, as well as the Bering Sea, Chukchi Sea, and Sea of Okhotsk (Fig. 5). Additional records from the Asian coast of the Sea of Japan (e.g., Lindberg and Krasyukova, 1987; Kanayama, 1991) may represent either *P. barbata* or *P. eryngia*. We found no representatives of this species from British Columbia, the U.S. west coast, or the Salish Sea. Specimens examined for this study were generally collected in shallow water, ranging from the intertidal zone to 36 m, but this species has been reported as deep as 128 m in the Bering Sea (USNM 59417: Love et al., 2005).

Remarks.—The type series of *P. barbata* includes two syntypes (NMW12103 and NMW 19835), both collected from Japanese waters, although in the original description Steindachner (1876:191) stated the locality as the Bering Strait, Hakodate, and Nangasaki [sic] in Japan. Sheiko and Mecklenburg (2004:18) stated that Steindachner's type series "evidently included specimens of both *barbata* and *aix*." In one of the syntypes (NMW 12103), presumably collected at "Nangasaki", although the label merely reads "Japan", the barbel length is very short (5.3% HL), the predorsal plate count is 12, the dorsolateral plate count is 35, the lateral line plate count is 46, the pelvic-anal plate count is 13, and the vertebral count is 46. All of these characters match the form distributed widely around the Pacific Rim from Alaska to northern Japan, and commonly recognized as *P. barbata*. In the other syntype (NMW 19835), collected at Hakodate, the barbel is much longer (55.1% HL), the predorsal plate count is 13, the dorsolateral plate count is 43, the lateral line plate count is 50, the pelvic-anal plate count is 15, and the vertebral count is 51. These characters match the form found only in Japanese waters, and later described by Jordan and Richardson (1907) as *Pallasina eryngia*. Thus, Steindachner's syntypes do indeed represent two separate species, but the second specimen (NMW 19835) is referable to *P. eryngia*, not *P. aix*.

There are two additional issues with Steindachner's description. The first is the stated locality of "Nangasaki", by which presumably the author meant Nagasaki, a large port city in the East China Sea in southern Japan. However, as first pointed out by Jordan et al. (1930), this locality is highly unlikely. The southernmost locality confirmed for any species of *Pallasina* examined for this study is near Kurobe in the Sea of Japan, over 500 km to the northeast of Nagasaki. Therefore, the collection locality of the remaining syntype of *P. barbata* remains uncertain.

The other issue with Steindachner's description is that the accompanying illustration (Steindachner, 1876:plate LXXIV) does not appear to faithfully represent either of the syntypes. The barbel length in the illustration is approximately 21% HL (vs. 5% and 55% HL in the two syntypes), and the prepelvic plates are preceded by a single plate in the illustration (vs. a pair of plates in both syntypes). However, the pelvic-anal, predorsal, and dorsolateral plate counts match those of NMW 12103, differing from the counts of NMW 19835, and thus the former specimen was more likely used as the basis of the illustration.

We hereby designate NMW 12103 as the lectotype of *Pallasina barbata*. Of the two syntypes, this specimen represents the species that agrees most closely with the accepted taxonomic application of the name (ICZN Recommendation 74A), and it most likely represents the specimen that served as the basis for the original illustration (ICZN Recommendation 74B). The other syntype (NMW 19835) represents *Pallasina eryngia*, and should be removed from the type series.

Pallasina eryngia **Jordan and Richardson, 1907**

Japanese name: higenaga-yagi-uo

Figures 6C, 7C; Tables 1–3

Pallasina eryngia Jordan and Richardson, 1907:264 (Type locality: Echigo, Japan. Holotype: CAS SU 20165).

Diagnosis.— A species of the genus *Pallasina* distinguished from its congeners by having a long chin barbel (>50% HL in 17 of 18 specimens), as well as a combination of relatively high counts of predorsal plates (12–15 vs. 10–13 in other *Pallasina*), dorsolateral plates (40–45 vs. 31–43 in other *Pallasina*), lateral line plates (49–54 vs. 44–52 in other *Pallasina*), pelvic-anal plates (14–16 vs. 12–15 in other *Pallasina*), and vertebrae (48–52 vs. 42–50 in other *Pallasina*).

Counts and Proportions.—See Tables 1–3.

Description.—Body elongate, nearly cylindrical, deepest near pectoral-fin base and tapering posteriorly to caudal peduncle, completely encased in dermal plates. Head elongate, conical, with narrow, protracted snout; single row of dermal plates on cheek. Mouth slightly upturned, positioned well anterior to orbit; lower jaw projecting beyond upper, with very long barbel extending anteriorly from dentary symphysis. Jaw teeth small, short, villiform, in 3–4 indistinct rows along most of premaxilla, expanding slightly near premaxillary symphysis, in 2–3 indistinct rows along most of dentary, expanding to 4–5 rows near dentary symphysis. Vomer with chevron-shaped patch of small teeth, interrupted along midline, with approximately 10–20 teeth on each side; palatine with approximately 5–15 small teeth arranged in single row. Eye round, its length 1/3 to 1/2 snout length; interorbital space narrow, distinctly concave, approximately half orbit diameter. Preopercular spines short, simple; first spine moderately pointed, extending posteriorly from posterior margin of preopercle on level of ventral margin of orbit; second spine shorter, more rounded, extending posteroventrally from preopercle; third spine present as small, rounded protuberance extending ventrally from preopercle. Upper opercular margin with strong posterior lobe; gill membranes free from narrow isthmus. Gill rakers short, rounded, rugose, 0–1 rakers on upper arch, 10–14 on lower arch.

Dermal plates organized into several longitudinal series on body (Table 2). Dorsolateral row (40–45 plates) extending bilaterally along dorsal surface of body from postoccipital region to caudal peduncle, merging posteriorly to form a single medial mid-dorsal row (5–9 plates), extending along dorsal midline to caudal fin. Supralateral row (36–40 plates) on lateral surface of body between dorsolateral row and lateral line, originating slightly anterior to first dorsal fin and extending to caudal fin. Lateral line row (49–54 plates) extending full length of lateral line, from upper opercular margin to caudal fin. Infralateral row (44–49 plates) on lateral surface of body ventral to lateral line, originating near pectoral-fin base and extending to caudal fin. Ventrolateral row (37–42 plates) extending bilaterally on ventral surface of body from pelvic-fin origin to caudal peduncle, merging posteriorly to form a single medial mid-ventral row (4–8 plates), extending along ventral midline to caudal fin. Prepelvic and prepectoral regions completely covered with dermal plates; 6–7 transverse rows of prepelvic plates, most commonly in a 1,2,1,1,1,2 pattern.

First dorsal fin short, rounded, originating well posterior to pelvic and pectoral origin, consisting of IV–VII flexible spines. Second dorsal fin short, rounded, consisting of 6–9 unbranched rays, separated from first dorsal fin by small gap. Anal fin longer than dorsal fins, originating approximately under posterior insertion of first dorsal fin, consisting of 8–11 unbranched rays. First dorsal-, second dorsal-, and anal-fin elements slightly exserted. Caudal peduncle elongate, narrow, its length 15–20 times its depth; caudal fin rounded. Pectoral fin broad, rounded, its dorsal insertion approximately even with middle of orbit, consisting of 11–12 rays; upper pectoral rays longest. Pelvic fins short, narrow, their bases touching on ventral midline. Anus immediately posterior to pelvic-fin bases. Lateral line originating near dorsal margin of opercle, slightly curving ventrally along body, and extending to caudal fin; lateral line canal opening through a single pore on each plate.

Coloration.— No consistent coloration differences were detected among species of *Pallasina* – see description of *P. aix*.

Distribution.—Specimens examined were collected in the Sea of Japan, from Toyama Bay on the west coast of Honshu to Cape Kamui on Hokkaido, and in the western North Pacific along the east coast of northern Honshu Island (Fig. 5). In contrast to the other two species of *Pallasina*, *P. eryngia* is generally found in deep water. Specimens examined for this study were collected at 75–231 m depth.

DISCUSSION

For decades, there has been debate about how many valid species of *Pallasina* should be recognized. In the most recent comprehensive treatments of the Agonidae, both Kanayama (1991) and Sheiko and Mecklenburg (2004) recognized *Pallasina* as a monotypic genus, including only *P. barbata*. This study provides morphological and molecular evidence which, in combination, indicates that all three nominal species in the genus are distinct and valid.

As first noted by Starks (1896), barbel length is an important character separating species of *Pallasina*. Although *P. barbata* and *P. aix* can be difficult to separate on this character alone, *P. eryngia* can be distinguished from the other two species using only barbel length, provided that the barbel is not damaged (Fig. 3). Barbel length was used to distinguish the species in both the original descriptions of *P. aix* (Starks, 1896) and *P. eryngia* (Jordan and Richardson, 1907), but later authors questioned the validity of this character. Kanayama (1991:115) examined a large sample of specimens from throughout the range of the genus, and noted that “the length of the lower jaw barbel varies, from very short or absent, off the coast of North America, to long in northern Honshu.” He interpreted this pattern as a continuous cline representing regional variation in a single species. While this is the same pattern noted here, Kanayama’s (1991:table 7) data on barbel length can alternatively be explained by the geographic distribution of the three species. Kanayama’s specimens from northern Honshu and parts of southern Hokkaido likely represent *P. eryngia*, while some of his material from northern Japan, Alaska, and the Bering Sea represent *P. barbata*, and his specimens from British Columbia likely represent *P. aix*. Likewise, the findings of Mecklenburg et al. (2016:117), who noted that the “chin barbel is as long as 33–56 % HL in specimens from the northern Bering Sea and Chukchi Sea and typically shorter to rudimentary in specimens from the southern Bering Sea and Gulf of Alaska,” are also consistent with our conclusions, as the specimens they examined were all within the geographic range of *P. barbata*, and the barbel lengths generally fall within the same range as the specimens of *P. barbata* that we examined.

Other morphological characters useful for distinguishing the species of *Pallasina* were also noted by previous authors. Starks (1896:560) remarked that *P. aix* differs from *P. barbata* “in having two median plates in front of ventrals in place of three”, which is equivalent to the character described here as prepelvic rows. Thus, the condition most typically found in *P. aix*, which is five prepelvic rows of plates, and can be described as “1,2,1,1,2”, denotes two median plates anterior to the posteriormost pair adjacent to the pelvic fins, as depicted in Figure 1. In contrast, both *P. barbata* and *P. eryngia* typically have six or seven rows of prepelvic plates, typically "1,2,1,1,1,2", which denotes three median plates anterior to the posterior pair. While there is a great deal of variation in the plate patterns found in these species, a simple count of prepelvic plate rows can be helpful in distinguishing *P. aix* from *P. barbata*.

The DNA barcode data currently available for these fishes, including sequence data generated for this study, provide additional evidence to corroborate the pattern indicated by morphological data. All specimens of *P. aix* for which sequence data are available ($n = 3$) share a single COI haplotype, differing from the other two known haplotypes found in *P. barbata* and *P. eryngia* by 2% sequence divergence. In a recent comprehensive study of snailfishes, Orr et al. (2019) found several congeneric species pairs that differed by less than 2% sequence divergence in the COI region. Similarly, all specimens of *P. barbata* ($n = 6$) share the same haplotype. Even if there is undiscovered haplotype diversity in these two species, the representative haplotypes surveyed here are different enough that the two species can be distinguished on the basis of their COI haplotype. Conversely, our sequence data for *P. eryngia* (n = 5) includes two haplotypes, the most common of which is identical to that found in *P. barbata*, and the two haplotypes differ only by a single base pair. Thus, although readily distinguished morphologically, *P. eryngia* cannot conclusively be distinguished from *P. barbata* on the basis of COI haplotype. The fact that these two species, which likely diverged only recently, can not be distinguished using COI sequences is not surprising. This phenomenon has been documented in closely related species of skates (Spies et al., 2006; Ward et al., 2008), as well as in bony fishes (Steinke et al., 2009a,b).

The overall morphological and genetic similarity among species of *Pallasina* is likely an indication that they have diverged very recently or possibly that there is still some genetic contact between them. For such similar species groups, the complimentary nature of morphological and molecular means of species delineation makes a combined approach particularly useful. In this case, the western North Pacific species (*P. eryngia*) is readily distinguished from the other two by morphological characters, while the two eastern North Pacific species (*P. aix* and *P. barbata*) are more similar morphologically. In contrast, the eastern North Pacific species (*P. aix*) is distinguishable from the other two species by as many as 11 fixed base pair differences within the COI gene, while the two western North Pacific species (*P. eryngia* and *P. barbata*) are much more genetically similar to each other, with no fixed base pair differences in this region.

The geographic distribution pattern for species of *Pallasina* is similar to that of the psychrolutid genus *Malacocottus*, with one eastern Pacific species in the Salish Sea region, a widely distributed northern species, and a western species in the Sea of Japan (Stevenson, 2015). The distribution of *P. eryngia* overlaps with that of *P. barbata* in the Sea of Japan, but *P. eryngia* has a much deeper depth distribution, preferring the outer shelf and upper continental slope, while its congeners are primarily found in shallow coastal and subtidal waters. Likewise, the distribution of *P. aix* may overlap with that of *P. barbata* in the eastern North Pacific, though our lack of material from the central Gulf of Alaska leaves this question open. Future collections of specimens and genetic material from both the Sea of Japan and the Gulf of Alaska may help to clarify the limits of distribution for the species of *Pallasina*, as well as the population demographics and evolutionary history of this genus.

KEY TO SPECIES OF *Pallasina*

1A Chin barbel elongate, usually greater than 50% head length; predorsal plates 12–15 (usually 13); dorsolateral plates 40–45; lateral line plates 49–54; pelvic-anal plates 14–16 (usually 15); vertebrae 48–52 .... ***Pallasina eryngia***

Sea of Japan, east coast of Honshu

1B Chin barbel variable in length, ranging from obsolete to 50% head length; predorsal plates 10–13 (usually 11 or 12); dorsolateral plates 31–43 (usually 31–40); lateral line plates 44–52; pelvic-anal plates usually 12–15 (usually 12–14); vertebrae 42–50 2

2A Chin barbel moderate in length, usually 10–50% head length; pectoral-fin rays usually 11; prepelvic plate rows usually 6 .... ***Pallasina barbata***

Gulf of Alaska to northern Japan; Bering Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan

2B Chin barbel obsolete or very short, <10% head length; pectoral-fin rays usually 12; prepelvic plate rows usually 5... ***Pallasina aix***

California to Gulf of Alaska; Salish Sea

MATERIAL EXAMINED

Pallasina aix (319 specimens): **Type**: SU 5040, Holotype, 103 mm, Salish Sea, near Port Ludlow. **Salish Sea**: BCPM 978-147, 86 mm, British Columbia, Satellite Channel; BCPM 978-165, 40 mm, Strait of Juan de Fuca, Sooke, Agate Beach; BCPM 978-170, 5, 45–55 mm, Strait of Juan de Fuca, Port Renfrew, 48.57°N, 124.4°W; BCPM 978-237, 6, 48–57 mm, west side of Portland I.; BCPM 978-238, 9, 42–67 mm, Sidney I.; BCPM 978-318, 2, 72–104 mm, James I., 48.65°N, 123.37°W; BCPM 978-332, 9, 68–80 mm, Vancouver I., Victoria, Ross Bay; BCPM

983-1570, 86, 50–65 mm, James I., 0–8 ft; SU 16503, 14, 57–69 mm, near Port Ludlow; SU 21365, 108 mm, Friday Harbor; SU 22264, 9, 45–65 mm, San Juan Islands; UW 553, 3, 38–46 mm, Friday Harbor; UW 28502, 2, 35–36 mm, San Juan I., Eagle Cove; UW 2976, 5, 40–57 mm, San Juan Archipelago, Lopez I., Iceberg Point; UW 3675, 78 mm, Strait of Juan de Fuca, Port Angeles; UW 5073, 80 mm, Edmonds, near Edwards Pt.; UW 14150, 63 mm, San Juan Archipelago, San Juan I., False Bay; UW 14156, 61 mm, San Juan Archipelago, off John's I.; UW 22066, 2, 42–48 mm, San Juan Archipelago, San Juan I., Eagle Cove; UW 28503, 103 mm, Skagit Bay; UW 28535, 45 mm, San Juan Archipelago, San Juan I., Deadman Cove; UW 40672, 79 mm, Port Townsend Bay; UW 48794, 101 mm, Discovery Bay, 48.08°N, 122.92°W, 17 fm; UW 119991, 121 mm, Strait of Juan de Fuca, 48.41°N, 124.32°W, 33–35 fm; UW 119992, 113 mm, off Lummi I., 48.71°N, 122.68°W, 7–13 fm; UW 158048, 111 mm, Puget Sound, 48.7°N, 122.651°W, 12 fm; UW 155862, 106 mm, Strait of Juan de Fuca, near Green Point, 48.12°N, 123.28°W. **Eastern North Pacific**: BCPM 948-005, 58 mm, British Columbia, Goose Island; BCPM 972-091, 59, 35–108 mm, Queen Charlotte Is., Graham I., Port Clements; BCPM 972-114, 2, 74–80 mm, Vancouver I., Ucluelet, Little Beach, 48.93°N, 125.55°W; BCPM 974-401, 4, 103–130 mm, British Columbia, head of Winter Inlet, 54.8°N, 130.42°W; BCPM 974-476, 125 mm, British Columbia, Griffith Harbour, 53.6°N, 130.53°W; BCPM 974-477, 11, 55–122 mm, British Columbia, Griffith Harbour, 53.6°N, 130.53°W; BCPM 975-667, 83 mm, British Columbia, Alert Bay, west of Turner I.; BCPM 977-179, 4, 43–61 mm, British Columbia, Hope Island, Roller Bay; BCPM 978-295, 4, 67–121 mm, Vancouver I., Ucluelet, Little Beach, 48.93°N, 125.55°W; BCPM 984-173, 2, 39–92 mm, British Columbia, Deer Island campsite; BCPM 984-505, 52 mm, British Columbia, Malcolm I., north of Port Hardy airport; BCPM 984-535, 117 mm, British Columbia, Malcolm I., near Port Hardy; BCPM 984-558, 50 mm, British

Columbia, Malcolm I., Malcolm Point; BCPM 984-562, 5, 50–62 mm, British Columbia, Malcolm I., near Port Hardy airport; BCPM 987-005, 68 mm, Vancouver I., Beaver Harbour; BCPM 987-007, 22, 57–78 mm, British Columbia, Malcolm I., Graeme Point; BCPM 987-025, 2, 58–105 mm, British Columbia, Deer I.; BCPM 988-798, 42 mm, British Columbia, Graham I., Masset Sound, 54°N, 132.14°W, 0–6 ft; BCPM 991-330, 107 mm, Queen Charlotte Is., Gowgaia Bay, 52.41°N, 131.6°W, 0–86 m; CAS 26307, 126 mm, California, Cleone Beach; CAS 28848, 52 mm, California, Arena Cove, 38.91°N, 123.72°W, 40–50 ft; CAS 59562, 41 mm, Oregon, off Gold Beach, 10 m; SU 61461, 120 mm, California, shallow bay N of San Francisco; UAM 4904, 2, 98–113 mm, Southeast Alaska, Samsing Cove, 56.98°N, 135.35°W; UAM 7737, 106 mm, Southeast Alaska, Auke Bay, 58.3°N, 134.72°W; UAM 7772, 130 mm, Southeast Alaska, Auke Bay, 58.34°N, 134.63°W; UAM 10065, 9, 33–48 mm, Southeast Alaska, Crab Bay, 57.74°N, 135.38°W; UW 1658, 89 mm, Alexander Archipelago, off Wrangell I., 15–20 fm; UW 2598, 107 mm, Alexander Archipelago, near Petersburg; UW 11732, 63 mm, Alexander Archipelago, False Bay; UW 11733, 94 mm, Alexander Archipelago, Frederick Sound; UW 14450, ?(damaged) mm, Queen Charlotte Is., Graham I., McIntyre Bay; UW 16532, 4, 64–71 mm, British Columbia, Porcher I., Oval Bay; UW 135045, 13 mm, British Columbia, Bamfield Marine Station, 48.84°N, 125.14°W.

Pallasina barbata (122 specimens): **Type**: NMW 12103, Lectotype, 117 mm, Japan. **Gulf of Alaska**: UAM 6268, 48 mm, Kachemak Bay, 59.617°N, 151.45°W, 2 m depth; UW 3903, 2, 84–90 mm, Cold Bay; UW 4206, 3, 82–97 mm, Wide Bay, 57.36°N, 156.35°W; UW 15575, 2, 112–120 mm, Cook Inlet, Kachemak Bay, 59.68°N, 151.21°W; UW 20690, 3, 109–133 mm, Kodiak I., Kaiugnak Bay, 57.07°N, 153.57°W; UW 22065, 3, 102–140 mm, Kodiak I., Ugak Bay, 57.50°N, 152.95°W; UW 28505, 122 mm, Trinity Is., 56.42°N, 154.31°W, 18 m; UW 28506, 113 mm, Wide Bay, 57.41°N, 156.27°W, 59 m; UW 28508, 2, 111–122 mm, Trinity Is., 56.42°N, 154.45°W, 18 m; UW 28509, 96 mm, Kodiak I., Ugak Bay. **Bering Sea**: BCPM 986-137, 100 mm, Norton Sound, 64.33°N, 164.23°W, 11 m; BCPM 986-142, 7, 95–120 mm, Norton Sound, 64.33°N, 162.26°W, 16 m; BCPM 986-152, 113 mm, Norton Sound, 64.66°N, 166.58°W, 15 m; BCPM 986-177, 130 mm, Norton Sound, 63.85°N, 162.37°W, 13 m; BCPM 986-178, 115 mm, Norton Sound, 64.5°N, 166.55°W, 22 m; BCPM 986-179, 125 mm, Norton Sound, 64.66°N, 166.99°W, 22 m; UW 28500, 128 mm, Bristol Bay; UW 28504, 107 mm, Norton Sound; UW28507, 137 mm, Norton Sound; UW 28511, 128 mm; UW 110393, 2, 96–98 mm, Port Moller, 55.71°N, 160.69°W; UW 110407, 114 mm, Port Moller, 55.8°N, 160.8°W, 15–20 m; UW 110416, 100 mm, Inner Port Moller Channel, 56°N, 160.55°W; UW 110426, 10, 77–129 mm, Inner Port Moller Channel, 56°N, 160.55°W; UW 110446, 79 mm, Port Moller; UW 112543, 87 mm, 57.99°N, 162.73°W; UW 113630, 106 mm, 58.33°N, 162.09°W; UW 114751, 113 mm, 59.36°N, 165.26°W; UW 119150, 71 mm, 59.64°N, 165.93°W, 25 m; UW 150314, 124 mm, 63.65°N, 161.57°W, 12 m; UW 150333, 53 mm, Bristol Bay, 58.846°N, 158.555°W; UW 150378, 2, 99–107 mm, Bristol Bay, 58.88°N, 160°W; UW 153878, 134 mm, southeastern Bering Sea; UW 112008, 128 mm, 59.17°N, 163.41°W; UW 150338, 50 mm, Bristol Bay, 58.59°N, 158.78°W; UW 150712, 96 mm, Norton Sound, 64.3°N, 161.53°W, 14 m; UW 200049, 7, 97–136 mm, Norton Sound, 64.33°N, 162.30°W, 19 m. **Chukchi Sea**: UAM 2923, 79 mm, 68.427°N, 166.829 °W, 25 m. **Western North Pacific**: FAKU 99548, 84 mm, Japan, Hokkaido, Akkeshi; SU 22325, 7, 76–109 mm, Russia, Kamchatka, Petropavlovsk; UW 40595, 88 mm, Kuril Islands, near Tanfilyeva I., 43.45°N, 145.96°E; UW 40599, 6, 46–68 mm, Kuril Islands, Shikotan I., Del'Fin Bay, 43.76°N, 146.64°E, 1 m; UW 42278, 107 mm, Kuril Islands, Shumshu I., 2 km south of Cape Pochtareva, 50.82°N, 156.51°E, 1 m. **Sea of Okhotsk**:

SU 5722, 4, 54–138 mm, Kuril Islands, Iturup I.; SU 26762, 5, 92–108 mm, Sakhalin I., Korsakov; UW 40593, 105 mm, Kuril Islands, Iturup I., east side of Chirip Pen., 45.34°N, 148.01°E, 1 m; UW 42286, 98 mm, Kuril Islands, Iturup I., east side of Chirip Pen., 45.34°N, 148.00°E, 1 m; UW 44793, 18, 32–77 mm, NW Sakhalin I., Sakhalinsky Bay, 53.47°N, 141.97°E, 1 m; UW 44930, 76 mm, Sakhalin I., W side of Cape Yelizavety, 54.39°N, 142.68°E, 1 m. **Sea of Japan**: SU 7862, 4, 71–87 mm, Hakodate, Sapporo.

Pallasina eryngia (18 specimens): **Type**: SU 20165, Holotype, 164 mm, Echigo, Japan. **Western North Pacific**: FAKU 97085, 173 mm, Japan, Iwate, Miyako, 75 m; NMW 19835 (former syntype of *Siphagonus barbatus*), 131 mm, Japan, Hakodate; SU 7861, 4, 71–100 mm, Japan, Aomori, Matsu Bay. **Sea of Japan**: FAKU 13586, 151 mm, Toyama Bay, Uozu; FAKU 13588, 128 mm, Toyama Bay, Uozu; FAKU 13589, 145 mm, Toyama Bay, Uozu; FAKU 132796, 158 mm, 38.42°N, 138.97°E, 170 m; FAKU 134400, 127 mm, Niigata, off Itoigawa; FAKU 136604, 148 mm, 39.65°N, 139.69°E, 231 m; FAKU 143190, 161 mm, 38.40°N, 138.91°E, 223 m; FAKU 145623, 152 mm, 38.41°N, 138.93°E, 210 m; FAKU 145624, 155 mm, 38.41°N, 138.93°E, 210 m; SU 26137, 2, 150–159 mm, Japan, Hokkaido.

COI sequence data (BOLD sequence ID or GenBank accession number within parentheses): *Pallasina aix*: UW 048794 (FMV 127-08), Puget Sound, 48.081°N, 122.92°W; UW 119991 (FMV 526-11), Strait of Juan de Fuca, 48.406°N, 124.322°W; UW 119992 (FMV 527-11), Puget Sound, 48.706°N, 122.676°W. *Pallasina barbata*: CAS 230148-1 (DSFAL 220-07), eastern Chukchi Sea, 67.004°N, 164.96°W, 28 m depth; CAS 230148-2 (DSFAL 223-07), eastern Chukchi Sea, 67.004°N, 164.96°W, 28 m depth; UAM 6268-1 (DSFAL 693-11), Gulf of Alaska, 59.617°N, 151.45°W, 2 m depth; UAM 6268-2 (DSFAL 694-11), Gulf of Alaska, 59.617°N, 151.45°W, 2 m depth; UAM 2923 (DSFIB045-11), eastern Chukchi Sea, 68.427°N, 166.829°W; SIO 05-184 (MFC368-08), Northwest Sakhalin Island, 53.468°N, 141.968°E. *Pallasina eryngia*: FAKU 132796 (LC491581), Sea of Japan, 38.42°N, 138.97°E; FAKU 134400 (LC491582), Sea of Japan, Niigata, off Itoigawa; FAKU 136604 (LC491583), Sea of Japan, 39.65°N, 139.69°E; FAKU 145623 (LC491584), Sea of Japan, 38.41°N, 138.93°E; FAKU 145624 (LC491585), 38.41°N, 138.93°E.

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FIGURE CAPTIONS

Fig. 1. Dermal plates in the prepelvic region of *Pallasina aix*. Rows with a single median plate are represented with a "1", while rows with paired medial plates are represented with a "2". Thus, the specimen illustrated here has five prepelvic plate rows, with a prepelvic plate count of "1,2,1,1,2."

Fig. 2. Plots of principal component (PC) scores for (A) meristic PC1 vs. meristic PC2, (B) morphometric PC2 vs. morphometric PC3, and (C) meristic PC1 vs. morphometric PC2 for *Pallasina aix* (open squares), *P. barbata* (dark circles), and *P. eryngia* (open triangles).

Fig. 3. Plot of head length vs barbel length for examined specimens of *Pallasina aix* (open squares), *P. barbata* (dark circles), and *P. eryngia* (open triangles).

Fig. 4. Plot of linear discriminant (LD) scores from discriminant analysis of species of *Pallasina*: *P. aix* (open squares), *P. barbata* (dark circles), and *P. eryngia* (open triangles).

Fig. 5. Geographic distribution of specimens examined and haplotypes for sequenced specimens of *Pallasina*: *P. aix* (dark squares); *P. barbata* (dark circles); *P. eryngia* (dark triangles); Haplotype 1 (open squares), Haplotype 2 (open circles), and Haplotype 3 (open triangles).

Fig. 6. Type specimens of species of *Pallasina*: (A) *Pallasina aix*, CAS SU5040, holotype, 103 mm; (B) *Pallasina barbata*, NMW 12103, lectotype, 117 mm; (C) *Pallasina eryngia*, CAS SU20165, holotype, 164 mm.

Fig. 7. Illustrations of type specimens of *Pallasina*: (A) *Pallasina aix* (after Starks, 1896); (B) *Pallasina barbata* (after Steindachner, 1876); and (C) *Pallasina eryngia* (after Jordan and Richardson, 1907).

Table 1. Frequency distributions of fin elements and vertebrae in *Pallasina aix*, *P. barbata*, and *P. eryngia*.

	First dorsal fin spines									Second dorsal fin rays							
	IV	V	VI	VII	VIII	IX	*n*	Mean	SD	5	6	7	8	9	*n*	Mean	SD
P. aix			4	33	9	2	48	7.2	0.6		5	29	14		48	7.2	0.6
P. barbata		6	23	34	8		71	6.6	0.8	1	8	33	23	4	69	7.3	0.8
P. eryngia	1	3	6	7			17	6.1	0.9		1	7	7	2	17	7.6	0.8

	Anal fin rays									Pectoral fin rays						
	8	9	10	11	12	13	*n*	Mean	SD	10	11	12	13	*n*	Mean	SD
P. aix			10	30	8		48	11.0	0.6		78	27	1	106	11.3	0.5
P. barbata		5	29	27	9	1	71	10.6	0.9	1	16	90	9	116	11.9	0.5
P. eryngia	1	6	8	2			17	9.6	0.8		17	1		18	11.1	0.2

	Vertebrae													
	42	43	44	45	46	47	48	49	50	51	52	*n*	Mean	SD
P. aix		2	14	12	15	5	2					50	45.3	1.2
P. barbata	1	1	1	10	19	18	13	9	1			73	46.8	1.5
P. eryngia							1	2	6	8	1	18	50.3	1.0

Table 2. Frequency distributions of dermal plates in *Pallasina aix*, *P. barbata*, and *P. eryngia*.

	Cheek Plates								
	3	4	5	6	7	8	*n*	Mean	SD
P. aix	1	2	14	25	6		48	5.7	0.8
P. barbata		8	29	21	13	1	72	5.6	1.0
P. eryngia			1	5	10	2	18	6.7	0.8

	Predorsal Plates								
	10	11	12	13	14	15	*n*	Mean	SD
P. aix	1	27	21				49	11.4	0.5
P. barbata		16	39	17			72	12.0	0.7
P. eryngia			1	12	4	1	18	13.3	0.7

	Dorsolateral Plates																
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	*n*	Mean	SD
P. aix	3	3	10	11	12	5	5									49	34.2	1.6
P. barbata			2	7	13	10	9	12	9	8		1	1			72	37.0	2.2
P. eryngia										2		7	5	3	1	18	42.6	1.3

	Mid-dorsal Plates											
	5	6	7	8	9	10	11	12	13	*n*	Mean	SD
P. aix			1	4	7	15	11	8	3	49	10.4	1.4
P. barbata		2	8	13	17	19	7	4	2	72	9.2	1.6
P. eryngia	2		6	6	4					18	7.6	1.2

	Total Dorsal Plates (Dorsolateral + Mid-dorsal)													
	42	43	44	45	46	47	48	49	50	51	52	*n*	Mean	SD
P. aix	2	7	13	16	8	3						49	44.6	1.2
P. barbata		1	8	13	21	15	9	3	2			72	46.2	1.5
P. eryngia							2	4	4	6	2	18	50.1	1.2

	Lateral Line Plates												
	44	45	46	47	48	49	50	51	52	53	54	*n*	Mean	SD
P. aix	1	10	15	11	7	3						47	46.5	1.2
P. barbata		1	10	14	20	13	9	3	1			71	48.1	1.5
P. eryngia						1	2	6	4	4	1	18	51.6	1.3

	Supralateral Plates											
	31	32	33	34	35	36	37	38	39	40	*n*	Mean	SD
P. aix	5	9	13	10	12						49	33.3	1.3
P. barbata		3	10	22	16	11	8	2			72	34.8	1.4
P. eryngia						1	2	6	5	4	18	38.5	1.2

	Infralateral Plates											
	40	41	42	43	44	45	46	47	48	49	*n*	Mean	SD
P. aix	4	13	19	7	6						49	42.0	1.1
P. barbata	4	5	16	12	16	15	3	1			72	43.3	1.6
P. eryngia					1	1	5	3	7	1	18	46.9	1.3

	Pelvic-Anal Plates							
	12	13	14	15	16	*n*	Mean	SD
P. aix	8	35	5	1		49	13.0	0.6
P. barbata	8	51	12	1		72	13.1	0.6
P. eryngia			2	11	5	18	15.2	0.6

	Ventrolateral Plates																			
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	*n*	Mean	SD
P. aix	1		1	1	2	9	18	8	7	2								49	32.0	1.7
P. barbata					2	1	6	6	12	10	10	13	7	3	2			72	35.3	2.3
P. eryngia												1	2	4	3	4	4	18	40.1	1.6

	Mid-ventral Plates									
	4	5	6	7	8	9	10	11	*n*	Mean	SD
P. aix		1	3	9	11	13	9	3	49	8.4	1.4
P. barbata	2	14	13	18	15	7	1	2	72	6.9	1.5
P. eryngia	1	4	6	5	2				18	6.2	1.1

	Total Ventral Plates (Ventrolateral + Mid-ventral)														
	36	37	38	39	40	41	42	43	44	45	46	47	48	*n*	Mean	SD
P. aix	1		4	4	14	16	6	4						49	40.5	1.4
P. barbata				3	5	17	18	10	16	2	1			72	42.2	1.5
P. eryngia									2	3	4	7	2	18	46.2	1.2

	Prepelvic Plate Rows						
	4	5	6	7	*n*	Mean	SD
P. aix		68	33	1	102	5.3	0.5
P. barbata	2	16	88	9	115	5.9	0.5
P. eryngia			9	9	18	6.5	0.5

Table 3. Proportional meristic characters and morphometric characters for *Pallasina aix*, *P. barbata*, and *P. eryngia*. Range followed by mean in parentheses; significance is reported as a *p* value for the ANCOVA (morphometrics) or ANOVA (meristics) followed in parenthesis by the results of the multiple comparisons test for differences among means (a = *P. aix*, b = *P. barbata*, e = *P. eryngia*, and * indicates the *p* value was obtained from the nonparametric Kruskal-Wallis rank-sum test).

	n	*P. aix*	*n*	*P. barbata*	*n*	*P. eryngia*	Significance
Standard length (mm)	93	33–130	98	42–138	18	71–173	
Total length (mm)	64	40–148	89	47–168	18	94–235	
Head length (mm)	84	9.4–30.5	86	10.2–35.6	18	16.9–38.4	
Meristics:							
First dorsal fin spines	48	6–9 (7.2)	71	5–8 (6.6)	17	4–7 (6.1)	<0.001 ($a^{b,e}$;b^{a};e^{a})*
Second dorsal fin rays	48	6–8 (7.2)	69	5–9 (7.3)	17	6–9 (7.6)	NS*
Anal fin rays	48	10–12 (11.0)	71	9–13 (10.6)	17	8–11 (9.6)	<0.001 (a^{e};b^{e};$e^{a,b}$)*
Pectoral fin rays	106	11–13 (11.3)	116	10–13 (11.9)	18	11–12 (11.1)	<0.001 (All)*
Vertebrae	50	43–48 (45.3)	73	42–50 (46.8)	18	48–52 (50.3)	<0.001 (All)*
Dermal plates:							
Cheek	48	3–7 (5.7)	72	4–8 (5.6)	18	5–8 (6.7)	<0.001 (a^{e};b^{e};$e^{a,b}$)*

Predorsal	49	10–12 (11.4)	72	11–13 (12.0)	18	12–15 (13.3)	<0.001 (All)*
Dorsolateral	49	31–37 (34.2)	72	33–43 (37.0)	18	40–45 (42.6)	
Mid-dorsal	49	7–13 (10.4)	72	6–13 (9.2)	18	5–9 (7.6)	
Dorsolateral + Mid-dorsal	49	42–47 (44.6)	72	43–50 (46.2)	18	48–52 (50.1)	<0.001 (All)*
Lateral line	47	44–49 (46.5)	71	45–52 (48.1)	18	49–54 (51.6)	<0.001 (All)*
Supralateral	49	31–35 (33.3)	72	32–38 (34.8)	18	36–40 (38.5)	<0.001 (All)*
Infralateral	49	40–44 (42.0)	72	40–47 (43.3)	18	44–49 (46.9)	<0.001 (All)*
Pelvic-anal	49	12–15 (13.0)	72	12–15 (13.1)	18	14–16 (15.2)	<0.001 (a^{e};b^{e};$e^{a,b}$)*
Ventrolateral	49	26–35 (32.0)	72	30–40 (35.3)	18	37–42 (40.1)	
Mid-ventral	49	5–11 (8.4)	72	4–11 (6.9)	18	4–8 (6.2)	
Ventrolateral + Mid-ventral	49	36–43 (40.5)	72	39–46 (42.2)	18	44–48 (46.2)	<0.001 (All)*
Prepelvic (rows)	102	5–7 (5.3)	115	4–7 (5.9)	18	6–7 (6.5)	<0.001 (All)*
Percentage of standard length:							
Head length	66	22.9–27.8 (25.2)	86	22.5–29.2 (24.8)	18	21.8–24.2 (23.0)	<0.001 (All)
Body width	38	5.9–11.5 (7.2)	61	5.0–11.6 (7.1)	18	4.3–5.8 (5.2)	<0.001 (a^{e};b^{e};$e^{a,b}$)*
Body depth	38	6.5–9.1 (7.3)	61	5.4–9.4 (6.9)	18	4.8–8.9 (5.8)	<0.001 (All)*

Predorsal length	38	39.9–46.2 (41.8)	61	37.6–45.6 (42.6)	18	39.9–44.2 (41.6)	<0.001 (a^{b};$b^{a,e}$;e^{b})
First dorsal-fin base length	38	11.9–16.5 (14.5)	61	10.3–16.7 (13.8)	18	9.7–14.3 (11.9)	<0.001 (a^{e};b^{e};$e^{a,b}$)*
Interdorsal length	38	1.4–6.3 (3.5)	60	0.6–6.8 (2.9)	18	2.1–6.2 (4.0)	<0.001 (b^{e};e^{b})
Second dorsal-fin base length	38	12.2–15.1 (13.5)	60	11.2–15.6 (13.5)	18	11.8–14.9 (13.0)	NS
Preanal length	38	49.1–55.5 (51.4)	61	46.8–55.5 (51.0)	18	49.1–54.7 (51.2)	NS
Anal-fin base length	38	18.2–22.9 (20.4)	61	16.2–22.7 (19.0)	18	14.0–17.9 (16.1)	<0.001 (All)
Snout to anus length	38	28.3–34.1 (31.8)	60	28.8–35.2 (31.0)	18	27.9–30.0 (28.9)	<0.001 (All)*
Prepelvic length	38	26.4–30.3 (28.2)	61	25.2–30.0 (27.9)	18	23.9–28.0 (26.7)	<0.001 (a^{e};b^{e};$e^{a,b}$)
Pelvic fin length	50	5.2–8.9 (7.2)	80	3.5–9.4 (6.4)	18	4.2–8.4 (5.8)	NS
Pelvic to anus length	38	2.0–6.5 (3.6)	60	1.9–6.5 (3.1)	18	1.6–3.3 (2.3)	<0.001 (All)*
Anus to anal fin length	38	17.8–24.3 (20.4)	60	14.6–23.7 (20.6)	18	20.5–25.9 (23.0)	<0.001(a^{e};b^{e};$e^{a,b}$)*
Pectoral fin length	38	15.0–17.3 (16.2)	61	13.8–18.8 (16.9)	18	12.6–17.2 (15.8)	<0.001 (a^{b};$b^{a,e}$;e^{b})
Pectoral-fin base length	38	2.6–4.0 (3.4)	61	2.8–4.3 (3.6)	18	2.7–3.6 (3.0)	<0.001 (All)*
Caudal peduncle length	38	25.1–31.1 (28.3)	61	25.4–34.3 (29.9)	18	30.4–36.3 (32.6)	<0.001 (All)
Caudal peduncle depth	38	1.2–2.1 (1.6)	61	1.1–1.7 (1.4)	18	1.0–1.8 (1.3)	<0.001 (a^{be};b^{a};e^{a})*
Caudal fin length	37	11.2–16.5 (14.1)	60	9.4–15.3 (12.9)	18	8.3–15.1 (12.5)	<0.001 (All)*
Percentage of head length:							

Snout length	38	37.4–43.9 (40.9)	61	30.3–45.4 (42.1)	18	39.8–49.3 (45.1)	<0.001 (All)*
Orbit length	38	13.7–19.0 (16.8)	61	12.6–19.8 (15.9)	18	13.5–18.5 (15.7)	NS
Postorbital head length	38	37.1–45.0 (41.7)	61	31.8–44.8 (41.5)	18	34.8–42.7 (39.5)	0.0015 (a^{e};b^{e};$e^{a,b}$)
Interorbital width	38	7.5–11.3 (9.2)	61	6.2–10.3 (8.3)	18	6.1–9.5 (7.8)	0.0067 (a^{be};b^{a};e^{a})
Maxilla length	38	21.7–25.1 (23.3)	61	17.7–27.3 (24.2)	18	20.4–24.6 (22.3)	<0.001 (All)
Barbel length	84	2.5–9.7 (5.5)	86	2.0–58.0 (15.2)	17	48.7–156.8 (102.9)	<0.001 (All)*

Table 4. Factor loadings for Principal Component Analysis (PCA) of meristic characters for *Pallasina aix* (*n* = 35), *P. barbata* (*n* = 57), and *P. eryngia* (*n* = 17).

	PC1	PC2	PC3
First dorsal fin spines	-0.058	0.068	0.045
Second dorsal fin rays	0.027	0.040	0.128
Anal fin rays	-0.048	0.067	0.241
Total vertebrae	0.313	0.305	0.019
Pectoral fin rays	-0.009	-0.071	0.013
Cheek plates	0.052	0.070	0.069
Lateral line plates	0.318	0.275	-0.124
Predorsal plates	0.106	0.078	-0.039
Mid-dorsal plates	-0.184	0.467	0.503
Dorsolateral plates	0.503	-0.174	-0.446
Supralateral plates	0.315	0.221	0.044
Infralateral plates	0.297	0.370	0.121

Ventrolateral plates	0.512	-0.238	0.486
Mid-ventral plates	-0.161	0.549	-0.440
Prepelvic plate rows	0.057	0.018	0.001
Pelvic-anal plates	0.120	0.113	-0.062

Table 5. Factor loadings for Principal Component Analysis (PCA) of morphometric characters for *Pallasina aix* (*n* = 35), *P. barbata* (*n* = 57), and *P. eryngia* (*n* = 17).

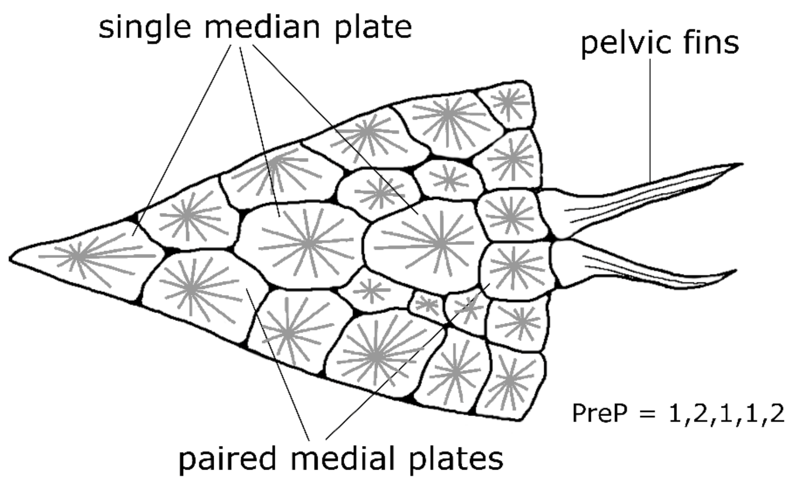
	PC1	PC2	PC3	PC4
Head length	-0.023	0.023	-0.004	0.046
Snout length	0.028	0.046	0.044	-0.076
Orbit length	-0.020	-0.040	-0.099	0.004
Postorbital head length	-0.017	-0.021	-0.017	0.078
Barbel length	0.970	-0.014	-0.146	0.161
Body width	-0.079	0.148	0.254	0.565
Interorbital width	-0.051	-0.088	-0.232	0.097
Maxilla length	-0.014	0.027	-0.022	-0.003
Body depth	-0.056	0.044	0.134	0.343
Predorsal length	-0.001	0.019	0.032	0.023
First dorsal fin length	-0.045	0.160	0.029	0.147
Interdorsal distance	0.027	-0.897	0.358	-0.044

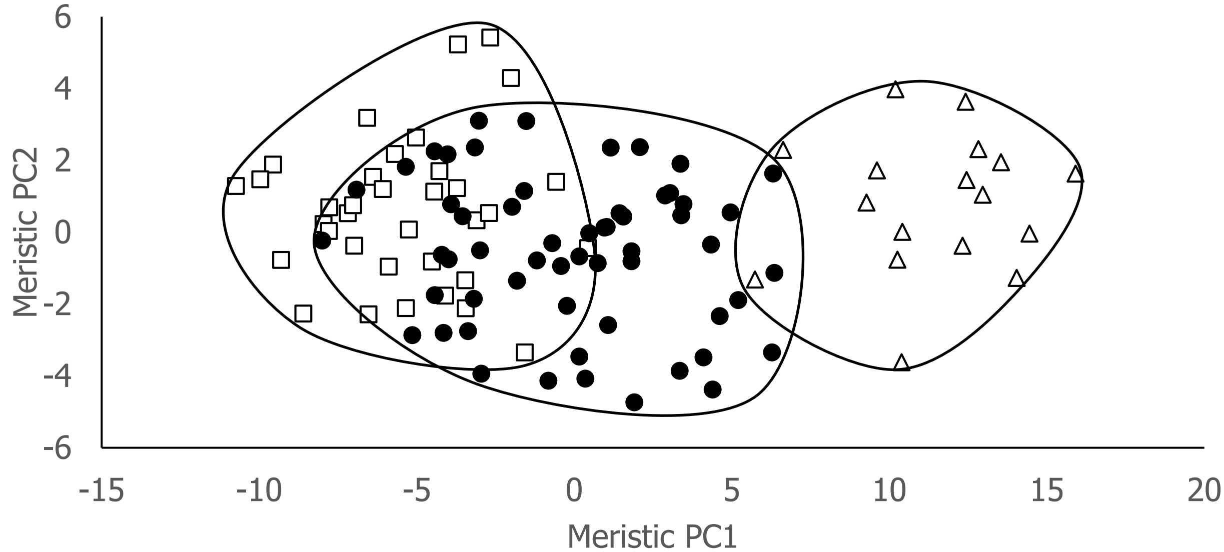
Second dorsal fin length	-0.014	0.022	-0.058	0.031
Pectoral fin length	-0.006	0.047	0.009	0.051
Pectoral fin base length	-0.029	0.094	0.130	0.191
Anal fin length	-0.069	-0.008	-0.040	0.109
Snout to pelvic base	-0.011	0.034	0.009	0.029
Snout to anus	-0.024	-0.010	-0.058	0.060
Preanal fin length	0.002	0.020	0.026	0.020
Pelvic fin length	-0.082	-0.012	-0.480	-0.379
Pelvic fin to anus	-0.142	-0.306	-0.626	0.456
Anus to anal fin	0.041	0.087	0.173	-0.045
Caudal peduncle depth	-0.067	-0.102	-0.104	0.231
Caudal peduncle length	0.037	-0.031	-0.036	-0.101
Caudal fin length	-0.037	-0.075	-0.102	0.120

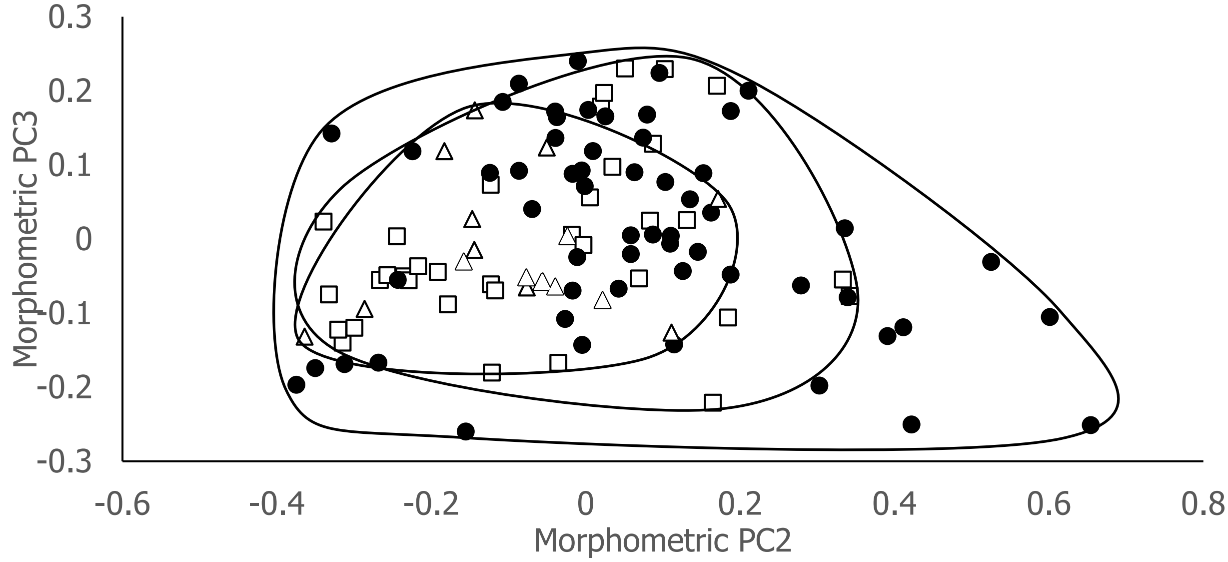
Table 6. Variable loadings for each of two linear discriminant (LD) functions in discriminant analysis of species of *Pallasina*.

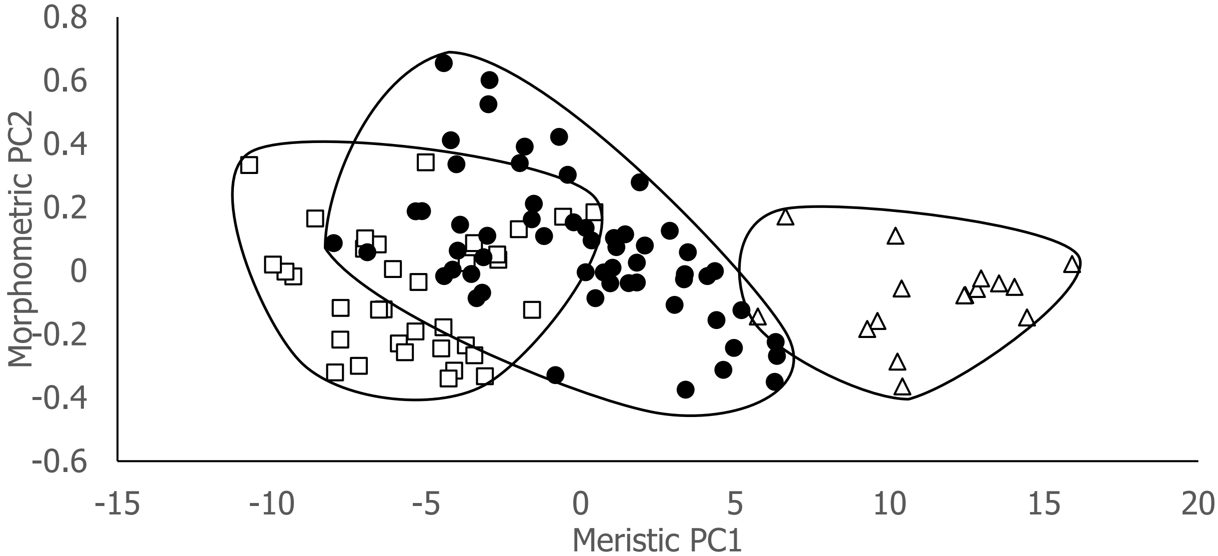
	LD1	LD2
Head length	58.094	39.241
Snout length	29.173	-7.727
Postorbital head length	4.462	-15.201
Barbel length	4.744	0.786
Body width	-17.365	-5.599
Interorbital width	16.392	-27.461
Maxilla length	-17.529	-49.990
Body depth	5.072	17.057
Predorsal length	-17.745	-32.494
First dorsal fin length	-0.937	2.162
Interdorsal distance	21.888	-13.806
Pectoral fin length	-18.020	-56.402
Pectoral fin base length	-26.673	-138.079

Anal fin length	-4.345	36.899
Snout to pelvic base	99.864	1.006
Snout to anus	-166.979	-30.065
Pelvic fin to anus	116.403	6.192
Anus to anal fin	-10.418	7.359
Caudal peduncle depth	109.113	177.605
Caudal peduncle length	-23.560	-13.686
Caudal fin length	-0.425	19.356
First dorsal fin spines	0.101	0.076
Anal fin rays	-0.645	-0.121
Total vertebrae	-0.117	0.357
Pectoral fin rays	-0.789	-1.328

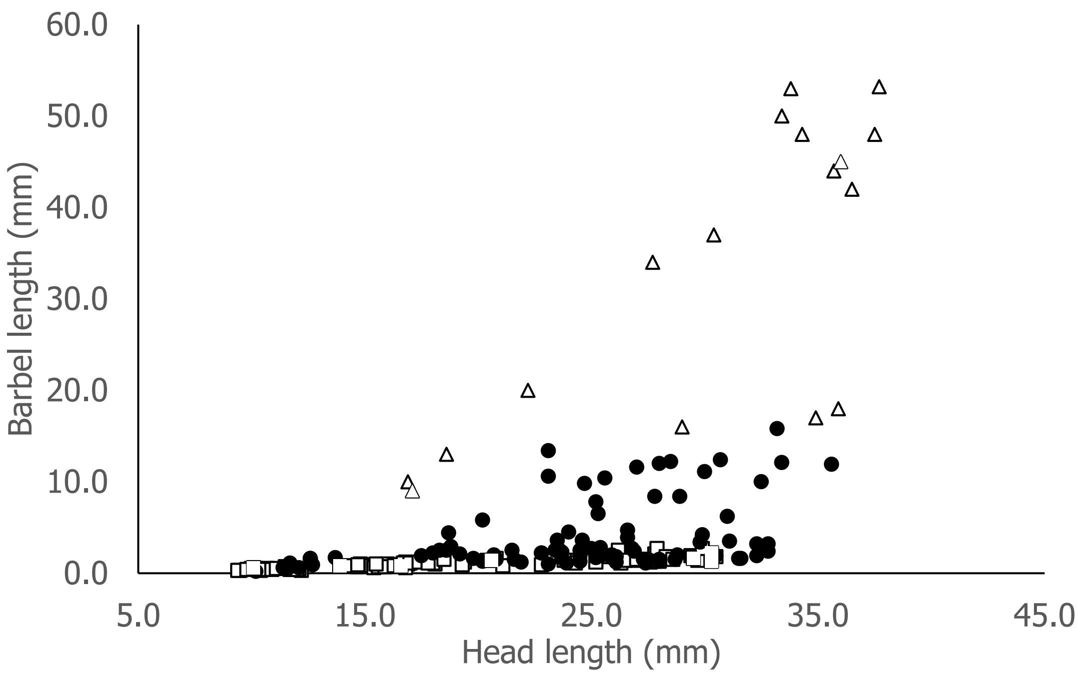

single median plate
pelvic fins
PreP = 1,2,1,1,2
paired medial plates


Meristic PC2
Meristic PC1
6
4
2
0
-2
-4
-6
-15
-10
-5
0
5
10
15
20

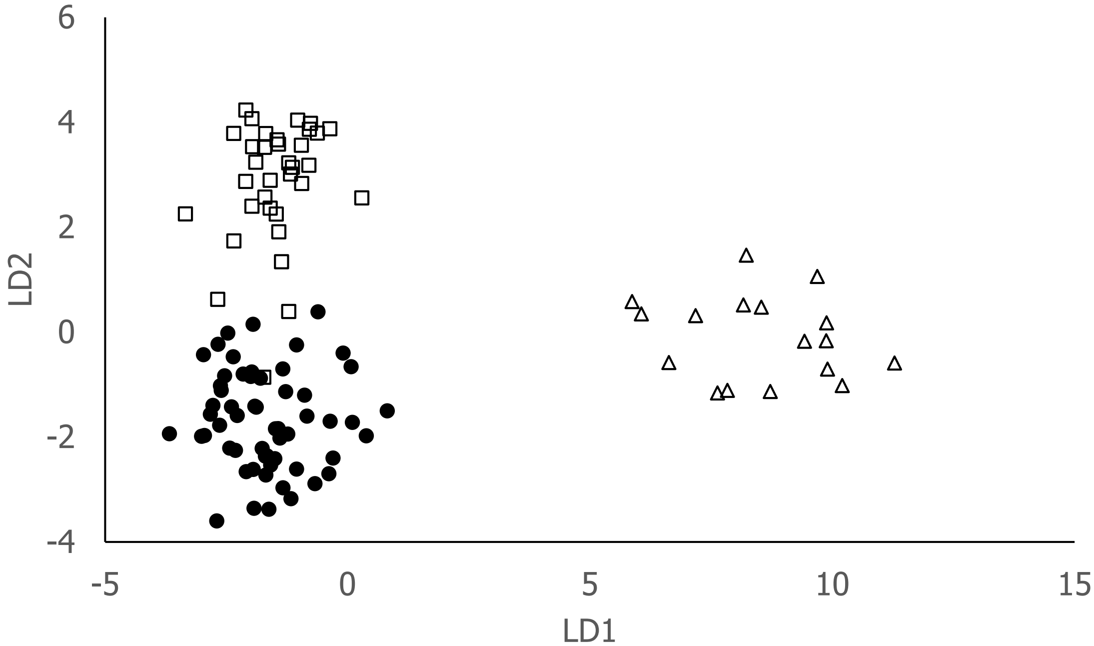

Morphometric PC3
Morphometric PC2
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8



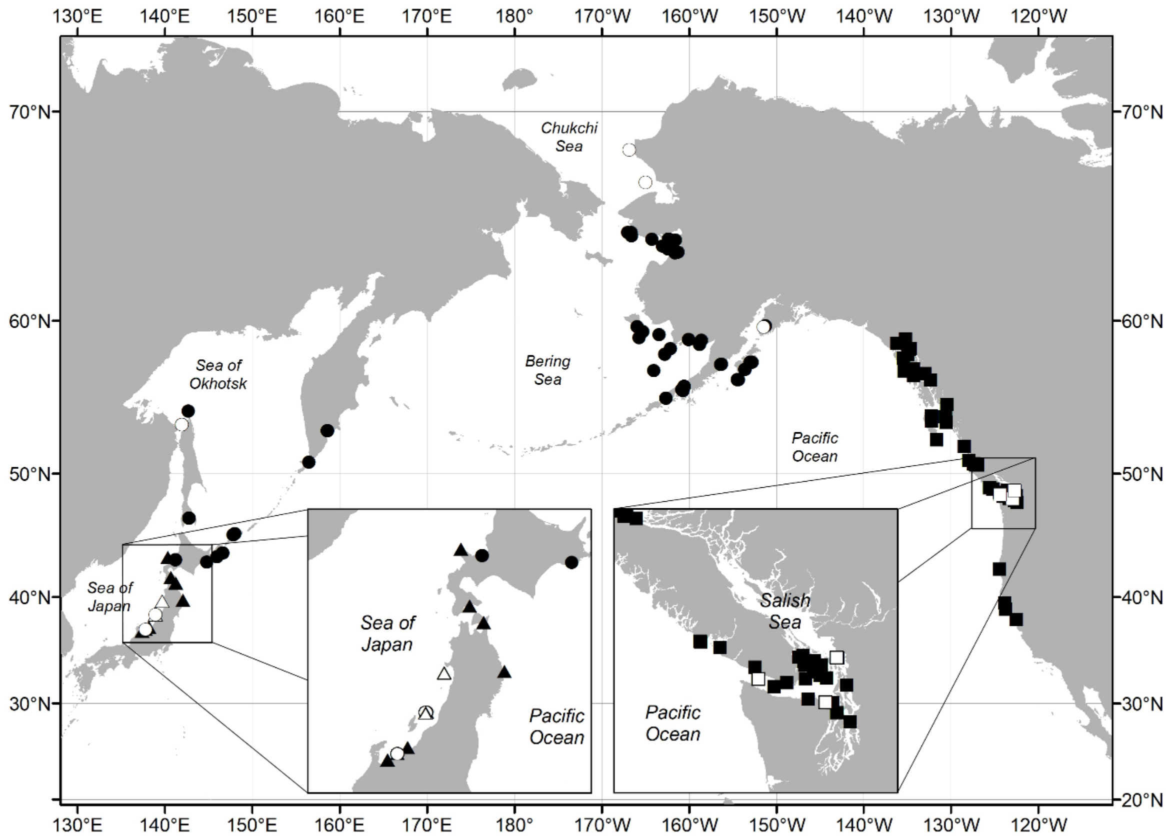
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Morphometric PC2
-15
-10
-5
0
5
10
15
20
Meristic PC1

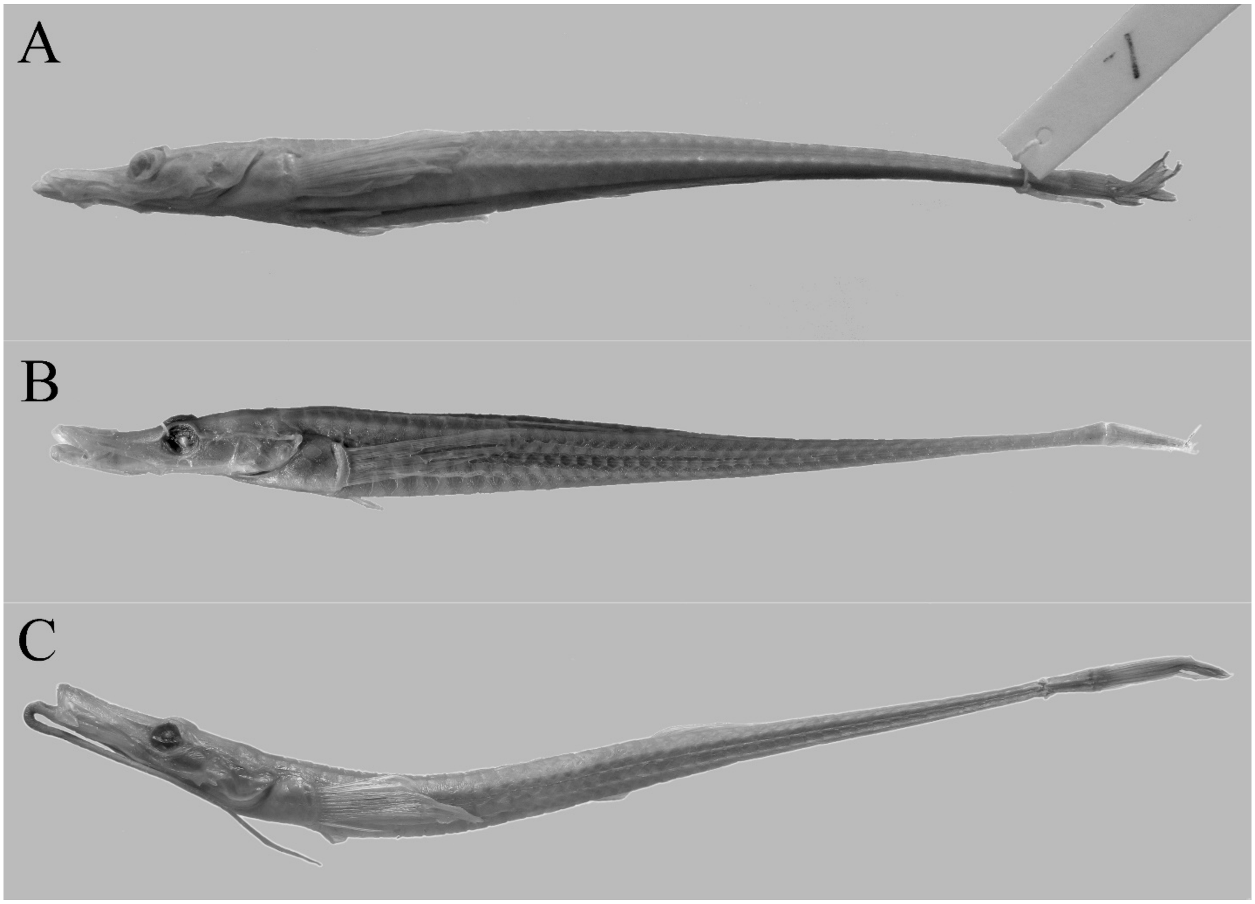


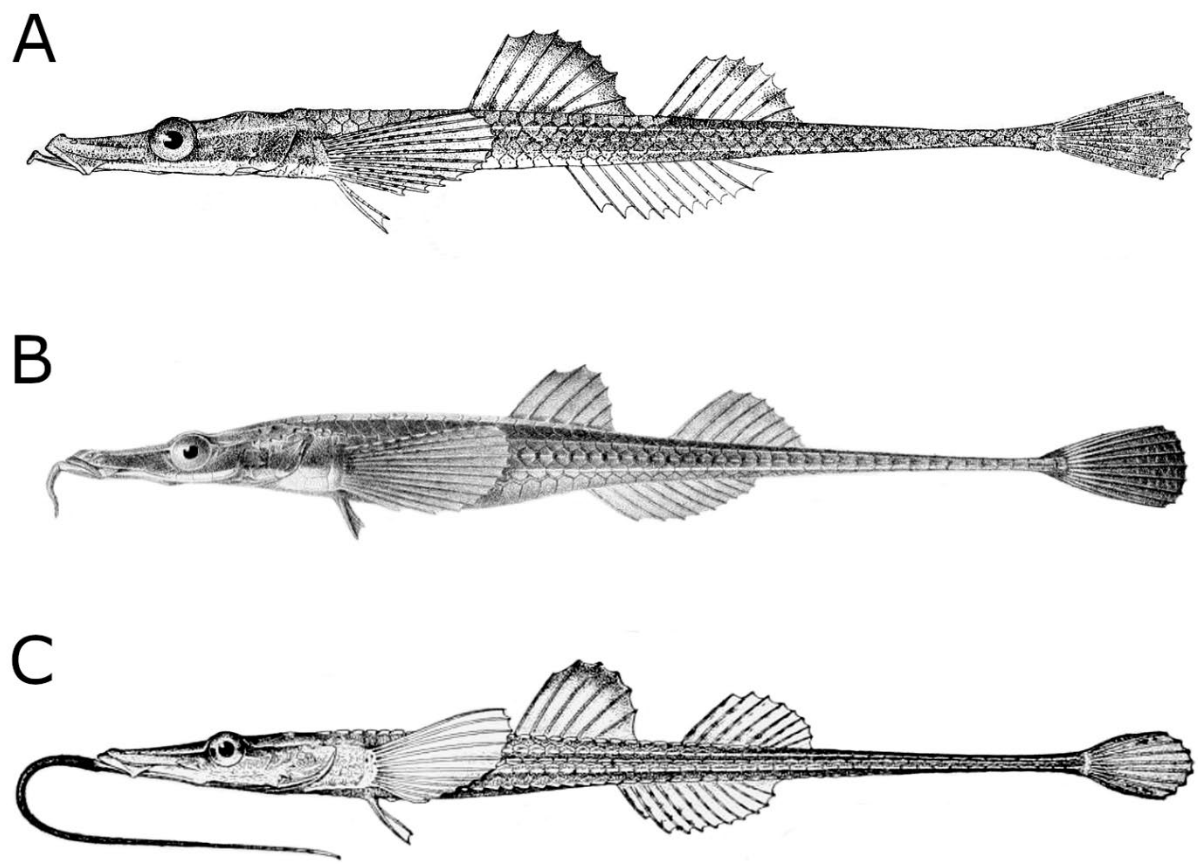
60.0
50.0
40.0
30.0
20.0
10.0
0.0
Barbel length (mm)
5.0
15.0
25.0
35.0
45.0
Head length (mm)



6
4
2
0
-2
-4
LD2
-5
0
5
10
15
LD1


130°E
140°E
150°E
160°E
170°E
180°
170°W
160°W
150°W
140°W
130°W
120°W
70°N
60°N
50°N
40°N
30°N
20°N
Chukchi Sea
Sea of Okhotsk
Bering Sea
Pacific Ocean
Sea of Japan
Sea of Japan
Pacific Ocean
Salish Sea
Pacific Ocean




A
B
C