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1 **A new species of *Zeuxo* (Crustacea: Peracarida: Tanaidacea) from Japan, with remarks**
2 **on carapace pigmentation as a potentially useful taxonomic character**

3

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10

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20

21 **Abstract**

22 We describe *Zeuxo ezoensis* sp. nov. from Hokkaido, Japan. This species closely resembles *Z.*
23 *phytalensis*, *Z. shitipingensis*, and *Z. turkensis* in having the pleopodal endopod with one inner
24 plumose seta, maxillipedal palp article 4 with one outer simple seta, the left mandible with a
25 wide, denticulate lacinia mobilis and one bifurcate accessory seta, and the right mandible with
26 a peg-like lacinia mobilis and two accessory setae. It differs from them in having (1) antennal
27 article 6 longer than wide, (2) the distal region of maxillipedal endite with four spiniform setae
28 and two circumplumose setae, (3) maxillipedal palp article 2 with one outer simple seta, (4) the
29 chelipedal carpus with three or four dorsodistal simple setae, (5) the chelipedal dactylus with
30 one inner simple seta, (6) the pereopod-1 basis with one or two ventrodistal simple setae, (7)
31 the pereopod-1 carpus with one ventrodistal simple seta, and (8) the uropod with four or five
32 articles (basal article plus three or four ramus articles). Partial nucleotide sequences for the
33 cytochrome *c* oxidase subunit I (COI) gene (655 nt) from *Z. ezoensis* specimens from four
34 localities in Hokkaido showed Kimura 2-parameter (K2P) divergences of 0–0.5% and 0.6–
35 1.5% within and between populations, respectively. Based on the COI data, we examined the
36 phylogenetic position of *Z. ezoensis* within *Zeuxo*. Six specimens used for morphological
37 observations and 10 specimens used for COI sequencing showed a similar dorsal pigmentation
38 pattern on carapace. We briefly discuss the validity of using this pattern as a diagnostic

39 character in *Zeuxo* taxonomy.

40

41 **KEYWORDS:** Malacostraca, Tanaididae, North Pacific, Hokkaido, Oshoro, DNA barcoding

42

43 **Introduction**

44 The genus *Zeuxo* Templeton, 1840, with 37 species (Bird 2019; but see the next paragraph), is
45 the most speciose genus in the family Tanaididae. *Zeuxo* differs from the other 19 confamilial
46 genera in having the following combination of characters: (1) five free pleonites, (2) the
47 length/width ratio of antennular article 1 more than 2.5, (3) the antenna with seven articles, (4)
48 no distal cluster of setae on antennal article 2, and (5) the uropod with the terminal article not
49 reduced (Sieg 1980; Bamber 2005; Bamber and Boxshall 2006; Chim and Tong 2019).

50 Species of *Zeuxo* have been found from tropical to subpolar regions worldwide. They are
51 tube-dwellers, making a self-woven tube in bottom sediments, on seagrasses, or on seaweeds
52 (Kakui 2016) and have been reported from depths of 0–30 m (García-Herrero et al. 2019).

53 Three species have been reported from Japan: *Zeuxo maledivensis* Sieg, 1980, *Zeuxo*
54 *coralensis* Sieg, 1980, and *Zeuxo normani* (Richardson, 1905). *Zeuxo maledivensis* was
55 synonymized with *Z. kurilensis* (Kussakin and Tzareva, 1974) by Sieg (1983), but here we
56 reinstate *Z. maledivensis* as a valid species because it morphologically differs from *Z.*
57 *kurilensis* (e.g., the number of inner plumose setae on the pleopodal endopod was one in the
58 former but three in the latter; Kussakin and Tzareva 1974; Sieg 1980). In Japan, *Zeuxo*
59 *maledivensis* and *Z. coralensis* were reported from Nagasaki Prefecture (Sieg 1980), and *Z.*
60 *normani* from Wakayama (Shiino 1951), Mie (Shiino 1951), and Hokkaido prefectures
61 (Takashima et al. 2002). However, their type localities are far away (Addu Atoll, Maldives for

62 *Z. coralensis*; Fadiffolu Atoll, Maldives for *Z. maledivensis*; Monterey Bay, USA for *Z.*
63 *normani*; Sieg 1980), so the occurrence of these species in Japan are suspect and need to be
64 checked.

65 Around Hokkaido, northern Japan, unidentified *Zeuxo* individuals all having a similar
66 pigmentation pattern on the carapace have been reported from Rishiri Island, Okushiri Island,
67 and Oshoro Bay (Kakui et al. 2014, 2017; Kakui 2015); specimens from Rebun Island reported
68 in Kakui et al. (2011) also show a similar pigmentation pattern (KK unpublished data).

69 Through morphological observations and molecular phylogenetic analyses, we found these
70 tanaidaceans to be conspecific and to represent an undescribed taxon. Here we describe it as
71 new and report partial sequences for the mitochondrial cytochrome *c* oxidase subunit I (COI) to
72 access its phylogenetic position within *Zeuxo*. Additionally, we briefly discuss the dorsal
73 pigmentation pattern on the carapace as a diagnostic character in *Zeuxo* taxonomy.

74

75 **Materials and methods**

76 Tanaidaceans were collected among brown algae in the intertidal zone at Oshoro and on Rebun,
77 Rishiri, and Okushiri islands. Some individuals from Oshoro were maintained for several
78 months in a small aquarium (20°C; 14h L/10h D; fed every 3 days), and one female and one
79 male hatched in the aquarium were photographed live to document their body pigmentation
80 pattern. All specimens were fixed and preserved in 70–99% ethanol. The methods used for

81 dissection, preparation of slides, light microscopy, scanning electron microscopy (SEM), and
82 drawing were as described by Kakui and Angsupanich (2012).

83 Orientation and terminology here follow Larsen (2003), except that the term “plumose
84 sensory seta(e)” (PSS; Bird 2011) is used instead of “broom seta(e)”, and two additional setal
85 terms are used: 'flattened denticulate seta' (Edgar 2008) and 'step-tipped plumose seta' (Kakui
86 et al. 2010). Body length (BL) was measured from the base of the antennules to the tip of the
87 pleotelson, and body width at the widest portion of the cephalothorax (CW, cephalothorax
88 width). Appendages were measured in holotype and allotype specimens. Measurements were
89 made axially with ImageJ (Rasband 2020) from digital images: dorsally on the body,
90 antennules, antennae, and uropods; laterally on the pereopods and pleopods.

91 Total DNA was extracted from the cheliped or whole body of 2, 2, 3, and 3 specimens from
92 Oshoro and Rebun, Rishiri, and Okushiri islands, respectively, by using a NucleoSpin Tissue
93 XS Kit (TaKaRa Bio, Japan); the carapace pigmentation patterns on these specimens were
94 photographed before extraction. After extraction, exoskeletons were recovered and preserved
95 in 99% ethanol. Part of the COI gene was amplified by PCR with primers LCO-1490 and
96 HCO-2198 (Folmer et al. 1994). PCR amplification conditions with TaKaRa Ex Taq DNA
97 polymerase (TaKaRa Bio) were 94°C for 1 min; 35 cycles of 98°C for 10 s, 50°C for 30 s, and
98 72°C for 50 s; and 72°C for 2 min. Nucleotide sequences were determined by direct sequencing
99 with a BigDye Terminator Kit ver. 3.1 and a 3730 Genetic Analyzer (Life Technologies, USA).

100 All sequences we determined were deposited in the International Nucleotide Sequence
101 Database (INSD) through the DNA Data Bank of Japan (DDBJ). MEGA7 (Kumar et al. 2016)
102 was used to align the 10 COI sequences we obtained (655 nt, no indels, encoding 218 amino
103 acids) and to calculate Kimura (1980) 2-parameter (K2P) and p distances within and among
104 populations.

105 The COI dataset for a phylogenetic analysis included the 10 COI sequences we determined
106 and eight sequences from the following species, obtained from INSD: *Zeuxo exsargasso* Sieg,
107 1980 (three sequences, accession numbers KF928318–928320; Larsen et al. 2014); *Zeuxo*
108 *holdichi* Bamber, 1990 (KF928322; Larsen et al. 2014); *Zeuxo koreaensis* Larsen, 2014
109 (KF928321; Larsen et al. 2014); *Zeuxo turkensis* Larsen, 2014 (KF928323; Larsen et al. 2014);
110 *Zeuxo cf. normani* (Richardson, 1905) (HM016203; Drumm 2010); and *Arctotanais alascensis*
111 (Richardson, 1899) (outgroup taxon; LC322249; Tanabe et al. 2017). The dataset was aligned
112 by using MAFFT ver. 7 (Katoh and Standley 2013) with the “Auto” strategy (“L-INS-i”)
113 selected (Katoh et al. 2005), after which the aligned sequences were trimmed in MEGA7 to the
114 shortest length among the sequences (389 nt). The optimal substitution models for different
115 partitions determined under the corrected AIC in PartitionFinder 2.1.1 (Lanfear et al. 2016)
116 were TVM+I for the first codon position, K81u+G for second position, and HKY for the third
117 position. A partitioned ML analysis was conducted in IQ-TREE ver. 1.6.8 (Nguyen et al. 2015;
118 Chernomor et al. 2016), with nodal support values obtained by ultrafast bootstrap analysis of

119 10,000 pseudoreplicates (Hoang et al. 2018). The ML tree was drawn by using FigTree v1.4.4
120 (Rambaut 2020).

121

122 **Systematics**

123 **Family Tanaididae Nobili, 1906**

124 **Genus *Zeuxo* Templeton, 1840**

125 [Japanese name: *Nami-tanaisu-zoku*]

126 *Zeuxo* Templeton, 1840: 203. Type species: *Zeuxo westwoodiana* Templeton, 1840

127

128 *Zeuxo ezoensis* sp. nov.

129 [New Japanese name: *Ezo-nami-tanaisu*]

130 (Figures 1–5)

131

132 *Anatanais normani* (not of Richardson 1905): Kito 1975, p. 152.

133 *Zeuxo* sp. 1: Kakui et al. 2011, p. 751; Kakui et al. 2012, p. 128, figure 1F; Kakui et al. 2017, p.

134 130, figures 4, 5.

135 *Zeuxo* spp.: Kakui et al. 2014, p. 9, figure 3Z1, Z2 (in part).

136 *Zeuxo* sp.: Kakui 2015, p. 2, figures 1, 4B–D.

137

138 ***Diagnosis***

139 Antennal article 2 with inner distal simple seta. Antennal article 6 longer than wide. Left
140 mandible with wide denticulate lacinia mobilis and bifurcate accessory seta. Right mandible
141 with peg-like lacinia mobilis and two accessory setae. Maxilliped with endite bearing four
142 spiniform setae and two circumplumose setae in distal region; palp article 4 with outer simple
143 seta. Chelipedal dactylus with inner simple seta. Male chelipedal fixed finger with nine outer
144 dorsal simple setae but without triangular mid-dorsal process on cutting surface. Pereopod 1
145 with coxa bearing slight dorsal process; basis with one or two ventrodistal simple setae; carpus
146 with ventrodistal simple seta. Pleopods 1–3 with endopod bearing inner plumose seta. Uropod
147 with four or five articles (including basal article). Carapace pigmentation comprising dark
148 background with V-shaped pattern of lighter, irregular spots.

149

150 ***Etymology***

151 The specific name is an adjective referring to the old name for Hokkaido Island, where the type
152 locality is located.

153

154 ***Material examined***

155 See Table I.

156

157 *Description of female, based primarily on holotype, with observation of maxillular palp from*

158 ***ICHUM6064***

159 Body (Figures 1A, a1, 3A, B) 5.34 times as long as wide, with reddish brown pigmentation
160 (retained in ethanol). Cephalothorax 0.22 times BL, with pair of mid-lateral simple setae and
161 pair of simple setae posterior to eyes; dorsal pigmentation comprising dark background with
162 V-shaped zone of lighter, irregular spots (Figures 1, 2). Pereonites 1–6 with length ratio
163 1.0:1.85:1.96:2.42:2.23:1.51; each pereonite with several pairs of simple setae. Pereonites 1–6
164 with width to length ratios 0.28, 0.46, 0.58, 0.79, 0.72, and 0.46, respectively. Pleonites 1–3
165 with one or two pairs of dorsolateral simple setae and two to five pairs of lateral plumose setae;
166 pleonites 4 and 5 with one to three pairs of lateral simple setae. Pleotelson with three to five
167 pairs of simple setae.

168 Antennule (Figure 3C) 0.59 times as long as cephalothorax; articles 1–4 with length ratio
169 1.00:0.42:0.40:0.05. Article 1 with one inner proximal, two inner distal, and three outer distal
170 simple setae and several proximal and distal PSS. Article 2 with four distal simple setae and
171 three distal PSS. Article 3 with three distal simple setae and distal PSS. Article 4 with three
172 shorter and eight longer simple setae, and five aesthetascs.

173 Antenna (Figure 3D) 1.06 times as long as antennule; articles 1–7 with length ratio
174 1.00:1.30:0.72:1.51:1.36:0.41:0.01. Articles 1 and 3 naked. Article 2 with one inner distal, one
175 dorsodistal, and two mid-ventral simple setae. Article 4 with five distal simple setae. Article 5

176 with three inner distal simple setae and three distal PSS. Article 6 longer than wide, with four
177 distal simple setae. Article 7 with six distal simple setae.

178 Labrum (Figure 3G) setulate distally. Mandibles (Figures 3H–J, 5) with well-developed
179 molar process bearing many small teeth on masticatory surface; left mandible (Figures 3H, 5A)
180 with smooth incisor, wide, denticulate lacinia mobilis, and bifid serrate accessory seta; right
181 mandible (Figures 3I, J, 5B) with smooth incisor, peg-like lacinia mobilis, and two serrate
182 accessory setae. Labium (Figure 3K) with inner and outer lobes setulate on distal margin; labial
183 palp setulate, articulated with outer lobe. Maxillule (Figure 3L, M) with endite bearing seven
184 distal spiniform setae and outer subdistal setation; palp (from paratype female ICHUM6064)
185 with six distal simple setae. Maxilla (Figure 3N) with finely serrate outer and distal margins.

186 Maxilliped (Figure 3O, P) with coxa bearing two simple setae. Basis with ventrodistal
187 simple seta. Endite with outer serration, two tiny dorso-subdistal and two distal spiniform
188 setae, and two ventro-subdistal circumplumose setae; ventrodistal region setulate. Palp article
189 1 with outer subdistal simple seta; article 2 with three inner ventral and one outer simple setae,
190 and three inner plumose setae; article 3 with 13 inner plumose setae; article 4 with outer simple
191 seta and 10 inner plumose setae. Epignath (Figure 3Q) with kidney-shaped lobe, margins finely
192 setulate; terminal seta setulate.

193 Cheliped (Figures 3B, 4A) with triangular articulation to cephalothorax via sclerite
194 (Figure 3B). Basis nearly as long as wide, with one outer dorsal and one ventrodistal simple

195 setae. Merus with two dorsal and two ventral simple setae. Carpus 1.46 times as long as wide,
196 with one dorsal, three dorsodistal, and three ventral simple setae. Propodal palm with three
197 outer simple setae and inner plumose seta at insertion of dactylus; fixed finger with three
198 ventral, five outer dorsal, and two inner subdistal simple setae, dorsal lamellar expansion
199 showing straight dorsal margin, and triangular claw. Dactylus as long as fixed finger, with
200 inner simple seta and row of ventral spiniform setae; unguis triangular.

201 Pereopods cylindrical, with length ratio 1.00:0.81:0.80:0.89:0.93:0.90 (unguis of
202 pereopod 3 broken, not measured). Pereopod 1 (Figure 4C) 0.29 times as long as BL, with
203 length ratio of basis, merus, carpus, propodus, and dactylus-unguis 1.00:0.26:0.34:0.60:0.30.
204 Coxa with slight dorsal process bearing dorsal simple seta. Basis cylindrical, narrow, 2.67
205 times as long as wide, with one dorso-subproximal and one ventrodistal simple setae and
206 dorso-subproximal PSS. Merus with ventrodistal simple seta. Carpus with one dorsodistal and
207 one ventrodistal simple setae, and dorsodistal spiniform seta. Propodus with one mid-inner,
208 one dorsodistal, and four ventrodistal simple setae, and mid-dorsal PSS. Dactylus with dorsal
209 simple seta; unguis length half dactylus length, naked. Pereopod 2 (Figure 4D) with length
210 ratio of articles from basis to dactylus-unguis 1.00:0.42:0.30:0.45:0.17. Coxa with dorsal
211 simple seta. Basis cylindrical, narrow, 3.50 times as long as wide, with one dorso-subproximal
212 and one ventrodistal simple setae, and dorso-subproximal PSS. Merus with one dorsodistal and
213 two ventrodistal simple setae and ventrodistal spiniform seta. Carpus with one dorsodistal and

214 one ventrodiscal simple setae, and four distal spiniform setae. Propodus with two dorsodistal,
215 one ventro-subdistal, and one ventrodiscal simple setae, and mid-dorsal PSS; dactylus with
216 dorsal simple seta; unguis as long as dactylus, naked. Pereopod 3 (Figure 4E) with length ratio
217 of articles from basis to dactylus 1.00:0.52:0.35:0.51:0.15; similar to pereopod 2, except basis
218 with two dorso-subproximal PSS, and carpus with five distal spiniform setae but without
219 ventrodiscal simple seta. Pereopod 4 (Figure 4F) with length ratio of articles from basis to
220 dactylus-unguis 1.00:0.44:0.37:0.49:0.39. Coxa naked. Basis thicker than in pereopods 1–3,
221 1.98 times as long as wide, with two ventrodiscal simple setae, three dorso-subproximal PSS,
222 and two ventro-subdistal PSS. Merus with two dorsodistal and one ventrodiscal simple setae,
223 and two ventrodiscal spiniform setae. Carpus with two dorsodistal simple setae and five distal
224 spiniform setae. Propodus with two dorsodistal, one outer distal, and one mid-ventral simple
225 setae, and dorsodistal PSS. Dactylus-unguis fused to form claw, strongly arched, with inner and
226 outer rows of ventral spines. Pereopod 5 (Figure 4G) with length ratio of articles from basis to
227 dactylus-unguis 1.00:0.48:0.44:0.56:0.37; similar to pereopod 4 except basis with one
228 ventro-subdistal PSS but without dorso-subproximal PSS. Pereopod 6 (Figure 4H, I) with
229 length ratio of articles from basis to dactylus-unguis 1.00:0.43:0.40:0.64:0.29. Basis, merus,
230 carpus, and dactylus-unguis similar to those of pereopod 4 except basis with two
231 dorso-subproximal PSS but without ventro-subdistal PSS. Propodus with two dorsodistal, one
232 outer distal, and one mid-ventral simple setae, dorsodistal PSS, and seven inner distal flattened

233 denticulate setae.

234 Pleopod 1 (Figure 4J) with basal article bearing one inner and five outer plumose setae;
235 endopod with one inner and nine outer plumose setae, and outer distal step-tipped plumose
236 seta; exopod 1.45 times as long as endopod, with 21 outer plumose setae. Pleopod 2 (Figure
237 4K) similar to pleopod 1 except exopod with 20 outer plumose setae (inner plumose seta on
238 basal article broken in holotype). Pleopod 3 (Figure 4L) with basal article bearing two outer
239 plumose setae; endopod with one inner and seven outer plumose setae, and outer distal
240 step-tipped plumose seta; exopod 1.38 times as long as endopod, with 17 outer plumose setae.

241 Uropod (Figure 4M) with four articles (basal article and triarticulate ramus). Basal article
242 with five distal simple setae. Ramus article 1 with distal simple seta and distal PSS; article 2
243 with four distal simple setae and two distal PSS; article 3 with six distal simple setae and two
244 PSS.

245

246 *Description of male, based on allotype*

247 Body (Figure 1B, b1) similar to female.

248 Antennule (Figure 3E) 0.92 times as long as cephalothorax; articles 1–4 with length ratio
249 1.00:0.34:0.25:0.05. Article 1 with setation similar to that of female. Article 2 with eight distal
250 simple setae and four PSS. Article 3 with four distal simple setae and two distal PSS. Article 4
251 with five shorter and 11 longer simple setae, and seven aesthetascs.

252 Antenna (Figure 3F) 0.88 times as long as antennule; articles 1–7 with length ratio
253 1.00:2.29:1.01:2.59:1.77:0.54:0.12. Articles 1 and 3 naked. Article 2 with one inner distal, one
254 dorsodistal, and one mid-ventral simple setae. Article 4 with four distal simple setae and distal
255 PSS. Article 5 with three distal simple and four distal PSS. Article 6 longer than wide, with
256 seven distal simple setae. Article 7 with eight distal simple setae.

257 Labrum, mandibles, labium, maxillule, and maxilla similar to those of female.

258 Maxilliped with coxa bearing three simple setae. Basis with two ventrodistal simple setae.
259 Endite similar to female. Palp article 1 with three (left) or two (right) outer subdistal simple
260 setae; article 2 with five inner ventral and one outer simple setae and three inner plumose setae;
261 article 3 with 11 inner plumose setae; article 4 with outer simple seta and 14 inner plumose
262 setae. Epignath similar to female.

263 Cheliped (Figure 4B) with triangular articulation to cephalothorax via sclerite. Basis and
264 merus similar to those of female. Carpus 0.90 times as long as wide, with one dorsal, four
265 dorsodistal, and five ventral simple setae. Propodal palm with six outer simple setae and inner
266 plumose seta at insertion of dactylus; fixed finger with five ventral, nine outer dorsal, and two
267 inner subdistal simple setae, dorsal lamellar expansion showing straight dorsal margin, and
268 triangular claw. Dactylus strongly arched ventrally, with inner simple seta and row of ventral
269 spiniform setae; unguis triangular.

270 Pereopods 1–6 with length ratio 1.00:0.82:0.77:0.83:0.84:0.88; pereopod 1 length 0.35

271 times BL. Pereopods similar to those of female, with following exceptions. Pereopod 1: basis
272 with two simple dorso-subproximal and one or two ventrodial simple setae; merus with
273 dorsodial simple seta; carpus with one or two dorsodial simple setae, propodus with six or
274 seven ventrodial simple setae. Pereopod 2: basis with two dorso-subproximal and three
275 ventrodial simple setae, and two dorso-subproximal PSS; merus with four ventrodial simple
276 setae; carpus with two dorsodial simple setae; propodus with one dorsodial and four
277 ventrodial simple setae. Pereopod 3: basis with two dorso-subproximal and two ventrodial
278 simple setae; merus with two dorsodial and three ventrodial simple setae; carpus with two
279 dorsodial simple setae; propodus with one dorsodial and two mid-ventral simple setae.
280 Pereopod 4: basis with three ventrodial simple setae; merus with three dorsodial and two
281 ventrodial simple setae; carpus with three dorsodial simple setae and six distal spiniform
282 setae. Pereopod 5: basis with three ventrodial simple setae and dorso-subproximal PSS;
283 merus with three dorsodial and two ventrodial simple setae; propodus with two mid-ventral
284 simple setae. Pereopod 6: basis with three ventrodial simple setae; merus with three
285 dorsodial and three ventrodial simple setae; carpus with three dorsodial simple setae;
286 propodus with two mid-ventral simple setae and 10 inner distal flattened denticulate setae.

287 Pleopods similar to those of female, with following exceptions: basal articles of pleopods
288 1–3 with six, six, and three outer plumose setae, respectively; endopods of pleopods 1–3 with
289 12, 13, and 11 outer plumose setae, respectively; exopods of pleopods 1–3 with 30, 32, and 25

290 outer plumose setae, respectively.

291 Uropod with five articles (basal article and 4-articulate ramus). Basal article with eight
292 distal simple setae. Ramus article 1 with two distal simple setae and distal PSS; article 2 with
293 six distal simple setae and distal PSS; article 3 with five distal simple setae and two distal PSS;
294 article 4 with six distal simple setae and two distal PSS.

295

296 ***Variation and stability***

297 In addition to the holotype and allotype, two female (ICHUM6061, 6064) and two male
298 (ICHUM6062, 6063) paratypes of *Zeuxo ezoensis* sp. nov. were dissected and all appendages
299 were observed. The morphological data we obtained are in Table SI. All specimens shared the
300 same character state for the following selected characters (for all characters, see Table SI): (1)
301 dorsal pigmentation pattern on carapace comprising dark background with V-shaped zone of
302 lighter, irregular spots; (2) antennal article 2 with one inner distal and one dorsodistal simple
303 setae; (3) left mandible with wide, denticulate lacinia mobilis and one bifurcate accessory seta;
304 (4) right mandible with peg-like lacinia mobilis and two accessory setae; (5) maxillipedal
305 endite with two tiny dorso-subdistal and two distal spiniform setae; (6) maxillipedal palp
306 articles 2 and 4 with one outer simple seta; (7) chelipedal basis with one outer dorsal simple
307 seta; (8) chelipedal dactylus with one inner simple seta and row of ventral spiniform setae; (9)
308 pereopod-1 carpus with one ventrodistal simple seta; (10) endopod of pleopods 1–3 with one

309 inner plumose seta; and (11) pleopod-3 basal article without inner plumose setae.

310 The following selected setae or articles varied in number among specimens (for all
311 characters, see Table SI) (ranges in parentheses): dorsodistal simple setae on chelipedal carpus
312 (3–4), ventrodistal simple setae on pereopod-1 basis (1–2), and articles of uropod (4–5).

313 Sexually dimorphic characters found in this species were typical for this genus: male
314 antennules and antennae were longer than those of females; male cheliped had a wider carpus
315 and a larger chela than that of females.

316

317 ***Phylogenetic analysis and genetic divergence***

318 Partial COI sequences (655 nt) were determined from 2, 2, 3, and 3 individuals
319 collected from populations at Oshoro and Rebun, Rishiri, and Okushiri islands, respectively. In
320 the ML tree (Figure 6) based on COI, the 10 sequences from Hokkaido form a clade (*Zeuxo*
321 *ezoensis* sp. nov.), with K2P distances of 0–0.5% within populations and 0.6–1.5% among
322 populations (Table II; the *p* distances were identical to the K2P distances). The *Z. ezoensis*
323 clade is the sister group to a clade comprising *Z. holdichi*, *Z. koreaensis*, and *Z. cf. normani*,
324 with 80% ultrafast bootstrap support (uBS), which in turn forms a clade with *Z. turkensis* (uBS,
325 93%), with *Z. exsargasso* comprising the sister group to the other *Zeuxo* species. Genetic
326 distances among the six *Zeuxo* species were 12–36% (K2P) or 11–29% (*p* distance), much
327 greater than the intraspecific distances for *Z. ezoensis*.

328

329 **Discussion**

330 The results that all our Hokkaido sequences form a single clade, with much lower genetic
331 distances within the clade than between it and other, previously described *Zeuxo* species,
332 indicate that our 10 specimens from four localities are conspecific. While there is relatively
333 little information in the literature on ranges of intraspecific variation for COI in Tanaidacea, the
334 K2P distances among populations we found were similar to those reported for the tanaidid
335 *Hexapleomera ulsana* Wi et al., 2018 (up to 1.1%; Wi et al. 2018), and distances within
336 populations were lower than within a single population of the kalliapseudid *Mesokalliapseudes*
337 *macsweenyi* (Drumm, 2003) (up to 3%; Drumm and Kreiser 2012). In the tree, our species
338 from Hokkaido was not in sister relation to another Japanese species, *Z. cf. normani*. This
339 implies that there may be multiple species groups in *Zeuxo*.

340 Among 38 congeners [37 in Bird (2019) plus *Z. maledivensis*], *Zeuxo ezoensis* sp. nov.
341 closely resembles *Z. phytalensis* Sieg, 1980 from the Kerguelen Islands, *Z. shitipingensis*
342 Tzeng and Hsueh, 2015 from Taiwan, and *Z. turkensis* from Turkey in having the following
343 combination of characters: (1) left mandible with wide denticulate lacinia mobilis and one
344 bifurcate accessory seta, (2) right mandible with peg-like lacinia mobilis and two accessory
345 setae, (3) maxillipedal palp article 4 with one outer simple seta, and (4) pleopodal endopod
346 with one inner plumose seta.

347 *Zeuxo ezoensis* differs from *Z. phytalensis* in the following characters (character states of
348 *Z. phytalensis* in parentheses; Sieg 1980): antennal article 6 longer than wide (shorter),
349 chelipedal basis with one outer dorsal simple seta (without the seta), chelipedal carpus with
350 three or four dorsodistal simple setae (one or two setae), chelipedal dactylus with one inner
351 simple seta (without the seta), and pleopod-3 basal article without inner plumose setae (with
352 one plumose seta). Additionally, male *Z. ezoensis* differs from male *Z. phytalensis* in having the
353 chelipedal fixed-finger with nine outer dorsal simple setae (six in *Z. phytalensis*).

354 *Zeuxo ezoensis* differs from *Z. shitipingensis* in the following characters (character states
355 of *Z. shitipingensis* in parentheses; Tzeng and Hseuh 2015): maxilipedal endite with two
356 circumplumose setae (four); chelipedal dactylus with one inner simple seta (without the seta),
357 dorsal process on pereopod-1 coxa slight (prominent), pereopod-1 carpus with one ventrodial
358 simple seta (without the seta), and uropod with four or five articles (six or seven). Additionally,
359 male *Z. ezoensis* differs from male *Z. shitipingensis* in having maxillipedal palp article 2 with
360 one outer simple seta (the seta is lacking in *Z. shitipingensis*), and the chelipedal fixed-finger
361 with nine outer dorsal simple setae (five in *Z. shitipingensis*).

362 *Zeuxo ezoensis* differs from *Z. turkensis* in the following characters (character states of *Z.*
363 *turkensis* in parentheses; Larsen 2014): antennal article 2 with one inner distal simple seta
364 (without the seta), distal region of maxillipedal endite with four spiniform setae (two setae),
365 chelipedal dactylus with one inner simple seta (without the seta), and pereopod-1 basis with

366 one or two ventrodistal simple setae (without setae in this position). Males of the two species
367 differ in the shape of the fixed finger: the dorsal margin is nearly straight in *Z. ezoensis* whereas
368 it bears one triangular mid-dorsal process in *Z. turkensis*. *Zeuxo ezoensis* was 29–31%
369 divergent (K2P) from *Z. turkensis* in the partial COI sequences (389 nt), and in our ML tree
370 (Figure 6) the two species are separated by the clade comprising *Z. koreaensis*, *Z. cf. normani*,
371 and *Z. holdichi*. These results support the conclusion from our morphological analysis, that *Z.*
372 *ezoensis* and *Z. turkensis* are different species.

373 The pigmentation pattern on the carapace differs between *Z. ezoensis* and *Z.*
374 *shitipingensis*. In *Z. ezoensis*, the carapace has a dark background, with a V-shaped zone of
375 lighter, irregular spots (Figures 1, 2); this pattern was the same in the six specimens studied
376 morphologically and the 10 specimens used for DNA sequencing (Figure 2). At least in one
377 female and one male of *Z. shitipingensis*, the anterior and middle regions of the carapace are
378 dark, while other regions lack dark pigmentation (Tzeng and Hsueh 2015: figures 6A, 9A).
379 Larsen et al. (2014) concluded that the pigmentation pattern on carapaces in *Zeuxo* can show
380 intraspecific variation, though his paper did not show the pigmentation patterns of specimens
381 actually used for sequencing DNA. While we observed slight differences in the degree of dark
382 pigmentation among *Z. ezoensis* specimens, and some specimens collected had strongly faded
383 pigmentation on the carapace (data not shown), the overall pattern was the same. Our
384 observation of multiple specimens suggests that carapace pigmentation patterns may be

385 consistent within species. If this is the case, differences among species may be consistent and
 386 provide a useful character for *Zeuxo* taxonomy in situations where “species discrimination is
 387 extremely difficult” (Bird 2019: p. 47). The validity of carapace pigmentation patterns as a
 388 diagnostic character in *Zeuxo* taxonomy should be tested with additional studies involving
 389 multiple individuals from populations, combined with molecular confirmation of
 390 conspecificity.

391

392 **Key to species of *Zeuxo* having the combination of characters referred in the Discussion**
 393 **section**

394 1. Antennal article 6 shorter than wide*Z. phytalensis*

395 Antennal article 6 longer than wide 2

396 2. Maxillipedal endite with four plumose setae; dorsal process on pereopod-1 coxa prominent;
 397 uropod with six or seven articles*Z. shitipingensis*

398 Maxillipedal endite with two plumose setae; dorsal process on pereopod-1 coxa slight or not
 399 appreciable; uropod with four or five articles 3

400 3. Maxillipedal endite with two distal spiniform setae; chelipedal dactylus without simple
 401 setae; ventrodiscal corner of pereopod-1 basis without simple setae; (in male) dorsal margin of
 402 fixed finger with one triangular mid-dorsal process *Z. turkensis*

403 Maxillipedal endite with four distal spiniform setae; chelipedal dactylus with one inner
 404 simple seta; ventrodiscal corner of pereopod-1 basis with one or two simple setae; (in male)

405 dorsal margin of fixed finger nearly straight*Z. ezoensis* **sp. nov.**

406

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413

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526

527 **Figure legends**

528

- 529 **Figure 1.** *Zeuxo ezoensis* sp. nov., paratype female (A, a1; ICHUM6068) and male (B, b1;
530 ICHUM6069), dorsal views. A, B, living individuals; a1, b1, anterior portion of body, ethanol
531 fixed specimens. Scales: 1 mm (A, B), 0.1 mm (a1, b1).

532

- 533 **Figure 2.** Carapaces of *Zeuxo ezoensis* sp. nov. specimens used for DNA extraction, ethanol
534 fixed, dorsal view. A, B, Oshoro specimens (ICHUM6066, 6067); C, D, Rebun Island
535 specimens (ICHUM6070, 6071); E–G, Rishiri Island specimens (ICHUM6072–6074); H–J,
536 Okushiri Island specimens (ICHUM6075–6077).

537

538 **Figure 3.** *Zeuxo ezoensis* sp. nov. A–D, G–K, M–Q, holotype, female; E, F, allotype, male; L,
539 paratype (ICHUM6064), female. A, B, body, dorsal (A) and lateral (B) views; C, E, antennule,
540 outer view of left (C) and inner view of right (E); D, F, left (D) and right (F) antenna, inner
541 view; G, labrum; H, left mandible (distal portion and molar); I, right mandible; J, distal portion
542 of right mandible; K, labium, L, maxillule; M, maxillular palp; N, maxilla; O, maxillipeds
543 (right palp, setal ornamentation and setation on right basis and left endite omitted), ventral
544 view; P, distal portion of maxillipedal endites (circumplumose setae on left endite omitted),
545 ventral view; Q, epignath. Scales: 1 mm (A, B); 0.1 mm (C–I, K–O, Q); 0.05 mm (J, P).

546

547 **Figure 4.** *Zeuxo ezoensis* sp. nov. A, C–M, holotype, female; B, allotype, male. A, B, right
548 cheliped, inner view; C–H, pereopods 1–6, inner (C, H) and outer (D–G) views; I, distal
549 portion of pereopod 6, inner view; J–L, right pleopods 1–3, setal ornamentation omitted; M,
550 uropod. Scales: 0.1 mm.

551

552 **Figure 5.** *Zeuxo ezoensis* sp. nov., paratype (ICHUM6065), female, SEM images. A, B, distal
553 portion of left (A) and right (B) mandibles, inner view. Scale: 10 μ m.

554

555 **Figure 6.** ML tree based on COI sequences (389 nt) from six *Zeuxo* species and an outgroup
556 taxon, *Arctotanais alascensis*. Numbers near nodes are ultrafast bootstrap values in percent
557 (80% or more). The scale indicates branch length in number of substitutions per site.
558

559 **Table I.** Collection information for specimens of *Zeuxo ezoensis* sp. nov. utilized in this study.

560 –, COI not determined; nd, no data.

561

ICHUM/INSD	Status	Sex; (mm)	BL/CW	Substratum; locality; date; collector
6059/–	Holotype	Female; 2.71/0.55		Brown algae; intertidal zone, west coast of Oshoro
6060/–	Allotype	Male; 3.70/0.81		Bay, Oshoro (43°12'40.3"N 140°51'24.2"E);
6061/–	Paratype	Female; 2.84/0.70		11.v.2018; NO
6062/–	Paratype	Male; 2.41/0.60		
6063/–	Paratype	Male; 2.23/0.51		
6064/–	Paratype	Female; 2.90/0.53		
6065/–	Paratype	Female; 1.64/0.36		
6066/529716	Paratype	Female; nd/0.59		<i>Sargassum confusum</i> ; intertidal zone, Uchikabuto,
6067/529717	Paratype	Female; nd/0.65		Oshoro (43°12'40.3"N 140°51'24.2"E);
				2.v.2012; KK
6068/–	Paratype	Female; nd/0.51		(hatched in aquarium; fixed on 11.i.2019)
6069/–	Paratype	Male; nd/0.57		<i>Neorhodomela aculeata</i> ; intertidal zone,
				Uchikabuto, Oshoro, 3.ix.2018; KK and NO
6070/529718	Nontype	Male; nd/0.47		<i>Sargassum</i> sp.; intertidal zone, Nishiuedomari,
6071/529719	Nontype	Male; nd/0.39		Rebun Island (45°24'27.2"N 140°59'29.3"E);
				17.x.2007; KK
6072/529720	Nontype	Male; nd/0.47		<i>Sargassum</i> sp.; intertidal zone, Motodomari,
6073/529721	Nontype	Female; nd/0.48		Rishiri Island (45°15'09.3"N 141°11'15.1"E);
6074/529722	Nontype	Female; nd/0.40		7.vii.2018; Shinri Tomioka
6075/529723	Nontype	Female; nd/0.77		<i>Sargassum thunbergii</i> ; intertidal zone, Monai,
6076/529724	Nontype	Female; nd/0.61		Okushiri Island (42°06'53.05"N
6077/529725	Nontype	Female; nd/0.56		139°25'04.98"E); 9.v.2010; KK

562

563

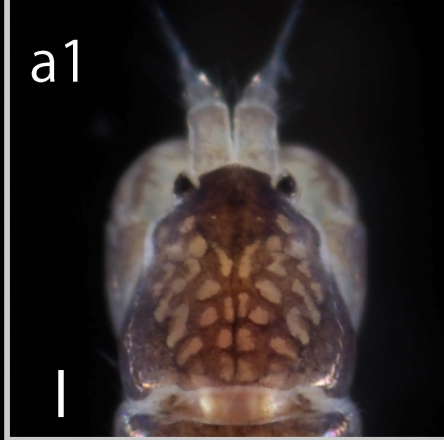
564 **Table II.** K2P distances (in percent) among COI sequences from four tanaidacean populations
 565 around Hokkaido (2, 2, 3, and 3 sequences from Oshoro and, Rebun, Rishiri, and Okushiri
 566 Islands, respectively; 655 nt). Average values are in parentheses.

567

	Oshoro	Rebun	Rishiri	Okushiri
Oshoro	0			
Rebun	1.2 (1.2)	0.5		
Rishiri	0.8 (0.8)	0.8–1.1 (0.9)	0–0.2 (0.1)	
Okushiri	1.1–1.4 (1.2)	1.1–1.5 (1.3)	0.6–1.1 (0.8)	0–0.3 (0.2)

568

569

A**B****A, B****a1****b1**

