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Author(s)	Okamoto, Nobuya; Oya, Yuki; Kakui, Keiichi
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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
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4	Nobuya Okamoto <sup>a</sup> , Yuki Oya <sup>a</sup> , and Keiichi Kakui <sup>b</sup>
5	
6	<sup>a</sup> Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan
7	<sup>b</sup> Faculty of Science, Hokkaido University, Sapporo 060-0810, Japan
8	Corresponding author: Nobuya Okamoto, nobu.okmt@gmail.com; Graduate School of
9	Science, Hokkaido University, N10 W8, Kita-ku, Sapporo 060-0810, Japan
10	
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## 21 Abstract

We describe Zeuxo ezoensis sp. nov. from Hokkaido, Japan. This species closely resembles Z. 2223phytalensis, Z. shitipingensis, and Z. turkensis in having the pleopodal endopod with one inner plumose seta, maxillipedal palp article 4 with one outer simple seta, the left mandible with a 2425wide, denticulate lacinia mobilis and one bifurcate accessory seta, and the right mandible with a peg-like lacinia mobilis and two accessory setae. It differs from them in having (1) antennal 2627article 6 longer than wide, (2) the distal region of maxillipedal endite with four spiniform setae and two circumplumose setae, (3) maxillipedal palp article 2 with one outer simple seta, (4) the 2829chelipedal carpus with three or four dorsodistal simple setae, (5) the chelipedal dactylus with 30 one inner simple seta, (6) the percopod-1 basis with one or two ventrodistal simple setae, (7) the pereopod-1 carpus with one ventrodistal simple seta, and (8) the uropod with four or five 31articles (basal article plus three or four ramus articles). Partial nucleotide sequences for the 32cytochrome c oxidase subunit I (COI) gene (655 nt) from Z. ezoensis specimens from four 33 localities in Hokkaido showed Kimura 2-parameter (K2P) divergences of 0-0.5% and 0.6-34351.5% within and between populations, respectively. Based on the COI data, we examined the phylogenetic position of Z. ezoensis within Zeuxo. Six specimens used for morphological 36 37observations and 10 specimens used for COI sequencing showed a similar dorsal pigmentation pattern on carapace. We briefly discuss the validity of using this pattern as a diagnostic 38

39 character in Zeuxo taxonomy.

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

### 43 Introduction

The genus Zeuxo Templeton, 1840, with 37 species (Bird 2019; but see the next paragraph), is 44the most speciose genus in the family Tanaididae. Zeuxo differs from the other 19 confamilial 45genera in having the following combination of characters: (1) five free pleonites, (2) the 46length/width ratio of antennular article 1 more than 2.5, (3) the antenna with seven articles, (4) 4748no distal cluster of setae on antennal article 2, and (5) the uropod with the terminal article not reduced (Sieg 1980; Bamber 2005; Bamber and Boxshall 2006; Chim and Tong 2019). 49Species of Zeuxo have been found from tropical to subpolar regions worldwide. They are 50tube-dwellers, making a self-woven tube in bottom sediments, on seagrasses, or on seaweeds 51(Kakui 2016) and have been reported from depths of 0-30 m (García-Herrero et al. 2019). 52Three species have been reported from Japan: Zeuxo maledivensis Sieg, 1980, Zeuxo 53coralensis Sieg, 1980, and Zeuxo normani (Richardson, 1905). Zeuxo maledivensis was 54synonymized with Z. kurilensis (Kussakin and Tzareva, 1974) by Sieg (1983), but here we 5556reinstate Z. maledivensis as a valid species because it morphologically differs from Z. kurilensis (e.g., the number of inner plumose setae on the pleopodal endopod was one in the 5758former but three in the latter; Kussakin and Tzareva 1974; Sieg 1980). In Japan, Zeuxo maledivensis and Z. coralensis were reported from Nagasaki Prefecture (Sieg 1980), and Z.  $\mathbf{59}$ normani from Wakayama (Shiino 1951), Mie (Shiino 1951), and Hokkaido prefectures 60 (Takashima et al. 2002). However, their type localities are far away (Addu Atoll, Maldives for 61

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

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dissection, preparation of slides, light microscopy, scanning electron microscopy (SEM), and 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

- 128 Zeuxo ezoensis sp. nov.
- 129 [New Japanese name: *Ezo-nami-tanaisu*]
- 130 (Figures 1–5)

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- 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.

## 138 Diagnosis

Antennal article 2 with inner distal simple seta. Antennal article 6 longer than wide. Left 139mandible with wide denticulate lacinia mobilis and bifurcate accessory seta. Right mandible 140with peg-like lacinia mobilis and two accessory setae. Maxilliped with endite bearing four 141 spiniform setae and two circumplumose setae in distal region; palp article 4 with outer simple 142seta. Chelipedal dactylus with inner simple seta. Male chelipedal fixed finger with nine outer 143dorsal simple setae but without triangular mid-dorsal process on cutting surface. Pereopod 1 144145with coxa bearing slight dorsal process; basis with one or two ventrodistal simple setae; carpus with ventrodistal simple seta. Pleopods 1-3 with endopod bearing inner plumose seta. Uropod 146with four or five articles (including basal article). Carapace pigmentation comprising dark 147148background with V-shaped pattern of lighter, irregular spots. 149**Etymology** 150The specific name is an adjective referring to the old name for Hokkaido Island, where the type 151locality is located. 152153Material examined 154See Table I. 155

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
- 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.

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
- dorsodistal, and two mid-ventral simple setae. Article 4 with five distal simple setae. Article 5

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

Cheliped (Figures 3B, 4A) with triangular articulation to cephalothorax via sclerite
(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	percopod 3 broken, not measured). Percopod 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 ventrodistal simple setae, and four distal spiniform setae. Propodus with two dorsodistal,
215	one ventro-subdistal, and one ventrodistal 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	ventrodistal 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 ventrodistal simple setae, three dorso-subproximal PSS,
222	and two ventro-subdistal PSS. Merus with two dorsodistal and one ventrodistal simple setae,
223	and two ventrodistal 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.

Antennule (Figure 3E) 0.92 times as long as cephalothorax; articles 1–4 with length ratio 1.00:0.34:0.25:0.05. Article 1 with setation similar to that of female. Article 2 with eight distal simple setae and four PSS. Article 3 with four distal simple setae and two distal PSS. Article 4 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 ventrodistal simple setae; merus with
273	dorsodistal simple seta; carpus with one or two dorsodistal simple setae, propodus with six or
274	seven ventrodistal simple setae. Pereopod 2: basis with two dorso-subproximal and three
275	ventrodistal simple setae, and two dorso-subproximal PSS; merus with four ventrodistal simple
276	setae; carpus with two dorsodistal simple setae; propodus with one dorsodistal and four
277	ventrodistal simple setae. Pereopod 3: basis with two dorso-subproximal and two ventrodistal
278	simple setae; merus with two dorsodistal and three ventrodistal simple setae; carpus with two
279	dorsodistal simple setae; propodus with one dorsodistal and two mid-ventral simple setae.
280	Pereopod 4: basis with three ventrodistal simple setae; merus with three dorsodistal and two
281	ventrodistal simple setae; carpus with three dorsodistal simple setae and six distal spiniform
282	setae. Pereopod 5: basis with three ventrodistal simple setae and dorso-subproximal PSS;
283	merus with three dorsodistal and two ventrodistal simple setae; propodus with two mid-ventral
284	simple setae. Pereopod 6: basis with three ventrodistal simple setae; merus with three
285	dorsodistal and three ventrodistal simple setae; carpus with three dorsodistal 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.

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

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#### 296 Variation and stability

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

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 <i>p</i> distances were identical to the K2P distances). The <i>Z. ezoensis</i>
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.

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

#### 329 **Discussion**

The results that all our Hokkaido sequences form a single clade, with much lower genetic
distances within the clade than between it and other, previously described *Zeuxo* species,

- 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
- K2P distances among populations we found were similar to those reported for the tanaidid
- 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
- implies that there may be multiple species groups in Zeuxo.

Among 38 congeners [37 in Bird (2019) plus *Z. maledivensis*], *Zeuxo ezoensis* sp. nov. closely resembles *Z. phytalensis* Sieg, 1980 from the Kerguelen Islands, *Z. shitipingensis* Tzeng and Hsueh, 2015 from Taiwan, and *Z. turkensis* from Turkey in having the following combination of characters: (1) left mandible with wide denticulate lacinia mobilis and one bifurcate accessory seta, (2) right mandible with peg-like lacinia mobilis and two accessory setae, (3) maxillipedal palp article 4 with one outer simple seta, and (4) pleopodal endopod 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 ventrodistal
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	
392 393	Key to species of <i>Zeuxo</i> having the combination of characters referred in the Discussion section
394	1. Antennal article 6 shorter than wideZ. phytalensis
395	Antennal article 6 longer than wide2
396	2. Maxillipedal endite with four plumose setae; dorsal process on pereopod-1 coxa prominent;
397	uropod with six or seven articlesZ. 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
400	3. Maxillipedal endite with two distal spiniform setae; chelipedal dactylus without simple
401	setae; ventrodistal corner of pereopod-1 basis without simple setae; (in male) dorsal margin of
402	fixed finger with one triangular mid-dorsal processs
403	Maxillipedal endite with four distal spiniform setae; chelipedal dactylus with one inner
404	simple seta; ventrodistal corner of pereopod-1 basis with one or two simple setae; (in male)

405	dorsal margin of fixed finger nearly straightZ. ezoensis sp. nov.			
406				
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413				
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526	
527 528	Figure legends
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, percopods 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  $\mu$ m.

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.

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

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

ICHUM/INSD	Status	Sex; BL/CW	Substratum; locality; date; collector
		(mm)	
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	Sargassum confusum; 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	Neorhodomela aculeata; intertidal zone,
			Uchikabuto, Oshoro, 3.ix.2018; KK and NO
6070/529718	Nontype	Male; nd/0.47	Sargassum 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	Sargassum 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	Sargassum thunbergii; 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

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

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	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)













91

Oshoro (LC529716) Rishiri (LC529722) Rishiri (LC529720) Rishiri (LC529721)

Okushiri (LC529724)

Okushiri (LC529723) Okushiri (LC529725)



Zeuxo ezoensis sp. nov