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First record of *Daphnia retrocurva* Forbes, 1882 (Crustacea, Cladocera, Daphniidae) outside its native North America (Shin Toyone Reservoir, Japan)

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Abstract. *Daphnia retrocurva* Forbes, 1882 (Crustacea, Cladocera, Daphniidae), a North American freshwater zooplankton species, was found in an artificial reservoir in central Japan. This represents the first record of *D. retrocurva* not only in Japanese and Asian freshwaters but also from outside North America. Our phylogenetic analysis based on mitochondrial DNA sequences revealed little differentiation between Japanese and North American populations. By combining geographical isolation and the lack of genetic differentiation, we consider Japanese *D. retrocurva* to be non-indigenous and relatively recently introduced.

Key words. Biogeography, DNA barcoding, freshwater zooplankton, non-indigenous species

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Introduction

The genus *Daphnia* O.F. Müller, 1785 (Crustacea, Cladocera, Daphniidae) includes 70–80 species (Benzie 2005; Kotov et al. 2013), and a critical review of this genus by Kotov (2015) counted 87 valid species. *Daphnia* mainly occurs in lentic freshwaters and plays an important role in the lentic food web, linking primary producers, such as phytoplankton, and higher consumers, such as fishes (Lampert and Sommer 1997). Lentic freshwaters have been exposed to various human activities, and as a result, the connectivity between water bodies has increased. Cladocerans, including *Daphnia*, can disperse outside their existing range using different natural vectors (Havel and Shurin 2004); however, anthropogenic dispersal has been prevailing (e.g. Kotov et al. 2022). At a global scale, there are 13 major geographical pathways through which anthropogenic dispersal has occurred in cladocerans, including several species of the genus *Daphnia*, such as *D. lumholtzi* Sars, 1885 and *D. magna* Straus, 1820 (Kotov et al. 2022).

Studies on *Daphnia* in Japan date back to the late 19th century (Ishikawa 1895), and many studies have been conducted on Japanese *Daphnia* species from taxonomical, ecological, and evolutionary perspectives (e.g. Uéno 1934a, 1934b; Tanaka 1997; Ishida and Taylor 2007; Ishida et al. 2011; Kotov et al. 2021). We recently collected individuals of *Daphnia* from the Shin Toyone Reservoir located in central Honshu Island, as part of National Census on River and Dam Environments in Japan (Suzuki et al. 2025, 2026). In the present study, the individuals were identified as *Daphnia retrocurva* Forbes, 1882 based on both external morphology and mitochondrial DNA sequence data. This species, which was found for the first time in Japan despite the long study history mentioned above, has only been reported from the northern part of the North American continent (Brooks 1957; Benzie 2005; Kotov et al. 2013), indicating that the Japanese population in this study represents the first record of *D. retrocurva* outside its native range.

Study area

According to the Shin Toyone Dam pamphlet, which is available on its website (Shin Toyone Dam 2013), the Shin Toyone Dam is used for flood control and hydroelectric power generation. The dam was constructed on the Oonyu (= Ōnyu) River, which is one tributary of the Oochise (= Ōchise) River. The latter

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river is a tributary of the Tenryu (= Tenryū) River, which ultimately flows into the Pacific Ocean in Iwata City, Shizuoka Prefecture. The dam construction began in 1969 and was completed in 1973. The catchment and surface areas of the reservoir are 136.30 km^2 and 1.56 km^2, respectively, and the total capacity is 53.5×10^6 m^3 (Shin Toyone Dam 2013).

Methods

Field collection was conducted on 1 October 2025 at an offshore station for monitoring reservoir water quality and plankton community structure (35.1300°N, 137.7598°E; Figure 1). Zooplankton bulk samples were collected by the vertical tow of a plankton net (mesh size 0.1 mm) from the bottom (depth, 62 m) to the water surface and immediately fixed with ethanol (concentration, ca. 70%). The ethanol in the sample bottles was replaced with 99% ethanol within the same day, and the bottles were kept cool (ca. 4 °C).

In the laboratory, 12 *Daphnia* parthenogenetic females with anterodorsally recurved helmets (Table A1) were carefully examined under an Olympus BX53 microscope at 40–400× magnification for the morphological characteristics listed in Table 1. Images were captured using a BX53 microscope equipped with a Leica HD170 camera.

All individuals were then used for Sanger sequencing. DNA was extracted individually. We attempted to retain voucher samples from six adult females (Table A1). In the case of a female carrying a well-developed embryo, the embryos were removed to extract DNA and the whole body was retained. In the case of a female carrying undeveloped subitaneous eggs or no eggs, the head region was separated from the rest of the body, and the former was used as the voucher and the latter for DNA extraction. Dissections were conducted under a Leica S9 stereomicroscope at 20–55× magnification equipped with a Leica HD170 camera. In six juvenile females, the whole body was used for DNA extraction (thus, no voucher samples except for microscopic images).

We used a Quick Extract DNA Extraction Solution (Biosearch Technologies) according to the manufacturer's protocols, except for the 6-h extraction period at 65 °C with the expectation of more efficient DNA extraction. We then obtained the partial nucleotide sequences of three mitochondrial genes, i.e. mitochondrial cytochrome *c* oxidase subunit I (mtCOI), 12S rDNA (mt12S), and NADH dehydrogenase 2 gene (mtND2), which were also used in *Daphnia* phylogeography studies (e.g. Ishida et al. 2006; Petrusek et al. 2008). The mtCOI Folmer region was primarily used for species delimitation, and the other two gene regions were used to evaluate the degree of sequence divergence among the 12 individuals.

We used KOD One PCR Master Mix (Toyobo) in the polymerase chain reaction (PCR). The ZplankF1_t1 and ZplankR1_t1 primer set of Prosser et al. (2013) was used to analyze the mtCOI Folmer region. The PCR cycle consisted of 1 s of initial denaturation at 98 °C; followed by 5 cycles of 10 s at 98 °C, 5 s at

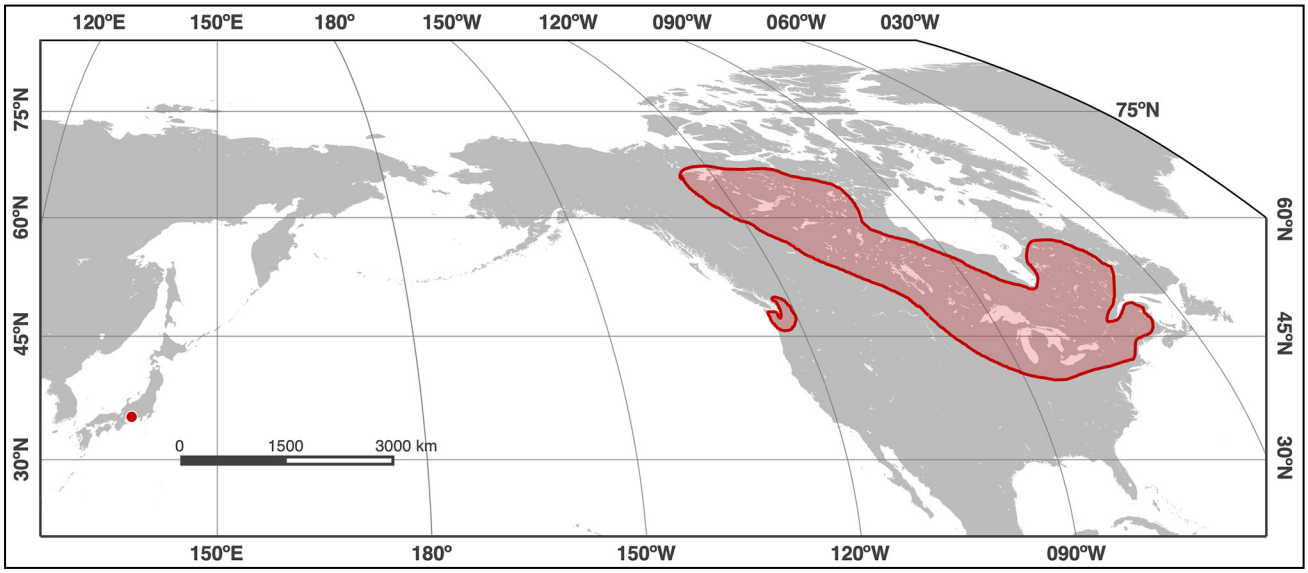

Figure 1. Map showing the *Daphnia retrocurva* collection location. The red circle denotes the newly recorded locality (Shin Toyone Reservoir, Aichi Prefecture, Japan), and the shaded areas represent previously known North American sites from Brooks (1957). The basal map was attributed to Kingfiser (CC0, via Wikipedia Commons) and modified by the authors.

Table 1. Comparison of morphological characteristics between *D. retrocurva* and resemble congeneric species (after Brooks 1957; Benzie 2005).

Character	*D. retrocurva*	*D. cristata*	*D. cucullata*	*D. dubia*	*D. galeata*	*D. longiremis*	*D. mendotae*	*D. parvula*
Length	0.7–1.8 mm	0.7–1.4 mm	1.0–2.0 mm	1.1–2.0 mm	Approximately 2.0 mm	0.5–2.4 mm	1.2–2.8 mm	0.7–1.5 mm
Tail spine	Variable, up to 0.7 carapace length	Variable, 0.5–1.0 carapace length	Variable, 0.5 or more of carapace length	Slender, long, 0.7 or more carapace length	Stout, short, 0.3–0.7, usually 0.5, carapace length	Long, >0.5 carapace length	Long, up to 0.7 length of carapace	Short, <0.3 carapace length
Head	Variable, rounded or triangular or with helmet anterodorsally recurved	Variable, rounded, to triangular sometimes with rounded, recurved helmet, never with spine at apex, frontal margin distinctly concave to nearly straight	Variable, broadly rounded, to strongly helmeted, with the helmet occasionally curved ventrally (procurved)	Rounded, more usually extended anteriorly with straight dorsal margin giving a triangular sometimes recurved helmet	Rounded, more usually extended anteriorly sometimes with straight dorsal margin to form broad triangular helmet, helmet never smoothly rounded, often with spine at apex	Of variable size and shape, rounded or triangular, rarely large, rounded, expanded dorsally	Rounded, often triangular with apical helmet resulting from anterior crest development, sometimes with a spine at apex, frontal margin straight or concave	Rounded, small relative to carapace, anterior margin concave between eye and rostrum
Eye	Small, distant from frontal margin of head	Small, optic vesicle large, can be distant from frontal margin of head	Small, close to frontal margin of head	Small-moderate, removed from frontal margin	Moderate to large, near frontal margin of head	Not close to frontal margin of head	Moderate, not always close to frontal margin of head	Close to frontal margin of head
Ocellus	Absent but inconspicuous small brown fleck may be present	Almost always present	Small, inconspicuous, or absent	Moderate-sized ocellus present	Small or absent	Very small or absent	Moderate-sized ocellus present	If present, inconspicuous; usually absent
Length of swimming seta which arises from base of second segment of three-segmented ramus of antenna	Extends well beyond the end of the ramus on which it is borne	Lacks this swimming seta altogether	Extends well beyond end of ramus on which it is borne	Extends well beyond end of ramus on which it is borne	Extends well beyond end of the ramus on which it is borne	Short, never reaching end of ramus	Extends well beyond end of ramus on which it is borne	Extends well beyond end of the ramus on which it is borne
Length of second postabdominal process relative to other ones	Long, at least half to two-thirds as long as first	Only first well developed	Intermediate between first and third	About one-fourth length of first	Half as long as first	Shorter than both first and third	Half as long as the first	The first two long, the first longer than the second; third much shorter
Postabdominal claw	With three external combs, spine size of comb 2 (middle) ≥ comb 1 (proximal) ≥ comb 3 (distal)	With three fine external combs with small spinules, spine size of comb 1 = comb 2 = comb 3	With three external combs, spine size of comb 2 large = comb 1 = comb 3	With three fine external combs, spine size of comb 1 = comb 2 = comb 3	With three fine external combs with small spinules, spine size of comb 1 = comb 2 = comb 3	With three external combs with small spinules, spine size of comb 2 > comb 1 = comb 3	With three fine external combs with small combs, spine size of comb 1 = comb 2 = comb 3	With three external combs, spine size of comb 2 > comb 1 ≥ comb 3

45 °C, and 3 s at 68 °C; then 35 cycles of 10 s at 98 °C, 5 s at 51 °C, and 3 s at 68 °C; and a final extension of 3 s at 68 °C. PCR primers for the mt12S region were the L13337-12S and the H13845-12S (Machida et al. 2004) and the PCR cycle consisted of 1 s of initial denaturation at 98 °C; followed by 35 cycles of 10 s at 98 °C, 5 s at 45 °C, and 3 s at 68 °C; and a final extension of 3 s at 68 °C. PCR primers for the mtND2 region were the MetF3 and TrpR (Ishida et al. 2006) and the PCR cycle was identical to that of mt12S except that the annealing temperature was 48 °C. After cleaning the PCR products with an ExoSap-IT Express kit (Thermo Fisher Scientific), we sent the products to Eurofins Genomics K.K. (Tokyo, Japan) for Sanger sequencing. In mtCOI and mt12S, the products were analyzed from both directions with the primer set of M13F and M13R (Prosser et al. 2013) and that of L13337-12S and H13845-12S for mtCOI and mt12S, respectively. In mtND2, the TrpR primer was used.

The sequences obtained were assembled and checked for mitochondrial pseudogenes (numts) by examining the presence of frameshift mutations and/or stop codons (in the cases of mtCOI and mtND2). The online version of MAFFT (Katoh et al. 2019) was used to align the assembled sequences in each gene region to detect haplotypes. All obtained haplotypes were submitted to the DDBJ/EMBL/GenBank databases under accession numbers LC909313 to LC909315.

In mtCOI, one haplotype obtained from the Shin Toyone Reservoir was screened against DDBJ/EMBL/GenBank to delimit the identity at the species level. A nucleotide BLAST search was performed using the Web BLASTn tool at the National Center for Biotechnology Information (NCBI) (Johnson et al. 2008) with default parameters, and we filtered the obtained subject sequences with 95–100% identity. We checked the assigned species name and, when available, microscopic images showing the head morphology of the "specimen_voucher" in each of the filtered subject sequences by clicking the hyperlink (to the related page in the BOLD Systems v. 5 website) shown in "db_xref" in the "source" feature (Table A2). All filtered subject sequences were then aligned with the haplotype obtained from the Shin Toyone Reservoir using the online version of MAFFT, and a TCS haplotype network (Clement et al. 2000) that illustrates all connections that have 95% probability of being the most parsimonious was drawn by the software PopART (Leigh and Bryant 2015) to visually understand the relationship between the haplotype obtained from the Shin Toyone Reservoir and the subject sequences. The same analysis was conducted on the mt12S and mtND2 haplotypes of the Shin Toyone Reservoir.

Results

***Daphnia retrocurva* Forbes, 1882**

Figure 2A–E

New records. JAPAN — Honshu Island • Aichi Prefecture, Kitashitara County, Toyone Village, the Shin Toyone Reservoir; 35.1300°N, 137.7598°E; alt. ca. 470 m; 1 Oct. 2025; I. Matsuba and K Nakamura leg.; 6 ♀ (dissected), TUMC 113008–113013; DDBJ accession number LC909313 for mtCOI, LC909314 for mt12S, and LC909315 for mtND2.

Identification. The specimens were identified as *D. retrocurva* based on Brooks (1957) and Benzie (2005), with external morphology (Figure 2A–E; Table 1) matching those descriptions. In short, each of our specimens had a head with anterodorsally recurved helmet (Figure 2A–C), which is one common characteristic of *D. retrocurva*, *Daphnia cristata* G.O. Sars, 1862, and *Daphnia dubia* Herrick, 1883. Our specimens always lacked ocellus (Figure 2A–C), which is present in *D. cristata* and *D. dubia* (Table 1). In addition, the length of the second postabdominal process relative to the first one was >0.5 (Figure 2D), and this relative length should be much smaller in *D. cristata* and *D. dubia* (Table 1). Additionally, our specimen possessed an enlarged middle pecten in the combs of spines on the outer sides of the postabdominal claws (Figure 2E, dotted line and red arrow). The enlarged middle pecten is another diagnostic morphological characteristic of *D. retrocurva* (Table 1), which is a member of the *D. pulex* group, whereas the middle pecten is not enlarged in *D. cristata* and *D. dubia*, both of which are members of the *D. longispina* group (Adamowicz et al. 2009; Chin and Cristescu 2021). Furthermore, while *D. cristata* always lack one of the swimming setae arising from the three-segmented ramus of the antenna, our specimens always possessed it (Figure 2A, red arrow). As such, we could clearly separate our specimens from *D. cristata* and *D. dubia*, and we conclude that *D. retrocurva* is the suitable scientific name for our specimens.

Anteriorly elongated helmets can also be observed on the heads of *Daphnia cucullata* G.O. Sars, 1862, *Daphnia galeata* G.O. Sars, 1864, *Daphnia longiremis* G.O. Sars, 1862, and *Daphnia mendotae* Birge, 1918 (Brooks 1957; Benzie 2005). However, our specimens were clearly differentiated from these four species as well. Specifically, the enlarged middle pecten in the combs of the postabdominal claw (Figure 2E) was different from those in *D. cucullata*, *D. galeata*, and *D. mendotae* (not enlarged; Table 1). In our specimens, the swimming seta arising from the base of the second segment of the three-segmented ramus of the antenna extended beyond the end of the ramus (Figure 2A). This characteristic showed that our specimens did not belong to *D. longiremis* (never reaching the end of the ramus; Table 1).

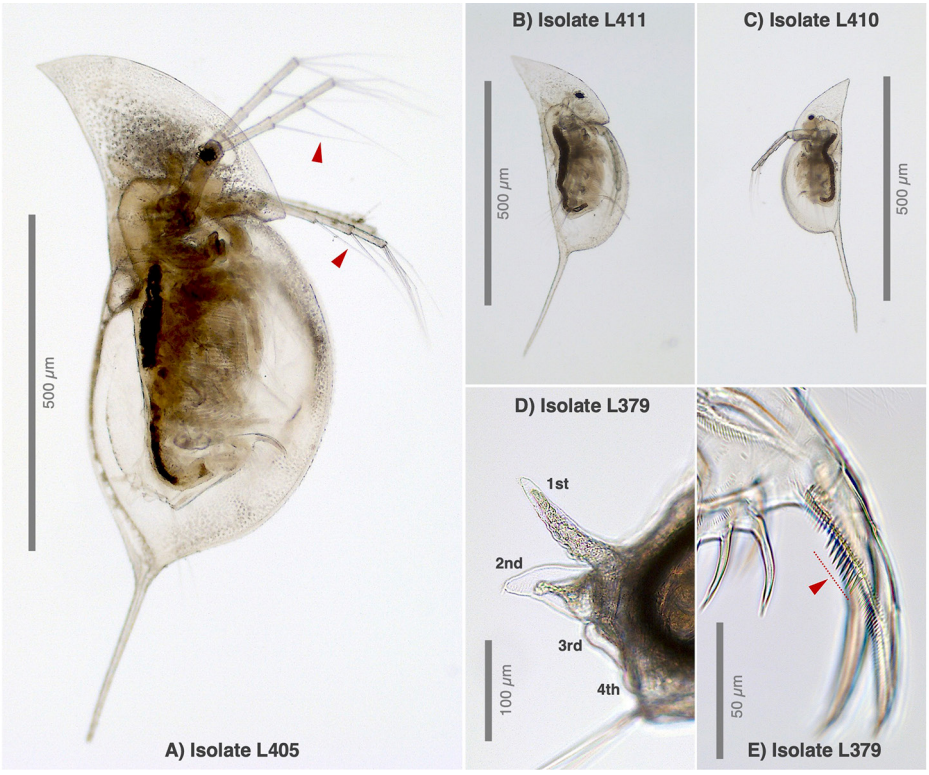

Figure 2. *Daphnia retrocurva*. **A.** Habitus of isolate L405 (lateral view). The tail spine is broken. The red arrows indicate the swimming seta arising from the base of the second segment of the three-segmented ramus of the antenna. **B.** Habitus of isolate L411 (lateral view). **C.** Habitus of isolate L410 (lateral view). The tail spine was slightly bent during specimen handling. **D.** The first to fourth postabdominal processes of isolate L379 (lateral view). **E.** Postabdominal claw of isolate L379 (lateral view). The red dotted line and arrow indicate an enlarged middle pecten.

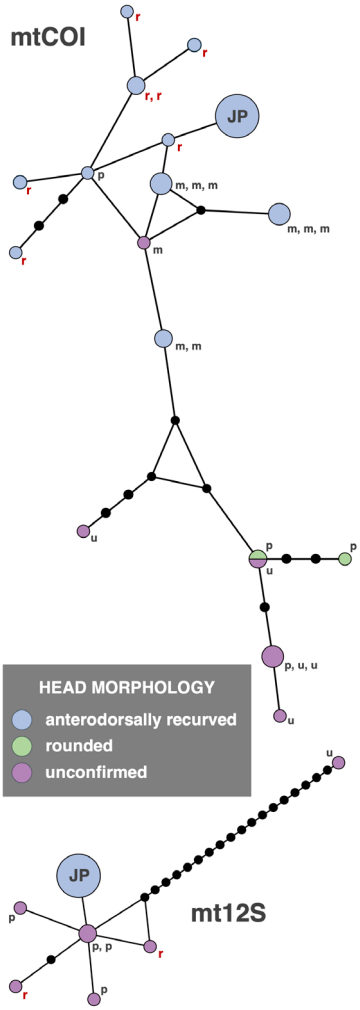

Figure 3. TCS haplotype networks for the mtCOI and mt12S sequences of *D. retrocurva* and its closely related species. The circle area corresponds to the number of individuals having the haplotype. The smallest circle corresponds to one individual, and the largest circle for the Shin Toyone Reservoir haplotype (inside "JP") corresponds to 12 individuals. Missing intermediate haplotypes are indicated in black. The alphabet(s) shown by a circle represents the scientific name assigned to each DNA sequence (r, *D. retrocurva*; p, *D. parvula*; m, *D. mendotae*; u, names with an unspecific term, either "sp." or "cf."). The circle colour represents the head morphology in the microscopic image(s) of the voucher sample.

In the Shin Toyone Reservoir, *D. retrocurva* was collected with *D. galeata*, which was present in the plankton sample at a concentration about three times that of *D. retrocurva*. In the reservoir, *D. galeata* did not have a head with an anterodorsally recurved helmet, which was always observed in *D. retrocurva* as explained above. In addition, *D. galeata* always possessed ocellus, whereas *D. retrocurva* always lacked ocellus. Thus, the two species in the reservoir were easily separated from each other. Besides *D. galeata*, some copepod species (*Eodiaptomus japonicus* (Burckhardt, 1913), *Mesocyclops dissimilis* Defaye and Kawabata, 1993, and *Thermocyclops crassus* (Fischer, 1853)) and cladoceran species (*Bosmina fatalis* Burckhardt, 1924, *Ceriodaphnia* cf. *lacustris* Birge, 1893, *Diaphanosoma dubium* Manujlova, 1964, and *Leptodora* cf. *kindtii* (Focke, 1844) were collected with *D. retrocurva*.

The sequence lengths of mtCOI, mt12S, and mtND2 were 658, 538, and 663 base pairs, respectively. Only one haplotype per gene region was obtained among the 12 individuals sequenced, indicating no intraspecific sequence variation. In mtCOI, our BLASTn search minded 25 subject sequences from North America: the sequence similarities to the Shin Toyone haplotype were more than 98% (Table A2). The identities of these subject sequences included *D. retrocurva*, *D. parvula*, *D. mendotae*, and other non-specific names. The mtCOI Shin Toyone haplotype was only one nucleotide different from the subject sequence obtained from Lake Erie (accession no. OP830195; Table A2). The identity of this particular subject sequence was *D. retrocurva*, and microscopic images of the voucher specimen showed an anterodorsally recurved helmet, the larger 2nd pecten than the 3rd pecten on the postabdominal claw, and the absence of ocellus (Table A2). The mtCOI haplotype network (Figure 3) revealed that the Shin Toyone haplotype (marked "JP") was at most five steps apart per 658 base pairs (thus, sequence divergences <1%) from the other haplotypes obtained from individuals with anterodorsally recurved helmet (i.e. the blue-coloured haplotypes in Figure 3) irrespective of their assigned species names. We noticed that at least two individuals assigned as *D. mendotae* lacked ocellus in the microscopic images, although *D. mendotae* should possess moderate-sized ocellus (Figure 3; Table 1).

In mt12S, our BLASTn search minded 5 subject sequences from North America, one from South America (Argentina), and one from Europe (France): the sequence similarities to the Shin Toyone haplotype were >95% (Table A2). The mt12S Shin Toyone haplotype was only one to two steps different from the subject sequences from North America and Europe, whose assigned names included *D. retrocurva* and *D. parvula* (Figure 3). The head morphology could not be checked because neither the subject sequence included information on the voucher specimen.

Our BLASTn search did not find sequences with >95% sequence similarity to the mtND2 Shin Toyone haplotype.

Discussion

Our record confirms the presence of *Daphnia retrocurva* in Japan in terms of both morphology (as mentioned above) and molecular phylogeny (see below). There are no other published records outside North America (Benzie 2005; Petrusek et al. 2008; Kotov et al. 2013), despite the fact that many studies on the genus *Daphnia* have been conducted, including the ones in adjacent China, South Korea, and Russian Far East in the last two decade (e.g. Jeong et al. 2014; Xiang et al. 2015; Zuykova et al. 2019, 2024). Thus, this is the first record of *D. retrocurva* occurrence outside its native range and that from the Palearctic region, resulting in a significant spatial gap in their geographical range.

North American *D. retrocurva* and *D. parvula* are sister species (Constanzo and Taylor 2010). The former is distributed from the central Midwest of the USA and to northern parts of Canada, whereas the latter is distributed from South America to the southern parts of Canada. The two species overlap largely near the southern extent of the glacial lake zone in North America where rare co-occurrence is documented (Brooks 1957). According to the hypothesis of Brooks (1957), *D. retrocurva* is a postglacial derivative of *D. parvula* because their occurrence is confined to the glaciated portion of the North American continent and typically appears in deep temperate glacial lakes (such as the Laurentian Great Lakes). The phylogenetic study of Constanzo and Taylor (2010) estimated the divergence time of the two species as ca. 20,000– 30,000 years ago, which supports Brooks's (1957) hypothesis. Constanzo and Taylor (2010) documented the intermediate genetic divergence pattern between panmixia and reciprocal monophyly among the two sister species in both mitochondrial and nuclear loci. Considering these previous results, it is not surprising that the Shin Toyone mtCOI and mt12S haplotypes were closely related to both *D. retrocurva* and *D. parvula* haplotypes.

The anterodorsally recurved helmet of *D. retrocurva* is, when present (see below), a determinative morphological characteristic that separates the species from *D. parvula*, which always has a rounded head (Brooks 1957; Benzie 2005; Constanzo and Taylor 2010). The microscopic images of voucher samples for the North American mtCOI haplotypes revealed the presence of an anterodorsally recurved helmet in some source individuals (Figure 3; Table A2). Thus, we could confidently identify such North American individuals (haplotypes) as *D. retrocurva*, leading us to conclude that our specimens were *D. retrocurva* in terms of both morphology and molecular phylogeny. As for the assigned name *D. mendotae* in individuals having anterodorsally recurved helmet on the microscopic images, we noticed that the individuals were recorded by the same study (Elías-Gutiérrez et al. 2018) and that at least two individuals lacked ocellus, which should be possessed by *D. mendotae*. Furthermore, the helmet shape of *D. mendotae* is mostly triangular (Brooks 1957; Benzie 2005) and not recurved as it was in the microscopic images. Thus, we simply consider that the name *D. mendotae* was a result of misidentification: the accurate name would have been *D. retrocurva*.

Daphnia parvula populations in Europe have been known since the 1970s and are considered non-indigenous (e.g. Schwenk et al. 2000; Riccardi et al. 2004). As mentioned above, our report on Japanese *D. retrocurva* is the first occurrence data outside its native North America. The Japanese and North American populations of *D. retrocurva* showed little divergence in terms of mtCOI and mt12S. This small genetic divergence is partially explained by the fact that *D. retrocurva* is a young species as a postglacial derivative of *D. parvula* (Brooks 1957; Constanzo and Taylor 2010). An additional possible explanation for the small genetic divergence is that *D. retrocurva* translocated with recent human activities. The occurrence of North American native, non-indigenous cladocerans, such as *Daphnia ambigua* Scourfield, 1947, *Daphnia pulicaria* Forbes, 1893, *Daphnia pulex* Leydig, 1860, and *Chydorus brevilabris* Frey, 1980, has already been confirmed in Japanese freshwaters, probably due to unintentional human introduction (Hanazato and Yasuno 1985; Urabe et al. 2003; So et al. 2015; Kotov et al. 2022; Makino et al. 2023). In the present study, only one haplotype per gene region was observed in the Shin Toyone Reservoir *D. retrocurva* population (12 individuals examined), implying a genetic bottleneck along with anthropogenic translocation. Since the Shin Toyone Reservoir also harbours North American Largemouth Bass *Micropterus nigricans* (Cuvier, 1828) and Bluegill *Lepomis macrochirus* Rafinesque, 1810 (Kyukamura Chausuyama Kogen 2022a, 2022b), this reservoir is somehow affected by factors from North America. The two non-native fish species have already spread to various reservoirs in Japan; however, *D. retrocurva* was not found in previous studies (e.g. Suzuki et al. 2025). Therefore, it remains unclear why the distribution of *D. retrocurva* is currently limited to the Shin Toyone Reservoir or how it was introduced into this reservoir.

In *D. retrocurva*, the degree of the anterodorsal extension of the head often undergoes pronounced seasonal changes. For example, the population of Bantam Lake (Connecticut, USA) lacked anterodorsal extension from April to mid-June, whereas it showed pronounced anterodorsal extension in summer (Brooks 1946). Further studies are needed to examine whether the *D. retrocurva* population of Shine Toyone Reservoir undergoes similar cyclomorphosis patterns. The anterodorsally recurved helmet reduces the vulnerability of *D. retrocurva* to invertebrate predators (Havel and Dodson 1985; Constanzo and Taylor 2010). Invertebrate predator cues can enhance helmet development (Brooks 1946). In Shin Toyone Reservoir, *M. dissimilis* and *L.* cf. *kindtii* can be invertebrate predators; however, they are not distributed in North America (note that North American *L. kindtii* is genetically different from Japanese *Leptodora*: Millette et al. 2011; Xu et al. 2011). If *D. retrocurva* in the Shin Toyone Reservoir was indeed recently translocated, it could mean that *D. retrocurva* develop helmet under the cues of invertebrate predators whom *D. retrocurva* did not encounter in the native range. Further studies are also needed in this regard. Similarly, whether the anterodorsally recurved helmet reduces the vulnerability of *D. retrocurva* to Japanese (or East Asian) invertebrate predators is also worth studying.

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Additional information

Conflict of interest
The authors declare that no competing interests exist.

Ethical statement
No ethical statement is reported.

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Author contributions
Conceptualization: WM, JU. Data curation: WM. Funding acquisition: JU. Investigation: WM, JU. Methodology: WM, JU. Resources: WM, JU. Supervision: JU. Visualization: WM. Project administration: JU. Validation: WM, JU. Writing – original draft: WM, JU. Writing – review and editing: WM, JU.

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Data availability
The collected specimen was deposited in the Tohoku University Museum Collection (TUMC 113008–113013). The obtained mtDNA sequences have been deposited at the DDBJ/EMBL/GenBank nucleotide sequence databases (accession number: LC909313–LC909315). Except for these, all data that support the findings of the present study are available in the main text and the Appendix (Tables A1, A2).

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Appendix

Table A1. A a list of 12 females of Shin Toyone Dam *Daphnia retrocurva*, which were used for DNA sequencing.

No.	Isolate name	Developmental stage	Body part usd for DNA extraction	Tohoku University Museum Collection (TUMC) no.	Content
1	L376	Juvenile	Whole body	No voucher sample	—
2	L377	Juvenile	Whole body	No voucher sample	—
3	L379	Adult, ovigerous	Embryo	113008	Whole body (dissected to isolete postabdomen) excluding embyo
4	L380	Adult, ovigerous	Parts other than head region	113009	Head region and embyro
5	L405	Adult, ovigerous	Parts other than head region	113010	Head region and embyro
6	L406	Adult, ovigerous	Embryo	113011	Whole body excluding embyo
7	L407	Adult, ovigerous	Parts other than head region and postabdomen	113012	Head region and postabdomen
8	L408	Adult, ovigerous	Parts other than head region	113013	Head region
9	L409	Juvenile	Whole body	No voucher sample	—
10	L410	Juvenile	Whole body	No voucher sample	—
11	L411	Juvenile	Whole body	No voucher sample	—
12	L412	Juvenile	Whole body	No voucher sample	—

Table A2. The list of mtCOI and mt12S sequences mined from DDBJ/EMBL/GenBank nucleotide sequence databases to construct the TCA haplotype networks in the main text (Figure 3).

	Characteristics of subject sequence obtained by BLASTn												Image(s) on BOLD website			
Gene region	Description	Scientific Name	Max score	Total score	Query cover	E value	Per. ident	Acc. len	Accession	Locality	Latitude, longitude	Reference	Process ID	Head, helmet morphology	Size of mid pecten of postabdominal claw	Ocellus
mtCOI	*D. retrocurva* voucher ZOOPS_0736 COI gene	*D. retrocurva*	1210	1210	100%	0	99.9	658	OP830195.1	Canada: Ontario, Lake Erie, GLNPO-ER61	41.946°N, 083.045°W	—	ZOOPS736-20	Anterodorsally recurved	Larger than third	Absent
	D. mendotae voucher BIOUG30454-F07 COI gene	*D. mendotae*	1199	1199	100%	0	99.5	658	MG450241.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1682-16	Anterodorsally recurved	No photo	Absent? Too dark
	D. mendotae voucher BIOUG30360-A08 COI gene	*D. mendotae*	1199	1199	100%	0	99.5	658	MG449784.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1243-16	Anterodorsally recurved	No photo	Absent? Too dark
	D. mendotae voucher BIOUG30360-A07 COI gene	*D. mendotae*	1199	1199	100%	0	99.5	658	MG449423.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1242-16	Anterodorsally recurved	No photo	Absent? Too dark
	D. retrocurva voucher ZOOPS_0740 COI gene	*D. retrocurva*	1195	1195	100%	0	99.4	658	OP830077.1	Canada: Ontario, Lake Erie, GLNPO-ER61	41.946°N, 083.045°W	—	ZOOPS740-20	Anterodorsally recurved	Larger than third	Absent? Too dark
	D. mendotae voucher BIOUG30348-D07 COI gene	*D. mendotae*	1194	1194	100%	0	99.4	658	MG448996.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1183-16	Anterodorsally recurved	No photo	Absent? Too dark
	D. mendotae voucher BIOUG30360-A09 COI gene	*D. mendotae*	1194	1194	100%	0	99.4	658	MG449874.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1244-16	Anterodorsally recurved	No photo	Absent
	D. retrocurva voucher ZOOPS_0739 COI gene	*D. retrocurva*	1194	1194	100%	0	99.4	658	OP830134.1	Canada: Ontario, Lake Erie, GLNPO-ER61	41.946°N, 083.045°W	—	ZOOPS739-20	Anterodorsally recurved	Larger than third	Absent
	D. mendotae voucher GZPL-030 COI gene	*D. mendotae*	1194	1194	100%	0	99.4	658	MG449950.1	Canada: Ontario, Guelph Lake	43.611°N, 080.209°W	Elías-Gutiérrez et al. 2018	BACZP220-15	no photo	No photo	No photo
	D. mendotae voucher BIOUG30348-D10 COI gene	*D. mendotae*	1188	1188	100%	0	99.2	658	MG449766.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1186-16	Anterodorsally recurved	No photo	Absent? Too dark
	D. mendotae voucher BIOUG30348-D09 COI gene	*D. mendotae*	1188	1188	100%	0	99.2	658	MG450140.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1185-16	Anterodorsally recurved	No photo	Absent? Too dark
	D. mendotae voucher BIOUG30348-D08 COI gene	*D. mendotae*	1188	1188	100%	0	99.2	658	MG449837.1	Canada: Ontario, Eel Lake	44.5631°N, 076.5535°W	Elías-Gutiérrez et al. 2018	BACZP1184-16	Anterodorsally recurved	No photo	Absent
	D. retrocurva voucher ZOOPS_0738 COI gene	*D. retrocurva*	1182	1182	100%	0	99.1	658	OP830204.1	Canada: Ontario, Lake Erie, GLNPO-ER61	41.946°N, 083.045°W	—	ZOOPS738-20	Anterodorsally recurved	Larger than third	Absent
	D. retrocurva voucher ZOOPS_0080 COI gene	*D. retrocurva*	1177	1177	98%	0	99.5	646	OP830209.1	USA: New York, Lake Ontario, GLNPO - ON69bw	43.319°N, 079.000°W	—	ZOOPS080-18	Anterodorsally retrocurved (slightly)	Larger than third	Absent
	D. parvula voucher BIOUG<CAN>:09BBCRU-0074 COI gene	*D. parvula*	1171	1171	100%	0	98.8	658	HM883963.1	USA	33.870°N, 096.826°W	—	—	—	—	—
	D. retrocurva voucher ZOOPS_0082 COI gene	*D. retrocurva*	1171	1171	98%	0	99.4	646	OP829982.1	USA: New York, Lake Ontario, GLNPO - ON69b	43.319°N, 079°W	—	ZOOPS082-18	Anterodorsally retrocurved (very slightly)	Larger than third	Absent
	D. retrocurva voucher ZOOPS_0083 COI gene	*D. retrocurva*	1168	1168	97%	0	99.5	641	OP830194.1	USA: New York, Lake Ontario, GLNPO - ON69b	43.319°N, 079.000°W	—	ZOOPS083-18	Anterodorsally retrocurved (slightly)	Larger than third	Absent
	D. sp. AS1b3 COI gene	*D.* sp. AS1b3	1160	1160	100%	0	98.5	658	KC616902.1	Mexico: Aguascalientes, Rincon de Romos, El Saucillo dam	22.249°N, 102.339°W	Prosser et al. 2013	—	—	—	—
	D. parvula voucher BIOUG<CAN>:09BBCRU-0111 COI gene	*D. parvula*	1155	1155	100%	0	98.3	658	HM883993.1	USA	33.8823°N, 096.7987°W	—	—	—	—	—
	D. sp. AS30b3 COI gene	*D.* sp. AS30b3	1153	1153	98%	0	98.9	645	KC616909.1	Mexico: Aguascalientes, San Jose de Gracia, El Canal pond	22.148°N, 102.346°W	Prosser et al. 2013	—	—	—	—
	D. sp. BOLD:AAE7849 voucher ZPLMX180 COI gene	*D.* sp. BOLD:AAE7849	1140	1140	99%	0	98.3	650	EU702140.1	Mexico	20.07°N, 099.56°W	Elías-Gutiérrez et al. 2008	—	—	—	—
	D. sp. BOLD:AAE7849 voucher ZPLMX181 COI gene	*D.* sp. BOLD:AAE7849	1131	1131	99%	0	98.0	650	EU702139.1	Mexico	20.07°N, 099.56°W	Elías-Gutiérrez et al. 2008	—	—	—	—
	D. parvula COI gene	*D. parvula*	1103	1103	96%	0	98.3	630	FJ427504.1	Mexico: Little Presa	—	Adamowicz et al. 2009	—	—	—	—
	D. parvula voucher NJPEL-00019 COI gene	*D. parvula*	1062	1062	90%	0	98.5	595	MG936477.1	Canada: Ontario, Point Pelee National Park, Lake Erie	41.9661°N, 082.5353°W	—	NJCGS1030-11	Retrocurved	No photo	Absent
	D. sp. AS1b2 COI gene	*D.* sp. AS1b2	904	904	79%	0	98.1	518	KC616915.1	Mexico: Aguascalientes, Rincon de Romos, El Saucillo dam	22.249°N, 0102.339°W	Prosser et al. 2013	—	—	—	—
mt12S	*D. parvula* small subunit ribosomal RNA gene	*D. parvula*	922	922	95%	0	99.2	528	FJ427441.1	Canada: Ontario, Kitchener, Columbia Lake	—	Adamowicz et al. 2009	—	—	—	—
	D. parvula from Canada 12S ribosomal RNA gene	*D. parvula*	883	883	90%	0	99.6	491	AY626358.1	Canada: Ontario	—	Penton and Crease 2004	—	—	—	—
	D. retrocurva from USA 12S ribosomal RNA gene	*D. retrocurva*	883	883	90%	0	99.6	488	AY626359.1	USA: Indiana	—	Penton and Crease 2004	—	—	—	—
	D. retrocurva small subunit ribosomal RNA gene	*D. retrocurva*	824	824	86%	0	98.9	469	FJ427449.1	USA: Indiana, Crooked Lake	—	Adamowicz et al. 2009	—	—	—	—
	D. parvula from France 12S ribosomal RNA gene	*D. parvula*	815	815	83%	0	99.6	447	AF277286.1	France	—	Schwenk et al. 2000	—	—	—	—
	D. parvula from Canada 12S ribosomal RNA gene	*D. parvula*	809	809	83%	0	99.3	447	AF277287.1	Canada	—	Schwenk et al. 2000	—	—	—	—
	D. cf. parvula sp. 2 Argentina small subunit ribosomal RNA gene	*D.* cf. *parvula* sp. 2 Argentina	725	725	86%	0	95.0	469	FJ427442.1	Argentina: Rio Coronda, Santa Fe (site #9)	—	Adamowicz et al. 2009	—	—	—	—