

1 **Lumping three nominal species into one: taxonomic revision of amphibian parasitic**
2 **leeches of *Torix* in Far East Asia (Hirudinea: Glossiphoniidae)**

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9

10 **Abstract.** While most members of the freshwater leech family Glossiphoniidae possess
11 the mid-body somites divided into three annuli, the genus *Torix* Blanchard, 1893 is
12 distinguished by its two-annuli somites. *Torix* shows high species richness in Far East
13 Asia, and three nominal species have been recognised in the Japanese Archipelago and
14 adjacent regions, which can be distinguishable by a combination of both internal and
15 external morphological characteristics. However, recent studies have shown that these
16 diagnostic features are ontogenetically variable, and this has resulted in taxonomic
17 confusion among *Torix* species endemic to the Japanese Archipelago. In this study, we
18 revisit the taxonomic accounts of *T. orientalis* (Oka, 1925) and *T. tagoi* (Oka, 1925), in
19 addition to that of the recently redescribed *T. tukubana* (Oka, 1935), to clarify the
20 diagnostic characteristics for each of the three species. Our morphological and
21 molecular phylogenetic analyses demonstrated that the three *Torix* species in Japan are
22 indistinguishable. We therefore conclude here that these species should be synonymized
23 and treated as a single species. Since the specific names *orientalis* and *tagoi* were
24 simultaneously established under the genus *Oligobdella* Moore, 1918, we herein act as

25 First Reviser and gave precedence to the name *O. tagoi*, and thus the valid name for the
26 Far East Asian *Torix* species is *T. tagoi* unless *T. orientalis* and *T. tagoi* are treated as
27 distinct species. Because there are several type localities for *T. tagoi* and the name-
28 bearing types have been lost, we designate a neotype for this species to obviate
29 zoological and nomenclatural issues.

30 ZooBank: urn:lsid:zoobank.org:pub:E2DBF999-3B51-456F-AB04-A7D138E0AF2D

31

32 **Short summary.** Freshwater leeches of the genus *Torix* Blanchard, 1893 in Japan have
33 considerable morphological variation, leading to taxonomic confusion. In this study, we
34 revisit the taxonomic accounts of *T. orientalis* (Oka, 1925) and *T. tagoi* (Oka, 1925) to
35 clarify the diagnostic characteristics for the three *Torix* species in Japan. Our
36 morphological and molecular phylogenetic analyses demonstrated that the Japanese
37 *Torix* species are indistinguishable. We therefore conclude here that the three *Torix*
38 species should be synonymized and treated as a single species.

39

40 **Additional keywords:** “Rhynchobdellida,” Glossiphoniiformes, redescription,
41 neotypification, synonymization, ectoparasite, blood sucking, Japan

42

43 Running title: Taxonomic revision of *Torix* endemic to Japan

44

45 **Introduction**

46 Leeches are carnivorous annelids with body segments superficially divided into annuli,
47 and they are thought to enhance the extensibility of the body (Sawyer 1986). The family
48 Glossiphoniidae is the most diverse group of freshwater leeches (Sket and Trontelj
49 2008), and most members of this family have mid-body somites divided into three
50 annuli (triannulate). Some species have reduced mid-body somites (biannulate), and
51 biannulate species have been thought to be phylogenetically closely related because of
52 their shared distinctive morphology. However, recent molecular phylogenetic analyses
53 have revealed that annular reduction has occurred independently in several
54 glossiphoniid lineages. Specifically, the North American biannulate species *Oligobdella*
55 *biannulata* (Moore, 1900) has been found to be derived within the triannulate genus
56 *Placobdella* Blanchard, 1893 (Light and Siddall 1999). The South American *O.*
57 *brasiliensis* Cordero, 1937 is known to form a monophyletic group with the other
58 triannulate genus *Haementeria* De Filippi, 1849 (Oceguera-Figueroa 2012).

59 *Torix* Blanchard, 1893 is another glossiphoniid genus that has been established
60 on the basis of its reduced annulation pattern. Currently, *Torix* comprises six species
61 distributed from Southeast Asia to New Zealand, and four species have been described
62 in Far East Asia: *T. cotylifer* Blanchard, 1898 from China; *T. orientalis* (Oka, 1925)
63 from Japan; *T. tagoi* (Oka, 1925) from Japan and Korea; and *T. tukubana* (Oka, 1935)
64 from Japan. Although the original systematic accounts were unclear because of a lack of
65 information after the original descriptions, *T. tukubana* was recently redescribed, and
66 phylogenetic analyses have revealed that this species forms a distinct lineage from other
67 known biannulate species that is closely related to the triannulate *Hemiclepsis*
68 *Vejdovsky*, 1884 (Kambayashi *et al.* 2020).

69 In the Japanese Archipelago, three *Torix* species have been described, and these
70 have been distinguished by the combination of the following morphological traits:
71 ventral annulation pattern (biannulate or triannulate), dorsal papillae (presence or
72 absence), number of eyes (one or two pairs), width of caudal sucker (larger or smaller
73 than the body width), and morphology of crop caeca (diverticulated or not). However,
74 recent studies have shown that morphologically distinct *Torix* species collected at a
75 single site are genetically identical (Kambayashi *et al.* 2019, 2020). These studies
76 highlight the fact that the features previously used for species identification are
77 ontogenetically variable; additional investigation is thus needed to identify diagnostic
78 characteristics suitable for defining each species.

79 In this study, we revisit the taxonomic accounts of the two unresolved *Torix*
80 species inhabiting Japan. Both *T. orientalis* and *T. tagoi* have multiple type localities,
81 and their name-bearing type specimens are thought to have been lost or destroyed
82 according to the present survey and Nakano and Itoh (2011). Therefore, we newly
83 collected their topotypic specimens and a diverse set of samples in Japan, and employed
84 an integrative approach that combines morphological and molecular data to reassess the
85 taxonomic status of Japanese *Torix* species.

86

87 **Materials and methods**

88 *Sampling and morphological examination*

89 Leech specimens were collected from 27 localities in Japan (Fig. 1 and Table 1),
90 including the five type localities: Akame (Mie Prefecture), Nemuro (Hokkaido), and
91 Yumoto (Tochigi Prefecture) for *T. orientalis*; Takayama (Gifu Prefecture) for *T. tagoi*;
92 and Mount Tsukubasan (Ibaraki Prefecture) for *T. tukubana*. Leeches were collected

93 from underneath rocks in mountain streams or from the surface of amphibians. Altitude
94 and coordinates for the localities were obtained using a Garmin eTrex GPS unit.

95 The collected leeches were individually kept at 16°C in the laboratory to digest
96 their blood meal. Subsequently, the specimens were relaxed by the gradual addition of
97 99% ethanol to freshwater. A quarter of the caudal sucker was taken from every
98 specimen for DNA extraction and the remaining bodies were fixed in 10% formalin and
99 preserved in 70% ethanol. The following four body measurements were taken: body
100 length from the anterior margin of the oral sucker to the posterior margin of the caudal
101 sucker (BL), maximum body width (BW), caudal sucker length from the anterior
102 margin to the posterior margin of the sucker (CL), and caudal sucker width from the
103 right to the left margins of the sucker (CW). Examination, dissection and drawing of the
104 specimens were accomplished under stereoscopic microscopes with a drawing tube
105 (Leica M125C and Olympus SZX7). Images of the specimens were captured with the
106 aid of a Leica MC170HD digital camera mounted on the Leica M125C, and assembled
107 using Leica Application Suite software (ver. 4.12, see <https://www.leica-microsystems.com/products/microscope-software/p/leica-application-suite/>). Specimens used in this
108 study have been deposited in the Zoological Collection of Kyoto University (KUZ).

110 The leech collection at the National Museum of Nature and Science, Tsukuba,
111 Japan (NSMT), including most of Oka's leech collection (Nakano 2010), was surveyed
112 to determine whether the type series of *Torix* species still exists. Although a portion of
113 Oka's collection is kept at The University Museum, The University of Tokyo (UMUT),
114 the type series was not discovered in the UMUT zoological collection (Nakano and Itoh
115 2011).

116 The somite numbering convention is based on Moore (1927): body somites are

117 denoted by Roman numerals and the annuli in each somite are given alphanumeric
118 designations.

119

120 *Molecular analyses*

121 Total DNA of 39 *Torix* specimens (Table 1) were extracted from the caudal suckers
122 using phenol/chloroform extraction. The partial sequence of mitochondrial cytochrome
123 *c* oxidase subunit I (*COI*), nuclear *18S* rRNA (*18S*), and Internal Transcribed Spacer 1
124 and 2 flanking the 5.8S rRNA (*ITS*) of representative specimens were PCR amplified
125 using the primers of LCO1490–HCO2198 and LCO-inerpo2–HCO-out (Folmer *et al.*
126 1994; Nakano 2016), A–B (Medlin *et al.* 1988; Apakupakul *et al.* 1999), and ITS5–
127 ITS4 (White *et al.* 1990), respectively. The PCR and cycle sequencing reactions were
128 performed according to Nakano (2012) for *COI* and *18S*, and de Carle *et al.* (2017) for
129 *ITS*, except for the use of PCR reaction kit, EmeraldAmp PCR Master Mix (Takara
130 Bio). The newly determined sequences were deposited in the International Nucleotide
131 Sequence Databases (INSD) through the DNA Data Bank of Japan (DDBJ).

132 We downloaded additional *COI* sequences from INSD and Barcode of Life
133 Data System (BOLD) of *Hemiclepsis* leeches, known to be most closely related to *Torix*
134 (Kabayashi *et al.* 2020), and species of *Glossiphonia* Johnson, 1816, which have been
135 used for delimitation analyses in Jovanović *et al.* (2021), as the outgroup taxa (Table 1).
136 The sequences obtained were aligned with MAFFT with the L-INS-i option (ver. 7.427,
137 see <https://mafft.cbrc.jp/alignment/software/>; Katoh and Standley 2013). After removing
138 identical sequences, phylogenetic trees were inferred with maximum likelihood (ML)
139 and Bayesian inference (BI) methods. The ML phylogeny was inferred using IQ-TREE
140 (ver. 1.6.12, see <http://www.iqtree.org/>; Nguyen *et al.* 2015), then nonparametric

141 bootstrapping (BS) was conducted with 1,000 replicates. BI tree and Bayesian posterior
142 probabilities (PP) were obtained using MrBayes (ver. 3.2.6, see [https://github.com/](https://github.com/NBISweden/MrBayes/)
143 [NBISweden/MrBayes/](https://github.com/NBISweden/MrBayes/); Ronquist *et al.* 2012). Two independent runs of four Markov
144 chains were conducted for 12 million generations, and a tree was sampled every 1,000
145 generations. The parameter estimates and convergence were checked using Tracer (ver.
146 1.7.1, see [https://github.com/](https://github.com/beast-dev/tracer/releases/tag/v1.7.1) [beast-dev/tracer/releases/tag/v1.7.1](https://github.com/beast-dev/tracer/releases/tag/v1.7.1); Rambaut *et al.* 2018),
147 and the first 10% of trees were discarded based on the result.

148 In order to assess the genetic differentiation within our dataset of *Torix*, five
149 different methods were used for species delimitation analyses: Automatic Barcode Gap
150 Discovery (ABGD) (Puillandre *et al.* 2012), Assemble Species by Automatic
151 Partitioning (ASAP) (Puillandre *et al.* 2020), Generalized Mixed Yule Coalescent model
152 (GMYC) (Fujisawa and Barraclough 2013), Bayesian implementation of Poisson Tree
153 Processes (bPTP) (Zhang *et al.* 2013), and multi-rate PTP (mPTP) (Kapli *et al.* 2017).
154 The analyses were based on the 53 *COI* sequences used in phylogenetic analyses. The
155 ABGD analysis was performed in a web-based interface
156 (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) with the following settings:
157 Pmin, 0.001; Pmax, 0.1; Steps, 10; X (relative gap width), 1.5; Nb bins (for distance
158 distribution), 20; distance, Kimura (K80) TS/TV 2.0. The ASAP analysis was conducted
159 using the online ASAP version (<https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html>)
160 with default settings and the K2P distance model. The GMYC analysis was executed
161 using the ‘splits’ package (ver. 1.0-19, T. Ezard, T. Fujisawa and T. G. Barraclough, see
162 <http://R-Forge.Rproject.org/projects/splits/>) in the R program. The bPTP analysis was
163 performed at the bPTP web server (<https://species.h-its.org>) with the following settings:
164 No. MCMC generations, 100,000; Thinning, 100; Burn-in, 0.1; Seed, 123. The mPTP

165 analysis was executed on the mPTP web server (<https://mptp.h-its.org>) with default
166 settings.

167 The *ITS* sequences obtained from 22 individuals were aligned with MAFFT,
168 and relationships between the obtained *ITS* haplotypes were estimated by statistical
169 parsimony network using PopART with the TCS option (ver. 1.7, see
170 <https://popart.maths.otago.ac.nz/>; Leigh and Bryant 2015). Pairwise comparisons of the
171 uncorrected *p*-distance for *COI* and *ITS* sequences between the representative
172 specimens of *Torix* obtained in this study and one collected from Mt. Tsukubasan,
173 Ibaraki Prefecture (INSD accession number LC538265), as well as a sample reported
174 from Liaoning Province, China (INSD accession number OL779256) were calculated
175 using MEGA X (ver. 10.1.7, see <https://www.megasoftware.net>; Kumar *et al.* 2018).

176

177 **Results**

178 *Molecular analyses*

179 Our *COI* alignment matrix comprised 1,267 bp representing 31 haplotypes of Japanese
180 *Torix*. The maximum uncorrected pairwise genetic distance among *Torix* collected in
181 this study was 5.2% (Table 2), which is smaller than the range of interspecific variation
182 observed in other glossiphoniid species (de Carle *et al.* 2017; Kaygorodova *et al.* 2020;
183 Jovanović *et al.* 2021).

184 Our ML ($\ln L = -7106.47$; Fig. 2) and BI ($\ln L = -7154.13$; not shown) trees
185 based on *COI* sequences revealed that all haplotypes detected in this study formed a
186 single well-supported clade (BS = 100%, PP = 1.0) along with the sequence collected in
187 China, which was previously identified by Zhu *et al.* (2023) as *T. tukubana*. In addition,
188 *Torix* leeches in Japan formed a monophyletic lineage (BS = 57%, PP = 0.92), and were

189 moderately supported to form two major clades in eastern (location #1–19, #21 in Table
190 1) (BS = 60%, PP = 0.98) and western Japan (location #20, #22–27) (BS = 80%, PP =
191 0.97). For *Torix* + *Hemiclepsis* + *Glossiphonia* leeches, the ABGD and ASAP analyses
192 resulted in 14 groups, the GMYC and bPTP in 20 groups, and mPTP in 4 groups; for
193 *Torix* species, ABGD and ASAP analyses resulted in one group and GMYC, bPTP, and
194 mPTP in two groups (Fig. 2). All of these results supported a one-species classification
195 of Japanese *Torix* species.

196 The *ITS* data revealed low genetic diversity within Japanese *Torix* individuals
197 (uncorrected *p*-distance < 1.1%), which is within the range of intraspecific variation in
198 *Placobdella* (de Carle *et al.* 2017). Network analysis indicated that *Torix* in Japan can
199 be broadly divided into the eastern and western lineages (Fig. 3), as indicated in the
200 phylogenetic analysis of *COI* (Fig. 2). The *18S* rRNA gene sequences of representative
201 specimens were identical to that of the *T. tukubana* topotype (INSD accession number
202 LC538285).

203

204 *Morphological examination*

205 As noted in previous studies (Kambayashi *et al.* 2019, 2020), the morphology of *Torix*
206 was highly variable. The results of our study confirmed that the dorsal papillae were
207 absent in juveniles. The papillae were usually present on the dorsal surface of mature
208 individuals, but some large individuals did not possess them (Fig. 4c). Some variation
209 was also observed in the number of eyes. Many individuals possessed two pairs of
210 *Hemiclepsis*-like eyes (Bolotov *et al.* 2019), and some individuals displayed a single
211 pair of fused eyes. In addition, CW was consistently smaller than BW in adult
212 individuals (Fig. 4a–d). However, in juveniles, CW was relatively large, sometimes

213 exceeding BW (Fig. 4e–f). The ventral mid-body somites were typically biannulate, but
214 in some adult individuals, they were superficially divided and formed triannulate mid-
215 body somites. In this study, we found that the morphology of the crop caeca was
216 variable. When the leeches were engorged, the tips of the 1st–6th crop caeca often
217 diverticulated into two or more sections (Fig. 4h), whereas after digesting the blood
218 meal, dissection revealed that they were simple and non-diverticulated (Fig. 5a).

219

220 **Discussion**

221 *Genetic divergence and biogeographical implications*

222 Our molecular-based analyses using mitochondrial *COI* and nuclear *ITS* sequences
223 showed that Japanese *Torix* are largely divided into eastern and western lineages, with
224 several sublineages (Figs 2–3). The geographic boundary between the two major
225 lineages of Japanese *Torix* was identified in the vicinity of locations #20 and #21 (Figs
226 1–2). This boundary is similar to that observed in a haemadipsid leech in Japan, which
227 is attributed to their expansion from northern and southern refugia (Morishima and
228 Aizawa 2019).

229 The genetic structure of ectoparasitic leeches is often concordant with that of
230 their host animals, which stems from parallel changes in their distributions (Morishima
231 *et al.* 2023). One of the boundaries of the *Rana tagoi* Okada, 1928 species complex, the
232 primary host amphibians of Japanese *Torix* is consistent with the boundary between the
233 eastern and western lineages of *Torix* (Eto *et al.* 2012), which suggests that the dispersal
234 of *Torix* is dependent on *R. tagoi*. Although, the boundaries between two major lineages
235 of the *R. tagoi* species complex (Clade A and B; Eto *et al.* 2012) and between the two
236 sister sublineages (Clade B-2a and B-2b) occur in the same area, whether these

237 correspond to the population divergence and dispersal events of *Torix* remains unclear.
238 *Rana tagoi* and *Onychodactylus japonicus* (Houttuyn, 1782), which are host
239 amphibians of *Torix* in Japan (Kambayashi *et al.* 2019, 2020), show high genetic
240 divergence within the Japanese Archipelago (Yoshikawa *et al.* 2008; Eto *et al.* 2012),
241 and genetic diversity among Japanese *Torix* populations is low. In light of the
242 vulnerability of parasites to climate change and their higher risk of extinction compared
243 with that of their hosts (Cizauskas *et al.* 2017), the expansion of *Torix* in Japan might be
244 a relatively recent event. To clarify the dispersal history of *Torix*, future comparative
245 analyses of the divergence time of the Japanese *Torix* is required.

246

247 *Taxonomic status of three Japanese Torix species*

248 The three *Torix* species in Japan have been distinguished on the basis of a combination
249 of morphological traits, some of which have been reported to be ontogenetic traits
250 (Kambayashi *et al.* 2019, 2020). The results of our study confirm the findings of the
251 previous studies and show that all of the conventional diagnostic features are highly
252 variable. The characteristics stated in the original description of *T. orientalis*, including
253 the biannulate segmentation pattern both dorsally and ventrally, two pairs of eyes,
254 smooth dorsal surface, and large caudal sucker, are common in juvenile individuals of
255 *Torix* in Japan. The conspicuous dorsal papillae and the small caudal suckers identified
256 on *T. tukubana*, are also typical of large individuals of *Torix* in Japan. Some large
257 individuals have been found without dorsal papillae (Fig. 4c), and this corresponds to
258 the morphology in the original description of *T. tagoi*.

259 In addition to the topotypes of *T. tukubana* used in Kambayashi *et al.* (2020),
260 we examined the newly collected specimens from the type localities of three *Torix*

261 species, as well as those from various localities of Japan. Although our phylogenetic
262 analyses revealed genetically differentiated lineages in Japanese *Torix*, no appropriate
263 diagnostic characteristics that can distinguish each nominal species or population were
264 found. According to the delimitation analysis, the merging of the Japanese *Torix* into a
265 single species was supported by all methods we employed (Fig. 2). Consequently, we
266 concluded that the three *Torix* species known in Japan should be treated as a single
267 species.

268 Of the three species, *T. tukubana* is the most recently described (Oka 1935) and
269 is considered a junior synonym of the others according to Article 23 of the International
270 Code of Zoological Nomenclature (International Commission on Zoological
271 Nomenclature 1999; hereinafter, the Code). However, since the other specific names
272 *orientalis* and *tagoi* were published simultaneously in Volume 10 of *Annotationes*
273 *Zoologicae Japonenses* on 31 March 1925 (Oka 1925a, b) under the genus *Oligobdella*,
274 and both have been accepted, the precedence between the two names cannot be
275 objectively determined. Although the specific name *orientalis* is a Latin adjective that
276 means “eastern,” the Oriental region is also inhabited by other congeners, including *T.*
277 *mirus* from Vietnam and *T. cotylifer* from continental China. The specific name *tagoi* is
278 dedicated to the Late Professor Katsuya Tago (1877–1943), a zoologist well-known for
279 his work on amphibians (e.g. Tago 1931). *Rana tagoi*, the primary host of the Japanese
280 *Torix*, is also named after the Late Professor Tago. According to Article 24.2.2 of the
281 Code, therefore, we herein act as First Reviser and assign precedence to the name *O.*
282 *tagoi*; thus, the valid name for the Far East Asian *Torix* species is *T. tagoi* unless *T.*
283 *orientalis* and *T. tagoi* are treated as distinct species. The specimens collected on the
284 Korean Peninsula, one of the type localities of *T. tagoi*, were not included in this study.

285 Since more than half of the delimitation analyses suggested that a specimen from China
286 (Zhu *et al.* 2023) should not be treated as the same species as Japanese *Torix* species,
287 additional surveys are needed to clarify the taxonomic status of the East Asian
288 continental *Torix* leeches.

289

290 **Systematics**

291 Family **GLOSSIPHONIIDAE** Vaillant, 1890

292 Genus *Torix* Blanchard, 1893

293 Type species: *Torix mirus* Blanchard, 1893, by monotypy

294

295 *Torix tagoi* (Oka, 1925)

296 (Figs 4–5)

297

298 *Oligobdella orientalis* Oka, 1925a: 311–315, figs 1–2; Autrum 1936: 35, fig. 23; Lukin
299 & Epshtein 1960: 812–814, figs 1–3; Soós 1969: 427; Lukin 1976: 286–289, figs
300 132–135; Yang 1996: 80–82, fig. 53. **New synonym.**

301 *Oligobdella tagoi* Oka, 1925: 330–333, figs 4–5; Autrum 1936: 34–35, fig. 22; Lukin &
302 Epshtein 1960: 814; Soós 1969: 427; Lukin 1976: 289–290, figs 136–137; Yang
303 1996: 82–83, fig. 54.

304 *Oligoclepsis tukubana* Oka, 1935: 66–68, one text figure; Autrum 1936: 36, fig. 24;
305 Lukin & Epshtein 1960b: 479; Soós 1969: 427; Lukin 1976: 290–291, fig. 138.
306 **New synonym.**

307 *Torix orientalis*: Sawyer 1986: 655; Sasaki 2019: 7–9, figs 1, 4.

308 *Torix tagoi*: Sawyer 1986: 655; Sasaki 2015: 5–8, figs 2–5; Bae *et al.* 2018: 519, fig. 1;

309 Sasaki 2019: 7–9, figs 2, 4.
310 *Torix tukubana*: Sawyer 1986: 655; Yoshida 2009: 47, figs 1, 2; Kambayashi *et al.* 2019:
311 664–665, fig. 1; Sasaki 2019: 8, figs 3, 5; Kambayashi *et al.* 2020: 59–71, figs 1–2;
312 Zhu *et al.* 2023: 388 (its taxonomic account should be clarified in future studies).
313 *Torix* sp.: Yoshinari *et al.* 2022: 10, fig. 2.

314

315 *Amended diagnosis.*

316 Body greenish. Caudal sucker ventral, oval. Somites XIII–XXIV dorsally biannulate,
317 ventrally triannulate. Anus between penultimate and last annuli. Male gonopore
318 between somites XI/XII, female gonopore between somite XII (a1 + a2)/a3, gonopores
319 separated by 1 annulus XII (a1 + a2). Eyes in 2 pairs; 1st pair inconspicuous on somite
320 II, 2nd pair on somite III. Dorsal papillae on IV–XXVI, max. 44 on every mid-body
321 annulus. Mouth pore on anterior margin of oral sucker. Salivary cells in 1 pair of
322 compact mass. Oesophagus simple, Oesophageal gland absent. Bacteriosomes absent.
323 Crop giving rise to 7 pairs of crop caeca, 1st–6th pairs diverticulated during
324 engorgement, 7th pair (post-crop caeca) diverticulated into 4 sections. Intersomital
325 testisacs in 6 pairs. Paired sperm ducts thick, strongly coiled. Atrial cornua directed
326 anterolaterally, developed ovate. Paired ovisacs tubular.

327

328 *Neotypification*

329 Six specimens examined in the original description of *T. tagoi* (Oka 1925b), were
330 automatically fixed as syntypes according to Article 73.2 of the Code. However, no type
331 series of this species were found at NSMT and UMUT, and the syntypes are believed to
332 have been lost or destroyed in the past according to our survey and Nakano and Itoh

333 (2011). The original description of *T. tagoi* is on the basis of specimens collected from
334 multiple localities, and individuals from each type locality are likely to belong to their
335 respective lineages (see Discussion), leading the nomenclatural status of this species
336 unclear. In order to prevent zoological and nomenclatural concerns on these species, we
337 propose neotype for *T. tagoi*. The neotype has been deposited in the KUZ, which
338 maintains a collection of Japanese leeches.

339 One newly collected specimen, KUZ Z4997, was selected as the neotype for *T.*
340 *tagoi*. This neotype possesses the characteristics outlined in the amended diagnosis, and
341 each body measurement was as follows: BL 20.6 mm, BW 5.83 mm, CL 3.04 mm, and
342 CW 2.90 mm (Fig. 4a–b). The original specimens of *T. tagoi* were collected in Hida
343 Province (currently Gero City, Hida City, Shirakawa Village, and Takayama City, Gifu
344 Prefecture) in Japan and Koryo (north of Seoul) on the Korean Peninsula. The neotype
345 was collected in Takayama City (36°12'56"N, 137°06'15"E; elev. 1213 m), which is
346 included in Hida Province, one of the original type localities.

347 Although this neotype differed in several characteristics compared with its
348 original descriptions, all these features were found to vary ontogenetically according to
349 a previous and the present survey (Kambayashi *et al.* 2019, 2020). Given the fact that
350 no other biannulate glossiphoniid species were found at the type locality of this species,
351 there is no doubt over the identity of the species as *T. tagoi*.

352

353 *Material examined.*

354 Neotype of *T. tagoi*: KUZ Z4997, a mature specimen, dissected, collected from Takayama
355 City, Gifu Prefecture, Japan, on 8 May 2021.

356 Additional material. In total, 17 matured specimens were examined and

357 dissected: KUZ Z4998 and Z5000 (two specimens), locality as for neotype of *T. tagoi*;
358 KUZ Z4975, Z4977–Z4978 (three specimens), collected from Nemuro City, Hokkaido,
359 Japan (= topotypes of *T. orientalis*); KUZ Z4982 (one specimen) collected from
360 Tomakomai City, Hokkaido, Japan; KUZ Z2972–Z2973 (two specimens) examined in
361 Kambayashi *et al.* (2020) and KUZ Z4989 (one specimen) collected from Mt.
362 Tsukubasan, Ibaraki Prefecture, Japan (= topotypes of *T. tukubana*); KUZ Z4992 (one
363 specimen) collected from Yumoto, Nikko City, Tochigi Prefecture, Japan (= topotype of
364 *T. orientalis*); KUZ Z5002, Z5004, and Z5005 (three specimens) collected from Akame,
365 Nabari City, Mie Prefecture, Japan (= topotypes of *T. orientalis*); KUZ Z5008 (one
366 specimen) collected from Katsuta-gun, Okayama Prefecture, Japan; KUZ Z5011–Z5013
367 (three specimens) collected from Hatsukaichi City, Hiroshima Prefecture, Japan.
368 Additionally, three juvenile specimens were examined: KUZ Z4980 (one specimen)
369 collected from Samani-gun, Hokkaido, Japan; KUZ Z4996 collected from Nakatsugawa
370 City, Gifu Prefecture, Japan; KUZ Z5014 collected from Hatsukaichi City, Hiroshima
371 Prefecture, Japan.

372

373 *Description of matured individuals*

374 Body lanceolate or ovate (Fig. 4a–d). Caudal sucker ventral, oval. Measurements (mean
375 \pm 1SD, followed by ranges in parenthesis; n = 18, including neotype): BL 16.6 ± 4.1
376 mm (10.7–22.7 mm), BW 6.15 ± 1.93 mm (3.39–10.1 mm), CL 3.15 ± 0.73 mm (2.14–
377 4.67) mm, CW 2.97 ± 0.74 mm (1.86–4.57 mm).

378 Somite I completely merged with prostomium. Somites II (= peristomium), III
379 uniannulate; Somites IV–VI often uniannulate, each with slight dorsal furrow, rarely
380 both dorsally and ventrally biannulate, $(a1 + a2) > a3$. Somite VII often both dorsally

381 and ventrally biannulate, $(a1 + a2) > a3$, rarely uniannulate with slight dorsal furrow.
382 Somites VIII–XII both dorsally and ventrally biannulate, $(a1 + a2) > a3$. Somites XIII–
383 XXIV variable; some both dorsally and ventrally biannulate, $(a1 + a2) > a3$, others
384 dorsally biannulate, $(a1 + a2) > a3$, ventrally triannulate, $a1 = a2 < a3$, ventral annular
385 furrow between $a1$ and $a2$ slightly shallow. Somite XXIV $a3$ being ventrally last
386 complete annulus. Somite XXV uniannulate. Annulation of somites XXVI and XXVII
387 comprising 3 annuli altogether; antepenultimate = penultimate $>$ last. Anus between
388 penultimate and last annuli.

389 Clitellum unobservable.

390 Male gonopore between XI/XII. Female gonopore between XII $(a1 + a2)/a3$.

391 Gonopores separated by 1 annulus.

392 Eyes in one or two pairs on anterior margin of II to anterior margin of III.

393 Dorsal papillae on IV–XXVI, max. 44 on every mid-body annulus, forming 1
394 inconspicuous transverse row on posterior margin of $(a1 + a2)$, and on middle of $a3$ of
395 each mid-body somite, respectively.

396 Nephridiopores undetectable.

397 Mouth pore on anterior margin of oral sucker. Proboscis in membranous sheath
398 reaching to XI/XII, without forming loop (Fig. 5a). Salivary cells arranged in 1 pair of
399 compact mass between somites IX $(a1 + a2)$ –XIII $a3$ (Fig. 5a); multiple ductules
400 inserting independently into base of proboscis in XI (Fig. 5a). Oesophagus simple (Fig.
401 5a), occasionally recurved; Oesophageal gland absent. Bacteriosomes absent. Crop
402 reaching to XIX/XX, giving rise to 7 pairs of crop caeca (Fig. 5a); 1st–6th pairs crop
403 caeca appearing simple and nondiverticulated when unfed, diverticulated in multiple
404 sections when engorged: 1st pair in XIII $(a1 + a2)$ – $a3$; 2nd pair in XIV $(a1 + a2)$ – $a3$;

405 3rd pair in XV (a1 + a2)–a3; 4th pair in XVI (a1 + a2)–a3; 5th pair in XVII (a1 + a2)–
406 a3; 6th pair in XVIII (a1 + a2)–a3; and 7th pair (post-crop caeca) diverticulated into 4
407 sections, in XIX (a1 + a2)–XXII a3. Intestinal caeca in 4 pairs (Fig. 5a): 1st pair in XIX
408 (a1 + a2)–XX (a1 + a2); 2nd pair in XX (a1 + a2)–a3; 3rd pair in XXI (a1 + a2)–a3; 4th
409 pair in XXII (a1 + a2)–a3. Rectum simple tubular (Fig. 5a), occasionally recurved.
410 Testisacs in 6 pairs, intersomital (Fig. 5a): 1st pair in XIII a3–XIV (a1 + a2); 2nd pair in
411 XIV a3–XV (a1 + a2); 3rd pair in XV a3–XVI (a1 + a2); 4th pair in XVI a3–XVII (a1 +
412 a2); 5th pair in XVII a3–XVIII (a1 + a2); 6th pair in XVIII a3–XIX (a1 + a2). Paired
413 sperm ducts thick, strongly coiled, in XI–XIII (Fig. 5a–b). Pair of muscular atrial
414 cornua directed anterolaterally, developed ovate, in XI a3–XII (a1 + a2) (Fig. 5b). One
415 pair of ovisacs tubular, thin-walled, slightly folded running alongside ventral nerve
416 cord, XII (a1 + a2) to XIII (a1 + a2)–XVIII (a1 + a2) (Fig. 5b); both ovisacs reaching to
417 XII (a1 + a2), then turned posteromedially toward female gonopore (Fig. 5b).

418

419 *Description of juveniles*

420 Measurements (mean, followed by ranges in parenthesis; n = 3): BL 3.69 mm (3.49–
421 3.80 mm), BW 1.13 mm (0.97–1.29 mm), CL 1.08 mm (0.96–1.24 mm), CW 1.03 mm
422 (0.84–1.22 mm). Somites I–V uniannulate, and VI–XXIV biannulate in KUZ Z4980
423 and Z5014. Somites I–VII uniannulate, and VIII–XXIV biannulate in KUZ Z4996. Eyes
424 in 2 pairs: 1st pair on posterior margin of II; 2nd pair on anterior margin of III. Male
425 and female gonopore undetectable. Dorsal papillae undeveloped. CW relative to BW is
426 larger than that found in mature individuals (Fig. 4a–f), occasionally CW is larger than
427 BW.

428

429 *Colouration.*

430 In life, dorsal surface uniform dark or light green, white and green mottled on distal
431 margin (Fig. 4g); ventral surface transparent (Fig. 4h). Colour faded in preservative;
432 uniform pale green or yellowish-gray (Fig. 4a–d).

433

434 *Host preference.*

435 All specimens of *T. tagoi*, with the exception of free-living individuals, were collected
436 from the body surface of amphibians. The observed amphibian host species of *T. tagoi*
437 are as follows: *Buergeria buergeri* (Temminck & Schlegel, 1838), *Rana ornativentris*
438 Werner, 1903, *R. tagoi*, *R. sakuraii* Matsui & Matsui, 1990, *R. pirica* Matsui, 1991, *R.*
439 *neba* Ryuzaki, Hasegawa & Kuramoto, 2014, *Hynobius retardatus* Dunn, 1923, *H.*
440 *kimurae* Dunn, 1923, *H. sematonotos* Tominaga, Matsui & Nishikawa, 2019,
441 *Onychodactylus japonicus*, and *O. kinneburii* Yoshikawa, Matsui, Tanabe & Okayama,
442 2013. The most frequently infested hosts are *R. pirica* in Hokkaido and *R. tagoi* in
443 Honshu and Shikoku. In Korea and China, *R. uenoi* Matsui, 2014 and *R. dybowskii*
444 Günther, 1876 have been recorded as the host animals, respectively (Bae *et al.* 2018;
445 Zhu *et al.* 2023).

446

447 *Remarks*

448 Examination of the topotypes of *T. tagoi*, *T. orientalis*, and *T. tukubana* revealed no
449 diagnostic characters that could be used to distinguish them. Because the genetic
450 divergence in the *COI* sequences among these species was low, we concluded that the
451 three *Torix* species should be treated as a single species and proposed *T. tagoi* as a valid
452 species name. The genus *Torix* contains four nominal species following this

453 synonymization: *T. mirus*, *T. cotylifer*, *T. novaezealandiae* (Dendy & Olliver, 1900), and
454 *T. tagoi*. *Torix tagoi* can be easily distinguished from the other congeneric species by the
455 following characters: 1) position of the male gonopore; 2) shape and number of the crop
456 caeca; and 3) shape of the ovisacs (Table 3).

457 The type species of *Torix*, *T. mirus*, was described as a biannulate species by
458 Blanchard (1893). In the subsequent redescription by Blanchard (1898), the male
459 gonopore was shown to be located at XI (a1 + a2)/a3, which differs from *T. tagoi*,
460 wherein the male gonopore is located at XI/XII. *Torix mirus* is known to prey on
461 mollusks (liquidsomatophagous), and its feeding behavior differs from that of *T. tagoi*,
462 which sucks blood from amphibians (haematophagous). Although both species share a
463 reduced annulation pattern, the annulation reduction can occur more frequently than
464 previously thought. In light of the aforementioned morphological and ecological
465 differences, *T. tagoi* and *T. mirus* might belong to separate lineages. *Torix tagoi* and *T.*
466 *orientalis* were originally described as members of the genus *Oligobdella*, and they
467 have been synonymized with *Placobdella* (Siddall *et al.* 2005). However, *T. tukubana*,
468 which is considered a new synonym of *T. tagoi*, was described under the genus
469 *Oligocleipsis* Oka, 1935. Future comparative studies are required in order to clarify the
470 taxonomic status of *T. tagoi*; if *T. tagoi* and *T. mirus* are found to belong to separate
471 lineages, the genus *Oligocleipsis* will be resurrected for *T. tagoi*.

472

473 **Data availability**

474 The data that support this study will be shared upon reasonable request to the
475 corresponding author.

476

477 **Conflicts of interest**

478 The authors declare that there are no conflicts of interest.

479

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669 **Table 1.** Samples with voucher numbers, collection localities, and International Nucleotide Sequences Database (INSD) or Barcode of
670 Life Data System (BOLD) accession numbers of the sequences used for molecular analyses. Sequences marked with an asterisk (*)
671 were obtained for the first time in the present study. Special remarks for each specimen are shown in parentheses. Acronyms: KUZ, the
672 Zoological Collection of Kyoto University; TRPM, Tottori Prefectural Museum.

Species	Locati on #	Locality	Voucher	INSD/BOLD			References
				<i>COI</i>	<i>18S</i>	<i>ITS</i>	
Ingroup (= <i>Torix tagoi</i>)							
(Topotype of <i>T. orientalis</i>)	1	Nemuro City, Hokkaido	KUZ Z4975	LC776047*	LC776025*	LC776026*	This study
			KUZ Z4976	LC776048*	–	–	This study
			KUZ Z4977	LC776049*	–	–	This study
			KUZ Z4978	LC776050*	–	–	This study
	2	Akkeshi-cho, Hokkaido	KUZ Z4979	LC776051*	–	LC776027*	This study
	3	Samani-gun, Hokkaido	KUZ Z4980	LC776052*	–	LC776028*	This study
	4	Yubari City, Hokkaido	KUZ Z4981	LC776053*	–	LC776029*	This study
	5	Tomakomai City, Hokkaido	KUZ Z4982	LC776054*	–	LC776030*	This study
			KUZ Z4983	LC776055*	–	–	This study
	6	Oshamanbe-cho, Hokkaido	KUZ Z4984	LC776056*	–	LC776031*	This study
	7	Ajigasawa-machi, Aomori Pref.	KUZ Z4985	LC776057*	–	–	This study
	8	Sendai City, Miyagi Pref.	KUZ Z4986	–	–	–	–
	9	Nagai City, Yamagata Pref.	KUZ Z4987	–	–	–	–
	10	Tamura City, Fukushima Pref.	KUZ Z4988	LC776058*	–	LC776032*	This study

(Topotype of <i>T. tukubana</i>)	11	Tsukuba City, Ibaraki Pref.	KUZ Z2972	LC538265	LC538285	LC776033*	Kambayashi <i>et al.</i> (2020); This study
			KUZ Z4989	LC776059*	–	–	This study
			KUZ Z4990	LC776060*	–	–	This study
			KUZ Z4991	LC776061*	–	–	This study
(Topotype of <i>T. orientalis</i>)	12	Yumoto, Nikko City, Tochigi Pref.	KUZ Z4992	LC776062*	–	LC776034*	This study
			KUZ Z4993	LC776063*	–	–	This study
	13	Nagano City, Nagano Pref.	KUZ Z4994	–	–	–	–
	14	Itoigawa City, Niigata Pref.	KUZ Z4995	LC776064*	–	LC776035*	This study
	15	Nakatsugawa City, Gifu Pref.	KUZ Z4996	LC776065*	–	LC776036*	This study
(Neotype of <i>T. tagoi</i>)	16	Takayama City, Gifu Pref.	KUZ Z4997	LC776066*	LC776024*	LC776037*	This study
(Topotype of <i>T. tagoi</i>)			KUZ Z4998	LC776067*	–	–	This study
			KUZ Z4999	LC776068*	–	–	This study
			KUZ Z5000	LC776069*	–	–	This study
	17	Taga-cho, Shiga Pref.	KUZ Z5001	LC776070*	–	LC776038*	This study
(Topotype of <i>T. orientalis</i>)	18	Akame, Nabari City, Mie Pref.	KUZ Z5002	LC776071*	LC776022*	LC776039*	This study
			KUZ Z5003	LC776072*	–	–	This study
			KUZ Z5004	LC776073*	–	–	This study
			KUZ Z5005	LC776074*	–	–	This study
	19	Nantan City, Kyoto Pref.	KUZ Z5006	LC776075*	–	–	This study
	20	Toyooka City, Hyogo Pref.	KUZ Z5007	LC776076*	–	LC776040*	This study
	21	Katsuta-gun, Okayama Pref.	KUZ Z5008	LC776077*	–	LC776041*	This study
	22	Saihaku-gun, Tottori Pref.	TRPM-AO-	LC776078*	–	LC776042*	This study
			0000256				

	23	Miyoshi City, Hiroshima Pref.	KUZ Z5010	LC776079*	–	LC776043*	This study
	24	Hatsukaichi City, Hiroshima Pref.	KUZ Z5011	LC776080*	LC776023*	LC776044*	This study
			KUZ Z5012	LC776081*	–	–	This study
			KUZ Z5013	LC776082*	–	–	This study
			KUZ Z5014	LC776083*	–	–	This study
	25	Okinoshima-cho, Shimane Pref.	KUZ Z5015	LC776084*	–	LC776045*	This study
	26	Mima City, Tokushima Pref.	KUZ Z5016	–	–	–	–
	27	Kumakougen-cho, Ehime Pref.	KUZ Z5017	LC776085*	–	LC776046*	This study
(Identified as <i>T. tukubana</i>)	28	Dandong City, Liaoning Province, China	–	OL779256	–	–	Zhu <i>et al.</i> (2023)
Outgroup							
<i>Hemiclepsis kasmiana</i> Oka, 1910		South Korea	Hir103/4	MN295423	–	–	Bolotov <i>et al.</i> (2019)
<i>Hemiclepsis khankiana</i> Bolotov, Klass, Bespalaya, Konopleva, Kondakov & Vikhrev, 2019		Primorsky Krai, Russia	Hir101	MN295420	–	–	Bolotov <i>et al.</i> (2019)
<i>Hemiclepsis marginata</i> (O. F. Müller, 1773)		France	–	AF003259	–	–	Siddall and Burreson (1998)
<i>Hemiclepsis myanmariana</i> Bolotov, Klass, Bespalaya,		Myanmar	Hir48/1	MN295394	–	–	Bolotov <i>et al.</i> (2019)

Konopleva, Kondakov & Vikhrev, 2019						
<i>Hemiclepsis schrencki</i>	Primorsky Krai, Russia	Hir88/1	MN295415	–	–	Bolotov <i>et al.</i> (2019)
Bolotov, Klass, Bepalaya, Konopleva, Kondakov & Vikhrev, 2019						
<i>Hemiclepsis tumniniiana</i>	Khabarovsk Krai, Russia	Hem1/2	MN295371	–	–	Bolotov <i>et al.</i> (2019)
Bolotov, Klass, Bepalaya, Konopleva, Kondakov & Vikhrev, 2019						
<i>Hemiclepsis yangtzenensis</i> Yang & Bolotov, 2021	Jingzhou, Hubei Province, China	–	MN106285	–	–	Yi <i>et al.</i> (2022)
<i>Glossiphonia balcanica</i> Grosser & Pešić, 2016	Dečani, Kosovo	Gbalc1	LCHME036	–	–	Jovanović <i>et al.</i> (2021)
<i>Glossiphonia baicalensis</i> (Stschegolew, 1922)	Lake Baikal, Russia	–	AY047329	–	–	Light and Siddall (1999)
<i>Glossiphonia complanata</i> (Linnaeus, 1758)	Ohrid Lake, North Macedonia	MAC1_1	LCHME020	–	–	Jovanović <i>et al.</i> (2021)
<i>Glossiphonia complanata</i>	Podgorica, Montenegro	MN1_1	LCHME008	–	–	Jovanović <i>et al.</i> (2021)
			-20			

<i>Glossiphonia concolor</i> (Apathy, 1888)	Mecklenburg-Vorpommern, Germany	Gcon1	LCHME041 -20	-	-	Jovanović <i>et al.</i> (2021)
<i>Glossiphonia concolor</i>	Ukraine	-	KM095097	-	-	Kaygorodova and Mandzyak (2014)
<i>Glossiphonia elegans</i> Verrill, 1872	Manitoba, Canada	ROMIZI115 05	MK479253	-	-	Mack and Kvist (2019)
<i>Glossiphonia nebulosa</i> Kalbe, 1964	Berlin, Germany	Gnebu4	LCHME044 -20	-	-	Jovanović <i>et al.</i> (2021)
<i>Glossiphonia cf. nebulosa</i>	Dečani, Kosovo	Gnebu1	LCHME042 -20	-	-	Jovanović <i>et al.</i> (2021)
<i>Glossiphonia verrucata</i> (Fr. Müller, 1844)	Sweden	-	AY962458	-	-	Siddall <i>et al.</i> (2005)
<i>Glossiphonia verrucata</i>	Croatia	ROMIZI117 53	MK479263	-	-	Mack and Kvist (2019)
<i>Glossiphonia verrucata</i>	Croatia	ROMIZI117 55	MK479264	-	-	Mack and Kvist (2019)
<i>Glossiphonia sp.</i>	Lake Izumrudnoe, Russia	H56	MH670835	-	-	Kaygorodova <i>et al.</i> (2020)

674 **Table 2.** Uncorrected *p*-distances for the mitochondrial *COI* sequences of representative *Torix* specimens. Location numbers in Table 1
 675 are presented in parentheses.

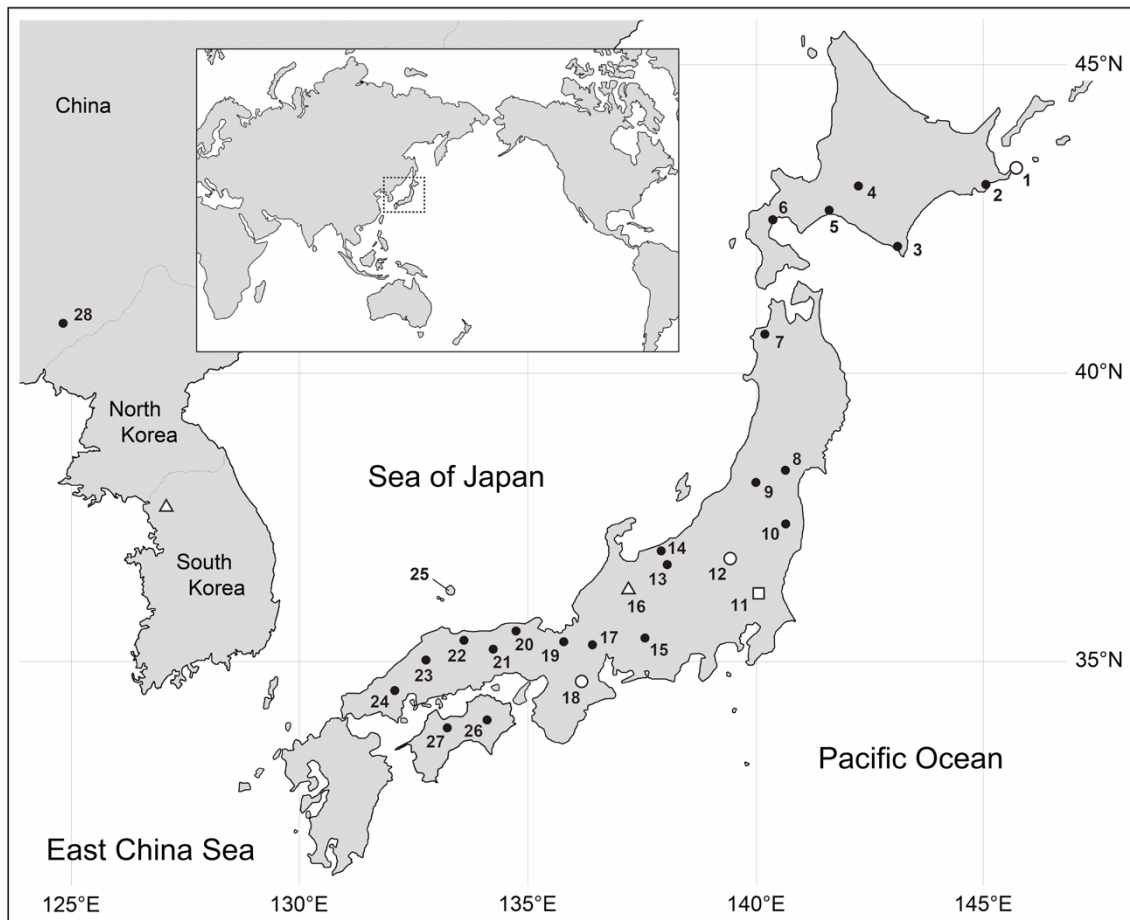
Voucher	1	2	3	4	5	6	7	8	9
1. KUZ Z4976; topotype of <i>T. orientalis</i> (1)									
2. KUZ Z4982 (5)	0.026								
3. KUZ Z2972; topotype of <i>T. tukubana</i> (11)	0.034	0.042							
4. KUZ Z4992; topotype of <i>T. orientalis</i> (12)	0.035	0.043	0.0039						
5. KUZ Z4997; neotype of <i>T. tagoi</i> (16)	0.035	0.043	0.030	0.031					
6. KUZ Z5002; topotype of <i>T. orientalis</i> (18)	0.034	0.043	0.032	0.035	0.024				
7. KUZ Z5011 (24)	0.037	0.052	0.039	0.040	0.035	0.041			
8. KUZ Z5017 (27)	0.035	0.043	0.034	0.034	0.034	0.039	0.019		
9. China; identified as <i>T. tukubana</i> (28)	0.048	0.057	0.051	0.051	0.042	0.044	0.044	0.040	

676

677 **Table 3.** Comparisons of morphological characters between *Torix tagoi* and three
 678 congeneric species.

Character	<i>Torix tagoi</i>	<i>Torix cotylifer</i>	<i>Torix mirus</i>	<i>Torix novaezealandiae</i>
Male gonopore	XI/XII	XI/XII	XI (a1 + a2)/a3	?
Crop caeca	7 pairs: 1st–6th pairs being equal-sized	7 pairs: 1st pair extending to lateral margin of body	?	6 pairs: 1st pair being very small
Ovisacs	tubular	globular	?	tubular

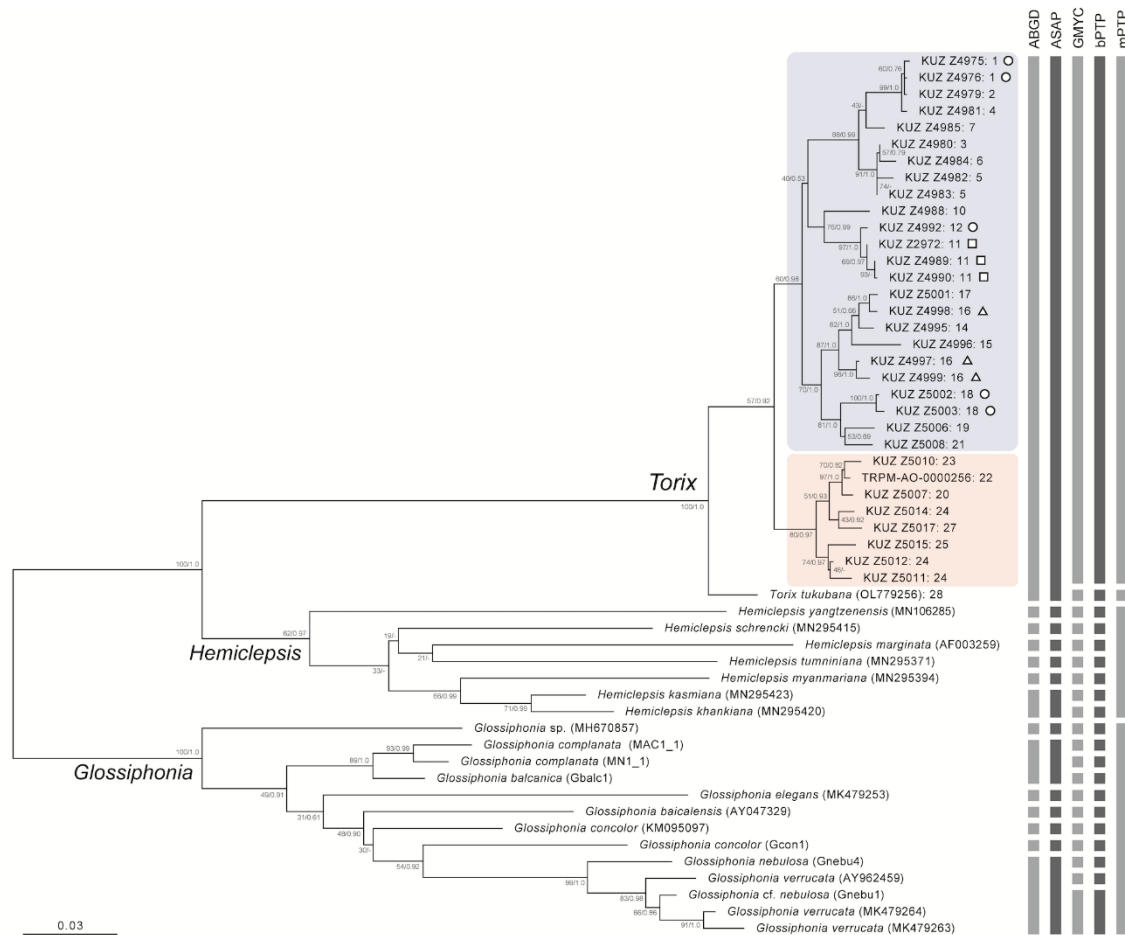
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680

681 **Fig. 1.** Map showing the sampling localities of *Torix* specimens used in this study. Open
 682 circles, the square, and triangles indicate the type localities of *T. orientalis*, *T. tukubana*,
 683 and *T. tagoi*, respectively. The numbers of localities are shown in Table 1.

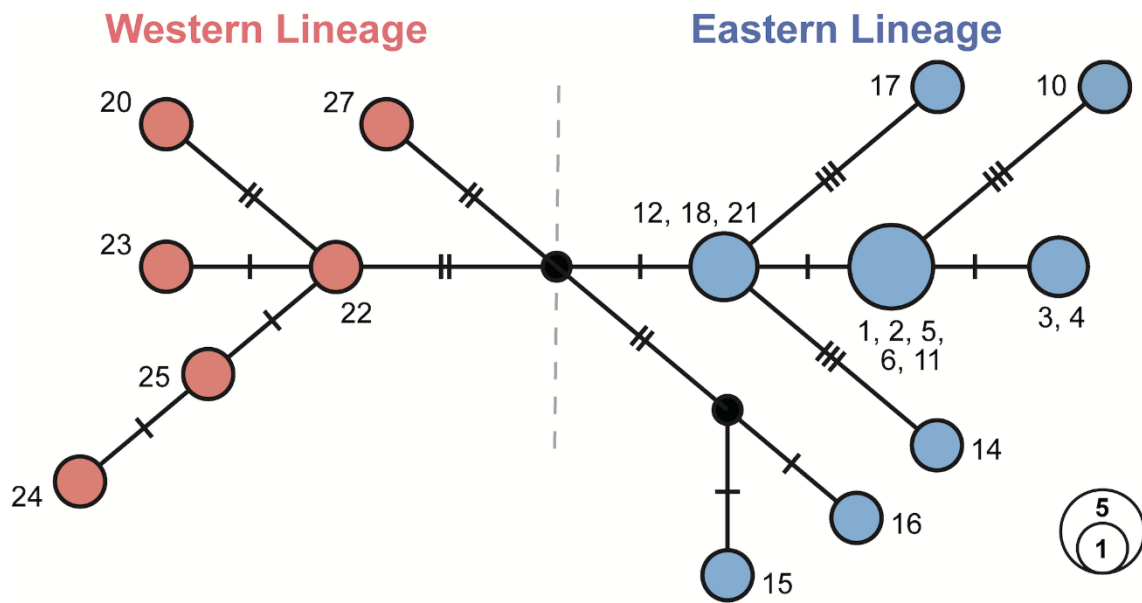
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685

686 **Fig. 2.** Maximum likelihood tree for 1,267 bp of the mitochondrial COI gene, along with
 687 the results of five species-delimitation analyses (ABGD, ASAP, GMYC, bPTP, and
 688 mPTP) as indicated by vertical bars. Voucher and location number corresponding to Table
 689 1 are presented for *Torix*. The blue and red shading indicate the eastern (locations #1–19,
 690 #21 in Table 1) and western (#20, #22–27) lineages of Japanese *Torix*, respectively. Open
 691 circles, the square, and triangles indicate the topotypes of *T. orientalis*, *T. tukubana*, and
 692 *T. tagoi*, respectively. Numbers on nodes represent bootstrap values for maximum
 693 likelihood and Bayesian posterior probabilities.

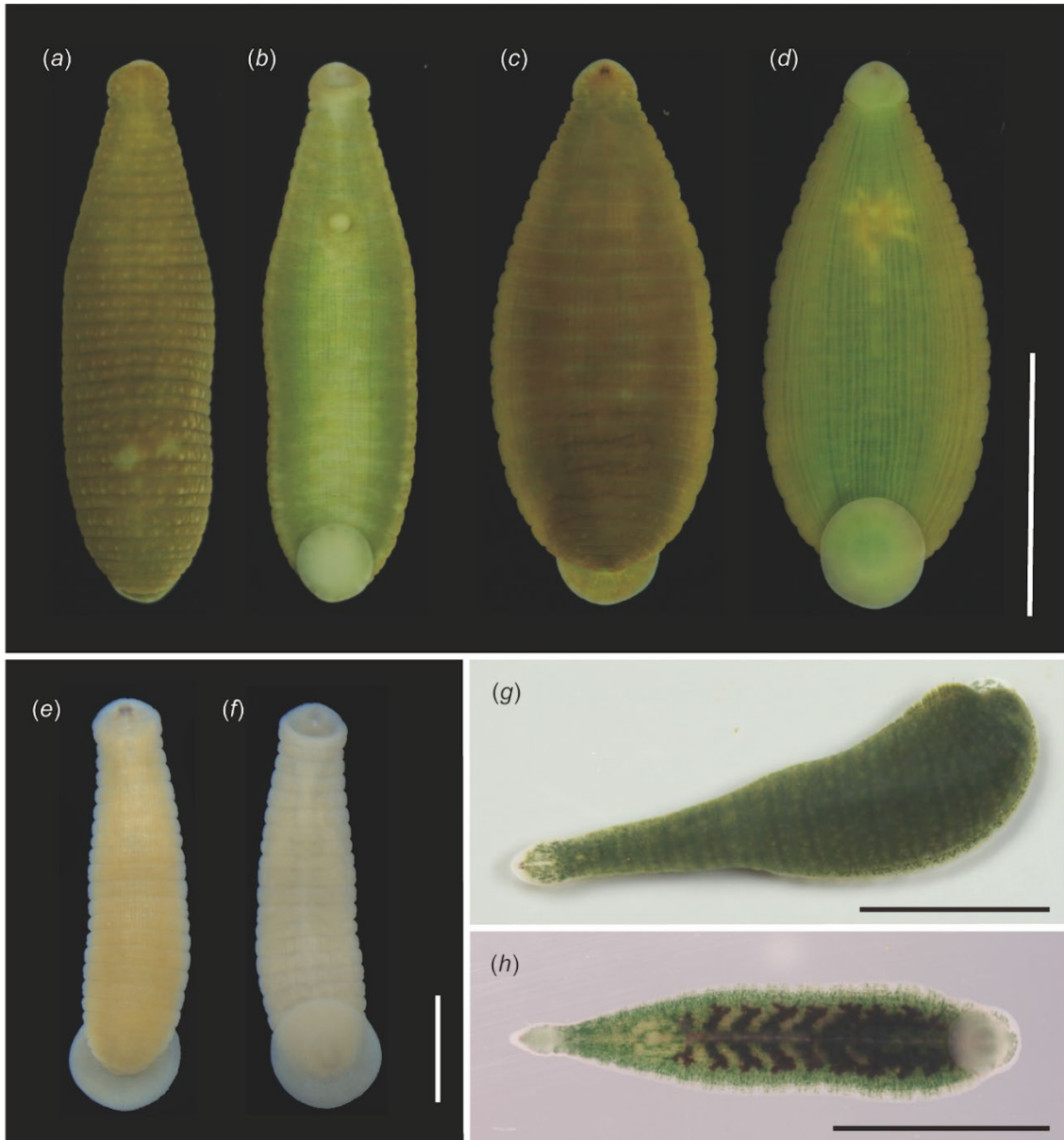
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695

696 **Fig. 3.** Statistical parsimony network of nuclear *ITS* haplotypes. The blue and red circles
 697 indicate haplogroups of the eastern and western lineages of Japanese *Torix* shown in Fig.
 698 2, respectively. Black circles indicate the missing haplotypes. The number on each circle
 699 corresponds to the location number in Table 1.

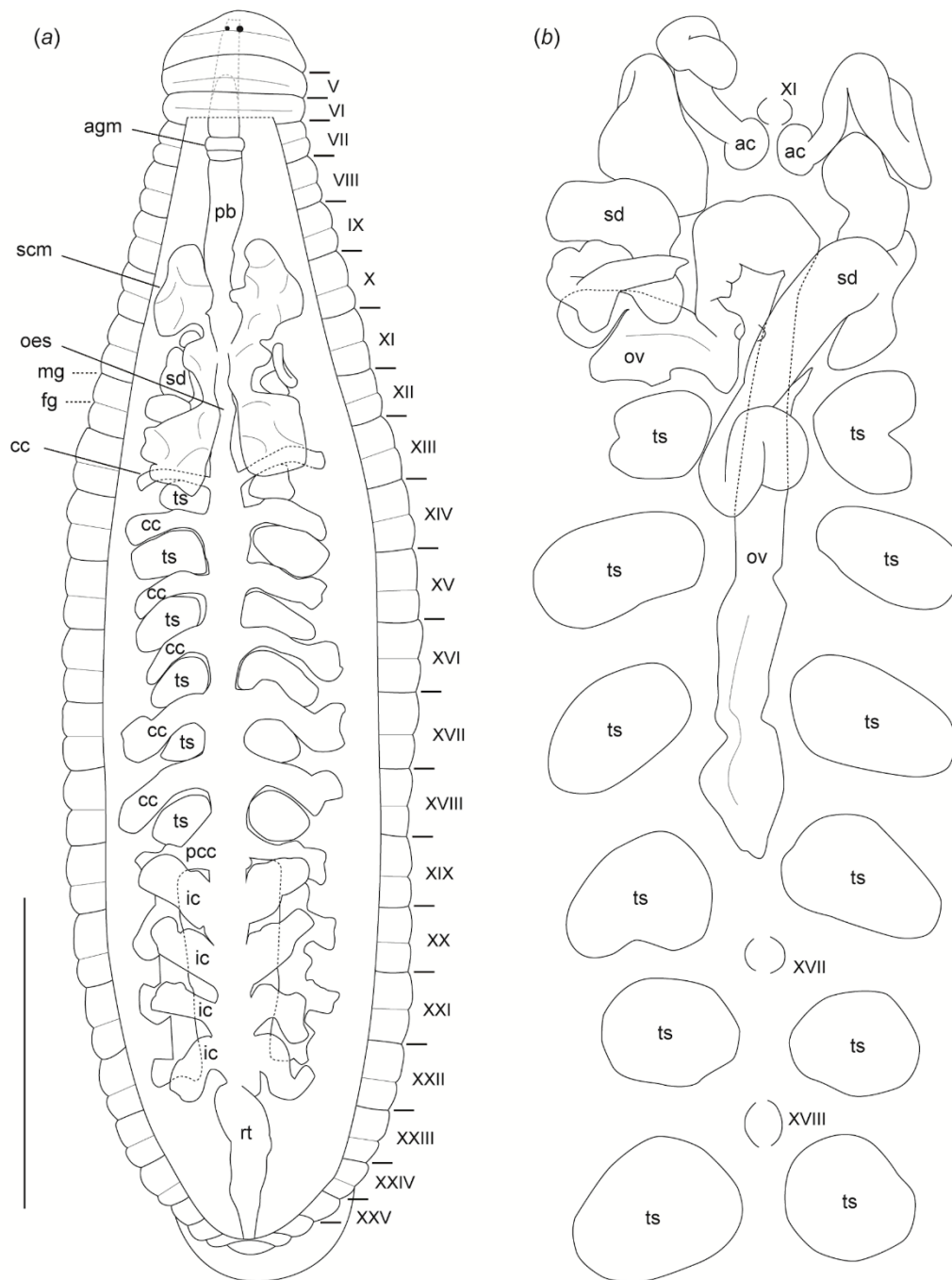
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701

702 **Fig. 4.** *Torix* specimens used in this study: (a) dorsal and (b) ventral views of the neotype
 703 of *T. tagoi* (KUZ Z4997); (c) dorsal and (d) ventral views of the topotype of *T. orientalis*
 704 (KUZ Z4975); (e) dorsal and (f) ventral views of a juvenile specimen (KUZ Z4980); (g)
 705 dorsal view of the live neotype of *T. tagoi*; (h) ventral view of live adult individual (KUZ
 706 Z5006). Scale bars: 10 mm (a–d, g–h), 1 mm (e–f).

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708

709 **Fig. 5.** *Torix tagoi*, neotype (KUZ Z4997): (a) dorsal view of the digestive tract and male
 710 genital organs; (b) dorsal view of the reproductive system and positions of ganglia XI–
 711 XVIII. Abbreviations: ac, atrial cornu; agm, anterior ganglionic mass; cc, crop cecum; fg,
 712 female gonopore; ic, intestinal cecum; mg, male gonopore; oes, oesophagus; ov, ovisac;
 713 pb, proboscis; pcc, post-crop cecum; rt, rectum; scm, salivary cells mass; sd, sperm duct;

714 ts, testisac. Scale bar: 5 mm (*a*), 1 mm (*b*).