Water mites of the genus *Hygrobates* Koch, 1837 (Acari: Parasitengona: Hygrobatidae) from Hokkaido, northern Japan

NORIKO MATSUMOTO¹, MATTHEW H. DICK², & SHUNSUKE F. MAWATARI¹

¹Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo, Japan, and ²21st Century COE Programme, Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo, Japan

(Accepted 4 November 2004)

Abstract
Nine species of *Hygrobates* (Acari: Parasitengona: Hygrobatidae) from Hokkaido, Japan are described or redescribed from newly collected material and historical specimens. Treated herein are eight species in the subgenus *Hygrobates*, including one new species, *H. bibi* sp. nov., as well as *H. calliger* Piersig, 1896; *H. foreli* (Lebert, 1874); *H. japonicus* Uchida, 1931; *H. longipalpis* (Hermann, 1804); *H. longiporus* Thor, 1898; *H. nigromaculatus* Lebert, 1879; and *H. sokolowi* Thor, 1927. Also treated is *H. ezoensis* Uchida, 1934 in the subgenus *Rivobates*. A lectotype and paralectotype are designated for *H. japonicus* Uchida, 1931. *Hygrobates* (s. str.) *heteropalpis* Imamura, 1954 is synonymized with *H. calliger* Piersig, 1896. The name *H. ezoensis* Uchida, 1934 is resurrected from synonymy with *H. diversiporus* Sokolow, 1927. Six species previously known from Hokkaido were collected in the study: *H. foreli*, *H. japonicus*, *H. longipalpis*, *H. longiporus*, *H. diversiporus*, and *H. ezoensis*. New records for both Hokkaido and Japan include *H. nigromaculatus* and *H. sokolowi*. A species previously recorded from Hokkaido, *H. taniguchii* Imamura, 1954, was not found in this study. Three new characters are proposed as useful for the taxonomy of the genus *Hygrobates*: the ratio of the distance between the P-4 ventral setae to P-4 length, the ratio of the length of the longest terminal seta on IV-L-5 to the length of IV-L-5, and the nature of the outer border of the genital plates.

Keywords: Collection, Hokkaido, Hygrobates, Japan, new species, Rivobates, synonymy, taxonomy, water mites

Introduction
So-called water mites, members of the Phalanx Hydrachnidia Krantz, 1978 (Acari: Parasitengona), are the most diverse group of mites living in aquatic habitats. More than 3000 species in seven superfamilies are assigned to the Hydrachnidia worldwide (Viets 1987). Over 250 species in 58 genera distributed among all the superfamilies have been
recorded from Japan. The genus *Hygrobates* Koch, 1837 is one of the largest genera of the family Hygrobatidae Koch, 1842. Most species of *Hygrobates* occur in still or slowly flowing waters, such as lakes, ponds, and the mid- and downstream parts of rivers, where they live among vegetation and between and underneath rocks. *Hygrobates* has a diversity of more than 150 species in 11 subgenera worldwide (Cook 1974; Tuzovskij and Gerecke 2003). In Japan, 14 nominal species from two subgenera have been previously recorded: 12 species of the subgenus *Hygrobates* Koch, 1837, including *H. biwaensis* Tuzovskij, 2003; *H. calliger* Piersig, 1896; *H. foreli* (Lebert, 1874); *H. heteropalpis* Imamura, 1954; *H. japonicus* Uchida, 1931; *H. longipalpis* (Hermann, 1804); *H. longiporus* Thor, 1898; *H. minutus* Imamura, 1953; *H. papillosus* Imamura, 1953; *H. rarus* Tuzovskij, 2003; *H. sinensis* Uchida and Imamura, 1951; and *H. variabilis* Tuzovskij, 2003; and two species of the subgenus *Rivobates* Thor, 1897, including *H. diversiporus* Sokolow, 1927 and *H. taniguchii* Imamura, 1954.

Despite much previous work on water mites in Japan, the taxonomy of many groups is poorly resolved due to insufficient original descriptions or inadequate evaluation of taxonomic characters; as a consequence, it is often difficult to identify specimens and recognize new species. To begin to address these problems, we conducted a taxonomic study of the genus *Hygrobates* on Hokkaido, Japan’s northernmost island. Among the 14 species of *Hygrobates* known from Japan, all except *H. biwaensis*, *H. minutus*, *H. papillosus*, *H. rarus*, *H. sinensis*, and *H. variabilis* were known to occur on Hokkaido (Uchida 1931, 1934, 1936b; Enami 1940; Imamura 1950, 1953a, 1953b, 1954, 1955, 1960, 1980; Tuzovskij 2003).

In this paper, we provide original descriptions or redescriptions of nine species of *Hygrobates* from Hokkaido detected through examination of extensive newly collected material and specimens in the collections of two previous workers, Uchida and Imamura. The species treated here comprise eight species of the subgenus *Hygrobates*, including one new species and two new records for Japan, and one species of the subgenus *Rivobates*. Among the species previously known from Hokkaido, this study identifies all but one, *H. taniguchii*. We recommend two nomenclatural changes: removal of the name *H. heteropalpis* through synonymy with *H. calliger*, and resurrection of the name *H. ezoensis* for Hokkaido specimens previously identified as *H. diversiporus*. We also nominate a lectotype and paralectotype for *H. japonicus* Uchida, 1931.

**Material and methods**

Most of the specimens examined in this study were collected by the first author during 2002–2003 at 35 localities across Hokkaido (Figure 1; Table I). Qualitative sampling was conducted in freshwater habitats (rivers, ponds, springs, and lakes) with a net of 250 μm mesh size. Specimens were either fixed and preserved in Koenike’s fluid, or collected into 80% ethanol and later transferred to Koenike’s fluid. There was no visible difference in effect on integument pattern between these two treatments. Specimens were dissected in lactic acid before mounting in polyvinyl alcohol (Danielsson 1985) or Euparal.

Specimens in Uchida’s collection in the Hokkaido University Museum and Imamura’s collection at Ibaraki University were also examined. Information on specimens examined in this study is noted in the “Material examined” section for each species.

Observations and measurements were made with a differential interference microscope (Olympus BH-2), and illustrations were prepared with the aid of a camera lucida. Measurements are given in micrometres; ratios are without units. Measurements of paired
Figure 1. Maps of Japan (below) and Hokkaido (above) indicating collecting sites (●). Numbers correspond to site numbers listed in Table I.
Table I. Collecting sites for *Hygrobates* spp. on Hokkaido (site numbers are correlated with numbers in Figure 1).

| No. | Collecting site | Date       | Species found | Mounted specimens |
|-----|-----------------|------------|---------------|-------------------|
|     |                 |            | Females | Males | Other |
| 1   | Inflow river to Akan Lake, Akan | 4 June 2002 | *H. ezoensis* | 1 |   |
| 1   | Inflow river to Akan Lake, Akan | 4 June 2002 | *H. foreli* | 1 | 1 |
| 2   | Akan-Lake, Akan | 5 June 2002 | *H. longipalpis* | 1 | 2 | >20 |
| 3   | Bekanbushigawa River, Akkeshi | 12 June 2002 | *H. bibi* sp. nov. | 20 | |
| 4   | Oboro-gawa River, Akkeshi | 13 June 2002 | *H. longipalpis* | 1 | |
| 5   | Bibi-River, Chitose | 10 May 2003 | *H. bibi* sp. nov. | 5 | 6 | >20 |
| 6   | Bibi-River, Tomakomai | 27 August 2002 | *H. longipalpis* | 1 | 2 | >20 |
| 7   | Bibi-River, Tomakomai | 8 September 2002 | *H. longipalpis* | 2 | 2 | >20 |
| 8   | Komaoi, Bihoro | 13 August 2002 | *H. ezoensis* | 1 | |
| 9   | Huruume, Bihoro | 13 August 2002 | *H. ezoensis* | 4 | 6 | |
| 10  | Moizari-gawa River, Eniwa | 11 May 2002 | *H. ezoensis* | 3 | |
| 10  | Moizari-gawa River, Eniwa | 30 July 2002 | *H. ezoensis* | 2 | |
| 11  | Kashiwagi-gawa River, Eniwa | 19 May 2002 | *H. ezoensis* | 1 | |
| 12  | Gokibiru-gawa River, Hamamasu | 31 August 2001 | *H. longiporus* | 1 | |
| 13  | Hokkaido Uni., Sapporo | 15 August 2003 | *H. longipalpis* | 1 | |
| 14  | Syumarinai-gawa River, Horokanai | 7 July 2002 | *H. longiporus* | 2 | 1 | |
| 15  | Juyonsen-gawa River, Horonobe | 20 August 2002 | *H. ezoensis* | 1 | |
| 16  | Pankerupeshupe-gawa River, Horonobe | 20 August 2002 | *H. longiporus* | 3 | 3 | |
| 17  | Tributary, Toikanbetu River, Horonobe | 20 August 2002 | *H. sokolowii* | 2 | 2 | |
| 18  | Iwana-sawa River, Hurano | 4 August 2002 | *H. foreli* | 1 | |
| 19  | Kiritappu-Marsh, Hamanaka | 13 June 2002 | *H. bibi* sp. nov. | 3 | |
| 20  | Kan-nokoike spring, Kiyosato | 12 August 2002 | *H. foreli* | 1 | 5 | >20 |
| 21  | Hukiage spring, Kyogoku | 14 May 2002 | *H. foreli* | 3 | 5 | >20 |
| 22  | Shirakawa River, Mori | 27 May 2002 | *H. longipalpis* | 2 | 2 | |
| 23  | Nanashigawa River, Niseko | 14 May 2002 | *H. calliger* | 5 | 5 | |
| 24  | Uraboro-gawa River, Obihiro | 30 June 2002 | *H. calliger* | 1 | |
| 25  | Monomannai-gawa River, Otoineppu | 7 July 2002 | *H. longiporus* | 1 | |
| 26  | Shiokari, Wassamu | 5 August 2003 | *H. longipalpis* | 1 | 1 | >20 |
| 27  | Shimokutuyo River, Turui, Akagun | 9 February 2001 | *H. ezoensis* | 3 | |
| 28  | Onnenai, Turui, Akagun | 15 July 2003 | *H. ezoensis* | 3 | |
| 29  | Onnenai, Turui, Akagun | 7 October 2002 | *H. japonicus* | 4 | |
| 30  | Shimoseturi, Turui, Akagun | 12 February 2001 | *H. longipalpis* | 2 | |
| 31  | Hokuto, Turui, Akagun | 19 February 2002 | *H. longipalpis* | 1 | |
| 32  | Tributary, Koetoi River, Wakanai | 19 August 2002 | *H. calliger* | 1 | |
| 32  | Tributary, Koetoi River, Wakanai | 5 August 2003 | *H. calliger* | 1 | 2 | |
| 33  | Masuhoro, Wakanai | 6 July 2002 | *H. ezoensis* | 1 | |

N. Matsumoto et al.
structures were made on only one member of the pair, haphazardly selected as to left or right. Where measurements were taken from multiple specimens, the mean is listed first, followed in parentheses by the range and number (n) of specimens measured. The number of specimens measured does not always equal the number of specimens examined because sometimes structures were missing or damaged. For Hygrobates bibi sp. nov. and H. japonicus, a “Variation in measurements” section follows the descriptions of the holotype and lectotype. Two ratios are given in the text as taxonomic characters. One is the ratio of the distance between the two ventral setae on P-4 to P-4 segment length; in the text this is abbreviated as “P-4 setae ratio”. The other is the ratio of the longest terminal seta on the tibia to the length of the tibia, I-L to IV-L; in the text this is abbreviated as “seta to tibia ratio”. “Integument pattern” refers to the sculpturing of the ventral integument in areas near the lateral margins.

Terminology follows Smith et al. (2001). Abbreviations are as follows: Palp: P-1, trochanter; P-2, femur; P-3, genu; P-4, tibia; P-5, tarsus. Genital acetabula: Ac1, anterior acetabulum; Ac2, medial acetabulum, Ac3, posterior acetabulum. Legs: I-L, first leg; II-L, second leg; III-L, third leg; IV-L, fourth leg. Leg segments are abbreviated by leg number followed by segment number from 1 to 6, proximal to distal, e.g. distalmost segment (tarsus) of first leg is I-L-6. Coxal plates: Cx1 to Cx4, anterior to posterior. Type specimens were deposited in the Hokkaido University Museum (HUM), Sapporo, Japan, with collection catalogue numbers prefaced by “ZIHU-”.

Diagnoses of the subgenera Hygrobates and Rivobates follow Cook (1974). Synonymy is provided only for Japanese specimens and for specimens that appeared in articles by Japanese authors. See K. H. Viets (1956) and K. O. Viets (1987) for more comprehensive synonymies.

**Taxonomy**

Family **HYGROBATOIDAE** Koch, 1842

Subfamily **HYGROBATINAE** Koch, 1842

Genus **Hygrobates** Koch, 1837

Subgenus **Hygrobates** Koch, 1837

**Hygrobates bibi** sp. nov.  
(Figures 2, 3)

**Hygrobates (s. str.) japonicus** Imamura 1953b, p 429–432, Figure 12; 1955, p 188.

**Hygrobates (Hygrobates) japonicus**: Imamura 1980, p 348–349, Figure 162A.

**Type locality**

Bibi River, Bibi, Chitose, Hokkaido, Japan.

**Etymology**

The species name refers to the type locality.

**Material examined**

Holotype: adult female (ZIHU-3106), dissected and mounted in polyvinyl alcohol, from type locality, 10 May 2003. Allotype: adult male (ZIHU-3107), dissected and mounted in
polyvinyl alcohol, from type locality, 10 May 2003. Paratypes: four adult males (ZIHU-3112, 3113, 3114, 3115), dissected and mounted in polyvinyl alcohol; four adult females (ZIHU-3108, 3109, 3110, 3111), dissected and mounted in polyvinyl alcohol, from type locality, 10 May 2003.

Figure 2. Hygrobates (Hygrobates) bibi sp. nov. (A–F) Female, holotype (ZIHU-3106). (A) Ventral side, scale 1; (B) palp, scale 3; (C) chelicera, scale 2; (D) coxoglandularium II, scale 3; (E) antenniform seta, scale 3; (F) genital fields, scale 3. (G) Male, allotype (ZIHU-3107), genital field, scale 3. Scale bars: 1, 2, 3 (B, F, G)=100 μm; 3 (D, E)=50 μm.
Figure 3. Hygrobes bibi sp. nov. Female, holotype (ZIHU-3106). (A) First leg; (B) second leg; (C) third leg; (D) fourth leg. Scale bar: 100 μm.
Additional specimens. Two males from Akkeshi, Hokkaido, 12 June 2003; three males from Hamanaka, Hokkaido, 13 June 2003. Uchida’s collection: one female (ZIHU-2334) and two males (ZIHU-2338, 2339) from Sapporo, Hokkaido, July 1932; two females (ZIHU-2335, 2336) and one male (ZIHU-2337) from Sapporo, Hokkaido, 16 May 1932; one female (ZIHU-2340) from Shakujii, Tokyo, 24 July 1935; one female (ZIHU-2341) from Shakujii, Tokyo, May 1934; one female (ZIHU-2342) from Myoshoji, Tokyo, 19 July 1935. Imamura’s collection: one female (collection number 940) and one male (collection number 938) from Toba River, Gifu, 20 October 1951; one male (collection number 1266) from Rakuju-en, Shizuoka, 15 May 1953.

Description of female

Cuticular features. Body spherical. Integument soft, finely striated, spacing of striae 2.7. Secondary sclerotization of coxoglandularia II weak (Figure 2D). Antenniform setae thickened, each located on a small, rounded base (Figure 2E), 45 in length. Without dorsalia.

Chelicera (Figure 2C). Total length 340, basal segment 233, claw 97, maximum height 65, length/height ratio 6, basal segment/claw ratio 2.

Palp (Figure 2B). Length/height: P-1 36/45, P-2 136/78, P-3 97/55, P-4 159/42, P-5 52/16. P-2 with prominent, rounded-conical projection having 38 denticles distributed all over the ventral surface. Ventral margin of P-3 swollen, evenly convex in outline, with 22 denticles in a central patch occupying about half the ventral length. P-4 with two setae on ventral side and 10 setae on lateral and dorsal sides; distance between two ventral setae 10; P-4 setae ratio 0.06. P-5 with two setae.

Capitulum (Figure 2A). Broadly fused with the first coxae, 139 in width; anterior margin of each half of capitulum with a rounded notch.

Coxae (Figure 2A). Length/width anterior coxal group 337/395. Length/width posterior coxal groups 318/272. Posterior end of anterior coxal group rounded-triangular; posterolateral apodemes extending slightly beyond sclerotization, 156 from tip to tip. Suture line between Cx1 and capitulum irregular, not curved. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 nearly straight, incomplete, extending to near glandularium of Cx4. Medial margin of Cx4 rounded; angle apodemes lacking.

Legs (Figure 3A–D). Swimming hairs absent. Claws with a ventral clawlet. Lengths of leg segments I-L-1 to I-L-6, 75/91/143/201/181/175; II-L-1 to II-L-6, 71/117/130/194/201/188; III-L-1 to III-L-6, 78/110/156/240/253/220; IV-L-1 to IV-L-6, 162/152/201/292/305/253. Seta to tibia ratio, I-L to IV-L, 0.36/0.32/0.23/0.26.

Genital field (Figure 2F). Entire genital field 230 wide. Genital plates with smooth, rounded-angular border. Right genital plates with 22 setae, left with 16. Setae lacking on membranous integument near genital plate. Length/width genital plates 149/75. Three genital acetabula on each side, arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 52/32, Ac2 52/32, Ac3 52/29. Pre- and postgenital sclerites with medially protruded apodemes. No setae on pregenital sclerite. Genital opening between pre- and postgenital sclerites 130 in length.
Description of male

Characters as given for female, except for genital field. Antenniform setae length 42.

Chelicera. Total length 201, basal segment 194, claw 91, maximum height 65, length/height ratio 6, basal segment/claw ratio 2.

Palp. Length/height P-1 32/39, P-2 117/78, P-3 87/58, P-4 143/39, P-5 55/19. P-2 with 30 denticles. P-3 with 31 denticles. P-4 with two setae on ventral side and 10 setae on lateral and dorsal sides; distance between two ventral setae 10; P-4 setae ratio 0.07. P-5 with two setae.

Capitulum. Width 123.

Coxae. Length/width anterior coxal groups 311/369. Length/width of posterior coxal group 305/262. Posterolateral apodemes of anterior coxal group 149 from tip to tip.

Legs. Lengths of leg segments I-L-1 to I-L-6, 81/110/123/175/165/156; II-L-1 to II-L-6, 71/104/123/175/181/175; III-L-1 to III-L-6, 71/104/136/214/227/214; IV-L-1 to IV-L-6, 162/143/188/272/279/240. Seta to tibia ratio, I-L to IV-L, 0.35/0.32/0.24/0.21.

Genital field (Figure 2G). Genital plate length/width 149/194. Genital plate with smooth, even border; anterior margin depressed, with a slight median projection; posterior margin deeply notched with a large, rounded median projection; apodemes lacking. Genital plate with 23 setae on right side and 25 on left. Three genital acetabula on each side, arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 45/23, Ac2 55/26, Ac3 52/32.

Variation in measurements, female

Antenniform setae length 49 (42–58, n=4).

Chelicera. Total length 327 (317–337, n=4), basal segment 225 (220–227, n=4), claw 102 (97–104, n=4), maximum height 65 (65–65, n=4), length/height ratio 6, basal segment/claw ratio 2.

Palp. Length/height P-1 32/44 (32–32/42–45, n=4), P-2 128/84 (123–130/81–88, n=4), P-3 99/60 (91–104/52–65, n=4), P-4 158/43 (156–162/39–45, n=4), P-5 57/19 (52–65/19–19, n=4). P-2 with 30 (26–38, n=4) denticles. P-3 with 27 (22–30, n=4) denticles. P4 with two ventral setae and 11 (10–12, n=4) setae on lateral and dorsal sides; P-4 setae ratio 0.07 (0.04–0.10, n=4). P-5 with two (2–2, n=4) setae.

Capitulum. Width 133 (123–143, n=4).

Coxae. Length/width anterior coxal group 323/374 (321–324/324–402, n=4). Length/width posterior coxal group 306/264 (292–311/259–266, n=4). Posterolateral apodemes of anterior coxal group 152 (130–162, n=4) from tip to tip.

Legs. Lengths of leg segments I-L-1 to I-L-6, 71/91/118/179/177/166 (65–79/91–91/113–123/175–181/168–188/162–175, n=3); II-L-1 to II-L-6, 69/96/125/184/191/181 (65–75/
84–104/123–130/175–194/181–201/175–188, *n* = 4); III-L-1 to III-L-6, 71/97/144/220/233/214 (65–78/91–104/136–156/214–227/227–246/207–227, *n* = 4); IV-L-1 to IV-L-6, 147/147/188/267/293/251 (130–162/143–162/168–207/233–292/285–311/240–227, *n* = 4). Seta to tibia ratio, I-L to IV-L, 0.37/0.32/0.24/0.24 (0.35–0.39/0.30–0.33/0.20–0.28/0.22–0.26, *n* = 4).

**Genital field.** Width of entire genital field 228 (217–240, *n* = 4). Right genital plate with 19 (18–20, *n* = 4) setae, left with 19 (17–22, *n* = 4). Length/width genital plates 143/83 (143–146/78–88, *n* = 4). Length/width of Ac1 50/32 (45–55/29–32, *n* = 4), Ac2 52/27 (39–64/23–32, *n* = 4), Ac3 49/33 (45–52/29–39, *n* = 4). Length of genital opening between pre- and post- genital sclerites 120 (97–149, *n* = 4).

**Variation in measurements, male**

Antenniform setae length 47 (45–49, *n* = 4).

**Chelicera.** Total length 287 (259–305, *n* = 4), basal segment 198 (175–214, *n* = 4), claw 89 (84–94, *n* = 4), maximum height 65 (65–65, *n* = 4), length/height ratio 6, basal segment/claw ratio 2 (2–2, *n* = 4).

**Palp.** Length/height P-1 31/40 (26–32/39–45, *n* = 4), P-2 109/72 (104–120/65–78, *n* = 4), P-3 83/51 (78–91/45–52, *n* = 4), P-4 140/38 (136–146/36–42, *n* = 4), P-5 52/17 (49–55/16–19, *n* = 4). P-2 with 28 (25–30, *n* = 4) denticles. P-3 with 28 (25–30, *n* = 4) denticles. P-4 with two ventral setae and 10 (10–10, *n* = 4) setae on lateral and dorsal sides. P-4 setae ratio 0.07 (0.04–0.09, *n* = 4). P-5 with two setae.

**Capitulum.** Width 127 (110–143, *n* = 4).

**Coxae.** Length/width anterior coxal group 151/241 (130–188/181–311, *n* = 4). Length/width posterior coxal group 297/251 (272–314/220–266, *n* = 4). Posterolateral apodemes of anterior coxal group 147 (130–159, *n* = 4) from tip to tip.

**Legs.** Lengths of leg segments I-L-1 to I-L-6, 61/89/105/160/159/154 (52–68/84–91/104–110/156–168/149–168/149–156, *n* = 4); II-L-1 to II-L-6, 59/97/113/168/175/170 (55–58/84–104/104–123/162–175/168–181/162–175, *n* = 4); III-L-1 to III-L-6, 70/100/128/203/207/196 (58–78/97–104/123–130/201–207/214–188–207, *n* = 4); IV-L-1 to IV-L-6, 133/139/173/248/272/231 (123–149/130–143/162–188/220–272/259–285/220–240, *n* = 4). Seta to tibia ratio, I-L to IV-L, 0.38/0.34/0.26/0.23 (0.35–0.42/0.24–0.42/0.23–0.35/0.22–0.34, *n* = 4).

**Genital field.** Length/width 139/188 (130–149/181–201, *n* = 4). Genital plate with 23 (22–24, *n* = 4) setae on right side and 23 (20–27, *n* = 4) setae on left. Length/width Ac1 41/28 (39–45/26–32, *n* = 4), Ac2 52/23 (45–58/19–32, *n* = 4), Ac3 47/32 (45–49/29–32, *n* = 4).

**Localities**

Akkeshi, Hamanaka, Sapporo, and Tomakomai on Hokkaido; Tokyo, Gifu, Shizuoka.

**Distribution**

Hokkaido, Gifu, Shizuoka; northern and middle Japan.
Remarks

_Hygrobes bibi_ sp. nov. is most similar to _H. calliger_, but differs from the latter in four of 18 characters (Table II). _Hygrobes bibi_ has a rounded projection on P-2, the ventral margin of P-3 convex, the pair of ventral setae on P-4 very close together, and an integument pattern of fine striation. In contrast, _H. calliger_ has a sharper, triangular P-2 projection, the ventral side of P-3 flat, the pair of ventral setae on P-4 farther apart, and an integument pattern of strong lineation.

Examination of the old collections revealed that the new species had already been collected from Japan prior to our study. Three of about 20 specimens labelled _H. japonicus_ in Uchida’s collection and both specimens labelled _H. japonicus_ in Imamura’s collection proved to be _H. bibi_. Imamura (1954) noted some differences in the morphology of P-3 between his specimens and the original description of _H. japonicus_ (Uchida, 1931), but concluded that these differences were due to the immaturity of his specimens. Examination of more than 20 specimens newly collected from Hokkaido has revealed that P-3 morphology is diagnostic between _H. japonicus_ and the new species. The character state Uchida (1931, p266) described for _H. japonicus_ as “Der gezackte Höcker auf den Beugeseite des dritten Gliedes ist niedrig, aber ziemlich breit” (serrated knob on the ventral side of P-3 is low, but relatively broad; our translation) is separable into “ventral side of P-3 with a low knob in the middle” (Figure 11B) in _H. japonicus_ and “ventral side of P-3 convex without a distinct knob” (Figure 2B) in _H. bibi_, without any transitional states.

Other characters previously used to distinguish species of _Hygrobes_ include the morphologies of P-2 and the genital plates, and the distribution of the ventral setae on P4. Uchida (1931, p265) mentioned for _H. japonicus_, “auf den Beugeseite des zweiten Palpengliedes befindet sich ein mit Spitzen besetzter stumpfer Zapfen” (on the ventral side of P-2 is a blunt projection occupied by points; our translation), but provided a poor illustration. Once again, the character state described by Uchida can be separated into two states: “projection narrow, with a truncated end” (Figure 11B) for _H. japonicus_ and “projection broad, with a round end” (Figure 2B) for _H. bibi_, also without any transitional states.

A comparison of character states between _H. bibi_ sp. nov. and _H. japonicus_ is summarized in Table II. The two species differ in 10 of the 18 characters compared, including the morphology of the P-2 projection and the ventral side of P-3, the P-4 setae ratio, the ratio of the longest terminal seta on IV-L-5 to length of IV-L-5, the shape of the male genital plate, and secondary sclerotization of the coxoglandularia.

Uchida (1931) noted that _H. japonicus_ has the two setae on ventral side of P-4 widely separate (Figure 11B). However, his specimens labelled _H. japonicus_ include specimens of _H. bibi_ that have these setae close together (Figure 2B). The ratio of the distance between the two setae to P-4 length does not overlap between _H. japonicus_ and _H. bibi_, and the means are significantly different (Figure 4). Finally, as a novel taxonomic character for distinguishing species of water mites, we propose here the ratio of the longest terminal seta on IV-L-5 to the length of IV-L-5. This ratio does not overlap between _H. japonicus_ and _H. bibi_, and the means are significantly different (Figure 5, also compare Figures 3D and 12D).

**Hygrobes calliger** Piersig, 1896
(Figures 6, 7)

_Hygrobes calliger_ Piersig 1896, p 439; Enami 1940, p 230–233, Text figures 23–25; Imamura 1953a, p 220–222, Figure 16.

_Hygrobes (s. str.) calliger_: Imamura 1953b, p 428–429, Figure 11; 1954, p 75; 1955, p 188.
Table II. Comparison of character states among species of *Hygrobates* subgenus *Hygrobates* from Hokkaido.

| Character                                                                 | bibi | calliger | foreli | japonicus | longipalpis | longiporus | nigromaculatus | sokolowi |
|---------------------------------------------------------------------------|------|----------|--------|-----------|-------------|-------------|----------------|----------|
| Secondary sclerotization of coxoglandularia 2: absent (0), weak (1), heavy (2) | 1    | 1        | 0      | 0         | 2           | 0           | 1              |          |
| Posterior end of anterior coxal group: round (0), triangular (1)          | 1    | 1        | 0      | 0         | 1           | 0           | 1              | 0        |
| Suture lines between Cx3 and Cx4: complete (0), incomplete (1)            | 1    | 1        | 1      | 1         | 0           | 0           | 1              | 1        |
| P-2 projection: weak (0), pronounced (1)                                   | 1    | 1        | 0      | 1         | 1           | 0           | 0              | 1        |
| End of P-2 projection: acute (0), rounded (1), square (2)                  | 1    | 0        | 1      | 2         | 1           | 1           | 1              | 0        |
| P-2 denticles: at tip of projection (0), or extending over less (1) or more (2) than half the ventral margin | 1    | 1        | 1      | 0         | 1           | 2           | 2              | 0        |
| Ventral outline P-3: flat (0), evenly convex (1), with more-or-less discrete knob (2) | 1    | 0        | 0      | 2         | 2           | 0           | 0              | 0        |
| Patch of P-3 denticles covers: less (0), or more (1) than half of ventral segment length | 1    | 1        | 1      | 0         | 0           | 1           | 1              | 1        |
| P-4 setae ratio: \( \leq 0.10 \) (0), variable (1), \( >0.10 \) (2)       | 0    | 1        | 0      | 2         | 0           | 0           | 0              | 2        |
| IV-L-5 seta to tibia ratio: \( \leq 0.30 \) (0), \( >0.30 \) (1)         | 0    | 0        | 1      | 1         | 1           | 1           | 0              | 0        |
| Anterior border male genital plate: unnotched with (0) or without (1) discrete median projection, or notched (2) | 1    | 1        | 0      | 0         | 2           | 2           | 0              | 1        |
| Posterior border male genital plate: having median projection not within (0) or within a deep notch, or notch only without projection (2) | 1    | 1        | 0      | 0         | 1           | 0           | 1              | 2        |
| Anterior end female genital plates: anterior (0), posterior (1) to anterior end pregenital sclerite | 1    | 1        | 1      | 1         | 0           | 0           | 1              | 1        |
| Posterior end female genital plates: anterior (0), posterior (1) to posterior end postgenital sclerite | 1    | 1        | 0      | 1         | 1           | 1           | 1              | 0        |
| Distance between Ac1 and Ac2: greater than or equal to (0), less than (1) width Ac1 | 0    | 0        | 0      | 0         | 0           | 1           | 0              | 1        |
| Distance between Ac1 and Ac3: less than (0), greater than (1) length of Ac1 | 0    | 0        | 0      | 0         | 0           | 0           | 0              | 1        |
| Outer border of genital plate(s) smooth (0), markedly crenate (1) or irregular (2) | 0    | 0        | 0      | 1         | 1           | 0           | 2              | 0        |
| Pattern of integument very fine striations (0), fine striations (1), strongly lineated (2) or irregular ridges (3) | 1    | 2        | 1      | 1         | 0           | 0           | 1              | 3        |
**Hygrobates calliger calliger**: Imamura 1960, p 41; 1980, p 348–349, Figure 162B.

**Hygrobates heteropalpis**: Imamura 1954, p 77–79, Figure 45.

**Material examined**

Five females and five males from Nanashi-gawa River, Niseko, 13 May 2002; one female from Urahoro-gawa River, Obihiro, 30 June 2002; one female from Koetoi, Wakkanai, 19 August 2002; one female and two males collected from Koetoi, Wakkanai, 5 August 2003; all from Hokkaido. From Imamura’s collection, holotype (female, collection number 1247) and one paratype (female, collection number 1248) of *H. heteropalpis* from Ebeotsu, Hokkaido, 19 June 1947.

**Description of female**

**Cuticular features.** Integument soft, strongly lineated, line spacing 2.0. Secondary sclerotization of coxoglandularia II weak (Figure 6D). Antenniform setae (Figure 6E) thin, located on small, rounded bases, length 58 (52–65, *n* = 5). Without dorsalia.

**Chelicera (Figure 6C).** Total length 330 (298–363, *n* = 5), basal segment 242 (227–266, *n* = 5), claw 101 (94–120, *n* = 5), maximum height 66 (58–71, *n* = 5), length/height ratio 5.0 (4.9–5.1, *n* = 5), basal segment/claw ratio 2.4 (2.1–2.7, *n* = 5).

**Palp (Figure 6B).** Length/height, P-1 33/45 (29–36/39–52, *n* = 5), P-2 133/91 (117–156/75–110, *n* = 5), P-3 111/64 (91–130/52–84, *n* = 5), P-4 167/41 (149–194/36–45, *n* = 5), P-5 56/18 (52–62/16–19, *n* = 5). P-2 with truncated projection. P-2 with a tapering,
blunt-triangular ventral projection having 26 (21–30, n=5) denticles distributed all over the surface. Ventral side of P-3 flat, with a patch of 27 (22–31, n=5) denticles occupying more than half the ventral length of segment, closer to distal end. P-4 with two ventral setae and 10 (9–11, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.1 (0.1–0.2, n=5). P-5 with three setae.

Capitulum (Figure 6A). Broadly fused with the first coxae, 152 (143–168, n=5) in width. Anterior portion of each half of capitulum deeply notched.

Coxae (Figure 6A). Length/width anterior coxal group 318/395 (285–337/369–421, n=5). Length/width posterior coxal groups 293/253 (279–305/240–272, n=5). Posterior end of anterior coxal group triangular, posterolateral apodemes extending slightly beyond sclerotization, 158 (143–175, n=5) from tip to tip. Suture line between Cx1 and capitulum nearly straight to irregular, not curved. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 incomplete, extending to near glandularia on Cx4. Medial margins of Cx4 acutely rounded, without angle apodemes.

Legs (Figure 7A–D). Swimming hairs absent, claws with a ventral clawlet. Seta to tibia ratio, I-L/IV-L 0.3/0.2 (0.2–0.4/0.2–0.2, n=5).

Genital field (Figure 6F). Entire genital field 232 (227–240, n=5) in width. Genital plates with smooth outer border. Right genital plate with 15 (13–16, n=5) setae, left with 14 (12–15, n=5). No setae on membranous integument near genital plate. Length/width genital
plates 135/77 (130–143/71–84, n=5). Three genital acetabula on each side arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width of Ac1 45/29 (39–49/19–32, n=5), Ac2 51/27 (42–58/23–29, n=5), Ac3 50/32 (39–58/32–36, n=5). Pre- and postgenital sclerites with medially protruded apodemes. Pregenital sclerite anterior to the anterior ends of genital plates, lacks setae. Postgenital sclerite anterior to the posterior ends of genital plates. Genital opening between pre- and post-genital sclerites 123 (97–149) in length.

Figure 6. *Hygrobates (Hygrobates) calliger*. (A–F) Female. (A) Ventral side, scale 1; (B) palp, scale 3; (C) chelicera, scale 2; (D) coxoglandularium II, scale 3; (E) antenniform seta, scale 3; (F) genital field, scale 3. (G) Male, genital field, scale 3. Scale bars: 1, 2, 3 (B, F, G)=100 μm; 3 (D, E)=50 μm.
Description of male

Characters as given for female, except for genital field. Antenniform setae length 51 (49–58, \(n=5\)).
Chelicera. Total length 330 (298–363, \(n=5\)), basal segment 203 (181–227, \(n=5\)), claw 87 (81–97, \(n=5\)), maximum height 57 (49–65, \(n=5\)), length/height ratio 4.9 (4.3–5.4, \(n=5\)), basal segment/claw ratio 2.3 (2.2–2.5, \(n=5\)).

Palp. Length/height P-1 30/41 (26–32/39–45, \(n=5\)), P-2 109/73 (97–130/65–97, \(n=5\)), P-3 84/48 (78–97/42–65, \(n=5\)), P-4 136/36 (130–162/32–39, \(n=5\)), P-5 51/17 (49–52/16–19, \(n=5\)). P-2 with 28 (24–33, \(n=5\)) denticles. P-3 with 25 (22–28, \(n=5\)) denticles. P-4 with two ventral setae and 11 (10–12, \(n=5\)) setae on lateral and dorsal sides. P-4 setae ratio 0.1 (0.1–0.1, \(n=5\)). P-5 with three setae.

Capitulum. Width 119 (110–136, \(n=5\)).

Coxae. Length/width anterior coxal group 187/351 (266–314/324–369, \(n=5\)). Length/width posterior coxal group 275/231 (259–305/207–266, \(n=5\)). Posterolateral apodemes of anterior coxal group 135 (123–149, \(n=5\)) from tip to tip.

Legs. Seta to tibia ratio, I-L/IV-L 0.3/0.2 (0.3–0.4/0.2–0.2, \(n=5\)).

Genital field (Figure 6G). Genital plate length/width 142/184 (139–143/175–194, \(n=5\)), anterior end flat, outer border smooth, posterior end deeply notched with a drop-shaped median projection; apodemes lacking. Genital plate with 20 (17–23, \(n=5\)) setae on right side and 20 (15–24, \(n=5\)) on left. Three genital acetabula arranged in an obtuse triangle on each side. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 40/29 (32–45/26–32, \(n=5\)), Ac2 51/25 (45–55/19–26, \(n=5\)), Ac3 50/32 (45–52/29–39, \(n=5\)).

Localities

Ebeotsu, Niseko, Obihiro, and Wakkanai on Hokkaido.

Distribution

Palaearctic region: Europe, Russia, Central Asia (Samarkand), Japan (southern Honshu, Hokkaido).

Remarks

Imamura (1954) described *Hygrobates heteropalpis* from Hokkaido as very similar to *H. calliger*, noting that the former has a longer ventral projection on P-2 compared to the latter. Two P-2 projections in the original illustration of *H. heteropalpis* (Imamura 1954, p 78, Figure 45b, c) certainly seem to be longer than those of *H. calliger calliger* illustrated by Imamura (1953a). However, the P-2 projections of three subspecies of *H. calliger* (*H. calliger calliger*, *H. calliger obtusipalpis*, and *H. calliger latilaminata*) illustrated by Viets (1930, p 378, Figures 13–15) do not seem to be shorter than those of *H. heteropalpis*. We addressed this problem by examining the shape variation of the P-2 projection among 11 specimens of the two species, including the holotype and paratype of *H. heteropalpis*, three specimens of *H. calliger* from Sicily and North Tuscany, Italy, and six specimens from a population at Nanashi-gawa river, Niseko, southern Hokkaido. As is clearly shown in Figure 8, there are
no diagnostic differences in the P-2 projection between the two nominal species. Both the length and shape of the projection in the types of *H. heteropalpis* fall within the range of variation of the Hokkaido population of *H. calliger*. The P-2 projection of the European specimens of *H. calliger* tends to be broader than that of either *H. calliger* or *H. heteropalpis* from Japan, but again the character overlaps (e.g. compare Figure 8B with 8E). Except for uncertainty regarding the male characters of *H. heteropalpis* (the male has not been described), *H. heteropalpis* and *H. calliger* overlap completely in P-2 morphology and other characters examined (Table II). With little doubt, *H. heteropalpis* Imamura, 1954 is a junior synonym of *H. calliger* Piersig, 1896.

*Hygrobates calliger* is most similar to *H. bibi* sp. nov. but differs from the latter in four of 18 characters (Table II). The former has a narrow, spike-like P-2 projection, the flat ventral side of P-3 flat, and a strongly lined integument, whereas the latter has a broad, rounded P-2 projection, the ventral side of P-3 convex (compare Figures 6B and 2B), and a finely striated integument. The P-4 setae ratio is somewhat greater in *H. calliger* than in *H. bibi*.

---

**Hygrobates foreli** (Lebert, 1874)

(Figures 9, 10)

*Compognatha foreli* Lebert 1874, p 645.

*Hygrobates foreli*: Uchida 1934, p 92, Figure 25.

*Hygrobates (s. str.) foreli*: Imamura 1954, p 75–77, Figures 43, 44.

**Material examined**

One female and one male from a stream in Akan, 4 June 2002; one male from Iwana-sawa River, Hurano, 4 August 2003; more than 20 females and males from Kan-noko-ike Spring, Kiyosato, 12 August 2002; more than 20 females and males from Hukidasi-Yusui, Kyogoku, 14 May 2002; all on Hokkaido.
Description of female

Cuticular features. Integument soft, finely striated, spacing of striae 1.6. Secondary sclerotization of coxoglandularia II weak (Figure 9D). Antenniform setae thin, each on a small, oval base (Figure 9E), length 67 (58–78, n=3). Without dorsalia.
Chelicera (Figure 9C). Total length 431 (408–447, n=3), basal segment 307 (285–324, n=3), claw 137 (136–139, n=3), maximum height 102 (97–104, n=3), length/height ratio 4.2 (4.2–4.3, n=3), basal segment/claw ratio 2.2 (2.1–2.4, n=3).

Figure 10. Hygrobates (Hygrobates) foreli, female. (A) First leg; (B) second leg; (C) third leg; (D) fourth leg. Scale bar: 100 μm.
**Palp (Figure 9B).** Length/height, P-1 41/49 (36–45/42–52, n=5), P-2 152/83 (130–168/71–97, n=5), P-3 132/56 (91–181/52–65, n=5), P-4 203/51 (162–240/36–58, n=5), P-5 64/25 (55–68/16–29, n=5). Ventral projection on P-2 negligible, a slightly raised knob with 16 (9–31, n=5) denticles. Ventral side of P-3 flat with a patch of 14 (12–16, n=5) setae. P-4 with two ventral setae and 14 (12–16, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.05 (0.03–0.07, n=5). P-5 with three setae.

**Capitulum (Figure 9A).** Broadly fused with first coxae, width 142 (123–181, n=5). Anterior portion of each half of capitulum is broadly and shallowly notched.

**Coxae (Figure 9A).** Length/width anterior coxal group 380/478 (324–389/395–505, n=5). Length/width posterior coxal groups 404/375 (305–460/360–405, n=5). Posterior end of anterior coxal group rounded, posterolateral apodemes extending scarcely beyond sclerotization, 228 (194–246, n=5) from tip to tip. Suture line between first coxae and capitulum nearly straight. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 incomplete, extending near to gland of Cx4. Medial margins of fourth coxae rounded, slightly angular, without angle apodemes.

**Legs (Figure 10A–D).** Swimming hairs absent. Claws with a ventral clawlet. Seta to tibia ratio, I-L/IV-L 0.3/0.3 (0.3–0.4/0.2–0.3, n=5).

**Genital field (Figure 9F).** Entire genital field 367 (311–434, n=5) in width, with smooth outer border. Length/width genital plates 191/117 (162–220/100–130, n=5). Right genital plate with 20 (16–25, n=5) setae, left with 19 (17–21, n=5). No setae on membranous integument near genital plate. Three genital acetabula on each side arranged in an acute triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width in Ac1 67/45 (55–84/32–58, n=5), Ac2 80/32 (65–97/26–39, n=5), Ac3 93/44 (78–104/29–58, n=5). Pre- and postgenital sclerites with apodemes medially. Pregenital sclerite located anterior to the anterior ends of genital plates, setae lacking. Postgenital sclerite extends slightly posterior to posterior ends of genital plates. Genital opening between pre- and postgenital sclerites 189 (175–207, n=5) in length.

**Description of male**

Characters as given for female, except for genital field. Antenniform setae length 70 (65–78, n=4).

**Chelicera.** Total length 394 (363–454, n=3), basal segment 279 (253–324, n=3), claw 129 (117–143, n=3), maximum height 97 (97–97, n=3), length/height ratio 4.1 (3.7–4.7, n=3), basal segment/claw ratio 2.2 (2.0–2.3, n=3), length/height P-1 39/41 (29–45/39–45, n=5), P-2 137/82 (130–156/71–97, n=5), P-3 99/54 (75–123/45–65, n=5), P-4 179/44 (156–201/42–49, n=5), P-5 62/21 (55–65/19–23, n=5). P-2 with 14 (9–21, n=5) denticles. P-3 with 15 (12–16, n=5) denticles. P-4 with two ventral setae and 13 (11–16, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.03 (0.0–0.08, n=5). P-5 with three setae.

**Capitulum.** Width 124 (84–143, n=5).
Coxae. Length/width anterior coxal group 352/456 (337–382/389–518, n=5). Length/width posterior coxal group 395/343 (376–434/292–395, n=5). Posterolateral apodemes of anterior coxal group 202 (181–214, n=5) from tip to tip.

Legs. Seta to tibia ratio, I-L/IV-L 0.3/0.3 (0.3–0.4/0.2–0.4, n=5).

Genital field (Figure 9G). Genital plate length/width 196/255 (165–233/220–292, n=5), with smooth, evenly curved outer border. Anterior end of genital plate with a low, broad, rounded median projection; posterior end depressed, with a mammiform median projection; apodemes lacking. Genital plate with 22 (21–23, n=5) setae on right side and 20 (18–22, n=5) on left. Three genital acetabula on each side arranged in an acute triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Acetabulum length/width Ac1 67/44 (62–71/42–52, n=5), Ac2 80/35 (71–91/29–42, n=5), Ac3 88/55 (78–97/42–71, n=5).

Localities
Akan, Hurano, Kiyosato, and Kyogoku, on Hokkaido.

Distribution
Palaearctic region: Europe, Russia, Japan (Hokkaido).

Remarks
Hygrobates foreli has previously been reported twice from Hokkaido (Uchida 1934; Imamura 1954). This species and H. longipalpis are both larger in overall body size than the other species treated. However, H. foreli is most similar to H. nigromaculatus; the two share 14 of 18 characters (Table II) and, among the species treated, are the only ones with rounded medial projections on both the anterior and posterior borders of the male genital plate. Next most similar to H. foreli is H. calliger and H. longipalpis, sharing nine of 18 characters.

Hygrobates japonicus Uchida 1931
(Figures 11, 12)

Hygrobates japonicus Uchida 1931, p 265–266, Abb. 5–8.
Hygrobates (s. str.) japonicus: Sokolow 1940, p 293, Figure 153a, b.
Hygrobates bituberosus Sokolow 1931, p 488–490, Figures 49, 50.

Material examined
Lectotype (ZIHU-2330): adult female, missing chelicerae, dissected and mounted in glycerin jelly, from Shakujii, Tokyo, 15 April 1928, labelled Hygrobates sp. in Uchida collection. Paralectotype (ZIHU-2331): adult male, missing the palps, dissected and mounted in glycerin jelly, from Shakujii, Tokyo, 15 April 1928, labelled Hygrobates sp. in Uchida collection; adult male from Shakujii, Tokyo, 17 August 1933; four females from Turui, Akan, Hokkaido, 7 October 2002.
Description of female

Lectotype, ZIHU-2330.

Cuticular features. Integument soft, finely striated, spacing of striae 1.8. Coxoglandularia II (Figure 11D) without secondary sclerotization. Antenniform setae (Figure 11E) thin, on small, oval base, length 23. Without dorsalia.

Figure 11. *Hygrobates (Hygrobates) japonicus*. (A–F) Female. (A) Ventral side, scale 1; (B) palp, scale 3; (C) chelicera, scale 2; (D) coxoglandularium II, scale 3; (E) antenniform seta, scale 3; (F) genital field, scale 3. (G) Male, paralectotype (ZIHU-2331), genital field, scale 3. Scale bars: 1, 2, 3 (B, F, G)=100μm; 3 (D, E)=50μm.
Chelicera. Missing.

*Palp (Figure 11B).* Length/height, P-1 45/65, P-2 175/123, P-3 117/84, P-4 227/55, P-5 71/19. P-2 with tapering, truncated projection, with seven denticles on flattened top. Ventral side of P-3 swollen into a rounded knob, with a dense patch of 27 denticles on top.
occupying less than one-quarter of the ventral segment length. P-4 with two ventral setae and seven setae on lateral and dorsal sides. P-4 setae ratio 0.2. P-5 with three setae.

**Capitulum (Figure 11A).** Broadly fused with the first coxae. Anterior border of each half of capitulum is irregularly truncate, without a notch.

**Coxae (Figure 11A).** Length/width anterior coxal group 356/330. Length/width posterior coxal groups 356/324. Posterior end of anterior coxal group rounded-triangular; posterolateral apodemes extending slightly beyond sclerotization, 207 from tip to tip. Suture line between first coxae and capitulum nearly straight. Coxoglandularium I on Cx2. Suture line between third and fourth coxae incomplete, extending to near glandularium of Cx4. Medial margin of Cx4 a rounded angle, with angle apodemes.

**Legs (Figure 12A–D).** Swimming hairs absent, claws with a ventral clawlet. Lengths of leg segments I-L-1 to I-L-6, 58/136/143/207/220/207; II-L-1 to II-L-6 84/110/156/240/–/–; III-L-1 to III-L-6, 79/123/168/253/279/272; IV-L-1 to IV-L-6, 149/181/233/369/162/324. Seta to tibia ratio, I-L to IV-L, 0.38/–/0.25/0.68 (II-L-5 and 6 are missing).

**Genital field (Figure 11F).** Entire genital field 194 in width. Length/width genital plates 201/100; outer border irregularly crenate except around smooth proximolateral portion; 19 setae on right side and 20 on left. No setae on membranous integument near genital plates. Three pairs of genital acetabula arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 78/45, Ac2 71/39, Ac3 71/45. Pre- and postgenital sclerites with medially protruded apodemes. No setae on pregenital sclerite. Pregenital sclerite extends slightly anterior to anterior ends of genital plates. Postgenital sclerite anterior to the posterior ends of genital plates. Genital opening between pre- and postgenital sclerites 162 in length.

**Description of male**

Paralectotype; ZIHU-2331. Characters as given for female, except for genital field. Chelicerae and palps missing.

**Capitulum.** Width 117.

**Coxae.** Length/width anterior coxal group 324/408. Length/width posterior coxal group 324/298. Posterolateral apodemes of anterior coxal group 188 from tip to tip.

**Legs.** Lengths of leg segments I-L-1 to I-L-6, 52/117/130/181/194/181; II-L-1 to II-L-6 45/117/130/181/194/181; III-L-1 to III-L-6, 78/123/168/253/279/272; IV-L-1 to IV-L-6, 162/168/233/343/350/305. Seta to tibia ratio, I-L to IV-L, 0.50/0.43/0.40/0.37.

**Genital field (Figure 11G).** Genital plate length/width 194/240; outer border irregularly crenate with three distinct lobes. Middle third of anterior border raised as a rounded projection; posterior border irregular, with a wide, shallow median notch; apodemes lacking. Genital plate with 22 setae on right side and 23 on left. Three genital acetabula on each side, arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 65/45, Ac2 75/39, Ac3 71/36.
Variation in measurements, female

ZIHU-3088, 3089, 3090, and specimens from first author's personal collection. Antenniform setae length 40 (36–42, n=3).

**Chelicera.** Total length 391 (369–421, n=4), basal segment 284 (266–311, n=4), claw 120 (117–123, n=4), maximum height 77 (71–81, n=4), length/height ratio 5.1 (4.9–5.2, n=4), basal segment/claw ratio 2.4 (2.3–2.5, n=4).

**Palps.** Length/height P-1 37/57 (32–39/52–58, n=4), P-2 154/97 (149–156/91–104, n=4), P-3 112/66 (104–117/58–78, n=4), P-4 213/46 (201–224/45–49, n=4), P-5 65/21 (65–65/19–26, n=4). P-2 with 18 (15–22, n=4) denticles. P-3 with 17 (13–24, n=4) denticles. Terminal end of P-4 with nine (8–11, n=4) setae. P-4 setae ratio 0.2 (0.2–0.3, n=4). P-5 with three setae.

**Capitulum.** Width 160 (149–175, n=4).

**Coxae.** Length/width anterior coxal group 335/403 (318–350/389–421, n=4). Length/width posterior coxal group 315/274 (288–337/266–285, n=4). Posterolateral apodemes of anterior coxal group 190 (168–201, n=4) from tip to tip.

**Legs.** Lengths of leg segments I-L-1 to I-L-6, 71/123/139/194/215/207 (65–78/117–130/136–143/188–201/207–227/201–214, n=4); II-L-1 to II-L-6 75/124/153/227/248/233 (71–78/97–139/146–162/220–233/240–259/227–240, n=4); III-L-1 to III-L-6, 79/141/178/274/306/285 (58–84/136–143/168–188/266–285/298–318/279–298, n=4); IV-L-1 to IV-L-6, 159/183/245/366/388/330 (149–175/162–207/227–259/356–376/382–399/324–337, n=4). Seta to tibia ratio, I-L to IV-L, 0.45/0.44/0.41/0.34 (0.42–0.47/0.38–0.50/0.36–0.45/0.32–0.40, n=4).

**Genital field.** Entire genital field 269 (243–292, n=4) in width. Length/width genital plates 169/96 (162–175/84–104, n=4). Genital plates with 15 (13–17, n=4) setae on right and 15 (14–16, n=4) on left. Length/width Ac1 61/35 (52–65/32–39, n=4), Ac2 71/33 (58–78/32–36, n=4), Ac3 60/42 (52–68/39–45, n=4). Genital opening between pre- and postgenital sclerites 133 (130–143, n=4) in length.

Variation in measurements, male

ZIHU-2333, Uchida collection.

**Chelicera.** Total length 363, basal segment 272, claw 123, maximum height 78, length/height ratio 4.7, basal segment/claw ratio 2.2.

**Palps.** Length/height P-1 32/52, P-2 143/91, P-3 104/58, P-4 214/42, P-5 71/23. P-2 with 19 denticles. P-3 with 18 denticles. P-4 with seven setae on end. P-4 setae ratio 0.2. P-5 with three setae.

**Capitulum.** Width 104.

**Coxae.** Length/width anterior coxal group 324/467. Length/width posterior coxal group 343/285. Posterolateral apodemes of anterior coxal group 194 from tip to tip.
Legs. Lengths of leg segments I-L-1 to I-L-6 65/130/149/201/227/214; II-L-1 to II-L-6, 65/117/162/233/253/246; III-L-1 to III-L-6, 78/117/279/318/398/298; IV-L-1 to IV-L-6, 181/194/240/363/389/337. Seta to tibia ratio, I-L to IV-L 0.5/0.5/0.4/0.4.

Genital field. Entire genital field 253 in width. Genital plates with 16 setae on right and 19 on left. Length/width Ac1 65/39, Ac2 78/32, Ac3 68/52. Genital opening between pre- and postgenital sclerites 136 in length.

Localities
Tokyo; Akan on Hokkaido.

Distribution
Middle and northern Japan; eastern Russia (Primorsk, Sokolow 1940). Uchida (1936a), in his redescription of \textit{H. japonicus} erroneously based on specimens of \textit{H. longipalpis} (see below), noted that “This species is common also in Sapporo”. In fact, his specimens labelled \textit{H. japonicus} from Sapporo include both \textit{H. longipalpis} and \textit{H. bibi}, but not \textit{H. japonicus}.

Remarks
Uchida (1931) described this species based on two specimens from Tokyo, Japan. We located these specimens in Uchida’s collection by comparing the collection data cited in the original description with information on the specimen labels. Since Uchida did not designate types for the species, we have designated one of the specimens as the lectotype and the other as a paralectotype for \textit{H. japonicus}. The male specimen designated as the paralectotype lacks palps; therefore, we used another specimen from Uchida’s collection, confirmed by us to be \textit{H. japonicus}, for observation of the male palps. These three specimens had been labelled by Uchida only as “\textit{Hygrobates sp.”} The collection contained another 25 specimens labelled as \textit{H. japonicus}. Among these, only one specimen proved to be \textit{H. japonicus}; the rest were either \textit{H. bibi} or \textit{H. longipalpis}.

Uchida (1936a) redescribed \textit{H. japonicus} on the basis of over 20 specimens collected from Kunashiri Island, off the north-west tip of Hokkaido. By comparing the collection data cited in his text with information on specimen labels, we located in Uchida’s collection the specimens he used for the redescription, all labelled \textit{H. japonicus}. Interestingly, all of these proved to be \textit{H. longipalpis}! Uchida’s redescription is far from current standards and of no use in discriminating \textit{H. japonicus} from \textit{H. longipalpis}, because nine characters we have found useful to distinguish between the two were poorly described, with no illustrations. For example, Uchida did not mention whether the posterior end of the anterior coxal group is round versus triangular, nor whether the suture line between Cx3 and Cx4 is complete versus incomplete, both of which are diagnostic between \textit{H. japonicus} and \textit{H. longipalpis}. Likewise, he indicated the shape of the P-2 projection only as “blunt” and failed to note the distribution of denticles, and he failed to describe adequately the shape of the male genital plate and the position of the pregenital sclerite of the female.

\textit{Hygrobates japonicus} is, in fact, most similar to \textit{H. longipalpis}; the two share nine of 18 characters (Table II). In particular, only these two species have P-3 with a prominent ventral convexity bearing a compact, limited denticulate patch. The most important
character diagnostic for *H. japonicus* is the flat end of the P-2 projection, which separates it from the other six Japanese species in the subgenus *Hygrobates*.

*Hygrobates longipalpis* (Hermann, 1804)  
(Figures 13, 14)  
*Hydrarachna longipalpis* Hermann 1804, p 55, Table 3, Figure 1.  
*Hygrobates longipalpis*: Uchida 1931, p 262–264, Abb. 1, 2; 1936b, p 313–314, Figures 3, 4; Imamura 1950, p 74–78, Figures 1–7.  
*Hygrobates japonicus*: Uchida 1936a, p 178–179.  
*Hygrobates (s. str.) longipalpis*: Imamura 1954, p 79–82, Figures 46, 47; 1955, p 188.  
*Hygrobates (Hygrobates) longipalpis*: Imamura 1980, p 348–349, Figure 162C.

**Material examined**

More than 20 adult females and males from Bibi-gawa River, Bibi, Chitose, 10 May 2003; one adult female from a pond at Hokkaido University, Sapporo, 15 August 2003; more than 20 adult females and adult males from a pond at Shiokari, Wassamu, 5 August 2003; more than 10 adult females and adult males from a spring at Turui, Akan-gun, 12 February 2001; more than 10 adult females and adult males from a spring at Turui, Akan-gun, 19 February 2002; two adult females and two adult males from Shira-kawa River, Mori, 27 May 2002; one adult female from Oboro-gawa River, Akkeshi, 13 June 2002. Uchida's collection: three adult females (ZIHU-2343, 2345, 1247) from Sapporo, 9 May 1932; one adult female (ZIHU-2344) from Sapporo, July 1932; one adult female (ZIHU 2346) from Sapporo, 16 May 1932; one adult female (ZIHU-2348) from Sapporo, 26 May 1935; three adult females (ZIHU-2389, 2390, 2391) and six adult males (ZIHU-2383, 2384, 2385, 2386, 2387, 2388) from Kunashiri Island, Kurile Islands, 2 September 1934.

**Description of male**

**Cuticular features.** Integument soft, very finely striated, spacing of striae 0.8. Coxoglandularia II (Figure 13D) without secondary sclerotization. Antenniform setae (Figure 13E) thickened and located on small, irregularly shaped bases, length 37 (32–39, n=4). Without dorsalia.

**Chelicera (Figure 13C).** Total length 405 (350–454, n=4), basal segment 292 (259–324, n=4), claw 126 (104–156, n=4), maximum height 90 (75–97, n=4), length/height ratio 4.5 (4.2–4.7, n=4), basal segment/claw ratio 2.3 (2.0–2.6, n=4).

**Palps (Figure 13B).** Length/height, P-1 52/62 (45–65/58–71, n=5), P-2 176/108 (168–194/91–123, n=5), P-3 128/80 (117–136/65–91, n=5), P-4 229/55 (207–253/45–65, n=5), P-5 78/28 (58–107/23–32, n=5). P-2 with low, rounded conical projection having 29 (28–32, n=5) denticles distributed to base. Ventral side of P-3 somewhat swollen distally, with a patch of 28 (20–41, n=5) denticles occupying less than half the ventral segment length, positioned near distal end. P-4 with two ventral setae and nine (6–12, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.4 (0.4–0.5, n=5). P-5 with three setae.

**Capitulum (Figure 13A).** Broadly fused with the first coxae, width 159 (130–207, n=5). Anterior portion of each half of capitulum with a shallow, rounded notch.
Coxae (Figure 13A). Length/width anterior coxal group 390/452 (376–441/369–544, n=5). Length/width posterior coxal groups 399/368 (347–454/324–408, n=5). Posterior end of anterior coxal group rounded; posterolateral apodemes extending beyond sclerotization, 193 (149–220, n=5) from tip to tip. Suture line between first coxae and capitulum nearly straight. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 complete, extending to near gland of Cx4. Medial border of Cx4 angular, without angle apodemes.
Legs (*Figure 14A–D*). Swimming hairs absent, claws with a ventral clawlet. Seta to tibia ratio, I-L/IV-L 0.4/0.4 (0.3–0.4/0.4–0.5, \( n=5 \)).

Genital field (*Figure 13G*). Genital plate length/width 211/281 (168–233/249–318, \( n=5 \)), with irregularly crenate outer border; anterior end with a squared median notch; posterior end depressed in middle, with a short, rounded median projection; apodemes lacking.
Genital plate with 29 (28–30, n=5) setae on right side and 29 (28–32, n=5) on left. Three genital acetabula on each side arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 86/51 (75–91/49–55, n=5), Ac2 82/48 (71–91/45–52, n=5), Ac3 89/52 (68–97/42–65, n=5).

Description of female

Characters as given for male, except for genital field. Antenniform setae length 38 (32–42, n=3).

Chelicera. Total length 503 (447–551, n=3), basal segment 365 (330–389, n=3), claw 151 (130–175, n=3), maximum height 110 (97–123, n=3), length/height ratio 4.6 (3.6–5.3), basal segment/claw ratio 2.4 (2.2–2.6).

Palp. Length/height P-1 51/62 (39–58/52–71, n=5), P-2 193/113 (156–220/97–136, n=5), P-3 131/79 (110–156/65–104, n=5), P-4 248/56 (207–285/49–71, n=5), P-5 70/27 (45–84/19–32, n=5). P-2 with 30 (20–36, n=5) denticles. P-3 with 27 (17–44, n=5) denticles. P-4 with two ventral setae and 10 (9–12, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.03 (0.03–0.03, n=5). P-5 with three setae.

Capitulum. Width 191 (123–233, n=5).

Coxae. Length/width anterior coxal group 395/477 (311–467/402–570, n=5). Length/width posterior coxal group 404/384 (350–454/337–424, n=5). Posterolateral apodemes of anterior coxal group 189 (130–227, n=5) from tip to tip.

Legs. Seta to tibia ratio, I-L/IV-L 0.4/0.5 (0.4–0.4/0.5–0.5, n=5).

Genital field (Figure 13F). Entire genital field 321 (285–369, n=5) in width, with irregularly crenate outer border. Length/width genital plates 225/111 (191–259/91–130, n=5); 27 (24–31, n=5) setae on right plate and 25 (21–28, n=5) on left. No setae on membranous integument near genital plate. Three genital acetabula on each side, arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 82/40 (65–91/32–52, n=5), Ac2 74/41 (65–94/32–55, n=5), Ac3 71/50 (58–78/39–71). Pre- and postgenital sclerites with medially protruded apodemes. No setae on pregenital sclerite. Pregenital sclerite located posterior to the anterior ends of genital plates. Postgenital sclerite located anterior to the posterior ends of genital plates. Genital opening between pre- and postgenital sclerites 185 (136–246, n=5) in length.

Localities

Turui, Akan, Akkeshi, Tomakomai, Chitose, Sapporo, Mori, and Wassamu, all on Hokkaido; Kunashiri, Kurile Islands.

Distribution

Holarctic region: America, Europe, Russia, Japan (Shizuoka, Kyushu, Tokyo, Hokkaido).
Remarks

There are several previous records of *H. longipalpis* from Hokkaido (Uchida 1936b; Imamura 1950, 1954). Among the eight species from Hokkaido, this species is most similar to *H. foreli*, *H. japonicus* (see Remarks section for that species) and *H. longiporus* which shares nine of 18 characters (Table II). *H. longipalpis* and *H. longiporus* exclusively share one coxal and two genital features: a complete suture line between the Cx3 and Cx4, a notched anterior border of the male genital plate, and the pregenital sclerite located posterior to the anterior ends of the female genital plates. This species was common in ponds, and in slowly flowing rivers close downstream from springs. It co-occurred with *H. bibi* sp. nov. in the Bibi-gawa River, Bibi, Chitose.

*Hygrobates longiporus* Thor, 1898

(Figures 15, 16)

*Hygrobates* (*Hygrobates*) *longiporus* Thor 1898, p 272–273; Imamura 1953a, p 216–219, Figures 14, 15; 1980, p 348–349, Figure 162D.

*Hygrobates* (s. str.) *longiporus*: Imamura 1953b, p 432; 1954, p 82.

Material examined

One adult female from Hamamasu, 31 July 2001; one adult female and one adult male from Gosen-gawa River, Horokanai, 7 July 2002; three adult females and three adult males from Horonobe, 20 August 2002; one adult female from Otoineppu, 7 July 2002.

Description of female

Cuticular features. Integument soft, very finely striated, spacing of striae 0.9. Coxoglandularia II (Figure 15D) with heavy secondary sclerotization. Antenniform setae (Figure 15E) very thin and located on small, ovoid bases, length 61 (58–62, n=4). Without dorsalia.

Chelicera (Figure 15C). Total length 439 (415–467, n=4), basal segment 319 (305–337, n=4), claw 133 (117–143, n=4), maximum height 92 (78–97, n=4), length/height ratio 4.8 (4.3–5.4, n=4), basal segment/claw ratio 2.4 (2.3–2.7, n=4).

Palp (Figure 15B). Length/height, P-1 40/56 (26–45/45–58, n=5), P-2 170/86 (156–181/52–110, n=5), P-3 118/71 (104–130/58–84, n=5), P-4 221/47 (214–230/45–52, n=5), P-5 70/29 (65–71/26–32, n=5). P-2 somewhat swollen distally into a blunt, angular ventral projection; 51 (38–59, n=5) denticles covering two-thirds of ventral segment length, from proximal half of projection to near proximal margin. Ventral side of P-3 flat with 34 (29–47, n=5) denticles in a patch covering nearly entire ventral length. P-4 with two ventral setae and 10 (8–12, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.04 (0.03–0.08, n=5). P-5 with three setae.

Capitulum (Figure 15A). Broadly fused with the first coxae and 140 (130–149, n=5) in width. Anterior portion of each half of capitulum with a rounded notch.

Coxae (Figure 15A). Length/width anterior coxal group 401/490 (350–437/460–531, n=5). Length/width posterior coxal groups 422/369 (395–447/337–421, n=5). Posterior end of
anterior coxal group triangular; posterolateral apodemes extending slightly beyond sclerotization, 200 (181–214, \( n = 5 \)) from tip to tip. Suture line between Cx1 and capitulum nearly straight or slightly curved. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 complete; glandularium on Cx4 located near suture line. Medial margin of Cx4 evenly rounded, without angle apodemes.
Legs (Figure 16A–D). Swimming hairs absent; claws with a ventral clawlet. Seta to tibia ratio, I-L/IV-L 0.2/0.3 (0.2–0.3/0.3–0.3, n=5).

Genital field (Figure 15F). Entire genital field 303 (298–337, n=5) in width. Genital plates with smooth outer border. Genital plates with 25 (23–26, n=5) setae on right plate and 24
Characters same as for female, except for genital field. Antenniform setae length 52 (42–58, \( n = 3 \)).

**Chelicera.** Total length 390 (366–408, \( n = 3 \)), basal segment 281 (266–305, \( n = 3 \)), claw 122 (113–136, \( n = 3 \)), maximum height 80 (78–84, \( n = 3 \)), length/height ratio 4.9 (4.7–5.1, \( n = 3 \)), basal segment/claw ratio 2.3 (2.0–2.6, \( n = 3 \)).

**Palp.** Length/height P-1 38/53 (32–42/49–58, \( n = 4 \)), P-2 151/87 (143–162/75–97, \( n = 4 \)), P-3 104/71 (104–104/65–78, \( n = 4 \)), P-4 194/48 (188–201/42–52, \( n = 4 \)), P-5 62/25 (58–65/23–26, \( n = 4 \)). P-2 with 51 (46–55, \( n = 4 \)) denticles. P-3 with 34 (31–39, \( n = 4 \)) denticles. P-4 with two ventral setae and nine (7–10, \( n = 4 \)) setae on lateral and dorsal sides. P-4 setae ratio 0.04 (0.0–0.07, \( n = 4 \)). P-5 with three setae.

**Capitulum.** Width 113 (104–123, \( n = 4 \)).

**Coxae.** Length/width anterior coxal group 363/429 (318–402/402–460, \( n = 4 \)). Length/width posterior coxal group 381/339 (356–415/285–382, \( n = 4 \)). Apodemes of anterior coxal group 147 (110–168, \( n = 4 \)) from tip to tip.

**Legs.** Seta to tibia ratio, I-L/IV-L 0.2 (0.2–0.3, \( n = 4 \))/0.3 (0.3–0.3, \( n = 3 \)).

**Genital field (Figure 15G).** Genital plate length/width 232/288 (227–240/272–318, \( n = 4 \)), with smooth, evenly rounded outer border. Anterior border of genital plate deeply notched, with a triangular projection in notch; posterior border with a small, mammiform median projection; apodemes lacking. Genital plate with 25 (24–27, \( n = 4 \)) setae on right side and 25 (23–28, \( n = 4 \)) on left. Three genital acetabula on each side arranged in the manner of an isosceles triangle. Distance between Ac1 and Ac2 approximately equal to width of Ac1; distance between Ac2 and Ac3 less than width of Ac1. Length/width Ac1 84/35 (81–87/26–32, \( n = 4 \)), Ac2 90/36 (84–97/32–39, \( n = 4 \)), Ac3 104/33 (104–104/26–39, \( n = 4 \)).

**Localities**
Hamamasu, Horokanai, Horonobe, and Otoineppu, all on Hokkaido.

**Distribution**
Palaearctic region: Europe, Russia, Japan (Kyushu, Hiroshima, Gifu, Hokkaido).
Remarks

Hygrobates longiporus has been previously recorded once from Hokkaido (Imamura 1954). It is most similar to H. longipalpis (see Remarks section for the latter) sharing nine of 18 characters with each (Table II). Among the eight Japanese species of this subgenus, only H. longiporus and H. sokolowi have the genital plate with the distance between Ac1 and Ac2 greater than the width of Ac1 in the female, and greater than or equal to the width of Ac1 in the male. Hygrobates longiporus is easily distinguished from the other seven Hygrobates species by two unique characters: heavy secondary sclerotization of coxoglandularium 2 and the long patch of denticles on P-2 occupying nearly the entire ventral segment length. This species was common among stones on the bottoms of rivers.

Hygrobates nigromaculatus Lebert, 1879
(Figures 17, 18)

Hygrobates (Hygrobates) nigromaculatus Lebert 1879, p 342–344.

Material examined

One female and two males from Pashikuru-gawa River, Otobetu, Hokkaido, 11 July 2002.

Description of male

Based on two specimens, ZIHU-3096 and 3097, collected by first author.

Cuticular features. Integument soft, finely striated, spacing of striae 2.0. Coxoglandularia II (Figure 17D) without secondary sclerotization. Antenniform setae (Figure 17E) thin and located on small, rounded-triangular bases, length 42 (39–45, n=2). Without dorsalia.

Chelicera (Figure 17C). Total length 356 (350–363, n=2), basal segment 266 (259–272, n=2), claw 110 (104–117, n=2), maximum height 81 (78–84, n=2), length/height ratio 4.4 (4.3–4.5, n=2), basal segment/claw ratio 2.4 (2.3–2.5, n=2).

Palp (Figure 17B). Length/height P-1 39/45 (39–39/45–45, n=2), P-2 84/75 (84–84/71–78, n=2), P-3 81/65 (78–84/65–65, n=2), P-4 149/42 (149–149/42–42, n=2), P-5 62/23 (58–65/23–23, n=2). P-2 swollen distally, but ventral border flat. Projection on P-2 broad, indistinct, rounded; 42 (32–51, n=2) denticles cover projection and occupy anterior two-thirds of the ventral segment length. P-3 somewhat swollen, but ventral side almost flat, with patch of 33 (31–34, n=2) denticles in middle. P-4 with two ventral setae and 10 (10–10, n=2) setae on lateral and dorsal sides. P-4 setae ratio 0.01 (0.0–0.02, n=2). P-5 with three setae.

Capitulum (Figure 17A). Broadly fused with the first coxae, width 126 (123–130, n=2). Anterior portion of each half of capitulum with a rounded notch.

Coxae (Figure 17A). Length/width anterior coxal group 340/399 (330–350/395–402, n=2). Length/width posterior coxal group 353/285 (350–356/272–298, n=2). Posterior end of anterior coxal group broadly rounded; posterolateral apodemes extending slightly beyond sclerotization, 159 (143–175, n=2) from tip to tip. Suture line between first coxae and
Figure 17. *Hygrobates* (*Hygrobates*) nigromaculatus. (A–E, G) Male. (A) Ventral side, scale 1; (B) palp, scale 3; (C) chelicera, scale 2; (D) coxoglandularium II, scale 4; (E) antenniform seta, scale 4; genital field, scale 3. (F) Female, genital field, scale 3. Scale bars: 1, 2, 3, 4=100 μm.
capitulum nearly straight. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 incomplete, extending to near gland of C4. Medial margin of C4 a rounded angle, without angle apodemes.

Legs (Figure 18A–D). Swimming hairs absent, claws with a ventral clawlet. Seta to tibia ratio, I-L/IV-L 0.1/0.3 (0.1–0.1/0.2–0.3, n=2).

Figure 18. Hygrobates (Hygrobates) nigromaculatus, male. (A) First leg; (B) second leg; (C) third leg; (D) fourth leg. Scale bar: 100 μm.
Genital field (Figure 17G). Genital plate length/width 207/243 (207–207/233–253, n=2). Outer border broadly and irregularly crenate; anterior and posterior margins slightly depressed in midline, each with a mammiform medial projection; apodemes lacking. Genital plate with 22 (20–24, n=2) setae on right side and 19 (18–20, n=2) on left. No setae in the membranous integument near genital plate. Three genital acetabula on each side arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 68/36 (65–71/32–39, n=2), Ac2 71–31 (68–75/32–39, n=2), Ac3 81–52 (75–87/45–58, n=2).

Description of female

Based on one specimen, ZIHU-3095, collected by first author. Characters same as for male, except for genital field. Antenniform setae length 39.

Chelicera. Total length 363, basal segment 279, claw 113, maximum height 84, length/height ratio 4.3, basal segment/claw ratio 2.5.

Palp. Length/height, P-1 39/52, P-2 104/84, P-3 91/71, P-4 156/45, P-5 58/26. P-2 with 26 denticles. P-3 with 26 denticles. P-4 with two ventral setae and 11 setae on lateral and dorsal sides. P-4 setae ratio 0.0. P-5 with three setae.

Capitulum. Width 136.

Coxae. Length/width anterior coxal group 363/421. Length/width posterior coxal groups 389/330. Apodemes of anterior coxal group 175 from tip to tip.

Legs. Seta to tibia ratio, I-L/IV-L 0.1/0.2.

Genital field (Figure 17F). Entire genital field 298 in width. Genital plates with irregular outer border. Right genital plate with 24 setae, left with 25. No setae in the membranous integument near genital plate. Length/width genital plates 207/110. Three genital acetabula on each side, arranged in an obtuse triangle. Distance between Ac1 and Ac2, and Ac2 and Ac3, less than width of Ac1. Length/width Ac1 81/29, Ac2 71/32, Ac3 62/45. Pre- and postgenital sclerites with medially protruded apodemes. No setae on pregenital sclerite. Pregenital sclerite extending anterior to the anterior ends of genital plates. Postgenital sclerite located anterior to the posterior ends of genital plates. Genital opening between pre- and postgenital sclerites 175 in length.

Locality

Otobetu on Hokkaido.

Distribution

Palaearctic region: Europe, Russia, Japan (Hokkaido).

Remarks

This is the first record of *H. nigromaculatus* from Japan. The species is known from Palaearctic Eurasia, with many records from Europe (Viets 1978). *Hygrobates nigromaculatus* is most
similar to *H. foreli* (see Remarks for that species), sharing 14 of 18 characters, and next most similar to *H. bibi*, with which it shares 10 of 18 characters (Table II). *Hygrobates nigromaculatus* and *H. longiporus* exclusively have denticles occupying more than half the ventral length of P-2.

**Hygrobates sokolowi** (Thor 1927)
(Figures 19, 20)

*Hygrobates (Rhabdotobates) sokolowi* Thor 1927, p 132–135, Figures 8–10.

**Material examined**

Two adult females and two adult males collected from Horonobe, 20 August 2002.

**Description of male**

Based on two specimens, ZIHU-3093 and 3094, collected by the first author.

**Cuticular features.** Integument soft, with irregular ridges. Coxoglandularia II (Figure 19D) with heavy secondary sclerotization. Antenniform setae (Figure 19E) thin, located on small, oval bases, 52 \( (n=1) \) in length. Without dorsalia.

**Chelicera** (Figure 19C). Total length 256 (253–259, \( n=2 \)), basal segment 194 (194–194, \( n=2 \)), claw 75 (71–78, \( n=2 \)), maximum height 57 (52–62, \( n=2 \)), length/height ratio 4.6 (4.2–4.9, \( n=2 \)), basal segment/claw ratio 2.6 (2.5–2.7, \( n=2 \)).

**Palp** (Figure 19B). Length/height, P-1 32/33 (32–32/26–39, \( n=2 \)), P-2 84/68 (71–97/65–71, \( n=2 \)), P-3 78/49 (78–78/45–52, \( n=2 \)), P-4 133/41 (130–136/39–42, \( n=2 \)), P-5 53/18 (49–58/16–19, \( n=2 \)). P-2 broad distally, with a long, tapering, acute projection at distal ventral margin; 15 (12–18, \( n=2 \)) denticles restricted to distal part of projection. Ventral side of P-3 flat, with a patch of 17 (15–18, \( n=2 \)) denticles covering approximately the anterior half of the ventral surface. P-4 with two ventral setae and 10 (9–11, \( n=2 \)) setae on lateral and dorsal sides. P-4 setae ratio 0.2 (0.2–0.2, \( n=2 \)). P-5 with three setae.

**Capitulum** (Figure 19A). Broadly fused with the first coxae, width 96 (94–97, \( n=2 \)). Anterior portion of each half of capitulum shallowly notched.

**Coxae** (Figure 19A). Length/width anterior coxal group 259/330 (253–266/330–330, \( n=2 \)). Length/width posterior coxal groups 274/224 (269–279/214–233, \( n=2 \)). Posterior end of anterior coxal group rounded-triangular; posterolateral apodemes extend slightly beyond sclerotization, 130 (123–136, \( n=2 \)) from tip to tip. Suture line between first coxae and capitulum nearly straight. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 incomplete, extending to near glandularium of Cx4. Medial margin of Cx4 acute or rounded-angular, with angle apodemes.

**Legs** (Figure 20A–D). Swimming hairs absent, claws with a ventral clawlet. Seta to tibia ratio, I-L/IV-L 0.4/0.3 (0.3–0.4/0.3–0.3, \( n=2 \)).

**Genital field** (Figure 19G). Genital plate length/width 137/206 (130–143/204–207, \( n=2 \)), with a smooth, undulating outer border; anterior end flat, coarsely crenate; posterior end
with a broad, deep median notch and weak apodemes. Genital plate with 16 (16–16, \( n = 2 \)) setae on right side and 17 (16–17, \( n = 2 \)) on left. Three genital acetabula on each side arranged in an isosceles triangle. Distance between Ac1 and Ac2 greater than width of Ac1; distance between Ac2 and Ac3 greater than or equal to width of Ac1. Length/width Ac1 29/18 (29–29/16–19, \( n = 2 \)), Ac2 36/16 (32–39/16–16, \( n = 2 \)), Ac3 28/19 (26–29/19–19, \( n = 2 \)).

Figure 19. *Hygrobates (Hygrobates) sokolowi*. (A–E, G) Male. (A) Ventral side, scale 1; (B) palp, scale 3; (C) chelicera, scale 2; (D) coxoglandularium II, scale 4; (E) antenniform seta, scale 4; (G) genital field, scale 3. (F) Female, genital field, scale 3. Scale bars: 1, 2, 3 (B, F, G)=100\( \mu \)m; 3 (D, E)=50\( \mu \)m.
Description of female

Based on two specimens, ZIHU-3091 and 3092, collected by the first author. Characters as given for male, except for genital field. Antenniform setae length 45 (45–45, \( n=2 \)).

**Chelicera.** Total length 295 (285–305, \( n=2 \)), basal segment 224 (214–233, \( n=2 \)), claw 84 (84–84, \( n=2 \)), maximum height 68 (65–71, \( n=2 \)), length/height ratio 4.4 (4.3–4.4, \( n=2 \)), basal segment/claw ratio 2.7 (2.5–2.8, \( n=2 \)).

**Palp.** Length/height P-1 32/34 (32–32/32–36, \( n=2 \)), P-2 115/67 (113–117/65–68, \( n=2 \)), P-3 84/52 (84–84/49–55, \( n=2 \)), P-4 150/39 (143–156/39–39, \( n=2 \)), P-5 50/18

---

Figure 20. *Hygrobates (Hygrobates) sokolowi*, male. (A) First leg; (B) second leg; (C) third leg; (D) fourth leg. Scale bar: 100\,\mu m.
(45–55/16–19, n=2). P-2 with 21 (19–23, n=2) denticles. P-3 with 24 (23–24, n=2) denticles. P-4 with two ventral setae and 11 (10–11, n=2) setae on lateral and dorsal sides. P-4 setae ratio 0.4/0.3 (0.3–0.4/0.2–0.3, n=2). P-5 with three setae.

Capitulum. Width 97 (78–117, n=2).

Coxae. Length/width anterior coxal group 243/340 (233–253/324–356, n=2). Length/width posterior coxal group 274/269 (269–279/259–279, n=2). Apodemes of anterior coxal group 136 (136–136, n=2) from tip to tip.

Legs. Seta to tibia ratio, I-L/IV-L 0.3/0.2 (0.3–0.4/0.2–0.3, n=2).

Genital field (Figure 19F). Entire genital field 206 (204–207, n=2) in width. Outer border of genital plates smooth; right genital plate with 14 (13–14, n=2) setae, left with 13 (12–14, n=2). No setae on the membranous integument near genital plate. Length/width genital plates 143/72 (143–143/65–78, n=2). Three genital acetabula on each side, arranged in an obtuse triangle. Distance between Ac1 and Ac2 greater than width of Ac1; distance between Ac2 and Ac3 less than width of Ac1. Length/width Ac1 31/23 (29–32/19–26, n=2), Ac2 39/18 (39–39/16–19, n=2), Ac3 34/21 (32–36/19–23, n=2). Pre- and postgenital sclerites with medially protruded apodemes. No setae on pregenital sclerite. Pregenital sclerite extends anterior to the anterior ends of genital plates. Postgenital sclerite extends posterior to the posterior ends of genital plates. Genital opening between pre- and postgenital sclerites 125 (120–130, n=2) in length.

Locality
Horonobe on Hokkaido.

Distribution
Eastern Europe and northern Japan: Caucasus, western Russia, Hokkaido.

Remarks
This is the first record of *H. sokolowi* from Japan. The species was previously known only from western Russia (Thor 1927; Sokolow 1940; Sokolow and Jankowskaja 1962; Viets 1978). Among the eight Hokkaido species in the subgenus *Hygrobates*, *H. sokolowi* is unique in having the acetabula small in relation to the area of the genital plate, so that most of the central portion of the plate is unoccupied by acetabula. At the Hokkaido locality, *H. sokolowi* was collected among stones on the bottom of a tributary of the Toikanbetsu River, together with two specimens of *H. longiporus*.

Subgenus *Rivobates* Thor, 1897

*Hygrobates ezoensis* (Uchida, 1934)
(Figures 21–23)

*Rivobates ezoensis* Uchida 1934, p 92–95, Figures 26–28.

*Hygrobates (Rivobates) ezoensis*: Imamura 1954, p 82–84, Figure 48.
Hygrobates (Rivobates) diversiporus: Imamura 1980, p 350–351, Figure 163B.
Hygrobates diversiporus: Uchida 1936b, p 314–315.

Material examined

Lectotype: ZIHU-2362, Uchida’s collection, adult male, dissected and mounted in glycerin jelly, from Chitose, Hokkaido, 6 February 1932, labelled Rivobates ezoensis collected by H.
Ishizuka. Allolectotype: ZIHU-2368, adult female with damaged chelicerae, Uchida's collection, adult male, dissected and mounted in glycerin jelly, from Chitose, Hokkaido, 6 February 1932, labelled *Rivobates ezoensis* collected by H. Ishizuka. Paralectotypes: adult males (ZIHU-2361, 2363) and adult females (ZIHU-2364, 2365, 2366, 2367), Uchida's collection, dissected and mounted in glycerin jelly, from Chitose, Hokkaido, 6 February 1932, labelled *Rivobates ezoensis* collected by H. Ishizuka.

Figure 22. *Hygrobates (Rivobates) ezoensis*, female. (A) First leg; (B) second leg; (C) third leg; (D) fourth leg. Scale bar: 100 μm.
Additional material. Two adult females (ZIHU-2381, 2382) and five adult males (ZIHU-2376, 2377, 2378, 2379, 2380), Uchida’s collection, dissected and mounted in glycerin jelly, from a river near Yuzhno-Sakhalinsk, Sakhalin, 4 August 1936, labelled *Rivobates diversiporus* collected by H. Yamaguchi. One adult female from a stream in Akan, 4 June 2002; five adult females and six adult males from a spring in Bihoro, 13 August 2002; three adult females from Moizari-gawa River, Eniwa, 11 May 2002; one adult male from Kashiwagi-gawa River, Eniwa, 19 May 2002; two adult males from Moizari-gawa River, Eniwa, 30 July 2002; one adult male from Horonobe, 20 August 2002; three adult females from a spring in Turui, 9 February 2001; one adult female from a spring in Turui, 26 February 2001; three adult females from a pond in Turui, 15 July 2003; one adult female from a spring in Masuhoro, Wakkanai, 6 July 2002.

Description of female

Description and measurements from allolectotype, ZIHU-2368; figures from other specimens.

Cuticular features. Integument soft, very finely striated, spacing of striae 0.7. Secondary sclerotization of coxoglandularia II weak (Figure 21D). Antenniform setae missing from specimen. Without dorsalia.

Chelicera. Damaged on this specimen.
Palp. Length/height P-1 32/39, P-2 78/78, P-3 104/78, P-4 149/45, P-5 58/19. P-2 with pronounced, tapering, acute ventral projection at distal margin, with 12 denticles distributed to base of projection. Ventral side of P-3 swollen, convex in outline, with a patch of 18 denticles occupying less than half the ventral side, offset toward distal end. P-4 with two ventral setae and 10 setae on lateral and dorsal sides. P-4 setae ratio 0.07. P-5 with three setae.

Capitulum (Figure 21A). Fused with the first coxae, 104 in width. Anterior portion of each half of capitulum with a rounded notch.

Coxae (Figure 21A). Length/width anterior coxal group 318/402. Length/width posterior coxal group 337/279. Posterior end of anterior coxal group broadly rounded; posterolateral apodemes extend slightly beyond sclerotization, 188 from tip to tip. Suture line between first coxae and capitulum irregular, not curved. Coxoglandularium I on Cx2. Suture line between Cx3 and Cx4 incomplete, extending to near glandularium of Cx4. Medial margin of Cx4 variable (evenly rounded or with a rounded angle projecting in middle), without angle apodemes.

Legs (Figure 22A–D). Swimming hairs absent, claws with a ventral clawlet. Lengths of leg segments I-L-1 to I-L-6, 71/84/117/181/194/181; II-L-1 to II-L-6 71/84/143/194/220/220; III-L-1 to III-L-6, 65/104/110/156/175/181; IV-L-1 to IV-L-6, 156/143/207/279/292/246. Seta to tibia ratio, I-L to IV-L, 0.40/0.35/0.44/0.31.

Genital field (Figure 21F). Entire genital field 318 in width. Genital plates with somewhat irregular outer border. Right genital plate with 16 setae, left with 16. No setae on membranous integument near genital plate. Length/width genital plates 149/91. Genital acetabula closely packed in each genital plate, seven on left side, six on right (Figure 21F is from a female specimen other than allolectotype). Pre- and postgenital sclerites each with a median apodeme. No setae on pregenital sclerite. Pregenital sclerite located anterior to the anterior ends of genital plates. Postgenital sclerite located anterior to the posterior ends of genital plates. Genital opening between pre- and postgenital sclerites.

Description of male

Lectotype, ZIHU-2362. Characters same as for female, except for genital field. Antenniform setae missing from specimen.

Chelicera. Missing from specimen.

Palp (Figure 21B). Length/height P-1 32/45, P-2 84/91, P-3 84/78, P-4 149/52, P-5 55/23. P-2 with 13 denticles. P-3 with 22 denticles. P-4 with two ventral setae and 10 setae on lateral and dorsal sides. P-4 setae ratio 0.1. P-5 with three setae.

Capitulum. Width 97.

Coxae. Length/width anterior coxal group 324/389. Length/width posterior coxal groups 324/311. Posterolateral apodemes of anterior coxal group 188 from tip to tip.
Legs. Lengths of leg segments I-L-1 to I-L-6, 84/130/130/175/181/181; II-L-1 to II-L-6 78/110/143/181/194/194; III-L-1 to III-L-6, 65/84/149/201/240/220; IV-L-1 to IV-L-6, 143/162/194/279/305/253. Seta to tibia ratio, I-L to IV-L, 0.38/0.47/0.30/0.26.

Genital field (Figure 21G). Genital plate length/width 188/227, with smooth outer border. Anterior end of genital plate a rounded obtuse angle, with a medial apodeme extending from anterior margin of gonopore. Posterior end of genital plate variable, from flat to curved, with one to three rounded apodemes (Figure 23A–K). Genital plate with 22 setae on right side and 25 on left. Genital acetabula eight on left side, seven on right; Figure 21G based on a specimen other than lectotype.

Variation in measurements, female
Antenniform setae length 70 (58–78, n=4).

Chelicera. Total length 313 (279–350, n=3), basal segment 231 (207–259, n=3), claw 95 (84–104, n=3), maximum height 67 (65–71, n=3), length/height ratio 4.7 (4.3–4.9, n=3), basal segment/claw ratio 2.4 (2.3–2.5, n=3).

Palp. Length/height P-1 30/38 (26–32/32–42, n=5), P-2 111/66 (104–117/58–74, n=5), P-3 80/47 (71–97/39–58, n=5), P-4 143/42 (136–149/39–55, n=5), P-5 51/20 (45–55/19–23, n=5). P-2 with nine (6–12, n=5) denticles. P-3 with 10 (6–17, n=5) denticles. P-4 with two ventral setae and 11 (8–13, n=5) setae on lateral and dorsal sides. P-4 setae ratio 0.1 (0.0–0.1, n=5). P-5 with three setae.

Capitulum. Width 87 (78–97, n=5).

Coxae. Length/width anterior coxal group 287/394 (272–298/356–486, n=5). Length/width posterior coxal groups 301/250 (272–324/214–266, n=5). Posterolateral apodemes of anterior coxal group 154 (146–162, n=5) in width.

Legs. Length of leg segments I-L-1 to I-L-6 60/92/114/158/170/171 (52–65/84–97/110–123/156–162/175/181–181, n=5); II-L-1 to II-L-6 62/98/114/165/183/184 (58–65/97–104/110–117/156–175/175–194/175–207, n=5); III-L-1 to III-L-6 66/106/136/197/211/211 (58–78/97–130/130–143/188–207/201–220/201–227, n=5); IV-L-1 to IV-L-6 130/150/193/257/271/192 (117–143/143–162/181–207/240–266/259–285/227–259, n=5, IV-L-6 only n=4). Seta to tibia ratio, I-L to IV-L 0.4/0.4/0.3/0.3 (0.3–0.4/0.3–0.4/0.3–0.3/0.3–0.3, n=5).

Genital field. Entire genital field 264 (207–298, n=5) in width. Right genital plate with 15 (15–16, n=5) setae, left with 13 (12–14, n=5). Length/width genital plates 131/79 (110–143/65–91, n=5). Genital acetabula eight (6–10, n=5) on left side, seven (6–9, n=5) on right. Genital opening between pre- and postgenital sclerites 148 (104–181, n=5) in length.

Variation in measurements, male
Antenniform setae length 58 (n=1).
Chelicera (Figure 22C). Total length 300 (272–311, $n=4$), basal segment 222 (201–233, $n=4$), claw 91 (84–97, $n=4$), maximum height 64 (58–68, $n=4$), length/height ratio 4.7 (4.2–5.2, $n=4$), basal segment/claw ratio 2.5 (2.3–2.6, $n=4$).

Palp. Length/height P-1 31/36 (26–32/32–45, $n=5$), P-2 105/67 (91–110/52–78, $n=5$), P-3 74/47 (65–84/39–52, $n=5$), P-4 139/40 (123–143/32–49, $n=5$), P-5 49/18 (42–52/13–23, $n=5$). P-2 with 11 (7–15, $n=5$) denticles. P-3 with 15 (13–17, $n=5$) denticles. P-4 with two ventral setae and 11 (9–12, $n=5$) setae on lateral and dorsal sides. P-4 setae ratio 0.05 (0.02–0.07, $n=5$). P-5 with three setae.

Capitulum. Width 87 (84–97, $n=5$).

Coxae. Length/width anterior coxal group 277/353 (246–292/324–376, $n=5$). Length/width posterior coxal group 290/250 (240–311/207–272, $n=5$). Posterolateral apodemes of anterior coxal group 149 (123–168, $n=5$) from tip to tip.

Legs. Length of leg segments I-L-1 to I-L-6 58/99/111/153/166/165 (52–65/78–110/104–117/136–162/149–175/149–181, $n=5$); II-L-1 to II-L-6 56/96/115/164/181/183 (45–65/78–110/104–117/136–162/149–175/162–207/168–201, $n=5$); III-L-1 to III-L-6 65/101/130/193/211/205 (52–71/91–110/117–143/175–201/188–227/188–214, $n=5$); IV-L-1 to IV-L-6 141/148/184/240/257/232 (130–156/130–162/168–194/207–266/227–272/207–246, $n=5$). Seta to tibia ratio, I-L to IV-L 0.4/0.3/0.3/0.3 (0.4–0.4/0.3–0.4/0.2–0.3/0.2–0.3, $n=5$).

Genital field. Length/width 158/202 (130–175/162–227, $n=5$). Genital plate with 22 (19–26, $n=5$) setae on right side and 21 (18–23, $n=5$) on left side. Genital acetabula eight (6–10, $n=5$) on left side, seven (6–9, $n=5$) on right.

Localities
Akan, Bihoro, Eniwa, Horinobe, Turui, Wakanai, all on Hokkaido.

Distribution
Sakhalin and Hokkaido.

Remarks
Uchida (1934, p 95) described *Hygrobates ezoensis* under the name of *Rivobates ezoensis*, based on “many specimens” collected by Mr H. Ishizuka from a spring in Chitose, Hokkaido on 6 February 1932. Soon after, however, Uchida (1936b) declared his species a junior synonym of *Rivobates diversiporus* Sokolow, 1927, based on “more than 10 examples collected by Mr. H. Yamaguchi on August 4, 1936 in a river near Toyohara”, Sakhalin Island.

We found in Uchida’s collection eight specimens separately mounted on slides and labelled “*Rivobates ezoensis*, Chitose (Hokkaido) Feb. 6, 1932”, and seven slides labelled “*Rivobates diversiporus* (Sokolow) Karahuto, Toyohara Aug. 4, 1936 H. Yamaguchi”. Karahuto is the Japanese name for Sakhalin Island and Toyohara is the old Japanese name for Yuzhno-Sakhalinsk on Sakhalin. In a careful examination, we could not detect any
diagnostic differences in characters among these specimens from Uchida’s collection and about 30 specimens we collected from various localities on Hokkaido for our study. Thus we confirmed that the species of the subgenus *Rivobates* that we collected on Hokkaido is the same that Uchida identified from both Hokkaido and Sakhalin. The question remained as to the species’ identity.

The taxonomy of *H. ezoensis/diversiporus* has been convoluted. In his original description, Uchida (1934, p 95) noted for *Rivobates ezoensis*, “The species is easily distinguished … from *R. diversiporus* (Sokolow) by the form of the third epimera and genital plates”. However, in later synonymizing *Rivobates ezoensis* with *R. diversiporus*, Uchida (1936b, p 314) concluded that “these differences are due to individual variations” and remarked that “Sokolow’s specimens are probably somewhat aberrant ones of the species”. Imamura (1954), on the other hand, did not agree with this synonymy and stated, “it [*H. ezoensis*] is distinguished from the latter [*H. diversiporus*] in the shapes of genital plates of both sexes”. Nonetheless, Viets (1956) accepted the synonymy, and Imamura (1980) listed *H. diversiporus* in an illustrated encyclopaedia of Japanese mites and ticks, to the exclusion of *H. ezoensis*.

We examined the male genital plate of 18 specimens from Sakhalin and Hokkaido, of which 11 are illustrated in Figure 23A–K, including three of Uchida’s specimens of *H. ezoensis* from Chitose, Hokkaido (Figure 23C, D, G); three of Uchida’s specimens from Sakhalin labelled as *H. diversiporus* (Figure 23H, J, K); and five specimens we collected from northern (Figure 23A, B, E) and central (Figure 23F, I) Hokkaido. In all 18 specimens examined, the male genital plate is irregularly ovoid, with the anterior border a rounded obtuse angle and the posterior border straight, irregularly convex, or broadly curved (that in Figure 23H is atypical, likely due to a developmental anomaly or healed wound). This form of the male plate is just as originally figured by Uchida (1934, p 93, Figure 26) for *Rivobates ezoensis*. It differs from the male plate (Figure 23L) of *H. diversiporus* originally described by Sokolow (1927) as “verkehrt-herzförmiger” (reverse-heart-shaped; our translation), with an acute anterior angle and a depressed posterior border having a broad, rounded median notch. We thus conclude that *H. ezoensis* (Uchida, 1934) is a valid species, distinct from *H. diversiporus* Sokolow, 1927, and that the name *H. ezoensis* should be restored. Unfortunately, the male genital plate seems to be the salient difference between the two species, as we detected no clear diagnostic differences in the female genital plates or other characters.

Since Uchida (1934) did not designate types for the species, one of the male specimens from his collection is here designated as lectotype (ZIHU-2362) and one of the female specimens (ZIHU-2368) is designated as allolectotype of *H. ezoensis* (Uchida, 1934).

Another Japanese species in the subgenus *Rivobates*, *H. taniguchii*, was described by Imamura (1954) on the basis of the two specimens collected from Kamishokotsu, Hokkaido. Despite extensive collecting across Hokkaido, we did not find this species.

**Discussion**

The confused state of *Hygrobates* taxonomy in northern Japan prior to our study is reflected in a number of misidentifications we detected in historical collections. For example, 25 specimens labelled *H. japonicus* in Uchida’s collection included three species: nine specimens were *H. bibi*, 15 were *H. longipalpis*, and one was *H. japonicus*. Similarly, two specimens labelled *Hygrobates japonicus* in Imamura’s collection turned out to be *H. bibi*. There are likely a number of reasons why these previous workers failed adequately to
diagnose species among their material. One was that the standard of description was somewhat lower than now. Uchida (1931, p 266), for example, originally described the P-2 projection of *H. japonicus* only as a blunt projection occupied by points, and his original figure (1931, Figure 6) shows a P-2 projection more like that of *H. longipalpis* than *H. japonicus*. In his redescription of *H. japonicus*, Uchida (1936, p 178) again described the P-2 projection as a blunt process covered with denticles and provided no new illustration. Our study shows that the P-2 projection is a diagnostic character among *H. bibi*, *H. longipalpis*, and *H. japonicus*, with a morphology that is broad and rounded, narrower and sharper, and squarely truncated, respectively.

Failure to separate species correctly, however, was due to more than what we would now consider as inadequate descriptions. In fact, Uchida’s original figure of *H. japonicus* accurately represents the forms of P-3 and the male genital plate, which taken together unambiguously diagnose this species. A further shortcoming was likely an overly broad estimation of intraspecific variation, that is, a failure to distinguish correctly inter- from intraspecific variation. Three of the most important characters for distinguishing among *H. japonicus*, *H. bibi*, and *H. longipalpis* are the forms of the P-2 projection, P-3, and the male genital plate. For each of these characters, it is possible to view variation as continuous, if one assumes a priori a broad range of intraspecific variation. For example, the ventral side of P-3 might seem to range from flat (*H. longipalpis*) to uniformly convex (*H. bibi*) to having a convex protrusion in the middle (*H. japonicus*), or the outline of the male genital plate from smooth (*H. bibi*) to moderately crenate (*H. japonicus*) to highly crenate (*H. longipalpis*). In a similar vein, Imamura (1953b) mistakenly attributed the discrepancies in palp morphology between his specimens and the original description of *H. japonicus* to ontogenetic variation within *H. japonicus*; thus, he failed to recognize the new species here described as *H. bibi*.

A final drawback of previous studies may have been examination of only limited material from a few localities. In all, our study examined approximately 300 newly collected specimens, 127 of which were prepared on slides, from 35 localities across Hokkaido.

Difficulties in correctly partitioning inter- from intraspecific variation will be magnified if undue weight is given to a single character. Here we have taken a polythetic approach, describing in detail numerous characters from each species encountered. Suites of characters, as shown in Table II, allow reliable identification of all species we have treated. However, many of the traditionally used characters are qualitative and in some cases require experience in interpretation. To improve species definition, we propose two new quantitative characters for the taxonomy of the genus *Hygrobates* that have not been considered significant in the previous literature. These are the ratio of the distance between the P-4 ventral setae to P-4 segment length, and the ratio of the length of the longest terminal seta on IV-L-5 to the length of IV-L-5. Although not diagnostic among all the species treated in our study, these characters are distinct, for example, between *H. japonicus* and *H. bibi* (Figures 4, 5). In addition, we have for the first time noted the sculpturing of the outer border of the genital plates, expecting an important role of this character in future taxonomy.

Representatives of the genus *Hygrobates* occur worldwide, on many islands and all continents, apparently except Antarctica. Some of the species on Hokkaido are broadly distributed in the Palaearctic (*H. calliger*, *H. foreli*, *H. longiporus*, *H. nigromaculatus*) or Holarctic (*H. longipalpis*) regions (Viets 1978). Prior to our study, all of these but *H. nigromaculatus* were known in Japan from Kyushu, Honshu and Hokkaido Islands (Enami 1940; Imamura 1950, 1953a, 1953b, 1954, 1955, 1960; Uchida 1931, 1934, 1936a, 1943).
1936b; N. Matsumoto, unpublished data). We recorded *H. nigromaculatus* for the first time from Hokkaido and also from Japan. This suggests that with further research, other widely distributed water mite species can be expected in Japan.

*Hygrobates ezoensis* and *H. bibi* are examples of species with narrow known distributions. Although *H. ezoensis* is common in springs in Hokkaido and occurs on adjacent Sakhalin Island, it has not been recorded elsewhere. *Hygrobates bibi* is so far known only from Hokkaido and central Honshu Islands, Japan.

*Hygrobates sokolowi* was previously thought to be a rare species with a limited distribution within Europe. Our records from a single locality on Hokkaido considerably extend the range to eastern Eurasia. Thus *H. sokolowi* may have a considerably broader distribution than was previously known, extending across northern Eurasia. If this broad range has previously gone undetected, it suggests much remains to be learned about the biogeography even of widely distributed species.

**Acknowledgements**

We are deeply grateful to the following colleagues for their generous help, and wish to extend our heartfelt thanks: Professor Haruo Katakura and Associate Professor Shin Tochinai, Hokkaido University, provided valuable assistance in numerous ways. Ms Tomiko Ito, Hokkaido Fisheries Experimental Station; Dr Kazuyuki Onimaru, Bihoro Museum; Dr Yoshikazu Takashima, Marine Biological Research Institute of Japan Co., Ltd; Mr Kazunori Saito, Asahikawa University; Ms Chiharu Sato, Graduate School of Education, Hirosaki University; and Mr Ko Tomikawa and Mr Shinpei Hiruta, Graduate School of Science, Hokkaido University, helped with collecting specimens or provided specimens. Dr Jun-ichi Aoki, Kanagawa Prefectural Museum of Natural History, shared his knowledge of acarology and helped with collecting. Dr Gen Takaku, Hokkaido University of Education, suggested useful techniques and provided other information. Dr Hiroshi Abe, Nihon University, helped obtain references and shared his knowledge of water mites. Dr Reinhard Gerecke, Tübingen, donated some European *Hygrobates* samples and likewise provided useful information on water mites. Dr Hiroshi Morino and Dr Yoshiaki Kikuchi, Ibaraki University, kindly loaned Imamura’s collection. This work was supported by a fellowship to N.M. from the Northern Advancement Center for Science and Technology, and by the COE Program on Neo-Science of Natural History, Graduate School of Science, Hokkaido University (M.H.D.).

**References**

Cook DR. 1974. Water mite genera and subgenera. Memoirs of the American Entomological Institute 21:I–VII, 1–860.

Danielsson R. 1985. Polyviol as mounting medium for aphids (Homoptera: Aphidoidea) and other insects. Entomologica Scandinavica 15:383–385.

Enami M. 1940. Water mites from Izu I. Rheophilous water-mites from River Inozawa. Science Reports of the Tohoku Imperial University, Fourth Series, Biology XV 2:203–259.

Hermann JF. 1804. Mémoire aptérologique. Strasbourg: Frédéric-Louis Hammer. 144 p.

Imamura T. 1950. On the life-history of a water-mite, *Hygrobates longipalpis* (Herm.). Gakugei, Hokkaido University 2:74–78. (Jpn).

Imamura T. 1953a. Some water-mites from Hiroshima Prefecture. Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology 11:193–260.

Imamura T. 1953b. Water-mites from Gifu Prefecture. Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology 11:411–471.
Imamura T. 1954. Studies on water-mites from Hokkaido. Journal of Hokkaido Gakugei University, Section B, Supplement 1:1–148.

Imamura T. 1955. Crenophilous and rheophilous water-mites from Mishima and its vicinity. Bulletin of the Biogeographical Society of Japan 16–19:181–192.

Imamura T. 1960. Water-mites from the River Hinuma. Bulletin of the Faculty of Arts and Sciences, Ibaraki University, Natural Science 11:39–52.

Imamura T. 1980. Hygrobatidae. In: Ehara S, editor. Illustrations of the mites and ticks of Japan Tokyo: Zenkoku Noson Kyoiku Kyokai. p 348–353. (Jpn).

Lebert H. 1874. Über den Werth und die Bereitung des Chitinskeletes der Arachniden für mikroskopische Studien. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 69:605–657.

Lebert H. 1879. Hydracarines du Léman. In: Forel FAC, editor. Matériaux pour servir a l’étude de la Faune profonde du Lac Léman. Série 6. Bulletin de la Société Vaudoise des Sciences Naturelles (Lausanne). p 475–525.

Piersig R. 1896. Einige neue Hydracarinen-Formen (Vorläufige Mittheilung). Zoologischer Anzeiger 19:438–441.

Smith IM, Cook DR, Smith BP. 2001. Water mites (Hydrachnida) and other arachnids. In: Thorp JHCovich AP, editors. Ecology and classification of North American freshwater invertebrates. 2nd ed. San Diego (CA): Academic Press. p 551–659.

Sokolow II. 1927. Beiträge zur Kenntnis der Hydracarinenfauna des Kaukasus. Travaux de la Station Biologique de Caucase du Nord, Gorsky Institut Agronomique 5(2):43–72.

Sokolow II. 1931. Beiträge zur Kenntnis der Hydracarinenfauna des Ussuri-Gebietes. I. Hydracarinen der stehenden Gewässer. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 61:453–522.

Sokolow II. 1940. Hydracarina (Part 1: Hydrachnellae). In: Sernov SAIStackelberg AA, editors. Faune de l’URSS. Arachnides. 5 (2), Moscow: Institut Zoologique de l’Academie des Sciences de l’URSS, No. 20, 511 p.

Sokolow II, Jankowskaja AI. 1962. Obzor fauny gidrakarin Lyeningradskoy oblasti i Karyelii. Trudy Zoologichyeskogo Instituta Akademii Nauk SSSR 31:389–428.

Thor S. 1898. Nye hydrachnideformer, fundne i Norge sommeren 1898, Foreløbig Meddelelse. Archiv für Mathematik og Naturvidenskab 20:272–279.

Thor S. 1927. Vorläufige Revision dir Gattung Hygrobates C. L. Koch 1837, mit phylogenetischen Bemerkungen. Norsk Entomologisk Tidsskrift 2:118–148.

Tuzovskij PV. 2003. Description of three new water mites species of the genus Hygrobates (Acariformes, Hygrobatidae). Zoologicheskii Zhurnal 82:1325–1338. (Rus with Eng summary).

Tuzovskij PV, Gerecke R. 2003. A new diagnosis and status for Mixobates Thor, 1905 (Acari, Hydrachnidia, Hygrobatidae), with a revision of the palaearctic species. Annales de Limnologie–International Journal of Limnology 39:151–174.

Uchida T. 1931. Einige Wassermilben aus Japan. Zoologischer Anzeiger 95:262–268.

Uchida T. 1934. Some rheophilous water-mites from Japan. Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology 3:67–116.

Uchida T. 1936a. Water mites from the Kurile islands. Bulletin of the Biogeographical Society of Japan 6:171–182.

Uchida T. 1936b. Water mites from Saghalien. Bulletin of the Biogeographical Society of Japan 6:309–323.

Viets KH. 1930. Zur Kenntnis der Hydracarinen-Fauna von Spanien. Archiv für Hydrobiologie 21:359–446.

Viets KH. 1956. Die Milben des Süßwassers und des Meeres. Hydrachnellae et Halacaridae (Acari) (Bibliographie, Katalog, Nomenklator). Zweiter und dritter Teil Jena: Veb Gustav Fischer Verlag. 870 p.

Viets KO. 1978. Hydracarina. In: Illies J, editor. Limnofauna Europaea. 2nd ed, Stuttgart: Gustav Fischer Verlag. p 154–181.

Viets KO. 1987. Die Milben des Süßwassers (Hydrachnellae und Halacaridae [part.], Acari) 2, Katalog. Hamburg: Paul Parey. 1012 p.