



## Distribution of ectosymbiotic species of *Cirrodrilus* (Annelida, Clitellata, Branchiobdellida) in northern Japan, with notes on their taxonomy

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### Abstract

Twelve species of *Cirrodrilus*, a genus of ectosymbiotic branchiobdellidans, have been recorded on the Japanese crayfish, *Cambaroides japonicus*, from the islands of Hokkaido and northern Honshu. To clarify the geographic distribution of these species, we examined branchiobdellidan assemblages from 71 locations on Hokkaido and 59 on northern Honshu. We found 11 morphologically distinct species. The following 8 species: *Cirrodrilus digitatus*, *Ci. cirratus*, *Ci. uchidai*, *Ci. sapporensis*, *Ci. nipponicus*, *Ci. japonicus*, *Ci. megalodontatus* and *Ci. homodontus* were exclusively recorded from Hokkaido, while *Ci. aomorensis* was restricted to Honshu. Two other species, *Ci. tsugarensis* and *Ci. iwakiensis*, had previously only been recorded from Honshu but were now also found on Hokkaido. The anomalous record of *Ci. digitatus* and *Ci. uchidai* on Honshu is known to be the result of crayfish being translocated from Hokkaido. No significant difference in the species composition was found between eastern and western regions on Hokkaido, where divergent lineages have been detected in the Japanese crayfish host. Overlaps in the diagnostic characters of *Ci. cirratus* and *Ci. uchidai* suggest that both taxa belong to either a single species or form a species complex.

**Key words:** Branchiobdellida, *Cirrodrilus*, distribution, morphological variations, northern Japan

### Introduction

Studies of Japanese branchiobdellidans, an ectosymbiotic group on Japan's only indigenous crayfish species, *Cambaroides japonicus* (De Haan, 1841), have been mostly taxonomic (Pierantoni 1905, 1906, 1912; Yamaguchi 1932a, b, c, 1934, 1935a, b; Gelder 1987; Gelder & Ohtaka 2000, 2002; Gelder *et al.* 2020; Ohtaka 2010; Ohtaka & Gelder 2015; Ohtaka *et al.* 2020). These descriptive works usually included approximate specimen collection locations in northern Japan, from which the distributions of branchiobdellidan species have been compiled (Gelder & Ohtaka 2002). The resurgence of interest in Japanese branchiobdellidans over the last 25 years has increased the number of sampled sites that led to new species being described (Gelder & Ohtaka 2000; Ohtaka & Gelder 2015) along with redescriptions of others (Gelder *et al.* 2020), currently resulting in 14 nominal species names.

A poorly preserved and distorted specimen formed the basis for the first description of a branchiobdellidan from Japan, *Cirrodrilus cirratus* Pierantoni, 1905. Yamaguchi (1932a: 362) provided an accurate redescription of the species to which Gelder (1987: 21) contributed additional details. Subsequent species from Japan were placed in a new genus *Stephanodrilus* Pierantoni, 1906 with the type species being *Stephanodrilus sapporensis* Pierantoni, 1906; however, Holt (1967: 3) showed that *Stephanodrilus* was a junior synonym of *Cirrodrilus* Pierantoni, 1905.

*Branchiobdella digitata* Pierantoni, 1906, was the only non-*Cirrodrilus* Japanese species to be reported on *Cambaroides japonicus* collected in Sapporo, Hokkaido. Pierantoni (1906) obtained his material in part from the Muséum National d'Histoire Naturelle de Paris, France, and the remainder directly from Japan (Oka 1907). To verify this was a *Branchiobdella* species, Yamaguchi (1934) and Gelder (1987) both made loan requests to the Museum for the *B. digitata* material and were told it could not be found; its absence was confirmed in another unsuccessful search of the Museum's collection by Subchev (2008). Yamaguchi (1934) noted that the external features and structure of the jaws of *B. digitata* resembled those in his newly described *Cirrodrilus inukaii* (Yamaguchi, 1934);

a view shared by Timm (1991: 328). During the examination of hundreds of Japanese branchiobdellidans by AO, morphological variations in the jaw structure of *Ci. inukaii* were identified, which resulted in *B. digitata* being reassigned and renamed *Cirrodrilus digitatus* (Pierantoni, 1906). Thus *Ci. inukaii* (Yamaguchi, 1934) became a junior synonym of *Ci. digitatus* (see Gelder *et al.* 2020).

Pierantoni (1912) examined the collection of crayfish from the Hamburg Museum, Germany, [now called the Museum of Nature Hamburg – Zoology] and found a new species of branchiobdellidan which he named *Cirrodrilus japonicus* (Pierantoni, 1912). A recent morphological comparison of the syntypes and the original description of *Ci. japonicus* with the syntypes of *Cirrodrilus ezoensis* (Yamaguchi, 1934) and newly collected material, demonstrated they were the same species; hence *Ci. ezoensis* was designated a junior synonym of *Ci. japonicus* by Ohtaka & Gelder (2023).

As *Ci. inukaii* and *Ci. ezoensis* have both become junior synonyms, there are currently only 12 valid branchiobdellidan species known from *Ca. japonicus* and all are members of the genus *Cirrodrilus*. According to Yamaguchi (1935a), nine of these species were reported on Hokkaido Island: *Ci. digitatus* (= *Ci. inukaii*), *Cirrodrilus homodontus* (Yamaguchi, 1932), *Ci. japonicus* (= *Ci. ezoensis*), *Cirrodrilus makinoi* (Yamaguchi, 1934), *Cirrodrilus megalodontatus* (Yamaguchi, 1934), *Cirrodrilus nipponicus* (Yamaguchi, 1932), *Ci. sapporensis*, *Cirrodrilus uchidai* (Yamaguchi, 1932), and *Ci. cirratus*. The remainder occur on northern Honshu: *Cirrodrilus aomorensis* (Yamaguchi, 1934), with recent additions of *Cirrodrilus tsugarensis* Gelder & Ohtaka, 2000 and *Cirrodrilus iwakiensis* Ohtaka & Gelder, 2015. Reviewing the collection sites reported by Yamaguchi (1932a, b, c, 1934, 1935a, b) and those compiled by Gelder & Ohtaka (2002), it was noticed that some areas within each branchiobdellidan's range had been sampled repeatedly while no collections had been made in others. The distribution of the host species, *Cambaroides japonicus*, used to be stated simply as present on northern Honshu and Hokkaido Islands, but a recent phylogeographic analysis of the crayfish demonstrated it had an unexpected evolutionary history on the Japanese archipelago (Koizumi *et al.* 2012). Their analyses showed that *Ca. japonicus* had western and eastern lineages. The western lineage had a slow, stepwise range expansion across western Hokkaido and through northern Honshu, in contrast to a rapid expansion of the eastern Hokkaido lineage bounded on the west by the Hidaka Mountains (Koizumi *et al.* 2012). This was not consistent with the known distribution of their ectosymbiotic branchiobdellidan species assemblages.

Following results of Koizumi *et al.* (2012) on the newly found regionalization of the crayfish, it was recognized that past distributional data on Japanese branchiobdellidans were inadequate to find either a comparable or different regionalization of their species assemblages. Therefore, a systematic search for the ectosymbionts was needed across northern Japan. Concomitantly, attention was also to be given to the morphology of the branchiobdellidan species as it was anticipated that the expanded search would reveal broader intraspecific variations and possibly new species. Such information would improve species descriptions and expose previously unknown micro-distributions, as well as providing a reassessment of the status of existing species.

## Materials and Methods

Specimens of branchiobdellidans used in the present study were obtained from crayfish preserved in 60–80% ethanol or 5–10% formalin solutions, which were collected by the authors and their colleagues from 71 locations on Hokkaido and 59 on northern Honshu Islands during 1994–2022 (Fig. 1, Table 1). The branchiobdellidans were recovered from the body surface of crayfish and the bottom debris in their collection containers. Specimens from formalin solutions were thoroughly washed in distilled water before being dehydrated in successively increasing ethanol solutions, cleared with methyl salicylate and mounted individually on slides in Canada balsam for morphological examination, while ethanol preserved specimens were introduced into the ethanol sequence at the appropriate level. Microscopical examinations were conducted on the mounted specimens using bright-field and differential interference contrast (DIC) illumination with various high quality research microscopes. The resulting morphological characters of body shape, form of the peristomium, jaw shape and dentation, and the male reproductive system were then used to identify the species with the taxonomic key by Gelder (2019) and for confirmation using the most up-to-date species description. After the removal of branchiobdellidans, a portion of each selected crayfish was preserved in 70% ethanol and deposited in the National Museum of Nature and Science, Tokyo, Japan (Accession numbers; NSMT-Cr 28707-28964) for future reference and projects. The branchiobdellidan specimens are held in AO's collection.

**TABLE 1.** List of *Cambaroides japonicus* (Japanese crayfish) collection sites in the study areas on northern Honshu and Hokkaido Islands.

No.	Island	Prefecture or region	Locality Name	Longitude	Latitude
1	Hokkaido	Eastern	Kanayama, Maruseppu Town	44.03	143.34
2	Hokkaido	Eastern	Toyooka, Bihoro Town	43.82	144.03
3	Hokkaido	Eastern	Kiyosato Town	43.78	144.63
4	Hokkaido	Eastern	Rubeshibe, Kitami City	43.74	143.33
5	Hokkaido	Eastern	Kunneppu Town	43.72	143.73
6	Hokkaido	Eastern	Oketo Town	43.67	143.58
7	Hokkaido	Eastern	Shibetsu Town	43.67	145.02
8	Hokkaido	Eastern	Chimikeppu, Tsubetsu Town	43.62	143.87
9	Hokkaido	Eastern	Nukabira, Kami-shihoro Town	43.36	143.19
10	Hokkaido	Eastern	Oribe, Kami-shihoro Town	43.25	143.39
11	Hokkaido	Eastern	Hamanaka Town	43.15	145.10
12	Hokkaido	Eastern	Tsutsujigaoka, Obihiro City	42.90	143.11
13	Hokkaido	Eastern	Samani Town	42.11	142.99
14	Hokkaido	Eastern	Lake Toyoni, Erimo Town	42.08	143.27
15	Hokkaido	Western	Sōya Cape, Wakkanai City	45.51	141.90
16	Hokkaido	Western	Wakkanai, Wakkanai City	45.43	141.66
17	Hokkaido	Western	Fujimi, Wakkanai City	45.42	141.64
18	Hokkaido	Western	Kafuka, Rebun Is., Rebun Town	45.34	141.04
19	Hokkaido	Western	Menashi-domari, Esashi Town	45.05	142.49
20	Hokkaido	Western	Toikanbetsu, Horonobe Town	44.98	142.11
21	Hokkaido	Western	Nakagawa Town	44.81	142.07
22	Hokkaido	Western	Enbetsu Town	44.66	141.79
23	Hokkaido	Western	Jinmon Fall, Oumu Town	44.45	142.62
24	Hokkaido	Western	Yagishiri Is., Haboro Town	44.43	141.41
25	Hokkaido	Western	Teuri Is., Haboro Town	44.42	141.31
26	Hokkaido	Western	Rikibiru, Tomamae Town	44.23	141.66
27	Hokkaido	Western	Ōbekkari, Mashike Town	43.81	141.46
28	Hokkaido	Western	Fukagawa City	43.77	142.19
29	Hokkaido	Western	Sōunkyo, Kamikawa Town	43.71	142.98
30	Hokkaido	Western	Gokibiru, Hamamasu Village	43.48	141.40
31	Hokkaido	Western	Furano City	43.34	142.38
32	Hokkaido	Western	Shiraiwa, Shakotan Town	43.32	140.50
33	Hokkaido	Western	Onenai River, Shakotan Town	43.29	140.35
34	Hokkaido	Western	Shukuzu, Otaru City	43.23	141.00
35	Hokkaido	Western	Yoichi City	43.20	140.75
36	Hokkaido	Western	Otaru City	43.19	140.99
37	Hokkaido	Western	Minami-Furano Town	43.16	142.56
38	Hokkaido	Western	Kamoenai Village	43.16	140.38
39	Hokkaido	Western	Tokiwa, Yoichi Town	43.09	140.95
40	Hokkaido	Western	Tomari Village	43.06	140.50
41	Hokkaido	Western	Jōzankei, Sapporo City	42.96	141.22
42	Hokkaido	Western	Ō-numa, Kyogoku Town	42.94	141.03
43	Hokkaido	Western	Ō-numa, Kyōwa Town	42.89	140.61

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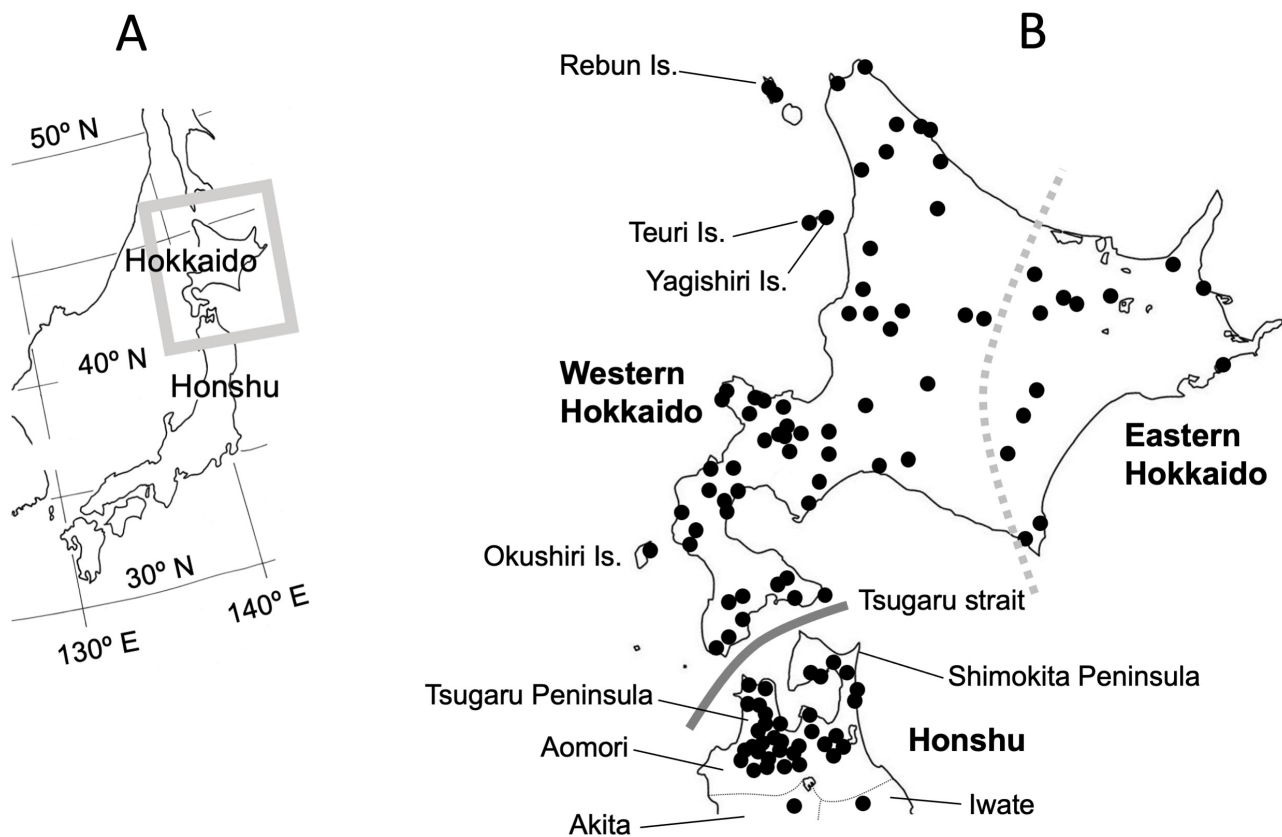
**TABLE 1.** (Continued)

No.	Island	Prefecture or region	Locality Name	Longitude	Latitude
44	Hokkaido	Western	Naga-numa, Kyōwa Town	42.89	140.58
45	Hokkaido	Western	Yumoto, Niseko Town	42.87	140.59
46	Hokkaido	Western	Eniwa City	42.86	141.32
47	Hokkaido	Western	Lake Hangetsu, Kutchan Town	42.84	140.75
48	Hokkaido	Western	Isoya, Suttu	42.83	140.34
49	Hokkaido	Western	Tomikawa, Niseko Town	42.80	140.68
50	Hokkaido	Western	Bisei, Memuro Town	42.78	142.89
51	Hokkaido	Western	Shimamaki Village	42.70	140.06
52	Hokkaido	Western	Sakae, Shimamaki Village	42.62	139.84
53	Hokkaido	Western	Usu Rive, Tomakomai City	42.66	141.53
54	Hokkaido	Western	Atsuma Town	42.66	141.91
55	Hokkaido	Western	Morino, Shiraoi Town	42.66	141.25
56	Hokkaido	Western	Kuromatsunai Town	42.65	140.32
57	Hokkaido	Western	Oshamanbe Town	42.51	140.37
58	Hokkaido	Western	Kyōritsu, Oshamanbe Town	42.58	140.36
59	Hokkaido	Western	Hogoshi Cape, Setana Town	42.26	139.77
60	Hokkaido	Western	Shinsei, Setana Town	42.32	139.78
61	Hokkaido	Western	Inaho, Okushiri Town	42.22	139.53
62	Hokkaido	Western	Komami, Kayabe Town	42.01	140.75
63	Hokkaido	Western	Mena, Assabu Town	41.92	140.16
64	Hokkaido	Western	Osatsube, Hakodate City	41.87	141.01
65	Hokkaido	Western	Todohokke, Hakodate City	41.81	141.16
66	Hokkaido	Western	Nakano, Hakodate City	41.76	140.84
67	Hokkaido	Western	Hakodate City	41.75	140.71
68	Hokkaido	Western	Yunotai, Kaminokuni Town	41.70	140.27
69	Hokkaido	Western	Ōkawa, Kikonai Town	41.69	140.33
70	Hokkaido	Western	Mogusa, Matsumae Town	41.50	140.01
71	Hokkaido	Western	Forest Park, Fukushima Town	41.49	140.25
72	Honshu	Aomori	Lake Usoriyama, Mutsu City	41.31	141.08
73	Honshu	Aomori	Kawauchi, Mutsu City	41.28	140.97
74	Honshu	Aomori	Yunokawa, Mutsu City	41.27	140.98
75	Honshu	Aomori	Taya, Higashidoori Village	41.26	141.28
76	Honshu	Aomori	Okunai, Mutsu City	41.24	141.31
77	Honshu	Aomori	Okoppe, Higashidoori Village	41.19	141.37
78	Honshu	Aomori	Wakinosawa, Mutsu City	41.18	140.83
79	Honshu	Aomori	Shiranuka, Higashidoori Village	41.17	141.37
80	Honshu	Aomori	Yokohama Town	41.06	141.28
81	Honshu	Aomori	Tōhoku Town	40.84	141.22
82	Honshu	Aomori	Ishizaka, Tōhoku Town	40.82	141.12
83	Honshu	Aomori	Tenmabayashi, Shichinohe Town	40.75	140.97
84	Honshu	Aomori	Tenmadate, Shichinohe Town	40.74	141.02
85	Honshu	Aomori	Kuraoka, Shichinohe Town	40.72	141.09
86	Honshu	Aomori	Hizamori, Shichinohe Town	40.71	141.16

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**TABLE 1.** (Continued)

No.	Island	Prefecture or region	Locality Name	Longitude	Latitude
87	Honshu	Aomori	Nonaihata, Hiranai Town	40.98	140.90
88	Honshu	Aomori	Yogoshiyama, Hiranai Town	40.91	140.98
89	Honshu	Aomori	Sotodōji, Hiranai Town	40.83	140.97
90	Honshu	Aomori	Stream 1, Imabetsu Town	41.22	140.55
91	Honshu	Aomori	Stream 2, Imabetsu Town	41.21	140.55
92	Honshu	Aomori	Sotogahama Town	41.14	140.38
93	Honshu	Aomori	Uemata River, Imabetsu Town	41.13	140.50
94	Honshu	Aomori	Seheji, Yomogita Village	40.99	140.56
95	Honshu	Aomori	Imaizumi, Nakadomari Town	40.97	140.47
96	Honshu	Aomori	Daitōgaoka, Goshogawara City	40.92	140.49
97	Honshu	Aomori	Tsutsugisaka, Tsugaru City	40.91	140.33
98	Honshu	Aomori	Maruoka, Tsugaru City	40.84	140.30
99	Honshu	Aomori	Komozuchi, Tsugaru City	40.84	140.32
100	Honshu	Aomori	Iizume River, Goshogawara City	40.84	140.51
101	Honshu	Aomori	Matsuki River, Goshogawara City	40.81	140.45
102	Honshu	Aomori	Koshimizu, Tsugaru City	40.79	140.29
103	Honshu	Aomori	Ushigogata, Aomori City	40.94	140.59
104	Honshu	Aomori	Chōbōsan, Aomori City	40.90	140.60
105	Honshu	Aomori	Maeda, Aomori City	40.89	140.64
106	Honshu	Aomori	Tsurugasaka, Aomori City	40.79	140.63
107	Honshu	Aomori	Daishaka, Aomori City	40.77	140.59
108	Honshu	Aomori	Magonai, Aomori City	40.75	140.63
109	Honshu	Aomori	Namioka, Aomori City	40.74	140.56
110	Honshu	Aomori	Aikozawa, Aomori City	40.74	140.76
111	Honshu	Aomori	Komagome, Aomori City	40.74	140.86
112	Honshu	Aomori	Komakino, Aomori City	40.73	140.73
113	Honshu	Aomori	Hosono, Aomori City	40.69	140.67
114	Honshu	Aomori	Arakawa, Aomori City	40.67	140.78
115	Honshu	Aomori	Hosoda, Aomori City	40.71	140.58
116	Honshu	Aomori	Namioka River, Aomori City	40.71	140.64
117	Honshu	Aomori	Ashiyamachi, Ajigasawa Village	40.69	140.22
118	Honshu	Aomori	Shirasawa, Ajigasawa Village	40.68	140.22
119	Honshu	Aomori	Nagatai, Ajigasawa Village	40.68	140.25
120	Honshu	Aomori	Matsushiro, Ajigasawa Village	40.67	140.22
121	Honshu	Aomori	Kosugisawa, Hirosaki City	40.67	140.36
122	Honshu	Aomori	Tokoshinai, Hirosaki City	40.73	140.33
123	Honshu	Aomori	Hyakusawa, Hirosaki City	40.65	140.35
124	Honshu	Aomori	Tokiwano, Hirosaki City	40.62	140.25
125	Honshu	Aomori	Moriyama, Hirosaki City	40.60	140.32
126	Honshu	Aomori	Ishikawa, Hirosaki City	40.53	140.52
127	Honshu	Iwate	Funada, Ninohe City	40.27	141.34
128	Honshu	Akita	Hayakuchi, Ōdate City	40.27	140.44
129	Honshu	Akita	Mochida, Ōdate City	40.27	140.52
130	Honshu	Akita	Osarizawa, Kazuno City	40.19	140.76



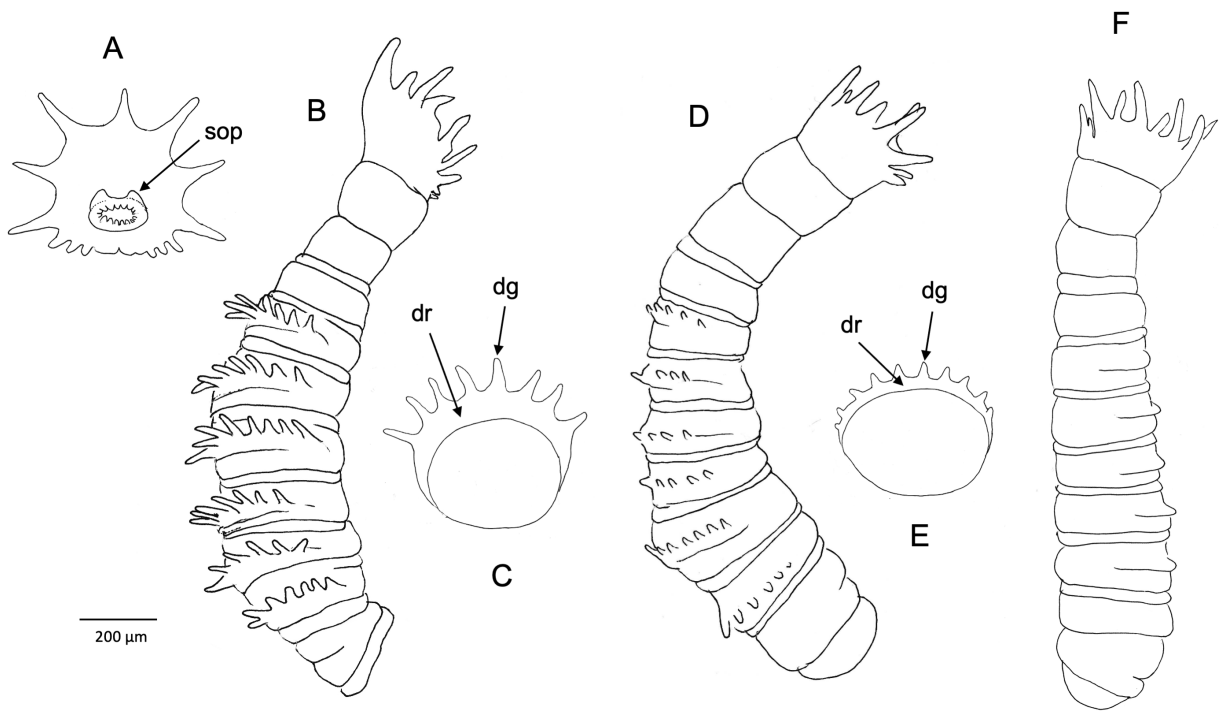
**FIGURE 1.** Location of Japanese archipelago (A), and the collection sites of *Cambaroides japonicus* in northern Japan (B), with the gray dashed line through Hokkaido indicating the boundary between eastern and western lineages of *Ca. japonicus* (according to Koizumi *et al.* 2012).

## Results

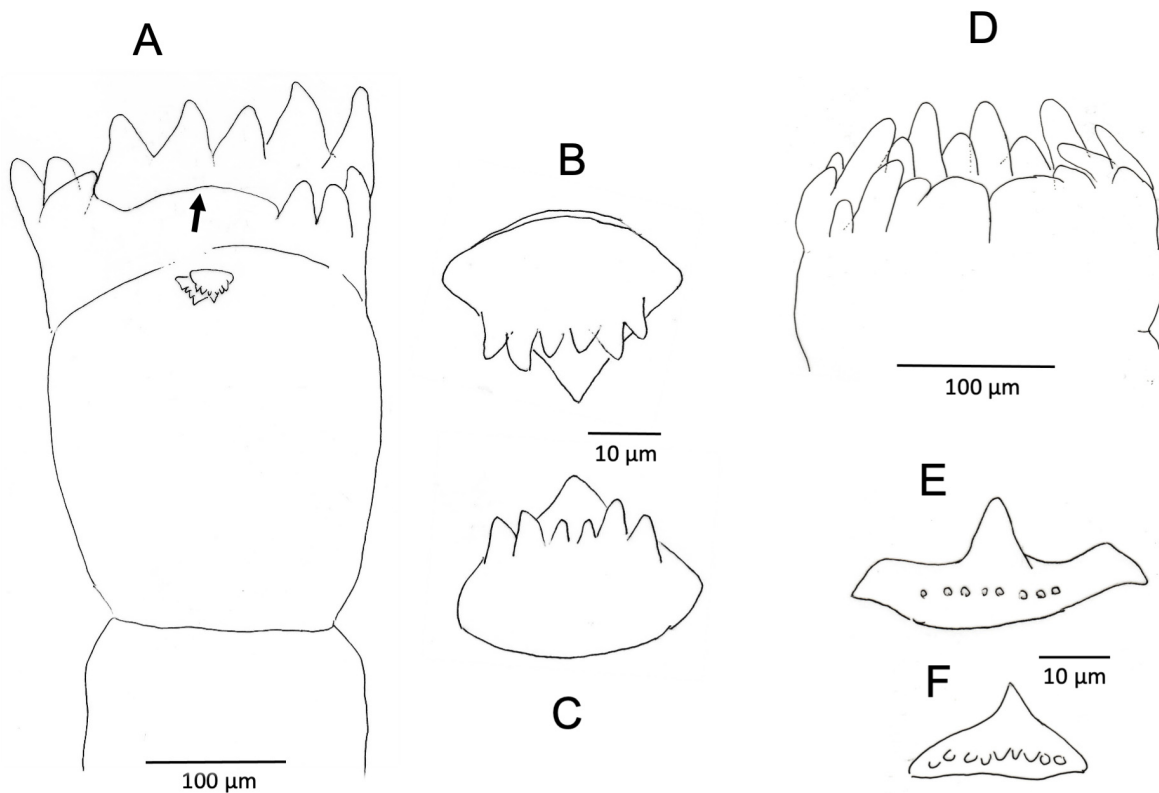
### *Reassessment of specific criteria and taxonomic notes on several species.*

During the identification of branchiobdellidans, inconsistencies in the species diagnoses of *Ci. cirratus* and *Ci. uchidai* forced us to reconsider their taxonomic status. In addition, the discovery of *Ci. tsugarensis* and *Ci. iwakiensis* outside of their Honshu range also revealed specimens with small morphological variations; see below.

The two morphological characteristics for identifying *Ci. cirratus* are the presence of a pair of supra-oral papillae (Fig. 2 A, sop) and prominent, dorsal transverse segment ridges bearing eight long digitiform appendages according to Yamaguchi (1934: 214; Pl. II D). Those specimens lacking supra-oral papillae, but with dorsal transverse ridges having 0–12 short dorsal segmental appendages were initially called *Ci. uchidai* (Yamaguchi 1932a: 367). Recognizing the dilemma caused by the range of dorsal segmental appendages, Yamaguchi (1934: 212, Fig. 15; 213) then divided the species into two groups: the “appendiculated form” for those specimens with a maximum of 12, short digitiform appendages on each of several dorsal ridges (Yamaguchi 1934: fig.15A, B), and the “unappendiculated form” for the specimens without any digitiform appendages on the dorsal ridges (Yamaguchi 1934: fig.15C–E). Gelder (1987) was able to mount and describe specimens on loan from the Museum of Nature Hamburg – Zoology, Germany, that had been donated by Prof. H. Yamaguchi sometime in the late-1930s. One specimen had supra-oral papillae, dorsal segmental transverse ridges and 8 digitiform appendages on segments 3 to 8 (Gelder 1987: 21), which he called *Ci. cirratus*, while the second had no supra-oral papillae, but had dorsal segmental ridges and 12 short digitiform appendages on segments 3 to 8 (Gelder 1987: 22) which he named *Ci. uchidai*.



**FIGURE 2.** *Cirrodrilus cirratus* (A–C) and *Ci. uchidai* (D–F). A, frontal view of oral region, Yamaguchi (1932a: Fig. 1C) was redrawn; B, dorso-lateral view of a specimen from Matsumae, Hokkaido (see Table 1, No. 70); C, the same, cross section of segment 6; D, dorso-lateral view of an appendiculated form from Kiyosato, Hokkaido (see Table 1, No. 3); E, the same, cross section of segment 6; F, a unappendiculated form from Erimo, Hokkaido (see Table 1, No. 14). Abbreviations: dg, digitiform appendages; dr, dorsal transverse ridges; sop, supra-oral papillae.



**FIGURE 3.** *Cirrodrilus tsugarensis* (A–C, from Sapporo, Hokkaido; see Table 1, No. 41) and *Ci. iwakiensis* (D–F, from Assabu, Hokkaido; see Table 1, No. 63). A and D, ventral views of the peristomium; B–C and E–F, dorsal and ventral jaws; arrow in A indicates the median point of the ventral lip where the median emargination would be seen in a live specimen.

In this study, over 100 specimens were identified as either *Ci. cirratus* or *Ci. uchidai* (Table 2). However, the application of the two criteria given above, presence or absence of supra-oral papillae, and the two versions of dorsal transverse segmental ridges with digitiform appendages, did not result in distinguishing two separate groups. The latter criterion proved to be a better discriminator for distinguishing *Ci. cirratus* from *Ci. uchidai*, as supra-oral papillae occurred in both groups. Therefore, the criterion used in this study for identifying *Ci. cirratus* (Fig. 2B, C) was prominent dorsal transverse segmental ridges with eight long digitiform appendages, while specimens with less prominent ridges and a variable number of short digitiform appendages, up to 12, or none, were named *Ci. uchidai* (Fig. 2D–F). A closer examination of *Ci. uchidai* material found that both appendiculated (Fig. 2D, E) and unappendiculated (Fig. 2F) forms were accompanied by variations in the prominence of the dorsal transverse segmental ridges. Some specimens from Hakodate (Table 1, No. 64) did not have ridges but still had several short digitiform appendages on segments 5–7. Although the stated criterion enabled us to assign specimens to either *Ci. cirratus* or *Ci. uchidai* for this survey, their taxonomic position based on morphological characters is unsatisfactory. Whether they are two valid species, or a species complex will require a future investigation using molecular sequencing techniques.

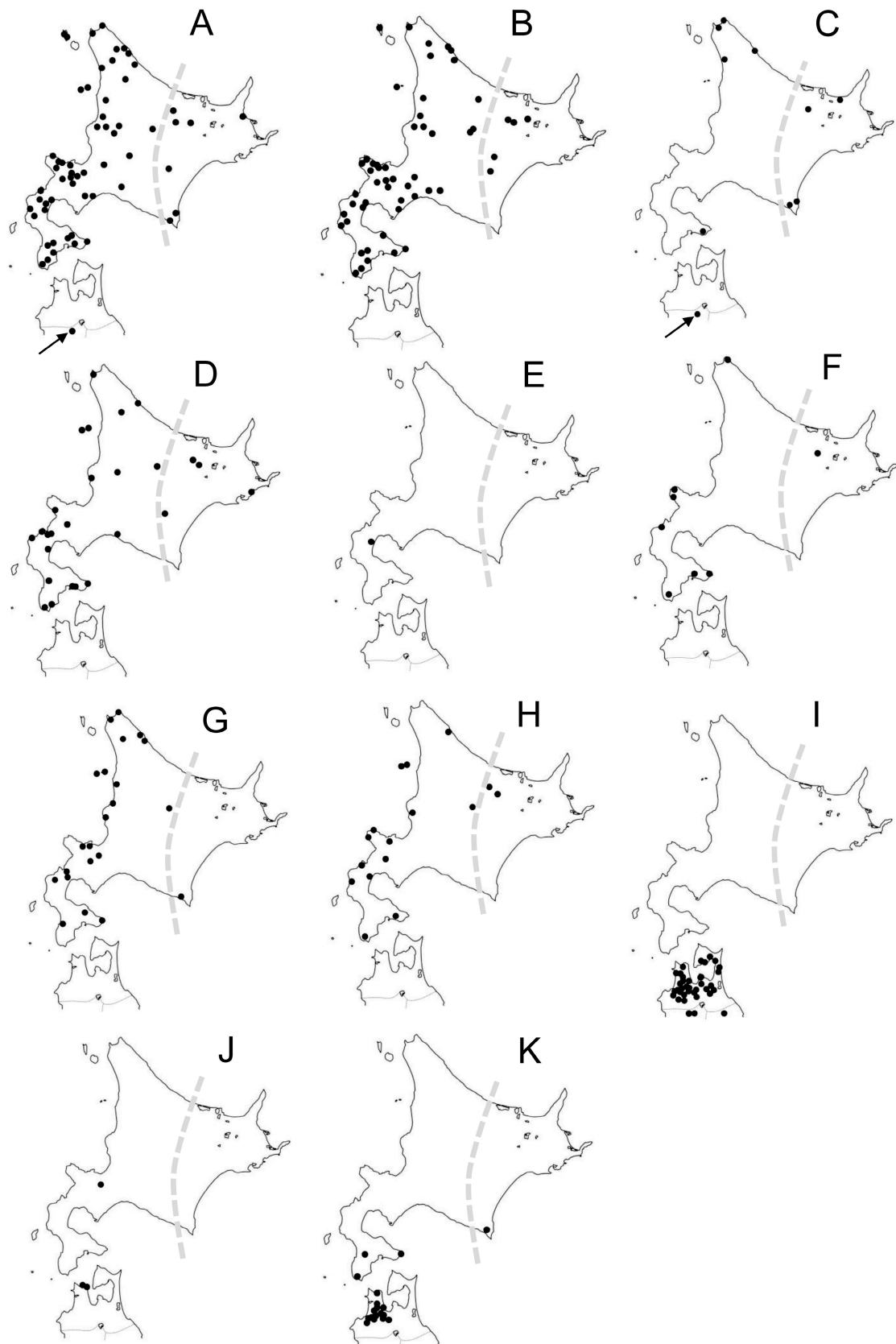
**TABLE 2.** The number of locations of each branchiobdellidan species in Honshu Prefectures with those on Hokkaido divided into eastern and western regions based on Japanese crayfish lineages (Koizumi *et al.* 2012).

	Hokkaido			Honshu				total
	West	East	total	Aomori	Iwate	Akita	total	
Number of localities studied	57	14	71	55	1	3	59	130
<i>Ci. digitatus</i>	49	7	56	0	0	1	1	57
<i>Ci. cirratus</i>	42	6	48	0	0	0	0	48
<i>Ci. uchidai</i>	4	4	8	0	0	1	1	9
<i>Ci. japonicus</i>	22	4	26	0	0	0	0	26
<i>Ci. megalodontatus</i>	1	0	1	0	0	0	0	1
<i>Ci. sapporensis</i>	14	2	16	0	0	0	0	16
<i>Ci. nipponicus</i>	7	1	8	0	0	0	0	8
<i>Ci. homodontus</i>	21	1	22	0	0	0	0	22
<i>Ci. aomorensis</i>	0	0	0	53	1	2	56	56
<i>Ci. iwakiensis</i>	3	1	4	20	0	0	20	24
<i>Ci. tsugarensis</i>	1	0	1	2	0	0	2	3

A single specimen of *Ci. tsugarensis* was identified from Sapporo, Hokkaido (Table 1, No. 41), making it the first record outside the type location in Imabetsu, Honshu (Fig. 4J). The peristomial tentacles (Fig. 3A) and jaws (Fig. 3B, C) are similar to those in the original description by Gelder & Ohtaka (2000: Fig. 1), but small variations in lateral tentacle length and width of the ventral lip were noted. These differences are most probably due to the 10% formalin solutions used by Gelder & Ohtaka (2000), in contrast to the 70% ethanol adopted for the Sapporo specimen. A difference in jaw widths was noted between the Sapporo specimen (dorsal 32 µm and ventral 30 µm wide) and the 7 topotypes from Imabetsu (23–29 µm wide), but this is not considered a significant difference.

Similarly, *Ci. iwakiensis* was only known from Honshu, until our survey found it in four new locations on Hokkaido as well as in its type area on Honshu (Fig. 4K). Eight long and seven short tentacles arranged alternately on the dorsal and lateral peristomium (Fig. 3D), and wing-like lateral tips on the dorsal jaw (Fig. 3E), differentiate *Ci. iwakiensis* from its congeners as pointed out by Ohtaka & Gelder (2015). The jaws (Fig. 3E, F) have a dental formula that ranges from 8/9 (3-1-4/4-1-4) to 11/11 (5-1-5/5-1-5) in the Hokkaido specimens, which is very similar to the type range of 10/9 (5-1-4/4-1-4) to 11/11 (5-1-5/5-1-5) reported by Ohtaka & Gelder (2015: 69).





**FIGURE 4.** Distribution of branchiobdellidan species in Japan arranged according to their location on Hokkaido or Honshu and then both: A, *Cirrodrilus digitatus*; B, *Ci. cirratus*; C, *Ci. uchidai*; D, *Ci. japonicus*; E, *Ci. megalodentatus*; F, *Ci. nipponicus*; G, *Ci. homodontus*; H, *Ci. sapporensis*; I, *Ci. aomorensis*; J, *Ci. tsugarensis*; K, *Ci. iwakiensis*; arrows in A and C indicate Osarizawa, Kazuno City, Akita Prefecture where crayfish were translocated from Hokkaido. Gray dashed lines through Hokkaido indicate the boundary between eastern and western lineages of *Cambaroides japonicus* (according to Koizumi *et al.* 2012).

Eight species were collected exclusively from Hokkaido (*Ci. digitatus*, *Ci. cirratus*, *Ci. uchidai*, *Ci. japonicus*, *Ci. megalodontatus*, *Ci. nipponicus*, *Ci. homodontus* and *Ci. sapporensis*; Fig. 4A–H), one species only from northern Honshu (*Ci. aomorensis*; Fig. 4I), and two species (*Ci. tsugarensis* and *Ci. iwakiensis*; Fig. 4J, K) from both Hokkaido and Honshu (Table 2). *Cirrodrilus digitatus* and *Ci. uchidai* were reported at Osarizawa, Kazuno City, Akita Prefecture, Honshu (Table 1, No. 130; Fig. 4A, C, arrows) and its unexpected presence on the island was explained by the host crayfish having been introduced from Hokkaido (Gelder & Ohtaka 2000). From the 71 collection sites on Hokkaido, *Ci. digitatus* was the most widely distributed being found at 56 locations (79%; Fig. 4A), followed by *Ci. cirratus* at 48 locations (68%; Fig. 4B), *Ci. japonicus* at 26 locations (37%; Fig. 4D) and *Ci. homodontus* at 22 locations (31%; Fig. 4G). *Cirrodrilus uchidai* was present at only 8 sites, this being far fewer than the closely related *Ci. cirratus*, and of these 8, both species were identified at three. Although the number of localities was fewer in the eastern region than in the western region on Hokkaido, all of these species were reported in both regions, except for *Ci. megalodontatus* which was only found at a single location (Table 1, No. 58) in the western region (Table 2). Branchiobdellidans were sought for the first time on four small offshore islands in the Sea of Japan off Hokkaido (Fig. 1B). These collections yielded *Ci. digitatus*, *Ci. cirratus*, *Ci. japonicus*, *Ci. homodontus*, and *Ci. sapporensis*; however, no branchiobdellidans were found on the 31 crayfish examined from Okushiri Island (Fig. 1B, Table 1, No. 61). *Cirrodrilus makinoi* was previously reported from Hokkaido (Yamaguchi 1934), while it was not recorded in the present study.

Sampling density was higher in northern Honshu, with 59 collection sites, where *Ci. aomorensis* was the most widely distributed species being found at 56 (93%; Fig. 4I) locations across Aomori Prefecture. However, it was absent in two neighboring streams in Imabetsu Town on the Tsugaru Peninsula (Table 1, Nos. 90, 91), where *Ci. tsugarensis* inhabited the local host crayfish (Fig. 4J). *Cirrodrilus iwakiensis* was often found in the western part of Aomori Prefecture, but at only four locations in southern Hokkaido (Figure 4K).

The number of branchiobdellidan species found at a single locality ranged from 0 to 6 with a mean of 2.7 on Hokkaido (N=71), and 1 to 2 with a mean of 1.4 on Honshu (N=59).

## Discussion

The distribution of branchiobdellidans on crayfish hosts is Holarctic, which would indicate ancestral ectosymbiotic associations may have formed across Laurasia as early as 200 million years ago (Ma) (Verdonschot 2015: 513). Following the breakup of Laurasia into Eurasia and Northern America, each region evolved its own unique fauna resulting in the modern distribution of 15 Nearctic and 8 Palaeartic branchiobdellidan genera (Gelder & Williams 2015: 552). Branchiobdellidan taxa in both zoogeographic regions are also divided into discrete eastern and western subregions by geographical barriers, namely the North American Continental Divide and the Himalayan-Siberian area. These four subregions can be more accurately defined using Bănărescu's (1990: 526) freshwater faunal subrealms: Eastern and Western North American, Euro-Mediterranean, and East Asian as described in Gelder (2020). The North American subrealms are separated by the North American Continental Divide, with species being unique to each subrealm, although *Cambarincola*, *Sathodrilus* and *Xironogiton* are known from both. The Palaeartic subrealms are widely separated by the High Asian uplift and the Siberian subrealms with only *Branchiobdella* being recorded in both Palaeartic subrealms (Gelder & Williams 2015).

At what point branchiobdellidans became ectosymbionts on freshwater astacoidean crayfish is unknown, and while the assumption that the phylogenies of symbionts and hosts should show congruity following Fahrenholz's rule (Fahrenholz 1913), no such phenomenon has been shown to date. According to Owen *et al.* (2015: Fig. 2) the origin of crayfish is estimated about 175 Ma with the Laurasia (Astacoidea) branch evolving into three families: the Cambaroididae, Astacidae and Cambaridae (after Crandall & De Graves 2017: Fig. 2). However, the ancient Cambaroididae contains one genus, *Cambaroides* Faxon, 1884, with six species (Crandall & De Grave 2017: 22) and they are endemic and restricted to the East Asian subrealm in the Palaeartic. The Astacidae contains the monophyletic *Pacifastacus*, endemic to the Western subrealm of Nearctic, and a monophyly of *Astacus*, *Austropotamobius* and *Pontastacus*, is located in the Euro-Mediterranean subrealm. The remaining 12 genera in the Cambaridae populate the Eastern subrealm of the Nearctic. Crayfish in the Palaeartic clearly evolved independently with *Cambaroides*

species having a greater diversity of branchiobdellidan genera (*Cirrodrilus*, *Branchiobdella*, *Hidejiodrilus* Gelder & Brinkhurst, 1990 and *Sinodrilus* Gelder & Brinkhurst, 1990) than the single genus *Branchiobdella* on the three Euro-Mediterranean crayfish genera. As *Branchiobdella* is the only extant genus with a single pair of testes in segment 5, it is unlikely that this apomorphic character arose more than once. How *Branchiobdella* came to be the only genus on more modern crayfishes in the Euro-Mediterranean subrealm is unknown. However, the broader associations of the branchiobdellidan–crayfish relationship are beyond the scope of this study and so the focus remains on the East Asian taxa and specifically Japan.

The current distribution of endemic East Asian branchiobdellidan–crayfish associations extend across the Korean Peninsula, northern China, Japan and southeast Russia including the Amur drainages (Timm 1991) and Sakhalin Island (Zhivoglyadova & Labay 2003). These associations involve 25 species of *Cirrodrilus*, 8 of *Branchiobdella*, and two monotypic genera, *Hidejiodrilus* and *Sinodrilus* (see Introduction for citations), on one or more of the four major *Cambaroides* species. On examination of these data, *Ca. japonicus* and its 12 species of *Cirrodrilus* only occur on the Japanese Islands of northern Honshu and Hokkaido (Ohtaka 2010; Ohtaka & Gelder 2015). Therefore, the remaining 23 species of *Cirrodrilus*, *Branchiobdella*, *Hidejiodrilus* and *Sinodrilus* can be referred to as Continental or “mainland” taxa (Timm 1991) along with the hosts, *Cambaroides dauricus* (Pallas, 1772), *Cambaroides schrenckii* (Kessler, 1874) and *Cambaroides similis* (Koelbel, 1892) (Kawai *et al.* 2016). Until recently this clear separation of branchiobdellidan species was marred by Pierantoni’s (1906) single report of *B. digitata* from Japan; however, Gelder *et al.* (2020) corrected its misidentification to *Cirrodrilus digitatus*, demonstrating that *Branchiobdella* is solely a Continental genus.

The continental crayfish species have reasonably discrete distributions with: *Ca. similis* on the Korean Peninsula and northern China, *Ca. dauricus* extending from northern Korea to the Amur River basin in China, and *Ca. schrenckii* extending along the Ussury and lower Amur River basins (Kawai *et al.* 2016). *Cambaroides schrenckii* was reported with *Cirrodrilus quadritentacularis* (Liu, 1984) in the northern portion of Sakhalin Island by Zhivoglyadova & Labay (2003). A subsequent search for crayfish and branchiobdellidans on the southern part of the island found none (Kawai *et al.* 2016), indicating the northern population had come from the adjacent mainland and had not spread southwards.

The uniqueness of the Japanese branchiobdellidan–crayfish association could be explained by *Cirrodrilus*-like worms on a *Cambaroides japonicus*-like host evolving in an area at the edge of the Eurasian continent. As the coastal region was subjected to geological events, it became separated from the mainland and formed the current offshore archipelago with the ectosymbiotic association surviving on what is now northern Honshu and Hokkaido Islands of Japan. Why branchiobdellidans and crayfish are not found on the rest of Honshu remains an enigma.

With such a hypothesis it is reasonable to expect that diversification in morphology would have evolved between the mainland and island species. Timm (1991: Fig. 46) compared the jaw morphology and variations in peristomial appendages in the *Cirrodrilus* species by arranging them into continental and Japanese groups. He could not find any differential trends in the peristomial forms, and neither could we. However, in all 13 continental species, both dorsal and ventral jaws are similar in form and size, while only six of the 12 Japanese species shared this character. In the remainder, the dorsal jaw is larger than the ventral: *Ci. aomomensis*, *Ci. digitatus*, *Ci. iwakiensis*, *Ci. japonicus*, *Ci. megalodentatus*, and *Ci. nipponicus*. Other apomorphic characters include multiple striations or ridges parallel to the median tooth in *Ci. japonicus* and *Ci. megalodentatus*, and the small teeth extending onto the lateral inwardly curling jaw tips in *Ci. nipponicus*. Another feature believed to be useful for phylogenetic assessment is that the majority of species in both groups have a large median tooth preceded by 6 to 10 small lateral teeth. In contrast, four species belonging to the Japanese (*Ci. sapporensis*) and continental (*Ci. suzukii*, *Ci. fimbriatus*, and *Ci. liaoningensis*) groups show these teeth condensing into a serrated margin, and in one continental species, *Ci. anodontus*, into a straight edge.

In the present study, three *Cirrodrilus* species were found on Honshu and nine on Hokkaido with two of the Honshu species being reported for the first time on Hokkaido. While the distribution of species on Hokkaido was significantly greater west of the Hidaka Mountains than to the east, no significant difference in species composition was found between the two regions. Yamaguchi (1934) reported finding *Ci. makinoi* and *Ci. megalodentatus* across Hokkaido, but our study did not find any *Ci. makinoi* on the island, and no specimens of *Ci. megalodentatus* in the eastern region. Perhaps the populations of crayfish may have decreased along with their branchiobdellidan assemblages since Yamaguchi’s study. Irrespective of the reasons for the reduced species composition detected in eastern compared to western Hokkaido, the presence of species with both similar and dissimilar jaws in both

Hokkaido and Honshu Islands suggests a non-monophyletic lineage of branchiobdellidan assemblages on both islands. While some biologists have suggested land bridges existed between Honshu and Hokkaido across the Tsugaru Strait in the middle and/or late Pleistocene (Dobson & Kawamura 1998; Suzuki *et al.* 2004), geologists have postulated their existence during the Last Glacial Maximum in the late Pleistocene (e.g., Ohshima 1990). Whether or not land bridges existed, they do not seem to be relevant to the composition of branchiobdellidans between Honshu and Hokkaido islands.

Koizumi *et al.* (2012) demonstrated that the Honshu populations of the Japanese crayfish were part of the western lineage and different from the eastern lineage. Our results showed that species distribution of Japanese branchiobdellidans differed more between Honshu and Hokkaido than those between the eastern and western ranges, and there appears to be little apparent congruence between branchiobdellidan assemblages and host crayfish. These results suggest that there are factors yet to be identified to explain these ectosymbiotic associations.

A future molecular phylogeographic study will be necessary to elucidate the distributional processes of Japanese branchiobdellidans, and with it, a probable explanation of the co-evolutionary history of the ectosymbiotic association of the branchiobdellidans and their Japanese crayfish hosts.

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