



Taxonomic Paper

New insights from museum specimens: a case of Viviparidae (Caenogastropoda: Mollusca) in Iwakawa's collection preserved in the National Museum of Nature and Science, Tokyo

Takumi Saito[‡], Osamu Kagawa[§]

[‡] Toho University, Narashino City, Chiba Pref., Japan

[§] Tohoku University, Sendai City, Miyagi Pref., Japan

Corresponding author: Takumi Saito (saito.zef@gmail.com)

Academic editor: Kenneth Hayes

Received: 19 Mar 2020 | Accepted: 21 Sep 2020 | Published: 21 Dec 2020

Citation: Saito T, Kagawa O (2020) New insights from museum specimens: a case of Viviparidae (Caenogastropoda: Mollusca) in Iwakawa's collection preserved in the National Museum of Nature and Science, Tokyo. Biodiversity Data Journal 8: e52233. <https://doi.org/10.3897/BDJ.8.e52233>

Abstract

Background

In this study, we clarify the classification of museum specimens of the family Viviparidae, which is composed of six species/subspecies in Japan, including three endangered species. We examined *Viviparus sclateri* specimens from the Tomotaro Iwakawa collection (1855-1933) in the National Museum of Nature and Science, Tokyo. The Iwakawa's collection was catalogued in 1919 and *Viviparus sclateri*, labelled with Naga-tanishi, the current Japanese name for *H. longispira*, which was, at the time, equivalent to *Viviparus sclateri*, was listed in this catalogue. The catalogue noted localities of *Viviparus sclateri* (Naga-tanishi) from outside Lake Biwa, including occurrences in Lake Kasumigaura and Lake Suwa. However, *Heterogen longispira* (Naga-tanishi) is currently considered to be endemic to Lake Biwa drainage. The actual status of *Viviparus sclateri* in Iwakawa (1919) has not been clarified until now.

New information

Our examination revealed that *Viviparus sclateri* from Iwakawa's catalogue included *H. japonica*, *H. longispira* and *Sinotaia quadrata histricea*, based on current taxonomy. Specimens assigned to *H. longispira* occurred only in Lake Biwa drainage. *Heterogen japonica* was confirmed to be present in all lots and some *H. japonica* from Lake Suwa had a distinctive morphology. *Sinotaia quadrata histricea* was only confirmed to occur in Lake Suwa. Furthermore, some specimens from southern Lake Biwa and the Seta River had intermediate characteristics between *H. japonica* and *H. longispira* and their populations are currently almost extinct.

Keywords

Ancient lake, endangered species, extinct population, freshwater molluscs, taxonomic history

Introduction

Museum specimens provide valuable insights into the evolutionary and ecological history of living and extinct populations, their taxonomy and knowledge for conservation biology (Suarez and Tsutsui 2004). For example, morphological and molecular data on historical specimens assist in the clarification of the classification and various other biological issues (Wandeler et al. 2007). In this study, we focused on specimens of endangered freshwater molluscs in a collection of Tomotaro Iwakawa from the National Museum of Nature and Science, Tokyo. Tomotaro Iwakawa (1855-1933) was an early contributor to zoology in Japan and he researched freshwater molluscs in Japan with particular attention (Taki 1933). Furthermore, he established one of the earliest systematic malacological lists in Japan (Taki 1933) and specimens of the list were deposited at the National Museum.

Viviparidae Gray, 1847, belonging to Caenogastropoda, is a family of freshwater gastropods with 125–150 valid described species globally and have a wide geographic range in Asia (Hirano et al. 2019b, Van Bocxlaer and Strong 2019, Stelbrink et al. 2020). Historically, Japanese viviparid gastropods have been classified as four species, based primarily on conchological features (Habe 1990, Masuda and Uchiyama 2004): *Cipangopaludina chinensis laeta* (Martens, 1860), *Cipangopaludina japonica* (Martens, 1861), *Heterogen longispira* (Smith, 1886) and *Sinotaia quadrata histricea* (Gould, 1859). Recently, some attributions were modified by Hirano et al. (2019b), namely, *Cipangopaludina japonica* was modified to *Heterogen japonica*, based on molecular phylogeny. Furthermore, molecular analyses have led to the recognition of two subspecies of *C. chinensis* in Japan: *C. c. laeta* and *C. c. chinensis* and the existence of an undescribed species of *Heterogen* sp was also suggested (Hirano et al. 2019a, Hirano et al. 2019b). Thus, based on all the above-mentioned work on Japanese Viviparidae, we consider six viviparid species/subspecies to exist in Japan. Of these six species/subspecies, *H. longispira* is listed on the IUCN Red List as EN (Köhler and Rintelen 2011).

Furthermore, *C. chinensis* is listed on the IUCN Red List as LC, although the subspecies is not designated (Köhler et al. 2012). These two species are also listed on the Red List issued by the Government of Japan as NT and VU, respectively (Ministry of the Environment, Government of Japan 2019). Furthermore, although *H. japonica* is invasive on some Continents (Van Bocxlaer and Strong 2016), it is also listed on the Japanese Red List as NT (Ministry of the Environment, Government of Japan 2019).

The highly-endangered *H. longispira* (Köhler and Rintelen 2011, Nakai 2016, Ministry of the Environment, Government of Japan 2019) is endemic to Lake Biwa drainage (Hirano et al. 2015, Hirano et al. 2019b) which consists of Lake Biwa, a river flowing from Lake Biwa, Lake Yogo (artificially drained from Lake Biwa) and Lake Biwa Canal (Fig. 1). Besides, Lake Biwa has an ancient origin with a remarkable biodiversity (Horie 1971, Yokoyama 1984, Kawanabe 1996, Rossiter 2000, Okuda et al. 2013). Prior to its description, *H. longispira* was included under *Paludina ingallsiana* Lea, 1856 (Kobelt 1879, Iwakawa 1895, Iwakawa 1897a, Iwakawa 1897b). Then, Pilsbry (1902) indicated that *P. ingallsiana* does not occur in Japan and *H. longispira* was included in *Vivipara sclateri* Frauenfeld, 1865. After this, *Vivipara sclateri* (or *Viviparus sclateri*) was adopted as the species name for specimens from Lake Biwa (Hirase 1909, Hirase 1910, Kobelt 1909, Lake Biwa fisheries experimental station 1915, Annandale 1916, Kawamura 1918, Iwakawa 1919). In addition, the name *Vivipara sclateri* was used for viviparid specimens from Japanese localities other than Lake Biwa (Kobelt 1909, Annandale 1916, Iwakawa 1919). Furthermore, Annandale (1921) pointed out the difference between *Vivipara sclateri* by Frauenfeld and the distinctive viviparid gastropods from Lake Biwa (= *H. longispira*), based on comparison with the type illustration of *Vivipara sclateri* and he described specimens from Lake Biwa as *Heterogen turris* Annandale, 1921. However, Smith (1886) had already described the endemic species in Lake Biwa as *Viviparus longispira* Smith, 1886, although this paper was not referred to by other malacologists at that time. Finally, Kuroda (1929) reclassified *Viviparus longispira* as *H. turris* and considered *Viviparus sclateri* to represent a regional subspecies of *H. japonica*, based on the type illustration of *V. sclateri*. Later, *Vivipara sclateri* was generally considered a junior synonym of *H. japonica* (Yagura 1935, Kuroda 1947b, Kuroda 1955, Kuroda 1963). As Annandale (1921) indicated, *H. longispira* is clearly different from typical *Vivipara sclateri*; however, the early malacologists have considered the species to occur in other regions beyond Lake Biwa (Kobelt 1879, Iwakawa 1895, Iwakawa 1897a, Iwakawa 1897b, Iwakawa 1919, Pilsbry 1902, Annandale 1916), although this conclusion remains uncertain. Iwakawa (1919) listed 12 museum lots from 10 localities labelled with 'Naga-tanishi', the current Japanese name for *H. longispira*, which was at the time equivalent to *Viviparus sclateri* and three of the 10 localities are outside Lake Biwa drainage. Although Kuroda (1929) said "these may be elongated *H. japonica*" without any examination, these "*H. longispira*" from areas outside Lake Biwa drainage in Iwakawa (1919) have not been sufficiently examined and have not been illustrated to date. In addition, there were two records of "*H. longispira*" from the southern part of Lake Biwa and the Seta River flowing from Lake Biwa; however, *H. longispira* is now very rare in this area (Nishino 1991, Kihira et al. 2003, Kihira et al. 2009, Nakai 2016). Furthermore, one locality of "*H. longispira*" was drained and is now terrestrial (Ozawa 2012) and the viviparid gastropods from these localities have not been examined. In this study, to clarify the actual

status of “*H. longispira*” (= *Viviparus sclateri*) from areas outside the current distribution and to classify extinct populations, we examined the collection of Tomotaro Iwakawa from the National Museum of Nature and Science, Tokyo.

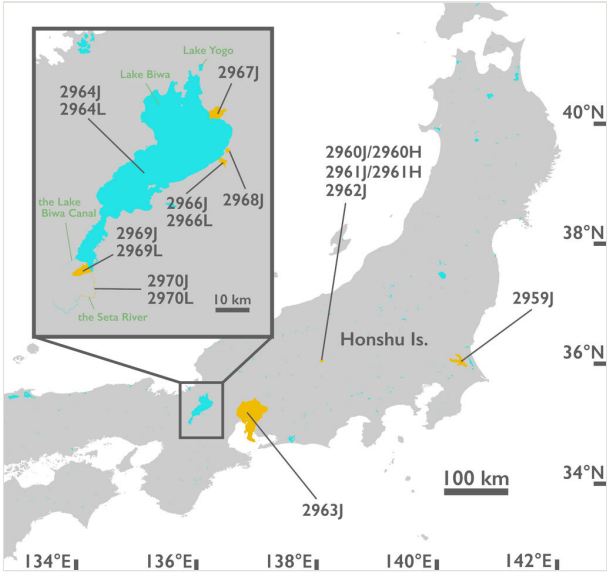


Figure 1. [doi](#)

A map of collected localities of *Viviparus scalateri* in Iwakawa's collection . Yellow parts show the estimated ranges, based on the label of the museum lots. Numbers indicate the sample numbers in this study (see also Table 1). Sample numbers 2964J and 2964L were collected from somewhere in Lake Biwa, but the entire Lake is not coloured to make it easier to see. Green letters and downstream of the Seta River are Lake Biwa drainage as defined in this paper. A map is created from digital national land information (Ministry of Land, Infrastructure and Transport of Japan: <https://nlftp.mlit.go.jp/ksj/index.html>).

Table 1.

List of examined viviparid lots deposited in the National Museum of Nature and Science, Tokyo, which were treated as *Viviparus sclateri* (Frauenfeld, 1865) in Iwakawa 1919. The number in each species/subspecies indicates examined individuals in each sample.

Sample No. in this study	Lot Acc. No. in the museum	Locality	<i>Heterogen japonica</i>	<i>Heterogen longispira</i>	<i>Sinotaia quadrata histrica</i>	Remarks
2959J	NSMT-Mo 2959	Japan, Ibaraki Pref., Lake Kasumigaura	3			Probably one of No. 2950 in Iwakawa (1919).
2960J	NSMT-Mo 2960	Japan, Nagano Pref., Lake Suwa	1			

Sample No. in this study	Lot Acc. No. in the museum	Locality	<i>Heterogen japonica</i>	<i>Heterogen longispira</i>	<i>Sinotaia quadrata histrica</i>	Remarks
2960H	NSMT-Mo 2960	Japan, Nagano Pref., Lake Suwa			1	
2961J	NSMT-Mo 2961	Japan, Nagano Pref., Lake Suwa	27			
2961H	NSMT-Mo 2961	Japan, Nagano Pref., Lake Suwa			5	
2962J	NSMT-Mo 2962	Japan, Nagano Pref., Lake Suwa	6			
2963J	NSMT-Mo 2963	Japan, The western part of Aichi Pref.	1			
2964J	NSMT-Mo 2964	Japan, Shiga Pref., Lake Biwa	1			
2964L	NSMT-Mo 2964	Japan, Shiga Pref., Lake Biwa		1		
2966J	NSMT-Mo 2966	Japan, Shiga Pref., Hikone City, Hikone	1			
2966L	NSMT-Mo 2966	Japan, Shiga Pref., Hikone City, Hikone		2		
2967J	NSMT-Mo 2967	Japan, Shiga Pref., Maibara City, Irie	7			
2968J	NSMT-Mo 2968	Japan, Shiga Pref., Tsukuma Lagoon	15			This locality was drained and converted into terrestrial areas
2969J	NSMT-Mo 2969	Japan, Shiga Pref., Otsu City, Zeze	4			
2969L	NSMT-Mo 2969	Japan, Shiga Pref., Otsu City, Zeze		6		<i>H. longispira</i> are almost extinct in this locality
2970J	NSMT-Mo 2970	Japan, Shiga Pref., the Seta River	2			
2970L	NSMT-Mo 2970	Japan, Shiga Pref., the Seta River		15		<i>H. longispira</i> are almost extinct in this locality

Materials and methods

All samples were from the mollusc collection of the National Museum of Nature and Science, Tokyo (NSMT-Mo). Specimens and labels were photographed using a digital single-lens reflex camera with a macro lens. Specimens were compared and identified by T. Saito based on mainly the references included in the full list of each species/subspecies synonymy (Suppl. material 1). In particular, the original descriptions of Japanese viviparid species and following references provided principal criteria for comparison and identification: Annandale (1921), Okada and Kurasawa 1950, Habe 1973, Masuda and Uchiyama (2004), Kihira et al. (2009), Hirano et al. (2015), Hirano et al. (2019a) and Hirano et al. (2019b). In addition, some specimens seemed to have an intermediate morphology and were tentatively identified to the species with which they are morphologically most similar.

The synonymy sections in the following text list only the first references for each combination of generic and specific names. As there are many references to Japanese viviparid species, it was impossible to list them all and also to establish objective quantitative criteria for selection. However, all references having the specific names, *sclateri* and *ingallsiana* from Japan were listed in the synonymy because of the main focus of this paper. To enhance reproducibility, we provide all the references that we examined in the synonymy list of Suppl. material 1.

Shell width (SW) of each specimen was measured using a Vernier micrometer (instrumental error: ± 0.03 mm). Furthermore, to compare quantitatively the shell shape of *Heterogen* species in Iwakawa's collection, we conducted elliptic Fourier (EF) analysis (Kuhl and Giardina 1982). The analysis was performed by Momocs 1.2.9 (Bonhomme et al. 2014) under R. 3.5.1 (R Core Team 2018). The EF coefficients were obtained from the images of 83 adult specimens in Iwakawa's collection and ten specimens figured in the published references (Frauenfeld 1865, Pilsbry 1902, Kobelt 1909, Annandale 1921). In addition, 143 images of *Heterogen* spp. studied by Hirano et al. (2019b) were also provided by these authors for analysis. The images were binarised before tracing shell outlines and the subsequent geometric normalisation was performed with Momocs. The number of harmonics was set to 40. Then, to summarise the results, a principal component analysis (PCA) was conducted using the obtained EF coefficients. Finally, the results of PCA and SW were graphed using Momocs and ggplot2 (Wickham 2016).

Data resources

Eleven out of 12 lots listed in Iwakawa (1919) were preserved in the National Museum and each lot contained several specimens (Fig. 1 and Table 1). No. 2965 from Kaizu, Omi [Kaizu, Takashima City, Shiga Pref.] in Iwakawa's catalogue (Iwakawa 1919) was not found in this investigation. To avoid confusion, we separated lots that contained several species/subspecies to species/subspecies-specific lots with modified sample numbers (Table 1). In general, a record No. in the Iwakawa catalogue (Iwakawa 1919) and the museum's registration No. (NSMT-Mo) match. There were two different records having the same

catalogue No. 2950 in Iwakawa's catalogue (Iwakawa 1919): one record was *Viviparus japonicus iwakawa* Pilsbry, 1902 from Nagahama, Iwashiro [Nagahama, Inawashiro City, Fukushima Pref.] and the other was *Viviparus sclateri* from Kasumigaura, Hitachi [Lake Kasumigaura, Ibaraki Pref.]. In addition, no record of No. 2959 existed in the catalogue. In the NSMT collection, there are NSMT-Mo 2950 without location data and NSMT-Mo 2959 from Kasumigaura instead of two 2950 records. Despite the lack of location data, the NSMT-Mo 2950 lot includes morphological *iwakawa* specimens, which are considered *Viviparus japonicus iwakawa* having No. 2950 from Nagahama, Iwashiro. Moreover, the NSMT-Mo 2959 lot was labelled with *Viviparus sclateri* and its collected locality was Kasumigaura. Accordingly, we presumed NSMT-Mo 2959 from Kasumigaura as one 2950 record, *Viviparus sclateri* from Kasumigaura, in Iwakawa's catalogue (Iwakawa 1919). Finally, all specimens information was deposited in the GBIF as an occurrence dataset (<https://doi.org/10.15468/mm7yye>).

Taxon treatments

Heterogen japonica (Martens, 1861)

Nomenclature

Synonyms:

- *Paludina japonica* von Martens 1861 : 44. Type locality: Japan. (original description).
- *Vivipara sclateri* Frauenfeld 1865: 531, pl. 22, unnumbered figs. Type locality: Japan. (original description); Pilsbry 1895: 158; Kobelt 1909: 102, pl. 16, figs. 3–6, 8 [part; pl. 16, fig. 9 and pl. 17, figs. 3 and 5 seemingly have the intermediate morphology between *H. japonica* and *H. longispira*, see discussion]; Annandale 1921: 46 [part].
- *Paludina ingallsiana* — Kobelt 1879: 124, pl. 10, fig. 14 [part; pl. 10, figs. 15–16 and 18 seemingly have intermediate morphology between *H. japonica* and *H. longispira*, see discussion]; Iwakawa 1895: 412, pl. 19, figs. 8–9 [part]; Iwakawa 1897a: 86, pl. 5, fig. 7 [part] (Japanese viviparid catalogue); Iwakawa 1897b: 5.
- *Paludina oxytropis* — Kobelt 1879: 123, pl. 11, fig. 6.
- *Paludina sclateri* — Kobelt 1879: 121, pl. 11, fig. 3; Tanba et al. 1883: 368; Tanba et al. 1891: 216; Iwakawa 1895: 357, pl. 19, fig. 2; Kitahara 1895: 89.
- *Paludina oxytropis* var. *japonica* — Iwakawa 1897a: 88, pl. 5, figs. 15 and 17 [Iwakawa noted that fig. 15 was an intermediate form between *P. oxytropis oxytropis* and *P. o. japonica*]; Iwakawa 1897b: 9, pl. 2, fig. 13.
- *Paludina oxytropis* var. *sclateri* — Iwakawa 1897a: 89, pl. 5, figs. 13–14 and 16 [Iwakawa noted that figs. 13 and 16 were an intermediate form between *P. oxytropis oxytropis* and *P. o. sclateri*]; Iwakawa 1897b: 9, pl. 2, figs. 7–9 and 11.
- *Vivipara oxytropis* — Pilsbry 1895: 158.
- *Viviparus japonicus* — Pilsbry 1902: 117, pl. 9, fig. 1.

- *Viviparus japonicus* var. *iwakawa* Pilsbry 1902: pl. 9, fig. 3. Type locality: Furukawa, Rikuzen [Furukawa City, Miyagi Pref., Japan]. (original description).
- *Viviparus sclateri* — Pilsbry 1902: 118 [part]; Iwakawa 1919: 72 [part].
- *Vivipara japonica* — Kobelt 1909: 99, pl. 15, figs. 1–4.
- *Vivipara japonica* var. *iwakawa* — Kobelt 1909: 100, pl. 15, figs. 5–7.
- *Idiopoma (Idiopoma) japonica* — Hannibal 1912: 194.
- *Viviparus japonicus iwakawa* — Iwakawa 1919: 71–72.
- *Viviparus japonicus* — Kanamaru 1920: 4, pl. 2, fig. 85. [sic].
- *Lecythoconcha japonica* — Annandale 1921: 401.
- *Lecythoconcha sclateri* — Annandale 1921: 401, fig.3; Annandale 1922: 133.
- *Viviparus (Idiopoma) japonicus* — Hirase 1927: 1380, fig. 2653.
- *Viviparus (Idiopoma) japonicus iwakawa* — Hirase 1927: 1381, fig. 2654.
- *Vivipara japonica* var. *iwakawae* — Prashad 1928: 173, pl. 19, fig. 12. [sic].
- *Viviparus (Cipangopaludina) japonicus* — Prashad 1928: 172.
- *Viviparus (Dactylochlamys) iwakawae* — Prashad 1928: 173, pl. 19, fig. 12. [sic].
- *Viviparus (Viviparus) sclateri* — Prashad 1928: 172, pl. 19, fig. 5 [part?].
- *Viviparus (Cipangopaludina) japonicus iwakawa* — Kuroda 1929: 102.
- *Viviparus (Cipangopaludina) japonicus sclateri* — Kuroda 1929: 102; Yagura 1932: 28.
- *Viviparus oxytropis* — Taki 1933 in Horikoshi and Itabashi 1994: 20.
- *Viviparus iwakawai* — Taki 1946: 202, fig. 8 [sic].
- *Cipangopaludina japonica* — Hirase and Kuroda 1947c: 1161, fig. 3304; Kuroda 1947b: 3.
- *Cipangopaludina japonica iwakawa* — Hirase and Kuroda 1947a: 1162, fig. 3305.
- *Cipangopaludina (Ussuriensis?) japonica* — Habe 1990: 4.
- *Heterogen japonica* — Hirano et al. 2019b: 5033, figs. 1, 4–5 and 8.

Materials

- scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Ibaraki; locality: Lake Kasumigaura; verbatimLocality: Kasumigaura (in Japanese) [Lake Kasumigaura]; year: before 1919; individualCount: 3; lifeStage: adults; preparations: shell (dried); catalogNumber: 2959J ex.NSMT-Mo 2959; occurrenceDetails: <https://www.gbif.org/occurrence/2864965303>; occurrenceRemarks: NMST-Mo 2959 from Kasumigaura was presumed as one record of 2950, *Viviparus sclateri* from Kasumigaura in Iwakawa's catalogue (1919) (see data resources).; recordNumber: Probably 2950 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2959J

- b. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Nagano; locality: Lake Suwa; verbatimLocality: Suwako (in Japanese) [Lake Suwa]; year: before 1919; individualCount: 1; lifeStage: adult; preparations: shell (dried); catalogNumber: 2960J ex.NSMT-Mo 2960; occurrenceDetails: <https://www.gbif.org/occurrence/2864965315>; recordNumber: 2960 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2960J
- c. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Nagano; locality: Lake Suwa; verbatimLocality: Suwako (in Japanese) [Lake Suwa]; year: before 1919; individualCount: 27; preparations: shell (dried); catalogNumber: 2961J ex.NSMT-Mo 2961; occurrenceDetails: <https://www.gbif.org/occurrence/2864965316>; recordNumber: 2961 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2961J
- d. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Nagano; locality: Lake Suwa; verbatimLocality: Tenryu-gawa-no-suigen (in Japanese) [The water source of Tenryu River = Lake Suwa]; year: before 1919; individualCount: 6; lifeStage: adult; preparations: shell (dried); catalogNumber: 2962J ex.NSMT-Mo 2962; occurrenceDetails: <https://www.gbif.org/occurrence/2864965304>; recordNumber: 2962 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2962J
- e. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Aichi; locality: western part of Aichi Prefecture; verbatimLocality: Owari (in Japanese) [Old name of western part of Aichi Prefecture]; year: before 1919; individualCount: 1; lifeStage: adult; preparations: shell (dried); catalogNumber: 2963J ex.NSMT-Mo 2963; occurrenceDetails: <https://www.gbif.org/occurrence/2864965307>; recordNumber: 2963 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the

- Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2963J
- f. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Lakw Biwa; verbatimLocality: Biwa-ko (in Japanese) [Lake Biwa]; year: before 1919; individualCount: 1; lifeStage: adult; preparations: shell (dried); catalogNumber: 2964J ex.NSMT-Mo 2964; occurrenceDetails: <https://www.gbif.org/occurrence/2864965302>; recordNumber: 2964 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2964J
- g. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Hikone, Hikone City; verbatimLocality: Hikone (in Japanese) [Hikone, Hikone City]; year: before 1919; individualCount: 1; lifeStage: adult; preparations: shell (dried); catalogNumber: 2966J ex.NSMT-Mo 2966; occurrenceDetails: <https://www.gbif.org/occurrence/2864965311>; recordNumber: 2966 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2966J
- h. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Maibara City, Irie; verbatimLocality: Irie-mura (in Japanese) [Irie Village, old name of Irie, Maibara City]; year: before 1919; individualCount: 7; lifeStage: adults; preparations: shell (dried); catalogNumber: 2967J ex.NSMT-Mo 2967; occurrenceDetails: <https://www.gbif.org/occurrence/2864965312>; recordNumber: 2967 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2967J
- i. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country:

- Japan; stateProvince: Shiga; locality: Tsukuma Ragoon; verbatimLocality: Tsukuma-uchiko (in Japanese) [Tsukuma Ragoon]; year: before 1919; individualCount: 15; lifeStage: 13 adults 2 young; preparations: shell (dried); catalogNumber: 2968J ex.NSMT-Mo 2968; occurrenceDetails: <https://www.gbif.org/occurrence/2864965309>; recordNumber: 2968 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2968J
- j. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Ohtsu City, Zeze; verbatimLocality: Zeze (in Japanese) [Zeze, Ohtsu City]; year: before 1919; individualCount: 4; lifeStage: 3 adults 1 young; preparations: shell (dried); catalogNumber: 2969J ex.NSMT-Mo 2969; occurrenceDetails: <https://www.gbif.org/occurrence/2864965310>; recordNumber: 2969 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; identificationRemarks: Some specimens seemingly have the intermediate morphology between *H. japonica* and *H. longispira* (see taxon discussion section); language: japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2969J
- k. scientificName: *Heterogen japonica* (Martens, 1860); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Oh-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: theSeta River; verbatimLocality: Seta-gawa (in Japanese) [the Seta River]; year: before 1919; individualCount: 2; lifeStage: 2 juveniles; preparations: shell (dried); catalogNumber: 2970J ex.NSMT-Mo 2970; occurrenceDetails: <https://www.gbif.org/occurrence/2864965317>; recordNumber: 2970 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; identificationRemarks: Some specimens seemingly have the intermediate morphology between *H. japonica* and *H. longispira* (see taxon discussion section); language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the Tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2970J

Diagnosis

Adult shell large and thick; shell shape subconical to pyramidal. Adult shell colour dark brown or brown or dark olive, often covered with many environmental attachments, such as alga; shell surface glossy, sometimes having weak hollows, growth lines and

spiral striae. Suture moderately deep. Young shell small, relatively thin and fragile; shell shape pyramidal. Young shell colour yellowish-olive; shell surface quite glossy with no spiral ridges on the upper part of the spire.

Taxon discussion

Heterogen japonica can be distinguished from other Japanese Viviparidae by the following criteria which are based on the illustrations and information from literature (Suppl. material 1).

H. japonica can basically be distinguished from *Cipangopaludina chinensis laeta* by its subconical to pyramidal shell shape (Kihira et al. 2009; Fig. 2). In addition, the spire is higher, the spire angle is narrower and the shell apex is more pointed than those of *C. c. laeta*. Furthermore, *C. c. laeta* often has a lipped aperture, but the aperture of *H. japonica* does not have a pronounced lip (Masuda and Uchiyama 2004). Next, the differences with *C. chinensis chinensis* are not fully revealed, as the shell morphology of *C. c. chinensis* in Japan was not examined in depth. Nevertheless, based on the analysis and illustration of Hirano et al. (2019a), the only study that explicitly examined Japanese *C. c. chinensis*, the shell shape of *C. c. chinensis* is similar to that of *C. c. laeta* except for the pointed shell apex of *C. c. chinensis*. In any case, *C. c. chinensis* is distributed only around Kyushu Island, the south-western part of Japan (Hirano et al. 2019a) and no specimens of this subspecies were included in our study.

Adult *Sinotaia quadrata histrica* is generally smaller than *H. japonica*. There is a high morphological diversity in the shell shape of *S. q. histrica* (Kihira et al. 2009); however, the body whorl and the spire whorl are more rounded and arched than that of *H. japonica*. In addition, the shell apex of *S. q. histrica* is more rounded and the aperture is relatively smaller than those of specimens of *H. japonica* having the similar shell shape, as the spire is dense. Moreover, the shell colour of *S. q. histrica* seems to be brighter than that in *H. japonica* and often has a yellowish colour.

H. japonica differs in shell shape from *H. longispira* (Hirano et al. 2019b). Quantitatively, *H. japonica* has a lower spire and a broader spiral angle than *H. longispira* (Kihira et al. 2009). In addition, *H. longispira* has a strong basal angulation even on the adult shell (Okada and Kurasawa 1950). Furthermore, the body whorl and the spire whorl of *H. longispira* are linear (like vertical) in lateral view and the upper periphery of the whorls turns sharply to nearly horizontal. Accordingly, the suture is quite deep and whorls have a strong shoulder just below the suture. This feature is extremely pronounced in juveniles and young shells and this morphological difference is diagnostic between two species (Okada and Kurasawa 1950, Hirano et al. 2019b). In addition, a difference that rarely appears in the shell shape is the distinct spiral ridges on the upper whorl of adult *H. longispira* (Hirano et al. 2019b). The early whorl of adult *H. japonica* does not have such spiral ridges. Moreover, *Heterogen* sp. has weak spiral ridges on the upper whorls and so this is a distinguishing feature from *Heterogen* sp., which is not distinguished by the shell shape (Hirano et al. 2019b). The spiral ridges of *H. longispira* are also pronounced on the body whorl of the adult shell. Furthermore,

some *H. japonica* usually has greenish shells without reddish colour (e.g. Fig. 2h), whereas the shell colour of most *H. longispira* contains reddish colour and accordingly are often brown or dark brown in colour.

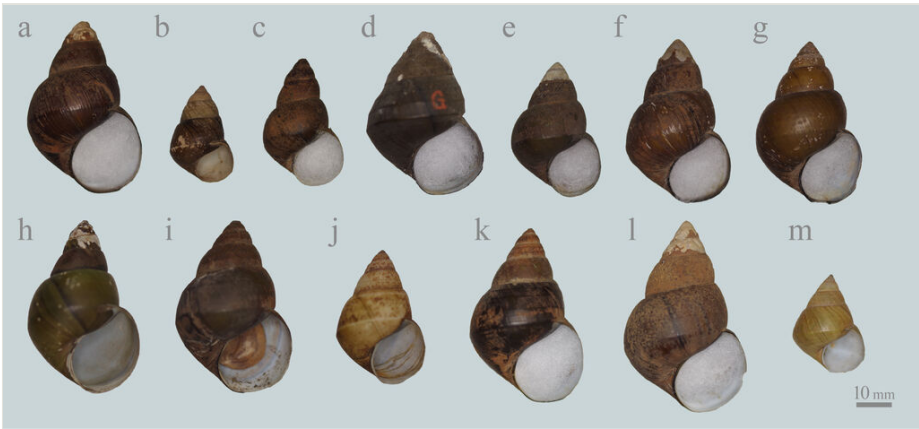


Figure 2. [doi](#)

Representative shells of *Heterogen japonica* (Martens, 1861) from Japan, deposited in the collection of the National Museum of Nature and Science, Tokyo, which were treated as *Viviparus sclateri* (Frauenfeld, 1865) in Iwakawa (1919). **a**: 2959J from Lake Kasumigaura, Ibaraki Pref. **b-g**: specimens from Lake Suwa, Nagano Pref. (**b**: 2960J, **c-e**: 2961J, **f-g**: 2962J). **h**: 2963J from the western part of Aichi Pref. **i**: 2964J from Lake Biwa, Shiga Pref. **j**: 2966J from Hikone City, Shiga Pref. **k**: 2967J from Maibara City, Shiga Pref. **l-m**: 2968J from Tsukuma Lagoon, Shiga Pref. (**l**: adult, **m**: young).

Besides, *H. japonica* has one morphotype, ver. *iwakawa*, which had been described and synonymised. This morphotype has a pyramidal shell shape, a broad spire angle and a strong basal angulation (e.g. Fig. 2d). Typical specimens of *Viviparus japonicus* var. *iwakawa* (Pilsbry 1902) is very easy to distinguish from any other Japanese Viviparidae; however, the morphology is continuous with *H. japonica* (Okada and Kurasawa 1950).

Notes

Heterogen japonica was identified in all 11 studied lots (Figs 2, 3). Some specimens (Fig. 2b-c, h and l) have the high spire and the narrow spire angle and the shell shapes of these specimens are relatively similar to *H. longispira*. However, specimens assigned to *H. japonica* lack a lot of the distinctive features of *H. longispira*. Lots Mo2969 and Mo2970 contained specimens with an intermediate morphology between *H. japonica* and *H. longispira* (e.g. Fig. 3c and g-h). Therefore, in this study, we treated only specimens that were clearly distinguished from *H. longispira* (e.g. Fig. 3a-b and l) as *H. japonica*.

Based on the previous taxonomy (Habe 1973), synonymy included species-group name, *iwakawa* (and its mandatory changes in spelling and incorrect subsequent

spellings) in addition to species-group name, *japonica* (and its mandatory changes in spelling and incorrect subsequent spellings). Furthermore, since *Paludina oxytropis* in Kobelt (1879) and *Vivipara oxytropis* in Pilsbry (1895) were later synonymised by the authors themselves (Kobelt 1909, Pilsbry 1902), these were also listed in synonymy. As to the species-group names *ingallsiana* and *sclateri*, we refer to the discussion.

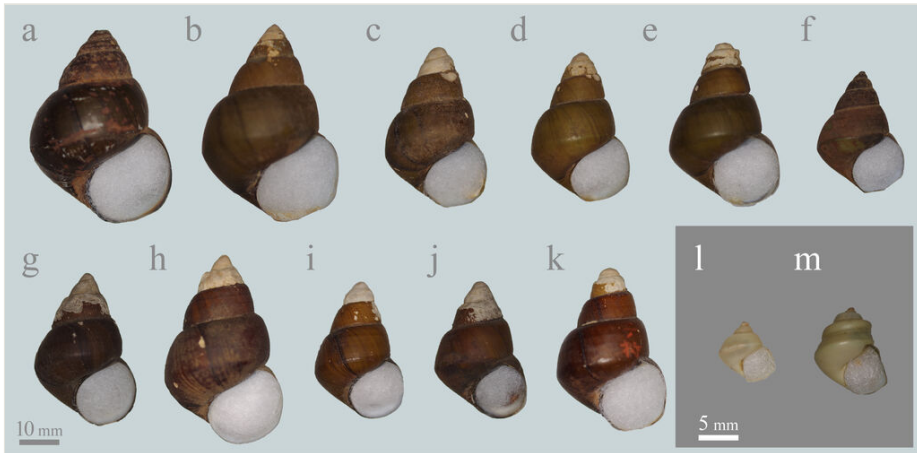


Figure 3. [doi](#)

Shells of *Heterogen japonica* (Martens, 1861), *H. longispira* (Smith, 1886), and the intermediate morphology between the two species stored at the National Museum of Nature and Science, Tokyo, which were treated as *Viviparus sclateri* (Frauenfeld, 1865) in Iwakawa's catalogue (1919). **a-b**: *H. japonica* in 2969J from Otsu City, Shiga Pref. **c-d**: non-typical *H. longispira* in 2969L from Otsu City, Shiga Pref. **e**: typical *H. longispira* in 2969L from Otsu City, Shiga Pref. **f**: subadult *H. japonica* in 2969J from Otsu City, Shiga Pref. **g-j**: non-typical and intermediate *H. longispira* in 2970L from the Seta River, Shiga Pref. **k**: typical *H. longispira* in 2970L from the Seta River, Shiga Pref. **l**: a juvenile shell of *H. japonica* in 2970J from the Seta River, Shiga Pref. **m**: a typical juvenile shell of *H. longispira* in 2970L from the Seta River, Shiga Pref.

Heterogen longispira (Smith, 1886)

Nomenclature

Synonyms:

- *Paludina ingallsiana* — Kobelt 1879: 124, pl. 10, figs. 15–18, pl. 11, fig. 2 [part; pl. 10, figs. 15–16 and 18 seemingly have the intermediate morphology between *H. japonica* and *H. longispira*, see discussion]; Tanba et al. 1883: 368; Iwakawa 1895: 412 [part]; Iwakawa 1897a: 86 [part]; Iwakawa 1897b: 5 [part].
- *Paludina longispira* Smith 1886: 57–58. Type locality: Lake Biwa. (original description).

- *Viviparus sclateri* — Pilsbry 1902: 118, pl.9, fig. 4 [part; see discussion]; Hirase 1909: 45 [part?]; Hirase 1910: 15 [part?]; Lake Biwa fisheries experimental station 1915: 30, fig. 13; Iwakawa 1919: 72 [part].
- *Vivipara sclateri* — Kobelt 1909: 102, pl. 16, figs. 7, 9, pl. 17, figs. 1–5. [part; pl. 16, fig. 9 and pl. 17, figs. 3, 5 seemingly have the intermediate morphology between *H. japonica* and *H. longispira*, see discussion]; Annandale 1916: 46 [part]; Kawamura 1918: 358, fig. 441 [part?].
- *Heterogen turris* Annandale 1921: 400, figs. 1–2. Type locality: Lake Biwa. (original description).
- *Viviparus (Heterogen) turris* — Hirase 1927: 1381, fig. 2655.
- *Viviparus (Heterogen) longispira* — Prashad 1928: 172, pl. 19, fig. 7.
- *Heterogen longispira* — Kuroda 1947b: 3.
- *Viviparus (Heterogen) turis* — Okada and Kurasawa 1950: 153, figs. 10–11, and 14, (in text), pl. 2, figs. 7–8, pl. 3, figs. 9–10, pl. 4, figs. a"–g". [sic].
- *Viviparus longispira* — Hirase and Taki 1951: pl. 77, fig. 10.
- *Cipangopaludina (Heterogen) longispira* — Kuroda and Habe 1965a: 48, fig. 151.

Materials

- a. scientificName: *Heterogen longispira* (Smith, 1886); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Naga-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Lake Biwa; verbatimLocality: Biwa-ko (in Japanese) [Lake Biwa]; year: before 1919; individualCount: 1; lifeStage: adult; preparations: shell (dried); catalogNumber: 2964L ex.NSMT-Mo 2964; occurrenceDetails: <https://www.gbif.org/occurrence/2864965305>; recordNumber: 2964 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2964L
- b. scientificName: *Heterogen longispira* (Smith, 1886); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Naga-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Hikone, Hikone City; verbatimLocality: Hikone (in Japanese) [Hikone, Hikone City]; year: before 1919; individualCount: 2; lifeStage: 1adult 1 young; preparations: shell (dried); catalogNumber: 2966L ex.NSMT-Mo 2966; occurrenceDetails: <https://www.gbif.org/occurrence/2864965303>; recordNumber: 2966 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2966L

- c. scientificName: *Heterogen longispira* (Smith, 1886); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Naga-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Zeze, Ohtsu City; verbatimLocality: Zeze (in Japanese) [Zeze, Ohtsu City]; year: before 1919; individualCount: 6; lifeStage: adults; preparations: shell (dried); catalogNumber: 2969L ex.NSMT-Mo 2969; occurrenceDetails: <https://www.gbif.org/occurrence/2864965313>; recordNumber: 2969 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; identificationRemarks: Some specimens are presumed to be hybrid species between *H. longispira* and *H. japonica* (see taxon discussion section).; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2969L
- d. scientificName: *Heterogen longispira* (Smith, 1886); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Naga-tanishi (in Japanese name); country: Japan; stateProvince: Shiga; locality: Seta River; verbatimLocality: Seta-gawa (in Japanese) [the Seta River]; year: before 1919; individualCount: 15; lifeStage: 11 adults 4 juveniles; preparations: shell (dried); catalogNumber: 2970L ex.NSMT-Mo 2970; occurrenceDetails: <https://www.gbif.org/occurrence/2864965314>; recordNumber: 2970 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; identificationRemarks: Some specimens are presumed to be hybrid species between *H. longispira* and *H. japonica* (see taxon discussion section).; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2970L

Diagnosis

Adult shell moderately large and very thick; shell shape subconical. Adult shell dark brown or greenish-brown sometimes covered with attachments; shell surface often having growth lines and several spiral ridges. Suture deeper than in any other viviparid from Japan; whorls strongly shouldered. Young shell small and relatively thin, but not fragile; shell shape pyramidal to subconical. Young shell bright olive; shell surface quite glossy having strong spiral ridges on upper part of spire. The shell size upon birth is larger than that of any other viviparid gastropod in Japan.

Taxon discussion

Heterogen longispira can be distinguished from other Japanese Viviparidae by criteria based on the illustrations and information from literature (Suppl. material 1). In particular, the juvenile and young shell have strong spiral ridges on the upper part of each whorl, this feature having crucial diagnostic value (Okada and Kurasawa 1950,

Hirano et al. 2019b). Furthermore, the shell size of the juvenile upon birth is larger than that of any other viviparid gastropods in Japan.

Firstly, *H. longispira* is easily distinguished from *Cipangopaludina* species/subspecies in Japan, based on the pyramidal shell shape, the higher spire, the narrower spire angle and the linear body whorl (Kihira et al. 2009; Fig. 4).

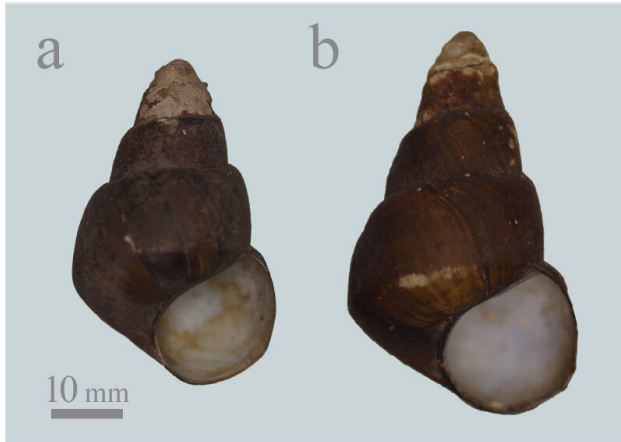


Figure 4. [doi](#)

Representative shells of *Heterogen longispira* (Smith, 1886) from Japan, deposited in the collection of the National Museum of Nature and Science, Tokyo, which were treated as *Viviparus sclateri* (Frauenfeld, 1865) in Iwakawa (1919). **a:** 2964L from Lake Biwa, Shiga Pref. **b:** 2966L from Hikone City, Shiga Pref.

Besides, adult *Sinotaia quadrata histricea* is generally smaller than *H. longispira*. There is a high morphological diversity in the shell shape of *S. q. histricea* (Kihira et al. 2009); however, the body whorl and the spire whorl are much more rounded and arched than those of *H. longispira*. In addition, the suture of *S. q. histricea* is shallower than that of *H. longispira*. The upper whorl of adult *S. q. histricea* does not have the pronounced spiral ridges. Moreover, the shell colour of *S. q. histricea* is brighter than that in *H. longispira* and often has a yellowish colour.

Both adult *H. longispira* and *Heterogen* sp. have the spiral ridges on the upper whorl (Hirano et al. 2019b), but the ridges of *H. longispira* are stronger than *Heterogen* sp. In addition, the shell shape of *Heterogen* sp. is indistinguishable from that of *H. japonica* and then there are some differences in the shell shape between *H. longispira* and *Heterogen* sp. (Hirano et al. 2019b; refer to taxon discussion on the section of *H. japonica* for the difference).

Notes

Heterogen longispira was identified in four of the 11 lots examined, which were all from Lake Biwa drainage only (Figs 3, 4). Lots Mo2969 and Mo2970 contained non-typical

H. longispira with an intermediate morphology to *H. japonica* and *H. longispira* (e.g. Fig. 3c and g-k). The shell shapes of these specimens tend to be slightly more similar to *H. japonica*; however, they have several distinctive morphological features of *H. longispira*, namely, the pronounced spiral ridges, the shouldered whorl, the deep suture, the strong basal angle and the high spire. Therefore these specimens were tentatively identified as *H. longispira* here (see also discussion).

Based on the previous taxonomy (Kuroda 1929), synonymy included the species-group name *turris* (and incorrect subsequent spellings) in addition to the species-group name *longispira*. For species-group names *ingallsiana* and *sclateri*, refer to the discussion.

***Sinotaia quadrata histrica* (Gould, 1859)**

Nomenclature

Synonyms:

- *Paludina histrica* Gould 1859: 41. Type locality: Ousima and Loo Choo [Amami-Oshima and the Ryukyu Islands]. (original description).
- [?]*Paludina nitens* Reeve 1863: pl. 10, fig. 59. Type locality: Japan. (original description).
- *Paludina ingallsiana* — Iwakawa 1897a: 86, pl. 5, figs. 5–6 [part]; Iwakawa 1897b: 5, pl. 2, fig. 6 [part].
- *Viviparus histicus* — Pilsbry 1902: pl. 9, fig. 5.
- *Vivipara histrice* — Kobelt 1909: 107, pl. 16, fig. 6.
- [?]*Vivipara nitens* — Kobelt 1909: 107.
- [?]*Vivipara lacustris* — Kawamura 1918: 358.
- *Viviparus quadratus* var. ? *histicus* — Hirase 1927: 1382, fig. 2656.
- *Cipangopaludina histrice* — Kuroda 1928: 32.
- *Viviparus (Viviparus) histicus* — Prashad 1928: 172.
- *Viviparus histicus* — Iwakawa 1919: 72.
- *Viviparus (Sinotaia) histicus* — Hirase and Kuroda 1947b: 1160, fig. 3301.
- *Taia (Sinotaia) histrice* — Kuroda 1947b: 4.
- *Sinotaia histrice* — Kuroda 1948: 26.
- *Viviparus (Idiopoma) histicus* — Okada and Kurasawa 1950: 149, figs. 3–4, 12–14 (in text), pl. 1, figs. 1–2, pl. 3, figs. a'–g'.
- *Sinotaia quadratus histrice* — Kuroda and Habe 1965b: 48, fig. 152.
- *Sinotaia quadrata histrice* — Habe and Kosuge 1967: 27, pl. 11, fig. 8.

Materials

- a. scientificName: *Sinotaia quadrata histrice* (Gould, 1859); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Hime-tanishi (in Japanese name); country: Japan; stateProvince: Nagano; locality: Lake Suwa; verbatimLocality: Suwako (in Japanese) [Lake Suwa]; year: before 1919; individualCount: 1; lifeStage: adult; preparations: shell (dried); catalogNumber: 2960H ex.NSMT-Mo 2960; occurrenceDetails: <https://www.gbif.org/occurrence/2864965306>; recordNumber: 2960 in Iwakawa 1919;

previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2960H

- b. scientificName: *Sinotaia quadrata histrica* (Gould, 1859); kingdom: Animalia; phylum: Mollusca; family: Viviparidae; vernacularName: Hime-tanishi (in Japanese name); country: Japan; stateProvince: Nagano; locality: Lake Suwa; verbatimLocality: Suwako (in Japanese) [Lake Suwa]; year: before 1919; individualCount: 5; lifeStage: adults; preparations: shell (dried); catalogNumber: 2961H ex.NSMT-Mo 2961; occurrenceDetails: <https://www.gbif.org/occurrence/2864965308>; recordNumber: 2961 in Iwakawa 1919; previousIdentifications: *Viviparus sclateri* (Frauenfeld, 1865) in Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; identifiedBy: Takumi Saito; dateIdentified: 2020-02-03/04; language: Japanese; bibliographicCitation: Tomotaro Iwakakawa. 1919. Catalogue of Japanese Mollusca in the Natural history department, Tokyo Imperial Museum, the tokyo Imperial Museum, Tokyo, Japan, p. 72.; institutionCode: NSMT; collectionCode: Mo; basisOfRecord: PreservedSpecimen; occurrenceID: paper:SK2020:2961H

Diagnosis

Adult shell small and thin, but not fragile; shell shape subconical to pyramidal. Adult shell bright brown or yellowish- or reddish-brown often covered with many attachments such as alga; shell surface slightly glossy, weak growth lines and spiral lines are usually present. Suture shallow; spire rounded. Young shell small, very thin and fragile; shell shape pyramidal with rounded angle. Young shell bright olive; shell surface quite glossy with no spiral ridges on upper part of the spire.

Taxon discussion

Sinotaia quadara histrica can be distinguished from other Japanese Viviparidae by the following features, based on the illustrations and information from literature (Suppl. material 1). In particular, the adult shell width tends to be relatively smaller than that of other Japanese Viviparidae (Masuda and Uchiyama 2004; for example, under 24 mm except for one exception in Kagawa et al. (2019)).

Firstly, *S. q. histrica* is easily distinguished from *Cipangopaludina* species/subspecies in Japan, based on the small shell width, pyramidal shell shape and the higher spire (Fig. 5).

The size of *Heterogen* sp. is larger and the apical whorls are also larger than those of *S. q. histrica*. In addition, *Heterogen* sp. has the weak spiral ridges on even the early whorls, whereas *S. q. histrica* does not have them. Diagnostic differences between *S.*

q. histrice vs. *H. japonica* and *H. longispira* have been provided above, so we refer to the taxon discussions of these latter two species.

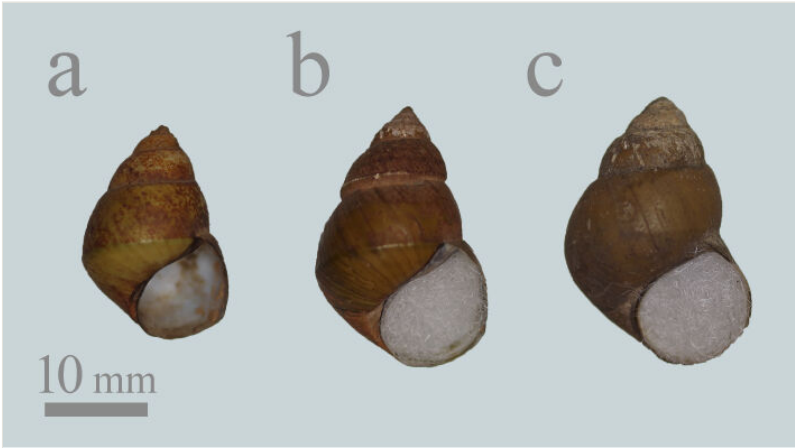


Figure 5. [doi](#)

Representative shells of *Sinotaia quadrata histrice* (Gould, 1859) from Japan, deposited in the collection of the National Museum of Nature and Science, Tokyo, which were treated as *Viviparus sclateri* (Frauenfeld, 1865) in Iwakawa (1919). **a-c**: Lake Suwa, Nagano Pref. (a: 2960H, b-c: 2961H).

Notes

Sinotaia quadrata histrice was identified in two of the 11 lots examined, which were from Lake Suwa (Fig. 5). Some specimens of *H. japonica* from Lake Suwa have a similar shell shape to *S. q. histrice*, but *S. q. histrice* has a more rounded shell apex, a broader spire angle, shallower sutures and a brighter colour than those of *H. japonica*.

We treated only the Japanese *Sinotaia* species for synonymy, as the taxonomic relationship between the continental *Sinotaia* and the Japanese *Sinotaia* species is not clear and not the point of this study. The species-group name, *nitens* was synonymised with a question mark by Pilsbry (1902) and we followed this treatment. *Vivipara lacustris* in Kawamura (1918) was documented as a small species that is distributed in the Kyushu Region. In the past, *S. q. histrice* was considered to be distributed in Kyushu Region (Pilsbry 1902) and so *V. lacustris* in Kawamura 1918 may be a junior synonym of *S. q. histrice*.

Analysis

The principal results of the PCA of EF analysis are shown in Fig. 6 and Fig. 7 (for full results of the PCA and SW, see Suppl. material 2). PC1 and PC2 explained 74.6% of the variance and the first five components explained 86.7% of the variance (PC1: 59.5%; PC2: 15.1%; PC3: 6.3%; PC4: 3.0%; PC5: 2.7%). *Heterogen japonica* and *H. longispira* from

Hirano et al. (2019b) had little overlap in each region and *Heterogen* sp. was fully included in the morphological range of *H. japonica*. Many of the *H. japonica* in Iwakawa's collection identified qualitatively by diagnostic features were within the morphological range of *H. japonica* from Hirano et al. (2019b), but some were located within the range of *H. longisira* from Hirano et al. (2019b) or in parts of the morphospace not covered by either. Some of *H. longisira* in Iwakawa's collection, which were identified qualitatively, were within the morphological range of *H. longisira* from Hirano et al. (2019b), but some were located within the morphological range of *H. japonica* from Hirano et al. (2019b) or in parts of the morphospace not covered by either.

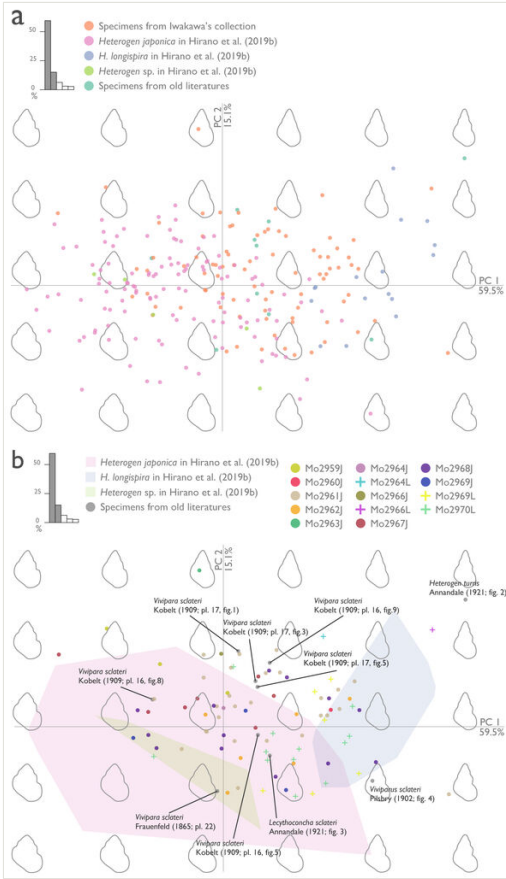


Figure 6. [doi](#)

a: Plots of principal component analysis (PCA) of all analysed specimens. The top left graph shows the proportion of variance of each component. Figures on the background indicate reconstructed shell morphology, based on principal components. **b:** Plots of PCA of Iwakawa's specimens and old literature specimens. The morphospace occupation by specimens from Hirano et al. (2019b) is shown as coloured polygons. The top left graph shows the proportion of variance of each component. Background outlines indicate the reconstructed shell morphology, based on principal components.

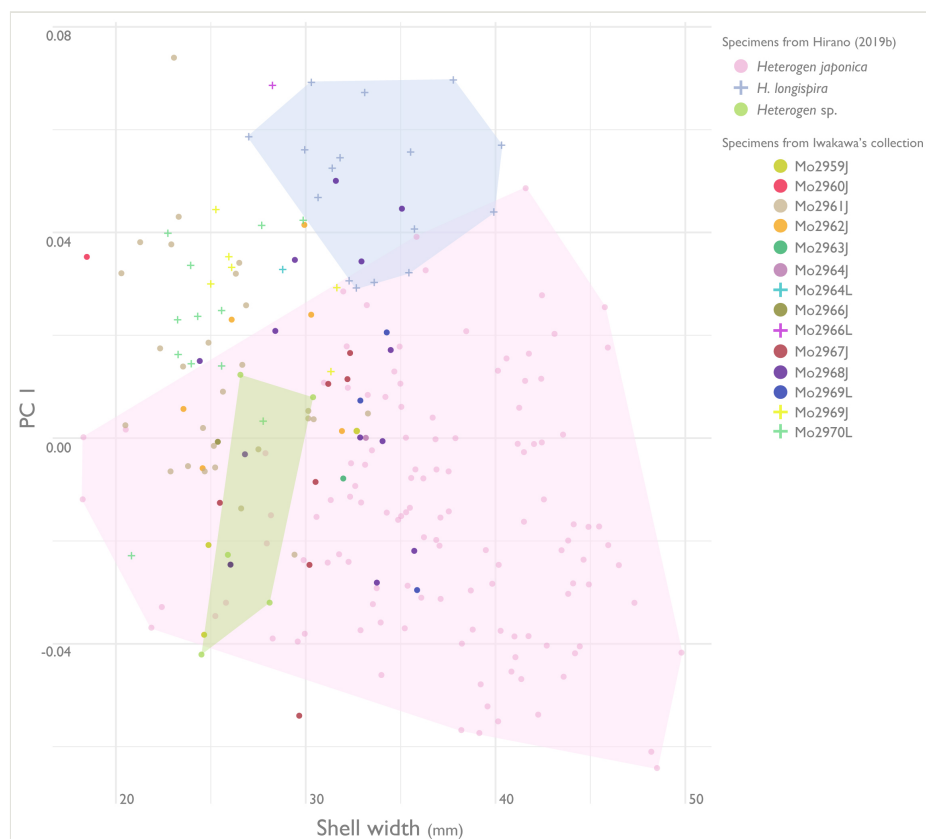


Figure 7. [doi](#)

Plots of principal component axis one versus shell width for specimens from Iwakawa and Hirano et al. (2019b). The morphospace occupation by specimens from Hirano et al. (2019b) is also shown as coloured polygons.

Discussion

All eleven lots in the Iwakawa collection in the NSMT were previously thought to consist of a single species, *Viviparus sclateri* in Iwakawa (1919), but now have been found to consist of at least three species/subspecies, *H. japonica*, *H. longispira* and *Sinotaia quadrata histrica*. *H. japonica* was found in all lots studied during our investigation; *H. longispira* was found amongst four of the lots, which were all from Lake Biwa drainage (Table 1 and Fig. 1). This result reflects the taxonomic understanding of the period, prior to *H. longispira* being recognised as a distinct species (as *H. turris* in Annandale (1921)). Furthermore, all specimens of *Viviparus sclateri* in Iwakawa (1919) from outside of Lake Biwa drainage differed from *H. longispira* (Fig. 2a-h and Fig. 5), because these specimens do not have spiral ridges on the upper part of each spire which is a distinctive character of *H. longispira* (Figs 2, 4; Annandale 1921, Kihira et al. 2003). Nevertheless, almost all of these

specimens seem to have a higher spire and narrower spire angle than *H. japonica* as illustrated and documented in literature (Suppl. material 1; e.g. Figure 2 in Hirano et al. 2015; Figure 1 in Hirano et al. 2019b). The higher spire and the narrower spire angle of the *H. japonica* that was listed as *Viviparus sclateri* in Iwakawa (1919) from outside of Lake Biwa basin are noteworthy. Our morphological analysis showed that some specimens of *Viviparus sclateri* in Iwakawa's collection differ in shell shape from specimens of *H. japonica* in Hirano et al. (2019b), which were collected from the entire native geographic range of the species (Fig. 6). The shell shapes of these specimens seemed to be more elongated (i.e. having the higher spire and the narrower spire angle) and some could not be distinguished from the shell shape of *H. longispira* in Hirano et al. (2019b), based on PC1 and PC2 of the EF analysis. The similarities of the shell shapes shown by the EF analysis may suggest the complexity of the taxonomic relationship between the two species. Nevertheless, most of them had the shallower suture and this seemingly differed from *H. longispira*. Furthermore, most specimens of *H. japonica* in Iwakawa's collection had a smaller shell width than *H. japonica* in Hirano et al. (2019b) (Fig. 7). This characteristic morphology seemed to be particularly abundant in *H. japonica* from Lake Suwa (2960J-2962J; e.g. Fig. 2c). The distinctive (see diagnosis and taxon discussion) shell morphology of *H. longispira* is considered to be a consequence of adaptation to its ancient lake habitat and this evolutionary change in morphology may have originated multiple times, based on examination of fossil specimens (Hirano et al. 2019b). Furthermore, plastic and/or adaptive morphological changes to the environment seem to occur easily both within and amongst species in viviparid gastropods (Hirano et al. 2019b, Kagawa et al. 2019, Stelbrink et al. 2020). Such morphological changes might have occurred in those *H. japonica* that have the elongated shell shape, as two of the three localities from where these specimens were collected are large lakes. In particular, Lake Suwa, where many distinctive specimens were found, was formed around 0.10 Ma (Anma et al. 1990) and *H. japonica* from Lake Suwa in Iwakawa's collection may represent an evolutionary distinct population.

On the other hand, *Sinotaia quadrata histrica* specimens were identified only from Lake Suwa (Fig. 5). These specimens were included in *Viviparus sclateri* of Iwakawa (1919). Fig. 6 of Iwakawa (1897a) and Figs. 5-6 of Iwakawa (1897b) shown as young specimens of *Paludina ingallsiana* may also be *S. q. histrica* from Lake Suwa. The existence of *S. q. histrica* in Lake Suwa might have resulted in further taxonomic confusion. *Sinotaia q. histrica* was considered to be only distributed in the southern part of Japan during that period (Pilsbry 1902, Kuroda 1929). Perhaps, *S. q. histrica* in the Iwakawa's collection may be the oldest record of the species from the eastern part of Japan. Now, *S. q. histrica* is a common viviparid gastropod throughout Japan, except for the Ryukyu Islands (Masuda and Uchiyama 2004). The species was considered to have been introduced after the prehistoric era, based on molecular phylogenetic studies and records of shell middens' records (Kurozumi 2001, Hirano et al. 2015, Kurozumi 2019). In a recent study, further complicated history of colonisation of *S. q. histrica* was estimated by genetic markers and multiple colonisations from the continent at different times were revealed (Ye et al. 2020). The time when population established in the eastern part of Japan was estimated around 7910 years ago in this paper. However, the distribution of *S. q. histrica* has been

considered to have recently expanded to the eastern part of Japan because there were few old records including from shell midden (Matsuoka 2001). Owing to the missing records, the history of the expansion of distribution have not been sufficiently clarified. Our probable oldest record from the eastern part of Japan may have implications for this, although further molecular and bibliographical studies are needed.

All samples from Lake Biwa drainage include *H. japonica*, though some lots contain both *H. japonica* and *H. longispira* (Table 1 and Fig. 1). The historically-documented co-existence of the two species differs from the current distribution of the two viviparid gastropods around Lake Biwa; *H. japonica* is rarely found within Lake Biwa at present (Horie 1971, Hirano et al. 2019b). Previous studies have stated that *H. longispira* is relatively common in the shallow area of southern Lake Biwa (Kuroda 1947a, Oyama and Kajiyama 1959, Kihira and Matsuda 1990). Although there is a possibility that each specimen was collected from several populations (including outside of the lake population), the co-existence of the two species in the same lot may be indicative of the past sympatric distribution of these species in Lake Biwa. Furthermore, some specimens from southern Lake Biwa and the Seta River flowing from Lake Biwa showed an intermediate morphology between *H. japonica* and *H. longispira* (Figs 3, 6; see also notes in taxon treatments of *H. longispira*). Some specimens, especially young and juvenile specimens, are easily assigned to one of the two species, based on the existence of spiral ridges and shell shapes (*H. japonica*: Fig. 3a, f and l; *H. longispira*: Fig. 3e, k and m). However, some specimens are difficult to distinguish. Namely, they have several distinctive morphological features of *H. longispira* (i.e. the pronounced spiral ridges, the shouldered whorls, the deep suture, the strong basal angle and the high spire), but the shell shapes of these specimens tend to be more similar to *H. japonica* (Fig. 6). In particular, many specimens from the Seta River have a distinctive morphology with a linear shape and smaller shell size, which is possibly indicative of a distinctive population (Figs 3, 6, 7). In addition, some specimens illustrated by past malacologists are presumed to be from southern Lake Biwa or the Seta River. For example, pl. 9, fig. 4 in Pilsbry (1902) (= pl. 16, fig. 7 in Kobelt 1909) from near Kyoto resembles specimens from the Seta River (Fig. 3i and j), which flows to Kyoto City, and pl. 10, fig. 18 in Kobelt (1879) (= pl. 16, fig. 9 in Kobelt 1909) looks similar to specimens from southern Lake Biwa (Fig. 3b). In fact, our analysis of literature illustrations and other specimens showed that the shell shapes of these specimens were similar to southern Lake Biwa or the Seta River specimens, whereas the shell shapes of illustrations of *Vivipara sclateri* from the original description were far from the shape of *H. longispira* (Fig. 6b). A molecular study using genome-wide genetic data suggested introgressive hybridisation between the two species and some genetic populations seemingly had been generated by hybridisation (Hirano et al. 2019b). As such, hybridisation may have been the cause of the formation of the populations with an intermediate morphology. To reveal the traits and origin of these unique specimens, we need to examine current specimens carefully and include molecular analyses whenever possible. However, *H. longispira* of southern Lake Biwa and the Seta River are extinct or almost extinct (Nishino 1991, Kihira et al. 2003, Kihira et al. 2009, Nakai 2016). Similarly, populations of *H. japonica* of Lake Kasumigaura and Lake Suwa are critically endangered or extinct (Kurasawa 1988,

Nishiwaki et al. 2008). Examining past specimens in the Museum may be the only way to elucidate the historical distribution of these species.

Acknowledgements

We are grateful to Dr. Kazunori Hasegawa for his assistance of our examination of viviparid specimens. In addition, we thank Dr. Takahiro Hirano for providing the morphological data for analysis. Moreover, we also thank handling editor and five reviewers for valuable suggestions. This research was partly supported by Grant-in-Aid for Japan Society for the Promotion of Science (JSPS) fellows number 19J00392.

Author contributions

T.S. planned and managed this study. T.S. and O.K. examined museum specimens. O.K. photographed all specimens. T.S. identified specimens. T.S. researched taxonomic history of the Japanese viviparid gastropods with major contribution of O.K.. T.S. wrote the manuscript and O.K. commented and approved the final manuscript under discussion.

References

- Anma K, Nagaoka M, Niwa S, Sekimoto K, Yoshikawa M, Fujine H (1990) A geological survey for the study on Neotectonic movement and geoenvironment of Lake Suwa, Nagano Prefecture. *Memoirs of the Geological Society of Japan* 36: 179-194. [In Japanese with English abstract].
- Annandale N (1916) Zoological results of a tour in the Far East. The Mollusca of Lake Biwa, Japan. *Memoirs of the Asiatic Society of Bengal* 6 (1): 39-74.
URL: <https://biodiversitylibrary.org/page/47681217>
- Annandale N (1921) Zoological results of a tour in the Far East. The viviparous water-snail of Lake Biwa, Japan. *Memoirs of the Asiatic Society of Bengal* 6 (7): 397-401.
URL: <https://biodiversitylibrary.org/page/47681678>
- Annandale N (1922) The macroscopic fauna of Lake Biwa. *Annotationes Zoologicae Japonenses* 10: 127-153.
- Bonhomme V, Picq S, Gaucherel C, Claude J (2014) Momocs: Outline analysis using R. *Journal of Statistical Software* 56 (13): 1-24. <https://doi.org/10.18637/jss.v056.i13>
- Frauenfeld GRV (1865) *Zoologische Miscellen. IV. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 15: 259-266.
URL: <https://www.biodiversitylibrary.org/page/16400700>
- Gould AA (1859) Dr. A. A. Gould read the following descriptions of new species of shells. *Proceedings of the Boston Society of Natural History* 7: 40-45.
URL: <https://www.biodiversitylibrary.org/page/9249577>
- Habe T, Kosuge S (1967) A standard illustrated handbook in natural color. III. Mollusca. Hoiku-sya, Osaka, 223 pp. [In Japanese].

- Habe T (1973) Mollusca. In: Ueno M (Ed.) The late Tamiji Kawamura freshwater biology of Japan, enlarged and revised edition. Hokuryu-kan, Tokyo, 309-341 pp. [In Japanese with English title].
- Habe T (1990) The list of Japanese freshwater mollusks: 1. Hitachiobi 54: 3-6. [In Japanese].
- Hannibal H (1912) A synopsis of the recent and tertiary freshwater Mollusca of the Californian province, based upon an ontogenetic classification. Proceedings of the Malacological Society of London 10: 112-211. URL: <https://www.biodiversitylibrary.org/page/15237075>
- Hirano T, Saito T, Chiba S (2015) Phylogeny of freshwater viviparid snails in Japan. Journal of Molluscan Studies 81 (4): 435-441. <https://doi.org/10.1093/mollus/eyv019>
- Hirano T, Saito T, Tsunamoto Y, Koseki J, Ye B, Do VT, Miura O, Suyama Y, Chiba S (2019a) Enigmatic incongruence between mtDNA and nDNA revealed by multi-locus phylogenomic analyses in freshwater snails. Scientific Reports 9 (1). <https://doi.org/10.1038/s41598-019-42682-0>
- Hirano T, Saito T, Tsunamoto Y, Koseki J, Prozorova L, Do VT, Matsuoka K, Nakai K, Suyama Y, Chiba S (2019b) Role of ancient lakes in genetic and phenotypic diversification of freshwater snails. Molecular Ecology 28 (23): 5032-5051. <https://doi.org/10.1111/mec.15272>
- Hirase S (1927) Mollusca. In: Uchida S (Ed.) An illustrated encyclopedia of the fauna of Japan. Hokuryu-kan, Tokyo. [In Japanese].
- Hirase S, Kuroda T (1947a) *Cipangopaludina japonica iwakawa* (Pilsbry). In: Uchida S (Ed.) An illustrated encyclopedia of the fauna of Japan, revised ver. Hokuryu-kan, Tokyo, 1162-1162 pp. [In Japanese].
- Hirase S, Kuroda T (1947b) *Viviparus (Sinotaia) histricus* (Gould). In: Uchida S (Ed.) An illustrated encyclopedia of the fauna of Japan, revised ver. Hokuryu-kan, Tokyo, 1160-1160 pp. [In Japanese].
- Hirase S, Kuroda T (1947c) *Cipangopaludina japonica* (Martens). In: Uchida S (Ed.) An illustrated encyclopedia of the fauna of Japan, revised ver. Hokuryu-kan, Tokyo, 1161-1161 pp. [In Japanese].
- Hirase S, Taki Is (1951) A handbook of illustrated shells in natural colors from Japanese Islands and their adjacent territories. Bunkyo-kaku, Tokyo, 134 pls and 43 pp. [In Japanese with English title].
- Hirase Y (1909) Introduction book of Mollusks. Hirase-kaikan, Kyoto, 112 pp. [In Japanese]. URL: <https://dl.ndl.go.jp/info:ndljp/pid/993608>
- Hirase Y (1910) One thousand kinds of shells existing in Japan. Hirase-kaikan, Kyoto, 48 pp. [In Japanese]. URL: <https://dl.ndl.go.jp/info:ndljp/pid/994074>
- Horie S (1971) Ancient inland waters in the world and Lake biwa as the natural heritage. In: The scientific investigation committee of Lake Biwa Quasi-national park (Ed.) The scientific report of Lake Biwa Quasi-national park. The scientific investigation committee of Lake Biwa Quasi-national Park, Otsu, 491-493 pp. [In Japanese].
- Horikoshi M, Itabashi Y (1994) Republication of "List of molluscs collected from Yokohama and its environs" compiled by the late Dr. Isao Taki in 1933 part 1. Natural History Report of Kanagawa (16): 17-28. URL: http://nh.kanagawa-museum.jp/files/data/pdf/nhr/16/nhr16_017_028horikoshi.pdf

- Iwakawa T (1895) Freshwater mollusks in Japan (2). Zoological Magazine 7 (86): 411-414. [In Japanese]. URL: https://dl.ndl.go.jp/view/download/digidepo_10825080_po_ART0003837109.pdf?contentNo=1&alternativeNo=
- Iwakawa T (1897a) Freshwater mollusks in Japan (2), with plate 2. Zoological Magazine 9 (99): 5-10. [In Japanese]. URL: https://dl.ndl.go.jp/view/download/digidepo_10825396_po_ART0003840054.pdf?contentNo=1&alternativeNo=
- Iwakawa T (1897b) Notes on the *Paludina*-species of Japan. Annotationes Zoologicae Japonenses 1: 83-92. URL: https://dl.ndl.go.jp/view/download/digidepo_10852805_po_ART0003842255.pdf?contentNo=1&alternativeNo=
- Iwakawa T (1919) Catalogue of Japanese Mollusca in the natural history department, Tokyo Imperial Museum. Tokyo Imperial Museum, Tokyo, 375 pp. [In Japanese]. <https://doi.org/10.5962/bhl.title.13147>
- Kagawa O, Saito T, Uchida S, Chiba S (2019) Phenotypic divergence in viviparid snails in a recently converted freshwater lagoon. Plankton and Benthos Research 14 (3): 189-196. <https://doi.org/10.3800/pbr.14.189>
- Kanamaru T (1920) An investigation report of Mollusca in Mie Prefecture. Mie Prefecture, Tsu, 17 pp. [In Japanese].
- Kawamura T (1918) Japanese freshwater biology. I. Shoka-bo, Tokyo, 362 pp. [In Japanese]. <https://doi.org/10.11501/956620>
- Kawanabe H (1996) Asian great lakes, especially Lake Biwa. Environmental Biology of Fishes 47 (3): 219-234. <https://doi.org/10.1007/bf00000495>
- Kihira H, Matsuda M (1990) Freshwater mollusks in Lake Biwa and the Yodo River. Tataru-syobo, Hirakata, 131 pp. [In Japanese].
- Kihira H, Matsuda M, Uchiyama R (2003) Freshwater Molluscs of Japan 1: Freshwater Molluscs of Lake Biwa and the Yodo River. Pisces, Tokyo, 159 pp. [In Japanese].
- Kihira H, Matsuda M, Uchiyama R (2009) Freshwater Molluscs of Japan 1: Freshwater Molluscs of Lake Biwa and the Yodo River, revised ver. Pisces, Tokyo, 159 pp. [In Japanese].
- Kitahara T (1895) Animals in Lake Kasumigaura. Zoological Magazine 7 (77): 87-90. [In Japanese]. URL: https://dl.ndl.go.jp/view/download/digidepo_10824909_po_ART0003801509.pdf?contentNo=1&alternativeNo=
- Kobelt W (1879) Fauna molluscorum extramarinorum Japoniae, nach den von Professor Rein gemachten Sammlungen. Christian Winter, Frankfurt a. M., 171 pp. <https://doi.org/10.5962/bhl.title.12881>
- Kobelt W (1909) Die Gattung *Paludina* Lam. (*Vivipara* Montfort) : neue Folge. In: Martini FHW, Chemnitz JH (Eds) Sytematisches Conchylien-Cabinet. Bd. 1 Abt. 21a. Verlag von Bauer und Raspe, Nürnberg, 98-430 pp. <https://doi.org/10.5962/bhl.title.119758>
- Köhler F, Rintelen T (2011) *Heterogen longispira*. IUCN Red List of Threatened Species <https://doi.org/10.2305/iucn.uk.2011-2.rlts.t189576a8750326.en>
- Köhler F, Do V, Jinghua F (2012) *Cipangopaludina chinensis*. IUCN Red List of Threatened Species <https://doi.org/10.2305/iucn.uk.2012-1.rlts.t166265a1124988.en>
- Kuhl FP, Giardina CR (1982) Elliptic Fourier features of a closed contour. Computer Graphics and Image Processing 18: 236-258. [https://doi.org/10.1016/0146-664X\(82\)90034-X](https://doi.org/10.1016/0146-664X(82)90034-X)
- Kurasawa H (1988) Pass down the Tenryu River, 9: A eutrophication in Lake Suwa and the biological community response. The Ministry of Construction of Japan, Construction

- Bureau in the Chubu region, the work office of the upper Tenryu River, Komagane, 67 pp. [In Japanese].
- Kuroda T (1928) A catalogue of mollusks in Amami-Oshima. Kagoshima Prefecture, Kagoshima, 120 pp. [In Japanese].
 - Kuroda T (1929) Notes on the nomenclature of the Japanese species of the genus *Viviparus*. *Venus* 1 (3): 98-102. [In Japanese]. https://doi.org/10.18941/venusomsj.1.3_98
 - Kuroda T (1947a) Freshwater mollusks of Lake Biwa (2). *Yume-hamaguri* (20): 2-15. [In Japanese].
 - Kuroda T (1947b) Classified list of freshwater shells from the Japanese Islands. *Mokuhachi-tengu-sya*, Kyoto, 22 pp. [In Japanese with English title].
 - Kuroda T (1948) A list of mollusks in Lake Biwa. *Yume-hamaguri* (22): 26-27. [In Japanese].
 - Kuroda T (1955) A list of freshwater molluscan shells of Japan. *Yume-hamaguri* (80) (Supplement): 1-12. [In Japanese with English title].
 - Kuroda T (1963) A catalogue of the non-marine mollusks of Japan, including the Okinawa and Ogasawara Islands. The Malacological Society of Japan, Tokyo, 70 pp. [In Japanese with English title].
 - Kuroda T, Habe T (1965a) *Cipangopaludina* (Heterogen) *longispira* (SMITH). In: Okada Y, Uchida S, Uchida T (Eds) New illustrated encyclopedia of the fauna of Japan (vol. 2). Hokuryu-kan, Tokyo, 48 pp. [In Japanese with English title].
 - Kuroda T, Habe T (1965b) *Sinotaia quadrata histrica* (GOULD). In: Okada Y, Uchida S, Uchida T (Eds) New illustrated encyclopedia of the fauna of Japan (vol. 2). Hokuryu-kan, Tokyo, 48 pp. [In Japanese with English title].
 - Kurozumi T (2001) Japanese crested ibis and Viviparid gastropods —Animals showing the transition of rice field. *Birder* 15 (4): 30-33. [In Japanese].
 - Kurozumi T (2019) Seeking unspoilt landscape in Japan using shells. In: Toyokawa K, Tomoda A, Yura H (Eds) 30th anniversary book of the Natural History Museum and Institute, Chiba. Chiba, 45-46 pp. [In Japanese]. URL: <http://www2.chiba-muse.or.jp/www/NATURAL/contents/1549010275781/simple/shell.pdf>
 - Lake Biwa fisheries experimental station (1915) Fisheries research report of Lake Biwa (2): Mollusks of Lake Biwa. Lake Biwa fisheries experimental station, Fukuman [Hikone], 36 pp. [In Japanese]. <https://doi.org/10.11501/928661>
 - Masuda O, Uchiyama R (2004) Freshwater mollusks of Japan 2: freshwater mollusks of Japan, including brackish water species. *Pisces*, Tokyo, 240 pp. [In Japanese].
 - Matsuoka K (2001) Freshwater mollusks in irrigation ponds. *Nature of irrigation pond* 34: 9-11. [In Japanese].
 - Ministry of the Environment, Government of Japan (2019) Red List of Ministry of the Environment, 2019. Ministry of the Environment, Government of Japan, Tokyo, 129 pp. [In Japanese]. URL: <https://www.env.go.jp/press/files/jp/110615.pdf>
 - Nakai K (2016) *Heterogen longispira*. In: Scientific Committee for Research into the Wildlife in Shiga Prefecture (Ed.) Red Data Book of Shiga Prefecture 2015. Sunrise Publishing, Hikone, 583-583 pp. [In Japanese].
 - Nishino M (1991) Benthos in Lake Biwa —Wildlife of the shores. *Mollusca*. Lake Biwa Research Institute, Shiga Prefecture, Otsu, 46 pp. [In Japanese].
 - Nishiwaki S, Masu H, Hanawa T (2008) Seasonal and regional variations in the number of shelled embryos of *Sinotaia quadrata histrica* in Lake Kasumigaura, Japan. *Venus* 67

(1-2): 73-80. [In Japanese with English abstract]. https://doi.org/10.18941/venus.67.1-2_73

- Okada Y, Kurasawa H (1950) A study of Viviparidae in Japan. In: Okada Y (Ed.) Studies of fishery animals (1). Japan Publishing Cooperation, Tokyo, 141-165 pp. [In Japanese]. <https://doi.org/10.11501/2470294>
- Okuda N, Watanabe K, Fukumori K, Nakano S, Nakazawa T (2013) Origin and diversification of freshwater fishes in Lake Biwa. Springer Briefs in Biology 1-19. https://doi.org/10.1007/978-4-431-54150-9_1
- Oyama K, Kajiyama H (1959) The relationship between *Heterogen turris* and *Cipangopaludina japonica* (a preliminary note). Yume-hamaguri (98): 1-4. [In Japanese].
- Ozawa S (2012) A study of the relationship between the designation of Lake Biwa as a Quasi-national Park and concurrent reclamation work on lagoons around the Lake. Landscape Research Japan Online 5: 5-16. [In Japanese with English title and abstract]. <https://doi.org/10.5632/jilaonline.5.5>
- Pilsbry HA (1895) Appendix I. List of land and freshwater mollusks collected in Japan by Frederick Stearns. In: Pilsbry HA (Ed.) Catalogue of the marine mollusks of Japan, with descriptions of new species and notes on others collected by Frederick Stearns. Frederick Stearn, Detroit, 155-159 pp. <https://doi.org/10.5962/bhl.title.32672>
- Pilsbry HA (1902) Revision of Japanese Viviparidae, with notes on *Melania* and *Bithynia*. Proceedings of the Academy of Natural Sciences of Philadelphia 54 (1): 115-121. URL: <https://www.jstor.org/stable/4062827>
- Prashad B (1928) Recent and fossil Viviparidae. A study in distribution, evolution, paleogeography. Memoirs of the Indian Museum 8 (4): 153-253.
- R Core Team (2018) R: A language and environment for statistical computing. 3.5.1. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>
- Reeve LA (1863) Monograph of the genus *Paludina*. Pl. X. In: Reeve LA (Ed.) Conchologia Iconica: or, Illustrations of the Shells of Molluscos Animals. 14. Lovell Reeve, London. URL: <https://www.biodiversitylibrary.org/page/10971864>
- Rossiter A (2000) Lake Biwa as a topical ancient lake. Advances in Ecological Research 31: 571-598. [https://doi.org/10.1016/s0065-2504\(00\)31031-5](https://doi.org/10.1016/s0065-2504(00)31031-5)
- Smith EA (1886) Descriptions of three new species of freshwater shells from Japan. Journal of Conchology 5: 57-59. URL: <https://biodiversitylibrary.org/page/31653661>
- Stelbrink B, Richter R, Köhler F, Riedel F, Strong EE, Van Bocxlaer B, Albrecht C, Hauffe T, Page TJ, Aldridge DC, Bogan AE, Du L, Manuel-Santos MR, Marwoto RM, Shirokaya AA, von Rintelen T (2020) Global diversification dynamics since the Jurassic: low dispersal and habitat-dependent evolution explain hotspots of diversity and shell disparity in river snails (Viviparidae). Systematic Biology, in press. <https://doi.org/10.1093/sysbio/syaa011>
- Suarez A, Tsutsui N (2004) The value of museum collections for research and society. BioScience 54 (1). [https://doi.org/10.1641/0006-3568\(2004\)054\[0066:tvomcf\]2.0.co;2](https://doi.org/10.1641/0006-3568(2004)054[0066:tvomcf]2.0.co;2)
- Taki Is (1933) The life of Prof. Iwakawa Tomotaro and a list of his papers on conchology (with a portrait). Venus 4 (2): 63-69. [In Japanese]. https://doi.org/10.18941/venusomsj.4.2_63
- Taki Is (1946) The freshwater mollusks in Musashino. Collecting and breeding 8 (11): 202. [In Japanese].

- Tanba K, Shibata S, Takamatsu K (1883) General Zoology. Shimamura Toshisuke, Maruya-zenshiti, and Tyu-kin-do, Tokyo, 397 pp. [In Japanese]. <https://doi.org/10.11501/832886>
- Tanba K, Shibata S, Takamatsu K (1891) General Zoology, revised ver. Shimamura Toshisuke, Maruzen, Nanko-do, and Umehara Kameshichi, Tokyo, 336 pp. [In Japanese]. <https://doi.org/10.11501/832887>
- Van Bocxlaer B, Strong E (2016) Anatomy, functional morphology, evolutionary ecology and systematics of the invasive gastropod *Cipangopaludina japonica* (Viviparidae: Bellamyinae). Contributions to Zoology 85 (2): 235-263. <https://doi.org/10.1163/18759866-08502005>
- Van Bocxlaer B, Strong EE (2019) Viviparidae, Gray 1847. In: Lydeard C, Cummings KS (Eds) Freshwater mollusks of the world: a distribution atlas. Johns Hopkins University Press, Baltimore, 43-50 pp.
- von Martens E (1861) Die Japanesischen Binnenschnecken im Leidner Museum. Malakozoologische Blätter 7: 32-61. URL: <https://biodiversitylibrary.org/page/15919572>
- Wandeler P, Hoeck PA, Keller L (2007) Back to the future: museum specimens in population genetics. Trends in Ecology & Evolution 22 (12): 634-642. <https://doi.org/10.1016/j.tree.2007.08.017>
- Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer-Verlag New York. URL: <https://ggplot2.tidyverse.org>
- Yagura H (1935) A research of viviparid gastropods and land snails. Bulletin of the Society for Hyogo Natural History (9): 7-13. [In Japanese].
- Yagura W (1932) A catalogue of Mollusca in Hyogo, new and revised ver. Konan-Kairuiso, Nishinomiya. [In Japanese]. <https://doi.org/10.11501/1903884>
- Ye B, Saito T, Hirano T, Dong Z, Do VT, Chiba S (2020) Human-geographic effects on variations in the population genetics of *Sinotaia quadrata* (Gastropoda: Viviparidae) that historically migrated from continental East Asia to Japan. Ecology and Evolution 10 (15): 8055-8072. <https://doi.org/10.1002/ece3.6456>
- Yokoyama T (1984) Stratigraphy of the Quaternary system around Lake Biwa and geohistory of the ancient Lake Biwa. In: Horie S (Ed.) Lake Biwa, Monographiae Biologicae. 54. Dr. W Junk Publishers, Dordrecht, 43-128 pp.

Supplementary materials

Suppl. material 1: Full list of synonyms and key publications of *Heterogen japonica*, *H. longispira* and *Sinotaia quadrata histrica* [doi](#)

Authors: Takumi Saito and Osamu Kagawa

Data type: References list

Brief description: The lists include synonyms and key publications of three viviparid species in Japan.

[Download file](#) (33.73 kb)

Suppl. material 2: The full results of morphological analysis [doi](#)

Authors: Takumi Saito and Kagawa Osamu

Data type: Morphological (data)

Brief description: The principal component values summarised from elliptic Fourier analysis and shell width measured directly.

[Download file](#) (613.07 kb)