

# Revisiting a 135-year-old Taxonomic Account of the Freshwater Snail *Semisulcospira multigranosa*: Designating its Lectotype and Describing a New Species of the genus (Mollusca: Gastropoda: Semisulcospiridae)

Naoto Sawada<sup>1,2,\*</sup> and Takafumi Nakano<sup>2</sup>

<sup>1</sup>Division of Applied Biosciences, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan.

\*Correspondence: E-mail: sawada.naoto.82w@st.kyoto-u.ac.jp (Sawada)

<sup>2</sup>Department of Zoology, Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan. E-mail: nakano@zoo.zool.kyoto-u.ac.jp (Nakano)

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The type series of *Semisulcospira multigranosa* Boettger, 1886 was found in the Malacological Collection at the Senckenberg Naturmuseum for the first time ca. 135 years after its original description. The syntypes consisted of 38 specimens that can be classified into four species. The examination of adult shell morphology of these original materials revealed that the current taxonomic account of *S. multigranosa* should be amended. Therefore, we designate a lectotype for *S. multigranosa*, and thus describe *S. multigranosa* auct. as *Semisulcospira davisii* sp. nov. *Semisulcospira davisii* can be discriminated from the other congeners by the characteristics of adult and embryonic shells, and radulae morphology. The present study resolves one of the fundamental taxonomic problems remaining in *Semisulcospira* snails.

**Key words:** Freshwater snail, Lake Biwa, Syntypes, Viviparous, Radula morphology.

## BACKGROUND

The freshwater snail genus *Semisulcospira* Boettger, 1886 contains 26 extant and 10 fossil species indigenous to inland waters of Japan, Korea, Taiwan, and China (e.g., Du et al. 2019; Matsuoka and Miura 2019). Among the 18 extant species described in Japan, 15 are endemic to the Lake Biwa water system (Watanabe and Nishino 1995). These 15 species have occasionally been placed within the subgenus *Biwamelania* Matsuoka and Nakamura, 1981 under *Semisulcospira* (Watanabe and Nishino 1995; Matsuoka and Miura 2019). However, its taxonomic status and even nomenclatural availability have remained controversial (Köhler 2016 2017; Matsuoka and Miura

2019). Comprehensive phylogenetic studies have also revealed that *Biwamelania* is non-monophyletic, consisting of two phylogroups, viz. *S. habeii*- and *S. decipiens*-groups (Nomoto 2001; Kamiya et al. 2011; Miura et al. 2019).

*Semisulcospira* was originally erected as a subgenus of the genus *Melania* Lamarck, 1799, and contained six species (Boettger 1886). Boettger (1886) examined Chinese and Japanese specimens obtained by Philipp Bernhard Schmacker, and described two species based on Schmacker's material, *M. (Sulcospira) schmackeri* Boettger, 1886 [synonymized with *Koreoleptoxis praenotata* (Gredler, 1884) by Du et al. (2019)], and *M. (Semisulcospira) multigranosa* Boettger, 1886 (currently *Semisulcospira multigranosa*).

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The latter species is the third oldest *Semisulcospira* species indigenous to Lake Biwa in Japan, and Boettger (1886) suggested that the species had been confused with *S. niponica* (Smith, 1876), which is the oldest species known from Lake Biwa. Since Boettger did not provide detailed morphological characteristics of *S. multigranosa* in the original description, the taxonomic account of *S. multigranosa* has been vague, and thus a wide range of morphological variations have been recognized in this species (e.g., Annandale 1916; Kuroda 1929; Habe and Kosuge 1967).

The current definition of *S. multigranosa* was established by Davis (1969). As the result of an overall examination of *Semisulcospira* snails inhabiting Japan, Davis (1969) redefined the taxonomic account of *S. multigranosa* based on the specimens collected by himself. Although measurements of *S. multigranosa* sensu Davis (1969) such as shell height and shell width are almost concordant with those in the original description, the counts of longitudinal rib and spiral cord number on the penultimate whorl of the former disagree with those of the latter. Additionally, Davis (1969) described the known morphological variants in *S. multigranosa* and *S. decipiens* (Westerlund, 1883) as *S. habei* Davis, 1969; he also recognized two subspecies in this species, viz., *S. h. habei* and *S. h. yamaguchi* Davis, 1969.

Since Boettger (1886) neither designated any name-bearing types for *S. multigranosa*, nor explicitly stated the number of the examined specimens of this species collected from Lake Biwa, it remains unclear how many specimens should receive the syntype status of *S. multigranosa*. A part of Schmacker's malacological collection is known to have been maintained at the Geosciences Collection of the University of Bremen (Lehmann 2018); nonetheless, Yen (1939) revisited Boettger (1886)'s Chinese specimens, including a *M. schmackeri* specimen kept at Senckenberg Naturmuseum, Frankfurt. Zilch (1942) subsequently added specimens to the specimens' catalogue, including semisulcospirid species that were not treated by Yen (1939). However, neither of these studies referred to the type series of *S. multigranosa*, and therefore the syntypes have been deemed missing. Given the discordance between the original description of *S. multigranosa* and its redefinition by Davis (1969), the taxonomic account of *S. multigranosa* should be revisited based on the examination of its type specimens.

Recently, we found the "missing" name-bearing types of *S. multigranosa* at Senckenberg Naturmuseum. In this study, we re-examine the types and designate a lectotype for the species. According to the present lectotypification, we redefine the taxonomic account

of *S. multigranosa*, and describe *S. multigranosa* sensu Davis (1969) as a new species based on newly collected snails.

## MATERIALS AND METHODS

### Samples

The name-bearing types of *S. multigranosa* examined in this study were kept in the Malacological Collection at Senckenberg Naturmuseum, Frankfurt (SMF).

In total, an additional 76 semisulcospirid snails were newly collected from five localities covering the range of *S. multigranosa* sensu Davis (1969) in Lake Biwa (Fig. 1): 15 from Tsukide, 20 from Kitafunaki, 14 from Yokohama, 12 from Okishima, and 14 from Yoshikawa. Except The snails were collected at a water depth of 5–7 m by snorkeling at all locations except Yoshikawa. At Yoshikawa, the specimens were obtained at a depth of 10–15 m by fishermen in the Katata fishermen's union using dredges. The newly collected specimens from this study were deposited in the Zoological Collection of Kyoto University (KUZ).

### Morphological examination

Morphometric characteristics of the specimens were measured following methods in previous studies (Watanabe 1984; Urabe 1992; Watanabe and Nishino 1995). Adult and embryonic shells were separated and cleaned using the method described by Sawada et al. (2020). Measurements were obtained from digital images using ImageJ 1.51k (Schneider et al. 2012). Color patterns of 10 newly collected adult and embryonic specimens at each locality were observed. The number of whorls of adult and embryonic shells were counted to 0.25 whorls. Radulae were extracted by soaking oral tissues in 1 M sodium hydroxide solution for a day. Extracted radulae were photographed with a Hitachi TM1000 scanning electron microscope. Reproductive organs were obtained from soft bodies separated from shells, and then observed under a Leica M125C stereoscopic microscope. Counts of adult shell sculptural features were obtained for all adult shells, except for four specimens whose sculptures were indistinct. The number of samples used for adult and embryonic shells, radulae and reproductive organs are shown in table 1.

Abbreviations of the morphological characters examined are as follows (Fig. 2): Adult shell: AH, aperture height; AL, aperture length; ASR, aperture slenderness ratio (the proportion of aperture length to

fourth aperture width); AW, aperture width; BCN, basal cord number; BWL, body whorl length; FWL, fourth whorl length; PWL, penultimate whorl length; RN, longitudinal rib number of penultimate whorl; SA, spire angle; SCN, spiral cord number of penultimate whorl; SH, shell height; SW, shell width; TWL, third whorl length; WER, whorl elongation ratio (the proportion of aperture height to fourth whorl length); WN, whorl number.

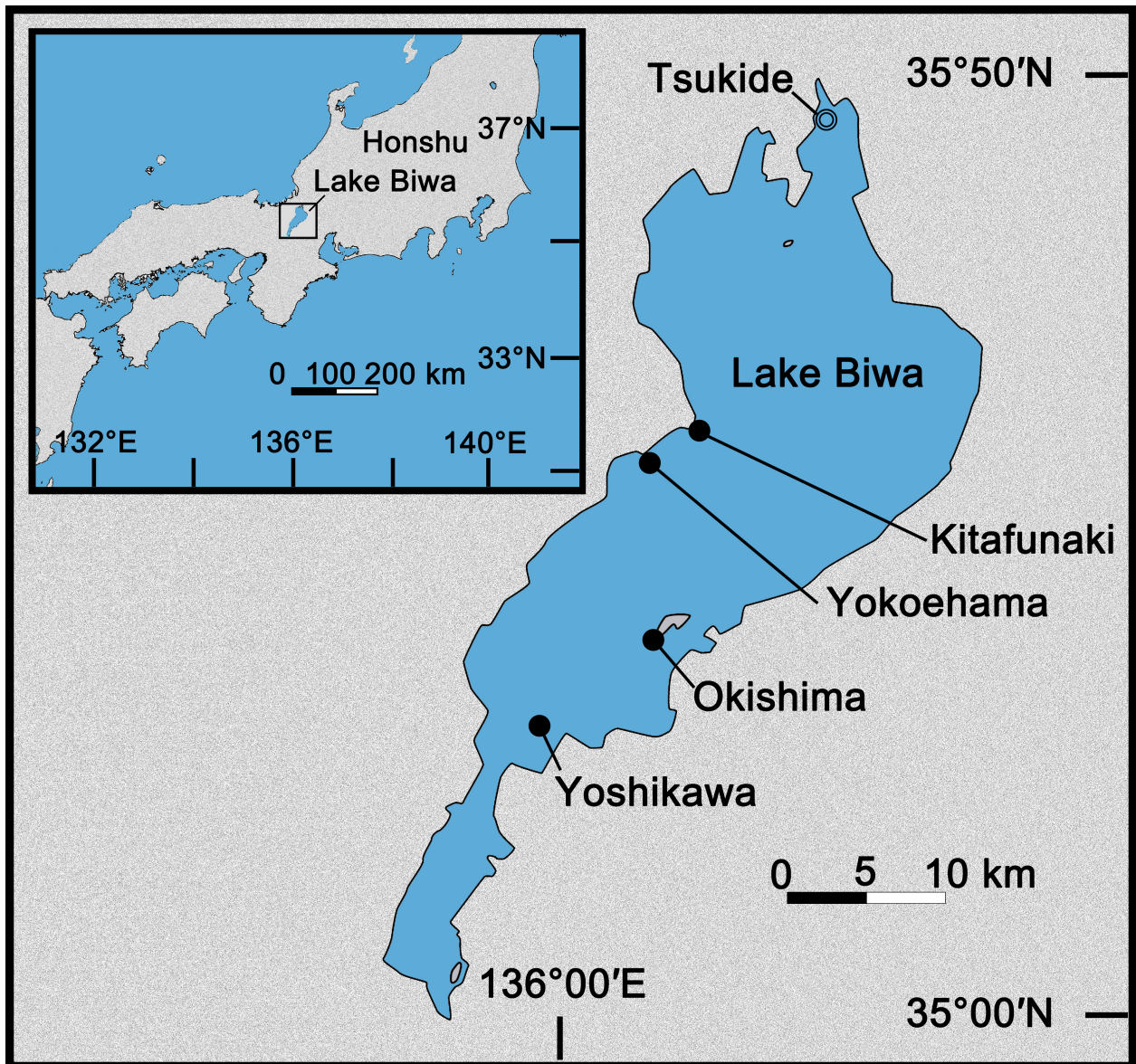
Embryonic shell: EN, number of embryos; RNE, longitudinal rib number of body whorl; SHE, shell height; SWE, shell width; WNE, whorl number.

**RESULTS**

**SYSTEMATICS**

**Family Semisulcospiridae Morrison, 1952**  
**Genus *Semisulcospira* Boettger, 1886**  
***Semisulcospira multigranosa* (Boettger, 1886)**  
 (Fig. 3)

*Melania* (*Semisulcospira*) *multigranosa* Boettger, 1886: 7–8 (part).  
*Melania multigranosa* – Pilsbry 1902: 119–120 (in part); Annandale 1916: 44–46, 55, 59, pl. 3, fig. 2A–E (part).  
*Semisulcospira multigranosa* – Kuroda 1929: 186, 189, pl. 5, figs. 34–36 (part); Fukuoka 1933: 114, 115, fig. 4.



**Fig. 1.** Map of Lake Biwa showing five sampling localities: double circle, Tsukide (type locality of *Semisulcospira davisi* sp. nov.); black circles, Kitafunaki, Yokoehama, Okishima, Yoshikawa.

**Table 1.** Morphometric characters of *Semisulcospira davisi* sp. nov. examined in the present and past studies. Measurements and counts: minimum–maximum value (mean ± SD) [except for Watanabe and Nishino (1995)]; (mean ± 95% confidence limits) [Watanabe and Nishino (1995)]

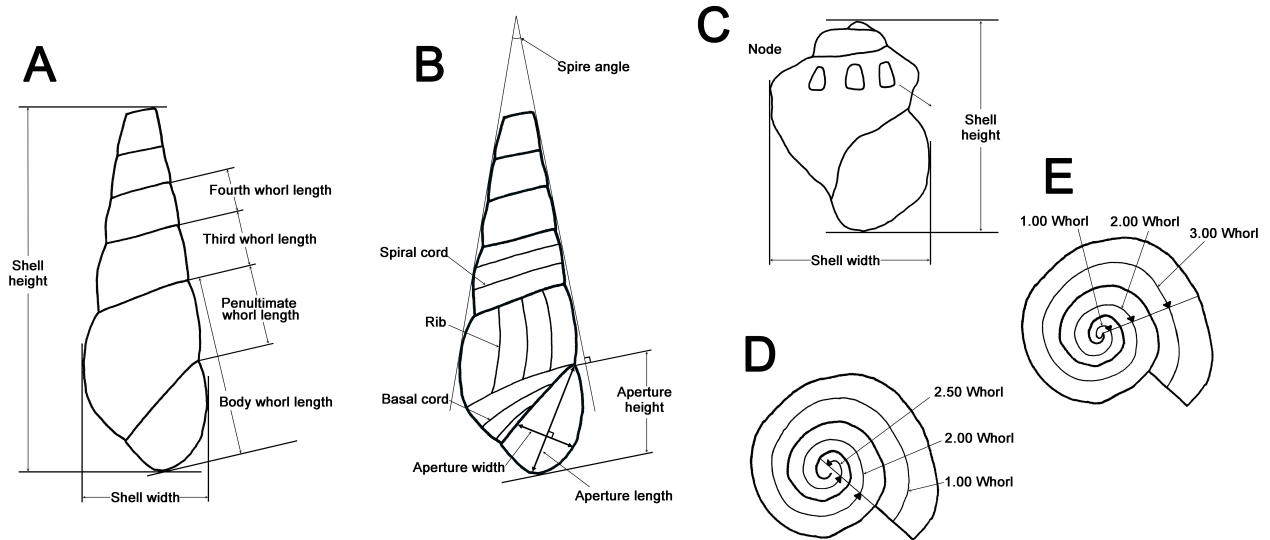
	Tsukide	Kitafunaki	Yokohama	Okishima	Yoshikawa	Davis (1969)	Watanabe and Nishino (1995)
specimen number of shells (adult / embryo)	15 / 7	20 / 10	14 / 10	12 / 9	14 / 8	25 / 16	30 / 10
specimen number of radulae	9	9	10	10	5	-	-
specimen number of reproductive organs (male / female)	3 / 8	4 / 8	2 / 10	0 / 10	1 / 5	-	-
<b>Morphological characters of adult shells</b>							
Aperture height (AH)	7.0–9.1 (8.1 ± 0.6)	7.3–8.9 (7.9 ± 0.4)	8.4–9.8 (9.1 ± 0.4)	6.7–8.7 (8.0 ± 0.5)	6.4–8.1 (7.2 ± 0.4)	-	-
Aperture length (AL)	7.1–9.7 (8.5 ± 0.8)	7.5–8.4 (8.0 ± 0.3)	8.7–10.4 (9.2 ± 0.4)	7.1–8.6 (8.3 ± 0.4)	6.8–7.8 (7.4 ± 0.3)	-	(9.42 ± 0.22)
Aperture slenderness ratio (ASR)	1.4–1.7 (1.5 ± 0.1)	1.3–1.6 (1.5 ± 0.1)	1.4–1.7 (1.5 ± 0.1)	1.3–1.7 (1.5 ± 0.1)	1.3–1.5 (1.4 ± 0.1)	-	-
Aperture width (AW)	4.5–6.5 (5.7 ± 0.5)	4.9–5.9 (5.3 ± 0.2)	5.5–6.7 (6.1 ± 0.4)	5.0–6.4 (5.7 ± 0.4)	4.7–5.5 (5.1 ± 0.3)	-	(5.44 ± 0.16)
Basal cord number (BCN)	1–3 (2.0 ± 0.4)	2–3 (2.1 ± 0.3)	2–4 (2.4 ± 0.6)	1–2 (1.9 ± 0.4)	1–3 (1.9 ± 0.5)	2–3	2–4
Body whorl length (BWL)	12.3–16.7 (14.4 ± 1.2)	12.8–14.8 (13.6 ± 0.5)	14.6–16.7 (15.7 ± 0.6)	12.0–15.0 (14.1 ± 0.8)	11.7–14.0 (13.0 ± 0.7)	(13.1 ± 1.24)	(15.65 ± 0.41)
Fourth whorl length (FWL)	3.6–5.1 (4.1 ± 0.4)	3.1–4.5 (3.6 ± 0.3)	3.5–4.5 (4.1 ± 0.3)	3.7–4.5 (4.0 ± 0.2)	3.3–4.6 (4.0 ± 0.4)	-	-
Penultimate whorl length (PWL)	5.4–7.6 (6.3 ± 0.6)	5.1–6.4 (5.7 ± 0.3)	5.9–7.4 (6.6 ± 0.4)	5.3–6.8 (6.1 ± 0.4)	4.7–6.8 (5.8 ± 0.6)	-	(6.84 ± 0.20)
Longitudinal rib number of penultimate whorl (RN)	18–30 (23.6 ± 2.9)	19–27 (22.6 ± 2.3)	16–26 (21.7 ± 3.0)	19–28 (22.5 ± 3.0)	19–26 (23.4 ± 2.0)	(23.2 ± 2.42)	-
Spire angle (SA)	13.0–20.5 (16.2 ± 1.9)	11.9–20.5 (16.9 ± 2.4)	15.8–20.7 (18.2 ± 1.4)	12.1–18.4 (15.4 ± 1.7)	11.1–17.9 (14.9 ± 1.9)	(14.2 ± 3.11)	(14.6 ± 0.5)
Spiral cord number of penultimate whorl (SCN)	7–10 (8.3 ± 1.3)	8–10 (8.6 ± 0.9)	8–10 (9.6 ± 0.8)	7–9 (8.2 ± 0.6)	7–10 (8.8 ± 1.9)	7–8	7–10
Shell height (SH)	25.4–40.4 (31.3 ± 3.7)	24.2–31.7 (27.8 ± 2.0)	29.2–35.5 (32.0 ± 2.2)	26.1–35.5 (30.2 ± 2.4)	23.9–30.5 (26.7 ± 1.8)	(26.0 ± -)	(32.60 ± 0.86)
Shell width (SW)	8.3–11.3 (9.6 ± 0.8)	8.5–10.3 (9.2 ± 0.4)	9.6–11.3 (10.6 ± 0.5)	8.4–10.6 (9.6 ± 0.5)	8.4–9.8 (9.0 ± 0.4)	(8.3 ± 0.60)	(9.87 ± 0.29)
Third whorl length (TWL)	4.3–6.1 (5.1 ± 0.5)	4.0–5.6 (4.7 ± 0.4)	4.6–6.1 (5.4 ± 0.5)	4.6–5.9 (5.1 ± 0.4)	4.0–5.4 (4.8 ± 0.4)	-	-
Whorl elongation ratio (WER)	1.7–2.3 (2.0 ± 0.2)	1.7–2.6 (2.2 ± 0.2)	1.9–2.6 (2.2 ± 0.2)	1.7–2.2 (2.0 ± 0.2)	1.5–2.1 (1.8 ± 0.2)	-	-
Whorl number (WN)	4.50–8.50 (5.5 ± 1.0)	3.50–7.50 (5.5 ± 1.2)	3.75–7.50 (5.9 ± 1.2)	3.50–8.50 (5.6 ± 1.3)	3.75–6.50 (4.8 ± 0.9)	-	-
<b>Morphological characters of embryonic shells</b>							
Number of embryos (EN)	2–8 (5.1 ± 2.1)	2–11 (5.4 ± 2.8)	2–21 (9.6 ± 5.4)	3–19 (11.9 ± 5.3)	2–8 (3.0 ± 0.9)	2–12 (5.2 ± 3.41)	(8.5 ± 2.9)
Longitudinal rib number of body whorl (RNE)	9–14 (10.7 ± 1.6)	9–12 (10.1 ± 0.9)	9–13 (10.2 ± 1.3)	10–13 (11.3 ± 0.9)	9–13 (10.9 ± 1.5)	-	(12.0 ± 1.0)
Shell height (SHE)	4.0–6.3 (5.3 ± 0.8)	3.4–4.6 (4.0 ± 0.5)	2.1–5.3 (3.9 ± 1.1)	2.5–5.7 (3.5 ± 1.1)	3.5–7.1 (5.1 ± 1.0)	-	(4.87 ± 0.43)
Shell width (SWE)	2.5–3.3 (3.0 ± 0.3)	2.2–2.8 (2.4 ± 0.2)	1.8–3.0 (2.5 ± 0.4)	1.6–2.9 (2.1 ± 0.5)	2.2–3.5 (2.8 ± 0.4)	-	(2.74 ± 0.16)
Whorl number (WNE)	4.00–6.00 (4.9 ± 0.7)	3.50–4.75 (3.9 ± 0.4)	2.50–4.50 (3.7 ± 0.7)	3.00–5.00 (3.7 ± 0.7)	3.75–5.00 (4.4 ± 0.4)	-	4.5–5.5
<b>Morphological characters of radulae</b>							
cuspid number of rachidian	7–8	7	7	7	7	-	-
cuspid number of lateral teeth	6–7	6–7	6–7	5–7	6	-	-
cuspid number of interior marginal teeth	5–7	5–8	6–8	6–7	5–7	-	-
cuspid number of exterior marginal teeth	5–7	5–8	5–8	5–7	5–7	-	-

*Semisulcospira decipiens* Kuroda 1941: 184 (part); Habe 1961: 25, pl. 11, fig. 9 (part); Habe and Kosuge 1967: 28, pl. 11, figs. 19, 20.

**Material examined:** Lectotype: SMF225654, adult shell, sex undetermined, collected from rice field near Lake Biwa in central Honshu island, Japan in 1885 by

[P.] B. Schmacker.

Paralectotypes: 37 specimens collected in and around Lake Biwa in 1885 by [P.] B. Schmacker: SMF 225655, 3 specimens; SMF 225656, 1; 225657, 1; 225658, 16; 225659, 2; 225660, 6; 358291, 3; 358294, 1; 358295, 1; 359900, 3. SMF 225655, 225658, 359900



**Fig. 2.** Schematic drawings indicating shell measurements of *Semisulcospira* species in this study. A–B, Adult shell. C, Embryonic shell. D, Whorl number of adult shell. E, Whorl number of embryonic shell.



**Fig. 3.** Lectotype of *Semisulcospira multigranosa* (SMF 225654). A, ventral view. B, lateral view. C, dorsal view. D, historical handwritten label. E, partly printed label. Scale bar = 10 mm.

from rice field near Lake Biwa; SMF 225656, 225659, 358291, 358294 from creek close to the lake; SMF 225657, 225660, 358295 from Lake Biwa.

*Amended diagnosis:* Adult shell elongated; 3–4 BCN, around 17–19 curved ribs with distinct or indistinct nodes; 5–6 SCN; 18.1–20.5 degrees SA; 1.7–1.8 ASR; 2.4–2.9 WER.

*Description:* Lectotype: AH 9.1 mm, AL 8.8 mm, ASR 1.7, AW 5.3 mm, BCN 3, BWL 14.4 mm, FWL 3.1 mm, PWL 5.4 mm, RN 17, SA 19.0 degrees, SCN 5, SH 27.3 mm, SW 9.3 mm, TWL 4.1 mm, WER 2.9, WN 5.0; shell elongated, suture slightly undulating, sides of whorls moderately convex, slightly curved longitudinal ribs partly nodulate in third to body whorl; ribs fade in body whorl; apex of shell eroded; shell surface colored brown to blackish brown with deposits; without operculum.

*Paralectotypes:* only four specimens in good condition examined. SMF 225655, 3 specimens; SMF 225656, 1. AH 7.6–8.1 mm, AL 7.9–8.4 mm, ASR 1.7–1.8, AW 4.6–5.0 mm, BCN 3–4, BWL 12.7–13.4 mm, FWL 3.0–3.5 mm, PWL 4.5–5.3 mm, RN 17–19, SA 18.1–20.5 degrees, SCN 5–6, SH 24.6–26.6 mm, SW 8.5–8.9 mm, TWL 3.6–4.3 mm, WER 2.2–2.6, WN 4.5–6.5; shell elongated, suture slightly to moderately undulating, sides of whorls slightly convex, moderately curved longitudinal ribs hardly or partly nodulated and fade in penultimate to body whorl in some specimens; apex of shell eroded; shell surface and operculums partly colored brown to blackish brown with deposits; operculum nearly pear to egg-shaped subcircular, paucispiral, nucleus subcentral.

*Remarks:* Among the paralectotypes of *S. multigranosa*, SMF 225657, 225660, 358291, 358294, 358295, 359900 may contain specimens that are actually other semisulcospirid species. SMF 225657 and 225660 can be identified as *Koreoleptoxis tegulata* (Martens, 1894) according to their smaller SL of the well-developed adult shells (about 16 mm) with moderately convex whorl sides, fewer distinguished longitudinal ribs from upper to lower whorls (about 16 RN), inconspicuous basal cords (3–4 BCN), and smaller SA (about 17 degrees). SMF 358291 and 358295 may belong to *S. reiniana* (Brot in Kobelt, 1876) in having more basal cords (7–8 BCN) and well-developed longitudinal ribs. SMF 358294 and 359900 may be *S. decipiens* in having smaller SA (about 17 degrees) and fewer basal cords (3 BCN).

The original description stated that the type specimens were collected mainly from rice fields and creeks close to Lake Biwa (Boettger 1886). However, the snails whose adult shell morphology corresponds to *S. multigranosa* have never been found in such habitats around the lake after Boettger (1886), but they

have been collected from inside the lake (e.g., Kuroda 1929; Fukuoka 1933; Watanabe 1970a). Since the type series also includes specimens that can be identified as Korean species with characteristics of SL, RN, BCN, SA, and shape of whorl sides, the original material of *S. multigranosa* may be composed of specimens collected from several locations in Japan and adjacent regions.

### ***Semisulcospira davis* sp. nov.**

[New Japanese name: Sazanami-kawanina]

(Figs. 4–7)

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*Melania multigranosa* – Pilsbry 1902: 119–120 (part); Annandale 1916: 44–46, 55, 59, pl. 3, fig. 2A–E (part).

*Semisulcospira multigranosa* – Kuroda 1929: 186, 189, pl. 5, figs. 34–36 (part); Burch 1968: 12, 26–29, pl. 4, figs. 1–3, pl. 5, fig. 6; Davis 1969: 255, 258, 260, 262, pl. 7, figs. 1–4, pl. 11, figs. 5–8; Watanabe 1970a: 13–30, fig. 15–2, -6, -7; Watanabe 1970b: 93–98, figs. 3–5; Oniwa and Kimura 1986: 1–2, 9–11, figs. 2–4.

*Semisulcospira decipiens* – Kuroda 1941: 184 (part); Kajiyama and Habe 1961: 167, figs. 4, 4a, 5, 5a; Habe 1961: 25, pl. 11, fig. 9 (part); Kuroda 1962: 86, 89; Habe 1965: 57.

*Semisulcospira (Biwamelania) multigranosa* – Watanabe and Nishino 1995: 1, 24, 30–34, app. pl. 1, fig. 7, app. pl. 2, figs. 20, 21; Kamiya et al. 2011: 23–34; Miura et al. 2019: 45–51, figs. 2–5.

*Biwamelania multigranosa* – Prozorova and Rasshepkina 2006: 130–132, fig. B.

*Material examined:* Holotype. KUZ Z3680, adult shell with embryonic shells treated with sodium hypochlorite, collected from a depth of 5–6 m of Lake Biwa (35°30'00"N, 136°09'48"E), Tsukide, Nishiazai-cho, Nagahama City, Shiga Prefecture, Japan, on 22 July 2020 by the first author. Paratypes. In total, 3 specimens collected with the holotype: KUZ Z3681–Z3683.

*Additional materials:* KUZ Z3684 collected with the holotype; KUZ Z3685, Z3686, collected from Kitafunaki, on 17 August 2017 (KUZ Z3685), and on 22 July 2020 (KUZ Z3686); KUZ Z3687, collected from Yokoehama, on 22 July 2020; KUZ Z3688, collected from Okishima, on 23 July 2020; KUZ Z3689, 3690, collected from Yoshikawa on 18 February 2018 (KUZ Z3689), and on 10 December 2019 (KUZ Z3690).

*Etymology:* The specific name is dedicated to Dr. George M. Davis, who greatly contributed to the systematics of Japanese *Semisulcospira*.

*Diagnosis:* Viviparous semisulcospirid. Adult shell elongated [SH 29.5 ± 3.2 (mean ± SD); SW 9.7 ± 1.2]; 2.1 ± 0.5 BCN; 22.8 ± 2.6 curved ribs with distinct or indistinct nodes; 8.8 ± 1.0 SCN; 16.4 ± 2.2 degrees SA; 1.5 ± 0.1 ASR; 2.1 ± 0.2 WER. Embryonic shell large (SHE 4.3 ± 1.1), with ribs on surface; color in black background or beige background with brown bands.

*Description of holotype:* Adult shell (Fig. 4A–

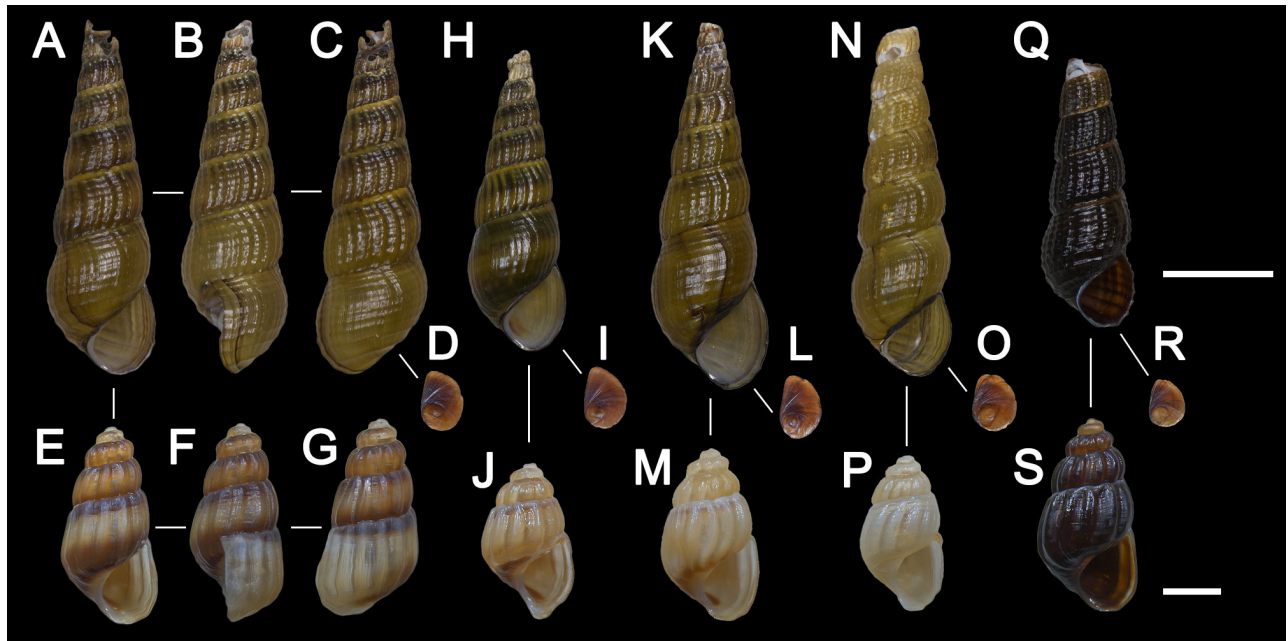
C): Female. Measurements and counts: AH 8.0 mm, AL 8.4 mm, ASR 1.5, AW 5.5 mm, BCN 2, BWL 14.1 mm, FWL 4.1 mm, PWL 6.1 mm, RN 25, SA 17.2 degrees, SCN 10, SH 32.3 mm, SW 10.1 mm, TWL 5.0 mm, WER 2.0, WN 6.00. Shell elongated. Slightly curved longitudinal ribs on whorls with indistinct spiral cords. Suture strongly undulating, sides of whorls moderately convex. Shell colored ocher in background with 1 olive color band on upper part of each whorl, 1 brown band on lower part of each whorl. Surface of shells covered with black deposits before treatment.

Operculum (Fig. 4D): 5.6 mm in long diameter. Nearly egg-shaped subcircular, paucispiral, comprising

3 whorls. Nucleus subcentral.

Embryonic shells (Fig. 4E–G): Measurements and counts: EN 7, RNE 10, SHE 4.9 mm, SWE 2.9 mm, WNE 5.00. Shell oval shape like rugby ball, with remarkable ribs. Shell colored beige background, with 1 distinct brackish brown band on upper part of each whorl and on basal part of the shell.

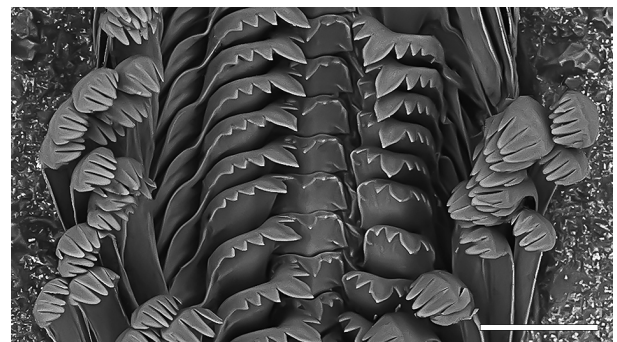
Radulae (Fig. 6): Taenioglossa consisting of rachidian in single, lateral teeth, interior and exterior marginal teeth in double row. Rachidian roughly triangular with large central pointed denticle and 3 minor pointed triangular cusps on each side. Approximately regular triangular central denticle of



**Fig. 4.** Shells of *Semisulcospira davisi* sp. nov. A–G, Holotype, KUZ Z3680. H–J, Specimen from Kitafunaki, KUZ Z3686. K–M, Specimen from Yokohama, KUZ Z3687. N–P, Specimen from Okishima, KUZ Z3688. Q–S, Specimen from Yoshikawa, KUZ Z3690. A–C, H, K, N, Q, Adult shell. D, I, L, O, R, Operculum. E–G, J, M, P, S, Embryonic shell. Scale bars: 10 mm (A–D, H–I, K–L, N–O, Q–R), 2 mm (E–G, J, M, P, S). All specimens were treated with 12% sodium hypochlorite.



**Fig. 5.** Living specimen of *Semisulcospira davisi* sp. nov. collected from Kitafunaki. Scale bar = 10 mm.



**Fig. 6.** Radula morphology of *Semisulcospira davisi* sp. nov. collected from type locality (KUZ Z3684). Scale bar = 100  $\mu$ m.

rachidian about 2.5 times longer than other triangular cusps. Lateral teeth with large central pointed and tapered denticle, 3 inner and 3 outer pointed cusps. Irregular triangular central denticle of lateral teeth about 2 times longer than other triangular cusps. Interior and exterior marginal teeth similar in shape with 5–6 rounded denticles.

Reproductive organs: Male (Fig. 7A). Gonad consisting of testes, vas deferens, and prostate without penis. Thin narrow vas deferens running from testes and connecting to posterior end of prostate. Posterior ventral part of inflated prostate, forming deep groove, observed as U-shape in transverse section. Anterior prostate tapering toward end of prostate opening to mantle cavity.

Female (Fig. 7B). Long narrow oviduct, emerging from ovary, entering near seminal receptacle without protrusion. Ventral edge of spermatophore bursa with groove with curved surface forming sperm gutter, extending toward mantle cavity. Brood pouch on dorsal side of spermatophore bursa, inflated dorsally, separated into many cells, including eggs and embryos. Eggs and embryos radially developing from base of brood pouch near seminal receptacle and embryos in anterior or dorsal cells more developed.

Variation (Table 1): Adult shell: Measurements: AH 6.4–9.8 mm [ $8.1 \pm 0.7$  (mean  $\pm$  SD)], AL 6.8–10.4 mm ( $8.2 \pm 0.8$ ), ASR 1.3–1.7 ( $1.5 \pm 0.1$ ), AW 4.5–6.7 mm ( $5.5 \pm 0.5$ ), BCN 1–4 ( $2.1 \pm 0.5$ ), BWL 11.7–16.7 mm ( $14.1 \pm 1.2$ ), FWL 3.1–5.1 mm ( $4.0 \pm 0.4$ ), PWL 4.7–7.6 mm ( $6.0 \pm 0.6$ ), RN 16–30

( $22.8 \pm 2.6$ ), SA 11.1–20.6 degrees ( $16.4 \pm 2.2$ ), SCN 7–10 ( $8.8 \pm 1.0$ ), SH 23.9–40.4 mm ( $29.5 \pm 3.2$ ), SW 8.3–11.3 mm ( $9.6 \pm 0.8$ ), TWL 3.9–6.1 mm ( $5.0 \pm 0.5$ ), WER 1.5–2.6 ( $2.1 \pm 0.2$ ), WN 3.50–8.50 ( $5.5 \pm 1.2$ ). Slightly to moderately curved longitudinal ribs on whorls sometimes form nodes with spiral cords. Suture slightly to strongly undulating, sides of whorls slightly to moderately convex. Shell colored ocher to olive or blackish brown in background with or without colored bands. Distinct to slightly indistinct colored bands on adult shells olive or brown in ochre background, brown in olive background. No colored band observed on shells in blackish brown background. One color band each found on upper, middle, or lower part of whorls, or on all of them.

Operculum: Nearly pear to egg-shaped subcircular, paucispiral, comprising 3 whorls. Nucleus subcentral.

Embryonic shells: Measurements: EN 2–21 ( $7.2 \pm 4.9$ ), SHE 2.1–7.1 mm ( $4.3 \pm 1.1$ ), SWE 1.6–3.5 mm ( $2.5 \pm 0.5$ ), RNE 9–14 ( $10.6 \pm 1.3$ ), WNE 2.50–6.00 ( $4.1 \pm 0.7$ ). Shell colored beige, olive or blackish brown in background with or without colored bands. Distinct colored bands brown to blackish brown in beige, olive background. No colored band found on shells in blackish brown background. One color band each lined on upper, middle, lower or basal part of whorls, or on all of them.

Radulae: Variation of the number and the size in cusps observed: rachidian, 1 central denticle flanked by 3–4 minor pointed cusps on each side, central denticle 2–3 times longer than marginal cusps; lateral teeth, 1

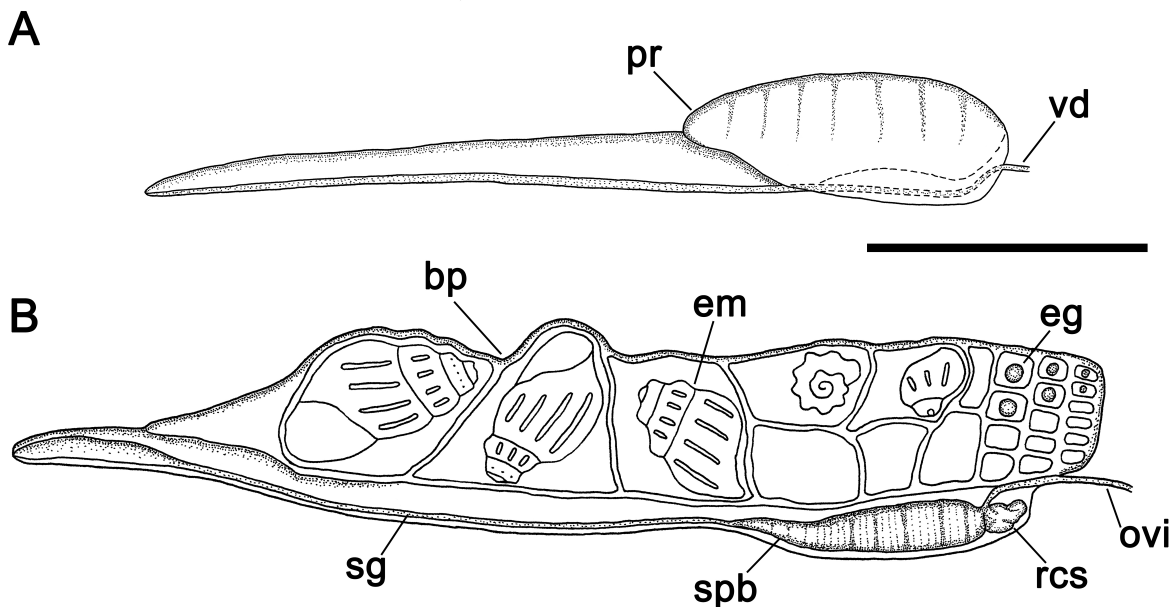


Fig. 7. Schematic drawings indicating reproductive organs of *Semisulcospira davisi* sp. nov. A, Male. B, Female. Scale bar = 5 mm.



central denticle with 2–3 inner and outer cusps, central denticle 2–3 times longer than other cusps; interior and exterior marginal teeth, 5–8 cusps.

Reproductive organs: Seminal receptacles with or without several short protrusions were observed in female reproductive organs.

*Distribution and ecology*: The new species was found from four sites of Lake Biwa in addition to its type locality: Kitafunaki, Yokohama, Okishima, and Yoshikawa (Fig. 1). Except at Yoshikawa, the new species inhabits sandy and muddy bottom at depths of 5–7 m. At Yoshikawa, the new species was collected from muddy bottom at the depth of 10–15 m. *Semisulcospira davisii* was found with several other congeners: *S. reticulata* Kajiyama and Habe, 1961, *S. decipiens* and *S. h. yamaguchi* at Tsukide, Kitafunaki and Yokohama; *S. decipiens* at Okishima; and *S. reticulata* at Yoshikawa.

*Remarks*: Morphological characters of adult and embryonic shells of the new species in five localities correspond closely to those of the species examined in the previous studies as *S. multigranosa* (Davis 1969; Watanabe and Nishino 1995; Table 1). Only the smallest value of SW in the present material was greater than that in Davis (1969). The reproductive organs of *S. davisii* are also nearly consistent with those of snails identified as *S. multigranosa* by Prozorova and Rasshepkina (2006). Although Prozorova and Rasshepkina (2006) observed several “long” protrusions in the female seminal receptacle, we detected several “short” protrusions only in about half of the dissected specimens.

Previous phylogenetic studies revealed that *S. davisii* belongs to the *S. decipiens*-group (Kamiya et al. 2011; Miura et al. 2019). Although allozyme analysis failed to show robust relationships within the *decipiens*-group (Kamiya et al. 2011), a phylogenomic study using a double digest restriction site associated DNA library revealed that *S. davisii* was closely related to *S. morii* Watanabe, 1984 (Miura et al. 2019). *Semisulcospira davisii* is clearly distinguishable from *S. morii* by having more SCN and smaller SA (Watanabe and Nishino 1995). Thus, the distinctiveness of *S. davisii* is unquestionably supported by both its morphological characteristics and phylogenetic position.

The examined specimens corroborate the previous finding that the new species (referred to as *S. multigranosa*) can be discriminated from *S. decipiens* by the morphology of rachidian and lateral teeth (Prozorova and Rasshepkina 2006), although *S. davisii* has similar radulae morphology with *S. decipiens* in the length and shape (Watanabe 1970b). The number of rachidian cusps is exceptional in that the number in *S. davisii* overlaps with that in *S. decipiens* (one central denticle with 3–4 minor cusps on each side; Table 1).

The present study shows that *S. davisii* seems to predominate in deep sandy and muddy sediments with *S. reticulata*. *Semisulcospira davisii* was collected with *S. reticulata* from the four collection sites. *Semisulcospira reticulata* has large embryonic shells, and prefers the deepest area of the lake (Davis 1969; Watanabe and Nishino 1995; Miura et al. 2019). Given that the two species share habitat preferences and large embryonic shells, the enlargement of embryonic shells may be an adaptation to deeper habitats.

## DISCUSSION

The taxonomic status of *Semisulcospira multigranosa* is revisited here for the first time in ca. 135 years after the original description based on the original material. However, the labels of the lectotype designated herein raise a question about the past taxonomic works on *S. multigranosa*. The historical handwritten label of the lectotype of *S. multigranosa* (Fig. 3D) is an original label made by Boettger (Sigrid Hof, personal communication). The specific name, the collection locality and the collector indicated on the label are concordant with those in the original description (Boettger 1886). Moreover, the words “= Niponica Kob.” is written on this label; Boettger (1886) considered *multigranosa* to be conspecific with *Niponica* sensu Kobelt (1876). Accordingly, we determined that this specimen as well as the other shells at SMF unquestionably belong to the original material of *S. multigranosa*.

The other partly printed label of SMF 225654 is problematic, since it indicates that this specimen is the “lectotypus” of *S. multigranosa* (Fig. 3E). To our knowledge, however, a lectotype for *S. multigranosa* has never been designated in any published work. This partly printed label was made by Adolf Zilch (Sigrid Hof, personal communication). Because Zilch listed and lectotypified a number of type specimens at SMF (e.g., Zilch 1942), the type specimens of *S. multigranosa* may have been relabeled simultaneously with other taxa without referring to it in his articles. However, it is possible that such a published work containing designation of SMF 225654 as a lectotype of *S. multigranosa* will be found in the future. To prevent prospective nomenclatural instability in *S. multigranosa*, therefore, we herein selected SMF 225654 as the lectotype for *S. multigranosa*.

Davis (1969) stated that *S. multigranosa* could be discriminated from other congeners with morphological characters on the adult shell: about 23.2 RN, 7–8 SCN. However, specimens with those characteristics were not detected among the syntypes. Therefore, we could

not follow Recommendation 74A of the Code (ICZN 1999), which restricts the application of the name in designation of a lectotype. Accordingly, we describe *S. multigranosa* sensu Davis (1969) as a new species. Given the fact that the original material consisted of several species belonging to both *habei-* and *decipiens-* groups, the identity of *S. multigranosa* provided by Boettger (1886) may have been vague.

By the present lectotypification for *S. multigranosa*, its taxonomic status can be unquestionably clarified. Since the soft-bodies and embryonic shells have not remained in the type series, however, their characteristics should be clarified by additional specimens whose adult shell characters accord with those of the lectotype of *S. multigranosa*. Moreover, taxonomic accounts of the other *Semisulcospira* species remain unsettled given the incongruence between the species classification based on morphological characters and snails' mitochondrial geneologies (Miura et al. 2013; Köhler 2016; Miura et al. 2020). Accordingly, the taxonomic status of *S. multigranosa* and other congeners, including the species described in the late 19th century, should be investigated in future systematic studies.

## CONCLUSIONS

Our discovery of the “missing” type specimens of *Semisulcospira multigranosa* sheds light on the correct taxonomic account for the first time after its original description (Boettger 1886). However, the adult shell morphology of the type series was not concordant with that of *S. multigranosa* sensu Davis (1969) and subsequent studies. Therefore, the prevailing taxonomic status of *S. multigranosa* should be revised, and thus *S. multigranosa* auct. is herein described as a new species, *S. davisii*.

*Semisulcospira* is a species-rich taxon, and its members exhibit an elaborate evolutionary history. Recent phylogenetic studies aimed to understand the incongruence between their morphology and mitochondrial phylogeny (e.g., Köhler 2016; Miura et al. 2020). However, *Semisulcospira* snails still have fundamental taxonomic and nomenclatural issues to be tackled. The present lectotypification can amend the vague taxonomic account of the original *S. multigranosa*, and thus resolve a 130-year-old taxonomic puzzle. Since the original material of *S. multigranosa* does not contain any embryonic shells or soft-body parts, the features of these characters should be described in a future study. Further systematic studies are also essential to elucidate the systematic account as well as phylogenetic position of *S. multigranosa* among

the *Semisulcospira* species.

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**Authors' contributions:** SN and NT designed the present study and drafted the manuscript. SN conducted the sample collection and the morphological examination. All authors drafted, read and approved the final manuscript.

**Competing interests:** The authors declare that they have no conflict of interests.

**Availability of data and materials:** The manuscript is incorporated in ZooBank. Materials are deposited in the collections of KUZ and SMF.

**Consent for publication:** Not applicable.

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