



Two Introduced Bithyniid Species Previously Attributed to *Parafossarulus* Annandale, 1924 (= *Pseudovivipara* Annandale, 1918; Caenogastropoda: Truncatelloidea) from China into Japan—Their Identification, Anatomical Redescriptions, and Generic Status

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TWO INTRODUCED BITHYNIID SPECIES PREVIOUSLY ATTRIBUTED TO
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1918; CAENOGASTROPODA: TRUNCATELLOIDEA) FROM CHINA INTO
JAPAN—THEIR IDENTIFICATION, ANATOMICAL REDESCRIPTIONS, AND
GENERIC STATUS

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ABSTRACT

Recently two nonindigenous species of the Bithyniidae were found in freshwater habitats of Honshū, Japan. Based on morphological examination and molecular phylogenetic analysis of their mitochondrial DNA, they were identified as *Pseudovivipara eximia* (Frauenfeld, 1864) and *Parafossarulus longicornis* (Benson, 1842), both of which are known to be distributed mainly in China. These species are anatomically similar to each other and included in a clade together with *Parafossarulus manchouricus* (Bourguignat, 1861). Therefore, *Parafossarulus* Annandale in Annandale & Prashad, 1924, was confirmed to be a junior synonym of *Pseudovivipara* Annandale, 1918. In Japan, introduced populations of *Pseudovivipara eximia* have been recorded from five prefectures (Aomori, Niigata, Ibaraki, Chiba, and Shiga) in northern to central Honshū, and *Pseudovivipara longicornis* is established only in Lake Kawaguchi, Yamanashi Prefecture. Middle Pleistocene fossils of *Pseudovivipara longicornis* have been reported around Lake Biwa in Shiga Prefecture, indicating that this species was previously found in Japan, but later became extinct, perhaps in the upper Pleistocene.

Key words: anatomy, Bithyniidae, conservation, exotic species, freshwater snail, nonindigenous species, parasitology, taxonomy.

摘要

齊藤 匠・澤田直人・叶 彬・秋山佳央・平野尚浩・木村昭一・千葉 聡・福田 宏：中国から.. 中国から日本に移入されたエゾマメタニシ科マメタニシ属2種（新生腹足類：クビキレガイ上科）の同定，解剖学的再記載および属の地位。最近，本州の淡水域でエゾマメタニシ科の外來種2種が発見された。両種は形態の検討およびミトコンドリアDNAの分子系統学的解析により，主に中国での分布が知られている *Pseudovivipara eximia* (Frauenfeld, 1864) オオマメタニシと *Parafossarulus longicornis* (Benson, 1842) コガシラマメタニシに同定された。この2種は解剖学的に互いに類似し，分子系統樹では *Pa. manchouricus* (Bourguignat, 1861) マメタニシとともに単系統群に含まれる。したがって *Parafossarulus* Annandale, 1924は *Pseudovivipara* Annandale, 1918の新参異名とみなされる。日本のオオマメタニシ移入個体群は本州北～中部の5県（青森・新潟・茨城・千葉・滋賀）で記録され，コガシラマメタニシは山梨県河口湖にのみ定着が確認されている。後種は滋賀県琵琶湖附近で中部更新統化石の産出が報告されており，その時代には日本にも分布していたものの，のちに絶滅した種である。

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INTRODUCTION

Introduced species often cause ecological, economic, and public health problems (Bellard et al., 2016; Pratt et al., 2017; Chinchio et al., 2020). Among the “One Hundred of the World’s Worst Invasive Alien Species,” six molluscan species have been identified due to their severe impacts on human society (ISSG, 2022). Of these, two are freshwater taxa, namely the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), which has caused economic losses exceeding US\$100 million (Strayer, 2008), and the golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), a major pest in rice cultivation with resulting secondary environmental and human health risks because of the use of chemical control measures (Halwart, 1994). Furthermore, molluscs frequently serve as intermediate hosts for parasites that cause human disease, and some introduced species are responsible for snail-borne parasitic infections (Q.-P. Wang et al., 2011; Lu et al., 2018). However, because public interest in molluscs is generally not high, and taxonomic knowledge and resources for molluscan research remain limited (Rosenberg et al., 2022), introduced molluscan species are often overlooked and only recognized after their establishment or spread (e.g., Fukuda, 2004; Herbert, 2012; Saito et al., 2018). Given these challenges, clarifying the taxonomy and distribution of introduced molluscs is a crucial task for malacologists.

The Japanese Archipelago is recognized as a biodiversity hotspot, with especially notable species diversity among terrestrial and freshwater molluscs (Strong et al., 2007; Cameron, 2016; Böhm et al., 2020). At the same time, Japan is a densely populated country with extensive anthropogenic activities, and accordingly, many introduced molluscs have been reported (e.g., Kurozumi, 2000; Hirano et al., 2022; Saito, 2022). Nevertheless, many aspects of introduced molluscs, such as the distributions and impacts on native fauna, remain poorly understood. Even species identification, which is fundamental to the management of introduced species, remains problematic (Kurozumi, 2000; Masuda & Uchiyama, 2004).

This study focused on the bithyniid genera *Parafossarulus* Annandale in Annandale & Prasad, 1924, and *Pseudovivipara* Annandale, 1918, in Japan where *Parafossarulus manchouricus* (Bourguignat, 1861) is the only native taxon of the genus, although the Japa-

nese populations have often been treated as a subspecies *Parafossarulus manchouricus japonicus* (Pilsbry, 1901) because their shell exhibits conspicuous spiral cords (Pilsbry, 1901; Habe, 1990; Masuda & Uchiyama, 2004; Fukuda, 2020a, b).

Species of *Parafossarulus* and *Pseudovivipara* are intermediate hosts of parasites, notably the Chinese liver fluke *Clonorchis sinensis* (Cobbold, 1875) 肝吸虫 causing clonorchiasis (Lu et al., 2018). Consequently, in the context of parasitology, the distribution of *Parafossarulus manchouricus japonicus* has been extensively studied, demonstrating that this subspecies was widely distributed across mainland Japan from the Tōhoku District to Kyūshū (Sugihara, 1979). However, the distribution range appears to be rapidly shrinking due to the deterioration of freshwater habitats by landfilling, reclamation, embankments, and pollution, and as a result, the subspecies has been evaluated as one of the most critically endangered taxa among freshwater gastropods of Japan (Fukuda, 2020a, b).

Despite their relevance as parasite hosts and conservation concerns, *Parafossarulus* and *Pseudovivipara* have not been critically examined taxonomically (e.g., Prozorova & Rasshepkina, 2017), and their phylogenetic relationships remain largely unresolved. A few studies using electrophoresis-based methods (B. Pan & Ji, 1995; B.-P. Pan & Y.-G. Zhang, 2002; B.-P. Pan & Y. Yang, 2003) suggested that *Parafossarulus manchouricus* [as *Parafossarulus striatulus* (W. H. Benson in Cantor, 1842)], *Parafossarulus longicornis* (Benson, 1842) (as *Alocinma longicornis*), and *Pseudovivipara eximia* (Frauenfeld, 1864) (as *Parafossarulus eximius*) are genetically distinct. However, due to methodological and sampling limitations, these studies did not provide further information on phylogenetic relationships.

The taxonomic relationships between *Parafossarulus* and *Pseudovivipara* require resolution. *Pseudovivipara* was proposed by Annandale (1918b) for *Pseudovivipara hypocrites* Annandale, 1918. The type species has been often regarded as a junior synonym of *Pseudovivipara eximia* (e.g., Zilch, 1938; Abbott, 1948; Habe, 1973). *Pseudovivipara eximia* has often been treated as *Parafossarulus eximius* (e.g., Yen, 1939; Lu et al., 2018). If *Pseudovivipara eximia* (= *Pseudovivipara hypocrites*) is closely related to *Parafossarulus manchouricus*, the type species of *Parafossa-*

rulus, then *Parafossarulus* should be treated as a junior synonym of *Pseudovivipara*. The possibility that they are synonymous has already been suggested (Ponder, 2003: 109), but it remains untested.

We discovered two additional *Parafossarulus/Pseudovivipara* species from Japan through our field surveys conducted in the 2000s. In this study, we examine and compare their morphological and molecular characteristics with *Parafossarulus manchouricus japonicus*. Our aims of this study were to (1) determine their taxonomic identity, (2) assess the phylogenetic relationships between *Parafossarulus* and *Pseudovivipara*, and (3) redescribe the introduced *Parafossarulus/Pseudovivipara* species in Japan. This study also results in updating the taxonomy of the Asian taxa attributed to *Parafossarulus* and *Pseudovivipara*.

MATERIALS AND METHODS

Taxon Sampling

Two introduced *Parafossarulus/Pseudovivipara* species were collected from five localities across three lakes in Japan during our field surveys (Fig. 1; Table 1). These contained two distinctly different morphs. In addition, misidentifications of one of the present species as “*Parafossarulus manchouricus japonicus*” were found in some literature records (Nomura, 2010a, b; Seki, 2012; Kurozumi, 2022; Murayama et al., 2025). To compare and identify these *Parafossarulus/Pseudovivipara* spp. and to reveal the phylogenetic relationships between *Parafossarulus* and *Pseudovivipara*, we utilized *Parafossarulus manchouricus japonicus* from Japan, and *Parafossarulus longicornis* and *Pseudovivipara eximia* from China (Fig. 1; Table 1).

Abbreviations for Specimen Depository

CBM, The Natural History Museum and Institute, Chiba, Chiba; KUZ, Zoological Collection of Kyoto University, Kyoto; NHMUK, The Natural History Museum, London; OKCAB, Conservation of Aquatic Biodiversity, Faculty of Agriculture, Okayama University, Okayama; TUMC, Center for Northeast Asian Studies, Tohoku University, Sendai, Miyagi; UMZC, University Museum of Zoology, Cambridge, UK.

Specimen Preparation and Anatomical Examination

Live animals were removed from the shells without damage by applying the *niku-nuki* method (Fukuda et al., 2008) of boiling for ~5–10 s in hot water at 95°C. This was successful in all specimens on which it was tried. Then muscular tissue (a part of the foot) was removed from the soft parts and fixed in 99% ethanol (EtOH) for DNA analysis. The remaining soft parts were fixed in 5% neutral seawater formalin for anatomical examination (used and drawn in the present study).

Anatomical investigation was undertaken by HF using a Leica stereoscopic microscope with a drawing apparatus as described by Fukuda (2023) and Fukuda & Kubo (2024). The methods for the extraction of the radulae were those used by Fukuda & Mitoki (1995). The radulae, together with the protoconchs, were examined by NS using a JSM-6510LV scanning electron microscope (SEM; JEOL Ltd., Tokyo, Japan) after platinum coating using a JEC-3000FC (JEOL Ltd.) sputter coater at the University of Tokyo.

Molecular Examination

Total DNA was extracted from each specimen using the DNeasy Blood and Tissue kit (Qiagen Inc., Hilden, Germany), following the manufacturer's protocol for animal tissues. To identify the collected specimens from Japan and estimate the phylogenetic relationship between *Parafossarulus* and *Pseudovivipara* spp., two mitochondrial loci (cytochrome oxidase subunit 1 [CO1] and 16S ribosomal DNA [16S]) were selected as molecular markers. Prior to DNA amplification, the total DNA samples were purified using the GeneReleaser DNA Extraction kit (Kaneka Eurogentec S.A., Seraing, Belgium). These loci were amplified using polymerase chain reaction (PCR) with the primers listed in Table 2. PCR amplifications were performed according to the protocols specified in Table 2, using KOD FX Neo DNA polymerase (Toyobo, Osaka, Japan). Each amplified fragment was purified using ExoSAP-IT (Affymetrix Inc., California, USA) and sequenced by Eurofins Genomics (Tokyo, Japan). All newly obtained sequences were deposited in the GenBank database (PV955415–PV955427, PV955662–PV955672).

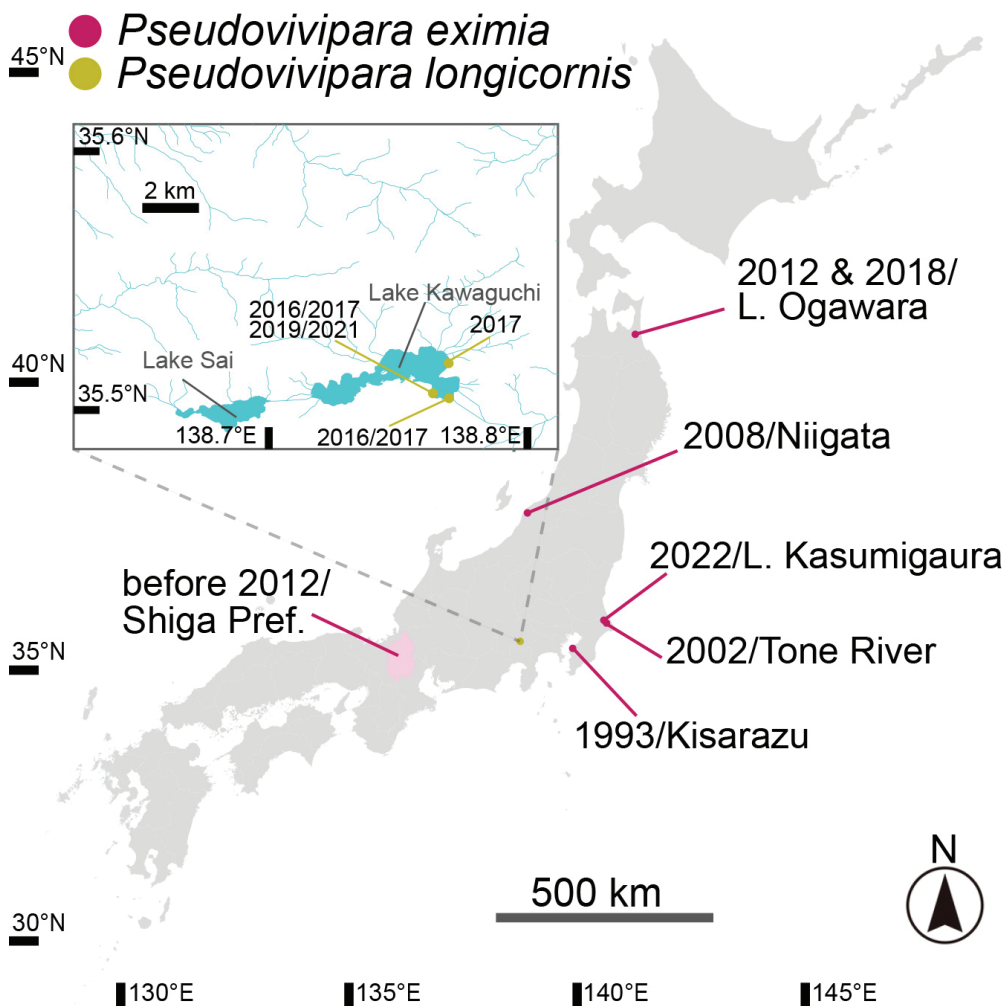


FIG. 1. Maps show the recorded localities of *Pseudovivipara* spp. in Japan. Red circles indicate *Pseudovivipara eximia* (Frauenfeld, 1864), and yellow circles indicate *Pseudovivipara longicornis* (Benson, 1842). The number with the locality indicates the year of collection. The record in Niigata Prefecture is based on Nomura (2010a, b) and Murayama et al. (2025). The record from Shiga Prefecture is based on Seki (2012), but the exact location was not specified.

Phylogenetic analyses were conducted for each DNA locus. Reference bithyniid sequences (up to three per species/subspecies) were retrieved from GenBank (Table 1), and the genus *Bythinella* Moquin-Tandon, 1856 was selected as an outgroup based on the phylogenetic results of Wilke et al. (2023). All sequences were aligned using MUSCLE v3.8.31 with the default settings (Edgar, 2004). To minimize alignment uncertainty in

the 16S dataset, poorly aligned regions were trimmed using trimAl v1.2 (Capella-Gutiérrez et al., 2009). After the alignments, identical haplotypes were collapsed using FaBox 1.61 (Villesen, 2007). The appropriate evolutionary models and partitioning schemes for each region were determined using PartitionFinder 2 (Lanfear et al., 2016), based on the Bayesian Information Criterion (BIC; Table 3). Phylogenetic trees were estimated under the selected

TABLE 1. The molecular samples in this study. The combination of genus and species names follows MolluscaBase (2024a, b, 2025a, b) and the species identifications basically followed the original papers and original registrations on GenBank. However, *Parafossarulus longicornis* instead of *Gabbia longicornis* and *Pseudovivipara eximia* instead of *Parafossarulus eximius* were used based on our literature consideration (see Systematics section). See also the references for further information on the localities. 1, This is originally published as *Bithynia* sp.; however, as the author later used *Gabbia cf. stenothyroides* for this entry (Ng et al., 2024), we treated it as the latter 2, This CO1 sequence was published as *Boreoelona ussuriensis* (Büttner & Ehrmann, 1927); however, based on the shell image in the supplementary file of the original article (Z. Hu et al., 2024), it was re-identified as *Parafossarulus cf. manchouricus*.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Bithynia cettinensis</i> Clessin, 1887	11Z22	Croatia, Zvečanje	MN013042	-	H47	-	Pešić et al., 2019
<i>Bithynia leachii</i> (Sheppard, 1823)	B1638-ZVLe16-06	Russia, Vyborg	MW138414	-	H59	-	GenBank
	B1533-BVIt03-52	Italy, Viterbo, L. Bolsena	MW138417	-	H57	-	GenBank
	B1511-BVIt01-01	Italy, Viterbo, L. Bolsena	MW138420	-	H58	-	GenBank
	DM1238	unknown	-	MT410857	-	H24	GenBank
<i>Bithynia pseudemmericia</i> Schütt, 1964	4343	Turkey, Isparta	OP339796	OP345365	-	H27	Wilke et al., 2023
<i>Bithynia tentaculata</i> (Linnaeus, 1758)	Bite4346	Turkey, Isparta, L. Egridir	FJ160291	FJ160288	H64	H26	Benke et al., 2009
	SERCIN- VERT1776	USA, District of Columbia	MK308073	-	H48	-	GenBank
	B1708- SGGB16-08	Belarus, Gomel, Chenki	MW138435	-	H49	-	GenBank
	AF445344	Germany, Müggelsee	-	AF445344	-	H21	Hausdorf et al., 2002
	HPL006	USA, New York	-	JX970531	-	H22	Wilke et al., 2012
<i>Bithynia troschelii</i> (Paasch, 1842)	B0021- MMCh08-01	Russia, Chelyabinsk	MW138384	-	H54	-	GenBank
	B0200-VKko11-03	Russia, Komi Republic	MW138410	-	H56	-	GenBank
	B0613-NENk-0613	Russia, Novosibirsk	MW138413	-	H56	-	GenBank
<i>Bithynia transsilvanica</i> (Bielz, 1853)	4919	Germany, Siemz-Niendorf	OP339799	OP345368	H55	H29	Wilke et al., 2023

(continues)

TABLE 1. Continued.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Bithynia zeta</i> Glöer & Pešić, 2007	1W32	Montenegro, Drume	MN013041	-	H62	-	Pešić et al., 2019
	1W30	Montenegro, Drume	MN013039	-	H62	-	Pešić et al., 2019
	1W29	Montenegro, Drume	MN013038	-	H62	-	Pešić et al., 2019
	ZMB191552	Indonesia, L. Poso	KY574006	-	H30	-	Van Bocxlaer et al., 2017
<i>Bithynia</i> sp.							
<i>Boreolona contortrix</i> (Lindholm, 1909)	B1538-GE-Bu01-01	Russia, Buryatia Republic, L. Gunda	MW138421	-	H50	-	GenBank
	B1545-GE-Bu01-08	Russia, Buryatia Republic, L. Gunda	MW138424	-	H50	-	GenBank
	B0079-ZCBk07-03	Russia, Buryatia Republic, L. Baikal	MW138427	-	H51	-	GenBank
	Bf3	Thailand	MT379921	-	H15	-	Bunchom et al., 2020
<i>Digoniostoma funiculatum</i> (B. Walker, 1927)	BfH2	Thailand	MW832388	-	H14	-	Bunchom et al., 2021
	BfH14	Thailand	MW832396	-	H16	-	Bunchom et al., 2021
	BfLpu4	Thailand	-	MW305292	-	H17	Bunchom et al., 2021
	BfS07-2	Thailand	-	MW305279	-	H17	Bunchom et al., 2021
<i>Digoniostoma siamense goniomphalos</i> (Morelet, 1866)	BfC18-2	Thailand	-	MW305267	-	H17	Bunchom et al., 2021
	CKc3	Cambodia, Khampong Cham	MN399641	-	H17	-	Tantrawatpan et al., 2019
	BsgH15	Thailand	MW832397	-	H19	-	Bunchom et al., 2021

(continues)

TABLE 1. Continued.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Digoniostoma siamense goniomphalos</i> (continued)	BsgH50	Thailand	MW832417	-	H18	-	Bunchom et al., 2021
	BsgS11-4	Thailand	-	MW305345	-	H18	Bunchom et al., 2021
	BsgS08-3	Thailand	-	MW305338	-	H19	Bunchom et al., 2021
	BsgA20-4	Thailand	-	MW305328	-	H19	Bunchom et al., 2021
<i>Digoniostoma siamense siamense</i> (I. Lea, 1856)	Bss3	Thailand	MT379912	-	H21	-	Bunchom et al., 2020
	BssH148	Thailand	MW832423	-	H22	-	Bunchom et al., 2021
	BssH195	Thailand	MW832462	-	H20	-	Bunchom et al., 2021
	BssS19-5	Thailand	-	MW305394	-	H20	Bunchom et al., 2021
	BssS19-1	Thailand	-	MW305390	-	H3	Bunchom et al., 2021
<i>Gabbia erawanensis</i> Chitramvong & Upatham, 1990	BssA07-4	Thailand	-	MW305383	-	H3	Bunchom et al., 2021
	JUT094	Thailand, Erawan	KY118673	-	H4	-	Kulsantiwong et al., 2013
	JUT091	Thailand, Erawan	KY118678	-	H4	-	Kulsantiwong et al., 2013
<i>Gabbia kiusiensis</i> (S. Hirase, 1927)	JUT093	Thailand, Erawan	KY118680	-	H4	-	Kulsantiwong et al., 2013
	KMC0002	Japan, Aichi	LC779811	-	H52	-	GenBank

(continues)

TABLE 1. Continued.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Gabbia kiusiensis</i> (continued)	G0455	Japan, Gifu	LC779809	-	H52	-	GenBank
	M754	Japan, Aichi	LC779792	-	H52	-	GenBank
	SOKN002	South Korea	KF966538	-	H53	-	GenBank
<i>Gabbia misella</i> (Gredler, 1884)	JUT096	Thailand, Mae Rim	KY118681	-	H10	-	Kulsantiwong et al., 2013
<i>Gabbia pygmaea</i> (Preston, 1908)	JUT097	Thailand, Mae Rim	KY118682	-	H10	-	Kulsantiwong et al., 2013
	JUT095	Thailand, Mae Rim	KY118683	-	H10	-	Kulsantiwong et al., 2013
	ABT41	Singapore, aquarium	KU318328	KU318355	H31	H5	Ng et al., 2016
<i>Gabbia cf. stenothyroides</i> (Dohm, 1857)	SIN20_02	Singapore	OR714244	-	H31	-	Ng & Tan, 2024
	SIN20_01	Singapore	OR714245	-	H32	-	Ng & Tan, 2024
	JUT180	Thailand	KY118693	-	H11	-	Kulsantiwong et al., 2013
<i>Gabbia wykoffi</i> (Brandt, 1968)	JUT143	Thailand	KY118728	-	H12	-	Kulsantiwong et al., 2013
	JUT046	Thailand	KY118740	-	H13	-	Kulsantiwong et al., 2013
	24452	Kenya, Mubwokhola	OP339804	OP345373	H6	H4	Wilke et al., 2023
<i>Gabbiella humerosa</i> (Martens, 1879) <i>Gabbiella humerosa kivuensis</i> Mandahl-Barth, 1968	UGSB 28072	Rwanda, Lake Kivu	PP510645	-	H7	-	Dusabe et al., 2024
	UGSB 27901	Rwanda, Lake Kivu	PP510648	-	H8	-	Dusabe et al., 2024
	UGSB 27868	Rwanda, Lake Kivu	PP510647	-	H9	-	Dusabe et al., 2024

(continues)

TABLE 1. Continued.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Gabbiella</i> sp.	24455	Uganda, Kiranga	OP339805	OP345374	H5	H3	Wilke et al., 2023
<i>Helicostoa sinensis</i> Lamy, 1926	MNH- IM-2000-33309	China, Chongqing	OP503947	OP503947	H33	H23	Wilke et al., 2023
<i>Hydrobioides nassa</i> (Theobald, 1866)	PYO-C2404	Thailand, Nakhon Sawan	MK640160	-	H34	-	Bunchom et al., 2019
	KPT-C0502	Thailand, Lopburi	MK640168	-	H35	-	Bunchom et al., 2019
	NSN-C0304	Thailand, Salokbat	MK640181	-	H36	-	Bunchom et al., 2019
	NSN-HnC0305	Thailand, Salokbat	-	MK629223	-	H31	Bunchom et al., 2019
	NSN-HnA1304	Thailand, Nakhon Sawan	-	MK629217	-	H31	Bunchom et al., 2019
	PYO-HnC2905	Thailand, Nakhon Sawan	-	MK629208	-	H31	Bunchom et al., 2019
<i>cf. Hydrobioides</i> sp.	5748	Myanmar, Khaungtaing	OP339806	OP345375	H3	H30	Wilke et al., 2023
<i>Parafossarulus longicornis</i> (Benson, 1842)	TUMCh320-2	China, Nanjing	PV955423	PV955668	H40	H11	This study
	TUMCB136	Japan, Yamanashi, L. Kawaguchi	PV955424	PV955669	H41	H12	This study
	TUMCB142	Japan, Yamanashi, L. Kawaguchi	PV955425	PV955670	H41	H12	This study
	TUMCh320-1	China, Nanjing	PV955426	PV955671	H42	H13	This study
<i>Parafossarulus cf. manchouricus</i> (Bourguignat, 1861)	SZ-2011	China, Anhui	HQ623174	HQ623158	H44	H15	Wilke et al., 2012
	TLBU ²	China, Inner Mongolia	OR990564	-	H45	-	Z. Hu et al., 2024

(continues)

TABLE 1. Continued.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Parafossarus manchouricus japonicus</i> (Pilsbry, 1901)	TUMCB81	Japan, Shiga, L. Biwa	PV955427	-	H43	-	This study
	TUMCB90	Japan, Shiga, L. Biwa	-	PV955672	-	H14	This study
<i>Pseudobithynia panetolis</i> Glöer, Albrecht, & Wilke, 2007	3283	Japan, Okayama	OP339803	OP345372	H46	H16	Wilke et al., 2023
	5167	Greece, Thestieis	OP339800	OP345369	H61	H25	Wilke et al., 2023
<i>Pseudobithynia pentheri</i> (Sturany, 1904)	4927	Turkey, Kayseri	OP339801	OP345370	H63	H28	Wilke et al., 2023
<i>Pseudobithynia trichonis</i> Glöer, Albrecht, & Wilke, 2007	5161	Greece, Thermo	OP339802	OP345371	H60	H25	Wilke et al., 2023
<i>Pseudovivipara eximia</i> (Frauenfeld, 1864)	TUMCB258	China, Nanjing	PV955422	PV955662	H39	H6	This study
	TUMCB259	China, Nanjing	PV955415	PV955667	H37	H10	This study
	TUMCB260	China, Nanjing	PV955416	PV955665	H37	H9	This study
	TUMCB313	Japan, Aomori	PV955417	-	H37	-	This study
	TUMCB321	Japan, Aomori	PV955419	PV955664	H37	H8	This study
	Nex713	Japan, Ibaraki, L. Kasumigaura (L. Sotona-sakaura)	PV955420	-	H37	-	This study
	Nex715	Japan, Ibaraki, L. Kasumigaura (L. Sotona-sakaura)	PV955421	PV955666	H37	H9	This study

(continues)

TABLE 1. Continued.

Taxon	Isolate	Locality	GenBank Acc. No. CO1	GenBank Acc. No. 16S	Hap. No. CO1	Hap. No. 16S	Reference
<i>Pseudovivipara eximia</i> (continued)	TUMCB314	Japan, Aomori	PV955418	PV955663	H38	H7	This study
<i>Wattebledia baschi</i> Brandt, 1968	JUT133	Thailand, Phunphin	KY118766	-	H25	-	Kulsantiwong et al., 2013
	JUT130	Thailand, Phunphin	KY118769	-	H25	-	Kulsantiwong et al., 2013
	JUT128	Thailand, Phunphin	KY118771	-	H26	-	Kulsantiwong et al., 2013
<i>Wattebledia crosseana</i> (Wattebled, 1884)	JUT217	Thailand	KY118792	-	H27	-	Kulsantiwong et al., 2013
	JUT017	Thailand	KY118794	-	H28	-	Kulsantiwong et al., 2013
	JUT209	Thailand	KY118798	-	H29	-	Kulsantiwong et al., 2013
<i>Wattebledia siamensis</i> Möllendorff, 1902	JUT106	Thailand, Khon Kaen	KY118799	-	H23	-	Kulsantiwong et al., 2013
	JUT102	Thailand, Khon Kaen	KY118802	-	H23	-	Kulsantiwong et al., 2013
	JUT100	Thailand, Khon Kaen	KY118804	-	H24	-	Kulsantiwong et al., 2013
Outgroups							
<i>Bythinella viridis</i> (Poiret, 1801)	2949/2951	France, Fontaine du Gris	FJ029099	FJ028884	H2	H1	Benke et al., 2009
<i>Bythinella reyniesii</i> (Dupuy, 1851)	6293	Germany, Kaltennordheim	FJ029019	FJ028854	H1	H2	Benke et al., 2009

TABLE 2. Primers and PCR conditions in this study.

Locus	Primer	Sequence 5'–3'	PCR condition	Reference
CO1	LCO1490	GGTCAACAAATCATAAAGATATTGG	94°C 2 min, (98°C 10 s, 48°C 30 s, 68°C 25 s) × 36, 68°C 1 min	Folmer et al., 1994
	HCO2198	TAAACTTCAGGGTGACCAAAAAATC		
16S	16Sar-L	CGCCTGTTTATCAAAAACAT	94°C 2 min, (98°C 10 s, 52°C 30 s, 68°C 20 s) × 29, 68°C 1 min	Palumbi et al., 1991
	16Sbr-H	CCGGTCTGAAGTCAGATCACGT		

evolutionary models and partitioning schemes. Maximum likelihood (ML) analyses were conducted using IQ-TREE2 v2.3.6 (Minh et al., 2020) with the -p option, which applies a shared set of branch lengths across partitions while allowing each partition to evolve at its own rate. Each tree topology was assessed using ultra-fast bootstrapping (UFB; Hoang et al., 2017; -B in IQ-TREE2 option) with 5,000 replicates, the Shimodaira-Hasegawa approximate likelihood ratio test (aLRT; Kishino & Hasegawa, 1989; Shimodaira & Hasegawa, 1999; -alrt) with 5,000 replicates, and a Bayesian-like transformation of aLRT (aBayes; Anisimova et al., 2011; -abayes). Bayesian inference (BI) analyses were performed using MrBayes 3.2.7a (Ronquist & Huelsenbeck, 2003). The MrBayes run included four simultaneous chains for one million generations, with tree sampling every 1,000 generations. After examining convergence and ensuring an effective sample size (ESS; > 500) using Tracer v1.7 (Rambaut et al., 2018), the first 101 trees were discarded as burn-in. The remaining trees were used to infer consensus phylogeny.

SYSTEMATICS

Superfamily Truncatelloidea J. E. Gray,
1840 クビキレガイ上科
Family Bithyniidae J. E. Gray, 1857
エゾマメタニシ科

Genus *Pseudovivipara* Annandale, 1918b
マメタニシ属

Pseudovivipara Annandale, 1918b: 309.

Type species: *Pseudovivipara hypocrites* Annandale, 1918b (= *Vivipara eximia* Frauenfeld, 1864 オオマメタニシ), by monotypy.

Synonym: *Parafossarulus* Annandale, in Annandale & Prashad, 1924: 28, **n. syn.** Type species: *Paludina striatula* Benson in Cantor, 1842: 488 (junior primary homonym of *Paludina striatula* Deshayes, 1825 in 1824–1837: 133, no. 12, pl. 15, figs. 15, 16, thus invalid; = *Bythinia* [sic] *manchourica* Bourguignat, 1861: 535, pl. 24, figs. 11–13; ?= *Bithynia striatula* var. *japonica* Pilsbry, 1901: 405–406; Pilsbry, 1902: 121, pl. 9, figs. 9–12 マメタニシ), by original designation.

Diagnosis

Shell conical to globose, thick; spiral cords present or absent. Protoconch of approximately one whorl; surface smooth except fine spiral striae. Operculum pyriform, paucispiral, calcified, thick, flat, opaque white; outer surface covered with thin horny layer; muscle scar occupying most of inner side. Head-foot pale grey with many yellowish or white spots; cephalic tentacles long; neck lobe distinct,

TABLE 3. The evolutionary models adopted for phylogenetic analyses in this study. These models were selected using PartitionFinder 2 (Lanfear et al., 2016).

Alignment	Evolutionary model for IQtree	Evolutionary model for MrBayes
CO1 (Codon Position 1/2/3)	GTR+G/TRN+G/HKY+I	GTR+G/GTR+G/HKY+I
16S	GTR+G	GTR+G

U-shaped. Gill well developed, consisting of 70–150 long, narrow filaments. Osphradium slender, elongate fusiform. Kidney extending forwards through mantle roof, with anterior lobe lying between rectum and gill. Radula taenioglossate; central teeth trapezoid, with three or four pairs of basal cusps laterally; lateral teeth with small cusps; inner marginal teeth with several tiny cusps; outer marginal teeth narrower than inner marginal teeth, with sharp cusps. Rectum straight on mantle roof. Testis very large, occupying two apical whorls; seminal vesicle well developed, highly convoluted. Prostate elongate oval, consisting of simple mass of small cells. Penis with long, flat accessory lobe; black glandular area present; accessory gland tubular, convoluted, buried in cephalic cavity, reaching inside of accessory lobe. Ovary large, bright orange. Renal (coiled) oviduct very narrow, fragile, with some distinct loops. Seminal receptacle variable in size, lying at middle portion of renal oviduct. Bursa copulatrix long, slender sac, lying on left side of capsule gland, opening anteriorly to ventral channel inside capsule gland; bursal content reddish brown. Female genital opening terminal as short slit. Cerebral commissure weakly developed. Tentacular nerves divided into two or three nerves distally. Right pleural and supraoesophageal ganglia abutting each other; pleuro-supraoesophageal connective rudimentary. Suboesophageal ganglia distinct, globular, separated from left pleural ganglion by distinct constriction. Globular propodial ganglia distinct. Metapodial ganglion and commissure not found.

Remarks

Our phylogenies supported the monophyly of *Parafossarulus* and *Pseudovivipara*, with species attributed to these two genera forming closely related sister clades (Figs. 104, 105). Each clade includes the type species, and both morphological similarity and genetic relatedness between *Parafossarulus* and *Pseudovivipara* provide no justification for maintaining them as different genera. Accordingly, *Parafossarulus* is regarded as a junior synonym of *Pseudovivipara*. At present, three species are included: *Pseudovivipara eximia*, *Pseudovivipara longicornis*, and *Pseudovivipara manchourica*.

Relationships among *Pseudovivipara* and other bithyniid genera are still obscure. *Parabithynia* Pilsbry, 1928, to which *Pseudovi-*

vipara longicornis has sometimes been attributed (e.g., Yu & H. Wang, 1977) and the type species *Parabithynia physcus* (Annandale, 1918a) from Inle Lake, Myanmar, exhibits morphological similarity to *Pseudovivipara*, especially to *Pseudovivipara longicornis*. However, a recent molecular phylogeny suggested that *Parabithynia physcus* is included in *Hydrobioides* G. Nevill, 1885, and is genetically different from *Parafossarulus* (L.-J. Zhang et al., 2025).

The internal anatomy of the three species investigated below is similar to each other but the shell varies from ovate conic with distinct spiral cords (*Pseudovivipara eximia* and *Pseudovivipara manchourica japonica*) to globose with a smooth surface (*Pseudovivipara longicornis*). Among the three congeners, some differences are found in the radula, the reproductive system, and the central nervous system: see below for a comparison with *Pseudovivipara manchourica japonica*.

Pseudovivipara eximia (Frauenfeld, 1864)

沼螺, 钝角沼螺 (刘 Y.-Y. Liu, 1961: 123, 127, 131), 大沼螺 (刘等 Y.-Y. Liu et al., 1979: 37) in Chinese

オオマメタニシ (大豆田螺, Ō-mame-ta-nishi; 瀧庸 Taki, 1940: 116),

フトスジマメタニシ (太筋豆田螺, Futo-suji-mame-ta-nishi; 黒田 Kuroda, 1949: 106) in Japanese

Figs. 2, 18, 19, 22–26, 32–37, 44, 47–51, 62, 65–68, 78, 79, 84, 87–91

Vivipara eximia Frauenfeld, 1864b: 149–150, pl. 5, fig. 2; 1864a: 604, no. 317; Brusina, 1870: 936.

Vivipara chinensis Frauenfeld, 1864a: 586, no. 155, with *Vivipara eximia* as synonym.

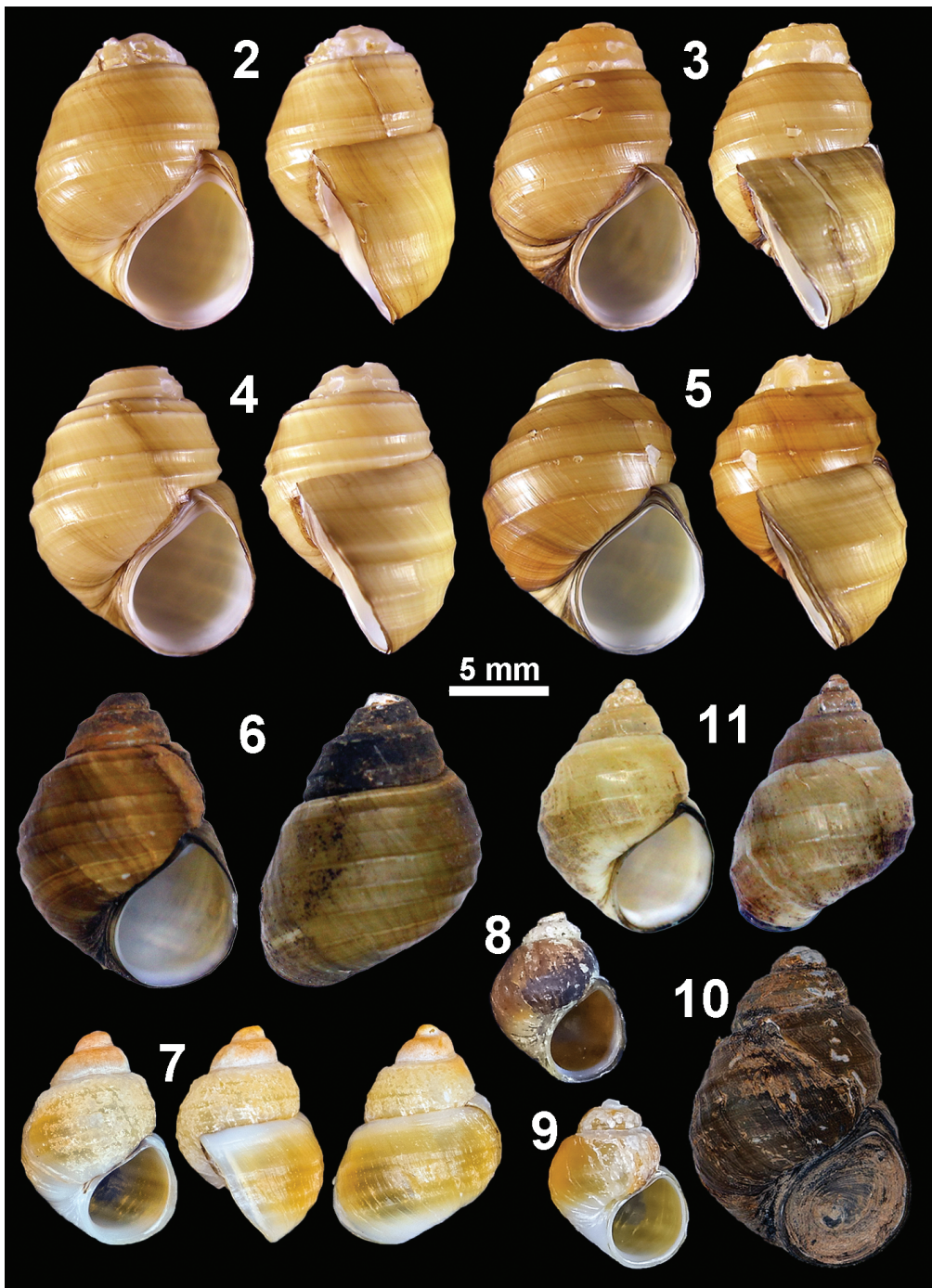
Bithynia subangulata Martens, 1875: 133, 134, no. 18, pl. 3, fig. 4; Gredler, 1887: 175, 176, no. 8; Heude, 1890: 170, no. 469, pl. 42, fig. 7, 7a, b (head with penis), with *Bithynia grandis* as synonym.

Bythinia [sic] subangulata.—Gredler, 1878: 105, no. 13; Möllendorff, 1888: 133, no. 2; Faust, 1924: 298.

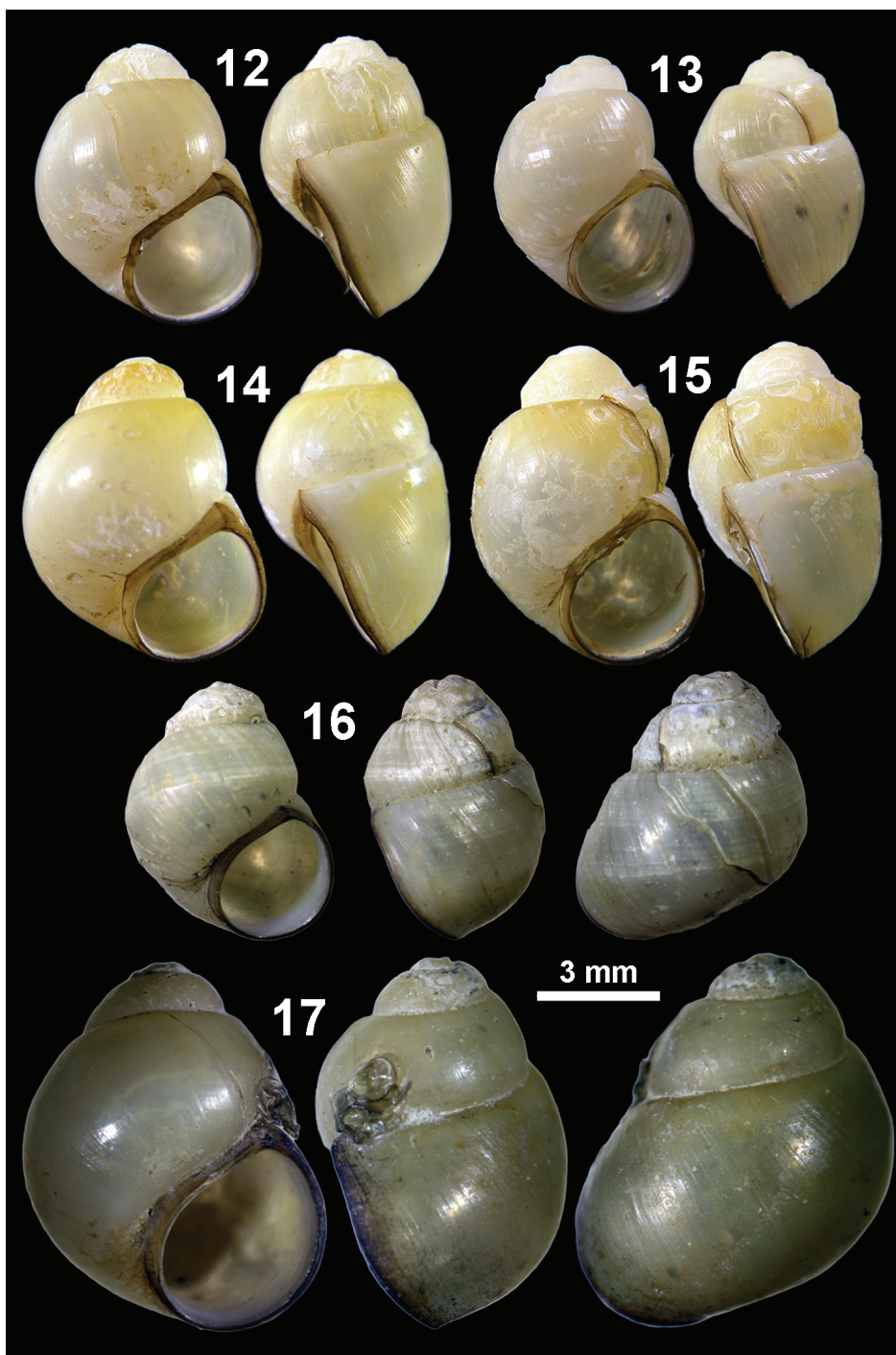
Paludina eximia.—Möllendorff, 1881: 43, no. 26.

Bythinia [sic] grandis Möllendorff, 1888: 132, 133, no. 1, pl. 4, fig. 1a, b.

Pseudovivipara hypocrites Annandale, 1918b: 310–312, text-figs. 4 (head with penis), 5 (radula), pl. 10, fig. 3, 3a; Walker, 1927: 221–223, text-fig. 4 (radula), pl. 14, fig. 9; Kuroda,



FIGS. 2–11. Shells of *Pseudovivipara eximia* (Frauenfeld, 1864). (2–6) Lake Ogawara, Aomori Prefecture, Japan (2–5, OKCAB M29800; 6, TUMC B314); (7–9) Lake Kasumigaura, Ibaraki Prefecture, Japan (KUJ Z4327); (10) Tone River, between Ibaraki and Chiba prefectures, Japan (CBM-ZM162779); (11) Nanjing, China (TUMC B260).



FIGS. 12–17. Shells of *Pseudovivipara longicornis* (Benson, 1842). (12–16) Lake Kawaguchi, Yamanashi Prefecture, Japan (12, OKCAB M30008; 13, OKCAB M30015; 14, 15, OKCAB M30004; 16, TUMC B142); (17) Nanjing, China (TUMC h320-2).

1949: 106, with *Parafossarulus sinensis* and *Parafossarulus eximius* as synonyms.

Parafossarulus subangulatus.—Walker, 1927: 218–220, pl. 14, fig. 7, with *Bythinia* [sic] *grandis* as synonym; Yen, 1937b: 7; Yen, 1939: 46, pl. 4, fig. 23 (“Paratypoid 25773”); Z. Sun et al., 2014: table 3.

Bulimus eximius.—Yen, 1936: 45.

Parafossarulus eximius.—Yen, 1937b: 22; 1939: 46, pl. 4, fig. 24 (“Hunan (25769, Typus von *Bithynia grandis* MlIdff”); 1942: 198; Abbott, 1948: 274, 277, fig. 8 [part], pl. 1, fig. 15, with *Bithynia subangulata*, *B. grandis*, and *Pseudovivipara hypocrites* as synonyms; Yen, 1948: 70; Dubois, 1951: 646, footnote 4; Y.-Y. Liu, 1961: 131; Kubota, 1962: 180, no. 227; Starobogatov, 1970: 201; Yamaguti, 1971: 816; Y.-Y. Liu et al., 1979: 24, 37, 131, 134, fig. 36, with *Vivipara exima* [sic], *Bithynia subangulata*, *B. grandis*, and *Pseudovivipara hypocrites* as synonyms; Combes et al., 1980: 185; R. Wang et al., 1988: 28, fig. 74; Huang & Z. Li, 1991: 58, 59, fig. 51; 1995: 102, no. 10; 105; B. Pan & Ji, 1995: 27, 31, tables 1, 2; Z. Li et al., 1995: 28; Y. Liu, 1998: 57, 58, fig. 65; B.-P. Pan & Y.-G. Zhang, 2002: 210, 212, 213, figs. 1–3, tables 1, 2; B.-P. Pan & Y. Yang, 2003: 7, 8, figs. 1–3, tables 2, 3; Z. Xie et al., 2005: 508; H.-J. Wang et al., 2006: 525, 526; Z.-Q. Hu et al., 2007: 525, no. 24; B. Pan et al., 2008: 809, no. 12; 2011: 253; 2016: 917, no. 20; Zhao et al., 2009: 1452, 1453, figs. 2–5, tables 1–3; Guo et al., 2009: 451, no. 8, 452; no. 17(18), fig. 8; 2015: 38, no. 7, 39; Shu et al., 2009: 1057; F. Gao et al., 2010: 2134, no. 15; D.-L. Li et al., 2011: 948; Y. Cai et al., 2014: tables 2, 3; J.-Y. Yang et al., 2014: 409, fig. 10, 410, no. 15; Y. Zhang et al., 2014: 19, 20, 22, 23; 2018: 62, table 2; Shu et al., 2014: 186; W. Zhang et al., 2015: 13; L. Chen et al., 2015: 125, fig. 9, table 2; H. Wang et al., 2015: 1239; Y. Wang et al., 2016: 191; Prozorova & Rasshepkina, 2017: 179, 180; Jia et al., 2018: 7013, 7017–7019; W. Zou et al., 2017: 1182; Kattel et al., 2018: 222, figs. 6, 7, 9, table 2; Lu et al., 2018: table 1; W. Wang, 2018: 126; D. Li et al., 2019: 14956–14958; L. Yang et al., 2019: 930, no. 13, 937 (pls. 1, 2), fig. E; Xing et al., 2019: appendix 1, no. 252; Z. Liu et al., 2020: 159, appendix 1, no. 22; Jiang et al., 2020: table A2; Jia et al., 2021: 1, 2, 4–7, figs. 2–4, table 1, appendix A, graphical abstract; F. Liu & Lu, 2021: 24; K. Wang et al., 2021: 3; L. Wang et al., 2021: 3, fig. 3, appendix A; L. Zou et al., 2021: 146, no. 10; Sheng et al., 2022: 6, 13; Fu et al., 2022: 6; J. Gao et al., 2023: 679; Ning et al., 2023: 011,

012, no. 1.3.1.2, text-fig. 8, pl. 4, figs. a–c, d (operculum), e (living animal), f (penis), g1–3 (radula); Q. Li et al., 2024: table 3, appendix 1; H. Zeng et al., 2024: 2, 5, 6, fig. 2; Y. Zhang et al., 2024: 5, 7, 11; Zhou et al., 2024: 4, table 1, fig. 2; Bai et al., 2024: appendix 2.

Pseudovivipara subangulata.—Zilch, 1938: 128–131, figs. 1 (“Paratypoid”), 2a, b (“Typus von *Bithynia grandis*”), 3 (“Zugleich Paratypoid von *Bithynia subangulata* und *Bithynia grandis*”), 4 (“Paratypoid von *Bithynia grandis*”), with *Bithynia grandis* and *Pseudovivipara hypocrites* as synonyms.

[No Latin name].—Taki, 1940: 116.

Bulimus (*Pseudovivipara*) *hypocrites*.—Miyadi & Habe, 1944: 363–365, no. 3, figs. 1e, f, 2A1–4 (radula).

Parafossarulus subangulata [sic].—Y.-Y. Liu, 1961: 123, 127, no. 12, pl. 1, fig. 9.

Pseudovivipara eximius [sic].—Habe, 1973: 318, with *Bythinia* [sic] *subangulata*, *Bythinia* [sic] *grandis*, and *Pseudovivipara hypocrites* as synonyms.

Parafossarulus eximius [sic].—Y. Liu et al., 1986: 72, 73, no. 9, pl. 1, fig. 9; J. Ma & H. Sun, 1997: 28, no. 12.

Parafossarulus euximius [sic].—Eschner, 2008: 21, 26.

Parafossarulus manchouricus japonicus.—Nomura, 2010a: unnumbered figs. (cover & back cover), 10, 13, 15, text-fig. 3; 2010b: 113, text-fig.; Seki, 2012: 78, text-fig.; Kurozumi, 2022: 234, text-fig. & cover; Murayama et al., 2025: 11, 15, 59, text-figs. [all misidentifications; not of Pilsbry, 1901].

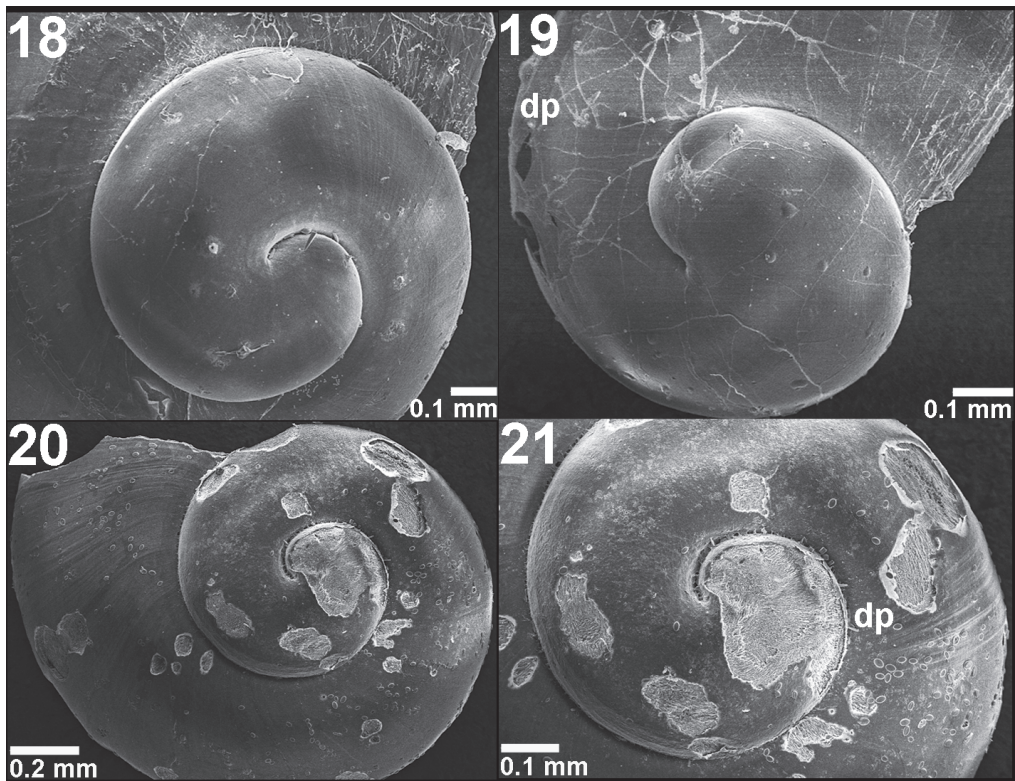
Material Examined

Qixia District, Nanjing City, Jiangsu Province, China, in a small pond 中华人民共和国江苏省南京市栖霞区 小池塘, April 24, 2018, collected by the authors (BY, TS, & TH). Three adults (sex unknown) and one juvenile (TUMC B258–260; Figs. 10, 26). Near Hanakiribashi Bridge, estuary of the Hanakiri-gawa River, southwestern coast of Lake Ogawara, Asahi-kita 4 chōme, Tōhoku-machi, Kamikita-gun, Aomori Prefecture, northern Honshū, 40°44′30.1″N, 141°16′33.8″E, among stones in standing water 青森県上北郡東北町旭北四丁目 小川原湖南西岸 花切川河口 花切橋附近, 止水 中転石間; August 5, 2018, collected by the first author (TS) & J. Koseki, five males, 15 females, three adults (sex unknown), and 16 juveniles (OKCAB M29800 and TUMC B313–314, B321; Figs. 2–6, 18, 19, 22–24, 32–37, 45, 62, 65–68,

78, 84, 87–91). Coast of Lake Sotonasakaura (a part of Lake Kasumigaura), Fukushima, Iwako-shi, Ibaraki Prefecture, central Honshū, 35°55'42.4"N, 140°35'42.6"E, among stones in standing water 茨城県潮来市福島 外浪逆浦, February 26, 2022, collected by the second author (NS) and T. Miyai, four females (KUZ Z4327; Figs. 7–9, 47–51). Tone River, between Takahama, Kamisu-shi, Ibaraki Prefecture and Omigawa, Katori-shi, Chiba Prefecture, central Honshū [~ 35°51'28.8"N, 140°38'06.3"E] 茨城県神栖市高浜と千葉県香取市小見川の間の利根川, November 8, 2002, collected by 平嶋賢治, one shell with operculum (CBM ZM162779; Fig. 10). Kaneda Fishing Port, Kisarazu-shi, Chiba Prefecture, central Honshū [~ 35°25'43.3"N, 139°54'16.7"E] 千葉県木更津市金田漁港, September 18, 1993, collected by 高谷正利, one empty shell (CBM ZM105197).

Description

Shell (Figs. 2–11). Large for family (measurements: Table 4), broadly ovate to ovate conic, thick, opaque, brownish. Spire variable from rather short to tall. Protoconch (Figs. 18, 19) with one weakly convex whorl (judging from specimens in egg mass just before hatching), surface smooth except for very fine spiral threads irregularly found near suture; demarcation point between protoconch and teleoconch obscure, with no varix or constriction (Figs. 18, 19). Teleoconch of ~ 2.5 rather convex whorls with distinct suture; surface weakly glossy with fine growth lines and a few thin, dark brown, slightly raised longitudinal varices; strong spiral cords on each whorl: three to six on last whorl and three or four on penultimate whorl. Aperture wide, pyriform, inside white;



FIGS. 18–21. Protoconchs (SEM). (18, 19) *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800); (20, 21) *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30008). dp, demarcation point between protoconch and teleoconch.

TABLE 4. Shell measurements of *Pseudovivipara eximia* (Frauenfeld, 1864) (mm).

		Shell length 殻長	Shell width 殻径	Body whorl length 体層長	Aperture length 殻口長	Aperture width 殻口径	Total number of whorls 螺層数
Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800)	♂ (n = 5)	15.9 ± 1.0 (14.9–17.1)	10.9 ± 0.6 (10.2–11.5)	13.2 ± 0.7 (12.2–14.2)	9.2 ± 0.6 (8.3–9.8)	6.6 ± 0.4 (6.0–6.9)	3.45 ± 0.11 (3.25–3.50)
	♀ (n = 15)	14.6 ± 1.1 (12.9–16.9)	10.6 ± 0.5 (9.4–11.2)	12.5 ± 0.8 (11.2–13.6)	8.6 ± 0.5 (7.8–9.5)	6.4 ± 0.5 (5.5–7.1)	3.43 ± 0.35 (3.00–4.25)
	Total (n = 20)	14.9 ± 1.2 (12.9–17.1)	10.6 ± 0.6 (9.4–11.5)	12.6 ± 0.8 (11.2–14.2)	8.8 ± 0.5 (7.8–9.8)	6.4 ± 0.4 (5.5–7.1)	3.44 ± 0.30 (3.00–4.25)
	♀ (n = 4)	10.5 ± 2.2 (8.7–13.6)	8.1 ± 1.5 (6.9–10.2)	8.5 ± 1.5 (7.4–10.6)	5.3 ± 0.9 (4.7–6.6)	4.0 ± 0.7 (3.4–5.0)	3.19 ± 0.24 (3.00–3.50)
Kasumigaura, Ibaraki Prefecture, Japan (KUZ Z432)							
Nanjing, China (TUMC B260)	Sex unknown	12.8	9.0	10.1	6.7	5.3	5.0
Total	♂ (n = 5)	15.9 ± 1.0 (14.9–17.1)	10.9 ± 0.6 (10.2–11.5)	13.2 ± 0.7 (12.2–14.2)	9.2 ± 0.6 (8.3–9.8)	6.6 ± 0.4 (6.0–6.9)	3.45 ± 0.11 (3.25–3.50)
	♀ (n = 19)	13.7 ± 2.2 (8.7–16.9)	10.0 ± 1.3 (6.9–11.2)	11.6 ± 1.9 (7.4–13.6)	7.9 ± 1.5 (4.7–9.5)	5.9 ± 1.1 (3.4–7.1)	3.38 ± 0.34 (3.00–4.25)
	Total (n = 25)	14.1 ± 2.2 (8.7–17.1)	10.2 ± 1.2 (6.9–11.5)	11.9 ± 1.8 (7.4–14.2)	8.1 ± 1.4 (4.7–9.8)	6.0 ± 1.0 (3.4–7.1)	3.46 ± 0.44 (3.00–5.00)

outer lip prosocline, with no varix; parietal lip rather long, nearly straight, covered with narrow, thick, shiny callus; columellar lip narrow, distinctly curved, with simple, blunt anterior end. Umbilicus closed or chink-like between parietal lip and last whorl.

Operculum (Figs. 22–26). Pyriform, calcified, thick, opaque; outer side flat, with rough concentric growth lines, covered with thin, pale brownish chitinous layer; nucleus eccentric, situated near middle part. Inner side opaque white, weakly convex, smooth, with muscle scar occupying most of inner surface.

Head-Foot (Figs. 32–35, 65–67). Majority of head-foot pale grey with many tiny yellowish spots on external surface. Cephalic tentacles (Figs. 65–67, ct) rather long, narrow, tapering with blunt tip. Distinct black eyes (e) in lateral bulges at outer bases just posterior to proximal end of cephalic tentacles. Snout (sn) short, wide, rectangular, distally bilobed; dorsal surface smooth. Exhalant siphon (epitaenial fold or neck lobe; nl) large, distinct, U-shaped lobe on right side of neck. Foot broad, elliptical; anterior edge simple; lateral edge almost parallel; posterior end simple, rounded. Sole broad, flat. Opening of anterior pedal mucous gland wide, transverse slit at anterior edge of foot; anterior pedal mucous gland composed of many small, white cells arranged in transverse row just behind slit.

Mantle Cavity. Long (depth of cavity ~ 25 mm), occupying approximately half of last whorl of shell. Dorsal mantle roof with a few broad, obscure bands of black pigmentation (Figs. 36, 37). Gill (ctenidial) filaments (Fig. 44, gf1, gf2) well developed, comprising ~ 140–150 conspicuous translucent filaments of gf1 and gf2 (*sensu* Davis et al., 1984: 170, fig. 6A); located on posterior portion of efferent vein near heart (auricle, au + ventricle, ve) on left side of cavity; gf1 long, narrow, abutting each other; gf2 arising from dorsal portion of each gf1, short, with same width as gf1, queueing with regular intervals. Osphradium (Fig. 44, os) long, narrow (~ 4 mm in length, 0.5 mm in width), elongate fusiform, containing short, elliptical osphradial ganglion (osg) at middle portion. Kidney colorless, translucent, extending forwards through mantle roof, with anterior lobe lying between rectum and gill. Hypobranchial gland not examined.

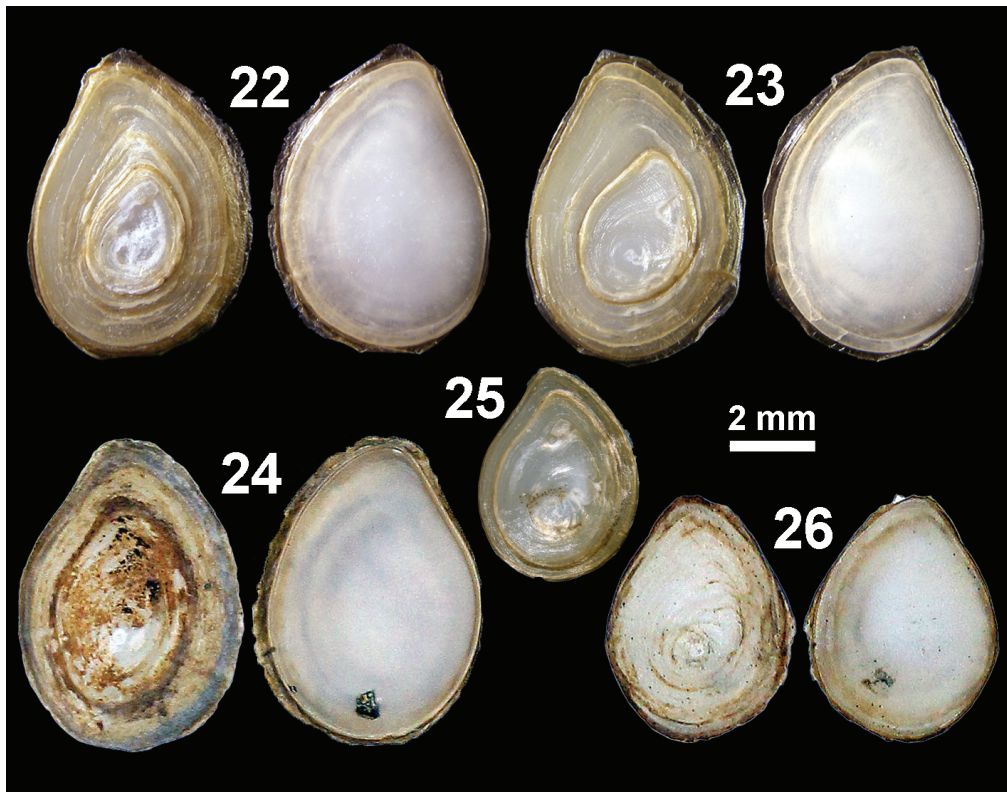
Digestive System. Mouth (Figs. 87, 88, m) opening between pair of muscular lips into buccal cavity. Buccal mass (bm) rather large, wide, occupying most of snout. Pair of

salivary glands (lsg, rsg) at posterior corner of dorsolateral sides of buccal mass, not passing through nerve ring; salivary glands colorless, short, simple, finger-like, strongly bent towards inner side. Buccal pouches probably weakly developed, not observed in gross anatomy. Radular sac short, not visible laterally.

Radula (Figs. 47–51). Taenioglossate, whole length ~ 1.4 mm (Fig. 47). Central teeth trap-ezoid; cutting edge approximately half of total width; with four small cusps on either side of median cusp; median cusp sharp, longest and widest, to three to four times as wide as adjacent cusps; lateral edges nearly straight, parallel-sided on upper part, then spread at angle of ~ 30° to cutting edge; four pairs of prominent basal cusps laterally; short, narrow basal process arising from middle part of ventral edge. Lateral teeth with cusp formula 2+1+5; cutting edge broad, median cusp longer and wider than adjacent cusps. Inner marginal teeth curved in distal portion, with parallel sides; cutting edge with ten tiny cusps in inner part and four or five wide cusps in outer part. Outer marginal teeth narrower than inner marginal teeth, with eight uniform, sharp cusps.

Oesophagus (Figs. 62, 87, 88, oe). Opening widely to buccal cavity; running nearly straight at posterior part of nerve ring; entering stomach on left side at junction of anterior and posterior chambers. Stomach (Fig. 62) consisting of large anterior and posterior chambers (ast, pst). Single opening to digestive gland (dgo) at ventral side of posterior chamber slightly behind oesophageal opening. Digestive gland rather small, surrounded by testis or ovary and not visible from outer side in apical whorls, composed of simple mass of globular cells with no distinct rows; pale lemon-yellow with many tiny reddish brown spots. Crystalline style sac (css) large, elongate bean-shaped, pale olive; anterior end blunt. Origin of intestine (int) at left anterior end of anterior chamber. Intestine tightly looped over middle of style sac before continuing to rectum; rectum running nearly straight, with no distinct curve on mantle roof. Oval faecal pellets queued diagonally in single file in intestine and rectum. Anus simple, slightly behind anterior mantle edge.

Male Reproductive System. Testis (Fig. 65, t) extremely large (~ 15 mm in length), occupying two apical whorls, bright orange, consisting of many small cells. Highly convoluted seminal vesicle (sv) arising from vas deferens on ventral side of testis. Posterior vas deferens (pvd) running from seminal vesicle as simple,

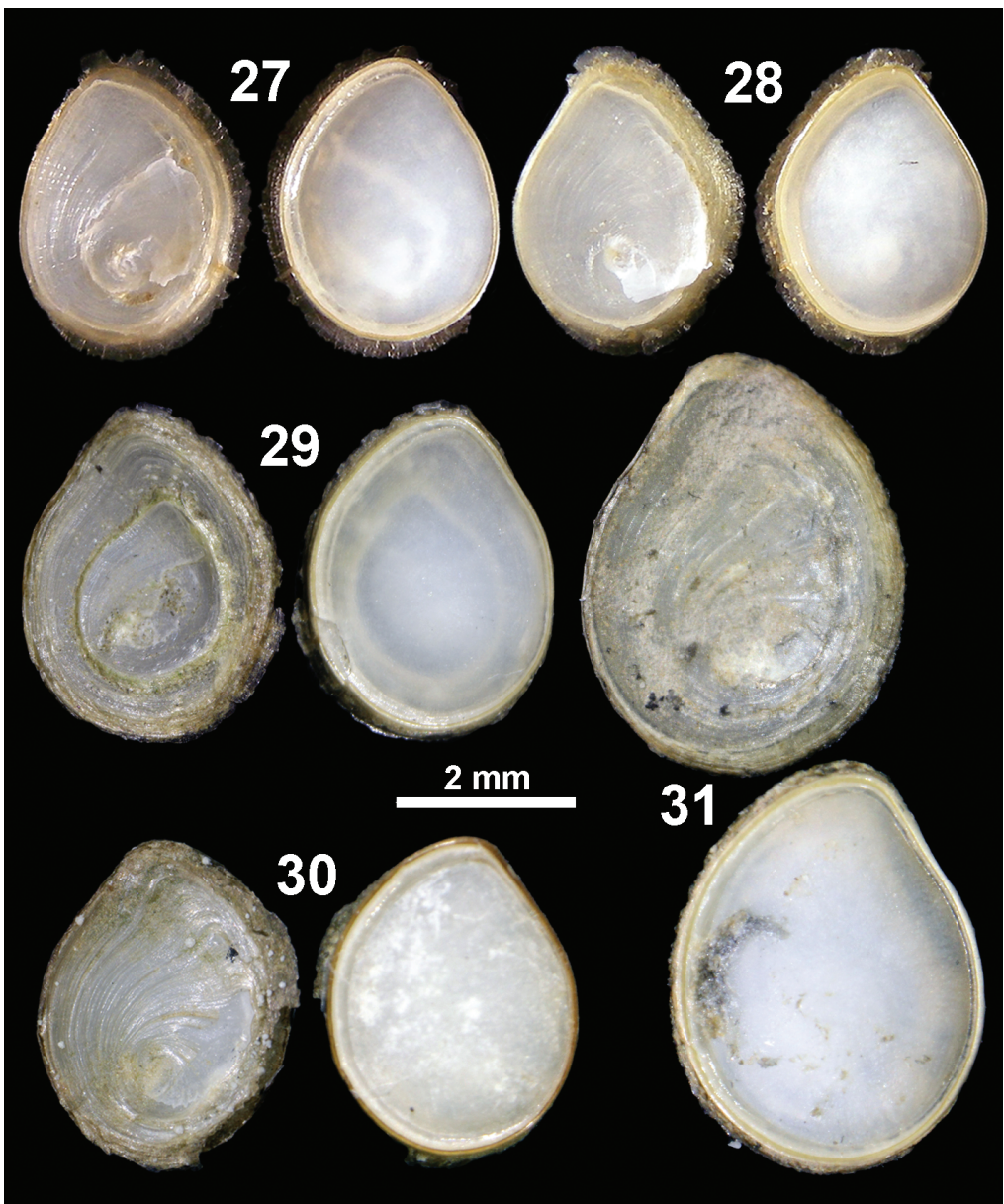


FIGS. 22–26. Opercula of *Pseudovivipara eximia* (Frauenfeld, 1864). Exterior views left, interior views right. (22–24) Lake Ogawara, Aomori Prefecture, Japan (22, 23, OKCAB M29800; 24, TUMC B314); (25) Lake Kasumigaura, Ibaraki Prefecture, Japan (KUZ Z4327; exterior view only); (26) Nanjing, China (TUMC B260).

narrow tube, running to posterior ventral part of prostate gland (pr) just within mantle cavity. Prostate gland long (~ 8 mm in length), approximately half within posterior mantle cavity, elongate bean-shaped consisting of many tiny, colorless cells. Anterior vas deferens (avd) emerging from ventral anterior part of prostate, nearly straight on mantle roof, then turning 90° three times and running towards proximal end of penis (Figs. 65–68, p). Penis large, approximately half of head width, rather long, muscular, attached to head ~ 2.5 mm behind eye (e) with wide base; dorsal surface of right side with wide, curved, black glandular area (bpg); distal end (po) weakly tapering, bluntly pointed but without papilla-like projection; penial duct (pd) distinctly undulating at central part. Accessory lobe (pa) long, flat, arising from left edge of middle part of penis; distal end slightly expanded. Accessory gland

(pag) tubular, buried in cephalic cavity, narrow, short, translucent, coiling several times, reaching accessory lobe as narrow, undulating duct along penial duct.

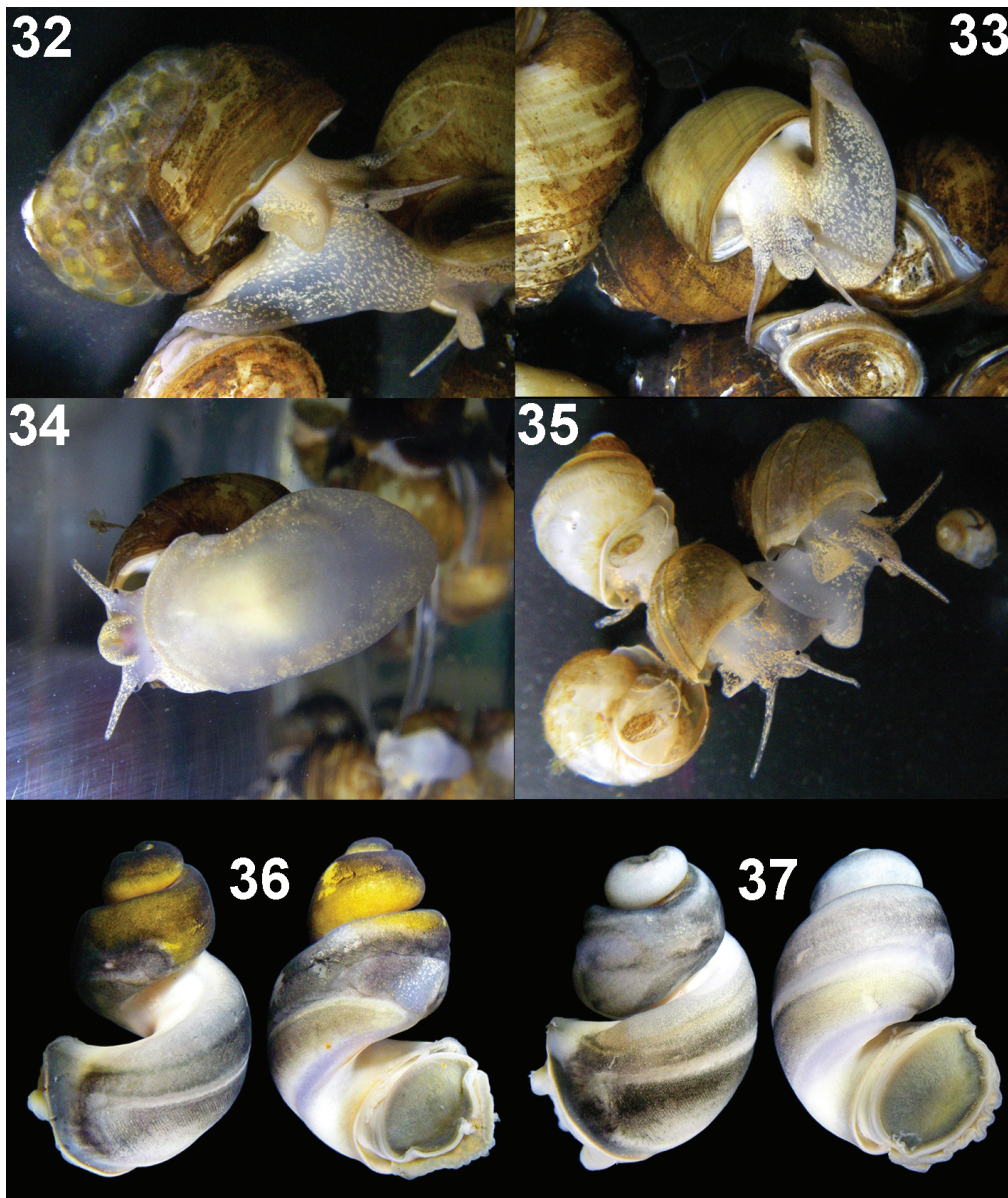
Female Reproductive System. Ovary (Fig. 84, ov) large (~ 3.5 mm in length), at mid-dorsal area of digestive gland, bright orange, consisting of several groups of bundles with many short lobes containing large oocytes. Posterior oviduct (Figs. 78, 79, od) arising from ventral edge of anterior region of ovary. Renal (coiled) oviduct (cov) very narrow, fragile, with one or two loops, then joining with lumen of albumen gland (ag). Seminal receptacle (sr) tiny, oval, pale brown, situated on middle portion of renal oviduct; seminal receptacle duct not observed in gross anatomy, apparently very short. Pallial oviduct (ag, cg) very long (~ 17 mm in length), narrow (~ 1.8 mm in maximum width), strongly curved on mantle roof; in dissection,



FIGS. 27–31. Opercula of *Pseudovivipara longicornis* (Benson, 1842). Exterior views left, interior views right. (27–30) Lake Kawaguchi, Yamanashi Prefecture, Japan (27, OKCAB M30008; 28, OKCAB M30004; 29, TUMC B142; 30, TUMC B136); (31) Nanjing, China (TUMC h320-2; exterior view uppermost).

clearly divided into albumen gland and capsule gland anteriorly; albumen gland opaque white; capsule gland translucent; inside with ventral channel. Bursa copulatrix (bc) extremely long,

narrow (~ 7 mm in length, 0.6 mm in width), running on left dorsal side of capsule gland (ag), opening anteriorly to ventral channel near genital opening (fgo), with no external bursal

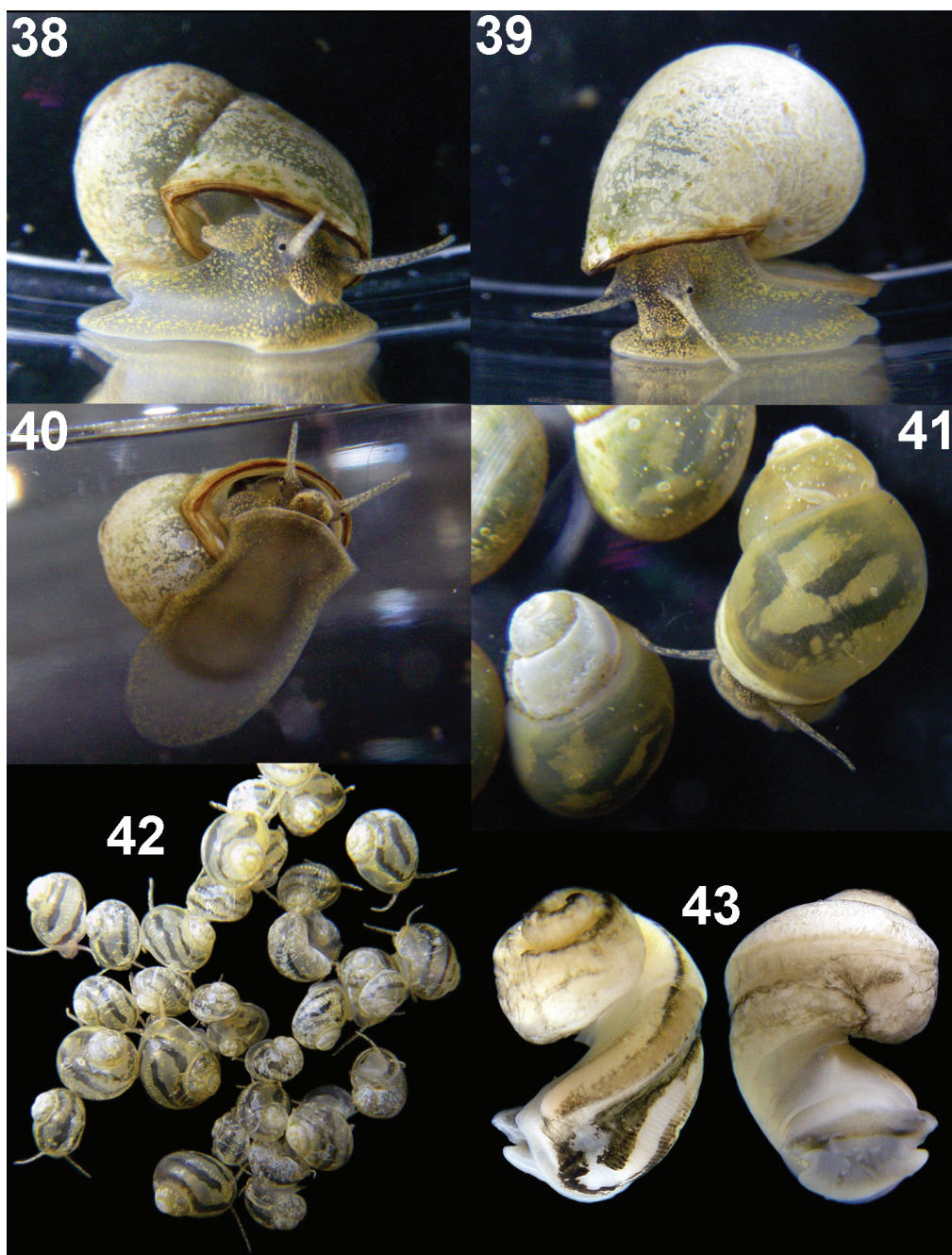


FIGS. 32–37. *Pseudovivipara eximia* (Frauenfeld, 1864), living animals (32–35) and soft parts after *niku-nuki* (36, 37), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800). (32) right lateral view, with egg mass; (33) dorsal view, showing left side of head-foot; (34) sole; (35) juveniles; (36) whole soft parts of male (shell length 16.8 mm); (37) whole soft parts of female (shell length 15.6 mm).

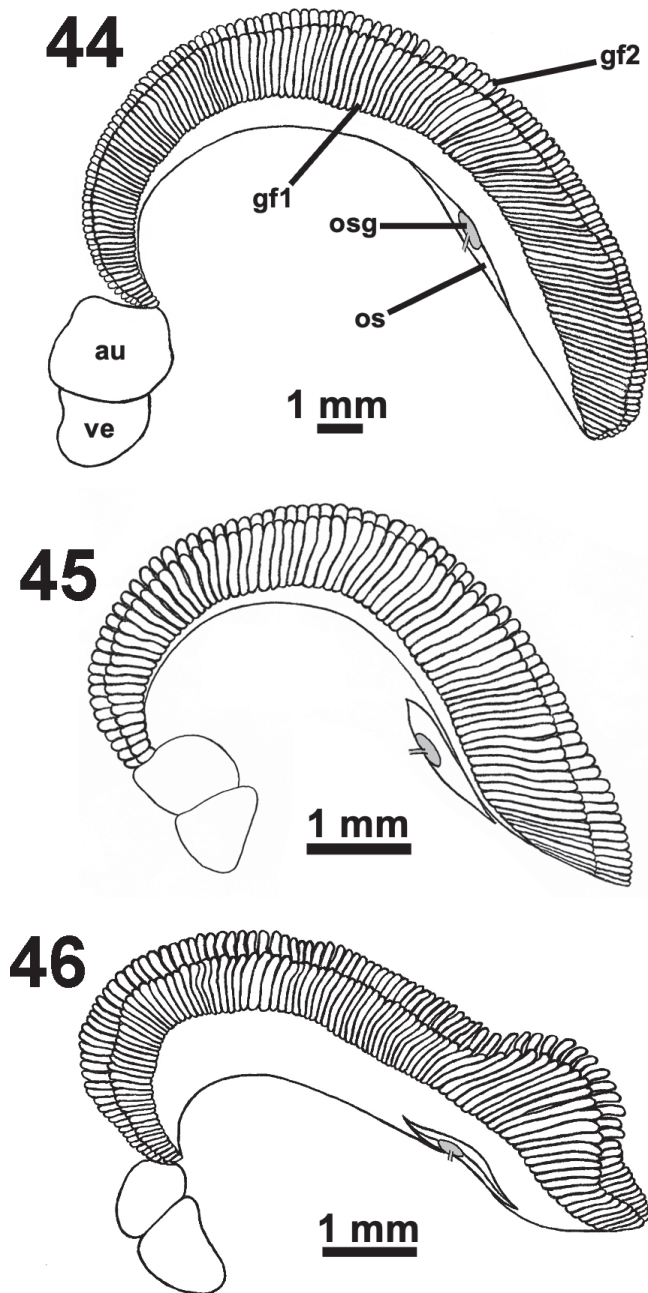
duct; bursal contents reddish brown. Female genital opening (fgo) at slightly posterior to anterior end of albumen gland.

Central Nervous System (Figs. 44, 87–91). Circumoesophageal nerve ring streptoneurous,

epiathroid, with ganglia moderately concentrated. Cerebral ganglia (rcg, lcg) ~ 0.5 mm in length, 0.3 mm in width, between posterior end of buccal mass (bm) and anterior portion of oesophagus (oe); right and left ganglia abutting



FIGS. 38–43. *Pseudovivipara longicornis* (Benson, 1842), living animals (38–42) and soft parts after *niku-nuki* (43); Lake Kawaguchi, Yamanashi Prefecture, Japan (38–40, 43, OKCAB M30030; 41, M30004; 42, M30008). (38) Right lateral view; (39) left lateral view; (40) sole; (41) dorsal view, black bands on mantle visible through translucent shell; (42) juveniles; (43) whole soft parts of female (shell length 6.6 mm).



FIGS. 44–46. Gills, osphradia, and hearts. (44) *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800); (45) *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30030); (46) *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Natajima, Yamaguchi Prefecture, Japan (OKCAB M25129). au, auricle; gf1, gf2, gill filaments 1 and 2; os, osphradium; osg, osphradial ganglion; ve, ventricle.

each other; cerebral commissure invisible, possibly rudimentary. Tentacular nerves (rtn, ltn) thicker than optic nerves (roptn, loptn), with no distinct swellings at their bases, each divided into two nerves, reaching cephalic tentacles. Optic nerves arising from midventral portion of cerebral ganglia. Cerebropedal and pleuropedal connectives (rcpc, lcpc, rppc, lppc) rather long (0.5 mm in length); left connectives slightly shorter than right ones in length, showing asymmetry. Buccal ganglia (rbg) small, globular, joined by long, narrow commissure at posterolateral sides of buccal mass. Right pleural ganglion (rpl) smaller than cerebral ganglia (0.4 mm in length, 0.2 mm in width), elongate oval, partially fused with right cerebral ganglion, separated by distinct constriction. Supraoesophageal ganglion (spg) distinct, oval, as large as right pleural ganglion; right pleural and supraoesophageal ganglia abutting each other; pleuro-supraoesophageal connective not found. Left pleural ganglion (lpl) smaller than left cerebral ganglion, separated by distinct constriction. Suboesophageal ganglion (sbg) globular, partially fused with left pleural ganglion; connective between these ganglia not visible; heavy mantle nerve (mtn) arising from suboesophageal ganglion as well as sub-visceral connective (sbv). Pedal ganglia (rpg, lpg) connected posteriorly to cerebral ganglia. Left and right pedal ganglia of approximately equal size (0.5 mm in length, 0.3 mm in width). Pedal commissure rudimentary, not visible. Propodial (rmg, lmg) ganglia small, globular, connected with pedal ganglia by distinct connectives; some heavy nerves (rmn, lmn) arising from these ganglia to foot. Metapodial ganglion and commissure not observed. Small statocysts (rst, lst) dorsal, at posterior ends of pedal ganglia. Osphradial ganglion (Fig. 44, osg) very small, slender, fusiform, on osphradium. Visceral ganglion (Fig. 91, vg) small, triangular; gonadal nerve (gn) and renal nerve (rn) arising from visceral ganglion.

Type Localities

"China borealis" [northern China] (*Vivipara eximia* and *V. chinensis*); "Kiukiang" (*Bithynia subangulata*); "in provincia Hunan" (*Bithynia grandis*); "Narrow creek at Tong Dong Ding, Tai-Hu, China" (*Pseudovivipara hypocrites*).

Distribution

Based on our investigation and literature records, the known localities of the species are listed below. Each representative locality in the Chinese provinces is shown in brackets:

China: Anhui Province 安徽省 (Hefei 合肥), Hebei Province 河北省 (Lake Baiyangdian 白洋淀), Hubei Province 湖北省 (Hankou 汉口, Wuhan 武汉), Hunan Province 湖南省 (Xiangtan 湘潭), Jiangsu Province 江苏省 (Nanjing 南京), Jiangxi Province 江西省 (Jiujiang 九江), Sichuan Province 四川省, Shandong Province 山东省 (Lake Weishan 南四湖), Zhejiang Province 浙江省 (Hangzhou 杭州), Shanghai 上海 (Jiading 嘉定). Japan (all introduced): Aomori Prefecture 青森県 (Lake Ogawara 小川原湖), Niigata Prefecture 新潟県 (Minami-ku, Niigata-shi 新潟市南区), Ibaraki Prefecture 茨城県 (Lake Sotonasakaura 外浪逆浦, a part of Lake Kasumigaura 霞ヶ浦), Tone River between Ibaraki and Chiba prefectures 茨城・千葉両県間の利根川, Chiba Prefecture 千葉県 (Kisarazu-shi 木更津市), Shiga Prefecture 滋賀県 (details unknown).

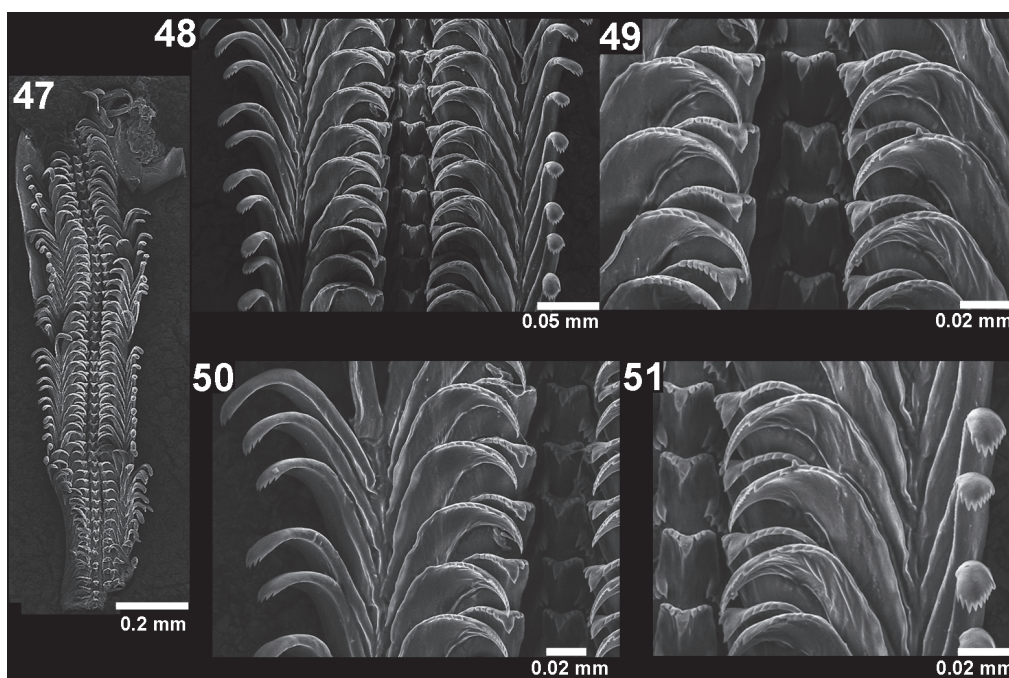
The species is widely distributed in the eastern part of China.

Ecology

The egg masses of the species were observed to be laid on the dorsal surface of adult shells (Fig. 32). Each consists of two parallel rows of interlocking hemispherical capsules, each of which contains a single egg/larva, as reported in *Pseudovivipara manchourica japonica* by Itagaki (1965: pl. 19, fig. 25) and Okino & Hatsushika (1993: fig. 1a).

Pseudovivipara eximia has been identified as a vector of *Angiostrongylus cantonensis* (Chen, 1935), causing angiostrongyliasis (Zhao et al., 2009; Lu et al., 2018). Although few parasitological, ecological, and physiological studies have specifically focused on *Pseudovivipara eximia* (e.g., Jia et al., 2021), some ecological insights have been obtained from broader research on freshwater macroinvertebrate communities in eastern China.

Stable isotope analysis suggested *Pseudovivipara eximia* as one of the most $\delta^{13}\text{C}$ -enriched consumers in the river-lake ecosystems in China (Zeng et al., 2024). This species inhabits a wide range of aquatic environments, including lakes, wetlands, rivers, and water channels (Taki, 1940; H. Wang et al., 2015; Jia et al.,



FIGS. 47–51. Radulae of *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Kasumigaura, Ibaraki Prefecture, Japan (KUZ Z4327).

2021; F. Liu & Lu, 2021; Q. Li et al., 2024), and it can sometimes be one of the dominant species in macroinvertebrate communities (F. Liu & Lu, 2021). Although *Pseudovivipara eximia* is considered an indicator of moderate water quality in the Yangtze River Delta (L. Wang et al., 2021), it seems to tolerate various environmental changes. Specifically, its abundance has been positively correlated with crab cultivation in Lake Yangcheng, Jiangsu Province (L. Chen et al., 2015). In addition, *Pseudovivipara eximia* is among the most drought-resistant molluscan species in a Chinese lake ecosystem (Y. Zhang et al., 2024). Its occurrence has also been positively associated with urbanization in Zhejiang Province (J. Gao et al., 2023). Furthermore, this species can tolerate habitats affected by mining activities, where bioaccumulation of arsenic has been reported (Jia et al., 2021).

Overall, *Pseudovivipara eximia* remains common within its native distributional range in China. However, its relative abundance in Lake Poyang might have declined since 2008 (Y. Cai et al., 2014). Nevertheless, it is still one

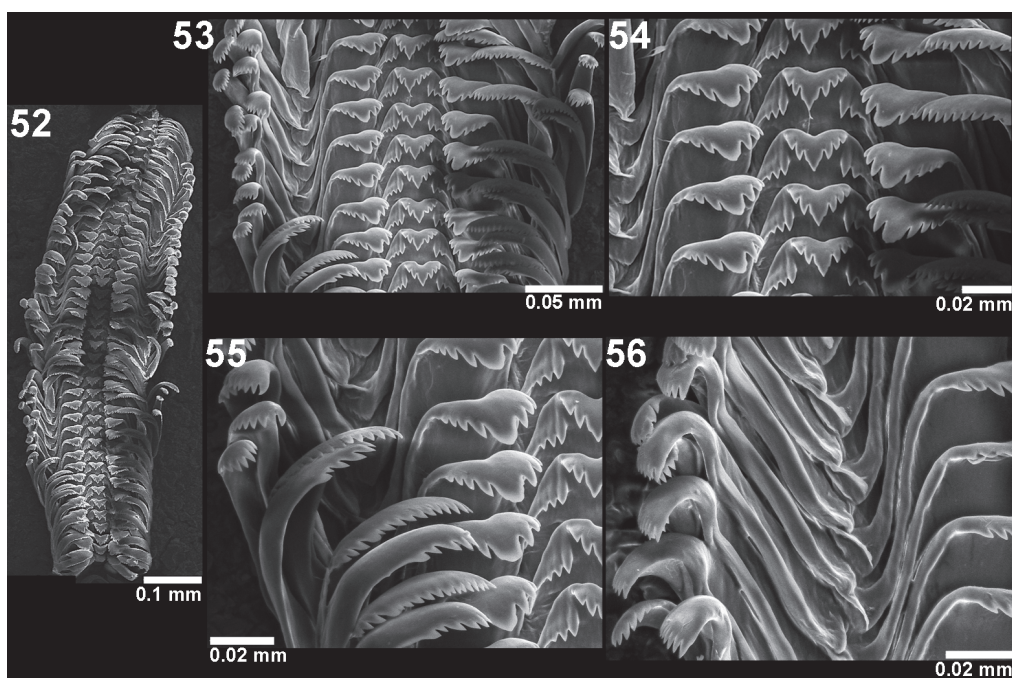
of the most abundant species in the lake (Zhou et al., 2024).

Remarks

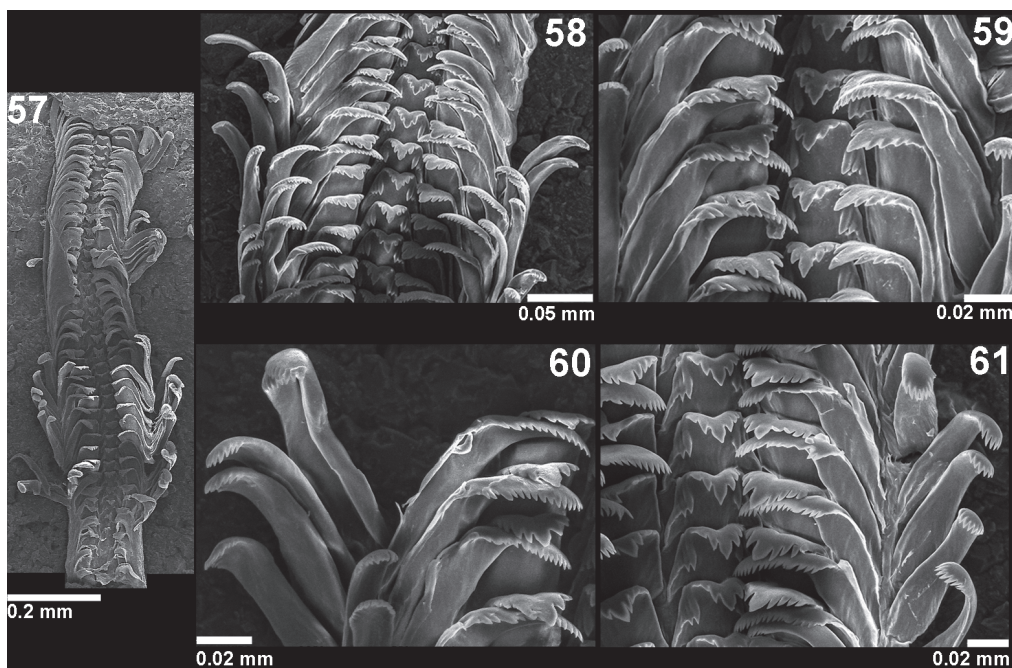
The type specimen of *Vivipara eximia* was illustrated by Frauenfeld (1864b). Zilch (1938) and Yen (1939) provided photographs of *Bithynia subangulata* (paratype, no. 25773) and *B. grandis* (holotype, no. 25769), both in the Senckenberg Museum, Germany. Zilch (1938) and Yen (1939) mentioned that all of them (and *Pseudovivipara hypocrites*) are conspecific with *Pseudovivipara eximia*. Abbott (1948) followed them.

The shell of *Pseudovivipara eximia* is somewhat similar to that of *Pseudovivipara manchourica*, but the former is much larger and wider than the latter. In *Pseudovivipara eximia* the number of the spiral cords on the penultimate whorl is usually less than five, whereas there are four or more in *Pseudovivipara manchourica*.

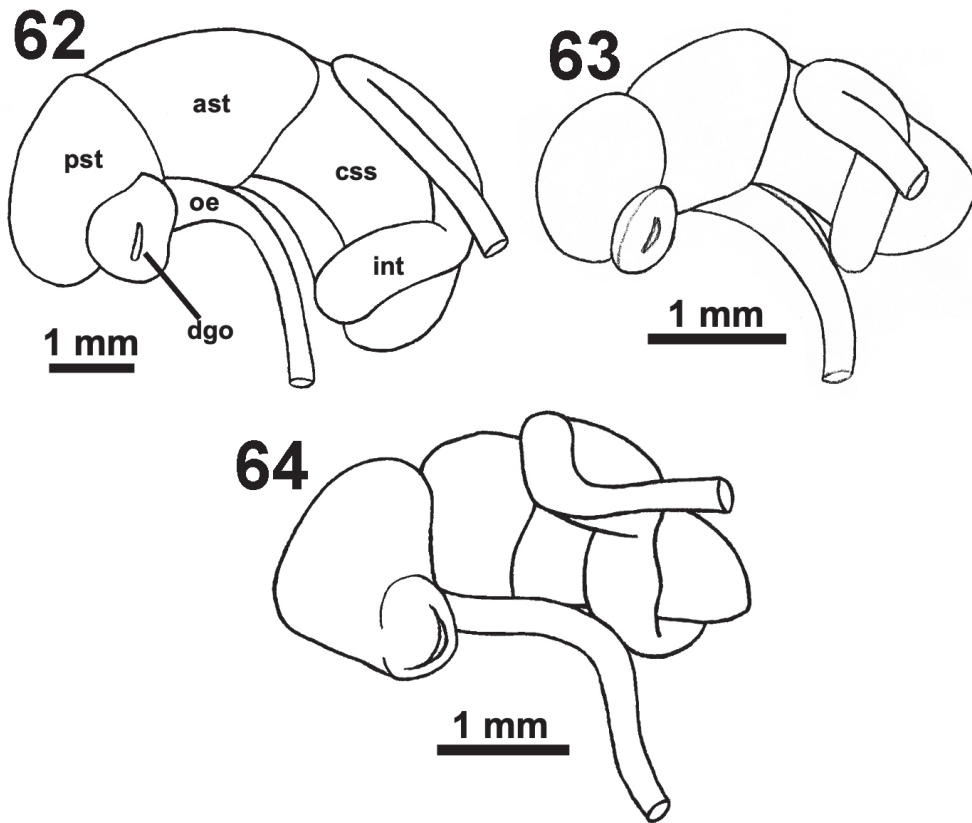
In Japan, the oldest record of the species was from Kisarazu-shi, Chiba Prefecture in



FIGS. 52–56. Radulae of *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (KUZ Z6014).



FIGS. 57–61. Radulae of *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Lake Kawaguchi, Yamanashi Prefecture, Japan (KUZ Z6013).



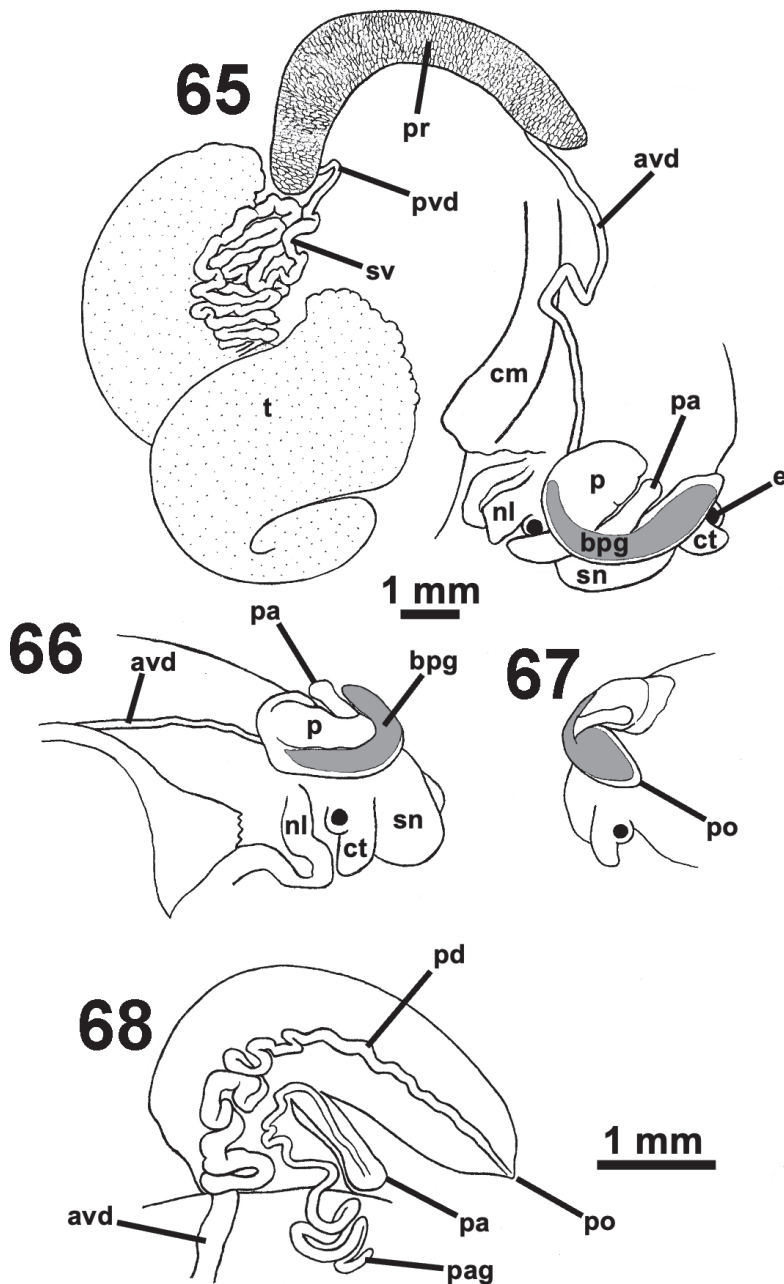
FIGS. 62–64. Stomachs. (62) *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800); (63) *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30030); (64) *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Natajima, Yamaguchi Prefecture, Japan (OKCAB M25129). ast, anterior chamber of stomach; css, crystalline style sac; dgo, opening of digestive gland; int, intestine; oe, oesophagus; pst, posterior chamber of stomach.

1993. The specimen (CBM ZM105197) is an eroded empty shell and it is uncertain that the population was actually present around the locality at that time.

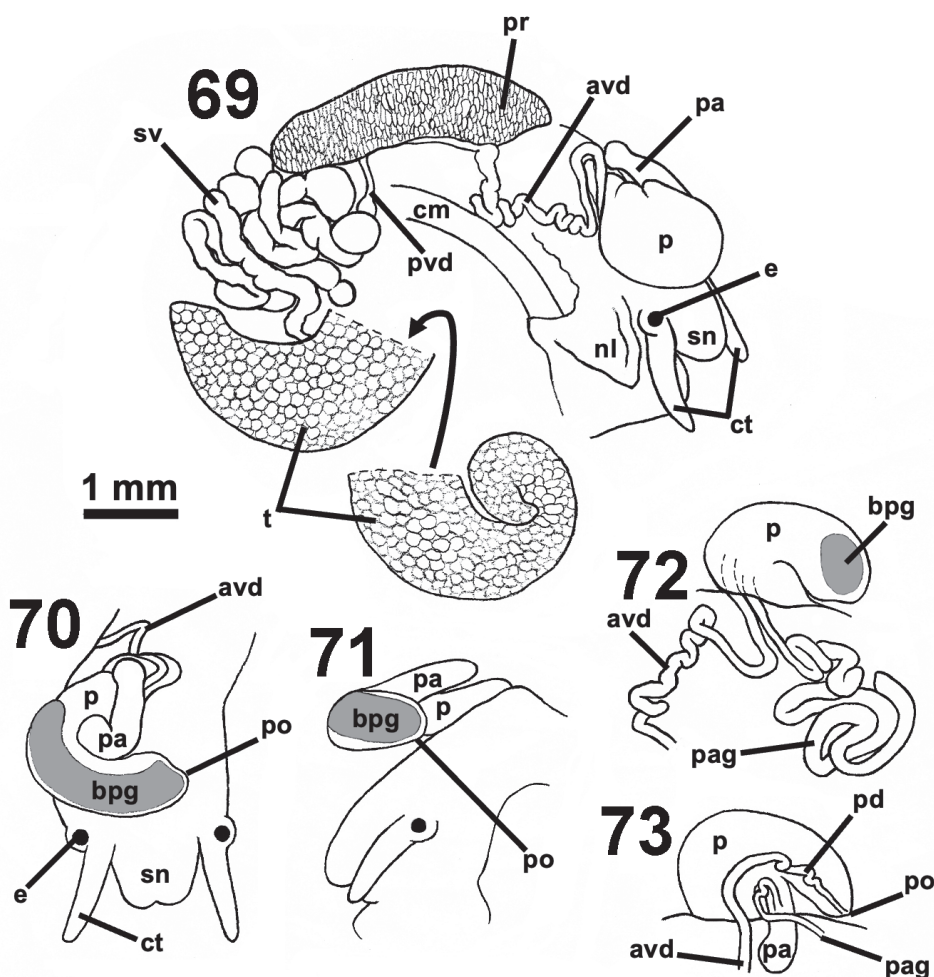
In 2002, a second specimen from Japan was collected from the Tone River between Ibaraki and Chiba prefectures. The voucher specimen (CBM ZM162779) is a large fresh shell with periostracum and the operculum and it is assumed to have been collected alive. However, no reliable records from around these prefectures have been provided until recently.

Nomura (2010a, b) and Murayama et al. (2025) reported “*Parafossarulus manchouricus japonicus*” from Niigata Prefecture and it was listed as “endangered” in the Red Data Book

of the Prefecture. However, his specimens are obviously *Pseudovivipara eximia* judging from the low spire of the shells, which have only three strong spiral cords on the penultimate whorl. The real *Pseudovivipara manchourica japonica* was recorded in the Niigata Prefecture (Hasegawa, 1979), but it became extinct after the 1980s and then an introduced population of *Pseudovivipara eximia* is thought to have established instead. Similarly, a photograph of a living animal as “*Parafossarulus manchouricus japonicus*” from Shiga Prefecture by Seki (2012; the same photograph was published by Kurozumi, 2022) is also identifiable as *Pseudovivipara eximia*. Then, one of the present authors (SK) discovered *Pseudovivipara exi-*



FIGS. 65–68. Male reproductive system of *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800). (65) Whole system; (66) right lateral view of penis; (67) left lateral view of penis; (68) accessory gland and inside of penis. avd, anterior vas deferens; cm, columellar muscle; ct, cephalic tentacle; e, eye; nl, neck lobe; p, penis; pa, penial accessory lobe; pag, penial accessory gland; pd, penial duct; po, penial opening; pr, prostate gland; pvd, posterior vas deferens; sv, seminal vesicle; sn, snout; t, testis.

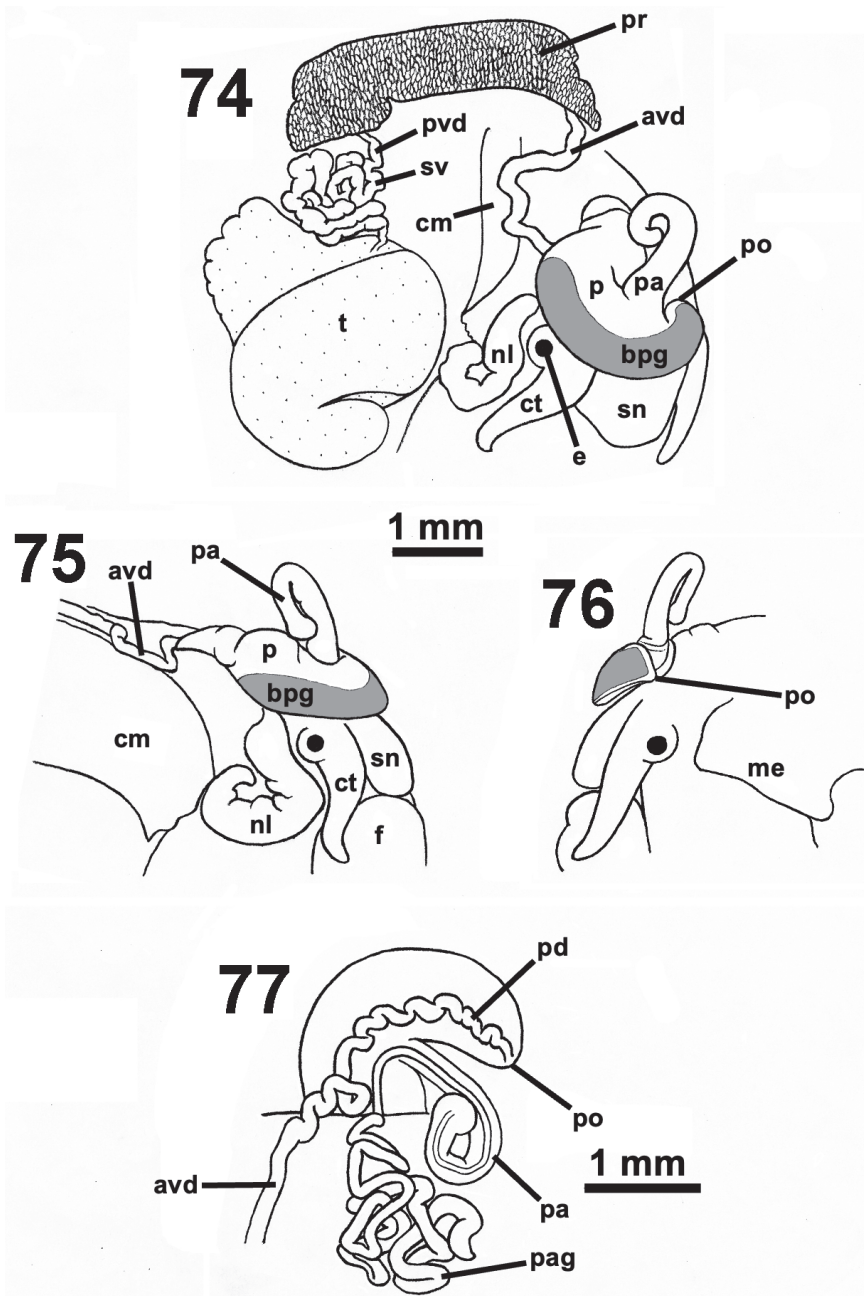


FIGS. 69–73. Male reproductive system of *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30030). (69) Whole system; (70) dorsal view of penis; (71) left lateral view of penis; (72) accessory gland; (73) inside of penis. avd, anterior vas deferens; bpg, black glandular area of penis; cm, columellar muscle; ct, cephalic tentacle; e, eye; nl, neck lobe; p, penis; pa, penial accessory lobe; pag, penial accessory gland; pd, penial duct; po, penial opening; pr, prostate gland; pvd, posterior vas deferens; sv, seminal vesicle; sn, snout; t, testis.

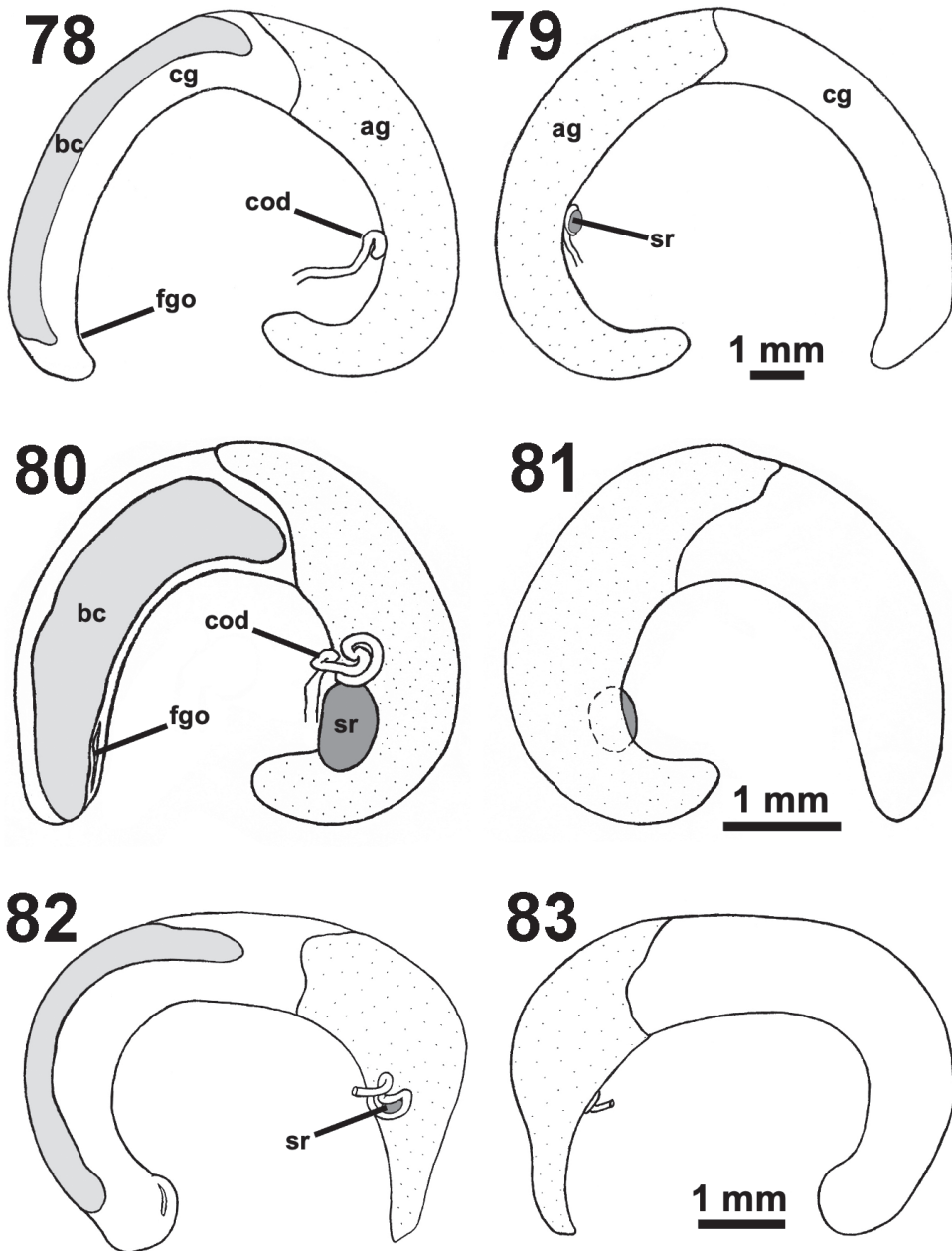
mia in Aomori Prefecture in 2012, and another author (NS) collected it from Ibaraki Prefecture in 2022.

The shell size and shape in fully mature specimens of this species are very variable among populations. Specimens from Lake Ogawara (Figs. 2–6) are large and tall with prominent spiral cords, but those from Lake Kasumigaura (Figs. 7–9) are much smaller with indistinct

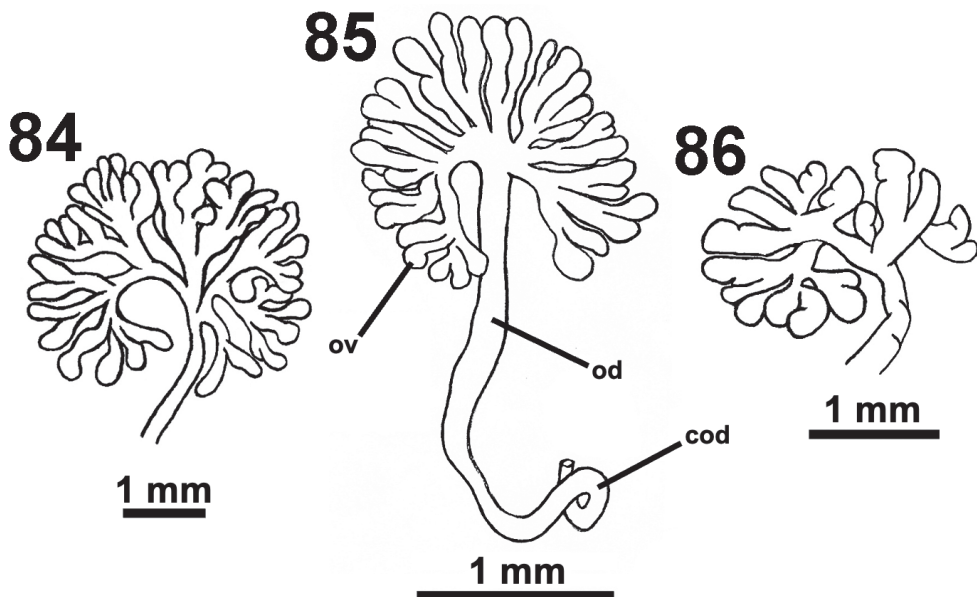
spiral cords. A specimen from Nanjing, China (Fig. 11) is intermediate between these forms. According to literature records from China, the mean shell length is 22.3 mm (9.0–28.0 mm; $n = 113$) in the lower region of the Yangtze River drainage (Zhao et al., 2009). Another report from Zhejiang Province documented the shell length as 16.2–19.2 mm and the shell width as 8.9–10.1 mm (Huang & Z. Li, 1991).



FIGS. 74–77. Male reproductive system of *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Natajima, Yamaguchi Prefecture, Japan (OKCAB M25129). (74) Whole system; (75) left lateral view of penis; (76) right lateral view of penis; (77) accessory gland and inside of penis. avd, anterior vas deferens; bpg, black glandular area of penis; cm, columellar muscle; ct, cephalic tentacle; e, eye; f, foot; me, mantle edge; nl, neck lobe; p, penis; pa, penial accessory lobe; pag, penial accessory gland; pd, penial duct; po, penial opening; pr, prostate gland; pvd, posterior vas deferens; sv, seminal vesicle; sn, snout; t, testis.



FIGS. 78–83. Pallial oviducts. (78, 80, 82) left (dorsal) side; (79, 81, 83) right (ventral) side. (78, 79) *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800); (80, 81) *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30030); (82, 83) *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Natajima, Yamaguchi Prefecture, Japan (OKCAB M25129). ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cod, coiled (renal) oviduct; fgo, female genital opening; sr, seminal receptacle.



FIGS. 84–86. Ovaries. (84) *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800); (85) *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30030); (86) *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Natajima, Yamaguchi Prefecture, Japan (OKCAB M25129). cod, coiled (renal) oviduct; od, oviduct; ov, ovary.

Pseudovivipara longicornis (Benson, 1842),
n. comb.

长角沼螺 (刘 Y.-Y. Liu, 1961: 123, 126),
长角涵螺, 角豆螺, B螺 (刘等 Y.-Y. Liu et al.,
1979: 33) in Chinese
コガシラメタニシ (小頭豆田螺,
Ko-gashira-mame-ta-nishi; 瀧庸 Taki, 1940:
113) in Japanese
Figs. 12–17, 20, 21, 27–31, 38–43, 45,
52–56, 63, 69–73, 80, 81, 85, 92–97

Paludina (*Bithynia*) *longicornis* Benson,
1842: 488; Ablett et al., 2019: text-fig. (syn-
type).

Paludina (*Bithynia* [sic]) *longicornis*.—Ben-
son, 1855: 130, 131.

Bithynia shuttleworthi Frauenfeld, 1862:
1148; Möllendorff, 1881: 43.

Bythinia [sic] *longicornis*.—Frauenfeld,
1864b: 622, no. 499; G. Nevill, 1885: 39, no.
21; Möllendorff, 1888: 135, no. 8; Annandale,
1918b: 306; Faust, 1924: 298; 1925: 292.

Bythinia [sic] *shuttleworthi*.—Frauenfeld,
1864a: 646, no. 759; Möllendorff, 1888: 135,
no. 8.

Bythinia [sic] *shuttleworthii* [sic].—Frauen-
feld, 1865: 527, pl. 9, unnumbered figs.

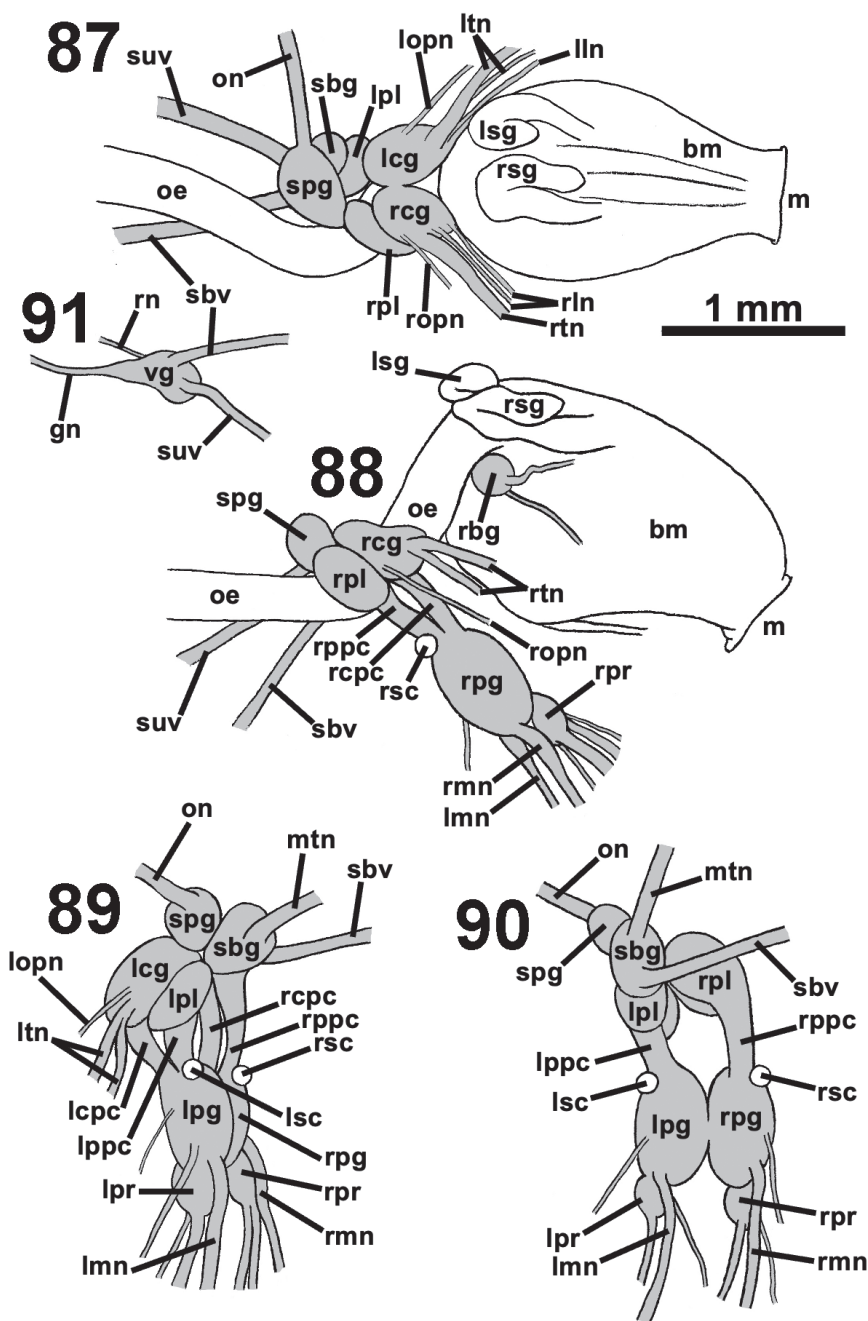
Stenothyra tonkiniana Morlet, 1886a: 5–6,
no. 12; 1886b: 263, no. 15, 287, 288, no. 13,
pl. 14, fig. 4, 4a, b; Mabille, 1887: 157, no. 15;
P. Fischer, 1891: 173 (89 in reprint); H. Fischer
& Dautzenberg, 1904: 420.

Bithynia longicornis.—Gredler, 1887: 176,
note at no. 8; Heude, 1890: 170, no. 470, pl.
42, fig. 4, 4a, b (head with penis), with *Bithynia*
shuttleworthi as synonym; [Y. Hirase], 1908:
169 (Japanese), 21 (English); Walker, 1927:
226–229, text-fig. 6 (radula), pl. 14, figs. 12,
13, *Bithynia shuttleworthi* and *Stenothyra*
tonkiniana as synonyms; Hsü & Chow, 1937:
349, 350; Galliard, 1939: 238, 240, 242, 244;
Yoshida, 2012: table 1; D. Wang et al., 2018:
162, table 1, with synonym “*Alocinma longicor-
nis*”; Wu et al., 2019: table 1.

Bithynia tonkiniana.—Dautzenberg & H.
Fischer, 1905: 416–417.

Bulimus longicornis.—Yen, 1936: 45; Taki,
1940: 113, 115–116.

Parafossarulus longicornis.—Yen, 1937a:
30–31, pl. 2, fig. 37, 37a; Yen, 1937b: 22; 1939:



FIGS. 87–91. Central nervous system of *Pseudovivipara eximia* (Frauenfeld, 1864), Lake Ogawara, Aomori Prefecture, Japan (OKCAB M29800). (87) Dorsal view of nerve ring and buccal mass; (88) right lateral view of nerve ring and buccal mass; (89) left lateral view of nerve ring; (90) rear view of nerve ring; (91) visceral ganglion. bm, buccal mass; gn, gonadal nerve; lcg, left cerebral ganglion; lcpc, left cerebropedal connective; lln, left labial nerve; lmn, left metapodial nerve; lopn, left optic nerve; lpg, left pedal ganglion; lpl, left pleural ganglion; lppc, left pleuropedal connective; lpr, left propodial ganglion; →

46, pl. 4, fig. 22; 1942: 198; 1948: 77; Y.-Y. Liu, 1961: 123, 126, no. 9, pl. 1, fig. 6; Starobogatov, 1970: 201; Yu & H. Wang, 1977: 3.

Bulimus (Parafossarulus) longicornis.—Miyadi & Habe, 1944: 361, 362, 365, 366, figs. 1c, 2C1–4 (radula); Yasuno, 1980: 107, 108, pl. 10, figs. 5–7.

Alocinma longicornis.—Abbott, 1948: 274, 278, fig. 8 [part], pl. 1, fig. 20, with *Stenothyra tonkiniana* as synonym; Tchang et al., 1964: 64; Muraoka, 1972: 33, no. 422; C.-Y. Chen et al., 1975: 371, 373, 375, 377–379, tables 1–3, 6, 7, 10, 13, 15, 18; Y.-Y. Liu et al., 1979: 24, 33, 34, 133, fig. 31; Matsuoka, 1981: 79–83, 85 (pl. 1), figs. 1a, b, 2, 3a, b, 4a, b, 5a, b; 1987: 70–72, 81, 88, 89, figs. 26, 27; Hong & San, 1993: 20, 21, appendix 4; Y. Liu et al., 1986: 72, 73, no. 6, pl. 1, fig. 6; R. Wang et al., 1988: 26, fig. 72; Y. Liu, 1990: 143, no. 32; 1998: 56, 57, fig. 63; Huang & Z. Li, 1991: 60, 61, fig. 53; 1995: 102, no. 13, 105; Higo & Gotō, 1993: 77, no. 986; Zeng & Qi, 1994: 171; B. Pan & Ji, 1995: 27, 31, table 2; Z. Li et al., 1995: 28; J. Ma & H. Sun, 1997: 28, no. 9; S.-L. Li et al., 2002: 214–216; Y.-J. Yan et al., 2002: 322–326, figs. 2–4, tables 1–3; Y. Yan & Liang, 2002: 374–376; B.-P. Pan & Y. Yang, 2003: 7, 8, figs. 1–3, tables 2, 3; Z. Xie et al., 2005: 508, table 2; X.-Q. Liu et al., 2006: figs. 5, 6, table 2; H.-J. Wang et al., 2006: 525, 526, 527; Z.-Q. Hu et al., 2007: 525, no. 21; Jing et al., 2007: table 2; Z.-C. Xie et al., 2007: 176, 178; Kimura et al., 2008: 57; Xiong et al., 2008: 292, tables 1, 3, 6; B. Pan et al., 2008: 809, no. 11; 2011: 248, 251, 253; 2016: 917, no. 19; Zhong et al., 2008: 831, 832, 834; Zhao et al., 2009: 1452, 1453, figs. 2–5, tables 1–3; Shu et al., 2009: 1057; 2014: 186, 187; Y. Cai et al., 2010: 52, 55; 2012: 42, 44, 46, 47; 2014: tables 2, 3; S. Ma et al., 2011: 12, 13, tables 1–3; Mao et al., 2011: 178, table 1; Y. Tang et al., 2012: table 2; Zheng et al., 2013: 98, text-figs.; Guo et al., 2013: 201, 202, fig. 1D, tables 1, 2; 2015: 38, no. 8, 39; J. Sun et al., 2013: 1; B.-Z. Pan et al., 2013: table 1; Chelomina et al., 2014: 805; Madsen & Hung, 2014: 111, fig. 2-22; Qin et al., 2014: table 5; Y. Zhang et al., 2014: 20, 23; 2018: 62, table 2; 2024: 5,

11; L.-H. Li et al., 2014: 24, 25, fig. 3; L. Chen et al., 2015: 124, 125, fig. 9, table 2; Doanh & Nawa, 2016: 17; Rong & Shan, 2016: 13443; Z.-L. Tang et al., 2016: 1, 3, figs. 1, 2; Chi et al., 2017: table 2; Prozorova & Rasshepkina, 2017: 180; W. Zou et al., 2017: 1182; Kattel et al., 2018: 222, figs. 6, 7, 9, table 2; Lu et al., 2018: table 1; Matsuoka & Miura, 2018: 60, with *Gabbia longicornis* as synonym; W. Wang, 2018: 124; F. Liu et al., 2019: table A1; Xing et al., 2019: appendix 1, no. 256; Z. Liu et al., 2020: appendix 1, no. 26; Jiang et al., 2020: tables 2, A2; R. Hu et al., 2020: 1561, 1562, appendix 1, no. 18; H. M. Nguyen, 2021: 2, 3, 6; L. Wang et al., 2021: fig. 3, appendix A; Ji et al., 2023: fig. 5; Y.-T. Yang et al., 2022: 409–411, fig. 2; Zhou et al., 2024: 4, table 1; Bai et al., 2024: appendix 2.

Alocima [sic] longicornis.—Komiya, 1967: 63, fig. 10, with *Bithynia? longicornis* as synonym.

Bithynia (Gabbia) longicornis.—Brandt, 1968: 223, 224, with *Bithynia shuttleworthi* and *Bithynia tonkiniana* as synonyms; 1974: 63, with *B. shuttleworthi* and *Bithynia tonkiniana* as synonyms.

Bithynia (Alocinna [sic]) longicornis.—Habe, 1973: 318.

Parabithynia longicornis.—Yu & H. Wang, 1977: 27, pl. 3, figs. 12a, b, 13a, b, 14a, b; Z. Sun et al., 2014: table 3.

Alocinna longicornis [sic].—Y.-Y. Liu et al., 1979: 131.

Alocima [sic] longicornis [sic].—B. Pan & Ji, 1995: table 1.

[No Latin name].—Matsuoka, 1998: 20, 26, fig. 4-4.

Alocinna longiconis [sic].—Ohara & Otani, 2002: 20.

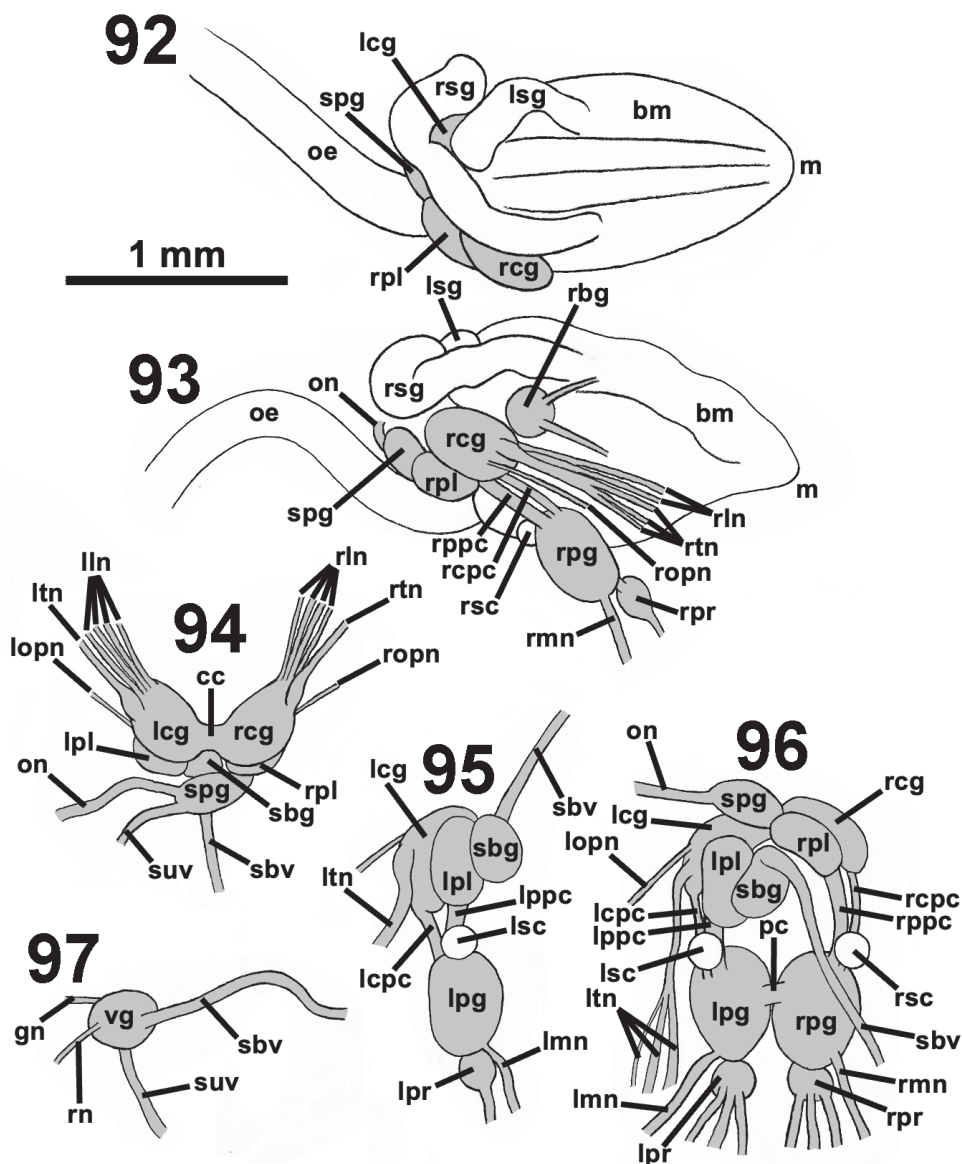
Arocinma [sic] longicornis.—B.-P. Pan & Y.-G. Zhang, 2002: 210, 212, 213, figs. 1–3, tables 1, 2; K. Wang et al., 2021: 3.

Parafossarulus manchouricus.—Min et al., 2004: 141 [part], fig. 168-1 [not fig. 168-2].

Bithynia (Alocinna) longicornis.—Rim, 2005: 271.

Bythinia [sic] shuttleworthi.—Eschner, 2008: 23.

FIGS. 87–91 (continued). lsc, left statocyst; lsg, left salivary gland; ltn, left tentacular nerve; m, mouth; mtn, mantle nerve; oe, oesophagus; on, osphradial nerve; rbg, right buccal ganglion; rcg, right cerebral ganglion; rcpc, right cerebropedal connective; rln, right labial nerve; rmn, right metapodial nerve; rn, renal nerve; ropn, right optic nerve; rpg, right pedal ganglion; rpl, right pleural ganglion; rppc, right pleuropedal connective; rpr, right propodial ganglion; rsc, right statocyst; rsg, right salivary gland; rtn, right tentacular nerve; sbg, suboesophageal ganglion; sbv, subvisceral connective; spg, supraoesophageal ganglion; suv, supravisceral connective; vg, visceral ganglion.



FIGS. 92–97. Central nervous system of *Pseudovivipara longicornis* (Benson, 1842), Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB M30030). (92) Dorsal view of nerve ring and buccal mass; (93) right lateral view of nerve ring and buccal mass; (94) dorsal view of nerve ring; (95) left lateral view of nerve ring; (96) rear view of nerve ring; (97) visceral ganglion. bm, buccal mass; cc, cerebral commissure; gn, gonadal nerve; lcg, left cerebral ganglion; lcpc, left cerebropedal connective; lln, left labial nerve; lmn, left metapodial nerve; lopn, left optic nerve; lpg, left pedal ganglion; lpl, left pleural ganglion; lppc, left pleuropedal connective; lpr, left propodial ganglion; lsc, left statocyst; lsg, left salivary gland; ltn, left tentacular nerve; m, mouth; oe, oesophagus; on, osphradial nerve; pc, pedal commissure; rbg, right buccal ganglion; rcg, right cerebral ganglion; rcpc, right cerebropedal connective; rln, right labial nerve; rmn, right metapodial nerve; rn, renal nerve; ropn, right optic nerve; rpg, right pedal ganglion; rpl, right pleural ganglion; rppc, right pleuropedal connective; rpr, right propodial ganglion; rsc, right statocyst; rsg, right salivary gland; rtn, right tentacular nerve; sbg, suboesophageal ganglion; sbv, subvisceral connective; spg, supraoesophageal ganglion; suv, supravisceral connective; vg, visceral ganglion.

Alocinma ongicornis [sic].—Guo et al., 2009: 451, no. 4, 452, no. 11(12), fig. 4.

Allocinma [sic] *longicornis*.—Hung et al., 2013: 233, 244, table 1; P.T.X. Nguyen et al., 2021: 955, 958, figs. 4, 5, tables 1, 2.

Alocinma longicorris [sic].—Jiang et al., 2020: 11, table 6.

Gabbia longicornis.—Matsuoka & Hirano, 2020: 236; Matsuoka, 2020: 40; Preece et al., 2022: 105, 420, fig. 43C–E (syntypes); Zhou et al., 2024: 4, table 1.

“Parafossarulus” longicornis.—Sawada et al., 2025: 42, 43, fig. 11, J.

Material Examined

Gulou District, Nanjing City, Jiangsu Prov., China, a water channel 中国江苏省南京市鼓楼区引水渠, April 20, 2018, collected by the authors (BY & TH), three adults (sex unknown) (TUMC h320-1–3; Figs. 16, 31).

All the following materials were collected from the southeastern to eastern coast of Lake Kawaguchi, Fujikawaguchiko-machi, Minamitsuru-gun, Yamanashi Prefecture, central Honshū 山梨県南都留郡富士河口湖町河口湖南東岸～東岸: Near boarding point, Funatsu, 35°30'14.49"N, 138°46'12.69"E, beneath stones in rocky shore at the edge of a sandy beach 船津, ボート乗場附近, 砂浜邊緣岩礫地 転石下, September 16, 2016, collected by the authors (TS & KA), two males, seven females, 14 sex unknown, 1 juvenile (OKCAB M30030 and TUMC B136–B142; Figs. 29, 30, 38–40, 42, 43, 45, 63, 69–73, 79, 85, 92–97). ~300 m south of Kawaguchiko-ō-hashi Bridge, Funatsu, 35°30'24.20"N, 138°45'49.27"E, on aquatic plants, 1–5 cm in depth, sandy mud flat 船津 河口湖大橋から南へ300 m, 平坦な砂泥底 水深1–5 cm 水草上, July 11, 2017, collected by the last author (HF), two males, three females, 41 juveniles (OKCAB M30008; Figs. 12, 27, 42). Asakawa, 35°30'17.70"N, 138°46'15.53"E, beneath stones on rocky shore at the edge of a sandy beach, 5–30 cm in depth 浅川, 砂浜邊緣岩礫地 水深5–30 cm 転石下, July 11, 2017, collected by the last author (HF), seven males, seven females, one sex unknown (OKCAB M30004; Figs. 14, 15, 28, 41). Kawaguchi, 35°31'03.38"N, 138°46'11.47"E, under beach drift on sandy mud flat, 1–3 cm in depth, 河口, 平坦な砂泥底 水深1–3 cm 漂着物下, July 11, 2017, collected by the last author (HF), one male, one female, one juvenile (OKCAB M30015; Fig.

13). ~200 m south of Kawaguchiko-ō-hashi Bridge, Funatsu, 35°30'28.9"N, 138°45'49.0"E, on piled rocks, 1–10 cm in depth 船津 河口湖大橋から南へ200 m, 水深1–10 cm 転石上, September 23, 2022, collected by the second author (NS), three adults (sex unknown) (KUZZ6014; Figs. 52–56).

Description

Shell (Figs. 12–17). Small (measurements: Table 5), globular, thick, translucent, ivory white or pale yellowish. Protoconch (Figs. 20, 21) similar to that of *Pseudovivipara eximia*. Teleoconch of ~2.5 convex whorls with weakly impressed suture; surface glossy with fine growth lines and a few thin, dark brown, slightly raised longitudinal varices; indistinct spiral threads irregularly found in some specimens. Aperture wide, semicircular, lips similar to those of *Pseudovivipara eximia*. Umbilicus closed.

Operculum (Figs. 27–31). Oval, shorter than that of *Pseudovivipara eximia*; outer side slightly concave, weakly glossy, with fine growth lines; edge of chitinous layer extending beyond edge of calcified part. Inner side weakly convex, opaque white.

Head-Foot (Figs. 38–41, 69–71). Similar to that of *Pseudovivipara eximia*, but darker in external color of head, neck, and anterior part of sole.

Mantle Cavity. Depth of cavity ~10 mm. Dorsal mantle roof with a few broad, distinct bands of black pigmentation (Figs. 41, 43); these bands distinct in juveniles (Fig. 42). Gill filaments (Fig. 45) well developed, comprising ~75–80 conspicuous translucent filaments of gf1 and gf2; both filaments wider than those of *Pseudovivipara eximia*. Osphradium (os) ~1.5 mm in length, 0.2 mm in width.

Digestive System. Buccal mass (Figs. 92, 93), oesophagus, stomach (Fig. 63), and intestine similar to those of *Pseudovivipara eximia* except for small size. Salivary gland long, extending beyond posterior end of buccal mass.

Radula (Figs. 52–56). Whole length ~0.7 mm (Fig. 52). Central teeth shorter than those of *Pseudovivipara eximia*; with three distinct cusps on either side of median cusp; median cusp sharp, longest and widest, up to two times as wide as adjacent cusps; lateral edges spread at angle of ~30° to cutting edge; three pairs of prominent basal cusps laterally; short, basal process short, narrow. Lateral teeth with cusp formula 3+1+4; median cusp blunt, wider than adjacent cusps. Inner marginal

TABLE 5. Shell measurements of *Pseudovivipara longicomis* (Benson, 1842) (mm).

		Shell length 殻長	Shell width 殻径	Body whorl length 体層長	Aperture length 殻口長	Aperture width 殻口径	Total number of whorls 螺層数	
Lake Kawaguchi, Yamanashi Prefecture, Japan (OKCAB)	M30004	♂ (n = 7)	7.2 ± 0.5 (6.5–7.9)	5.5 ± 0.3 (5.0–6.0)	6.2 ± 0.4 (5.7–6.8)	4.0 ± 0.3 (3.6–4.3)	3.3 ± 0.2 (3.0–3.5)	3.46 ± 0.22 (3.25–3.75)
		♀ (n = 7)	6.9 ± 0.4 (6.3–7.3)	5.6 ± 0.2 (5.2–5.7)	6.2 ± 0.2 (5.9–6.4)	4.0 ± 0.1 (3.8–4.2)	3.3 ± 0.1 (3.2–3.5)	3.32 ± 0.19 (3.25–3.75)
		Total (n = 14)	7.0 ± 0.4 (6.3–7.9)	5.5 ± 0.2 (5.0–6.0)	6.2 ± 0.3 (5.7–6.8)	4.0 ± 0.2 (3.6–4.3)	3.3 ± 0.2 (3.0–3.5)	3.39 ± 0.21 (3.25–3.75)
	M30008	♂ (n = 2)	6.8 ± 0.4 (6.5, 7.0)	5.4 ± 0.1 (5.3, 5.5)	6.1 ± 0.0 (6.1, 6.1)	4.0 ± 0.1 (3.9, 4.0)	3.2 ± 0.0 (3.2, 3.2)	3.25 ± 0.0 (3.25, 3.25)
		♀ (n = 3)	6.6 ± 0.3 (6.4–6.9)	5.3 ± 0.2 (5.1–5.5)	6.0 ± 0.3 (5.7–6.2)	4.0 ± 0.1 (4.0–4.1)	3.2 ± 0.1 (3.1–3.3)	3.17 ± 0.14 (3.00–3.25)
	Total (n = 5)	6.7 ± 0.3 (6.4–7.0)	5.3 ± 0.2 (5.1–5.5)	6.0 ± 0.2 (5.7–6.2)	4.0 ± 0.1 (3.9–4.1)	3.2 ± 0.1 (3.1–3.3)	3.20 ± 0.11 (3.00–3.25)	
	M30015	♂ (n = 1)	6.4	5.0	5.6	3.9	3.0	3.25
		♀ (n = 1)	6.3	5.0	5.7	3.8	3.0	3.25
		Total (n = 2)	6.4 ± 0.1 (6.3, 6.4)	5.0 ± 0.0 (5.0, 5.0)	5.7 ± 0.1 (5.6, 5.7)	3.9 ± 0.1 (3.8, 3.9)	3.0 ± 0.0 (3.0, 3.0)	3.25 ± 0.00 (3.25, 3.25)
	M30030	♂ (n = 2)	6.6 ± 0.4 (6.3, 6.8)	5.5 ± 0.2 (5.3, 5.6)	6.1 ± 0.4 (5.8, 6.3)	4.1 ± 0.1 (4.0, 4.2)	3.3 ± 0.1 (3.2, 3.3)	3.25 ± 0.00 (3.25, 3.25)
		♀ (n = 6)	7.2 ± 0.5 (6.5–7.7)	6.0 ± 0.3 (5.7–6.4)	6.6 ± 0.3 (6.2–6.9)	4.4 ± 0.2 (4.2–4.7)	3.5 ± 0.2 (3.3–3.9)	3.29 ± 0.10 (3.25–3.50)
		Total (n = 8)	7.0 ± 0.5 (6.3–7.7)	5.8 ± 0.3 (5.3–6.4)	6.5 ± 0.4 (5.8–6.9)	4.3 ± 0.2 (4.0–4.7)	3.5 ± 0.2 (3.2–3.9)	3.28 ± 0.09 (3.25–3.50)

(continues)

TABLE 5. Continued.

		Shell length 殻長	Shell width 殻径	Body whorl length 体層長	Aperture length 殻口長	Aperture width 殻口径	Total number of whorls 螺層数
Total	♂ (n = 12)	6.9 ± 0.5 (6.3–7.9)	5.4 ± 0.3 (5.0–6.0)	6.1 ± 0.4 (5.6–6.8)	4.0 ± 0.2 (3.6–4.3)	3.2 ± 0.2 (3.0–3.5)	3.38 ± 0.20 (3.25–3.75)
	♀ (n = 17)	6.9 ± 0.4 (6.3–7.7)	5.6 ± 0.4 (5.0–6.4)	6.3 ± 0.4 (5.7–6.9)	4.1 ± 0.2 (3.8–4.7)	3.3 ± 0.2 (3.0–3.9)	3.28 ± 0.15 (3.00–3.75)
	Total (n = 29)	6.9 ± 0.5 (6.3–7.9)	5.5 ± 0.3 (5.0–6.4)	6.2 ± 0.4 (5.6–6.9)	4.1 ± 0.2 (3.6–4.7)	3.3 ± 0.2 (3.0–3.9)	3.32 ± 0.17 (3.00–3.75)
	Sex unknown	9.2	7.1	7.6	5.1	4.5	3.50
Nanjing, China (TUMC h320-2)							
Total (n = 30)		7.0 ± 0.6 (6.3–9.2)	5.6 ± 0.4 (5.0–7.1)	6.2 ± 0.4 (5.6–7.6)	4.1 ± 0.3 (3.6–5.1)	3.3 ± 0.3 (3.0–4.5)	3.33 ± 0.18 (3.00–3.75)

teeth with 15–18 uniform, small cusps. Outer marginal teeth with seven uniform, sharp cusps.

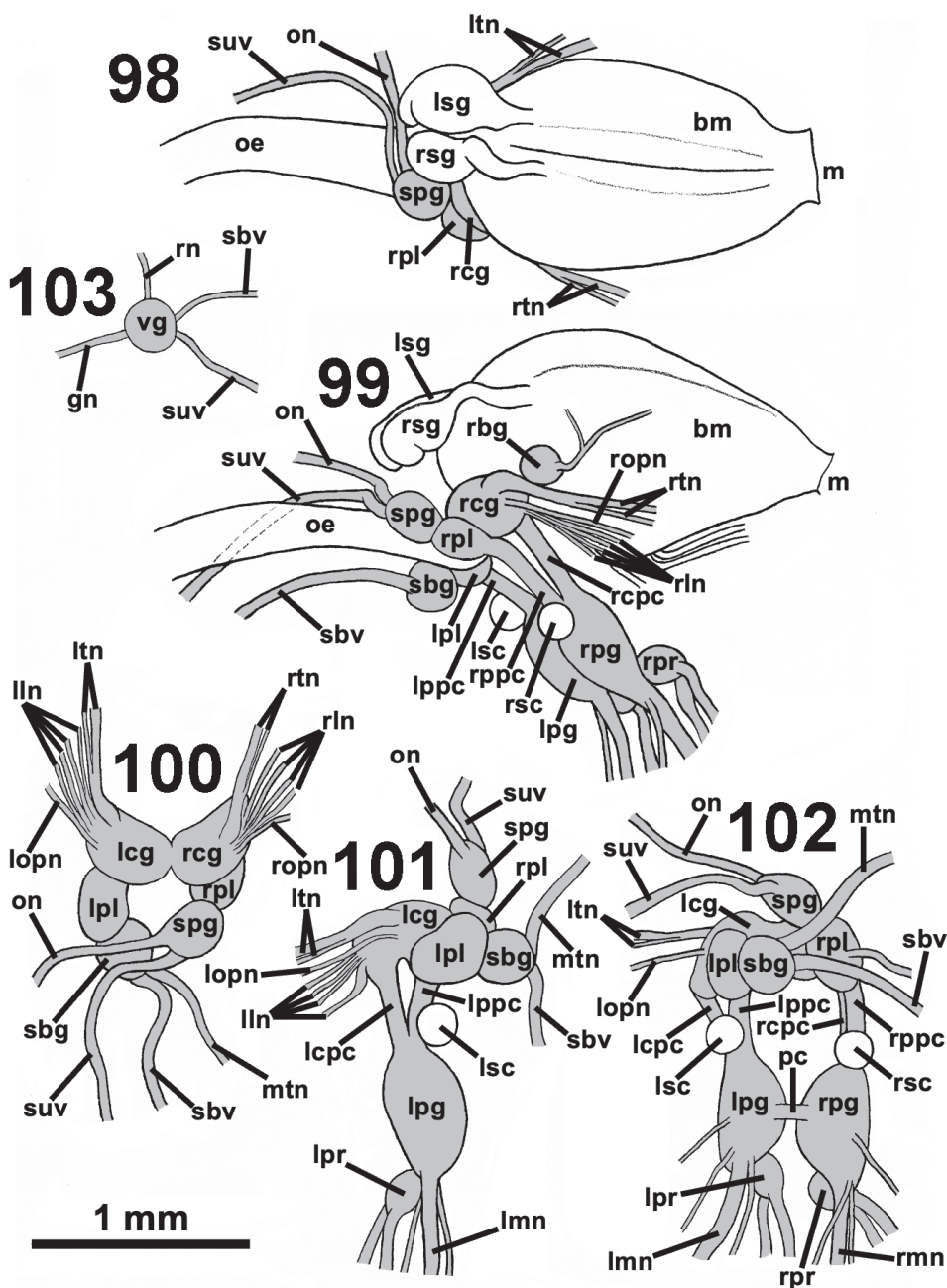
Male Reproductive System (Figs. 69–73). Testis (Fig. 69, t) large (~ 10 mm in length), occupying two apical whorls, bright orange, consisting of many globular, distinct cells. Seminal vesicle (sv) highly convoluted. Prostate gland (pr) ~ 2.8 mm in length. Anterior vas deferens (avd) strongly undulating before reaching proximal end of penis (Figs. 69–73, p). Penis smaller than that of *Pseudovivipara eximia*, attached to head ~ 1 mm behind eye (e); black glandular area (bpg) distinct; distal end (po) blunt with no projection; penial duct (pd) weakly undulating. Accessory lobe (Figs. 70, 73, pa) long. Accessory gland (Fig. 72, pag) longer than that of *Pseudovivipara eximia*.

Female Reproductive System (Figs. 80, 81, 85). Ovary (Fig. 85, ov) ~ 1.5 mm in length, smaller than that of *Pseudovivipara eximia*. Renal (coiled) oviduct (cov) narrow but distinct, with some large loops. Seminal receptacle (Fig. 80, sr) very large, oval, opening at middle portion of renal oviduct, lying on left ventral side of albumen gland. Pallial oviduct (Figs. 80, 81, ag, cg) long (~ 8 mm in length), rather wide (~ 1 mm in maximum width). Bursa copulatrix (bc) long, wide (~ 3.5 mm in length, 0.8 mm in width), elongate triangular, running on left lateral side of capsule gland (ag). Female genital opening (fgo) long slit.

Central Nervous System (Figs. 92–97). Generally similar to that of *Pseudovivipara eximia* except for several differences: cerebral commissure (cc) short but distinct, wide (0.1 mm in length, 0.2 mm in width). Tentacular nerves (rtn, ltn) with weak swellings at their bases, each divided into three nerves distally. Cerebropedal and pleuropedal connectives (rcpc, lcpc, rppc, lppc) right and left with same length, not showing asymmetry. Mantle nerve from suboesophageal ganglion not observed. Statocysts (rst, lst) large for size of pedal ganglia (rpg, lpg). Visceral ganglion (vg) distinct, globular.

Type Localities

“Chusan” [= Zhoushan 舟山, Zhejiang 浙江省, China] (*Paludina (Bithynia) lon-*



FIGS. 98–103. Central nervous system of *Pseudovivipara manchourica japonica* (Pilsbry, 1901), Natajima, Yamaguchi Prefecture, Japan (OKCAB M25129). (98) Dorsal view of nerve ring and buccal mass; (99) right lateral view of nerve ring and buccal mass; (100) dorsal view of nerve ring; (101) left lateral view of nerve ring; (102) rear view of nerve ring; (103) visceral ganglion. bm, buccal mass; gn, gonadal nerve; lcg, left cerebral ganglion; lcp, left cerebropedal connective; lln, left labial nerve; lmn, left metapodial nerve; lopn, left optic nerve; lpg, left pedal ganglion; lpl, left pleural ganglion; lppc, left pleuropedal connective; lpr, left propodial ganglion; lsc, left statocyst; lsg, left salivary gland; ltn, left tentacular nerve; m, mouth; mtan, mantle nerve; oe, oesophagus; on, osphradial nerve; pc, pedal

→

gicornis); "In der kaiserlichen Sammlung von Shuttleworth aus Nordchina, in Cuming's Sammlung aus Shanghai" (*Bithynia shuttleworthi*); "fluviales du Tonkin" (*Stenothyra tonkiniana*).

Distribution

The known localities of the species are listed below. Representative locality in each Chinese province is shown in brackets: China: Anhui Province 安徽省 (Hefei 合肥), Fujian Province 福建省, Guangdong Province 广东省 (Xijiang River 西江), Guangxi Zhuang Autonomous Region 广西壮族自治区, Guizhou Province 贵州省 (Sanjiangkou 三江口), Hebei Province 河北省 (Shijiazhuang 石家庄), Henan Province 河南省, Hubei Province 湖北省 (Yichang 宜昌), Hunan Province 湖南省 (Xiangtan 湘潭), Jiangsu Province 江苏省 (Nanjing 南京), Jiangxi Province 江西省, Shandong Province 山东省 (Lake Weishan 微山湖), Shaanxi Province 陕西省; Shanxi Province 山西省, Sichuan Province 四川省 (Guang'an 广安), Yunnan Province 云南省 (Lake Fuxian 抚仙湖), Zhejiang Province 浙江省 (Zhoushan 舟山), Beijing 北京, Chongqing 重庆 (Lake Hanfeng 汉丰湖), Shanghai 上海 (Jiading 嘉定), Hong Kong 香港 (Siu Lam 小欖); Vietnam: northern region, Thanh Hoa Province (Ha Trung), Yen Bai Province (Yen Binh); South Korea (Suwon 수원시 水原); Japan (introduced): Lake Kawaguchi 河口湖.

The species is widely distributed around the eastern and southeastern parts of China and the northern part of Vietnam as the southern limit. In addition to the above regions, Y.-T. Yang et al. (2022) also suggested records from Heilongjiang Province 黑龙江省, Liaoning Province 辽宁省, and Xinjiang Uygur Autonomous Region 新疆维吾尔自治区 of China, but specific details were not provided.

In South Korea, Annandale (1918b: 306) mentioned that "I have recently examined a number of specimens from Suigen [= Suwon] in Corea (T. Kawamura [川村多實二]) which agree closely with them [= 'three co-types of Benson's species in the collection of the Zoological Survey of India']". Min et al. (2004)

illustrated two specimens of "*Parafossarulus manchouricus*" from South Korea, and one of them (fig. 268-1) is identifiable as *Pseudovivipara longicornis* judging from the shell characters, whereas another one (fig. 268-2) is *Pseudovivipara manchourica*.

This species was reported from the Middle Pleistocene Hiraen Clay Member, Katata Formation, Kobiwako Group in Shiga Prefecture, central Honshū 滋賀県中部更新統古琵琶湖層群堅田層比良園粘土層 (Yasuno, 1980; Matsuo, 1981, 1987, 1998, 2020; Kimura et al., 2008) but it later became extinct.

Ecology

Pseudovivipara longicornis is one of the vectors of *Clonorchis sinensis*, causing clonorchiasis (Hsü & Chow, 1937; Lim, 2005; Lu et al., 2018) and, as a result, its distribution has been relatively well studied (Lim, 2005). However, other ecological aspects were not well documented, with limited insights suggested from ecological studies on freshwater macroinvertebrate communities in China.

In Lake Biandantang, *Pseudovivipara longicornis* primarily forages on detritus throughout the year (X.-Q. Liu et al., 2006), and stable isotope analysis suggested that this species as one of the most $\delta^{13}\text{C}$ -enriched consumers in Lake Taihu (Mao et al., 2011). Detailed life-history studies conducted in Lake Biandantang indicated that this species has a lifespan of 1–1.5 yr, a reproductive season from April–May, and an annual production-to-biomass ratio ranging from 4.00–4.36 (Y.-J. Yan et al., 2002).

This species inhabits various aquatic environments, primarily lakes and rivers (Galliard, 1939; Taki, 1940; C.-Y. Chen et al., 1975; Xiong et al., 2008; Y. Zhang et al., 2018; Wu et al., 2019). It is often a dominant species in macroinvertebrate communities (C.-Y. Chen et al., 1975; Xiong et al. 2008; Y. Zhang et al., 2018). In lake habitats, *Pseudovivipara longicornis* tends to be more abundant in areas with macrophytes (C.-Y. Chen et al., 1975;

FIGS. 98–103 (continued). commissure; rbg, right buccal ganglion; rcg, right cerebral ganglion; rcpc, right cerebropedal connective; rln, right labial nerve; rmn, right metapodial nerve; rn, renal nerve; ropn, right optic nerve; rpg, right pedal ganglion; rpl, right pleural ganglion; rppc, right pleuropedal connective; rpr, right propodial ganglion; rsc, right statocyst; rsg, right salivary gland; rtn, right tentacular nerve; sbg, suboesophageal ganglion; sbv, subvisceral connective; spg, supraoesophageal ganglion; suv, supravisceral connective; vg, visceral ganglion.

L. Chen et al., 2015; Ji et al., 2023; Y. Zhang et al., 2024), whereas in river habitats, it has been reported to be more abundant in areas without macrophytes (S. Ma et al., 2011). Although this species has often been observed with *Pseudovivipara eximia* in the same lakes, their microhabitat preferences seem to differ slightly (Z. Xie et al., 2005; L. Chen et al., 2015; Y. Zhang et al., 2018, 2024). Moreover, unlike *Pseudovivipara eximia*, this species might be susceptible to drought (Y. Zhang et al., 2024). Although no experimental evidence is documented, observations suggest that *Pseudovivipara longicornis* can exhibit high salt tolerance, because it has been found in estuaries and mangrove habitats (Hong & San, 1993; Jing et al., 2007). In the Yangtze River Delta, this species is considered an indicator of moderate water quality (Qin et al., 2014; L. Wang et al., 2021). Although *Pseudovivipara longicornis* remains common, some studies have reported potential population declines in response to recent environmental changes (Y. Cai et al., 2014; Kattel et al., 2018; Jiang et al., 2020).

Remarks

Ablett et al. (2019) provided a photograph of a syntype of *Paludina* (*Bithynia*) *longicornis* (UMZC I.104440.A–D). Preece et al. (2022) also illustrated the above syntype as well as another syntype (NHMUK 1842.9.30.23–26). Specimens examined in this study agree well with these illustrated type specimens.

The species was originally described as belonging to the viviparid genus *Paludina* Férussac, 1812 (= *Viviparus* Montfort, 1810; but also included in the subgenus *Bithynia*), with the generic position being unstable since then. As shown in the above synonymy, many authors assigned this species to *Gabbia* Tryon, 1865 or *Alocinma* Annandale & Prashad, 1919, chiefly because of the resemblance of the smooth, globose shell. However, the species is here regarded as a member of *Pseudovivipara* based on our molecular phylogenetic analysis. This result is also supported by the similarities in anatomy of the pallial organs: the reproductive and central nervous systems that are mentioned in the above diagnosis of the genus. These also include the few wide bands of black pigment on the dorsal surface of the mantle (Figs. 41, 42) shared with *Pseudovivipara eximia* (Figs. 36, 37) and *Pseudovivipara manchourica*. In other bithyniid genera,

most species exhibit many distinct white spots on black ground of the external mantle surface [e.g., *Bithynia tentaculata* (Linnaeus, 1758) and *Digoniostoma siamense* (I. Lea, 1856): Fukuda, 2025a, and pers. obs.; *Bithynia inabai* Habe, 1985; Tatara et al., 2010: fig. 20, R; Fukuda, 2020b; *Gabbia kiusiuensis* (S. Hirase, 1927): Fukuda, 2010, 2020b; *Pseudobithynia yildirimi* Odabaşı, Kebapçı, & Akbulut, 2013: Odabaşı et al., 2013: fig. 2G].

Shell size is not very variable among specimens from Lake Kawaguchi (Fig. 16), but a specimen from Nanjing, China (Fig. 17) is much larger than them. In a previous study, shell length in fully mature specimens from the lower region of the Yangtze River drainage was reported showing a mean of 7.2 mm (4.1–10.0 mm; n = 240) (Zhao et al., 2009). Another study on specimens from Lake Bao'anhui reported the shell length as ~ 7.2 mm (Y.-J. Yan et al., 2002). In addition, specimens from the Zhejiang Province showed 7.6–8.0 mm in length and 5.2–5.8 mm in width (Huang & Z. Li, 1991).

COMPARISON WITH *PSEUDOVIVIPARA MANCHOURICA JAPONICA*

The internal anatomy of *Pseudovivipara manchourica japonica* was described in detail by Itagaki (1965) (and also *Pseudovivipara manchourica manchourica* based on Korean specimens by Kim, 2005), but the morphology of the bursa copulatrix, some ganglia, connectives and commissures of the nervous system, and so on are not informative in their descriptions. Thus, we here redescribe the anatomy of *Pseudovivipara manchourica japonica* and compare the results with the two introduced congeneric species. The following new data were added to the above diagnosis for *Pseudovivipara*.

Specimens examined were ten males and 11 females from rice fields in Shōwa-nishi, Natajima, Yamaguchi-shi, Yamaguchi Prefecture, western Honshū, Japan 山口県山口市名田島 昭和西, 34°02'53"N, 131°23'58"E, June 24, 2008, collected by the last author (HF), OKCAB M25129 (Figs. 46, 64, 69–73, 82, 83, 86, 98–103). The radula is from ~ 200 m south of Kawaguchiko-ō-hashi Bridge, Lake Kawaguchi, Funatsu, Fujikawaguchiko-machi, Minamitsuru-gun, Yamanashi Prefecture, Japan, 35°30'28.9"N, 138°45'49.0"E, on piled rocks, 1–10 cm in depth 山梨県南都留郡富士河口湖町船津 河口湖 河口湖大橋から南へ200 m, 水深1–10 cm 転石上, June 8, 2024, collected

by the second author (NS), three adults (sex unknown), KUZ Z6013 (Figs. 57–61).

Pseudovivipara manchourica japonica is anatomically similar to *Pseudovivipara eximia* and *Pseudovivipara longicornis* and specifically *Pseudovivipara manchourica japonica* and *Pseudovivipara eximia* share the following character conditions: extremely minute seminal receptacle and narrow renal oviduct (Figs. 82, 83); very long and narrow bursa copulatrix; and thick mantle nerve arising from the suboesophageal ganglion (Figs. 101, 102, mtn). On the other hand, the pedal commissure (Fig. 102, pc) observed in *Pseudovivipara manchourica japonica* and *Pseudovivipara longicornis*, is not visible because the pedal ganglia closely abut each other in *Pseudovivipara eximia*.

Gill filament number is different in these three taxa: 140–150 in *Pseudovivipara eximia* (Fig. 44), 75–80 in *Pseudovivipara longicornis* (Fig. 45), and 100–110 in *Pseudovivipara manchourica japonica* (Fig. 46). Ponder (2003: 24, fig. 6) pointed out that the shape and size of the whole gill differs in species of *Gabbia*. Also, Kim (2005: 137, 138) mentioned that “the numbers of [gill] lamellae varied in species. Generally, bigger species such as *Bithynia siamensis* [= *Digoniostoma siamense*] had about 70 lamellae, but smaller species, *Bithynia leachi* [sic; = *Bithynia leachii* (Sheppard, 1823)], had less than 40 lamellae”. Accordingly, the gill size and the filament number are thought to be useful diagnostic characters for bithyniid species.

The central radular teeth (Figs. 57–61) are low trapezoid with three pairs of basal cusps. They are similar to those of *Pseudovivipara longicornis* (Figs. 52–56), but different from those of *Pseudovivipara eximia*, which are taller with nearly straight lateral edges in the upper part (Figs. 47–51).

The length of the penial accessory gland differs among the three species, as shown in many Australian taxa of *Gabbia* by Ponder (2003: 24, 25, fig. 25). In *Pseudovivipara*, the longest is *Pseudovivipara manchourica* (Fig. 77) and the shortest is *Pseudovivipara eximia* (Fig. 68).

In the female genital organs, the seminal receptacle is large and conspicuous in *Pseudovivipara longicornis* but is extremely small in *Pseudovivipara eximia* and *Pseudovivipara manchourica japonica* (Figs. 79, 80, 82, sr). The shape and size (length and width) of the bursa copulatrix (Figs. 78, 80, 82, bc) are other important diagnostic characters, with the bursa of *Pseudovivipara eximia* and *Pseudovivipara*

manchourica japonica being very long and narrow, whereas in *Pseudovivipara longicornis*, it is rather wide.

Kim (2005: 138, fig. 8) illustrated a distinct “metapodial ganglion” of “*Bithynia striatula*” (= *Pseudovivipara manchourica*), but we did not find that ganglion in the three species examined in the present study (Figs. 91, 97, 103). Further, Kim (2005: 144) mentioned that “I could not find [a] visceral ganglion” and “I cannot completely exclude the possibility that I missed an isolated visceral ganglion” in *Pseudovivipara manchourica*. In the present study, the presence of the visceral ganglion was confirmed in all three species examined. It is globular in *Pseudovivipara longicornis* and *Pseudovivipara manchourica japonica* (Figs. 97, 103) but elongate triangular in *Pseudovivipara eximia* (Fig. 91).

MOLECULAR RESULTS

In both CO1 and 16S phylogenies (Figs. 104, 105), *Parafossarulus/Pseudovivipara* species formed a strongly supported monophyletic clade (CO1; BPP = 1.00/UFB = 98/aBayes = 1.00/LRT = 98 and 16S; BPP = 1.00/UFB = 98/aBayes = 1.00/LRT = 98). In the CO1 phylogeny, the *Parafossarulus* + *Pseudovivipara* clade comprised three well-supported monophyletic subclades (support values for all clades > 0.95 and 95, except for a single aLRT value; Fig. 104). These subclades consisted of *Parafossarulus longicornis*, *Parafossarulus manchouricus*, and *Pseudovivipara eximia*, respectively. The clades of *Parafossarulus longicornis* and *Pseudovivipara eximia* each contained three haplotypes, with few genetic differences. The *Parafossarulus manchouricus* clade was divided into two lineages: one consisting of *Parafossarulus manchouricus japonicus* from Lake Biwa, Japan, and the other comprising *Parafossarulus* cf. *manchouricus* from China and *Parafossarulus manchouricus japonicus* from Okayama, Japan. The latter lineage formed a moderately supported clade (0.98/95/0.98/84). The *Parafossarulus manchouricus* clade was sister to the *Parafossarulus longicornis* clade, and together they formed a partially supported clade (0.98/94/0.87/83). This clade was, in turn, sister to the *Pseudovivipara eximia* clade. However, the phylogenetic position of the *Parafossarulus* + *Pseudovivipara* clade within the family Bithyniidae was not well resolved. In the 16S phylogeny, the overall tree topology for *Parafossarulus* and *Pseudovivipara* was

FIGS. 104. Bayesian phylogenetic tree estimated from mitochondrial cytochrome oxidase subunit 1 sequences (658 bp). Each sample label includes the haplotype number and corresponding scientific name. For *Parafossarullus* and *Pseudovivipara* haplotypes, collected localities are provided, with Japanese localities indicated in blue. Four support values are displayed at each branch, except for terminal nodes. For further information of each sample, see Table 1. *Ps*, *Pseudovivipara*; *Pa*, *Parafossarullus*; *B*, *Bithynia*; *G*, *Gabbia*; *W*, *Wattebledia*; *H*, *Hydrobioides*.

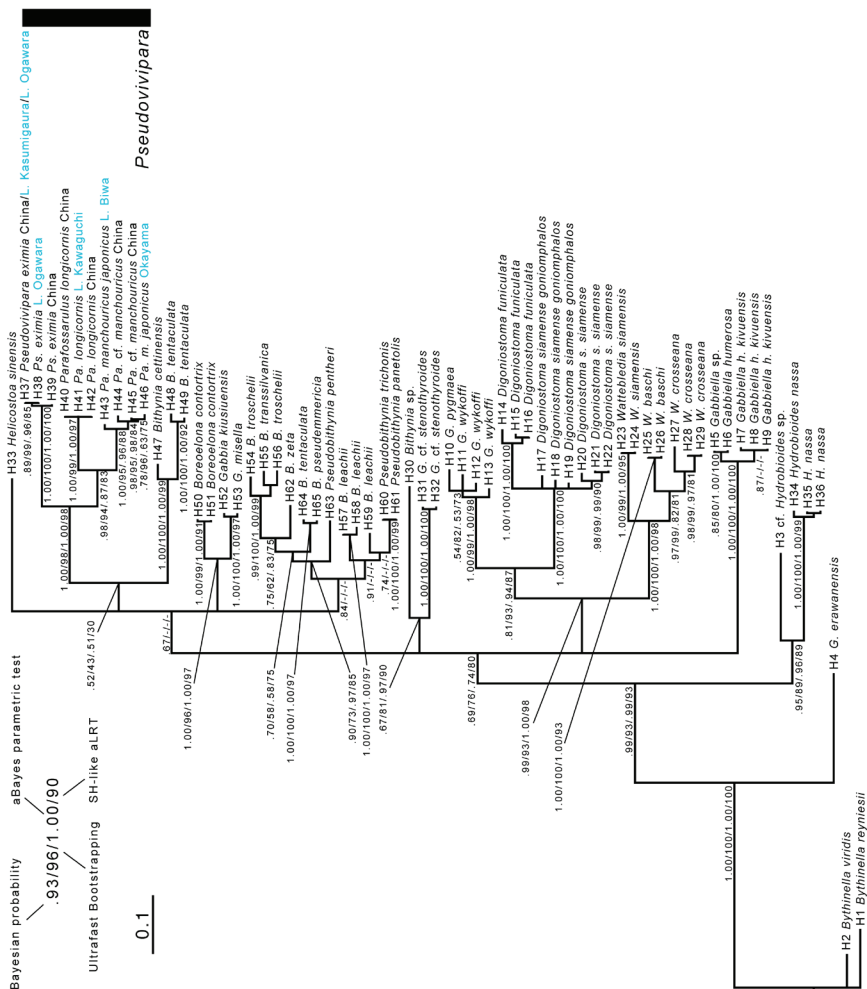
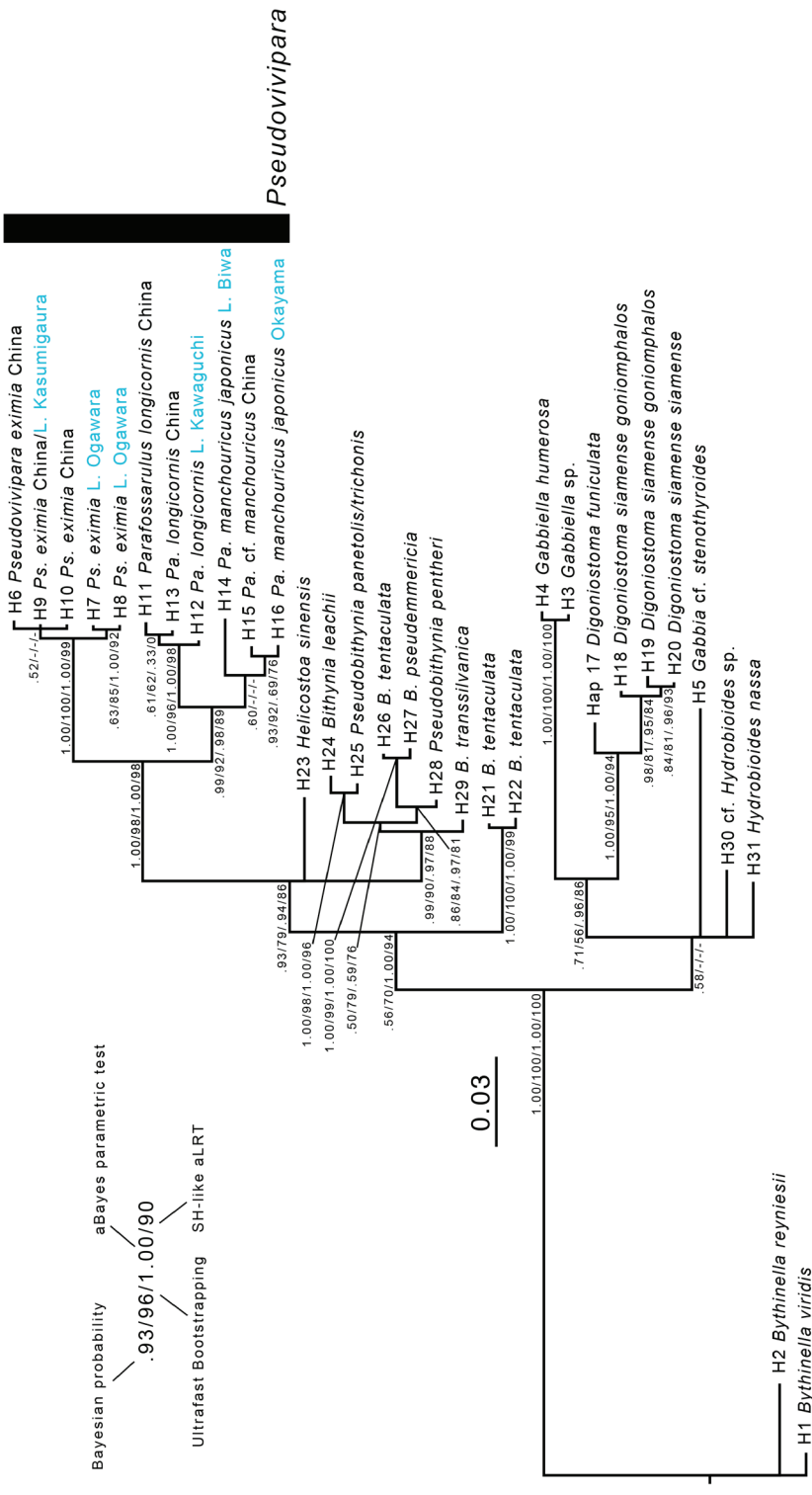


FIG. 105. Bayesian phylogenetic tree estimated from mitochondrial 16S ribosomal RNA sequences (467 bp). Each sample label includes the haplotype number and corresponding scientific name. For *Parafossarulus* and *Pseudovivipara* haplotypes, collected localities are provided, with Japanese localities indicated in blue. Four support values are displayed at each branch, except for terminal nodes. For further information of each sample, refer to Table 1. *Ps*, *Pseudovivipara*; *Pa*, *Parafossarulus*; *B*, *Bithynia*.



congruent with that observed in the CO1 phylogeny (Fig. 105), although support values for the *Parafossarulus manchouricus* clade were low (0.60/-/-).

Two CO1 haplotypes (H37 and H38) of *Pseudovivipara eximia* from Japan were observed in this study, and one CO1 haplotype was shared among samples from China and two Japanese lakes (Fig. 104). Within *Parafossarulus longicornis*, a single CO1 haplotype (H41) was detected in Japan, and it was slightly distinct from two Chinese haplotypes (H40 and H42). Similarly, three 16S haplotypes (H7, H8, and H9) of *Pseudovivipara eximia* were observed from Japan, and one haplotype (H9) was shared among samples from China and Japan (Fig. 105). Within *Parafossarulus longicornis*, a single 16S haplotype (H12) was detected from Japan and it was slightly distinct from two Chinese haplotypes (H11 and H13).

DISCUSSION

Our morphological and molecular results have demonstrated that the *Pseudovivipara* species recently observed in Japan are *Pseudovivipara eximia* and *Pseudovivipara longicornis*. Prior to this study, these two species had not been recorded in Japan, except for the fossil records of *Pseudovivipara longicornis* (Yasuno, 1980; Matsuoka, 1981, 1987, 1998, 2020; Kimura et al., 2008). The observed genetic variation in CO1 and 16S sequences (Figs. 104, 105) within Japanese populations were limited, and the genetic differences between Japanese and native Chinese populations (Yen, 1939) were few. These findings suggest that *Pseudovivipara longicornis* and *Pseudovivipara eximia* in Japan were recently introduced.

Based on our study, *Pseudovivipara eximia* was recorded from five localities: Lake Ogawara, Aomori Prefecture; a water channel, Niigata Prefecture; the Tone River between Ibaraki and Chiba prefectures; Lake Sotona-sakaura (a part of Lake Kasumigaura), Ibaraki Prefecture; Kisarazu, Chiba Prefecture (broken empty shell) (Fig. 1). Specimens in Japan from Ibaraki and Chiba prefectures were collected in 1993 and 2002 but these records were not previously published, and one of us (NS) discovered them during a survey of the collection of the Natural History Museum and Institute, Chiba. This species has not been reported subsequently in those areas and so might not have become established. Later,

Pseudovivipara eximia was found in Niigata Prefecture in 2008, but was misidentified as *Pseudovivipara manchourica japonica* (as *Parafossarulus manchouricus japonicus*; Nomura, 2010a, b; Murayama et al., 2025). In Lake Ogawara, *Pseudovivipara eximia* was collected from the same site in 2012 and 2018, with numerous individuals. Therefore, we can regard *Pseudovivipara eximia* as established in Japan.

Pseudovivipara longicornis has been recorded exclusively from Lake Kawaguchi in Yamanashi Prefecture, Japan, and was found at four collecting sites in that lake. The first observation was in 2016, then in 2017, 2019, and 2021 (Fig. 1). Although fossil records of *Pseudovivipara longicornis* exist in Japan (Yasuno, 1980; Matsuoka, 1981, 1987, 1998, 2020), the extant population in Lake Kawaguchi likely represents a recent introduction from China. The genetic differences between Japanese and Chinese sequences are few (i.e., 1 bp in CO1). In addition, we know of no specimens or literature records of *Pseudovivipara longicornis* in Japan prior to 2016. Considering its size and distinctive morphology from other Japanese freshwater snails, it is improbable that the occurrence of this species has been overlooked prior to its recent discovery.

The mechanisms for the introduction of species of *Pseudovivipara* in Japan (or elsewhere) remain unclear. Various possibilities could be considered, such as the aquarium trade (e.g., Patoka et al., 2017), accompanying fish releases (e.g., Fuller, 2015), and attaching to migratory birds (e.g., Saito et al., 2023). Our molecular results indicate that introduced *Pseudovivipara* share haplotypes with Chinese samples from Nanjing, Jiangsu Province. However, due to limited genetic data on *Pseudovivipara eximia* and *Pseudovivipara longicornis* across their native distributions, it is difficult to accurately identify their origins. Nevertheless, because bithyniid gastropods exhibit geographically structured populations based on genetic data (Bunchom et al., 2019, 2021), the source population of the introduction is most likely from the Yangtze River basin, including Nanjing. In addition, most records of *Pseudovivipara* in Japan are from large lakes and rivers like Lake Ogawara, Lake Kasumigaura, Lake Kawaguchi, and the Tone River. These water bodies have many intended and unintended introduced species, including those from China (e.g., Harako & Murai, 1995; Hirabayashi & Yoshida, 1998; Ito, 2007;

Hagiwara, 2017; Saito, 2022; Ishii et al., 2024). These water bodies are subject to frequent human activities such as fisheries and tourism, thus providing opportunities for accidental or deliberate introduction. Given that some sites appear to be unestablished (e.g., the Tone River), introduction opportunities from China to Japan through various human or animal vectors could be frequent, leading to establishment after repeated introductions. This process can be recognized as a typical example of invasion debut for introduction (Rouget et al., 2015).

Although introduced *Pseudovivipara* spp. in Japan have primarily been recorded in lakes, they are not restricted to that type of water body. They are also recorded from water channels, rivers, and wetlands within their native distributions and *Pseudovivipara eximia* has also been recorded in a water channel in Niigata Prefecture (Taki, 1940; Nomura, 2010a, b; Jia et al. 2021; F. Liu & Lu, 2021). Thus, the distributions of introduced *Pseudovivipara* spp. in Japan might expand in the future. Fortunately, the three *Pseudovivipara* spp. found in Japan exhibit distinct shell morphology, allowing for accurate identification, facilitating evaluation of any impacts of the introductions.

The introduced *Pseudovivipara* spp. are important intermediate hosts for parasites that cause human diseases, including *Angiostrongylus cantonensis* and *Clonorchis sinensis* (Hsü & Chow, 1937; Lim, 2005; Lu et al., 2018). These diseases could potentially pose a threat to human activities in Japan (Asato et al., 2004; Yoshida, 2012). It is unclear whether the introduction of *Pseudovivipara eximia* can exhibit an impact on the epidemiology of *A. cantonensis* infection, because other intermediate hosts, e.g., *Physella acuta* (Draparnaud, 1805) and *Orientogalba ollula* (Gould, 1859), are already widespread in Japan (Masuda & Uchiyama, 2004; Lu et al., 2018). In contrast, *Pseudovivipara longicornis* could influence the epidemiology of *C. sinensis*, because its dominant native intermediate host, *Pseudovivipara manchourica japonica*, is rapidly decreasing in Japan (Fukuda, 2020a, b). However, *C. sinensis* exhibits genetic differentiation across geographic regions and might have a different host specificity (J. Sun et al., 2013; Chelomina et al., 2014). Thus, it remains unclear whether *C. sinensis* in Japan can efficiently utilize *Pseudovivipara longicornis* from China as the intermediate host.

The only native species of *Pseudovivipara* in Japan, *Pseudovivipara manchourica japonica*,

is regarded as critically endangered (Fukuda, 2020a, b), and its potential habitats, e.g., lakes, can overlap with those of the introduced species (Sugihara, 1979). *Pseudovivipara manchourica japonica* was abundant in Lake Kawaguchi until the 1980s (Sawada et al., 2025), and one of us (N. S.) recorded *Pseudovivipara manchourica* there in 2021 and 2024 (but it is unclear whether this population is native; Sawada et al., 2025). In Lake Kawaguchi, *Pseudovivipara manchourica japonica* had already decreased before the 2000s (Fukuda, 2020a), and the introduction of *Pseudovivipara longicornis* should not be the direct cause. Nonetheless, introduced *Pseudovivipara* spp. could pose an additional threat due to ecological similarities between these taxa.

This study documented the introductions of two bithyniid gastropods, provided detailed redescriptions, and clarified the taxonomic relationships between the genera *Parafossarulus* and *Pseudovivipara* based on morphological and molecular results. Our results confirm that *Pseudovivipara* includes at least the three species examined here and that other *Parafossarulus* species should also be automatically reassigned to *Pseudovivipara*. However, many bithyniid genera are polyphyletic (e.g., Kulsantiwong et al., 2013; Figs. 104, 105) and further taxonomic studies are required to address this issue. Because the relationship between *Pseudovivipara manchourica manchourica* in China and *Pseudovivipara manchourica japonica* in Japan remains unclear, future taxonomic and phylogenetic studies will be required to clarify their relationship.

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