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Meretrix taiwanica (Bivalvia: Veneridae), a previously misidentified new species in Taiwan

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ABSTRACT
This paper describes a new Asian hard clam, *Meretrix taiwanica* sp. n., found in the Tamsui River estuary in northern Taiwan. This species was formerly identified as *M. lusoria*, and was considered to be a descendant of a clam that originated in Japan. A molecular phylogenetic analysis, however, demonstrated that *Meretrix taiwanica* sp. n. is closely related to *M. petechialis* and *M. lusoria*. *Meretrix taiwanica* is distinguished by its smaller socket width and shorter posterior dorsal margin. This species is distributed throughout the coast of Taiwan on the southern coast of China.

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KEYWORDS
Asian hard clams; COI-DNA barcoding; *Meretrix lusoria*; *Meretrix petechialis*; Tamsui River

Introduction

Asian hard clams of the genus *Meretrix* belong to the family Veneridae, and are commercially important bivalves in East Asia, Southeast Asia and East Africa (Yoosukh and Matsukuma 2001). They inhabit the lower reaches of sandy beaches, estuaries and tidal flats, and there are 15 recognised species in the genus (MolluscaBase 2022): *M. astricta* (Reeve, 1864), *M. attenuata* (Dunker, 1863), *M. aurora* (Hornell, 1917), *M. casta* (Gmelin, 1791), *M. lamarckii* (Deshayes, 1853), *M. lusoria* (Röding, 1798), *M. lyrata* (G.B. Sowerby II, 1851), *M. marisarabicum* (C. Martin & Matsukuma, 2020), *M. meretrix* (Linnaeus, 1758), *M. morphina* (Lamarck, 1818), *M. petechialis* (Lamarck, 1818), *M. planisulcata* (G.B. Sowerby II, 1854), *M. subtrigona* (Dunker, 1857), *M. tigris* (Lai & Nien, 2008), and *M. vestita* (Reeve, 1864).

Taiwan's cultivated Asian hard clam species has been identified as *M. lusoria* for almost a century (Chen 1984). With a harvest of 49,501 tons and an economic value of more than US$155 million in 2019 (Fisheries Agency 2020), it is a major commercial aquaculture species in Taiwan.

Taxonomic research on *Meretrix* in Taiwan, including *M. petechialis*, *M. lamarckii* and *M. lyrata*, was first conducted by Kuroda (1941). Two additional species from Taiwan, *M. meretrix* and *M. lusoria*, were added by Wu (1980). An additional species, *M. tigris*, was described by Lai and Nien (2008), but recent research indicates that the colour pattern of the shell of *M. tigris* is only a different pattern of the common hard clam, with no others having been found thus far (Hsu *et al.* 2020). Of these species, *M. lyrata* can be easily identified by the unique commarginal ribs of its shell; the shell of *M. lamarckii*, which usually inhabits shallow subtidal sandy flats and beaches, is thick, triangularly ovate, and sometimes has faint concentric stria. However, because *M. meretrix*, *M. lusoria* and *M. petechialis* have simple shell shapes with diverse colour patterns and their external morphological differences are relatively small, using morphological characteristics to identify them is difficult; these similarities can lead to frequent erroneous identifications, and notations to this effect are found in shell books, reports and references (Yamakawa *et al.* 2008).

With the development of molecular technologies, allozyme (Yamakawa *et al.* 2008) and polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) (Yamakawa and Imai 2013) have been applied to studies of hard clam taxonomies of Japan, China, South Korea and Taiwan. The results suggested that *M. lusoria* and *M. petechialis* are closely related, having small genetic distances, and are allopatric (Yamakawa *et al.* 2008). The Taiwanese *Meretrix* is genetically different from *M. lusoria* and *M. petechialis* (Yamakawa and Imai 2013). Moreover, Hsiao *et al.* (2019) revealed that Asian hard clams found in the Tamsui River estuary in Taiwan formed a distinctively different cluster from *M. lusoria* and *M. petechialis* in phylogenetic analysis based on the mitochondrial DNA cytochrome c oxidase I (COI) gene. The topology revealed that *Meretrix taiwanica* sp. nov. and *M. petechialis* are more closely related to one another than

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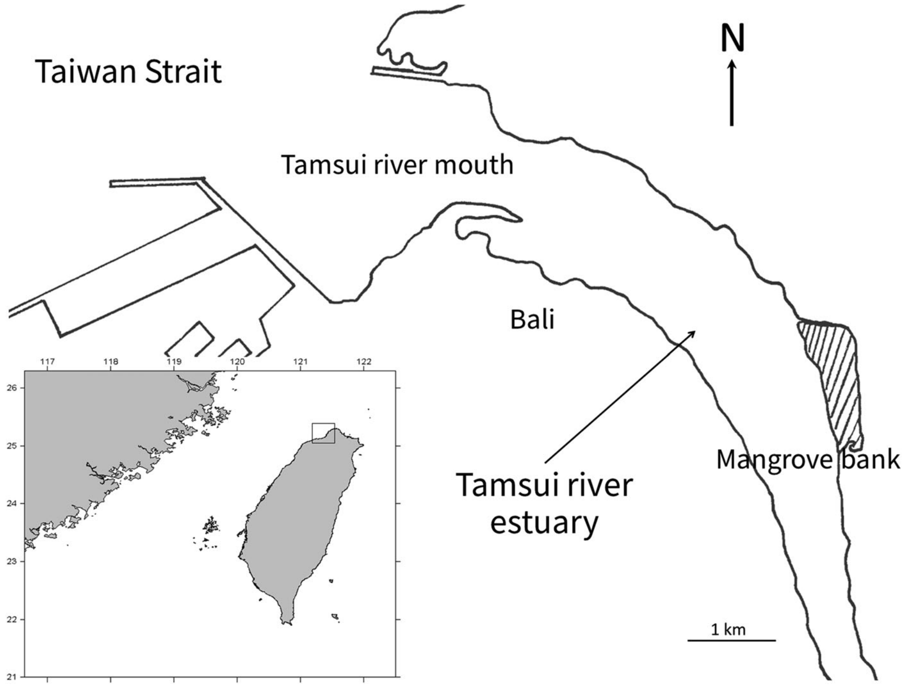

Figure 1. The type locality of *Meretrix taiwanica* sp. n. in the Tamsui River estuary, northern Taiwan.

to *M. lusoria*. Eighty years after the distribution of *Meretrix* was initially reported in Taiwan, our results indicate that Taiwanese *Meretrix* represents a distinct evolutionary lineage that is both genetically and morphologically distinct from its congeners and is thus described herein as a new species.

Material and methods

Sample collection

Specimens of the *Meretrix* species were collected from Taiwan. The adductor muscle tissue (approximately 0.5×0.5 cm) of specimens was collected and stored in 95% alcohol prior to analysis. The holotype and paratypes were collected with a bull raker at the Tamsui River estuary in New Taipei City, Taiwan (Figures 1 and 2). In order to examine the status of *Meretrix* species, we also collected samples from Hsinchu, Changhua, Tainan and Kinmen in western Taiwan.

Specimens of *M. petechialis* were obtained from a supermarket in Mie Prefecture, Japan; the packaging was labelled 'imported from China'. Specimens of *M. lusoria* were obtained from Shirakawa, Kumamoto Prefecture, Japan. All reference samples were deposited at the Molecular Systematic Laboratory, Marine Fisheries Division, Fisheries Research Institute.

The name *Cytheraea formosa* (G.B. Sowerby II, 1851) is not accepted and is synonymised with *M. lusoria*. Two syntype specimens are kept at the British Museum of Natural History (BMNH) (BMNH 20120227). To clarify the relationships of the two syntypes with the present species, we used two-dimensional digital images from BMNH to obtain relevant morphological data for comparison.

Morphological examinations

Shell measurements, partially consistent with those outlined by Torii *et al.* (2010), included shell length (L), shell height (H), anterior shell length (AL), socket width (SW), socket length (SL), upper shell height (UH), length of posterior dorsal margin (LPM), height of posterior dorsal margin (HPM), shell breadth (B), ligament length (LL), and pallial sinus length (PL) (Figure 3). The last 10 measurements were divided by shell length for standardisation (Table 3). Characters of the right shell valve were photographed with a digital camera and then measured with image analysis software, ImageJ v. 1.51 K (Abramoff *et al.* 2004).

Canonical discriminant analysis (CDA) was used to assess the 10 standardised characteristics using R-plot (R Core team, 2015). The method of multivariate analysis was partly based on Torii *et al.* (2010).

Molecular methods

Mitochondrial COI was selected as the target gene. DNA was extracted using a Gentra Puregene Tissue Kit (Gentra, Minneapolis, MN, USA). The LCO-1490 (forward primer, 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′) and HCO-2198 (reverse primer, 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′) primers were set and used to amplify the COI barcode (Folmer *et al.* 1994). The amplification of the COI gene followed the protocol described in our previous study (Hsiao *et al.* 2019).

The PCR products were examined through electrophoresis on 1% agarose gel to confirm that the

Figure 2. **A,** Environment of type locality; **B,** local fisherman catches Asian hard clams in single small boat; **C,** use of a bull raker as harvesting gear; **D,** harvested wild Asian hard clams.

correct length of fragment had been obtained; they were subsequently eluted using the QIAquick Gel Extraction kit (Qiagen, Hilden, Germany). The purified PCR products were sent to MB Mission Biotech (Taipei, Taiwan) for DNA sequencing.

The *Meretrix* species, the collecting locality of the samples and GenBank accession numbers of specimens that were used in this study are listed in Table 1. The sequence data were manually edited and automatically assembled using BioEdit 7.2.5 (Hall 1999), and sequence divergence statistics were then calculated using Clustal X programs (Thompson *et al.* 1997). The phylogenetic relationships among the samples were inferred using both neighbour-joining (NJ) and maximum parsimony (MP) methods. NJ trees were constructed using MEGA X (Kumar *et al.* 2018) under the Kimura two-parameter model of base substitution with 1000 bootstrap repetitions. The MP tree topology was estimated using the tree bisection–reconnection algorithm. Bayesian phylogenetic trees were created using MrBayes v. 3.2 (Ronquist *et al.* 2012) with 10^7 cycles and an HKY85 + G substitution model, as determined by jModelTest v. 2 (Darriba *et al.* 2012).

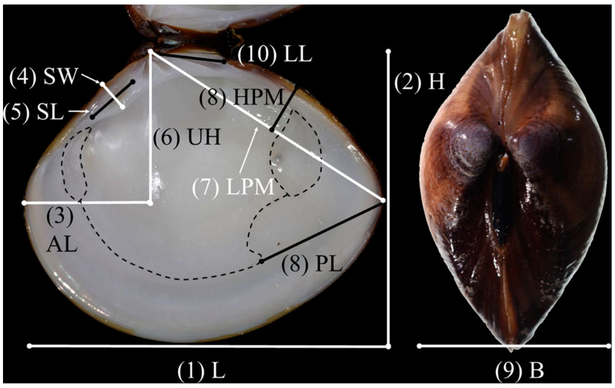

Figure 3. Morphometric measurements of right valve and shell. L: shell length, H: shell height, B: shell breadth, AL: anterior shell length, SW: socket width, SL: socket length, UH: upper shell height, LPM: length of posterior dorsal margin, HPM: height of posterior dorsal margin, LL: ligament length, and PL: pallial sinus length.

Results

Systematics

Superfamily Veneroidea Rafinesque, 1815
Family Veneridae Rafinesque, 1815
Genus *Meretrix* Lamarck, 1799

Meretrix taiwanica **Hsiao & Chuang, sp. n.**
http://zoobank.org:act:AB345172-30F1-4CDD-AADD-CEADB57EB3D6
Figures 4 and 5.

Meretrix lusoria.— Kuo 1964: 32, left shell in figure; Wu 1980: 112, 109, pl. III, fig. N; Wu and Liu 1989: 51–52; The Malacological Society of Taiwan 1994: 95, pl. 61, fig. 386; Lam 1999: 51–52, figs 1, 7; Wu 1997: 76–77 (with 2 figs); Wu and Jian 2008: 195, fig. 108 (not of Röding, 1798).

Meretrix meretrix.—Wu and Liu 1989: 49–61; Higo and Goto 1993: 661; Wu and Jian 2008: 196, fig. 109 (not of Linnaeus, 1758).

Meretrix petechialis.—Kuroda 1941: 65–216; Kuo 1964: 32, middle shell in figure (not of Lamarck, 1818).

Table 1. Table of species, sample collecting localities and GenBank accession numbers that were used in this study.

Species	Collecting locality	GenBank no.
Meretrix taiwanica sp. n.	Taiwan	MN275933–MN275941 MZ453092–MZ453103 (this study) Holotype, MT622847 (this study) Paratype, MT622848, MT622849 (this study)
Meretrix lusoria	China	JN898935, GQ903339, JQ294065, JN043624
	Japan	KX534323, AB280786, AB853864, MT418596
	South Korea	AB853870
Meretrix lamarckii	China	JN043625, KY318175
	Japan	AB059420, KP244452
Meretrix lyrata	Philippines	KF009624
	China	HQ703198, JN898944, KC832317
Meretrix meretrix	China	DQ399402 (*M. petechialis*), KP976274 (*M. petechialis*), MF038859 (*M. petechialis*), GQ463598 (*M. petechialis*), JN898949 (*M. petechialis*)
Meretrix petechialis	China	EU145977, KY318078, KX534315
	South Korea	JX503043
	Japan (from market)	MN308465-MN308468

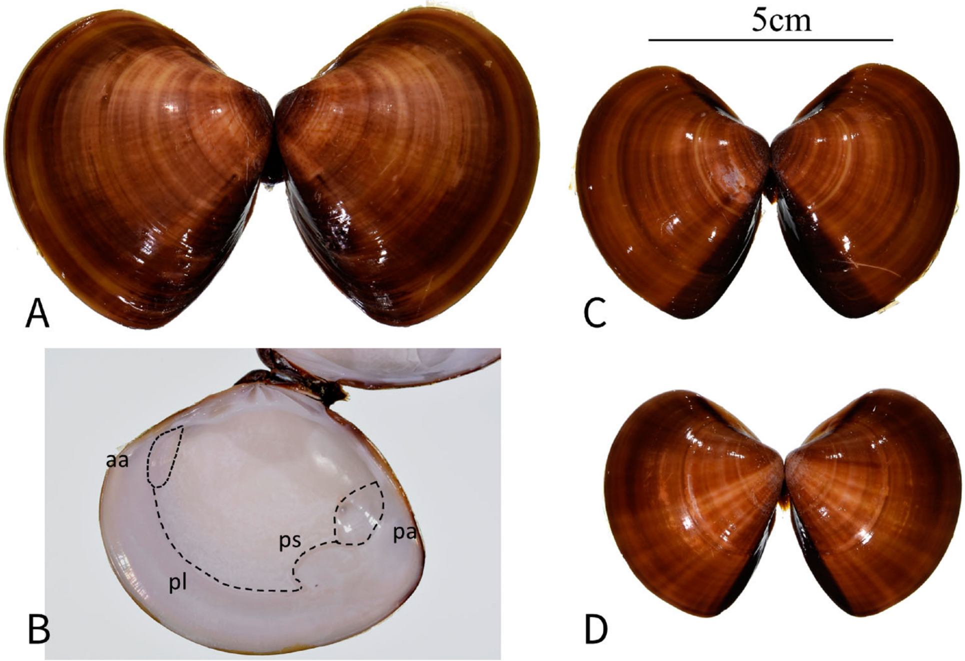

Figure 4. **A,** Holotype, FRIM10028, paired valves; **B,** inner shell of right valve of holotype, aa: anterior adductor scar, pl: pallial line, ps: pallial sinus, pa: posterior adductor scar; **C,** paratype, FRIM10029; **D,** paratype, FRIM10030.

Meretrix formosana.—Kuo 1964: 32, right shell in figure (not of G.B. Sowerby II, 1851).

Holotype. Tamsui River estuary, New Taipei City, Taiwan, 25°09′02.2"N, 121°27′11.8"E, coll. S.T. Hsiao and S.C. Chuang, 15 May 2019 (FRIM10028, paired valves, length 67.9 mm, height 57.2 mm) (Figure 4A, B; Table 2).

Paratypes. Tamsui River estuary, New Taipei City, Taiwan, 25°09′51.3"N, 121°25′51.8"E, coll. S.T. Hsiao and S.C. Chuang, 21 Jun. 2018 (FRIM10029, paired valves, length 56.5 mm, height 45.2 mm) (Figure 4C; Table 2); Tamsui River estuary, New Taipei City, Taiwan, 25°09′52.5"N, 121°26′28.0"E, coll. S.T. Hsiao and S.C. Chuang, 21 Jun. 2018 (FRIM10030, paired valves, length 49.4 mm, height 37.8 mm) (Figure 4D; Table 2).

Material examined

Type material. See above. *Other material.* ***M. taiwanica* sp. n.**: New Taipei City, coll. S.T. Hsiao and S.C. Chuang, 26 Jul. 2018 (FRIM10031, 16 paired valves); New Taipei City, coll. S.T. Hsiao and S.C. Chuang, 20 Oct. 2018 (FRIM10032, 35 paired valves); New Taipei City, coll. S.T. Hsiao and S.C. Chuang, 20 Jul. 2018 (FRIM10035, 7 paired valves); Tainan, coll. S.T. Hsiao, 18 Aug. 2020 (FRIM10036, 3 paired valves); Changhua, coll. S.T. Hsiao, 18 Aug. 2020 (FRIM10037, 3 paired valves); Hsinchu, coll. S.T. Hsiao and S.C. Chuang, 20 Jun. 2018 (FRIM10038, 4 paired valves); Kinmen, coll. S.T. Hsiao, 6 Nov. 2018 (FRIM10039, 2 paired valves). ***M. petechialis***: collected at supermarket, Mie Prefecture, Japan, coll. S.T. Hsiao and J.H. Wu, 7 Nov. 2018 (FRIM10033, 17 paired valves). ***M. lusoria***: collected on Shirakawa, Kumamoto Prefecture, Japan,

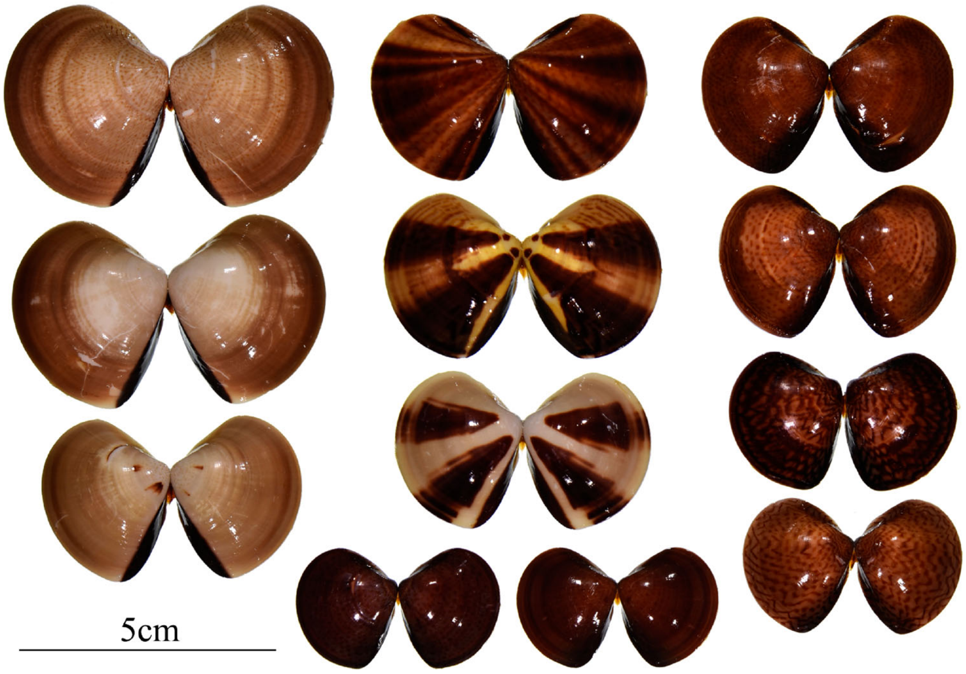

Figure 5. Colour patterns of *Meretrix taiwanica* sp. n., FRIM10031.

Table 2. Measurements (in mm) of type specimens of *Meretrix taiwanica* sp. n.
L: shell length; H: shell height; AL: anterior shell length; SW: socket width; SL: socket length; UH: upper shell height; LPM: length of posterior dorsal margin; HPM: height of posterior dorsal margin; B: shell breadth; LL: ligament length; PL: pallial sinus length.

ID	L	H	AL	SW	SL	UH	LPM	HPM	B	LL	PL
Holotype (FRIM10028)	67.9	57.2	14.7	4.1	16.3	22.6	49.0	8.3	32.6	11.9	15.6
Paratype (FRIM10029)	56.5	45.2	10.6	4.3	21.8	20.3	40.6	7.3	30.3	10.1	12.8
Paratype (FRIM10030)	49.4	37.8	11.6	4.9	13.4	19.2	36.3	5.8	29.5	9.6	11.5

Table 3. Ten characters standardised against shell length calculated in *M. taiwanica* sp. n. (N = 70), *M. petechialis* (N = 17), *M. lusoria* (N = 24) and *C. formosa* (N = 2) (unavailable name-bearing types). Avg.: mean, Std.: standard deviation, L: shell length, H: shell height, B: shell breadth, AL: anterior shell length, SW: socket width, SL: socket length, UH: upper shell height, LPM: length of posterior dorsal margin, HPM: height of posterior dorsal margin, LL: ligament length, and PL: pallial sinus length.

Species	H/L	AL/L	SW/L	SL/L	UH/L	LPM/L	HPM/L	B/L	LL/L	PL/L
M. taiwanica sp. n.										
Avg.	0.797	0.375	0.087	0.291	0.393	0.730	0.104	0.524	0.223	0.368
Std.	0.028	0.035	0.006	0.043	0.022	0.082	0.014	0.020	0.026	0.040
M. petechialis										
Avg.	0.789	0.381	0.091	0.267	0.410	0.742	0.128	0.497	0.220	0.317
Std.	0.022	0.019	0.005	0.042	0.020	0.023	0.012	0.015	0.018	0.025
M. lusoria										
Avg.	0.806	0.374	0.080	0.291	0.423	0.754	0.117	0.518	0.202	0.339
Std.	0.018	0.023	0.005	0.029	0.012	0.018	0.009	0.059	0.040	0.016
C. formosa *										
Avg.	0.740	0.322	0.063	0.172	0.363	0.772	0.091	/	0.170	0.308
Std.	0.007	0.007	0.014	0.010	0.010	0.004	0.011	/	0.049	0.034

**C. formosa* was measured using digital images, not actual samples; B/L value was not available.

coll. Y. Henmi, 20 Jun. 2019 (FRIM10034, 24 paired valves). ***Cytheraea formosa***: BMNH catalogue number: 20120227, 2 individual images from BMNH, length 70.8–89.2 mm, unavailable name-bearing types (https://data.nhm.ac.uk/object/cadd6f3c-b54d-412f-9ec9-df01d37420f1/1623715200000).

Type locality

Taiwan, New Taipei City, Tamsui River estuary (25° 09′02.2"N; 121°27′11.8"E), water depth approximately 2.41 m, sandy to muddy bottoms.

Distribution

Western coast of Taiwan, southern coast of China to northern Vietnam.

Description

Shells in our collection medium-sized, length of up to 86.69 mm. Solid, triangular-ovate shaped, inequivalve, have a rounded ventral margin, fairly straight dorsal edge; posterior margin length approximately

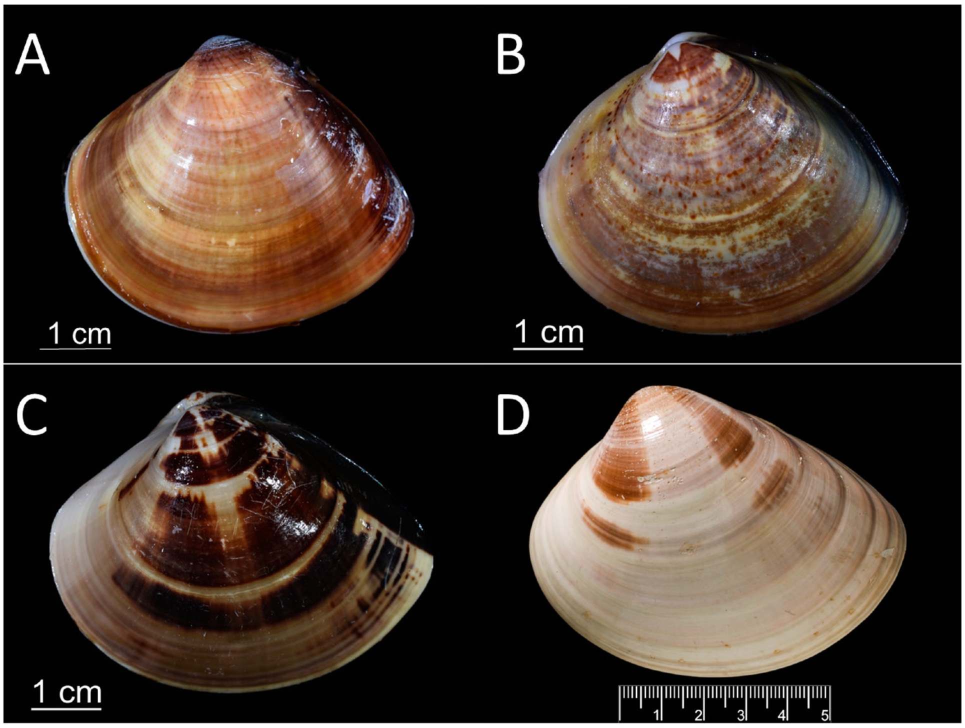

Figure 6. Shells of hard clams **A,** *Meretrix taiwanica* sp. n.; **B,** *M. petechialis*; **C,** *M. lusoria;* **D,** *Cytheraea formosa* (unavailable name-bearing types, syntype, digital image cited from BMNH HP collection, 20120227).

0.65–0.78 times shell length. Umbones elevated well above the hinge line. Shells topped with ligaments behind the umbones. Umbones slightly biased towards the front. Shell posterior margin longer than anterior margin, the posterior has an escutcheon, usually a dark-brown colour, anterior sides have a clear lunule.

Shell exterior smooth, having fine growth lines but no grooves on the surface. Shells have highly variable colour patterns roughly divided into yellow-white,

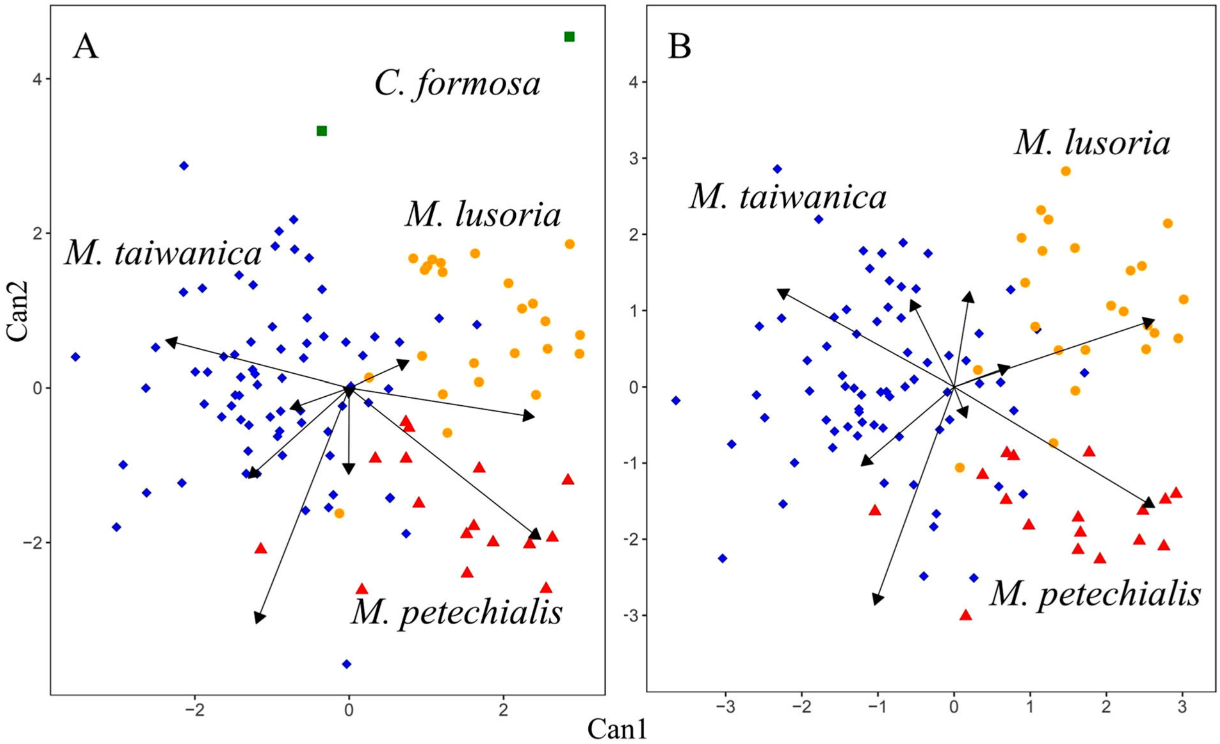

Figure 7. Two-dimensional scatterplots of canonical discriminant analysis. **A,** Analysis including the species *Meretrix taiwanica* sp. n., *M. petechialis*, *M. lusoria* and *C. formosa*; **B,** analysis including the species *Meretrix taiwanica* sp. n., *M. petechialis* and *M. lusoria*.

Table 4. Centroids of canonical variates (Can.) 1 and 2 for 10 standardised characters of *Meretrix taiwanica* sp. n., *M. petechialis*, and *M. lusoria*. L: shell length, H: shell height, B: shell breadth, AL: anterior shell length, SW: socket width, SL: socket length, UH: upper shell height, LPM: length of posterior dorsal margin, HPM: height of posterior dorsal margin, LL: ligament length, and PL: pallial sinus length.

	H/L	AL/L	SW/L	SL/L	UH/L	LPM/L	HPM/L	B/L	LL/L	PL/L
Can. 1	0.205	0.162	−1.044	−0.569	2.632	0.732	2.634	0.113	−1.220	−2.322
Can. 2	1.251	−0.409	−2.866	1.144	0.877	0.266	−1.583	0.139	−1.038	1.278

reddish-brown, dark-brown mottling, W-shaped markings and dark green.

Shell interior thin and shiny, creamy-white colour, posterior sections of deep purple; hinge area with fine sculpture, with three cardinal teeth. Teeth attached to each other at the top of the shell and extend to outer edge in arrow shapes. Length of socket is approximately 0.04–0.044 times shell length. One anterior lateral tooth. One small, clear oblong anterior adductor scar, length 0.20–0.24 times shell length. One large, oval posterior adductor scar approximately 0.21–0.25 times shell length. Pallial sinuses shallow, reaching end of cardinal tooth. Pallial line almost reaches middle of posterior adductor scar; length of the pallial sinus approximately 0.21–0.44 times shell length.

Etymology

We name this species '*taiwanica*' in reference to the collection locality in Taiwan. Additionally, this species is the most abundant and widely distributed hard clam in Taiwan.

Diagnosis

Shell surface of *M. lyrata* has commarginal ribs; ventral margins of *M. taiwanica* sp. n., *M. lamarckii* and *M. lusoria* smooth, flat and round, respectively. *Meretrix taiwanica* sp. n. similar in shape to *M. lusoria* and *M. petechialis* (Figure 6A–C) but differs in several morphological features. Posterior dorsal margin of *M. lusoria* relatively straight, causing rear shell angle to be sharper, socket narrower. Shell-shaped posterior margin of *M. petechialis* rounded,with wider socket. Posterior margin of *M. taiwanica* sp. n. rounded with narrower socket than *M. petechialis*.

To compare the posterior margin sizes of *M. taiwanica* sp. n., *M. petechialis* and *M. lusoria*, we used the ratio of the length of each species' posterior dorsal margin to its shell length (LPM/L) (Table 3). For *M. taiwanica* sp. n. (N = 70), the range was 0.65–0.78, with an average of 0.74. The range for *M. petechialis* (N = 17) was 0.69–0.78 with an average of 0.74, and for *M. lusoria* (N = 24) the range was 0.73–0.81 with an average of 0.75. The syntypes of the two *Cytheraea formosa* in Sowerby (1851) both had a ratio of 0.77. In measured specimens, the LPM/L of *M. taiwanica* sp. n. and *M. petechialis* did not significantly differ from each other ($P = 0.6446$), whereas they were shorter than *M. lusoria* ($P = 0.00437$, $P < 0.01$, respectively) and perhaps *C. formosa*.

Multivariate analysis

Because the shell breadths of the two syntypes of *C. formosa* were not measurable, these measurements were excluded in the first CDA. The results of the analysis demonstrated that the two *C. formosa* specimens were distinct from the samples of the other three species (Figure 7A). However, because of the small sample sizes, those two were excluded in the second CDA.

Meretrix taiwanica sp. n., *M. petechialis* and *M. lusoria* were clearly separated by this CDA using the standardised 10 morphological characteristics (Table 3; Figure 7B). The proportions of variation explained by canonical variates 1 and 2 were 61.4% and 38.6%, respectively. The absolute values of SW/L, UH/L, HPM/L, LL/L and PL/L were more than 0.5 in the centroid of canonical variates 1 and 2 (Table 4). These results demonstrated that *M. taiwanica* sp. n. has a rounder posterior dorsal margin than *M. lusoria* and a smaller socket width than *M. petechialis*.

Molecular and phylogenetic analyses

Phylogenetic analysis of the COI gene with new samples of *Meretrix taiwanica* sp. n. resulted in a tree concordant with that of Hsiao *et al.* (2019, fig. 2), with all species supported (Figure 8).

In the clade of *M. petechialis*, some sequences from The National Center for Biotechnology Information (NCBI) (JN898949, GQ463598, MF038859, KP976274 and DQ399402) were identified as *M. meretrix* and one sequence (AB853870) was identified as *M. lusoria*. The most samples collected from China and South Korea were *M. petechialis* but had previously been misidentified as belonging to other taxa.

Our results support the presence of a new species (herein named *Meretrix taiwanica*) in a monophyletic clade with *M. petechialis*, *M. lusoria*, *M. lyrata* and *M. lamarckii*. The average nucleotide sequence divergence is 7.59% between *M. taiwanica* sp. n. and *M. petechialis* and 9.53% between *M. taiwanica* sp. n. and *M. lusoria*. Nucleotide diversity is 1.13% within *M. taiwanica*

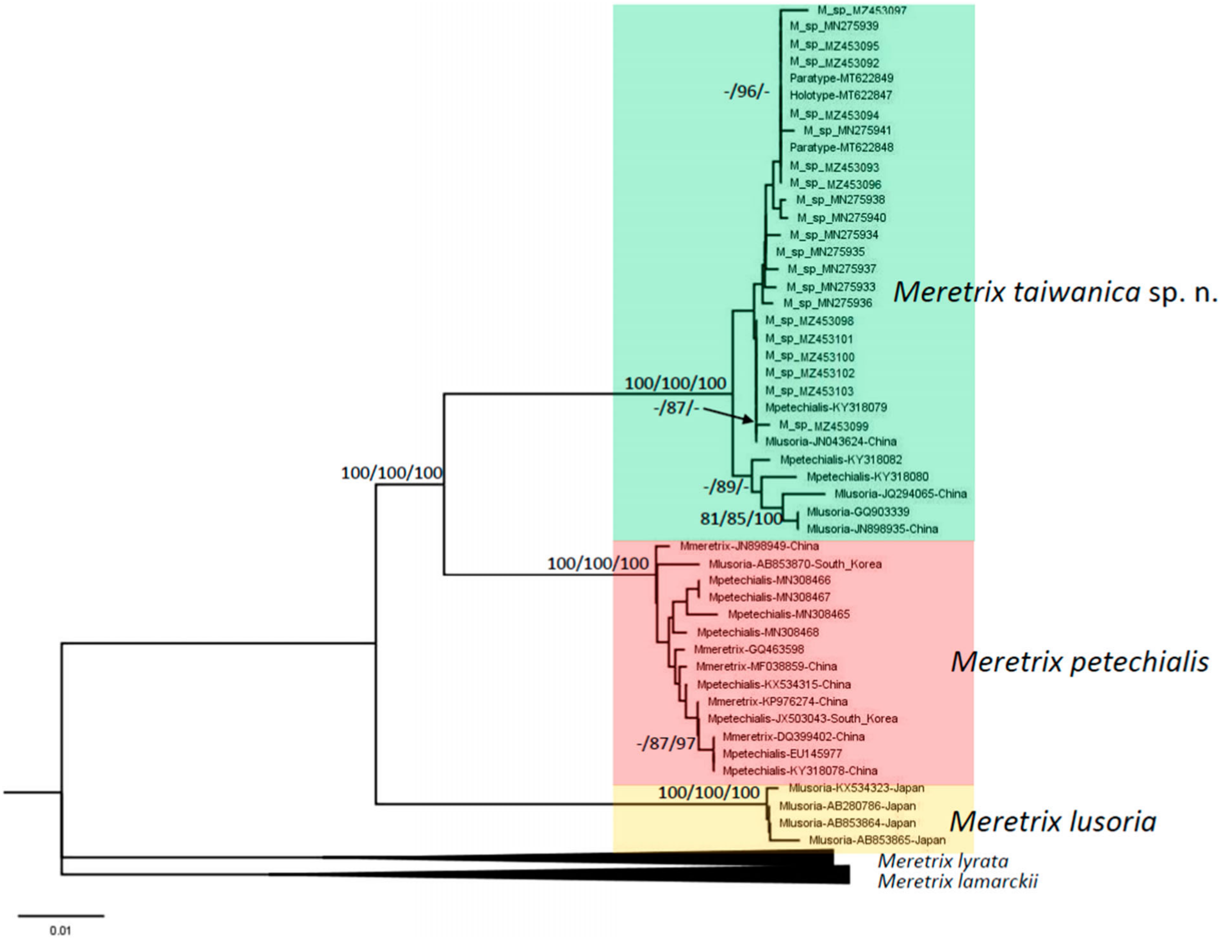

Figure 8. Phylogenetic tree constructed for *Meretrix* spp. and reference sequences based on the cytochrome c oxidase I gene barcode sequence. Branch support values estimated by bootstrap pseudo-replicates in maximum parsimony and neighbour-joining are displayed above each branch. A minus sign (-) indicates that the bootstrap values were <75%.

sp. n. The topology of the phylogenetic tree indicates that *M. taiwanica* sp. n. and *M. petechialis* are more closely related to one another than to *M. lusoria*.

All of the samples that we collected from western Taiwan, including the holotype and paratypes, were clustered together in a single clade as *Meretrix taiwanica* sp. n., excluding *M. petechialis* and *M. lusoria*.

Discussion

Sowerby (1851) described the new species *Cytheraea formosa*, and this species is currently listed as a synonym of *M. lusoria*. The source of the specimen was Hugh Cuming's collection. The type specimen has not been specified, and thus the type locality is unknown. According to Sowerby II's description of *C. formosa* in p.620, 'the shell is thinner, more oblique and more elongated than *C. meretrix*, which it otherwise greatly resembles'. The shells of *M. taiwanica* sp. n. and *C. formosa* exhibit clear morphological differences (Figure 6A, D).

The syntypes deposited in the BMNH are supposed to be from Japan, based on the original label with the M.C. (Museum Cuming) sticker and according to the museum's curator, although 'Formosa' is a previous name for Taiwan. However, no distribution of *M. taiwanica* sp. n. has been found in Japan. Therefore, *C. formosa* should be considered a variant and synonym of *M. lusoria*.

Habe (1977) posited that the Asian hard clams produced in Taiwan are *Meretrix meretrix*, which has a range centred on the Indian Ocean. *Meretrix meretrix* has been reported to be primarily distributed in the South China Sea (Zhang *et al.* 2012), Thailand (Supmee *et al.* 2020), Southeast Asia (Trang *et al.* 2018) and along the East African coast (Branch *et al.* 2010). The shells of *M. meretrix* are oval and broader in shell breadth (Supmee *et al.* 2020) than those of *M. taiwanica* sp. n. Based on our results, *M. taiwanica* sp. n., *M. petechialis* and *M. lusoria* cannot be accurately distinguished using single morphological characteristics. However, these species can be distinguished from each other through multivariate analysis using multiple shell morphological characteristics.

Wang *et al.* (2017) indicated that *M. petechialis* in China has two different population groups: the northern lineage (including the Bohai Sea, Yellow Sea and East China Sea) and the south lineage (including the East China Sea and South China Sea). However, we discovered that the mtDNA haplotypes of this southern lineage form a highly supported monophyletic clade with those of *M. taiwanica* sp. n. On the other hand, the haplotypes of the northern lineage clustered in the same clade as those of *M. petechialis*. Therefore, the southern lineage as distinguished from the northern lineage by Wang *et al.* (2017) represents populations of *M. taiwanica* sp. n. in southern China rather than those of *M. petechialis*.

Although they are morphologically similar, *M. lusoria*, *M. petechialis*, *M. meretrix* and *M. taiwanica* sp. n. have distinct geographical distributions. *Meretrix lusoria* is mainly distributed in Japan and South Korea. *Meretrix petechialis* is distributed from the south-western coasts of South Korea to the coast of China (Torii *et al.* 2010; Wang *et al.* 2017). The distribution of *Meretrix meretrix* includes coastal areas of South and Southeast Asia (Trang *et al.* 2018), and *M. taiwanica* sp. n. is distributed in Taiwan (the present study) and the southern coast of China to northern Vietnam (Wang *et al.* 2017).

The Taiwanese hard clam was previously identified as *M. lusoria* and is considered to be a descendant of a clam that originated in Japan and was introduced to Taiwan during the Japanese colonial period (Chen 1984). We examined specimens from the National Taiwan Museum, National Museum of Natural Science and Shihsanhang Museum of Archaeology collections. We discovered that all the Taiwanese specimens labelled as *M. lusoria* in those institutions are actually *M. taiwanica* sp. n. and that wild *M. lusoria* clams do not occur in Taiwan.

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Disclosure statement

No potential conflict of interest was reported by the authors.

References

Abramoff, M.D., Magalhaes, P.J. & Ram, S.J. (2004) Image Processing with ImageJ. *Biophotonics International* 11, 36–42.

Branch, G.M., Griffiths, C.L., Branch, M.L. & Beckley, L.E. (2010) *Two Oceans, a Guide to the Marine Life of Southern Africa*. Struik Nature, Cape Town.

Chen, H.C. (1984) Recent innovations in cultivation of edible molluscs in Taiwan, with special reference to the small abalone *Haliotis diversicolor* and the hard clam *Meretrix lusoria*. *Aquaculture* 39, 11–27. doi:10.1016/0044-8486(84)90256-4

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest2: more models, new heuristics and parallel computing. *Nature Methods* 9, 772. doi:10.1038/nmeth.2109

Fisheries Agency (2020) *Fisheries Statistical Yearbook 2019, Taiwan. Fisheries Agency, Council of Agriculture*. Executive Yuan, Taipei, Taiwan.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3, 294–299.

Habe, T. (1977) *Systematics of Mollusca in Japan, Bivalvia and Scaphopoda* 244–275. Tokyo: Zukan-No-Hokuryukan.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41, 95–98.

Higo, S. & Goto, Y. (1993) *A Systematic List of Molluscan Shells from the Japanese Islands and the Adjacent Areas*. Eru Malacological Publisher, Osaka.

Hsiao, S.T., Chuang, S.C., Wu, Y.H., Chang, J.W., Chin, C.P., Yeh, H.M., Henmi, Y. & Chen, J.R. (2019) Preliminary studies for the habitat conditions of the asian hard clam *Meretrix* spp. in Tamsui Estuary, Taiwan. *Proceedings of the 2019 Climate Change, Disaster Management and Environmental Sustainability International Conference, Kumamoto, Japan*, pp. 474–482.

Hsu, T.H., Huang, C.W. & Gong, H.Y. (2020) The past and present of Taiwanese hard clams. 2020 *Annual Forum for the Fisheries Society of Taiwan*, Tainan, Taiwan, p. 127. [In Chinese].

Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35, 1547–1549. doi:10.1093/molbev/msy096

Kuo, H. (1964) *The investigation on Taiwan economic molluscs*. The Council of Agriculture, Special Publication No. 38, 32–50.

Kuroda, T. (1941) A catalogue of molluscan shells from Taiwan (Formosa). *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University* 22, 194–195.

Lai, Y.L. & Nien, Y.G. (2008) A new species of *Meretrix* from Taiwan (Bivalvia: Veneridae). *Bulletin of Malacology* 31, 23–30.

Lam, T.C. (1999) Natural history of Asian hard clam. *The Pei-Yo* 25, 44–53. [In Chinese].

Linnaeus, C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata [10th revised edition], vol. 1: 824 pp. Laurentius Salvius: Holmiae.

MolluscaBase (2022) MolluscaBase. *Meretrix* Lamarck, 1799. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?*p* = taxdetails&id = 204011 [accessed 11 Dec. 2022].

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. https://www.R-project.org/.

Röding, P. F. (1798) Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried Bolten, M. D. p. d. per XL. annos proto physicus Hamburgensis. Pars secunda continens Conchylia sive Testacea univalvia, bivalvia and multivalvia. Trapp, Hamburg. viii, 199 pp.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. &

Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61, 539–542. doi:10.1093/sysbio/sys029

Sowerby, II, G.B. (1851) Monograph of the genus *Cytheraea*. In: G.B. Sowerby, II (Ed.), *Thesaurus conchyliorum, or Monographs of Genera of Shells*. (Vol. 2: pp. 611–648, pls 127–136). London: privately published.

Supmee, V., Sangthong, P., Songrak, A. & Suppapan, J. (2020) Population genetic structure of Asiatic Hard Clam (*Meretrix meretrix*) in Thailand based on Cytochrome Oxidase subunit I gene sequence. *Biodiversitas Journal of Biological Diversity* 21, 2702–2709. doi:10.13057/biodiv/d210943

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25, 4876–4882. doi:10.1093/nar/25.24.4876

Torii, H., Sato, S., Hamaguchi, M., Henmi, Y. & Yamashita, H. (2010) The comparison of shell morphology and genetic relationship between *Meretrix lusoria* and *M. petechialis* in Japan and Korea. *Plankton and Benthos Research* 5, 231–241. doi:10.3800/pbr.5.231

Trang, V.T., Quynh, L.T., Thiet, C.C.C., Duc, N.H. & Ha, T.T.T. (2018) Genetic relationship of asiatic hard clam populations collected in northern coastal provinces in Vietnam based on mtDNA sequence analysis. *Journal of Aquaculture & Marine Biology* 7, 00184. doi:10.15406/jamb.2018.07.00184.

Wang, X., Kong, L., Chen, J., Matsukuma, A. & Li, Q. (2017) Phylogeography of bivalve *Meretrix petechialis* in the Northwestern Pacific indicated by mitochondrial and nuclear DNA data. *PLOS ONE* 12, e0183221. doi:10.1371/journal.pone.0183221.

Wu, W.L. (1980) The list of Taiwan bivalve fauna. *Quarterly Journal of the Taiwan Museum* 33, 65–206.

Wu, W.L. (1997) *The Economic Mollusks in Taiwan*. The Council of Agriculture, Executive Yuan, Taipei.

Wu, W.L. & Jian, S.J. (2008) *The Mollusks of Taoyuan, Hsinchu, and Miaoli Area, Taiwan*. Academia Sinica, Taipei.

Wu, W.L. & Liu, H.P. (1989) Malacological research on *Meretrix* resources in Taiwan II. History review and evaluation on the studies of the Taiwan *Meretrix*. *Bulletin of Malacology* 14, 49–61.

Yamakawa, A.Y. & Imai, H. (2013) PCR-RFLP typing reveals a new invasion of Taiwanese *Meretrix* (Bivalvia: Veneridae) to Japan. *Aquatic Invasions* 8, 407–415. doi:10.3391/ai.2013.8.4.04

Yamakawa, A.Y., Yamaguchi, M. & Imai, H. (2008) Genetic relationships among species of *Meretrix* (Mollusca: Veneridae) in the western Pacific Ocean. *Pacific Science* 62, 385–394. doi:10.2984/1534-6188(2008)62[385:GRASOM]2.0.CO;2

Yoosukh, W. & Matsukuma, A. (2001) Taxonomic study on *Meretrix* (Mollusca: Bivalva) from Thailand. *Phuket Marine Biological Center Special Publication* 25, 451–460.

Zhang, S., Wang, H. & Xu, F. (2012) Taxonomic study on *Meretrix* (Bivalvia, Veneridae) from China seas. *Acta Zootaxonomica Sinica* 37, 473–479. [In Chinese with English abstract].