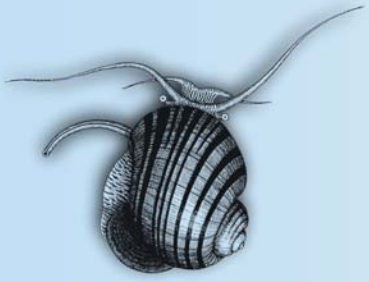

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TAXONOMY OF *MACRIDISCUS* SPECIES (BIVALVIA: VENERIDAE) FROM THE WESTERN PACIFIC: INSIGHT BASED ON MOLECULAR EVIDENCE, WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT

The genus *Macridiscus* Dall, 1902 contains a few species present in warm temperate to tropical faunas of the western Pacific. *Macridiscus* was widely accepted as a subgenus of *Gomphina* until a recent suggestion that it should be separated from *Gomphina* and elevated to an independent genus, based on morphology and molecular data. The taxonomy of the genus *Macridiscus* has in the past been based solely on shell characters and there has been no agreement about the number of valid species. In this study, we explore the taxonomy and phylogeny of *Macridiscus* species in order to resolve the systematics of the genus, based not only on shell characters but also on mitochondrial and nuclear DNA sequences. The morphological characters, the sequences of the cytochrome *c* oxidase subunit I of mitochondrial DNA and the first internal transcribed spacer region (ITS1) between the 18S and 5.8S ribosomal DNA were highly concordant and clearly suggested that three species should be recognized in the genus *Macridiscus*: *M. multifarius* new species, *M. semicancellata* (Koch, in Philippi, 1843) and *M. melanaegis* (Römer, 1860). The morphological characters and geographical distribution of the three species are redescribed based on the molecular data.

INTRODUCTION

The marine bivalve genus *Macridiscus* Dall, 1902 contains a few species present in warm temperate to tropical regions of the Western Pacific. *Macridiscus* was first proposed by Dall (1902) as a section of the subgenus *Gomphina*, which he placed in the genus *Chione*. Since then, *Macridiscus* has been widely accepted as a subgenus of the genus *Gomphina* (e.g. Habe, 1951; Zhuang, 1964; Keen, 1969; Fischer-Piette & Métivier, 1971; Yoo, 1976; Zhuang, 2001). However, Mikkelsen *et al.* (2006) published a detailed phylogeny of the superfamily Veneroidea, based on morphology and four molecules from over 100 taxa, including *Macridiscus melanaegis* and *Gomphina undulosa* (the type species of *Gomphina* Mörch, 1853). The morphological and molecular results strongly supported placement of *M. melanaegis*, but not *G. undulosa*, within the subfamily Tapetinae (see detail in Mikkelsen *et al.*, 2006). Mikkelsen *et al.* (2006) used the name '*Macridiscus melanaegis*' rather than the widely accepted '*Gomphina* (*Macridiscus*) *melanaegis*', which implied that *Macridiscus* should be elevated from subgeneric to generic level. Indeed, there are two major morphological differences between *G. undulosa* and *Macridiscus* species. First, the shell microstructure is different. The shell structure of the middle and outer layers of *Macridiscus* species indicates its classification into type II in which crossed-lamellar structure is not developed, while *Gomphina* species were classified into type III in which composite prismatic structure is not developed (Shimamoto, 1986). Second, *G. undulosa* has anterior and posterior marginal lamellae, but *Macridiscus* species do not. Here, we accept the generic status of *Macridiscus* for a group endemic to the Western Pacific, whose classification and nomenclature remains problematic.

Since Chemnitz (1795), five names have been proposed for species of this group, i.e. *Venus donacina* 'Chemnitz, 1795', *Donax veneriformis* Lamarck, 1818, *Donax aequilatera* Sowerby, 1825, *Venus semicancellata* Philippi, 1843, *Venus melanaegis* Römer, 1860, and different opinions exist concerning how many species should be recognized. Fischer-Piette & Métivier (1971) considered that the group contained only one species and synonymized all the binominal names under '*Gomphina aequilatera*'. Kuroda, Habe & Oyama (1971) remarked that *G.* (*M.*) *melanaegis* seemed to be a form of *G.* (*M.*) *veneriformis*, and later Habe (1981) synonymized *G.* (*M.*) *melanaegis* and *G.* (*M.*) *veneriformis* under *G.* (*M.*) *aequilatera*. Higo, Callomon

& Goto (1999) also thought the subgenus contained only one species, and synonymized *G.* (*M.*) *melanaegis* under *G.* (*M.*) *veneriformis*. However, a number of Japanese malacologists, such as Kira (1959) and Habe (1977), considered that the group contained two species, i.e. *G.* (*M.*) *melanaegis* and *G.* (*M.*) *veneriformis*, and Tanaka (1979) showed that *G.* (*M.*) *melanaegis* and *G.* (*M.*) *veneriformis* can be distinguished by differences in shell sculpture of the umbonal region. Matsukuma (2000) also recognized two different species, *G.* (*M.*) *melanaegis* and *G.* (*M.*) *semicancellata*. Most Chinese malacologists considered that this group contained only one species (e.g. Zhang *et al.*, 1962; Qi *et al.*, 1989; Zhuang, 2001; Xu & Zhang, 2008). Although Zhuang (1964) initially considered that there were two species in the group, *G.* (*M.*) *melanaegis* and *G.* (*M.*) *veneriformis*, he synonymized *G.* (*M.*) *melanaegis* and *G.* (*M.*) *veneriformis* under *G.* (*M.*) *aequilatera* in 2001. In Korea, Yoo (1976) separated *G.* (*M.*) *melanaegis* and *G.* (*M.*) *veneriformis*. Kwon, Park & Lee (1993) classified *G.* (*M.*) *melanaegis* as a subspecies of *G.* (*M.*) *veneriformis* and listed two subspecies from coastal waters of Korea, *G.* (*M.*) *veneriformis melanaegis* and *G.* (*M.*) *veneriformis veneriformis*, but later Min (2004) synonymized *G.* (*M.*) *melanaegis* under *G.* (*M.*) *veneriformis*. Most recently Lutaenko (2001) suggested that the group should be divided into three species: *G.* (*M.*) *semicancellata*, *G.* (*M.*) *melanaegis* and *G.* (*M.*) sp. ('*aequilatera* auctt.'), based on conchological characters of more that 300 specimens from South China, the Sea of Japan and the Pacific coast of Japan.

We show that the use of molecular techniques can resolve this debate. We sequenced both a mitochondrial gene, the first subunit of cytochrome *c* oxidase (COI), and a nuclear DNA marker, the internal transcribed spacer region 1 (ITS1) between the 18S and 5.8S ribosomal DNA genes, in order to clarify the systematics of *Macridiscus*.

MATERIAL AND METHODS

Institutional abbreviations

KYUM, Kyushu University Museum, Fukuoka, Japan.
LSGB, Laboratory of Shellfish Genetics and Breeding, Fisheries College, Ocean University of China, Qingdao, China.
NSM, Nishinomiya Shell Museum, Nishinomiya, Japan.

Sampling, synonymies and geographical distribution

Shell material stored in the following institutes was studied: KYUM, LSGB and NSM. Samples for DNA analysis were collected from the coast of China during 2006–2008 and Japan in 2009 (Table 1), and specimens were preserved in 95% ethanol. Synonymies attempt to be as complete as possible for significant taxonomic works. Distribution maps are based on examined material and reliable literature records.

Shell morphology

Four shell characters were measured for each individual to the nearest 0.1 mm with vernier callipers: shell length (SL), shell height (SH), shell convexity (C) and anterior extent of pallial sinus (PSD, measured from anterior end of pallial sinus to posterior shell margin). The hinge teeth were examined under a stereomicroscope.

DNA extraction, PCR amplification and sequencing

Total genomic DNA was extracted from 10 to 20 mg of tissue dissected from the adductor muscle using the Qiagen DNeasy Blood & Tissue kit (Qiagen, catalogue no. 69504), eluted in 200 µl AE buffer (Qiagen, 10 mM Tris–HCl, 0.5 mM EDTA, pH 9.0) and kept at 4°C for short-term use. Polymerase chain reaction (PCR) amplification of the mitochondrial COI gene was carried out with the forward and reverse primers: 5′-ATYGGNGGNTTYGGNAAYTG-3′ and 5′-ATNGCRAA YTTYGGNTC-3′ (N = A, G, C, T; R = A, G; Y = C, T; Matsumoto & Hayami, 2000). The ITS1 between the 18S and 5.8S ribosomal DNA genes was amplified for a subset of the samples with the primers ITS-A (5′-GGTTTCTGTAGGTG AACCT-3′) and ITS-B (5′-CTGCGTTCTTCATCGACC C-3′) (Hedgecock *et al.*, 1999). All individuals analysed for ITS1 were selected based on the topology of the COI sequences to detect whether the phylogenetic pattern was congruent and to check for interspecific hybrids. The 12-µl volume reaction mixture contained 0.3 U of Ex-Taq DNA polymerase (Takara), 1× Ex-Taq reaction buffer, 0.25 mM of each dNTP, 0.5 µM of each primer, and 1 µl template DNA. The PCR amplification was carried out in a GeneAmp® 9700 PCR System (Applied Biosystems) under the following conditions: 3 min initial denaturation at 94°C, and 35 cycles of 30 s at 94°C for denaturation, 1 min at 52°C (COI) and 55–

Table 1. Details of *Macridiscus* specimens for sequencing in this study.

Species	Location	Code	COI	Accession no.	ITS1	Accession no.
M. multifarius n. sp.	Haiyang, Shandong, China	hy	6	HM357296–HM357301	1	HM357261
	Rizhao, Shandong, China	rz	4	HM357302–HM357305	1	HM357262
	Fujitsukahama, Shibata, Niigata, Japan	fuj	6	HM357306–HM357311	1	HM357263
	Iwafune, Murakami, Niigata, Japan	iwa	2	HM357312–HM357313	1	HM357264
	Gotsu, Shimane, Japan	got	6	HM357314–HM357314	2	HM357265–HM357266
	Karatsu, Japan	kar	7	HM357320–HM357326	2	HM357267–HM357268
	Shima-machi, Fukuoka, Japan	shi	4	HM357327–HM357330	2	HM357269–HM357270
M. semicancellata	Zhoushan, Zhejiang, China	zs	5	HM357331–HM357335	1	HM357271
	Yangjiang, Guangdong, China	yj	5	HM357336–HM357340	1	HM357272
	Weizhou Island, Guangxi, China	wz	5	HM357341–HM357345	2	HM357273–HM357274
	Fangchenggang, Guangxi, China	fcg	5	HM357346–HM357350	–	–
M. melanaegis	Weihai, Shandong, China	wh	5	HM357275–HM357279	1	HM357256
	Lianyungang, Jiangsu, China	ly	6	HM357280–HM357285	1	HM357257
	Fujitsukahama, Shibata, Niigata, Japan	fuj	3	HM357286–HM357288	1	HM357258
	Iwafune, Murakami, Niigata, Japan	iwa	6	HM357289–HM357294	1	HM357259
	Kagoshima, Japan	kag	1	HM357295	1	HM357260

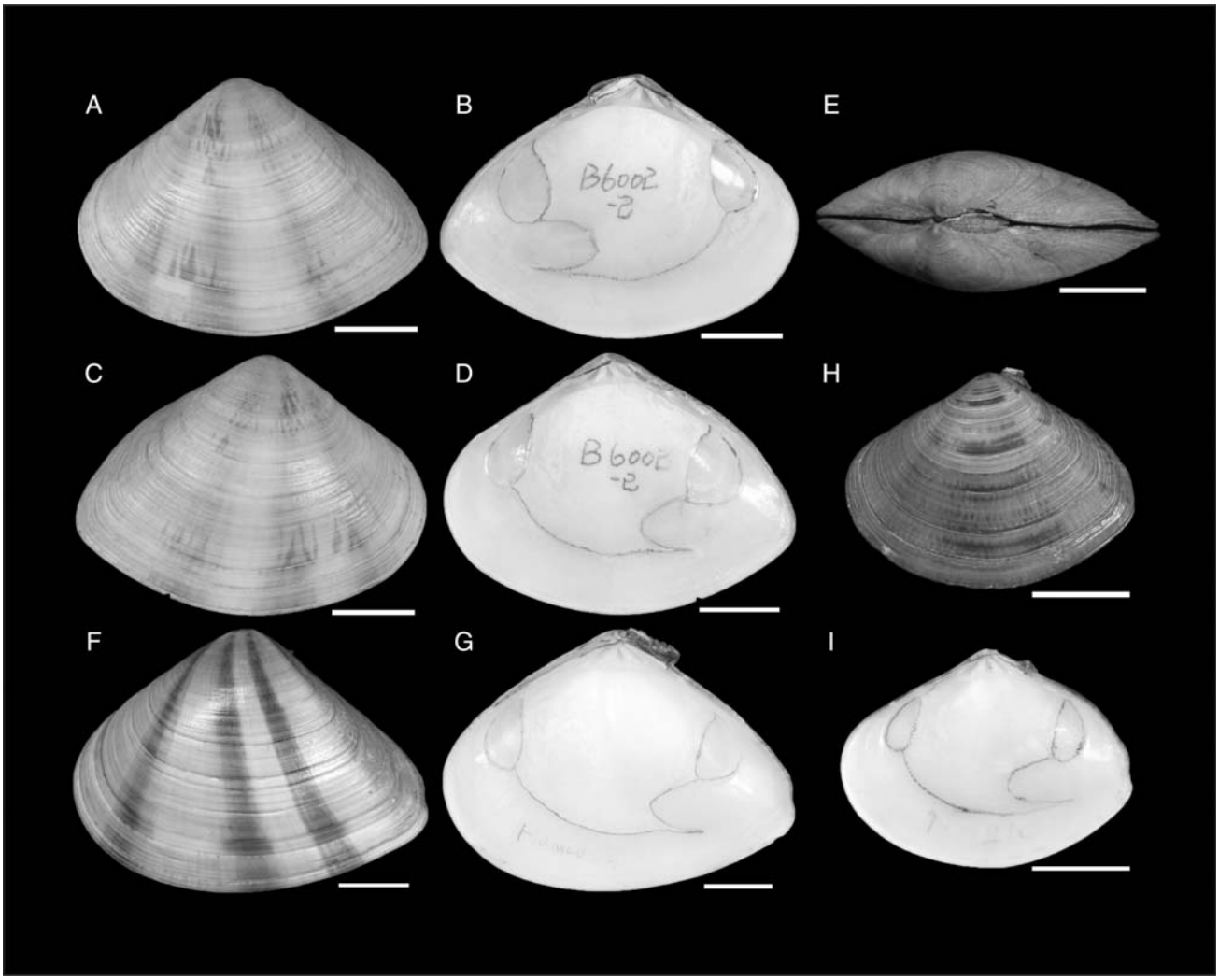

Figure 1. *Macridiscus multifarius* n. sp. **A–E.** Holotype, LSGB-B6002-2, Daxinjia, Haiyang, Yantai, Shandong Province, China, shell length 42.2 mm. **A.** Left valve. **B.** Inside view of left valve. **C.** Right valve. **D.** Inside view of right valve. **E.** Dorsal view of conjoined valve. **F, G.** Paratype, LSGB-B6015-4, Gotsu, Shimane Prefecture, Japan; shell length 50.6 mm. **F.** Left valve. **G.** Inside view of right valve. **H, I.** Paratype, LSGB-B6011-6 Fujitsukahama, Shibata, Niigata prefecture, Japan; shell length 29.5 mm. **H.** Left valve. **I.** Inside view of right valve. Scale bars = 1 cm.

57°C (ITS1) for annealing and 2 min at 72°C for extension, and a final extension at 72°C for 7 min. Amplification products were purified using ExoSAP-IT® (USB Corporation) according to manufacturer's instructions. The purified product was used as the template DNA for cycle-sequencing reactions performed using BigDye Terminator Cycle Sequencing Kit (v. 3.1, Applied Biosystems). Sequencing was carried out in an ABI 3100 Capillary Electrophoresis Genetic analyzer. Both DNA strands were sequenced.

DNA sequence analysis

The forward and reverse sequences were assembled automatically using SeqMan in DNASTAR, and the assembled files were checked by eye. We obtained a total of 76 sequences of COI and 19 of ITS1. Sequences were deposited in GenBank with the accession numbers HM357275–HM357350 for COI, and HM357256–HM357274 for ITS1 (Table 1).

Multiple alignments were performed with MEGA 4 (Tamura *et al.*, 2007) using ClustalW (Thompson, Higgins & Gibson, 1994) under the default parameters. For COI the sequences were translated with MEGA 4 using the invertebrate mitochondrial genetic code to test for the amplification of pseudogenes. No stop codons were found, indicating that the sequences were mitochondrial. For the ITS1 region the boundaries of the coding and spacer regions were determined by comparison with the sequence of *Macridiscus multifarious* n. sp., which we describe below (as *Gomphina melanaegis*, AB377660, S. Chow, unpubl.). To achieve a consensus dataset across all taxa, the length of analysed sequence was truncated in MEGA to the shortest common length. The final alignment of 561 bp of COI and 641 bp (gaps included) of ITS1 was used for phylogenetic analysis. The Kimura 2-parameter (K2P) model of base substitution (Kimura, 1980) was used as a simple measure of pairwise sequence distances.

Consistency of phylogenetic signal in the data was tested by two methods of phylogenetic reconstruction: maximum parsimony (MP) using PAUP* 4.0b10 software (Swofford, 2003), and neighbour joining (NJ) using MEGA. *Marcia japonica* of the subfamily Tapetinae (GenBank HM357351) was chosen as outgroup in the COI analysis. A COI sequence of *M. melanaegis* (AB076948, Matsumoto, 2003) and an ITS1 sequences of *M. multifarious* (as *Gomphina melanaegis*, AB377660,

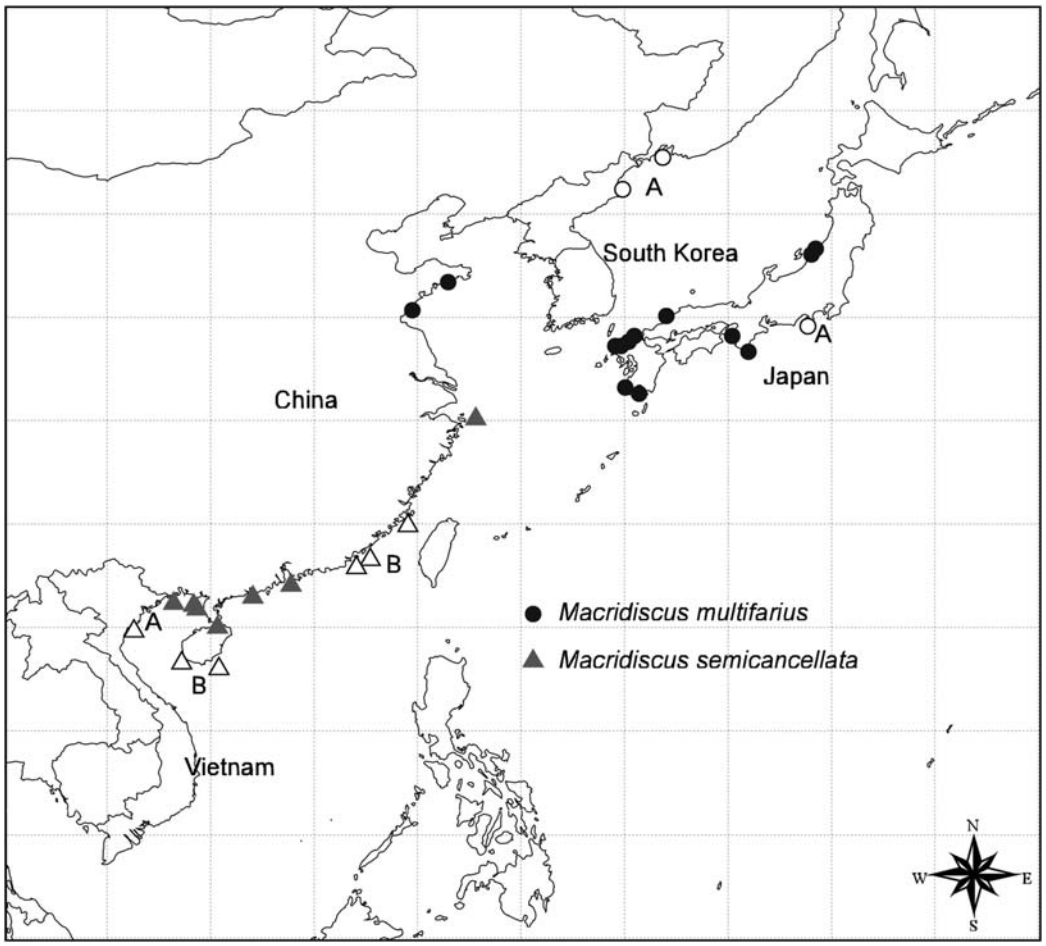

Figure 2. Geographical distribution of *Macridiscus multifarius* n. sp. and *M. semicancellata* based on material examined (solid dots and triangles) and cited literature records (hollow dots and triangles) (A: Lutaenko, 2001; B: Zhuang, 1964).

S. Chow, unpubl.) from GenBank were also included in the phylogenetic analysis. For MP, we conducted an unweighted analysis with a heuristic search, TBR branch-swapping, and 10 random-addition repetitions using program PAUP*. To indicate nodal support, we conducted a subsequent bootstrap analysis with 1,000 replications. Indels within the ITS1 alignment were coded with the SeqState program (Müller, 2005), which uses the 'simple indel coding' method of Simmons & Ochoterena (2000). The NJ tree was bootstrapped with 1,000 pseudoreplicates carried out using the K2P model of base substitution and the pairwise deletion option.

SYSTEMATIC DESCRIPTIONS

Family Veneridae Rafinesque, 1815

Subfamily Tapetinae H. & A. Adams, 1857

Genus *Macridiscus* Dall, 1902

Type species: *Venus semicancellata* Koch, in Philippi, 1843.

Original diagnosis: "valves more equilateral, trigonal and compressed, less heavy and sometimes with feeble striation distally; nymphs and teeth entire, smooth".

Rediagnosis: Shell subovate, subtrigonal to trigonal, compressed, thick and solid; exterior glossy, sometimes with posterodorsal radial striations; both valves ornamented with numerous fine commarginal lines; colour variable, usually with three brownish radial rays; hinge plate triangular, with three cardinal teeth in each shell, no lateral teeth, cardinal teeth 2b in left valve and 1 in right valve with groove; nymphs smooth; anterior and posterior adductor muscle scars nearly same size; pallial line and sinus well impressed; escutcheon and lunule weak.

Macridiscus multifarius Kong, Matsukuma & Lutaenko, new species

(Fig. 1A–I)

Donax aequilatera Sowerby, 1825: 12 (*nom. nud.* or *nom. dub.*).

Venus donacina—Sowerby, 1853: 739, pl. 159, figs 165, 166, 167. Reeve, 1863: sp. 95 (not Gmelin, 1791; not Chemnitz, 1795).

Gomphina (*Macridiscus*) *veneriformis*—Habe, 1951: 179. Kira, 1959: 143, pl. 56, fig. 20. Zhuang, 1964: 87, pl. 7, fig. 2. Kuroda *et al.*, 1971: 657, pl. 90, fig. 12. Yoo, 1976: pl. 31, fig. 2. Habe, 1977: 268. Qi *et al.*, 1989: 220, pl. 11, fig. 12. Higo *et al.*, 1999: 511 (in part). Min, 2004: 469, figs 1543 (not Lamarck, 1818).

Gomphina veneriformis—Tanaka, 1979: 61–65, Fig. 3D–I (not Lamarck, 1818).

Gomphina (*Macridiscus*) *veneriformis veneriformis*—Kwon *et al.*, 1993: 369, pl. 12, figs. 86-10-1, 86-10-2 (not Lamarck, 1818).

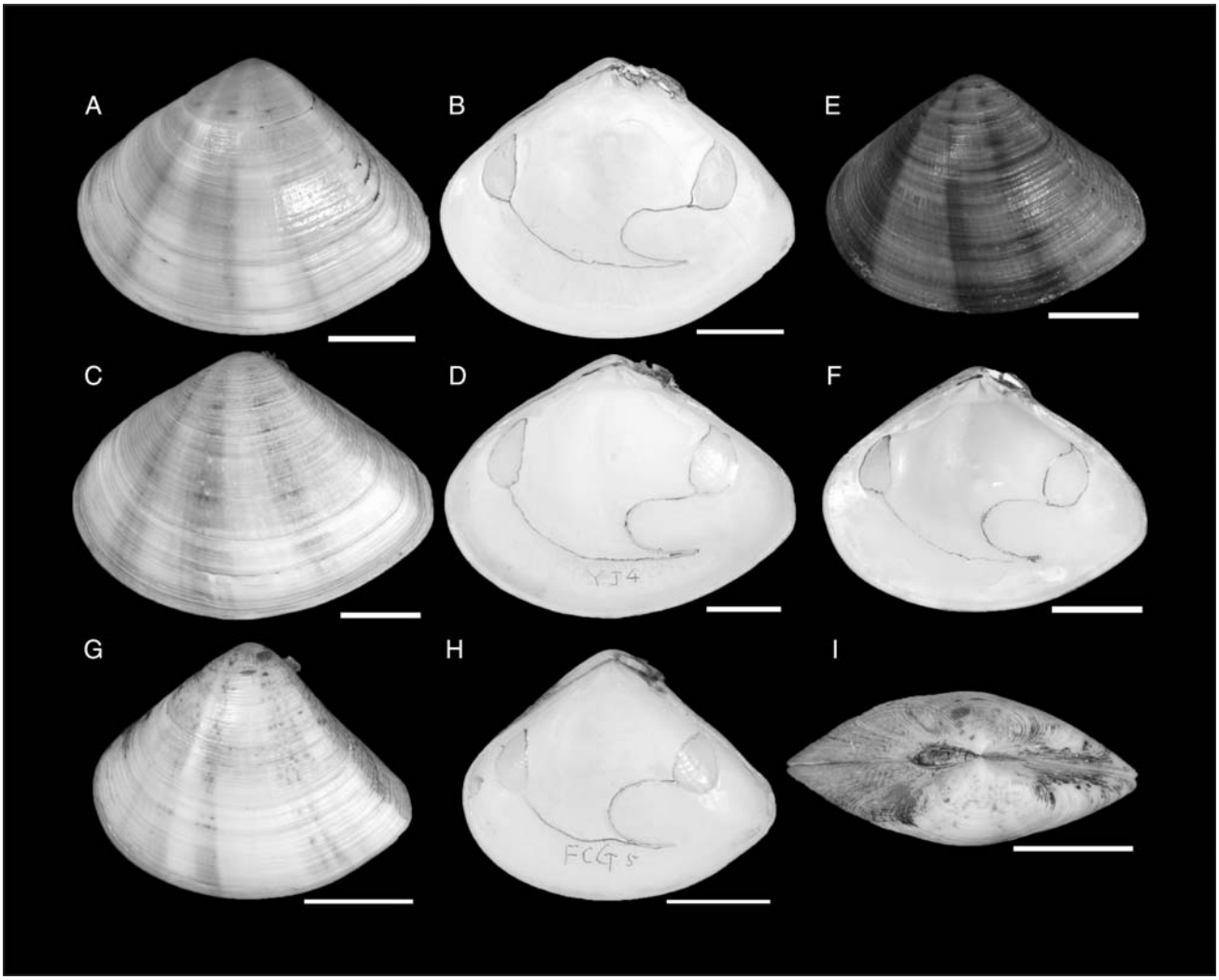

Figure 3. *Macridiscus semicancellata*. **A, B.** LSGB-B6005-3, Zhoushan, Zhejiang province, China; shell length 40.6 mm. **A.** Left valve. **B.** Inside view of right valve. **C, D.** LSGB-B6006-4, Yangjiang, Guangdong province, China; shell length 45.5 mm. **C.** Left valve. **D.** Inside view of right valve. **E, F.** LSGB-B6007-2, Weizhou Island, Beihai, Guangxi province, China; shell length 34.9 mm. **E.** Left valve. **F.** Inside view of right valve. **G–I.** LSGB-B6008-5, Fangchenggang, Guangxi province, China; shell length 27.9 mm. **G.** Left valve. **H.** Inside view of right valve. **I.** Dorsal view of conjoined valve. Scale bar = 1 cm.

Gomphina semicancellata—Matsukuma in Okutani, 2000: 1015, pl. 505, fig. 61 (not Koch in Philippi, 1843).
Gomphina (*Macridiscus*) sp. ('*aequilatera* auctt.') Lutaenko, 2001: 465–486, pl. 2, figs 1–4, 7; pl. 3, 5–8; pl. 4, figs 1, 2.
Gomphina aequilatera—Lutaenko & Yakovlev, 1999: 147–154, fig. 3; Okutani, 2006: 124 (not Sowerby, 1825).

Type material: Holotype (Fig. 1A–E): LSGB-B6002-2, Daxinjia, Haiyang, Yantai, Shandong Province, China, 1 conjoined specimen, 15 May 2006, Coll. LK. 40 paratypes: LSGB-B6002-1, LSGB-B6002-3 to LSGB-B6002-12, Daxinjia, Haiyang, Yantai, Shandong Province, China, 11 conjoined specimens, 15 May 2006, Coll. LK; KYUM-Mo5005, 5 conjoined specimens, Daxinjia, Haiyan, Shandong Province, China, 5 conjoined specimens, 15 May 2006, Coll. LK; LSGB-B6003, Rizhao, Shandong Province, China, 4 conjoined specimens, 9 May 2008, Coll. XZ; LSGB-B6011, Fujitsukahama, Shibata, Niigata Prefecture, Japan, 7 conjoined specimens, 19 June 2009, Coll. IH & YT; LSGB-B6015, Gotsu, Shimane Prefecture, Japan, 6 conjoined specimens, 6 July 2009, Coll. SI; LSGB-B6017, Hamatama, Karatsu, Saga Prefecture, Japan, 7 conjoined specimens, 22 August 2009, Coll. AM.

Other material examined: Seventy-five specimens from 10 localities (Supplementary material Appendix 1).

Etymology: From Latin *multifarius*, meaning many and of various types, referring to the geographical variation in the shell form of this species.

Measurements: Table 2.

Description: Shell subtrigonal, solid, equivalve. Anterodorsal margin straight and anterior end rounded; ventral margin broadly rounded; posterodorsal margin straight or slightly convex; posterior end shortly truncated. Exterior glossy, smooth; sometimes with weak radial riblets from the umbo extend to posterior slope; both valves ornamented with numerous fine commarginal lines; usually with 3 brownish radial rays; colour variable. Interior white or yellowish, sometimes bright yellow around adductor muscle scar and pallial sinus. Hinge plate triangular; teeth strong; left valve with weakly grooved 2b; right valve with strong and bifid 1, and elongated and weakly grooved 3b. Ligament strong, raised, protruding. Escutcheon elongated, depressed; lunule

Table 2. Shell parameters for *Macridiscus multifarius* n. sp., *M. semicancellata* and *M. melanaegis*.

	SL	SH	C	PSD	SL/SH	C/SH	PSD/SL
M. multifarius n. sp.							
Holotype	42.20	31.20	16.90	18.50	1.35	0.54	0.44
Paratypes ($n = 40$)							
Mean	36.04	26.75	14.61	14.86	1.35	0.54	0.41
Range	21.9–57.9	16.1–43.9	8.1–25.5	9.3–22.4	1.29–1.45	0.48–0.60	0.37–0.46
Std. dev.	9.30	6.88	4.41	3.52	0.04	0.03	0.02
Total ($n = 111$)							
Mean	33.05	24.69	13.21	14.03	1.34	0.53	0.43
Range	11.1–60.2	7.8–45.7	3.7–25.7	4.8–24.8	1.11–1.45	0.41–0.62	0.37–0.48
Std. dev.	8.65	6.58	3.98	3.47	0.04	0.03	0.02
M. semicancellata ($n = 42$)							
Mean	32.55	25.67	13.75	15.92	1.27	0.54	0.49
Range	22.5–45.5	16.5–35.1	8.1–19.1	10.9–21.2	1.11–1.36	0.49–0.60	0.43–0.55
Std. dev.	6.16	4.60	2.49	2.46	0.05	0.02	0.03
M. melanaegis ($n = 69$)							
Mean	50.75	37.16	18.98	20.00	1.36	0.52	0.40
Range	16.1–92.9	11.9–65.5	6.4–32.8	6.6–37.5	1.30–1.43	0.47–0.61	0.36–0.45
Std. dev.	19.99	14.27	6.86	7.66	0.03	0.03	0.02

Abbreviations: SL, shell length; SH, shell height; C, shell convexity; PSD, anterior extent of pallial sinus; *n*, number of examined specimens (specimens of only one valve were excluded).

lanceolate, separated from shell surface by sharp grooves. Adductor muscle scar and pallial sinus relatively deeply impressed, but weak in juveniles. Pallial sinus moderately deep.

Geographical distribution (Fig. 2): Niigata and southward in Sea of Japan; Boso Peninsula and southward to Kyushu along Pacific coast of Japan; Peter the Great Bay in Russia; Korean Peninsula; Liaoning to Jiangsu on north coast of China.

Habitat: Sand bottom, middle intertidal zone to 50 m deep.

Remarks: According to Lutaenko (2001) the widely used name *Donax aequilatera* Sowerby, 1825 is a *nomen nudum* or a *nomen dubium*, so he left the name as *Gomphina* (*Macridiscus*) sp. ('*aequilatera* auctt.'). Here, substantial evidence from molecular, shell morphology and distributional data (see below) allows us to describe *G.* (*M.*) sp. as a new species. *Macridiscus multifarius* differs from *M. melanaegis* in having a subtrigonal shell and in being more inflated, and from *M. semicancellata* in that the pallial sinus is not so deep and broad and with a different geographical distribution. *Macridiscus multifarius* is found in Japan, Peter the Great Bay in Russia, Korean Peninsula and northern China (north of Changjiang River), while *M. semicancellata* is found around southern coasts of China (south of Changjiang River), Taiwan, Beibu Gulf and Vietnam. Some conchologists of Japan considered that the northern limit of *M. multifarius* in the Japan Sea was the Noto Peninsula (Habe, 1951; Kira, 1959; Kuroda *et al.*, 1971), but there are some specimens of *M. multifarius* among our examined material sympatric with *M. melanaegis* in Niigata Prefecture (north of Noto Peninsula). *Macridiscus multifarius* exhibits considerable geographical variation in shell form.

Macridiscus semicancellata (Koch in Philippi, 1843)

(Fig. 3A–I)

Venus donacina Chemnitz, 1795: 231, pl. 202, figs 1983, 1984. Lischke, 1869: 120 (nonbinominal; not Gmelin, 1791).

Venus semicancellata Koch in Philippi, 1843: 40, pl. 1, figs 2, 3. Dautzenberg & Fischer, 1906: 218.

Gomphina (*Macridiscus*) *melanaegis*—Zhuang, 1964: 87, pl. 6, fig. 9 (not Römer, 1864).

Gomphina veneriformis—Hu & Tao, 1995: 205, pl. 116, fig. 6 (not Lamarck, 1818).

Gomphina aequilatera—Hu & Tao, 1995: 205, pl. 116, figs 8, 9. Qi, 2004: 310, pl. 169, fig. E. Xu & Zhang, 2008: 247, fig. 781. Zhang, 2008: 351 (not Sowerby, 1825).

Gomphina (*Macridiscus*) *semicancellata*—Lutaenko, 2001: 465–486, pl. 3, figs 1–4.

Gomphina (*Macridiscus*) *aequilatera*—Zhuang, 2001: 211, fig. 131 (not Sowerby, 1825).

Gomphina semicancellata—Thach, 2007: 223, pl. 74, fig. 1232.

Material examined: Forty-eight specimens from seven localities (Supplementary material Appendix 1).

Measurements: Table 2.

Description: Shell subtrigonal or equilateral triangular, solid, compressed, equivalve. Anterodorsal margin straight; anterior end rounded; ventral margin broadly rounded; posterodorsal margin straight or slightly concave; posterior end produced, nearly beak-like. Exterior glossy, smooth; both valves ornamented with numerous fine commarginal lines; with conspicuous radial riblets from the umbo extend to posterior slope, resulting in cancellate pattern particularly near umbo. Colour variable, usually with 3 brownish radial rays. Interior always white, porcellanous, glossy in area of pallial sinus, along ventral margin and in muscle scars. Hinge plate triangular; left valve with elongate 2a, weakly grooved 2b; right valve with trigonal, bifid 1, slightly bifid 3b, and weak 3a. Ligament strong, raised, protruding. Escutcheon elongated, depressed. Lunule elongated, separated from shell surface by sharp grooves. Adductor muscle scar and pallial sinus relatively deeply impressed, but weak in juveniles. Pallial sinus broad, deep, about 1/2 shell length.

Geographical distribution: South coast of China (south of Changjiang River); Taiwan; Beibu Gulf; Vietnam (Fig. 2).

Habitat: Sand bottom in lower intertidal zone.

Remarks: *Macridiscus semicancellata* differs from *M. melanaegis* and *M. multifarius* by possession of much deeper and broader pallial

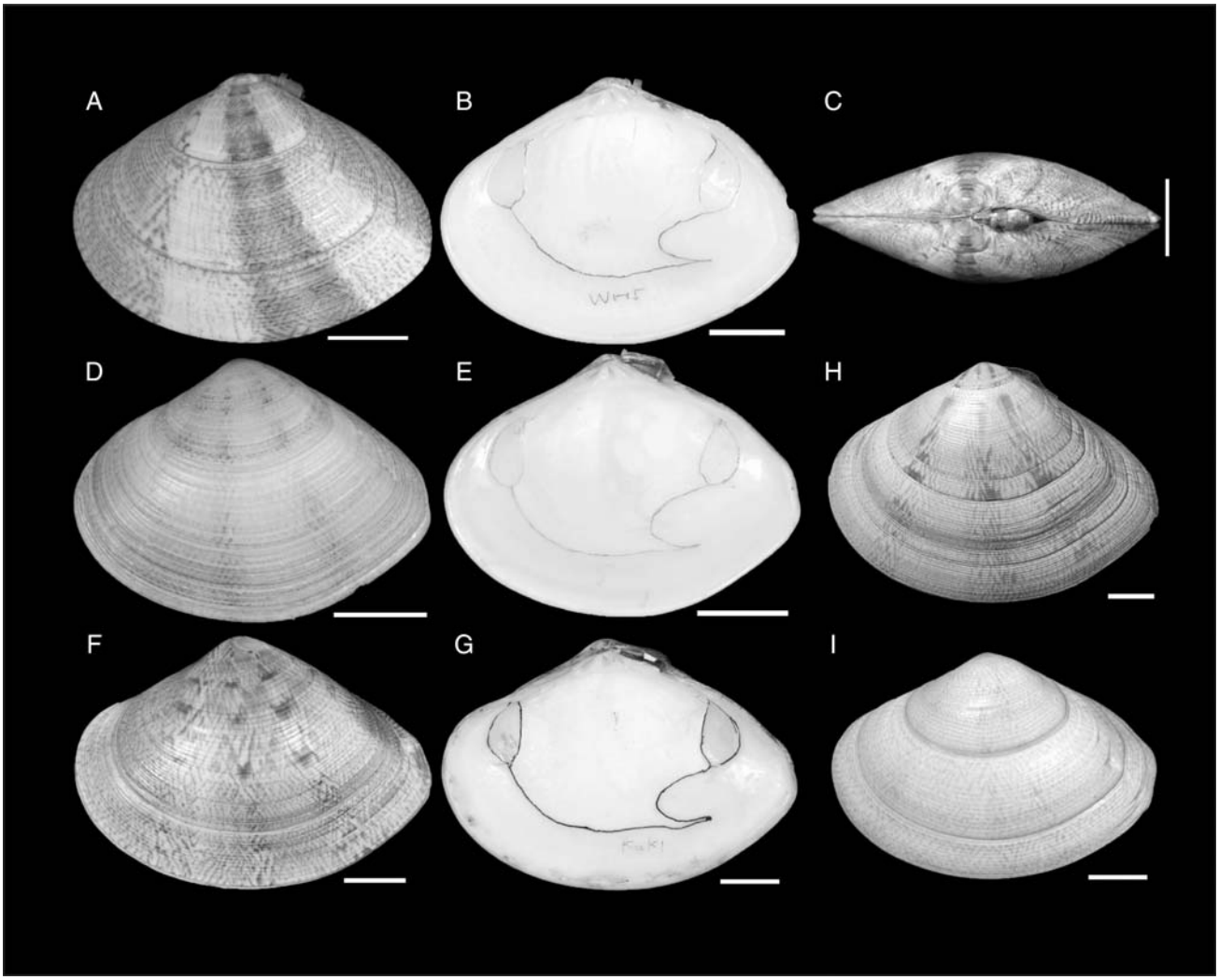

Figure 4. *Macridiscus melanaegis*. **A–C.** LSGB-B6001-5, Weihai, Shandong Province; shell length 46.4 mm. **A.** Left valve. **B.** Inside view of right valve. **C.** Dorsal view of conjoined valve. **D, E.** LSGB-B6012-5, Iwafune, Murakami, Niigata Prefecture, Japan; shell length 38.2 mm. **D.** Left valve. **E.** Inside view of right valve. **F, G.** LSGB-B6014, Kagoshima Bay, Kagoshima Prefecture, Japan; shell length 58.5 mm. **F.** Left valve. **G.** Inside view of right valve. **H.** KUM, Sato collection, reg. no. 1100-1, Akita Prefecture, Japan; shell length 72.7 mm. Left valve. **I.** KUM, Sato collection, reg. no. 1097, Fukui Prefecture, Japan; shell length 53.9 mm. Left valve. Scale bar = 1 cm.

sinus, and from *M. melanaegis* by conspicuous radial riblets extending from the umbo to the posterior slope. Lutaenko (2001) considered the key feature distinguishing *M. semicancellata* and *M. multifarius* [as *M.* sp. ('*aequilatera* auctt.')] to be the pallial sinus reaching the median line dividing the shell from the umbones ventrally in the former. This is not the case, although most individuals of *M. semicancellata* have a deeper pallial sinus than that in *M. multifarius*. The pallial sinus of some individuals of *M. semicancellata* from Zhoushan, Zhejiang province and Yangjiang, Guangdong province, do not reach the median line (PSD/SL range, 0.43–0.55, Table 2).

Macridiscus melanaegis (Römer, 1860)

(Fig. 4A–I)

Venus aequilatera—Sowerby II, 1853: 739, pl. 159, figs 168, 169. Reeve, 1863: sp. 92 (not Sowerby, 1825).

Venus melanaegis Römer, 1860: 157–158. Lischke, 1874: 86, pl. 7, figs 10, 11.

Gomphina melanaegis—Dunker, 1862: 40, pl. 12, figs 12, 13. Tanaka, 1979: 61–65, Fig. 3A–C. Matsukuma in Okutani, 2000: 1015, pl. 505, fig. 60. Okutani, 2006: 124.

Gomphina (*Macridiscus*) *melanaegis*—Habe, 1951: 179, figs 415, 416. Kira, 1959: 143, pl. 56, fig. 21. Habe & Ito, 1965: 135, pl. 45, fig. 8. Yoo, 1976: 132, pl. 31, fig. 1. Habe, 1977: 268, pl. 55, figs 11, 12. Lutaenko, 2001: 465–486, pl. 2, figs 5, 6, 8–12; pl. 4, fig. 5; pl. 5, figs 1–7.

Gomphina aequilatera—Abbott & Dance, 1982: 364 (not Sowerby, 1825).

Gomphina (*Macridiscus*) *veneriformis melanaegis*—Kwon *et al.*, 1993: 368, pl. 12, figs 86-9-1, 86-9-2.

Gomphina (*Macridiscus*) *veneriformis*—Higo *et al.*, 1999: 511 (in part) (not Lamarck, 1818).

Material examined: Seventy specimens from 23 localities (Supplementary material Appendix 1).

Measurements: Table 2.

Description: Shell subovate, thick, bilaterally compressed, equivalve. Anterodorsal margin straight to slightly concave; anterior end always smoothly rounded; posterodorsal margin slightly convex and rounded; posterior end rounded or shortly

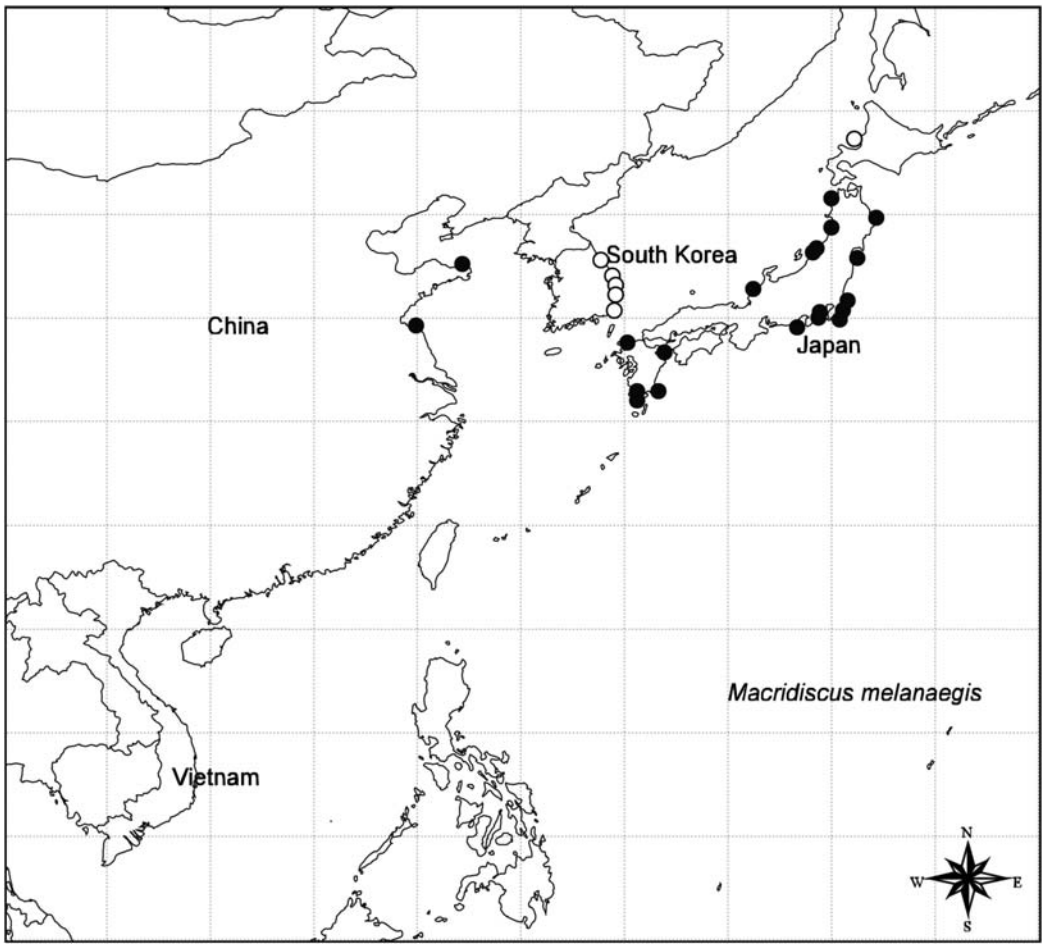

Figure 5. Geographical distribution of *Macridiscus melanaegis* based on material examined (solid dots) and cited literature records (hollow dots, Lutaenko, 2001).

truncated; ventral margin broadly arcuate. Escutcheon lanceolate, not well expressed. Lunule weak, elongate, with fine grooves separating it from shell surface. Exterior glossy; both valves ornamented with fine commarginal lines. Colour variable; exterior often cream, brownish or white with three brown rays consisting of zigzag lines. Interior white, porcellanous, glossy in area of pallial sinus, along ventral margin and in muscle scars. Umbones orthogyrate or weakly prosogyrate. Hinge plate triangular; left valve with three strong cardinal teeth, of which 2b is slightly bifid; right valve with weak 3a, trigonal and bifid tooth 1, elongated and slightly bifid 3b. Ligament strong, relatively short, protruding. Adductor muscle scars and pallial line well impressed and easily visible, muscle scars subequal, elongated dorsoventrally. Pallial sinus round, moderately deep.

Geographical distribution: Southwest Hokkaido to Kyushu, Japan; Korean Peninsula; Liaoning to Jiangsu on northeastern coast of China (Fig. 5).

Habitat: Sand substrates; lower intertidal zone to 50 m deep.

Remarks: Adult specimens of *M. melanaegis* can be easily distinguished from those of *M. multifarius* and *M. semicancellata* by possession of more ovate shells. However, the shell form of small individuals (1–4 cm) of *M. melanaegis* is very similar to those of *M. multifarius*. Small individuals of *M. melanaegis* and *M. multifarius* can be distinguished by combining three characteristics, although each character is not absolute. The first one is whether the interior colour of the shell is white or yellowish. The interior colour of *M. melanaegis* is usually white and *M. multifarius* usually yellowish. The second one is whether the anterodorsal margin is slightly concave. The anterodorsal margin of *M. melanaegis* is usually slightly concave but that of *M. multifarius* usually straight. The third one is whether the posterodorsal ridge is present or not. *Macridiscus multifarius* usually has obvious posterodorsal ridges but these are not present in *M. melanaegis*. Lutaenko (2001) considered that *M. melanaegis* has a thinner shell than the other two species, but we found that adult specimens of *M. melanaegis* usually have thick and solid shells similar to the other two species. Clerical errors in the description of hinge teeth by Lutaenko (2001; he wrongly put the cardinal teeth 3b under the left valve and 2a, 2b, 4b under the right valve) are corrected here. Tanaka (1979) said that *M. melanaegis* can be distinguished from *M. multifarious* (as '*Gomphina veneriformis*') based on the shell sculpture of their umbonal region when young (shell length below 3 mm).

PHYLOGENETIC ANALYSIS

Alignment of 561 bp of 77 sequences from the partial COI gene revealed 454 constant and 107 variable characters; 99 of the latter were parsimony-informative. The ITS1 alignment for 20 sequences contained 641 bp (after exclusion of the ambiguous region) with 534 constant sites and 56 variable

Table 3. Intraspecies K2P distances (±SE) of *Macridiscus* species.

	COI	ITS1
M. multifarius n. sp.	0.005 ± 0.001	0.001 ± 0.001
M. semicancellata	0.007 ± 0.002	0.003 ± 0.001
M. melanaegis	0.002 ± 0.001	0.002 ± 0.002

Table 4. Mean K2P pairwise distances among species of *Macridiscus*.

	M. melanaegis	*M. multifarius* n. sp.	*M. semicancellata*
M. melanaegis	–	0.080 ± 0.011	0.081 ± 0.012
M. multifarius n. sp.	0.150 ± 0.018	–	0.015 ± 0.004
M. semicancellata	0.157 ± 0.017	0.064 ± 0.011	–

Mean K2P distances (±SE) of COI gene and ITS1 region are in the lower triangle and the upper triangle, respectively.

sites, of which 51 were parsimony-informative. The mean K2P distances between the three clades and within the clades are summarized in Tables 3 and 4. Intraclade variation ranged from 0.2% to 0.7% for COI and 0.1% to 0.3% for ITS1 genes (Table 3); interclade variation ranged from 6.4% to 15.7% for COI and 1.5% to 8.1% for ITS1 genes (Table 4). Not surprisingly, the interclade differences were generally greater than intraclade differences.

Phylogenetic analysis based on MP and NJ for the COI gene gave generally consistent trees and clearly divides all the sequences into three lineages (Fig. 6). The phylogeny produced from the ITS1 dataset also resolved the genus *Macridiscus* into three lineages with strong bootstrap support (>95%).

DISCUSSION

We completed a phylogenetic analysis of the genus *Macridiscus* based on a representative sampling across its distributional range and analyses of both mitochondrial and nuclear genetic markers. We found three well-supported evolutionary lineages (Fig. 6). The three lineages could be ascribed to the species described by Lutaenko (2001): *M. melanaegis*, *M.* sp. ('*aequilatera* auctt.') (described as *M. multifarius* n. sp. herein) and *M. semicancellata*, respectively, except that Lutaenko placed *Macridiscus* as a subgenus of *Gomphina*. The morphological differences and distribution of the three species were corrected based on the new molecular data.

The K2P distances of COI sequence between *M. melanaegis* and *M. multifarius*, *M. melanaegis* and *M. semicancellata* were 15.0% and 15.7%, respectively, which are within the range observed among congeners of other bivalves (e.g. *Arcopsis solida vs A. adamsi*: 12.9%, *Mytilus edulis vs M. trossulus*: 15.3%, Luttikhuizen, Drent & Baker, 2003), and also similar to results observed in other congeners of Tapetinae (17.2–32.2%, Chen *et al*., 2010). *Macridiscus melanaegis* has diagnostic shell characters compared with *M. multifarius* and *M. semicancellata* (e.g. shape of the shell, and the radial riblets from the umbo extending to posterior slope). In addition, the overlapping distributional range of between *M. melanaegis* and *M.* sp. ('*aequilatera* auctt.') suggests reproductive isolation of the two species, because this deep phylogenetic structure is achieved by lack of interbreeding and by subsequent lineage sorting over time. Thus, the molecular, morphological and geographical distribution evidence provides ample justification for recognizing *M. melanaegis* as a distinct species.

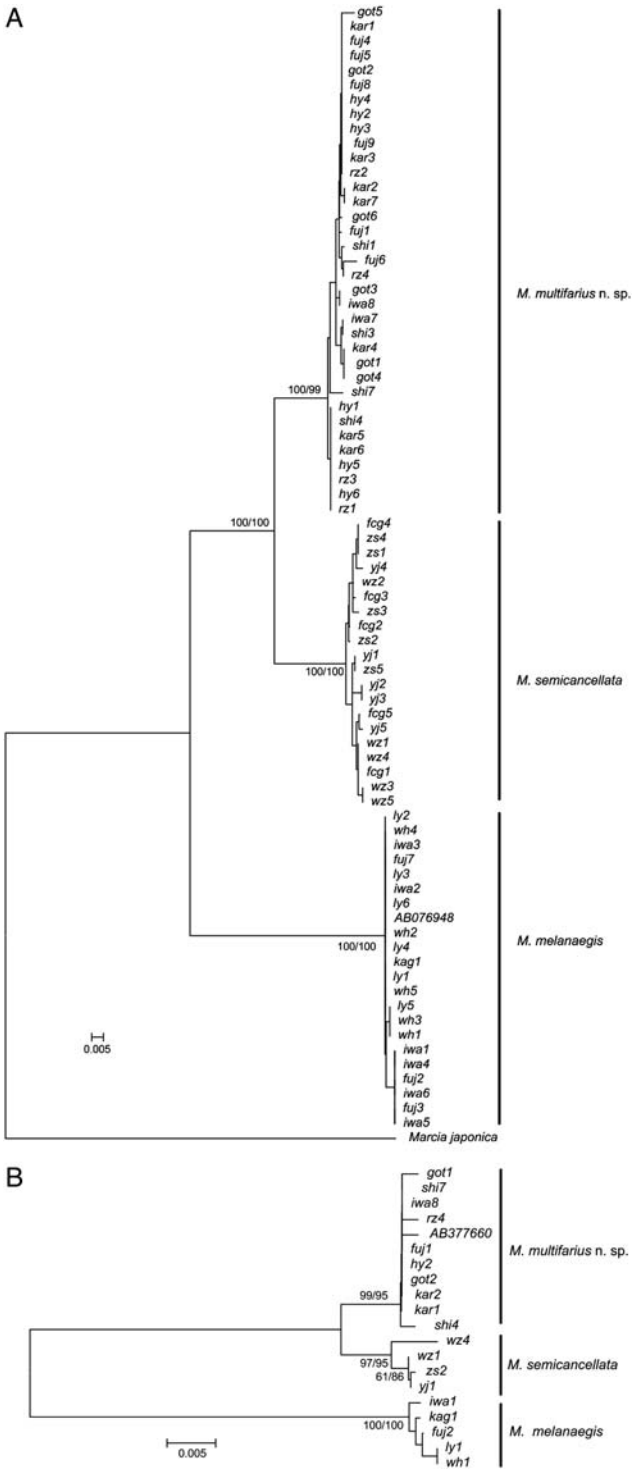

Figure 6. Neighbour-joining phylogram for the COI **A.** and ITS1 **B.** datasets based on K2P distance. Support values are indicated at nodes (MP and NJ bootstrap values, respectively).

However, species delimitation in allopatry is problematic and controversial, and there is a case in this study which should be addressed: *M. multifarius* and *M. semicancellata*. To our knowledge, the two 'species' have nonoverlapping geographical ranges: *M. multifarius* is found in Japan, Peter the Great Bay in Russia, Korean Peninsula and northern China, while *M. semicancellata* occurs only in southern China (south of

Changjiang River), Taiwan, Beibu Gulf and Vietnam. The K2P distance of COI sequence between the two species was 6.4%, which although within the range in some groups of bivalves (*Crassostrea* spp., 2.55–29.29%, Lam & Morton, 2003), is lower than the 'typical' value (17.2–32.2%) found in other congeners of Tapetinae. Here, according to the unified species concept (De Queiroz, 2007), which comprises the biological species concept without the need to prove actual reproductive isolation, we proposed that *M. multifarius* and *M. semicancellata* should be recognized as different species, because (1) the two entities were reciprocally monophyletic at two independently inherited marker loci (COI, Fig. 6A and ITS1, Fig. 6B), which thus represent 'separately evolving metapopulation lineages'; and (2) the depth of the anterior extent of the pallial sinus (PLD) is quite different between the two entities. The ratio of the anterior extent of pallial sinus to shell length (PLD/SL) of *M. semicancellata* is significantly larger than that of *M. multifarius* (0.49–0.43, Table 2; $P < 0.01$, *t*-test, data not shown). There are several cases in which morphologically similar allopatric entities have been recognized as separate species in molluscs. For example, data from three genes (COI, 28S rRNA and 16S rRNA) allowed recognition of two sister pairs of allopatric species of *Bulla* (Malaquias & Reid, 2008). Based on the unified species concept, Pfenninger *et al.* (2010) delimited *Tudorella* species with mitochondrial (COI and 16S) and nuclear (ITS1) genetic data and suggested that there are eight allopatric species in the genus.

In conclusion, we demonstrate that a combination of both morphological and genetic analyses is effective for the clarification of taxonomic status, especially in groups that were difficult to resolve using morphological characters alone.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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