INTRODUCTION

Populations of the Asian (overbite) clam, *Corbula (Potamocorbula) amurensis* Schrenck, 1861, in San Francisco Bay, USA, have markedly increased since 1986. They were introduced to the region through ballast waters from a cargo ship that had stopped in East Asia (Carlton et al. 1990, Nichols et al. 1990). It is known that the waters adjacent to Japan and Korea in the Northwest Pacific are inhabited by at least 4 species of the subgenus *Potamocorbula* Habe, 1955. These species are distinguishable from each other by 6 morphological characteristics: shell size, shell outline, shell inflation, shell thickness, posterior...
margin and position of the umbo (Zhuang & Cai 1983, Habe 1994, Horikoshi & Okamoto 1994, Tsuchida & Okamura 1997). However, Sato (2002, 2005) and Sato & Kanazawa (2004) reported that there were high geographic variations in these morphological characteristics, making it challenging to distinguish among these species.

Corbula (Potamocorbula) amurensis is regarded as an invasive species in San Francisco Bay and may have a significant impact on the estuarine ecosystem of the bay (Carlton 1999, Coan 2002, Kimmerer 2002, Greene et al. 2011). In addition, fossil specimens of this species have been used as indicators of a cool climate or brackish water during reconstructions of the paleoenvironments of the Late Pleistocene and Holocene in Japan (Matsushima 1984, Habe 1994). However, these may not be accurate until the relationships between the geographic distribution and morphological characteristics of Corbula (Potamocorbula) spp. are fully understood at both population and species levels. To clarify the relationships among members of Corbula (Potamocorbula) spp., it will be necessary to investigate the morphological and genetic characteristics of populations from various localities. There have been several discussions of the genetic characteristics of Corbula (Potamocorbula) spp. For example, Duda (1994) reported that C. (P.) amurensis from San Francisco Bay, California, shows high genetic variation. Further, Smith et al. (2012) indicated that C. (P.) amurensis from San Francisco Bay and the Ariake Sea, western Japan, can be identified using the same genetic marker, 18S ribosomal DNA. However, they did not simultaneously discuss the relationships between the morphological and genetic characteristics. In the present study, we investigated the geographic distribution of the morphological and genetic characteristics of the populations from the waters adjacent to Japan, Korea and San Francisco Bay through canonical discriminant analysis (CDA) of 8 shell characteristics and through the DNA sequences of mitochondrial cytochrome c oxidase subunit 1 (CO1) and nuclear internal transcribed spacer 2 (ITS2) regions.

MATERIALS AND METHODS

Sampling

Corbula (Potamocorbula) spp. were collected from 8 localities shown in Fig. 1: Rokkaku River Estuary, Saga Prefecture, Ariake Sea, western Japan (N = 25 individuals collected on 12 July 1998 and 23 November 2008); Dong River Estuary, Suncheon-si, southern Korea (N = 30, 20 August 2011); Mangyeong River Estuary, Gunsan-si, western Korea (N = 30, 3 May 2000 and 11 July 2008); Ganghwa-do, intertidal muddy sand flat, western Korea (N = 30, 8 May 1998 and 18 August 2011); Maeho Lake, Yangyang-gun, eastern Korea (N = 30, 16 July 2008); Hinuma Lake, Ibaraki Prefecture, central Japan (N = 30, 31 May 1998 and 30 July 2011); Obuchi Swamp, Aomori Prefecture, northern Japan (N = 46, 3 September 1998 and 27 July 2009); and San Francisco Bay, California,

![Fig. 1. Localities where the samples were collected. Rr: Rokkaku River Estuary (33°11’N, 130°12’E); Dr: Dong River Estuary (34°31’N, 127°30’E); Mr: Mangyeong River Estuary (35°51’N, 126°40’E); Gd: Ganghwa-do (37°36’N, 126°22’E); Ml: Maeho Lake (37°56’N, 128°46’E); Hl: Hinuma Lake (36°16’N, 140°30’E); Os: Obuchi Swamp (40°57’N, 141°22’E); Sf: San Francisco Bay (37°27’N, 122°1’W)
Morphological analysis

Eight shell characteristics (in mm): shell length (L), shell breadth (B), shell height of left valve (HL), shell height of right valve (HR), thickness of shell margin (T), height of umbo (U), posterior shell length (PL) and upper shell height (UH) were measured on each individual (Fig. 2). For measurement of L, HR, U, PL and UH, the outside of the right shell valve was photographed with a digital camera, and then each characteristic was measured using image analysis software, ImageJ ver. 1.45s. Further, L, B, HL, HR and T were measured using a digital slide caliper (accuracy ± 0.01 mm). L and HR were measured using both methods, but there were no significant differences (p > 0.05) between them. Then, to standardize the variability for size, all characteristics were log-transformed (using base 10 logs), and the 7 characteristics excluding L were divided by the log L. CDA was tested with the standardized 7 characteristics using SPSS (Ver. 16.0).

Polymerase chain reaction (PCR)

CO1 and ITS2 regions were amplified using Premix Taq (Takara) and a PCR Thermal Cycler PERSONAL (Takara). The following primers were newly designed for the present study: 5'-TCW ACA AAT CAY AAA GAT ATT GG-3' (forward) and 5'-ACY TCM GGR TGM CCA AAA AAT CA-3' (reverse) for the CO1 region, and 5'-ATT GCA GGA CAC ATT GAA CAT CG-3' (forward) and 5'-GTT ACT GAG GGA ATC CTT GTT A-3' (reverse) for the ITS2 region. The conditions for PCR amplification were as follows: denaturation at 94°C for 30 s, annealing at 54°C for 30 s (CO1) and 55°C for 30 s (ITS2) and extension at 72°C for 60 s. These steps were repeated 30 times. The PCR products were purified using ExoSAP-IT (USB), and cycle-sequencing reactions were performed using BigDye Terminator Version 3.1 Cycle Sequencing Kit (ABI PRISM). The sequences were compiled using a 3130 Genetic Analyzer (ABI PRISM) from both the 5' and 3' directions. These sequences were registered in the DNA Data Bank of Japan (CO1: AB740093 to AB740137 and AB827932 to AB827935, ITS2: AB740177 to AB740218 and AB827936 to AB827938).

Genetic analysis

In the analysis of genetic variation in the CO1 region, the sequences of Varicorbula dissimilis (AF 120669), Solidicorbula erythrodon (AB740137), and Corbula (Potamocorbula) fasciata (AB740136) were included as outgroups. After alignment using Clustal W Version 1.8 (Thompson et al. 1997), sites that contained gaps or those that could not be confirmed by homology were removed from the analysis. A molecular phylogenetic tree was reconstructed using maximum-likelihood (ML) and Bayesian methods, respectively. The ML method was performed by PAUP Version 4.0*b10 (Swofford 2002). The tree search algorithm was a likelihood ratchet algorithm (2000 times) (Vos 2003), and the model for the ML method was selected using Modeltest Version 3.7 (Posada & Crandall 1998). A bootstrap test was conducted 1000 times. The Bayesian method was performed by MrBayes Version 3.1.2 (Ronquist & Huelsenbeck 2003). This program was run for 5,000,000 generations, with sampling every 1000th generation. The model for the Bayesian method was determined using Mrmodeltest Version 2.3 (Posada & Buckley 2004).

In the analysis of genetic variation in the ITS2 region, the sequences were aligned using Clustal W
Version 1.8 (Thompson et al. 1997). Sites that contained gaps and those that could not be confirmed by homology were removed from the analysis. Further, a haplotype network was built using TCS Version 1.21 (Clement et al. 2000).

RESULTS

Canonical discriminant analysis

Shells of representative individuals collected from each locality are shown in Fig. 3. According to the results of CDA, individuals from Ganghwa-do can be clearly separated from those of all the other localities by the 7 standard morphological characteristics (Fig. 4). The proportions of Canonical Variates 1 and 2 were 84.6 and 8.3%, respectively (Table 1). The centroid of Canonical Variate 1 in individuals from Ganghwa-do was less than −6, but those from the other 7 localities were all more than −2. The shell characteristics that largely affect Canonical Variate 1 were shell height and height of umbo (Table 2). Namely, individuals from Ganghwa-do have smaller shell heights and umbos rather than those from the other 7 localities (Fig. 3).

The other 7 samples beside Ganghwa-do cannot be clearly separated from each other (Fig. 4). However, individuals from Maeho Lake and Hinuma Lake have similar shell morphology, and those from Rokkaku River Estuary, Mangyeong River Estuary and San Francisco Bay were also of similar shell shape (Fig. 4). The samples from Dong River Estuary and Obuchi Swamp were slightly different from the other 5 samples, but some individuals overlapped morphologically (Fig. 4). In conclusion, though these 7 samples have a characteristic shell morphology, they cannot be distinguished because of the high morphological variability.

Among the samples from each locality, the percent of correct cases in multivariate discriminant analysis ranged between 100 and 60.0% (Table 3). All indi-

![Fig. 3. Corbula (Potamocorbula) spp. Representative individuals collected from each locality. For each locality the upper 2 rows display the right valve and the lower 2 rows display the left valve. Scale bars: 5 mm. Rr: Rokkaku River Estuary; Dr: Dong River Estuary; Mr: Mangyeong River Estuary; Gd: Ganghwa-do; Ml: Maeho Lake; Hl: Hinuma Lake; Os: Obuchi Swamp; Sf: San Francisco Bay](image)
Fig. 4. *Corbula* (*Potamocorbula*) spp. Two-dimensional scattergrams of *Corbula* (*Potamocorbula*) spp. from 8 localities obtained with canonical discriminant analysis. The values of Canonical Variates 1 and 2 for each individual and the centroids for individuals from each locality are shown. *Rr*: Rokkaku River Estuary; *Dr*: Dong River Estuary; *Mr*: Mangyeong River Estuary; *Gd*: Ganghwa-do; *Ml*: Maeho Lake; *Hl*: Hinuma Lake; *Os*: Obuchi Swamp; *Sf*: San Francisco Bay

Table 1. *Corbula* (*Potamocorbula*) spp. Standardized coefficients of 7 characteristics, eigenvalue and proportion of Canonical Variates 1 and 2 for 8 groups. *L*: shell length; *B*: shell breadth; *HL*: shell height of left valve; *HR*: shell height of right valve; *T*: thickness of shell margin; *U*: height of umbo; *PL*: posterior shell length; *UH*: upper shell height

<table>
<thead>
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<th>Characteristics</th>
<th>Canonical Variates:</th>
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<tr>
<td>log (B/L)</td>
<td>−0.248</td>
<td>1.115</td>
<td></td>
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<tr>
<td>log (HL/L)</td>
<td>0.385</td>
<td>0.255</td>
<td></td>
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<tr>
<td>log (HR/L)</td>
<td>0.361</td>
<td>−0.475</td>
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<tr>
<td>log (T/L)</td>
<td>0.357</td>
<td>−0.199</td>
<td></td>
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<tr>
<td>log (U/L)</td>
<td>0.451</td>
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<td>log (PL/L)</td>
<td>−0.200</td>
<td>0.227</td>
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<tr>
<td>log (UH/L)</td>
<td>0.095</td>
<td>−0.853</td>
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<tr>
<td>Eigenvalue</td>
<td>11.314</td>
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<tr>
<td>Proportion</td>
<td>84.6</td>
<td>8.3</td>
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</tbody>
</table>

Table 2. *Corbula* (*Potamocorbula*) spp. Centroids of Canonical Variates 1 and 2 for individuals from 8 localities. *Rr*: Rokkaku River Estuary; *Dr*: Dong River Estuary; *Mr*: Mangyeong River Estuary; *Gd*: Ganghwa-do; *Ml*: Maeho Lake; *Hl*: Hinuma Lake; *Os*: Obuchi Swamp; *Sf*: San Francisco Bay

<table>
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<tr>
<th>Locality</th>
<th>Centroid of Canonical Variate:</th>
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<tr>
<td><em>Rr</em></td>
<td>1.589</td>
<td>−0.440</td>
<td></td>
</tr>
<tr>
<td><em>Dr</em></td>
<td>−1.377</td>
<td>0.702</td>
<td></td>
</tr>
<tr>
<td><em>Mr</em></td>
<td>1.496</td>
<td>−0.809</td>
<td></td>
</tr>
<tr>
<td><em>Gd</em></td>
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<td>0.651</td>
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<tr>
<td><em>Ml</em></td>
<td>3.127</td>
<td>1.317</td>
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<tr>
<td><em>Hl</em></td>
<td>4.008</td>
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<td></td>
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<tr>
<td><em>Os</em></td>
<td>−1.822</td>
<td>−0.238</td>
<td></td>
</tr>
<tr>
<td><em>Sf</em></td>
<td>−0.077</td>
<td>−1.980</td>
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</table>
Individuals from Ganghwa-do were classified correctly, but 25.0% of the individuals from the other 7 localities were classified incorrectly (43 out of 172 ind.) (Table 3).

Genetic variation of the CO1 region

DNA sequences of 606 bp in length were compiled for 47 individuals. They were 5 sequences from Rokkaku River Estuary, 4 from Dong River Estuary, 8 from Mangyeong River Estuary, 8 from Ganghwa-do, 3 from Maeho Lake, 4 from Hinuma Lake, 8 from Obuchi Swamp and 7 from San Francisco Bay. After the alignment, a 594 bp sequence was used for the genetic analysis. Genetic variation among the sequences was found at 64 nucleotide sites (11%); however, the sequences of some individuals were identical. The sequences that were translated to amino acids were the same in all the individuals from the 8 localities. There were 25 amino acid substitutions between the ingroup and the outgroup *Corbula (Potamocorbula) fasciata*.

In the ML method, the K81uf+G model was selected by Modeltest Version 3.7 and the likelihood index (−ln L) was 2593.56183. In the Bayesian method, the GTR+G model was selected by Mrmodeltest. A strict consensus tree was computed from these 2 trees (Fig. 5). In the strict consensus tree, all individuals from the 8 localities formed a monophyletic group and *Corbula (Potamocorbula) fasciata* was identified as a sister group of the monophyletic group. The individuals from

![Figure 5](image_url)

Table 3. *Corbula (Potamocorbula)* spp. Discrimination scores using multivariate discriminant analysis among individuals from 8 localities. *Rr*: Rokkaku River Estuary; *Dr*: Dong River Estuary; *Mr*: Mangyeong River Estuary; *Gd*: Ganghwa-do; *Ml*: Maeho Lake; *Hl*: Hinuma Lake; *Os*: Obuchi Swamp; *Sf*: San Francisco Bay

<table>
<thead>
<tr>
<th></th>
<th>No. of total cases</th>
<th>No. of correct cases</th>
<th>Percent of correct cases</th>
<th>No. of classified cases</th>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rr</em></td>
<td>25</td>
<td>19</td>
<td>76.0</td>
<td></td>
</tr>
<tr>
<td><em>Dr</em></td>
<td>30</td>
<td>27</td>
<td>90.0</td>
<td></td>
</tr>
<tr>
<td><em>Mr</em></td>
<td>30</td>
<td>18</td>
<td>60.0</td>
<td></td>
</tr>
<tr>
<td><em>Gd</em></td>
<td>30</td>
<td>30</td>
<td>100.0</td>
<td></td>
</tr>
<tr>
<td><em>Hl</em></td>
<td>28</td>
<td>24</td>
<td>83.7</td>
<td></td>
</tr>
<tr>
<td><em>Os</em></td>
<td>20</td>
<td>19</td>
<td>95.0</td>
<td></td>
</tr>
<tr>
<td><em>Sf</em></td>
<td>30</td>
<td>20</td>
<td>66.7</td>
<td></td>
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<tr>
<td>Total</td>
<td>222</td>
<td>179</td>
<td>80.6</td>
<td>27 31 34 31 27 29 20 23</td>
</tr>
</tbody>
</table>

No. of No. of Percent of Number of classified cases

Table 3. *Corbula (Potamocorbula)* spp. Discrimination scores using multivariate discriminant analysis among individuals from 8 localities. *Rr*: Rokkaku River Estuary; *Dr*: Dong River Estuary; *Mr*: Mangyeong River Estuary; *Gd*: Ganghwa-do; *Ml*: Maeho Lake; *Hl*: Hinuma Lake; *Os*: Obuchi Swamp; *Sf*: San Francisco Bay

- *Corbula (Potamocorbula) fasciata* Genealogy
- *Corbula (Potamocorbula) fasciata* Branch
- *Solidicorbula erythrodon* Genealogy
- *Varicorbula dissimilis* Genealogy
- 0.1 substitutions/site

Fig. 5. *Corbula (Potamocorbula)* spp. Molecular phylogenetic tree on the basis of the DNA sequences of the mitochondrial cytochrome c oxidase subunit 1 region. A filled circle on a node indicates a bootstrap value >50% and a Bayesian posterior probability of >0.90 for the respective monophyletic clade. Branch length was calculated using the maximum-likelihood method. *Rr*01 to 08: individuals from Rokkaku River Estuary; *Dr*01 to 04: Dong River Estuary; *Mr*02 to 10: Mangyeong River Estuary; *Gd*01 to 09: Ganghwa-do; *Ml*02 to 05: Maeho Lake; *Hl*01 to 04: Hinuma Lake; *Os*01 to 10: Obuchi Swamp; *Sf*02 to 13: San Francisco Bay
Ganghwa-do formed a monophyletic group, and it was a sister group of the other 7 localities. Some individuals from Rokkaku River Estuary, Mangyeong River Estuary and San Francisco Bay formed monophyletic groups (Fig. 5).

Genetic variation of the ITS2 region

Sequences of 384 to 393 bp in length were compiled for 45 individuals. They were 5 sequences from Rokkaku River Estuary, 3 from Dong River Estuary, 8 from Mangyeong River Estuary, 8 from Ganghwa-do, 4 from Maeho Lake, 4 from Hinuma Lake, 6 from Obuchi Swamp and 7 from San Francisco Bay. After the alignment, a 377 bp sequence was used for genetic analysis. Genetic variation among the sequences was found at 16 sites (4%).

The haplotype network is shown in Fig. 6, and it revealed 10 unique haplotypes forming 2 groups. The highest divergence among them was 11 bp. One group included only individuals from Ganghwa-do, and the other group was composed of the remaining individuals. In the Ganghwa-do group, 3 haplotypes were identified, and the highest divergence was 3 bp. In the group containing all the other individuals, 7 haplotypes were identified, and the highest divergence was 4 bp. One haplotype was found in the samples from 6 investigated localities, except for those from Dong River Estuary and Ganghwa-do (Fig. 6).

DISCUSSION

According to the criteria of Zhuang & Cai (1983), the samples from Rokkaku River Estuary, Mangyeong River Estuary and San Francisco Bay were identified as Corbula (Potamocorbula) amurensis, those from Ganghwa-do as a morphological type of C. (P.) laevis Hinds, 1843, those from Maeho Lake and Hinuma Lake as C. (P.) ustulata (Reeve 1844) and those from Dong River Estuary and Obuchi Swamp as C. (P.) rubromuscula (Zhuang & Cai 1983). However, Horikoshi & Okamoto (1994) identified the samples from Rokkaku River Estuary as C. (P.) cf. laevis. Tsuchida & Okamura (1997) identified the
samples from Hinuma Lake as *C. (P.) ustulata*, in agreement with Zhuang & Cai (1983), though Huber (2010) defined this species as a junior synonym of *C. (P.) nimbosa* Hanley, 1843.

On the basis of their classification, *Corbula (Potamocorbula)* spp. distributed in the waters adjacent to Japan and Korea are divided into at least 4 species. If the classification is accurate, then these groups could be indicated through the analysis of morphological and molecular characteristics. However, the investigated samples did not form any species groups, except for the group composed of samples from Ganghwa-do. In the CDA results, samples from Ganghwa-do were clearly separated from those of the other 7 localities. Among the CO1 and ITS2 sequences, which were used to analyze intra-species relationships, the greatest difference was found between the groups composed of samples from Ganghwa-do and those composed of the remaining samples. This difference was larger than the largest difference among the samples from the other 7 localities. Therefore, the samples from Ganghwa-do can be distinguished from those of the other localities on the basis of both morphological and genetic characteristics. Furthermore, the samples from Ganghwa-do inhabited the intertidal zone of a muddy sand coast. Therefore, reproductive isolation may have occurred between the Ganghwa-do population and the populations from the other localities. On the other hand, no differences in CO1 amino acid sequences, which has been frequently applied as a criterion for differences between species, were identified among any of the investigated samples. This suggests that the reproductive isolation occurred relatively recently.

Although the populations of Dong River Estuary, Mangyeong River Estuary, Maeho Lake and Obuchi Swamp are native to these places, we found no population-specific substitutions in CO1 and ITS2 regions. Further, the geographical distance between these localities would make it difficult for the populations inhabiting them to exchange genes. Thus, it may be concluded that these populations originated from a common, historically large population. In contrast, it is known that the populations of Rokkaku River Estuary, Hinuma Lake and San Francisco Bay were artificially introduced from other localities (Carlton et al. 1990, Nichols et al. 1990, Horikoshi & Okamoto 1994, Tsutsumi et al. 1997). Some individuals from Mangyeong River Estuary and Rokkaku River Estuary formed a clade with those from San Francisco Bay in the phylogenetic tree, and the samples from all the investigated localities, except for those from Dong River Estuary and Ganghwa-do, contained the same haplotype in the haplotype network. These facts suggest that the artificially introduced populations also belonged to the same historically large population. Therefore, it may be that the historical population was naturally or artificially separated and that the populations of the 7 localities were recently formed. Further, the population of Ganghwa-do may have separated from the historical population earlier than those of the other localities.

Nichols et al. (1990) and Nicolin & Penry (2000) reported that *Corbula (Potamocorbula) amurensis* is euryhaline and inhabits seawater with salinity ranging from 5 to 25‰. In addition, the populations of Rokkaku River Estuary, Mangyeong River Estuary and San Francisco Bay have been commonly shown to increase quickly after sudden environmental changes such as reclamation (Takayasu et al. 2000, Sato et al. 2001, Sato 2002, 2005, Sato & Azuma 2002, Sato & Kanazawa 2004). These facts could cause high variations in morphological characteristics. Although *Corbula (Potamocorbula)* spp. have been treated as indicators of a cool climate or brackish water in the past, the results of the present study do not support this. The smaller shells of the Ganghwa-do population might indicate a high population density, but it is not clear whether genetic or environmental factors caused the shell reduction. Therefore, *Corbula (Potamocorbula)* spp. may not be used as a paleoenvironmental indicator.

The present study showed that *Corbula (Potamocorbula)* spp. distributed in the waters adjacent to Japan and Korea are divided into 2 groups on the basis of morphological and genetic characteristics. The 2 groups are closely related genetically; however, reproductive isolation between them is possible. Hence, currently, it seems appropriate to treat them as at least 2 distinct species. The classification of the subgenus *Potamocorbula* should be re-examined at the species level.

Hallan & Willan (2010) described 2 species of genus *Lentidium* from northern Australia. *Lentidium* conspicuously resembles the subgenus *Potamocorbula* in shell morphology. Thus, *Lentidium* and *Potamocorbula* could be closely related, but further information on both morphological and genetic characteristics is needed to investigate the relationship between the 2 genera (cf. Hallan et al. 2013).
Acknowledgements. We deeply thank Emr. Prof. I. Hayami, Prof. K. Kanazawa and Prof. A. Hino (Kanagawa University) for their support of this study. We are indebted to Prof. T. Yamaguchi (Kanagawa University) and Prof. J. T. Carlton (Williams College) for valuable comments, to Dr. R. Naka-shima (AIST) for fruitful discussions and to Drs T. Haga (JAMSTEC) and J. K. Thompson (U.S. Geological Survey) for donating the samples and providing valuable comments. We are also grateful to 2 anonymous reviewers for useful comments. We acknowledge the Japan/Korea Tidal-Flats Joint Survey Group for their help in collecting the samples. This work was supported by a Grant-in-Aids for Scientific Research from the Japan Society for the Promotion of Science (19650219 and 21500861 to S.S.) and a grant from the National Institute of Biological Resources, funded by the Ministry of Environment of the Republic of Korea (NIBR No. 2013-02-001).

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Editorial responsibility: Nikolaos Schizas, Mayagüez, Puerto Rico, USA

Submitted: January 2, 2013; Accepted: September 11, 2013

Proofs received from author(s): November 1, 2013