UNIVERSITY OF COPENHAGEN

Genus-specific commensalism of the galeommatoid bivalve Koreamya arcuata (A. Adams, 1856) associated with lingulid brachiopods

Sato, Shin'ichi; Owada, Masato; Haga, Takuma; Hong, Jae-Sang; Lützen, Jørgen; Yamashita, Hiroyoshi

Published in:
Molluscan Research

Publication date:
2011

Document version
Publisher's PDF, also known as Version of record

Document license:
Unspecified

Citation for published version (APA):
Sato, S., Owada, M., Haga, T., Hong, J-S., Lützen, J., & Yamashita, H. (2011). Genus-specific commensalism of the galeommatoid bivalve *Koreamya arcuata* (A. Adams, 1856) associated with lingulid brachiopods. *Molluscan Research*, *31*(2), 95-105.

Download date: 08. apr.. 2020

Molluscan Research 31(2): 95–105
http://www.mapress.com/mr/
ISSN 1323-5818
Magnolia Press

Genus-specific commensalism of the galeommatoid bivalve *Koreamya arcuata* (A. Adams, 1856) associated with lingulid brachiopods

SHIN'ICHI SATO[1], MASATO OWADA[2], TAKUMA HAGA[3], JAE-SANG HONG[4], JØRGEN LÜTZEN[5] & HIROYOSHI YAMASHITA[6]

[1]The Tohoku University Museum, 6-3 Aoba, Aramaki, Aoba-ku, Sendai 980-8578, Japan.
Corresponding author - Email: kurosato@m.tohoku.ac.jp.
[2]Department of Biological Sciences, Kanagawa University, 2946 Tsuchiya, Hiratsuka 259-1293, Japan
[3] Marine Biodiversity Research Program, Institute of Biogeosciences, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan
[4]Department of Oceanography, Inha University, Incheon 402-751, South Korea
[5] Section of Marine Biology, Biological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
[6]Association of Conservation Malacology, 3-1-26-103 Kugenuma-Mastugaoka, Fujisawa 251-0038, Japan

Abstract

We compared shell morphology and DNA sequences of the ectosymbiotic bivalves *Koreamya* (Montacutidae) attached to two different species of inarticulate brachiopods *Lingula* collected from South Korea. There are some differences in shell morphology between *K. arcuata* (A. Adams, 1856) attached to *Lingula anatina* and *K.* sp. attached to *L. adamsi*, such as shell outline, periostracum and hinge teeth. However, there are very few differences in DNA sequences of COI and ITS1 suggesting that the two forms of *Koreamya* are genetically conspecific. While many ectosymbiotic Galeommatoidea species have been reported to live commensally with only one host species, this study suggested that *K. arcuata* lives commensally with at least two species of *Lingula* and that its shell morphology may vary according to the host species.

Key words: Galeommatoid bivalve, Ectosymbiosis, *Lingula*, Mitochondrial COI gene, Montacutidae, Nuclear ITS, Shell morphology, South Korea

Introduction

Ectosymbiotic bivalves of the superfamily Galeommatoidea have already been reported from various invertebrate hosts such as Porifera, Coelenterata, Sipunculoidea, Echiuroidea, Bryozoa, Annelida, Mollusca, Arthropoda, Brachiopoda and Echinodermata (Boss 1965; Morton and Scott 1989; Kato 1998; Lützen *et al.* 2009). However, among them, only one species, *Koreamya arcuata* (A. Adams, 1856) has been recorded living commensally with a brachiopod. The hosts of *K. arcuata* are the inarticulate brachiopods *Lingula anatina* Lamarck, 1801 from South Korea (Hong *et al.* 2007; Lützen *et al.* 2009) and the Philippines (Savazzi 2001), *L. translucida* Dall, 1921 from SE India (Fernando and Fernando 1983) and *L.* sp. from Western Australia (Lützen *et al*. 2009). However, there are no studies comparing the shell morphology of the bivalves attached to different species of *Lingula* Bruguière, 1791 or investigating their DNA sequences.

In May 2003, we found a population of *Koreamya* Lützen, Hong & Yamashita, 2009 attached to *Lingula adamsi* Dall, 1873 on the southwestern coasts of South Korea (Sato *et al*. 2004). *Koreamya* sp. attached to *L. adamsi* is very similar to *K. arcuata* attached to *L. anatina* from South Korea, but Lützen *et al*. (2009) noted that the shells of *K.* sp. are generally smaller, thinner and more rounded than those of *K. arcuata*. In the present study, we collected more specimens of *Koreamya* from South Korean tidal-flats, and compared their shell morphology in detail and their DNA sequences of mitochondrial cytochrome oxidase subunit I (COI) and nucleic internal transcribed spacer 1 (ITS1) to test whether or not two species can be recognized.

Materials and methods

Specimens of *Koreamya arcuata* attached to *Lingula anatina* (Fig. 1A) were collected from a sandy mud substatum in the middle intertidal zone of the following tidal-flats: Seondo-ri, Biin-myeon, Seocheon-gun, Chungcheongnam-do, (36° 08' 02" N, 126° 34' 36" E) (A in Fig. 2) on 3 April and 10 July 2008 (9 individuals, TUMC110962-110964); Sura, Okbong-ri, Okseo-myeon, Gunsan-si, Jeollabuk-do (35° 55' 55" N, 126° 36' 15" E) (B in Fig. 2) on 5 May, 2003 (3 individuals, JKTS 148); Geojeon, Simpo-ri, Jinbong-myeon, Gimje-si, Jeollabuk-do (35° 50' 36" N, 126° 41' 00" E) (C in Fig. 2) on 16 August 2002 and 25 September 2003 (29 individuals, TUMC110956-110958 and JKTS 141-147); Daehang-ri, Byeonsan-myeon, Buan-gun, Jeollabuk-do (35° 41' 15" N, 126° 31' 59" E) (D in Fig. 2) on 2 September 2007 (9 individuals, TUMC110959-110961); Seojeon, Hajeon-ri, Simwon-myeon, Gochang-gun, Jeollabuk-do (35° 32' 33" N, 126° 33' 54" E) (E in Fig. 2) on 27 March 2009 (3 individuals, TUMC110965); Waon, Sangnae-ri, Haeryong-myeon, Suncheon-si, Jeollanam-do (34° 51' 00" N, 127° 31' 16" E) (F in Fig. 2) on 30 April 2010 (20 individuals). Specimens of *Koreamya* sp. attached to *Lingula adamsi* (Fig. 1B) were collected from the middle to low intertidal zone of

COPYRIGHT © 2011 MALACOLOGICAL SOCIETY OF AUSTRALASIA & SOCIETY FOR THE STUDY OF MOLLUSCAN DIVERSITY

the mud tidal-flats at Woldoo, Yongjeong-ri, Hyeongyeong-myeon, Muan-gun, Jeollanam-do (35° 04' 47" N, 126° 23' 49" E) (J in Fig. 2) on 8 April 2008 (15 individuals, TUMC110966–110969). Individuals of *Lingula* spp. were dug up using a shovel at low tide, and the bivalves were removed from the shells of *Lingula* spp. and preserved in 99.5% ethanol.

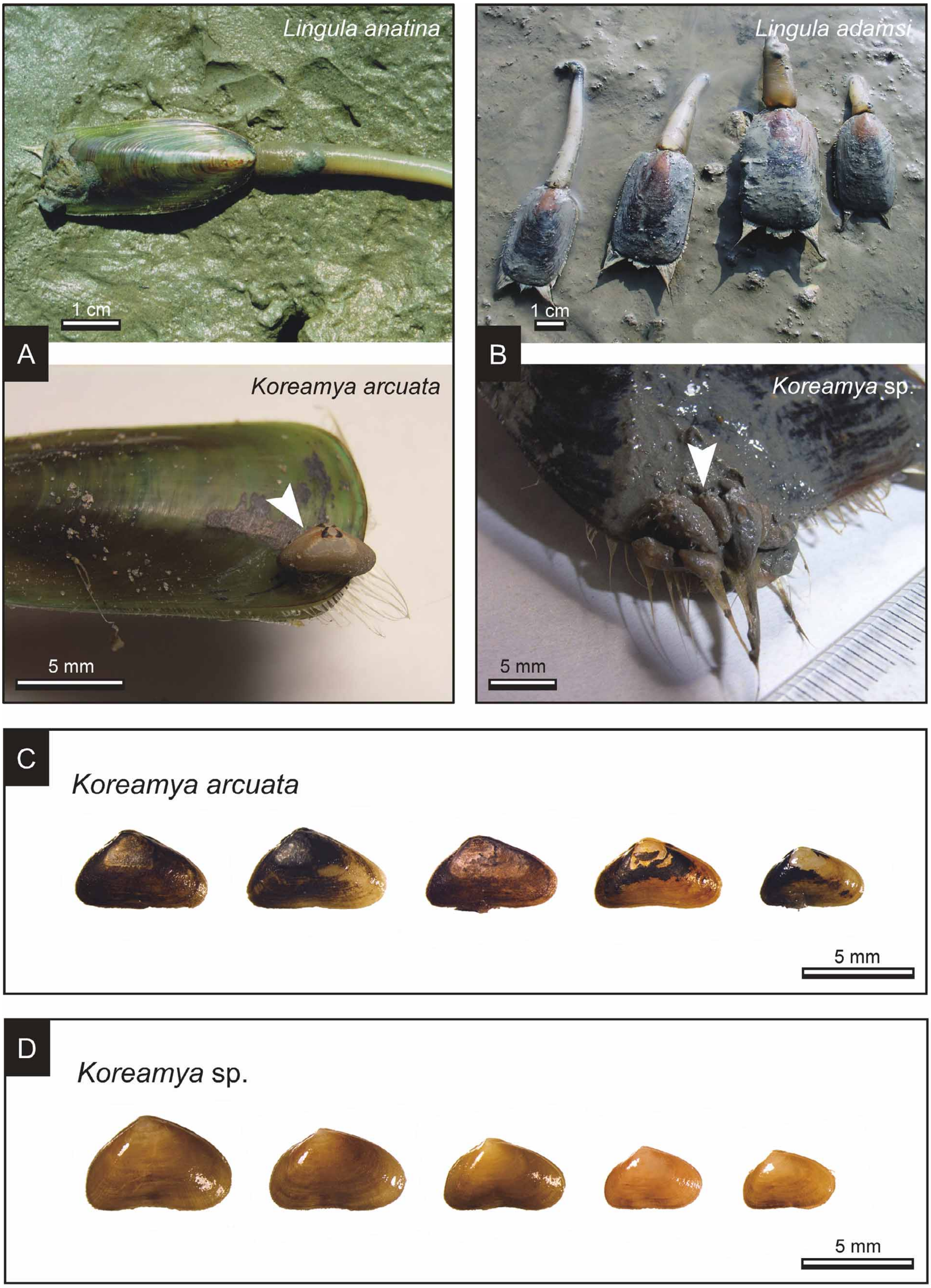

FIGURE 1. A. *Koreamya arcuata* attached to *Lingula anatina*. **B**. *Koreamya* sp. attached to *Lingula adamsi*. **C**. Shells of *Koreamya arcuata* (TUMC110962). **D.** Shells of *Koreamya* sp. (TUMC110969).

FIGURE 2. Distribution of *Koreamya* in South Korea. **A–I**. *K. arcuata*. **J**. *K.* sp. ○ present population, × extinct population. **A**. Seondo-ri. **B**. Sura, Okpong-ri. **C**. Geojeon, Simpo-ri. **D**. Daehang-ri. **E**. Seojeon, Hajeon-ri. **F**. Waon, Sangnae-ri. **G**. Gaehwa-ri. **H**. Yubu-do Island. **I**. Deokgyo-dong. **J**. Woldoo, Yongjeong-ri.

Shell height (SH) and shell length (SL) in eight individuals from Seocheon-gun (A in Fig. 2) and 12 individuals from Gimje-si (C in Fig. 2) as *Koreamya arcuata* and 14 individuals from Muan-gun (J in Fig. 2) as *K.* sp. were measured using a slide caliper (accuracy ± 0.05mm). The height of the shell anterior margin (HA, see Fig. 4) was measured using image analysis software (Scion Image ver. 1.63, available as freeware) in nine individuals from Seocheon-gun, 20 individuals from Gimje-si as *Koreamya arcuata* and 15 individuals from Muan-gun as *K.* sp. SL was analyzed with reduced major axis regression against SH, and HA were done in the same way against SL. The slopes and positions of reduced major axis regression were compared between the two forms using a significance test at 99% confidence level (Hayami and Matsukuma 1971). Nine shells coated with platinum (JEOL JFC-1600) and 11 uncoated shells were observed by scanning electron microscopes (JEOL JSM-T20, JSM-T330A or JSM-840A). We compared the shell morphology details in eight to 13 specimens of *K. arcuata* from three localities (Seocheon-gun, Gimje-si, Buan-gun) and six specimens of *K.* sp. from Muan-gun using a scanning electron microscope (SEM). The anatomy was examined using a stereoscopic microscope in five specimens of *K. arcuata* from Suncheon-si and three of *K.* sp. from Muan-gun.

TABLE 1. Amplification and sequencing primers for the COI and ITS1 regions. CO1-F and CO1-R were designed according to Matsumoto and Hayami (2000) and the others were anew. CO1-D and CO1-Dr were used only in DNA sequencing.

primer	5′ — 3′
CO1-F	ATYGGNGGNTTYGGNAAYTG
CO1-R	ATNGCRAANACNGCNCCYAT
CO1-D	TGRTTYTTYGGNCAYCCNGA
CO1-Dr	TCNGGRTGNCCRAARAAYCA
ITS1-F	GGAAGTAAAAGTCGTAACAAGG
ITS1-R	CGATGTTCAATGTGTCCTGCAAT

Total DNA was extracted from ethanol-preserved tissues of the samples of *K. arcuata* from Seocheon-gun and *K.* sp. from Muan-gun by DNeasy Blood and Tissue Kit (QIAGEN). COI and ITS1 regions were amplified by Premix Ex Taq and PCR thermal cycler PERSONAL (TaKaRa). The conditions of PCR amplification were denaturation (94 °C and 30 sec.), annealing (COI: 57 °C and 30 sec., ITS1: 58 °C and 30 sec.), extension (72 °C and 1 min.) for 25 cycles. The primers used in this study are shown in Table 1. PCR products were purified by ExoSAP-IT (GE Healthcare), and direct cycle sequencing was performed on 3130 Genetic Analyzer (ABI PRISM) in both directions using the BigDye Terminator v3.1 Cycle Sequencing Kit (ABI PRISM). These sequences were registered in the DNA Data Bank of Japan (Table 2).

TABLE 2. Accession numbers of investigated samples. TUMC110962-1 to 5: *Koreamya arcuata* from Seondo-ri, Seocheon-gun. TUMC-110969-1 to 5: *Koreamya* sp. from Woldoo, Yongjeong-ri, Muan-gun.

species	specimen	accession number	
		CO1	ITS1
Koreamya arcuata	TUMC110962-1	AB474955	AB499832
	TUMC110962-2	AB474956	AB499833
	TUMC110962-3	AB474957	AB499834
	TUMC110962-4	AB474958	AB499835
	TUMC110962-5	AB474959	AB499836
Koreamya sp.	TUMC110969-1	AB474950	AB499827
	TUMC110969-2	AB474951	AB499828
	TUMC110969-3	AB474952	AB499829
	TUMC110969-4	AB474953	AB499830
	TUMC110969-5	AB474954	AB499831

Obtained sequences were aligned by CLUSTALW (Thompson *et al*. 1997). Maximum likelihood phylogenetic analyses of the COI sequences were conducted using PAUP* 4.0 beta 10 (Swofford 1998) comprising 1,000 bootstrap replicates. Models to be used in phylogenetic analyses were estimated by using Modeltest version 3.7 (Posada and Crandall 1998), and the substitution model chosen was HKY+G. *Meretrix petechialis* (Lamarck, 1818) (accession number: EU145977) and *Ruditapes philippinarum* (Adams & Reeve, 1850) (accession number: AB244335; this study validates the genus *Ruditapes* Chiamenti, 1900 instead of *Venerupis* Lamarck, 1818) were used as the outgroup. The monophyly of *Koreamya arcuata* and *Koreamya* sp. was also tested by the SH-test (Shimodaira and Hasegawa 1999). The number of substitutions on the ITS1 sequences were also investigated.

Abbreviations: TUMC—Tohoku University Museum Collection, Sendai; JKTS—Japan/Korea Tidal Flat Joint Survey Group, Fujisawa.

Results

Distribution

In addition to the present study (see Materials and methods), *Koreamya arcuata* attached to *Lingula anatina* is recorded by Lützen *et al*. (2009) from Gaehwa-ri, Gaehwa-myeon, Buan-gun, Jeollabuk-do (35° 47’11” N, 126º 337’09” E) (G in Fig. 2), Yubu-do Island, Seocheon-gun, Chungcheongnam-do (36° 00’20” N, 126º 37’55” E) (H in Fig. 2), and Deokgyo-dong, Jung-gu, Incheon (37° 25’58” N, 126º 24’59” E) (I in Fig. 2), South Korea. Therefore, *K. arcuata* associated with *L. anatina* is now known from nine localities, i.e. eight localities along the western coast and one on the southern coast of South Korea (A-I in Fig. 2). Three of these populations (Okpong-ri, Simpo-ri, Gaehwa-ri) have subsequently been lost to the Saemangeum Reclamation Project (Hong *et al*. 2007). *Koreamya* sp. attached to *Lingula adamsi* was recorded to date from only one locality (Muan-gun) on the southwestern coast of South Korea (J in Fig. 2).

Comparison of shell morphology and anatomy

Shell outlines of both *Koreamya arcuata* and *K*. sp. are subequilateral triangular and the anterior ends are long (Fig. 1C, Fig. 3A–D). The antero-dorsal and postero-dorsal margins of *K. arcuata* are nearly straight, whilst those of *K*. sp. are rather rounded (Fig. 3 A–D). Roundness of the antero-dorsal margin reflects the height of shell anterior margin (HA in Fig. 4). The slope of reduced major axis regression in HA against SL is not significantly different between *K. arcuata* and *K*. sp. ($K = 0.88$; $p > 0.05$), but their positions (the y-intercepts of reduced major axis regression) are significantly different ($K = 2.90$; $p < 0.01$) (Fig. 4). *K. arcuata* also seems more elongate than *K*. sp. (Fig. 3A–D), however the difference between SH and SL was not statistically significant ($K = 1.68$; $p>0.05$, Fig. 5). In both forms, the posterior cardinal tooth of the right valve has a thickened spoon-like crest which on its inside is hollowed out by a shallow groove (Fig. 3G, H). However, the crest of the cardinal tooth of *K*. sp. is wider than *K. arcuata* (Fig. 3C, D, G, H). In *K. arcuata*, the anterior elongate lateral tooth of the right valve is narrow and straight, but in *K*. sp. it is rather wide and slightly curved (Fig. 3E, F).

The prodissoconch II in two specimens of *K. arcuata* measures 464 × 291 µm (SL × SH) and 610 × 362 µm (SL × SH; Fig. 6C), and one from a juvenile *K*. sp. measures 414 × 303 µm (SL × SH; Fig. 6D). The shell surface and periostracum of *K. arcuata* is heavily corroded from the umbo to the center during growth (Fig. 6A), in contrast to *K*. sp., in which corrosion was less and the periostracum covered the umbo even in the adult shell (Fig. 6B). The periostracum of *K. arcuata* is dark brownish and thick, while that of *K*. sp. is light brownish, glossy and thinner (Fig. 1). In both forms, the periostracum is ornamented with narrow discontinuous lamellae width *ca*. 20–30 µm (Fig. 6H). There are no radial ribs on the outermost shell surface, whilst many periostracal striae form a lattice pattern crossing with commarginal periostracal lamellae (Fig. 6E, F, H). The spaces between each periostracal lamella in *K. arcuata* are filled by many grains of sediment (Fig. 6G).

Gross anatomical features of *K*. sp. were identical with those of *K. arcuata* as reported by Lützen et al (2009). *K. arcuata* associated with *L. anatina* had consistently the same shell characters in all the nine surveyed populations in South Korea. Because *K*. sp. on *L. adamsi* was known from only one locality, only its intrapopulation variation could be assessed.

Analyses of DNA sequences

Sequencing of COI and ITS1 regions yielded 903 and 524 bp, respectively, from 10 investigated individuals. The heterozygosity of COI and ITS1 was not observed. In the COI sequences, there were 4–16 bp (0.4–1.7 %) nucleotide differences; the maximum number of intraform was 12 bp on Muan-gun and 14 bp on Seochon-gun, respectively, and that of interform was 16 bp. However, there were no differences between them in inferred amino acid sequences due to synonymous substitutions. In the ITS1 sequences, nucleotide differences were 0–1 bp (0–0.2 %); the maximum number of intra- and interform was 1 bp together. The maximum likelihood phylogenetic tree for the COI data showed that both *Koreamya arcuata* and *Koreamya* sp. were polyphyletic ($-\ln L = 2960.546$) (Fig. 7). However, the SH-test did not reject monophyly of each form (Δ-ln $L = 14.628$; $p > 0.05$).

Discussion

Some differences in shell morphology exist between *Koreamya arcuata* attached to *Lingula anatina* and *Koreamya* sp. attached to *L. adamsi*, such as shell outline, teeth and periostracum (Figs 1, 3, 4, 6). However, DNA sequences of COI and ITS1 revealed that there are very few differences between the two forms suggesting that *K. arcuata* and *K*. sp. are genetically similar and probably the same species (Fig. 7). If they are indeed conspecific, these findings suggest that *K. arcuata* can live commensally with two different species of *Lingula*, and the shell morphology may vary according to the host species. The shell of *Lingula adamsi* (adult dorsal shell length *ca*. 60 mm) is much larger than that of *L. anatina* (*ca*. 35 mm). The maximum dorsal shell length of the former may exceed 70 mm (Sato *et al*. 2004), and its burrow is much larger than that of *L. anatina*. Most individuals of *L. anatina* were collected from sandy mud bottom, but *L. adamsi* was only collected from mud tidal-flats. The shell morphology in *K. arcuata* may be influenced by differences between the two host species such as shell size, life history traits, and habitats.

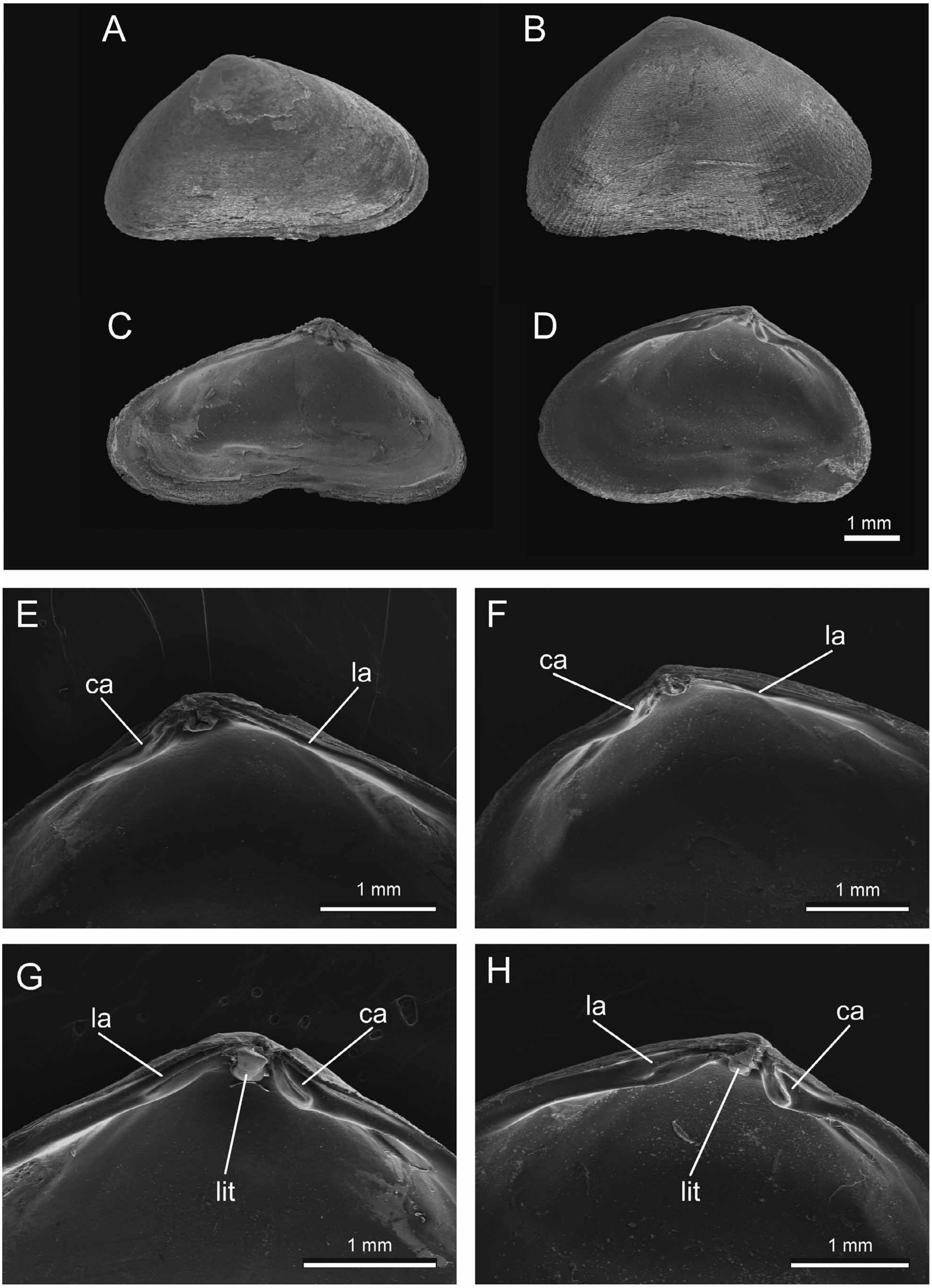

FIGURE 3. SEM images of the shell and hinge of *Koreamya*. **A**, **C**, **G**. Right valve of *Koreamya arcuata*. **E**. Left valve of *K. arcuata*. **B**, **D**, **H**. Right valve of *K.* sp. **F**. Left valve of *K.* sp. ca, cardinal tooth; la, lateral tooth; lit, lithodesma.

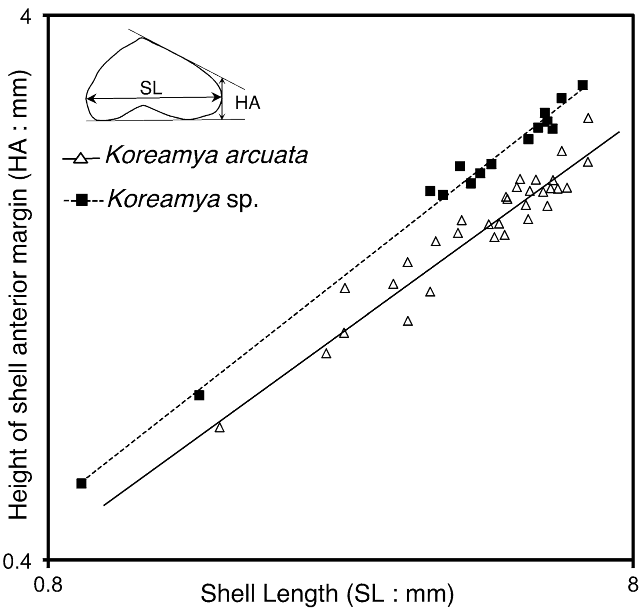

FIGURE 4. Plots of log-transformed height of shell anterior margin (HA: mm) against log-transformed shell length (SL: mm) with reduced major axis regression for *Koreamya arcuata* (HA = 0.598 $SL^{0.845}$) and *Koreamya* sp. (HA = 0.491 $SL^{0.805}$).

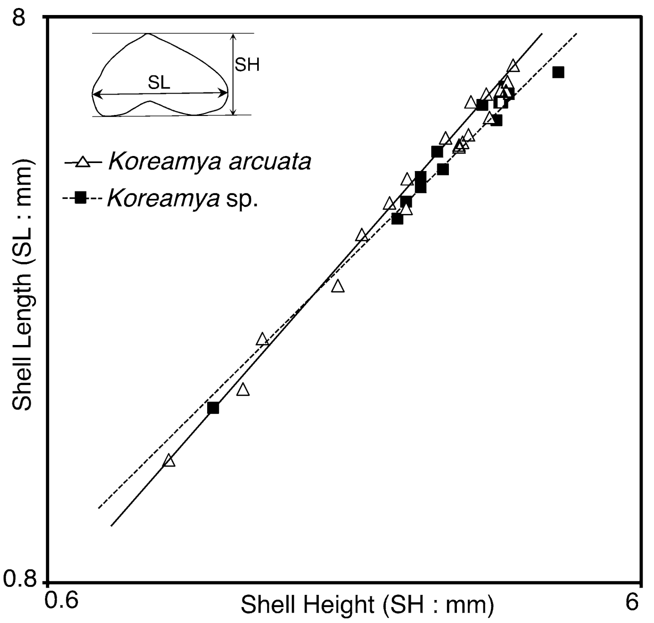

FIGURE 5. Plots of log-transformed shell length (SL: mm) against log-transformed shell height (SH: mm) with reduced major axis regression for *Koreamya arcuata* (SL = 1.380 $SH^{1.174}$) and *Koreamya* sp. (SL = 1.446 $SH^{1.089}$).

There are many ectosymbiotic species among the Galeommatoidea. Most of these are reported to live commensally with only a single host species. However, some species have been confirmed to be associated with several host species. Among the ectosymbiotic galeommatoid species collected from Japan, Korea and China, 23 species are reported to attach directly on the body or shell of only one host species, while six species (*Pseudopythina macrophthalmensis* Morton and Scott, 1989, *Montacuta echinocardiophila* Habe, 1964, *Koreamya arcuata*, *Nipponomysella subtruncata* (Yokoyama, 1922), *Peregrinamor ohshimai* Shoji, 1938 and *Curvemysella paula* (Adams, 1856)) have been demonstrated to live with several species (Table 3). One of these species, *N. subtruncata*, has been reported to live with two different host species, *Siphonosoma cumanense* (Keferstein, 1867) and *Sipunculus nudus* Linnaeus, 1766, but the latter is now considered a misidentification of *S. cumanense*. For example, Habe (1970) misidentified *S. cumanense* as *S. nudus* in his Plate 1, and subsequent authors have followed the misidentification (Table 3). The host of *N. subtruncata* in the figures of Matsukuma (2000), Hamamura (2004) and Aichi Environmental Research Center (2009) are identified as *S. cumanense*, but there is no photographic evidence of *N. subtruncata* living commensally with *S. nudus* in the literature. *N. subtruncata* living commensally with *S. cumanense* has been found from six localities in Japan (Hiroshima, Yamaguchi, Oita, Saga, Kumamoto and Okinawa Prefectures; H. Yamashita, unpublished data).

Three species (*Ps. macrophthalmensis*, *Pe. ohshimai* and *K. arcuata*) are now known to live commensally with multiple host species belonging to the same genus (*Macrophthalmus* Desmarest, 1823, *Upogebia* Borradaile, 1903, and *Lingula*, respectively). The present study has revealed that *K. arcuata* is in a genus-specific commensal relationship with *Lingula anatina* (Savazzi 2001; Lützen *et al*. 2009), *L. adamsi* (the present study), and most probably with *L. translucida* (Fernando and Fernando 1983) and *L.* sp. (Lützen *et al*. 2009). *K. arcuata* is, however, exceptional in that it is the only ectosymbiotic galeommatoid species in which shell morphology is known to differ between populations from the different host species.

Acknowledgments

We are grateful to Mr. Kyung-Won Kim, Mr. Dong-Pil Oh, Mr. Kil-Wook Yoe, Mr. Yung-Ki Ju, Mr. Hidemi Osada and Ms. Yae Mizuma, as well as members of the Japan/Korea Tidal-flats Joint Survey Group, for their help in collecting samples and for photographs. We also thank Dr. Teruaki Nishikawa for his valuable advice and two anonymous reviewers and Dr. Winston F. Ponder for helpful comments and suggestions that improved the manuscript. This work was supported by the Toyota Foundation, Takagi Fund for Citizen Science, Heiwa Nakajima Foundation, Suncheon City and Grant-in-Aids for Scientific Research from the Japan Society for the Promotion of Science (No. 15740308, 19650219 and 21500861 for S.S.).

References

Aichi Environmental Research Center (Ed.) (2009) *Threatened Wildlife of Aichi Prefecture, Red Data Book Aichi 2009, Animals*. Department of the Environment, Aichi Prefectural Government, Aichi (in Japanese).

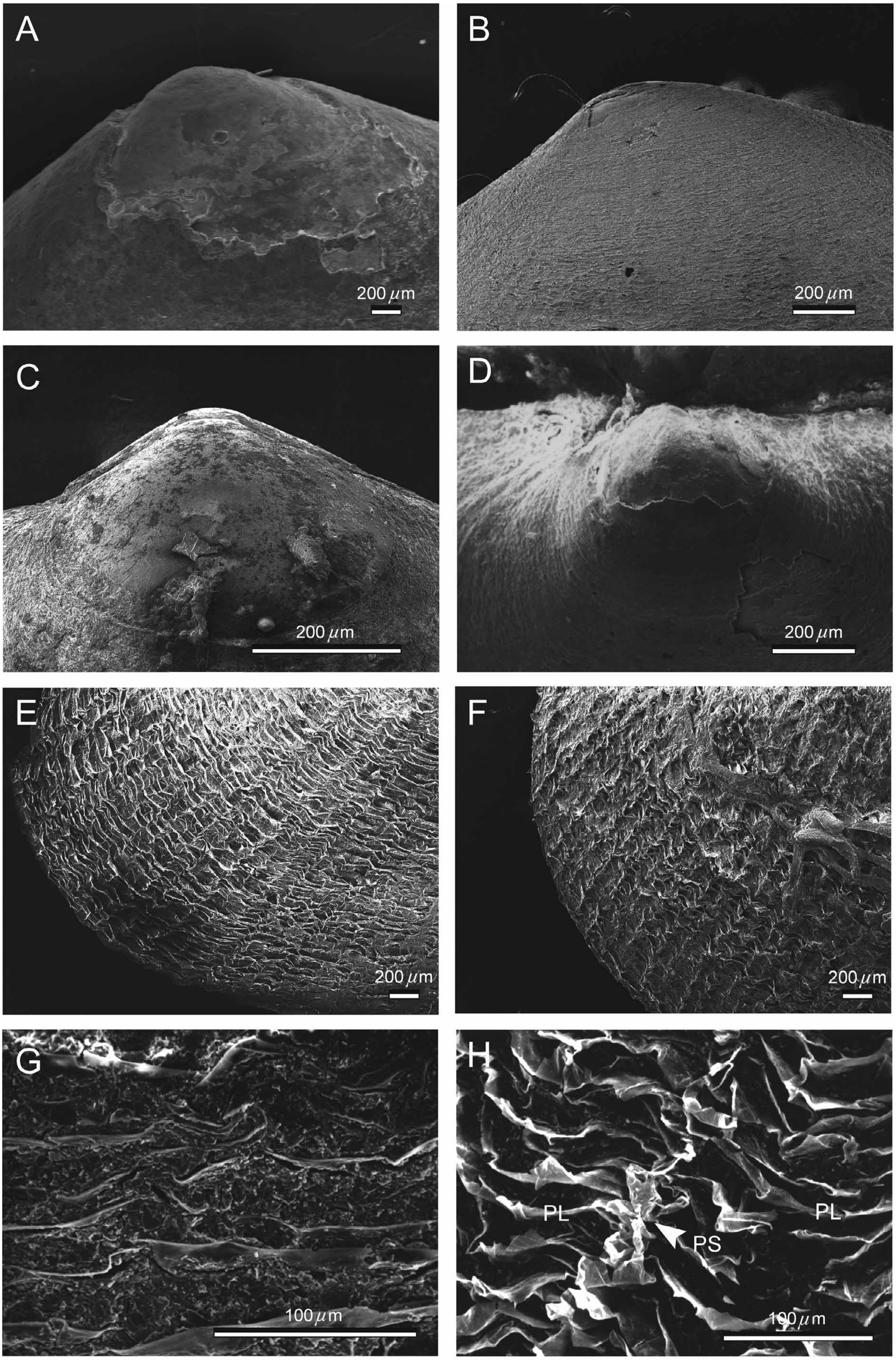

FIGURE 6. SEM images of the shell and prodissoconch of *Koreamya*. **A**, **C**, **E**, **G**. *Koreamya arcuata*. **B**, **D**, **F**, **H**. *K*. sp. **A, B, C, D**. Umbo and prodissoconch of right valve. **E, F, G, H**. Periostracum. PL, periostracal lamella; PS, periostracal stria.

TABLE 3. Partial list of ectosymbiotic galeommatoid species and their hosts recorded from Japan, Korea and China.

Galeommatoid bivalve		Host animal			References
Family	species	No. of Host species	species	taxon	
Lasaeidae	*Litigiella pacifica* Lützen & Kosuge, 2006	1	*Sipunculus nudus* Linnaeus, 1799	Sipuncula	Lützen & Kosuge 2006
Lasaeidae	*Salpocola philippinensis* Habe & Kanazawa, 1981	1	*Sipunculus nudus* Linnaeus, 1799	Sipuncula	Habe & Kanazawa 1981; Kosuge & Kubo 2002; Lützen *et al*. 2008
Leptonidae	*Arthritica japonica* Lützen & Takahashi, 2003	1	*Xenophthalmus pinnotheroides* White, 1846	Arthropoda	Lützen & Takahashi 2003
Kellidae	*Pseudopythina ariakensis* (Habe, 1959)	1	*Protankyra bidentata* (Woodward & Barrett, 1858)	Echinodermata	Morton & Scott 1989
Kellidae	*Pseudopythina macrophthalmensis* Morton & Scott, 1989	6	*Macrophthalmus latreillei* (Desmarset, 1822)	Arthropoda	Morton & Scott 1989; Bernard *et al*. 1993; Higo *et al*. 1999
			Macrophthalmus convexus Stimpson, 1898	Arthropoda	Kosuge & Itani 1994; Jespersen *et al*. 2001
			Macrophthalmus milloti Crosnier, 1965	Arthropoda	Kosuge 2005
			Macrophthalmus brevis (Herbst, 1804)	Arthropoda	Kosuge 2005
			Macrophthalmus serenei Takeda & Komai, 1991	Arthropoda	Hayase *et al*. 2009
			Macrophthalmus telescopicus (Owen, 1839)	Arthropoda	Yamashita *et al*. 2005
Kellidae	*Pseudopythina maipoensis* Morton & Scott, 1989	1	*Discapseudes* sp.	Arthropoda	Morton & Scott 1989; Bernard *et al*. 1993
Kellidae	*Pseudopythina nodosa* Morton & Scott, 1989	1	*Sipunculus nudus* Linnaeus, 1799	Sipuncula	Morton & Scott 1989
Kellidae	*Pseudopythina ochetostomae* Morton & Scott, 1989	1	*Ochetostoma erythrogrammon* Leuckart and Rüppell, 1828	Echiura	Morton & Scott 1989; Bernard *et al*. 1993; Jespersen *et al*. 2002
Kellidae	*Pseudopythina tsurumaru* (Habe, 1959)	1	*Protankyra bidentata* (Woodward & Barrett, 1858)	Echinodermata	Morton & Scott 1989; Lützen *et al*. 2004
Kellidae	*Pseudopythina subsinuata* (Lischke, 1871)	1	*Squilla oratoria* De Haan, 1844	Arthropoda	Habe 1977; Morton & Scott 1989; Higo & Goto 1993; Bernard *et al*. 1993; Higo *et al*. 1999; Jespersen *et al*. 2009; Yamashita unpubilshed data
Montacutidae	*Barrimysia siphonosomae* Morton & Scott, 1989	1	*Siphonosoma cumanense* (Keferstein, 1867)	Sipuncula	Morton & Scott 1989; Bernard *et al*. 1993; Jespersen *et al*. 2002
Montacutidae	*Brachiomya stigmatica* (Pilsbry, 1921)	1	*Brissus latecarinatus* (Leske, 1778)	Echinodermata	Yamamoto & Habe 1974; Ishikawa 1979; Higo & Goto 1993; Higo *et al*. 1999; Matsukuma 2000
Montacutidae	*Curvemysella paula* (Adams, 1856)	2	*Diogenes edwarsii* (De Haan, 1849)	Arthropoda	Morton & Scott 1989; Tanaka 1991; Goto *et al*. 2007
			Spiropagurus spiriger (De Haan, 1849)	Arthropoda	Goto *et al*. 2007
Montacutidae	*Devonia semperi* (Ohshima, 1930)	1	*Protankyra bidentata* (Woodward et Barrett, 1858)	Echinodermata	Ohshima 1930; Habe 1977; Higo & Goto 1993; Bernard *et al*. 1993; Higo *et al*. 1999
Montacutidae	*Anisodevonia oshimai* (Kawahara, 1942)	1	*Leptosynapta ooplax* (von Marenzeller, 1882)	Echinodermata	Kawahara 1942; Habe 1977; Higo & Goto 1993; Kato 1998; Higo *et al*. 1999; Lützen *et al*. 2005
Montacutidae	*Entovalva lessonothuriae* Kato, 1998	1	*Holothuria* (*Lessonothuria*) *pardalis* Selenka, 1867	Echinodermata	Kato 1998; Lützen *et al*. 2005
Montacutidae	*Fronsella ohshimai* Habe, 1958	1	*Sipunculus nudus* Linnaeus, 1799	Sipuncula	Habe 1958, 1977; Higo & Goto 1993; Higo *et al*. 1999

Table 3. continued.

Galeommatoid bivalve		Host animal			References
Family	species	No. of Host species	species	taxon	
Montacutidae	*Koreamya arcuata* (A. Adams, 1856)	4	*Lingula anatina* (Lamarck, 1801)	Brachiopoda	Hong *et al*. 2007; Lützen *et al*. 2009; the present study
			Lingula adamsi Dall, 1873	Brachiopoda	Sato *et al*. 2004; Lützen *et al*. 2009; the present study
			Lingula translucida Dall, 1920	Brachiopoda	Fernando & Fernando 1983
			Lingula sp.	Brachiopoda	Lützen *et al*. 2009
Montacutidae	*Montacuta divaricata* Gould, 1861	1	*Schizaster lacunosus* (Linnaeus, 1758)	Echinodermata	Habe 1977; Higo & Goto 1993; Higo *et al*. 1999
Montacutidae	*Montacuta echinocardiophila* Habe, 1964	2	*Echinocardium cordatum* (Pennant, 1777)	Echinodermata	Habe 1964, 1977; Higo & Goto 1993; Higo *et al*. 1999; Matsukuma 2000
			Lovenia elongata (Gray, 1845)	Echinodermata	Komatsu 1986; Higo & Goto 1993; Higo *et al*. 1999
Montacutidae	*Montacutona mutsuwanensis* Yamamoto & Habe, 1959	1	*Cerianthus filiformis* Carlgren, 1893	Cnidaria	Bernard *et al*. 1993; Higo *et al*. 1999
Montacutidae	*Nipponomontacuta actinariophila* Yamamoto & Habe, 1961	1	*Halcampella maxima* Hertwig, 1888	Cnidaria	Yamamoto & Habe 1961; Habe 1973, 1977; Higo & Goto 1993; Matsukuma 2000
Montacutidae	*Nipponomysella oblongata* (Yokoyama, 1922)	1	*Ophioplocus japonicus* H. L. Clark, 1911	Echinodermata	Yamamoto & Habe 1959; Habe 1977; Higo & Goto 1993; Higo *et al*. 1999; Matsukuma 2000
Montacutidae	*Nipponomysella subtruncata* (Yokoyama, 1927)	2	*Sipunculus nudus* Linnaeus, 1799	Sipuncula	Habe 1970, 1977; Oyama 1973; Higo & Goto 1993; Higo *et al*. 1999; Matsukuma 2000
			Siphonosoma cumanense (Keferstein, 1867)	Sipuncula	Inaba 1982; Higo & Goto 1993; Higo *et al*. 1999; Lützen *et al*. 2001b; Hamamura 2004; Aichi Environmental Research Center 2009
Montacutidae	*Peregrinamor gastrochaenans* Kato & Itani, 2000	1	*Upogebia carinicauda* (Stimpson, 1860)	Arthropoda	Kato & Itani 2000; Itani 2002
Montacutidae	*Peregrinamor ohshimai* Shoji, 1938	6	*Upogebia major* (de Haan, 1841)	Arthropoda	Shoji 1938; Higo & Goto 1993; Bernard *et al*. 1993; Sakai *et al*. 1995; Kato & Itani 1995, 2000; Higo *et al*. 1999; Lützen *et al*. 2001a; Itani *et al*. 2002
			Upogebia issaeffi (Balss, 1913)	Arthropoda	Horikoshi 1994 (in Sakai *et al*. 1995); Sakai *et al*. 1995; Higo *et al*. 1999; Kato & Itani 2000
			Upogebia natutensis Sakai, 1986	Arthropoda	Kato & Itani 2000; Itani 2002
			Upogebia yokoyai Makarov, 1938	Arthropoda	Horikoshi 1994 (in Sakai *et al*. 1995); Kato & Itani 2000; Itani 2002
			Upogebia pugnax de Man, 1905	Arthropoda	Itani 2002
			Upogebia trispinosa Sakai, 1991	Arthropoda	Horikoshi 1994 (in Sakai *et al*. 1995)
Montacutidae	*Tellimya torishimensis* Callomon, 1999	1	*Lovenia*	Echinodermata	Okutani 1962; Higo *et al*. 1999
Galeommatidae	*Sagamiscintilla thalassemicola* (Habe, 1962)	1	*Anelassorhynchus mucosus* (Ikeda, 1904)	Echiura	Habe 1962, 1977; Higo & Goto 1993; Higo *et al*. 1999
Galeommatidae	*Scintillona brissae* Morton & Scott, 1989	1	*Brissus latecarinatus* (Leske, 1778)	Echinodermata	Morton & Scott 1989; Bernard *et al*. 1993

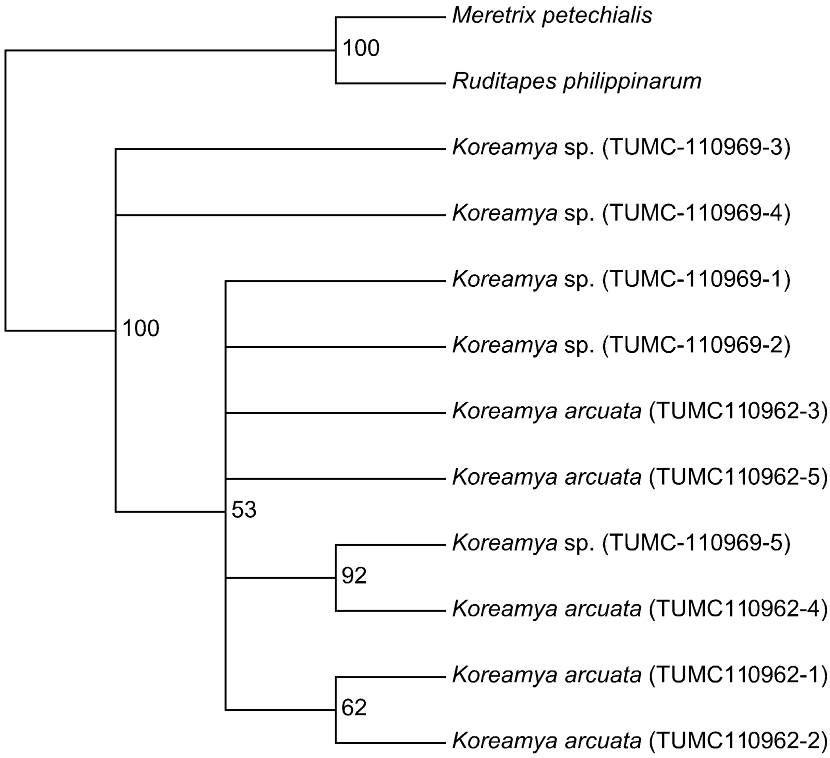

FIGURE 7. Maximum likelihood phylogenetic tree of *Koreamya arcuata* and *Koreamya* sp. inferred from COI sequence data. The numbers on the nodes indicate the bootstrap value.

Bernard, F.R., Cai, Y.Y. & Morton, B. (1993) *Catalogue of the Living Marine Bivalve Molluscs of China*. Hong Kong University Press, Hong Kong.

Boss, K.J. (1965) Symbiotic erycinacean bivalves. *Malacologia* 3, 183–195.

Fernando, S.A. & Fernando, O.J. (1983) Association of *Pythina arcuata*, Adams 1856, an erycinid bivalve with *Lingula translucida* Dall, 1921, from Indian waters. *Current Science* 52, 940.

Goto, R., Hamamura, Y. & Kato, M. (2007) Obligate commensalism of *Curvemysella paula* (Bivalvia: Galeommatidae) with hermit crabs. *Marine Biology* 151, 1615–1622.

Habe, T. (1958) Descriptions of five new bivalves from Japan. *Venus* 20, 173–180.

Habe, T. (1962) *Achasmea thalassemicola* sp. nov., a new commensal bivalve found in an echiuroid, *Thalassema mucosum* Ikeda. *Venus* 22, 117–119.

Habe, T. (1964) Two commensal bivalves from the west coast of Kyushu, Japan. *Venus* 23, 137–139.

Habe, T. (1970) Sujihoshimushi-no-yadorigai. *Chiribotan* 6, Pl. 1 (in Japanese).

Habe, T. (1973) *Halcampella maxima* Hertwig, host of *Nipponomontacuta actinariophila* Yamamoto & Habe. *Venus* 31, 157 (in Japanese).

Habe, T. (1977) *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda*. Hokuryukan, Tokyo (in Japanese).

Habe, T. & Kanazawa, T. (1981) A new commensal bivalve from the Philippines (Montacutidae). *Venus* 40, 123–125.

Hamamura, H. (2004) *Marine mollusks in the Geinan provinces*. Ranto Cultural Promotion Foundation, Hiroshima (in Japanese).

Hayami, I. & Matsukuma, A. (1971) Mensuration of fossils and statistics -Analysis of allometry and variation. *Memoirs of the Faculty of Science, Kyūsyū University. Series D, Geology* 10, 135–160 (in Japanese with English abstract).

Hayase, Y., Ueno, S., Matsunaga, Y. & Shakema, T. (2009) New distribution record of *Pseudopythina macrophthalmensis* Morton & Scott, 1989 from northern part of Suruga Bay, Kuzura, Numazu City, Shizuoka Prefecture, central Japan. *Chiribotan* 40, 15–19 (in Japanese).

Higo, S., Callomon, P. & Goto, Y. (1999) *Catalogue and bibliography of the marine shell-bearing mollusca of Japan. Gastropoda, Bivalvia, Polyplacophora, Scaphopoda*. Elle Scientific Publications, Osaka.

Higo, S. & Goto, Y. (1993) *A systematic of molluscan shells from the Japanese Islands and the adjacent area*. Elle Scientific Publications, Osaka (in Japanese).

Hong, J.S., Yamashita, H. & Sato, S. (2007) The Saemangeum Reclamation Project in South Korea threatens to collapse a unique mollusk, ectosymbiotic bivalve species attached to the shell of *Lingula anatina*. *Plankton & Benthos Research* 2, 70–75.

Inaba, A. (1982) *Molluscan fauna of the Seto Inland Sea, Japan*. Hiroshima shell Club, Hiroshima (in Japanese).

Ishikawa, H. (1979) Notes on the ecological observation of *Scintillona stigmatica* (Pilsbry, 1921) (Bivalvia, Montacutidae). *Nanki Seibutsu* 21, 115–116 (in Japanese).

Itani, G. (2002) Distribution and host specificity of two species of *Peregrinamor* symbiotic with upogebiid shrimps. *Venus* 61, 114 (in Japanese).

Itani, G., Kato, M. & Shirayama, Y. (2002) Behaviour of the shrimp ectosymbionts, *Peregrinamor ohshimai* (Mollusca: Bivalvia) and *Phyllodurus* sp. (Crustacea: Isopoda) through host ecdyses. *Journal of the Marine Biological Association of the United Kingdom* 82, 69–78.

Jespersen, Å., Kosuge, T. & Lützen, J. (2001) Sperm dimorphism and spermatozeugmata in the commensal bivalve *Pseudopythina macrophthalmensis* (Galeommatoidea, Kelliidae). *Zoomorphology* 120, 177–189.

Jespersen, Å., Lützen, J. & Itani, G. (2009) Sperm structure and sperm transfer in *Pseudopythina subsinuata* (Bivalvia; Galeommatoidea). *Zoologischer Anzeiger* 248, 57–67.

Jespersen, Å., Lützen, J. & Morton, B. (2002) Ultrastructure of dimorphic sperm and seminal receptacle in the hermaphrodites *Barrimysia siphonosomae* and *Pseudopythina ochetostomae* (Bivalvia, Galeommatoidea). *Zoomorphology* 121, 159–172.

Kato, M. (1998) Morphological and ecological adaptations in montacutid bivalves endo- and ecto-symbiotic with holothurians. *Canadian Journal of Zoology* 76, 1403–1410.

Kato, M. & Itani, G. (1995) Commensalism of a bivalve, *Peregrinamor ohshimai*, with a thalassinidean burrowing shrimp, *Upogebia major*. *Journal of the Marine Biological Association of the United Kingdom* 75, 941–947.

Kato, M. & Itani, G. (2000) *Peregrinamor gastrochaenans* (Bivalvia: Mollusca), a new species symbiotic with the thalassinidean shrimp *Upogebia carinicauda* (Decapoda: Crustacea). *Species Diversity* 5, 309–316.

Kawahara, T. (1942) On *Devonia ohshimai* sp. nov., a commensal bivalve attached to the Synaptid *Leptosynapta ooplax*. *Venus* 11, 153–164 (in Japanese with English abstract).

Komatsu, S. (1986) Shells of the surroundings of Mukaishima Island, the Inland Sea of Japan (I). *Chiribotan* 17, 36–37 (In Japanese).

Kosuge, T. (2005) Seasonal changes in the number and size frequency distributions of the crab-associated bivalve *Pseudopythina macrophthalmensis* (Bivalvia: Galeommatoidea) from *Macrophthalmus milloti* (Brachyura: Ocypodidae) in Ishigaki Island, Okinawa, Japan. *The Biological Magazine, Okinawa* 43, 21–25 (in Japanese with English abstract).

Kosuge, T. & Itani, G. (1994) A record of the crab associated bivalve, *Pseudopythina macrophthalmensis* from Iriomote Island, Okinawa, Japan. *Venus* 53, 241–244.

Kosuge, T. & Kubo, H. (2002) Records of the sipunculid-associated bivalve *Fronsella philippinensis* from the Ryukyu Islands, southwestern Japan. *Chiribotan* 33, 41–46 (in Japanese with English abstract).

Lützen, J., Hong, J.S. & Yamashita, H. (2009) *Koreamya arcuata* (A. Adams, 1856) gen. nov. (Galeommatoidea; Montacutidae), a commensal bivalve associated with the inarticulate brachiopod *Lingula anatina*. *Journal of Conchology* 39, 669–679.

Lützen, J., Jespersen, Å., Takahashi, T. & Kai, T. (2004) Morphology, structure of dimorphic sperm, and reproduction in the hermaphroditic commensal bivalve *Pseudopythina tsurumaru* (Galeommatoidea: Kellidae). *Journal of Morphology* 262, 407–420.

Lützen, J., Kato, M., Kosuge, T. & O'Foighil, D.O. (2005) Reproduction involving spermatophores in four bivalve genera of the superfamily Galeommatoidea commensal with holothurians. *Molluscan Research* 25, 99–112.

Lützen, J. & Kosuge, T. (2006) Description of the bivalve *Litigiella pacifica* n. sp. (Heterodonta: Galeommatoidea: Lasaeidae), commensal with the sipunculan *Sipunculus nudus* from the Ryukyu Islands, Japan. *Venus* 65, 193–202.

Lützen, J., Kosuge, T. & Jespersen, Å. (2008) Morphology of the Bivalve *Salpocola philippinensis* (Habe & Kanazawa, 1981) n. gen. (Galeommatoidea: Lasaeidae), a commensal with the Sipunculan *Sipuinculus nudus* from Cebu Island, the Philippines. *Venus* 66, 147–159.

Lützen, J., Sakamoto, H., Taguchi, A. & Takahashi, T. (2001a) Reproduction, dwarf males, sperm dimorphism, and life cycle in the commensal bivalve *Peregrinamor ohshimai* Shoji (Heterodonta: Galeommatoiedea: Montacutidae). *Malacologia* 43, 313–325.

Lützen, J. & Takahashi, T. (2003) *Arthritica japonica*, sp. nov. (Bivalvia: Galeommatoidea: Leptonidae), a commensal with the pinnotherid crab *Xenophthalmus pinnotheroides* White, 1846. *The Yuriyagai: Journal of the Malacozoological Association of Yamaguchi* 9, 11–20.

Lützen, J., Takahashi, T. & Yamaguchi, T. (2001b) Morphology and reproduction of *Nipponomysella subtruncata* (Yokoyama), a galeommatoidean bivalve commensal with the sipunculan *Siphonosoma cumanense* (Keferstein) in Japan. *Journal of Zoology* 254, 429–440.

Matsukuma, A. (2000) Superfamily Galeommatacea. In: Okutani, T. (Ed.), *Marine Mollusks in Japan*. Tokai University Press, Tokyo, pp. 937–941 (in Japanese).

Matsumoto, M. & Hayami, I. (2000) Phylogenetic analysis of the family Pectinidae (Bivalvia) based on mitochondrial cytochrome c oxidase subunit 1. *Journal of Molluscan Studies* 66, 477–488.

Morton, B. & Scott, P.H. (1989) The Hong Kong Galeommatacea (Mollusca: Bivalvia) and their hosts, with descriptions of new species. *Asian Marine Biology* 6, 129–160.

Ohshima, H. (1930) Preliminary note on *Entovalva semperi* sp. nov., a commensal bivalve living attached to the body of a synaptid. *Annotationes zoologicae Japonenses* 13, 25–27.

Okutani, T. (1962) Report on the archibenthal and abyssal lamellibranchiate mollusca mainly collected from Sagami Bay and adjacent waters by the R. V. Soyo-Maru during the years 1955–1960. *Bulletin of the Tokai Regional Fisheries Research Laboratory* 32, 1–40.

Oyama, K. (1973) Revision of Matajiro Yokoyama's type mollusca from the tertiary and quaternary of the Kanto area. *Paleontologial Society of Japan, Special papers* 17, 1–148.

Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* 14, 817–818.

Sakai, K., Maeda, S. & Hayashi, K. (1995) A remarkable commensal bivalve, *Peregrinamor ohshimai* (Gaimardiidae, Pelecypoda) attached to two upogebiids, *Upogebia major* and *U. issaeffi* (Thalassinidea, Decapoda, Crustacea) from Tachibana Inlet, Tokushima. *Bulletin of Shikoku University ser. B.* 4, 45–50 (in Japanese with English abstract).

Sato, S., Endo, K. & Yamashita, H. (2004) Morphological and genetic comparisons of *Lingula adamsi* Dall, 1873 from South Korea and Japan. *Japanese Journal of Benthology* 59, 14–19 (in Japanese with English abstract).

Savazzi, E. (2001) A review of symbiosis in the Bivalvia, with special attention to macrosymbiosis. *Paleontological Research* 5, 55–73.

Shimodaira, H. & Hasegawa, M. (1999) Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* 16, 1114–1116.

Shoji, K. (1938) A new commensal bivalve attached to a burrowing shrimp. *Venus* 8, 119–128.

Swofford, D. (1998) *PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Sinauer Associates, Sunderland, Massachusetts.

Tanaka, T. (1991) Symbiotic state of *Curvemysella paula* (A. Adams). *Chiribotan* 21, 82–84 (in Japanese).

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* 24, 4876–4882.

Yamamoto, G. & Habe, T. (1959). Fauna of shell-bearing mollusks in Mutsu Bay. Lamellibranchia (2). *The Bulletin of the Marine Biological Station of Asamushi* 9, 85–122.

Yamamoto, T. & Habe, T. (1961) *Nipponomontacuta actinariophila* gen. et sp. nov., a new commensal bivalve of the sea anemone. *Publications of the Seto Marine Biological Laboratory* 9, 265–266.

Yamamoto, T. & Habe, T. (1974) *Scintillona stigmatica* (Pilsbry) new to Japan. *Venus* 33, 116 (in Japanese with English abstract).

Yamashita, H., Kurozumi, T., Osuga, K., Nawa, J., Osada, H., Maekawa, S. & Kaihatsu, N. (2005) Discovery of some rare molluscan species from the Awase Tidal-flat and the present condition of conservation measure. *Venus* 64, 71 (in Japanese).