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Worm-riding clam: description of *Montacutona sigalionidcola* sp. nov. (Bivalvia: Heterodonta: Galeommatidae) from Japan and its phylogenetic position

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Abstract

A new galeommatid bivalve, *Montacutona sigalionidcola* **sp. nov.**, is described from an intertidal flat in the southern end of the Kii Peninsula, Honshu Island, Japan. Unlike other members of the genus, this species is a commensal with the burrowing scale worm *Pelogenia zeylanica* (Willey) (Annelida: Sigalionidae) that lives in fine sand sediments. Specimens were always found attached to the dorsal surface of the anterior end of the host body. This species has a ligament lithodesma between diverging hinge teeth, which is characteristic of *Montacutona* Yamamoto & Habe. However, it is morphologically distinguished from the other members of this genus in having elongate-oval shells with small gape at the posteroventral margin and lacking an outer demibranch. Molecular phylogenetic analysis based on the four-gene combined dataset (18S + 28S + H3 + COI) indicated that this species is monophyletic with *Montacutona, Nipponomontacuta* Yamamoto & Habe and *Koreamya* Lützen, Hong & Yamashita, which are commensals with sea anemones or *Lingula* brachiopods. This result suggests that host shifting across different phyla occurred at least twice in this clade.

Key words: ectocommensal, Galeommatoidea, host shift, polychaete, scale worm, Sigalionidae, symbiosis

Introduction

The Galeommatidae *sensu* Ponder, 1998 is the most species-rich bivalve family, comprising about 620 described species and numerous undescribed species (Huber 2015). This family contains small to minute bivalves and exhibits high species diversity especially in tropical warm shallow waters (Bouchet *et al.* 2002; Paulay 2003; Lützen & Nielsen 2005). Many of them are commensals that live attached to host body surface or host burrow wall (Boss 1965; Morton & Scott 1989). The host taxa of the galeommatids are highly diverse as a whole, including crustaceans, annelids, echinoderms, cnidarians and brachiopods, although each galeommatid generally has high host specificity to particular host taxa (Boss 1965; Morton 1988; Morton & Scott 1989; Goto *et al.* 2012, 2014, 2018; Li *et al.* 2012).

Polychaetes are ones of the major host groups for galeommatids. *Neaeromya rugifera* (Carpenter, 1864) occurs in the respiratory cavity of the scale worm *Aphrodita* spp., although it also occurs on the ventral surface of the mud shrimp *Upogebia pugettensis* (Dana, 1852) (Narchi 1969; Ó Foighil 1985; Li & Ó Foighil 2012). *Aligena elevata* (Stimpson, 1851) lives attached to the lower end of the tube of the bamboo worm *Clymenella torquata* (Leidy, 1855) (Gage 1968). *Kurtiella bidentata* (Montagu, 1803) has been collected from the burrows of the polychaetes, *Perinereis cultrifera* (Grube, 1840) and *Nereis irrorata* (Malmgren, 1867), although this species is also collected from burrows of various invertebrates (see the review of Ockelmann & Muus 1978). *Montacuta* sp. lives attached to the tube of the polychaete *Eunereis longissima* (Johnston, 1840) (Anthony 1916). *Kurtiella tumida* (Carpenter, 1864) lives within the exhalant halo of the host *Mesochaetopterus taylori* Potts, 1914 (Sendall *et al.* 1995). *Orobitella floridana* (Dall, 1899) and *Aligena* sp. are associated with the polychaete *Americonuphis magna* (Andrews, 1891) (Fox 1979). Two undescribed species were recorded as commensals with the polychaetes, *Notomastus lobatus* Hartman, 1947 and *Lepidasthenia varia* Treadwell, 1917, respectively, in the southeastern coast of the United States (Fox 1979; Ruppert & Fox 1988).

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An undescribed galeommatid species is known to live attached to the body surface of the scale worm *Pelogenia zeylanica* (Willey, 1905) (Annelida: Sigalionidae), which burrows in fine sand sediments, in Kii and Boso Peninsulas, Honshu Island, Japan (Otani *et al.* 2005; Yanagi 2018). This species was tentatively assigned to the genus *Nipponomysella* Yamamoto & Habe, 1959 (Otani *et al.* 2005), although it has not been described yet.

In this study, we described this species as *Montacutona sigalionidcola* **sp. nov.** based on the four specimens newly collected in Kamiura Beach, Kushimoto, Kii Peninsula, Japan. In addition, we performed molecular phylogenetic analyses to understand how a symbiotic association with *Pelogenia* Schmarda, 1861 evolved in Galeommatidae.

Materials and methods

Sampling and study sites. Field observations and sampling of galeommatids ectocommensal with *Pelogenia zeylanica* were made in Kamiura Beach, Kushimoto, Kii Peninsula, Japan (Figs. 1, 2), between 2000 to 2017. One additional observation was made at Tsubaki, Shirahama, Kii Peninsula, Japan (Fig. 1). We dug the soft sand sediments in the tidepool to about 20–50 cm in depth by using scoop shovels in order to collect *P. zeylanica*. If *P. zeylanica* harbored ectocommensal galeommatids, we recorded the number of bivalves per host. We collected four bivalve specimens from two individuals of *P. zeylanica* in Kamiura Beach on 3 May 2011 and 28 May 2017 for species description. Three specimens collected from the same individual of *P. zeylanica* in 2011 were preserved in a dry state and designated as paratypes, whereas a single specimen collected from *P. zeylanica* in 2017 was preserved in 99.5 % ethanol and designated as holotype. We photographed the latter in a living state with and without the host before preservation and used the foot tissue for molecular analyses.

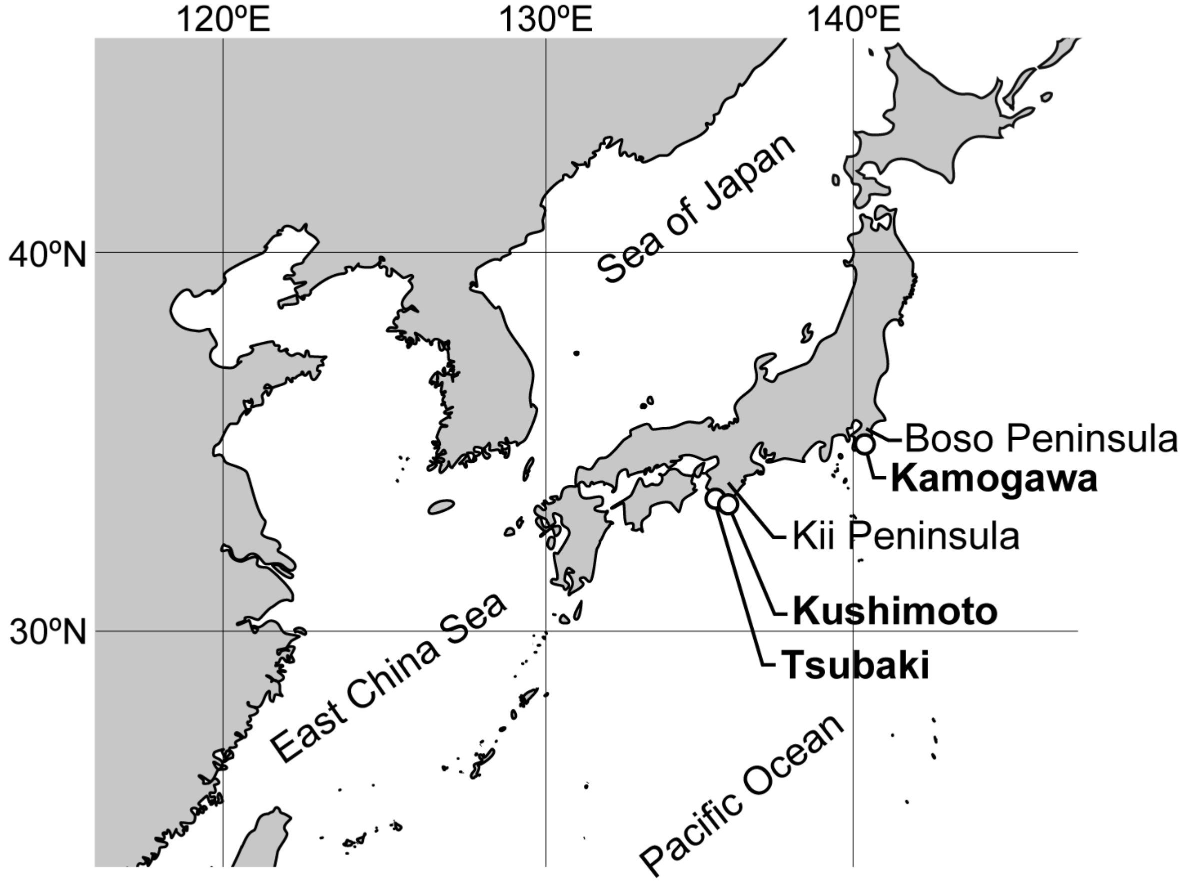

FIGURE 1. Sampling localities and previous records of *Montacutona sigalionidcola* **sp. nov.** Kushimoto (type locality), Wakayama prefecture, Japan (this study); Tsubaki, Shirahama, Wakayama Prefecture, Japan (this study; Otani *et al.* 2005); and Kamogawa, Chiba Prefecture, Japan (Yanagi *et al.* 2017).

Shell characteristics of these specimens and internal anatomy of the specimen collected in 2017 were observed under stereoscopic microscope. The hinge structure and nepioconch were taken by a scanning electron microscope (SEM, Real Surface View Microscope VE-9800, Keyence Corp.).

To investigate the phylogenetic position of this species within Galeommatidae, we performed molecular analyses based on the sequence data obtained in previous studies (mainly Goto *et al.* 2012, 2014) and those newly collected in this study (Table 1).

TABLE 1. List of species used for molecular phylogenetic analyses and their accession numbers. Accession numbers with an asterisk indicate the sequences obtained in this study.

Family	Species	18S rRNA	28S rRNA	H3	COI
Galeommatidae	*Anisodevonia ohshimai*	AB714754	AB714797	AB714838	AB714878
	Arthritica japonica	AB714755	AB714798	AB714839	AB714879
	Basterotia carinata	AB714780	AB714823	AB714861	AB714902
	Basterotia gouldi	AB714781	AB714824	AB714862	AB714903
	Basterotia sp. 1	AB714782	AB714825	AB714863	AB714904
	Borniopsis aff. *ariake*	AB714776	AB714819	AB714858	AB714899
	Borniopsis aff. *nodosa*	AB714777	AB714820	AB714859	AB714900
	Borniopsis macrophthalmensis	AB714775	AB714818	AB714857	AB714898
	Borniopsis ochetostomae	AB714773	AB714816	AB714855	–
	Borniopsis subsinuata	AB714774	AB714817	AB714856	AB714897
	Borniopsis yamakawai	AB714756	AB714799	AB714840	AB714880
	Brachiomya stigmatica	AB714753	AB714796	–	AB714877
	Curvemysella paula	AB714757	AB714800	AB714841	AB714881
	Devonia semperi	AB714758	AB714801	AB714842	AB714882
	Divariscintilla toyohiwakensis	AB714745	AB714788	AB714831	AB714869
	Entovalva lessonothuriae	AB714759	AB714802	AB714843	AB714883
	Ephippodonta gigas	AB714746	AB714789	AB714832	AB714870
	Galeomma sp. 1	AB714747	AB714790	AB714833	AB714871
	Kellia porculus	AB714760	AB714803	AB714844	AB714884
	Koeamya setoensis	AB907562	AB907568	AB907573	AB907574
	Koreamya arcuata	AB907557	AB907563	AB907569	AB47955
	Kurtiella aff. bidentata	AB714765	AB714808	–	AB714889
	Kurtiella bidentata	KF741629	KF741655	–	–
	Kurtiella pedroana	–	KX376195	KX375917	–
	Kurtiella tumida	–	KX376206	KX375841	–
	Lasaea undulata	AB714761	AB714804	AB714845	AB714885
	Litigiella pacifica	AB714762	AB714805	AB714846	AB714886
	Melliteryx puncticulata	AB714763	AB714806	AB714847	AB714887
	Montacutona sigalionidcola	LC485247*	LC485248*	LC485249*	LC485250*
	Montacutona sp. 1	AB714764	AB714807	AB714848	AB714888
	Mysella charcoti	KC429372	KC429474	KC429205	–
	Mysella sp. 1	–	KX376208	KX375946	–
	Mysella vitrea	AM774519	AM779693	KX375945	–
	Neaeromya rugifera	AB714766	AB714809	AB714849	AB714890
	Nipponomontacuta actinariophila	AB714767	AB714810	AB714850	AB714891
	Nipponomysella oblongata	AB714768	AB714811	AB714851	AB714892
	Nipponomysella subtruncata	AB714769	AB714812	AB714852	AB714893
	Paraborniola matsumotoi	AB714770	AB714813	AB714853	AB714894
	Peregrinamor gastrochaenans	AB714771	AB714814	–	AB714895

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TABLE 1. (Continued)

Family	Species	18S rRNA	28S rRNA	H3	COI
	Peregrinamor ohshimai	AB714772	AB714815	AB714854	AB714896
	Platomysia rugata	LC126833	LC126832	–	–
	Pseudogaleomma sp. 1	AB714748	AB714791	AB714834	AB714872
	Pythina deshayesiana	AB714778	AB714821	–	–
	Salpocola philippinensis	AB714779	AB714822	AB714860	AB714901
	Scintilla aff. hydatina	AB714750	AB714793	AB714835	AB714874
	Scintilla rosea	AB714749	AB714792	–	AB714873
	Scintilla sp.1	AB714751	AB714794	AB714836	AB714875
	Scintilla sp.2	AB714752	AB714795	AB714837	AB714876
Outgroups					
Solecurtidae	*Azorinus minutus*	AB714783	AB714826	AB714864	AB714905
Gastrochaenidae	*Gastrochaena cuneiformis*	AB714784	AB714827	AB714865	–
Veneridae	*Irus mitis*	AB714785	AB714828	AB714866	AB714906
Mactridae	*Meropesta nicobarica*	AB714786	AB714829	AB714867	–
Trigoniidae	*Neotrigonia margaritacea*	AF411690	DQ279963	AY070155	U56850
Nuculanidae	*Nuculana pella*	AY070111	AJ307553	AY070148	AY070138
Solemyidae	*Solenmya velum*	AF120524	AY145421	AY070146	U56852
Solenidae	*Solen strictus*	AB714787	AB714830	AB714868	AB714907

* Sequences obtained for this study are marked with an asterisk.

FIGURE 2. Kamiura Beach, Kushimoto, Wakayama Prefecture, Japan (type locality of *Montacutona sigalionidcola* **sp. nov.)**

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Repository of type materials. The holotype and two paratype specimens are deposited in the National Museum of Nature and Science, Tokyo, Japan (NSMT; NSMT-Mo 79031–79033). One paratype is in the Smithsonian National Museum of Natural History, USA (USNM 1571983).

Molecular analysis. Total genomic DNA was isolated from the foot tissue of the bivalve specimen (NSMT-Mo 79031) using DNeasy Blood & Tissue Kit (Qiagen) following the manufacture's protocol. Polymerase chain reactions (PCRs) were used to amplify 1384 bp of 18S, 1040 bp of 28S, 328 bp of H3 and 658 bp of COI. Amplification was performed in 25.23 μL mixtures consisting of 0.3 μL of forward and reverse primers (10 μM each; Table 2), 2.5 μL 10x ExTaq buffer, 2.0 μL dNTPs (2.5 μM each), 0.13 μL ExTaq polymerase (TaKaRa, Otsu, Japan), 17.5 μL of distilled water and 2.5 μL of genomic DNA. Thermal cycling was performed with an initial denaturation for 3 min at 94 °C , followed by 30 cycles of 30 s at 94 °C. 30 s at 49 °C (COI) or 55 °C (18S, 28S, and H3) and 2 min at 72 °C , with a final 3 min extension at 72 °C . PCR products were cleaned using ExoSAP-IT (Thermo Fisher Scientific, Tokyo, Japan). The sequencing reaction was performed in Eurofins Genomics (Tokyo, Japan) using PCR primers and internal primers (Table 2). The obtained sequences were deposited in the DDBJ/EMBL/GenBank databases with accession numbers LC485247–485250 (Table 1).

TABLE 2. Primers used for PCR amplification and sequencing in this study.

Primer	Direction	Sequence 5'–3'	References
18S rRNA			
PCR amplification and sequencing			
1F	Forward	TACCTGGTTGATCCTGCCAGTAG	Giribet *et al*. (1996)
3F	Forward	GTTCGATTCCGGAGAGGGA	Giribet *et al*. (1996)
5R	Reverse	CTTGGCAAATGCTTTCGC	Giribet *et al*. (1996)
9R	Reverse	GATCCTTCCGCAGGTTCACCTAC	Giribet *et al*. (1996)
18Sa2.0	Forward	ATGGTTGCAAAGCTGAAAC	Giribet *et al*. (1996)
18Sbi	Reverse	GAGTCTCGTTCGTTATCGGA	Giribet *et al*. (1996)
28S rRNA			
PCR amplification and sequencing			
D1	Forward	ACCCSCTGAAYTTAAGCAT	Colgan *et al*. (2003)
D3	Reverse	GACGATCGATTTGCACGTCA	Vonnemann *et al*. (2005)
Sequencing			
D2F	Forward	CCCGTCTTGAAACACGGACCAAGG	Vonnemann *et al*. (2005)
C2R	Reverse	ACTCTCTCTTCAAAGTTCTTTTC	Dayrat *et al*. (2001)
H3			
PCR amplification and sequencing			
H3F	Forward	ATGGCTCGTACCAAGCAGACVGC	Colgan *et al*. (1998)
H3R	Reverse	ATATCCTTRGGCATRATRGTGAC	Colgan *et al*. (1998)
COI			
PCR amplification and sequencing			
LCO1490	Forward	GGTCAACAATCATAAAGATATTGG	Folmer *et al*. (1994)
HCO2198	Reverse	TAAACTTCAGGGTGACCAAAAAATC	Folmer *et al*. (1994)

Sequences of the 18S, 28S, H3, and COI genes were aligned using the program Muscle (Edgar 2004) as implemented in the software Seaview (Galtier *et al.* 1996; Gouy *et al.* 2010) with default settings; poorly aligned regions were corrected by eye. The alignments of H3 and COI sequences (328 and 658 bp, respectively) had no indels and were therefore unambiguous. We employed Gblocks v0.91b (Castresana 2000; Talavera & Castresana 2007) to eliminate ambiguously aligned regions for 18S and 28S datasets. Lengths of sequences prior to and following the Gblocks treatment were 2029 and 1724 (18S) and 1352 and 920 (28S), respectively.

Phylogenetic trees were constructed based on the combined dataset (18S + 28S + H3 + COI) using Bayesian inference and maximum likelihood (ML) methods. The Bayesian analysis was performed using MrBayes 3.2.5 (Ronquist & Huelsenbeck 2003) with substitution models chosen by Kakusan 4 (Tanabe 2011) for each gene and codon position [18S: K80_GAMMA, 28S: GTR_GAMMA, H3: GTR_GAMMA, GTR_GAMMA, and JC69_Homogeneous (for each codon), COI: HKY85_GAMMA, GTR_GAMMA, and GTR_GAMMA (for each codon)]. Two independent runs of Metropolis-coupled Markov chain Monte Carlo were carried out simultaneously for 4,000,000 generations, sampling trees every 100 generations. The initial 25% of the sampled trees were discarded as burn-in. We confirmed that analyses reached stationarity well before the burn-in period both by checking the ASDSFs and plotting the ln-likelihood of the sampled trees against generation time.

Maximum likelihood (ML) analysis was performed using RAxML (Stamatakis 2014) as implemented in raxmlGUI 1.5 (Silvestro & Michalak 2012). Datasets were partitioned by gene and codon position and GTR + GAMMA model was implemented for all partitions. Robustness of tree topology was evaluated by bootstrap support values (BS) from 1,000 replications. We mapped the host taxa and host use pattern on a part of tree to show how *M. sigalionidcola* evolutionarily achieved the association with *Pelogenia*. The information of the host taxa and host use pattern is based on Goto *et al.* (2012), Goto *et al.* (2014) and Li *et al.* (2016).

Systematics

Superfamily Galeommatoidea J.E. Gray, 1840

Family Galeommatidae *sensu* Ponder, 1998

Genus *Montacutona* Yamamoto & Habe, 1959

Diagnosis. Shell typically suborbicular in shape with submedian umbones. Two pronounced and spread laterals in left and right valves. A calcified, white portion (*i.e.*, lithodesma) situated in-between the spread laterals. Outer demibranch significantly reduced or absent.

Montacutona sigalionidcola sp. nov.

[Japanese name: Sunaurokomushi-yadori-gai]
Figs. 3–5

Nipponomysella sp. Otani *et al.* 2005: 73, pl. 5, fig. 5
Sunaurokomushi-yadori-gai Yanagi 2017: 10

Material examined. Holotype (Figs. 3, 4): NSMT-Mo 79031 (SL 3.9 mm, SH 2.6 mm, Kamiura Beach, 28 May 2017). Paratype 1 (Fig. 5A): NSMT-Mo 79032 (SL 4.8 mm, SH 3.5 mm, Kamiura Beach, 3 May 2011), paratype 2 (Fig. 5B): USNM 1571983 (SL 4.9 mm, SH 3.1 mm, Kamiura Beach, 3 May 2011), paratype 3 (Fig. 5C): NSMT-Mo 79033 (SL 2.9 mm, SH 1.9 mm, Kamiura Beach, 3 May 2011).

Type locality. Kamiura Beach, Kushimoto, Wakayama, Kii Peninsula, Japan (33°27'N, 135°46'E; Figs. 1, 2).

Habitat. Intertidal sand (Fig. 2).

Diagnosis. Shell ovate-elongate in shape with a small gape at posteroventral margin. Only inner demibranch present.

Description. Adult shell (Figs. 3–5) small (up to 4.9 mm), thin, fragile, anteroposteriorly ovate-elongate, dorsally subtrigonal, equivalve, inequilateral. Shell inflated posteriorly. Umbo prominent; beak opisthogyrate, located slightly posterior to mid-length of shell. Shell color pale yellowish but slightly whitish and polished around the beak. Height/length about 0.73–0.63.

Anterior shell margin rounded; posterior margin roundly subtruncate; anterodorsal margin straight; posteroventral margin nearly straight but slightly incurved near umbo; posteroventral margin nearly straight. Shell margins meeting at the all points except for small gape along the posteroventral margin (Fig. 3C). Byssal threads extending from the base of the foot through the posteroventral gape of the shell to the outside. Shell sculpture consisting of many closely-set commarginal growth lines and evenly spaced fine radial ribs.

Hinge of left valve consisting of thickened marginal lateral teeth, diverging approximately 90° (Fig. 4E). Hinge of right valve consisting of distinct lamella-like teeth, diverging approximately 90° (Fig. 4F). Resilium (internal ligament) on left and right valves located immediately below umbo and between anterior and posterior tooth, with a rounded to trapezoid lithodesma anteriorly slightly curved (Fig. 4E, F). No external ligament.

Prodissoconch I and II indistinct. The nepioconch/adult shell boundary with SL = 1220 μm, SH = 612 μm in holotype (Fig. 4G, H)

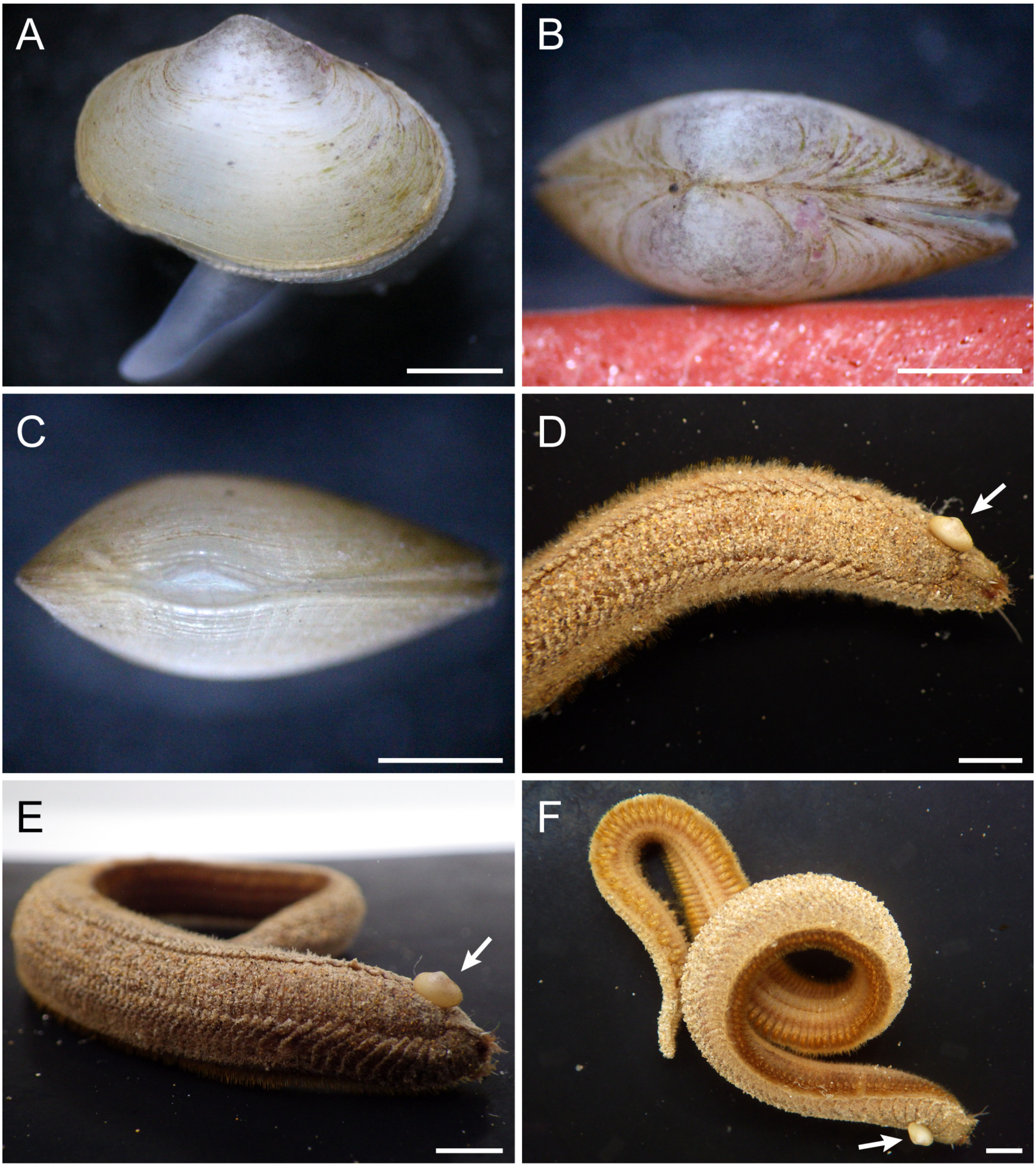

FIGURE 3. *Montacutona sigalionidcola* **sp. nov.** (holotype, NSMT-Mo 79031, SL 3.9 mm) and its host *Pelogenia zeylanica*. (**A**) A crawling individual of *M. sigalionidcola.* (**B, C**) Dorsal and ventral sides of *M. sigalionidcola.* (**D–F**) *Pelogenia zeylanica* with *M. sigalionidcola* attached (arrowed). Scale bar: 1 mm (A–C), 5 mm (D–F). Photo credits: R. Goto (A–F).

Soft parts: Mantle not reflected, without tentacles. Mantle edge narrowly extending beyond margin of shell and somewhat rugose (Fig. 3A). Both anterior and posterior adductor muscles elongate ovate and located in relatively dorsal position (Fig. 4C, D). Ctenidia consisting of inner demibranch with ascending and descending lamellae (Fig. 4C, D). Labial palps small (Fig. 4C, D). Foot slender, laterally compressed, rounded in front (Fig. 3A). Byssal gland located at the base of the foot.

Distribution. Kushimoto (this study) and Tsubaki (Otani *et al.* 2005; this study), Kii Peninsula, Wakayama Prefecture, and Uchiura, Kamogawa, Boso Peninsula, Chiba Prefecture, Japan (Yanagi 2017) (Fig. 1).

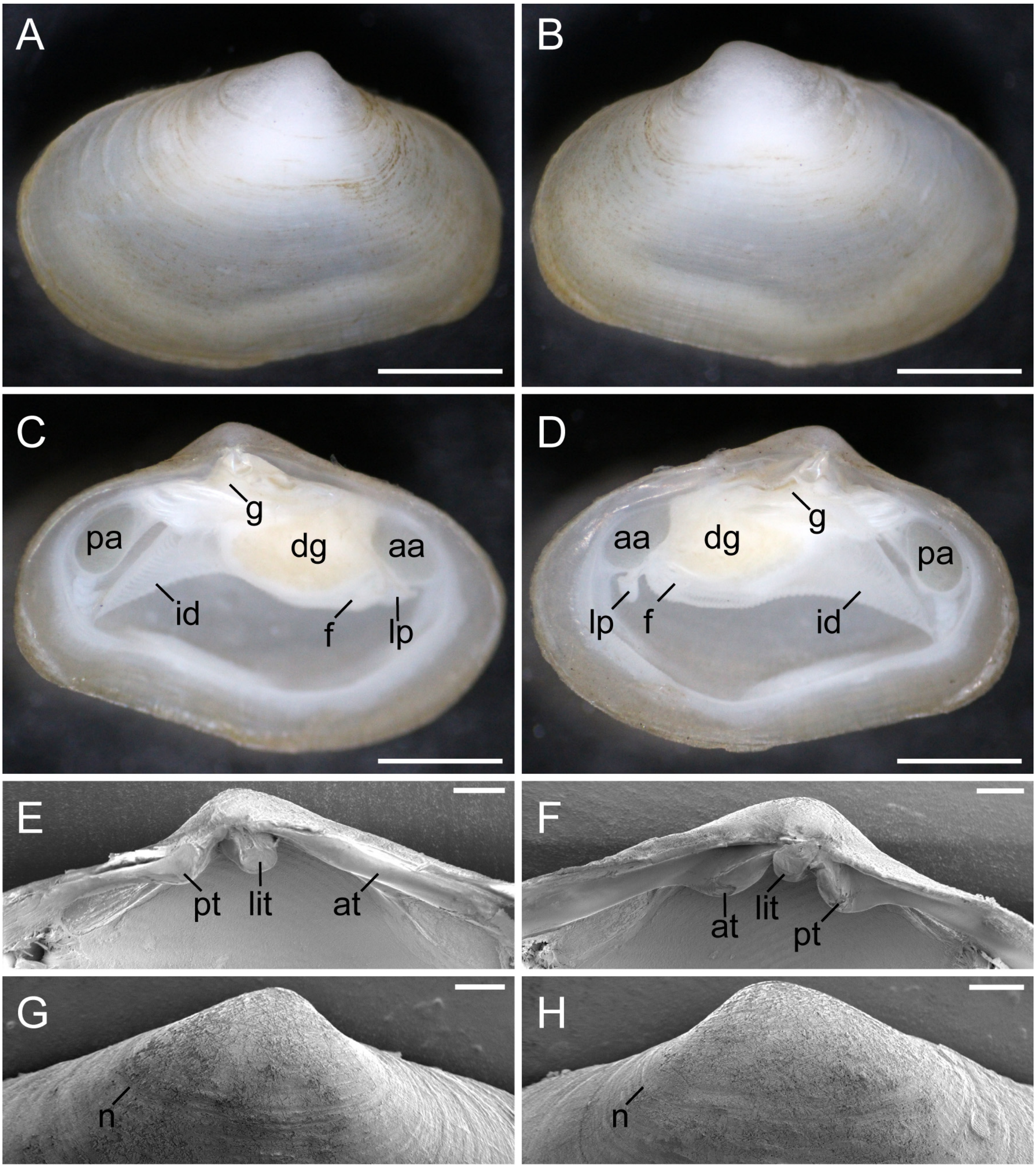

FIGURE 4. Holotype of *Montacutona sigalionidcola* **sp. nov.** (NSMT-Mo 79031, SL 3.9 mm). (**A, C**) Left valve. (**B, D**) Right valve. The foot was removed for DNA analysis. (**E, F**) Hinge structure of left and right valves. (**G. H**) Umbos of left and right valves. Abbreviations: aa, anterior adductor muscle; at, anterior lateral tooth; dg, digestive gland; f, foot; g, gonad; id, inner demibranch; lp, labial palp; lit, lithodesma; n, nepioconch-adult shell boundary; pa, posterior adductor muscle; pt, posterior lateral tooth. Scale bar: 1 mm (A–D), 200 µm (E–H). Photo credits: R. Goto (A–H).

Host. *Pelogenia zeylanica* (Annelida: Sigalionidae) (Fig. 3D–F).

Host association. This species is tightly attached to the dorsal surface of the anterior end of the host by byssal threads (Fig. 3). The anterior end of the holotype was directed towards the anterior end of the host. The number of *M. sigalionidcola* per host ranged from one to four (Table 3). The infestation rate by *M. sigalionidcola* is high: roughly 80% of *P. zeylanica* harbored commensal bivalves (Tanaka, personal observations).

Phylogenetic analysis. Figure 6 shows the phylogenetic position of *M. sigalionidcola* in Galeommatidae. This species forms a monophyletic group with *Montacutona, Nipponomontacuta,* and *Koreamya* [Bayesian posterior probabilities (PP) = 1.00, ML bootstrap rates (BS) = 99].

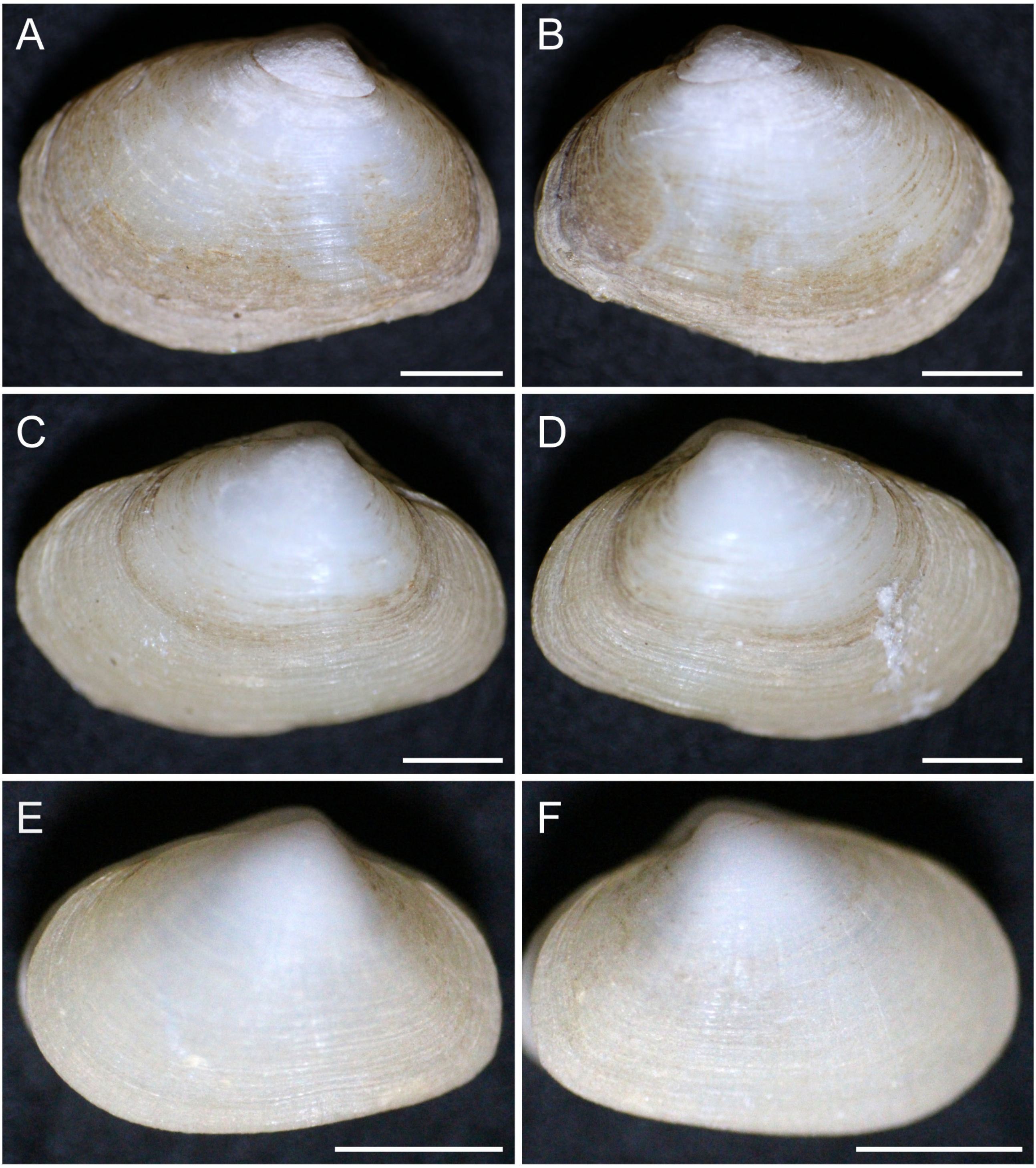

FIGURE 5. Paratypes of *Montacutona sigalionidcola* **sp. nov.** (**A, B**) Left and right valve of paratype 1 (NSMT-Mo 79032, SL 4.8 mm). (**C, D**) Left and right valve of paratype 2 (USNM 1571983, 4.9 mm). (**E, F**) Left and right valve of paratype 3 (NSMT-Mo 79033, 2.9 mm). Scale bar: 1 mm. Photo credits: R. Goto (A–F).

TABLE 3. Number of *Montacutona sigalionidcola* per host with its sampling localities and sampling dates.

Date	Sampling locality	Number of individuals per host
15 May 2000	Tsubaki, Shirahama, Wakayama, Japan	2
20 July 2008	Kamiura Beach, Kushimoto, Wakayama, Japan	4
3 May 2011	Kamiura Beach, Kushimoto, Wakayama, Japan	3 (paratypes)
4 June 2011	Kamiura Beach, Kushimoto, Wakayama, Japan	2
7 June 2015	Kamiura Beach, Kushimoto, Wakayama, Japan	4
10 June 2017	Kamiura Beach, Kushimoto, Wakayama, Japan	1 (holotype)

Etymology: The species name is derived from the family name of the host and the suffix *cola* (Latin), meaning a dweller or inhabitant.

Discussion

The genus *Montacutona* Yamamoto & Habe, 1959 comprises about ten species, although the species border is often difficult to determine (Huber 2015). The biology of many members of this genus remains unknown, but several species (e.g., *M. mutsuwakensis* Yamamoto & Habe 1959 and *M. ceriantha* Ponder, 1971) are commensal with burrowing sea anemones of *Cerianthus* Delle Chiaje, 1841 (Ponder 1971; Morton 1988; Morton & Scott 1989), whereas *M. compacta* (A. A. Gould, 1861) is free-living or perhaps commensal with corals (Morton 1980). Our finding adds a new commensal species to this genus.

The members of the genus *Montacutona* have a calcified lithodesma between diverging lateral tooth (Morton 1980; Huber 2015). *Montacutona sigalionidcola* also has such a lithodesma. Most species of *Montacutona* have a reduced outer demibranch (Morton 1980; Huber 2015), whereas *M. sigalionidcola* lacks an outer demibranch. Shell shape of *Montacutona* is rounded to trigonal (Huber 2015), whereas that of *M. sigalionidcola* is ovate-elongate. In addition, *M. sigalionidcola* is distinguished from other members of this genus in having a small gape along the posteroventral margin. *Montacutona sigalionidcola* attaches strongly to the host body surface by byssal threads, which are extended through this small gape. Thus, the small gape of the shell is considered to be a morphological specialization to their ectocommensal lifestyle.

Montacutona sigalionidcola was previously treated as *Nipponomysella* sp. (Otani *et al.* 2005) probably because this species has an elongated oval shell. However, molecular phylogenetic analyses in the present study suggest that *M. sigalionidcola* is not monophyletic with *N. oblongata* (Yokoyama, 1922)*,* the type species of *Nipponomysella* (Fig. 6)*,* but is monophyletic with *Montacutona, Nipponomontacuta* Yamamoto & Habe, 1959 and *Koreamya* Lützen, Hong & Yamashita, 2009 (Fig. 6). Considering that *Koreamya* and *Nipponomontacuta* also have a lithodesma between diverging lateral tooth and a reduced outer demibranch (Goto *et al.* 2014), it may be reasonable that these genera are synonymized with *Montacutona.*

Montacutona sigalionidcola attaches only to the dorsal surface of the anterior end of the host scale worm. Many ectocommensal galeommatids are known to have a similar attachment-site specificity (Kato & Itani 1995; Goto *et al.* 2014, 2018). It has been suggested that the attachment site allows the commensal to effectively receive water currents created by the hosts and use them for filter feeding and respiration. This may also be applied for *M. sigalionidcola.* On the other hand, *Pelegenia zeylanica* autotomizes a body part when it is shocked (Goto, personal observations). By attaching to the anterior end of *P. zeylanica*, the bivalves may reduce the risk of being left behind during an autotomizing event.

Montacutona sigalionidcola has been recorded only from Kii and Boso Penisulas, Honshu Island, Japan (Fig. 1). Considering that the host scale worm *P. zeylanica* has also been recorded from more southern localities (e.g., Iriomote Island and Izu Oshima Island, Japan, and Indonesia) (Imajima 2007), *M. sigalionidcola* also may occur at those localities.

Host shift is a common speciation process in symbiotic and parasitic organisms (Coyne & Orr 2004). Host shifts revealed by molecular phylogenetic analyses occurred mostly between closely related host taxa (e.g. Hafner & Nadler 1988; Shaw 1988; Faucci *et al.* 2006; Tsang *et al.* 2009). However, recent molecular phylogenetic analyses of Galeommatidae suggest that host shifts across distantly related host taxa (*e.g.* phyla) are common in some clades (Goto *et al.* 2012, 2014; Li *et al.* 2016). In the present study, *M. sigalionidcola,* a commensal with a sigalionid scale worm, forms a monophyletic group with commensal species associated with sea anemones and species associated with *Lingula* brachiopods (Fig. 6). This suggests host shifts across phyla occurred at least twice in this clade. Sigalionid scale worms, burrowing sea anemones, and *Lingula* brachiopods are ecologically similar in inhabiting fine sand sediments. This suggests that the habitat preference for specific sediments type may more strongly constrain the diversification of this galeommatid clade than preference for specific host taxa. Our analysis included *Neaeromya rugifera,* which is also known as an ectocommensal of the scale worm, *Aphrodita* spp. (Li & Ó Foighil 2012). They were not monophyletic in the phylogenetic tree (Fig. 6), suggesting that ectocommensal associations with scale worms evolved at least twice in the Galeommatidae.

Sea anemones and *Lingula* brachiopods, the hosts of *Montacutona, Nippponomontacuta,* and *Koreamya*, are nearly sessile animals. In contrast, sigalionid scale worms, the host of *M. sigalionidcola,* are much more mobile. Shells of *M. sigalionidcola* are dorsoventrally flatter than those of other *Montacutona.* Perhaps, it is an adaptation to reduce the friction against sediments around the hosts when it moves sediments.

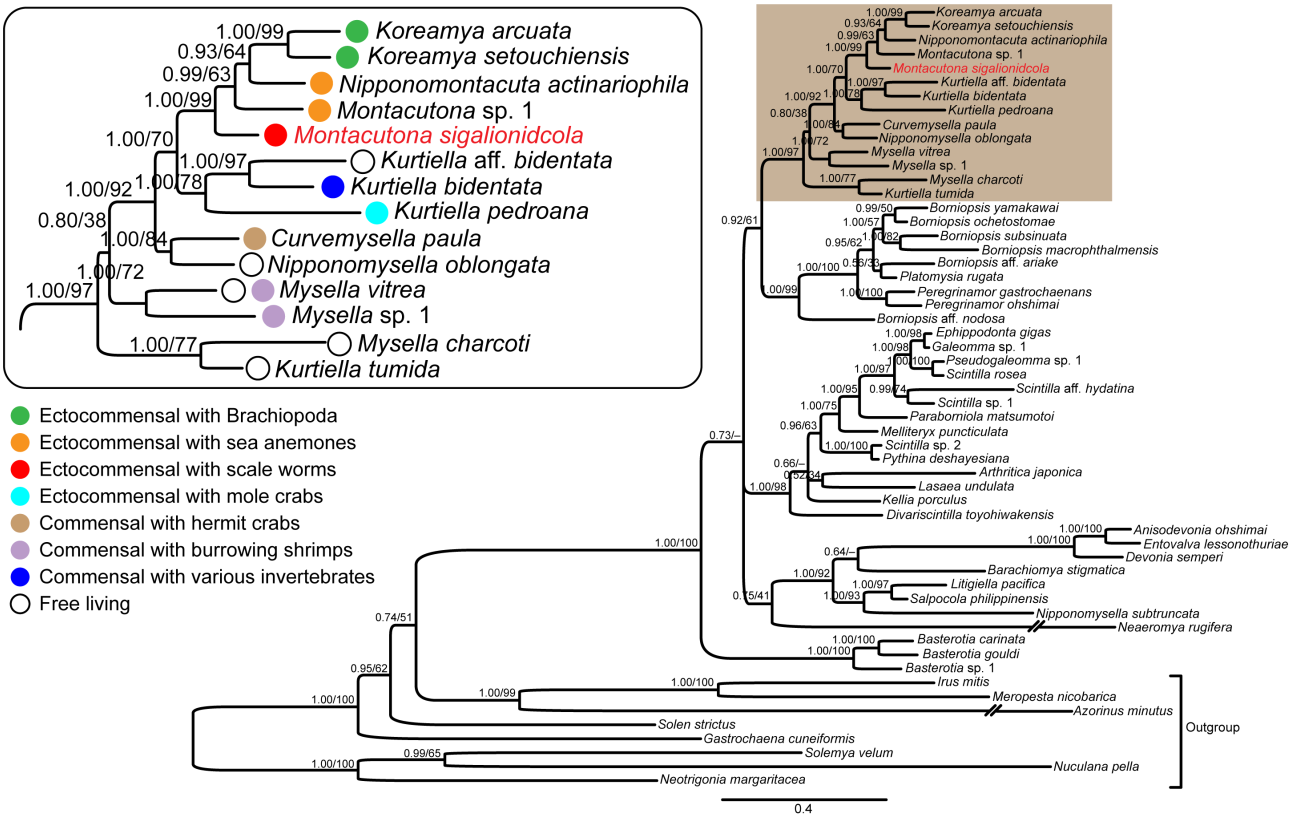

FIGURE 6. Bayesian phylogenetic tree of Galeommatidae, including *Montacutona sigalionidcola* **sp. nov.**, based on the combined dataset of 18S, 28S, H3 and COI genes. Numbers above branches indicate Bayesian posterior probabilities followed by maximum likelihood bootstrap support values. A part of the galeommatid tree is closed up to show evolutionary pattern of host associations.

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