Description of a New Species of the Intertidal Limpet Patelloida (Patellogastropoda: Lottiidae) from Wakayama and Kochi, Japan

Faith Jessica Paran^{1,*}, Takenori Sasaki², Akira Asakura^{1,3}, and Tomoyuki Nakano^{1,3,*}

¹Seto Marine Biological Laboratory, Biological Sciences Department, Graduate School of Science, Kyoto University, Shirahama-cho, Nishimuro-gun, Wakayama Prefecture, Japan 649-2211. *Correspondence: E-mail: faith.jessica.paran@gmail.com (Paran) E-mail: asakurasetombl@gmail.com (Asakura)

- ²The University Museum, University of Tokyo, Hongo, Bunkyo City, Tokyo 113-0033. E-mail: sasaki@um.u-tokyo.ac.jp (Sasaki)
- ³*Field Science Education and Research, Kyoto University, Sakyo-ku, Kyoto Prefecture, Japan 606-8502.* **Correspondence: E-mail: nakano.tomoyuki.2a@kyoto-u.ac.jp (Nakano)*

(Received 25 April 2024 / Accepted 23 April 2025 / Published -- 2025) Communicated by Benny K.K. Chan

This study presents a comprehensive examination of a recently identified intertidal limpet species, *Patelloida parva* n. sp., utilizing a multidisciplinary approach that combines molecular analyses and detailed morphological investigations. Molecular analysis, involving mitochondrial (16S rRNA) and recently reported single nucleotide polymorphism markers, has been instrumental in distinguishing *Patelloida parva* n. sp. from its congeners. In addition to genetic divergence, this study provides a description of both morphology and species distribution, revealing key features that set *Patelloida parva* n. sp. apart from closely related *Patelloida* species found in Japan. *Patelloida parva* n. sp. is known from the upper intertidal of the Pacific coasts of Wakayama and Kochi Prefectures, Japan, but morphological analysis suggests that there are also populations on the Ryukyu Islands. Furthermore, this study hypothesizes the tropical origin of *Patelloida parva* n. sp., attributing its distribution pattern to the influence of the Kuroshio Current. Genetic analyses indicate a closer sequence divergence (5%) to the tropical *P. saccharinoides* compared to the *P. lanx* (11%) co-occurring in intertidal rocky shores. This study not only contributes to the understanding of the species' ecology but also underscores the importance of considering both genetic and morphological aspects in the taxonomy of limpets within *Patelloida*.

Keywords: Mollusca, Gastropoda, Patellogastropoda, Kuroshio current, Biogeography

Citation: Paran FJ, Sasaki T, Asakura A, Nakano T. 2025. Description of a new species of the intertidal limpet Patelloida (Patellogastropoda: Lottiidae) from Wakayama and Kochi, Japan. Zool Stud **64:**26.

BACKGROUND

The genus *Patelloida*, a prominent member of the diverse patellogastropod family Lottiidae (Gray, 1840), boasts a wide distribution on the Indo-West Pacific (Quoy & Gaimard, 1834). Notably, *Patelloida* can be categorized into two distinct groups: the *P. saccharina* species group, characterized by robust radial ribs inhabiting rocky intertidal shores, and the *P. pygmaea* group, distinguished by rounded shells found across various substrates (Nakano and Ozawa 2004 2007).

Within the *P. saccharina* group, known for its broad Indo-West Pacific distribution, the presence of cryptic species has been well-documented (Kirkendale and Meyer 2004). Initial classifications recognized two subspecies, *P. saccharina saccharina* in the Ryukyu Islands and southward, and *P. saccharina lanx* in temperate Japan (Okutani 2017; Sasaki 1999). Recent molecular investigations, considering data on demographic history and environmental differentiation, have elevated these subspecies to distinct species status (Paran et al. 2023). This reclassification prompted the identification of an unidentified *Patelloida* species (hereafter referred to as *Patelloida parva* n. sp.) in Kushimoto, Wakayama Prefecture, central Japan. Interestingly, this new species can easily be misidentified as *P. lanx*, especially when co-occurring in the same habitat. Using the mitochondrial marker 16S rRNA alone, this species exhibited 11% and 12% species divergence from *P. lanx* and *P. saccharina*, respectively. Furthermore, SNP markers underscored the separation of *Patelloida parva* n. sp. samples as a distinct group within the *P. saccharina* species complex.

Previous records by Sasaki (1999) highlighted the occurrence of a similar *Patelloida parva* n. sp. inhabiting the upper intertidal zones of Okinawa, Amami-Oshima Islands, southern Kyushu, Kochi, and Wakayama. Despite potential confusion with *P. lanx* due to similar shell coloration and cohabitation in the upper intertidal zone, this *Patelloida parva* n. sp. is distinct with a smaller shell size, prominent secondary radial ribs, and a preference for higher tidal levels.

This study delves into the taxonomic characterization of this species, elucidating both its morphological features and molecular phylogeny in comparison to *P. lanx* and other *Patelloida* species. Using 16S DNA marker, our examination of newly collected samples from Wakayama and Kochi confirmed the monophyletic grouping of *Patelloida parva* n. sp., thereby also substantiating its

occurrence in Kochi Prefecture. This comprehensive study contributes valuable insights into the taxonomy of the genus *Patelloida* and enhances our understanding of the diversity within the *Patelloida saccharina* species complex.

MATERIALS AND METHODS

Sample collection

Patelloida sp. specimens were collected from Kochi and Wakayama Prefectures where this species is known to occur (Fig. 1, locality colored in red). Archived specimens from the National Museum of Nature and Science (NMNS), Tsukuba, Japan identified as *Patelloida* sp. were also used for shell morphology observations (Fig. 1, archived samples collected in Kochi and Wakayama are colored in blue).



Fig. 1. Locality map of the occurrence of *Patelloida parva* n. sp. used in this study. Inset: Map of Japan showing the present-day routes of Tsushima and Kuroshio currents.

Radula morphology

Radular segments were observed and dissected from the specimens, soaked in household bleach for 20 s, and rinsed in distilled water. Radulae were examined and photographed using a scanning electron microscope (SEM).

DNA extraction and PCR amplification

A small amount of tissue was taken from the muscular foot of collected samples and preserved in salt-saturated DMSO (ssD) buffer. Due to the difficulty of extracting DNA from museum archives, the specimens from NMNS were not used for DNA sequencing. Protocols for DNA extraction and PCR amplification of the 16S rRNA mitochondrial region previously reported in Paran et al. (2023) were followed. Sequences were assembled in GENEIOUS R6.

Phylogenetic analysis

The best-fit nucleotide substitution model, determined based on the corrected Akaike Information Criterion (AICc) and the Bayesian Information Criterion (BIC) in JMODELTEST v2.1 (Darriba et al. 2012; Guindon and Gascuel 2003), was the TPM3 model with discrete gamma shape parameter with invariant sites (TPM3 + G + I; where G = 0.25 and I = 0.61). TPM3 assumes equal DNA substitution rates (Darriba et al. 2012). Bayesian tree reconstruction was conducted in MRBAYES 3.2 (Ronquist et al. 2012) using the GTR model, which is the best substitution model corresponding to TPM3. The *invgamma* function was activated as suggested by the best-fit nucleotide substitution model. The chain length was set at 1 million generations by sampling every 10,000 generations, with a burn-in fraction at 25% of the chain length.

The tree was rooted with outgroups that included *P. saccharinoides* (Habe and Kosuge 1966), *P. saccharina, P. lanx,* and evolutionary species units of *P. saccharina* (Kirkendale and Meyer 2004). Pairwise sequence divergence was calculated in MEGA 11 (Tamura et al. 2021).

RESULTS

Comparative molecular analysis reveals significant genetic divergence of *Patelloida parva* n. sp. from morphologically similar species

In this study, we subjected 21 samples from Wakayama and 2 samples from Kochi to 16S rRNA mitochondrial region sequencing. This dataset included 4 previously sequenced *Patelloida parva* n. sp. from Wakayama (GenBank Accession Numbers: OP532865–OP532868), two of which were also subjected to SNP marker sequencing (Paran et al. 2023). To facilitate comprehensive analysis, we included 19 *P. saccharina* and 97 *P. lanx* sequences (OP532869–OP532975), culminating in a total of 142 sequences (Table 1). A 510 bp 16S assembly, yielding 9 haplotypes, was generated, with 3 haplotypes attributed to *Patelloida parva* n. sp.

Locality	Patelloida parva n. sp.	Patelloida lanx	Patelloida saccharina	Total
Aomori		5		5
Fukui		10		10
Kagawa		6		6
Kagoshima		31		31
Kochi	2			2
Nagasaki		3		3
Okinawa		9	16	25
Wakayama	24	23		47
Yamaguchi		3		3
GenBank		7	3	10
Total	26	97	19	142

Table 1. Sample distribution of *P. saccharina* species complex

The sequence alignment recovered 436 conserved positions, featuring 74 variable sites, 68 parsimony-informative sites, and 6 singletons. For *Patelloida parva* n. sp. sequences exclusively, 506 out of 510 sites were conserved, with 3 polymorphic sites, 3 singletons, and no parsimony-informative sites, suggesting possible individual variations or sequencing errors. In the comparison between *P. lanx* and *Patelloida parva* n. sp., 447 sites were conserved, 62 sites were polymorphic, 62 sites were parsimony-informative, and no singletons were observed. The assembly between *P. saccharina* and *Patelloida parva* n. sp. revealed greater genetic distance, recovering 440 conserved sites, 70 variable sites, 64 parsimony-informative sites, and 6 singletons. Additionally, an 8bp insertion was present in all 26 *Patelloida parva* n. sp. sequences, further substantiating the genetic divergence of this new species from *P. lanx* and *P. saccharina*. Three haplotypes of *Patelloida parva* n. sp. were identified, with one major haplotype comprising 22 sequences shared between WAK and KCH, and 2 singletons from WAK (Table 2).

1 71			
Haplotype	Kochi	Wakayama	Total
HAP1.1		1	1
HAP2.24	2	22	24
HAP3.1		1	1
Total	2	24	26

Table 2. Haplotype distribution of *Patelloida parva* n. sp. samples

Zoological Studies 64:26 (2025)

Phylogenetic relationships among the *Patelloida* sp. haplotypes and other *Patelloida* species were elucidated using a Bayesian approach, revealing high posterior probability values. All three haplotypes of the unknown *Patelloida parva* n. sp. were monophyletic but clustered with the tropical *P. saccharinoides* (Fig. 2). In contrast, the *P. saccharina* and the *P. lanx* species group were divergent from *Patelloida parva* n. sp. Sequence divergence estimates with *P. lanx* and *P. saccharina* were calculated at 11.1% and 11.8%, respectively (Table 3).



Fig. 2. Bayesian-inferred phylogenetic tree of *Patelloida parva* n. sp rooted with *P. lanx*, *P. saccharina*, and outgroups. Branch lengths are annotated in posterior probability values. Tree was generated in MrBayes.

For comparative purposes, shell specimens archived at the National Museum of Nature and Science (NMNS), Tsukuba, Japan, were included in this study (Fig. S1). Beyond Kochi and Wakayama, additional specimens were collected from the Ryukyu Archipelago in Amami-Oshima Island, signifying a sub-tropical species distribution. These shells share a similar structure with *Patelloida parva* n. sp. in this study, featuring prominent secondary radial ribs. However, shells from the Ryukyu Islands exhibit a whiter apex and characteristic dark chevron markings reminiscent of *P. saccharina*, coupled with a pearly white ventral side. These colorations align with the habitat characteristics of sedimentary and coralline substrates prevalent in Okinawa and Amami-Oshima

Islands. This taxonomic description enhances our understanding of the unique shell morphology and distribution of this sub-tropical species.

A supplementary BLAST search was conducted to determine whether this species had been previously reported. Sequences with the highest genetic identity, at 93.6%, were *P. saccharinoides* isolates collected in China and Hong Kong. A voucher specimen of *P. saccharinoides* from Java, Indonesia (GenBank Accession Number: AB238392), exhibited a sequence similarity of 91% with the *Patelloida parva* n. sp. from this study and was ruled out as the same species due to the geographic distance.

The Hong Kong (AN: AB106488) and Guandong, China (AN: OQ170797–OQ170806) sequences were found to be 96% genetically similar to the *P. saccharinoides* voucher specimen. The sequence divergence rate (Table 3) between the *P. saccharinoides* from Hong Kong and Guandong, China was calculated at 5% (uncorrected *p*-distance).

Table 3. Species divergence of *Patelloida* species complex for the 16S rRNA region. Intraspecific divergence is presented within the diagonal and interspecific divergence below the diagonal. Values are in percentage

Species ID	Patelloida parva n. sp.	P. lanx	P. saccharina	P. saccharinoides
Patelloida parva n. sp.	0.00			
P. lanx	11.1	0.00		
P. saccharina	11.8	2.05	1.00	
P. saccharinoides	5.01	10.2	10.7	2.00

P. saccharina and *P. lanx* sequences used in this analysis are from Paran et al., 2023 (GenBank AN: OP532865–OP532975, Japan). *P. saccharinoides* sequences used for this analysis are from Nakano and Ozawa, 2007 (GenBank AN: AB106488, HongKong; GenBank AN: AB238392, Java) and (AN: OQ170797–OQ170806, Guandong)

SYSTEMATIC

Family Lottiidae Gray, 1840 Genus *Patelloida* Quoy & Gaimard, 1834

Patelloida parva n. sp.

(Figs. 3a–3r; Fig. S2)

urn:lsid:zoobank.org:pub:DFE627F4-B2C7-4C79-90B4-9E67A6A85FF3

Patelloida sp.—Sasaki, 1999:39.

Type material: Holotype: University Museum, The University of Tokyo (UMUT)-RM34074 (see Fig. 3p), Shionomisaki, Kushimoto, Wakayama., Japan. Selected paratypes: Paratype 1 (UMUT-RM34046), Shionomisaki, Kushimoto, Wakayama., Japan. Paratype 2 (UMUT-RM34048), Shionomisaki, Kushimoto, Wakayama., Japan. Paratype 3 (UMUT-RM34061), Kashiwajima, Kochi., Japan. Paratype 4 (UMUT-RM34062), Kashiwajima, Kochi., Japan. Paratype 5 (UMUT-RM34049), Shionomisaki, Kushimoto, Wakayama., Japan. Paratype 6 (UMUT-RM34065), Shionomisaki, Kushimoto, Wakayama., Japan.

Type locality: Ogokuda Beach, Cape Shionomisaki, Kushimoto, Wakayama Prefecture, Japan *Description*: Shell (Fig. 3) conical. Sculpture consists usually of 8–12 radial ribs, highly variable in thickness. The major ribs are thicker, while thinner secondary ribs intersperse between the primary ones. The apex is positioned anteriorly, projecting ribs in a distinctive stellate pattern. External shell coloration ranges from greyish blue to brown reticulate markings, complemented by a whitish eroded apex.



Fig. 3. Shell morphology of *Patelloida parva* n. sp. A–P, Specimens collected from Shionomisaki, Kushimoto, Wakayama. Holotype specimen is PS315WAK (Figure 3P). Q–R, Specimens collected from Kashiwajima, Kochi. See Table S1 for shell measurements.

Zoological Studies 64:26 (2025)

Ventral view reveals a smooth and lustrous interior, featuring blue and yellow shadings on the apex, along with white or blue projections in the ribs. Dark blue to black margins encircle the shell. Measurements indicate variations in shell length (9.4–16.5 mm), width (6.6–12.8 mm), and height (1.8–6.7 mm) (Table S1).

Radula morphology: The radular structure of *Patelloida parva* n. sp. is docoglossate, featuring three pairs of lateral teeth and two pairs of marginal teeth, as illustrated in figure 4A. The first lateral teeth exhibit tapering stalks culminating in triangular pointed ends. The second lateral teeth are distinctive, extending prominently with a curved, kite-like tongue, featuring a deeply dented base. Notably, the third lateral teeth are notably thin and pointed, positioned on the sides of the second lateral teeth. Stacked on the upper portion of each other, the marginal teeth share a high degree of similarity, characterized by narrow stalks and rounded cusps.

The radula sac comprises approximately 50 rows of teeth (Fig. 4B), with Row 1 representing the oldest set of teeth located in the mouth. Rows 1–30 are characterized by substantial mineralization and exhibit minimal variation. In contrast, Rows 31–50 show weaker mineralization and display observable variation in size and shape. The radula ribbon, maintaining a copper-like hue, gradually lightens towards the younger, posterior end.

Etymology: The specific name *parva* is derived from the Latin word *parvus*, meaning "small," in reference to the diminutive size of the species compared to its genetically closest relative, Pate*lloida saccharinoides*, and the morphologically similar species, *Patelloida saccharina* and *Patelloida lanx*.

Distribution: Patelloida parva n. sp. is limited to the intertidal zones in the southernmost parts of Kochi and Wakayama Prefectures, Japan facing the Pacific Ocean. Museum archives have recorded its occurrence in Amami-Oshima Island in the Ryukyu Archipelago.



Fig. 4. Radula morphology of *Patelloida parva* n. sp. A, Radular teeth at 280X–350X magnification. Kochi specimen is the first photo to the left at the top panel and the rest are radular teeth of specimens collected in Wakayama. B, Whole radula sac photographed in segments from the first row situated in the mouth to the 50th row in the posterior sac. Row numbers are written in red.

WD:22.6

а

DISCUSSION

Patelloida parva n. sp. is morphologically and genetically distinct from its Patelloida sister species

In this study, we delineated the genetic differences of *Patelloida parva* n. sp. in comparison to the *P. lanx*, a sister species co-occurring in the same intertidal shores. In addition, despite *P. saccharinoides* having high genetic similarities in the BLAST sequences database, we established its clear divergence with *P. parva* n. sp. Genetic verification was based on phylogenetic analysis, corroborating the genetic assignment analysis that used mitochondrial and the recently reported SNP markers in Paran et al. (2023).

Shell size could differentiate *P. parva* n. sp. from *P. lanx* species found in the waters of Japan. However, despite a prevalent pattern of larger shell sizes in *P. lanx* samples across Japan, our observations reveal that *P. lanx* specimens from Wakayama were only slightly larger than *P. parva* n. sp. samples from the same region, possibly due to the diet available in the area. But shell structure further distinguishes the two species, with *P. parva* n. sp. exhibiting a more eroded apex and different radial rib characteristics, as shown in Figure S2. The depression in the base of the second lateral teeth of the radula is less pronounced in *P. lanx*.

While genetic evidence from archived museum samples is lacking, their shell size and radial rib configurations align with those of *P. parva* n. sp. from Wakayama and Kochi, strengthening the morphological distinctions observed in this study. Caution is advised when employing shell colorations as primary differentiation features, as archived *Patelloida parva* n. sp. samples from the Ryukyu Islands exhibit distinct characteristics, including a white dorsal shell background, pearly white internal shell, and chevron markings, differing significantly from those collected from Honshu Island. It is crucial to recognize that shell color patterns are influenced by habitat substrate, particularly the coralline sands in the tropical Ryukyu archipelago.

In addition, the archived samples from Ryukyu Islands could be easily misidentified as *P*. *saccharina*, but careful examination of the shells shows that they are likely to be *P. parva* n. sp. For example, *P. saccharina* displays a much whiter shell background and more acute radial ribs compared to the blunt edges observed in the radial ribs of *P. parva* n. sp. from the Ryukyu Islands. The taxonomic and genetic distinctions observed are substantive evidence supporting the recognition of *Patelloida parva* n. sp. as a novel species within the *Patelloida* complex.

Comparison of Patelloida parva n. sp. with Patelloida saccharinoides

The genetic characteristics of *Patelloida parva* n. sp. were compared with those of *Patelloida saccharinoides*, a tropical species exhibiting 93% genetic similarity. Although this study did not perform side-by-side comparisons between *P. parva* n. sp and *P. saccharinoides*, substantial morphological differences were observed based on the original description published on *P. saccharinoides* by Habe and Kosuge (1966). Below, we discuss the differences with the *P. saccharinoides*, justifying the recognition of *P. parva* n. sp. as a distinct species.

P. parva n. sp. exhibits a conical shell with 8–12 radial ribs of varying thickness. The major ribs are thicker, while thinner secondary ribs intersperse between the primary ribs, forming a distinctive stellate pattern. In contrast, *P. saccharinoides* (Fig. S3) possesses six prominent radial ribs that are thicker and paired, projecting outward radially. Externally, *P. parva* n. sp. displays greyish-blue to brown reticulate markings with a whitish eroded apex. The ventral view reveals a smooth and lustrous interior with blue and yellow shadings on the apex and dark blue to black margins encircling the shell. In contrast, *P. saccharinoides* exhibits a dark outer coating with black margins except at the rib ends, and a uniformly white internal surface. Shell size also differs significantly. *P. parva* n. sp. is smaller in size, while *P. saccharinoides* has larger dimensions, with lengths of 36.3–40.4 mm, widths of 32.0–35.5 mm, and heights of 8.5–11.2 mm (See Table S1 for shell dimensions of *P. parva* samples).

Despite a 93% genetic similarity between *P. parva* n. sp. and *P. saccharinoides*, mitochondrial 16S rRNA analysis revealed sequence divergence rates of 5.01%, a sufficient threshold to distinguish them as separate species. Phylogenetic analysis using Bayesian inference confirmed the monophyly of *P. parva* n. sp., clustering it with *P. saccharinoides* but maintaining clear genetic distinctiveness. In terms of ecological distribution, *P. parva* n. sp. is confined to the intertidal zones of Kochi and Wakayama Prefectures, Japan, with additional occurrences in Amami-Oshima Islands. Its distribution is influenced by the Kuroshio Current, which likely facilitated its migration from the tropics. The type locality of *P. saccharinoides* is in Zamboanga, Mindanao, Philippines.

However, the sequences of *P. saccharinoides* available in GenBank lack corresponding morphological data, raising the possibility that they do not represent the true *P. saccharinoides* as originally described by Habe and Kosuge (1966). Furthermore, no genetic sequences collected from the type locality of *P. saccharinoides* have been analyzed, increasing the risk of misidentification. Additional morphological and molecular studies, particularly involving specimens from the type locality, are necessary to confirm the genetic status of *P. saccharinoides* and its relationship to *P. parva* n. sp.

Distribution of Patelloida parva n. sp. is influenced by the Kuroshio current and tropical waters

Sasaki (1999) documented the presence of *P. parva* n. sp. in Okinawa and Amami-Oshima Islands, as well as Kagoshima, Kochi, and Wakayama Prefectures. Unlike the widely distributed *P. lanx* in the Pacific Ocean, Sea of Japan, and Seto Inland Seas, *P. parva* n. sp. is confined to the Pacific coasts. Our study reveals its preference for capes and coasts near the open ocean, contrasting with *P. lanx*, which also inhabits bays and inland shores.

All *P. parva* n. sp. samples sequenced in this study were collected from Kashiwajima, Kochi Prefecture, and Kushimoto, Wakayama Prefecture—coastal areas significantly influenced by the Kuroshio current. Both locations are impacted by the Bungo Channel and Kii Channel, with Kashiwajima closer to the entrance to Sukumo Bay than Kushimoto to the entrance of Kii Channel. Kashiwajima, Kochi, with more than 800 reported species, and Kushimoto, Wakayama, experience a diverse coastal fish fauna due to the Kuroshio current's influence.

The selected type locality for *P. parva* n. sp., Ogokuda beach in Cape Shionomisaki, Kushimoto (Fig. S4), boasts the highest shellfish diversity on Honshu Island (CBD 2015). The northern limit of *P. parva* n. sp. along southern Wakayama aligns with the existing northern limit of coral reefs (Nakabayashi et al. 2019). The species' occurrence in Japan is likely influenced by warm waters from the Kuroshio current, possibly originating from the tropical waters of the Indo-west Pacific. Its absence from the Tsushima current region suggests a preference for higher salinity and lower nutrient concentration, distinctive differences between of the Kuroshio and Tsushima currents. However, further investigation is necessary to comprehend the species abundance, ecology, and distribution in its habitat range.

The possible tropical origin of this new species could be linked to the phylogenetic distance of *Patelloida parva* n. sp. closer to the *P. saccharinoides*, a tropical species, compared to the *Patelloida saccharina* species complex in Japan. This hypothesis corroborates previous descriptions that the morphology of our undescribed species is similar to *Patelloida saccharinoides* (Sasaki 1999). Divergence time was not estimated as the divergence rate for the 16S rRNA region in gastropods remains to be elucidated, but several inferences can be made. Tropical marine gastropods in Japan were reported to have expanded their habitat ranges northward during the Late Neogene (\sim 5–2 Ma) when sea surface temperatures were warmer (Tomida & Kitao, 2002; Yokoyama, 1911). During this period, the

Kuroshio current was also believed to have existed in some form (Tomida et al. 2013), facilitating the migration from the tropics. Formal confirmation of the occurrence of this species in the Ryukyu Islands could also strengthen the hypothesis of a tropical origin. Overall, these evolutionary processes may have influenced the demographic history and present-day structure of *Patelloida parva* n. sp.

CONCLUSIONS

Our study provides a combination of morphological, genetic, and geographical evidence that supports the recognition of *Patelloida parva* n. sp. as a novel species, including comparisons to other closely related *Patelloida* species. In addition, the new species' confinement to Pacific coasts along the Japanese archipelago, particularly in regions influenced by the Kuroshio current, as well as its genetic similarity closer to a tropical species, the *P. saccharinoides*, suggest a tropical evolutionary origin.

Acknowledgments: We thank Dr. Kazunori Hasegawa for the loan of specimens from the National Museum of Nature and Science (NMNS). We are also highly indebted to Ms. Moe Shimizu and the University of Tokyo University Museum for the assistance in the genetic and morphological laboratory work. This work was financially supported by the Seto Marine Biological Laboratory, Kyoto University to FJP, AA, and TN.

Authors' contributions:

Competing interests:

Availability of data and materials: mtDNA sequence data were deposited in GenBank (OQ9999906-OQ999927).

Consent for publication:

Ethics approval consent to participate:

REFERENCES

- CBD. 2015. Report of the regional workshop to facilitate the description of ecologically or biologically significant marine areas in the seas of East Asia. UNEP.
- Gray JE. 1840. Shells of molluscous animals. *In*: Synopsis of the contents of the British Museum, ed. **42:**105–152.
- Habe T, Kosuge S. 1966. New genera and species of the tropical and subtropical Pacific molluscs. Venus (Japanese Journal of Malacology) 24:312–341. doi:10.18941/venusjjm.24.4 312.
- Kirkendale LA, Meyer CP. 2004. Phylogeography of the *Patelloida profunda* group (Gastropoda: Lottidae): Diversification in a dispersal-driven marine system. Mol Ecol 13:2749–2762. doi:10.1111/j.1365-294X.2004.02284.x.
- Nakabayashi A, Yamakita T, Nakamura T, Aizawa H, Kitano YF et al. 2019. The potential role of temperate Japanese regions as refugia for the coral *Acropora hyacinthus* in the face of climate change. Sci Rep **9**:1–12. doi:10.1038/s41598-018-38333-5.
- Nakano T, Ozawa T. 2004. Phylogeny and historical biogeography of limpets of the order Patellogastropoda based on mitochondrial DNA sequences. J Molluscan Stud **70:**31–41. doi:10.1093/mollus/70.1.31.
- Nakano T, Ozawa T. 2007. Worldwide phylogeography of limpets of the order Patellogastropoda: Molecular, morphological and palaeontological evidence. J Molluscan Stud 73:79–99. doi:10.1093/mollus/eym001.
- Okutani T. 2017. Marine mollusks in Japan. 2nd edn, vol 2. Tokai University Press.
- Paran FJ, Ikeo K, Asakura A, Nakano T. 2023. Species divergence despite minimal morphological differentiation and habitat overlap in the *Patelloida saccharina* (Patellogastropoda: Lottiidae) species complex. Biol J Linn Soc 139:173–191. doi:10.1093/biolinnean/blad019.
- Quoy, HE, Gaimard, P. 1834. Mollusques. Zoologie. *In*: Voyage de découvertes de l'Astrolabe, exécuté par ordre du Roi, pendant les années 1826-1827-1828-1829, sous le commandement de M. J. Dumont d'Urville **3**:1–366.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542. doi:10.1093/sysbio/sys029.
- Sasaki T. 1999. The present state and problems of the taxonomy of Japanese patellogastropod limpets. Part II: Lottiidae. Chiribotan **29:**37–46.
- Tomida S, Akazaki H, Kawano T. 2013. A janthinid gastropod from late Neogene Miyazaki Group of Southwestern Japan, and a status of *Hartungia*. Bull Mizunami Fossil Mus **39:**59–63.

- Tomida S, Kitao F. 2002. Occurrence of *Hartungia* (Gastropoda: Janthinidae) from the Tonohama Group, Kochi Prefecture, Japan. Bull Mizunami Fossil Mus **29:**157–160.
- Yokoyama M. 1911. Climatic changes in Japan since the Pliocene Epoch. J Geol Soc Japan 18:1–18. doi:10.5575/geosoc.18.217_1.

Zoological Studies 64:26 (2025)

Supplementary materials

Table S1. Shell measurement of Patelloida parva n. sp. samples and museum archives.

Fig. S1. Shell morphology of *Patelloida* sp. archived at the National Museum of Nature and Science (NMNS), Tsukuba, Japan. See Table S1 for shell measurements.

Fig. S2. Shell morphology of *Patelloida parva* n. sp., *P. saccharina*, and *P. lanx*. *P. parva* n. sp. differs from *P. lanx* with its irregular secondary radial ribs, and it differs from *P. saccharina* with the distinct chevron markings in the latter.

Fig. S3. Digital scan of the *Patelloida saccharinoides* holotype from Habe & Kosuge (1966). The scanned specimen represents the original morphological description of *P. saccharinoides*, providing a reference for comparative analysis with *Patelloida parva* n. sp. Key diagnostic features, including radial rib patterns, shell shape, and coloration, are visible, aiding in the assessment of species delineation.

Fig. S4. Habitat of *Patelloida parva* n. sp. in Ogokuda Beach, Cape Shionomisaki, Kushimoto, Wakayama Prefecture, Japan (type locality).