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Two new species of *Pseudoneilonella* Laghi, 1986 (Bivalvia: Neilonellidae) from the southwestern Japan and a redescription of *Neilonella kuroshimaensis* Okutani, 2011

Kazutaka Amano[1] & Chong Chen[2]

1 *Joetsu University of Education, 1 Yamayashiki, Joetsu, Niigata 943-8512, Japan; amano@juen.ac.jp*
https://orcid.org/0000-0002-8320-8661
2 *X-STAR, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan; cchen@jamstec.go.jp*
https://orcid.org/0000-0002-5035-4021

Abstract. Neilonellid bivalves are commonly found in the sediments of the deep sea. Here, we describe two new species of the genus *Pseudoneilonella* from cold seeps in the Nankai Trough, Japan, the first report of this genus from the northwestern Pacific Ocean. *Pseudoneilonella costata* n. sp. is characterised by having an oblique posterior margin, some crenulations on the anterior inner shell surface, and a large, 300–310 μm prodissoconch. *Pseudoneilonella fusca* n. sp. is characterised by having an acutely rounded posterior end, a thick, dark-brown periostracum, a deeply depressed lunule, and a rather large, 285 μm prodissoconch. We also re-examined the type series and additional topotypes of *Neilonella kuroshimaensis* Okutani, 2011 from the Kuroshima Knoll seep on the Ryukyu Arc. This species is redescribed, shown to be separate from the above two new species, and transferred to *Pseudoneilonella*, as *P. kuroshimaensis* n. comb.

Key words. Deep-sea, Protobranchia, methane seep, Nuculanoidea, redescription, Nankai Trough

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Introduction

Neilonellids are protobranch bivalves that typically inhabit muddy substrates in the deep sea (e.g. Higo *et al.* 1999; Coan *et al.* 2000; La Perna 2007; Kurozumi *et al.* 2017). The neilonellid genus *Pseudoneilonella* was first established by Laghi (1986), based on the fossil species *Nucula pusio* Philippi, 1844 from the Plio-Pleistocene of Calabria, southern Italy. The genus is characterised by shells having strong commarginal ribs and an opisthodetic ligament. Until now, four living *Pseudoneilonella* species—*P. atossa* (Dall, 1908), *P. latior* (Jeffreys, 1876), *P. salicensis* (Seguenza, 1877), and *P. virens* (Dall, 1890)—have been recorded from the Atlantic Ocean, the Mediterranean Sea, and the southeastern Pacific Ocean.

We recovered empty valves of neilonellid bivalves from abyssal cold-seep sites in the Nankai Trough (Fig. 1), southwestern Japan. Morphological examinations revealed them to represent two undescribed species of *Pseudoneilonella*, constituting the first report of the genus from the western Pacific Ocean. Furthermore, we re-examined the type specimens and a few additional specimens of *Neilonella kuroshimaensis* Okutani, 2011, which was described from the upper bathyal Kuroshima Knoll cold seep on the Ryukyu Arc, southern Japan. This revealed it to be a *Pseudoneilonella.* In the sections below, we describe the two new species, *P. costata* n. sp. and *P. fusca* n. sp., as well as provide a redescription of *N. kuroshimaensis* and move it to *Pseudoneilonella*, as *P. kuroshimaensis* n. comb.

Materials

Neilonellid bivalve specimens were collected by the human-occupied vehicle (HOV) *Shinkai 6500* or the remotely operated vehicle (ROV) *Hyper-Dolphin* from three cold seep sites in the Nankai Trough (Chen *et al.* 2025) and the Kuroshima Knoll Seep Site on the Ryukyu Arc (Fujikura *et al.* 2003), southwestern Japan (Fig. 1).

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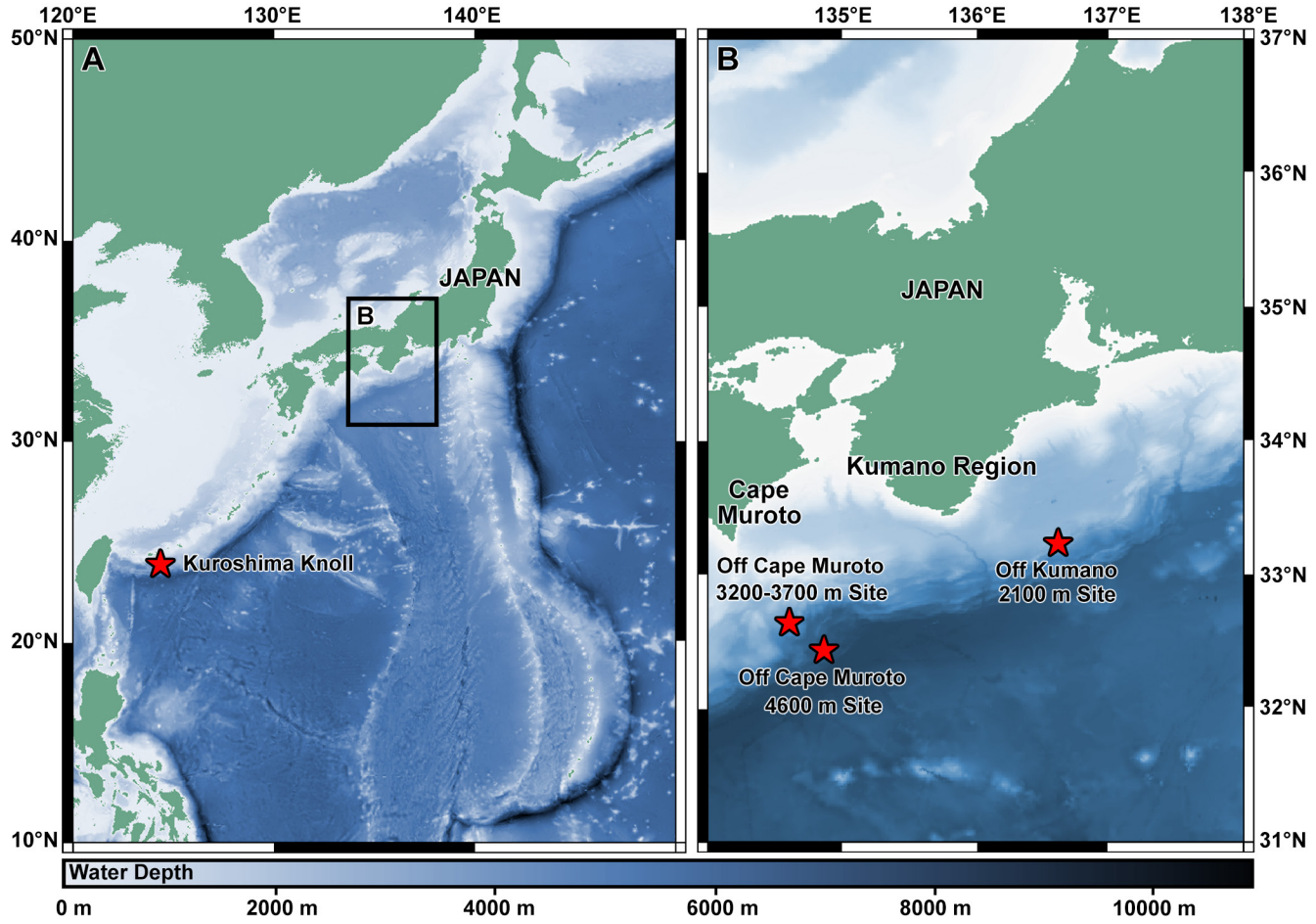


Figure 1. Map of localities where the three *Pseudoneilonella* species studied herein were sampled. Bathymetry was generated an using equidistant cylindrical projection using publicly available data on GEBCO (General Bathymetric Chart of the Oceans, https://www.gebco.net/).

From a deepwater cold-seep site, officially called "Off Cape Muroto 3,200–3,700 m Seep Site (32°21′N, 134°56′E)" in Nankai Trough, Japan (Nakajima *et al.* 2014), one empty conjoined shell, one right valve, and one left valve of *Pseudoneilonella costata* n. sp. were recovered. These were obtained by a scoop sampler operated by the manipulators of the HOV *Shinkai 6500* during the R/V *Yokosuka* cruise YK25-09C (Chen *et al.* 2025). The scoop samples targeted colonies of the large vesicomyid clam *Abyssogena kaikoi* (Okutani & Métivier, 1986). On board the research vessel, sediments from the scoop samples were sieved on a 0.5 mm mesh, which revealed the bivalve shells.

Seven empty neilonellid shells (one conjoined shell, three right valves, and three left valves) of *Pseudoneilonella fusca* n. sp. were recovered from the "Off Cape Muroto 3,200–3,700 m Seep Site (32°32–35′N, 134°41–43′E)" in Nankai Trough, by HOV *Shinkai 6500* during R/V *Yokosuka* cruise YK05-08 Leg 1 (Nakajima *et al.* 2014). Additionally, two more conjoined shells of this species were obtained from the "Off Kumano 2,100 m Seep Site (33°15.780′N, 136°43.056′E)" in Nankai Trough (Nakajima *et al.* 2014), by HOV *Shinkai 6500* during the same cruise.

In addition to the re-examination of the holotype (NSMT-Mo 77381) and two paratypes (NSMT-Mo 77382a, b) of *Neilonella kuroshimaensis* Okutani, 2011 (= *Pseudoneilonella kuroshimaensis* n. comb.) stored at the National Museum of Nature and Science, Tsukuba (NSMT), four empty conjoined valves were newly collected and examined. These were obtained from the type locality, Kuroshima Knoll Cold-seep Site, on the Ryukyu Arc (24°07.830′N, 124°11.556′E, 641 m deep), sampled by ROV *Hyper Dolphin* during R/V *Natsushima* cruise NT04-03 Leg 2.

All specimens treated herein are deposited in the Mollusca collection of the Department of Zoology, National Museum of Nature and Science in Tsukuba, Japan and given the specimen prefix NSMT-Mo.

Taxonomy

Family Neilonellidae Schileyko, 1989

Genus *Pseudoneilonella* Laghi, 1986

Saturnia Seguenza 1877: 1178, *non Saturnia* Schrank, 1802 (homonym).

Pseudoneilonella Laghi 1986: 191. Type species: *Nucula pusio* Philippi, 1844, from the Plio-Pleistocene of Calabria, southern Italy (by monotypy).

Diagnosis. Shell subovate to subtrigonal-elongate, inflated, thick; subequilateral to inequilateral, with posterior end longer; periostracum thin to thick, adherent; sculpture of heavy commarginal ribs to fine striae, sometimes with additional faint radial striae; umbones prominent, orthogyrate to prosogyrate; hinge plate wide; taxodont teeth moderate to heavy, in two series, separated by narrow to wide subumbonal area; ligament opisthodetic, mostly external, but with small sunken portion under beaks; pallial sinus wide (slightly modified from Valentich-Scott *et al.* 2020).

Remarks. *Pseudoneilonella* was proposed by Laghi (1986) as a replacement name for *Saturnia* Seguenza, 1877 (*non* Schrank, 1802). *Pseudoneilonella* is similar to *Neilonella* Dall, 1881 but has an opisthodetic ligament, and *Neilonella* has an amphidetic ligament and a rather continuous series of teeth (La Perna 2007).

Austrotindaria Fleming, 1948 from New Zealand shares the opisthodetic ligament with *Pseudoneilonella*. However, according to La Perna (2007), the type species of *Austrotindaria*, *A. wrighti* Fleming, 1948 has a small, elongate ligament pit between the anterior and posterior teeth which is never seen in *Pseudoneilonella*. Moreover, the convex postero-dorsal margin of *Austrotindaria* also helps us to separate it from *Pseudoneilonella*.

The tindariid genus *Tindaria* Bellardi, 1875 shares the commarginal ribs and opisthodetic ligament with *Pseudoneilonella*. However, the hinge of *Tindaria* shows continuous series, not breaking in the central part of hinge (Coan *et al.* 2000). Moreover, *Tindaria* has a broadly rounded posterior end, not acutely rounded as in the neilonellids.

Pseudoneilonella costata n. sp.

[New Japanese name: Arasuji-hatomugi-sode-gai]

Figures 2, 3

ZooBank registration. urn:lsid:zoobank.org:act:74D6493D-EEB8-47FC-B374-D8107A4B2E32

Type locality. Off Cape Muroto 4,600 m Seep Site (32° 21.6436′ N, 134° 56.3388′ E, 4,637 m deep), Nankai Trough, Japan (see Chen *et al.* 2025 for details, including *in situ* photographs); HOV *Shinkai 6500* dive #1858, 9 June 2025, R/V *Yokosuka* cruise YK25-09C.

Type material. Holotype, empty conjoined valves, NSMT-Mo 82431, collected by scoop sampler among *Abyssogena kaikoi*. Paratype #1, a disarticulated right valve, NSMT-Mo 82432 and paratype #2, a disarticulated left valve, NSMT-Mo 82433, same HOV *Shinkai 6500* dive at the same seep site but from a different *A. kaikoi* colony (32° 21.4756′ N, 134° 56.4420′ E; 4,673 m deep).

Diagnosis. *Pseudoneilonella* with oblique posterior margin, olive-coloured periostracum, around 20 commarginal riblets separated by wider interspaces in anterior to central part of disc, but smooth in posterior part. Some indistinct crenulations observed on inside of ventral anterior part. Lunule indistinct; escutcheon indistinct, narrow, lanceolate.

Description. Shell rather large for genus, attaining 9.9 mm in length, rather thin, nuculaniform (H/L = 0.65–0.68), moderately inflated (T/L = 0.27–0.30). Antero-dorsal margin broadly arcuate and transitioning into rounded anterior margin; postero-dorsal margin nearly straight and gently sloping into oblique posterior margin; posterior end not pointed; ventral margin broadly arcuated. Umbo produced above dorsal line. Beak orthogyrate and located anterior ⅓–⅔. Shell surface sculptured by about 20 narrow, erect commarginal riblets on anterior to medial portions of shell, separated by wider interspaces on anterior and central part of disc. Surface of posterior part of disc smooth, except for fine commarginal lines. Lunule indistinct; escutcheon indistinct, narrow, and lanceolate. Ligament opisthodetic (Fig. 3A, B). Shell surface covered by olive-coloured periostracum. Inner surface of anterior margin to central part of ventral margin weakly crenulated (Fig. 2I). Taxodont teeth separated into two arcs by small central pit (Fig. 3C) or ridge (Fig. 3A, B); anterior teeth 9 or 10; posterior teeth 17–19. Anterior adductor muscle scar indistinct; posterior one small, elongate-ovate scar just above moderately deep, U-shaped pallial sinus (Fig. 2J). Prodissoconch large for genus, 300–310 μm long; subquadrate, sculptured by undulated commarginal ribs and irregular radial riblets, forming a reticulate pattern (Fig. 3E).

Measurements. Table 1.

Etymology. *Costatus*, Latin adjective, meaning "ribbed". This species is named for its remarkable commarginal ribs.

Remarks. Table 2 compares the key morphological characters and habitat information of known *Pseudoneilonella* species, including our new species. Detailed comparative remarks for the most morphologically similar species are included as follows.

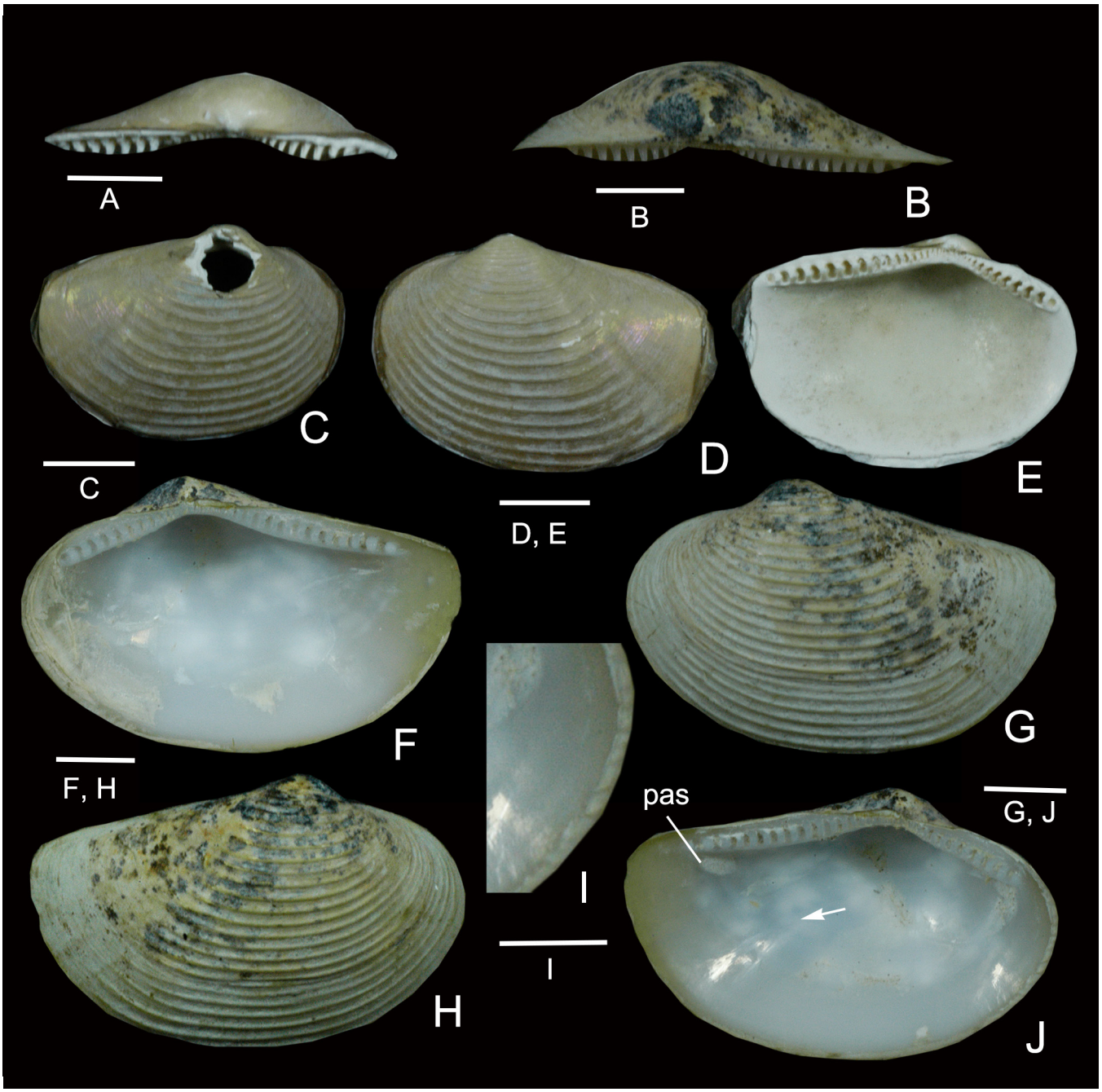


Figure 2. Type specimens of *Pseudoneilonella costata* n. sp. **A**, **D**, **E**, paratype #2, left valve, NSMT-Mo 82433. **B**, **F–J**, holotype, NSMT-Mo 82431: (**B**, **F**, **H**) right valve; (**G**, **I**, **J**) left valve; (**I**) enlarged view of inner surface of anterior part. **C**, paratype #1, right valve, NSMT-Mo 82432. Abbreviation: pas, posterior adductor muscle scar. White arrow indicates top of pallial sinus. Scale bars = 2 mm.

Table 1. Measurements of *Pseudoneilonella costata* n. sp. Abbreviations: L, shell length; H, shell height; AL, anterior shell length; T, thickness of one valve; AT, number of anterior teeth, PT, number of posterior teeth, NR, number of commarginal ribs.

Specimen	Type status	L (mm)	H (mm)	AL (mm)	T (mm)	H/L	AL/L	T/L	AT	PT	NR	Valve
NSMT-Mo 82431	Holotype	9.9	6.5	3.3	2.7	0.66	0.33	0.27	10	19	20	Right
NSMT-Mo 82432	Paratype #1	6.9	4.7	2.8	2.1	0.68	0.41	0.30	9	18	19	Left
NSMT-Mo 82433	Paratype #2	7.1	4.6	2.4	2.0	0.65	0.34	0.28	10	17	12+	Left

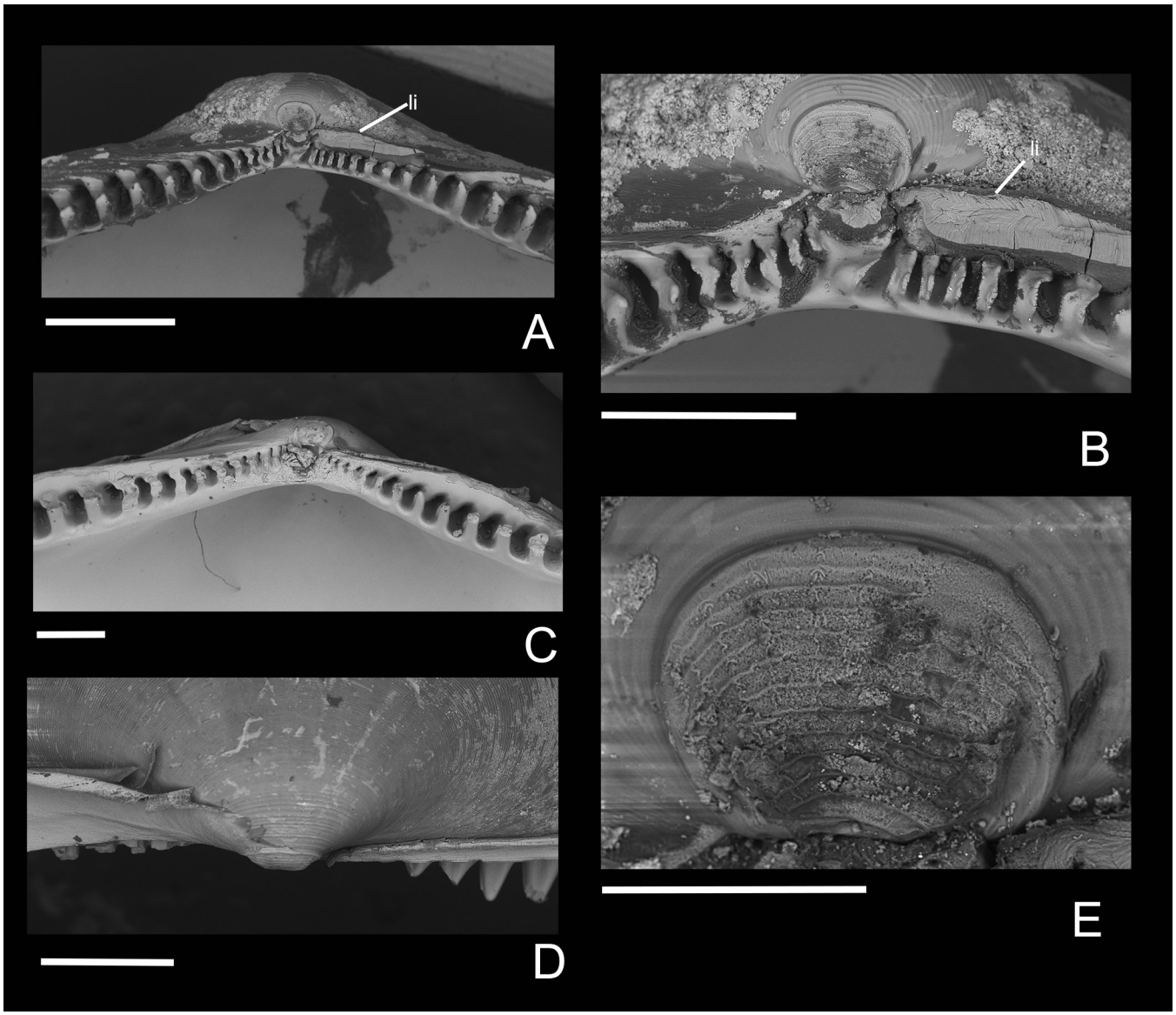


Figure 3. SEM micrographs showing hinge plate and prodissoconch of *Pseudoneilonella costata* n. sp. **A**, **B**, **E**, hinge plate and the prodissoconch of right valve, paratype #1 (NSMT-Mo 82432): (**A**) hinge plate; (**B**) enlargement of the central part of hinge; (**E**) prodissoconch. **C, D**, hinge plate and dorsal view of the beak of left valve, paratype #2 (NSMT-Mo 82433): (**C**) hinge plate; (**D**) dorsal view of the beak. Abbreviation: li, ligament. Scale bars: 500 μm in A–D: 200 μm in E.

Pseudoneilonella costata n. sp. differs from *P. fusca* n. sp. (Fig. 4) described below by having an indistinct lunule, an oblique posterior margin, and the lack of a blunt ridge from the beak to posterior end defining the escutcheon and a larger prodissoconch (300–310 μm long) sculptured by undulated commarginal ribs and irregular radial riblets (Table 2). Moreover, *P. costata* n. sp. has more numerous (about 20) commarginal ribs that diminish towards the posterior part of the disc.

Pseudoneilonella kuroshimaensis n. comb. (Fig. 5) from the Kuroshima Knoll on the Ryukyu Arc, Japan is similar to *P. costata* n. sp. in sharing the opisthodetic ligament and remarkable commarginal ribs separated by wider interspaces. However, *P. costata* n. sp. differs from *P. kuroshimaensis* n. comb. in having taller, fewer commarginal ribs with wider interspaces, lacking an acutely rounded posterior margin, lacking a blunt ridge demarcating the escutcheon, having inner crenulations on the inside of anterior and ventral margins, and having olive-coloured (not pale brown to pale yellow) periostracum. Moreover, *P. costata* n. sp. was collected from abyssal depth around 4,600 m deep in the Nankai Trough, while *P. kuroshimaensis* n. comb. was found

Table 2. Key morphological characteristics and distribution of living *Pseudoneilonella* species. Abbreviations: IC, inner crenulations; WIR, wider interspaces between erect commarginal ribs.

	***P. costata* n. sp.**	***P. fusca* n. sp.**	***P. kuroshimaensis* (Okutani, 2011) n. comb.**	***P. latior* (Jeffreys, 1876)**	***P. salicensis* (Seguenza, 1877)**	***P. atossa* (Dall, 1908)**	***P. virens* (Dall, 1890)**
Max. shell length (mm)	9.9	8.6	8.9	2.5–4.0	10.7	9.0	6.0
Posterior margin	Oblique	Acutely rounded	Acutely rounded	Acutely rounded	Acutely rounded	Pointed	Broadly rounded
Periostracum	Olive	Dark brown	Pale brown to pale yellow	?	Pale brown	Olive	Light yellowish brown
Escutcheon	Indistinct	Distinct	Distinct	Distinct	Distinct	Distinct	Poorly demarcated
Lunule	Indistinct	Deeply depressed	Depressed	Depressed	Depressed	Shallowly depressed	?
WIR	+	+	+	–	–	–	–
IC	+	–	–	–	–	–	–
Prodissoconch (μm)	300–310	285	250	?	215	?	?
Distribution	NW Pacific	NW Pacific	NW Pacific	Atlantic, Mediterranean	Atlantic	SE Pacific	SE Pacific
Depth (m)	4,673	2,071–3,257	641	200–3,100	100–4,829	805–2,700	70–821
Reference	This study	This study	This study	Laghi 1986; Warén 1989	Allen & Sanders 1997; La Perna 2007; Huber 2010	Valentich-Scott *et al.* 2020	Valentich-Scott *et al.* 2020

at a much shallower depth (641 m deep) on the Ryukyu Arc.

Pseudoneilonella latior (= *Neilonella striolata* (Brugnon, 1876) *sensu* Warén 1989) living in the Atlantic Ocean and the Mediterranean Sea is somewhat similar to *P. costata* n. sp. However, *P. latior* has a smaller shell, with the broader posterior area and many fine commarginal ribs with narrower interspaces (Laghi 1986; Warén 1989).

Distribution. Only known from the type locality.

Pseudoneilonella fusca n. sp.

[New Japanese name: Kuro-hatomugi-sode-gai]
Figures 4, 6A, E, G

Neilonella kuroshimaensis Okutani—Kurozumi *et al.* 2017: pl. 464, fig. 17. *Non Neilonella kuroshimaensis* Okutani, 2011.

ZooBank registration. urn:lsid:zoobank.org:act:B1E56AC4-E1B5-4C5B-8DBD-7864B573C894

Type locality. Off Cape Muroto 3,200–3,700 m Seep Site, Nankai Trough, Japan (32° 34.902′N, 134° 41.502′E; 3,257 m deep); HOV *Shinkai 6500* dive #884, 18 June 2005, R/V *Yokosuka* cruise YK05-08 Leg 1.

Type material. Holotype, empty conjoined valves, NSMT-Mo 82434. Paratype #1, left valve, NSMT-Mo 82435; paratype #2, left valve, NSMT-Mo 82436; paratype #3, left valve, NSMT-Mo 82437; paratype #4, right valve, NSMT-Mo 82438; paratype #5, right valve, NSMT-Mo 82439; paratype #6, left valve, NSMT-Mo 82440; all with same data as holotype.

Other material examined. Two empty articulated valves (NSMT-Mo 82441, 82442) from the Off Kumano 2,100 m Seep Site (33°15.780′N, 136°43.056′E; 2,071 m deep), Nankai Trough, Japan; HOV *Shinkai 6500* dive #883, 17 June 2005, R/V *Yokosuka* cruise YK05-08 Leg 1.

Diagnosis. *Pseudoneilonella* with thick, dark-brown periostracum, 12–19 strong commarginal ribs separated by wider interspaces; posterior end forming acute angle; postero-dorsal margin straight and blunt radial ridge running from umbo to posterior end defining narrow escutcheon; lunule narrow, distinctly depressed, demarcated by sharp ridge.

Description. Shell rather large for genus, moderately inflated (T/L = 0.26–0.48, mean 0.31), attaining 8.6 mm in

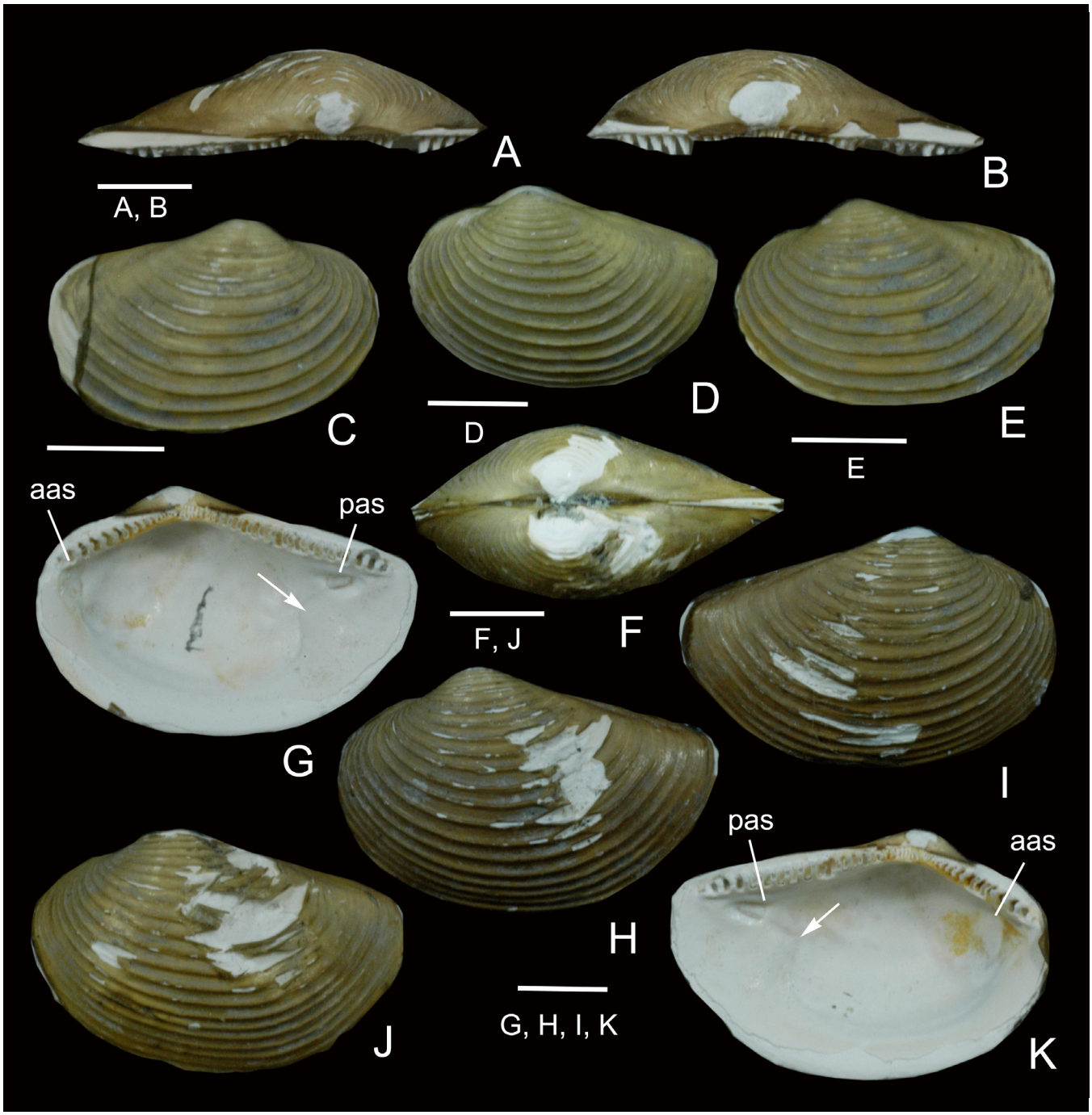


Figure 4. *Pseudoneilonella fusca* n. sp. **A**, **B**, **G**, **H**, **I**, **K**, holotype, NSMT-Mo 82434: (**A**, **H**, **K**) left valve; (**B**, **G**, **I**) right valve. **C**, paratype #4, NSMT-Mo 82438, right valve. **D**, NSMT-Mo 82442, left valve. **E**, paratype #1, NSMT-Mo 82439, left valve. **F**, **J**, NSMT-Mo 82441: (**F**) dorsal view of conjoined valves; (**J**) left valve. Abbreviations: aas, anterior adductor muscle scar; pas, posterior adductor muscle scar. White arrow indicates deepest point of pallial sinus. Scale bars = 2 mm.

length. Postero-dorsal margin straight and gently sloping, forming acute angle to well-rounded ventral margin. Antero-dorsal margin slightly convex, transitioning into subcircular anterior margin. Blunt radial ridge running from umbo to posterior end defining escutcheon (Fig. 4 A, B, F). Beak slightly prosogyrate, situated at anterior ⅓–⅔ of length (AL/L = 0.16–0.42; mean 0.33). Periostracum thick, dark brown. Surface sculptured by 12–19 (mean 14.6) strong commarginal ribs, separated by wider interspaces on whole surface but becoming indistinct near postero-dorsal margin.

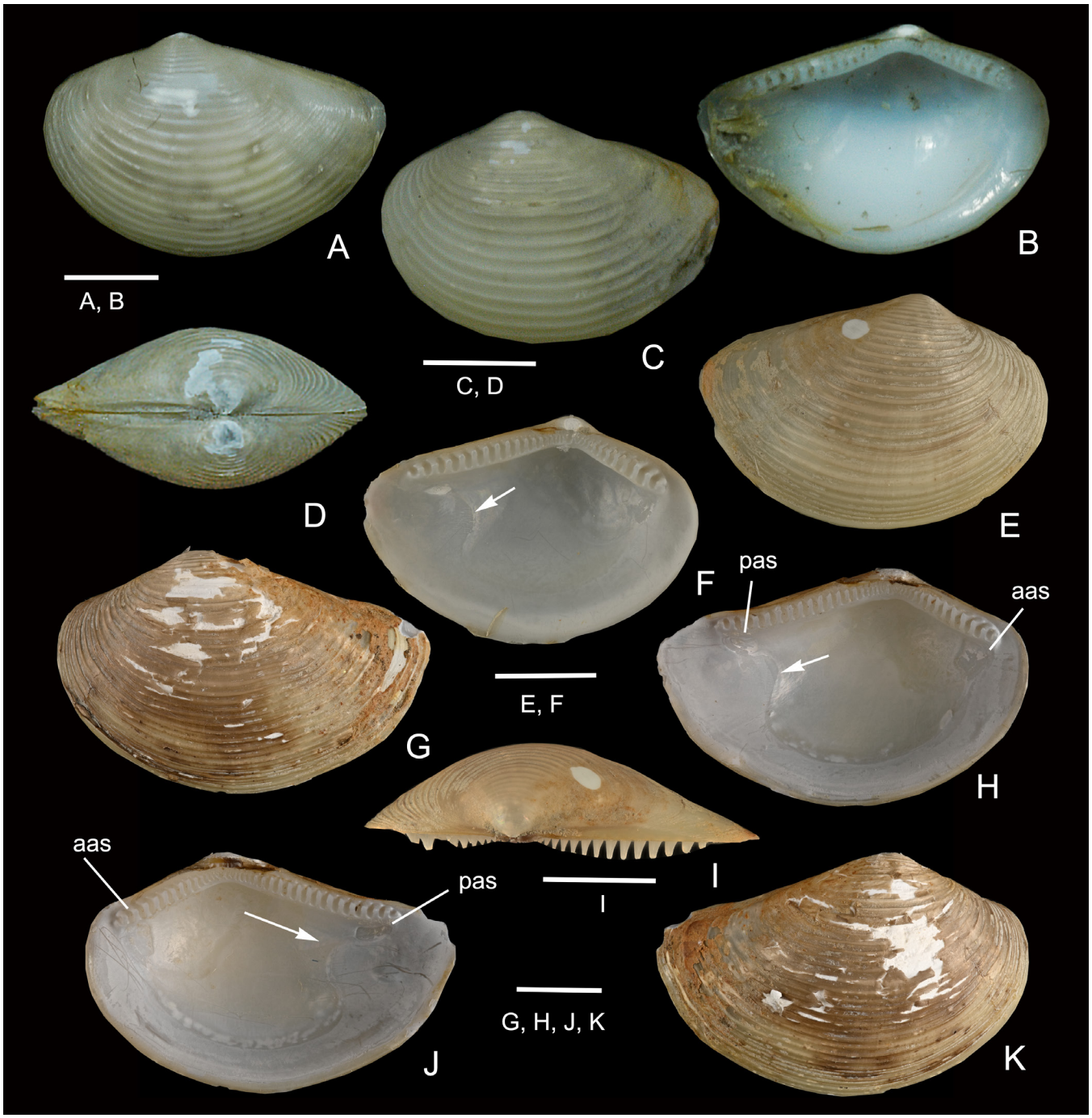


Figure 5. *Pseudoneilonella kuroshimaensis* (Okutani, 2011) n. comb. **A**, **B**, NSMT-Mo 82445, left valve (illustrated as "holotype" by Okutani 2011: fig. 1). **C**, **D**, NSMT-Mo 82443: (**C**) left valve; (**D**) dorsal view of conjoined valves. **E**, **F**, **I**, paratype #2, NSMT-Mo 77382b: (**E**) external right valve, (**F**) inner left valve, (**I**) dorsal view of right valve. **G, H, J, K**, holotype, NSMT-Mo 77381: (**G**, **H**) left valve; (**J**, **K**) right valve. Abbreviations: aas, anterior adductor muscle scar; pas, posterior adductor muscle scar. White arrow indicates deepest point of pallial sinus. Scale bars = 2 mm.

Lunule narrow, distinctly depressed, demarcated by sharp edge (Fig. 4F); escutcheon narrow, lanceolate, depressed, and bounded by ridge running from beak to posterior end. Ligament itself missing in specimens examined but with distinct external posterior furrow (Fig. 6A, C). Anterior arc of hinge with 10–13 teeth; posterior arc with 16–19 teeth; these arcs interrupted by central small pit (Fig. 6A, C). Pallial sinus wide and shallow (Fig. 4G, K). Anterior adductor

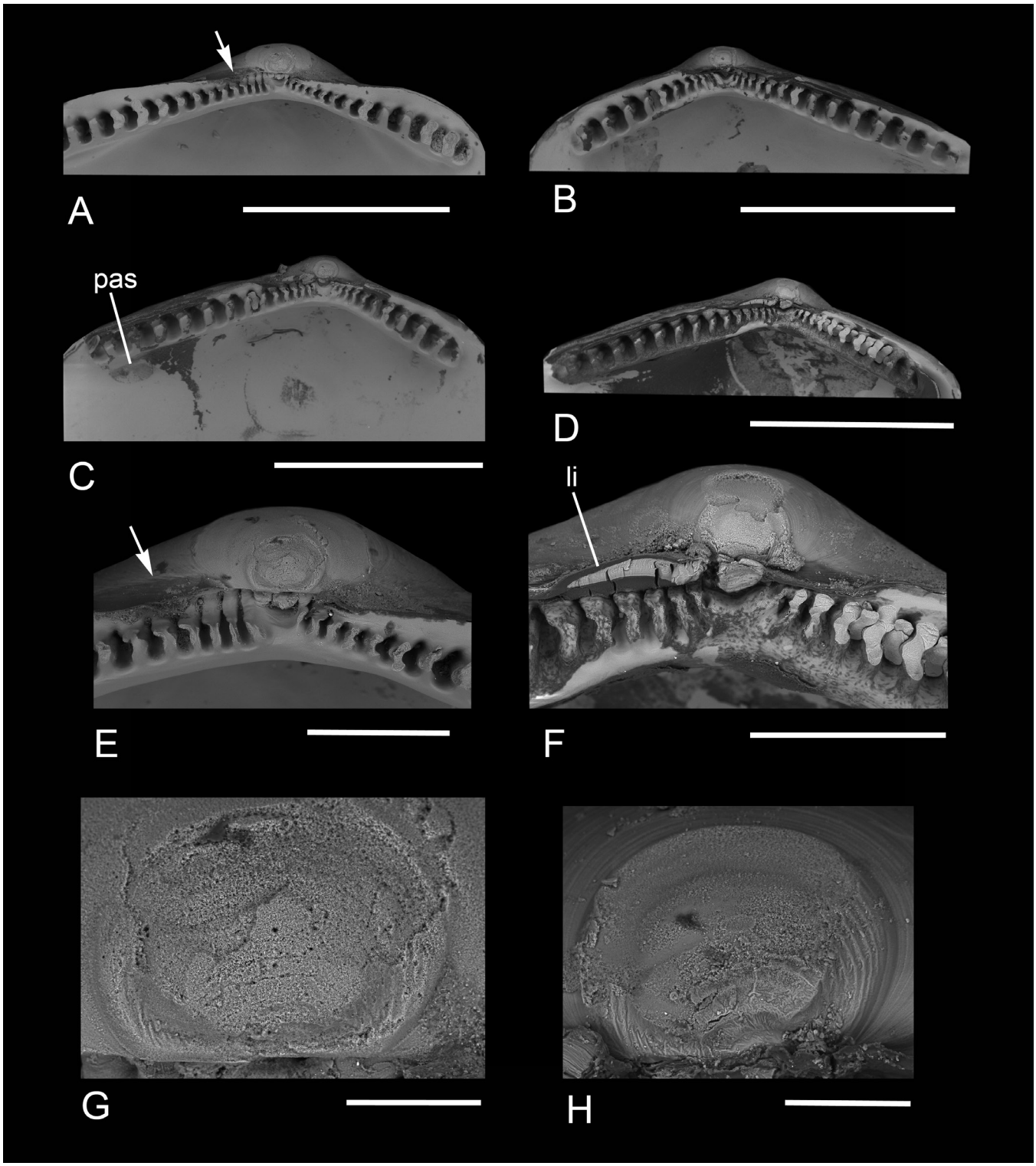


Figure 6. SEM micrographs showing hinge plate and prodissoconch of *Pseudoneilonella fusca* n. sp. and *P. kuroshimaensis* (Okutani, 2011) n. comb. **A**, **E**, **G**, *P. fusca* n. sp., paratype #1, NSMT-Mo 82435: (**A**) hinge plate of the left valve; (E) enlargement of **A**; (G) prodissoconch. **B–D**, **F**, **H**, *P. kuroshimaensis* n. comb.: (**B**, **C**) NSMT-Mo 82444; (**B**) hinge plate of the right valve; (**C**) hinge plate of the left valve; (**D**, **F**) NSMT-Mo 82446; (**D**) hinge plate of the left valve; (**F**) enlargement of **D**; (**H**) prodissoconch. Abbreviations: li, ligament; pas, posterior adductor muscle scar. White arrow indicates posterior external furrow for ligament insertion. Scale bars: 2 mm in A–D: 500 μm in E, F: 100 μm in G, H.

muscle scar ovate, larger than posterior adductor muscle scar; posterior adductor muscle scar small and trigonal (Fig. 4G, K). Prodissoconch 285 μm in length, ill-preserved but probably sculptured by commarginal ribs (Fig. 6G).

Measurements. Table 3.

Etymology. *Fuscus*, Latin adjective, meaning "dark". This species is named for its dark-brown periostracum.

Remarks. Kurozumi *et al.* (2017) previously illustrated this new species as *Neilonella kuroshimaensis* (= *P. kuroshimaensis* n. comb.). Although there was no mention of the locality for the specimen they figured, the illustrated specimen (Kurozumi *et al.* 2017: pl. 464, fig. 17) corresponds to a specimen from the Off Kumano 2,100 m Seep Site. We examined this specimen and illustrate it again (Fig. 4F, J). See Table 2 for a comparison of key morphological and habitat differences among known *Pseudoneilonella* species, including *P. fusca* n. sp. *Pseudoneilonella kuroshimaensis* n. comb. is the most similar species to *P. fusca* n. sp. in both shell size and shell shape. However, *P. fusca* n. sp. has a deeply depressed, shorter lunule demarcated by a sharp edge and has a more distinct, shorter escutcheon. In addition, *P. fusca* n. sp. has generally less numerous (12–19 *vs* 16–30 in *P. kuroshimaensis* n. comb.), strong commarginal ribs separated by wider interspaces, a slightly larger prodissoconch (285 μm *vs* 250 μm in *P. kuroshimaensis* n. comb.; Fig. 6H), and a thicker, darker periostracum. The habitat of the two species also differs, with *P. kuroshimaensis* n. comb. living in much shallower water (641 m deep) than *P. fusca* n. sp. (2,071–3,500 m deep).

The Atlantic *Pseudoneilonella salicensis* shares some characters with *P. fusca* n. sp., including the numerous commarginal ribs, a pointed posterior end, and a radial ridge running from the beak to the posterior end. However, *P. salicensis* has a higher shell with more produced umbo, bears many fine, lower commarginal ribs with wider interspaces, and has a much smaller (215 μm long) prodissoconch than *P. fusca* (Allen & Sanders 1997; La Perna 2007; Huber 2010).

Distribution. Off Cape Muroto 3,200–3,700 m Seep Site, and Off Kumano 2,100 m Seep Site (Nakajima *et al.* 2014), both in Nankai Trough, Japan.

Pseudoneilonella kuroshimaensis (Okutani, 2011) n. comb.

[Japanese name: Sudare-hatomugi-sode-gai]

Figures 5, 6B–D, F, H

Neilonella kuroshimaensis Okutani 2011: 203–204. *Non* Kurozumi *et al.* 2017: pl. 464, fig. 17.

Type material. Holotype, conjoined valves, NSMT-Mo 77381. Paratype #1, conjoined valves, NSMT-Mo 77382a; paratype #2, conjoined valves, NSMT-Mo 77382b; all from Kuroshima Knoll, 24°7.830′N, 124°11.556′E (641 m deep), sampled during ROV *Hyper-Dolphin* dive #291, 14 April 2004, R/V *Natsushima* NT04-03 Leg 2.

Other material examined. Four empty articulated valves (NSMT-Mo 82443, 82444, 82445, 82446), collected from the type locality together with the type specimens.

Diagnosis. *Pseudoneilonella* with pale-brown to pale-yellow periostracum, 16–33 commarginal ribs separated by wider interspaces. Lunule long, depressed, narrow, but not demarcated by edge. Escutcheon long and well-defined.

Supplementary redescription. Shell rather large for genus, moderately inflated (W/L = 0.42–0.55, mean 0.49), attaining 8.9 mm in length. Beak orthogyrate, situated at anterior ⅔ of disc (AL/L = 0.37–0.56; mean 0.42). Periostracum pale brown to pale yellow. Surface sculptured by 16–33 (mean

Table 3. Measurements of *Pseudoneilonella fusca* n. sp. Abbreviations: L, shell length; H, shell height; T, thickness of one valve A; AL, anterior shell length; AT, number of anterior teeth, PT, number of posterior teeth, NR, number of commarginal ribs.

Specimen NSMT-Mo	Type status	L (mm)	H (mm)	AL (mm)	T (mm)	H/L	AL/L	T/L	AT	PT	NR	Valve	Locality
82434	Holotype	8.6	5.2	3.0	2.2	0.60	0.35	0.26	13	19	18	Right	Off Muroto
82435	Paratype 1	5.9	4.0	2.5	1.5	0.68	0.42	0.25	12	19	12	Left	Off Muroto
82436	Paratype 2	6.2	3.6	2.4	1.6	0.58	0.39	0.26	10	17	13	Left	Off Muroto
82437	Paratype 3	5.8	4.4	1.5	2.2	0.76	0.26	0.38	12	17	15	Right	Off Muroto
82438	Paratype 4	5.0	3.5	2.1	2.4	0.70	0.42	0.48	12	17	14	Right	Off Muroto
82439	Paratype 5	5.5	3.6	0.9	1.2	0.65	0.16	0.22	10	16	12	Left	Off Muroto
82440	Paratype 6	5.0	3.5	1.7	1.7	0.70	0.34	0.34	—	—	12	Right	Off Muroto
82441	—	8.3	5.2	3.1	—	0.63	0.37	—	—	—	19	Right	Off Kumano
82442	—	5.9	4.3	1.7	—	0.73	0.29	—	—	—	16	Right	Off Kumano

22.9) commarginal ribs, separated by wider interspaces in young stage but narrower interspaced toward ventral margin in adults. Blunt ridge running from umbo to posterior end demarcating long and narrow escutcheon; lunule narrow, depressed, distinctly demarcated by low edge (Fig. 5D, I). Ligament external and opisthodetic (Fig. 6D, F). Anterior arc of hinge with 8–13 teeth; posterior arc with 13–19 teeth. Anterior adductor muscle scar large and quadrate; posterior adductor muscle scar small and elongate-ovate (Fig. 5H, J). Pallial sinus wide, moderately deep; deepest point rounded (Fig. 5F, H, J). Prodissoconch 250 μm long, sculptured by a few commarginal cords (Fig. 6H).

Measurements. Table 4.

Remarks. The opisthodetic ligament revealed from our re-examination of types and additional specimens from the type series indicates that this species belongs to *Pseudoneilonella* instead of *Neilonella*, according to the diagnosis of *Pseudoneilonella* by Laghi (1986). As such, we here transfer this species to *Pseudoneilonella*, as *P. kuroshimaensis* n. comb.

Our examination of the type series of *P. kuroshimaensis* n. comb. stored in NSMT revealed that the specimen illustrated by Okutani (2011) as the holotype is not the actual holotype, but a non-type specimen. We have located the specimen illustrated by Okutani (2011) (NSMT-Mo 82445; Fig. 5A, B), but its sculpture and size of this specimen do not match the description of the holotype. The specimen stored in NSMT as the holotype (NSMT-Mo 77381) does match the original description of the holotype in the shell size and is presumed to be the real holotype; it is figured here (Fig. 5G, H, J, K).

Furthermore, Okutani (2011) also reported three small (non-type) specimens (NSMT-Mo 77387) presumed to be conspecific with *P. kuroshimaensis* n. comb. collected by R/V *Hakuho Maru* cruise KH-05-1 from off Amami-Oshima Island (28°32.2′–31.1′N, 127°01.8′– 01.5′E, 576–594 deep). Upon re-examination of these specimens, however, it was revealed that they have translucent shells with amphidetic ligament. As such, they do not belong to the genus *Pseudoneilonella* and cannot be conspecific with *P. kuroshimaensis* n. comb.

Distribution. Kuroshima Knoll (641 m deep).

Discussion

Our findings constitute the first reports of genus *Pseudoneilonella* from the northwestern Pacific Ocean, but it is likely that additional Pacific neilonellid species previously assigned to *Neilonella* belong to *Pseudoneilonella*, like *P. kuroshimaensis* n. comb. More attention to the ligament morphology and investigations of the type specimens are needed to ascertain their generic assignments of known Pacific neilonellids.

All three *Pseudoneilonella* species treated here were collected from sediments of hydrocarbon seep habitats. Another neilonellid bivalve recorded from cold seeps is *Neilonella profunda* Okutani & Fujiwara, 2005 from 5,225 m deep in the Japan Trench (Okutani & Fujiwara 2005). Although these neilonellids have not been found in habitats other than seeps, they are unlikely to be seep endemics (Okutani 2008). Instead, they probably occur in higher densities at cold seeps due to the increased food availability from local chemosynthetic primary production, as no neilonellid bivalve has been shown to host symbiotic bacteria. The effect of biased sampling at chemosynthetic habitats compared to the ambient seafloor is also a factor.

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Table 4. Measurements of *Pseudoneilonella kuroshimaensis* (Okutani, 2011) n. comb. Abbreviations: L, shell length; H, shell height; AL, anterior shell length; W, width of conjoined valve; AT, number of anterior teeth, PT, number of posterior teeth, NR, number of commarginal ribs.

Specimen NSMT-Mo	Type status	L (mm)	H (mm)	AL (mm)	W (mm)	H/L	AL/L	W/L	AT	PT	NR	Valve
77381	Holotype	8.8	5.7	3.3	4.6	0.65	0.38	0.52	12	19	33	Left
77382a	Paratype #1	6.6+	4.4	2.8	2.9	—	—	—	—	—	26	Right
77382b	Paratype #2	6.5	4.3	2.6	3.3	0.66	0.40	0.51	13	17	29	Right
82443	—	6.0	3.6	2.2	3.3	0.60	0.37	0.55	—	—	19	Left
82444	—	4.9	3.9	1.8	2.3	0.80	0.37	0.47	—	—	18	Right
82445	—	7.3	5.3	3.1	—	0.73	0.42	—	8	13	19	Right
82446	—	5.0	3.3	2.8	2.1	0.66	0.56	0.42	—	—	16	Left

laborative "SHINKAI" expedition (research cruise YK25-09C) and cruise YK05-08 Leg 1; and extend the same to those on-board R/V *Natsushima* during cruise NT04-03 Leg 2. We also extend our gratitude to the HOV *Shinkai 6500* team and the ROV *Hyper-Dolphin* team for their tireless support of our sampling activities. Research cruise YK25-09C was co-funded by JAMSTEC and the Nippon Foundation – Nekton Ocean Census (https://oceancensus.org/) through a Cooperative Research Agreement. We thank Ocean Census for supporting and accelerating species discovery in this work. Akinori Yabuki (JAMSTEC) is gratefully acknowledged for leading the cruise YK25-09C, and Michelle Taylor (Nippon Foundation – Nekton Ocean Census) for leading the Nippon Foundation – Nekton Ocean Census team on-board; Chiaki Kato (JAMSTEC) is acknowledged for leading the cruise YK05-08 Leg 1 and Hiroyuki Yamamoto (JAMSTEC) for leading the cruise NT04-03 Leg 2. We thank Kazunori Hasegawa (NSMT) and Takuma Haga (NSMT) for their curatorial work in depositing the specimens treated herein and for photographing the types of *Pseudoneilonella kuroshimaensis* n. comb. We also thank Gennady M. Kamenev (A.V. Zhirmunsky National Scientific Center of Marine Biology) and Paul Valentich-Scott (Santa Barbara Museum of Natural History) for providing useful comments that improved an earlier version of this paper.

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