Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Research Article

Cite this article: Kobayashi I, Hibino M, Yamamoto M, Fujita T (2024). Description of a new *Luidia* species (Asteroidea: Paxillosida: Luidiidae) from Japan with molecular phylogenetic analysis of the genus *Luidia*. *Journal of the Marine Biological Association of the United Kingdom* **104**, e22, 1–12. https://doi.org/10.1017/S0025315424000158

Received: 17 September 2023
Revised: 21 December 2023
Accepted: 29 January 2024

Keywords:
Asteroidea; Echinodermata; phylogenetics; taxonomy

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Description of a new *Luidia* species (Asteroidea: Paxillosida: Luidiidae) from Japan with molecular phylogenetic analysis of the genus *Luidia*

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Abstract

Luidia iwakiensis n. sp. (Asteroidea, Echinodermata) is described in Japanese waters. A molecular phylogenetic analysis including 18 *Luidia* species supported Döderlein L (1920, *Siboga Expedition* 4, 193–291) four morphogroups. Morphological reconsideration revealed three of the eight criteria of the morphogroup adopted by Döderlein were justified, but the remaining five characters were rejected. The placement of the new species in the Ciliaris-group was supported by molecular as well as morphological evidence, however, it varies from other species of Ciliaris-group by arm number, length of major inferomarginal spines, and pedicellariae on actinal plates.

Introduction

Luidia is the sole genus of the family Luidiidae, characterized by long, slender, and flat arms, small paxilliform superomarginal plates that are not block-like, and knob-ending tube feet (Clark and Downey, 1992). They are found on the sandy bottoms of the littoral to sublittoral zones and are typically distributed in the range of tropical and temperate oceans in the world (Blake, 1983; Clark, 1989; Lawrence, 2013). The genus encompasses 48 species (Clark, 1989; Liao and Clark, 1995; Liu *et al.*, 2006a, 2006b; Hopkins and Knott, 2010; Mah and Blake, 2012), among which, six species, viz *Luidia avicularia* Fisher, 1913, *Luidia hardwicki* (Gray, 1840), *Luidia maculata* Müller and Troschel, 1842, *Luidia quinaria* von Martens, 1865, *Luidia sagamina* Döderlein, 1920, and *Luidia savignyi* (Audouin, 1826) have been found in Japan (Kogure, 2018).

The genus *Luidia* has been divided into ten subgenera that were classified into four morphogroups; Alternata-group, Clathrata-group, Ciliaris-group, and Quinaria-group by Döderlein (1920). These subgenera were rarely referred to, and are currently considered invalid (Clark, 1989). However, several authors have used the morphogroups for sorting of this genus (e.g., Clark, 1953; Clark and Rowe, 1971; Blake, 1973, 1982; Xiao *et al.*, 2013), since they are morphologically distinct (Döderlein, 1920). These morphogroups, however, have not been taxonomically considered as subgenera or separate genera. Recently, Xiao *et al.* (2013) and Lee and Shin (2018) used partial sequences of the mitochondrial cytochrome c oxidase subunit I gene (COI) for shedding light on the interspecific phylogeny of the *Luidia* species. While confirming the distinction between the Alternata- and Quinaria-groups, these analyses, however, could not completely elaborate on the phylogenetic relationships among the four morphogroups due to the low statistical supports.

In this study, we have introduced a new species of the genus *Luidia* found in the sublittoral waters in northern Japan. Furthermore, we revisited the classification of these morphogroups. We conducted a molecular phylogenetic analysis of the genus *Luidia* to verify the distinction between four morphogroups and discussed phylogenetic relationships among these groups.

Materials and Methods

Sample collection and morphological observations

The holotype of the new species was procured by the R/V *Iwaki-Maru* of Fukushima Prefectural Fisheries and Marine Science Research Centre from a depth of 175 m, during a bottom-trawl survey conducted on 8th March 2021. The specimen was fixed with 70% ethanol and preserved in 99.5% ethanol following procurement. The holotype specimen of the new species was deposited in the National Museum of Nature and Science, Tsukuba (NSMT).

We examined five *Luidia* species: including two specimens of *Luidia avicularia* (NSMT E-14357, 14358), one specimen of *L. hardwicki* (NSMT E-14359), one specimen of *L. maculata* (NSMT E-14356), two specimens of *L. quinaria* (NSMT E-14360, 14361), and one

Table 1. Specimens examined for morphological comparisons with *Luidia iwakiensis* n. sp

Species	Catalog number	Locality	Coordinates	Depth	Date of sampling
L. avicularia	NSMT E-14357	off Tanabe Bay, Wakayama Prefecture, Japan	33°41.142′N, 135°13.987′E	104–105 m	April 27, 2018
	NSMT E-14358	off Tanabe Bay, Wakayama Prefecture, Japan	33°41.207′N, 135°13.565′E	107–108 m	April 27, 2018
L. hardwicki	NSMT E-14359	Oomuro Hole, Japan	34°32.685′N, 139°26.752′E	197 m	May 18, 2016
L. maculata	NSMT E-14356	south of Chichijima Island, Ogasawara Islands, Japan	27°00.142′N, 142°11.590′E	134–137 m	July 13, 2016
L. quinaria	NSMT E-14360	northwest of Nishinoomote, Tanegashima Island, Kagoshima Prefecture, Japan	30°47.239′N, 130°55.354′E	79–86 m	May 23, 2017
	NSMT E-14361	off Toba, Mie Prefecture, Japan	34°34.000′N, 136°52.900′E	27 m	October 14, 2016
L. s. sagamina	NSMT E-14363	off Aduchiooshima Island, Nagasaki Prefecture, Japan	33°33.952′N, 129°30.869′E	77–79 m	October 20, 2015

specimen of *L. sagamina sagamina* (NSMT E-14363) for morphological and molecular comparisons with the new species. Detailed information on the collecting location, coordinates, and dates of these specimens has been depicted in Table 1. An MZ8 dissecting microscope (Leica, Germany) was used for inspecting the specimens. Lengths of major radius (R) and minor radius (r) were measured from the centre of the mouth opening to unbroken arm tips and the connection of each proximal part of 2 arms, respectively. The arrangement of the underlying abactinal, marginal, and actinal plates were observed after removing the epidermis and paxillar spines from the proximal portions of the arms by applying commercial bleach (about 5% sodium hypochlorite). The removed spines and pedicellariae were collected in the holotype specimen of this new species for observation under a scanning electron microscope (SEM). Also, some abactinal, superomarginal, and inferomarginal plates were isolated to observe their sizes and shapes. These isolated spines, pedicellariae, and plates were immersed in a drop of commercial bleach for a few minutes which was followed by washing with deionized water to clean remnant tissues. The samples were then mounted on brass SEM stubs and desiccated in the air. Finally, these ossicles were observed under a JSM-6380LV SEM (JEOL, Japan) after coating them with gold-palladium. The semi-dried holotype specimen was scanned using an inspeXio SMX-225CT FPD HR micro-computed tomography (micro-CT) scanner (Shimadzu, Japan), at a tube voltage of 115 kV and a tube current of 70 μA for 30 min, which revealed the fasciolar grooves between the inferomarginal plates. Three-dimensional images were reconstructed with the software VGSTUDIO Max 3.2 (Volume Graphics, Germany).

DNA extraction, gene amplification, and molecular analysis

DNA was extracted from chopped tube feet of six Japanese *Luidia* species (NSMT E-14356, NSMT E-14357, NSMT E-14359, NSMT E-14360, NSMT E-14363, and NSMT E-14364) by boiling the tissues with Chelex-100 resin (Bio-Rad, Inc., USA) in ultrapure water for 30 min, followed by rapid cool down on the ice for ten minutes. Polymerase chain reaction (PCR) was carried out by using 5.0 μl of 2 × PCR Buffer (Takara Bio, Inc., Japan), 0.2 μl TKs Gflex Polymerase (Takara Bio, Inc., Japan), 0.2 μl of each primer pair (10 μM), 1.0 μl of extracted DNA, and 3.4 μl of ultrapure water (3.4 μl). Two primer pairs, COIceF (5'-ACTGCCCACG CCCTAGTAATGATATTTTTTATGGTNATGCC-3') and COIceR (5'-TCGTGTGTCTACGTCCATTCCTACTGTRAACATRTG-3'), and 16SaL (5'- CGCCTGTTTATCAAAAACAT −3') and 16SAN-R (5'- GCTTACGCCGGTCTGAACTCAG -3') targeted the partial sequences of the mitochondrial COI and 16S rRNA gene (16S), respectively (Palumbi, 1994; Zanol *et al.*, 2010; Hoareau and Boisson, 2010). The protocol used for PCR amplification was as follows: preheating at 94 °C for 1 min; 30 cycles of 98 °C for 10 s, 55 °C for 15 s, and 68 °C for 30 s. Following purification using ExoSAP-IT Cleanup Regent (Thermo Fisher Scientific, Inc., USA), Big Dye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, Inc., USA) was used for sequencing the PCR products using the Applied Biosystems 3500xL Genetic Analyzer (Life Technologies, Inc., USA). Assembly of the sequenced data was carried out using GeneStudio Professional Edition ver. 2.2.0.0 (GeneStudio, Inc., USA), which successfully provided COI (598–709 bp) and 16S (555–638 bp) sequences of all specimens. In addition, 15 registered sequences from the GenBank were obtained, and a total of 21 sequences for each gene marker were aligned by MAFFT ver. 7.222 (Katoh and Standley, 2013). The outgroups in our datasets were represented by two species with registered COI and 16S sequences, that belonged to the closest clades of the paraphyletic sister family Astropectinidae to the family Luidiidae (Mah and Foltz, 2011). For the COI dataset, the stop codons were removed by manually editing the sequence errors using MEGA ver. 7.0.26 (Kumar *et al.*, 2016). The 16S dataset was trimmed with the gappyout option by using trimAL 1.2rev59 (Capella-Gutiérrez *et al.*, 2009). GTR + G was selected as a best-fit substitution model by Kakusan4 (Tanabe, 2011) to construct phylogeny for the maximum likelihood (ML) analysis. Both datasets were partitioned by gene region, and the COI dataset was additionally partitioned based on the codon position. ML tree was inferred using RAxML ver. 8.2.9 (Stamatakis, 2014). Bootstrap values (BS) were calculated from 1000 replicates. MEGA ver. 7.0.26 (Kumar *et al.*, 2016) was used to calculate the interspecific Kimura 2-parameter (K2P) distance.

Results

Systematics

Family Luidiidae Forbes, 1839
Genus *Luidia* Forbes, 1839
Luidia iwakiensis n. sp.
(https://zoobank.org/NomenclaturalActs/9B98B65F-6D0E-4666-938FC21890F172BA)
(New Japanese name: Sazare-suna-hitode)

Type Material

Holotype. NSMT E-14364, off Iwaki, Fukushima Prefecture, Japan, 36°53.41'N, 141°16.44'E (Figure 1), 175 m, on March 8, 2021, 3 arms were detached, fixed in 99.5% ethanol, and 1 detached arm was dried.

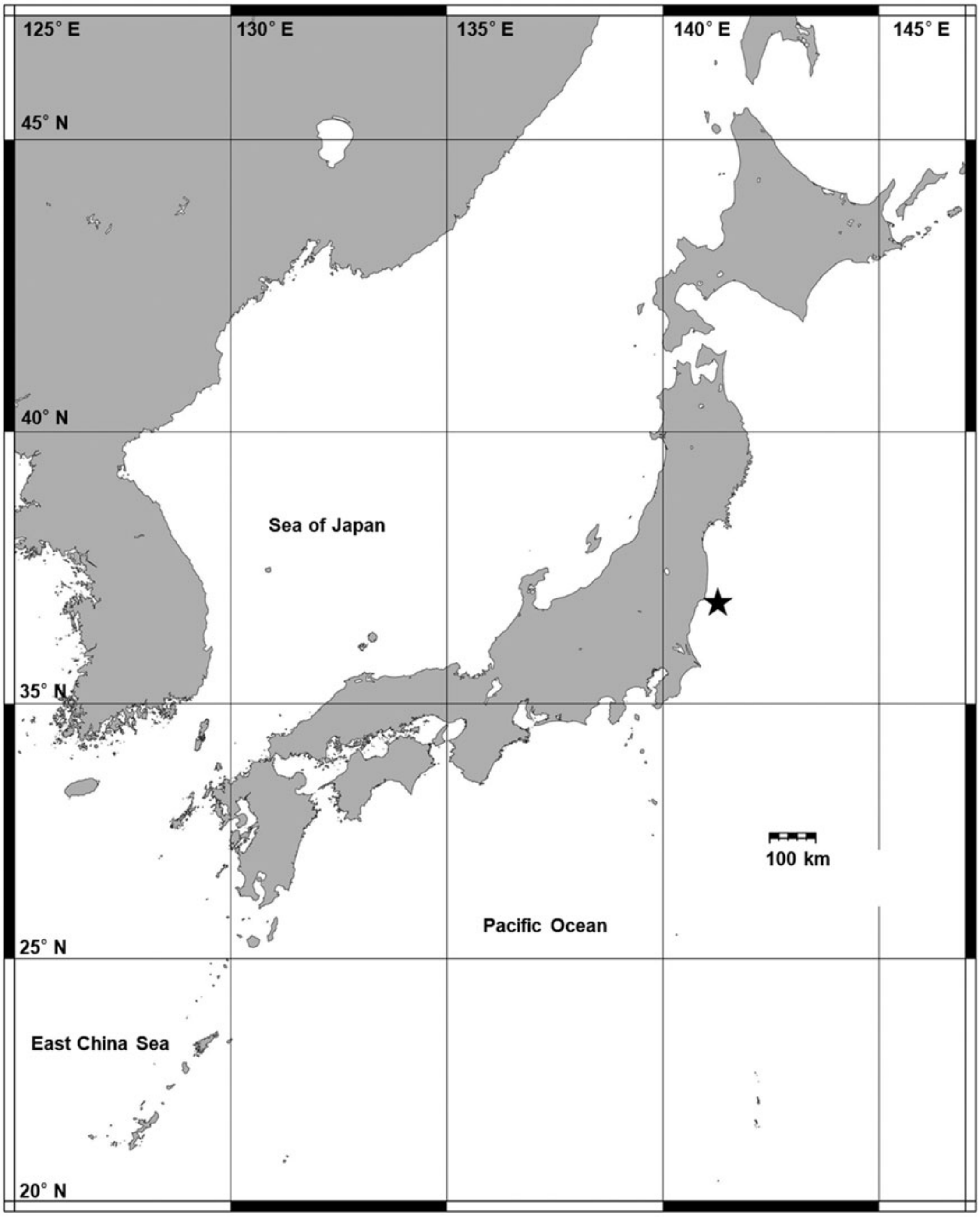

Figure 1. Locality of sampling site (indicated by solid stars) of *Luidia iwakiensis* n. sp.

Etymology

The specific name derives from the type locality, Iwaki City in Fukushima Prefecture, Japan. The Japanese name 'sazare' is derived from the pebbles called 'sazare-ishi' in Japanese, referring to the numerous pebble-like pedicellariae on the abactinal side. 'Suna-hitode' comes from the Japanese name of the genus *Luidia*.

Diagnosis

Arms five, slender. Abactinal spines almost uniform in size and shape. Abradial-most abactinal series contains 1.5 times or more plates than adjacent superomarginal series. Major inferomarginal spines longest in abactinal-most one, as long as nearby 2–3 inferomarginal plates. Minor inferomarginal spines half lengths of inferomarginal fasciolar grooves having equal depth and length. Pedicellariae present on proximal to middle abactinal, almost all actinal, and all oral plates. Body colour solid, lacking pattern.

Description

Arms five, flat, slender, and gradually tapering to the arm tip (Figures 2A, B & 3A). R 86.3 mm, r 9.3 mm, and R/r ratio 9.3r. Abactinal surface covered by numerous paxillae (Figure 2C, 2D). These paxillae composed of abactinal plates bearing spines and no or one pedicellaria on pawn-shaped ridges (Figure 4A, 4B). Abactinal plates round or quadrilobate. Round abactinal plates bearing 9–17 abactinal spines irregularly arranged in disc

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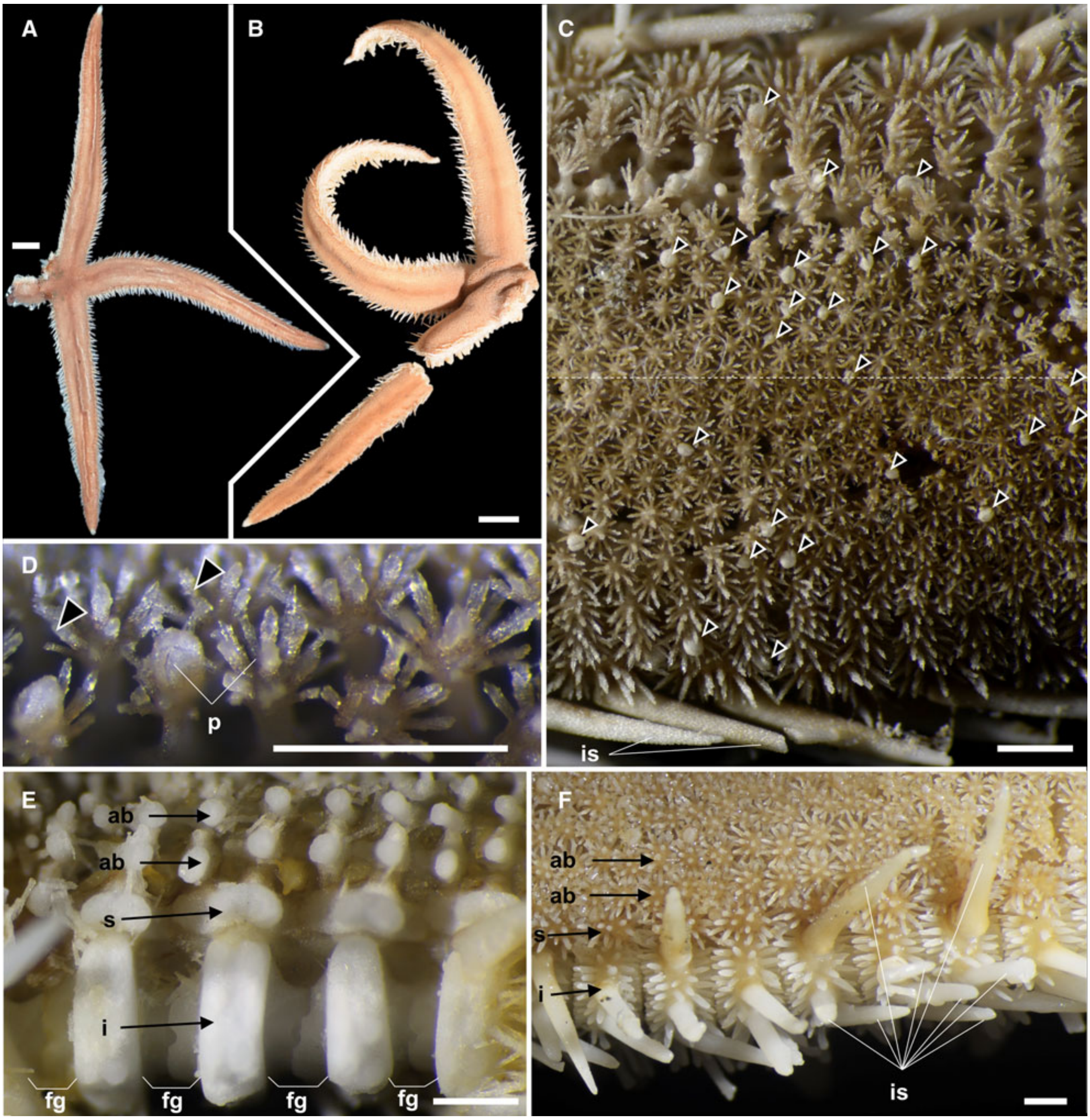

Figure 2. *Luidia iwakiensis* n. sp., holotype, NSMT E-14364. A, Whole body of live specimen, abactinal view, B, whole body of ethanol preserved specimen, abactinal view; C, abactinal surface of the middle portion of the arm, showing abactinal pedicellariae (arrowheads); D, abactinal paxillae from the proximal portion of arm, showing abactinal pedicellariae (arrowheads); E, denuded abactinal to lateral surface of the middle portion of arm; F, lateral to abactinal surface of the proximal portion of arm. Abbreviations: ab, abactinal series; fg, fasciolar groove; i, inferomarginal series; is, major inferomarginal spines; p, paxilla; s, superomarginal series. Scale bars indicate 10 mm for A, B, 1 mm for C–F. Proximal is left in C–F.

and along midradial line of arms. Quadrilobate plates bearing 15–23 abactinal spines arranged in 2–3 longitudinal series in abactinolateral portion of arm. Quadrilobate abactinal plates three times longer and wider than round abactinal plates. Abactinal spines 0.2–0.3 mm in length, straight, cylindrical, and uniformly smooth, except for distal half of spines with sparse serration by splayed thorns (Figure 4C). Abactinal pedicellariae round-shaped and bivalvate or trivalvate (Figure 4D). Each papular area contains no or one branched papula. Madreporite located at the extremity of the disc.

Superomarginal plates longitudinally elongated, two times longer than the adjacent abactinal plates, quadrilobate with crescent-shaped rides (Figure 4E), and arranged in one longitudinal series at abactinolateral portion of arm (Figure 2E, 2F). Each superomarginal series composed of 68–74 plates, corresponding to 140–149 abactinal plates of abradial-most abactinal series. Inferomarginal plates transversely elongated, two times wider than adjacent superomarginal pates, quadrilobate with oblong ridges (Figure 4F), and arranged in one longitudinal series at lateral portion of arms (Figures 2E & 3B). U-shaped fasciolar grooves between ridges of two consecutive inferomarginal plates have equal depth and length (Figures 2E & 3B, 3C). Each superomarginal plate possesses 21–38 spines. Each inferomarginal plate bears three major spines and numerous minor spines (Figures 2F & 3D). Major inferomarginal spines 1.5–3.6 mm in length, straight, conical, and uniformly smooth (Figure 4G). These spines arranged in one vertical row on each inferomarginal plate, and these rows alternately positioned abactinally and

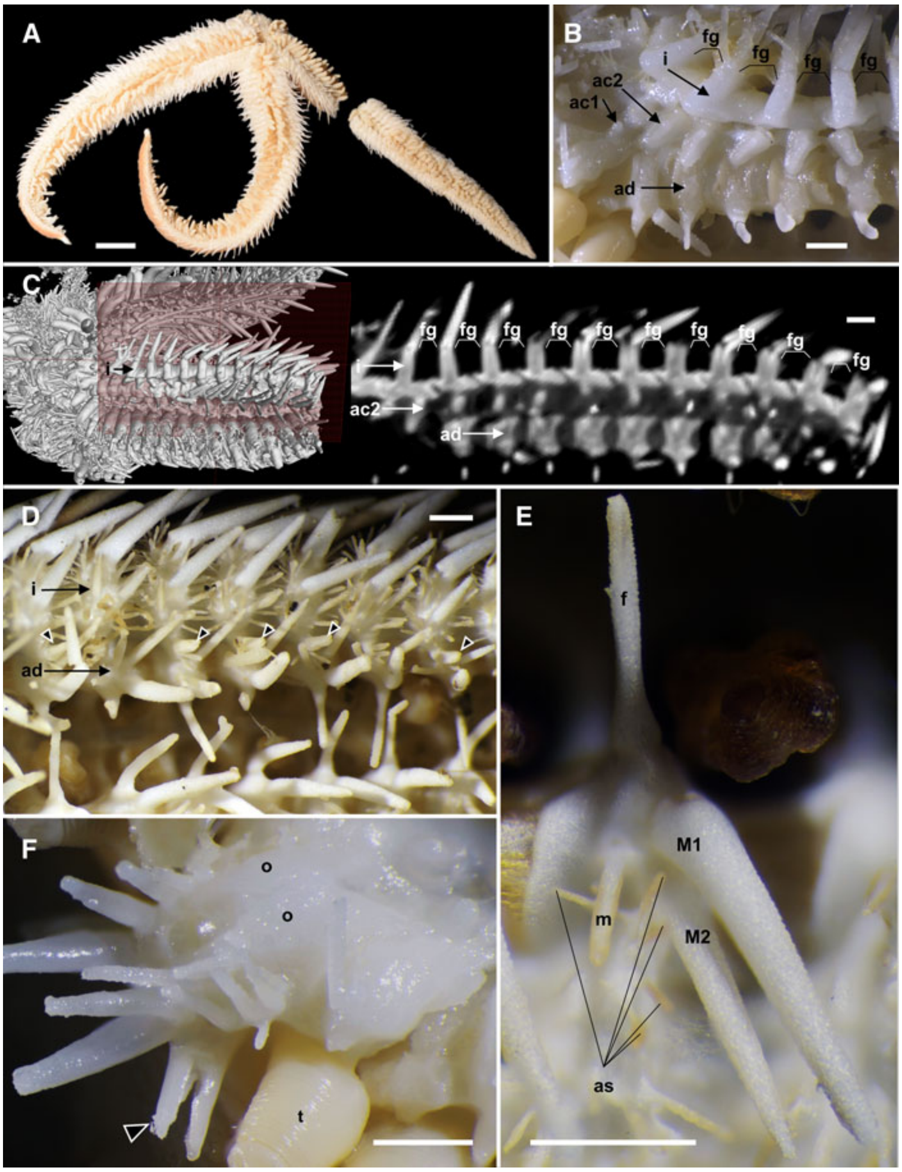

Figure 3. *Luidia iwakiensis* n. sp., holotype, NSMT E-14364. A, Whole body of ethanol preserved specimen, actinal view; B, denuded actinal surface of the proximal portion of the arm; C, horizontal section of the denuded inferomarginal plates using micro-CT (right), showing the sectioned plane (left, red rectangle); D, actinal surface of the proximal portion of arm, showing actinal pedicellariae (arrowheads); E, spines on adambulacral and actinal plates; F, oral region, showing oral pedicellariae (arrowheads). Abbreviations: ac1, first actinal series; ac2, second actinal series; ad, adambulacral series; as, actinal spines; f, furrow spine; fg, fasciolar groove; i, inferomarginal series; M1, major subambulacral spine positioned adradially; M2, major subambulacral spine positioned abradially; m, minor subambulacral spines; o, oral plates; t, tube feet. Scale bars indicate 10 mm for A, 1 mm for B–F. Proximal is left in B–F.

actinally on lateral sides of neighbouring inferomarginal plates. Abactinal-most major inferomarginal spines longest, as long as 2–3 nearby inferomarginal plates (Figures 2F & 3F, 3G). Minor spines closely located on surfaces of inferomarginal ridges and densely filled fasciolar grooves (Figure 2F). Minor spines half lengths of fasciolar grooves. Pedicellariae absent on all supero- and inferomarginal plates.

Actinal plates transversely elongated, ovoid with round ridges, and arranged in two longitudinal series (Figure 3B). First series composed of only two plates confined within each interradial disc. Second series exceeds two-thirds of arm length, reaching nearly to arm tips. Each actinal plate bears three to six spines (Figure 3E), and most actinal plates bear one bicuspid pedicellaria (Figures 3D & 4H).

Adambulacral plates transversely elongated, longitudinally constricted at median part of each plate, and arranged in one longitudinal series along ambulacral furrow (Figure 3B, 3C). Adambulacral plates constantly bear one furrow and two major subambulacral spines arranged in one transverse row and one or two minor subambulacral spines positioned proximal to this row (Figure 3D, 3E). These spines conical and uniformly smooth as major inferomarginal spines, however, furrow and first subambulacral spines curved. Pedicellariae absent on all adambulacral plates.

Each oral plate bears 10–18 oral spines arranged in two rows (Figure 3F). Each oral spine straight, conical, uniformly smooth, and gradually decreases in size towards distal side of each plate. One bicuspid pedicellaria present on the proximal edge of each oral plate, one-third of length of oral plates (Figures 3F & 4I).

Colour in living and ethanol-preserved specimen appears uniform yellow with dark midradial line on abactinal side and white on actinal side (Figures 2A, 2B & 3A). Abactinal-most inferomarginal spines yellow and become gradually white coloured towards tips (Figure 2F).

Distribution

Luidia iwakiensis n. sp. has only been known from the type locality, off Iwaki, Fukushima Prefecture, Japan, at a depth of 175 m.

Phylogenetic analysis

The phylogenetic tree (Figure 5) demonstrated four distinct clades (A–D) with moderate to high bootstrap supporting values (74–96%). Of these four clades, Clade-A was branched from the others at first and Clade-B was branched at second. A sister relationship between Clade-C and Clade-D was supported with moderate bootstrap values (68%).

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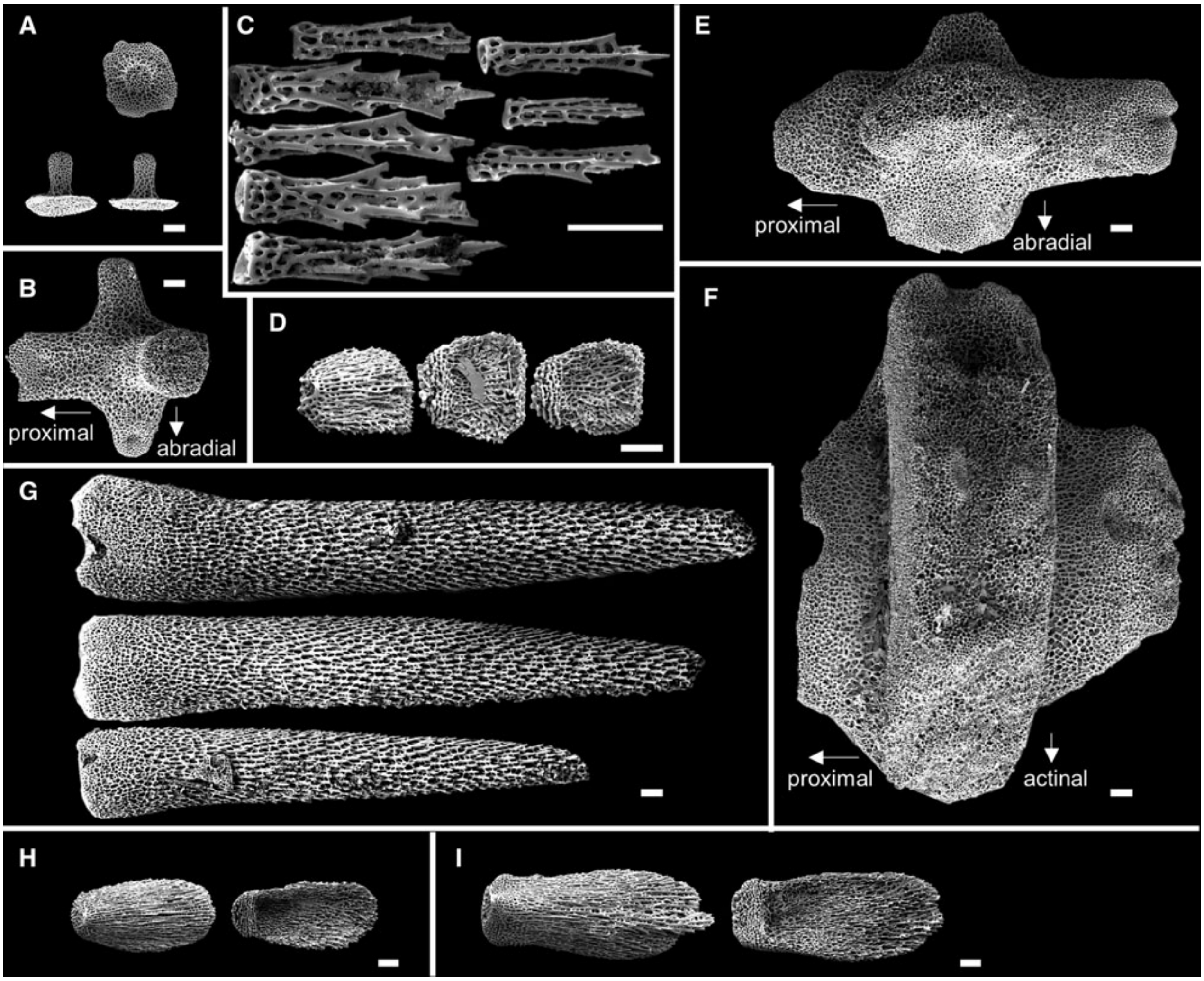

Figure 4. SEM images of ossicles of *Luidia iwakiensis* n. sp., holotype, NSMT E-14364. A, Round abactinal plates, abactinal (above) and lateral (below two) views; B, quadrilobate abactinal plate in the abradial-most abactinal series; C, abactinal spines; D, detached valves of the abactinal pedicellaria, outside (left one) and inside (right two) views; E, superomarginal plate, abactinal view; F, inferomarginal plate, lateral view; G, major inferomarginal spines on the inferomarginal plate shown in F, borne on the abactinal (above), the lateral (middle), and the actinal (below) area of the plate; H, detached vaves of the actinal pedicellaria, outside (left) and inside (right) views; I, detached valves of the oral pedicellaria, outside (left) and inside (right) views. Ossicles in A–B and E–G were collected from the middle portion of arm showed in Figure 2D. Scale bar indicates 0.1 mm in all images. Bottom is left in C, D, G–I.

Among the eighteen analysed species, *L. hardwicki* and *L. quinaria*, belonged to Clade-A, *L. avicularia*, *L. ciliaris* (Philippi, 1837), *L. iwakiensis* n. sp., *L. sagamina*, and *L. sarsii* Düben & Koren in Düben, 1844, belonged to Clade-B, *L. alternata* (Say, 1825), *L. maculata*, *L. magnifica* Fisher, 1906b, *L. savignyi*, and *L. sibogae* Döderlein, 1920, belonged to Clade-C, and *L. barbadensis* Perrier, 1881, *L. clathrata* (Say, 1825), *L. foliolata* Grube, 1866, *L. lawrencei* Hopkins and Knott, 2010, *L. ludwigi* Fisher, 1906a, and *L. senegalensis* (de Lamarck, 1816), belonged to Clade-D (Figure 5). The new species, *L. iwakiensis* n. sp., was most closely related to *L. sarsii* with 13.8% in K2P distance.

Discussion

Molecular and morphological evidence for 4 species groups within Luidia

Four monophyletic clades were evident from our molecular analysis (Figure 5). A morphological comparison of species belonging to these four clades by observing eight specimens of six Japanese species (Table 1) and surveying previous descriptions of each species (see the legend of Figure 5) exhibited three characters among the eight characters outlined in Döderlein's (1920) diagnosis clearly defined each clade. These three characteristics were as follows: presence/absence of elongated superomarginal plates corresponding to 1.5 times or more abactinal plates, a mottled and/or banded pattern on ethanol specimens, and oral pedicellariae (Figure 5). Based on these three diagnostic characters, Clade-A, B, C, and D were identified with the Quinaria-, Ciliaris-, Alternata-, and Clathrata-groups, respectively, and *Luidia* species were re-classified into these morphogroups as shown in Table 2. However, the remaining five characters indicated by Döderlein (1920); which included the presence/absence of enlarged spines on the paxillae, presence of pedicellariae on the actinal and adambulacral plates, presence of two furrow spines, and two or more actinal series were inconsistent with the clades supported by molecular data.

In our phylogenetic tree, the Quinaria-group was at the most basal position, and the clades of the the Alternata- and Clathrata-group were at the terminal (Figure 5). Alternata- and Clathrata-groups were also placed at the terminal position in a report by Lee and Shin (2018). In accordance with the original suggestions of Döderlein (1920), the Clathrata-group was basal since it shared the absence of pedicellariae with the other Paxillosida species. Xiao *et al.* (2013) placed the representative species of the Alternata- and Clathrata-groups in the basal

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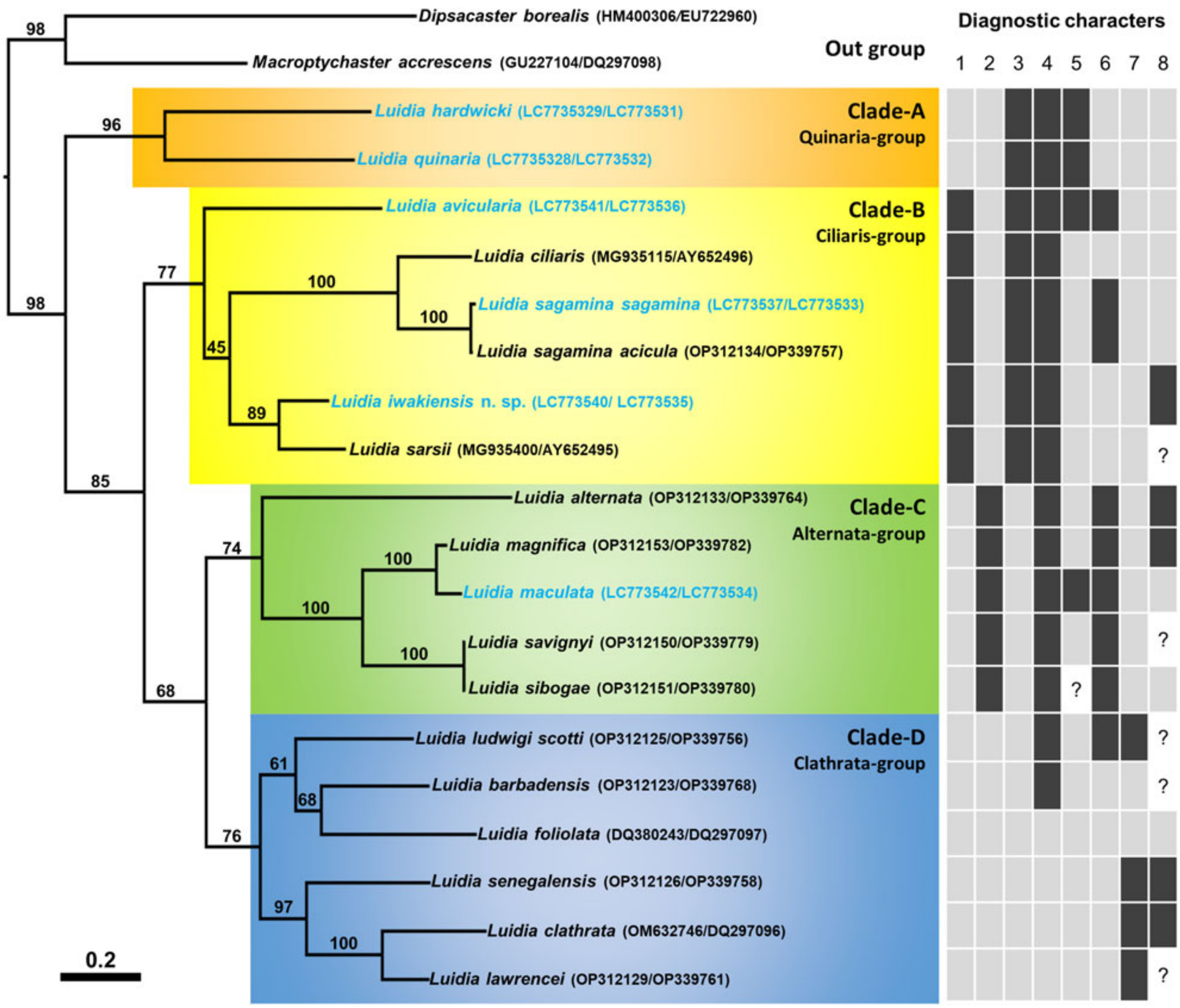

Figure 5. Molecular phylogenetic tree of 18 *Luidia* species based on concatenated sequences of COI and 16S genes (1207 bp) by the maximum likelihood analysis. The values on branches indicate bootstrap support. The scale bar indicates substitutions per site in branch length. GenBank accession numbers of COI and 16S are depicted before and after the slashes, respectively, in parentheses. Blue OTUs indicate the sequences newly obtained in this study. Presence (black rectangle), absence (grey rectangle), or both (black and grey) of eight diagnostic characters of morphogroups indicated by Döderlein (1920) are shown for each species: 1, the abradial-most abactinal series contains 1.5 times or more plates than the adjacent superomarginal series; 2, mottled and/or banded colour pattern; 3, oral pedicellariae; 4, actinal pedicellariae; 5, adambulacral pedicellariae; 6, enlarged abactinal spines on the centre of paxillae; 7, two furrow spines on each adambulacral plate; 8, two or more actinal series (Perrier, 1884; Koehler, 1895; Fisher, 1906b, 1911, 1913, 1919; Goto, 1914; Döderlein, 1920; Mortensen, 1933; Clark, 1953, 1982; Clark and Rowe, 1971; Downey, 1973; Hayashi, 1973; Walenkamp, 1976; Clark and Downey, 1992; Liao and Clark, 1995; Hopkins and Knott, 2010; Kogure, 2015). Question marks mean unknown.

position, and Blake (1973) indicated some ossicle similarities between Alternata- and Clathrata-groups and the other Paxillosida species, thereby supporting this hypothesis. In contrast with this hypothesis, our molecular tree indicated two groups with oral pedicellariae, Quinaria- and Ciliaris-groups, were basal in the genus *Luidia*. This suggested that oral pedicellariae might have evolved in the common ancestor of *Luidia*, and secondarily lost in the Alternata- and Clathrata-groups.

The distinct characters of the four morphogroups of *Luidia*, as proposed by Döderlein (1920), find strong support from our molecular analysis, suggesting that these morphogroups could be classified as separate taxa. Twelve synonymized genera or subgenera were established in the genus *Luidia* by previous papers, and we assigned them into four morphogroups after reviewing the descriptions of type species as follows:

(1) Quinaria-group: *Petalaster* Gray, 1840, *Armaster* Döderlein, 1920, *Denudaster* Döderlein, 1920, *Integuraster* Döderlein, 1920, *Penangaster* Döderlein, 1920, *Quinaster* Döderlein, 1920.
(2) Ciliaris-group: *Luidia* Forbes, 1839, *Astrella* Perrier, 1882, *Hemicnemis* Müller & Troschel, 1840.
(3) Alternata-group: *Alternaster* Döderlein, 1920, *Maculaster* Döderlein, 1920.
(4) Clathrata-group: *Platasterias* Gray, 1871, *Senegaster* Döderlein, 1920

However, since we analysed specimens of only a limited number of *Luidia* species, we hesitate to classify the morphogroups as separate subgenera or genera herein.

Comparisons of new species with the other species

Luidia iwakiensis n. sp. is placed within the Ciliaris-group in having the abradial-most abactinal series composed of 1.5 times or more numerous plates than the adjacent superomarginal series, the pedicellariae on the oral plates, and the solid body colour lacking pattern (Figures 2A, 2B, 2D & 3F). Fourteen species and subspecies of *Luidia* were assigned to the Ciliaris-group: eight

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Table 2. An updated classification of *Luidia* species into four morphogroups based on three diagnostic characters (1, the abradial-most abactinal series contains 1.5 times or more plates than the adjacent superomarginal series; 2, mottled and/or banded colour pattern; 3, oral pedicellariae).

Species	1	2	3	References for three diagnostic characters	Previous (sub)genus assignments (References)	Previous morphogroup assignments (References)
Quinaria-group						
L. amurensis	A	A	P	Döderlein, 1920	*Quinaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920)
L. armata	A	A	P	Ludwig, 1905; Clark, 1982	*Armaster* (Döderlein, 1920) *Alternaster* (Fell, 1963)	**Alternata** (Döderlein, 1920)
L. changi	A	A	P	Liu *et al.*, 2006b		
L. denudata	A	U	U	Koehler, 1910	*Denudaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920)
L. gymnochora	A	A	P	Fisher, 1919	*Denudaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920)
L. hardwicki	A	A	P	Clark, 1953; Clark and Rowe, 1971; Fatemi and Fatemi, 2018; present study	*Petalaster* (Gray, 1840) *Quinaster* (Fell, 1963)	Quinaria (Döderlein, 1920; Clark and Rowe, 1971)
L. integra	A	U	U	Koehler, 1910	*Integraster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920)
L. longispina	A	A	P	Sladen, 1889; Döderlein, 1920	*Quinaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920)
L. penangensis	A	A	P	de Loriol, 1891; Döderlein, 1920; Clark and Rowe, 1971; Vandenspiegel *et al.*, 1998	*Penangaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920; Clark and Rowe, 1971)
L. prionota	A	A	P	Fisher, 1919; Clark and Rowe, 1971	*Quinaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Clark and Rowe, 1971)
L. quinaria	A	A	P	present study	*Quinaster* (Döderlein, 1920; Fell, 1963)	Quinaria (Döderlein, 1920; Blake, 1973)
Ciliaris-group						
L. asthenosoma	P	A	P	Fisher, 1906a	*Hemicnemis* (Döderlein, 1920)	Ciliaris (Döderlein, 1920; Blake, 1973)
L. atlantidea	P	A	P	Clark and Downey, 1992		Ciliaris (Clark, 1953)
L. avicularia	P	A	P	Döderlein, 1920; Fisher, 1913, 1919; present study	*Integraster* (Döderlein, 1920; Fell, 1963)	**Quinaria** (Döderlein, 1920)
L. ciliaris	P	A	P	Döderlein, 1920; Clark and Downey, 1992	*Hemicnemis* (Müller and Troschel, 1840a, 1840b; Döderlein, 1920)	Ciliaris (Döderlein, 1920; Blake, 1973)
L. heterozona	P	A	P	Fisher, 1940; Clark and Downey, 1992	*Integraster* (Fell, 1963)	Ciliaris (Fisher, 1940) **Quinaria** (Clark, 1953)
L. neozelanica	P	A	P	Mortensen, 1925		Ciliaris (Clark, 1953; Blake, 1973)
L. orientalis	P	A	P	Fisher, 1919	*Hemicnemis* (Döderlein, 1920)	Ciliaris (Döderlein, 1920)
L. porteri	P	A	P	Clark, 1917a		Ciliaris (Clark, 1953)
L. sagamina	P	A	P	Döderlein, 1920; present study	*Hemicnemis* (Döderlein, 1920)	Ciliaris (Döderlein, 1920)
L. sarsii	P	A	P	Clark and Downey, 1992	*Astrella* (Milne-Edwards, 1882) *Hemicnemis* (Döderlein, 1920)	Ciliaris (Döderlein, 1920)
L. iwakiensis	P	A	P	Present study		
Alternata-group						
L. alternata	A	P	A	Döderlein, 1920; Downey, 1973; Clark, 1982; Clark and Downey, 1992	*Alternaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Blake, 1973)
L. aspera	A	P	A	Sladen, 1889; Clark, 1953; Clark and Rowe, 1971	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Clark and Rowe, 1971)
L. australiae	A	P	A	Döderlein, 1920	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920)
L. bellonae	A	P	A	Lütken, 1864; Madsen, 1956	*Alternaster* (Döderlein, 1920; Fell, 1963)	
L. difficilis	A	P	A	Liu *et al.*, 2006a		Alternata (Liu *et al.*, 2006a)
L. herdmani	A	P	A	Clark, 1953; Clark and Rowe, 1971		Alternata (Clark and Rowe, 1971)

(*Continued*)

https://doi.org/10.1017/S0025315424000158 Published online by Cambridge University Press

Table 2. (*Continued.*)

Species	1	2	3	References for three diagnostic characters	Previous (sub)genus assignments (References)	Previous morphogroup assignments (References)
L. hexactis	U	P	A	Clark, 1938; Clark and Rowe, 1971	*Maculaster* (Fell, 1963)	**Quinaria** (Clark, 1953); Alternata (Clark and Rowe, 1971)
L. maculata	A	P	A	Döderlein, 1920; Clark and Rowe, 1971; present study	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Clark and Rowe, 1971; Blake, 1973)
L. magnifica	A	P	A	Fisher, 1906b; Clark and Rowe, 1971	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Clark and Rowe, 1971; Blake, 1973)
L. mauritiensis	A	P	A	Koehler, 1910; Clark and Rowe, 1971	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Clark and Rowe, 1971)
L. phragma	A	P	A	Clark, 1910	*Armaster* (Döderlein, 1920) *Alternaster* (Fell, 1963)	Alternata (Döderlein, 1920; Blake, 1973)
L. savignyi	A	P	A	Clark and Rowe, 1971; Kogure, 2015	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Clark and Rowe, 1971)
L. sibogae	A	P	A	Döderlein, 1920; Clark and Rowe, 1971	*Maculaster* (Döderlein, 1920; Fell, 1963)	Alternata (Döderlein, 1920; Clark and Rowe, 1971)
L. varia	A	P	A	Mortensen, 1925	*Maculaster* (Fell, 1963)	Alternata (Clark, 1953)
Clathrata-group						
L. barbadensis	A	A	A	Perrier, 1884; Downey, 1973; Clark, 1982; Clark and Downey, 1992	*Alternaster* (Döderlein, 1920; Fell, 1963)	**Alternata** (Döderlein, 1920)
L. clathrata	A	A	A	Döderlein, 1920; Downey, 1973; Clark and Downey, 1992	*Petalaster* (Döderlein, 1920; Fell, 1963)	Clathrata (Döderlein, 1920)
L. columbia	A	A	A	Clark, 1953	*Petalaster* (Döderlein, 1920; Fell, 1963)	Clathrata (Clark, 1953; Blake, 1973)
L. ferruginea	A	A	A	Ludwig, 1905	*Petalaster* (Döderlein, 1920; Fell, 1963)	Clathrata (Döderlein, 1920)
L. foliolata	A	A	A	Fisher, 1911	*Petalaster* (Döderlein, 1920; Fell, 1963)	Clathrata (Döderlein, 1920) **Alternata** (Blake, 1973)
L. latiradiata	A	A	A	Fell, 1963; Blake, 1982	*Platasterias* (Blake, 1972, 1982)	Clathrata (Blake, 1982)
L. lawrencei	A	A	A	Hopkins and Knott, 2010; Shilling *et al.*, 2022		
L. l. ludwigi	A	A	A	Fisher, 1906a, 1911	*Armaster* (Döderlein, 1920) *Alternaster* (Fell, 1963)	**Alternata** (Döderlein, 1920; Blake, 1973)
L. l. scoti	A	A	A	Clark, 1982; Clark and Downey, 1992	*Alternaster* (Fell, 1963)	Clathrata (Clark, 1953)
L. magellanica	U	A	A	Leipoldt, 1895; Madsen, 1956		**Alternata** (Döderlein, 1920)
L. patriae	A	A	A	Clark and Downey, 1992		Clathrata (Clark, 1953)
L. senegalensis	A	A	A	Downey, 1973; Walenkamp, 1976; Clark and Downey, 1992	*Senegaster* (Döderlein, 1920; Fell, 1963)	Clathrata (Döderlein, 1920; Blake, 1973)
L. superba	A	A	A	Clark, 1917b		**Alternata** (Clark, 1953)
L. tessellata	A	A	A	Lütken, 1859; Clark, 1910 (described as *L. columbia*); Döderlein, 1920 (described as *L. columbia*)	*Petalaster* (Fell, 1963)	Clathrata (Döderlein, 1920)

Following Blake's (1972, 1982) classification, we include *Luidia latiradiata* here, while this species has been classified as Somasteroidea (Fell, 1963). P: presence, A: absence, U: unknown. Previous assignments to genus or subgenus (currently synonymized with *Luidia*) and morphogroup (if different in bold) are also shown.

Atlantic species and subspecies, *Luidia atlantidea* Madsen, 1950; *Luidia ciliaris* (Philippi, 1837); *Luidia heterozona barimae* John and Clark, 1954; *Luidia heterozona heterozona* Fisher, 1940; *Luidia sagamina acicula* Mortensen, 1933; *Luidia sarsii sarsii* Düben & Koren in Düben, 1844; *Luidia sarsii africana* Sladen, 1889; *Luidia sarsii elegans* Perrier, 1875; six Pacific species, *Luidia asthenosoma* Fisher, 1906a; *Luidia avicularia* Fisher, 1913; *Luidia neozelanica* Mortensen, 1925; *Luidia orientalis* Fisher, 1913; *Luidia porteri* Clark, 1917a; *Luidia sagamina sagamina* Döderlein, 1920 (Table 2). Among these species, *L. avicularia*, *L. ciliaris*, *L. h. barimae*, and *L. h. heterozona* have six to ten arms, and can be readily distinguished from the *L. iwakiensis* n. sp. (Fisher, 1913, 1919, 1940; Döderlein, 1920; John and Clark, 1954; Clark and Downey, 1992). Furthermore, *L. atlantidea*, *L. neozelanica*, *L. orientalis*, *L. s. acicula*, and *L. s. sagamina* are clearly discriminated from *L. iwakiensis* n. sp. by having the abactinal-most major inferomarginal spines longer than three nearby inferomarginal plates (Fisher, 1919; Clark, 1917a; Döderlein, 1920; Mortensen, 1925; Clark and Downey, 1992; Gallardo-Roldán *et al.*, 2015). The presence/absence of pedicellariae enables the distinction of the new species from the remaining five related species and subspecies.

Luidia iwakiensis n. sp. has pedicellariae on proximal to middle abactinal, almost all actinal, and all oral plates, whereas *L.*

asthenosoma and *L. porteri* also have pedicellariae on the supero- and inferomarginal plates (Fisher, 1906a; Clark, 1917a), and *L. s. africana*, *L. s. elegans*, and *L. s. sarsii* lack pedicellariae on the middle to distal actinal plates (Clark, 1982). Clark (1953) pointed out that the presence of pedicellariae varies based on the body size in some *Luidia* species. Comparison of similar-sized specimens of the holotypes of *L. iwakiensis* n. sp. ($R = 86.3$ mm), *L. asthenosoma* ($R = 86$ mm in Fisher, 1906a), *L. porteri* ($R = 98$ mm in Clark, 1917a), and three subspecies of *L. sarsii* ($R = 90$–190 mm in Clark and Downey, 1992) confirmed the above-mentioned differences with regards to the occurrence of pedicellariae.

Our phylogenetic analysis based on COI and 16S gene markers supported the morphological classification of *Luidia iwakiensis* n. sp. as a member of the Ciliaris-group and demonstrated relationship between *L. iwakiensis* n. sp. and the Atlantic species *L. sarsii* (Figure 5). The K2P genetic distance between *L. iwakiensis* n. sp. and *L. sarsii* was 13.8%, which was long enough to consider them as genetically and geographically distinct species (Hebert *et al.*, 2003; Shilling *et al.*, 2022).

Key to the recognized species of *Luidia* in Japanese waters

In this study, we report a seventh *Luidia* species in Japanese waters. This key to the seven Japanese species is based on our observations and previous descriptive papers (Döderlein, 1920; Liao & Clark, 1995; Hayashi, 1973; Kogure, 2015).

1. Superomarginal plates that are shorter than or as long as the adjacent abactinal plates; the abradial-most abactinal series and superomarginal series contain almost identical numbers of plates 2
– Superomarginal plates are considerably longer than the adjacent abactinal plates; the abradial-most abactinal series contains 1.5 times or more plates than the adjacent superomarginal series; oral plates bear pedicellariae (Ciliaris-group) 5
2. Oral plates bear pedicellariae; abactinal surface lack mottled and/or banded colour pattern (Quinaria-group) 3
– Oral plates lack pedicellariae; abactinal surface has mottled and/or banded colour pattern (Alternata-group) 4
3. Adambulacral plates lack pedicellariae or only proximal 1–3 adambulacral plates bear pedicellariae; furrow and subambulacral spines are arranged in 1 or 2 zigzag transverse rows; abactinal surface is uniform orange-cinnamon . . . . . *L. hardwicki*
– Adambulacral plates bear pedicellariae; furrow and subambulacral spines are arranged in a transverse row; abactinal surface is brown with a longitudinal dark stripe along the midradial line . . . . . *L. quinaria*
4. Arms 6; some abactinal paxillae bear enlarged central spines . . . . . *L. savignyi*
– Arms 7–9; abactinal paxillae lack enlarged central spines . . . . . *L. maculata*
5. Arms 9–10 . . . . . *L. avicularia*
– Arms 5 6
6. Abactinal plates lack pedicellariae; the abactinal-most major inferomarginal spines longer than three nearby inferomarginal plates . . . . . *L. s. sagamina*
– Abactinal plates bear pedicellariae; the abactinal-most major inferomarginal spines as long as 2–3 nearby inferomarginal plates . . . . . *L. iwakiensis* n. sp.

Data availability. The data that support the findings of this study are available from the corresponding author, IK, upon reasonable request.

Acknowledgements. We would like to express our sincere gratitude to Takashi Iwasaki, Masato Ikegawa, and the captain and crew of R/V *Iwaki-Maru* (Fukushima Prefectural Fisheries and Marine Science Research Centre) for providing the holotype of *Luidia iwakiensis* n. sp. (NSMT E-14364). We also thank to the captain and crew of following research vessels for collecting specimens: R/V *Seisui-Maru* (Mie University): *L. avicularia* (NSMT E-14357, 14358) and *L. quinaria* (NSMT E-14361); R/V *Toyoshio-Maru* (Hiroshima University): *L. sagamina sagamina* (NSMT E-14363) and *L. quinaria* (NSMT E-14360); R/V *Shinsei-Maru* (Japan Agency for Marine-Earth Science and Technology): *L. hardwicki* (NSMT E-14359); R/V *Koyo* (Tokyo Metropolitan Ogasawara Fisheries Center): *L. maculata* (NSMT E-14356). We acknowledged the following researchers for managing research cruise and/or providing processed specimens: NSMT: Akito Ogawa, Hironori Komatsu, and Mikihito Arai; Hiroshima University: Susumu Otsuka; Mie University: Shoichi Kimura and Taeko Kimura. We are grateful to Gento Shinohara, Shuhei Nomura, Takahiko Kutsuna, and Yasunari Shigeta (NSMT) for their help in manipulating micro-CT, and Takeshi Furukawa, Masamitsu Iwata, Makoto Kuraishi, and Subaru Joukura (Marine Science Museum, Fukushima Prefecture, Aquamarine Fukushima) for their helpful advice and encouragement. We appreciate the suggestive and helpful comments on the present study by anonymous reviewers. The authors would like to thank Enago (www.enago.jp) for the English language review.

Authors' contributions. MH provided the specimen of *L. iwakiensis* n. sp. All authors performed morphological observations and molecular analyses. IK and TF drafted this manuscript. All authors commented on and approved the final manuscript.

Financial support. This study was partly supported by JSPS KAKENHI Grant Number 21K06327 and the National Museum of Nature and Science projects 'Geological, biological, and anthropological histories in relation to the Kuroshio Current', 'Biological Properties of Biodiversity Hotspots in Japan', and 'Collection of mitochondrial genome data of invertebrates and its application to taxonomy and phylogeny'.

Competing interests. None.

Ethical standards. Not applicable.

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