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Morphological and Genetic Features of *Culmenella prashadi* (Heterobranchia: Planorbidae) Newly Discovered in Fukushima Prefecture, Japan

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Abstract: *Culmenella prashadi* (Clench, 1931) is a critically endangered freshwater snail whose habitats have significantly declined despite its wide recorded distribution. The authors discovered a new population of *Cu. prashadi* in a small mountain pond in Fukushima Prefecture, northern Honshu, Japan, from where the species had not been previously recorded. Morphological examination of the shell, head-foot, and digestive, reproductive, and central nervous systems revealed that the examined population had similar features to previously dissected snails from Ishikawa Prefecture, while exhibiting intraspecific variations in the accessory preputial organs and radulae. The present anatomical observations confirmed that *Cu. prashadi* can be distinguished from its congeners and the closely related *Camptoceras hirasei* Walker, 1919 based on morphological differences in the mantle flap, male reproductive organs, and central nervous system. Base substitutions were also identified between the haplotypes of the populations in Fukushima and Aomori Prefectures.

Keywords: anatomy, nervous system, diagnosis, endangered species, mitochondrial haplotype

Introduction

The freshwater snail genus *Culmenella* Clench, 1927 consists of five valid species, native to East Asia (Japan and Russia) and South-east Asia (Bengal and Kashmir Regions and Thailand) (Brandt, 1974; Hubendick, 1967; MolluscaBase eds, 2025; Starobogatov & Prozorova, 1990). *Culmenella* species are characterized by their unusual, ovate shells and features of the male genital organs (Hubendick, 1978). The genus has been treated as a subgenus (Clench, 1931) or junior synonym (Hubendick, 1955a, 1967) of the genus *Camptoceras* Benson, 1843, whose members have a more slender shell than *Culmenella* species, but has recently been considered a full genus (MolluscaBase eds, 2025; Saito *et al.*, 2018b). The shell and genital morphologies of these two genera have been examined in several studies, establishing their extraordinary shell shapes and features of the male genital organs and radulae as useful for their genus-level identification (Hubendick, 1955a, 1959, 1967; Starobogatov, 1957; Starobogatov & Prozorova, 1990). Within *Culmenella*, morphological differences have been detected in the shell aperture, radula, and inner penial wall of Japanese, Russian, and Thai species (Hubendick, 1959, 1967; Starobogatov & Prozorova, 1990).

Culmenella prashadi (Clench, 1931) has been the only species found in Japan since the establishment of the genus approximately 100 years ago (Hubendick, 1967; MolluscaBase eds, 2025). This species was described from Morotsutsumi-Mura, Osaka (not Koka-Mura) in central Japan, and was recorded in 15 prefectures in Honshu and Hokkaido (Clench, 1927, 1931; Matsuda,

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Table 1. Previous and present occurrence records of *Culmenella prashadi* and its prefectural Red Data Book evaluations. The evaluation criteria in parentheses are the corresponding criteria of the Ministry of the Environment (2020).

Prefecture	Evaluation by the latest prefectural Red Data Book	Occurrence record	Reference
Hokkaido	Unevaluated		
		Unspecified	Personal communication by Y. Kuwahara
Aomori	D rank (DD)		Oyagi (2020)
		Hirosaki City	Matsuda (1998)
		Obuchi Pond, Obuchi, Rokkasho-Mura, Kamikita-Gun	Matsuda (1998)
		Mountainous ponds and irrigation canals of the Tsugaru and Shimokita Peninsulas	Oyagi (2020)
		Pond near Lake Ogawara	Oyagi (2020)
Iwate	Critically Endangered + Endangered (CR+EN)		Nature Conservation Division, Environment and Lifestyle Department, Iwate Prefectural Government (2024)
		Ichinoseki City	Nature Conservation Division, Environment and Lifestyle Department, Iwate Prefectural Government (2020)
Fukushima	Unevaluated		
		Central region	This study
Niigata	Endangered (EN)		Environmental Planning Division, Environmental Policy Department, Niigata Prefectural Government (2001: 105)
		Lake Toyano, Chuo-ku, Niigata City	Environmental Planning Division, Environmental Policy Department, Niigata Prefectural Government (2001: 105), Hasegawa (1979)
Gunma	Extinct (EX)		Natural Environment Division, Environment and Forestry Department, Gunma Prefecture (2022: 243)
		Annaka-Cho, Usui-Gun (currently Annakka City)	Natural Environment Division, Environment and Forestry Department, Gunma Prefecture (2022: 243), Takahashi (1984)
		Shimokawabuchi-Mura, Seta-Gun (currently Shimokawabuchi District, Maebashi City)	Natural Environment Division, Environment and Forestry Department, Gunma Prefecture (2022: 243), Takahashi (1984)
Tokyo	Extinct (EX)		Kurozumi (2023)
		Unspecified	Mori (1938)
		Akabane, Kita-Ku	Matsuda (1998)
		Kamata, Oota-Ku	Kurozumi (2023)
Nagano	Critically Endangered + Endangered (CR+EN)		Nature Conservation Division, Environment Department, Nagano Prefecture (2015)
		Lake Kizaki, Taira, Omachi City	Matsuda (1998)
		Lake Nakatsuna, Taira, Omachi City	Matsuda (1998)
Ishikawa	Critically Endangered + Endangered (CR+EN)		Ishihara (2020)
		Lake Shibayama, Kaga City	Hubendick (1959), Ishihara (2020)
Fukui	Extinct (EX)		Natural Environment Division, Department of Safety and Environment, Fukui Prefecture (2016: 261)
		Sakai-Gun (currently Sakai City and surrounding areas)	Mori (1938)
		Kibe (currently Kibe District), Sakai-Cho, Sakai City	Natural Environment Division, Department of Safety and Environment, Fukui Prefecture (2016: 261)
Shizuoka	Critically Endangered (CR)		Kato (2019)
		Okegaya Pond, Iwai, Iwata City	Kato (2019)
Aichi	Extinct (EX)		Kimura (2020)
		Sukaguchi, Kiyosu City	Kimura (2020)
		Kaba Pond, Ushikawa-Cho, Toyohashi City	Kimura (2020)
Shiga	Data Deficient (DD)		Matsuda (2021)
		Lake Biwa	Matsuda (1998)
Kyoto	Extinct (EX)		Kondo (2015)
		Ogura Pond, Uji City	Kondo (2015), Matsuda (1998)
Osaka	Extinct (EX)		Osaka Biodiversity Conservation Network (2014)
		Morotsutsumi-Mura, Kitakawachi-Gun (currently Tsurumi-Ku, Osaka City)	Kira (1941), Mori (1938)

1998; Table 1). *Culmenella prashadi* was originally described as *Bulinus* (*Culmenella*) *hirasei* Clench, 1927 (type species of *Culmenella*), and was subsequently transferred to *Camptoceras* based on shell morphological features (Clench, 1931). However, as its specific name of "*hirasei*" was preoccupied by Japanese *Ca. hirasei* Walker, 1919, the species was described as *Cu. prashadi* in the same study. In recent years, *Cu. prashadi* has been considered an independent species endemic to Japan (*e.g.*, Ishihara, 2020; Kihira *et al.*, 2009: 55; Masuda & Uchiyama, 2010: 160; Natural Environment Division, Environment and Forestry Department, Gunma Prefecture [NEDEFDGP], 2022: 243; Vinarski & Kantor, 2016), or conspecific with *Cu. rezvoji* (Lindholm, 1929) described from Russia (Kato, 2019; Kimura, 2020; Oyagi, 2020) or subspecies of it (Nature Conservation Division, Environment Department, Nagano Prefecture [NCDELDIPG], 2020). In the present study, the Japanese populations were tentatively treated as *Cu. prashadi* according to a comprehensive review of the genus (Hubendick, 1967).

Japanese *Cu. prashadi* is one of the most morphologically studied species in the genus. Conchological traits of *Cu. prashadi* were examined using specimens collected from Osaka (type locality), Tokyo, and Fukui (Mori, 1938), and many photographs of the shell specimens provided in the prefectural Red Data Books (Kato, 2019; Kimura, 2020; Kurozumi, 2023). However, knowledge of the anatomical traits of this species has been limited; dissection was conducted based only on a few specimens from one population in Ishikawa Prefecture (Hubendick, 1959). Although traits of digestive and reproductive systems of *Cu. prashadi* were clarified in the study, intraspecific variation was not sufficiently investigated owing to the limited specimen numbers. Furthermore, the nervous system has not been elucidated in any of *Culmenella* species.

The current distribution of *Cu. prashadi* has declined significantly despite its historically wide range (Matsuda, 1995, 1998). In recent years, the species has been found only in water bodies in Aomori, Iwate, and Nagano Prefectures (Masuda & Uchiyama, 2010: 160; Nakai, 2014; NCDELDIPG, 2020), and has been listed as either extinct or critically endangered on the national and prefectural Red Lists (Table 1). In addition, nucleotide sequences have been obtained from only two populations in Aomori Prefecture (Saito *et al.*, 2018b).

A new population of *Cu. prashadi* was recently discovered by the authors in Fukushima Prefecture, northern Honshu, where this species has not been previously recorded. In this study, morphological and genetic examinations, as well as an investigation of its habitat, were conducted for this new population, with the aim of increasing our knowledge of *Cu. prashadi* and the genus *Culmenella*.

Materials and Methods

Field survey and specimen preparation

A field survey of *Culmenella prashadi* was conducted in central Fukushima Prefecture on 24 October 2024. Detailed information on the locality is unpublished to protect the habitat and population. The habitat substrates and rough abundances of *Culmenella* snails and sympatric freshwater mollusks were visually investigated for two hours by the two authors. Sympatric mollusk species were identified according to Korniushin (1999), Masuda & Uchiyama (2010), and Saito *et al.* (2018a). Scientific names follow Aksenova *et al*. (2024) and Hirano *et al*. (2019). Ten *Culmenella* specimens were prepared by boiling for eight seconds in water at 80°C referring to Fukuda *et al.* (2008). Shells were dried, tips of head-feet were preserved in 99% ethanol, and the rest of the soft bodies were frozen at –20°C until dissection. Newly collected specimens of *Cu. prashadi* were deposited at the Zoological Collection of Kyoto University (KUZ Z6010–Z6012).

Morphological observation

Shells and soft bodies of ten specimens were observed using a YS05T stereomicroscope

(Micronet Inc., Kawaguchi, Japan) and photographed using a Swiftcam SC1003-CK camera (SwiftCam Technologies Group Co., Ltd., Kwai Chung, Hong Kong) attached to the stereomicroscope. The following shell measurements were obtained from digital images using ImageJ v1.51 (Schneider *et al.*, 2012), following Mori (1938) and Hubendick (1967): shell length, shell width, aperture height, aperture width, whorl number, index α (shell width / shell length), and index γ (aperture width / aperture height). The surface structures of the teleoconch and protoconch were observed in three specimens using a JSM-6510LV scanning electron microscope (JEOL Ltd., Tokyo, Japan) after platinum coating using a JEC-3000FC (JEOL Ltd.).

Anatomical investigation of the defrosted soft bodies was performed using the YS05T stereomicroscope. The nomenclature of the internal organs was based on Hubendick (1959, 1978), and Paraense & Pointier (2003). After dissection, the radulae were extracted from the buccal masses of three specimens using 1 M sodium hydroxide. The radulae were observed using the scanning electron microscope as with the shell specimens.

Genetic analysis

Genomic DNA was extracted from the two specimens following the procedure outlined by Okamoto *et al.* (2006). Polymerase chain reaction and nucleotide sequencing were performed following the methods of Saito *et al.* (2018b) and Sawada *et al.* (2021). However, the annealing temperature for 16S ribosomal RNA gene (16S) was modified to 48°C and the primer set was changed from 16Sar-L/16Sbr-H to 16S-H/16S-R sets for efficiency. Consequently, the following primer sets were used in the present study: LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer *et al.*, 1994) for mitochondrial cytochrome c oxidase subunit 1 (COI); 16S-H (5′-CGCCTGTTTATCAAAAACAT-3′) and 16S-R (5′-CCGGTCTGAACTCAG ATCACGT-3′) (Simon *et al.*, 1994) for mitochondrial 16S. The newly obtained sequences were deposited in the International Nucleotide Sequence Database (INSD) through the DNA Databank of Japan (LC866792– LC866795).

The newly obtained two sequences were compared with those of two *Cu. prashadi* from Aomori Prefecture (COI – LC429448, LC429549; 16S – LC428897, LC428997), three *Culmenella* sp. from Russia (COI – LC429424, LC429425, LC429497; 16S – LC428874, LC428875, LC428946), and two *Ca. hirasei* (COI – LC429453, LC429562; 16S – LC428902, LC429010) provided by Saito *et al.* (2018b). Nine sequences were aligned using ClustalW option (Thompson *et al.*, 1994) implemented in MEGA v11 (Tamura *et al.*, 2021) with the default settings (gap opening penalty – 15.00; gap extension penalty – 6.66; DNA weight matrix – IUB; transition weight – 0.50; use negative matrix – off; delay divergent cutoff – 30%). Their variations were visually evaluated using MEGA. Subsequently, non-conserved regions of the nine aligned sequences were trimmed using Gblocks v0.91b (Castresana, 2000) with the default settings (minimum sequence number for conserved position – 5; minimum sequence for flanking position – 7; maximum number of contiguous non-conserved positions – 8; minimum length of block – 10; without allowing gaps). Genetic variation between the nine specimens were visualized by statistical parsimony (Clement *et al.*, 2000) using PopART v1.7 (Leigh & Bryant, 2015).

Results

Morphological description

Shell (Figs 1, 2A, 2B, Table 2): Sinistral, elongated helicoid, small (3.9–5.3 mm in shell length, 2.6–3.2 mm in shell width) with 2.50–2.75 whorls, thin, translucent, colored light brown. Index α (shell width / shell length) = 0.58–0.67. Whorls convex; rapidly and regularly expanding in lower whorls. Suture well impressed. Umbilicus deep, narrow. Protoconch of about 0.75 whorls; heterostrophic at angle of 170 degrees to teleoconch axis, forming pointed spire; hardly subsumed

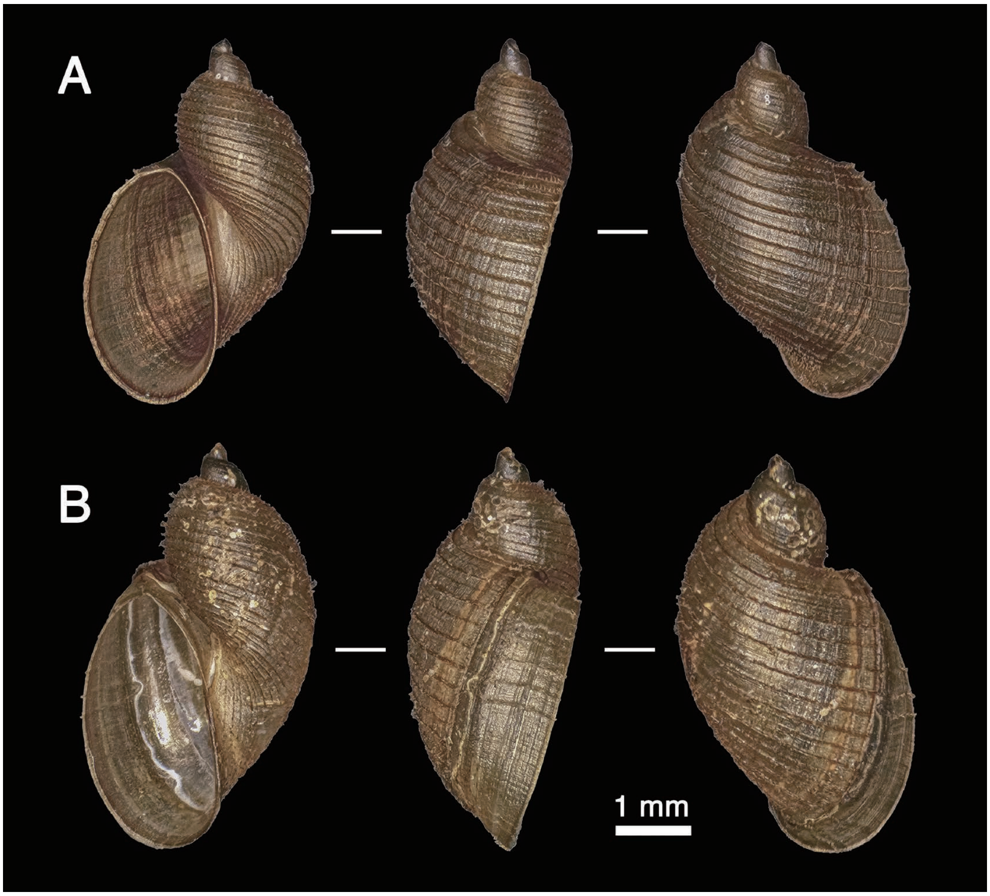

Fig. 1. Shell specimens of *Culmenella prashadi* found from central Fukushima Prefecture, KUZ Z6012 (**A**, **B**).

in first teleoconch whorl; dorsal surface almost smooth with weak spiral ridges; lateral surface uneven with many small depressions. Boundary between protoconch and teleoconch indistinct, with weak longitudinal ridge (Fig. 2B). Teleoconch composed of 1.75–2.00 whorls; whole surface sculptured with distinct, uplifted spiral ridges accompanying short hairs and fine longitudinal striae, without depressions; weak and strong ridges alternating in central part of whorls. Aperture large, 63%–69% total length of shell (2.6–3.5 mm in aperture height, 1.3–1.8 mm in aperture width), rounded ovate, slightly separated from penultimate whorl; lip thin, slightly reflected with weak projection of spiral ridges on palatal lip. Index γ (aperture width / aperture height) = 0.47–0.54.

Head–foot (Figs 3, 4A): Lower part of snout (sn), sides of foot (f), edge of cephalic tentacles (ct) colored pale pink (when living), light grey (preserved); basal part of snout, central part of cephalic tentacles colored dark grey (preserved); mass of tiny light beige granules at snout, cephalic tentacles and sides of foot (living); granules visible only at proximal portions of eyes (e) (preserved). Snout broad, rounded, spread laterally. Cephalic tentacles long, slightly shorter than snout, with horizontally grooved dorsal surfaces (preserved). Eyes conspicuous, colored black, at inner basal portions of cephalic tentacles.

Mantle cavity (Fig. 3): Mantle cavity deep (depth of cavity around 2.5 mm). Dorsal mantle roof (mr) opaque with mass of microscopic black spots. Kidney opening (ko) indistinct, in left anterior portion of mantle roof (near dorsal edge of mantle flap). Kidney (k) large, opaque white,

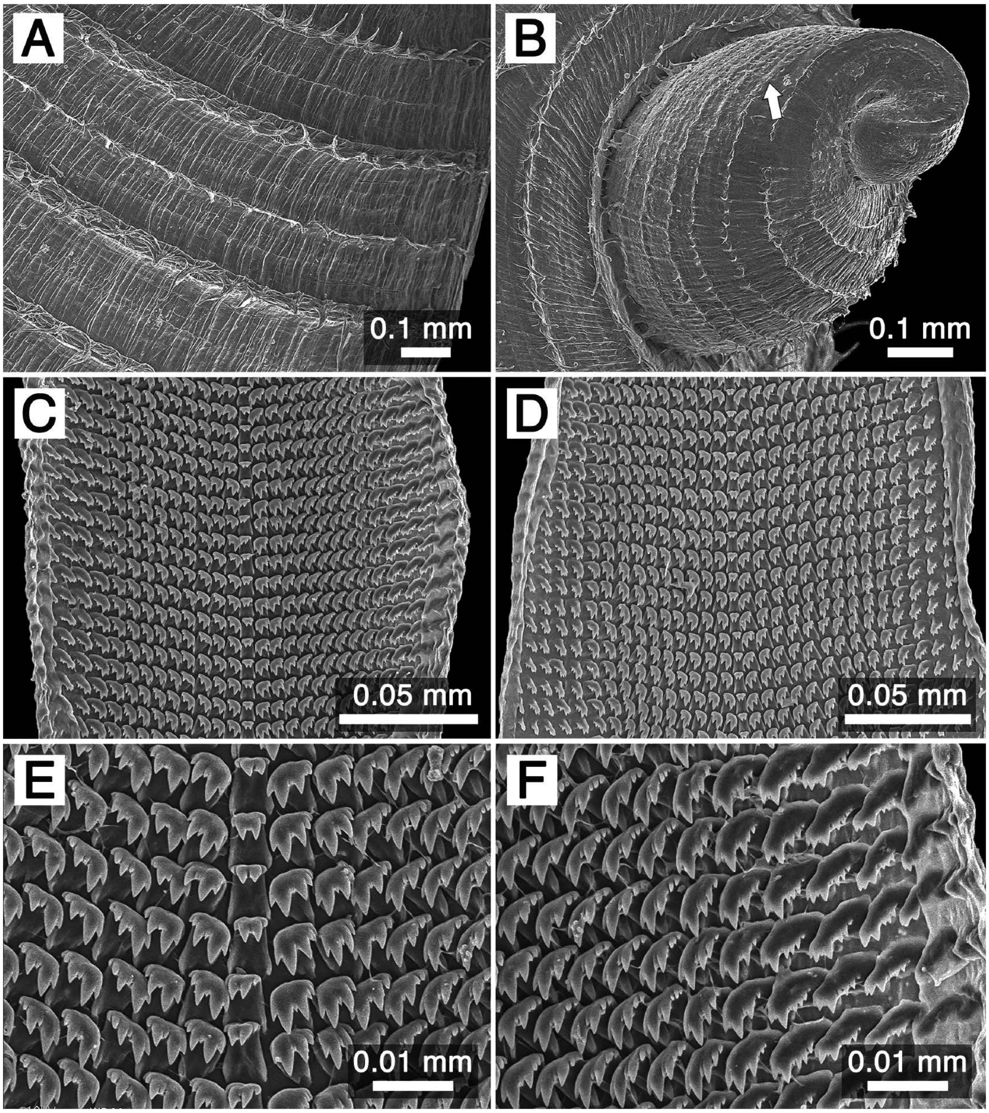

Fig. 2. Shell surface structures and radulae of *Culmenella prashadi*. **A.** Central body whorl of teleoconch, KUZ Z6012. **B.** Shell apex capturing protoconch and the beginning of teleoconch, KUZ Z6012. An arrow indicates boundary between protoconch and teleoconch. **C, D.** Central rows of radula, KUZ Z6011 (**C**), KUZ Z6010 (**D**). **E.** Rachidian and lateral teeth of radula, KUZ Z6011. **F.** Lateral and marginal teeth of radula, KUZ Z6011.

on mantle roof; wide in right posterior part of roof (near heart); intricated by narrow folds. Urethra (ur) arising from kidney, tapering, meandering at anterior portion of mantle roof. Pulmonary (pv) and renal veins (rv) thick, translucent, running parallel to kidney; minor, intricated blood vessels visible near pulmonary and renal veins, mantle edge (me) and right portion of kidney. Auricle (au) and ventricle (ve), globular, colored light pink; auricle opening to pulmonary vein; separated from ventricle by constriction. Mantle flap (mf) large, rectangular, adhering to right posterior portion of mantle roof; narrow aperture of mantle cavity lying on posterior-dorsal side of mantle flap.

Digestive system (Figs 2C–F, 3, 4A): Mouth (m) opens at back side of central depression of

Table 2. Measurements, average, and standard deviation of ten specimens of *Culmenella prashadi* examined in this study.

Specimen (voucher) number	Shell length (mm)	Shell width (mm)	Aperture height (mm)	Aperture width (mm)	Whorl number	α (shell width / shell length)	γ (aperture width / aperture height)
1 (KUZ 6010)	4.7	2.7	3.2	1.7	2.50	0.58	0.51
2 (KUZ 6011)	4.3	2.8	2.9	1.6	2.50	0.65	0.54
3 (KUZ 6012)	5.3	3.2	3.5	1.8	2.50	0.59	0.53
4 (KUZ 6012)	4.3	2.8	2.7	1.3	2.50	0.64	0.47
5 (KUZ 6012)	4.8	3.0	3.0	1.6	2.75	0.62	0.54
6 (KUZ 6012)	4.3	2.7	2.9	1.5	2.50	0.64	0.52
7 (KUZ 6012)	4.2	2.7	2.8	1.5	2.50	0.64	0.53
8 (KUZ 6012)	3.9	2.6	2.6	1.3	2.50	0.66	0.52
9 (KUZ 6012)	4.2	2.6	2.8	1.4	2.50	0.62	0.50
10 (KUZ 6012)	4.1	2.7	2.8	1.4	2.50	0.67	0.51
Average	4.41	2.78	2.92	1.52	2.53	0.63	0.52
Standard deviation	0.42	0.18	0.27	0.17	0.08	0.03	0.02

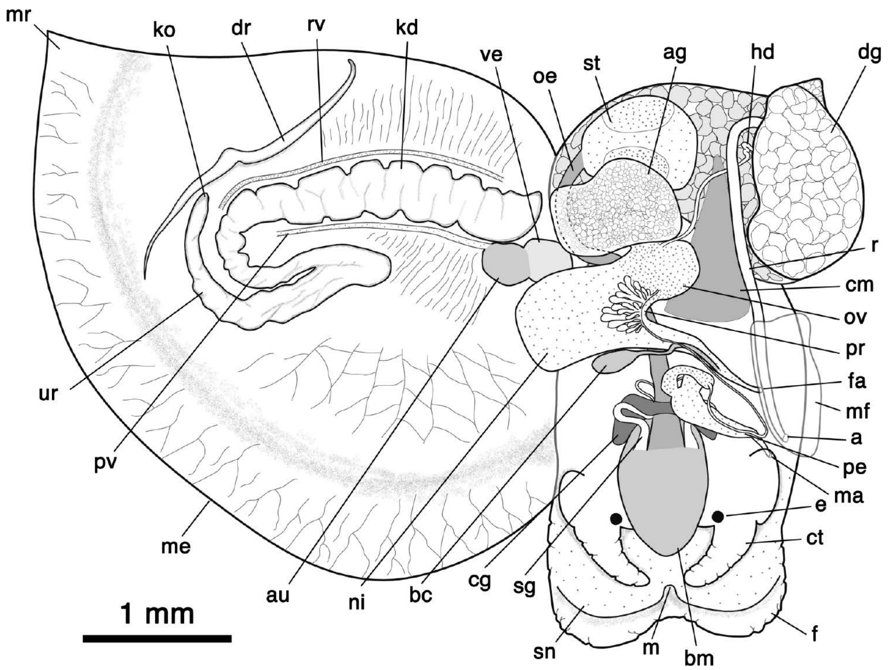

Fig. 3. Illustration of whole animal of *Culmenella prashadi*. Mantle roof was unfolded to the right side of the body. Abbreviations: a – anus; ag – albumen gland; au – auricle; bc – bursa copulatrix; bm – buccal mass; cg – cerebral ganglia; cm – columellar muscle; ct – cephalic tentacle; dg – digestive gland; dr – dorsal ridge; e – eye; f – foot; fa – female genital opening; hd – hermaphrodite duct; i – intestine; kd – kidney; ko – kidney opening; m – mouth; ma – male genial opening; me – mantle edge; mf – mantle flap; mr – mantle roof; ni – nidamental gland; oe – oesophagus; ov – oviduct; pe – penis; pr – prostate gland; pv – pulmonary vein; r – rectum; rv – renal vein; sg – salivary gland; sn – snout; st – stomach; ur – urethra; ve – ventricle.

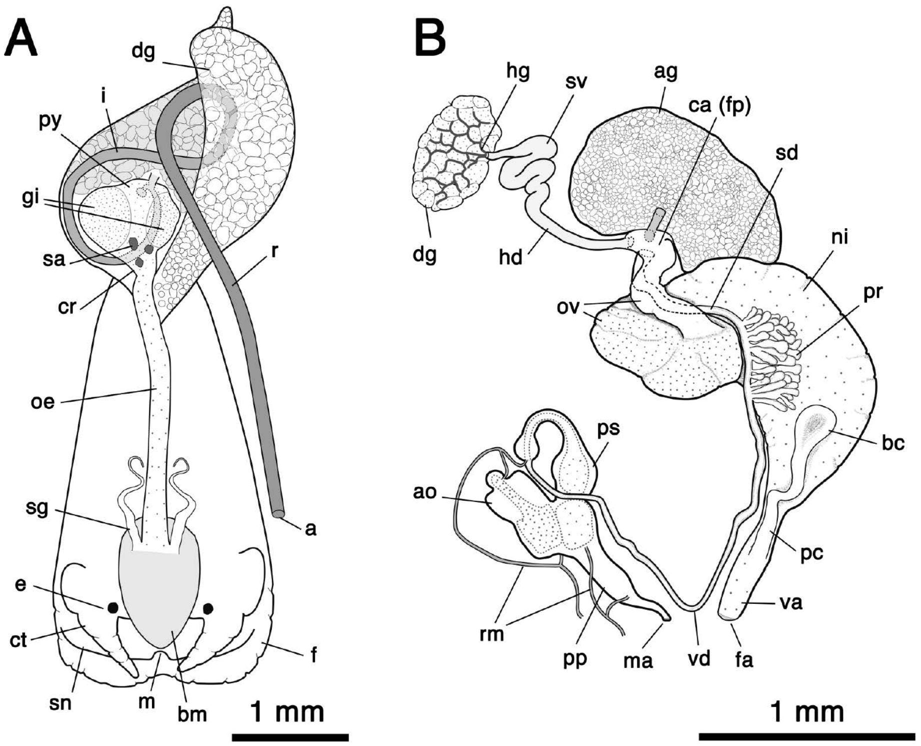

Fig. 4. Illustration of digestive (**A**) and reproductive (**B**) systems of *Culmenella prashadi*. Abbreviations: a – anus; ag – albumen gland; ao – accessory preputial organ; bc – bursa copulatrix; bm – buccal mass; ca (fp) – carrefour (fertilization pouch); cr – crop; ct – cephalic tentacle; dg – digestive gland; e – eye; f – foot; fa – female genital opening; gi – gizzard; hd – hermaphrodite duct; hg – hermaphrodite gland; i – intestine; m – mouth; ma – male genial opening; ni – nidamental gland; oe – oesophagus; ov – oviduct; pc – pedunculus; ps – penial sheath; pp – preputium; pr – prostate gland; py – pylorus; r – rectum; rm – retractor mascle; sa – sand crystal; sd – seminal duct; sg – salivary gland; sn – snout; st – stomach; sv – seminal vesicle; va – vagina; vd – vas deferens.

snout into buccal cavity. Buccal mass (bm) large (around 1.0 mm in length), oval, colored light beige. Salivary glands (sg) long, tapering, colored light yellow, connecting to dorsal posterior side of buccal mass; meandering where passing nerve ring; not fusing in posterior portion. Radular sac invisible outside buccal mass. Jaw solid, thin, colored dark brown, lying at anterior side of buccal mass; blade-shaped on dorsal side; narrow, near L-shaped on lateral side at frontal view.

Radula colorless, translucent, with 30–41 teeth per transverse row. Rachidian teeth rectangular (around 4 μm in width), with 2 large, pointed cusps and 2 minor rounded cusps (approximately 1/4 length of larger cusps). Lateral and marginal tooth elongate pentagonal (around 5–6 μm in width), their boundaries ambiguous without interstice; with 1 large, pointed mesocone, 1 small pointed endocone (approximately 1/3 to 1/2 lengths of mesocone), 2–4 ectocones (4–6 cusps in total); one ectocone rather large (approximately 1/2 length of mesocone), pointed, other small, rounded (about 1/7 to 1/5 lengths of mesocone); mesocone and endocone smaller at outer sides of marginal teeth; marginal teeth weaker at outermost portions of row.

Oesophagus (oe) colored opaque white; opens widely to buccal cavity; curves ventrally in passing nerve ring; extends slightly off body midline to right; curves laterally in front of stomach (st); enters stomach. Crop (cr) colorless, translucent, at anterior portion of stomach; contains several sand crystals (sa). One pair of gizzards (gi) at middle portion of stomach; colored opaque white to light beige; fibrous on outside; several coarse folds on inside. Pylorus (py) colorless, translucent, situated at posterior portion of stomach. Single narrow opening at end of stomach to intestine (i) and digestive gland (dg). Digestive gland around 3.0 mm in length, colored light brown; composed of mass of large vesicles at central region; vesicles smaller at anterior and apical portions. Intestine looped under stomach and over middle of digestive gland before connecting to rectum (r). Rectum long, continuing almost straight to anus. Anus (a) simple opening on anterior surface of mantle flap.

Reproductive system (Fig. 4B): Hermaphrodite gland (hg) narrow, colored opaque white; tips interpenetrate digestive gland (dg); assembles at basal portion; connecting to hermaphrodite duct (hd). Hermaphrodite duct immediately swells, forming meandering seminal vesicle (sv) at anterior to central portions of duct; continuing to carrefour (ca) [fertilization pouch (fp)]. Openings of hermaphrodite duct, albumen gland duct, oviduct (ov), seminal duct (sd) situated at carrefour. Albumen gland (ag) around 1.1 mm in length, colored light grey, composed of many small vesicles. Anterior portion of oviduct thick tubular, colorless, translucent; posterior part wide, opaque white, with deep wrinkles. Nidamental gland (ni) arising from oviduct, around 1.0 mm in length, colored light grey, posterior portion connecting to vagina. Pedunculus (pc) of bursa copulatrix (bc) connecting to vagina. Bursa copulatrix approximately 0.25 mm in length, elongate oval, colored opaque white, translucent at periphery, light pink, nebulous at central portion. Seminal duct wide at proximal portion of carrefour, narrower at distal part; situated along oviduct; connecting to prostate gland (pr). Prostate gland around 0.5 mm in length, colored light grey; adhering to nidamental gland; composed of bundles with single or several elongate lobes; each bundle connected with narrow ventral duct. Vas deferens (vd) arising from prostate gland, narrow, translucent, lying along nidamental gland and vagina; central portion buried in columellar muscle (cm) between male and female genital openings (fa); connecting to penial sheath (ps). Duct leading to vas deferens passes through penial sheath. Penial sheath elongated (around 0.8 mm in length); its anterior and posterior portions swelling; connecting to preputium. Preputium (pp) tapering (around 0.7 mm in length), muscular, translucent in proximal portion of genital opening, opaque in distal part; entering male genital opening (ma). Accessory preputial organ (ao) near rectangular (around 0.3 mm in length), muscular, opaque, with single short, blunt projection at tip; projection connecting to internal core. Retractor muscles (rm) quite narrow, translucent; attached near middle and basal parts of preputium, tips of penial sheath and accessory preputial organ.

Central nervous system (Fig. 5): Circumoesophageal nerve ring streptoneurous, epiathroid, with ganglia strongly concentrated. Cerebral ganglia (rcg, lcg) elongate oval (approximately 0.29 mm in length), near posterior end of buccal mass (bm) and dorsal portion of anterior oesophagus (oe); several deep wrinkles on surface. Cerebral commissure (cc) long, wide (approximately 0.16 mm in length). Tentacular nerves (tn) thicker than optic nerves (opn); branching from thick nerve leaving cerebral ganglia near basal tentacle; thick nerve arising from cerebral ganglia without distinct swellings at their bases, running parallel to optic nerves near its basal portion. Optic nerves branching from narrow nerve arising from just inside tentacular nerves at its distal portion. Labial nerves (ln) slightly narrower than tentacular nerves; extending anteriorly alongside buccal mass. Pleural ganglia (rplg, lplg) small (approximately 0.14 mm in length), oval, adhering ventrally to cerebral ganglia; separated by constriction. Parietal ganglia (rpag, lpag) rather large, oval, asymmetric; left ganglion (approximately 0.19 mm in length) larger than right one (0.15 mm); adhering to pleural and visceral ganglia (vg). Visceral ganglia rather large (approximately 0.22 mm in length), elongate oval. One thick nerve from each of pleural and visceral ganglia extends posteriorly. Buccal ganglia (rbg, lbg) small (approximately 0.14 mm in length), globular, joined by short, narrow commissure (bcc) at postero-dorsal sides of buccal mass. Thin nerves extend anteriorly from lateral and dorsal portions of buccal ganglia; lateral nerves connect to anterior sides of cerebral ganglia. Pedal ganglia (rpg, lpg) large (approximately 0.28 mm in length), globular,

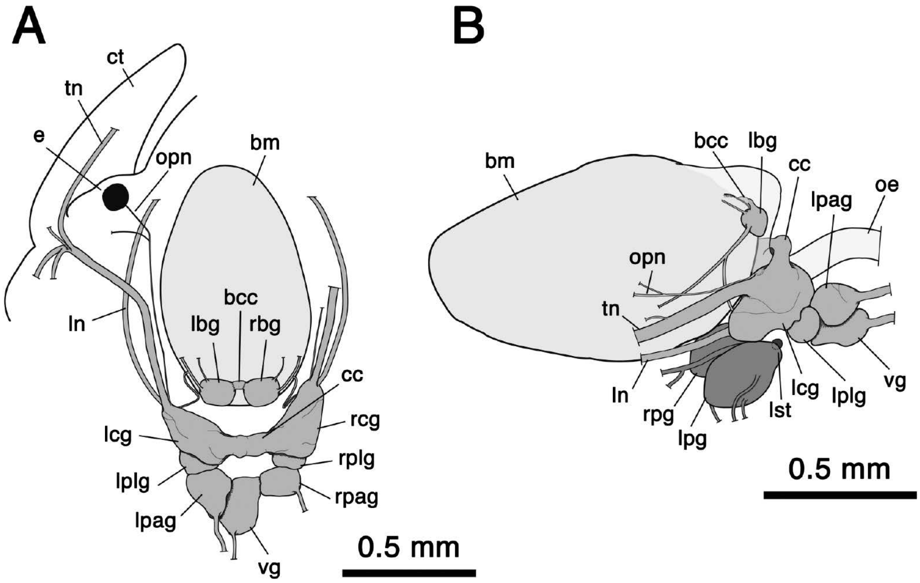

Fig. 5. Illustration of central nervous system of *Culmenella prashadi*. **A**. Dorsal view. **B**. Left lateral view. Abbreviations: bcc – buccal commissure; bm – buccal mass; cc – cerebral commissure; ct – cephalic tentacle; e – eye; lbg – left buccal ganglion; lcg – left cerebral ganglion; ln – labial nerve; lpag – left parietal ganglion; lpg – left pedal ganglion; lplg – left pleural ganglion; oe – oesophagus; opn – optic nerve; rbg – right buccal ganglion; rcg – right cerebral ganglion; rpag – right parietal ganglion; rpg – right pedal ganglion; rplg – right pleural ganglion; st – statocyst; tn – tentacular nerve; vg – visceral ganglion.

connected dorsally to cerebral ganglia. Left and right pedal ganglia of about equal size; tightly adhering to each other at lateral sides. Three thin nerves arising from lateral and basal sides of pedal ganglia visible; one thick nerve from dorsal surface. Small statocysts (lst) at postero-dorsal portions of pedal ganglia.

Habitat

Culmenella prashadi was found in a small pond surrounded by broadleaved mountain forests in central Fukushima Prefecture. The pond water was cloudy, and the sandy bottoms expanded the pond shore. Sandy mud containing fallen leaves and branches was deposited approximately 1 m from the shore, and the substrate deepened towards the center of the pond (Fig. 6A). *Culmenella* snails were observed mainly on the underside of the branches, half-buried in sandy mud at a depth of 0.5 m or more. Several individuals crawled on the surface and underside of deciduous leaves (Fig. 6B). More than 100 individuals of various shell sizes, ranging from juveniles with approximately 3 mm shell length to adults, were found during a two-hour survey by the two authors. In the pond, *Cu. prashadi* occurred with *Cipangopaludina laeta* (Martens, 1860), *Radix plicatula* (Benson, 1842), *Ferrissia californica* (Rowell, 1863), and *Odhneripisidium uejii* (Mori, 1938).

Genetic analysis

Haplotypes of the 655 bp COI and 436 bp 16S sequences of the two *Cu. prashadi* specimens obtained in this study were identical for each. A single-base substitution was observed between the haplotypes of *Cu. prashadi* collected from Fukushima and Aomori Prefectures (82nd position in the 655 bp aligned COI sequences). Two specimens of *Cu. prashadi* from Fukushima Prefecture and one Aomori specimen (LC428897) showed an identical haplotype in the 485 bp aligned 16S

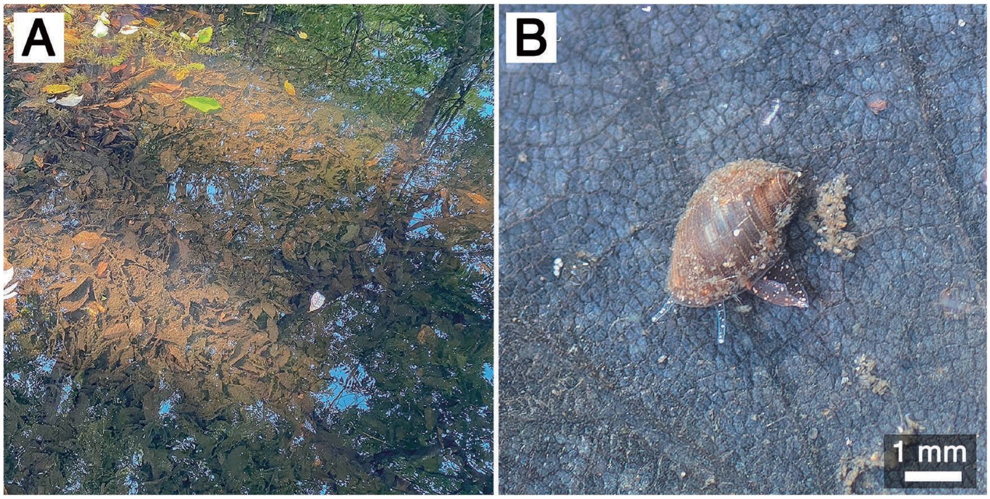

Fig. 6. Habitat (**A**) and wild individual (**B**) of *Culmenella prashadi* in central Fukushima Prefecture.

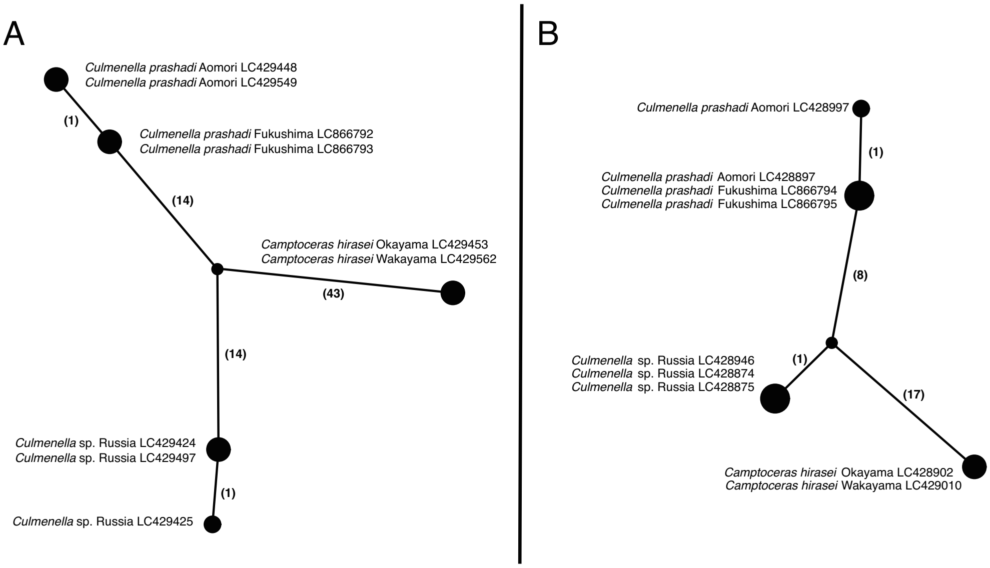

Fig. 7. Statistical parsimony network of a partial COI (**A**) and 16S (**B**) sequences showing the relationships between *Culmenella prashadi*, *Culmenella* sp., and *Camptoceras hirasei*. Each connection indicates a single mutation, and numbers represent missing intermediate haplotypes.

sequences. The remaining Aomori specimen (LC428997) had a haplotype with one substitution in the 300th position from the other three samples. Between the haplotypes of *Cu. prashadi* from Fukushima Prefecture and *Culmenella* sp. from Russia, 28–29 (COI) and nine (16S) base substitutions were detected (Fig. 7).

Discussion

The shell and soft body features of the *Culmenella* snails collected from Fukushima Prefecture were almost identical to those in previous reports of *Cu. prashadi* (Hubendick, 1959; Mori, 1938). Their mitochondrial haplotypes, which were similar to those of the Aomori populations, also confirmed that these snails were *Cu. prashadi*. On the other hand, the following morphological variations were observed between Hubendick (1959) and the present study: the accessory preputial organ was previously described as tapering, but was of constant thickness throughout this study; 33 teeth per row were observed previously in the radula, but the present samples had 30–41 teeth per row. These differences are likely intraspecific variations that were previously unclarified in *Cu. prashadi*. Shell length of the present mature specimens (3.9–5.3 mm) was also within the range observed previously [Clench (1927) – 2.7–3.4 mm; Mori (1938), Hubendick (1967) – 6.1 mm]. Although maturation of smaller specimens has not been verified by Clench (1927), present study confirmed that this species matures from 3.9 mm shell length.

In *Culmenella*, anatomical traits have been clarified in the Japanese *Cu. prashadi*, Russian *Cu. rezvoji*, and Thai *Cu. jiraponi* (Hubendick, 1967) (Hubendick, 1959, 1967; Starobogatov, 1957). In the original description of *Cu. subspinosa* Annandale & Prashad, 1920, *Cu. lindholmi* Starobogatov & Prozorova, 1990, and *Cu. buldowskii* Starobogatov & Prozorova, 1990, only the male genitalia were investigated. The mantle flap was drawn as a single mass in *Cu. prashadi* (separated into two tissues in *Cu. jiraponi*) and the dorsal ridge as almost straight in *Cu. prashadi* (meandering in *Cu. jiraponi*), although those differences were not mentioned by Hubendick (1959). Additionally, the accessory preputial organs of *Cu. prashadi* and *Cu. rezvoji* were shorter than in *Cu. jiraponi*. The lateral teeth in the central part of the radula also have four cusps in *Cu. prashadi* instead of the three cusps in *Cu. rezvoji*, as indicated by Hubendick (1959). These features of *Cu. prashadi* were almost concordant with the present results, and thus, these anatomical differences could be diagnostic between the three species.

The two sister genera *Culmenella* and *Camptoceras* have been distinguished mainly by differences in the interstices of the marginal radular teeth and penial thickness, based on dissections of *Cu. prashadi*, *Cu. jiraponi*, and *Ca. hirasei* (Hubendick, 1955a, 1959, 1967). The present examination of the central nervous system further showed that *Cu. prashadi* possesses unfused pleural and visceral ganglia. Unlike other planorbid species, the pleural and visceral ganglia were illustrated as fused in *Ca. hirasei* (Hubendick, 1955a, 1955b), and the differences in the nervous system between *Cu. prashadi* and *Ca. hirasei* may be useful in identifying both the two species and the two genera.

Anatomical traits and their intraspecific variation, as well as genetic features, have been insufficiently studied in most species of *Culmenella* and *Camptoceras*, despite disagreements between studies regarding treatment as species or subspecies and their validity (*e.g.*, Hubendick, 1967; Kimura, 2020; Masuda & Uchiyama, 2010: 160; NCDELDIPG, 2020; Vinarski & Kantor, 2016). Especially in the case of *Cu. prashadi* and *Cu. rezvoji*, where only minor morphological differences were indicated by Hubendick (1959), their distinctiveness was placed in question again by the variations observed in the present study. Considering the variation of accessory preputial organ observed between the previous and present *Cu. prashadi* specimens, the identities of Russian species, which were established from male genital morphologies, should also be re-examined (Starobogatov & Prozorova, 1990). Therefore, further comprehensive comparisons based on integrative analyses are required to regularize their taxonomic accounts.

COI and 16S haplotypes of the two sequenced *Cu. prashadi* were similar to those obtained from populations in Aomori Prefecture, and base substitutions were observed between these populations. Although they could be either variations among the few samples analyzed or true differences between populations, settling this will require comparison of many specimens from a wide range of populations. However, habitats for *Cu. prashadi* have been rapidly lost in Japan in recent years, with only a few populations remaining (Matsuda, 1998). The possibility that populations of this species survive in narrow areas, as in the present case, applies also to other regions of the country.

It is therefore important for the conservation of *Cu. prashadi* to prevent environmental degradation in areas with potential habitats, and to monitor existing populations.

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福島県から初めて見出されたヒダリマキモノアラガイ（異鰓亜綱：ヒラマキガイ科）の形態的・遺伝的特徴

澤田直人・宮井卓人

要　約

ヒダリマキモノアラガイ *Culmenella prashadi*（Clench, 1931）は本州の広い地域から記録されており，近年に生息地が急激に縮小しているヒラマキガイ科淡水貝類の絶滅危惧種である。著者らはこれまでに記録のなかった福島県において，県中部の山中の小さな池で本種の新たな個体群を発見した。

殻および，軟体部の外部形態，内部形態（消化器系，生殖器系，中枢神経系）の検討の結果，この個体群は過去に解剖学的に研究された石川県の個体群と概ね同一の特徴を有する一方で，陰茎の包皮付属器や歯舌の形態にこれまで知られていなかった種内変異を示した。本研究の解剖学的な検証によって，ヒダリマキモノアラガイは外套の肉弁や歯舌，雄性生殖器，中枢神経系の特徴によって同属の他種や姉妹属のカワネジガイ *Camptoceras hirasei* Walker, 1919 から識別されることが確かめられた。また，新たに見出された福島県の個体群と過去に遺伝解析が行われた青森県の個体群の間では，2 つのミトコンドリア遺伝子のハプロタイプにそれぞれ 1 つずつの塩基置換が特定された。

本研究はヒダリマキモノアラガイ属 *Culmenella* Clench, 1927 の中枢神経系を初めて記載した。本属やカワネジガイ属 *Camptoceras* Benson, 1843 に属するほとんどの種では，形態学的，遺伝学的研究が 1960 年代からほとんど進展しておらず，分類の再検討に必要な情報が不足している。このような状況にも関わらず，本邦ではこれら 2 属の生息地が急速に失われていることから，ヒダリマキモノアラガイをはじめとする希少な淡水貝類の現存個体群の減少を防ぐとともに，本研究で発見されたような潜在的な生息地を有する地域の保全を進めることが急務と考えられる。