

A new marine tardigrade genus and species (Arthrotardigrada, Styraconyxidae) with unique pockets on the legs

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Abstract

A marine heterotardigrade *Cyaegharctus kitamurai* **gen. et sp. nov.** (Arthrotardigrada, Styraconyxidae) is described from Daidokutsu, a submarine cave off Iejima island, Okinawa Islands, Ryukyu Archipelago, Japan. It is easily distinguished from all other styraconyxids by its pocket organs (putative sensory structures) on all legs in addition to the usual leg sensory organs. Its combination of other character states, such as the dorso-ventrally flattened body, ovoid primary clavae, conical secondary clavae, large terminal anus, internal digits with proximal pads and peduncles, external digits with developed peduncles and all digits with three-pointed claws in adult female, supports the erection of a new genus and species.

Key Words

meiofauna, Pacific Ocean, sensory organs, submarine cave, Tardigrada

Introduction

Marine tardigrades, specifically arthrotardigrades, exhibit remarkable morphological diversity (see comprehensive drawings of arthrotardigrade genera in Fontoura et al. (2017) and drawings of additional genera in Fujimoto and Yamasaki (2017) and Fujimoto and Ohtsuka (2019)). Styraconyxidae Kristensen and Renaud-Mornant, 1983 is one of the arthrotardigrade families and it is comprised of 38 species and subspecies of ten genera: *Angursa* Pollock, 1979 (eight species), *Bathyechiniscus* Steiner, 1926 (monotypic), *Lepoarctus* Kristensen and Renaud-Mornant, 1983 (monotypic), *Paratanarctus* D'Addabbo Gallo et al., 1992 (monotypic), *Pleocola* Cantacuzène, 1951 (monotypic), *Raiarctus* Renaud-Mornant, 1981a (five species), *Rhomboarctus* Renaud-Mornant, 1984 (three species), *Styraconyx* Thulin, 1942 (15 species and subspecies), *Tetrakentron* Cuénot, 1892 (monotypic) and *Tholoarctus* Kristensen and Renaud-Mornant, 1983 (three species and subspecies) (Guidetti and Bertolani 2005; Degma and Guidetti 2007; Degma et al. 2019; Pérez-Pech

et al. 2020). In addition to these ten genera, Fujimoto et al. (2017) reported an undescribed genus related to *Styraconyx* and *Tetrakentron* from a submarine cave in Japan (for detail of this cave see Yamamoto et al. 2009). However, Fujimoto et al. (2017) did not make any remarks on the undescribed genus' morphology and only provided two voucher micrographs of a specimen used for their molecular phylogenetic study (provided by MorphoBank (O'Leary and Kaufman 2012) at <http://doi.org/10.7934/P2234>). Herein, we describe this taxon as a new genus and species, based on detailed morphological observation of additional material collected from the same cave.

Material and methods

The type material was collected from Daidokutsu, a submarine cave off Iejima island, Okinawa Islands, Ryukyu Archipelago, Japan (26°43'N, 127°50'E) (Yamamoto et al. 2009) in 2013 and 2019 by Koshin Yasumura (KY) and the first author (SF). For extraction of meiofauna, the cave

sediment samples were stirred with tap water and the supernatants were concentrated using a 30 µm opening mesh net to separate coarse sediment and to wash away seawater. Subsequently, the meiofauna and fine sediment were separated using LUDOX HS-40 colloidal silica (Sigma-Aldrich Co., St. Louis) and a 32 µm opening mesh net (e.g. Giere 2009). The type material was sorted under a stereomicroscope and fixed in 2–4% buffered formaldehyde. Specimens for light microscopy were mounted in distilled water for brief observation (only for the holotype) and mounted in glycerol. Differential interference contrast microscopy (DIC) was conducted using an Olympus BX53 and phase contrast microscopy (PhC) was conducted using an Olympus BX41. One specimen for scanning electron microscopy (SEM) was post-fixed in 2% OsO₄ for 2 h, dehydrated through a series of ethanol and acetone, critical point dried (BAL-TEC CPD-030), osmium coated (Filgen OPC40) and observed using JEOL JSM-7001F. Type material was deposited in the Zoological Collection of Kyoto University (KUZ). Adobe Illustrator CS6 and Photoshop CS6 were used to prepare figures and to obtain morphometric data.

Systematics

Family Styraconyxidae Kristensen & Renaud-Mornant, 1983

Cyaegharctus gen. nov.

<http://zoobank.org/5F0BA732-F1A4-4BBE-B1E0-691BFB410C2A>

Type species. *Cyaegharctus kitamurai* gen. et sp. nov.

Diagnosis. Styraconyxidae with dorso-ventrally flattened body; cuticle smooth; epicuticular pillars present; cephalic region with complete set of cephalic cirri, ovoid primary clavae and compact conical secondary clavae; median cirrus and internal cirri at anterior margin of cephalic region; external cirri latero-ventral to internal cirri; lateral cirri and primary clavae sharing common base at antero-lateral position of cephalic region; secondary clavae between internal and external cirri; buccal apparatus with stylet supports; cirri E spine-like; seminal receptacle ducts opening anterior to gonopore; terminal anus with pair of large longitudinally elongate lobes; dorsal side of each leg with usual sensory organ on proximal part of femur and pocket organs at distal margin of femur; internal digits each with proximal pad and thin peduncle; external digits with proximal developed peduncles; claw sheaths present; adult female with three-pointed claws on all digits; four-claw juvenile with three-pointed claws on internal digits and single-pointed claws on external digits; three-pointed claws each with accessory and secondary hooks less developed compared to primary hook.

Etymology. The genus name is masculine and derives from two words, *Cyäegha*, a deity of darkness and caves

in the Cthulhu Mythos from Eddy C. Bertin's short story *Darkness, My Name Is* and *arctus*, a Latinised Greek word meaning bear.

Remarks. The presence of pocket organs distinguishes the new genus and species from all other members of the phylum (see **Description of holotype** and **Discussion** for further information on the new structure). For this uniqueness, it is difficult to infer the new taxon's taxonomic position, based solely on this morphology. Here we use other comparable morphological characters to infer its taxonomic position. The new taxon's three-pointed claws and peduncles indicate its affinity to the following four genera of Styraconyxidae: *Raiarctus*, *Styraconyx*, *Tetrakentron* and *Tholoarctus* (van der Land 1975; Kristensen and Higgins 1984; Jørgensen et al. 2014).

The new taxon's epicuticular pillars are not developed to the degree of *Raiarctus*'s characteristic pillars (Jørgensen et al. 2014). In addition, the new taxon has its seminal receptacles opening near the gonopore, in contrast to those of the latter genus opening laterally apart from the gonopore (Jørgensen et al. 2014).

Styraconyx harbours species covering a wide range of character states and has been regarded as a non-monophyletic group (Kristensen and Renaud-Mornant 1983; Kristensen and Higgins 1984). Due to this problematic state, many of the new taxon's character states fall within the range of *Styraconyx*, i.e. morphology of cephalic cirri, primary clavae, usual leg sensory organs, claws and digits (including peduncles) and seminal receptacles (Kristensen and Higgins 1984). However, the new taxon's compact conical secondary clavae differ from *Styraconyx*'s flat sac to dome-shaped ones (Kristensen and Higgins 1984). Further, although it is not included in the generic diagnosis (Kristensen and Higgins 1984), it is apparent from all the original descriptions of *Styraconyx* species that they have a cylindrical body shape differing from the new taxon's dorso-ventrally flattened body and also the anus is not known to be developed as the large bi-lobed anus of the new taxon (Thulin 1942; Robotti 1971; Kristensen 1977; Renaud-Mornant 1981b; Pollock 1983; Kristensen and Higgins 1984; D'Addabbo Gallo et al. 1984, 1989; Chang and Rho 1998; Bartels et al. 2015; Pérez-Pech et al. 2020).

The new taxon and *Tetrakentron* both have a dorso-ventrally flattened body, but the latter genus has short legs with strongly developed claws (van der Land 1975). The latest diagnosis of *Tetrakentron* by van der Land (1975) is brief and we here present some other differences, based on information that van der Land (1975) did not implement in the diagnosis and additional information provided by subsequent literature (Kristensen 1980; Kristensen and Hansen 2005). One difference is that, in contrast to the new taxon, *Tetrakentron* has unique peduncles, which van der Land (1975) called 'drop-shaped' (already illustrated in its original description (Cuénot 1892); for detailed drawing see van der Land (1975)).

Another difference is that the new taxon and *Tetrakentron* have differently arranged cephalic appendages: i) the new taxon's primary clavae are positioned laterally apart from the secondary clavae, whereas the two clavae are situated close together in *Tetrakentron* and ii) the new taxon's secondary clavae are positioned posterior from the anterior margin of the cephalic region, whereas those of *Tetrakentron* are at the antero-lateral margin (see detailed drawings and SEM in Kristensen (1980)). The presence of epicuticular pillars in the new taxon further differentiates it from *Tetrakentron* without pillars (Kristensen 1980). On the other hand, the new taxon and *Tetrakentron* have similar secondary clavae morphology and they both have their seminal receptacles opening anterior to their gonopores (Kristensen and Hansen 2005). It is also noteworthy that these two taxa, as well as *Angursa*, have a terminal anus (Kristensen and Hansen 2005; Fujimoto and Hansen 2019). Whether these morphological similarities between the new taxon and *Tetrakentron* are phylogenetic signals or not need to be verified with molecular data.

The new taxon has a dorso-ventrally flattened body differing from *Tholoarctus*'s cylindrical body with a large detached outer epicuticle (Jørgensen et al. 2014). Further, the new taxon has ovoid primary clavae and conical secondary clavae, in contrast to *Tholoarctus* with cone-shaped primary clavae and large secondary clavae surrounding the internal and external cirri (Jørgensen et al. 2014).

For the morphological differences indicated above, the new taxon's designation to any of the four genera is not plausible and the erection of a new genus and species is justified.

Cyaegharctus kitamurai gen. et sp. nov.

<http://zoobank.org/04BDD214-AC65-44F3-B7C5-3AD160927E36>

Figs 1–3

Styraconyxidae gen. sp. (Fujimoto et al. 2017): partial sequence of the nuclear 28S rRNA available at DDBJ/GenBank under accession number LC103153 and voucher micrographs provided by MorphoBank (O'Leary and Kaufman 2012) at <http://doi.org/10.7934/P2234>.

Material examined. Holotype: KUZ Z2624 (on microscope slide in glycerol), an adult female collected from Daidokutsu (type locality) on 28 July 2019 by KY. Paratypes: KUZ Z2625 (on microscope slide in glycerol), an adult female collected on 13 May 2019 by SF; KUZ Z2626 (on microscope slide in glycerol), an adult female collected on 26 August 2013 by KY; KUZ Z2627 (on SEM stub), a four-claw juvenile collected on 13 May 2019 by SF. All paratypes were collected from the type locality.

Type locality. Muddy bottom of Daidokutsu (28 m below sea level), off Iejima Island, Okinawa Islands, Ryukyu Archipelago, Japan (26°43'N, 127°50'E).

Diagnosis. *Cyaegharctus* with median, internal and external cirri each with basal swelling (cirrophore?) and short

subdivision; lateral cirri each with short subdivision; cirri E on cirrophores arising from round lateral processes between legs III and IV; seminal receptacle ducts run postero-laterally with U-shaped bend (vesicles unknown); leg I sensory organs spine-like, each with distal subdivision and terminal pore; legs II and III sensory organs spine-like without subdivisions; leg IV sensory organs papillate with short distal tubes.

Description of holotype. Adult female (Figs 1, 2A–J). Dorso-ventrally flattened body 202 µm in length and 117 µm wide at level of leg III (Figs 1A, 2A). Outer epicuticle loose from pillar layer as artefact of formaldehyde fixation (for further information see **Remarks on paratypes**). Fine epicuticular pillars recognised.

Cephalic region (head) (Figs 1A, 2B–D) with unpaired median cirrus, paired internal cirri, paired external cirri, paired lateral cirri, paired primary clavae, paired secondary clavae and antero-ventral directed mouth. Median, internal and external cirri (7 µm, 10 µm and 10 µm, respectively) with proximal swelling (cirrophore?) and short, distal subdivision terminating in pore. Lateral cirri (19 µm), each with short, distal subdivision with terminal pore. Primary clavae ovoid (6 µm) with distal pore and van der Land's body at base. Secondary clavae compact and conical (4 µm wide at base). Internal cirri at anterior margin of head and dorsal median cirrus at slightly posterior position. External cirri latero-ventral to internal cirri. Secondary clavae between internal and external cirri. Dorsal lateral cirri and ventral primary clavae share common base at antero-lateral margin of head. Buccal apparatus consists of buccal tube (38 µm), paired stylets, paired stylet supports (inserted 29 µm from mouth opening), three simple placoids (11 µm) and pharyngeal bulb. Observation of buccal apparatus incomplete due to dissolved structures after permanent preparation and difficulty in recognising pharyngeal bulb's margin after squeezing of specimen.

Paired spine-like cirri E (38 µm) (Figs 1A, 2E) on cirrophores arise from round lateral processes at level between legs III and IV.

Rosette-like gonopore 9 µm anterior to anus (Figs 1A, 2E). Gonopore morphology disturbed when cleaning specimen and only contour recognisable after permanent preparation (8 µm in diameter). Anus 16 µm wide at posterior most part of body between legs IV and consists of paired longitudinally elongate lobes. Paired seminal receptacles open immediately anterior to gonopore. Seminal receptacle ducts first run laterally, bent in U-shape and run postero-laterally. Terminal vesicles of seminal receptacles not recognised.

Four pairs of legs (Figs 1, 2F–J) each with usual leg sensory organ on dorsal side of femur's proximal portion, pocket organ on dorsal side of femur's distal margin and four digits terminating in claws. Legs I each with spine-like sensory organ (10 µm) with distal subdivision. Legs II each with spine-like sensory organs

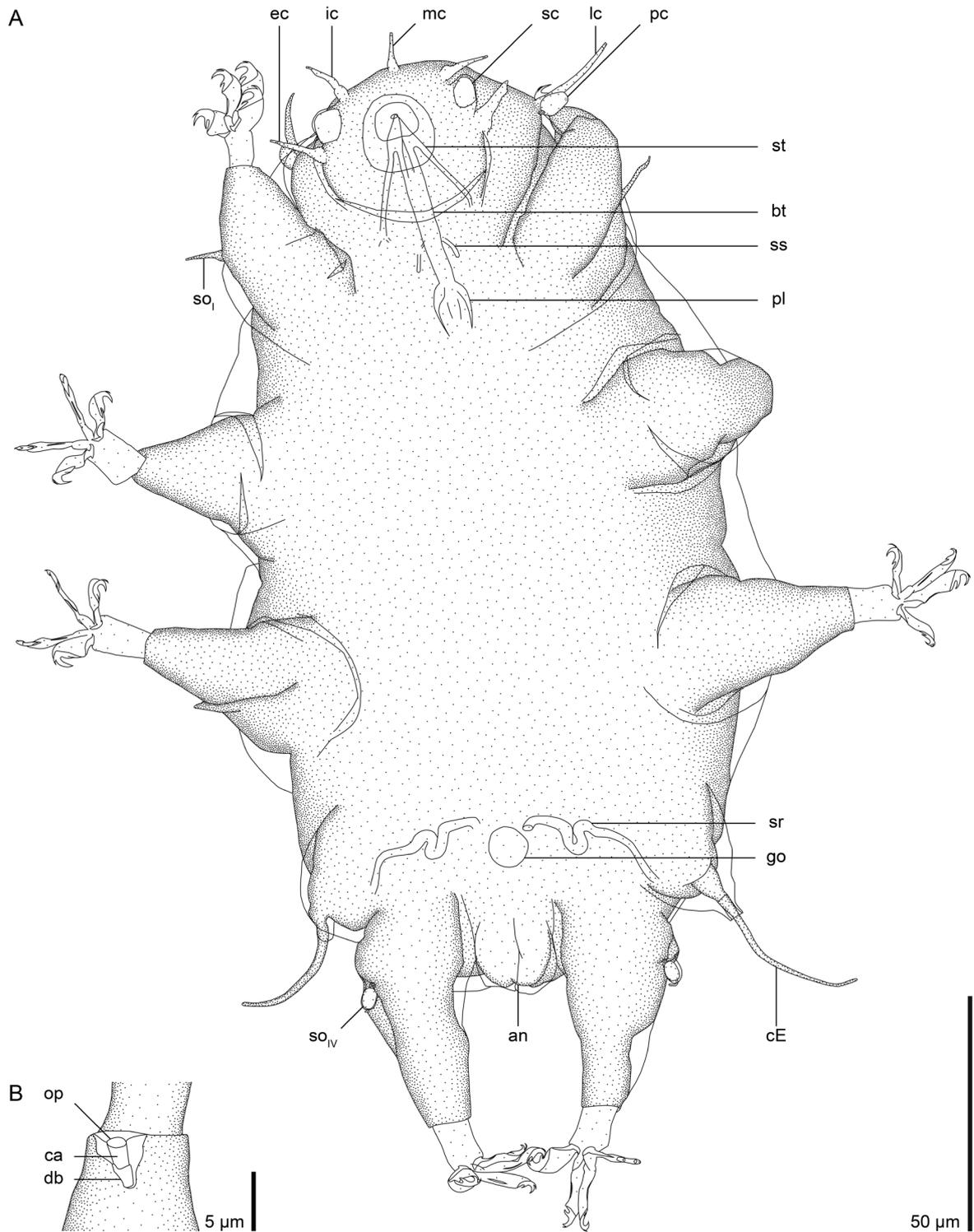


Figure 1. Drawings of *Cyaegharcus kitamurai* gen. et sp. nov., holotype KUZ Z2624. **A.** Habitus (ventral view). **B.** Leg IV pocket organ. **an** anus, **bt** buccal tube, **ca** cavity, **cE** cirrus E, **db** dense body, **ec** external cirrus, **go** female gonopore (detail not available), **ic** internal cirrus, **lc** lateral cirrus, **mc** median cirrus, **pc** primary clava, **pl** placoid, **op** opening, **sc** secondary clava, **so_{I,IV}** legs I and IV sensory organs, **sr** seminal receptacles, **ss** stylet support, **st** stylet.

which lack subdivisions (length not measured due to bad orientation). No sensory organs recognised on legs III but presence likely (recognised in paratypes; see **Remarks on paratypes**). Legs IV each with sensory organ (7 μm) consisting of papilla (4 μm) with distal tubular

portion (2 μm). Pocket organ consists of small opening, cavity and apparent dense body. No difference recognised amongst legs I–IV pocket organs besides protruded opening of leg II pocket organ. Leg IV pocket organ in good orientation for observation of whole structure

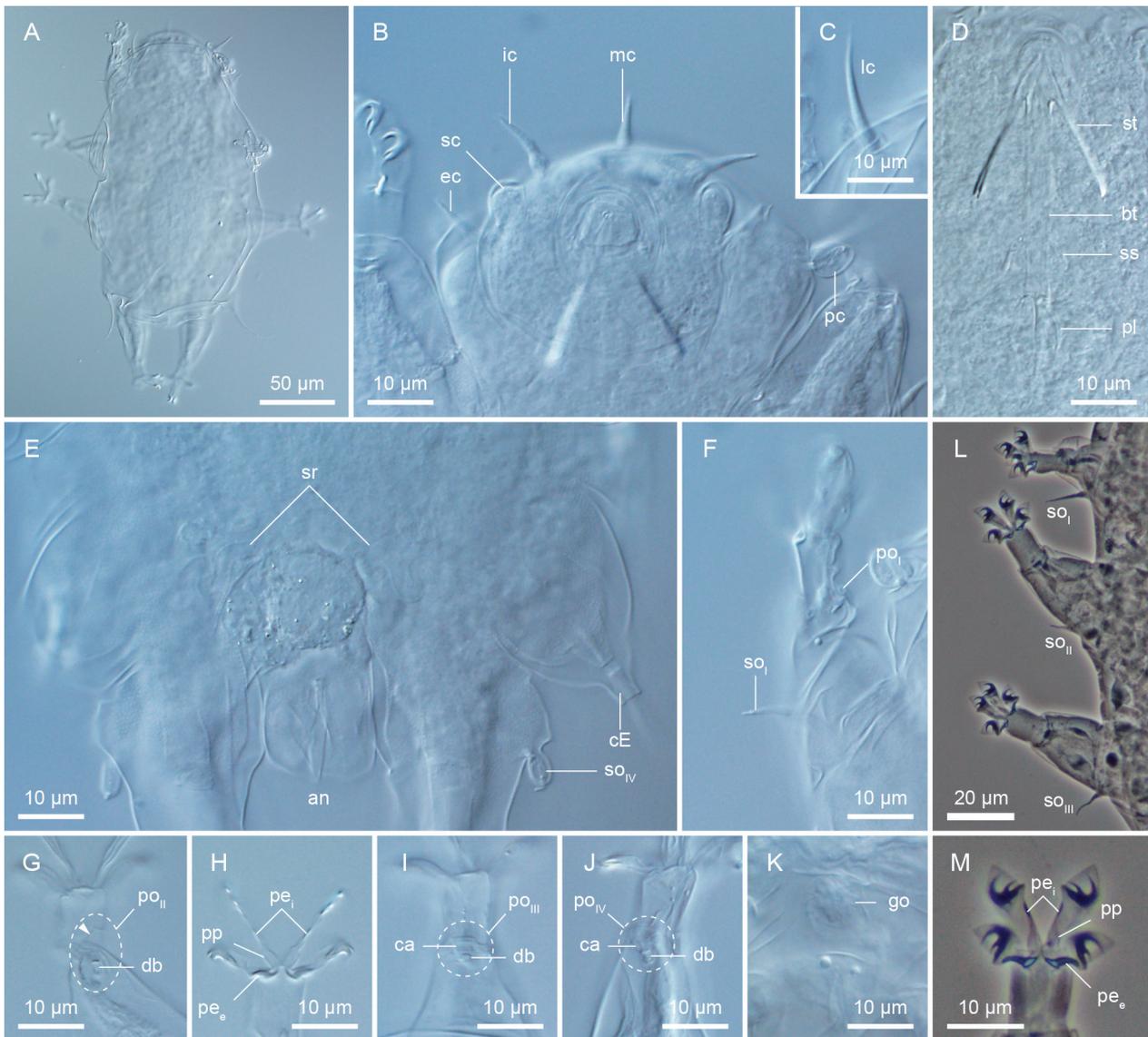


Figure 2. DIC and PhC micrographs of *Cyaegharctus kitamurai* gen. et sp. nov., adult female. **A.** Habitus (dorsal view). **B.** cephalic region (ventral view). **C.** Lateral cirrus. **D.** Buccal apparatus. **E.** Caudal region (ventral view) (epicuticle pillars visible). **F.** Leg I sensory organ and pocket organ. **G.** Leg II pocket organ (arrowhead indicates protruding portion). **H.** Leg II digits and claws. **I.** Leg III pocket organ. **J.** Leg IV pocket organ. **K.** female gonopore. **L.** Legs I–III sensory organs. **M.** Leg III digits and claws. **A–J.** holotype KUZ Z2624, **K.** paratype KUZ Z2625, **L, M.** paratype KUZ Z2626. **an** anus, **bt** buccal tube, **ca** cavity, **cE** cirrus E, **db** dense body, **ec** external cirrus, **go** gonopore, **ic** internal cirrus, **lc** lateral cirrus, **mc** median cirrus, **pc** primary clava, **pe_{i,e}** peduncles of internal and external digits, **pl** placoid, **po_{I–IV}** legs I–IV pocket organs, **pp** proximal pad, **sc** secondary clava, **so_{I–IV}** legs I–IV sensory organs, **sr** seminal receptacles, **ss** stylet support, **st** stylet.

(Fig. 1B). Internal digits each with proximal pad and thin peduncle that do not reach claws, subdivided into proximal and distal portion. Internal digits longer than external digits. Each claw of both internal and external digits with three points: primary hook and less-developed, secondary and accessory hooks. Digits and peduncles slightly longer than those of preceding leg pairs (legs I: internal digits 13 µm (peduncles 3 µm), external digits 10 µm (peduncles 5 µm); legs II: 14 µm (3 µm), 10 µm (5 µm); legs III: 15 µm (4 µm), 10 µm (5 µm); legs IV: 16 µm (4 µm), 10 µm (6 µm)).

Remarks on paratypes. Fixation of specimens using formaldehyde seems to have introduced an artefact in the cuticle, i.e. the detached (or loose) outer epicuticle. When the specimens were sorted in distilled water before fixation, the outer epicuticle did not look loose at 63× magnification (all four specimens) and also at 400× magnification (only observed for KUZ Z2627) as it would appear in *Tholoarctus*. Although these are only brief observations and we did not conduct any experiment to test this artefact, we consider the outer epicuticle’s detached state as an artefact and excluded this character state from the diagnoses of this genus and species.

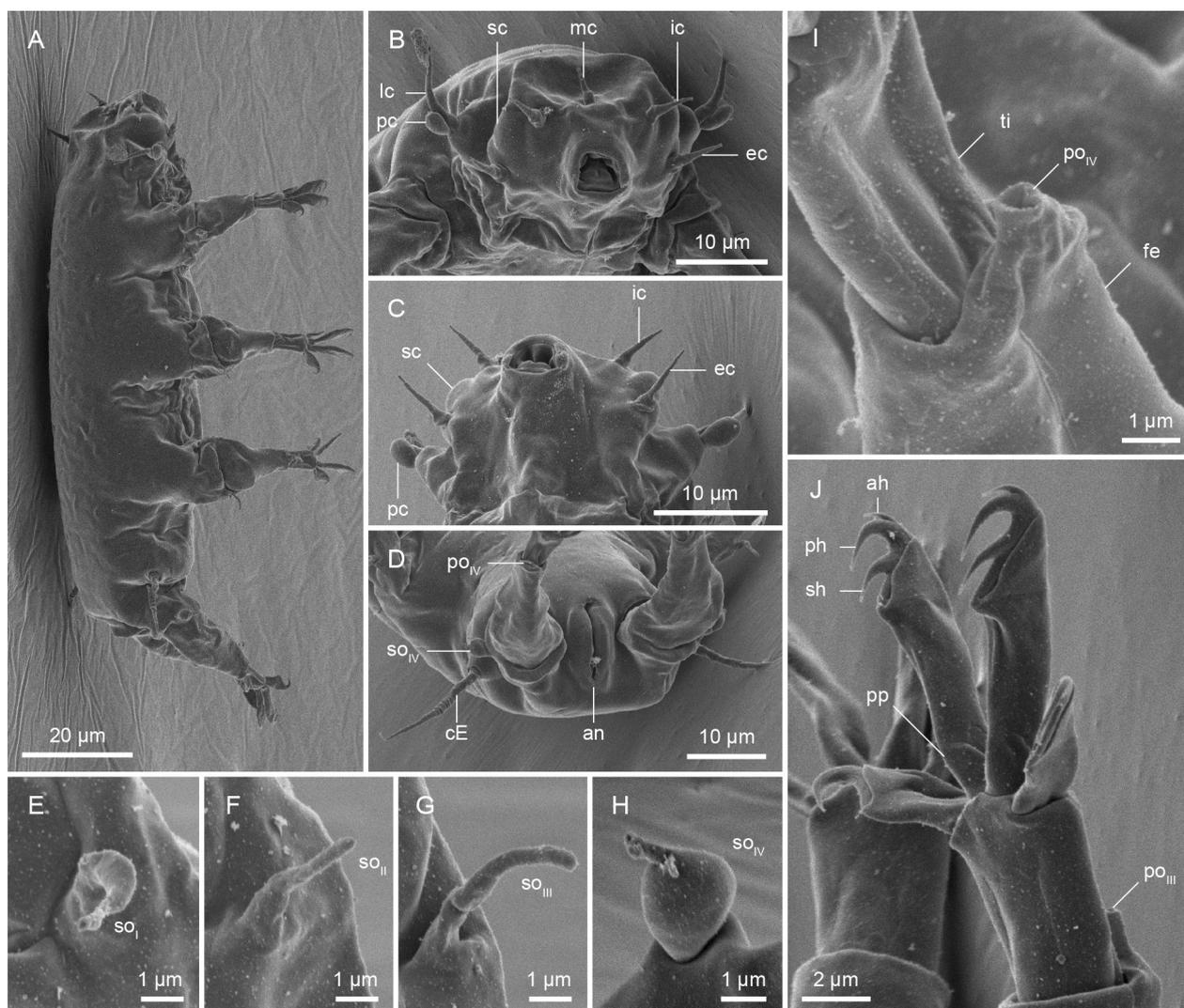


Figure 3. SEM micrographs of *Cyaegharcus kitamurai* gen. et sp. nov., four-claw juvenile paratype KUZ Z2627. **A.** Habitus (lateral view). **B.** Cephalic region (frontal view). **C.** Cephalic region (ventral view). **D.** Anus. **E.** Leg I sensory organ. **F.** Leg II sensory organ. **G.** Leg III sensory organ. **H.** Leg IV sensory organ. **I.** Leg IV pocket organ. **J.** Leg III digits and claws. **ah** accessory hook, **an** anus, **cE** cirrus E, **ec** external cirrus, **fe** femur, **ic** internal cirrus, **lc** lateral cirrus, **mc** median cirrus, **pc** primary clava, **ph** primary hook, **po_{III,IV}** legs III and IV pocket organs, **pp** proximal pad, **sc** secondary clava, **sh** secondary hook, **so_{I-IV}** legs I–IV sensory organs, **ti** tibia.

The adult female paratype KUZ Z2625 revealed the presence of a cuticular ring surrounding the rosette gonopore (Fig. 2K) and the presence of the spine-like leg III sensory organs with no subdivisions. In the adult female paratype KUZ Z2626, the legs I–III sensory organs, claws and peduncles were orientated better than the holotype and the other paratype for observation (Fig. 2L, M). However, the pocket organs were not recognised for this specimen, probably due to the excessively-squeezed state. Other character states, recognised in these two paratypes, confirmed the observation of the holotype. The morphometrics are as follows (KUZ Z2625, Z2626): body length (159 µm, 210 µm), body width (83 µm, 110 µm), median cirrus (5 µm, 8 µm), internal cirrus (10 µm, 12 µm), external cirrus (9 µm, 12 µm), lateral cirrus (17 µm, 19 µm), primary clava (6 µm, 6 µm), secondary clava width (4 µm, 6 µm), cirrus E (33 µm, 33 µm), leg I sen-

sory organ (7 µm, 12 µm), leg II sensory organ (8 µm, 7 µm), leg III sensory organ (10 µm, 11 µm), leg IV sensory organ (4 µm, 7 µm), gonopore (6 µm, -), anus length (-, µm), anus width (-, -), gonopore-anus distance (5 µm, -) (- represents ‘not measured’).

The SEM of a four claw juvenile (Fig. 3) confirmed the results of light microscopy and also provided further detail. However, this SEM specimen also seems to have its outer epicuticle detached. If the outer epicuticle is attached to the underlying layer, a pattern is recognised on the surface of the body due to the pillar layer, but no such indentations were found, suggestive of the detached state of the outer cuticle (for ultrastructure of cuticle, see Kristensen and Neuhaus 1999). The proximal part of each leg has an inflated appearance (Fig. 3A) not recognised in light microscopy. The view of the cephalic region (Fig. 3B, C) revealed the three-dimensional morphology and

the arrangement of the cephalic appendages and also confirmed the presence of terminal pores on the cephalic cirri and the primary clavae. The conical shape of the secondary clavae seems not as evident as in light microscopy probably due to the overlying outer epicuticle. The large anus is not on the ventral surface and rather directed posteriorly (Fig. 3D). The leg sensory organs were recognised (Fig. 3E–H) and those of legs I and IV revealed to have terminal pores. The pocket organs (Fig. 3I, J) were recognised on all legs, however, with slightly different degrees of protruded appearances. The protruded state might be an artefact caused during specimen preparation since specimens on microscope slides do not always have these appearances (Figs 1B, 2F, I, J) or the pocket organs are capable of moving. In the latter case, since no muscles seem to be attached to the structures, a passive movement is likely. Regarding claw/digit morphology, the peduncles (internal structures) were not recognised but the three hooks of the internal claws and the single-pointed external claws were recognised (Fig. 3J).

Etymology. The species is dedicated to Prof. Dr. Akihisa Kitamura (Shizuoka University), who has been studying Daidokutsu and its bivalve assemblage to understand the paleo-environment (e.g. Kitamura et al. 2007).

Discussion

We consider the dense body inside the pocket organs of *Cyaegharctus kitamurai* gen. et sp. nov. to be related to the van der Land's body, often situated at the base of the primary clavae and leg IV sensory organs and suggest that the pocket organs are chemoreceptors. However, Kristensen (1981) is the only one who investigated the function and ultrastructure of arthrotardigrade sensory organs by transmission electron microscopy and, with our poor knowledge on arthrotardigrade sensory organs, this remains a matter of speculation. Another possibility for the new structure is a secretory organ. However, no gland was recognised in its vicinity and there is no evidence supporting this hypothesis. To understand the true functions and evolutionary significance of the pocket organs, comparative ultrastructure studies of arthrotardigrades (including *C. kitamurai* gen. et sp. nov.) are necessary.

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