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ORIGINAL ARTICLE

A new species of the genus *Actinimenes* Ďuriš and Horká, 2017 (Crustacea: Decapoda: Palaemonidae) from the Arabian Sea, Lakshadweep Islands, India

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ABSTRACT

A new species, *Actinimenes koyas* sp. nov. (Decapoda: Palaemonidae) was collected at a depth of 1.0–2.0 m from the coral atoll of Agatti Island, Lakshadweep, Arabian Sea. The species was associated with the sea anemone, *Heteractis magnifica* (Quoy and Gaimard, 1833). It is the second representative of the genus *Actinimenes* Ďuriš and Horká, 2017 described from the Arabian Sea. *Actinimenes koyas* sp. nov. is closely related to *A. ornatellus* in terms of morphological traits. *Actinimenes koyas* sp. nov. is distinguished from *Actinimenes ornatellus* (Bruce, 1979) by the presence of a biramous outer antennular flagellum with three proximal segments fused, a shorter free ramus consisting of 7 to 8 segments with 12–14 groups of aesthetascs, a fourth thoracic sternite with V-shaped median incision and features of the telson and third maxilliped. The present new species is easily distinguished from the other three described species in the genus *Actinimenes* by the structural variation in the fourth sternal plate with a median notch. Additionally, a phylogenetic analysis inferred by Maximum Likelihood using the mitochondrial genes COI and 16S rRNA shows a close relationship of *Actinimenes koyas* sp. nov. with *Actinimenes inornatus* (Kemp, 1922). Pairwise genetic distances estimated using the COI and 16S data provided divergences between *A. koyas* sp. nov. and other congeneric species.

KEYWORDS

Actinimenes koyas sp. nov., anemone associated fauna, Arabian Sea, Lakshadweep, morphology, phylogenetic tree

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Introduction

Palaemonid shrimps commonly have symbiotic associations with various marine organisms such as sponges, cnidarians, echinoderms, mollusks, polychaetes, ascidians, fish, and even other crustaceans (Bruce, 1995; Hayashi and Ohtomi, 2001; Thiel and Baeza, 2001; Bruce and Okuno, 2006; Komai *et al.,* 2010). The ecological interactions between palaemonid shrimps and their hosts are mainly to avoid predators, for mating and molting processes, as a source of food, and as secondary mutualism like cleaning (Fautin *et al.,* 1995; Spotte, 1996; Richardson *et al.,* 1997; Jonsson *et al.,* 2001; Duffy, 2003; Bauer, 2004; Huebner and Chadwick, 2012; Ory *et al.*, 2013). The symbiotic relationship between shrimps and their hosts is typically described as commensalism, and shrimp are associated with a wide range of taxa. For example, Coleman's shrimp *Periclimenes colemani* Bruce, 1975 is associated with echinoderms, the pearl oyster shrimp *Pontonia margarita* Smith in Verrill, 1869 with pen shells, and the sea star shrimp *Zenopontonia soror* (Nobili, 1904) is associated with shallow-water sea stars (Omori *et al.,* 1994; Baeza, 2008; Góngora-Gómez *et al.*, 2015; Antokhina and Britayev, 2020). During this symbiotic association, it has been suggested that shrimp get more benefits (Olliff, 2013).

Generally, palaemonid shrimp in the genus *Periclimenes* O.G. Costa, 1844 are considered to be a polyphyletic and highly diverse group (Chow *et al.*, 2021). In recent decades, this group was divided into many new genera, for example: *Exoclimenella* Bruce, 1995; *Periclimenella* Bruce, 1995; *Manipontonia* Bruce, Okuno and Li, 2005; *Unguicaris* Marin and Chan, 2006; *Ancylomenes* Okuno and Bruce, 2010. Similarly, species of *Actinimenes* Ďuriš and Horká, 2017 were formally considered part of the *Periclimenes brevicarpalis* (Schenkel, 1902) (see Bruce and Svoboda, 1983; Bruce, 2010) and *Periclimenes inornatus* Kemp, 1922 groups (Fransen, 1989). The *P. inornatus* group has been assigned to the separate genus *Actinimenes* by the structure of the fourth thoracic sternite and the shape of chela on the first and second pereopods (Ďuriš and Horká, 2017). The genus contains three species and is commonly associated with sea anemones (Fransen, 1989; Müller, 1993). These species are *Actinimenes inornatus* (associated with *Discosoma* Rüppell and Leuckart, 1828: Corallimorpharia), *Actinimenes ornatellus* (Bruce, 1979), associated with the Actiniaria *Heteractis malu* (Haddon and Shackleton, 1893), and *Actinimenes ornatus* (Bruce, 1969) (associated with Actiniaria). These three species are widely distributed in the tropical regions of the Indo-West Pacific, Red Sea, Kenya to Japan, Marshall Islands, and Fiji waters (Kemp, 1922; Bruce, 1969; 1976; 1979; 1980; Miyake and Fujino, 1968; Fransen, 1989; Ďuriš and Horká, 2017).

The genus *Actinimenes* has a close phylogenetic relationship with species in the genus *Zenopontonia* Bruce, 1975, which are echinoderm associates (Gan *et al.,* 2016; Horká *et al.,* 2016; 2018) and are widely distributed in the Indo-West Pacific region (Bruce, 1975; 1978; 1982; Kou *et al.,* 2016). Furthermore, the morphological characteristics of *Zenopontonia* are also very similar to *Actinimenes* due to the presence of an incised transverse ridge on the fourth thoracic sternite, the deep subspatulate chelae of the first pereopod, and the location of the antennal and hepatic spines (Bruce, 1989). However, this group differs from species in the genus *Actinimenes* by the presence of a more down-curved rostrum, pectination on fingers of the first pereopod, and a small distoventral tooth on the dactylus of the ambulatory pereopods (Marin, 2012).

The present study describes a new species in the genus *Actinimenes,* based on morphology and molecular data. This is the first representative of *Actinimenes* collected from the Lakshadweep islands, Arabian Sea, India. The major objective of the study is to provide a detailed morphological description with illustrations of the new species. We also provide the mitochondrial DNA sequences and infer the phylogenetic relationship of this species based on the cytochrome oxidase I (COI) and 16S rRNA (16S) gene data to confirm the species identification and to detect the phylogenetic position of the species relative to closely related species.

Materials and Methods

Study site and sampling

The sampling location was near the airport of Agatti Island, Lakshadweep, Arabian Sea, India (10°49'13"N 72°10'07"E), around 250 m distance from

the shore (Fig. 1). During low tide, the specimens were collected by a scoop net at a depth ranging between 1.0 to 2.0 m, where the shrimps were associated with anemones. The collected live animals were immediately transported to the Indian Council of Agricultural Research (ICAR) – National Bureau of Fish Genetic Resources (NBFGR) and Department of Biotechnology (DBT), Germplasm Resource Centre, Agatti Island, Lakshadweep, for further study. A closed bucket with a portable aerator was used for transporting the animals from the collection site to the laboratory. Seventeen specimens were collected and examined, and specimens were preserved in 96 % ethanol for further studies.

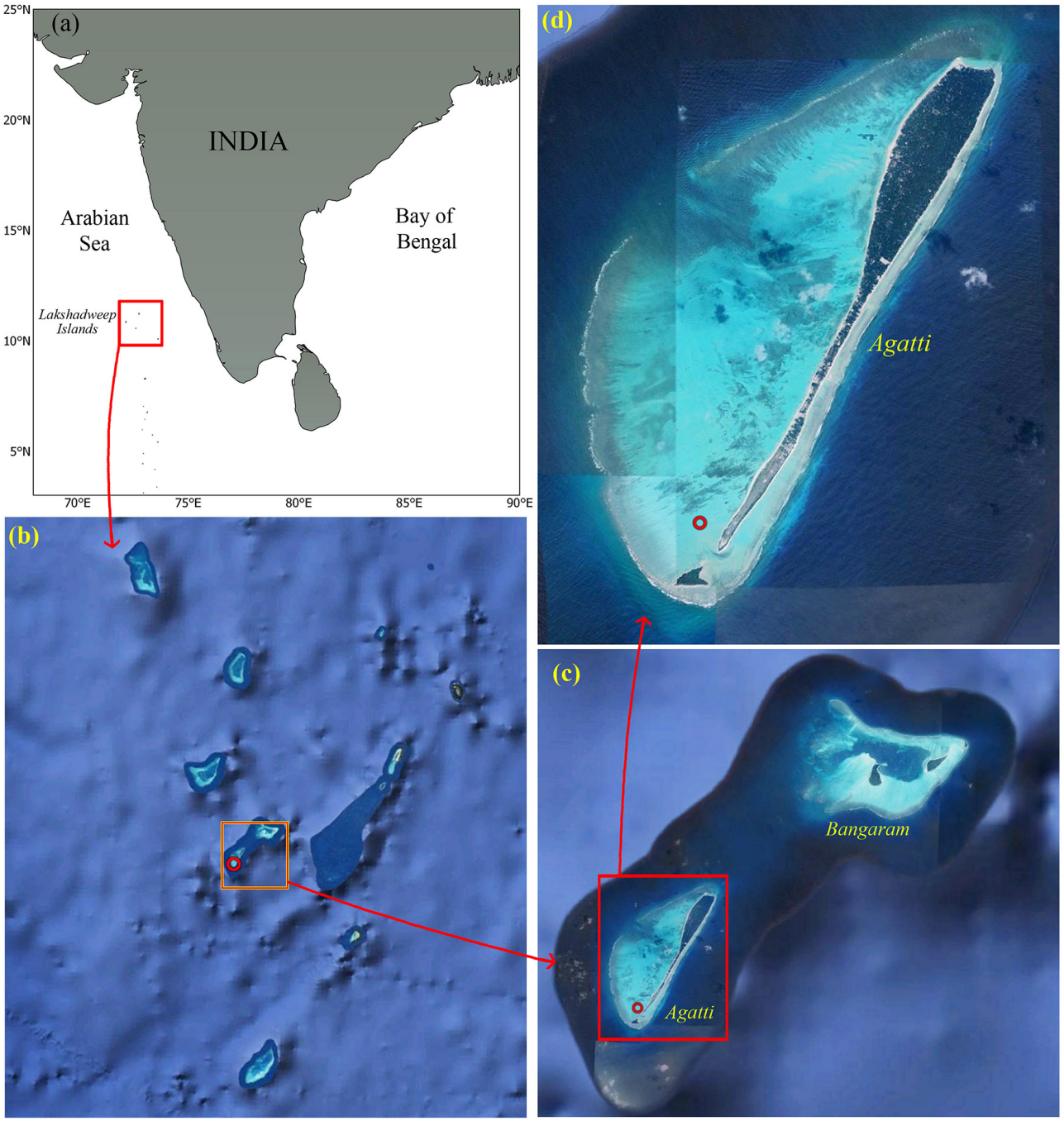

Figure 1. Map showing (**a–d**) location of Agatti Island, Lakshadweep, India, the type locality of *Actinimenes koyas* sp. nov.

Morphology

The specimens in good condition were chosen for detailed taxonomic study and compared with the key characters of palaemonid shrimp in the published literature, such as Bruce (1969; 1979) and Ďuriš and Horká (2017). The specimens were dissected and rinsed with 75 % ethanol using a stereomicroscope (Magnus MSZ-TR). Close observations were carried out with a stereo zoom microscope (0.5–8×, Nikon SMZ1270, Japan) and a compound microscope (10×, Leica D750). Images were captured and processed with a Camera Control Unit DS-L4 and the imaging software NIS-Elements (Nikon, Japan). Furthermore, drawing and image processing of illustrations were done with the GNU Image Manipulation Program (version 2.10.12). Sizes of the specimens, carapace (CL, from the posterior orbital angle to the posterior margin of the carapace in the dorsal midline), and rostrum length (RL, from the apex to the base of the rostrum at the posterior level of the inner orbital margin) were measured using 0.1 mm calipers. The specimens were deposited at the National Fish Museum and Repository of the ICAR-NBFGR, Lucknow, India (NBFGR/PALAKOY–01, 02). Two paratype specimens were deposited in the National Museum of Zoological Survey of India (ZSI: C8867/2).

DNA extraction, amplification, and sequencing

Total genomic DNA extractions from holotype and paratype specimens were performed using a DNeasy Blood and Tissue kit (Qiagen), according to the manufacturer's protocol. Partial sequences of the mitochondrial COI and 16S genes (5' to 3' direction) were amplified by polymerase chain reaction (PCR) using the universal invertebrate primers (Palumbi *et al.*, 1991; Folmer *et al.*, 1994); 25 µL reaction cocktail containing genomic DNA (0.6 µg μL^{-1}), *Taq* DNA polymerase (0.05 U μL^{-1}), 1X buffer, $MgCl_2$ (1.0 mM), 5 pM μL^{-1} of each primer, dNTPs (200 µM), and 11.0 µL of sterilized distilled water. The PCR amplification was performed with an initial denaturation at 95 °C for 5 minutes, followed by 35 cycles of denaturation at 94 °C for 1 minute, annealing at 52 °C for 1 minute, extension at 72 °C for 1.5 minutes, and a final extension at 72 °C for 5 minutes. The quantity and quality of amplified PCR products were verified by 1.5 % agarose gel electrophoresis with ethidium bromide and visualized under a Gel Doc™ XR+ (Bio-Rad, India). Sequencing was performed using the dideoxy chain termination method with Big-Dye Ready-Reaction kit v 3.1 (Applied Biosystems) on an ABI Prism 3770 automated sequencer at SciGenom Centre (Cochin, India) with the same primers used for the PCR reaction.

Phylogenetic analysis

The quality of DNA sequences was reviewed using ABI Seq Editor v 1.0. COI nucleotide sequences were translated into amino acids, using EMBOSS Seqret (https://www.ebi.ac.uk/Tools/sfc/emboss_seqret/) to check for pseudogenes (Tsang *et al.*, 2008). Further, we searched for homologous COI and 16S sequences with the nblast program from the National Center for Biotechnology Information (NCBI, http://blast.ncbi.nlm.nih.gov/Blast.cgi:GenBank). All DNA sequences of the genera *Actinimenes*, *Zenopontonia*, and the sequence of *Ancylocaris brevicarpalis* Schenkel, 1902 were retrieved from GenBank and used as an outgroup (Tab. 1). The sequence alignment of COI sequences was performed in BioEdit 5.0.9 (Hall, 1999) with the Clustal W algorithm (Thompson *et al.*, 1994). Finally, seven sequences of *A. koyas* sp. nov. and two sequences of *A. inornatus* were submitted to GenBank (Tab. 1). The pairwise genetic distances for COI and 16S were estimated in MEGA 10.0.5 (Kumar *et al.*, 2018). For phylogenetic analysis, PAUP* 4.0 was used to find out the optimized model for COI and 16S data with the corrected Akaike Information Criterion (AICc) (Akaike, 1974). The Maximum likelihood (ML) analysis was implemented to estimate the phylogenetic relationship with the General time-reversible model with gamma distribution and invariable sites (GTR+G+I) for COI data and Hasegawa-Kishino-Yano model and Gamma distribution (HKY+G) for 16S data with 1,000 replications.

Table 1. Details of DNA sequences of *Actinimenes koyas* sp. nov., two other *Actinimenes* species and outgroup species obtained from GenBank.

S. Nº	Voucher code	Species	16S	COI
1	NBFGR: DBTLDA59	*Actinimenes koyas* sp. nov.	MT396167	MW239171
2	NBFGR: DBTLDA62	*Actinimenes koyas* sp. nov.	MT396168	MW239172
3	NBFGR: DBTLD63	*Actinimenes koyas* sp. nov.	MT396169	-
4	NBFGR: DBTLD64	*Actinimenes koyas* sp. nov.	MT396170	-
5	NBFGR: DBTLD66	*Actinimenes koyas* sp. nov.	MT396171	-
6	NBFGR: DBTLD112A	*Actinimenes inornatus*	-	MZ087704
7	NBFGR: DBTLD112B	*Actinimenes inornatus*	-	MZ087705
8	MTQ W-33160	*Actinimenes inornatus*	KU064841	KU064997
9	UO<CZE>:V08-80	*Actinimenes ornatus*	KU064843	KU065001
10	-	*Actinimenes ornatus*	JX025181	-
11	UO<CZE>:V08-105	*Zenopontonia rex*	KU064867	KU065024
12	MNHN-Na 15892	*Zenopontonia noverca*	KU356302	-
13	MSLKHC-CA22Pebre	*Ancylocaris brevicarpalis*	MK470834	-
14	UO<CZE>:V08-22	*Ancylocaris brevicarpalis*	-	KU064990

Systematics

Order Decapoda Latreille, 1802

Infraorder Caridea Dana, 1852

Superfamily Palaemonoidea Rafinesque, 1815

Family Palaemonidae Rafinesque, 1815

Genus *Actinimenes* Ďuriš and Horká, 2017

***Actinimenes koyas* sp. nov.**
(Figs. 2–6)
Zoobank: urn:lsid:zoobank.org:pub:45058CD0-568E-4CEA-A4EE-CE7490617076

Material examined. Holotype: ovigerous female (CL 3.0 mm; accession nº: NBFGR/PALAKOY—01), ID nº DBTLDA59, 10°49'13"N 72°10'07"E, depth 1.0–2.0 m, scoop net, associated with *Heteractis magnifica* (Quay and Gaimard, 1833), Agatti Island, Lakshadweep, India, Arabian Sea, on December 2019.

Paratypes: male (CL 3.2 mm; accession nº: NBFGR/PALAKOY—02), ID nº DBTLDA62, same data as holotype. 1 female and 1 male (CL 2.0–2.5 mm; accession nº: ZSI: C8867/2), ID nº DBTLDA111A, DBTLDA111B, 10°49'20"N 72°10'15"E, depth 1.0–2.0 m, scoop net, associated with *H. magnifica*, Agatti Island, Lakshadweep, India, in March 2020. 7 females (CL 1.9–4.2 mm), ID nº DBTLDA60—64, DBTLDA66—67; 6 males (CL 1.9–3.0 mm), ID nº DBTLDA68—73, 10°49'13"N 72°10'07"E, depth 1.0–2.0 m, scoop net, associated with *H. magnifica*, Agatti Island, Lakshadweep, India, in December 2019.

Description. Small-sized palaemonid shrimp, body (Fig. 2A, B) usually glabrous. Rostrum (Fig. 3A, B) well developed, straight or slightly depressed, about 0.65–0.72 times as long as carapace, reaching distal margin of the third antennular peduncle; dorsal margin bearing 5 to 8 acute teeth, slightly decreasing in size, distally with a row of 7–14 long plumose setae on rostrum underneath of each tooth; first dorsal tooth found posterior to posterior orbital margin; ventral margin convex with small ventral tooth at 0.7 of length.

Carapace (Fig. 3A, B) smooth, glabrous, without epigastric or supraorbital spines; inferior orbital angle well developed, acute in lateral view; antennal spine moderate in size, marginal, found in bottom of inferior orbital angle, slightly exceeding distal end of orbital angle; hepatic spine prominent, smaller than antennal, situated slightly lower than level of antennal spine; anterolateral angle of carapace region simply rounded.

Eyes (Fig. 3C) well developed with globular-shaped cornea and distinct accessory pigment spot present posterodorsally; eyestalks almost equal in length to proximal width and slightly swollen proximally.

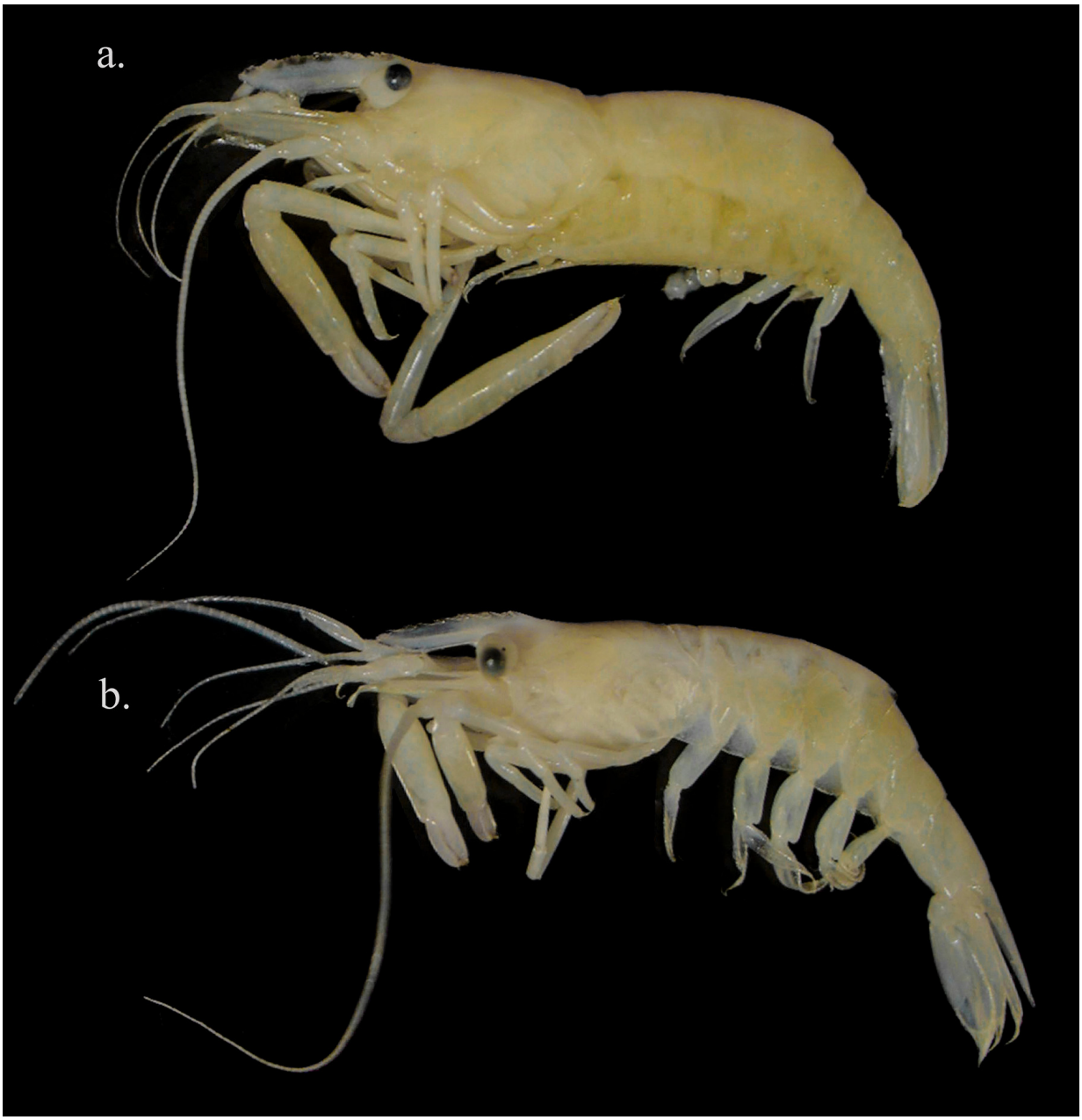

Figure 2. *Actinimenes koyas* sp. nov. from Agatti island, India. (**a**) Holotype: ovigerous female (CL 3.5 mm, NBFGR/PALAKOY—01); (**b**) paratype, male (CL 3.2 mm, NBFGR: DBTLDA62, Ethanol preserved).

Antennular peduncle (Fig. 3A, E) reaching distal margin of scaphocerite. Proximal segment broad, thin, about 1.9 times longer than central width; lateral margin barely convex, anterolateral margin produced angular lobate with small acute distolateral tooth, row of plumose long setae on proximal margin; ventral margin with small submedian tooth found at 0.4 the length of segment. Stylocerite well developed, slender, acute reaches near middle of proximal segment. Intermediate segment short, about 1.1 times longer than width with small lateral lobe, 0.78 times as long as distal segments, and together equals 0.66 times of proximal segment length. Antennular flagellum (Fig. 3E) long, tapered; outer flagellum biramous, proximal three segments of rami fused, shorter free ramus consists of 7 to 8 segments with 12–14 groups of aesthetascs, longer free ramus filiform, with 29–31 segments; inner flagellum slender, filiform, almost equal to outer one with 34–36 segments.

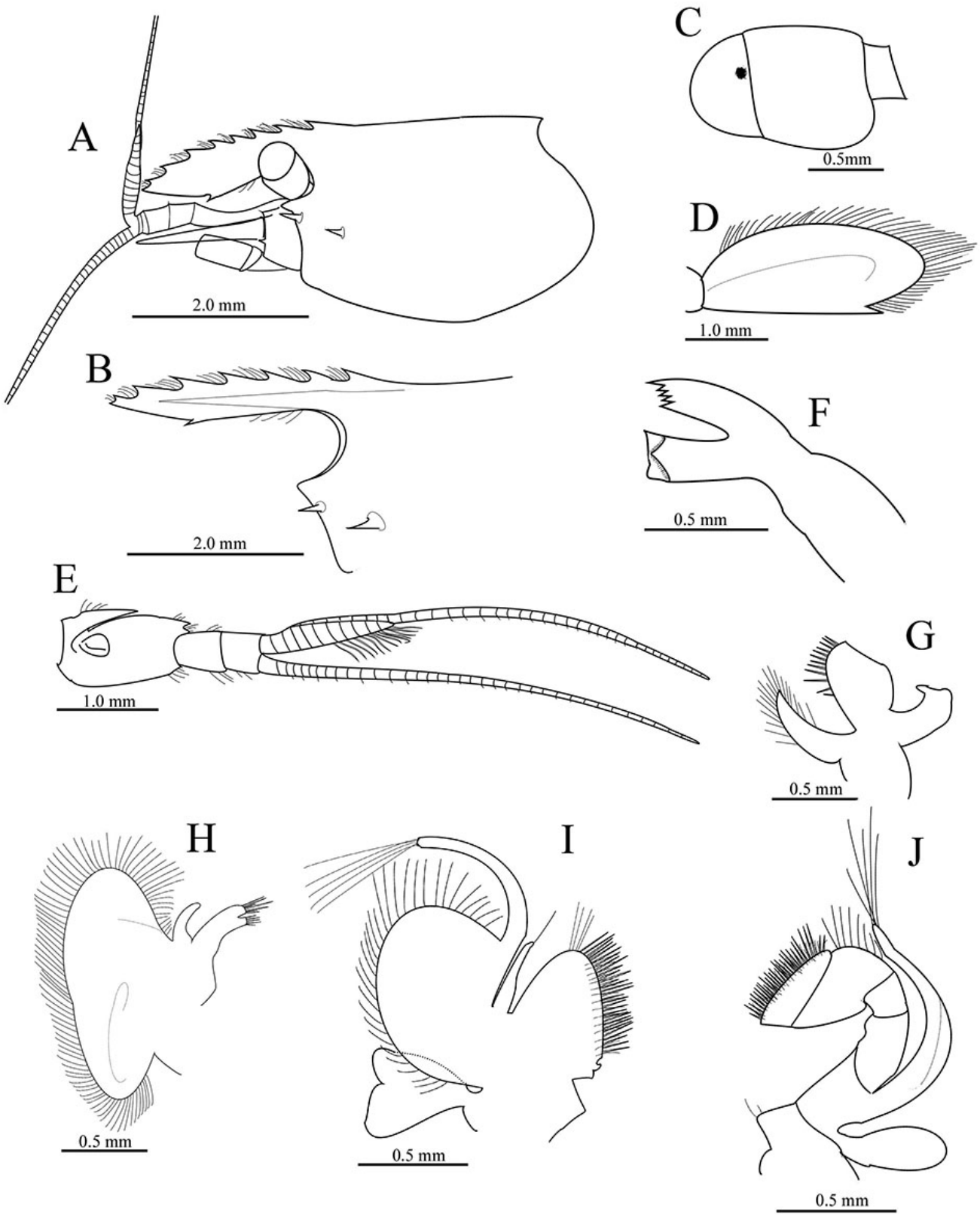

Figure 3. *Actinimenes koyas* sp. nov., from Agatti island, India. **A**, Carapace of ovigerous female (CL 3.5 mm, NBFGR/PALAKOY—01, lateral view); **B**, anterior part of male carapace (DBTLDA62, lateral view; **C**, dorsal view of cornea and eyestalk); **D**, dorsal view of right scaphocerite; **E**, dorsal view of antennular peduncle and flagellum; **F**, left mandible (outer view); **G**, left maxillula (outer view); **H**, left maxilla (outer view); **I**, left first maxilliped (outer view); **J**, left second maxilliped (outer view).

Antenna: basicerite bearing acute distolateral tooth. Ischiocerite and merocerite short. Carpocerite reaching middle of scaphocerite. Scaphocerite (Fig. 3D) long with lamella reaching just beyond distal margin of distal antennular peduncle; lateral margin straight, with well-developed distolateral tooth; lamella rounded, about 2.1–2.3 times longer than breadth, with long distal plumose setae, extending beyond the distolateral tooth.

Mandible (Fig. 3F) without palp; the molar process stout, subcylindrical with 2 blunt teeth distally, numerous rows of small stout setae sub-distally; incisor processes short, slightly tapering distally, obliquely truncate, with 5 teeth distally and lateral-most slightly enlarged. Maxillula (Fig. 3G) normal form, palp feebly bilobed, outer lobe obscure, inner lobe with few small setae; upper lacinia with 10 stout long spines, several spiniform setae and plumose setae; lower lacinia subcylindrical, tapering distally, with numerous long setae.

Maxilla (Fig. 3H) with broad scaphognathite, without setae on inner and outer surfaces, anterior lobe wider than posterior with numerous long setae terminally; basal endite bilobed with spine-like long setae distally.

First maxilliped (Fig. 3I) endopodite short, slender, reaching distal margin of basal segment, with single long seta distally. Basal endite broad, rounded with long setae marginally, median margin with slender simple marginal setae. Coxal endite broadly rounded, elevated from basal endite by notch. Flagellum of exopodite well developed with 3 to 4 long plumose distal setae. Caridean lobe well developed; epipod bilobed without setae.

Second maxilliped (Fig. 3J) dactylus segment narrow, densely fringed with numerous serrulate setae. Propodal segment longer than dactylus, distomedial margin produced, with 10 long spiniform setae. Carpus and merus short without setae. Ischium fused with basal segment. Coxal segment triangular-shaped medially with single setae. Exopod slender, with few long plumose setae distally.

Third maxilliped (Fig. 4A) slender, reaching middle of antennal scaphocerite. Ultimate segment tapering, about 4.0 times longer than proximal width, 0.63 times as long as penultimate segment, with rows of short serrulate setae laterally, numerous longer setae distally. Penultimate segment slender, about 6.5 times longer than maximum width, 0.82 times as long as antepenultimate, with rows of long simple setae laterally. The antepenultimate segment slightly convex, about 4.5 times as long as proximal width. Coxa with small rounded epipod. Exopod slender, reaching distal end of antepenultimate segment, with few plumose setae distally.

First pereopod (Fig. 4B) slender, extended beyond the distal end of scaphocerite by chela; fingers slender, sub-equal, concave, dactylus about 1.3–1.4 times longer than palm length, with small hooked terminal tooth, with numerous long setae; fixed finger with 6 to 7 groups serrulate setae on dorsal side. Palm short, sub-cylindrical, proximal region with row of setae. Carpus sub-cylindrical, about 4.6 times long as distal width, 2.9–3.0 times longer than palm, with distoventral cleaning setae. Merus cylindrical, about 0.9–0.95 times as long as carpus, 5.2 times longer than maximum width. Ischium equal to basis, about 0.35 times of merus length. Coxa with small setae on the medial process.

Second pereopod: major and minor chelipeds (Fig. 4C, D) well developed, similar, barely unequal in length, overreaching beyond the distal margin of antennular peduncle by length of chela. Major cheliped (Fig. 4C, C1, C2): fingers slender, less than half of palm length (0.45–0.47 times); dactylus slender, about 3.8 times as long as proximal depth, slowly tapering distally with stout terminal tooth, proximal half with 2 acute teeth, distal half of cutting edge concave, with numerous long setae; fixed finger with 4 to 5 teeth proximally, distal half concave with terminal tooth, with numerous long setae. Palm sub-cylindrical, about 2.9–3.0 times longer than maximum width. Carpus short, stout, about 1.1–1.3 times as long as distal width, tapering proximally, unarmed. Merus cylindrical, uniform, unarmed, about 2.1 times as long as carpus, 4.5 times as long as wide. Ischium with 0.7–0.78 times as long as merus, 0.45 times of palm length.

Minor cheliped (Fig. 4D): fingers slender, less than half of palm length (0.50–0.51 times); dactylus slender, about 4.5 times as long as proximal depth, slowly tapering distally with stout terminal tooth, sub-proximal half with 2 acute teeth. Carpus, merus, and ischium similar with major cheliped.

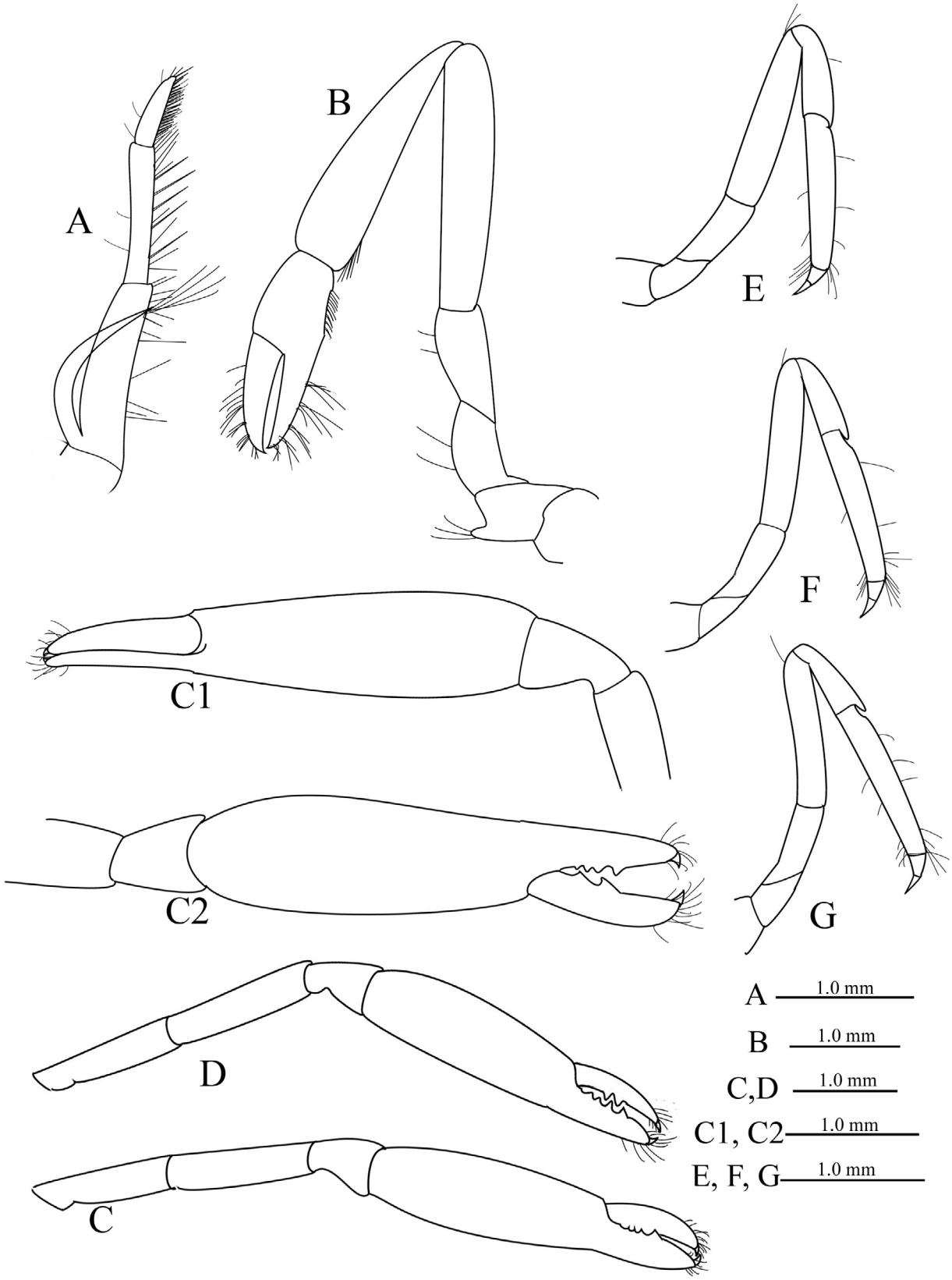

Figure 4. *Actinimenes koyas* sp. nov. paratype, male, (CL 3.2 mm), NBFGR: DBTLDA62. **A**, Left third maxilliped (outer view); **B**, left first pereopod (lateral view); **C**, major second pereopod (left, lateral view); **C1**, lateral view of major chela of the second pereopod; **C2**, dorsal view of major chela of same; **D**, minor second pereopod, right (lateral view); **E**, left third pereopod (lateral view); **F**, right fourth pereopod (lateral view); **G**, right fifth pereopod (lateral view).

Ambulatory pereopods (Fig. 4E–G): slender, similar in structure, and moderately long. Third pereopod (Fig. 4E) extending beyond distal margin of scaphocerite by length of dactylus; dactylus acute, slender, about 0.28 times propodus length, 2.1 times as long as proximal width, with curved unguis, terminal end sharp with numerous long setae (Fig. 5B). Propodus about 5.5 times as long as width, with numerous short and long setae distally. Carpus, merus, and ischium are about 0.60, 1.17, and 0.55 times propodus length, respectively. Fourth pereopod (Fig. 4F) and fifth pereopod (Fig. 4G) slightly longer than third; dactylus about 0.25 times as long as propodus, 2.1 times longer than proximal width; propodus about 6.4 times as long as wide; carpus, merus, and ischium about 0.52, 1.06, and 0.55 times propodus length, respectively.

Fourth thoracic sternite (Fig. 5A) with angular broad lateral ridges and "V"-shaped median notch.

First pleopods: exopod broad, outer margin fringed with long setae; endopod short, about 0.38 times as long as exopod, lateral border with row of 9 plumose setae. Male second pleopod with appendix masculina short and stout, reaching middle of exopod, distal outer margin fringed with few long setae; exopod broad, outer margin with long setae.

Abdominal segments (Fig. 2A, B) smooth, glabrous, about 2.8 times as long as carapace; third abdominal tergite not produced in entire posterior margin. Fourth and fifth abdominal segments posterior-dorsally rounded; sixth abdominal segment elongate, about 1.6 times as long as fifth, produced barely pointed posteroventral angle, posterolateral angle acute. Pleura of first to fifth abdominal segments broadly rounded; fourth and fifth slightly produced posteriorly and rounded.

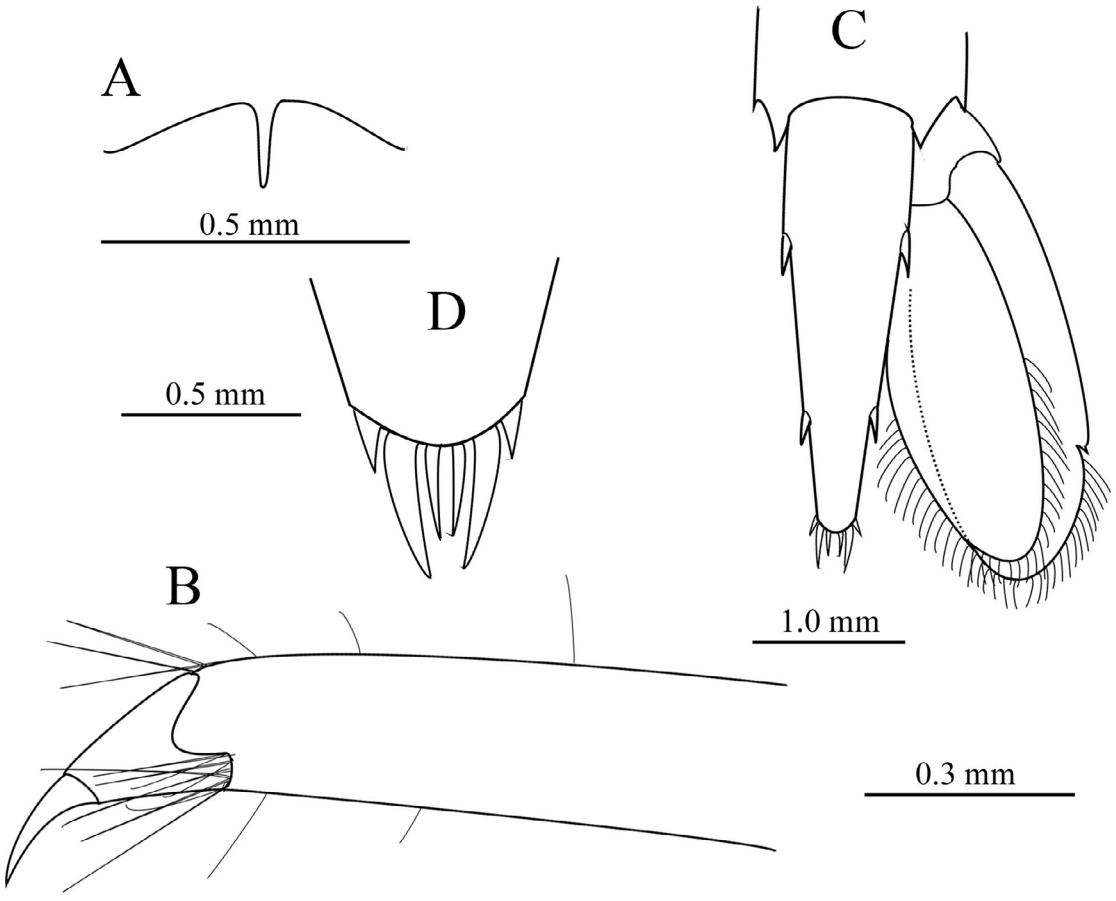

Figure 5. *Actinimenes koyas* sp. nov. holotype, ovigerous female, CL 3.5 mm, NBFGR/PALAKOY–01. **A**, Fourth sternal plate with median incision (inner view); **B**, left dactylus of the third pereopod (closer view); **C**, dorsal view of telson with uropod; **D**, posterior end of telson (closer view).

Telson (Fig. 5C, D) slender, about 1.5 times as long as sixth abdominal segment, 3.5 times longer than anterior width, with 2 pairs of movable, well-developed dorsal spines appearing at 0.25 and 0.6 of telson length. Posterior margin triangular-shaped, 0.30 times anterior width, with 3 pairs of spines; lateral spine short and subequal to dorsal spines; intermediate spines well developed, slender, about 0.16 times telson length, 1.6 times length of submedian spines. Uropods exceeding length of telson; exopod slightly longer than endopod, about 2.25 times as long as width, with small fixed distolateral tooth; endopod with leaf-like structure, outer and inner margin bearing long setae.

Coloration in life. Body and appendages are transparent or pale brownish (Fig. 6). Hepatic pancreas and cardiac regions visible as pale orange through integument. Abdominal segments and telson are almost fully translucent without any spots. Eyes are greenish with a dark mark posterior-dorsally.

Distribution and habitat. Presently known from the coral atolls of Agatti Island (near Kalpetti Island), Lakshadweep, India. The specimen *A. koyas* sp. nov. was found in two locations at the sampling site. This species was seen in association with the magnificent sea anemone *H. magnifica*, assemblages (Fig. 6) belonging to the order Actiniaria, which is widely distributed in the Lakshadweep islands. It was noticed that the shrimp mostly appeared in between the tentacles of the sea anemone, where they can easily hide from predators. The aggregations of shrimps on the sea anemone were typically observed in the daytime only. We recorded a salinity of 34 ppt and a temperature of 26 °C at the sampling locations. It was observed that several peacock-tail anemone shrimp *A. brevicarpalis* and marbled shrimp *Saron marmoratus* (Olivier, 1811) were also found in the same collection site. However, *A. koyas* sp. nov. was the dominant (~93 %) species group on the sea anemone assemblage. The faunal assemblage and habitat of *A. koyas* sp. nov.

Figure 6. Collection site, assemblages of *Heteractis magnifica* at Agatti Island, Lakshadweep, India with live coloration of *Actinimenes koyas* sp. nov. (Depth 1–2 m).

were documented as a video (https://youtu.be/jb9DmGSRn_o). Further, ornamental fishes were also noticed in the collection site such as the swallowtail cardinalfish, *Verulux cypselurus* (Weber, 1909); blue-spotted cardinalfish, *Apogon apogonides* (Bleeker, 1856); Kashmir snapper, *Lutjanus kasmira* (Forsskål, 1775); three spot damsel, *Dascyllus trimaculatus* (Rüppell, 1829); cleaner wrasse, *Labroides dimidiatus* (Valenciennes 1839); blue-green damsel, *Chromis viridis* (Cuvier, 1830); scarlet soldierfish, *Myripristis pralinia* Cuvier, 1829; twinspot damselfish, *Chrysiptera biocellata* (Quoy and Gaimard, 1825); moon wrasse, *Thalassoma lunare* (Linnaeus, 1758); black streak surgeon, *Acanthurus nigricauda* Duncker and Mohr, 1929; and Maldive anemonefish, *Amphiprion nigripes* Regan, 1908.

Etymology. Koyas are an important ethnic community of Lakshadweep. Koyas have made a significant contribution to the development and preservation of the heritage of the society at Lakshadweep. The present species is named "Koyas" to honor the local community at Lakshadweep.

DNA barcodes. COI and 16S sequences from the holotype and paratype, and *A. inornatus* were obtained and submitted to GenBank (Tab. 1).

Remarks. Generally, shrimps in the genus *Actinimenes* are associated with sea anemones and commonly distributed in Indo-West Pacific regions (Kemp, 1922; Bruce, 1969; 1976; 1979; 1980; Miyake and Fujino, 1968; Suzuki and Hayashi, 1977; Fransen, 1989; Ďuriš and Horká, 2017). *Actinimenes koyas* sp. nov. is the fourth species in the genus and has the following morphological characters similar to the three existing species in the genus (Tab. 2): (i) rostrum reaching or exceeding the antennular peduncles; (ii) rostral formula: 5–10 in dorsal and 0–2 teeth in ventral; (iii) antennal spine acute or only minutely produced; (iv) shorter free ramus of the outer antennular flagellum with 7–8 segments and 8–14 groups of aesthetascs; (v) the fourth thoracic sternal plate produced anteriorly with a "U" or "V"-shaped median, narrow and deep notch; (vi) first pereopod: length ratio of finger and palm is 1.0–1.4 times, length ratio of carpus and palm is 1.2 to 3.0 times; (vii) second pereopod merus is 0.66–0.75 times as long as palm; (viii) the dactylus of ambulatory pereopods have minute spinulate or simple structure around the base of unguis (Bruce, 2010; Ďuriš and Horká, 2017).

Actinimenes koyas sp. nov. showed some remarkable morphological differences between the sexes: the rostrum of the male is mostly horizontal and reaches the distal end of the antennular peduncle (Fig. 3B), whereas in the female the rostrum is slightly depressed and barely reaches the distal end of the antennular peduncle (Fig. 3A). The range of the rostral dorsal teeth is five to seven for males and eight for females. The inferior orbital angle of the male is slightly wider than in females; five to six cleaning setae are present on the distoventral region of carpus of the first pereopod for males and six to eight are present in females.

Among the three allied species, *A. ornatellus* is morphologically most similar to *A. koyas* sp. nov. by the shape of the rostrum; general appearance of the hepatic spine on the carapace; and the length ratio and width of the scaphocerite (Tab. 2). In both species, the stylocerite is slender and reaches near the middle of the first antennular segment; the first pereopods have subspatulate fingers; there is dentition on the chela of the second pereopod; and the telson has two pairs of dorsal and three pairs of posterior spines. However, *A. koyas* sp. nov. differs from *A. ornatellus* (summarized in Tab. 2) by having biramous outer antennular flagellum with proximal three segments of rami fused (*vs.* four in *A. ornatellus*); a shorter free ramus consisting of seven to eight segments with 12–14 groups of aesthetascs (*vs.* shorter free ramus with only four segments and eight to nine groups of aesthetascs in *A. ornatellus*); the length of the telson is 3.5 times longer than anterior width (2.4 times for *A. ornatellus*); fourth thoracic sternite with V-shaped median incision (*vs.* U-shaped for *A. ornatellus*); third maxilliped penultimate segment 0.82 times as long as antepenultimate (0.75 times as long in *A. ornatellus*); and dactylus of ambulatory pereopods are without spinulation on the base of unguis (spinulated minutely in *A. ornatellus*) (Bruce, 1979; 2010; Ďuriš and Horká, 2017). Consequently, *A. ornatellus* was reported only from the Marshall Islands and Heron Island (Bruce, 1977; 2010).

Table 2. Comparison of morphological features of *Actinimenes koyas* sp. nov. and other *Actinimenes* spp.: Anp–Antennular peduncle and TeL–Telson length.

S. No.	Characters	*Actinimenes inornatus* (Kemp, 1922)	*Actinimenes ornatellus* (Bruce, 1979)	*Actinimenes ornatus* (Bruce, 1969)	*Actinimenes koyas* sp. nov.
1	Rostrum	Little beyond Anp	Exceed Anp	Equal to Anp	Equal to Anp
2	Rostral formula (dorsal/ventral)	6—8 / 0—2	7—10 / 1—2	7 / 1	5—8 / 1
3	Inferior orbital angle	Round lobe, slightly pointed	Acute, without lower border	Minutely produced	Produced, angular
4	Antennal spine	Slender, marginal	Acute and sub-marginal	Slender, marginal	Moderate size, marginal
5	Hepatic spine	Situated behind the level of antennal spine	Robust, slightly lower level of antennal spine	Robust, distinctly lower level of antennal spine	Prominent, slightly lower level of antennal spine
6	Scaphocerite (Length: width)	2.25 times	2.3 times	2.3 times	2.1—2.3 times
7	Antennular flagellum (outer)	Biramous, proximal 3 segments fused, shorter free ramus with 3 segments and 8 groups of aesthetascs	Biramous, proximal 4 segments fused, shorter free ramus with 4 segments and 8—9 groups of aesthetascs	Biramous, proximal 4 segments fused, shorter free ramus with 4 segments 7 groups of aesthetascs	Biramous, proximal 3 segments fused, shorter free ramus with 7—8 segments and 12—14 groups of aesthetascs
8	TeL: 6th somite a. TeL: Anterior width	1.33 times 2.8 times	1.4 times 2.4 times	1.5 times 2.9 times	1.5 times 3.5 times
9	4th sternal plate	Broad, low transverse ridge with an open median notch	Strongly elevated with a faint median notch	Centrally elongated transverse ridge with a deep close median notch	Angular, broad lateral ridges with 'V' shaped median notch
10	1st pereopod a. Fingers: palm b. Carpus: palm c. Merus: carpus	1.1 times 2.8 times Equal	1.2 times 2.5 times Sub-equal	Sub-equal 2.7 times Sub-equal	1.3—1.4 times 2.9—3.0 times 0.9—0.95 times
11	2nd pereopod a. Fingers: palm b. Carpus: palm c. Merus: palm	≤ 0.5 times 0.35 times 0.71 times	≥0.5 times 0.22 times 0.75 times	>0.5 times 0.25 times 0.72 times	0.45—0.47 times 0.33 times 0.7 times
12	3rd – 5th pereopods a. Dactylus length: width b. Dactylus: propodus	2.6 times 0.20 times	3.0 times 0.25 times	3.2 times 0.24 times	2.1—2.5 times 0.25—0.28 times
13	Type locality	Port Blair, Andaman	Eniwetok Atoll, Marshall Islands	Lung Ha Wan, Hong Kong	Agatti Island, Lakshadweep
14	Associated with	*Discosoma*	*Heteractis malu* (formerly *Radianthus malu*)	Actiniarian	*Heteractis magnifica*
15	Depth	Shallow	1.0—2.0 m	3.6 m	1.0—2.0 m

Further, *A. ornatus* and *A. inornatus* are similar to *A. koyas* sp. nov. with characters like a marginal antennal slender spine; hepatic spine appears nearly behind the level of antennal spine; and the dactylus of ambulatory pereopods is slender and smooth. However, *A. ornatus* differs from the new species in the presence of a fourth thoracic sternite with a centrally elongated transverse ridge with a deep median notch (*vs.* angular broad lateral ridges in *A. koyas* sp. nov.). *Actinimenes ornatus* is known from the Pacific Ocean: Hong Kong (Bruce, 1969; 1979), Japan (Suzuki and Hayashi, 1977), Eniwetok Atoll, the Marshall Islands (Bruce, 1979), Indonesia, Korea, the Red Sea (Bruce and Svoboda, 1983), Kenya, and Vietnam (Marin, 2006; Lee and Ko, 2011).

Similarly, *A. inornatus* varied from *A. koyas* sp. nov. by having a broad low transverse ridge, with an open median notch in the fourth thoracic sternite (angular broad lateral ridges with deep median incision in *A. koyas* sp. nov.) (Fransen, 1989; Bruce, 2010; Ďuriš and Horká, 2017). *Actinimenes inornatus* is widely distributed in Kenya (Bruce, 1976), Grand Comoro Island near Madagascar (Bruce, 1971), Seychelles Islands (Bruce, 1971; 1976), Andaman Islands (Kemp, 1922), Maldives and Laccadive Islands, Bay of Bengal, Mariana Island (Bruce, 1976; 1984), Heron Island (Bruce, 2010), Ryukyu Islands, Indonesia, South China Sea, Great Barrier Reef, Fiji, and Caroline Islands (Chace and Bruce, 1993).

Color patterns are one of the important taxonomic characters for palaemonid shrimps and are mostly species-specific for the *Actinimenes* group (Fransen, 1989; Ďuriš, 2017; Ďuriš and Horká, 2017). The coloration of *A. koyas* sp. nov. is similar to that of *A. inornatus* and *A. ornatellus,* where the carapace, rostrum, and abdominal region have a transparent and faint brownish color. However, *A. inornatus* and *A. ornatellus* are distinguished from *A. koyas* sp. nov. by the presence of a broad dorsal white band on the eyestalks, cardiac region, and presence of a broad medial ventral white band extended longitudinally from the posterior end of the stomach to the anterior end of the fifth abdominal segment (absent on *A. koyas* sp. nov.) (Bruce, 1979; Fransen, 1989; Salvat and Bacchet, 2011; Ďuriš and Horká, 2017). *Actinimenes ornatus* differs from *A. inornatus*, *A. ornatellus*, and *A. koyas* sp. nov. by having finely striated, longitudinally and alternating rows of minute red and white chromatophores extended over the pleura, the antennal peduncles and scaphocerite with purple and white spots (especially along the dorsum of the eyestalk and across the ophthalmic somite) transparent pereopods and uropods with numerous paired purple and whitish chromatophores (Bruce, 1979; Fransen, 1989; Lee and Ko, 2011).

Host range. *Actinimenes koyas* sp. nov. was found with the magnificent sea anemone, *H. magnifica* along with another anemone-associated shrimp *A. brevicarpalis* in the Agatti Island of Lakshadweep at a depth of 1–2 m. Similarly, *A. inornatus* was observed on *Discosoma* sp. with *A. brevicarpalis* and occurred with *H. magnifica*, *Pocillopora damicornis* (Linnaeus, 1758), *Pocillopora verrucosa* (Ellis and Solander, 1786), *Seriatopora hystrix* Dana, 1846, *Stylophora pistillata* (Esper, 1792), and *Acropora* spp. (see Patton, 1966; Fransen, 1989). *Actinemenes ornatus* specimens were noticed from the actinian sea anemones: *Heteractis crispa* (Hemprich and Ehrenberg in Ehrenberg, 1834), *H. magnifica*, *H. malu, Entacmaea actinostoloides* (Leuckart in Rüppell and Leuckart, 1828), *Entacmaea* spp., *Gyrostoma* sp., *Parasicyonis actinostoloides* (Wassilieff, 1908), *Parasicyonis maxima* (Wassilieff, 1908), and *Cryptodendrum adhaesivum* (Klunzinger, 1877) (see Bruce, 1979; Suzuki and Hayashi, 1977; Marin *et al.*, 2004). *Actinimenes ornatellus* was only found on *H. malu*. According to earlier reports, the species of the genus *Actinimenes* are generalist symbionts, inhabiting a significant number of hosts.

In the molecular analysis, the ML tree was reconstructed using the mitochondrial COI gene (Fig. 7A), which revealed that *A. koyas* sp. nov. forms a monophyletic clade and has a close relationship to *A. inornatus* and *A. ornatus,* with significant nodal support (bootstrap values 72 % and 99 % respectively). The sequences of *Zenopontonia rex* (Kemp, 1922) and *A. brevicarpalis* were used as the outgroup species (Gan *et al.*, 2016; Horká *et al.*, 2016; 2018). Similarly, the tree topology of 16S gene sequences showed similar clade patterns for *A. koyas* sp. nov. and other *Actinimenes* species (Fig. 7B). Unfortunately, COI and 16S sequences are not available for *A. ornatellus* in GenBank. The genetic divergence between *A. koyas* sp. nov. and the other species of *Actinimenes* ranged from 15.7 to 18.7 % for COI (Tab. 3) and 1.2 to 6.5 % for 16S (Tab. 4). These high genetic differences are generally considered species-specific for decapod crustaceans (Malay and Paulay, 2010, Komai and Tsuchida, 2015; Chakraborty *et al.*, 2015; Purushothaman *et al.*, 2019). The present molecular analyses are strongly supported by the morphological identification of *A. koyas* sp. nov. from Lakshadweep, India. Furthermore, *A. koyas* sp. nov. differs considerably both in morphological traits and coloration from its sister species. These sea anemone-associated shrimps exhibit remarkable color patterns; *A. inornatus* and *A. ornatellus* have eyestalks with a broad dorsal white band and *A. ornatus* has minute red and white chromatophores on the body (Bruce, 1979; Fransen, 1989; Lee and Ko, 2011; Salvat and Bacchet, 2011; Ďuriš and Horká, 2017). The color patterns of the new species are rather dull and without band patterns. Furthermore, *A. koyas* sp. nov. showed significant differences with *A. inornatus*, *A. ornatellus*, and *A. ornatus* in morphological characters related to the antennular flagellum, sternal plate, and length of pereopods (Tab. 2).

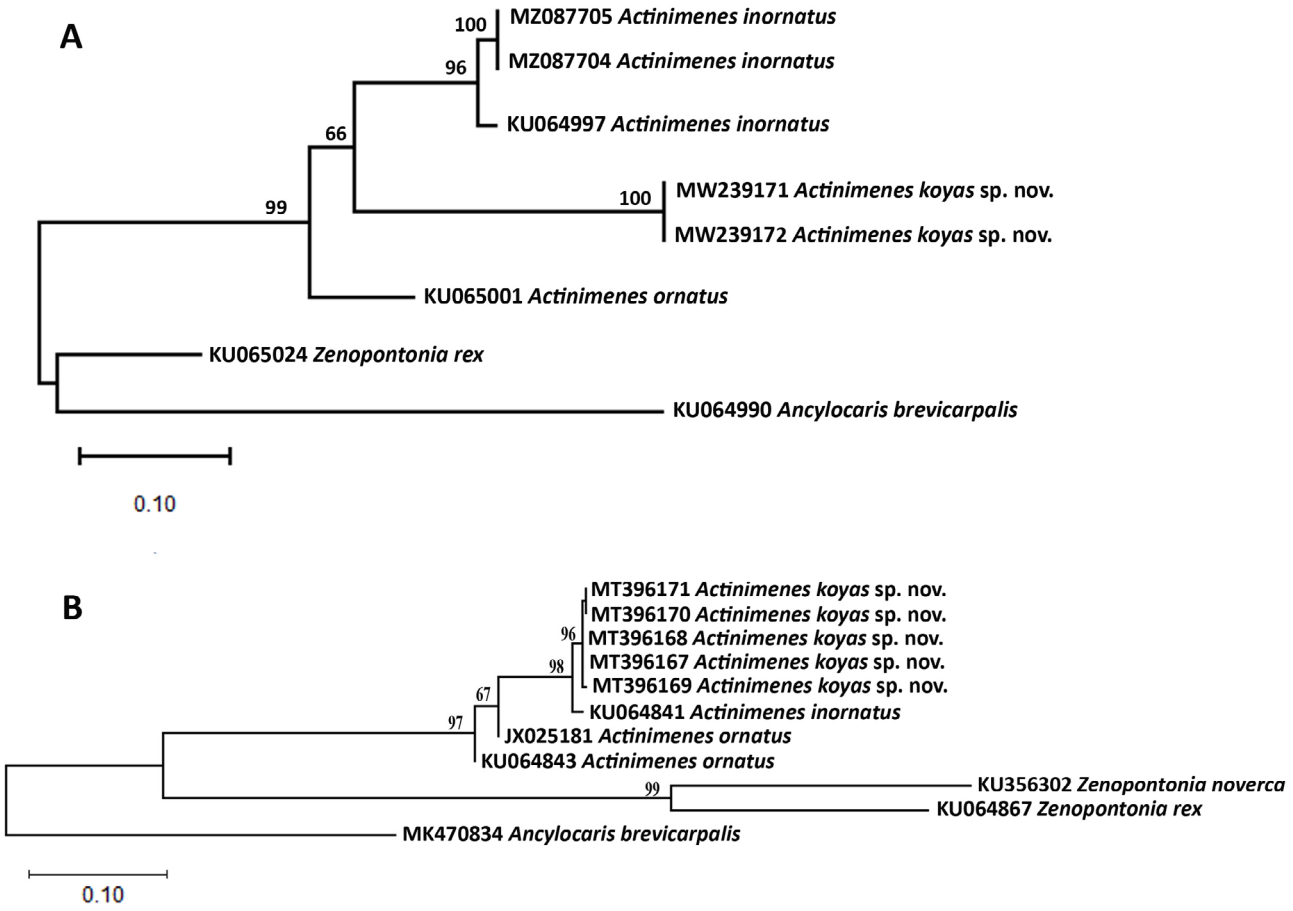

Figure 7. Maximum Likelihood phylogenetic tree based on partial COI (**A**) and 16S (**B**) sequences of *Actinimenes koyas* sp. nov. and two other *Actinimenes* species obtained from GenBank (Scale bar = 10 % divergence; significant bootstrap value > 60).

Table 3. Pairwise genetic distances calculated using Kimura 2-parameter model with COI sequences of genus *Actinimenes, Ancylocaris* and *Zenopontonia.*

Sl. Nº	Species	1	2	3	4	5	6	7	8
1	*Actinimenes koyas* sp. nov. MW239171								
2	*Actinimenes koyas* sp. nov. MW239172	0.000							
3	*Actinimenes inornatus* MZ087704	0.181	0.181						
4	*Actinimenes inornatus* MZ087705	0.181	0.181	0.00					
5	*Actinimenes inornatus* KU064997	0.183	0.183	0.025	0.025				
6	*Actinimenes ornatus* KU065001	0.187	0.187	0.159	0.159	0.157			
7	*Zenopontonia rex* KU065024	0.261	0.261	0.209	0.209	0.219	0.206		
8	*Ancylocaris brevicarpalis* KU064990	0.388	0.388	0.293	0.293	0.301	0.306	0.287	

Table 4. Pairwise genetic distances calculated using Kimura 2-parameter model with 16S sequences of genus *Actinimenes, Ancylocaris* and *Zenopontonia.*

Sl. Nº	Species	1	2	3	4	5	6	7	8	9	10
1	*Actinimenes koyas* sp. nov. MT396167										
2	*Actinimenes koyas* sp. nov. MT396168	0.00									
3	*Actinimenes koyas* sp. nov. MT396169	0.002	0.002								
4	*Actinimenes koyas* sp. nov. MT396170	0.00	0.000	0.002							
5	*Actinimenes koyas* sp. nov. MT396171	0.000	0.000	0.002	0.000						
6	*Actinimenes inornatus* KU064841	0.012	0.012	0.014	0.012	0.012					
7	*Actinimenes ornatus* JX025181	0.051	0.051	0.054	0.051	0.051	0.054				
8	*Actinimenes ornatus* KU064843	0.062	0.062	0.065	0.062	0.062	0.065	0.014			
9	*Zenopontonia noverca* KU356302	0.316	0.317	0.321	0.317	0.317	0.326	0.318	0.308		
10	*Zenopontonia rex* KU064867	0.332	0.333	0.337	0.333	0.333	0.328	0.315	0.310	0.195	
11	*Ancylocaris brevicarpalis* MK470834	0.262	0.262	0.262	0.262	0.262	0.262	0.263	0.272	0.334	0.381

Conclusion

A new symbiotic species from the palaemonid shrimp genus *Actinimenes* is described and illustrated from Lakshadweep, India. *Actinimenes koyas* sp. nov. was obtained from the magnificent sea anemone *Heteractis magnifica* (Actiniaria). Sea anemone-associated species of the genus *Actinimenes* are widely distributed in the tropical regions of the Indo-West Pacific, and *A. koyas* sp. nov. is reported for the first time from the Arabian Sea. Additionally, molecular information from mitochondrial markers (COI and 16S) are provided and the ML tree suggests that *A. koyas* sp. nov. is sister to a clade of *A. inornatus*.

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Additional information and declarations

Disclosure statement

All authors declare that there are no competing interests.

References

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19: 716–723.

Antokhina, T.I. and Britayev, T.A. 2020. Host recognition behaviour and its specificity in pontoniine shrimp *Zenopontonia soror* (Nobili, 1904) (Decapoda: Caridea: Palaemonidae) associated with shallow-water sea stars. *Journal of Experimental Marine Biology and Ecology*, 524: 151302.

Baeza, J.A. 2008. Social monogamy in the shrimp *Pontonia margarita*, a symbiont of *Pinctada mazatlanica*, off the Pacific coast of Panama. *Marine Biology*, 153: 387–395.

Bauer, R.T. 2004. Remarkable Shrimps: Adaptations and Natural History of the Carideans. Norman, University of Oklahoma Press, 243p.

Bruce, A.J. 1969. Preliminary descriptions of sixteen new species of the genus *Periclimenes* Costa, 1844 (Crustacea, Decapoda Natantia, Pontoniinae). *Zoologische Mededelingen*, 43: 253–278.

Bruce, A.J. 1971. Pontoniinid shrimps from the ninth cruise of RV Anton Bruun, IIOE, 1964: I. *Palaemonella* Dana and *Perclimenes* Costa. *Smithsonian Contributions to Zoology*, 82: 1–13.

Bruce, A.J. 1975. *Periclimenes colemani* sp. nov., a new shrimp associate of a rare sea urchin from Heron Island, Queensland (Decapoda Natantia, Pontoniinae). *Records of the Australian Museum*, 29: 486–502.

Bruce, A.J. 1976. A report on some pontoniinid shrimps collected from the Seychelle Islands by the FRV Manihine, 1972, with a review of the Seychelles pontoniinid shrimp fauna. *Zoological Journal of the Linnean Society*, 59: 89–153.

Bruce, A.J. 1977. Pontoniine shrimps in the collections of the Australian Museum. *Records of the Australian Museum,* 31: 39–81.

Bruce, A.J. 1978. A report on a collection of pontoniine shrimps from Madagascar and adjacent seas. *Zoological Journal of the Linnaean Society,* 62: 205–290.

Bruce, A.J. 1979. A report on a small collection of pontoniine shrimps from Eniwetok Atoll. *Crustaceana,* Supplement 5: 209–230.

Bruce, A.J. 1980. On some pontoniine shrimps from Nouméa, New Caledonia. *Cahiers de l'Indo-Pacifique,* 2: 1–39.

Bruce, A.J. 1982. The pontoniine shrimp fauna of Hong Kong. p. 234–284. In: B.S. Morton and C.K. Tseng (eds), Proceedings of the First International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, 1980. Hong Kong, Hong Kong University Press.

Bruce, A.J. 1984. Marine caridean shrimps of the Seychelles. p. 141–169. In: D.R. Stoddart (ed), Biogeography and Ecology of the Seychelles Islands. The Hague, Boston, Lancaster, Junk Publishers.

Bruce, A.J. 1989. *Periclimenes gonioporae* sp. nov. (Crustacea: Decapoda: Palaemonidae), a new coelenterate-associated shrimp. Beagle: *Records of the Museums and Art Galleries of the Northern Territory*, 6: 149.

Bruce, A.J. 1995. A synopsis of the Indo-west Pacific genera of the Pontoniinae (Crustacea: Decapoda: Palaemonidae). *Theses Zoologicae,* 25: 1–172.

Bruce, A.J. 2010. More pontoniine shrimps (Crustacea: Decapoda: Palaemonidae) from the Coral reefs 2009 Heron Island expedition. *Zootaxa*, 2604: 20–36.

Bruce, A.J. and Okuno, J. 2006. *Periclimenes dardanicola* n. sp., a new species of hermit crab associated shrimp (Crustacea, Decapoda, Palaemonidae) from the western Pacific. *Zoosystema,* 28: 367–377.

Bruce, A.J. and Svoboda, A. 1983. Observations upon some pontoniine shrimps from Aqaba, Jordan. *Zoölogische Verhandelingen*, 205: l–44.

Chace, F.A.Jr. and Bruce, A.J. 1993. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine expedition 1907–1910, Part 6: Superfamily Palaemonoidea. *Smithsonian Contributions to Zoology,* 543: 1–152.

Chakraborty, R.D.; Chan, T.Y.; Maheswarudu, G.; Kuberan, G.; Purushothaman, P.; Chang, S.C. and Jomon, S. 2015. On *Plesionika quasigrandis* Chace, 1985 (Decapoda, Caridea, Pandalidae) from southwestern India. *Crustaceana,* 88: 923–930.

Chow, L.H.; De Grave, S. and Tsang, L.M. 2021. Evolution of protective symbiosis in palaemonid shrimps (Decapoda: Caridea) with emphases on host spectrum and morphological adaptations. *Molecular Phylogenetics and Evolution*, 162: 107201.

Duffy, J.E. 2003. The ecology and evolution of eusociality in sponge-dwelling shrimp. p. 217–252. In: T. Kikuchi; S. Higashi and N. Azuma (eds), Genes, Behavior, and Evolution in Social Insects. Sapporo, Japan, University of Hokkaido Press.

Ďuriš, Z. 2017. Palaemonid shrimps (Crustacea: Decapoda) of Saudi Arabia from the 'Red Sea biodiversity survey' 2011–2013, with 11 new records for the Red Sea. *Marine Biodiversity,* 47: 1147–1161.

Ďuriš. Z. and Horká, I. 2017. Towards a revision of the genus *Periclimenes*: resurrection of *Ancylocaris* Schenkel, 1902, and designation of three new genera (Crustacea, Decapoda, Palaemonidae). *ZooKeys,* 646: 1–25.

Fautin, D.G.; Guo, C.C. and Hwang, J.S. 1995. Costs and benefits of the symbiosis between the anemone shrimp *Periclimenes brevicarpalis* and its host *Entacmaea quadricolor*. *Marine Ecology Progress Series,* 129: 77–84.

Folmer, O.; Black, M.; Hoeh, W.; Lutz, R. and Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial Cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology,* 3: 294–299.

Fransen, C.H.J.M. 1989. Notes on caridean shrimps collected during the Snellius-II Expedition. I. Associates of Anthozoa. *Netherlands Journal of Sea Research,* 23: 131–147.

Gan, Z.B.; Li, X.Z.; Chan, T.Y.; Chu, K.H. and Kou, Q. 2016. Phylogeny of Indo-West Pacific pontoniine shrimps (Crustacea: Decapoda: Caridea) based on multilocus analysis. *Journal of Zoological Systematics and Evolutionary Research*, 53: 282–290.

Góngora-Gómez, A.M.; Muñoz-Sevilla, N.P.; Hernández-Sepúlveda, J.A. and García-Ulloa, M. 2015. Association between the pen shell *Atrina tuberculosa* and the shrimp *Pontonia margarita*. *Symbiosis,* 66: 107–110.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41: 95–98.

Hayashi, K.I. and Ohtomi, J. 2001. A new species of the genus *Periclimenes* (Decapoda: Caridea: Palaemonidae) collected from hydrothermal vent fields in Kagoshima Bay, Japan. *Crustacean Research*, 30: 160–171.

Horká, I.; De Grave, S.; Fransen, C.H.; Petrusek, A. and Ďuriš, Z. 2016. Multiple host switching events shape the evolution of symbiotic palaemonid shrimps (Crustacea: Decapoda). *Scientific Reports*, 6: 26486.

Horká, I.; De Grave, S.; Fransen, C.H.; Petrusek, A. and Ďuriš, Z. 2018. Multiple origins and strong phenotypic convergence in fish-cleaning palaemonid shrimp lineages. *Molecular Phylogenetics and Evolution,* 124: 71–81.

Huebner, L.K. and Chadwick, N.E. 2012. Patterns of cleaning behaviour on coral reef fish by the anemone shrimp *Ancylomenes pedersoni*. *Journal of the Marine Biological Association of the United Kingdom*, 92: 1557–1562.

Jonsson, L.G.; Lundälv, T. and Johannesson, K. 2001. Symbiotic associations between anthozoans and crustaceans in a temperate coastal area. *Marine Ecology Progress Series*, 209: 189–195.

Kemp, S.W. 1922. Notes on Crustacea Decapoda in the Indian Museum. XV. Pontoniinae. *Records of the Indian Museum,* 24: 113–288.

Komai, T. and Tsuchida, S. 2015. New records of Alvinocarididae (Crustacea: Decapoda: Caridea) from the southwestern Pacific hydrothermal vents, with descriptions of one new genus and three new species. *Journal of Natural History,* 49: 1789–1824.

Komai, T.; Nemoto, S. and Tsuchida, S. 2010. *Periclimenes cannaphilus*, new species, the second palaemonid shrimp (Crustacea: Decapoda: Caridea) associated with sibogrinid tube worm inhabiting hydrothermal vents. *Journal of the Marine Biological Association of the United Kingdom*, 90: 799–808.

Kou, Q.; Li, X. and Bruce, A.J. 2016. Designation of a new genus *Bathymenes* for the deep-sea pontoniine shrimps of the '*Periclimenes alcocki* species group' (Decapoda, Caridea, Palaemonidae), with a checklist of the species assigned to the genus. *Chinese Journal of Oceanology and Limnology*, 34: 170–176.

Kumar, S.; Stecher, G.; Li, M.; Knyaz, C. and Tamura, K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution,* 35: 1547–1549.

Lee, K.H. and Ko, H.S. 2011. First records of two pontoniid shrimps (Crustacea: Decapoda: Caridea: Palaemonidae) from Korea. *Animal Systematics, Evolution and Diversity,* 27: 239–245.

Malay, M.C.M.D. and Paulay, G. 2010. Peripatric speciation drives diversification and distributional pattern of reef hermit crabs (Decapoda: Diogenidae: Calcinus). *Evolution,* 64: 634–662.

Marin, I.N. 2006. Description of *Crinotonia anastasiae*, new genus, new species, a new crinoid associated pontoniine shrimp (Crustacea: Caridea) from Nha Trang Bay, Vietnam, with inclusion of *Periclimenes attenuatus* Bruce, 1971, in the new genus. *The Raffles Bulletin of Zoology*, 54: 321–340.

Marin, I. 2012. New records and associations of pontoniine shrimps (Crustacea: Decapoda: Caridea: Palaemonidae: Pontoniinae) from the Nhatrang Bay, Vietnam; with taxonomic remarks on some species from the Indo-West Pacific region. *Benthic fauna of the Bay of Nhatrang, Southern Vietnam*, 2: 345–405.

Marin, I.N.; Britayev, T.A. and Anker, A. 2004. Pontoniine shrimps associated with cnidarians: new records and list of species from coastal waters of Viet Nam. *Arthropoda Selecta. Russian Journal of Arthropoda Research*, 13: 199–218.

Miyake, S. and Fujino, T. 1968. Pontoniid shrimps from the Palau Islands (Crustacea, Decapoda, Palaemonidae). *Journal of the Faculty of Agriculture, Kyushu University,* 14: 399–431.

Müller, H.G. 1993. Catalogue of the Indo-Pacific Pontoniine Shrimps. Wetzlar, Germany, Wissenschafticher Verlag H.G. Müller, 159p.

Olliff, R.R. 2013. Symbiosis of the sea star shrimp, *Periclimenes soror* Nobili, 1904 (Decapoda, Palaemonidae), and cushion star, *Culcita novaeguineae* Müller and Troschel, 1842 (Echinodermata, Asteroidea, Oreasteridae): host finding and benefits. Crustaceana, 86: 564–577.

Omori, K.; Yanagisawa, Y. and Hori, N. 1994. Life history of the caridean shrimp *Periclimenes ornatus* Bruce associated with a sea anemone in southwest Japan. *Journal of Crustacean Biology*, 14: 132–145.

Ory, N.C. and Thiel, M. 2013. Host-use patterns and factors influencing the choice between anemone and urchin hosts by a caridean shrimp. *Journal of Experimental Marine Biology and Ecology*, 449: 85–92.

Palumbi, S.; Martin, A.; Romano, S.; McMillan, W.O.; Stice, L. and Grabowski, G. 1991. The simple fools guide to PCR Version 2.0. Honolulu, HI: Department of Zoology and Kewalo Marine Laboratory, University of Hawaii. Available at https://searchworks.stanford.edu/view/9267895. Accessed on 11 March 2022.

Patton, W.K. 1966. Decapod Crustacea commensal with Queensland branching corals. *Crustaceana*, 10: 271–295.

Purushothaman, P.; Chakraborty, R.D.; Kuberan, G. and Maheswarudu, G. 2019. Integrative taxonomy of commercially important deep-water penaeoid shrimps from India. *Journal of Genetics,* 98: 12.

Richardson, C.A.; Kennedy, H.; Duarte, C.M. and Proud, S.V. 1997. The occurrence of *Pontonia pinnophylax* (Decapoda: Natantia: Pontoninae) in *Pinna nobilis* (Mollusca: Bivalvia: Pinnidae) from the Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, 77: 1227–1230.

Salvat, B. and Bacchet, P. 2011. Guide des récifs coralliens de Tahiti et ses îles. Papéete, Au Vent des Iles, 365p.

Spotte, S. 1996. Supply of regenerated nitrogen to sea anemones by their symbiotic shrimp. *Journal of Experimental Marine Biology and Ecology*, 198: 27–36.

Suzuki, K. and Hayashi, K.I. 1977. Five caridean shrimps associated with sea anemones in central Japan. *Publications of the Seto Marine Biological Laboratory*, 24: 193–208.

Thiel, M. and Baeza, J.A. 2001. Factors affecting the social behaviour of crustaceans living symbiotically with other marine invertebrates: a modelling approach. *Symbiosis*, 30: 163–190.

Thompson, J.D.; Higgins, D.G. and Gibson, T.J. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22: 4673–4680.

Tsang, L.M.; Ma, K.Y.; Ahyong, S.T.; Chan, T.Y. and Chu, K.H. 2008. Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. *Molecular Phylogenetics and Evolution,* 48: 359–368.