A new species of the genus *Cristimenes* Ďuriš & Horká, 2017 (Decapoda, Caridea, Palaemonidae)

Jin-Ho Park¹, Sammy De Grave², Won Kim¹

¹ School of Biological Sciences, Seoul National University, Seoul, 08826, Republic of Korea ² Oxford University Museum of Natural History, Oxford University, Parks Road, Oxford, OX1 3PW, UK

Corresponding author: Won Kim (wonkim@plaza.snu.ac.kr)

Abstract

A new species of crinoid-associated shrimp, *Cristimenes brucei* sp. nov., is described based on specimens from Korea, although the species also occurs in Hong Kong and is likely more widespread. The new species is morphologically very similar to *C. commensalis*, but can be distinguished by the reduced supraorbital tooth on the carapace. *Cristimenes brucei* sp. nov. is clearly recovered as a monophyletic species through COI barcode and molecular phylogenetic analyses based on four genetic markers (COI, 16S, H3, 18S).

Keywords

*Cristimenes brucei* sp. nov., crinoid associate, Indo-West Pacific, Hong Kong, Korea, phylogeny

Introduction

The genus *Cristimenes* Ďuriš & Horká, 2017 is associated with echinoderms (Ďuriš and Horká 2017) and currently consists of three species: *C. cristimanus* (Bruce, 1965), *C. zanzibaricus* (Bruce, 1967) (both associated with echinoids), and *C. commensalis* (Borradaile, 1915), associated with crinoids. All three species are widespread across the tropical regions of the Indo-West Pacific, and morphologically easily distinguished from related genera by the unique carpo-propodal articulation of the second pereiopod (Borradaile 1915; Barnard 1958; Bruce 1965, 1967, 1982a, 1984, 1989, 1996; Hayashi and Honma 2004; Marin and Savinkin 2007; Ďuriš and Horká 2017).
Cristimenes commensalis differs from the other two species by its host affiliation and can also be easily distinguished by the morphology of the ambulatory dactyli (Bruce 1965, 1967, 1980; Ďuriš and Horká 2017). The species has been recorded from various host crinoid species across the Indo-West Pacific, after it was described from Murray Island, Torres Strait, Australia in 1915 (Barnard 1958; Bruce 1982b; Marin and Savinkin 2007). Bruce (1979) already remarked upon variation in the supraorbital tooth and the lateral carina of specimens from Hong Kong in comparison to Indonesian specimens (Bruce 1982a, 1983). Specimens matching this morphology were obtained from Korea, and based on a morphological comparison as well as a molecular analysis are herein reported as a new species.

Materials and methods

Fieldwork for this study was carried out and organised in Korea (2012–2018), the Philippines (2014, 2018), and Vietnam (2016–2018) by Seoul National University (SNU), Korea Institute of Ocean Science and Technology (KIOST), the University of the Philippines Visayas (UPV), and the Institute of Tropical Biology (ITB). Host crinoids were collected during scuba diving and associated shrimps separated. All shrimps and tissue of host crinoids were preserved in 80% ethanol. The type series is deposited in the Marine Arthropod Depository Bank of Korea, Seoul National University, Seoul, Korea (MADBK); National Institute of Biological Resources, Incheon, Korea (NIBR) and the Oxford University Museum of Natural History, Oxford, United Kingdom (OUMNH.ZC). Postorbital carapace length (pocl, in mm) is used as the standard size measurement.

Molecular phylogenetic analyses were performed to elucidate the phylogenetic position of the new species within Cristimenes. Four species of Cristimenes (C. commensalis, C. cristimanus, C. zanzibaricus, and the new species) and three crinoid-associated shrimps Araiopontonia odontorhyncha Fujino & Miyake, 1970, Laomenes amboinensis (De Man, 1888), and Unguicaris pilipes (Bruce & Zmarzly, 1983) were selected as the ingroup, with Palaemonella potti (Borradaile, 1915) as the outgroup. Total genomic DNA was isolated from fifth pleopod tissue or eggs using the QI Amp® DNA Micro Kit (QIAGEN, Hilden, Germany), according to the manufacturer’s instructions. Two mitochondrial DNA fragments (cytochrome c oxidase subunit I (COI) and 16S rRNA) and two nuclear DNA fragments (histone 3 (H3) and 18S rRNA (18S)) were amplified by polymerase chain reaction (PCR) with the primer pairs LCO1490/HCO2198 (Folmer et al. 1994), 16S-ar/16S-1472 (Crandall and Fitzpatrick 1996; Palumbi et al. 2002), H3F/H3R (Colgan et al. 1998), 18Sa2.0/18S9r (Whiting 2002), respectively. PCR protocols followed Horká et al. (2016), with PCR products sent to Macrogen Inc. (Seoul, Korea) for purification and Sanger sequencing. Geneious v11.1.5 (http://www.geneious.com) was used to manipulate and confirm the sequencing data from both DNA strands before data analysis. Newly obtained sequences and additional sequences from GenBank are listed in Table 1.
Table 1. Specimens used in the phylogenetic analysis, with collection location, GenBank accession numbers (COI, 16S, H3, and 18S), and source references. N/A - not available.

| Taxa                        | Location | Voucher ID | GenBank accession numbers | Source         |
|-----------------------------|----------|-----------|---------------------------|----------------|
| Cristimenes brucei sp. nov. | Korea    | MADBK 120532_012 | MK688394 MK688410 MK688426 MK688442 | Present study  |
|                             | Korea    | SNU KR H537  | MK688395 MK688411 MK688427 MK688443 | Present study  |
|                             | Korea    | MADBK 120532_015 | MK688396 MK688412 MK688428 MK688444 | Present study  |
|                             | Korea    | MADBK 120532_015 | MK688397 MK688413 MK688429 MK688445 | Present study  |
| Cristimenes commensalis     | Philippines | SNU PH PI13  | N/A MK688414 MK688430 MK688446 | Present study  |
|                             | Philippines | SNU PH PI36  | N/A MK688415 MK688431 MK688447 | Present study  |
|                             | Philippines | SNU PH PI261 | MK688398 N/A N/A N/A | Present study  |
|                             | Philippines | SNU PH PI263 | MK688399 N/A N/A N/A | Present study  |
|                             | Philippines | SNU PH PI264 | MK688400 MK688416 MK688432 MK688448 | Present study  |
|                             | Taiwan    | UO Tw12-48B  | KU064993 KU170697 KU065081 KU064912 | Horká et al. 2016 |
| Cristimenes cristimanus     | Philippines | SNU PH PC49  | MK688401 MK688417 MK688433 MK688449 | Present study  |
|                             | Vietnam   | SNU VI V1109 | MK688402 MK688418 MK688434 MK688450 | Present study  |
|                             | Vietnam   | SNU VI V1110 | MK688403 MK688419 MK688435 MK688451 | Present study  |
|                             | Vietnam   | UO V08-34   | KU064994 KU064838 KU065082 KU064913 | Horká et al. 2016 |
| Cristimenes zanzibaricus    | Taiwan    | UO Tw12-86  | KU065011 KU170696 KU065096 KU064925 | Horká et al. 2016 |
| Laomenes amboinensis        | Philippines | SNU PH12    | MK688405 MK688420 MK688436 MK688452 | Present study  |
|                             | Philippines | SNU PH PH76  | MK688404 MK688421 MK688437 MK688453 | Present study  |
|                             | Taiwan    | UO Tw12-49  | KU064979 KU064825 KU065063 KU064898 | Horká et al. 2016 |
| Unguicaris pilipes          | Philippines | SNU PH PI57  | MK688406 MK688422 MK688438 MK688454 | Present study  |
|                             | Philippines | SNU PH PI68  | MK688407 MK688423 MK688439 MK688455 | Present study  |
| Unguicaris sp.              | Taiwan    | NTOU 6687-09 | KU065020 KU064863 KU065108 KU064937 | Horká et al. 2016 |
| Palaemonella potii          | Philippines | SNU PH PI56  | MK688408 MK688424 MK688440 MK688456 | Present study  |
|                             | Philippines | SNU PH PI58  | MK688409 MK688425 MK688441 MK688457 | Present study  |

COI sequence divergence within and between species were calculated using the Neighbor-Joining method (Saitou and Nei 1987) and the Kimura 2-parameter (K2P) distance method (Kimura 1980) within the MEGA6 (Tamura et al. 2013). Multiple sequence alignment was performed using MAFFT v7 (Katoh and Standley 2013) under the default parameters and then checked by eye; phylogenetic trees for the combined dataset were constructed by maximum likelihood (ML) analysis and Bayesian Inference (BI) approaches. The best-fitting substitution model for COI (HKY+I+G), 16S (HKY+G), H3 (GTR) and 18S (GTR+I+G) was determined by jModelTest v2.1.10 (Darriba et al. 2012) according to the Akaike Information Criterion (AIC; Akaike 1974). The ML analysis was carried out using RAxML v8.2.4 (Stamatakis 2006) using the model GTRGAMMA for each partition with 1,000 bootstrap runs. The BI analysis was carried out using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). The combined dataset was run for 10 million generations, sampling every 500 generations, with the first 50% trees discarded as burn-in. Phylogenetic trees were visualised in iTOL v4.0.3 (Letunic and Bork 2016).
Systematics

Infraorder Caridea Dana, 1852
Family Palaemonidae Rafinesque, 1815
Genus Cristimenes Ďuriš & Horká, 2017

Cristimenes brucei sp. nov.
http://zoobank.org/05D90862-52D5-4C2F-A5CF-5E4F3251A40E
Figures 1–7, 8A–B, 9A–C, 10A–C

Periclimenes commensalis: Bruce 1982a: 236–238, fig. 2.

Material examined. Holotype. KOREA – Jeju Special Self-Governing Province • 1 ov. ♀ (pocl 3.80 mm); Munseom Island; 33°13’37”N, 126°34’8”E; depth 20 m; 16 Oct. 2015; JH Park leg.; on Annessia japonica (Müller, 1841); NIBRIV0000841118; Paratypes. KOREA – Jeju Special Self-Governing Province • 3 ♀♂ (pocl 2.2, 1.86, 1.83 mm); Munseom Island; 33°13’37”N, 126°34’8”E; depth 20 m; 16 Oct. 2015; JH Park leg.; on A. japonica; MADBK 120532_006 • 1 ov. (pocl 3.65 mm); same data; 16 Oct. 2015; JH Park leg.; on A. japonica; OUMNH.ZC.2018-03-022 • 2 ♀♂, 1 ♂ (pocl 3.34, 3.1, 1.6 mm); same data; 17 Oct. 2015; JH Park leg.; on A. japonica; MADBK 120532_007 • 3 ♀♂, 1 ♂ (pocl 2.85, 2.2, 1.5, 1.98 mm); same data; 08 Jul. 2016; JH Park leg.; on A. japonica; NIBRIV0000841119 • 1 ♀ (pocl 1.67 mm); same data; 08 Aug.2016; JH Park leg.; on A. japonica; OUMNH.ZC.2018-03-023 • 1 ♀ (pocl 2.45 mm); same data; 31 Mar. 2018; JH Park leg.; on A. japonica; MADBK 120532_017.

Additional material. KOREA – Dadohaesang National Park • 1 ♀ (pocl 2.7 mm); Geomundo Island; 34°3’35”N, 127°16’57”E; depth 20 m; 5 Jul. 2014; JH Park leg.; on A. japonica; MADBK 120532_002 – Gyeongsangbuk-do • 1 ♀, 3 ♀♂ (pocl 1.95, 2.0, 1.7, 1.6 mm); Pohang-si, Guryongpo; 36°0’25”N, 129°35’10”E; depth 15 m; 22 Sep. 2016; JH Park leg.; on A. japonica; MADBK 120532_015 – Jeju Special Self-Governing Province • 5 ♀♂, 1 ♂ (pocl 2.5, 2.3, 2.2, 1.7, 1.45, 2.0 mm); Beomseom Island; 33°13’7”N, 126°30’50”E; depth 20 m; 28 Feb. 2015; JH Park leg.; on A. solaster (Clark, 1907); MADBK 120532_003 • 8 ♀♂, 1 ♂ (pocl 2.77, 2.6, 2.6, 2.5, 2.5, 2.4, 2.3, 2.1, 1.9 mm); same data; 16 May 2015; JH Park leg.; on Catoptometra rubroflava (Clark, 1908); MADBK 120532_004 • 1 ov. ♀, 6 ♀♂, 3 ♀♂ (pocl 3.43, 3.48, 3.21, 3.08, 2.37, 2.3, 2.89, 2.54, 1.97 mm); same data; 17 May 2015; JH Park leg.; on A. japonica; MADBK 120532_005 • 1 ♂, 1 ♂ (pocl 1.83, 1.83 mm); Saeseom Island; 33°14’2”N, 126°33’49”E; depth 20 m; 30 Jan. 2016; JH Park leg.; on A. japonica; MADBK 120532_011 • 3 ♀♂, 2 ♂♂ (pocl 2.45, 2.24, 1.2, 2.0, 1.68 mm); Seopseom Island; 33°13’55”N, 126°35’51”E; depth 15 m; 28 Jan. 2016; JH Park leg.; on A. japonica; MADBK 120532_010 • 1 ♂, 2 ♂♂ (pocl 3.0, 2.16, 1.89 mm); same data; 28 Apr. 2016; JH Park leg.; on A. japonica; MADBK 120532_013 • 1 ♂ (pocl 2.27 mm); same data; 28 Apr. 2016; JH Park leg.; on A. japonica; OUMNH.ZC.2018-03-024 • 1 ♀ (pocl 3.5 mm); same data; 28 Apr. 2016; JH Park leg.;
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Figure 1. Cristimenes brucei sp. nov., lateral aspect. Ovigerous female holotype pocl 3.65 mm (NIBRIV0000841118).

Diagnosis. Rostrum well developed, with dorsal and ventral teeth. Carapace smooth, without epigastric tooth; lateral carinae feebly developed; supraorbital tooth reduced, blunt; inferior orbital angle pointed; antennal and hepatic teeth well developed. Fourth thoracic sternite without median process. Abdomen with rounded pleura. Telson with two pairs of small dorsal spiniform setae, and with three pairs of posterior spiniform setae. Eyes with hemispherical cornea. Basal antennular segment with two acute distolateral teeth. Antennal basicerite with sharp distoventral tooth; scaphocerite with large distolateral tooth, not reaching distal end of lamella. Epistome rounded. Mandible without palp; molar process robust; incisor process with four or five terminal teeth. Maxillula with simple palp. Maxilla with blunt palp, basal endite well developed, bilobed. First maxilliped with simple palp; basal and coxal endites fused; exopod with developed caridean lobe; epipod bilobed. Second maxil-
lipped with subquadrate epipod, without podobranch. Third maxillipeds with slender exopod; arthrobranch rudimentary. Second pereiopods equal in shape and subequal in size; palm articulated subproximally; cutting edges of fingers feebly dentate proximally, serrated distally. Dactyli of ambulatory pereiopods biunguiculate; corpus with two or three acute dorsodistal spinules, with acute preterminal accessory tooth. Uropodal exopod with distolateral tooth and movable acute spine.

**Description.** Rostrum (Figs 2A, B, 9A, B) well developed, slightly overreaching distal end of antennular peduncle; upper margin slightly convex with 6–8 dorsal teeth, ventral margin convex with 0–3 ventral teeth. Carapace (Figs 2A, B, 9A, B) smooth without epigastric tooth; lateral carinae feebly developed; supraorbital tooth reduced, blunt (Fig. 9C); inferior orbital angle pointed; antennal and hepatic teeth (Fig. 2C) well developed, antennal tooth long and slender, hepatic tooth larger than antennal tooth; pterygostomial angle rounded. Thoracic sternite (Fig. 3D) without special features; fourth thoracic sternite without finger-like median process. Abdomen (Fig. 1) smooth; pleura of first to fifth segments rounded; sixth segment with pointed posterolateral angle, posteroventral angle blunt (Fig. 2E).
Telson (Fig. 2D, E) 0.78 of pocl, 3.2 times longer than proximal width; two pairs of small dorsal spiniform setae at 0.53 and 0.82 of telson length, with three pairs of posterior spiniform setae, outer pair short, inner pair long and stout.

Eye (Figs 2B, 3A) with hemispherical cornea, dorsolaterally with nebenauge; eye-stalk 1.2 times as long as wide.

Antennule (Fig. 3B) well developed; basal segment with two acute distolateral teeth, with submarginal medioventral tooth; stylocerite reaching to middle of proximal segment; intermediate and distal segment subequal in length; upper flagellum biramous, proximal four segments fused, shorter free ramus with five segments, 0.3 of longer free ramus.

Antenna (Fig. 3C) well developed; basicerite with sharp distoventral tooth; ischiocerite and merocerite unarmed; carpocerite reaching to 0.4 of scaphocerite; scaphocerite 2.4 times as long as maximal wide, distolateral tooth large, not reaching distal end of lamellae.

Mandible (Fig. 4A) without palp; molar process robust, with four strong teeth and brush-like setae; incisor process with four or five terminal teeth.

Maxillula (Fig. 4B) with bilobed palp; upper lacinia broad, with stout and simple spines, with plumose setae on lower margin; lower lacinia robust with long spines distally, with plumose setae on lower margin.

Figure 3. Cristimenes brucei sp. nov., female pocl 2.74 mm (MADBK 120532_012). A eye, interocular region, and epistome, dorsal view B antennule, ventral view C antenna, ventral view D fifth (top) and fourth thoracic sternite.
Maxilla (Fig. 4C) with blunt palp, with sparsely plumose setae; coxal endite obsolete; basal endite well developed, bilobed, with sparsely plumose setae; scaphognathite 2.9 times as long as wide.

First maxilliped (Fig. 4D) with long simple palp, with sparsely plumose setae along the medial margin of the palp; basal and coxal endites fused, with serrulate setae medially; exopod with developed caridean lobe, flagellum with long simple seta; epipod bilobed.

Second maxilliped (Fig. 4E) with subquadrate epipod, without podobranch; merus and carpus without special features; propodus with slender simple setae; dactylus 2.7 times as long as wide, with dense serrulate setae distally.

Third maxilliped (Fig. 4F) with endopod slightly overreaching distal end of carpocerite; ischiomerus approximately six times longer than wide, medially sparsely setose; penultimate segment 0.56 length of ischiomerus, medially with long serrulate setae; terminal segment tapering, slightly downcurved distally, subequal to penultimate segment, with transverse rows of setae and group of terminal hamate setae; exopod slender with plumose setae distally; coxa with large rounded epipod, arthrobranch rudimentary.

First pereiopod (Fig. 5A, B) overreaching distal end of scaphocerite; ischium 0.56 length of merus, unarmed; merus and carpus subequal in length; carpus 1.36
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Figure 6. *Cristimenes brucei* sp. nov., female pocl 2.74 mm (MADBK 120532_012). A minor right second pereiopod, ventrolateral view B major left second pereiopod, lateral view C same, carpo-propodal articulation, dorsal view D same, dactylus, lateral view E same, distal margin of cutting edge of dactylus.

Fourth pereiopod (Fig. 5E) with ischium 0.57 length of merus, unarmed; merus 0.80 times length of propodus, unarmed; carpus 0.42 times length of propodus, unarmed; propodus with four distolateral spiniform setae including two distoventral ones; dactylus 0.18 times length of propodus, biunguiculate; corpus with two acute dorsodistal spinules, with acute preterminal accessory tooth, ventral margin straight, with simple distal setae laterally; unguis 0.64 times as long as corpus.

Fifth pereiopod (Fig. 5F) with ischium 0.54 length of merus, unarmed; merus 0.74 times length of propodus, unarmed; carpus 0.38 times length of propodus, unarmed; propodus with five mesial spiniform setae, distolateral one absent; dactylus 0.18 times length of propodus, biunguiculate; corpus with two acute dorsodistal spinules, with acute preterminal accessory tooth, ventral margin straight, with simple distal setae laterally; unguis 0.70 times as long as corpus.

Pleopods as usual for genus. First pleopod of male (Fig. 7A) with endopod 2.8 times longer than wide. Second pleopod of male (Fig. 7B) with appendix masculina with stout, long setae; appendix interna slightly longer than appendix masculina. Second pleopod of female (Fig. 7C) as usual for genus.
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Uropod (Fig. 2E) overreaching distal end of telson; exopod with distolateral tooth and movable acute spine.

**Etymology.** The new species is named in honour of Dr AJ (Sandy) Bruce, in recognition of his considerable contribution to the systematics of Palaemonidae.

**Colour.** Body colour (Fig. 8A, B) orange or reddish-brown adapted to the colour of the host crinoids; creamy white line extending from the tip of the rostrum to the posterior dorsal margin of the carapace; similar, but thinner and lighter line extending from posterior ventral angle of the sixth abdominal segment to the lateral side of the first antennular peduncle.

**Ecology.** The specimens were collected from the crinoids *Anneissia japonica*, *A. solaster* and *Catoptometra rubroflava* at a depth of 15 – 27 m. Bruce (1982a) reported that the Hong Kong specimens were collected from *Tropiometra afra* (Hartlaub, 1890).

**Distribution.** Presently only known from the type locality, Jeju Special Self-Governing Province, Korea as well as Hong Kong (Bruce 1982a).

**Remarks.** The new species is morphologically very similar to the other crinoid-associated species in the genus, *C. commensalis* (Fig. 8C). Within the genus, both species
share the following characteristics: subspatulate fingers of the first pereiopods; proximally dentate and distally serrate cutting edges of the fingers of the second pereiopods (Fig. 10C, D); and the presence of accessory spinules on the anterior margin of the dactyli of the ambulatory pereiopods. The new species can, however, be easily distinguished from *C. commensalis* by the reduced, blunt supraorbital tooth (Fig. 9A–C) and reduced rostral carinae (vs. well-developed supraorbital tooth (Fig. 9D) and rostral carinae in *C. commensalis*).

*Cristimenes brucei* sp. nov. can easily be distinguished from the echinoid-associated species *C. cristimanus* (Fig. 8D) and *C. zanzibaricus* by the reduced supraorbital tooth and rostral carinae (vs. extremely developed supraorbital tooth and rostral carinae), the presence of accessory spinules on the anterior margin of the ambulatory dactylus (vs. absent), and a different host affiliation, with the latter two species being associated with echinoids.

The crinoid-associated genera *Araiopontonia* Fujino & Miyake, 1970, *Laomenes* Clark, 1919, and *Unguicaris* Marin & Chan, 2006 are phylogenetically closely related to *Cristimenes*. The new species shares a morphological trait with *Araiopontonia odontorhyncha* Fujino & Miyake, 1970 in having accessory spinules on the anterior margin of the ambulatory dactylus, but the new species can easily be distinguished from *A. odontorhyncha* by the reduced supraorbital teeth and rostral carinae, the presence of a hepatic tooth on the carapace, and the low and rounded epistome (vs. developed supraorbital tooth and rostral carinae, absence of hepatic tooth, and well developed rounded epistomial horns in *A. odontorhyncha*). All species in the genus *Laomenes* can
be distinguished from the new species by having more strongly developed supraorbital teeth and rostral carinae, well developed sharp epistomial horns and simple biunguiculat ambulatory dactylus. The new species is morphologically similar to *U. novaecaledoniae* (Bruce, 1968) among species of the genus *Unguicaris*. The new species shares with *U. novaecaledoniae* similar first chelipeds, proximally dentate but distally serrate cutting edges of the fingers of the second pereiopods, and the presence of well-developed accessory spinules on the anterior margin of the ambulatory dactyli. The new species can, however, be distinguished from *U. novaecaledonia* by the presence of reduced supraorbital teeth (vs. absent).

**Phylogenetic analyses**

We obtained fragments of 658, 462, 293, and 655 bp for the COI, 16S, H3, and 18S markers, respectively. Barcode COI regions were calculated for 13 specimens across all four species of *Cristimenes*, with the maximum K2P intraspecific divergence being 0.15%, 1.09% and 1.25% in *Cristimenes brucei* sp. nov., *C. commensalis*, and *C. cristi-manus* (Table 2), whilst mean K2P interspecific distances between *C. brucei* sp. nov.
Figure 10. Cristimenes brucei sp. nov., female pocl 2.7 mm (MADBK 120532_002) (A, C, D), female pocl 3.34 mm (MADBK 120532_007) (E, F), Cristimenes commensalis from Vietnam, female pocl 2.0 mm (SNU VI_VI155) (B) A, B chela and carpus of second pereiopod C same, distally serrate margin of fixed finger D same, proximally dentate margins of fingers E dactylus and distal propodus of third pereiopod F same, distal dorsal spinules of dactylar corpus, and unguis.

and C. commensalis, C. cristimanus and C. zanzibaricus being 18.2%, 13.8%, and 15.1%, respectively (Table 2).

Phylogenetic analyses were conducted on 21 specimens of seven species of four genera (Table 1). The combined 2068 bp fragments had 253 parsimony-informative sites for COI, 145 for 16S, 42 for H3, and 102 for 18S. The ML and BI analyses showed the same topology, except for Laomenes and Unguicaris (Fig. 11). The resulting
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phylogeny clearly indicates the monophyly of Cristimenes with high support values, both in ML and BI analyses. Cristimenes brucei sp. nov. is clearly recovered as a monophyletic species but as a sister group to the echinoid associated C. cristimanus, whilst the crinoid associated C. commensalis is a sister group to the clade containing C. brucei sp. nov., C. cristimanus, and C. zanzibaricus.
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