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Two new species of planktonic *Caligus* O.F. Müller 1785 (Copepoda: Caligidae) from Türkiye with an updated review and checklist of planktonic caligids

ARGUN AKIF ÖZAK[1], TUBA TERBIYIK KURT[2], SEYIT ALI KAMANLI[3], GÜRKAN AKBULUT[2], ALPER YANAR[4] & GEOFFREY A. BOXSHALL[5]

[1]*Department of Fish Diseases, Faculty of Fisheries, University of Çukurova, 01330 Sarıçam, Adana, Türkiye*
ozargun@gmail.com, ozargun@cu.edu.tr; https://orcid.org/0000-0001-6743-4178
[2]*Department of Basic Sciences, Faculty of Fisheries, University of Çukurova, 01330 Sarıçam, Adana, Türkiye*
tubaterbiyik@gmail.com, tterbiyik@cu.edu.tr; https://orcid.org/0000-0002-2937-6816
ggurkan-1988@hotmail.com; https://orcid.org/0000-0002-9593-154X
[3]*Department of Biology, Faculty of Art and Science, Burdur Mehmet Akif Ersoy University, Burdur 15030, Türkiye*
alikamanli06@gmail.com; https://orcid.org/0000-0002-9118-4591
[4]*Department of Marine Sciences, Faculty of Marine Sciences and Technology, Iskenderun Technical University, Iskenderun-Hatay 31200, Türkiye*
alperynr@gmail.com, alper.yanar@iste.edu.tr; https://orcid.org/0000-0002-9293-7647
[5]*Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
g.boxshall@nhm.ac.uk; https://orcid.org/0000-0001-8170-7734

Abstract

Two new species of caligid sea lice, *Caligus izmiriensis* sp. nov., and *Caligus sarosensis* sp. nov. are described, based on specimens collected from the zooplankton in the Gulf of Sığacık and the Gulf of Saros off the Aegean Sea coast of Türkiye. Detailed examination of the morphology of these two new species and comparisons with other closely related caligid species, especially *Metacaligus yucatanensis* Suárez-Morales, Kim & Escamilla, 2012, resulted in the recognition of the genus *Metacaligus* Thomsen 1949 as a junior synonym of C*aligus* O.F. Müller, 1785. Based on this proposed synonymy, all species of the genus *Metacaligus* are here transferred to *Caligus*: *Metacaligus trichiuri* (Krøyer, 1863), *M. rufus* (Wilson, 1908), and *M. unguidentatus* (Rangnekar & Murti, 1950) all return to their original combinations as *Caligus trichiuri* Krøyer, 1863, *Caligus rufus* Wilson, 1908, and *Caligus unguidentatus* Rangnekar & Murti, 1950, respectively; *Metacaligus yucatanensis* Suárez-Morales, Kim& Escamilla, 2012, becomes *Caligus yucatanensis* (Suárez-Morales, Kim & Escamilla, 2012) comb. nov.; transferring *Metacaligus latus* Ho & Lin, 2002 would create a secondary homonym of *Caligus latus* Byrnes 1987, so a replacement name is proposed as *Caligus cultellus* nom. nov. We recognise *C. yucatanensis* as a member of the *C. undulatus*-group. The four other species previously placed in *Metacaligus* form a cluster which represents a new species group, the *Caligus trichiuri*-group. An updated list of planktonic caligids is presented, together with keys to species of the *C. undulatus*-group and of the newly proposed *C. trichiuri*-group. The subgenus *Subcaligus* Heegaard, 1943 was originally proposed to accommodate *Caligus* (*Subcaligus*) *bocki* Heegaard, 1943, and was characterised by its unusual stylet-like sternal furca. This subgenus has not been treated as valid by subsequent authors and we here formally propose to treat *Subcaligus* Heegaard 1943 as a junior synonym of *Caligus*.

Key words: Caligidae, planktonic, copepod, Türkiye, sea lice

Introduction

The parasitic copepod family Caligidae Burmeister, 1835 is the most species-rich family in the entire Copepoda and it currently comprises more than 500 valid species (Walter & Boxshall 2023). Members of the family are commonly known as sea lice which typically utilize wild or cultured marine fish species as their hosts (Boxshall 2018; Costello 2009; Johnson *et al.* 2004). It has been estimated that approximately 60% of all copepod infestations in fin-fish farming in marine and brackish water environments are attributable to sea lice (Johnson *et al.* 2004). Species belonging to the genera *Caligus* O.F. Müller, 1785, and *Lepeophtheirus* von Nordmann, 1832 in particular,

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have been reported to cause significant economic losses in aquaculture (Mackenzie 2022), with losses due to sea lice in the salmon farming industry alone estimated to be in excess of $1 billion p.a. (Boxaspen *et al.* 2022).

The majority of sea lice have direct life cycles incorporating only a short free-swimming phase consisting of two non-feeding naupliar stages and the infective first copepodid stage (Boxshall & Özak 2022), but in recent years the discovery of numerous adult *Caligus* species within the zooplankton community has prompted a re-evaluation of the lifestyle of these parasites and has led to the frequent occurrence of the term "planktonic caligid" in recently published papers. In their review and checklist, Venmathi Maran *et al*. (2016) listed a total of 32 species of caligids belonging to the genera *Caligus*, *Lepeophtheirus* and *Metacaligus* Thomsen, 1949, which have been collected from the plankton. We note that 19 of the species listed by (Venmathi Maran *et al.* 2016) have also been sampled from fish hosts, while the remaining 13 species have been found exclusively in the plankton.

In the present study, we describe two new species of *Caligus*, *C. izmiriensis* sp. nov. and *C. sarosensis* sp. nov. based on specimens found in zooplankton samples taken from Aegean Sea waters, off the Turkish coast. Based on the comparative morphological data obtained from these new species descriptions, we explored the boundaries between the genus *Metacaligus* and *Caligus*, concluding that these genera are synonymous. In addition, all available previous reports on planktonic caligids were revisited and we collated several additional old records of planktonic caligids that had been overlooked in recent reviews. We note that at least 44 caligid species have been reported from plankton samples (Table 1).

TABLE 1. Caligid species recorded as adults free-swimming in plankton[1].

Group*	Species	Specimens	Locality	Source	Notes
N/A	*Anchicaligus nautili* Stebbing, 1900	1 male	07º 53'S, 116º 18'E	Heegaard, 1972	as *Caligulina ocularis* (see Dojiri & Ho, 2013)
C.mac	*Caligus aduncus* Shen & Li, 1959	2 females	Tsingtao Harbour (China)	Shen & Li, 1959	
C.pro	*Caligus affinis* Heller, 1865	1 male	Loanda Harbour (Gulf of Guinea)	Scott, 1894	as *C. bengoensis* (see Hayes, *et al*., 2012)
UA	*Caligus calotomi* Shiino, 1954	1 male	Tokushima (Japan)	Venmathi Maran *etal*., 2012a	
C.und	*Caligus chelifer* Wilson, 1905	1 male	Gulf of Mexico	Suárez-Morales *et al*., 1998	
		1 female 1 male	Off Rockport, Texas (USA)	Heegaard, 1966	as *C. hyalinae* (see Boxshall & Bernot, 2023)
UA	*Caligus chiastos* Lin & Ho, 2003	1 male	Gulf of Thailand	Venmathi Maran *et al*., 2012b	
C.pse	*Caligus chinglonglini* Ohtsuka & Boxshall, 2019	1 male	Iki Island (Japan)	Ohtsuka & Boxshall, 2019	
UA	*Caligus coryphaenae* Steenstrup & Lütken, 1861	4 males	Nansei Islands (Japan)	Venmathi Maran & Ohtsuka, 2008	
		1 male	Loanda Harbour (Gulf of Guinea)	Scott, 1894	as *C. thymni* (see Hayes, *et al*., 2012)
		1 female	unknown	Wilson, 1905	
		1 male	Easter Island (Chile)	Wilson, 1905	
		1 male	Mindanao (Philippines)	Wilson, 1905	
		7 females 3 males	Various stations in North Atlantic and Indian Oceans	Heegaard, 1972	Material from Dana Expedition
C.dia	*Caligus costatus* Shen & Li, 1959	2 males	Tsingtao Harbour (China)	Shen & Li, 1959	Recognised here as member of *C. diaphanus* group
UA	*Caligus curtus* Müller, 1785	1 specimen	Bermuda	Wilson, 1936	Sex unspecified
UA	*Caligus dubius* Scott, 1894	1 female 5 males	Loanda Harbour (Gulf of Guinea)	Scott, 1894	Redescribed by Boxshall & Gurney,1980

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TABLE 1 (Continued)

Group*	Species	Specimens	Locality	Source	Notes
UA	*Caligus elongatus* von Nordmann, 1832	females & males	British coastal waters	Todd *et al*., 1996	Common in coastal plankton samples
		1 male	Gulf of Mexico	Wilson, 1950	as *C. rapax*
UA	*Caligus epidemicus* Hewitt, 1971	multiple specimens	Mitchel River (Australia)	Hewitt, 1971	
C.und	*Caligus evelynae* Suárez-Morales, Camisotti & Martin, 2012	1 female 1 male	Bay of Amuay (Venezuela)	Suárez-Morales *et al*., 2012a	
UA	*Caligus hyalinus* Czerniavski, 1868	1 male	Black Sea	Czerniavski, 1868	
UA	*Caligus ilhoikimi* Suárez-Morales & Gasca, 2016	16 females 14 males	Xcalak Reef (Mexico)	Suárez-Morales & Gasca, 2016	
C.und	*Caligus izmiriensis* sp. nov.	3 females 2 males	İzmir Bay (Türkiye)	Present account	
C.pse	*Caligus latigenitalis* Shiino, 1954	1 male	Seto Inland Sea (Japan)	Venmathi Maran *et al*., 2012b	
UA	*Caligus littoralis* Luque & Cezar, 2000	13 females 5 males	Western Caribbean (off Venezuela)	Kim *et al*., 2019	
C.mac	*Caligus longicaudatus* Brady, 1899	1 male	Port Chalmers (New Zealand)	Brady, 1899	
C.und	*Caligus longiramus* Venmathi Maran,Ohtsuka & Jitchum, 2012	1 female	Amami Island (Japan)	Venmathi Maran *et al*., 2012b	
C.mac	*Caligus macarovi* Gusev, 1951	1 male	California (USA)	Heegaard, 1966	
		1 male	San Francisco (USA)	Heegaard, 1972	Material from Dana Expedition
UA	*Caligus minimus* Otto, 1821	1 female	Gulf of Iskenderun (Türkiye)	Kamanli, 2023	
C.und	*Caligus ogawai* Venmathi Maran, Ohtsuka & Shang, 2012	2 females 1 male	Seto Inland Sea (Japan) Hirado Island (Japan)	Venmathi Maran *et al*., 2012a	
C.mac	*Caligus orientalis* Gusev, 1951	2 females 1 male	Yellow River (China)	Shen, 1957	as *C. laticorpus*
		1 female 1 male	Mankyong River (South Korea)	Venmathi Maran & Ohtsuka, 2008	
		1 female 1 male	Amoy (China) Ariake Sea (Japan)	Venmathi Maran *et al*., 2012a	
UA	*Caligus pelagicus* Kurian, 1955	3 females	Kayamkulam (India)	Kurian, 1955	
		3 males			
UA	*Caligus planktonis* Pillai, 1979	1 female	Off Trivandrum (India)	Pillai, 1979	
UA	*Caligus praetextus* Bere, 1936	1 male	Gulf of Cariaco (Venezuela)	Kim *et al*., 2019	
C.pro	*Caligus productus* Dana, 1852-1853	1 female	California (USA)	Wilson, 1935	
		7 females 7 males	Various stations in North Atlantic and Indian Oceans	Heegaard, 1972	Material from Dana Expedition
C.mac	*Caligus punctatus* Shiino, 1955	12 females 8 males	China	Shen, 1957	most from plankton, as *C. communis*
C.mac	*Caligus quadrigenitalis* Venmathi Maran, Ohtsuka & Shang, 2012	1 female	Iheya Island (Japan)	Venmathi Maran *et al*., 2012a	
UA	*Caligus rufimaculatus* Wilson, 1905	1 female 4 males	Laguna Chelem (Mexico)	Suárez-Morales *et al*., 2012b	
		1 male	Turpialito (Venezuela)	Kim *et al*., 2019	
C. tri	*Caligus rufus* Wilson, 1908	3 females 1 male	Laguna Chelem (Mexico)	Suárez-Morales *et al*., 2012b	as *Metacaligus rufus*
C.und	*Caligus sarosensis* sp.nov.	1 female	Gulf of Saros (Türkiye)	Present account	

.....continued on the next page

TABLE 1 (Continued)

Group*	Species	Specimens	Locality	Source	Notes
UA	*Caligus savala* Gnanamuthu, 1948	12 females 5 males	Madras (India)	Gnanamuthu, 1948	
C.mac	*Caligus sclerotinosus* Roubal, Armitage & Rohde, 1983	1 female	Uwajima (Japan)	Venmathi Maran & Ohtsuka, 2008	
C.dia	*Caligus torpedinis* Heller, 1866	1 male	Fujian Province (China)	Venmathi Maran *et al*., 2012a	as *C. rotundigenitalis* (see Boxshall & Bernot, 2023)
C.tri	*Caligus trichiuri* Krøyer, 1863	1 female	Osaka Port (Japan)	Venmathi Maran *et al*., 2012a	as *Metacaligus* uruguayensis
C.und	*Caligus tripedalis* Heegaard, 1972	2 females 1 male	New Zealand	Heegaard, 1972	
C.und	*Caligus undulatus* Shen & Li, 1959	24 females 34 males	Kiaochow Bay (China)	Shen & Li, 1959	
		1 male	Mandapam (India)	Pillai, 1966	
		75 females	Baiá de Paranaguá (Brazil)	Montú, 1982	including ovigerous and non-ovigerous females
		1 male	Ariake Sea (Japan)	Venmathi Maran & Ohtsuka, 2008	
		1 male	Seomjin River (South Korea)	Venmathi Maran & Ohtsuka, 2008	
		1 female	Ube, Seto Inland Sea (Japan)	Venmathi Maran & Ohtsuka, 2008	
		2 males	Laguna Chelem (Mexico)	Suárez-Morales *et al*., 2012b	
		1 male	Bonny River delta (Nigeria)	Heegaard, 1955	as *C. hamatus*, see Boxshall & Bernot,2023
		2 females 1 male	Takamatsu Port (Japan)	Venmathi Maran *et al*., 2012a	
		5 females 4 males	Southern & southwestern coast of South Korea	Moon & Park, 2019	
C.und	*Caligus yucatanensis* (Suárez-Morales, Kim & Escamilla, 2012)	1 female 2 males	Laguna Chelem (Mexico)	Suárez-Morales *et al*., 2012b	as *M. yucatanensis*
N/A	*Lepeophtheirus alvaroi* Suárez-Morales & Gasca, 2012	2 females	Bahia Wafer (Costa Rica)	Suárez-Morales & Gasca, 2012	
N/A	*Lepeophtheirus parviventris* Wilson, 1905	1 female	Bering Sea	Venmathi Maran *et al*., 2012a	
N/A	*Lepeophtheirus semicossyphi* Yamaguti, 1939	1 female	Iheya Island (Japan)	Wilson, 1905	

*Abbreviations for species groups within *Caligus*: *C.dia* = *C. diaphanus*-group, *C.mac* = *C. macarovi*-group, *C.pro* = *C. productus*-group, *C.pse* = *C.pseudorhombi*-group, *C.tri* = *C.trichiuri*-group, *C.und* = *C.undulatus* group; N/A = not applicable; UA = unattributed (i.e. not yet placed in a species group).

[1] A single male of *Caligus tetrodontis* Barnard, 1948 was reported from Brazilian plankton by Montú (1982) but this was considered a misidentification by Hayes *et al*. (2021) and is not included here.

Material and methods

The *Caligus* specimens examined in the present study were collected during two different projects conducted off the Aegean Sea coast of Türkiye; the Oceanographic monitoring project (İZİZ Project) and the Integrated Marine Pollution Monitoring (DE-NİZ Project). In both projects zooplankton samples were collected vertically using a WP-2 net with 200-µm mesh. Fifteen stations were visited in each project and mean volume of water filtered by the net was 6.8 l. Collected zooplankton samples were immediately preserved in seawater-formalin solution (4%) in the field. Subsequently, all *Caligus* specimens were sorted from the fixed zooplankton samples. A total of 6 Caligus

specimens were collected. *Caligus* specimens were later cleared in lactic acid for 2 h prior to examination using a Nikon SMZ 800N dissecting stereomicroscope and an Olympus BX51 microscope equipped with differential interference contrast (DIC). Subsequently, specimens were mounted as temporary preparations in a drop of lactic acid on a cavity slide for taking measurements and making drawings. Measurements were made using an ocular micrometer and drawings were made with the aid of a drawing tube. All measurements are given in millimetres unless otherwise stated and are presented as the range followed by the mean in parentheses where possible. Confocal laser scanning microscope (CLSM) imaging techniques applied by Kamanli *et al.* (2017) were used to visualise some of the appendages of the new species using a Zeiss LSM 700 CLSM and Drishti software (version 2.6.4) (Limaye 2012) was used to process CLSM images and videos. The videos are provided as Supplementary Video (SV) in .wmv format and named as SV-IZM1–4 for *Caligus izmiriensis* sp. nov., and for *C. sarosensis* sp. nov. as SV-SAR5–6, respectively. The morphological terminology for the copepods follows Boxshall (1990) and Huys & Boxshall (1991). The scientific and common names of fishes presented in this study follow Froese & Pauly (2023). Type specimens are deposited at the Natural History Museum, London and the remaining material is stored in the collections of the Aquatic Parasitology Museum at the Faculty of Fisheries, University of Cukurova in Adana, Türkiye.

Results

Family: Caligidae Burmeister, 1835

Genus: *Caligus* O.F. Müller, 1785

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Caligus izmiriensis sp. nov.

LSIDurn:lsid:zoobank.org:act:B6978259-447A-4470-9D74-E1868246E546

Type material

Holotype adult female stored in collections of the Natural History Museum, London (Reg, No,. NHMUK 2022. 201). Type Locality: Stn ILBSW1**;** Ildır Bay, İzmir, Türkiye (38°23′38.69″N 26°23′55.95″E): depth 60 m; date 28.02.2020.

Paratype young female stored in the collections of Aquatic Parasitology Museum of the Faculty of Fisheries, University of Çukurova (CUMAP), Adana, Türkiye (Reg. No. CUMAPCOP/2023. Locality: Stn S3; Akarca Cape, Seferihisar (Aegean Sea, Türkiye) (38°09′40.13″N; 26°48′35.70″E): depth 10 m; date 13.06.2020.

Allotype adult male stored in collections of the Natural History Museum, London (Reg, No,. NHMUK 2022. 202). Type Locality: Stn Sta20; İzmir Bay, off Urla (Aegean Sea, Türkiye) (38°27′07.41″N; 26°51′19.37″E): depth 50 m; date 07.05.2021.

Additional material: 1 young adult female and 1 adult male from İzmir Bay were prepared for confocal laser scanning microscopy; and were eventually dissected to allow scanning of individual limbs.

Etymology: The species name refers to the type locality.

Description (Figs. 1–7).

Adult female (Fig. 1A). Body typical for the genus comprising dorsal cephalothoracic shield, free fourth pedigerous somite, genital complex, and 1-segmented abdomen. Total body length 2.73 mm measured from mid-anterior margin of frontal plate to posterior end of caudal rami, excluding caudal setae; adult female 1.1 times longer than total body length of young female (Fig.1B). Dorsal cephalothoracic shield longer than wide (1.32 × 0.93 mm) with slightly convex lateral margins, posterior part about 2 times wider than anterior; frontal plate narrow, bearing pair of large lunules ventrally, ornamented with strip of narrow marginal membrane; thoracic zone of shield slightly wider than long (0.69 × 0.75 mm) with posterior margin forming posterior sinuses on either side, each sinus bearing flap-like hyaline membrane, posterior edge of thoracic zone extending beyond posterior margins of lateral zones. Dorsal cephalothoracic shield comprising about 48% of total body length. Fourth pedigerous somite sub-trapezoidal, wider than long (0.17 × 0.31 mm), distinctly separated from cephalothorax and genital complex. Genital complex longer than wide (0.82 × 0.59 mm), subrectangular with parallel lateral margins; anterolateral

corners rounded, posterolateral corners distinctly lobate; genital complex length about 60% length of cephalothorax; posteroventral margin with pair of flap-like processes concealing copulatory pores (Fig. 1C). Free abdomen (Fig. 1A, C) unsegmented, about 1.9 times longer than wide (0.34 × 0.18 mm), with parallel lateral margins. Combined length of genital complex and abdomen comprising about 87% of cephalothorax length. Caudal ramus subrectangular, longer than wide (0.10 × 0.06 mm), armed with 6 plumose setae and ornamented with fine setules along inner margin.

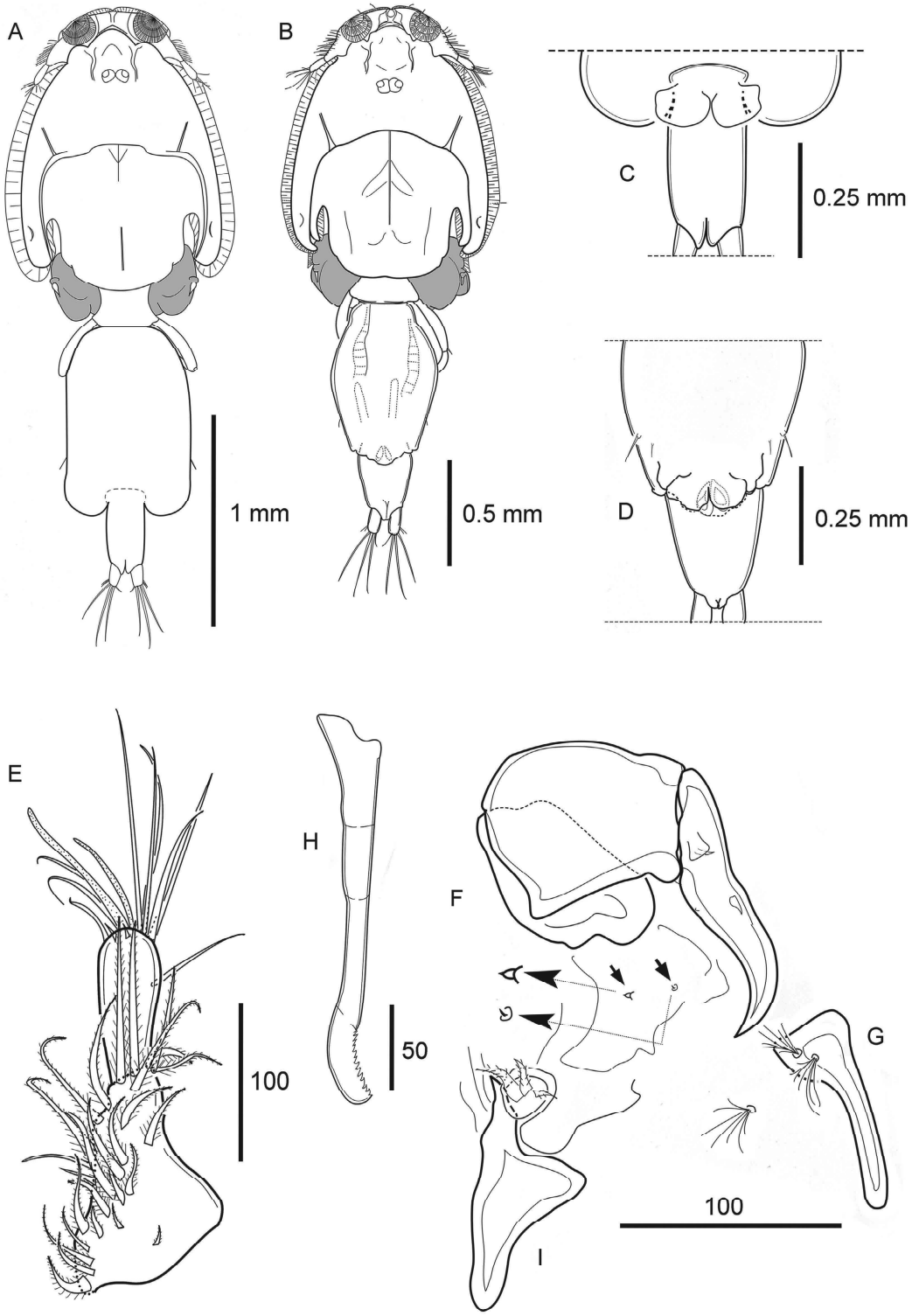

FIGURE 1. *Caligus izmiriensis* sp. nov. A. Adult female habitus (dorsal), B. Young adult female habitus (dorsal), C. Pair of flap-like processes on posteroventral margin of adult female genital complex, D. The same processes on young adult female genital complex, E. Antennule, F. Antenna; minute papilla-like process with tiny denticle at apex and single sensilla on ventral cephalothoracic surface(arrows), G. Postantennal process, H. Mandible, I. Maxillule.

Young adult female (Fig. 1B). Total body length 2.49–2.51 mm (n = 2). Dorsal cephalothoracic shield subrectangular with convex lateral margins, slightly longer than wide (1.28–1.34 × 0.93–0.95 mm); thoracic zone of shield slightly wider than long (0.70–0.72 × 0.76–0.79 mm), comprising about 55% of overall length of cephalothorax. Dorsal cephalothoracic shield comprising about 50% of total body length. Fourth pedigerous somite sub-trapezoidal, wider than long (0.13–0.15 × 0.33–0.34 mm), distinctly separated from cephalothorax and genital complex. Genital complex longer than wide (0.77–0.83 × 0.51–0.56 mm), elongate with convex lateral margins; maximum width in middle, about 1.5 times greater than width at posterior end; posterolateral corners indented, posterior margin v-shaped and extending back over anterior surface of abdomen (Fig. 1B). Oviducts and cement glands visible inside genital complex, posteroventral margin with pair of flap-like processes concealing copulatory pores and partially concealing pair of attached spermatophores (Fig. 1D). Free abdomen (Fig. 1B, D) 1-segmented, longer than wide (0.36–0.41 × 0.26–0.28 mm), tapering posteriorly, anterior part about 2 times wider than posterior, lateral margins more-or-less linear. Combined length of genital complex and abdomen comprising about 88% of cephalothorax length. Caudal ramus subrectangular, about 2 times longer than wide (0.12–0.13 × 0.06–0.07 mm), armed with 6 plumose setae.

Antennule (Fig. 1E) 2-segmented; proximal segment about 1.4 times longer than distal segment, armed with 25 plumose setae along anteroventral surface plus 2 naked unequal dorsal setae; distal segment cylindrical, about 2.5 times longer than wide, armed with 1 subterminal seta on posterior margin and 11 naked setae plus 2 aesthetascs around apex.

Antenna (Fig. 1F) uniramous, 3-segmented; proximal segment lacking posterior process; middle segment subrectangular, 1.5 times longer than wide and unarmed; distal subchela tapering towards sharply pointed curved claw, armed with small distal seta located at mid-length and large, papilliform, cuticular swelling proximally bearing tiny apical seta. Minute papilla-like process bearing tiny denticle at apex and single sensilla present on ventral cephalothoracic surface near proximal segment (Fig. 1F, arrows). Postantennal process (Fig. 1G) with almost straight, blunt-tipped tine and ornamented with 2 papillae each bearing 7 sensillae, plus similar papilla with 7 sensillae located on adjacent ventral cephalothoracic surface, near base of postantennal process. Mandible (Fig. 1H) stylet-like, armed with 12 inner teeth distally. Maxillule (Fig.1I) comprising anterior papilla carrying 3 unequal pinnate setae and posteriorly-directed dentiform process with rounded tip. Maxilla (Fig. 2A) 2-segmented, proximal segment (lacertus) large, unarmed; slender distal segment (brachium) with large subterminal hyaline membrane (flabellum) on inner margin plus short canna and long calamus distally; canna ornamented with strips of serrated membranes bilaterally, calamus with spirally arranged strips of serrated membrane. Maxilliped (Fig. 2B) subchelate; protopodal segment (corpus) elongate and ornamented with single pore on myxal area, distal subchela divided by partial surface suture delimiting terminal claw; subchela bearing lateral seta plus second seta at base of terminal claw. Sternal furca (Fig. 2C) (SV-IZM1) with subcircular box and straight, blunt-tipped tines positioned immediately next to each other.

Leg 1 (Figs. 2D, E, 3A) biramous with 2-segmented exopod and vestigial endopod (apparently 2-segmented). Sympod bearing lateral and inner plumose setae; ornamented with patch of tiny spinules on ventral surface (Fig. 2D). First exopodal segment robust, ornamented with row of setules along posterior margin; armed with small spine at outer distal corner. Distal exopodal segment (Figs. 2E, 3A) with 3 plumose setae posteriorly plus 4 terminal elements; outermost element (spine 1) smallest; middle 2 elements (spines 2 and 3) more or less equal in length, each bearing slender, spiniform accessory process; innermost element (seta 4) distinctly longer than spines, about equal to length of segment.

Leg 2 (Figs. 2F, 3B) biramous, with distinct coxa and basis; coxa short, bearing long plumose inner seta and with sensilla on ventral surface; basis armed with short naked seta on outer distal corner plus extensive marginal membrane along posterior margin and sensilla near middle of posterior margin. Exopod (Figs. 2F, 3C) (SV-IZM2) 3-segmented; first segment with inner plumose seta, outer spine slightly curved, extending obliquely across surface of ramus and almost reaching posterior margin of second segment, spine with pecten-like membrane at base; segment ornamented with row of setules along inner margin; second exopodal segment smallest, with inner plumose seta and minute outer spine (Figs. 2F arrow, 3C arrow) (SV-IZM2) extending parallel to outer margin of segment: third exopodal segment with 3 spines and 5 inner plumose setae; proximalmost spine simple and smallest (Figs. 2F arrowhead, 3C arrowhead), second spine with marginal membrane along inner margin, and terminal spine with outer marginal membrane and row of fine setules along inner margin. Endopod (Figs. 2F, 3D) 3-segmented; first segment bearing inner plumose seta; second segment elongate, armed with 2 inner plumose setae, and ornamented

with rows of fine setules along outer edge; third segment smallest, with 6 distal plumose setae plus tuft of fine setules proximally on outer margin.

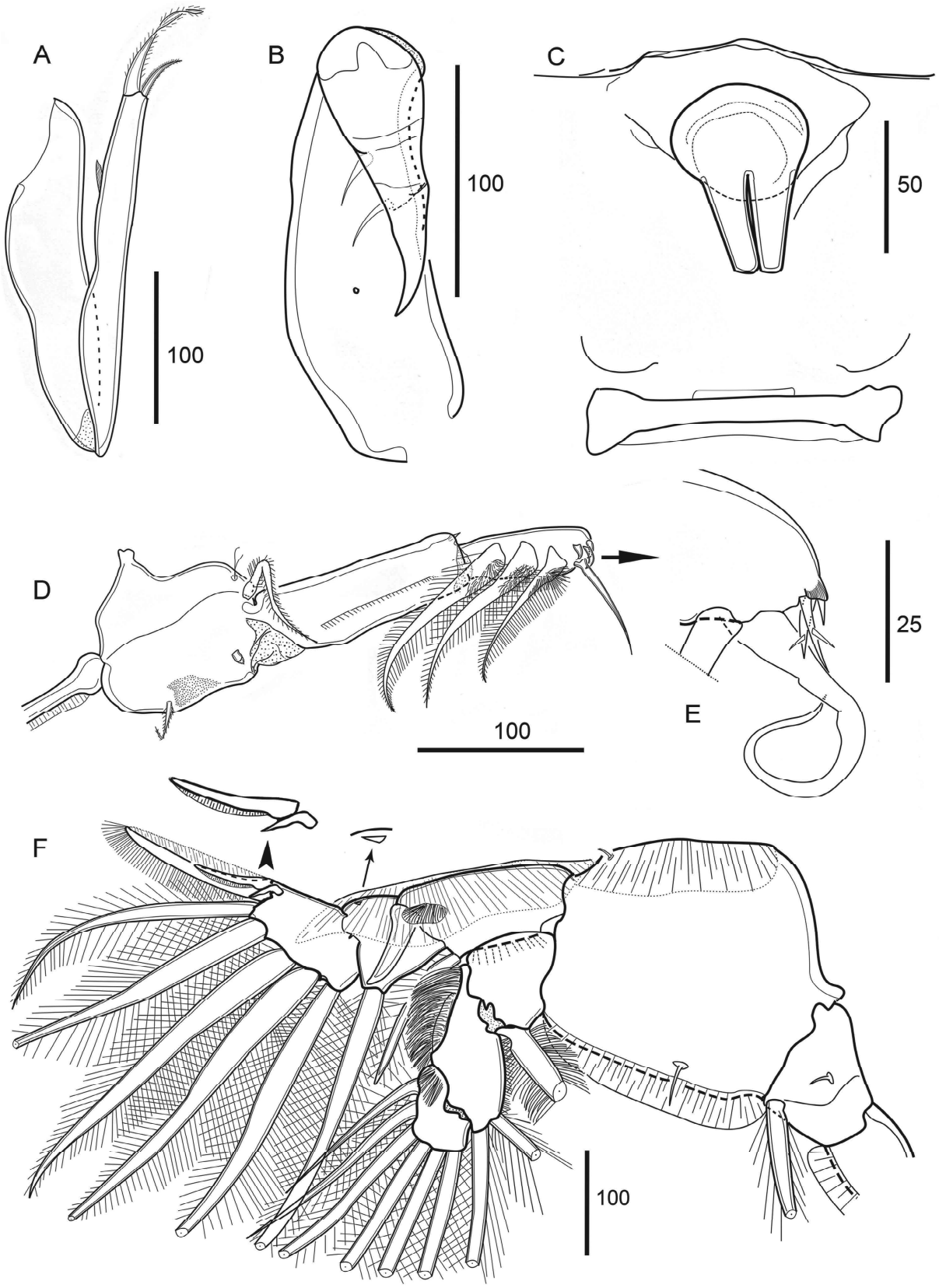

FIGURE 2. *Caligus izmiriensis* sp. nov. Adult female. A. Maxilla; B. Maxilliped; C. Sternal furca and intercoxal sclerite of leg1; D. Leg 1; E. Terminal elements on distal exopodal segment of leg 1; F. Leg 2.

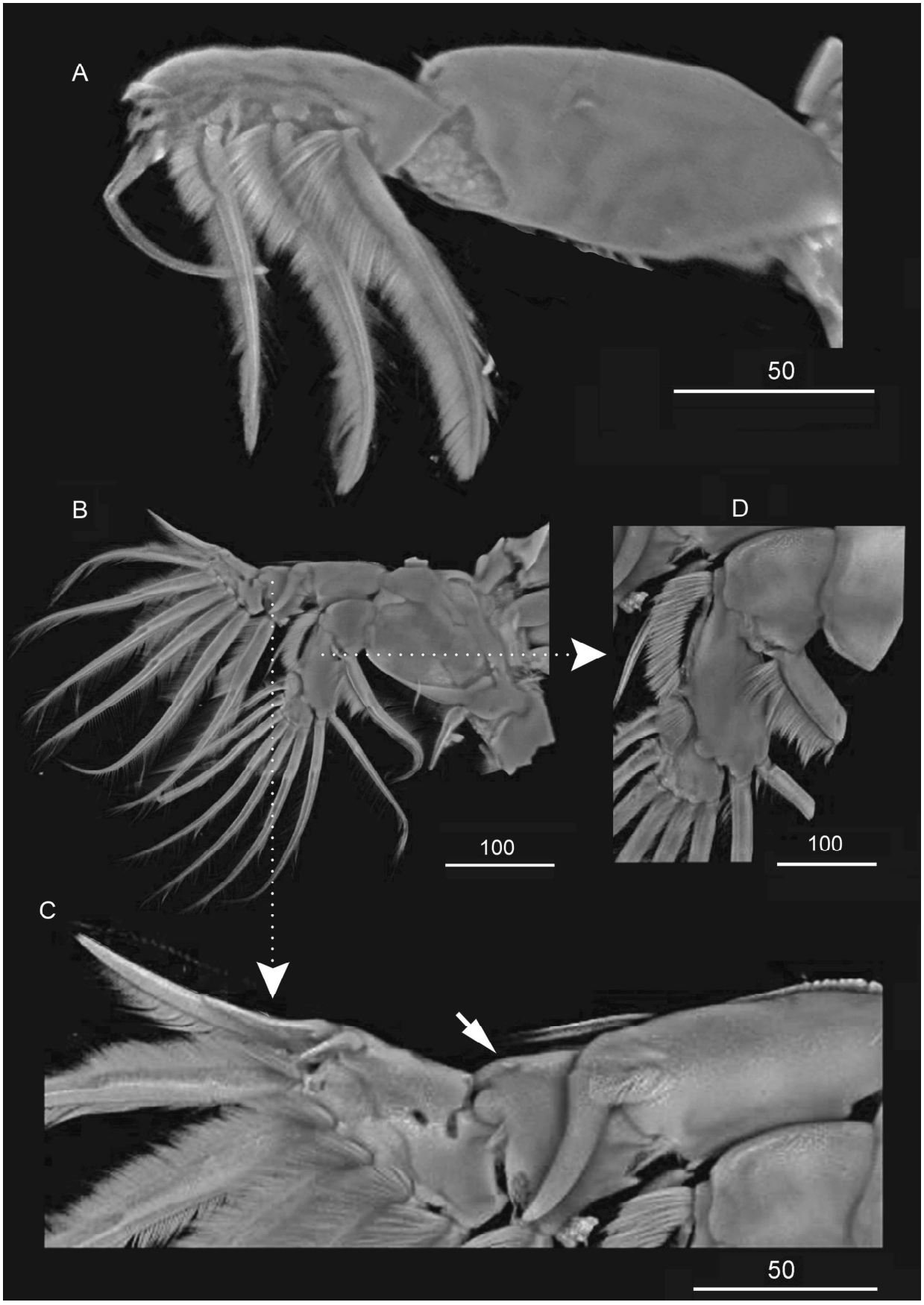

FIGURE 3. *Caligus izmiriensis* sp. nov. Adult female. Drishti applied confocal laser scanning microscope images (CLSM-D). A. Exopod of leg 1; B. Leg 2; C. Spines on exopodal segments of leg 2, minute outer spine on second exopodal segment arrowed; D. Ornamentations on endopodal segments of Leg 2.

Leg 3 (Figs. 4A, 5A) biramous with rami separated by large gap; flattened apron-like sympod carrying extended strips of hyaline membrane along lateral and free posterior margins plus rows of spinules on outer surface and corrugated pad on mid-ventral surface (Figs. 4A, 5B); armed with inner coxal seta and outer basal seta positioned at base of exopod. Intercoxal sclerite narrow, with flap of hyaline membrane along posterior margin. Exopod 3-segmented: first segment with straight outer spine not reaching articulation between second and third segments, pecten-like strip of membrane present at base of outer spine; second segment with slender outer spine and inner plumose seta; third segment with 3 subequal outer spines and 4 short pinnate setae. Endopod 2-segmented; first segment extending laterally to form elongate velum closing off gap between bases of rami, segment armed with long inner pinnate seta; second endopodal segment bearing 6 pinnate setae and ornamented with row of long setules along outer margin.

Leg 4 (Figs. 4B, 5C) uniramous. Slender protopodal segment with outer distal seta. Exopod 2-segmented (Figs. 4C, 5C); first segment armed with slender outer distal spine ornamented with strips of membrane bilaterally; second segment with 1 lateral spine and 3 distal margin spines increasing in length from outer to inner, middle spine extending beyond middle of inner spine; inner and middle spines each with pecten at base. Spine (Roman numerals) and seta (Arabic numerals) formula of rami of legs 1–4 as follows:

	Exopod	Endopod
Leg 1	I-0; III,1,3	vestigial
Leg 2	I-1; I-1; II,I,5	0–1; 0–2; 6
Leg 3	I-0; I-1; III,4	0–1; 6
Leg 4	I-0; I,III	absent

Leg 5 (Fig. 4D) located ventrally near posterolateral corners of genital complex and represented by 2 papillae; outer (protopodal) papilla bearing single plumose seta; inner (exopodal) papilla carrying 2 equal plumose setae: seta on outer papilla longest.

Adult male (Fig. 6A) Total body length 1.93–2.08 mm (*n* = 2); dorsal cephalothoracic shield slender, longer than wide (1.05–1.10 × 0.70–0.72 mm) excluding hyaline membranes, narrowing anteriorly and with broad marginal membranes on lateral zones. Thoracic zone of shield slightly wider than long (0.57–0.58 × 0.59–0.60 mm) and comprising about 54% of cephalothorax length. Fourth pedigerous somite short, much wider than long (0.05–0.06 × 0.23–0.24 mm) and distinctly separated from cephalothorax and genital complex. Genital complex elongate, longer than wide (0.40–0.43 × 0.26–0.27 mm), lateral margins indented anteriorly, with slightly convex lateral margins and straight posterior edge, about 38% of cephalothorax length. Abdomen 2-segmented; first free abdominal somite subrectangular, about 1.4 times wider than long (0.14–0.17 × 0.20–0.24 mm), anterior part slightly wider than posterior part; anal somite longer than wide (0.22–0.27 × 0.14–0.17 mm) and about 1.57 times longer than preceding abdominal somite: combined length of genital complex and entire abdomen about 72% of length of cephalothorax. Caudal rami slightly longer than wide (0.10–0.13 × 0.06–0.08 mm), about 45% of anal somite length, carrying 6 plumose setae.

Antennule as in female. Antenna (Figs. 6B,C, 7A) 3-segmented; proximal segment elongate, with corrugated adhesion pad distally on ventral surface; middle segment largest with corrugated pads on medial and distal surfaces (Figs. 6C, 7A) (SV-IZM3); posteriorly-directed distal segment with 2 fused subrectangular and overlapping plates (Figs. 6C, 7A), first (upper) plate ornamented with slightly curved cuticular ridge (Fig. 7A arrow), second plate subrectangular and spatulate, armed with 2 slender basal setae. Postantennal process (Fig. 6D) more curved than that of female and with tapering tine. Maxillule (Fig. 6E) comprising tapering posterior dentiform process and anterior papilla bearing 3 subequal naked setae. Mandible and maxilla as in female. Maxilliped (Figs. 6F, 7B, C) with massive corpus produced into large conspicuous triangular process in myxal area plus small subtriangular process proximally (Figs. 6G, 7B, C arrowheads) (SV-IZM4); distal surface of small myxal process covered with slight corrugations (Fig. 6G). Subchela armed with 2 small sensilla plus another longer seta at base of claw (Figs. 6F, 7B arrows). Sternal furca (Figs. 6H, 7C) with tines positioned immediately next to each other, tines about 1.3 times longer than tines of female.

Legs 1–4 as in female. Leg 5 (Fig. 6I) represented by 2 papillae located on posterolateral margin of genital complex: outer papilla with 1 long plumose seta and inner (exopodal) papilla with 2 equal plumose setae. Leg 6 (Fig. 6I) represented by single papilla on margin of genital operculum, bearing 2 equal pinnate setae.

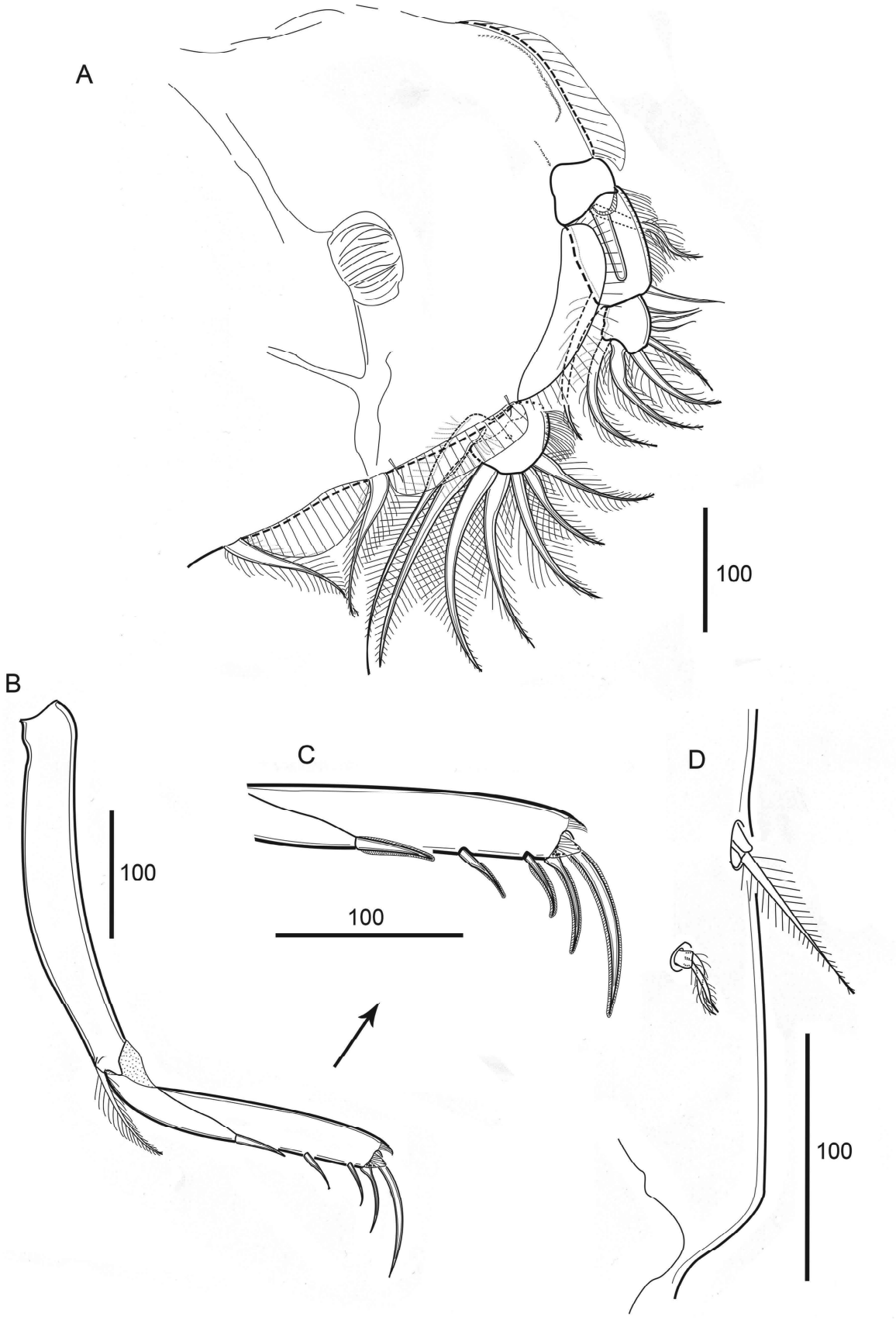

FIGURE 4. *Caligus izmiriensis* sp. nov. Adult female. A. Leg3; B. Leg 4; C. Exopodal spines of leg 4; D. Leg 5.

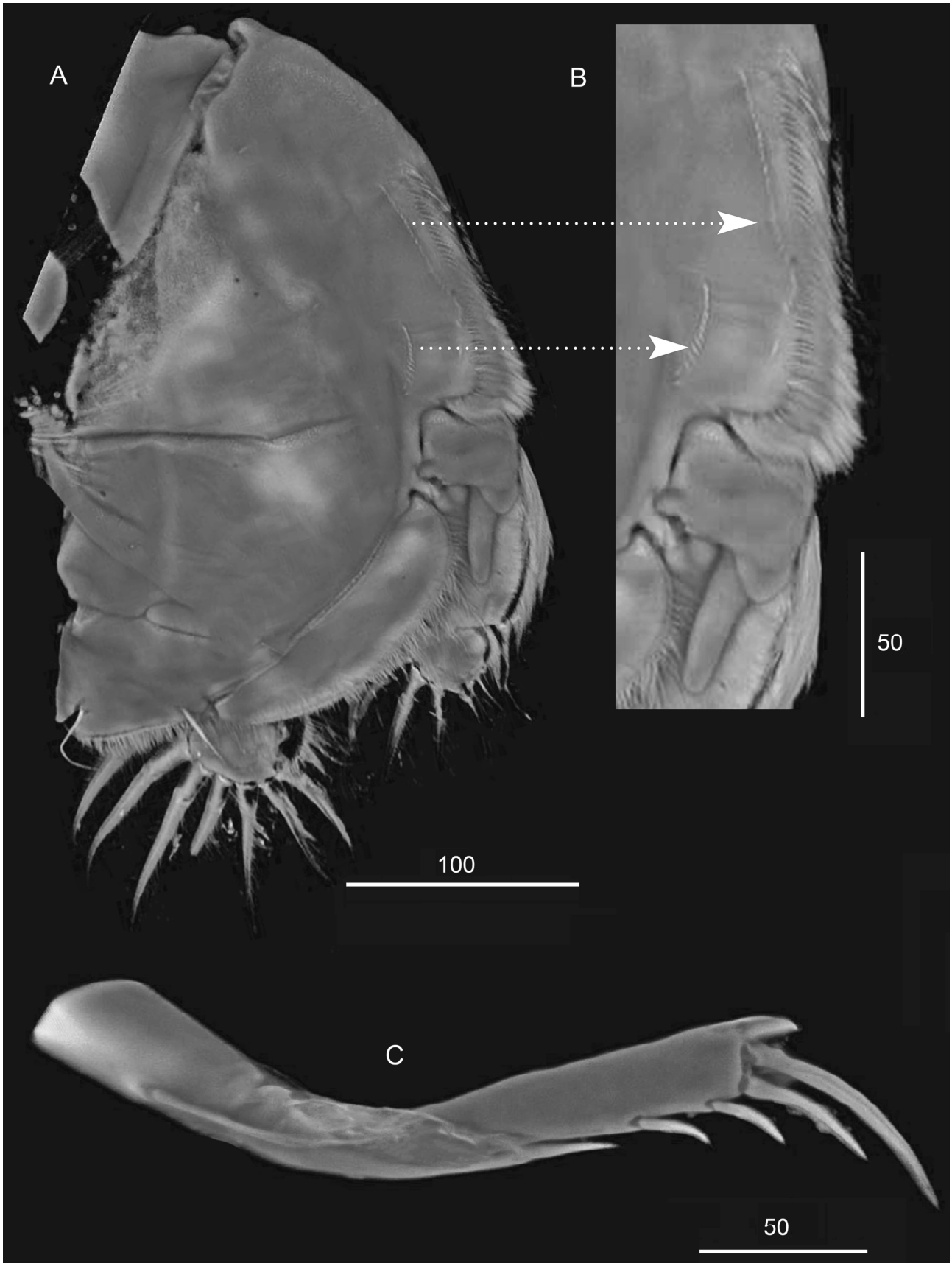

FIGURE 5. *Caligus izmiriensis* sp. nov. Adult female. Drishti applied confocal laser scanning microscope images (CLSM-D). A. Leg 3; B. Spinular ornamentations on ventral surface of Leg 3 outer apron; C. Leg 4.

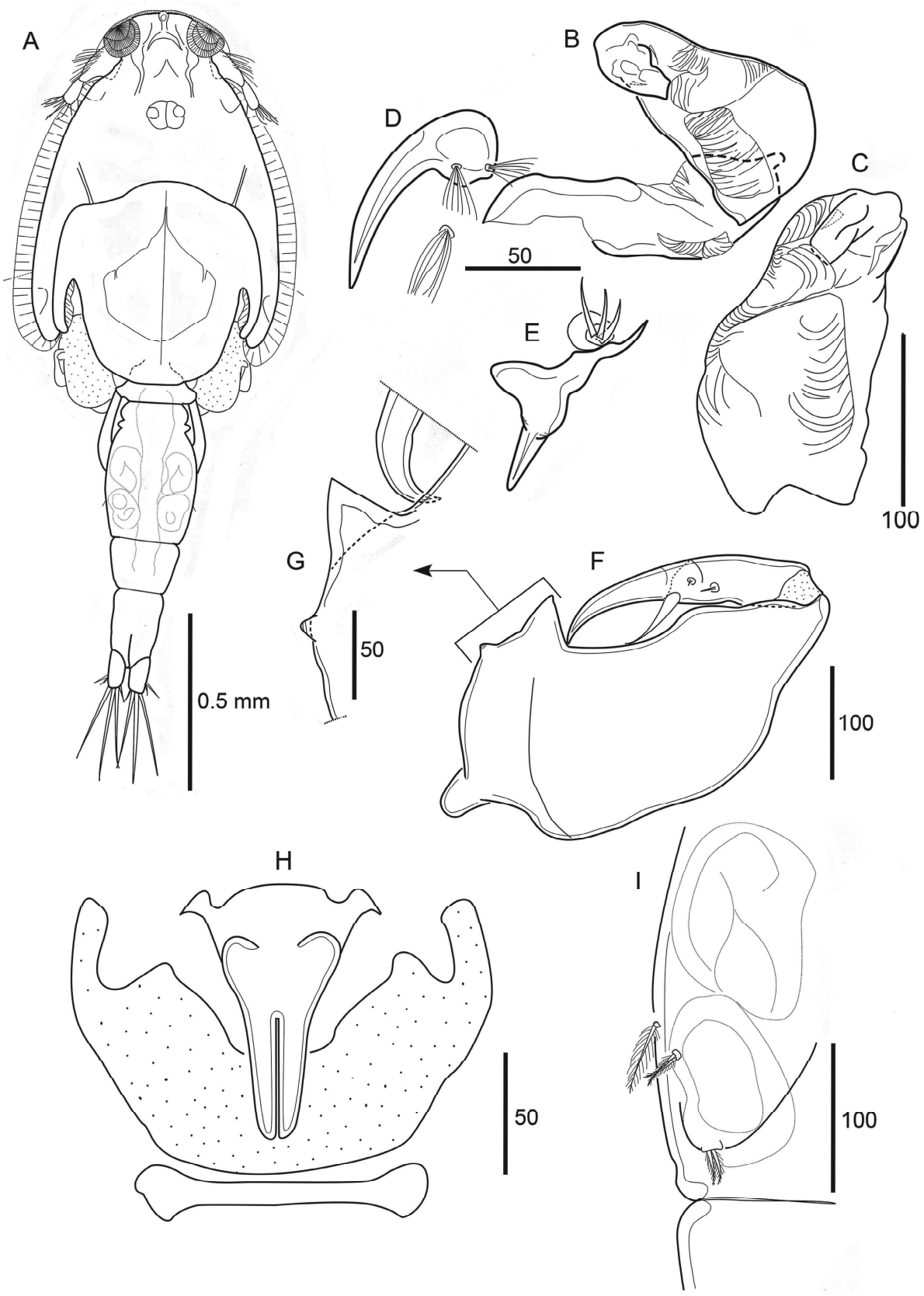

FIGURE 6. *Caligus izmiriensis* sp. nov. Adult male. A. Habitus dorsal; B. Antenna; C. Middle and terminal segments of antenna from different angle; D. Postantennal process; E. Maxillule; F. Maxilliped; G. Details of myxal processes; H. Sternal furca and intercoxal sclerite of leg 1, in situ; I. Legs 5 and 6.

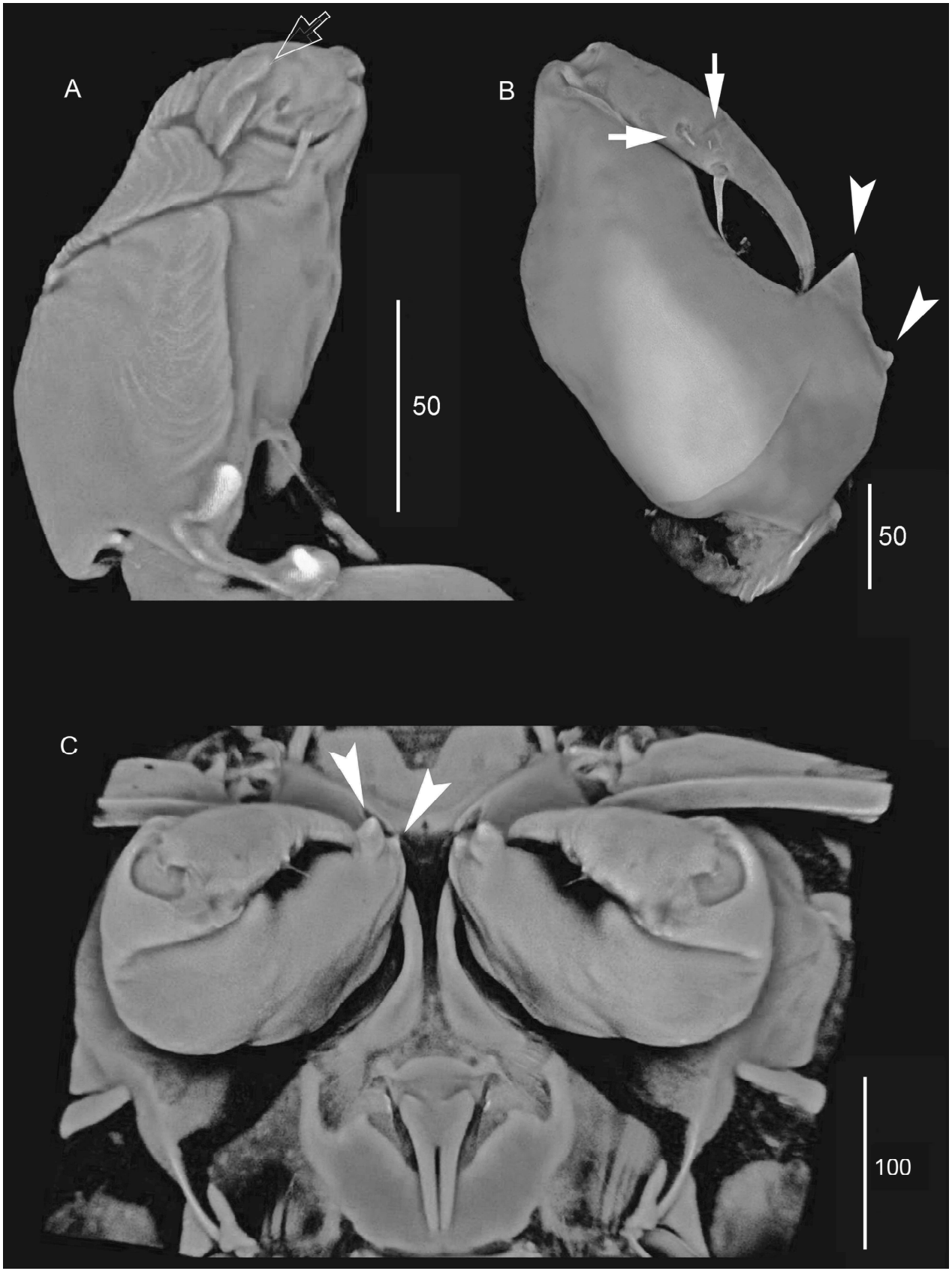

FIGURE 7. *Caligus izmiriensis* sp. nov. Adult male. Drishti applied confocal laser scanning microscope images (CLSM-D). A. Middle and distal segments of the antenna, overlapping plates on terminal segment arrowed; B. Maxilliped (lateral view) with two triangular myxal processes (arrowheads) on corpus and 2 small sensillae (arrows) on subchela; C. Maxillipeds from a different angle showing two myxal processes (arrowheads) and position of sternal furca.

Remarks

The new species, *C. izmiriensis* sp. nov., displays several distinctive character states, the most prominent of which is the unusual form of the sternal furca. In both sexes the tines of the sternal furca are well defined but closely adpressed to each other along their entire length. This form of sternal furca is unique within the genus, although a similar, highly modified form of furca was reported for *Caligus bocki* Heegaard, 1943 by Heegaard (1943) who described this species as having the tines of the furca fused to form a tapering median spine. Solely based on this character Heegaard (1943) proposed a new subgenus *Subcaligus* Heegaard 1943 to accommodate *C. bocki*. This subgenus, based on a single autapomorphy, has not gained acceptance and was not even mentioned by Dojiri & Ho (2013) in their phylogenetic analysis of caligid genera. In the related caligiform genus *Dissonus* Wilson, 1906 the sternal furca is modified as a short tapering median stylet in one species, *D. manteri* Kabata, 1966, but in other congeneric species the furca is either lacking or has the typical structure with paired tines (Boxshall *et al.* 2008). In *Caligus*, as in *Dissonus*, such a level of variation in sternal furca expression can be readily accommodated within the genus, and we treat the subgenus *Subcaligus* as a junior subjective synonym of *Caligus*. *Caligus bocki* lacks plumose setae on the posterior margin of the distal exopodal segment of leg 1 (Heegaard 1943) and the absence of these setae led (Boxshall & El-Rashidy 2009) to place *C. bocki* in the *C. productus*-group of species. The possession of 3 plumose setae on the posterior margin serves to distinguish *C. izmiriensis* sp. nov. from *C. bocki*.

Caligus izmiriensis sp. nov. shares the same unusual form of leg 1 as *Metacaligus yucatanensis* Suárez-Morales, Kim & Escamilla, 2012 and a second new species from Turkish coastal waters, which is described below as *C. sarosensis* sp. nov. Detailed comparison of the two new species and *M. yucatanensis* is given below in the Remarks section for *C. sarosensis* sp. nov. Another remarkable feature of *C. izmiriensis* sp. nov. is the presence of paired flaps on the posteroventral surface of the genital complex of the female. Their function appears to be to partially conceal and presumably protect the attached spermatophores which discharge their contents into the copulatory pores of the female. As far as we can ascertain, these flaps are unique to *C. izmiriensis* sp. nov. within the genus. Their absence from other caligid species that spend extended periods of time swimming free in the plankton away from the host (i.e. species included in the *Caligus undulatus*-group) suggests that they are not associated with a more planktonic life style.

The shape of the genital complex differs remarkably between the young female and the holotype female, and we infer that this difference indicates that the holotype has undergone a post-mating metamorphosis, which is common in female caligids (see Boxshall & Özak 2022). In *C. izmiriensis* sp. nov. this metamorphosis involves a marked change in the shape of the genital complex from having convex lateral margins with the maximum width about in the middle to becoming subrectangular with parallel lateral margins, plus the development of distinct lobes at the posterolateral corners. In the young female the posterolateral corners are slightly indented and the posterior margin is v-shaped.

Mating in caligid copepods has been observed to take place on the surface of the host (Anstensrud 1992) but mating behavior is currently unknown for the members of the *Caligus undulatus*-group. However, the presence in the plankton of both young females carrying recently deposited spermatophores and adult females that are postmetamorphic, suggests that the metamorphosis may take place away from any host in these planktonic forms.

***Caligus sarosensis* sp. nov.**

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Type material

Holotype adult female stored in collections of the Natural History Museum, London (Reg, No, NHMUK 2022. 200). Type Locality: Stn. SABSW1**,** Gulf of Saros, Türkiye (40°37′52.52″N 26°43′39.70″E): depth 60 m; date 20.02.2019.

Etymology: The species name refers to the Gulf of Saros (Çanakkale, Türkiye) where the material was collected.

Description

Adult female [Figs. 8–14]. Body (Figs. 8A, 9A) comprising cephalothorax, free fourth pedigerous somite, genital complex, and 1-segmented abdomen. Total body length 2.06 mm including caudal rami. Dorsal cephalothoracic shield

longer than wide, 1.06 × 0.77, narrowing anteriorly towards narrow frontal plate bearing pair of large lunules; lateral margins convex, with broad hyaline membrane around lateral margins. Cephalothorax comprising approximately half of total body length. Thoracic zone of shield about as long as wide, 0.56 × 0.63, forming large posterior sinuses on either side; posterior margin extending beyond posterior end of lateral zones. Fourth pedigerous somite about 2.6 times wider than long (0.10 × 0.26). Genital complex (Figs. 8A, B, 9A) 0.54 × 0.38, subrectangular, with parallel lateral margins and weakly lobate posterolateral corners, anterior part indented, forming folded narrow transition between fourth pedigerous somite and genital complex; lateral indentation and partial surface suture present on anteroventral surface of genital complex at about one third of complex length (Figs. 8B black arrows, 9B white arrows). Two subrectangular flap-like processes on medioventral surface either side of median line (Figs. 8B, 9B, 9C arrowheads) (SV-SAR5), left and right processes subequal (41 × 74 μm, 45 × 74 μm, respectively). Posteroventral surface of genital complex swollen and produced into lobate posterolateral corners overlying oviduct openings (egg sac attachment area) (Figs. 8C, 9D). Free abdomen 1-segmented, slender, 2.3 times longer than wide (0.32 × 0.14), genital complex and abdomen fused laterally, abdomen with numerous overlapping cuticular folds anterolaterally (Figs. 8C black arrows, 9D white arrows) (SV-SAR6): abdomen with paired swellings on anteroventral surface either side of mid-line, inner margins of each swelling connecting to another digitiform cuticular medial swelling carrying two tiny, triangular papilliform processes (Figs. 8C arrowheads, 9D arrowheads) (SV-SAR6), mid-anteroventral surface ornamented with 2 sensilla (Figs. 8C long arrows, 9D long arrows) (SV-SAR6). Combined length of genital complex and abdomen about 84% of length of cephalothorax. Caudal ramus (Figs. 8C, 9D) subrectangular, about 1.6 times longer than wide (0.08 × 0.05), bearing 6 plumose setae plus tuft of spinules along inner margin.

Antennule (Fig. 8D) 2-segmented; proximal segment about 1.7 times longer than slender distal segment; proximal segment armed with 25 plumose setae anteroventrally near anterior margin plus 2 naked dorsal setae (Fig. 8D arrowheads); slender distal segment carrying 1 subterminal seta on posterior margin and 11 terminal setae plus 2 aesthetascs (Fig. 8D arrows). Antenna (Figs. 10A, 11A) 3-segmented; proximal segment without posterior process; middle segment subrectangular; distal segment forming acutely curved claw, with minute distal seta on outer margin at mid-length (Figs. 10A arrowhead, 11A arrowhead) plus proximal seta. Postantennal process (Figs. 10B, 11B) weakly curved, carrying accessory tine proximally (Fig. 11B arrowhead) plus two papillae on basal part, each with 6 sensilla; similar papilla with 6 sensilla present on adjacent ventral surface. Maxillule (Figs. 10C, 11C) comprising slightly curved dentiform posterior process, anterior papilla bearing 1 long and 2 small setae; posterior part of dentiform process ornamented with narrow marginal flange bilaterally. Mouth tube (Fig. 10D) approximately 1.1 times longer than wide. Distal margins of labium and labrum fringed with hyaline membrane. Labrum with submarginal row of minute denticles. Mandible (Fig. 10E) curved distally and bearing 12 inner teeth near apex. Maxilla (Fig. 10F, 11D) 2-segmented, brachiform; proximal segment (lacertus) unarmed; distal segment (brachium) armed with small subdistal outer hyaline membrane (flabellum) plus 2 elements at apex (short canna and long calamus) (Fig 11E), canna with bilaterally serrated hyaline membrane, calamus longer than canna and ornamented with spirally arranged strips of serrated membrane (Figs. 10F, 11E). Maxilliped (Figs. 10G, 11F) comprising large proximal segment (corpus) and distal subchela representing fused endopodal segments plus curved terminal claw; subchela armed with small seta at base of claw, tip of claw extending almost to middle of corpus; myxal area smooth. Sternal furca (Fig. 10H) with short, straight, weakly divergent tines rounded at tip, tines with marginal flanges.

Leg 1 (Fig. 12A) biramous, with 2-segmented exopod and lobate vestigial endopod carrying minute denticle at apex (Fig. 12B). Sympod armed with lateral plumose seta and inner seta. First exopodal segment (Fig. 12A) bearing small spine at outer distal corner but lacking row of setules along free posterior margin (Figs. 12A, 14A). Distal exopodal segment (Figs. 12C, 14A) with 4 terminal elements (spines 1–3 and inner seta 4) on distal margin; spine 1 (outermost) shortest, middle 2 spines almost equal in length and each bearing single accessory process (Fig. 12C), seta 4 (innermost) about 4 times longer than middle two spines 2 and 3 and slightly longer than segment; posterior margin with three plumose setae (Fig. 14A), each distinctly longer than segment.

Leg 2 (Fig. 12D) biramous with 3-segmented rami. First exopodal segment with pinnate seta on inner margin and long spine at outer distal corner reflexed obliquely back across surface of second exopodal segment; second segment lacking outer spine, armed only with pinnate seta on inner margin (Figs. 12E, 14B): third exopodal segment with 5 inner plumose setae plus 3 spines; proximal outer spine (smallest) naked and slender (Figs. 12E,F, 14B arrow), middle spine with hyaline membrane bilaterally; terminal spine ornamented with hyaline membrane along outer margin and row of setules along inner margin (Figs. 12E, F, 14B). First endopodal segment armed with inner

plumose seta; second endopodal segment armed with 2 inner plumose setae and ornamented with rows of setules along outer and inner margins; third segment with 6 plumose setae and bearing tuft of setules proximal to outermost seta (Fig. 12G).

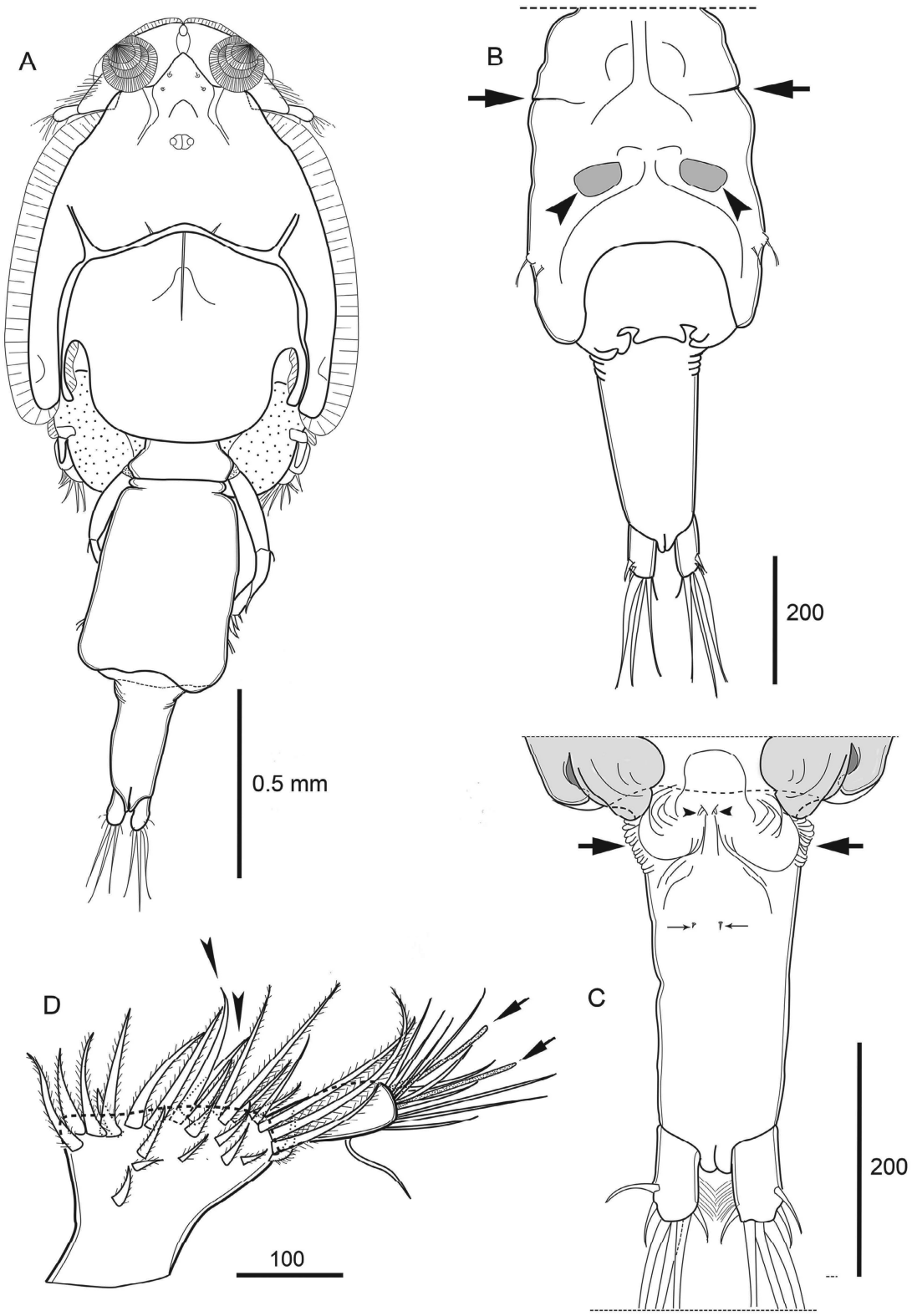

FIGURE 8. *Caligus sarosensis* sp. nov. Adult female. A. Habitus dorsal; B. Genitoabdomen (ventral) with partial surface suture on anteroventral surface of genital complex (arrows) and two subrectangular flap like processes (arrowheads); C. Abdomen (ventral) with overlapping cuticular folds (arrows) on anterolateral parts and digitiform cuticular medial swelling carrying two tiny triangular papilliform processes (arrowheads) plus 2 sensillae (long arrows) on mid-anteroventral surface; D. Antennule with 2 naked dorsal setae (arrowheads) on proximal segment and 2 aesthetascs (arrows) on distal segment.

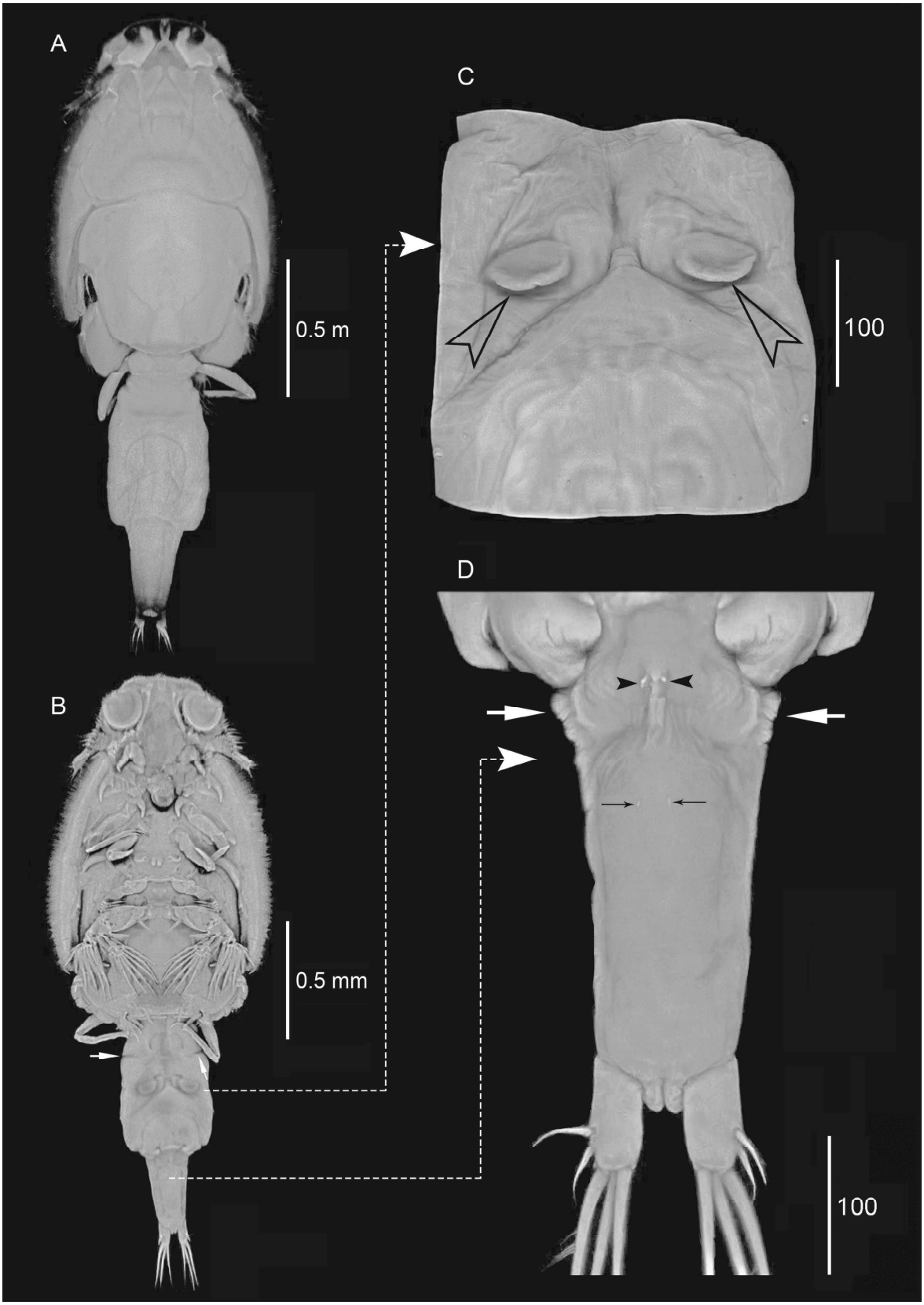

FIGURE 9. *Caligus sarosensis* sp. nov. Adult female. Drishti applied confocal laser scanning microscope images (CLSM-D). A. Habitus dorsal; B. Habitus ventral; C. Two subrectangular flap like processes (arrowheads) on either side of the medioventral surface of genital complex (arrowheads); D. Abdomen (ventral) with overlapping cuticular folds (white arrows) on anterolateral parts, digitiform cuticular medial swelling carrying two tiny triangular papilliform processes (arrowheads) and 2 sensillae (long black arrows) on mid-anteroventral surface.

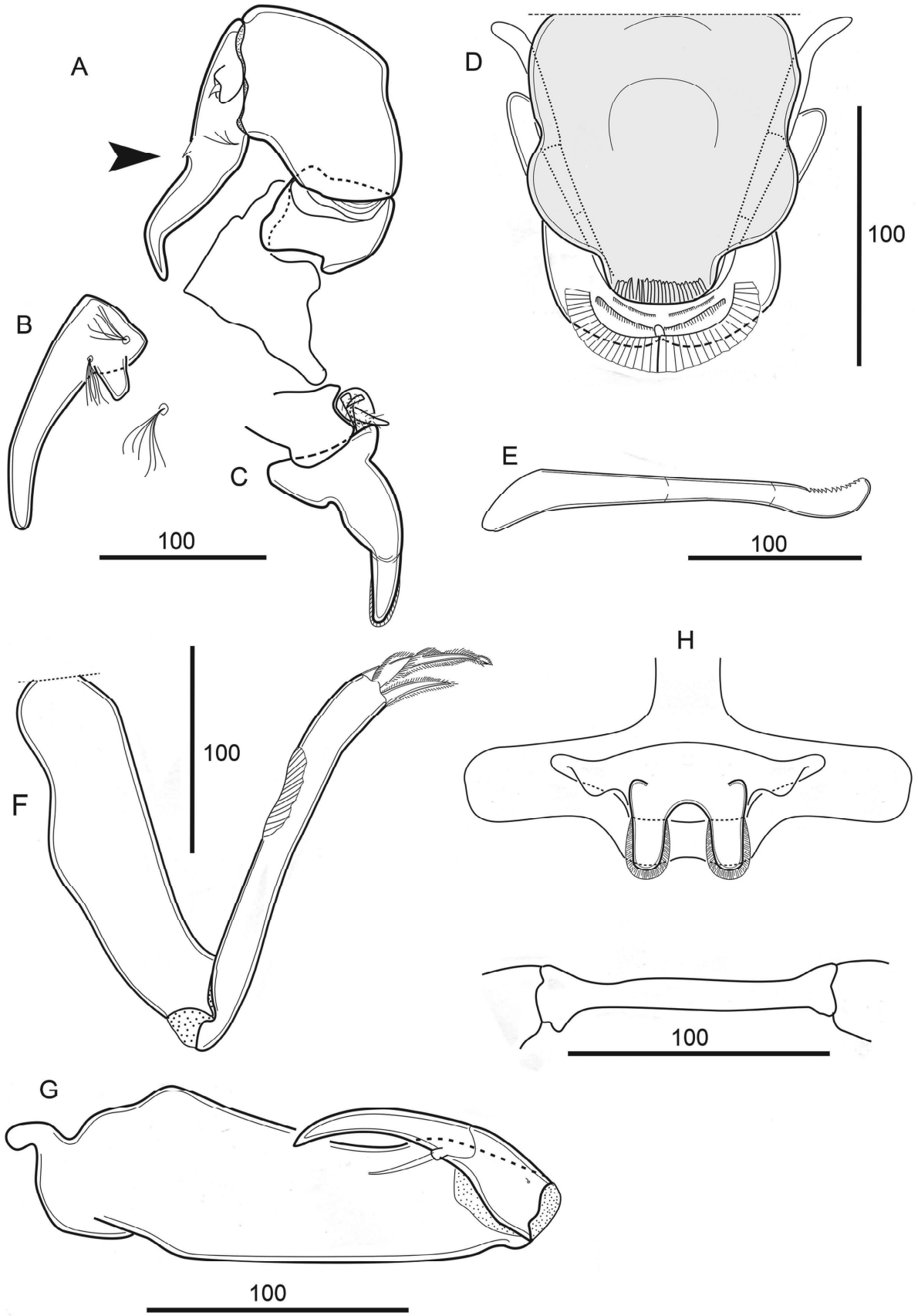

FIGURE 10. *Caligus sarosensis* sp. nov. Adult female. A. Antenna, minute distal seta (arrowhead) on outer margin at mid-length of terminal claw; B. Postantennal process; C. Maxillule; D. Mouth cone; E. Mandible; F. Maxilla; G. Maxilliped; H. Sternal furca and intercoxal sclerite of leg 1.

FIGURE 11. *Caligus sarosensis* sp. nov. Adult female. Drishti applied confocal laser scanning microscope images (CLSM-D). A. Antenna, minute distal seta (black arrowhead) on outer margin at mid-length of terminal claw; B. Postantennal process with accessory tine at base (white arrowhead); C. Maxillule; D. Maxilla; E. Distal segment of maxilla with spirally arranged strips of serrated membrane on calamus and bilaterally serrated membrane on canna; F. Maxilliped.

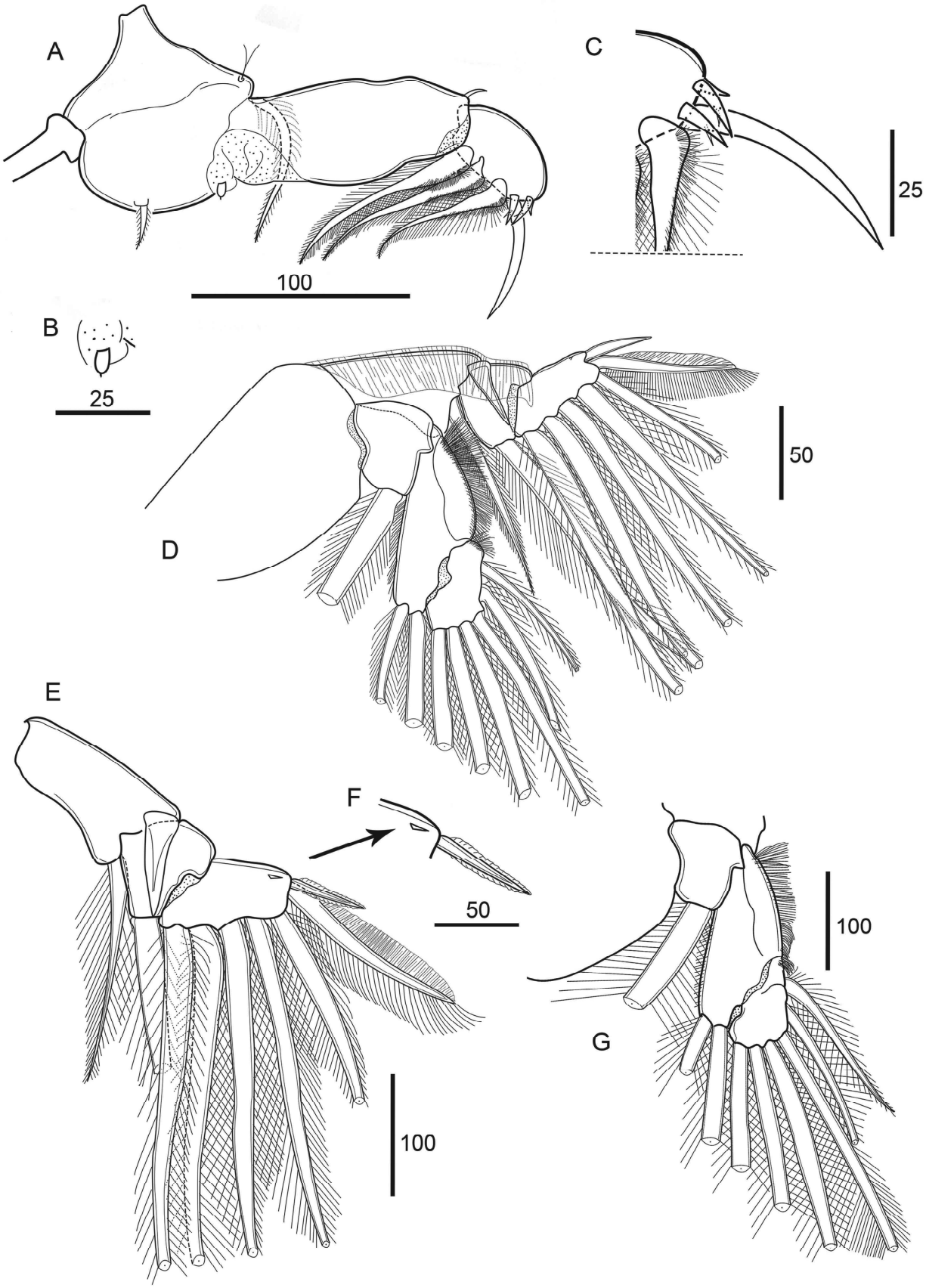

FIGURE 12. *Caligus sarosensis* sp. nov. Adult female. A. Leg 1 ; B. Endopod; C. Terminal elements on distal segment of leg 1; D. Leg 2; E. Exopod of leg 2; F. Proximal outer spine on third exopodal segment of leg 2; G. Endopod of leg 2.

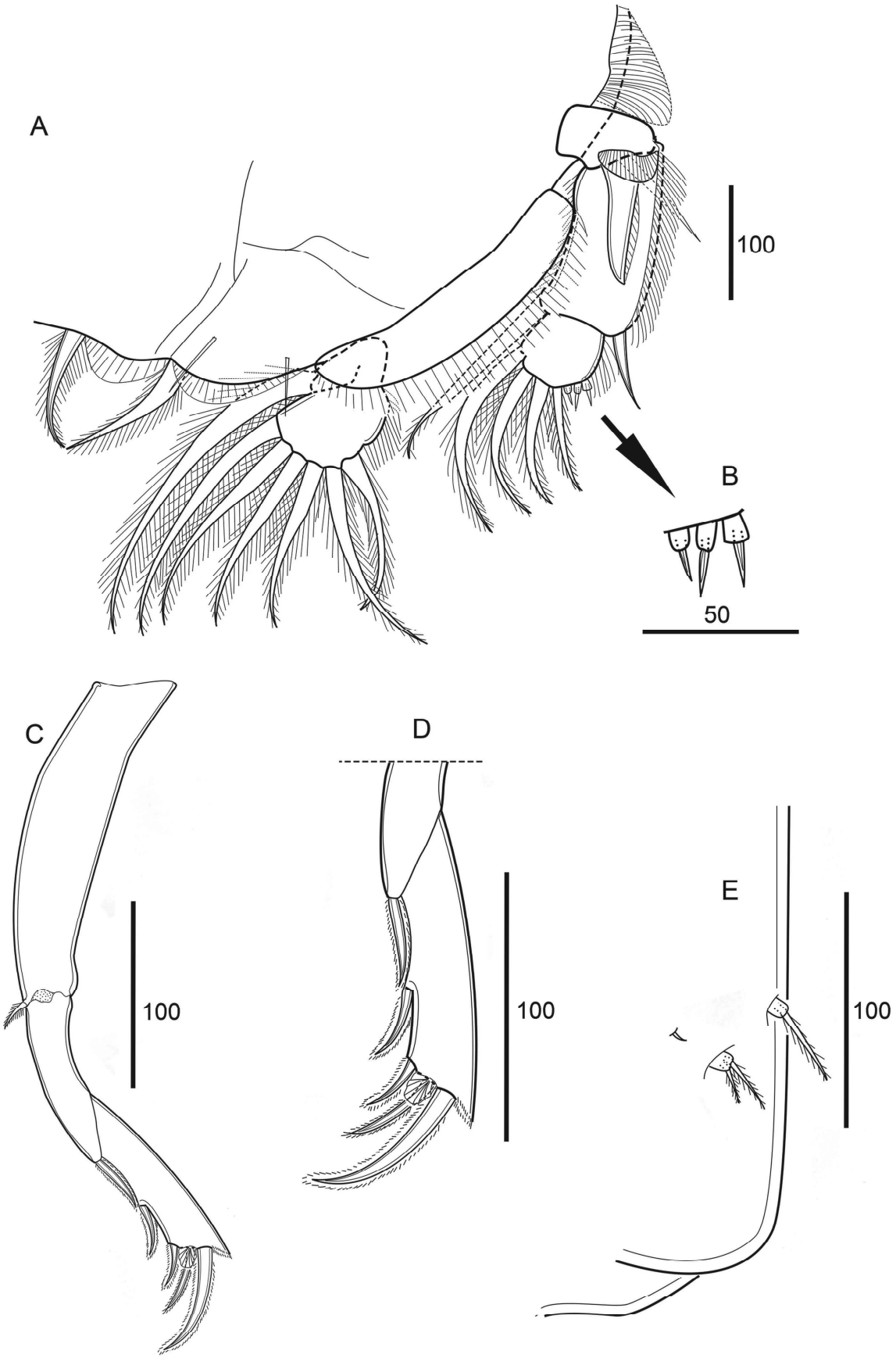

FIGURE 13. *Caligus sarosensis* sp. nov. Adult female. A. Leg 3; B. Outer spines on third exopodal segment of leg 3; C. Leg 4; D. Exopodal spines on leg 4; E. Leg 5.

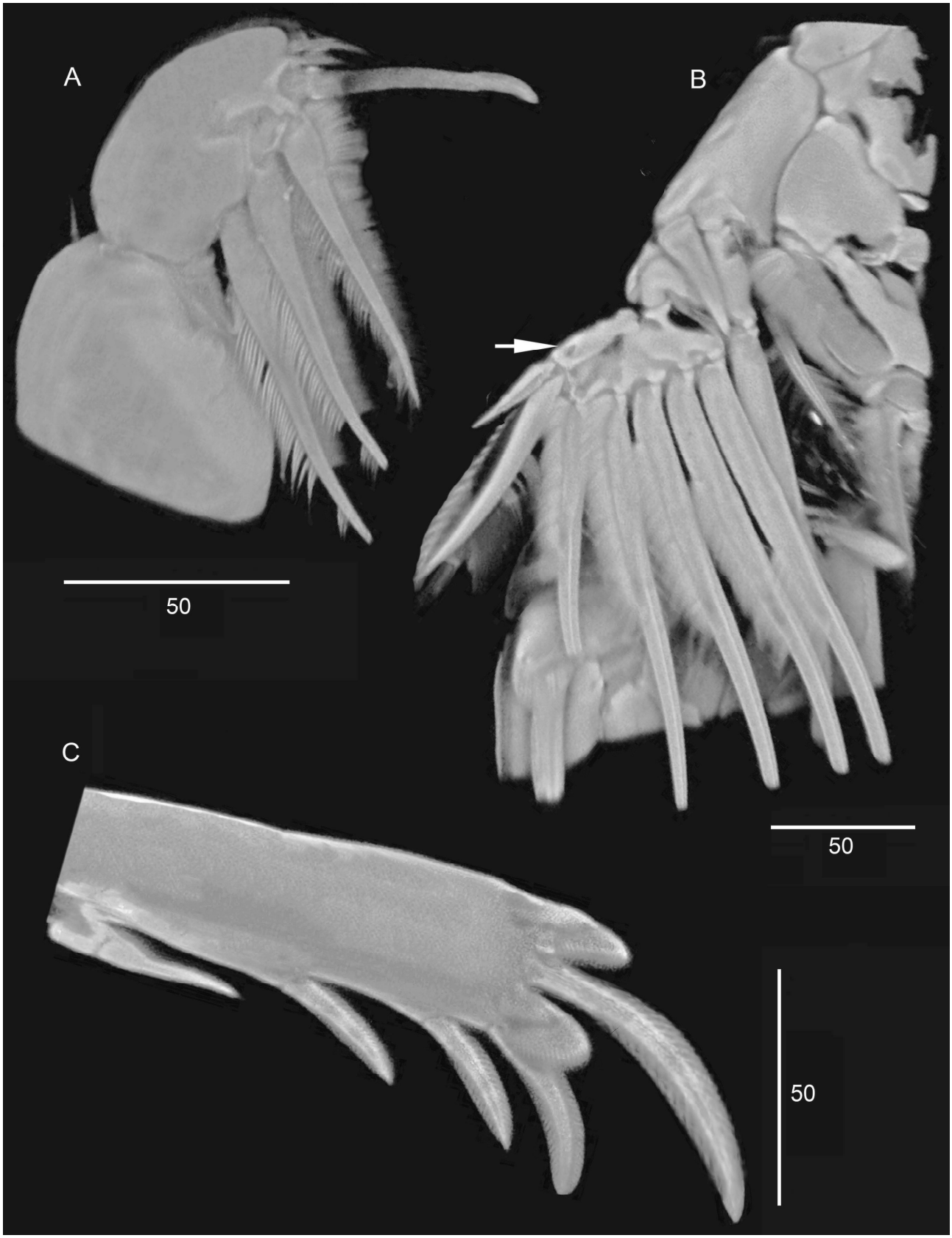

FIGURE 14. *Caligus sarosensis* sp. nov. Adult female. Drishti applied confocal laser scanning microscope images (CLSM-D). A. Distal segment of leg 1; B. Exopod of leg 2, proximal outer spine on third exopodal segment arrowed; C. Leg 4 exopodal spines surrounded with serrated hyaline membrane.

Leg 3 (Fig. 13A) with narrow intercoxal sclerite, coxa and basis fused into flattened apron-like protopod ornamented with extended strips of hyaline membrane along lateral and posterior margins. Inner coxal seta and outer basal seta both pinnate. Exopod 3-segmented, first segment with outer spine extending beyond middle of second segment, orientated parallel with longitudinal axis of ramus, base of spine with pecten-like strip of with hyaline membrane; second segment with outer spine and inner plumose seta, plus setules along outer margin; third segment with outer row of setules and 3 outer spines (Fig. 13B) (first and second spines almost equal in length, third spine slightly shorter than first 2) plus 4 pinnate setae (Fig. 13A). Endopod (Fig. 13A) 2-segmented; first segment armed with long, inner pinnate seta and forming flap-like velum extending to base of exopod, ornamented with row of fine setules along free posterior margin; second segment bearing 6 pinnate setae and bearing row of long setules along outer margin.

Leg 4 (Fig. 13C) uniramous. Protopodal segment with outer seta derived from basis. Exopod 2-segmented; first segment armed with long slender, bilaterally flanged, outer distal spine; compound distal segment with 1 lateral spine and 3 apical spines along oblique distal margin; inner apical spine longest. Inner and middle apical spines each with pecten at base (Figs. 13D, 14C). Armature of rami of legs 1–4 as follows (Roman numerals indicating spines and Arabic numerals indicating setae).

	Exopod	Endopod
Leg 1	I-0; III,1,3	vestigial
Leg 2	I-1; 0-1; II, I, 5	0–1; 0–2; 6
Leg 3	I-0; I-1; III, 4	0–1; 6
Leg 4	I-0; I, III	absent

Leg 5 (Fig. 13E) located on posterolateral ventral surface of genital complex and represented by 2 small papillae; outer (protopodal) papilla with single long pinnate seta; inner (exopodal) papilla carrying 2 shorter unequal pinnate setae; sensilla located on surface close to inner papilla.

Remarks

The new species, *C. sarosensis* sp. nov. exhibits numerous detailed similarities in the structure and setation of legs 1 to 4 with *C. izmiriensis* sp. nov. (described above) and *Metacaligus yucatanensis* is very similar to both new species, having an unusual leg 1 with a rounded distal margin on the second exopodal segment and spines 1 to 3 are small and clustered close to the base of seta 4. In addition, spines 2 and 3 each bear an accessory process and seta 4 is longer than the segment. This configuration differs from that of *M. yucatanensis* only in the lack of accessory processes on spines 2 and 3, which are absent according to Suárez-Morales *et al.* (2012b).

In *C. izmiriensis* sp. nov. the second exopodal segment of leg 2 carries a tiny vestige of an outer margin spine but both *C .sarosensis* sp. nov. and *M. yucatanensis* lack any vestige of this spine. The loss of this spine is an extremely rare character state in *Caligus*. In leg 3 of *C. izmiriensis* sp. nov. the gap between the rami is smaller than in the other two species, so the velum is not quite so broad, but all three share an elongate second exopodal segment and the outer spine on the first exopodal segment is straight and reaches only about two thirds of the distance along the second segment. There is also a pecten-like, rounded strip of hyaline membrane positioned across the base of the outer spine on the first exopodal segment in all these species. The segmentation and armature of leg 4 is similar in these three species and all have the same arrangement of pectens. Despite these detailed similarities, these species can be readily distinguished by the sternal furca: in *C. izmiriensis* sp. nov. the sternal furca has long, closely adpressed tines, compared with short, widely separated tines in *C. sarosensis* sp. nov., and by the complete absence of the sternal furca in *M. yucatanensis*.

The paired cephalothoracic appendages of the two new species are rather generic and lack any distinctive characteristics. However, the sensory papillae associated with the postantennal process are multisensillate in both species and the presence of 6 or 7 sensilla per papilla is unusually high as there are rarely more than 4 in the great majority of *Caligus* species where the number is known. The presence of an accessory tine on the postantennal process of *C sarosensis* sp. nov., serves to distinguish it from *C. izmiriensis* sp. nov. which lacks such an accessory tine.

The new species from the Gulf of Saros exhibits a slender dorsal cephalothoracic shield which narrows anteriorly towards the frontal plate which bears the paired lunules, and the lateral margins of the shield are provided with unusually broad marginal membrane. This general morphotype is typical of so-called "planktonic" caligids, such as *Caligus undulatus* Shen & Li, 1959. Ohtsuka *et al.* (2020) listed the narrow frontal plate as a diagnostic characteristic of their newly proposed *Caligus undulatus*-group of species which comprised five, possibly six, species, each of which had originally been described from plankton samples rather than from material obtained from a host fish. As defined by Ohtsuka *et al.* (2020), the *C. undulatus*-group is characterized by: 1), leg 4 is 3-segmented with IV spines on compound distal exopodal segment; 2), three plumose setae are present on posterior margin of second exopodal segment of leg 1; 3), outer spines on distal exopodal segment of leg 2 are small or reduced; 4), antenna with weak or well-developed process on proximal segment; 5), body with relatively narrow frontal plate; 6), female genital complex longer than wide, sometimes with outer margin undulated; and 7), male urosome slender, with 2-segmented abdomen. In addition to *C. undulatus*, Ohtsuka *et al.* (2020) included in this species group *C. evelynae* Suárez-Morales, Camisotti & Martin, 2012, *C. longiramus* Venmathi Maran, Ohtsuka & Jitchum, 2012, *C. ogawai* Venmathi Maran, Ohtsuka & Shang, 2012, *C. tripedalis* Heegaard, 1972, and possibly *C. hyalinae* Heegaard, 1966. Subsequently, Boxshall & Bernot (2023) considered that *C. hyalinae* should be treated as a junior subjective synonym of *C. chelifer* Wilson, 1905, and they confirmed that this species does also belong in the *C. undulatus*-group. Both new species share *C. undulatus*-group characteristics 1, 2, 4, 5, and 6. *Caligus izmiriensis* sp. nov. also shares character 7 but the male (and, therefore, the state of characteristic 7) is unknown in *C. sarosensis* sp. nov. Characteristic 4 is not robust since it incorporates the two extremes (and presumably all states in between) of a well-developed process on the proximal segment of the antenna versus proximal process lacking. Characteristic 3 is also variably expressed within the species group, ranging from minute in *C. ogawai* (Venmathi Maran *et al.* 2012a), via slender and setiform in *C. evelynae* (Suárez-Morales *et al.* 2012a), to about the same size as the distal outer spine in *C. longiramus* (Venmathi Maran *et al.* 2012b). In *C. sarosensis* sp. nov. the proximal outer spine on the distal exopodal segment of leg 2 is minute and in *C. izmiriensis* sp. nov. it is small.

Caligus izmiriensis sp. nov. and *C. sarosensis* sp. nov. both exhibit the same general morphotype as members of the *C. undulatus*-group, especially the narrow frontal plate and the broad marginal membrane around the dorsal cephalothoracic shield. We propose to place them in the *C. undulatus*- group together with *C. undulatus*, *C. evelynae*, *C. longiramus*, *C. ogawai*, *C. tripedalis* and *C. chelifer*. Interestingly *Metacaligus yucatanensis* also shares *C. undulatus*-group characteristics 1, 2, 4, 5, 6 and 7. Regarding characteristic 3, the proximal outer spine on exopodal segment 3 of leg 2 in *M. yucatanensis* is long although extremely slender and setiform in appearance (Suárez-Morales *et al.* 2012b), somewhat like that of *C. evelynae*. Despite this impressive array of shared character states, the two new species can be readily distinguished from *M. yucatanensis* by the presence of a sternal furca in both new species. All species currently placed in *Metacaligus* lack a sternal furca (Dojiri & Ho 2013; Suárez-Morales *et al.* 2012b) and the presence of a sternal furca prevents the placement of the new species in *Metacaligus*. However, in view of the close similarity between the new species and *M. yucatanensis*, it is necessary to review the validity of *Metacaligus* as a generic level taxon.

Validity of *Metacaligus* Thomsen 1949

Metacaligus was originally established by Thomsen (1949) as a subgenus of *Caligus* in order to accommodate a new species, *Caligus* (*Metacaligus*) *uruguayensis* Thomsen, 1949, which was based on material collected from *Trichiurus lepturus* (Linnaeus, 1758) caught in the estuary of the Rio de la Plata, Uruguay. His species lacked a sternal furca and Thomsen (1949) transferred three other species, *Caligus rufus* Wilson, 1908, *C. afurcatus* Wilson, 1913 and *C. enormis* Wilson, 1913, into his new subgenus because they apparently shared the lack of a sternal furca. Ho & Bashirullah (1977) proposed to raise *Metacaligus* to generic status and, in addition to the type species *M. uruguayensis* (Thomsen, 1949), they included two other species in the genus, *M. rufus* (Wilson, 1908) and *M. hilsae* (Shen, 1957). *Metacaligus rufus* was collected from an ariid catfish, *Bagre marinus* (Mitchill, 1815) (Wilson, 1908) and *M. hilsae* from a dorosomatid clupeiform host, *Tenualosa reevesii* (Richardson, 1846) (as *Hilsa reevesii*). After re-examination of the type material of *Caligus afurcatus* and *C. enormis*, Ho & Bashirullah (1977) excluded both species from *Metacaligus* even though the sternal furca is absent, because they lacked the "*Metacaligus* type" of leg 1 (with a large spine 1 and progressively smaller spines 2 and 3 (both lacking an accessory process), a long seta 4, plus 3 reduced plumose setae along the posterior margin of the distal exopodal segment). In *C. afurcatus*

spine 1 is minute and spines 2 and 3 each have an accessory process, and in *C. enormis* spine 1 is apparently absent and spines 2 and 3 each have an accessory process. Boxshall & El-Rashidy (2009) placed the latter species in the *Caligus productus*-species group due to the loss of 2 plumose setae and the reduction of the third from the posterior margin of the same segment.

Pillai (1985) recognized that *Caligus hilsae* Shen, 1957 was a junior synonym of *Caligus unguidentatus* Rangnekar & Murti, 1950 but placed this species in *Caligus* due to Thomsen's proposal of a new subgenus having "apparently failed to get accepted". *Caligus unguidentatus* was transferred to *Metacaligus* by Ho & Lin (2002) who considered it to be a valid genus, and they added a fourth species, *M. latus* Ho & Lin, 2002, taken from the same host species, *Trichiurus lepturus*, as the type species. Hayes *et al.* (2012) recognized that *Caligus trichiuri* Krøyer, 1863, originally reported from the same host (as *Trichiurus haumala*), was a senior synonym of *Metacaligus uruguayensis* and transferred it as *Metacaligus trichiuri* (Krøyer, 1863). Finally, Suárez-Morales *et al.* (2012b) added another species, *M. yucatanensis*, found in the plankton in a coastal lagoon in the Gulf of Mexico. In their analysis of the systematics of caligid genera, Dojiri & Ho (2013) treated *Metacaligus* as a valid genus and noted four diagnostic character states the combination of which could be used to separate this genus from *Caligus*, namely: 1, the lack of a sternal furca; 2, the lack of accessory processes on spines 2 and 3 on the distal margin of the second exopodal segment of leg 1; 3, the 3 plumose setae on the posterior margin of the same segment are short (i.e. shorter than the segment); and 4, there is only 1 outer spine on the third exopodal segment of leg 2. As pointed out by Dojiri & Ho (2013), all these character states can be found individually in particular species of *Caligus,* but the full combination is found only in species of *Metacaligus*. [The description of *M. yucatanensis* only appeared in 2012, presumably after Dojiri & Ho (2013)'s analysis of caligid systematics had gone to press, and therefore, this species was not included in their discussion.]

Metacaligus, as currently constituted, is heterogeneous: *M. yucatanensis* shares characters 1 and 2 of Dojiri & Ho (2013) but the plumose setae on the exopod of leg 1 (character 3) are long, and it retains 2 outer spines on the third exopodal segment of leg 2 (character 4). The four other *Metacaligus* species share additional character states, including the lack of a posterior process on the proximal segment of the female antenna and the major reduction or loss of the tine of the postantennal process. However, these two character states are widespread within *Caligus* and are shared with members of the *C. diaphanus*-group, which is also characterized by the lack of accessory processes on spines 2 and 3 on the distal margin of the second exopodal segment of leg 1 (Boxshall 2018), another *Metacaligus* characteristic regarded as diagnostic by Dojiri & Ho (2013). Based on the numerous detailed similarities between *Metacaligus yucatanensis* and the two new species *Caligus* described here, we propose to transfer *Metacaligus yucatanensis* Suárez-Morales, Kim & Escamilla, 2012, to *Caligus* as *C. yucatanensis* (Suárez-Morales, Kim & Escamilla, 2012) comb. nov. We recognize *C. yucatanensis* as a member of the *C. undulatus*-group.

The characters listed by Dojiri & Ho (2013) as supporting the recognition of *Metacaligus* as a valid genus are not robust. The loss of the sternal furca has occurred at least three times independently within the genus *Caligus*: in *C. enormis* (a member of the *C. productus*-group), in *C. yucatanensis* (*C. undulatus*-group), and in *C. afurcatus*. The reduced length of the 3 plumose setae on the posterior margin of the distal exopodal segment of leg 1 is typical of members of the *C. confusus*-group and is also found in some other species such as *C. pauliani* Nuñes-Ruivo & Fourmanoir, 1956, a member of the *C. bonito*-group (as *C. biseriodentatus* Shen, 1957). The absence of accessory processes from spines 2 and 3 on the distal exopodal segment of leg 1 is found in members of the *C. diaphanus*-group and in numerous other *Caligus* species. The loss of the proximal outer spine of the third exopodal segment of leg 2 is rare in *Caligus*, however, it is lacking in *C. chinglonglini* Ohtsuka & Boxshall, 2019 and is reduced in size in members of the *C. pseudorhombi*-group and *C. undulatus*-group (Ohtsuka *et al.* 2020; Ohtsuka & Boxshall 2019; present account). In the light of this, we consider the case for maintaining *Metacaligus* as a separate genus is extremely weak and we therefore propose to treat *Metacaligus* Thomsen, 1949 as a synonym of *Caligus* O.F. Müller, 1785. We also propose to transfer its species to *Caligus*: *Metacaligus trichiuri*, *M. rufus*, and *M. unguidentatus* all return to their original combinations as *Caligus trichiuri*, *Caligus rufus*, and *Caligus unguidentatus*, respectively. Transferring *Metacaligus latus* would create a secondary homonym of *Caligus latus* Byrnes, 1987, so we propose a replacement name *Caligus cultellus* nom. nov. So, *Metacaligus latus* Ho & Lin, 2002 becomes *Caligus cultellus* nom. nov., with the new name derived from the Latin *cultellus* which is the root of the English word cutlass, referring to the cutlass fish host (*Trichiurus lepturus*) of this species.

Excluding *Caligus yucatanensis* (Suárez-Morales, Kim & Escamilla, 2012) comb. nov., which is a member of the *C. undulatus*-group, this cluster of the remaining four species formerly placed in *Metacaligus* represents a

new species group, the *Caligus trichiuri*-group, characterized by the following combination of character states: the lack of a posterior process on the proximal segment of the female antenna; the reduction or loss of the tine of the postantennal process; the lack of a sternal furca; the lack of accessory processes on spines 2 and 3 on the distal margin of the second exopodal segment of leg 1; the small size of the 3 plumose setae on the posterior margin of the same segment (i.e. they are shorter than the segment); the presence of only 1 outer spine on the third exopodal segment of leg 2; leg 4 is 3-segmented with a 2-segmented exopod armed with I, IV spines. The *C. trichiuri*-group shares several of these character states with the *C. diaphanus*-group but can readily be distinguished by the state of leg 4, which is 4-segmented with a 3-segmented exopod armed with I, I, III spines in the latter group.

Key to species of *Caligus trichiuri*-group (females only)

1. Abdomen 1-segmented, shorter than genital complex . . . 2
- Abdomen 2-segmented, longer than genital complex . . . *C. unguidentatus*
2. Genital complex wider than long, with convex lateral margins . . . *C. cultellus* nom. nov.
- Genital complex longer than wide, with more-or-less parallel lateral margins . . . 3
3. Genital complex large, almost as long as cephalothorax . . . *C. trichiuri*
- Genital complex small, less than half length of cephalothorax . . . *C. rufus*

Updated key to species of *Caligus undulatus*-group (females only)

1. Distal segment of antennule short (less than 2.5 times length of proximal segment) . . . 2
- Distal segment of antennule elongate (about 2.5 times length of proximal segment) . . . *C. longiramus*
2. Sternal furca present . . . 3
- Sternal furca absent . . . *C. yucatanensis* comb. nov.
3. Genital complex at least 3 times longer than abdomen . . . *C. evelynae*
- Genital complex less than 3 times longer than abdomen . . . 4
4. Postantennal process with accessory tine on base part . . . *C. sarosensis* sp. nov.
- Postantennal process simple, lacking accessory tine . . . 5
5. Sternal furca with tines closely adpressed along midline . . . *C. izmiriensis* sp. nov.
- Tines of sternal furca clearly separated . . . 6
6. Abdomen distinctly 2-segmented and about as long as genital complex . . . *C. chelifer*
- Abdomen 1-segmented and shorter than genital complex . . . 7
7. Abdomen more than 2 times longer than wide . . . *C. undulatus*
- Abdomen less than 2 times longer than wide . . . 8
8. Dorsal cephalothoracic shield subtriangular, with straight lateral margins . . . *C. tripedalis*
- Dorsal cephalothoracic shield rounded, with evenly convex lateral margins . . . *C. ogawai*

Discussion

The two new species, *C. izmiriensis* sp. nov. and *C. sarosensis* sp. nov., have a slender dorsal cephalothoracic shield which narrows anteriorly towards the frontal plate bearing the lunules and they share this shape with most of the other members of the *C. undulatus*-group, namely: *C. chelifer* (Figs. 15A–B), *C. evelynae* (Figs. 15C–D), *C. longiramus* (Fig. 15E), *C. tripedalis* (Fig. H–I), *C. undulatus* (Figs. 15J–K), and *C. yucatanensis* comb. nov. (Figs. 15L; 16A). Where both sexes are known, both exhibit the same distinctive shape. Only *C. ogawai* (Figs. 15F–G) has a more rounded dorsal cephalothoracic shield as found in most of the other species of *Caligus* reported as free-swimming in the plankton, such as *C. aduncus* (Fig. 16B), *C. chinglonglini* (Fig. 16C), and *C. quadrigenitalis* (Fig. 16D) which are currently known only from the plankton, having never been recorded from a host. There are, however, a few species such as *C. rufus* (Figs. 16E–F) and *C. planktonis* (Fig. 16G) appear somewhat intermediate in cephalothoracic shape and there is a wide range of shapes exhibited although *C. undulatus*-group species tend to cluster at the narrow end of that shape spectrum. The three species of *Lepeophtheirus* reported from plankton samples, *L. alvaroi* Suárez-Morales & Gasca, 2012 (Fig. 16H), *L. parviventris* Wilson, 1905 (Figs. 16I–J) and *L. semicossyphi* Yamaguti, 1939 (Figs. 16K–L), also have a rounded dorsal cephalothoracic shield, as in the majority of the *Caligus* species. We infer that the narrower tapering shape of the *C. undulatus*-group species is linked to the extended periods they spend swimming up in water column.

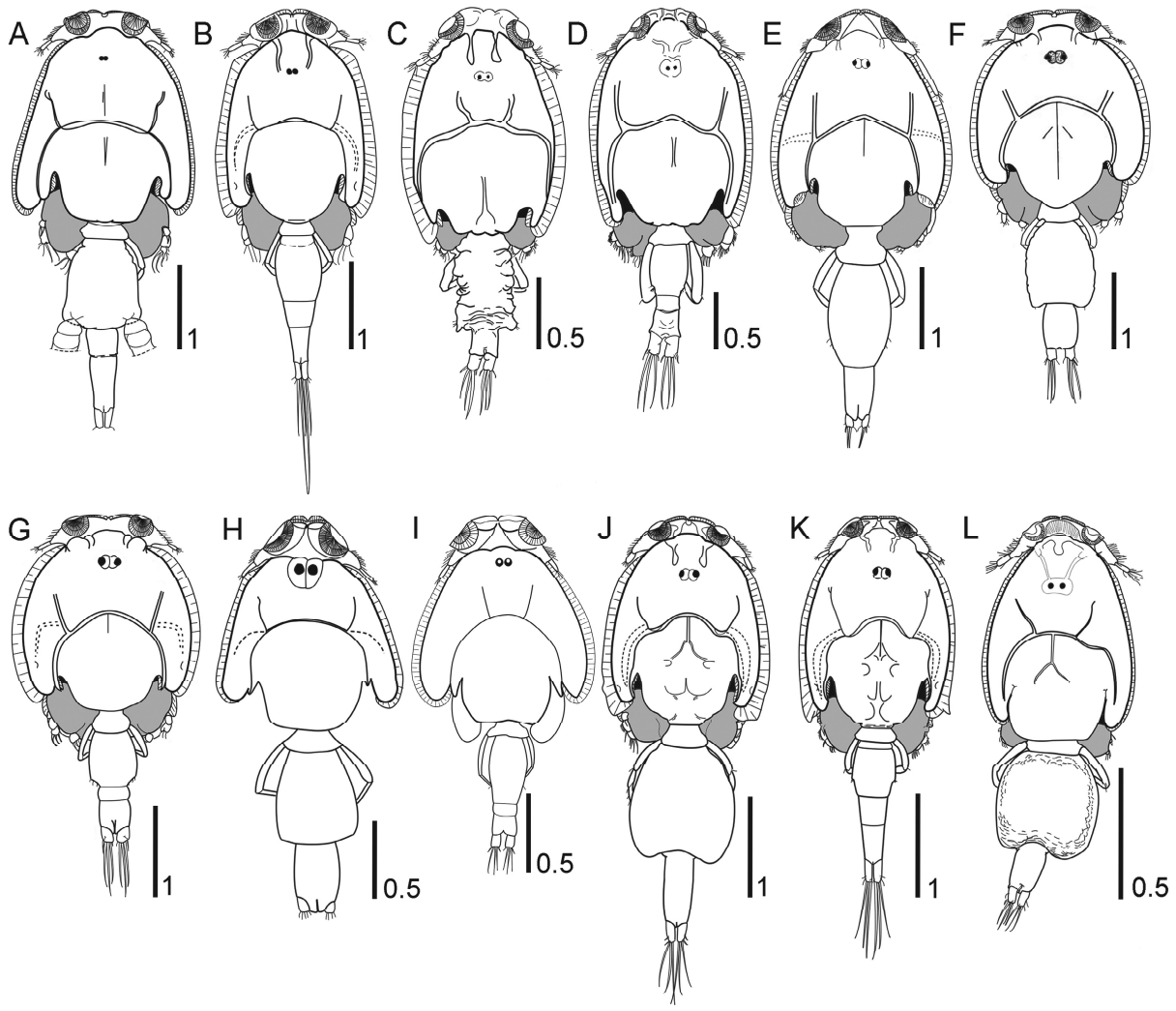

FIGURE 15. A–B. *Caligus chelifer* Wilson C.B., 1905 (female; male); C–D. *Caligus evelynae* Suárez-Morales, Camisotti & Martín, 2012 (female; male); E. *Caligus longiramus* Venmathi Maran, Ohtsuka & Jitchum, 2012 (female); F–G. *Caligus ogawai* Venmathi Maran, Ohtsuka & Shang, 2012 (female; male); H–I. *Caligus tripedalis* Heegaard, 1972 (female; male); J–K. *Caligus undulatus* Shen & Li, 1959 (female; male); L. *Caligus yucatanensis* nov. comb. (Suárez-Morales, Kim I.H. & Escamilla, 2012) (female).

Reduction in the size or number of setation elements along the outer margin of the exopod of leg 2 occurs in the *C. undulatus*-group, the *C. pseudorhombi*-group and the newly proposed *C. trichiuri*-group. Within the genus, the complete absence of the outer margin spine from exopodal segment 2 is reported only in *C. yucatanesis* comb. nov. and *C. sarosensis* sp. nov., but this spine is reduced to a tiny vestige in *C. izmiriensis* sp. nov. This marked reduction or loss appears to be a robust synapomorphy linking these three species, and they are here placed together in the *C. undulatus*-group. The same spine is also reduced in size in *C. cultellus* nom. nov. but it retains an ornamentation of bilateral marginal membranes (see Ho & Lin 2004, as *Metacaligus latus*).

The reduction and loss of the proximal outer spine on the third exopodal segment of leg 2 is a character state exhibited in representatives of all three of these species groups. In *C. sarosensis* sp. nov. this proximal spine is reduced to a tiny vestige, but in both *C. izmiriensis* sp. nov. and *C. yucatanensis* it is slender but well developed. In species of the *C. pseudorhombi*-group this spine and the distal outer margin spine are both generally reduced and in one species, *C. chinglonglini*, the proximal spine appears to be absent but is perhaps represented by a minute knob-like process on the margin of the segment (Ohtsuka & Boxshall 2019). In species of the *C. trichiuri*-group this spine is absent. We infer that the reduction and loss of the outer margin setation elements on leg 2 is a convergent trend within *Caligus*.

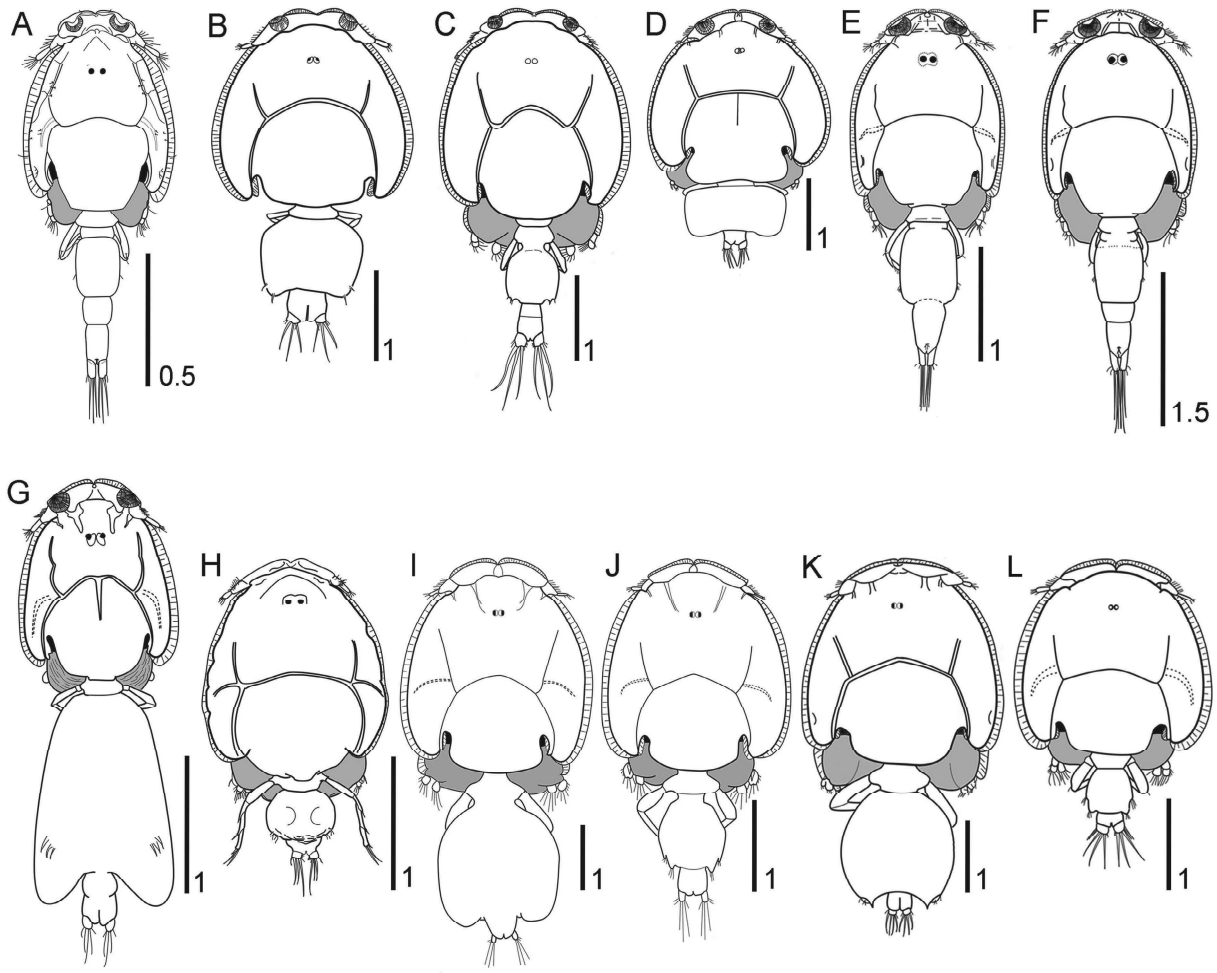

FIGURE 16. A. *Caligus yucatanensis* nov. comb. (Suárez-Morales, Kim I.H. & Escamilla, 2012) (male); B. *Caligus aduncus* Shen & Li, 1959 (female); C. *Caligus chinglonglini* Ohtsuka & Boxshall, 2019 (male); D. *Caligus quadrigenitalis* Venmathi Maran, Ohtsuka & Shang, 2012 (female); E–F. *Caligus rufus* (Wilson C.B., 1908) (female; male); G. *Caligus planktonis* Pillai N.K., 1979 (female); H. *Lepeophtheirus alvaroi* Suárez-Morales & Gasca, 2012 (female); I–J. *Lepeophtheirus parviventris* Wilson C.B., 1905 (female; male); K–L. *Lepeophtheirus semicossyphi* Yamaguti, 1939 (female; male).

A surprising diversity of caligid species has been recorded swimming free up in the water column. At least 40 species of *Caligus* have been reported from the plankton (Table 1). These represent six of the eight currently recognized species groups within the genus, but the list also includes several that have not yet been assigned to a species group. This behavior may be more widespread than currently appreciated. Caligids have also been reported free-swimming in artificial situations such as aquaria (e.g. *Caligus calotomi*) (see Shiino 1954). Experimental laboratory studies on *Lepeophtheirus salmonis* (Krøyer 1837) have demonstrated significant levels of inter-host transfer (Hull *et al.* 1998) and that adult males of *L. salmonis* transferred more often than adult females. Males are also recorded more frequently from the plankton than females, with 26 (39%) of the individual reports in Table 1 based on the presence of males only, 22 (33%) on males and females, and only 16 (24%) on females only. Two (3%) of the records did not specify the sex of the specimens. Boxshall & Özak (2022) inferred that the more frequent presence of adult males in the plankton was likely linked to their more active role in mate location. Lee *et al*. (2022) reported seven species of *Caligus* taken in light traps deployed in shallow coastal waters around the coast of South Korea but these are not included in Table 1 because it seems possible that these caligids may have left the host in response to the light source stimulus and that they may not swim freely in the water column as part of their normal behavior.

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References

Anstensrud, M. (1992) Mate guarding and mate choice in two copepods, *Lernaeocera branchialis* (L.) (Pennellidae) and *Lepeophtheirus pectoralis* (Müller) (Caligidae), parasitic on flounder. *Journal of Crustacean Biology*, 12, 31–40. https://doi.org/10.2307/1548716

Barnard, K.H. (1948) New records and descriptions of new species of parasitic Copepoda from South Africa. *Annals and Magazine of Natural History*, Series 12, 1 (4), 242–254. https://doi.org/10.1080/00222934808653905

Bassett-Smith, P.W. (1898) Some new or rare parasitic copepods found on fish in the Indo-tropic region. *Annals and Magazine of Natural History*, Series 7, 2 (11), 357–372. https://doi.org/10.1080/00222939808678056

Bere, R. (1936) Parasitic copepods from Gulf of Mexico fish. *American Midland Naturalist*, 17, 577–625. https://doi.org/10.2307/2419936

Boxaspen, K.K., Karlsen, Ø., Svåsand, T. & Asplin, L. (2022) Impacts of sea lice. *In*: Treasurer, J., Bricknell, I. & Bron, J. (Eds.), *Sea Lice Biology and Control*. 5M Books Ltd., Essex, pp. 531–547.

Boxshall, G.A. (1990) The skeletomusculature of siphonostomatoid copepods, with an analysis of adaptive radiation in structure of the oral cone. *Philosophical Transactions of the Royal Society of London*, Series B, 328, 167–212. https://doi.org/10.1098/rstb.1990.0113

Boxshall, G.A. (2018) The sea lice (Copepoda: Caligidae) of Moreton Bay (Queensland, Australia), with descriptions of thirteen new species. *Zootaxa*, 4398 (1), 1–172. https://doi.org/10.11646/zootaxa.4398.1.1

Boxshall, G.A. & Bernot, J.P. (2023) Resolving taxonomic and nomenclatural problems in the genus *Caligus* O.F. Müller, 1785 (Copepoda: Caligidae). *Zootaxa*, 5360 (4), 545–567. https://doi.org/10.11646/zootaxa.5360.4.5

Boxshall, G.A. & El-Rashidy, H.H. (2009) A review of the *Caligus productus* species group, with the description of a new species, new synonymies and supplementary descriptions. *Zootaxa*, 2271 (1), 1–26. https://doi.org/10.11646/zootaxa.2271.1.1

Boxshall, G.A. & Gurney, A.R. (1980) Description of two new and one poorly known species of the genus *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida). *Bulletin of the British Museum (Natural History)*, Zoology Series, 39, 161–178. https://doi.org/10.5962/p.13270

Boxshall, G.A. & Özak, A.A. (2022) Introduction to sea lice morphology and biology. *In*: Treasurer, J., Bricknell, I. & Bron, J. (Eds.), *Sea Lice Biology and Control*. 5M Books Ltd., Essex, pp. 13–49.

Boxshall, G.A., Lin, C.-L., Ho, J.-S., Ohtsuka, S., Venmathi Maran, B.A. & Justine, J.-L. (2008) A revision of the family Dissonidae Kurtz, 1924 (Copepoda: Siphonostomatoida). *Systematic Parasitology*, 70, 81–106. https://doi.org/10.1007/s11230-008-9132-z

Brady, G.S. (1899) On the marine Copepoda of New Zealand. *Transactions of the Zoological Society of London*, 15 (2), 31–54. https://doi.org/10.1111/j.1096-3642.1899.tb00018.x

Burmeister, H. (1835) Beschreibung einiger neuen oder weniger bekannten Schmarotzerkrebse, nebst allgemeinen Betrachtungen über die Gruppe, welcher sie angehören. *Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum*, 17, 269–336. https://doi.org/10.5962/bhl.title.39131

Byrnes, T. (1987) Caligids (Copepoda: Caligidae) found on the bream (*Acanthopagrus* spp.) of Australia. *Journal of Natural History*, 21, 363–404. https://doi.org/10.1080/00222938700771071

Costello, M.J. (2009) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society Biological Sciences*, Series B, 276 (1672), 3385–3394. https://doi.org/10.1098/rspb.2009.0771

Czerniavski, V. (1868) Materialia ad zoographiam ponticam comparatam. *Travaux de la Societe des Naturalistes de St.*

Petersbourg, 1, 19–136.
Dana, J.D. (1852) Conspectus crustaceorum, quae in orbis terrarum circumnavigatione, Carolo Wilkes, e classe Reipublicae foederatae duce, lexit et descripsit Jacobus D. Dana. Pars II. *Proceedings of the American Academy of Arts and Sciences*, 2, 9–61.
https://doi.org/10.5962/bhl.title.53615
Dana, J.D. (1853) *Crustacea. Part II. United States Exploring Expedition. During the year 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. United States Exploring Expedition*, 14, 691–1618.
https://doi.org/10.5962/bhl.title.69333
Dojiri, M. & Ho, J.-S. (2013) *Systematics of the Caligidae, copepods parasitic on marine fishes*. *Crustaceana Monographs 18*. Brill, Leiden and Boston, 448 pp.
https://doi.org/10.1163/9789004204256
Froese, R. & Pauly, D. (Eds.) (2023) FishBase. World Wide Web Electronic Publication. Available from: http://www.fishbase.org/ (accessed 31 January 2024)
Gnanamuthu, C.P. (1948) Notes on the Anatomy and Physiology of *Caligus savala*, n. sp., a parasitic copepod from Madras Plankton. *Proceedings of the Zoological Society of London*, 118, 591–606.
https://doi.org/10.1111/j.1096-3642.1948.tb00401.x
Gusev, A.V. (1951) Paraziticheskie Copepoda s nekotorykh morskikh ryb. *Parazitologica Papers of the Zoological Institute, Parazitologicheskij Sbornik*, 13, 394–463. [in Russian]
Hayes, P., Justine, J.-L. & Boxshall, G.A. (2012) The genus *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida): two new species from reef associated fishes in New Caledonia, and some nomenclatural problems resolved. *Zootaxa*, 3534 (1), 21–39.
https://doi.org/10.11646/zootaxa.3534.1.2
Hayes, P.M., Christison, K.W., Vaughan, D.B., Smit, N.J. & Boxshall, G.A. (2021) Sea lice (Copepoda: Caligidae) from South Africa, with descriptions of two new species of Caligus. *Systematic Parasitology*, 98, 369–397.
https://doi.org/10.1007/s11230-021-09984-2
Heegaard, P.E. (1943) Some New Caligids from the Gilbert Islands. *Arkiv för Zoologi*, Series A, 34, 1–12.
Heegaard, P.E. (1955) Parasitic copepods from Tropical West Africa. *Atlantide Reports*, 3, 41–56.
Heegaard, P.E. (1966) Parasitic copepods from Texas. *Videnskabelige Meddelelser fra Dansk Naturhistoriske Forening, Copenhagen*, 129, 187–197.
Heegaard, P.E. (1972) *Caliginae* and *Euryphorinae* of the Dana Expedition (Crustacea Copepoda, Caligidae). *Steenstrupia*, 2, 295–317.
Heller, C. (1865) *2 Crustaceen*. Kaiserlich-Königliche Hof- und Staatsdruckerei, Wein, 280 pp., 25 pls.
Heller, C. (1866) Carcinologische Beitrage zur Fauna des Adriatischen Meeres. *Verhandlungen der Kaiserlich-Koniglichen Zoologisch-Botanischen Gesellschaft in Wien*, 15, 723–760.
Hewitt, G.C. (1971) Two species of *Caligus* (Copepoda, Caligidae) from Australian waters, with a description of some developmental stages. *Pacific Science*, 25, 145–164.
Ho, J. & Bashirullah, A. (1977) Two species of caligid copepods (Crustacea) parasitic on marine fishes of Venezuela, with discussion of *Metacaligus* Thomsen, 1949. *Journal of Natural History*, 11, 703–714.
https://doi.org/10.1080/00222937700770601
Ho, J. & Lin, C.-L. (2002) New species of *Metacaligus* (Caligidae, Copepoda) parasitic on the Cutlassfish (*Trichiurus lepturus*) of Taiwan, with a cladistic analysis of the family Caligidae. *Zoological Science*, 19, 1363–1375.
https://doi.org/10.2108/zsj.19.1363
Ho, J.-S. & Lin, C.-L. (2003) Two species of rare sea lice (Copepoda, Caligidae) parasitic on marine fishes of Taiwan. *Journal of The Fisheries Society of Taiwan*, 30, 147–158.
https://doi.org/10.29822/JFST.200306.0004
Ho, J.-S. & Lin, C.-L. (2004) *Sea lice of Taiwan: (Copepoda : Siphonostomatoida : Caligidae*. The Sueichan Press, Keelung, 388 pp.
Hull, M.Q., Pike, A.W., Mordue, A.J. & Rae, G.H. (1998) Patterns of pair formation and mating in an ectoparasitic caligid copepod *Lepeophtheirus salmonis* (Krøyer, 1837): implications for its sensory and mating biology. *Philosophical Transactions of the Royal Society London*, 353, 753–764.
https://doi.org/10.1098/rstb.1998.0241
Huys, R. & Boxshall, G.A. (1991) *Copepod evolution*. Ray Society, London, 468 pp.
Johnson, S.C., Treasurer, J.W., Bravo, S., Nagasawa, K. & Kabata, Z. (2004) A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies*, 43, 229–243.
Kabata, Z. (1966) Copepoda parasitic on Australian fishes. V. Genus *Dissonus* (Dissonidae). *Annals and Magazine of Natural History*, 13, 211–226.
https://doi.org/10.1080/00222936608656047
Kamanli, S.A. (2023) First report of *Caligus minimus* Otto, 1821 (Copepoda: Siphonostomatoida: Caligidae) from plankton samples collected from Türkiye. *Commagene Journal of Biology*, 7 (1), 50–57.
https://doi.org/10.31594/commagene.1261446
Kamanli, S.A., Kihara, T.C., Ball, A.D., Morritt, D. & Clark, P.F. (2017) A 3D imaging and visualization workflow, using

confocal microscopy and advanced image processing for brachyuran crab larvae. *Journal of Microscopy*, 266, 307–323. https://doi.org/10.1111/jmi.12540
Kim, I.-H., Suárez-Morales, E. & Márquez-Rojas, B. (2019) Caligid copepods (Copepoda: Siphonostomatoida: Caligidae) as zooplankters off the Venezuelan coast, western Caribbean Sea. *Thalassas: An International Journal of Marine Sciences*, 35, 607–618. https://doi.org/10.1007/s41208-019-00130-w
Krøyer, H. (1837) Om Snyltekrebsene, isaer med Hensyn til den danske Fauna. *Naturhistoriske Tiddskrift*, 1 (6), 605–628.
Krøyer, H. (1863) Bidrag til Kundskab om Snyltekrebsene. *Naturhistorisk Tidsskrift*, Series III, 2, 75–320.
Kurian, C.V. (1955) Parasitic copepods of Travancore-Cochin. *Bulletin of the Central Research Institute, University of Travancore*, 4, 113–116.
Lee, J., Chang, C.Y. & Kim, I.-H. (2022) Symbiotic copepods (Cyclopoida and Siphonostomatoida) collected by light trap from Korea. *ZooKeys*, 1115, 1–71. https://doi.org/10.3897/zookeys.1115.83266
Limaye, A. (2012) Drishti: a volume exploration and presentation tool. *In*: Stock, S.R. (Ed.), Proceedings of SPIE. Vol. 8506 SPIE. *Developments in X-Ray Tomography VIII, Bellingham, Washington*, 85060X, 17 October 2012, pp. 1–9. https://doi.org/10.1117/12.935640
Lin, C.-L. & Ho, J. (2003) Two Species of Rare Sea Lice (Copepoda, Caligidae) Parasitic on Marine Fishes of Taiwan. *Journal of The Fisheries Society of Taiwan*, 30 (2), 147–158. https://doi.org/10.29822/JFST.200306.0004
Linnaeus, C. (1758) *Systema naturae per Regna tria naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio decima, reformata.* Impensis Direct. Laurentii Salvii, Holmiae, ii + 824 pp. https://doi.org/10.5962/bhl.title.542
Luque, J.L. & Cezar, A.D. (2000) Two new species of *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida: Caligidae) parasitic on *Xenomelaniris brasiliensis* (Quoy & Gaimard, 1824) (Osteichthyes: Atherinidae) from the costal [sic] zone of the state of Rio de Janeiro, Brazil. *Contribuiçoes Avulsas Sobre a História Natural do Brasil*, Série Zoologia, Seropédica, 14, 1–10.
Mackenzie, K. (2022) Caligids in Global Aquaculture. *In*: Treasurer, J., Bricknell, I. & Bron, J. (Eds.), *Sea Lice Biology and Control*. 5M Books Ltd., Essex, pp. 69–86.
Mitchill, S.L. (1815) The fishes of New-York, described and arranged. *Transactions of the Literary and Philosophical Society of New York*, 1, 355–492.
Montú, M. (1982) Alguns copépodos parasitas de peixes do sul do Brasil. *Arquivos de Biologia e Tecnologia*, 25, 329–339.
Moon, S.Y. & Park, J.S. (2019) Occurrence of sea lice, *Caligus undulatus* Shen and Li, 1959 (Copepoda: Siphonostomatoida: Caligidae) in plankton samples collected from Korea. *Journal of Species Research*, 8 (4), 365–372. https://doi.org/10.12651/JSR.2019.8.4.365
Müller, O.F. (1785) *Entomostraca seu Insecta Testacea, quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit Otho Fridericus Müller*. F.W. Thiele, Lipsiae and Havniae, 134 pp. https://doi.org/10.5962/bhl.title.14414
Nordmann, A. von (1832) *Mikrographische Beiträge zur Naturgeschichte der Wirbellosen Thiere*. G. Reimer, Berlin, 150 pp.
Nuñes-Ruivo, L. & Fourmanoir, P. (1956) Copépodes parasites de poissons de Madagascar. I. Parasitic copepods of fish from Madagascar. I. *Mémoires de l'Institut Scientifique de Madagascar*, Series A, 10, 69–80.
Ohtsuka, S. & Boxshall, G.A. (2019) Two new species of the genus *Caligus* (Crustacea, Copepoda, Siphonostomatoida) from the Sea of Japan, with a note on the establishment of a new species group. *ZooKeys*, 893, 91–113. https://doi.org/10.3897/zookeys.893.46923
Ohtsuka, S., Nawata, M., Nishida, Y., Nitta, M., Hirano, K., Adachi, K., Kondo, Y., Venmathi Maran, B.A. & Suárez-Morales, E. (2020) Discovery of the fish host of the "planktonic" caligid *Caligus undulatus* Shen & Li, 1959 (Crustacea: Copepoda: Siphonostomatoida). *Biodiversity Data Journal*, 8, e52271. https://doi.org/10.3897/BDJ.8.e52271
Otto, A.G. (1821) *Conspectus animalium quorundam maritimorum nondum editorum pars prior quam patri dilectissimo ad cineres usque venerando Bernhardo Crristiano Otto pro celebrando die laetissimo XI. Maji MDCCCXXI quo ante decem lustra honores doctorales acceperat*. Typis Universitatis, Vratislaviae, 20 pp.
Pillai, N.K. (1961) Copepods parasitic on South Indian fishes. Part. 1. Caligidae. *Bulletin of the Research Institute, University of Kerala*, 8, 87–130.
Pillai, N.K. (1966) Notes on copepods parasitic on South Indian marine fishes. *Journal of the Marine Biological Association of India*, 8, 123–140.
Pillai, N.K. (1979) *Caligus planktonis* sp. nov. from the plankton collected off the Trivandrum coast. *Aquatic Biology*, 4, 29–32.
Pillai, N.K. (1985) *Fauna of India. Parasitic copepods of marine fishes*. Zoological Survey of India, Calcutta, 900 pp.
Rangnekar, P.G. & Murti, N.N. (1950) A new caligid copepod parasitic on the fish *Clupea toli*. *Journal of the University of Bombay*, Series B, 18, 21–28.
Richardson, J. (1846) Report on the ichthyology of the seas of China and Japan. *Report of the British Association for the*

Advancement of Science 15th Meeting, 1845, 187–320.
https://doi.org/10.5962/bhl.title.59530
Roubal, F.R., Armitage, J. & Rohde, K. (1983) Taxonomy of metazoan ectoparasites of snapper, *Chrysophrys auratus* (Family Sparidae), from southern Australia, eastern Australia and New Zealand. *Australian Journal of Zoology*, Supplemental Series, 94, 1–68.
https://doi.org/10.1071/AJZS094
Scott, T. (1894) Report on *Entomostraca* from the Gulf of Guinea, collected by John Rattray, B.Sc. *Transactions of the Linnean Society of London*, Series 2, Zoology, 6, 1–161.
https://doi.org/10.1111/j.1096-3642.1894.tb00660.x
Shen, C. (1957) Parasitic copepods from fishes of China. II. Caligoida, Caligidae (1). *Acta Zoologica Sinica*, 9 (4), 351–378.
Shen, C.J. & Li, H.L. (1959) Parasitic copepods from fishes of China. IV. Caligoida, Caligidae (3). *Acta Zoologica Sinica*, 11, 12–20.
Shiino, S.M. (1954) On the new copepod, *Caligus calotomi* n. sp., parasitic on the fish, *Calotomus japonicus* (C. & V.). *Bulletin of the Japanese Society of Scientific Fisheries [Nippon Suisan Gakkaishi]*, 20, 16–20.
https://doi.org/10.2331/suisan.20.16
Shiino, S.M. (1955) A new piscicola copepod belonging to the genus *Caligus* from Matusima Bay. *Bulletin of the Biogeographical Society of Japan*, 16–19, 135–140.
Stebbing, T.R.R. (1900) On Crustacea brought by Dr. Willey from the South Seas. *In*: Willey, A. (Ed.), *Zoological Results based on material from New Britain, New Guinea, Loyalty Islands and Elsewhere collected during the years 1895, 1896 and 1897. Part V*. Cambridge University Press, Cambridge, pp. 668–670.
Steenstrup, J.J.S. & Lütken, C.F. (1861) Bidrag til Kundskab om det aabne Havs Snyltekrebs og Lernaeer samt om nogle andre nye eller hidtil kun ufuldstaendigt kjendte parasitiske Copepoder. *Kongelige Danske Videnskabernes Selskabs Skrifter, naturhistorisk og mathematisk Afdeling*, 5 (5), 341–432.
https://doi.org/10.5962/bhl.title.59539
Suárez-Morales, E. & Gasca, R. (2012) A new *Lepeophtheirus* (Copepoda: Siphonostomatoida: Caligidae) from Isla del Coco National Park, Costa Rica, Eastern Tropical Pacific. *Revista de Biología Tropical*, 60 (S3), 235–242.
https://doi.org/10.15517/rbt.v60i3.28371
Suárez-Morales, E. & Gasca, R. (2016) A new species of *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida: Caligidae) from coral reef plankton in the Mexican Caribbean. *Zootaxa*, 4174 (1), 424–436.
https://doi.org/10.11646/zootaxa.4174.1.26
Suárez-Morales, E., Camisotti, H. & Martín, A. (2012a) A new species of *Caligus* (Copepoda, Siphonostomatoida) from the plankton of the Caribbean coast of Venezuela with a key to species. *ZooKeys*, 201, 59–71.
https://doi.org/10.3897/zookeys.201.3099
Suárez-Morales, E., Kim, I.-H. & Escamilla, B.J. (2012b) On some Caligids (Copepoda: Caligidae) from plankton of a coastal lagoon in the Gulf of Mexico with a description of a new species of *Metacaligus*. *Zoological Studies*, 51, 804–818.
Suarez-Morales, E., Kim, I.H. & Lopez-Salgado, I. (1998) An illustrated record and range extension of *Caligus chelifer* (Copepoda, Siphonostomatoida) in the Gulf of Mexico. *Gulf Research Reports*, 10, 57–60.
https://doi.org/10.18785/grr.1001.06
Thomsen, R. (1949) Copépodos parásitos de los peces marinos del Uruguay. *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo*, 3, 1–41.
Todd, C.D., Laverack, M.S. & Boxshall, G.A. (1996) *Coastal Marine Zooplankton: A Practical Manual for Students*. 2nd Edition. Cambridge University Press, Cambridge, 106 pp.
Venmathi Maran, B.A. & Ohtsuka, S. (2008) Descriptions of caligiform copepods in plankton samples collected from East Asia: Accidental occurrences or a new mode of life cycle? *Plankton and Benthos Research*, 3, 202–215.
https://doi.org/10.3800/pbr.3.202
Venmathi Maran, B.A., Ohtsuka, S. & Jitchum, P. (2012a) Occurrence of caligid copepods (Crustacea) in plankton samples collected from Japan and Thailand, with the description of a new Species. *Species Diversity*, 17, 87–95.
https://doi.org/10.12782/sd.17.1.087
Venmathi Maran, B.A., Ohtsuka, S. & Shang, X. (2012b) Records of adult caligiform copepods (Crustacea: Copepoda: Siphonostomatoida) in marine plankton from East Asia, including descriptions of two new species of *Caligus* (Caligidae). *Species Diversity*, 17, 201–219.
https://doi.org/10.12782/sd.17.2.201
Venmathi Maran, B.A., Suárez-Morales, E., Ohtsuka, S., Soh, H.Y. & Hwang, U.W. (2016) On the occurrence of caligids (Copepoda: Siphonostomatoida) in the marine plankton: a review and checklist. *Zootaxa*, 4174 (1), 437–447.
https://doi.org/10.11646/zootaxa.4174.1.27
Walter, T.C. & Boxshall, G.A. (2023) World of Copepods database. Caligidae Burmeister, 1835. Accessed through: World Register of Marine Species. Available from: https://www.marinespecies.org/aphia.php?p=taxdetails&id=135513 (accessed 30 January 2024)
Wilson, C.B. (1905) North American parasitic copepods belonging to the family Caligidae, Part I.—The Caliginae. *Proceedings of the United States National Museum*, 28, 479–672.
https://doi.org/10.5479/si.00963801.28-1404.479

Wilson, C.B. (1906) Report on some parasitic Copepoda collected by Professor Herdman, at Ceylon, in 1902. *In*: Herdman, W.A. (Ed.), *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar*, 1906, pp. 189–210.
Wilson, C.B. (1908) North American parasitic copepods: New genera and species of Caliginae. *Proceedings of the United States National Museum*, 33, 593–627.
https://doi.org/10.5479/si.00963801.33-1580.593
Wilson, C.B. (1913) Crustacean parasites of West Indian fishes and land crabs, with descriptions of new genera and species. *Proceedings of the United States National Museum*, 44, 189–227.
https://doi.org/10.5479/si.00963801.44-1950.189
Wilson, C.B. (1935) Parasitic Copepods from the Pacific Coast. *American Midland Naturalist*, 16, 776.
https://doi.org/10.2307/2420107
Wilson, C.B. (1936) Plankton of the Bermuda Oceanographic Expeditions IV. Notes on Copepoda. *Zoologica Scientific Contributions of the New York Zoological Society, New York*, 21, 89–93.
https://doi.org/10.5962/p.203698
Wilson, C.B. (1950) Copepods gathered by United States Fisheries Steamer. *Bulletin of United States National Museum*, 14, 141–441.
Yamaguti, S. (1936) *Parasitic copepods from fishes of Japan. Part 2. Caligoida I*. Published by the author, Kyoto, 22 pp., 12 pls. [private publication]
Yamaguti, S. (1939) Parasitic copepods from fishes of Japan. Part 5. Caligoida, III. *Jubilar Vol. for Prof. Sadao Yoshida*, 2, 443–487.

SUPPLEMENTARY VIDEO LEGENDS

SV-IZM1. *Caligus izmiriensis* sp. nov. Drishti applied 3D-CLSM video of female sternal furca SV-IZM2. *Caligus izmiriensis* sp. nov. Drishti applied 3D-CLSM video of female leg 2 exopod SV-IZM3. *Caligus izmiriensis* sp. nov. Drishti applied 3D-CLSM video of male antenna

SV-IZM4. *Caligus izmiriensis* sp. nov. Drishti applied 3D-CLSM video of male maxilliped

SV-SAR5. *Caligus sarosensis* sp. nov. Drishti applied 3D-CLSM video of female genital complex (ventral)

SV-SAR6. *Caligus sarosensis* sp. nov. Drishti applied 3D-CLSM video of female abdomen (ventral)