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Parasitic copepods of the common sole, *Solea solea* (L.), from the Eastern Mediterranean coast of Turkey

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Abstract There is increasing interest in the common sole, *Solea solea* (Linnaeus), as an alternative fish species in aquaculture in the Mediterranean region, and parasitic copepods are a potential hazard for farmed finfish. This paper provides taxonomic information on two species of sea lice (family Caligidae) collected from *S. solea* in eastern Mediterranean waters off the Turkish coast. *Caligus brevicaudatus* A. Scott, 1901 and *Caligus apodus* (Brian, 1924) were both found and this is the first report of *C. brevicaudatus* in Turkish waters. The discovery of *C. apodus* on *S. solea* is a new host record. Key diagnostic characters of both species are reported, supported by light and scanning electron microscopy observations. During a 12-month survey a prevalence of 28% was recorded for *C. brevicaudatus*, whereas for *C. apodus* peak prevalence was much lower (3%).

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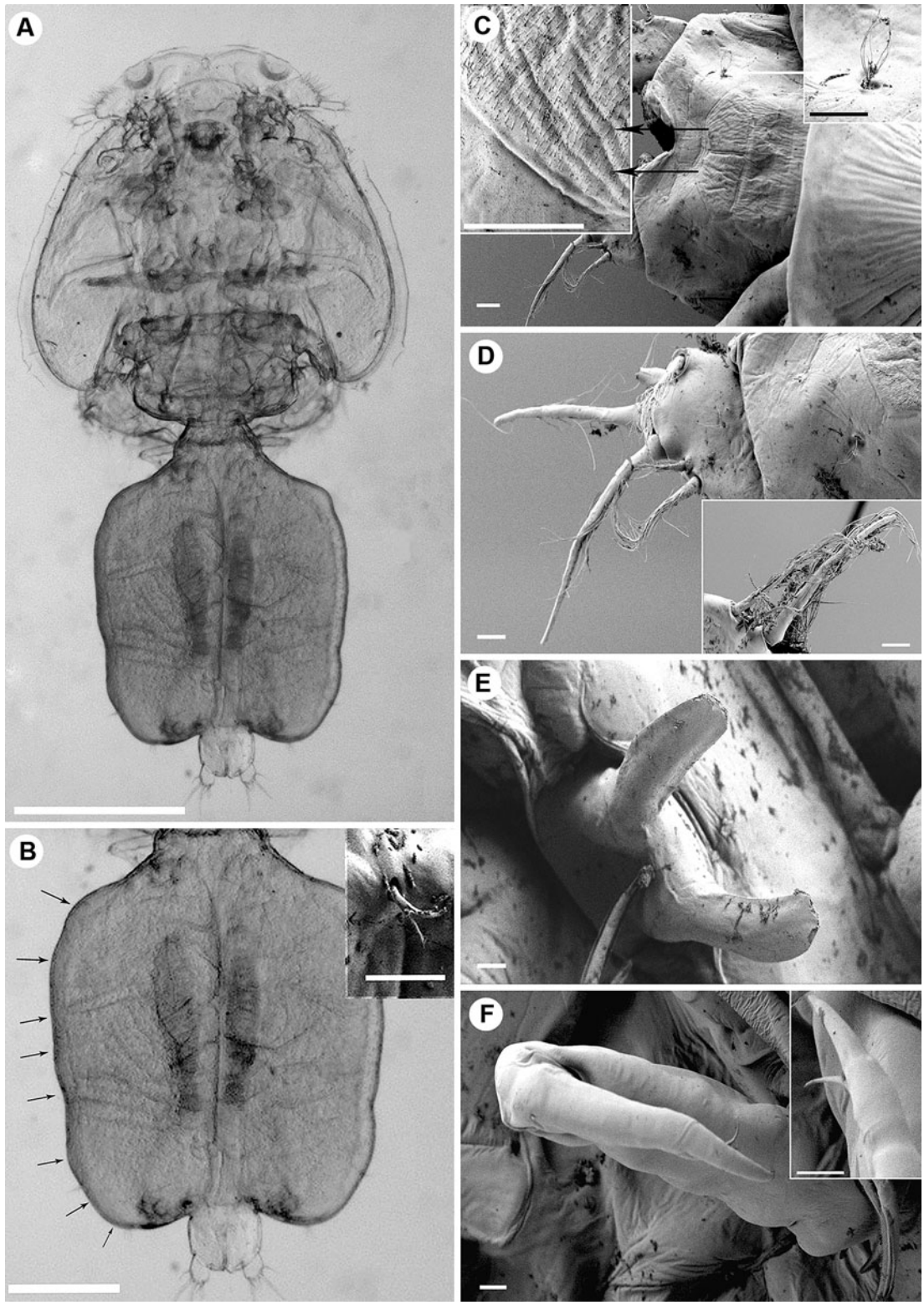
Introduction

The common sole, *Solea solea* (Linnaeus), is one of the most economically important fish species in the Mediterranean due to its high market value. Since about 30 years ago, this flat fish has been considered one of the most promising species for marine aquaculture (Imsland et al., 2009) and, to the best of our knowledge, at least three fish farming companies have recently started cultivation trials in Turkey. The successful commercialization of sole aquaculture will require improved knowledge of diseases and the development of parasite and disease management strategies.

At least one viral (Viral nervous necrosis) and five bacterial (Blackpatch necrosis, Vibriosis, Tailrot, Furunculosis and Redspot) diseases have thus far been reported during the cultivation trials of common sole (Flütchter, 1979; Baudin-Laurencin, 1986; Bernadet et al., 1990; Starkey et al., 2001; Imsland et al., 2003). In addition, many parasite species including haemoflagellates, ichthyobdellid leeches, trematodes, isopods and copepods have been reported from *S. solea* across its range (Claus, 1864; Slinn, 1970; Boxshall, 1974; Kirmse, 1987; Palm et al., 1999; Kabata, 2003; Kayis and Ceylan 2011). Among these groups of parasites infecting *S. solea*, the copepods, with nine species reported, are the most species rich.

Parasitic copepods are known as disease causing agents in marine and brackish-water fish culture (e.g. Cruz-Lacierda et al., 2011). In particular, species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◀**Fig. 1** *Caligus brevicaudatus* (Female). A, Habitus, dorsal view; B, Compound sensillae aligned along the lateral margins of the genital complex (black arrows), *inset*: bifid sensilla; C, Abdomen, ventral view, *insets:* patch of spinules (black arrows) and compound sensilla (white arrow); D, Caudal ramus, *inset:* unequal outermost two setae; E, Sternal furca with diverging tines; F, Maxilliped, *inset:* tip of maxilliped. *Scale-bars*: A, 1 mm; B, 0.5 mm; B *inset*, 10 μm; C, C *insets*, 30 μm; D *inset*, 15 μm; D, E, F, F *inset*, 20 μm

belonging to the family Caligidae, the sea lice, cause high mortalities in aquaculture (Johnson et al., 2004) and may also serve as vectors for other disease agents (Nylund et al., 1994). Sea lice also adversely affect growth rate and fecundity of marine fish in culture species, as has recently been emphasised in disease reports worldwide (e.g. Johnson et al., 2004; Lester & Hayward, 2006; Cruz-Lacierda et al., 2011). The aim of this research was to determine which sea lice species naturally infect *S. solea* in the eastern Mediterranean off the Turkish coast. A one-year parasitological survey was conducted in İskenderun Bay, Turkey. Morphological examination of the collected parasites revealed the presence of two species of caligids: *Caligus brevicaudatus* Scott, 1901 and *Caligus apodus* (Brian, 1924) both of which inhabited the upper surface of S. *solea*. Their characteristic features are briefly described.

Materials and methods

A one-year (December 2011–December 2012) parasitological survey was conducted to determine which parasitic copepods were present on *Solea solea* (L.) in İskenderun Bay, Turkey. Fish were caught monthly by Sole trammel nets in İskenderun Bay, near Yumurtalık (36°45′30.11″N, 35°43′08.75″E), Karataş (36°30′01.88″N, 35°23′14.60″E) and Konacık (36°21′51.23″N, 35°45′46.74″E). The body surface (upper and lower),

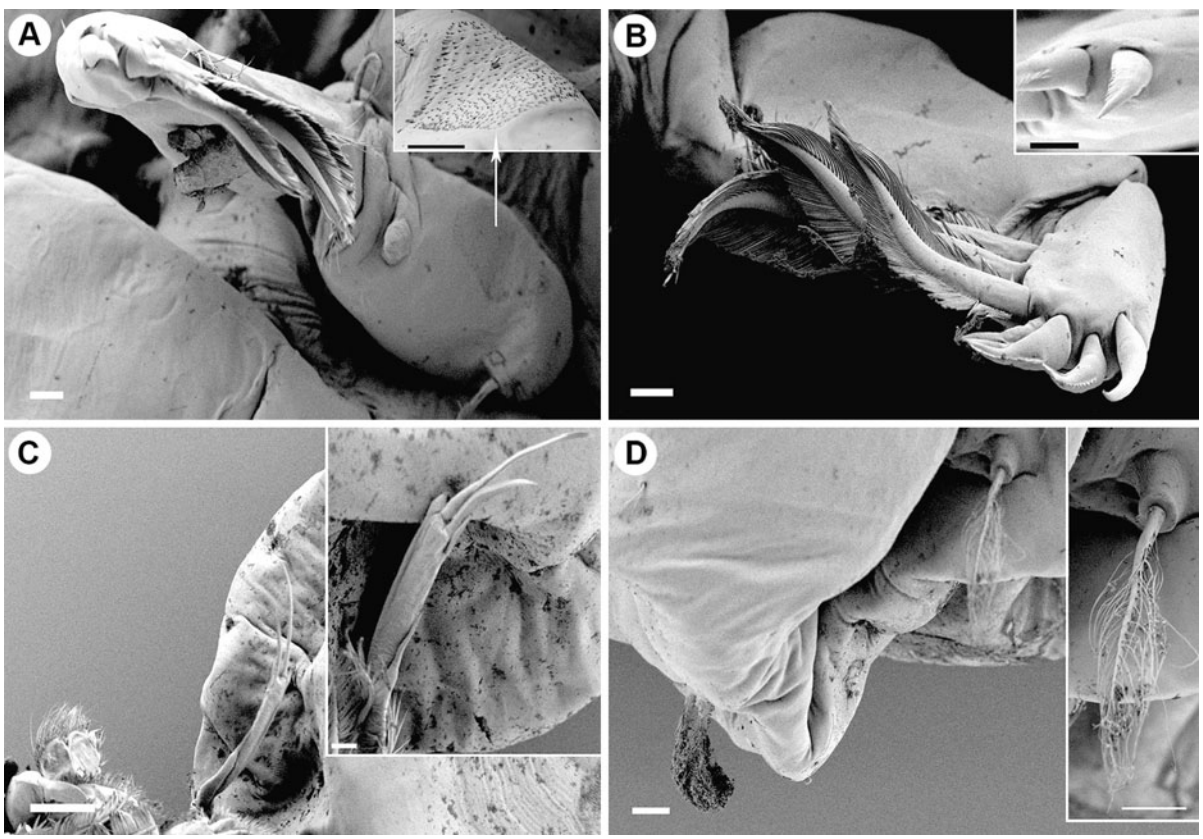

Fig. 2 *Caligus brevicaudatus* (Female). A, Leg 1, *inset:* patch of spinules on protopod (white arrow); B, Distal exopodal segment of leg 1, *inset:* outermost terminal element (spine 1); C, Two-segmented exopod of leg 4, *inset:* tip of leg; D, Leg 5, *inset:* isolated plumose seta of leg 5. *Scale-bars*: 20 μm

gill cavities and gill filaments of the fish were examined. The fish ($n = 3{,}316$) ranged in total length from 11 to 23 cm.

Parasitic copepods were collected from the upper body surface of the infested fish and immediately preserved in 70% ethyl alcohol. Specimens were cleared in lactic acid for 2 h prior to examination using an Olympus SZX16 dissecting microscope and Olympus BX51 compound microscope. Intact specimens and individual appendages were photographed with a digital camera on both microscopes. The scientific and common names of fishes follow Froese & Pauly (2013) and the morphological terminology for the copepods follows Huys & Boxshall (1991). All measurements are in millimetres unless otherwise stated.

The protocols for preparing crustaceans for scanning electron microscopy (SEM) outlined by Felgenhauer (1987) were followed. Ethanol-fixed specimens were hydrated to distilled water and post-fixed in 1–2% osmium tetroxide (OsO_4) in buffer for 2 h, washed in distilled water, dehydrated through graded acetone series, critical point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with platinum. Coated specimens were examined on a Zeiss Supra 55 (FE-SEM, Germany) field emission scanning electron microscope at 1–3 kV.

Results

Two species of *Caligus* were found. *Caligus brevicaudatus* was originally described by A. Scott (1901) and subsequently redescribed by Kabata (1979) and Choi et al. (1995). *Caligus apodus* was originally described by Brian (1924) (as *Pseudocaligus apodus*) and subsequently redescribed by Brian (1935) and Ben Hassine (1983). Here, only the characteristics important for accurate identification are highlighted and illustrated by light and scanning electron micrographs.

Caligus brevicaudatus A. Scott, 1901

Material examined

Collection of the Natural History Museum, London: 32 females collected from mouth of *Chelidonichthys lucerna* (Linnaeus) (as *Trigla lucerna*) in Luce Bay, 1912 and submitted by T. & A. Scott (BMNH Reg. Nos 1913.9.18.77-86).

Newly collected material: Twenty-nine ovigerous females collected from the upper surface of *Solea solea* (L.) caught in İskenderun Bay, Turkey were examined. Five female *C. brevicaudatus* are deposited at the Natural History Museum, London (BMNH 2013.68-72); the remaining parasites are in the personal collection of the first author.

Prevalence: 28% (928 of 3,316 hosts parasitised) over the 12-month period of study.

Description (Figs. 1–2)

Adult female. Total body length 3.82 (3.48–4.1) ($n = 10$); cephalothorax longer than wide, 2.01 × 1.7; genital complex (Fig. 1B) subrectangular, longer than wide, 1.45 × 1.36, about 5.8 times longer than 1-segmented abdomen (Fig. 1C), 0.25 × 0.35 mm. Genital complex with distinctive ornamentation of about 8 compound sensillae aligned along lateral margins of genital complex (Fig. 1B, inset); abdomen ornamented with sensillae and with patch of spinules on central part of ventral surface (Fig. 1C, insets). Cephalothorax 1.7, approximately 1.18 times longer than combined length of genital complex and abdomen. Caudal rami (Fig. 1D) each with 6 pinnate setae plus fringe of pinnules along inner margin; outermost seta about twice as long as adjacent seta (Fig. 1D, inset).

Sternal furca with slightly diverging tines, with blunt tips, and square box (Fig. 1E). Maxilliped (Fig. 1F) comprising robust protopod (corpus) with smooth medial margin; distal subchela armed with short, tapering claw carrying single seta more than half length of claw (Fig. 1F, inset). Swimming leg 1 (Fig. 2A) biramous; with 2-segmented exopod and vestigial, lobate endopod. Protopod (Fig. 2A, inset) armed with plumose seta on anterodistal corner and plumose seta on posteromedial margin, ornamented with patch of spinules on ventral surface near base. Distal exopodal segment (Fig. 2B) with 4 terminal elements about equal in length, outermost element (spine 1) finely serrated on inner margin (Fig. 2B, inset), middle two elements (spines 2 and 3) each bearing single accessory process, and ornamented with fine serrations along inner and outer margins, innermost element (seta 4) at inner distal angle, unarmed; posterior margin with 3 long plumose setae.

Leg 4 uniramous, comprising protopod plus 2-segmented exopod. Protopod armed with long outer plumose seta and ornamented with multi-sensillate papilla. Exopod (Fig. 2C) slender; first exopodal segment bearing finely serrated outer distal spine, terminal segment with 3 finely serrated, unequal apical setae (Fig. 2C, inset). Spine (Roman numerals) and seta (Arabic numerals) formula of legs 1–4 as follows:

	Exopod	Endopod
Leg 1	I-0; III, I, 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; III	absent

Leg 5 (Fig. 2D) comprising single seta on isolated papilla (Fig. 2D, inset) plus papilla with 2 setae, about equal in length, located on posterolateral margin of genital complex. Bifid sensillae present on body surface in vicinity of leg 5 papillae.

Remarks

Caligus brevicaudatus was first reported as parasitic on *Eutrigla gurnardus* (Linnaeus) from Liverpool Bay by A. Scott (1901). It was subsequently also reported from *Chelidonichthys lucerna* (Linnaeus) in British waters (Scott & Scott, 1913; Scott, 1929). *Caligus brevicaudatus* has also been reported from other parts of the world, including the Baltic Sea, Table Bay (South Africa), the Barents Sea (Russia), the Gulf of Naples (Italy), Kamak Bay (Korea), the Gulf of Tunisia (Tunisia), the North Sea and from off the Portuguese Coast (van Oorde-de Lint & Schuurmans Stekhoven 1936; Barnard, 1955; Markevich, 1956; Reichenbach-Klinke, 1956; Rohde, 1980; Choi et al., 1995; Benmansour & Ben Hassine, 1997; Palm et al., 1999; Marques et al., 2006, 2009). Although *C. brevicaudatus* has most commonly been reported from gurnards (family Triglidae), it has also been found on two flatfish species: *Paralichthys olivaceus* (Temminck & Schlegel) and *S. solea* (see Choi et al., 1995; Marques et al., 2009).

The morphological characteristics of our adult females were similar to those of *C. brevicaudatus*, as described by A. Scott (1901), Kabata (1979) and Choi et al. (1995). In particular, the similarities included: (i) the subrectangular shape of the genital complex; (ii) the presence of about eight sensillae along the lateral margins of the genital complex; and (iii) the short 1-segmented abdomen. In addition, the ornamentation and setation of legs 1 and 4 were identical in fine detail. We also report two previously unrecognised characters which are of taxonomic value. First, there is a patch of spinules on the central part of the ventral surface of abdomen (see Fig. 1C, insets); and secondly, there is a patch of fine spinules on the ventral surface of the basal part of leg 1 (Fig. 2A, inset).

Our Turkish specimens have a smaller mean body length of 3.82 mm when compared with the previous measurements reported from Korea (4.06 mm) and Britain (5.30 mm), respectively (Choi et al., 1995; A. Scott, 1901). Detailed comparison between the Turkish specimens and the specimens identified and presented by T. & A. Scott, stored in the collection of the Natural History Museum, London (BMNH Reg. Nos. 1913.9.18.77-86), revealed close similarities in all morphological features and in body proportions. However, the re-measured mean total body length of Scott's females was 4.48 mm (4.13–4.76) ($n = 10$), about 1.2 times longer than the Turkish females. In the absence of any significant differences in limb structure, setation and ornamentation, we infer that the size differences represent geographical variation. Such a size difference between the British and Mediterranean specimens may be correlated with temperature differences.

In the redescription of *C. brevicaudatus* from Korea (Choi et al., 1995) the outermost two setae of the caudal rami were illustrated as equal in length but in the Turkish material, our SEM images showed these two outermost setae as very unequal in length (Fig. 1D, inset). Again, in the absence of other differences, we interpret this as representing regional variation.

Caligus apodus (Brian, 1924)

Syns *Pseudocaligus apodus* Brian, 1924; *Pseudolepeophtheirus mediterraneus* Paperna, 1964

Material examined

Two syntype females, MNHN-Cp-267, collected by A. Brian on 3 January 1923 (Brian, 1924). The data on the label in the vial are "sur *Mugil cephalus*, 3-1-23". One syntype female, MNHN-Cp-269, collected by A. Brian on 13 August 1923 (Brian, 1924). The data on

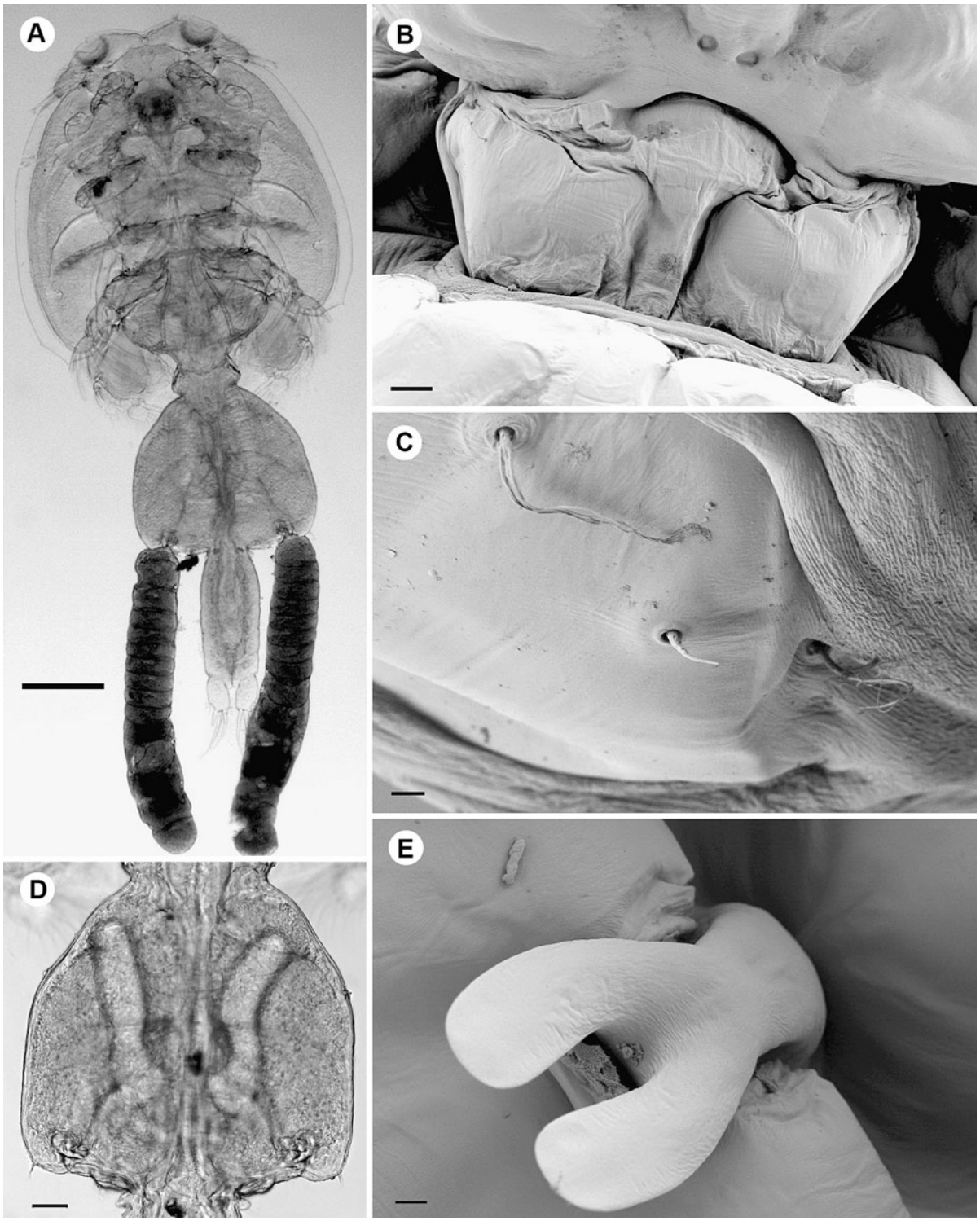

Fig. 3 *Caligus apodus* (Female). A, Habitus, dorsal view; B, Fourth pedigerous somite, dorsal view; C, Sensillae and spiniform structure on posterolateral corner of fourth pedigerous somite; D, Genital complex; E, Sternal furca with rounded spatulate tips. *Scale-bars*: A, 0.5 mm; B, 40 μm; C, 4 μm; D, 0.1 mm; E, 10 μm

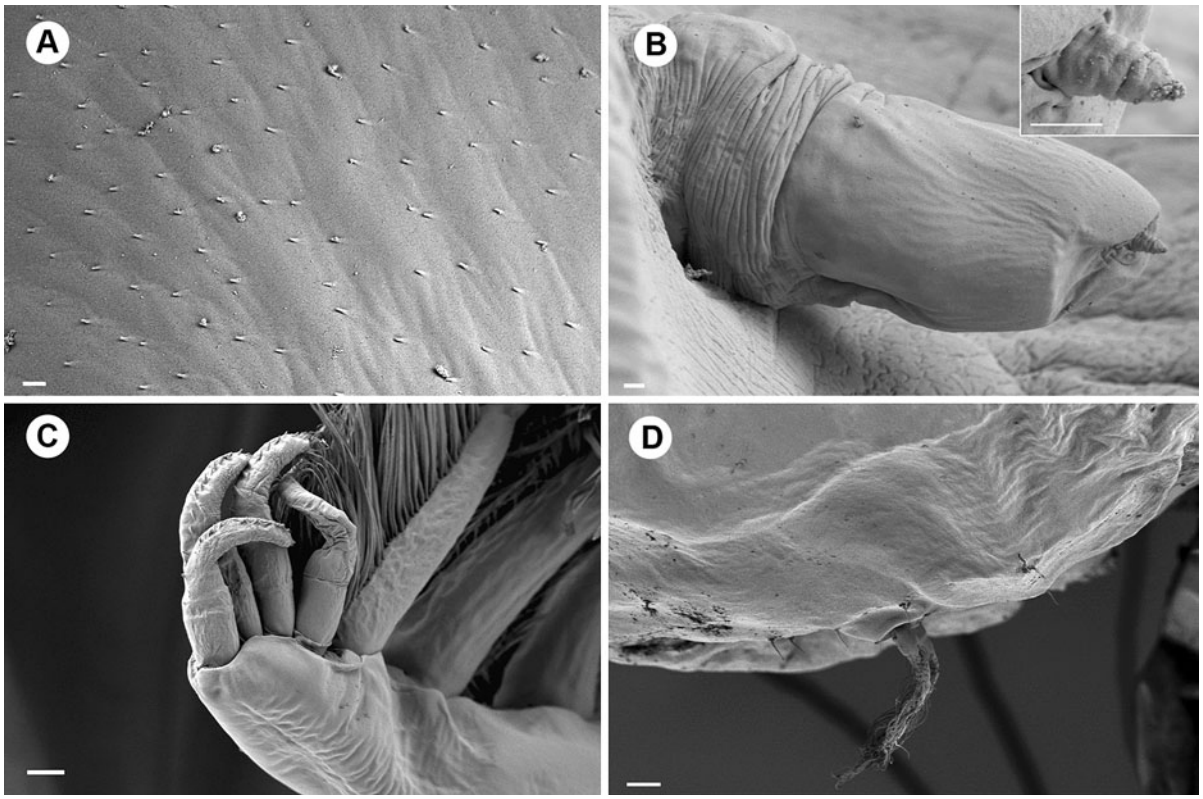

Fig. 4 *Caligus apodus* (Female). A, Patch of spinules on protopod of leg1; B, Vestigial endopod of leg1, *inset*: tiny spiniform structure at apex; C, Tip of distal exopodal segment of leg1; D, Leg 5 with three plumose setae, and sensillae on adjacent body surface. *Scale-bars*: A, B, B *inset*, 1 μm; C, D, 10 μm

the label in the vial are "squalide 402, surpeaudorsale, 13 août 1923".

Five females and three males from upper surface of *Solea solea* (L.) caught in İskenderun Bay, Turkey were examined. Two females and one male *C. apodus* are stored at the Natural History Museum, London (BMNH 2013.73-75); the remaining parasites are in the personal collection of the first author.

Prevalence: 3% (99 of 3,316 hosts parasitised) over the 12-month period of study.

Description (Figs. 3-6)

Adult female. Total body length 4.30 (4.22–4.38) ($n = 5$), with suborbicular cephalothorax and slightly longer than wide, 2.06 × 2.03. Fourth pedigerous somite (Fig. 3B) wider than long, 0.23 × 0.41, and without trace of fourth leg; surface ornamented with 2 sensillate papillae in mid-margin plus spiniform structure posterolaterally (Fig. 3C). Genital complex (Fig. 3D) as long as wide, 0.94 × 0.94, tapering gradually anteriorly and with rounded posterolateral corners. Abdomen 1-segmented, 0.89 × 0.38, about four times longer than caudal rami. Caudal rami longer than wide, 0.22 × 0.13. Cephalothorax 2.06 long, slightly longer than combined length of genital complex and abdomen, 1.83 mm. Tines of sternal furca slightly incurved, spatulate, with rounded tips (Fig. 3E). Swimming leg 1 biramous, with 2-segmented exopod and vestigial endopod. Protopod armed with lateral plumose seta and short medial seta (both derived from basis) and ornamented with patch of fine spinules (Fig. 4A). Lobate endopod (Fig. 4B) with single tiny spine-like vestige at tip (Fig. 4B, inset). First exopodal segment fringed with row of setules on inner margin, and bearing small spine at outer distal corner. Terminal exopodal segment (Fig. 4C) with 3 unequal plumose setae on inner

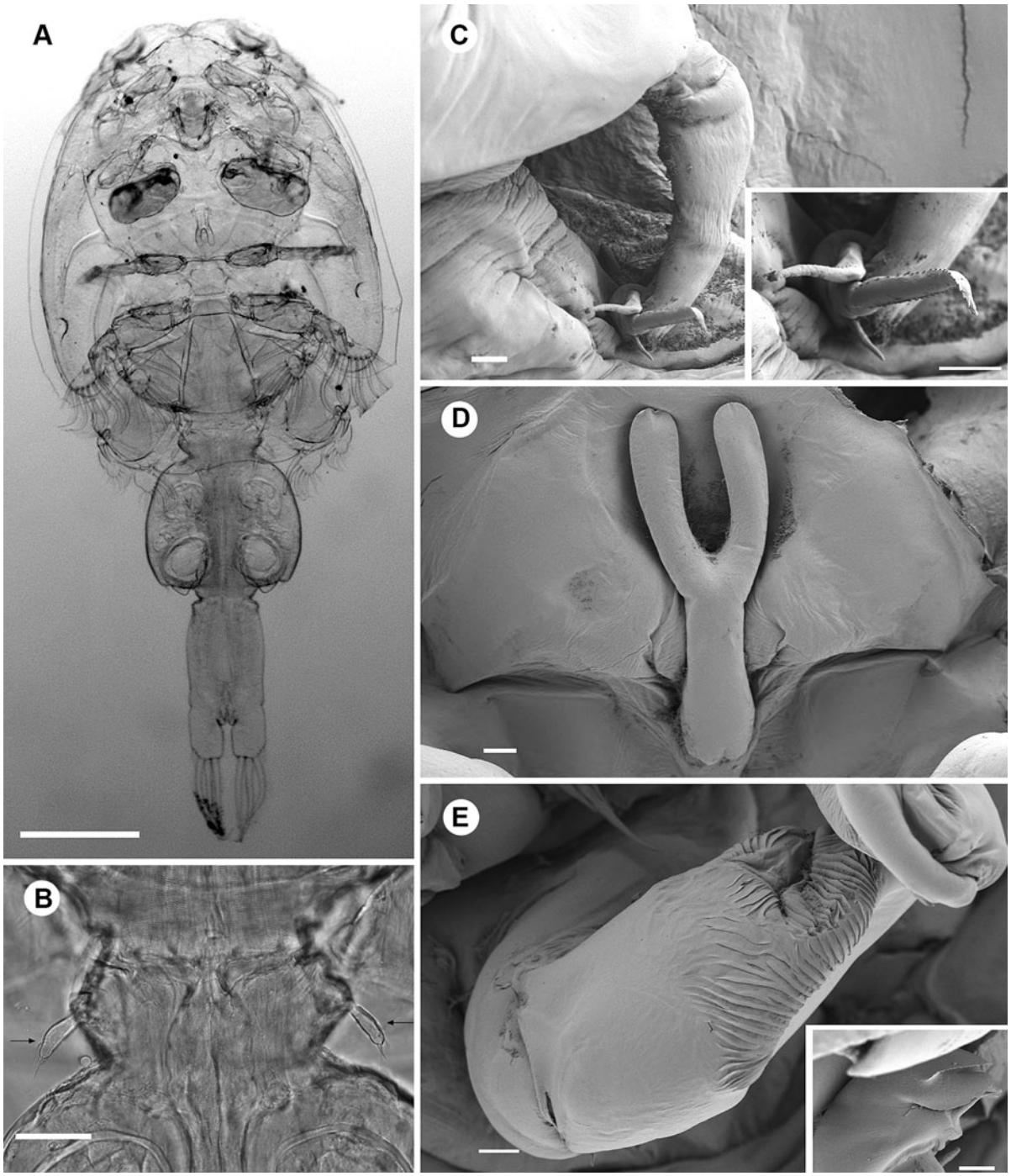

Fig. 5 *Caligus apodus* (Male). A, Habitus, ventral view; B, Fourth pedigerous somite with vestigial leg 4 (black arrows); C, Vestigial fourth leg, *inset*: detailed structure of terminal elements; D, Sternal furca; E, Middle segment of antenna with adhesion pads, *inset*: tip of distal segment of antenna with overlapping flaps. *Scale-bars*: A, 0.5 mm; B, 0.1 mm; C, C *inset*, 10 μm; D, E, 20 μm; E *inset*, 10 μm

margin, plus 4 spiniform elements about equal in length along distal margin. Outermost element (spine 1) and middle 2 elements (spines 2 and 3) finely serrated along margins, element (seta 4) at inner distal angle, unarmed. Spine (Roman numerals) and seta (Arabic numerals) formula of legs 1–4 as follows:

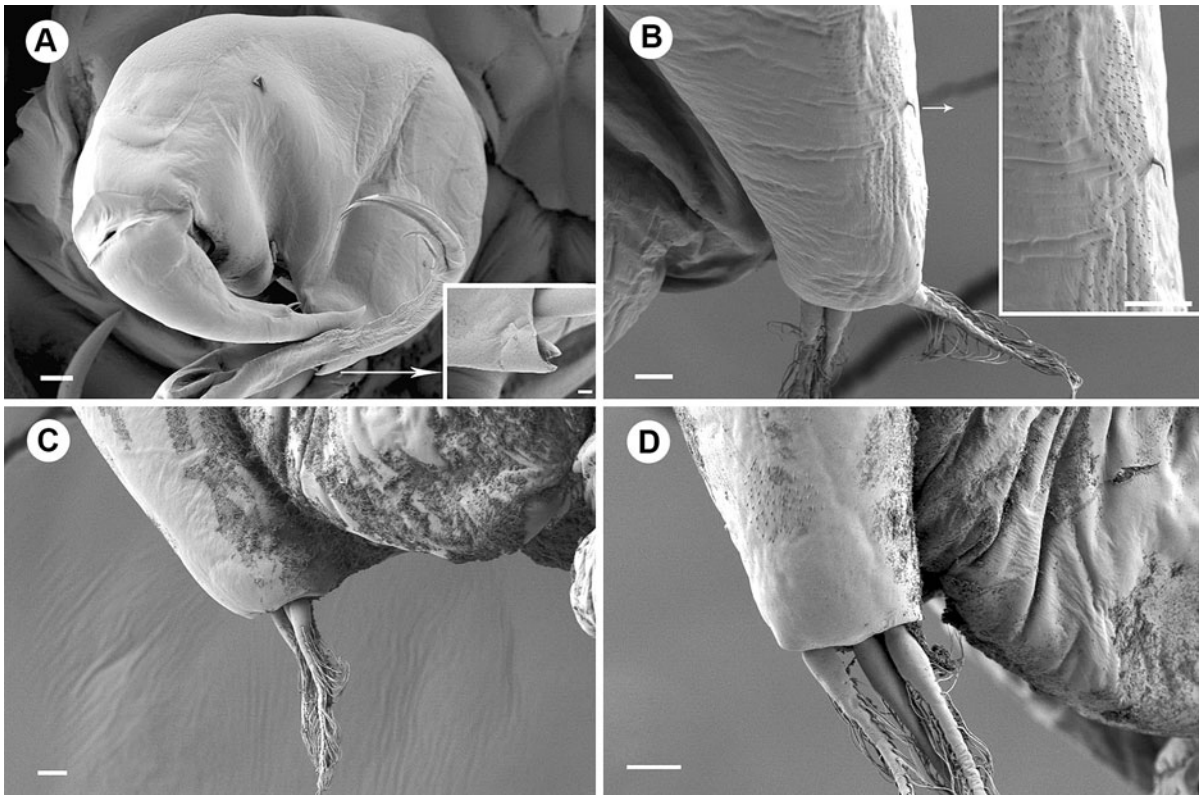

Fig. 6 *Caligus apodus* (Male). A, Maxilliped, *inset*: double points of myxal process (white arrow); B, Leg 5 (white arrow), *inset*: patches of spinules; C, Leg 6 with three plumose setae; D, Patch of spinules on anterior part of Leg 6. *Scale-bars*: A, 30 μm; A *inset*, B, B *inset*, C, D, 10 μm

	Exopod	Endopod
Leg 1	I-0; III, I, 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	vestigial	absent

Leg 5 (Fig. 4D) comprising single papilla with 3 plumose setae; sensillate papillae present on body surface in vicinity of leg.

Male (Fig. 5A). Total body length 3.19 (3.17–3.21) ($n = 3$), with suborbicular cephalothorax slightly longer than wide, 1.59 × 1.32. Fourth pedigerous somite (Fig. 5B) wider than long, 0.17 × 0.35, carrying paired vestige of fourth legs posterolaterally (Fig. 5C). Genital complex (Fig. 5D) wider than long, 0.57 × 0.64, bearing two protrusions on posterior margin; abdomen 0.54 × 0.32, 1-segmented. Cephalothorax about 1.43 times longer than combined length of genital complex and abdomen. Caudal rami longer than wide, 0.20 × 0.13. Antenna (Fig. 5F) 3-segmented; middle segment bearing 2 broad adhesion pads; distal segment terminating in 3 overlapping cuticular flaps, each with rounded free margin, armed with 2 unequal slender setae. Maxilliped (Fig. 6A) with robust corpus produced into conspicuous bifid-pointed process on myxal margin; shaft claw more than half length of corpus, armed with seta at base of claw (Fig. 6A, inset). Tines of sternal furca (Fig. 5E) almost parallel, slightly longer (0.14) than rectangular box (0.12), rounded at tip. Leg 4 reduced, indistinctly 3-segmented, located posterolaterally on somite (Fig. 5C). Middle segment bearing 1 pinnate spine at outer distal corner, terminal segment with 3 unequal spiniform elements at apex (Fig. 5C, inset), lateral margins of outer and middle spines finely serrated, serrations very small; innermost element shortest and unarmed. Leg 5 (Fig. 6B) represented by single papilla on posterolateral margin of genital complex bearing single spiniform, posteriorly-curved process; body

surface ornamented with patches of spinules in vicinity of papilla (Fig. 6B, inset). Leg 6 (Fig. 6C) comprising papilla carrying 3 plumose setae located on posterolateral corner of genital complex, ornamented with dorsolateral patch of spinules on surface (Fig. 6C, inset).

Remarks

Caligus apodus was first described by Brian (1924) as *Pseudocaligus apodus* and was recorded on *Mugil cephalus* (Linnaeus) and *Galeorhinus galeus* (Linnaeus) (as *Eugaleus galeus*) caught off the coast of Mauritania (Brian, 1924). No type was designated but the description was based on a female of length "environs 5 mm" which is the length given in the text for the four specimens from *M. cephalus* (L.). We conclude that the type-host is *M. cephalus* (L.). The report from an elasmobranch host is atypical and we consider it most likely to represent contamination within the net by host transfer while the fish were being landed. The type-series as listed by Brian (1924) comprised five females and no males.

Subsequently this parasite was reported on different members of the Mugilidae from around the coast of Africa, from different parts of the Mediterranean, and from further afield (Rose & Vaissiere, 1953; Rangnekar, 1955; Capart, 1959; Paperna, 1964; Paperna & Lahav, 1971, 1974; Raibaut et al., 1971; Paperna, 1975; Raibaut & Ben Hassine, 1977; Braun, 1981; Paperna & Overstreet, 1981; Radujkovic, 1982; Altunel, 1983; Ben Hassine, 1983; Arru et al., 1988; Ragias et al., 2004). Paperna (1964) described *Pseudolepeophtheirus mediterraneus* Paperna, 1964 on the basis of material from *Liza ramada* (Risso) (as *Mugil capito*), but Paperna & Lahav (1974) subsequently recognised this species to be a synonym of *P. apodus*, as was later confirmed by Raibaut & Ben Hassine (1977). The synonymy of *Pseudocaligus* A. Scott, 1901 and *Caligus* O.F. Müller, 1785 is reviewed in the discussion below.

Pseudocaligus apodus Brian, 1924, was placed in the genus *Pseudocaligus* A. Scott, 1901 due to the complete absence of the fourth leg in the female. However, Ben Hassine (1983) redescribed *P. apodus* based on specimens collected from grey mullets caught off Tunisia and noted the presence of vestigial fourth legs in both females and males. In contrast to Ben Hassine (1983), we did not observe even a trace of the fourth leg in our females (Fig. 3B). In addition, our females are distinguishable from the Tunisian material in the possession of a sternal furca which has its tines slightly inwardly curved (*vs* slightly divergent); the swimming leg 1 has a vestigial endopod bearing only one tiny but noticeable spiniform process on its apex (*vs* one small spiniform process plus two minute denticle-like structures) and is ornamented with a patch of spinules on the protopod (*vs* none); and leg 5 comprises a single papilla carrying three plumose setae (*vs* a setate papilla plus an anterior spine).

We also observed differences between our males and the description of the male given by Ben Hassine (1983). These include: the maxilliped claw bears only a single seta at its base (*vs* one seta plus a minute second seta anteriorly), the tips of the two myxal processes lack any ornamentation (*vs* ornamented with tiny denticles); the distal segment of the antenna consists of three overlapping cuticular flaps with rounded free margins (*vs* sharply pointed tips) and is armed with two slender basal setae (*vs* one slender basal seta plus two equal small denticles); the postantennal process bears two multi-sensillate papillae plus one similar multi-sensillate single papilla (*vs* plus three) located on body surface adjacent to postantennal process; leg 5 comprises a papilla carrying a single, posteriorly-curved spiniform process on the posterolateral margin of the genital complex (*vs* a single papilla carrying three plumose setae at the posterolateral corner of the genital complex); and leg 6 comprises a papilla sited at the posterolateral corner of the genital complex and carrying three plumose setae (*vs* with two small knob-like processes on the posterior margin of the genital complex).

The presence or absence of a vestigial fourth leg in females of *P. apodus* was the major discrepancy observed between the Turkish and Tunisian material. In the original description Brian (1924) emphasised the complete absence of the fourth legs in females. We re-examined the type-material of *Pseudocaligus apodus* Brian, 1924 stored in the Muséum national d'Histoire naturelle in Paris. There were two lots: MNHN-Cp-267, which contained two ovigerous adult females, one of which was distorted in preservation and could not be readily observed, and MNHN-Cp-269, which contained a single adult female. No males were present in the type-series. Close examination of the female syntypes revealed that one of the two females had no trace of the fourth leg while the second female

carried a minute, rod-like trace of a possible fourth leg on one side only of the pedigerous somite. Both females were ornamented with two sensillate papillae plus a spiniform structure located near the posterolateral corner of the fourth pedigerous somite, identical to that reported here for females from Turkish waters (Fig. 3C). In addition, other morphological features of adult females from Turkey were similar both in shape and morphometrics to the re-examined syntypes. However, the Turkish females differed slightly in having a smaller body length from those reported from *Mugil cephalus* (L.) by Brian (1924) (4.30 *vs* 5.00 mm).

The general morphology and body proportions of Turkish males of *P. apodus* were also similar to Brian's (1935) description, based on material from *M. cephalus* (L.) and *Mugil* sp. from Italy, although the total body length of our male is slightly shorter than Brian's (1935) (3.19 *vs* 4.00 mm). The vestigial fourth leg of our males carried three unequal, spiniform terminal elements at the apex while Brian (1935) described his males as carrying two spiniform terminal elements. We were unable to confirm the validity of this difference, in the absence of male syntypes.

Discussion

Kabata (1965) expressed strong reservations concerning the validity of using the state of the fourth legs as a generic-level character, diagnostic for the genera *Pseudocaligus* and *Pseudolepeophtheirus* Markevich, 1940. He considered that *Pseudocaligus* and *Pseudolepeophtheirus* should probably be synonymised with their respective related genera, *Caligus* and *Lepeophtheirus* von Nordmann, 1832. Ben Hassine (1983) also noted the lack of any significant differences between *Caligus* and *Pseudocaligus.* She placed *P. apodus* in the genus *Caligus* and used the combination *Caligus apodus*. Finally, Kabata's suggestions (Kabata, 1965, 1979) concerning the relegation of the genera *Pseudocaligus* to synonymy with the genus *Caligus* were revisited by Dojiri & Ho (2013) who formally recognised *Pseudocaligus* as a junior synonym of *Caligus*; however, they did not deal with the nomenclatural problems arising from that decision.

As a consequence of the genus-level synonymy, *Pseudocaligus brevipedis* (Bassett-Smith, 1896) and *P. parvus* (Bassett-Smith, 1898) revert to their original combinations of *Caligus brevipedis* Bassett-Smith, 1896 and *C. parvus* Bassett-Smith, 1898, respectively. *Pseudocaligus apodus* Brian, 1924 becomes *Caligus apodus* (Brian, 1924), as already proposed by Ben Hassine (1983). Three more species become new combinations: *Pseudocaligus subparvus* Hameed, 1977 becomes *Caligus subparvus* (Hameed, 1977), *Pseudocaligus laminatus* Rangnekar, 1955 becomes *Caligus laminatus* (Rangnekar, 1955), and *Pseudocaligus uniartus* Ho, Kim, Cruz-Lacierda & Nagasawa, 2004 becomes *Caligus uniartus* (Ho, Kim, Cruz-Lacierda & Nagasawa, 2004). However, three species of *Pseudocaligus* become secondary homonyms as a result of the generic level synonymy between *Pseudocaligus* and *Caligus* (see Dojiri & Ho, 2013): *Pseudocaligus fistulariae* Pillai, 1961 and *Caligus fistulariae* Yamaguti, 1936, *Pseudocaligus fugu* Yamaguti, 1936 and *Caligus fugu* Yamaguti & Yamasu, 1959, and *Pseudocaligus indicus* Hameed, 1977 and *Caligus indicus* Pillai, 1967.

In the first of these examples, *Caligus fistulariae* Yamaguti, 1936 has priority and so a substitute name is required for *Pseudocaligus fistulariae* Pillai, 1961 on transfer. According to Article 60.2 of the International Code for Zoological Nomenclature if a rejected junior homonym has available valid synonyms, then the oldest of these becomes the valid name of the taxon. In this case *Pseudocaligus tenuicauda* Shiino, 1964, which was placed in the synonymy of *Pseudocaligus fistulariae* by Pillai (1985), is the oldest available valid name. The new combination *Caligus tenuicauda* (Shiino, 1964) thus becomes the valid name for the junior secondary homonym *Pseudocaligus fistulariae* Pillai, 1961.

In the case of the secondary homonymy resulting from the transfer of *Pseudocaligus fugu* Yamaguti, 1936 to *Caligus*, it is *Caligus fugu* Yamaguti & Yamasu, 1959 that becomes the junior homonym. In the recent revision of the *Caligus productus* group by Boxshall & El-Rashidy (2009) *Caligus lagocephali* Pillai, 1961 was treated as a subjective synonym of *Caligus fugu* Yamaguti & Yamasu, 1959. Since *Caligus fugu* Yamaguti & Yamasu, 1959 is the junior secondary homonym, the oldest available valid name for this taxon is *Caligus lagocephali* Pillai, 1961 as pointed out to us by Freeman & Ogawa (pers. comm.).

In the third case of homonymy, *Caligus indicus* Pillai, 1967 retains priority as the senior homonym,

even though it has been treated as a subjective synonym of *Caligus cossacki* Bassett-Smith, 1898. *Pseudocaligus indicus* Hameed, 1977 becomes the junior secondary homonym upon transfer and requires a replacement name. We propose the substitute name *Caligus keralensis* nom. nov. as it was reported from Kerala, India.

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