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The discovery of *Lepeophtheirus lichiae* Barnard, 1948 (Copepoda: Caligidae) parasitic on leerfish, *Lichia amia* (Linnaeus) in the Mediterranean Sea

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Abstract *Lepeophtheirus lichiae* Barnard, 1948 (Copepoda: Caligidae), a very rare and poorly known sea louse, is redescribed based on a single newly collected female. The specimen was collected from the dorsal body surface of the leerfish, *Lichia amia* (Linnaeus) caught in north-eastern Mediterranean waters off the Turkish coast. The original and only available description of *L. lichiae* was incomplete and with only three illustrations: the dorsal view of the female habitus, the sternal furca, and the postantennal process. Here, we present a full re-description of female of *L. lichiae* and report it from the Mediterranean Sea for the first time.

Introduction

The common leerfish, *Lichia amia* (Linnaeus) (Teleostei: Carangidae), is one of the twenty species of carangid fishes widely distributed in the Mediterranean. Besides being a popular game fish, it is marketed commercially fresh, frozen, smoked, and salted, and it is also utilised for fishmeal and oil (Smith-Vaniz, 1986). Across its geographic range, this economically important fish has been recorded as host to nine different species of parasitic copepods belonging to eight genera, *Bomolochus unicirrus* Brian, 1902, *Caligus dakari* van Beneden, 1892, *Caligus lichiae* Brian, 1906, *Colobomatus lichiae* (Richiardi, 1877), *Eobrachiella elegans* (Richiardi, 1880), *Lepeophtheirus lichiae* Barnard, 1948, *Lernaeenicus gracilis* (Heller, 1865), *Lernanthropus gisleri* van Beneden, 1852 and *Nemesis lamna* Risso, 1826, although some of these records are almost certainly erroneous. Three of these species, *Caligus dakari*, *C. lichiae* and *Lepeophtheirus lichiae* are sealice, members of the family Caligidae Burmeister, 1835, which are known to cause serious commercial losses in marine finfish aquaculture. The first of these sealice, *C. dakari* (syn. *C. mauritanicus*), is a well-known member of the genus *Caligus* O. F. Müller, 1785 which has been reported many times on different host fishes (Capart, 1959; Pillai, 1967; Oldewage & van As, 1989; Radujkovic & Raibaut, 1989; Raibaut et al., 1998; Dippenaar, 2005; Boxshall & El-Rashidy, 2009; Öktener & Trilles, 2009). In contrast, the other two species, *C. lichiae* and *L. lichiae*, were regarded as extremely rare and poorly known copepods.

Caligus lichiae was first described over a century ago by Brian (1906) based on the material found on *Lichia amia* from off Genoa and the island of Elba

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(Italy). More than a century after its first discovery, *C. lichiae* was recently re-discovered and redescribed (Özak et al., 2019), based on specimens collected from its type-host, *L. amia* and from *Seriola dumerili* (Risso) caught in northeastern Mediterranean waters off the Turkish coast. Özak et al. (2019) concluded that *C. lichiae* is the senior synonym of *C. aesopus* Wilson C. B., 1921, a well-known and widely distributed parasite of carangid fishes.

The third sea louse species, *L. lichiae*, which belongs to *Lepeophtheirus* von Nordmann, 1832, the second largest caligid genus after *Caligus*, and was originally described by Barnard (1948) based on females collected on *L. amia* caught in the western Indian Ocean waters off Natal (Durban), South Africa. Unfortunately, the brief original description was supported by only three drawings: female habitus, the sternal furca, and the postantennal process (referred to as "maxilla 2" by Barnard, 1948). Just as for *C. lichiae*, *L. lichiae* had never been reported again since its original description. In the present study, *L. lichiae* is fully described based on the newly collected female from *L. amia* caught in northeastern Mediterranean waters off the Turkish coast.

Materials and methods

Three common leerfish, *Lichia amia* (Linnaeus) (mean total body length: 62.8 cm) were caught by long-line fishing in northeastern Mediterranean waters, near Tuzla (Karataş), Turkey on 20 September 2018. The body surface, mouth, inner and upper surface of the operculum, gill cavity and gill filaments of the fish were examined for the presence of parasitic copepods. A single female caligid was found on lateral body surface and immediately preserved in 70% ethanol. Subsequently, the specimen was mounted as a temporary preparation in a drop of lactic acid on a cavity slide for examination and taking measurements. Measurements were made using an ocular micrometer and drawings were made with the aid of a drawing tube. All measurements are in millimetres unless otherwise stated. The scientific and common name of the host fish follows Froese & Pauly (2018) and the morphological terminology for the copepod follows Boxshall (1990) and Huys & Boxshall (1991). The single female of *L. lichiae* (CUMAP-COP/2018-5) is deposited in the collections of the Aquatic Parasitology Museum at the Faculty of Fisheries, Cukurova University, Adana, Turkey. In addition, a total of five intact female specimens of *L. lichiae* (NHMUK 1979.949-952 and NHMUK 1979.954-955), stored in the collections of Natural History Museum, London, UK, were examined by one of us (GAB) for comparative purposes. The deposited females were collected from *Lichia amia* caught in western Indian Ocean waters off Natal (Durban), South Africa.

Family Caligidae Burmeister, 1835
Genus *Lepeophtheirus* von Nordmann, 1832

Lepeophtheirus lichiae Barnard, 1948

Host: *Lichia amia* (Linnaeus) (Perciformes: Carangidae).
Locality: Eastern Mediterranean waters off the Turkish coast.
Site on host: Lateral body surface, near to left pectoral fin.
Prevalence: 33.3% (1 of 3 hosts infected).
Voucher material: 1 female of *L. lichiae* (CUMAP-COP/2018-5) stored in the collections of the Aquatic Parasitology Museum at the Faculty of Fisheries, Cukurova University, Adana, Turkey

Description (Figs.1–6)

Adult female. Body (Fig. 1A) caligiform, comprising cephalothorax incorporating first to third pedigerous somites, free fourth pedigerous somite, genital complex and 1-segmented abdomen. Total body length 6.34 mm including caudal rami. Dorsal cephalothoracic shield subcircular, slightly longer than wide, 3.59 × 3.18, excluding marginal membranes, 2.1 times longer than length of thoracic zone of shield and 1.29 times longer than combined length of fourth pedigerous somite, genital complex, abdomen, and caudal rami (excluding setae); lateral margins evenly convex and ornamented with array of about 14 small dorsal sensilla plus 13 small compound sensilla beneath marginal membrane along each side (Fig. 1B); anteromedial part of frontal plate ornamented with numerous sensilla. Thoracic zone of shield wider than long (1.71 × 2.18); posterior margin of thoracic zone convex, extending beyond posterior ends of lateral zones. Fourth pedigerous somite distinctly separated from genital complex, wider than long (0.43 × 1.31).

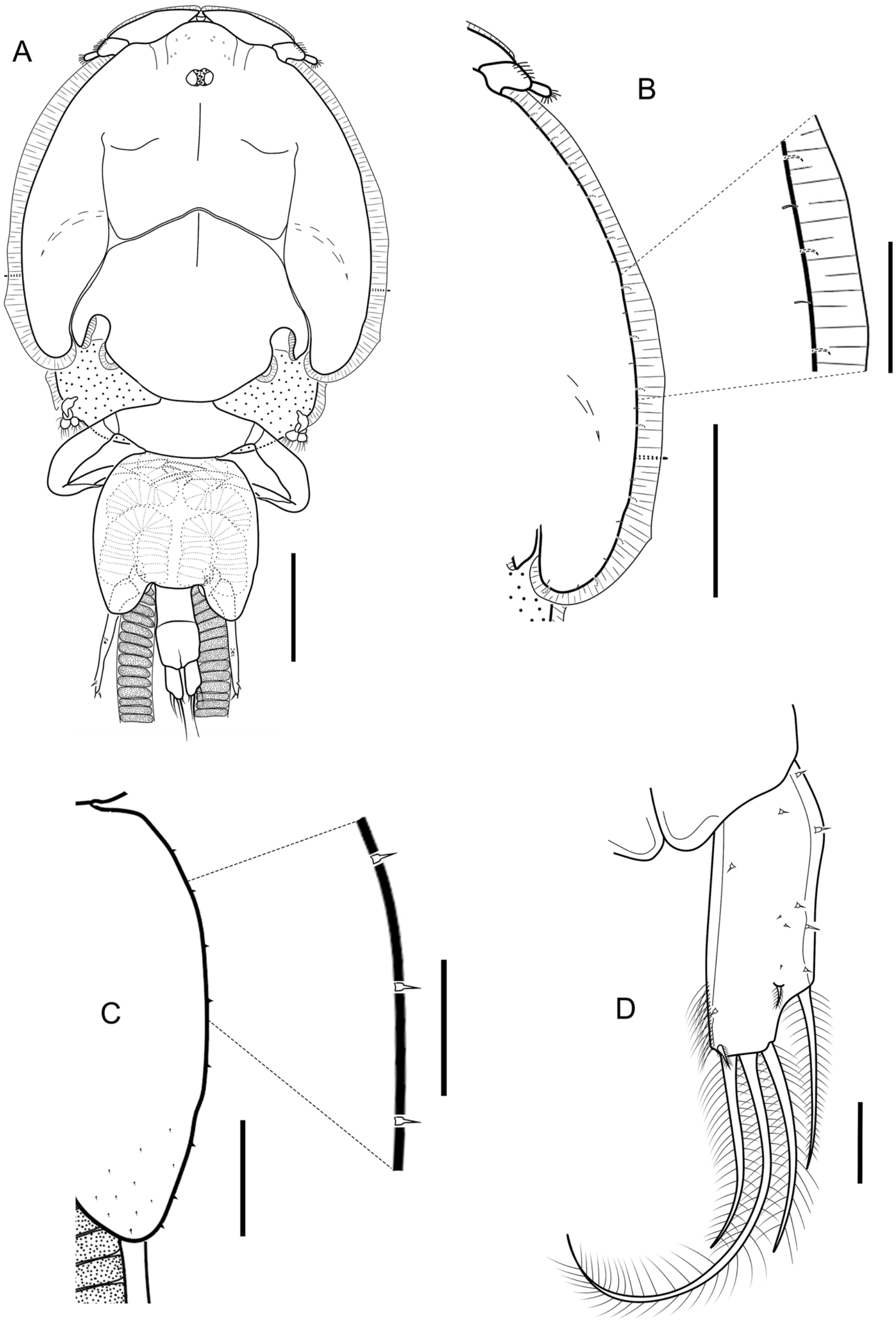

Fig. 1 *Lepeophtheirus lichiae* Barnard, 1948. Female. A, Habitus, dorsal view; B, Sensilla beneath marginal membrane of cephalothorax; C, Sensilla along lateral margin and on dorsal surface of posterolateral lobe of genital complex; D, Caudal ramus. *Scale-bars*: A, 1 mm; B, (left) 1 mm, (right) 400 µm; C, (left) 400 µm, (right) 200 µm; D, 100 µm

Genital complex wider than long (1.25×1.56), convex lateral margins ornamented with array of about 8 small sensilla (Fig. 1C); posterolateral corners distinctly lobate, extending posteriorly about to posterior margin of first abdominal segment; dorsal surface of posterolateral lobes ornamented with minute sensilla (Fig. 1C). Abdomen 2-segmented; longer than wide, 0.75×0.40, comprising 60% of length of

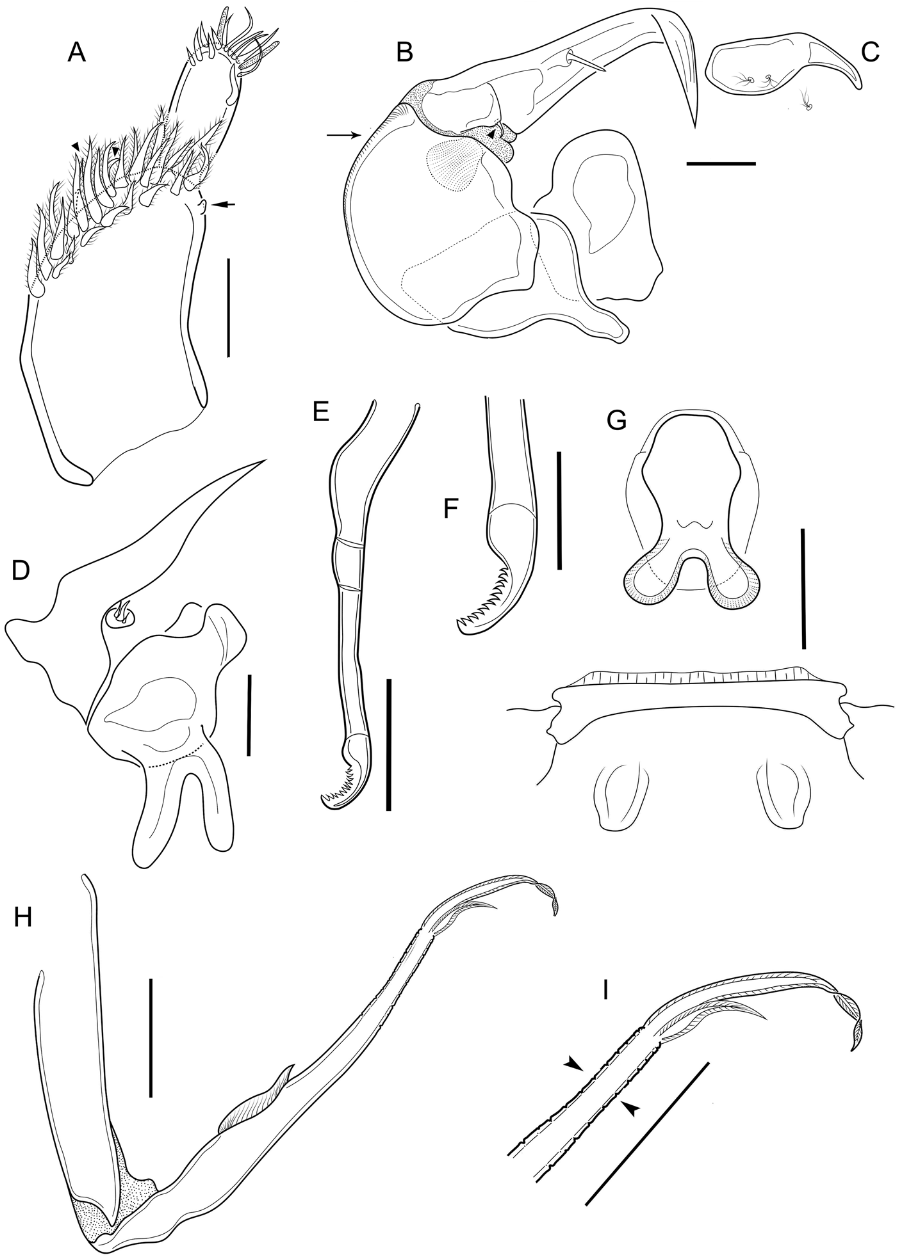

Fig. 2 *Lepeophtheirus lichiae* Barnard, 1948. Female. A, Antennule, note two setae (*arrowheads*) on dorsal surface and small knob-like process (*arrow*) on ventrodistal corner of proximal segment; B, Antenna, note narrow corrugations along outer margin of middle segment and small spine-like seta proximally (*arrowhead*) on claw; C, Postantennal process; D, Maxillule; E, Mandible; F, Tip of mandible; G, Sternal furca and intercoxal sclerite of leg 1, *in situ*; H, Maxilla; I, Small indentations (*arrowheads*) on inner and outer distal margin of brachium. *Scale-bars*: A–E, 100 µm; F, 50 µm; G–I, 200 µm

genital complex; first abdominal somite about as long as wide, 0.32 × 0.31; anal somite slightly longer than wide, 0.43 × 0.40, 1.34 times longer than first abdominal somite. Caudal ramus (Fig. 1D) nearly 3 times longer than wide, 0.34 × 0.12, about 45% of length of entire abdomen: armed with 6 pinnate setae, outer dorsal seta and inner seta shorter than other 4 setae, second outer seta located at outer distal corner of ramus and distinctly separated from other 3 apical setae; outer half of posterior margin deeply indented, dorsal surface of ramus ornamented with scattered sensilla; inner margin ornamented with short row of fine setules distally.

Antennule (Fig. 2A) 2-segmented, proximal segment *c.*2.7 times wider than distal segment and *c.*1.6 times longer; armed with 25 plumose setae on anterior and antero-ventral surfaces plus 2 unarmed setae located dorsally (Fig. 1C, arrowheads), small knob-like process present at ventrodistal corner of proximal segment (Fig. 1C, arrow); distal segment short, armed with 1 subterminal seta on posterior margin and 11 setae plus 2 aesthetascs around apex. Antenna (Fig. 2B) uniramous, 3-segmented; with subrectangular cuticular process near base; proximal segment produced posteriorly into blunt spinous process; middle segment with narrow corrugations along outer margin (Fig. 2B, black arrow), and bearing large inner distal adhesion pad on dorsal surface; distal segment forming sharply curved claw armed with small spine-like seta proximally and longer seta distally. Postantennal process (Fig. 2C) weakly curved; carrying 2 papillae each with 4 sensilla; similar papilla with 4 sensilla located on body surface adjacent to process. Mandible (Fig. 2E) curved inward distally, armed with 12 teeth on medal margin near apex (Fig. 2F). Maxillule (Fig. 2D) bifid with unequal tines; outer tine shorter and more slender than inner: anterior papilla bearing 3 small, unequal setae. Maxilla (Fig. 2H) 2-segmented, brachiform; proximal segment (lacertus) unarmed; slender distal segment (brachium) bearing large flabellum (hyaline membrane) on inner margin plus short canna and long calamus distally; inner and outer margin of brachium ornamented with small indentations distally (Fig. 2H, I, arrowheads). Maxilliped (Fig. 3A) with long, robust proximal segment (corpus), inner margin of corpus bearing prominent rounded protrusion proximally, anteromedial margin of protrusion ornamented with fine setules; proximal part of corpus forming slender, blunt-tipped, apodeme-like process extending into ventral body cavity; small, slender spiniform outgrowth present on ventral body surface near base of corpus: distal subchela representing fused endopodal segments plus short claw; subchela armed with small proximal knob (Fig. 3A) on ventral surface and simple seta at base of claw; concave margin of claw with small, angular expansion. Sternal furca (Fig. 2G) with short rounded, divergent tines, each tine surrounded with flange, tines not extending as far as intercoxal sclerite of leg 1; subrectangular box *c.*2.5 times longer than tines.

Leg 1 (Fig. 3B) biramous with 2-segmented exopod and vestigial lobate endopod. Sympod armed with lateral plumose seta and inner seta plus papilla with four sensilla (Fig. 3B, arrowhead). First exopodal segment ornamented with row of setules along posterior margin and bearing small spine at outer distal corner (Fig. 3C). Distal exopodal segment (Fig. 3D) with 3 plumose setae posteriorly plus 4 terminal elements; outermost element (spine 1) finely serrated, middle 2 elements (spines 2 and 3) each bearing single prominent accessory process and ornamented with fine serrations along inner and outer margins, innermost element (seta 4) with setules along inner and outer margins: Spines 1–3 each with pecten at base.

Leg 2 (Fig. 4A) biramous with distinct coxa and basis; coxa short, bearing long inner plumose seta plus sensillum on ventral surface; basis large, armed with short pinnate seta on outer distal corner, ornamented with flap of membrane anteriorly reflexed back across dorsal surface of segment, plus small strip of membrane along posterior margin and sensillum near middle of margin. Exopod (Fig. 4B) 3-segmented: first segment, largest, subrectangular, ornamented with flap of membrane anteriorly reflexed back across dorsal surface of ramus, armed with long, bilaterally serrate, outer spine with pecten at base and inner plumose seta; segment 2 with outer spine and inner plumose seta; segment 3 armed with posteriorly-directed, bilaterally-serrate proximal spine; laterally-directed, bilaterally-serrate, curved middle spine; apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopod (Fig. 4C) 3-segmented; first and second endopodal segments with 1 and 2 inner plumose setae, respectively; segment 3 with 6 plumose setae; outer margins of all segments ornamented with fine setules.

Leg 3 (Fig. 5A) with coxa and basis fused into flattened apron-like sympod: sympod and intercoxal sclerite with extended strips of hyaline membrane along lateral and free posterior margins, plus crescent-shaped corrugations forming adhesion pad on anteroventral surface, near lateral margin. Inner coxal seta and outer basal seta both pinnate. Exopod 3-segmented (Fig. 5C): first segment bearing narrow hyaline membrane laterally, 3 lateral setules, and

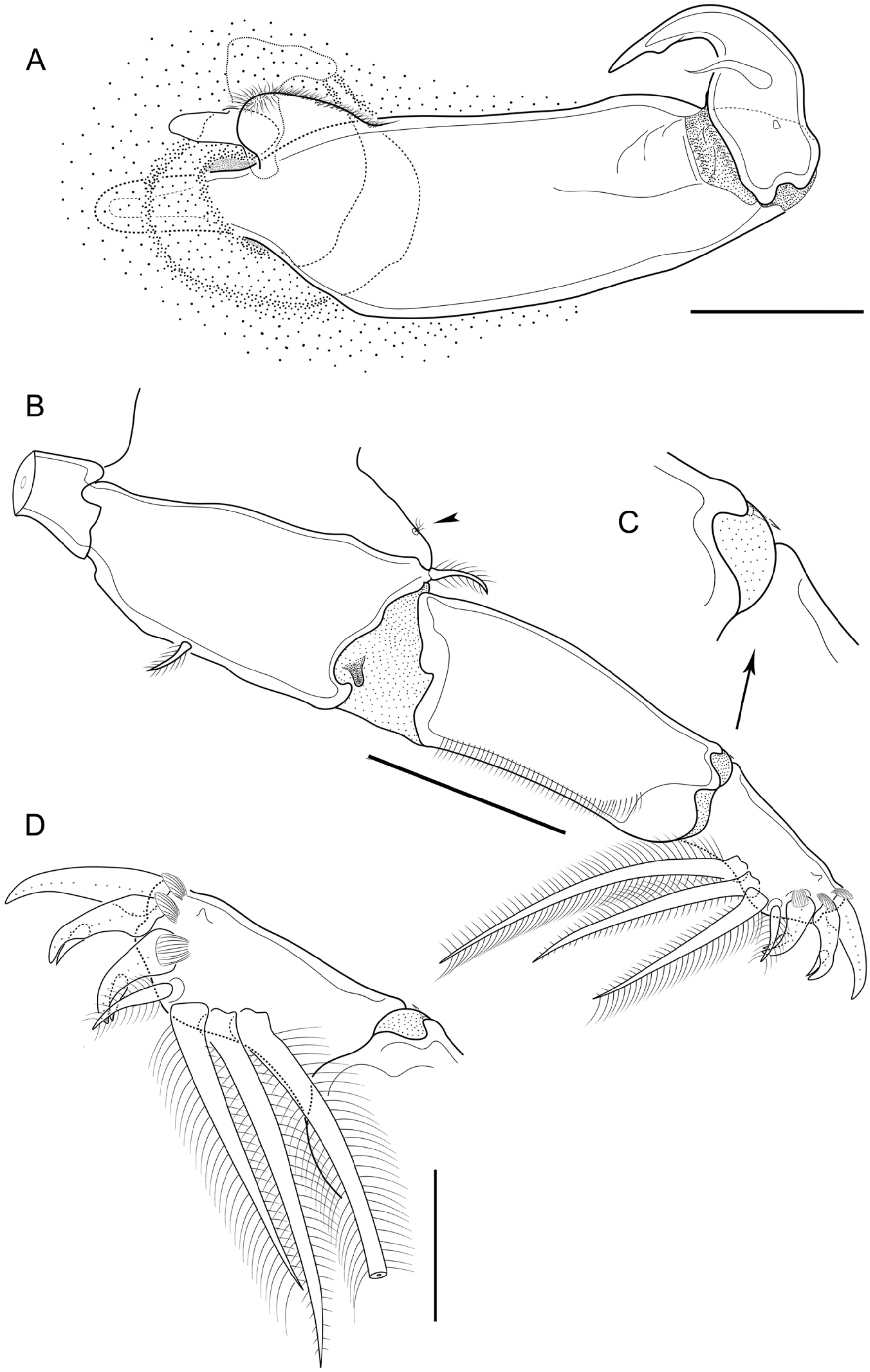

Fig. 3 *Lepeophtheirus lichiae* Barnard, 1948. Female. A, Maxilliped; B, Leg 1, note papilla with four sensilla on sympod; C, Spine at outer distal corner of first exopodal segment of leg 1; D, Distal exopodal segment of leg 1. *Scale-bars*: A–B, 200 µm; C, 50 µm; D, 100 µm

slightly curved outer spine; outer margin of spine ornamented with lateral membrane; second segment ornamented with row of fine setules along inner and outer margins, and carrying outer spine plus inner plumose seta; third segment with 3 outer spines and 5 short pinnate setae; dorsal surface of segment with

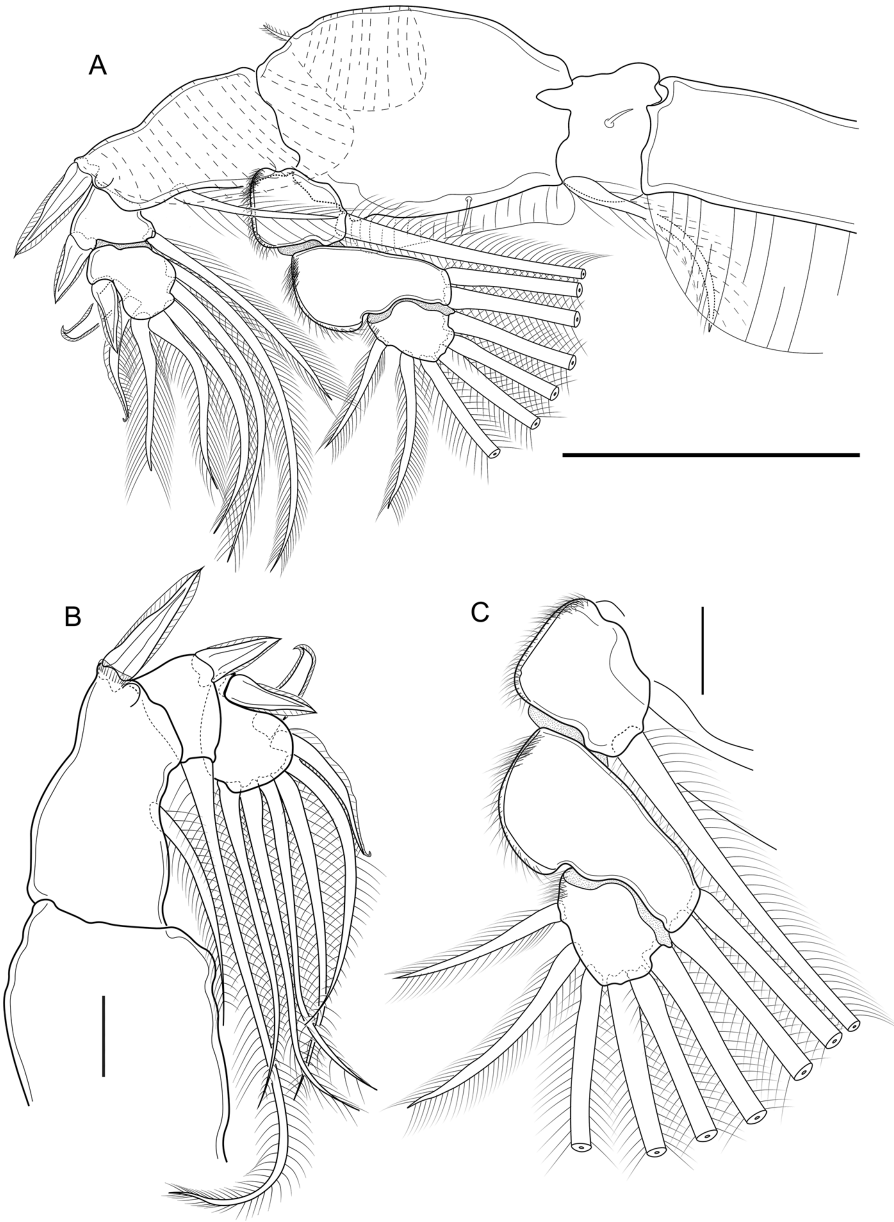

Fig. 4 *Lepeophtheirus lichiae* Barnard, 1948. Female. A, Leg 2; B, Exopod of leg 2; C, Endopod of leg 2. *Scale-bars*: A, 500 µm; B, C, 100 µm

cuticular outgrowth near outer margin. Endopod (Fig. 5D) 2-segmented: proximal segment expanded laterally to form short velum closing space between bases of rami, armed with long inner plumose seta, and ornamented with setules along margin of velum; compound distal segment with 6 plumose setae and ornamented with rows of setules along outer and inner margins.

Leg 4 (Fig. 6A) uniramous, long protopodal segment armed with outer seta derived from basis, ornamented with scattered sensilla. Exopod 3-segmented: first segment with 1 tiny distal spine and adjacent outer knob surrounded with pecten (Fig. 6B); middle segment with longer bilaterally serrate spine at outer distal corner (Fig. 6B); terminal segment with 3 apical spines decreasing in size laterally; longest spine

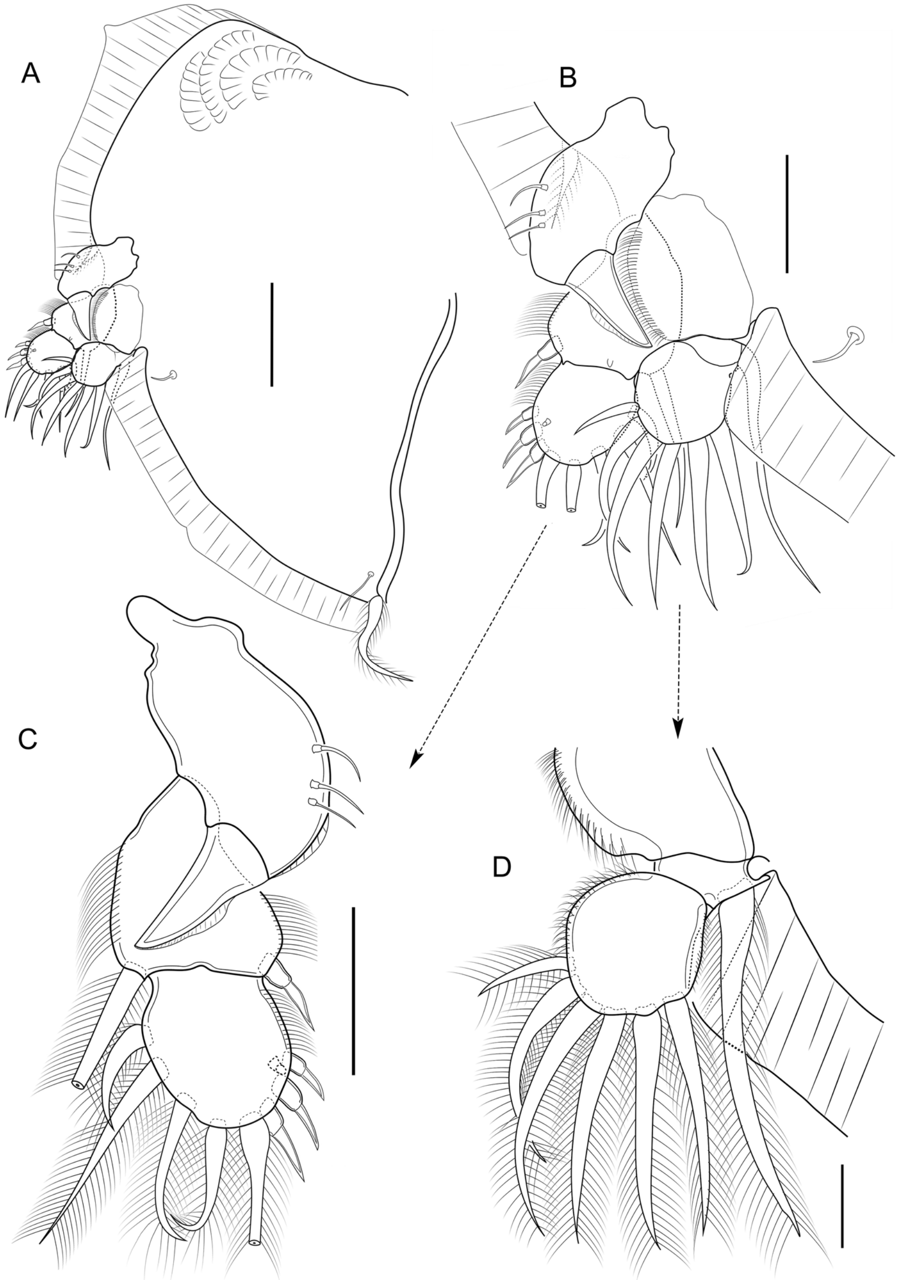

Fig. 5 *Lepeophtheirus lichiae* Barnard, 1948. Female. A, Leg 3; B, Detail of leg 3 rami; C, Exopod of leg 3; D, Endopod of leg 3. *Scale-bars*: A, 200 μm; B, C, 100 μm; D, 50 μm

with serrate membrane along inner margin (Fig. 6B), middle and outermost spines distinctly shorter than inner spine and with serrate membranes along inner and outer margins. Middle spine slightly less than half-length of longest spine, and outermost spine smallest; all exopodal segments ornamented with numerous surface sensilla and outer margin of each segment finely serrated; each spine on exopod with pecten at base. Spine (Roman numerals) and seta (Arabic numerals) formula of legs 1–4 as follows:

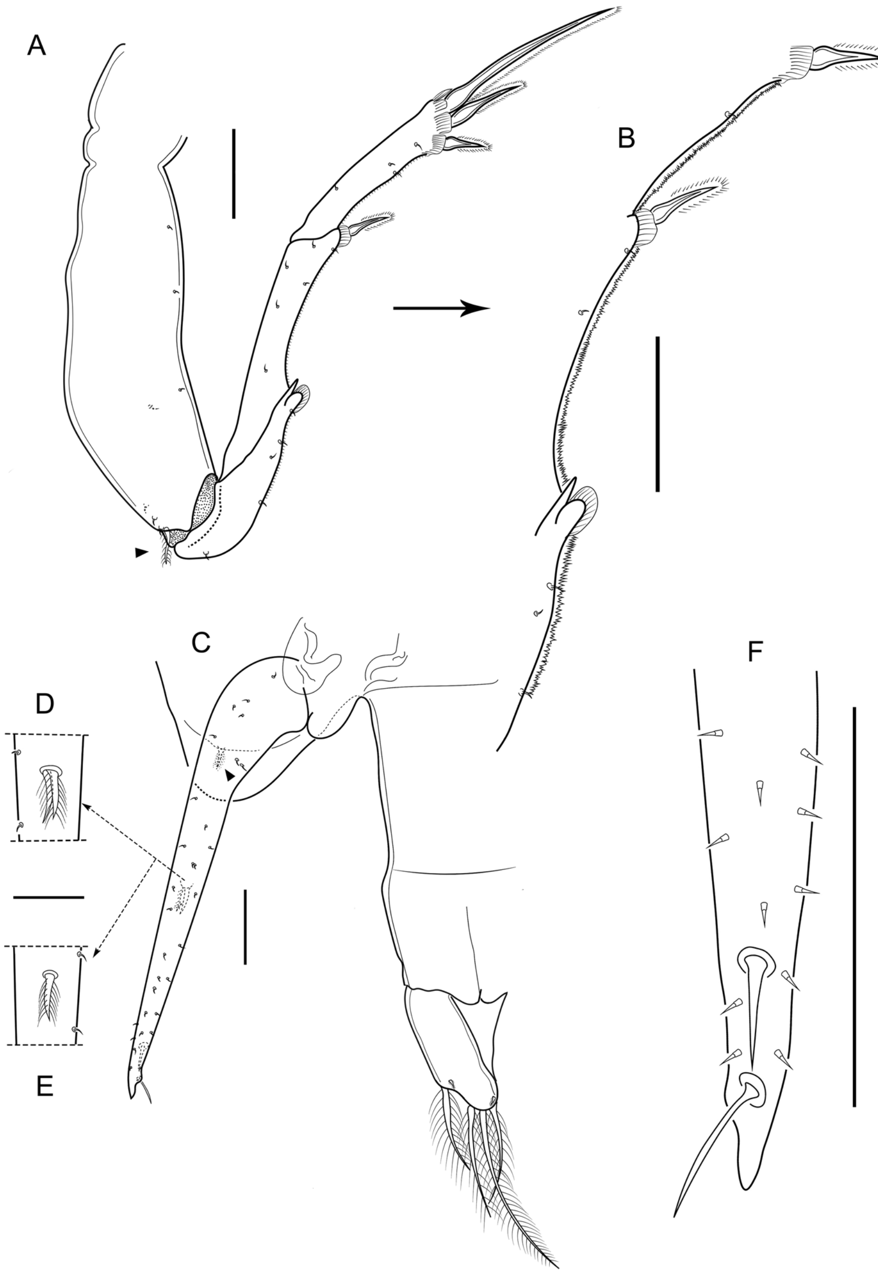

Fig. 6 *Lepeophtheirus lichiae* Barnard, 1948. Female. A, Leg 4; B, Detail of inner margins of exopodal segments of leg 4; C, Leg 5, note small pinnate seta (*arrowhead*) behind leg 5 on ventral surface of posterolateral corner of genital complex; D, Inset showing mediodorsal papilla with 2 adjacent setae located at mid-length of process of right fifth leg; E, Inset showing mediodorsal papilla with1 plumose seta located at mid-length of process of left fifth leg; F, Tip of fifth leg showing 2 subapical naked setae plus scattered sensilla. *Scale-bars*: A–C, F, 200 µm; D, E, 100 µm

	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, 5	0-1; 6
Leg 4	I-0; I, III	absent

Leg 5 (Fig. 6C) represented by conical, spinous process located behind lobate posterolateral corner of genital complex and extending posteriorly slightly beyond mid-length of caudal ramus. Length of spinous fifth leg about 83% of length of genital complex. Right fifth leg carrying mediodorsal papilla with 2 adjacent setae located at mid-length of process (Fig. 6D) whereas similar papilla on left fifth leg with 1 plumose seta (Fig. 6E); outer seta on papilla of right fifth leg simple and slightly longer than adjacent inner plumose seta (Fig. 6D). Each fifth leg bearing 2 additional subapical naked setae and ornamented with numerous sensilla (Fig. 6F).

Remarks

In his original description, Barnard (1948) presented only three drawings of the female of *L. lichiae*; dorsal habitus, sternal furca, and the postantennal process (as the second maxilla "mx2"). The strongest similarities between our specimen of *L. lichiae* and Barnard's material are: (i) the shape of the 2-segmented abdomen; (ii) the shape of the posterolateral lobes on the genital complex, which extend as far as the posterior margin of the first abdominal somite; (iii) the extent of the spiniform fifth legs which reach to the tip of the caudal rami; (iv) the shape of the sternal furca which has short rounded tines; and (v) the weakly curved tine on the postantennal process.

The Mediterranean female differs from Barnard's type female in having: (i) a shorter body (6.34 *vs* 7.50 mm); (ii) a dorsal cephalothoracic shield that is 1.12 times longer than wide (*vs* as long as wide); (iii) a free thoracic zone of the shield with a convex (*vs* straight) posterior margin that extends beyond (*vs* extending to) the posterior ends of lateral zones; (iv) a female genital complex that is 1.20 times (*vs* 1.40 times) longer than the combined length of the abdomen plus caudal rami; (v) a spinous fifth leg that is about 83% (*vs* about 75%) of the length of the genital complex; and (vi) a caudal ramus that is 2.2 times longer than wide (*vs* 1.6 times). We interpret these differences as reflecting intraspecific variation. Given the small sample available to Barnard (1948) and the single specimen from the Mediterranean, we are not in a position to robustly assess variability across the geographical range of *L. lichiae*.

Table 1 Comparison between the specimens of *Lepeophtheirus lichiae* Barnard, 1948 collected from the Mediterranean Sea and Western Indian Ocean

Species	TBL (mm)	GC (W:L)	LGC: LEAB + LCR	Caudal rami (L:W)	P3exp. segments	P3 exp. formula	P3 endp. formula	Reference
L. lichiae (n = 1)	7.50	1.10:1	1.40:1	1.60:1	–	–	–	Barnard (1948)
L. lichiae (n = 1)	6.34	1.20:1	1.20:1	2.20:1	3	I-0; I-1; III, 5	0-1; 6	Present study
L. lichiae (n = 5)[a]	5.95–6.85 (6.48)	1.23–1.37 (1.30):1	1.16–1.22 (1.19):1	1.4–2.2 (1.70):1	3	I-0; I-1; III, 5	0-1; 6	Specimens from NHMUK

[a]Measurements, given for the 5 specimens from NHMUK (1979.949-952 and 1979.954-955), are presented as the minimum and maximum values followed by the mean in parenthesis. *Abbreviations*: TBL, total body length; GC, genital complex; W, width; L, length; LGC, length of the genital complex; LEAB, length of the entire abdomen; LCR, length of caudal rami; exp, exopodal; endp, endopodal; –, not illustrated

Table 2 Comparison of some characters of species of *Lepeophtheirus* (n = 13) with extremely developed, spiniform leg 5 in female

Species	TBL (mm)	GC (W:L)	GC lobes	LGC: LEAB +LCR	Number of ABS	CR(L:W)	P3 exp. segments	P3 exp. formula	P3 endp. formula	Reference
L. anguilli Hameed, 1976	2.7	1.1:1	absent	6.66:1	1	*c.*1.0:1	3	I-0;I-1;III,4	0-1; 6	Hameed (1976)
L. cossyphi Krøyer, 1863	3.35	1.2:1	absent	5.75:1	1	*c.*1.6:1	3	I-0;I-1;III,5	0-1; 6	Wilson (1905)
L. crassus (Bere, 1936)	7.52	1.5:1	present	1.06:1	2	*c.*1.6:1	3	I-0;I-1;III,4	0-1; 6	Bere (1936)
L. curtus (Wilson, 1913)	3.13–3.60	2.1:1	absent	0.95:1	1	*c.*2.0:1	2	I-1; IV,5	0-1; 6	Wilson (1913)
L. krishnai Kaliyamurthy, 1990	1.96	1.6:1	present	1.73:1	1	*c.*2.3:1	2	I-1;?	0-1:?	Kaliyamurthy (1990)
L. lewisi (Hewitt, 1971)	3.08 – 3.45	1.9:1	absent	1.57:1	1	*c.*2.0:1	3	I-0; I-1; III,4	0-1; 6	Hewitt (1971)
L. lichiae Barnard, 1948	6.34	1.2:1	present	1.20:1	2	*c.*2.2:1	3	I-0; I-1; III,5	0-1; 6	Present study
L. litus (Lewis, 1964)	3.45 – 3.90	2.1:1	absent	1.13:1	1	*c.*1.0:1	2	I-1; IV,5	0-1; 6	Lewis (1964b)
L. longicaudus (Cressey, 1966)	5.6	1.8:1	present	1.29:1	1	*c.*4.0:1	2	I-?; IV,3	0	Cressey (1966)
L. plotosi Barnard, 1948	3.5	1.0:1	absent	5.00:1	1	*c.*1.1:1	NI	NI	NI	Barnard (1948)
L. robertae Boxshall, 2018	2.71	2.1:1	absent	1.64:1	1	*c.*2.3:1	2	I-0; IV,1	0-1; 4	Boxshall (2018)
L. spinifer Kirtisinghe, 1937	4.0	1.4:1	present	2.00:1	2	*c.*1.0:1	2	I-1; ?	0-1; ?	Kirtisinghe (1937)
L. uluus (Lewis, 1964)	6.00–7.13	1.1:1	present	2.27:1	1	*c.*1.0:1	3	I-0; I-1; III,4	0-1; 6	Lewis (1964b)

Abbreviations: TBL, total body length; GC, genital complex; L, length; W, width; LGC, length of the genital complex; LEAB, length of the entire abdomen; LCR, length of caudal rami; ABS, abdominal segment; CR, caudal rami; exp, exopodal; endp, endopodal; ?, not clear from descriptions of Kirtisinghe (1937), Cressey (1966), and Kaliyamurthy (1990)

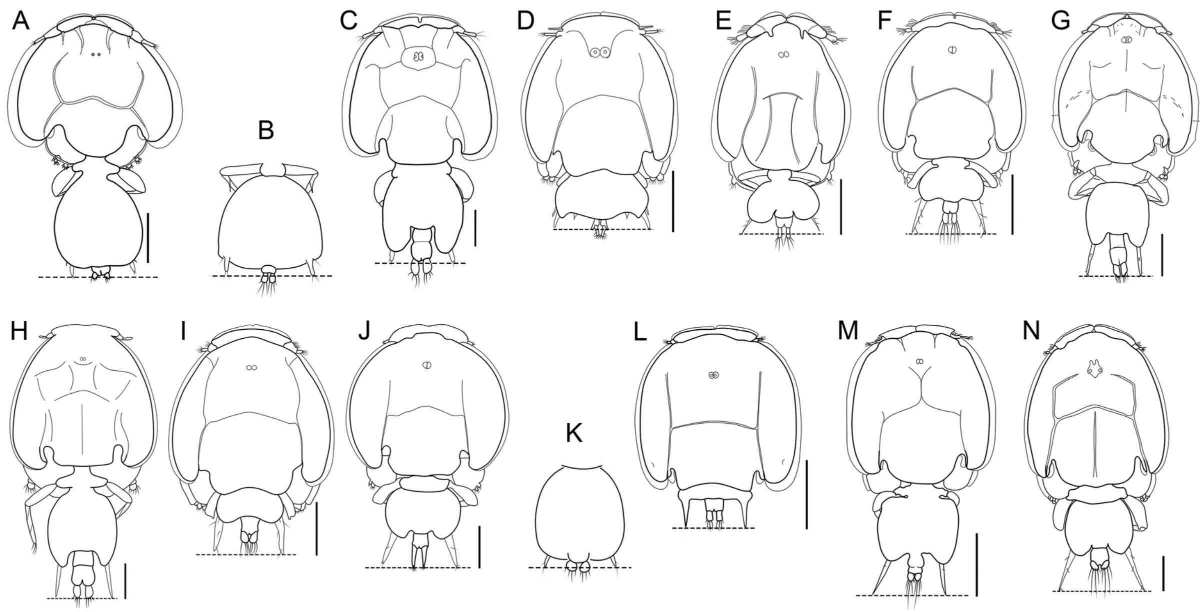

Fig. 7 Reproduced drawings of the female *Lepeophtheirus* having extremely developed leg 5. A, *L. anguilli* Hameed, 1976; B, *L. cossyphi* Krøyer, 1863; C, *L. crassus* (Bere, 1936); D, *L. curtus* (Wilson, 1913); E, *L. krishnai* Kaliyamurthy, 1990; F, *L. lewisi* (Hewitt, 1971); G, *L. lichiae* Barnard, 1948 (Mediterranean material); H, *L. lichiae* Barnard, 1948 (South African material); I, *L. litus* (Lewis, 1964); J, *L. longicaudus* (Cressey, 1966); K, *L. plotosi* Barnard, 1948; L, *L. robertae* Boxshall, 2018; M, *L. spinifer* Kirtisinghe, 1937; N, *L. uluus* (Lewis, 1964). *Scale-bars*: A, E, 0.5 mm; C, D, F–J, L–N, 1 mm; B, K, scale-bar not available

Comparison between the Mediterranean specimen and the five females of *L. lichiae* [NHMUK 1979.949-952 (*n* = 3); NHMUK 1979.954-955 (*n* = 2)] stored in the collections of the Natural History Museum, London, revealed closer resemblance in terms of body length and body proportions relative to the type-material described by Barnard (1948) (Table 1). The details of the cephalothoracic appendages and legs 1-5 were identical.

The most obvious distinguishing character of *L. lichiae* is the extreme development of the spiniform fifth legs (Fig. 6C). Within the family Caligidae a few species belonging to three genera; *Lepeophtheirus*, *Alebion* Krøyer, 1863 and *Tuxophorus* Wilson, 1908, are characterised by the presence of long, spiniform fifth legs in females in contrast to the majority of other species in these genera, which have fifth legs in the form of setiferous papillae (Dojiri & Ho, 2013).

According to Boxshall (2018), this distinguishing character, "extreme development of the fifth leg of the female", is exhibited by a cluster of eight species within *Lepeophtheirus*, most of which were formerly placed in a separate genus, *Dentigryps* Wilson, 1913 (see Lewis 1964b). These are: *L. bifurcatus* (Lewis, 1964), *L. curtus* (Wilson, 1913), *L. lichiae*, *L. litus* (Lewis, 1964), *L. longicaudus* (Cressey, 1966), *L. robertae* Boxshall, 2018, *L. spinifer* Kirtisinghe, 1937 and *L. uluus* (Lewis, 1964). Five of these, *L. bifurcatus*, *L. curtus*, *L. litus*, *L. longicaudus* and *L. uluus*, were originally established as members of *Dentigryps,* which was treated as a valid genus by Wilson (1913) and Lewis (1964a, b). The validity of the *Dentigryps* was questioned by Pillai (1966) and Hewitt (1971) proposed to synonymise it with *Lepeophtheirus*, transferring all five species of *Dentigryps* to *Lepeophtheirus*. On transfer *Dentigryps bifurcatus* Lewis, 1964 would have become *Lepeophtheirus bifurcatus* (Lewis, 1964) but this combination was preoccupied, so to avoid the secondary homonymy with *Lepeophtheirus bifurcatus* Wilson, 1905, Hewitt (1971) proposed *Lepeophtheirus lewisi* Hewitt, 1971 as the replacement name [p. 333 in Hewitt (1971)]. We note here that *L. lewisi* was listed erroneously as *L. bifurcatus* (Lewis, 1964) in Boxshall (2018). Six years later, after Hewitt's (1971) transfer, Ho & Dojiri (1977) re-instated *Dentigryps* as a valid genus and increased the number of species to seven by transferring *Lepeophtheirus lichiae* and *L. spinifer*

Kirtisinghe, 1937. Kabata (1979) subsequently considered that the gradation in the length of fifth legs was not sufficient to retain these two as distinct genera. However, the genus *Dentigryps* remained separate until Dojiri & Ho (2013) re-synonymized them and transferred all seven species back to *Lepeophtheirus*. The discovery of *L. robertae* brings the number of species of *Lepeophntheirus* that are characterised by a pair of extremely developed, spiniform fifth legs in the female, to eight (Boxshall, 2018).

A wider comparison across the 124 valid species of *Lepeophtheirus* reveals that there are three different forms of fifth leg. The first is the extremely developed, spiniform fifth leg (Fig. 6C) which is present in the eight species listed by Boxshall (2018), as mentioned above. The second is a fifth leg represented by a posteriorly directed, conical or subtriangular, spinous projection that is shorter and less extreme than the first form, and can be found in a number of species such as *L. azoricus* Özak, Rodrigues, Vieira, Rosa, Yanar, Koyuncu & Boxshall, 2018; *L. gonistii* Yamaguti, 1936 and *L. sigani* Ho, Kim, Cruz-Lacierda & Nagasawa, 2004. The third form of fifth leg comprises of setiferous papillae only, and can be found in the majority of *Lepeophtheirus* species including the type-species *L. pectoralis* (Müller, O. F., 1776), *L. acutus* Heegaard, 1943 and *L. rhinobati* Luque, Chaves & Cezar, 1999. These species can readily be distinguished from those with the first two forms of leg but separating the first two leg types is more problematic.

Using a quantitative distinction, such as the length to width ratio of the spiniform fifth legs was not possible, as descriptions of several species were incomplete (e.g. Barnard, 1948; Pearse, 1952; Krøyer, 1863). Estimating the ratio between the length of the genital complex and the spiniform process of the fifth leg (see Ho & Dojiri, 1977) is also problematic because the base of the spiniform fifth leg often overlooked in drawings (e.g. *L. krishnai* and *L. spinifer*). This has resulted in the use of more qualitative definitions, such as "strongly projecting spike-like", "extremely long posterior process" or "extremely developed spiniform" (Lewis, 1964b; Ho & Dojiri 1977; Dojiri & Ho 2013; Boxshall, 2018). The extent of the spiniform fifth legs (relative to the caudal rami was used in some previous descriptions (Lewis, 1964b; Ho & Dojiri, 1977), but this was also not adequate for distinguishing between the first two forms of fifth leg.

In the present study, we used the length of the fifth leg relative to the posterior margin of the entire abdomen as the key reference line. This allowed us to clearly distinguish a total of 13 species of *Lepeophtheirus* which have a spiniform fifth leg that extends to or beyond the posterior margin of the entire abdomen including the caudal rami. Various body proportions and the extension of the fifth legs relative to the tips of the caudal rami of these 13 species are compared in Table 2 and in Fig. 7A–N. Unfortunately, drawings of the dorsal cephalothoracic shield of *L. cossyphi* and *L. plotosi* are unavailable (see Fig. 7B, K) because whole body illustrations have never been published (see Wilson, 1905; Barnard, 1948). These comparisons demonstrate a continuum in fifth leg development from small but distinct, as in *L. anguilli*, to longer than the genital complex, as in *L. uluus*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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