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**The “Very Thankless Task”: Revision of *Luniceps* Clay and  
Meinertzhagen, 1939 (Insecta: Phthiraptera: Ischnocera:  
Phlopteridae), with descriptions of six new species and one new  
subspecies**

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## Abstract

The louse genus *Luniceps* Clay and Meinertzhagen, 1939, parasitic on shorebirds (Charadriiformes: Scolopacidae) is revised. Six new species and one new subspecies of *Luniceps* Clay and Meinertzhagen, 1939 parasitic on shorebirds (Charadriiformes, Scolopacidae) are described. They are *L. enigmaticus* sp. nov. from Stilt Sandpiper *Micropalama himantopus* (Bonaparte, 1826), *L. kukri* sp. nov. from Long-billed Curlew *Numenius americanus* Bechstein, 1812, *L. mintoni* sp. nov. from Great Knot *Calidris tenuirostris* (Horsfield, 1821), *L. rothkoi* sp. nov. from Buff-breasted Sandpiper *Tryngites subruficollis* (Vieillot, 1819), *L. schismatus* sp. nov. from Dunlin *Calidris alpina* (Linnaeus, 1758), *L. superciliosus* from Sharp-tailed Sandpiper *Calidris acuminata* (Horsfield, 1821) and Long-toed Stint *Calidris subminuta* (Middendorff, 1853), and *L. numenii madagascariensis* ssp. nov. from Far Eastern Curlew *Numenius madagascariensis* (Linnaeus, 1766). Furthermore, the species *L. cabanisi* Timmermann, 1954, and *L. pusillus* are placed as new junior synonyms of *L. incoenis* (Kellogg and Chapman, 1899); the species *L. haematopi* Timmermann, 1954, *L. oliveri* Timmermann, 1954, and *L. husainii* Ansari, 1956, are placed as new junior synonyms of *L. numenii numenii* (Denny, 1842), *L. numenii phaeopi* (Denny, 1842), and *L. falcinellus* Timmermann, 1954, respectively, and the subspecies *L. holophaeus timmermanni* Bechet, 1968, is regarded as a new junior synonym of *L. falcinellus* Timmermann, 1954. *Luniceps limosella limosa* Bechet, 1968, which was previously considered a junior synonym of *L. limosella* Timmermann, 1954, is resurrected as a valid species. *Luniceps wilsoni* Carriker, 1956, is considered a nomen dubium, and *L. parabolicus* Eichler (in Niethammer), 1953, is removed to the genus *Quadriceps* Clay and Meinertzhagen, 1939 as *Quadriceps parabolicus* comb. nov., although its status in *Quadriceps* needs further attention. All species and subspecies of *Luniceps* are illustrated and re-described, and a key is provided for their identification. Three populations, from which only poor or limited data are available, are placed as incerta sedis.

**Key words:** Chewing lice, *Luniceps*, Philopteridae, shorebirds, sandpipers, curlews, godwits, whimbrel, new species, new synonymies, redescriptions, key to species

## Introduction

The species of the genus *Lunaceps* Clay and Meinertzhagen, 1939 are notoriously difficult to separate morphologically (e.g. Waterston, 1915; Timmermann, 1954a; Keirans, 1967; Ledger, 1980). Waterston (1915) thought the “series of *Nirmus* of the general type *holophaeus* (Nitzsch)” were “extremely similar”, differing only in intensity of colour, size and “minute differences in the male genitalia”. He concluded that this series could be divided into three forms: a small form on *Calidris* and *Philomachus*, a medium-sized form on *Limosa* and a large form on *Numenius*. In the end, he treated them all as the same species, but also included what is now *Quadriceps strepsilaris* in this species.

*Lunaceps* is indeed a morphologically homogeneous genus, and apart from size, proportions, and hosts, many species are difficult to separate. This is reflected in the cursory descriptions given to most species. Timmermann (1954a), who described most of the species recognised today, relied mainly on measurements and host relations, while Eichler (1953) simply stated that his species could clearly be separated from all others, but neglected to detail specific morphological differences between them.

Hopkins and Clay (1952) listed 13 species in *Lunaceps*, but three of them were considered synonymous with other species (*L. inaequalis*, *L. oliveri* and *L. phaeopodis*), and they included Osborn’s *Nirmus cordatus* Osborn, 1896, placed by Edwards (1952) in *Rotundiceps* Edwards, 1952, where it remains today (Price *et al.*, 2003).

Timmermann (1954a) added 11 species, but considered two of them [*L. trimaculatus* (Piaget, 1880) and *L. bicolor* (Piaget, 1880)]—accepted by Hopkins and Clay (1952) as valid—to be junior synonyms. He divided the genus into four groups, depending on size and host-relationships: a small sandpiper group, a *Limosa* group, a *Numenius* group, and a *Haematopus-Dromas* group; the *Numenius* group was further split into two subgroups, based on features of the male genitalia, in one of his rare acknowledgements of the morphological differences between *Lunaceps*-species. Nevertheless, he considered the species of *Lunaceps* as “landmarks, within the field of variation” (Timmermann, 1954a), and noted that it would also be equally appropriate to treat the entire genus as a single species as it would be to treat every population from a given host species as a unique *Lunaceps* species. He remarked that sorting out the species of *Lunaceps* would be “a very thankless task”, and left it to future authors.

Emerson (1972) considered Timmermann’s (1954a) four groups to be species, and Timmermann’s species to be subspecies. Conversely, Price *et al.* (2003) largely agrees with Timmermann (1954a), but kept the seven species on *Numenius* as subspecies of *Lunaceps numenii* in spite of these being the only ones which Timmermann (1954a) clearly illustrated morphological differences.

Based on molecular data, Gustafsson and Olsson (2012) found evidence of ten species, which revealed several instances of conflict with current taxonomy (Timmermann, 1954a; Price *et al.*, 2003). We here present a revision of the genus *Lunaceps* based on the combined evidence of a comprehensive morphological study and the phylogenetic analysis of Gustafsson and Olsson (2012), including formal descriptions of the unnamed clades obtained by that study.

## Material and methods

Mounted material was obtained from the Natural History Museum (London, United Kingdom—NHML), the Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand—MONZ), the Essig Museum of Entomology (University of California, Berkeley, California, United States—EMEC), the Price Institute for Phthirapteran Research (PIPeR, University of Utah, Salt Lake City, Utah, United States—PIPeR), the Oklahoma State University (Stillwater, Oklahoma, United States—OSU) and the Museum für Naturkunde (Berlin—MFN). Some wet material was obtained from the Tsurumi Collection (Yamashina Institute for Ornithology, Chiba, Japan—YIO). Additional material studied belongs to either the Gothenburg Museum of Natural History (Gothenburg, Sweden—GNM) or the Swedish Museum of Natural History (Stockholm, Sweden—SMNH).

Fresh material was collected by DG at: Ottenby Bird Observatory (Sweden), in 2007; Tori-no-Umi (Sendai Prefecture, Japan); Broome Bird Observatory and Eighty Mile Beach (both in Western Australia) in 2008; and Boundary Bay and surroundings (British Columbia, Canada) in 2009. Additional fresh material was collected by: David Lank (Simon Fraser University, Canada) in 2008; Veli-Matti Pakanen (University of Oulu, Finland) at Lumijoki (Finland); and Pavel Pinchuk near Turov (Belarus) during 2009. This material was mounted on

microscopy slides by the first author following DNA extraction, and deposited at the Gothenburg Museum of Natural History (GNM), Gothenburg, the Swedish Museum of Natural History (SMNH), Stockholm, and at the Yamashina Institute for Ornithology, Chiba, Japan (YIO). The location of all studied material is given after each entry, however, note that the GNM and the SMNH do not provide voucher numbers for slides deposited with them.

DNA was extracted after dividing the lice, either between the head and the mesothorax, or between the meso- and pterothorax. After extraction, the exoskeletons were placed in 95% ethanol for ten minutes, followed by absolute ethanol for ten minutes, and oil of cloves for ten minutes. The exoskeletons were mounted in Canada balsam and reassembled carefully. These were allowed to stand over-night without a cover glass, to be able to correct the placement of the head when the balsam had hardened, and to prevent the body and the head from separating when the cover glass was applied. One drop of Canada balsam was added on day two, and the cover glass was put in place gently. Slides were stored in an oven for 1–3 months.

For each species, a maximum of 10 individuals of each sex were photographed with ACT-1, using a Nikon DXM1200 camera mounted on an Olympus BX60 microscope. Measurements were made in MicroImage (Olympus Co.). Some individual specimens in poor condition were not measured, including those with abdominal plates dislodged during mounting, those with a twisted abdomen, and those mounted in pieces. Exceptions are *Lunaceps rileyi*, because most available material lacks parameres, and *L. superciliosus ex C. subminuta* because the heads had been cut off for DNA extraction. Line drawings were made using a *camera lucida* on the same Olympus BX60 microscope. These images were scanned and then collated and edited in GIMP ([www.gimp.org](http://www.gimp.org)).

Head setal terminology follows Clay (1951), with the exception of the marginal temporal setae and ocular setae, where I follow Smith (2000) in naming Clay's (1951) MTS1 the post-ocular seta (POS), and renumbering the other MTS accordingly, from one to five (see Fig. 1). Specific terms for thoracic setae are outlined in Fig. 2. Abdominal setal terminology follows Smith (2000). Male genitalia nomenclature (Fig. 3) is based on Lyal (1986), but freely interpreted, and the designations of the various parts should not be taken as a statement of homology.

All known references to the individual species of *Lunaceps* have been listed under their respective entries, with the number after the colon denoting page number. Balát (1977) and Huldén (1984) have been excluded from these lists, as no hosts are provided in his lists, and it therefore becomes impossible to suggest synonymies.

Most of Eichler's material at the MFN lack collection data on the slides. The location of any index of collection data is unknown (J. Deckert, pers. comm.).

## ***Lunaceps* Clay and Meinertzhagen, 1939: 450**

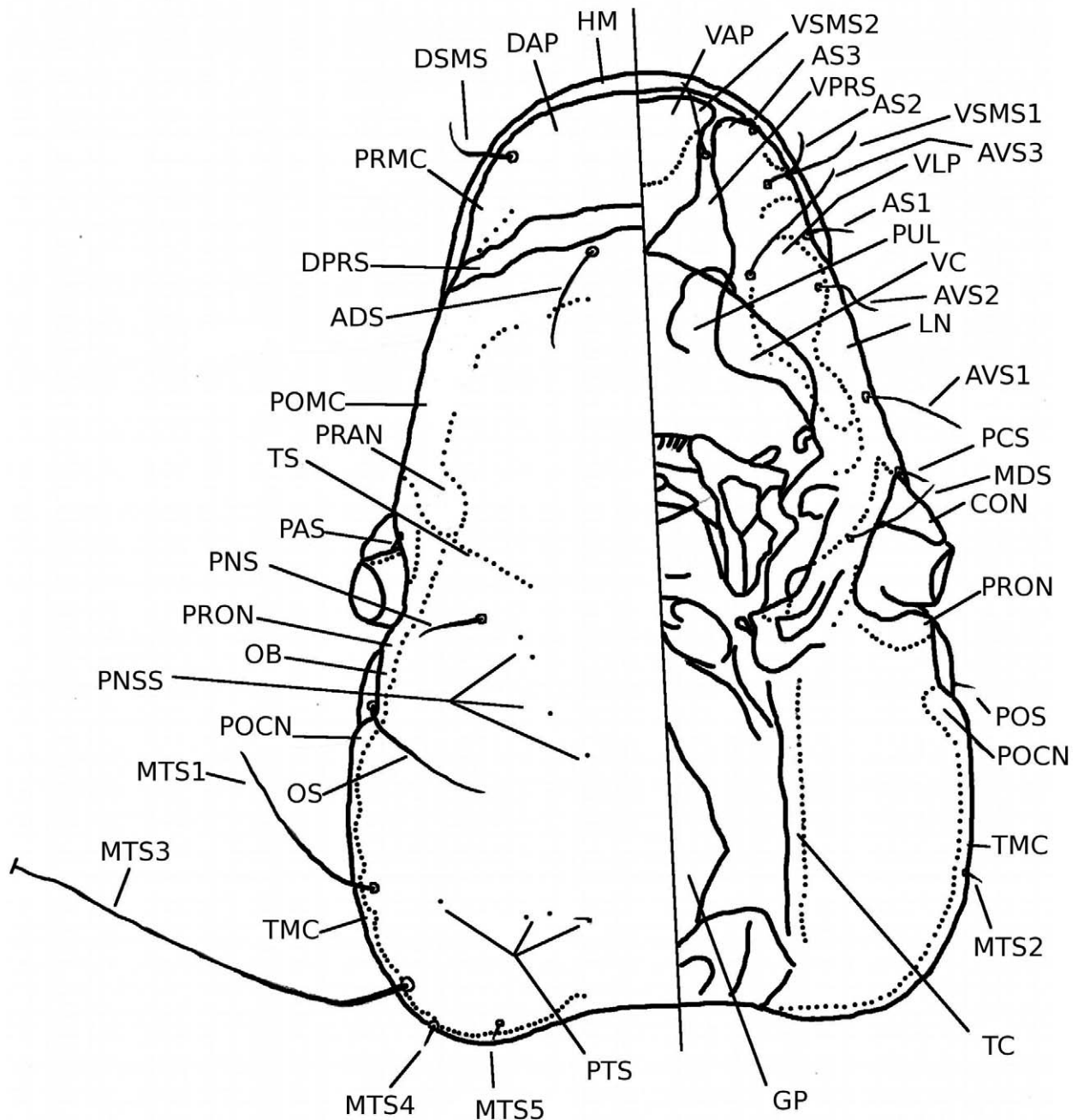
(Fig. 1–5)

**Type species:** *Nirmus actophilus* (Kellogg and Chapman, 1899) (by original designation).

**Diagnosis:** Colour whitish, pale brown, amber, to dark brown, with darker border markings, particularly on abdomen and head. Sexes differ in size, chaetotaxy, terminalia, and genitalic elements.

Head roughly ovoid with broad concave indentation of the posterior margin (Fig. 1). Hyaline margin narrow, extending laterally to the point where the dorsal preantennal suture reaches the lateral sides of the head. Dorsal anterior plate roughly crescent-shaped. Dorsal preantennal suture arched, and is usually continuous across the head or interrupted medially (but missing in *L. limosae* and *L. paschalis*, and interrupted sublaterally in *L. holophaeus*). Ventral anterior plate of different shape, and may be rounded, pointed, tapering or flat posteriorly. Pulvinus large and transparent, and associated with one or two pairs of dark structures at the postero-lateral ends. Marginal carina usually clearly defined laterally, though in most species interrupted at least dorsally by the dorsal preantennal suture. Anteriorly, the marginal carina may be interrupted at least ventrally by the anterior extensions of the ventral preantennal suture, which delimit the ventral anterior plate. The marginal carina typically widens inwards at the anterior end of the head, augmenting the ventral anterior plate. Just posterior to the dorsal preantennal suture, there is a broadening of the marginal carina, here termed the lateral nodus, from which the dark preantennal band arises. This band veers off medially, but is usually narrow and fades out as it approaches the middle of the head. In most species, the posterior margin of this band is more clearly defined than the anterior margin. Just before the antennae, the marginal carina broadens ventrally and turns inwards towards the mandibles, for which it seems to provide a socket. An extension of the marginal carina reaches the ventral carina, which is usually well defined posteriorly, but fades when it reaches the dorsal preantennal suture. Dorsally, the marginal carina forms a nodus just anterior to

the antennal base, but a usually ill-defined and vaguely pigmented extension continues past the antenna to connect with the preocular nodus, the ocular band, and the postocular nodus, from which it continues as the temporal marginal carina. A thin line runs medially from this nodus to disappear above the mandibles, and we have interpreted this as being what Clay and Meinertzhagen (1939) termed the transversal suture. This line, however, is



**FIGURE 1.** Head of *Lunaceps kukri* sp. nov., showing setae and internal and external structures. Setae (following Clay, 1950, apart from as indicated in the text): ADS—Anterior dorsal setae; AS—Anterior setae; AVS—Anterior ventral setae; DSMS—Dorsal submarginal setae; MDS—Mandibular setae; MTS—Marginal temporal setae; OS—Ocular setae; PCS—Preconal setae; PAS—Post-antennal setae; PNS—Post-nodular setae; PNSS—Post-nodular subsidiary setae; POS—Post-ocular setae; PTS—Post-temporal setae. External and internal structures (following Clay, 1950): CON—Conus; DAP—Dorsal anterior plate; DPRS—Dorsal preantennal suture; GP—Gular plate; HM—Hyaline margin; LN—Lateral nodus; OB—Ocular band; POCN—Post-ocular nodus; PRAN—Preantennal nodus; PRON—Pre-ocular nodus; PUL—Pulvinus; TC—Temporal carina; TMC—Temporal marginal carina; TS—Transverse suture; VAP—Ventral anterior plate; VC—Ventral carina; VLP—Ventral lateral plate; VPRS—Ventral preantennal suture.

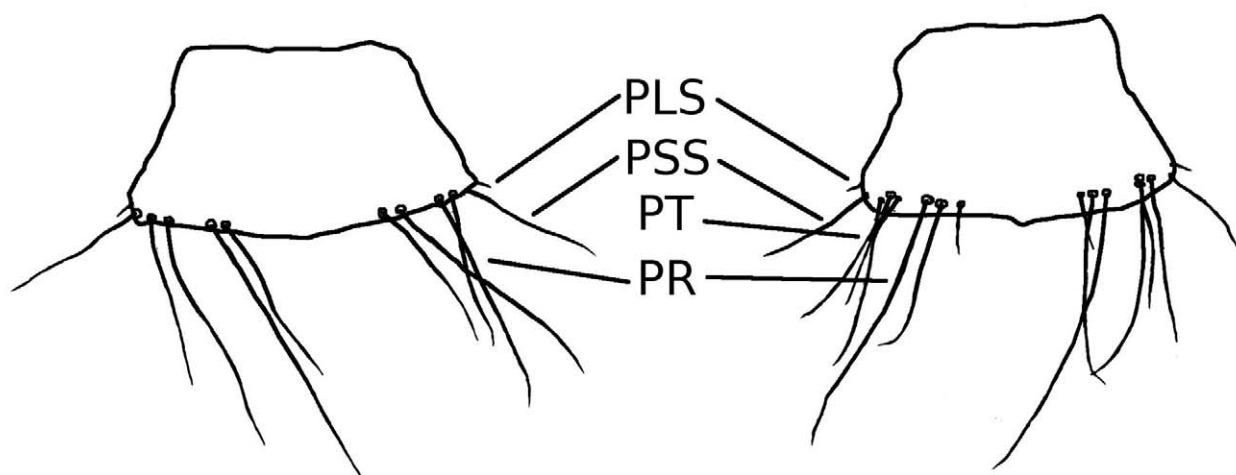
often very hard to see. Ventrally, the marginal carina divides in two just posterior to the mandibles, with one section continuing as the ventral part of the temporal marginal carina, and the other continuing as the temporal carina. The temporal carina fades out quite abruptly near the posterior margin of the head, and does not seem to reconnect to the temporal marginal carina. Gular plate prominent and usually spade-shaped, in some species with short extensions laterally.

Head setal arrangement as in Fig. 1, though with some variation in relative position. One small spot anterior to the PAS and 3–4 small spots postero-lateral to this, as well as one setae median to MTS1 all probably microsetae. POS positioned on eye. MTS3 and sometimes MTS1 macrosetae, whereas MTS2, MTS4, and MTS5 are small or thorn-shaped.

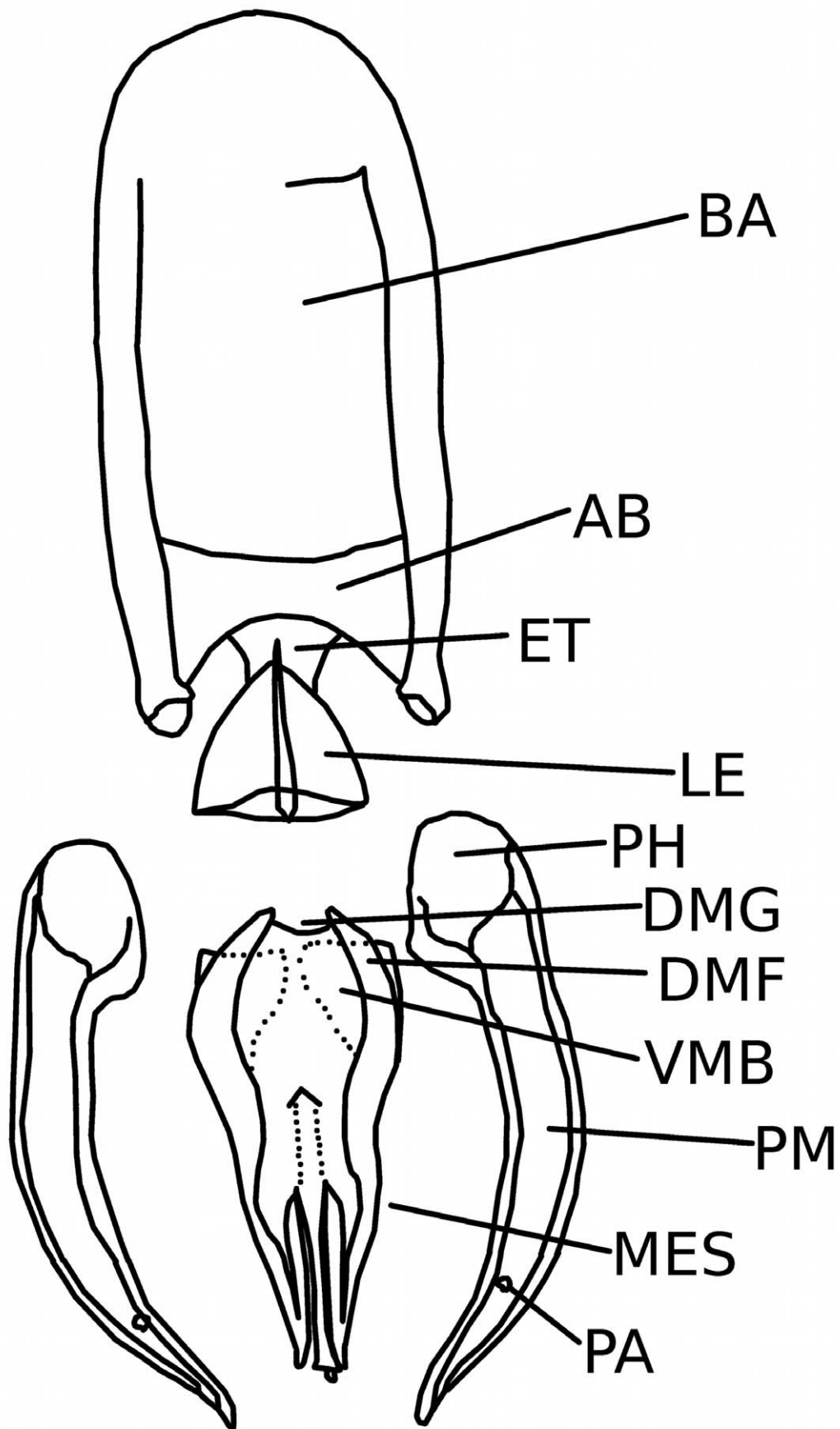
Mesothorax with lateral sides parallel, shorter than wide. Pterothorax roughly as broad as long in small species or broader than long in larger species, with lateral sides parallel, subparallel, or divergent. In males, three sublateral setae form a triangle (the pterothoracic triangle, see Fig. 2A) at the posterior margin. Median to this are three setae (the pterothoracic row, see Fig. 2A), of which the outermost one is a macroseta. In females, four setae form a row along the pterothoracic margin (pterothoracic row, see Fig. 2B), with a gap between setae number 2 and 3.

Abdomen usually long and slender; widest segment usually V. Tergites transversely continuous apart from segments VIII in males and segment X/XI of both sexes; these are divided medially. Anterior margin of some tergites may be indented medially. Spiracles opening on tergites. Laterally, the tergites wrap around the edge of the abdomen and form paratergal plates on the ventral side. These differ in shape between different species, and are sometimes associated with dark border markings. Tergites III–VII indented antero-laterally by a lighter area, associated with a small bar which extends laterally (Fig. 4). This bar forms a cap covering the anterior-lateral end of the tergite, and may be elongated anteriorly and re-entrant into preceding segment. Sternites transversely continuous but usually do not reach the lateral margins of the abdomen. Median third of sternite VII in both sexes extended posteriorly, in males to reach posterior end of abdomen. Sternite of female segment VIII divided medially. Setal arrangement almost invariable, apart from size. Intermediate setae of segments III–V macrosetae in both sexes.

Male genitalia as in Fig. 3. Exophallus enveloped by mesomere, which is roughly triangular and interlocks with the parameres anteriorly. Dorsally, there are two anterior thickenings (“dorsal mesomeral fingers”, Fig. 3), which may be convergent or divergent at tip. These are separated by a small gap (“dorsal mesomeral groove”, Fig. 3). Ventrally, the two sides of the mesomere are divided into a pair of squares (“ventral mesomeral blades”, Fig. 3). Laterally, one or more setae can be seen in larger species. Lower endomere kidney-shaped or semicircular. Basal apodeme often with apodemal bridge. Parameres with well developed heads in proximal end, and more or less slender fingers in distal end.

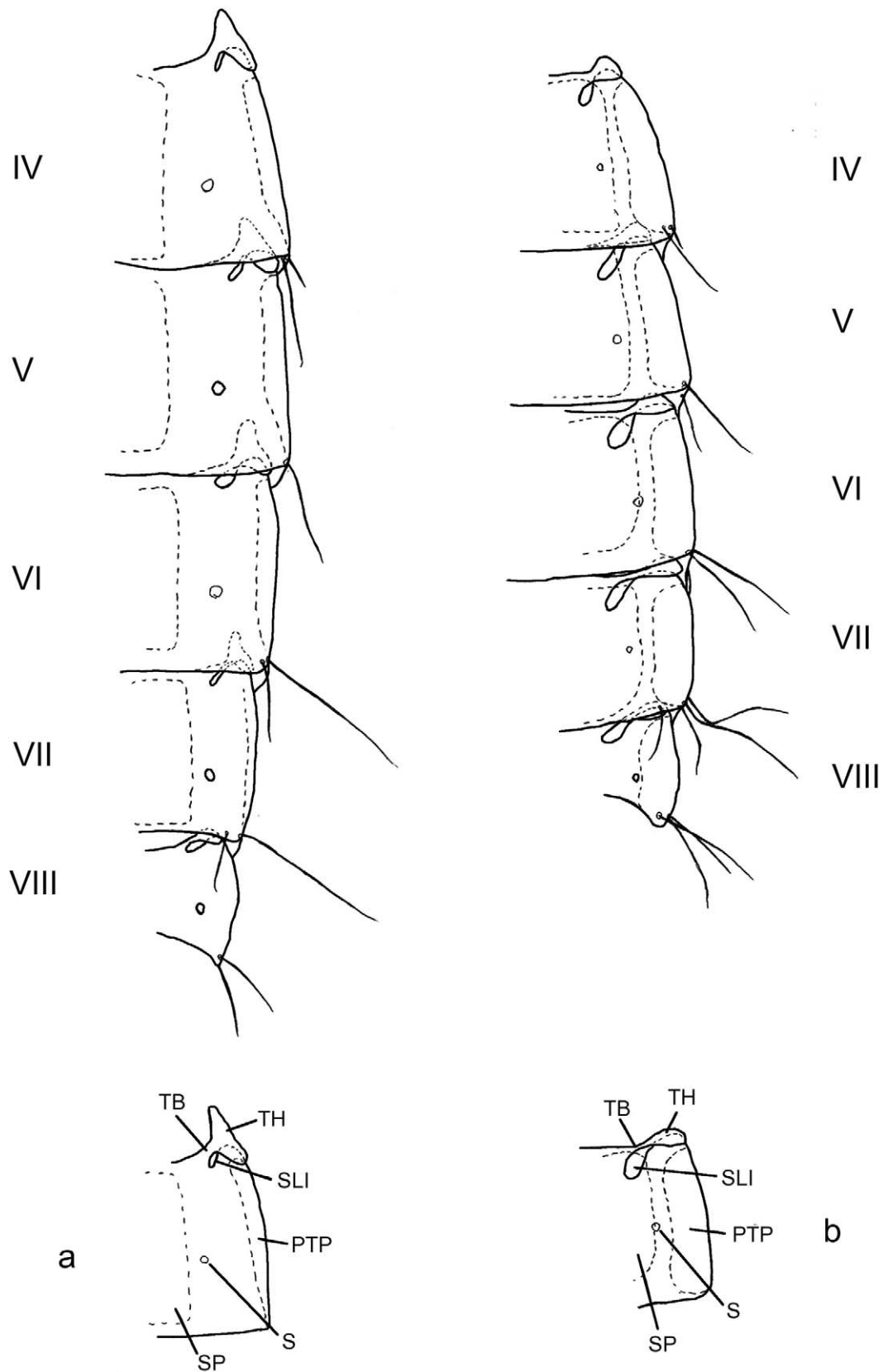


**FIGURE 2.** Pteronota of *Lunaceps numenii numenii*. A) Male. B) Female. Abbreviations: PLS—Pterothoracic lateral setae; PR—Pterothoracic row; PSS—Pterothoracic sublateral setae; PT—Pterothoracic triangle.



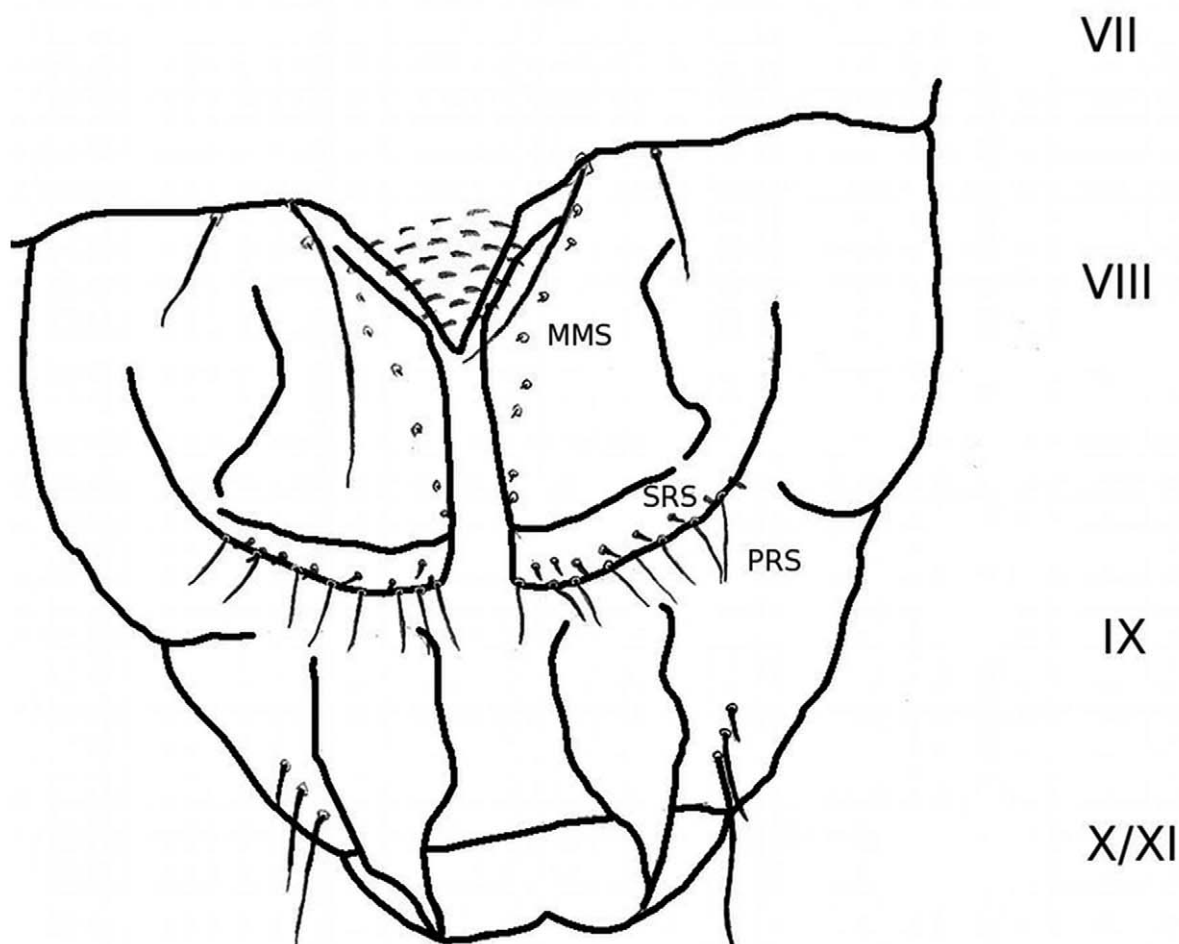
**FIGURE 3.** Male genitalia of *Lunaceps hopkinsi*, showing the structures: AB—Apodemal bridge; BA—Basal apodeme; DMF—Dorsal mesomeral fingers; DMG—Dorsal mesomeral groove; ET—Endomer triangle; LE—Lower endomere; MES—Mesomere; PA—Parameral aperture; PH—Parameral head; PM—Paramere; VMB—Ventral mesomeral blades.





**FIGURE 4.** Overview of the lateral sides of male abdominal segments IV–VIII. A) *Lunaceps incoenis*. B) *Lunaceps actophilus*. PTP—Paratergal plate; S—Spiracle opening; SLI—Sublateral indentation; SP—Sternal plate; TB—Tergal bar; TH—Tergal head.

In females, the median part of sternite VII is extended posteriorly into a wedge, which runs between two halves of sternite VIII. Sternite VIII has three sets of setae (Fig. 5): the posterior marginal setae (often long and slender), the sub-marginal setae (often thorn-shaped or stout, but short), and the median marginal setae (often microsetae). Sternite IX also divided medially, and fused with, extending over, or replacing sternites X/XI. The ventral side of segment IX has three pairs of setae, with the most posterior one typically being longest. Wedge-like extension of sternite VII in some species with dark markings, forming an “amphitheatre”.



**FIGURE 5.** Female genitalia of *Lunaceps lissmanni*, showing the three sets of genital setae: MMS—Median marginal setae; PRS—Posterior marginal setae; SRS—Sub-marginal setae.

**Etymology:** There is no indication of etymology of *Lunaceps* in the original generic description. One interpretation is that this name refers to the crescent-shaped dorsal anterior plate of the head. *Luna* is Latin for “the Moon”; *-ceps* is Latin for “head”.

**Discussion:** *Lunaceps* is easily separated from *Quadriceps* and other louse genera found on shorebirds by the preantennal area, particularly the shape of the dorsal preantennal suture and the dorsal anterior plate. The male genitalia are quite uniform within the genus, and dissimilar to those of most *Quadriceps*, but superficially similar to those of *Quadriceps* spp. ex *Tringa* spp. There is a tendency in some species for the dorsal preantennal suture to bulge posteriorly to encapsulate the apertures of the AVS, although these extensions never become as extensive as the narrow, elongated furrow in *Quadriceps*.

The female genital setae appear to be very fragile, and vary somewhat between different individuals of the same population, and even between different sides of the same individual. The numbers given are average numbers for all studied material, and we recommended that future work include the study of several individuals before any

conclusions are drawn from this set of characters alone. Also, the median-most sub-marginal setae of the female genitalia are occasionally displaced anteriorly, forming a second sub-marginal set. This differs between individuals of the same species, and sometimes between sides of the same individual, and therefore we counted all the sub-marginal setae as one row.

The species *Nirmus cordatus* Osborn, 1896, was included in *Lunaceps* by Hopkins and Clay (1952). Edwards (1952) erected the monotypic genus *Rotundiceps* for *N. cordatus*, but Timmermann (1972: 104) regarded *Rotundiceps* as a subgenus of *Lunaceps*. However, there are many differences between these two taxa. *Rotundiceps* is more “head louse” shaped, with a broad, almost circular abdomen, and a wide head. The head setal arrangement also differs, with MTS1 and MTS2 being long, and the POS being as short and thorn-like as the OS in *Rotundiceps*. The male genitalia are quite similar, but differ with *Rotundiceps* having a more constricted mesomere and somewhat more angular parameres than *Lunaceps*. In contrast, the female genitalia differ widely. The two genera are likely to be closely related.

## Species level taxonomy

### *Lunaceps actophilus* (Kellogg and Chapman, 1899)

(Fig. 6a–d; Table 1)

### Type species of genus *Lunaceps* (Clay and Meinertzhagen, 1939)

*Nirmus actophilus* Kellogg and Chapman, 1899: 78

*Nirmus phaeopi* Denny; Waterston, 1915: 33 (partim)

*Degeeriella actophila* (Kellogg and Chapman); Harrison, 1916: 107

*Degeeriella actophila* (Kellogg and Chapman); Peters, 1936: 16 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Clay and Meinertzhagen, 1939: 450

*Lunaceps actophila* (Kellogg and Chapman); Ansari, 1947: 280

*Lunaceps actophilus* (Kellogg and Chapman); Hopkins and Clay, 1952: 201

*Lunaceps actophilus* (Kellogg and Chapman); Timmermann, 1953: 628 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Malcomson, 1960: 191

*Lunaceps holophaeus actophilus* (Kellogg and Chapman); Emerson, 1961: 253

*Lunaceps holophaeus actophilus* (Kellogg and Chapman); Emerson, 1965: 49

*Lunaceps holophaeus* (Burmeister, 1838); Keirans, 1967: 113 (by implication)

*Lunaceps actophilus* (Kellogg and Chapman); Fedorenko, 1968: 72

*Lunaceps actophilus* (Kellogg and Chapman); Hackman and Nyholm, 1968: 80

*Lunaceps holophaeus actophilus* (Kellogg and Chapman); Emerson, 1972: 93

*Lunaceps actophilus* (Kellogg and Chapman); Eichler and Hackman, 1973: 92

*Lunaceps actophilus* (Kellogg and Chapman); Ledger, 1980: 169 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Rékási and Kiss, 1980: 76

*Lunaceps actophilus* (Kellogg and Chapman); Pilgrim and Palma, 1982: 21

*Lunaceps actophilus* (Kellogg and Chapman); Forrester, 1995: 27

*Lunaceps acrophilus* [sic!] (Kellogg and Chapman); Mayberry *et al.*, 2000: 60

*Lunaceps actophilus* (Kellogg and Chapman); Price *et al.*, 2003: 196 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Holt, 2003: 32

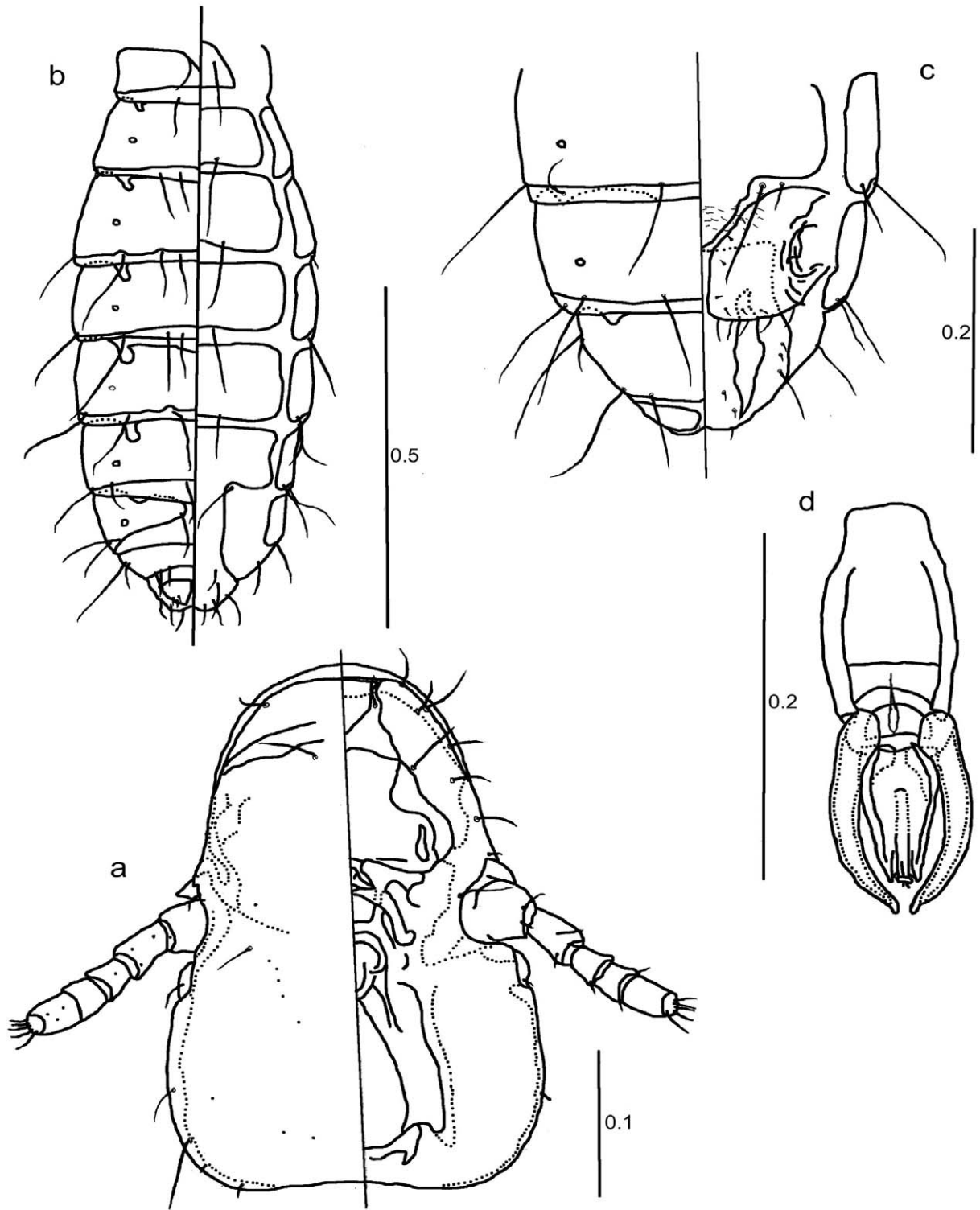
*Lunaceps actophilus* (Kellogg and Chapman); Palma and Jensen, 2005: 56 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Rékási, 2006: 183

*Lunaceps actophilus* (Kellogg and Chapman) (“Clade 6”); Gustafsson and Olsson, 2012: 94 (Fig. 1, 2).

**Type host:** *Calidris alba* (Pallas, 1764).

**Diagnosis:** Head ovoid, with posterior margin almost flat (Fig. 6a). Marginal carina well demarcated along its length, though weakened somewhat at dorsal preantennal suture. Dorsal preantennal suture clearly demarcated except medially, where it widens and encircles the apertures of the ADS. Ventral anterior plate pointed posteriorly. Preantennal nodus with dark margins and pale interior. In males, dark preantennal band prominent, but missing or very weak in females. This band usually forms several connections with the ventral lateral plates and the ventral carina, forming small bright “islands”. AVS3 anterior to AVS2.



**FIGURE 6.** *Lunaceps actophilus* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Abdominal tergite II in females with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width; no or very shallow indentation in males. Segments II–III, sometimes also IV, very pale, approaching whiteness. The rest of the abdomen also pale, but markedly darker lateral to the spiracle openings. Females paler than males. Paratergal plates wide. Tergal heads small and transparent, sometimes re-entrant on segment III (Fig. 6b); this is more developed in males than in females.

**TABLE 1.** Measurements of *Lunaceps* species according to host species and host subspecies (where relevant). Abbreviations: S = N: Sex = number measured; TL = Total length; HL = Head length; HW = Head width; PRW = Prothorax width; PTW = Pterothorax width; AW = Abdomen width; PL = Paramere length. Abbreviations for host and louse genera: *A* = *Aphrica*; *C* = *Calidris*; *E* = *Eurynorhynchus*; *L* = *Lunaceps*; *Lc* = *Limicola*; *Ls* = *Limosa*; *M* = *Micropalama*; *N* = *Numenius*; *P* = *Philomachus*; *Q* = *Quadriceps*; *T* = *Tryngites*; *V* = *Vanellus*.

Species	Host	S = N	TL	HL	HW	PRW	PTW	AW	PL
<i>L. actophilus</i>	<i>C. alba</i>	M = 10	1.44 (1.40–1.47)	0.36 (0.35–0.37)	0.25 (0.24–0.26)	0.18 (0.17–0.18)	0.24 (0.23–0.26)	0.32 (0.30–0.36)	0.11 (0.10–0.12)
		F = 10	1.58 (1.47–1.72)	0.36 (0.33–0.39)	0.26 (0.24–0.28)	0.18 (0.17–0.20)	0.25 (0.23–0.28)	0.36 (0.32–0.42)	
<i>L. clayae</i>	<i>Ls. fedoa</i>	M = 9	1.71 (1.56–1.85)	0.45 (0.43–0.46)	0.30 (0.28–0.34)	0.23 (0.2–0.24)	0.33 (0.30–0.36)	0.40 (0.38–0.43)	0.15 (0.13–0.16)
		F = 6	1.81 (1.63–2.01)	0.46 (0.45–0.47)	0.32 (0.31–0.33)	0.23 (0.22–0.24)	0.34 (0.31–0.36)	0.44 (0.43–0.45)	
<i>L. drosti</i>	<i>C. canutus canutus</i>	M = 10	1.53 (1.48–1.64)	0.38 (0.37–0.39)	0.26 (0.23–0.27)	0.19 (0.18–0.20)	0.26 (0.24–0.28)	0.33 (0.30–0.39)	0.11 (0.10–0.11)
		F = 10	1.73 (1.66–1.79)	0.37 (0.36–0.38)	0.26 (0.25–0.27)	0.19 (0.18–0.20)	0.26 (0.24–0.28)	0.36 (0.33–0.41)	
	<i>C. canutus rogersi</i>	M = 10	1.49 (1.41–1.57)	0.37 (0.35–0.38)	0.25 (0.24–0.26)	0.18 (0.18–0.19)	0.23 (0.22–0.25)	0.32 (0.30–0.34)	0.11 (0.09–0.12)
		F = 10	1.61 (1.59–1.64)	0.36 (0.35–0.37)	0.25 (0.25–0.26)	0.18 (0.18–0.19)	0.24 (0.23–0.26)	0.35 (0.34–0.36)	
	<i>C. canutus rufus</i>	M = 10	1.52 (1.43–1.72)	0.37 (0.35–0.38)	0.25 (0.24–0.26)	0.19 (0.18–0.19)	0.24 (0.23–0.25)	0.32 (0.30–0.34)	0.11 (0.10–0.12)
		F = 10	1.61 (1.59–1.64)	0.37 (0.36–0.37)	0.25 (0.25–0.26)	0.19 (0.18–0.19)	0.25 (0.24–0.27)	0.35 (0.34–0.36)	
	<i>A. virgata</i>	M = 2	1.50 (1.46–1.54)	0.38 (0.38–0.38)	0.26 (0.26–0.26)	0.19 (0.18–0.20)	0.25 (0.23–0.26)	0.35 (0.33–0.35)	0.13 (0.13)
		F = 6	1.74 (1.60–1.88)	0.39 (0.36–0.41)	0.27 (0.26–0.30)	0.20 (0.20–0.20)	0.27 (0.26–0.30)	0.40 (0.34–0.44)	
<i>L. enigmaticus</i>	<i>M. himantopus</i>	M = 3	1.58 (1.54–1.65)	0.41 (0.40–0.42)	0.29 (0.28–0.30)	0.21 (0.20–0.22)	0.27 (0.26–0.29)	0.36 (0.34–0.38)	0.10 (0.09–0.11)
		F = 6	1.76 (1.72–1.80)	0.41 (0.39–0.42)	0.28 (0.24–0.30)	0.21 (0.18–0.22)	0.29 (0.25–0.31)	0.39 (0.37–0.40)	
<i>L. falcinellus</i>	<i>Lc. falcinellus falcinellus</i>	M = 4	1.48 (1.41–1.55)	0.40 (0.40–0.41)	0.24 (0.23–0.25)	0.18 (0.17–0.18)	0.24 (0.23–0.25)	0.29 (0.28–0.33)	0.08 (0.08–0.10)
		F = 10	1.62 (1.50–1.74)	0.40 (0.39–0.42)	0.24 (0.23–0.25)	0.17 (0.16–0.19)	0.25 (0.23–0.26)	0.33 (0.28–0.36)	
	<i>Lc. falcinellus sibirica</i>	M = 1	1.44	0.38	0.23	0.16	0.21	0.25	0.08
		F = 2	1.56 (1.55–1.56)	0.39 (0.38–0.39)	0.24 (0.24–0.24)	0.17 (0.16–0.18)	0.23 (0.21–0.25)	0.30 (0.29–0.30)	
	<i>C. ferruginea</i>	M = 10	1.55 (1.45–1.68)	0.39 (0.37–0.41)	0.24 (0.22–0.26)	0.18 (0.17–0.19)	0.25 (0.21–0.27)	0.30 (0.26–0.34)	0.09 (0.8–0.10)
		F = 10	1.76 (1.61–1.83)	0.40 (0.39–0.41)	0.25 (0.25–0.26)	0.19 (0.18–0.19)	0.26 (0.26–0.28)	0.35 (0.34–0.37)	
	<i>C. minuta</i>	M = 8	1.49	0.37	0.22	0.16	0.21	0.25	0.08
		F = 10	1.63 (1.51–1.80)	0.38 (0.36–0.39)	0.23 (0.22–0.25)	0.17 (0.16–0.19)	0.23 (0.21–0.26)	0.29 (0.26–0.34)	
	<i>C. ruficollis</i>	M = 10	1.54 (1.44–1.65)	0.38 (0.36–0.40)	0.23 (0.22–0.25)	0.18 (0.16–0.19)	0.23 (0.20–0.25)	0.29 (0.26–0.33)	0.09 (0.8–0.10)
		F = 10	1.67 (1.59–1.78)	0.39 (0.36–0.40)	0.24 (0.21–0.26)	0.18 (0.16–0.19)	0.24 (0.19–0.27)	0.31 (0.26–0.37)	
<i>L. holophaeus</i>	<i>P. pugnax</i>	M = 10	1.57 (1.51–1.81)	0.36 (0.35–0.38)	0.23 (0.22–0.24)	0.18 (0.16–0.18)	0.22 (0.20–0.23)	0.26 (0.22–0.27)	0.09 (0.08–0.10)
		F = 10	1.71 (1.59–1.78)	0.37 (0.35–0.38)	0.24 (0.23–0.25)	0.18 (0.17–0.19)	0.24 (0.22–0.27)	0.30 (0.28–0.31)	
<i>L. hopkinsi</i>	<i>N. tahitiensis</i>	M = 10	1.94 (1.82–2.01)	0.50 (0.47–0.51)	0.33 (0.31–0.35)	0.25 (0.23–0.26)	0.35 (0.31–0.38)	0.48 (0.41–0.52)	0.19 (0.17–0.20)
		F = 10	2.13 (2.02–2.21)	0.51 (0.50–0.53)	0.35 (0.34–0.37)	0.27 (0.25–0.28)	0.38 (0.34–0.40)	0.53 (0.46–0.55)	
<i>L. incoenis</i>	<i>C. mauri</i>	M = 10	1.55 (1.49–1.62)	0.37 (0.35–0.38)	0.23 (0.22–0.24)	0.17 (0.15–0.17)	0.22 (0.18–0.24)	0.26 (0.22–0.30)	0.10 (0.09–0.10)

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TABLE 1 (continued)

Species	Host	S = N	TL	HL	HW	PRW	PTW	AW	PL
<i>L. kukri</i>	<i>C. pusillus</i>	F = 10	1.68 (1.62–1.75)	0.37 (0.35–0.39)	0.24 (0.23–0.25)	0.17 (0.15–0.17)	0.23 (0.21–0.25)	0.30 (0.28–0.32)	
		M = 10	1.58 (1.50–1.66)	0.38 (0.36–0.40)	0.24 (0.23–0.26)	0.17 (0.16–0.19)	0.23 (0.22–0.26)	0.26 (0.23–0.31)	0.10 (0.09–0.10)
		F = 10	1.74 (1.66–1.85)	0.38 (0.37–0.40)	0.25 (0.24–0.27)	0.18 (0.16–0.19)	0.24 (0.21–0.28)	0.31 (0.26–0.37)	
	<i>C. minutilla</i>	M = 6	1.55	0.37	0.23	0.17	0.21	0.21	0.08
		F = 3	1.69	0.38	0.24	0.17	0.20	0.25	
	<i>L. kukri</i>	<i>N. americanus americanus</i>	M = 10	2.18 (1.99–2.34)	0.55 (0.51–0.57)	0.37 (0.32–0.39)	0.28 (0.24–0.31)	0.41 (0.33–0.45)	0.55 (0.44–0.61)
F = 10			2.25 (2.00–2.41)	0.55 (0.52–0.57)	0.38 (0.34–0.40)	0.30 (0.27–0.31)	0.44 (0.41–0.46)	0.62 (0.56–0.66)	
<i>N. americanus parvus</i>		M = 0	–	–	–	–	–	–	–
<i>L. limosae</i>	<i>Ls. limosa limosa</i>	F = 2	2.12 (2.07–2.18)	0.54 (0.53–0.54)	0.35 (0.35–0.35)	0.27 (0.27–0.28)	0.41 (0.41–0.41)	0.56 (0.54–0.58)	
		M = 2	1.45 (1.42–1.47)	0.39 (0.37–0.40)	0.28 (0.25–0.32)	0.21 (0.19–0.23)	0.29 (0.25–0.32)	0.38 (0.31–0.45)	0.13 (0.11–0.13)
	<i>Ls. limosa melanuroides</i>	F = 10	1.68 (1.51–1.83)	0.38 (0.37–0.41)	0.28 (0.25–0.30)	0.20 (0.19–0.22)	0.29 (0.26–0.31)	0.40 (0.35–0.43)	
		M = 10	1.59 (1.56–1.64)	0.37 (0.36–0.39)	0.25 (0.24–0.26)	0.19 (0.18–0.20)	0.26 (0.25–0.28)	0.34 (0.32–0.36)	0.11 (0.10–0.12)
<i>L. limosella</i>	<i>Ls. lapponica lapponica</i>	F = 10	1.80 (1.73–1.88)	0.37 (0.36–0.39)	0.27 (0.26–0.27)	0.19 (0.18–0.21)	0.28 (0.26–0.29)	0.39 (0.36–0.43)	
		M = 10	1.53 (1.46–1.64)	0.40 (0.38–0.42)	0.29 (0.27–0.31)	0.21 (0.19–0.22)	0.29 (0.26–0.32)	0.39 (0.35–0.43)	0.12 (0.12–0.13)
	<i>Ls. lapponica baueri</i>	F = 10	1.81 (0.75–1.87)	0.41 (0.40–0.42)	0.32 (0.30–0.33)	0.23 (0.22–0.23)	0.32 (0.30–0.34)	0.47 (0.45–0.49)	–
		M = 10	1.49 (1.37–1.58)	0.38 (0.35–0.40)	0.27 (0.26–0.30)	0.20 (0.18–0.21)	0.28 (0.24–0.31)	0.38 (0.36–0.40)	0.11 (0.10–0.12)
		F = 10	1.77 (1.64–1.87)	0.40 (0.39–0.43)	0.30 (0.29–0.33)	0.21 (0.20–0.23)	0.32 (0.29–0.36)	0.46 (0.39–0.53)	
<i>Ls. lapponica menzbieri</i>	M = 2	1.65 (1.64–1.67)	0.39 (0.39–0.39)	0.27 (0.26–0.27)	0.19 (0.19–0.19)	0.27 (0.26–0.27)	0.35 (0.34–0.36)	0.11 (0.10–0.11)	
<i>L. lissmanni</i>	<i>N. minutus</i>	F = 1	1.53	0.36	0.26	0.29	0.26	0.33	
		M = 9	1.78 (1.54–1.95)	0.45 (0.42–0.46)	0.28 (0.26–0.29)	0.22 (0.20–0.23)	0.29 (0.26–0.31)	0.39 (0.33–0.42)	0.17 (0.16–0.18)
	F = 10	2.01 (1.93–2.10)	0.45 (0.44–0.47)	0.30 (0.28–0.31)	0.22 (0.21–0.24)	0.31 (0.28–0.33)	0.45 (0.39–0.50)		
<i>L. mintoni</i>	<i>C. tenuirostris</i>	M = 9	1.52 (1.46–1.59)	0.39 (0.37–0.41)	0.26 (0.24–0.27)	0.20 (0.19–0.21)	0.26 (0.24–0.28)	0.37 (0.34–0.41)	0.11 (0.10–0.12)
<i>L. nereis</i>	<i>C. maritima</i>	F = 10	1.63 (1.53–1.70)	0.39 (0.37–0.41)	0.27 (0.25–0.29)	0.20 (0.20–0.21)	0.27 (0.25–0.29)	0.41 (0.37–0.45)	
		M = 5	1.36 (1.30–1.39)	0.36 (0.35–0.37)	0.27 (0.26–0.28)	0.19 (0.19–0.20)	0.27 (0.25–0.27)	0.35 (0.33–0.38)	0.10 (0.09–0.11)
	F = 5	1.52 (1.43–1.59)	0.36 (0.35–0.37)	0.28 (0.27–0.29)	0.19 (0.19–0.20)	0.27 (0.25–0.28)	0.38 (0.35–0.39)		
	<i>C. ptilocnemis</i>	M = 2	1.40 (1.33–1.47)	0.37 (0.35–0.39)	0.28 (0.26–0.29)	0.19 (0.19–0.20)	0.27 (0.26–0.28)	0.36 (0.36–0.37)	0.10 (0.10–0.11)
		F = 5	1.46 (1.35–1.69)	0.37 (0.35–0.41)	0.30 (0.29–0.31)	0.20 (0.20–0.21)	0.28 (0.26–0.32)	0.39 (0.38–0.41)	
<i>L. numenii numenii</i>	<i>N. arquata arquata</i>	M = 10	2.20 (2.14–2.32)	0.56 (0.54–0.58)	0.38 (0.36–0.41)	0.29 (0.27–0.31)	0.41 (0.39–0.45)	0.56 (0.51–0.59)	0.21 (0.20–0.22)
		F = 10	2.31 (2.19–2.39)	0.56 (0.53–0.57)	0.39 (0.38–0.39)	0.29 (0.28–0.31)	0.42 (0.40–0.45)	0.57 (0.54–0.61)	
	<i>N. arquata lineata</i>	M = 3	2.18 (2.11–2.23)	0.55 (0.53–0.56)	0.37 (0.36–0.37)	0.28 (0.28–0.29)	0.39 (0.38–0.40)	0.54 (0.50–0.56)	0.21 (0.20–0.22)
		F = 9	2.34 (2.25–2.43)	0.56 (0.54–0.57)	0.39 (0.38–0.41)	0.29 (0.28–0.30)	0.42 (0.41–0.45)	0.59 (0.51–0.62)	

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TABLE 1 (continued)

Species	Host	S = N	TL	HL	HW	PRW	PTW	AW	PL
<i>L. numenii</i> <i>madagascariensis</i>	<i>N. madagascariensis</i>	M = 10	2.09 (2.02–2.14)	0.52 (0.51–0.53)	0.35 (0.34–0.36)	0.27 (0.25–0.28)	0.36 (0.34–0.40)	0.49 (0.47–0.55)	0.19 (0.18–0.20)
		F = 10	2.33 (2.24–2.42)	0.54 (0.52–0.56)	0.38 (0.37–0.39)	0.28 (0.27–0.30)	0.39 (0.37–0.43)	0.50 (0.47–0.59)	
<i>L. numenii</i> <i>phaeopi</i>	<i>N. phaeopus phaeopus</i>	M = 10	1.90 (1.79–2.07)	0.48 (0.44–0.51)	0.31 (0.29–0.33)	0.23 (0.22–0.25)	0.33 (0.30–0.35)	0.43 (0.37–0.48)	0.17 (0.15–0.19)
		F = 10	2.09 (2.02–2.17)	0.49 (0.47–0.51)	0.33 (0.30–0.35)	0.25 (0.22–0.26)	0.35 (0.33–0.38)	0.48 (0.44–0.52)	
	<i>N. phaeopus hudsonicus</i>	M = 5	1.85 (1.76–1.94)	0.47 (0.46–0.48)	0.31 (0.29–0.32)	0.23 (0.23–0.25)	0.32 (0.32–0.33)	0.42 (0.40–0.45)	0.19 (0.18–0.20)
		F = 7	2.07 (1.99–2.16)	0.49 (0.48–0.51)	0.33 (0.32–0.35)	0.25 (0.24–0.27)	0.35 (0.33–0.37)	0.48 (0.42–0.54)	
	<i>N. phaeopus variegatus</i>	M = 10	2.05 (2.01–2.07)	0.50 (0.47–0.51)	0.32 (0.30–0.33)	0.25 (0.23–0.25)	0.36 (0.32–0.38)	0.42 (0.39–0.46)	0.19 (0.18–0.20)
		F = 10	2.21 (2.07–2.32)	0.51 (0.46–0.53)	0.34 (0.32–0.35)	0.26 (0.24–0.27)	0.37 (0.34–0.40)	0.44 (0.42–0.47)	
<i>L. paschalis</i>	<i>Ls. haemastica</i>	M = 2	1.49 (1.39–1.58)	0.40 (0.38–0.41)	0.29 (0.28–0.30)	0.21 (0.21–0.22)	0.29 (0.28–0.30)	0.40 (0.36–0.45)	0.12 (0.12–0.12)
		F = 4	1.55 (1.41–1.71)	0.38 (0.37–0.41)	0.30 (0.29–0.32)	0.21 (0.20–0.23)	0.30 (0.28–0.34)	0.45 (0.42–0.50)	
<i>L. proximus</i>	<i>N. tenuirostris</i>	M = 4	2.00 (1.86–2.12)	0.50 (0.47–0.51)	0.33 (0.32–0.35)	0.28 (0.24–0.29)	0.39 (0.33–0.42)	0.50 (0.48–0.52)	0.20 (0.20–0.21)
		F = 2	2.12 (2.10–2.14)	0.52 (0.51–0.53)	0.35 (0.35–0.35)	0.29 (0.28–0.30)	0.42 (0.41–0.42)	0.54 (0.52–0.55)	
<i>L. rileyi</i>	<i>N. borealis</i>	M = 5 <sup>1</sup>	1.62 (1.52–1.68)	0.44 (0.39–0.47)	0.30 (0.26–0.32)	0.23 (0.21–0.24)	0.32 (0.30–0.34)	0.46 (0.39–0.51)	0.19
		F = 4	2.01 (1.89–2.12)	0.48 (0.47–0.50)	0.35 (0.34–0.36)	0.25 (0.24–0.26)	0.36 (0.34–0.37)	0.56 (0.50–0.60)	
<i>L. rothkoi</i>	<i>T. subruficollis</i>	M = 5	1.58 (1.55–1.64)	0.39 (0.38–0.40)	0.23 (0.21–0.24)	0.17 (0.16–0.17)	0.22 (0.21–0.23)	0.29 (0.26–0.32)	0.09 (0.08–0.10)
		F = 1	1.78	0.41	0.26	0.18	0.26	0.37	
<i>L. schismatus</i>	<i>C. alpina alpina</i>	M = 10	1.34 (1.25–1.40)	0.36 (0.33–0.37)	0.25 (0.23–0.25)	0.18 (0.17–0.19)	0.24 (0.21–0.26)	0.31 (0.27–0.32)	0.10 (0.09–0.11)
		F = 10	1.47 (1.36–1.62)	0.36 (0.33–0.39)	0.26 (0.24–0.27)	0.19 (0.17–0.21)	0.25 (0.24–0.29)	0.34 (0.31–0.36)	
	<i>C. alpina schinzii</i>	M = 10	1.34 (1.31–1.38)	0.36 (0.35–0.38)	0.25 (0.25–0.27)	0.18 (0.17–0.19)	0.25 (0.24–0.27)	0.30 (0.28–0.33)	0.10 (0.09–0.11)
		F = 10	1.42 (1.20–1.53)	0.36 (0.33–0.38)	0.27 (0.23–0.29)	0.18 (0.15–0.20)	0.26 (0.21–0.29)	0.33 (0.29–0.37)	
	<i>C. alpina arctica</i>	M = 1	1.42	0.37	0.28	0.19	0.27	0.33	0.12
		F = 2	1.44 (1.43–1.45)	0.36 (0.35–0.36)	0.26 (0.25–0.26)	0.17 (0.17–0.17)	0.24 (0.24–0.24)	0.32 (0.29–0.34)	
<i>L. superciliosus</i>	<i>C. acuminata</i>	M = 10	1.67 (1.61–1.72)	0.38 (0.36–0.39)	0.23 (0.21–0.24)	0.17 (0.16–0.18)	0.23 (0.21–0.24)	0.27 (0.24–0.30)	0.10 (0.09–0.10)
		F = 10	1.84 (1.62–1.91)	0.38 (0.35–0.39)	0.24 (0.21–0.26)	0.18 (0.15–0.19)	0.24 (0.20–0.27)	0.32 (0.27–0.35)	
	<i>C. subminuta</i>	M = 0	–	–	–	–	–	–	–
		F = 3	1.66 (1.58–1.79)	0.36 (0.35–0.38)	0.22 (0.21–0.24)	0.15 (0.14–0.15)	0.19 (0.19–0.21)	0.25 (0.24–0.27)	
<i>Incerta sedis</i>	<i>C. melanotos</i>	M = 2	1.56 (1.50–1.62)	0.38 (0.36–0.41)	0.23 (0.21–0.25)	0.18 (0.17–0.19)	0.23 (0.21–0.26)	0.29 (0.27–0.31)	0.10 (0.10–0.10)
		F = 5	1.77 (1.70–1.85)	0.38 (0.37–0.39)	0.24 (0.23–0.24)	0.17 (0.16–0.18)	0.24 (0.23–0.26)	0.33 (0.30–0.36)	
	<i>C. temminckii</i>	M = 10	1.49 (1.45–1.55)	0.38 (0.37–0.40)	0.22 (0.21–0.23)	0.17 (0.16–0.17)	0.22 (0.20–0.23)	0.26 (0.24–0.29)	0.09 (0.08–0.09)
		F = 10	1.62 (1.50–1.67)	0.38 (0.37–0.39)	0.23 (0.22–0.24)	0.17 (0.16–0.18)	0.22 (0.21–0.24)	0.29 (0.26–0.31)	

..... continued on the next page

TABLE 1 (continued)

Species	Host	S = N	TL	HL	HW	PRW	PTW	AW	PL
	<i>E. pygmeus</i>	M = 3	1.62 (1.60–1.66)	0.41 (0.40–0.42)	0.28 (0.28–0.29)	0.21 (0.19–0.23)	0.28 (0.26–0.30)	0.36 (0.33–0.40)	0.10 (0.09–0.10)
		F = 7	1.76 (1.69–1.83)	0.42 (0.41–0.43)	0.28 (0.27–0.30)	0.21 (0.20–0.22)	0.31 (0.29–0.37)	0.41 (0.39–0.45)	
<i>Q. parabolicus</i>	<i>V. resplendens</i>	M = 6	1.60 (1.56–1.64)	0.46 (0.45–0.47)	0.32 (0.31–0.33)	0.21 (0.20–0.21)	0.30 (0.30–0.31)	0.40 (0.39–0.41)	0.08 (0.06–0.09)
		F = 6	2.03 (1.98–2.09)	0.50 (0.48–0.52)	0.35 (0.33–0.36)	0.23 (0.23–0.24)	0.35 (0.34–0.36)	0.50 (0.47–0.51)	

Female genital lobes with 5 posterior marginal setae, 3 sub-marginal setae, and 5 median marginal setae (Fig. 6c). Parameres gently curved, of roughly equal width until distal fourth. Lower endomere broad and bean-shaped. Distal ends of mesomere slender; dorsal fingers stout (Fig. 6d).

**Discussion:** Similar to *L. schismatus* sp. nov., but females separable by being very pale, making the dark paratergal plates seem more distinct; this is less obvious in males. In fresh material, the white blotch (usually) covering abdominal segments II–III is very distinctive, and has not been found in any other species; this character can be hard to see in prepared material. Populations from the two hosts are well separated genetically (Gustafsson and Olsson, 2012), and the population from *C. alpina* sp. is described below as *L. schismatus* sp. nov.

Males of *L. actophilus* lack the wedge-shaped indentations of the tergites found in most other species, apart from tergite II, which is sometimes shallowly indented. The preantennal area is distinctive, with many secondary connections between the dark preantennal band and the ventral carina and ventral lateral plates, but these characters can be seen to a much lesser extent in other species as well. The dark borders and pale interior of the preantennal nodi differentiates *L. actophilus* from most other species, but some individuals of *L. nereis* have the same pattern, although these are readily separated from *L. actophilus* by the shape of the head and the extreme thinness of the marginal carina.

*Luniceps actophilus* was reported from *Charadrius hiaticula* by Zunker (1932), but this may be a misidentification (as argued by Mehl *et al.*, 1982). Older reports of this species on hosts other than *C. alba* are plentiful (*e.g.* Waterston, 1922). Some of these may refer to *Luniceps actophilus* as defined here, while others may refer to *Luniceps* in general, as *Luniceps actophilus* was one of the few species described at the time. These records have here been listed under the *Luniceps* species normally inhabiting that host, under the assumption that most refer to a different louse species.

**Etymology:** From *act* = the shore, or *actit* = shore dweller and *philo* = lover, loving. *Actophilus* is a junior synonym of *Calidris*, and the choice of name may indicate that this is the “*Nirmus*” found on *Calidris* sandpipers, which are all “shore lovers”.

#### Material examined:

*Ex. Calidris alba* (synonyms: *Crocethia alba*, *Calidris arenaria*).

Holotype: ♀1, USA: California: Pacific Grove, 472c (EMEC).

Paratypes: ♀2, USA: California: Pacific Grove, 472c (EMEC).

Non-types: ♀8f, ♂12, United Kingdom: Sussex, December 1934, Meinertzhagen Collection 2260 (NHML). ♀3, ♂9, United Kingdom: England: Sussex, December 1934, Meinertzhagen Collection 2244 (NHML). ♀11, ♂19, United Kingdom: England: Norfolk, January 1946, Meinertzhagen Collection 15564 (NHML). ♀4, ♂4, United Kingdom: England: Norfolk, January 1946, Meinertzhagen Collection 15569 (NHML). ♀4, ♂6, United Kingdom: England: Norfolk, January 1940, Meinertzhagen Collection 13756 (NHML). ♀11, ♂9, Egypt, May 1936, Meinertzhagen Collection, 4698 (NHML). ♀1, ♂2, United Kingdom: Scotland: Hebrides: North Uist, September 1941, Meinertzhagen Collection 14606 and 14607 (NHML). ♀1, ♂1, Ireland: County Sligo, 278 (NHML). ♀1, ♂1, Germany: Hamburg: Neuwerk, 17 September 1931, Hopkins Collection (NHML). ♂2, Mauritius: Port Louis: Mer Rouge, 14 February, 1974, BM1975-161 (NHML). ♀1, ♂3, United Kingdom: Wales: Glamorganshire: Aberthaur, 8 September, 1935, BM 1980-40 (NHML). ♀2, ♂1, Ireland: County Sligo: Lislary, 22 September, 1938, BM 1980-40 (NHML). ♀1, ♂2, United Kingdom: Shetlands: Fair Isle Bird Observatory, 27 August, 1957, BM 1958-166 (NHML). ♀3, ♂3, Denmark: Faroes Islands: Nólsoy, 9 September, 2000 (MONZ). ♀1, New Zealand: Waimakariri Beach, 13 January, 1938, R.L.C. Pilgrim collection, C Mu AV 2476 (MONZ). ♀1, ♂1, India: Tamil Nadu: Point



Calimere, 22 November 1970, K.C. Emerson Collection (OSU). ♀1, ♂1, [Collection data not given on slide], K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Ohio: Sandusky, 19 September 1925, K.C. Emerson Collection (OSU). ♂3, India: Tamil Nadu: Point Calimere, 12 November 1969, K.C. Emerson Collection (OSU). ♀6, ♂6, United States: Texas: Galveston, 6 December 1947 and 15 November 1946, K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Mississippi: Ship Island, K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Florida: Sanibel, K.C. Emerson Collection (OSU). ♀2, ♂1, [Collection data not given on slide], 7814a, c, d (MFN). ♀1, [Collection data not given on slide], 20066a (MFN). ♀2, ♂1, Australia: West Australia: Broome: Coconut Wells, 9 November, 2008, ID: 807, Band Number: 042-43289, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 30 July, 2007, ID: 243, Band number: 3533646, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 31 July, 2007, ID: 264, Band number: 3534065, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 30 July 2007, ID: 239, Band number: 3533645, D. Gustafsson (SMNH). ♀1, ♂1, Australia: Western Australia: Broome Area: Coconut Wells, 9 November 2008, ID: 804, 805, Band numbers: 042-43278 and 042-43280, D. Gustafsson (SMNH).

*Ex Calidris alpina* (synonym: *Erolia alpina*) (possibly stragglers):

♂1, Germany, K.C. Emerson Collection (OSU).

Material of uncertain status due to poor condition:

*Ex Calidris alba* (as *Crocethia alba*):

♂1, United States: Texas: Galveston, November 13<sup>th</sup> 1946, BM 1960-518 (NHML).

### ***Lunaceps clayae* Timmermann, 1954**

(Fig. 7a–d; Table 1)

*Lunaceps clayae* Timmermann, 1954a: 629

*Lunaceps clayae* Timmermann; Malcomson, 1960:191

*Lunaceps limosella clayae* Timmermann; Emerson, 1972: 94

*Lunaceps clayae* Timmermann; Price *et al.*, 2003: 196

**Type host:** *Limosa fedoa* (Linnaeus, 1758)

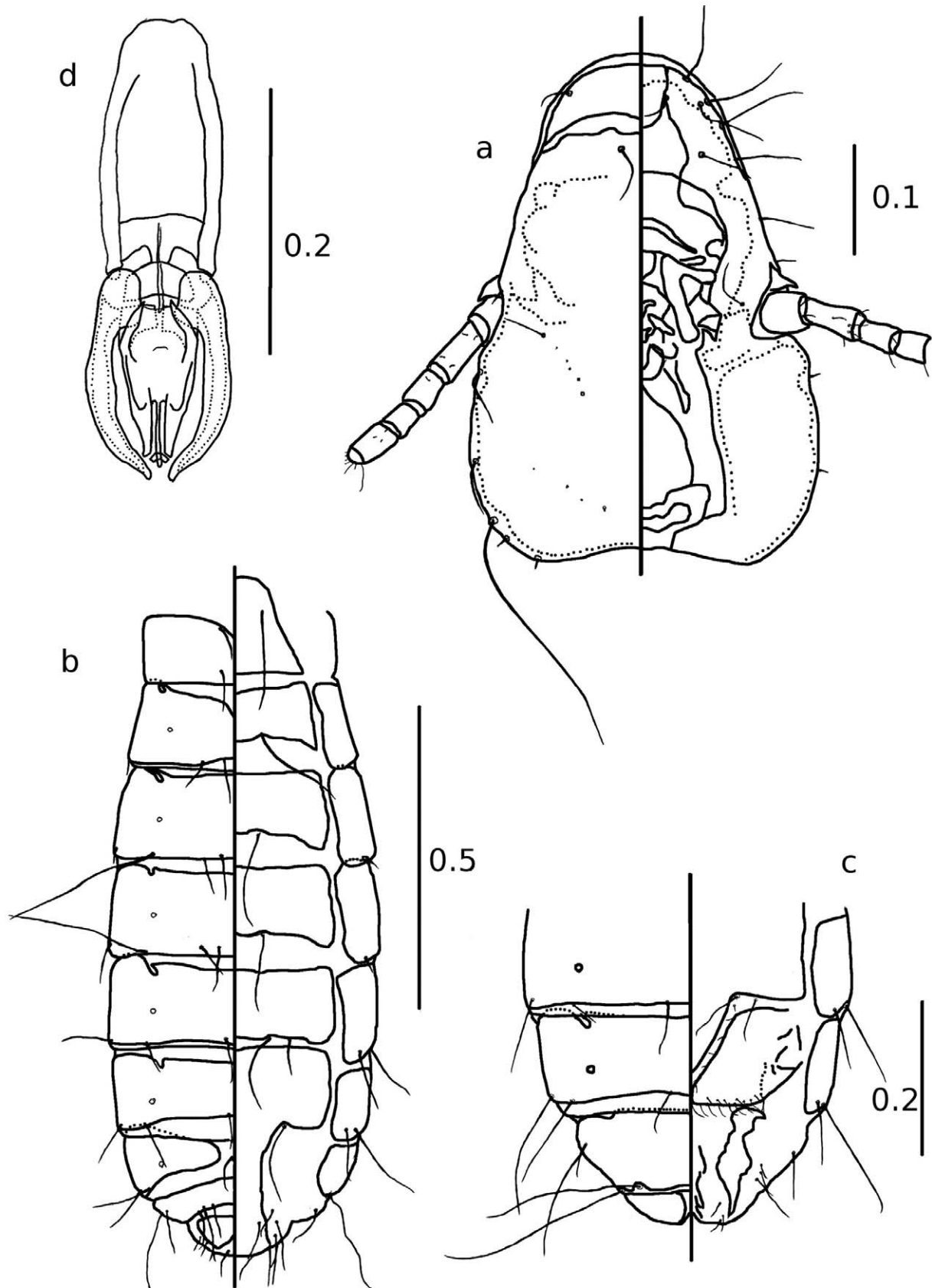
**Diagnosis:** Hyaline margin thin or missing. Marginal carina uninterrupted along the preantennal area, but transparent anteriorly and less well demarcated anterior to the AVS2 (Fig. 7a). Ventral anterior plate broad and distal half convergent. Dorsal preantennal suture continuous across the head, but narrows laterally. Preantennal setae very long and slender. AVS2 and AVS3 aligned, and positioned markedly posterior to the ADS. Eyes sunken in, and not visible. OS quite long and thick, but not similar to MTS3. POS sometimes positioned posterior to eye. MTS4 and MTS5 stout and thorn-like.

Abdominal tergites II–III in males and II–IV in females with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width (Fig. 7b). In both sexes, the ventral setae of segment II are positioned in the anterior half of the segment, similar to *L. rileyi*. Female dorsal intermediate setae on segment VII shorter than median setae. Female dorsal intermediate setae on segment IX long and thick. Males have an extra submedian pair of setae on the sternite of segment VII. Male subgenital plate wide. Sternites of male segments IV–VI very narrow, with the posterior margin being concave; this is not always as pronounced in females. Tergal heads very small, and present only in segments III–IV.

Female genital lobes with 8–10 posterior marginal setae, 5–6 thorn-like sub-marginal setae, and 6–7 thorn-like median marginal setae (Fig. 7c). Parameres broad and gently curved (Fig. 7d). Mesomere large, with a slight lateral bulge at distal half. Dorsal fingers broad and extending slightly beyond the anterior edge of ventral blades. Lower endomere broad and wide, almost square-shaped in some individuals. Apodemal bridge subtle, but not clearly demarcated.

**Discussion:** *Lunaceps clayae* differs from other *Lunaceps* parasitizing *Limosa* (*Lunaceps limosella*, *Lunaceps limosae*, and *Lunaceps paschalis*) in the male genitalia, which are larger and more similar to those of *Lunaceps* from *Numenius* (e.g. Fig. 23e). As in e.g. *Lunaceps hopkinsi* (Fig. 12), the female dorsal intermediate setae on abdominal segment IX are long and thick, more similar to the dorsal intermediate setae of segments IV–V than to

the median setae of these segments. However, *L. clayae* differs from *Lunaceps* species from *Numenius* in several key characters, including the OS and MTS1, which are short in *L. clayae*, and the setae of the pterothoracic rows in both sexes of *L. clayae*.



**FIGURE 7.** *Lunaceps clayae* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

The most distinctive character is the dorsal submedian setae of male segment VII, which is unique within *Lunaceps*. For both sexes, the far anterior position of the ventral setae of abdominal segment II, along with the general shape of the body and head, sets it apart from all other species. This character can be found on *L. rileyi*, *L. nereis*, and *L. schismatus* sp. nov. as well, but other characters of these species are sufficiently different to avoid misidentification. The head of *L. nereis* is smaller and rounder with a thin, unbroken marginal carina, and the dorsal sublateral setae of female abdominal segment IX are smaller, as in *L. schismatus* sp. nov. *Lunaceps rileyi* is quite different with its large number of ventral setae in both sexes, and its distinct parameres.

A single female from *Limnodromus scolopaceus* is known, but it is uncertain whether this is a contamination or if *Limnodromus scolopaceus* is a natural host of *L. clayae*.

**Etymology:** Named after the well-known phthirapterist Miss Theresa Clay formerly of the British museum (of Natural History), now the NHML.

#### **Material examined:**

*Ex Limosa fedoa:*

Holotype: ♂1, United States: California, March 1939, Meinertzhagen Collection 12997 (NHML).

Allotype: ♀1, United States: California, March 1939, Meinertzhagen Collection 12997 (NHML).

Paratypes: ♀26, ♂26, United States: California, March 1939, Meinertzhagen Collection 12714, 12730, 12738, 12756, 12897, 12997, 12998 (NHML). ♀2, ♂1, United States: Texas, Meinertzhagen Collection 8121 (NHML).

Non-type material: ♀4, ♂7, United States: California, NM 18555 (MONZ). ♀2, ♂2, Canada: Saskatchewan: Old Wives Lake, BM 1960-443 (NHML). ♂2, Canada: Manitoba: Anola, 5 July 1932, Hopkins Collection (NHML). ♀2, Mexico?: Chiapan, J. Waterston Collection BM1930-232 (NHML). ♀1, ♂2, United States: California, J. Waterston Collection BM 1930-232 (NHML). ♀4, ♂8, Mexico: Yucatan: Cozumel Island, February 1886, J. Waterston Collection BM1930-232 (NHML).

*Ex Limnodromus scolopaceus* (synonym: *Macroramphus griseus scolopaceus*)

♀1, Canada: British Columbia, May 1920, Meinertzhagen Collection (4302) (NHML).

#### ***Lunaceps drosti* Timmermann, 1954**

(Fig. 8a–d; Table 1)

*Nirmus actophilus* Kellogg and Chapman; Kellogg and Mann, 1912: 61 (partim)

*Degeeriella actophila* (Kellogg and Chapman); Peters, 1936: 15

*Lunaceps drosti* Timmermann, 1954a: 627

*Degeeriella holophaea* (Nitzsch); Blagoveshtchensky, 1958: 376

*Lunaceps drosti* Timmermann; Malcomson, 1960: 191

*Lunaceps holophaeus* (Burmeister); Keirans, 1967: 113 (by implication)

*Lunaceps holophaeus drosti* Timmermann; Emerson, 1972: 93

*Lunaceps* sp. “ab *Calidris c. canutus*” Eichler and Hackman, 1973: 92

*Lunaceps drosti* Timmermann; Ledger, 1980: 169

*Lunaceps drosti* Timmermann; Pilgrim and Palma, 1982: 21

*Lunaceps drosti* Timmermann; Forrester *et al.*, 1995: 27

*Lunaceps drosti* Timmermann; Palma and Barker, 1996: 191

*Lunaceps drosti* [sic!] Timmermann; Mayberry *et al.*, 2000: 60

*Lunaceps drosti* Timmermann; Price *et al.*, 2003: 196

*Lunaceps drosti* Timmermann; Palma and Jensen, 2005: 56

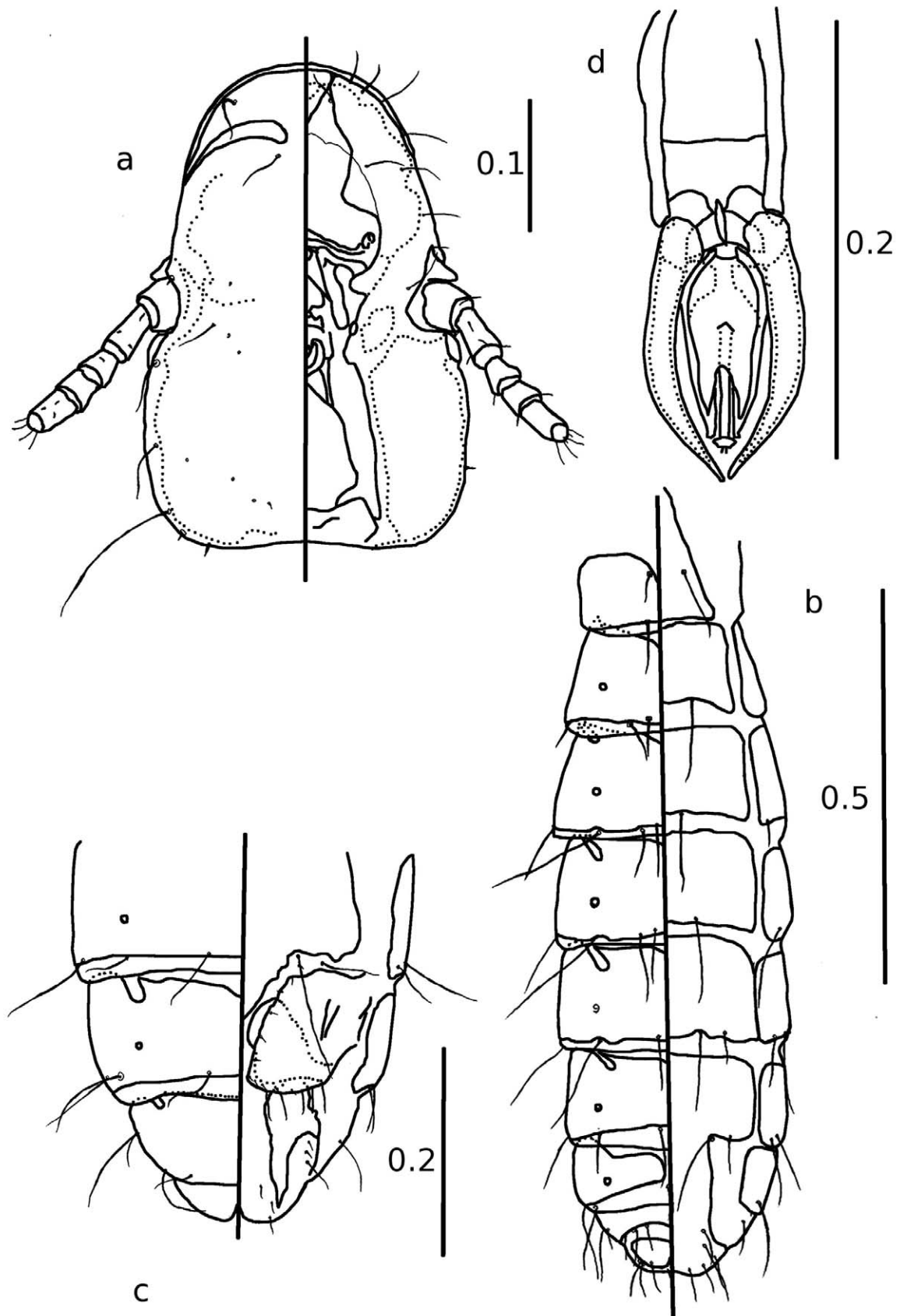
*Lunaceps drosti* Timmermann (“Clade 7”); Gustafsson and Olsson, 2012: 94 (Fig. 1, 2).

**Type host:** *Calidris canutus* (Linnaeus, 1758)

**Other hosts:** *Calidris canutus rufus* (Wilson, 1813), *Calidris canutus rogersi* (Mathews, 1913), *Aphriza virgata* (J.F. Gmelin, 1789).

**Diagnosis:** Marginal carina narrow (Fig. 8a), but bulges out at DSMS. Dorsal preantennal suture may be interrupted medially, and in females bends anteriorly to reach or envelop the ADS. Ventral anterior plate small, and triangular (occasionally rounded posteriorly). Lateral nodi moderately developed, and dark preantennal bands weak but broad. AVS3 slightly anterior to AVS2.

Abdominal tergites II–III in both sexes with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width (Fig. 8b). Indentations present in segments IV–V as well, but these are generally less pronounced. Paratergal plates broad. Tergal heads small and dark, appearing only as dark bars.



**FIGURE 8.** *Lunaceps drosti* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Female genital lobes with 5–6 posterior marginal setae, 4–6 sub-marginal setae, and 5–6 median marginal setae (Fig. 8c). Parameres gently curved, and very slender distally (Fig. 8d). Mesomere roughly triangular, with straight lateral sides. Lower endomere connected to apodemal bridge by a small triangle.

**Discussion:** Similar to *L. mintoni* sp. nov., but differs in the median indentations of the tergites, and in the shape of the parameres. Also, these two species are well separated genetically (Gustafsson and Olsson, 2012). The marginal carina is as thin as in *L. nereis*, but is not of even thickness as in this species.

No significant differences have been found between material from *C. canutus canutus*, *C. canutus rogersi*, and *C. canutus rufus*. The material from *Aphriza virgata* differs slightly from that from *C. canutus* in that the females are overall longer and broader, they lack the wedge-shaped indentation of tergite III, and have only 5 median marginal setae. The males are more similar in morphology and measurements, but the shape of the mesomere is slightly different, and the parameres are longer in *A. virgata* material than in *C. canutus ssp.* material. However, not enough specimens of *Lunaceps* from *A. virgata* are available to draw any definite conclusion about their taxonomic status.

**Etymology:** Named in honour of Rudolf Drost (1892–1971), Director of the Vogelwarte Helgoland, Institut für Vogelforschung, in Wilhelmshaven, who among other things studied factors that influenced bird migration and aging and sexing criteria for captured birds (Thomson, 1973).

### Material examined:

*Ex. Calidris canutus* (synonym: *Erolia canutus*, *Tringa canutus*):

Holotype: ♂1, United Kingdom: Scotland: Hebrides: N. Uist, September 1941, Meinertzhagen Collection 14599 (NHML).

Allotype: ♀1, United Kingdom: Scotland: Hebrides: N. Uist, September 1941, Meinertzhagen Collection 14599 (NHML).

Paratypes: ♀25, ♂29, United Kingdom: England: Norfolk, January, 1940, Meinertzhagen Collection 13758-9 (NHML). ♀26, ♂24, United Kingdom: Scotland: Hebrides: N. Uist, September 1941, Meinertzhagen Collection 14599 (NHML). ♀1, ♂1, United Kingdom: Scotland: Hebrides: N. Uist, September 1944, Meinertzhagen Collection 14599 (NHML). ♀1, ♂1, United Kingdom: Scotland: Hebrides: N. Uist, September 1941, K.C. Emerson Collection (OSU).

Non-types: ♀1, ♂1, Denmark: Faroes Islands: Nólsoy, 13 September 2000 (MONZ). ♀1, ♂4, Mauritania: Banc d'Arguin: Iwik, 27 November 2002 (MONZ). ♀4f, ♂4, United Kingdom: Scotland: Skerryvore, 17 September 1988 (MONZ). ♀1, ♂2, United States: New York, May 1932, Meinertzhagen Collection 11149 (NHML). ♂1, The Netherlands: Vlieland, 4 January 1972, BM1973-271 (NHML). ♂1, Canada: Manitoba: Churchill, 17 June 1947, BM 1956-302 (NHML). ♀2, ♂2, United Kingdom: Wales: Bardsey Island, 4 September 1957, BM1958-142 (NHML). ♀1, ♂2, Orient, L.I., N.Y., G.B. Thompson Collection 234, BM1980-40 (NHML). ♀2, ♂3, England, L. Harrison Collection (NHML). ♀1, ♂2, Ireland: Dublin: Rogerstown, 25 December 1939, Hopkins Collection (NHML). ♀1, ♂2, United Kingdom: Shetlands: Fair Isle Bird Observatory, 1953 (NHML). ♀1, ♂1, Thailand: Samutprakan: Bang Pu, 17 September 1965, K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Florida: Miami, 14 August 1924, K.C. Emerson Collection (OSU). ♀3, ♂3, United States: Texas: Galveston, 15 November 1946, K.C. Emerson Collection (OSU). ♀2, ♂2, United States: Florida: Sanibel, 19 October 1983, K.C. Emerson Collection (OSU). ♀8, ♂10, United States: California, March 1939, Meinertzhagen Collection (12892, 12966-67) (NHML). ♀1, [Collection data not given on slide], 4000a (MFN). ♂2, [Collection data not given on slide], 4010c, i (MFN). ♀3, ♂1, [Collection data not given on slide], 2990a, b, c, e (MFN). ♀1, ♂5, [Collection data not given on slide], 439 (MFN). ♂1, Sweden: Öland: Ottenby Bird Observatory, 27 July 2007, ID: 220, Band Number: 4562313, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 24 July 2007, ID: 177, Band Number: 4539175, D. Gustafsson (SMNH). ♂1, Sweden: Öland: Ottenby Bird Observatory, 23 July 2007, ID: 171, Band Number: 4539170, D. Gustafsson (SMNH).

*Ex Calidris canutus rufus*

♂1, Brazil: Sao Paulo: Iguape, 6 November, 1900, Hopkins Collection (NHML).

*Ex Calidris canutus rogersi*

♀1, ♂1, New Zealand: Campbell Island, Meinertzhagen Collection 16276 (NHML). ♀12, ♂12, New Zealand:

Campbell Island, 21 December 1945, DM 13076 and 13077 (MONZ). ♀1, Australia: Western Australia: Broome area, 11 November 2008, ID: 824b, Band Number: Not recorded, D. Gustafsson, (GNM). ♀1, Australia: Western Australia: Broome area, 11 November, 2008, ID: 820, Band Number: 042-89445, D. Gustafsson (SMNH). ♀1, Australia: Western Australia: 80 Mile Beach, 17 November, 2008, ID: 823, Band number: 042-00208, D. Gustafsson (SMNH).

*Ex Aphriza virgata*

♀2, Locality unknown, 99130 (EMEC). ♀2, ♂4, North America (NHML). ♀7, ♂2, United States: California, Meinertzhagen Collection 12730 (NHML).

*Ex Calidris ferruginea* (synonym: *Calidris testacea*) (possible stragglers):

♀1, ♂2, India: Tamil Nadu: Thanjavur: Point Calimere, 27 September 1969, K. C. Emerson Collection (OSU). ♀1, [Collection data not given on slide], 20070n (MFN).

Material of uncertain status due to condition of specimen:

*Ex Calidris canutus*

♀1, [Collection data not given on slide], 3187a (MFN).

***Lunaceps enigmaticus* sp. nov.**

(Fig. 9a–d; Table 1)

*Lunaceps nereis* Timmermann, 1954a: 628 (partim)

*Lunaceps holophaeus nereis* Timmermann; Emerson, 1972: 94 (partim)

*Lunaceps nereis* Timmermann; Forrester *et al.*, 1995: 28 (partim)

*Lunaceps nereis* Timmermann; Price *et al.*, 2003: 196 (partim)

**Type host:** *Micropalama himantopus* (Bonaparte, 1826)

**Diagnosis:** Head elongated ovoid (Fig. 9a). Marginal carina interrupted laterally and anterior-laterally, more or less disappearing anterior to the ADS2. Hyaline margin comparatively broad. Ventral anterior plate roughly triangular, but with rounded posterior margin. Bulge in marginal carina augmenting ventral anterior plate. Dorsal preantennal suture broad. AS1 and AVS3 aligned with ADS, AVS2 markedly posterior to AVS3. Lateral nodus missing. Ventral carina of uneven thickness. OS and MTS1 small, not approaching MTS3.

Posterior margin of pterothorax convergent with a small median point (Fig. 9b).

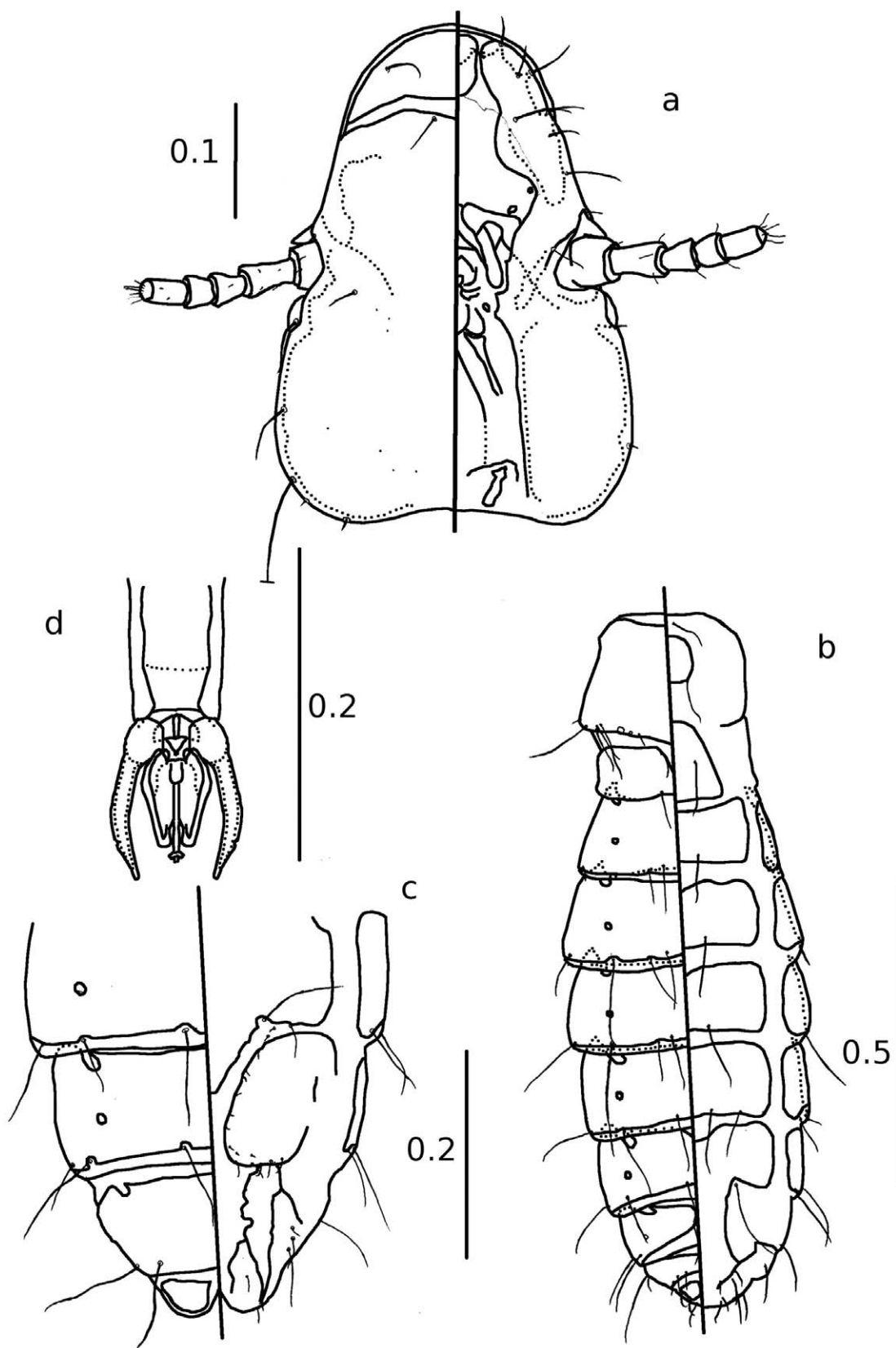
Abdominal tergites II in males and II–III in females with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width. Paratergal plates broad with very narrow dark border marking, and males appear to lack them entirely in segments VII–VIII. Tergal heads transparent, with those of segments III–IV (sometimes V) slender and pointed, and those of segments V–VII squat, sometimes pointed. Tergal heads of segment V–VII blunt, almost rounded, in females. Anterior sublateral indentation very narrow (Fig. 9b).

Female genital lobes with 5–6 posterior marginal setae, 3–4 sub-marginal setae, and 6–9 median marginal setae (Fig. 9c). Parameres slender and gently curved, with a visible aperture one third of the length from the tip. Mesomere stout. Lower endomere kidney-shaped. Apodemal bridge broad but weakly coloured (Fig. 9d).

**Discussion:** *L. enigmaticus* sp. nov. is well separated from other species on *Calidris* s. lat., with many characters of the preantennal area being more similar to those of *Lunaceps* parasitic on *Numenius* species. *Lunaceps enigmaticus* sp. nov. is somewhat reminiscent of *L. mintoni*, but differs in the shape of the paratergal plates and in the number of female genital setae. *Lunaceps* from *Micropalama himantopus* has previously been identified as *L. nereis* (e.g. Price *et al.*, 2003), but *L. enigmaticus* sp. nov. can be separated from *L. nereis* by the shape of the head, the interruption of the marginal carina, the shape of the tergal heads and the male genitalia.

The type host of *L. enigmaticus* sp. nov. is also a somewhat aberrant species, which has occasionally been placed in *Calidris* and sometimes in its own genus, *Micropalama*. Recent studies have placed it well inside *Calidris sensu lato* (Borowik and McLennan, 1999; Hebert *et al.*, 2004; Thomas *et al.*, 2004a; Baker *et al.*, 2007; Gibson, 2010), but its exact placement differs among studies.

**Etymology:** The name refers to the dissimilarities between this species of *Lunaceps* and other *Lunaceps* species on *Calidris sensu lato*.



**FIGURE 9.** *Lunaceps enigmaticus* sp. nov. A) Male head, dorsal and ventral views. B) Male pterothorax and abdomen, dorsal and ventral views; some pterothoracic setae missing in the specimen. C) Female terminalia, dorsal and ventral views. D) Male genitalia. All available male genitalia are either obscured or distorted. In this illustration, the left side of the genitalia is a mirror image of the right side.

**Material examined:***Ex Micropalama himantopus*

Holotype: ♂1, North and Central America (NHML).

Paratype (on same slide): ♀1, North and Central America (NHML).

Non-type material: ♀5, ♂1, Trinidad and Tobago: Trinidad: Caroni Swamp, 21 October 1959, TRVL 3329 (BM 1974-636) (NHML). ♀1, ♂1, Barbados, L. Harrison (NHML). ♀1, ♂1, [Collection data not given on slide], BM 1970-558 (NHML) (another slide with the same number and coming from the same host species, appears to contain no lice that can definitely be assigned to *L. enigmaticus*). ♂1, Canada: Manitoba: Churchill, June 1936, Meinertzhagen Collection 4794 (NHML). ♀2, ♂2, United States: Florida: Miami, 26 July 1919, K.C. Emerson Collection (OSU).

*Ex Tringa flavipes* (possibly stragglers):

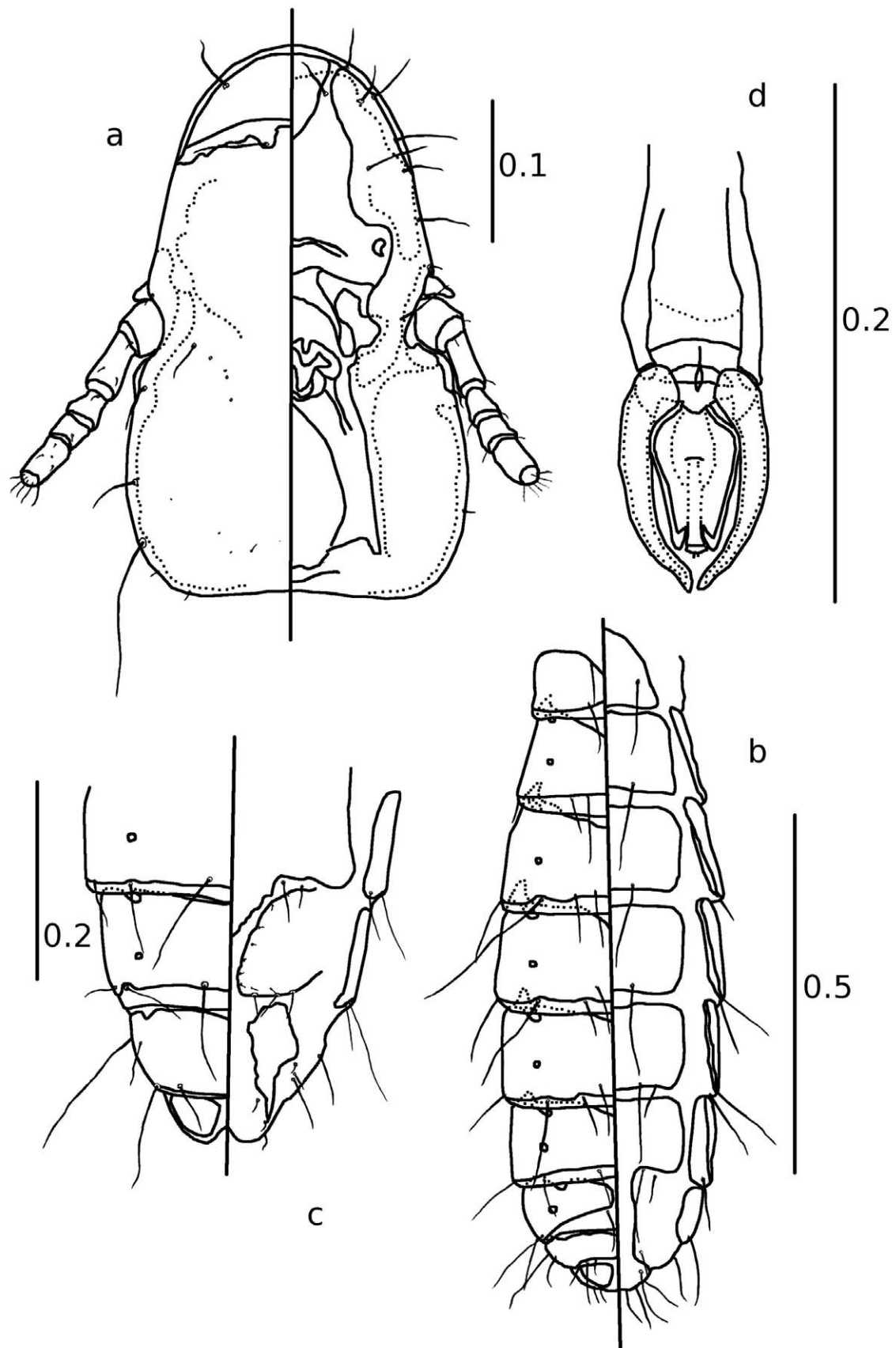
♀1, ♂1, Canada: Manitoba: Whitewater Lake, 27 August 1996, Coll. T.D. Galloway/ D. Wytrykush/L.M. Babey (MONZ).

***Lunaceps falcinellus* Timmermann, 1954**

(Fig 10a–d; Table 1)

*Nirmus actophilus* Kellogg and Chapman; Waterston, 1914: 283 (partim)*Lunaceps falcinellus* Timmermann, 1954a: 627 (partim)*Lunaceps incoenis* (Kellogg and Chapman); Timmermann, 1954a: 623 (partim)*Lunaceps cabanisi* Timmermann, 1954a: 625 (partim)*Lunaceps husainii* Ansari, 1956: 49 **New synonymy***Lunaceps husainii* Ansari, 1958: 98*Lunaceps holophaeus incoenis* (Kellogg and Chapman); Bechet, 1968: 126*Lunaceps holophaeus timmermanni* Bechet, 1968: 126*Lunaceps falcinellus* Timmermann; Fedorenko, 1968: 73*Lunaceps incoenis* (Kellogg and Chapman); Fedorenko, 1968: 73 (partim)*Lunaceps sp. II* Fedorenko, 1968: 73*Lunaceps holophaeus timmermanni* Bechet; Eichler and Hackman, 1973: 92 **New synonymy***Lunaceps sp.* “ab *Limicola f. falcinellus*” Eichler and Hackman, 1973: 92*Lunaceps sp.* Rékási and Kiss, 1977: 105*Lunaceps cabanisi* Timmermann; Ledger, 1980: 169*Lunaceps sp.* Rékási and Kiss, 1980: 76*Lunaceps incoenis* (Kellogg and Chapman) *s. l.*; Pilgrim and Palma, 1982: 21*Lunaceps holophaeus* (Burmeister); Literák, 1983: 743*Lunaceps sp.* [ex *Calidris ruficollis*] Palma, 1999: 380*Lunaceps falcinellus* Timmermann; Price *et al.*, 2003: 196 (partim)*Lunaceps cabanisi* Timmermann; Price *et al.*, 2003: 196 (partim)*Lunaceps incoenis* (Kellogg and Chapman); Price *et al.*, 2003: 196 (partim)*Lunaceps timmermanni* Bechet; Price *et al.*, 2003: 196*Lunaceps incoenis* (Kellogg and Chapman); Rékási, 2006: 183*Lunaceps timmermanni* Bechet; Rékási, 2006: 183*Lunaceps timmermanni* Bechet; Adam, 2007a: 137*Lunaceps drosti* Timmermann; Dik *et al.*, 2010: 869 (identified in images)*Lunaceps drosti* Timmermann; Inci *et al.*, 2010: 215*Lunaceps incoenis* (Kellogg and Chapman); Dik *et al.*, 2010: 869*Lunaceps incoenis* (Kellogg and Chapman); Inci *et al.*, 2010: 215*Lunaceps falcinellus* Timmermann (“Clade 1”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2)*Lunaceps incoenis* (Kellogg and Chapman) (“Clade 1”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2) (in partim)*Lunaceps timmermanni* Bechet (“Clade 1”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2).*Lunaceps sp. ex Calidris ruficollis* (“Clade 1”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2).**Type host:** *Limicola falcinellus falcinellus* (Pontoppidan, 1763)**Other hosts:** *Limicola falcinellus sibirica* Dresser, 1876, *Calidris ferruginea* (Pontoppidan, 1763), *Calidris ruficollis* (Pallas, 1776), *Calidris minuta* (Leisner, 1812).





**FIGURE 10.** *Lunaceps falcinellus*. A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. Individual with extra submedian setae on ventral side of segment VII. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

**Diagnosis:** Head elongated ovoid (Fig. 10a). Posterior margin flat or nearly flat. Marginal carina clearly defined, but not very heavily pigmented, especially anterior to the dorsal preantennal suture. Ventral anterior plate triangular. No lateral nodus, and dark preantennal band very vague. Dorsal preantennal suture broad, enveloping the apertures of the AVS in some individuals, and interrupted medially by a narrow bridge. AVS3 aligned with, or slightly posterior to, AVS2. Very rarely is AVS3 anterior to AVS2. In all cases, both AVS3 and AVS2 are markedly posterior to the ADS.

Paratergal plates narrow, narrowing further posteriorly (Fig. 10b). Tergal heads long, blunt, and re-entrant, with a broad tergal bar. In females, the tergal heads may be very broad, in some individuals they are approximately as broad as long. Paratergal plates and tergal heads less heavily pigmented in segment III than in more posterior segments. Tergal head on segment VII squat but pointed, and is usually transparent in females. Tergite III partially divided medially. Females pale. Many males with an extra submedian seta on ventral side of segment VII.

Female genital lobes oval with 3–5 posterior marginal setae, 3 sub-marginal setae, and 6 median margin setae (Fig. 10c). Mesomere particularly short and stocky (Fig. 10d). Dorsal mesomeral fingers very slender. Lower endomere narrow, with more or less parallel anterior and posterior margins. Apodemal bridge diffuse anteriorly.

**Discussion:** Gustafsson and Olsson (2012) found that *Luniceps* populations from *C. minuta*, *C. ferruginea*, *L. falcinellus*, and *C. ruficollis* were genetically identical. The oldest available name for this clade is *L. falcinellus*. For a discussion on *L. incoenis*, the identity of its type specimen, and the assignment of host associations, see the entry for *L. incoenis* below.

*Luniceps falcinellus* is almost indistinguishable from *L. incoenis*, but the tergal heads of abdominal segment VII are broader and blunter in *L. falcinellus* than in *L. incoenis*. In *L. falcinellus*, many males have two ventral setae on abdominal segment VII but, because they are sometimes missing, it is not a reliable character. Apart from *L. incoenis*, the most similar species to *L. falcinellus* is *L. superciliosus* sp. nov. Females of *L. falcinellus* and *L. superciliosus* sp. nov. differ in the number of genital setae, but this character is somewhat unreliable, and should not be used exclusively because the posterior marginal setae in particular have a tendency to fall off or perhaps never develop fully. Most males of *L. superciliosus* sp. nov. have a small suture medio-posterior to the antennae which readily separates it from *L. falcinellus*. However, this character can be hard to see in some individuals, and is missing entirely in female *L. superciliosus*.

It should be noted that Timmermann (1954a) included several individuals of an unidentified *Quadriceps* species among his paratypes for *L. falcinellus*, but both the type and the allotype are *Luniceps*.

Ansari's (1956) description of *L. husainii* mentions that this species could be separated from all other species of the genus by the shape of the head and body, and by the male genitalia. This is reiterated in his second description of the species (Ansari, 1958); however this is accompanied by illustrations matching *L. falcinellus* as defined here. Price *et al.* (2003) listed *L. husainii* as a junior synonym of *L. incoenis*, following Ledger (1980: 168). Therefore, ours is a new synonymy for *L. husainii* under *L. falcinellus*.

Bechet (1968) mentioned “cut-off” paramere extremities in his description of *L. timmermanni*, but nothing resembling this has been found in any specimen from *C. ferruginea* studied by us. In the photo included with the original description it is not clear what that feature would look like, and the possibility that this is due to Bechet's material being damaged cannot be excluded. The material studied by us cannot be morphologically separated from those collected from other hosts of *L. falcinellus*, and therefore we regard *L. holophaeus timmermanni* as a junior synonym of *L. falcinellus*.

**Etymology:** After the species name of the type host, *Limicola falcinellus*. The name means “little sickle”, and likely refers to the shape of the bill.

#### **Material examined:**

*Ex Limicola falcinellus falcinellus*

**Holotype:** ♂1, Pakistan?: Mekran Coast: Aisnee, 16 February 1872, J. Waterston Collection 1930-232 (NHML). [Note: The Mekran Coast lies in Iran and Pakistan, but the locality is given as “India” on slide. We have been unable to locate “Aisnee”.]

**Allotype:** ♀1, Pakistan: Karachi [slide has the locality as “India”], 8 February, 1872, J. Waterston Collection 1930-232 (NHML).

**Paratypes:** ♂1, Pakistan?: Mekran Coast: Aisnee, 16 February 1872, J. Waterston Collection 1930-232 (NHML). ♀1, ♂2, Pakistan: Karachi [slide has the locality as “India”], 8 February, 1872, J. Waterston Collection

1930-232 (NHML). ♀1, India: Calcutta, 28 December 1872, J. Waterston Collection 1930-232 (NHML). ♀1, Pakistan?: Mekran Coast: Aisnee, 16 February 1872, J. Waterston Collection 1930-232 (NHML). ♀2, Karrachee [= Pakistan: Karachi?], 1 February 1872. J. Waterston Collection 1930-232 (NHML). ♂3, Norway: Finnmark, 22 November 1883, J. Waterston Collection 1930-232 (NHML). ♀1, Karalla Klang [= Malaysia: Selangor: Karala: Klang?], 15 January, 1880, J. Waterston Collection, 1930-232 (NHML).

Non-types: ♂1, Namibia [Slide has the locality as “South West Africa”]: Sandwich Harbour, 26 January, 1973, BM 1974-33 (NHML). ♂2, India (NHML). ♂1, Poland: Piaseczno: [Konstancin-]Jeziorna, 27 August 1954, Yurezyk, 42/ac/1-1 (MFN). ♀3, ♂2, [Collection data not given on slide], 20070g, m, o, p, r (MFN). ♂1, Sweden: Öland, Ottenby Bird Observatory, 25 May 2007, ID: 103, Band number: 3531454, D. Gustafsson (SMNH). ♀1, Sweden: Öland: Ottenby Bird Observatory, 25 May 2007, ID:106, Band number: 3531453, D. Gustafsson (SMNH). ♀1, Sweden: Öland: Ottenby Bird Observatory, 29 May 2007, ID: 134, Band number: ob29312, D. Gustafsson (SMNH). ♂1, Sweden: Öland, Ottenby Bird Observatory, 25 May 2007, ID: 103, Band number: 3531454, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 25 May 2007, ID:106, Band number: 3531453, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 29 May 2007, ID: 134, Band number: OB29312, D. Gustafsson (GNM).

#### *Ex Limicola falcinellus sibirica*

♂1, Australia: Western Australia: Broome Area: Richard’s Point, 11 November 2008, ID: 830, Band Number: 042-43332, D. Gustafsson (GNM). ♀1, Australia: Western Australia: Broome Area: Richard’s Point, 11 November 2008, ID: 829, Band Number: 042-43330, D. Gustafsson (SMNH). ♀1, Australia: Western Australia: 80 Mile Beach, Near Anna Plain Cattle Station, 17 November 2008, ID: 892, Band Number: 042-43482, YIO-P-01156, D. Gustafsson (YIO).

#### *Ex Calidris ferruginea* (synonyms: *Erolia ferruginea* or *Erolia testacea*)

♀10, ♂5, Morocco, October 1939, 11953 (NHML). ♀1, New Zealand: Lake Ellesmere, January 1928, E.F. Stead, R.C.L. Pilgrim Collection (Cmu Av L588) (MONZ). ♂1, Australia: Victoria: Western Port Bay: Stockyard Point, 13 January 1996, W. Steele (MONZ). ♀3, ♂10, Estonia, August 1934, Meinertzhagen Collection, 1444 (NHML). ♀1, ♂1, Sudan, May 1936, Meinertzhagen Collection 7946 (NHML). ♀6, ♂5, Papua New Guinea: Western District: near Wando, 14 October 1969, I.L., Owen, 691014/11b, BM 1970-381 (NHML). ♀1, ♂1, Angola: Port Alexander, 20 September 1912, 964, BM 1954-318 (NHML). ♀1, ♂4, Kenya, April 1916, Meinertzhagen Collection 3880 (NHML). ♀2, ♂6, Seychelles: Aldabra: South Island: Cing Cases, January 1968, B. Cogan and A. Hutson, Roy. Soc. Exp., BM 1968-333 (NHML). ♀1, United Kingdom: England: Weymouth, 8 October 1910, J. Waterston Collection BM 1930-232 (NHML). ♀1, Malawi: Lake Chilwa [slide has this as “Nyasaland”], 21 November, 1960 (NHML). ♀1, ♂1, Mauritius, 30 November 1973, BM 1974-4 (NHML). ♀1, ♂1, Kenya: Nakuru, January 1956, Meinertzhagen Collection 20420 (NHML). ♀1, ♂1, Sri Lanka [as “Ceylon”]: Northern Province: Mullaitivu, 25 March 1955, BM 1955-299 (NHML). ♀1, Cyprus: Akrotiri, 21 September 1967, K.C. Emerson Collection (OSU). ♀4, ♂5, India: Tamil Nadu: Point Calimere, June–September, 1969, K.C. Emerson Collection (OSU). ♀2, ♂2, Thailand: Samutprakan: Bang Pu, 29 September 1965, K.C. Emerson Collection (OSU). ♂1, Australia: Western Australia: Broome Area: Richard’s Point, 11 November 2008, ID: 842, Band Number: 042-43406, D. Gustafsson (GNM). ♂1, Australia, Western Australia, Broome Area: Richard’s Point, 11 November 2008, ID: 840, Band Number: 042-43364, D. Gustafsson (SMNH). ♂1, Australia, Western Australia, Broome Area: Richard’s Point, 11 November 2008, ID: 838, Band Number: 042-43353, YIO-P-01157, D. Gustafsson (YIO). ♀1, Sweden: Öland: Ottenby Bird Observatory, 30 July 2007, ID: 253a-1, Band number: 3533877, D. Gustafsson (YIO). ♀1, Sweden: Öland: Ottenby Bird Observatory, 23 July 2007, ID: 168a-1, Band number: 3532199, YIO-P-01158, D. Gustafsson (YIO). ♀1, Sweden: Öland: Ottenby Bird Observatory, 30 July 2007, ID: 253a-2, Band number: 3533877, YIO-P-01159, D. Gustafsson (YIO). ♀1, Sweden: Öland: Ottenby Bird Observatory, 23 July 2007, ID: 168a-2, Band number: 3532199, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 23 July 2007, ID: 167, Band number: 3532168, D. Gustafsson (SMNH). ♀1, Sweden, Öland: Ottenby Bird Observatory, 25 July 2007, ID: 196, Band number: 3532705, D. Gustafsson (SMNH). ♂1, Sweden: Öland: Ottenby Bird Observatory, 30 July 2007, ID: 253a-1, Band number: 3533877, D. Gustafsson (SMNH). n#1, Sweden: Öland: Ottenby Bird Observatory, 26 July 2007, ID: 208, Band number: 3533046, D. Gustafsson (SMNH). ♀1, Sweden: Öland: Ottenby Bird Observatory, 21 May 2007, ID:72, Band number:

3531328, D. Gustafsson (GNM). ♀1, ♂1, Sweden: Öland: Ottenby Bird Observatory, 24 July 2007, ID: 178-1, 178-2, Band number: 3532387, D. Gustafsson (GNM). ♂1, Sweden: Öland: Ottenby Bird Observatory, 25 July 2007, ID: 196-s, Band number: 3532705, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 25 July 2007, ID: 199, Band number: 3532812, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 30 July 2007, ID: 250, Band number: 3533595, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 2 August 2007, ID: 279, Band number: 3534673, D. Gustafsson (GNM).

*Ex Calidris minuta* (synonym: *Erolia minuta*)

♀1, ♂1, Israel: Kfar Masaryk, 26 August 1958, BM 1959-56 (NHML). ♀2, ♂1, Kenya, March 1936, Meinertzhagen Collection (7264, 7268) (NHML). ♀4, ♂1, Uganda, April 1936, Meinertzhagen Collection (7712) (NHML). ♀1, ♂1, Yemen: Aden, December 1948, Meinertzhagen Collection (17948) (NHML). ♀1, Arabia, January, 1948, Meinertzhagen Collection (17123) (NHML). ♀1, Angola: Port Alexander, 23 October 1912, 1092, BM1954-318 (NHML). ♀2, ♂1, Uganda: Kanyanja?: Tolo?, 28 April 1944, Hopkins Collection (NHML). ♀1, ♂1, V. Dvár?, 9 September 1950, Coll. Dr. F. Balát (NHML). ♀1, Iraq: Baghdad, L. Harrison (NHML). ♂1, Sri Lanka [as “Ceylon”]: Southern Province: Bundala, 24 September 1954, BM 1954-699 (NHML). ♂1, Sri Lanka [as “Ceylon”]: Hambantona District: Bundala lagoon, 6 March 1955, BM 1955-332 (NHML). ♀3, India: Tamil Nadu: Thanjavur: Point Calimere, 26 September 1969, K.C. Emerson Collection (OSU). ♂2, India: Rajasthan: Bharatpur, 15 February 1971, K.C. Emerson Collection (OSU). ♂1, Sweden: Öland: Ottenby Bird Observatory, 21 May 2007, ID 71-1, Band number: 2kn50208, D. Gustafsson (SMNH). ♂1, Sweden: Öland: Ottenby Bird Observatory, 21 May 2007, ID 71-2, Band number: 2kn50208, D. Gustafsson (GNM). ♂1, Sweden: Öland: Ottenby Bird Observatory, 21 May 2007, ID 77-1, Band number: 2kn50207, D. Gustafsson (SMNH). ♂1, Sweden: Öland: Ottenby Bird Observatory, 21 May 2007, ID 77-2, Band number: 2kn50207, D. Gustafsson (GNM).

*Ex Calidris ruficollis* (synonyms: *Erolia ruficollis*, *Ereunetes ruficollis*, *Ereunetes minuta ruficollis* or *Pisobia minuta ruficollis*)

♀2, ♂2, Australia: Western Australia: Perth, August 1967, R. H. Stranger, BM 1969-48 (NHML). ♀3, ♂3, Australia: Tasmania: Ralphs Bay, 20 November 1981, K. Heiden (MONZ). ♂1, New Zealand: Rangitikei River Mouth, 28 February 1983, F. Sibley, NM 22743 (MONZ). ♀1, Japan: Tyototen?, 31 August 1957, BM 1958-245 (NHML). ♀1, Papua New Guinea: Western District: Wando, 14 October 1969, I. L. Owen, 691014/3c, BM 1970-381 (NHML). ♀1, Myanmar: Rangoon, April 1900, Meinertzhagen Collection 4297 (NHML). ♀3, ♂6, Philippines: Luzon: Batangas: Calatagan, September–December 1964, K.C. Emerson Collection (OSU). ♀1, ♂1, Thailand: Samutprakan: Chao Praya River, 23 September 1965, K.C. Emerson Collection (OSU). ♀1, Australia: Western Australia: Broome Area: Two Dog Hermit, 12 November 2008, ID: 844, Band number: 036-13725, D. Gustafsson (SMNH). ♂1, Australia: Western Australia: Broome Area: Coconut Wells, 9 November 2008, ID: 817, Band number: 036-13701, D. Gustafsson (GNM).

*Ex Xenus cinereus* (synonym: *Tringa terek*) (possibly stragglers):

♂1, Sri Lanka [as “Ceylon”]: Hambantota: Bundala, 23 October 1955, W. W. A. Phillips, 1956-133 (NHML). ♂1, India: Tamil Nadu: Point Calimere, 7 July 1969, K.C. Emerson Collection (OSU).

***Lunaceps holophaeus* (Burmeister, 1838)**

(Fig. 11a–d; Table 1)

*Nirmus holophaeus* Burmeister, 1838: 427

*Nirmus bicolor* Piaget, 1880: 175

*Nirmus phaeopi* Denny; Waterston, 1915: 33 (partim)

*Degeeriella holophaea* (Burmeister); Harrison, 1916: 115

*Degeeriella bicolor* (Piaget); Harrison, 1916: 109

*Degeeriella bicolor* (Piaget); Séguy, 1944: 279

*Degeeriella holophaea* (Nitzsch); Séguy, 1944: 285

*Quadriceps holophaea* (Nitzsch); Ansari, 1947: 279

*Degeeriella holophaea* (Burmeister); Blagoveshtchensky, 1948: 280

*Lunaceps holophaeus* (Burmeister); Hopkins and Clay, 1952: 201

*Lunaceps bicolor* (Piaget); Hopkins and Clay, 1952: 201  
*Lunaceps holophaeus* (Burmeister); Timmermann, 1954a: 625  
*Lunaceps holophaeus* (Burmeister); Ansari, 1956: 49  
*Lunaceps holophaeus* (Burmeister); Ansari, 1958: 98  
*Lunaceps holophaeus* (Burmeister); Malcomson, 1960: 190  
*Lunaceps holophaeus* (Burmeister); Malcomson, 1960: 191  
*Lunaceps bicolor* (Piaget); Touleshkov, 1964: 132  
*Lunaceps holophaeus* (Burmeister); Touleshkov, 1964: 132  
*Lunaceps holophaeus* (Burmeister); Keirans, 1967: 113  
*Lunaceps holophaeus holophaeus* (Burmeister); Bechet, 1968: 125  
*Lunaceps holophaeus holophaeus* (Burmeister); Emerson, 1972: 93  
*Lunaceps holophaeus holophaeus* (Burmeister); Eichler and Hackman, 1973: 92  
*Lunaceps holophaeus* (Burmeister); Rékási and Kiss, 1977: 105  
*Lunaceps holophaeus* (Burmeister); Ledger, 1980: 169  
*Lunaceps holophaeus* (Burmeister); Rékási and Kiss, 1980: 76  
*Lunaceps bicolor* (Piaget); Rékási and Kiss, 1980b: 104  
*Lunaceps holophaeus* (Burmeister); Literák, 1983: 741  
*Lunaceps holophaeus* (Burmeister); Price *et al.*, 2003: 196  
*Lunaceps holophaeus* (Burmeister); Martín Mateo, 2006: 26  
*Lunaceps holophaeus* (Burmeister); Dik *et al.*, 2010: 869  
*Lunaceps holophaeus* (Burmeister); Inci *et al.*, 2010: 215  
*Lunaceps holophaeus* (Burmeister) (“Clade 2”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2)

**Type host:** *Philomachus pugnax* (Linnaeus, 1758)

**Other host:** *Vanellus vanellus* (Linnaeus, 1758) (possibly straggler)

**Diagnosis:** Head elongated ovoid (Fig. 11a). Marginal carina thick and continuous around the anterior margin of the head. Dorsal preantennal suture does not reach the lateral margins of the head. In some individuals, the dorsal preantennal suture is further subdivided into a median section, and two small kidney-shaped sections anterior-lateral to the ADS. In many, but not all, individuals the dorsal preantennal suture bulges posteriorly to envelope the apertures of the ADS. Ventral anterior plate triangular. Ventral carina, ventral lateral plates and ventral anterior plate ill defined. AVS3 and AVS2 more or less aligned. PCS very small, and cannot be seen in all individuals. Coni very broad and rounded. Postantennal area square-shaped, but posterior margin of head slightly concave. MTS4-5 thorn-like.

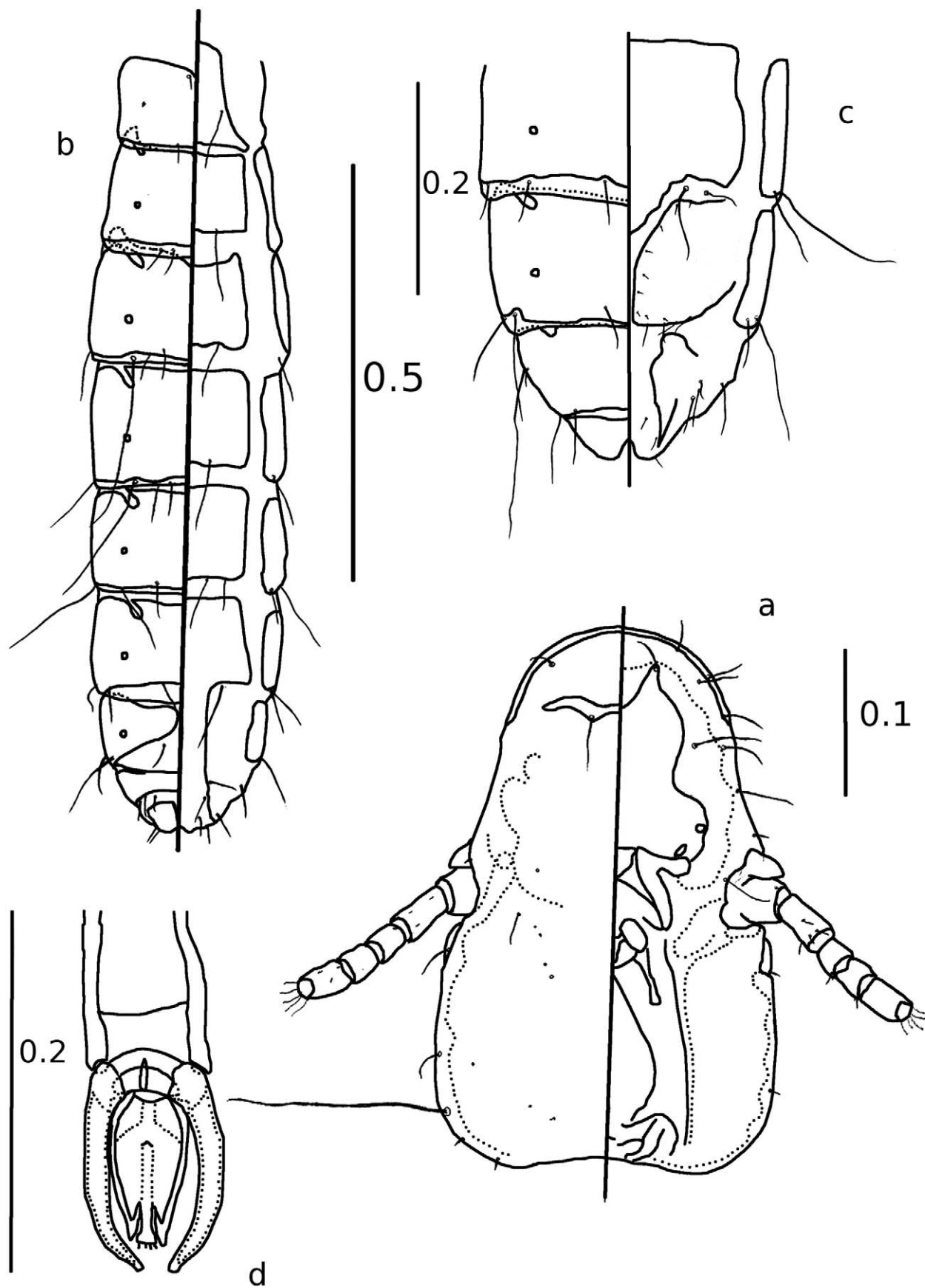
Paratergal plates narrow and dark. Re-entrant tergal heads present in segments III–IV (Fig. 11b), but small and transparent, and hard to see in some individuals. On more posterior segments, tergal heads are still transparent, but blunt and not re-entrant. Many females are missing the re-entrant tergal heads entirely.

Female genital lobes with 4 posterior marginal setae, 3 sub-marginal setae, and 6 median marginal setae (Fig. 11c). Notably, the median marginal setae are shorter than the sub-marginal setae. Parameres slender with small heads (Fig. 11d). Mesomere almost triangular with straight lateral sides. Lower endomere crescent-shaped. Apodemal bridge indistinct.

**Discussion:** Overall, *L. holophaeus* is morphologically similar to *L. falcinellus* (which, according to molecular data, it is closely related to; Gustafsson and Olsson, 2012) and *L. incoenis*, particularly in the male genitalia and in preantennal characters, but its paratergal plates and tergal heads are more similar to *L. actophilus*, *L. drosti*, *L. mintoni*, and *L. schismatus*. *Lunaceps holophaeus* is the only *Lunaceps* species for which the dorsal preantennal suture does not reach the lateral edges of the head.

*Lunaceps holophaeus* has been reported from a variety of atypical hosts, including *Limosa limosa* (Blagoveshtchensky, 1948; Golikova, 1959) [Ref: Fedorenko, 1968]), *Numenius arquata* (Blagoveshtchensky, 1948; Rékási, 1993), *Calidris ruficollis* (Belopolskaya, 1959 [Ref: Fedorenko, 1968]), *Xenus cinereus* (Blagoveshtchensky, 1948), *Calidris temminckii* (Blagoveshtchensky, 1948), and *Tringa totanus* (Rékási, 1993), and two non-charadriiform hosts *Asio flammeus* (Blagoveshtchensky, 1948), *Somateria mollissima* (Rékási, 1993). Some of these may be stragglers or misidentifications.

Timmermann (1954a) synonymised *Lunaceps bicolor*, originally described from *Vanellus vanellus*, with *L. holophaeus*, based on size and shape, and under the assumption that it was a straggler on *V. vanellus*. The measurements of the *L. bicolor* and *L. holophaeus* specimens studied by Timmermann (1954a) match each other. However, Timmermann (1954a) does not mention any morphological characters, and thus this synonymisation may



**FIGURE 11.** *Lunaceps holophaeus* A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

be unjustified. Eichler (1959) mentions having in his collection a single individual of *L. bicolor*, which supposedly has male genitalia similar to those of *Abumarkub koenigi* (= *Neophilopterus platyclypeatus*; see Tandan and Hajela, 1962) in their general structure. Eichler's specimen (located at the MFN) has its genitalia covered with a blotch of Canada balsam on the cover slide, but the details that can be seen are typical for a *Lunaceps*, and unlike that of Eichler's (1959) illustration of the male genitalia of *Abumarkub koenigi*. The specimen is a *Lunaceps schismatus* sp. nov. The only other collections of *L. bicolor* are cited by Touleshkov (1964) and Rékási and Kiss (1980b).

Timmermann (1971) suggested that the lice parasitic on *Vanellus vanellus* are more closely related to the lice parasitic on other boreal shorebirds than to the lice from other *Vanellus* species. *Quadriceps junceus* from *Vanellus vanellus* appear to be more closely related to *Quadriceps charadrii* from *Pluvialis apricaria* and *Quadriceps hospes* from *Pluvialis squatarola* than to *Quadriceps renschi* from the Australian *Vanellus miles* (Gustafsson and Olsson, *in prep.*). No *Lunaceps* have been found on *Vanellus vanellus* examined in Sweden (n = 2)

**Etymology:** From *holo* = whole, and *phae* = dusky. Probably a reference to the even brown colour that characterises most members of the genus.

### Material examined:

*Ex Philomachus pugnax* (synonym: *Machetes pugnax*)

Neotype: ♂1, United Kingdom: England: Suffolk, August 1926, Meinertzhagen Collection 4921 (NHML).

Neallotype: ♀1, United Kingdom: England: Suffolk, August 1926, Meinertzhagen Collection 4921 (NHML).

Neoparatypes: ♀11, ♂9, United Kingdom: England: Suffolk, August, 1926, Meinertzhagen Collection 4921 (NHML) (one of these slides contains several divided individuals, all mixed together). ♀7, ♂3, United Kingdom: Scotland: Hebrides: N. Uist, August 1941, Meinertzhagen Collection 14531 (NHML). ♀4, ♂1, Palestine, April 1953, Meinertzhagen Collection BM 1953-225 (NHML). ♀28, ♂25, Estonia, August 1934, Meinertzhagen Collection 1540 (NHML) (one of these slides also contain an unidentified *Quadriceps*, a female *L. schismatus* and what may be a male *L. limosella*, but the individual is pale and some characters are difficult to see).

Non-types: ♀20, ♂18, Uganda: Bunyoro: Butiaba, 10 May 1935, Hopkins Collection (NHML). ♂2, United Kingdom: England: Kent: Stoke Lagoon, 22 August 1964, BM 1966-165 (NHML). ♂1, Wells, 26 August, 1892, J. Waterston Collection BM 1930-232 (NHML). ♀1, ♂2, n#1, India: Uttar Pradesh: Etawah, 19 September 1865 (NHML). ♀1, ♂1, Israel: Kfar Masaryk, 27 August 1958, 488, BM1959-56 (NHML). ♀1, ♂1, Israel: Kfar-Rupin, 29 March 1960, 1046/7 (NHML). ♂1, Sri Lanka [as "Ceylon"]: Leaway: Palatopana, 27 November 1955, BM1956-133 (NHML). ♀1, ♂1, United Kingdom: Shetlands: Lerwick, 7 September 1957, BM 1956-724 (NHML). ♀3, ♂2, South Africa: Guderstepoort, 18 September 1930, G.B. Thompson Collection, BM1980-40 (NHML). ♀1, ♂2, Canada: Saskatchewan: Regina, 8 May 1965 (PIPeR). ♀1, ♂1, Poland: Near Gdansk: Mikoszewo, 31 July 1963, Zuige, 42/y/18 and 42/y/12 (MFN). ♂1, [Collection data not given on slide], 20064a (MFN). ♀1, Sweden: Öland: Ottenby Bird Observatory, 7 August 2007, ID: 321, Band number: 6130114, D. Gustafsson (SMNH).

### *Lunaceps hopkinsi* Timmermann, 1954

(Fig. 12a–d; Table 1)

*Lunaceps* sp. Thompson, 1948: 200

*Lunaceps hopkinsi* Timmermann, 1954a: 634

*Lunaceps hopkinsi* Timmermann; Malcomson, 1960: 190

*Lunaceps* sp. Butler, 1961: 382 (uncertain)

*Lunaceps* sp. Butler and Usinger, 1963: 8

*Lunaceps numenii hopkinsi* Timmermann; Emerson, 1972: 94

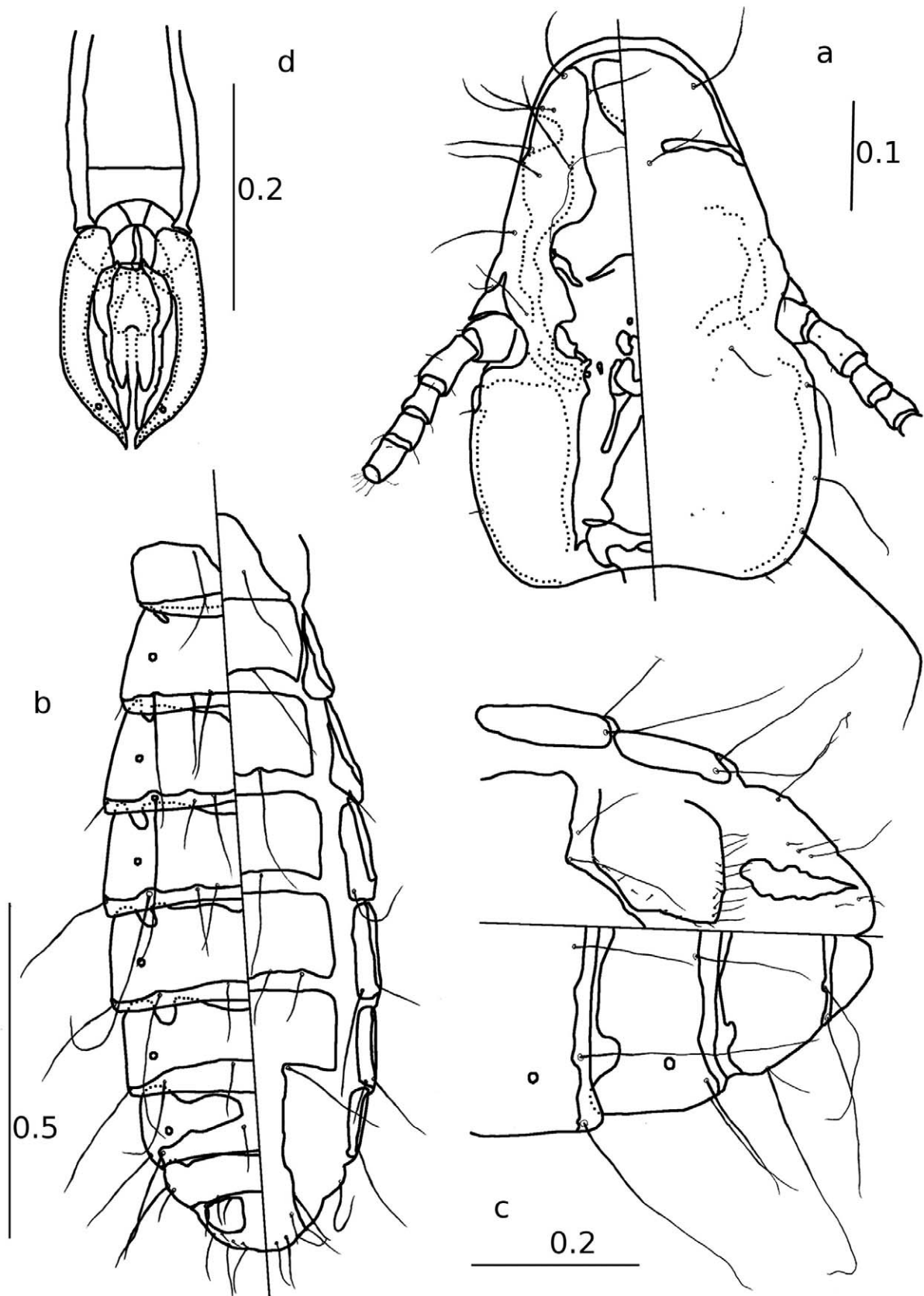
*Lunaceps hopkinsi* Timmermann; Ward and Downey, 1973: 394

*Lunaceps numenii hopkinsi* Timmermann; Price *et al.*, 2003: 196

**Type host:** *Numenius tahitiensis* (J.F. Gmelin, 1789)

**Diagnosis:** Hyaline margin comparatively broad, even on lateral sides (Fig. 12a). Marginal carina broad and well demarcated, with pronounced lateral nodi. Anterior to dorsal preantennal suture, the marginal carina is visible only in two prominent dark lateral patches between AS1 and AS2. DSMS very long. Ventral anterior plate broad and tapering to a point, and augmented by a pronounced U-shaped thickening, clearly defined on both sides.

Preantennal nodi very dark. Dorsal preantennal suture interrupted medially, and bulges posteriorly to envelop the apertures of the ADS. Preantennal setae long and slender. AVS2 and AVS3 aligned (or with AVS3 slightly anterior to AVS2), in males also aligned with ADS, but markedly posterior to this in females.



**FIGURE 12.** *Lunaceps hopkinsi* A) Male head, dorsal and ventral views. Mandible missing in the specimen. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.



Pterothorax with rounded posterior margin.

Abdomen slender (Fig 12b). Anterior margin of segments II–III in males and II–IV in females with narrow wedge-shaped median indentation. Paratergal plated narrow, with a thin dark border marking. Tergal heads missing entirely. Ventral sublateral setae of segments IV–VIII very long, trichoid in both sexes. Both sexes with intermediate macrosetae on segment III and with ventral setae on segment VI trichoid and of roughly equal length. Other abdominal setae also long, and usually very slender. Female abdominal setae long, but not as slender as in the males.

Female genital lobes with 8–10 posterior marginal setae, 6–8 sub-marginal setae, and 7–8 median marginal setae (Fig 12c). Parameres slender, and gently curved, with an inconspicuous ventral aperture in distal fourth. Mesomere with lateral bulge in distal half, with two small lateral apertures (Fig. 12d). Dorsal fingers convergent, extending anteriorly to the ventral blades. Distal end of mesomere elongated and narrow. Lower endomere broad and wide, approaching a triangle in shape, but with convex lateral sides, and connected to the apodemal bridge by a narrow triangle.

**Nymphs:** One nymph examined, which also seems to have the intermediate macrosetae on abdominal segment III, but the abdomen of the specimen is distorted. Dorsal anterior suture thin, and ends abruptly well anterior of antennal base.

**Discussion:** The hook-shaped endomeral apices mentioned by Timmermann (1954a) are artefacts of mounting, and can be seen in many species, and cannot be used as a differentiating character.

The male genitalia of *L. hopkinsi* have characters that are an amalgamation of genitalic characters of, *L. rileyi*, *L. kukri* sp. nov. and *L. proximus*, and those of *L. numenii phaeopi*. The shape of the mesomere is similar to *L. rileyi*, *L. kukri* sp. nov. and *L. proximus*, whereas the parameres are more similar to those of *L. numenii phaeopi*. The female is almost identical to *L. kukri* sp. nov., but differs in the genital setae and the lateral setae of abdominal segment III, both of which are longer in *L. kukri* sp. nov. than in *L. hopkinsi*. The narrow median indentations of the anterior abdominal segments are almost identical in extent to those of *L. lissmanni* and *L. rileyi*. In both sexes, the abdominal setae are quite long and slender, with many lateral or sublateral setae are almost trichoid; this feature is similar to that in *L. proximus*, but the abdomen of *L. proximus* is broader. Both sexes of *L. hopkinsi* can be separated from all other species by the presence of dorsal intermediate macrosetae on abdominal segment III.

**Etymology:** Named in honour of George Henry Evans Hopkins (1898–1973), a well-known phthirapterist, who worked at the Zoological Museum, Tring.

#### Material examined:

##### *Ex Numenius tahitiensis*

Holotype: ♂1, Palau: Malakai, 25 July 1920 (NHML) (genitalia on separate slide).

Allotype: ♀1, Kiribati: Phoenix Group: Canton Island, 3 July 1889 (NHML).

Paratypes: ♂3, Palau: Malakai, 25 July 1920 (NHML). ♂3, Kiribati: Phoenix Group: Canton Island, 3 July 1889 (NHML) (also one slide containing only male genitalia, although no matching body has been found).

Non-types: n#1, Kiribati: Phoenix Group: Canton Island, 3 July 1889 (NHML). ♀1, ♂3, Pacific Ocean: Niue Island, 8 November 1972, DM 17759 (MONZ). ♀11, ♂13, Pacific Ocean: Cook Islands: Palmerston Atoll, 1 July 1960, NM 15355 (MONZ).

#### *Lunaceps incoenis* (Kellogg and Chapman, 1899)

(Figs. 13a–d for specimens from *Calidris mauri* and *Calidris pusilla*; Figs. 14a–d for specimens from *Calidris minutilla*; Table 1)

*Nirmus incoenis* Kellogg and Chapman, 1899: 81

*Degeeriella incoenis* (Kellogg and Chapman); Harrison, 1916: 115

*Degeeriella actophila* (Kellogg and Chapman); Peters, 1934: 36 (partim)

*Degeeriella actophila* (Kellogg and Chapman); Peters, 1936: 16 (partim)

*Lunaceps incoenis* (Kellogg and Chapman); Hopkins and Clay, 1952: 201

*Lunaceps incoenis* (Kellogg and Chapman) (partim); Timmermann, 1954a: 623

*Lunaceps cabanisi* Timmermann, 1954a: 625. **New synonymy**

*Lunaceps pusillus* Carriker, 1956: 74. **New synonymy**

*Lunaceps incoenis* (Kellogg and Chapman); Malcomson, 1960: 190

*Lunaceps cabanisi* Timmermann; Malcomson, 1960: 190  
*Lunaceps holophaeus* (Burmeister); Keirans, 1967: 113 (by implication)  
*Lunaceps* sp. Keirans, 1967: 116  
*Lunaceps holophaeus incoensis* (Kellogg and Chapman); Emerson, 1972: 93  
*Lunaceps holophaeus cabanisi* Timmermann; Emerson, 1972: 93  
*Lunaceps holophaeus pusillus* Carriker; Emerson, 1972: 94  
*Lunaceps holophaeus pusillus* Carriker; Taft and Schaper, 1979: 698  
*Lunaceps holophaeus* (Burmeister); Taft and Schaper, 1979: 698 (partim)  
*Lunaceps incoensis* [sic!] (Kellogg and Chapman); Ledger, 1980: 168  
*Lunaceps cabanisi* Timmermann; Ledger, 1980: 169  
*Lunaceps cabanisi* Timmermann; Forrester *et al.*, 1995: 27, 28  
*Lunaceps pusillus* Carriker; Mayberry *et al.*, 2000: 60  
*Lunaceps cabanisi* Timmermann; Price *et al.*, 2003: 196 (partim)  
*Lunaceps incoensis* (Kellogg and Chapman); Price *et al.*, 2003: 196 (partim)  
*Lunaceps cabanisi* Timmermann (“Clade 4”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2).  
*Lunaceps pusillus* Carriker (“Clade 4”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2).

**Type host:** *Pluvialis squatarola* (Linnaeus, 1758)

**Other hosts:** *Calidris mauri* (Cabanis, 1857), *Calidris pusilla* (Linnaeus, 1766), *Calidris minutilla* (Vieillot, 1819)

**Diagnosis of material from *C. mauri* and *C. pusilla*:** Head elongated ovoid (Fig. 13a), often with a slight concavity at the posterior margin. Marginal carina unbroken anteriorly. Ventral anterior plate long and tapered, reaching the posterior margin of the dorsal preantennal suture. Ventral preantennal suture does not divide ventral anterior plate from ventral lateral plates entirely. Dorsal preantennal suture broad and interrupted medially. AVS3 sometimes anterior to AVS2, but usually aligned with it.

Paratergal plates very narrow (Fig. 13b), and the tergal re-entrant heads less intensely coloured than the anterior-lateral ends of the tergites. Dark border markings narrow. Tergal head of segment VII usually narrow and pointed.

Female genital lobes with 4–5 posterior marginal setae, 3 sub-marginal setae, and 5–7 median marginal setae (Fig. 13c). Parameres very slender, lower endomere narrow and mesomere slender, almost triangular (Fig. 13d). No apertures visible on distal third of parameres. Posterior margin of apodemal bridge more clearly demarcated than anterior margin.

**Diagnosis of material from *C. minutilla*:** As above, with the following exceptions:

Pterothorax and abdomen generally narrower, and on the whole shorter (Table 1). Posterior margin of head markedly concave (Fig. 14a). Marginal carina very distinct. Hyaline margin visible only in anterior end, and very narrow or missing antero-laterally. Ventral anterior plate almost triangular. AVS3 markedly anterior to AVS2, but both posterior to ADS. PCS very small.

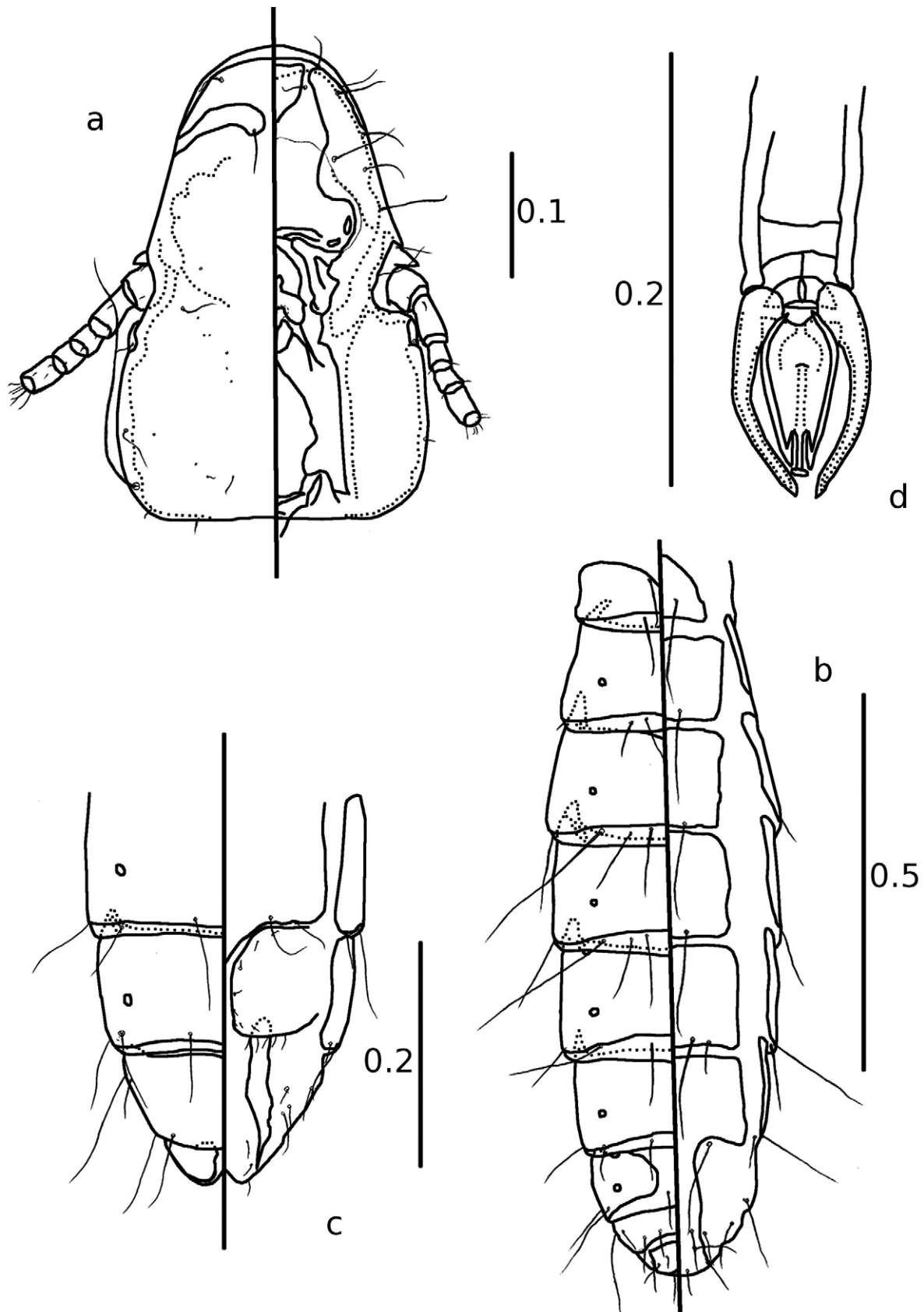
Abdominal sides virtually parallel, and re-entrant heads of tergites more or less completely overlapping with paratergal plate in front (Fig. 14b). Median margins of paratergal plates and dark border marking clearly delimited, and giving the appearance of a pair of dark “railway tracks” running along the abdomen. Re-entrant tergal heads not always as dark as border markings. Anterior sublateral indentation largely overlapping with paratergal plates and may appear to be missing in some segments. Spiracle openings positioned above the paratergal plate.

Female genital lobes narrow and pointed, with 3 posterior marginal setae, 2 sub-marginal setae, and 5 median marginal setae (Fig. 14c). Parameres slender, with somewhat rectangular heads (Fig. 14d). Apodemal bridge vaguely delimited.

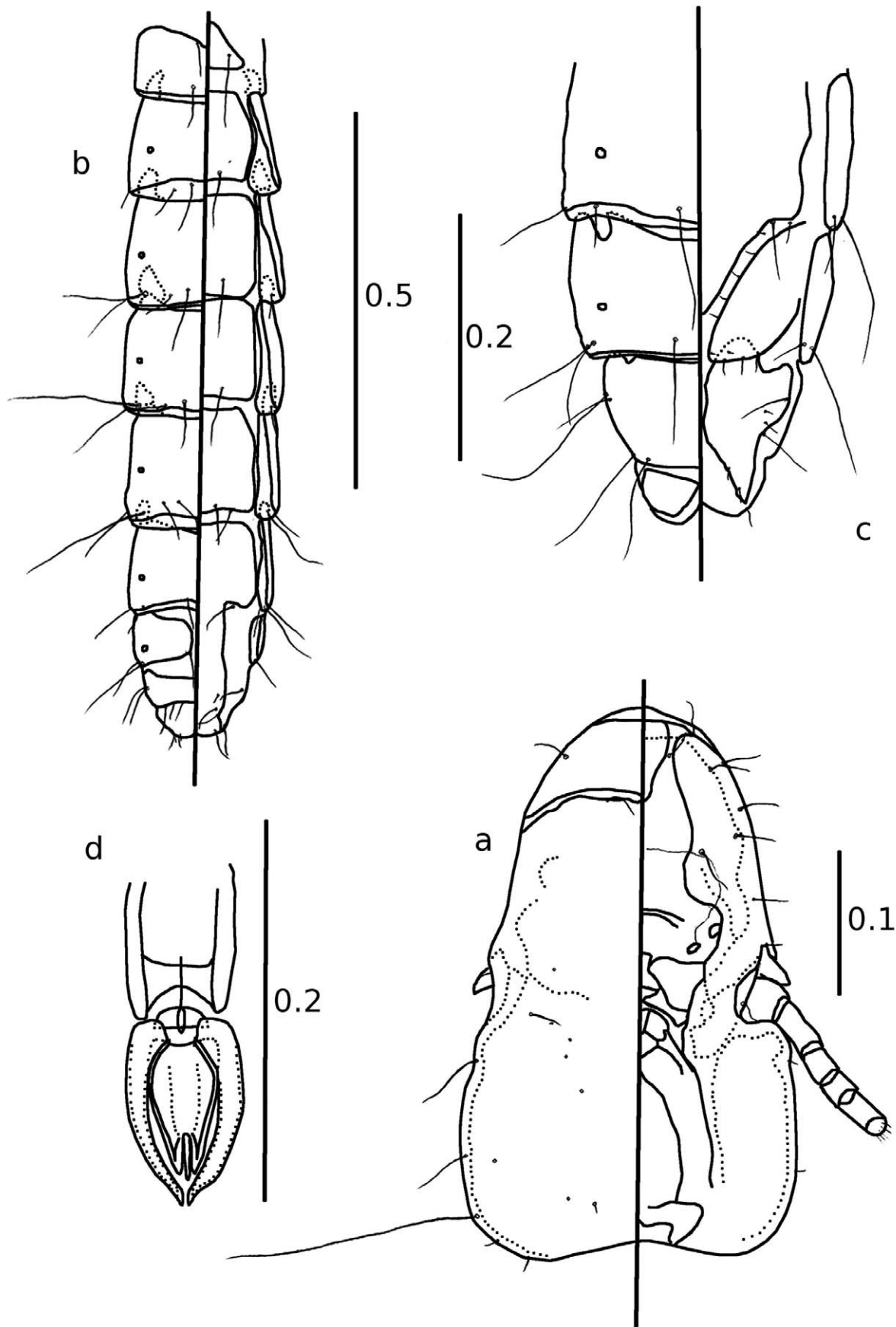
**Discussion:** Using molecular data, Gustafsson and Olsson (2012) showed that the *Lunaceps* on smaller sandpipers and stints form two geographically widely distributed clades, one in the Palaearctic and one in the Nearctic. Material in that study nominally belonging to *L. incoensis* was placed in the Palaearctic clade 1, whereas the Nearctic clade 4 included *L. pusillus* and *L. cabanisi*. However, naming the Palaearctic clade as *L. incoensis* is problematic for reasons outlined below.

*L. incoensis* was described (Kellogg and Chapman, 1899) from *Pluvialis squatarola*. However, the holotype—a single female—is generally considered a straggler from an unidentified species of *Calidris* (Timmermann, 1954a; Emerson, 1972; Ledger, 1980). Timmermann (1954a) proposed *Calidris temminckii* as the most likely original host and *C. minuta* as a secondary host, both based on agreement with measurement between the NHML material from these species and the type of *L. incoensis*. Ledger (1980) recommended that Timmermann’s (1954a) interpretation

should be accepted “for reasons of stability”. However, both of these hosts are Palaearctic, and considered rare accidentals in Alaska with very few records in the Pacific Northwest (Paulson, 1993). This makes them unlikely original hosts for a louse collected in California.



**FIGURE 13.** *Lunaceps incoenis ex Calidris mauri* A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.



**FIGURE 14.** *Lunaceps incoenis ex Calidris minutilla* A) Female head, dorsal and ventral views. Left antenna removed. B) Male abdomen, dorsal and ventral views. Tergal heads included on ventral side to highlight the lateral “rails”. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

The holotype of *L. incoenis* is very old and in poor condition, making many characters of the head difficult to see, thus making certain identification difficult. The AVS3 is anterior to the AVS2, as in much of the material from North American hosts, whereas the tergal heads of abdominal segment VII are intermediate between those of *L. falcinellus* and those of *L. cabanisi*. Paratergal bars are narrow, and the posterior margin of the head is slightly concave, as in other North American material, but unlike that of the Palaearctic hosts.

As no *Lunaceps* have been found on *Pluvialis squatarola* examined in Sweden ( $n = 8$ ), and there has been no further records of *Lunaceps* from this host to our knowledge, we agree with earlier authors (Timmermann, 1954a; Emerson, 1972; Ledger, 1980) that the holotype is most likely a straggler. In the light of the morphological correspondence between the holotype and other North American material, we conclude that *L. cabanisi* and *L. incoenis* represent the same species, and that the former is a junior synonym of the latter.

*L. incoenis* is similar to *L. falcinellus*, but can be separated by the shape of the tergal heads of abdominal segment VII, which are narrow and pointed in *L. incoenis* and broader and blunter in *L. falcinellus*. There are other minor differences, but most of them fall within the variation within each separate species. In many *L. incoenis*, the AVS3 is positioned anterior to the AVS2, which only rarely happens in *L. falcinellus*. The posterior margin of the head is often flatter in *L. falcinellus* than in *L. incoenis*. Further, the paratergal bar is generally broader in *L. falcinellus* than in *L. incoenis*.

Carriker (1956) stated that his *L. pusillus ex Calidris pusilla* might closely resemble *L. cabanisi*, for which he had no material to compare with. Gustafsson and Olsson (2012) found populations of *Lunaceps* on *C. mauri*, *C. minutilla* and *C. pusilla* genetically identical. The holotype of *L. pusillus* is longer than Timmermann's (1954a) measurements for *L. cabanisi*, but other measurements correspond well between the two species, and we have found no consistent morphological differences between them.

Material from *C. minutilla* is enigmatic, as there are several morphological differences between this population and material from other hosts. They can readily be separated in a dissection microscope by the intensity of the dark "railway track"-like paratergal plates along the abdominal sides, the shape of the female genital lobes, and the narrower body. However, the two populations are genetically identical (Gustafsson and Olsson, 2012), and many of the structural differences between them can be ascribed to the narrower abdomen in specimens from *C. minutilla*, which could be the result of living on a smaller host (Message and Taylor, 2005). The space between the feather barbs may be smaller in *C. minutilla* than in other host species, but we have no data on this character. This difference, if present, may explain the morphological differences without corresponding genetic difference. Other explanations may include recent divergence or a history of hybridization. We feel it is prudent for now to keep the two populations within the bounds of one species until more is known about their relationships and the plasticity of body shapes in *Lunaceps*.

**Etymology:** From *in* = not, and *coen* = common. Possibly a reference to the fact that only a single female was found on the host.

#### Material examined:

*Ex Pluvialis squatarola* (in error?)

Holotype: ♀1, United States: California: Pacific Grove (EMEC).

*Ex Calidris mauri* (synonyms: *Ereunetes mauri*, *Calidris pusillus mauri*) Holotype of *L. cabanisi*: ♂1, United States: California, February 1939, Meinertzhagen Collection 12760-61 (NHML).

Allotype of *L. cabanisi*: ♀1, United States: California, February 1939, Meinertzhagen Collection, 12760-61 (NHML).

Paratypes of *L. cabanisi*. ♀8, ♂12, United States: California, February 1939, Meinertzhagen Collection 12760-61, 12840-41, 12948 (NHML). ♀1, ♂1, United States: California, February 1939, K.C. Emerson Collection (OSU).

Non-types: ♀3, United States: California, May 1923, Meinertzhagen Collection 4301 (NHML). ♂1, United States: Utah: Toole County: Dugway Proving Ground: Dog Area, 16 July 1958, K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Alaska: Anchorage, 22 May 1962, K.C. Emerson Collection (OSU). ♀1, United States: Florida: Sanibel, 12 June 1982, K.C. Emerson Collection (OSU). ♀2, ♂2, United States: Utah: Toole County: Skull Valley, 12 August 1954, K. C. Emerson Collection (OSU). ♀3, ♂2, United States: Utah: Toole County: Sewerline, 22 April 1953, K.C. Emerson Collection (OSU). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay,

10 July 2009, ID: 1484, Band number: 1401-64523, D. Gustafsson (SMNH). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 10 July 2009, ID: 1487, Band number: 1401-64530, D. Gustafsson (SMNH). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 30 July 2009, ID: 1586, Band number: 1401-65712, D. Gustafsson (GNM). ♂1, Canada: British Columbia: Vancouver: Simon Fraser University, 29 July 2008, ID: 591, Band number: not recorded, YIO-P-01160, D. Lank (YIO).

*Ex Calidris pusilla* (synonym: *Ereunetes pusillus*)

♀4, ♂6, Suriname: Paramaribo, 6 September, 1971, BM1973-561 (NHML). ♀1, ♂1, Suriname: Paramaribo, 8 January 1971, BM 1973-561 (NHML). ♀3, ♂3, Trinidad and Tobago: Trinidad: Fernandez Factory, 30 October 1959, TRVL3402 etc. BM1961-606 (NHML). ♀2, ♂1, United States: New York: Jamaica, 17 September 1944, K.C. Emerson Collection (OSU). ♀3, ♂3, United States: Indiana: Hamilton County, 1 September 1962, K.C. Emerson Collection (OSU). ♀2, ♂2, United States: Texas: Galveston, K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Alaska: Cape Thompson, 22 July 1960, K.C. Emerson Collection (OSU). ♀3, ♂4, United States: Mississippi: Pascaguola, 27 August 1937, K.C. Emerson Collection (OSU). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 10 July 2009, ID: 1489, Band number: 1401-64531, D. Gustafsson (SMNH). ♀1, Canada: British Columbia: Vancouver Area: Boundary Bay, 29 July 2009, ID: 1545, Band number: 1401-65702, YIO-P-01161, D. Gustafsson (YIO). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 17 July 2009, ID: 1499, Band number: 1401-64565, D. Gustafsson (GNM). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 29 July 2009, ID: 1544, Band number: 1401-65703, D. Gustafsson (GNM).

*Ex Calidris minutilla*

♀2, ♂2, Canada: Saskatchewan: Aberdeen, 17 September, 1957, R. Connell, BM 1959-376 (NHML). ♀1, ♂2, Canada: Labrador: Turnavik, H. Lance (NHML). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 17 July 2009, ID: 1491, Band number: 1401-64552, D. Gustafsson (SMNH). ). ♂1, Canada: British Columbia: Vancouver Area: Boundary Bay, 17 July 2009, ID: 1494, Band number: 1401-64558, D. Gustafsson (SMNH).

*Ex Tringa melanoleuca* (possibly stragglers):

♀2, Canada: Manitoba: Whitewater Lake, 27 August 1996, Coll. T.D. Galloway/ D. Wytrykush/L.M. Babey (MONZ).

*Ex Tringa flavipes* (possibly stragglers):

♀1, Canada: Manitoba: Whitewater Lake, 27 August 1996, Coll. T.D. Galloway/ D. Wytrykush/L.M. Babey (MONZ).

Material of uncertain status due to poor condition:

*Ex Calidris mauri* (synonym: *Ereunetes mauri*)

♀2, ♂1, United States: Alaska: Cape Thompson, 2 August 1960, K.C. Emerson Collection (OSU).

***Lunaceps kukri* sp. nov.**

(Fig. 15a–d; Table 1)

*Nirmus numenii* Denny, 1842: 53 (partim)

*Degeeriella* sp. Peters, 1936: 15 (uncertain)

*Lunaceps numenii* (Denny); Timmermann, 1954a: 631 (partim)

*Lunaceps numenii numenii* (Denny); Emerson, 1972: 94 (partim)

*Lunaceps numenii numenii* (Denny); Butler and Pfaffenberger, 1981: 537 (partim)

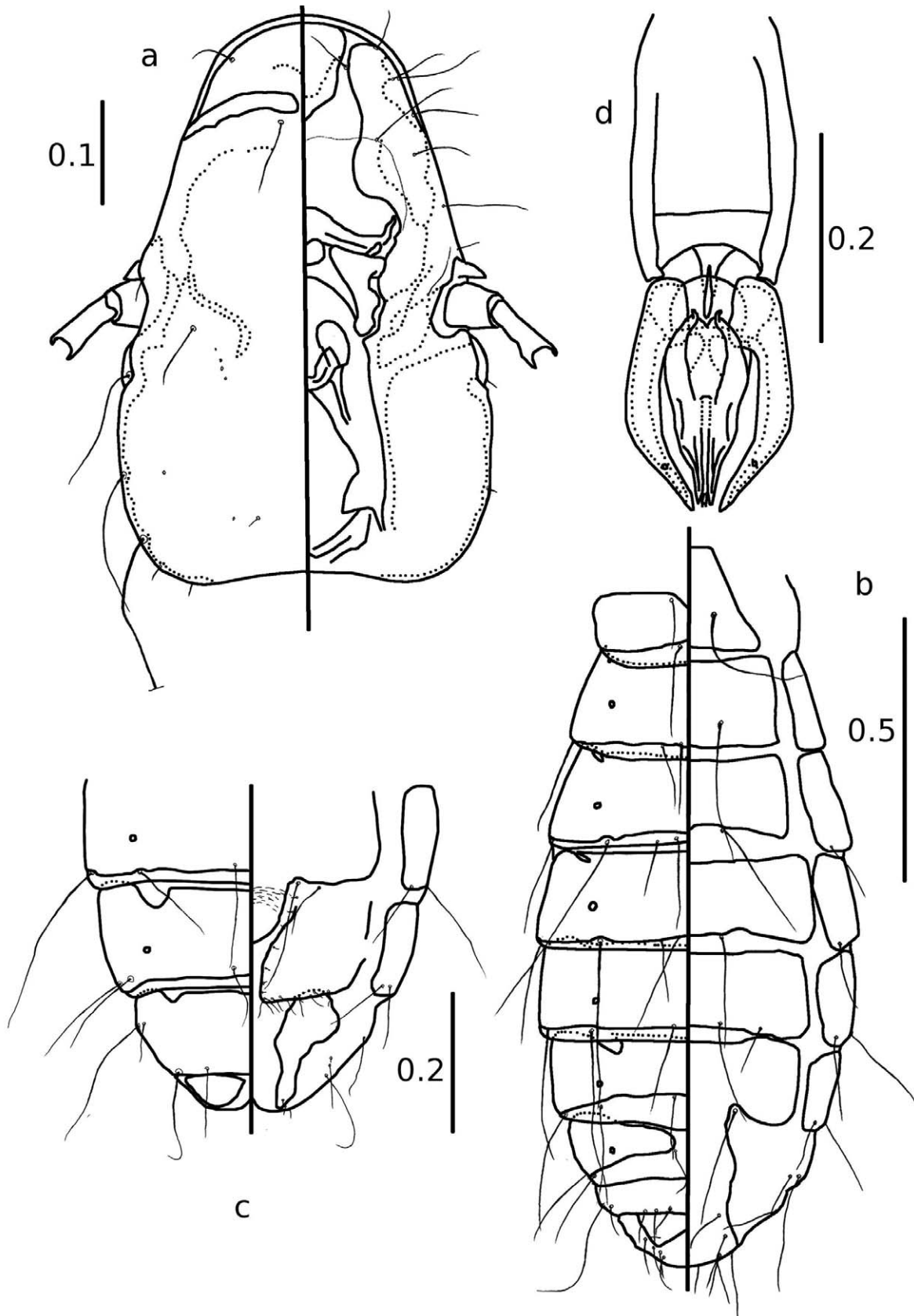
*Lunaceps numenii numenii* (Denny); Price *et al.*, 2003: 196 (partim)

**Type host:** *Numenius americanus americanus* Bechstein, 1812

**Other host:** *Numenius americanus parvus* Bishop, 1910

**Diagnosis:** Head quite elongated, but ovoid (Fig. 15a). Hyaline margin broad. Marginal carina present anterior to the dorsal preantennal suture only as a small hint between the AS1 and AS2. Dorsal preantennal suture interrupted medially. Ventral anterior plate long and broad, with a rounded posterior margin. Central thickening of

this plate (remnant of marginal carina) small and shallowly U-shaped in females, more V-shaped in males. Prominent dark band transversing preantennal area, and interrupted medially. AVS2 and AVS3 aligned, but both posterior to ADS. MTS and MTS3 slender and long.



**FIGURE 15.** *Lunaceps kukri* sp. nov. A) Female head, dorsal and ventral views. Distal parts of antennae removed. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Pterothorax with rounded posterior margin.

Paratergal plates very broad with blunt anterior ends (Fig. 15b), apart from segments III–IV where the anterior-lateral ends are sometimes narrow. In segments III–IV, the sublateral indentation is also very narrow, and can be hard to see in some individuals. Tergites of segments V–VI have blunt anterior-lateral ends, and narrow sublateral indentations. No tergal heads. Long lateral setae of segment III in both sexes.

Female genital lobes with 8–10 posterior marginal setae, 5–7 sub-marginal setae, and 7–8 median marginal setae (Fig. 15c). Median marginal setae quite long. Parameres bulges distally, and become wider before turning inwards (Fig. 15d). Ventral aperture on distal third. Dorsal side of mesomere roughly triangular, and extended distally. Lateral sides with bulge in distal half, and one minute lateral setae at about a third from distal end, visible only in everted genitalia. Dorsal fingers very broad with divergent tips, extending anteriorly to the ventral blades, and median groove deep and pointed. Lower endomere semi-circular, with posterior margin flat dorsally and concave ventrally. Apodemal bridge connected to lower endomere by diffuse triangle.

**Discussion:** Very similar to *L. numenii*, but differs in the male genitalia, which is more similar to that of *L. lissmanni* or *L. rileyi*, with abruptly turning parameres and bulging lateral sides of the mesomere. However, *L. kukri* lacks the second, more distal, parameral bend of *L. lissmanni* and *L. rileyi*, and the existing bend is not as pronounced. Males can be separated from *L. proximus* by the lack of parallel extension of the parameres.

Females identical to *L. numenii*, but on average have more posterior marginal setae, and the paratergal plates are broader in *L. kukri*. The long lateral setae of female abdominal segment III can be found also in *L. proximus* which has more posterior marginal and sub-marginal setae.

Apart from size (Table 1), no differences have been found between material collected between the two host subspecies.

**Etymology:** Refers to the shape of the parameres, which are reminiscent of the traditional Ghurkha knife, the *kukri*.

#### Material studied:

Ex *Numenius americanus americanus*

Holotype: ♂1, United States: Texas, 19 December 1935, DM 16315 (MONZ).

Paratypes: ♀8, ♂4, United States: Texas, 19 December 1935, DM 16315 (MONZ).

Non-types: ♀1, United States: California, 2 February 1860, DM2546 (MONZ). ♀7, ♂6, United States: California, March 1939, Meinertzhagen Collection 13005 (NHML). ♀7, ♂3, United States: California, March 1939, Meinertzhagen Collection 13003 (NHML). ♀3, ♂3, United States: California, March 1941, Meinertzhagen Collection 13006 (NHML). ♂1, Canada: British Columbia: near Armstrong, BM 1956-302 (NHML). ♂2, N. America (NHML). ♀1, ♂5, United States: Texas, October 1912, Meinertzhagen Collection 4421 (NHML).

Ex *Numenius americanus parvus*

♀3, ♂1, Canada: Alberta: Alta: Sullivan Lake, 23 July 1926, DM18553 (MONZ).

#### *Lunaceps limosae* Bechet, 1968

(Fig. 16a–d; Table 1)

*Lunaceps limosella* Timmermann, 1954a: 629 (partim)

*Lunaceps limosella limosae* Bechet, 1968: 127

*Cummingsiella limosae* (Timmermann, 1956 [sic!]), Rékási and Kiss, 1977: 104 (uncertain)

*Lunaceps limosella* Timmermann; Ledger, 1980: 169 (partim)

*Lunaceps limosella* Timmermann; Cabot, 1975: 146

*Lunaceps limosella* Timmermann [ex *Limosa limosa melanuroides*]; Pilgrim and Palma, 1982: 20

*Lunaceps limosella* Timmermann; Price *et al.*, 2003: 196 (partim)

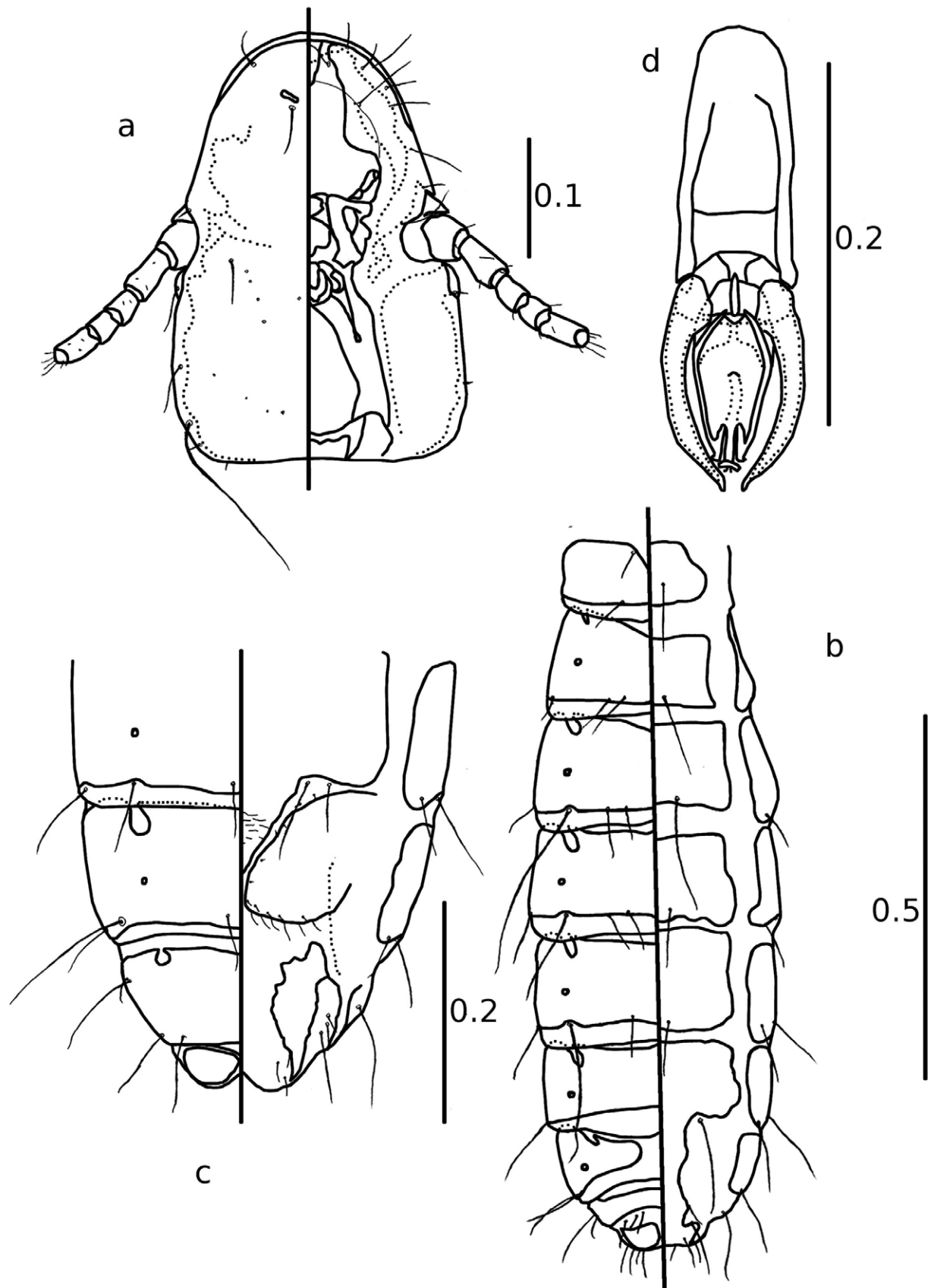
*Lunaceps limosella* Timmermann; Adam, 2007a: 137

*Lunaceps limosella* Timmermann; Adam, 2007b: 151

**Type host:** *Limosa limosa limosa* (Linnaeus, 1758)

**Other host:** *Limosa limosa melanuroides* Gould, 1846.





**FIGURE 16.** *Lunaceps limosae* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

**Diagnosis:** Marginal carina continuous across the head (Fig. 16a), but transparent or missing anterior to the AVS2, except for at the ventral anterior plate, where it bulges slightly. Dorsal preantennal suture missing, or present only as a pair of kidney-shaped vestiges anterior-lateral to the ADS. Ventral anterior plate small and irregular, triangular or quadratic. AVS3, AVS2 and ADS more or less aligned, the ventral setae sometimes both slightly anterior to ADS.

Abdominal tergites II in males and II–III in females with wedge-shaped median indentation of the anterior margin (Fig. 16b), reaching more than a third of the tergite width. Paratergal plates broad. Tergal heads transparent and broad. Sublateral anterior indentations of tergites deep.

Female genital lobes with 5–6 posterior marginal setae, 4–6 sub-marginal setae, and 5–6 median marginal setae (Fig. 16c). Parameral heads elongated. Shape of mesomere approaching elongated triangle, with straight lateral edges. Lower endomere wide and connected to a broad and clearly delimited apodemal bridge by an equally clearly demarcated triangle (Fig 16d).

**Discussion:** Very similar to *L. limosella*, with which it was synonymised (Price *et al.*, 2003), but the dorsal preantennal suture of *L. limosae* is much reduced or missing, making the preantennal area more similar to that of *L. paschalis*. However, the abdomen of *L. limosae* is much longer and more slender than that of *L. paschalis*, and there are further differences in the male genitalia and the preantennal setal arrangement.

There are minor but consistent differences between material collected from the two host subspecies. For instance, populations from *L. l. melanuroides* have four sub-marginal setae on the female genital lobes, and there are differences in the relative size of the setae on several abdominal segments. However, very few males from the nominate host subspecies are available, and the differences, though consistent, are perhaps not significant enough to justify taxonomic recognition, but should be kept in mind when examining material from East Asia and Australia.

**Etymology:** From *limus* = mud. Refers to the host name *Limosa*, a group of birds that can often be found on mudflats and along shores.

#### **Material examined:**

##### *Ex Limosa limosa*

♀1, ♂1, Ireland: Galway, 4 February 1965, D. Cabot, BM 1965-566 (NHML). ♀3, India: Rajputana, January 1936, Meinertzhagen Collection (4774) (NHML). ♀6, ♂1, Iraq, January 1923, Meinertzhagen Collection (4420) (NHML). ♀2, India: [Rajasthan?:] Near Ajmere, 27 March 1868, J. Waterston Collection BM 1930-232 (NHML). ♀1, United Kingdom: Wales: Carmarthenshire: Pendine, 19 September 1935, J. G. Wilson, BM 1980-40 (NHML). ♂1, Belarus: Turov, ID: 1660-1, Band number: F00262, P. Pinchuk (SMNH). ♀1, Belarus: Turov, ID: 1660-2, Band number: F00262, P. Pinchuk (GNM).

##### *Ex Limosa limosa melanuroides* (synonym: *Limosa melanura melanuroides*)

♀15, ♂19, New Zealand: Auckland Island: Enderby Island, 8 December 1976, J. A. Battle (MONZ). ♀5, ♂5, Russia: East Siberia: Amur Bai, 27 September 1893, Dorries, J. Waterston Collection BM 1930-232 (NHML). ♀7, ♂4, [China?:] Tonghoo, 2 October, 1845, R. G. Wardlaw, J. Waterston Collection BM 1930-232 (NHML).

##### *Ex Limosa lapponica* (possibly stragglers)

♀4, ♂1, United Kingdom: Sussex: Pagham, 4 September, 1869, Alfred Grant, J. Waterston Collection, BM 1930-232 (NHML).

##### *Ex Limosa sp.*

♀1, New Zealand, 20 November 1927, A. W. Parrot, in R.L.C. Pilgrim Collection (MONZ).

#### ***Lunaceps limosella* Timmermann, 1954**

(Fig. 17a–d; Table 1)

*Lunaceps limosella* Timmermann, 1954a: 629 (partim)

*Lunaceps limosella limosella* Timmermann; Emerson, 1972: 94

*Lunaceps limosella limosella* Timmermann; Eichler and Hackman, 1973: 92

*Lunaceps limosella* Timmermann; Ledger, 1980: 169 (partim)

*Lunaceps limosella* Timmermann [ex *Limosa lapponica baueri*]; Pilgrim and Palma, 1982: 21

*Lunaceps limosella* Timmermann; Price *et al.*, 2003: 196 (partim)

**Type host:** *Limosa lapponica lapponica* (Linnaeus, 1758)

**Other hosts:** *Limosa lapponica menzbieri* Portenko, 1936, *Limosa lapponica baueri* J. F. Naumann, 1836

**Diagnosis:** Marginal carina narrow and sometimes transparent anteriorly (Fig. 17a). Dorsal preantennal suture continuous across the head. Ventral anterior plate small and triangular. Lateral nodi small. Dark preantennal band very narrow and faint. AVS3 and AVS2 more or less aligned, but both posterior to ADS.

Abdominal tergites II–III in both sexes with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width. Paratergal plates broad and roughly rectangular. Tergal heads broad and blunt, with short bars (Fig. 17b).

Female genital lobes with 6 posterior marginal setae, 5 sub-marginal setae, and 6 median marginal setae (Fig. 17c). Parameres gently curved (Fig. 17d). Lower endomere small. The mesomere plump, with blunt and wide distal ends and curved lateral edges. Dorsal fingers extend anteriorly to ventral blades. The apodemal bridge is weakly delineated and no connection between the apodemal bridge and the lower endomere visible.

**Discussion:** *Lunaceps limosella* can be differentiated from *L. paschalis* and *L. limosae* by the presence of a dorsal preantennal suture. Further separated from all other species parasitic on *Limosa* spp. by the male genitalia being relatively shorter and stouter, and with a much smaller lower endomere. The genitalia of *L. limosella* are more similar to *Lunaceps* species from *Calidris* spp., but are easily separated from *Lunaceps* on *Calidris* sp. by size and by the number of female genital setae (although some *L. drosti* have the same number).

Most similar to *L. limosae*, with which it was previously considered conspecific (Price *et al.*, 2003), but it differs in the shape and size of the male genitalia, the number of female posterior marginal setae, and the presence of a median wedge-shaped indentation in the anterior margin of male tergite III. In general, *L. limosella* is wide in the abdomen and its head is rounder than in *L. limosae*.

Material from *L. lapponica menzbieri* is slightly different from that from nominate subspecies and from *L. l. baueri*, with a more oblong head, more clearly defined marginal carina, and with AVS2 far anterior to AVS3 (even aligned with ADS in one specimen). However, too few specimens from *L. l. menzbieri* are available to draw any conclusions about their status.

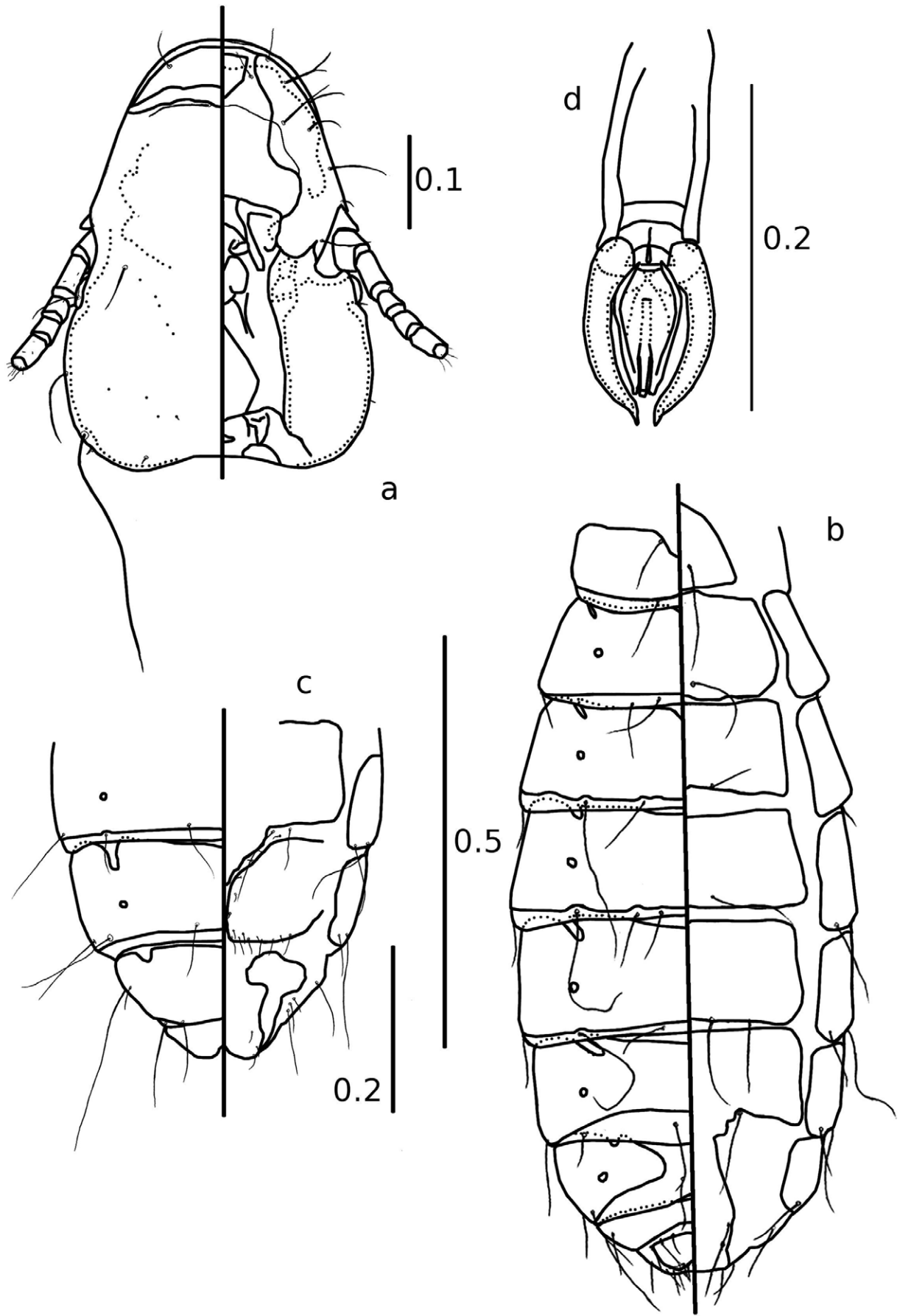
**Etymology:** From *limus* = mud, and *-ella* = small. A reference to the host name *Limosa*, which can often be found on mudflats.

#### Material examined:

##### *Ex Limosa lapponica*

Paratypes: ♀19, ♂9, United Kingdom: Scotland: Ross-shire, Oct. 1935, Meinertzhagen Collection 4352 (NHML). ♀2, ♂1, United Kingdom: Scotland: Hebrides: South Uist, Jan. 1935, Meinertzhagen Collection 2742 (NHML). ♀2, United Kingdom: England: Norfolk, Dec. 1934, Meinertzhagen Collection 2294 (NHML). n#2, United Kingdom: England: Norfolk, Jan. 1946, Meinertzhagen Collection 15560 (NHML). ♀7, ♂5, United Kingdom: Scotland: Hebrides: North Uist, Sept. 1941, Meinertzhagen Collection 14631 (NHML). ♀26, ♂18, United Kingdom: Scotland: Hebrides: North Uist, Sept. 1941, Meinertzhagen Collection 14662 (NHML) (slide also contains a *Carduiceps*). ♀22, ♂12, United Kingdom: Scotland: Hebrides: North Uist, Sept. 1941, Meinertzhagen Collection 14660 (NHML).

Non-type: ♀1, ♂3, The Netherlands: Vlieland, 12 September 1972, E. van den Broek, collection 1973-561 (NHML). ♀1, ♂1, United Kingdom: Wales: Bardsey Island, 3 September 1957, A. Comber, BM 1958-149 (NHML). ♂1, United Kingdom: England: Cheshire: Mersey Estuary, 22 September 1934, H. Bostock (NHML). ♀1, ♂1, United Kingdom: Wales: Glamorganshire: Aberthaw, 7 September 1935, J. G. Williams, BM 1980-40, at NHML. ♂3, United Kingdom: England: Kent: New Romney, 19 September 1889, Col. Irby, J. Waterston Collection BM 1930-232 (NHML). ♂1, United Kingdom: Scotland: Aberlady, 23 September 1911, Ogilvie for H.M., J. Waterston Collection, BM 1930-232 (NHML). ♀8, ♂2, United Kingdom: England: Sussex: Pagham, 4 September 1869, Alfred Grant, J. Waterston Collection, BM 1930-232 (NHML). ♀1, ♂1, Poland: Near Swinoujście: [Gmina] Międzydroje, 26 September 1961, E. Woik, 42/m/126 and 42/m/174 (MFN). ♀1, [Collection data not given on slide], 7824c (MFN) [Note: a second slide, 7824b, contains the head of what appear to be a *Lunaceps*, but the body is missing and the head is in the mounting medium *outside* the cover slide, and cannot be correctly identified].



**FIGURE 17.** *Lunaceps limosella* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

*Ex Limosa lapponica baueri*

♀9, ♂9, New Zealand: Greymouth, 21 October 1973, W. Pulley, R.L.C. Pilgrim collection (MONZ). ♀5, ♂5, New Zealand: Kaikoura, 22 October 1973, C. J. Horning, R.L.C. Pilgrim collection (MONZ). ♀2, ♂2, New Zealand: Heathcote Estuary, October 18th 1973, F. R. B. Allison, R.L.C. Pilgrim collection (MONZ). ♀3, ♂2, New Zealand: Campbell Island, 8 January 1961, J. M. Moreland (MONZ). ♀1, ♂1, New Zealand: Campbell Island, 8 January 1961, J. M. Moreland, BM 1963-502 (NHML). ♀3, ♂3, New Zealand: South Brighton, 20 December 1962, CU #935, N. C. A. S., R. C. L. Pilgrim collection (MONZ). ♀1, United States: California, Meinertzhagen Collection 12715 (NHML). ♀1, Australia: New South Wales: Wollongong, 6 January 1968, J. McKean, BM1975-80 (NHML).

*Ex Limosa lapponica menzbieri*

♀1, ♂2, Australia: Western Australia: Broome, 28 September 1998, P. F. Battley (MONZ).

***Lunaceps lissmanni* Timmermann, 1954**

(Fig. 18a–d; Table 1)

*Lunaceps lissmanni* Timmermann, 1954a: 634

*Lunaceps numenii lissmanni* Timmermann; Price *et al.*, 2003: 196

**Type host:** *Numenius minutus* Gould, 1841

**Diagnosis:** Head very elongated, with marked concave posterior margin (Fig. 18a). Hyaline margin broad. Marginal carina interrupted laterally where the dorsal preantennal suture reached the side of the head. Anteriorly, the marginal carina is present only between the AS1 and AS2. A thickening associated with the middle of the ventral anterior plate may be part of marginal carina, but is weak and ill-defined. Ventral anterior plate long and broad, with irregular posterior margin. Dorsal preantennal suture broad and may be interrupted medially. AVS2 and AVS3 aligned, in males also aligned with ADS, but markedly posterior to this in females. Marginal temporal carina very broad, particularly in anterior end. MTS1, MTS4 and MTS5 quite slender, not thorn-like.

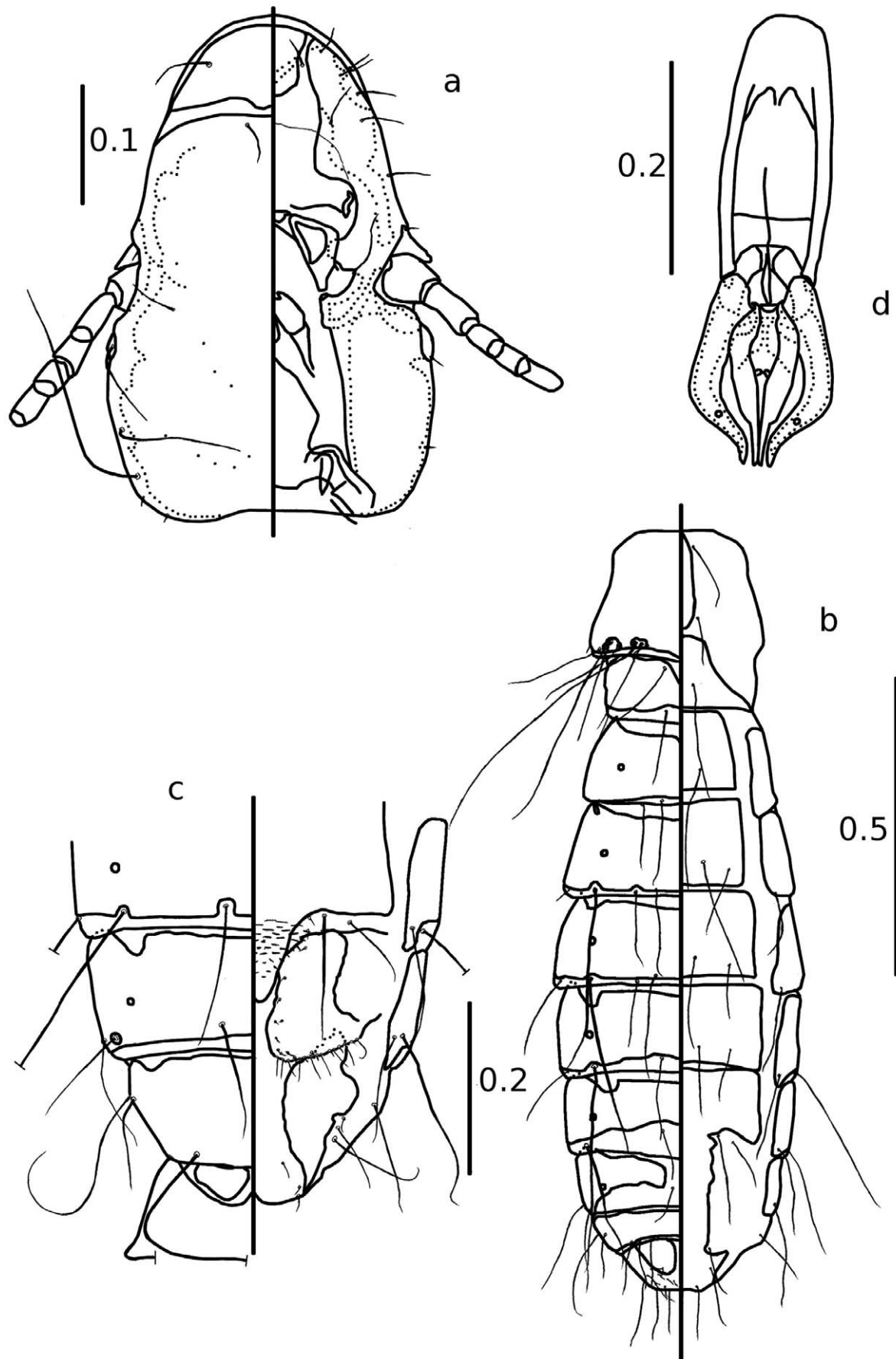
Posterior margin of pterothorax with median point, with the two halves concave (Fig. 18b).

All abdominal setae very stout and long (Fig. 18b). Setal arrangement very distinct in both sexes, with two pairs of ventral setae on segments IV–V and VII (sometimes also in III) in males, and an extra submedian pair of ventral setae in the female segment VI. Anterior margin of segments II–III in males and II–IV in females with narrow wedge-shaped median indentation. Antero-lateral ends of tergites broadly pointed in segments III–VI, without tergal heads. Sublateral indentation missing in segment III, narrow in segment IV, and broad in segments V–VII. Paratergal plates broad. Sternite of segment II very broad posteriorly, sometimes reaching the lateral margins of the abdomen.

Female genital lobes rounded with 8–9 posterior marginal setae, 8–10 sub-marginal setae, and 7–8 median marginal setae (Fig. 18c). The inner three sub-marginal setae are typically smaller than the others, and not thorn-like, as are the outer ones. Parameres with abrupt turn about one third from distal tip, ends roughly parallel, and parameral heads elongated and almost triangular (Fig. 18d). One ventral aperture visible in distal fourth of paramere. Mesomere with bulging lateral sides and an elongated distal end. Dorsal fingers stout, and divergent anteriorly, forming small hooks. Lower endomere broad and semicircular, connected to apodemal bridge by narrow triangle.

**Discussion:** *Lunaceps lissmanni* is a very distinct species, separable from other *Lunaceps* by a large array of characters. It is most similar to *L. rileyi*, with which it shares extra abdominal setae, but *L. rileyi* is broader and shorter. Also the parameres of *L. rileyi* are not as abruptly bent as those of *L. lissmanni*, and the mesomeral lateral margins are less straight in *L. rileyi*. Females of these two species are more similar, having similar numbers of genital setae, but can be separated by the shape of the head, which is generally longer and narrower anteriorly in *L. lissmanni*. Both sexes can be separated by the broad dorsal preantennal suture of *L. lissmanni*, which is narrow and sometimes hard to see in *L. rileyi*, and by the shape of the pterothorax. The hosts of *L. lissmanni* and *L. rileyi* appear to be closely related (Thomas *et al.*, 2004a), and this suggests that the lice also might be closely related.

*L. lissmanni* can be separated from other *Lunaceps* species by its additional abdominal setae and the shape of the pterothorax. The male genitalia are quite unique in shape, particularly the parameres, and the female genital setal numbers, especially the sub-marginal and median marginal setae, place it apart from other species.



**FIGURE 18.** *Lunaceps lissmanni* A) Male head, dorsal and ventral views. B) Male pterothorax and abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

**Etymology:** Named in honour of Hans Werner Lissman (1909–1995) at the University of Cambridge, England.

**Material examined:**

*Ex Numenius minutus*

Holotype: ♂1, Russia: Siberia, Meinertzhagen Collection 11015 (NHML).

Allotype: ♀1, Russia: Siberia, Meinertzhagen Collection 11015 (NHML).

Paratypes: ♀11, ♂6, Russia: Siberia, Meinertzhagen Collection (11015) (NHML).

Non-types: ♀11, ♂8, Australia: Western Australia: Broome, 26 October 1999 (MONZ). ♂3, Far East, BM 8943 (NHML). ♀1, Papua New Guinea: Western District: Near Wando, 16 October 1969, BM 1970-381 (NHML).

***Lunaceps mintoni* sp. nov.**

(Fig. 19a–d; Table 1)

*Lunaceps drosti* Timmermann, 1954a: 627 (partim)

*Lunaceps holophaeus drosti* Timmermann; Emerson, 1972: 93 (partim)

*Lunaceps drosti* Timmermann; Price *et al.*, 2003: 196 (partim)

*Lunaceps drosti* Timmermann (“Clade 10”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)

**Type host:** *Calidris tenuirostris* (Horsfield, 1821)

**Diagnosis:** Head ovoid (Fig. 19a). Hyaline margin very thin, and cannot be seen in some individuals. Marginal carina clearly demarcated along its length. Ventral anterior plate broad but short, with flat or slightly bulging posterior margin. Dorsal preantennal suture interrupted medially, and may bulge posterior to encapsulate the apertures of the ADS. AVS3 and ADS aligned, but AVS2 markedly posterior to these. Temporal marginal carina thick dorsally. MTS3 comparatively long and thick.

Abdominal tergites II in males and II–III in females with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width (Fig. 19b). Paratergal plates broad and blunt, not much darker than tergites. Tergal heads of segments III–V slightly pointed or hook-shaped, otherwise broad and blunt. In males, dorsal intermediate setae of segment VII are shorter and more slender than median setae.

Female genital lobes with 4–5 posterior marginal setae, 3–4 sub-marginal setae, and 5–6 median marginal setae (Fig. 19c). Posterior marginal setae quite short and slender. Parameres gently curved and slender (Fig. 19d). Mesomere triangular. Lower endomere narrow. Apodemal bridge broad but very faint.

**Nymphs:** Marginal carina very prominent, and evenly thick, uninterrupted, along its length. Dorsal preantennal suture C-shaped, and at least as broad as the marginal carina. Preantennal setae very small, except for the AVS3, which is markedly longer, and perhaps proportionately as long as in the adult individual. Ventral anterior plate almost wholly obscured by the dorsal anterior plate, but appears to be roughly triangular.

**Discussion:** Included by Timmermann (1954a) in *L. drosti*, but *Lunaceps* populations on these two host species are genetically distinct (uncorrected “p” distance for COI = 19.2%; Gustafsson and Olsson, 2012). Both sexes of *L. mintoni* sp. nov. can be distinguished from *L. drosti* by the shape of the ventral anterior plate and by the tergal heads. Females generally have more sub-marginal setae in *L. drosti* than in *L. mintoni*.

**Etymology:** Named in honour of Clive Minton, who for several decades has been leading the expeditions of the Australasian Wader Study Group to North West Australia. It was during one of those expeditions that the first author collected some of the material on which this new species is based.

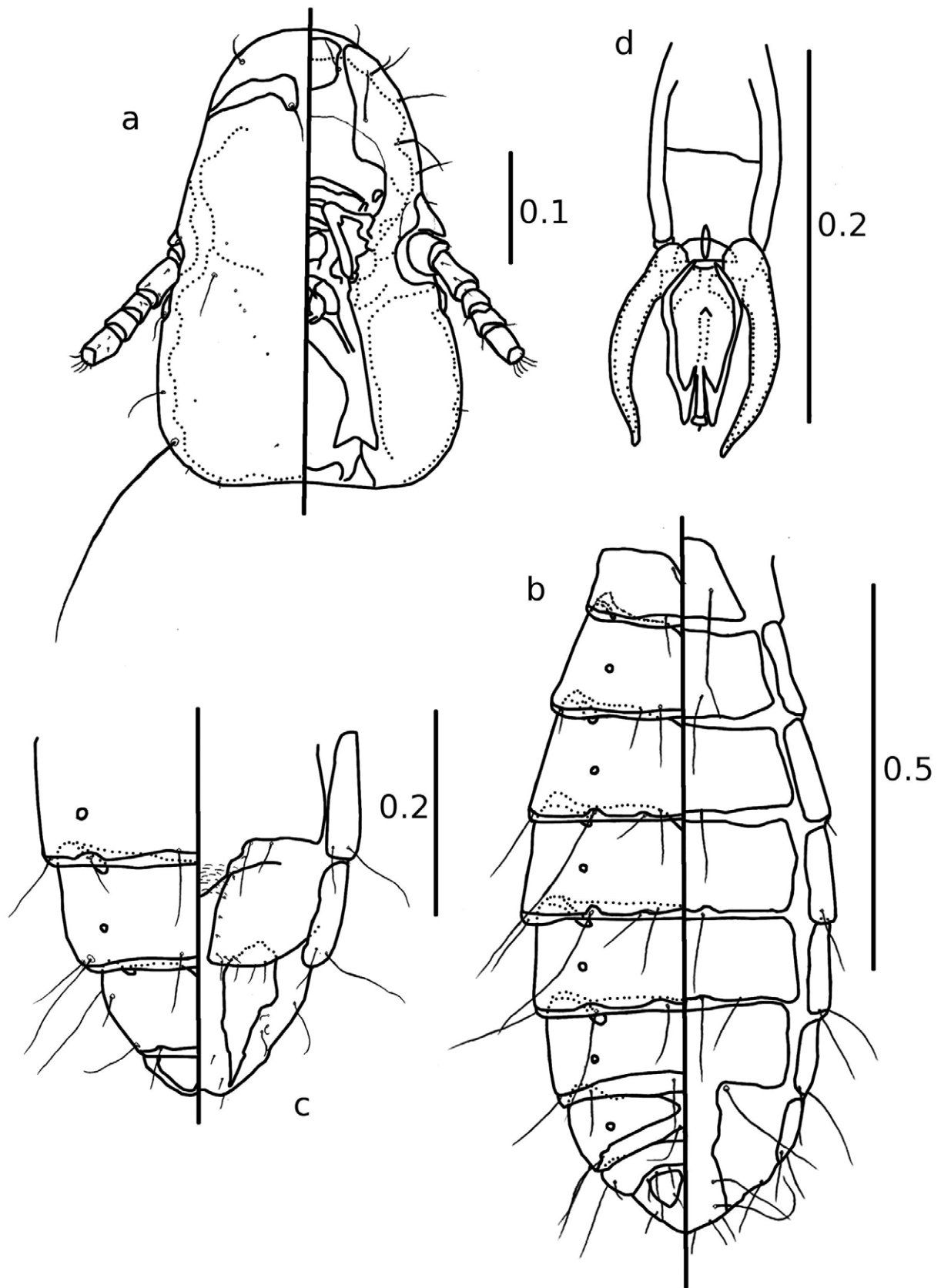
**Material examined:**

*Ex Calidris tenuirostris* (synonym: *Erolia tenuirostris*)

Holotype: ♀1, Australia: Western Australia: 80 Mile Beach: Near Anna Plains Cattle Station, 18 November 2008, ID: 900, Band number: 063-03628, D. Gustafsson, (GNM).

Paratype: ♀1, Australia: Western Australia: 80 Mile Beach: Near Anna Plains Cattle Station, 17 November 2008, ID: 895, Band number: 063-03474, D. Gustafsson, (SMNH).

Non-type: ♀21, ♂14, Japan, Meinertzhagen Collection (11012) (NHML). ♀1, ♂2, Philippines: Luzon: Batangas: Calatanga, 10 August 1966, BM 1968-86 (NHML) (one of these slides also contains an unidentified female *Quadriceps*). ♀4, ♂4, n#4, Australia: Western Australia: Mandurah, 1970, BM 1970-144 (NHML). ♀2, ♂2, Philippines: Luzon: Batangas: Calatanga, 10 August 1966, K.C. Emerson Collection (OSU).



**FIGURE 19.** *Lunaceps mintoni* sp. nov. A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.



## *Lunaceps nereis* Timmermann, 1954

(Fig. 20a–d; Table 1)

*Degeeriella actophilus* (Kellogg and Chapman); Waterston, 1922: 253

*Degeeriella actophilus* (Kellogg and Chapman); Ferris, 1923: 11

*Lunaceps nereis* Timmermann, 1954a: 628

*Lunaceps nereis* Timmermann; Malcomson, 1960: 191

*Lunaceps holophaeus nereis* Timmermann; Emerson, 1972: 94

*Lunaceps nereis* Timmermann; Price *et al.*, 2003: 196 (partim)

*Lunaceps nereis* Timmermann; Palma and Jensen, 2005: 56

**Type host:** *Calidris maritima* (Brünnich, 1764).

**Other host:** *Calidris ptilocnemis* (Coues, 1873), *Calidris ptilocnemis couesi* (Ridgway, 1880).

**Diagnosis:** Head wide and short (Fig. 20a). Hyaline margin extremely narrow or missing. Marginal carina narrow and even along its length. Dorsal preantennal suture interrupted medially, but a more weakly coloured area surrounds its inner ends, and connects them. Ventral anterior plate small and quadratic (occasionally triangular). Ventral carina weakly coloured and narrow. Lateral nodus small. Dark preantennal band only a blotch near lateral sides of head. AVS3 and ADS more or less aligned, but AVS2 posterior to these. Marginal temporal carina dark at eye.

Abdominal tergites II–III in males and II–IV, sometimes V, in females with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width (Fig. 20b). Paratergal plates broad, only marginally darker than tergites. Tergal heads large and blunt, but transparent. In males, the paratergal heads may be re-entrant and pointed in segment III. Ventral setae aligned with the anterior dorsal setae of segment II of both sexes.

Female genital lobes with 4–5 posterior marginal setae, 3 sub-marginal setae, and 5 median marginal setae (Fig. 20c). Parameres slender with slight sudden bent (Fig. 20d). Distal ends of mesomere broad, with convex lateral sides, and dorsal fingers slender and barely reaching anterior to the ventral blades. Lower endomere semicircular, with pointed postero-lateral edges, and connected to apodemal bridge by an indistinct triangle.

**Nymphs:** Marginal carina narrow and continuous around head. Ventral anterior plate continuous with ventral lateral plates. Dorsal preantennal suture bent and wide, enveloping the ADS, and continuing posteriorly to the preantennal nodi. Faint traces of transverse sutures appearing near preantennal nodi and continuing anteriorly and medially; these may be continuous with dorsal preantennal suture. Thorax similar to that of adults. Tergites and sternites transparent, but paratergal plates weakly pigmented. Intermediate setae similar to median setae in length and thickness in all segments.

**Discussion:** *L. nereis* is similar to *L. schismatus* sp. nov., with similar colouration and position of the ventral setae of abdominal segment II. However, *L. nereis* and *L. schismatus* sp. nov. differ in the preantennal area, with the former having a thinner marginal carina and a smaller ventral anterior plate. The overall shape of the head of *L. nereis* is rounder and stouter, with a narrower dorsal anterior plate.

Material from *C. ptilocnemis* is identical to that of *C. maritima*, and therefore is included in *L. nereis*, although only a few individuals are available. Both hosts inhabit similar environments, and are closely related (Borowik and McLennan, 1999).

**Etymology:** From *nerei* = a sea nymph. Though Timmermann (1954a) gives no derivation to this name, it is probably attributable to the maritime habits of the host, which is often found on the smallest of rocks that barely reach above the waves.

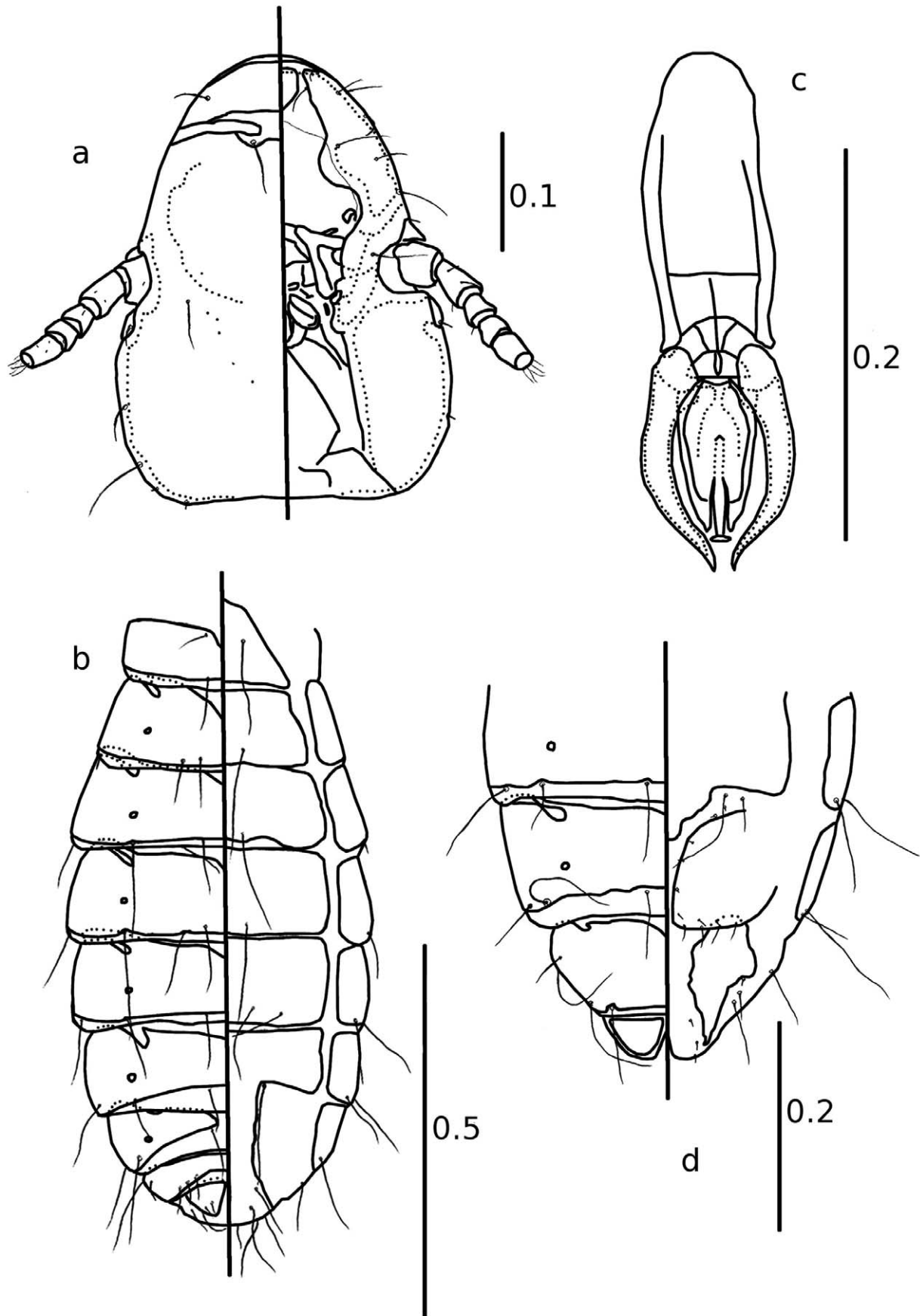
### Material examined:

Ex *Calidris maritima* (synonyms: *Erolia maritima*, *Alipsa actophilus*)

Holotype: ♂1, [Sweden?:] Lapland, March 1938, Meinertzhagen Collection 11071-72 (NHML).

Allotype: ♀1, [Sweden?:] Lapland, March 1938, Meinertzhagen Collection 11071-72 (NHML).

Paratypes: ♀6, ♂4, [Sweden?:] Lapland, March 1938, Meinertzhagen Collection 11071-72 (NHML). ♀1, ♂3, United Kingdom: England: Norfolk, December 1934, Meinertzhagen Collection 2286 (NHML). ♀1, ♂2, United Kingdom: Scotland: Hebrides: South Uist, January 1934, Meinertzhagen Collection 104, 105, 130 (NHML). ♀8, ♂9, United Kingdom: Scotland: Tabaltness, December 1934, Meinertzhagen Collection 2346, 2366, 2364, 2368 (NHML).



**FIGURE 20.** *Lunaceps nereis* A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Non-types: ♀5, ♂5, n#4, United Kingdom: Scotland: Skerryvore, 22 October 1990 (MONZ). ♀1, ♂1, Denmark: Faroes Islands: Nólsoy, 5 March 1999 (MONZ). ♀1, ♂1, Norway: Spitsbergen: Klaas Billen Bay, 15 August 1921, Spitzbergen Expedition, 1922-114 (NHML). ♀1, ♂2, n#1, Denmark: West Greenland, August 1955, Meinertzhagen Collection 20378, BM 1955-650 (NHML).

*Ex Calidris ptilocnemis*

♀1, ♂1, United Kingdom: Alaska: E. Killing Gd, 2 August 1964, K.C. Emerson Collection (OSU).

*Ex Calidris ptilocnemis couesi*

♀4, ♂1, United States: Alaska: Aleutian Isles: Amchitka, 10 March, 1959 (NHML).

***Lunaceps numenii numenii* (Denny, 1842)**

(Fig. 21a–d; Table 1)

*Nirmus numenii* Denny, 1842: 53

*Nirmus inaequalis* Piaget, 1880: 176

*Nirmus phaeopi* Denny; Waterston, 1915: 33 (partim)

*Degeeriella numenii* (Denny); Harrison, 1916: 119

*Degeeriella numenii* (Denny); Séguy, 1944: 289

*Degeeriella numenii* (Denny); Blagoveshtchensky, 1948: 279

*Lunaceps numenii* (Denny); Hopkins and Clay, 1952: 201

*Lunaceps numenii* (Denny); Timmermann, 1954a: 631

*Lunaceps haematopi* Timmermann, 1954a: 635. **New synonymy**

*Lunaceps haematopi* Timmermann; Malcomson, 1960: 190

*Lunaceps numenii* (Denny); Malcomson, 1960: 190

*Lunaceps numenii* (Denny); Touleshkov, 1964: 132

*Lunaceps numenii* (Denny); Fedorenko, 1968: 73

*Lunaceps phaeopi* (Denny); Brander, 1969: 7 [Ref: Eichler and Hackman, 1973: 92]

*Lunaceps numenii numenii* (Denny); Emerson, 1972: 94 (partim)

*Lunaceps haematopi* Timmermann; Emerson, 1972: 93

*Lunaceps numenii* (Denny); Eichler and Hackman, 1973: 92

*Lunaceps numenii* (Denny); Rékási and Kiss, 1977: 104

*Lunaceps numenii* (Denny); Ledger, 1980: 169

*Lunaceps haematopi* Timmermann; Ledger, 1980: 169

*Lunaceps numenii* (Denny); Rékási and Kiss, 1980: 75

*Lunaceps numenii numenii* (Denny); Mayberry *et al.*, 2000: 60

*Lunaceps numenii numenii* (Denny); Price *et al.*, 2003: 196 (partim)

*Lunaceps haematopi* Timmermann; Price *et al.*, 2003: 196

*Lunaceps numenii numenii* (Denny); Palma and Jensen, 2005: 56

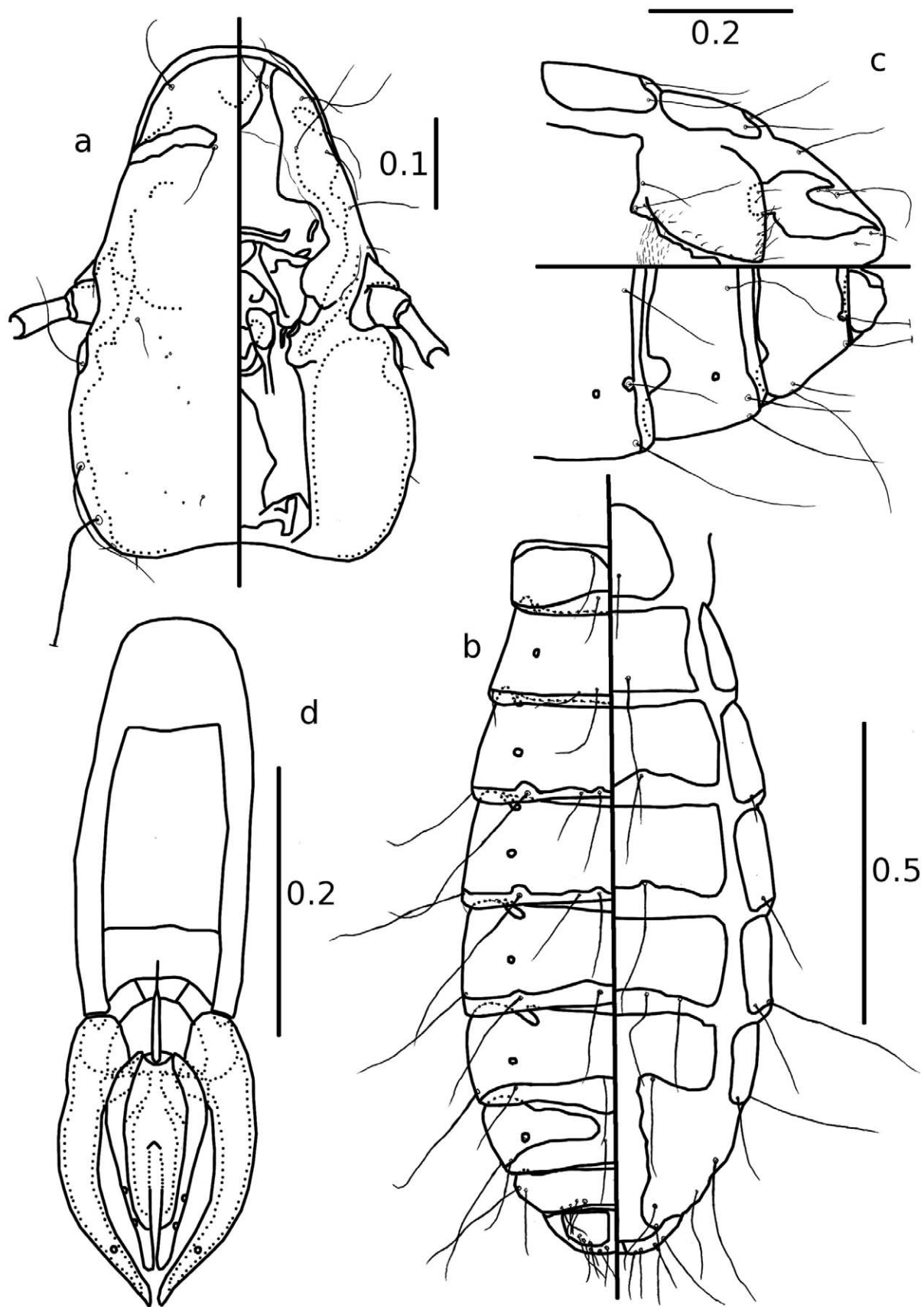
*Lunaceps numenii* (Denny) (“Clade 9”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)

**Type host:** *Numenius arquata arquata* (Linnaeus, 1758)

**Other hosts:** *Numenius arquata orientalis* C.L. Brehm, 1831, *Haematopus ostralegus* Linnaeus, 1758, *Haematopus bachmani* Audubon, 1838, *Dromas ardeola* Paykull, 1805

Note: The two species of *Haematopus* are listed by Price *et al.* (2003: 196, 289) as hosts for *L. haematopi* (= *L. numenii*), one as the type host and the other taken from Emerson (1972: 93), who merely stated that *H. bachmani* and *H. palliatus* Temminck, 1820, were likely hosts. No other record of *L. haematopi* being found on any of the North American *Haematopus* species is known to us.

**Diagnosis:** Hyaline margin comparatively broad (Fig. 21a). Marginal carina interrupted or weakened by dorsal preantennal suture. Anterior to dorsal preantennal suture most clearly visible as an “island” near the AS1 and AS2, however there is a colourless connection between this and the medio-anterior bulge of the marginal carina, which forms a prominent extension (commonly pointed in males, rounded in females) that augments the ventral anterior plate. Dorsal preantennal suture interrupted medially, bulging to envelop the ADS. Preantennal setae quite long and thick. Lateral nodus small but distinct. Dark preantennal band narrow, and almost continuous across the head. AVS2 and AVS3 aligned, in males and most females both are aligned with ADS. MTS1 and OS slender, but long, particularly in females where they approach the size of the MTS3.



**FIGURE 21.** *Lunaceps numenii numenii* A) Female head, dorsal and ventral views. Distal parts of antennae removed. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Pterothorax with rounded posterior margin.

Abdomen relatively broad (Fig. 21b). Only in segment II is the anterior margin of the tergite indented medially. Paratergal plates broad. Antero-lateral ends of tergites III–IV broadly pointed, but without tergal heads. The type of *Lunaceps inaequalis* studied has perhaps more pointed antero-lateral ends of tergites than is standard in *L. numenii numenii*, but is otherwise similar. Sublateral indentation narrow and long in all segments. Lateral setae of segment III not thorn-like on either sex.

Female genital lobes with 7–8 (9 in *Haematopus* material) posterior marginal setae, 5–6 (6–7 in *Haematopus* material, 8 in *Lunaceps numenii inaequalis*) sub-marginal setae, and 7–9 median marginal setae (Fig. 21c). Parameres gently curved, with a ventral aperture approximately one fifth from distal tip (Fig. 21d). Mesomere roughly triangular but elongated posteriorly, with straight or nearly straight lateral sides which are interrupted in distal half by two small apertures, only rarely with visible setae (though these are usually visible in material from *H. ostralegus*). Dorsal fingers convergent and extending anteriorly to ventral blades, with median groove broad and shallow. Ventral blades thickened medially. Lower endomere semi-circular, with posterior margin flat dorsally and concave ventrally, and connected to apodemal bridge by vaguely defined triangle.

**Nymphs:** Ventral carina very angular. Dorsal preantennal suture long and broad, bending posteriorly and almost reaching the base of antennae.

**Discussion:** *Lunaceps numenii* is easily distinguished by the narrow and almost complete dark preantennal band, which is only barely interrupted medially. Overall, the head is heavily sclerotized, reminiscent of *L. actophilus*. The ventral anterior plate is quite large, but similar to that of *L. numenii phaeopi* and *L. kukri* sp. nov., and differs somewhat between the sexes.

Most similar to *L. kukri* sp. nov., with which it was previously considered conspecific, but males of these two species differ in the genitalia, particularly in the shape of the mesomeres and parameres. Females identical to *L. kukri* sp. nov. apart from the number of genital setae.

*Lunacepsnumenii numenii* is also similar to *L. numenii phaeopi*, but they differ in size—*L. numenii numenii* and *L. kukri* sp. nov. are the only *Lunaceps* species measuring above 2 mm—and in the shape of the male genitalia. In general, *L. numenii numenii* is broader in the abdomen than *L. numenii phaeopi*, and the paratergal plates are narrower, with a dark border marking, which is missing in *L. numenii phaeopi*. The ventral sublateral setae of abdominal segment III is long and slender in both sexes, which immediately sets it apart from *L. numenii phaeopi*.

No significant consistent differences were found between material from the two subspecies of *Numenius arquata*.

The type of *Lunaceps inaequalis* differs only very slightly from *Lunaceps numenii*, in the number of sub-marginal setae of the female genitalia and perhaps in the shape of the antero-lateral ends of tergites. These differences are small, and do not in our opinion warrant recognition of *Lunaceps inaequalis* as a separate species. We therefore accept the synonymisation of *Lunaceps inaequalis* with *Lunaceps numenii* (Hopkins and Clay, 1952; Price *et al.*, 2003).

There is a small series of *Lunaceps* specimens collected from *Haematopus ostralegus* and *Dromas albeola* at the NHML, which Timmermann (1954a) described as *Lunaceps haematopi*. Even in the original description, Timmermann seems to have had some doubts on the validity of the species, as so few individuals were available despite the type host (*H. ostralegus*) having been frequently sampled. However, in his review of ischnoceran lice from the Charadriiformes, Timmermann (1957: 81) appears more certain about the validity of *L. haematopi*, as he wrote: “Obwohl keine Veranlassung besteht, ihr normales Vorkommen bei *Haematopus* und *Dromas* anzuzweifeln, dürfte es sich doch empfehlen, mit einem abschliessenden Urteil über die Art zu warten, bis sie besser bekanntgeworden ist, da *L. haematopi* auffallenderweise auf beiden Wirten ziemlich selten zu sein scheint.” (“Although there is no reason to doubt its natural occurrence on *Haematopus* and *Dromas*, it might be advisable to wait with a final judgement about this species until it is better known, as *L. haematopi* seems to be quite rare on both hosts.”; our translation)

Both *Dromas* and *Haematopus* would be atypical hosts for *Lunaceps*, as *Haematopus* appears to be more closely related to avocets and stilts (*e.g.*, Paton *et al.*, 2003; Thomas *et al.*, 2004b; Fain and Houde, 2007), and *Dromas* more closely related to gulls and terns (Thomas *et al.*, 2004a) or pratincoles and coursers (Pereira and Baker, 2010). It is possible that some populations of *Dromas* and/or *Haematopus* are hosts to *Lunaceps*. However, we feel it is best to include this material in *L. numenii numenii* until additional specimens have been collected. The *Lunaceps* from these two host species are similar in size, and both the male genitalia and the preantennal area of the

lice from these two host species are virtually identical. The lateral setae of the mesomere appear to be longer and easier to see in material from *H. ostralegus* than in that of *N. arquata*, and there are some differences in the female genital setae. However, there is some overlap in setal counts, particularly in the sub-marginal setae. There are, above all, no clear characters to separate them.

The specimens from *Dromas ardeola* differs slightly from that of *Numenius arquata* and *Haematopus ostralegus* in head setal characters, male and female genital characters, as well as some small differences in abdominal setal arrangement. The material from *D. ardeola* comes from two samples with a small total number of individuals (see below). If this collection proves to represent a natural population on *Dromas ardeola*, it will be necessary to study them further to establish if they deserve species recognition but, at present, we prefer to include it in *L. numenii numenii* until more material becomes available.

**Etymology:** From *numeni* = curlew, the new moon. The name refers to the host genus, which in turn is named after the second meaning of *numenii*, as their beaks can be likened to thin moon crescents.

### Material examined:

#### *Ex Numenius arquata*

Nontype material: ♀5, ♂5, United Kingdom: Scotland: Hebrides: South Uist, January 1934, Meinertzhagen Collection 73-110, 237, 273-425 (NHML). ♀1, ♂1, Denmark: Faroes Islands: Nólsoy, 29 January 1985 (MONZ). ♀9, ♂11, United Kingdom: England: Sheffield Park, 15 December 1975 (MONZ). ♀1, ♂3, United Kingdom: Wales: Radnorshire: Llanbrochlllyn, 27 April 1933, BM 1980-40 (NHML). ♀1, United Kingdom: England: Lancashire: Langton: Preston, 23 January 1923, BM1980-40 (NHML). ♂3, Hungary, November 1936, Meinertzhagen Collection 8035 (NHML). ♀1, ♂1, [Collection data not given on slide], 1913 (NHML) (as *Nirmus inaequalis*). ♀2, ♂1, United Kingdom: Cheshire: Lace, 25 February 1933, Hopkins Collection (NHML). ♀1, Slovenia: Ljubljana: Iziea?, 23 May 1950, BM 1959-232 (NHML). ♀13, ♂9, United Kingdom: Scotland: Hebrides: North Uist, August 1941, Meinertzhagen Collection 14563 (NHML). n#4, Europe, 2 December 1968, BM 1968-213 (NHML). ♀1, United Kingdom: Scotland: Dornoch Firth, December 1934, Meinertzhagen Collection 2244 (NHML). ♀5, ♂3, United Kingdom: Scotland: Ross-shire, October 1935, Meinertzhagen Collection 4536 (NHML). ♀2, ♂2, United Kingdom: England: Boston: Lines, 2 March 1938, 222 (NHML). ♀35, ♂40, United Kingdom: Orkney Islands, August-September 1938, Meinertzhagen Collection 11626 (one slide in Hopkins Collection), some marked BM 1951-171 (NHML). ♀3, [Collection data not given on slide], marked "ENTOMOLOGY, Mallophaga, Louse/Parasite of Curlew", BM 1980-40 (NHML). ♂1, [Collection data not given on slide], unmarked (NHML). ♀17, ♂8, Glos [=United Kingdom: England: Gloucestershire?], November 1936, Meinertzhagen Collection 8025 and 8027 (NHML). ♀13, ♂6, United Kingdom: England: Suffolk, September 1935, Meinertzhagen Collection 4003 (NHML). ♀3, ♂3, United Kingdom: Scotland: Hebrides: South Uist, September 1953, Meinertzhagen Collection 20230, BM 1953-658 (NHML). ♀8, ♂3, United Kingdom: Scotland: Hebrides: South Uist, December 1933, Meinertzhagen Collection 73 (NHML). ♂2, Glos [= United Kingdom: England: Gloucestershire?], October 1936, Meinertzhagen Collection 8027 (NHML). ♀2, ♂2, United Kingdom: England: Northumberland: Monk's House Bird Observatory, 21 May 1954, BM1980-40 (one of these slides also contains a female *L. falcinellus*) (NHML). ♂5, United Kingdom: Scotland: Watherspoon, L. Harrison Collection (NHML). ♀3, ♂3, n#1, [Collection data not given on slide], 2688 131 (MFN). ♀2, ♂2, [Collection data not given on slide], 2824 vih and vgh (MFN). ♀2, ♂3, [Collection data not given on slide], 20046e, f, h, i, k (MFN). ♀4, ♂4, [Collection data not given on slide], 3047a-h (MFN).

#### *Ex Numenius arquata orientalis* (synonym: *Numenius arquata lineata*)

♀9, ♂3, Arabia, March 1948, Meinertzhagen Collection 17569 (NHML). ♀2, ♂2, n#1, Maldives: Gan-Addu Atoll, 6 December 1958, BM 1959-560 (NHML).

#### *Ex Haematopus ostralegus* (possibly stragglers)

Holotypes, allotypes, and paratypes of *L. haematopi*: ♀34, ♂17, Ireland, September 1937, Meinertzhagen Collection 10568 (NHML).

#### *Ex Dromas ardeola* (possibly stragglers)

♀6, ♂3, Tanzania: Zanzibar, October 1912, Meinertzhagen Collection 3591 (NHML). ♂1, East Africa (NHML).

Ex *Numenius* sp.

♀1, ♂1, [Collection data not given in slide], 2259 fi and 2250 fh (MFN). ♀1, [collection data not given on slide], 2259 [as *Lunaceps inaequalis*] (MFN).

Ex *Limosa limosa* (possibly stragglers)

♀1, ♂2, England, L. Harrison Collection (NHML).

Material of uncertain status due to condition of slide:

Ex *Numenius arquata*:

♂1, Asia, L. Harrison Collection (NHML). ♂1 (male genitalia only), United Kingdom: Shetlands: Ronas Voe, 23 March 1911, J. Waterston Collection BM1930-232 (NHML). ♀1, ♂1, [Collection data not given on slide], 2824 w ae (MFN) (as *Lunaceps phaeopi numenii*). ♀1, [Collection data not given on slide], 716 (MFN) (as *Lunaceps phaeopii numenii*).

Ex *Circus aeruginosus* (possibly straggler):

♀1, [Collection data not given on slide], 1758a (MFN).

### ***Lunaceps numenii madagascariensis* ssp. nov.**

(Fig. 22a–d; Table 1)

*Lunaceps numenii* (Denny); Timmermann, 1954a: 631 (partim)

*Lunaceps numenii numenii* (Denny); Pilgrim and Palma, 1982: 20

*Lunaceps numenii numenii* (Denny); Price *et al.*, 2003: 196 (partim)

**Type host:** *Numenius madagascariensis* (Linnaeus, 1766)

**Diagnosis:** As nominate subspecies, but with slight differences in size. Head very similar (Fig. 22a). Antero-lateral ends of tergites similar to those of the nominate, but the sublateral indentation rounder and broader, but still with a narrow opening (Fig. 22b). In segment V, the tergal bar occasionally extends laterally to form a small, transparent tergal head.

In the male genitalia (Fig. 22d), the median dorsal groove of the mesomere is narrow and deep, the lower endomere is not as long as in the nominate, and the lateral setae of the mesomere are more commonly visible in *L. n. madagascariensis* than in *L. n. numenii*. The parameres are on average shorter in *L. n. madagascariensis*. In some individuals, there is a colour difference in the male genitalia, with the basal apodeme and lower endomere being greyish brown, and the parameres and mesomere more yellowish.

There is a tendency in the female genitalia towards having fewer posterior marginal setae (typically 7, sometimes 8) (Fig. 22c), but they fall within the range variation for *L. n. numenii*.

**Discussion:** The *Lunaceps* populations on *N. arquata* and *N. madagascariensis* are very similar, and some females cannot be separated, suggesting that they are closely related. However, we found that consistent differences among the males justify giving the *Lunaceps* populations from *N. madagascariensis* the status of subspecies. Furthermore, with other *Lunaceps* species (e.g. *L. falcinellus* and *L. incoenis*) we have found that small morphological differences may still correspond to great genetic differences, and this may be the case with the subspecies of *L. numenii*. However, we feel that the morphological differences alone are not sufficient to separate them into different species until more data, including genetic data, has been collected.

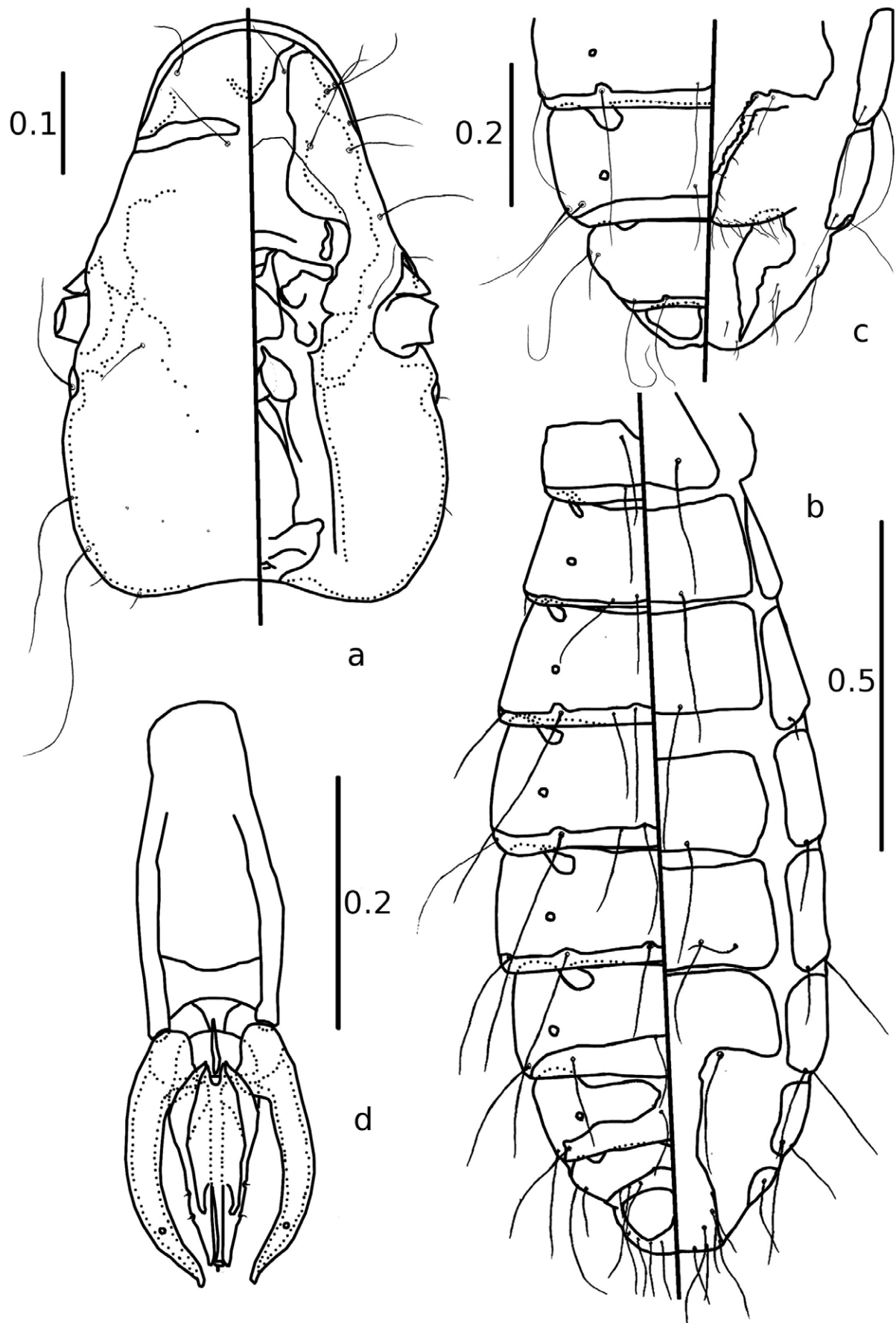
### **Material examined:**

Ex *Numenius madagascariensis*

Holotype: ♂1, Australia: Tasmania: Sandford, 4 May 1958, BM 1959-667 (NMHL).

Paratypes (on same slide): ♀1, ♂1, Australia: Tasmania: Sandford, 4 May 1958, BM 1959-667 (NHML).

Non-types: ♀9, ♂3, Russia: Kamtschatka, Meinertzhagen Collection 11016 (NHML). ♀1, Australia: South Australia, DM4136 (MONZ). ♀17, ♂19, New Zealand: Stewart Island: Masons Bay, 12 November 1976, R.C.L. Pilgrim Collection (MONZ). ♂2, Russia: Kamtschatka, Meinertzhagen Collection 11016 (NHML).



**FIGURE 22.** *Luniceps numenii madagascariensis* ssp. nov. A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia



## *Lunaceps numenii phaeopi* (Denny, 1842)

(Fig. 23a–d; Table 1)

- Nirmus phaeopi* Denny, 1842: 54  
*Nirmus phaeopodis* Giebel, 1874: 166  
*Nirmus trimaculatus* Piaget, 1880: 174  
*Nirmus phaeopi* Denny; Piaget, 1880: 177  
*Nirmus phaeopi* Denny; Mjöberg, 1910: 139  
*Nirmus trimaculatus* Nitzsch; Mjöberg, 1910: 145 [Mjöberg uncertain]  
*Degeeriella oliveri* Johnston and Harrison, 1912: 367  
*Nirmus phaeopi* Denny; Waterston, 1915: 33  
*Degeeriella phaeopi* (Denny); Harrison, 1916: 120  
*Degeeriella trimaculatus* (Piaget); Harrison, 1916: 125  
*Degeeriella oliveri* (Johnston and Harrison); Harrison, 1916: 119  
*Degeeriella* sp. Peters, 1936: 15  
*Degeeriella oliveri* Johnston and Harrison; Thompson, 1939: 120  
*Degeeriella phaeopi* (Denny); Séguy, 1944: 296  
*Lunaceps phaeopi* (Denny); Hopkins and Clay, 1952: 202  
*Lunaceps trimaculata* (Piaget); Hopkins and Clay, 1952: 202  
*Lunaceps phaeopi* (Denny); Timmermann, 1954a: 631  
*Lunaceps phaeopi* (Denny); Emerson, 1958: 57  
*Lunaceps phaeopi* (Denny); Malcomson, 1960: 190  
*Lunaceps numenii phaeopi* (Denny); Keirans, 1967: 115  
*Lunaceps phaeopi* (Denny); Hackman and Nyholm, 1968: 80  
*Lunaceps numenii phaeopi* (Denny); Emerson, 1972: 95  
*Lunaceps phaeopi* (Denny); Eichler and Hackman, 1973: 92  
*Lunaceps phaeopi* (Denny); Ledger, 1980: 169  
*Lunaceps numenii oliveri* (Johnston and Harrison); Pilgrim and Palma, 1982: 20  
*Lunaceps numenii phaeopi* (Denny); Price *et al.*, 2003: 196  
*Lunaceps numenii oliveri* (Johnston and Harrison); Price *et al.*, 2003: 196  
*Lunaceps numenii phaeopi* (Denny); Palma and Jensen, 2005: 56  
*Lunaceps phaeopi* (Denny) (“Clade 9”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)  
*Lunaceps oliveri* (Johnston and Harrison) (“Clade 9”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)

**Type host:** *Numenius phaeopus* (Linnaeus, 1758)

**Other hosts:** *Numenius phaeopus hudsonicus* Latham, 1790, *Numenius phaeopus variegatus* (Scopoli, 1786), *Ciconia episcopus* (Boddaert, 1783) (in error?)

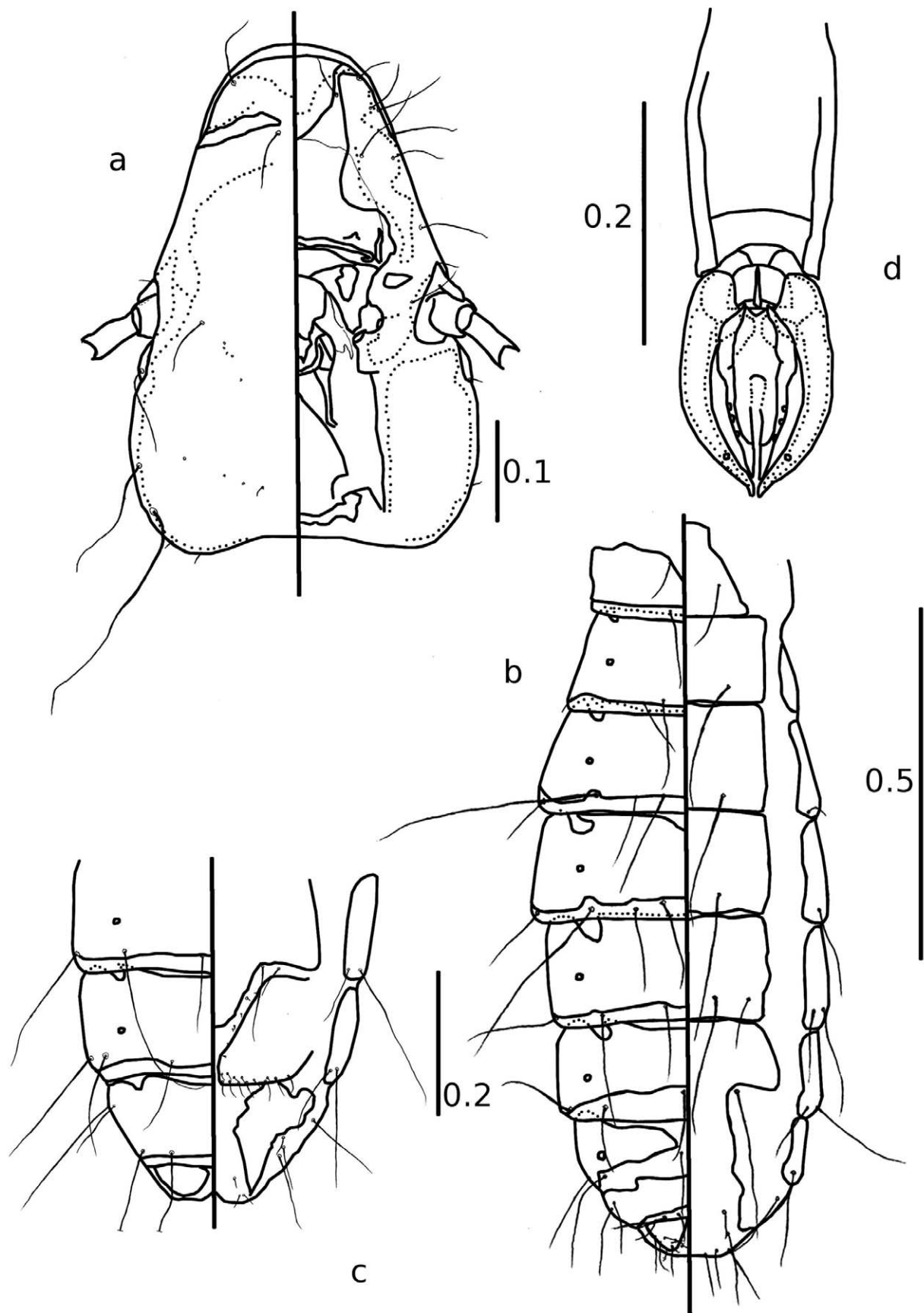
**Diagnosis:** Overall very pale. Head narrows anteriorly (Fig. 23a). Hyaline margin comparatively broad. Marginal carina interrupted or vague anteriorly, anterior to the dorsal preantennal suture present only as a pair of dark dorsal lines between the AS1 and AS2, and a pair of small ventral “islands”. Dorsal anterior suture quite narrow and interrupted medially. Ventral anterior plate broad, with a pointed, but irregular, posterior margin, and augmented by a central thickening. Lateral nodi well developed. AVS2 and AVS3 more or less aligned, and both markedly posterior to ADS (in material from *N. ph variegatus* all three sets are aligned). Marginal temporal carina narrow.

Pterothorax with rounded posterior margin.

Abdomen slender, usually with subparallel lateral sides (Fig. 23b). Ventral setae on segment II positioned at middle of sternite, or slightly anterior to the middle (in material from *N. ph variegatus*). Paratergal plates narrow anteriorly, but broaden posteriorly, and with narrow dark border markings in males. Antero-lateral ends of tergites pointed in segments III–IV, rounded in V–VIII. Sublateral indentation broad, but variable. Tergal bars in segments IV–V sometimes nearly reach the anterior-lateral end of the tergite, but never form proper tergal heads. Tergites very pale, except laterally where they are as darkly coloured as other species. This pale area overlaps with the gap between the paratergal plate and the sternite.

Female genital lobes with 7–8 posterior marginal setae, 5 sub-marginal setae, and 7 median marginal setae (Fig. 23c). Parameres slender and gently curved, with a ventral aperture on distal fourth (Fig. 23d). Lower endomere dark brown or black, in clear contrast to the other parts of the genitalia, which are more yellow. Basal apodeme also darker than parameres and mesomere, but not nearly as dark as the lower endomere. Mesomere elongated distally, with a bulge in the distal half, associated with three pairs of lateral microsetae, usually visible only as three pairs of apertures. Dorsal fingers convergent and extending anteriorly of the ventral blades. Lower

endomere broad and wide, attached to the apodemal bridge by a narrow triangle. Apodemal bridge clearly defined both anteriorly and posteriorly.



**FIGURE 23.** *Lunaceps numenii phaeopi* A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

**Nymphs:** Ventral carina rounded. Dorsal preantennal suture broad and clearly defined. Abdomen hard to assess due to transparency, but seems slender.

**Discussion:** The populations of *Lunaceps* on *N. phaeopus phaeopus*, *N. phaeopus variegatus*, and *N. arquata* are almost identical genetically (Gustafsson and Olsson, 2012), but can be distinguished morphologically. Until a more thorough study has been made of the *Lunaceps* from species of *Numenius*, we prefer to keep these three populations, as well as that of *N. madagascariensis*, as subspecies of the same species. The two populations from *N. phaeopus* ssp. are genetically identical, and are here synonymised.

*Lunaceps numenii phaeopi* is a very slender subspecies, with a head that is typically narrow in the preantennal area. The paleness of this subspecies, more than anything, sets it apart from the other subspecies. This is especially noticeable in the head, where the various dark markings are starkly contrasted with what appears to be an almost white centre, but also in the abdomen of many specimens (especially females). The pale area of the tergites overlap with the gap between the sternite and the paratergal plates, which gives the whole abdomen a very pale, almost striped, appearance, making the subspecies easily recognisable even in a stereomicroscope.

*Lunaceps numenii phaeopi* is quite similar to the nominate subspecies, but is more slender, and with different male genitalia, where the mesomere abruptly narrows at about mid-length in *L. numenii phaeopi*, but more gradually in *L. numenii numenii*. The distal ends of the mesomere are also broader and blunter in *L. numenii numenii*. In *L. numenii phaeopi* there is a colour difference between the lightly coloured mesomere and parameres, and the darkly coloured lower endomere and basal apodeme, with the former being even darker. The same contrast can be found in some specimens of *Lunaceps numenii madagascariensis* ssp. nov.

Other than the subspecies of *L. numenii*, *L. n. phaeopi* is perhaps most similar to *L. hopkinsi*, but it lacks the intermediate pair of macrosetae of abdominal segment III of *L. hopkinsi*; there are some other differences in the relative sizes of abdominal setae, but these are often hard to assess without large samples. For instance, the sublateral setae of abdominal segment IV are longer and more slender in *L. hopkinsi*, and thus more similar to the median ones, whereas the same setae in *L. numenii phaeopi* are much shorter.

No significant differences have been found between the material from *N. phaeopus phaeopus* and *N. phaeopus hudsonicus* (cf. Timmermann, 1954a). Specimens from *N. phaeopus variegatus* (formerly *Lunaceps numenii oliveri*) are generally larger and paler than those from other host subspecies, and with slight differences in head setal arrangement; females often have fewer posterior marginal setae. Nevertheless, Gustafsson and Olsson (2012) showed that these populations are genetically identical to those of the nominate host subspecies, and the two louse populations are synonymised again in this paper (as in Hopkins and Clay, 1952; Keirans, 1967). *Lunaceps oliveri* was not mentioned by Timmermann (1954a).

Timmermann (1954a) noted that the holotype male of *L. trimaculatus* agreed well with *L. numenii phaeopi* in its measurements, and synonymised both under the assumption that *L. trimaculatus*, from a stork, was a straggler. Piaget's (1880) illustration is quite similar to *L. numenii numenii*, in that it appears to lack any elaborate structures in the preantennal area, and the lateral and sublateral setae of the abdomen are long, however it could also be said to be similar to *L. numenii phaeopi* or other *Lunaceps* from *Numenius*. We follow Timmermann (1954a) in regarding *L. trimaculatus* as a junior synonym of *L. numenii phaeopi*.

**Etymology:** From *phaeo* = dusky and *pūs* = foot. Named after the host, which can be separated from other curlews by a number of characters, of which the colour of the legs is not the most prominent one. *Lunaceps oliveri* was named after W. R. B. Oliver (1883–1957) of the Dominion Museum, Wellington, and one of the leaders of the expedition to the Kermadec Islands during which the original material was collected.

#### **Material examined:**

Ex *Numenius phaeopus*

♀27, ♂24, Ireland, September 1937, Meinertzhagen Collection 10580 (NHML). ♀4, ♂3, Maldives: North Male Atoll, 6 February 1957, BM 1957-283 (NHML). ♀18, ♂18, United Kingdom: Wales: Bardsey Island, 13 May 1953, BM 1980-40 (NHML). ♀24, ♂26, United Kingdom: Shetlands, August 1939, Meinertzhagen Collection 13616 (NHML). ♀6, ♂5, United Kingdom: Scotland: Hebrides: South Uist, September 1953, Meinertzhagen Collection 20223, BM1953-658 (NHML). ♀2, ♂2, n#2, Cameroon [as "French Cameroons"]: Louala, June 1959, BM 1960-295 (NHML). ♂1, France: Brittany: Ouessant [as "Ushant"], April 1935, Meinertzhagen Collection 3415 (NHML). ♀12, ♂7, Egypt, May 1936, Meinertzhagen Collection 4715 (NHML). ♀1, ♂1, Madagascar: Maroantsetra, January 1964 (NHML). ♀1, ♂1, Ireland, August 1934, Hopkins Collection (NHML). ♀1, ♂1,

France: Brittany: Ouessant [as “Ushant”], April 1935, Hopkins Collection (NHML). ♀1, ♂3, Iceland, August 1934, Meinertzhagen Collection 2090 (NHML). ♀1, ♂1, Slovenia: Ljubljana, 6 April 1954, BM 1958-661 (NHML). ♀6, ♂9, Norway, DM 2585 (MONZ). n#3, Philippines: Batangas: Calatagan, 11 September 1966, 6E-0602 (NHML). n#3, Philippines: Batangas: Calatagan, 12 September 1966, 6E-0699 (NHML). ♂3, Russia: Kobyayskiy: North of Yakutsk: Lena River, 4 June 1975, Sb. Yanaja? [Slide text in Russian] (MFN). n#1, Sweden: Öland: Ottenby Bird Observatory, 4 August 2007, ID: 299, Band number: 7066021, D. Gustafsson (SMNH).

*Ex Numenius phaeopus hudsonicus*

♀10, ♂7, United States: California, Meinertzhagen Collection 12732 (NHML). ♀1, Canada: British Columbia: Vancouver Area: Lulu Island, 30 April 1941, BM 1956-302 (NHML). ♀1, United States: California, May 1912, Meinertzhagen Collection 4422 (NHML). ♀1, ♂1, Brazil: Bahia: Ilha Madre Deus Est, February 1933, Hopkins Collection (NHML). ♀2, ♂2, Canada: Manitoba, Meinertzhagen Collection 11150 (NHML). ♀3, ♂1, United States: Virginia: Cobbs Island, 24 May 1881 (MONZ).

*Ex Numenius phaeopus variegatus*

♀1, ♂2, Indonesia: North Borneo: Tanjung Aru Beach, 21 September 1960, B; 1964-163 (NHML). ♀1, ♂1, Philippines: Batangas: Calatagan, 12 August 1965, BM 1968-86 (NHML). ♀10, ♂10, New Zealand: Taranaki: Puniha: Paeora Rol, 25 October 1979 (MONZ). ♀1, Australia: Western Australia: 80 Mile Beach: Near Anna Plains Cattle Station, 21 November 2008, ID: 933a-1, Band number: 083-23776, D. Gustafsson (SMNH).

*Ex Ibidorhyncha struthersii* (possibly straggler):

♀1, N. Tibet, 1798 (NHML).

*Ex Limosa lapponica* (possibly straggler):

♂1, England, L. Harrison Collection (NHML).

Material of uncertain status:

*Ex Numenius phaeopus*:

♂1 (genitalia only), United Kingdom: Shetlands: Lerwick, J. Waterston Collection, BM 1930-232 (NHML).

***Lunaceps paschalis* Timmermann, 1954**

(Fig. 24a–d; Table 1)

*Lunaceps paschalis* Timmermann, 1954a: 630

*Lunaceps paschalis* Timmermann; Malcomson, 1960: 191

*Lunaceps limosella paschalis* Timmermann; Keirans, 1967: 114

*Lunaceps limosella paschalis* Timmermann; Emerson, 1972: 94

*Lunaceps paschalis* Timmermann; Price *et al.*, 2003: 196

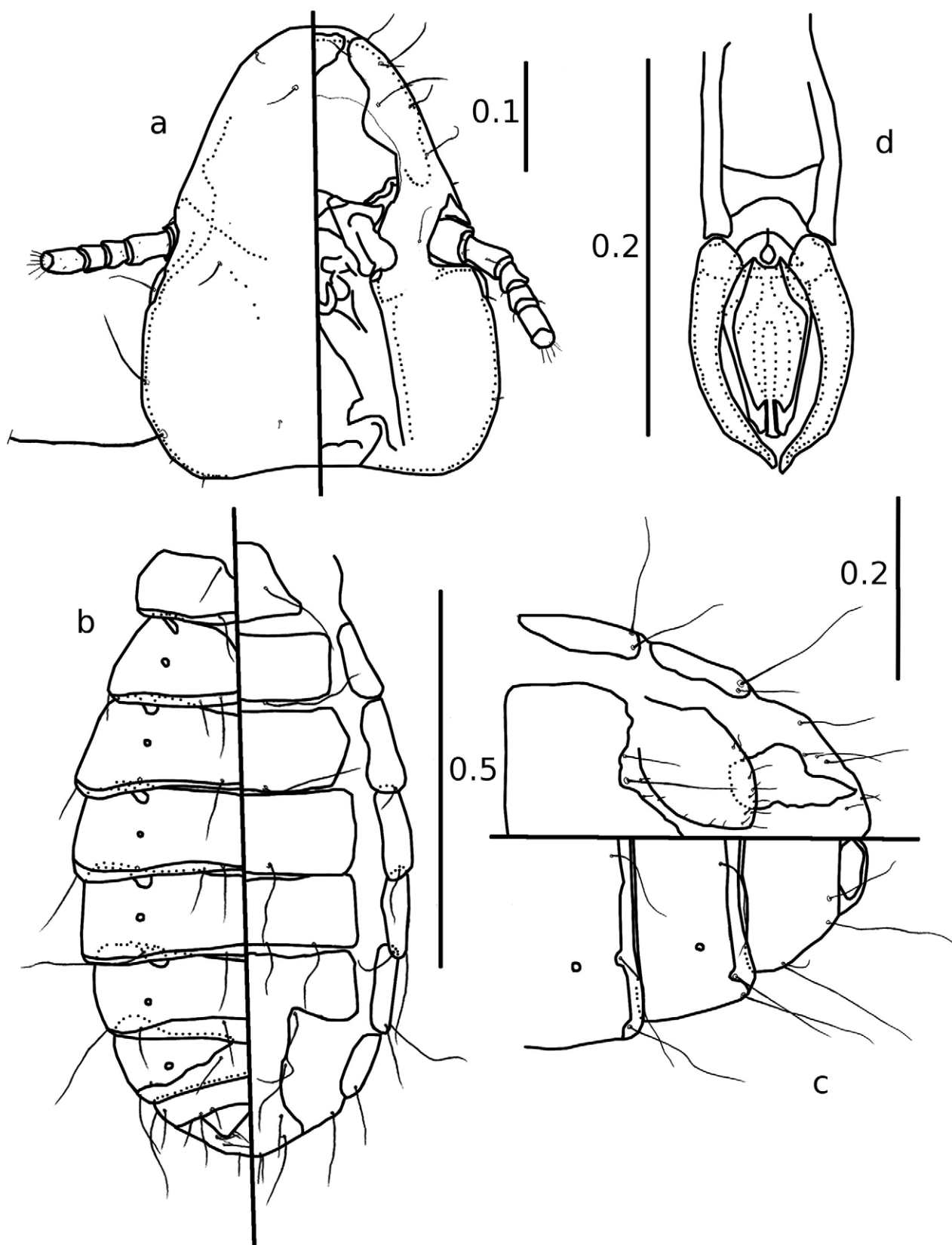
**Type host:** *Limosa haemastica* (Linnaeus, 1758)

**Diagnosis:** Head roughly triangular (Fig. 24a). Marginal carina very narrow, and evenly thick around the head; anterior portion on marginal carina may be virtually invisible. Ventral anterior plate small, often with indistinct posterior margin. Dorsal preantennal suture and dark preantennal band missing entirely. Lateral nodi small and pointed. Marginal temporal carina weak and narrow. Pre- and post-ocular nodi reduced. Head setae weak. AVS2 and AVS3 aligned, but somewhat posterior to the ADS.

Antero-median indentation of tergites variable. Some males with only II–IV indented, whereas others have II–VII. In females, the type has II–VII indented, whereas other females have only II–VI indented. Female dorsal intermediate setae on segment VII approximately as long as the median setae. Female dorsal intermediate setae on segment IX medium size and slender. Paratergal plates very broad and those on segments IV–VII overlap (Fig. 24b). Tergal heads missing, or may be present as a very narrow bar. Males have a submedian pair of setae on the ventral side of segment VIII.

Female genital lobes with 6 posterior marginal setae, 7 sub-marginal setae, and 5–6 median marginal setae (Fig. 24c). Sub-marginal setae quite stout, but short. Parameres gently rounded, parameral heads not elongated

(Fig. 24d). Mesomere elongated, and bulging slightly in distal half. Lower endomere narrow. Apodemal bridge vaguely delimited, and appears narrow.



**FIGURE 24.** *Lunaceps paschalis* A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. Sublateral setae of segments IV, V, and VIII missing in slide. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

**Discussion:** Without a dorsal preantennal suture, and with a similar shape of the head and abdomen, *L. paschalis* is morphologically close to *Rotundiceps cordatus* (Osborn, 1896), originally described from the same host (Edwards, 1952). However, *R. cordatus* has an even rounder abdomen, a much wider heart-shaped head, and different pterothoracic and marginal temporal chaetotaxy. The male genitalia are similar in the two species and the genera are probably closely related, but the mesomere of *R. cordatus* is constricted in the middle, and the parameres are more angular, with almost pincer-like distal ends. There is also a great difference in size, *R. cordatus* being at least 0.84 mm longer and twice as broad in the head and abdomen (Osborn, 1896; Timmermann, 1954a). Edwards (1952) stated that he could find no *R. cordatus* on the type host, *Limosa haemastica*, but plenty on *L. fedoa*, and apparently transferred the type host status to this species in his description of *Rotundiceps*.

Kellogg and Mann's (1912) description of *Nirmus lucidus* states that the species is close to *R. cordatus* (as "*N. cordatus*"). Emerson (1972) synonymised *N. lucidus* under *R. cordatus*, and Price *et al.* (2003) followed his decision. *Nirmus lucidus* is also longer and wider than most *Lunaceps*, but supposedly more slender than *R. cordatus*. Timmermann (1954a) mentions *N. lucidus* only in the summary, where he mentions that this species was "described from [the] wrong host", but does not elaborate.

Whether or not *N. lucidus* and *R. cordatus* are synonymous, and whether or not either, or both, of these are the same as *L. paschalis*, the existence of two similar species on the same host highlights the need for further louse collection from *Limosa haemastica*, as well as from *L. fedoa*, in order to establish whether *N. lucidus* is distinct from *R. cordatus*. Edwards' (1952) remarks that the niche differentiation of the two genera is not necessarily helpful, as I have observed *Lunaceps* sp. on the head of fumigated birds several times (unpublished data).

Within *Lunaceps*, *L. paschalis* is probably closest to *L. limosae*, which also lacks the dorsal preantennal suture, but differs from this species in the preantennal setal arrangement, and in the details of the genitalia of both sexes. The ventral submedian setae on abdominal segment VIII, found only in males, is unique within the genus. The preantennal setal arrangement is similar to that of *L. clayae*, but *L. paschalis* differs in the male genitalia and the female genital setal arrangement, and in the lack of a dorsal preantennal suture. However, only a very small number of have been examined.

**Etymology:** The term *paschalis* is apparently a form of "Pascal", meaning "Easter child". Whether this is the intended etymology and, if so, what this refers to, is not mentioned by Timmermann (1954a).

#### **Material examined:**

*Ex Limosa haemastica* (sometimes as *Limosa hudsonica*)

Holotype: ♀1, United States: Texas: Brownsville, 20 October 1891, J. Waterston Collection, BM 1930-232 (NHML).

Allotype: ♂1, United States: Texas: Brownsville, 4 May 1890, J. Waterston Collection BM 1930-232 (NHML).

Paratypes: ♀3, United States: Texas: Brownsville, 4 May 1890, J. Waterston Collection. BM 1930-232 (NHML). ♀2, ♂1, United States: Dakota, 25 May 1924, DM 16317 (MONZ). ♂1, United States: Texas: Brownsville, 20 October 1891, J. Waterston Collection, BM 1930-232 (NHML).

#### ***Lunaceps proximus* (Blagoveshtchensky, 1948)**

(Fig. 25a–d; Table 1)

*Degeeriella proxima* Blagoveshtchensky, 1948: 279

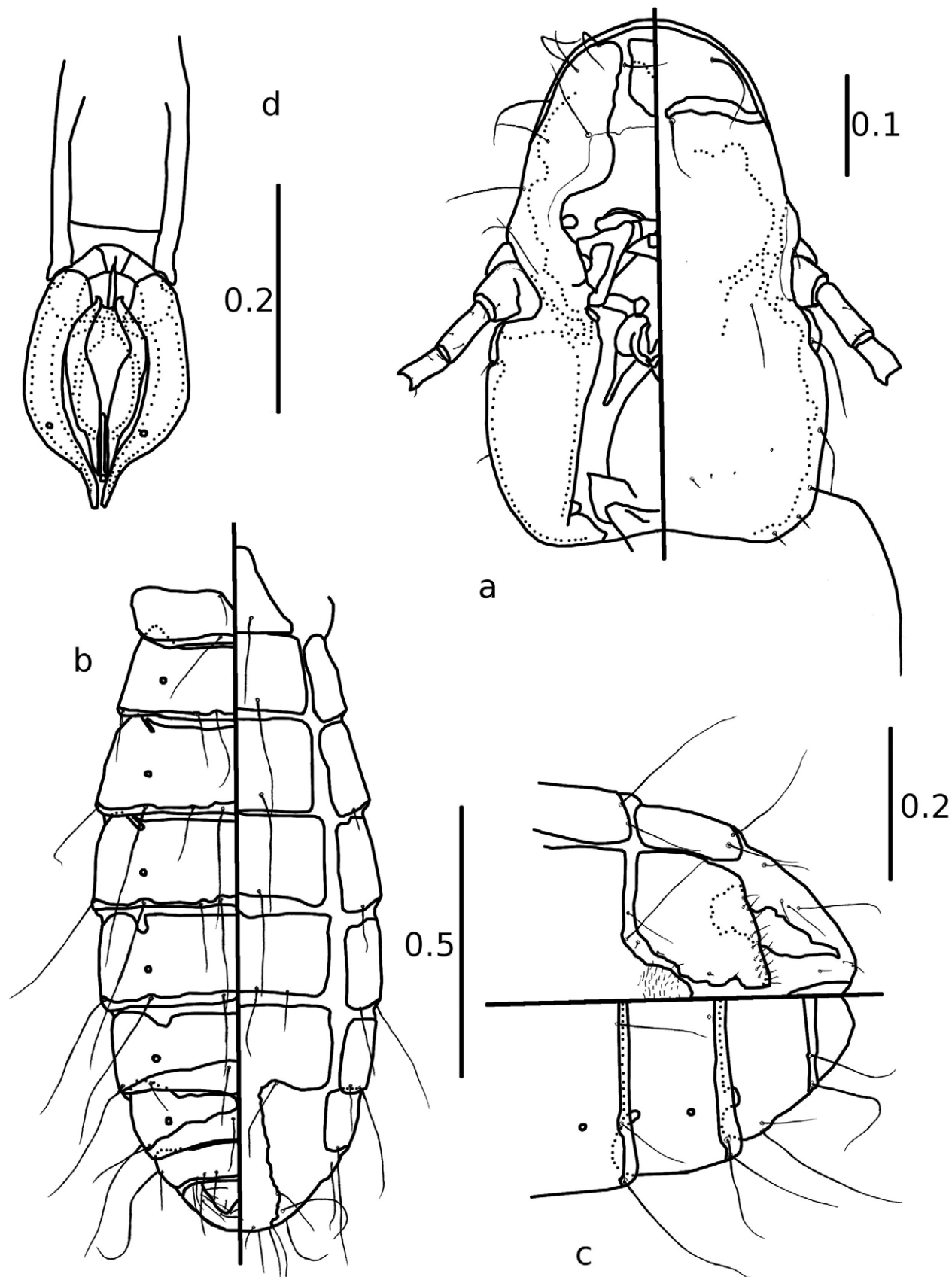
*Lunaceps proximus* (Blagoveshtchensky); Hopkins and Clay, 1952: 202

*Lunaceps proximus* (Blagoveshtchensky); Timmermann, 1954a: 635

*Lunaceps numenii proximus* (Blagoveshtchensky); Price *et al.*, 2003: 196

**Type host:** *Numenius tenuirostris* Vieillot, 1817

**Diagnosis:** Head elongated (Fig. 25a). Marginal carina weakly coloured anterior to the dorsal preantennal suture, except a small marking associated with the ventral anterior plate and a pair of dark carina "islands" between the AS1 and AS2. Dorsal preantennal suture interrupted medially, and bulges to envelop the apertures of the ADS. Ventral anterior plate with parallel lateral sides in anterior half, but tapering quickly posteriorly. Lateral nodi pronounced, but often very slender. Dark preantennal band narrow. AVS2 and AVS3 aligned, but markedly posterior to ADS. OS and MTS1 long, but not approaching MTS3.



**FIGURE 25.** *Lunaceps proximus* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. Dorsal median setae on segment IX missing in all available specimens. D) Male genitalia.

Pterothorax with flat or sometimes slightly rounded posterior margin.

Abdominal tergite II narrow. Abdomen broad and suboval (Fig. 25b). Paratergal plates broad and square-shaped. Antero-lateral end of tergite III pointed and without sublateral indentation. In segments IV–V, sublateral indentation is present, but very narrow and can be hard to see. Antero-lateral end of tergites grow progressively blunter more anteriorly. Median dorsal setae very long, similar to intermediate setae. Female lateral setae on segment III long and slender, not thorn-like. Setae on male segment X/XI very long.

Female genital lobes with 10–11 posterior marginal setae, which are thick at base but tapers, 6 thorn-like submarginal setae, and 5–6 median marginal setae (Fig. 25c). Parameres uniquely shaped, with two abrupt bends, and a distal elongation, making the tips parallel or subparallel (Fig. 25d). Small ventral aperture in distal fourth. Mesomere reminiscent of a short-necked violin, extended distally. Lower endomere semicircular and connected to apodemal bridge by narrow triangle.

**Discussion:** Males are clearly separated from all males of all other *Lunaceps* species by the shape of the parameres and mesomere. Females similar to *L. numenii* and *L. hopkinsi*, but the shape of the ventral anterior plate is more rectangular. The extremely high number of posterior marginal setae is also distinctive within the genus.

The only known host, the Slender-billed Curlew *Numenius tenuirostris*, is now very rare (IUCN, 2011a). No nests of this bird has been found since 1924 (Ushakov, 1925), and it was believed to be extinct when it disappeared from wintering grounds in Morocco. However, occasional sightings are still made both on potential breeding grounds (Bojko and Nowak, 1996) and on migration stop-over points (e.g., Nankinov, 1991), suggesting that the valiant efforts to find their elusive breeding grounds (Danilenko *et al.*, 1996; Boere and Yurlov, 1998) may be looking in the wrong places. Whether or not *Lunaceps proximus* and other lice endemic to this host survive is at present an open question.

**Etymology:** From *proxim* = the nearest. It is unclear what this refers to.

#### Material examined:

Ex *Numenius tenuirostris*

♂3, Italy, January 1918, Meinertzhagen Collection (4424) (NHML). ♀3, ♂2, Russia, Meinertzhagen Collection (11017) (NMHL). ♀1, [Collection data not given in slide], 3058b (MFN).

#### *Lunaceps rileyi* Timmermann, 1954a

(Fig. 26a–d; Table 1)

*Lunaceps rileyi* Timmermann, 1954a: 635

*Lunaceps rileyi* Timmermann; Malcomson, 1960: 190

*Lunaceps numenii rileyi* Timmermann; Emerson, 1972: 95

*Lunaceps numenii rileyi* Timmermann; Price *et al.*, 2003: 196

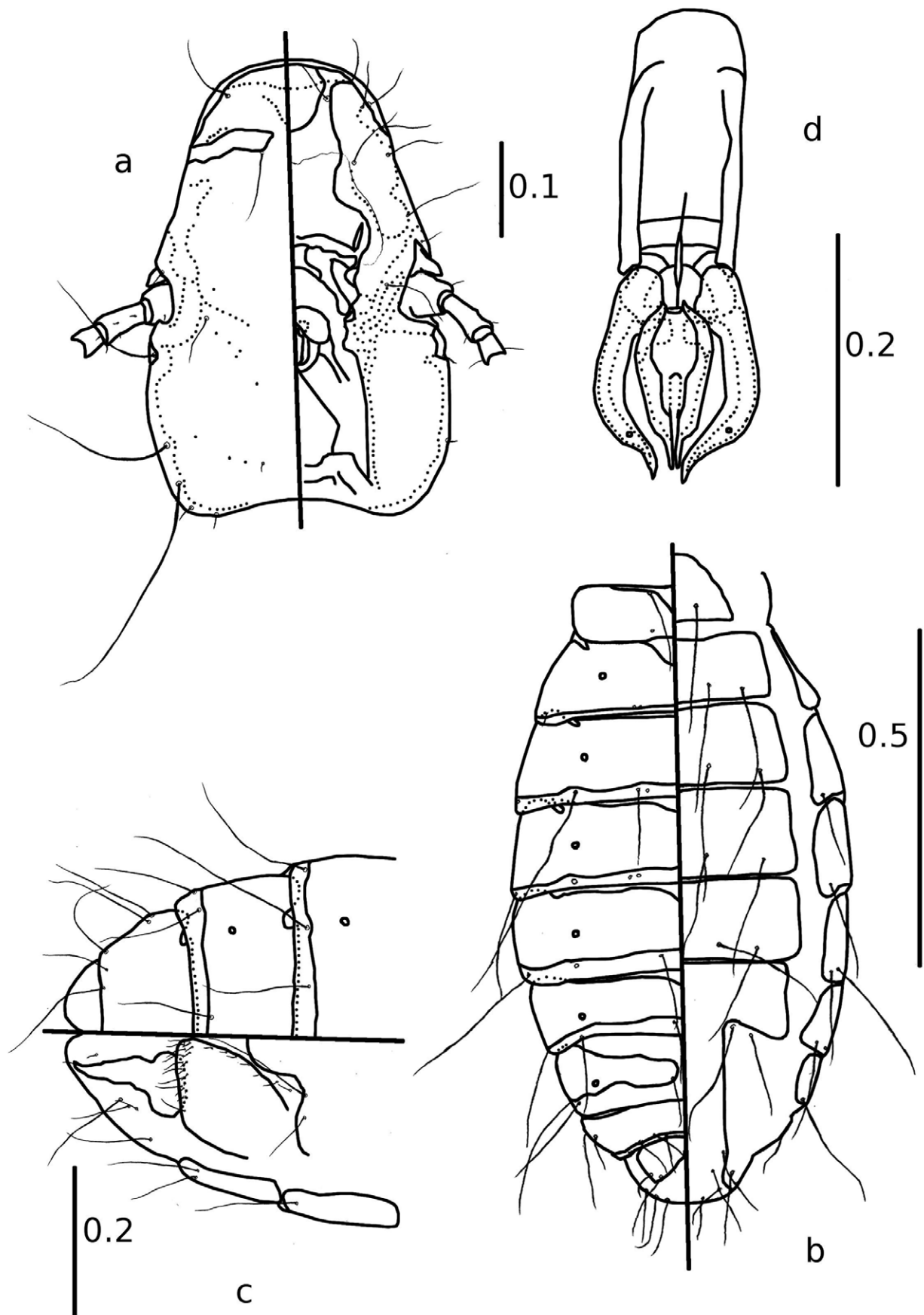
**Type hosts:** *Numenius borealis* (Forster, 1772)

**Diagnosis:** Head ovoid (Fig. 26a). Marginal carina interrupted laterally and antero-laterally, but present at the ventral anterior plate, which it augments, bulging posteriorly and extending across the ventral preantennal suture. One portion of this extension seems to reach the dorsal side. Dorsal preantennal suture appears to be missing in type, but is present in other material, where it is narrow, widely interrupted medially, and not bulging to envelop the apertures of the ADS. Lateral nodi broad and blunt. Dark preantennal band very short and thin, appearing as a pair of triangular darkening near the lateral nodi. AVS2 anterior to AVS3, at least in males and some females, but both pairs of setae markedly posterior to ADS.

Pterothorax with rounded posterior margin.

Setal arrangement of abdomen very distinct in both sexes (Fig. 26b). Ventral setae of segment II often far anterior, aligned with the anterior dorsal pair. Males with two pairs of ventral setae on segments IV–V and VII (sometimes also in III). Females with an extra submedian pair of ventral setae in segment VI. Anterior margin of segments II–III in males and II–IV in females with narrow wedge-shaped median indentation. Dorsal median and submedian setae of males positioned very close together. Paratergal plates broad. Sublateral indentations clearly visible only in segments III–V, but shallow and narrow. No tergal heads, and the anterior-lateral end of most tergites blunt and broad.





**FIGURE 26.** *Lunaceps rileyi* A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. Many dorsal setae as well as second sublateral dorsal setae of segment VII, missing in all available slides. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Female genital lobes rounded with 8 posterior marginal setae, 8 sub-marginal setae, and 7 median marginal setae (Fig. 26c). Sub-marginal setae thorn-like and quite long. Parameres with abrupt turn about one third from distal tip, and another, in the opposite direction, roughly one fifth from distal tip, with ends approaching parallel (Fig. 26d). One ventral aperture visible in distal fourth of paramere. Ventral side of mesomere triangular, but whole structure with very bulging lateral sides and elongated, very slender, distal end. No visible setae or apertures along lateral margins of mesomere. Dorsal mesomeral fingers stout, and divergent anteriorly, forming small hooks. Mesomeral groove wide and quite deep, square-shaped, but with rounded corners. Lower endomere broad and semicircular, connected to apodemal bridge by broad triangle. Apodemal bridge diffuse. Basal apodeme relatively short.

**Discussion:** Like *L. lissmanni*, the male has an extra pair of setae on the ventral side of several abdominal segments, and the parameres are abruptly bent at approximately two fifths from the distal end. These characters are sufficient to separate males of *L. rileyi* from all other *Lunaceps*, except *L. lissmanni*. The shape of the head and the width of the abdomen separates *L. rileyi* from *L. lissmanni*, and in general the abdominal setae are more slender in *L. rileyi* than in *L. lissmanni*. Females can be separated from all other species, except *L. lissmanni*, by the number of sub-marginal setae, but differ from *L. lissmanni* by the number of abdominal setae.

The host, the Eskimo Curlew *Numenius borealis*, is now believed to be extinct (IUCN, 2011b), and it is unlikely that any species of louse endemic to this bird species has survived.

**Etymology:** Named in honour of Norman Denbigh Riley (1890–1979), Keeper of the Department of Entomology of the (then) British Museum (Natural History) in London.

#### **Material examined:**

Ex *Numenius borealis*

Holotype: ♂1, USA, Meinertzhagen Collection 12546 (NHML).

Allotype: ♀1, USA, Meinertzhagen Collection 12546 (NHML).

Paratypes: ♀4, ♂3, USA, Meinertzhagen Collection 12546 (NHML).

Non-types: ♂2, Barbados, 5 September 1886, J. Waterston Collection BM 1930-232 (NHML).

#### ***Lunaceps rothkoi* sp. nov.**

(Fig. 27a–d; Table 1)

*Lunaceps falcinellus* Timmermann, 1954a: 627 (partim)

*Lunaceps falcinellus* Timmermann; Price *et al.*, 2003: 196 (partim)

*Lunaceps falcinellus* Timmermann (“Clade 5”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)

**Type host:** *Tryngites subruficollis* (Vieillot, 1819)

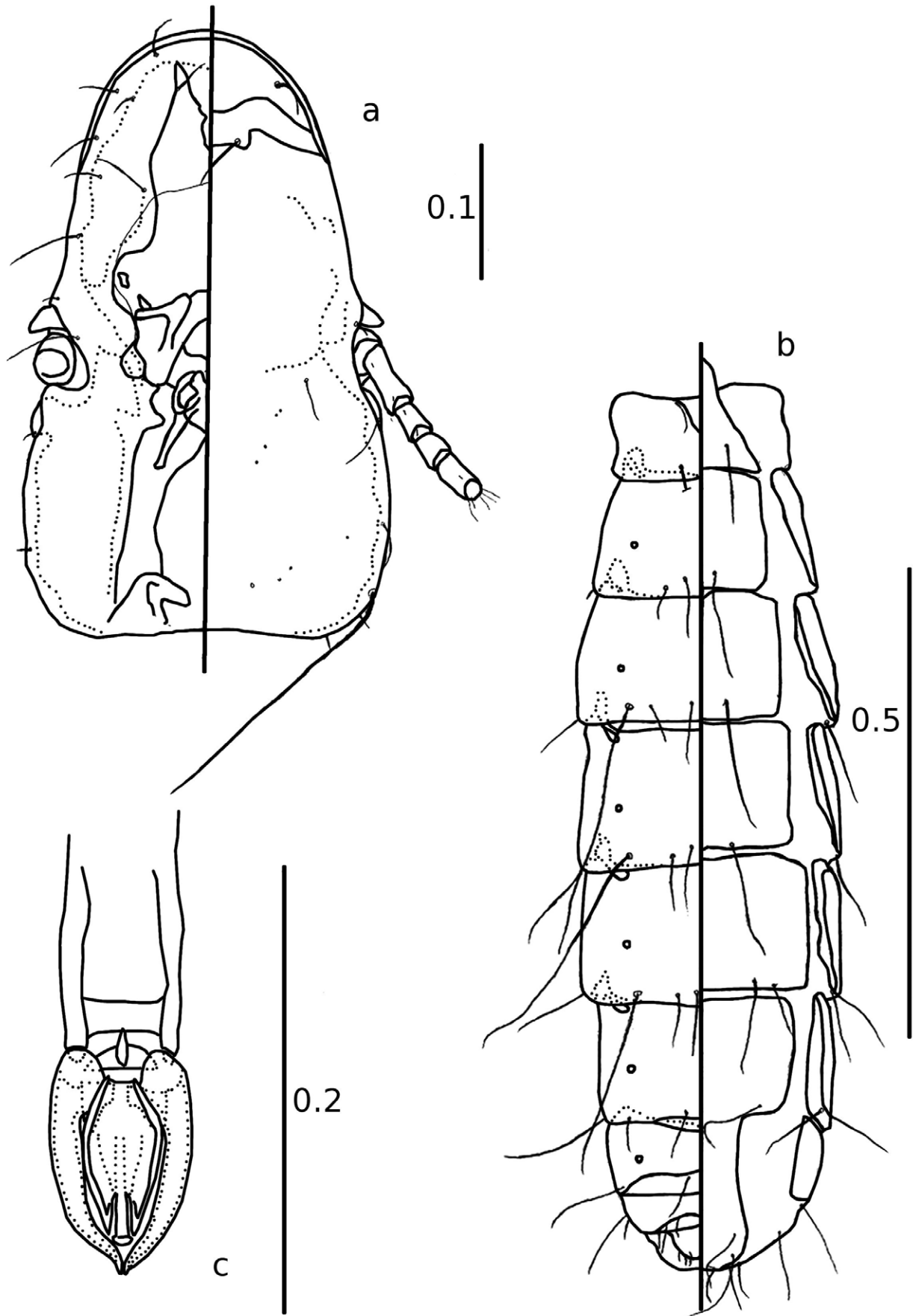
**Diagnosis:** Head oblong, almost rectangular (Fig. 27a). Hyaline margin thin. Marginal carina clearly demarcated around the preantennal area, and broad anteriorly, but it becomes more transparent at the dorsal preantennal suture. Ventral anterior plate triangular and elongated, reaching well posterior to the dorsal preantennal suture. AVS32 slightly anterior to AVS3, but both markedly posterior to ADS. Dorsal preantennal suture wide, and enveloping the apertures of the ADS. Lateral nodi well developed. Dark preantennal band present only as a pair of dark marks near the lateral nodi.

Paratergal plates narrow (Fig. 27b). In males, the tergal heads are large, almost triangular, and are often more lightly coloured than the paratergal plates. In females available, the tergal heads are smaller.

Parameres slender and gently bent (Fig. 27c). Mesomere roughly trapezoid dorsally. Lower endomere crescent-shaped. Apodemal bridge diffuse.

**Discussion:** The *Lunaceps* population on *Tryngites subruficollis* was first separated from *L. falcinellus*, the species it was previously placed with, by DNA (Gustafsson and Olsson, 2012). All available females have their genitalia obscured by gut content, and the number of genital setae and other features are unknown.

Similar to *L. holophaeus*, but can be separated from this species by the shape of the dorsal preantennal suture, which reaches the lateral sides of the head, and by the shape of the head. Male genitalia similar to those of *L. incoenis*, with which it is closely related (Gustafsson and Olsson, 2012: Fig. 1, 2), but the shape of the head and the ventral anterior plate clearly separate them. The dorsal anterior plate is elongated and tapering posteriorly, unlike all other *Lunaceps* species.



**FIGURE 27.** *Lunaceps rothkoi* sp. nov. A) Female head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Male genitalia.

One slide of material from *Bartramia longicauda* has a mixture of Phthiraptera species; The middle specimen (a female) appears to be *L. rothkoi* sp. nov. but, if there are truly *Lunaceps* on *Bartramia*—which is possible, given its supposed phylogenetic position (Hebert *et al.*, 2004; Thomas *et al.*, 2004a; Baker *et al.*, 2007; Gibson, 2010)—more material would be needed to ascertain if the specimen on this slide is *L. rothkoi*, and if *L. rothkoi* occurs on both hosts naturally. The two hosts use similar stop-over spots and wintering grounds.

**Etymology:** Named in honour of the painter Mark Rothko (1903–1970), whose painting *Saffron* (1957) is somewhat reminiscent of the colouration and distribution of dark and light areas in the head of the holotype. He is also one of the first author's favourite painters.

#### Material examined:

*Ex Tryngites subruficollis* (synonym: *Tringites rufescens*)

Holotype: ♂1, Canada, USA (NHML).

Paratypes: ♀1, ♂5, Canada, USA (NHML).

Non-types: ♂2, Barbados, R. S. M., 6 October 1888, J. Waterston Collection BM 1930-232 (NHML). ♂1, Barbados, R. S. M., 6 October 1888, J. Waterston Collection, BM 1930-232 (NHML). ♀1, Sweden: Öland: Ottenby Bird Observatory, 12 October 2007, ID: 500, Band number: 3536135, D. Gustafsson, (SMNH).

Material of uncertain status due to poor condition:

*Ex Tryngites subruficollis*:

♀2 (abdomen only), Barbados, R. S. M., 6 October, 1888, J. Waterston Collection, BM 1930-232 (NHML).

#### *Lunaceps schismatus* sp. nov.

(Fig. 28a–d; Table 1)

*Nirmus actophilus* Kellogg and Chapman, 1899: 78 (partim)

*Degeeriella actophila* (Kellogg and Chapman); Peters, 1933: 71 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Timmermann, 1954a: 628 (partim)

*Degeeriella holophaea* (Nitzsch); Blagoveshtchensky, 1958: 376

*Lunaceps* sp. Keirans, 1967: 116

*Lunaceps* sp. I Fedorenko, 1968: 73

*Lunaceps holophaeus actophilus* (Kellogg and Chapman); Emerson, 1972: 93 (partim)

*Lunaceps* sp. “ab *Calidris a. alpina*” Eichler and Hackman, 1973: 92

*Lunaceps actophilus* (Kellogg and Chapman); Cabot, 1975: 146 (partim)

*Lunaceps* sp. [1] *ex Charadrius hiaticula* Cabot, 1975: 146 (uncertain)

*Lunaceps* sp. [2] *ex Calidris alpina* Cabot, 1975: 146 (uncertain)

*Lunaceps* sp. Haarløv, 1977: 38

*Lunaceps* sp. Rékási and Kiss, 1977: 105

*Lunaceps nereis* Timmermann; Forrester *et al.*, 1995: 28 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Price *et al.*, 2003: 196 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Palma and Jensen, 2005: 56 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Rékási, 2006:183 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Dik *et al.*, 2010: 869 (partim)

*Lunaceps actophilus* (Kellogg and Chapman); Inci *et al.*, 2010: 215 (partim)

*Lunaceps actophilus* (Kellogg and Chapman) (“Clade 8”); Gustafsson and Olsson, 2012: 94 (Figs. 1, 2)

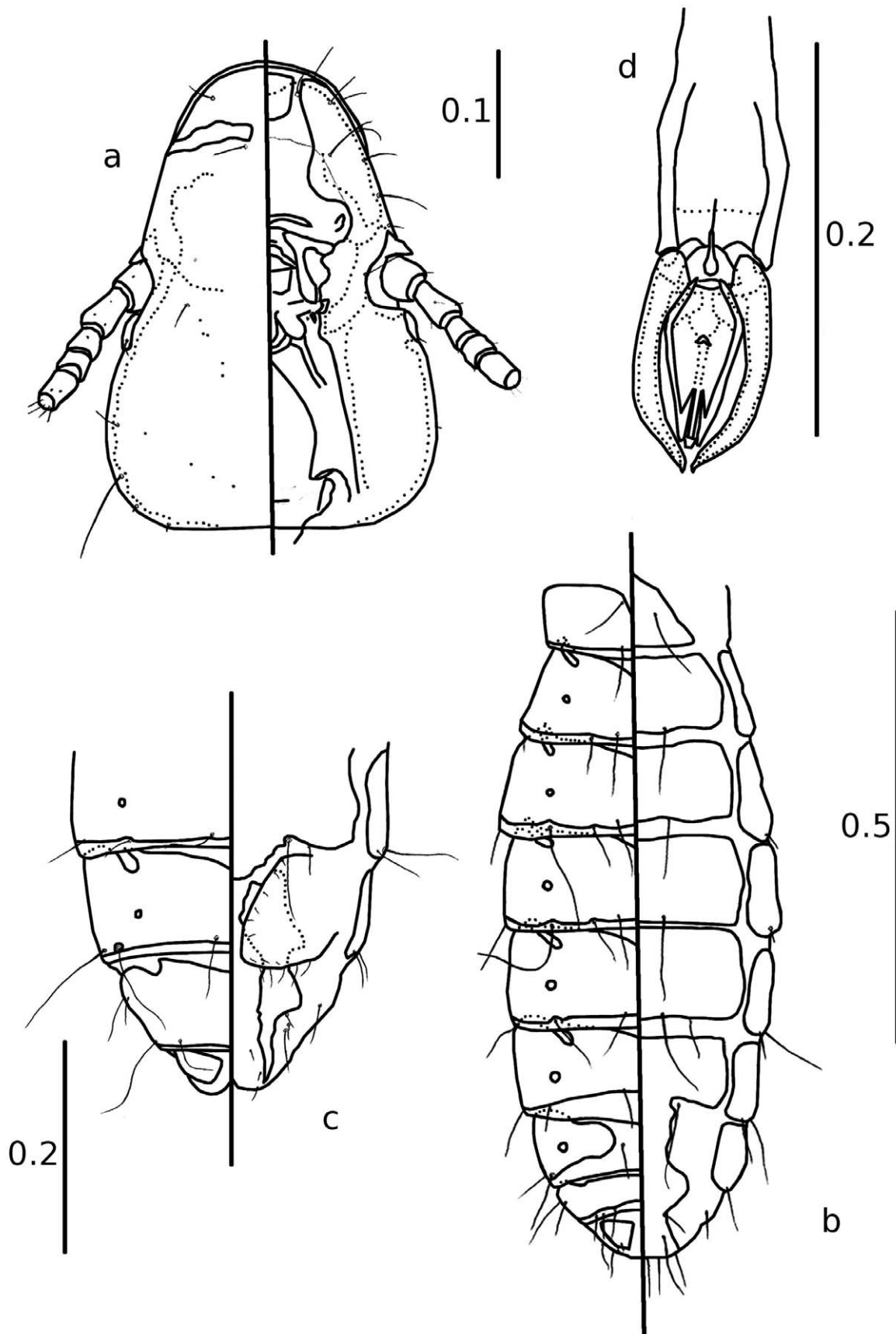
**Type host:** *Calidris alpina alpina* (Linnaeus, 1758)

**Other hosts:** *Calidris alpina schinzii* (C. L. Brehm and Schilling, 1822), *Calidris alpina sakhalina* (Vieillot, 1816).

**Diagnosis:** Marginal carina continuous and broad along anterior margin of head (Fig. 28a). Dorsal preantennal suture not continuous across head, but interrupted medially by a bridge. Ventral anterior plate quite large and roughly quadratic, with rather straight anterior margin. Dark preantennal band narrow. AVS3, AVS2 and ADS more or less aligned.

Abdominal tergites II–III, sometimes also IV, in males and II–V, sometimes also VI, in females with wedge-shaped median indentation of the anterior margin, reaching more than a third of the tergite width. Paratergal plates

broad (Fig. 28b). Broad tergal bars lead to narrow, blunt tergal heads, which may be re-entrant in segment III of males. Ventral median setae of segment II positioned on anterior margin of segment.



**FIGURE 28.** *Lunaceps schismatus* sp. nov. A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.

Female genital lobes with 5 posterior marginal setae, 3 sub-marginal setae, and 6 median marginal setae (Fig. 28c). Parameres gently curved (Fig. 28d). Lower endomere semicircular. Mesomere slender, with straight sides, very narrowed distally. Apodemal bridge diffuse anteriorly.

**Discussion:** Similar to *L. actophilus*, with which it was previously considered conspecific, following Timmermann (1954a). However, the colouration of the abdomen is different, and there are slight differences in the genitalia of both sexes, as well as in the partial divisions of the tergites. *Lunaceps actophilus* and *Lunaceps schismatus* are well separated genetically (Gustafsson and Olsson, 2012).

The shape of the male genitalia is similar to that of *L. drosti* or *L. nereis*, although the mesomere is not as stout in *L. schismatus* as in those species. The anterior margin of the tergites are partially divided in more segments in females of *L. schismatus* than in other species, but some females of *L. nereis* have the same pattern. The shape of the head is different from *L. nereis* but virtually identical to that of *L. drosti* or *L. actophilus*.

No differences have been found among specimens from the three studied host subspecies, which is concordant with the recent diversification of these subspecies (Wenink *et al*, 1996).

**Etymology:** From *schism* = a split or division. Refers both to the partial division of the tergites and to the interruption of the dorsal preantennal suture.

### Material examined:

*Ex Calidris alpina* (synonym: *Erolia alpina*)

Holotype: ♂1, Mauritania: Banc d'Arguin: Iwik, 1 December 2002 (MONZ).

Paratypes: ♀8, ♂6, Mauritania: Banc d'Arguin: Iwik, 1 December 2002 (MONZ).

Non-types: ♀1, ♂1, Canada: British Columbia: Vancouver Area: Lulu Island, 18 November 1953, BM 1956-302 (NHML). ♀1, Ireland: Tipperary: Banaghen, 19 December 1946 (NHML). ♀2, ♂2, Ireland: County Dublin: Rogerstown, 6 January 1940, Hopkins Collection (NHML). ♀1, ♂3, United Kingdom: England: Kent: Stoke, 31 July 1965, BM 1966-165 (NHML). ♀2, ♂2, United Kingdom: Shetlands: Fair Isle, 13 August 1955, BM 1955-795 (NHML). ♀2, ♂1, United Kingdom: England: Lines: Gibraltar Port, 13 September 1950, BM 1980-40 (NHML). ♀1, ♂1, Denmark: Faroes Islands: Sumla, 1 April 1998 (MONZ). ♀4, ♂2, Germany, K.C. Emerson Collection (OSU). ♀1, ♂1, United States: Alaska: Anchorage, 22 May 1962, K.C. Emerson Collection (OSU). ♀1, ♂1, India: Rajasthan: Bharatpur, 1 January 1970, K.C. Emerson Collection (OSU). ♀1, India: Tamil Nadu: Tanjavur: Point Calimere, K.C. Emerson Collection (OSU). ♀23, ♂11, United Kingdom: England: Lines, December 1936, Meinertzhagen Collection 8132-8141 (NHML). ♀1, ♂3, Estonia, August 1934, Meinertzhagen Collection 1496, 1562 (NHML). ♀1, ♂2, United Kingdom: Scotland: Dornoch Firth, December 1934, Meinertzhagen Collection 2348 (NHML). ♀3, ♂2, United Kingdom: England: Kent, April 1934, Meinertzhagen Collection 686, 690, 692 (NHML). ♀9, ♂13, Morocco, October 1938, Meinertzhagen Collection 11964-66 (NHML). ♂1, [Collection data not given on slide], 20067b (MFN). ♀5, ♂1, [Collection data not given on slide], 139d, e, i, p, s, y (MFN). ♀1, [Collection data not given on slide], 438 (MFN). ♀1, Sweden: Öland: Ottenby Bird Observatory, 10 May 2007, ID: 10a-1, Band number: 3531149, D. Gustafsson (SMNH). ♂1, Sweden: Öland: Ottenby Bird Observatory, 10 May 2007, ID: 10a-s, Band number: 3531149, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 25 May 2007, ID: 104-1, Band number: 3531458, D. Gustafsson (SMNH). ). ♀1, Sweden: Öland: Ottenby Bird Observatory, 25 May 2007, ID: 104-2, Band number: 3531458, D. Gustafsson (GNM). ♀1, Sweden: Öland: Ottenby Bird Observatory, 11 May 2007, ID: 22-1, Band number: 3531151, YIO-P-01162, D. Gustafsson (YIO). ♂1, Sweden: Öland: Ottenby Bird Observatory, 11 May 2007, ID: 22-2, Band number: 3531151, D. Gustafsson (GNM).

*Ex Calidris alpina schinzii*

♀8, ♂16, United Kingdom: Scotland: Hebrides: North Uist, September 1941, Meinertzhagen Collection 14622-25 (NHML). ♀2, Ireland: County Sligo, 22 September 1939, 279 (NHML). ♂1, United Kingdom: Wales: Bardsey Island, 13 May 1953, BM 1980-40 (NHML). ♀3, ♂2, Ireland: County Sligo: Lislary, 22 September, 1938, BM 1980-40 (NHML). ♀1, ♂1, United Kingdom: Wales: Glamorganshire: Aberthaur, 25 August 1935, BM 1980-40 (NHML). ♂1, United Kingdom: England: Monmouthshire: Peterstone Wentlooge, 2 May 1935, BM 1980-40 (NHML). ♀2, ♂4, Morocco, October 1938, Meinertzhagen Collection 11945 (NHML). ♀1, ♂4, United Kingdom: England: Norfolk, February 1934, Meinertzhagen Collection 284 (NHML). ♀2, ♂2, United Kingdom: England: Sussex, December 1934, Meinertzhagen Collection 2264 (NHML). ♀1, Sweden: Öland: Ottenby Bird

Observatory, 22 May 2007, ID: 84-1, Band number: 3531402, D. Gustafsson (SMNH). ♂1, Sweden: Öland: Ottenby Bird Observatory, 22 May 2007, ID: 84-2, Band number: 3531402, D. Gustafsson (GNM). ♂1, Finland: Oulu: Lumijoki, ID: 1640-1, Band number: KT3150, V.-M. Pakanen (SMNH). ♀1, Finland: Oulu: Lumijoki, ID: 1640-2, Band number: KT3150, V.-M. Pakanen (GNM).

*Ex Calidris alpina sakhalina*

♀13, ♂20, United States: California, March 1939, Meinertzhagen Collection 1290 (NHML). ♂1, Japan: Miyagi Prefecture: Sendai: Watari: Tori-no-Umi, 25 October 2008, ID: 774, Band number: 3E21763, YIO-P-01163, D. Gustafsson (YIO). ♀1, Japan: Miyagi Prefecture: Sendai: Watari: Tori-no-Umi, 26 October 2008, ID: 782, Band number: 3E21769, YIO-P-01164, D. Gustafsson (YIO). ♀1, Japan: Miyagi Prefecture: Sendai: Watari: Tori-no-Umi, 30 October 2008, ID: 800, Band number: 3E21781, YIO-P-01165, D. Gustafsson (YIO).

*Ex Vanellus vanellus* (possibly straggler):

♂1, [No collection data given on slide], 333b (MFN).

*Ex Limicola falcinellus* (possibly straggler):

♀1, Poland: Piaseczno: [Konstancin-]Jeziorna, 27 August 1954, Jurnyk, 42/ac/2-1 (MFN).

*Ex Calidris minuta* (possibly straggler):

♀1, [Collection data not given in slide], 7832i (MFN).

*Ex Stercorarius parasiticus* (possibly stragglers):

♀10, ♂7, [Collection data not given on slide], 20074a–q (MFN).

Material of uncertain status due to poor condition:

*Ex Calidris alpina*

♂1, United Kingdom: England: Yorkshire: Spurn Bird Observatory, 20 September 1952, BM 1980-40 (NHML). ♀2, [collection data not given on slide], 3003k, s (MFN).

*Ex Arenaria interpres* (possible stragglers)

♀1, ♂1, [Collection data not given on slide], 7555b, d (MFN).

***Lunaceps superciliosus* sp. nov.**

(Fig. 29a–d; Table 1)

*Lunaceps* sp. [*ex Calidris acuminata*] Palma, 1999: 380

*Lunaceps incoenis* (Kellogg and Chapman); Price *et al.*, 2003: 196 (partim)

*Lunaceps incoenis* (Kellogg and Chapman) (“Clade 3”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)

*Lunaceps* sp. *ex Calidris subminuta* (“Clade 3”); Gustafsson and Olsson (2012): 94 (Figs. 1, 2)

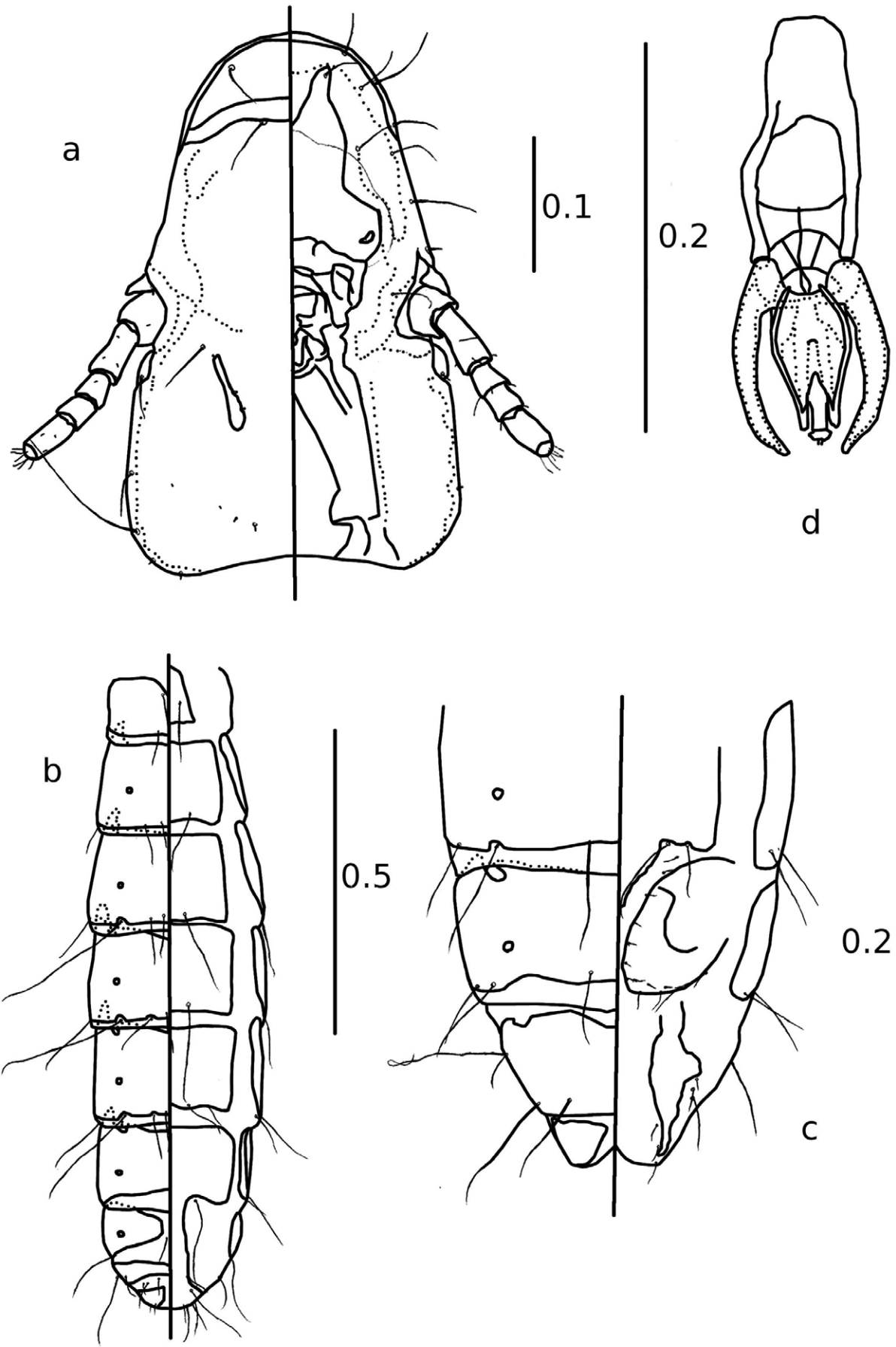
**Type host:** *Calidris acuminata* (Horsfield, 1821)

**Other host:** *Calidris subminuta* (Middendorff, 1853)

**Diagnosis:** Head elongated (Fig. 29a). Marginal carina weakly coloured anterior to DSMS. Dorsal preantennal suture broad, enveloping the apertures of the ADS. Lateral nodi small or non-existent. Ventral anterior plate triangular. AVS3 anterior to AVS2, but both posterior to ADS. In many males, a short, narrow suture arises from near PNS and goes medially and posteriorly. This character is generally missing in material from *C. subminuta*.

Male paratergal plates of segments IV–VI relatively broad and of equal width except posterior fourth (Fig. 29b). Re-entrant heads long and broad. Tergal bars quite narrow.

Female genital lobes with 5 posterior marginal setae, 4 sub-marginal setae, and 6 median marginal setae (Fig. 29c). Parameres slender with small aperture at distal third. Basal apodeme narrow, and apodemal bridge not clearly defined anteriorly (Fig. 29d). Apodemal triangle weakly coloured.



**FIGURE 29.** *Lunaceps superciliosus* sp. nov. A) Male head, dorsal and ventral views. B) Male abdomen, dorsal and ventral views. C) Female terminalia, dorsal and ventral views. D) Male genitalia.



**Discussion:** *Lunaceps superciliosus* is genetically distinct (Gustafsson and Olsson, 2012), but often virtually impossible to separate from *L. incoenis* and *L. falcinellus* on morphological characters. The small dorsal suture arising near the PNS is unique within *Lunaceps*, but is not reliable, as it is missing in material from *C. subminuta* and in all females, and is difficult to see in many males collected from *C. acuminata*. The tergal re-entrant heads are generally longer and most distinct in *L. superciliosus* than in the other two species, but there is as always some variation. The head shape approaches that of *L. rothkoi*, but tapers markedly anterior to the antennae. The pronounced re-entrant tergal heads, as well as the shape of the dorsal preantennal suture, easily separates it from *L. holophaeus*.

We separate this species primarily based on genetic data and the presence of the small suture near the PNS on some males examined. A larger series of specimens may reveal further diagnostic characters. No significant differences have been found between the material from the two host species.

**Etymology:** From *supercilium* = eyebrow. Refers to the two small sutures near the PNS, which are reminiscent of eyebrows, and unique within the genus.

#### Material examined:

##### Ex *Calidris acuminata*

Holotype: ♂1, New Zealand: Kermadec Islands: Raoul Island, 17 October 1982, M. Fraser (MONZ).

Paratypes: ♀9, ♂11, New Zealand: Kermadec Islands: Raoul Island, 17 October 1982, M. Fraser (MONZ).

Non-types: ♀1, New Zealand: Lake Ellesmore, January 1929, E. F. Stead, C Mu Av 4596, R. C. L. Pilgrim Collection (MONZ). ♀8, ♂4, Papua New Guinea: Western District: Wando, October 1969, I.L. Owen 691014/12c, Brit Mus. 1970-381 (NHML). ♀2, ♂1, Papua New Guinea: Western District: Wando, October 1969, I.L. Owen 691016/17b, Brit Mus. 1970-381 (NHML). ♂1, Papua New Guinea: Western District: Wando, October 1969, I.L. Owen 691014/16b, Brit Mus. 1970-381, (NHML). ♀1, Japan: Miyagi Prefecture: Sendai: Watari: Tori-no-Umi, 26 October 2008, ID: 784a-1, Band number: 4A20704, YIO-P-01166, D. Gustafsson (YIO). ♀1, Australia: Western Australia: 80 Mile Beach, Near Anna Plain Cattle Station, 15 November 2008, ID: 871a-1, Band number: 042-61414, D. Gustafsson (SMNH).

##### Ex *Calidris subminuta*

♀1, Australia: Western Australia: Broome Area: Lake Eda, 23 November 2008, ID: 1451a-1, Band number: 036-48094, D. Gustafsson (SMNH). ♀1, Australia: Western Australia: Broome Area: Lake Eda, 23 November 2008, ID: 1451a-2, Band number: 036-48094, D. Gustafsson (GNM). ♀1, Australia: Western Australia: Broome Area: Lake Eda, 23 November 2008, ID: 966a-1, Band number: 036-48095, YIO-P-01167, D. Gustafsson (YIO).

#### *Lunaceps wilsoni* Carriker, 1956, nomen dubium

*Lunaceps wilsoni* Carriker, 1956: 76

*Lunaceps wilsoni* Carriker; Price *et al.*, 2003: 196

**Type host:** *Charadrius wilsonia wilsonia* Ord, 1814

**Other host:** *Charadrius wilsonia beldingi* (Ridgway, 1919)

**Discussion:** The only *Lunaceps* described from a *Charadrius* plover. No material was studied, but Carriker's (1956) description would place this species near *L. incoenis*, as the re-entrant heads of the tergites are clearly visible in his drawing. Carriker's measurements fit well with those of *L. incoenis* and their genitalia are also similar.

The species was described from a single male—though a second male is mentioned in a footnote—and a partial drawing, lacking the middle segments of the abdomen is included. The shape of the “acetabular bars of the 2nd pair of coxae” is the only distinct character of Carriker's (1965) description, however similar structures can be seen in many other species, and this seems to be an artefact of mounting caused by the bending of the lateral edges of the dorsal thoracic plates.

While only a study of the original material can establish whether *Lunaceps wilsoni* is really a distinct species or not, the low number of known individuals, and their similarity to other species makes the status of *L. wilsoni* uncertain. It is likely to be synonymous with *L. incoenis*, originating on one of its hosts, but an origin from either *C. bairdii* or *C. fuscicollis* cannot be excluded.

**Etymology:** Named after the host species, which in turn is named in honour of Alexander Wilson (1766–1813), ornithologist and painter, who published the book series *American Ornithology* (1808–1814).

**Material examined:**

None. Attempts have been made to gain access to the holotype, but they have been fruitless.

***Species incerta sedis***

We consider the following populations impossible to place in any known species of *Lunaceps* with any confidence. The material studied is minimal, and the differences between these populations and named populations above are often slight. All three populations are similar to either *L. incoenis* or *L. falcinellus*, but we prefer to keep them separate and undescribed until more samples and data are collected, considering that morphological differences are, in any case, minimal between *L. incoenis*, *L. falcinellus*, and *L. superciliosus*. None of these populations were studied genetically by Gustafsson and Olsson (2012).

***Lunaceps incerta sedis 1***

**Host:** *Calidris melanotos* (Vieillot, 1819)

**Discussion:** Most similar to *L. incoenis*, but differs from this species by the number of median marginal setae of the females (7 instead of 6), and by the general appearance of the paratergal plates, but very few individuals have been studied. The AVS3 is often positioned anterior to the AVS2, as in *L. incoenis*. Gustafsson and Olsson (2012) found that *Lunaceps* from hosts that prefer inland freshwater stop-over and wintering grounds (e.g., *L. superciliosus*) differ from those that prefer more coastal stop-over and wintering habitat (e.g., *L. falcinellus*). Therefore, we here place the population on *C. melanotos*, which prefers inland habitats (Piersma, 2003) as *incerta sedis*, awaiting additional specimens and its inclusion in a genetic study.

**Material examined:**

Ex *Calidris melanotos* (synonym: *Pisobia maculata*)

♀2, ♂2, locality unknown, 6 September 1958, Coll: R. Connell, BM 1960-443 (NMHL). ♀3, Trinidad and Tobago: Trinidad: Laventille Swamp, 13 November 1959, TRUL 3570, BM 1961-606 (NHML). ♀1, ♂1, United States: Texas: Corpus Christi, F.B. Armstrong, E. Mus. O.S. and F.D.G., J. Waterston Collection BM 1930-232 (NHML).

***Lunaceps incerta sedis 2***

**Host:** *Calidris temminckii* (Leisner, 1812)

**Discussion:** Material from *Calidris temminckii* was not available for genetic studies by Gustafsson and Olsson (2012), but is morphologically almost identical to *Lunaceps* from *C. minuta*, and was placed in *L. incoenis* by Timmermann (1954a). It differs from *L. falcinellus*, where material from *C. minuta* is now placed, in having somewhat broader border markings on the paratergal plates, however as *L. falcinellus* and *L. superciliosus* are also virtually identical, but differ genetically, we find that this morphological similarity may not be indicative of relationships between *L. falcinellus* and the population on *C. temminckii*, especially as *C. temminckii* prefers inland habitats (Piersma, 2003). Until this population has been studied genetically, we prefer not to place it with any species.

**Material examined:**

Ex *Calidris temminckii* (synonym: *Erolia temminckii*)

♀15, ♂17, Sudan, December 1947, Meinertzhagen Collection (16883) (NHML).

***Lunaceps incerta sedis 3***

**Host:** *Eurynorhynchus pygmeus* (Linnaeus, 1758)

**Discussion:** *Lunaceps* from *Eurynorhynchus pygmeus* is similar to *L. falcinellus*, but the only known specimens are noticeably paler than material from the other hosts of *L. falcinellus*, tend to have fewer posterior marginal setae in the female genitalia, and the lateral sides of the abdominal segments are more divergent posteriorly, making them much broader. However, as all studied material is from one collection event, we cannot rule out that these differences are due to the preservation process.

*Eurynorhynchus pygmeus* is among the rarest of the *Luniceps* hosts (IUCN, 2011c), and the *Luniceps* population, if distinct from other *Luniceps* species, should perhaps be considered as endangered as its host, and should ideally be included in conservation programs for the hosts, unless the recent population decline in *E. pygmeus* (e.g., Zöckler *et al.*, 2010) has already driven its lice to extinction. Only one louse species (*Haematopinus oliveri* Mishra and Singh, 1978) is included in the IUCN Red List (IUCN, 2011); however, others have been suggested (Perez and Palma, 2001; Whiteman and Parker, 2005), and many have already been lost in recent times (Mey, 1990; Gompper and Williams, 1998; Mey, 2005).

**Material examined:**

Ex *Eurynorhynchus pygmeus*

♀8, ♂4, China (NHML).

**Species transferred to other genus**

***Quadriceps parabolicus* Eichler [in Niethammer], 1953, comb. nov.**

(Fig. 30a–e; Table 1)

*Luniceps parabolicus* Eichler [in Niethammer], 1953: 270

*Luniceps parabolicus* Eichler; Hopkins and Clay, 1955: 183

*Luniceps parabolicus* Eichler; Price *et al.*, 2003: 196

**Type host:** *Vanellus resplendens* (Tschudi, 1843)

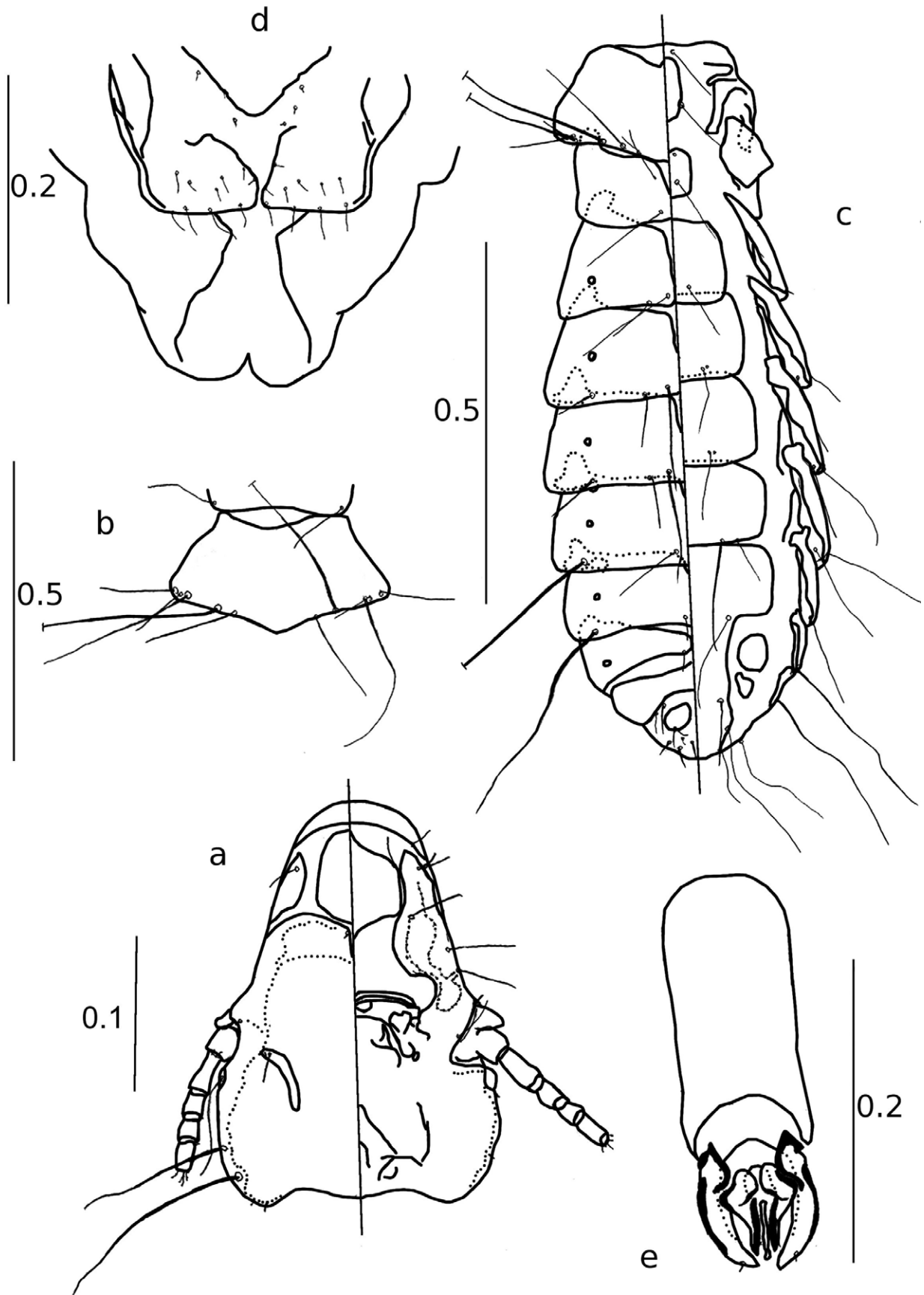
**Diagnosis:** Hyaline margin extensive and spatulate, enclosing the marginal carina laterally (Fig. 30a). Dorsal anterior plate clearly defined, and roughly quadrate, but with posterior edge rounded. Marginal carina interrupted laterally by the dorsal preantennal suture, as well as anteriorly by the ventral preantennal suture. Ventral carina clearly defined. On dorsal side, the post-marginal carina turns inwards and forms a broad band across the head, which is interrupted medially by a thin posterior extension of the dorsal preantennal suture. Ventrally, this inward extension of the post-marginal carina is thinner, and follows the anterior edge of the dorsal extension. No transverse suture. PNS associated with a long occipital suture bending medially and posteriorly. OS long and quite broad; POS short and positioned just posterior to the post-ocular nodus. MTS1 and MTS3 macrosetae, all others MTS microsetae. Gular plate indistinct, but usually triangular, and only vaguely sclerotized internally.

Pterothoracic dorsal plate indented anteriorly; more obvious in males (Fig. 30b, c). Setal arrangement in both sexes similar to that of *Luniceps* species.

Tergal plates divided medially in segment II–III of both sexes (Fig. 30c). In females, tergites of segments IV–VII divided partially, and those of segments VIII–IX at least indented anteriorly. In males, tergite IV divided partially, and tergite V weakly indented. Paratergal plates present in segments II–VIII and apparently variable, but always quite narrow, and lacking overlap with sternites. Tergal heads pointed and re-entrant. In segments II–III, these re-entrant heads sometimes shaped as coarse hooks. Male abdominal segments VIII–IX have subsidiary ventral plates.

Female genital lobes with 4 posterior marginal setae, 4 sub-marginal setae, and 5 median marginal setae (Fig. 30d). Similar to *Luniceps*, but the sub-marginal setae are positioned further from the posterior margin, and the lobes are of different shape. Laterally, the lobes are thickened. Parameres are broad and together form a circle surrounding the mesomere almost completely (Fig. 30e). One small seta is positioned on the outward side of each paramere, about one fifth of the length from the distal tip. Parameral heads complex, with median thickening and an anteriorly protruding point. Basal endomere missing. Mesomere pointed and narrow distally. Lower apodeme simple, with no lateral thickenings (*contra* Eichler, 1953).

**Discussion:** Timmermann (1957) suggested that *L. parabolicus* might be a straggler, but in all likelihood, it is identical to *Quadriceps hoplopteri inca* Timmermann (1954b). Eichler's original description is almost singularly unhelpful, stating only that "Die neue Art ist durch den vorgezogenen Clypeus von *L. actophilus* deutlich unterschieden" ("The new species can be clearly separated from *L. actophilus* by the advanced clypeus"; our translation), with a reference to two illustrations.



**FIGURE 30.** *Quadraceps parabolicus* nov. comb. A) Female head, dorsal and ventral views. B) Female pterothoracic margin and pteronotum. C) Male pterothorax and abdomen. D) Male genitalia. E) Female terminalia, dorsal and ventral views.

However, the illustration of the head seems to be a mixture of the dorsal and the ventral side, and any dorsal characters of the clypeus that would separate it from *L. actophilus* are crowded out. In the characters that can be seen, there are some that would place it in *Lunaceps* and some that would place it outside *Lunaceps*. For instance, the anterior end seems to show a crescent-shaped anterior dorsal plate, separated by a narrow suture, as in a typical *Lunaceps*. On the other hand, the POS is positioned posterior to the eye, not on it as in *Lunaceps* and there is a pair of structures that bend medially from the site of the lateral nodi that is unlike anything in *Lunaceps*. The significance of any of these characters is difficult to assess from Eichler's drawing.

The second drawing, of the male genitalia, is more straightforward, as it is dissimilar to those found in *Lunaceps*, but almost identical to Timmermann's (1954b) drawings of the genitalia of *Q. hoplopteri incai*. The lower endomere, present in all *Lunaceps*, is missing in both Eichler's and Timmermann's drawings, and although the parameres are shorter and blunter in Eichler's drawings than in Timmermann's, the shape of the mesomere with its contorted form is more or less identical, as is the shape of the basal apodeme.

The matter is made clear in the type material and the series located at PIPeR, all of which are specimens of a *Quadriceps* (Fig. 30). Some preliminary studies at the NHML have shown that their *Q. hoplopteri incai* specimens are virtually identical to the *Lunaceps parabolicus* material studied. It is also dissimilar to that of other South American lapwings, precluding the possibility of contamination. We therefore conclude that *Lunaceps parabolicus* Eichler, 1953, is identical to *Quadriceps hoplopteri incai* Timmermann, 1954b, which would make them synonyms, with Eichler's name having priority. Price *et al.* (2003) listed *Q. incai* as a full species, and this species should now be known as *Quadriceps parabolicus* (Eichler, 1953).

**Etymology:** *para* = beyond, beside, and *bole* = a throw. It is unclear from Eichler's (1953) short description and drawings exactly what this refers to, but may refer to the parameres, which have a somewhat parabolic shape.

#### Material examined:

Note on Eichler's type series. In his description, Eichler (1953) states that the holotype is slide 3896b and the allotype is slide 3896c. No other slides are mentioned in the description. This does not correspond to the labels on the slides. Slide 3698b and 3698c are both labelled "Paratypoid", whereas slide 3698e is labelled "Allotypoid". Slide 3698d has been labelled before, but the label has fallen off, and only the glue outline remains. Handwritten on this slide is "Holotypus?". We here assume that the text of the description has precedence, and that specimen 3896b is the holotype, despite what it says on the slide. As specimen 3896c is also a male, this cannot be an allotype, and is here referred to as a paratype. The other three slides are here referred to as non-types, as they are not mentioned in the original description.

*Ex Vanellus resplendens* (synonym: *Ptiloscelys splendens*):

Holotype: ♂1, [Collection data not given on slide], 3896b (MFN).

Paratype: ♂1, [Collection data not given on slide], 3896c (MFN).

Non-type material: ♂3, [Collection data not given in slide], 3896a, d, e (MFN). ♀6, ♂6, Ecuador: Cotopaxi Province: 24 km W of Latacuya: Near Signiquingre, RC-712 (PIPeR).

These specimens was compared with material from the following species to ascertain what *Lunaceps parabolicus* is:

*Quadriceps hoplopteri ex Vanellus spinosus* (synonym: *Hoplopterus spinosus*)

♀12, ♂12, Uganda: Toro: Kaganya, 28 April 1944, Hopkins Collection BM1958-686 (NHML).

*Quadriceps hoplopteri incai ex Vanellus resplendens* (synonyms: *Ptiloscelus splendens* or *Ptilocelys* [sic!] *resplendens*)

Holotype: ♂1, Peru: Sta. Lucia, 24 April 1931, 2706, BM1954-596 (NHML).

Allotype: ♀1, Peru: Sta. Lucia, 24 April 1931, 2706, BM1954-596 (NHML). ♀2, ♂2, Peru: Jauja Province: Paca Pond, 2 June 1969, BM1975-308 (NHML).

*Quadriceps hoplopteri guimaraesi ex Vanellus chilensis lampronotus* (synonym: *Belanopterus chilensis lampronotus*)

Holotype: ♂1, Brazil: Pará: Fóy do Gurana [?], 2 December 1936, BM-1954-596 (NHML).

Allotype: ♀1, Brazil: Pará: Fóy do Gurana [?], 2 December 1936, BM-1954-596 (NHML).

*Quadriceps hasei ex Vanellus cayanus* (synonym: *Hoploscypterus cayanus*)

Holotype: ♂1, Brazil: Mato Grossoa: Rio Parana, 10 November 1939, BM1954-596 (NHML).

## Key to species of *Lunaceps*:

- 1) Lateral sides of abdominal segments with broad, colourless or weakly coloured paratergal plates. Tergal heads not or insignificantly re-entrant into preceding segment, or re-entrant only into segment II . . . . . 2
  - Lateral sides of abdominal segments with narrow, dark paratergal plates. Tergal heads re-entrant into preceding segment . . . 21
- 2) OS and MTS1 short and thin. Marginal carina more or less uninterrupted anterior to dorsal preantennal suture . . . . . 4
  - OS and MTS1 long and thick. Marginal carina interrupted or weak anterior to dorsal preantennal suture . . . . . 14
- 4) Tergal heads pointed in at least some segments beyond segment II . . . . . *L. enigmaticus* sp. nov.
  - Tergal heads rounded in all segments (may be pointed in segment II) . . . . . 5
- 5) Dorsal preantennal suture absent, or present only as a small kidney-shaped remain, anterior to the ADS . . . . . 6
  - Dorsal preantennal suture present . . . . . 7
- 6) Males with ventral submedian setae on abdominal segment VIII. AVS2 and AVS3 aligned, but markedly posterior to ADS . . . . . *L. paschalis*
  - AVS2, AVS3 and ADS all aligned . . . . . *L. limosae*
- 7) Dorsal preantennal suture does not reach lateral margins of head . . . . . *L. holophaeus*
  - Dorsal preantennal suture does reach lateral margins of head . . . . . 8
- 8) Ventral median setae of abdominal segment II in anterior half of sternite . . . . . 9
  - Ventral median setae of abdominal segment II in posterior half of sternite . . . . . 11
- 9) Males with dorsal submedian setae on abdominal segment VII. Females with dorsal intermediate setae of abdominal segment IX long and thick . . . . . *L. clayae*
  - Not as described above . . . . . 10
- 10) Hyaline margin missing or very narrow. Marginal carina narrow. Ventral anterior plate small and pointed in posterior margin . . . . . *L. nereis*
  - Not as described above . . . . . *L. schismatus* sp. nov.
- 11) Abdominal segments II-III (sometimes IV) markedly paler than more posterior segments, often approaching white in fresh material. Male tergites not indented anteriorly; in females only tergite II indented. Preantennal nodus with pale interior and narrow dark borders . . . . . *L. actophilus*
  - Not as above . . . . . 12
- 12) Dorsal preantennal suture continuous across head . . . . . *L. limosella*
  - Dorsal preantennal suture interrupted medially . . . . . 13
- 13) Ventral anterior plate triangular. AVS2 and AVS3 aligned. . . . . *L. drostii*
  - Ventral anterior plate square-shaped. AVS3 markedly posterior to AVS2 . . . . . *L. mintoni* sp. nov.
- 14) Parameres with two distinct bends. Distal ends more or less subparallel. Dorsal fingers of mesomere divergent. . . . . 15
  - Parameres with one or no distinct bend. Distal ends converging. Dorsal fingers of mesomere convergent. . . . . 17
- 15) Males with one pair of ventral setae on abdominal segments IV-VII. Females with one submedian setae on the ventral side of abdominal segment VI . . . . . *L. proximus*
  - Males with two pairs of ventral setae on abdominal segments IV-VII. Females with two submedian setae on the ventral side of abdominal segment VI . . . . . 16
- 16) Posterior marginal of pterothorax rounded, without median point. Ventral setae on abdominal segment II often aligned with anterior dorsal pair. Abdomen broad and rounded . . . . . *L. rileyi*
  - Posterior marginal of pterothorax with median point flanked by concave sides. Body slender . . . . . *L. lissmanni*
- 17) Parameres with one distinct bend . . . . . *L. kukri* sp. nov.
  - Parameres gently curved . . . . . 18
- 18) Dorsal intermediate macrosetae on abdominal segment III in both sexes . . . . . *L. hopkinsi*
  - No intermediate setae on abdominal segment III in either sex . . . . . *L. numenii* ssp. 19
- 19) Mesomeres narrowing slowly. Broad and long (> 2mm) . . . . . 20
  - Mesomeres narrowing suddenly. Slender, often very pale, and shorter (> 2mm) . . . . . *L. numenii phaeopi*
- 20) Mesomeral groove narrow and deep. . . . . *L. numenii madagascariensis* ssp. nov.
  - Mesomeral groove broad and shallow . . . . . *L. numenii numenii*
- 21) Abdomen very slender, with paratergal plates forming overlapping “rails” along the lateral margins. Spiracle openings overlaps with paratergal plates. Female genital lobes compressed and elongated posteriorly. Parameral heads almost square-shaped . . . . . *L. incoenis ex Calidris minutilla*
  - Not as described . . . . . 22
- 22) Head oblong, almost rectangular. Ventral anterior plate drawn out and tapering posteriorly . . . . . *L. rothkoi* sp. nov.
  - Head ovoid. Ventral anterior plate not tapering posteriorly . . . . . 23
- 23) Both lateral setae on abdominal segment IV long, reaching approximately half (or more) of tergite length. At least some males (not from *C. subminuta*) with suture associated with the PNS . . . . . *L. superciliosus* sp. nov.
  - Ventral lateral setae on abdominal segment IV shorter than dorsal, reaching approximately a fourth of tergite length . . . . . 24
- 24) Tergal heads of abdominal segment VII broad and blunt, but still re-entrant. Only rarely with AVS3 anterior to AVS2. Tergal bars usually broad. On Old World sandpipers . . . . . *L. falcinellus*
  - Tergal heads of abdominal segment VII pointed. Often with AVS3 anterior to AVS2. Tergal bars usually narrow. On New World sandpipers. . . . . *L. incoenis*

## Discussion

The genus *Lunaceps* has been reviewed and reworked, with six new species (*L. schismatus*, *L. enigmaticus*, *L. kukri*, *L. mintoni*, *L. rothkoi*, and *L. superciliosus*) and one new subspecies (*L. numenii madagascariensis*) being described and illustrated. One species (*L. limosae*), previously placed in synonymy (e.g. Price *et al.*, 2003) has been resurrected. Another species (*L. parabolicus*) has been transferred to *Quadriceps*, and six nominal species (*L. cabanisi*, *L. pusillus*, *L. haematopi*, *L. oliveri*, *L. husainii* and *L. timmermanni*) are new junior synonyms. One species (*L. wilsoni*) is deemed as a *nomen dubium*. This brings the total number of valid species in the genus to 21, plus two subspecies (see Table 4).

Of these 21 species, 10 were included in the molecular analysis of Gustafsson and Olsson (2012) and are known to be genetically distinct. Most of the *Lunaceps* species parasitizing *Numenius* and *Limosa* hosts were not included, however, and it is presently unknown whether or not they are as distinct genetically as they are morphologically. Of the *Lunaceps* species parasitizing *Calidris*, the species exhibiting re-entrant heads of tergites group together (“Clades 1–5”; Gustafsson and Olsson, 2012), but at low support (Posterior probability = 0.57). In general, the *Lunaceps* species with dark, narrow paratergal plates and re-entrant heads of tergites parasitize smaller sandpipers, whereas *Lunaceps* species on larger hosts have broad paratergal plates with no re-entrant heads. Surprisingly, despite their morphological similarity, *L. drosti* and *L. mintoni* sp. nov. are not closely related, and *L. mintoni* sp. nov. may be the sister species of all other *Lunaceps*.

However, this revision cannot be seen as final because several host species or potential host species have no records of *Lunaceps*. Peters (1936) noted that *Calidris fuscicollis* is host to *L. actophilus*, an association that is missing in subsequent checklists (Forrester *et al.*, 1995; Price *et al.*, 2003), but *L. actophilus* is also listed under *C. pusilla* and *C. canutus rufus*, and *Lunaceps* from *C. fuscicollis* is probably not *L. actophilus*. Apart from this record (from Massachusetts), no *Lunaceps* from *C. fuscicollis* are known. No *Lunaceps* have been reported from *Calidris bairdii*, and to the extent that parasite distribution can be predicted from host phylogeny, *Bartramia longicauda* is also a likely candidate for hosting *Lunaceps*, possibly *L. rothkoi*.

The lack of reports of *Lunaceps* from *C. fuscicollis* and *C. bairdii* may be due to limited sampling. It should be noted, however, that the first author has collected lice indiscriminately from *Calidris* sandpipers and found that *Lunaceps* is by far the most commonly encountered louse genus on all examined host species (Gustafsson, *in prep.*), yet all three of the less common genera (i.e. *Actornithophilus*, *Carduiceps* and *Saemundssonina*) are known from both *C. fuscicollis* and *C. bairdii*. On the other hand, Hunter and Colwell (1994) examined a total of 58 *C. mauri*, *C. pusilla* and *C. alpina* without finding a single *Lunaceps*, although their study was limited to collecting from the birds' heads.

Several other host species treated here (*Calidris ptilocnemis*, *Aphriza virgata*, *Eurynorhynchus pygmeus*) have *Lunaceps* populations which may or may not represent good species in their own right, but the known material is too limited to draw definite conclusions. Finally, further collections from *Dromas ardeola* and perhaps also *Vanellus vanellus* and *Haematopus ostralegus* are needed to ascertain whether or not these are actually hosts to the *Lunaceps* populations ascribed to them, or if they are the results of misattributions, contamination or straggling.

*Lunaceps* is a homogenous genus, separated from other ischnoceran genera found on the Charadriiformes by the shape of the male genitalia and details of the preantennal area, both of which are simple compared to those in *Quadriceps* and *Carduiceps*. Interspecific variation is mainly in the shape of the male genitalia, the tergal heads and paratergal plates, and dimensions but, on the whole, *Lunaceps* is morphologically well-defined and easy to identify.

At least two of the species of *Lunaceps* are likely to be extinct, or very close to extinction. The IUCN Red List of Threatened Species states that the world population of *Numenius tenuirostris* is probably below 50 individuals, if it survives at all (no confirmed sightings since 2001; IUCN, 2011b). *Numenius borealis* is probably extinct, not having been captured since 1963, and not reliably observed since 1981 (IUCN, 2011a). Both these species are officially considered “Critically endangered”, and it is unlikely that either of their lice (*L. proximus* and *L. rileyi*, respectively) will have straggled and thus outlived their hosts.

A third *Lunaceps* population, that from *Eurynorhynchus pygmeus*, is also parasitizing a host that is rapidly disappearing (Tomkovich *et al.*, 2002; Zöckler *et al.*, 2010; IUCN, 2011c), at least partly due to the exploitation of its wintering grounds and stop-over points in China and South-East Asia (see e.g., Bird *et al.*, 2010). This population is here treated as “*Lunaceps incerta sedis* 3” since only one sample of few *Lunaceps* is known from *E.*

*pygmeus* (see above). However, there are morphological differences between those few specimens and populations from other hosts. If more material could be collected before it is too late, there may show to be a valid species.

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