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A NEW SPECIES OF SUCKING LOUSE FROM THE LONG-TAILED GROUND SQUIRREL, *UROCITELLUS UNDULATUS,* FROM MONGOLIA, WITH A KEY TO SPECIES, AND A REVIEW OF HOST ASSOCIATIONS AND GEOGRAPHICAL DISTRIBUTIONS OF MEMBERS OF THE GENUS *LINOGNATHOIDES* (PSOCODEA: ANOPLURA: POLYPLACIDAE)

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KEY WORDS

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Anoplura
Linognathoides
New Species
Mongolia
Dichotomous Key
Host Associations
Geographical Distributions

ABSTRACT

Members of the genus *Linognathoides* are ectoparasites of ground squirrels and marmots (Rodentia: Sciuridae) in the Nearctic, Palearctic, and Afrotropical regions. *Linognathoides urocitelli* n. sp. is described based on adult male and female and third-instar nymphal specimens collected from the long-tailed ground squirrel (*Urocitellus undulatus*) in Mongolia. The new species is compared morphologically to other members of the genus *Linognathoides*. Additionally, DNA sequences of a 610–base pair (bp) fragment of the nuclear *18S rDNA* gene, a 452-bp fragment of the mitochondrial *12S rrnS* gene, and a 363-bp fragment of the mitochondrial *16S rrnL* gene are provided. Host associations and geographical distributions of the 11 previously recognized species of the genus, and of *Linognathoides urocitelli* n. sp., are reviewed. A dichotomous identification key to adults of all known species in the genus *Linognathoides* is provided.

The sucking louse genus *Linognathoides* Cummings is assigned to the family Polyplacidae Fahrenholz as designated by Kim and Ludwig (1978). All known members of the genus *Linognathoides* are ectoparasites of sciurid rodents, namely, ground-dwelling squirrels belonging to the subfamily Xerinae in the Nearctic, Palearctic, or Afrotropical regions (Kim and Adler, 1982; Durden and Musser, 1994). Most species of *Linognathoides* parasitize ground squirrels or marmots belonging to the Holarctic tribe Marmotini, but 2 species parasitize ground-dwelling squirrels belonging to the African tribe Xerini. To date, 11 valid species of *Linognathoides* have been recognized (Kim and Adler, 1982; Durden, 1991; Durden and Musser, 1994).

In this paper, a new species of *Linognathoides* is described from the long-tailed ground squirrel, *Urocitellus undulatus* (Pallas) (Rodentia, Sciuridae), from Mongolia, and host associations and geographical distributions are reviewed for members of the genus *Linognathoides*. We also provide an identification key for adults of this sucking louse genus. The long-tailed ground squirrel is a Palearctic sciurid that ranges from eastern Kazakhstan to southern Siberia, northern and central Mongolia, and Heilungjiang province and Xinjiang autonomous region in northern China (Thorington and Hoffmann, 2005).

Members of the family Polyplacidae are characterized within the suborder Anoplura (sucking lice) of the insect order Psocodea (parasitic and nonparasitic lice) as having the following morphological characters as designated by Kim and Ludwig (1978), who illustrate all of the mentioned structures:

(1) Medium to small sized sucking lice (adult lengths, ~0.7–1.5 mm).
(2) Head lacking eyes, with 5-segmented antennae which are often sexually dimorphic.
(3) Thoracic sternal plate in adults usually well developed.
(4) Forelegs small and slender, smaller than mid- and hindlegs, all with a distinct tibio-tarsal claw.
(5) Abdomen usually with 6 pairs of spiracles.
(6) Paratergal plates well developed.
(7) Sternal plate of abdominal segment 2, if present, not extended laterally to articulate with the corresponding paratergal plate on either side.
(8) Male genitalia with well-developed basal apodeme, parameres, and pseudopenis.

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(9) Female genitalia with well-developed subgenital plate and gonopods VIII and IX.

The genus *Linognathoides* was erected by Cummings (1914), but Kim and Adler (1982) provided additional taxonomic details for this genus and morphologically defined adults of *Linognathoides* as having the following additional morphological characters:

(1) Head slightly longer than wide, with basal antennal segment lacking a stout seta, and third antennal segment sometimes with a stout spiniform seta in males (spiniform seta always absent in females); ventral principal head seta (VPHS) distinct.
(2) Thoracic sternal plate rounded posteriorly or convex, sometimes with slightly produced posterolateral angles.
(3) Forelegs small, each with a small acuminate or bifid claw; mid- and hindlegs larger and usually subequal in size, each with a robust claw.
(4) Abdominal tergites and sternites highly reduced or absent, except for ventral genital plates.
(5) Paratergal plates reduced with anterior portions often membranous; some paratergal plates bearing very long setae.
(6) Most abdominal segments with numerous long setae; segments 3–6 each with 2–3 rows of dorsal setae.

MATERIALS AND METHODS

As part of a larger project examining the diversity and coevolution of northern latitude mammals and parasites (Cook et al., 2017), 3 long-tailed ground squirrels (*Urocitellus undulatus*) were collected from 3 sites in Huvsgul, Arkhangai, and Bayan Ulgii Provinces in northwestern Mongolia (50°33′13.8384″N, 100°29′54.6864″E; 48°7′58.1088″N, 100°5′53.8296″E; and 49°24′37.8432″N, 89°5′25.5912″E) during July and August 2015 and found to host 5 lice belonging to the new species (1 adult male, 3 adult females, and 1 third-instar nymph). Collected lice were stored in 95% ethanol in the field using fine forceps to allow for later morphological and molecular examination. Ground squirrels were collected following field methods (Galbreath et al., 2019) and guidelines of the institutional animal care and use committees as well as the American Society of Mammalogists Guide for Use of Wild Mammals in Research (Sikes et al., 2011). Examined host specimens are housed at the Museum of Southwestern Biology, University of New Mexico under catalog numbers MSB:Mamm: 288931, 289043, and 289396.

DNA was extracted from 2 adult lice and 1 nymph as follows. Louse specimens stored in 95% ethanol were transferred to ultrapure water. A small hole was made in the abdomen using a 0.155-mm minuten insect pin and each louse was transferred to a 1.5-ml microcentrifuge tube along with 10 μl of 20 mg/ml proteinase K, 95 μl of ultrapure water and 95 μl of 2x digestion buffer (Zymo Research, Irvine, California), followed by incubation at 58 C overnight. Following incubation, the lysate was transferred to a new 1.5-ml microcentrifuge tube, quickly followed by the addition of 80% ethanol to the original tube with the louse exoskeleton, which was then permanently slide mounted. Two hundred microliters of isopropanol was added to the new tube with the DNA lysate, vortexed, and placed at –20 C for at least 2 hr to precipitate DNA. Precipitated DNA was centrifuged at 13,300 *g* for 15 min, the supernatant removed, washed in 70% ethanol, centrifuged at 13,300 *g* for 5 min (×2), the supernatant removed, dried for 15 min at 58 C, and resuspended in 45 μl of ultrapure water for 2 hr at room temperature. Polymerase chain reaction (PCR) amplification and sequencing of a 452–base pair (bp) fragment of the mitochondrial *12S rrnS* gene and a 363-bp fragment of the mitochondrial *16S rrnL* gene were accomplished using the respective primers 12SA–12SB and 16SF–Lx16SR designed by Dong et al. (2014). PCR amplification and sequencing of a 610-bp fragment of the nuclear *18S rDNA* gene was accomplished using the primers NS1 and NS2a (Barker et al., 2003). Amplified fragments were purified using ExoSAP-it (Affimetrix, Santa Clara, California) and sequenced in both directions using the original PCR primers. Sequence chromatograms were trimmed, assembled, and edited using Geneious version 11.0.4 (Biomatters Ltd., Auckland, New Zealand).

Louse specimens from which DNA had been extracted were slide-mounted from ethanol directly into polyvinyl alcohol (PVA) medium (Bioquip Products, Rancho Dominguez, California). Lice from which DNA had not been extracted were cleared for ~24 hr in 10% potassium hydroxide, rinsed in distilled water, dehydrated through an ethanol series, further cleared in xylene, and then slide mounted in Canada balsam. Line drawings were prepared by examining specimens at 100–400× with an Olympus BH-2 phase contrast high-power microscope (Olympus Corporation of the Americas, Center Valley, Pennsylvania) connected to an Ikegami MTV-3 video camera attachment and monitor (Ikegami Electronics, Neuss, Germany). Measurements were made using a calibrated ocular micrometer. Standardized descriptive format for Anoplura follows Kim and Ludwig (1978) and Durden et al. (2018). Differential interference contrast microscopy images were taken with a Nikon Eclipse Ni-U research microscope equipped with a Nikon DS-L3 camera (Nikon Inc., Melville, New York). Images were stitched together using the "Photomerge" automation application in Adobe Photoshop Creative Cloud 2018 (Adobe Inc., San Jose, California).

Names of anopluran morphological structures, including setae, follow Kim and Ludwig (1978) and Durden et al. (2018). Taxonomy, including common names, of Holarctic ground squirrels follows Helgen et al. (2009). Taxonomy and common names of other squirrels mentioned follow Thorington and Hoffmann (2005).

DESCRIPTION

Linognathoides urocitelli, n. sp.
(Figs. 1–3)

Male (Figs. 1A–D, 2A, B) (n = 1): Total body length of holotype, 1.128 mm. Head, thorax and abdomen moderately sclerotized.

Head (Figs. 1A, 2A): Slightly longer than wide with broadly curved lateral margins posterior to antennae and extended medioanteriorly; maximum head width, 0.190 mm. Antennae 5-segmented with broad basal segment and elongated second segment; third segment not highly modified. One distinct VPHS, 2 sutural head setae (SHS), 4 dorsal marginal head setae (DMHS), 1 dorsal anterior central head seta (DAnCHS), 1 dorsal posterior head seta (DPoHS), 1 extremely long dorsal principal head seta (DPHS), 1 small dorsal accessory head seta

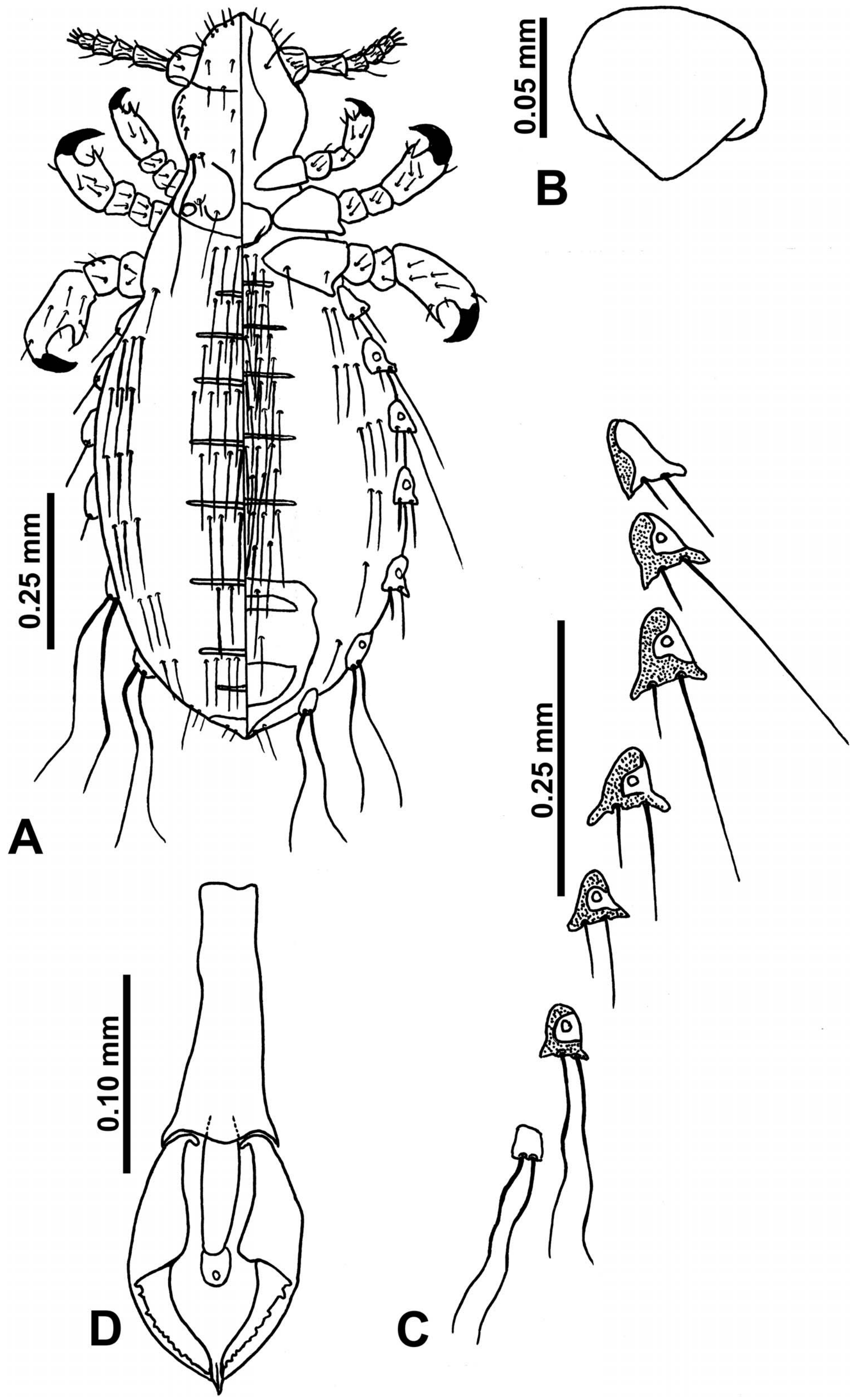

Figure 1. *Linognathoides urocitelli* n. sp., male. (**A**) Dorsoventral drawing of whole louse (dorsal features on left side, ventral features on right). (**B**) Thoracic sternal plate. (**C**) Paratergal plates. (**D**) Genitalia.

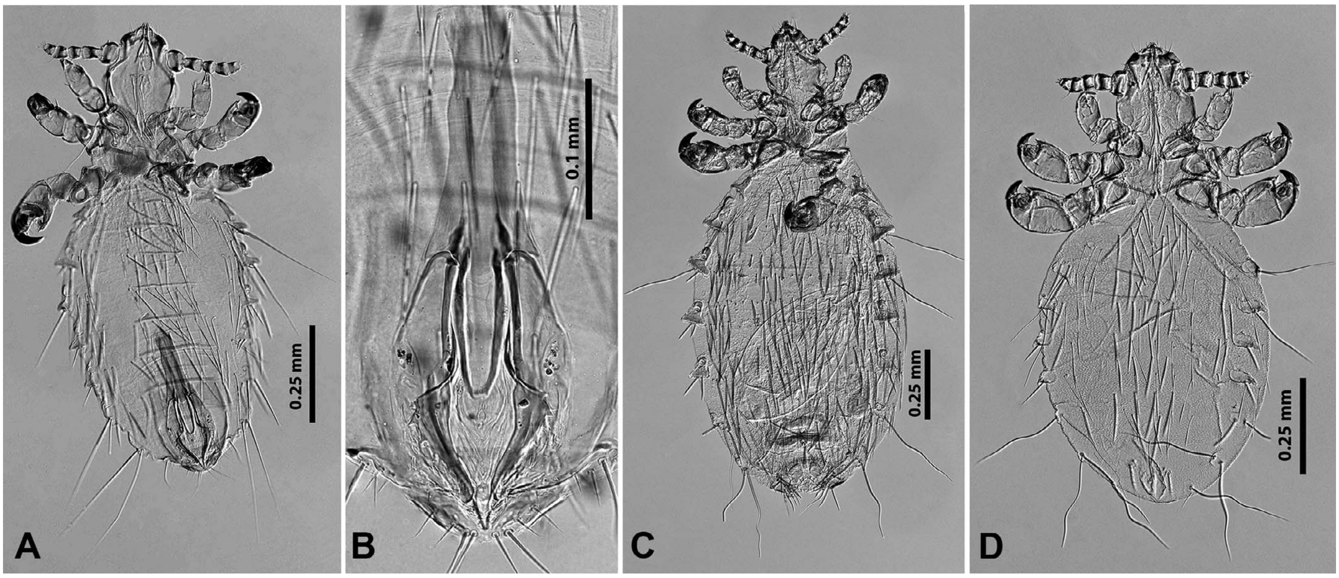

Figure 2. *Linognathoides urocitelli* n. sp. Differential interference contrast photomicrographs of cleared specimens. (**A**) Male. (**B**) Male genitalia. (**C**) Female (note sclerotized outline of egg inside abdomen). (**D**) Third-instar nymph.

(DAcHS), 2 supra-antennal head setae (SpAtHS), 1 small dorsal preantennal head seta, and 4 apical head setae (ApHS) on each side.

Thorax (Figs. 1A, 2A): Broader than head; maximum thorax width, 0.260 mm. Thoracic sternal plate (Fig. 1B) subelliptical, broadly rounded anteriorly and laterally, and with distinct posterior extension. Thoracic fragma distinct. Mesothoracic spiracle diameter, 0.018 mm. Dorsal principal thoracic seta (DPTS) length, 0.105 mm. Legs each terminating in tibio-tarsal acuminate claw; forelegs distinctly smaller than other legs; midlegs slightly smaller than hindlegs; leg coxae subtriangular with small posterolateral extensions on second and third coxae.

Abdomen (Figs. 1A, 2A): Broader than thorax with 8 narrow, short tergites and 5 narrow, short sternites. Eight rows of 5–8 long dorsal central abdominal setae (DCAS)—each row associated with abdominal segment; rows 2–8 each associated with tergites. Seven rows of 1–3 long dorsal marginal abdominal setae (DMAS) on each side; row 1 with 1 DMAS on each side, rows 2–6 each with 3 DMAS on each side, and row 7 with 2 DMAS on each side. Fourteen rows of ventral central abdominal setae (VCAS), each with 2–6 VCAS; 2 rows of long VCAS associated with each abdominal segment anterior to subgenital plate; 6 rows of 2–6 long ventral marginal abdominal setae (VMAS); rows 1 and 4 each with 2 VMAS on each side, rows 2 and 3 each with 3 VMAS on each side, rows 5 and 6 each with 1 VMAS on each side.

Paratergal plates (Figs. 1C, 2A): Present on abdominal segments II–VIII; plates on segments II–VII subtriangular; plates on segments III–VII each with spiracle; plates differentially sclerotized. Plate on abdominal segment II with 1 long seta and 1 seta of moderate length; plates on segments III and IV each with 1 very long seta and 1 seta of moderate length; plates on segments V and VI each with 2 setae of moderate but slightly different lengths; plates on segments VII and VIII each with 2 very long setae.

Genitalia (Figs. 1D, 2B): Basal apodeme slightly longer than parameres. Posterolateral angles of basal apodeme acute with curved convex posterior margin between angles; parameres broadly curved, each with small anteromedial hook-like process; lateral margins of pseudopenis distinctly dentate; apex of pseudopenis extending slightly beyond posterior confluence of parameres. Subgenital plate (Fig. 1A) extending anteriorly to abdominal segment VI, with almost straight anterior margin, curved lateral margins, and tapering posteriorly; 2 distinct lacunae present, anterior lacuna elongated bilaterally, posterior lacuna larger with almost straight anterior margin and curved, tapering, posterior-lateral margin.

Female (Figs. 2C, 3A–D) (n = 3): Total body length of allotype, 1.600 mm; mean, 1.507 mm; range, 1.445–1.600 mm. Head, thorax, and abdomen as in male unless indicated otherwise.

Head (Figs. 2C, 3A): Maximum head width of allotype, 0.211 mm; mean, 0.210 mm; range, 0.205–0.215 mm.

Thorax (Figs. 2C, 3A): Thoracic sternal plate (Fig. 3B) with slightly shorter, less acute posterior extension than in male. Maximum thorax width of allotype, 0.295 mm; mean, 0.308 mm; range, 0.295–0.325 mm. DPTS length of allotype, 0.145 mm; mean, 0.141 mm; range, 0.138–0.145 mm. Mesothoracic spiracle diameter of allotype, 0.022 mm; mean, 0.020 mm; range, 0.018–0.022 mm.

Abdomen (Figs. 2C, 3A): Lacking tergites and sternites except for ventral subgenital plate. Fourteen rows of 6–10 long DCAS; 12 rows of 3–4 DMAS on each side, rows 1–4 and 12 each with 3 setae on each side and rows 5–11 each with 4 setae on each side. Twelve rows of 4–16 long VCAS; 10 rows of 3 VMAS on each side. Some abdominal setae dagger-shaped, especially on ventral surface.

Paratergal plates (Figs. 2C, 3C): Differential sclerotization and lengths of apical setae on plates of abdominal segments IV and V slightly different than in male as shown in Figure 3C. Number of shorter apical setae on paratergal plates on segments II and III slightly variable: On plate of segment II, allotype female has 1 shorter seta on 1 side and 2 on the other side; 2 paratype females have 2 shorter setae on both sides; on plate of segment III,

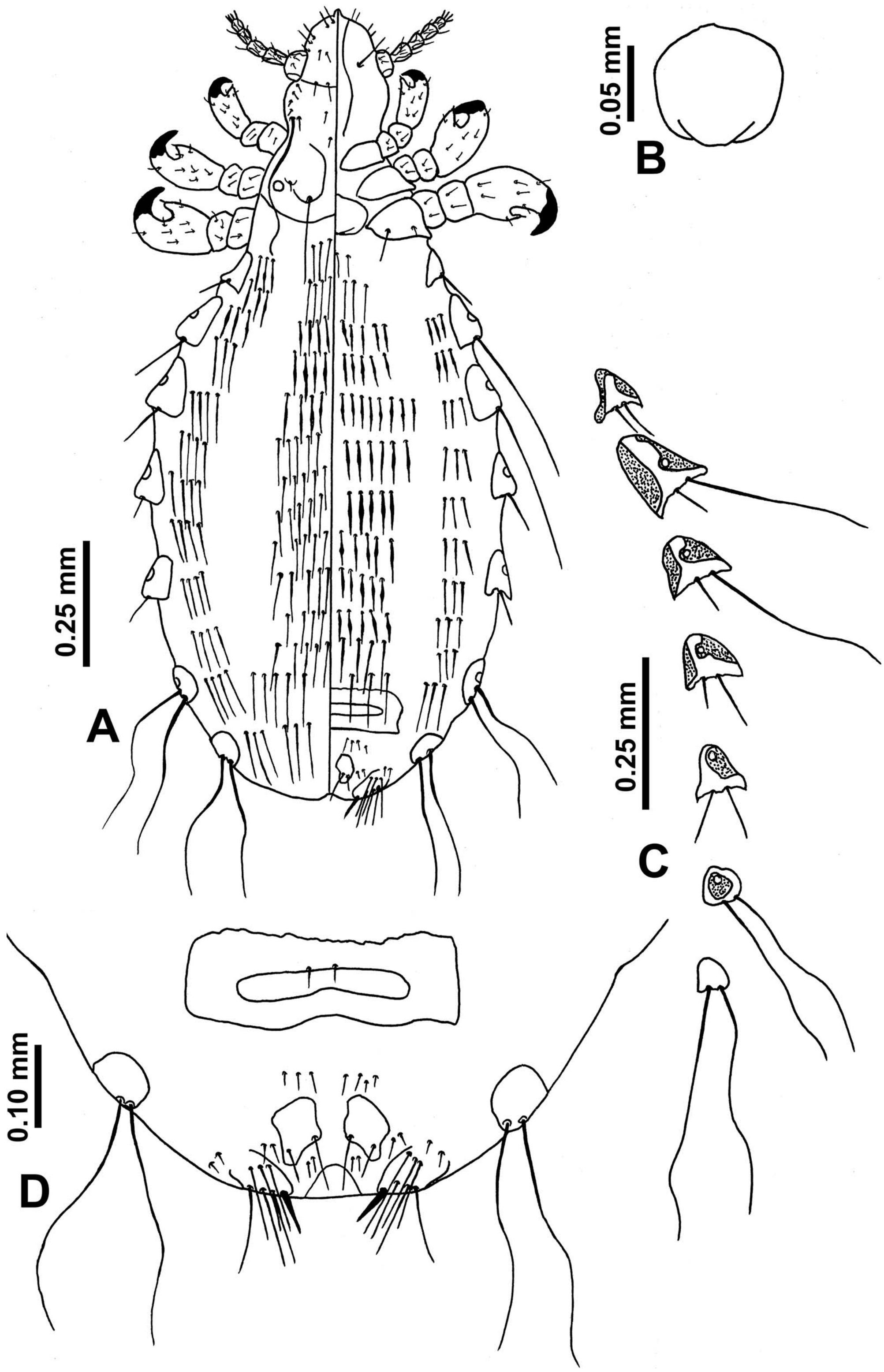

Figure 3. *Linognathoides urocitelli* n. sp., female. (**A**) Dorsoventral drawing of whole louse (dorsal features on left side, ventral features on right). (**B**) Thoracic sternal plate. (**C**) Paratergal plates. (**D**) Genitalia.

allotype female and 1 paratype female have 1 shorter seta on both sides; another female paratype has 1 shorter seta on 1 side and 2 on the other side.

Genitalia (Fig. 3D): Subgenital plate subrectangular, much wider than long, with slightly concave, irregular anterior margin and slightly concave, smoothly rounded posterior margin; with single large central lacuna and 2 small central setae anterior to lacuna. Three–four small setae anterior to gonopod VIII on each side. Gonopods VIII irregularly shaped and medially situated, each with 1 longer medial seta and 1 shorter lateral seta. Gonopods IX less distinct and more lateral than gonopods VIII, each with 2 rows of 3 long setae, followed by 1 short stout seta. ~Six small setae on each side adjacent to gonopods.

Nymph (third instar) (Fig. 2D) ($n = 1$): Total body length of paratype nymph, 1.170 mm. Overall body shape wider than in adults.

Head: Broadly rounded anteriorly with small anteromedial projection; lateral margins almost straight posterior to antennae. Maximum head width, 0.201 mm. Ventrally, 1 anterolateral denticle, 1 anteromedial denticle, and pair of denticles just medial to first antennal segment on each side; 1 denticle near mediolateral margin of first antennal segment on each side. Four DMHS, 2 SuHS, 1 long DPTS, and 1 short DAcHS both borne on small protuberance, 1 SpAtHS, 1 DPaHS, 4 ApHS, 1 VPHS, and 1VPaHS on each side. Antennae five-segmented; first segment much wider than long; second segment slightly longer than wide, third and fourth segments about as long as wide; fifth segment tapering distally.

Thorax: Wider than head; maximum thorax width, 0.262 mm. Overall shape of thorax and legs similar to those in adults except tibio-tarsal leg segments broader. No thoracic sternal plate. DPTS length, 0.122 mm. Mesothoracic spiracle diameter, 0.017 mm.

Abdomen: Wider than thorax; integumental sculpting distinct; some morphological features of developing adult female visible beneath nymphal exoskeleton. Eleven rows of 2–5 long DCAS. Eight rows of DLAS; rows 1, 3, and 5 each with 2 long setae, row 2 with 2 long and 1 shorter seta, rows 4 and 6 each with 1 long seta, and rows 7 and 8 each with 1 small seta, on each side. Seven rows of 2–5 long VCAS. Five rows of long VLAS each with 1–2 VLAS on each side.

Paratergal plates: Eight lightly sclerotized plates present on each side associated with abdominal segments II–IX. Plates on segments II and IX small and irregularly shaped; plates on segments III–VI each subtriangular and produced posterolaterally on 1 side; plates on segments VII and VIII both subrectangular. Plate on abdominal segment II with 1 long apical seta; plates on segments III and IV each with 1 very long seta and 1 shorter seta; plates on segments V and VI each with 1 short seta; plates on segments VII and VIII each with 2 long setae; plate on segment IX with 1 long and 1 short seta. Spiracles present on each of plates on abdominal segments III–VII.

Taxonomic summary

Type and only known host: Long-tailed ground squirrel, *U. undulatus* (Pallas) (Rodentia: Sciuridae).

Specimens deposited: One male holotype, 1 female allotype, 2 female paratypes, 1 nymph (third instar) paratype, Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, accession numbers: MSB:Para:28811 (holotype), MSB:Para:28813 (allotype), MSB:Para:28814 and 28815 (2 paratype females), and MSB:Para:28812 (paratype nymph).

Type locality: Mongolia: Arkhangai Province, Zurkh Mountain (48°7′58.1088″N, 100°5′53.8296″E) (holotype male, 1 paratype female, and paratype nymph), 21 and 27 July 2015. Collectors: S. E. Greiman, J. A. Cook, B. S. McLean, and N. Batsaikhan.

Other localities: Mongolia: Huvsgul Province, Heegtsar River Valley (50°33′13.8384″N, 100°29′54.6864″E) (allotype female), 19 August 2015; Mongolia: Bayan Ulgii Province, Huljaa River Valley (49°24′37.8432″N, 89°5′25.5912″E) (1 paratype female), 5 August 2015. Collectors: S. E. Greiman, J. A. Cook, B. S. McLean and N. Batsaikhan. Although it is desirable to select type specimens from the same host individual, this was not possible because no more than 2 lice were collected from the same host individual and male and female lice were not collected from the same individual.

Site of infestation: Skin surface and fur.

ZooBank registration: urn:lsid:zoobank.org:act:15566E70-921B-473E-840E-11D796F2E3C4

Etymology: The specific epithet is derived from the host genus name.

DNA sequence data: An *18S rDNA* sequence was generated for 1 of the 3 louse samples (male holotype, GenBank: MK478719). Based on a sequence alignment with 2 other *Linognathoides* species, *Linognathoides marmotae* (HQ124301) and *Linognathoides laeviusculus* (HM171411), *L. urocitelli* n. sp. is closest to *L. marmotae* (90.2% similar). *18S rDNA* sequences of the 3 species of *Linognathoides* are between 82.2 and 90.2% similar. This large variation is due mostly to the presence or absence of 2 long insertions, ranging from 22 to 85 bp in length. *16S rrnL* DNA sequences were successfully generated for 2 of 3 louse samples (male holotype, GenBank: MK478723; female allotype, GenBank: MK478724). Slight intraspecific variation was detected within this gene for the 2 samples, with 1-bp difference between the 2 lice (362/363 bp). *12S rrnS* DNA sequences were successfully generated for all 3 louse samples (male holotype, GenBank: MK474720; nymph paratype, GenBank: MK478721; female allotype, GenBank: MK478722), although, of the 450 bp the PCR primers amplified, only 412 could be successfully sequenced. No intraspecific variation was detected within this gene for the 3 samples (412 bp).

Remarks

Linognathoides urocitelli can most easily be separated from its congeners based on morphology of the genitalia in adults of both sexes, the paratergal plates (especially lengths of the apical setae) and the thoracic sternal plate. We provide a dichotomous key to facilitate identification of adults of all known members of the genus *Linognathoides*. Following identification to species using this key, we recommend comparing specimens to the original descriptions, especially if lice are collected from host species that have not previously been reported to be parasitized by lice belonging to the genus *Linognathoides*. We state this because of the possibility that additional species of *Linognathoides* may await discovery and description. Conversely, it is also possible that some louse species may parasitize multiple host species (as is the case for *L. laeviusculus*, for example).

Males of *L. urocitelli* n. sp. have heavily serrated lateral margins to the pseudopenis (Figs. 1D, 2B). Although males of some other species of *Linognathoides* (*Linognathoides baibacinae, L. laeviusclus, L. marmotae, Linognathoides palaearctus, Linognathoides relictus,* and *Linognathoides schizodactylus*) have distinctly serrated margins of the pseudopenis, none of these species has serrations as large as those of *L. urocitelli* n. sp., or arranged in the same pattern. The lengths of the apical setae attached to the paratergal plates are also unique in males (and females) of *L. urocitelli* n. sp. Notably, in *L. urocitelli* n. sp., both sexes have much shorter setae on the paratergal plates of abdominal segments V and VI compared to lengths of apical setae of other paratergal plates. In *L. baibacinae, Linognathoides citelli, Linognathoides cynomyis, Linognathoides faurei*, *L. laeviusculus*, *L. marmotae*, *L. palaearctus*, *L. relictus,* and *Linognathoides traubi,* all of the paratergal plates have at least 1 very long apical seta. Although *Linognathoides pectinifer* and *L. schizodactylus* both have shorter apical setae on the paratergal plates of abdominal segments V and VI, those setae are subequal in length on each plate, compared to being distinctly different in length on each of these plates in the male of *L. urocitelli* n. sp. (Fig. 1C), and significantly different in length on the paratergal plate on abdominal segment V in the female of *L. urocitelli* n. sp. (Fig. 3C). Although lengths of the apical setae on the paratergal plates of *L. urocitelli* are unique for both sexes, females of *L. urocitelli* n. sp. are most easily distinguished from all other congeners of the same sex based on the shape of the subgenital plate (Fig. 3D). No other species in the genus has a similarly shaped subgenital plate that is at least twice as wide as long, and with a large, central lacuna. The shape of the thoracic sternal plate is also unique in both sexes of *L. urocitelli* n. sp. (Figs. 1B, 3B). This plate has a distinct posterior medial projection or lobe in *L. urocitelli* n. sp. The only other species of *Linognathoides* with a posterior medial lobe or extension on the thoracic sternal plate are *L. laeviusculus, L. pectinifer, L. relictus,* and *L. schizodactylus*. However, this plate is also extended laterally on both sides in *L. laeviusculus* (versus not extended in *L. urocitelli*), is much wider than long and has an anterior projection in *L. pectinifer* (versus about as wide as long and lacking an anterior projection in *L. urocitelli* n. sp.), and is slightly extended anteriorly in both *L. relictus* and *L. schizodactylus* (versus broadly rounded anteriorly in *L. urocitelli* n. sp.). The thoracic sternal plate of *L. schizodactylus* also has a small postero-medial pointed extension which differs from the large posterior lobe present in *L. urocitelli* n. sp.

The third-instar nymph we describe for *L. urocitelli* n. sp. was apparently collected and placed in ethanol when it was in the process of molting to an adult female. This is evident because parts of the developing adult female integument (notably, gonopods VIII) are visible beneath the nymphal integument. Adult female sucking lice are invariably larger than conspecific male lice, so it is not unexpected that the single third-instar nymphal louse we describe for *L. urocitelli* n. sp. is slightly larger (1.170 mm long) than the conspecific single male (1.128 mm long). We assume the third-instar nymph of *L. urocitelli* n. sp. is unique but the only other species of *Linognathoides* for which the third-instar nymph has been documented are *L. marmotae* and *L. pectinifer*, which were described by Kim and Adler (1982) and *L. cynomyis* which was described by Kim (1986). The third-instar nymph of *L. marmotae* was also illustrated by Kim (1987). This nymphal stage of *L. urocitelli* n. sp. differs from the same stage of *L. cynomyis, L. marmotae* and *L. pectinifer* in several ways, including the presence of 11 rows of DCAS (versus 13 rows in *L. pectinifer*, and 9 rows in both *L. cynomyis* and *L. marmotae*), 8 rows of DLAS (versus 5 rows in *L. marmotae*, 6 rows in *L. cynomyis*, and 7 rows in *L. pectinifer*), 1 long apical seta on each paratergal plate on abdominal segment II (vs. no plate on this segment in *L. cynomyis,* and 2 apical setae on this plate in both *L. marmotae* and *L. pectinifer*—2 shorter setae in *L. marmotae* and 1 long and 1 short seta in *L. pectinifer*). Further, the combination of lengths and numbers of apical setae on the paratergal plates differs between each of these 4 species in the third-instar stage.

Key to adults of known species of the genus *Linognathoides*

1a. Thoracic sternal plate not visible (poorly sclerotized) in both sexes; tip of male abdomen with ~5 thick spines on each side (on *Spermophilopsis leptodactylus,* central Asia).............................. ***L. citelli***

1b. Thoracic sternal plate distinct (well sclerotized) in both sexes; tip of male abdomen lacking thick spines.. 2

2a. Thoracic sternal plate narrow and elongate, more than twice as long as wide, and tapering to anterior apex (on *Xerus*, southern Africa)............. ***L. faurei***

2b. Thoracic sternal plate about as long as wide, wider than long, or only slightly longer than wide.......... 3

3a. Thoracic sternal plate broadly rounded anteriorly 4

3b. Thoracic sternal plate prolonged anteriorly and tapering apically.................................... 8

4a. Thoracic sternal plate much wider than long with a lateral lobe on each side (on *Atlantoxerus getulus*, north Africa)............................ ***L. pectinifer***

4b. Thoracic sternal plate about as wide as long 5

5a. Paratergal plates on abdominal segments V and VI each with distinctly shorter apical setae than paratergal plates on segments III, IV, VII, and VIII 6

5b. Paratergal plates on abdominal segments III–VIII all with at least one long apical seta..................... 7

6a. Thoracic sternal plate lacking posterior lobe; male parameres distinctly longer than basal apodeme (on *Cynomys ludovicianus*, western North America) .... ***L. cynomyis***

6b. Thoracic sternal plate with distinct posterior lobe; male parameres slightly shorter than basal apodeme (on *Urocitellus undulatus*, Mongolia, possibly also in other adjacent regions) .... ***L. urocitelli* n. sp.**

7a. Thoracic sternal plate broadest posteriorly; male parameres about the same length as the basal apodeme (on many species of ground squirrels, Holarctic region) .... ***L. laeviusculus***

7b. Thoracic sternal plate broadest anteriorly; male parameres distinctly shorter than basal apodeme (on *Urocitellus glacialis,* northern Asia; only known as a subfossil) .... ***L. relictus***

8a. Thoracic sternal plate with distinct anterior projection; male parameres broadest posteriorly (on *Notocitellus adocetus*, Mexico) .... ***L. traubi***

8b. Thoracic sternal plate without anterior projection; male parameres broadest anteriorly.................. 9

9a. Paratergal plates on abdominal segments V and VI each with 2 short apical setae (much shorter than apical setae on paratergal plates on segments III, VII, and VIII); female subgenital plate more than twice as wide as long (on *Spermophilus suslicus*, central and eastern Europe).......... ***L. schizodactylus***

9b. Paratergal plates on abdominal segments V and VI each with 2 very long apical setae (about as long as apical setae on paratergal plates III, VII, and VIII); female subgenital plate about as wide as long...... 10

10a. Thoracic sternal plate with posterolateral angles produced into small posteriorly-directed points; anterior margin of female subgenital plate concave (on *Marmota* spp., western North America) .... ***L. marmotae***

10b. Thoracic sternal plate without postero-lateral angles produced into small posteriorly directed points; anterior margin of female subgenital plate not concave 11

11a. Thoracic sternal plate with anterior, lateral lobe on each side; male second abdominal tergite with straight posterior margin (on *Marmota* spp.; central and eastern Asia)....................... ***L. palaearctus***

11b. Thoracic sternal plate without lateral lobes; male second abdominal tergite with curved posterior margin (on *Marmota baibacina*; central Asia) .... ***L. baibacinae***

Host associations and geographical distributions of members of the genus *Linognathoides*

Linognathoides baibacinae (Blagoveshtchensky, 1965)

Host: Marmota baibacina Kastschenko, 1899 (gray marmot).

Known distribution of parasite: Kazakhstan (Alma-Ata Province).

Host distribution: southwestern Siberia, southeastern Kazakhstan, Kyrgyzstan, Mongolia, and Xinjiang autonomous region, China; it has also been introduced into the Caucasus mountains in Russia (Thorington and Hoffmann, 2005).

Taxonomic notes: Blagoveshtchensky (1965) originally assigned this louse to the genus *Neohaematopinus* but, based on taxonomic reinterpretations established by Kim and Adler (1982), it was reassigned to *Linognathoides* by Durden (1991).

Linognathoides citelli Cummings, 1916

Host: Spermophilopsis leptodactylus (Lichtenstein, 1823) (long-clawed ground squirrel).

Known distribution of parasite: Turkmenistan (Transcaspia) (Cummings, 1914; Durden and Musser, 1994).

Host distribution: Turkmenistan, Uzbekistan, southeastern Kazakhstan, western Tajikistan, northeastern Iran, and northwestern Afghanistan (Thorington and Hoffmann, 2005).

Taxonomic notes: Linognathoides spermophili Cummings, 1914 (preoccupied) is a junior synonym, and *Neohaematopinus citelli* (Cummings) of Ferris (1923) is a previous combination for this species.

Linognathoides cynomyis Kim, 1986

Host: Cynomys ludovicianus (Ord, 1815) (black-tailed prairie dog)

Known distribution of parasite: United States: South Dakota (Kim, 1986; Kim et al., 1986; Kietzmann, 1987), Nebraska (Kucera et al., 2007), New Mexico (Eads, 2019).

Host distribution: Canada (Saskatchewan), United States (Montana, Nebraska, New Mexico, western Texas, southeastern Arizona) to Mexico (northeastern Sonora and northern Chihuahua states) (Thorington and Hoffmann, 2005).

Linognathoides faurei Bedford, 1920

Type host: Xerus inauris (Zimmermann, 1780) (South African ground squirrel).

Known distribution of parasite: Angola, Botswana, Namibia, South Africa, Zimbabwe (Ferris, 1923; Ledger, 1980; Durden and Musser, 1994).

Distribution of type host: Angola, Botswana, Namibia, South Africa, Zimbabwe (Thorington and Hoffmann, 2005).

Other host: Xerus princeps (Thomas, 1929) (Damara ground squirrel).

Distribution of other host: southern Angola, western Namibia (Thorington and Hoffmann, 2005).

Taxonomic notes: Neohaematopinus faurei (Bedford) of Ferris (1923) is a previous combination for this species.

Linognathoides laeviusculus (Grube, 1851)

Type host: Urocitellus parryii (Richardson, 1825) (Arctic ground squirrel).

Known distribution of parasite: Widely distributed across the Holarctic region (Ferris, 1923; Kim et al., 1986; Durden and Musser, 1994); also recorded in Mexico as *Neohaematopinus patiki* (Rubin, 1946; Sánchez-Montes et al., 2013).

Distribution of type host: United States (Alaska), northwestern Canada, far western Russia (Thorington and Hoffman, 2005).

Other hosts: Ammospermophilus leucurus (Merriam, 1889) (white-tailed antelope squirrel), *Callospermophilus lateralis* (Say, 1823) (golden-mantled ground squirrel), *Ictidomys mexicanus* (Erxleben, 1777) (Mexican ground squirrel), *Ictidomys tridecemlineatus* (Mitchill, 1821) (13-lined ground squirrel), *Otospermophilus beecheyi* (Richardson, 1829) (California ground squirrel), *Otospermophilus variegatus* (Erxleben, 1777) (rock squirrel), *Poliocitellus franklinii* (Sabine, 1822) (Franklin's ground squirrel), *Spermophilus alashanicus* Büchner, 1888 (Alashan ground squirrel), *Spermophilus citellus* (L., 1766) (European ground squirrel), *Spermophilus dauricus* Brandt, 1843 (Daurian ground squirrel), *Spermophilus erythrogenys* Brandt, 1841 (red-cheeked ground squirrel), *Spermophilus fulvus* (Lichtenstein, 1823) (yellow ground squirrel), *Spermophilus major* (Pallas, 1778) (russet ground squirrel), *Spermophilus pygmaeus* (Pallas, 1778) (little ground squirrel), *Spermophilus suslicus* (Güldenstaedt, 1770) (speckled ground squirrel), *Urocitellus beldingi* Merriam, 1888 (Belding's ground squirrel), *Urocitellus brunneus* (Howell, 1928) (Idaho ground squirrel), *Urocitellus columbianus* (Ord, 1815) (Columbian ground squirrel), *Urocitellus richardsonii* (Sabine, 1822) (Richardson's ground squirrel), *Urocitellus townsendii* Bachman, 1839 (Townsend's ground squirrel), *Urocitellus undulatus* (Pallas, 1778) (long-tailed ground squirrel), *Urocitellus washingtoni* (Howell, 1938) (Washington ground squirrel) (Kéler, 1967; Durden and Musser, 1994; Kim et al., 1986, Yensen et al., 1996; Kristofik, 1999; Sánchez-Montes et al., 2013).

Distribution of other hosts: Together, the many sciurid hosts of this louse are widely distributed across the Holarctic region, including Mongolia.

Taxonomic notes: The following names are synonyms or previous combinations for this taxon (see Durden and Musser, 1994): *Pediculus laeviusculus* Grube, 1851; *Haematopinus laeviusculus* (Grube, 1851); *Haematopinus montanus* Osborn, 1896; *Haematopinus columbianus* Osborn, 1900; *Polyplax laeviuscula* (Grube, 1851); *Polyplax columbiana* (Osborn, 1900); *Linognathoides montanus* (Osborn, 1896); *Enderleinellus laeviusculus* (Grube, 1851); *Neohaematopinus laeviusculus* (Grube, 1851); *Neohaematopinus patiki* Rubin, 1946. Touleshkov (1957) described and illustrated a subspecies, *Neohaematopinus laeviusculus bulgaricus*, 1957.

Linognathoides marmotae (Ferris, 1923)

Type host: Marmota flaviventris (Audubon and Bachman, 1841) (yellow-bellied marmot).

Known distribution of parasite: Widely distributed in the western United States and parts of western Canada (Ferris, 1923; Kim et al., 1986; Durden and Musser, 1994); also recorded in Mexico as *Neohaematopinus mathesoni* Rubin (Rubin, 1946; Sánchez-Montes et al., 2013).

Distribution of type host: Alberta and British Columbia (Canada) south to California, Nevada, northern New Mexico, and southern Utah (United States) (Thorington and Hoffmann, 2005).

Other hosts: Marmota caligata (Eschscholtz, 1829) (hoary marmot), *Marmota monax* (L., 1758) (woodchuck). Also recorded (as *N. mathesoni* which is a synonym) from *Otospermophilus variegatus couchii* (Baird, 1855) (rock squirrel) from Nuevo Leon state, Mexico, which is considered to represent an atypical host association for this louse.

Distribution of other hosts: Together, across much of North America except parts of the southeastern Unied States (Thorington and Hoffmann, 2005).

Taxonomic notes: The following two names are a previous combination and a synonym, respectively, for this species (see Durden and Musser, 1994): *Neohaematopinus marmotae* Ferris, 1923; *Neohaematopinus mathesoni* Rubin, 1946.

Linognathoides palaearctus (Olsoufiev, 1938)

Type host: Marmota caudata (Geoffroy, 1844) (long-tailed marmot).

Known distribution of parasite: Afghanistan, China (Gansu, Qinghai, Sichuan, Yunnan Provinces), India (Jammu and Kashmir State), Kyrgyzstan, Mongolia, Russian Federation (Altay, Transbaikalia), Tibet, Turkmenistan (Olsoufjev, 1938; Durden and Musser, 1994; Kristofik, 1999; Meng et al., 2008).

Distribution of type host: Afghanistan, China (Xinjiang and Xizang Provinces), Kyrgyzstan, India (Kashmir), Pakistan, Tajikistan.

Other hosts: Marmota baibacina Kastschenko, 1899 (gray marmot), *Marmota bobak* Müller, 1776 (bobak marmot), *Marmota himalayana* (Hodgson, 1841) (Himalayan marmot), *Marmota sibirica* (Radde, 1862) (tarbagan marmot).

Distribution of other hosts: Together, the recorded hosts of *L. palaearctus* range across much of the eastern Palearctic region.

Taxonomic notes: Neohaematopinus palaearctus Olsoufjev, 1938 is a previous combination; *Neohaematopinus palaearcticus* [sic.] *tarbagani* Dubinina, undetermined date, is a synonym (see Durden and Musser, 1994).

Linognathoides pectinifer (Neumann, 1909)

Type host: Atlantoxerus getulus (L., 1758) (Barbary ground squirrel).

Known distribution of parasite: Algeria, Morocco (Ferris, 1923; Durden and Musser, 1994).

Distribution of host: Algeria, Morocco (Thorington and Hoffmann, 2005).

Taxonomic notes: The following names are previous combinations or synonyms: *Haematopinus setosus* Piaget, 1885 (preoccupied), *Haematopinus* (*Polyplax*) *pectnifer* Neumann, 1909, *Linognathides setosus* Piaget, 1885, *Lutegus pectinifer* (Neumann, 1909), *Neohaematopinus pectinifer* (Neumann, 1909) (see Durden and Musser, 1994). Ferris (1951) incorrectly stated that the type specimens of *L. pectinifer* were collected in South Africa.

Linognathoides relictus (Dubinin, 1948)

Type host: Urocitellus glacialis (Vinogradov, 1948) (no common name)—recent DNA analysis places this taxon within *Urocitellus parryii* (see Faerman et al., 2017).

Known distribution of parasite: Russian Federation: Yakutia-Sakha (Dubinin, 1948; Durden and Musser, 1994).

Distribution of host: Russian Federation: Yakutia-Sakha (or, the Holarctic region, for *U. parryii*).

Taxonomic notes: Neohaematopinus relictus Dubinin, 1948 is a previous combination; *Neohaematopinus relectus* Dubinin, 1948 is a synonym. This louse species was collected from ~30,000-yr-old subfossil remains on mummified ground squirrels (Dubinin, 1948; Faerman et al. 2017). This parasite taxon is not currently known in present-day faunas.

Linognathoides schizodactylus (Gerwel, 1954)

Type host: Spermophilus suslicus (Güldenstaedt, 1770) (speckled ground squirrel).

Known distribution of parasite: Poland, Romania, and Ukraine (Gerwel, 1954; Durden and Musser, 1994).

Distribution of host: Poland, Romania, and Ukraine north to the Oka river and east to the Volga river in the Russian Federation (Thorington and Hoffmann, 2005).

Taxonomic notes: Neohaematopinus schizodactylus Gerwel, 1954 represents a previous combination for this species.

Linognathoides traubi (Rubin, 1946)

Type host: Notocitellus adocetus (Merriam, 1903) (tropical ground squirrel).

Known distribution of parasite: Mexico: Michoacan (Rubin, 1946; Sánchez-Montes et al., 2013).

Distribution of host: Mexico (Jalisco, Michoacan and Guerrero provinces) (Thorington and Hoffmann, 2005).

Taxonomic notes: Neohaematopinus traubi Rubin, 1946 is a previous combination for this species.

Linognathoides urocitelli **Durden, Robinson, Cook, McLean, Batsaikhan, and Greiman, n. sp.**

Type host: Urocitellus undulatus (Pallas, 1778) (long-tailed ground squirrel).

Known distribution of parasite: Mongolia.

Distribution of host: Russian Federation (Siberia, Transbaikalia), Kazakhstan, Mongolia, China (Heilungjiang and Xinjiang) (Thorington and Hoffmann, 2005).

DISCUSSION

The discovery of this new species adds to our knowledge of the host associations and geographical distribution of the genus *Linognathoides* and reinforces associations of the genus with ground-dwelling squirrels across the Palearctic region. Given that sucking lice have not been recorded from several other species of ground-dwelling squirrels, especially in the Palearctic and Afrotropical regions, additional new species of *Linognathoides* may await discovery. We suspect that many of the known species of *Linognathoides* have larger geographical distributions than currently reported and that some may occur throughout the ranges of their hosts. This is likely true for *L. urocitelli* n. sp. as well, given the large distribution of its host across the central Asian region (McLean et al., 2018). Further collecting of ectoparasites from these host species will provide more data on the geographical distributions of these lice. From a phylogenetic perspective, the host associations of the genus *Linognathoides* are very broad. Although all recorded hosts are ground-dwelling squirrels, they represent 2 different tribes within the subfamily Xerinae. There are additional members and tribes of this subfamily in Africa that are more scansorial/arboreal that could be parasitized by undescribed species of lice.

It is not currently known if lice belonging to this genus are vectors of any pathogens. However, some species (*L. citelli, L. laeviusculus, L. urocitelli* n. sp., and possibly also *L. schizodactylus*) parasitize central Asian ground squirrels that are known to be reservoir hosts of plague bacilli. *Linognathoides laeviusculus* also parasitizes various species of ground squirrels in plague-endemic regions of North America. Further, *L. cynomyis* parasitizes black-tailed prairie dogs in parts of western North America, where sylvatic plague circulates in some prairie dog populations (Durden and Hinkle, 2019; Eads, 2019). Given that the human body louse (*Pediculus humanus humanus*) is a competent laboratory vector of *Yersinia pestis,* the causative agent of plague (Houhamdi et al., 2006), *Linognathoides* lice could be supplementary enzootic vectors of this zoonotic pathogen between rodents in central Asia and perhaps in North America (Eads, 2019). Similarly, *Rickettsia typhi* Wolbach and Todd, 1920, the causative agent of murine typhus, has been detected in the sucking louse *Enderleinellus marmotae* Ferris, 1919, in South Carolina (Reeves et al., 2005). Therefore, it should be considered that *R. typhi* could also be detected in *L. marmotae*, because both species of lice parasitize *M. monax* as documented by Kim et al. (1986) and Durden and Musser (1994). Further research on the possible role of these and other species of sucking lice that parasitize wild mammals, as enzootic vectors of zoonotic disease agents, is warranted.

The sucking louse fauna of Mongolia has been documented by Kéler (1967) and Kristofik (1999), but evidently is still incompletely known. We advocate further collections and studies of ectoparasites, including sucking lice, of Mongolian mammals from both a taxonomic and vectorial perspective.

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