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A new genus and new species of sucking louse (Phthiraptera: Anoplura: Enderleinellidae) from the particoloured flying squirrel (*Hylopetes alboniger*) in Laos, and an updated identification key to enderleinellid genera

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Abstract

Hylophthirus spinosus, **new genus and new species** (Phthiraptera: Anoplura: Enderleinellidae), is described from specimens collected from the particoloured flying squirrel, *Hylopetes alboniger* in Khammouane Province, Laos (Lao People's Democratic Republic). Both sexes of the new louse are illustrated with stacked microphotographs, scanning electron micrographs and line drawings. An updated morphological identification key to the six genera (*Atopophthirus, Enderleinellus, Hylophthirus, Microphthirus, Phthirunculus* and *Werneckia*) now recognised within the family Enderleinellidae is presented. The new genus is unique within the Enderleinellidae in having massive spines (modified setae) on some abdominal sternites, partially bulbous 5th antennal segments, mesothoracic spiracles borne on protuberances and the morphology of the genitalia of both sexes. Tables showing all genera of sucking lice that include species parasitising sciurids (squirrels, chipmunks, susliks and marmots), and all known species of enderleinellids, with their known host associations and geographical distributions are included and briefly discussed in relation to the new genus and species.

Key words: Phthiraptera, Anoplura, Enderleinellidae, sucking lice, new genus, new species, *Hylophthirus spinosus, Hylopetes alboniger*, host associations, Laos

Introduction

Sucking lice (Phthiraptera: Anoplura) are permanent, hemimetabolous, haematophagous ectoparasitic insects of eutherian mammals that, as a group, co-occur throughout the world with their various hosts (Durden 2019). Currently, 16 families, 49 genera and more than 550 species of sucking lice are recognised with several additional species yet to be described (Durden & Musser 1994; Durden *et al.* 2022). Significant host specificity has been reported for most species of sucking lice with many species parasitising a single host species (Durden & Musser 1994). However, some species parasitise a small cluster of closely related, usually congeneric, host species, while a few species, such as *Enderleinellus suturalis* (Osborn) and the mouse louse, *Polyplax serrata* (Burmeister), parasitise several different (but phylogenetically closely related) host species (Kim *et al.* 1986; Durden & Musser 1994; Martinů *et al.* 2018).

Members of the sucking louse family Enderleinellidae Ewing are exclusively parasites of sciurid rodents (squirrels, chipmunks, susliks and marmots), and are widely distributed on this group of hosts in North and South America, Eurasia, and Africa (Ferris 1919; Werneck 1947; Kim 1966, 2006; Musser *et al.* 2010). Enderleinellid lice are the smallest parasitic lice known, with adult body lengths ranging from 0.35 mm to 0.8 mm. Five genera are currently recognised within the Enderleinellidae: *Enderleinellus* Fahrenholz, 1912 is the most speciose

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genus with 47 recognised species that collectively occur throughout most of the global range of the Sciuridae (Kim & Ludwig 1978); *Werneckia* Ferris, 1951 is the next most speciose genus with five known species that parasitise squirrels in the Afrotropical region (Ledger 1980; Pajot 2000); the monotypic *Microphthirus* Ferris, 1919 parasitises North American flying squirrels (Kim *et al.* 1986), and members of the remaining two described enderleinellid genera, *Atopophthirus* Kim, 1977 (with two species), and *Phthirunculus* Kuhn & Ludwig, 1965 (monotypic) are ectoparasites of large flying squirrels (*Petaurista* spp.) in Southeast Asia (Kuhn & Ludwig 1965; Kim 1977).

In this paper, we describe a new species and a new genus, the sixth within the family Enderleinellidae. Like members of *Atopophthirus* and *Phthirunculus*, the new species parasitises a species of flying squirrel native to Southeast Asia, a pygmy flying squirrel (genus *Hylopetes*), and has several unique morphological characters that warrant its placement in a new genus of sucking lice. We also provide a user-friendly dichotomous key for the morphological identification of the six genera of adult lice belonging to the family Enderleinellidae. Finally, we briefly discuss the host associations and geographical distributions of some members of these genera in relation to the new louse species.

Material and methods

Collection of samples: Specimens (host and lice) examined in this study were collected during a field trip to Laos (Lao People's Democratic Republic) in November 2008. The small mammal survey was carried out in Khammouane Province, 18 km north of Thakhek, near Ban Doy Village, (17º33′26″N, 104º49′28″E), 140 m above sea level. A single *Hylopetes alboniger* specimen was obtained from the food market in Ban Doy Village. Lice were brushed from the host pelage, collected and then stored in a labeled vial containing 70% ethanol.

Specimen preparations: Selected lice (6 males, 3 females) were removed from the vial and the ventral anterior abdomen was punctured with a size 000 insect pin. These lice were then slide-mounted for light microscopy following Palma (1978) with minor modifications. Lice were cleared in a 10% potassium hydroxide solution for ~24 hours and then neutralised in 10% aqueous acetic acid for ~30 min, rinsed in distilled water for ~1 hour, dehydrated through an ethanol series (70%, 95%, 100% X 2 each for 15 min), further cleared in xylene for 15 min, slide-mounted in Canada balsam and oven-dried for 4 weeks. Additionally, two louse specimens from which DNA had been extracted, were slide-mounted from ethanol directly into Polyvinyl Alcohol (PVA) medium (Bioquip Products, Rancho Dominguez, California, U.S.A.).

Morphological examination: Slide-mounted lice were examined at 100–400X magnification under an Olympus BH-2 phase contrast high-power microscope (Olympus Corporation of the Americas, Center Valley, Pennsylvania) with an Ikegami MTV-3 video camera attachment and monitor (Ikegami Electronics, Neuss, Germany). Measurements were made using a calibrated ocular micrometer. Images of slide-mounted specimens were prepared using a BK Plus Lab System (Visionary Digital, Boulder, Colorado, U.S.A.), stacked with Helicon Focus version 4.77. Descriptive format and abbreviations for morphological structures and setae follow Kim & Ludwig (1978) and Durden *et al.* (2022). Host sciurid names follow Thorington & Hoffmann (2005) with updated nomenclatural changes to Holarctic ground squirrel taxa by Helgen *et al.* (2009) as listed in the Mammal Diversity Database (https://www.mammaldiversity.org/index.html).

Scanning electron microscopy: Specimens were prepared for scanning electron microscopy (SEM) as follows: dehydrated in a graded ethanol series; 70% for 30 min, 80% for 30 min, 90% for 1 hr, 95% overnight, and 100% for 24 hr. Then, specimens were chemically dried using a graded ethanol/hexamethyldisilazane (HMDS) series; 2(EtOH):1(HMDS) for 2 hr, 1:1 for 2 hr, 1:2 for 3 hr, 1:3 overnight, pure HMDS for 6 hr, followed by replacement of HMDS with new pure HMDS, and allowed to evaporate overnight. Dried specimens were mounted on aluminum stubs, sputter coated with gold/palladium, and visualised on a JEOL JSM6610LV Scanning Electron Microscope (JEOL U.S.A., Peabody, Massachusetts) at 15KV. Multiple images were captured and stitched together using the photomerge function in Adobe Photoshop CC.

DNA extraction: DNA was extracted from two selected lice, for potential gene sequencing following techniques detailed in Durden *et al*. (2022). Unfortunately, no louse DNA could be amplified for sequencing.

Systematics

Phthiraptera Haeckel, 1896
Phthiraptera Haeckel, 1896: 703.

Anoplura Leach, 1815
Anoplura Leach, 1815: 77.

Enderleinellidae Ewing, 1929
Enderleinellidae Ewing, 1929: 132.

Hylophthirus Durden, Beati, Greiman & Abramov, new genus
Type species: *Hylophthirus spinosus* new species

Diagnosis. Morphologically, *Hylophthirus* differs from all other enderleinellid genera by several unique features. In the head, *Hylophthirus* lacks large, ventral protuberances (present in *Microphthirus*). The antennae of *Hylophthirus* are 5-segmented (4-segmented in *Phthirunculus*) and have an elongate, slightly bulbous terminal segment (shorter and parallel-sided in all other enderlenellid genera). The small mesothoracic spiracles of *Hylophthirus* are each uniquely borne on a dorsal thoracic protuberance. The thoracic sternal plate is well developed and very broad in *Hylophthirus* (absent in *Atopophthirus*), whereas this structure is typically longer than broad in other enderleinellids. On the abdomen of *Hylophthirus*, there are no paired accessory sternal plates on segment two (which are diagnostic for members of the genus *Enderleinellus*) or on any other abdominal segments. The presence of paratergal plates on each side of abdominal segments 2, 3, 4, 7 and 8 in *Hylophthirus* is unique. *Phthirunculus* lacks paratergal plates and members of the other enderleinellid genera have paratergal plates on other abdominal segments. Males and females of *Hylophthirus* have distinct abdominal sternites and broad tergites (sternites and tergites are absent in *Werneckia*) and the sternites have massive lateral spines (modified setae) in both sexes, which is unique within the Enderleinellidae. The male genitalia of *Hylophthirus* have uniquely very narrow, curved parameres posterior to a broad basal apodeme. The female genitalia in *Hylophthirus* have unique gonopods that are extremely large, especially gonopods IX, that extend well beyond the apex of the abdomen.

Description: Very small size (body length of adults, ~0.450–0.585 mm). Head longer than wide with broadly rounded anterior and lateral margins; distinct dorsal head suture present; antennae 5-segmented with slightly bulbous terminal segment; no sexually dimorphic antennal segments (Fig. 1). Thorax wider than long, lacking notal pit; thoracic sternal plate broad (Figs, 3B, 4B); mesothoracic spiracles small, each borne on protuberance; forelegs and midlegs small, each with small acuminate tibiotarsal claw; hindlegs much larger with massive tibiotarsal claw (Figs 3–4). Abdomen wider than thorax with five paratergal plates on each side—borne on abdominal segments 2, 3, 4, 7 and 8; paratergal plate I small, lacking spiracle and with pair of short paratergal setae (PrS); paratergal plate II with small spiracle and pair of slightly longer PrS; paratergal plate III with small spiracle and pair of long PrS; paratergal plate IV lacking spiracle and with pair of long PrS; paratergal plate V lacking spiracle and with pair of extremely long PrS; small lateral spiracles present on each of abdominal segments 5 and 6 (Figs 2–4); Tergites broad and relatively unmodified; sternites present—some anterior sternites with unique massive lateral spines (modified setae). No sternal accessory plates on segment two or on other abdominal segments (Figs 3–4). Male genitalia highly modified with very narrow parameres, which are shorter than basal apodeme (Fig. 3D). Female genitalia highly modified with small subcircular subgenital plate, flanked on each side by broad accessory plate; gonopods, especially gonopods IX, very large and extending well beyond apex of abdomen (Fig. 4D).

Host distribution: Only known from the particoloured flying squirrel, *Hylopetes alboniger* (Hodgson) (Rodentia: Sciuridae).

Geographical range: Currently, the new louse genus is only known from Laos.

Etymology. The new genus name is derived from the first four letters of the host genus and appended by *phthirus* from *phtheir*, Greek for louse. Gender masculine.

Identification Key to genera of adult lice in the family Enderleinellidae

1a. Antennae 5-segmented; abdomen with paratergal plates 2
1b. Antennae 4-segmented; abdomen without paratergal plates (on *Petaurista*, Southeast Asia) . . . . . *Phthirunculus* Kuhn & Ludwig
2a. Ventral head and first antennal segment each with a sclerotised plate bearing 3–5 large protuberances (on *Glaucomys*, North America) . . . . . *Microphthirus* Ferris
2b. Ventral head and first antennal segment lacking plates and protuberances 3
3a. Thoracic sternal plate absent (on *Petaurista*, Southeast Asia) . . . . . *Atopophthirus* Kim
3b. Thoracic sternal plate present and distinct 4
4a. Abdominal segment 2 with a distinct ventral sclerite on each side (on various sciurids, North America, South America, Eurasia, Africa). . . . . *Enderleinellus* Fahrenholz
4b. Abdominal segment 2 lacking a distinct ventral sclerite on each side 5
5a. Abdomen lacking sternal and tergal plates (on various squirrels, Africa) . . . . . *Werneckia* Ferris
5b. Abdomen with distinct sternal and tergal plates (on *Hylopetes,* Southeast Asia) . . . . . *Hylophthirus* new genus

Hylophthirus spinosus Durden, Beati, Greiman & Abramov, new species

(Figs. 1–4)

Type Host: *Hylopetes alboniger* (Hodgson, 1836)—particoloured flying squirrel (Rodentia: Sciuridae: Pteromyinae).

Type locality: Laos.

Description

Male (n = 6) (Figs. 1A, 2A, 3A, 3B, 3C, 3D). Total length of Holotype, 0.495 mm (mean, 0.486 mm, range, 0.464–0.525 mm). Integument distinctly mamillated in certain areas and smooth in other regions (Fig. 2A). Head longer than wide with broadly rounded lateral margins and broadly tapering anterior margin; maximum head width of Holotype, 0.095 mm (mean, 0.093 mm, range, 0.091–0.097 mm); dorsal head suture wide and distinct. Ventral head with large, sclerotised plate with anterolateral lobe on each side. One dorsal posterior central head seta, 2 dorsal marginal head setae, 2 sutural head setae, 1 supraantennal head seta, 2 preantennal head setae, 1 dorsal anterior head seta, 2 anterior marginal head setae and 1–2 oral setae on each side. Antennae five-segmented; segment 1 wider than long, segments 2 and 5 much longer than wide, segments 3 and 4 slightly longer than wide, segment 5 slightly bulbous and bearing terminal sensilla. Thorax wider than head; maximum thorax width of Holotype, 0.154 mm (mean, 0.156 mm, range, 0.154–0.159 mm). Thoracic sternal plate (Fig. 3B) very broad and subtrapezoidal with acuminate anterolateral apex on each side. Notal pit absent. Mesothoracic spiracles small (diameter, 0.005 mm in all specimens) and each borne on distinct protuberance; dorsal mesothoracic seta adjacent to spiracle; two shorter more central dorsal setae present on each side of thorax. Forelegs and midlegs each terminating in small tibiotarsal claw, hindlegs terminating in massive tibiotarsal claw with distinct striations; all legs with subtriangular coxae, fore and mid coxae abutting each other ventrally, gap present between mid and hind coxae ventrally. Abdomen wider than thorax with 9 broad tergites dorsally, abutting each other; tergite 2 extending posteriorly on each side to partially cover sternite 3 laterally. Dorsally, 1 small tergal abdominal seta (TeAS) on each side on tergite 1, 2 small TeAS on each side on tergite 2, 2 longer TeAS on each side on tergites 3 and 4, 1 long TeAS on each side on tergites 5–7, 1 long medial TeAS and 1 short lateral TeAS on each side on tergite 8 and 1 short TeAS on each side on tergite 9. Posteriorly, ~4 short Dorsal Central Abdominal Setae (DCAS), followed by 1 short DCAS and 4 longer terminal setae on each side. Ventrally, 4 narrow sternites (on segments 3–6); 2 long, narrow Ventral Central Abdominal Setae (VCAS) on each side, followed by 2 long, robust Sternal Abdominal Setae (StAS) on each side on each sternite, then 1 long VCAS, 1 short VCAS and 2 short VCAS on each side. Lateral StAS on sternites 2–4 massive, each curving to acuminate posterior apex (Fig. 3C). Paratergal plates (Fig.3C) present on abdominal segments 2, 3, 4, 7 and 8; all plates subtriangular; paratergal plate I small, lacking spiracle and with pair of short PrS; paratergal plate II with small spiracle and pair of slightly longer PrS; paratergal plate III with small spiracle and pair of long PrS; paratergal plate IV lacking spiracle and with pair of long PrS; paratergal plate V lacking spiracle and with pair of extremely long PrS; small lateral spiracles, unaccompanied by paratergal plates, present on each of abdominal segments 5 and 6 (between paratergal plates III and IV).

Genitalia (Figs 3A, 3D) with subgenital plate (Fig. 3A) extending anteriorly to abdominal segment 7, with sinuous anterior and lateral margins, narrowing centrally, then expanding posteriorly. Basal apodeme (Fig. 3D) broad, terminating in large, wide, bifid arms posteriorly; parameres (Fig. 3D) curved and extremely narrow; pseudopenis

with very narrow anterior margins and extending posteriorly well beyond apices of parameres; aedeagus (Fig. 3D) elongated and narrowing posteriorly to gonopore.

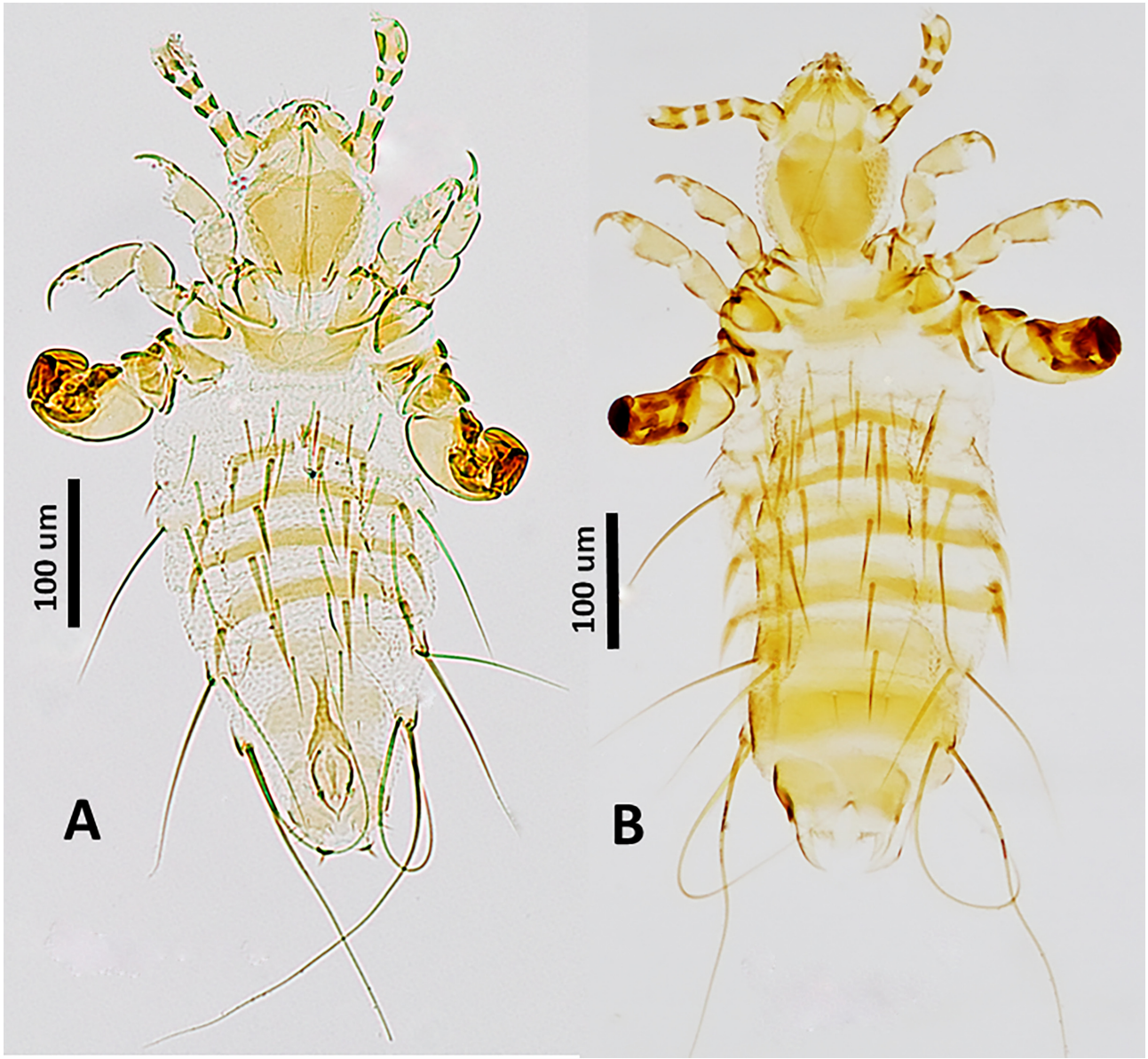

FIGURE 1. *Hylophthirus spinosus* **n. gen., n. sp.** *C*leared, slide-mounted specimens. **A.** Male. **B.** Female.

Female (n = 3) (Figs. 1B, 2B, 4A, 4B, 4C, 4D). Morphology as in male unless otherwise stated. Total body length of Allotype, 0.545 mm (mean, 0.554 mm, range, 0.534–0.583 mm). Maximum head width in Allotype, 0.099 mm (mean, 0.100 mm, range, 0.099–0.110 mm), with ventral sclerotised plate differing slightly in shape from that of male (Figs. 2B, 4A). Maximum thorax width, 0.164 mm (mean, 0.162 mm, range, 0.158–0165 mm); thoracic sternal plate (Fig. 4B) similar to that of male but subterminal hump present anterolaterally on each side. Abdomen with 6 broad, well separated, tergites dorsally and 6 sternites ventrally; sternites 1–5 narrow, sternite 6 broad. One long DCAS anteriorly, then 2 long TeAS on tergites 1–4, followed by 1 short TeAS on tergite 5 on each side. Sternite 1 with 2 long, narrow StAS, sternites 2–5 each with 2 extremely stout StAS, with lateral StAS as massive acuminate spines, and sternite 6 with 1 short StAS on each side. Paratergal plates, paratergal spiracles and PrS as in male although exact shape of paratergal plates slightly different (Fig. 4C). Genitalia (Fig. 4D) with small, poorly sclerotised, subcircular subgenital plate with broadly curved posterior and anterior margins; anterior margin with shallow central notch; posterior margin with 10 small setae; subgenital plate flanked on each side by broad accessory plate each bearing 4 small setae along curved posterior margin. Gonopods VIII and IX greatly enlarged and extending well beyond apex of abdomen; gonopods VIII smaller than, and internal to, gonopods IX, with

straight lateral margins and each bearing 2 small setae, medial seta smaller than lateral seta; gonopods IX massive and possibly having expandable integument (see one gonopod IX in Fig. 2B), curving medially to acuminate apex and bearing 2 small setae near both medial and lateral margins. Genital opening flanked by 8–10 small setae and one longer seta on each side; 3 short setae on each side at apex of abdomen.

The host specimen is deposited in the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg, Russia (ZIN). Collection data: Nº ZIN 98664; field Nº AA, AT 106; 17 November 2008; Laos: Khammouane Province, 18 km north of Thakhek, near Ban Doy Village (17⁰33’26”N, 104⁰49’28”E), elevation 140 m. Collectors: A.V. Abramov and A.N. Tikhonov.

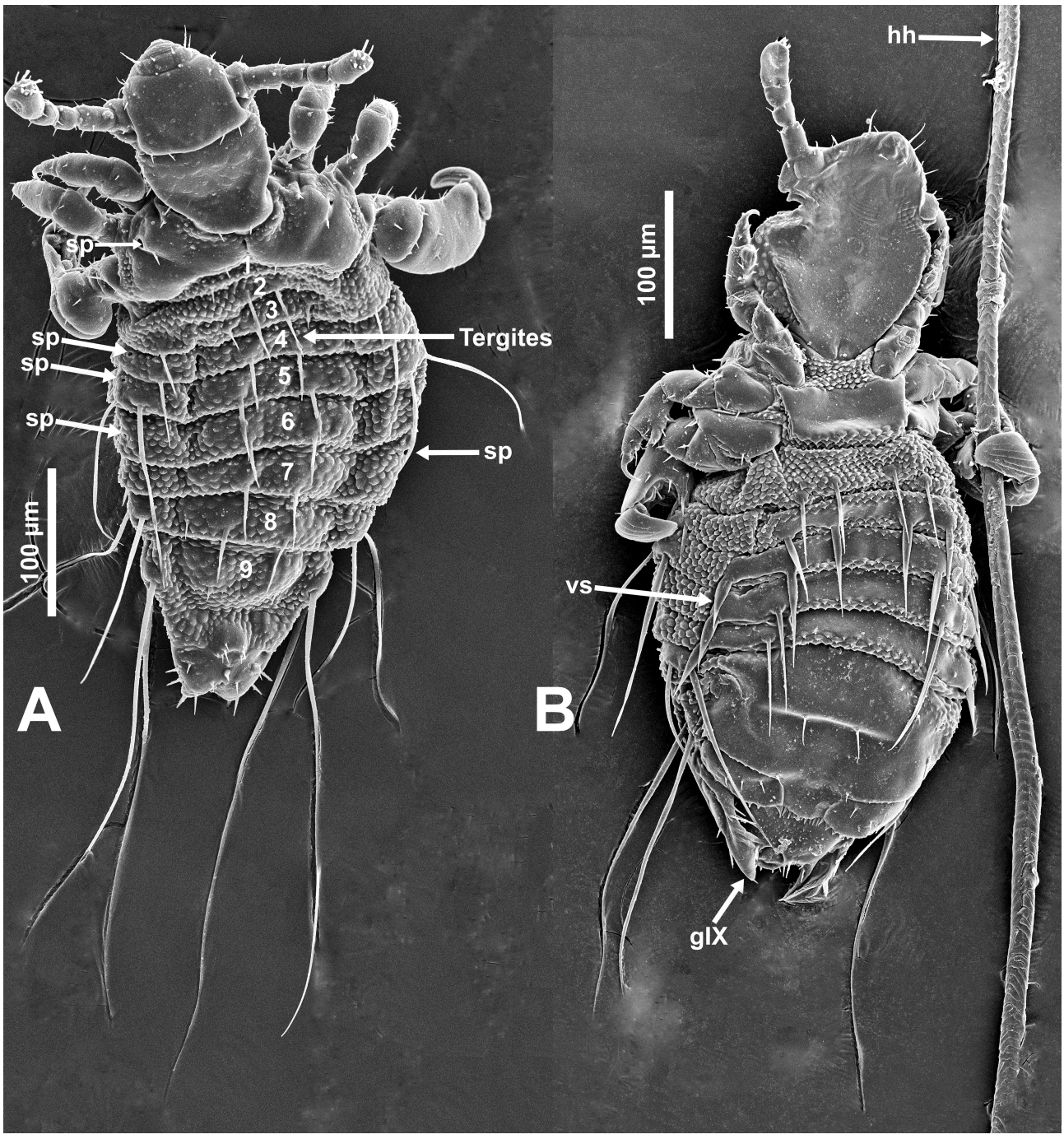

FIGURE 2. *Hylophthirus spinosus* **n. gen., n. sp.** Scanning electron micrographs of adults. **A.** Dorsal male. **B.** Ventral female (with hind tibiotarsal claw grasping host underfur hair). Numbers refer to abdominal tergites 1 through 9. (gIX = gonopod IX, hh = host hair, sp = spiracles, vs = ventral abdominal spine).

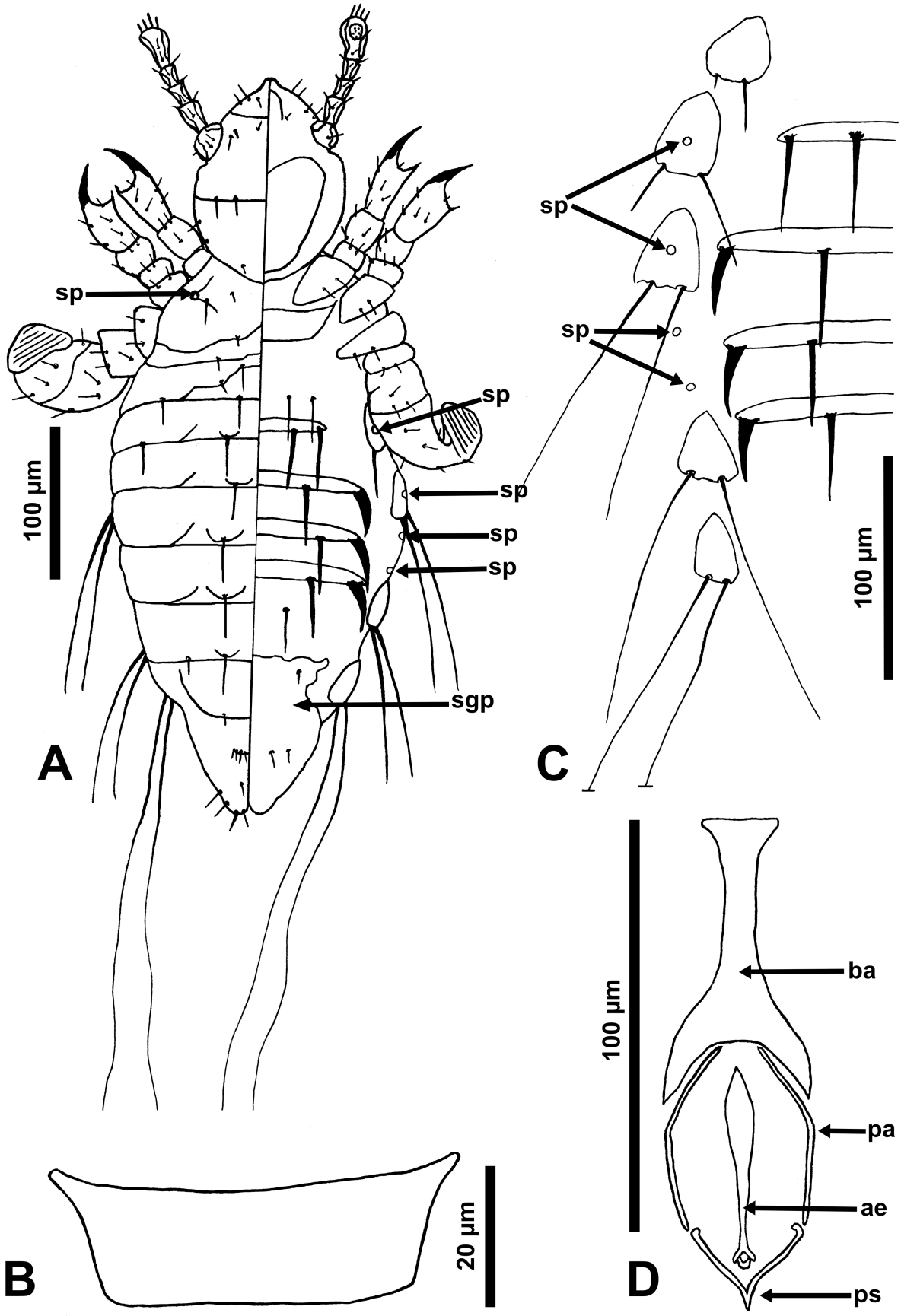

FIGURE 3. *Hylophthirus spinosus* **n. gen., n. sp.** line drawings of male. **A.** Dorsoventral views (dorsal view on left of midline; ventral view on right of midline). **B.** Thoracic sternal plate. **C.** Paratergal plates and adjacent sections of ventral sternites showing spines. **D.** Genitalia (ae = aedeagus, ba = basal apodeme, pa = paramere, ps = pseudopenis; sgp = subgenital plate; sp = spiracles).

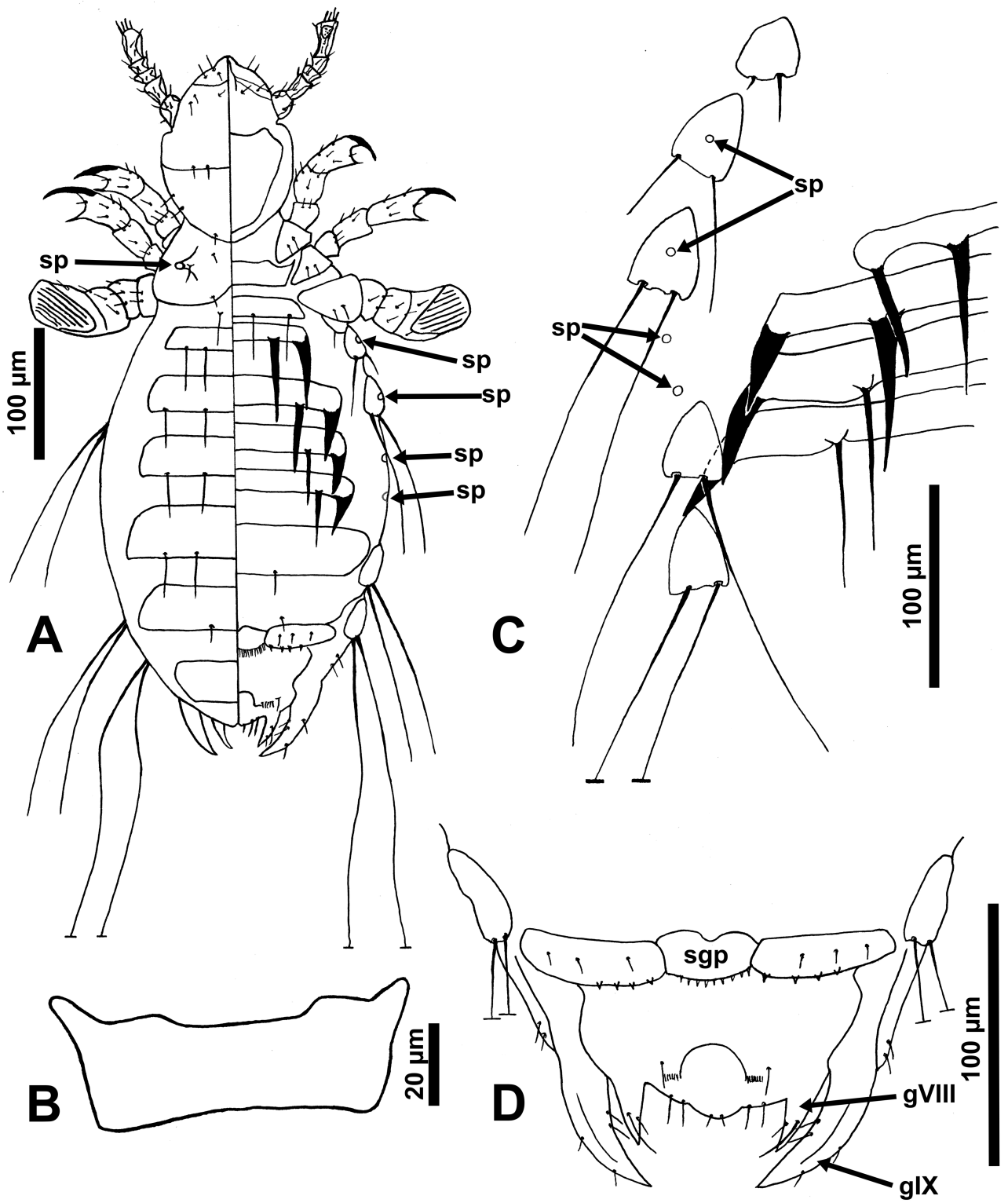

FIGURE 4. *Hylophthirus spinosus* **n. gen., n. sp.** line drawings of female. **A.** Dorsoventral views (dorsal view on left of midline; ventral view on right of midline). **B.** Thoracic sternal plate. **C.** Paratergal plates and adjacent sections of ventral sternites showing spines. **D.** Genitalia and adjacent structures (gVIII = gonopod VIII, gIX = gonopod IX, sgp = subgenital plate, sp = spiracles).

Material examined

Type material. Holotype ♂ with data as above for the host (USNMENT 00981917); deposited in the Department of Entomology, U.S. National Museum of Natural History (Smithsonian Institution), Washington D.C., U.S.A.

(USNMNH). **Paratypes:** 1♂, 2♀ (USNMENT 00981918) same data as holotype, deposited in USNMNH. 1♂, 1♀ (L3865, L3866) same data as holotype, deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia. 1♂, 1♀ (L3861, L3862) same data as holotype, deposited in the collection of the first author which is willed to the USNMNH.

Non-type material: 2♂ (L3863, L3864), same data as type material. These specimens are slightly distorted following DNA extractions. Deposited in the collection of the first author.

Etymology. The species epithet refers to the robust spines (modified setae) on the ventral abdomen of both sexes of the new species.

Discussion

The description of *Hylophthirus* increases the number of known genera of enderleinellid sucking lice from five to six. The updated identification key to genera of adult Enderleinellidae presented above is partly based on the key published by Kim (1977), but it has been modified to exclude morphological characters that may be difficult for non-experts to visualise in some specimens (whether or not paratergal plates are connected to other sclerotised abdominal plates).

Hylophthirus spinosus is the second smallest species of parasitic louse in the world, after the Nearctic *Microphthirus uncinatus* Ferris, which is the smallest known species (adult male body length, 0.35 mm; adult female body length, 0.45 mm) (Kim *et al.* 1986). The new louse is smaller than 34 other species of enderleinellids examined by us during this study and smaller than the sizes listed for the types of other described enderleinellids. The size was not given for a few of the early enderleinellid descriptions. The diminutive size of the new louse may explain, in part, why it has remained undocumented until now. Larger lice have been reported from three other species of Southeast Asian pygmy flying squirrels belonging to the genus *Hylopetes*: *Neohaematopinus kinabalensis* Johnson has been reported from *Hylopetes lepidus* (Horsfield) (grey-cheeked flying squirrel) and *Neohaematopinus capitaneus* Johnson has been reported from both *Hylopetes phayrei* (Blyth) (Indochinese flying squirrel) and *Hylopetes spadiceus* (Blyth) (red-cheeked flying squirrel) (Johnson 1959, 1964; Durden & Musser 1994, Kazim *et al*. 2022). Furthermore, nymphs of an undetermined and possibly undescribed species of *Neohaematopinus* (in the collection of the first author, accession number L3867) were collected from *Hylopetes alboniger* in Laos (the same host individual from which *Hylophthirus spinosus* was collected). If adults of this *Neohaematopinus* species are collected from *H. alboniger* in the future, they should be compared to other species of *Neohaematopinus* from southeast Asia to determine their taxonomic status. It is intriguing to speculate whether other species of *Hylopetes* might also be parasitised by undescribed species belonging to *Hylophthirus*. Future collections of ectoparasites, including very small species that may have been overlooked in the past, should answer this question. *Hylophthirus spinosus* may occur in some other parts of Southeast Asia in addition to Laos, because the geographical distribution of the host, *H. alboniger*, ranges from Nepal and northern India to Indochina and China (Thorington & Hoffmann 2005).

Hylopetes alboniger may not be the only host of *Hylophthirus spinosus*, because several species of sucking lice, including some species of enderleinellids, have been recorded from multiple host species. Examples are: *Atopophthirus setosus* Chin, known to parasitise two species of *Petaurista* (giant flying squirrels); *Enderleinellus arizonensis* Werneck, *Enderleinellus deppei* Kim and *Enderleinellus hondurensis* Werneck, all known to parasitise multiple species of *Sciurus* (tree squirrels); *Enderleinellus dremomydis* Ferris, known from two species of *Dremomys* (Asian montane ground squirrels); *Enderleinellus kumadai* Kaneko, known from four species of *Callosciurus* (Oriental tree squirrels), and *Enderleinellus heliosciuri* Ferris, known from four species of *Heliosciurus* (sun squirrels), two species of *Protoxerus* (African giant squirrels), one species of *Paraxerus* (African bush squirrels) and one species of *Epixerus* (palm squirrel) (Table 2). Furthermore, two species of enderleinellids that parasitise Nearctic ground squirrels have been recorded from multiple hosts: *Enderleinellus osborni* Kellogg & Ferris, recorded from five ground squirrel species belonging to three different genera, and *Enderleinellus suturalis* (Osborn), recorded from 12 species of ground squirrel and two species of prairie dog, collectively belonging to nine different genera (Table 2). Therefore, it is possible that *Hylophthirus spinosus* could parasitise other species of flying squirrels belonging to the genus *Hylopetes*, or other closely related squirrels. As stated above, some other (larger) species of sucking lice are known to parasitise some species of *Hylopetes*, but very small lice, like *Hylophthirus*, may have been overlooked in previous ectoparasitological studies of these hosts.

TABLE 1. Families and genera of sucking lice that include species parasitic on members of the Sciuridae (squirrels, chipmunks, susliks and marmots).

Louse Families &Genera	Number of species	Host Tribe/s	Geographical Distributions
Enderleinellidae			
Atopophthirus	2	Pteromyini	Southeast Asia
Enderleinellus [b]	47	Nannosciurini, Funambulini, Protoxerini, Pteromyini, Sciurini	North America, South America, Eurasia, Africa
Hylophthirus new genus	1	Pteromyini	Southeast Asia
Microphthirus	1	Pteromyini	North America
Phthirunculus	1	Pteromyini	Southeast Asia
Werneckia	5	Protoxerini	Sub-Saharan Africa
Hoplopleuridae			
Hoplopleura Enderlein, 1904b [a,b]	19	Nannosciurini, Marmotini, Sciurini, Pteromyini	North America, Southern Asia
Paradoxophthirus Chin, 1989	1	Marmotini	Southeast Asia
Polyplacidae			
Johnsonpthirus Benoit, 1961	5	Protoxerini	Africa
Linognathoides Cummings, 1914	11	Marmotini, Xerini	North America, Central America, Eurasia, Africa
Neohaematopinus Mjöberg, 1910[a,b]	30	Nannosciurini, Pteromyini, Sciurini	North America, South America, Eurasia[c]
Polyplax Enderlein, 1904a[a]	1	Marmotini	Europe

[a] Except for *Hoplopleura, Neohaematopinus* and *Polyplax*, all known species in the remaining genera exclusively parasitise sciurid rodents.

[b] Three species of squirrel-associated lice, *Enderleinellus longiceps, Hoplopleura sciuricola* and *Neohaematopinus sciuri*, have accompanied their host, the eastern grey squirrel, *Sciurus carolinensis* Gmelin, from North America to some other parts of the world as intentional or accidental squirrel introductions [Thompson 1935; Davis 1951 (louse misidentified as *Neohaematopinus sciurinus*), Durden & Musser 1994].

[c] *Neohaematopinus callosciuri* has accompanied its intentionally introduced host, *Callosciurus erythraeus* (Pallas squirrel), from Taiwan to Japan (Shinozaki *et al*. 2003, 2004).

A rich fauna of sucking lice parasitises sciurids (squirrels, chipmunks, susliks and marmots) with representatives of 12 different louse genera known to be associated with members of this family of rodents throughout the world (Table 1). This far exceeds the number of sucking louse genera associated with any other family of mammals (Durden & Musser 1994; Kim 2006; Musser *et al.* 2010). The finding of a new genus parasitising a sciurid poses the possibility that additional sucking lice (new genera or species) might parasitise other sparsely studied sciurids. For example, no sucking lice have been reported from members of several other flying squirrel genera such as *Aeretes, Aeromys, Belomys, Biswamoyopterus, Eoglaucomys, Eupetaurus, Iomys, Pteromyscus* and *Trogopterus,* probably because members of these genera have not been examined, or have been inadequately sampled, for ectoparasites. Further, no sucking lice have been documented from any members of the Afrotropical family Anomaluridae (scaly-tailed squirrels). Collections of ectoparasites from these and other poorly studied squirrels will likely yield additional undescribed sucking lice and other parasites.

With the addition of *Hylophthirus spinosus*, the family Enderleinellidae comprises 55 species parasitic on sciurid rodents throughout the world (Table 2), (Ferris 1919; Werneck 1947; Kim 1966, 2006; Durden & Musser 1994). Members of the most speciose genus, *Enderleinellus,* are found worldwide except in southern Africa, where they are replaced by members of the genus *Werneckia* (Table 2). Members of the other four enderleinellid genera are exclusively ectoparasitic on flying squirrels, three of them (*Atopophthirus, Hylophthirus* and *Phthirunculus*) primarily in Southeast Asia (Kuhn & Ludwig 1965; Kim 1977), and *Microphthirus* in North America (Kim *et al.* 1986). However, one species currently assigned to the genus *Enderleinellus*—(*E. replicatus* Redikorzev, 1937, recorded from the Siberian flying squirrel, *Pteromys volans* in the Tatarstan Republic and eastern Siberia,

Russia—has a descriptive line drawing lacking certain morphological features present in other members of *Enderleinellus.* Additionally, *E. replicatus* exhibits distinct characters that suggest it could belong to an undescribed genus of enderleinellid lice associated with flying squirrels. The types of this louse need to be re-examined and re-evaluated.

TABLE 2. Species of Enderleinellinae, their known hosts and geographical distributions.

Louse Species	Host/s[a]	Geographical Distributions[b]
Atopophthirus emersoni Kim	*Petaurista elegans* (Müller)	Peninsular Malaysia
Atopophthirus setosus Chin	*Petaurista philippensis* (Elliot) *Petaurista alborufus* Milne-Edwards	China
Enderleinellus arizonensis Werneck	*Sciurus arizonensis* Coues *Sciurus alleni* Nelson *Sciurus nayaritensis* Allen	U.S.A., México
Enderleinellus blagoveshtchenskyi Sosnina & Ozerova	*Marmota baibacina* Kastschenko	Kyrgyzstan
Enderleinellus corrugatus Johnson	*Tamiops mcclellandii* (Horsfield) *Callosciurus erythraeus* (Pallas)	China, Thailand
Enderleinellus deppei Kim	*Sciurus deppei* Peters *Sciurus aureogaster* Cuvier *Sciurus granatensis* Humboldt	México, Nicaragua, Panamá
Enderleinellus disparilis Blagoveschtchensky	*Urocitellus undulatus* (Pallas)	Russia
Enderleinellus dolichocephalus Blagoveschtchensky	*Marmota camtschatica* (Pallas)	Russia
Enderleinellus dremomydis Ferris	*Dremomys pernyi* (Milne-Edwards) *Dremomys rufigenis* (Blanford)	China, Thailand
Enderleinellus euxeri Ferris	*Euxerus erythropus* (Geoffroy Saint-Hilaire)	Benin, Kenya, Liberia, Nigeria, Sudan
Enderleinellus extremus Ferris	*Sciurus aureogaster* Cuvier *Sciurus deppei* Peters	Guatemala, México
Enderleinellus ferrisi (Touleshkov)	*Spermophilus citellus* (Linnaeus)	Eastern Europe
Enderleinellus gambiani Kuhn &Ludwig	*Heliosciurus punctatus*(Temmiinck)	Liberia

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TABLE 2. (Continued)

Louse Species	Host/s[a]	Geographical Distributions[b]
Enderleinellus heliosciuri Ferris	*Heliosciurus undulatus* (True) *Heliosciurus gambianus* (Ogilby) *Heliosciurus ruwenzorii* (Schwann), *Heliosciurus rufobrachium* (Waterhouse), *Epixerus ebii* (Temminck) *Paraxerus cepapi* (Smith) *Protoxerus aubinnii* (Gray) *Protoxerus stangeri* (Waterhouse)	Angola, Democratic Republic of the Congo, Kenya, Liberia, Tanzania, Uganda
Enderleinellus hondurensis Werneck	*Sciurus variegatoides* Ogilby *Sciurus yucatanensis* Allen	Colombia, Honduras, México. Nicaragua, Panamá
Enderleinellus insularis Werneck	*Sciurus granatensis* Humboldt	Venezuela
Enderleinellus kaibabensis Kim	*Sciurus aberti* Woodhouse	U.S.A.
Enderleinellus kelloggi Ferris	*Sciurus griseus* Ord	North America
Enderleinellus krochinae Blagoveschtchensky	*Sciurus anomalus* Gmelin	Azerbaijan, Syria, Turkey
Enderleinellus kumadai Kaneko	*Callosciurus erythraeus* (Pallas) *Callosciurus finlaysoni* (Horsfield) *Callosciurus nigrovittatus* (Horsfield) *Callosciurus prevostii* (Desmarest)	Borneo, Malaysia, Taiwan, Thailand [c]
Enderleinellus larisci Ferris	*Lariscus insignis* (Cuvier)	Borneo
Enderleinellus longiceps Kellogg & Ferris	*Sciurus carolinensis* Gmelin *Sciurus niger* (Linnaeus)	North America [d]
Enderleinellus malaysianus Ferris	*Callosciurus caniceps* (Gray) *Callosciurus notatus* (Bodaert) *Callosciurus prevostii* (Desmarest)	Borneo, Malaysia, Myanmar, Thailand
Enderleinellus marmotae Ferris	*Marmota monax* (Linnaeus)	U.S.A.
Enderleinellus menetensis Ferris	*Menetes berdmorei* (Blyth)	Thailland
Enderleinellus mexicanus Werneck	*Sciurus aureogaster* Cuvier	México
Enderleinellus microsciuri Werneck	*Microsciurus mimulus* (Thomas) *Microsciurus alfari* (Allen)	Colombia, Panamá
Enderleinellus nannosciuri Ferris	*Nannosciurus melanotis* (Müller)	Java
Enderlenellus nayaritensis Kim	*Sciurus nayaritensis* Allen	México
Enderleinellus nishimarui Kaneko	*Funambulus pennanti* Wroughton	India, Nepal
Enderleinellus nitzschi Fahrenholz	*Sciurus vulgaris* Linnaeus	Eurasia

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TABLE 2. (Continued)

Louse Species	Host/s[a]	Geographical Distributions[b]
Enderleinellus oculatus Kim	*Sciurus oculatus* Peters *Sciurus alleni* Nelson	México
Enderleinellus osborni Kellogg & Ferris	*Otospermophilus beecheyi* (Richardson) *Otospermophilus variegatus* (Erxleben) *Urocitellus beldingi* (Merriam) *Xerospermophilus mohavensis* (Merriam) *Xerospermophilus tereticaudus* (Baird)	North America, México
Enderleinellus paralongiceps Kim	*Sciurus aberti* Woodhouse	U.S.A.
Enderleinellus platyspicatus Ferris	*Funambulus palmarum* (Linnaeus)	Sri Lanka
Enderleinellus pratti Kim	*Sciurus colliaei* Richardson	México
Enderleinellus propinquus Blagoveschtchensky	*Spermophilus fulvus* (Lichtenstein), *Spermophilus citellus* (Linnaeus), *Spermophilus suslicus* (Güldenstädt)	Eastern Europe, Kazakhstan
Enderleinellus puvensis Blagoveschtchensky	*Callosciurus inornatus* (Gray) *Callosciurus pygerythrus* (Geoffroy Saint Hilaire)	China
Enderleinellus replicatus Redikorzev	*Pteromys volans* (Linnaeus)	Russia
Enderleinellus sciurotamiasis Ferris	*Sciurotamias davidianus* (Milne-Edwards)	China
Enderleinellus suturalis (Osborn)	*Ictidomys tridecemlineatus* (Mïitchill), *Ammospermophilus harrisii* (Audubon & Bachman) *Ammospermophilus nelsoni* (Merriam), *Callospermophilus lateralis* (Say) *Cynomys gunnisoni* (Baird) *Cynomys leucurus* Merriam *Ictidomys mexicanus* (Erxleben), *Otospermophilus variegatus* (Erxleben), *Poliocitellus franklinii* (Sabine) *Urocitellus beldingi* (Merriam) *Urocitellus richardsonii* (Sabine) *Urocitellus townsendii* Bachman *Xerospermophilus spilosoma* (Bennett) *Xerospermophilus tereticaudus* (Baird)	North America, México
Enderleinellus tamiasciuri Kim	*Tamiasciurus hudsonicus* (Erxleben) *Tamiasciurus douglasii* (Bachman)	North America
Enderleinellus tamiasis Fahrenholz	*Eutamias sibiricus* (Laxmann)	Korea, Mongolia [c]
Enderleinellus tamiopsis Chin	*Tamiops* sp.	China

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TABLE 2. (Continued)

Louse Species	Host/s[a]	Geographical Distributions[b]
Enderleinellus urosciuri Werneck	*Sciurus igniventris* Wagner	Brazil
Enderleinellus venezuelae Ferris	*Sciurus granatensis* Humboldt	Venezuela
Enderleinellus zonatus Ferris	*Paraxerus ochraceus* (Huet) *Paraxerus palliatus* (Peters)	Kenya, South Africa
Hylophthirus spinosus Durden, Beati, Greiman & Abramov	*Hylopetes alboniger* (Hodgson)	Laos
Microphthirus uncinatus (Ferris)	*Glaucomys sabrinus* (Shaw) *Glaucomys volans* (Linnaeus)	North America
Phthirunculus sumatranus Kuhn & Ludwig	*Petaurista petaurista* (Pallas) *Petaurista alborufus* (Milne-Edwards) *Petaurista philippensis* (Elliot)	Southeast Asia
Werneckia africana Kaneko	*Funisciurus* sp.	Nigeria
Werneckia funisciuri Benoit	*Funisciurus carruthersi* Thomas	Central Africa
Werneckia minuta (Werneck)	*Paraxerus ochraceus* (Huet) *Paraxerus cepapi* (Smith) *Heliosciurus rufobrachium* (Waterhouse)	Central & East Africa
Werneckia nigeriensis Kaneko	*Funisciurus* sp.	Nigeria
Werneckia paraxeri (Werneck)	*Paraxerus palliatus* (Peters) *Paraxerus cepapi* (Smith)	Kenya, Namibia

[a] The type host for each species of louse is listed first if there are multiple recorded host species.
[b] Geographical distributions reflect known distributions for the lice; in almost all cases, known host distributions are larger.
[c] *Enderleinellus kumadai* has also been recorded on introduced, non-native *Callosciurus erythraeus* in Japan (Katahira *et al*. 2022) and in Belgium and France (Dozières *et al*. 2010).
[d] *Enderleinellus longiceps* has also been recorded on introduced, non-native *Sciurus carolinensis* in some other parts of the world (e.g, Britain) (Thompson 1935; Durden & Musser 1994).
[e] *Enderleinellus tamiasis* has also been recorded in France on introduced, non-native *Eutamias sibiricus* (Beaucournu *et al*. 2008).

Morphologically, all known enderleinellid lice have small forelegs and midlegs with small tibiotarsal claws and much larger hind legs with correspondingly much larger tibiotarsal claws (Werneck 1947; Kim 1966). The hindleg tibiotarsal claws serve as the main host attachment organs for enderleinellid lice (Fig. 2B). However, due to their small size, enderleinellid lice are only capable of grasping the underfur hairs of their hosts (Musser *et al.* 2010), which are the smallest and narrowest hairs of the host pelage (Knecht 2011). Larger sucking lice belonging to other genera, especially *Hoplopleura* Enderlein, 1904b and *Neohaematopinus* Mjöberg, 1910 may parasitise the same host species and even the same host individual (Durden 1980; Kim *et al.* 1986) but these larger lice have larger tibiotarsal claws that are adapted for grasping thicker (larger shaft diameter) coat or guard hairs. Consequently, it is possible for at least three species of sucking lice of different size groups to coexist on the same sciurid host utilizing different microhabitats while being physically adjacent to one another. This differential utilization of fine-scale resources may facilitate coexistence of members of various genera and species of lice on the same host. Cannon

(2010) showed that the diameter encompassed by anopluran tibiotarsal claws positively correlates with host hair diameters for host-specific sucking lice.

The discovery of a new genus and species of sucking louse on a pygmy flying squirrel warrants the need for further examination of other sciurids for lice, including members of other genera and species of flying squirrels, particularly the small and often challenging to sample enderleinellid lice. The intimate, and often unique, nature of these host-parasite associations, combined with the declining populations of many of the host species, also warrant co-conservation considerations. The adaptation and partial radiation of members of five out of the six enderleinellid genera with flying squirrels in North America and Asia suggest a strong selection for the evolution of unique morphotypes of these small lice on these highly specialised hosts. Hence, additional undescribed genera and species of enderleinellids may be found on members of other genera of flying squirrels.

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References

Beaucournu, J.-C., Pisanu, B. & Chapuis, J.-L. (2008) *Enderleinellus tamiasis* Fahrenholz, 1916 (Anoplura: Enderleinellidae), espèce importèe, implantèe, et nouvelle pour la faune de France. *Parasite*, 15, 175–178. https://doi.org/10.1051/parasite/2008152175

Benoit, P. L. G. (1961) Anoploures du Centre Africain. *Revue de Zoologie et de Botanique Africaines*, 63, 231–241.

Cannon, S.M. (2010) *Size correlations between sucking lice and their hosts including a test of Harrison's rule.* M.S. Thesis, Georgia Southern University, Statesboro, Georgia, 131 pp.

Chin, T.-H. (1989) *Paradoxophthirus*, a new generic name for *Hoplopleura emarginata* Ferris, 1922 (Anoplura: Polyplacidae). *Journal of Guiyang Medical College*, 14, 251–255. [in Chinese with English summary]

Cummings, B.F. (1914) Descriptions of five new species of Anoplura and Mallophaga. *Bulletin of Entomological Research*, 5, 155–177 https://doi.org/10.1017/S0007485300034039

Davis, D.H.S. (1951) First record of a louse (*Neohaematopinus sciurinus*) from the American grey squirrel in the Cape. *Journal of the Entomological Society of South Africa*, 14, 26. [https://hdl.handle.net/10520/AJA00128789_4405]

Dozières, A., Pisanu, B., Gerriet, O., Lapeyre, C., Stuyck, J. & Chapuis, J.-L. (2010) Macroparasites of Pallas's squirrels (*Callosciurus erythraeus*) introduced into Europe. *Veterinary Parasitology*, 172, 172–176. https://doi.org/10.1016/j.vetpar.2010.04.021

Durden, L A. (1980) Seasonal abundance of fleas (Siphonaptera) and sucking lice (Anoplura) on gray squirrels, *Sciurus carolinensis*, in central Tennessee, U.S.A. *Journal of Medical Entomology*, 17, 483–484. https://doi.org/10.1093/jmedent/17.5.483

Durden, L.A. (2019) *Lice* (*Phthiraptera*). *In:* Mullen, G.R. & Durden, L.A. (Eds.), *Medical and Veterinary Entomology*. *3rd Edition*. Elsevier Press, London, pp. 79–106 https://doi.org/10.1016/B978-0-12-814043-7.00007-8

Durden, L.A. & Musser, G.G. (1994) The sucking lice (Insecta, Anoplura) of the world: a taxonomic checklist with records of mammalian hosts and geographical distributions. *Bulletin of the American Museum of Natural History*, 218, 1–90. [http://hdl.handle.net/2246/825]

Durden, L.A., Robinson, C., Cook, J.A., Bell, K.C., Nyamsuren, B. & Greiman, S.E. (2022) Sucking lice (Phthiraptera: Anoplura) parasitizing Mongolian rodents with the description of a new species of *Hoplopleura* from mountain voles (*Alticola* spp.). *Journal of Parasitology*, 108, 353–365. https://doi.org/10.1645/22-2

Enderlein, G. (1904a) Läuse-Studien. Über die Morphologie, Klassifikation und sytematische Stellung der Anopluren nebst Bemerkungen zur Systematik der Insektenordnungen. *Zoologischer Anzeiger*, 28, 121–147.
Enderlein, G. (1904b) Läuse-Studien. II. *Zoologischer Anzeiger*, 28, 220–223.
Ewing, H.E. (1929) *A manual of external parasites*. Baillière, Tindall & Cox, London, xvi + 225 pp. https://doi.org/10.2307/3271887
Fahrenholz, H. (1912) Diagnosen neuer Anopluren. *Zoologischer Anzeiger*, 39, 54–56.
Ferris, G.F. (1919) Contributions toward a monograph of the sucking lice. Part I. *Leland Stanford Junior University Publications University Series* (No Volume Number), 1–51.
Ferris, G, F. (1951) The sucking lice. *Memoirs of the Pacific Coast Entomological Society*, 1, 1–320. https://doi.org/10.5962/bhl.title.149669
Haeckel, E. (1896) *Systematische Phylogenie. 2. Theil. Systematische Phylogenie der wirbellosen Thiere (Invertebrata).* Verlag von Georg Reimer, Berlin, 720 pp. https://doi.org/10.1515/9783111443935
Helgen, K.M, Cole, F.R., Helgen, L.E. & Wilson, D.E. (2009) Generic revision of the Holarctic ground squirrel genus *Spermophilus*. *Journal of Mammalogy*, 90, 270–305. https://doi.org/10.1644/07-MAMM-A-309.1
Johnson, P.T. (1959) The rodent-infesting Anoplura (sucking lice) of Thailand, with remarks on some related species. *Proceedings of the United States National Museum*, 110, 569–598. https://doi.org/10.5479/si.00963801.110-3421.569
Johnson, P.T. (1964) The hoplopleurid lice of the Indo-Malayan subregion (Anoplura: Hoplopleuridae). *Miscellaneous Publications of the Entomological Society of America*, 4, 67–102. https://doi.org/10.4182/QZCU7927.4-3.3
Katahira, H., Eguchi, Y., Hirose, S., Ohtani, Y., Banzai, A., Ohkubo, Y. & Shimamaoto, T. (2022) Spillover and spillback risks of ectoparasites by an invasive squirrel *Callosciurus erythraeus* in Kanto region of Japan. *International Journal for Parasitology: Parasites and Wildlife*, 19, 1–8. https://doi.org/10.1016/j.ijppaw.2022.07.006
Kazim, A.-R., Houssaini, J., Tappe, D. & Heo, C.-C. (2022) An annotated checklist of sucking lice (Phthiraptera: Anoplura) from domestic and wild mammals in Malaysia, with lists of hosts and pathogens. *Zootaxa*, 5214 (3), 301–336. https://doi.org/10.11646/zootaxa.5214.3.1
Kim, K.C. (1966) The species of *Enderleinellus* (Anoplura, Hoplopleuridae) parasitic on the Sciurini and Tamiasciurini. *Journal of Parasitology*, 52, 988–1024. https://doi.org/10.2307/3276551
Kim, K.C. (1977) *Atopophthirus emersoni*, new genus and new species (Anoplura: Hoplopleuridae) from *Petaurista elegans* (Rodentia: Sciuridae), with a key to the genera of Enderleinellinae. *Journal of Medical Entomology*, 14, 417–420. https://doi.org/10.1093/jmedent/14.4.417
Kim, K.C. (2006) Blood-sucking lice (Anoplura) of small mammals: true parasites. *In*: Morand, S, Krasnov, B. & Poulin, R. (Eds.), *Micromammals and macroparasites: from evolutionary ecology to management.* Springer, New York, New York, pp. 141–160. https://doi.org/10.1007/978-4-431-36025-4_9
Kim, K.C. & Ludwig, H.W. (1978) The family classification of the Anoplura. *Systematic Entomology*, 3, 249–284. https://doi.org/10.1111/j.1365-3113.1978.tb00120.x
Kim, K.C., Stojanovich, C.J. & Pratt, H.D. (1986) *The sucking lice of North America—An illustrated manual for identification.* The Pennsylvania State University Press, University Park & London, xii + 241 pp.
Knecht, L. (2011) The use of hair morphology in the identification of mammals. *In*: Huffman, J.E. & Wallace, J.R. (Eds.), *Wildlife forensics: methods and applications.* John Wiley & Sons, Chichester, West Sussex, pp. 129–143. https://doi.org/10.1002/9781119953142.ch8
Kuhn, H.-J. & Ludwig, H.W. (1965) *Phthirunculus sumatranus* n. gen., n. sp., eine Laus des Flughörnchens *Petaurista petaurista* (Hoplopleuridae, Anoplura). *Senckenbergiana Biologica*, 48, 245–250.
Leach, W.E. (1815) Entomology. *In*: Brewster, D. (Ed.), *The Edinburgh Encyclopaedia*. *Vol. 9*. William Blackwood & Sons, Edinburgh, pp. 57–172.
Ledger, J.A. (1980) The arthropod parasites of vertebrates in Africa south of the Sahara. IV. Phthiraptera (Insecta). *Publications of the South African Institute for Medical Research*, 56, 1–327.
Martinů, J., Hypša, V. & Štefka, J. (2018) Host-specificity driving genetic structure and diversity in ectoparasite populations: coevolutionary patterns in *Apodemus* mice and their lice. *Ecology and Evolution*, 8, 10008–10022. https://doi.org/10.1002/ece3.4424
Mjöberg, E.G. (1910) Studien über Mallophagen und Anopluren. *Arkiv för Zoologi, Stockholm*, 6 (13), 1–297, 5 pls. https://doi.org/10.5962/bhl.part.26907
Musser, G.G., Durden, L.A., Holden, M.E. & Light, J.E. (2010) Systematic review of endemic Sulawesi squirrels (Rodentia, Sciuridae), with descriptions of new species of associated sucking lice (Insecta, Anoplura), and phylogenetic and zoogeographic assessment of sciurid lice. *Bulletin of the American Museum of Natural History*, 339, 1–260. https://doi.org/10.1206/695.1

Pajot, F.-X. (2000) *Les poux (Insecta, Anoplura) de la region afrotropicale. Collection Faune et Flore tropicales 37*. Éditions de I'IRD, Institut de Recherche pour le Développement, Paris, 293 pp.

Palma, R. L. (1978) Slide-mounting lice: a detailed description of the Canada balsam technique. *New Zealand Entomologist*, 6, 432–436.
https://doi.org/10.1080/00779962.1978.9722313

Redikorzev, V. (1937) A parasite of *Sciuropterus volans* (L.). *Parasitology*, 29, 4–6.
https://doi.org/10.1017/S0031182000026159

Shinozaki, Y., Shiibashi, T., Yoshizawa, K., Murata, K., Kimura, J., Maruyama, S., Hayama, Y., Yoshida, H. & Nogami, S. (2004) Ectoparasites of the Pallas squirrel, *Callosciurus erythraeus*, introduced to Japan. *Medical and Veterinary Entomology*, 18, 61–63.
https://doi.org/10.1111/j.0269-283x.2004.0475.x

Shinozaki, Y., Yoshizawa, K., Murata, K., Shiibashi, T., Kimura, J., Maruyama, S., Hayama, Y., Yoshida, H. & Nogami, S. (2003) The first record of sucking louse, *Neohaematopinus callosciuri*, infesting Pallas squirrels in Japan. *Journal of Veterinary Medical Science*, 66, 333–335.
https://doi.org/10.1292/jvms.66.333

Thompson, G.B. (1935) The parasites of British birds and mammals IV – Records of mammal parasites. *Entomologists' Monthly Magazine*, 71, 214–219.

Thorington Jr., R.W. & Hoffmann, R.S. (2005) Sciuridae. *In:* Wilson, D.E. & Reeder, D.M. (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference. 3rd Edition*. The Johns Hopkins University Press, Baltimore, Maryland, pp. 754–818.

Werneck, F.L. (1947) Notas sôbre o gênero *Enderleinellus* (Anoplura). *Memórias do Instituto Oswaldo Cruz*, 45, 281–305, 1 pl.
https://doi.org/10.1590/S0074-02761947000200001