Medical and Veterinary Entomology

Medical and Veterinary Entomology (2018), doi: 10.1111/mve.12314

Fleas of the genus *Neotyphloceras* associated with rodents from Bolivia: new host and distributional records, description of a new species and remarks on the morphology of *Neotyphloceras rosenbergi*

J. SANCHEZ[1], M. LARESCHI[2], J. SALAZAR-BRAVO[3] and S. L. GARDNER[4]

[1]Centro de Investigaciones y Transferencia del Noroeste de la Provincia de Buenos Aires (CIT NOBA) (CONICET-UNNOBA), Pergamino, Argentina, [2]Centro de Estudios Parasitológicos y de Vectores (CEPAVE) (CCT La Plata-CONICET-UNLP), La Plata, Argentina, [3]Department of Biological Sciences, Texas Tech University, Lubbock, TX, U.S.A. and [4]Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum, University of Nebraska Lincoln, Lincoln, NE, U.S.A.

Abstract. The flea genus *Neotyphloceras* Rothschild (Siphonaptera: Ctenophthalmidae) includes five species and two subspecies distributed from Venezuela to southern Chile and Argentina. Only *Neotyphloceras crassispina hemisus* Jordan has been registered in Bolivia. The present study examines species of *Neotyphloceras* collected in Bolivian localities in the Departments of La Paz, Cochabamba and Tarija, and describes the morphology of the modified abdominal segments in males and females of *Neotyphloceras rosenbergi* Rothschild on the basis of type material and specimens collected from Tarija. A new species, *Neotyphloceras boliviensis* n. sp., is described and new host associations are reported for *N. rosenbergi*, *Neotyphloceras crassispina crassispina* and *N. crassispina hemisus*. *Neotyphloceras c. crassispina* and *N. rosenbergi* are reported for the first time in Bolivia. The distribution of *N. rosenbergi* is extended 1600 km to the south. Given the potential medical and veterinary significance of fleas as disease vectors, and considering that in the Departments of La Paz and Tarija several human cases of plague have been reported, and species of flea have been identified as main vectors of these diseases, the new records of fleas in Bolivia reported herein may be useful for epidemiological studies on flea-borne diseases.

Key words. Ctenophthalmidae, Neotyphloceratini, Siphonaptera, Andean region.

Introduction

Between 1984 and 2000, the American Museum of Natural History (AMNH) (New York, NY, U.S.A.), the Museum of Southwestern Biology (MSB) (University of New Mexico, Albuquerque, NM, U.S.A.), the Harold W. Manter Laboratory of Parasitology (HWML) (University of Nebraska Lincoln, Lincoln, NE, U.S.A.). and the Bolivian National Museum of Natural History (La Paz, Bolivia) conducted collaborative collecting expeditions throughout Bolivia to survey sylvatic mammals and their parasites. An authoritative synthesis of the work on mammals was published by Anderson (1997) in 'Mammals of Bolivia: taxonomy and distribution', and many groups of parasites collected are still being studied. For most of the mammals collected by these expeditionary research teams in Bolivia, data on habitat, habits and biological associates (e.g. helminth, protozoan and arthropod parasites) were also collected and archived in museum collections. The current paper summarizes data on some of the fleas obtained from rodent specimens during these fieldwork campaigns.

Correspondence: Juliana Sanchez, Centro de Investigaciones y Transferencia del Noroeste de la Provincia de Buenos Aires (CONICET-UNNOBA), Ruta Provincial 32 Km 3,5, 2700 Pergamino, Argentina. Tel.: + 54 2477 409500; E-mail: julianasanchez@unnoba.edu.ar

Fleas in the genus *Neotyphloceras* Rothschild are parasites of both rodents and marsupials, and are currently known only from Neotropical mammals (Hopkins & Rothschild, 1966; Sanchez *et al*., 2012; Bazán-León *et al*., 2013; Sanchez & Lareschi, 2014). Currently, *Neotyphloceras* includes six species and subspecies: *Neotyphloceras rosenbergi* (Rothschild, 1904); *Neotyphloceras crassispina crassispina* Rothschild, 1914; *Neotyphloceras chilensis* Jordan, 1936; *Neotyphloceras crassispina hemisus* Jordan, 1936; *Neotyphloceras crackensis* Sanchez & Lareschi, 2014, and *Neotyphloceras pardinasii* Sanchez & Lareschi, 2014. These are characterized by the chaetotaxy of the head, thorax and legs, the presence of abdominal spinelets, and by morphological differences in the characteristics of the modified abdominal segments and genitalia in both sexes (Rothschild, 1904, 1914; Jordan, 1936; Sanchez *et al*., 2012; Sanchez & Lareschi, 2014; López Berrizbeitia *et al*., 2015).

The geographical distributions of known species of *Neotyphloceras* range from the northernmost record in Venezuela southward to southern Chile and Argentina. These distributions include an extensive range of habitats that vary in diversity from the Lower Montane wet forest, the Montane rain forest and Paramo in Venezuela, to Yungas and Puna in Bolivia and the Patagonian Forest and Monte Desert in Argentina (Hopkins & Rothschild, 1966; Hastriter, 2001; Beaucournu *et al*., 2014; Sanchez & Lareschi, 2014; López Berrizbeitia *et al*., 2015). Of the species of *Neotyphloceras*, only *N. crassispina hemisus* has been previously reported in several localities in central Bolivia (Hopkins & Rothschild, 1966).

One of the important aspects of the biology of fleas is that they are intimately associated with, and act as vectors for, many zoonotic bacterial diseases, including those caused by *Rickettsia*, *Bartonella* and *Yersinia*. In particular, within the genus *Neotyphloceras*, *N. rosenbergi* has been found to be naturally infected with plague in Ecuador [Disease Vector Ecology Profile (DVEPS): Ecuador, 1998].

Although the pathogens transmitted by fleas cause diseases in humans and domestic and wild animals, which, in some cases, are severe, little is known about the prevalence and distribution of flea species in Bolivia (Bitam *et al*., 2010; Eisen & Gage, 2012). For example, several human cases of plague and typhus have been reported and various species of flea have been identified as main vectors of these diseases (DVEPS: Bolivia, 1998; Ruiz, 2001). In particular, within the reservoir–flea–pathogen system in South America (and elsewhere), rodents have been shown to be the primary reservoir hosts of several pathogens that are of great significance to public health (Marshall, 1981; Linardi & Guimarães, 2000; Krasnov, 2008; Schneider *et al*., 2014).

The present paper reports a study of fleas of the genus *Neotyphloceras* that were collected from several species of rodent captured in Bolivia, extends knowledge of the morphology and distribution of this genus and contributes to knowledge of flea diversity in the region. These new data on the species diversity of potential or actual vectors of diseases may enable scientists to more easily predict emergences or outbreaks of disease before they can cause problems in human or domestic animal populations (Brooks *et al*., 2014).

Materials and methods

Fleas were collected from mammals in line with the guidelines approved by the American Society of Mammalogists (Sikes & Gannon, 2011). Following the methods of Gardner (1996), captured animals were assigned a field identification number, and the locality, date of capture and general ecological data were recorded in field notebooks [an update on the methods can be found in Gardner & Jiménez-Ruiz (2009)]. The mammal was then killed by chloroform vapour inhalation, brushed and inspected for ectoparasites, and searched for endoparasites (chloroform was used instead of other types of euthanizing chemical to ensure that all ectoparasites were killed in order to prevent fleas from transferring to other hosts). All fleas were preserved in glass vials in 70% ethanol until examination.

In the laboratory, fleas were cleared with 10% KOH, dehydrated through a series of ethanol (80–100%), cleared with eugenol, and mounted permanently on glass microscope slides in Canada balsam for study under a microscope equipped with a drawing tube. The fleas studied were drawn, photographed and identified using the original description and figures of the species (Rothschild, 1904, 1914; Jordan, 1936). For comparative purposes, holotypes and paratypes of all species and subspecies of *Neotyphloceras* deposited at the Rothschild Collection, Natural History Museum (NHM), London, and Colección de Entomología del Museo de La Plata (MLP), La Plata, Buenos Aires Province, Argentina, were examined. Morphology nomenclature followed Rothschild & Traub (1971).

Flea specimens collected during this work were deposited in the HWML. Specimens of mammals were deposited in the Department of Mammalogy, AMNH, the Museo Noel Kempff Mercado (MNKN), Santa Cruz de la Sierra, Bolivia, the Colección Boliviana de Fauna (CBF), La Paz, Bolivia, or the Division of Mammals, MSB. The numbers assigned to each specimen deposited in the HWML are given in the section for each species below. To enable ease of use and compatibility with previous publications, mammal taxonomies and specific locations, the present report follows Anderson (1997), Salazar-Bravo *et al*. (2003) and updates in Patton *et al*. (2015).

Neotyphloceras rosenbergi (Rothschild, 1904)

Taxonomic summary

Type host and locality. *Metachirus opossum* (= *Philander opossum*) (Linnaeus 1758); Cayembe, Ecuador. (Note: the name currently includes *Metachircus canus* Osgood, 1913, *Metachircus crucialis* Thomas, 1923, *Metachircus fuscogriseus* J.A. Allen, 1900, *Metachircus grisescens* J.A. Allen, 1901, *Metachircus melantho* Thomas, 1923, *Metachircus melanurus* Thomas, 1899, *Metachircus pallidus* J.A. Allen, 1901, and *Metachircus virginianus* Tiedemann, 1808.)

Other known hosts. Akodon mollis Thomas, 1894, *Caluromys philander* (Linnaeus, 1758), *Didelphis pernigra* J.A. Allen, 1900 [note: Tipton & Machado-Allison (1972) reported

N. rosenbergi from *Didelphis azarae* from Merida, Venezuela; however, *D. azarae* is no longer a valid name and the only species of *Didelphis* known from Merida is *D. pernigra* J.A. Allen, 1900], *Gracilinanus dryas* (Thomas 1898), *Heteromys anomalus* (Thompson, 1815) [note: Tipton & Machado-Allison (1972) reported this flea from *H. anomalus* from Caracas, Venezuela; however, there are two species of *Heteromys* currently recognized from the vicinity of Caracas: *H. anomalus* (Thompson, 1815) and *Heteromys catopterius* R. P. Anderson and Gutiérrez, 2009, and currently it appears that *H. anomalus* is certainly much more common and widespread], *Melanomys caliginosus* (Tomes, 1860), *Aegialomys xanthaeolus* (Thomas, 1894), *Nephelomys caracolus* (Thomas, 1914), *Nephelomys meridensis* (Thomas, 1894), *Oecomys trinitatis* (J.A. Allen & Chapman, 1893), *Microryzomys minutus* (Tomes, 1860), *Rheomys* sp., *Rhipidomys leucodactylus* (Tschudi, 1845), *Rhipidomys venustus* (Thomas, 1900), *Sigmodon* sp., *Notosciurus granatensis* (Humboldt, 1811), *Thomasomys princeps* (Thomas, 1895), *Thomasomys emeritus* Thomas, 1916, *Thomasomys dispar* Anthony, 1925, *Aepeomys lugens* (Thomas, 1896), *Thomasomys hylophilus* Osgood, 1912, *Thomasomys vestitus* (Thomas, 1898), *Thomasomys* sp. (Rothschild, 1904; Johnson, 1957; Hopkins & Rothschild, 1966; Tipton & Machado-Allison, 1972).

Known geographical distribution. **Venezuela:** Caracas, Trujillo, Merida, Monagas, Tachira; **Colombia:** Huila, Cundinamarca, Bogotá, Antioquia; **Ecuador:** Quito, Llava, Ibarra, Iliniza, Pichincha, Chimborazo, Loja, Chinchil, Malacatos, Baiza; **Peru:** La Laguna (Piura), Huancabamba, Cascas (Rothschild, 1904; Johnson, 1957; Hopkins & Rothschild, 1966; Tipton & Machado-Allison, 1972).

Material examined. La Paz: Rio Unduavi (16°18′ S, 67°51′ W; 2500 m a.s.l.), 7 August 1992, one male from *Akodon fumeus* (MSB 68551); Rio Aceromarca (16°19′ S, 67°53′ W; 2990 m a.s.l.), 1–3 August 1992, five males and three females from *A. fumeus* [catalogue nos. two from Colección Boliviana de Fauna (CBF) 2578, AMNH 264832, MSB 68508, AMNH 264829, two from AMNH 264839, CBF 2575], one male from *Thomasomys ladewi* (catalogue no. AMNH 264778).

Diagnosis. Neotyphloceras rosenbergi presents abdominal spinelets. This characteristic is shared only with *N. crassispina hemisus*, and other species and subspecies of *Neotyphloceras* lack abdominal spinelets. *Neotyphloceras rosenbergi* differs from all species and subspecies of *Neotyphloceras* by the combination of the following characters: (a) the location of two frontal rows of setae, anterior to the preoral edge (Fig. 1), which are situated above or posterior to the preoral margin in all others; (b) the presence of eight or nine equidistant setae in the first frontal row (Fig. 1C) (all other species in the genus possess six or seven setae in the same location; (c) length of the labial palpus, which is short and extends only to about the middle of the forecoxa (all other species in the genus have long labial palpi that extend to about the distal edge of the forecoxa); (d) length of the two antesensilial setae, one being shorter than the other (Figs 1A, B; 2A) (in all other species both setae are the same length), and (e) the presence of seven dorsomarginal notches on the hind tibia (Fig. 1D) (all other species possess eight). Males of *N. rosenbergi* can be recognized by a unique combination of the following characters: (a) the fixed process of the clasper is very triangular, with five or six setae on the dorsal edge, and the last seta very close to the clasper tip (Fig. 2A); (b) the movable process of the clasper is large and rounded at the apex and almost straight in the middle; the apex has one large and lightly pigmented seta on each side and three small sharply pointed setae (Fig. 2A); (c) the apex of the distal arm of sternum IX is rounded and bears three curved, spine-like pigmented setae (Fig. 2B), and (d) the apex of the crochet of the aedeagus is triangular in shape (Fig. 2C). Females of *N. rosenbergi* can be recognized as unique by the combination of the following characters: (a) the shape and chaetotaxy of sternum VII, which has four setae; the contour of the distal margin is rounded or convex in the final third of its total length (Fig. 2D), and (b) the shape of tergum VIII, which has a distal margin with three small lobes; the second lobe has three wide spiniform, pigmented setae and the third lobe has four short setae (Fig. 2D).

Description. The head has a rounded front, about four times longer than high, with two frontal rows of setae located before the preoral edge; the first row has eight or nine equidistant setae, the tips of the setae exceed the insertion of the setae in the next row, and the second row has three equidistant setae; the longest seta extends past the distal end of the longest spine of the genal comb (Fig. 1). The head segment has two or three placoid pits along the frontal margin. The occipital region has four rows of setae (Fig. 1C). The first antennal segment has five to 10 small setae; the second antennal segment has nine to 11 short setae reaching the first segment of the clavus; the antennal clavus is shorter in length than the first antennal segment in males (Fig. 1A) and twice the length in females (Fig. 1B). A row of small setae borders the antennal fossa numbering 20–25 in males and nine to 15 in females and is restricted to the posterior edge of the head. The genal comb has four pointed spines; the first two spines overlap and the fourth spine is shorter than the others ($\leq 60\%$ of the length of the longest spine) (Fig. 1C). The preoral edge has two setae on each side. The genal process is sharp and narrow, shorter in length than the longest spine of the genal comb. The maxillary lobe is sharp, extending beyond the basal half of the maxillary palpus. The maxillary palpus has four segments reaching to about the middle of the forecoxa; the first, second and fourth segments are of about same size, whereas the third segment is a little over half their length. The labial palpus has five segments and is short, extending to about the middle of the forecoxa; the last segment is a little longer than the fourth and half as long again as the second. The lacinia is slightly serrated and shorter in length than the labial palpus.

The pronotum (Fig. 1A, B) has one row of four or six long equidistant setae; the pronotal comb has nine spines on each side; the length of the longest spine is less than the width of the pronotum. The mesonotum is very setose, with two regular

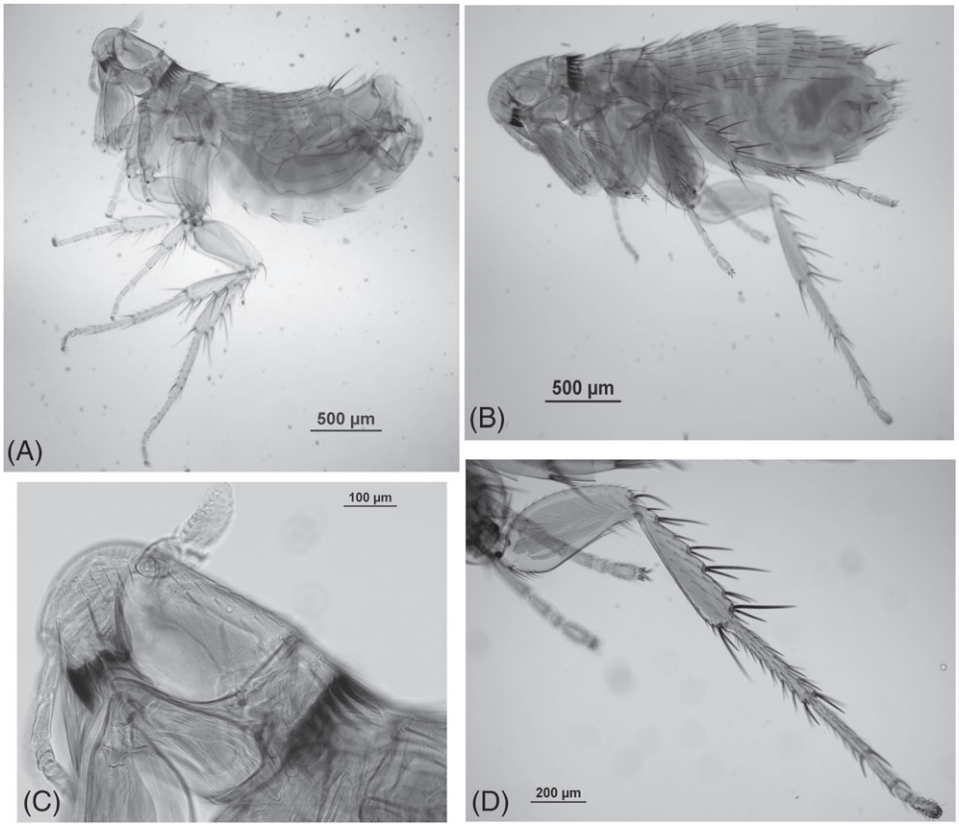

Fig. 1. *Neotyphloceras rosenbergi* (Rothschild, 1904). (A) Male, optical microscope view. (B) Female, optical microscope view. (C) Head and pronotum. (D) Hind leg.

rows of setae and numerous other setae in front of them; near the apex of the mesonotum are two or three seta-like spines on either side. The mesepisternum has three small setae on the anterior region and two long setae posteriorly. The mesepimere has four setae before the middle and two setae behind. The metanotum has two anterior rows of six short setae and one apical row of six long setae; the lateral metanotal area is long, roughly equal to the pleural arch and has two long setae; the pleural arch and ridge are well developed. The metepisternum has one long seta and one small seta; the furca of the metasternum is about one fourth the length of the pleural ridge; the metepimere has two rows of long setae (4, 2) and five small setae distributed in the surfaces.

The forecoxa has 40–50 setae distributed over the entire surface and one long seta on the posterior margin. The middle and hind coxae have setae distributed in three rows only on the anterior margin. The forefemur (Fig. 1A, B) has a dorsal marginal row of 10–12 small setae and two rows of setae (3, 6) on the inner side. The middle and hind femurs (Fig. 1A B) on the inner side have two long ventral setae and a dorsal row of five to six setae restricted to the distal region, with one ventral pair of pigmented setae on the proximal margin and one dorsal pair of setae on the distal margin; the longest seta reaches the second notch of the tibia. The tibiae (Figs 1A, B; 2A) has six or seven dorsomarginal notches bearing large setae from the apex to base as follows: foretibia (1, 2, 1, 2, 2, 3); middle tibia (2, 2, 1, 2, 2, 2, 3), and hind tibia (2, 2, 1, 2, 2, 2, 3). The longest caudal seta extends to beyond the middle of the first tarsal segment. The first tarsal hind segment is longest and the fourth segment is shortest; the first segment is three times as long as the third, four times as long as the fifth, and more than five times as long as the fourth segment.

On the abdomen, each abdominal tergite has two rows of setae, and one or two additional setae on the back. Tergites II and III have apical spinelets. Tergites II–VI have two rows of setae (4, 8–10); the setae of the anterior row are shorter than those of the posterior row. Tergum VII has two antesensilial setae on each side; in the male, one of these setae is about three times shorter than the other, whereas in the female one is about half the length of the other. The fossa of the spiracle of tergites II–VII is short and cone-shaped. The sensilium is strongly convex posteriorly, with 17–20 sensilial pits. The first abdominal sternite is without setae; the second has three, and the others have four setae on each side.

Modified abdominal segments of the male. Sternum VII has three or four setae on each side. Tergum VIII has three or four setae above the spiracle. The fixed process of the clasper (Fig. 2A) is cone-shaped or very triangular, with one row of five or six setae on the dorsal edge, with the last seta very proximal to its tip (Fig. 2A). The movable process is large and rounded at the apex and slightly constricted or almost straight in the middle; the apex has one large and lightly pigmented seta on each side and three small, sharply pointed setae. The ventral

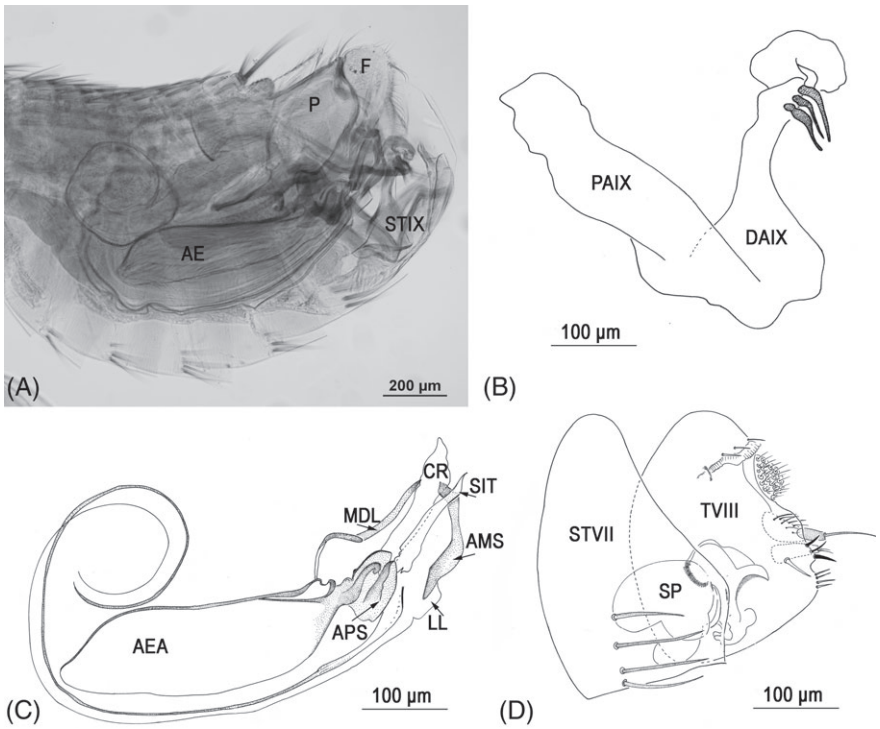

Fig. 2. *Neotyphloceras rosenbergi* (Rothschild, 1904). (A) Modified abdominal segments of the male. AE, aedeagus; F, movable process of the clasper; P, fixed process of the clasper; STIX, sternite IX. (B) Male: sternite IX. DAIX, distal arm of sternite IX; PAIX, proximal arm of sternite IX. (C) Male: aedeagus. AEA, aedeagal apodeme; APS, apodemal strut of aedeagus; CR, crochet; MDL, median dorsal lobe of aedeagus; LL, lateral lobes of aedeagus; SIT, sclerotized inner tube. (D) Female: sternite VII (STVII), spermatheca (SP) and tergite VIII (TVIII).

margin has a row of 12 small unpigmented setae along its edge, with the last seta larger than the others. There are two manubria: the upper manubrium is hook-shaped, and shorter and narrower than the lower manubrium. The acetabulum has a vertical row of seven small spiniform setae; below this row is a wide, strongly pigmented spatulate spine. Sternum IX (Fig. 2B) has a proximal arm and distal arm that are unequal in length; the distal arm has a rounded apex bearing three curved, spine-like and pigmented setae, the second of which is shorter and narrower than the others. The dorsal anal lobe is cone-shaped and long, roughly equal to the fixed process of the clasper; the ventral anal lobe is conical, shorter than the dorsal anal lobe, with two relatively long ventral setae on each side.

The aedeagus (Fig. 2C) has a long aedeagal apodeme that is over five times as long as it is broad. The median dorsal lobe is strongly sclerotized. The lateral lobes are convex at the base and extend to the apex of the crochet to form a right angle. The sclerotized inner tube is long, straight and narrow. The apical median sclerite is strongly pigmented and roughly equal in length to the inner tube. The crochet of the aedeagus is apical and large, with a long, robust base, and an apex that is triangular in shape or forms a sharp projection. There are two long apodemal struts; the proximal strut is greater than the distal strut and has a sclerotized dorsoproximal margin. The crescent sclerite is conspicuous above the apodemal strut. The penis rod is uncoiled, with a fold in the anterior portion and roughly equal or longer than the tendon of sternite IX.

Modified abdominal segments of the female. Sternum VII has four setae, the apical margin is strongly rounded and twice as narrow as the base, the contour of the distal margin is rounded or convex in the final third of the total length (Fig. 2D). Sternum VIII is narrow, elongated and less sclerotized than the other segments. Tergum VIII is wider than sternum VII and has long, narrow, oblique spiracles, with three small setae placed above; the upper lateral seta is situated at a variable distance from the ventral margin to the lowest level of the spiracular fossa; the distal margin has three small lobes in the lower portion, the second lobe has three wide spiniform and pigmented setae and the third lobe has four short setae (Fig. 2D). The anal lobes are short and conical; the dorsal anal lobe is wider than the ventral anal lobe. The anal stylet is subapical, is more than twice as long as it is broad at the base, with long apical setae twice the length of the anal stylet. On the spermatheca, the bulga is larger than the hilla, and the cribiform area is circular and heavily sclerotized (Fig. 2D). The bursa copulatrix is strongly sclerotized and bifurcated (Y-shaped).

Remarks

New characteristics of diagnostic importance are provided for the male and female of *N. rosenbergi*. The species is new for Bolivia and the current data extend its range over 1600 km to the south from Cascas, La Libertad, Peru (7°34′ S, 78°53′ W) to

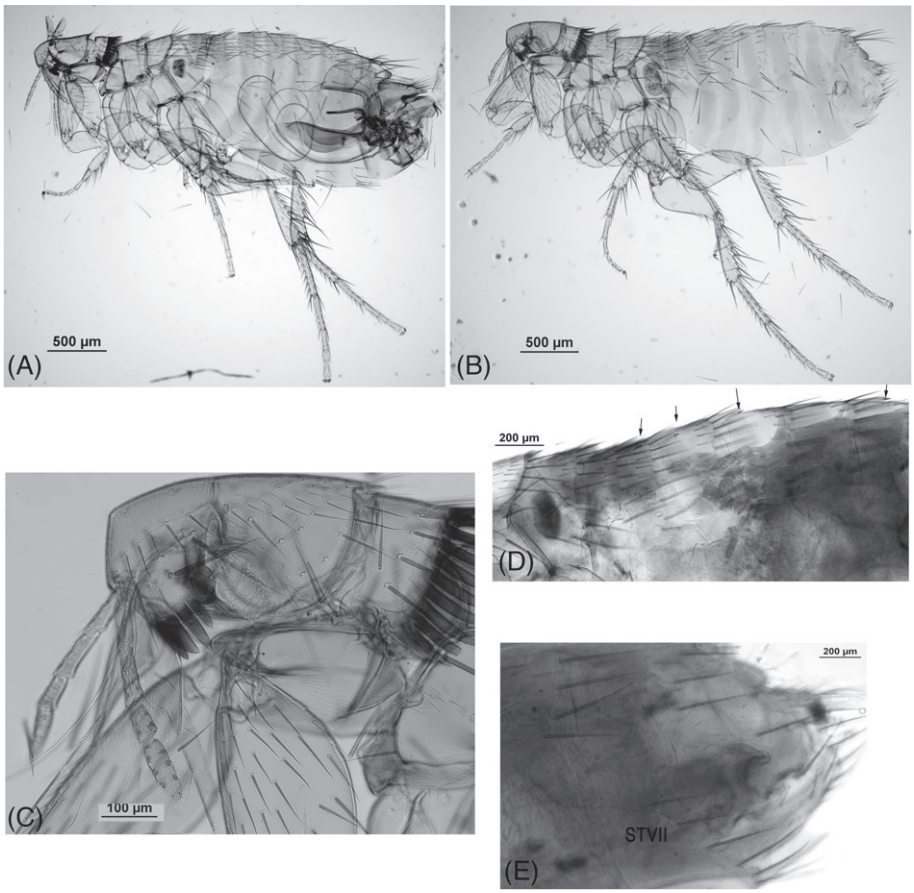

Fig. 3. *Neotyphloceras boliviensis* n. sp. (A) Male, optical microscope view. (B) Female, optical microscope view. (C) Head and pronotum. (D) Tergites II–V (TII–TV) with spinelets, optical microscope view. (E) Female: sternite VII (STVII).

Rio Aceromarca, La Paz, Bolivia (16°19′ S, 67°53′ W). *Akodon fumeus* is a new host for this flea.

Neotyphloceras boliviensis **Sanchez, Lareschi, Salazar-Bravo & Gardner, n. sp.**

urn:lsid:zoobank.org:act:B3B74BA9-1320-46C0-A208-E8E05998F87A

Type material

Holotype male ex *Oxymycterus paramensis* Thomas, 1902 [catalogue no. MSB 67279 (NK22855)], Tinkursiri, 17 km east of Totora, Cochabamba, Bolivia (17°45′ S, 65°02′ W; 2950 m a.s.l.), 30 May 1991; allotype female: same locality data as holotype [catalogue no. MSB 67280 (NK22833)]. Paratypes: Cochabamba: Tinkursiri, 17 km east of Totora (17°45′ S, 65°02′ W; 2950 m a.s.l.), 30 May 1991, one female of *O. paramensis* [catalogue no. MSB 67280 (NK22833)], one female of *Akodon lutescens* J.A. Allen, 1901 [catalogue no. AMNH 264269 (NK22857)]; 16.5 km northwest of Colomi (17°13′ S, 65°57′ W; 3500 m a.s.l.), 28 July 1993, one male and one female of *O. paramensis* [catalogue nos. NK30526, NK30530 (both to be catalogued at the CBF)]; 13 km north of Colomi (17°13′ S, 65°53′ W; 3152 m a.s.l.), 12 June 1993, two females from *Oligoryzomys destructor* (Tschudi, 1844) [catalogue no. MSB 70406 (NK29721)]; Corani (17°12′43″ S, 65°52′09″ W; 2630 m a.sl.), 30 July 1993, one male from *Akodon mimus* [catalogue no. AMNH 268806 (NK30597)]; Tarija: 3 km southeast of Cuyambuyo (22°16′ S, 64°33′ W; 900 m a.s.l.), 5 August 1991, one female from *Akodon pervalens* Thomas, 1925 [catalogue no. AMNH 264414 (NK23801)].

Diagnosis

Neotyphloceras boliviensis n. sp. is unique in the shape of its front, which is angled or sharp (Fig. 3A–C), whereas it is rounded in all other species and subspecies within the genus. *Neotyphloceras boliviensis* n. sp. resembles *N. rosenbergi* and *N. crassispina hemisus*, and differs from the other species and subspecies of *Neotyphloceras* in the presence of abdominal spinelets. However, *N. boliviensis* n. sp. has spinelets on tergites II–V (Fig. 3D), whereas *N. crassispina hemisus* and *N. rosenbergi* have spinelets on tergites II and III only. *Neotyphloceras boliviensis* n. sp. and *N. rosenbergi* share the

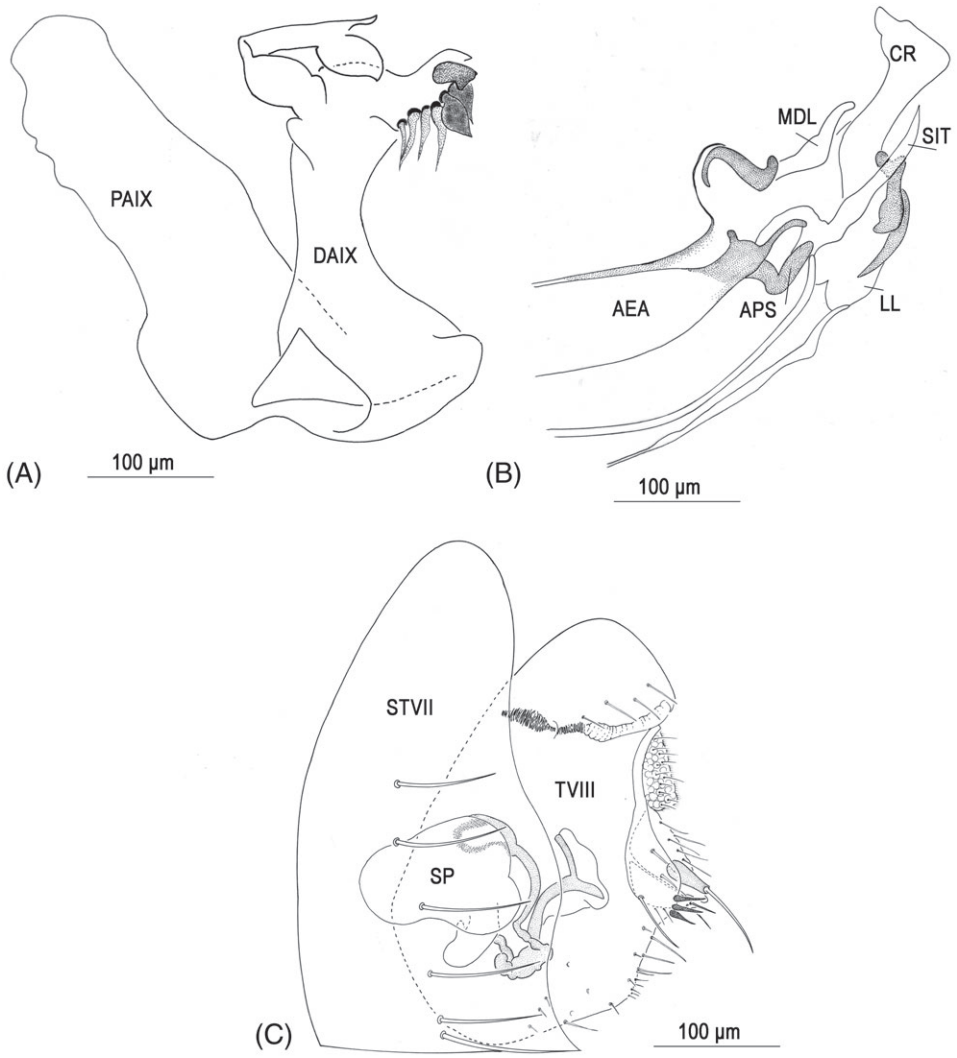

Fig. 4. *Neotyphloceras boliviensis* n. sp. (A) Male: sternite IX. DAIX, distal arm of sternite IX; PAIX, proximal arm of sternite IX. (B) Male: aedeagus. AEA, aedeagal apodeme; APS, apodemal strut of aedeagus; CR, crochet; MDL, median dorsal lobe of aedeagus; LL, lateral lobes of aedeagus; SIT, sclerotized inner tube. (C) Female: sternite VII (STVII), spermatheca (SP) and tergite VIII (TVIII).

presence of seven dorsomarginal notches on the hind tibia. Males of *N. boliviensis* n. sp. are unique in the combination of the following characters: (a) the apex of the distal arm of sternum IX forms a strongly concave projection that bears three wider strongly pigmented setae located near the apex, and four slender lightly pigmented setae, located in a ventral row that is rounded (Fig. 4A), and (b) the crochet of the aedeagus has a long, robust base and hammer-shaped apex (Fig. 4B). Females of *N. boliviensis* n. sp. are unique in the combination of the following characters: (a) the shape and chaetotaxy of sternum VII, which has five or (usually) six setae, and the contour of the distal margin, which is convex in the lower half, with a small notch in the lower corner (Figs 3E, 4C), and (b) the shape of tergum VIII, of which the distal margin has a small lobe with three short, wide, strongly pigmented spiniform setae and the lower portion is straight, with numerous small setae (Fig. 4C).

Description. The front of the head is angled or sharp and the ventral margin is more sclerotized (Fig. 3A–C), with two frontal rows of setae: the first row consists of six equidistant setae, the tips of the setae exceed the insertion of setae in the next row; the second row has three equidistant setae, the longest of which extends distal to the end of the longest spine of the genal comb (Fig. 3C). Two or three placoid pits are apparent along the margin of the front. The occipital region has four rows of setae (Fig. 3A,B). The first antennal segment has about 10 small setae; the second antennal segment has nine to 11 short setae reaching the first segment of the clavus; the antennal clavus is shorter in length to the first antennal segment in males and is twice the length in females. A row of small setae border the antennal fossa (25–30 in males, 15–20 in females) and are restricted to the posterior edge of the head. The genal comb has four pointed spines, the first two of which overlap, whereas the

fourth spine is shorter than the others (≤ 60% of the length of the longest spine) (Fig. 3C). The preoral edge has two setae on each side. The genal process is sharp and narrow, shorter in length to the longest spine of the genal comb. The maxillary lobe is sharp and extends beyond the basal half of the maxillary palpus. The maxillary palpus has four segments reaching to about the middle of the forecoxa; the first, second and fourth segments are about the same size, whereas the third segment is a little over half their length. The labial palpus has five segments and is long, extending to about the distal edge of the forecoxa; the last segment is a little longer than the fourth and half as long again as the second. The lacinia is slightly serrated and shorter in length to the labial palpus.

The pronotum (Fig. 3C) has one row of four or six long, equidistant setae; the pronotal comb has nine or 10 spines on each side; the length of the longest spine is less than the width of the pronotum. The mesonotum is very hairy and has two regular rows of setae, in front of which are numerous other setae; near the apex of the mesonotum on either side are two or three seta-like spines. The mesepisternum has three small setae on the anterior region and two long setae posteriorly. The mesepimere has four setae located before the middle and two setae behind. The metanotum has two anterior rows of six short setae and one apical row of six long setae; the lateral metanotal area is long, roughly equal to to the pleural arch and has two long setae; the pleural arch and ridge are well developed. The metepisternum has one long seta and one small seta. The furca of the metasternum is about one-quarter the length of the pleural ridge. The metepimere has two rows of long setae (4, 2) and five small setae distributed in the surfaces.

The forecoxa has about 50 setae distributed over the entire surface, with one long seta on the posterior margin. The middle and hind coxae show setae distributed in three rows only on the anterior margin. The forefemur has a dorsal marginal row of small setae and two rows of setae (3, 6) on the inner side. The middle and hind femurs on the inner side have two long ventral setae and a dorsal row of five or six setae restricted to the distal region, and one ventral pair of pigmented setae on the proximal margin and one dorsal pair of setae on the distal margin; the longest seta reaches the second notch of the tibia. The tibiae (Fig. 3A, B) have seven or eight dorsomarginal notches bearing large setae from the apex to base as follows: foretibia (2, 2, 2, 2, 2, 2, 3); middle tibia (2, 2, 1, 2, 2, 2, 2, 3), and hind tibia (2, 2, 1, 2, 2, 1–2, 2, 3). The longest caudal setae extend to beyond the middle of the first tarsal segment. The first tarsal hind segment is the largest and the fourth segment the shortest; the first segment is three times longer than the third, four times longer than the fifth and more than five times longer than the fourth segment.

On the abdomen, each tergite bears two rows of setae, with one or two additional setae to the back. Tergites II–V have one to three apical spinelets (Fig. 3D). Tergites II–VI have two rows of setae (4, 8–10) and the setae in the anterior row are shorter than those in the posterior row. Tergum VII has two antesensilial setae of the same length on each side. The fossa of the spiracle of tergites II–VII is short and cone-shaped. The sensilium is strongly convex posteriorly, with about 20 sensilial pits. The first abdominal sternite is without setae, the second bears three and the others bear four setae on each side.

Modified abdominal segments of the male. Sternum VII has three or four setae on each side. Tergum VIII has three setae above the spiracle. The upper lobe of the fixed process of the clasper) (Fig. 3A) is cone-shaped and robust, with three or four submarginal setae and one row of eight to 10 dorsomarginal setae; the last seta is located at a distance equal to the width of the fixed process at the point of attachment of the seta (Fig. 3B). The lower lobe of the fixed process has a sharp distal edge, without setae. The movable process has one strongly pigmented seta on each side and five or six small setae on the apex; the distal margin is rounded; the ventral margin is very indented, with a row of 15–17 small setae along its edge. There are two manubria. The upper manubrium is hook-shaped, and shorter and narrower than the lower manubrium. The acetabulum has a vertical row of 11–13 small spiniform setae; below this row is a wide, strongly pigmented spatulated spine and two narrow, pigment-free setae. Sternum IX (Fig. 4A) has a proximal arm and a distal arm that are roughly equal in length; the distal arm has an apex that forms a strongly concave projection and bears three wider, strongly pigmented setae near the apex, and four slender, lightly pigmented setae in a ventral row (Fig. 4A). The dorsal anal lobe is long, narrow and cone-shaped; the ventral anal lobe is conical, shorter than the dorsal anal lobe, and has two long ventral setae on each side.

The aedeagus (Fig. 4B) has a long aedeagal apodeme, more than five times as long as it is broad. The median dorsal lobe is strongly sclerotized. Lateral lobes are present. The sclerotized inner tube is long, straight and narrow. An apical median sclerite is present, strongly pigmented and roughly equal in length to inner tube. The crochet of the aedeagus is apical and large, with a long, robust base and hammer-shaped apex. There are two long apodemal struts; the proximal strut is greater than the distal strut and the dorsoproximal margin is sclerotized. The crescent sclerite is conspicuous above the apodemal strut. The penis rod is uncoiled, with a fold in the anterior portion and shorter in length than the tendon of sternite IX.

Modified abdominal segments of the female. Sternum VII has five or (usually) six setae; the apical margin is strongly rounded and the contour of the distal margin convex in the lower half, with a small notch in the lower corner (Fig. 4C). Sternum VIII is narrow, elongated and less sclerotized than the other segments. Tergum VIII has long, narrow, oblique spiracles, with four small setae placed above; the upper lateral seta is situated at a variable distance from the ventral margin to the lowest level of the spiracular fossa; the distal margin has a small lobe with three short, wide, strongly pigmented spiniform setae; the lower portion is straight, with numerous small setae (Fig. 4C). The anal lobes are short and conical; the dorsal anal lobe is wider than the ventral anal lobe. The anal stylet is subapical, more than three times as long as it is broad at the base, with long apical setae twice the length of the anal stylet. The spermatheca has a larger bulga than hilla; the cribiform area is circular and heavily sclerotized (Fig. 4C). The bursa copulatrix is strongly sclerotized and bifurcated (Y-shaped).

Etymology

This species is named for the country in which its type specimens were collected, Bolivia.

Neotyphloceras crassispina crassispina Rothschild, 1914

Taxonomic summary

Type host and locality. *Rattus* sp.; Pachacayo, Peru.

Other known hosts. *Auliscomys boliviensis* (Waterhouse 1846), *Abrothrix hirtus modestior* [syn. *Abrothrix longipilis* (Waterhouse, 1837)], *Abrothrix olivacea* (Waterhouse, 1837), *Chinchillula sahamae* Thomas, 1898, *Geoxus valdivianus* (Philippi, 1858), *Octodon degus* (G. I. Molina, 1782), *Oligoryzomys longicaudatus* (Bennett, 1832), *Phyllotis lutescens* [syn. *Phyllotis xanthopygus* (Waterhouse, 1837)], *Phyllotis osilae* J.A. Allen, 1900, *Phyllotis amicus* Thomas, 1900, *Phyllotis arenarius* [syn. *Phyllotis xanthopygus* (Waterhouse, 1837)], *Phyllotis darwini* (Waterhouse, 1837), *Rattus rattus* (Linnaeus, 1758) (Rothschild, 1914; Johnson, 1957; Hopkins & Rothschild, 1966; Bazán-León *et al*., 2013).

Known geographical distribution. **Peru:** Pachacayo, Puno, Matucana, Caylloma, Caccachara; **Argentina:** Rio Negro; **Chile:** Valparaiso, Fray Jorge, Santiago, Dichato, Concepcion, Curicó, Petorca, Linares, San Antonio (Johnson, 1957; Hopkins & Rothschild, 1966; Alarcón, 2000, 2003; Bazán-León *et al*., 2013; Beaucournu *et al*., 2014).

Material examined. La Paz: Rio Aceromarca (16°19′ S, 67°53′ W; 2990 m a.s.l.), 1–3 August 1992, one male from *T. ladewi* Anthony, 1926 [catalogue no. MSB 68485 (NK25742)], two males and one female from *A. mimus* (Thomas, 1901) [catalogue nos. MSB 68509 (NK25805), CBF 2557 (NK25808), MSB 68514 (NK25798)]; 8.5 km west of San Andres de Machaca (16°59′04″ S, 69°01′53″ W; 3850 m a.s.l.), 3 August 1993, one male and two females from *Abrocoma cinerea* Thomas, 1919 [catalogue nos. MSB 70580 (NK30666), AMNH 268933 (NK30670)]. Cochabamba: Poseidon, Laguna de Corani 12.5 km north of Colomi (17°14′ S, 65°53′ W; 3200 m a.s.l.), 27 July 1993, one male from *O. paramensis* Thomas, 1902 [field catalogue no. NK30512 (to be catalogued at CBF)]; 16.5 km northwest of Colomi (17°13′ S, 65°57′ W; 3500 m a.s.l.), 28 July 1993, one female from *A. fumeus* Thomas, 1902 [catalogue no. CBF3500 (NK30523)]; 7.5 km southeast of Rodeo Curubamba (17°40′ S, 65°36′ W; 4000 m a.s.l.), 25 July 1993, one female from *O. paramensis* [catalogue no. NK30482 (to be catalogued at CBF)].

Remarks

This is the first record of *N. crassispina crassispina* for Bolivia. Other hosts include the rodents *O. paramensis*, *A. cinerea*, *A. fumeus*, *A. mimus* and *T. ladewi*.

Neotyphloceras crassispina hemisus Jordan, 1936

Taxonomic summary

Type host and locality. *Andinomys edax* Thomas, 1902, with type locality Bolivia, Chuquisaca Department, Posta 'El Cabrado', 3500 m a.s.l., as recently amended by Jayat *et al*. (2017).

Other known hosts. *Abrothrix andina* (Philippi, 1858), *Akodon albiventer* Thomas, 1897, *Akodon boliviensis* Meyen, 1833, *Akodon mollis* Thomas, 1894, *Akodon simulator* Thomas, 1916, *Akodon spegazzinii* Thomas, 1897, *Calomys lepidus* (Thomas, 1884), *Calomys callosus* (Rengger, 1830), *Cuniculus paca* (Linnaeus, 1766), *Eligmodontia bolsonensis* Mares, Braun, Coyner, and van den Bussche, 2008, *Eligmodontia puerulus* (Philippi, 1896), *Eligmodontia hirtipes* (Thomas, 1902), *Galea musteloides* Meyen, 1833, *Graomys griseoflavus* (Waterhouse, 1837), *Graomys medius* [syn. *Graomys chacoensis* (J.A. Allen, 1901)], *Hesperomys muriculus* (syn. *Calomys callosus*), *Necromys lactens* (Thomas, 1918), *Oligoryzomys destructor* (Tschudi, 1844), *Oxymycterus paramensis* Thomas, 1902, *Aegialomys xanthaeolus* (Thomas, 1894), *Phyllotis xanthopygus* (Waterhouse, 1837), *Phyllotis osilae* J.A. Allen, 1901, *Rattus rattus* (Linnaeus, 1758), *Rattus norvegicus* (Berkenhout, 1769), *Reithrodon auritus* (G. Fischer, 1814), *Reithrodon caurinus* Thomas 1920 [syn. *R. auritus* (G. Fischer, 1814)], *Thylamys elegans* (Waterhouse, 1839) (Johnson, 1957; Hopkins & Rothschild, 1966; López Berrizbeitia *et al*., 2015; Lareschi *et al*., 2016).

Known geographical distribution. **Bolivia:** Potosi Department (Potosi), Chuquisaca Department (Padilla, Sucre, Serrano), Santa Cruz Department (Pucara, Valle Grande), and Cochabamba Department (Aiquile); **Peru:** Llampa; **Argentina:** Catamarca Province, Salta Province, Jujuy Province, Tucuman Province, San Juan Province, Mendoza Province, Neuquen Province, Rio Negro Province; **Chile:** Atacama, Cautin, Copiapo, Coyhaique, Aysen, Iquique, Magallanes, Paranicota, General Carrera, Tamarugal (Johnson, 1957; Hopkins & Rothschild, 1966; Beaucournu *et al*., 2014; Lareschi *et al*., 2016).

Material examined. Cochabamba: 1.3 km west of Jamachuma (17°31′32″ S, 66°07′29″ W; 2800 m a.sl.), 22 July 1993, three males and two females from *Didelphis albiventris* Lund, 1840 [catalogue no. MSB 70285 (NK30427)]. Curubamba: 7.5 km southeast of Rodeo (17°41′ S, 65°36′W; 4000 m a.s.l.), 25 July 1993, two males and six females from *O. paramensis* Thomas, 1902 [catalogue nos. NK30493, NK30490, NK30491, NK30492 (all to be catalogued at CBF)]. Tinkursiri: 17 km east of Totora (17°45′ S, 65°02′ W; 2950 m a.sl.), 30 May 1991, one male from *O. paramensis* [catalogue no. MSB 67281 (NK22859)]. La Paz: Rio Aceromarca (16°19′ S, 67°53′ W; 2900 m a.s.l.), 1 August 1992, one male from *T. ladewi* [catalogue no. MSB 68483 (NK25743)]; 8.5 km

west of San Andres de Machaca (16°59′04″ S, 69°01′ W; 3850 m a.s.l.), 3 August 1993, one female from *A. cinerea* [catalogue no. CBF3657 (NK30665)]. Tarija: 61 km east of Tarija, Rancho Tambo (21°27′ S, 64°19′ W; 2100 m a.s.l.), 22 September 1986, one male from *A. edax* [catalogue no. MSB 57099 (NK14603)], one female from *Phyllotis caprinus* (catalogue no. AMNH 262987).

Remarks

New rodent hosts for *N. crassispina hemisus* include *A. edax* Thomas, 1902, *A. cinerea* Thomas, 1919, *P. caprinus* Pearson, 1958, *T. ladewi* Anthony, 1926, and the marsupial *D. albiventris* Lund, 1840.

Discussion

The general morphological characteristics of the specimens studied here are consistent with those of species allocated to the genus *Neotyphloceras*. In addition, the present study adds the shape of the head as a new characteristic of diagnostic importance in differentiating species of this genus: the front is angled or sharp in *N. boliviensis*, but is rounded in all other species and recognized subspecies of *Neotyphloceras*.

Although there are several prior studies on the systematics of South American fleas (Linardi & Guimarães, 2000; Beaucournu *et al*., 2014; Lareschi *et al*., 2016), information on fleas from Bolivia is still lacking. The current study describes a new species of flea in the genus *Neotyphloceras* and adds three new species to knowledge of flea diversity in the country. In addition, *N. crassispina hemisus* is recorded for the first time from mammals in the Departments of Cochabamba, La Paz and Tarija, and all of the fleas identified and included in this work show extended ranges of hosts. This indicates that there is still much diversity in the Siphonaptera that has not been described in the Neotropics.

The study of fleas is important from an epidemiological point of view because they are largely known for their ability to transmit agents of infectious diseases (Bitam *et al*., 2010). Plague is the most notorious of the zoonotic flea-borne diseases known to affect humans, has been recorded worldwide and is believed to have originated in Asia, although most current human transmission occurs in Africa, South America and North America, as well as Asia (Eisen & Gage, 2012). As this re-emerging zoonotic disease has a global distribution and can severely affect public health, the implementation of biodiversity surveys and subsequent vector control strategies is urgent (Brooks *et al*., 2014). In Bolivia, plague is endemic in the Andean region, mainly in the mountainous areas of the Departments of La Paz, Chuquisaca, Santa Cruz and Tarija, and several rodent species have been identified as natural reservoirs (DVEP: Bolivia, 1998; Ruiz, 2001; Álvaro *et al*., 2013; Schneider *et al*., 2014; Bonvicino *et al*., 2015). Specifically, members of the genus of *Neotyphloceras* have a mainly Andean–Patagonian distribution (Sanchez *et al*., 2012).

Acknowledgements

The authors thank Maria Cristina Estivariz (CEPAVE) for the drawings and Luis Giambelluca (CEPAVE) for the photographs used in this paper. Theresa Howard and Erica McAlister [Natural History Museum (NHM), London, U.K.] kindly assisted ML during her visit to study specimens deposited at the Rothschild Collection at the NHM. The visit of ML to the NHM was funded by the Universidad Nacional de La Plata and Agencia Nacional de Promoción Científica y Tecnológica, Argentina. This work was supported by the U.S. National Science Foundation (grants BSR8612329, BSR9024816, DEB9496263, DEB9631295 to SLG; BSR8408923, DEB8920617 to T. L. Yates; OISE 9417252 to T. L. Yates and JS-B; BSR8316740 to S. Anderson). Additional support was provided directly by the American Museum of Natural History, the Museum of Southwestern Biology, Texas Tech University, the Tinker Foundation, and the Harold W. Manter Laboratory of Parasitology Development Fund. The following organizations provided logistic support in the field: Museo Nacional de Historia Natural, La Paz; Museum of Southwestern Biology, University of New Mexico, and Instituto Boliviano de Biología de la Altura, La Paz. The authors also thank the cadres of faculty, staff and students of the natural history collections in Bolivia, who are hard at work learning about the natural heritage of the country in order to conserve it for the future.

The authors declare no conflicts of interest.

References

Alarcón, M. (2000) Present state of the knowledge of Siphonaptera in Chile (Insect: Siphonaptera). *Gayana*, **64**, 1–17.

Alarcón, M. (2003) Sifonapterofauna de tres especies de roedores de Concepcion, VIII Region-Chile. *Gayana*, **67**, 16–24.

Álvaro, A., Faccini-Martínez, H. & Sotomayor, A. (2013) Reseña histórica de la peste en Suramérica: una enfermedad poco conocida en Colombia. *Biomédica*, **33**, 8–27.

Anderson, S. (1997) Mammals of Bolivia: taxonomy and distribution. *Bulletin of the American Museum of Natural History*, **231**, 1–652.

Bazán-León, E.A., Lareschi, M., Sanchez, J.P., Soto-Nilo, G., Lazzoni, I. & Vásquez, R.A. (2013) Fleas (Insecta: Siphonaptera) associated with non-flying small mammal communities from northern and central Chile; with new host and locality records. *Medical and Veterinary Entomology*, **27**, 450–459.

Beaucournu, J.C., Moreno, L. & González-Acuña, D. (2014) Fleas (Insecta-Siphonaptera) of Chile: a review. *Zootaxa*, **3900**, 151–203.

Bitam, I., Dittmar, K., Parola, P., Whiting, M.F. & Raoult, D. (2010) Fleas and flea-borne diseases. *International Journal of Infectious Diseases*, **14**, 667–676.

Bonvicino, C., Oliveira, J.A., Cordeiro-Estrela, P., D'Andrea, P.S. & Almeida, A.M. (2015) A taxonomic update of small mammal plague reservoirs in South America. *Vector Borne and Zoonotic Diseases*, **15**, 571–579.

Brooks, D.R., Hoberg, E.P., Boeger, W.A. *et al.* (2014) Finding them before they find us: informatics, parasites, and environments in accelerating climate change. *Comparative Parasitology*, **81**, 155–164.

Disease Vector Ecology Profile: Bolivia (1998) Defense Pest Management Information Analysis Center, Armed Forces Pest Management Board, Forest Glen Section, Walter Reed Army Medical Center, Washington, DC. www.dtic.mil/dtic/tr/fulltext/u2/a604938.pdf [accessed on 15 December 2017].

Disease Vector Ecology Profile: Ecuador (1998) Disease Vector Ecology Profile – Ecuador. Defense Pest Management Information Analysis Center, Armed Forces Pest Management Board, Forest Glen Section, Walter Reed Army Medical Center, Washington, DC. http://www.dtic.mil/dtic/tr/fulltext/u2/a604926.pdf [accessed on 15 December 2017].

Eisen, R.J. & Gage, K.L. (2012) Transmission of flea-borne zoonotic agents. *Annual Review of Entomology*, **57**, 61–82.

Gardner, S.L. (1996) Essential techniques for collection of parasites during surveys of mammals. *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals* (ed. by D.E. Wilson, R. Cole, J.D. Nichols, R. Rudran & M. Foster), pp. 291–298. Smithsonian Institution Press, Washington, DC.

Gardner, S.L. & Jiménez-Ruiz, F.A. (2009) Methods of endoparasite analysis. *Ecological and Behavioral Methods for the Study of Bats* (ed. by T. Kunz & S. Parsons), pp. 795–805. Johns Hopkins University Press, Baltimore, MD.

Hastriter, M.W. (2001) Fleas (Siphonaptera: Ctenophthalmidae and Rhopalopsyllidae) from Argentina and Chile with two new species from the rock rat *Aconaemys fuscus* in Chile. *Annals of Carnegie Museum*, **70**, 169–178.

Hopkins, G.H. & Rothschild, M. (1966) *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History). Vol. IV: Ctenophthalminae, Dinopsyllinae; Doratopsyllinae and Listropsyllinae*. British Museum (Natural History), London.

Jayat, J., D'elía, G., Torres, R. *et al.* (2017) Integration of morphological, ecological, and genetic evidence suggests that the genus *Andinomys* (Rodentia, Cricetidae) is monospecific. *Journal of Mammalogy*, **98**, 1060–1077.

Johnson, P.T. (1957) A Classification of Siphonaptera of South America. Memoirs of the Entomological Society of Washington, Washington, DC.

Jordan, K. (1936) Some Siphonaptera from South America. *Novitates Zoologicae*, **39**, 305–310.

Krasnov, B.R. (2008) Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology. Cambridge University Press, Cambridge.

Lareschi, M., Sanchez, J.P. & Autino, A.G. (2016) A review of the fleas (Insecta: Siphonaptera) from Argentina. *Zootaxa*, **4103**, 239–258.

Linardi, P.M. & Guimarães, L.R. (2000). Sifonápteros do Brasil. Museu de Zoología da Universidade de São Paulo, São Paulo, SP.

López Berrizbeitia, M.F., Sanchez, J.P., Díaz, M.M., Barquez, R.M. & Lareschi, M. (2015) Redescription of *Neotyphloceras crassispina hemisus* Jordan (Siphonaptera: Ctenophthalmidae: Neotyphloceratini). *Journal of Parasitology*, **10**, 145–149.

Marshall, A. (1981) . *The Ecology of Ectoparasitic Insects*. Academic Press, London.

Patton, J., Pardiñas, U. & D'elia, G. (2015) . *Mammals of South America. Vol. 2 – Rodentia*. University of Chicago Press, Chicago, IL.

Rothschild, N.C. (1904) Description of a new species of Siphonaptera from South America. *Revista Chilena de Historia Natural*, **8**, 147.

Rothschild, N.C. (1914) New Siphonaptera from Peru. *Novitates Zoologicae*, **21**, 239–251.

Rothschild, M. & Traub, R. (1971) . *A Revised Glossary of Terms Used in the Taxonomy and Morphology of Fleas. An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History). Vol. V*. British Museum (Natural History), London.

Ruiz, A. (2001) Plague in the Americas. *Emerging Infectious Diseases*, **7**, 539–540.

Salazar-Bravo, J., Tarifa, T., Aguirre, L.F., Yensen, E. & Yates, T. (2003) Revised checklist of Bolivian mammals. *Museum of Texas Tech University, Occasional Papers*, **220**, 1–28.

Sanchez, J.P. & Lareschi, M. (2014) Two new species of *Neotyphloceras* (Siphonaptera: Ctenophthalmidae) from Argentinean Patagonia. *Zootaxa*, **3784**, 159–170.

Sanchez, J.P., Amor, V., Bazan-Leon, E.A., Vasquez, R.A. & Lareschi, M. (2012) Redescription of *Neotyphloceras chilensis* Jordan, new status (Siphonaptera: Ctenophthalmidae: Neotyphloceratini). *Zootaxa*, **3259**, 51–57.

Schneider, M.C., Najera, P., Aldighieri, S. *et al.* (2014) Where does human plague still persist in Latin America? *PLoS Neglected Tropical Diseases*, **8**, e2680.

Sikes, R.S. & Gannon, W.L. (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, **92**, 235–253.

Tipton, V. & Machado-Allison, C.E. (1972) Fleas of Venezuela. *Brigham Young University, Science Bulletin, Biological Series*, **17**, 1–115.

Accepted 16 May 2018

