Abrocomaphthirus hoplai, a new genus and species of sucking louse from Chile and its relevance to zoogeography

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Abstract. Both sexes of Abrocomaphthirus hoplai, new genus and new species (Anoplura: Polyplacidae), are described and illustrated. The endemic Chilean chinchilla rat Abrocoma bennetti Waterhouse (Rodentia: Abrocomidae) is the type host. The definition of the family Polyplacidae is amended to accommodate the new genus. Polyplax longa (Werneck), also referred to in the literature as Neohaematopinus longus Werneck, is reassigned to Abrocomaphthirus. The host of A. longus comb.n., is Abrocoma cinerea Thomas, another chinchilla rat, which inhabits parts of Argentina, Bolivia, Chile and Peru. The erection of Abrocomaphthirus as a distinct genus has important zoogeographical and evolutionary implications. The tenuous anomaly of P. longa being the sole native representative of the genus Polyplax in South America, possibly with African affinities, is now refuted. Instead, partial colonization of the neotropics by native species of both Polyplax and Neohaematopinus appears to have been relatively recent and from North America. The phylogenetic affinities of Abrocomaphthirus are unknown, but it appears to be closely related to other, more ancient, native South American polyplacid louse genera, such as Cuyana, Eulinognathus, Galeophthirus, and Lagidiophthirus. Arguments are presented in support of an ancestral zoogeographical link to Africa for these louse genera.

Key words. Abrocomaphthirus hoplai, A. longus, Polyplax, Anoplura, Phthiraptera, new combination, new genus and species, neotropics, sucking lice, zoogeography, Chile, Peru.

Introduction

Although Vanzolini & Guimaraes (1955a, b) and Traub (1980) provided lucid accounts of the zoogeography and host associations of neotropical mammal lice, one louse species, Polyplax longa (Werneck), originally described as Neohaematopinus longus Werneck, did not easily conform with their hypotheses. Polyplax is a speciose sucking louse genus currently with 79 recognized species (Durden & Musser, 1994a; Chin, 1995) and with most representatives inhabiting the Old World (Africa and Eurasia) but with three species native to North America (Kim et al., 1986). Two additional species, Polyplax serrata (Burmeister) and P. spinulosa

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(Burmeister), which parasitize commensal Old World mice and rats, respectively, have accompanied their hosts in their colonizations throughout of much of the world, including North and South America (Durden & Musser, 1994a). Although historical faunal connections between Africa and South America are documented (Goldblatt, 1994), if Polyplax had accompanied ancestral African rodents that colonized South America, it seems likely that more than one native species of Polyplax would now be established on the latter continent. Furthermore, collection records of native New World species of Polyplax are confined to North America and Central America as far south as Panama (Durden & Musser, 1994a). In fact, a gradual reduction in the number of species of native Polyplax from North America to Panama, from which just one species is known, suggests that this louse genus has colonized the neotropics from the north. A similar north to

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south colonization route has been demonstrated for *Polyplax* in eastern Asia (Durden & Traub, 1990).

The discovery of a new species of Chilean sucking louse with close morphological affinities to *Polyplax longa*, prompted us to compare these two lice and to analyse their morphological traits with respect to other polyplacid sucking lice. Based on this study, we describe the new species and erect a new genus to accommodate both species of lice. Next, we briefly discuss the zoogeographical significance of these taxonomic actions. Finally, we consider any medical or veterinary importance that these lice may have.

Materials and Methods

Lice were collected from rodents in central Chile by Robert E. Martin in 1975 and later forwarded to us for analysis. Specimens were cleared in 10% potassium hydroxide, dehydrated in a series of ethanol changes of ascending strength, further cleared in xylene and then slide-mounted in Canada balsam, as described by Kim et al. (1986). The new material, and types of Polyplax longa on loan from the Museum of Comparative Zoology (MCZ), Harvard University, were examined and compared by compound light microscopy. In the descriptions that follow, abbreviations established by Kim & Ludwig (1978) are used but are spelled out when first mentioned in this paper. Measurements were made using a calibrated eyepiece graticule.

Results

Although the new louse genus is clearly a typical polyplacid as characterized by Kim & Ludwig (1978), representatives of the new genus have five abdominal spiracles rather than six. This trait necessitates amending the characters that define the family Polyplacidae. Although the number of abdominal spiracles present is generally constant for higher taxa of sucking lice, with six being the plesiomorphic (primitive) state, an apomorphic (derived) reduction in this number occurs in representatives of some families such as the Enderleinellidae (Kim & Ludwig, 1978). Thus, although the number of abdominal spiracles is a fundamental and constant trait in most families of sucking lice, intrafamilial variation of this number is not unprecedented.

Family Polyplacidae – amended description (adapted from Kim & Ludwig, 1978)

Medium to small Anoplura. Head with 5-segmented antennae, usually sexually dimorphic; postantennal angles variable. Thorax with mesothoracic phragmata usually evident; sternal plate usually well developed and rarely absent; notal pit absent. Forelegs always small and slender, each with acuminate claw; mid- and hindlegs subequal in size and shape or hindlegs larger than midlegs. Abdomen with paratergites usually highly developed and occasionally represented by

small sclerites or completely lacking; 5 or 6 pairs of spiracles present; tergal and sternal plates usually highly developed and at times reduced or lacking; sternal plate of segment 2 not extending laterally to articulate with corresponding paratergites. Male genitalia with well developed but variously shaped basal apodeme, parameres and pseudopenis. Female genitalia with well developed subgenital plate and gonopods VIII and IX; spermatheca usually indistinct.

Abrocomaphthirus Durden & Webb, gen.n.

Small Anoplura. Head produced into rounded apex; antennae 5-segmented, not sexually dimorphic. Thoracic sternal plate well developed with broadly rounded anterior and lateral margins and slightly extended posterior margin; thoracic phragmata distinct; dorsal mesothoracic setae (DMsS) absent. Forelegs small and weak with small acuminate claw; mid- and hindlegs progressively larger, each with larger acuminate claw. Abdomen with narrow tergites and sternites, or tergites absent in male; paratergites well developed; paratergites II-V each with 1 or both posterolateral angles extended; 5 abdominal spiracles - on paratergites II-VI. Dorsal lateral abdominal setae (DLAS) and ventral lateral abdominal setae (VLAS) present in both sexes. Male basal apodeme, parameres and pseudopenis well developed; male subgenital plate weakly sclerotized. Female genitalia with small but well sclerotized subgenital plate; gonopods VIII and IX distinct; vulvar fimbriae indistinct.

Included species. A. hoplai sp.n.; A. longus (Werneck) comb.n.

Hosts. Chinchilla rats (Rodentia: Abrocomidae) in Andean South America.

Collection data and deposition of types. (1) For A. hoplai, see species description below; (2) For A. longus, types ex Abrocoma cinerea Thomas, Puno Department, Peru (Werneck, 1948; Ferris, 1951, 1953; Durden & Musser, 1994a), types deposited in the MCZ, Harvard University.

Type species. A. longus (Werneck).

Etymology. Named for the type host genus, Abrocoma.

Abrocomaphthirus hoplai Durden & Webb, sp.n. (Figs 1, 2)

Male (Fig. 1)

Length of holotype, 0.76 mm. Head, thorax and abdomen moderately sclerotized.

Head. Longer than wide with slightly extended, rounded apex; 3 dorsal ApHS (apical head setae), 2 ventral ApHS, 2 dorsal anterior head setae (DAnHS), 1 supraantennal head seta (SpAtHS), 2 sutural head setae (SHS), 2 dorsal marginal head setae (DMHS), 1 dorsal anteror central head seta (DAnCHS), 1 dorsal posterior central head seta (DPoCHS), 1 dorsal principal head seta (DPHS), 1 dorsal accessory head seta (DAcHS), 1 ventral principal head seta (VPHS), and 1 ventral preantennal

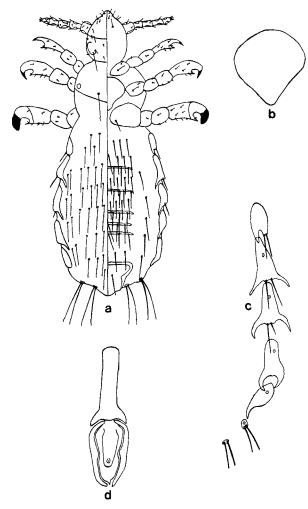


Fig. 1. Abrocomaphthirus hoplai, new genus and species; male (a) whole louse showing dorsal morphology to the left of the midline and ventral features to the right; (b) thoracic sternal plate; (c) paratergal plates; (d) genitalia.

head seta (VPaHS) on each side; medial SHS slightly longer than lateral SHS; DPHS and DAcHS borne on flap-like structure. Antennae 5-segmented with basal segment distinctly larger than other segments, slightly wider than long; third antennal segment unmodified.

Thorax. Broad with rounded margins; thoracic sternal plate (Fig. 1b) broadly rounded anteriorly and laterally but with extended posterior apex; mesothoracic spiracle small (0.0125 mm in diameter); dorsal principal thoracic seta (DPTS) moderate in length (0.075 mm); no other thoracic setae present except on legs. Legs with subtriangular fore coxae; forelegs small with narrow acuminate claw; mid- and hind legs progressively larger with correspondingly larger acuminate claws.

Abdomen. Slightly wider than thorax with leathery integument; 1 narrow sternite ventrally on segments 3, 4 and 6; 2 narrow sternites ventrally on segment 5; no tergites dorsally; ventrally, 1 row of 6 ventral central abdominal setae (VCAS)

anteriorly, followed posteriorly by a row of 7 VCAS, then successively by 6 sternal abdominal setae (StAS), 8 intersternal abdominal setae (InStAS), 8 StAS, 8 InStAS, 6 StAS, 5 StAS, 5 StAS, 4 VCAS, and 2 VCAS; 1 VLAS present on each of segments 3-7; dorsally, 2 rows of 4 dorsal central abdominal setae (DCAS) anteriorly, followed successively by 3 rows of 8 DCAS, 2 rows of 6 DCAS, and 1 row of 2 DCAS; 2 DLAS present on each of segments 3-6; ventral abdominal setae stouter than dorsal abdominal setae. Paratergal plates (Fig. 1c) present on segments 2-8; plates II-VI each with small spiracle; plate I with deep medial depression; plates II-IV each with extended ventral and dorsal apices; plate V with extended ventral apex; plates VI and VII small and indistinct; plate I with 2 long dorsal paratergal setae (DPrS), plate II with DPrS and ventral paratergal seta (VPrS) both long, plate III with short DPrS and long vPrS, plates IV and V lacking setae, plates VI and VII each with 2 very long setae.

Genitalia (Fig. 1d). Slightly distorted as shown in figure; basal apodeme slightly longer than parameres and pseudopenis, concave posteriorly; parameres stout, well sclerotized, and with blunt medial indentation; pseudopenis extending approximately to apex of parameres; subgenital plate (Fig. 1a) poorly sclerotized and indistinct, U-shaped with small medial projection on each side.

Female (Fig. 2)

Length of allotype, 0.98 mm; length of paratype female, 0.94 mm; mean length, 0.96 mm. Head, thorax and abdomen as in male unless indicated otherwise.

Head. 2-3 ApHS present on each side; head distinctly broader posterior to antennae.

Thorax. Thoracic sternal plate (Fig. 2b) distinctly extended posteriorly to truncate apex; mesothoracic spiracle diameter, 0.015 mm; DPTS length, 0.08 mm. Legs with fore- and mid coxae subtriangular.

Abdomen. Distinctly broader than thorax, with 14 narrow plates ventrally and 12 dorsally; ventrally, sternites 1 and 2 broader than other sternites, and sternites 1, 10, 11, 13 and 14 shorter than adjacent sternites; 4 StAS on sternite 1, then 6-8 StAS on sternites 2-9 and 12, and 4-5 StAS on sternites 10, 11, 13 and 14; 5 rows of 1-2 VLAS present; dorsally, tergites 1 and 2 each with 4 TeAS; tergites 3-9 each with 6-8 TeAS, tergites 10 and 11 each with 4 TeAS, and tergite 12 with 2 TeAS; 1 DCAS posterior to tergite 12; 11 rows of 1-4 DLAS present. Paratergal plates (Fig. 2c) as in male but 1 long DPrS present on plate II, 1 long VPrS and 1 short DPrS on plate IV, and 1 short seta on plate V.

Genitalia (Fig. 2d). Small but well sclerotized subgenital plate slightly extended anterolaterally on each side, with medial indentation posteriorly and 1 small seta on each side; gonopods VIII each with 3 apical setae of moderate length; gonopods IX small, with 2 fairly stout setae (appearing as 3 due to the presence of dorsal seta in the same region); vulvar fimbriae indistinct.

Collection data. All three type specimens were recovered from different individuals of the chinchilla rat, Abrocoma bennetti Waterhouse, trapped by R. E. Martin in Santiago Province, Chile, at an elevation of 900 m. The precise type

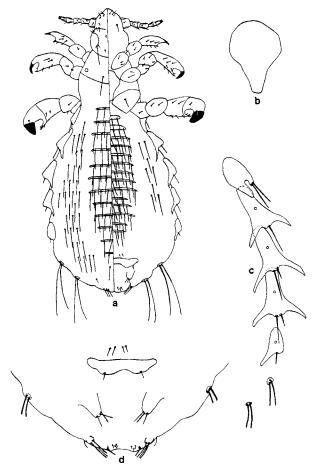


Fig. 2. Abrocomaphthirus hoplai, new genus and species; female (a) whole louse showing dorsal morphology to the left of the midline and ventral morphology to the right; (b) thoracic sternal plate; (c) paratergal plates; (d) genitalia.

locality is 2.5 km north-east of Cerro Manquehue at the site of a Trappist monastery (33°20′ S, 70°33′30″ W). The holotype male of *A. hoplai* was collected from an adult female chinchilla (field no. REM 1229) on 1 August 1975, the allotype female louse from a subadult female chinchilla (REM 1189) on 10 April 1975 and the paratype female louse from an adult female chinchilla (REM 1208) on 1 June 1975.

Deposition of types. Holotype male and allotype female deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington DC. Paratype female deposited in the Natural History Museum, London.

Etymology. This new species is named for our trusted friend and colleague, Professor Cluff E. Hopla, a renowned authority on ectoparasites and vector-borne diseases.

Abrocomaphthirus longus (Werneck, 1948), comb.n.

Neohaematopinus longus Werneck, 1948. Neohaematopinus longus Werneck: Ferris, 1951. Polyplax longa (Werneck): Ferris, 1953.

Polyplax longus (Werneck): Durden & Musser, 1994a, b.

This louse shares many characters with Abrocomaphthirus hoplai, sp.n. It also parasitizes a congeneric chinchilla rat in the same approximate geographical region of the neotropics (southern Peru). Clearly, this louse is a congener of A. hoplai, sp.n. For this reason, we have reassigned it to the new genus as Abrocomaphthirus longus, comb.n.

Since it was first described in 1948, the precise generic assignment of this louse has been debated. Clearly, it does not belong to the genus Neohaematopinus because it lacks morphological characters of that genus such as: (1) a posteriorly emarginate second tergite on abdominal segment 2; (2) a posteriorly emarginate thoracic sternal plate; (3) a specialized third antennal segment in the male; (4) characteristic male genitalia. Although Ferris (1953) reassigned this louse from Neohaematopinus to Polyplax, a genus with which it undoubtedly shares several characters, he expressed reservations about retaining this louse in Polyplax. He stated, 'There remains a question as to what genus it should be referred or as to whether or not a new genus should be named for it.' (Ferris, 1953; p. 53). Despite sharing some morphological characters with Polyplax, both A. longus and A. hoplai have five abdominal spiracles rather than the six that distinguish Polyplax, Neohaematopinus, and other polyplacids. Males of Polyplax also have a highly modified third antennal segment, which remains unmodified in males Abrocomaphthirus. However, because Abrocomaphthirus is a typical polyplacid genus in all other respects, we have taken what we consider to be the most prudent action by slightly amending the definition of the family Polyplacidae in order to accomodate it. Although other traits of Abrocomaphthirus such as the narrow abdominal tergites and sternites, the relatively large number of DLAS and VLAS and the shape of the reproductive structures are unusual, a few species of Polyplax share one or more of these characters. However, Abrocomaphthirus also shares certain morphological characters with other native neotropical polyplacid genera, namely Cuyana, Eulinognathus, Galeophthirus and Lagidiophthirus, and we believe that it is phylogenetically more closely related to these genera than to Polyplax. Its morphological similarity to Polyplax may be due, in part, to convergent evolution. Interestingly, Eulinognathus, as currently interpreted, is well represented in both South America and Africa.

Discussion

Selection pressures associated with parasitizing South American abrocomid rodents have resulted in the evolution of several taxa of ectoparasites. In addition to the new sucking louse genus described here, a unique family of chewing lice, the Abrocomophagidae, is associated with abrocomids (Emerson & Price, 1976). Further, the ixodid tick *Ixodes sigelos* Keirans, Clifford & Corwin, and the rhopalopsyllid fleas *Delostichus coxalis* (Rothschild) and *Tetrapsyllus corfidii* (Rothschild) parasitize *A. bennetti* and some of its close

ecological rodent associates in Chile (Keirans et al., 1976; Smit. 1987).

Interestingly, some convergent morphological evolution seems to have occurred between the sucking louse, A. hoplai, and the chewing louse, Abrocomophaga chilensis Emerson & Price, both of which parasitize A. bennetti. Both lice have narrow abdominal plates, relatively abundant lateral abdominal setae, and five abdominal spiracles (on segments 3-7), presumably reflecting evolutionary responses to the same selection pressures associated with parasitizing A. bennetti.

The taxonomic action of erecting a new genus for the sucking lice associated with abrocomids has zoogeographical implications. Foremost, no native species of Polyplax are now known to inhabit South America. Three noteworthy papers have discussed the zoogeography of neotropical mammal lice. The authors of the earlier of these, Vanzolini & Guimaraes (1955a, b), treated A. longus as a member of the polyplacid genus Neohaematopinus and stated that it reflected a recent invasion of this genus from North America after the Panamanian landbridge formed 2.5-3 million years ago, i.e. during the 'great American interchange' (Vrba, 1992). Although Neohaematopinus does indeed appear to have colonized Central and South America from North America, which is inhabited by 10 native species belonging to this genus (Kim et al., 1986; Durden, 1991), a sharp reduction in the number of species in this genus is evident in the neotropics. Thus, although 10 species of Neohaematopinus are native to the United States, seven species are known from Mexico, two from other Central American countries and just one (N. semifasciatus Ferris) from Venezuela (Johnson, 1972b; Durden, 1991; Durden & Musser, 1994a). This, and the documented Nearctic rodent invasions of South America during the great American interchange, provide circumstantial evidence that Neohaematopinus has recently infiltrated the neotropics from the north. Thus, if A. longus did belong to the genus Neohaematopinus as originally believed (Werneck, 1948), there would be a significant gap between Venezuela and southern Peru in which Neohaematopinus is apparently absent. Although polyplacid louse extinctions could have occurred in this region, the above explanation of the derivation of the extant zoogeography of Neohaematopinus seems more plausible. Further, 30 of the 32 recognized species of Neohaematopinus parasitize sciurid rodents and the remaining two parasitize sigmodontine rodents (woodrats, Neotoma spp.), with none associated with other rodent families such as the abrocomids (Durden, 1991; Durden et al., 1997). Regardless, the neotropical distribution for this genus described by Vanzolini & Guimaraes (1955a) is refuted.

Similarly, when A. longus was thought to belong to the genus Polyplax (Ferris, 1953; Durden & Musser, 1994a, b), it represented a zoogeographical anomaly because no other native species of the latter genus are known south of Panama in the neotropics. Similar to the case for Neohaematopinus, a reduction in the number of native species of Polyplax occurs from the United States (three species), southwards to Guatemala and Honduras (two species, including an undescribed species at hand) and Panama (one species -P. auricularis Kellogg & Ferris) (Johnson, 1972a; Durden &

Musser, 1994a). Therefore, if A. longus did belong to the genus Polyplax, there would again be a sizeable gap between Panama and southern Peru, from which no native species of Polyplax are known. Because native species of Polyplax do not appear to have colonized the neotropics any further south than Panama, they may not have dispersed further into the region after the Panamanian landbridge formed.

Unlike Vanzolini & Guimaraes (1955a, b), who did not consider continental drift in their zoogeographical analyses, Traub (1980) believed this form of vicariance zoogeography to be important in shaping the distributions of vertebrates and their parasites. He advocated that some neotropical sucking lice had African affinities, highlighting the fact that Eulinognathus is well represented on both continents and that three closely related monotypic native polyplacid genera, Cuyana, Galeophthirus and Lagidiophthirus, also inhabit South America. Although Traub (1980) acknowledged that any physical connection between Africa and South America predated the evolution of the Anoplura, he believed that certain ancestral African rodents accompanied by their lice, could have 'island-hopped' between the two continents when they were physically closer in the geological past. Given the lack of rigorous alternative scenarios, this certainly seems to be a plausible hypothesis for Eulinognathus and its allies (Cuyana, Galeophthirus and Lagidiophthirus) because these louse genera are all absent from North America and other landmasses with potential relevance to this issue such as Antarctica, Australia and India (Durden & Musser, 1994a). Because Abrocomaphthirus is also allied to this cluster of neotropical polyplacid genera, it seems likely that they share ancestral African affinities. In fact, based on currently available data, this seems to be the most likely route of neotropical colonization by these sucking lice.

The evolutionary and zoogeographical history of South American caviomorph rodents such as the abrocomids may also favour ancient African origins. Two competing views of late-Eocene caviomorph colonization of South America exist (Vrba, 1992; Wyss et al., 1993); one advocates dispersal of ancestral forms from North America prior to the formation of the Panamanian landbridge, whereas the other favours dispersal from Africa. Fossil evidence presented by Wyss et al. (1993) promotes the African connection. Interestingly, the derivation of the extant neotropical polyplacid sucking louse fauna supports both ancient African origins (for Abrocomaphthirus, Cuyana, Eulinognathus, Galeophthirus and Lagidiophthirus) as well as more recent North American origins (for Neohaematopinus and Polyplax). The louse data therefore support the contention that there were two major waves of rodent colonization into South America; an ancient one from Africa and a recent one from North America. Future phylogenetic analyses of neotropical rodents and their lice, particularly with respect to host-parasite cospeciation, should provide a test of these hypotheses.

It is presently unknown whether A. hoplai and A. longus have any medical or veterinary importance. However, some sucking lice of rodents are enzootic vectors of zoonotic pathogens such as the causative agents of murine typhus and epidemic typhus (Traub et al., 1978; Durden & Musser, 1994b). Related species of sucking lice are vectors of the agents of murine eperythrozoonosis and haemobartonellosis to their rodent hosts (Durden & Musser, 1994b). If rodent ectoparasites are vectors of hantaviruses as advocated by some researchers (e.g. Meng et al., 1996), then South American lice such as A. hoplai and A. longus could be enzootic vectors of these pathogens. Increasing recognition of hantaviral infection of humans in Chile has recently been documented (Espinoza et al., 1998; Toro et al., 1998).

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References

- Chin, T.-H. (1995) A new species of sucking louse from Cricetulus longicaudatus Milne-Edwards (Anoplura: Polyplacidae). Acta Zootaxonomica Sinica, 20, 97-101 (In Chinese).
- Durden, L.A. (1991) A new species and an annotated world list of the sucking louse genus *Neohaematopinus* (Anoplura: Polyplacidae). *Journal of Medical Entomology*, 28, 694-700.
- Durden, L.A., Banks, C.W., Clark, K.L., Belbey, B.V. & Oliver, J.H. Jr (1997) Ectoparasite fauna of the eastern woodrat, *Neotoma floridana*: composition, origin, and comparison with ectoparasite faunas of western woodrat species. *Journal of Parasitology*, 83, 374–381.
- Durden, L.A. & Musser, G.G. (1994a) The sucking lice (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.
- Durden, L.A. & Musser, G.G. (1994b) The mammalian hosts of the sucking lice (Anoplura) of the world: a host-parasite list. Bulletin of the Society for Vector Ecology, 19, 130-168.
- Durden, L.A. & Traub, R. (1990) Zoogeographical implications from rodent ectoparasites in Sulawesi. *Insects and the Rain Forests of South East Asia (Wallacea)* (ed. by W. J. Knight and J. D. Holloway), pp. 57-62. Royal Entomological Society, London.
- Emerson, K.C. & Price, R.D. (1976) Abrocomophagidae (Mallophaga: Amblycera), a new family from Chile. Florida Entomologist, 59, 425-428.
- Espinoza, R., Vial, P., Noriega, L.M., Johnson, A., Nichol, S.T., Rollin, P.E., Wells, R., Zaki, S., Reynolds, E. & Ksiazek, T. (1998) Hantavirus pulmonary syndrome in a Chilean patient with recent travel in Bolivia. *Emerging Infectious Diseases*, 4, 93-95.
- Ferris, G.F. (1951) The sucking lice. Memoirs of the Pacific Coast Entomological Society, 1, 1-320.
- Ferris, G.F. (1953) Illustrations of three species of sucking lice, with

- notes on a fourth species (Insecta; Anoplura). Microentomology, 18, 19-22
- Goldblatt, P., ed. (1994) Biological Relationships Between Africa and South America. Yale University Press, New Haven.
- Johnson, P.T. (1972a) On the rodent-infesting Anoplura of Panama. Great Basin Naturalist, 32, 121-136.
- Johnson, P.T. (1972b) Sucking lice of Venezuelan rodents, with remarks on related species (Anoplura). Brigham Young University Science Bulletin, Biological Series, 17 (5), 1-62.
- Keirans, J.E., Clifford, C.M. & Corwin, D. (1976) Ixodes sigelos, n. sp. (Acarina: Ixodidae), a parasite of rodents in Chile, with a method for preparing ticks for examination by scanning electron microscopy. Acarologia, Paris, 18, 217-225.
- Kim, K.C. & Ludwig, H.W. (1978) The family classification of the Anoplura. Systematic Entomology, 3, 249–284.
- Kim, K.C., Pratt, H.D. & Stojanovich, C.J. (1986). The Sucking Lice of North America: an Illustrated Manual for Identification. The Pennsylvania State University Press, University Park.
- Meng, Y.-C., Zhuge, H.-X., Lan, M.-Y. & Zhou, H.F. (1996) The natural infection, experimental transmission and maintenance of HFRS virus in gamasid mites (Mesostigmata). Acarology IX, Vol. 1. Proceedings (ed. by R. Mitchell, D. J. Horn, G. R. Needham and W. C. Welbourn), pp. 451–452. Ohio Biological Survey, Columbus.
- Smit, F.G.A.M. (1987) An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History) with Keys and Short Descriptions for the Identification of Families, Genera, Species and Subspecies of the Order, VII. Malacopsylloidea (Malacopsyllidae and Rhopalopsyllidae). Oxford University Press, Oxford and The British Museum (Natural History), London.
- Toro, J., Vega, J.D., Khan, A.S., Mills, J.N., Padula, P., Terry, W., Yadón, Z. et al. (1998) An outbreak of hantavirus pulmonary syndrome, Chile, 1997. Emerging Infectious Diseases, 4, 687-694.
- Traub, R. (1980) The zoogeography and evolution of some fleas, lice and mammals. Fleas: Proceedings of the International Conference on Fleas (ed. by R. Traub and H. Starcke), pp. 93–172. A. A. Balkema, Rotterdam.
- Traub, R., Wisseman, C.L. Jr & Azad, A.F. (1978) The ecology of murine typhus: a critical review. *Tropical Diseases Bulletin*, 75, 237-317.
- Vanzolini, P.E. & Guimaraes, L.R. (1955a) Lice and the history of South American land mammals. Revista Brasileira de Entomologia, 3, 13-46.
- Vanzolini, P.E. & Guimaraes, L.R. (1955b) South American land mammals and their lice. Evolution, 9, 345-347.
- Vrba, E.S. (1992) Mammals as a key to evolutionary theory. *Journal of Mammalogy*, 73, 1–28.
- Werneck, F.L. (1948) 'Neohaematopinus longus' n.sp. (Anoplura, Haematopinidae). Revista Brasileira de Biologia, 8, 173-175.
- Wyss, A.R., Flynn, J.J., Norell, M.A., Swisher, C.C. III, Charrier, R., Novacek, M.J. & McKenna, M.C. (1993) South America's earliest rodent and recognition of a new interval of mammalian evolution. *Nature, London*, 365, 434–437.

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