Biological Journal of the Linnean Society, 2008, **95**, 598–610. With 3 figures

Rodent louse diversity, phylogeny, and cospeciation in the Manu Biosphere Reserve, Peru

VINCENT S. SMITH[1], JESSICA E. LIGHT[2]* and LANCE A. DURDEN[3]

[1]*Entomology Department, The Natural History Museum, London SW7 5BD, UK*
[2]*Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA*
[3]*Department of Biology and Institute of Anthropodology & Parasitology, PO Box 8042, Georgia Southern University, Statesboro, GA 30460, USA*

Received 12 January 2008; accepted for publication 11 March 2008

We investigated the diversity, cophylogenetic relationships, and biogeography of hoplopleurid sucking lice (Phthiraptera: Anoplura) parasitizing rodents (Muridae: Sigmodontinae) in the Manu National Park and Biosphere Reserve. Our morphological and molecular studies reveal that 15 distinct louse species parasitize 19 rodent species. Three of these louse species are new to science, and all but two of the host associations were previously unknown. We find that hoplopleurid lice in South America parasitize multiple host species across a large geographic area, and that Peru represents a new geographic locality for almost all the louse species collected in the present study. Phylogenetic analyses of mitochondrial and nuclear data reveal that the louse family Hoplopleuridae and the genera *Hoplopleura* and *Pterophthirus* are not monophyletic, and lice do not appear to group by host tribe, collecting locality, or collection elevation. The lack of monophyly for these apparently natural groups (taxonomic, locality, and elevation) indicates that host switching with or without parasite speciation may be prevalent among hoplopleurid lice.

ADDITIONAL KEYWORDS: Anoplura – biodiversity – biogeography – cophylogeny – *Hoplopleura* – Peru – rodents – Sigmodontinae – sucking lice.

INTRODUCTION

The Manu National Park and Biosphere Reserve in southeastern Peru is one of the richest biodiversity regions in the world, largely due to its physical location in central Amazonia and its elevational heterogeneity. This reserve includes the eastern slope of the Andes and adjacent Amazonian lowlands, resulting in an elevational gradient of 3000 m and a wide diversity of habitats (from lowland tropical forests to montane cloud forests; Tantaleán & Chavez, 2004; Patterson, Stotz & Solari, 2006a, b). Despite the documentation of more than 190 species of mammals and 900 species of birds within this region (Pacheco, 2003; Fitzpatrick, unpubl. data), much remains to be learned about the biodiversity found within the Manu Biosphere Reserve.

Rodents, specifically muroid rodents, account for over 40% of all mammal diversity (Weksler, 2003; Jansa & Weksler, 2004; Wilson & Reeder, 2005) and the sigmodontine rodents are the most diverse subfamily-level mammal clade in the Neotropics with over 70 genera and 350 species (Musser & Carleton, 1993, 2005; Weksler, 2003; D'Elia *et al.*, 2006; Weksler, Percequillo & Voss, 2006). Excluding bats (Chiroptera), sigmodontine rodents belonging to the tribes Oryzomyini, Akodonini, and Thomasomyini encompass the majority of the mammal species found within the Manu Biosphere Reserve (Solari *et al.*, 2006). Comparatively little is known about the parasitic fauna of these rodent groups. Although diverse parasite faunas have been recorded from other Neotropical hotspots, such as Panama and Venezuela

*Corresponding author. E-mail: jlight@flmnh.ufl.edu

(Wenzel & Tipton, 1966; Tipton & Handley, 1972), Peru is arguably the least known given its species richness and diversity of potential vertebrate hosts. In particular, sucking lice (Phthiraptera: Anoplura) infesting mammals from the tropical Andes are one of the least well known groups of parasites.

Members of the Anoplura (sucking lice) are blood-feeding obligate ectoparasitic insects, some of which have medical and veterinary significance as parasites, pests, and vectors of animal and human disease agents. Sucking lice are distributed worldwide and, for the most part, are highly host-specific, occurring on most major groups of eutherian mammals. Approximately 550 species of Anoplura have currently been described, with the majority (71%) collected from rodents (Kim, 1988; V. S. Smith & J. E. Light, unpubl. data). Lice belonging to the genus *Hoplopleura* Enderlein (family Hoplopleuridae; 150 species) almost exclusively parasitize rodents, with half of all species recorded from a single rodent host species. Although a high degree of host specificity is often expected from obligate parasites, multi-host parasitism is relatively common among lice (Banks & Paterson, 2005; V. S. Smith & J. E. Light, unpubl. data) and may arise through various biological processes (e.g. host switching, failure of the parasite to speciate) or artefacts of taxonomy (e.g. cryptic speciation). Untangling the complex associations between *Hoplopleura* and their rodent hosts requires a detailed study of their distribution, taxonomy, and phylogeny. Although there have been several recent studies of Sigmodontinae relationships (D'Elia, Gonzalez & Pardinas, 2003; Weksler, 2006; Weksler *et al.*, 2006), no such studies exist for *Hoplopleura*. Indeed, no more than 20 species of Anoplura have ever been studied phylogenetically, making it impossible to establish the factors that might explain deviations from host specificity observed within this group of rodent lice.

In the present study, we provide a preliminary assessment of the diversity of sucking lice parasitizing rodents found within the Manu Biosphere Reserve. We concentrate our diversity assessment on the hoplopleurid lice parasitizing sigmodontine rodents, specifically the tribes Akodontini, Oryzomyini, and Thomasomyini, although sucking lice were also examined from additional rodent families (Sciuridae, Echimyidae, and Caviidae). These data provide a baseline inventory of rodent Anoplura in the Manu Biosphere Reserve. In addition, we examine host associations, louse cophylogenetic relationships, and biogeographic data to provide a preliminary assessment of the cophylogenetic patterns between these lice and their Neotropical rodent hosts. These findings are examined in light of other cophylogenetic studies on parasitic lice to consider possible explanations for patterns of host specificity exhibited by anopluran species infesting rodents.

MATERIAL AND METHODS

Collecting and sample preparation

In a series of three annual trips between 1999 and 2001, ectoparasites were collected from rodents at a series of eight field sites (Fig. 1) within the Manu Biosphere Reserve. A full account of these trips and details on the collection localities are provided elsewhere (Patterson *et al.*, 2006a). Hosts were fumigated in ethyl ether to immobilize ectoparasites, and then a stiff brush was applied to the host pelage to loosen ectoparasites adhering to the fur. All collected ectoparasites were placed in 95% ethanol for future sorting and identification. Lice were identified to genus using a dissecting microscope, and stored at –70 °C.

Louse diversity was assessed by morphological identification of lice collected from each host species across the reserve (Table 1). Male and female lice (if both were present) were cleared using 10% KOH and mounted on slides in Canada Balsam using standard louse preparation protocols (although xylene, rather than clove oil, was used to fix the lice; Palma, 1978). Subsamples of lice from the same hosts were chosen for molecular work (Table 1) using louse-specific protocols (Cruickshank *et al.*, 2001; Johnson & Clayton, 2003) and the DNeasy Tissue Kit (Qiagen Inc.) to isolate genomic DNA from each louse. After DNA extraction, lice were retained as vouchers and mounted on slides as explained above, although the 10% KOH treatment was omitted because specimens were cleared during the extraction process. After lice were mounted on slides, they were identified to species with the aid of a compound microscope (Olympus BH-2 phase contrast; ×40 to ×400) and by comparison with the literature (Johnson, 1972; Castro, 1979, 1982, 1984; Castro & Gonzalez, 1997; González-Acuña, Castro & Moreno-Salas, 2003; González-Acuña *et al.*, 2005) and previously identified, cleared, slide-mounted specimens.

Amplification and sequencing

DNA extractions were used in polymerase chain reaction (PCR) amplifications of portions of two genes: the mitochondrial cytochrome *c* oxidae subunit I (CO *I*; 387 bp) and the nuclear elongation factor 1-alpha (EF1α; 351 bp) genes. The primers L6625 and H7005 (Hafner *et al.*, 1994) and EF1-For1 and EF1-Cho10 (Danforth & Ji, 1998) were used to amplify CO *I* and EF1α, respectively, using protocols described in Johnson & Clayton (2000). PCR clean-ups and sequencing reactions were performed according to Light & Hafner (2007a). Sequences were edited using Se-Al Sequence Alignment Editor, version 2. 0a11

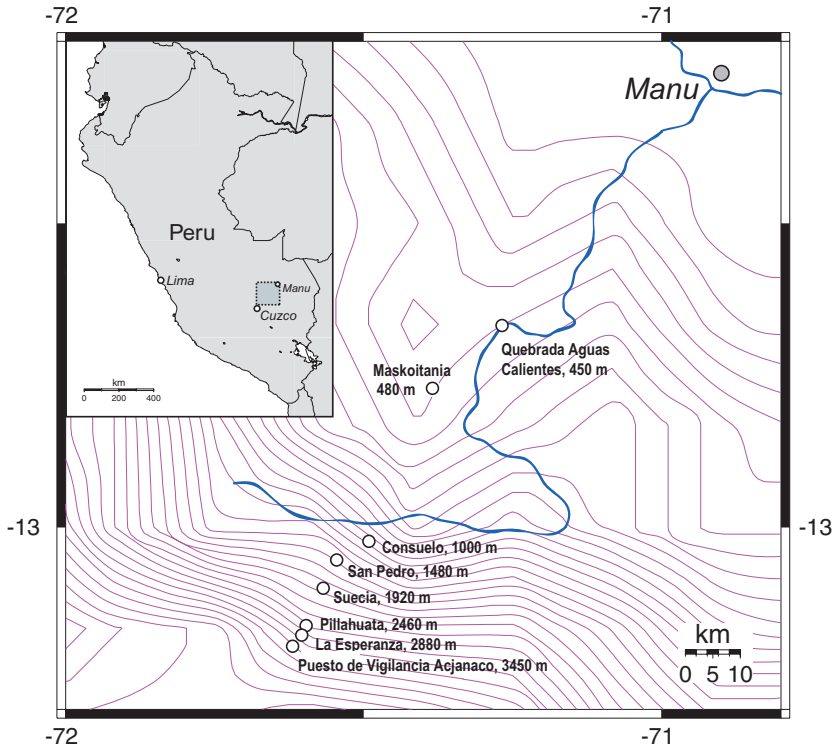

Figure 1. Collection localities within the Manu Biosphere Reserve of rodent and sucking louse specimens (Table 1).

(Rambaut, 2002) and aligned by eye. Primer sequences were removed and sequences were trimmed in reference to the translated protein sequence. All sequences were deposited in Genbank (EU375756–EU375776 for CO *I* and EU375777–EU375797 for EF1α). Exemplars of louse suborders closely related to Anoplura [*Bovicola bovis* (Linnaeus) and *Felicola subrostratus* (Burmeister), Phthiraptera: Ischnocera, and *Haematomyzus elephantis* Piaget, Phthiraptera: Rhynchophthirina] were chosen as outgroup taxa in the phylogenetic analyses (Genbank Accession Numbers AF38009, AF545680, and AF545700 for CO *I*; AF385028, AF320370, and AF320398 for EF1α).

Phylogenetic analysis

Each louse specimen represented in the phylogenetic and cophylogenetic analyses was treated as a unique taxonomic unit, *sensu* Page *et al.* (2004). Phylogenetic analyses of a combined CO *I* and EF1α dataset for 27 taxa (Table 1) were performed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian approaches. PAUP*4.0b10 (Swofford, 2003) was used to perform equally weighted MP searches with 100 random addition replicates and tree-bisection-reconnection branch swapping. To assess nodal support, nonparametric bootstrap analyses (500 pseudoreplicates and ten random sequence addition additions per replicate) were performed (Felsenstein, 1985).

To generate the best ML tree, MODELTEST, version 3.7 (Posada & Crandall, 1998) was used to examine the fit of 56 models of nucleotide substitution to the sequence data. Models of evolution providing the best approximation of the data using the fewest parameters were chosen for subsequent analyses according to the Akaike Information Criterion (Huelsenbeck & Rannala, 1997; Posada & Buckley, 2004). The TIM model (a transitional general time reversible model), including among-site rate variation and invariable sites (TIM+I+Γ; Yang, 1994; Gu, Fu & Li, 1995), was chosen as the best model of evolution for the combined dataset. Full heuristic ML and bootstrap searches (200 pseudo-replicates) were conducted using the preferred model in PAUP* 4.0b10 (Swofford, 2003).

Bayesian phylogenetic analyses were performed using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). A general time reversible model including invariable sites and among-site rate variation was used in the Bayesian analyses and model parameters were treated as unknown variables with uniform priors. Bayesian analyses were initiated with random starting trees, run for 10 million generations with four incrementally heated chains (Metropolis-coupled Markov chain Monte Carlo; Huelsenbeck & Ronquist, 2001), and

Table 1. List of hoplopleurid lice assessed in the present study

Louse species	Host species	Locality
Rodentia: Cricetidae: Sigmodontinae: Akodontini		
Hoplopleura aitkeni – 174952*	*Akodon aerosus*	Cusco: Paucartambo; Consuelo, 1000 m
Hoplopleura aitkeni – 172177	*Akodon aerosus*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura aitkeni – 172182	*Akodon aerosus*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura aitkeni – 172194	*Akodon aerosus*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura aitkeni – 172191	*Akodon aerosus*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura aitkeni – 170485	*Akodon subfuscus*	Cusco: Paucartambo; Puesto de Vigilancia Acjanaco, 3450 m
Hoplopleura aitkeni – 175017*	*Akodon torques*	Cusco: Paucartambo; La Esperanza, 2880 m
Hoplopleura aitkeni – 172213	*Akodon torques*	Cusco: Paucartambo; Pillahuata, 2460 m
Hoplopleura aitkeni – 170516*	*Akodon torques*	Cusco: Paucartambo; Puesto de Vigilancia Acjanaco, 3450 m
Hoplopleura fonsecai – 175215	*Oxymycterus inca*	Madre de Dios: Manu; Maskoitania, 480 m
Hoplopleura fonsecai – 175207*	*Oxymycterus inca*	Madre de Dios: Manu; Maskoitania, 480 m
Rodentia: Cricetidae: Sigmodontinae: Oryzomyini		
Hoplopleura multilobata – 175197*,†	*Euryoryzomys nitidus*	Cusco: Paucartambo; Consuelo, 1000 m
Hoplopleura multilobata – 175198	*Euryoryzomys nitidus*	Cusco: Paucartambo; Consuelo, 1000 m
Hoplopleura brasiliensis – 175181*,‡	*Hylaeamys megacephalus*	Madre de Dios: Manu; Maskoitania, 480 m
Hoplopleura brasiliensis – 175193*,‡	*Hylaeamys megacephalus*	Madre de Dios: Manu; Maskoitania, 480 m
Hoplopleura rimae – 175034*	*Microryzomys minutus*	Cusco: Paucartambo; La Esperanza, 2880 m
Hoplopleura rimae – 172241	*Microryzomys minutus*	Cusco: Paucartambo; Pillahuata, 2460 m
Hoplopleura rimae – 170569*	*Microryzomys minutus*	Cusco: Paucartambo; Puesto de Vigilancia Acjanaco, 3450 m
Hoplopleura rimae – 170579	*Microryzomys minutus*	Cusco: Paucartambo; Succia, 1920 m
Hoplopleura quadridentata – 172246*	*Neacomys* sp.	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura new sp. 1 – 172250	*Neacomys* sp.	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura quadridentata – 172253	*Nectomys squamipes*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura quadridentata – 172262	*Nectomys squamipes*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura quadridentata – 172263	*Nectomys squamipes*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura quadridentata – 175091	*Nectomys squamipes*	Cusco: Paucartambo; Consuelo, 1000 m
Hoplopleura multilobata – 172332*,§	*Nephelomys keaysi*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura multilobata – 172325	*Nephelomys keaysi*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura quadridentata – 172305	*Nephalomys keaysi*	Cusco: Paucartambo; San Pedro, 1480 m
Hoplopleura multilobata – 170666	*Nephelomys keaysi*	Cusco: Paucartambo; Succia, 1920 m
Hoplopleura multilobata – 170650	*Nephelomys keaysi*	Cusco: Paucartambo; Succia, 1920 m
Hoplopleura travassosi – 175102*	*Oligoryzomys destructor*	Cusco: Paucartambo; La Esperanza, 2880 m
Hoplopleura travassosi – 172279	*Oligoryzomys destructor*	Cusco: Paucartambo; Pillahuata, 2460 m
Hoplopleura sp. – 172287¶	*Oligoryzomys destructor*	Cusco: Paucartambo; Pillahuata, 2460 m
Hoplopleura travassosi – 172290	*Oligoryzomys destructor*	Cusco: Paucartambo; Pillahuata, 2460 m
Hoplopleura rimae – 175054	*Oligoryzomys minutus*	Cusco: Paucartambo; La Esperanza, 2880 m
Hoplopleura sp. – 172298¶	*Oligoryzomys* sp.	Cusco: Paucartambo; Pillahuata, 2460 m

Table 1. *Continued*

Louse species	Host species	Locality
Rodentia: Cricetidae: Sigmodontinae: Thomasomyini		
Hoplopleura new sp. 2 – 172369	*Thomasomys aureus*	Cusco: Paucartambo; Pillahuata, 2460 m
Hoplopleura new sp. 2 – 170689*	*Thomasomys aureus*	Cusco: Paucartambo; Succia, 1920 m
Hoplopleura tiptoni – 175243*	*Thomasomys oreas*	Cusco: Paucartambo; La Esperanza, 2880 m
Hoplopleura tiptoni – 170706	*Thomasomys oreas*	Cusco: Paucartambo; Puesto de Vigilancia Acjanaco, 3450 m
Pterophthirus imitans – 170706**	*Thomasomys oreas*	Cusco: Paucartambo; Puesto de Vigilancia Acjanaco, 3450 m
Rodentia: Sciuridae		
Hopleopleura sciuricola – 170302	*Microsciurus flaviventer*	Madre de Dios: Manu; Quebrada Aguas Calientes, 450 m
Enderleinellus new sp. – 170302	*Microsciurus flaviventer*	Madre de Dios: Manu; Quebrada Aguas Calientes, 450 m
Hoplopleura sciuricola. – 170303*	*Sciurus spadiceus*	Madre de Dios: Manu; Quebrada Aguas Calientes, 450 m
Rodentia: Caviidae		
Pterophthirus imitans – 170718*	*Cavia tschudii*	Cusco: Paucartambo; Puesto de Vigilancia Acjanaco, 3450 m
Rodentia: Echimyidae		
Pterophthirus splendida – 170724	*Proechimys simonsi*	Madre de Dios: Manu; Quebrada Aguas Calientes, 450 m
Pterophthirus splendida – 170726*	*Proechimys simonsi*	Madre de Dios: Manu; Quebrada Aguas Calientes, 450 m
Additional Louse Taxa Used in Molecular Analyses		
Haematopinus suis – GLA.M02*	*Sus scrofa*	
Haematopinus tuberculatus – GLA.M01*	*Bubalus bubalis*	
Hoplopleura sciuricola – GLA.M120*	*Sciurus carolinensis*	
Hoplopleura trispinosa – GLA.M29*	*Glaucomys volans*	
Linognathoides marmotae – CF01.01*,††	*Marmota flaviventris*	
Linognathoides marmotae – GLA.M42*	*Marmota* sp.	
Linognathus africanus – GLA.M06*,††	*Capra hircus*	
Linognathus ovillus – GLA.M09*,††	*Ovis aries*	

Louse specimens are grouped by host taxonomy and followed by host museum number (all are from the Field Museum of Natural History; FMNH). Asterisks indicate taxa included in the molecular analyses. All collection localities are in Peru and shortened specific localities are in accordance with Patterson *et al.* (2006b); full specific localities are available from the FMNH database. Accession numbers for additional outgroup louse taxa correspond to the Glasgow University Louse Specimen Database (LouseBASE; GLA.M)

†*Hoplopleura multilobata* – 175222 (from *Euryoryzomys*) was sequenced only for the EF1α gene.

‡*Hoplopleura brasiliensis* – 175181 was sequenced only for the CO I gene, whereas *Hoplopleura brasiliensis* – 175193 was sequenced only for the EF1α gene. Because these louse specimens parasitize the same host species (*Hylaeamys megacephalus*) from the same host locality, they are treated as a singular specimen and only *Hoplopleura brasiliensis* – 175193 is listed in the phylogenetic and cophylogenetic trees.

§*Hoplopleura multilobata* – 172332 (from *Nephelomys keaysi*) was sequenced only for the EF1α gene.

¶Due to insufficient material, these louse specimens could not be identified.

**This louse association likely reflects a straggler or contamination.

††These specimens were sequenced only for the CO *I* gene.

sampled at intervals of 1000 generations. To avoid entrapment on local optima, two independent Bayesian analyses were run and log-likelihood scores were compared for convergence (Huelsenbeck & Bollback, 2001; Leaché & Reeder, 2002). Log-likelihood scores of sample points were plotted against generation time to assess stationarity and all burn-in points (the first 5000 trees) were discarded. The retained equilibrium samples were used to generate a 50% majority rule consensus tree with the percentage of samples recovering any particular clade representing that clade's posterior probability. The executable file of louse data is available at TreeBASE (http://www.treebase.org; study accession number S2002).

Alternative phylogenetic hypotheses were compared statistically using the Kishino–Hasegawa and Shimodaira–Hasegawa tests as implemented in PAUP*4.0b10 (MP and ML analyses using resampling estimated log-likelihood optimization and 1000 bootstrap replicates; Kishino & Hasegawa, 1989; Shimodaira & Hasegawa, 1999; Goldman, Anderson & Rodrigo, 2000).

Comparisons with host tree

Coevolutionary comparisons included only the ingroup louse taxa and their respective rodent hosts (Sigmodontinae, Sciuridae, Caviidae, and Echimyidae; Table 1). Host and parasite trees were assessed for similarity using tree-based methods, which consider similarities between trees as possible instances of codivergence. These methods compare only the branching structure of host and parasite trees to determine whether more codivergence events are present than would be observed by chance. Host trees were compiled from the literature (D'Elia *et al.*, 2003; Pacheco, 2003; Weksler, 2003; Herron, Castoe & Parkinson, 2004; Steppan, Storz & Hoffman, 2004; Weksler, 2006; Weksler *et al.*, 2006) in accordance with the taxonomy of Weksler *et al.* (2006) and conservatively using the hystricomorph rodents (Caviidae and Echimyidae) as the base of the rodent tree (current data suggest a polytomy among major rodent lineages; Bininda-Emonds *et al.*, 2007). Because of the basal polytomy among the three sigmodontine tribes (M. Weksler, pers. comm.), three different analyses were performed, each using a different combination of two of the three host tribes (Akodontini and Oryzomyini; Akodontini and Thomasomyini; and Oryzomyini and Thomasomyini). Only the parasite tree resulting from ML analysis was chosen for comparison with the host tree.

Two tree-based methods were used to test for phylogenetic congruence between host and parasite trees: reconciliation analysis (TREEMAP 2.0β; Page, 1994; Charleston, 1998; Charleston & Page, 2002) and generalized parsimony (TREEFITTER 1.0; Ronquist, 1995, 2000, 2003). Reconciliation analysis, as implemented in TREEMAP 2.0β, was used to find the least costly reconstruction of host–parasite relationships at the same time as maximizing the number of cospeciation events. The default settings of TREEMAP were used (assigning a cost of zero for cospeciation events and a cost of 1 for host switches, losses, and duplications). The parasite tree was randomized 100 times and the observed number of cospeciation events was compared with the resulting null distribution of cospeciation events to determine whether the number of cospeciation events recovered from the reconciliation analysis was significant. Generalized parsimony, implemented in TREEFITTER 1.0, was used to reconcile host and parasite phylogenies by searching for the minimum cost reconstruction under various event cost assignments for each historical event (cospeciation, duplication, extinction, and host switching). Host–parasite relationships were reconstructed in TREEFITTER using the same cost assignments as in TREEMAP to estimate overall cost and frequency of each event. To assess the significance of the historical reconstruction, the host tree was randomized on the parasite tree with 1000 random permutations (generated by a Markov process) of parasite tree terminals.

RESULTS

Louse diversity and host associations

Although not all louse specimens could be identified due to insufficient material, 15 definitive louse species were found parasitizing 19 rodent species in the Manu Biosphere Reserve (considering the two *Neacomys* Thomas specimens to be the same species; Table 1). Three of the 15 louse species are new to science. On the sigmodontine rodents alone, ten distinct *Hoplopleura* species were found and all except for two [*Microryzomys minutus* (Tomes) and *Nectomys squamipes* (Brants)] represent new host associations (see Appendix, Table A1). *Cavia tschudii* Fitzinger and *Thomasomys oreas* Anthony also represent new host associations for *Pterophthirus imitans* Werneck. Peru, specifically the Manu Biosphere Reserve, represents a new geographic locality for all previously described hoplopleurid species except *Hoplopleura aitkeni* Johnson, *Hoplopleura quadridentata* (Neumann), and *Hoplopleura sciuricola* Ferris (see Appendix, Table A1).

Phylogenetic analyses

Of the 738 characters examined, 294 bp were potentially parsimony informative. MP analysis produced one most parsimonious tree (length, 1613; consistency index = 0.368; retention index = 0.448; rescaled con-

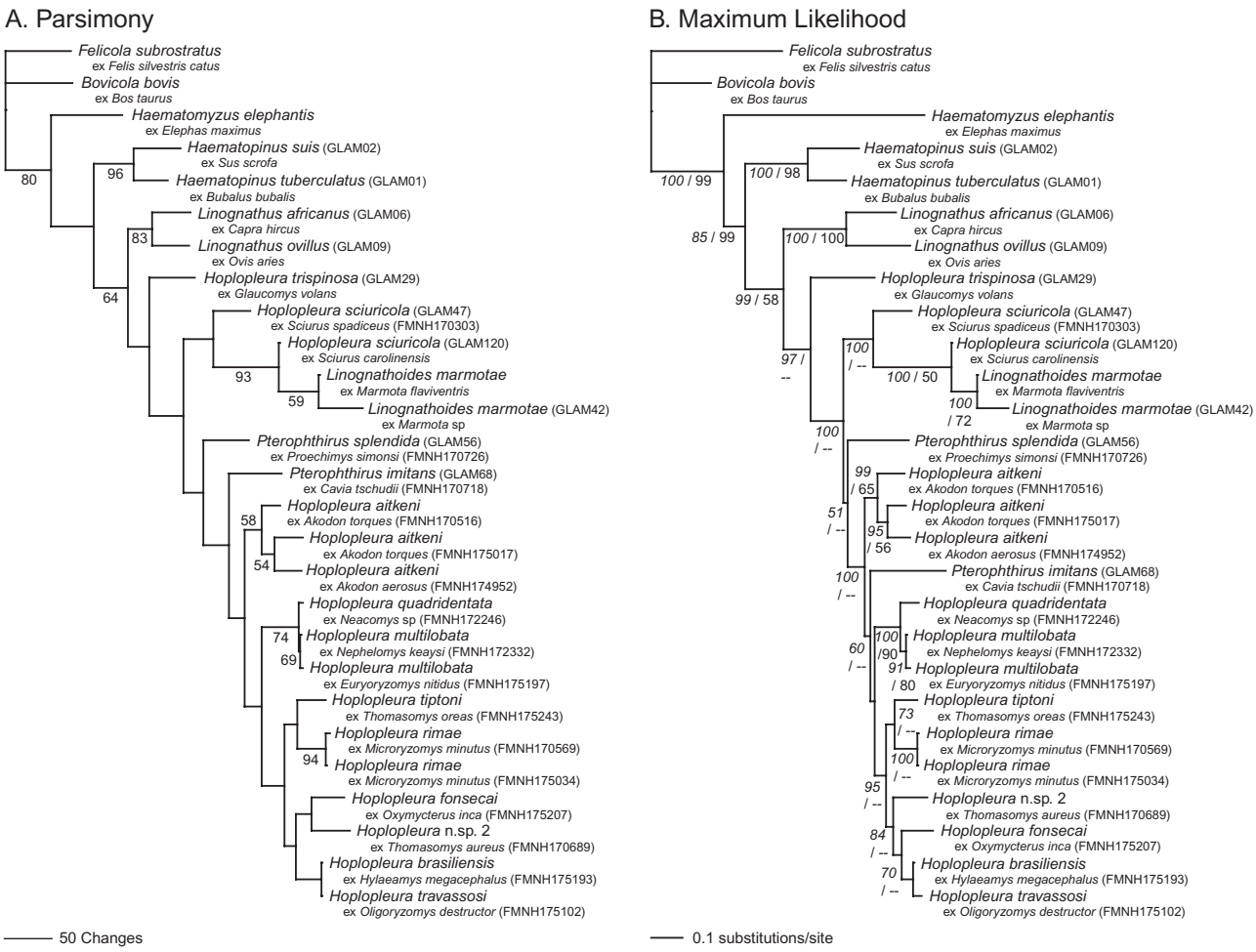

Figure 2. Phylogenetic relationships among rodent lice from the Manu Biosphere Reserve based on sequence data from the mitochondrial cytochrome *c* oxidase subunit I and the nuclear elongation factor 1-alpha genes. A, maximum parsimony phylogram with parsimony bootstrap support values greater than 50% indicated at the nodes. B, maximum likelihood phylogram with Bayesian posterior probabilities and likelihood bootstrap support values greater than 50% indicated at the nodes. Host and parasite names are followed by museum specimen number (Table 1).

sistency index = 0.165; Fig. 2A). ML and Bayesian analyses yielded nearly identical trees (Fig. 2B; Bayesian topology available upon request) that differed only in lack of resolution at two terminal nodes. These trees differed from the MP tree only in the placement of *Pterophthirus imitans* – 170718, which was located more basally in the MP tree (Fig. 2A). All analyses showed strong support for monophyly of Anoplura (MP bootstrap, 99; ML bootstrap, 80; Bayesian posterior probability = 100; Fig. 2). However, bootstrap support within these trees was generally lacking especially at more terminal nodes (Fig. 2). Monophyly of Hoplopleuridae, *Hoplopleura*, and *Pterophthirus* Ewing is not supported, and constraining these groups to be monophyletic yielded trees with likelihood scores that were significantly worse than the best tree (all KH and SH tests $P < 0.0001$).

COPHYLOGENETIC ANALYSES

Because Hoplopleuridae is not monophyletic, *Linognathoides* Cummings (Fig. 2) was included in all cophylogenetic comparisons. Reconciliation and general parsimony analyses using TREEMAP 2.0β and TREEFITTER 1.0 detected significant cophylogeny between lice and their hosts for all combinations of host tribal relationships ($P < 0.05$; Fig. 3, Table 2) and higher-level rodent relationships (current data suggest a polytomy among major rodent lineages; Bininda-Emonds *et al.*, 2007).

DISCUSSION

Our preliminary assessment of sucking louse diversity (using morphological identifications and molecu-

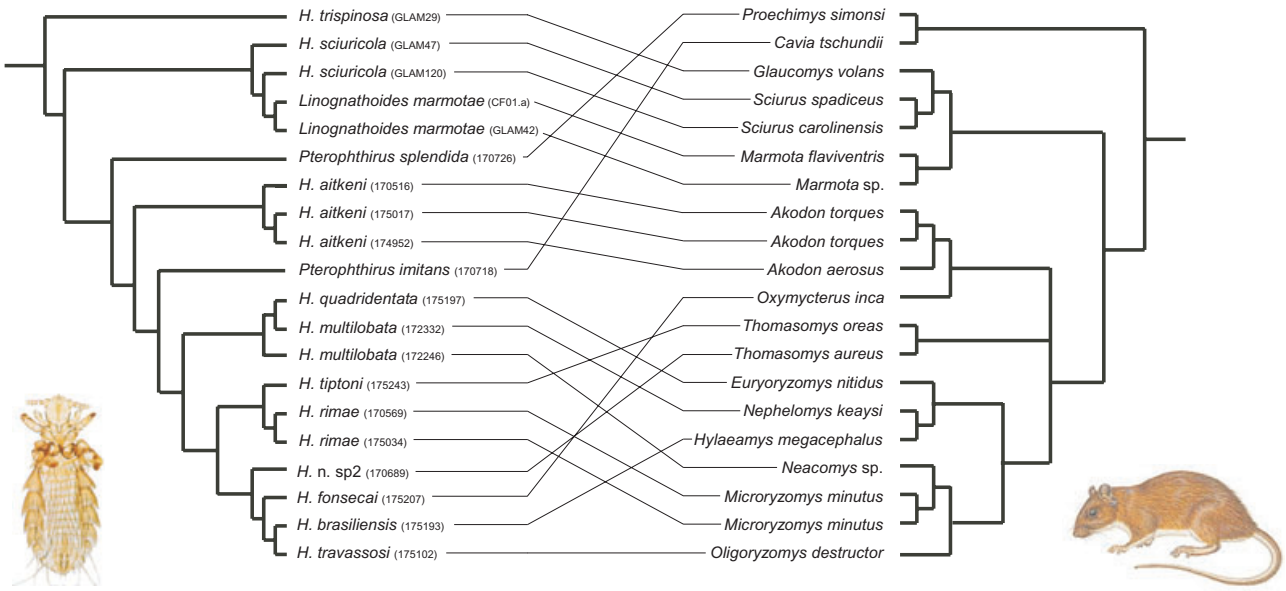

Figure 3. Results of reconciliation analysis (TREEMAP 2.0β) for rodents of the Manu Biosphere Reserve and their ectoparasitic sucking lice. Grey lines between taxa indicate host-parasite associations. The number of reconstructed codivergence events for each topological comparison (see Appendix, Table A1) was greater than expected by chance ($P < 0.05$).

Table 2. Results of cophylogenetic comparisons between lice and their rodent hosts

Comparison	Cost	Codivergence	Duplication	Extinction	Host switching	Solutions
TREEMAP						
Akodontini and Oryzomyini	35	20*	14	15	4	1
Akodontini and Thomasomyini	27	12*	12	12	4	1
Oryzomyini and Thomasomyini	25	20*	10	12	3	1
TREEFITTER						
Akodontini and Oryzomyini	10†	7–9*	0	0–2	8–10	–
Akodontini and Thomasomyini	6†	6*	0	0	6†	–
Oryzomyini and Thomasomyini	9†	6–9*	0	0–3	6–9†	–

TREEMAP and TREEFITTER results are given for all three combinations of host tribal relationships (Akodontini, Oryzomyini, and Thomasomyini). Columns show the cost, number of each event type necessary to reconcile the host and parasite trees, and the number of equally probable reconstructions. The full comparison including all louse and rodent taxa is shown in Fig. 3.

*The observed value is significantly greater than that for randomized trees ($P < 0.05$).

†The observed value is significantly less than that for randomized trees ($P < 0.05$).

lar work) reveals that louse diversity within the Manu Biosphere Reserve is high (15 species), and notably includes three species previously unknown to science. The discovery of these new species within a relatively small geographic area (compared with all of Peru or the Neotropics) suggests that additional sampling will uncover more louse species, some of which are likely to be undescribed. The Manu Biosphere Reserve is therefore a biodiversity hotspot not only for vertebrate taxa (Patterson *et al.*, 2006a, b), but also for invertebrate taxa (Tantaleán & Chavez, 2004; present study) and additional studies are necessary to determine the true diversity within this region.

Although we found that there were almost equal numbers of louse and rodent species, a review of the literature shows that none of the hoplopleurid species examined as a part of the present study are host specific (not including the three new species; see Appendix, Table A1). Within *Hoplopleura*, *Hoplopleura fonsecai* Werneck and *Hoplopleura tiptoni* Johnson parasitize multiple species within one host genus (*Oxymycterus* Waterhouse and *Thomasomys*

Coues, respectively), whereas the majority of *Hoplopleura* species parasitize multiple host genera. *Hoplopleura aitkeni*, *H. quadridentata*, and *Hoplopleura travassosi* Werneck appear to be host generalists, parasitizing different tribes within Sigmodontinae (see Appendix, Table A1). Multi-host parasitism observed among these *Hoplopleura* species is also typical among other louse species (Banks & Paterson, 2005; V. S. Smith & J. E. Light, unpubl. data) and, given the wide geographic distribution of these *Hoplopleura* species (see Appendix, Table A1), it is probable that the lack of host specificity may be the result of cryptic parasite species or host switching without speciation. For example, host switching is the most likely explanation of the diverse host associations of *H. aitkeni*, *H. multilobata* Werneck, *H. quadridentata*, and *H. travassosi* (see Appendix, Table A1). Alternatively, failure of lice to speciate (i.e. cophylogenetic inertia: Paterson & Banks, 2001) could also explain the large geographic ranges of *Hoplopleura* lice if hosts are closely related. This is probably the case for *H. aitkeni* parasitizing *Akodon* Meyen and *Phyllotis* Waterhouse (but not both host genera; D'Elia *et al.*, 2006), *H. fonsecai* parasitizing *Oxymycterus* Waterhouse, and *H. tiptoni* parasitizing *Thomasomys* Coues (see Appendix, Table A1). In addition to data from the literature and the findings from recent collections, an examination of the molecular data can also elucidate potential causes of multi-host parasitism among hoplopleurid lice.

Phylogenetic analyses of the mitochondrial CO *I* and nuclear EF1α data reveal that the louse family Hoplopleuridae and the genera *Hoplopleura* and *Pterophthirus* are not monophyletic, and lice do not appear to group together by host tribe (e.g. Oryzomyini or Thomasomyini) collecting locality or elevation (Fig. 2, Table 1), regardless of how the data are analyzed. The lack of monophyly for these apparently natural groups (taxonomic, locality, and elevation) indicates that failure of lice to speciate and host switching may be prevalent among hoplopleurid lice. Additionally, louse individuals belonging to the same species are monophyletic (*H. aitkeni*, *H. multilobata*, *Hoplopleura rimae* Johnson) regardless of which host species they parasitize (Fig. 3, Table 1), which further supports host switching (*H. multilobata*) and failure to speciate (*H. aitkeni* and likely *H. rimae*) of hoplopleurid lice in the Manu Biosphere Reserve.

Although the use of two molecular markers together yielded an enhanced phylogenetic signal than when either dataset was analyzed independently (data available upon request), bootstrap support was often very low (Fig. 2). This low support may be due, in part, to the high genetic diversity observed in both of these genes. In the CO *I* gene, for example, uncorrected *p* distances average 14% within *H. aitkeni* specimens, 13% within *H. tiptoni* and *H. rimae* specimens, and 18% within *Hoplopleura brasiliensis* Werneck, *H. fonsecai*, *H. travassosi*, and *Hoplopleura* sp. nov. 2. Recent louse studies using mitochondrial markers have found genetic divergences up to 18% within species (Johnson *et al.*, 2002; Light & Hafner, 2007a) and approximately 20% between species (Johnson *et al.*, 2002, 2003; Reed *et al.*, 2004; Light & Hafner, 2007a, b). The genetic divergences within *Hoplopleura* species therefore appear to be typical for lice, and a lack of topological support may be the result of other factors such as those related to taxon and gene sampling. In common with many other cophylogenetic studies of parasitic lice, the difficulties of specimen collection mean that taxon sampling is not high and molecular markers could not be obtained from all louse taxa (Table 1). Additional sampling, data collection, and analysis will be necessary to improve support in the phylogenetic trees.

Despite the significant diversity (both taxonomic and genetic) of hoplopleurid sucking lice in the Manu Biosphere Reserve, it is surprising that these lice show a significant pattern of cophylogeny with their rodent hosts (Fig. 3, Table 2). In general, cophylogenetic studies of lice tend to find a strong positive association between the degree of host specificity and patterns of phylogenetic congruence between host and associate trees (Clayton & Johnson, 2003; J. E. Light & M. S. Hafner, 2008). In the present study, it is interesting to note that, although both TREEMAP and TREEFITTER find significant numbers of codivergence events, these methods also find large numbers of other historical events such as parasite duplication, extinction, or host switching (Table 2). It is possible that the significance of both sets of events may be a statistical anomaly caused by the small number of taxa (less than 20 for all comparisons) included in each analysis. Alternatively, a significant pattern of codivergence may be a real pattern within this assemblage. Future studies involving more taxa as well as a better-resolved host tree will be necessary to verify these results.

This preliminary assessment of hoplopleurid lice from the Manu Biosphere Reserve indicates that these louse taxa are highly diverse and parasitize multiple host species across a large geographic area. Taxonomically, we found a lack of monophyly of a family of 150 species (Hoplopleuridae) as well as the genera *Hoplopleura* and *Pterophthirus*. These results are not too surprising given that the present study is one of only a handful of molecular assessments of anopluran taxonomy (Reed *et al.*, 2004, 2007; Light & Hafner, 2007a). Future phylogenetic studies using both molecular and morphological data are therefore vital to better understand relationships within this

louse suborder and relationships between lice and their rodent hosts. With a better understanding of taxonomy, we can then obtain better estimates of louse diversity from regions all over the world.

ACKNOWLEDGEMENTS

C. Dick and B. Patterson provided information regarding host identifications and collection localities. We thank B. Patterson, M. Weksler, and J. D. Hanson for help determining the rodent phylogeny and M. Gitzendanner and the Florida Museum of Natural History Phyloinformatics Cluster for Higher Performance Computing in the Life Sciences for analytical support. This work was supported by National Science Foundation Biological Inventories (DEB-9870191) and Systematic Biology (DEB-00717165) grants.

REFERENCES

Banks JC, Paterson AM. 2005. Multi-host parasite species in cophylogenetic studies. *International Journal of Parasitology* **35:** 741–746.

Barros-Battesti DM, Arzua M, Linardi PM, Bothelo JR, Sbalqueiro IJ. 1998. Interrelationship between ectoparasites and wild rodents from Tijucas do Sul, State of Paraná, Brazil. *Memorias do Instituto Oswaldo Cruz* **93:** 719–725.

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A. 2007. The delayed rise of present-day mammals. *Nature* **446:** 507–512.

Castro D del C. 1978. Nuevas citas de Anoplura para Argentina (Insecta). *Neotropica* **24:** 78.

Castro D del C. 1979. Las especies del genero *Hoplopleura* Enderlein de la Republica Argentina (Insecta, Anoplura). *Acta Zoologica Lilloana* **35:** 361–363.

Castro D del C. 1982. Las especies del grupo *travassosi* del genero *Hoplopleura* Enderlein, 1904 en la Republica Argentina (Insecta, Anoplura). *Revista de la Sociedad Entomológia Argentina* **41:** 171–182.

Castro D del C. 1984. Contribución al conocimiento do los Anoplura neotropicales II. *Revista de la Sociedad Entomológia Argentina* **43:** 159–163.

Castro D del C, Gonzalez A. 1997. Las especies del genero *Hoplopleura* Enderlein, 1904 (Phthiraptera, Insecta) parasitas de roedores de la región neotropical. *Papéis Avulsos de Zoologia, Museu de Zoologia da Universidade de São Paulo* **40:** 203–215.

Charleston MA. 1998. Jungles: a new solution to the host/parasite phylogeny reconciliation problem. *Mathematical Biosciences* **149:** 191–223.

Charleston MA, Page RDM. 2002. *TREEMAP,* Version 2.0. *Applications for Apple Macintosh*. Oxford: University of Oxford.

Clayton DH, Johnson KP. 2003. Linking coevolutionary history to ecological process: doves and lice. *Evolution* **57:** 2335–2341.

Cruickshank RH, Johnson KP, Smith VS, Adams RJ, Clayton DH, Page RDM. 2001. Phylogenetic analysis of partial sequences of elongation factor 1α identifies major groups of lice (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution* **19:** 202–215.

Danforth BN, Ji S. 1998. Elongation factor-1α occurs as two copies in bees: implications for phylogenetic analysis of EF-1α sequences in insects. *Molecular Biology and Evolution* **15:** 225–235.

D'Elia G, Gonzalez EM, Pardinas UFJ. 2003. Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus Deltamys. *Mammalian Biology* **68:** 351–364.

D'Elia G, Luna L, González EM, Patterson BD. 2006. On the sigmodontinae radiation (Rodentia, Cricetidae): an appraisal of the phylogenetic position of *Rhagomys*. *Molecular Phylogenetics and Evolution* **38:** 558–564.

Durden LA, Musser GG. 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.

Felsenstein J. 1985. Confidence limits on phylogenies with a molecular clock. *Systematic Zoology* **38:** 406–407.

Goldman N, Anderson JP, Rodrigo AG. 2000. Likelihood-based tests of topologies in phylogenetics. *Systematic Biology* **49:** 652–670.

González-Acuña DA, Castro D del C, Moreno-Salas L del C. 2003. Contribución al conocimiento de los Phthiraptera (Anoplura, *Hoplopleura*) parásitos de roedores en Chile. *Gayana Zoología* **67:** 117–119.

González-Acuña DA, Castro D del C, Moreno-Salas L del C, Torres-Mura JC, Mey E. 2005. New records of sucking lice (Insecta: Phthiraptera: Anoplura) on rodents (Mammalia: Rodentia: Muridae) from Chile. *Mastozoología Neotropical* **12:** 249–251.

Gu X, Fu Y-X, Li W-H. 1995. Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. *Molecular Biology and Evolution* **12:** 546–557.

Hafner MS, Sudman PD, Villablanca FX, Spradling TA, Demastes JW, Nadler SA. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* **265:** 1087–1090.

Herron MD, Castoe TA, Parkinson CL. 2004. Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (*Spermophilus*). *Molecular Phylogenetics and Evolution* **31:** 1015–1030.

Huelsenbeck JP, Bollback JP. 2001. Empirical and hierarchical Bayesian estimation of ancestral states. *Systematic Biology* **50:** 351–366.

Huelsenbeck JP, Rannala B. 1997. Phylogenetic methods come of age: testing hypothesis in an evolutionary context. *Science* **276:** 227–232.

Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* **17:** 754–755.

Jansa SA, Weksler M. 2004. Phylogeny of muroid rodents: relationships within and among major lineages as revealed by nuclear IRBP gene sequences. *Molecular Phylogenetics and Evolution* **31:** 256–276.

Johnson KP, Clayton DH. 2000. Nuclear and mitochondrial genes contain similar phylogenetic signal for pigeons and doves (Aves: Columbiformes). *Molecular Phylogenetics and Evolution* **14:** 141–151.

Johnson KP, Clayton DH. 2003. Coevolutionary history of ecological replicates: comparing phylogenies of wing and body lice to columbiform hosts. In: Page RDM, ed. *Tangled trees: cophylogeny, cospeciation, and coevolution*. Chicago, IL: The University of Chicago Press, 262–286.

Johnson KP, Cruickshank RH, Adams RJ, Smith VS, Page RDM, Clayton DH. 2003. Dramatically elevated rate of mitochondrial substitution in lice (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution* **26:** 231–242.

Johnson KP, Williams BL, Drown DM, Adams RJ, Clayton DH. 2002. The population genetics of host specificity: genetic differentiation in dove lice (Insecta: Phthiraptera). *Molecular Ecology* **11:** 25–38.

Johnson PT. 1972. Sucking lice of Venezuelan rodents, with remarks on related species. *Brigham Young University Science Bulletin. Biological Series* **17:** 1–62.

Kim KC. 1988. Evolutionary parallelism in Anoplura and eutherian mammals. In: Service MS, ed. *Biosystematics of haematophagous insects*. Systematics Association Special, Vol. 37. Oxford: Clarendon Press, 91–114.

Kishino H, Hasegawa M. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order of the Hominoidea. *Journal of Molecular Evolution* **29:** 170–179.

Leaché AD, Reeder TW. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulates*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology* **51:** 44–68.

Light JE, Hafner MS. 2007a. Phylogeny and host associations of *Fahrenholzia* sucking lice (Phthiraptera: Anoplura). *Systematic Entomology* **32:** 359–370.

Light JE, Hafner MS. 2007b. Disparate rates of evolution in sympatric lineages of chewing lice on pocket gophers. *Molecular Phylogenetics and Evolution* **45:** 997–1013.

Light JE, Hafner MS. 2008. Codivergence in heteromyid rodents (Rodentia: Heteromyidae) and their sucking lice of the genus *Fahrenholzia* (Phthiraptera: Anoplura). *Systematic Biology* **57:** 449–465.

Musser GG, Carleton MD. 1993. Family Muridae. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference*, 2nd edn. Washington, DC: Smithsonian Institution Press, 501–753.

Musser GG, Carleton MD. 2005. Superfamily Muroidea. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore, MD: Johns Hopkins University Press, 894–1531.

Pacheco VR. 2003. Phylogenetic analyses of the Thomasomyini (Muroidea: Sigmodontinae) based on morphological data. DPhil Thesis, City University of New York.

Page RDM. 1994. Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics* **10:** 155–173.

Page RDM, Cruickshank RH, Dickens M, Furness RW, Kennedy M, Palma RL, Smith VS. 2004. Phylogeny of 'Philoceanus complex' seabird lice (Phthiraptera: Ischnocera) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **30:** 633–652.

Palma RL. 1978. Slide-mounting of lice: a detailed description of the Canada balsam technique. *New Zealand Entomologist* **6:** 432–436.

Paterson AM, Banks JC. 2001. Analytical approaches to measuring cospeciation of hosts and parasites: through a glass darkly. *International Journal for Parasitology* **31:** 1012–1022.

Patterson BD, Stotz DF, Solari S. 2006a. *Mammals and birds of the Manu Biosphere Reserve, Peru*. Chicago, IL: Fieldiana: Zoology, New Series No. 110, 1–49.

Patterson BD, Stotz DF, Solari S. 2006b. Biological surveys and inventories in Manu. In: Patterson BD, Stotz DF, Solari S, eds. *Mammals and birds of the Manu Biosphere Reserve, Peru*. Chicago, IL: Fieldiana: Zoology, New Series No. 110, 3–12.

Posada D, Buckley TR. 2004. Model selection and model averaging in phylogenetics: advantages of the AIC and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53:** 793–808.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14:** 817–818.

Rambaut A. 2002. *Se-Al sequence alignment editor,* Version 2.0a11. Oxford: Department of Zoology, University of Oxford. Available at http://tree.bio.ed.ac.uk/software/seal/

Reed DL, Light JE, Allen JM, Kirchman JJ. 2007. Pair of lice lost or regained: the evolutionary history of anthropoid primate lice. *BMC Biology* **5:** 7.

Reed DL, Smith VS, Hammond SL, Rogers AR, Clayton DH. 2004. Genetic analysis of lice supports direct contact between modern and archaic humans. *PLoS Biology* **2:** 1972–1983.

Ronquist F. 1995. Reconstructing the history of host-parasite associations using generalised parsimony. *Cladistics* **11:** 73–89.

Ronquist F. 2000. *TreeFitter*. Computer program distributed by the author. Uppsala: University of Uppsala.

Ronquist F. 2003. Parsimony analysis of coevolving species associations. In: Page RDM, ed. *Tangled trees: cophylogeny, cospeciation, and coevolution*. Chicago, IL: The University of Chicago Press, 22–64.

Shimodaira H, Hasegawa M. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* **16:** 1114–1116.

Solari S, Pacheco V, Luna L, Velazco PM, Patterson BD. 2006. Mammals of the Manu Biosphere Reserve. In: Patterson BD, Stotz DF, Solari S, eds. *Mammals and birds of the Manu Biosphere Reserve, Peru*. Chicago, IL: Fieldiana: Zoology, New Series No. 110, 13–22.

Steppan SJ, Storz BL, Hoffman RS. 2004. Nuclear DNA phylogeny of squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. *Molecular Phylogenetics and Evolution* **30:** 703–709.

Swofford DL. 2003. *PAUP*: Phylogenetic analysis using parsimony (* and other methods)*. Version 4.0b10. Sunderland, MA: Sinauer Associates.

Tantaleán M, Chavez J. 2004. Wild animals endoparasites (Nemathelminthes and Platyhelminthes) from the Manu Biosphere Reserve, Peru. *Revista Peruana de Biología* **11:** 219–222.

Tipton VJ, Handley CO Jr. 1972. Ectoparasites of Venezuela. *Brigham Young University Science Bulletin. Biological Series* **17**. 371 pp.

Weksler M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. *Molecular Phylogenetics and Evolution* **29:** 331–349.

Weksler M. 2006. Phylogenetic relationships of oryzomyine rodents (Muridae: Sigmodontinae): separate and combined analyses of morphological and molecular data. *Bulletin of the American Museum of Natural History* **296:** 1–149.

Weksler M, Percequillo AR, Voss RS. 2006. Ten new genera of oryzomyine rodents (Cricetidae: Sigmodontinae). *American Museum Novitates* **3537:** 1–29.

Wenzel RL, Tipton VJ. 1966. *Ectoparasites of Panama*. Chicago, IL: Field Museum of Natural History.

Werneck FL. 1932a. Sobre uma especie nova de *Hoplopleura*. *Revista Médico-Cirurgica do Brasil* **40:** 345–346.

Werneck FL. 1932b. Sur une nouvelle espèce de pou (*Hopopleura* [*sic*] *brasiliensis*). *Société de Biologie de Rio de Janeiro (Société de Biologie de Paris Comptes Rendus)* **109:** 754–755.

Werneck FL. 1934. Sobre duas especies de Anoplura encontradas em ratos sylvestres do Brasil. *Memorias do Instituto Oswaldo Cruz* **27:** 407–415.

Werneck FL. 1942. '*Pterophthirus imitans*' n. sp. (Anoplura, Haematopinidae). *Revista Brasileira de Biologia* **2:** 317–320.

Werneck FL. 1954. Contribuçáo ao conhecimento dos Anopluros. V. *Revista Brasileira de Biologia* **14:** 109–117.

Wilson DE, Reeder DM. 2005. *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore, MD: Johns Hopkins University Press.

Yang Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable sites over sites: approximate methods. *Journal of Molecular Evolution* **39:** 306–314.

APPENDIX

Table A1. List of hoplopleurid lice collected from rodents in the Manu Biosphere Reserve

Hoplopleura aitkeni Johnson, 1972
Geographic Distribution: Argentina, Bolivia, Brazil, Chile, Ecuador, Peru, Venezuela
Host Associations: Cricetidae: Sigmodontinae: Akodontini: *Akodon aerosus**, *A. azarae*, *A. budini*, *A. caenosus*, *A. iniscatus*, *A. molinae*, *A. mollis*, *A. nucus*, *A. puer*, *A. subfuscus**, *A. torques**, *A. urichi*
Cricetidae: Sigmodontinae: Phyllotini: *Phyllotis gerbillus*, *P. xanthopygus*, *P. vaccarum*
References: Johnson (1972); Castro (1984); Durden & Musser (1994); Castro & Gonzalez (1997); González-Acuña *et al.* (2005); present study

Hoplopleura brasiliensis Werneck, 1932
Geographic Distribution: Brazil, Peru*, Trinidad
Host Associations: Cricetidae: Sigmodontinae: Oryzomyini: *Hylaeamys megacephalus**, *Oryzomys capito*
References: Werneck (1932a); Johnson (1972); Durden & Musser (1994); Castro & Gonzalez (1997); present study

Hoplopleura fonsecai Werneck, 1934
Geographic Distribution: Argentina, Brazil, Peru*, Uruguay
Host Associations: Cricetidae: Sigmodontinae: Akodontini: *Oxymycterus hispidus*, *O. inca**, *O. paramensis*, *O. roberti*, *O. rufus*
References: Werneck (1934); Johnson (1972); Castro (1979); Durden & Musser (1994); Castro & Gonzalez (1997); present study

Hoplopleura multilobata Werneck, 1954
Geographic Distribution: Brazil, Colombia, Peru*, Venezuela
Host Associations: Cricetidae: Sigmodontinae: Oryzomyini: *Euryoryzomys nitidus**, *Microryzomys minutus*, *Nephelomys keaysi**, *Oecomys concolor*, *O. trinitatis*, *Oryzomys albigularis*
Echimyidae: *Proechimys iheringi* (probably a straggler)
References: Werneck (1954); Johnson (1972); Durden & Musser (1994); Castro & Gonzalez (1997); present study

Hoplopleura quadridentata (Neumann, 1909)
Geographic Distribution: Argentina, Mexico, Paraguay, Peru, Trinidad, Venezuela
Host Associations: Cricetidae: Sigmodontinae: Oryzomyini: *Neacomys* sp.*, *Nectomys palmipes*, *N. squamipes*, *Nephelomys keaysi**, *Oligoryzomys fulvescens*, *O. rostratus*
Cricetidae: Sigmodontinae: Akodontini: *Scapteromys tumidus*
References: Johnson (1972); Castro (1979); Durden & Musser (1994); Castro & Gonzalez (1997); present study

Table A1. *Continued*

Hoplopleura rimae Johnson, 1972
Geographic Distribution: Peru*, Venezuela
Host Associations: Cricetidae: Sigmodontinae: Oryzomyini: *Microryzomys minutus*, *Oligoryzomys minutus**, *Oryzomys albiglaris*
References: Johnson (1972); Durden & Musser (1994); Castro & Gonzalez (1997); present study

Hoplopleura sciuricola Ferris, 1921
Geographic Distribution: North, Central, and South America (introduced to some other regions such as Britain on introduced *Sciurus carolinensis*). Previous South American country records are from Bolivia, Brazil, Colombia, Peru, and Venezuela
Host Associations: Sciuridae: *Microsciurus flaviventer**, *Sciurus aberti*, *S. aestuans*, *S. arizonensis*, *S. carolinensis*, *S. granatensis*, *S. ignitus*, *S. igniventris*, *S. griseus*, *S. niger*, *S. spadiceus*, *Tamiasciurus douglasii*, *T. hudsonicus.*
References: Durden & Musser (1994); Castro & Gonzalez (1997); Barros-Battesti *et al.* (1998); present study

Hoplopleura tiptoni Johnson, 1972
Geographic Distribution: Peru*, Venezuela
Host Associations: Cricetidae: Sigmodontinae: Thomasomyini: *Thomasomys laniger*, *T. oreas**
References: Johnson (1972); Durden & Musser (1994); Castro & Gonzalez (1997); present study

Hoplopleura travassosi Werneck, 1932
Geographic Distribution: Argentina, Brazil, Chile, Peru*, Uruguay, Venezuela
Host Associations: Cricetidae: Sigmodontinae: Phyllotini: *Calomys callosus*, *C. laucha*
Cricetidae: Sigmodontinae: Oryzomyini: *Oecomys speciosus*, *O. trinitatis*, *Oligoryzomys delticola*, *O. destructor**, *O. flavescens*, *O. fulvescens*, *O. longicaudatus*
References: Werneck (1932b); Johnson (1972); Castro (1979, 1982); Durden & Musser (1994); Castro & Gonzalez (1997); González-Acuña *et al.* (2003, 2005); present study

Hoplopleura sp.
Geographic Distribution: Peru*
Host Associations: Cricetidae: Sigmodontinae: Oryzomyini: *Oligoryomys destructor*, *O.* sp.
References: present study

Hoplopleura new sp. 1
Geographic Distribution: Peru*
Host Associations: Cricetidae: Sigmodontinae: Oryzomyini: *Neacomys* sp.
References: present study

Hoplopleura new sp. 2
Geographic Distribution: Peru*
Host Associations: Cricetidae: Sigmodontinae: Thomasomini: *Thomasomys aureus**
References: present study

Pterophthirus imitans Werneck, 1942
Geographic Distribution: Argentina, Brazil, Peru*, Uruguay
Host Associations: Caviidae: *Cavia aperea*, *C. tschudii**
Cricetidae: Sigmodontinae: Thomasomyini: *Thomasomys oreas** (probably a straggler)
References: Werneck (1942); Johnson (1972); Castro (1978); Durden & Musser (1994); present study

Pterophthirus splendida Johnson, 1972
Geographic Distribution: Bolivia, Brazil, Ecuador, Peru*, Suriname, Trinidad, Venezuela
Host Associations: Echimyidae: *Proechimys cayennensis*, *P. semispinosus*, *P. simonsi*, *P. trinitatus*
References: Johnson (1972); Durden & Musser (1994); Durden, unpubl. – record from Suriname; present study

Geographic distributions, host associations, and references are listed for each louse species.
*New host associations and geographic localities.