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Sucking Lice (Insecta, Anoplura) from Indigenous Sulawesi Rodents: a New Species of *Polyplax* from a Montane Shrew Rat, and New Information About *Polyplax wallacei* and *P. eropepli*

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ABSTRACT

Polyplax melasmothrixi, a new species of polyplacid sucking louse, is described from *Melasmothrix naso*, a small-bodied shrew rat known only from tropical upper montane rain forest in Central Sulawesi, Indonesia. The male of *Polyplax wallacei* is described from specimens collected from *Bunomys chrysocomus* trapped in tropical lowland evergreen rain forest in Central Sulawesi. A further specimen of *Polyplax eropepli*, a taxon previously known only from the type series, is documented from *Eropeplus canus* from tropical upper montane rain forest also in Central Sulawesi. Host and habitat associations for these three species of sucking lice are discussed. *Polyplax melasmothrixi* and *P. eropepli* are both known only from montane habitats in Central Sulawesi and both appear to be host specific (to *M. naso* and *E. canus*, respectively). Contrastingly, *P. wallacei* parasitizes two species of *Bunomys* in lowland forests and is known from North and Central Sulawesi.

INTRODUCTION

Melasmothrix naso, *Bunomys chrysocomus*, and *Eropeplus canus* are three murine rodents found only in forests on the Indonesian island of Sulawesi (Musser, 1987; Musser and Holden, 1991). The shrew rat, *M. naso*, and the large-bodied *E. canus* have been recorded only from montane rainforest formations in the mountainous central part

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of the island. *Bunomys chrysocomus* also occurs in montane forest but is most frequently encountered at lower altitudes in lowland tropical evergreen rain forest. These three species of rats are phylogenetically distant from each other, but they share, in addition to their endemicity to Sulawesi, an important trait: they are all parasitized by species of sucking lice (Anoplura) belonging to the genus *Polyplax*.

The descriptions of these lice, along with notes about the rodent hosts and their habitats, form the body of the present report. We describe and illustrate a new species of *Polyplax* based on specimens removed from the fur of *Melasmothrix naso*. We also describe the male of *Polyplax wallacei*, a louse originally known only by female examples (Durden, 1987); this ectoparasite has been collected from *Bunomys chrysocomus* trapped in lowland evergreen rain forest in northeastern and Central Sulawesi, and from *Bunomys fratrorum*, which occurs only in the northeast arm of the island. Finally, we document an additional specimen of *Polyplax eropepli*, which until now was only known from the type series; this louse is apparently a specific parasite of *Eropeplus canus*.

Durden and Musser (1991) have summarized the taxa of sucking lice and their hosts so far recorded from Sulawesi. The present report extends our knowledge beyond that summary and is one of a series intended to document the diversity of ectoparasites, some of which possess unusual or unique morphological traits, found on the array of murine host species that are endemic to the forests of Sulawesi. This and future papers will contain descriptions of new or poorly known species of ectoparasites that have recently been removed from the skins (both dry and preserved in fluid) of Sulawesian rodents housed in major museum collections.

More than 40 indigenous species of rats and mice have been recorded from Sulawesi and its offshore islands (Musser and Holden, 1991). It is important to document the diversity of ectoparasites and their host associations. Results will form another set of data that may be significant for testing hypotheses of zoogeographical relationships among hosts and their ectoparasites (Durden and Traub, 1990).

Information derived from these descriptive surveys will also be significant in a wider context. Eventually, phylogenetic data will be available for both hosts and parasites, and hypotheses focusing on host-parasite coevolution can be formulated and tested. The relationships between ectoparasites and their hosts have always intrigued biologists. Recently, a growing body of literature has described coevolution between groups of hosts and parasites based on comparisons of their phylogenies (Brooks, 1988; Hafner and Nadler, 1988, 1990; Hellenthal and Price, 1991; May and Anderson, 1983; Page, 1991; Toft and Karter, 1990) as well as apparent coevolution that in reality reflects host-induced morphology of the parasite (Downes, 1990). Preceding this more complex level of analysis are surveys simply describing the parasites and documenting their host species; the results that we present here reflect that level of inquiry.

Abbreviations and Procedures

Specimens examined and referred to here are deposited in the collections of the American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); Lance A. Durden (LAD); Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB); South Australian Museum, Adelaide, Australia (SAM); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Other abbreviations used in the descriptive portions of this work are as follows:

DAcHS	Dorsal accessory head setae
DAnHS	Dorsal anterior head setae
DCAS	Dorsal central abdominal setae
DMHS	Dorsal marginal head setae
DMsS	Dorsal mesothoracic setae
DPHS	Dorsal principal head setae
DPoCHS	Dorsal posterior central head setae
DPrS	Dorsal paratergal setae
DPTS	Dorsal principal thoracic setae
DPtS	Dorsal prothoracic setae
OrS	Oral setae
SHS	Sutural head setae
SpAtHS	Supraantennal head setae
StAS	Sternal abdominal setae
TeAS	Tergal abdominal setae
VPaHS	Ventral preantennal head setae
VPHS	Ventral principal head setae
VPrS	Ventral paratergal setae

Descriptive format and terminology follow Kim (1966), Kim and Ludwig (1978), and Durden and Musser (1991). Drawings of entire lice conventionally illustrate dorsal morphology to the left of the midline and ventral features to the right. Measurements were made using a calibrated eyepiece micrometer inserted into a high-power phase contrast microscope. Values of measurements and weights are reported in millimeters (mm) and grams (g). All rodent hosts discussed here (*Melasmothrix naso*, *Eropeplus canus*, *Bunomys chrysocomus*, and *Bunomys fratrorum*) are members of the subfamily Murinae, which Carleton and Musser (1984) place in the family Muridae of Rodentia.

ACKNOWLEDGMENTS

We are grateful to Michael D. Carleton (USNM) and Paula D. Jenkins (BMNH) who arranged for various murine study skins under their curation to be examined for ectoparasites. Lance Durden's fieldwork in Sulawesi was funded by a grant from the Committee for Research and Exploration of the National Geographic Society; he was sponsored in Indonesia by the Lembaga Ilmu Pengetahuan Indonesia (LIPI) and the Royal Entomological Society of London. Guy Musser's field collections in Sulawesi were partly supported by the Celebes Fund of the American Museum as well as Archbold Expeditions, Inc.; his sponsorship in Indonesia came from LIPI and MZB. He was also assisted by members of United States Navy Medical Research Unit No. 2 (NAMRU-2) in Jakarta. Donna Moore Smith skillfully prepared the drawings included in this paper. Drs. Richard G. Robbins and Nixon Wilson critically reviewed an earlier draft of the manuscript.

Polyplax melasmothrixi, new species

HOLOTYPE: Male collected by L. A. Durden from pelt of adult male *Melasmothrix naso* (AMNH 225100) collected by G. G. Musser at 2255 m on Gunung Nokilalaki (1°16′S, 120°10′E), Central Sulawesi, Indonesia on 29 April, 1975. Deposited in the MZB.

REFERRED SPECIMENS: Seven additional adult lice (2 males, 5 females) all removed by L. A. Durden from pelts of *M. naso* from animals trapped on Gunung Nokilalaki by G. G. Musser in March and April, 1975. Allotype female and one paratype female from the same host individual as holotype; three paratype females ex male *M. naso* (AMNH 225091) at 2255 m; one paratype male ex male *M. naso* (AMNH 225105) at 2285 m; one male ex female *M. naso* (AMNH 225106) at 2285 m. In addition, five immature lice were removed from AMNH 225106. Allotype female: MZB. Paratypes: BMNH, LAD, USNM.

DISTRIBUTION: Known by four collections from *Melasmothrix naso* collected at 2225 and 2285 m (tropical upper montane rain forest) on or close to the summit of Gunung Nokilalaki (2285 m), Central Sulawesi (Sulawesi Tengah), Indonesia.

ETYMOLOGY: The species is named for the type host genus.

DIAGNOSIS: *Polyplax melasmothrixi* is distinctive. It is easily distinguished from all other species of *Polyplax* by the unusual appearance of the male genitalia and by the setation of gonopods VIII and IX in the female. The following combination of characters also serves to distinguish this species: (1) DPHS, DAcHS, and DPoCHS all stout; DPHS and DAcHS displaced posterolaterally; (2) the shape of the thoracic sternal plate; (3) the presence of some short stout setae, in addition to longer stout setae, on the abdominal tergites and sternites; (4) the shape of the paratergal plates and the lengths of the setae borne on these plates.

DESCRIPTION: **Male** (fig. 1). Length of holotype 1.02 mm (mean for series 1.00; range 0.96–1.03; N = 3). Head, thorax, and abdomen well sclerotized.

Head. About as wide as long with blunt anterior apex; 2 DAnHS, 1 DMHS, 1 OrS, 1 SHS (2 present on 1 side of 1 specimen), 1 SpAtHS, and 2 VPaHS on each side; DPHS relatively short and stout, extending about half distance to thoracic spiracle, with 1 stout DAcHS distal to DPHS on each side; both DPHS and DAcHS displaced posteromarginally; 1 stout peglike DPoCHS on each side; VPHS long and fairly stout. *Antennae* 5-segmented with basal segment much larger than second segment, wider than long; third antennal segment with anterior projection as typical for males of *Polyplax* spp.

Thorax. Broad with almost parallel outer

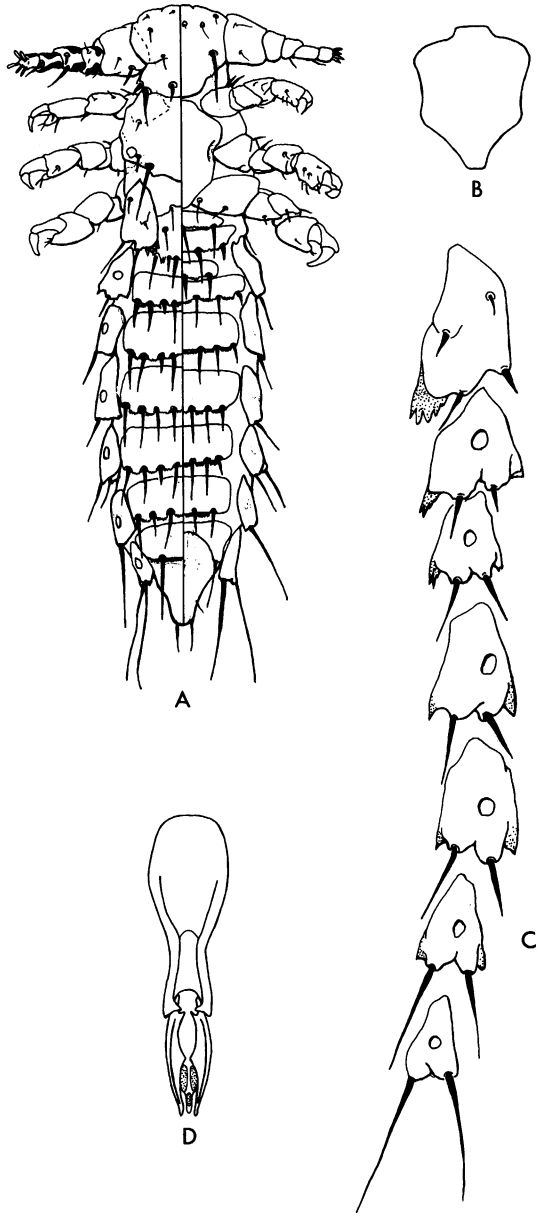

Fig. 1. *Polyplax melasmothrixi*, male. **A,** habitus; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

margins; thoracic sternal plate (fig. 1B) tapering to slightly prolonged, rounded, posterior apex, with central, blunt, anterior projection, and slightly concave, lateral margins; mesothoracic spiracle moderate in size (0.018 mm in diameter); DPTS short (0.098 mm); 1 DMsS and 1 DPtS on each side. *Legs.* Mid and hind coxae subtriangular; forelegs small, each with narrow acuminate claw; mid and hind legs progressively larger and with correspondingly larger acuminate claws.

Abdomen. Slightly wider than thorax; one broad plate per segment dorsally (on segments 2–8) and ventrally (on segments 4–7); two narrow plates ventrally on each of segments 2 and 3; curving, concave plate ventrally on segment 8; most plates with finely crenulated posterior margins; dorsal plates on segments 2–7 each with 6–8 thickened TeAS; dorsal plate on segment 8 with 2 long TeAS; ventral plates 1–3 and 8 each with 3–4 StAS; ventral plates 4–7 each with 6–7 thickened StAS; ventral plate 9 with 2 long marginal StAS; some TeAS and StAS short and stout. *Paratergal plates* (fig. 1C) present on segments 2–8; all plates with 2 apical setae each, with DPrS slightly longer than corresponding VPrS of same plate: plates I and II with short setae, plates III–V with setae of intermediate length, and plates VI and VII with longer setae; all plates subtriangular; plates IV and V with both apical angles produced into points; plates II–VII each with moderately sized spiracle.

Genitalia (fig. 1D). Basal apodeme deeply concave posteriorly and with differential sclerotization; parameres flanged medially, notched anteriorly, and appearing to articulate with posterior projections of basal apodeme; pseudopenis short, extending approximately to apices of parameres, and with three sclerotized patches.

Female (fig. 2). Length of allotype 1.18 mm (mean for series 1.18; range 1.14–1.24; N = 5).

Head, thorax, and legs. As in male unless indicated otherwise. Third antennal segment not modified; thoracic sternal plate (fig. 2B) posteriorly more prolonged than in male.

Abdomen. With one broad plate dorsally on each of segments 2, 3, and 8, and two broad plates dorsally on each of segments 4–7; two broad plates ventrally on each of segments 2–7; dorsal plates 1, 10, and 11 each with four thickened TeAS; dorsal plates 2–9 each with 6–7 thickened TeAS; ventral plate 1 with two thickened StAS, ventral plate 2 with four thickened StAS, and ventral plates 3–12 each with 5–7 thickened StAS; StAS elongated on ventral plate 12; some TeAS

and StAS short and stout; most tergal and sternal abdominal plates with fine crenulations along posterior margins. *Paratergal plates* (fig. 2C) present on segments 2–8 and all bearing 2 apical setae each; DPrS longer than corresponding VPrS on plates I, II, IV, and V; plates I–III with short apical setae, plates IV and V with setae of intermediate length, and plates VI and VII with longer setae; plates I and II subtriangular; plates II–VI with both apical angles produced into points; plates II–VII each with moderately sized spiracle.

Genitalia (fig. 2D). Subgenital plate subtriangular; gonopods VIII each with one long lateral seta and one short seta situated close to center of gonopod; gonopods IX each with one short stout seta but with smaller anterior lobe also bearing short seta; vulvar fimbriae distinct.

REMARKS: Morphologically, *P. melasmothrixi* is an unusual louse when compared to its congeners. Some head setae and most abdominal setae are stout, particularly in the male. Both *Polyplax phthisica* Ferris and *P. smallwoodae* Johnson, which are parasites of African murines (*Lemniscomys* spp.), similarly possess stout abdominal setae (Johnson, 1960) but otherwise these lice do not appear to be closely related to *P. melasmothrixi*. Genitalic characters of *P. melasmothrixi* also are unusual. The male pseudopenis is unique in possessing three sclerotized distal patches. Similarly, the proximally notched parameres that appear to articulate with the distal arms of the basal apodeme are very unusual. The setation of the female gonopods VIII and IX is also distinct.

These and other characters strongly suggest that *P. melasmothrixi* is morphologically unique and not closely related to any other known species in the genus *Polyplax*. The host species, *M. naso*, is unique from two perspectives. It is the only known member of *Melasmothrix*. Its closest phylogenetic relatives are the small-bodied shrew rats *Tateomys rhinogradoides* and *T. macrocercus*, also endemic to the mountains of Central Sulawesi, and they along with *M. naso* form a monophyletic group without apparent close relatives either on Sulawesi or elsewhere in the Indo-Australian region (Musser, 1982; Breed and Musser, 1991). We would also expect the morphology of sucking lice from the other two species of shrew rats to resemble that characterizing *Polyplax melasmothrixi*; unfortunately, no lice were found on any of the preserved specimens of *Tateomys*.

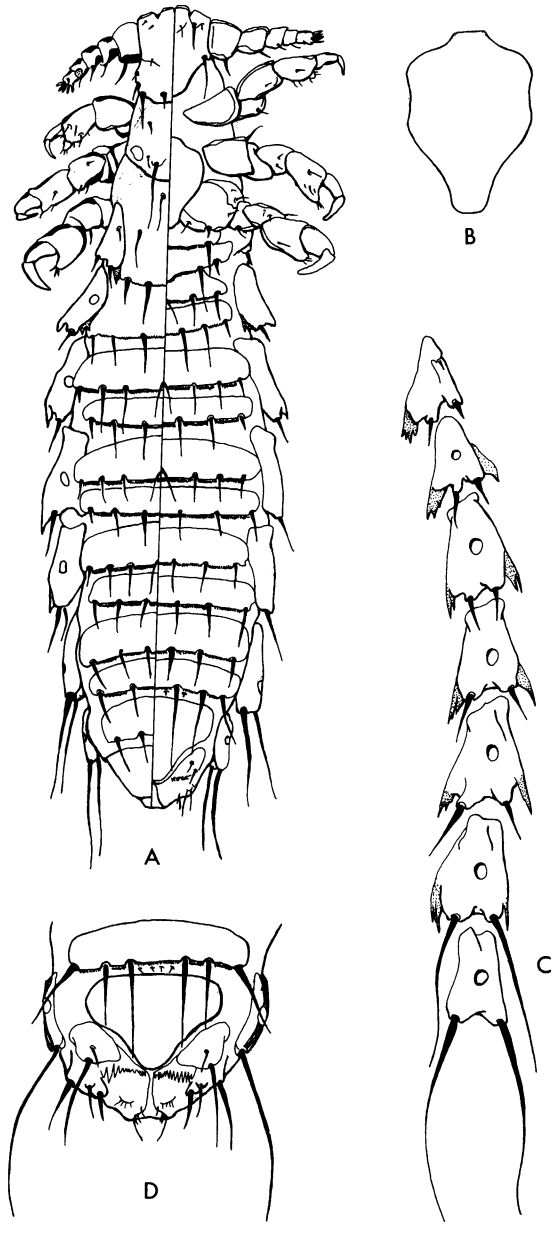

Fig. 2. *Polyplax melasmothrixi*, female. **A**, habitus; **B**, thoracic sternal plate; **C**, paratergal plates; **D**, genitalia.

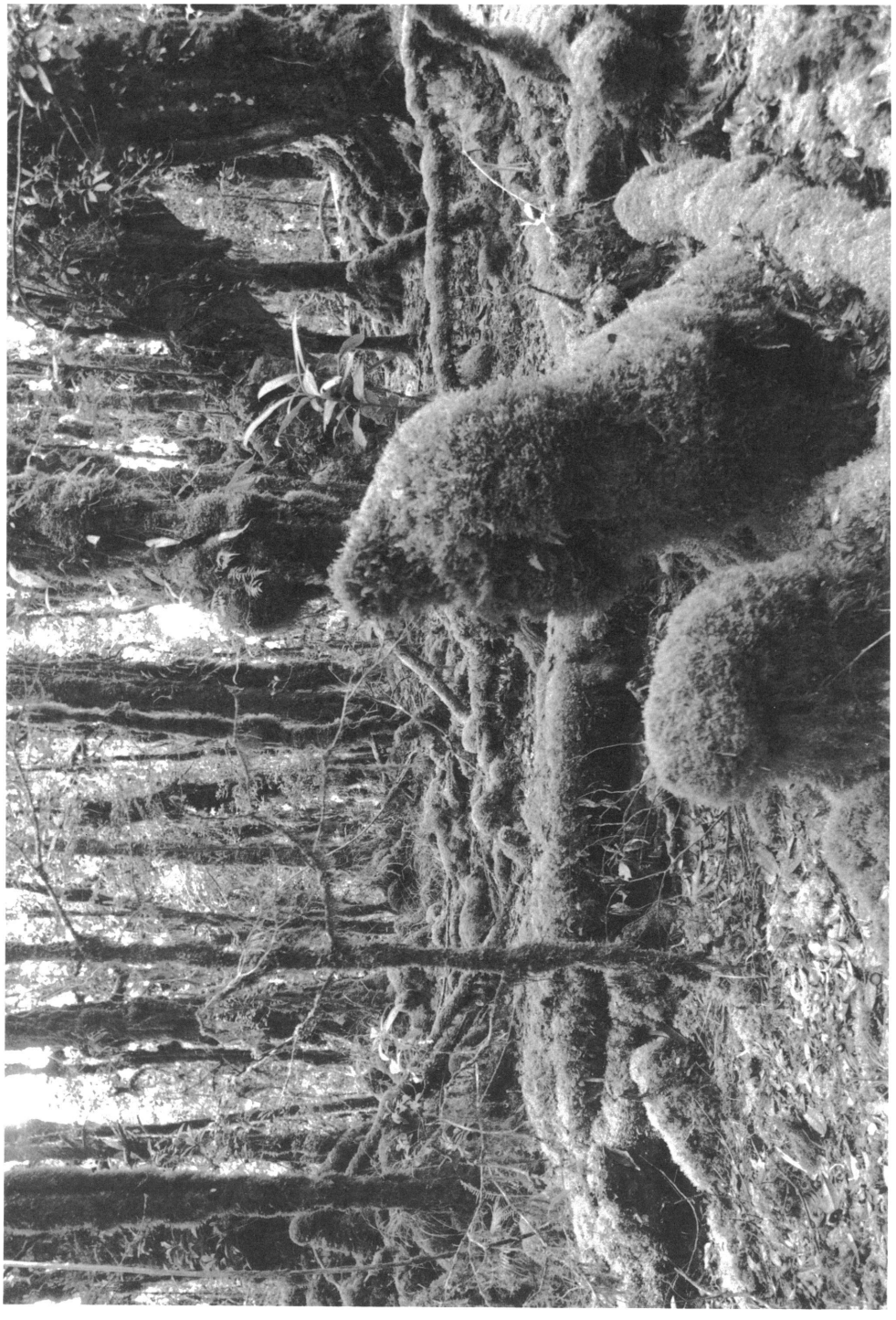

Fig. 3. Upper montane rain forest at 7500 ft near the summit of Gunung Nokilalaki, Central Sulawesi, 1974. This cool and wet mossy forest is the habitat of small-bodied Sulawesi shrew rats. *Melasmothrix naso* was trapped in damp runways beneath the moss-covered rotting trunks and sometimes seen during the day dashing across the open ground from beneath trunks to other cover.

Fig. 4. *Melasmothrix naso*, the host of *Polyplax melasmothrixi*. An adult male caught during the day on the summit of Gunung Nokilalaki in habitat similar to that shown in figure 3.

HOST HABITAT: All three species of Sulawesian small-bodied shrew rats are known to occur only in the mountainous central core of Sulawesi. Records of *Melasmothrix naso* are from 6000 ft at Rano Rano (1°30′S, 120°28′E) where the holotype (USNM 219752) was obtained (Miller and Hollister, 1921), and between 6400 and 7500 ft on the southwest slope and near the summit of Gunung Nokilalaki (1°16′S, 120°10′E) where 35 specimens were collected (Musser, 1982).

Cool, wet, and mossy forest above 6000 ft is the general habitat where all examples of *M. naso* have been encountered (fig. 3). Among the characteristics of this formation are the short canopy; small trees representing species associations and morphologies distinctive to mountain environments; low diversity in species of trees, shrubs, palms, and other plants; dense moss cover; and high frequency and long duration of rain and mist. Quantitative details, other descriptive observations, and other places where the shrew rats were trapped are documented by Musser (1982: 71).

Melasmothrix naso is small in body size with an elongate head and muzzle, small eyes and ears, chunky body, short tail, elongate claws on the front feet, and velvety dark chestnut fur (fig. 4). It is diurnal and terrestrial, uses mossy and earthen runways concealed beneath moss-covered rotting treefalls or root entanglements, and apparently feeds primarily on earthworms and fungus gnats (Musser, 1982).

Polyplax wallacei Durden

Polyplax wallacei Durden, 1987: 812.
Polyplax wallacei Durden. Durden and Traub, 1990: 57 (zoogeography).
Polyplax wallacei Durden. Durden and Musser, 1991: 7 (faunal relationships).

HOLOTYPE: Female designated by Durden (1987). In USNM. Allotype male removed by L. A. Durden from pelt of a male *Bunomys chrysocomus* (AMNH 226924) collected by G. G. Musser at 1000 m near Tomado (1°19′S, 120°03′E), Danau (Lake) Lindu, Central Sulawesi, Indonesia on 22 July, 1973. Deposited in the MZB.

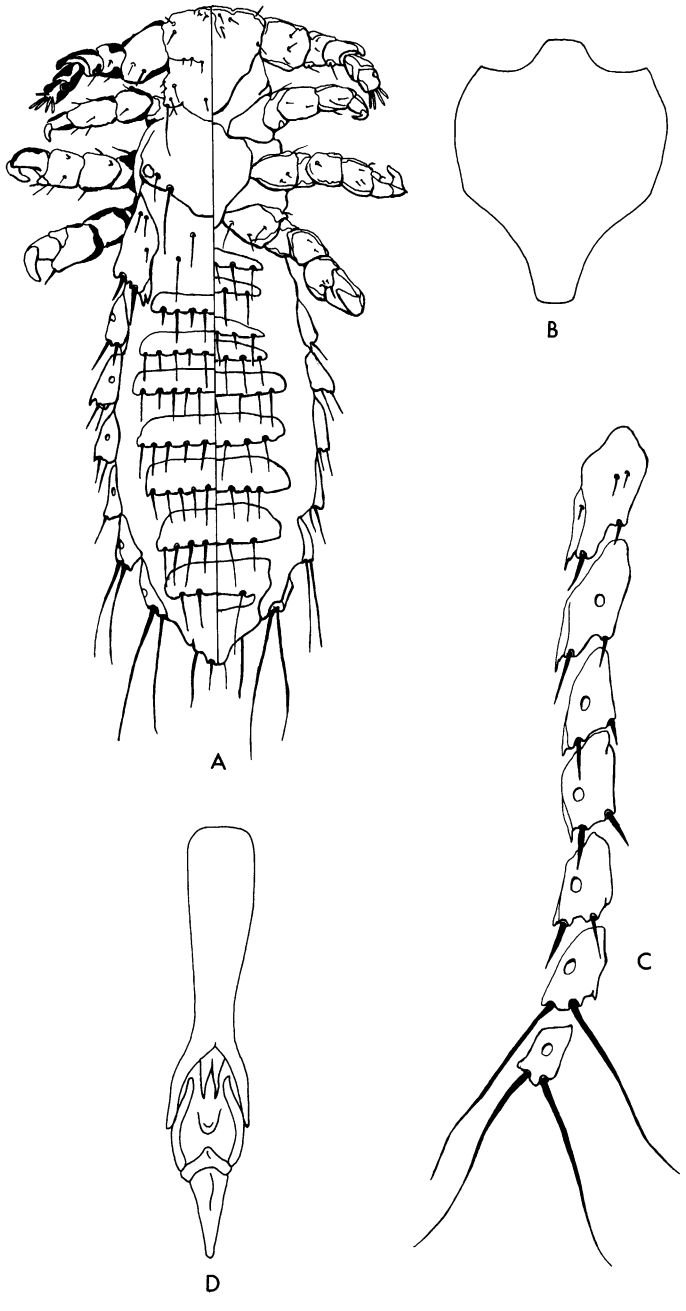

Fig. 5. *Polyplax wallacei*, male. **A,** habitus; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

REFERRED SPECIMENS: Eight additional lice (4 males, 4 females). Of these, an additional male and one female were removed from the same pelt from which the allotype was taken. One male louse was removed from the pelt of a *B. chrysocomus* female (AMNH 223038) bearing the same locality data as the allotype host but collected on 21 July, 1975. The remaining five specimens, most of which are in relatively poor condition, were located in the USNM slide-mounted Anoplura collections where they had been misidentified as

Polyplax spinulosa Burmeister. These specimens were also collected from Tomado; one male and two female lice were collected on 22 January, 1972 and bear the field collection number DJ.M-2366, while two male lice were collected on 24 January, 1972 (field collection no. DJ.M-2455). Hosts for both of these collections were originally labeled on the slides as "*Rattus penitus penitus*," which we have since determined to be *Bunomys chrysocomus*. Both of these 1972 collections were made by members of NAMRU-2 teams. Paratypes: BMNH, LAD, MZB, USNM.

DISTRIBUTION: Known from both North and Central Sulawesi (Sulawesi Utara and Sulawesi Tengah, respectively) from two species of forest rats belonging to the genus *Bunomys*. All known collections from North Sulawesi are from Dumoga-Bone National Park (0°34′N, 123°54′E), at an altitude of 230 m, while those from Central Sulawesi all originate from Tomado near Danau (Lake) Lindu (elevation 1000 m).

DIGANOSIS: The female of *P. wallacei* was described and diagnosed by Durden (1987). The male, described in this paper, has morphological similarities to *Polyplax spinulosa* Burmeister, a widespread parasite of domestic *Rattus*. The male of *P. wallacei* can be distinguished from *P. spinulosa* and from other species of *Polyplax* by a combination of the following traits: (1) distinctively shield-shaped thoracic sternal plate with extended anterolateral angles (fig. 5B); (2) the shapes and lengths of the attached apical setae for the paratergal plates (fig. 5C); (3) the shapes and proportions of the genitalic structures (fig. 5D).

DESCRIPTION: **Male** (fig. 5). Length of allotype 0.98 mm (mean for series 0.98; range 0.97–1.00; N = 5). Head, thorax, and abdomen well sclerotized.

Head. About as wide as long with anterior apex broadly rounded; 2 DAcHS (both anteromedial to DPHS), 2 DAnHS, 2 DMHS, 1 DPoCHS, 3 OrS, 3 SHS, and 2 SpAtHS on each side; DPHS almost extending to thoracic spiracle; VPHS short and close to insertion of first antennal segment. *Antennae* 5-segmented with first segment much larger than second, about as wide as long; third segment prolonged anterolaterally as is characteristic of male *Polyplax*.

Thorax. Slightly broader than long; thoracic sternal plate (fig. 5B) distinctive with rounded, central, anterior apex, angulate less well-developed anterolateral angles, and tapering to broadly rounded posterior apex; mesothoracic spiracle small (0.016 mm in diameter); DPTS moderate in length (0.115 mm), extending beyond insertions of first DCAS; *Legs.* With subtriangular coxae; forelegs with small acuminate claw; hindlegs slightly larger than midlegs, both with strong, pointed claws.

Abdomen. Wider than thorax; two anterior rows of 2 DCAS followed by one broad plate dorsally on each of segments 2–8; dorsal plates 1–6 (on abdominal segments 2–7) each with 8–10 TeAS; dorsal plate 7 (on abdominal segment 8) with 4 TeAS; two narrow plates ventrally on each of segments 2 and 3, and one broad plate ventrally on each of segments 4–7; ventral plates 1 and 3–7 each with 5–7 StAS; ventral plates 2 and 8 each with 4 StAS; some TeAS and StAS short. *Paratergal plates* (fig. 5C) present on segments 2–8; plates I–V subtriangular, each with two short apical setae; plates VI and VII each with two long apical setae; DPrS longer than corresponding VPrS on plates I–III; plates I–VI with dorsal angles developed into points; plates II–VII each with moderately sized spiracle.

Genitalia (fig. 5D). Subgenital plate with medial lacuna and one long lateral seta on each side of plate immediately anterior to lacuna; basal apodeme much longer than parameres, forked posteriorly; parameres smoothly curved; pseudopenis thick, extending appreciably beyond apices of parameres.

REMARKS: In addition to the new records from Central Sulawesi recorded here, Durden (1987) collected the following specimens of *P. wallacei* from tropical lowland evergreen rain forest (altitude 230 m) in Dumoga-Bone National Park, North Sulawesi, during February 1985:

2 females ex male *B. chrysocomus* (LAD no. 24),
2 females ex male *B. chrysocomus* (LAD no. 32),
2 females ex female *B. chrysocomus* (LAD no. 51),
4 females ex female *B. chrysocomus* (LAD no. 69),
1 female ex female *Bunomys fratrorum* (LAD no. 43),
1 female ex female *B. fratrorum* (LAD no. 53),
1 female ex female *Taeromys* sp. (LAD no. 73).

Unfortunately, the last host specimen listed (LAD no. 73) was not retained as a voucher but our subsequent examination of collection records indicates this animal was not a species of *Taeromys*. Consequently, all reliable known host records for *P. wallacei* pertain to *Bunomys chrysocomus* and *B. fratrorum*.

Polyplax wallacei may be restricted to populations of *Bunomys* living at low altitudes, at least between 230 and 1000 m, the elevations from which the louse has been recorded. The known hosts, however, are not similarly ecologically bracketed. In Central Sulawesi, samples of *Bunomys chrysocomus* were collected by Musser from 300 m up through lowland evergreen rainforest to the interface with tropical lower montane rain forest (about 1300 m) and higher into montane habitats between 1370 and 1515 m (AMNH 223566–223568, 223570, 225148 are the montane voucher specimens). The species has also been obtained in montane formations up to 6000 ft on Gunung Tambussissi (Musser, 1991), above 6000 ft on Gunung Lehio (USNM 218673 and 218681), at 2200 m on Pegunungan Latimojong (AMNH 196578–196584) in the central part of the island, and at 1500 and 2000 m at Tanke Salokko on Pegunungan Mekongga in the southeastern arm (Musser, 1991). Durden unsuccessfully sought lice from the fur of these montane samples, which consisted of study skins and fluid-preserved specimens.

In contrast to *Bunomys chrysocomus*, which occurs throughout most of Sulawesi (at least where collectors have sampled) between about 300 and 1800 m (Musser, MS), *B. fratrorum* has been found only in the northeastern arm of Sulawesi east of the Gorontalo region. Most samples come from lowlands and middle altitudes, but the species also reaches montane forest environments as documented by samples from 1780 m on Gunung Maujat (SAM m12644 and m12681) and 2000 m on the slopes of Gunung Klabat (USNM 217581, 217582, and 217585). We have not surveyed these animals for lice. That *Polyplax wallacei* may be restricted to habitats at low and middle altitudes in tropical lowland evergreen rain forest while their hosts are not so confined is the obvious hypothesis to be tested by sampling freshly caught rats collected in montane situations.

Additional survey of the other species of *Bunomys* is needed to determine what kinds of sucking lice they may harbor. For example, in Central Sulawesi, *B. andrewsi* occurs in tropical lowland evergreen rain forest, and *B. penitus* is the common *Bunomys* in montane habitats except where the mountain *B. prolatus* is found (Musser, 1991; Musser and Holden, 1991). Samples of *B. chrysocomus* have been taken at some of the same places that yielded specimens of *B. penitus* and *B. andrewsi* (Musser, MS), and close to *B. prolatus* (Musser, 1991). Is *Polyplax* part of their ectoparasite fauna and, if so, do they all share the same species of sucking louse? If *Polyplax wallacei* is actually restricted to hosts living at low and middle altitudes, we would not expect to find it parasitizing either *B. penitus* or *B. prolatus* but would not be surprised if it occurred on *B. andrewsi*, which is morphologically more similar to *B. fratrorum* than to any other species of *Bunomys* (Musser, MS).

Another facet of the association between *P. wallacei* and *Bunomys* is the low frequency of louse infestation on *B. fratrorum*. Durden (1987: 814) noted that *B. chrysocomus* appeared to be the primary host of *P. wallacei* and that its occurrence on *B. fratrorum* "could represent accidental infestations through ecological associations." This suggestion could be tested by surveying freshly caught *B. fratrorum* specimens from localities where it does not occur together with *B. chrysocomus*. Also, if *B. chrysocomus* is really the primary host and accidental infestation of other species is a possibility, *P. wallacei* might also be found on other species of *Bunomys* that are sympatric with *B. chrysocomus*.

Whether or not *B. fratrorum* is an accidental or primary host of *P. wallacei*, because the louse has been found on that host and not on a murine in another genus suggests evolutionary specificity between *P. wallacei* and the genus *Bunomys*. Throughout its geographic range, *B. chrysocomus* occurs in the same habitat and in Central Sulawesi was collected at the same sites as *Rattus hoffmanni*, *Maxomys hellwaldii*, and *M. muschenbroekii*, other Sulawesian endemic murines, but those hosts are parasitized by species of *Hoplopleura*, not *Polyplax* (Durden, 1990; Durden and Musser, 1991).

Fig. 6. *Bunomys chrysocomus*, the host of *Polyplax wallacei*. An adult female from Sungai Tokararu, 1150 m.

HOSTS AND HABITAT: *Bunomys chrysocomus* is of medium body size (see measurements listed in tables 1 and 2 in Musser, 1991), with a tail shorter than head and body, small eyes and ears, a long snout, and covered by dark, soft fur (fig. 6). Musser (fieldnotes in AMNH) found it to be an opportunistic feeder, subsisting on insects, earthworms, snails, small frogs and lizards, and sometimes fruit.

In Central Sulawesi, Musser encountered *B. chrysocomus* most commonly in the wetter and cooler parts of tropical lowland evergreen rain forest (fig. 7), usually under dense cover along the sides of wet ravines and small streams. It was rarely collected higher on slopes, ridgetops, or beneath open understory, where the ambient environment is slightly drier than that characteristic of ravines and streamside habitats. At higher elevations within the boundaries of tropical lower montane rain forest, *B. chrysocomus* was also found in wetter areas of the forest with good cover.

In its morphology and external appearance, *B. fratrorum* is a larger version of *B. chrysocomus* (compare the values listed in tables 1–3 *in* Musser, 1991), and examples of it have often been misidentified as the smaller species in museum collections. In addition to its much larger size, *B. fratrorum* has a longer tail relative to head and body length, the distal portion of the tail is white in most specimens, and cusp patterns of molars are less complex. *Bunomys fratrorum* likely occurs in similar habitat as *B. chrysocomus* because specimens of both have been collected at the same place (although no information on microhabitats was provided), and they may have a similar diet. The stomach of one specimen we studied contained remains of insects and earthworms.

Polyplax eropepli (Ewing)

Eremophthirius eropepli Ewing, 1935: 209.
Polyplax eriopepli [sic] Ewing. Ferris, 1951: 207 (catalog).

Fig. 7. Lowland evergreen rain forest along Sungai Tokararu at 1150 m, Central Sulawesi, 1973. Examples of *Bunomys chrysocomus* were trapped beneath the dense streamside vegetation.

Polyplax eropepli (Ewing). Johnson, 1958a: 47 (lectotype designated).
Polyplax eropepli (Ewing). Durden, 1987: 814 (redescription).
Polyplax eropepli (Ewing). Durden and Traub, 1990: 57 (zoogeography).
Polyplax eropepli (Ewing). Durden and Musser, 1991: 7 (faunal relationships).

REFERRED SPECIMEN: One female louse removed by L. A. Durden from the pelt of an *Eropeplus canus* female (USNM 219711) trapped at 1800 m at Rano Rano, Central Sulawesi, Indonesia, by H. C. Raven on 15 December, 1917 (Miller and Hollister, 1921). Deposited in the USNM.

REMARKS: Until now, *P. eropepli* was known only from four specimens (two males, two females) removed from the same pelt listed here for the new specimen (Ewing, 1935; Ferris, 1951; Johnson, 1958a; Durden, 1987). These four specimens are mounted on the same microscope slide, which bears the USNM type number 44906. All five *P. eropepli* specimens are in poor condition, but the new specimen has retained some intact structures that are damaged in the type series. Both female paralectotypes are missing all leg segments other than the coxae; the new specimen, however, has intact legs and these do not differ significantly from those illustrated by Durden (1987) for the male. Other differences noted for the new specimen are as follows: (1) a small, anterior, central projection is present on the thoracic sternal plate; (2) on paratergal plate VII, one apical seta remains intact; it is much longer than the corresponding setae on the paralectotypes suggesting setal damage in those specimens; (3) on gonopods VIII, the lateral setae (broken on both sides in the paralectotypes) are long, extending beyond the outline of the abdomen for about 40% of their length; (4) on each gonopod IX, a single stout seta, rather than two narrow setae, is present.

Polyplax eropepli has never been collected from murine species other than *Eropeplus canus* and it is probably host specific to that animal. However, the uniqueness of this association has to be tested by surveying *Lenomys meyeri* for sucking lice. That murine is endemic to Sulawesi and is the closest known relative of *E. canus*, as revealed by shared distinctive cranial and pelage traits (Musser, 1981) as well as spermatozoal morphology (Breed and Musser, 1991). *Lenomys* is represented by few specimens in museums, and unfortunately we have not found lice on any of those we examined.

HOST AND HABITAT: *Eropeplus canus* is a member of the montane murine fauna endemic to Central Sulawesi (Musser and Holden, 1991: 406). Although infrequently encountered by collectors, it is documented by 13 examples from the following places: Gunung Nokilalaki (1°16′S, 120°10′E) at 5950 ft (AMNH 225119 and 225120), 7200 ft (AMNH 223553, 223554, 223557), 7250 ft (AMNH 225121–225123), and 7500 ft (AMNH 223555, 223556, 225124); Rano Rano (1°30′S, 120°28′E) at 6000 ft (USNM 219711); Gunung Lehio (1°33′S, 110°53′E) above 6000 ft (USNM 218707, holotype); Pegunungan Quarles, Bulu Karua (2°56′S, 119°39′E) at 6000 ft (BM 40.386 and 40.387); and Pegunungan Latimojong (3°30′S, 121°23′E) at 2200 m (AMNH 196592).

Eropeplus canus is large and bulky with a very long bicolored tail (fig. 8). Among five adults from Gunung Nokilalaki, the range in length of head and body is 230–255 mm, length of tail is 270–296 mm, length of hind foot is 46–48 mm, length of ear is 21–27 mm, and weight is 190–315 g. Long and thick gray fur covers the body and proximal portion of the tail.

Tropical montane rain forest (generally described by Whitmore, 1984) is the general habitat of *E. canus* (fig. 9). Musser (1982) and Musser and Dagosto (1987) provide descriptions of this environment on Gunung Nokilalaki. Musser trapped the rats on wet ground near and within rock clusters covered with moss and held together by tree roots, alongside rotting trunks, and 15 ft above ground on a woody vine. Fruits, leaves, palm hearts, and some kinds of insects were eaten by captive rats (Musser, fieldnotes in AMNH).

ASSOCIATED MORPHOLOGICAL DIVERGENCE IN HOST AND PARASITE

Because evolutionary parallelism at the levels of genera and species is a relationship between sucking lice that is widespread (Kim, 1985, 1988), we might expect each species of

Fig. 8. *Eropeplus canus*, the host of *Polyplax eropepli*. An adult female from near the summit of Gunung Nokilalaki, 7500 ft.

louse associated with the species of *Melasmothrix*, *Eropeplus*, and *Bunomys* to also be unique, possibly at the generic level. *Melasmothrix naso*, the louse found on the shrew rat, *M. naso*, is diagnosed by a set of characters unique to it (stout setae, male pseudopenis with three sclerotized distal patches, proximally notched parameres that articulate with distal arms of the basal apodeme, and characteristic setation of female gonopods VIII and IX), suggesting remote affinity with any other described relative. However distinct it is, this louse does not appear to be part of a monophyletic group different from that formed by other species of *Polyplax*, a new monotypic genus, for example.

Polyplax eropepli, the sucking louse specific to *Eropeplus canus*, is not as distinctive in its morphology as is *P. melasmothrixi*. Some characters of *P. eropepli* are shared with *P. spinulosa*, a louse found on commensal *Rattus* species (table 1; Durden, 1987; Durden and Page, 1991) that occur on Sulawesi but are not native to the island (Musser and Holden, 1991). *Polyplax wallacei*, which parasitizes *Bunomys chrysocomus* and *B. fratrorum*, also resembles *P. spinulosa* in some features and shares one trait (the general shape of the thoracic sternal plate) with *P. cutchicus*, a parasite of the Indian rat *Cremnomys cutchicus* (table 1; Durden, 1987).

These relationships suggest that the reported evolutionary parallelism between sucking lice and host taxa cited by Kim (1988) does not describe the discordant degree of morphological divergence that exists between host and louse among certain species of Indo-Australian murine rodents. *Melasmothrix naso* is in a clade with two other species of small-bodied shrew rats endemic

Fig. 9. Upper montane rain forest near the summit of Gunung Nokilalaki, 7500 ft, Central Sulawesi, 1973. In this cool, mossy, and misty environment, *Eropeplus canus* was caught in the dark recesses beneath the upturned rotting tree base at the right of the photograph.

TABLE 1

Principal Hosts and Known Geographical Distributions of *Polyplax* spp. Sucking Lice Parasitic on Murine Rodents[a]

Louse species	Host species	Distribution	Reference
P. abyssinica	*Arvicanthus niloticus*	N. & E. Africa	Johnson (1960)
P. acomydis	*Acomys spinosissimus*	Mozambique	Kim and Emerson (1970)
P. antennata	*Apodemus mystacinus*	E. Europe	Smetana (1960)
P. arvicanthis	*Rhabdomys pumilio*	E. & Southern Africa	Johnson (1960)
P. asiatica	*Nesokia indica*	Southern Asia & Near East	Durden et al. (1990)
P. blanfordi	*Cremnomys blanfordi*	India	Mishra (1981)
P. brachyrrhyncha	*Acomys cahirinus*	N. Africa to Pakistan	Durden (1991)
P. bullimae	*Bullimus bagopus*	Philippines: Mindanao	Johnson (1958b)
P. cummingsi	*Dasymys* spp.	Africa	Durden (1991)
P. cutchicus	*Cremnomys cutchicus*	India	Mishra (1981)
P. dacnomydi	*Dacnomys millardi*	China: Yunnan	Chin (1990)
P. dolichura	*Acomys cahirinus*	Sudan	Johnson (1962b)
P. eropepli	*Eropeplus canus*	Indonesia: Sulawesi	Durden and Musser (1991)
P. expressa	"*Rattus* sp."	Philippines: Luzon	Johnson (1964)
P. gracilis	*Micromys minutus*	Eurasia	Beaucournu (1968)
P. grammomydis	*Grammomys dolichurus*	Southern Africa	Johnson (1960)
P. hoogstraali	*Acomys* spp.	Egypt	Johnson (1960)
P. humae	*Cremnomys blanfordi*[b]	Pakistan	Khan and Khan (1985)
P. indica	*Golunda ellioti*	India	Mishra (1981)
P. insulsa	*Leopoldomys sabanus*	Malaysia, Natuna Is.	Johnson (1964)
	L. edwardsi[c]	China	Chin (1980)
P. kondana	*Millardia kondana*	India	Mishra (1981)
	Millardia meltada	Pakistan	Durden et al. (1990)
P. melasmothrixi	*Melosmothrix naso*	Indonesia: Sulawesi	Present report
P. meridionalis	*Acomys spinosissimus*[d]	Botswana	Johnson (1962a)
P. oxyrrhyncha	*Acomys* spp.	N. & E. Africa	Durden (1991)
P. phloeomydis	*Phloeomys cumingi*	Philippines: Luzon	Cuy (1982)
P. phthisica	*Lophuromys* spp.	E. & Central Africa	Durden (1991)
P. praomydis	*Aethomys namaquensis*	S. Africa & Namibia	Johnson (1960)
P. pricei	*Niviventer confucianus*[e]	N. Thailand	Kim (1968)
P. serrata	*Mus musculus*	Cosmopolitan	Durden et al. (1990)
P. smallwoodae	*Lophuromys* spp.	W. & Central Africa	Durden (1991)
P. solivaga	*Aethomys chrysophilus*	S. Africa	Johnson (1962b)
P. spinulosa	*Rattus norvegicus*, *R. rattus*	Cosmopolitan	Durden (1991)
	Rattus argentiventer	S.E. Asia to New Guinea	Durden (1987)
	Rattus exulans	Indo-Pacific region	Durden (1987)
P. tarsomydis	*Tarsomys apoensis*	Philippines: Mindanao	Ewing (1935)
P. thamnomydis	*Grammomys rutilans*	Central Africa	Johnson (1960)
P. vicina	*Rattus losea*[f]	China	Blagoveshchensky (1972)
P. visenda	*Leopoldomys sabanus*[f]	Vietnam	Blagoveshchensky (1972)
P. wallacei	*Bunomys chrysocomus*	Indonesia: Sulawesi	Durden (1987)
P. waterstoni	*Mastomys* spp., *Praomys* spp.	Southern Africa	Durden (1991)

[a] An additional 39 species of *Polyplax* are known. Collectively, they parasitize mammals belonging to eight other subfamilies of Muridae (in the sense of Carleton and Musser, 1984) and to the families Sciuridae and Soricidae.

[b] There are no substantiated records of *Cremnomys blanfordi* from Pakistan. This murine is endemic to peninsular India and to Sri Lanka. We assume that the correct type host of *Polyplax humae* is either *Millardia gleadowi* or *M. meltada*.

[c] We have not seen the louse or host material reported by Chin (1980) for *P. insulsa* from *L. edwardsi*.

[d] The type host of *Polyplax meridionalis* was listed as *Acomys cahirinus* by Johnson (1962a). However, *A. spinosissimus* is the only murine of the genus *Acomys* that is known from Botswana (Dippenaar and Rautenbach, 1986).

[e] The type host of *Polyplax pricei* was listed as *Rattus niveiventer* [sic] (=*Niviventer niviventer*). This murine does not occur in northern Thailand (Marshall, 1977) and we have since determined the type host to be *Niviventer confucianus*.

[f] We have not seen the louse or host material reported by Blagoveschensky (1972).

to Sulawesi, *Tateomys rhinogradoides* and *T. macrocercus*. *Eropeplus canus* and *Lenomys meyeri* form a separate clade that is phylogenetically distant from the group of shrew rats (Musser, 1982; Breed and Musser, 1991). *Bunomys* and *Rattus* are part of a clade that includes genera that are native not only to Sulawesi but to other islands and continents in the Indo-Australian region (Musser and Heaney, 1992; Kitchener et al., 1991), and one that is not phylogenetically closely related to either the shrew rat or *Eropeplus-Lenomys* clades. Similarly, the Indian rat, *Cremnomys cutchicus*, is not closely related to any of the endemic Sulawesi murines. Yet it and species in the other three clades are parasitized by species of sucking lice in the same supposed monophyletic group, *Polyplax*. These and other known examples of murine/*Polyplax* host-parasite associations are listed in table 1. Most of the lice shown in table 1 are clearly host specific (monoxenous). However, because diverse murine hosts with various Old World distributions (except for two species that have accompanied their cosmopolitan hosts around the globe) are parasitized, host-parasite coevolution in the strict sense (i.e., Fahrenholz' rule) does not appear to have occurred at the genus and species levels. These observations are based on morphological characters and need to be compared with results from analyses of other kinds of systems, molecular traits for example. Some other ectoparasites of Sulawesi rodents may show clearer host-parasite morphological coevolution. For example, many undescribed genera and species of Sulawesian rodent fleas are known, and distinct flea genera appear to parasitize distinct murine genera in many cases (Durden and Traub, 1990; R. Traub, personal commun.).

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