The Genus *Hoplopleura* (Anoplura: Hoplopleuridae) from Murid Rodents in Sulawesi, with Descriptions of Three New Species and Notes on Host Relationships

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ABSTRACT *Hoplopleura chrysocomi, H. sembeli,* and *H. musseri* are described and illustrated as new species from bioendemic murid rodents, and *H. pacifica* Ewing is documented from commensal murids from Sulawesi Utara, Indonesia. *H. chrysocomi* parasitized only *Bunomys chrysocomus* (Hoffmann), and *H. musseri* was taken only from *Maxomys musschenbroeki* (Jentink). *H. sembeli* was collected from three species of sympatric murids but parasitized principally *Maxomys hellwaldi* (Jentink). Similarities between *H. musseri* from Sulawesi and *H. pectinata* (Cummings) from mainland Southeast Asia and Borneo corroborate host taxonomies that propose close phylogenetic relationships between their spiny rat hosts. Brief comment is made on possible coevolution between the regionally bioendemic Sulawesi macaques and their pedicinid sucking lice.

KEY WORDS Insecta, coevolution, *Hoplopleura,* rodents

THE SUCKING LICE (Anoplura) associated with murid rodents in Sulawesi, Indonesia, are inadequately known. Three species of *Polyplax* Enderlein have been documented from the murid fauna of this island (Durden 1987), and the present paper considers, in similar fashion, the genus *Hoplopleura* Enderlein. Together, these two large louse genera parasitize an assortment of small to medium-sized mammals (particularly rodents) on an almost global basis with each currently represented by 74 (*Polyplax*) and 134 (*Hoplopleura*) described species.

This paper documents four species of *Hoplopleura* collected by the author from Sulawesian murids. One of these species, *H. pacifica* Ewing, is a common louse of commensal (anthropophilic) *Rattus* throughout Indo-Australia, whereas the other three, described here as new species, were collected only from bioendemic forest rats and, like their hosts, are probably confined zoogeographically to Sulawesi. Also noted in this paper are some apparent evolutionary host–parasite relationships that suggest common geographical origins for the mammal–louse associations under consideration.

The disease relationships, if any, for the *Hoplopleura* discussed here are unknown, but Traub et al. (1978) note that some lice belonging to this genus are naturally infected and capable of experimental intramurid transmission of *Rickettsia typhi* Wolbach & Todd, the etiologic agent of murine (endemic) typhus. Traub et al. (1978) also state that these lice should be considered as potential sources of murine typhus transmission to humans by the aerosol route (via inhalation of dust from infected louse feces).

Methods and Materials

Sucking lice were collected from wild mammals in Sulawesi Utara (North Sulawesi) as part of an ectoparasite survey undertaken during Project Wallace (Durden 1986). Bioendemic murids were live-trapped in primary lowland rain forest, and commensal murids were taken in human dwellings or in secondary scrub vegetation. Lice were collected mainly by intense visual pelage searches of hosts subjected to prolonged anesthesia (administered using systemic ketamine hydrochloride), but a few animals were processed for ectoparasite removal by the use of skin digestion techniques (Cook 1954).

Collection records for *H. pacifica* and records, descriptions, and illustrations for the three new species follow. Terminology and format designated by Kim (1966, 1986) and by Kim & Ludwig (1978) are followed. Drawings of whole specimens conventionally illustrate dorsal morphology to the left of the midline and ventral morphology to the right. Abbreviations used to designate specific louse setae in the species accounts that follow are: AnMHS, anterior marginal head setae; ApHs, apical head setae; DAcHS, dorsal accessory head setae; DAnCHS, dorsal anterior central head setae; DAnHS, dorsal anterior head setae; DCAS, dorsal central abdominal setae; DMHS, dorsal marginal head setae; DPaHS, dorsal preantennal head setae; DPHS, dorsal principal head setae; DPoCHS, dorsal posterior central head setae; DPTS, dorsal principal thoracic setae; SHS, sutural head setae; SpAtHS, supraantennal head setae; StAS, sternal

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abdominal setae; TeAS, tergal abdominal setae; VPaHS, ventral preantennal head setae; VPHS, ventral principal head setae.

Depositories and their acronyms are as follows: BMNH, British Museum (Natural History), London, U.K.; LAD, author's collection; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; NMNH, National Museum of Natural History, Washington, D.C.

Hoplopleura pacifica Ewing

Material Examined. All collections are from Dumoga, Bolaang Mongondow Province, Sulawesi Utara, Indonesia, 200–300 m elevation, II-1985, L. A. Durden: 1 ♂, 1 second instar, ex ♂ *Rattus exulans* (Peale) (LAD No. 27) from scrub vegetation; 4 ♀♀, 3 second instars, ex ♂ *R. exulans* (LAD No. 28), from scrub vegetation; 1 ♂, 1 ♀, 1 third instar, 1 second instar, ex ♂ *Rattus argentiventer* (Robinson & Kloss) (LAD No. 29), from scrub vegetation; 5 ♀♀, 3 third instars, 2 second instars, 2 first instars, ex ♀ *R. argentiventer* (LAD No. 41), in base camp building; 1 ♀ ex ♀ *R. argentiventer* (LAD No. 80), in base camp building.

Specimens deposited in NMNH and LAD.

Remarks. *Hoplopleura pacifica* was originally described from specimens collected from commensal rats throughout Indo-Malaysia and Polynesia. Some of the original material (documented by Ewing [1924]) was collected from *R. exulans* (identified by Ewing as *Rattus raveni* and *R. raveni eurous*) from Sulawesi Utara. Pritchard (1947) repeated Ewing's (1924) *H. pacifica* records from Sulawesi but followed Ferris (1935) in treating *H. pacifica* as a synonym of *H. oenomydis* Ferris. Ferris (1951) adhered to this synonymy despite doubts expressed by Hopkins (1949). However, *H. pacifica* and *H. oenomydis* are not synonyms (Johnson 1964, 1972; Voss 1966; Kim et al. 1986). *H. oenomydis* is principally parasitic on the east African murid rodent *Oenomys hypoxanthus* (Pucheran), whereas *H. pacifica* parasitizes commensal *Rattus* in Asia and the Pacific region (and now throughout the Western Hemisphere also). It is important to refute this synonymy, not only in connection with the species records noted here but also because there has been considerable confusion in the literature.

Hoplopleura chrysocomi Durden, n. sp. (Fig. 1–8)

Male. Total length of allotype 0.73 mm (mean for series, 0.73; range, 0.71–0.75; $n = 5$). Head, thorax, and abdomen well sclerotized.

Head. Slightly longer than wide, anterior apex rounded; 2 SHS and 4 DMHS distinct on each side; DPHS fairly short, not extending to thoracic spiracle, with 1 DAcHS medial to DPHS on each side; 1 DPaHS, 2 DAnHS on each side; VPHS, ApHS, and AnMHS distinct. *Antennae.* 5-segmented with basal segment larger than 2nd segment, slightly wider than long.

Thorax. Broader than long; thoracic sternal plate with concave anterior apex and extended but evenly rounded posterior apex; mesothoracic spiracle (0.016 mm in diameter) moderate in size; DPTS moderate in length (0.091 mm), extending to 1st paratergal plate; no other thoracic setae present. *Legs.* Coxae subtriangular; fore and midlegs small, each with acuminate tarsal claw; hind legs large, each with robust rounded tarsal claw.

Abdomen. Wider than thorax, with 1 plate per segment dorsally and (starting at segment 4) 2 plates per segment ventrally; 2 rows of DCAS each with 2 setae followed by 7 rows of TeAS, each with 4–8 setae (TeAS of 2 distinct lengths); 12 rows of StAS, each with 2–8 setae, rows 1–10 with 6–8 setae, rows 11 and 12 each with 2 setae; sternites of segments 2 and 3 extending completely across ventral surface to articulate with corresponding paratergal plate as characteristic of genus; sternite on segment 3 with 2 robust setae on each side. Paratergites present on segments 1–8: plate I without setae; plates II and III each with 2 setae of moderate length; plates IV–VI each with 1 moderate and 1 short seta; plates VII and VIII each with 2 long setae; dorsal and ventral angles of plates II–VII subtriangular, produced into points; plates III–VII each with a spiracle; plates IV–VI with apical sculpting. *Genitalia.* With distinct subgenital plate; basal apodeme longer than parameres; parameres narrow at both ends and with central "elbow"; pseudopenis long and narrow, extending well beyond apices of parameres.

Female. Total length of holotype 1.02 mm (mean for series, 1.03; range, 0.94–1.09; $n = 23$). *Head, thorax,* and *legs.* As in male unless described otherwise; fore and hind coxae with small, spiny protuberances; DPTS length, 0.098 mm.

Abdomen. With 2 rows of DCAS on 1st segment (each with 2 and 4 setae, respectively) followed by 1 tergite on each of abdominal segments 2 and 3 (each with 4 and 6 TeAS, respectively) and 3 tergites on each of segments 4–7 (each with 4–7 TeAS); total of 17 rows of TeAS, each consisting of 2–7 setae; TeAS on 1st tergite elongated; 16 rows of StAS, each with 6–8 setae and with 3 sternites on each 4th–7th segment; 16th sternite widened and with 4 short central setae and 4 longer StAS (2 on each side).

Genitalia. Subgenital plate poorly sclerotized, subrectangular; gonopods VIII each with 1 short medial seta and 2 longer lateral setae; gonopods IX each with stout central seta; vulvar fimbriae distinct.

Type Material. ♀ Holotype, ♂ Allotype, 4 ♂♂ and 22 ♀♀ Paratypes ex *Bunomys chrysocomus* (Hoffmann), Dumoga-Bone National Park (123°53′E, 0°34′N), Bolaang Mongondow Province, Sulawesi Utara, Indonesia, about 240 m elevation, II-1985, L. A. Durden. Individual collections are as follows: 2♂♂, 10♀♀ (including holotype), ex ♀ *B. chrysocomus*

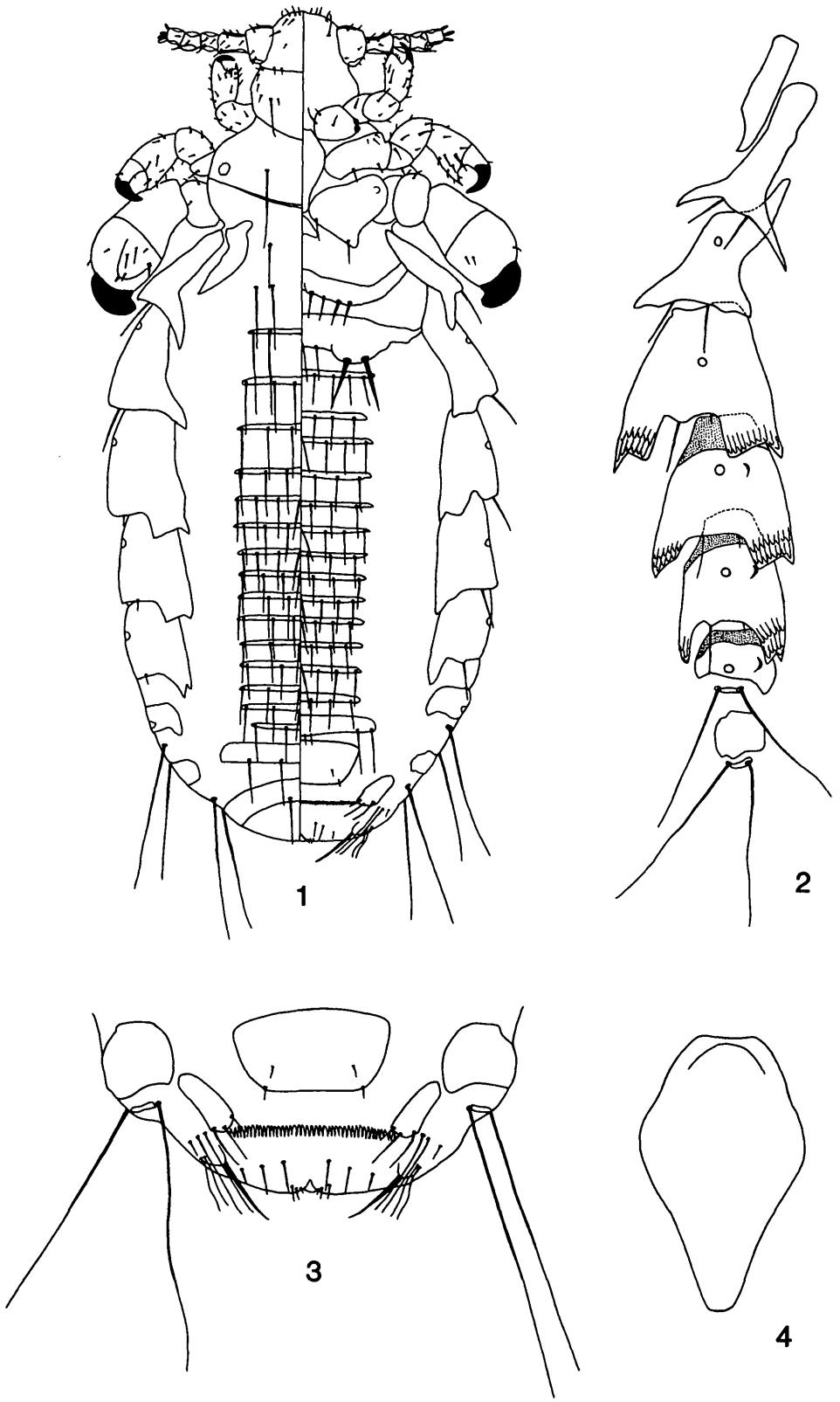


Fig. 1–4. *H. chrysocomi* Durden, n. sp., female. (1) Dorsal-ventral view. (2) Paratergal plates. (3) Genitalia. (4) Thoracic sternal plate.

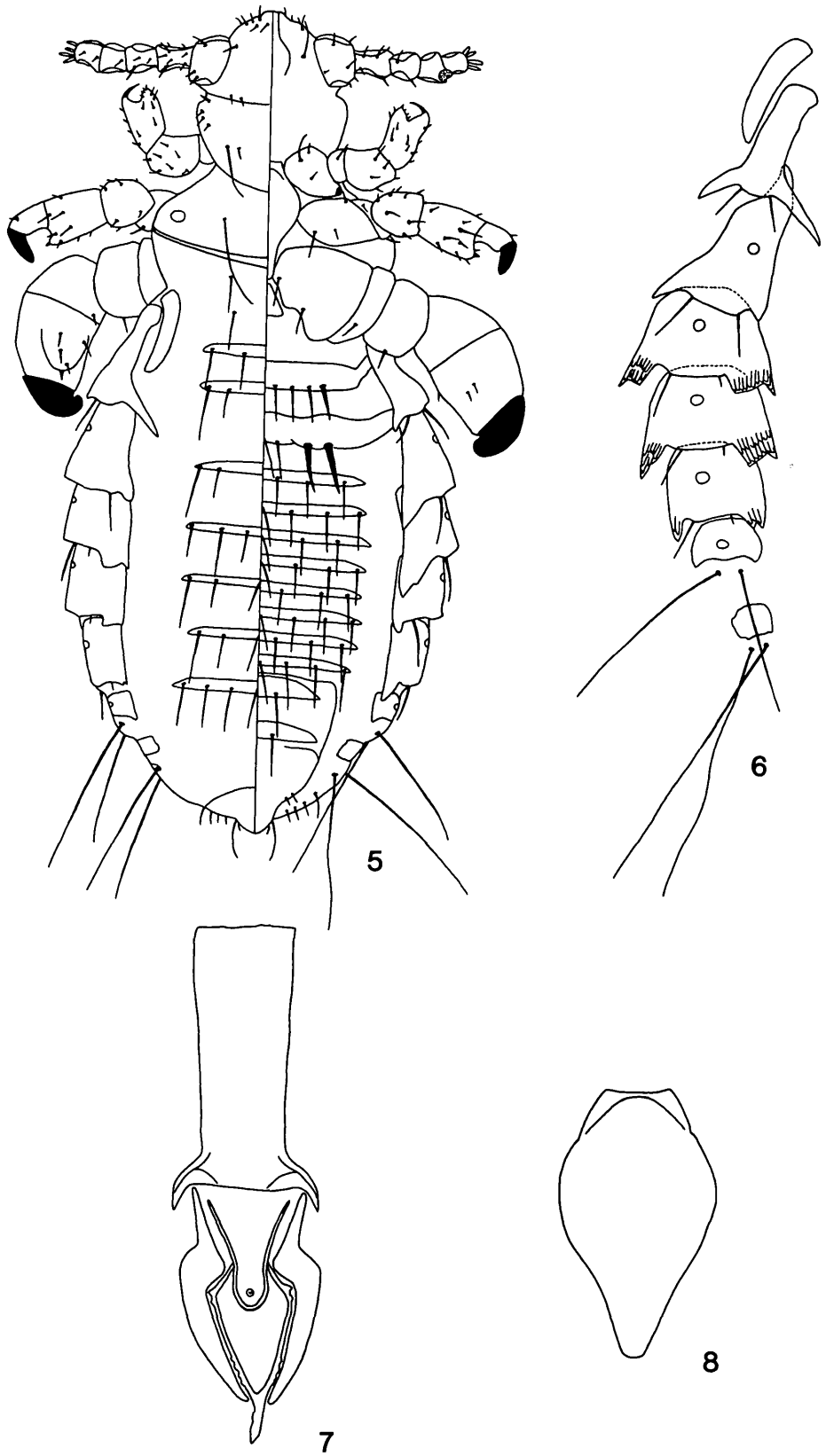


Fig. 5–8. *H. chrysocomi* Durden, n. sp., male. (5) Dorsal-ventral view. (6) Paratergal plates. (7) Genitalia. (8) Thoracic sternal plate.

(LAD No. 69); 1♂, 2♀♀, ex ♀ *B. chrysocomus* (LAD No. 18); 3♀♀, ex ♂ *B. chrysocomus* (LAD No. 24); 1♂ (allotype), 3♀♀, ex ♂ *B. chrysocomus* (LAD No. 32); 1♂, 5♀♀, ex ♀ *B. chrysocomus* (LAD No. 81). Holotype and allotype deposited in NMNH, paratypes deposited in BMNH, MZB, NMNH, and LAD.

Remarks. The specific epithet for this new species is derived from that of its host, *B. chrysocomus*. *H. chrysocomi* is a fairly typical member of its genus, although the reduction in thoracic setation is notable. It is similar to *H. pacifica* and can be identified by the shape, sculpting, and setation of the paratergal plates; the anterior concavity of the thoracic sternal plate; and characteristics of the genitalia. *H. chrysocomi* appears to be host specific to *B. chrysocomus*, a murid bioendemic to, but widely distributed within, Sulawesi (Musser 1987). Because all the lice documented herein are from North Sulawesi, it will be interesting to ascertain if this murid is parasitized by this species elsewhere in Sulawesi.

Hoplopleura sembeli Durden, n. sp.
(Fig. 9–16)

Male. Total length of holotype 0.95 mm (mean for series, 0.94; range, 0.84–1.00; n = 19). Head, thorax, and abdomen well sclerotized.

Head. About as long as wide; anterior apex with shallow depression; 2 SHS and 4 DMHS distinct on each side; DPHS fairly short, not extending to thoracic spiracle, with 1 DAcHS medial to DPHS on each side; 1 DPaHS, 1 SpAtHS, and 1 DPoCHS on each side; VPHS and 1 VPaHS distinct on each side; ApHS and AnMHS present. *Antennae.* 5-segmented, basal segment larger than 2nd segment, slightly wider than long.

Thorax. Broader than long; thoracic sternal plate with rounded but narrowed anterior apex and extended, blunter posterior apex; mesothoracic spiracle (0.025 mm in diameter) large; DPTS moderate in length (0.115 mm), extending to 1st paratergal plate; no other thoracic setae present. *Legs.* Coxae of different shapes but those of mid and hind legs mainly subtriangular; fore and midcoxae each with tubercle, well developed in former; fore legs small, each with narrow, acuminate claw; hind legs robust, each with large, blunt claw; midlegs intermediate in size between fore and hind legs.

Abdomen. Wider than thorax, 1 plate per segment dorsally and 2 plates ventrally on each of segments 3–7; 1 row of DCAS with 2 setae followed by 8 rows of TeAS, each with 4–7 setae (TeAS on tergites 1–7 of 2 distinct lengths); 12 rows of StAS, rows 1–10 each with 7–8 setae, row 11 with 4 setae, row 12 with 2 setae; few shorter setae present in regular pattern in StAS rows 4–10; StAS on 3rd sternite consisting of 2 robust lateral setae on each side, 1 short seta medial to these on each side, and longer central seta of regular thickness; sternites of segments 2 and 3 extending completely across ventral surface to articulate with corresponding paratergal plates. Paratergites present on segments 1–8: plate I without setae; plates II and III each with 2 setae of moderate length; plates IV–VI each with 1 moderate and 1 minute seta (the latter often difficult to locate because not always situated at extreme plate margin); plates VII and VIII each with 2 long setae; plates II–VII mainly subtriangular, dorsal and ventral angles showing some development into points, although lobulated appearance also characterizes plates III–VI, these apical lobes each with surface sculpting; paratergites III–VII each with large spiracle. *Genitalia.* Basal apodeme longer than parameres; parameres thickened basally and narrow apically; pseudopenis long and narrow, extending beyond apices of parameres.

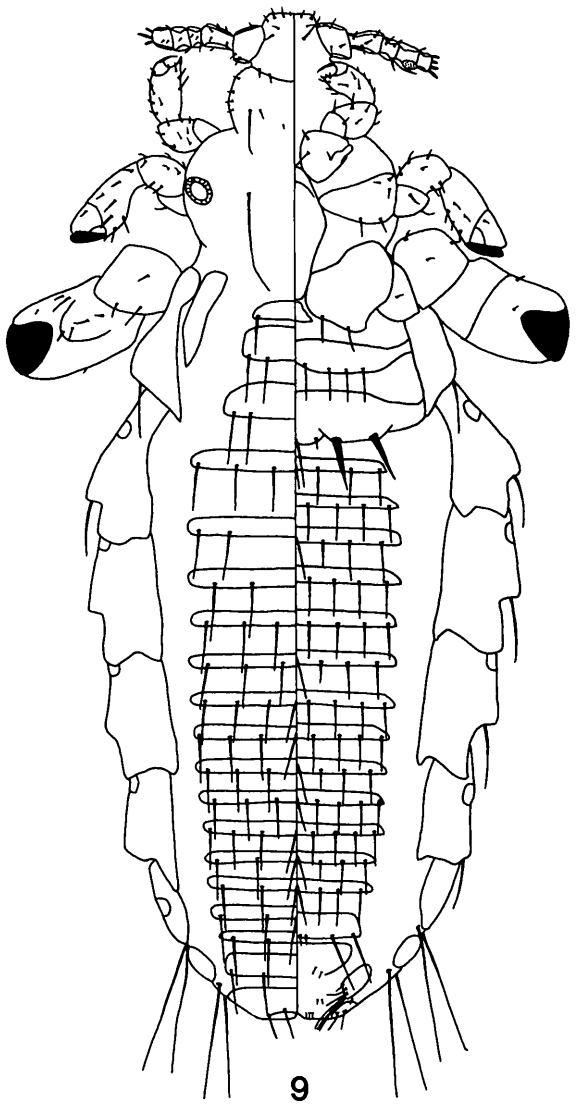
Female. Total length of allotype 1.21 mm (mean for series, 1.21; range, 0.98–1.38; n = 36). *Head, thorax,* and *legs.* As in male unless described otherwise; middle coxae without obvious protuberances; thoracic sternal plate not narrowed as much apically.

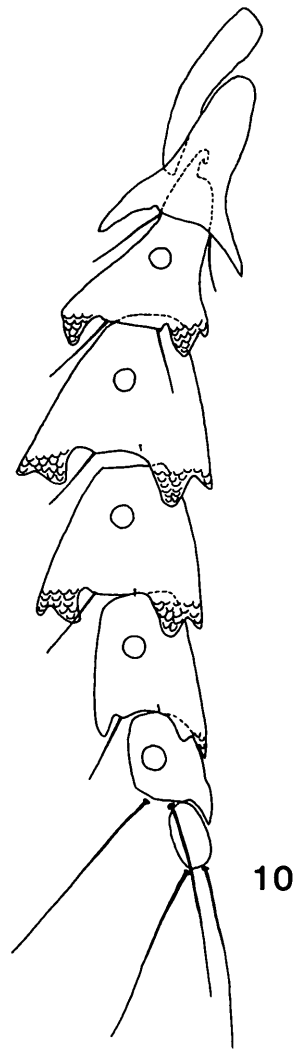
Abdomen. With 3 tergites per segment starting at segment 4 and with total of 19 tergites and corresponding rows of TeAS comprising 2 setae in 1st row and 4–7 setae in each of following rows; all TeAS about equal in length; 16 rows of StAS each with 7–8 setae and 3 sternites on each of segments 3–7; 16th sternite wider, with 4 short central setae and 4 longer StAS (2 on each side). *Genitalia.* Subgenital plate triangular, poorly sclerotized; gonopods VIII each with 1 short medial seta and 2 longer lateral setae; gonopods IX each with 2 unthickened setae; vulvar fimbriae indistinct.

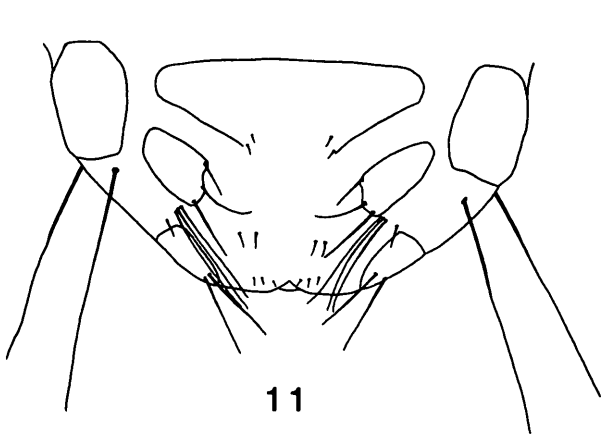
Type Material. HOLOTYPE: ♂, ex ♀ *Maxomys hellwaldi* (Jentink) (LAD No. 68), Dumoga-Bone National Park (123°53′E, 0°34′N), Bolaang Mongondow Province, Sulawesi Utara, Indonesia, about 240 m elevation, II-1985, L. A. Durden. ALLOTYPE: ♀, same data as holotype except ex ♀ *M. hellwaldi* (LAD No. 56). PARATYPES: 7♂♂, 20♀♀, same data as holotype, with individual collections as follows: 2♂♂, 5♀♀ ex ♀ *M. hellwaldi* (LAD No. 44); 1♂, 2♀♀, ex ♂ *M. hellwaldi* (LAD No. 54); 1♂, 3♀♀, ex ♀ *M. hellwaldi* (LAD No. 59); 2♀♀ ex ♂ *M. hellwaldi* (LAD No. 65); 2♂♂, 7♀♀, ex ♀ *M. hellwaldi* (LAD No. 68); 1♂, 1♀, ex ♀ *M. hellwaldi* (LAD No. 79). Holotype and allotype deposited in NMNH; paratypes deposited in BMNH, MZB, NMNH, and LAD.

Additional Material Examined. All specimens with same data as holotype except: 3♂♂, 4♀♀, ex ♂ *Rattus hoffmanni* (Matschie) (LAD No. 62); 5♂♂, 8♀♀, ex ♂ *Bunomys fratrorum* (Thomas) (Lad No. 26); 1♂, 1♀, ex ♂ *B. fratrorum* (LAD No. 30); 2♂♂, 1♀, ex ♂ *B. fratrorum* (LAD No. 61).

Remarks. This species is named for D. T. Sembel of Sam Ratulangi University, Manado, Sulawesi Utara, in recognition of his indispensable cooperation in my ectoparasite studies in Sulawesi. Again, this is a fairly typical species of *Hoplopleura* and is similar in many respects to *H. pacifica*. A com-







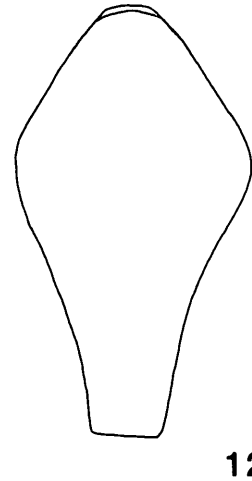


Fig. 9–12. *H. sembeli* Durden, n. sp., female. (9) Dorsal-ventral view. (10) Paratergal plates. (11) Genitalia. (12) Thoracic sternal plate.

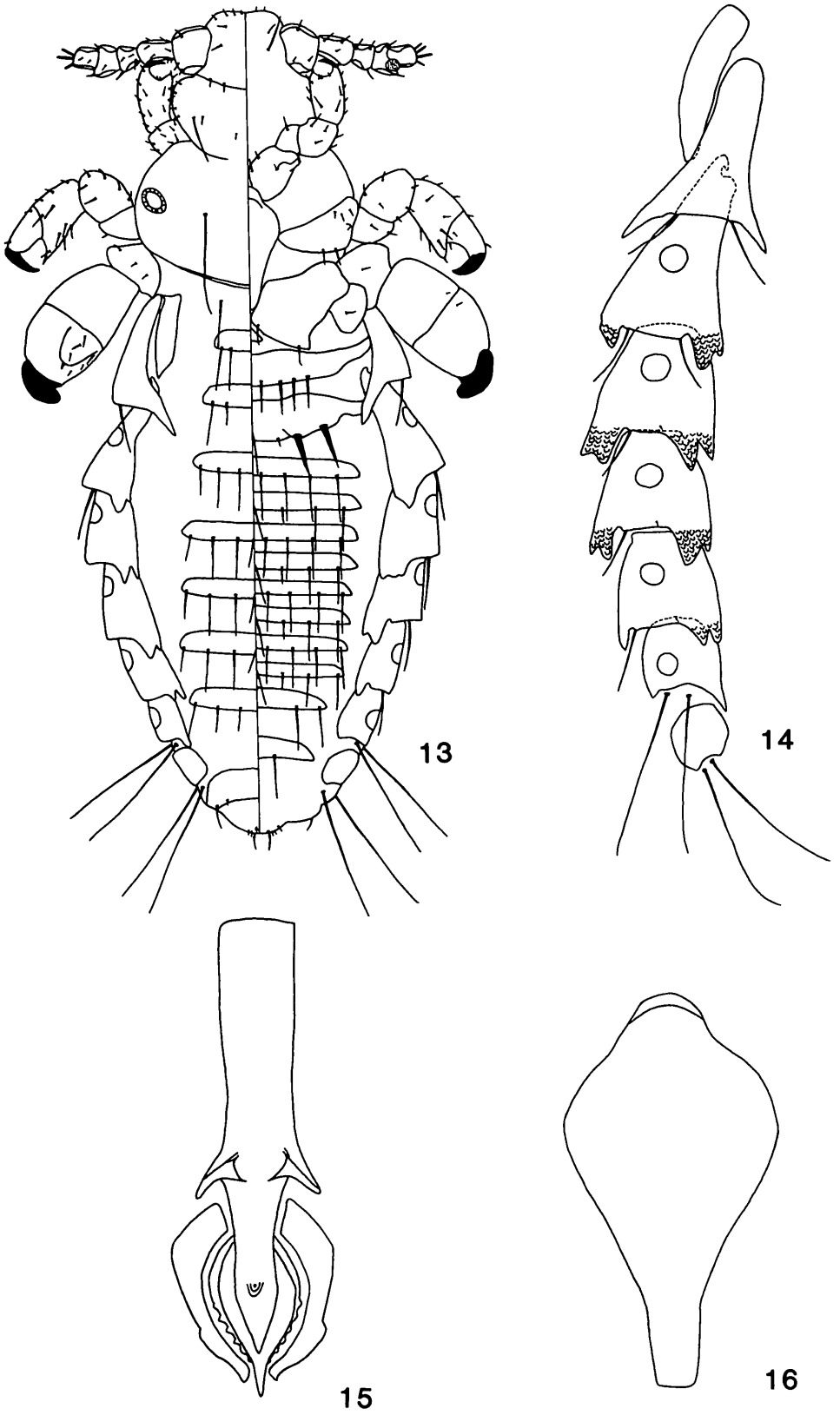


Fig. 13–16. *H. sembeli* Durden, n. sp., male. (13) Dorsal-ventral view. (14) Paratergal plates. (15) Genitalia. (16) Thoracic sternal plate.

bination of the following characters distinguishes *H. sembeli*: the shape, sculpting and setation of the paratergal plates; the shape of the thoracic sternal plate; the large spiracles; the presence of two small medial setae on the third abdominal sternite; and the characteristics of the genitalia. Although *H. sembeli* is a common ectoparasite of the murid *M. hellwaldi*, it also was collected from the sympatric murids *R. hoffmanni* and *B. fratrorum*. In this respect, *H. sembeli* is similar to *Polyplax wallacei* Durden, which also parasitizes sympatric murids at comparable elevations in the same forests (Durden 1987).

Hoplopleura musseri Durden, n. sp.
(Fig. 17–27)

Male. Total length of holotype, 1.21 mm (mean for series, 1.22; range, 1.13–1.30; $n = 8$). Head, thorax, and abdomen well sclerotized.

Head. Slightly longer than wide with blunt, rounded apex and finely crenulated lateral margins posterior to antennae; 2 SHS distinct on each side but DMHS absent; DPHS displaced laterally, average in length, almost extending to mesothoracic spiracle; 1 DAnCHS, 1 DPoCHS, 1 DPaHS, 1 SpAtHS, and 1 VPHS on each side; ApHS distinct.

Thorax. Broader than long, anterior angles squared and mesothoracic spiracle (0.029 mm in diameter) displaced laterally with part clearly visible ventrally; thoracic sternal plate rounded anteriorly but with subapical indentation on each side, elongated posteriorly to broad apex; DPTS and other thoracic setae absent. *Legs.* Fore and hind coxae subtriangular, midcoxae with elongate protuberance; spinous thickenings on fore and hind legs; fore legs smaller than mid and hind legs, all with pointed tarsal claws.

Abdomen. Wider than thorax with 1 broad plate per segment dorsally and 2 thinner plates on segments 4–6 ventrally; 7 rows of TeAS, each with 4–11 setae; 12 rows of StAS, the 1st 10 rows each with 6–8 setae, 11th row with 4 setae, 12th row with 2 setae; StAS on 3rd sternite consisting of 1 robust lateral seta on each side and 5 setae of regular thickness between them; sternites of segments 2 and 3 extending completely across ventral surface to articulate with corresponding paratergal plates. Paratergites present on segments 1–8; plate II with 1 short seta, plates VII and VIII each with 2 long setae but other plates devoid of setae; plates with surface sculpting and of various shapes, but plate VIII with ventral angle tapering to elongated point; plates III–VII each with a spiracle. *Genitalia.* Basal plate longer than parameres; parameres curved and noticeably sclerotized anteriorly; pseudopenis thick and extending well beyond apices of parameres.

Female. Total length of allotype 1.72 mm (mean for series, 1.58; range, 1.42–1.81; $n = 19$). *Head, thorax, legs,* and *paratergites.* As in male unless described otherwise; thoracic sternal plate extended anteriorly to rounded apex.

Abdomen. With 2 tergites on each of segments 2 and 3, 3 tergites on each of segments 4–7, 1 tergite on segment 8; 3 sternites on each of segments 3–6; 17 rows of TeAS, each with 4–7 setae (except row 17 with 2 setae); 15 rows of StAS, each with 2–7 setae. Paratergites with sculpting largely restricted to apical regions of plates III–VIII; plate VIII with dorsal and ventral angles extended to elongated points. *Genitalia.* Subgenital plate subtriangular but with deep anterior indentations; gonopods VIII fairly small, each with 3 long setae; gonopods IX each with 1 thick apical seta; vulvar fimbriae indistinct; 8 elongate protuberances positioned terminally, each with fairly long apical seta, lateral protuberance on each side larger than 6 central ones, with larger, thicker apical seta.

Third Instar. Total length: mean, 0.86 mm; range, 0.77–0.92; $n = 6$.

Head. Head and first 4 antennal segments with ventral tubercles (with 6 distinct tubercles on head proper); SHS, ApHS, AnMHS, and VPHS distinct, but other head setae (except those on antennae) absent; lateral border of head behind antennae finely crenulated.

Thorax. Without sternal plate or setae, with laterally positioned mesothoracic spiracle. *Legs.* Coxae subtriangular, fore and midcoxae each with 3 large setae and hind coxae each with 2 large setae; hind tibiae with wrinkled appearance along part of length.

Abdomen. Membranous and sculpted over entire surface but without setae or paratergites.

Second Instar. Total length: mean, 0.70 mm; range, 0.69–0.75; $n = 11$. Similar to third instar but with following differences: 8 distinct ventral tubercles on head proper; no wrinkling of hind tibiae.

First Instar. Total length: mean, 0.61 mm; range, 0.58–0.63; $n = 10$.

Head. Head with 8 ventral tubercles; 1 SHS and 1 VPHS on each side, but other setae (except those on antennae) absent; lateral border of head behind antennae finely crenulated.

Thorax. Without sternal plate or setae, with lateral spiracles. *Legs.* All coxae each with 3 large setae; tubercles present on coxae and trochanters of fore and midlegs and on tibiae of midlegs.

Abdomen. Membranous and sculpted over entire surface, without paratergites, with pair of long subterminal setae.

Type Material. ♂ Holotype, ♀ Allotype, 7♂♂, 18♀♀ Paratypes, 6 third instars, 11 second instars, 10 first instars, ex *Maxomys musschenbroeki* (Jentink), Bolaang Mongondow Province, Sulawesi Utara, Indonesia, II-1985, L. A. Durden. Individual collections are as follows: 7♂♂ (including holotype), 14♀♀ (including allotype), 4 third instars, 10 second instars, 9 first instars, ex ♂ *M. musschenbroeki* (LAD No. 39) near Danau (Lake) Moajat (124°29'E, 0°45'N), about 1,300 m elevation; 2♀♀, ex ♂ *M. musschenbroeki* (LAD No. 11), Dumoga-Bone National Park (123°53'E, 0°34'N), about 240 m elevation;

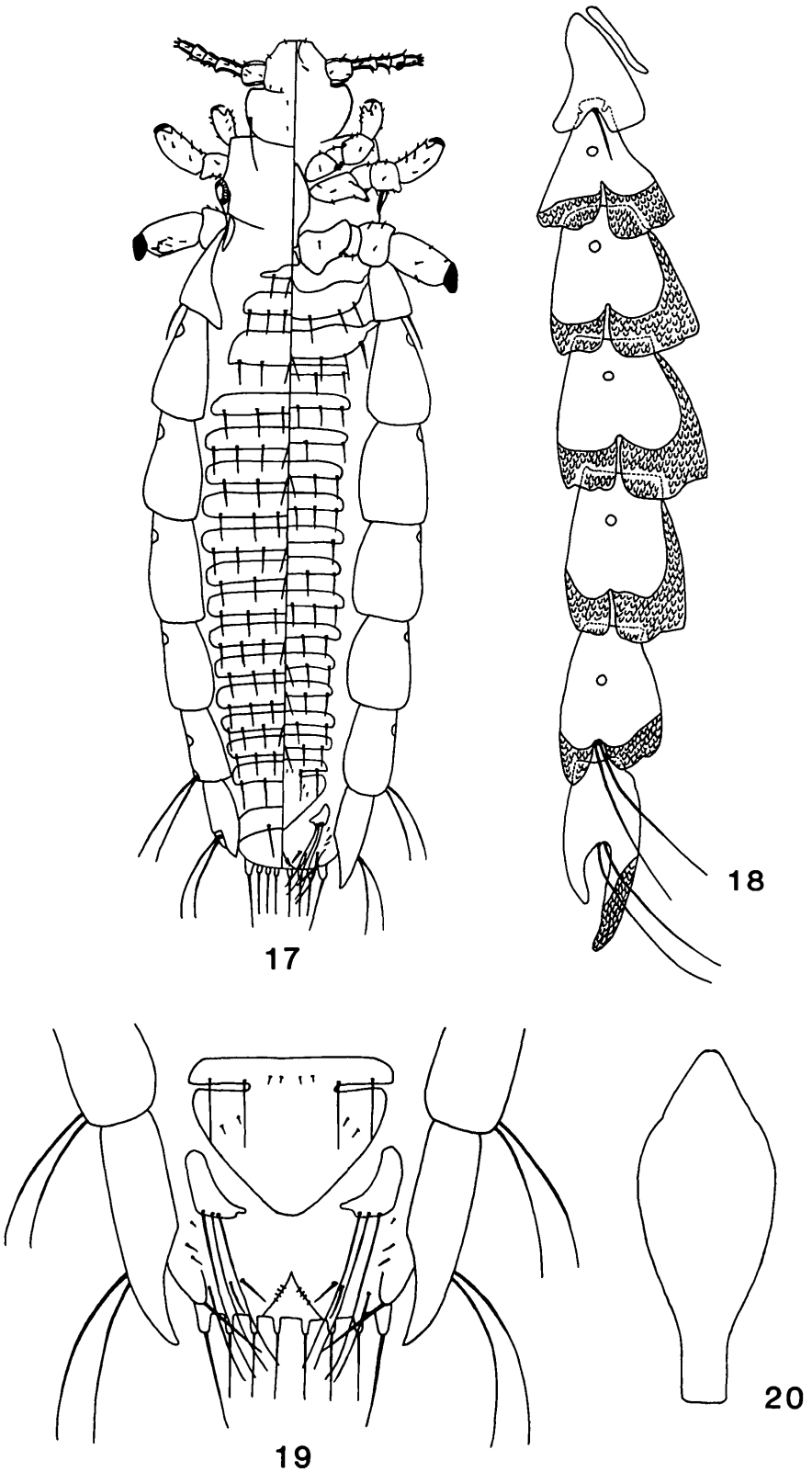


Fig. 17–20. *H. musseri* Durden, n. sp., female. (17) Dorsal-ventral view. (18) Paratergal plates (sculpting interrupted to show outline of plate beneath in dotted lines). (19) Genitalia. (20) Thoracic sternal plate.

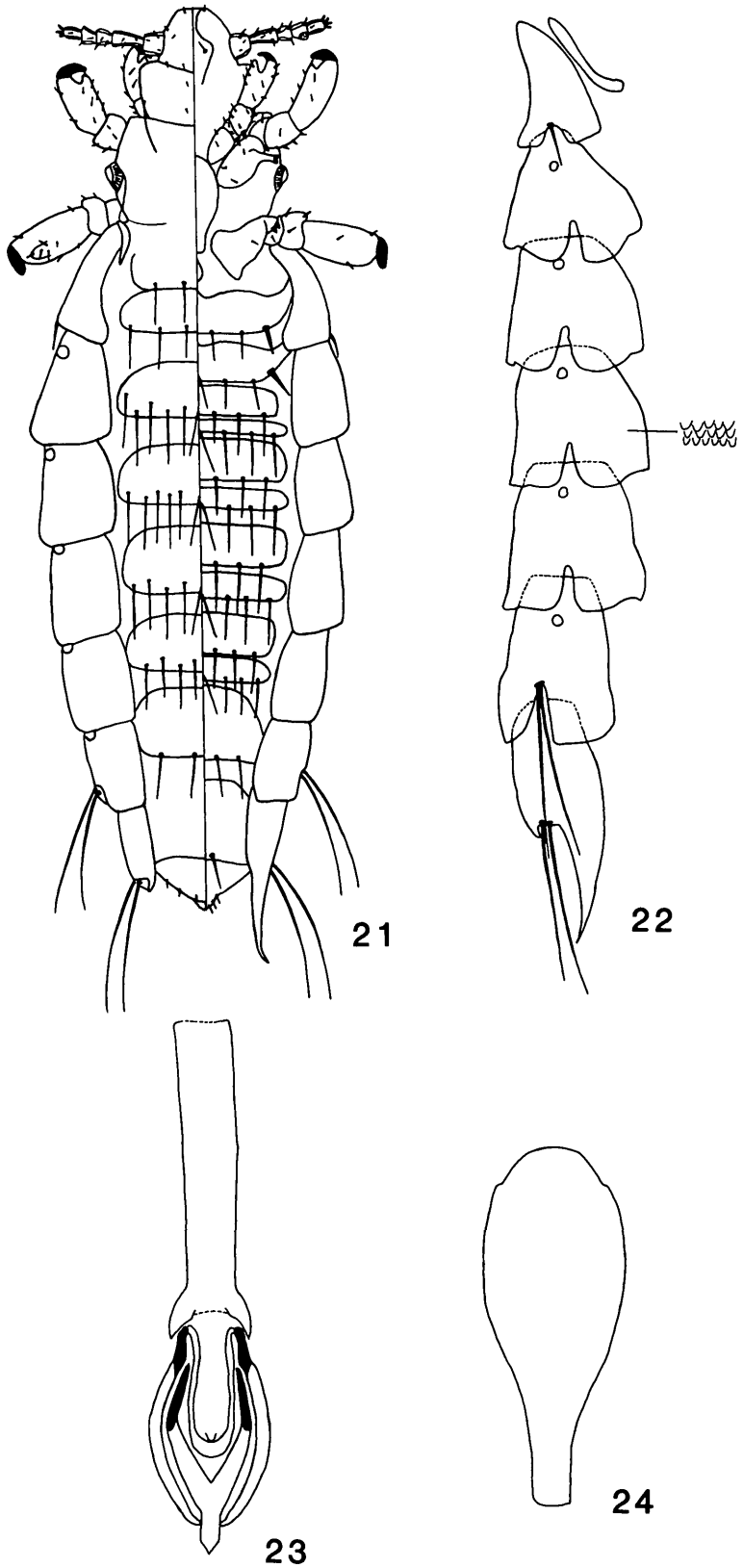


Fig. 21–24. *H. musseri* Durden, n. sp., male. (21) Dorsal-ventral view. (22) Paratergal plates. (23) Genitalia. (24) Thoracic sternal plate.

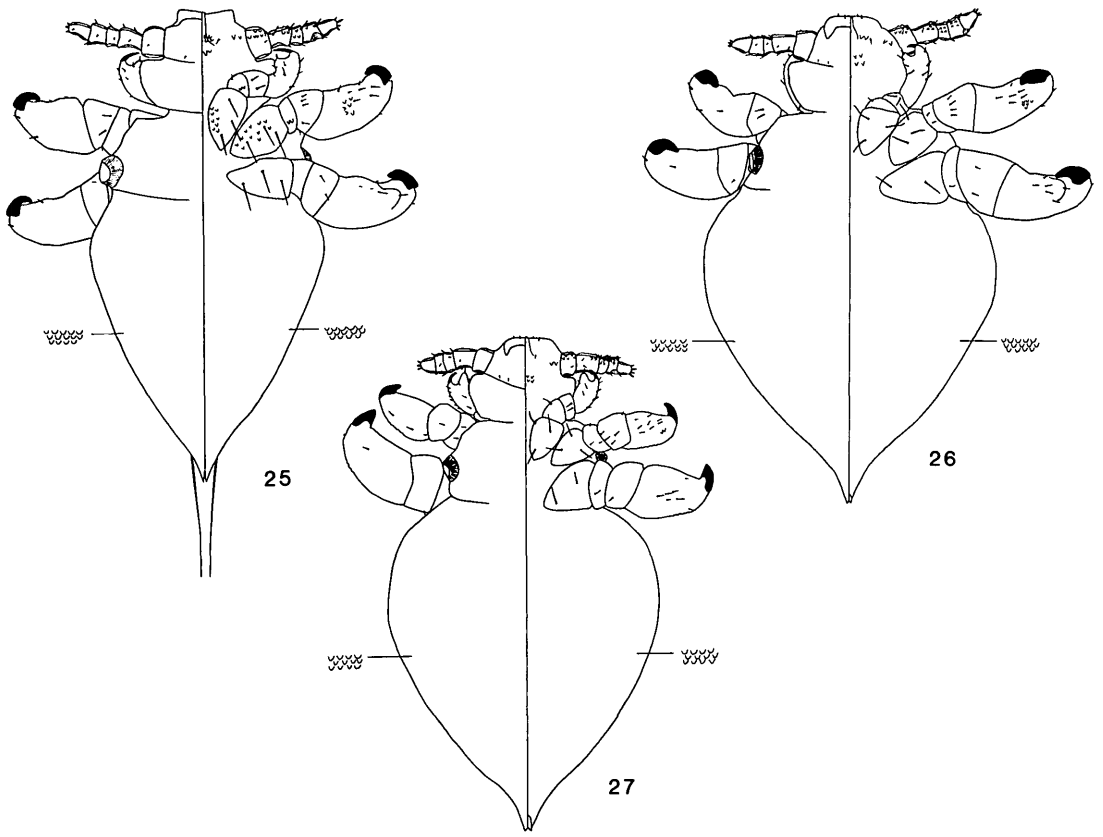


Fig. 25–27. *H. musseri* Durden, n. sp., dorsal-ventral views of nymphs. (25) First instar. (26) Second instar. (27) Third instar.

1♂, 1♀, 1 third instar, 1 second instar, 1 first instar, ex ♂ *M. musschenbroeki* (LAD No. 14), Dumoga-Bone National Park as above; 2♀♀, ex ♀ *M. musschenbroeki* (LAD No. 57), Dumoga-Bone National Park as above; 1 third instar, ex ♂ *M. musschenbroeki* (LAD No. 60), Dumoga-Bone National Park as above. Holotype and allotype deposited in NMNH; paratypes deposited in the BMNH, MZB, NMNH, and LAD.

Remarks. This species is named for Guy G. Musser of the American Museum of Natural History, New York, in recognition of his scholarly studies on the taxonomy of Sulawesian mammals and for his continued interest and help with my studies.

H. musseri is atypical in comparison with all but one of its congeners, *H. pectinata* Cummings. Adults of *H. musseri* and *H. pectinata* share a number of identifying characters, most notably the following: the lateral positioning of the mesothoracic spiracle and the DPHS; the squarish anterior border of the thorax; the absence of DMHS and thoracic setae; the thickenings and protuberances on the legs; the elongated, tapering eighth paratergal plates; and the eight spiny protuberances situated terminally on the female abdomen (probably functional during mating or oviposition). Differences between adults of these two similar species include the larger lateral terminal protuberances on the abdomen of *H. musseri* females, the precise morphology of the genitalia, and the presence of two small setae on paratergal plates III–VI in *H. pectinata* (these are absent in *H. musseri*).

The nymphs of *H. musseri* and *H. pectinata* are more typical for *Hoplopleura*; ventral tubercles are characteristic of nymphs of this genus. However, the overall reduction in setation (except on the antennae and legs), the laterally positioned thoracic spiracles, and the extensive abdominal sculpting are unusual features for immatures of *Hoplopleura*. Nymphs of *H. musseri* and *H. pectinata* can be separated by the following characters: *H. pectinata* possess a few small setae on the thorax and abdomen (absent in *H. musseri*); in *H. musseri*, ventral thoracic tubercles occur only on the fore and midcoxae of first instars, whereas they are present in all instars of *H. pectinata* (also, ventral thoracic tubercles are not confined to the legs in *H. pectinata*); the abdominal sculpting is fairly uniform in *H. musseri* nymphs but is interrupted by "plaques" in *H. pectinata* immatures. The nymphal instars of *H. pectinata* have been described and illustrated by Johnson (1972).

Hoplopleura musseri is probably host-specific to the spiny forest rat, *M. musschenbroeki*, a wide-

spread and fairly common bioendemic murid which occurs throughout Sulawesi (Musser et al. 1979).

Discussion

Although additional new taxa of Anoplura are likely to be collected when more of Sulawesi's bioendemic rodents are examined for ectoparasites, some interesting trends relating to host–louse coevolution already can be noted. Musser (1987) has shown that most of the 69 species of bioendemic mammals known from Sulawesi are representatives of species clusters, and that this and certain zoogeographical data suggest that early mammalian colonization of this island was principally by rafting from Southeast Asia. A cladistic analysis of Indo-Australian *Hoplopleura* for comparison with accepted host cladograms (a test of host–parasite coevolution) is not yet possible for Sulawesi's poorly known louse fauna. Agreements between host and louse phylogenies, particularly with regard to areas of origin, would corroborate accepted scenarios for the mammalian origins, whereas incongruences would require reappraisal of one of the data sets. Such analyses rely on the principle that coevolution between vertebrates and their ectoparasites (Fahrenholz's rule) is widespread for lice on mammals, although in certain cases, resource tracking has apparently taken place in addition to (or as an alternative to) phyletic tracking (Timm 1983; Lyal 1986, 1987; Hafner & Nadler 1988).

Hoplopleura pectinata was originally described from the spiny rat, *Maxomys surifer* (Miller), from peninsular Malaysia. Referring to this louse, Ferris (1921) stated, "This is a peculiar and isolated species, . . . not intimately connected with any other known form." Johnson (1964) made similar comments on the unusual morphology of *H. pectinata,* which she recorded from *M. surifer* and also from the related spiny rats *M. whiteheadi* (Thomas), *M. alticola* (Thomas), and *M. rajah* (Thomas) from Malaysia and Borneo. In their taxonomic revision, Musser et al. (1979) defined the sundaic murid genus *Maxomys* as consisting of 16 related species previously included in the unwieldy genus *Rattus* (including *M. surifer, M. alticola, M. whiteheadi, M. rajah, M. musschenbroeki,* and *M. hellwaldi,* the last two species bioendemic to Sulawesi) ranging from the Indo-China Peninsula to Sulawesi. Therefore, the lice documented here (particularly *H. musseri,* which is host-specific to *M. musschenbroeki*) provide a check for this murid taxonomy. Comparison of *H. musseri* with *H. pectinata* reveals a high degree of similarity, particularly in characters that are unusual for this louse genus. No other lice are currently known that possess the unusual morphological traits of these two species (although other *Maxomys* spp. rats from Sulawesi and elsewhere have yet to be intensively processed for lice), and they should be considered sister taxa. Evidence from these two lice, therefore, suggests they are closely related phylogenetically, and, if host–louse coevolution has occurred, their hosts also must be closely related; this would agree with the taxonomic revision of hosts presented by Musser et al. (1979).

Hoplopleura sembeli, although recorded mainly from *Maxomys hellwaldi* in this survey, is very different from *H. musseri.* However, not all *M. hellwaldi* individuals have spiny pelage (Musser et al. 1979); this louse is not host-specific to this murid, so the selective pressures that have influenced the morphology of *H. sembeli* must be very different.

Another case of probable Anoplura–mammal coevolution on Sulawesi involves the bioendemic macaques (*Macaca* spp.) and their pedicinid lice. Although agreement is not universal, Sulawesi probably has four species of *Macaca,* all of which are regionally bioendemic. *Macaca maura* F. Schinz, confined to South Sulawesi, is usually considered to be the least specialized of the four species and to represent the ancestral macaque stock that first colonized the island (Groves 1980, Musser 1987). *M. ochreata* (Ogilby) occurs in the southeastern arm of Sulawesi, whereas *M. tonkeana* (Meyer) inhabits much of central and North Sulawesi and *M. nigra* (Desmarest) the distal third of the northern arm (Fooden 1969, Groves 1980, Musser 1987). The species most distant from the probable ancestral form is, therefore, *M. nigra;* this species seems most specialized, so that physical distance from South Sulawesi could reflect evolutionary distance to a certain degree in this group. Although the lice of Sulawesian macaques are poorly known, preliminary data suggest coevolution between these partners. *M. maura,* the probable ancestral form, is parasitized by *Pedicinus obtusus* (Rudow) (Kuhn & Ludwig 1967), a relatively unspecialized pedicinid louse which also occurs on other macaque species throughout Southeast Asia. *P. cynopitheci* Kuhn & Ludwig shows slightly more specialized morphology (mainly with respect to setal arrangements), however, and is known only from "*Macaca hecki,*" a form which Kuhn & Ludwig (1967) stated to be a race of *M. nigra* but which is currently considered to be the subspecies of *M. tonkeana* that occupies the proximal two-thirds of the northern arm of Sulawesi (Groves 1980). The picture is rudimentary at present, however, because lice are not yet documented from *M. ochreata.* Also, a few *P. obtusus* have been collected from *M. nigra* in zoos (Hopkins 1949, Kuhn & Ludwig 1967), although these individuals almost certainly originated from other primate species caged nearby.

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References Cited

Cook, E. F. 1954. A modification of Hopkins' technique for collecting ectoparasites from mammalian skins. Entomol. News 65: 35–37.

Durden, L. A. 1986. Ectoparasites and other arthropod associates of tropical rain forest mammals in Sulawesi Utara, Indonesia. Nat. Geogr. Res. 2: 320–331.

1987. The genus *Polyplax* (Anoplura: Polyplacidae) in Sulawesi, Indonesia, with the description of a new species. Proc. Entomol. Soc. Wash. 89: 811–817.

Ewing, H. E. 1924. Ectoparasites of some Polynesian and Malaysian rats of the genus *Rattus*. Bull. Bernice P. Bishop Mus. 14: 7–11.

Ferris, G. F. 1921. Contributions toward a monograph of the sucking lice. Part II. Stanford Univ. Publ., Biol. Sci. 2: 57–133.

1935. Contributions toward a monograph of the sucking lice. Part VIII. Stanford Univ. Publ., Biol. Sci. 2: 527–634.

1951. The sucking lice. Memoir 1, Pacific Coast Entomological Society, San Francisco.

Fooden, J. 1969. Taxonomy and evolution of the monkeys of Celebes. Bibl. Primatol. 10: 1–148.

Groves, C. P. 1980. Speciation in *Macaca*: the view from Sulawesi, pp. 84–124. *In* D. G. Lindburg [ed.], The macaques. Studies in ecology, behavior and evolution. Van Nostrand Reinhold, New York.

Hafner, M. S. & S. A. Nadler. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. Nature (Lond.) 332: 258–259.

Hopkins, G. H. E. 1949. The host associations of the lice of mammals. Proc. Zool. Soc. Lond. 119: 387–604.

Johnson, P. T. 1964. The hoplopleurid lice of the Indo-Malayan subregion (Anoplura: Hoplopleuridae), pp. 67–102. *In* Miscellaneous Publication 4, Entomological Society of America, College Park, Md.

1972. Some Anoplura of the Oriental region. A study of *Hoplopleura pacifica* Ewing and allies. J. Med. Entomol. 9: 219–227.

Kim, K. C. 1966. The species of *Enderleinellus* (Anoplura, Hoplopleuridae) parasitic on the Sciurini and Tamiasciurini. J. Parasitol. 52: 988–1024.

1986. A new species of *Linognathoides* (Polyplacidae: Anoplura) from black-tailed prairie dog, *Cynomys ludovicianus* (Ord) (Sciuridae: Rodentia). Proc. Entomol. Soc. Wash. 88: 354–359.

Kim, K. C. & H. W. Ludwig. 1978. The family classification of the Anoplura. Syst. Entomol. 3: 249–284.

Kim, K. C., H. D. Pratt & C. J. Stojanovich. 1986. The sucking lice of North America. An illustrated manual for identification. Pennsylvania State University Press, University Park.

Kuhn, H.-J. & H. W. Ludwig. 1967. Die Affenläuse der Gattung *Pedicinus*. Z. Zool. Syst. Evolutionsforsch. 5: 144–297.

Lyal, C. H. C. 1986. Coevolutionary relationships of lice and their hosts: a test of Fahrenholz's rule, pp. 77–91. *In* A. R. Stone & D. L. Hawksworth [eds.], Coevolution and systematics. Clarendon, Oxford.

1987. Co-evolution of trichodectid lice (Insecta: Phthiraptera) and their mammalian hosts. J. Nat. Hist. 21: 1–28.

Musser, G. G. 1987. The mammals of Sulawesi, pp. 73–93. *In* T. C. Whitmore [ed.], Biogeographic evolution of the Malay archipelago. Clarendon, Oxford.

Musser, G. G., J. T. Marshall & Boedi. 1979. Definition and contents of the sundaic genus *Maxomys* (Rodentia, Muridae). J. Mammal. 60: 592–606.

Pritchard, A. E. 1947. *Hoplopleura oenomydis* Ferris, a louse found on domestic rats in the United States. J. Parasitol. 33: 374–375.

Timm, R. M. 1983. Fahrenholz's rule and resource tracking: a study of host-parasite coevolution, pp. 225–265. *In* M. H. Nitecki [ed.], Coevolution. University of Chicago Press, Chicago.

Traub, R., C. L. Wisseman, Jr., & A. Farhang-Azad. 1978. The ecology of murine typhus—a critical review. Trop. Dis. Bull. 75: 237–317.

Voss, W. J. 1966. A lectotype designation for *Hoplopleura pacifica* Ewing (Anoplura: Hoplopleuridae). Pac. Insects 8: 29–32.

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