

TAXONOMIC RELATIONSHIPS OF *NEOHAEMATOPINUS* TO *JOHNSONPHIRUS* AND *LINOGNATHOIDES* (POLYPLACIDAE: ANOPLURA)¹

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Abstract. Of the known species of *Neohaematopinus* s. lat. (sensu Ferris 1951), the 3 genera *Johnsonphirus*, *Linognathoides* and *Neohaematopinus* s. str. are recognized and redefined on the basis of nymphs and adults. *Johnsonphirus* is a senior synonym of *Alenaphirus*. The adults and 3 nymphal instars of *J. spinosissimus* are redescribed and illustrated, and the lectotype of *J. helioscouri* is designated. The inclusive species for each genus are listed with host and distribution data.

While studying a long series of *Neohaematopinus* from African tree and bush squirrels (*Funisciurus* and *Paraxerus*), we discovered many specimens of the 2nd and 3rd nymphal instars that were molting to the adult stage. They were identical to the types of *Alenaphirus spinosissimus* Benoit (1969) collected from *Paraxerus boehmi* (as *Tamiscus vulcanorum*). Much earlier, we recognized that the type specimens of *A. spinosissimus* described and figured were not adults but rather the 3rd-instar nymphs in the process of molting, and that these specimens showed nymphal characters superimposed on adult characters. This observation was confirmed by examination of the type specimens, which are deposited in Tervuren, Belgium.

We further discovered that the nymphs of another *Neohaematopinus* species from *Funisciurus* and *Paraxerus*, which turned out to be *Johnsonphirus chlorotalpae* Benoit (1961), had numerous ventral tubercles on the head, antennae and coxae, more resembling immature *Hoplopleura* than typical *Neohaematopinus*. This observation led us to reexamine the nymphs of all available *Neohaematopinus* species.

The genus *Alenaphirus* Benoit was first established on the basis of *A. spinosissimus* by monotypy. Adults of *spinosissimus* are very similar to, and key out to, *Neohaematopinus*. However, the nymphs do

not resemble typical *Neohaematopinus*. The genus *Johnsonphirus* Benoit (1961) was established on the basis of 3 females, 1 male and 3 nymphs collected from *Chlorotalpa stuhlmanni* (Chrysochloridae, Insectivora) in Kivu, Congo, with *J. chlorotalpae* as the type species. The adults of *chlorotalpae* closely resemble *Neohaematopinus*, whereas the nymphs are more like immature *Alenaphirus*. Further examination showed that both adults and nymphs of *Johnsonphirus* are very similar to those of *Alenaphirus* and they are clearly congeneric. Accordingly, the name *Johnsonphirus* is a senior synonym of *Alenaphirus*.

Cummings (1914) recognized *Linognathoides* for *L. citelli* Cummings, which was later synonymized with *Neohaematopinus* by Ferris (1923). The adults of *citelli* deviate considerably in morphology from other *Neohaematopinus* adults, although they would be diagnosed as *Neohaematopinus* sensu Ferris (1923, 1951). However, the nymphs do not resemble immature *Neohaematopinus*. A study of the nymphs revealed that *citelli* and its related species form a distinct group whose adults are superficially similar to *Neohaematopinus* and *Johnsonphirus* but whose nymphs are clearly different. Accordingly, the name *Linognathoides* is resurrected for this taxon.

In this paper, we (1) discuss taxonomic relationships between *Johnsonphirus*, *Linognathoides*, and *Neohaematopinus*, (2) redescribe and illustrate the adults and 3 nymphal instars of *J. spinosissimus*, (3) designate a lectotype for *J. helioscouri* (Cummings), and (4) redefine the genera *Johnsonphirus*, *Linognathoides*, and *Neohaematopinus* with known inclusive species.

Materials for this study were made available by Dr K. C. Emerson, 560 Boulder Drive, Sanibel, Florida 33957, and by the National Museum of Natural History, Smithsonian Institution. The classification and nomenclature used for mammals follows Simpson (1945) for the world, Meester & Setzer (1971) for African fauna, and Corbet (1978) for Palaearctic fauna. Morphological terms and chaetotaxy used in this paper are those of Kim &

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Ludwig (1978). Measurements are given in millimetres, with means for the series followed by the range in parentheses.

TAXONOMY AND HOST ASSOCIATIONS OF
Neohaematopinus S. LAT.

Species of *Neohaematopinus* s. lat. are primary parasites of squirrels (Sciuridae) in the Ethiopian, Holarctic and Oriental regions. Some species, in more recent evolutionary times, invaded other hosts beyond the Sciuridae, such as the North American *Neotoma* (Cricetidae) and African golden moles, *Chrysochloris* (Chrysochloridae, Insectivora). *Neohaematopinus* as defined by Ferris (1923, 1951) is a heterogeneous group including a number of aberrant species, such as *pectinifer* (Neumann) and *cielli* (Cummings) for which *Lulegus* Fahrenholz and *Linognathoides* Cummings were respectively recognized.

The genus *Neohaematopinus* was first recognized by Mjöberg (1910) on the basis of *Haematopinus sciuropteri* Osborn. In the same paper he also recognized the genus *Acanthopinus* for *Acanthopinus sciurinus* (n. n. for *Haematopinus antennatus* Osborn). Later, Cummings (1914) erected *Linognathoides* for *L. cielli* Cummings, and Fahrenholz (1916) established *Lulegus* for *Haematopinus pectinifer* Neumann. Ferris (1923, 1951) considered that these taxa constituted a natural group and rejected these generic names. However, the 2 additional names were again proposed without satisfactory justification: *Ahaematopinus* Fwing (1929) with *N. inornatus* Kellogg & Ferris as type, and *Petauristophthirus* Eichler (1949) with *N. petauristae* Ferris as type. *Neohaematopinus* s. lat. (Ferris 1951) is different from other polyplacids by having (1) the 2nd tergal plate of the 2nd abdominal segment in the male at least slightly modified, with its posterior margin emarginate and 2 groups of radially arranged setae at each end of the emargination (if this tergite is reduced, the row of setae is still modified), (2) the paratergites of the 2nd abdominal segment entire and (3) paratergites on abdominal segments 2-8.

In light of the rediscovery of *Johnsonphthirus spinosissimus*, we have examined the nymphs of 27 species previously assigned to *Neohaematopinus*. Of these, the nymphs of 5 species were definitely *Johnsonphthirus*, with more than 20 ventral tubercles on the head, 1 on the basal antennal segment, and more than 3 microtubercles with a blunt posterior

spur on each coxa (Fig. 3, 4). The adults of *Johnsonphthirus* also differ distinctly from *Neohaematopinus* by having 1 spiniform seta on the apical part of the 3rd antennal segment in the male (Fig. 5) and the thoracic sternal plate usually truncate posteriorly with posterolateral emarginations (Fig. 26a, b, c). The head setae, particularly OSTIS (outer sutural head setae) and 3rd DMHS (dorsal marginal head setae), are long and thickened.

On the other hand, the males of *Neohaematopinus* have 2 spines or spiniform setae on the 3rd antennal segment (Fig. 8), and in both males and females the posterior margin of the thoracic sternal plate is strongly emarginate with posterolateral angles prolonged (Fig. 28a-l). The nymphs of *Neohaematopinus* are completely devoid of ventral tubercles on the head and coxae, although the basal antennal segment occasionally bears a single blunt, but often obscure, tubercle.

Of the 35 species examined, 9 previously assigned to *Neohaematopinus* were recognized as forming a distinct taxon referable to *Linognathoides*. The nymphs of *Linognathoides* differ from *Johnsonphthirus* and *Neohaematopinus* by having 2-10 tubercles, often blunt, on the ventral side of the head, 1 large, blunt ventral tubercle on the basal antennal segment, and 1 large, blunt posterior spur without microtubercles on each coxal plate (Fig. 16-19). The adults of *Linognathoides* are also separable from the allied groups by having the abdominal tergites and sternites as well as paratergites highly reduced and the thoracic sternal plate posteriorly rounded or convex without posterolateral projections (Fig. 21, 22, 24, 25).

Each of the 3 taxa, *Johnsonphthirus*, *Linognathoides* and *Neohaematopinus*, is confined to a different host group. *Johnsonphthirus* is parasitic on African tree squirrels (Funambulini) restricted to the Ethiopian Region, whereas *Linognathoides* is on the ground squirrels: Marmotini (Northern ground squirrels) of the Holarctic Region and Xerini (African ground squirrels) of the Ethiopian Region. Considering a large collection of *J. chlorotalpae* from *Paraxerus*, *Funiscurus* and *Helioscirus*, the original collection of *J. chlorotalpae* from *Chrysochloris stuhlmanni* Marsch (as *Chlorotalpa stuhlmanni*) might have been a contamination or straggler, and the type host may be an accidental host. *Neohaematopinus* s. str. is more widely distributed and is parasitic on 4 major groups of squirrels of the Holarctic and Oriental regions: Sciurini, Tamiasciurini, Petauristini, and Callosciurini.

Genus **Johnsonphirus** Benoit

Johnsonphirus Benoit, 1961. Rev. Zool. Bot. Afr. **63**: 238 (type-species: *Johnsonphirus chlorotalpae* Benoit).

Aleataphirus Benoit, 1969. Rev. Zool. Bot. Afr. **80**: 108 (type-species: *Aleataphirus spinosissimus* Benoit). **New synonymy.**

Neohaematopinus (partum) Cummings, 1912. Bull. Entomol. Res. **3**: 383 (limited to *N. helioscivri* Cummings) (Ferris, 1915. Proc. Calif. Acad. Sci. 4th Ser. **6**: 168 (limited to *N. helioscivri* Cummings); 1923. Stanford Univ. Publ. Univ. Ser. Biol. Sci. **2**: 237 (limited to *N. helioscivri* Cummings, *N. kenae* Ferris, *N. subhelios*); 1951. Mem. Pan. Par. Entomol. Soc. **1**: 185 (limited to the species from Funambuline scutids) —Johnson, 1960. Tech. Bull. U.S. Dep. Agric. **1211**: 43 [not *N. pectinifer* (Neumann), *N. laura* (Bedford)].

Type-species: *Johnsonphirus chlorotalpae* Benoit, by original designation.

Description (Fig. 1–7, 26a–d). Anoptina without eyes. ADU:LS (Fig. 1, 2). **Head** (Fig. 3) As long as wide or slightly longer, with postantennal angle convex; antennae 5-segmented, basal segment with or without posterolateral angle usually bearing a stout seta, ♂ with 3rd segment usually somewhat produced anterolaterally and bearing 1 strong spine or spiniform seta; ♀ with 3rd segment not bearing a strong spine or seta; VPIS present and sometimes very thin. **Thorax**. With sternal plate posteriorly truncate with posterolateral emargination (Fig. 26a–d). **Legs**. Forelegs small and weak with acuminate claw, mid- and hindlegs larger and usually subequal or with hindlegs slightly larger, each with a strong claw. **Abdomen**. With paratergal plates well developed on 2nd to 8th segment, plates 3–6 varying from small and triangular in some species to large and subquadrate angular in others, each bearing a dorsal and ventral paratergal seta, plates 7–8 usually ellipsoid with long slender setae, tergites and sternites highly developed; dorsally and ventrally well covered with rows of setae usually arising from posterior margin of plates, 2nd plate of 2nd tergite usually emarginate posteriorly with a group of setae on each lateral knob. NYMPHS (Fig. 3, 4). **Head**. With 5-segmented antennae, basal and 2nd segments having ventral tubercles and 1 dorsal spin; ventral side with small, pointed tubercles, sometimes as many as 20 or more. **Thorax**. With sparse setae, but usually with DPIS distinct. **Legs**. As in adult except coxae with 3 or more small tubercles and 1 blunt posterolateral spin. **Abdomen**. Surface usually minutely scaly, always with less setae than adult; paratergites visible in N2 and strongly demiform with a rounded base.

Distribution and hosts. Funambulini; Africa.

Included species.

- chlorotalpae* (Benoit), ex *Chrysochloris stuhlmanni*; N and NE Zaire, Uganda, Tanzania.
- helioscivri* (Cummings), ex *Paraxerus palliatus*, *P. ochraceus*, *P. cepapi*; South Africa (Natal), SE Mozambique, Zimbabwe, Malawi, Tanzania, E Kenya and S Somalia.
- kenae* (Ferris), ex *Helioscivrus gambianus*, *H. ruwenzori*, *Paraxerus cepapi*; Kenya, Zaire, Mozambique, Tanzania, Namibia.
- spinosissimus* (Benoit), ex *Paraxerus boehmi*; Rwanda, Zaire.

- sunhelicus* (Ferris), ex *Paraxerus ochraceus*, *P. palliatus*, *P. cepapi*; Africa.

Lectotype designation for

Johnsonphirus helioscivri (Cummings)

Neohaematopinus helioscivri was described by Cummings (1912) from 1 male and 3 females collected 2 March 1912, ex *Paraxerus* (as *Helioscivrus*) *palliatus* (Peters) in the Uchweni Forest, Kenya (British East Africa). However, Cummings failed to designate a type specimen for the name *Neohaematopinus helioscivri*. The type (male) and paratype (females) designations on the slides were affixed at a later date without formal designation.

The original series of *N. helioscivri* is mounted on 3 slides, the male and 1 female separately and 2 females together. All 3 slides are labelled *Neohaematopinus helioscivrus* (sic). Here, in order to fix the type, we designate the aforementioned male as lectotype and the 3 females as paralectotypes. Type specimens are deposited in the British Museum (Natural History), London.

Johnsonphirus spinosissimus (Benoit)

FIG. 1–7, 26a

Aleataphirus spinosissimus Benoit, 1969. Rev. Zool. Bot. Afr. **80**: 108–11, fig. 8–13.

Redescription. ♂ (Fig. 2, 5, 6). Total body length ($n = 15$) 1.16 (1.08–1.25). **Head** (Fig. 5) About as long as wide; postantennal angles moderately developed, each with 1 DMHS (dorsal marginal head setae). 3rd DMHS large, spiniform. DPMS (dorsal principal head setae) long with a strong DACHS (dorsal accessory head setae); DPoCHS (dorsal posterior central head setae) strong, spiniform, displaced laterally behind DACHS; 2 SHS (supraantennal head setae) long; DANCHS (dorsal anterior central head setae) and supraantennal setae distinct, VPIS (ventral principal head setae) long, strong; anterior, apical and oral head setae distinct. **Antenna**. 5-segmented; basal segment enlarged with posterolateral angle produced and bearing a stout spiniform seta; segment 3 dorsally with 1 short, recurved spine at its apex; segment 4 constricted basally. **Thorax**. Broader than head; prothoracic and mesothoracic pleural apophyses slender; mesothoracic pleural apophyses encompassing the mesothoracic spine and medially connected; DPIS (dorsal prothoracic setae) and DMS (dorsal mesothoracic setae) strong and DPIS (dorsal principal thoracic setae) long, slender; thoracic sternal plate (Fig. 26a) with rounded anterior margins sloping to sharp posterolateral angles and with posterior margin truncate. **Legs**. Forelegs small with acuminate claw; mid- and hindlegs similar in size and shape, both larger than forelegs, each with a strong claw. **Abdomen**. Elliptical; tergal, sternal, and paratergal plates well developed; with 6 distinct spiracles on each side; 2nd plate of 2nd tergite strongly emarginate posteriorly with 3 to 4 setae on each knob; succeeding tergal plates each bearing 15 to 15 slender setae (9 on last tergal plate); segments 2 to 7 each with 2 sternal plates; sternal plates each with 6 to 8 slender setae (1 on last sternal plate); segments 3 to 6 each with long gonopatergites subquadrate angular; each paratergite with the posterior angles produced into

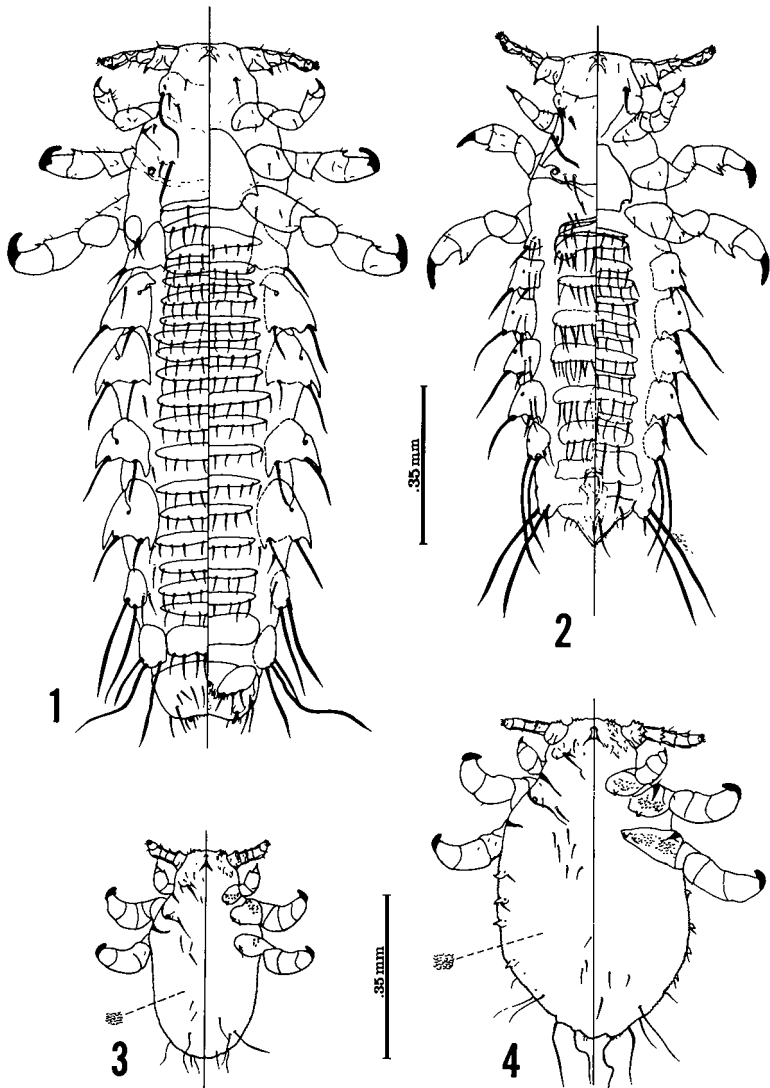


FIG. 1-4. *Jobsoniphthirus spinosissimus*: 1, ♀; 2, ♂; 3, nymph 1; 4, nymph 2.

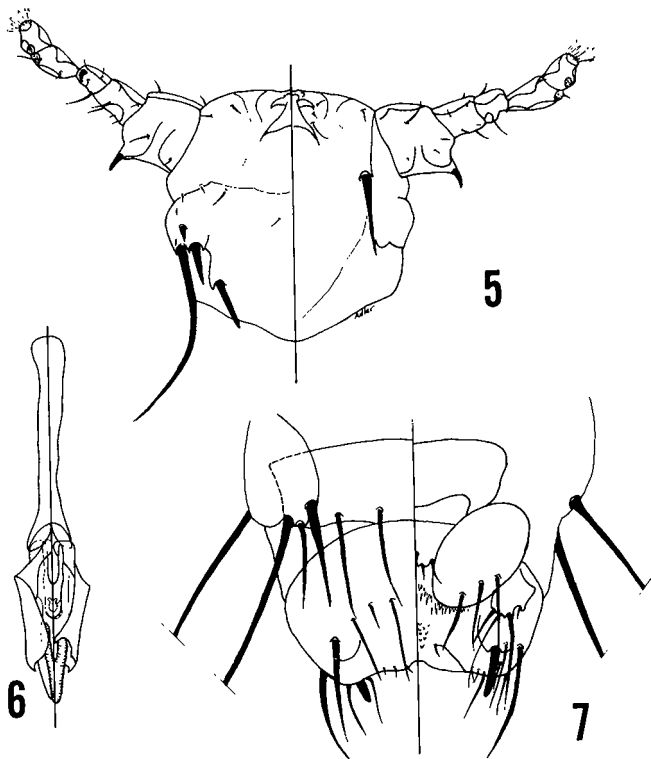


FIG. 5-7. *Johnsonophthorus spino-ossimus*: 5. ♂ head; 6. ♂ genitalia; 7. ♀ terminalia.

a strong tooth and with a dorsal paratergal seta and a shorter ventral paratergal seta; paratergites of segment 7 and 8 oval with a pair of extremely long setae. *Genitalia* (Fig. 6). With basal apodeme slender and extending to middle of 6th tergite; parameres sloping strongly from the base and forming a sharply pointed lateral shoulder; outline of the parameres forming a diamond, skewed apically; pseudopenis slender, Y-shaped, and longer than paramer; dorsal endometre slender and U-shaped.

♀ (Fig. 1, 7). Total body length ($n = 15$) 1.69 (1.51-1.83); head as in ♂ but medial SHS stronger; thorax and legs as in ♂. Antennae as in ♂ but 3rd segment without a spine and 4th segment less constricted basally. Abdomen as in ♂ but segments 2 to 7 each usually with 3 tergites and sternites; each tergal plate with 8 to 10 setae. *Genitalia* (Fig. 7). Gonopod VIII elliptical, with 3 distinct setae; gonopod IX with a thick, blunt seta in addition to numerous other setae.

Nymph (N) 1 (Fig. 3). Total body length ($n = 5$) 0.53 (0.48-0.59) *Head* Slightly wider than long with a cluster of

small tubercles at the anterior margin and 7 additional ventral tubercles distributed as far as the posterior antennal margin; 2 small DMHS; DPHS strong with a small DACHS; DPOCHS and DANCHS present; 2 SHS distinct; 1 supraantennal seta present; VPHS long and thin; apical or oral setae present. *Antenna*, 5-segmented; basal segment with 8 to 10 ventral tubercles, 2nd segment with about 6 ventral tubercles. *Thorax* Broader than head, with 1 strong DP1S, a small DMS; mesothoracic spiracle distinct. *Legs*. Forelegs weak with acuminate claw; mid- and hindlegs large with strong claw; all coxae each with 10 to 15 ventral tubercles in addition to a distinct, blunt spine near the coxal base. *Abdomen* Obovate and minutely scaled; a group of 6 DGAS (dorsal central abdominal setae), marginal abdominal setae long and slender; no indication of tergites, sternites or paratergites; abdominal spiracles indistinct.

N2 (Fig. 4). Total body length ($n = 6$) 0.72 (0.69-0.76). Identical to N1 except VPaHS present, each coxa having 20 to 60 ventral tubercles; a few additional dorsal abdominal setae,

parategites represented by 4 small, very stout teeth with rounded bases; abdominal spiracles faintly apparent.

N3. Total body length N3 ♂ ($n = 1$) 1.01; N3 ♀ ($n = 2$) 1.08 (0.96–1.20). Similar to N2 except anterior margin of head with more ventral tubercles (ca. 15 on each side), and abdomen with a few more dorsal setae.

Type data. Holotype ♀ and allotype ♂ 3rd-instar nymphs, RWANDA: Uinka (Shanguru), 11.VI.1962. A. Eibl, ex *Tamiscus vulcanorum* Thomas [= *Paraxerus boehmi* (Reichenow, 1886)] (A. Eibl F. 683). Deposited in the collection of the Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

Specimens examined. ZAIRE [all labeled "CONGO" (=Belgian Congo)], ex *Fanicus anerythrus*: Irangi, 3.I.1960, 4 ♂ (#1740); 22.VI.1968, 1 ♂ (#628); Juchere, 23.III.1969, 2 ♂ (#1926); ex *Fanicus* sp.: Irangi, 21.III.1969, 1 ♂ (#1928); 2.XII.1968, 1 ♂ (#1466); 25.II.1969, 1 ♀ (#1790); 24.II.1969, 1 ♀ (#1953); Karacui, 8.X.1968, 1 ♂ (#1160); Mifutu, 13.IX.1968, 1 ♀ (#1014); 4.XI.1968, 1 ♀ (#1291); 15.I.1969, 1 ♀ (#1719); Marieje Kangi, 27.III.1969, 1 ♀ (#2018); Kangi Kalolo, 24.III.1969, 1 ♀ (#1949); ex *Paraxerus* (vs *Tamiscus*) sp.: no location, 15.IX.1968, 1 ♂ (#1097); 25.II.1969, 2 ♂ (#1795); 15.IX.1968, 1 ♀ (no #); Irangi, 13.IX.1968, 3 ♂ (#1020); 19.VIII.1968, 1 ♀ (#916); 15.VIII.1968, 1 ♀ (#915); 24.III.1969, 1 ♂ (#1937); 4.XII.1968, 1 ♂ (#1497); 14.VII.1968, 5 ♂, 2 ♀ (#547); 16.I.1969, 1 ♀ (#1725); 7.X.1968, 1 ♀ (#1149); 25.II.1969, 1 ♀ (#1779); 24.II.1969, 2 ♀ (#1777); 19.VIII.1968, 2 ♀ (#921 & 923); Juchere, 23.III.1969, 1 ♀, 1 N1 (#1929); 23.III.1968, 1 ♂, 3 ♀, 1 N2 (#1930); 23.III.1969, 2 ♂ (#1925); 23.III.1969, 1 N1 (#1928); Mifutu, 14.IX.1968, 1 ♀ (#1081); 13.IX.1968, 1 ♂ (#1016); 19.VIII.1968, 1 ♂, 1 ♀, 1 N2 (#948); 19.VIII.1968, 1 ♂, 1 N1 (#945); 19.VIII.1968, 1 ♂, 1 ♀ (#911); 13.IX.1968, 2 ♀ (#1018); Kangi, 19.VII.1968, 1 ♂ (#919); Juchere, 16.X.1968, 2 ♀ (#1223); Karacui, 11.I.1969, 3 ♂, 1 ♀ (#1616); Mashere, 12.VII.1968, 1 ♂, 2 ♀, 1 N2 (#1662); Kalolo, 24.III.1969, 3 ♂, 1 ♀ (#1951); Karambi, 7.I.1969, 1 ♂ (#1152); 13.IX.1968, 2 ♀ (#1009); near Lake Kivu, 10.XI.1969, 2 ♀ (#LR2); 10.XII.1969, 1 ♂ (#1R4); ex *P. boehmii emini*: 14.IX.1968, 1 ♂, 4 ♀ (#1053); 14.IX.1968, 1 ♂ (#1058); Irangi, 3.XI.1968, 1 ♀, 1 N3 ♂ (#1278); 14.IX.1968, 1 ♀, 2 N3 ♀ (#1048); Hombo, 24.XI.1966, 1 ♂, 1 ♀, 1 N1, 1 N2 (#9129); ex *P. alexandri*: Karambi, 9.X.1968, 1 ♂ (#1168), 9.X.1968, 2 ♂ (#1170).

Specimens of other Johnsonophthirius spp. examined.

J. chlorotylus: ZAIRE [all labeled "CONGO" (=Belgian Congo)], ex *Paraxerus* sp.: Bitale Bulobo, 23.II.1967, 1 ♂, 5 ♀; Fout, 5.XII.1968, 1 N3 ♂; Irangi, VII–IX, XII.1968, 1 III.1969, 80 ♂, 121 ♀, 2 N2 ♂; Juchere, IX–X.1968, 1 ♂, 8 ♀; Juchere, I, III, V, III 1969, 33 ♂, 234 ♀; Kalolo, 14, 24.III.1969, 23 ♂, 13 ♀; Kangi, 19.VIII, 2.XII.1968, 2 ♀; Karambi, 7.I, 2.II.1969, 23.VII, 11–12.IX, 7, 11 X, 8.XI.1968, 20 ♂, 39 ♀, 1 N3 ♂, 1 N3 ♀; Karacui, 23.VII, 13.IX, 8–9.X, 3.XI.1968, 15 ♂, 20 ♀; Mahé, 6.XII.1968, 1 ♂, 2 ♀; Mashere, 12.VII.1968, 1–II.1969, 6 ♂, 4 ♀, 2 ♀ N3 ♀; Mifutu, 19.VII, 12.IX, 13.X.1968, 15.1, 25.III.1969, 36 ♂, 52 ♀, 1 N3 ♂; Mashere, 19.I, 22.II.1969, 1 ♂, 7 ♀, 3 N3 ♀; near Lake Kivu, 10.IX.1969, 2 ♀; no location, 14–15.IX.1968, 25.II.1969, 6 ♂, 13 ♀; ex *P. alexandri*: Karambi, 9.X.1968, 1 ♂, 8 ♀, 1 N3 ♀; Mifutu, 3.XI.1968, 2 ♂, 2 ♀, 2 N3 ♂; ex *P. boehmii emini* or *alexandri*: Irangi, 6.VI.1968, 6 ♂, 6 ♀; ex *P. boehmii emini*: Hombo, 24.XI.1969, 3 ♂, 3 ♀; Irangi, 11, 14.IX.1968, 3–5.XI.1968, 20 ♂, 19 ♀, 3 N3 ♂, 2 N3 ♀; Kalumba, 22.XI.1966, 1 ♂, 2 ♀; Mifutu, 3, 5.XI.1968, 2 ♂, 4 ♀; no location, 14–15.IX.1968, 3 ♂, 10 ♀; ex *Fanicus* sp.: Irangi, V, VII, X, XII.1968, 1–II.1969, 13 ♂, 32 ♀, 1 N3 ♂; Juchere,

23.III, 13.IX.1969, 3 ♂, 1 ♀; Kangi, 24.III.1969, 2 ♀; Karambi, 7.X.1968, 1 ♂, 2 ♀; Karacui, 14.IX, 8.X, 7.XI.1968, 1 ♂, 1 ♀; Kashewe, 27.II.1969, 1 ♀; Mifutu, 4.XI.1968, 23.II, 24.III.1969, 2 ♀, 4 ♀; Mulitaba, 18.VI.1968, 1 ♀; Mukosa, 22.III.1969, 1 ♀; no location, 14.IX.1968, 11 ♀; ex *F. anerythrus* on *pyrrhuloxa*: 31.I.1969, 4 ♂, 4 ♀; ex *F. anerythrus*: Juchere, 3.XI.1968, 1 ♀; Irangi, 14.IX.1968, 2 ♀; Mifutu, 4.XI.1968, 2 ♀; Ishibau, 20.IV.1966, 1 ♂, 3 ♀; ex *Hohococcus infobrachium*: Kalumi, 27.V.1968, 1 ♂.

J. helioscavi, ex *Paraxerus palliatus*, KI NYA: Uchweni Forest, 2.III.1912, 1 ♂ lectotype, 3 ♀ paratype; ex *Paraxerus cepapi*, SOUTH AFRICA: Kruger, Natl. Park, 7.XI.1953, (USNM), 2 ♂, 2 ♀ (KNP 128–130), MOZAMBIQUE: Moamba, 11.III.1964, 1 ♂ (#950)

J. kenta, ex *Hohococcus ruwenzori*, U.GANDA: Mubuku Vat, Mt Ruwenzori (USNM), 1 ♀ paratype (#172921); ex *Paraxerus* sp.: ZAIRE: Mashere, 22.II.1969, 2 ♂, 1 N3 ♂ (#1749); 22.II.1969, 1 ♀ (#1751); 12.VII.1968, 1 ♀ (#1622); Karambi, 8.I.1969, 1 ♂ (#1627); ex *Paraxerus boehmii emini*, ZAIRE: Kalumba, 22.XI.1966, 1 ♂, 1 ♀ (#9094); Ishibau, 5 ♂, 4 N3 ♂, 1 N3 ♀; ex *Fanicus* sp.: ZAIRE: Irangi, 10.V.1968, 1 ♂, 4 ♀, 2 N3 ♂ (#212); 14.I.1969, 1 ♂, 1 ♀ (#1701); 24.II.1969, 1 ♀ (#1772); 15.IX.1968, 2 ♀ (#1120); 29.I.1968, 1 N3 ♀ (#16854); 31.I.1969, 1 ♀ (#1711); 25.II.1969, 1 ♂ (#1790); Juchere, 13.IX.1969, 1 ♀ (#1012); 2.XI.1968, 1 ♂, 3 ♀ (#1225); Mashere, 22.II.1969, 1 ♂ (#1797); Mifutu, 24.III.1969, 1 ♂ (#1937); 25.III.1969, 1 ♂ (#1987); ex *Fanicus anerythrus*, ZAIRE: Irangi, 14.IX.1968, 1 ♂, 1 ♀ (#1068); date unknown, 1 ♀ (#1041); 22.I.1966, 4 ♀ (#9095); Karambi, 5.XI.1968, 1 ♀ (#1307); Oshobo, 28.XI.1968, 2 ♂, 2 ♀ (#22165); ex *Hohococcus gambiana*, UGANDA: Bumba Toro, IX.1916, 1 ♂, 3 ♀ (BMNH).

J. suahilicus, ex *Paraxerus cepapi*, MOZAMBIQUE: Moamba, 11.III.1964, 4 ♂, 4 ♀ (#950); ex *Paraxerus cepapi arvensis*, 1 ANGANYIKA: Arusha, Temi Riv, 5 of Ienguru, 915 m, 3.VIII.1956, (R.SNM), Hoogstraal & Kohls, 1 ♂, 1 ♀, 1 N1 (#III11245); Arusha, Makumire Riv, 1250 m, 30.VII.1956 (USNM), Hoogstraal & Kohls, 4 N1, 1 N2 (#III1193); ex *Paraxerus palliatus ornatus*, SOUTH AFRICA: Ngoya Hills, Natal, 1 ♂, 2 ♀ paratypes (#14472) (USNM).

Genus *Linognathoides* Cummings 1914

Linognathoides Cummings, 1914, Bull. Entomol. Res. 5: 159 (type-species: *Linognathoides citelli* Cummings as *L. spermophilii*).

Linognathoides (partim): Kellogg & Ferris, 1915, I clamid Stanford Junior Univ. Publ. Univ. Ser. 20: 23 (limited to *L. montanus*, a synonym of *L. laevisculus* (Gübbe))—Ferris, 1916, Proc. Calif. Acad. Sci. 4th Ser. 6: 158 (except *L. uornatus* Kellogg & Ferris).

Lutegus (Fahrenholz, 1916, Arch. Naturgesch. Abt. A 81: 31 (type-species: *Haematopus pectinifer* Neumann)).

Neohammatopus (partim): Ferris, 1923, Stanford Univ. Publ. Univ. Ser. Biol. Ser. 2: 237 (limited to the species of *Linognathoides*); 1951, Mem. Pan Pac. Entomol. Soc. 1: 185 (limited to the species from Marmotini and Xerini sciurids)—Johnson, 1960, Tech. Bull. U. S. Dep. Agric. 1211: 43 (limited to *N. pectinifer* Neumann, *N. favea* Bedford).

Type-species: *Linognathoides citelli* Cummings.

Description (Fig. 16 25, 27a–c). Anopluta without eyes. ADULTS (Fig. 20–25). Body stout. Head slightly longer than wide with postantennal angles variable; 5-segmented antennae, basal segment without posteroapical angle and a stout seta, ♂ with 3rd segment bearing 1 or no spiniform seta (Fig. 20, 23); ♀ with 3rd segment bearing no spiniform seta; P.III distinct. **Thorax.** With sternal plate posteriorly rounded or convex, its posterolateral angles produced or rounded or completely ab-

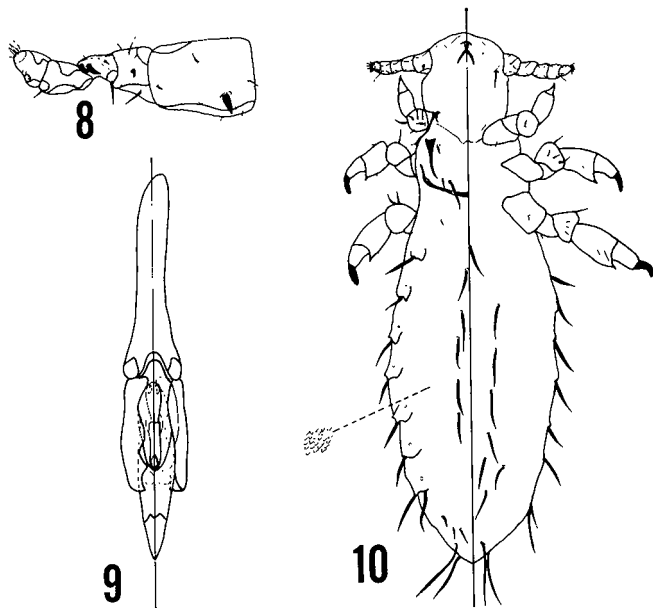


FIG. 8-10. *Neoharmatophis sensuopteri*: 8, ♂ antenna; 9, ♂ genitalia; 10, nymph 2

scut (Fig. 21, 22, 24, 25, 27). *Legs*. Forelegs small and weak with acuminate or bifid claw, mid- and hindlegs larger and usually subequal, with strong claws. *Abdomen*. Tergites and sternites highly reduced or completely lacking except genital plates, paratergites reduced, often with anterior part membranous; each of segments 3-6 with 2-3 rows of dorsal setae; ♂ having vestiges of 2nd tergite with a faint indication of posterior emargination and a group of setae. *NYMPHS*. *Head*. With 5-segmented antennae, without ventral tubercles, with 1 dorsal spin; ventral side with 2-10 pointed or blunt small tubercles. *Thorax*. With sparse setae but DPIS distinct. *Legs*. As in adult except coxae with 1 blunt posterolateral spin but without ventral tubercles. *Abdomen*. With fewer setae than adult; paratergites visible in N2 and N3.

Distribution and hosts. Mai motini and Xerini; Holarctic and Ethiopian regions.

Included species.

1. *ciethi* Cummings, ex *Spermophilopsis leptodactylus*; Russian Turkistan.
2. *faurei* (Bedford), ex *Xerus mauris*, *X. princeps*; Angola, Namibia, Botswana, Zimbabwe, South Africa (Orange Free State).
3. *laeviusculus* (Grube), ex *Spermophilus undulatus*,

S. parryi, *S. pygmaeus*, *S. dauricus*, *S. columbianus*, *S. variegatus*; Holarctic Region.

4. *marmotae* (Ferris), ex *Marmota* spp., *Cynomys ludovicianus*; North America.
5. *palaearectus* (Olsoufjev), ex *Marmota caudata*; Russian Turkistan, Afghanistan, Kashmir.
6. *pectinifer* (Neumann), ex *Atlantoxerus getulus*; NW Africa, Morocco, Algeria.
7. *relictus* (Dubinin), ex *Spermophilus gracilis* (fossil); Palaearctic Region.
8. *schizodactylus* (Gerweil), ex *Spermophilus suslicus*; S European Russia to SE Poland, NE Rumania.
9. *traubi* (Rubin), ex *Spermophilus adocetus*; Mexico.

Specimens examined.

L. ciethi: ex *Spermophilopsis leptodactylus*, USSR Transkaspien, III.1913, J. Wagner, 1 ♂ 1 ♀
1 faurei: ex *Xerus mauris*, SOU-FH AFRICA: Cape Prov. Ahwal, 1 2.VIII.1968, 1 ♂, 1 ♀, 2 N1, 5 N2, 2 N3 (AVW1.2005); Grobblershoop, 7.VI.1968, 1 ♂, 1 ♀ (SJI-2225); Transvaal, Bloemhof I onbard Native Reserve, 6.III.1957, F Zumpt (#54, SAJMR), 1 ♂ 1 ♀, 3 NII.1956, F Zumpt, 1 ♂, 1 N3; 22.VII.1966, 2 ♂, 2 ♀, 3 N1, 9 N2, 1 N3 (RDH 670); Orange Free State, Philippolis, 27.IV.1968, 1 ♂, 1 ♀ 2 N1, 2 N2, 5 N3

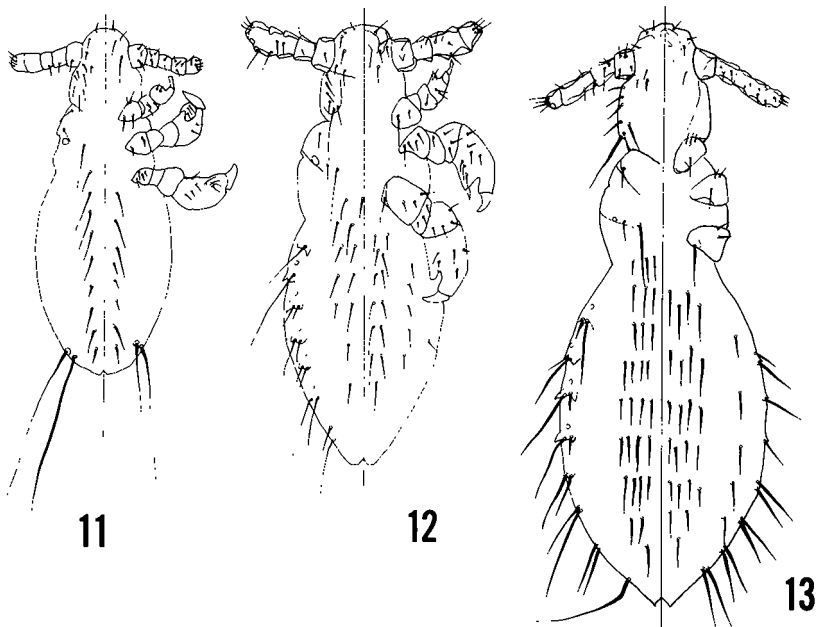


FIG. 11-13. *Neohaematopinus callosicuri*, ex *Callosicurus erythraeus centralis*, Puli, Nam, Tou Hsien, Formosa: 11, nymph 1; 12, nymph 2; 13, nymph 3

(AVWL-1050); Sterkspruit, 23.II.1968, 1 ♂, 1 ♀ (IHS-6238); Bechuanaland: Maboane, 18.XI.1965, 1 ♂, 1 ♀ (TNI-115); BOTSWANA: Mabua Sefulus Ram, 11.II.1967, 1 N2, 2 N3 (TNI-2335); NAMIBIA: Skaamskolk, I.V.1966, 1 ♂, 1 ♀, 4 N2, 4 N3 (RDI-459).

L. taemusculus: ex *Spermophilus beecheyi*, CALIFORNIA: Monterey Co., Bell Ranch, 16.VII.1972, Yescout, 3 ♂, 2 ♀, 3 N1, 3 N2, 3 N3; Monterey Co., 13.V.1976 (USNM), 2 ♂, 2 ♀, 10 N1, 11 N2, 6 N3; ex *Spermophilus bolingi*, CALIFORNIA: Bridgeport, 12.VII.1950 (lot #90, RT B-9950), J. Poll, 1 N2; OREGON: Keno 15.VIII.1934 (#17019), H. H. Stage, 3 ♀, 4 N3; ex squirrel, CALIFORNIA, San Diego, 1933-1934, P. H. Rodent Survey, 2 ♂, 2 N3 (#285); 1 N3 ♂. (#169); 2 ♂, 1 N1, 1 N3 (#501).

L. marmota: ex *Cynomys ludovicianus*, N. DAKOTA: Billings Co., 7 V.UL.1976 (T140, R102), 1 ♂; ex *Marmota* sp., IDAHO: Shoshone Falls, 20.VI.1941, Burroughs, 1 ♂; ex *Marmota flaviventris*, CALIFORNIA: Modoc Co., 29.VI.1949 (#73027, RJS-8385), Kirkwood, 1 N1, 6 N2, 4 N3; ex *Marmota flaviventris nevada*, IDAHO: St. Maries, 9.V.1932 (#19040), H. H. Stage, 8 ♂, 7 ♀; ex woodchuck, UTAH: Logan, 20.V.1939 (#39-8277), Knowlton & Nye, 1 ♂, 1 ♀, 1 N2, 1 N3; ex Rock Chuck, UTAH: Logan Canyon, 6.VII.1951 (#32-3676), G. E. Knowlton, 1 ♂, 1 ♀

L. palaeacutus: ex *Marmota caudata*, WEST PAKISTAN: Hazara Dist.: Burawai, I.IX.1963, 1 N1, 4 N2, 3 N3 (B67460).

L. pectinifer: ex *Atlantoxerus getulus*, MOROCCO: Agadir Prov.: Aquinet Torkoz, 6.XI.1969, 7 ♂, 6 ♀, 3 N1, 5 N2 (MGH-183); Tafraoute, 10.III.1970, 2 ♂, 2 ♀, 1 N1, 5 N2 (MGH-1327); Tammi, 13.IV.1970, 3 N1, 16 N2, 2 N3 (MGH-1391-92, 1394); Tafava Prov.: Tuisgui Remz, 12.XII.1969, 4 N1, 6 N2, 1 N3 (MGH-464).

L. traulsi: ex *Spermophilus adocetus*, MEXICO: Apatzingan, Michoacan, 3.VIII.1941 (USNM), Hoag & Wouder, 1 ♂, 1 ♀, 1 N2 (paratypes) (#57681).

Genus *Neohaematopinus* Mjöberg

Neohaematopinus Mjöberg, 1910, Ark. Zool., 6: 160 (type-species: *Haematopinus scurpenti* Osborn).

Neohaematopinus (partim): Ferris, 1916, Proc. Calif. Acad. Sci. 1th Ser., 6: 168 (not *N. helio-scuri* Cummings); 1923, Stanford Univ. Publ. Univ. Ser. Biol. Sci., 2: 237 (not the species of *Linognathodes* and *Lutegus*); 1932, *ibid.* 2: 283 (*Ahaematopinus* Ewing); 1951, Mem. Pan Pac. Entomol. Soc., 1: 185 (sinks *Petauristophthirus* Eichler).—Johnson, 1960, Tech. Bull. U.S. Dep. Agric., 1211: 43; 1964, Misc. Publ. Entomol. Soc. Am., 4: 77 (limited to the species of *Neohaematopinus* s. str.).

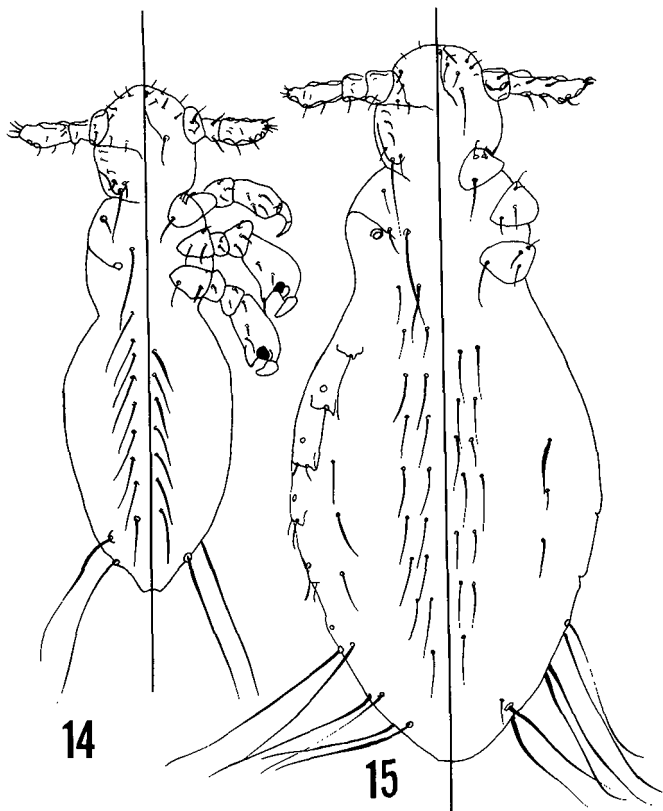


FIG. 14-15. *Neohaematopinus petauristar*, ex *Petauriste elegans*, Chiang Mai, Doi Pui, Thailand: 14, nymph 1; 15, nymph 2.

- Acanthopinus* Mjöberg, 1910, Ark. Zool. 6: 160 (type-species: *Acanthopinus securinus* Mjöberg, n. n. for *Haematopinus austriacus* Osborni preocc.).
Ahaematopinus Ewing, 1929, Man. Ext. Parasites, 197 (type-species: *Neohaematopinus inornatus* Kellogg & Ferris).
Lnognathoides (partim): Kellogg & Ferris, 1915, Leland Stanford Junior Univ. Publ. Univ. Ser. 20: 23 (limited to *L. inornatus* Kellogg & Ferris).—Ferris, 1916, Proc. Calif Acad. Sci. 4th Ser. 6: 158 (limited to *L. inornatus* Kellogg & Ferris).
Petauristophilus Fichler, 1919, Boll. Soc. Entomol. Ital. 79: 12 (type-species: *Neohaematopinus petauristar* Ferris).

Type-species: *Haematopinus sciuropteri* Osborn, by original designation.

Redescription (Fig. 8-15, 28a-h). Anopluta without eyes. ADU 1S (Fig. 8, 9). **Head.** As long as wide or slightly longer, with postantennal angles convex; 5-segmented antennae, basal segment with or without posteroapical angle usually bearing a stout seta, ♂ with 3rd segment usually somewhat produced anteroapically and always bearing 2 strong spines or spiniform setae at apex; ♀ with 3rd segment not bearing a strong spine or seta. **Thorax.** Usually with sternal plate posteriorly emarginate or truncate and having distinct posterior angles produced (Fig. 28a-h). **Legs.** Forelegs small and weak with unimacate claw, mid- and hindlegs larger and usually subequal or with hindleg slightly larger, each with a strong claw. **Abdomen.** With paratergal plates well developed on the 2nd to 8th segment, plates 3-6 usually subquadrangular or triangular, each bearing a dorsal

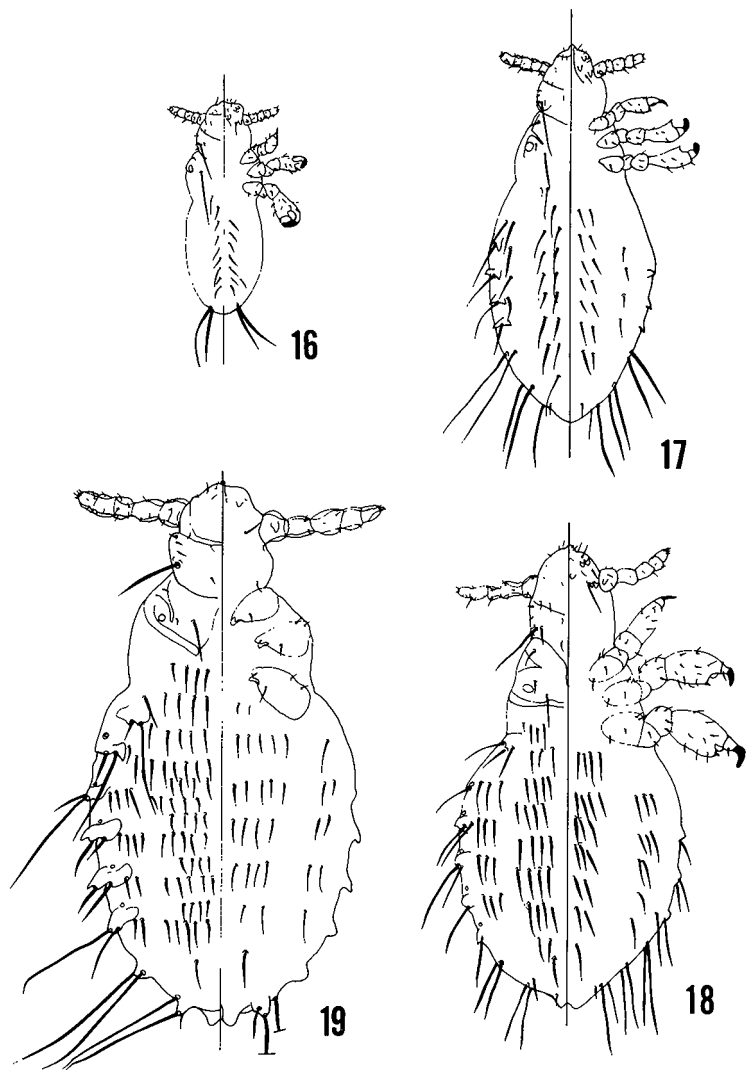


FIG. 16-19 16-18. *Linognathoides marwotae*: 16, nymph 1; 17, nymph 2; 18, nymph 3. 19. *Linognathoides pectinifera*: nymph 3.

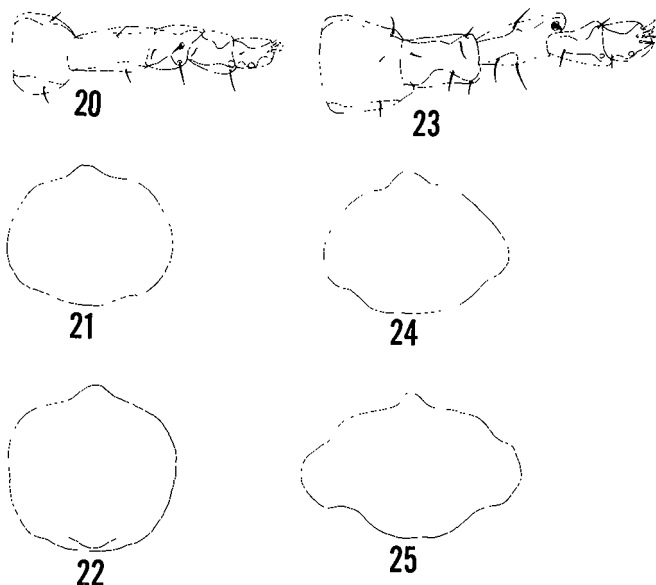


FIG. 20-25. *Linognathodes*. 20-22. *L. marmorata*; 23-25. *L. pectinifer*: 20, 23. ♂ antennae; 21, 24. ♂ thoracic sternite plates; 22, 25. ♀ thoracic sternite plates.

and ventral paratergal seta; plates 7-8 usually ellipsoid with slender setae; tergites and sternites well developed; dorsally and ventrally covered with rows of setae. 2nd plate of the 2nd tergite usually emarginate posteriorly with a group of setae on each lateral knob. NYMPHS (Fig. 10-15). *Head*. With 3-segmented antennae, basal segment without ventral tubercle and 1 or no dorsal spur; no tubercles present on ventral surface of head; 1 long, thick DPHS present. *Thorax*. With 1 DPHS. *Legs*. Forelegs small and weak with acuminate claw; mid- and hind-legs large and generally subequal with a strong claw; coxae without ventral tubercles but occasionally with 1 or no small blunt posterolateral spur. *Abdomen*. Usually immature but distinctly scaly; paratergites present in N2 and N3; dorsum and venter with at least a few setae per segment with terminal setae longest; tergites and sternites absent.

Distribution and hosts. Sciurini, Tamiasciurini, Petauristini, and Callosciurini; Holarctic and Oriental regions.

Included species.

1. *appressus* Johnson, ex *Tamiops rodolphez*: Laos.
2. *batuanae* Ferris, ex *Petaurista batuana*: Batu Is, Malaysia.

3. *callosciuri* Johnson, ex *Callosciurus finlaysoni*, *C. caniceps*, *C. erythraeus*, *C. nigrovittatus*, *C. notatus*, *C. tenuis*, *C. prevosti*, *Glyphotes simus*, *Lariscus insignis*; Malaysia and Thailand.
4. *capitaneus* Johnson, ex *Hylopetes phayrei*: Thailand.
5. *ceylonicus* Ferris, ex *Funambulus palmarum*; Sri Lanka.
6. *chinensis* Blagoveschtchensky, ex *Dremomys rufigenis ornatus*: China and Vietnam.
7. *citellinus* Ferris, ex *Ammospermophilus harrisi*, *Cynomys gunnisoni zuniensis*, *Spermophilus leucurus*, *S. tereticaudus*, *S. variegatus grammurus*; SW US and Mexico.
8. *cognatus* Johnson, ex *Callosciurus jentinki*, *Dremomys* spp., *Menetes berdmorei*, *Nannosciurus schilleheedi*; North Borneo and Thailand.
9. *echinatus* (Neumann), ex *Funambulus palmarum*, *F. pennanti*: India.
10. *elbeli* Johnson, ex *Dremomys rufigenis*; Thailand and Malaysia.

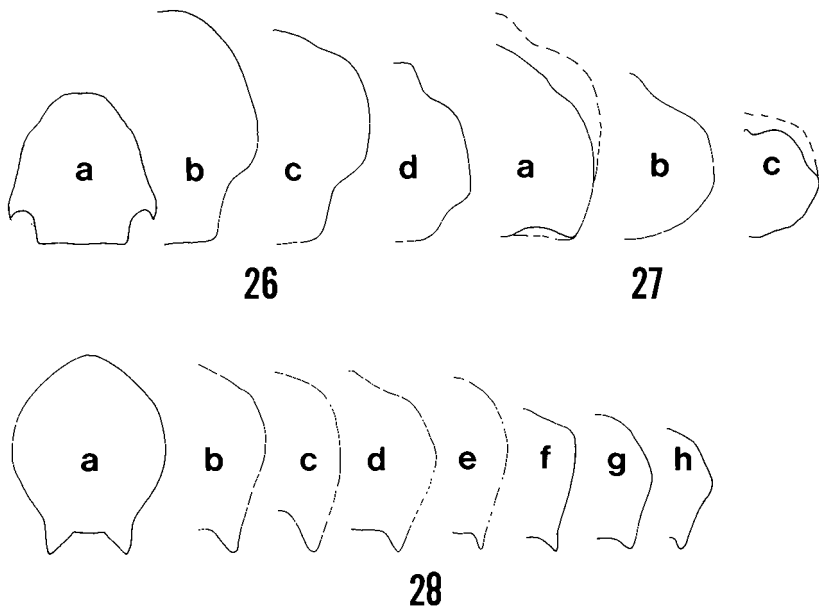


FIG. 26-28. Thoracic sternal plates. 26, *Johnsonphthirus*: a, *J. spinosissimus*; b, *J. sudanicus*; c, *J. kennari*; d, *J. helveticus*. 27, *Linognathoides*: a, *L. normotae*; b, *L. traubi*; c, *L. laevusculus*. 28, *Neohaemaphysalis*: a, *N. sciuopteri*; b, *N. sciurinus*; c, *N. syriacus*; d, *N. callosicuri*; e, *N. uotomae*; f, *N. sciuri*; g, *N. citellinus*; h, *N. spilosomae*.

11. *griseicollis* Ferris, ex *Sciurus griseus*; California.
12. *inornatus* (Kellogg & Ferris), ex *Neotoma cinerea*; W North America.
13. *kinabalensis* Johnson, ex *Hylapetes sagitta*; Thailand.
14. *neotomae* Ferris, ex *Dipodomys ordii*, *Neotoma aleni*, *Neotoma albigula*, *N. fuscipes*, *N. lepida*, *N. mexicana*, *N. micropus*, *N. streatoris*; W US.
15. *pacificus* Kellogg & Ferris, ex *Eutamias quadri- vittatus*, *Neotamias alpinus*, *N. hindsi*, *N. merriami*, *N. speciosus*, *N. townsendii*; W US.
16. *pallidus* Johnson, ex *Petaurista petaurista*, *P. taylori*; Malaya and Thailand.
17. *pansus* Johnson, ex *Petaurillus hosei*; Sabah.
18. *petauristae* Ferris, ex *Petaurista inornata*, *P. taylori*; Kashmir and Thailand.
19. *pteromydis* Blagoveshtchensky, ex *Pteromys volans*; Russia.
20. *robustus* Johnson, ex *Petaurista elegans*; Malaya.
21. *sciuri* Jancke, ex *Callosciurus caniceps*, *C. finlaysoni*, *S. poltopus*, *S. vulgaris*; Europe, Malaya, US, Mexico.
22. *sciurinus* (Mjöberg), ex *Sciurus* spp., *Tamiasciurus hudsonicus*; Germany, Malaya, North, Central, and South America.
23. *sciuopteri* (Osborn), ex *Eutamias amoenus*, *Glaucomys sabrinus*, *G. volans*; US.
24. *semifasciatus* Ferris, ex *Tamiasciurus* sp.; North America.
25. *spilosomae* Stojanovich & Pratt, ex *Spermophilus spilosoma*; SW US.
26. *syriacus* Ferris, ex *Sciurus anomalus*; Syria.

Specimens examined. Adults and nymphs of the following species were studied: *apprissus*, *callosicuri*, *capitanicus*, *citellinus*, *cognatus*, *echinatus*, *elloti*, *inornatus*, *kinabalensis*, *neotomae*, *pallidus*, *pansus*, *petauristae*, *robustus*, *sciuri*, *sciurinus*, *sciuopteri*, *spilosomae*, and *syriacus*. Only adult specimens of the following were examined: *batuanae*, *teslioniensis*, *chircensis*, *griseicollis*, *pacificus*, *pteromydis*, and *semifasciatus*.

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