

Revision of the Chewing Louse Genus *Eutrichophilus* (Phthiraptera: Trichodectidae) from the New World Porcupines (Rodentia: Erethizontidae)

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Abstract

A systematic revision of the chewing louse genus *Eutrichophilus* Mjöberg was undertaken to delineate the species present and clarify their hosts and distributions. This genus has been particularly problematic in that, in some cases, two or three species have been described from the same host taxon. Furthermore, the critical type material is widely scattered in collections (some was even destroyed during World War II), and the host porcupines have not been revised.

We now recognize 18 species of *Eutrichophilus*, all restricted to the mammalian family Erethizontidae, the New World porcupines. We redescribe the 12 previously described species that we recognize herein and describe 6 species of *Eutrichophilus* new to science. A key is provided for the identification of all recognized species. We found four of the older species names (*E. cercolabes* Mjöberg, *E. minor* Mjöberg, *E. cordiceps* Mjöberg, and *E. lobatus* Ewing) to represent complexes of species, thereby accounting for the six new species: (1) the *cercolabes* group consists of *E. cercolabes*, *E. andersoni*, n. sp., *E. australis* Ewing, *E. duellmani*, n. sp., and *E. maximus* Bedford; (2) the *minor* group consists of *E. minor*, *E. emersoni*, n. sp., and *E. claytoni*, n. sp.; (3) the *cordiceps* group consists of *E. cordiceps* and *E. paraguayensis*, n. sp.; and (4) the *lobatus* group consists of *E. lobatus* and *E. hershkovitzi*, n. sp. Lectotypes are designated for *E. cercolabes*, *E. minor*, and *E. cordiceps*. Identities for all host species are evaluated and corrected where necessary.

Resumen

Se realizó la revisión sistemática de los piojos del género *Eutrichophilus* Mjöberg para delinear las especies incluidas en este género y clarificar sus huéspedes y sus distribuciones. Este género ha sido particularmente problemático porque en ciertos casos dos o tres especies fueron descritas desde el mismo huésped. Además, el material tipo está depositado en diferentes colecciones, algunas de las cuales fueron destruidas durante la Segunda Guerra Mundial y los huéspedes puercoespines no han sido revisados sistemáticamente.

En el presente trabajo se reconocen 18 especies de *Eutrichophilus*, todas ellas restringidas a Erethizontidae, familia de mamíferos puercoespines del Nuevo Mundo. Se describen 12 de las especies previamente descritas, y que se reconocen como tales, y se describen seis nuevas especies de *Eutrichophilus*. Se presenta una clave de identificación de todas las especies reconocidas. Los resultados muestran que cuatro de los nombres específicos antiguos (*E. cercolabes* Mjöberg, *E. minor* Mjöberg, *E. cordiceps* Mjöberg y *E. lobatus* Ewing) representan grupos de especies y por lo tanto las seis nuevas especies se incluyen en las siguientes agrupaciones taxonómicas: (1) el grupo *cercolabes* incluyendo *E. cercolabes*, *E. andersoni*, n. sp., *E. australis*

Ewing, *E. duellmani*, n. sp., y *E. maximus* Bedford; (2) el grupo *minor* incluyendo *E. minor*, *E. emersoni*, n. sp., y *E. claytoni*, n. sp.; (3) el grupo *cordiceps* incluyendo *E. cordiceps* y *E. paraguayensis*, n. sp.; y (4) el grupo *lobatus* con *E. lobatus* y *E. hershkovitzi*, n. sp. Se designan lectotipos para *E. cercolabes*, *E. minor*, y *E. cordiceps*. Las identificaciones de todos los huéspedes fueron evaluadas y corregidas cuando fue necesario.

Introduction

Eleven species have been recognized in the chewing louse genus *Eutrichophilus* Mjöberg, with two additional names placed as junior synonyms (Werneck, 1950). The members of this genus are the sole constituents of the subfamily Eutrichophilinae Kéler and are restricted to the New World porcupines of the caviomorph rodent family Erethizontidae. The first two species of porcupine lice were described in the genus *Trichodectes* Nitzsch: *T. setosus* by Giebel (1861) from the North American porcupine, *Erethizon dorsatum*, and *T. mexicanus* by Rudow (1866) from the Mexican hairy porcupine, *Coendou mexicanus*. The genus *Trichodectes* contained most of the mammal-infesting ischnoceran chewing lice known at that time. Mjöberg (1910) erected a new genus, *Eutrichophilus*, for all of the previously described porcupine and deer lice, and added three new species of porcupine lice: *E. cercolabes*, *E. cordiceps*, and *E. minor*. All were reported from a porcupine that Mjöberg called "Quendu-Stachelschwein" and assumed to be *Coendou prehensilis*. Stobbe (1913) described *E. coendou* from *C. mexicanus*; it has been considered a junior synonym of *E. mexicanus* by Werneck (1950) and others. Ewing (1936) described two species of porcupine lice, *E. australis* from a porcupine he called *C. villosus* in Paraguay and *E. lobatus* from *C. pruinus* in Venezuela. The former species has been considered a junior synonym of *E. cercolabes* by Werneck (1950) and others. Bedford (1939) described the species *E. maximus* from *C. rothschildi* in Panama and erected a new genus, *Tricholipeurus*, for those species of chewing lice found on deer. Werneck (1945) described *E. moojeni* from the distinctive bristle-spined porcupine, *Chaetomys subspinosus*, of southeastern Brazil, and, in 1950, described the last three species in the genus, *E. comitans* from *C. pruinus* in Venezuela and *E. exiguus* and *E. guyanensis*, both from *C. melanurus* in Guyana.

Although the taxonomic history of the species within *Eutrichophilus* has been relatively stable,

the subfamily Eutrichophilinae has been the subject of a wide variety of different views. Kéler (1938), in reviewing the trichodectid lice, raised the Trichodectidae to superfamily level and included within it the three families Trichodectidae, Bovicolidae, and Dasyonygidae. Within the Trichodectidae, he proposed recognition of four new subfamilies: Eutrichophilinae, Eurytrichodectinae, Felicolinae, and Trichodectinae. However, he placed the Eutrichophilinae in the family with reservation. His subfamily Eutrichophilinae included three genera, *Eutrichophilus*, *Procavicola* Bedford, and *Procaviphilus* Bedford. Eichler (1941) transferred the subfamilies Eutrichophilinae and Eurytrichodectinae to the family Dasyonygidae, with the Eutrichophilinae still containing the same three genera. In a later classification of the Trichodectoidea, Kéler (1944) transferred the Eutrichophilinae to the family Bovicolidae and apparently included within it another genus, *Lymeon* Eichler (Lyal, 1985). Hopkins (1949) treated the 1938 subfamilies of Kéler (including the Eutrichophilinae), and several other groups, as tribes within the family Bovicolidae. In his classification of the Mallophaga, Eichler (1963) followed Kéler in treating the Eutrichophilinae as a subfamily of the family Bovicolidae but included within it only the single genus *Eutrichophilus*. Kéler (1969), in his final classification of the Mallophaga, also considered the subfamily Eutrichophilinae to contain only the single genus *Eutrichophilus*. Lyal (1985), in his cladistic analysis of the trichodectid lice, recognized five subfamilies within the family Trichodectidae: Eutrichophilinae, Bovicolinae, Dasyonyginae, Neotrichodectinae, and Trichodectinae. He, as had the previous authors, restricted the subfamily Eutrichophilinae Kéler to the single distinctive genus *Eutrichophilus*, the porcupine-infesting phthirapterans. We have no disagreement with the content of Eutrichophilinae and its placement in this fashion.

Our understanding of the systematics and host-parasite relationships of the Eutrichophilinae is hindered by the fact that many of the original

species descriptions and much of the taxonomic work on the genus *Eutrichophilus* predate modern detailed descriptions and illustrations, thereby making the identification of specimens extremely difficult. Compounding this, it is likely that most of the older collections, including some types, available to the early German workers were destroyed during World War II. The Mjöberg collection was housed at the Hamburg Museum, which was destroyed in the firebombing of Hamburg by Allied forces in July 1943, resulting in the destruction of much slide-mounted material, but not the collections preserved in alcohol (Weidner, 1966).

Even though Werneck (1945, 1950) redescribed most of the species, and Emerson and Price (1975) reviewed the type hosts and distributions and provided illustrations for the species of *Eutrichophilus* found in northern South America, there are still inadequacies and a need for further study. An enigma of the genus is that some host species, and even perhaps individual porcupines, have two or three sympatric species of *Eutrichophilus* described from them; in most other species of mammals that are parasitized by chewing lice, a single species of a louse genus per host (host specificity) is most common. The array of morphological variation that exists between species of porcupine lice further complicates the species-level problems. Additionally, the South American porcupines have never been revised, and, unfortunately, a variety of names has been used over the years for these animals, resulting in a truly confusing array of specific names in the genus *Coendou*. The phylogeny in Lyal (1985) treated to species all of the genera within the family Trichodectidae, except two: *Eutrichophilus* and *Geomydoecus* Ewing. The latter genus, the pocket gopher lice, includes 122 taxa (now recognized as two genera: *Geomydoecus* and *Thomomydoecus* Price and Emerson—see Hellenthal & Price, 1991).

Eutrichophilus has been of interest to us for some time, but, because of the problematic literature and the fact that the necessary type material was either widely scattered in collections or possibly destroyed, we were reluctant to study these lice. We, and we assume other workers, had been hampered by the confusing taxonomic literature available for this genus and for the host porcupines.

We recently obtained a collection of *Eutrichophilus* from the bicolor-spined porcupine, *Coendou bicolor bicolor*, from southeastern Peru, stimulating us to study the available literature and species descriptions in an attempt to identify these specimens. Despite the considerable body of lit-

erature on *Eutrichophilus*, most species could not be identified with any certainty using the published literature. The dimensions, details of setal numbers and placement, and aspects of the genitalia that we use today to distinguish species of chewing lice were not treated in sufficient detail by many authors in the original written descriptions of most of these species of *Eutrichophilus*. Additionally, not all members of this genus have been illustrated adequately. To alleviate this situation, we undertook a comprehensive revision of the genus. These lice are large and seem to have a number of characters previously overlooked that are useful in diagnosing species. We were able to reexamine all of the described species and, where possible, the type material, with the exception of *E. maximus*. We now recognize 18 species in the genus *Eutrichophilus*, all of which are restricted to the mammalian family Erethizontidae, the New World porcupines. The purposes of this paper are to (1) describe six species of *Eutrichophilus* new to science, (2) redescribe 12 previously named species, (3) provide a key for the identification of species, and (4) discuss the host relationships and geographic distribution of all species. We hope that the detailed descriptions, illustrations, brief literature review, and keys presented herein will make additional systematic and ecological studies possible on these poorly known lice, their porcupine hosts, and the host-parasite system.

Methods

All measurements are given in millimeters. Abbreviations designating museum collections where specimens of the hosts are deposited are as follows: AMNH = American Museum of Natural History, New York; KU = Museum of Natural History, University of Kansas, Lawrence; LACM = Los Angeles County Museum, Los Angeles; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; USNM = U.S. National Museum of Natural History, Washington, D.C. We associate museum catalog numbers with the hosts/localities wherever possible as the state of porcupine taxonomy is in considerable flux. Brackets are used to designate our additions or corrections to locality data or host identifications. If we believe the type host in the original published description was erroneously identified, we note it as such in the synonymy and provide additional details and other host names within the discussion section.

Systematics

Subfamily Eutrichophilinae Kéler, 1938

Eutrichophilinae Kéler, 1938:393. Type genus: *Eutrichophilus* Mjöberg.

Since Kéler (1938) first proposed subfamilial status for the Eutrichophilinae, it has continued as a distinctive taxon of chewing lice even though its constituents and relationships to other trichodectids have been uncertain (see brief review of the critical papers in the Introduction).

Lyal (1985) recognized the Eutrichophilinae as a well-supported clade within the Trichodectidae. He characterized the clade as having the following six unique apomorphic states: (1) posterior temple margins produced and convex, (2) median extension of mesomeral arch absent, (3) basiparameral sclerites present and either fused to parameres or free, (4) male flagellum very long, (5) abdominal spiracle VIII present, and (6) pleurum VIII [misstated as VII by Lyal (1985, p. 211) for character 140] with tuft of very long setae.

To paraphrase Lyal (1985, p. 265), the subfamily and genus may be characterized as follows: Anterior head with osculum present or absent, but pulvinus always attaining margin; dorsal preantennal sulcus absent; clypeal marginal carina with median expansion absent or slight, or present as broad or narrow parallel-sided bar with transverse margins convex, straight, or concave; anterolateral head margin straight or convex; head preantennal portion long or short; outline triangular, rounded, or broadly trapezoid. Temple margin convex or with posterolateral angle; temples greatly expanded posteriad. Male scape expanded, with longitudinal row of two setae; male flagellomeres fused; female flagellomeres fused or flagellum of two flagellomeres; male flagellum very long, with two basally articulated "teeth." Head dorsum with short or long setae, sometimes longer anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with short to moderately long dorsal setae marginally or submarginally on posterior of prothorax and pterothorax, absent from disc of both; one or two long setae on posterolateral pterothorax margins.

Abdomen oval, elongate. Abdominal spiracles on segments III–VIII. Abdominal setae short or moderately long, with tufts of very long setae on at least pleurum VIII, sometimes also pleurum VII

(males) or IX (females); anterior setae present only on pleura, absent from terga and sterna; posterolateral setae present. Abdominal pleura lacking dorsal or ventral projections. Sclerites present on terga, sterna, and pleura (where present) of all pregenital abdominal segments except, sometimes, tergum I; at least male abdominal terga of segments V and VI with anterior and posterior sclerites.

Gonapophyses often large, broadly triangular or rounded, ventral margin lacking lobe but with more or less dense medium to long marginal setae. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotized band. Ventral vulval margin not sclerotized; smoothly convex, with or without median indentation or setose projection; subgenital lobe absent.

Male subgenital plate with sternites VII and VIII present and fused to subgenital plate rods, IX absent or, if present, fused to subgenital plate rods. Pseudostyli absent. Male genital opening dorsal, male segment IX posterior. Parameres long or short, narrow or broad; with basiparameral sclerite or flange sometimes present and fused medially, thus linking parameres, but otherwise unfused. Mesomeres present, fused apically to form arch with no median extension; arch smoothly rounded, or with lateral desclerotizations, in which case median portion straight and at right angles to lateral portions, very poorly sclerotized and thin, or absent.

Genus *Eutrichophilus* Mjöberg, 1910

Eutrichophilus Mjöberg, 1910:71. Type species: *Eutrichophilus cercolabes* Mjöberg, by subsequent designation (Harrison, 1916, p. 21).

Mjöberg (1910) erected the genus *Eutrichophilus* and included in it four species that he described as new in the same paper: *E. cercolabes*, *E. cordiceps*, *E. minor*, and *E. mexicanus*. The first three species were from porcupines and the last from a brocket deer (*Cervus mexicanus* = *Mazama americana*). Bedford (1939) subsequently erected the genus *Tricholipeurus* for the species found on deer. Our telegraphic translation of the generic description in German of *Eutrichophilus* from Mjöberg (1910) is as follows: Body of moderate size. Head broad, more or less heart-shaped; male antennal groove very deep due to robust antennae, and anterior head sharply separated from posterior por-

tion; clypeus anteriorly either truncated or emarginated; furrow for food very clearly developed; antennae very robust in male, with basal segment very long and thick, second segment much narrower than third; third segment arched slightly to inside, this last segment always carrying on inner edge two small blunt setae and, in addition, two clear sensory pits. Thorax of three segments not always clearly visible; prothorax considerably variable, sometimes broad, sometimes narrowed anteriorly; with distinct prothoracic pair of spiracles visible often as tubercle-like elevation. Legs surprisingly similar to those of some species of *Pedicinus*; long pointed seta on inner corner of tibia and elongated well-developed process present on second tarsal segment; claw very long, pointed. Abdominal segments with narrow lateral sclerites and broad yellowish crossbands; only one transverse row of setae on each segment; first tergite, even though small, always present, with only few setae (2–4); last sternite always strongly developed in male; spiracles, large and similar in sculpture to Anoplura, present on segments 3–8. Sculpture of integument more or less scale-like. Eggs surrounded by very large mass of slime.

The characterization of this genus by Mjöberg (1910) and Lyal (1985) is problematic, as so many features present extremes of variation, being either present or absent, large to small, and so on. This has caused us concern as to how homogeneous (monophyletic) this genus truly is, but we opt for no generic changes at this time. Perhaps this extreme heterogeneity was the reason that Lyal (1985, p. 223) does not resolve further the *Eutrichophilus* clade.

Lyal (1985, pp. 266–267) provides several illustrations of *Eutrichophilus* (his figs. 87–93). We were able to examine the specimens he used for illustrations and note the following corrections. His Figure 90, stated to be the female terminalia of *E. maximus*, actually represents the female terminalia of *E. mexicanus*. The specimen is from well within the known range for both this louse species and its host and is typical of all other *E. mexicanus* we have examined. Also, in couplet 27 of the key to the genera, Lyal (1985, p. 339) refers to Figures 100, 101, and 102, which correctly should be Figures 89, 91, and 93, respectively.

In his initial generic description, Mjöberg (1910) misspelled the name *Eutrichophilus*, spelling it *Entrichophilus*. Hopkins and Clay (1952) concluded, and we concur, that this was an error, as he consistently spelled this new genus *Eutrichophilus* throughout the remainder of the paper. Un-

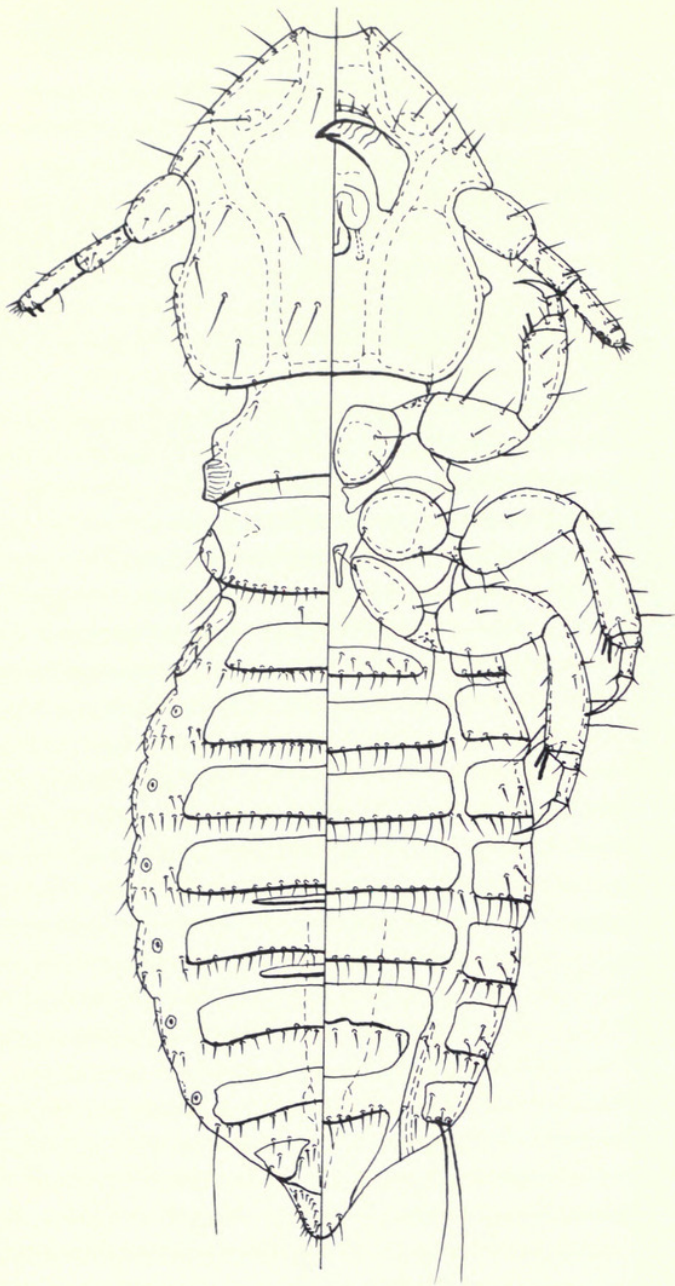
der Article 32(d) of the International Code of Zoological Nomenclature, incorrect spellings are to be corrected (ICZN, 1985).

Eutrichophilus setosus (Giebel, 1861) (figs. 1–5)

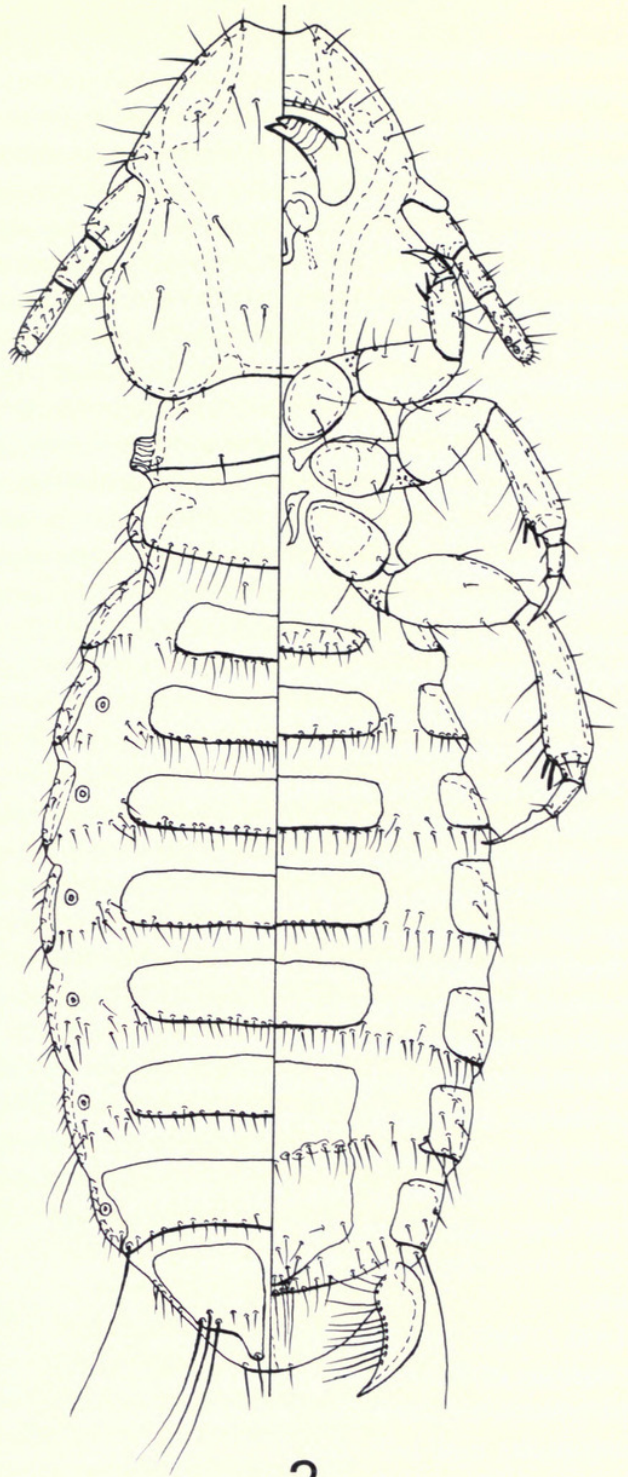
Trichodectes setosus Giebel, 1861:86. Type host: (*Hystrix dorsata*) = *Erethizon dorsatum* (Linnaeus).

MALE—As in Figure 1. Head longer than wide, with slight medioanterior concavity; relatively long dorsal setae; 4 middorsal setae aligned transversely; scape slightly enlarged. Pronotum with 1, less often 2, medioposterior setae on each side. Metanotum with long outer marginal seta and total of 14–20 setae between them; longest seta of metapleuron subequal to long adjacent metanotal seta. Tergal setae short: I, 2; II, 24–31; III–V, 28–42; VI, 24–33; VII, 17–27; VIII, 8–12; IX with 10–16 short anterior setae; terminal segment tapered, with patch of minute dorsal setae. Very long setae on pleuron VIII and lateral tergum VIII. Small accessory tergal plate on V–VI. Spiracles large. Sternal setae slightly longer than tergal setae: II–IV, 21–30; V–VI, 18–23; VII–VIII, 12–15. Genitalia (fig. 3) with slender tapered paired parameres, ring-like fused mesomeres with slight medioposterior concavity, and small accessory structures at base of parameres; small weakly spinose sac; sides of basal apodeme straight, but slightly diverging. Dimensions: temple width (TW), 0.40–0.46; head length (HL), 0.45–0.52; scape length (SL), 0.11–0.12; scape width (SW), 0.08–0.09; prothorax width (PW), 0.34–0.38; metathorax width (MW), 0.37–0.42; abdomen width at IV (AWIV), 0.56–0.66; total length (TL), 1.62–1.90; genitalia width at mesomeres (GW), 0.09–0.11; genitalia paramere length (GPL), 0.17–0.18; genitalia basal apodeme length (GBAL), 0.19–0.21.

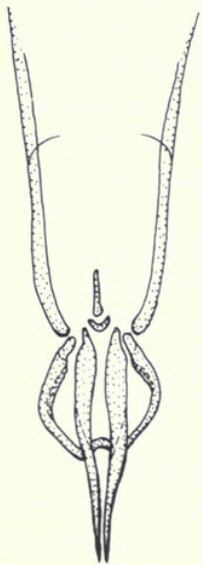
FEMALE—As in Figure 2. Much as for male, except as follows. Head about as long as wide; scape small. Longer metanotal and tergal setae. Tergal setae: II, 29–36; III–VI, 36–48; VII, 31–38; VIII, 13–17. Last segment (fig. 5) with cluster of 3 very long dorsal setae on each side and 5–10 short setae between them. No accessory tergal plates. Sternal setae: II–VI, 27–36; VII, 20–25; chaetotaxy and shape of sterna II–III as in Figure 4. Ventral terminalia (fig. 5) with moderate-sized gonapophyses, slender, tapered to point, each with 8–14 marginal setae, and total of 31–47 setae between their bases, these much longer medially than laterally;



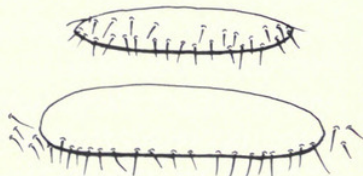
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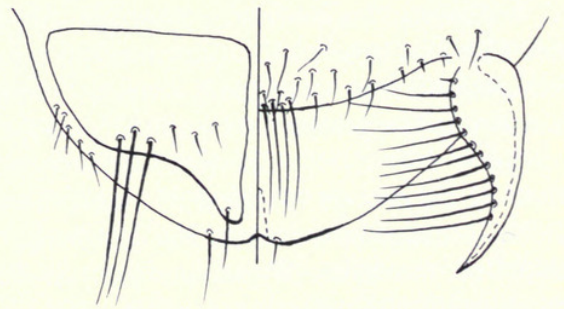
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FIGS. 1-5. *Eutrichophilus setosus*: 1, male. 2, female. 3, male genitalia. 4, female sternites II-III. 5, female terminalia.

margin of subgenital plate slightly convex. Dimensions: TW, 0.54–0.65; HL, 0.55–0.62; PW, 0.45–0.50; MW, 0.50–0.55; AWIV, 0.81–0.92; TL, 2.04–2.46.

MATERIAL EXAMINED—Ex *Erethizon dorsatum dorsatum*: CANADA: Quebec: Oka, 5 males, 5 females. USA: Michigan: Benzie Co.: 2 females. Minnesota: Mahnomen Co.: Big Hill Fireway, 1 male, 1 female; Itasca State Park, 2 males, 2 females. New Hampshire: Strafford Co.: Durham, 1 male, 5 females. Ex *Erethizon dorsatum epixanthum*: USA: California: Placer Co.: 6 males, 4 females. Colorado: Archuleta Co.: Pagosa Springs, 1 female. Montana: Ravalli Co.: Darby, 1 female. Utah: Tooele Co.: Simpson Mt., 5 males, 5 females. Wyoming: Uinta Co.: Evanston, 2 males, 1 female. Ex *Erethizon dorsatum myops*: USA: Alaska: North Fork Kuskowin River, 6 females; Ladd AFB, 2 males, 2 females; no specific locality, 9 males, 7 females. Ex *Erethizon dorsatum nigrescens*: CANADA: British Columbia: Tuolumne, 1 male, 3 females. Ex *Erethizon dorsatum* no subspecies: Zoo hosts: NYC Zoo, 3 males, 3 females. California: San Diego Zoo, 1 male, 4 females. Washington, D.C.: U.S. National Zoological Park, 1 male, 1 female. No data: 3 males, 2 females.

REMARKS—*Eutrichophilus setosus* is distinct from all other known species of the genus by having both sexes with the longer dorsal head setae, the female with gonapophyses and ventral terminalia chaetotaxy as in Figure 5, and the male with the mesomeres fused to form a circle (fig. 3).

Eutrichophilus setosus is restricted in distribution to a single host species, the North American porcupine *Erethizon dorsatum*. It is the only louse species known from *E. dorsatum*, apparently occurring throughout the very broad host range. This porcupine occurs across much of the United States and Canada from the Atlantic to the Pacific coasts and from northern Alaska and Canada to northern Mexico.

In addition to the material we examined, *Eutrichophilus setosus* has been recorded in the literature off *Erethizon dorsatum* in the following states: Nebraska (Osborn, 1896), New Hampshire (Werneck, 1945), New Mexico (Cockerell, 1902), Oregon (Werneck, 1945), and Texas (Wilson & Oliver, 1979). We see no reason not to accept these records as valid. However, we do not believe that the two females that Werneck (1950) reported from *Coendou laenatus* [= *mexicanus*] from Honduras constitute a valid record. Werneck (1950) reported one host for this species as *Erethizon epixanthum*; *E. epixanthum* is now considered the subspecies

of *E. dorsatum* occurring in the western United States. The host species reported by Morse (1903, p. 618) and later Werneck (1950, p. 58) as "*Erethizon ermineus*" is *E. dorsatum* also, as Morse recorded it as a porcupine from "Neb." [Nebraska]. Curiously, and erroneously, Kellogg and Ferris (1915, p. 59) reported, "This species [*E. setosus*] is apparently common to the porcupines of both Europe and America." There are no porcupines, either erethizontids or hystrichids, endemic to Europe.

Lyal (1985) erroneously listed the year of authorship for Giebel's species description as 1874. The correct date of publication is 1861.

***Eutrichophilus mexicanus* (Rudow, 1866) (figs. 6–10)**

Trichodectes mexicanus Rudow, 1866:109, Figure 1.

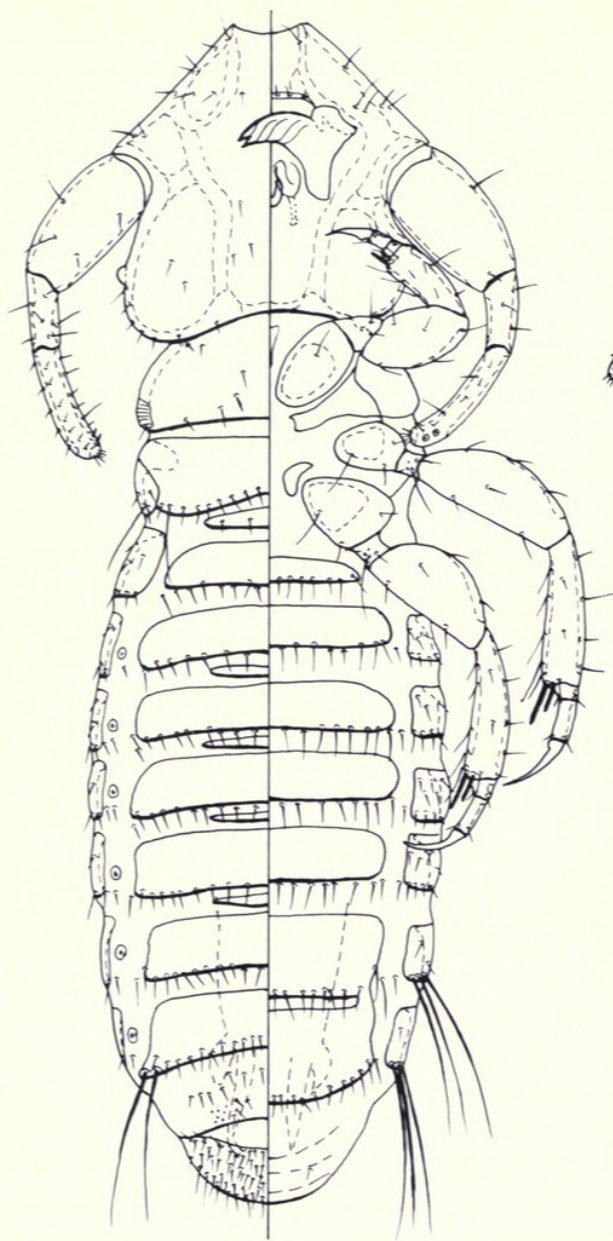
Type host: *Coendou mexicanus* (Kerr).

Eutrichophilus coendou Stobbe, 1913:566, Figure 5.

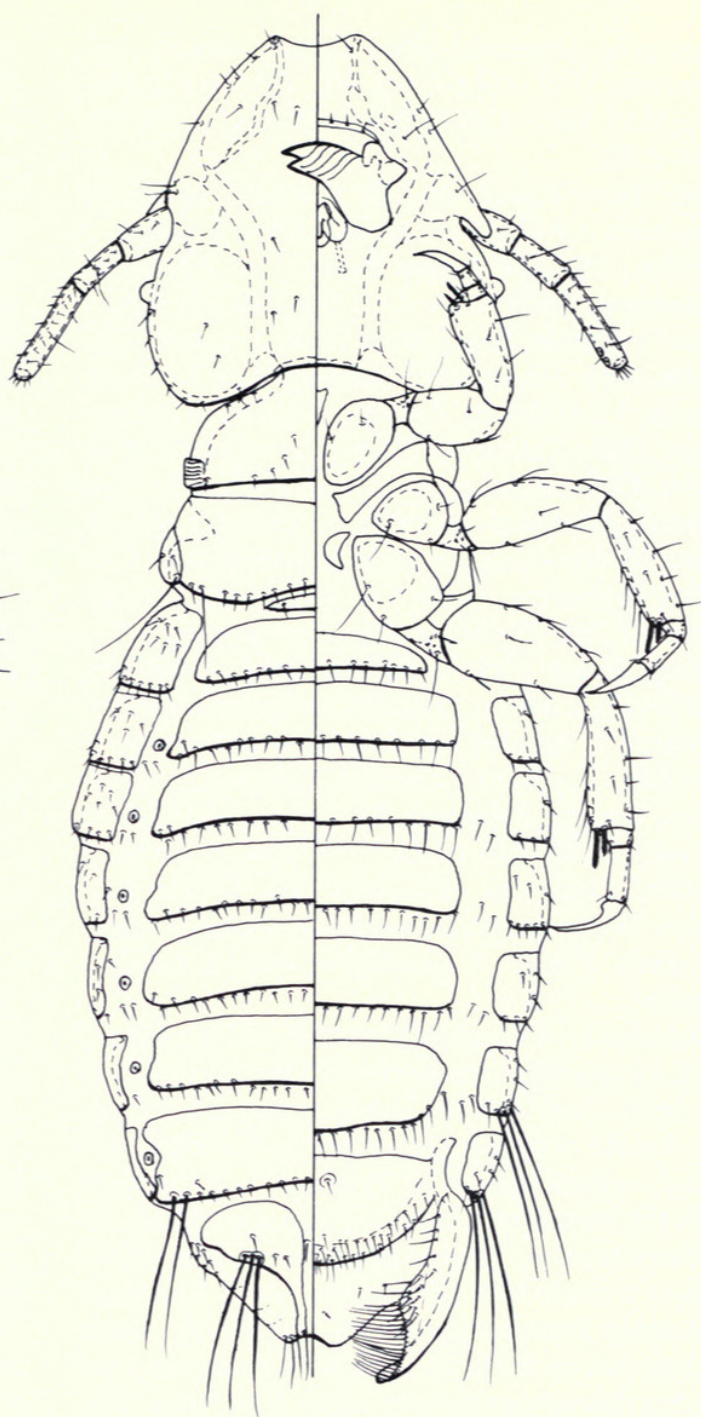
Type host: *Coendou mexicanus*.

MALE—As in Figure 6. Head about as long as wide, with slight medioanterior concavity; with short dorsal setae; median pair of middorsal setae distinctly medioanterior to outer pair; scape much enlarged. Pronotum with 3–5 medioposterior setae on each side. Metanotum with long outer marginal seta and total of 14–20 setae between them; longest seta of metapleuron subequal to long adjacent metanotal seta. Tergal setae short: I, 2; II–III, 13–19; IV–VI, 17–22; VII, 22–26; VIII, 26–32; IX, 23–27, with patch of 6–8 sensilla on each side; terminal segment broadly rounded, with numerous short dorsal setae. Pleura VII and VIII and lateral tergum VIII with very long setae. Small accessory tergal plate on III–VI. Spiracles large. Sternal setae slightly longer than tergal setae: II, 11–15; III–VI, 13–19; VII, 17–21; VIII, 18–26. Genitalia (fig. 8) with long slender parameres, short mesomeres, and wide slender connection at base of parameres; very large spinose sac; sides of basal apodeme relatively straight, slightly diverging. Dimensions: TW, 0.49–0.56; HL, 0.48–0.53; SL, 0.26–0.30; SW, 0.11–0.15; PW, 0.39–0.45; MW, 0.41–0.49; AWIV, 0.60–0.73; TL, 2.01–2.27; GW, 0.23–0.29; GPL, 0.20–0.22; GBAL, 0.28–0.32.

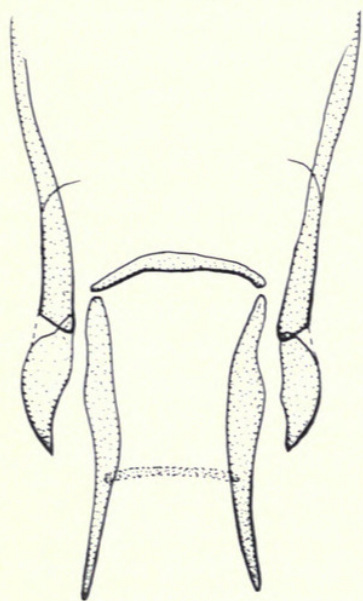
FEMALE—As in Figure 7. Much as for male, except as follows. Head wider than long. Scape much smaller. Metanotum with 15–22 marginal setae between long outer setae. Tergal setae: III–VIII, 18–29. Last segment (fig. 10) with cluster of 3 very



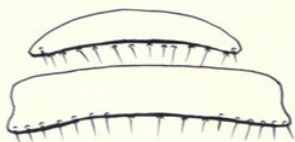
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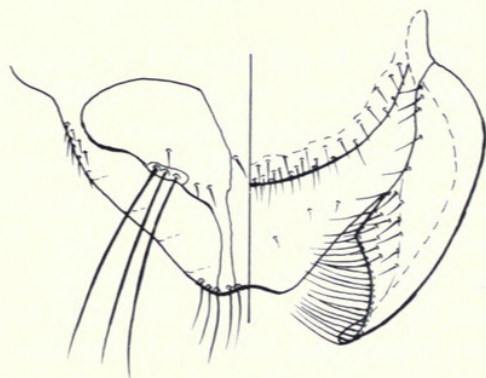
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9



10

FIGS. 6-10. *Eutrichophilus mexicanus*: 6, male. 7, female. 8, male genitalia. 9, female sternites II-III. 10, female terminalia.

long dorsal setae on each side and 7–10 short setae anterior and mediad of them. No accessory tergal plates. Sternal setae: II, 10–14; III–VII, 15–22; chaetotaxy and shape of sterna II–III as in Figure 9. Ventral terminalia (fig. 10) with large angulate gonapophyses, each with 33–46 relatively short fringe and submarginal setae and total of 41–51 setae on subgenital plate, these of fairly uniform short length; margin of subgenital plate strongly convex. Dimensions: TW, 0.54–0.65; HL, 0.49–0.56; PW, 0.44–0.48; MW, 0.53–0.59; AWIV, 0.72–0.91; TL, 1.99–2.28.

MATERIAL EXAMINED—Ex *Coendou mexicanus laenatus*: COSTA RICA: Guanacaste: Buenos Aires de Santa Cruz, 2 males, 2 females (LACM 25160); El Cacao de Santa Cruz, 14 males, 23 females (LACM 24836). Limón: Las Cuevas, 1 mi NW Limón, 16 males, 33 females (LACM 25146). NICARAGUA: Carazo: 3 km N, 4 km W Diriamba, 8 males, 8 females (KU 110572), 40 males, 51 females (KU 110573), 1 male, 1 female (KU 110574), 3 males, 6 females (KU 110575). Ex *Coendou mexicanus mexicanus*: GUATEMALA: no locality; 2 males, 2 females (USNM 61243). MEXICO: Oaxaca: 20 mi NW La Ventura, 12 males, 12 females. Veracruz: Misantla, 1 male, 1 female. Ex *Coendou mexicanus yucataniae*: MEXICO: Campeche: 46 km S Champotón, 3 males, 2 females (KU 93792). Yucatán: Gruta de Balankanche [4.5 km E of Chichén Itzá], 4 males, 5 females; Tekom, 4 males, 9 females.

REMARKS—The unmodified legs II–III, presence of a symmetrical head with the inner pair of mid-dorsal setae medioanterior to outer pair, and at least three median pronotal setae on each side, in combination with the details of the male genitalia (fig. 8) and the female terminalia (fig. 10), set *E. mexicanus* apart from all other known taxa of the genus.

This is the only louse known from *Coendou mexicanus*; it apparently is found on this host throughout its range from southern Mexico southward through Central America to western Panama. Werneck (1950) reported that he had examined a great number of specimens of both sexes from Mexico and Guatemala, all from *C. mexicanus*. Both series of lice we examined from Costa Rica were labeled as from *C. rothschildi* and identified by K. C. Emerson as *E. maximus*; however, these specimens clearly are conspecific with *E. mexicanus*, and we believe the identification was erroneously applied owing to misidentification of the host as one that does not occur in Costa Rica. First and second instars were found on a host collected on 13 August 1967.

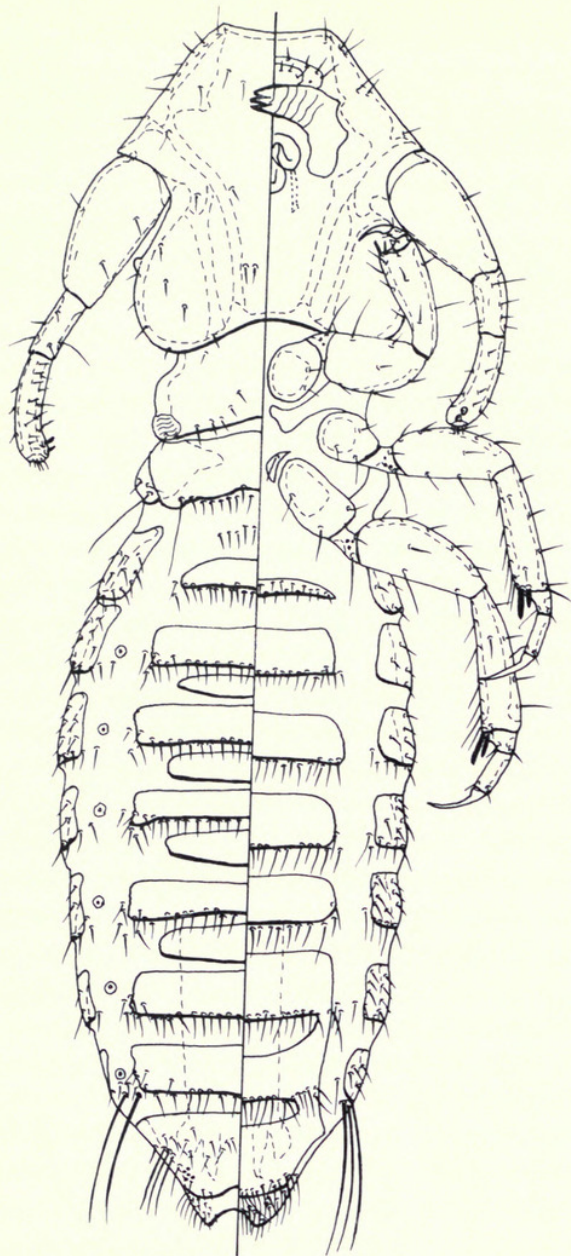
Eutrichophilus cercolabes Mjöberg, 1910 (figs. 18–20)

Eutrichophilus cercolabes Mjöberg, 1910:72, Figures 7, 8. Type host: *Coendou prehensilis* (Linnaeus)—misidentification.

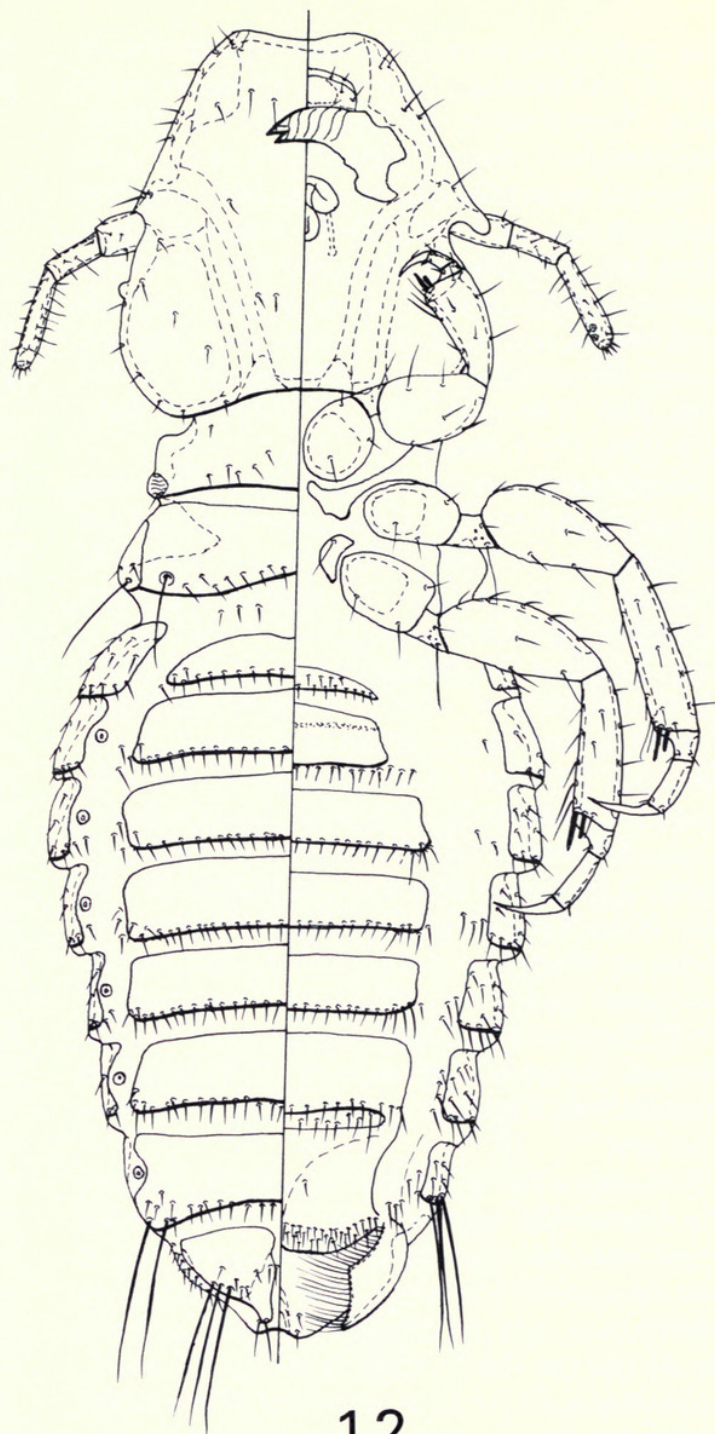
MALE—Much as for *E. andersoni* (fig. 11). Head longer than wide with broad shallow medioanterior concavity; short dorsal setae; inner pair of mid-dorsal head setae variably medioanterior to or aligned transversely between outer pair; scape much enlarged. Pronotum with 3–5 medioposterior setae on each side. Metanotum with total of 21–29 marginal setae between long corner setae; longest seta of metapleuron subequal to long adjacent metanotal seta. Tergal setae short: I, 5–9; II, 23–27; III, 28–37; IV–VIII, 33–42; IX with patch of 15–24 conspicuous sensilla (fig. 19) on each side; terminal segment with posterior margin broadly rounded to flattened (fig. 19). Pleuron VIII and lateral tergum VIII with very long setae. Large accessory tergal plate on III–VI. Spiracles large. Sternal setae similar in length to tergal setae; II, 31–40; III–VI, 26–34; VII–VIII, 23–33. Genitalia near to Figure 13, with broad apically tapered and curved parameres, short broad mesomeres, and bridge connecting bases of parameres broader in middle; with large spinose sac; sides of basal apodeme straight, parallel. Dimensions: TW, 0.66–0.70; HL, 0.73–0.74; SL, 0.42–0.45; SW, 0.18–0.22; PW, 0.59–0.62; MW, 0.64–0.66; AWIV, 0.91–0.96; TL, 3.07–3.19; GW, 0.29–0.32; GPL, 0.18–0.19; GBAL, 0.52–0.57.

FEMALE—Much as for *E. andersoni* (fig. 12). As for male, except as follows. Head slightly wider than long. Scape much smaller. Tergal setae: I, 3–9; II, 25–30; III–VIII, 29–41. Last segment with 19–27 short setae anterior to and mediad of long setae (fig. 20). No accessory tergal plates. Sternal setae: II, 28–40; III–VI, 20–32; VII, 28–35; chaetotaxy and shape of sterna II–III as in Figure 18, with sternite II strongly arched, III with large partitioned anterior portion nestled into sternite II. Ventral terminalia (fig. 20) with large angulate gonapophyses, each with 30–42 marginal setae; total of 39–50 short setae on subgenital plate, with distinct space between setae and posterior margin of plate; patch of about 10 short setae beneath each gonapophysis; margin of subgenital plate relatively straight, with median indentation. Dimensions: TW, 0.78–0.82; HL, 0.69–0.73; PW, 0.64–0.66; MW, 0.81–0.85; AWIV, 0.92–1.08; TL, 2.77–2.99.

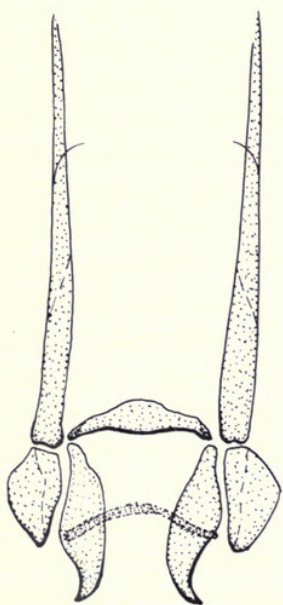
TYPE MATERIAL—Ex *Coendou spinosus*: lectotype female, 4 female paralectotypes, BRAZIL:



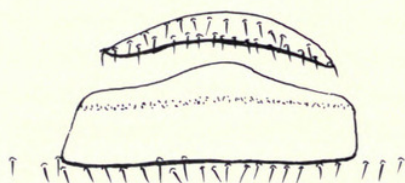
11



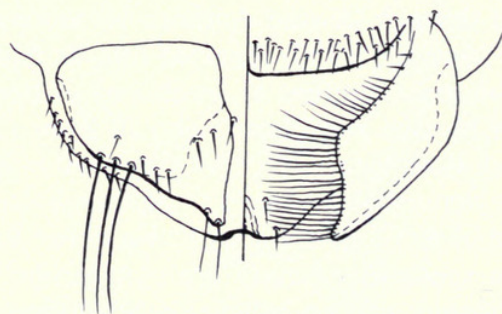
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14



15

FIGS. 11-15. *Eutrichophilus andersoni*: 11, male. 12, female. 13, male genitalia. 14, female sternites II-III. 15, female terminalia.

Rio Grande do Sul: Colonia de Sta. Cruz, 10.VII.1899, coll. Fr. Stieglmayr; in collection of Zoologisches Museum, Hamburg. *Other Material*—*Ex Coendou spinosus*: BRAZIL: Santa Catarina: Nova Teutônia, 35 males, 23 females.

REMARKS—This species is readily separated from the following four members of the *cercolabes* group by dimensional differences and/or the male with the rounded terminalia and a larger more conspicuous sensilla patch on each side of the last tergite and the female with the configuration of sternites II–III as in Figure 18 and the setae of the subgenital plate placed well anterior of the margin (fig. 20).

Upon determining that *Eutrichophilus cercolabes* represented a complex of species, it became imperative to confirm if our concept of the species based upon the published description and subsequent use in the literature matched the identity of the material that Mjöberg (1910) used for his original description. In his species description of *E. cercolabes*, Mjöberg (1910) stated that he had few specimens of the species from the collection of the Hamburg Museum from a male(?) *Cercolabes prehensilis*. Originally, we were pessimistic in our pursuit of Mjöberg's specimens since we were unaware of any mention of the type series in the literature after 1910 and we knew that the lice preserved on slides in the Zoologisches Museum in Hamburg were destroyed in World War II during the Allied forces firebombing in 1943. However, through the generous assistance of H. Strümpel, we were able to locate a vial containing five fluid-preserved adult females from Mjöberg's original type series in the Hamburg Museum. After mounting and studying these specimens, we are convinced that we have interpreted his species correctly. To stabilize the species further, we herein designate one of these females as a lectotype, with the remaining four assuming the status of paralectotypes. Mjöberg (1910) gives descriptive details and dimensions for a male and a female, even though we found only females in his vial of type specimens; these described specimens were likely slide-mounted and are presumably destroyed.

Mjöberg (1910) originally described *Eutrichophilus cercolabes* from a porcupine he called "Quendu-Stachelschwein" and assumed to be *Coendou prehensilis*. Werneck (1936, 1945, 1950) was the first to doubt that Mjöberg's type host(s) for the species *E. cercolabes*, *E. cordiceps*, and *E. minor* were identified correctly. Hopkins and Clay (1952), however, without comment, corrected the host to *C. villosus*. We assume that the "correction" by Hopkins and Clay (1952) on the type host

for Mjöberg's three species is an extension of the view of Hopkins (1949, p. 487) in which he stated, "All the above were described from a 'Quendu-Stachelschwein' which Mjöberg assumed to have been *C. prehensilis*. As all three forms have been taken many times in great numbers from specimens of *C. villosus* it seems almost certain that Mjöberg's assumption was incorrect." Werneck (1936) stated that he examined a large number of examples of this species of both sexes from *C. villosus*, and later Werneck (1950) reported that *C. villosus* is the only host species for *E. cercolabes* that has been properly verified. *Coendou villosus* we are now treating as a junior synonym of *C. spinosus*. This represents the first of three species taken from *C. spinosus* apparently from the same locality, Colonia de Sta. Cruz, Rio Grande do Sul, Brazil, and perhaps from the same host individual. Although this specific locality is associated with Mjöberg's specimens, Weidner (1966) reported that the Mallophaga in the Hamburg Museum used by Mjöberg in his dissertation were, without exception, from an animal from the zoo. This now calls into question the accuracy of this locality. Quite often with older zoo specimens, the localities associated with them represent the point from which they were exported from the country rather than a specific locality of capture. Given that this was a captive animal, it is possible that several individuals were housed or shipped together, thus allowing for louse transfer.

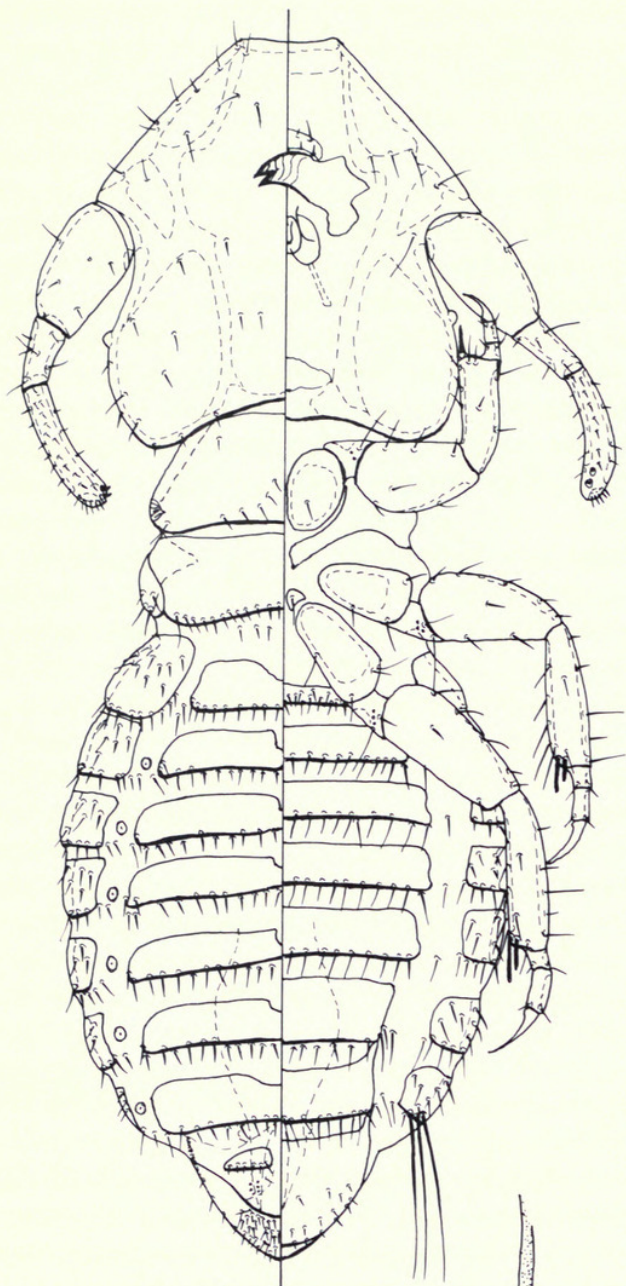
The material examined herein from Nova Teutônia had been identified previously by K. C. Emerson as *Eutrichophilus cercolabes* even though he believed the type host of this louse was *Coendou prehensilis*. *Eutrichophilus australis* was considered a junior synonym of *E. cercolabes* by Werneck (1950) and subsequent workers; however, we here recognize these as two distinct species that are separable by the characters listed below in the account of *E. australis*.

Coendou spinosus, the orange-spined hairy dwarf porcupine, occurs in extreme northeastern Argentina, southern Brazil, eastern Paraguay, and Uruguay.

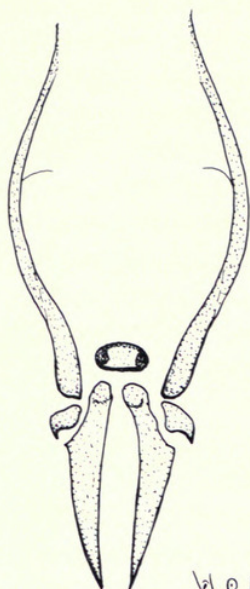
Eutrichophilus australis Ewing, 1936

Eutrichophilus australis Ewing, 1936:239. Type host: *Coendou villosus* (F. Cuvier) [= *C. spinosus* (F. Cuvier)].

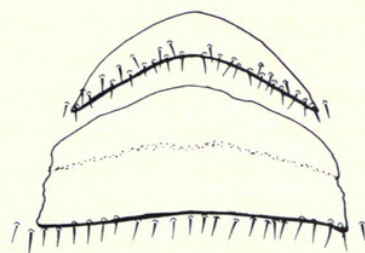
MALE—Very close to *E. cercolabes*, except as follows. Margin of metanotum with total of 20–



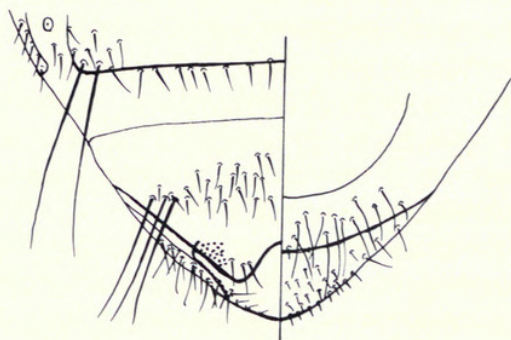
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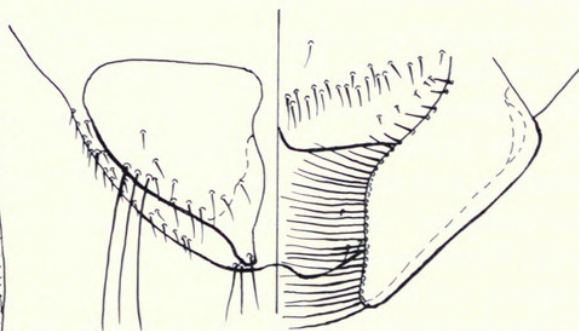
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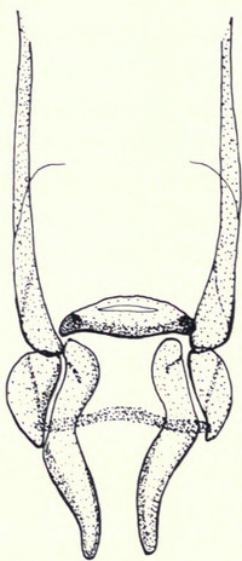
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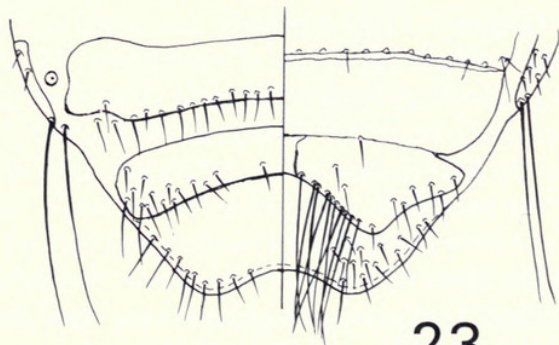
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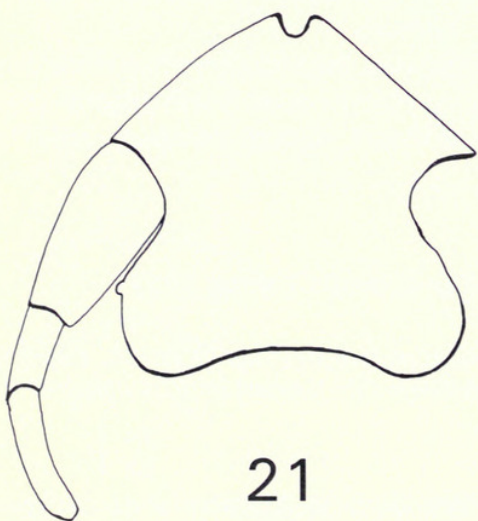
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23



21

22 setae between longer corner setae. Sternal setae: II, 23–30; III, 23–29; IV–VI, 25–30. Smaller dimensions: TW, 0.57–0.61; HL, 0.65–0.67; SL, 0.37–0.40; SW, 0.16–0.21; PW, 0.51–0.55; MW, 0.54–0.56; AWIV, 0.81–0.88; TL, 2.68–2.86; GW, 0.23–0.26; GPL, 0.14–0.17; GBAL, 0.46–0.50.

FEMALE—Very close to *E. cercolabes*, except as follows. Margin of metanotum with total of 19–23 setae between longer corner setae. Sternal setae: II, 24–31; III, 18–25; IV–VI, 23–29; VII, 26–30. Gonapophyses each with 22–34 marginal setae and total of 32–45 setae on subgenital plate. Smaller dimensions: TW, 0.65–0.71; HL, 0.63–0.66; PW, 0.54–0.60; MW, 0.63–0.73; AWIV, 0.75–0.92; TL, 2.25–2.56.

TYPE MATERIAL—Ex *Coendou spinosus*: holotype female, paratype male, PARAGUAY: [Paraguairí]: Sapucaí. Other Material—Ex *Coendou spinosus*: ARGENTINA: Misiones: Iguazú, 1 male, 1 female. PARAGUAY: [Paraguairí]: Sapucaí, 2 males, 2 females. [Guairá]: Villarrica, 15 males, 15 females (USNM 115123).

REMARKS—Werneck (1950), Hopkins and Clay (1952), and subsequent workers considered *Eutrichophilus australis* to be a junior synonym of *E. cercolabes*. While it is similar to that species, we feel the consistently much smaller dimensions of both sexes, along with a tendency for fewer metanotal and sternal setae, justify its resurrection and recognition as a distinct species. Ewing (1936, p. 240) considered *E. australis* similar to *E. cercolabes* but described it as differing in “having the forehead trapezoidal instead of subtriangular, a much broader hair-groove, and the sides of the abdomen subparallel.” The host was given as *Coendou villosus*, but, as mentioned above, we now treat that name as a junior synonym of *C. spinosus*. *Coendou spinosus* was treated as *C. paraguayensis* by Emmons and Feer (1990).

The locality Ewing (1936, p. 239) gave for the type, “Sapucay, Paraguay,” is without doubt Sapucaí, in northern Paraguairí Province on the railway southeast of Asunción at 220 m. Sapucay is an older and often used spelling. Ewing reported that his small series was collected from two host porcupines that are deposited in the U.S. National Museum of Natural History, and he published the catalog numbers (115121 and 115123). Ewing list-

ed USNM 115121 as the host porcupine from which the type female of *Eutrichophilus australis* was taken, but that specimen is actually an opossum (*Didelphis*). The collections of the USNM do contain two specimens of porcupines from “Sapucay, Paraguay,” USNM 115122 and 115123. We examined both of these specimens and they represent *C. spinosus*, and, accordingly, we report the true host of *E. australis* to be *C. spinosus*.

Examination of Ewing’s type slides revealed a discrepancy between what Ewing (1936) said was on the slides and what is actually there. According to Ewing’s published description, the slide based on USNM skin 115121 [= 115122] was to have the type female, and the other slide, based on USNM skin 115123, was to have another female and three immatures. Actually, the type slide does have a single female that we assume to be the holotype [labeled in weak pencil “*australis*”], but it also has a headless male [labeled in weak pencil “different sp.”]. However, the reason for this latter comment escapes us, as the male conforms perfectly with the other males of our series of *Eutrichophilus australis*. The second slide has only two immatures instead of the female and three immatures supposedly on it. Judging from the condition of the specimens and the mounting medium (balsam), it does not appear that any of these specimens were remounted at a later date.

Eutrichophilus andersoni, new species
(figs. 11–15)

Type host: *Coendou bicolor simonsi* Thomas.

MALE—As in Figure 11. Head slightly longer than wide, with broad shallow medioanterior concavity; short dorsal setae; 4 middorsal setae usually aligned transversely, less often with inner pair medioanterior to outer pair; scape much enlarged. Pronotum with 3–5 medioposterior setae on each side. Metanotum with long outer marginal seta and total of 11–17 setae between them; longest seta of metapleuron subequal to long adjacent metanotal seta. Tergal setae short: I, 5–9; II, 22–29; III, 25–30; IV–VIII, 24–37; IX with 3 variably medium to long lateral setae and patch of 4–10

FIGS. 16–23. Figs. 16, 17. *Eutrichophilus minor*: 16, male. 17, male genitalia. Figs. 18–20. *Eutrichophilus cercolabes*: 18, female sternites II–III. 19, male terminalia. 20, female terminalia. Figs. 21–23. *Eutrichophilus lobatus*: 21, male head outline. 22, male genitalia. 23, male terminalia.

obscure sensilla on each side with irregular patch of short setae connecting them; terminal segment concave. Pleuron VIII and lateral tergum VIII with very long setae. Large accessory tergal plate on III–VI. Spiracles large. Sternal setae similar in length to tergal setae: II, 29–38; III–VIII, 22–33. Genitalia (fig. 13) with broad apically tapered and curved parameres, short broad mesomeres, and bridge connecting bases of parameres broader in middle; with large spinose sac; sides of basal apodeme straight, parallel. Dimensions: TW, 0.64–0.69; HL, 0.67–0.71; SL, 0.35–0.37; SW, 0.15–0.17; PW, 0.53–0.58; MW, 0.58–0.64; AWIV, 0.81–0.88; TL, 2.70–2.88; GW, 0.28–0.31; GPL, 0.16–0.18; GBAL, 0.42–0.47.

FEMALE—As in Figure 12. Much as for male, except as follows. Head slightly wider than long. Scape much smaller. Tergal setae: I, 5–7; II, 21–27; III–VIII, 27–37. Last segment (fig. 15) with cluster of 3 very long dorsal setae on each side and 12–16 short setae anterior and mediad of them. No accessory tergal plates. Sternal setae: II, 29–42; III, 20–29; IV–VII, 25–35; chaetotaxy and shape of sterna II–III as in Figure 14, with II only slightly arched and III with only small anterior portion subdivided from posterior part. Ventral terminalia (fig. 15) with large angulate gonapophyses, each with 25–32 marginal setae and 44–52 uniformly short setae on subgenital plate arranged in irregular double row near margin of plate; patch of about 10 short setae beneath each gonapophysis; margin of subgenital plate relatively straight, with median indentation. Dimensions: TW, 0.70–0.78; HL, 0.65–0.73; PW, 0.53–0.61; MW, 0.67–0.75; AWIV, 0.86–1.04; TL, 2.45–2.73.

TYPE MATERIAL—Ex *Coendou bicolor simonsi* (AMNH 214615): holotype female, BOLIVIA: Beni: Puerto Caballo on the Mamore River, 13°43'S, 65°21'W, 22 Sep 1965, coll. Sydney Anderson #6077; in collection of the American Museum of Natural History. Paratypes: BOLIVIA: 27 males, 31 females, same data as holotype; 3 males, 5 females, same except AMNH 214610, Mamore River, 13°35'S, 65°20'W, 25 Sep 1965, coll. Sydney Anderson #6113; paratypes distributed among American Museum of Natural History, National Museum of Natural History, Oklahoma State University, The Natural History Museum (London), and University of Minnesota.

ETYMOLOGY—This new species is named in honor of Sydney Anderson, AMNH, the collector of all specimens that are known, and in recognition of his extensive contributions to South American mammalogy.

REMARKS—*Eutrichophilus andersoni* is associated with the *cercolabes* group of five species but is recognizable from the other four by the combination of the indentation of the male terminalia (fig. 11), the female sternite II only slightly curved and sternite III with only a small anteriorly demarcated area (fig. 14), the female subgenital plate with the setae irregularly placed near the posterior margin (fig. 15), and the much smaller dimensions of both sexes.

The only specimens that we have seen from *Coendou bicolor simonsi* are those representing this new species. This material had been labeled as representing *Eutrichophilus cercolabes* by K. C. Emerson. As we discuss below, this host species has one other species of *Eutrichophilus* parasitizing it on a different subspecies of *C. bicolor* occurring in a different region of its broad geographic range.

Eutrichophilus duellmani, new species

Type host: *Coendou bicolor bicolor* (Tschudi).

MALE—Essentially as for *E. andersoni*, except as follows. Head wider than long. Metanotum with total of 18–23 setae between long corner setae. Tergal setae: III, 27–33; IV–VII, 30–38; VIII, 32–44. Sternal setae: II, 31–40; III–VI, 26–34; VII–VIII, 23–28. Much larger dimensions: TW, 0.82–0.87; HL, 0.79–0.84; SL, 0.41–0.45; SW, 0.18–0.20; PW, 0.61–0.69; MW, 0.70–0.75; AWIV, 0.97–1.05; TL, 3.23–3.47; GW, 0.32–0.36; GPL, 0.20–0.22; GBAL, 0.49–0.56.

FEMALE—Essentially as for *E. andersoni*, except as follows. Metanotum with total of 18–23 setae between long corner setae. Tergal setae: I, 6–13; II, 24–30; III, 28–32; IV–VII, 30–40. Much larger dimensions: TW, 0.89–0.96; HL, 0.81–0.87; PW, 0.63–0.72; MW, 0.83–0.89; AWIV, 1.06–1.19; TL, 3.03–3.26.

TYPE MATERIAL—Ex *Coendou bicolor bicolor* (KU 144560): holotype female, PERU: Madre de Dios: 14 km E Puerto Maldonado, Reserva Cuzco Amazónico, 200 m, 12°33'S, 69°03'W, 19 Jan 1990, coll. Errol D. Hooper #1; in collection of Snow Entomological Museum, University of Kansas, Lawrence. Paratypes: 7 males, 13 females, same data as holotype; in collections of Field Museum of Natural History, Museo Javier Prado (Lima, Peru), National Museum of Natural History, Oklahoma State University, University of Kansas, and University of Minnesota.

ETYMOLOGY—This species is named after William E. Duellman, University of Kansas, in recognition of his many contributions to systematic biology in the Neotropics and for his efforts in making RMT's work in Peru possible, productive, and enjoyable.

REMARKS—*Eutrichophilus duellmani* is very close to *E. andersoni*, being distinguished from it by its consistently much larger dimensions and the larger number of marginal metanotal setae.

***Eutrichophilus maximus* Bedford, 1939**

Eutrichophilus maximus Bedford, 1939:118, Figure 14. Type host: *Coendou rothschildi* Thomas.

MALE—Unknown.

FEMALE—*Eutrichophilus maximus* is represented only by the single female type specimen collected in Gamboa, Canal Zone, Panama. We have not studied this individual but have noted from the descriptive details by Bedford (1939) and Werneck (1950) that it is of large size, approximately comparable to that of *E. duellmani*. However, both authors show only a total of 14 or 16 marginal metanotal setae, as opposed to at least 20 for *E. duellmani*. Because the specimen is from a taxon of host different from that of *E. duellmani* and because the male has not been collected, we feel the most conservative action is to continue to recognize it as different from the Peruvian series.

Rothschild's porcupine, *Coendou rothschildi*, the host of *Eutrichophilus maximus*, occurs throughout most of Panama to western Colombia west of the Andes. Some authors consider *C. rothschildi* conspecific with *C. bicolor*, treating these northern populations as the subspecies *C. bicolor rothschildi* (Corbet & Hill, 1991). Emmons and Feer (1990, p. 198) probably correctly stated, "If *C. rothschildi* is a valid species, the *C. 'bicolor'* west of the Andes are probably that species."

***Eutrichophilus minor* Mjöberg, 1910
(figs. 16, 17)**

Eutrichophilus minor Mjöberg, 1910:77, Figures 44, 47, 48. Type host: *Coendou prehensilis* (Linnaeus)—misidentification.

MALE—As in Figure 16. Head wider than long, with moderately wide slightly indented anterior

portion; short dorsal setae; 4 middorsal setae aligned transversely; scape moderately enlarged. Pronotum with 3–5 medioposterior setae on each side. Metanotum with only medium outer marginal seta and total of 19–25 somewhat shorter setae between them; metapleuron lacking any longer setae. With at most only vague suggestion of weak median division of tergites. Tergal setae: I, 3–6; II–III, 21–25; IV–VII, 23–29; VIII, 16–21; IX with each side having 5–6 setae on small plate followed by patch of sensilla and several minute setae; terminal segment evenly rounded, with dense patch of minute to short dorsal setae. Very long setae on pleuron VIII. Without evident accessory tergal plates. Spiracles large. Sternal setae slightly longer than tergal setae: II, 18–26; III–VI, 17–22; VII, 15–17; VIII, 16–23. Genitalia (fig. 17) with tapering straight parameres, small mesomeres, and oval accessory structure at base of parameres; with very small lightly spiculate sac; sides of basal apodeme arched outward through entire length. Dimensions: TW, 0.46–0.56; HL, 0.46–0.52; SL, 0.17–0.20; SW, 0.11–0.12; PW, 0.35–0.42; MW, 0.40–0.46; AWIV, 0.59–0.66; TL, 1.61–1.83; GW, 0.10–0.11; GPL, 0.13–0.15; GBAL, 0.24–0.28.

FEMALE—Much as in Figure 25. As for male, except as follows. Scape smaller. Longer corner metanotal and metapleural setae. Tergal setae: I, 3–10; II, 19–24; III, 26–32; IV–VII, 28–38; VIII, 26–32. Last segment (fig. 28) with cluster of 3 very long setae on each side and 7–10 short setae anterior to and mediad of them. Sternal setae: II, 24–36; III–VII, 22–31; chaetotaxy and shape of sterna II–III as in Figure 27. Ventral terminalia (fig. 28) with very large gonapophyses having striated surface texture, each with 43–53 short to medium marginal setae, patch of medium setae beneath each gonapophysis, and gonapophyses so large as to be sprung out from body; total of 50–65 setae on subgenital plate, with longer setae toward midline situated on lobe of plate. Dimensions: TW, 0.65–0.71; HL, 0.51–0.60; PW, 0.46–0.52; MW, 0.53–0.63; AWIV, 0.83–0.95; TL, 2.24–2.51.

TYPE MATERIAL—Ex *Coendou spinosus*: lectotype male, 16 male, 26 female paralectotypes on slides, 30 male, 69 female paralectotypes in alcohol, BRAZIL: Rio Grande do Sul: Colonia de Sta. Cruz, 10.VIII.1899, coll. Fr. Stieglmayr; lectotype and most paralectotypes in collection of Zoologisches Museum, Hamburg; other paralectotypes in collections of Field Museum of Natural History, National Museum of Natural History, Oklahoma State University, The Natural History Museum, and University of Minnesota. *Other*

Material—Ex *Coendou spinosus*: URUGUAY: Montevideo Zoo, 2 males.

REMARKS—*Eutrichophilus minor* is easily separated from other species in the genus by the male's unique genitalic features (fig. 17) and lack of accessory tergal plates and the female with the very large sprung gonapophyses and unique shape and chaetotaxy of the subgenital plate.

This is the first of three species in the *minor* group for which the males apparently lack accessory abdominal tergal sclerites. This is at variance with the generic characterization by Lyal (1985, p. 265) in which he stated "... male terga, at least of abdominal segments V and VI, with anterior and posterior sclerites."

In his description of *Eutrichophilus minor*, Mjöberg (1910) stated that he had a large amount of both sexes from a female *Coendou prehensilis* from the collections of the Hamburg Museum. As with *E. cercolabes*, Mjöberg (1910) originally reported the type host for *E. minor* as *C. prehensilis*, and Werneck (1936) reported examining a large number of examples of both sexes from *C. villosus*. Hopkins and Clay (1952) formally corrected the identification of the type host to *C. villosus*, and we further alter this to *C. spinosus*. This represents the second of three species apparently occurring together on *C. spinosus* in Brazil.

In a situation parallel to that of *Eutrichophilus cercolabes*, once we found that what had been recognized as *E. minor* by various workers was actually a complex of species, it became imperative to determine on which of these Mjöberg had based his species. Fortunately, we obtained two vials with 142 adult specimens from the Zoologisches Museum, Hamburg, representing the Mjöberg type series of *E. minor*. To stabilize the species *E. minor*, we are here designating a male as lectotype and the remainder of the series as paralectotypes.

***Eutrichophilus emersoni*, new species
(figs. 24–28)**

Type host: *Coendou spinosus* (F. Cuvier).

MALE—As in Figure 24. Head about as long as wide, with moderately wide slightly indented anterior portion; 4 middorsal setae variably aligned transversely to having inner pair medioanterior to outer; scape moderately enlarged. Pronotum with 3–5 medioposterior setae on each side. Metanotum with only medium outer marginal seta and total of 20–25 shorter setae between them; metapleuron lacking longer seta. Tergal setae: I, 5–8;

II, 20–25; III–VII, 21–29; VIII, 18–22; IX with each side having 6–7 short setae on small plate followed by patch of sensilla and few small setae; terminal segment rounded, with patch of minute to short dorsal setae. Very long setae on pleuron VIII and long seta on lateral tergum VIII. Without evident accessory tergal plates. Spiracles large. Sternal setae slightly longer than tergal setae: II, 23–31; III–VI, 18–25; VII, 16–20; VIII, 19–24. Genitalia (fig. 26) with tapering curved parameres, elongate mesomeres, and elongate accessory structure at base of parameres; with medium spinose sac; sides of basal apodeme arched outward in middle. Dimensions: TW, 0.56–0.59; HL, 0.54–0.56; SL, 0.20–0.22; SW, 0.10–0.11; PW, 0.42–0.47; MW, 0.47–0.51; AWIV, 0.67–0.75; TL, 1.97–2.06; GW, 0.14–0.16; GPL, 0.10–0.12; GBAL, 0.32–0.38.

FEMALE—As in Figure 25; sterna II–III as in Figure 27; terminalia as in Figure 28. Apparently inseparable from that of *E. minor*. Dimensions: TW, 0.64–0.73; HL, 0.58–0.62; PW, 0.51–0.53; MW, 0.61–0.64; AWIV, 0.90–0.98; TL, 2.50–2.61.

TYPE MATERIAL—Ex *Coendou spinosus*: holotype male, BRAZIL: Santa Catarina: Nova Teutônia, 6 Jun 1941, F. Plaumann; in collection of Field Museum of Natural History. Paratypes: 22 males, 24 females, same data as holotype; in collections of Field Museum of Natural History, National Museum of Natural History, Oklahoma State University, The Natural History Museum, University of Minnesota, and Zoologisches Museum, Hamburg.

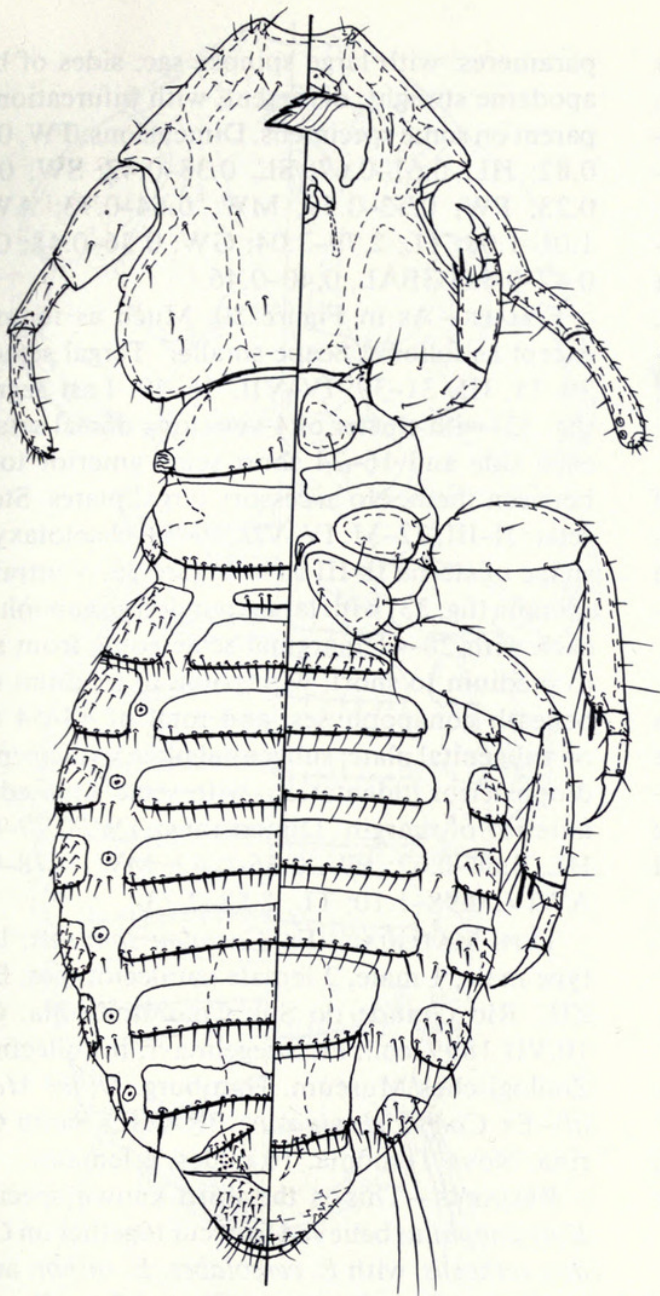
ETYMOLOGY—This species is named in honor of the late K. C. Emerson in recognition of his numerous publications on chewing louse taxonomy and his establishment at Oklahoma State University of one of the world's foremost collections of chewing lice that made this study, as well as many other studies, possible.

REMARKS—*Eutrichophilus emersoni*, while having many similarities to *E. minor*, is quite different for the male in aspects of chaetotaxy, dimensions, and genitalia.

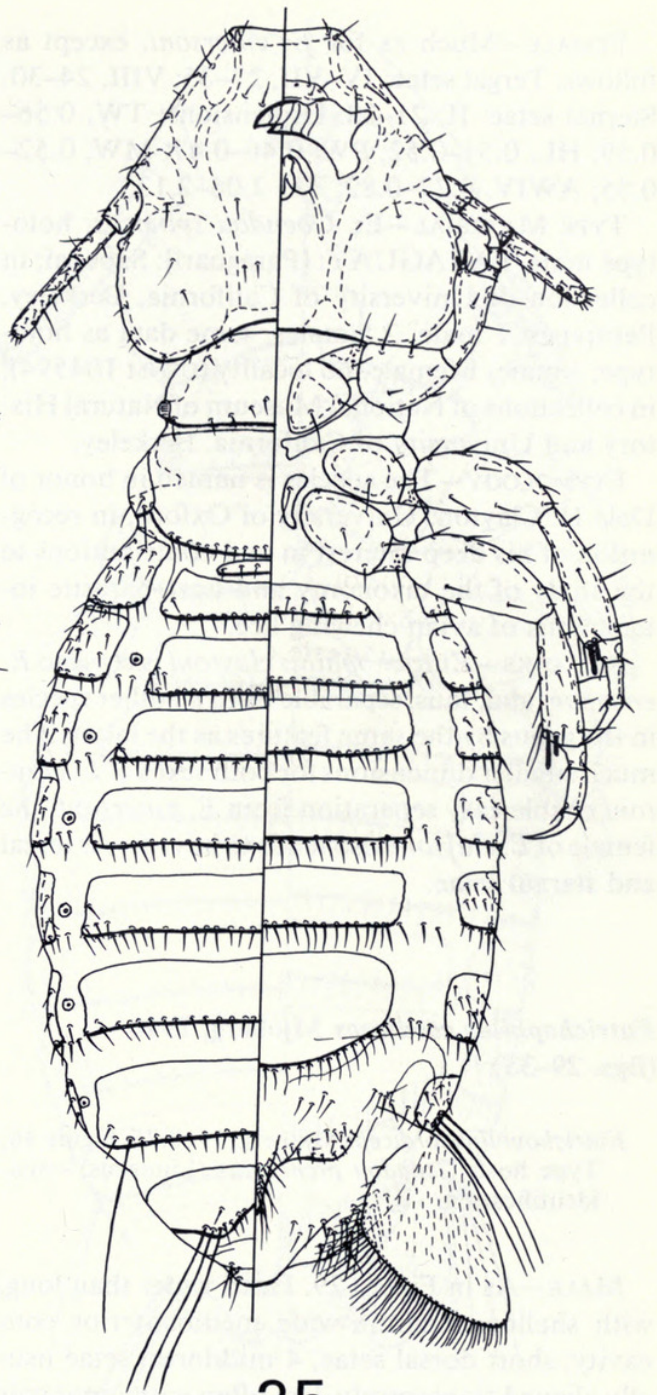
***Eutrichophilus claytoni*, new species**

Type host: *Coendou spinosus* (F. Cuvier).

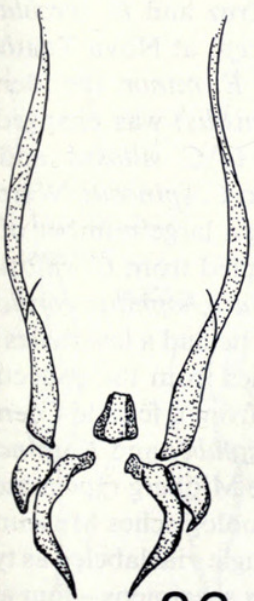
MALE—Much as for *E. emersoni*, except as follows. Dimensions: TW, 0.51–0.52; HL, 0.50–0.51; SL, 0.18–0.20; PW, 0.40–0.41; MW, 0.43–0.44; AWIV, 0.65–0.66; TL, 1.71–1.73; GW, 0.13–0.14; GBAL, 0.30–0.31.



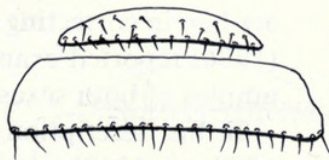
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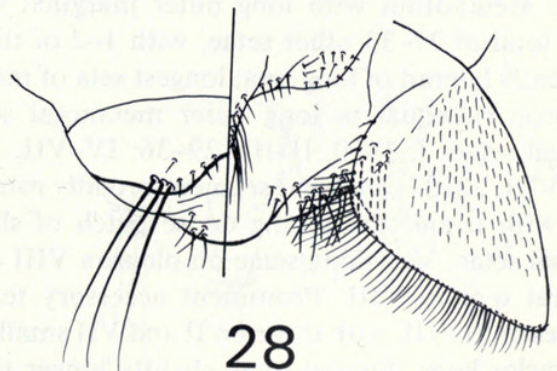
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FIGS. 24-28. *Eutrichophilus emersoni*: 24, male. 25, female. 26, male genitalia. 27, female sternites II-III. 28, female terminalia.

FEMALE—Much as for *E. emersoni*, except as follows. Tergal setae: IV–VII, 27–35; VIII, 24–30. Sternal setae: II, 21–28. Dimensions: TW, 0.56–0.59; HL, 0.51–0.52; PW, 0.46–0.47; MW, 0.52–0.55; AWIV, 0.77–0.82; TL, 2.06–2.13.

TYPE MATERIAL—Ex *Coendou spinosus*: holotype male, PARAGUAY: [Paraguarí]: Sapucaí; in collection of University of California, Berkeley. Paratypes: 1 male, 2 females, same data as holotype; 1 male, 1 female, no locality (USNM 104594); in collections of National Museum of Natural History and University of California, Berkeley.

ETYMOLOGY—The species is named in honor of Dale H. Clayton, University of Oxford, in recognition of his deep interest in and contributions to the study of the taxonomy and host–parasite interactions of avian chewing lice.

REMARKS—*Eutrichophilus claytoni* is close to *E. emersoni* and, thus, separable from all other species in the genus by the same features as the latter. The much smaller dimensions for both sexes of *E. claytoni* enable easy separation from *E. emersoni*; the female of *E. claytoni* also tends to have fewer tergal and sternal setae.

***Eutrichophilus cordiceps* Mjöberg, 1910 (figs. 29–33)**

Eutrichophilus cordiceps Mjöberg, 1910:75, Figure 46.

Type host: *Coendou prehensilis* (Linnaeus)—misidentification.

MALE—As in Figure 29. Head wider than long, with shallow medium-wide medioanterior concavity; short dorsal setae; 4 middorsal setae usually aligned transversely, less often with inner pair medioanterior to outer pair; scape much enlarged. Pronotum with 5–8 medioposterior setae on each side. Metanotum with long outer marginal seta and total of 27–33 other setae, with 1–2 of these typically laterad of long seta; longest seta of metapleuron subequal to long outer metanotal seta. Tergal setae: I, 3–10; II–III, 29–36; IV–VII, 32–48; VIII, 28–37; terminal segment broadly rounded, with it and IX having dense patch of short dorsal setae. Very long setae on pleuron VIII and lateral tergum VIII. Prominent accessory tergal plates on II–VII, with those on II and VII smallest. Spiracles large. Sternal setae slightly longer than tergal setae: II–III, 23–33; IV–VI, 27–38; VII, 29–37; VIII, 30–41. Genitalia (fig. 31) with large pointed blade-like parameres, short broad mesomeres, and slender transverse structure at base of

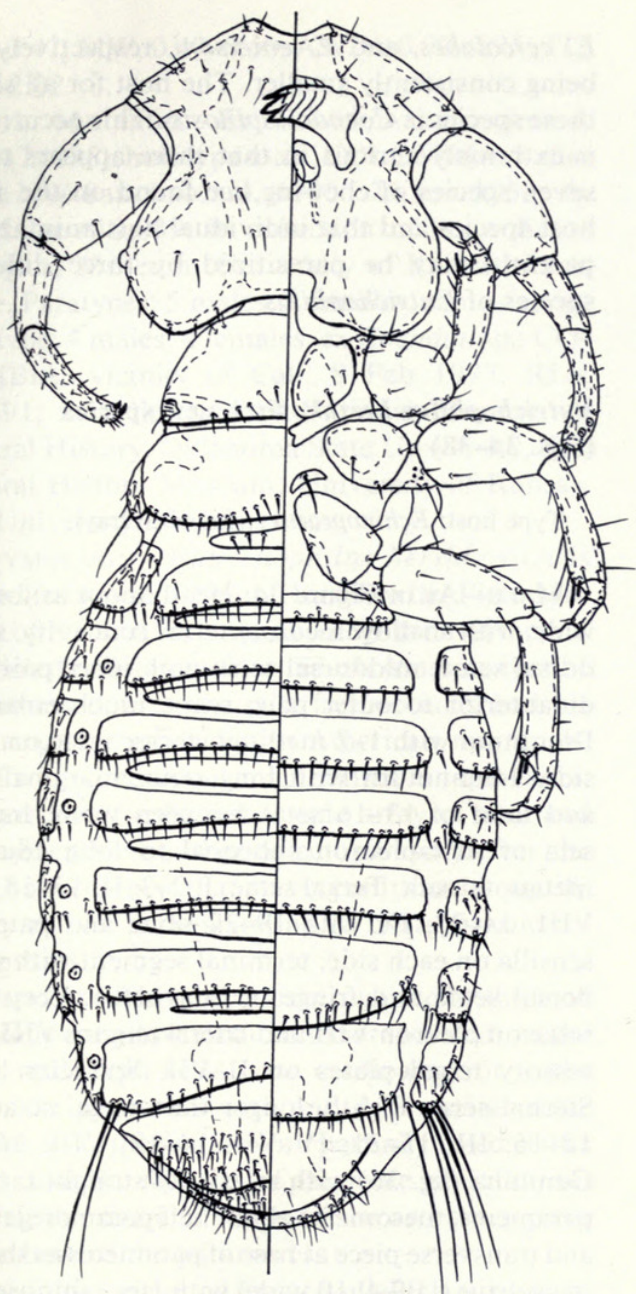
parameres; with large spinose sac; sides of basal apodeme straight, divergent, with bifurcation apparent on some specimens. Dimensions: TW, 0.71–0.82; HL, 0.61–0.67; SL, 0.38–0.42; SW, 0.18–0.23; PW, 0.53–0.59; MW, 0.64–0.73; AWIV, 1.01–1.08; TL, 2.79–3.04; GW, 0.36–0.42; GPL, 0.42–0.45; GBAL, 0.40–0.46.

FEMALE—As in Figure 30. Much as for male, except as follows. Scape smaller. Tergal setae: II, 30–35; III, 31–39; IV–VII, 36–49. Last segment (fig. 33) with cluster of 4 very long dorsal setae on each side and 16–24 short setae anterior to and between them. No accessory tergal plates. Sternal setae: II–III, 22–31; IV–VII, 26–38; chaetotaxy and shape of sterna II–III as in Figure 32. Ventral terminalia (fig. 33) with large rounded gonapophyses, each with 28–41 marginal setae going from short to medium to short, with patch of medium setae beneath gonapophyses, and total of 43–54 setae on subgenital plate; subgenital plate with deep medioposterior indentation, with setae situated well anterior of margin. Dimensions: TW, 0.77–0.82; HL, 0.64–0.67; PW, 0.56–0.62; MW, 0.78–0.85; AWIV, 0.98–1.10; TL, 2.58–2.73.

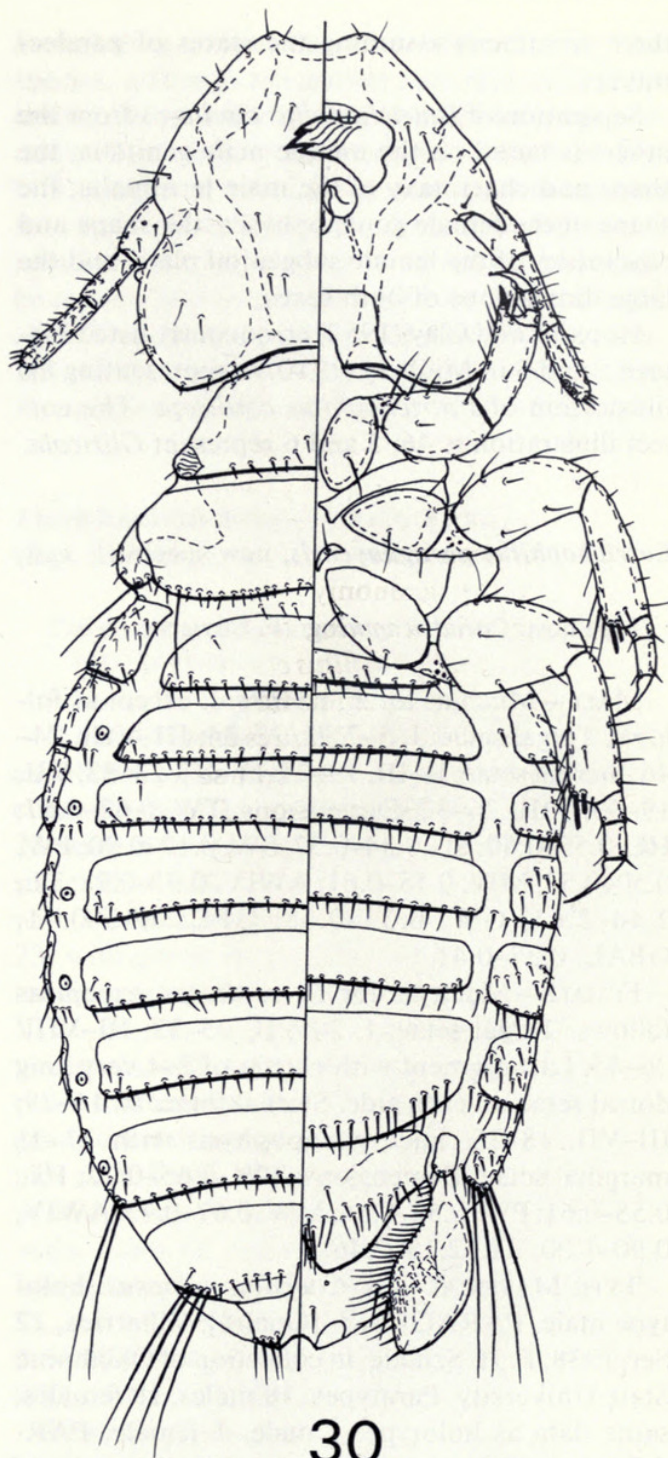
TYPE MATERIAL—Ex *Coendou spinosus*: lectotype male, 1 male, 2 female paralectotypes, BRAZIL: Rio Grande do Sul: Colonia de Sta. Cruz, 10.VII.1899, coll. Fr. Stieglmayr; in collection of Zoologisches Museum, Hamburg. *Other Material*—Ex *Coendou spinosus*: BRAZIL: Santa Catarina: Nova Teutônia, 10 males, 8 females.

REMARKS—This is the third known species of *Eutrichophilus* believed to occur together on *Coendou spinosus*, with *E. cercolabes*, *E. minor*, and *E. cordiceps* all having been collected from Brazilian hosts at Colonia de Sta. Cruz and *E. cercolabes*, *E. emersoni*, and *E. cordiceps* at Nova Teutônia. As with *E. cercolabes* and *E. minor*, the identity of the type host (*C. prehensilis*) was changed by Hopkins and Clay (1952) to *C. villosus*, and we are herein correcting that to *C. spinosus*. Werneck (1936) reported examining a large number of examples of both sexes collected from *C. villosus*.

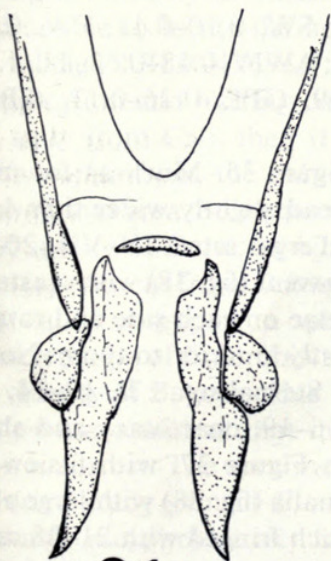
In his description of *Eutrichophilus cordiceps*, Mjöberg (1910) stated that he had a few males and a few females of this species from the collections of the Hamburg Museum from a female *Coendou prehensilis*. As with *E. cercolabes* and *E. minor*, it was necessary to obtain the Mjöberg type material of *E. cordiceps* from the Zoologisches Museum to confirm its identity. The single vial labeled as types of *E. cordiceps* contained six specimens—four adult *E. cordiceps*, one female of *E. minor*, and one immature specimen. From these, we designate here a male as lectotype of *E. cordiceps*, with the other



29



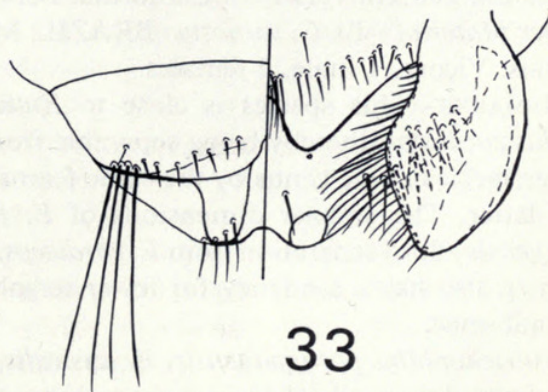
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FIGS. 29-33. *Eutrichophilus cordiceps*: 29, male. 30, female. 31, male genitalia. 32, female sternites II-III. 33, female terminalia.

three specimens assuming the status of paralectotypes.

Separation of *Eutrichophilus cordiceps* from the others is based on the unique male genitalia, the shape and chaetotaxy of the male terminalia, the shape of the female gonapophyses, the shape and chaetotaxy of the female subgenital plate, and the large dimensions of both sexes.

Hopkins and Clay (1952) erroneously listed Figures 5 and 6 in Mjöberg (1910) as representing his illustration of *Eutrichophilus cordiceps*. The correct illustration is 46; 5 and 6 represent *Gliricola*.

Eutrichophilus paraguayensis, new species

Type host: *Coendou spinosus* (F. Cuvier).

MALE—Much as for *E. cordiceps*, except as follows. Tergal setae: I, 3–7; II, 22–34; III–VIII, 24–46. Sternal setae: II–III, 19–29; IV–VI, 23–33; VII, 19–30; VIII, 26–32. Dimensions: TW, 0.62–0.67; HL, 0.55–0.60; SL, 0.34–0.37; SW, 0.17–0.20; PW, 0.50–0.53; MW, 0.58–0.61; AWIV, 0.91–0.98; TL, 2.44–2.61; GW, 0.33–0.38; GPL, 0.38–0.41; GBAL, 0.37–0.41.

FEMALE—Much as for *E. cordiceps*, except as follows. Tergal setae: I, 2–5; II, 23–35; III–VIII, 26–45. Last segment with cluster of 2–4 very long dorsal setae on each side. Sternal setae: II, 16–29; III–VII, 18–35. Each gonapophysis with 22–31 marginal setae. Dimensions: TW, 0.65–0.72; HL, 0.55–0.61; PW, 0.52–0.56; MW, 0.67–0.73; AWIV, 0.90–1.00; TL, 2.18–2.46.

TYPE MATERIAL—Ex *Coendou spinosus*: holotype male, PARAGUAY: [Guairá]: Villarrica, 12 Sep 1938, F. H. Schade; in collection of Oklahoma State University. Paratypes: 18 males, 19 females, same data as holotype; 1 male, 1 female, PARAGUAY: [Paraguarí]: Sapucaí; in collections of Oklahoma State University, The Natural History Museum, and University of California, Berkeley. *Other Material*—Ex *C. spinosus*: BRAZIL: Minas Gerais: Viçosa, 1 male, 2 females.

REMARKS—This species is close to *Eutrichophilus cordiceps*, thereby being separable from all other species in the genus by the same features as the latter. The smaller dimensions of *E. paraguayensis* afford separation from *E. cordiceps*. The former also has a tendency for fewer tergal and sternal setae.

Eutrichophilus paraguayensis, *E. australis*, and *E. claytoni* were all taken in what appears to be the same collection at Sapucaí, Paraguay, and each is separable from its nearest species, *E. cordiceps*,

E. cercolabes, and *E. emersoni*, respectively, by being consistently smaller. The host for all six of these species is *Coendou spinosus*. This occurrence is extremely curious in that there appears to be seven species of chewing lice found on the same host species and that individual host animals apparently may be parasitized by three different species of *Eutrichophilus*.

Eutrichophilus hershkovitz, new species (figs. 34–38)

Type host: *Echinoprocta rufescens* (Gray).

MALE—As in Figure 34. Head about as long as wide, with shallow medioanterior concavity; short dorsal setae; middorsal setae with inner pair medioanterior to outer pair; scape much enlarged. Pronotum with 1–2 medioposterior setae on each side. Metanotum with long outer marginal seta and total of 13–16 setae between them; longest seta of metapleuron subequal to long adjacent metanotal seta. Tergal setae: I, 2–3; II, 13–18; III–VIII, 14–22; IX with 19–22 setae and patch of sensilla on each side; terminal segment with short dorsal setae and fringe of long setae. Very long setae on pleuron VIII and lateral tergum VIII. Accessory tergal plates on II–VII. Spiracles large. Sternal setae slightly longer than tergal setae: II, 12–16; III, 15–21; IV–VII, 14–18; VIII, 16–20. Genitalia (fig. 36) with relatively straight tapered parameres, mesomeres about half paramere length, and transverse piece at base of parameres as shown, measuring 0.09–0.10 wide; with large spinose sac; sides of basal apodeme relatively straight, slightly divergent. Dimensions: TW, 0.44–0.47; HL, 0.44–0.48; SL, 0.20–0.22; SW, 0.10–0.11; PW, 0.35–0.37; MW, 0.37–0.42; AWIV, 0.58–0.62; TL, 1.68–1.79; GW, 0.18–0.19; GPL, 0.16–0.17; GBAL, 0.28–0.30.

FEMALE—As in Figure 35. Much as for male, except as follows. Head slightly wider than long; scape not enlarged. Tergal setae: IV–VII, 20–25; VIII, 13–16. Last segment (fig. 38) with cluster of 3 very long dorsal setae on each side and total of 8–10 short setae mostly anterior to them. No accessory tergal plates. Sternal setae: II, 12–14; III–V, 17–21; VI–VII, 16–19; chaetotaxy and shape of sterna II–III as in Figure 37, with fusion laterally. Ventral terminalia (fig. 38) with large elongate gonapophyses each fringed with 21–28 setae, and total of 40–47 setae on subgenital plate, these short and following curved margin of plate. Dimensions: TW, 0.48–0.51; HL, 0.47–0.50; PW,

0.38–0.42; MW, 0.47–0.50; AWIV, 0.70–0.75; TL, 1.88–2.02.

TYPE MATERIAL—Ex *Echinoprocta rufescens* (MVZ 124088): holotype male, COLOMBIA: Valle: 4 km NW San Antonio, 6500', 25 Jun 1958, A. H. Miller #10,039; in collection of Snow Entomological Museum, University of Kansas, Lawrence. Paratypes: 5 males, 3 females, same data as holotype; 4 males, 4 females, ex *Coendou* sp.: COLOMBIA: vicinity of Cali, 8 Feb 1977, RLR #42691; in collections of National Museum of Natural History, Oklahoma State University, The Natural History Museum, University of Kansas, and University of Minnesota.

ETYMOLOGY—*Eutrichophilus hershkovitzi* is named in honor of Philip Hershkovitz, Field Museum of Natural History, in recognition of the unparalleled collections from South America that he has amassed over the past five decades and his enduring studies on South American mammals, and for his interest in mammalian ectoparasites. He personally collected a wide array of taxa and a considerable number of ectoparasites over the past half century that have contributed significantly to our understanding of host–parasite relationships.

REMARKS—This species is recognized by the head with only a shallow medioanterior indentation, the inner middorsal head setae medioanterior to the outer, the pronotum with only 1–2 median setae on each side, the female with partially fused sterna II–III, and the features of the male genitalia, including the size and shape of the accessory piece at the base of the parameres.

Our initial series of *Eutrichophilus hershkovitzi* is from a porcupine identified only as *Coendou* sp. and from “vicinity of Cali, Colombia.” We have been unable to locate the host porcupine, which was labeled “RLR-42691,” to confirm the host identification and locality data. If this porcupine was truly from Cali, then it should represent *C. bicolor richardsoni*, the only porcupine known to occur in that area. Subsequently, after an analysis of all species of *Eutrichophilus*, we obtained a series of specimens from *Echinoprocta rufescens*, the short-tailed porcupine, a species found only in a restricted area of Colombia’s eastern cordillera in the vicinity of Bogotá. This was a wild-shot host and we are confident that this host–louse association is correct. The specimens we obtained from the dried study skin of *E. rufescens* are indistinguishable morphologically from our initial series of *E. hershkovitzi*. In no other instance do we see a single species of *Eutrichophilus* on two different host species. Thus, we are skeptical that *E. hersh-*

kovitzi does indeed occur on both of these host species, although we cannot rule that out. There is also the possibility that the *Coendou* sp. represented a misidentified captive animal or that both species of porcupines were housed together in a zoo. Cali is a major commercial center, and animals captured elsewhere in Colombia might have been held in captivity there and then shipped elsewhere. Because of the confusion over the identity of the porcupine from Cali, we are designating *E. rufescens* as the type host of *E. hershkovitzi*.

***Eutrichophilus lobatus* Ewing, 1936 (figs. 21–23)**

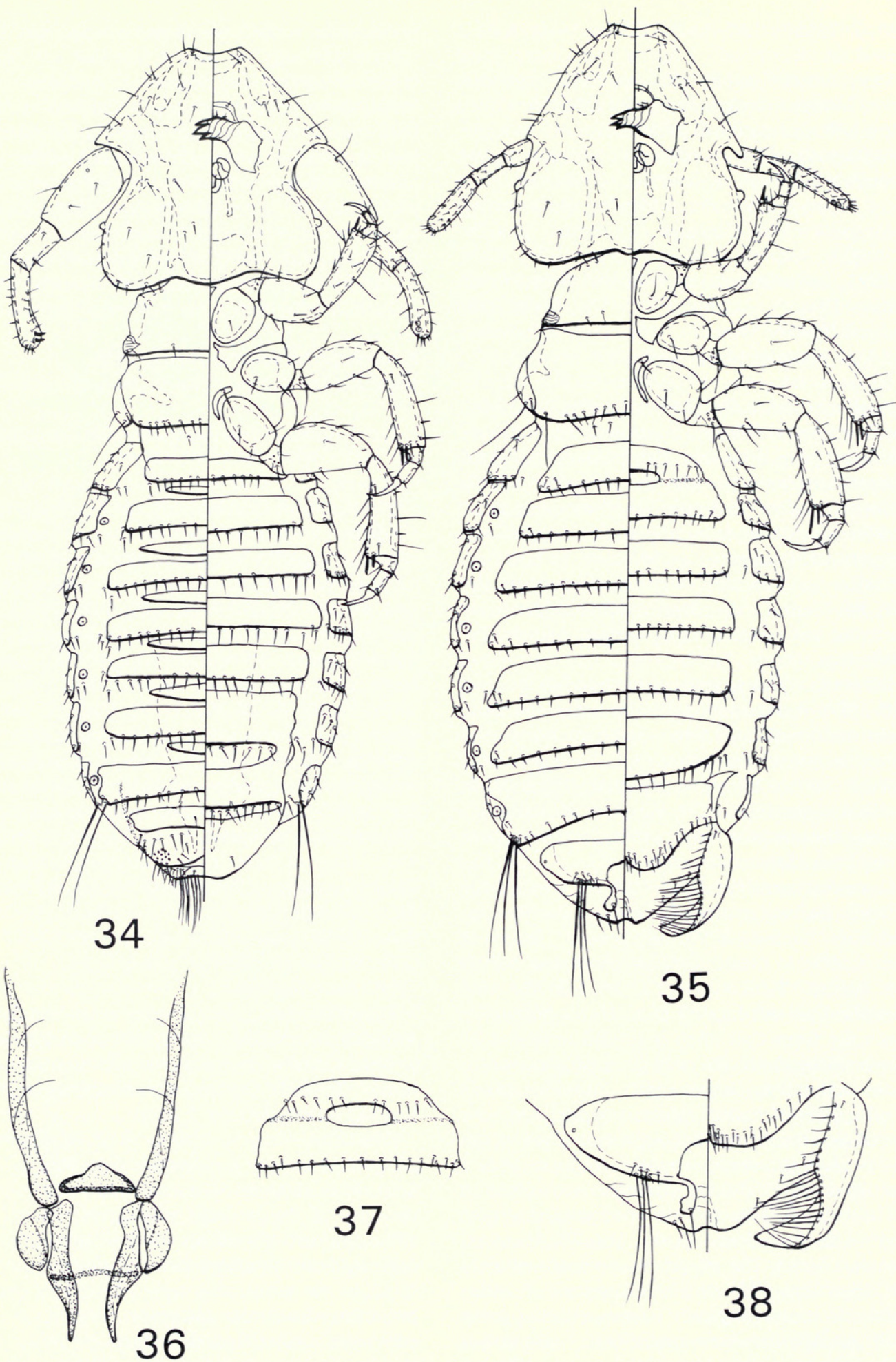
Eutrichophilus lobatus Ewing, 1936:238, Figure 2. Type host: *Coendou pruinosus* Thomas.

MALE—Much like that of *E. hershkovitzi*, except as follows. Head with narrow deep medioanterior concavity (fig. 21). Margin of metanotum with 19–22 setae between long corner setae. More tergal setae: II, 17–20; III, 21–22; IV–VIII, 25–31; IX with 15 setae on each side; terminal segment (fig. 23) with gentle indentation, fringed with short to medium setae. More sternal setae: II, 16–17; III–V, 21–24; VI, 18–21; VII, 21–22; VIII, 24. Ventral terminalia with cluster of long setae associated with other shorter setae (fig. 23). Genitalia (fig. 22) with gently curved tapered parameres, mesomeres about half their length, and transverse piece associated with the base of parameres as shown, 0.13–0.14 wide; sides of basal apodeme straight, parallel. Larger dimensions: TW, 0.49–0.50; HL, 0.49–0.50; SL, 0.27–0.29; SW, 0.13–0.14; PW, 0.38; MW, 0.44; AWIV, 0.64–0.67; TL, 1.82–1.85; GW, 0.22; GPL, 0.19–0.20; GBAL, 0.28–0.31.

FEMALE—Unknown.

TYPE MATERIAL—Ex *Coendou pruinosus*: South America: no specific locality, 1 male on type slide (USNM 172985). *Other Material*—Ex *Coendou vestitus*: COLOMBIA: Cundinamarca: Quipile (W of Bogotá) (AMNH 70529), 1 male.

REMARKS—This species is close to *Eutrichophilus hershkovitzi* but readily separated by differences in size and shape of transverse piece at the base of the genitalic parameres, overall dimensions, and placement of setae on the terminalia. At first we thought the differences, especially those of the terminalia, were illusionary due to mounting distortion. However, close study has convinced us that these differences are actual, and this conclusion is supported by other features of chaetotaxy.



FIGS. 34-38. *Eutrichophilus herskovitzi*: 34, male. 35, female. 36, male genitalia. 37, female sternites II-III. 38, female terminalia.

Ewing (1936) did not designate a holotype but, rather, based his description on the type slide specimen as was his usual practice. We have studied this slide (USNM 50060) and found that it contains a mix of two species. The slide contains one adult male, one adult female, and three immatures. Of the three immatures, one is definitely a male of *Eutrichophilus comitans* within the third-instar skin; the other two immatures are too young to identify. We believe the single female is also that of *E. comitans*, but this is difficult to say for certain. Werneck (1950) postulated that the females of *E. lobatus* and *E. comitans* are so similar that they may not be separated. Both of these species are sympatric on the same host individuals. Circumstantially, we believe that the only females available to us from *Coendou pruinosus* represent *E. comitans* and that we have yet to see females of *E. lobatus*; we further suspect that the female of *E. lobatus*, when known, will have similarities to that of *E. hershkovitzi*, not *E. comitans*. This then leaves the single male on the type slide as the type of *E. lobatus* and, as such, there is no need for lectotype designation here. Ewing (1936) devoted three times as much space to the description of the male, giving many more details than for the female, and his only illustration was that of the male genitalia. Therefore, the application of the male description to *E. lobatus* and consignment of the female to *E. comitans* is consistent with Ewing's emphasis.

Coendou pruinosus is considered by some as a subspecies of *C. vestitus* (see Woods, 1993); if that arrangement is followed, the type host would be called *C. vestitus pruinosus*.

***Eutrichophilus comitans* Werneck, 1950 (figs. 39–43)**

Eutrichophilus comitans Werneck, 1950:56, Figures 42, 43. Type host: *Coendou pruinosus* Thomas.

MALE—As in Figure 39. Head about as long as wide, with narrow medioanterior concavity; short dorsal setae; middorsal head setae with inner pair medioanterior to outer pair; scape much enlarged. Pronotum with 1, less often 2, medioposterior setae on each side. Metanotum with long outer marginal seta and total of 13–14 setae between them; metapleuron with only short setae. Tergal setae: I, 2; II, 16–18; III, 16–21; IV–VIII, 18–24; IX with 22–26 short setae; terminal segment dorsally with scattered short to medium setae. Very long setae on pleuron VIII. Accessory tergal plates on III–

VII, with those on III–IV smallest. Sternal setae slightly longer than tergal setae: II, 14–16; III–VIII, 15–20. Genitalia (fig. 41) with long tapered parameres, short oblong mesomeres, and no apparent accessory structures at base of parameres; with medium spiny sac; sides of basal apodeme relatively short, straight, widely divergent. Dimensions: TW, 0.46–0.47; HL, 0.45–0.46; SL, 0.23–0.24; SW, 0.11–0.12; PW, 0.34–0.37; MW, 0.39–0.41; AWIV, 0.57–0.61; TL, 1.65–1.68; GW, 0.16–0.17; GPL, 0.21–0.23; GBAL, 0.16–0.22.

FEMALE—As in Figure 40. Much as for male, except as follows. Head slightly wider than long; scape not enlarged. Metanotum with total of 12–17 setae between longer corner setae. Tergal setae shorter on VII–VIII than on III–VI: II, 17–23; III–VII, 22–30; VIII, 17–23. Last segment (fig. 43) with 12–16 very short setae across posterior margin of tergum IX. No accessory tergal plates. Sternal setae: II, 14–18; III, 17–22; IV–VI, 20–25; VII, 19–23; chaetotaxy and shape of sterna II–III as in Figure 42. Ventral terminalia (fig. 43) with very small gonapophyses, tapered, each with only 4–6 widely spaced marginal setae, and total of 14–22 setae on subgenital plate, with margin of plate evenly curved. Dimensions: TW, 0.50–0.54; HL, 0.45–0.53; PW, 0.38–0.41; MW, 0.47–0.50; AWIV, 0.68–0.75; TL, 1.78–1.98.

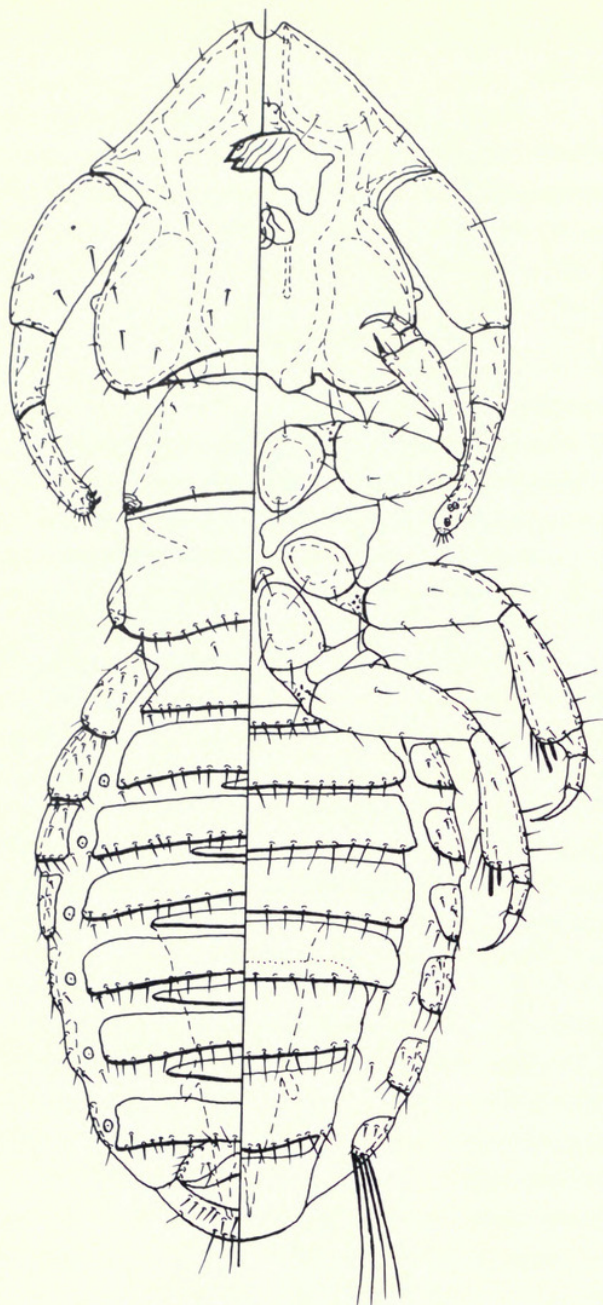
TYPE MATERIAL—Ex *Coendou pruinosus*: holotype male, 2 male and 1 female paratypes, VENEZUELA: [Mérida]: Mérida (AMNH 21350). **Other Material**—Ex *Coendou pruinosus*: VENEZUELA: Mérida, 3 females (2 of them headless) labeled *E. lobatus* on type slide (AMNH 21350); South America—on type slide of *E. lobatus* (USNM 172985), 1 female; no locality (USNM 172985), 5 females.

REMARKS—*Eutrichophilus comitans* is readily recognized from others of the genus by its symmetrical head and configuration of middorsal head setae, with the inner pair medioanterior to the outer, along with the unique male genitalia and the extremely small female gonapophyses with so few marginal setae on each.

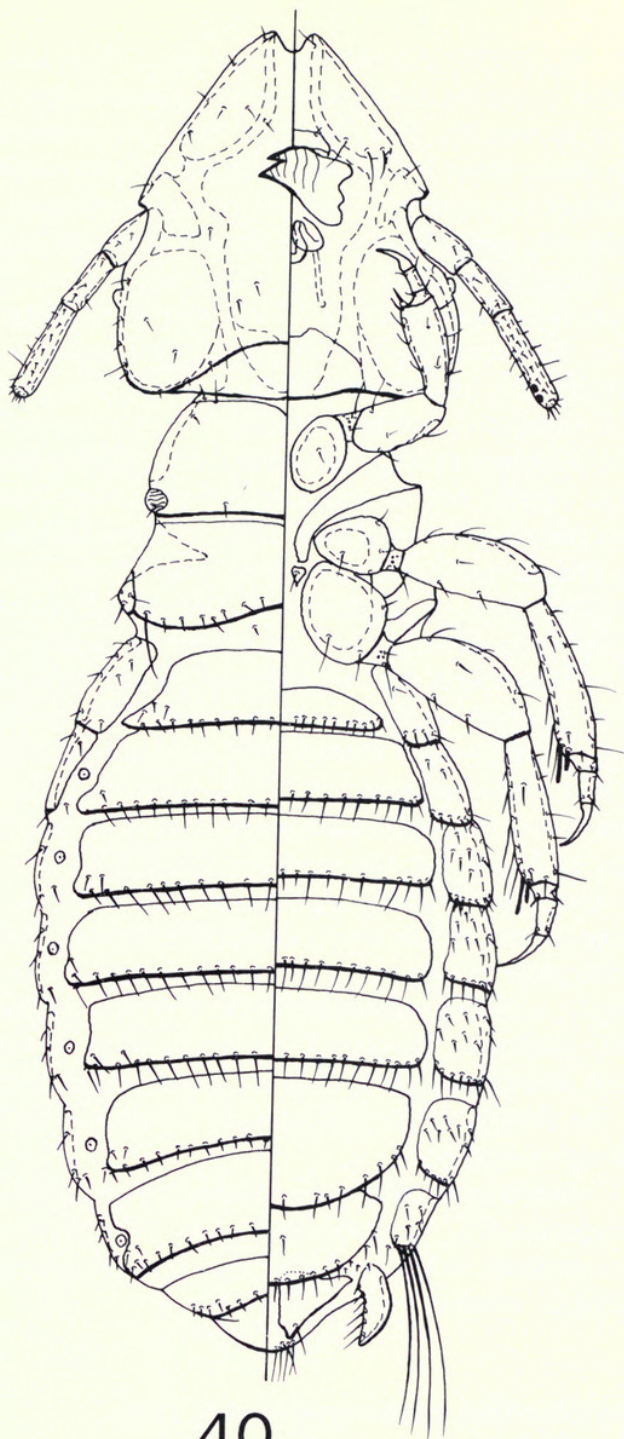
The status of the female of *E. comitans* and that of *E. lobatus*, both of which are sympatric on *C. pruinosus*, has been discussed under the latter species and will not be repeated here.

***Eutrichophilus guyanensis* Werneck, 1950 (figs. 44–48)**

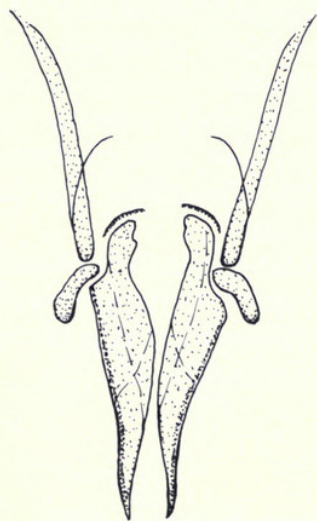
Eutrichophilus guyanensis Werneck, 1950:49, Figures 29–35. Type host: *Coendou melanurus* (Wagner).



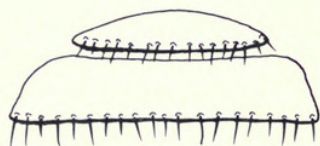
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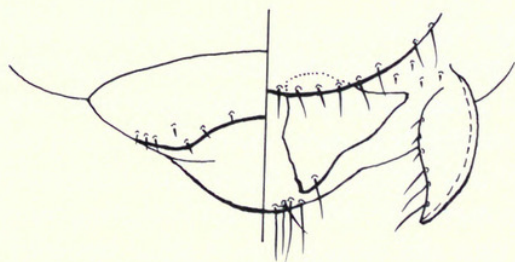
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FIGS. 39-43. *Eutrichophilus comitans*: 39, male. 40, female. 41, male genitalia. 42, female sternites II-III. 43, female terminalia.

MALE—As in Figure 44. Head distinctly longer than wide, with asymmetrically broad flattened medioanterior portion and compression of carinae on shortened side; minute to short dorsal setae; middorsal head setae minute, longitudinally aligned on each side; scape much enlarged. Pronotum with only 1–2 minute medioposterior setae on each side. Metanotum and metapleuron with only short to minute setae, total on metanotal margin of 16–19. Tergal setae: I, 0; II, 15–17; III, 16–19; IV–VI, 18–22; VII, 21–24; VIII, 13–16; IX and terminal segment with dorsal patches of short setae. Very long setae on pleuron VIII and lateral tergum VIII. Accessory tergal plates on V–VII, progressively larger from front to back. Spiracles large. Sternal setae longer than tergal setae: II, 10–12; III–VIII, 16–24. Genitalia (fig. 46) with broad acute parameres, mesomeres and accessory structures apparently fused with parameres, as shown; with large spinous sac; sides of basal apodeme essentially straight, parallel. Dimensions: TW, 0.67–0.72; HL, 0.74–0.80; SL, 0.45–0.47; SW, 0.18–0.21; PW, 0.51–0.55; MW, 0.49–0.57; AWIV, 0.81–0.88; TL, 2.46–2.74; GW, 0.19–0.21; GPL, 0.20–0.23; GBAL, 0.34–0.39.

FEMALE—As in Figure 45. Much as for male, except as follows. Head about as wide as long; scape small. Metanotum marginally with total of 14–17 setae. Tergal setae minute: II, 14–17; III, 17–24; IV–VI, 20–27; VII, 23–31; VIII, 16–20. Last segment (fig. 48) with cluster of 2–3 very long dorsal setae on each side and 4 minute setae between them. No accessory tergal plates. Sternal setae: II, 10–17; III–IV, 15–24; V–VII, 21–30; chaetotaxy and shape of sterna II–III as in Figure 47, with II nestled into anterior margin of III. Ventral terminalia (fig. 48) with small gonapophyses, rounded, each with 12–13 marginal setae, and total of 19–20 setae on subgenital plate, with margin of plate angulate. Dimensions: TW, 0.77–0.80; HL, 0.72–0.78; PW, 0.57–0.61; MW, 0.58–0.65; AWIV, 0.86–0.94; TL, 2.61–2.93.

TYPE MATERIAL—Ex *Coendou melanurus*: holotype male, 1 male and 1 female paratypes, GUY-ANA: Mazaruni-Potaro: Kartabo, 24 Mar 1924, coll. Wm. Beebe (AMNH 142955). *Other Material*—Ex *Coendou melanurus*: SURINAM: Marowijne: Moengo, 2 males, 2 females.

REMARKS—*Eutrichophilus guyanensis* is the first of two species recognized by the asymmetry associated with the anterior head. It is further differentiated from *E. exiguus*, the only other asymmetrical species of the genus, by the unique dorsal chaetotaxy and the details of the male genitalia and female terminalia.

Emerson and Price (1975) reported specimens from a porcupine collected at Moengo, Surinam; this locality, as noted above, is well within the range of *Coendou melanurus*, the type host.

Eutrichophilus exiguus Werneck, 1950 (figs. 49–53)

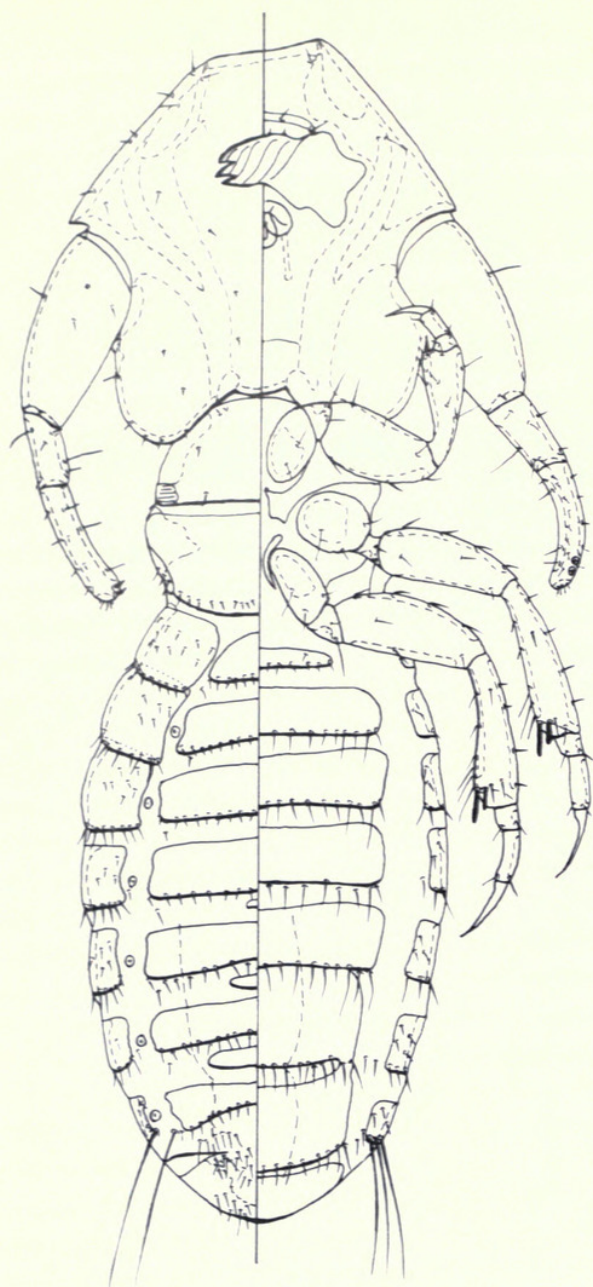
Eutrichophilus exiguus Werneck, 1950:52, Figures 36–41. Type host: *Coendou melanurus* (Wagner).

MALE—As in Figure 49. As for *E. guyanensis*, except as follows. Narrower medioanterior head margin; many head setae missing or represented only by alveoli; middorsal setae with inner pair medioanterior to outer; metanotum with long corner seta and 17–21 minute setae between them. Tergal setae shorter toward midline; I, 2; II, 16–19; III–VII, 18–26; VIII, 16–18; IX rounded, with short setae; terminal segment truncate, with patch of minute setae. With very long setae only on pleuron VIII. Accessory tergal plates on IV–VII. Sternal setae: II, 10; III, 15–18; IV–VII, 18–22; VIII, 16–18. Genitalia (fig. 51) with slender acute parameres, broad mesomeres, and narrow bridge connecting base of parameres; with small spinous sac; sides of basal apodeme straight, divergent. Much smaller in all dimensions: TW, 0.46–0.47; HL, 0.48–0.50; SL, 0.21–0.23; SW, 0.10–0.11; PW, 0.37; MW, 0.39–0.40; AWIV, 0.59–0.62; TL, 1.52–1.54; GW, 0.17; GPL, 0.16; GBAL, 0.21–0.22.

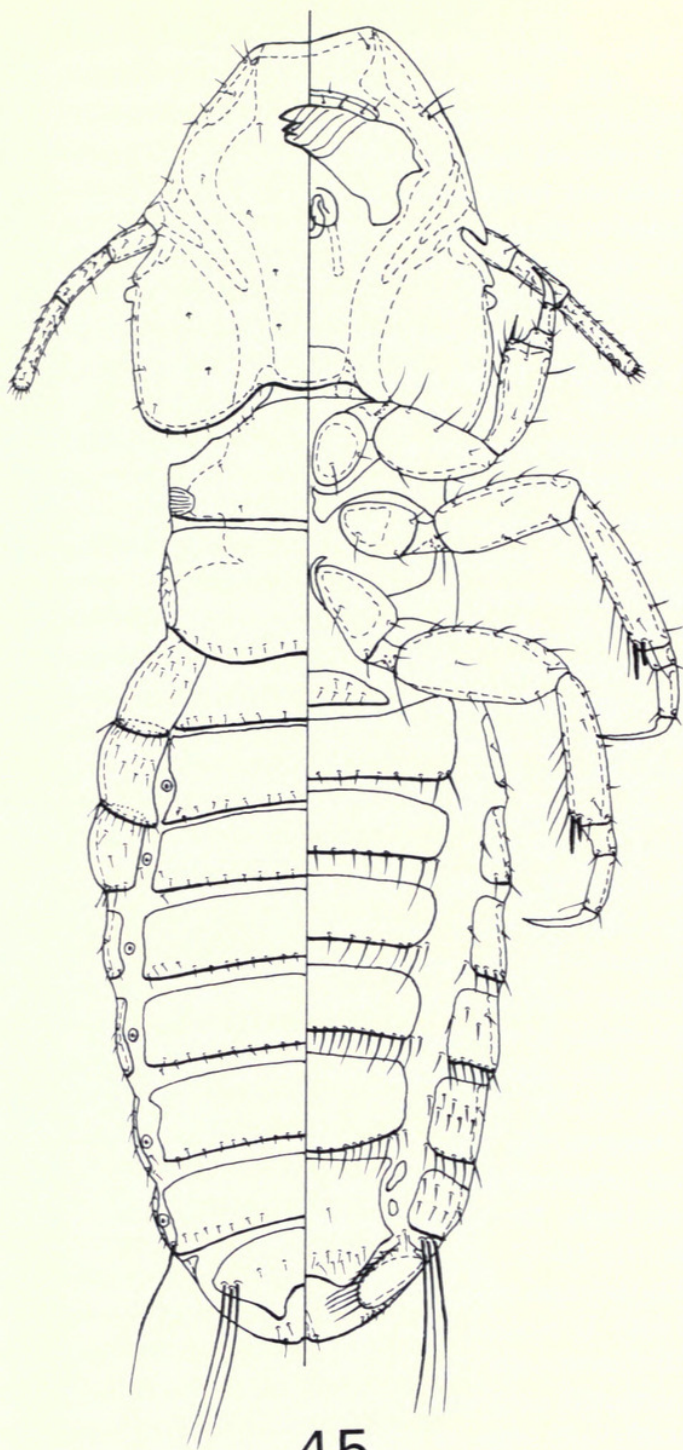
FEMALE—As in Figure 50. Much as for male, except as follows. Head wider than long; scape small. Last segment (fig. 53) with cluster of 3 very long setae on each side and 8 minute setae between them. Tergal setae all of fairly uniform length. No accessory tergal plates. Chaetotaxy and shape of sterna II–III as in Figure 52. Ventral terminalia (fig. 53) with small gonapophyses, rounded, each with only 5–6 short to medium setae, and total of 18 setae on subgenital plate, with margin of plate only slightly concave medially. Dimensions: TW, 0.54; HL, 0.51; PW, 0.41; MW, 0.47; AWIV, 0.70; TL, 1.86.

TYPE MATERIAL—Ex *Coendou melanurus*: holotype male, 1 male and 1 female paratypes. GUY-ANA: Mazaruni-Potaro: Kartabo, 24 Mar 1924, coll. Wm. Beebe (AMNH 142955).

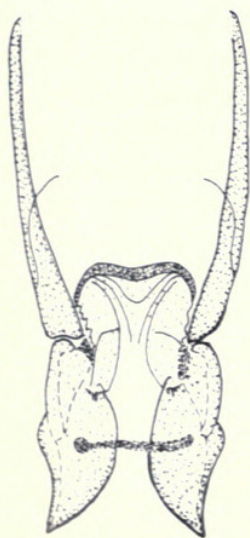
REMARKS—This and *Eutrichophilus guyanensis* are the only known members of *Eutrichophilus* that have an asymmetrical anterior head. In addition, they have minute dorsal head setae and unique male genitalia and female terminalia, to name some of the more obvious differences. The



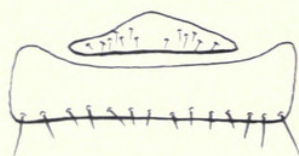
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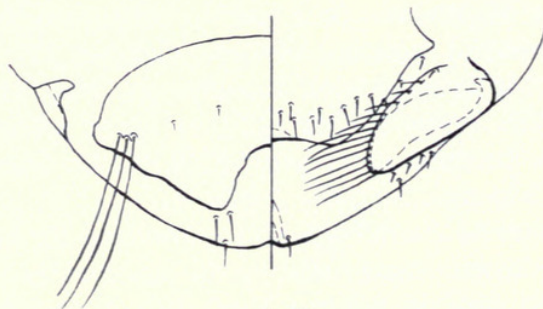
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48

FIGS. 44-48. *Eutrichophilus guyanensis*: 44, male. 45, female. 46, male genitalia. 47, female sternites II-III. 48, female terminalia.

two species are easily separated from each other by the gross differences in size, head shape, general body shape, and other features.

It is interesting that the two species with the head asymmetry are sympatric on *Coendou melanurus* and they represent the only lice known from this host taxon. Woods (1993) considered *C. insidiosus* to be the correct name for the porcupines of Surinam. Curiously, *C. melanurus* does not seem to have been reported previously from Guyana.

***Eutrichophilus moojeni* Werneck, 1945
(figs. 54–58)**

Eutrichophilus moojeni Werneck, 1945:143, Figures 63–68. Type host: *Chaetomys subspinosus* (Olfers).

MALE—As in Figure 55. Head about as long as wide; with only slight medioanterior indentation and appearance of being nearly round; short dorsal setae; middorsal setae with inner pair medioanterior to outer pair; much enlarged scape. Pronotum with 1 medioposterior seta on each side. Metanotum with long outer marginal seta and total of 2 setae between them; metapleuron with long seta subequal to that of the metanotum. Legs II–III grossly modified, distinctly different from first pair. Tergal setae: I, 2; II, 12–15; III, 18–19; IV–VI, 21–25; VII, 14–19; VIII with 2–3 very long corner setae and 14–17 very short setae between them; IX with medioposterior concavity and patch of very short dorsal setae; terminal segment rounded, with minute to short dorsal setae. Very long setae on pleura VII and VIII and lateral tergum VIII. Accessory tergal plate on II–VII. Spiracles very small. Sternal setae: II, 8–10; III, 12–13; IV–VIII, 13–19. Genitalia (fig. 58) with markedly curved parameres flared at distal tip, oval mesomeres, and elongate accessory structure at base of parameres; sides of basal apodeme as shown. Dimensions: TW, 0.51–0.53; HL, 0.52; SL, 0.27–0.30; SW, 0.14–0.15; PW, 0.43–0.46; MW, 0.47–0.51; AWIV, 0.74–0.77; TL, 2.26–2.34; GW, 0.23–0.26; GPL, 0.18–0.19; GBAL, 0.32–0.35.

FEMALE—As in Figure 54. Much as for male, except as follows. Scape not enlarged; flagellum with weak indication of terminal division. Tergal setae: III, 16–22; IV–VII, 18–27. Last segment (fig. 56) with cluster of 3–4 very long setae on each side and 16–18 short setae anterior to and between them. No accessory tergal plates. Sternal setae: II, 10–14; III, 12–14; IV–V, 15–17; VI, 20–21; VII, 24–25; chaetotaxy and shape of sterna II–III as in

Figure 57. Ventral terminalia (fig. 56) with very large sharply angulate gonapophyses, each with 28–31 long marginal setae, and total of 44–45 setae on subgenital plate, these setae being markedly longer medially; subgenital plate margin only slightly concave medially. Dimensions: TW, 0.53–0.54; HL, 0.53; PW, 0.46–0.47; MW, 0.56–0.58; AWIV, 0.82–0.87; TL, 2.43–2.44.

TYPE MATERIAL—Ex *Chaetomys subspinosus*: holotype male, allotype female, 1 male and 1 female paratypes, BRAZIL: Espírito Santo: Santa Teresa.

REMARKS—*Eutrichophilus moojeni* is so distinctively different from all other porcupine lice that a case could be made for description of a new, monotypic genus for this species. The head shape, the unique modification of legs II–III, the small spiracles, and the unusual shape of the male genitalic parameres are some of the more obvious gross differences.

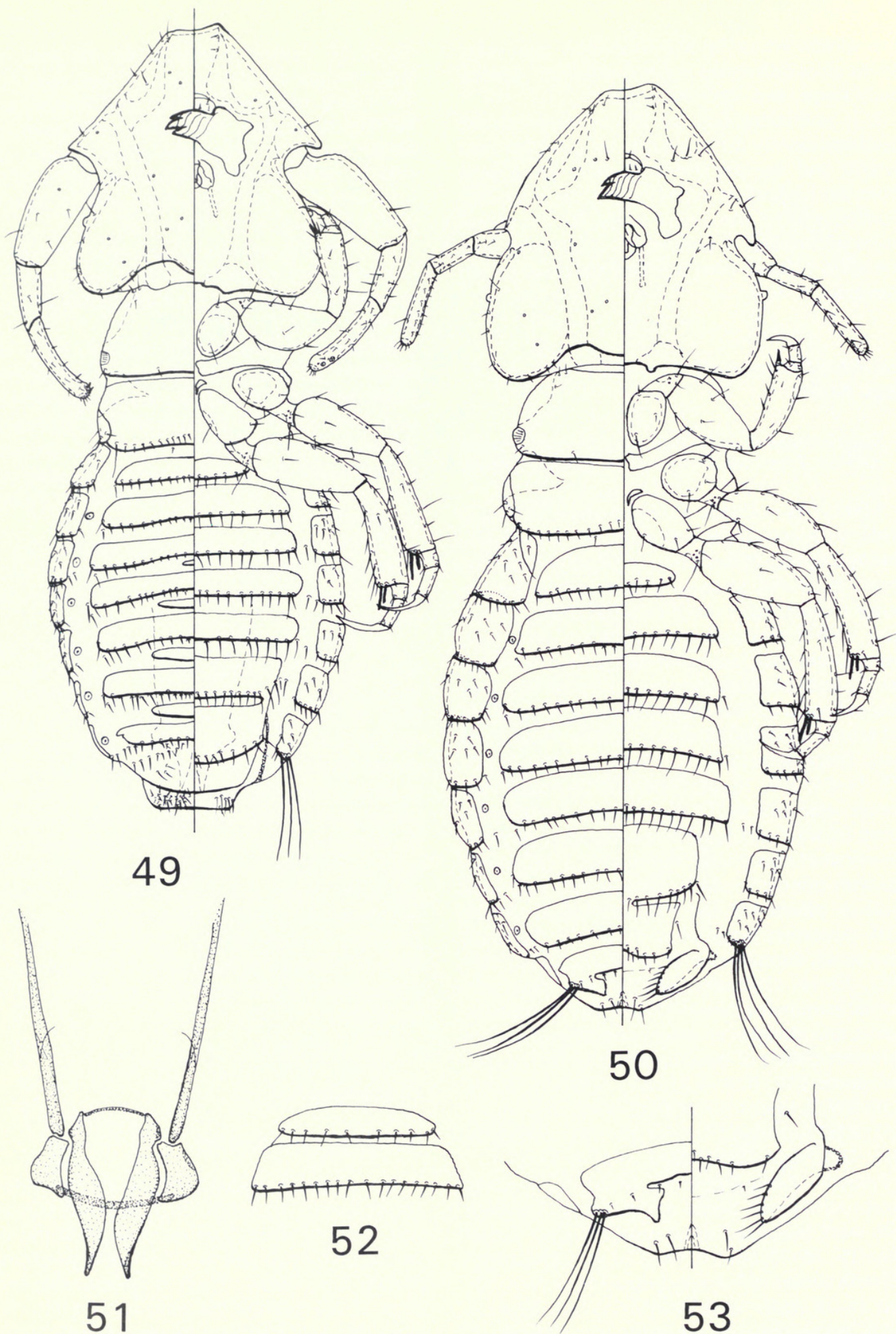
Werneck (1950) believed that the long legs of *Eutrichophilus moojeni* were an adaptation for the large diameter quills of the host, *Chaetomys subspinosus*.

The bristle-spined porcupine, *Chaetomys subspinosus*, of the Atlantic Forest region of Brazil is quite distinctive morphologically from all other New World porcupines. *Chaetomys*, like other members of the Atlantic coastal fauna, is clearly an old species, and its evolutionary relationships to other erethizontids are unclear. It has long been placed as a monotypic genus in the porcupine family Erethizontidae; however, it does share characters with the spiny rats of the family Echimyidae and some recent authors consider it an echimyid (see Discussion, below). Oliver and Santos (1991) provided a recent review of conservation problems concerning the bristle-spined porcupines and a discussion of the confusion surrounding their distribution.

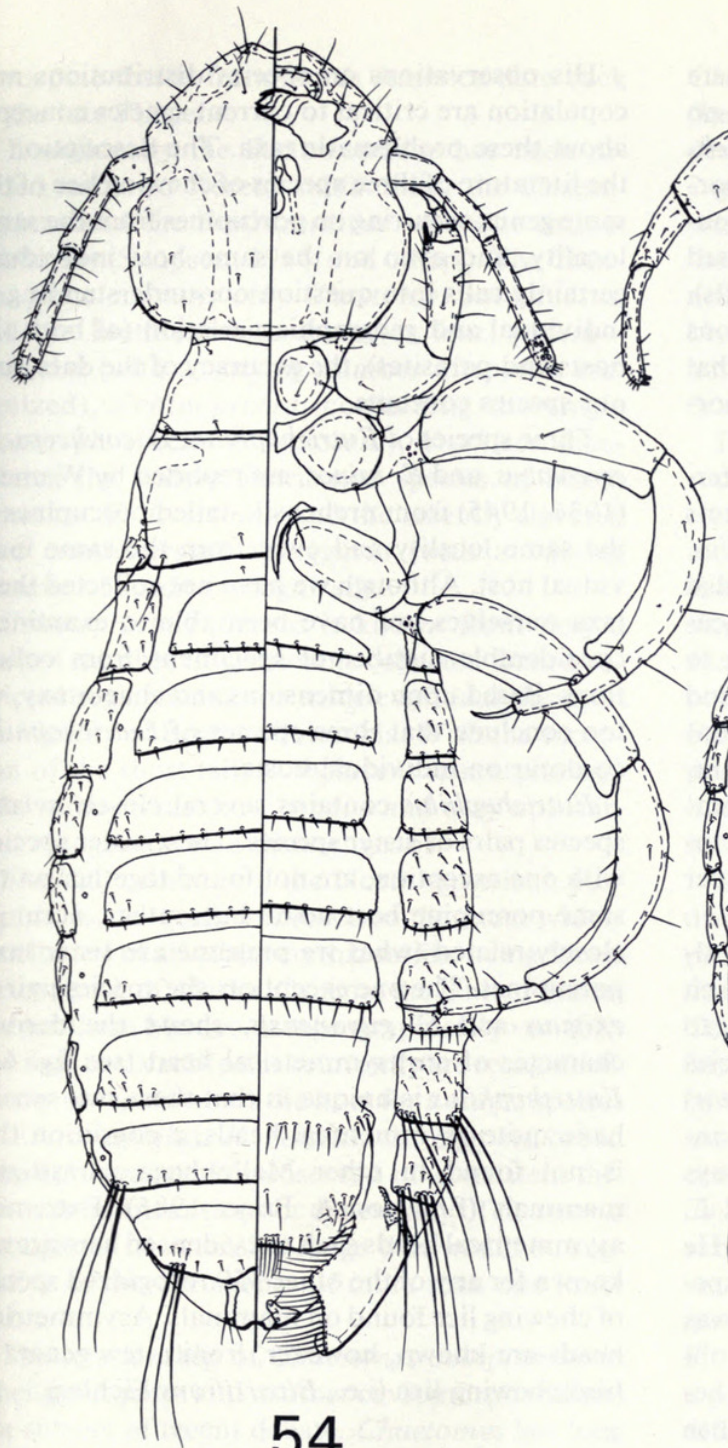
Discussion

Biology of *Eutrichophilus*

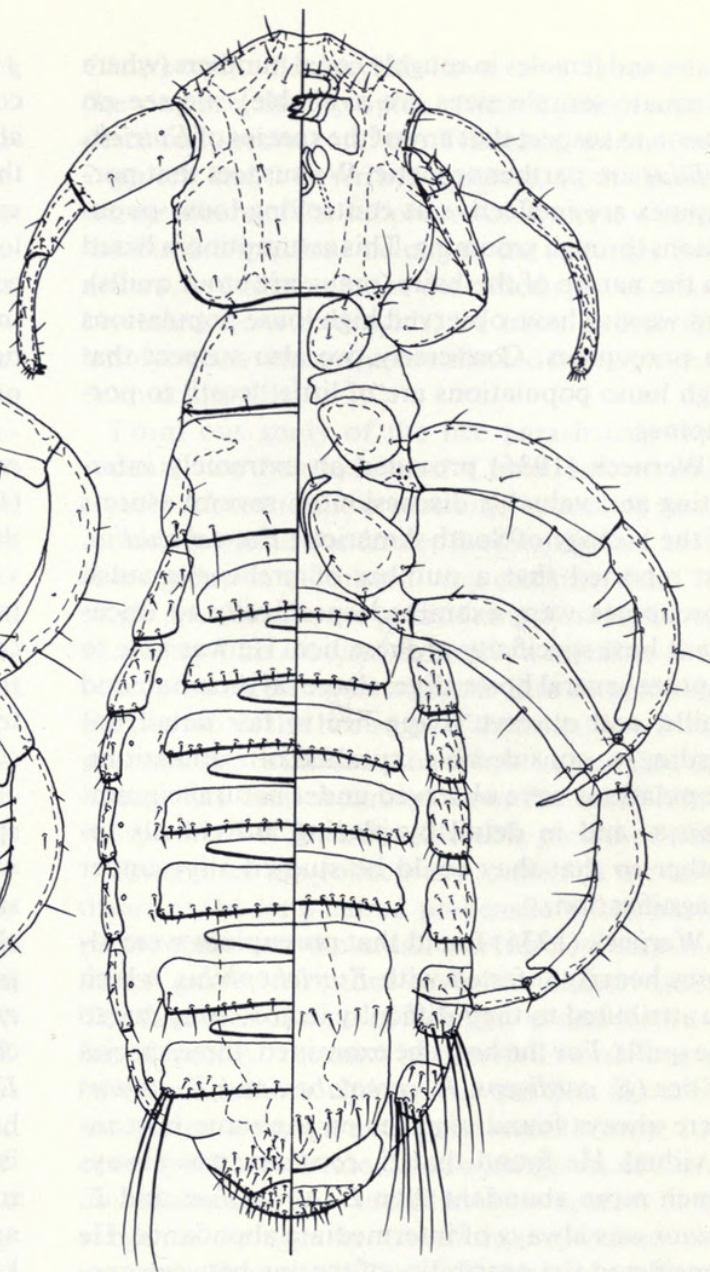
Eutrichophilus is found only on the New World porcupines of the family Erethizontidae; it is absent from all other families of New World caviomorph rodents and the Old World porcupines (family Hystricidae). There is considerable variation among species, but little intraspecific variation. We now recognize 18 species in the genus, and we suspect that additional species will be found on the South American porcupines. As we see both



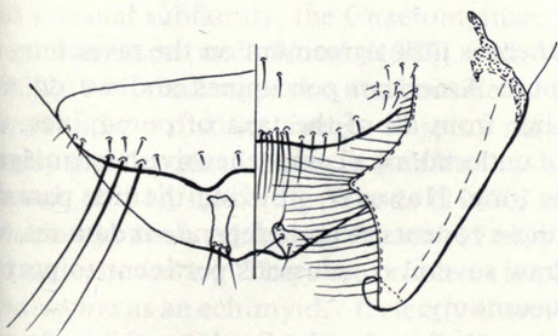
FIGS. 49-53. *Eutrichophilus exiguus*: 49, male. 50, female. 51, male genitalia. 52, female sternites II-III. 53, female terminalia.



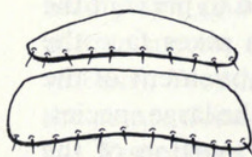
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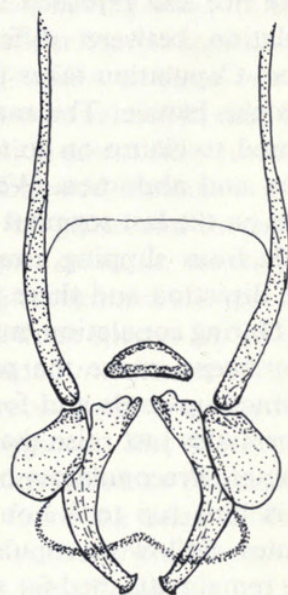
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FIGS. 54-58. *Eutrichophilus moojeni*: 54, female. 55, male. 56, female terminalia. 57, female sternites II-III. 58, male genitalia.

males and females in roughly equal numbers (where adequate sample sizes are available), we see no reason to suspect that any of the species of *Eutrichophilus* are parthenogenetic. We suspect that porcupines are ineffective at controlling louse populations through grooming. This assumption is based on the nature of the hairs (many are stout quills), and we also have observed high louse populations on porcupines. Conversely, we also suspect that high louse populations are of little "cost" to porcupines.

Werneck (1936) provided an extremely interesting and valuable discussion on several aspects of the biology of South American *Eutrichophilus*. He reported that a number of prehensile-tailed porcupines were examined specifically to document host specificity of these lice. He was able to capture several hosts alive, shave off their hair and quills, and observe living lice in fair detail, including a considerable number of copulations. Copulations were observed under natural circumstances and in detail by placing individuals together so that they could be studied alive under magnification.

Werneck (1936) found that porcupines were always heavily infested with *Eutrichophilus*, which he attributed to their difficulty in grooming due to the quills. For the hosts he examined, three species of lice (*E. cordiceps*, *E. cercolabes*, and *E. minor*) were always found together on the same host individual. He found that *E. cordiceps* was always much more abundant than *E. cercolabes*, and *E. minor* was always of intermediate abundance. He considered the possibility of mating between species of lice and reported that in no instance was copulation between different species ever observed. Copulation takes place with the male beneath the female. The male's enlarged antennae are used to clamp on to the female between her thorax and abdomen. Werneck reports that the spines on the last segment are used to prevent the female from slipping away. Both sexes face the same direction and there is no movement of the legs. During copulation, males of the large species, *E. cordiceps*, curve the posterior portion of the abdomen upwards and forwards. The smaller *E. minor* males just raise the distal extremity of the abdomen. Precopulatory behavior in all three species is long (up to 2 hours); copulation takes 5 minutes. Following copulation, the male and female remain attached for some time. He concluded that *E. cordiceps*, *E. cercolabes*, and *E. minor* are indeed separate species and that individual porcupines are parasitized by more than one species of louse.

His observations on species distributions and copulation are critical to current species concepts about these problematic taxa. The description in the literature of three species of chewing lice of the same genus occurring on porcupines from the same locality, and even on the same host individual, certainly calls into question our understanding of individual and geographic variation (of both the hosts and parasites), the accuracy of the data, and our species concepts.

Three species of *Eutrichophilus*, *E. cordiceps*, *E. cercolabes*, and *E. minor*, are reported by Werneck (1936, 1945) from prehensile-tailed porcupines at the same locality and even from the same individual host. Although we have not collected these taxa ourselves, we have been able to examine a considerable number of specimens from collections. Based upon dimensions and chaetotaxy, we too conclude that three species of *Eutrichophilus* co-occur on individual hosts.

Eutrichophilus contains several closely related species pairs or sister species. These sister species, with one exception, are not found together on the same porcupine host taxon but, rather, occur on closely related (what we presume are sister taxa) porcupines. The one exception, the species pair *E. exiguus* and *E. guyanensis*, shows the derived character of an asymmetrical head (see fig. 44). *Eutrichophilus* is unique in that these two species have quite asymmetrical heads, a condition that is not found in other Mallophaga parasitizing mammals (Emerson & Price, 1985). Extremely asymmetrical heads such as evidenced here are not known for any of the other 350 recognized species of chewing lice found on mammals. Asymmetrical heads are known, however, from a few genera of bird chewing lice (i.e., *Bizarriifrons* Eichler).

Host Relationships

As there is little agreement on the taxonomy of the South American porcupines and we do not have lice from all of the taxa of porcupines, we are not undertaking a comprehensive host analysis at this time. However, utilizing the lice parasitizing these rodents as an independent data set, we can draw several conclusions pertinent to porcupine taxonomy.

The porcupine family Erethizontidae almost certainly originated in South America and secondarily dispersed into Central America and North America. The oldest fossil porcupines known are from the Oligocene of South America. The oldest

porcupine fossils from North America date back to the late Pliocene.

Traditionally the Erethizontidae has been divided into two Recent subfamilies, the Chaetomyinae and the Erethizontinae, and one extinct subfamily (Simpson, 1945, and others). The Chaetomyinae contains only *Chaetomys subspinosus*, and the Erethizontinae three (or four) genera—*Coendou* (with a varying number of species recognized), *Echinoprocta* (containing the single monotypic species *E. rufescens*), *Erethizon* (containing the widely distributed species in North America, *E. dorsatum*), and the recently elevated (and controversial) *Sphiggurus* (with a varying number of species recognized).

Echinoprocta rufescens is known from only a limited number of specimens collected from a restricted region along the midelevational slopes in the vicinity of Bogotá, Colombia. With the exception of the short tail, *E. rufescens* is morphologically quite similar to *Coendou* and may not warrant recognition as a distinct genus.

Erethizon dorsatum, the North American porcupine, is the northernmost and the most widely distributed of all of the erethizontids, being found across much of Alaska, Canada, the United States, and northern Mexico. It is geographically variable, and four to six subspecies currently are recognized. *Erethizon dorsatum* is the host for a single species of *Eutrichophilus*, *E. setosus*, through its broad geographic range. We observed no consistent differences in dimensions or chaetotaxy of *E. setosus* throughout its extensive range that would be suggestive of the occurrence of more than one louse taxon.

The relationship of *Chaetomys subspinosus* to other porcupines and to other caviomorph rodents is a subject of recent debate. *Chaetomys* has long been treated as a true porcupine in the family Erethizontidae. It is so different, however, from all other porcupines that it has ranked as a distinct and unusual subfamily, the Chaetomyinae. However, Patterson and Wood (1982) and Woods (1982, 1984) challenged this and considered *Chaetomys* to be a distinct lineage of spiny rat of the family Echimyidae, giving it subfamilial status. Nowak (1991), following Woods (1984), treated *Chaetomys* as an echimyid. Woods (1984, p. 437) did state, however, "There are problems in placing *Chaetomys* as an echimyid." It clearly shares characters with erethizontids that are believed to be derived.

The lice parasitizing the echimyid rodents are clearly quite distinct and long separated lineages from the lice found on erethizontids (including

Chaetomys). Echimyids have two families of chewing lice, the Gyropidae (with 2 genera and 39 described species) and the Trimenoponidae (with 2 genera and 2 described species). Both families are members of the suborder Amblycera, whereas the Eutrichophilinae belong to the suborder Ischnocera. In addition to the described species of amblycerans from echimyids, we have undescribed amblycerans that we have collected in recent years from echimyids.

From our study of the lice parasitizing these rodents, we conclude that *Chaetomys* is most closely related to the erethizontids, and we would include it within the family Erethizontidae, as the sister group to all other living erethizontids. The single species of louse parasitizing *C. subspinosus*, *Eutrichophilus moojeni*, is clearly a member of the porcupine-infesting lineage, the Eutrichophilinae. Furthermore, the lice suggest that the New World porcupines are indeed monophyletic and that this lineage has been separated from the other caviomorph rodents for a considerable period of time.

Sphiggurus are collectively known as the hairy dwarf or the long-haired prehensile-tailed porcupines; these are the small porcupines with long dorsal guard hairs that cover the shorter quills. The taxonomic status of *Sphiggurus* and the number of species it contains has been variously treated by recent authors. *Sphiggurus* was first described as a genus, although until quite recently most 20th century authors treated it as a subgenus of *Coendou*. Cabrera (1961) included three species in the subgenus *Sphiggurus* (*insidiosus*, *spinosus*, and *vestitus*). Husson (1978, p. 488) elevated *Sphiggurus* to full generic level stating only, "I follow F. Cuvier [1825] in considering *Sphiggurus* to be a genus distinct from *Coendou*, as these two taxa differ so strongly both in external and in skull characters, that their separation seems fully justified." Honacki et al. (1982) followed Husson in recognizing *Sphiggurus* as a full genus and included in it four species (*insidiosus*, *spinosus*, *vestitus*, and *villosus*). Woods (1982) recognized six species in the genus *Coendou* and three species in *Sphiggurus*. Eisenberg (1989) added *mexicanus* to *Sphiggurus*. Nowak (1991) recognized two species of *Coendou* and six *Sphiggurus*. The Neotropical porcupines variously considered as belonging to *Sphiggurus* include the following taxa: *insidiosus*, *melanurus*, *mexicanus*, *pallidus*, *pruinus*, *sneiderni*, *spinosus*, *vestitus*, and *villosus*.

In contrast, Emmons and Feer (1990) discussed the controversy but treated all these as species of the genus *Coendou*. Recently, Handley and Pine (1992), as part of a description of a new species

of diminutive Brazilian prehensile-tailed porcupine, reexamined all of the characters that had been used previously to assign porcupines to either *Coendou* or *Sphiggurus*. In rigorously examining the characters across all species, they concluded that “[i]n no case do they characterize groups of species” and that there is no justification for splitting *Coendou* into two genera or even subgenera. *Sphiggurus* was regarded by them as a junior synonym of *Coendou* (but see Concepcion & Molinari, 1991). Thus, in recent years, there has been little agreement on how to treat these porcupines.

Based solely on the species of lice and their relationships, we suggest that Handley and Pine (1992) are correct in regarding *Sphiggurus* as a junior synonym of *Coendou*. There is simply no clear distinction between either the morphology or taxonomic relationships of the *Eutrichophilus* found on the members of the *Coendou*–*Sphiggurus* complex that would suggest a major dichotomy in the hosts. We would also include *Echinoprocta rufescens* with the long-tailed porcupines because their lice suggest that all three groups of hosts form a single, quite closely related clade. There are, however, two very distinctive *Eutrichophilus* that clearly represent outgroups to the *Coendou*–*Sphiggurus*–*Echinoprocta* complex of lice, these being *E. moojeni* on *Chaetomys subspinosus* and *E. setosus* on *Erethizon dorsatum*.

The fact that *Coendou bicolor* is parasitized by different, albeit closely related, species of *Eutrichophilus* in different parts of its range suggests that it might be a species complex in need of further study.

In a study of both fossil and Recent forms, Woods and Hermanson (1985) concluded that the erethizontoids (minus *Chaetomys*) are a monophyletic lineage and that this lineage split from its sister group, the octodontoids, at least as far back as the Deseadan (34 MYBP). The octodontid (family Octodontidae) rodents include five genera and eight species and are parasitized by sucking lice of the suborder Anoplura, and not by chewing lice. Octodontids have a single genus of sucking louse, *Hoplopleura* (Hoplopleuridae) and several described species, although the group is in need of revision. Judging from the parasitic lice known from the erethizontids, echimyids, and octodontids, the host lineages are indeed old. We would add from our study of the lice that the New World porcupines, the genera *Chaetomys*, *Coendou* (including *Sphiggurus*), *Echinoprocta*, and *Erethizon* are a monophyletic lineage and that the split from its sister lineage is indeed old.

The South American porcupines are in need of major revision. The lack of agreement in recent years on how to treat these porcupines at both the specific and generic levels is indicative of the tremendous array of geographic and individual variation present in these animals. Hopefully our study of the parasitic lice will contribute to a better understanding of speciation in the erethizontids.

Additional collections of chewing lice from South American porcupines undoubtedly will produce additional species new to science and help clarify host distributions and relationships. Much remains to be learned about this interesting and extremely complex host–parasite relationship.

**Key to the Species of
*Eutrichophilus***

1. Legs II–III highly modified, femur and tibia curved, with median flange (figs. 54, 55); spiracles small. Ex *Chaetomys subspinosus* *moojeni* Werneck
 Legs II–III not modified, similar to leg I, but larger (fig. 1); spiracles large 2
2. Medioanterior head margin essentially straight, asymmetrically slanted (figs. 44, 49). Ex *Coendou melanurus* 3
 Medioanterior head margin symmetrical, flattened to concave (figs. 1, 21) 4
3. Large. Male TW over 0.60. Female TW over 0.70 *guyanensis* Werneck
 Small. Male TW under 0.50. Female TW under 0.60 *exiguus* Werneck
4. Long dorsal head setae (figs. 1, 2). Male genitalia with long slender parameres and circular fused mesomeres (fig. 3). Female subgenital plate smoothly curved, with median group of long setae (fig. 5). Ex *Erethizon dorsatum* *setosus* (Giebel)
 Shorter dorsal head setae (fig. 6). Male genitalia otherwise. Female with subgenital plate shape and/or chaetotaxy otherwise 5

5. With only 1–2 median pronotal setae on each side (figs. 34, 39) 6
 With at least 3 median pronotal setae on each side (fig. 1) 8
6. Male genitalia as in Figure 41. Female gonapophyses small, with fewer than 10 marginal setae (fig. 43). Ex *Coendou pruinosus* *comitans* Werneck
 Male genitalia otherwise (figs. 22, 36). Female gonapophyses larger, with over 20 marginal setae (fig. 38) 7
7. Head with deep medioanterior concavity (fig. 21). Male terminalia posteriorly concave, with chaetotaxy as in Figure 23; genitalia (fig. 22) with accessory piece at base of parameres over 0.12 wide. Female unknown. Ex *Coendou pruinosus* *lobatus* Ewing
 Head only slightly concave medioanteriorly (fig. 34). Male terminalia posteriorly flattened, with chaetotaxy as in Figure 34; genitalia (fig. 36) with accessory piece at base of parameres under 0.11 wide. Ex *Echinoprocta rufescens* *hershkovitzi*, n. sp.
8. Male without accessory tergal sclerites (figs. 16, 24); genitalia as in Figure 17 or 26. Female subgenital plate medioposteriorly attenuate, with cluster of long setae (fig. 28); with very large “sprung” gonapophyses with broken surface striation and overlying patch of conspicuous setae (fig. 28). Ex *Coendou spinosus* 9
 Male with accessory tergal sclerites (figs. 6, 11, 29); genitalia much as in Figure 8, 13, or 31. Female subgenital plate evenly rounded to medioposteriorly indented; gonapophyses otherwise 11
9. Male genitalia as in Figure 17 *minor* Mjöberg
 Male genitalia as in Figure 26 10
10. Large. Male TW over 0.54, MW over 0.46. Female TW over 0.63, MW over 0.59 *emersoni*, n. sp.
 Small. Male TW under 0.54, MW under 0.46. Female TW under 0.61, MW under 0.57 *claytoni*, n. sp.
11. Male terminalia broadly rounded, with many dorsal setae (figs. 6, 29); genitalia as in Figure 8 or 31. Female sternite III lacking partitioned anterior area (figs. 9, 32) 12
 Male terminalia otherwise (figs. 11, 19); genitalia much as in Figure 13. Female sternite III having partitioned anterior area (figs. 14, 18) 14
12. Male with small accessory tergal plates on III–VI (fig. 6); genitalia as in Figure 8. Female with evenly rounded subgenital plate and angulate gonapophyses (figs. 7, 10). Ex *Coendou mexicanus* *mexicanus* (Rudow)
 Male with larger accessory tergal plates on II–VII (fig. 29); genitalia as in Figure 31. Female with deep medioposterior indentation of subgenital plate and rounded gonapophyses (figs. 30, 33). Ex *Coendou spinosus* 13
13. Large. Male TW over 0.70, MW over 0.63. Female TW over 0.75, MW over 0.76 *cordiceps* Mjöberg
 Small. Male TW under 0.68, MW under 0.62. Female TW under 0.74, MW under 0.75 *paraguayensis*, n. sp.
14. Male terminalia tapered, narrowly rounded (fig. 19). Female sternite III with large anterior partitioned area, nestling into arched sternite II (fig. 18); subgenital plate with setae set well anterior of posterior margin (fig. 20). Ex *Coendou spinosus* 15
 Male terminalia with medioposterior indentation (fig. 11). Female sternite III with smaller anterior partitioned area behind relatively straight sternite II (fig. 14); subgenital plate with setae near posterior margin (fig. 15) 16
15. Large. Male TW over 0.64, GW over 0.28. Female TW over 0.75, MW over 0.78 *cercolabes* Mjöberg
 Small. Male TW under 0.63, GW under 0.27. Female TW under 0.73, MW under 0.76 *australis* Ewing
16. Small. Male TW under 0.72, GPL under 0.19. Female TW under 0.81. Ex *Coendou bicolor simonsi* *andersoni*, n. sp.
 Large. Male TW over 0.78, GPL over 0.19. Female TW over 0.85 17
17. Fewer than 18 marginal metanotal setae. Ex *Coendou rothschildi* *maximus* Bedford
 At least 20 marginal metanotal setae. Ex *Coendou bicolor bicolor* *duellmani*, n. sp.

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