PHYLOGENETIC RELATIONSHIPS IN THE MITE FAMILY SARCOPTIDAE (ACARI: ASTIGMATA)

BY

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Phylogenetic Relationships in the Mite Family Sarcoptidae (Acari: Astigmata)

by

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ABSTRACT

Klompen, J.S.H. 1991. Phylogenetic relationships in the mite family Sarcoptidae (Acari: Astigmata). Misc. Publ. Univ. Michigan, Mus. Zool., 180: 1–155, 265 figs. A phylogenetic analysis of relationships among the 117 recognizable species of the mite family Sarcoptidae Murray, 1877 is carried out based on 215 morphological and ontogenetic characters. The putative sister group of the Sarcoptidae, the family Rhyncoptidae, and more distantly related families in the Sarcoptoidea (Psoroptidae, Lobalgidae, Myocoptidae) are used as outgroups. All of these taxa are obligate, permanent ectoparasites of mammals.

Due to the large quantity of missing data and the overall size of the matrix, the analysis is carried out in parts. Initial analyses, including only those taxa for which the quantity of missing data is low, are used to establish a hypothesis of relationships among the larger subgroups. Relationships within each subgroup are analyzed separately. The subgroup analyses are rooted using hypothetical ancestors which are constructed based on the results of the initial analyses.

A new classification of the Sarcoptidae is proposed based on the results of the systematic analysis. The family is divided in three subfamilies, the Diabolicoptinae Fain & Domrow, 1974 (2 genera, 3 species), Sarcoptinae Murray, 1877 (4 genera, 8 species) and Teinocoptinae Fain, 1959 (9 genera, 106 species). These groupings include two newly described genera and 18 newly described species. Within the Sarcoptinae, the genus *Pithesarcoptes* Fain, 1965 is synonymized with *Prosarcoptes* Lavoipierre, 1960 and the subgenus *Trixacarus* (*Caviacoptes*) Fain et al., 1972 with *Trixacarus* (*s.s.*) Sellnick, 1944. At the species level, *Prosarcoptes faini* Lavoipierre, 1970 is synonymized with *P. pitheci* (Philippe, 1948). The Teinocoptinae includes the formerly recognized families Teinocoptidae Fain, 1959 and Bakerocoptidae Fain, 1962, as well as the subfamily Notoedrinae Fain, 1968 (Sarcoptidae). Within this lineage the genus *Bakerocoptes* Fain, 1962 is synonymized with *Nycteridocoptes* Oudemans, 1898, the subgenus *Chirnyssoides* (*Carollicoptes*) Fain & Lukoschus, 1971 with *Chirnyssoides* (*s.s.*) Fain, 1959, and the genera *Chirnyssus* Fain, 1959 and *Suncicoptes* Fain & Lukoschus, 1976, and subgenera *Notoedres* (*Neonotoedres*) Fain, 1963, *N.* (*Metanotoedres*) Fain, 1959, and *N.* (*Jansnotoedres*) Fain, 1965 with *Notoedres* (*s.s.*) Railliet, 1893. At the species level, *Notoedres dohanyi* Klompen et al., 1983 is synonymized with *N. tadaridae* Fain, 1959, *N. schoutedeni hyatti* Fain, 1963 with *N. chiropteralis* (Trouessart, 1896), and *N. douglasi* Lavoipierre, 1964 with *N. centrifera* Jansen, 1963. New combinations include *Tychosarcoptes amphipterinon* (Klompen et al., 1984) and *Chirobia brevior* (Fain et al., 1982), both transferred from *Teinocoptes; Teinocoptes harpyionycteris* (Klompen & OConnor, 1987), transferred from *Chirobia; Notoedres* (*Bakeracarus*) *plecoti* Fain, 1959, transferred from *N.* (*Notoedres*); *N.* (*B.*) *eptesicus* (Fain & Lukoschus, 1971), *N.* (*B.*) *corynorhini* (Fain, 1961), and *N.* (*B.*) *anisothrix* (Fain & Lukoschus, 1975), formerly subspecies of *N.* (*B.*) *lasionycteris* (Boyd & Bernstein, 1950).

Data on ecology, pathology and host associations are summarized for all species of the family, and identification keys to all species are included.

Key words: *Acari, Astigmata, cladistics, classification, ectoparasites, Mammalia, ontogeny, phylogeny, Sarcoptidae.*

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INTRODUCTION

The Sarcoptidae form a large family of parasitic mites, all members of which are obligate, permanent parasites of mammals. Their host associations include primarily marsupials, primates, bats, rodents, and insectivores, but a few species have colonized hosts in other orders of mammals. Some species have gained some notoriety by becoming pest species of humans and domestic animals (e.g. *Sarcoptes scabiei, Notoedres cati*).

The evolution of host associations in this group has been hypothesized to be characterized by cospeciation (Andrews, 1983; Fain, 1976a, 1982, 1984; OConnor, 1984). However, these hypotheses are severely hampered by our poor understanding of relationships in the Sarcoptidae. The goal of this study is to reexamine existing classifications of the Sarcoptidae using the methods of phylogenetic systematics and to present testable hypotheses of relationships among these mites.

The family Sarcoptidae is included in the Psoroptidia, a large, monophyletic assemblage of families classified as a cohort or supercohort in the suborder Astigmata (OConnor, 1982). Most taxa in this assemblage are associated with birds or mammals in all life stages. Although a detailed study of family relationships in the Psoroptidia has not been conducted, some larger groupings have been proposed. Based on a number of shared derived character states, OConnor (1982) proposed a division into four superfamilies: Pterolichoidea, Analgoidea (both exclusively bird parasites), Pyroglyphoidea (most taxa parasitic on birds, some free living), and Sarcoptoidea (exclusively mammal parasites). Within the Sarcoptoidea, OConnor recognized 14 families, one of which is the Sarcoptidae.

A review of the history of classification and systematics within the Sarcoptidae can be relatively brief. The most recent review of the family (Fain, 1968) provides an excellent summary of those aspects of sarcoptid research up to the mid 1960's. However, since this revision some significant developments have taken place in both sarcoptid taxonomy and systematics. In addition, a few remarks should be made regarding some groups that Fain (1968) excluded from the Sarcoptidae but that may belong in this family.

Fain (1968) recognized two subfamilies: the Sarcoptinae, including the genera *Cosarcoptes, Pithesarcoptes, Prosarcoptes, Sarcoptes,* and *Trixacarus,* and the Notoedrinae, including *Chirnyssoides, Chirnyssus, Chirophagoides, Notoedres,* and *Nycteridocoptes.* In addition, he recognized 5 subgenera within *Notoedres.* The subfamilies were defined by the number of setae on tarsi I–II which are transformed into spines (2 in the Sarcoptinae, 4 in the Notoedrinae), and by the presence/absence of fusion of tarsus and tibia IV in the male (fused in the Sarcoptinae, free in the Notoedrinae) (Fain, 1968).

Within the context of the two existing subfamilies three subsequent genera have been described: *Kutzerocoptes* Lavoipierre, 1970 from a cebid monkey, *Tychosarcoptes* Fain, 1976 from an unknown host (both placed in the Sarcoptinae), and *Suncicoptes* Fain & Lukoschus, 1976 from a shrew (placed in the Notoedrinae). In addition, two subfamilies, Diabolicoptinae Fain & Domrow, 1974 and Caenolestocoptinae Fain & Lukoschus, 1976, have been subsequently proposed. The Diabolicoptinae includes two genera, *Diabolicoptes* Fain & Domrow, 1974 and *Satanicoptes* Fain & Laurence, 1975, and was defined by the lack of fusion of the tibiae and tarsi of all legs (tarsus and tibia III–IV in the immatures and female are fused in both Sarcoptinae and Notoedrinae), and by the retention of cuticular spines on the tarsi (Fain & Domrow, 1974). Both of these character states, however, are ancestral for the family. The Caenolestocoptinae contains only a single species, *Caenolestocoptes inca* Fain & Lukoschus, 1976, and was originally defined by the loss of setae *vi* in all stages, the presence of a single spine-like seta on each anterior tarsus, the presence of small, retrorse processes on the palps, and the presence of adanal discs in the male (Fain & Lukoschus, 1976). These characters are either ancestral (presence of adanal discs), or uniquely derived characters for the family Rhyncoptidae to which *Caenolestocoptes* should be transferred (Klompen, in press). *Caenolestocoptes* will be considered here only in the context of belonging to an outgroup for the Sarcoptidae.

Not included in Fain's concept of the Sarcoptidae (Fain, 1968) were the genera *Teinocoptes* and *Chirobia.* These taxa were placed in a separate family, Teinocoptidae Fain, 1959, based on the derived morphology of the nymphs and females (Fain, 1959b). Fain (1968) did recognize the similarity of members of the two families (both have some tarsal setae transformed into spines), and grouped the two families as a superfamily Sarcoptoidea (*sensu* Fain, 1968, not *sensu* OConnor, 1982). Another taxon that has not previously been included in the Sarcoptidae is the highly paedomorphic species *Bakerocoptes cynopteri* Fain, 1962. Initially placed in its own subfamily, Bakerocoptinae, within the Teinocoptidae (Fain, 1962b), it was elevated to family rank by Lavoipierre et al. (1967), once again based on the degree of difference between it and other sarcoptids.

Relationships between the genera (and families) have received relatively little attention. Fain (1959e, 1965b, 1968, 1976a, 1982, 1984) approached the problem in a traditional way. Initially Fain (1959e, 1965b, 1968) based his views on the structure of the posterior coxal apodemes in the male, in particular on the point of junction between coxal apodemes IV and either the transverse or median apodeme. As shown in the discussion of morphology (characters 156, 157), this structure proved to be of dubious value in the present analysis, since it has a high level of intraspecific variability. Fain's more recent ideas (Fain, 1976a, 1982, 1984) stress the reduction in the number of dorsal setae. The first use of phylogenetic methodology in sarcoptid systematics was by OConnor (1982, 1984). Although not presenting a specific set of relationships within the family, OConnor (1982) suggested that the Teinocoptidae (and Bakerocoptidae) be synonymized with the Sarcoptidae, since recognition of the Teinocoptidae would leave the Sarcoptidae as a paraphyletic group. OConnor (1984) also provided the first phylogenetic analysis of generic relationships for the subfamily Sarcoptinae.

My objectives are to present a study of morphological variation in the Sarcoptidae (including the Teinocoptidae and Bakerocoptidae), analyze phylogenetic relationships at the species or species group level, and, based on the results of that analysis, present diagnoses for all monophyletic lineages. The latter section also includes a new classification and a discussion of all species. Keys to the species are included in Appendix 1.

MATERIAL AND METHODS

Terminology

Development in the Sarcoptidae includes five different stages: egg, larva, protonymph, tritonymph, and adult. The deutonymph, present in most non-psoroptidid Astigmata, is lost in all Psoroptidia (OConnor, 1982). Probably, the Sarcoptidae have also lost the prelarva (Fain & Herin, 1978). Distinct sexual dimorphism can occur as early as the tritonymph. The two forms of the tritonymph developing into respectively an adult female and an adult male are identified in the text as "female tritonymph" and "male tritonymph." The adults are identified as "female" or "male."

The nomenclature of body structures of the mites follows Krantz (1978). Setae and solenidia of specific legs are identified in the text by adding the number(s) of the leg(s) in Roman numerals to the setal designation, e.g. setae *f* II–IV, refers to setae *f* on legs II–IV.

The term diagnosis as used in the discussion of lineages and classification refers exclusively to synapomorphies of lineages, not to a listing of identifying characters for recognized taxa. Finally, lineages which are not identified by a taxon name are referred to by listing the two "extreme" taxa, top to bottom, as indicated in the figures.

Specimen Collection and Preparation

Mite specimens were obtained from two different sources. The majority of specimens examined were collected by hand with forceps and/or needles, while examining potential hosts under a dissecting microscope (10–25X magnification). Most of these collections were made by B.M. OConnor and the author (respectively BMOC and HK mite collection numbers). Samples of all collected mites were cleared in lactophenol and mounted on microscope slides in Hoyer's medium. Additional mite specimens were borrowed from museum collections. Specimens were examined at 300–1600X magnification using a compound microscope with phase and interference contrast. Drawings were made using a drawing tube.

All measurements presented in this study were made using a digitizer (Houston Instruments) connected to a IBM-PC XT. This method allowed accurate measurements of curved objects such as setae, coxal apodemes, and the bursa copulatrix. The legs were measured from the tip of the tarsus to the anterior edge of the trochanter. Measurements of the entire leg are of limited use in Sarcoptidae since the legs tend to curl up, but are presented to provide comparative data with earlier studies. The measurement paths for the coxal apodemes are illustrated by arrows in Fig. 1. When available, 10 females and 10 males of each new species were measured. Measurements of undescribed adult stages of other species were restricted to 5 specimens each. Larger samples were measured in species where taxonomic confusion existed, or where the host range was exceptionally broad and host race formation was suspected. Measurements of immature stages are not included due to time and space constraints. All measurements are summarized in tabular form. Standard deviations and range are presented for sample sizes of 5 or more, only the range for sample sizes between 3 and 5, and individual measurements for samples of 1 or 2. All measurements are in micrometers (μm) unless otherwise indicated.

1

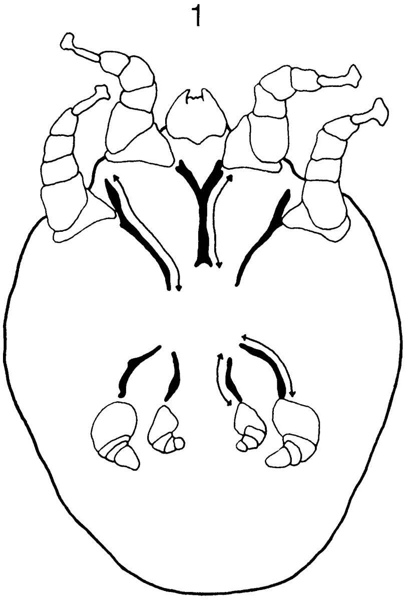


Fig. 1. Measurement path for each of the four coxal apodemes (indicated by arrows).

The section on behavior and ecology is based on published descriptions of site choice and pathology, and new observations. Most new observations were made during a five month stay in the Philippines, a project undertaken as part of a survey of mammals in the central Philippines. During this period live sarcoptid mites were collected from freshly killed hosts, allowing limited observations on live mites and accurate estimates of population densities on individual hosts. Population densities could also be estimated based on a variety of new collections from hosts in Ecuador, Egypt, Indonesia (lesser Sundas), Madagascar, Paraguay, Peru, and the Philippines. For all of the above collections, the collectors kindly agreed to wrap freshly killed hosts in a few layers of cheesecloth, which prevented contamination and loss of parasites. Collections from most preserved hosts in museums should not be used to estimate population densities. Many parasites are lost during the process of collecting and preparing the host specimens, and contamination with parasites washed from other hosts is a common problem. However, this type of collecting does offer an unrivaled taxonomic and geographical range of hosts. For Sarcoptidae, museum collecting tends to be more rewarding than for many other groups of ectoparasites; losses are relatively limited due to the tendency of these mites to burrow into the skin.

The nomenclature for the mammal hosts is based on Honacki et al. (1982), with a few exceptions. I follow Carleton & Musser (1984) in recognizing an expanded version of the Muridae (including the Arvicolidae, Cricetidae, etc.), and I recognize *Eonycteris robusta* Miller, 1913 (Chiroptera: Pteropodidae) as a species separate from *E. major* Andersen, 1910 (L.R. Heaney, pers. comm.).

In the species discussions, the "host and locality" section refers exclusively to mite specimens examined during this study. Unless otherwise indicated all of these specimens are in the collection of the University of Michigan Museum of Zoology. Studied specimens borrowed from other institutions are identified by a brief statement regarding their nature and source, e.g. "paratype, specimen in collection BMNH." A summary of all previously published host and locality records is included in the "literature records" section. The information in the host and locality section is organized as follows: host name and author, host synonymies (only names cited in prior sarcoptid literature), locality (country, province/state, town, longitude/latitude), collection date, collector (+ host field number), host depository (+ accession number), mite collection number. In many instances one or more of these items are unavailable, and for those collections the missing items are ignored. Where multiple host specimens with the same field data were examined, listings are restricted to the host field number, host accession number, and mite collection number for all but the first collection.

Institutions serving as sources of material (both mites and hosts) and/or depositories for mite specimens are abbreviated as follows: American Museum of Natural History, New York, New York (AMNH); Australian National Insect Collection, Canberra (ANIC); Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); R.M. Bohart Museum of Entomology, University of California, Davis, California (BME); The Natural History Museum, London (BMNH); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CMNH); Cornell University Insect Collection, Ithaca, New York (CUIC); Field Museum of Natural History, Chicago, Illinois (FMNH); Institute for Medical Research, Kuala Lumpur (IMR); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN); Michigan State University Museum, East Lansing, Michigan (MSU); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ); Nationaal Natuurhistorisch Museum, Leiden (NNML); The Acarology Laboratory, The Ohio State University, Columbus, Ohio (OSU); Philippine National Acarological Collection, at Visayas State College of Agriculture, Leyte (PNC); Philippine National Museum, Manila (PNM); U.S. National Museum of Natural History, Washington, D.C. (NMNH); University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); Western Australian Museum, Perth, Western Australia (WAM); Zoological Institute, Academy of Sciences, St. Petersburg (ZIAC); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (MAK); Zoologisches Institut und Zoologisches Museum, Hamburg (ZIZM).

PHYLOGENETIC ANALYSIS

The phylogenetic analysis is intended to be comprehensive. It includes all 117 valid known species in the Sarcoptidae; the actual data matrix (Appendix 2), however, contains only 102 terminal taxa. This reduction is due to two different problems. The first concerns *Bakerocoptes cynopteri,* the type species of the Bakerocoptidae, a species that is paedomorphic in nearly every aspect examined (Fain, 1962b). Its inclusion in the analysis leads to numerous very dubious and probably false homologies, and it seemed preferable to include it *a posteriori.*

The second problem is largely an artifact of the large amount of missing data. In several cases two or more species could not be distinguished based on the characters examined. This problem usually involves one species for which most character states could be determined and one or more other species for which most of the stages (and thus many character states) are unknown. For each of these clusters I have entered only the species with the most available data in the matrix. It should be noted that all species within a cluster are distinct based on characters not included in the matrix. The following clusters of species are treated as a single terminal taxon (the species mentioned first is entered in the data matrix): *Chirobia jagori* and *C. minor; Teinocoptes astridae* and *T. rousetti; T. auricularis* and *T. ituriensis; Notoedres* (*Bakeracarus*) *paraguayensis* and *N.* (*B.*) *plecoti; Notoedres* (*Notoedres*) *nigricans, N.* (*N.*) *myoticola, N.* (*N.*) *myotis,* and *N.* (*N.*) *roesleri; N.* (*N.*) *alexfaini* and *N.* (*N.*) *cheiromeles; N.* (*N.*) *dewitti, N.* (*N.*) *ismaili, N.* (*N.*) *ovatus,* and *N.* (*N.*) *tristis; N.* (*N.*) *chiropteralis* and *N.* (*N.*) *schoutedeni; N.* (*N.*) *pahangi, N.* (*N.*) *jamesoni, N.* (*N.*) *paucipilis,* and *N.* (*N.*) *galagoensis.*

The majority of the characters examined relate to adult external morphology or to its ontogeny. Very little is known about internal anatomy or genetics of these mites. Characters considered extrinsic to the mites studied are excluded. The evolution of some of these characters (e.g. host associations) will be examined in future studies. Within these general constraints, all characters available are included if they met the criteria of low intraspecific variability and definable states (no continuous variation).

One very important character set deals with ontogenetic information. The most accurate method for including this information in a systematic analysis is by treating the ontogenetic transformations themselves as characters (Kluge & Strauss, 1985; de Queiroz, 1985). This method has been made explicit in acarine systematics by using entire ontogenetic transformation patterns as character states (Klompen & OConnor, 1989). Unfortunately, it requires knowledge of entire ontogenetic transformation patterns, information which is unavailable for most taxa in this analysis. In the character discussion, I opted for a compromise by coding characters as transformations between two subsequent stages. For a given character (e.g. the addition of a pair of setae), modifications in transformations between each set of life stages are coded separately, with the restriction that duplicates, involving changes in the same set of taxa, are avoided. For example, a pair of setae may be added in the larva, protonymph, or tritonymph. Assuming addition in the larva is ancestral, two characters are defined as follows "addition delayed (1), added in the larva (0)" and "addition delayed (1), added in the larva or protonymph (0)." Even if information on one of the stages is unavailable, the state for at least one of the characters can be determined. This method does not allow comparison of total ontogenetic transformation series but it allows maximal use of the available information on ontogenetic change.

The resulting matrix includes 215 characters (Appendix 2). All but three of these are entered as two-state characters. Characters 12, 18, and 45 for which (1) absence is the ancestral condition, (2) two or more states of presence (i.e. shapes) occur, and (3) a transformation series including all observed states cannot be established, are treated as unordered, multistate characters. For those characters for which absence is one derived state and a shape modification, not inferred to lead to absence, is another, absence is coded as missing data for the character(s) involving the shape modification(s). Characters were not weighted to avoid the arbitrariness of *a priori* weighting procedures.

Character polarization of both the morphological and ontogenetic characters is based on outgroup comparison, as outlined by Maddison et al. (1984). Outgroups are the Rhyncoptidae, the presumed sister group of the Sarcoptidae (Klompen, in press), and other taxa in the Sarcoptoidea, in particular the families Psoroptidae, Lobalgidae, and Myocoptidae. The analysis was carried out using a hypothetical ancestor, with all character states 0.

The phylogenetic analyses were carried out using both PAUP 3.0 (David L. Swofford, Illinois Natural History Survey, Champaign, 1989), implemented on Macintosh, and Hennig86 (James S. Farris, Port Jefferson Station, New York, 1988), implemented on IBM compatibles. Alternative hypotheses (e.g. hypotheses based on existing classifications) were tested using the "constraints" option in PAUP, which generates the most parsimonious tree given a specified topological constraint. Character optimization (as presented in the discussion of lineages) is based on the ACCTRAN (accelerated transformation) option in PAUP but is modified to better reflect probabilities of change. The modifications are based on the assumption that losses and reductions are more probable than gains of new structures. Therefore, the character optimization used favors multiple losses over multiple gains (given an equal number of steps).

Tree length and consistency index are the statistics used to compare the different hypotheses of relationships generated. The consistency index (CI) is a measure of the amount of homoplasy in the data. Calculated as the ratio of the minimum possible number of steps (no homoplasy in any characters) to the actual number of steps, its value ranges from 1 (no homoplasy) down to, but not including, 0. Presented is the CI excluding uninformative characters (autapomorphies) for the particular analysis under discussion.

MORPHOLOGY AND CHARACTER ANALYSIS

The following discussion is intended to describe the variation in morphology among the taxa in the Sarcoptidae and to define the characters used in the phylogenetic analysis. The listing of the taxa in which each character state occurs gives a general impression of the range of these states. It is not intended to be exhaustive. The exact state assignment for each character in all taxa is given in the data matrix (Appendix 2).

In order to facilitate the discussion of variation over the taxa in the study group, I will use some of the new supraspecific concepts that are discussed in detail in the discussion of lineages. These concern the subfamily Teinocoptinae (including the formerly recognized families Teinocoptidae Fain, 1959 and Bakerocoptidae Fain, 1962, and the subfamily Notoedrinae Fain, 1968), the genera *Prosarcoptes* (including *Pithesarcoptes* Fain, 1965 and *Cosarcoptes* Fain, 1967), *Nycteridocoptes* (including *Bakerocoptes* Fain, 1962), *Cynopterocoptes* nov. gen., *Rousettocoptes* nov. gen., *Tychosarcoptes* (including *Teinocoptes amphipterinon* Klompen et al., 1984), and *Notoedres* (including *Chirnyssus* Fain, 1959 and *Suncicoptes* Fain & Lukoschus, 1976). Within *Notoedres* two subgenera are recognized: *Bakeracarus* (including *Notoedres plecoti* Fain, 1959, but excluding *N. schoutedeni* Fain, 1959) and *Notoedres* (including *Metanotoedres* Fain, 1959, *Jansnotoedres* Fain, 1965, and *Neonotoedres* Fain, 1963).

In addition to these named groupings, I will use the terms "Sarcoptinae associated with primates" for the assemblage of *Kutzerocoptes, Sarcoptes,* and *Prosarcoptes;* "*Teinocoptes* group" for the assemblage of *Rousettocoptes, Tychosarcoptes, Chirobia,* and *Teinocoptes;* "*myoticola* group" for a lineage in *Notoedres* including part of *Chirnyssus* Fain, 1959 and *N.* (*Metanotoedres*) Fain, 1959 (*philippinensis-roesleri* in Fig. 57); and "*lasionycteris* group" for a lineage in *Notoedres* (*Bakeracarus*) consisting largely of species described as subspecies of *N.* (*B.*) *lasionycteris* (*anisothrix-americanus* in Fig. 57).

GNATHOSOMA

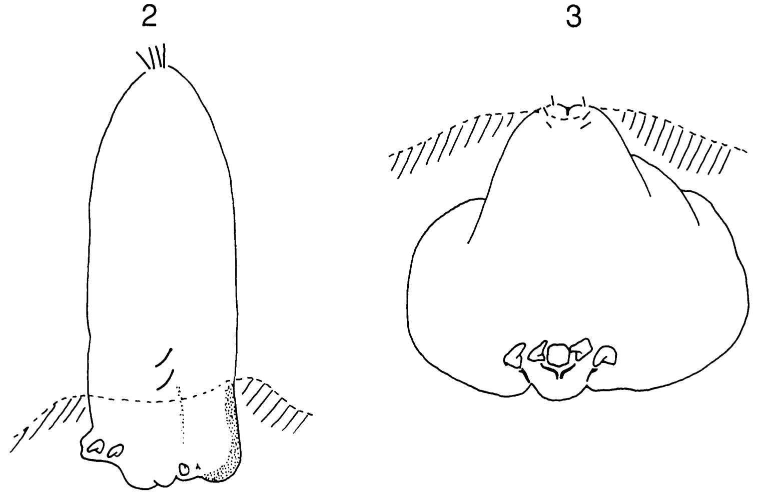
The gnathosoma in the Sarcoptidae shows relatively little variation in morphology. It is partly or completely (*Teinocoptes* group) enveloped by transparent flaps, originating from the rutellar lobes. The subcapitulum carries a single, ventral pair of setae. Ancestrally, a pair of palpal supracoxal setae is present dorsal or dorsolateral on the gnathosoma. This pair of setae has been observed in a number of Sarcoptidae: *Trixacarus eliurus, T. diversus, Sarcoptes, Prosarcoptes scanloni,* and most *Nycteridocoptes* species. It appears to be absent in the Diabolicoptinae, *Cynopterocoptes,* the *Teinocoptes* group, *Chirophagoides, Chirnyssoides,* and *Notoedres,* but given the extreme difficulty of seeing these setae (they are always very small), this character has not been used in the analysis.

The palps are one-segmented, each ancestrally with 3 setae, *cm* (dorsal, distal), *dm* (dorsal, proximal), and α *l* (ventral, proximal), and a small solenidion omega (OConnor, 1981). Some of these structures may be absent in females and immatures of *Cynopterocoptes* and the *Teinocoptes* group. These potential losses are also excluded from the analysis due to difficulty in observation. In females of *Notoedres* (*myoticola* group) the base of palpal setae α *l* is strongly inflated, a character state unique for this group of species (Figs. 235, 253).

1. Base of palpal setae α *l in the female inflated (1), vs. not inflated (0).*

BODY SHAPE

Most Sarcoptoidea are dorsoventrally flattened, with the anus in a terminal position. In most Sarcoptidae (not in the Diabolicoptinae) the body of at least the female is more



FIGS. 2, 3. Female, body shape (the position of the host tissue is indicated by hatchmarks): *Teinocoptes philippinensis* (2), *Nycteridocoptes cynopteri* (3).

rounded. The anus is distinctly dorsoterminal or dorsal in the immatures and females of most Teinocoptinae. The condition for *Chirophagoides* is unclear and coded as missing data, since fresh specimens were not available for study (it is often difficult to interpret from material mounted on slides).

2. Anus position in the female dorsoterminal or dorsal (1), vs. terminal (0).

Dorsoventral elongation of the body is pronounced in several taxa of the Teinocoptinae. Extreme dorsoventral elongation (height > 2 X length) is found in the females of most *Teinocoptes, Chirnyssoides noctilionis, C. amazonae, C. caparti, Notoedres* (*Bakeracarus*), *N.* (*N.*) *chiropteralis*, and *N.* (*N.*) *schoutedeni* (Fig. 2). More moderate levels of dorsoventral elongation (height between 1–2 X length) are present in *Nycteridocoptes*, most species in the *Teinocoptes* group, most *Chirnyssoides*, and some *Notoedres*. In *Nycteridocoptes* and most *Chirnyssoides* this elongation is limited to the female but in the other taxa listed the body of both immatures and females is dorsoventrally elongated.

3. Height of the body of the female exceeding the length (1), vs. height distinctly less than the length (0).

4. Height of the body of the female over twice the length (1), vs. height/length ratio less than two (0).

5. Height of the body of both females and immatures exceeding the length (1), vs. only for the females or never (0).

In the genus *Nycteridocoptes* the body of ovigerous females is uniquely modified by a combination of lateral and dorsoventral expansion. The anal region projects slightly out of the bulk of the body on what superficially appears to be a broad tube (Fig. 3). This unique modification is poorly developed in the relatively small females of *N. microphallus* and *N. rousetti*, but very distinct in all other species, including the highly paedomorphic *N. cynopteri*.

6. Body of ovigerous females with anus projecting on a dorsal "tube" (1), vs. body shape different (0).

7. Dorsal "tube" well developed, lateral and dorsoventral elongation of the body pronounced (1), vs. tube poorly developed and elongation of the body relatively weak, or body shape different (0).

IDIOSOMAL SHIELDS

The pattern of sclerotized areas (= shields) on the dorsum of immature and female Sarcoptoidea is simple. Ancestrally a single propodosomal (= anterior median) shield is present, a condition retained in the Sarcoptinae (with the exception of *Kutzerocoptes*) and *Chirophagoides*. The shield is lost in all other Sarcoptidae.

8. Anterior median shield in the female and immatures absent (1), vs. present (0).

The pattern of sclerotized areas in the males is more complex. Ancestrally, the propodosoma bears a single (anterior median) shield which does not encompass the bases of setae *sci*. This condition is retained in the Sarcoptinae and *Chirophagoides*. In most Teinocoptinae the bases of setae *sci* are included in the shield. In *Nycteridocoptes, Chirnyssoides*, and most *Notoedres*, the anterior median shield is expanded anteriorly beyond the line between the bases of setae *sce*, a state not found in the outgroups. The anterior median shield is absent in the Diabolicoptinae and *Notoedres centrifera* (all dorsal shields are absent in these taxa).

9. Dorsal shields in the male absent (1), vs. present (0).

10. Anterior median shield including the bases of setae sci *(1), vs. not including setae* sci*, or shield absent (0).*

The males of most Teinocoptinae have anterior lateral shields in addition to the anterior median shield, a unique state within the Sarcoptoidea. These shields are fused to the anterior median shield in *Nycteridocoptes* and *Notoedres* (*myoticola* group) (Figs. 103, 242) while free in the other taxa (Figs. 150, 211). The character relating to the fusion of the shields is treated as unordered.

11. Anterior lateral shields in the male present (1), vs. absent (0).

12. Anterior lateral shields not fused to the anterior median shield (2), fused (1), or absent (0).

The ancestral configuration of shields on the hysterosoma of the male includes a single shield encompassing the posterior median and anal shields, including the base of setal pair *d 1*. This condition of the median and anal shields is retained in *Trixacarus eliurus, T. diversus, Kutzerocoptes, Chirobia, Teinocoptes, Chirophagoides, Chirnyssoides,* and some *Notoedres* (Figs. 61, 190). The posterior median shield is reduced in size, no longer including the bases of setae *d 1*, in *Trixacarus caviae, Sarcoptes, Prosarcoptes,* and *Notoedres cati.* The anal shields are not connected to any other shields in *Trixacarus caviae, Sarcoptes,* most *Nycteridocoptes, Tychosarcoptes ptenochirus,* and some *Notoedres* (Fig. 120). They are connected to each other, but not to the posterior median shield, in *Tychosarcoptes orphanus, Notoedres miniopteri, N. namibiensis, N. yunkeri, N. dewitti,* and *N. muris.* Finally, in *Nycteridocoptes heidemanni* and *Cynopterocoptes* the anal shields are connected to the posterior median shield, but not to each other.

The posterior median shield in most *Nycteridocoptes* and *Chirophagoides* has a variously well developed lateral notch, which is absent in the other ingroup taxa as well as in the outgroups.

13. Posterior median shield of the male absent or reduced, not including the bases of setae d 1 *(1), vs. shield present, including the bases of these setae (0).*

14. Anal shields not fused together (1), vs. fused (0). Shields absent coded as missing data.

15. Anal shields not fused to the posterior median shield (1), vs. fused (0). Shields absent coded as missing data.

16. Posterior median shield with a lateral notch (1), vs. lateral edge smooth, or shield absent (0). Shield absent coded as missing data.

The males of most taxa in the Sarcoptinae and Teinocoptinae have more or less well developed posterior lateral shields, in addition to the posterior median and anal shields (Figs. 103, 190, 242). These shields are absent in most outgroups as well as in the Diabolicoptinae, *Trixacarus, Prosarcoptes,* and some *Notoedres.* They are poorly developed (not including the bases of setae *c 2*) in *Caenolestocoptes* (Rhyncoptidae), *Kutzerocoptes,* and *Sarcoptes,* but well developed in most Teinocoptinae. Posterior lateral shields were not observed in *Tychosarcoptes ptenochirus* and *Chirobia haplonycteris.* However, these observations are tentative, since all males examined in these two taxa were pharates.

17. Posterior lateral shields in the male present (1), vs. absent (0).

18. Posterior lateral shields poorly developed, not including the bases of setae c 2 *(2), well developed (1), or absent (0). This character is treated as unordered.*

CUTICULAR SPINES AND SCALES

Ancestrally, the cuticle of sarcoptoid mites is simply striated, a condition retained in the Diabolicoptinae, *Chirnyssoides, Notoedres,* and immature *Nycteridocoptes.* In contrast, the cuticle in the remaining taxa shows a range of modifications in addition to striations. These include large spines (e.g. Sarcoptinae [Fig. 66], female *Chirophagoides*), small spines (e.g. female *Nycteridocoptes* [Fig. 93]), and scales (e.g. female *Teinocoptes* [Fig. 207]). Based on the following evidence, I consider these three types of structures to be homologous.

Positionally, the patterns of large spines, small spines and/or scales correspond well across taxa. A striking example concerns the female of *Teinocoptes strandtmanni.* In this species small spines cover the same area of the dorsum covered with scales in most other *Teinocoptes* species. In general, the area covered by the combination of scales and the lateral spine series in females of the *Teinocoptes* group matches very closely the area of small spines of female *Nycteridocoptes.* The different types of structures can occur in different stages of the same species. The female tritonymph of *Nycteridocoptes heidemanni* has large spines, and the female small spines (Figs. 91, 93). Finally, transitional forms occur. The different host races of *Nycteridocoptes microphallus* have small spines or scales in the preanal zone, with intermediate forms occurring. A transition between small spines and scales in a single individual is evident in the lateral spine series of nymphal and female *Chirobia.* The small spines gradually merge into the scaly area (Figs. 189, 193, 200).

In addition to suggesting homology of these three types of cuticular structures, the character state distributions (see discussion characters 19–46) suggest that they are part of a transformation series, from no structure (as observed in the outgroups) to large spines, to small spines, to scales. Each state in this transformation series occurs only in a subset of the taxa in which the previous state occurs.

Apart from characters associated with occurrence and type of cuticular structure, the pattern of these structures provides an additional character set. In *Cynopterocoptes* and the *Teinocoptes* group the pattern of spines and/or scales has a strong ontogenetic component: the area covered by spines/scales increases from protonymph to tritonymph to female (Figs. 161–163, 166, 167). A transformation series can be recognized for the pattern of spines/scales in the immatures and females, rooted by outgroup comparison: spines/scales absent, spines/scales only in small discrete patches near setae *c 1*, patches connected into a U-shaped band, spines/scales covering the hysterosoma from setae *c 1* to the anus, and spines/scales continuing posterior to the anus. This transformation series is assumed to be valid for all taxa in the Sarcoptidae.

DISCUSSION OF INDIVIDUAL CHARACTERS BY STAGE.—*Larva.* Spines and/or scales are found in the larvae of the Sarcoptinae, *Cynopterocoptes,* and the *Teinocoptes* group. They are absent in the larvae of the Diabolicoptinae and most of the remaining Teinocoptinae. The larva of *Chirophagoides* is unknown. In the Sarcoptinae the larvae have large spines, while larvae in the *Teinocoptes* group may have spines (intermediate between large and small type) and/or scales. Scales occur in *Cynopterocoptes, Tychosarcoptes ptenochirus, Chirobia,* and a few *Teinocoptes;* spines in *Rousettocoptes, Tychosarcoptes,* and most *Teinocoptes.* In the Sarcoptinae, spines cover most of the hysterosoma; in *Cynopterocoptes* and the *Teinocoptes* group spines/scales may occur in patches, cover the hysterosoma anterior to the anus, or extend posterior to the anus.

The scale-like striations on the dorsum of some *Notoedres* (*s.s.*) larvae are not homologous with the scales observed in the above taxa. The "scales" on the dorsum of these *Notoedres* species do not extend from the body, nor do they overlap, two characteristics of the spine-derived "real" scales in *Cynopterocoptes* and the *Teinocoptes* group. These cuticular modifications are dealt with below (characters 56, 57).

19. Spines or scales in the larva present (1), vs. absent (0).

20. Spines posterior to the anus (1), vs. only anterior to the anus or absent (0).

21. Scales present (1), vs. absent (0).

22. Scales extending to the anus (1), vs. only in two separate patches near setae c 1 *or absent (0).*

23. Scales extending posterior to the anus (1), vs. only anterior to the anus or absent (0).

An additional modification of the scales occurs in some larval *Chirobia.* In *C. brevior, C. cynopteri, C. jagori,* and *C. minor,* some scales have pointed tips (Fig. 185). These structures are clearly a secondary derivation from scales and are not considered to be homologous to the spines in the larvae of *Rousettocoptes, Tychosarcoptes,* or *Teinocoptes.*

24. Pointed scales in the larva present (1), vs. absent (0).

Protonymph. As in the larva, spines and/or scales occur in the Sarcoptinae, *Cynopterocoptes,* and the *Teinocoptes* group, with large spines occurring in the Sarcoptinae and small spines and scales in *Cynopterocoptes* and the *Teinocoptes* group. The pattern of spines in the protonymph of the Sarcoptinae resembles that observed in the larva. Scales cover a large part of the dorsum in *Cynopterocoptes, Tychosarcoptes ptenochirus,* and most *Chirobia,* but cover only small areas or are absent in most of the other taxa of the *Teinocoptes* group.

25. Spines or scales in the protonymph present (1), vs. absent (0).

26. Small spines or scales present (1), vs. only large spines present, or spines/scales absent (0).

27. Spines/scales extending at least to a U-shaped band across the dorsum (1), vs. only patches or spines/scales absent (0).

28. Spines/scales posterior to the anus (1), vs. only anterior to the anus or absent (0).

Tritonymph. Spines and/or scales are present in tritonymphs of the Sarcoptinae, *Cynopterocoptes,* and the *Teinocoptes* group, as well as the female tritonymphs of most *Nycteridocoptes.* Spines/scales are absent in the male tritonymphs of *Nycteridocoptes.* Female tritonymphs of the Sarcoptinae and *Nycteridocoptes heidemanni* have large spines but female tritonymphs of most other *Nycteridocoptes* species have few (< 10) to many (> 20) small spines. Tritonymphs of *Cynopterocoptes* and the *Teinocoptes* group have only small spines and/or scales. The variation in the scale patterns of tritonymphs is similar to that observed in protonymphs. The latter type of variation is therefore not included in the analysis to avoid duplication.

29. Spines/scales in the female tritonymph present (1), vs. absent (0).

30. Small spines or scales present (1), vs. only large spines present, or spines/scales absent (0).

31. Scales present (1), vs. scales absent (0).

Female. Spines and/or scales occur in the females of all Sarcoptinae and Teinocoptinae, with the exception of *Chirnyssoides* and *Notoedres.* Large spines occur in the Sarcoptinae and *Chirophagoides,* small spines in *Nycteridocoptes, Cynopterocoptes,* and the *Teinocoptes* group, and scales in *Nycteridocoptes microphallus, N. rousetti, Cynopterocoptes,* and the *Teinocoptes* group. The pattern of spines in female Sarcoptinae is quite similar to that in the larva and nymphs. However, the variation in pattern in *Nycteridocoptes* and the *Teinocoptes* group is extensive. Since transformation series of complete patterns cannot be made with any degree of confidence (there is no ontogenetic evidence since female *Nycteridocoptes* are the only stage in that genus with well developed spine/scale areas), characters are defined by area of the dorsum. Each of these characters is polarized using outgroup comparison.

Some *Notoedres* females have scale-like striations on the dorsum, but these cuticular modifications are not considered homologous with the scales found in *Nycteridocoptes, Cynopterocoptes,* and the *Teinocoptes* group (see discussion for characters 19–23 and 56, 57).

32. Spines/scales in the female present (1), vs. absent (0).

33. Small spines or scales present (1), vs. only large spines present, or spines/scales absent (0).

34. Scales present (1), vs. absent (0).

35. Spines/scales in the area between setae sci *and* c 1 *(1), vs. spines/scales in this zone absent (0).*

36. Spines/scales in a continuous transverse band between setae sci *and* c 1 *(1), vs. only patches in this zone or spines/scales absent (0).*

37. Spines/scales in the area between setae c 1 *and* d 1 *(1), vs. spines/scales in this zone absent (0).*

38. Spines/scales in the area between setae d 1 *and the anus (1), vs. spines in this zone absent (0).*

39. Spines/scales lateral to the anus (1), vs. spines/scales in this zone absent (0).

40. Spines/scales posterior to the anus (1), vs. spines/scales in this zone absent (0).

A narrow band of small spines extends laterally from the dorsum to an area near leg III in females of *Nycteridocoptes, Cynopterocoptes,* and the *Teinocoptes* group. This pattern of spines is not found in any other Sarcoptidae or in the outgroups. In some *Chirobia* and *Teinocoptes* this band is expanded to a more or less oval field. Finally, the posterior spine in the series is very large (> 10 μm) in *Tychosarcoptes,* a unique state in the Sarcoptidae.

41. Female with spines in a zone lateral to leg III (1), vs. spines in this zone absent (0).

42. Lateral spines arranged in a field (1), vs. arranged linearly or absent (0).

43. Most posterior spine in the lateral group very large (> 10 μm) (1), vs. posterior spine smaller or lateral spines absent (0).

Females of a few species of *Nycteridocoptes* have an additional spinose zone ventrolaterally on the hysterosoma, quite distant from the anus. The presence of this zone is considered an apomorphy. The character relating to the shape of this zone is treated as unordered.

44. An isolated ventrolateral zone of small spines in the female present (1), vs. absent (0).

45. Ventrolateral spines arranged in a field with a distinct notch (Figs. 131, 132) (3), in a roughly oval field (Figs. 136, 137) (2), linearly (1), or ventrolateral spines absent (0).

Male. Cuticular spines occur in the males of the Sarcoptinae (except in *Kutzerocoptes*), *Tychosarcoptes, Teinocoptes strandtmanni,* and *T. harpyionycteris.* They are absent in all other taxa in the Sarcoptidae.

46. Spines in the male present (1), vs. absent (0).

MISCELLANEOUS CUTICULAR STRUCTURES

The females of *Sarcoptes* and *Prosarcoptes* have more or less well developed tubercles in an area posterolateral to legs IV (Fain, 1968; OConnor, 1984). These structures are unique among the in- and outgroup taxa examined. They are well developed in *Prosarcoptes,* poorly developed in *Sarcoptes.*

47. Posterior ventral tubercles in the female present (1), vs. absent (0).

48. Posterior ventral tubercles well developed (1), vs. relatively small or absent (0).

A number of unique cuticular modifications are found in females of the *Teinocoptes* group. In many species the females have a well developed sclerotized zone posterior to the genital area (Fig. 215). Also quite common among females in this genus is a "verrucous" zone anterolateral to legs III, consisting of rounded protuberances or spine-like structures (Figs. 159, 208). This zone extends in a narrow band between coxae III in *Teinocoptes eonycteris* and *T. johnsoni.* Finally, a sclerotized or spinose band extends between the distal ends of coxal apodemes II in some female *Teinocoptes.*

49. Well developed sclerotized zone posterior to the genital area in the female (1), vs. postvulvar sclerotization absent (0).

50. Verrucous zone anterolateral to legs III present (1), vs. absent (0).

51. Verrucous zone extending in a band between coxae III (1), vs. only lateral to coxae III or verrucous zone absent (0).

52. Sclerotized or spinose band between the distal ends of coxal apodemes II present (1), vs. absent (0).

Distinct median ventral outgrowths at the posterior margin of coxal fields II are present in the males of *Chirobia* and *Teinocoptes* (Figs. 191, 210, 219). This type of ventral "spines" does not occur in the other ingroup taxa or in the outgroups. Possible precursors exist in some Sarcoptinae, *Nycteridocoptes,* and *Tychosarcoptes* in the form of the sclerotized, rounded edges of striations on coxal fields II. In males of *Chirobia* and *Teinocoptes* these structures extend out from the body and have become much larger. Three morphologies can be recognized: short and blunt (Fig. 191), short and pointed (Fig. 210), and elongated and pointed (Fig. 219). Given the above information short and blunt is considered the most primitive condition, elongated and pointed the most derived.

53. Median ventral outgrowths in the male present (1), vs. absent (0).

54. Median ventral outgrowths pointed (1), vs. blunt or absent (0).

55. Median ventral outgrowths elongated (1), vs. short or absent (0).

In most taxa in the Sarcoptidae, as well as in the outgroups, the idiosoma of the immatures and females is covered with parallel striations. In female *Notoedres cati, N. musculi,* and *N. oudemansi* the striation pattern is modified to yield a scale-like structure. As mentioned in the discussion for characters 19–23, these "scales" are not considered homologous to the scales found in *Nycteridocoptes, Cynopterocoptes,* and the *Teinocoptes* group. A less distinct pattern of scale-like striations is found in the larvae of *N. cati* and *N. musculi.* Scale-like striations are indicated but very poorly developed in the larvae of *Nycteridocoptes heidemanni* and *N. hoogstraali,* as well as in the immatures and female of *N. cynopteri.*

An additional modification of the striation pattern occurs in a number of taxa in *Notoedres,* where large parts of the dorsum of the female (and nymphs) are smooth, bearing no striations at all.

56. Larva with scale-like striations (1), vs. such striations absent (0).

57. Female with scale-like striations (1), vs. such striations absent (0).

58. Over 20% of the dorsum in the female bare (1), vs. dorsum with striations, spines, scales, etc. (0).

DORSAL BODY SETATION

Variation in shape, addition pattern, and position of the idiosomal setae in the Sarcoptidae is extensive. Since there is considerable confusion in the literature regarding setal nomenclature in the Sarcoptidae and Sarcoptoidea, it seems appropriate to briefly discuss the system (chaetotaxy) adopted for this study. In doing this, I have concentrated on the assumptions made and methods used in determining setal homologies.

The chaetotaxy used in this study was developed by Griffiths et al. (1990) for the Astigmata. The system can be used for the Sarcoptidae without any major modifications. As in a number of chaetotaxy systems developed earlier (Grandjean, 1939b; OConnor, 1981, 1982) it is based on the assumption of retention of the ancestral segmental structure of the body, even though segmental boundaries are no longer visible in astigmatid mites. A second basic assumption in all of these systems is that segments are added in the paraproctal region during ontogeny. The terminal segment always includes the anus even when the body shape, and thus the segmental boundaries, become distorted. Finally, a very important, although often unstated assumption is that the setae of an ancestral segment always remain associated with that segment.

Systems for setal nomenclature usually concentrate on the hysterosoma, since the propodosomal setation is quite simple and segmental boundaries are unclear. The propodosoma bears at most three pairs of setae in the Sarcoptidae: the internal verticals (*vi*) and two pairs of scapular setae (*sci, sce*) (Figs. 59, 93, 234).

Segmental boundaries can be hypothesized for the hysterosoma. In the Astigmata, each of the ancestral segments is assumed to have the following maximum complement of setae (Griffiths et al., 1990): segment C with *c 1, c 2, cp,* and *c 3,* segment D with *d 1* and *d 2,* segment E with *e 1* and *e 2,* segment F with *f 2,* segment H with *h 1, h 2,* and *h 3,* segment PS with *ps 1, ps 2,* and *ps 3,* and segment AD with *ad 1, ad 2,* and *ad 3.* Since segments and their associated setal rows are assumed not to overlap, it is possible to draw hypothetical segmental boundaries, including the appropriate setae and incorporating the distortion of the body as indicated by the position of the anus. This approach is a very useful tool in hypothesizing setal homologies.

Another important tool in determining setal homologies is setal ontogeny. The ancestral setal addition sequence in the Astigmata as hypothesized by Griffiths et al. (1990) can be summarized as follows. Ancestrally all setae of segments C, D, and E, plus setae *h 1* and *h 2,* are fundamental (= present in the first free living stage, the larva). Setae *f 2, h 3,* and the three *ps* setae are added in the protonymph. Ancestrally the *ad* setae are added in the deutonymph but in the Psoroptidia, which have lost the deutonymphal stage, they appear in the tritonymph. The Psoroptidia never add the setae of the AN segment (OConnor, 1982). As discussed below, numerous modifications of this sequence occur in the Sarcoptidae.

Within the framework of the Griffiths et al. (1990) system, setal homologies in this study have been determined by a combination of data on position (segmental boundaries, position relative to other setae, etc.) and setal ontogeny. Setal shape is used, but setae in the Sarcoptidae can change shape drastically between life stages and this criterion is used only if the results of the other methods are inconclusive. Parsimony is used as the criterion for deciding between alternative hypothesis of setal homology. In the following paragraphs a number of complex situations involving problems in setal nomenclature will be discussed before proceeding to discuss individual character states.

The first case involves the missing pair of setae in the propodosomal/anterior hysterosomal area of the Diabolicoptinae. Ancestrally the following setal pairs can be present: *vi, sci, sce, c 1,* and *c 2.* In the Sarcoptinae and Teinocoptinae all five pairs are present. In the Diabolicoptinae setae *vi* are present but one of the other pairs of setae is absent. Based on positional and shape comparisons with the remaining Sarcoptidae and the Rhyncoptidae (the sister group to the Sarcoptidae), two likely hypotheses can be proposed regarding the missing setal pair.

In their description of *Diabolicoptes,* Fain & Domrow (1974) proposed that setal pair *c 1* ("*d 1*" *sensu* Fain & Domrow) is absent. This requires a transformation of setae *sci* from simple to layered in the Sarcoptidae, and a reversal from layered to simple in the Teinocoptinae. It also requires a transformation of setae *c 1* from simple to layered in the ancestor of the Sarcoptidae and Rhyncoptidae, reversed in the Teinocoptinae, and a loss of *c 1* in the Diabolicoptinae (from the layered state). A problem with this hypothesis is that it requires that setae *sce* in the Diabolicoptinae ("*sci*" *sensu* Fain & Domrow, 1974) are positioned as close to each other as setae *sci.* Setae *sce* are usually much more widely spaced. However, the situation is not unique: setae *sci* and *sce* are in similar relative positions in the nymphs and females of the *Teinocoptes* group.

The alternative hypothesis assumes that setal pair *sci* is missing. This requires the loss of setae *sci* in the Diabolicoptinae (from a simple shape) and a transformation from simple to layered in the Sarcoptinae. For setae *c 1,* it requires a transformation from simple to layered in the ancestor of the Rhyncoptidae and Sarcoptidae, reversed to simple in the Teinocoptinae. The positional problems of the first hypothesis do not exist, since setal pair *sci* is absent. This hypothesis is accepted as more parsimonious, requiring four transformational steps, compared to five for the first hypothesis.

The chaetotaxy of the hysterosoma presents a number of problems, the first of which involves the ancestral setal complement for the Sarcoptidae. The maximum number of setae added during ontogeny in the Rhyncoptidae is five, in the Sarcoptidae four. In most species all of these setae are added in the protonymph, leading to the conclusion that the *ad* setae are never added in either family. Compared to the Rhyncoptidae the Sarcoptidae add one fewer setal pairs. The missing pair is hypothesized to be *ps 3.* Positional arguments strongly support the addition of setae *f 2* (between setal rows *e* and *h*), and *ps 1* and *ps 2* (very close to the anus), but evidence for the addition of setae *h 3* instead of *ps 3* as the fourth pair of setae added is less strong. Absence of setal pair *ps 3* is hypothesized since a potential addition of setae *ps 3* requires more contorted hypothetical segmental boundaries in *Nycteridocoptes* and *Cynopterocoptes* than the addition of setae *h 3.* Given this ancestral setal complement of the hysterosoma, major modifications have taken place within the family, which I will discuss by subfamily.

In the Diabolicoptinae, *Satanicoptes armatus* does not add setae during ontogeny. Given that all setae present are fundamental and given their relative position, I hypothesize that setae *c 1, c 2, cp, c 3, d 2, e 1, e 2, h 1,* and *h 2* are present, while setae *d 1* are absent. Females of *S. phascogale* have two additional pairs of setae in the perianal region, probably *ps 1* and *ps 2* based on position. In contrast, larvae of *Diabolicoptes* have only seven pairs of setae on the hysterosoma but add five in the protonymph. The larvae lack the usual two pairs near the anus (*h 1* and *h 2*), which are added in the protonymph. Based on the assumption that all setae present in adult *Satanicoptes* are also present in *Diabolicoptes,* the remaining setae added in *Diabolicoptes* most probably are *f 2, ps 1,* and *ps 2.*

The Sarcoptinae are relatively uniform in their setal complement. *Trixacarus eliurus* and the Sarcoptinae associated with primates add three pairs in the protonymph: one between setal rows *e* and *h,* and two near the anus. These setae correspond positionally with *f 2, ps 1,* and *ps 2.* The newly added setae, especially *f 2,* are often relatively small in the protonymph but distinctly more developed in the following life stages. *Trixacarus diversus* and *T. caviae* lack setal pair *e 2* in all life stages and do not add setae *f 2.*

Variation in setal complements is much richer in the Teinocoptinae. The setal complement of *Chirophagoides* resembles that of the Sarcoptinae: setae *f 2, ps 1,* and *ps 2* are present in the tritonymph and adults. Data on ontogeny are limited since the larva is unknown and the protonymph is incompletely described.

The setal complement in *Nycteridocoptes* is the richest of all Sarcoptidae. Although delayed additions are common among the species of *Nycteridocoptes,* all but one species add setae *f 2, h 3, ps 1,* and *ps 2* during ontogeny. The highly paedomorphic species *N. cynopteri* does not add setae to its larval complement.

Cynopterocoptes has the same setal complement as *Nycteridocoptes,* but the species of the *Teinocoptes* group add only one or two pairs of hysterosomal setae during ontogeny. Homologies for the added setae can once again be inferred using position, ontogeny, and shape of the perianal setae. The larvae of *Cynopterocoptes* and the *Teinocoptes* group have three pairs of setae near the anus, positionally corresponding to setae *e 1, h 1,* and *h 2.* Nymphs, females, and males have four pairs in that position. The added pair is characteristically smaller than the others in the protonymph, although usually of equal size in the following stages, and is hypothesized to be *ps 1.* Another pair of often very small setae, absent in all stages in several species of *Chirobia*, is added posterior to the anus. This pair could be either *f 2*, *h 3*, or *ps 2*, all of which are present in *Cynopterocoptes* and *Nycteridocoptes*. In the males of these taxa setae *f 2* are always positioned on the anal shield, setae *h 3* off the shield, and setae *ps 2* on the inner edge of the shield. The setal pair in males of the *Teinocoptes* group is inserted on the inside edge of the shield. Moreover, setae *f 2* and *h 3* in *Cynopterocoptes* are more poorly developed than setae *ps 2*, making retention of *ps 2* more likely. The pair of setae posterior to the anus is therefore hypothesized to be *ps 2*. The above hypothesis does create the problem that both *ps* setae in *Cynopterocoptes* and the *Teinocoptes* group are positioned posterior to the anus, *ps 1* close, but *ps 2* often far removed (e.g. Fig. 167). This problem can be explained as a result of the deformation of segment *ps* due to the movement of the anus to a mid dorsal position. Although the segment is "dragged along" with the anus, the bulk of its area can be expected to be trailing, leaving the *ps* setae in positions often far removed from the anus.

The remaining taxa, *Chirnyssoides* and *Notoedres*, add at most two pairs of perianal setae, corresponding to *ps 1* and *ps 2*. In *Chirnyssoides* setal additions are often delayed, but nearly all species add the *ps* setae. The exception, *C. surinamensis*, never adds setae to its larval complement. In an unusual ontogenetic modification (similar to that previously noted for *Diabolicoptes*), some species of *Chirnyssoides* lack the *h* setae in the larvae, but add them during ontogeny.

The setal complement in *Notoedres* is the most reduced in the family: species in this genus never add the *ps* setae. The larva has only a single pair of setae near the anus (hypothesized to be *h 1*), adding a second (*h 2*) in the protonymph. The addition of setae *h 2* is delayed in *Notoedres* (*Bakeracarus*) *corynorhini*, and the setae are never added in *N.* (*B.*) *eptesicus* and *N.* (*B.*) *americanus*. In some species a pair of small structures resembling alveoli is present close to the anus, posterior to setae *h 2* (Figs. 242, 252). This may be a remnant of a pair of *ps* setae.

DISCUSSION OF INDIVIDUAL SETAL CHARACTERS.—Setal pair *vi* is present in most of the in- and outgroup taxa, but absent in all stages of the Rhyncoptidae, the female of *Cynopterocoptes*, and the nymphs and females of most species in the *Teinocoptes* group. Due to the difficulty of establishing the presence of setae *vi* in the taxa of the *Teinocoptes* group, the character related to the absence of setae *vi* is defined very broadly.

59. Setae vi *in the nymphs and female absent (1), vs. present in either the nymphs or the female (0).*

Setae *sci* are relatively short and filiform in all life stages of the outgroups examined. They are absent in the Diabolicoptinae, minute (< 5 μm) in the nymphs and females of most taxa in the *Teinocoptes* group and some *Chirnyssoides* and *Notoedres*, and very long (> 20 μm) in females of *Trixacarus*, *Chirnyssoides noctilionis*, and some *Notoedres*.

60. Setae sci *in all stages absent (1), vs. present (0).*

61. Setae sci *in the female very long (> 20 μm) (1), vs. shorter (0). Setae absent coded as missing data.*

62. Setae sci *in the female minute (< 5 μm) (1), vs. longer (0). Setae absent coded as missing data.*

The shape of setae *sci* varies considerably over the various taxa as well as over ontogeny. The setae are short, broad spines in all stages of the Sarcoptinae associated with primates and *Chirophagoides*. In immatures and females of *Nycteridocoptes*, *Cynopterocoptes*, the *Teinocoptes* group, some *Notoedres*, and *Caenolestocoptes* (Rhyncoptidae), they are less well developed, thinner spines. Setae *sci* are elongated spines in the larvae of most species of *Nycteridocoptes* and are especially long (length >4X width) in the larvae of *N. malayi* and *N. orientalis*. A similar elongated shape is found in the males of most *Nycteridocoptes*. Finally, the setae are thin, spine-like rods with bifurcate tips in the protonymphs and male tritonymphs of a number of *Nycteridocoptes* species. In the following characters absence of the setae is coded as missing data.

63. Setae sci *in the female spine-like (1), vs. filiform (0).*

64. Setae sci *in all stages broad, short spines (1), vs. small or thin spines, or filiform (0).*

65. Setae sci *in the larva elongate spines (length >4X width) (1), vs. shorter or filiform (0).*

66. Setae sci *in the protonymph and male tritonymph thin, spine-like rods with bifurcate tips (1), vs. short spines or filiform (0).*

67. Setae sci *in the male distinct, thin and elongate spines (1), vs. broad spines, or filiform (0).*

In most Sarcoptinae (except *Trixacarus diversus* and *T. caviae*) setae *sci* appear to be layered. In *Trixacarus eliurus*, the setae consist of a long filiform and a basal flat part, the latter wrapping partly around the filiform part. This structure is remarkably similar to the structure of some median hysterosomal setae in the Rhyncoptidae. In the Sarcoptinae associated with primates the thin basal part (or parts) appears to overlie the spine-like bulk of the setae.

68. Setae sci *layered (1), vs. simple (0). Setae absent coded as missing data.*

Setae *sce* are long and filiform in all stages in most outgroups, as well as in most taxa in the Sarcoptidae. They are minute (< 5 μm) in the nymphs and females of most taxa in the *Teinocoptes* group (but well developed in *Rousettocoptes*) and in *Notoedres* (*lasionycteris* group), as well as in *Ursicoptes*, *Saimirioptes*, and *Audycoptes* (Rhyncoptidae). The setae are also minute in the female of *Cynopterocoptes* (not in the nymphs).

In the males of most *Nycteridocoptes* and *Chirnyssoides* setae *sce* are long spines (although the tip may be more or less filiform, e.g. *N. poppei*), a condition not found among any of the outgroups.

69. Setae sce *in the female minute (1), vs. well developed (0).*

70. Setae sce *in the nymphs and female minute (1), vs. well developed (0).*

71. Setae sce *in the male long spines (1), vs. filiform, thinner (0).*

Setal pair *c 1* is well developed and filiform in most outgroup taxa but absent in all stages of some Psoroptidae and *Rhyncoptes* (Rhyncoptidae). Setae *c 1* are minute in the larvae, nymphs, and females of most *Chirnyssoides* and some *Notoedres*, as well as in the nymphs and females of the *Teinocoptes* group (except *Rousettocoptes*). The setae are well developed in the known males of these taxa. Setae *c 1* are unusually long (> 20 μm) in *Trixacarus* and some *Notoedres*.

72. Setae c 1 *in the larva minute (< 3 μm) (1), vs. well developed (0).*

73. Setae c 1 *in the nymphs and female minute (< 5 μm) (1), vs. well developed (0).*

74. Setae c 1 *in the female long (> 20 μm) (1), vs. shorter (0).*

The shape modifications found in setal pair *c 1* are comparable to those for setae *sci.* In all stages of the Diabolicoptinae, the Sarcoptinae associated with primates, and *Chirophagoides,* setae *c 1* are short, broad spines. In the larvae and protonymphs of *Nycteridocoptes* and *Cynopterocoptes* they are transformed into thin, spine-like rods with bifurcate tips. This condition is retained in the male tritonymphs of most of these taxa, but not in *N. heidemanni.*

75. Setae c 1 *in all stages short, broad spines (1), vs. thin spines or filiform (0).*

76. Setae c 1 *in the male tritonymph thin, spine-like rods with bifurcate tips (1), vs. of different shape (0).*

Setae *c 1* are layered in most taxa of the Rhyncoptidae (absent in *Rhyncoptes*) and Diabolicoptinae (not in *Satanicoptes armatus*), in *Trixacarus eliurus,* and in the Sarcoptinae associated with primates. They are simple (or absent) in the other in- and outgroup taxa. The layered structure of setae *c 1* and *c 2* most probably arose in the ancestor of the Rhyncoptidae and Sarcoptidae.

77. Setae c 1 *layered (1), vs. not layered (0).*

Setae *c 2* are simple, filiform, and well developed in all stages of most outgroup taxa. They are minute in the nymphs and females of the *Teinocoptes* group, most *Chirnyssoides,* and some *Notoedres.*

78. Setae c 2 *in the nymphs and female minute (< 5 μm) (1), vs. well developed (0).*

Setae *c 2* are spines in all stages of the Diabolicoptinae, the Sarcoptinae associated with primates, *Nycteridocoptes* and *Caenolestocoptes* (Rhyncoptidae), and in females of *Cynopterocoptes,* the *Teinocoptes* group, *Chirophagoides,* and some *Notoedres* (*myoticola* group). In most of these taxa setae *c 2* are small and/or thin spines, but in the Diabolicoptinae, the Sarcoptinae associated with primates, and *Chirophagoides* they are short, broad spines.

79. Setae c 2 *in the female well developed spines (1), vs. filiform or thin spines (0).*

80. Setae c 2 *in the male spines (1), vs. filiform (0).*

81. Setae c 2 *in all life stages short, broad spines (1), vs. filiform or thin spines (0).*

Setae *c 2* are layered in the females of most Rhyncoptidae (not in *Ursicoptes, Rhyncoptes*), and in all stages of the Diabolicoptinae (not in *Satanicoptes armatus*), *Trixacarus eliurus,* and the Sarcoptinae associated with primates. The setae are simple in all other in- and outgroup taxa studied.

82. Setae c 2 *in the female layered (1), vs. not layered, simple (0).*

Setal pair *cp* is well developed in all stages of most outgroup taxa examined, although reduced in *Saimirioptes* (Rhyncoptidae), and absent in *Audycoptes* and *Rhyncoptes* (Rhyncoptidae). These setae are reduced to various degrees in the larvae, nymphs, and females of the Teinocoptinae (except in *Chirophagoides*). The ontogenetic reduction patterns are analyzed by stage.

83. Setae cp *in the larva minute, vestigial, or absent (1), vs. distinct (0).*

84. Setae cp *in the larva vestigial or absent (1), vs. present (0).*

85. Setae cp *in the protonymph and male tritonymph minute, vestigial, or absent (1), vs. distinct (0).*

86. Setae cp *in the protonymph vestigial or absent (1), vs. present (0).*

87. Setae cp *in the male tritonymph vestigial or absent (1), vs. present (0).*

88. Setae cp *in the female vestigial or absent (1), vs. present (0).*

In the males of *Chirnyssoides caparti* and *C. brasiliensis* setae *cp* have been modified to long, spine-like rods with bifurcate tips. This modification is unique for those taxa.

89. Setae cp *in the male long, spine-like rods with bifurcate tips (1), vs. filiform or short (0).*

Setae *c 3* are well developed and filiform in all stages of the outgroup taxa examined. They are reduced in the females of some taxa in the *Teinocoptes* group, of most *Chirnyssoides,* and of some *Notoedres* (*lasionycteris* group).

A shape transformation to distinct spines has taken place in all stages of the Diabolicoptinae. Setae *c 3* in the males of some *Notoedres* are transformed into spines (*myoticola* group) or setae with thickened bases (*N. africanus*).

90. Setae c 3 *in the female minute, vestigial, or absent (1), vs. distinct (0).*

91. Setae c 3 *in the female vestigial or absent (1), vs. present (0).*

92. Setae c 3 *in the immatures and female distinct spines (1), vs. filiform (0). Setae absent coded as missing data.*

93. Setae c 3 *in the male spines or with distinctly thickened bases (1), vs. filiform (0).*

The absence of setae *d 1* is characteristic for the Diabolicoptinae. The setae are present in all other Sarcoptidae as well as in the outgroups.

The relative size of setae *d 1* and *d 2* is variable. They are of similar size in the adults of the outgroups that have both setae (setae *d 2* is absent in the Rhyncoptidae), but setae *d 1* are much longer than *d 2* in the males of some *Nycteridocoptes.* In the immatures and females of *Notoedres* (*lasionycteris* group), setae *d 1, e 1,* and *h 1* have a unique shape, more or less spine-like with a thickened, rounded (spatulate) tip.

94. Setae d 1 *absent (1), vs. present (0).*

95. Setae d 1 *in the male twice the size of setae* d 2 *(1), vs. subequal or shorter (0). Setae* d 1 *absent coded as missing data.*

96. Setae e 1 *(and* d 1 *and* h 1 *if present) in the immatures and female spine-like with thickened, rounded tips (1), vs. shape different (0).*

The nymphs and females of *Cynopterocoptes* and the *Teinocoptes* group are characterized by four pairs of setae (*e 1, h 1, h 2, ps 1*) arranged very close to the anus. In the females of some taxa of this group, these perianal setae are more or less membranous in structure, rounded at the tips, and often lobed. This morphology is unique among the taxa examined.

97. Perianal setae in the female membranous, with rounded tips (1), vs. filiform or spine-like (0).

Setae *e 2* are present in all in- and outgroup taxa examined with the exception of *Trixacarus diversus* and *T. caviae.* The loss of setae *e 2* in all developmental stages is considered an apomorphy for these two species.

98. Setae e 2 *in all stages absent (1), vs. present (0).*

Setae *f 2* are added in the protonymph in the outgroups, *Diabolicoptes,* most Sarcoptinae, *Cynopterocoptes,* and possibly *Chirophagoides.* Addition of these setae is usually delayed in *Nycteridocoptes,* and the setae are never added in the remaining Sarcoptidae. The following transformation series is hypothesized: added in the protonymph, delayed to the tritonymph, delayed to the adults, never added.

In addition to presence/absence through ontogeny, variation exists in the degree of development of setae *f 2*. Setae *f2* are well developed in addition in the outgroups, but within *Nycteridocoptes* and *Cynopterocoptes* the setae are often minute in some or all stages.

99. Addition of setae f 2 *delayed or setae never added (1), vs. added in the protonymph (0).*

100. Setae f 2 *in the protonymph and male tritonymph minute or absent (1), vs. well developed (0).*

101. Addition of setae f 2 *delayed to the adults or setae never added (1), vs. added in the nymphs (0).*

102. Setae f 2 *in the female tritonymph short, minute, or absent (1), vs. relatively long (> 10 μm) (0).*

103. Setae f 2 *never added (1), vs. added in some developmental stage (0).*

Setae *h 1* are fundamental in most taxa in the Sarcoptidae, as well as in the outgroups. In *Diabolicoptes* and some *Chirnyssoides* an ontogenetic shift has taken place whereby setae *h 1* are absent in the larva but added in the protonymph.

In the larvae of some *Notoedres* setae *h 1* are distinctly longer than all other hysterosomal setae. This unique condition is considered derived.

104. Addition of setae h 1 *delayed to the protonymph (1), vs. setae* h 1 *fundamental (0).*

105. Setae h 1 *in the larva longer than the other hysterosomal setae (1), vs. subequal or shorter (0). Setae absent coded as missing data.*

Setal pair *h 2* is fundamental in the outgroups and most Sarcoptidae. Its addition is delayed in *Diabolicoptes* (to the protonymph), some *Chirnyssoides* (in some species to the adult), and *Notoedres*. In most species of *Notoedres* the addition of setae *h 2* is delayed to the protonymph but in some species of *N.* (*Bakeracarus*) addition is delayed to the adult (*N.* (*B.*) *corynorhini*), or setae *h 2* are never added at all (*N.* (*B.*) *eptesicus*, *N.* (*B.*) *americanus*).

106. Addition of setae h 2 *delayed or setae never added (1), vs. present in the larva (0).*

107. Addition of setae h 2 *delayed or setae never added (1), vs. added in the protonymph or larva (0).*

108. Addition of setae h 2 *delayed or setae never added (1), vs. added in the nymphs or larva (0).*

109. Setae h 2 *never added (1), vs. added in some developmental stage (0).*

Setae *h 2* and *ps 2* are transformed into spines in the males of *Diabolicoptes* and *Nycteridocoptes*. In the remaining ingroup taxa, as well as in the outgroups, these setae are filiform. These spine-like setae can be thin and short (a condition most closely resembling the outgroup state), thick and relatively short, or thin and relatively long. For the taxa in which setae *h 1* and/or *ps 2* are absent the following characters are coded as missing data.

110. Setae h 2 *and* ps 2 *in the male spine-like (1), vs. filiform (0).*

111. Setae h 2 *and* ps 2 *in the male thick spines (1), vs. thin spines or filiform (0).*

112. Setae h 2 *and* ps 2 *in the male long spines (1), vs. short spines or filiform (0).*

In the outgroups setae *h 3* are added in the protonymph. In the Sarcoptidae these setae are added only in *Nycteridocoptes* and *Cynopterocoptes*. Within *Nycteridocoptes* addition can be delayed to the female tritonymph or adults.

113. Addition of setae h 3 *delayed or setae never added (1), vs. added in the protonymph (0).*

114. Addition of setae h 3 *delayed or setae never added (1), vs. added in the protonymph or male tritonymph (0).*

115. Setae h 3 *never added (1), vs. added in some developmental stage (0).*

Ancestrally setae *ps 1* are added in the protonymph. This condition is retained in the Diabolicoptinae, Sarcoptinae, and most Teinocoptinae. The addition of these setae is delayed in some *Chirnyssoides*. Setae *ps 1* are never added in *Nycteridocoptes cynopteri*, *Chirnyssoides surinamensis*, and *Notoedres*.

116. Addition of setae ps 1 *delayed or setae never added (1), vs. added in the protonymph (0).*

117. Addition of setae ps 1 *delayed or setae never added (1), vs. added in the proto- or tritonymph (0).*

118. Setae ps 1 *never added (1), vs. added in some developmental stage (0).*

The addition sequence for setae *ps 2* in the outgroups is similar to that for setae *ps 1*. In *Chirnyssoides*, addition of both pairs of setae is similarly delayed in some species. Setae *ps 2* are never added in *Nycteridocoptes cynopteri*, *Chirnyssoides surinamensis*, and *Notoedres*. In most *Chirobia* setae *ps 2* are not added in the nymphs and females. However, vestigial alveoli or small clear spots are often retained. In those species where the females retain at least spots, the males retain small but distinct setae. The setae are absent in the males of the remaining species of *Chirobia*.

119. Setae ps 2 *in the nymphs and female absent (1), vs. vestigial alveoli or distinct setae present (0).*

120. Setae ps 2 *in the nymphs and female absent or vestigial alveoli present (1), vs. distinct setae present (0).*

Setae *ps 3* are added in the protonymph in the distant outgroups (e.g. Myocoptidae, Makialginae [Psoroptidae]) and the Rhyncoptidae. They are never added in the Sarcoptidae.

121. Setae ps 3 *never added (1), vs. added (0).*

VENTRAL BODY SETATION

The ventral body setation in psoroptidid mites is relatively simple. The larva has a single pair of setae on each of coxal fields I and III (*1 a, 3 b sensu* Griffiths et al., 1990; *cx I, cx III sensu* Fain, 1963e). In the protonymph a pair of genital setae (*g*) is added, usually at the level of legs III (Fig. 64). Two additional pairs are added in the tritonymph, one anterior to setae *g*, and a pair loosely associated with coxal fields IV (Fig. 65). Griffiths et al. (1990) concluded that these two pairs were ancestral coxal field setae, and not aggenital or genital setae as previously assumed (Fain, 1963e). The anterior pair (*3 a*) is assumed to have originated on coxal fields III, the posterior pair (*4 a*) on coxal fields IV (Griffiths et al., 1990).

Not all ventral setae are added in all taxa of the Sarcoptidae and it is not always evident which setae are missing. The homologies proposed in the following discussion are developed based on position and ontogeny and are consistent with shape data. Setae *3 a*, *g*, and *4 a* in the Sarcoptidae are hypothesized to be arranged in the same relative positions in all developmental stages: setae *3 a* anterior, fairly widely spaced; setae *g* median, widely spaced; and setae *4 a* posterior, closely spaced. In the female this results in setae *3 a* anterior to the oviporus (Fig. 60, ovi), setae *g* on the genital valves, flanking the oviporus, and setae *4 a* posterior to the oviporus (Figs. 60, 67, 94). In the male, setae *3 a* are inserted anterior to the genital area, usually close to coxal fields III, setae *g* lateral to the genital area, and setae *4 a* on the cuticle overlying the genital area (Figs. 62, 77, 104). Although setae *4 a* appear to be inserted on the genital area in the male, these setae are clearly inserted on a cuticular fold overlying the posterior part of the genital area, and not on the genital valves themselves.

This hypothesis of homology is based on the following evidence. In the Sarcoptinae associated with primates no setae are added in the protonymph, and two pairs are added in the tritonymph (Figs. 87, 88). The positions of these setae in the adults (one pair anterior, one posterior to the oviporus in the female, one pair anterior to, one over the genital area in the male) is consistent with the interpretation that setae *g* are never added in this group of taxa. Similarly, setae *g* and *3 a* are absent in *Chirnyssoides* and *Notoedres* (no setae added in the protonymph, one pair added in the tritonymph, inserted posterior to the oviporus in the female, over the genital area in the male) (Figs. 232, 233, 235, 243).

The above interpretation is consistent with the observations on shape and degree of development. For example, in *Nycteridocoptes* setae *4 a* are generally poorly developed in the nymphs, while setae *g* and *3 a* are always well developed and distinct (Fig. 117). In the female the pair of setae posterior to the genital area is distinctly smaller than the pairs anterior to and flanking the genital area in all females studied (Figs. 94, 119). Likewise, in the male the pair of setae over the genital area is much smaller than the two other pairs, and may even be absent in some specimens (Figs. 104, 121).

Although the above hypothesis provides an excellent fit with most of the available data, problems arise interpreting homologies in the female of *Cynopterocoptes*. The protonymph in this genus adds a pair of setae, and the tritonymph adds a second pair (Figs. 139–141). Given that the male has setae in the positions of setae *3 a* and *g* (Fig. 151), I suggest that the pair added in the tritonymph is *3 a*. However, the female has only one pair of setae, posterior and lateral to the oviporus, more or less on coxal field IV (Fig. 143). Although it requires a shift in position, I interpret this pair of setae as *g*, since the presence of setae *4 a*, with the concomitant loss of setae *3 a* and *g*, would be less parsimonious.

DISCUSSION OF INDIVIDUAL CHARACTERS.—Coxal setae *1 a* and *3 b* are filiform in most in- and outgroup taxa. These setae show relatively little variation in the Sarcoptidae. Setae *1 a* are often poorly developed or absent in the nymphs and females of the *Teinocoptes* group, especially in *Chirobia*. Given the average size and position of these setae (partially hidden under cuticular folds originating on the gnathosoma and anterior legs), it is extremely difficult to determine character states in the majority of taxa in the *Teinocoptes* group. This character is not included in the analysis.

Setae *3 b* are spine-like, or have at least a distinctly thickened base, in all stages of the Diabolicoptinae and the larvae and males of *Notoedres* (*myoticola* group) and *N. africanus*.

122. Setae 3 b *in the larva and male spine-like or with thickened bases (1), vs. filiform (0).*

The genital setae (*g*) are added in the protonymph in the outgroups, the Diabolicoptinae, *Trixacarus*, *Nycteridocoptes*, *Cynopterocoptes*, and possibly *Chirophagoides*. They are extremely reduced or absent in the nymphs and females of *Teinocoptes* but always present in the males of these taxa. In the Sarcoptinae associated with primates, *Nycteridocoptes cynopteri*, *Chirnyssoides*, and *Notoedres*, setae *g* are never added.

In the outgroups and most Sarcoptidae retaining these setae, setae *g* are filiform. In the Diabolicoptinae (nymphs and female) and some *Nycteridocoptes* (female tritonymph and male) setae *g* are spines.

123. Setae g *in the nymphs and female not added (1), vs. added (0).*

124. Setae g *never added (1), vs. added in at least the male (0).*

125. Setae g *in the female tritonymph spines (1), vs. filiform (0). Setae absent coded as missing data.*

126. Setae g *in the male spines (1), vs. filiform (0). Setae absent coded as missing data.*

Setae *3 a* are added in the tritonymph of the outgroups, the Diabolicoptinae, most Sarcoptinae, *Nycteridocoptes*, *Cynopterocoptes*, and *Chirophagoides*. In *Diabolicoptes* and *Cynopterocoptes* setae *3 a* are added in the tritonymph but lost in respectively the male and female. In *Prosarcoptes scanloni* and the *Teinocoptes* group the setae are extremely reduced or absent in the nymphs and female but well developed in the male. The setal pair is never added in *Nycteridocoptes cynopteri*, *Chirnyssoides*, and *Notoedres*.

In the outgroups and most ingroup taxa, setae *3 a* are filiform. In the tritonymphs and females of the Diabolicoptinae as well as in some female tritonymphs and some males of *Nycteridocoptes*, setae *3 a* are modified into spines.

127. Setae 3 a *in the tritonymph or female not added (1), vs. added (0).*

128. Setae 3 a *never added (1), vs. added in some developmental stage (0).*

129. Setae 3 a *in the female tritonymph spines (1), vs. filiform (0). Setae absent coded as missing data.*

Setae *4 a* are added in the tritonymph of the outgroups and most ingroup taxa. In *Nycteridocoptes cynopteri*, *Cynopterocoptes*, the *Teinocoptes* group, most *Chirnyssoides*, and some *Notoedres*, setae *4 a* are never or rarely (*Notoedres musculi*) added.

Setae *4 a* are filiform in the outgroups and most Sarcoptidae but transformed to well developed spines in the tritonymphs and females of the Diabolicoptinae and the males of some *Notoedres* (*myoticola* group).

130. Setae 4 a *rarely or never added (1), vs. added (0).*

131. Setae 4 a *in the tritonymph and female distinct spines (1), vs. filiform (0). Setae absent coded as missing data.*

132. Setae 4 a *in the male spines (1), vs. filiform (0). Setae absent coded as missing data.*

GENITAL AREA AND REPRODUCTION

The shape of the female oviporus in most outgroups is triangular due to the incomplete median fusion of the genital valves. In the Sarcoptidae and *Ursicoptes* (Rhyncoptidae) the valves are completely fused medially, resulting in a transverse oviporus (Fig. 60, ovi).

133. Oviporus in the female transverse (1), vs. triangular or longitudinal (0).

The male aedeagus in the outgroup taxa and in most Sarcoptidae is no longer than the width of the genital area. In *Nycteridocoptes macrophallus, N. cynopteri,* and *Chirnyssoides* the aedeagus is at least twice as long as the width of the genital area. The hypothesis of homology for these three instances of modification of the aedeagus is tentative, since the structure of the aedeagus in Sarcoptidae is difficult to determine.

134. Male aedeagus strongly elongated (1), vs. aedeagus relatively short (0).

Genital papillae in the adults are vestigial but present in most Sarcoptoidea as well as in the Diabolicoptinae. They are completely lost in the Sarcoptinae and Teinocoptinae.

135. Vestiges of the genital papillae absent (1), vs. present (0).

In the male adanal discs are present in nearly all outgroups, including the Rhyncoptidae. Adanal discs are lost in all Sarcoptidae, a potential apomorphy for the family.

136. Adanal discs in the male absent (1), vs. present (0).

Reproduction in most Sarcoptoidea is by ovipary. In the sister group of the Sarcoptidae, the Rhyncoptidae, as well as in *Cynopterocoptes* and the *Teinocoptes* group, reproduction is by ovovivipary.

A unique modification of the egg deposition system is found in the genera *Chirnyssoides* and *Notoedres.* Eggs deposited by species in these genera have stalks by which they are anchored to the substrate. In contrast to the Sarcoptinae, which deposit their eggs separately, these species deposit their eggs in groups, united by the fused bases of the egg stalks. The stalks are strongly reduced or absent in those species of *Notoedres* parasitizing hosts other than bats.

137. Reproduction by ovovivipary (1), vs. ovipary (0).

138. Eggs anchored to the substrate by well developed stalks (1), vs. stalks absent (0).

APODEMES

In contrast to shields and other forms of surface sclerotization, apodemes are internal structures. Most apodemes in the Sarcoptidae are associated with the coxal fields, although they often extend beyond the coxal fields. A few, such as the median apodeme in the male, may have a different origin.

Coxal apodemes I in the female are fused into a short sternum in the outgroups and most Sarcoptidae. In the nymphs and females of *Cynopterocoptes* and the *Teinocoptes* group they are very short, barely touching each other. In a number of taxa, including *Notoedres* (*Bakeracarus*) and *Notoedres* (*myoticola* group), coxal apodemes I run parallel, but are not completely fused.

Finally, in *Chirnyssoides noctilionis, Notoedres dewitti, N. ismaili, N. ovatus,* and *N. tristis,* coxal apodemes I are fused over most of their length but separated at the distal end, creating a bifurcate appearance.

139. Coxal apodemes I in the female parallel but not fused together (1), vs. fused (0).

140. Coxal apodemes I very short, barely touching each other (1), vs. longer, forming a sternum (0).

141. Distal end of the sternum bifurcate (1), vs. not bifurcate (0). Sternum absent coded as missing data.

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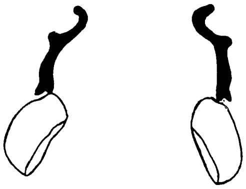

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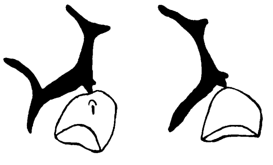


FIGS. 4, 5. Coxal apodemes: morphology of coxal apodemes III for the larva of *Teinocoptes malayi* (4), morphology of coxal apodemes III and IV for the female of *Chirnyssoides amazonae* (5).

Coxal apodemes II in the immatures and females of *Chirobia* are strongly elongated, with an anterolateral projection (Figs. 189, 193, 204). This condition is unique among all taxa examined. Coxal apodemes II in the females of *Notoedres rajamanickami* and *N. elongatus* have a distinct sclerotized flange, another unique condition of coxal apodemes II.

142. Coxal apodemes II in the immatures and female elongated, with an anterolateral projection (1), vs. shorter, without a projection (0).

143. Coxal apodemes II with a sclerotized flange (1), vs. without a flange (0).

Coxal apodemes III are simple in the outgroups and most ingroup taxa, each consisting of a long main branch (projecting anteromedial) and a small basal branch (projecting towards the body margin). In the larvae of *Cynopterocoptes* and the *Teinocoptes* group, the main branch of each coxal apodeme III has a distinct anterolateral projection (Figs. 4, 160). The distal end of the main branch of each coxal apodeme III in the immatures and females is bifurcate in nearly all *Chirnyssoides* (not in *C. noctilionis*). The basal branch is exceptionally well developed in some *Chirnyssoides,* and has a bifurcate distal end (Fig. 5). Coxal apodemes III are extremely reduced (< length trochanter III) in the nymphs and females of *Chirobia.*

144. Each coxal apodeme III in the larva with an anterolateral projection (1), vs. without a projection (0).

145. Distal end of the main branch of each coxal apodeme III in the immatures and female bifurcate (1), vs. simple (0).

146. Basal branch of each coxal apodeme III well developed and ending bifurcate (1), vs. more poorly developed and/or not bifurcate (0).

147. Coxal apodemes III in the nymphs and female extremely reduced (1), vs. well developed (0).

Coxal apodemes IV in the immatures and females of the outgroups are similar in shape to coxal apodemes III. This ancestral state is retained in most Sarcoptidae. In *Chirnyssoides amazonae, C. caparti,* and *C. parvisuctus* the distal end of each coxal apodeme IV is bifurcate (Fig. 5). Coxal apodemes IV are very poorly developed or absent in *Nycteridocoptes cynopteri* and the *Teinocoptes* group.

148. Distal end of each coxal apodeme IV in the nymphs and female bifurcate (1), vs. simple (0).

149. Coxal apodemes IV extremely reduced or absent (1), vs. well developed (0).

The apodemal structure in the males is more complex due to the presence of a few unpaired apodemes that are absent in the immatures and females as well as in the outgroups. The transverse apodeme extends along the anterior margin of coxal fields III–IV, forming an unbroken, straight apodeme between the bases of setae *c 3* (Figs. 223, 243, 259). It is found in *Chirophagoides, Chirnyssoides, Notoedres* (*s.s.*), and most *Notoedres* (*Bakeracarus*). It is absent in the other Sarcoptidae as well as in the outgroups.

150. Transverse apodeme in the male present (1), vs. absent (0).

The median apodeme extends along the body axis in the area between coxae IV (Fig. 77). A similar structure is present in some Atopomelidae but overall, it is rare in the Sarcoptoidea. A median apodeme is present in most Sarcoptinae and Teinocoptinae (not in the *Teinocoptes* group). It is very poorly developed or absent in *Trixacarus* and some *Nycteridocoptes.* The posterior end of this apodeme is distinctly bifurcate in *Kutzerocoptes, Sarcoptes,* and *Prosarcoptes.* In the latter two genera it is fused to the apodemes around the genital area.

151. Median apodeme in the male present (1), vs. absent (0).

152. Median apodeme bifurcate posteriorly (1), vs. simple or absent (0).

153. Median apodeme fused to the apodemes of the genital area (1), vs. not fused or absent (0).

In the Sarcoptinae, *Notoedres* (*Bakeracarus*), and most *Notoedres* (*s.s.*), small apodemes extend from the posterior end of the genital area to coxae IV. These genital apodemes may be derived from the posterior coxal apodemes IV. Genital apodemes are absent in the other Sarcoptidae as well as in the outgroups examined.

154. Genital apodemes in the male present (1), vs. absent (0).

Coxal apodemes I in male Sarcoptidae are nearly always fused into a sternum. In the outgroups, the Diabolicoptinae, *Cynopterocoptes,* the *Teinocoptes* group, and some *Notoedres,* this sternum is relatively short, not reaching the level of the distal tips of coxal apodemes II. In the other taxa it reaches or passes this level. Coxal apodemes II in the male reach to the midline of the body in *Nycteridocoptes, Cynopterocoptes, Chirophagoides, Chirnyssoides,* and most *Notoedres.* These apodemes are much shorter in the outgroups and remaining Sarcoptidae. However, these characters show a considerable amount of intra-specific variability and have not been used for the analysis.

Each coxal apodeme II in all males of *Nycteridocoptes* has a well sclerotized spur-like internal projection (Figs. 104, 121). This structure is unique among the in- and outgroup taxa examined. Males in the *Teinocoptes* group may have some projection in this area but it is always weakly developed.

155. Coxal apodemes II of the male with a sclerotized spur-like internal projection (1), vs. such a projection absent (0).

The structure of the posterior coxal apodemes of the male in the outgroups is variable. In *Ursicoptes, Rhyncoptes* (Rhyncoptidae), and some Makialginae and Cebalginae (Psoroptidae) coxal apodemes III are fused to apodemes IV. However, these apodemes are not fused in most Psoroptinae (Psoroptidae), Lobalgidae, and the most basal genus of Rhyncoptidae, *Caenolestocoptes.* I therefore consider the condition "all posterior coxal apodemes free" as ancestral for the Sarcoptidae. Coxal apodemes III are fused to apodemes IV in most Sarcoptinae (not in *Trixacarus diversus, T. caviae*) and Teinocoptinae (not in *Tychosarcoptes, Chirobia,* some *Teinocoptes,* and some *Notoedres* [*Bakeracarus*]). Coxal apodemes III are fused together medially in *Kutzerocoptes, Chirophagoides, Chirnyssoides,* and most *Notoedres* (not in *N.* [*B.*] *eptesicus, N.* [*B.*] *americanus*).

156. Coxal apodemes III in the male fused to coxal apodemes IV (1), vs. not fused (0).

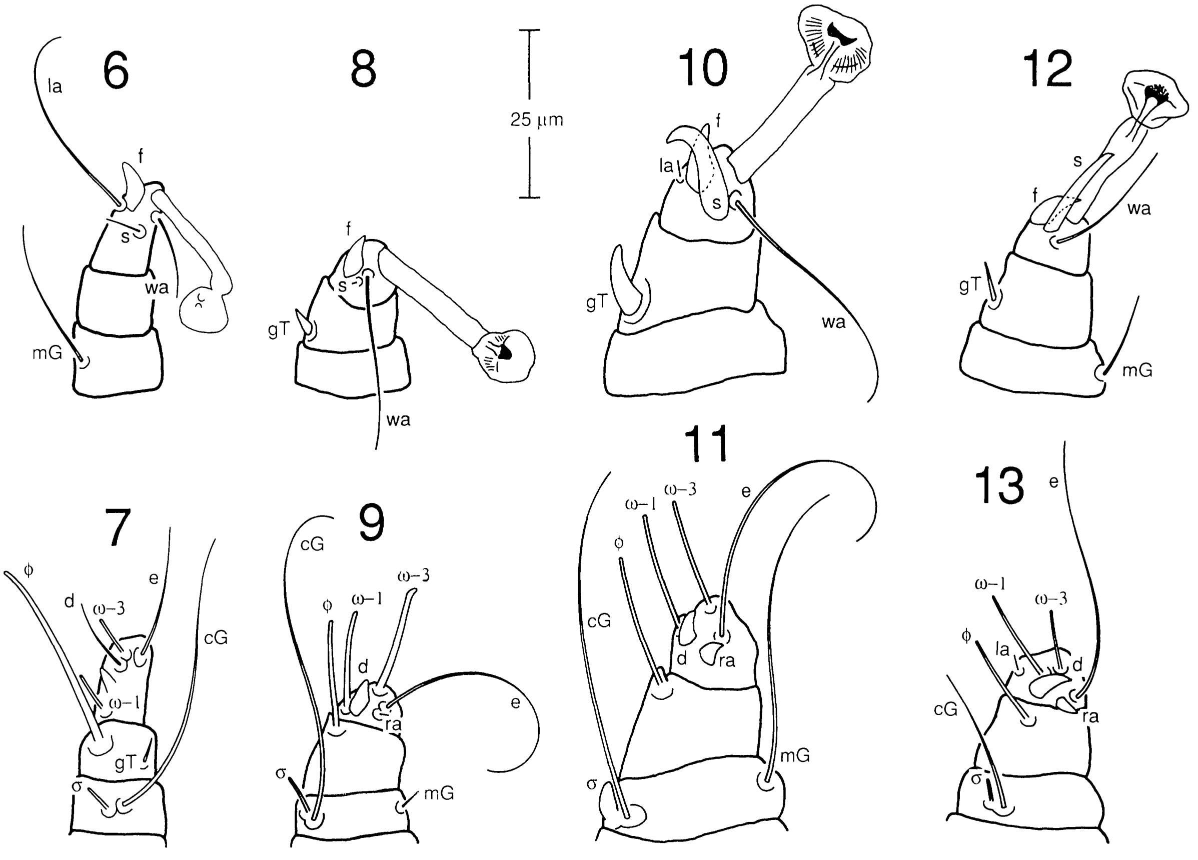
157. Coxal apodemes III fused together medially (1), vs. not fused (0).

If coxal apodemes III and IV are connected, coxal apodemes IV may be fused to the median apodeme, to the junction of the median and the transverse apodeme, or to the transverse apodeme. Earlier studies on the evolution of Sarcoptidae (Fain, 1959e, 1965b, 1968) stressed the importance of the point of fusion of coxal apodemes IV as an indicator of relationships. However, a number of problems occur in interpreting this character. The junction of the median and transverse apodemes is often characterized by a broad and irregularly shaped sclerotized zone, making judgments on the exact point of fusion of coxal apodemes IV problematic. Secondly, intra-specific variability is often substantial, including at least two of the three possible states. For these reasons the point of fusion of coxal apodemes IV has not been used in this analysis.

ANTERIOR LEGS

Although Fain (1968) discussed the variation in the number of spine-like setae on the tarsi, leg setation in the Sarcoptidae has never been discussed in detail. As with the idiosomal setae, the hypotheses of homologies for the leg setae are based on positional and, when available, ontogenetic evidence. For the positional evidence the distortions caused by the strong compression of leg segments in some taxa of the Sarcoptidae are taken into account. The leg chaetotaxy adopted in this study was developed by Grandjean (1939a).

Ancestrally the following set of setae could have been present on each anterior leg of the Sarcoptidae (Grandjean, 1939a; OConnor, 1981, 1982): tarsus *d, f, e, ba, s, la, wa,* and *ra;* tibia *gT;* genu *cG* and *mG;* femur *vF;* trochanter *pR.* Tarsal setae *aa, u, v, p,* and *q* as well as tibial seta *hT* are not present in the Sarcoptoidea (OConnor, 1982). In addition to the setae, the following solenidia could have been present (Grandjean, 1939a; OConnor 1981): tarsus I omega-1 and omega-3 (ω-1, ω-3) (solenidion ω-2 is absent in the Sarcoptoidea [OConnor, 1982]); tarsus II omega (ω); tibiae I–II phi (φ); genu I sigma-1 and sigma-2 (σ-1, σ-2); genu II sigma (σ). Solenidion σ-2 on genu I is always absent in the Sarcop-



FIGS. 6–13. Male, ventral (top) and dorsal (bottom) view of genu, tibia, and tarsus I: *Satanicoptes armatus* (6, 7), *Kutzerocoptes grunbergi* (8, 9), *Nycteridocoptes notopteris* (10, 11), *Notoedres namibiensis* (12, 13).

tidae and Rhyncoptidae. The Rhyncoptidae also lack the remaining genual solenidia.

The maximum observed complement of setae and solenidia on legs I–II in the Sarcoptidae corresponds reasonably with the above listing. It differs by having at most seven setae on each of the anterior tarsi, not eight (Figs. 6–21). The following hypothesis of homology for this missing seta is based on a comparative study among Sarcoptoidea (especially the Psoroptidae), focusing on positional comparisons.

The ancestral positions of the tarsal setae (Grandjean, 1939a; OConnor, 1981) are: *d* dorsal, either median or posterior, relatively distal; *f* and *e* dorsal to lateral, respectively anterior and posterior, distal; *ba* dorsal, close to solenidion ω-1, always distal; *s* ventral, median to posterior; *la, wa,* and *ra* ventral, proximal group, *la* anterior, *wa* anteromedian, *ra* posterior. In many Psoroptidae (e.g. *Psoroptes, Acaroptes, Psoralges*) all eight ancestral tarsal setae are present (Fain, 1963e). In these taxa, one seta is inserted very close to respectively solenidia ω-1 I and ω II. This seta is most probably seta *ba.* Since there is no seta in the corresponding position in the Sarcoptidae, seta *ba* is hypothesized to be the missing seta on all anterior tarsi.

DISCUSSION OF INDIVIDUAL CHARACTERS.—Setae *d* I–II in most outgroup taxa as well as in the immatures and females of the Diabolicoptinae are filiform. They are transformed into spines in the primary outgroup, the Rhyncoptidae, and all stages of the Sarcoptinae and Teinocoptinae. In male Diabolicoptinae, setae *d* I are filiform while setae *d* II are transformed into spines.

158. Setae d *I–II in the immatures and female spines (1), vs. filiform (0).*

Setae *f* I–II are filiform in the outgroups and in the immatures and females of the Diabolicoptinae. These setae are spines in male Diabolicoptinae, as well as in all developmental stages in the Sarcoptinae and Teinocoptinae.

159. Setae f *I–II in the immatures and female spines (1), vs. filiform (0).*

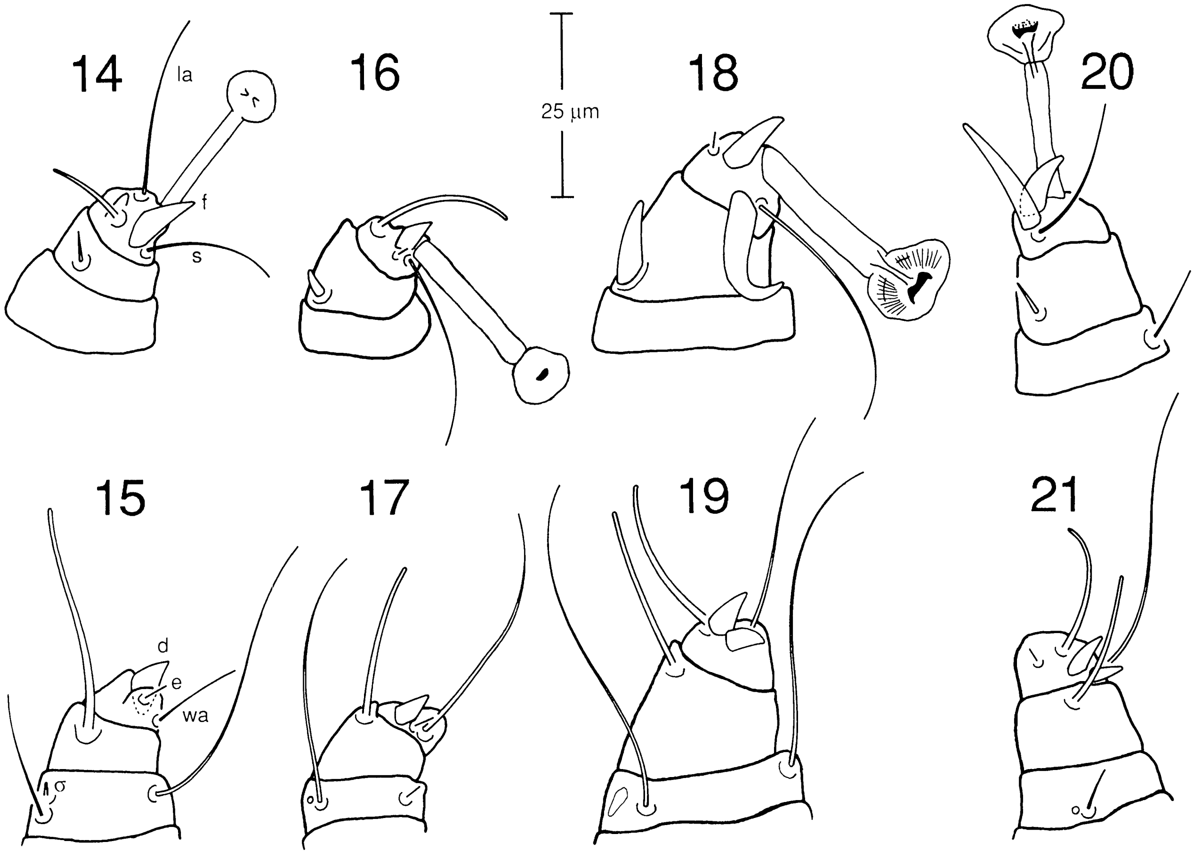
160. Setae f *I–II in the male spines (1), vs. filiform (0).*

Setae *e* and *wa* I–II are filiform in the outgroups and in all taxa of the Sarcoptidae. The only variation existing in these setae within the Sarcoptidae is in absolute and relative size, characters that are not used in this analysis.

Setae *s* I–II are filiform in the distant outgroups, the Diabolicoptinae, and the Sarcoptinae. These setae are absent in the Rhyncoptidae and are spines in the Teinocoptinae.

161. Setae s *I–II in all stages spines (1), vs. filiform (0). Absence is coded as missing data.*

Setae *ra* I–II are filiform in the outgroups, the Diabolicoptinae, and the Sarcoptinae. They are spines in most Teinocoptinae. However, setae *ra* I–II are filiform in males of



FIGS. 14–21. Male, ventral (top) and dorsal (bottom) view of genu, tibia, and tarsus II: *Satanicoptes armatus* (14, 15), *Kutzerocoptes grunbergi* (16, 17), *Nycteridocoptes notopteris* (18, 19), *Notoedres namibiensis* (20, 21).

the *Teinocoptes* group, *Notoedres* (*Bakeracarus*) *americanus*, and *Notoedres* (*N.*) *dewitti*.

162. Setae ra *I–II in the immatures and female spines (1), vs. filiform (0).*

163. Setae ra *I–II in the male spines (1), vs. filiform (0).*

Setae *la* I–II are distinct and filiform in the outgroups. They are absent in the females of *Cynopterocoptes*, the *Teinocoptes* group, *Notoedres* (*myoticola* group), and most *Nycteridocoptes* (present in the nymphs of *Nycteridocoptes*), as well as in all stages of *Kutzerocoptes* and most *Chirnyssoides*. The setae are present in all stages of *Nycteridocoptes cynopteri*.

164. Setae la *I–II in the female absent (1), vs. distinct (0).*

165. Setae la *I–II in the male absent (1), vs. present (0).*

The tibial setae *gT* I–II are ancestrally filiform and positioned anteroventral on the tibia (Grandjean, 1939a; OConnor, 1981). Within the Sarcoptidae their shape is quite variable; in the immatures and females they vary from filiform to spine-like, with all possible intermediates. In the males of *Kutzerocoptes*, *Nycteridocoptes*, *Chirnyssoides*, *Notoedres* (*myoticola* group), and *N. africanus*, these setae are transformed to large spines.

166. Setae gT *I–II in the male large spines (1), vs. filiform (0).*

The genual setae are generally well developed and filiform in the outgroups and most taxa in the Sarcoptidae but setae *cG* are minute or absent in females of some *Chirnyssoides* and *Notoedres* (*lasionycteris* group). In many *Notoedres* setae *cG* II are considerably shorter than setae *cG* I. Setae *mG* are extremely reduced in nymphal and female *Teinocoptes*. Their precise status is very difficult to determine given the difficulty in observing the anterior legs of taxa in the *Teinocoptes* group.

167. Setae cG *I–II in the female extremely reduced or absent (1), vs. present, distinct (0).*

Setae *vF* I–II are well developed in most Sarcoptidae and the outgroups. In most Sarcoptidae setae *vF* I are much smaller than setae *vF* II. In the nymphs and females of *Cynopterocoptes* and the *Teinocoptes* group setae *vF* I–II are very poorly developed. They are completely absent in *Cynopterocoptes*, *Chirobia*, and some *Tychosarcoptes* and *Teinocoptes*.

168. Setae vF *I in the nymphs and female absent (1), vs. present (0).*

169. Setae vF *II in the nymphs and female absent (1), vs. present (0).*

In the outgroups and most Sarcoptidae setae *pR* I–II are added as filiform setae in the tritonymph. Setae *pR* I–II are added in the males of the *Teinocoptes* group but are poorly developed or absent in the tritonymphs and females. They are never added in *Nycteridocoptes cynopteri*.

170. Setae pR *I in the tritonymph and female not added (1), vs. added (0).*

171. Setae pR *II in the tritonymph and female not added (1), vs. added (0).*

The tarsal and tibial solenidia of legs I–II in the Sarcoptidae vary in size (both absolute and relative to each other) but are always present and morphologically similar. More variation exists in the genual solenidia. Only the Diabolicoptinae retain solenidion σ on both legs I and II in all developmental stages (the ancestral condition). All other Sarcoptidae have lost solenidion σ on legs II in the immatures and female, and only the *Teinocoptes* group retains this solenidion in the male. Solenidion σ on legs I is lost in the immatures and females in *Cynopterocoptes*, the *Teinocoptes* group, *Chirophagoides*, *Chirnyssoides*, and *Notoedres*. Solenidion σ on legs I is lost in all developmental stages in *Chirnyssoides* and some *Notoedres*.

In the males of some *Nycteridocoptes* the morphology of solenidia σ I is modified. In these species they are thick and spine-like (Fig. 11) instead of thin and rod-like, the morphology found in all other taxa examined.

172. Solenidia σ I in the immatures and female absent (1), vs. present (0).

173. Solenidia σ I in the male absent (1), vs. present (0).

174. Solenidia σ I in the male thick, spine-like (1), vs. thin, rod-like (0). Solenidia absent coded as missing data.

175. Solenidia σ II in the immatures and female absent (1), vs. present (0).

176. Solenidia σ II in the male absent (1), vs. present (0).

The pretarsi in the Sarcoptoidea consist of well developed ambulacra, each consisting of a stalk and a disc. The ambulacra of most Sarcoptidae have well developed discs, each with a poorly to moderately well developed central sclerite and a well developed system of rays (Atyeo, 1978). The ambulacra of legs I–II are well developed in all stages of the outgroups and most Sarcoptidae. In female *Nycteridocoptes* (except for *Nycteridocoptes cynopteri*), *Cynopterocoptes*, and the *Teinocoptes* group the ambulacral discs of legs I–II are absent. In the *Teinocoptes* group these discs are also absent in the nymphs.

177. Ambulacral discs on legs I–II of the female absent (1), vs. present (0).

178. Ambulacral discs on legs I–II of the nymphs and female absent (1), vs. present (0).

Legs I–II, especially the tarsi, are adorned with cuticular spines in most taxa in the Sarcoptoidea. Apart from cuticular outgrowths on the femora such spines are largely absent in the Sarcoptidae, and only the Diabolicoptinae retain cuticular spines on the tarsi and trochanters. The Diabolicoptinae also share with the Rhyncoptidae, Makialginae, and Listropsoralginae (Psoroptidae) the presence of spines on the tibia and genu. Interpretation of this character will have to be postponed until family level relationships in the Sarcoptoidea have been clarified. The two species of *Satanicoptes* share the presence of a unique bifid process anteroventral on the trochanters. The Listropsoralginae (Psoroptidae) have a small, single process on the trochanter but structurally these processes do not appear to be homologous.

179. Cuticular spines on tarsi I–II absent (1), vs. present (0).

180. Trochanters II each with a bifid anteroventral process (1), vs. such cuticular process absent (0).

POSTERIOR LEGS

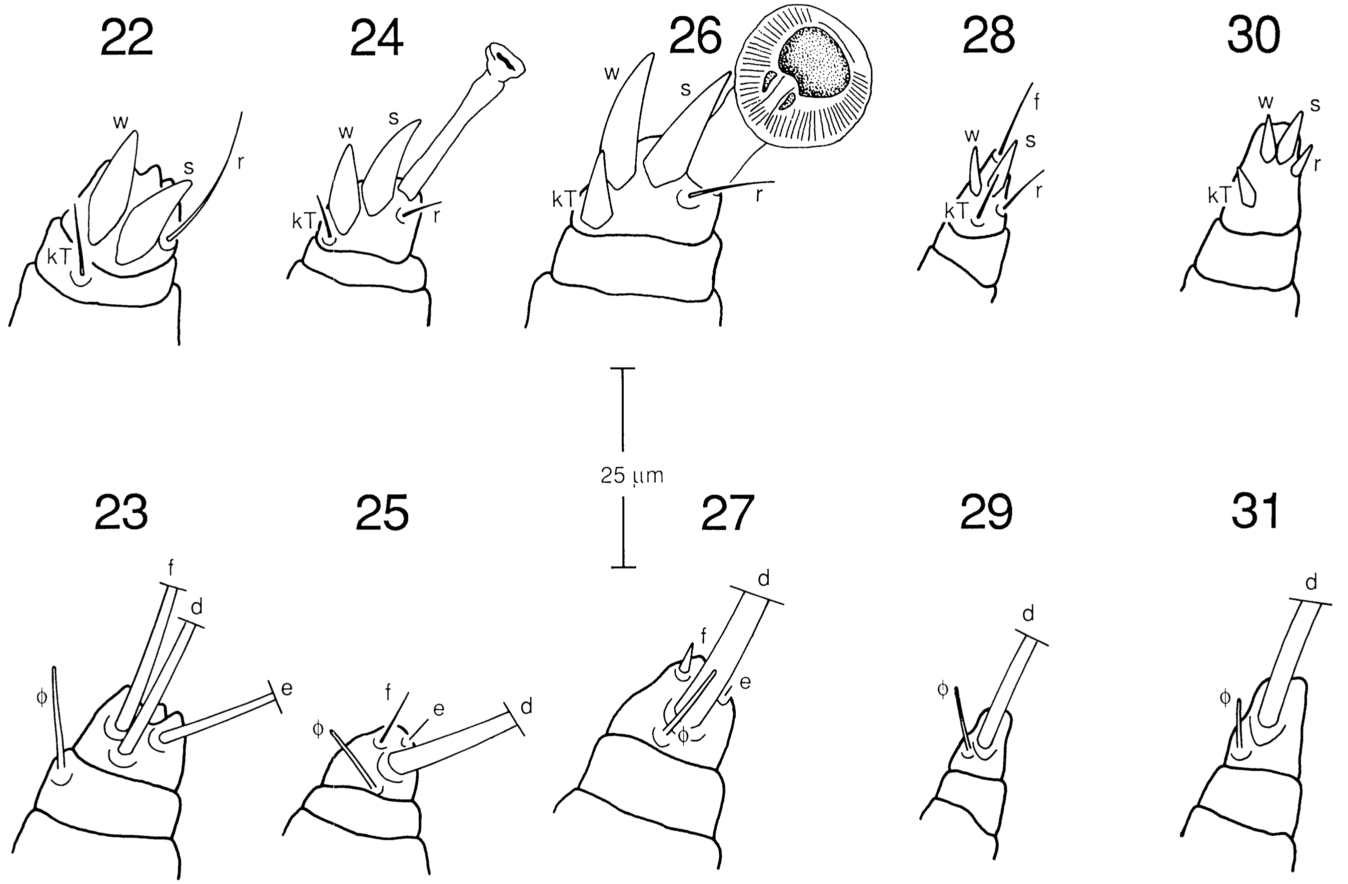
The setation of the posterior legs in the Sarcoptidae is more variable than that of the anterior legs. In addition to various changes in morphology, setae are often delayed in ontogeny or lost. As before, the setal homologies proposed in the following character discussion were established using a combination of positional and ontogenetic evidence.

The following setae are potentially present on the posterior legs of the Sarcoptoidea (OConnor, 1981, 1982): on the tarsi *d, f, e, s, w,* and *r;* on the tibiae *kT,* and on trochanters III *sR.* Tarsal setae *u, v, p,* and *q* are absent in the ancestor of the Sarcoptoidea (OConnor, 1982). Solenidia σ III are absent in all Sarcoptidae, Rhyncoptidae, and a large number of other Sarcoptoidea, but solenidion ϕ can be present on each of the tibiae. The ancestral positions of the tarsal setae are: seta *d* dorsal, median to posterior, distal; setae *f* and *e* dorsal to lateral, respectively anterior and posterior, distal; seta *s* ventral, median to posterior, median; setae *w* and *r* ventral, respectively anterior and posterior, proximal.

As in all Acari the larva has only three pairs of legs, with the fourth pair ancestrally added in the protonymph. However the setation of legs IV in the protonymph is never complete. Each leg IV may have setae *d, w,* and *r* present, but the addition of setae *f, e, s, kT,* and solenidion ϕ is delayed to the deutonymph (in the Psoroptidia to the tritonymph) in all Astigmata (OConnor, 1981). The maximum number of setae observed on each tarsus IV of the Sarcoptidae is five, the maximum number for each tarsus III is six. The missing seta on tarsus IV is assumed to be the same in all Sarcoptidae. In most Sarcoptidae the protonymph has the ancestral psoroptidid complement of three setae on each tarsus IV: seta *d* median dorsal, setae *w* and *r* ventral and proximal. Therefore it is most parsimonious to assume that the seta which is never added is either *f, e,* or *s.* Setae *d, w,* and *r* of tarsus III can be homologized by comparison with the setae on tarsi IV. In addition to these setae, tarsus III have two dorsal, distal setae (*f, e*) and one ventral, proximal seta (*s*) (Figs. 22–31). The two dorsal, distal setae may be present on tarsus IV, but the ventral, proximal seta is always absent (Figs. 32–43). Based on these observations the most parsimonious hypothesis for the identity of the missing seta of tarsus IV is that it is seta *s.*

A hypothesis of homology for the ventral proximal setae of tarsi III–IV poses a problem with respect to shape and/or position changes. In nymphal and female Sarcoptinae and Teinocoptinae, each tarsus III has three ventral, proximal setae (*w, r,* and *s*), and each tarsus IV has two (*w* and *r*). The anterior and median setae on tarsus III, and both setae on tarsus IV are spines in all of these taxa, the posterior seta on tarsus III is usually filiform. The anterior seta, based on position, is assumed to be *w.*

For the remaining setae two hypotheses can be proposed based respectively on retention of shape and retention of position. In the first hypothesis the spine-like setae on tarsus III are homologous with those on tarsus IV. In this hypothesis the median proximal seta on tarsus III is seta *r,* the posterior proximal seta is *s.* The advantage of this hypothesis is that homologous setae on both tarsi retain the same shape. However, it requires an unusual positional shift in that seta



FIGS. 22–31. Male, ventral (top) and dorsal (bottom) view of tibia and tarsus III: *Diabolicoptes sarcophilus* (22, 23), *Kutzerocoptes grunbergi* (24, 25), *Nycteridocoptes macrophallus* (26, 27), *Teinocoptes eonycteris* (28, 29), *Chirnyssoides amazonae* (30, 31).

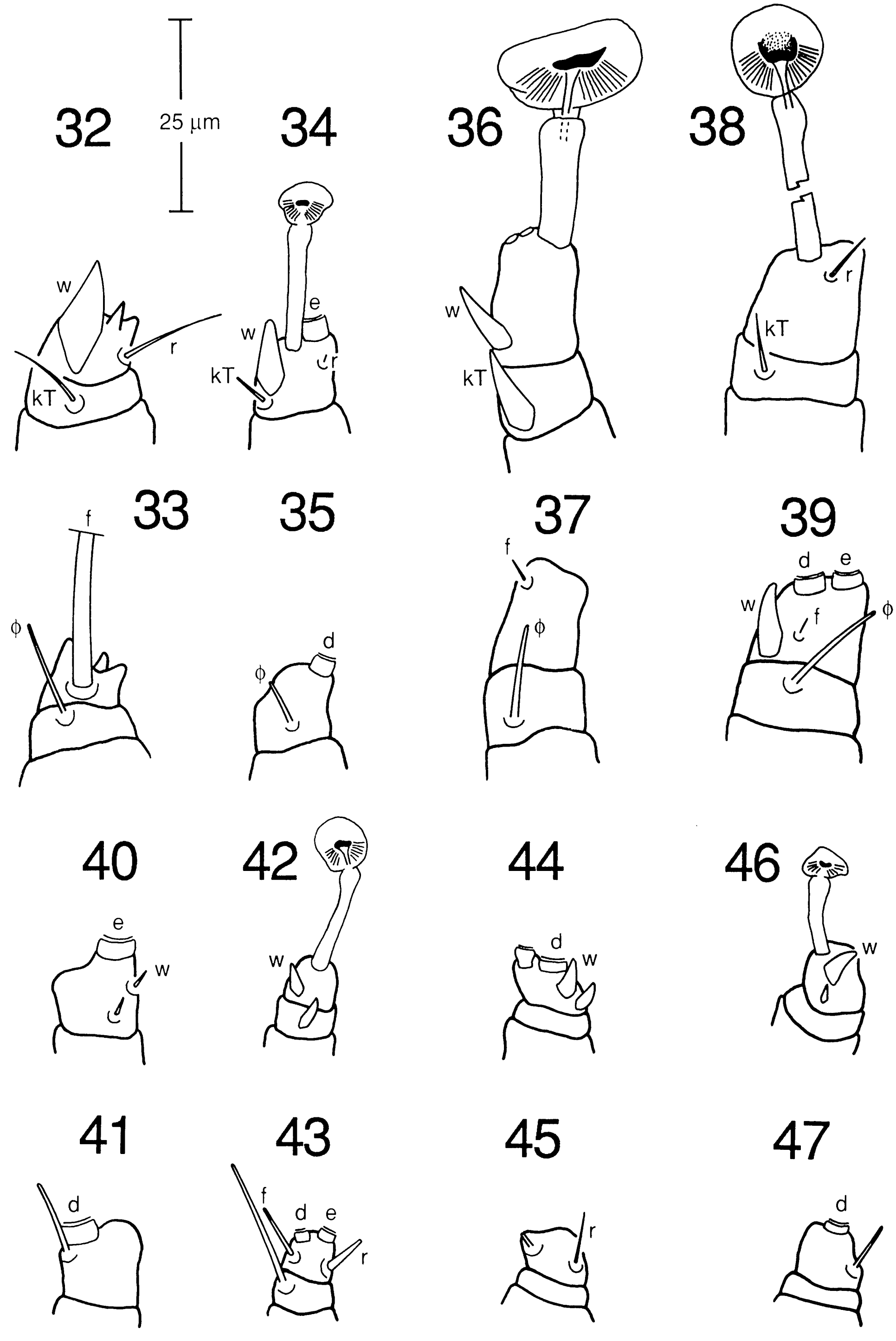
s is posterior to seta *r* on tarsus III. In the second hypothesis the posterior seta on tarsus III is homologous with the posterior seta on tarsus IV (*r*), irrespective of the shape differences. The median spine-like seta on tarsus III is therefore seta *s*. This hypothesis is supported by the observation that seta *r* IV in the males is usually filiform. Hypothesis 1 requires a shape change in seta *r* in the male between tarsi III and IV; hypothesis 2 does not. For this study hypothesis 2 is accepted; both hypotheses require shape changes of homologous setae between the tarsi, but hypothesis 2 is more consistent with positional evidence.

Another setal modification on the posterior legs concerns setae *d* and *e* IV in the male. Setae *d* and *e* are transformed to small suckers in the males of the lineage comprising the Acaroidea, Hypoderatoidea, and Psoroptidia (Grandjean, 1939a; OConnor, 1981, 1982). These small suckers are absent in the Diabolicoptinae and *Nycteridocoptes*. However, unlike the condition in the Rhyncoptidae, where the shape of these setae has changed (reversed to filiform), setae *d* and *e* in the male of the Diabolicoptinae and *Nycteridocoptes* are hypothesized to be lost. Support for the hypothesis that the remaining dorsal, distal seta on each tarsus IV of the males in *Nycteridocoptes* is seta *f*, and not seta *d* or *e*, is provided by the observation that the males of some *Nycteridocoptes* retain vestiges of the small suckers (Figs. 36, 37).

In some *Notoedres* species (Figs. 44–47), and possibly in *Chirnyssoides noctilionis*, one of the two small suckers on each tarsus IV is lost. The remaining sucker is assumed to be derived from seta *d*, since this seta is also present on tarsi III–IV of the other stages (setae *e* III–IV are absent in the immatures and females of these taxa).

DISCUSSION OF INDIVIDUAL CHARACTERS.—Setae *d* III–IV are long and filiform in the immatures and females of the outgroups and most Sarcoptidae. In the nymphs and females of a few *Chirobia* species setae *d* III are minute (< 5 µm) or absent. All leg IV setae (including setae *d*) are absent in the protonymphs, female tritonymphs, and females of the *Teinocoptes* group and *Nycteridocoptes cynopteri* (this species never adds legs IV). Setae *d*, *w*, and *r* IV are present in the male tritonymph of *Tychosarcoptes*, but absent in *Chirobia* and *Teinocoptes* (condition for *Rousettocoptes* unknown). All taxa and stages mentioned are characterized by the absence or extreme reduction of legs IV.

The outgroup condition for setae *d* III in the males is long and filiform; setae *d* IV are shaped as small suckers. In the Diabolicoptinae and *Nycteridocoptes* setae *d* IV are absent, al-



FIGS. 32–47. Male, ventral (top) and dorsal (bottom) view of tibia and tarsus IV: *Diabolicoptes sarcophilus* (32, 33), *Kutzerocoptes grunbergi* (34, 35), *Nycteridocoptes macrophallus* (36, 37), *Notoedres alexfaini* (38, 39), *Tychosarcoptes orphanus* (40, 41), *Chirophagoides mystacopis* (42, 43), *Notoedres centrifera* (44, 45), *Notoedres pahangi* (46, 47).

though vestiges of these setae are present in some *Nycteridocoptes* (Figs. 36, 37). The entire legs IV including all setae are absent in *Nycteridocoptes cynopteri.* Setae *d* IV retain the ancestral shape in all other Sarcoptidae.

181. Setae d *III in the nymphs and female strongly reduced (< 5 μm) or absent (1), vs. well developed (0).*

182. Setae d, w, *and* r *IV in the male tritonymph absent (1), vs. present (0).*

183. Setae d, w, *and* r *IV in the protonymph, female tritonymph, and female absent (1), vs. present (0).*

184. Setae d *IV in the male absent (1), vs. present (0).*

Setae *f* III–IV are filiform in all stages in the distant outgroups but are completely absent in the Rhyncoptidae. Setae *f* III–IV are also absent in all stages of *Chirnyssoides* and most *Notoedres,* as well as in the nymphs and females of *Chirobia.* In addition, setae *f* IV are absent in the males of *Trixacarus, Kutzerocoptes,* and most taxa in the *Teinocoptes* group.

In the males of *Chirophagoides* and some *Nycteridocoptes* setae *f* IV are modified into spines.

185. Setae f *III in the tritonymph and female absent (1), vs. present (0).*

186. Setae f *III in the male absent (1), vs. present (0).*

187. Setae f *IV in the male absent (1), vs. present (0).*

188. Setae f *IV in the male spines (1), vs. filiform (0). Setae absent coded as missing data.*

Setae *e* III–IV in the tritonymph and female, and setae *e* III in the male, are usually similar in shape to setae *f* III–IV in the outgroups in which they are present. Setae *e* III–IV are absent in the Rhyncoptidae. Setae *e* III–IV in the tritonymph and female, as well as setae *e* III in the male, are absent in *Prosarcoptes scanloni* (the condition for the other species of *Prosarcoptes* is unknown), most species in the *Teinocoptes* group, *Chirnyssoides,* and *Notoedres.*

Setae *e* IV in the male are ancestrally modified into small suckers. They are absent in the males of the Diabolicoptinae, *Nycteridocoptes,* and some *Notoedres.* These setae may also be absent in *Chirnyssoides noctilionis* but the available specimens did not allow a good view of tarsi IV.

189. Setae e *III–IV in the tritonymph and female absent (1), vs. present (0).*

190. Setae e *III in the male absent (1), vs. present (0).*

191. Setae e *IV in the male absent (1), vs. present (0).*

Setae *w* III–IV are filiform in the outgroups, as well as in the Diabolicoptinae. Setae *w* IV are absent in nearly all nymphs and females (see discussion of setae *d* III–IV) and in most males of the *Teinocoptes* group.

Setae *w* III–IV are transformed into well developed spines in nearly all immature and female Sarcoptinae and Teinocoptinae (setae *w* IV are absent in some immature and female Teinocoptinae). These setae are similarly transformed in the males of all Sarcoptidae, although setae *w* IV have reversed to very thin spines in *Tychosarcoptes orphanus* and are absent in some other taxa.

192. Setae w *IV in the male absent (1), vs. present (0).*

193. Setae w *III in the immatures and female spines (1), vs. filiform (0).*

194. Setae w *III in the male spines (1), vs. filiform (0).*

Setae *r* III–IV are filiform in the outgroup taxa and most Sarcoptidae. The reduction of setae *r* IV in the nymphs and females of the *Teinocoptes* group has been discussed with setae *d* III–IV. In the males setae *r* IV are absent in most *Nycteridocoptes,* the *Teinocoptes* group, *Chirnyssoides phyllostomus,* and some *Notoedres.*

Setae *r* III are transformed into spines in *Chirophagoides, Chirnyssoides,* and *Notoedres.* Setae *r* IV (when present) are spines in the immatures and females of all Sarcoptinae and Teinocoptinae and the males of *Chirophagoides* and some *Chirnyssoides* and *Notoedres.* Absence is coded as missing data for characters 197 and 198.

195. Setae r *IV in the male absent (1), vs. present (0).*

196. Setae r *III in all stages spines (1), vs. filiform (0).*

197. Setae r *IV in the immatures and female spines (1), vs. filiform (0).*

198. Setae r *IV in the male spines (1), vs. filiform (0).*

Tibial setae *kT* III–IV are spines in the Rhyncoptidae and filiform in the more distant outgroups and most Sarcoptidae. In the males setae *kT* III–IV are large spines in *Nycteridocoptes, Chirophagoides, Chirnyssoides,* and some *Notoedres.* In the other Sarcoptidae these setae are at best spine-like or very thin spines. Setae *kT* IV are absent in all stages of *Nycteridocoptes cynopteri* and the nymphs and females of the *Teinocoptes* group, once again related to the absence or poor development of legs IV.

199. Setae kT *III–IV in the male large spines (1), vs. thin spines, spine-like or filiform (0).*

Trochanteral setae *sR* III are added as filiform setae in the tritonymph of the outgroups and most Sarcoptidae. The setae are never added in *Nycteridocoptes cynopteri* or in the tritonymph and female of some *Tychosarcoptes* and *Teinocoptes,* all *Chirobia,* and some *Chirnyssoides.*

Setae *sR* III are distinct spines in both female and male *Notoedres* (*myoticola* group), and in male *Chirnyssoides* and *Notoedres africanus.*

200. Setae sR *III in the female not added (1), vs. added (0).*

201. Setae sR *III in the female spines (1), vs. filiform (0). Absence is coded as missing data.*

202. Setae sR *III in the male spines (1), vs. filiform (0).*

The outgroup condition for presence/absence of pretarsal ambulacra on the posterior legs is equivocal. Ambulacra are absent from legs III–IV in all stages of the primary outgroup, the Rhyncoptidae, but they are present in most lineages of the Psoroptidae. I consider absence the ancestral state for the immatures and females in the Sarcoptidae (not in the Sarcoptoidea). Tentatively, absence is also considered the ancestral state for the males.

Among immature and female Sarcoptidae, ambulacra are present on the posterior legs of the females of *Kutzerocoptes,* the tritonymphs and females of most *Prosarcoptes,* and the tritonymphs of *Nycteridocoptes.* Ambulacra on legs III of the male are found in *Kutzerocoptes,* most *Prosarcoptes,* and all *Nycteridocoptes.* Legs IV of the males have ambulacra in most Sarcoptinae associated with primates (not in *P. talapoini*) and, with the exception of *Cynopterocoptes* and the *Teinocoptes* group, in all Teinocoptinae. Ambulacra are absent in all other stages and species of this family.

203. Ambulacra on legs III–IV of the female tritonymph present (1), vs. absent (0).

204. Ambulacra on legs III–IV of the female present (1), vs. absent (0).

205. Ambulacra on legs III of the male present (1), vs. absent (0).

206. Ambulacra on legs IV of the male present (1), vs. absent (0).

The pretarsi of legs III–IV, if present, generally resemble those on legs I–II. However, the ambulacra on legs III–IV of many female tritonymphs and legs III of many males of *Nycteridocoptes* are quite different in structure. The ambulacral stalk is much thicker and shorter and the morphology of the ambulacral disc is quite distinct: the central sclerite is big, two small unguiform sclerites are present, and the rays are not limited to the basal section of the disc but extend over almost the entire disc (Fig. 26) (terminology following Atyeo, 1978).

207. Ambulacra on legs III–IV of the female tritonymph and legs III of the male modified, with a short stalk and unguinal sclerites (1), vs. with a long stalk and without unguinal sclerites, or ambulacra absent (0).

In the distant outgroups and the Diabolicoptinae all segments of the posterior legs are free (in the Rhyncoptidae the genu and femur of legs III–IV are always fused). In the Sarcoptinae and Teinocoptinae the tarsus and tibia of legs III–IV of the immatures and females and the tarsus and tibia of legs III of the males are fused. Tarsus and tibia of legs IV of the males are fused in the Sarcoptinae, *Cynopterocoptes,* the *Teinocoptes* group, and some *Notoedres.* The genu and femur of legs III in the nymphs and females are fused in *Chirobia.* Legs IV can be even more reduced: they consist of at the most two free segments in the nymphs and females of the *Teinocoptes* group. The complete absence of these legs is common in the protonymphs of the *Teinocoptes* group but also occurs in some tritonymphs and females. In *Chirobia* legs IV are present in some protonymphs and a few (male) tritonymphs but always absent in the female. The genu and femur of legs IV are fused in most male *Teinocoptes* and some male *Chirobia.*

Legs IV are never added in *Nycteridocoptes cynopteri.* This reduction pattern is quite different from that found in the *Teinocoptes* group and should not be homologized with the reductions observed in the *Teinocoptes* group.

208. Tarsus and tibia of legs III fused (1), vs. free (0).

209. Tarsus and tibia of legs IV of the male fused (1), vs. free (0).

210. Genu and femur of legs III of the nymphs and female fused (1), vs. free (0).

211. Genu and femur of legs IV of the male fused (1), vs. free (0).

212. Legs IV of the nymphs and females with no more than two free segments (1), vs. four or more free segments (0).

213. Legs IV of the protonymph absent (1), vs. present (0).

214. Legs IV of the tritonymph absent (1), vs. present (0).

215. Legs IV of the female absent (1), vs. present (0).

PHYLOGENETIC ANALYSIS

The phylogenetic analysis of species relationships was carried out in several steps. Given the size of the matrix and the large quantity of missing data, it became impractical to execute the entire analysis in one step. As an alternative, multiple analyses were executed using a reduced matrix. The results of each of these partial analyses were used to reexamine the assumptions of the other partial matrices. The hypotheses of relationships presented below are the result of numerous partial analyses.

The initial (partial) analysis included all 77 terminal taxa for which males are known. The rationale for this analysis was that the amount of missing data for these taxa is relatively low. With two exceptions (*Tychosarcoptes orphanus* and *Notoedres verheyeni*), every species for which the male is known has a described female and often described immatures. Low amounts of missing data are important, since this decreases the number of trees generated, allowing more accurate analyses. This partial matrix also provided a good taxonomic spread: only the monobasic genus *Rousettocoptes* was not represented. The next step involved using the results of the above analysis to construct a set of ancestral character states for each of four large monophyletic groupings: *Nycteridocoptes, Cynopterocoptes* + the *Teinocoptes* group, *Chirnyssoides,* and *Notoedres.* By substituting a single hypothetical ancestor for all individual taxa in a group, the overall data matrix for analyzing relationships among the genera was reduced to a more manageable size. Subsequent analyses of relationships within the large groupings were performed with the data matrix reduced to the hypothetical ancestor and the constituent taxa.

Fig. 48 shows the first of two most parsimonious cladograms resulting from an analysis of all species in the smaller genera and the hypothetical ancestors of the four large groupings. The second most parsimonious cladogram differs only in the arrangement of the Teinocoptinae (Fig. 49). Both have a length of 258 and a consistency index (CI) of 0.520 (tree statistics and topologies are identical using PAUP or Hennig86). The topologies depicted in these cladograms allow a number of conclusions:

1. The Sarcoptidae, excluding *Caenolestocoptes* (included in the Rhyncoptidae) but including the Teinocoptidae, form a monophyletic group.

2. The subfamilies Diabolicoptinae and Sarcoptinae (*sensu* Fain & Domrow, 1974) are monophyletic. A note of caution is warranted, since an arrangement including a sister group relationship between the Sarcoptinae associated with primates (*Kutzerocoptes, Sarcoptes,* and *Prosarcoptes*) and the Teinocoptinae requires only two more steps (an analysis including this constraint generated a single most parsimonious tree of length 260 and CI = 0.515; Fig. 50). A second alternative topology requiring a sister group relationship between *Trixacarus* (associated with rodents) and the Teinocoptinae is notably less parsimonious (one most parsimonious tree, length 263, CI = 0.509).

3. Relationships within the Sarcoptinae are completely resolved. The present analysis provides more resolution than that of OConnor (1984) but is compatible with the results of that analysis.

4. The subfamily Notoedrinae *sensu* Fain, 1968 (*Chirophagoides, Nycteridocoptes, Chirnyssoides,* and *Notoedres*) is paraphyletic with respect to the Teinocoptidae *sensu* Fain, 1959b (*Chirobia* and *Teinocoptes*). This confirms previous suggestions of the paraphyletic nature of the Sarcoptidae *sensu* Fain, 1968 (i.e. excluding the Teinocoptidae) (Klompen & OConnor, 1987; OConnor, 1982).

5. Within the Teinocoptinae (new concept) basal relationships are less clear. The cladogram presented in Fig. 48 sug-

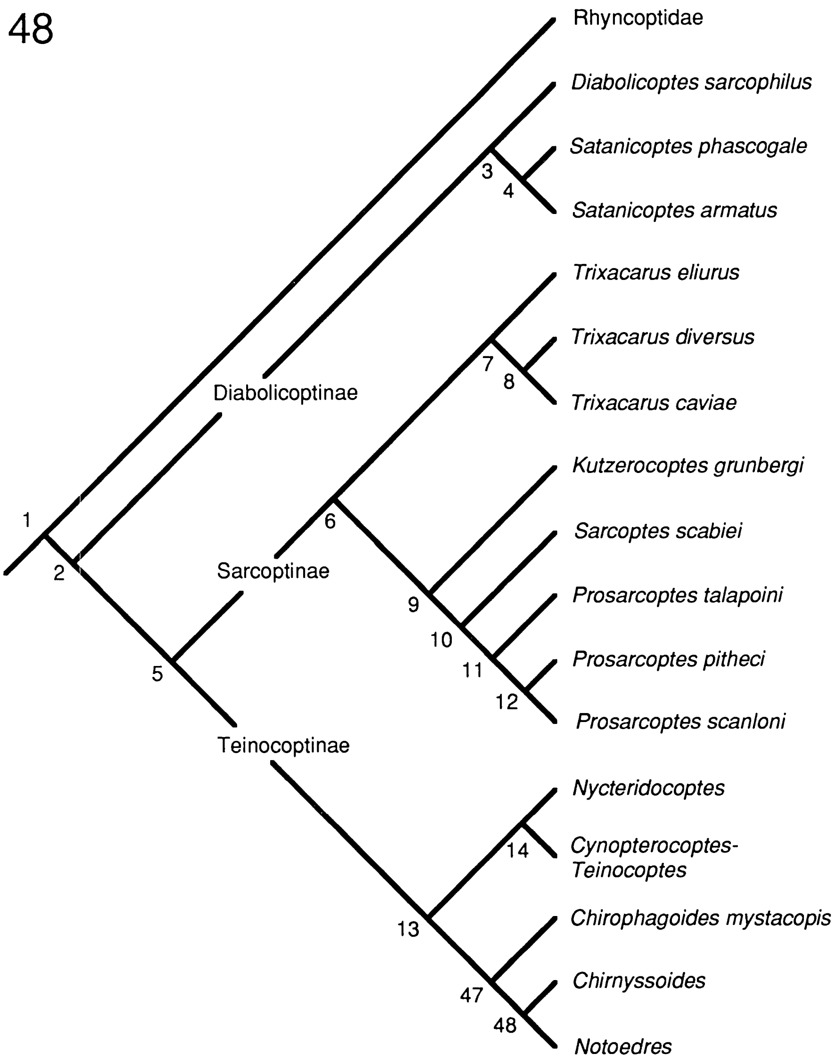


FIG. 48. Relationships among the species of the Diabolicoptinae and Sarcoptinae, and the basal groups of the Teinocoptinae: cladogram 1 of 2 (length 258, CI = 0.520). The various nodes are identified by numbers.

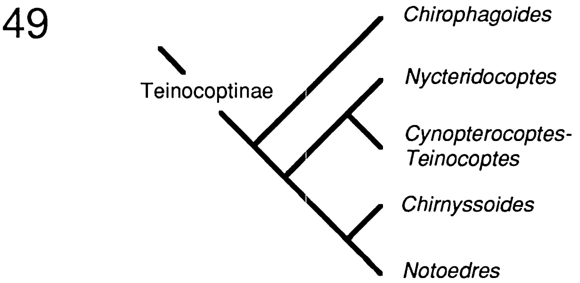


FIG. 49. Relationships among the species of the Diabolicoptinae and Sarcoptinae, and the basal groups of the Teinocoptinae: cladogram 2 of 2 (length 258, CI = 0.520), in part. Topology for the Diabolicoptinae and Sarcoptinae as in Fig. 48.

gests the *Nycteridocoptes-Teinocoptes* group as the sister group of the remaining taxa and *Chirophagoides* as the sister group to the *Chirnyssoides/Notoedres* clade, but an equally parsimonious cladogram (Fig. 49) suggests a sister group relationship between *Chirophagoides* and a *Nycteridocoptes-Notoedres* lineage. In the species discussion I have chosen to use the topology presented in Fig. 48. This topology requires only a single change in each of two characters which are unique for the Sarcoptidae: in the male the presence of a transverse apodeme (150), and in all stages the transformation of setae *r* III from filiform to spines (196). Both of these characters support the grouping of *Chirophagoides, Chirnyssoides,* and *Notoedres.* In contrast, the relevant branches of the alternative hypothesis (Fig. 49) are not supported by any unique characters.

50

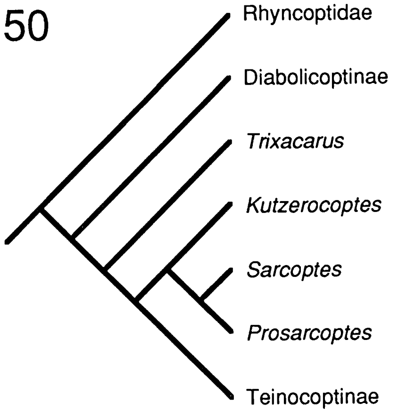


FIG. 50. Phylogenetic tree of relationships among the species of the Diabolicoptinae and Sarcoptinae, and the basal groups of the Teinocoptinae, with the constraint that the assemblage comprising the Sarcoptinae associated with primates (*Kutzerocoptes-Prosarcoptes*) plus the Teinocoptinae is monophyletic (length 260, CI = 0.515). Topology for the Diabolicoptinae and the Teinocoptinae as in Fig. 48.

The first partial analysis of the large groups involves the genus *Nycteridocoptes* and produced 10 most parsimonious trees of length 80 and CI = 0.553 (tree statistics and topologies are identical using PAUP or Hennig86). Resolution in the strict consensus tree (Fig. 51) is poor, a result due almost exclusively to one species, *N. malayi*. While all other species are known for four or more life stages, *N. malayi* is known only for the female and larva. Removing *N. malayi* from the analysis results in a single most parsimonious tree (length 78, CI = 0.556) and complete resolution (Fig. 52). This is a good example of the phenomenon of poor resolution overall due to large amounts of missing data in a few species.

"*Bakerocoptes*" *cynopteri* was not included in the analysis due to its high degree of paedomorphosis (see p. 3). The tentative *a posteriori* inclusion of *Bakerocoptes cynopteri* in *Nycteridocoptes* is based on the following evidence. Tarsi I–II have four spine-like setae, arranged in the same pattern as in all other Teinocoptinae. It is significant to note that setae *ra* I–II are spine-like in the male, not filiform as in males of the *Teinocoptes* group, the putative sister group (Fain, 1962b). Setae *r* III are filiform, not spine-like as in all stages of *Chirophagoides, Chirnyssoides,* and *Notoedres*. These characters are similar to the conditions observed in *Nycteridocoptes*. More compelling evidence of association with *Nycteridocoptes* is provided by a few characters that are not affected by paedomorphosis: 1, the cyst structure and body shape of the female (6, 7; Fig. 3) are identical to those observed in other *Nycteridocoptes;* 2, the male shows weakly sclerotized but distinct internal projections on coxal apodemes II (155). Both of these character states are unique for *Nycteridocoptes*. At present there is no evidence indicating that *Bakerocoptes* is the sister group to *Nycteridocoptes* and I propose to synonymize the two genera, transferring *B. cynopteri* to *Nycteridocoptes* as *N. cynopteri* (Fain, 1962) new combination.

The second grouping includes *Cynopterocoptes* and the *Teinocoptes* group. This is the largest grouping (34 terminal taxa) analyzed as a single unit. The consensus tree in Fig. 53 is based on 255 equally parsimonious trees with a length of 201 and CI = 0.423 (tree statistics and topologies are identical using PAUP or Hennig86). It is important to note that relationships within *Teinocoptes* are unstable. Resolution in this genus disappears almost completely in consensus trees based on the hundreds of equally parsimonious trees that are only one or two steps longer. A second note of caution in interpreting these results concerns the monobasic genus *Rousettocoptes*. This is the only genus without an associated male, and its position on the tree may very well change with the discovery and description of the male. Resolution improved slightly in an analysis including only the species in the *Cynopterocoptes-Teinocoptes* clade for which the male is known (6 most parsimonious trees, length 169, CI = 0.497; Fig. 54). Relationships hypothesized in the two analyses are compatible.

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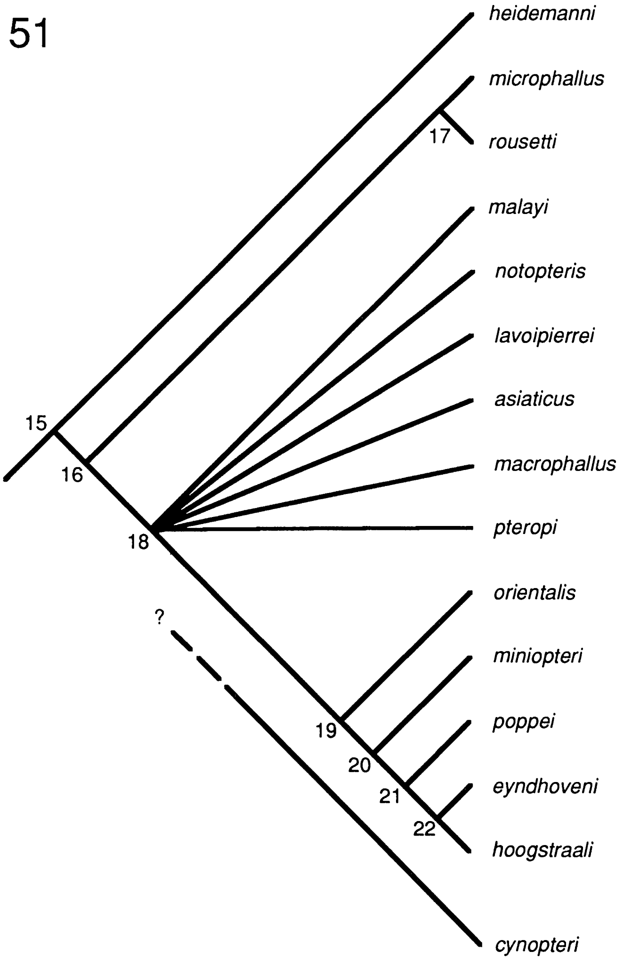

FIG. 51. Strict consensus tree of relationships in the genus *Nycteridocoptes* (10 trees, length 80, CI = 0.553). The position of *N. cynopteri* (not included in the analysis) is unclear.

The set of relationships presented in Fig. 53 requires a few changes in classification in order to reflect monophyly of the resulting groupings: *Teinocoptes amphipterinon* is transferred to *Tychosarcoptes, Teinocoptes brevior* to *Chirobia* and *Chirobia harpyionycteris* to *Teinocoptes*. A previous hypothesis as-

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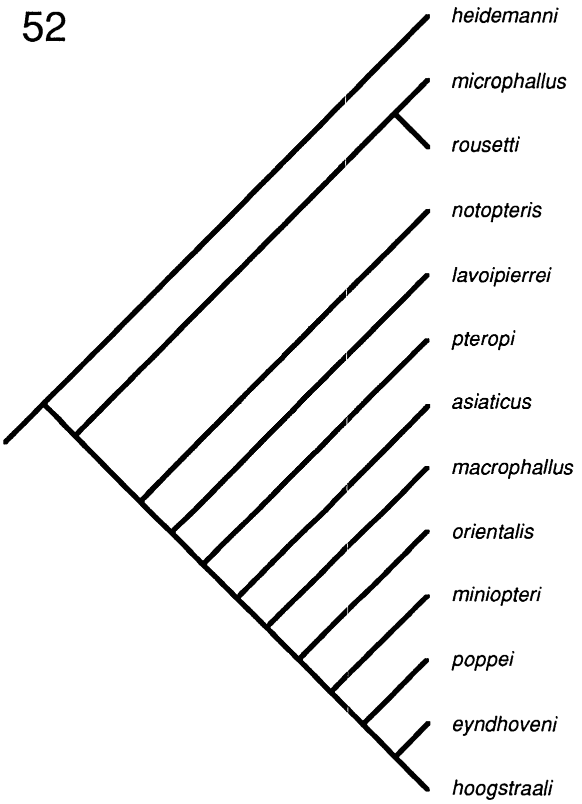

FIG. 52. Cladogram of relationships within the genus *Nycteridocoptes*, excluding *N. malayi* (length 78, CI = 0.556).

suming monophyly of *Chirobia sensu* Klompen & OConnor, 1987 (i.e. including *C. harpyionycteris*) is rejected since such a topology requires at least four more steps (> 600 trees, length 205, CI = 0.414).

Relationships in the third group, the genus *Chirnyssoides*, are well resolved. The analysis generated a single most parsimonious tree with length 43 and CI = 0.794 (tree statistics and topology are identical using PAUP or Hennig86). The topology in Fig. 55 is largely congruent with previous hypotheses on relationships within the genus (Klompen & OConnor, 1989), although the positions of *C. stenoderma* and *C. parvisuctus* are reversed.

Relationships in the fourth and last subgroup, the genus *Notoedres*, are very poorly resolved. Once again this is associated with large amounts of missing data: males are undescribed for 9 of the terminal taxa (and all but 2 of the 12 species that are not included in the analysis), and poorly described for 5 more; nymphs are unknown for 10 terminal taxa. The consensus tree presented in Fig. 56 is based on over 600 most parsimonious trees with length 114 and CI = 0.533 (tree statistics and topologies are identical using PAUP or Hennig86). Resolution in the consensus tree improves slightly by excluding a single species, *N. indicus*, from the analysis (> 600 most parsimonious trees, length 113, CI = 0.538; Fig. 57). This species has been described from three damaged females, with no data on the other life stages. In order to facilitate the discussion of lineages in *Notoedres*, I will discuss that group based on the analysis excluding *N. indicus*. An analysis including only those species for which the males have been described resulted in a single most parsimonious tree (length 106, CI = 0.561; Fig. 58), presumably related to the smaller amount of missing data.

Although the overall resolution in *Notoedres* is poor, a few conclusions can be drawn. Continued recognition of the genera *Chirnyssus* (*myoticola* and *africanus*) and *Suncicoptes* (*indicus*) leaves *Notoedres* as a paraphyletic group and those two genera are therefore synonymized with *Notoedres*. Within *Notoedres* a dichotomy can be recognized between the *paraguayensis-americanus* lineage and the *philippinensis-pahangi* lineage (Figs. 56, 57). The former lineage corresponds largely to the subgenus *Bakeracarus* (*sensu* Fain, 1965b), with the exclusion of *N. schoutedeni* and the inclusion of *N. plecoti*. This lineage is retained as the subgenus *Bakeracarus* (new concept). The *philippinensis-pahangi* lineage is retained as the nominate subgenus, *Notoedres* (new concept). Once again, this arrangement is not very stable. A topology including the constraint that *Bakeracarus* (new concept) is not monophyletic requires only 1 more step (> 300 trees, length 115, CI = 0.533; analysis included *N. indicus*).

The results of all partial analyses can be summarized into a tree topology for all taxa of the Sarcoptidae included in the matrix. Such a procedure results in trees with a minimum length of 691 and a predictably poor consensus index (CI = 0.32).

DISCUSSION OF LINEAGES AND CLASSIFICATION

The goal of this section is to interpret the results of the phylogenetic analysis by discussing the various groupings within the Sarcoptidae in terms of their derived character states. Only the most parsimonious hypotheses of relationships (as presented in the previous section) are discussed. The proposed classification for the Sarcoptidae corresponds first of all to the results of the phylogenetic analysis. Where modifications of existing concepts are necessary to satisfy the above condition, a minimum number of changes have been made. A secondary consideration is that a classification should avoid redundancy in nomenclature. The latter consideration became applicable in *Trixacarus* and the Sarcoptinae associated with primates.

Included in this section is a species revision with descriptions of some new taxa and several previously undescribed stages, and a summary of published and new data on ecology and pathology, as well as on host associations and geographic distribution. In order to facilitate cross referencing between this and previous sections, the numbers of the characters are cited in parentheses where appropriate. As stated in the "Material and Methods" section, the diagnoses for each of the species and lineages include only character states that are derived at the level discussed. Additional characters which are typical for the lineage or species but which have not been discussed in the character analysis are listed separately.

A sister group relationship of the families Rhyncoptidae and Sarcoptidae cannot be rejected based on the present analysis. The presence of layering in setae *c 1* and *c 2* (77, 82), the spine-like shape of setae *c 2* (79, 80), and the trans-

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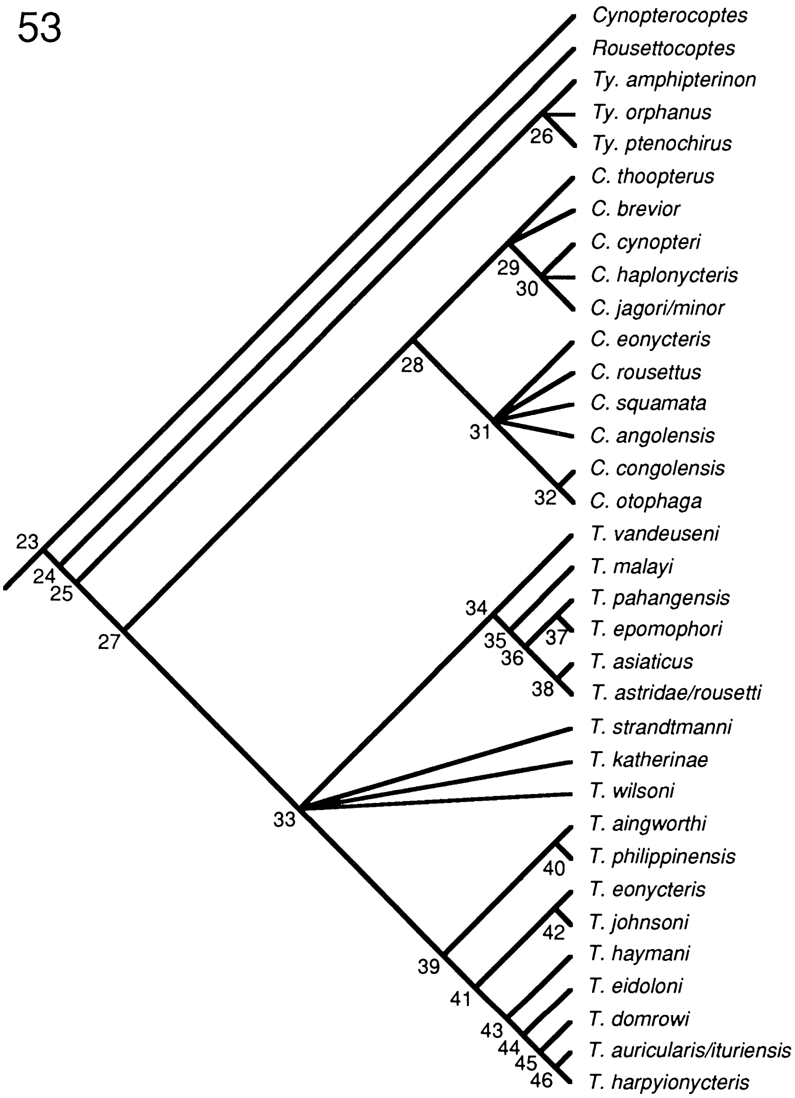

FIG. 53. Strict consensus tree of relationships in the assemblage comprising *Cynopterocoptes* and the *Teinocoptes* group (255 trees, length 201, CI = 0.423). Abbreviations for the genera: *Ty.* = *Tychosarcoptes*, *C.* = *Chirobia*, *T.* = *Teinocoptes*.

formation of setae *d* I–II from filiform to spines (158), are characters providing support for this relationship.

A number of characters support a hypothesis of monophyly for the family Sarcoptidae (new concept) (node 2, Fig. 48).

Sarcoptidae Murray, 1877

Sarcoptidae, Murray, 1877: 291.
Teinocoptidae Fain, 1959b: 119.
Bakerocoptidae Fain, 1962b, Lavoipierre et al., 1967: 1.

Diagnosed in all stages by the loss of setae *h 3* (113–115) and *ps 3* (121); in the female by a transverse oviporus (133); in the male by the loss of the adanal discs (136) and the transformation of leg setae *f* I–II and *w* III from filiform to spine-like (160, 194). In addition, the epigynium, a sclerite anterior to the oviporus, is present in most female Sarcoptoidea but absent in the Sarcoptidae. Characters 113–115 are reversed within the family (see *Nycteridocoptes, Cynopterocoptes*).

Within the Sarcoptidae, the first dichotomy is between a lineage corresponding to the subfamily Diabolicoptinae Fain & Domrow, 1974, and the remaining taxa (Fig. 48).

Diabolicoptinae Fain & Domrow, 1974

Diabolicoptinae Fain & Domrow, 1974: 124.

Diagnosed in all stages by the absence of sclerotized shields (8, 9, 13), the loss of opisthosomal setae *sci* and *d 1* (60, 94), the transformation from filiform to spine-like of setae *c 3* and *3 b* (92, 93, 122), and the unequal size and shape of legs I and II; in the immatures and females by the trans-

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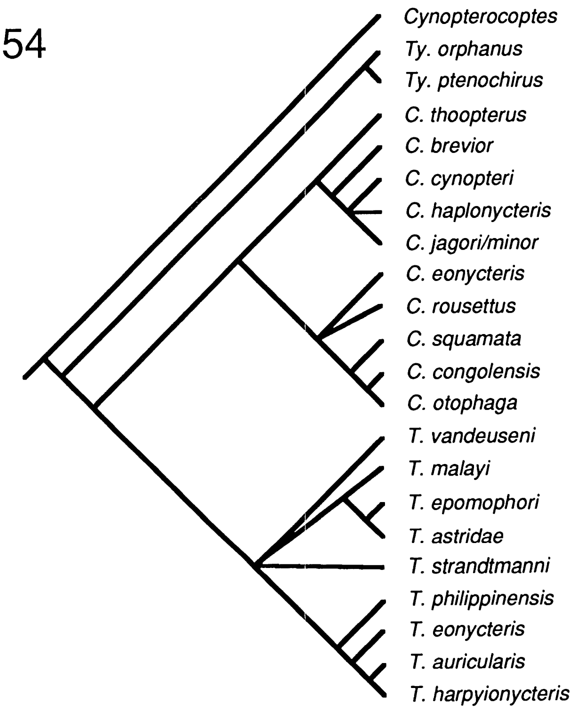

FIG. 54. Strict consensus tree of relationships in the assemblage comprising *Cynopterocoptes* and the *Teinocoptes* group, including only those species for which the male has been described (6 trees, length 169, CI = 0.497). Abbreviations for the genera as in Fig. 53.

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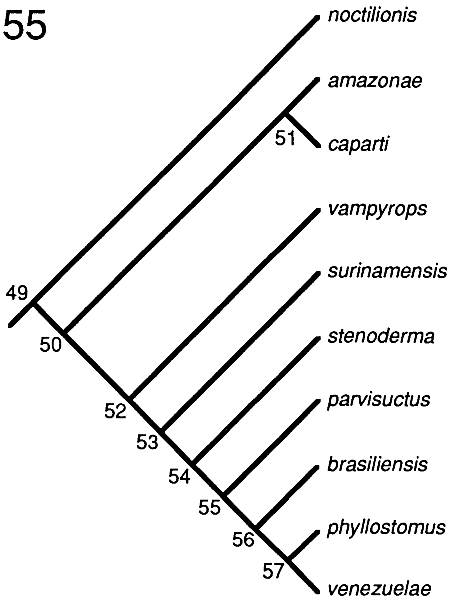

FIG. 55. Cladogram of relationships in the genus *Chirnyssoides* (length 43, CI = 0.794).

formation of setae *d* I–II to filiform (reversal) (158); in the nymphs and female by the transformation of setae *c 1* and *c 2* from filiform or spine-like to short, broad spines (75, 81), and setae *g* and *4 a* to spines (125, 131); in the male by the loss of leg setae *d* and *e* IV (184, 191).

All taxa in this subfamily are associated with Australian marsupials. Within the Diabolicoptinae (node 3), the two named genera, *Diabolicoptes* and *Satanicoptes,* appear to be monophyletic.

Diabolicoptes Fain & Domrow, 1974

Diabolicoptes Fain & Domrow, 1974: 124.

Diagnosed by the addition pattern of the *h* setae (setae *h 1* and *h 2* absent in the larva but added, together with setae *f 2, ps 1,* and *ps 2,* in the protonymph) (104, 106); in the female by parallel, not fused, coxal apodemes I (139); in the male by the transformation of setae *h 2* and *ps 2* to long spines (110, 112). In addition setae *3 a* are added in the tritonymph, retained in the female, but lost in the male.

The opisthosomal setae are spine-like in the adults but filiform in the immatures. The genus includes a single species, *Diabolicoptes sarcophilus* Fain & Domrow, 1974.

Diabolicoptes sarcophilus Fain & Domrow, 1974
(Figs. 22, 23, 32, 33)

Diabolicoptes sarcophilus Fain & Domrow, 1974: 124.

Diagnosed by the characters of the genus. *Diabolicoptes sarcophilus* has been described for all life stages (Fain & Domrow, 1974).

Material examined: Larva, tritonymph, female, and male.

Host (Marsupialia: Dasyuridae) and locality: *Sarcophilus harrisii* (Boitard, 1841). AUSTRALIA: TASMANIA, Launceston, 17 November 1972 (holotype, allotype, paratypes, specimens in collection ANIC).

Literature records: on *Sarcophilus harrisii* from AUSTRALIA (Fain & Domrow, 1974 [Type series]).

Satanicoptes Fain & Laurence, 1975

Satanicoptes Fain & Laurence, 1975: 415.

Diagnosed in all stages by the absence of setae *f 2* (99–103), and the presence of a bifurcate hook or spine on trochanter II (180).

The opisthosomal setae are filiform/setiform in all stages, never spine-like. Setae *h 1* and *h 2* are present in the larva.

Type species *Satanicoptes armatus* Fain & Laurence, 1975.

Satanicoptes armatus Fain & Laurence, 1975
(Figs. 6, 7, 14, 15)

Satanicoptes armatus Fain & Laurence, 1975: 415.

Diagnosed in all stages by never adding setae *ps 1* and *ps 2* (116–120), and the transformation of setae *c 1* and *c 2* from layered to simple (reversal) (77, 82).

The body shape is more elongate than in the other Diabolicoptinae. All stages have been described previously (Fain & Laurence, 1975).

Material examined: Female and male.

Host (Marsupialia: Dasyuridae) and locality: *Sarcophilus harrisii* (Boitard, 1841). GREAT BRITAIN: London, Lon-

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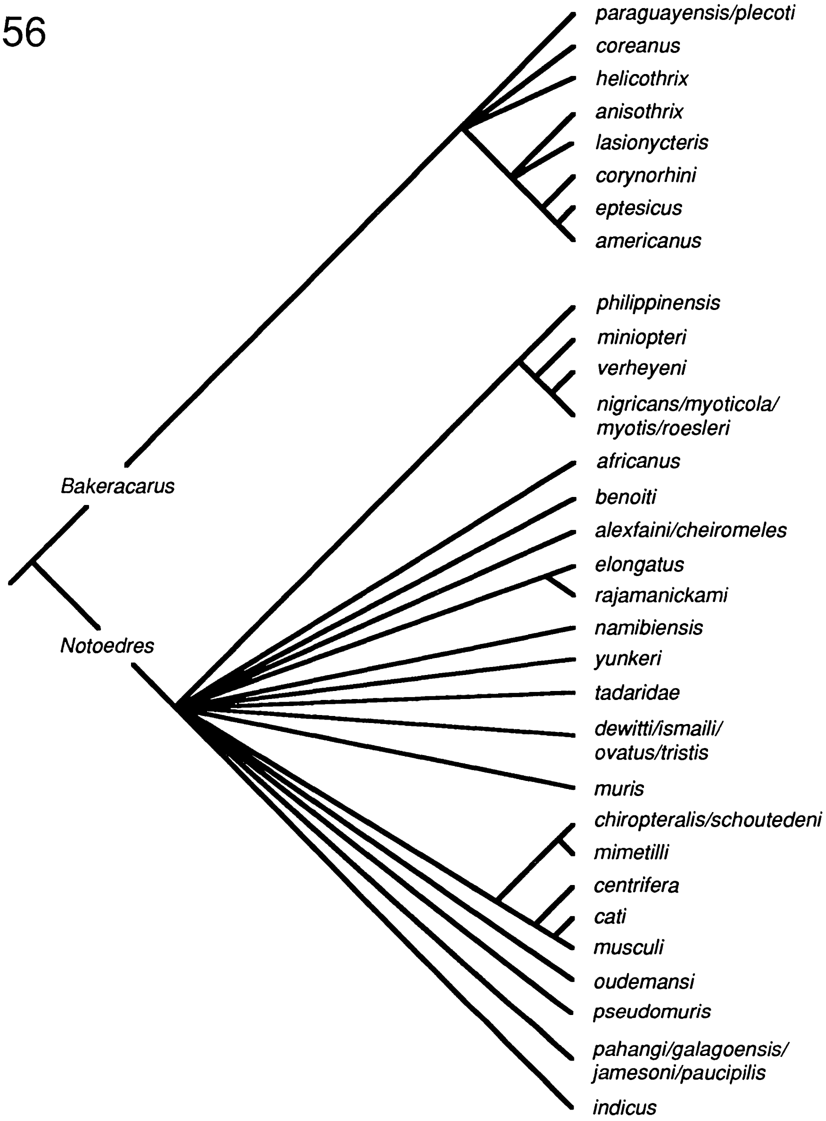

FIG. 56. Strict consensus tree of relationships in the genus *Notoedres* (> 600 trees, length 114, CI = 0.533).

don Zoo, 15 May 1968 (paratypes, specimens in collection OSU).

Literature records: on *Sarcophilus harrisii* from GREAT BRITAIN (captivity) (Fain & Laurence, 1975 [Type series]).

Satanicoptes phascogale (Fain & Domrow, 1974)

Diabolicoptes phascogale Fain & Domrow, 1974: 129.

Satanicoptes phascogale (Fain & Domrow), Fain & Laurence, 1975: 415.

This species differs from *S. armatus* by the presence of setae *ps 1* and *ps 2* in the female (the immatures and male are undescribed), by the layered structure of setae *c 1* and *c 2,* and by a more rounded body shape.

Material examined: Female.

Host (Marsupialia: Dasyuridae) and locality: *Phascogale tapoatafa* (Meyer, 1793). AUSTRALIA: VICTORIA, Christmas Hills, August 1973 (holotype, specimen in collection ANIC).

Literature records: on *Phascogale tapoatafa* from AUSTRALIA (Fain & Domrow, 1974 [Type series]).

The sister group of the Diabolicoptinae is the assemblage of the Sarcoptinae and Teinocoptinae (node 5, Fig. 48). Diagnosed in all stages by the loss of the vestiges of the genital papillae (135), the absence of solenidia σ II (175, 176), the loss of cuticular spines on the tarsi (179), and the fusion of tibia and tarsus III (208); in the immatures and female by the transformation of leg setae *f* I–II, *w* III–IV, and *r* IV from filiform to spines (159, 193, 197), and the fusion of the tibia and tarsus of legs IV; in the female tritonymph by the presence of spines or scales (29); in the female by the presence of dorsal spines in the area between setae *sci* and the

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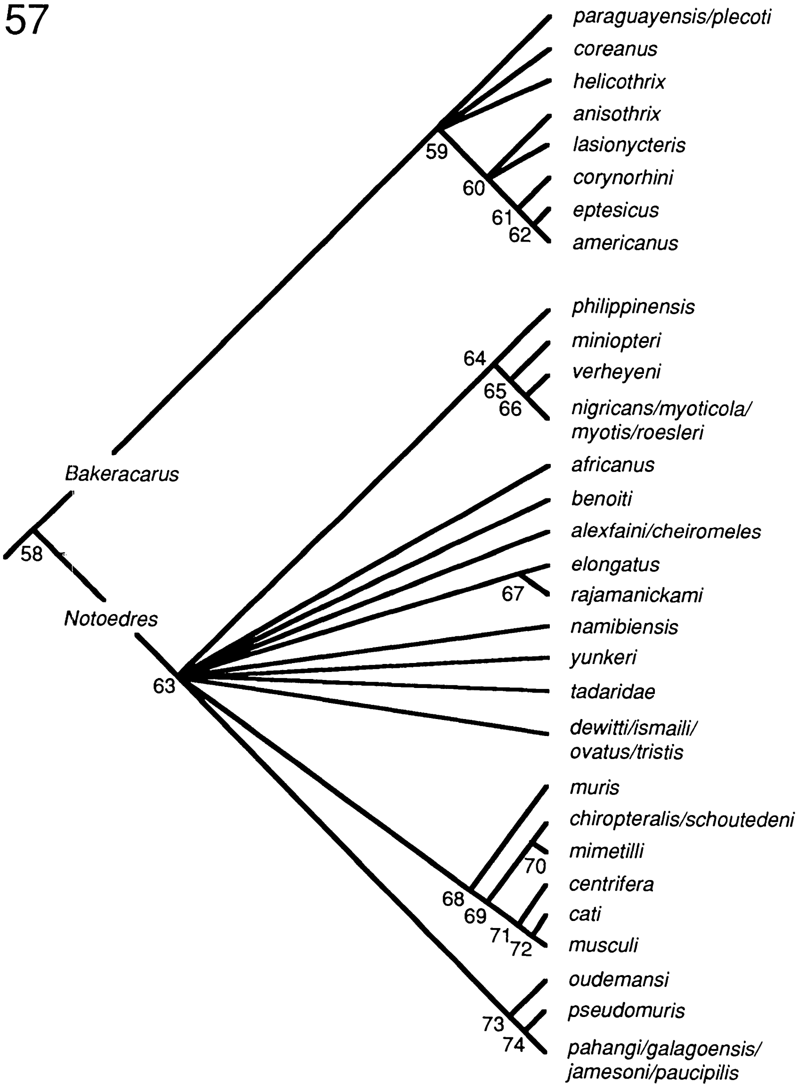

FIG. 57. Strict consensus tree of relationships in the genus *Notoedres*, excluding *Notoedres indicus* (> 600 trees, length 113, CI = 0.538).

anus (32, 35, 36, 37, 38), and the transformation of setae *sci* into spines (63); in the male by the presence of posterior lateral shields (17) and a median apodeme (151), the fusion of coxal apodemes III and IV (156), and the presence of ambulacra on legs IV (206).

All taxa in this group are associated with placental mammals, with some secondary colonization of marsupials. Within this lineage, the first dichotomy is between a lineage corresponding to the subfamily Sarcoptinae Murray, 1877 (*sensu* Fain, 1968), and a large lineage including the Teinocoptidae (*sensu* Fain, 1959b), Bakerocoptidae (*sensu* Lavoipierre et al., 1967), *Tychosarcoptes,* and the Notoedrinae (*sensu* Fain, 1968). The oldest available name, Teinocoptinae, is used for the latter assemblage.

Sarcoptinae Murray, 1877

Sarcoptinae Murray, 1877: 291.

Diagnosed in all stages by the presence of large spines on the dorsum (19, 25, 46), and the layered structure of setae *sci* (68); in the nymphs by the presence of spines extending to at least a U-shaped band across the dorsum (27); in the male by the presence of genital apodemes (154), and the fusion of the tibia and tarsus of legs IV (209).

The first dichotomy in the Sarcoptinae is between the genus *Trixacarus* and the remaining taxa (node 9).

Trixacarus Sellnick, 1944

Trixacarus Sellnick, 1944: 248.

Trixacarus (*Caviacoptes*) Fain et al., 1972: 74, new synonymy.

Diagnosed in the adults by long and filiform dorsal setae (61, 63, 74, 79, 80); in the male by the loss of the posterior lateral shields (reversal) (17), the loss of setae *f* IV (187), and the loss of the ambulacrum of legs IV (reversal) (206).

The filiform shape of the body setae may represent a

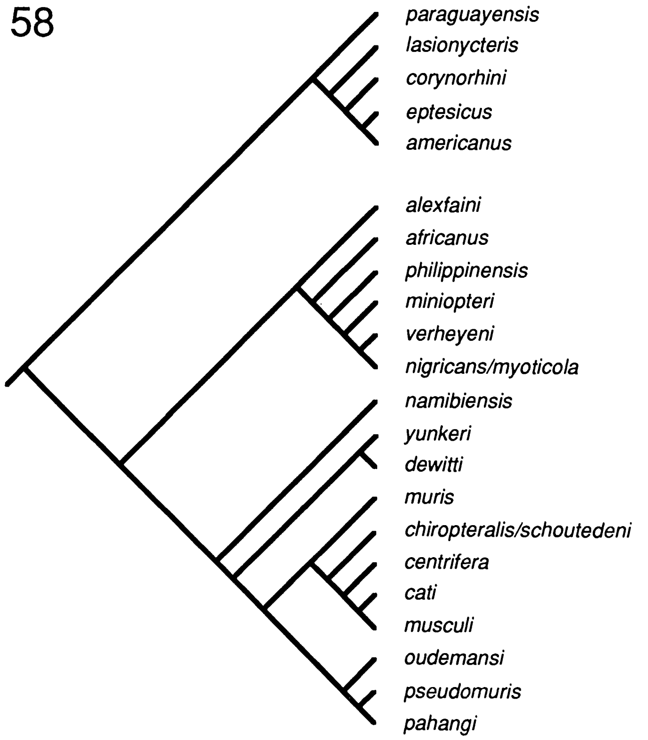

FIG. 58. Cladogram of relationships in the genus *Notoedres*, including only those species for which the male has been described (length 106, CI = 0.561).

terminal ontogenetic addition. In the immatures most of these setae are spine-like rods with a bifurcate tip (Figs. 63–65), the shape found in all stages of the other Sarcoptinae. All three species of *Trixacarus* are associated with rodents.

Type species *Trixacarus diversus* Sellnick, 1944.

The sister group relationship between *Trixacarus diversus* and *T. caviae* (node 8) is well supported. The lineage including these two species is diagnosed in all stages by the loss of the layered structure of setae *sci, c 1*, and *c 2* (reversal) (68, 77, 82), and the loss of setae *e 2* (98) and *f 2* (99–103); in the male by the absence of fusion between coxal apodemes III and IV (reversal) (156). In view of this relationship within the genus, I propose to synonymize the subgenus *Caviacoptes* Fain et al., 1972, erected for *T. caviae*, with *Trixacarus* (*s.s.*). The alternative, proposing a new subgenus for *T. eliurus*, would create three monobasic subgenera. Such redundancy in classification does not add to our understanding of the evolution of the group and should be avoided.

Trixacarus ***eliurus*** nov. spec.
(Figs. 59–62)

Diagnosed in the female by the reduction of the area covered by spines (reversal) (35, 36, 38); in the male by the loss of the median apodeme (reversal) (151).

This species retains the layered structure of setae *sci, c 1*, and *c 2* and adds setae *e 2* and *f 2*.

Larva: Unknown.

Protonymph: Dorsal spines extending from halfway between setae *sci* and *c 1* to the level of setae *e 1*. Setae *ps 2* long and filiform, setae *f 2* and *h 2* very small, all other opisthosomal setae spine-like rods with bifurcate tips. Setae *g* present. Legs I–III well developed, legs IV each with only three setae on the tibiotarsus.

Tritonymph: Resembling the protonymph in spine pattern and opisthosomal setae but setae *h 2* long and filiform. Setae *3 a, 4 a, pR* I–II, and *sR* III, and solenidia ω-3 added. Setation of each leg IV complete (6 setae; 1 solenidion). Sexual dimorphism at this stage not observed.

Female (Figs. 59, 60): Spine covered area smaller than in the nymphs, extending from setae *c 1* to setae *d 2* (Fig. 59). Setae *d 1, d 2, e 1*, and *e 2* transformed from spine-like to long and filiform. Oviporus between the posterior borders of coxal fields II. Opisthosomal gland opening (gla) between setae *e 2* and *f 2*, poorly defined (this structure is unclear in the immatures). Measurements in Table 1.

Male (Figs. 61, 62): Resembling the female in spine pattern, setal structure, and position of the gland opening. Posterior median and anal shields fused, weakly sclerotized. Genital area between trochanters IV. Measurements in Table 1.

Most specimens were found in lesions inhabited (and presumably made) by large chiggers (Trombiculidae). Associated pathology was not observed.

Material examined: Nymphs, female, and male.

Host (Rodentia: Muridae) and locality: *Eliurus myoxinus webbi* Milne-Edwards, 1885. MADAGASCAR: FIANARANTSOA, 9 km ESE Kianjavato, Vatovavy, ca 21°24′S 47°57′E, elev. 400 m, 4 August 1988, G.K. Creighton (GKC 2768), NMNH #449368, BMOC 88–1550–065 (holotype female, allotype male).

Etymology: The specific name is derived from the generic name of the type host, *Eliurus myoxinus webbi*.

Deposition of specimens: Holotype female and allotype male in collection NMNH. Paratypes in NMNH, IRSN, and UMMZ.

Trixacarus diversus Sellnick, 1944
(Figs. 63–85)

Trixacarus diversus Sellnick, 1944: 249.
Sarcoptes anacanthos Guilhon, 1946a: 108.

Trixacarus diversus was described almost simultaneously by Sellnick (1944) as *Trixacarus diversus* and Guilhon (1946a, 1946b) as *Sarcoptes anacanthos*. These names were synonymized by Lavoipierre (1960) and the adults have been redescribed by Fain (1968).

Trixacarus diversus differs from *T. caviae* in the male by the retention of a complete opisthosomal (median + anal) shield, and in the female by the absence of spines lateral to the anus. The female may have a weakly sclerotized opisthosomal shield (Fain, 1968), which would be unique in the Sarcoptidae/Rhyncoptidae clade. Some indication of the presence of such a shield was observed in the specimens from *Rattus* but it was not observed in the (not optimally cleared) specimens from *Calomys*. All figures presented are based on material collected from *Calomys*.

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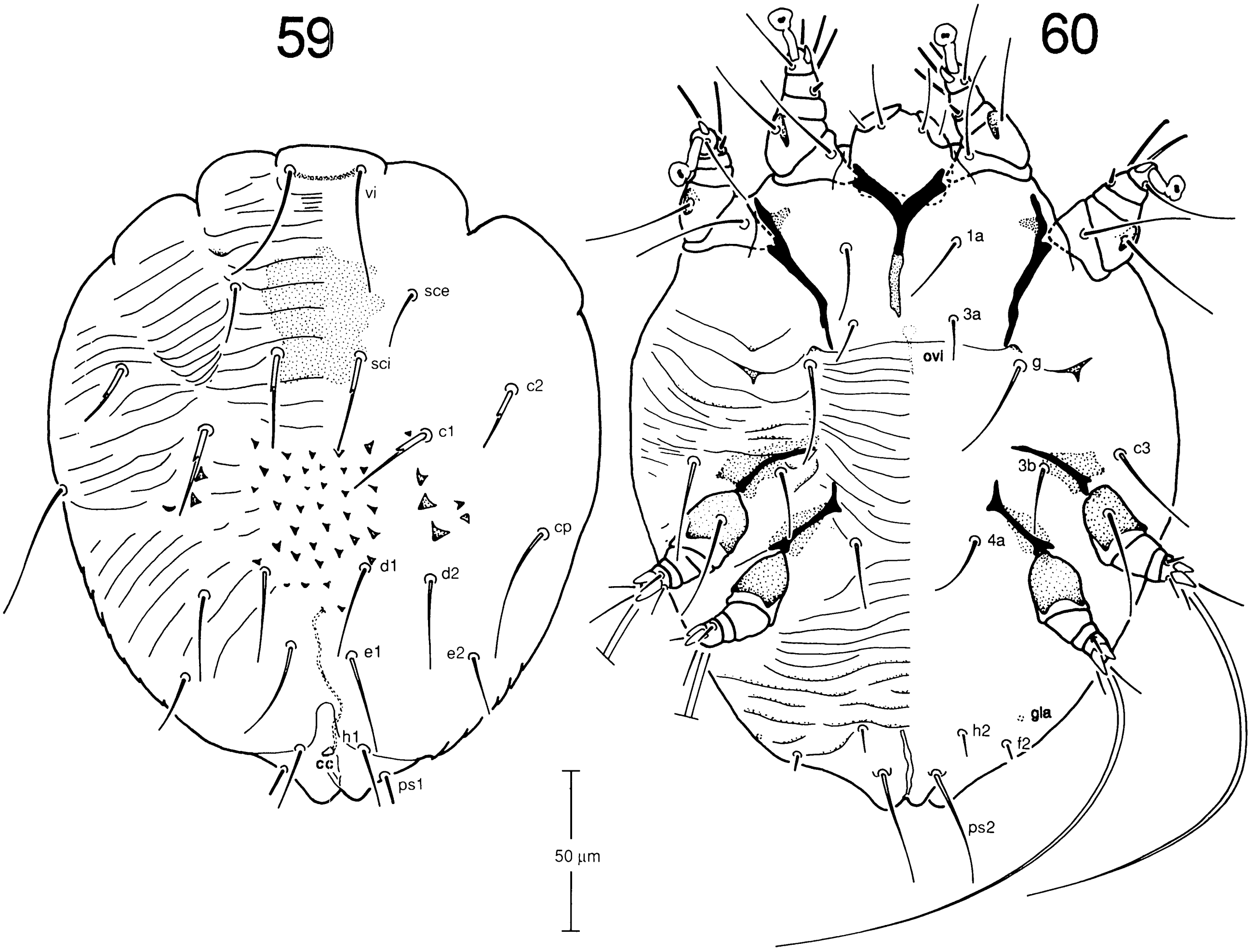


FIGS. 59, 60. *Trixacarus eliurus,* female, dorsal (59) and ventral (60) view. cc = copulatory cone, gla = opisthosomal gland, ovi = oviporus.

A few additions to previous descriptions can be made, mostly related to ontogeny. In the larva and nymphs (Figs. 63–65), dorsal spines cover the area between setae *sci* and *h 2*. In the larva (Fig. 63), opisthosomal setae *d 2, e 1, h 1,* and *h 2* are spine-like rods with a bifurcate tip, while setae *d 1* are long and filiform. In the protonymph (Fig. 64) the newly added *ps* setae are spine-like, while setae *h 1* and *h 2* are transformed to filiform. Setae *e 1* transform to filiform in the tritonymph (Fig. 65), and setae *d 2* and *ps 2* become filiform in the adults (Figs. 66, 76). Spine pattern in the adults (Figs. 66, 76) reduced, extending posteriorly no further than setae *d 2* and *e 1.* Position of the opisthosomal gland opening similar to that in *T. eliurus.* Measurements of females and the single male are summarized in Table 1.

Previously known only from Europe on *Rattus norvegicus* (type host) and *R. rattus,* specimens indistinguishable from *T. diversus* in both shape and measurements have been found during this study on an endemic South American rodent, *Calomys musculinus.* The mites caused severe hair loss and skin crusting all over the body, especially on the head and the tail area. In areas of the hosts body with relatively low numbers of mites, females were found at the bottom of small, trunk-like outgrowths projecting from the skin (1–3 mm). These projections appeared to become confluent in areas with high mite densities.

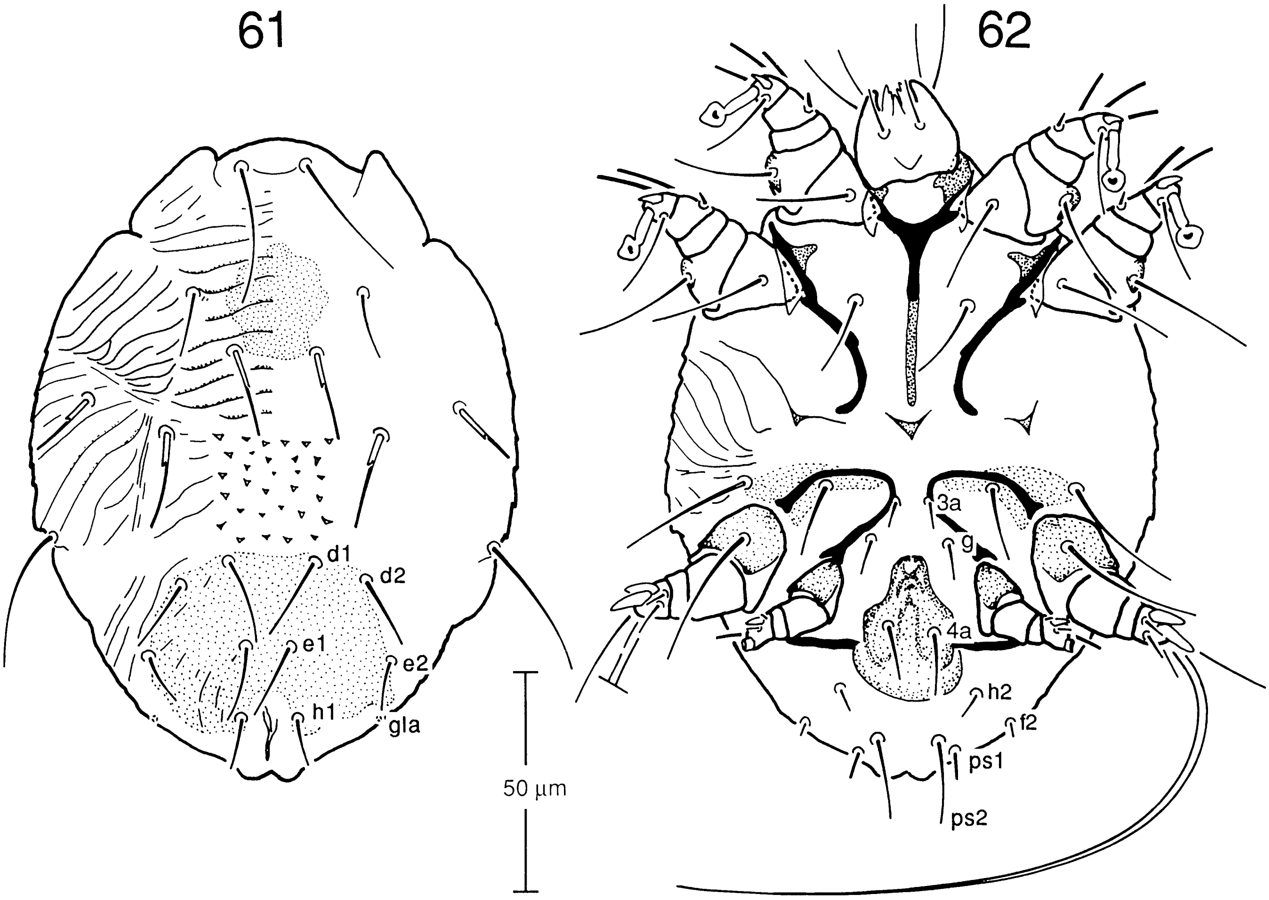
Material studied: All stages.

Hosts (Rodentia: Muridae) and locality: *Rattus norvegicus* (Berkenhout, 1769). Type host. FRANCE: Alfort, J. Guilhon (type series of *Sarcoptes anacanthos;* specimens in collection OSU).

Calomys musculinus (Thomas, 1913). ARGENTINA: BUENOS AIRES, Partido de Balcarce, Ruta 226, km 98, Campo Caralite, ca 37°45′S 58°15′W, 16 March 1970, P. Dalby, MSU #18685, HK 84–0716–4.

Literature records: on *Rattus norvegicus* from GERMANY: HAMBURG (Sellnick, 1944 [Type series]), and FRANCE (Guilhon, 1946a, 1946b); on *Rattus rattus* (Linnaeus, 1758) from GREAT BRITAIN (Lavoipierre, 1960); on *Mesocricetus auratus* (Waterhouse, 1839) from GERMANY (lab colony) (Enigk & Grittner, 1951).

Deposition of specimens (from *Calomys*): CUIC, MSU, IRSN, and UMMZ.



FIGS. 61, 62. *Trixacarus eliurus,* male, dorsal (61) and ventral (62) view.

Trixacarus caviae Fain, Hovell, & Hyatt, 1972

Trixacarus (*Caviacoptes*) *caviae* Fain et al., 1972: 74.

Diagnosed in the female by the presence of spines in the area lateral to the anus (39); in the male by the loss of the posterior median shield, and the loss of fusion between the anal shields (13, 14, 15).

A few additions can be made to the existing descriptions, all related to ontogeny. The dorsal spines in nymphal and adult *T. caviae* are characteristically elongated and pointed. In the larva, this morphology is found on the posterior dorsum, but anteriorly the spines are shorter and more blunt, strongly resembling the type of spines in other *Trixacarus.* Setal morphology is also variable over ontogeny. In the larva setae *d 1, d 2, e 1,* and *h 1* are spine-like rods; in all other stages these setae are more or less filiform. Setae *h 2* are filiform throughout ontogeny.

Trixacarus caviae is a cosmopolitan associate of captive guinea-pigs. It has never been reported from a wild caught host.

Material examined: All stages.

Host (Rodentia: Caviidae) and locality: *Cavia porcellus* (Linnaeus, 1758). GREAT BRITAIN: London, London Zoo, B. Brewster, AL-2096 (specimens in collection OSU); NETHERLANDS: UTRECHT, Utrecht, Veterinary School, #D 76/106, F.S. Lukoschus.

Literature records: on *Cavia porcellus* from GREAT BRITAIN (Fain et al., 1972 [Type series]; Beresford-Jones et al., 1976), AUSTRALIA (Collins et al., 1986), NETHERLANDS (Dorrestein & v. Bronswijk, 1979), continental USA (McDonald & Lavoipierre, 1980; Kummel et al., 1980), and HAWAII (Goff & Conant, 1985).

The sister group of *Trixacarus* is formed by five species, all primarily associated with primates (node 9, Fig. 48). This lineage is diagnosed in all stages by the short and broad shape of setae *sci* (64), and the loss of setae *g* (123, 124); in the female by the transformation of setae *c 1* and *c 2* from filiform or spine-like to short, broad spines (75, 81); in the male by the presence of poorly developed lateral shields (18 state 2), and a well developed and posteriorly bifurcate median apodeme (152).

All five species in this lineage are very similar in morphology, and synonymy of the five formerly recognized genera into a single genus, *Sarcoptes,* could be supported to avoid redundancy. However, I have chosen to reject synonymy of all five genera because different generic names set these taxa apart from the numerous subspecies and host races of *Sar-*

Table 1. Comparative measurements of female and male *Trixacarus*.

	eliurus					*diversus*			
	female N=5			male N=2		female N=12			male N=1
	av	SD	range			av	SD	range	
gnathosoma									
length	30	3	28–34	23	22	32	4	26–40	21
width	32	2	31–34	21	23	35	2	32–38	22
subcapitular seta	17	2	16–20	11	10	15	6	8–23	10
body									
length	225	9	211–235	153	158	238	35	197–296	143
width	177	13	157–191	108	112	188	25	158–223	105
seta *vi*	38	1	37–40	32	29	44	2	39–48	35
seta *sci*	29	1	27–30	21	20	40	3	37–48	27
seta *sce*	17	1	16–19	15	16	20	3	14–25	14
seta *c 1*	28	2	26–29	21	23	45	3	39–49	35
seta *c 2*	19	1	24–33	17	15	29	2	25–33	26
seta *cp*	42	3	38–45	37	31	43	3	38–48	31
seta *c 3*	31	3	28–34	30	26	37	2	32–39	28
seta *d 1*	27	1	26–29	19	20	42	3	36–47	27
seta *d 2*	26	2	24–28	20	14	41	2	39–46	27
seta *e 1*	29	3	24–33	18	16	38	2	35–42	29
seta *e 2*	21	7	17–29	12	12				
seta *f 2*	10	1	10	2	3				
seta *h 1*	19	1	17–20	10	12	52	2	49–54	29
seta *h 2*	4	1	4	5	4	37	5	31–48	16
seta *ps 1*	7	1	6–8	5	5	11	1	10–13	6
seta *ps 2*	36	3	33–40	19	18	22	3	15–29	6
seta *1 a*	22	2	19–24	20	15	38	5	25–43	31
seta *3 a*	12	2	11–15	6	6	28	2	24–30	15
seta *3 b*	20	1	19–22	16	18	32	3	25–37	27
seta *4 a*	20	2	17–21	13	11	25	1	23–27	28
seta *g*	33	3	30–36	9	7	32	3	25–38	8
copulatory cone	3	1	2–4			4	1	3–7	
bursa copulatrix	20	1	19–22			61	6	53–76	
genital area									
length				27	28				21
width				20	19				22
coxal apodemes I	48	2	45–51	49	48	58	9	33–68	50
coxal apodemes II	47	2	44–50	47	46	59	5	51–68	43
coxal apodemes III	29	2	27–31	30	31	26	3	22–31	22
coxal apodemes IV	28	2	25–30	20	20	27	2	24–31	18
leg I	45	2	42–47	31	40	40	9	30–58	34
leg II	44	2	42–47	29	41	43	9	32–60	35
leg III	43	2	40–46	36	39	41	5	36–55	32
leg IV	38	1	37–40	26	27	39	4	33–48	24
seta *pR* I	34	5	28–40	21	23	38	5	29–45	27
seta *pR* II	37	3	32–41	26	27	42	8	21–50	27
seta *sR* III	34	4	27–37	31	35	23	5	16–31	18
seta *vF* I	27	1	26–27	23	23	35	2	31–37	25
seta *vF* II	37	2	35–40	30	25	40	4	34–48	32
seta *cG* I	39	2	37–42	32	31	37	7	28–49	29
seta *cG* II	38	3	34–41	25	25	35	5	26–44	31
seta *e* III	21	2	18–23	27	26	69	6	62–84	66
seta *e* IV	16	2	14–18			28	8	19–48	
seta *d* III	148	6	143–157	144	141	165	7	152–178	141
seta *d* IV	155	9	141–164			183	6	175–192	

Table 1 (continued).

			eliurus					*diversus*	
		female		male			female		male
		N=5		N=2			N=12		N=1
	av	SD	range			av	SD	range	
solenidion σ I	4	1	4–5	6	4	4	1	3–5	4
solenidion φ I	16	1	15–16	12	11	14	1	12–17	12
solenidion φ II	23	1	21–24	16	16	22	2	18–25	17
solenidion φ III	10	1	9–11	7	8	8	1	7–10	7
solenidion φ IV	6	1	6–7	10	12	6	1	4–8	8
solenidion ω01 I	15	1	14–16	14	13	16	1	14–18	12
solenidion ω-3 I	12	1	12	11	11	13	2	11–16	9
solenidion ω II	20	1	18–21	16	15	20	2	18–22	16
ambulacral stalk I	10	1	9–11	10	10	15	3	11–19	12
ambulacral stalk II	11	1	10–12	10	8	14	2	10–17	11

coptes scabiei, many of which are still referred to as distinct species in the literature. In a compromise which retains monophyly of all recognized taxa, I propose a limited synonymy: *Kutzerocoptes* and *Sarcoptes,* the first two branches in the cladogram for this group, are retained as separate genera, while *Pithesarcoptes* and *Cosarcoptes* are synonymized with *Prosarcoptes.* This solution is compatible with the host associations: each of the three genera (new concept) is associated with a single family of primates.

The sister group of *Kutzerocoptes* is a lineage (node 10) diagnosed in the female by the presence of posterior ventral tubercles (47); in the male by reduced opisthosomal shields (13), and fusion of the median apodeme to the apodemes of the genital area (153). This lineage diverges into the genera *Sarcoptes* and *Prosarcoptes* (new concept).

Kutzerocoptes Lavoipierre, 1970

Kutzerocoptes Lavoipierre, 1970: 378.

Diagnosed in all stages by the loss of setae *la* I–II (164, 165); in the immatures and female by the loss of the anterior median shield (8); in the female by the presence of ambulacra on legs III–IV (204); in the males by the loss of cuticular spines (remnants in the form of blunt outgrowths are still present) (reversal) (46), the medial fusion of coxal apodemes III (157), the transformation of setae *gT* I–II to spines (Figs. 8, 16) (166), the loss of setae *f* IV (187), and the presence of ambulacra on legs III (205).

The genus includes a single species, *Kutzerocoptes grunbergi* Lavoipierre, 1970.

Kutzerocoptes grunbergi Lavoipierre, 1970
(Figs. 8, 9, 16, 17, 24, 25, 34, 35, 86–88)

Prosarcoptes pitheci Kutzer & Grünberg, 1967: 291, not Philippe, 1948.

Prosarcoptes pitheci Fain, 1968: 140, not Philippe, 1948.

Kutzerocoptes grunbergi Lavoipierre, 1970: 378.

With the characters of the genus.

All stages have been described under the name *Prosarcoptes pitheci* (Kutzer & Grünberg, 1967; Fain, 1968). Lavoipierre (1970) noted significant differences between these descriptions and the original description of *P. pitheci* (Philippe, 1948) and reclassified the specimens collected by Kutzer & Grünberg as a new genus and species, *Kutzerocoptes grunbergi.* This view is supported by the results of the present analysis.

Material examined: All stages.

Host (Primates: Cebidae) and locality: *Cebus capucinus* (Linnaeus, 1758). AUSTRIA (captivity), E. Kutzer & W. Grünberg.

Literature records: on *Cebus capucinus* from AUSTRIA (Kutzer & Grünberg, 1967 [Type series]; Fain, 1968; Lavoipierre, 1970).

Sarcoptes Latreille, 1802

Sarcoptes Latreille, 1802: 64.

Diagnosed in the male by the almost complete loss of the posterior median shield, and the loss of fusion between the anal shields (14, 15).

Type species *Acarus siro* var. *scabiei* (Linnaeus, 1758).

Sarcoptes scabiei (Linnaeus, 1758)

Acarus siro var. *scabiei* Linnaeus, 1758: 116.

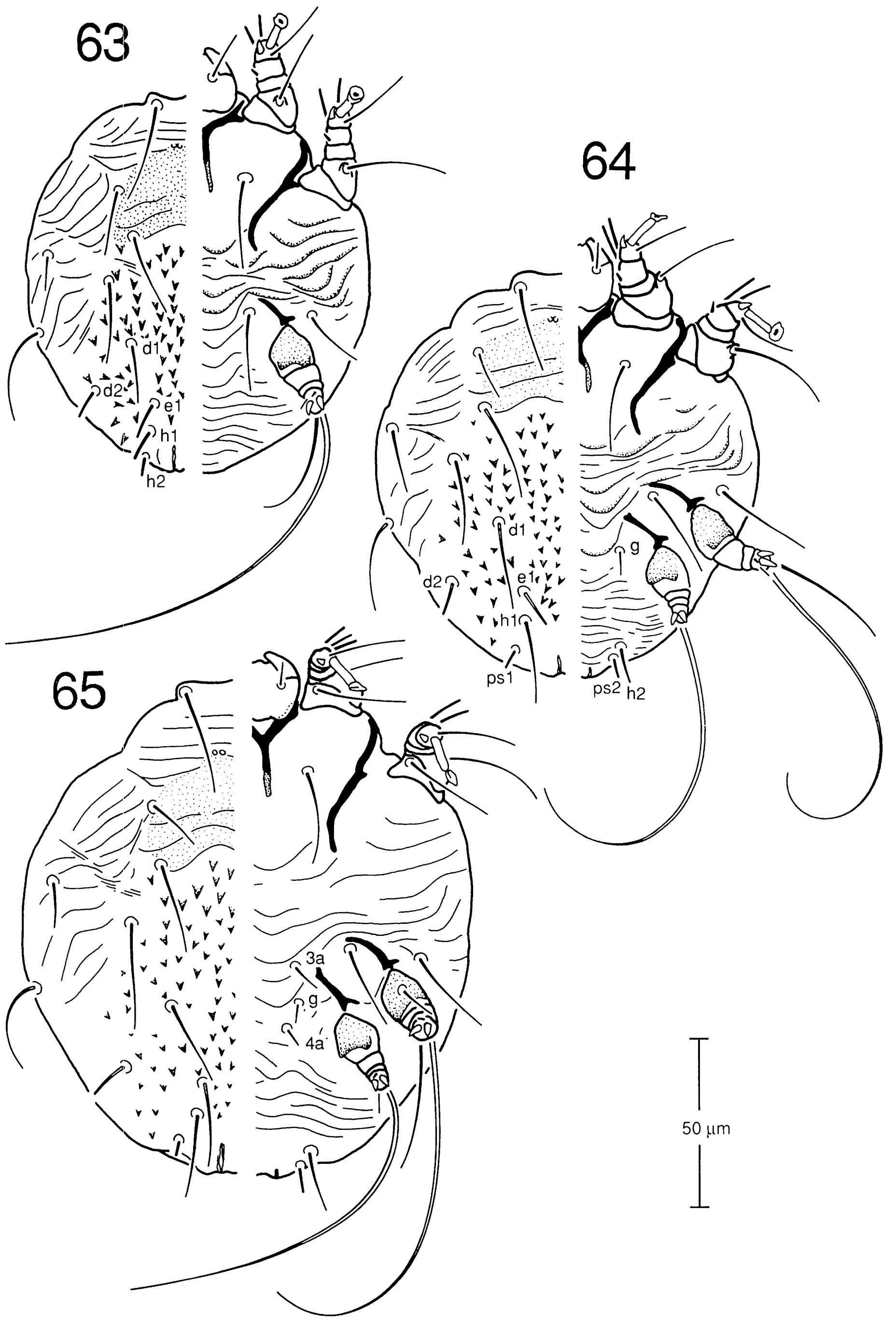
Sarcoptes scabiei (Linnaeus), Latreille, 1802: 64.

With the characters of the genus.

A complete history of the nomenclature of this species, including all synonymies made, was presented by Fain (1968) and will not be repeated for this study. Similarly, its morphology and ontogeny has been discussed in detail (Fain, 1968). The single addition to Fain's excellent redescription concerns the presence of a pair of very small palpal supracoxal setae, dorsal on the subcapitulum.

Only one species of *Sarcoptes* is recognized in this study. The notion of morphologically different (host) races or species of *Sarcoptes* was rejected by Fain (1968) and Pence et al. (1975), based on observations of significant within-population variability and inconsistent between-host variability. However, cross infectivity experiments (e.g. Arlian et al., 1984) provide some indications that physiological host race formation may be taking place.

Ecology, epidemiology, and pathology of this mite has



FIGS. 63–65. *Trixacarus diversus*, immatures, dorsal (left) and ventral (right) view of the larva (63), protonymph (64), and tritonymph (65).

been studied extensively, covering associations with humans, domestic animals, and wild hosts (e.g. Dubinin, 1955; Fain, 1968, 1978; Okoniewski & Stone, 1983; Pence et al., 1983; Stone et al., 1972, 1974; Trainer & Hale, 1969).

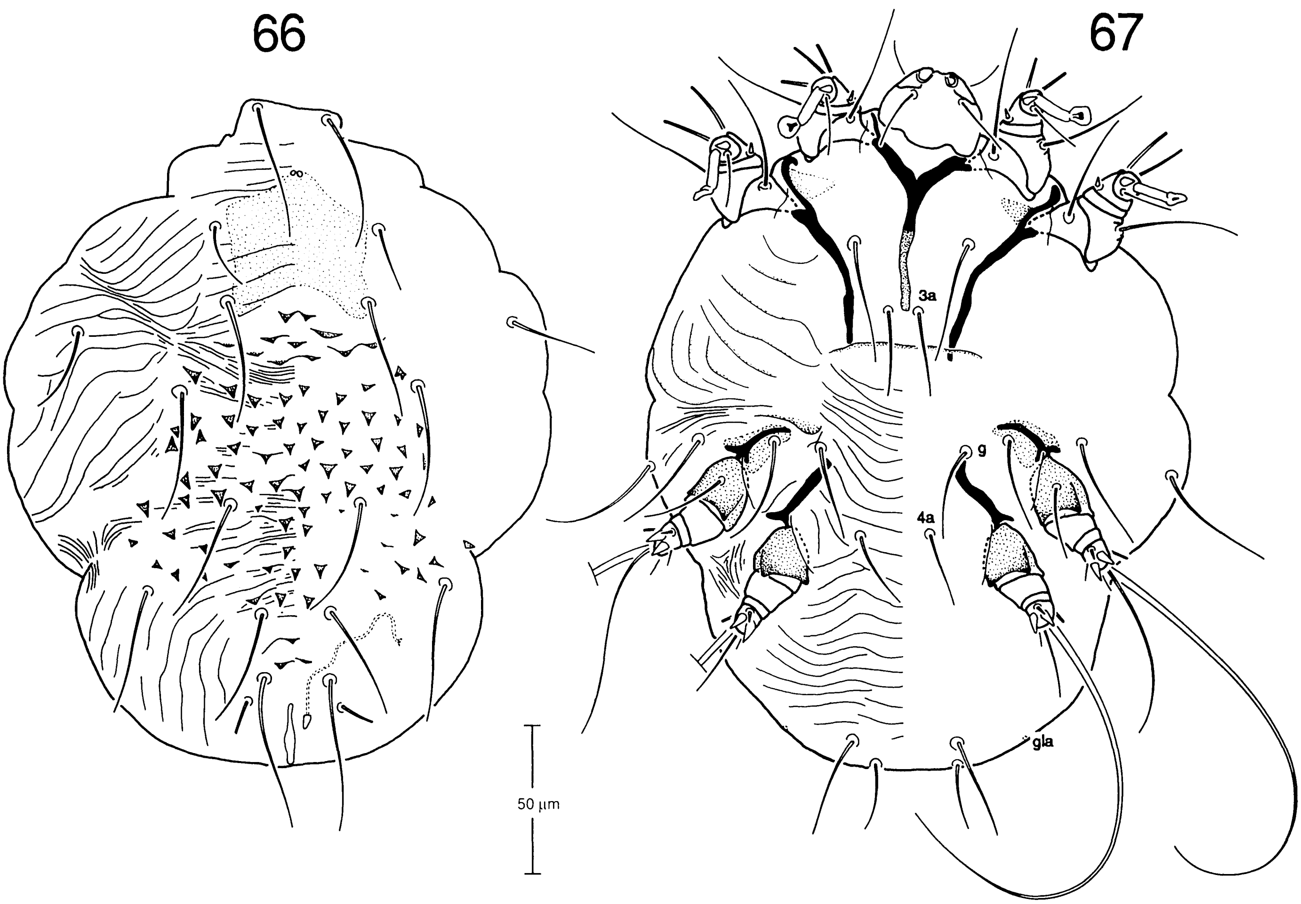
Material examined: All stages.

Hosts and localities: *Homo sapiens* Linnaeus, 1758 (Primates: Hominoidea). NETHERLANDS: NOORD HOLLAND, Amsterdam, 28 May 1973, J. v. Bronswijk; UTRECHT, Utrecht, September 1974, J. v. Bronswijk; UTRECHT, Driebergen, 11 October 1974, J. v. Bronswijk.

Bos taurus Linnaeus, 1766 (Artiodactyla: Bovidae). USA: NEW YORK, Erie Co., Alden, February 1976, F. Walter, BMOC 76–0303–1.

Sus scrofa Linnaeus, 1758 (Artiodactyla: Suidae). USA: SOUTH CAROLINA, 10 August 1982, BMOC 82–0816–1.

Canis lupus (= *Canis familiaris*) Linnaeus, 1758 (Carnivora:



FIGS. 66, 67. *Trixacarus diversus*, female, dorsal (66) and ventral (67) view.

Canidae). AUSTRALIA: WESTERN AUSTRALIA, Mitchell Plateau, 18 October 1976, Kimberley Exp. #3010, F.S. Lukoschus.

Vulpes vulpes (= *Vulpes fulva*) (Linnaeus, 1758) (Carnivora: Canidae). USA: NEW YORK, Tompkins Co., September 1975, BMOC 75–1022–7.

Erinaceus europaeus Linnaeus, 1758 (Insectivora: Erinaceidae). ISRAEL: Gedera, 1974, HK 86–0326–1.

Literature records: The host range of *Sarcoptes* is extremely broad. In the latest revision of the genus Fain (1968) cited host species in the orders Marsupialia, Primates, Carnivora, Artiodactyla, Perissodactyla, Rodentia, and Lagomorpha (a total of 16 families within those orders). Since that revision, numerous new records have been published, including records from at least one new host order and two new host families (*Erinaceus europaeus* [Insectivora: Erinaceidae; Tadmor & Rauchbach, 1972] and *Ursus americanus* [Carnivora: Ursidae; Schmitt et al., 1987]).

Prosarcoptes Lavoipierre, 1960

Prosarcoptes Lavoipierre, 1960: 168.
Pithesarcoptes Fain, 1965a: 252, new synonymy.
Cosarcoptes Fain, 1968: 146.

Diagnosed in the female by very well developed posterior ventral tubercles (48); in the male by the loss of posterior lateral shields (reversal) (17, 18 state 0).

Type species *Sarcoptes pitheci* Philippe, 1948.

Within the genus, the lineage of *P. pitheci* and *P. scanloni* is the sister group of *P. talapoini*. This lineage (node 12, Fig. 48) is diagnosed in the tritonymph and adults by the presence of ambulacra on legs III–IV (203–205).

Prosarcoptes talapoini (Fain, 1965), new combination

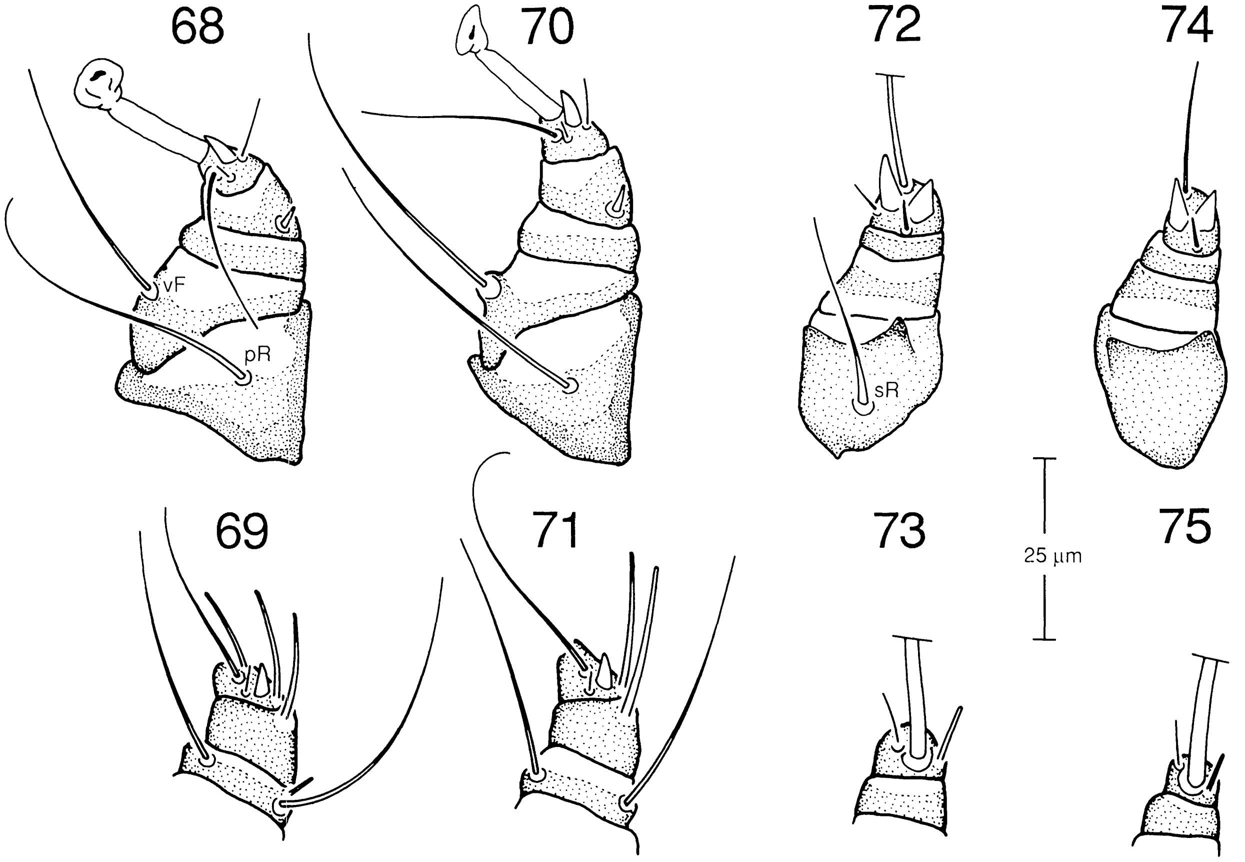
Pithesarcoptes talapoini Fain, 1965a: 252.

Diagnosed in the female by the presence of spines lateral to the anus (39), and the fusion of coxal apodemes III and IV; in the male by the loss of the ambulacrum of legs IV (reversal) (206).

Prosarcoptes talapoini caused discrete mange on the backs of three monkeys (Fain, 1965a). All stages burrowed into the epidermis and the females produced small cysts.

Material examined: None.

Literature records: on *Cercopithecus* (*Miopithecus*) *talapoin*



Figs. 68–75. *Trixacarus diversus*, female, ventral (top) and dorsal (bottom) view of legs I (68, 69), II (70, 71), III (72, 73), and IV (74, 75).

Schreber, 1774 (Primates: Cercopithecidae) from BELGIUM: Antwerp Zoo, recently imported from central Africa (Fain, 1965a [Type series]).

Prosarcoptes pitheci (Philippe, 1948)

Sarcoptes pitheci Philippe, 1948: 599.
Prosarcoptes pitheci (Philippe), Lavoipierre, 1960: 168.
Prosarcoptes faini Lavoipierre, 1970: 377, new synonymy.

The original description of *P. pitheci* (Philippe, 1948) is inadequate by modern standards, but the descriptions of *P. faini* are relatively detailed and cover all ontogenetic stages (Lavoipierre, 1970; Smiley, 1982). *Prosarcoptes pitheci* and *P. faini* were distinguished by differences in the shape of the central dorsal spines and setae *1 a, 3 a* (spine-like vs. setiform) and *f 2* (setiform vs. spine-like) (Lavoipierre, 1970). However, the shape and number of dorsal spines is quite variable in *Sarcoptes* (Fain, 1968; Pence et al., 1975), and may reasonably be expected to be variable in other Sarcoptinae. Furthermore, the quality of the original illustrations of *P. pitheci* is insufficient to allow an adequate evaluation of small differences in setal morphology, and the types of *P. pitheci* are apparently lost. Based on the available data, I propose a synonymy of *P. faini* with *P. pitheci*. Synonymy also provides a better fit with the host data (both forms occur on the same host species).

Material examined: None.

Literature records: on *Papio hamadryas* (Linnaeus, 1758) (= *P. papio, P. ursinus*) (Primates: Cercopithecidae) from GUINEA: Kindia (captivity) (Philippe, 1948 [Type series], host identified as *P. papio*); USA: San Diego Zoo (captivity) (Lavoipierre, 1970 [Type series of *P. faini*], host identified as *P. ursinus*); on *Cercopithecus aethiops* (Linnaeus, 1758) from GUINEA: Kindia (captivity) (Philippe, 1948).

Prosarcoptes scanloni Smiley, 1965

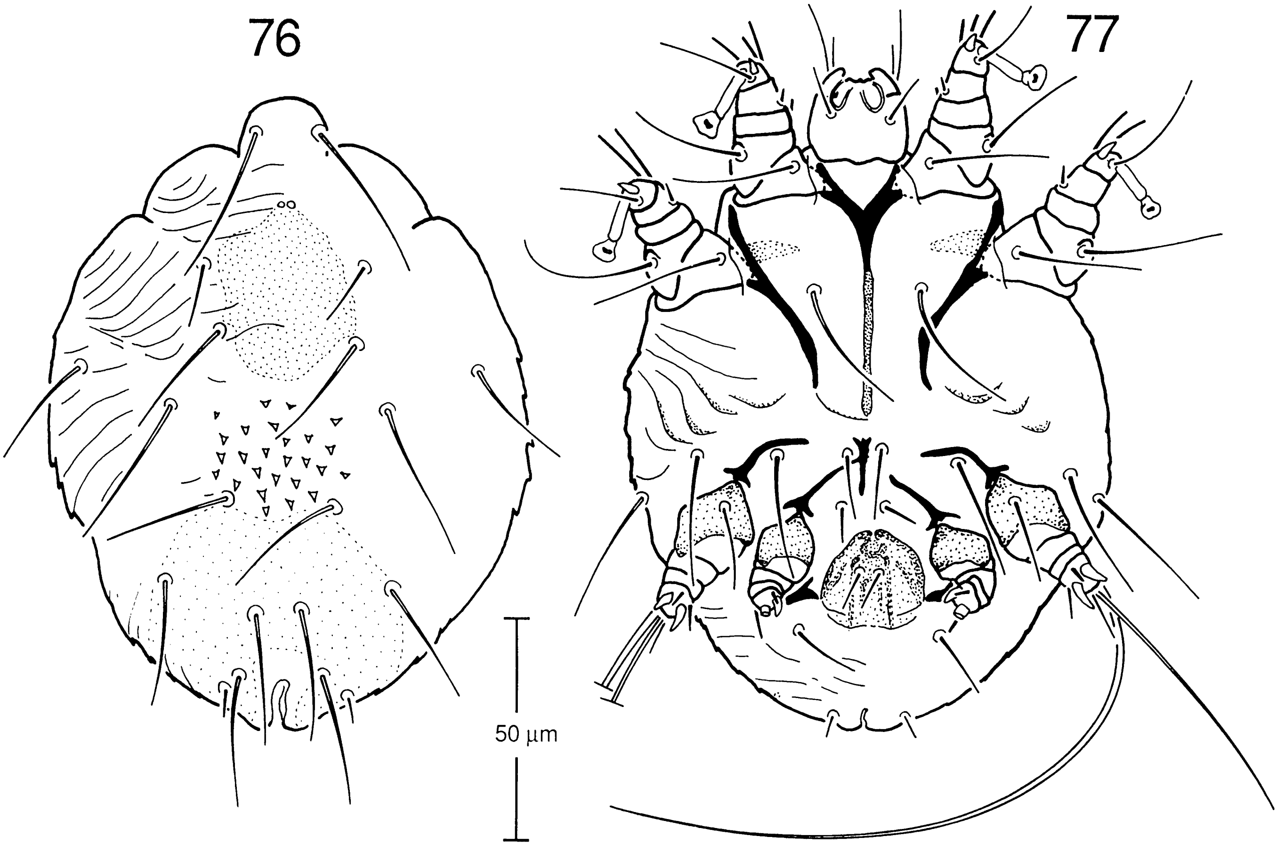
Prosarcoptes scanloni Smiley, 1965: 166.
Cosarcoptes scanloni (Smiley), Fain, 1968: 146.

Diagnosed in the tritonymph and female by the loss of setae *3 a* (present in the male) (127), and *e* III–IV (189); in the male by the loss of setae *e* III (190). Another derived feature is the further reduction (compared to other *Prosarcoptes* species) of the opisthosomal shield in the male (OConnor, 1984).

All stages have been described previously (Smiley, 1965; Smiley & OConnor, 1980).

Material examined: All stages.

Host (Primates: Cercopithecidae) and locality: *Macaca*



FIGS. 76, 77. *Trixacarus diversus,* male, dorsal (76) and ventral (77) view.

arctoides (Geoffroy, 1831). USA: NEW YORK, Ithaca, New York State Veterinary College (captivity), 20 February 1976, B.M. OConnor, BMOC 76–0221–1.

Literature records: on *Macaca fascicularis* (Raffles, 1823) (= *M. irus*) from THAILAND (Smiley, 1965 [Type series]); on *Macaca arctoides* from USA (Smiley & OConnor, 1980).

The sister group of the Sarcoptinae is the subfamily Teinocoptinae (new concept) (node 13, Fig. 48).

Teinocoptinae Fain, 1959

Teinocoptidae Fain, 1959b: 119.
Bakerocoptidae Fain, 1962b; Lavoipierre et al., 1967: 1.
Notoedrinae Fain, 1968: 14.

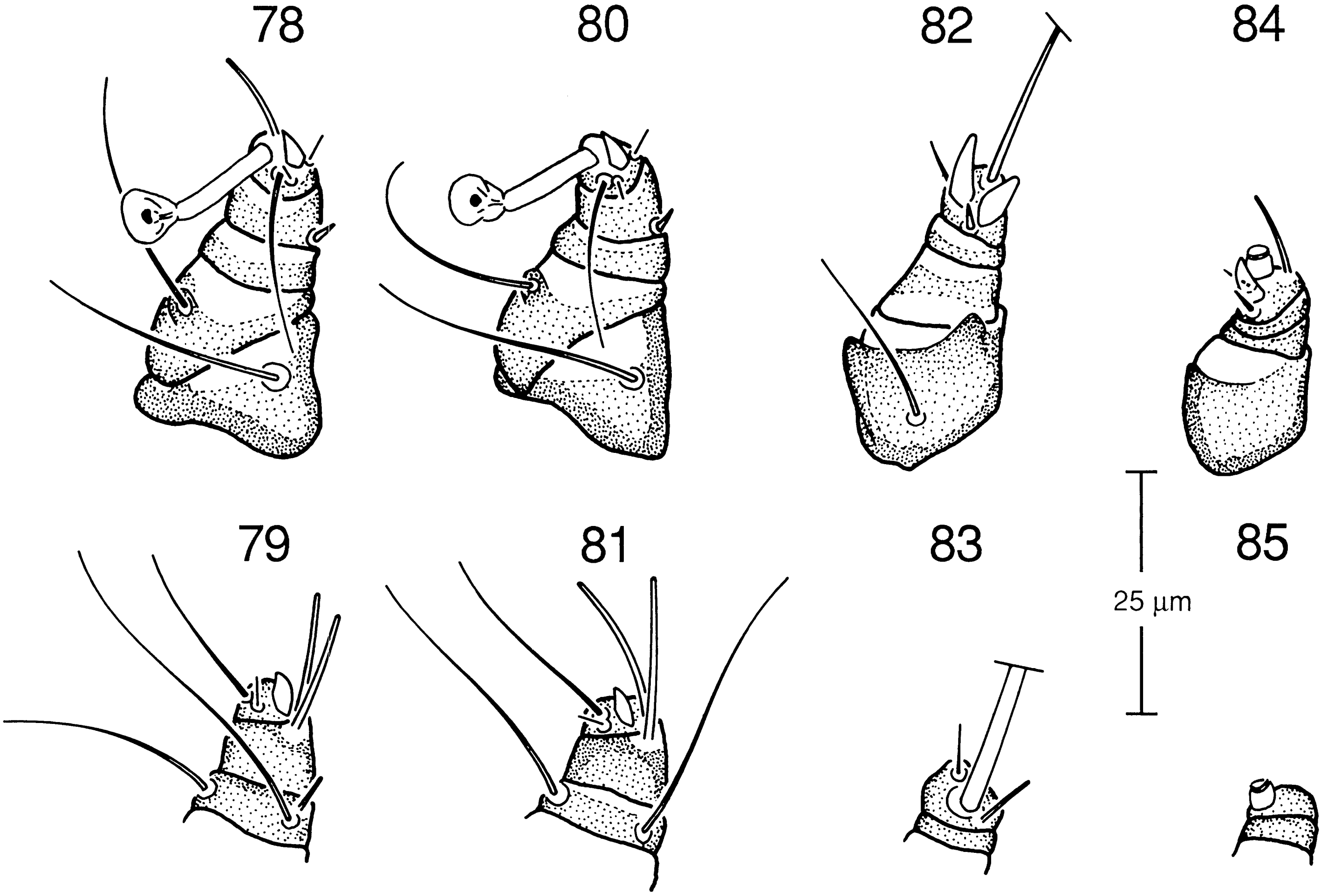
Diagnosed in all stages by the transformation of setae *c 1* and *c 2* from layered to simple (reversal) (77, 82), and the transformation of leg setae *s* I–II and *ra* I–II to spines (161–163); in the immatures by the reduction of setae *cp* (83, 85); in the nymphs by the delay in addition and weak development of setae *f 2* (99, 100); in the tritonymph and female by the loss of setae *e* III–IV (189); in the female by the dorsoterminal or terminal position of the anus (2), and the relative increase of the height of the body (3); in the male by the presence of free anterior lateral shields (11, 12 state 2), well developed posterior lateral shields (18 state 1), and the transformation of setae *kT* III–IV to spines (199).

Species in this lineage are ancestrally associated with bats, with some transfer to other groups of small mammals.

The first dichotomy within the Teinocoptinae is between a lineage including the formerly recognized family Teinocoptidae, plus the genera *Nycteridocoptes, Cynopterocoptes, Rousettocoptes,* and *Tychosarcoptes,* and the assemblage of the genera *Chirophagoides, Chirnyssoides,* and *Notoedres* (Fig. 48).

The *Nycteridocoptes-Teinocoptes* lineage (node 14) is diagnosed in all stages by the addition of setae *h 3* during ontogeny (reversal) (115); in the male tritonymph by the transformation of setae *c 1* to thin spine-like rods with bifurcate tips (76); in the immatures and female by the loss of the anterior median shield (8); in the female by the presence of small spines and/or scales (33), the presence of spinose zones extending laterally from the dorsum to the area of legs III (41), the loss of setae *la* I–II (164), and the loss of the ambulacral disc on legs I–II (177); in the male by the extension of the anterior median shield to include the bases of setae *sci* (10), separation of the anal shields (14), and the loss of setae *e* III (190).

All taxa in this clade are associated with bats, mostly Old World fruit bats, family Pteropodidae. The first dichotomy within this lineage is between the genus *Nycteridocoptes* and the remaining genera.



FIGS. 78–85. *Trixacarus diversus*, male, ventral (top) and dorsal (bottom) view of legs I (78, 79), II (80, 81), III (82, 83), and IV (84, 85).

Nycteridocoptes Oudemans, 1898

Nycteridocoptes Oudemans, 1898: 277.
Bakerocoptes Fain, 1962b: 406, new synonymy.

Diagnosed in the female tritonymph by the spine-like shape of setae *g* and *3 a* (125, 129), and the presence of ambulacra on legs III–IV (203); in the female by the shape of the body (6, 7); in the male by the fusion of the anterior lateral shields to the anterior median shield (12 state 1), the elongate, spine-like shape of setae *sci* (67), the relative length of the *d* setae (setae *d 1* at least twice as long as setae *d 2*) (95), the spine-like shape of setae *h 2*, *ps 2*, and *g* (110, 126); the presence of an internal spur on coxal apodemes II (155), the spine-like shape of setae *gT* (166), the loss of setae *d* and *e* IV (184, 191), and the presence of ambulacra on legs III (205). The genus is also characterized by very distinct sexual dimorphism in the tritonymph.

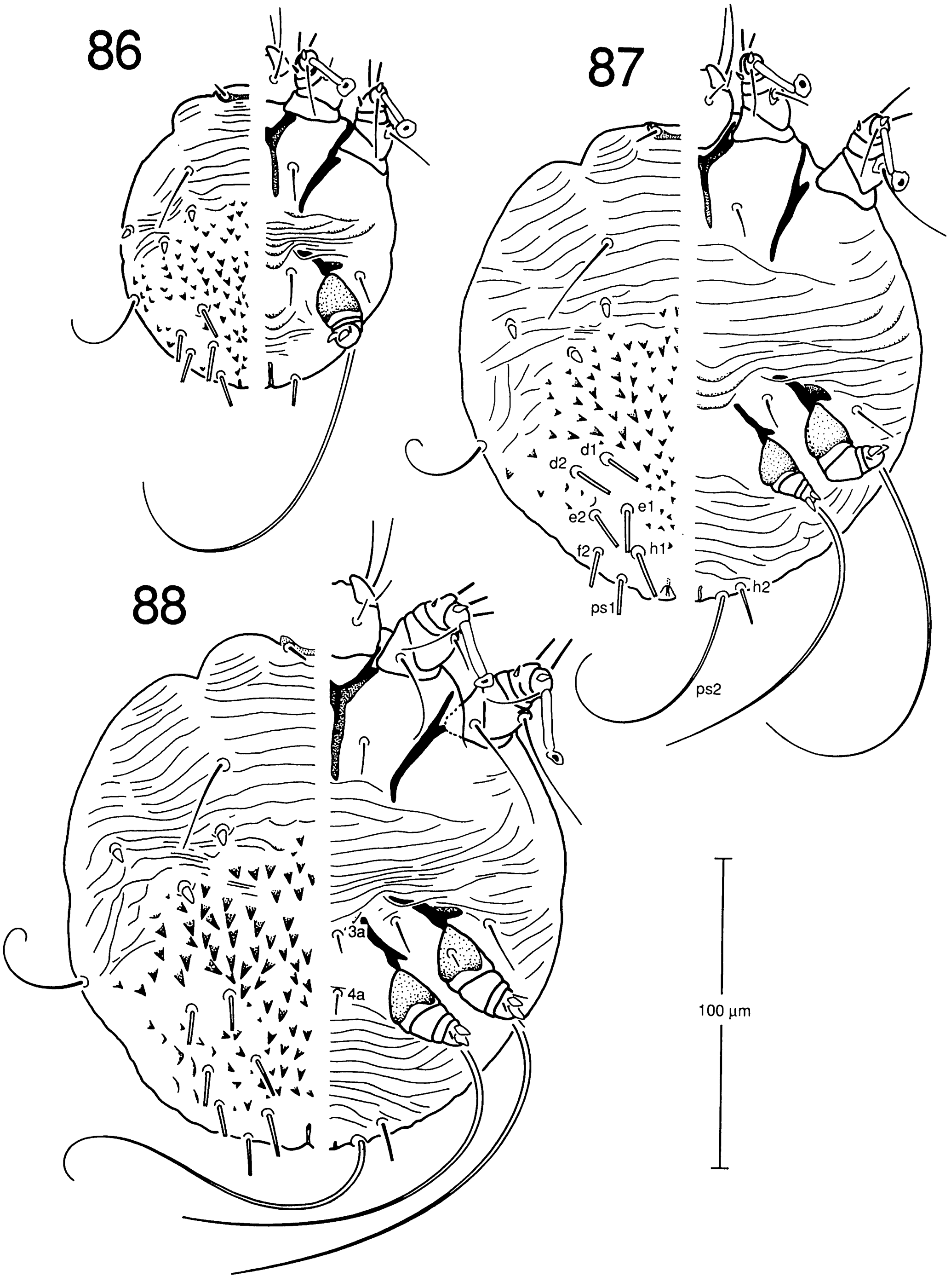
Type species *Nycteridocoptes poppei* Oudemans, 1898.

The first dichotomy within *Nycteridocoptes* is between *N. heidemanni* and a lineage including all remaining taxa (Fig. 51). The latter lineage (node 16) is diagnosed in the female tritonymph and male by the modified shape of the ambulacrum of respectively legs III–IV and legs III (207); in the male by the loss of fusion between the posterior median and anal shields (15), the transformation of setae *sce* into long spines (71), and the thick shape of setae *h 2* and *ps 2* (111).

A small lineage including *N. microphallus* and *N. rousetti* diverges from a larger one including the remaining species. The small lineage (node 17) is diagnosed in the immatures by the ontogeny and degree of development of setae *f 2* (101, 102); in the female tritonymph by the loss of dorsal spines (reversal) (29); in the females by a reduction in size (reversal) (7), the presence of scales (34), the loss of spines and/or scales in the area between setae *sci* and *c 1* (reversal) (35, 36), and parallel, but not fused, coxal apodemes I (139).

Nycteridocoptes **heidemanni** nov. spec.
(Figs. 89–112)

Diagnosed in all stages by the well developed setae *cp* (reversal) (83, 85); in the protonymph by the addition of setae *h 3* (reversal) (113, 114); in the male tritonymph by the transformation of setae *c 1* from thin, spine-like rods to filiform



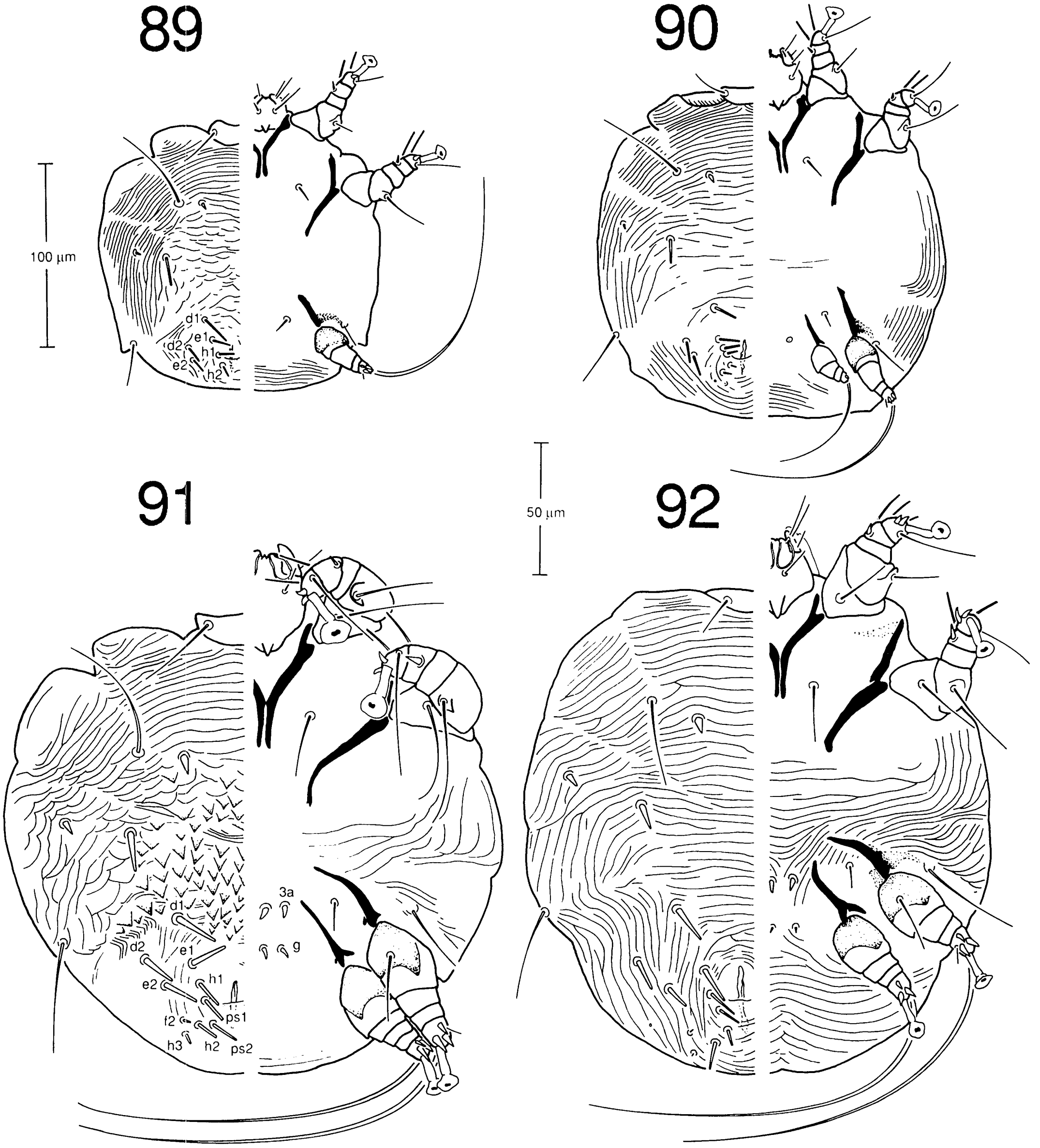
FIGS. 86–88. *Kutzerocoptes grunbergi*, immatures, dorsal (left) and ventral (right) view of the larva (86), protonymph (87), and tritonymph (88).

(reversal) (76); in the male by the loss of the median apodeme (reversal) (151) and the loss of setae *r* IV (195).

Larva (Fig. 89): Parts of the dorsum with a weakly developed, scale-like striation. Setae *c 1* and the perianal setae elongate, spine-like rods with slightly bifurcate tips. Coxal apodemes I parallel but not fused. Legs well developed. Pretarsi of legs I–II with a well developed ambulacral disc.

Protonymph (Fig. 90): Striation not scale-like. Setae *h 3*, *ps 1*, *ps 2*, and *g* and legs IV added. The *ps* setae short but distinct, setae *h 3* very small to minute, setae *g* very small. Setae *f 2* represented by vestigial alveoli.

Female tritonymph (Fig. 91): Large spines present on the central part of the dorsum. Setae *f 2* and *h 3* small but distinct, *ps* setae well developed. Setae *g* and *3 a* more or less



FIGS. 89–92. *Nycteridocoptes heidemanni*, immatures, dorsal (left) and ventral (right) view of the larva (89), protonymph (90), female tritonymph (91), and male tritonymph (92) (Figs. 90–92 same scale).

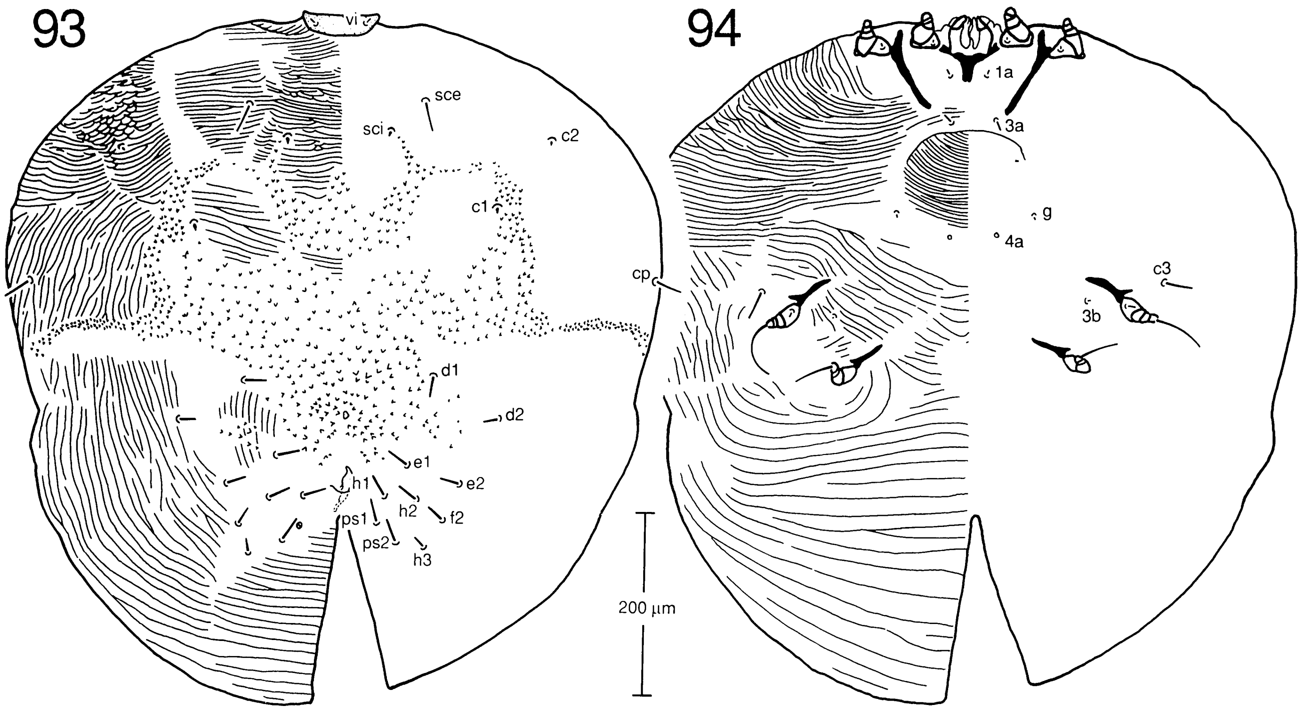
spine-like, setae *4 a* not observed in the single, damaged, specimen available. Pretarsi of legs III–IV with well developed ambulacra, resembling those of legs I–II. Trochanteral setae and solenidia ω-3 added. Setation of legs IV complete for the genus.

Male tritonymph (Fig. 92): Resembling the protonymph but setae *c 1* not elongate and setae *f 2* present (small). Legs as in the female tritonymph, with well developed pretarsi on legs III–IV. Setae *3 a* small spines. Setae *4 a* not observed.

Female (Figs. 93–102): Very large. Characterized by the pattern of dorsal spines, and the subequal lengths of the opisthosomal setae. Setae *4 a* present. Legs (Figs. 95–102) compressed. Tibial setae *gT* I–II and *kT* III–IV spine-like, femoral and trochanteral setae short. Translucent flaps on femora I–II relatively small. Solenidia σ-1 I thin but well developed. Measurements in Table 2.

Male (Figs. 103–112): Anal and posterior median shields partially fused. Opisthosomal gland opening (gla) between setae *e 2* and *f 2* (not observed in other stages). Setae *4 a* very poorly developed or absent. Legs (Figs. 105–112) well developed. Setae *s* I–II elongated spines. Ambulacra of all legs similar in shape. Measurements in Table 3.

All stages were found on the wings of the hosts. Most specimens were attached to the wing membrane, some to the skin overlying the arm and finger bones. One male was collected from the lower lip of a *Ptenochirus minor*. Unlike other species in this genus, female tritonymphs and males of *N. heidemanni* were not found in the mouth of their hosts. The



Figs. 93, 94. *Nycteridocoptes heidemanni*, female, dorsal (93) and ventral (94) view.

females produce large cysts, resembling those described for *N. cynopteri* (see Lavoipierre et al., 1967).

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Ptenochirus minor* Yoshiyuki, 1979. Type host. PHILIPPINES: Leyte, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 22 March 1987, P.D. Heideman (PDH 3226), NMNH #459234, HK 87–0322–4 (holotype female); same locality, 17 March 1987, J.S.H. Klompen (JSHK 6), PNM, HK 87–0317–3 (allotype male); 19 March 1987, JSHK 24, NMNH, HK 87–0319–2; 20 March 1987, JSHK 30, NMNH #459215, HK 87–0320–4 (wash); Leyte, 10 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 320 m, 10 March 1987, PDH 3112, NMNH, HK 87–0310–2; same locality, 11 March 1987, PDH 3126, NMNH #459224, HK 87–0311–3.

Ptenochirus jagori (Peters, 1861). PHILIPPINES: Camarines Sur, 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N 123°20'E, elev. 475 m, L.R. Heaney (LRH 3975), NMNH #573726, HK 88–0824–1; Leyte, Biliran Is., 11°32'N 124°32'E, elev. 700 m, 29 April 1984, PDH 2493, UMMZ #161280, HK 84–0719–2; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 8 February 1983, PDH 1494, UMMZ #160037, BMOC 83–1600–84.

Cynopterus brachyotis (Muller, 1838). INDONESIA: Lombok, September 1987, D. Kitchener (L 6), WAM, HK 88–0411–1; MALAYSIA: Sabah, Pulau Tiga, 7°21'N 117°03'E, 15 April 1988, S.M. Goodman, UMMZ #155506–165511, BMOC 88–0527–5.

Haplonycteris fischeri Lawrence, 1939. PHILIPPINES: Catanduanes, 9 km W Gigmoto, 13°47'N 124°19'E, elev. 200 m, 21 February 1988, E.A. Rickart (EAR 1674), NMNH #573222, HK 88–0828–7; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 4 July 1982, PDH 512, UMMZ #159836, HK 83–1210–1; same locality, 6 July 1982, PDH 538, UMMZ #159838, HK 83–1217–3; 30 July 1982, PDH 640, UMMZ #159841, HK 83–1213–2; 1 August 1982, PDH 682, UMMZ #159848, HK 83–1216–4; 1 August 1982, PDH 683, UMMZ #159849, HK 83–1214–2; 27 August 1982, PDH 778, UMMZ #159860, HK 83–1218–2; 4 November 1982, PDH 1034, UMMZ #159879, HK 83–1217–1; 4 November 1982, PDH 1043, UMMZ #159887, HK 83–1216–1; 8 November 1982, PDH 1086, UMMZ #159898, HK 83–1211–1; 4 March 1983, PDH 1561, UMMZ #159933, HK 88–0118–2.

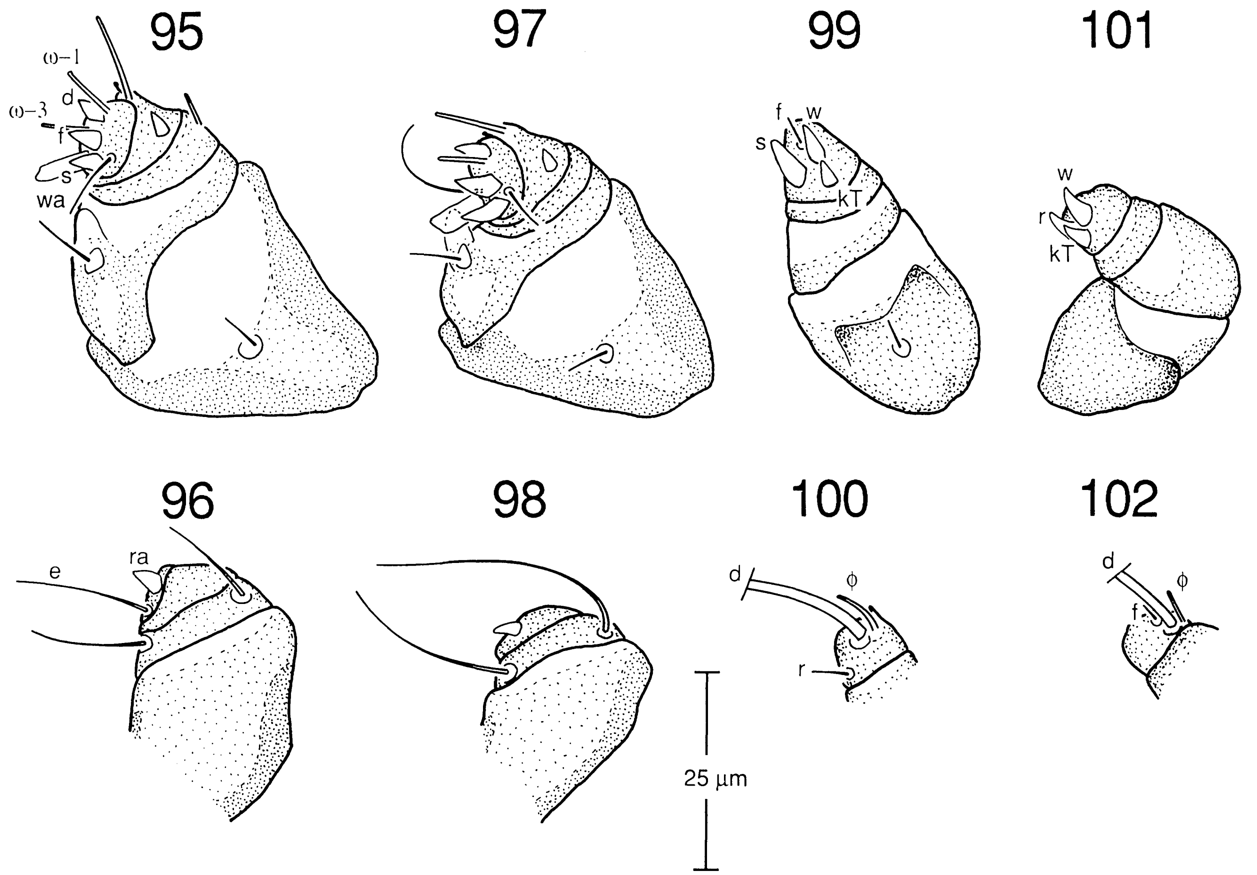
Etymology: This species is named in honor of Dr. P.D. Heideman, in recognition for his studies on the ecology of *Haplonycteris* and *Ptenochirus*, the principal hosts of this new species.

Deposition of specimens: Holotype female and allotype male in collection NMNH. Paratypes in BMNH, FMNH, IRSN, NMNH, PNC, UMMZ, and WAM.

Nycteridocoptes microphallus Fain, 1959
(Figs. 113–115)

Nycteridocoptes microphallus Fain, 1959f: 347.
Nycteridocoptes microphallus celebensis Fain, 1963c: 251.

Diagnosed in the male by having a lateral notch on the median opisthosomal shield (16). The diagnostic character mentioned by Fain (1959f), the small size of the genital area



Figs. 95–102. *Nycteridocoptes heidemanni,* female, ventral (top) and dorsal (bottom) view of legs I (95, 96), II (97, 98), III (99, 100), and IV (101, 102).

in the male, may be a characteristic for the lineage of *N. microphallus* and *N. rousetti* but it does not clearly distinguish the two species (Table 3).

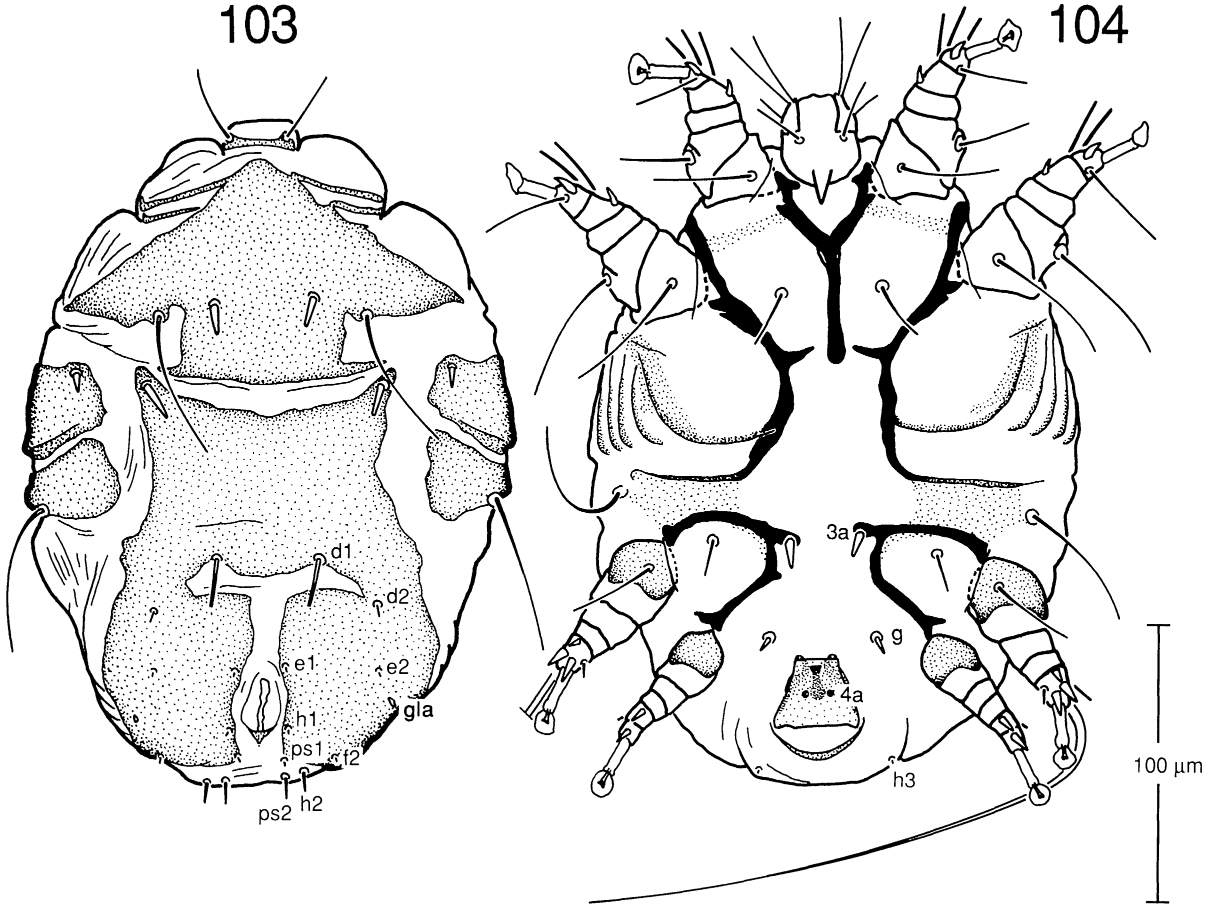
The type series was collected from *Eonycteris spelaea,* a common host of this mite species. A separate subspecies, *N. microphallus celebensis,* was subsequently described from *Rousettus celebensis* (Fain, 1963c). The female of this subspecies is characterized by long, instead of short, setae *h 1,* and preanal scales, instead of a field of blunt spines. A third form was found during this study combining elements of both named subspecies: short setae *h 1* and scales instead of spines. This form was found on *Harpyionycteris whiteheadi, Dobsonia moluccensis* and *Rousettus amplexicaudatus.* In addition, specimens of *N. microphallus* were found on *Thoopterus nigrescens* and *Cynopterus brachyotis* but the females collected from these hosts are in poor condition and the structure of the preanal spines/scales could not be determined. Setae *h 1* in specimens from both collections are short. The above observations may be indicative of either a species complex or a highly variable species. Given the limited amount of available material from several of the "host races," I will retain all populations within a single species, *N. microphallus.*

The adults and female tritonymph have been described by Fain (1959f, 1963c). The other immature stages (Figs. 113–115) have not been described previously. Setae *sci* are relatively small in all immatures. Addition of setae *f 2* and *h 3* is delayed to the female tritonymph, although setae *f 2* are represented by vestigial alveoli in the male tritonymph. Setae *g* are added in the protonymph and setae *3 a* and *4 a* are added in the male tritonymph. All of these setae are small to minute.

Nycteridocoptes microphallus occurs mainly on the wings but female tritonymphs and males are often found in the mouth of their hosts, or in rare cases (host *Eonycteris*) on the ear or hind leg. On *Dobsonia* and *Harpyionycteris* males and females regularly occur in and around the nostrils but rarely in the mouth. In several cases males were found in the same cyst with a female tritonymph (on the wing). Few data are available on pathology. Female cysts are often congregated (3–6 cysts) near holes in the wing membrane but it is not clear whether the mites caused the damage to the wing membrane. The other stages are much smaller than the females and appear to induce little host reaction.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Eonycteris spelaea* (Dobson, 1871). Type host. INDONESIA: Lombok, Batu Koq, 8°19'S 116°26'E, 7 October 1987, D. Kitchener (P 409), WAM, HK 88–0406–1; same locality, 31 October 1987,

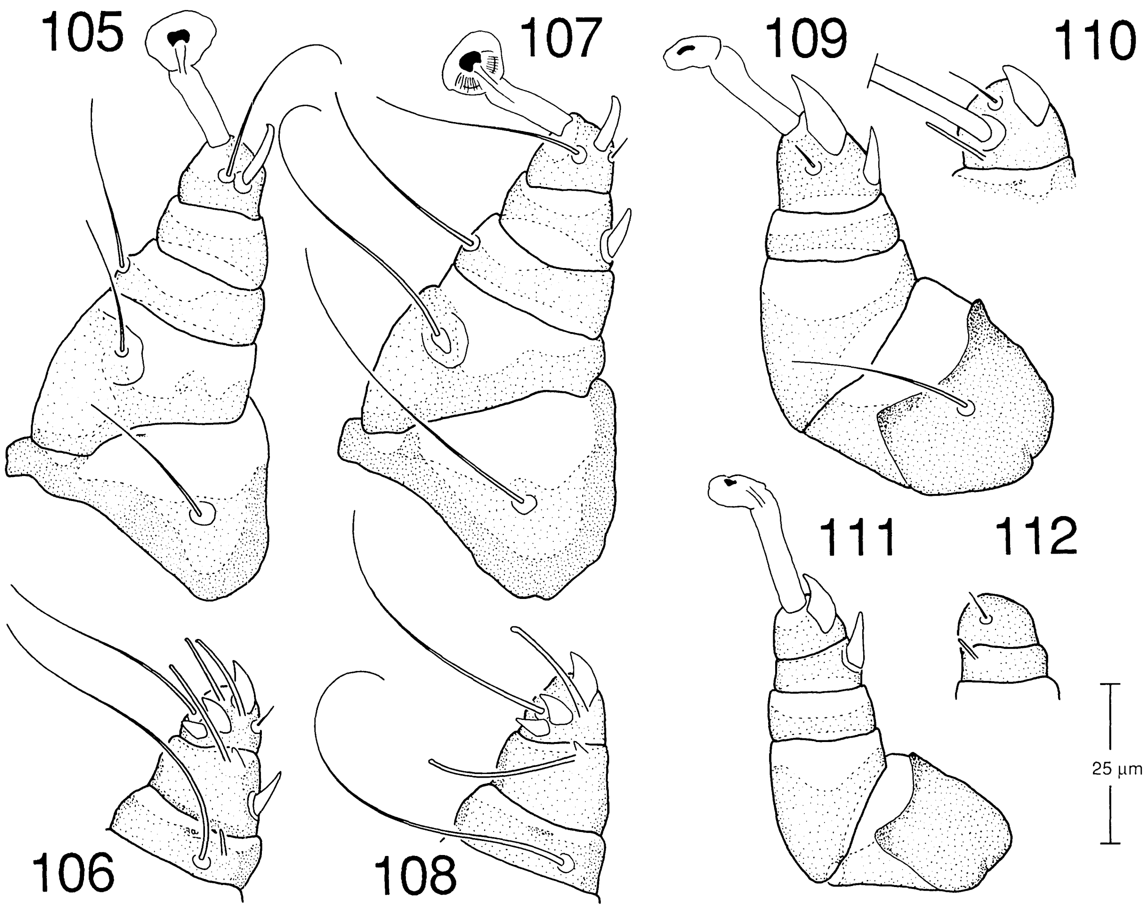


FIGS. 103, 104. *Nycteridocoptes heidemanni*, male, dorsal (103) and ventral (104) view.

D. Kitchener (L 201), WAM, HK 88–0410–1; Lombok, Pelangan, 12 October 1987, L 271, WAM, HK 88–0421–1; same locality, 13 October 1987, L 300, WAM, HK 88–0413–1; Sumbawa, Desa Belo Jereweh, 8°52'S 116°50'E, 15 May 1988, D. Kitchener (S 212), WAM, HK 89–0208–2; Sumbawa, Teluk Santong, 8°44'S 117°54'E, 21 May 1988, S 294, WAM, HK 89–0208–1; MALAYSIA: Pahang, Raub Cave, 13 May 1979, Rudnick, IMR; Pahang, Bentong, Bukit Chintamani, 13 October 1982, F.S. Lukoschus; PHILIPPINES: Leyte, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 5 April 1987, J.S.H. Klompen (JSHK 74), NMNH, HK 87–0405–1; Leyte, 4 km S, 1 km E Inopacan, 10°28'N 124°45'E, elev. 50 m, 28 May 1984, P.D. Heideman (PDH 2735), UMMZ #161427, MAH 85–0131–5; Leyte, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 26 March 1987, R.B. Utzurrum (RBU 155), NMNH, HK 87–0326–6; same locality, 27 March 1987, JSHK 38, NMNH, HK 87–0327–3; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 10 October 1982, PDH 970, UMMZ #158919, BMOC 83–1600–50; same locality, 4 November 1982, PDH 1028, UMMZ #158920, BMOC 83–1600–57; Negros Oriental, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 10 May 1987, PDH 3569, NMNH, HK 87–0510–1; same locality, 10 May 1987, PDH 3570, NMNH, HK 87–0510–6; Negros Oriental, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 22 February 1987, L.R. Heaney (LRH 2907), NMNH #459070, HK 87–0222–3 (wash); same locality, 22 February 1987, E.A. Rickart (EAR 1258), NMNH #458166, HK 87–0222–7; Negros Oriental, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 24 October 1982; PDH 1017, UMMZ #158941, HK 84–0411–1; same locality, 24 March 1983, PDH 1673, UMMZ #159844, HK 84–0329–1; 11 June 1987, JSHK 97, NMNH #458164, HK 87–0611–2.

Eonycteris robusta Miller, 1913. PHILIPPINES: Catanduanes, 1 km N, 8 km W Gigmoto, 13°48'N 124°19'E, elev. 200 m, 24 February 1988, EAR 1695, NMNH #573211, HK 88–0713–2; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 6 May 1983, PDH 1816, UMMZ #158917, BMOC 83–1600–96.

Cynopterus horsfieldi Gray, 1843. MALAYSIA: Kelantan, Pulai, 4°48'N 101°57'E, 18 July 1970, Yong Ghong Chong, AMNH #233953, HK 86–0813–14.



Figs. 105–112. *Nycteridocoptes heidemanni*, male, ventral (top) and dorsal (bottom) view of legs I (105, 106), II (107, 108), III (109, 110), and IV (111, 112).

Dobsonia exoleta Andersen, 1909. INDONESIA: Sulawesi, Gumbara, ca 1°S 121°E, elev. 105 m, 26 May 1973, NAMRU-2, AMNH #227302, HK 86–0815–8.

Dobsonia moluccensis (Quoy & Gaimard, 1830). INDONESIA: Irian Barat, Biak Is., Korim, 0°54'N 136°02'E, 16 August 1976, NAMRU-2, AMNH #252258, HK 86–0815–7; same data, AMNH #252259, HK 86–0815–6.

Harpyionycteris whiteheadi Thomas, 1896. PHILIPPINES: Leyte, Biliran Is, 11°32'N 124°32'E, elev. 920 m, 1 May 1984, PDH 2514, UMMZ #161303, HK 84–0621–8; Leyte, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 21 March 1987, PDH 3214, NMNH #459113, HK 87–0321–3; same locality, 22 March 1987, PDH 3228, NMNH #459114, HK 87–0322–5; Leyte, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 24 May 1984, LRH 2667, UMMZ #161306, HK 84–0730–1; same locality, 23 March 1987, LRH 3030, NMNH, HK 87–0323–1; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 28 August 1982, PDH 820, UMMZ #158903, BMOC 83–1600–28; same locality, 1 September 1982, PDH 853, UMMZ #162376, BMOC 83–1600–34; 4 October 1982, PDH 919, UMMZ #158904, BMOC 83–1600–38; 4 October 1982, PDH 923, UMMZ #158905, BMOC 83–1600–41; 8 February 1984, RBU 252, UMMZ #161302, HK 84–0621–10.

Pteropus pumilus Miller, 1911. PHILIPPINES: Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 4 October 1982, PDH 924, UMMZ #158894, BMOC 83–1600–42 (wash).

Rousettus amplexicaudatus (Geoffroy, 1810). PHILIPPINES: Leyte, 7 km N Baybay, 10°45'N 124°48'E, elev. 10 m, 11 March 1987, PDH 3119, NMNH #458478, HK 87–0311–1; Negros Oriental, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 25 February 1987, D. Kitchener (P 7), NMNH #459298, HK 87–0225–4; same locality, 10 May 1987, EAR 1565, NMNH #459293, HK 87–0510–2.

Rousettus celebensis Andersen, 1907. INDONESIA: Sulawesi, Sumalata, 0°59'N 122°30'E, 5 November 1914, R.C. Raven, FMNH #44141, HK 86–0227–2; same data, NMNH #199773, HK 88–0827–1; NMNH #199774, HK 88–0827–2; Sulawesi, Lake Lindu, Tomado, 1°18'S 120°05'E, elev. 950 m, 29 January 1972, G.G. Musser, AMNH #240481, HK 86–0812–2.

Thoopterus nigrescens (Gray, 1870). INDONESIA: Su-

Table 2. Comparative measurements of female *Nycteridocoptes*. 1.

	heidemanni			*microphallus*			*rousetti*		*malayi*	*notopteris*	
		N=5			N=10		N=2		N=1	N=3	
	av	SD	range	av	SD	range				av	range
gnathosoma											
length	59	9	48–70	47	3	43–52	48	41	56	69	60–75
width	50	1	49–50	41	3	36–45	38	40	46	55	50–58
body											
length	799	–	–	445	78	337–514	–	575	1139	955	–
width	754	–	–	401	116	289–521	–	601	1197	848	–
seta *vi*	6	2	2–8	5	1	3–7	–	7	4	3	2–3
seta *sci*	7	1	6–7	5	1	4–8	7	7	6	6	5–7
seta *sce*	29	2	26–32	4	1	3–6	6	6	20	6	5–8
seta *c 1*	6	1	5–8	7	1	6–8	8	8	7	8	7–8
seta *c 2*	5	1	4–6	3	1	2–5	5	4	4	4	4–5
seta *cp*	31	6	24–39	4	1	3–5	6	4	18	3	3–4
seta *c 3*	30	7	20–38	21	4	16–28	22	26	25	34	27–38
seta *d 1*	22	4	18–28	39	5	30–45	38	43	16	21	15–25
seta *d 2*	16	2	14–18	30	4	24–37	29	32	12	9	8–10
seta *e 1*	25	5	18–30	38	5	29–45	37	34	23	24	23–26
seta *e 2*	20	3	16–22	3	1	1–4	4	3	19	10	7–11
seta *f 2*	17	2	16–19	2	1	1–2	2	1	22	15	14–15
seta *h 1*	25	3	21–28	4	1	3–6	5	5	24	21	18–26
seta *h 2*	24	5	21–31	36	4	30–42	31	30	24	22	16–26
seta *h 3*	13	1	11–15	1	1	1–2	2	1	21	10	9–11
seta *ps 1*	25	3	20–27	11	1	10–15	17	15	22	23	22–24
seta *ps 2*	27	3	21–30	9	4	4–16	16	16	24	24	21–25
seta *1 a*	6	1	5–8	5	2	2–7	6	8	4	3	2–3
seta *3 a*	9	2	7–11	3	1	1–6	7	5	5	8	5–10
seta *3 b*	3	1	2–4	2	1	1–2	2	1	2	4	4
seta *4 a*	–			2	–	2	2	–	1	5	5
seta *g*	5	1	3–5	6	1	4–8	9	11	3	9	9–10
copulatory cone	–			4	1	4–5	–	–	–	12	12–14
bursa copulatrix	–			–			–	–	–	79	69–88
coxal apodemes I	55	2	53–57	52	5	45–63	53	52	54	64	61–66
coxal apodemes II	107	7	99–116	88	7	76–99	77	83	106	110	106–113
coxal apodemes III	44	7	37–55	28	5	22–36	32	29	36	31	28–33
coxal apodemes IV	35	3	33–39	24	4	19–30	29	28	34	32	29–35
leg I	48	4	43–55	38	5	31–50	40	41	43	49	43–54
leg II	47	6	41–54	41	4	35–49	37	38	46	48	44–54
leg III	44	2	42–46	34	4	30–41	35	35	45	46	44–47
leg IV	39	2	36–41	32	4	26–38	33	34	41	44	42–46
seta *sR* III	5	1	3–7	2	1	1–4	4	–	6	8	7–10
seta *d* III	57	14	44–73	44	7	33–56	41	57	47	61	54–71
seta *d* IV	45	9	39–62	39	7	25–49	39	36	45	54	38–66
solenidion σ I	7	–	6–7	5	1	4–6	–	–	–	6	6
solenidion ϕ I	12	–	12	7	1	6–8	8	13	10	9	9
solenidion ϕ II	12	2	9–15	7	1	7–8	10	10	11	10	10–12
solenidion ϕ III	9	2	7–11	12	2	10–16	11	10	10	13	12–13
solenidion ϕ IV	6	1	5–8	6	1	5–7	7	8	4	7	6–7
solenidion ω-1 I	8	1	6–9	8	1	7–9	10	11	6	10	8–11
solenidion ω-3 I	7	1	6–7	6	1	5–8	8	9	–	6	5–6
solenidion ω II	10	2	8–12	9	1	7–10	12	11	7	10	9–11

LAWESI, Lake Lindu, Tomado, 1°18′S 120°05′E, elev. 950 m, 23 January 1972, G.G. Musser, AMNH #240478, HK 86–0814–5; same locality, 29 January 1972, G.G. Musser, AMNH #240479, HK 86–0814–4; Sulawesi, Donggala, Lake Lindu, 1°18′S 120°05′E, January 1972, NAMRU-2 2471, NMNH #502107, HK 88–0829–14; same data, NAMRU-2 2511, NMNH #502112, HK 88–0829–15.

Literature records: on *Eonycteris spelaea* from MYANMAR (formerly BURMA): Tenasserim, Farm Caves (Fain, 1959f [Type series]) and MALAYSIA (Fain, 1963c); on *Harpyionycteris whiteheadi* from the PHILIPPINES (Klompen & OConnor, 1987); on *Rousettus celebensis* from INDONESIA: Sulawesi (Fain, 1963c [*N. microphallus celebensis*]).

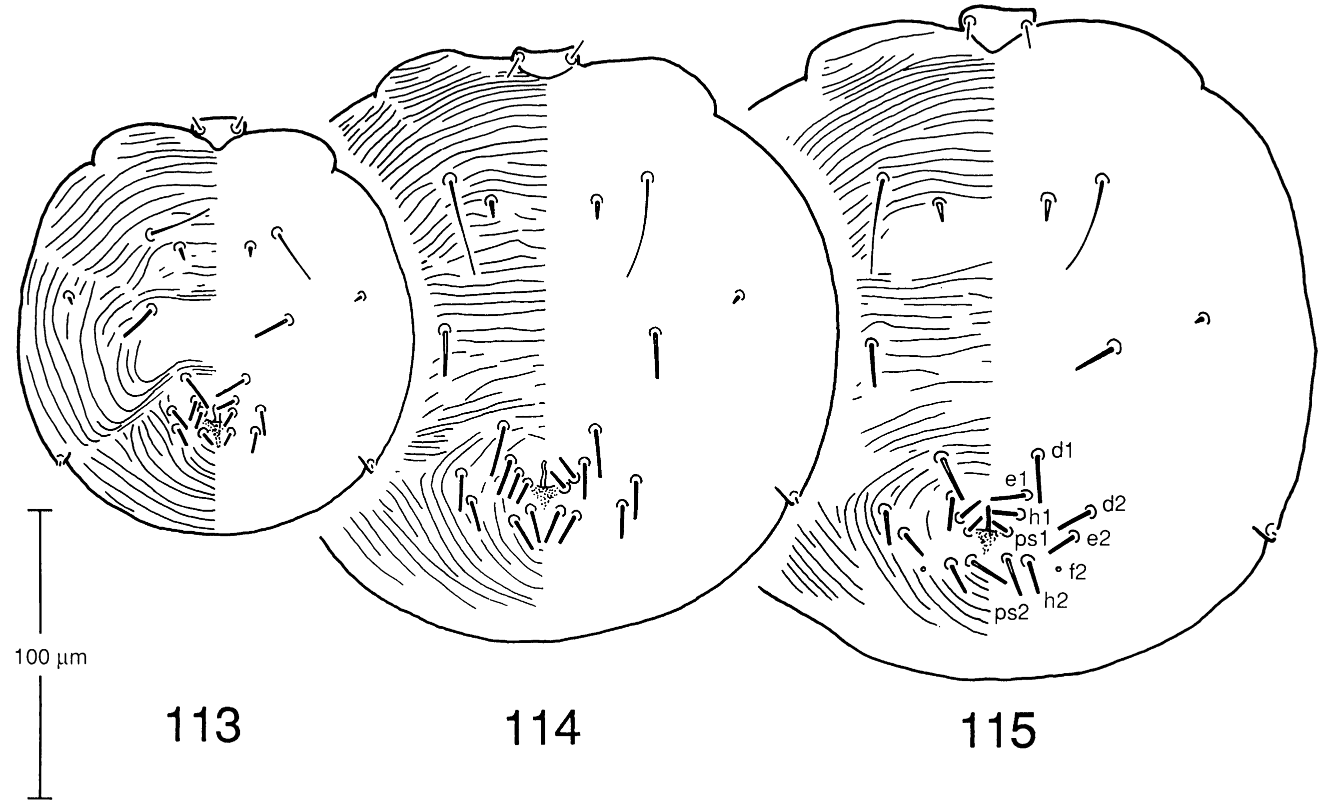
Deposition of specimens: AMNH, BMNH, CUIC,

Table 3. Comparative measurements of male *Nycteridocoptes*.

	heidemanni			*microphallus*			*rousetti*		*notopteris*			*orientalis*	
	N = 15			N = 10			N = 2		N = 6			N = 2	
	av	SD	range	av	SD	range			av	SD	range		
gnathosoma													
length	33	2	30–34	36	2	32–40	34	30	39	3	33–41	40	41
width	32	2	30–35	26	1	24–28	24	28	31	2	28–33	30	42
subcapitular seta	11	2	9–15	14	3	10–19	9	13	12	2	10–15	17	–
body													
length	300	42	250–413	225	16	197–255	195	210	278	24	251–310	253	307
width	214	33	167–266	186	13	164–205	158	164	205	3	199–210	200	236
seta *vi*	34	6	24–47	10	2	7–13	10	11	7	1	5–7	28	28
seta *sci*	9	1	8–12	10	1	9–13	11	12	7	1	7–8	9	9
seta *sce*	55	9	41–69	29	2	25–30	24	21	56	4	51–61	–	46
seta *c 1*	10	2	9–13	9	1	7–11	9	9	8	1	7–10	9	11
seta *c 2*	7	1	5–8	9	1	7–10	9	9	7	1	6–10	7	8
seta *cp*	54	6	43–64	19	4	13–23	14	14	16	4	12–24	65	71
seta *c 3*	45	3	39–53	52	10	39–70	50	44	73	7	66–82	50	–
seta *d 1*	17	2	13–20	19	2	17–22	18	20	15	1	13–16	–	15
seta *d 2*	5	1	3–7	4	1	2–5	6	7	4	1	3–6	7	6
seta *e 1*	4	1	1–6	5	1	4–6	8	8	1	1	1–2	4	4
seta *e 2*	2	1	1–3	3	1	2–4	5	6	1	1	1–2	4	5
seta *f 2*	2	1	1–3	2	1	2–3	4	4	3	1	2–4	4	4
seta *h 1*	3	1	2–5	5	1	4–7	9	9	1	1	1–2	6	6
seta *h 2*	7	1	5–10	10	1	9–11	11	12	10	1	8–12	12	7
seta *h 3*	3	1	2–4	4	1	3–5	6	4	4	1	3–5	5	5
seta *ps 1*	3	1	2–5	6	1	5–7	9	9	2	1	1–3	6	6
seta *ps 2*	8	1	6–10	14	2	10–17	16	17	11	2	9–13	14	17
seta *1 a*	21	4	17–31	18	5	13–25	14	14	16	3	12–19	18	17
seta *3 a*	9	1	7–11	15	2	12–18	12	13	2	1	1–3	4	5
width seta *3 a*	2.8	0.4	2.2–3.1	4.5	0.6	3.8–5.4	4.6	5.0	0.6	0.1	0.5–0.7	0.5	0.5
seta *3 b*	16	2	11–19	11	2	9–17	9	10	17	3	12–21	11	6
seta *4 a*	1	–	–	9	2	6–12	5	4	2	1	1–2	4	2
seta *g*	6	1	4–8	13	1	12–15	13	14	10	1	9–11	5	4
width seta *g*	1.8	0.4	1.4–2.2	4.5	0.5	3.9–5.5	4.4	4.6	1.0	0.2	0.7–1.2	0.5	0.5
genital area													
length	37	9	18–46	19	4	13–24	21	19	32	7	23–38	23	24
width	29	2	24–33	17	4	13–22	18	22	29	5	23–34	28	29
coxal apodemes I	73	8	62–83	82	8	62–91	72	77	102	3	99–107	93	99
coxal apodemes II	76	11	61–93	95	6	83–105	75	79	106	3	102–109	91	92
coxal apodemes III	48	7	36–55	46	4	38–50	46	46	54	5	48–61	47	57
coxal apodemes IV	44	3	41–52	43	3	39–47	42	45	50	4	45–55	46	46
leg I	65	5	57–73	61	10	51–80	51	53	69	7	58–77	49	74
leg II	68	5	59–77	64	8	56–84	51	57	72	3	65–76	61	65
leg III	63	5	55–72	68	8	58–80	53	53	65	4	62–73	51	66
leg IV	55	4	48–62	62	7	54–77	48	47	57	5	47–61	49	58
seta *pR* I	37	3	30–42	33	12	20–55	34	45	33	3	29–36	37	–
seta *pR* II	46	7	29–57	50	11	40–73	32	39	55	11	41–70	33	–
seta *sR* III	28	5	20–35	31	12	12–51	36	33	37	6	31–48	28	–
seta *vF* I	26	2	23–29	27	3	22–31	22	24	28	2	26–29	24	–
seta *vF* II	53	5	42–60	56	5	49–64	43	52	70	5	63–74	47	–
seta *cG* I	47	5	39–52	42	5	33–48	37	41	51	9	38–64	33	50
seta *mG* I	25	3	22–28	32	5	24–39	22	36	28	3	22–31	21	–
seta *d* III	215	19	186–248	264	20	228–228	234	229	286	26	256–302	242	260
solenidion σ I	5	1	4–6	4	1	2–5	3	3	5	1	5–7	4	–
solenidion ϕ I	18	1	16–19	18	2	16–22	17	16	21	2	18–23	19	20
solenidion ϕ II	21	1	20–23	25	3	22–31	21	21	24	2	21–28	27	25
solenidion ϕ III	11	1	9–12	11	2	8–13	7	9	8	1	6–9	9	–
solenidion ϕ IV	5	1	4–6	4	1	2–6	4	3	12	3	10–17	12	6
solenidion ω-1 I	16	1	15–17	16	1	15–17	16	15	18	2	16–21	19	20
solenidion ω-3 I	12	1	1–14	14	1	12–16	13	12	17	1	15–18	17	14
solenidion ω II	18	1	16–19	21	2	19–24	20	20	19	5	12–24	23	19
ambulacral stalk I	14	1	12–16	19	2	18–22	17	17	23	2	21–25	21	–
ambulacral stalk II	14	1	13–16	20	2	18–23	18	17	22	2	20–24	20	27

Table 3 (continued).

	heidemanni			*microphallus*			*rousetti*		*notopteris*			*orientalis*	
	N=15			N=10			N=2		N=6			N=2	
	av	SD	range	av	SD	range			av	SD	range		
ambulacral stalk III	15	1	14–17	16	4	9–21	13	14	13	3	11–18	24	27
ambulacral stalk IV	17	2	14–20	21	2	18–23	20	20	24	1	23–26	25	26



FIGS. 113–115. *Nycteridocoptes microphallus,* immatures, dorsal view of the larva (113), protonymph (114), and male tritonymph (115).

FMNH, IRSN, MAK, NMNH, OSU, PNC, UMMZ, WAM, and ZIAC.

Nycteridocoptes rousetti Fain, 1958

Nycteridocoptes rousetti Fain, 1958: 245.

Only the male has been described (Fain, 1958). During this study all other life stages were collected. They strongly resemble the corresponding stages in *N. microphallus. Nycteridocoptes rousetti* differs from *N. microphallus* by the absence of a lateral notch in the posterior median shield in the male and some small differences in measurements for both females and males (setae *ps 1* and *ps 2* of the female, and setae *e 1* and *ps 1* of the male are distinctly longer than in *N. microphallus;* Tables 2, 3).

Males and female tritonymphs were found in the mouth and on the wings of the host, the other stages only on the wings.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus angolensis* (Bocage, 1898). CAMEROON: Mont Koupee, 4°47'N 9°43'E, elev. 1600 m, 6 December 1966, Eisentraut, MAK #69.481, HK 85–0621–10; ZAIRE: HAUT-ZAIRE, 20 mi S Irumu, Mt. Hoyo Cave, 1°13'N 28°49'E, 4 May 1955, W.L. Schmitt & E.W. Baker, NMNH #301708, HK 88–0831–6; same data, NMNH #301712, HK 88–0901–1.

Rousettus lanosus Thomas, 1906. ETHIOPIA: KEFA, Ghera Region, Afallo, 7°41'N 36°20'E, 2 May 1971, M. Desfayes, FMNH #105409, HK 86–0226–4.

Rousettus madagascariensis Grandidier, 1928. MADAGAS-

CAR: FIANARANTSOA, 4 km E Kianjavato, ca 21°23'S 47°54'E, elev. 125 m, 3 August 1988, G.K. Creighton (GKC 2748), NMNH #449274, HK 88–0926–1.

Literature records: on *Rousettus aegyptiacus* (Geoffroy, 1810) (Type host) from ZAIRE: KIVU, Katana, Mahyusa (Fain, 1958 [Type series]); ZAIRE (BAS-ZAIRE and KIVU) (Fain, 1959f).

Deposition of specimens: FMNH, MAK, NMNH, and UMMZ.

The sister group of the *N. microphallus*/*N. rousetti* lineage (node 18) is diagnosed in the larva, protonymph, and male tritonymph by the absence or vestigial character of setae *cp* (84, 86); in the male by the presence of setae *e* III (reversal) (190), and the loss of setae *r* IV (195).

As mentioned previously in the discussion of the results of the phylogenetic analyses, the large amount of missing data for *N. malayi* results in very poor resolution within the sister group of the *heidemanni-rousetti* lineage (compare Figs. 51, 52). Seven lineages, six of which are monobasic, arise at node 18.

Nycteridocoptes malayi Fain, 1963

Nycteridocoptes malayi Fain, 1963c: 256.

Diagnosed in the larva by the elongation of setae *sci* (length > 4 X width) (65); in the female by the presence of spines lateral to the anus (39).

The species was described from a single female (Fain, 1963c). During this study one more female and a few larvae were collected. The dorsum of the larva shows some poorly defined scale-like striation and the perianal setae are subequal. The female is characterized by the large proportion of the dorsum covered with spines.

The female produces a large cyst in the wing membrane.

Material examined: Larva and female.

Host (Chiroptera: Pteropodidae) and locality: *Aethalops alecto* (Thomas, 1923). Type host. MALAYSIA, before 1970, Yong Ghong Chong, AMNH #232510, HK 86–0814–7.

Literature records: on *Aethalops alecto* from MALAYSIA: PAHANG, Cameron Highlands, Mt. Brinchang (Fain, 1963c [Type series]).

Deposition of specimens: UMMZ.

Nycteridocoptes **notopteris** nov. spec.
(Figs. 10, 11, 18, 19, 116–121)

Diagnosed in the protonymph by the addition of a pair of well developed setae *f 2* (reversal) (99, 100); in the female tritonymph by the loss of spines or scales on the dorsum (reversal) (29), and the transformation of setae *3 a* to filiform (reversal) (129); in the female by the loss of spines between setae *c 1* and the anus (reversal) (37, 38); in the male by the shape transformations of setae *g* to filiform (reversal) (126), solenidia σ I to spine-like structures (174), and setae *f* IV to spines (188), and by the loss of setae *e* III (190).

Larva: Dorsum striate. Setae *e 2* and *h 2* (to a lesser degree setae *d 2*) much smaller than setae *d 1*, *e 1*, and *h 1*. Setae *sci* and *c 2* very small, alveoli of setae *c 3* very large, but setae not observed.

Protonymph: Setae *h 2* and *ps 2* subequal to setae *d 1*, distinctly longer than the other opisthosomal setae. Setae *f 2* short, setae *h 3* represented by vestigial alveoli or minute setae. Setae *g* very small.

Female tritonymph (Figs. 116, 117): Setae *g* spine-like, setae *3 a* filiform, setae *4 a* minute. Setae *sce* long spines, setae *h 3* small.

Male tritonymph: Only a single, damaged specimen available. Resembling the protonymph. Setae *3 a* added, setae *h 3* and *4 a* not observed.

Female (Figs. 118, 119): Spine pattern reduced to a narrow band stretching from leg III, between setae *c 1* and *sci*, to leg III on the other side. Setae *d 2*, *e 2*, and *h 3* relatively small. Setae *4 a* present. Measurements in Table 2.

Male (Figs. 10, 11, 18, 19, 120, 121): Setae *sce* long and spine-like. Median apodeme well developed. Setae *3 a* and *4 a* minute. Leg setae *d* and *e* IV represented by small protuberances. Measurements in Table 3.

Males and female tritonymphs were found in the mouth and on the wing, the other stages only on the wings. Infestation levels were low and pathology was not observed.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Notopteris macdonaldi* Gray, 1859. Type host. FIJI: VITI LEVU Is., Suva, Colombo Cave, 18°08'S 178°25'E, 22 March 1950, F.C. Wonder, FMNH #31199, HK 87–0904–3 (holotype female); same data, FMNH #31198, HK 87–0904–1 (allotype male); FMNH #31202, HK 87–0904–2; FMNH #31235, HK 89–0715–3; FMNH #31246, HK 89–0715–2; NEW CALEDONIA: Sarramea, Col d'Amieu, Reserve Forestiere, 21°37'S 165°48'E, August 1986, C.A. Ross & S.L. Brochot, NMNH #463929, HK 88–0827–6; same data, NMNH #463930, HK 88–0827–5.

Etymology: The specific name is derived from the generic name of the type host, *Notopteris macdonaldi.*

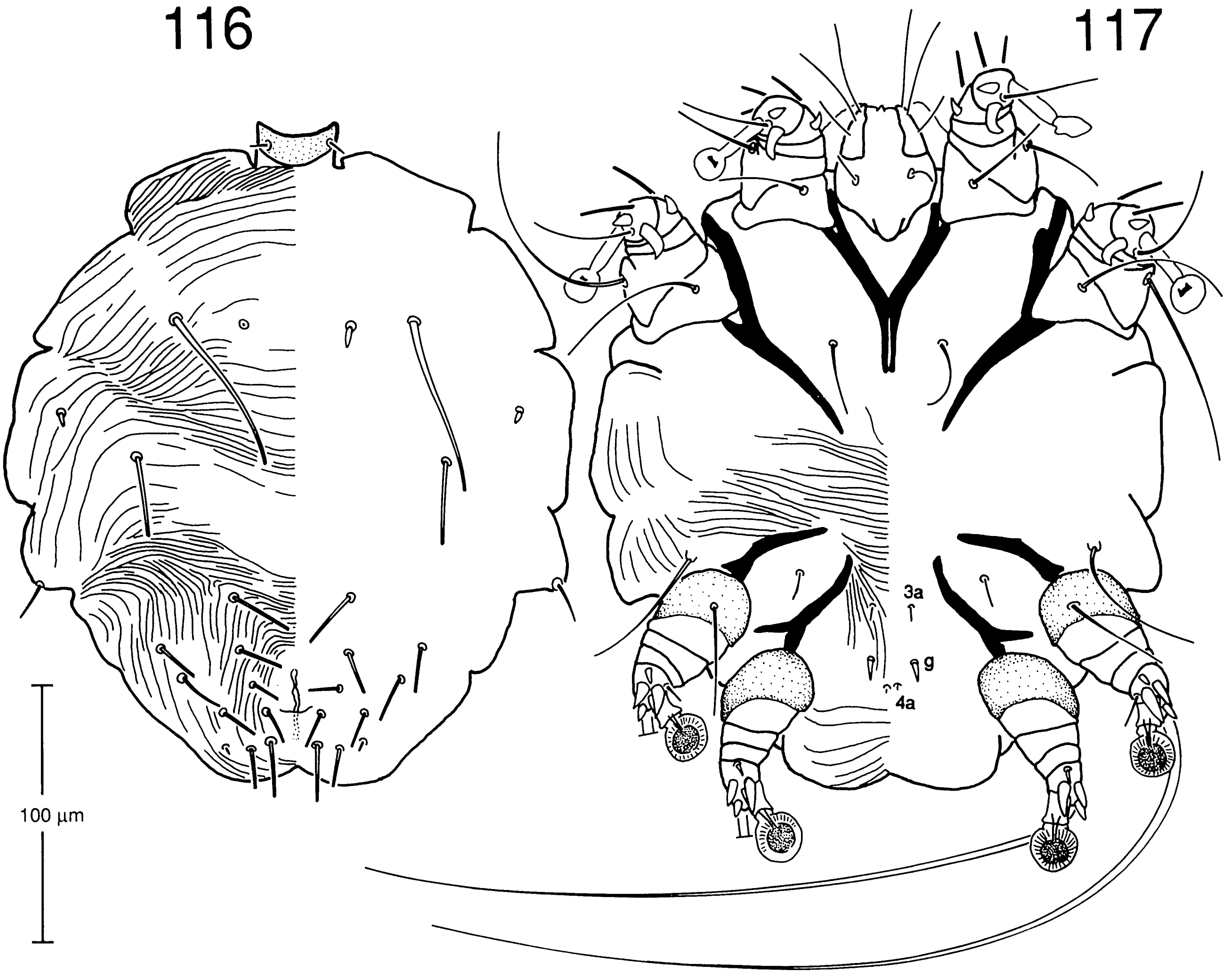
Deposition of specimens: Holotype female and allotype male in FMNH. Paratypes in BMNH, FMNH, IRSN, NMNH, OSU, and UMMZ.

Nycteridocoptes lavoipierrei Fain, 1958

Nycteridocoptes lavoipierrei Fain, 1958: 244.

Diagnosed in the protonymph and male tritonymph by the shape of setae *sci* (thin spine-like rods with bifurcate tips) (66), and the addition of well developed setae *f 2* (reversal) (99, 100); in the female by the loss of spines between setae *d 1* and the anus (reversal) (38), and the presence of spines lateral to the anus (39); in the male by the shape transformation of setae *g* to filiform (reversal) (126), and solenidia σ I to spine-like structures (174).

Only the male has been described previously (Fain, 1958, 1959f). The larva, protonymph, and male tritonymph are characterized by the size distribution of the perianal setae (the posterior setae are 1/2 to 2/3 the size of setae *d 1*), by the addition of setae *f 2* in the protonymph, and by the complete absence of setae *h 3*. The female closely resembles that of *N. asiaticus* (Figs. 122, 123). Differences include shorter setae *sce* (11–12 vs. 25 μm) and a spine zone lateral to the anus that



FIGS. 116, 117. *Nycteridocoptes notopteris*, female tritonymph, dorsal (116) and ventral (117) view.

extends beyond the posterior end of the anus (to the posterior end of the anus in *N. asiaticus*). Measurements in Table 4.

The ecology of *N. lavoipierrei* generally resembles that of *N. notopteris*. On one *Rousettus madagascariensis* four females were found closely associated with a hole in the wing membrane. However, it is not clear to what extent the presence of the females contributed to the wing damage.

Material examined: Larva, protonymph, male tritonymph, female, and male.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus angolensis* (Bocage, 1898). CAMEROON: Mont Koupee, 4°47′N 9°43′E, 6 December 1966, Eisentraut, MAK #69.481, HK 85–0621–10.

Rousettus lanosus Thomas, 1906. UGANDA: Ruwenzori range, Old Kalangi, 0°48′S 30°54′E, 5 February 1925, E. Heller, NMNH #260141, HK 88–0902–10.

Rousettus madagascariensis Grandidier, 1928. MADAGASCAR: FIANARANTSOA, 1 km N Kianjavato, 21°23′S 47°52′E, elev. 300 m, July–August 1987, L.H. Emmons (LHE 658), NMNH #448882, HK 88–0105–1; FIANARANTSOA, 4 km E Kianjavato, ca 21°23′S 47°54′E, elev. 125 m, 3 August 1988, G.K. Creighton (GKC 2748), NMNH #449274, HK 88–0926–1; same locality and date, GKC 2752, NMNH #449275, HK 88–0922–1; GKC 2753, NMNH #449276, HK 88–0922–2; GKC 2754, NMNH #449277, HK 88–0922–3; GKC 2755, NMNH #449278, HK 88–0922–4.

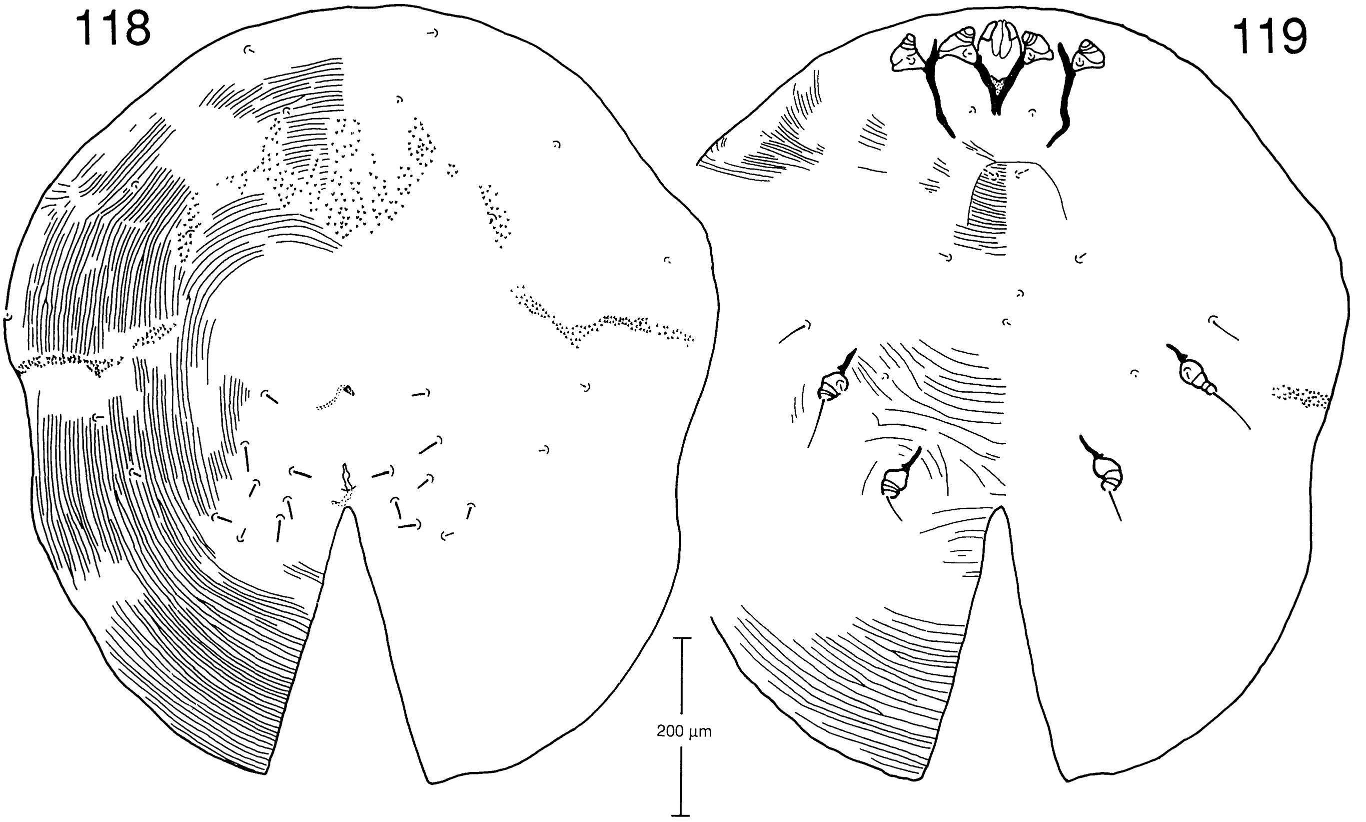
Literature records: on *Rousettus aegyptiacus* (Geoffroy, 1810) (Type host) from ZAIRE: KIVU, Katana, Mahyusa (Fain, 1958 [Type series]); ZAIRE (BAS-ZAIRE and KIVU) (Fain, 1959f).

Deposition of specimens: MAK, NMNH, and UMMZ.

Nycteridocoptes asiaticus Fain, 1959
(Figs. 122, 123)

Nycteridocoptes asiaticus Fain, 1959f: 349.

Diagnosed in the female tritonymph by the presence of small spines on the dorsum (30), and the transformation of setae *g* and *3 a* to filiform (reversal) (125, 129); in the male by the presence of a lateral notch in the posterior median shield (16). In addition this species shares all the derived character states mentioned for *N. lavoipierrei*.



FIGS. 118, 119. *Nycteridocoptes notopteris*, female, dorsal (118) and ventral (119) view.

This species strongly resembles *N. lavoipierrei.* Males of *N. asiaticus* differ from those of *N. lavoipierrei* by the presence of a lateral notch of the posterior median shield and a short, instead of a long, median apodeme. Differences between the females have been listed in the discussion of *N. lavoipierrei.*

The male is the only developmental stage described previously (Fain, 1959f). The larvae, protonymphs, and male tritonymphs are highly similar to those of *N. lavoipierrei.* The female tritonymph resembles that of *N. macrophallus* (see Fain, 1959f) but with fewer anterior spines. It adds a pair of short setae *h 3*. Most of the dorsum of the female is covered by spines (Figs. 122, 123), although the spine zones are less well developed than in *N. lavoipierrei.* The perianal setae are subequal in length, spine-like with bifurcate tips. Measurements in Table 4.

Site choice as in *N. notopteris.* The observed infestation levels were always low, with no apparent pathology.

Material examined: All stages.

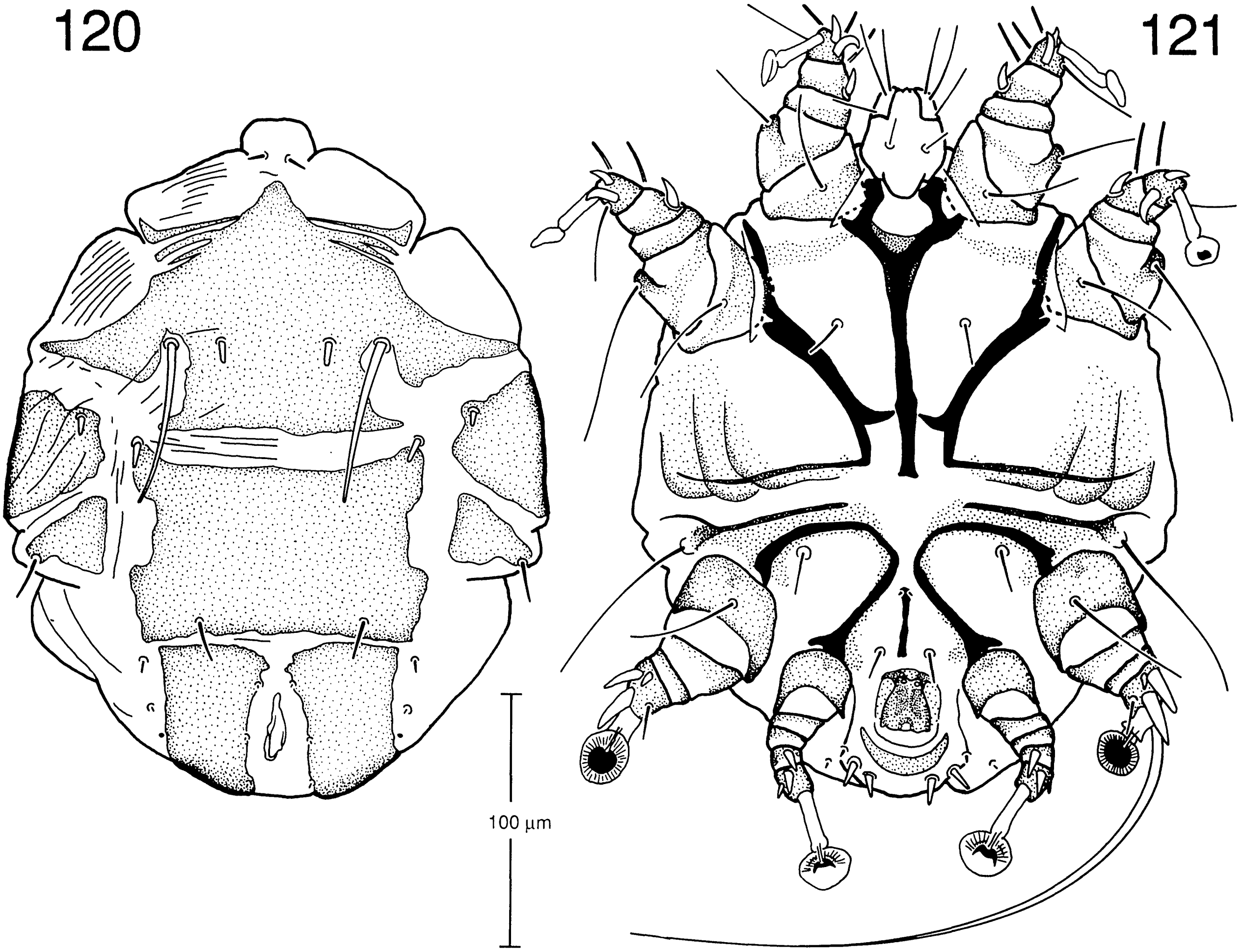
Hosts (Chiroptera: Pteropodidae) and localities: *Eonycteris spelaea* (Dobson, 1871). Type host. INDONESIA: LOMBOK, Batu Koq, 8°19'S 116°26'E, 7 October 1987, D. Kitchener (P 409), WAM, HK 88–0406–1; same locality, 31 October 1987, D. Kitchener (L 201), WAM, HK 88–0410–1; LOMBOK, Pelangan, 8°19'S 116°26'E, 13 October 1987, L 300, WAM, HK 88–0413–1; MALAYSIA: PAHANG, Bentong, Bukit Chintamani, 13 October 1982, F.S. Lukoschus; PAHANG, Raub Cave, 13 May 1979, Rudnick, IMR; PHILIPPINES: NEGROS ORIENTAL, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 10 May 1987, P.D. Heideman (PDH 3569), NMNH, HK 87–0510–1; NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 22 February 1987, L.R. Heaney (LRH 2907), NMNH #459070, HK 87–0222–3; NEGROS ORIENTAL, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 24 October 1982, PDH 1017, UMMZ #158941, HK 84–0411–1; same locality, 24 March 1983, PDH 1673, UMMZ #158944, HK 84–0329–1.

Eonycteris robusta Miller, 1913. PHILIPPINES: NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 6 May 1983, PDH 1816, UMMZ #158917, BMOC 83–1600–96.

Aethalops alecto (Thomas, 1923). MALAYSIA: before 1970, Yong Ghong Chong, AMNH #232511, HK 86–0814–6.

Penthetor lucasi (Dobson, 1880). MALAYSIA: SELANGOR, Fraser's Hill, 3°42'N 101°45'E, elev. 1600 m, 17 April 1969, Yong Ghong Chong, AMNH #216743, HK 86–0814–1; same data, AMNH #216744, HK 86–0814–2.

Rousettus amplexicaudatus (Geoffroy, 1810). INDONESIA: LOMBOK, Suranadi, 8°33'S 116°14'E, 26 September 1987, L 19, WAM, HK 88–0420–1; SUMBAWA, Batu Tering, 8°48'S 117°22'E, 25 May 1988, D. Kitchener (S 370), WAM, HK 89–0215–1; PHILIPPINES: BOHOL, 1 km S, 1 km E Bilar, 9°44'N 124°07'E, elev. 320 m, 19 June 1987, PDH 3684, NMNH, HK 87–0619–9; LEYTE, 10 km N, 4 km E Baybay,



FIGS. 120, 121. *Nycteridocoptes notopteris,* male, dorsal (120) and ventral (121) view.

10°47′N 124°50′E, elev. 700 m, 20 March 1987, J.S.H. Klompen (JSHK 28), NMNH #459278, HK 87–0320–3; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21′N 123°11′E, elev. 850 m, 12 February 1983, PDH 1515, UMMZ #161616, HK 85–0730–2; NEGROS ORIENTAL, Dumaguete, 9°18′N 123°18′E, elev. 5 m, 29 September 1982, PDH 889, UMMZ #161535, HK 85–0809–1; same locality, 29 September 1982, PDH 890, UMMZ #161537, HK 85–0808–1; 24 October 1982, PDH 1006, UMMZ #161553, HK 86–0309–1; 30 December 1982, PDH 1338, UMMZ #161600, HK 85–0815–2; 26 January 1983, PDH 1465, UMMZ #161614, HK 85–0725–2; 26 January 1983, PDH 1466, UMMZ #161615, HK 85–0725–3; 26 February 1983, PDH 1537, UMMZ #161625, HK 86–0312–2; 24 April 1983, PDH 1779, UMMZ #161665, HK 86–0413–1; 25 February 1987, D. Kitchener (P 7), NMNH #459298, HK 87–0225–4; ROMBLON, Sibuyan Is., 1 km S, 1 km E Magdiwang, Tampayan, 12°29′N 122°31′E, elev. 10 m, 24 May 1989, S.M. Goodman (SMG 3048), FMNH #136987, HK 89–0711–9.

Rousettus leschenaulti (Desmarest, 1820). PAKISTAN: NORTHWEST FRONTIER, Malakand Agency, Malakand, 34°34′N 71°56′E, 19 September 1966, C.J. Phillips 572, NMNH #429338, HK 88–0901–6.

Literature records: on *Eonycteris spelaea* from MYANMAR: TENASSERIM, Farm Caves (Fain, 1959f [Type series]); on *Rousettus leschenaulti* from THAILAND (Uchikawa & Suzuki, 1980).

Deposition of specimens: AMNH, BMNH, CUIC, FMNH, MAK, IRSN, NMNH, OSU, PNC, UMMZ, WAM, and ZIAC.

Nycteridocoptes macrophallus Fain, 1958
(Figs. 26, 27, 36, 37, 124, 125)

Nycteridocoptes macrophallus Fain, 1958: 245.

Diagnosed in the male tritonymph by the vestigial or absent condition of setae *cp* (87); in the male by a strongly elongated aedeagus (134), and the loss of the median apodeme (reversal) (151). In addition *N. macrophallus* shares the majority of derived states listed for *N. asiaticus*. It does not share the addition of well developed setae *f 2* (99, 100) in the protonymph and male tritonymph (these setae are absent or vestigial in those stages).

The female tritonymph and the male have been described previously (Fain, 1958, 1959f). The other immature stages differ from those of *N. lavoipierrei* by the absence of setae *f 2,*

Table 4. Comparative measurements of female *Nycteridocoptes*. 2.

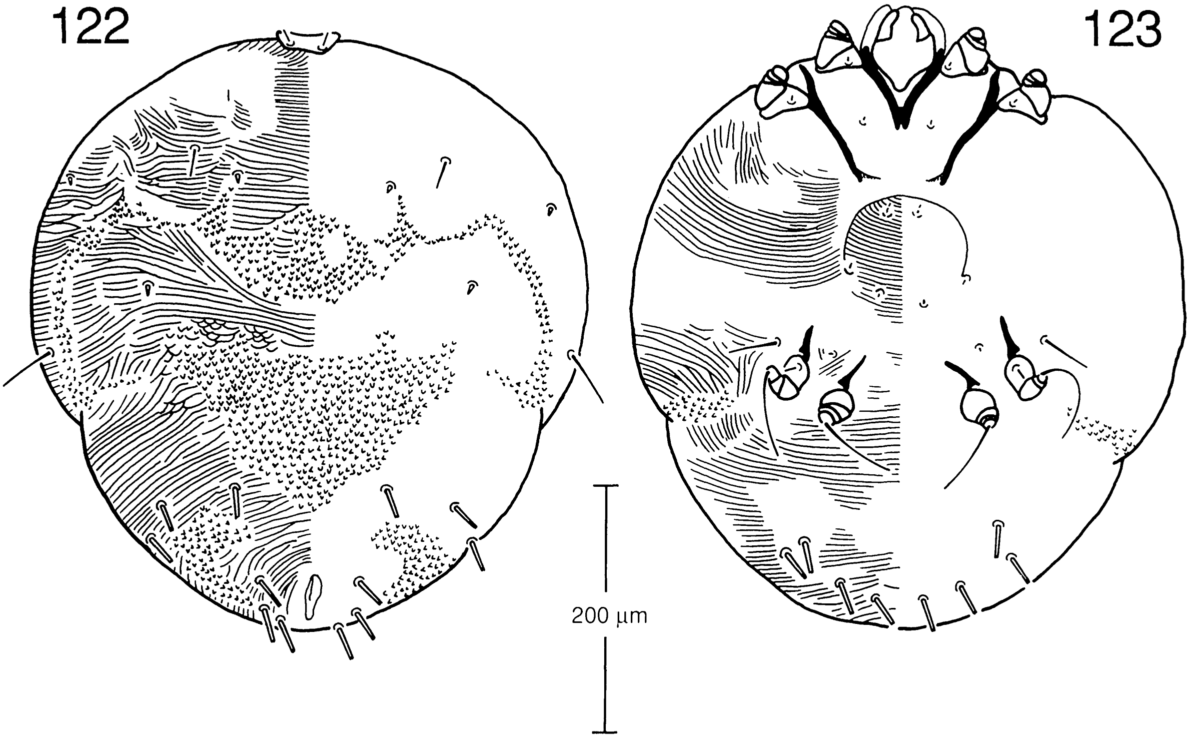
	lavoipierrei N=3		*asiaticus* N=2		*macrophallus* N=2		*orientalis* N=2		*miniopteri* N=1	*eyndhoveni* N=1
	av	range								
gnathosoma										
length	66	–	–	59	51	69	65	68	91	82
width	49	46–52	–	54	52	55	60	59	67	62
body										
length	558	417–644	–	494	–	363	–	–	–	–
width	507	409–556	–	563	–	375	–	–	–	–
seta *vi*	8	6–10	–	8	8	4	–	–	–	8
seta *sci*	6	4–8	–	6	5	6	7	5	5	5
seta *sce*	11	11–12	–	25	4	7	16	12	15	18
seta *c 1*	8	6–9	–	6	7	6	7	5	4	4
seta *c 2*	5	4–6	–	4	3	3	4	4	4	3
seta *cp*	33	30–37	–	42	4	12	27	22	20	16
seta *c 3*	22	17–25	25	38	4	7	18	15	36	27
seta *d 1*	29	29–30	26	24	27	28	42	–	18	27
seta *d 2*	28	27–29	24	23	20	19	11	–	8	18
seta *e 1*	29	27–31	22	30	25	28	38	–	28	24
seta *e 2*	30	27–31	27	26	19	20	21	17	11	23
seta *f 2*	30	28–33	27	24	14	20	16	12	13	17
seta *h 1*	32	31–33	27	26	25	26	37	33	25	26
seta *h 2*	30	30–31	27	30	21	22	16	20	15	21
seta *h 3*	26	26–27	–	23	16	17	6	–	8	11
seta *ps 1*	30	29–31	26	26	22	23	34	31	25	22
seta *ps 2*	30	27–32	24	27	19	18	20	20	16	20
seta *1 a*	4	–	–	4	3	3	6	–	11	11
seta *3 a*	9	8–10	–	8	4	4	5	–	6	9
seta *3 b*	3	3–4	–	4	2	2	3	3	3	3
seta *4 a*	3	2–3	–	3	1	2	3	–	4	3
seta *g*	10	10	–	6	3	3	7	–	8	9
copulatory cone	5	5	–	–	–	–	–	–	–	–
bursa copulatrix	88	–	–	–	139	206	–	–	–	–
coxal apodemes I	58	54–62	–	64	63	62	69	67	79	75
coxal apodemes II	96	95–97	–	102	–	96	111	109	113	111
coxal apodemes III	37	34–38	33	36	27	37	45	38	32	38
coxal apodemes IV	33	29–35	30	32	–	33	35	26	27	31
leg I	47	46–47	–	46	43	44	50	56	60	55
leg II	48	46–49	–	47	37	41	53	60	51	45
leg III	46	45–46	44	41	36	33	49	48	37	46
leg IV	40	37–42	41	38	34	29	43	44	31	40
seta *sR* III	5	4–6	6	14	4	5	10	8	2	10
seta *d* III	70	67–72	68	72	42	47	61	37	59	61
seta *d* IV	64	60–66	66	73	36	59	54	47	70	57
solenidion σ I	7	6–7	–	–	10	8	–	–	6	7
solenidion ϕ I	11	10–11	–	10	9	9	12	11	11	9
solenidion ϕ II	11	9–12	–	14	9	11	16	13	11	11
solenidion ϕ III	10	9–11	11	11	12	11	16	13	9	13
solenidion ϕ IV	10	9–11	9	9	9	9	13	13	6	9
solenidion ω-1 I	11	10–11	–	12	7	8	10	11	9	10
solenidion ω-3 I	7	7	–	8	5	7	7	6	7	8
solenidion ω II	13	13–14	–	13	9	10	14	14	11	11

and by perianal setae that are subequal in length (the posterior perianal setae are smaller than the anterior ones in *N. lavoipierrei*). The pattern of spines in the female (Figs. 124, 125) resembles that of *N. asiaticus* but the median dorsal spine zone and the zones lateral to the anus are smaller and made up of much smaller, poorly developed spines (Fig. 124: A, B, C). All perianal setae subequal in size. Measurements in Table 4.

The observed site choice in *N. macrophallus* was the same as in *N. notopteris*. Pathology was not observed.

Material studied: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus aegyptiacus* (Geoffroy, 1810). Type host. CYPRUS: Paralimni, April 1968, G. Walson, NMNH #520996, HK 88–0829–11; EGYPT: CAIRO, Cairo, 30°03'N 31°15'E, 2 February 1984, S.M. Goodman (SMG 809), UMMZ #161044, HK 84–1123–



Figs. 122, 123. *Nycteridocoptes asiaticus,* female, dorsal (122) and ventral (123) view.

1; same locality and date, SMG 810, UMMZ #161045, HK 84–1119–1; SMG 811, UMMZ #161046, HK 84–1127–1.

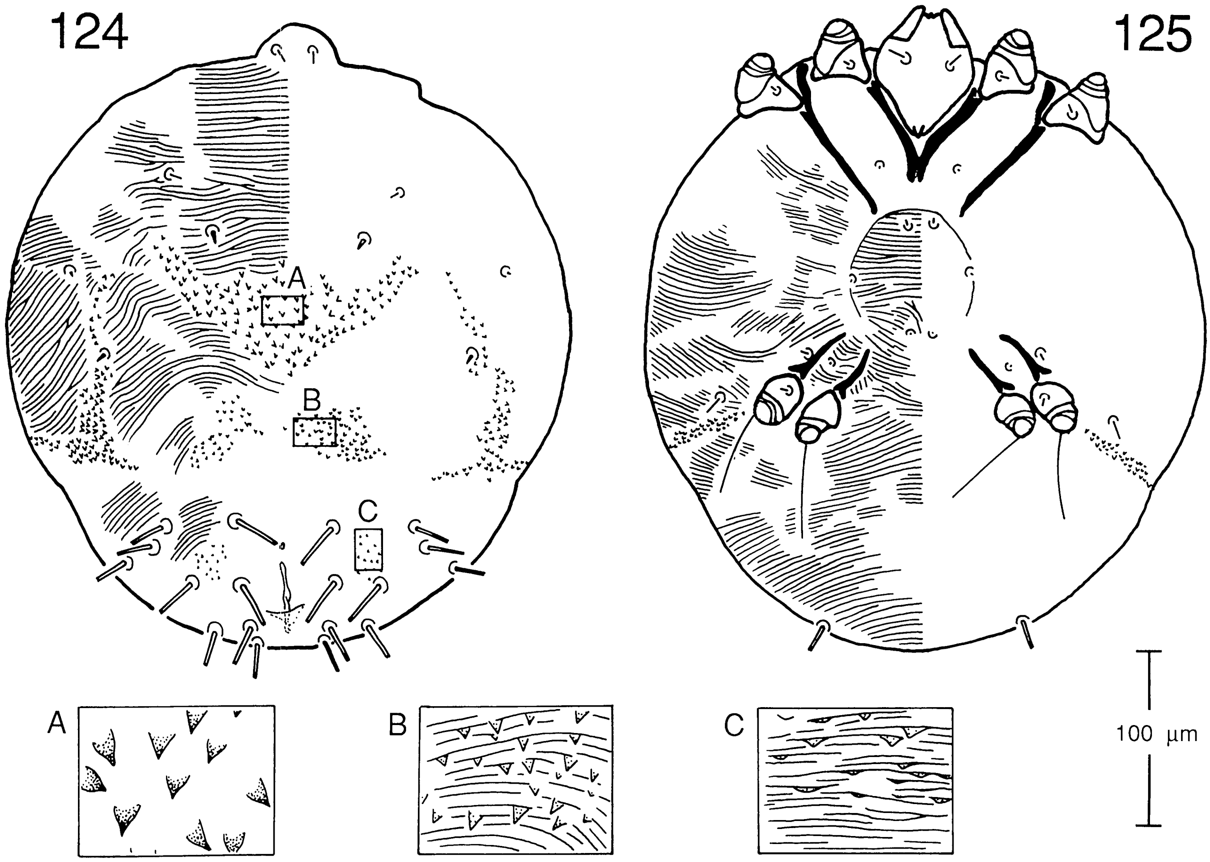
Rousettus amplexicaudatus (Geoffroy, 1810). INDONESIA: Lombok, Suranadi, 8°33'S 116°14'E, 26 September 1987, D. Kitchener (L 19), WAM, HK 88–0420–1; Sumbawa, Batu Tering, 8°48'S 117°22'E, 25 May 1988, D. Kitchener (S 370), WAM, HK 89–0215–1; PAPUA NEW GUINEA: Madang, 9 mi N Madang, Maiwara, 21 July 1969, W.Z. Lidecker, MVZ #138510, HK 86–0520–2; Madang, Madang, 23 July 1969, J. Kikhawa, MVZ #138505, HK 86–0520–1; PHILIPPINES: Bohol, 1 km S, 1 km E Bilar, 9°44'N 124°07'E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3707), NMNH #459273, HK 87–0618–8; same locality, 19 June 1987, P.D. Heideman (PDH 3684), NMNH, HK 87–0619–9; Leyte, 7 km N Baybay, 10°45'N 124°48'E, elev. 10 m, 27 March 1987, J.S.H. Klompen (JSHK 37), NMNH #459279, HK 87–0327–2; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 12 February 1983, PDH 1515, UMMZ #161616, HK 85–0730–2; Negros Oriental, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 20 July 1982, PDH 611, UMMZ #161493, HK 86–0308–1; same locality, 23 August 1982, PDH 737, UMMZ #161494, HK 86–0424–1; 23 August 1982, PDH 746, UMMZ #161501, HK 86–0424–2; 23 August 1982, PDH 750, UMMZ #161504, HK 86–0425–1; 24 October 1982, PDH 1006, UMMZ #161553, HK 86–0309–1; 29 November 1982, PDH 1149, UMMZ #161577, HK 86–0403–1; 30 December 1982, PDH 1339, UMMZ #161601, HK 85–0815–1; 30 December 1982, PDH 1338, UMMZ #161600, HK 85–0815–2; 26 January 1983, PDH 1465, UMMZ #161614, HK 85–0725–2; 26 January 1983, PDH 1466, UMMZ #161615, HK 85–0725–3 (wash); 31 May 1983, PDH 1973, UMMZ #161678, HK 85–0829–3; 31 May 1983, PDH 1975, UMMZ #161679, HK 85–0829–1; 20 February 1987, E.A. Rickart (EAR 1251), NMNH #458509, HK 87–0220–7; 25 February 1987, D. Kitchener (P 7), NMNH #459298, HK 87–0225–4; 10 May 1987, EAR 1565, NMNH #459293, HK 87–0510–2.

Rousettus lanosus Thomas, 1906. KENYA: Rift Valley, Mt. Menengai, 0°14'S 36°06'E, 8 June 1948, Hoogstraal et al., FMNH #85450, HK 86–0226–12.

Rousettus madagascariensis Grandidier, 1928. MADAGASCAR: Fianarantsoa, 1 km N Kianjavato, 21°23'S 47°52'E, elev. 300 m, 10 August 1987, G.K. Creighton (GKC 2571), NMNH #448880, HK 87–1122–1; same locality and date, GKC 2572, NMNH #448881, BMOC 87–1500–25; Fianarantsoa, 4 km E Kianjavato, ca 21°23'S 47°54'E, elev. 125 m, 3 August 1988, GKC 2748, NMNH #449274, HK 88–0926–1; same locality and date, GKC 2753, NMNH #449276, HK 88–0922–2; GKC 2754, NMNH #449277, HK 88–0922–3; GKC 2755, NMNH #449278, HK 88–0922–4.

Eonycteris robusta Miller, 1913. PHILIPPINES: Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 6 May 1983, PDH 1816, UMMZ #158917, BMOC 83–1600–96.

Eonycteris spelaea (Dobson, 1871). INDONESIA: Lombok, Batu Koq, 8°19'S 116°26'E, 31 October 1987, L 201, WAM, HK 88–0410–1; Sumbawa, Teluk Santong, 8°44'S 117°54'E, 21 May 1988, S 294, WAM, HK 89–0208–1; PHILIPPINES: Leyte, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 26 March 1987, R.B. Utzurrum (RBU 155), NMNH, HK 87–



FIGS. 124, 125. *Nycteridocoptes macrophallus*, female, dorsal (124) and ventral (125) view. A, B, and C illustrate the spine structure for different parts of the dorsum.

0326–6; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 4 October 1982, PDH 920, UMMZ #158918, BMOC 83–1600–39; NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 22 February 1987, LRH 2907, NMNH #459070, HK 87–0222–3.

Literature records: on *Rousettus aegyptiacus* from ZAIRE: KIVU, Katana, Mahyusa (Fain, 1958 [Type series]); ZAIRE (BAS-ZAIRE, DJONDA and KIVU) (Fain, 1959f); on *Rousettus amplexicaudatus* from MYANMAR (Fain, 1959f); on *Eonycteris spelaea* from MYANMAR (Fain, 1959f) and MALAYSIA (KUALA LUMPUR and SARAWAK) (Fain, 1963c).

Deposition of specimens: BMNH, CUIC, FMNH, IRSN, MAK, NMNH, OSU, PNC, UMMZ, WAM, and ZIAC.

Nycteridocoptes pteropi Rodhain & Gedoelst, 1921

Nycteridocoptes pteropi Rodhain & Gedoelst, 1921: 51.
Nycteridocoptes pteropodi Rodhain, 1923: 17.

Diagnosed in the protonymph and male tritonymph by the addition of well developed setae *h 3* (reversal) (114). In addition *N. pteropi* shares most of the derived character states listed for *N. asiaticus*. It does not share the transformation of setae *g* and *3 a* in the female tritonymph and male to filiform (125, 126, 129) (these setae remain spine-like in *N. pteropi*).

The larva, female tritonymph, female, and male were described in some detail by Rodhain (1923). The male was redescribed by Fain (1958) based on new material.

Nycteridocoptes pteropi occurs in the same general sites as *N. notopteris*. In cases of high infestation levels, multiple females may occupy a single cyst on the body or in the membrane over the arm bones (Rodhain, 1923). Even with numerous cysts present, the bat hosts usually do not seem to be negatively affected, unless very old or sick (Rodhain, 1923).

Material examined: Protonymph, female tritonymph, and male.

Host (Chiroptera: Pteropodidae) and locality: *Eidolon helvum* (Kerr, 1792). Type host. ETHIOPIA: ILUBABOR, Gambela, 8°15'N 34°35'E, 3 December 1973, J.S. Ash, NMNH #462720, HK 88–0823–9; same locality, 13 December 1973, J.S. Ash, NMNH #497602, HK 88–0823–8; 14 December 1973, J.S. Ash, NMNH #520895, HK 88–0828–6.

Literature records: on *Eidolon helvum* from ZAIRE: BAS-ZAIRE, Boma and Kinshasa (Rodhain & Gedoelst, 1921 [Type series]; Fain, 1958, 1959f; Rodhain, 1921, 1923); ZAIRE

(EQUATEUR and SHABA) (Fain, 1958, 1959f); RUANDA (Fain, 1958). On *Rousettus aegyptiacus* from ZAIRE (Fain, 1958), probably accidental (Fain, 1959f).

Deposition of specimens: NMNH and UMMZ.

The last lineage at the polychotomy (node 19) is diagnosed in the female tritonymph by the transformation of setae *g* and *3 a* to filiform (reversal) (125, 129); in the female by the loss of spines in the area between setae *c 1* and the anus (reversal) (37, 38), and the presence of an isolated, ventrolateral spinose zone (see Figs. 131, 132, 136) (44); in the male by the subequal length of setae *d 1* and *d 2* (reversal) (95), and the transformation of setae *g* to filiform (reversal) (126).

Nycteridocoptes orientalis diverges from a lineage including the four species of *Nycteridocoptes* associated with Microchiroptera (node 20). This lineage (*miniopteri-hoogstraali*) is diagnosed in the female tritonymph by the presence of small spines on the dorsum (30); in the female by the shape of the isolated, ventrolateral spinose zone (see Figs. 131, 132) (45 state 3); in the male by the presence of a lateral notch in the posterior median shield (16), the transformations of setae *sci* from elongate and rod-like to short and spine-like (reversal) (67), setae *h 2* and *ps 2* from thick to thin spines (reversal) (111), and setae *f* IV from filiform to spines (188).

The first dichotomy within this lineage involves *N. miniopteri* and a lineage (node 21) diagnosed in the protonymph by the addition of well developed setae *f 2* (reversal) (99, 100); in the male tritonymph by the addition of setae *h 3* (reversal) (114); in the male by the loss of setae *e* III (reversal) (190). *Nycteridocoptes poppei* diverges from the two species associated with Rhinolophidae. The latter lineage (node 22) is diagnosed in the female by a modification of the ventrolateral spinose zone (to oval, without a notch; Fig. 136) (45 state 2); in the male by the elongate (vs. short) setae *h 2* and *ps 2* (112).

Nycteridocoptes orientalis Fain, 1963
(Figs. 126, 127)

Nycteridocoptes orientalis Fain, 1963c: 252.

Diagnosed in the larva by the elongation of setae *sci* (65); in the protonymph and male tritonymph by the transformation of setae *sci* from filiform to thin, spine-like rods (66); in the female tritonymph by the absence of spines and scales from the dorsum (reversal) (29); in the female tritonymph and male by the reversal of the modification of the posterior ambulacra (207); in the male tritonymph by vestigial or absent setae *cp* (87); in the female by the linear shape of the ventrolateral spine zone (45 state 1), and the presence of setae *e* III–IV (reversal) (189); in the male by the transformation of setae *sce* from spine-like to filiform (reversal) (71), and the presence of setae *r* IV (reversal) (195). The male is characterized by the very weak dorsal sclerotization.

Nycteridocoptes orientalis was described from the female, although notes were made on a female tritonymph and male that were tentatively associated with the female (Fain, 1963c). Based on pharate individuals in the newly collected material, that association can be confirmed. All life stages have been collected during this study.

The immatures of *N. orientalis* are characterized by the addition of setae *f 2* in the male tritonymph (very small), and the distinctly unequal size of the perianal setae. The female tritonymph (Figs. 126, 127) adds setae *h 3* (very small); setae *g, 3 a,* and *4 a* are present; and both dorsum and venter are less sclerotized than in other *Nycteridocoptes* (in this respect it resembles *N. heidemanni*). Measurements of the female and male are summarized in Tables 3 and 4.

All stages in the type series and the new collections were found on and in the wing membrane of their hosts.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Pteropus alecto* Temminck, 1837. Type host. INDONESIA: SULAWESI, Buka Is., 1909 (paratype female tritonymph and male, specimens in collection NMNH); SULAWESI, Tringgula, 1°01'N 122°11'E, 29 August 1914, R.C. Raven, NMNH #199759, HK 88–0825–8.

Pteropus poliocephalus Temminck, 1825. PAPUA NEW GUINEA: NEW BRITAIN Is., 21 November 1909, ZIZM #T845, F.S. Lukoschus (specimens in collections NNML and UMMZ).

Literature records: on *Pteropus alecto* from INDONESIA: SULAWESI (Fain, 1963c [Type series]); on *Pteropus hypomelanus geminorum* from MYANMAR: Mergui Archipelago (Fain, 1963c).

Deposition of specimens: NMNH, PNC, and UMMZ.

Nycteridocoptes miniopteri Fain, 1959
(Figs. 128–132)

Nycteridocoptes miniopteri Fain, 1959f: 342.

Diagnosed in the protonymph by the presence of setae *cp* (reversal) (86), and in the protonymph and male tritonymph by the absence of setae *f 2* (101).

Nycteridocoptes miniopteri has been described for the female tritonymph and male, with brief notes on the other immatures (Fain, 1959f). The other immatures are characterized by the very poor development of the posterior perianal setae (Figs. 128–130). The female tritonymph has strongly reduced ambulacra on legs III–IV (Fain, 1959f). In the female (Figs. 131, 132) all perianal setae are present but their length is strongly unequal (Table 4). The ventrolateral spine zone in the female has a well developed ventral notch.

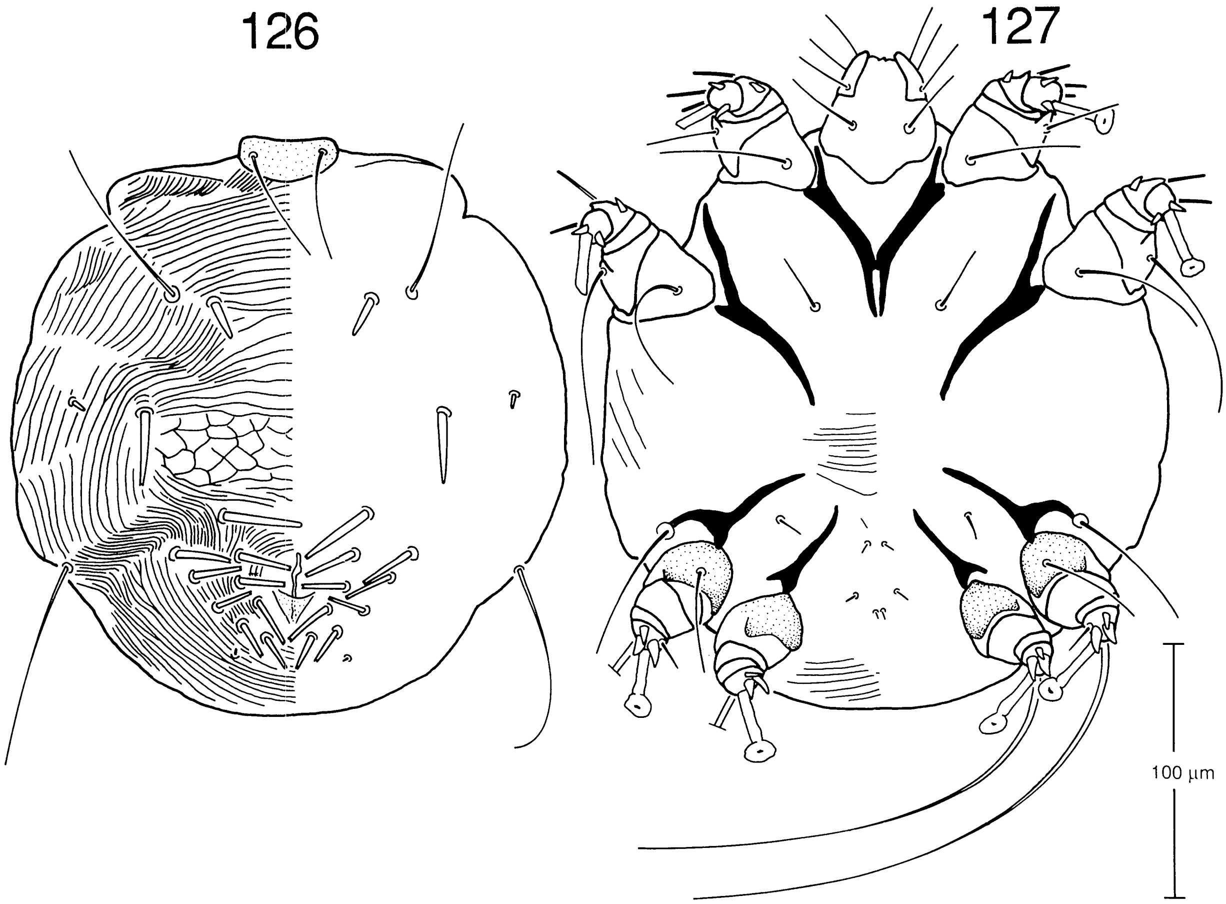
Immatures and males were found on the wing membrane and uropatagium but some female tritonymphs were collected on the ear (Fain, 1959f; Fain, 1960a; present study). Two females were also collected from the ear lobes (Fain, 1960a). Pathology has not been observed.

Material examined: All stages.

Hosts (Chiroptera: Vespertilionidae) and localities: *Miniopterus inflatus* Thomas, 1903. Type host. ZAIRE: KIVU, Mulungu; BAS-ZAIRE, Thysville (paratypes, specimens in collection IRSN).

Miniopterus australis Tomes, 1858. INDONESIA: SUMBAWA, 2 km E Bata Dulang, 3 November 1988, D. Kitchener (S 987), WAM, HK 89–0201–2 (two larvae, tentatively associated with *N. miniopteri*).

Miniopterus schreibersi (Kuhl, 1819). ITALY: TOSCANA (paratypes, specimens in collection IRSN); MADAGASCAR: FIANARANTSOA, 1 km N Kianjavato, 21°23'S 47°52'E, elev.



FIGS. 126, 127. *Nycteridocoptes orientalis*, female tritonymph, dorsal (126) and ventral (127) view.

300 m, 12 August 1987, G.K. Creighton (GKC 2583), NMNH #448888, HK 88–0117–2.

Literature records: on *Miniopterus inflatus* from ZAIRE (Fain, 1959f [Type series]); on *Miniopterus schreibersi* from ITALY (Fain, 1959f), and FRANCE (Fain, 1960a).

Deposition of specimens: NMNH and UMMZ.

Nycteridocoptes poppei Oudemans, 1898

Nycteridocoptes poppei Oudemans, 1898: 277.

Diagnosed in the protonymph by the addition of setae *h 3* (reversal) (113).

All stages of this mite species have been described previously (Dusbabek, 1963; van Eyndhoven, 1954; Fain, 1958, 1959c; Oudemans, 1898). It shares with *N. miniopteri* the apparent absence of setae *g* in the protonymph. Unlike *N. miniopteri*, which has a strongly modified setal addition pattern during ontogeny, *N. poppei* adds all setae in the ancestral pattern (Fain, 1958, 1959c).

Nycteridocoptes poppei occurs predominantly on the wings (Lukoschus, 1962; Rack, 1962), with female cysts occurring on both the wings and the ear pinnae (Dusbabek, 1963; Fain, 1958; Fain & Aellen, 1961). Infestations including large numbers of females have been associated with considerable pathology, usually expressed as severe damage to the wing membrane and the edge of the pinnae (Fain & Aellen, 1961; Lukoschus, 1962; Rack, 1962).

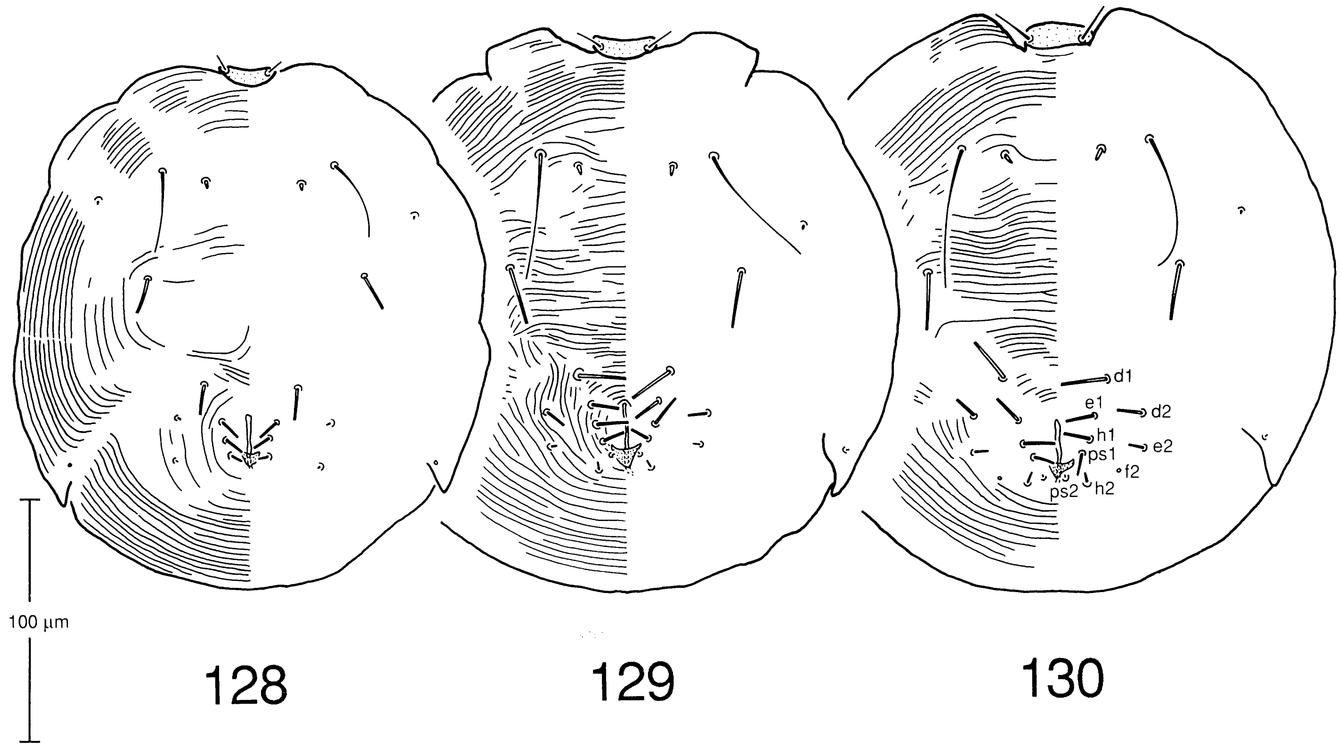
Material examined: All stages.

Hosts (Chiroptera: Vespertilionidae) and localities: *Myotis myotis* (Borkhausen, 1797). GERMANY: SCHLESWIG-HOLSTEIN, Bad Segeberg, ca 54°N 10°E, 1 September 1960, F.S. Lukoschus; Berlin, winter 1935 (specimen in collection BMNH).

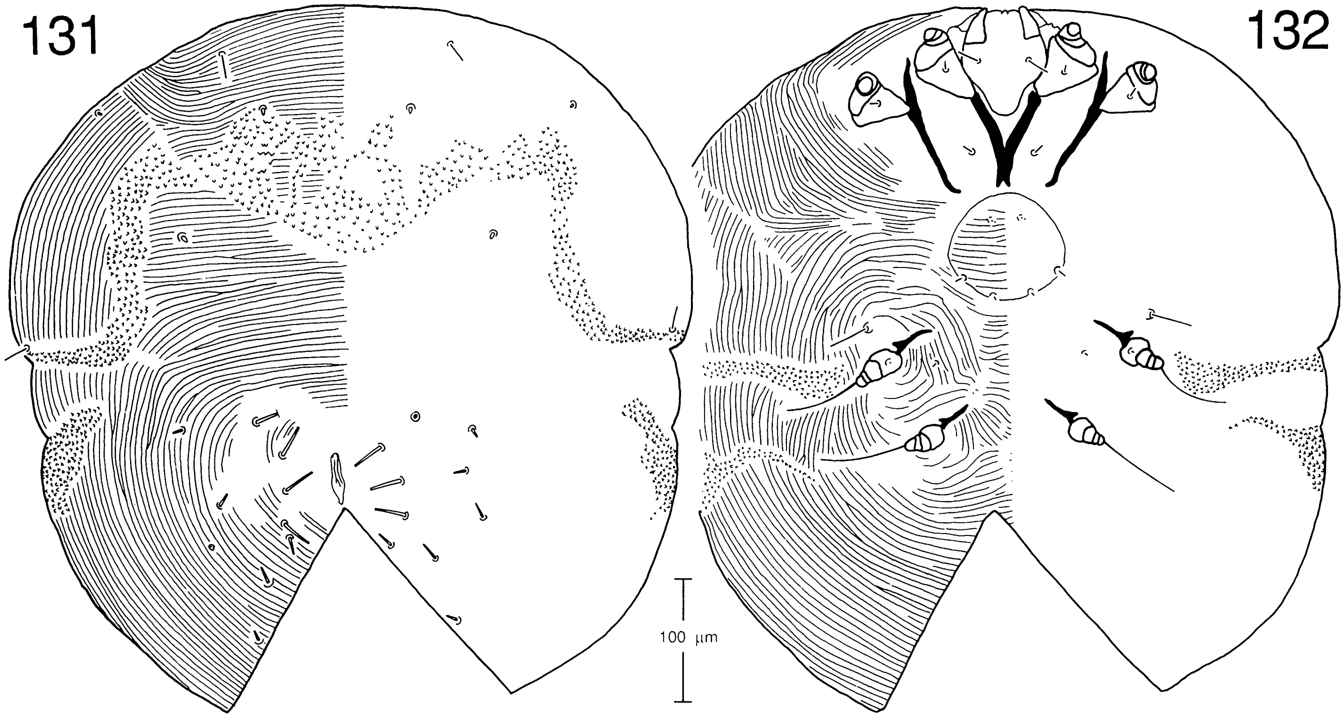
Myotis daubentoni (Kuhl, 1819). GREAT BRITAIN: NORFOLK, Norwich, 19 August 1977 (specimen in collection BMNH).

Myotis goudoti (Smith, 1834). MADAGASCAR: Fiv. de Taolanara, Mandena, 15 September 1989, G.K. Creighton (GKC 3024), NMNH, BMOC.

Literature records: on *Vespertilio murinus* Linnaeus, 1758 from GERMANY: BREMEN, Vegesack (Oudemans, 1898 [Type series]); on *Eptesicus serotinus* Schreber, 1774, *Myotis bechsteini* (Kuhl, 1818) and *Myotis nattereri* (Kuhl, 1818) from GERMANY (Lukoschus, 1962); on *Myotis blythii* (Tomes, 1857) from FRANCE (Fain & Aellen, 1961); on *Myotis daubentoni* from BELGIUM (Fain, 1959f), FRANCE, GERMANY (Lukoschus, 1962) and SWITZERLAND (Fain & Aellen, 1961); on *Myotis myotis* from BELGIUM (Fain,



FIGS. 128–130. *Nycteridocoptes miniopteri*, immatures, dorsal view of the larva (128), protonymph (129), and male tritonymph (130).



FIGS. 131, 132. *Nycteridocoptes miniopteri*, female, dorsal (131) and ventral (132) view.

1958), BULGARIA (Beron, 1970), CZECHOSLOVAKIA (Dusbabek, 1963), GERMANY (Lukoschus, 1962; Rack, 1962), NETHERLANDS (van Eyndhoven, 1954), and POLAND (Haitlinger, 1979); on *Plecotus auritus* (Linnaeus, 1758) from GERMANY (Lukoschus, 1962) and SWITZERLAND (Fain, 1960a); on *Rhinolophus euryale* Blasius, 1853 (Chiroptera: Rhinolophidae) from CZECHOSLOVAKIA (Dusbabek, 1963) and SPAIN (Fain & Lukoschus, 1969).

Deposition of specimens: NMNH and UMMZ.

Nycteridocoptes eyndhoveni Fain, 1959
(Figs. 133–137)

Sarcoptes chiropteralis (Trouessart) in part, Fain, 1959d: 332.
Nycteridocoptes eyndhoveni Fain, 1959d: 332.

Diagnosed in the tritonymph and female by the presence of setae *e* III–IV (reversal) (189).

The male was described as *Sarcoptes chiropteralis* Trouessart, 1896, a species reclassified as *Prosopodectes chiropteralis* (Trouessart) by Canestrini (1897). Fain (1959d) synonymized *Prosopodectes* with *Notoedres,* with the female of *Prosopodectes chiropteralis* as the lectotype of *Notoedres chiropteralis* (Trouessart). In the same paper the male of *Sarcoptes chiropteralis* Trouessart was included in a new species *Nycteridocoptes eyndhoveni* Fain, 1959.

The species has been described for the female tritonymph and male, with notes on the larva and male tritonymph. Immatures (larva, protonymph, male tritonymph) are characterized by long perianal setae (Figs. 133–135). Setae *f 2* in the protonymph are small and setae *g* are present. Setae *h 3* are absent in the protonymph, small in the male tritonymph. The female (Figs. 136, 137) is characterized by the spine pattern on the dorsum, and the insertion pattern of the perianal setae. Measurements in Table 4.

All collections reported have been from the wings of the hosts. Data on possible pathology are not available.

Material examined: Larva, protonymph, male tritonymph, and female.

Hosts (Chiroptera: Rhinolophidae) and localities: *Rhinolophus ferrumequinum* (Schreber, 1774). Type host. BELGIUM (paratypes, specimens in collection IRSN); GREAT BRITAIN: PEMBROKESHIRE, 1 July 1979 (specimen in collection BMNH).

Rhinolophus clivosus Cretzschmar, 1828. ZAIRE (specimens in collection IRSN).

Literature records: on *Rhinolophus ferrumequinum* from BELGIUM: NAMUR, Floreffe (Fain, 1959d [Type series]); BELGIUM, ITALY, NETHERLANDS (Fain, 1959f), BULGARIA (Beron, 1970), and FRANCE (Fain, 1959f; Trouessart, 1896); on *Rhinolophus blasii* Peters, 1867, *Rhinolophus clivosus,* and *Rhinolophus hildebrandti* Peters, 1878 from ZAIRE (Fain, 1959f); on *Rhinolophus fumigatus* Ruppell, 1842 (= *R. aethiops*) from ANGOLA (Fain, 1959f).

Nycteridocoptes hoogstraali Fain, 1961

Nycteridocoptes hoogstraali Fain, 1961c: 138.

Diagnosed in the larva and the protonymph by the presence of setae *cp* (reversal) (84, 86); in the protonymph by the addition of setae *h 3* (reversal) (113).

This species was described for the female only (Fain, 1961c). During this study immatures and males were collected from the type host. The immatures differ from those of *N. eyndhoveni* by a more complete setation (setae *cp* and *h 3* are present in the nymphs). In addition the larva and protonymph of *N. hoogstraali* show weak, but distinct, scale-like striations on the central part of the dorsum. These striations are absent in the male tritonymph. The three males available were severely damaged in the posterior region, not allowing a detailed description.

All specimens (including the females) were collected from the wings of their hosts (Fain, 1961c; present study).

Material examined: Larva, protonymph, male tritonymph, and male.

Host (Chiroptera: Rhinolophidae) and locality: *Triaenops persicus* Dobson, 1871. Type host. MOZAMBIQUE: TETE, 10 mi E Massamba, Muchena, 15°41'S 33°48'E, 29 July 1964, R.M. Davis & J.C. Lingebach, NMNH #367537, HK 88–0827–9; same data, NMNH #367538, HK 88–0826–3; NMNH #367541, HK 88–0827–7; NMNH #367543, HK 88–0826–5; NMNH #367545, HK 88–0827–8.

Literature records: on *Triaenops persicus* (= *T. afer*) from TANZANIA: TANGA, Sigi River (Fain, 1961c [Type series]).

Deposition of specimens: NMNH and UMMZ.

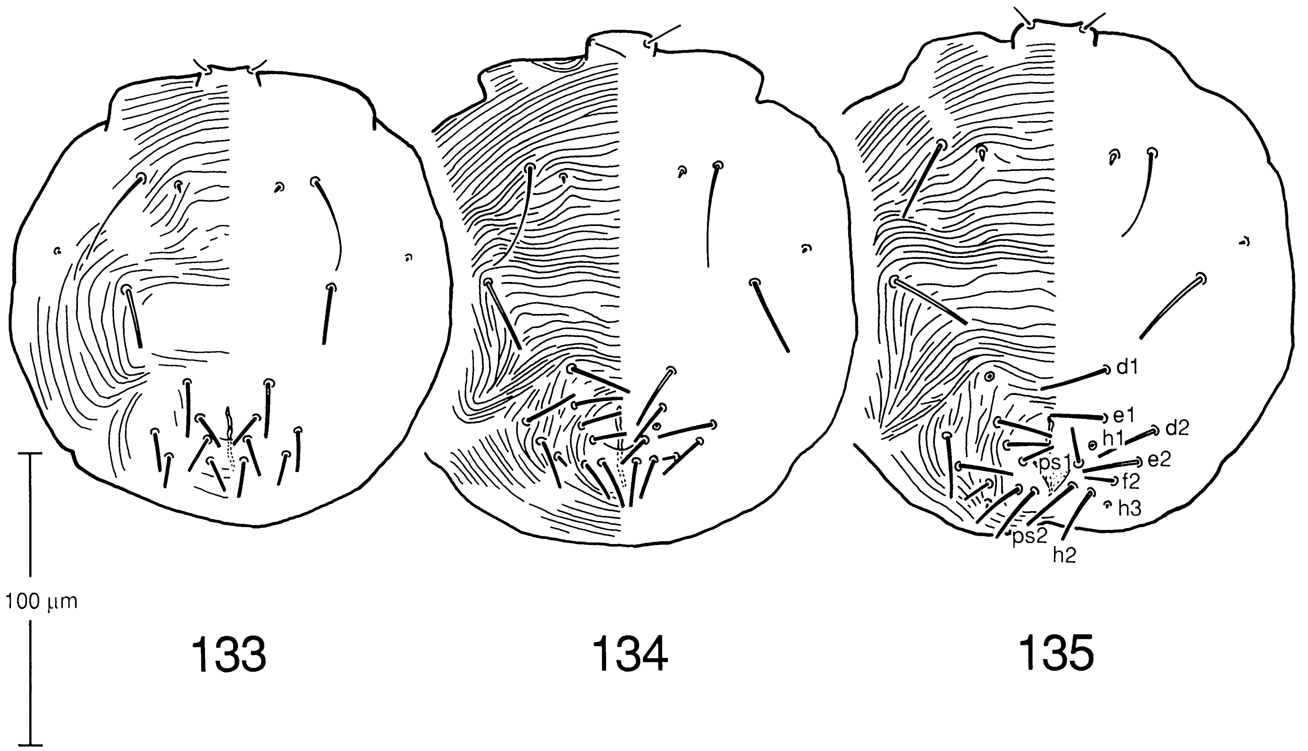
Nycteridocoptes cynopteri (Fain, 1962), new combination
(Fig. 3)

Bakerocoptes cynopteri Fain, 1962b: 406.

This species differs from all other Sarcoptidae by not adding legs IV in any life stage (Fain, 1962b). A few additions can be made to the original description, all related to ontogeny. Fain (1962b) mentioned a male emerging from a nymph having no solenidion ω-3 on tarsus I, a nymph he could not distinguish from a protonymph. This suggests that males might develop from protonymphs (Fain, 1964). During this study a large number of molting males and females were examined. Both adult stages develop in nymphs with a very small solenidion ω-3 on tarsus I (3–5 μm); therefore they develop in tritonymphs.

In general, immatures resemble each other very closely and differentiation of the stages is not always possible. Although both larvae and protonymphs occur (molting protonymphs were examined), I found no consistent morphological differences between those stages. Similarly, sexual dimorphism in the tritonymphs is restricted to very small differences in the length of solenidia ω-3 (4.5–5 μm in the female tritonymph vs. 3–4.5 μm in the male tritonymph), solenidia φ I (10–12 vs. 8–9 μm) and some body setae.

The ecology of this species has been studied in some detail. Females produce cysts within the tissues of the wing membrane (Lavoipierre et al., 1967) measuring 1.5–2 mm in diameter. Up to seven cysts have been observed on a single bat (Lavoipierre et al., 1967). The cysts in *N. cynopteri* differ from those observed in other *Nycteridocoptes* species in one aspect: they contain not only the female and eggs (and occasionally a male) but all the immature stages. The loss of the dispersal behavior of the immatures is interpreted as paedomorphic. Very few young cysts have been observed, leading to the hypothesis that either the cysts develop very rapidly,



Figs. 133–135. *Nycteridocoptes eyndhoveni,* immatures, dorsal view of the larva (133), protonymph (134), and male tritonymph (135).

or all cysts result from a single invasion (Beck, 1969). Transmission is assumed to be from mother to young, but adult to adult transmission is possible, aided by the colonial roosting of the bat host (Beck, 1969; Lavoipierre et al., 1967).

Incidence levels in Malaysia (based on presence of female cysts only) have been estimated at 4.9% (sample size 450 bats) (Beck, 1971). However, material from the Philippines, collected during this study, indicates that incidence rates vary strongly based on locality and possibly season.

At the cellular level host reaction includes hyperplasia in the connective tissue, thickening of the epidermis near the cyst, and marked hyperkeratosis near the cyst opening (Lavoipierre et al., 1967). Some mites appear to burrow through the layer of epidermal cells lining the cyst wall, into the stratum corneum (Lavoipierre et al., 1967). However, infestation levels per bat are not sufficiently high to cause any serious injury to the hosts.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Cynopterus brachyotis* (Muller, 1838). Type host. INDONESIA: Sumbawa, Merente, 8°33'S 117°01'E, 20 May 1988, D. Kitchener (S 120), WAM, HK 89–0215–2; MALAYSIA: Pahang, Taman Negara, 19 October 1982, F.S. Lukoschus; Kuala Lumpur, 4 November 1982, F.S. Lukoschus; Selangor, Gombak Forest, 6 November 1982, F.S. Lukoschus; Sabah, Pulau Tiga, 7°21'N 117°03'E, 15 April 1988, S.M. Goodman, UMMZ #165506–165511, BMOC 88–0527–5; SRI LANKA: Kandy, August 1979, O. Bain, F.S. Lukoschus.

Ptenochirus jagori (Peters, 1861). PHILIPPINES: Leyte, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 10 April 1987, E.A. Rickart (EAR 1432), NMNH #458334, HK 87–0410–1; same locality and date, EAR 1433, NMNH #458335, HK 87–0410–2; EAR 1434, NMNH #458336, HK 87–0410–3; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 8 February 1984, R.B. Utzurrum (RBU 247), BMOC 84–1575–3; same locality, RBU 227.

Ptenochirus minor Yoshiyuki, 1969. PHILIPPINES: Leyte, 10 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 320 m, 10 March 1987, P.D. Heideman (PDH 3115), NMNH, HK 87–0310–3.

Literature records: on *Cynopterus brachyotis* from INDONESIA: Mentawi Archipelago, Pagi Is. (Fain, 1962b [Type series]), MALAYSIA (Beck, 1969, 1971; Lavoipierre et al., 1967) and SINGAPORE (Lavoipierre et al., 1967).

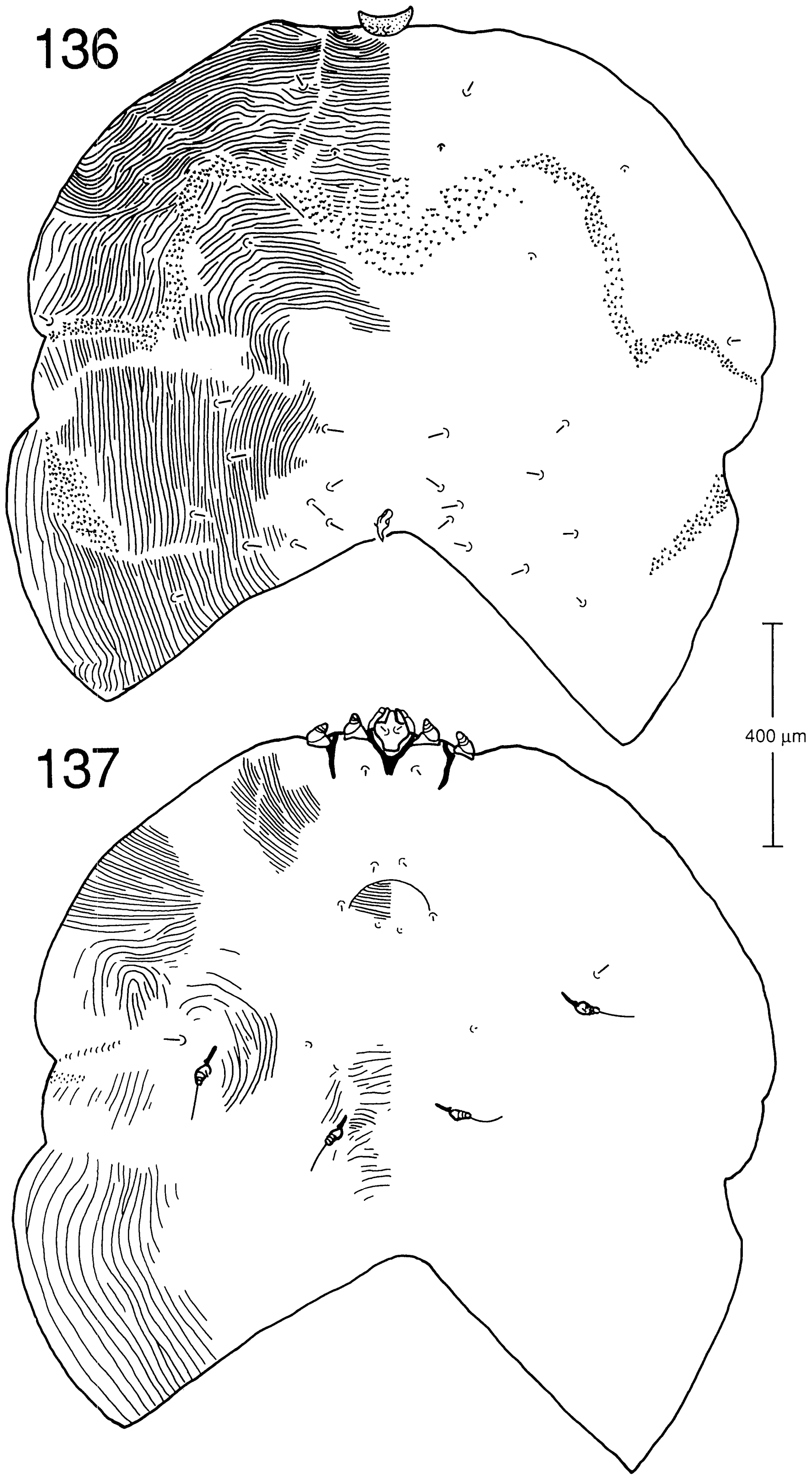
Deposition of specimens: NMNH, PNC, UMMZ, and WAM.

A few specimens of an additional species of *Nycteridocoptes* have been recovered. The material is sufficient to indicate a potentially new species, but too limited to allow an adequate description.

Nycteridocoptes sp. 1

Material examined: Larvae and 1 female.

Hosts (Chiroptera: Rhinolophidae) and locality: *Rhinolophus inops* Andersen, 1905. PHILIPPINES: Leyte, 8 km N,



FIGS. 136, 137. *Nycteridocoptes eyndhoveni*, female, dorsal (136) and ventral (137) view.

2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 4 April 1987, R.B. Utzurrum (RBU 179), NMNH, HK 87–0404–1.

The sister group of *Nycteridocoptes* is made up of *Cynopterocoptes* nov. gen. and the *Teinocoptes* group (Fig. 48). The lineage (node 23, Fig. 53) is diagnosed by a large number of derived character states. In all stages: setae *4 a* never added (130); in the larva: spines or scales present (19), and each coxal apodeme III with an anterolateral projection (144); in the immatures and female: the loss of solenidia σ I (172); in the nymphs and female: scales present (25, 26, 30, 31, 34), and setae *c 2* minute (78); in the tritonymph: setae *f 2* short (102); in the female: scales extending lateral and posterior to the anus (39, 40), setae *sci* and *sce* minute (62, 69), perianal setae membranous (97), reproduction by ovovivipary (137), very short coxal apodemes I (140), and the loss of setae *vF* I (168); in the male: setae *c 2* transformed from spines to filiform (reversal) (80), solenidia σ II present (reversal) (176), setae *kT* III–IV transformed to filiform (reversal) (199), ambulacra on legs IV of the male lost (reversal) (206), and tarsus and tibia of legs IV fused (209).

The first dichotomy in this lineage is between *Cynopterocoptes* and the *Teinocoptes* group (Fig. 53).

Cynopterocoptes nov. gen.

Diagnosed in the larva by the presence of scales (21) extending to the anus (22); in the protonymph by the presence of scales in a U-shaped band across the body at the level of setae *c 1* (27), and the addition of setae *f 2* and *h 3* (reversal) (99, 113, 114); in the female by the reduced height of the body (reversal) (3), the reduction of setae *c 3* (90), and the loss of setae *vF* II (169).

Type species *Cynopterocoptes heaneyi* nov. spec.

Etymology: The name of this genus is a combination of the name of the major host group, pteropodid bats in the *Cynopterus* section of the Pteropodidae, and the latinized Greek "kopto," for cut or bite.

Cynopterocoptes **heaneyi** nov. spec.

(Figs. 138–157)

With the characters of the genus.

Larva (Fig. 138): In general appearance resembling a *Nycteridocoptes* larva. Setae *c 1* spine-like, setae *e 2* very small. Perianal setae spine-like rods. Coxal apodemes III with an anterolateral projection.

Protonymph (Fig. 139): Resembling the larva but perianal setae *e 1*, *h 1*, *h 2*, and *ps 1* membranous, slightly foliate. Setae *ps 1* considerably smaller than the other perianal setae. Setae *f 2*, *h 3*, and *ps 2* added but very small. Setae *g* added. Coxal apodemes III as in the larva.

Female tritonymph (Fig. 140): Resembling the protonymph in most characters. The *d* and perianal setae are large, membranous, and trilobed. Setae *ps 1* similar in size to the other perianals. Setae *e 2* small, membranous. Setae *3 a* added.

Male tritonymph (Fig. 141): Closely resembling the protonymph. Setae *d 1*, *d 2*, and the perianal setae membranous, but not lobed. Setae *3 a* added.

Female (Figs. 142–149): Resembling the female tritonymph, but with the perianal setae more, and the *d* setae less, developed. Anterior dorsal setae small to minute. Setae *vi* not observed, setae *c 3* very small. Setae *3 a* absent and setae *g* on coxal fields IV, far behind the oviporus. Palpal setae α *l* rod shaped. Anterolateral projection of coxal apodemes III absent. Legs more compact, and with shorter setae than in the nymphs. Femoral setae *vF* I–II not observed. Trochanteral and femoral lobes of legs I–II well developed. Measurements in Table 5.

Male (Figs. 150–157): Shields poorly sclerotized. Anterior lateral shields free, anal shields not fused to each other. Posterior edges of coxal field II sclerotized, without any free projections. Leg setation and solenidiotaxy nearly complete for the subfamily, only setae *e* III absent. Measurements in Table 6.

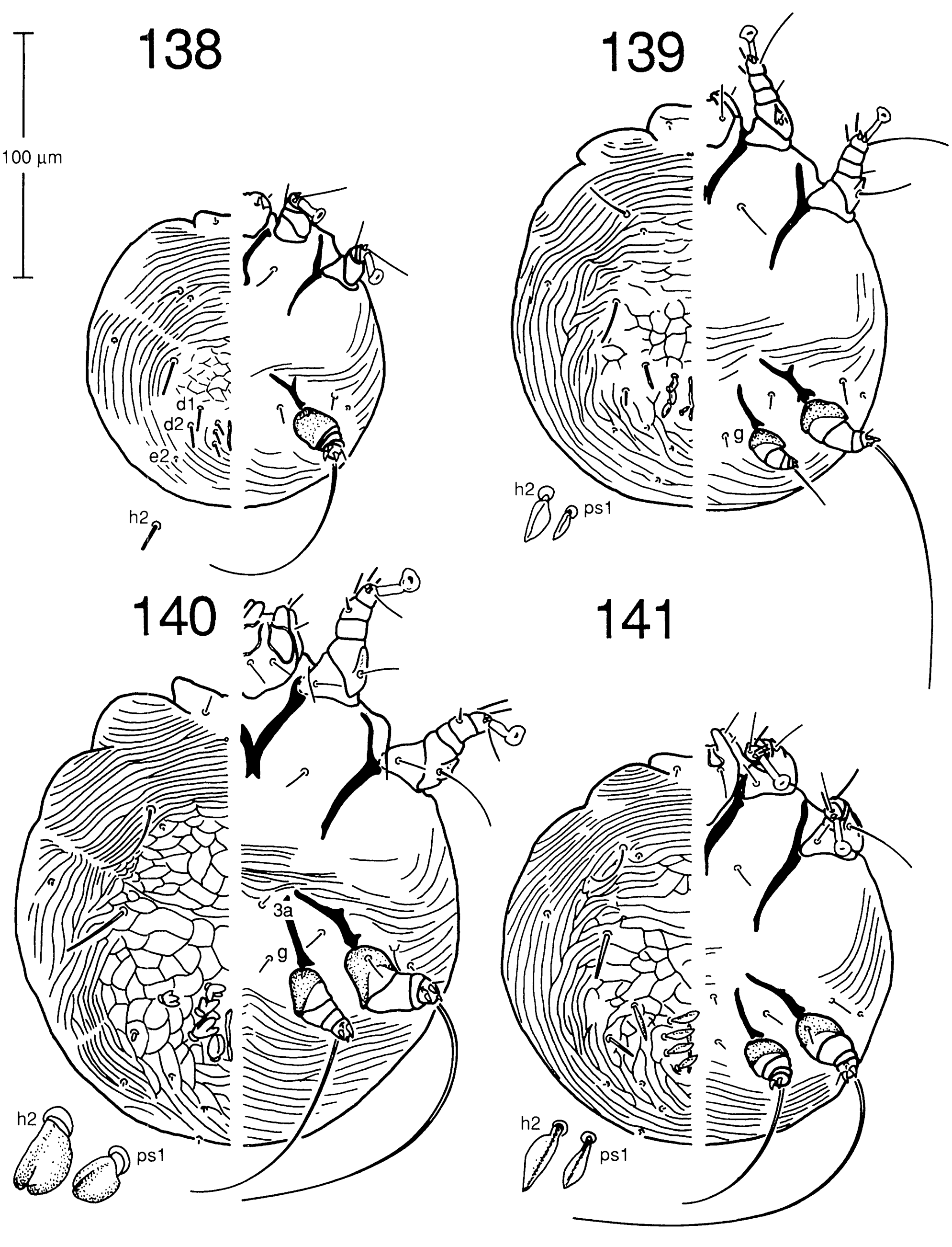
Throughout ontogeny the area covered with scales increases from a small zone anterior to the anus in the larva, to over half of the dorsum in the female. Sexual dimorphism in the tritonymphs is distinct, although not as pronounced as in *Nycteridocoptes*.

The free larvae, protonymphs, and male tritonymphs occur on the wing membrane and, more rarely, on the membrane over the wrist bones. The female tritonymphs and females occur on the face, either on the lips (in *Ptenochirus* spp.) or on (not in) the nose (most other hosts). Only a few males have been collected, all of which were still in the tritonymphal cuticle. Female tritonymphs and females were found in relatively high frequency, the other stages were less common. Associated pathology has not been observed.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Haplonycteris fischeri* Lawrence, 1939. Type host. PHILIPPINES: NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 1 July 1982, P.D. Heideman (PDH 480), UMMZ #159832 (holotype female); same locality, 30 June 1982, PDH 466, UMMZ #159830, HK 83–1216–3; 30 July 1982, PDH 627; 30 July 1982, PDH 640, UMMZ #159841, HK 83–1213–2; 27 August 1982, PDH 771, UMMZ #159855, HK 83–1215–4; 27 August 1982, PDH 779, UMMZ #159861, HK 83–1215–6; 4 November 1982, PDH 1041, UMMZ #159886, HK 83–1210–2; 5 November 1982, PDH 1049, UMMZ #159889, HK 83–1219–1; 6 November 1982, PDH 1064, UMMZ #159894, HK 83–1211–2; 6 November 1982, PDH 1067; UMMZ #159895, HK 83–1214–3; 11 December 1982, PDH 1232, UMMZ #159915, HK 88–0215–2; 9 January 1983, PDH 1323, UMMZ #159920, HK 88–0215–1; 10 February 1983, PDH 1501, UMMZ #159930, HK 88–0111–2 (allotype male); 7 April 1983, PDH 1725, UMMZ #159947, HK 88–0111–1; 9 April 1983, PDH 1742, UMMZ #159949, HK 88–0215–3; 28 April 1983, PDH 1786, UMMZ #159962; HK 86–1013–4; 5 May 1983, PDH 1794, UMMZ #159951, HK 88–0105–4; 8 February 1984, R.B. Utzurrum (RBU 255), HK 85–0131–4.

Aethalops alecto (Thomas, 1923). INDONESIA: WEST JAVA, Sukabumi, Gunung Masigit, 19 May 1972, NAMRU-2 (2724), NMNH #501862, HK 87–0728–14; MALAYSIA, before 1970, Yong Ghong Chong, AMNH #232511, HK 86–0814–6.



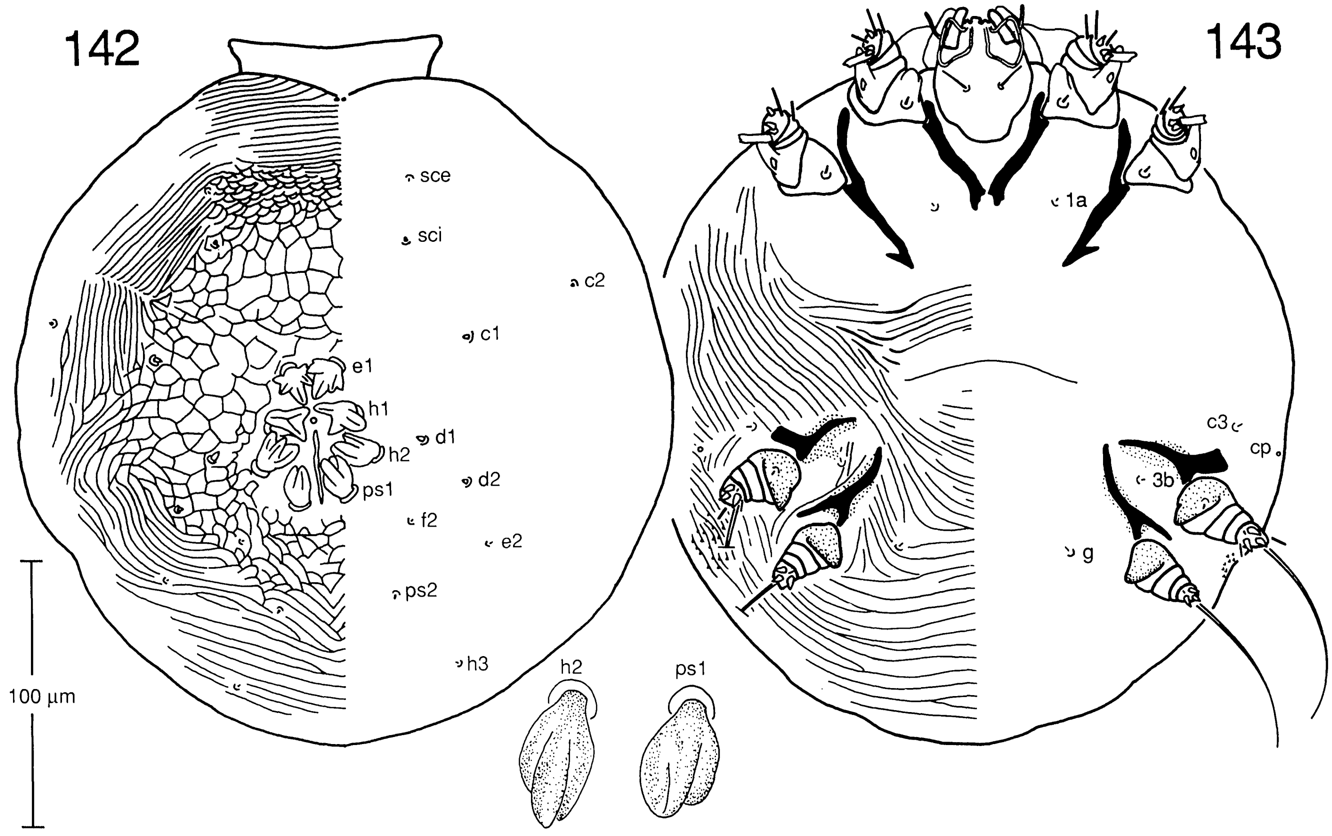
FIGS. 138–141. *Cynopterocoptes heaneyi*, immatures, dorsal (left) and ventral (right) view of the larva (138), protonymph (139), female tritonymph (140), and male tritonymph (141).

Balionycteris maculata (Thomas, 1893). MALAYSIA: PAHANG, Krau Game Reserve, Kuala Lompat, 102°17'N 3°42'E, 23 February 1970, Yong Ghong Chong, AMNH #233964, HK 86–0813–6; same locality and collector, 25 February 1970, AMNH #233967, HK 86–0813–7; 27 February 1970, AMNH #233970, HK 86–0813–5; 27 February 1970, AMNH #233971, HK 86–0813–8; SELANGOR, Kepong, Bukit Lagong Forest Reserve, 3°15'N 101°37'E, 20 March 1953, Lim Boo Liat (R 31829), FMNH #109058, HK 87–0903–7; same locality, 7 October 1953, R 34047, FMNH #109060, HK 87–0903–8.

Chironax melanocephalus (Temminck, 1825). INDONESIA: WEST JAVA, Bandung, Cibuni, 14 August 1972, NAMRU-2 3368, NMNH #501361, HK 87–0729–11; MALAYSIA: PAHANG, Genting Sempah, 3°21'N 101°47'E, elev. 700 m, 8 March 1969, Yong Ghong Chong, AMNH #216740, HK 86–0815–9; SELANGOR, Fraser's Hill, 3°42'N 101°45'E, elev. 1600 m, 12 April 1969, Yong Ghong Chong, AMNH #216741, HK 86–0815–11; same locality, 19 April 1969, Yong Ghong Chong, AMNH #216742, HK 86–0815–12.

Cynopterus horsfieldi Gray, 1843. INDONESIA: LOMBOK, Pelangan, 8°48'S 115°56'E, 16 October 1987, D. Kitchener (L 347), WAM, HK 88–0429–1.

Nyctimene rabori Heaney & Peterson, 1984. PHILIP-



FIGS. 142, 143. *Cynopterocoptes heaneyi*, female, dorsal (142) and ventral (143) view.

PINES: NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 10 October 1982, PDH 973, UMMZ #158885, BMOC 83–1600–51.

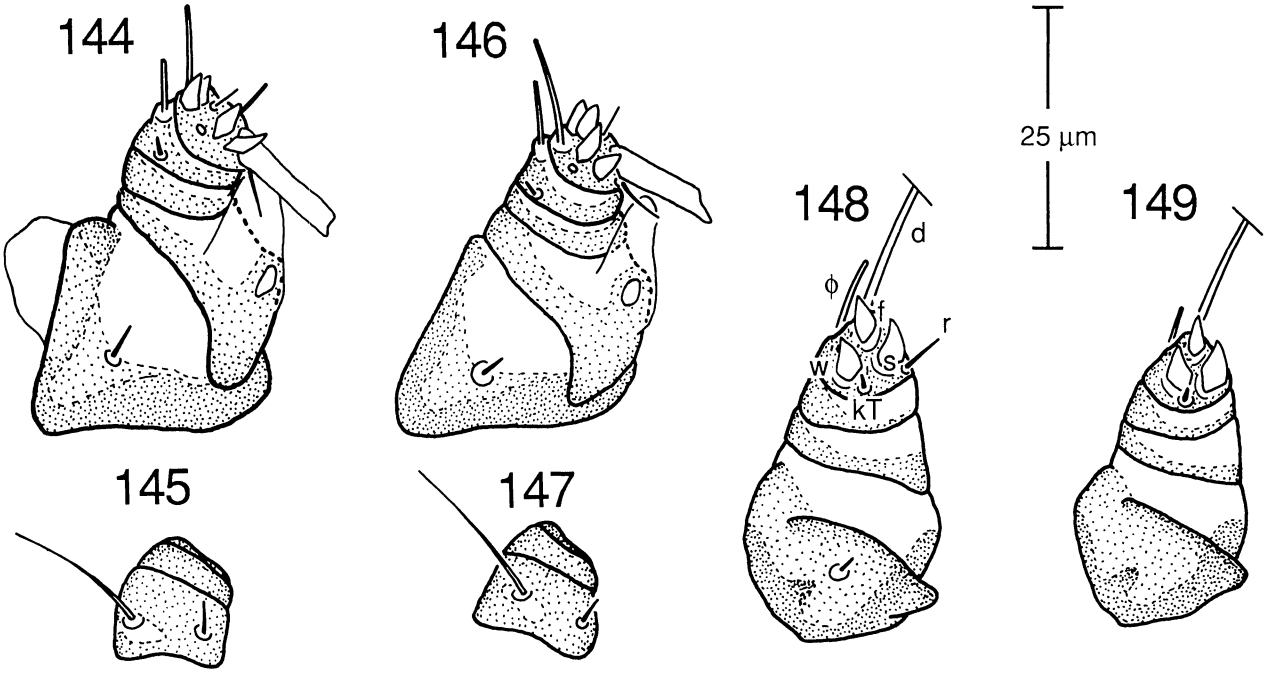
Ptenochirus jagori (Peters, 1861). PHILIPPINES: CAMARINES SUR, 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N 123°20'E, elev. 475 m, 5 March 1988, L.R. Heaney (LRH 3975), NMNH #573726, HK 88–0824–1; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 4 November 1982, PDH 1027, UMMZ #160000, HK 83–1202–1; BOHOL, 1 km S, 1 km E Bilar, 9°43'N 124°07'E, elev. 320 m, 18 June 1987, LRH 3692, NMNH #459264, HK 87–0618–4; same locality, 18 June 1987, LRH 3700, NMNH #459170, HK 87–0618–6; LEYTE, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 12 March 1987, PDH 3140, NMNH #458318, HK 87–0312–1; same locality, 27 March 1987, J.S.H. Klompen (JSHK 40), NMNH #458320, HK 87–0327–4; 11 April 1987, LRH 3181, NMNH #458315, HK 87–0411–5; 11 April 1987, E.A. Rickart (EAR 1437), NMNH #458339, HK 87–0411–1; LEYTE, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 3 April 1987, RBU 167, NMNH #458342, HK 87–0403–2; same locality, 6 April 1987, LRH 3131, NMNH, HK 87–0406–1.

Ptenochirus minor Yoshiyuki, 1979. PHILIPPINES: LEYTE, Biliran Is., 3 km S, 5 km W Caibiran, 11°32'N 124°32'E, elev. 700 m, 28 April 1984, LRH 2545, UMMZ #161227, HK 84–0725–3; LEYTE, 10 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 320 m, 10 March 1987, PDH 3115, NMNH, HK 87–0310–3; same locality, 10 March 1987, EAR 1318, NMNH #458424, HK 87–0310–4; LEYTE, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 4 April 1987, RBU 177, NMNH #459237, HK 87–0404–3; LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 16 March 1987, PDH 3156, NMNH #458409, HK 87–0316–6; same locality, 19 March 1987, JSHK 24, NMNH, HK 87–0319–2; 20 March 1987, JSHK 27, NMNH #458419, HK 87–0320–2; 20 March 1987, JSHK 30, NMNH #459215, HK 87–0320–4.

Etymology: This species is named in honor of Dr. L.R. Heaney, for his contributions to the study of the biogeography, ecology, and systematics of cynopterine bats.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in AMNH, BMNH, CUIC, FMNH, IRSN, MAK, NMNH, OSU, PNC, UMMZ, WAM, ZIAC, and ZIZM.

The sister group of *Cynopterocoptes*, the *Teinocoptes* group (node 24, Fig. 53), is diagnosed by the following derived character states: in all stages setae *f 2* (101, 103) and *h 3* (115) not added; in the protonymph legs IV not added (213); in the protonymph, female tritonymph, and female setae *d*, *w*, and *r* IV not added (183); in the nymphs the ambulacral discs of legs I–II absent (178); in the nymphs and female setae *sce* minute (70), coxal apodemes IV extremely reduced



FIGS. 144–149. *Cynopterocoptes heaneyi*, female, ventral (top) and dorsal (bottom) view of legs I (144, 145) and II (146, 147), ventral view of legs III (148) and IV (149).

(149), and legs IV reduced to no more than two free segments (212); in the tritonymph and female setae *pR* I not added (170).

The next dichotomy is between *Rousettocoptes mammophilus* and the remaining taxa (node 25).

Rousettocoptes nov. gen.

Diagnosed in the female by the relative reduction in height of the body (reversal) (3), the presence of a verrucous area anterolateral to legs III (shared with several *Teinocoptes*) (50), the loss of setae *vF* II (169), and the presence of a large internal spur on trochanter III (a unique character for this taxon).

Type species *Rousettocoptes mammophilus* nov. spec.

Etymology: The name of this genus is a combination of the generic name of the type host, *Rousettus,* and the latinized Greek "kopto," for cut or bite.

Rousettocoptes **mammophilus** nov. spec.

(Figs. 158, 159)

With the characters of the genus.

Larva: Dorsum with 60–70 dorsal spines in a pattern similar to that in *Teinocoptes vandeuseni* (Fig. 205). Setae in the *d, e,* and *h* rows subequal in length.

Protonymph: Cuticle striate, with a few scales near setae *c 1*. Perianal setae long and filiform. Length of setae *d 1* 1.5–2.0 X the length of setae *d 2, e 2,* and *ps 2*. Trochanters III without internal spurs. Legs IV not observed.

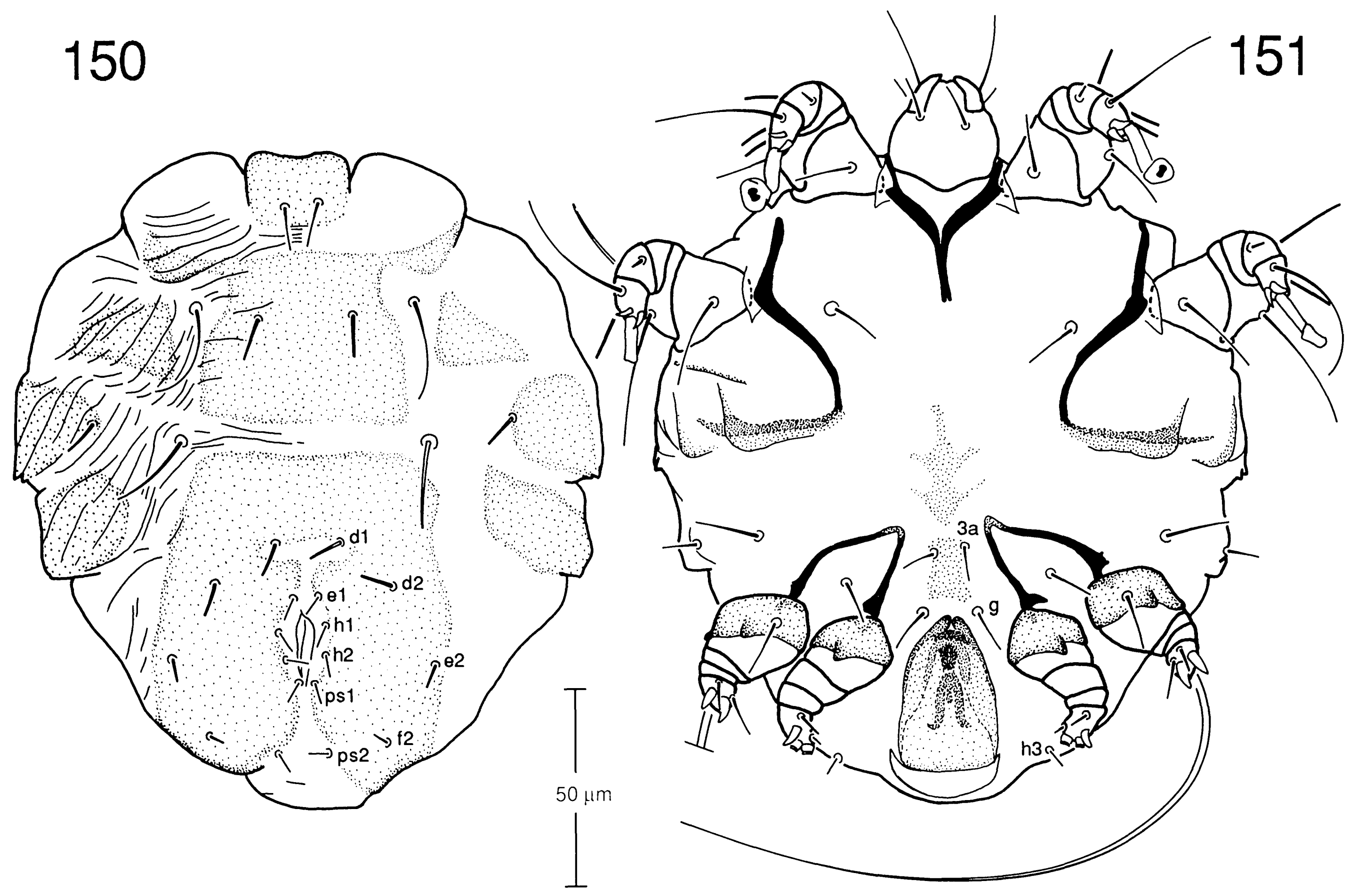
Female tritonymph: Scales in patches near setae *c 1* and anterior to the anus. Perianal setae membranous. Length of setae *d 1* over twice the length of setae *d 2,* and 3–4 X the length of setae *e 2* and *ps 2*. Trochanters III with small internal spurs. Legs IV small, without a solenidion.

Female (Figs. 158, 159): Scale pattern continuous from setae *c 1* to the area posterior to the anus. Setae as in the tritonymph but setae *c 1* and *d 1* more developed. Setae *g* present near the oviporus. Legs IV with a very small solenidion or solenidion absent. Bursa copulatrix very long. Measurements in Table 5.

All specimens (immatures and females) have been collected from the nipples of their host.

Material examined: Larva, protonymph, female tritonymph, and female.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus amplexicaudatus* (Geoffroy, 1810). Type host. PHILIPPINES: BOHOL, 1 km S, 1 km E Bilar, 9°44′N 124°07′E, elev. 320 m, 19 June 1987, P.D. Heideman (PDH 3684), NMNH, HK 87–0619–9 (holotype female); LEYTE, 7 km N Baybay, 10°45′N 124°47′E, elev. 10 m, 4 March 1987, E.A. Rickart (EAR 1292), NMNH #459285, HK 87–0304–4; same locality, 11 March 1987, PDH 3119, NMNH #458478, HK 87–0311–1; 27 March 1987, J.S.H. Klompen (JSHK 37), NMNH #459279, HK 87–0327–2; NEGROS ORIENTAL, Dumaguete, 9°18′N 123°18′E, elev. 5 m, 29 September 1982, PDH 890, UMMZ #161537, HK 85–0808–1; same locality, 31 May 1983, PDH 1970, UMMZ #161677, HK 85–0902–1; 22 June 1983, PDH 2121, UMMZ #161680, HK 85–0419–1; 22 June 1983, PDH 2127, UMMZ #161681, HK 85–0419–2; 12 June 1987, JSHK 108, NMNH #458506, HK 87–0612–1; ROMBLON, Sibuyan Is., 1 km S, 1 km E Magdiwang, Tam-



FIGS. 150, 151. *Cynopterocoptes heaneyi*, male, dorsal (150) and ventral (151) view.

payan, 12°29'N 122°31'E, elev. 10 m, 24 May 1989, S.M. Goodman (SMG 3048), FMNH #136987, HK 89–0711–9; same locality, elev. 50 m, 1 June 1989, SMG 3237, FMNH #136988, HK 89–0711–5.

Rousettus leschenaulti (Desmarest, 1820). PAKISTAN: NORTHWEST FRONTIER, Malakand Agency, Malakand, 34°34'N 71°56'E, 19 September 1966, C.J. Phillips (569), NMNH #429347, HK 88–0901–5; same locality and date, C.J. Phillips (572), NMNH #429338, HK 88–0901–6.

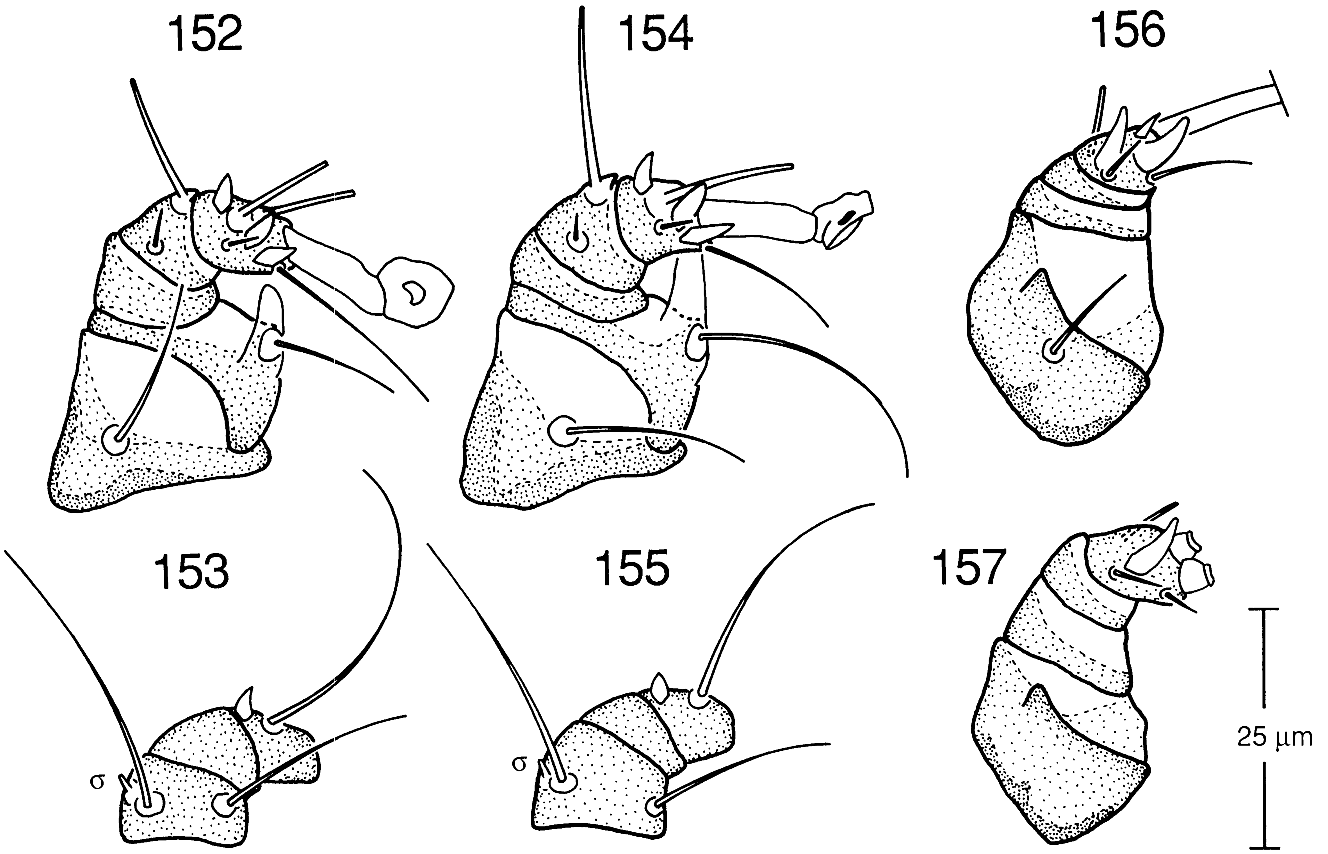
Eonycteris spelaea (Dobson, 1871). PHILIPPINES: NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 22 February 1987, L.R. Heaney (LRH 2907), NMNH #459070, HK 87–0222–3.

Etymology: The specific name is a combination of "mamma," Latin for breast, teat, and "philia," latinized Greek for love, affection. The name refers to the habitat of this mite species.

Deposition of specimens: Holotype female in collection NMNH. Paratypes in BMNH, FMNH, IRSN, NMNH, PNC, UMMZ, and WAM.

The sister group of *Rousettocoptes* (node 25) is diagnosed in the protonymph by vestigial or absent setae *cp* (86); in the male tritonymph by the transformation of setae *c 1* from elongate rods to small spine-like setae (reversal) (76); in the immatures by the shape of the body (the height exceeding the length) (5); in the nymphs and female by the loss of setae *vi* (59); in the female by the minute setae *c 1* (73); in the male by the loss of the median apodeme (reversal) (151), the filiform shape of setae *ra* I–II (reversal) (163), and the loss of setae *f* (187) and *r* IV (195). The characters referring to the male tritonymph and male are provisionally included at this level. Once these stages of *Rousettocoptes* have been discovered, some of these characters may be found to diagnose the entire *Teinocoptes* group (node 24).

At the next dichotomy a lineage including three species (node 26) diverges from the lineage including the remaining species. Since the type species of the genus *Tychosarcoptes*, *T. orphanus*, is included in this lineage, I propose to apply the generic name *Tychosarcoptes* to all three species. *Tychosarcoptes* is unusual in that it contains one species known only from the male, another known only from the immatures and female, and only one known for all stages. The possibility that the immatures and female described as *T. amphipterinon* are really the immatures and female of *T. orphanus* cannot be excluded. However, given the lack of evidence I will treat all three species separately.



FIGS. 152–157. *Cynopterocoptes heaneyi*, male, ventral (top) and dorsal (bottom) view of legs I (152, 153) and II (154, 155), ventral view of legs III (156) and IV (157).

Tychosarcoptes Fain, 1976

Tychosarcoptes Fain, 1976b: 145.

Diagnosed in the larva by the presence of spines posterior to the anus (20); in the female by the huge size of the posterior spine in the lateral spine zone (43); in the male by the reduction of the posterior median shield (13), and the presence of spines on the dorsum (46).

Type species *Tychosarcoptes orphanus* Fain, 1976.

Tychosarcoptes ***ptenochirus*** nov. spec.
(Figs. 160–183)

Diagnosed in the larva by the presence of scales (21); in the protonymph by the presence of a U-shaped band of scales (27); in the male tritonymph by the loss of setae *cp* (87); in the tritonymph and female by the absence of setae *pR* II (171); in the female by well developed setae *sci* (reversal) (62); in the male by the reduction of the dorsal shields (reversal) (11, 12 state 0), and the loss of fusion between coxal apodemes III and IV (reversal) (156).

Larva (Fig. 160): Two well developed patches of scales present near setae *c 1,* almost fused medially. Over 100 spines on the dorsum, strongly flattened posterior to the anus. Setae in the *d, e,* and *h* rows subequal in length.

Protonymph (Fig. 161): Cuticle of the anterior dorsum almost completely covered by scales. Scales absent from the posterior dorsum. Most perianal setae slightly membranous, setae *ps 1* small and filiform. Setae *g* and *cp* not observed. Legs IV not added.

Female tritonymph (Figs. 162, 164): Scales present on the posterior dorsum. Lateral spine series present but with small spines. All perianal setae subequal in size, membranous. Setae *g* and sometimes *3 a* present as vestigial alveoli. Legs IV present (one segment with solenidion ϕ) (Fig. 164). Resembling the protonymph in most other characters.

Male tritonymph (Figs. 163, 165): Resembling the female tritonymph but pattern of scales as in the protonymph. Lateral spine series absent. Perianal setae smaller than in the female tritonymph. Setae *g* and *3 a* present, minute. Legs IV 2-segmented, with setae *w, r,* and *d* and solenidion ϕ (Fig. 165).

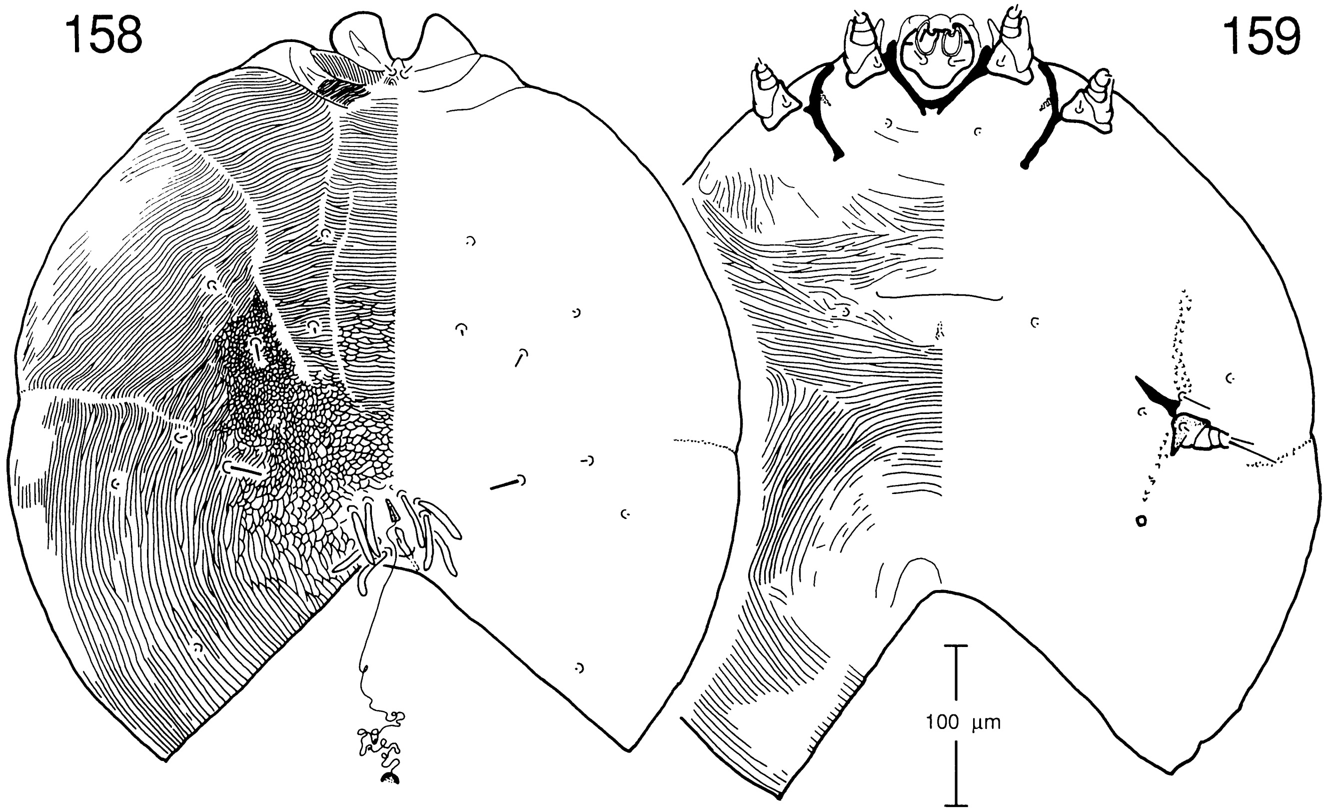
Female (Figs. 166–175): Resembling the female tritonymph in most characters. Scaling expanded on the posterior dorsum and between setae *sci.* Lateral spine series well developed (Fig. 169). Setae *d 1* distinctly membranous. Perianal setae larger than in the nymphs. Setae *g* and *3 a* absent, setae *cp* minute. Legs IV 1-segmented, with solenidion ϕ only. Anterior legs (Figs. 170–173) resembling those of *Nycteridocoptes* but setae *mG* I–II, *vF* I, and the trochanteral

Table 5. Comparative measurements of female *Cynopterocoptes*, *Rousettocoptes*, *Tychosarcoptes*, and *Chirobia*.

	Cynopterocoptes heaneyi N = 35			*Rousettocoptes mammophilus* N = 10			*Tychosarcoptes ptenochirus* N = 10			*Chirobia thoopterus* N = 10		
	av	SD	range	av	SD	range	av	SD	range	av	SD	range
gnathosoma												
length	44	5	35–52	50	5	42–59	45	4	36–53	39	2	34–41
width	43	5	36–51	46	5	41–56	33	3	30–38	34	2	30–38
subcapitular seta	8	1	6–11									
body												
length/height	325	52	219–396	561	55	473–644	419	32	381–485	308	27	267–348
width	288	47	201–365	443	33	390–475	361	22	316–388	280	38	222–323
distance *d 1*-*d 2*				40	7	27–49	40	6	30–52	30	7	19–36
distance *d 2*-*e 2*				53	7	41–65	51	4	45–56	40	6	32–48
distance *e 2*-*ps 2*				107	13	92–129	70	4	65–78	56	8	46–71
distance *ps 2*-*ps 2*				44	10	36–64	45	7	32–57	64	4	58–72
seta *vi*	–			6	1	5–8	–			–		
seta *sci*	3	1	1–5	3	1	3–4	4	1	4–5	2	1	1–2
seta *sce*	2	1	1–7	1	1	1–2	3	1	2–4	1	1	1–2
seta *c 1*	6	1	2–8	8	2	6–10	2	1	1–2	1	1	1–2
seta *c 2*	2	1	1–3	2	1	1–5	2	1	1–2	1	1	1–2
seta *cp*	1	1	1	1	1	0–1	3	1	1–5	–		
seta *c 3*	3	1	1–4	25	4	20–32	2	1	1–3	–		
seta *d 1*	5	1	4–8	20	4	14–25	18	2	15–20	46	4	38–52
seta *d 2*	4	1	2–5	4	1	2–7	3	1	2–4	47	5	37–55
seta *e 1*	17	4	11–27	35	5	25–42	22	2	20–26	31	5	23–38
seta *e 2*	1	1	1–2	1	1	1–2	1	1	1–2	1	1	1
seta *f 2*	1	1	1–2	–			–			–		
seta *h 1*	19	4	13–28	36	3	32–40	24	2	22–27	32	4	27–37
seta *h 2*	20	4	15–29	35	4	25–41	25	3	21–29	31	3	27–34
seta *h 3*	1	1	1–3	–			–			–		
seta *ps 1*	19	4	13–28	33	3	25–38	24	2	20–26	30	5	24–37
seta *ps 2*	1	1	1–3	1	1	1–2	1	1	1–2	–		
seta *1 a*	3	1	1–4	1	1	1–2	2	1	1–3	–		
seta *3 b*	2	1	1–3	2	1	2–3	2	1	1–2	–		
seta *4 a*	2	1	1–5	–			–			–		
seta *g*	–			1	1	1–2	–			–		
longest spine in the lateral row				–			16	2	14–21	5	1	4–6
copulatory cone	4	1	3–5	14	1	12–16	7	1	6–8	15	1	13–16
bursa copulatrix	57	9	38–70	419	47	382–499	163	19	132–197	107	14	92–143
coxal apodeme I	47	5	40–57	40	2	38–45	37	3	32–44	35	2	32–38
coxal apodeme II	69	8	53–84	71	5	61–79	49	3	43–53	108	7	100–122
coxal apodeme III	33	4	26–41	6	1	5–8	19	1	17–21	5	2	2–9
coxal apodeme IV	36	7	27–52									
leg I	38	4	33–49	40	4	32–44	31	5	22–39	26	2	22–29
leg II	36	4	29–46	35	5	29–43	28	2	23–32	25	3	21–29
leg III	33	3	28–39	35	2	30–38	28	2	22–31	5	2	2–9
leg IV	33	5	25–49	7	1	5–10	4	1	3–5	–		
seta *pR* I	6	2	3–10									
seta *pR* II	5	1	1–7	30	4	25–35	–			–		
seta *sR* III	2	1	1–4	4	1	3–7	2	1	1–3	–		
seta *d* III	58	12	25–85	33	6	26–42	31	4	25–40	3	1	3
seta *d* IV	43	10	22–63									
solenidion σ I	–											
solenidion φ I	6	1	4–8									
solenidion φ II	7	1	5–10									
solenidion φ III	12	2	9–16	16	1	15–18	10	1	9–11	6	1	5–7
solenidion φ IV	4	1	3–5	1			4	1	3–5	–		
solenidion ω-1 I	10	1	8–13									
solenidion ω-3 I	7	1	6–9									
solenidion ω II	12	2	8–15									

Table 6. Comparative measurements of male *Cynopterocoptes*, *Tychosarcoptes*, and *Chirobia*.

	Cyn. heaneyi N=4		*Ty. ptenochirus* N=2		*Ty. orphanus* N=1	*Chirobia thoopterus* N=4		*Chirobia brevior* N=2		*Chirobia cynopteri* N=4		*Chirobia haplonycteris* N=8		
	av	range				av	range			av	range	av	SD	range
gnathosoma														
length	28	27–29	24	26	43	27	25–27	–	23	29	27–30	32	1	31–33
width	26	21–29	29	27	46	27	25–28	–	28	28	27–29	27	1	26–28
subcapitular seta	10	9–12	22	15	30	16	13–19	–	14	14	13–17	15	2	14–16
body														
length	182	164–198	235	–	300	233	–	–	–	224	221–230	229	11	217–246
width	154	143–173	–	204	228	172	–	–	–	169	153–180	181	16	159–205
seta *vi*	11	10–12	32	–	50	30	29–32	22	26	26	22–30	23	4	17–28
seta *sci*	10	9–10	33	29	30	24	22–25	24	23	23	21–25	20	4	13–26
seta *sce*	25	15–34	28	29	57	39	38–42	31	37	33	29–37	39	6	30–49
seta *c 1*	22	20–24	42	34	52	22	21–24	28	28	23	18–25	44	4	37–52
seta *c 2*	9	8–10	37	25	33	20	18–21	20	22	20	17–22	17	4	10–22
seta *cp*	8	6–10	42	32	87	10	9–11	13	14	26	22–29	17	3	11–21
seta *c 3*	17	15–20	41	37	82	39	36–44	35	47	30	29–32	35	6	22–42
seta *d 1*	8	8–9	22	22	7	15	13–18	18	17	17	15–18	19	3	14–24
seta *d 2*	8	7–8	35	26	13	17	13–21	19	20	17	15–20	20	4	15–26
seta *e 1*	5	5–6	12	10	4	5	4–5	5	5	10	8–11	6	1	4–7
seta *e 2*	4	4–5	29	–	7	5	5	6	6	9	8–9	5	1	3–7
seta *f 2*	4	4–5	–	–	–	–		–	–	–		–		
seta *h 1*	6	5–6	11	11	6	5	4–5	5	6	9	8–9	5	1	4–6
seta *h 2*	5	4–6	11	11	5	5	5	4	5	7	7	6	1	4–7
seta *h 3*	4	4	–	–	–	–		–	–	–		–		
seta *ps 1*	6	5–6	10	10	4	5	4–5	4	4	7	7–8	5	1	4–6
seta *ps 2*	6	5–6	16	13	6	–		–	–	3	2–5	4	1	3–5
seta *1 a*	12	10–15	33	32	28	17	13–21	15	15	15	13–17	28	2	25–32
seta *3 a*	8	7–10	22	17	14	8	7–9	8	9	9	8–9	7	1	4–9
seta *3 b*	11	9–12	27	24	16	14	13–17	13	17	15	14–15	14	1	12–16
seta *g*	11	10–12	20	15	10	9	8–12	8	7	10	8–11	9	2	6–11
genital area														
length	40	36–43	40	49	42	31	27–37	–	29	48	46–52	40	4	34–46
width	28	24–32	30	28	29	22	20–28	–	19	32	25–42	25	7	21–41
coxal apodeme I	37	34–42	47	64	74	50	42–55	–	56	41	41–42	44	2	41–48
coxal apodeme II	58	55–61	63	66	118	63	60–65	–	60	55	51–60	47	11	36–64
coxal apodeme III	28	25–33	34	29	45	30	28–32	–	31	27	25–29	26	2	20–29
coxal apodeme IV	22	21–23	22	23	49	24	18–26	–	22	21	19–24	26	4	19–31
leg I	42	37–47	60	59	104	50	41–65	50	48	60	49–66	57	8	46–65
leg II	40	31–46	53	59	105	53	47–60	52	63	61	50–66	56	8	46–67
leg III	33	33–34	37	46	69	36	32–40	32	39	38	37–40	39	5	32–45
leg IV	36	34–38	22	28	47	16	14–20	–	18	20	19–21	18	2	15–21
seta *pR* I	15	12–20	38	38	50	31	26–35	26	34	33	30–38	37	7	29–47
seta *pR* II	22	19–24	35	33	60	32	29–34	28	38	32	29–34	37	4	30–41
seta *sR* III	13	11–17	33	23	21	28	26–31	–	35	21	20–22	24	8	15–36
seta *vF* I	17	10–20	40	–	49	26	24–27	21	27	26	23–30	27	2	24–29
seta *vF* II	33	28–41	33	30	–	42	35–48	31	37	38	35–43	43	4	37–47
seta *cG* I	31	26–37	47	–	66	43	42–45	28	40	43	41–44	43	6	39–48
seta *mG* I	22	18–27	38	32	58	38	35–43	27	39	34	29–38	31	2	29–32
seta *d* III	150	132–167	156	144	252	176	162–189	125	146	138	120–149	166	20	140–188
solenidion σ I	–		4	3	6	4	4–5	3	4	5	3–6	4	1	2–4
solenidion σ II	2	–	3	–	7	5	4–6	4	–	4	3–5	4	1	3–5
solenidion ϕ I	12	10–13	16	14	19	13	12–14	11	14	13	12–14	16	2	13–19
solenidion ϕ II	21	18–23	19	18	24	21	20–22	17	20	21	19–22	21	2	17–24
solenidion ϕ III	8	7–9	11	10	10	6	5–6	7	8	6	6–7	8	2	5–11
solenidion ϕ IV	6	4–7	4	5	9	2	2	–	3	2	2–3	3	1	2–5
solenidion ω-1 I	12	11–14	15	14	24	15	15–16	17	17	17	16–19	19	2	16–21
solenidion ω-3 I	10	9–10	14	13	20	11	10–11	7	11	12	12	12	1	10–13
solenidion ω II	15	13–17	19	18	24	21	20–22	17	20	18	17–20	22	2	19–24
ambulacral stalk I	13	12–13	13	13	23	14	13–15	14	13	14	13–15	13	1	12–15
ambulacral stalk II	14	12–15	12	12	24	13	11–14	12	13	13	12–14	13	1	11–16



FIGS. 158, 159. *Rousettocoptes mammophilus*, female, dorsal (158) and ventral (159) view.

setae absent. Femoral flaps I–II and trochanteral flap I very well developed. Posterior legs strongly reduced. Setae *kT* III minute, coxal apodemes IV extremely reduced. Measurements in Table 5.

Male (Figs. 176–183): Median part of the dorsum covered with spines. Anterior median shield poorly sclerotized, anal shields free. Lateral and posterior median shields absent. All posterior opisthosomal setae well developed. Striation at the posterior end of coxal fields II with thick edges but no median ventral outgrowths (see characters 53–55). Genital area oval-shaped. Legs with some indication of cuticular spines on tarsi, tibiae, and femora I–II. Setae *ra* I–II filiform. Measurements in Table 6.

Specimens were collected from a variety of sites. Females and immatures were recovered from the nipples and legs but most often from the skin overlying the arm bones. The males were found on the limbs.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Ptenochirus jagori* (Peters, 1861). Type host. PHILIPPINES: CAMARINES Sur, 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N 123°20'E, elev. 475 m, 5 March 1988, L.R. Heaney (LRH 3975), NMNH #573726, HK 88–0824–1 (holotype female, allotype male); CAMARINES SUR, 5 km N, 20 km E Naga, Mt. Isarog, 13°40'N 123°21'E, elev. 1125 m, 24 March 1988, S.M. Goodman (SMG 2332), NMNH #573742, HK 88–0824–2; BOHOL, 1 km S, 1 km E Bilar, 9°43'N 124°07'E, elev. 320 m, 18 June 1987, LRH 3697, NMNH #458291, HK 87–0618–5; LEYTE, Biliran Is., 3 km S, 5 km W Caibiran, 11°32'N 124°32'E, elev. 700 m, 29 April 1984, P.D. Heideman (PDH 2493), UMMZ #161280, HK 84–0719–2; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 8 February 1984, R.B. Utzurrum (RBU 247), BMOC 84–1575–3.

Ptenochirus minor Yoshiyuki, 1979. PHILIPPINES: LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 16 March 1987, PDH 3156, NMNH #458409, HK 87–0316–6; same locality, 20 March 1987, J.S.H. Klompen (JSHK 30), NMNH #459215, HK 87–0320–4; 22 March 1987, PDH 3226, NMNH #459234, HK 87–0322–4.

Etymology: The specific name is derived from the generic name of the type host, *Ptenochirus jagori*.

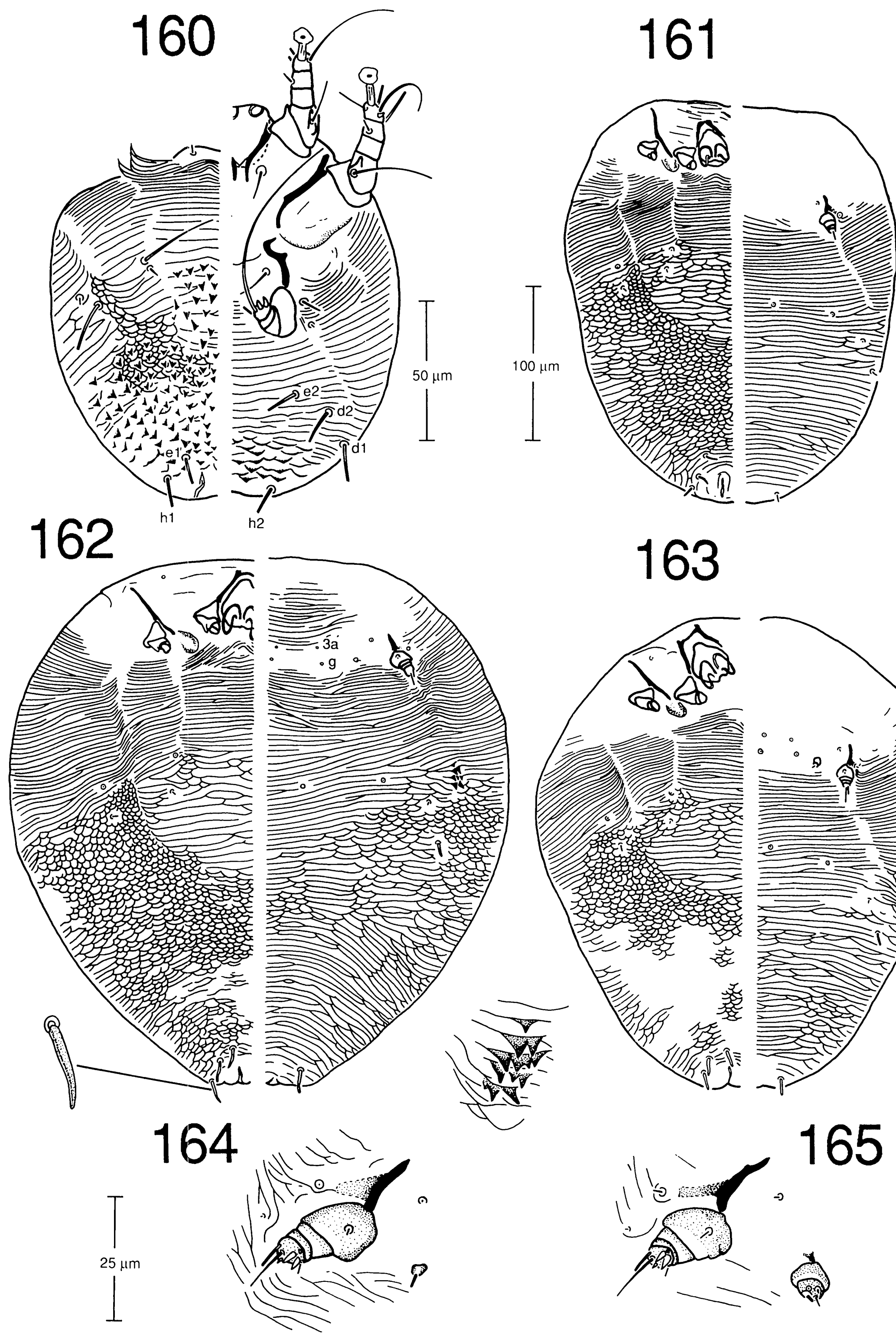
Deposition of specimens: Holotype female and allotype male in collection NMNH. Paratypes in BMNH, FMNH, IRSN, NMNH, OSU, PNC, UMMZ, and WAM.

Tychosarcoptes orphanus Fain, 1976
(Figs. 40, 41)

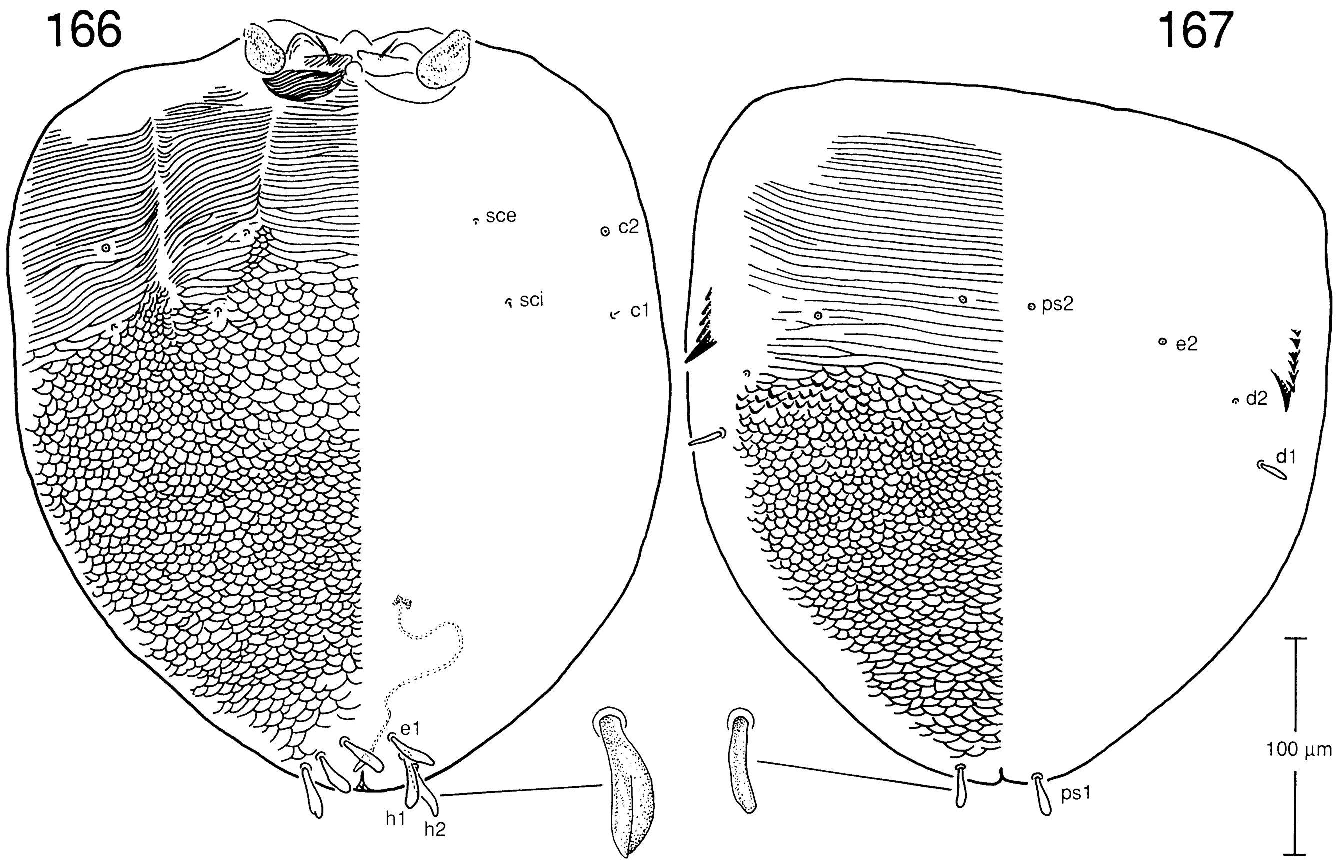
Tychosarcoptes orphanus Fain, 1976b: 148.

Diagnosed in the male by the lack of fusion between the anal shields and the posterior median shield (15).

The male is the only stage known. It differs from *T. ptenochirus* by having more developed dorsal shields (the posterior median and lateral shields are present), fewer dorsal spines, and differences in setal length (Table 6). The shape



FIGS. 160–165. *Tychosarcoptes ptenochirus*, immatures: dorsal (left) and ventral (right) view of the larva (160); anterior (left) and posterior (right) view of the protonymph (161), female tritonymph (162, including a detail drawing of the lateral spines), and male tritonymph (163) (Figs. 161–163 same scale); details of legs III–IV of the female tritonymph (164) and male tritonymph (165). Figs. 164, 165 same scale.



FIGS. 166, 167. *Tychosarcoptes ptenochirus,* female, anterodorsal (166) and posterodorsal (167) view.

of setae *w* IV, filiform to spine-like rather than a distinct spine (Fig. 40), is unique within the family.

Material examined: Male.

Host and locality: unknown (holotype, specimen in collection IRSN).

Literature records: Fain, 1976b (Type series).

Tychosarcoptes amphipterinon
(Klompen, Lukoschus, Fain, & Nadchatram, 1984)
new combination

Teinocoptes amphipterinon Klompen et al., 1984: 63.

Diagnosed in the female by the absence of spines or scales lateral to the anus (reversal) (39), the presence of setae *vF* I (168) and *pR* I (170) (reversal), the absence of setae *sR* III (200), and the loss of legs IV (215).

The larva and female have been described in detail (Klompen et al., 1984) but the nymphs were mentioned only briefly. The cuticle in the protonymph and male tritonymph is almost completely striate, with some scales medially between setae *c 1* and the anus. The protonymph lacks legs IV, the male tritonymph has 2-segmented legs IV (with solenidion ϕ and several setae; see Fig. 165). Female tritonymphs were not available for study.

During this study some females were collected from the nipples of their host; no other information on site choice is available.

Material examined: Larva, protonymph, male tritonymph, and female.

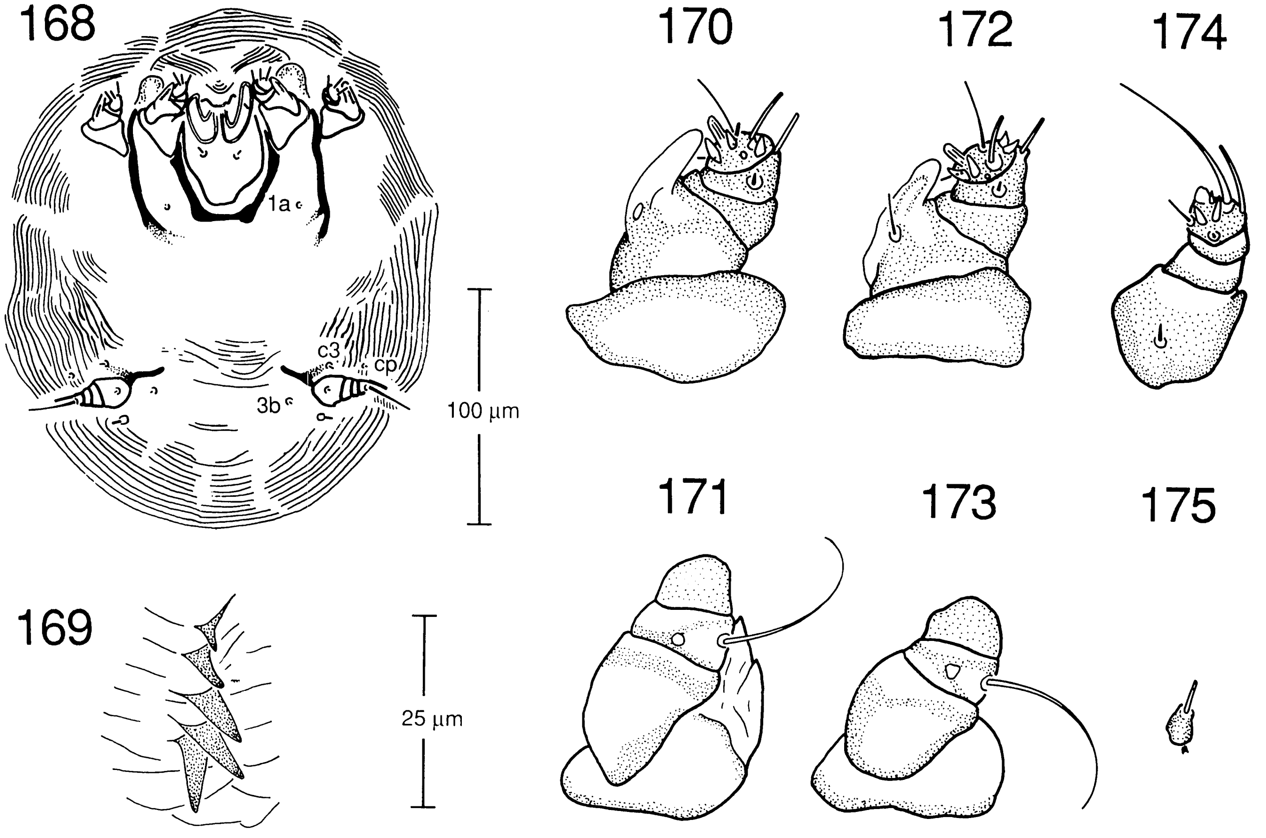
Host (Chiroptera: Pteropodidae) and localities: *Cynopterus brachyotis* (Muller, 1838). MALAYSIA: KUALA LUMPUR, 4 and 6 November 1982, F.S. Lukoschus; PAHANG, Taman Negara, 19 October 1982 (both paratypes); SABAH, Pulau Tiga, 7°21'N 117°03'E, 15 April 1988, S.M. Goodman, UMMZ #165506–165511, BMOC 88–0527–4.

Literature records: on *Cynopterus brachyotis* from MALAYSIA: PAHANG (Klompen et al., 1984 [Type series]).

Deposition of specimens: UMMZ.

The sister group of *Tychosarcoptes* (node 27) is diagnosed in the male tritonymph by the reduction of legs IV to one segment without setae (182); in the nymphs and female by vestigial or absent setae *cp* (87, 88), and the absence of setae *3 a* (127); in the female by the loss of scales posterior to the anus (reversal) (40), and the transformation of the perianal setae from membranous to filiform (reversal) (97); in the male by the fusion of the anal shields (reversal) (14), the presence of median ventral outgrowths (53), and the loss of setae *w* IV (192).

The first dichotomy within this lineage involves the two



FIGS. 168–175. *Tychosarcoptes ptenochirus*, female: ventral view (168), lateral spine series (169), ventral (top) and dorsal (bottom) view of legs I (170, 171) and II (172, 173), ventral view of legs III (174) and IV (175). Figs. 169–175 same scale.

remaining genera: *Chirobia* (excluding *C. harpyionycteris* which is transferred to *Teinocoptes*, and including *Teinocoptes brevior*), and *Teinocoptes* (excluding *T. amphipterinon* and *T. brevior* which are transferred to respectively *Tychosarcoptes* and *Chirobia*, and including *C. harpyionycteris*).

Chirobia Fain, 1959

Chirobia Fain, 1959b: 131.

Diagnosed in the larva by the presence of scales (21) extending to the anus (22), and vestigial or absent setae *cp* (84); in the protonymph by the presence of scales in at least a U-shaped band (27); in the immatures and female by the elongation of coxal apodemes II (142); in the nymphs and female by the reduction of setae *ps 2* to vestigial alveoli (120), the reduction of coxal apodemes III (147), the loss of all femoral and trochanteral setae (169, 171, 200), the loss of setae *f* III (185), and the fusion of genu and femur III (210); in the female by the loss of setae *c 3* (90, 91), and the loss of legs IV (215); in the male by the loss of fusion of coxal apodemes III and IV (reversal) (156).

Type species *Chirobia congolensis* Fain, 1959.

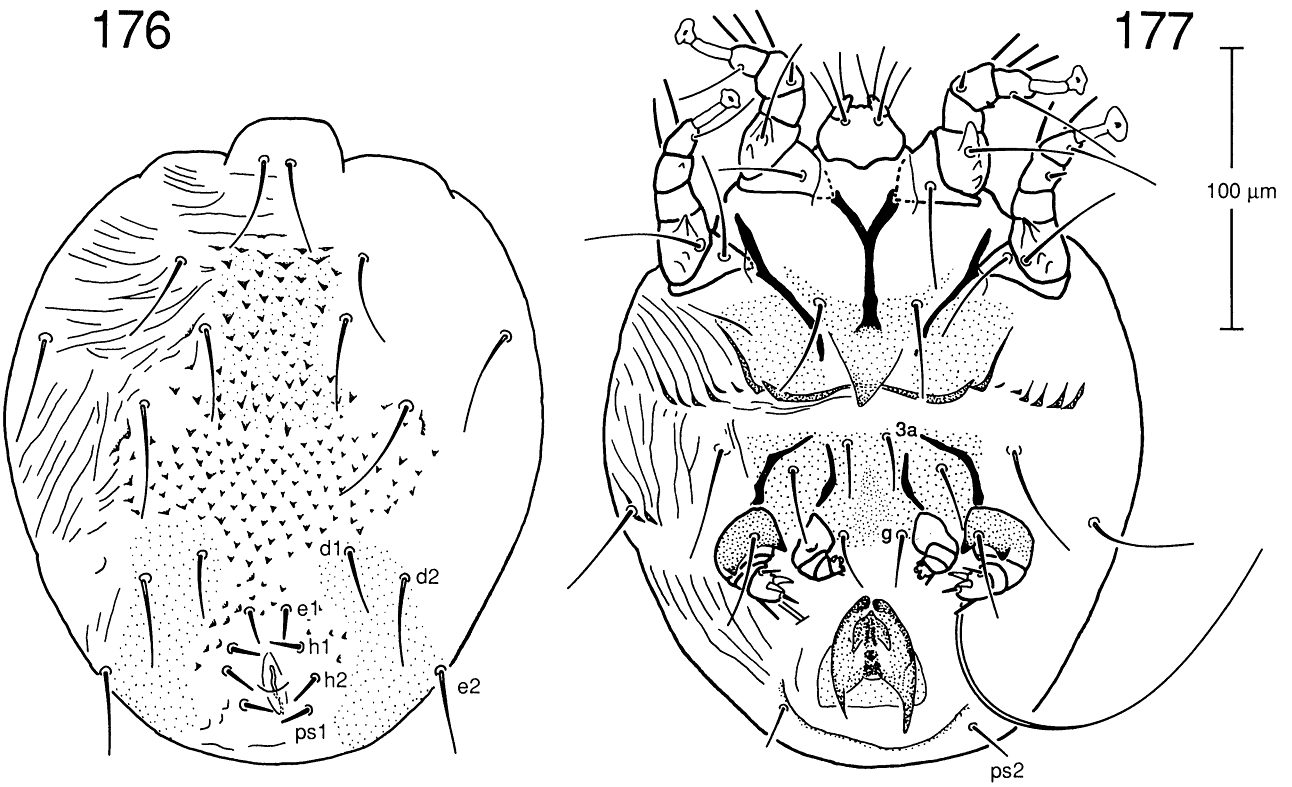
Within *Chirobia* the first dichotomy is between those species primarily associated with cynopterine Pteropodidae (*thoopterus-minor*), and those associated with rousettine, macroglossine and epomophorine Pteropodidae (*eonycteris-otophaga*) (Fig. 53).

The lineage including the cynopterine associates (node 29) is diagnosed in the nymphs and female by the strong reduction or loss of setae *d* III (181); in the female by having the lateral spine series arranged in a field (42). Within this group three lineages diverge, two monobasic (*C. brevior* and *C. thoopterus*), the third with four species. The latter lineage (node 30) is diagnosed in the larva by the presence of pointed scales (see Fig. 185) (24); in the immatures and female by the presence of scales posterior to the anus (23, 28, 40).

Relationships among the remaining species, *C. cynopteri*, *C. haplonycteris*, and *C. jagori/minor*, are unresolved. *Chirobia jagori* and *C. minor* were entered as a single taxon in this analysis, since the states for the characters examined were identical for both species (see p. 3). *Chirobia cynopteri* and *C. haplonycteris* share the presence of setae *3 a* in the male tritonymph (reversal) (127), while *C. jagori/minor* and *C. haplonycteris* share the presence of legs IV in the protonymph (reversal) (213).

Chirobia ***thoopterus*** nov. spec.
(Figs. 186, 188–191)

This species differs from the remaining cynopterine associates, and particularly from the highly similar *C. brevior*, by



FIGS. 176, 177. *Tychosarcoptes ptenochirus*, male, dorsal (176) and ventral (177) view.

the absence of pointed scales on the dorsum of the larva and by measurement differences. Setae *d 1* and *d 2* of the female are filiform, very long (45–50 µm), and subequal in length, a unique combination within *Chirobia.*

Larva (Fig. 186): Scales present anterior to the anus but absent posterior to the anus. Setae *e 1* subequal to the *d* setae.

Protonymph: Scale pattern as in the female (Fig. 188). Lateral spine series absent. Legs IV not added.

Tritonymph: Highly similar to the protonymph, but legs IV present as undifferentiated structures, at least in the male tritonymph.

Female (Figs. 188, 189): Lateral spine field well developed. Perianal setae shorter than the *d* setae. Measurements in Table 5.

Male (Figs. 190, 191): Setae *sci, c 2,* and the *d* setae thin spines. Genital area round to oval. A flap of tissue overlies the anterior section of both coxal apodemes I. Legs IV with four free segments. Measurements in Table 6.

All stages occur on the wing membrane.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Thoopterus nigrescens* (Gray, 1870). INDONESIA: SULAWESI, Lake Lindu, Tomado, 1°18′S 120°05′E, elev. 950 m, 23 January 1972, G.G. Musser, AMNH #240478, HK 86–0814–5 (holotype female); same locality, 29 January 1972, G.G. Musser, AMNH #240479, HK 86–0814–4; SULAWESI, Donggala, Lake Lindu, 1°18′S 120°05′E, January 1972, NAMRU-2 2471, NMNH #502107, HK 88–0829–14 (allotype male); same locality and date, NAMRU-2 2511, NMNH #502112, HK 88–0829–15.

Etymology: The specific name is derived from the generic name of the type host, *Thoopterus nigrescens.*

Deposition of specimens: Holotype female and allotype male in collection NMNH. Paratypes in AMNH, BMNH, IRSN, OSU, and UMMZ.

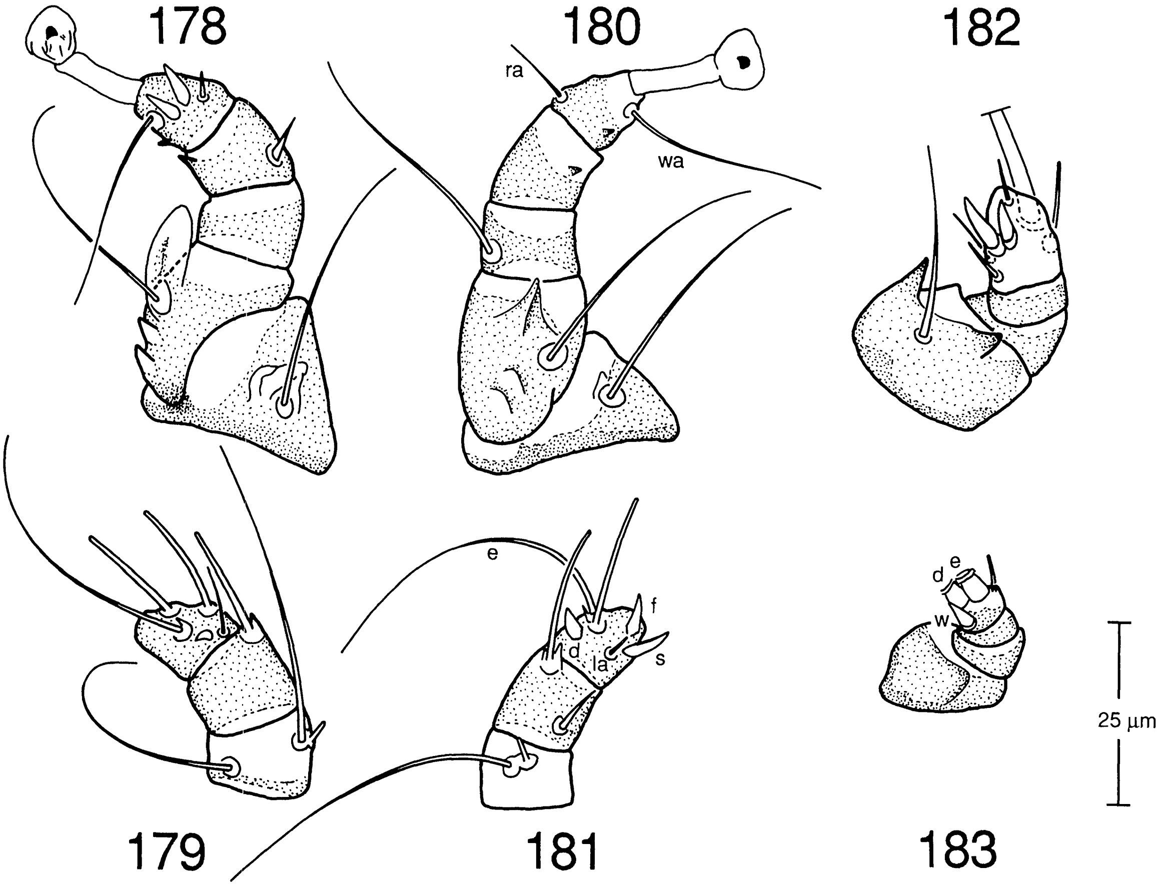
Chirobia brevior
(Fain, Lukoschus, & Nadchatram, 1982)
new combination

Teinocoptes brevior Fain et al., 1982: 78.

Diagnosed in the larva by the presence of pointed scales on the dorsum (24); in the tritonymph by the loss of legs IV (214).

This species was described from a single, damaged female containing a well developed larva, and its taxonomic status (whether a *Teinocoptes* or a *Chirobia*) was considered provisional (Fain et al., 1982). The type specimen was found in the fur of a rat, a host assumed to be accidental (Fain et al., 1982). During this study many specimens corresponding in structure and measurements to the description of the female and larva were collected from *Chironax melanocephalus* and *Rousettus celebensis,* the likely true host(s).

Chirobia brevior resembles *C. thoopterus* in most characters. Apart from the differences listed in the species diagnoses, it differs in the female by the shorter *d* (35–40 µm vs. 45–50



FIGS. 178–183. *Tychosarcoptes ptenochirus*, male: ventral (top) and dorsal (bottom) view of legs I (178, 179) and II (180, 181), ventral view of legs III (182) and IV (183).

µm) and perianal (20–25 µm vs. 30–35 µm) setae (Table 7). The males resemble each other very closely in both shape and measurements (Table 6).

All stages occur on the wing membrane.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Chironax melanocephalus* (Temminck, 1825). MALAYSIA, SELANGOR, Fraser's Hill, 3°42'N 101°45'E, elev. 1600 m, 12 April 1969, Yong Ghong Chong, AMNH #216741, HK 86–0815–11.

Rousettus celebensis Andersen, 1907. INDONESIA: SULAWESI, Likupang, 1°41'N 125°04'E, 1 February 1916, H.C. Raven, NMNH #217067, HK 88–0827–3; SULAWESI, Sumalata, 0°59'N 122°30'E, 5 November 1914, H.C. Raven, FMNH #44141, HK 86–0227–2; same data, NMNH #199774, HK 88–0827–2; NMNH #199785, HK 88–0827–4; SULAWESI, Lake Lindu, Tomado, 1°18'S 120°05'E, elev. 950 m, 22 January 1972, G.G. Musser, AMNH #240480; same locality, 23 January 1972, G.G. Musser, AMNH #240481, HK 86–0812–2; SULAWESI, Donggala, Lake Lindu, 1°18'S 120°05'E, 22 January 1972, NAMRU-2 2393, NMNH #501375, HK 88–0829–13.

Literature records: on *Rattus hoffmanni* (Matchie, 1901) (Rodentia: Muridae) from INDONESIA (Fain et al., 1982 [Type series]).

Deposition of specimens: AMNH, BMNH, FMNH, IRSN, NMNH, OSU, and UMMZ.

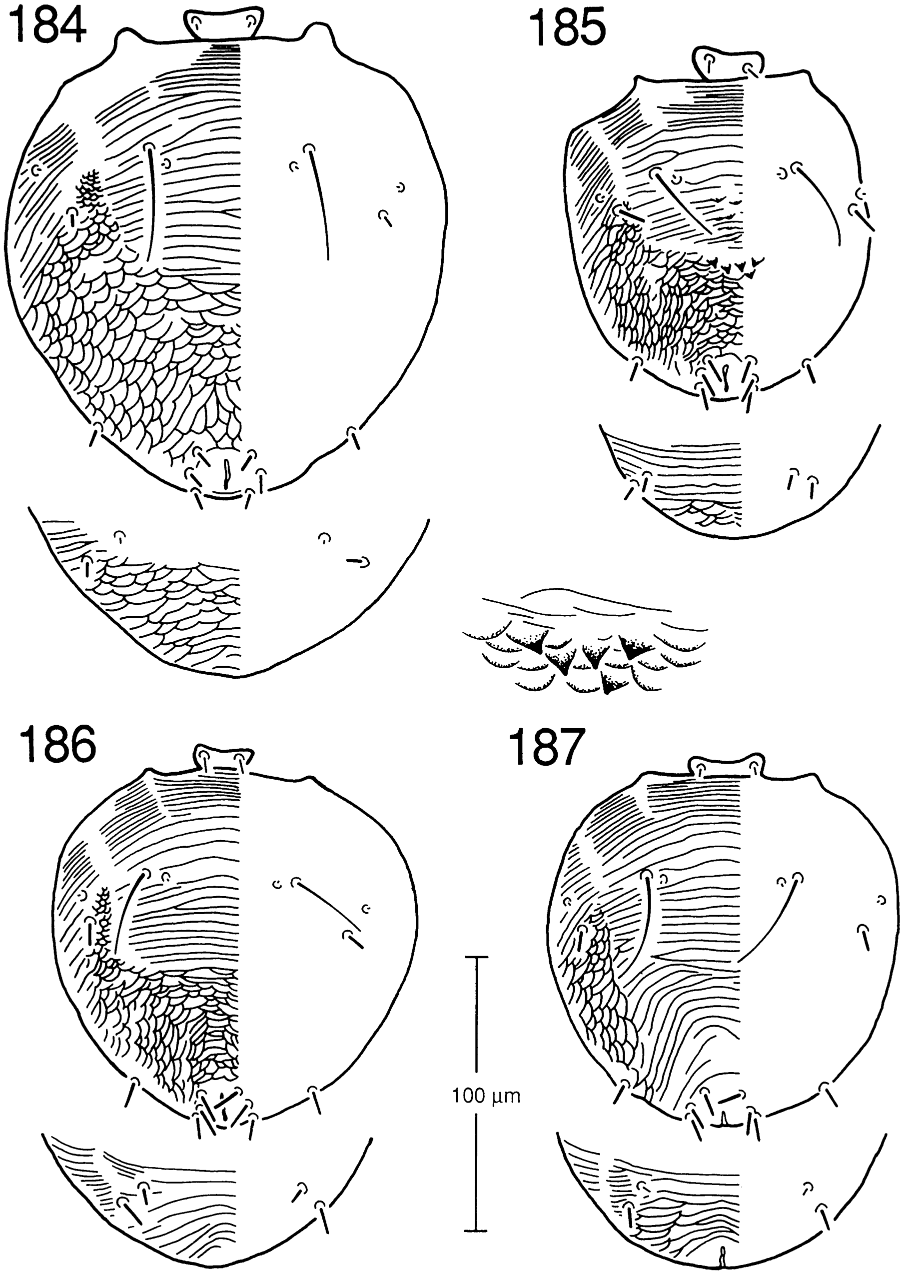
Chirobia cynopteri Klompen, Lukoschus, & Nadchatram, 1985

Chirobia cynopteri Klompen et al., 1985: 63.

Diagnosed in the male tritonymph by the presence of vestigial to minute setae *3 a* (reversal) (127); in the female by the linear arrangement of the lateral spine series (reversal) (42).

This species differs from all other *Chirobia* associated with cynopterines by the shape of setae *d 1* in the female, which are spine-like rods instead of long and filiform setae. Setae *d 1* in the nymphs and female are much longer than setae *d 2*, a characteristic shared with *C. jagori* and *C. minor*.

Specimens collected during this study allow a few additions to the original description of the male (Klompen et al., 1985). Weakly sclerotized anterior and posterior lateral shields are present, in addition to the anterior and posterior median shields. The flap covering the anterior section of coxal apodemes I, described for *C. thoopterus* and *C. brevior*, is also present. The genital area, damaged in the allotype, is elongate, resembling the genital areas of *C. haplonycteris*, *C. jagori*, and *C. minor* (see Figs. 198, 202). Measurements in Table 6.

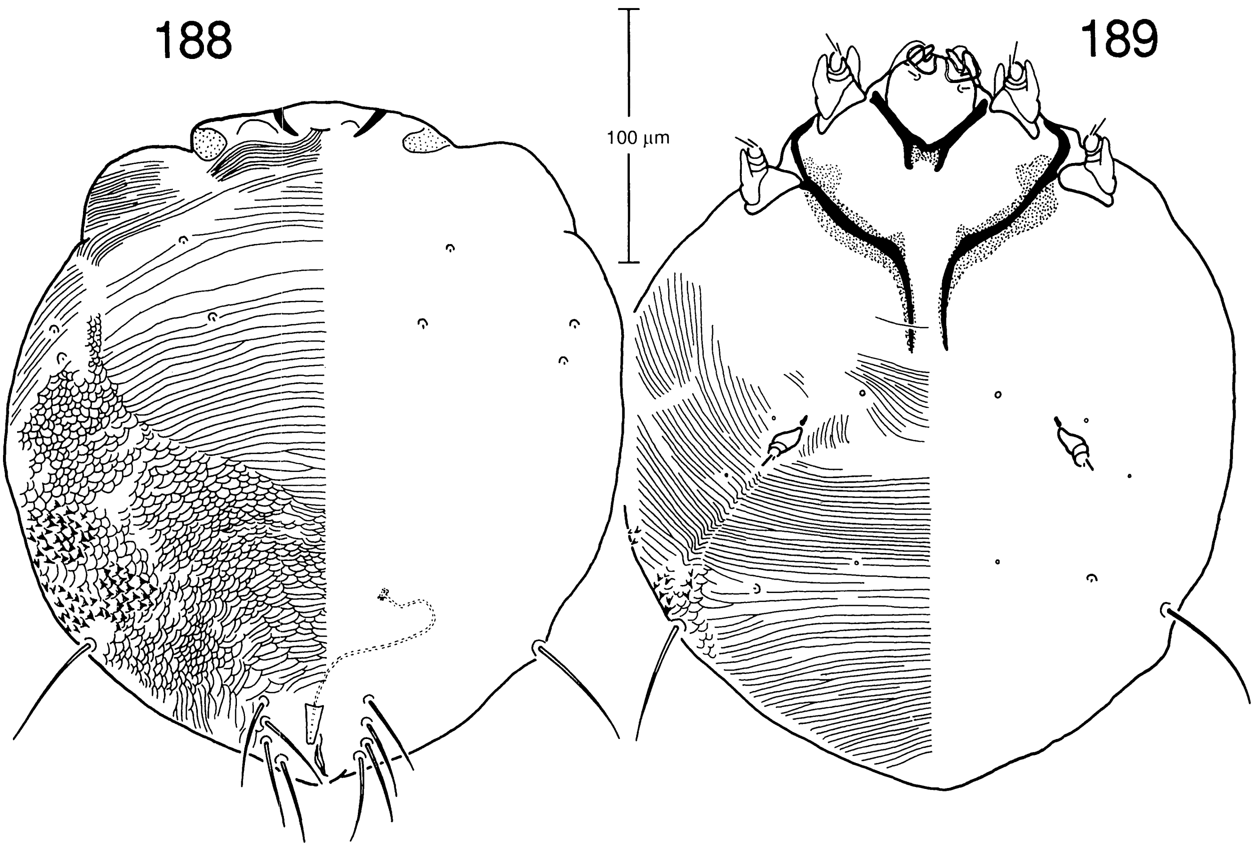


FIGS. 184–187. *Chirobia*, larvae, anterodorsal (top), and posterodorsal (bottom) view: *C. haplonycteris* (184), *C. jagori* (185, including details of the spinose scales), *C. thoopterus* (186), *C. angolensis* (187).

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Cynopterus horsfieldi* Gray, 1843. Type host. MALAYSIA: PAHANG, Taman Negara, 19 October 1982, F.S. Lukoschus (paratypes); KELANTAN, Pulai, 4°48'N 101°57'E, 14 July 1970, Yong Ghong Chong, AMNH #233952, HK 86–0813–15; same locality, 18 July 1970, Yong Ghong Chong, AMNH #233953, HK 86–0813–14.

Cynopterus brachyotis (Muller, 1838). INDONESIA: LOMBOK, September 1987, D. Kitchener (L 6), WAM, HK 88–0411–1; SUMBAWA, Merente, 8°33'S 117°01'E, 9 May 1988, D. Kitchener (S 68), WAM, HK 89–0208–3; SUMBAWA, Teluk Santong, 8°44'S 117°54'E, 22 May 1988, S 300, WAM, HK 89–0301–1; MALAYSIA: SABAH, Pulau Tiga, 7°21'N 117°03'E, 15 April 1988, S.M. Goodman, UMMZ #165506–165511, BMOC 88–0527–1 & 88–0527–5; PHILIPPINES: CATANDUANES, 8 km W Gigmoto, 13°47'N 124°19'E, elev. 250 m, 16 February 1988, E.A. Rickart (EAR 1651), NMNH



Figs. 188, 189. *Chirobia thoopterus,* female, anterodorsal view (188), and posterodorsal and ventral view (189).

#573193, HK 88–0823–1; Bohol, 1 km S, 1 km E Bilar, 9°44′N 124°07′E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3679), NMNH #458002, HK 87–0618–3.

Cynopterus titthaecheilus (Temminck, 1825). INDONESIA: Lombok, September 1987, L 7, WAM, HK 88–0425–1; Lombok, Pelangan, 8°48′N 115°56′E, 12 October 1987, L 277, WAM, HK 88–0407–1; same locality, 13 October 1987, L 292, WAM, HK 88–0422–1.

Literature records: on *Cynopterus horsfieldi* and *C. brachyotis* from MALAYSIA: Pahang (Klompen et al., 1985 [Type series]).

Deposition of specimens: AMNH, BMNH, CUIC, FMNH, MAK, NMNH, PNC, UMMZ, WAM, and ZIAC.

Chirobia ***haplonycteris*** nov. spec.
(Figs. 184, 192–198)

Diagnosed in the larva by the absence of pointed scales (reversal) (24); in the protonymph by the presence of legs IV (reversal) (213); in the male tritonymph by the presence of setae *3 a* (reversal) (127); in the nymphs and female by the presence of setae *ps 2* (reversal) (120), and well developed setae *d* III (reversal) (181); in the male by the loss of the anterior lateral shields (11, 12 state 0), and the presence of setae *e* III (190) (unique reversals within the *Chirobia*/*Teinocoptes* clade).

Larva (Fig. 184): Scales present both anterior and posterior to the anus. Setae *e 2* much smaller than the *d* setae.

Protonymph: Scales present both anterior and posterior to the anus. Setae *e 1* much smaller than the other perianal setae. The *d* setae relatively short, filiform. Setae *g* present as vestigial alveoli in some specimens (ventral area unclear in most others). Legs IV present in some specimens (without solenidion ϕ) (Fig. 194).

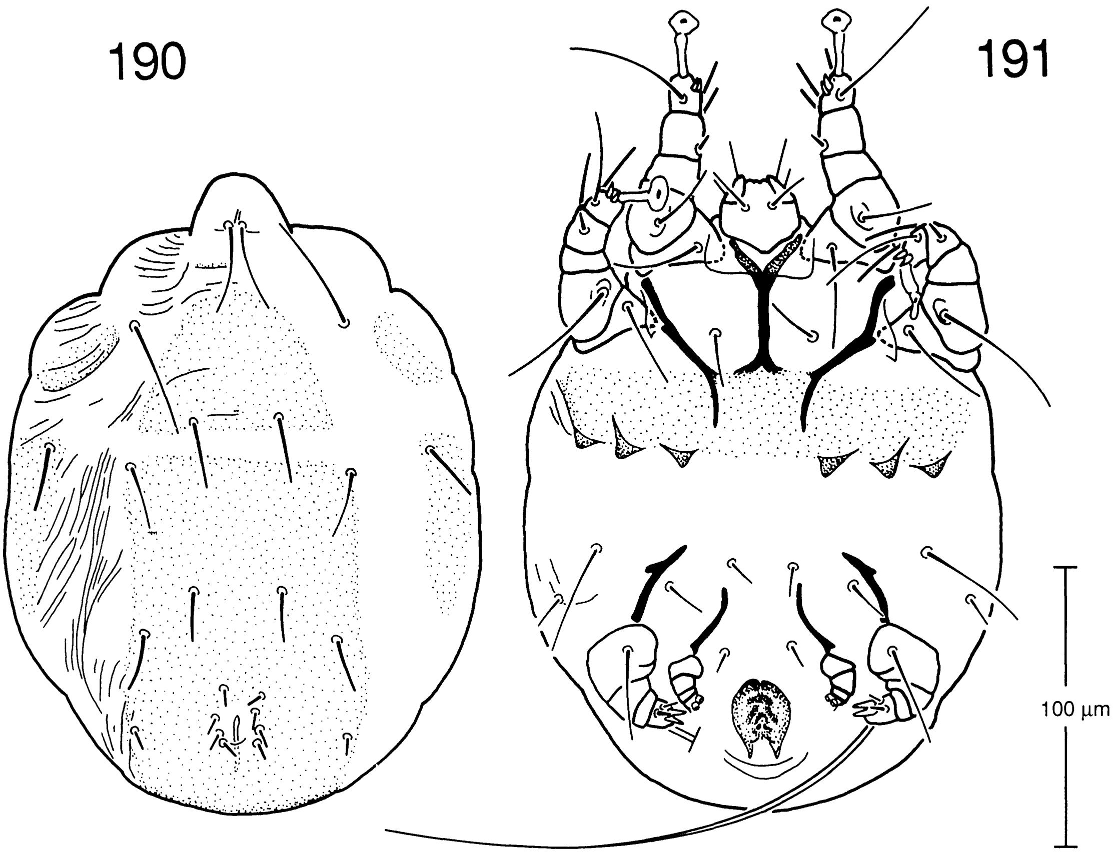
Female tritonymph: Resembling the protonymph but opisthosomal setae longer. Setae *g* and legs IV not observed (Fig. 195).

Male tritonymph: Resembling the female tritonymph but setae *g* and *3 a* vestigial alveoli, and legs IV present (with a small solenidion ϕ) (Fig. 196).

Female (Figs. 192, 193): Resembling the female tritonymph but opisthosomal setae longer. Setae *d 2* almost twice as long as setae *d 1.* Lateral spine field, absent in the protonymph and small in the tritonymphs, very well developed. Internal end of the bursa copulatrix tube-like and well sclerotized. Measurements in Table 7.

Male (Figs. 197, 198): Resembling the male of *C. thoopterus* but sclerotization of the dorsal shields much weaker, an elongate instead of a round to oval genital area, and the flap covering the anterior section of both coxal apodemes I absent. Measurements in Table 6.

All stages were collected from the wing membrane.



Figs. 190, 191. *Chirobia thoopterus,* male, dorsal (190) and ventral (191) view.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Haplonycteris fischeri* Lawrence, 1939. PHILIPPINES: Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21′N 123°11′E, elev. 850 m, 4 October 1982, P.D. Heideman (PDH 914), NMNH #548564, HK 83–1109–1 (holotype female); same locality, 1 August 1982, PDH 682, UMMZ #159848, HK 83–1216–4; 27 August 1982, PDH 777, UMMZ #159859, BMOC 83–1600–25; same date, PDH 778, UMMZ #159860, HK 83–1218–2 (allotype male); 4 November 1982, PDH 1034, UMMZ #159879, HK 83–1217–1; same date, PDH 1043, UMMZ #159887, HK 83–1216–1; 5 November 1982, PDH 1049, UMMZ #159889, HK 83–1219–1; same date, PDH 1063, UMMZ #159893, HK 83–1206–3; 6 November 1982, PDH 1064, UMMZ #159894, HK 83–1211–2; 8 November 1982, PDH 1086, UMMZ #159898, HK 83–1211–1; 6 December 1982, PDH 1187, UMMZ #159903, HK 88–0208–2; 10 December 1982, PDH 1224, UMMZ #159911, HK 88–0202–2; 9 January 1983, PDH 1352, UMMZ #159924, HK 88–0118–3; 10 February 1983, PDH 1501, UMMZ #159930, HK 88–0111–2; 5 May 1983, PDH 1794, UMMZ #159951, HK 88–0105–4; Negros Oriental, 2 km S, 3 km W Valencia, 9°16′N 123°13′E, elev. 500 m, 11 April 1988, E.A. Rickart (EAR 1934), NMNH #573657, HK 88–0828–8; Bohol, 1 km S, 1 km E Bilar, 9°44′N 124°07′E, elev. 320 m, 20 June 1987, L.R. Heaney (LRH 3751), NMNH #459083, HK 87–0620–3; Catanduanes, 8 km W Gigmoto, 13°47′N 124°19′E, elev. 200 m, EAR 1674, NMNH #573222, HK 88–0828–7; Leyte, Biliran Is., 3 km S, 5 km W Caibiran, 11°32′N 124°32′E, 30 April 1984, LRH 2592, UMMZ #161361, MAH 85–0131–3; Leyte, 10 km N, 4 km E Baybay, 10°47′N 124°50′E, elev. 700 m, 15 March 1987, PDH 3149, NMNH #458189, HK 87–0315–1; same locality, 19 March 1987, PDH 3182, NMNH #459087, HK 87–0319–6.

Etymology: The specific name is derived from the generic name of the type host, *Haplonycteris fischeri.*

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, FMNH, IRSN, NMNH, OSU, PNC, UMMZ, and WAM.

The assemblage of *Chirobia jagori* and *C. minor* is diagnosed by the presence of legs IV in the protonymph (reversal) (213).

These species differ from all other *Chirobia* by the combination of the following characters: pointed scales in the larva present, setae *d 1* and *d 2* in the female filiform, and setae *d 1* in the female much longer than setae *d 2.*

Chirobia ***jagori*** nov. spec.
(Figs. 185, 199–202)

Distinguished by the characters mentioned above.

Larva (Fig. 185): Scales both anterior and posterior to the

Table 7. Comparative measurements of female *Chirobia*.

	brevior			*haplonycteris*			*jagori*			*minor*		
	N=5			N=10			N=10			N=10		
	av	SD	range	av	SD	range	av	SD	range	av	SD	range
gnathosoma												
length	32	3	27–36	51	5	39–59	44	2	42–47	46	2	44–49
width	27	3	22–39	39	4	34–45	32	2	29–36	35	4	29–41
body												
length/height	308	32	271–344	398	57	292–495	342	29	303–391	395	30	337–433
width	248	26	218–288	328	32	254–357	329	32	265–379	375	18	342–397
distance *d 1-d 2*	32	8	20–39	50	13	28–70	32	6	20–38	35	3	30–40
distance *d 2-e 2*	41	6	36–51	39	6	30–48	40	5	31–47	47	3	42–53
distance *e 2-ps 2*	42	1	41–43	56	9	43–71	67	3	62–71	69	6	56–74
diatance *ps 2-ps 2*	24	1	24	27	4	21–34	51	7	40–60	50	9	37–66
seta *vi*	–			–			–			–		
seta *sci*	1	1	1–2	2	1	2–3	2	1	1–2	2	1	1–2
seta *sce*	1	1	1	1	1	1–2	1	1	1	1	1	1–2
seta *c 1*	1	1	1	1	1	1–2	1	1	1–2	1	1	1–2
seta *c 2*	1	1	1	1	1	1–2	1	1	1–2	1	1	1–2
seta *cp*	–			–			–			–		
seta *c 3*	–			–			1	1	1–2	–		
seta *d 1*	37	2	34–40	30	8	19–44	30	5	21–37	18	3	14–22
seta *d 2*	36	4	32–41	63	7	53–77	15	5	6–22	8	2	5–10
seta *e 1*	23	1	21–24	9	2	5–13	38	7	28–52	28	3	24–32
seta *e 2*	1	1	1–2	1	1	1	1	1	1	1	1	1–2
seta *h 1*	23	2	20–26	40	5	33–49	38	5	29–45	31	4	26–39
seta *h 2*	24	5	19–30	42	4	37–49	36	5	30–43	30	3	26–35
seta *ps 1*	23	2	20–25	41	2	39–45	37	5	29–45	31	4	26–38
seta *ps 2*	–			1	1	1	–			–		
seta *1 a*	–			1	–	–	–			–		
seta *3 b*	–			1	1	1	–			–		
seta *g*	–			–			–			–		
longest spine in lateral row	4	1	3–5	7	1	5–8	4	1	2–5	4	1	3–5
copulatory cone	15	1	13–16	15	1	13–17	16	1	15–18	14	1	12–16
bursa copulatrix	94	6	85–100	177	28	133–213	129	13	105–147	123	15	104–138
postvulvar sclerotization												
length	–			–			–			–		
width	–			–			–			–		
coxal apodemes I	29	1	27–29	38	2	35–40	39	2	35–42	37	2	35–41
coxal apodemes II	84	7	5–91	86	9	78–109	118	5	111–126	116	8	98–126
coxal apodemes III	3	1	2–3	9	3	3–15	5	2	3–9	3	1	2–4
leg I	24	2	23–27	32	3	26–37	29	3	26–37	36	5	26–41
leg II	21	2	20–24	29	4	23–37	29	3	24–34	29	3	26–33
leg III	3	1	2–3	13	2	9–15	5	2	3–9	3	1	2–4
leg IV	–			–			–			–		
seta *pR* II	–			–			–			–		
seta *sR* III	–			–			–			–		
seta *d* III	–			16	4	10–21	7	–	–	–		
solenidion φ III	5	1	4–6	8	1	6–11	5	1	5–6	5	1	5
solenidion φ IV	–			–			–			–		

anus. About 5–10 pointed scales present, median dorsal. Setae *e 2* subequal to the *d* setae.

Nymphs: as in *C. haplonycteris* but setae *d 2* shorter than setae *d 1*.

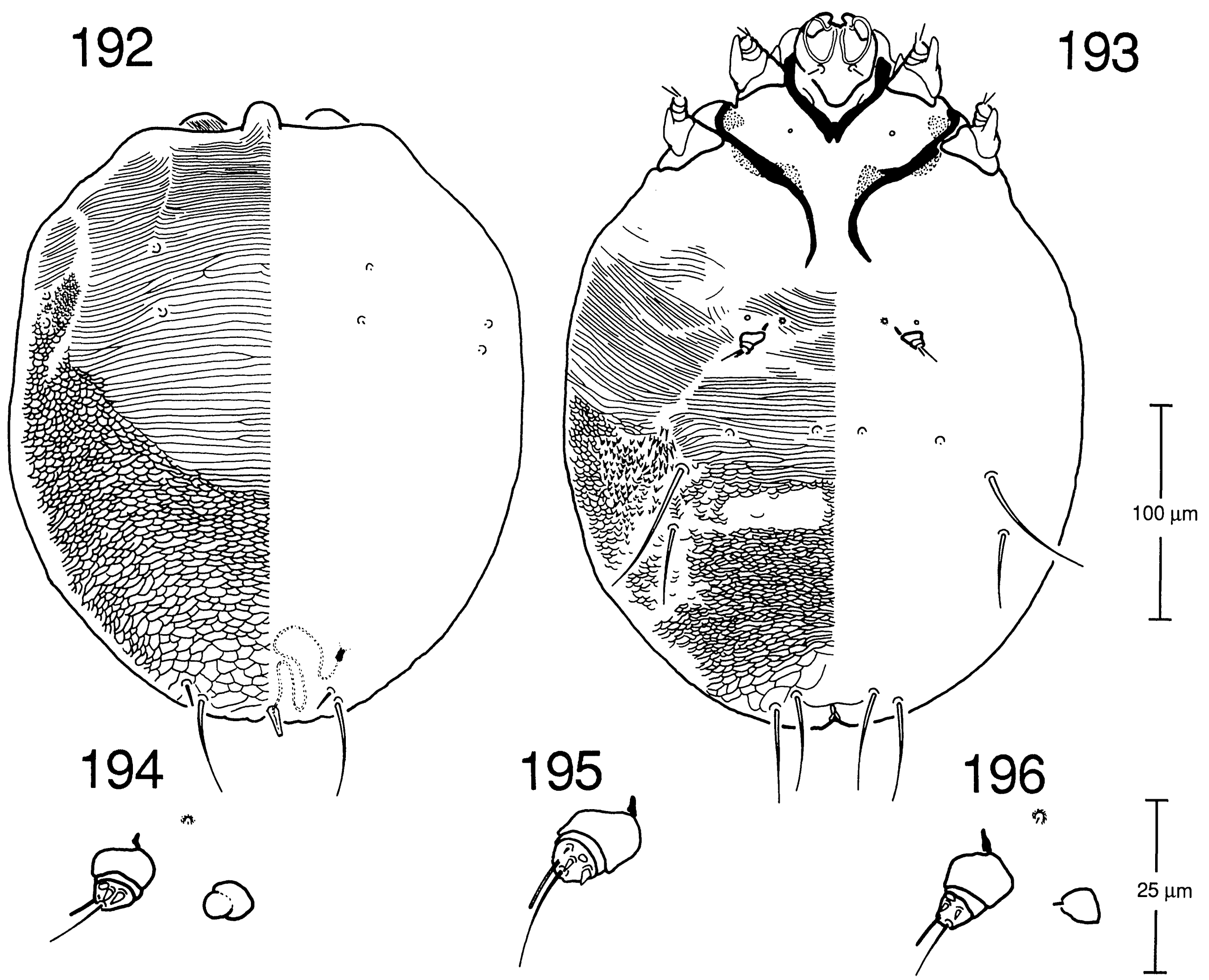
Female (Figs. 199, 200): Lateral spine field well developed. Setae *d 1* 2–3 X as long as setae *d 2*. Internal end of the bursa copulatrix small, disc-like. Legs IV absent. Measurements in Table 7.

Male (Figs. 201, 202): Resembling the male of *C. thoopterus* but with relatively long perianal setae (Table 8) and an elongate genital area.

All stages occur on the wing membrane.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Ptenochirus jagori* (Peters, 1861). PHILIPPINES: Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 5 November 1982, P.D. Heideman (PDH 1056), UMMZ #160004, HK 83–1125–1 (holotype fe-



FIGS. 192–196. *Chirobia haplonycteris:* female, anterodorsal view (192), and posterodorsal and ventral view (193); legs III–IV of the protonymph (194), female tritonymph (195), and male tritonymph (196) (Figs. 194–196 same scale).

male); same locality, 3 July 1982, PDH 508, UMMZ #159991, HK 83–1203–2; 30 August 1982, PDH 842, UMMZ #159994, HK 83–1202–4; 1 September 1982, PDH 852, UMMZ #159995, HK 83–1111–3; 4 October 1982, PDH 917, UMMZ #159996, HK 83–1123–1; same date, PDH 918, HK 83–1111–1; PDH 922, UMMZ #159997, HK 83–1109–2 (allotype male); 4 November 1982, PDH 1026, UMMZ #159999, HK 83–1202–2; same date, PDH 1027, UMMZ #160000, HK 83–1202–1; 5 November 1982, PDH 1054, UMMZ #160003, HK 83–1031–3; same date, PDH 1055, HK 83–1121–2; PDH 1059, UMMZ #160005, HK 83–1031–1; PDH 1061, HK 83–1111–4; 6 November 1982, PDH 1069, UMMZ #160007, HK 83–1203–1; 8 February 1983, PDH 1494, UMMZ #160037, BMOC 83–1600–84; 8 February 1984, R.B. Utzurrum (RBU 247), BMOC 84–1575–3; NEGROS ORIENTAL, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 10 May 1987, E.A. Rickart (EAR 1567), NMNH #459201, HK 87–0510–5; BOHOL, 1 km S, 1 km E Bilar, 9°44'N 124°07'E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3697), NMNH #458291, HK 87–0618–5; same locality and date, LRH 3700, NMNH #459170, HK 87–0618–6; CAMARINES SUR, 5 km N, 20 km E Naga, Mt. Isarog, 13°40'N 123°21'E, elev. 1125 m, 24 March 1988, S.M. Goodman (SMG 2332), NMNH #573742, HK 88–0824–2; CAMARINES SUR, 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N 123°20'E, elev. 475 m, 5 March 1988, LRH 3975, NMNH #573726, HK 88–0824–1; LEYTE, Maripipi Is., 2 km N, 3 km W Maripipi, 11°47'N 124°18'E, elev. 740 m, 18 April 1987, PDH 3335, NMNH #458345, HK 87–0418–3; LEYTE, Biliran Is., 3 km S, 5 km W Caibiran, 11°32'N 124°32'E, elev. 700 m, 29 April 1984; PDH 2493, UMMZ #161280, HK 84–0719–2; LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 21 March 1987, PDH 3216, NMNH #458319, HK 87–0321–4; LEYTE, 4 km S, 1 km E Inopacan, 10°28'N 124°45'E, elev. 50 m, 6 March 1987, D. Kitchener (P 89), NMNH, HK 87–0306–2; LEYTE, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 12 March 1987, PDH 3140, NMNH #458318, HK 87–0312–1; same locality, 27 March 1987, J.S.H. Klompen (JSHK 40), NMNH #458320, HK 87–0327–4; ROMBLON, Sibuyan Is., 1 km S, 1

FIGS. 197, 198. *Chirobia haplonycteris*, male, dorsal (197) and ventral (198) view.

km E Magdiwang, Tampayan, 12°29'N 122°31'E, elev. 10 m, 28 April 1989, LRH 4263, FMNH #136984, HK 89-0711-10.

Etymology: The specific name is derived from that of the type host, *Ptenochirus jagori*.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, CUIC, FMNH, IRSN, NMNH, OSU, PNC, UMMZ, WAM, ZIAC, and ZIZM.

Chirobia ***minor*** nov. spec.

This species closely resembles *C. jagori* but differs by the much smaller size of the *d* and perianal setae in the female (setae *d 1* 18 vs. 30 µm; setae *d 2* 8 vs. 15 µm; perianal setae 28–31 vs. 36–38 µm) (Table 7). The two species may also differ by the presence or absence of spine-like structures dorsomedial to setae *c 1* in the larva. These structures are not pointed scales (there are no scales in that region of the dorsum), but are directly derived from striations. They are poorly developed in *C. jagori* (Fig. 185) but very distinct in *C. minor*. Including the pointed scales, larvae of *C. minor* have 15–20 "spines," compared to the 5–10 in *C. jagori*. However, the degree of development of these structures is variable within and between populations. The males appear to be very similar, and the single available male of each did not allow a study of variation. Measurements in Table 8.

All stages were found on the wing membrane.

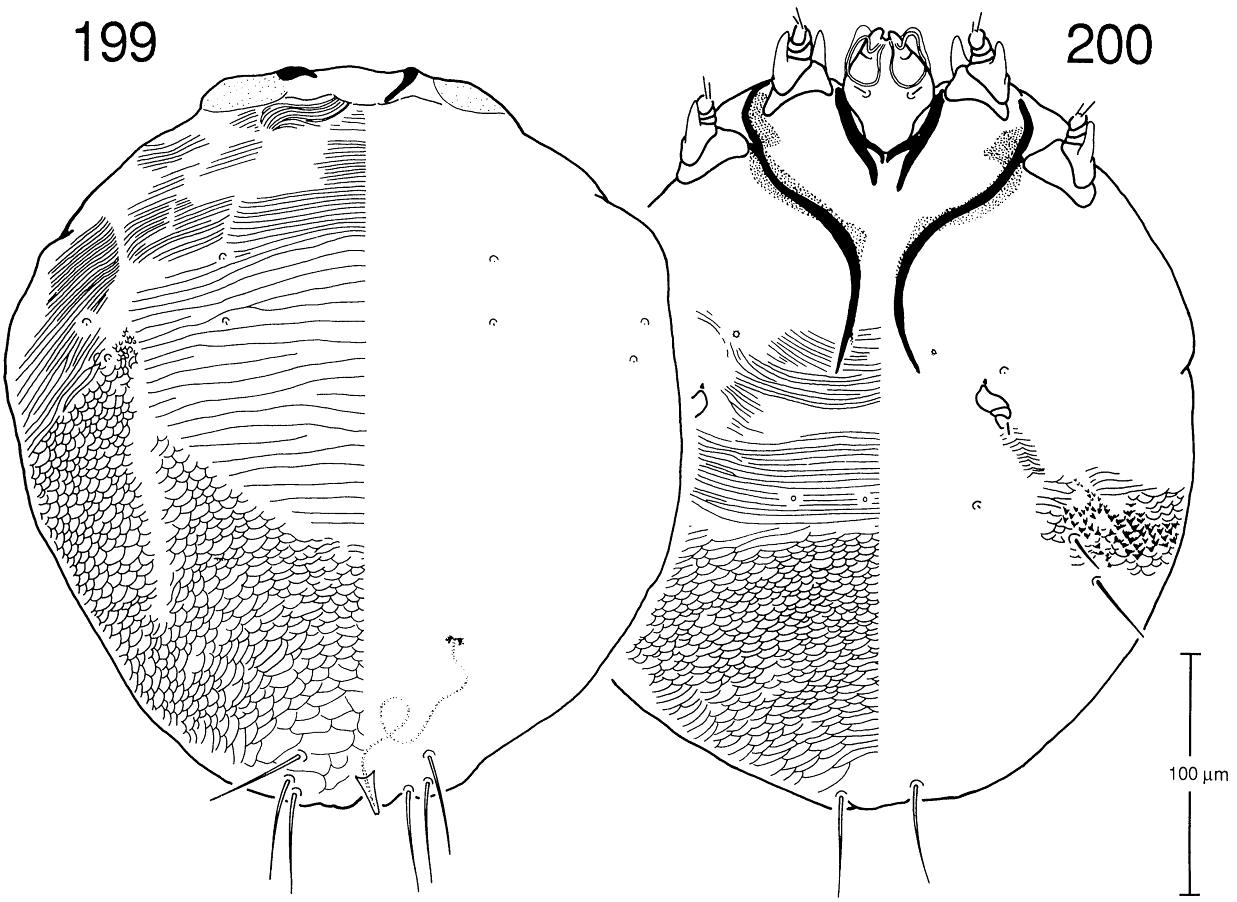
Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Ptenochirus minor* Yoshiyuki, 1979. PHILIPPINES: LEYTE, 10 km N, 2 km E Baybay, 10°47'N 124°49'E, elev. 320 m, 11 March 1987, P.D. Heideman (PDH 3126), NMNH #459224, HK 87-0311-3 (holotype female); same locality, 10 March 1987, PDH 3112, NMNH, HK 87-0310-2; same date, PDH 3115, NMNH, HK 87-0310-3; E.A. Rickart (EAR 1318), NMNH #458424, HK 87-0310-4; LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 16 March 1987, PDH 3156, NMNH #458409, HK 87-0316-6; same locality, 17 March 1987, J.S.H. Klompen (JSHK 9), NMNH, HK 87-0727-16 (wash); 22 March 1987, PDH 3226, NMNH #459234, HK 87-0322-4 (allotype male); LEYTE, Biliran Is., 3 km S, 5 km W Caibiran, 11°32'N 124°32'E, elev. 700 m, 28 April 1984, L.R. Heaney (LRH 2545), UMMZ #161227, HK 84-0725-3.

Etymology: The specific name is derived from that of the type host, *Ptenochirus minor*.

Deposition of specimens: Holotype female and allotype male in collection NMNH. Paratypes in BMNH, FMNH, NMNH, PNC, and UMMZ.

Most of the species in the sister group of the lineage associated with cynopterines (node 31) are associated with hosts in the genus *Rousettus*. This lineage is diagnosed in the trito-



Figs. 199, 200. *Chirobia jagori*, female, anterodorsal (199) and posterodorsal/-ventral (200) view.

nymph by the loss of legs IV (214); in the nymphs and female by the relative reduction in height of the body (reversal) (3, 5), and the complete loss of setae *g* (123); in the female by the loss of the lateral spine zone (reversal) (41); in the male by the fusion of the femur and genu of legs IV (211). Setae *d 1* and *d 2* in the nymphs and females are spine-like rods with slightly bifurcate tips.

Basal relationships within this lineage are poorly resolved as evidenced by the five lineages arising at node 31, four of which are monobasic.

Chirobia eonycteris
Klompen, Lukoschus, Fain, & Nadchatram, 1982

Chirobia eonycteris Klompen et al., 1982: 51.

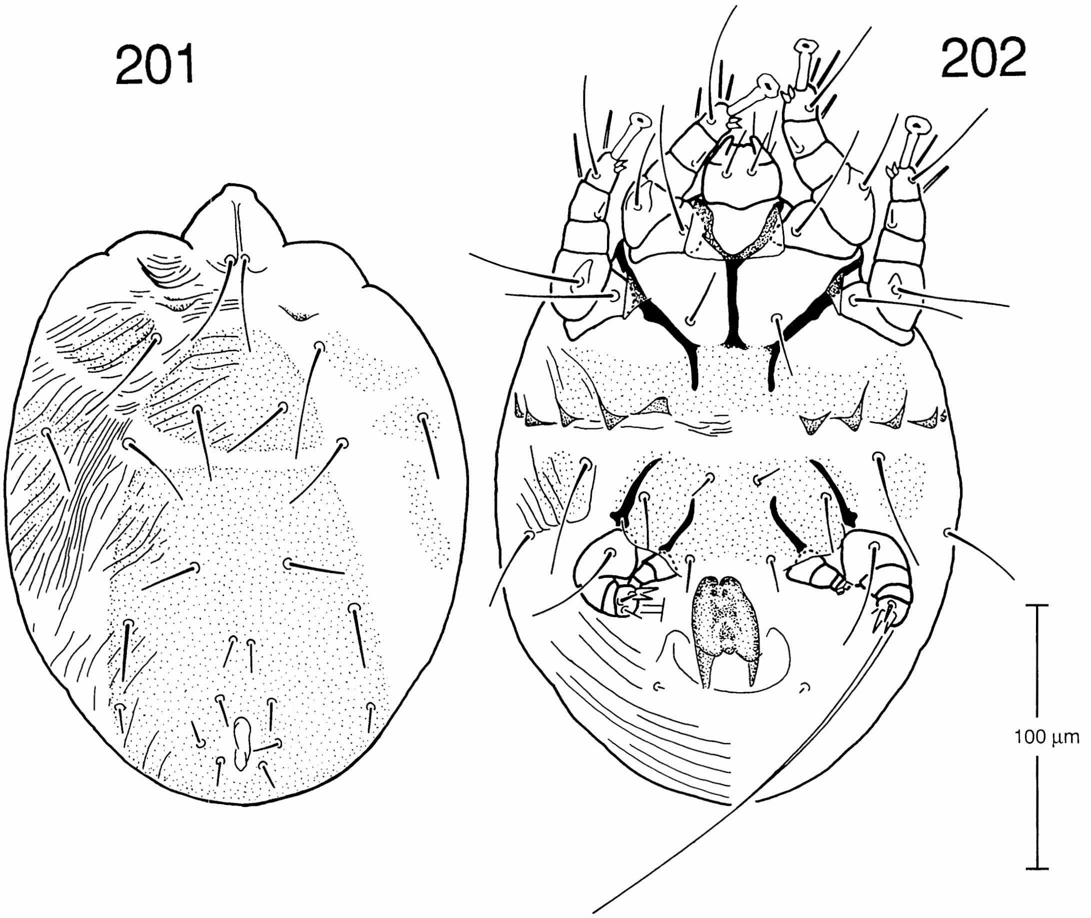
Diagnosed in the nymphs and female by the complete loss of setae *ps 2* (119); in the female by the presence of scales posterior to the anus (40).

The larva, female, and male have been described previously (Klompen et al., 1982). Scales are absent immediately anterior to the anus of the nymphs. The presence of setae *4 a* in the male, indicated in the original description, is erroneous. Examination of several males and reexamination of the allotype, showed these setae to be absent. Measurements of females and males in Tables 8 and 9.

All stages occur on the wing membrane.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Eonycteris spelaea* (Dobson, 1871). Type host. INDONESIA: Lombok, Batu Koq, 8°19'S 116°26'E, 7 October 1987, D. Kitchener (P 409), WAM, HK 88–0406–1; same locality, 31 October 1987, D. Kitchener (L 201), WAM, HK 88–0410–1; Lombok, Pelangan, 8°48'S 115°56'E, 12 October 1987, L 271, WAM, HK 88–0421–1; same locality, 13 October 1987, L 300, WAM, HK 88–0413–1; Sumbawa, Teluk Santong, 8°44'S 117°54'E, 21 May 1988, D. Kitchener (S 294), WAM, HK 89–0208–1; MALAYSIA: Pahang, Raub Cave, 13 May 1979, Rudnick, IMR, F.S. Lukoschus (paratypes); Pahang, Bentong, Bukit Chintamani, 13 October 1982, F.S. Lukoschus; PHILIPPINES: Bohol, 1 km S, 1 km E Bilar, 9°43'N 124°07'E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3704), NMNH #459052, HK 87–0618–7; Leyte, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 5 April 1987, J.S.H. Klompen (JSHK 74), NMNH, HK 87–0405–1; Negros Oriental, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 24 October 1982, P.D. Heideman (PDH 1017), UMMZ #158941, HK 84–0411–1; same locality, 24 March 1983, PDH 1673, UMMZ #158944, HK 84–0329–1; 11 June 1987, JSHK 97, NMNH #458164, HK 87–0611–2; same date, JSHK 98, NMNH #458165, HK 87–0611–1; Negros Ori-



Figs. 201, 202. *Chirobia jagori*, male, dorsal (201) and ventral (202) view.

ental, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 22 February 1987, LRH 2907, NMNH #459070, HK 87–0222–3; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 4 October 1982, PDH 920, UMMZ #158918, BMOC 83–1600–39; same locality, 4 November 1982, PDH 1028, UMMZ #158920, BMOC 83–1600–57.

Eonycteris robusta Miller, 1913. PHILIPPINES: Catanduanes, 8 km W, 1 km N Gigmoto, 13°48'N 124°19'E, elev. 200 m, 24 February 1988, E.A. Rickart (EAR 1695), NMNH #573211, HK 88–0713–2; Maguindanao, Cotabato City, 7°13'N 124°15'E, 26 December 1946, W. Alcasid, FMNH #56576, HK 86–0225–16; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 5 May 1983, PDH 1809, UMMZ #158916, HK 84–0415–2; same locality, 6 May 1983, PDH 1816, UMMZ #158917, BMOC 83–1600–96.

Literature records: on *Eonycteris spelaea* from MALAYSIA: Pahang (Klompen et al., 1982 [Type series]).

Deposition of specimens: AMNH, BMNH, CUIC, FMNH, IRSN, MAK, NMNH, OSU, PNC, UMMZ, WAM, and ZIAC.

Chirobia ***rousettus*** nov. spec.

Diagnosed in the nymphs and female by the complete loss of setae *ps 2* (119).

This species closely resembles *C. eonycteris* in all stages. It differs in the female by the more reduced scaling (no scales posterior to the anus vs. scales present in *C. eonycteris*), and shorter dorsal setae (*d* setae 8–9 vs. 13–14 µm; perianal setae 25–27 vs. 33–39 µm) (Table 9). The males also differ in some measurements: setae *1 a* and *g* are longer in *C. rousettus* (respectively 22 vs. 15 µm and 9 vs. 5 µm), and setae *d* III are shorter (158 vs. 189 µm) (Table 8). An interesting aberration was found in one female with setae *d* III extremely short (3 µm) and thin. The usual length of these setae is 10–13 µm.

All stages occur on the wing membrane.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Rousettus amplexicaudatus* (Geoffroy, 1810). PHILIPPINES: Negros Oriental, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 24 March 1983, P.D. Heideman (PDH 1671), UMMZ #161642, HK 86–0306–2 (holotype female); same locality, 20 July 1982, PDH 608, UMMZ #161491, HK 86–0306–4; same

Table 8. Comparative measurements of male *Chirobia* and *Teinocoptes*.

	C. jagori N=1	*C. minor* N=1	*C. eonycteris* N=5			*C. rousettus* N=6			*C. squamata* N=1	*C. otophaga* N=3		*T. vandeuseni* N=6		
			av	SD	range	av	SD	range		av	range	av	SD	range
gnathosoma														
length	28	26	26	1	25–28	25	1	24–26	29	30	28–31	31	2	29–33
width	29	28	29	2	27–33	24	1	23–26	30	29	27–31	27	1	26–30
subcapitular seta	16	16	17	3	13–22	13	3	9–17	20	15	13–18	12	1	11–14
body														
length	235	217	216	16	201–239	185	8	172–191	222	207	195–219	194	28	145–216
width	174	183	168	11	155–181	139	9	130–153	167	164	157–171	147	23	115–186
seta *vi*	31	31	25	2	22–28	24	2	22–27	24	26	19–35	22	1	20–23
seta *sci*	26	22	19	3	17–22	20	1	18–21	18	20	19–23	24	1	23–25
seta *sce*	33	38	36	2	33–38	35	2	32–38	40	33	31–38	16	3	10–20
seta *c 1*	24	27	12	4	8–17	15	2	13–17	14	15	14–18	25	3	22–29
seta *c 2*	21	21	16	2	13–18	18	1	17–20	15	17	16–19	25	1	24–26
seta *cp*	23	30	7	3	4–10	7	1	5–9	12	4	2–6	13	2	11–15
seta *c 3*	34	42	43	2	42–46	40	3	36–44	42	23	21–25	29	1	27–31
seta *d 1*	18	19	13	3	10–17	14	1	12–15	13	13	11–15	19	2	17–21
seta *d 2*	20	19	12	2	8–14	14	2	12–16	13	10	8–13	24	2	21–27
seta *e 1*	9	12	4	1	3–6	5	1	4–7	6	6	5–7	8	2	7–11
seta *e 2*	8	10	4	1	4–5	5	1	4–6	4	4	4–5	18	2	17–21
seta *h 1*	9	12	4	1	4–6	5	1	5–6	5	6	5–7	7	1	6–8
seta *h 2*	7	9	4	1	3–5	5	1	3–5	5	5	4–6	6	1	5–7
seta *ps 1*	8	9	6	2	3–7	5	1	4–6	5	4	3–5	6	1	5–7
seta *ps 2*	4	4	–			–			–	1	1–2	9	2	7–11
seta *1 a*	18	24	15	3	12–18	22	3	18–25	18	14	10–19	19	1	18–20
seta *3 a*	7	9	6	1	5–7	7	1	7	8	6	6–7	14	1	11–15
seta *3 b*	16	20	10	1	10–11	14	1	13–15	11	16	14–18	18	1	16–18
seta *g*	9	10	5	1	4–6	9	1	7–11	7	7	5–8	20	1	19–22
genital area														
length	45	44	31	4	27–37	29	1	28–30	29	36	34–38	40	3	36–43
width	40	24	22	4	19–30	25	4	21–29	19	25	24–26	32	3	28–35
coxal apodeme I	41	44	42	2	40–46	37	1	36–39	45	42	40–43	42	1	40–43
coxal apodeme II	54	57	61	3	58–65	47	4	42–53	66	58	52–63	54	4	49–61
coxal apodeme III	29	27	27	3	24–31	25	1	22–26	31	28	25–31	32	1	31–34
coxal apodeme IV	23	20	25	3	22–28	23	4	18–28	27	20	19–22	33	2	30–35
leg I	58	64	60	6	53–70	53	6	45–59	73	49	–	66	3	63–69
leg II	59	56	61	6	56–70	52	5	46–57	75	56	51–60	66	3	61–71
leg III	37	41	41	2	39–44	34	2	32–35	47	39	36–42	43	3	38–46
leg IV	20	17	21	3	17–25	16	2	13–17	19	16	15–18	24	2	20–27
seta *pR* I	40	34	33	2	30–36	33	3	27–33	36	21	–	37	7	23–42
seta *pR* II	40	41	36	4	32–40	34	4	29–42	37	31	26–36	37	4	32–41
seta *sR* III	38	–	34	7	25–42	36	6	29–43	32	20	17–23	33	2	30–35
seta *vF* I	23	27	24	4	19–28	23	1	22–25	24	24	23–26	27	3	20–29
seta *vF* II	38	42	42	4	38–47	36	5	28–43	46	38	36–40	43	4	36–49
seta *cG* I	39	42	40	3	35–42	38	3	34–43	44	44	41–46	38	4	33–43
seta *mG* I	38	42	34	3	32–38	33	3	29–38	33	31	30–32	32	6	22–37
seta *d* III	157	147	189	10	176–198	158	11	147–174	199	152	151–153	215	20	194–253
solenidion σ I	4	4	3	1	2–4	3	1	2–4	5	3	2–3	4	1	3–4
solenidion σ II	4	4	3	1	2–5	4	1	3–4	4	3	3–4	4	1	3–5
solenidion φ I	14	14	10	1	9–11	8	1	7–9	11	12	12	10	1	9–12
solenidion φ II	18	20	15	2	13–18	11	1	10–12	14	15	13–16	12	1	12–13
solenidion φ III	6	6	8	1	7–9	6	1	6	8	7	7–8	7	1	7–8
solenidion φ IV	4	2	3	1	3–4	2	1	2–3	3	2	2–3	3	1	3
solenidion ω-1 I	18	18	15	1	14–16	12	1	11–13	18	17	15–19	14	1	13–15
solenidion ω-3 I	13	11	9	1	8–11	9	1	8–10	11	11	11	8	1	7–8
solenidion ω II	20	21	18	1	17–19	15	1	14–15	21	18	17–19	15	1	14–16
ambulacral stalk I	14	12	15	1	14–17	12	1	11–14	17	13	13	11	1	11–12
ambulacral stalk II	13	12	15	1	14–15	12	1	11–12	17	12	12	11	1	10–12

date, PDH 610, UMMZ #161492, HK 86–0308–2; 23 August 1982, PDH 737, UMMZ #161494, HK 86–0424–1; same date, PDH 746, UMMZ #161501, HK 86–0424–2; PDH 750, UMMZ #161504, HK 86–0425–1; 28 September 1982, PDH 878, UMMZ #161530, HK 85–0806–1; 29 September 1982, PDH 889, UMMZ #161536, HK 85–0809–1; same date, PDH 890, UMMZ #161537, HK 85–0808–1 (allotype male); 24 October 1982, PDH 1006, UMMZ #161553, HK 86–0309–1; same date, PDH 1018, UMMZ #86–0308–3, HK 86–0308–3; 25 October 1982, PDH 1021, UMMZ #161559, HK 86–0309–2; 29 November 1982, PDH 1145, UMMZ #161573, HK 86–0405–1; same date, PDH 1149, UMMZ #161577, HK 86–0403–1; 30 December 1982, PDH 1331, UMMZ #161594, HK 86–0504–1; same date, PDH 1338, UMMZ #161600, HK 85–0815–2; PDH 1339, UMMZ #161601, HK 85–0815–1; 26 January 1983, PDH 1460, UMMZ #161613, HK 85–0725–1; same date, PDH 1466, UMMZ #161615, HK 85–0725–3; 25 February 1983, PDH 1531, UMMZ #161623, HK 86–0312–1; 26 February 1983, PDH 1537, UMMZ #161625, HK 86–0312–2; 24 April 1983, PDH 1775, UMMZ #161663, HK 86–0413–2; 31 May 1983, PDH 1970, UMMZ #161677, HK 85–0902–1; same date, PDH 1975, UMMZ #161679, HK 85–0829–1; 22 June 1983, PDH 2121, UMMZ #161680, HK 86–0419–1; same date, PDH 2127, UMMZ #161681, HK 86–0419–2; 20 February 1987, E.A. Rickart (EAR 1251), NMNH #458509, HK 87–0220–7; 10 May 1987, EAR 1565, NMNH #459293, HK 87–0510–2; 12 June 1987, J.S.H. Klompen (JSHK 108), NMNH #458506, HK 87–0612–1; 12 June 1987, JSHK 109, NMNH #459295, HK 87–0612–2; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 12 February 1983, PDH 1515, UMMZ #161616, HK 85–0730–2; BOHOL, 1 km S, 1 km E Bilar, 9°43'N 124°07'E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3707), NMNH #459273, HK 87–0618–8; LEYTE, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 4 April 1987, EAR 1293, NMNH #459286, HK 87–0304–3; LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 20 March 1987, JSHK 28, NMNH #459278, HK 87–0320–3; DAVAO, Sitio Tegato, Luangbay Cave, Hoogstraal et al. (1093), FMNH #61368, HK 87–0903–6; ROMBLON, Sibuyan Is., 1 km S, 1 km E Magdiwang, Tampayan, 12°29'N 122°31'E, elev. 10 m, 24 May 1989, S.M. Goodman (SMG 3048), FMNH #136987, HK 89–0711–9; INDONESIA: IRIAN BARAT, 40 km N Baliem Valley, Bokondini, 3°35'S 138°32'E, elev. 1400 m, 23 November 1961, L. & S. Quate, AMNH #221837, HK 86–0812–3; LOMBOK, Suranadi, 8°33'S 116°14'E, 26 September 1987, D. Kitchener (L 19), WAM, HK 88–0420–1; LOMBOK, Pelangan, 8°48'S 115°56'E, 12 October 1987, L 272, WAM, HK 88–0429–3; SUMBAWA, Batu Tering, 8°48'S 117°22'E, 25 May 1988, D. Kitchener (S 370), WAM, HK 89–0215–1; PAPUA NEW GUINEA: MADANG, Madang, 23 July 1969, J. Kikhawa, MVZ 138505, HK 86–0520–1; MADANG, 9 mi N Madang, Maiwara, 21 July 1969, W.Z. Lidecker, MVZ 138510, HK 86–0520–2.

Etymology: The specific name is derived from the generic name of the type host, *Rousettus amplexicaudatus*.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in AMNH, BMNH, CUIC, FMNH, IRSN, MAK, NMNH, OSU, PNC, UMMZ, WAM, ZIAC, and ZIZM.

Chirobia ***angolensis*** nov. spec.
(Figs. 187, 203, 204)

Diagnosed in the larva by the reduction of the area with scales to two patches near setae *c 1* (reversal) (22); in the female by the presence of scales posterior to the anus (40).

Larva (Fig. 187): Scales limited to two patches extending from setae *c 1* to setae *d 1*. Setae *e 2* much smaller than the *d* setae.

Nymphs: Scales both anterior and posterior to the anus. Setae *ps 2* at best represented by clear spots. Legs IV not added.

Female (Figs. 203, 204): Resembling the nymphs but with longer setae. Setae *ps 2* represented by either clear spots or vestigial alveoli. Internal end of the bursa copulatrix disc-like. Measurements in Table 9.

The immatures and females were found on the wing membrane.

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus angolensis* (Bocage, 1898). Type host. ZAIRE: HAUT-ZAIRE, 20 mi S Irumu, Mt. Hoyo Cave, 1°13'N 28°49'E, 4 May 1955, W.L. Schmitt & E.W. Baker, NMNH #301712, HK 88–0901–1 (holotype female); CENTRAL AFRICAN REPUBLIC: BAMINGUI-BANGORAN, Manovo-Gounda-St. Floris National Park, 8°21'N 21°12'E, CMNH #73597, HK 86–0702–11; ETHIOPIA: KEFA, Ghera region, 20 km NE Afallo, Challa, ca 7°41'N 36°20'E, 8 May 1971, M. Desfayes, FMNH #105410, HK 86–0226–5; WELEGA, Didesa river, ca 9°N 36°E, January 1972, J.S. Ash, NMNH #497488, HK 88–0825–5; NIGERIA: KANO, Kano Buk, 24 October 1979, M.E. Dyer, HZM #20.II.914, HK 85–0705–3.

Myonycteris torquata (Dobson, 1878). CAMEROON: Eseka, 3°37'N 10°45'E, 16 June 1973, L.W. Robbins, AMNH #238279, HK 86–0812–4.

Etymology: The specific name is derived from that of the type host, *Rousettus angolensis*.

Deposition of specimens: Holotype female in collection NMNH. Paratypes in AMNH, BMNH, IRSN, NMNH, OSU, and UMMZ.

Chirobia squamata Fain, 1959

Chirobia squamata Fain, 1959b: 134.

Diagnosed in the nymphs and female by the complete loss of setae *ps 2* (119); in the female by the loss of scales in the area between setae *d 1* and the anus, and lateral to the anus (reversals) (38, 39).

This species has been described from the female only (Fain, 1959b). All immatures share a similar scale pattern: scales are present in a U-shaped arc connecting the bases of setae *c 1* but absent immediately anterior to the anus. Setae *e 2* in the larva subequal to the *d* setae. The males resemble those of *C. eonycteris*, with setae *ps 2* absent. Measurements in Table 8.

All stages occur on the wing membrane (Fain, 1959b; pre-

Table 9. Comparative measurements of female *Chirobia* and *Teinocoptes*.

	Chirobia eonycteris N = 10			*Chirobia rousettus* N = 10			*Chirobia angolensis* N = 10			*Teinocoptes vandeuseni* N = 10		
	av	SD	range	av	SD	range	av	SD	range	av	SD	range
gnathosoma												
length	33	2	30–38	33	2	31–38	37	3	29–40	58	4	53–66
width	28	2	25–31	27	3	23–33	32	2	29–34	41	3	38–47
body												
length	297	29	255–335	277	38	250–333	301	30	268–340	604	73	496–668
width	280	34	232–336	246	35	200–302	313	17	289–327	398	45	353–501
distance *d 1-d 2*	22	3	16–27	16	2	12–20	27	6	19–38	101	18	72–122
distance *d 2-e 2*	25	5	18–33	22	3	18–29	34	7	21–46	54	7	45–65
distance *e 2-ps 2*	93	5	87–98	–			80	6	74–86	76	13	61–108
distance *ps 2-ps 2*	35	1	34–36	–			25	6	21–29	62	12	45–79
seta *vi*	–			–			–			–		
seta *sci*	2	1	1–3	2	1	1–2	2	1	1–3	2	1	1–2
seta *sce*	1	1	1	1	1	1	1	1	1–2	1	1	1
seta *c 1*	1	1	1–2	1	1	1–2	1	1	1	2	1	1–2
seta *c 2*	1	1	1–2	1	1	1	1	1	1–2	1	1	1–2
seta *cp*	–			–			–			–		
seta *c 3*	–			–			–			8	1	6–9
seta *d 1*	14	1	13–16	9	2	6–11	10	2	8–14	33	4	27–44
seta *d 2*	13	1	11–14	8	1	6–10	7	1	6–11	45	4	41–54
seta *e 1*	33	4	27–40	25	2	23–29	27	2	24–29	40	7	31–47
seta *e 2*	1	1	1–2	1	1	1	1	1	1–2	2	1	1–2
seta *h 1*	37	5	30–45	27	2	24–30	28	3	24–34	42	5	35–47
seta *h 2*	39	4	34–46	27	2	24–30	29	3	24–32	43	4	39–48
seta *ps 1*	37	3	33–43	26	4	20–30	30	4	24–35	41	3	36–44
seta *ps 2*	–			–			–			1	1	1–2
seta *1 a*	–			–			–			4	1	3–5
seta *3 b*	–			–			–			5	1	3–6
seta *g*	–			–			–			–		
longest spine in lateral row	–			–			–			2	1	2–3
copulatory cone	11	2	7–13	6	1	5–8	11	2	8–15	10	2	7–12
bursa copulatrix	116	26	68–166	81	15	63–112	91	16	65–108	210	15	193–235
postvulvar sclerotization												
length	–			–			–			95	6	90–99
width	–			–			–			56	1	55–56
coxal apodemes I	26	1	24–28	28	2	25–30	31	2	28–34	40	3	35–45
coxal apodemes II	95	4	88–104	90	5	83–99	92	7	79–102	72	3	67–78
coxal apodemes III	3	1	2–4	3	1	2–4	3	1	2–5	40	9	27–53
leg I	22	2	19–25	22	3	17–27	26	3	20–29	37	3	32–42
leg II	23	2	20–28	22	2	19–26	26	2	21–29	33	2	29–37
leg III	15	1	13–15	14	1	12–15	14	1	12–17	34	2	30–36
leg IV	–			–			–			8	1	6–9
seta *pR* II	–			–			–			4	1	3–5
seta *sR* III	–			–			–			7	2	4–10
seta *d* III	14	4	9–23	11	2	9–17	12	3	8–16	40	8	30–52
solenidion ϕ III	7	1	5–9	6	1	6–7	6	1	4–7	12	2	10–15
solenidion ϕ IV	–			–			–			5	1	3–6

sent study), with some females attached to the skin overlying the arm bones.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus lanosus* Thomas, 1906. KENYA: Rift Valley, Mt. Menengai, 0°14'S 36°06'E, 8 June 1948, Hoogstraal et al., FMNH #85450, HK 86–0226–12; UGANDA: Ruwenzori Range, Old Kalangi, ca 0°48'S 30°54'E, 5 February 1925, E. Heller, NMNH #260141, HK 88–0902–10.

Rousettus madagascariensis Grandidier, 1928. MADAGASCAR: Fianarantsoa, 1 km N Kianjavato, 21°23'S 47°52'E, elev. 300 m, 12 August 1987, L.H. Emmons (LHE 658), NMNH #448882, HK 88–0105–1; same locality and date, G.K. Creighton (GKC 2571), NMNH #448880, HK 87–

1122–1; GKC 2572, NMNH #448881, BMOC; FIANARANTSOA, 4 km E Kianjavato, 21°23'S 47°54'E, elev. 125 m, 3 August 1988, GKC 2748, NMNH #449274, HK 88–0926–1; same locality and date, GKC 2752, NMNH #449275, HK 88–0922–1; GKC 2753, NMNH #449276, HK 88–0922–2; GKC 2754, NMNH #449277, HK 88–0922–3; GKC 2755, NMNH #449278, HK 88–0922–4.

Literature records: on *Rousettus* sp. from RUANDA: Astrida (Fain, 1959b [Type series]); on *Rousettus angolensis* from ZAIRE (Fain, 1959b).

Deposition of specimens: BMNH, FMNH, NMNH, and UMMZ.

The lineage including the remaining two species of *Chirobia* (node 32) is diagnosed in the larva and protonymph by the reduction of the area with scales to patches near setae *c 1* (reversals) (22, 27); in the nymphs and female by the complete loss of setae *ps 2* (119); in the female by the loss of scales between setae *c 1* and *d 1* and lateral to the anus (reversals) (37, 39).

Chirobia congolensis Fain, 1959

Chirobia congolensis Fain, 1959b: 131.

Diagnosed in the female by the reduction of the area covered with scales to small patches near setae *c 1* (reversals) (36, 38).

The larva, female, and male have been described previously (Fain, 1959b). The nymphs closely resemble the female in the structure of the setae and the reduction of the scaling to two patches near setae *c 1*.

All stages occur on the wing membrane.

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus aegyptiacus* (Geoffroy, 1810). Type host. ANGOLA: CUANZA SUL, 30 km S Gabela, ca 10°51'S 14°22'E, 27 July 1954, G. Heinrich, FMNH #84034, HK 86–0226–6; EGYPT: CAIRO, Cairo, 30°03'N 31°15'E, 2 February 1984, S.M. Goodman (SMG 807), UMMZ #161042, HK 84–1201–1.

Rousettus leschenaulti (Desmarest, 1820). INDIA: MADHYA PRADESH, Guva, Gadi, 11 March 1975, K. Bhadnagar, AMNH #244990, HK 86–0813–13.

Literature records: on *Rousettus aegyptiacus* from ZAIRE: KIVU, Mahyusa (Fain, 1959b [Type series]).

Deposition of specimens: AMNH, BMNH, FMNH, and UMMZ.

Chirobia otophaga Fain, 1959

Chirobia otophaga Fain, 1959j: 339.

The female is characterized by the very small *d* setae (4–9 μm), and the unusual pattern of scaling: scales near setae *c 1* and anterior to the anus but not in the area in between. In the larva and nymphs scales are limited to small patches near setae *c 1*. Setae *e 1* of the larva are minute. The previously undescribed male closely resembles that of *C. congolensis*. Setae *ps 2* are very small or absent. The genital area is round to oval. Measurements in Table 8.

Females have been found in the ear canal of their host (Fain, 1959j) but all specimens collected during this study were collected from the wing membrane.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Epomophorus wahlbergi* (Sundevall, 1846). Type host. MOZAMBIQUE: GAZA, 2 mi N Can Phumo, 25°58'S 32°34'E, 17 May 1948, T. Larson, MVZ #117094, HK 86–0521–11.

Epomophorus angolensis Gray, 1870. ANGOLA: NAMIBE, Mocamedes, Koelae-ai-Kasinga, ca 15°S 12°E, 7 May 1887, P.J. van der Kellen, NNML #25752, HK 85–0607–6.

Epomophorus gambianus (Ogilby, 1835). SENEGAL: CASAMANCE, 20 km E Zinguinchor, Diabane, 12°33'N 16°05'W, 27 December 1982, P.L. Ames, FMNH, HK 86–0226–1.

Epomophorus labiatus (Temminck, 1837). KENYA: COAST, Lamu Is., 2°17'N 40°52'E, 15 December 1982, L.J. Moritz, MSU #33405, HK 84–0607–1; SUDAN: BAHR EL GHAZAL, 20 mi SE Wau, Mbili, 7°01'N 27°59'E, 10 September 1982, L.J. Moritz, MSU #33393, HK 84–0710–3; BAHR EL GHAZAL, 2 mi S Wau, Ngosulugu, 7°42'N 28°00'E, 26 September 1982, L.J. Moritz, MSU #33395, HK 84–0518–1; same data, MSU #33396, HK 84–0607–2; BAHR EL GHAZAL, 200 mi NW Wau, Rajaj, 10°55'N 24°43'E, 27 November 1982, L.J. Moritz, MSU #33401, HK 84–0605–1; WESTERN Equatorial, 100 mi NW Juba, Jabal Mundri, 50°23'N 30°22'E, 7 December 1982, L.J. Moritz, MSU #33402, HK 84–0606–1; same data, MSU #33403, HK 84–0710–1.

Hypsignathus monstrosus Allen, 1861. ETHIOPIA: SIDAMO, Bulcha, ca 5°N 39°E, 21 June 1974, J.S. Ash (52197), NMNH #462724, HK 88–0826–11.

Literature records: on *Epomophorus wahlbergi* from TANZANIA: ZANZIBAR (Fain, 1959j [Type series]).

Deposition of specimens: BMNH, FMNH, MSU, NMNH, NNML, and UMMZ.

In addition to the 12 species discussed above small collections have been made of what may represent two more new species of *Chirobia*. However, the available material does not allow a complete description and I will only list these collections without descriptions.

Chirobia sp. 1

Material examined: 3 nymphs.

Hosts (Chiroptera: Pteropodidae) and localities: *Aethalops alecto* (Thomas, 1923). INDONESIA: WEST JAVA, Sukabumi, Gunung Masigit, 19 May 1972, NAMRU-2 2724, NMNH #501862, HK 87–0728–14; MALAYSIA: before 1970, Yong Ghong Chong, AMNH #232510, HK 86–0814–7.

Chirobia sp. 2

Material examined: 5 nymphs and 1 male.

Hosts (Chiroptera: Pteropodidae) and localities: *Penthetor lucasi* (Dobson, 1880). MALAYSIA: SABAH, Upper Tongod, SE Kampong Kipalieu, 5°16'N 116°58'E, 29 May 1962, A.K. Shipway, AMNH #241670, HK 86–0814–3; SELANGOR, Fraser's Hill, 3°42'N 101°45'E, elev. 1600 m, 17 April 1969, Yong Ghong Chong, AMNH #216743, HK 86–0814–1;

FIGS. 203, 204. *Chirobia angolensis*, female, dorsal (203) and ventral (204) view.

same locality, 17 April 1969, Yong Ghong Chong, AMNH #216744, HK 86–0814–2.

The sister group of *Chirobia* (node 33, Fig. 53), is the genus *Teinocoptes* (new concept).

Teinocoptes Rodhain, 1923

Teinocoptes Rodhain, 1923: 29.

Diagnosed in the female by the very pronounced increase in the height of the body (4), and the strong reduction of the area covered by scales (reversals) (37–39); in the male by the presence of pointed median ventral outgrowths (54), and the fusion of femur and genu IV (211).

Type species *Teinocoptes epomophori* Rodhain, 1923.

Resolution of the basal lineages in *Teinocoptes* is relatively poor. Five lineages diverge at node 33, three of which are monobasic. The first lineage (*vandeuseni-rousetti*) (node 34) is diagnosed in the nymphs and female by the loss of setae *g* (123); in the female by the presence of a verrucous area anterolateral to legs III (50).

Within this lineage the first dichotomy is between *T. vandeuseni* and a lineage (node 35) diagnosed in the protonymph by the presence of legs IV (reversal) (213); in the nymphs and/or female by the presence of setae *vi* (reversal) (59); in the female by the presence of a sclerotized, postvulvar zone (49). The next dichotomy involves *T. malayi* and a lineage (node 36) diagnosed in the female by the presence of a sclerotized or spinose band connecting the distal ends of coxal apodemes II (52), and the presence of distinct setae *cp* (reversal) (88). A lineage including *T. pahangensis* and *T. epomophori* diverges from a lineage including the three remaining species. The first lineage (node 37) is diagnosed in the tritonymph and female by the loss of setae *pR* I (170); in the female by the absence of the verrucous zone anterolateral to legs III (reversal) (50). The sister group of the *pahangensis*/*epomophori* lineage (node 38) is diagnosed in the nymphs and female by the presence of setae *g* (reversal) (123). It includes three species, *T. asiaticus*, *T. astridae*, and *T. rousetti*.

Teinocoptes vandeuseni Mitchell & Fain, 1963
(Figs. 205, 207–210)

Teinocoptes vandeuseni Mitchell & Fain, 1963: 486.

Diagnosed in the larva by vestigial or absent setae *cp* (84); in the tritonymph by not adding legs IV (214); in the tritonymph and female by the presence of setae *pR* I in the female (reversal) (170); in the female by the arrangement of the lateral spines into a field (42).

The females collected during this study were inconsistent with the original description in having longer *d* and perianal setae (ranges of respectively 27–54 and 35–48 μm vs. 22–39 and 17–35 μm in the description). However, measurements of two paratype females indicated that the setal lengths of these paratypes are in the same range as those for the new specimens. The extensive new collections allow notes on all life stages, including the previously undescribed nymphs and male. The larva (Fig. 205) has about 50 spines on the dorsum (vs. 70–80 in *T. pahangensis* and none in *T. malayi*), and setae *d 2* are much longer than setae *d 1* or *e 1*. Only a few scales are present near setae *c 1* in the protonymph, but in the tritonymph and female (Figs. 207, 208) scales form a narrow U-shaped band. Postvulvar sclerotization in the female is weak or absent and the verrucous area is well developed. The distance between setae *d 1* and *d 2* distinctly exceeds the distance between setae *d 2* and *e 2*. Measurements in Table 9. The male (Figs. 209, 210) resembles the male of *T. malayi* (Figs. 211, 212) but is smaller and the median ventral outgrowths are pointed, rather than blunt. Measurements in Table 8.

All stages occur on the posterior edge of the wing. Additional immatures and females were collected from the nipples of their hosts.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Rousettus amplexicaudatus* (Geoffroy, 1810). INDONESIA: IRIAN BARAT, Japen Is., 29 October 1962 (paratypes, specimens in collection BPBM); PAPUA NEW GUINEA: MADANG, Madang, 23 July 1969, J. Kikhawa, MVZ #138505, HK 86–0520–1; MADANG, 9 mi N Madang, Maiwara, 21 July 1969, W.Z. Lidecker, MVZ #138510, HK 86–0520–2; NEW BRITAIN Is., Gunanur Plantation, 6 August 1979, J.D. Smith (JD5 5370) (specimens in collection OSU); PHILIPPINES: NEGROS ORIENTAL, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 24 October 1982, P.D. Heideman (PDH 1006), UMMZ #161553, HK 86–0309–1; 20 February 1987, E.A. Rickart (EAR 1252), NMNH #459290, HK 87–0220–1; ROMBLON, Sibuyan Is., 1 km S, 1 km E Magdiwang, Tampayan, 12°29'N 122°31'E, elev. 10 m, 24 May 1989, S.M. Goodman (SMG 3048), FMNH #136987, HK 89–0711–9.

Literature records: on *Rousettus amplexicaudatus* (= *R. stresemanni*) from INDONESIA: IRIAN BARAT (Mitchell & Fain, 1963 [Type series]).

Deposition of specimens: BMNH, FMNH, NMNH, OSU, PNC, UMMZ, and WAM.

Teinocoptes malayi Fain & Nadchatram, 1962
(Figs. 4, 211, 212)

Teinocoptes malayi Fain & Nadchatram, 1962: 248.

Diagnosed in the larva by the absence of spines (19), and vestigial or absent setae *cp* (84); in the female by the presence of setae *vF* I (reversal) (168), and the loss of setae *vF* II (169); in the male by the presence of blunt, not pointed, median ventral outgrowths (reversal) (54).

The female and larva have been described previously (Fain & Nadchatram, 1962); descriptions of the nymphs and male are presented here for the first time. Scaling develops from 1–4 scales near setae *c 1* in the protonymph, to patches in the tritonymph, to a narrow U-shaped band in the female. The *d* setae are long and filiform in the nymphs and female. The distance between setae *d 1* and *d 2* is smaller than that between setae *d 2* and *e 2* (Table 10). The male (Figs. 211, 212) corresponds largely with the male of type A as mentioned by Fain et al. (1982). The dorsal shields are well sclerotized, and the perianal setae are very small (6–9 μm; Table 11). Genital area oval in shape.

The females and nymphs attach to the posterior trailing edge of the wing (Fain & Nadchatram, 1962; five collections in the present study). Young immatures (larvae, protonymphs) and molting males were found near the eye (eight collections).

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Eonycteris spelaea* (Dobson, 1871). INDONESIA: LOMBOK, Pelangan, 8°48'S 115°56'E, 13 October 1987, D. Kitchener (L 300), WAM, HK 88–0413–1; MALAYSIA: PAHANG, Raub Cave, 13 May 1979, Rudnick, IMR; PAHANG, Bentong, Bukit Chintamani, 13 October 1982, F.S. Lukoschus; Kuala Lumpur, 16 October 1982, F.S. Lukoschus; PHILIPPINES: BOHOL, 1 km S, 1 km E Bilar, 9°44'N 124°07'E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3704), NMNH #459052, HK 87–0618–7; LEYTE, 4 km S, 1 km E Inopacan, 10°28'N 124°45'E, elev. 50 m, 28 May 1984, P.D. Heideman (PDH 2736), UMMZ #161429, HK 84–0622–8; same locality, 5 March 1987, E.A. Rickart (EAR 1305), NMNH #458089, HK 87–0305–1; LEYTE, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 27 March 1987, J.S.H. Klompen (JSHK 38), NMNH, HK 87–0327–3; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 4 October 1982, PDH 920, UMMZ #158918, BMOC 83–1600–39; NEGROS ORIENTAL, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 24 March 1983, PDH 1673, UMMZ #158944, HK 84–0329–1; same locality, 11 June 1987, JSHK 98, NMNH #458165, HK 87–0611–1; NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 22 February 1987, LRH 2907, NMNH #459070, HK 87–0222–3; NEGROS ORIENTAL, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 10 May 1987, PDH 3570, NMNH, HK 87–0510–6.

Eonycteris robusta Miller, 1913. PHILIPPINES: NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 6 May 1983, PDH 1816, UMMZ #158917, BMOC 83–1600–96; CATANDUANES, 1 km N, 8 km W Gigmoto, 13°48'N 124°19'E, elev. 200 m, 24 February 1988, EAR 1695, NMNH #573211, HK 88–0713–2.

Rousettus celebensis Andersen, 1907. INDONESIA: SULAWESI, Donggala, Lake Lindu, 1°18'S 120°05'E, 22 January 1972, NAMRU-2 2393, NMNH #501375, HK 88–0829–13.

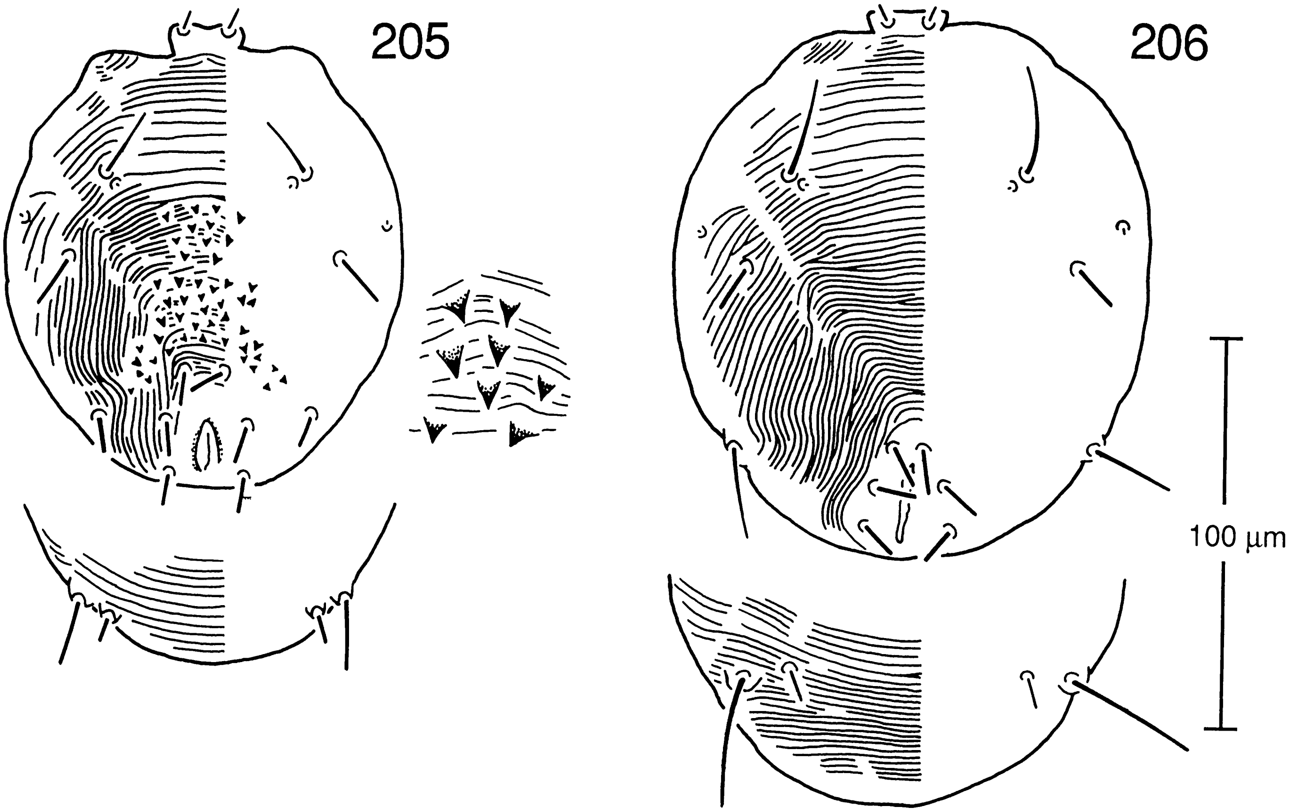
Literature records: on *Macroglossus* sp. from MALAYSIA: Ulu Kelantan, Fort Betis (Fain & Nadchatram, 1962 [Type series]); on *Eonycteris spelaea* from MALAYSIA (Fain et al., 1982).

Deposition of specimens: BMNH, FMNH, NMNH, OSU, PNC, UMMZ, and WAM.

Teinocoptes pahangensis Fain, Lukoschus, & Nadchatram, 1982

Teinocoptes pahangensis Fain et al., 1982: 75.

Diagnosed in the larva by vestigial or absent setae *cp* (84).



Figs. 205, 206. *Teinocoptes*, larvae, anterodorsal (top) and posterodorsal (bottom) view: *T. vandeuseni* (205, including details of the spine structure), *T. philippinensis* (206).

The female and the larva have been described previously (Fain et al., 1982). A few remarks can be made regarding nymphal morphology and ontogeny. The area covered with scales varies through ontogeny from almost completely absent in the protonymph, to patches near setae *c 1* in the tritonymph, to a narrow U-shaped band in the female. The distance between setae *d 1* and *d 2* in both the nymphs and female exceeds that between setae *d 2* and *e 2* (Table 10). Setae *d 1* and *d 2* are short and spine-like in the nymphs, long in the female.

Site specificity appears to be high. Nearly all specimens collected were attached in or on the ears of their hosts. A single female was collected near the eye.

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Pteropodidae) and localities: *Eonycteris spelaea* (Dobson, 1871). Type host. INDONESIA: Sumbawa, Teluk Santong, 8°44'S 117°54'E, 21 May 1988, D. Kitchener (S 294), WAM, HK 89–0208–1; MALAYSIA: Pahang, Bentong, Bukit Chintamani, 13 October 1982, F.S. Lukoschus; PHILIPPINES: Negros Oriental, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 10 May 1987, P.D. Heideman (PDH 3569), NMNH, HK 87–0510–1.

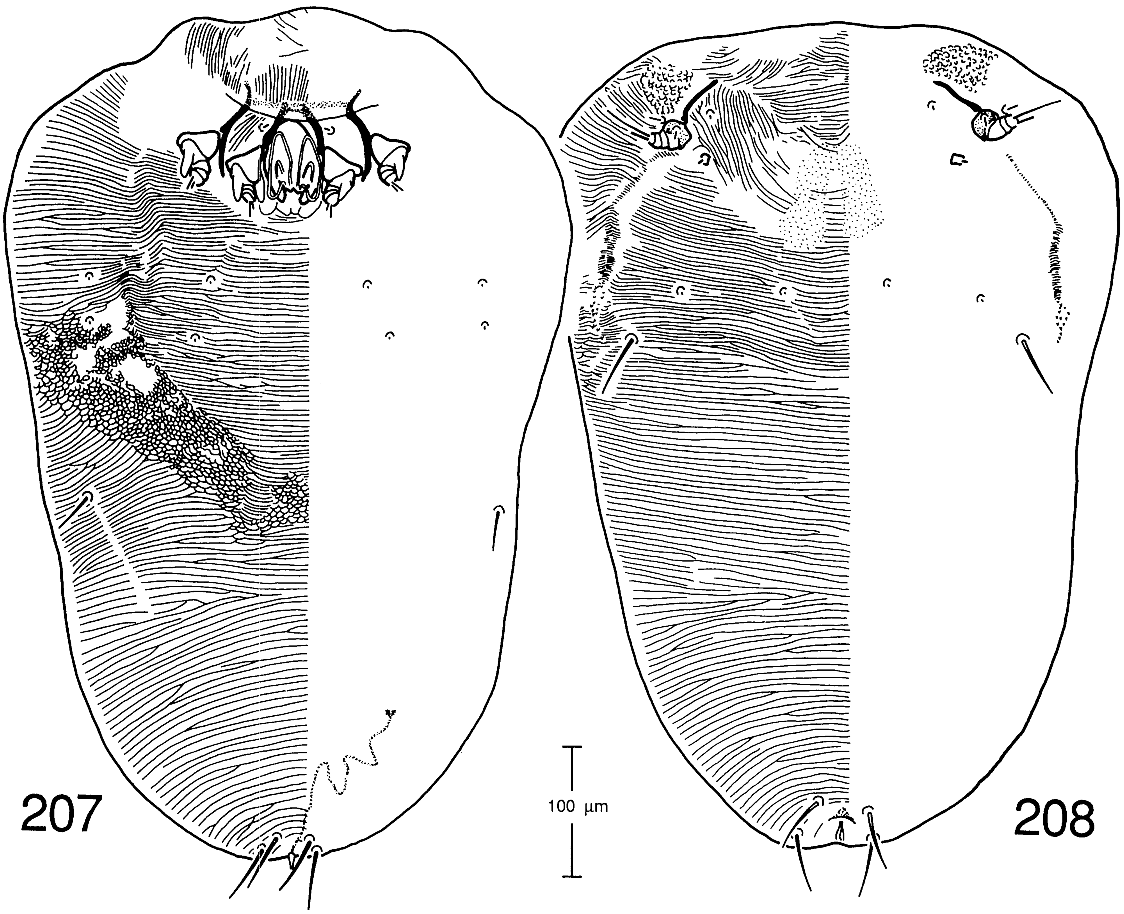
Rousettus aegyptiacus (Geoffroy, 1810). ANGOLA: Cuanza Sul, 30 km S Gabela, ca. 10°51'S 14°22'E, 27 July 1954, G. Heinrich, FMNH #84034, HK 86–0226–6; CYPRUS: Paralimni, April 1968, G. Walson, NMNH #520996, HK 88–0829–11; EGYPT: Cairo, Cairo, 30°03'N 31°15'E, 2 February 1984, S.M. Goodman (SMG 807), UMMZ #161042, HK 84–1201–1.

Rousettus amplexicaudatus (Geoffroy, 1810). PAPUA NEW GUINEA: Madang, Madang, 23 July 1969, J. Kikhawa, MVZ #138505, HK 86–0520–1; Madang, 9 mi N Madang, Maiwara, 21 July 1969, W.Z. Lidecker, MVZ #138510, HK 86–0520–2; PHILIPPINES: Leyte, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 27 March 1987, J.S.H. Klompen (JSHK 37), NMNH #459279, HK 87–0327–2; same locality, 9 April 1987, L.R. Heaney (LRH 3161), NMNH #459282, HK 87–0409–2; Negros Oriental, Dumaguete, 9°18'N 123°18'E, elev. 5 m, 20 July 1982, PDH 608, UMMZ #161491, HK 86–0306–4; Romblon, Sibuyan Is., 1 km S, 1 km E Magdiwang, Tampayan, 12°29'N 122°31'E, elev. 10 m, 24 May 1989, S.M. Goodman (SMG 3048), FMNH #136987, HK 89–0711–9.

Rousettus madagascariensis Grandidier, 1928. MADAGASCAR: Fianarantsoa, 4 km E Kianjavato, 21°23'S 47°54'E, elev. 125 m, 3 August 1988, G.K. Creighton (GKC 2753), NMNH #449276, HK 88–0922–2.

Literature records: on *Eonycteris spelaea* from MALAYSIA: Pahang, Raub (Fain et al., 1982 [Type series]).

Deposition of specimens: FMNH, NMNH, PNC, UMMZ, and WAM.



FIGS. 207, 208. *Teinocoptes vandeuseni*, female, anterior (207) and posterior (208) view.

Teinocoptes epomophori Rodhain, 1923

Teinocoptes epomophori Rodhain, 1923: 29.

Diagnosed in the larva by the presence of scales (21); in the female by the arrangement of the lateral spines into a field (42).

All life stages have been described previously (Rodhain, 1923; Fain, 1959b). Comparative measurements for the male are included in Table 11.

Immatures and especially females attach to the posterior edge of the wing (Rodhain, 1923, 1926; Fain, 1959b) but males do not attach (Rodhain, 1923). The development of the female includes a period of rapid growth lasting about two weeks, after which they gradually diminish in size and disappear (at about four weeks) (Rodhain, 1926).

Material examined: Larva, male tritonymph, female, and male.

Hosts (Chiroptera: Pteropodidae) and locality: *Epomophorus gambianus* (Ogilby, 1835). NIGERIA: Ibadan, 7/8 August 1976, W. Bergmans (117), F.S. Lukoschus.

Micropteropus pusillus (Peters, 1867). NIGERIA: Ife, 21 August 1976, W. Bergmans (158), F.S. Lukoschus.

Literature records: on *Epomophorus wahlbergi* (Sundevall, 1846) from ZAIRE: BAS-ZAIRE, Boma (Rodhain, 1923 [Type series]; Fain, 1959b); on *Epomophorus labiatus* (Temminck, 1837) from RUANDA (Fain, 1959b as *E. anurus*) and ZAIRE (Fain, 1959b); on *Epomops franqueti* (Tomes, 1860) from ZAIRE (Rodhain, 1926); on *Micropteropus pusillus* from ZAIRE (Rodhain, 1923).

Deposition of specimens: UMMZ.

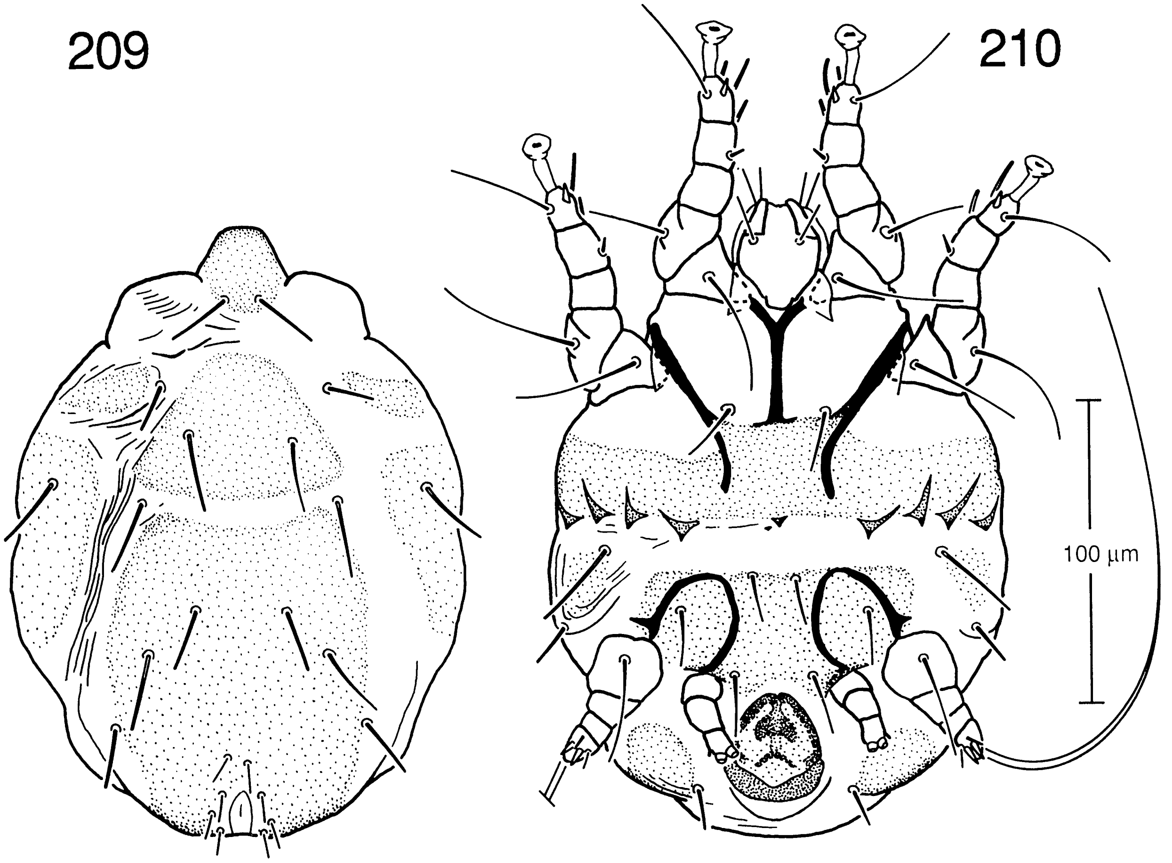
Teinocoptes asiaticus Fain & Domrow, 1961

Teinocoptes asiaticus Fain & Domrow, 1961: 179.

Diagnosed in the male tritonymph by the presence of distinct setae *cp* (reversal) (87); in the female by the presence of scales in the area between setae *c 1* and the anus (37, 38).

The female (Fain & Domrow, 1961) and the larva (Fain & Nadchatram, 1962) have been described previously. Scaling in the protonymph is restricted to a narrow, U-shaped band. From this band a median zone of scales extends posterior to the level of setae *d 1* in the tritonymph. This zone becomes much broader and extends down to the anus in the female. Legs IV are added in the tritonymph. In other aspects the nymphs resemble the female.

Immatures and females are collected most often from the nipples (Fain & Domrow, 1961; present study). However immatures, especially larvae and protonymphs, have been collected several times from the eye region (present study).



Figs. 209, 210. *Teinocoptes vandeuseni,* male, dorsal (209) and ventral (210) view.

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Pteropodidae) and localities: *Cynopterus brachyotis* (Muller, 1838). Type host. INDONESIA: Lombok, September 1987, D. Kitchener (L 6), WAM, HK 88–0411–1; Sumbawa, Merente, 8°33'S 117°01'E, 9 May 1988, D. Kitchener (S 51), WAM, HK 89–0301–4; same locality and date, S 68, WAM, HK 89–0208–3; MALAYSIA: Sabah, Pulau Tiga, 7°21'N 117°03'E, 15 April 1988, S.M. Goodman, UMMZ #165506–165511, BMOC 88–0527–4; PHILIPPINES: Palawan, Langogan River, 19 June 1984, B. Hargar, UMMZ, HK 84–0808–1.

Ptenochirus jagori (Peters, 1861). PHILIPPINES: Bohol, 1 km S, 1 km E Bilar, 9°43'N 124°07'E, elev. 320 m, 18 June 1987, L.R. Heaney (LRH 3700), NMNH #459170, HK 87–0618–6; Leyte, 7 km N Baybay, 10°45'N 124°47'E, elev. 10 m, 27 March 1987, J.S.H. Klompen (JSHK 40), NMNH #458320, HK 87–0327–4; same locality, 10 April 1987, E.A. Rickart (EAR 1434), NMNH #458336, HK 87–0410–3; 11 April 1987, EAR 1437, NMNH #458339, HK 87–0411–1; 11 April 1987, LRH 3181, NMNH #458315, HK 87–0411–5; Leyte, 4 km S, 1 km E Inopacan, 10°28'N 124°45'E, elev. 50 m, 6 March 1987, D. Kitchener (P89), NMNH, HK 87–0306–2; Leyte, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 4 April 1987, R.B. Utzurrum (RBU 171), NMNH, HK 87–0404–2; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 6 November 1982, P.D. Heideman (PDH 1069), UMMZ #160007, HK 83–1203–1; same locality, 8 February 1984, RBU 247, BMOC 84–1575–3; 2 July 1987, JSHK 135, NMNH #459202, HK 87–0702–7.

Literature records: on *Cynopterus brachyotis* from MALAYSIA: Selangor, Rantau Panjang (Fain & Domrow, 1961 [Type series]); MALAYSIA (Fain, 1963a) and PHILIPPINES: Palawan (Mitchell & Fain, 1963); on *Macroglossus* sp. from MALAYSIA (Fain & Nadchatram, 1962).

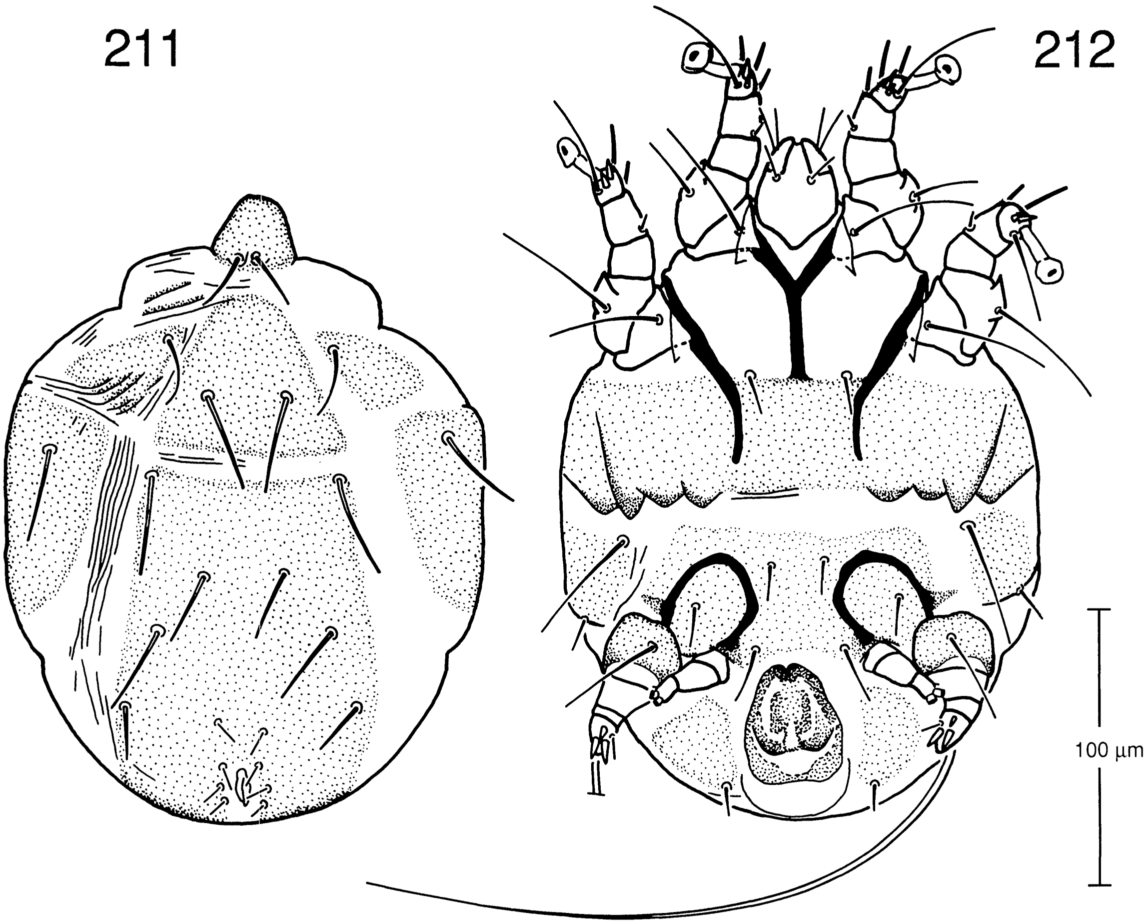
Deposition of specimens: NMNH, PNC, UMMZ, and WAM

The sister lineage to *T. asiaticus* includes two African species, *T. astridae* and *T. rousetti* (*T. rousetti* was not included as a terminal taxon in the analysis, see p. 3). This grouping is diagnosed in the female by the arrangement of the lateral spines in a field (42), and the loss of the postvulvar sclerotization (reversal) (49).

Teinocoptes astridae Fain, 1959

Teinocoptes astridae Fain, 1959b: 129.

This species was described for the larva, nymphs, and female (Fain, 1959b). Scales in the nymphs are limited to



Figs. 211, 212. *Teinocoptes malayi,* male, dorsal (211) and ventral (212) view.

patches, very distant in the protonymph, almost touching along the midline in the tritonymph. The previously undescribed male closely resembles that of *T. vandeuseni* but is larger. Measurements for the single male in Table 11.

All specimens collected were attached to the posterior edge of the wing (Fain, 1959b; present study).

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Rousettus madagascariensis* Grandidier, 1928. MADAGASCAR: Fianarantsoa, 1 km N Kianjavato, 21°23'S 47°52'E, elev. 300 m, 10 August 1987, G.K. Creighton (GKC 2572), NMNH #448881, BMOC 87–1500–25; Fianarantsoa, 4 km E Kianjavato, ca. 21°23'S 47°54'E, elev. 125 m, 3 August 1988, GKC 2753, NMNH #449276, HK 88–0922–2.

Literature records: on *Rousettus* sp. from RUANDA: Astrida (Fain, 1959b [Type series]).

Deposition of specimens: BMNH, NMNH, and UMMZ.

Teinocoptes rousetti Fain, 1959

Teinocoptes rousetti Fain, 1959b: 127.

This species very closely resembles *T. astridae.* It differs in the larva by the number and pattern of spines on the dorsum (22–30 vs. 38–47 in *T. astridae*), and in the female by thicker perianal setae (6 vs. 4 µm) (Fain, 1959b).

The type series was collected from the posterior edge of the wing (Fain, 1959b).

Material examined: None.

Literature records: on *Rousettus aegyptiacus* from ZAIRE: Kivu, Mahyusa (Fain, 1959b [Type series]).

The next three lineages originating at node 33 are monobasic. All three are associated with hosts in the fruitbat genus *Dobsonia.*

Teinocoptes strandtmanni Mitchell & Fain, 1963

Teinocoptes strandtmanni Mitchell & Fain, 1963: 483.

Diagnosed in the tritonymph by not adding legs IV (214); in the tritonymph and female by the loss of trochanteral setae *sR* III (200); in the female by the absence of scales in a continuous band between setae *sci* and *c 1* (reversal) (36), the presence of postvulvar sclerotization (49), and the transformation of the perianal setae from filiform to membranous

Table 10. Comparative measurements of female *Teinocoptes*.

	malayi			*pahangensis*			*philippinensis*			*eonycteris*		
	N=5			N=5			N=10			N=10		
	av	SD	range	av	SD	range	av	SD	range	av	SD	range
gnathosoma												
length	66	5	61–73	77	1	77–78	63	3	58–67	41	6	34–50
width	52	6	47–60	55	5	51–59	48	3	44–54	33	3	29–37
body												
length	658	161	502–925	684	104	564–777	762	139	451–910	338	19	317–367
width	473	51	407–533	475	70	408–574	446	45	343–514	275	22	254–329
distance *d 1*-*d 2*	43	9	33–56	113	22	77–135	43	5	36–51	79	8	68–93
distance *d 2*-*e 2*	62	7	54–72	67	13	46–76	73	7	61–82	45	5	37–52
distance *e 2*-*ps 2*	94	19	72–119	94	14	75–110	95	11	77–109	48	5	42–60
distance *ps 2*-*ps 2*	77	5	70–83	109	15	85–126	62	11	40–70	37	3	35–42
seta *vi*	7	–	7	4	1	1	–			4	2	2–5
seta *sci*	2	1	1–2	2	1	1–2	1	1	1–2	1	1	1–2
seta *sce*	1	1	1	1	1	1–2	1	1	1–2	1	1	1
seta *c 1*	1	1	1–2	1	1	1	1	1	1–2	1	1	1–2
seta *c 2*	1	1	1	1	1	1–2	1	1	1–2	1	1	1
seta *cp*	1	–	–	1	1	1	–			–		
seta *c 3*	24	4	18–28	31	9	23–42	13	4	9–20	4	1	2–5
seta *d 1*	88	10	78–104	69	8	60–78	68	6	61–77	14	3	11–18
seta *d 2*	94	6	86–103	69	6	64–77	74	11	58–89	11	2	8–13
seta *e 1*	63	6	55–68	42	9	32–51	62	7	49–71	17	2	17–19
seta *e 2*	1	1	1–2	2	1	1–2	1	1	1–2	1	1	1–2
seta *h 1*	66	6	57–72	43	6	34–51	65	5	59–71	18	1	16–20
seta *h 2*	65	5	60–70	43	4	39–50	65	8	51–74	18	2	15–20
seta *ps 1*	59	8	51–70	46	8	37–52	63	8	52–75	16	1	13–18
seta *ps 2*	1	1	1	2	1	1–2	1	1	1	1	1	1–2
seta *1 a*	4	1	3–4	4	1	4–5	3	1	2–5	1	1	1
seta *3 b*	3	1	1–4	5	1	4–6	4	1	2–5	2	1	1–3
seta *g*	–			–			–			–		
longest spine in lateral row	3	1	3–4	2	1	1–3	3	1	2–4	2	1	1–3
copulatory cone	19	2	15–21	8	1	8–10	24	3	19–27	8	2	5–10
bursa copulatrix	254	86	196–375	334	55	269–399	152	14	137–176	105	17	80–128
postvulvar sclerotization												
length	131	9	119–141	181	15	160–194	254	36	193–304	83	13	68–102
width	96	12	81–108	143	24	115–165	103	6	92–112	52	6	46–59
coxal apodemes I	53	5	46–58	58	5	52–61	45	2	41–50	32	2	30–36
coxal apodemes II	90	6	81–97	92	6	82–98	81	8	76–102	59	5	53–66
coxal apodemes III	37	4	31–42	34	10	26–45	34	3	30–40	2	–	2
leg I	47	2	44–49	54	5	48–60	42	4	38–47	30	5	20–37
leg II	39	7	32–49	48	6	42–54	35	3	30–39	28	3	25–33
leg III	37	5	28–41	42	5	34–46	33	2	30–36	27	1	24–28
leg IV	8	1	7–10	11	2	9–13	7	1	6–9	4	1	3–7
seta *pR* II	3	2	1–4	5	2	3–7	–			16	2	14–20
seta *sR* III	4	1	2–5	9	3	7–14	3	1	2–4	2	1	2–3
seta *d* III	50	13	33–64	47	7	35–54	48	7	37–59	23	3	17–28
solenidion ϕ III	17	1	16–17	17	2	14–19	14	1	13–17	11	2	7–13
solenidion ϕ IV	5	1	4–5	7	1	6–7	6	1	4–6	4	1	3–6

(97); in the male by the presence of dorsal spines (46), and the loss of fusion between coxal apodemes III and IV (reversal) (156). In both the nymphs and female the scales are transformed to pointed spines.

The female and larva have been described previously (Mitchell & Fain, 1963). In the protonymph the spines are restricted to small patches near setae *c 1*. These patches are slightly larger in the tritonymph and female. Setae *d 2* in the nymphs and female flattened, rounded at the tips, and much longer than setae *d 1*. Anal setae small and swollen in the nymphs, larger and membranous in the female. The previously undescribed male has about ten small spines in the area between the anterior and posterior median shields. The shields appear poorly sclerotized, but the only available male is a

Table 11. Comparative measurements of male *Teinocoptes*.

	malayi N=4		*epomophori* N=1	*astridae* N=1	*strandtmanni* N=1	*philippinensis* N=3		*eonycteris* N=3		*auricularis* N=1	*harpyionycteris* N=6		
	av	range				av	range	av	range		av	SD	range
gnathosoma													
length	37	34–38	41	34	29	40	39–43	29	28–30	32	46	4	41–51
width	33	30–36	36	31	27	37	35–38	25	24–25	28	45	2	42–47
subcapitular seta	13	9–18	14	14	13	16	12–20	15	–	14	31	4	25–35
body													
length	246	244–249	346	227	224	305	–	212	184–229	223	436	28	404–465
width	180	177–184	231	146	155	234	–	152	138–165	160	327	42	257–361
seta *vi*	23	20–26	25	24	26	20	16–23	39	36–44	17	69	8	59–80
seta *sci*	33	30–35	21	27	24	26	24–28	37	35–38	32	57	5	52–65
seta *sce*	25	22–31	27	25	46	37	34–41	31	29–33	24	29	7	22–40
seta *c 1*	35	32–37	17	22	17	20	20	25	24–26	46	100	9	88–110
seta *c 2*	32	31–34	23	21	22	22	21–22	36	34–38	31	48	3	44–52
seta *cp*	12	11–14	20	10	22	13	13–14	28	28	16	84	12	72–97
seta *c 3*	47	38–51	25	27	31	37	29–44	39	35–41	30	52	4	47–57
seta *d 1*	27	25–28	18	21	17	25	24–26	28	27–29	34	45	3	39–48
seta *d 2*	31	29–33	22	25	28	30	30–31	34	34	35	49	5	42–54
seta *e 1*	9	8–11	7	6	9	7	6–8	21	20–22	11	30	2	27–32
seta *e 2*	19	18–21	11	17	12	13	11–15	31	30–32	15	32	5	27–38
seta *h 1*	7	6–7	6	6	8	7	7	17	17	11	29	3	26–33
seta *h 2*	7	6–8	6	6	8	7	7	18	17–19	8	34	3	31–38
seta *ps 1*	6	3–8	6	5	10	6	5–7	16	–	9	36	3	32–39
seta *ps 2*	9	6–12	8	10	8	9	–	13	12–14	10	24	2	23–26
seta *1 a*	14	11–16	15	16	15	13	12–13	32	27–39	13	58	1	58–60
seta *3 a*	10	9–11	8	13	9	6	–	18	18–19	13	29	2	27–31
seta *3 b*	13	12–15	14	18	12	12	12–13	23	22–26	25	48	2	46–51
seta *g*	21	20–23	12	15	12	14	13–15	20	19–21	10	25	3	23–30
genital area													
length	44	37–53	59	42	49	57	53–62	44	42–45	28	111	6	100–116
width	32	28–37	47	32	43	42	34–47	32	32	25	105	7	97–113
coxal apodeme I	51	46–61	58	47	48	56	53–61	38	37–38	40	67	2	64–69
coxal apodeme II	66	63–69	76	65	68	77	73–82	49	45–52	60	86	1	85–88
coxal apodeme III	37	35–41	45	36	32	44	43–45	32	32	32	54	2	51–57
coxal apodeme IV	35	33–41	45	39	14	43	38–47	38	35–39	21	30	5	24–38
leg I	69	62–77	86	58	68	71	59–82	49	40–58	54	110	5	104–115
leg II	67	62–73	84	52	59	77	74–80	55	52–58	48	107	4	104–113
leg III	43	37–50	61	43	45	60	54–67	35	30–42	40	91	3	88–94
leg IV	26	22–32	35	24	16	28	22–33	17	14–20	20	59	2	57–62
seta *pR* I	47	41–53	38	32	39	39	34–46	33	–	27	72	10	62–86
seta *pR* II	47	38–53	35	37	42	38	34–43	25	–	47	69	13	58–92
seta *sR* III	42	39–45	12	25	–	33	32–34	25	20–29	26	55	4	51–60
seta *vF* I	26	23–31	34	30	28	31	28–37	24	–	27	56	4	51–61
seta *vF* II	48	44–51	49	47	50	57	50–63	39	–	43	86	3	82–89
seta *cG* I	40	37–45	50	45	50	48	43–57	33	–	43	75	5	67–81
seta *mG* I	38	35–39	50	40	39	52	47–56	26	–	43	63	7	53–70
seta *d* III	225	211–232	233	212	189	246	219–274	150	141–164	195	325	12	309–338
solenidion σ I	4	3–4	–	3	5	3	2–3	5	4–5	–	5	1	4–6
solenidion σ II	4	3–4	5	4	4	3	2–3	4	4--5	–	4	1	3–5
solenidion φ I	10	10–11	17	12	12	14	12–16	12	12–13	17	23	1	22–25
solenidion φ II	13	11–14	18	13	16	18	16–18	16	14–18	20	25	1	24–27
solenidion φ III	12	11–13	13	10	8	12	11–12	9	7–11	10	13	3	11–18
solenidion φ IV	3	3–4	4	2	2	4	3–5	3	3–4	2	5	1	4–5
solenidion ω-1 I	14	13–15	15	15	14	14	13–15	15	13–16	23	25	1	23–26
solenidion ω-3 I	11	10–11	13	11	–	11	10–12	9	8–9	14	15	1	13–16
solenidion ω II	18	18	21	17	19	18	17–19	15	14–16	23	30	2	28–33
ambulacral stalk I	16	15–18	14	14	18	15	14–16	10	10–11	15	21	1	21–23
ambulacral stalk II	15	14–16	13	13	16	14	13–16	9	9–10	13	19	1	18–20

pharate and is not fully developed. Measurements in Table 11.

All specimens collected during this study were attached to the posterior edge of the wing.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Dobsonia moluccensis* (Quoy & Gaimard, 1830). INDONESIA: IRIAN BARAT, Nabire, 8 September 1962 (paratypes, specimens in collection BPBM); IRIAN BARAT, Biak Is., Korim, 0°54′S 136°02′E, elev. 5 m, 16 August 1976, NAMRU-2, AMNH #25225, HK 86–0815–7.

Literature records: on *Dobsonia moluccensis* from INDONESIA: IRIAN BARAT (Mitchell & Fain, 1963 [Type series]).

Deposition of specimens: AMNH and UMMZ.

Teinocoptes katherinae Mitchell & Fain, 1963

Teinocoptes katherinae Mitchell & Fain, 1963: 484.

Diagnosed in the female by the absence of scales in a continuous band between setae *sci* and *c 1* (reversal) (36).

The female is characterized by the linear arrangement of the perianal setae (Mitchell & Fain, 1963). Scaling of the dorsum is restricted to small patches near setae *c 1*. Site information is not available.

Material examined: Larva and female.

Host (Chiroptera: Pteropodidae) and locality: *Dobsonia inermis* Andersen, 1909. PAPUA NEW GUINEA: BOUGAINVILLE, Buka Is., Sia Cave, 8 December 1959 (paratypes, specimens in collection BPBM).

Literature records: on *Dobsonia inermis* from PAPUA NEW GUINEA: BOUGAINVILLE (Mitchell & Fain, 1963 [Type series]).

Teinocoptes wilsoni Mitchell & Fain, 1963

Teinocoptes wilsoni Mitchell & Fain, 1963: 482.

Diagnosed in the female by the absence of scales in a continuous band between setae *sci* and *c 1* (reversal) (36).

The female differs from that of *T. katherinae* by the relatively large scaly patches, which nearly touch along the midline. In addition only three (rather than four) pairs of perianal setae are arranged linearly (Mitchell & Fain, 1963). The *d* setae in the female are slightly modified, with a flattened shape and a rounded tip (Mitchell & Fain, 1963). This setal shape is less distinct in *T. katherinae*. Site information is not available.

Material examined: Female.

Host (Chiroptera: Pteropodidae) and locality: *Dobsonia moluccensis* (Quoy & Gaimard, 1830). INDONESIA: IRIAN BARAT, Nabire, 8 September 1962 (paratype, specimen in collection BPBM).

Literature records: on *Dobsonia moluccensis* from INDONESIA: IRIAN BARAT (Mitchell & Fain, 1963 [Type series]).

The fifth and last lineage arising at node 33 (node 39) is diagnosed in the nymphs by the absence of scales (reversal) (25, 26, 29, 30, 31); in the nymphs and female by the loss of setae *g* (123); in the female by the absence of scales in a continuous band between setae *sci* and *c 1* (reversal) (36), and the presence of postvulvar sclerotization (49). The first dichotomy in this lineage includes a small lineage (*aingworthi*/*philippinensis*), diagnosed in the larva by the loss of dorsal spines and/or scales (19), and a larger assemblage (node 41) diagnosed in the protonymph by the presence of legs IV (reversal) (213) and in the male by the presence of pointed and elongated median ventral outgrowths (55). Within the larger assemblage, a lineage including *T. eonycteris* and *T. johnsoni* diverges from the remaining species. The former lineage (node 42) is diagnosed in the nymphs and female by the presence of setae *vi* (reversal) (59); in the female by a relative decrease in the height of the body (reversal) (4), the presence of a verrucous zone anterolateral to legs III (50) extending across the body (51), and the presence of setae *vF* I (reversal) (168).

Teinocoptes aingworthi Mitchell & Fain, 1963

Teinocoptes aingworthi Mitchell & Fain, 1963: 481.

Diagnosed in the female by the arrangement of the lateral spines in a field (42).

The position of setae *e 1*, distinctly anterior to the anus and the other perianal setae, is characteristic for the female (Mitchell & Fain, 1963). The *d* setae are filiform and subequal in length. The perianal setae are very small (10 µm). Site information is not available.

Material examined: Larva and female.

Host (Chiroptera: Pteropodidae) and locality: *Nyctimene* sp. INDONESIA: IRIAN BARAT, Central Mts., Archbold Lake, 26 November/3 December 1961 (paratypes, specimens in collection BPBM).

Literature records: on *Nyctimene* sp. from INDONESIA: IRIAN BARAT (Mitchell & Fain, 1963 [Type series]).

Teinocoptes ***philippinensis*** nov. spec.
(Figs. 2, 206, 213–217)

Diagnosed in the larva by vestigial or absent setae *cp* (84); in the male by blunt, not pointed, median ventral outgrowths (reversal) (54).

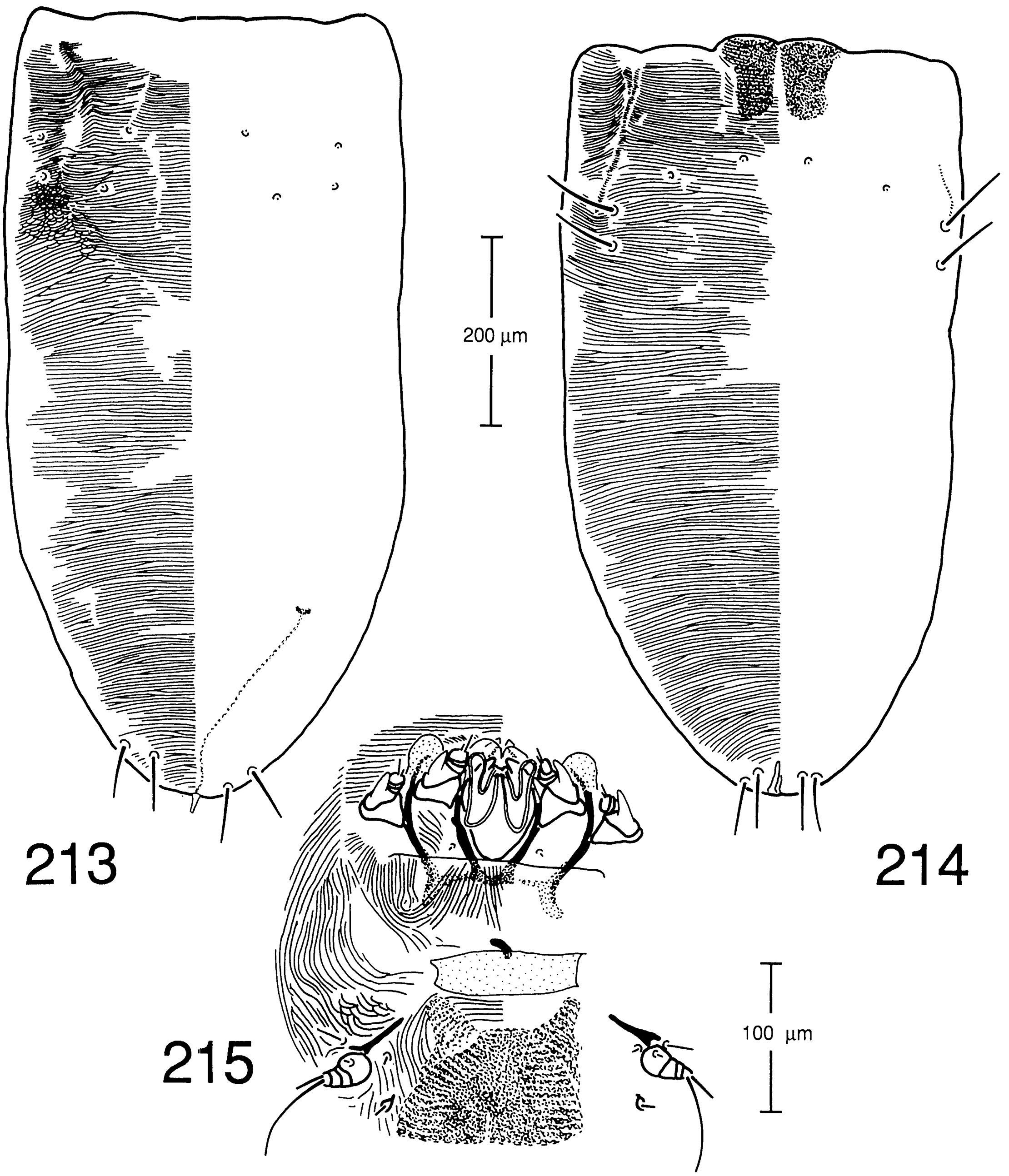
Larva (Fig. 206): Resembling the larva of *T. aingworthi* and *T. malayi* by the complete absence of spines and scales. Setae *d 2* 3–4 X the length of setae *e 2*.

Nymphs: Scales absent, the entire dorsum striated. Lateral spine series absent. Distribution and relative size of the body setae as in the female but all setae slightly shorter. Legs IV added in the tritonymph.

Female (Figs. 2, 213–215): Scales in two small patches near setae *c 1*. Lateral spine series poorly developed. All *d* and perianal setae long and filiform. Setae *d 2* longer than setae *d 1*. Distance between setae *d 1* and *d 2* smaller than the distance between setae *d 2* and *e 2*. Postvulvar sclerotization very well developed. Verrucous area anterolateral to legs III absent, although some scale-like striations are present (Fig. 215). Measurements in Table 10.

Male (Figs. 216, 217): Resembling the male of *T. malayi*. Dorsal shields well sclerotized. Posterior lateral shields appear to be divided. Genital area large, oval to triangular. Measurements in Table 11.

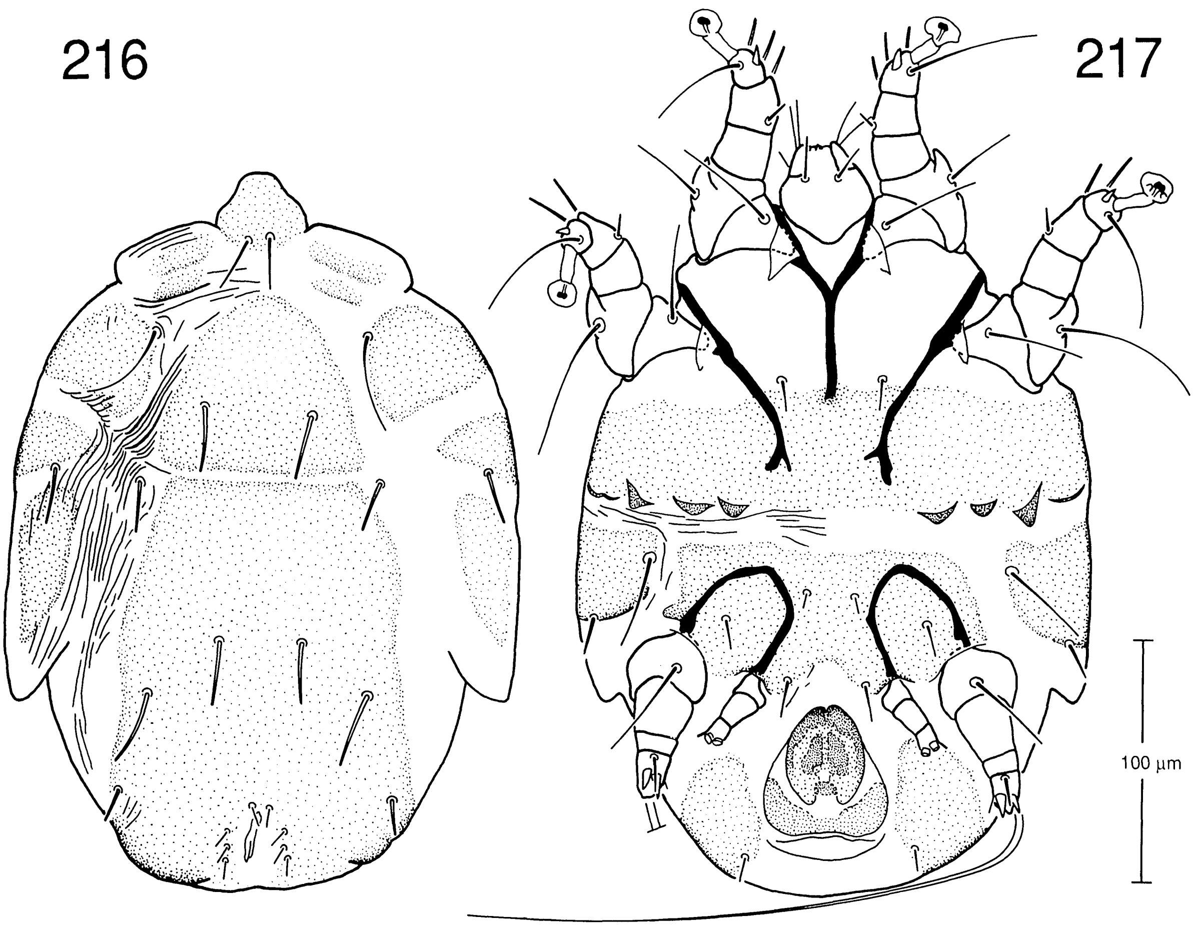
The immatures and females attach to the posterior edge of the wing.



Figs. 213–215. *Teinocoptes philippinensis*, female, anterodorsal (213), posterodorsal (214), and ventral (215) view.

Material examined: All stages.

Host (Chiroptera: Pteropodidae) and localities: *Harpyionycteris whiteheadi* Thomas, 1896. PHILIPPINES: Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21′N 123°11′E, elev. 850 m, 8 February 1984, R.B. Utzurrum (RBU 252), UMMZ #161303, HK 84–0621–10 (holotype female and allotype male); same locality, 28 August 1982, P.D. Heideman (PDH 820), UMMZ #158903, BMOC 83–1600–28; 1 September 1982, PDH 853, UMMZ #162376, BMOC 83–1600–34; 2 September 1982, PDH 857, FMNH, BMOC 83–1600–35; 4 October 1982, PDH 921, PNM, BMOC 83–1600–40; Camarines Sur, 4 km N, 18 km E Naga, Mt Isarog, 13°40′N 123°20′E, elev. 475 m, E.A. Rickart (EAR 2052), NMNH #573660, HK 88–0822–12; Leyte, Biliran Is., 11°32′N 124°32′E, elev. 920 m, 1 May 1984, PDH 2514, UMMZ #161303, HK 84–0621–8; Leyte, 8 km N, 2 km E Baybay, 10°46′N 124°49′E, elev. 500 m, 24 May 1984, L.R. Heaney (LRH 2667), UMMZ #161306, HK 84–0730–1; same locality, 23 March 1987, LRH 3030, NMNH, HK 87–0323–1; Leyte, 10 km N, 4 km E Baybay,



FIGS. 216, 217. *Teinocoptes philippinensis,* male, dorsal (216) and ventral (217) view.

10°47'N 124°50'E, elev. 700 m, 20 March 1987, PDH 3200, NMNH #459111, HK 87–0320–5; same locality, 21 March 1987, PDH 3214, NMNH #459113, HK 87–0321–3.

Etymology: The specific name is derived from the name of the country, the Philippines, where the type series was collected.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, IRSN, NMNH, OSU, PNC, and UMMZ.

Teinocoptes eonycteris Fain, Lukoschus, & Nadchatram, 1982 (Figs. 218, 219)

Teinocoptes eonycteris Fain et al., 1982: 77.

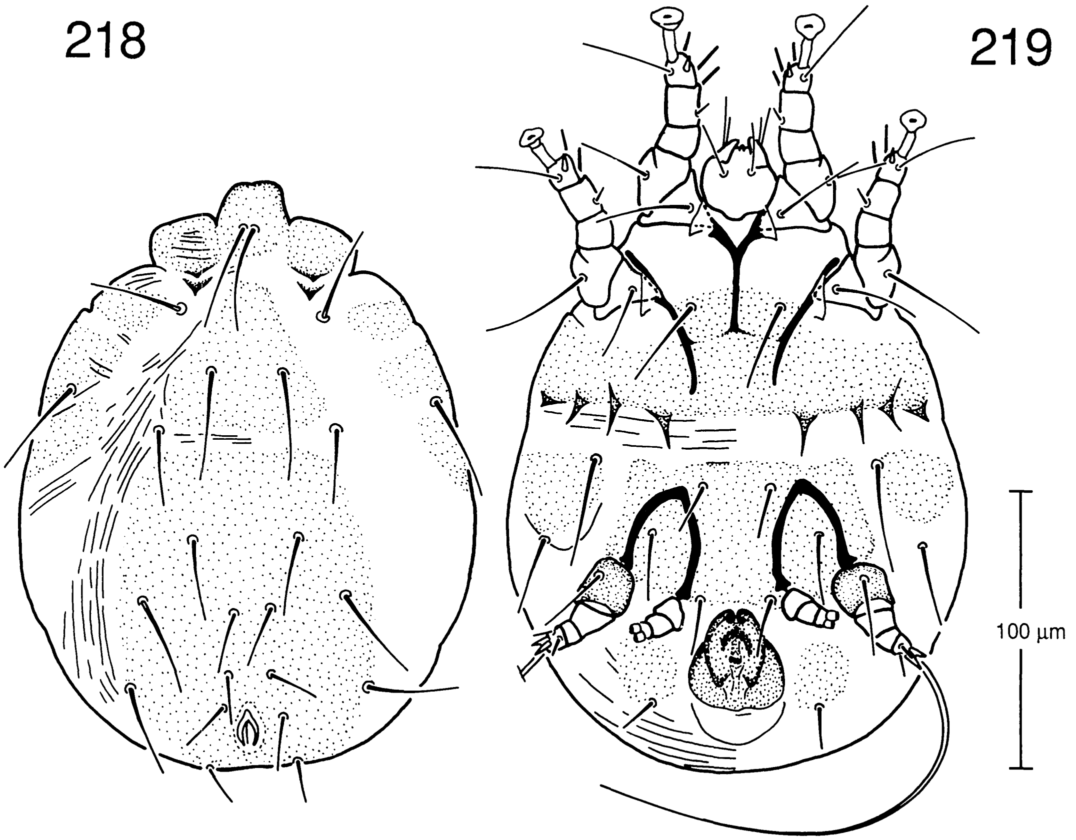
Diagnosed in the tritonymph and female by the loss of setae *pR* II (171); in the female by the presence of a spinose or sclerotized band between the distal ends of coxal apodemes II (52), the reduction of setae *c 3* to minute or absent (90), and the presence of membranous perianal setae (97).

Described from the holotype female only (Fain et al., 1982). The larva has 80–90 dorsal spines, distributed to include the entire area between setae *sci* and setae *d 1* and *e 1*. Setae *d 2* are subequal in length to setae *e 2*. The cuticle of the nymphs is without scales. Setae *d 1* and the perianal setae are small, not membranous. The female has a unique scale pattern, consisting of separate patches near setae *c 1* and *d 1*. Setae *d 1* and the perianal setae are membranous, setae *d 2* spine-like. The distance between setae *d 1* and *d 2* exceeds that between setae *d 2* and *e 2*. Measurements in Table 10. The male (Figs. 218, 219) corresponds to the male of type B as mentioned by Fain et al. (1982). It resembles the male of *T. auricularis* but has only a single pair of anterior dorsal spines (7–9 in *T. auricularis*) and coxal apodemes III and IV are fused (free in *T. auricularis*). Measurements in Table 11.

This species occurs on a variety of sites, including the legs, arms, neck, ears, and nipple, but not on the wing membrane.

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Eonycteris spelaea* (Dobson, 1871). Type host. INDONESIA: LOMBOK, Batu Koq, 8°19'S 116°26'E, 31 October 1987, D. Kitchener (L 201), WAM, HK 88–0410–1; MALAYSIA: PAHANG, Bentong, Bukit Chintamani, 13 October 1982, F.S. Lukoschus; PHILIPPINES: LEYTE, 4 km S, 1 km E Inopacan, 10°28'N 124°45'E, elev. 50 m, 28 May, 1984, P.D. Heideman (PDH 2734), UMMZ #161427, MAH 85–0131–1; same locality and date, PDH 2737, UMMZ #161430; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N



Figs. 218, 219. *Teinocoptes eonycteris,* male, dorsal (218) and ventral (219) view.

123°11′E, elev. 850 m, 4 November 1982, PDH 1028, UMMZ #158920, BMOC 83–1600–57; Negros Oriental, 4 km N Manjuyod, 9°43′N 123°10′E, elev. 50 m, 22 February 1987, L.R. Heaney (LRH 2907), NMNH #459070, HK 87–0222–3; same locality and date, E.A. Rickart (EAR 1258), NMNH #458166, HK 87–0222–7.

Rousettus aegyptiacus (Geoffroy, 1810). EGYPT: Cairo, Cairo, 30°03′N 31°15′E, 2 February 1984, S.M. Goodman (SMG 810), UMMZ #161045, HK 84–1119–1; same locality and date, SMG 811, UMMZ #161046, HK 84–1127–1.

Rousettus amplexicaudatus (Geoffroy, 1810). INDONESIA: Sumbawa, Batu Tering, 8°48′S 117°22′E, 25 May 1988, D. Kitchener (S 370), WAM, HK 89–0215–1; PAPUA NEW GUINEA: Madang, 9 mi N Madang, Maiwara; 21 July 1969, W.Z. Lidecker, MVZ #138510, HK 86–0520–2; PHILIPPINES: Leyte, 7 km N Baybay, 10°45′N 124°48′E, elev. 10 m, 27 March 1987, J.S.H. Klompen (JSHK 37), NMNH #459279, HK 87–0327–2; Negros Oriental, Dumaguete, 9°18′N 123°18′E, elev. 5 m, 23 August 1982, PDH 746, UMMZ #161501, HK 86–0424–2; same locality and date, PDH 750, UMMZ #161504, HK 86–0425–1; 29 November 1982, PDH 1149, UMMZ #161577, HK 86–0403–1; 30 December 1982, PDH 1338, UMMZ #161600, HK 85–0815–2; 24 March 1983, PDH 1671, UMMZ #161642, HK 86–0306–2; 20 February 1987, EAR 1252, NMNH #459290, HK 87–0220–1.

Literature records: on *Eonycteris spelaea* from MALAYSIA: Pahang, Raub (Fain et al., 1982 [Type series]).

Deposition of specimens: BMNH, CUIC, FMNH, IRSN, NMNH, OSU, PNC, UMMZ, WAM, ZIAC, and ZIZM.

Teinocoptes johnsoni Fain, 1963

Teinocoptes johnsoni Fain, 1963a: 101.

Diagnosed in the female by the presence of scales in the area anterior and lateral to the anus (36–39).

All females (the only known stage) have been found on the nipples of their host (Fain, 1963a; present study).

Material examined: Female.

Host (Chiroptera: Pteropodidae) and localities: *Thoopterus nigrescens* (Gray, 1870). INDONESIA: Sulawesi, Bada, 1917–1918 (paratype, specimen in collection NMNH); Sulawesi, Donggala, Lake Lindu, 1°18′S 120°05′E, January 1972, NAMRU-2 2376, NMNH #501357, HK 88–0831–2; same locality and date, NAMRU-2 2471, NMNH #502107, HK 88–0829–14.

Literature records: on *Thoopterus nigrescens* from INDONESIA: Sulawesi (Fain, 1963a [Type series]).

Deposition of specimens: NMNH and UMMZ.

The sister group of the *eonycteris/johnsoni* lineage (Fig. 53, node 43) is diagnosed in the female by the presence of distinct setae *cp* (reversal) (88). The first dichotomy in this lineage is between *T. haymani* and a lineage (node 44) diagnosed in the female by the complete loss of scales (34, 35). The next dichotomy separates *T. eidoloni* from a lineage (node 45) diagnosed in the female by a relative decrease in height (reversal) (4). *Teinocoptes domrowi* diverges from a lineage including the remaining three species (node 46) diagnosed in the tritonymph and female by the loss of setae *pR* II (171); in the female by the reduction of setae *c 3* to minute or absent (90), and the loss of setae *vF* II (169); in the male by the loss of fusion between coxal apodemes III and IV (reversal) (156), and the loss of fusion between femur and genu IV (reversal) (211).

Teinocoptes haymani Fain, 1963

Teinocoptes haymani Fain, 1963a: 103.

The female is characterized by the relative length of the *d* setae: setae *d 2* are much longer than setae *d 1* (Fain, 1963a). The *d* setae have rounded tips (Fain, 1963a).

The type specimens (females and larvae) were attached posteroventrally on the body, close to the uropatagium (Fain, 1963a).

Material examined: Larva and female.

Host (Chiroptera: Pteropodidae) and locality: *Notopteris macdonaldi* Gray, 1859. VANUATU: Tana Is. (paratypes, specimens in collection BMNH, #25–12–14–11–12).

Literature records: on *Notopteris macdonaldi* from VANUATU (Fain, 1963a [Type series]).

Teinocoptes eidoloni Fain, 1959

Teinocoptes eidoloni Fain, 1959b: 130.

Diagnosed in the larva by the presence of a small number of scales (21).

Described for the larva and the female (Fain, 1959b). In the female the distance between setae *d 1* and *d 2* exceeds that between setae *d 2* and *e 2*.

Females attach to the nipples of their host (Fain, 1959b).

Material examined: Larva and female.

Host (Chiroptera: Pteropodidae) and locality: *Eidolon helvum* (Kerr, 1792). RUANDA: Astrida, Nyarutovu (paratypes, specimens in collection OSU).

Literature records: on *Eidolon helvum* from RUANDA (Fain, 1959b [Type series]).

Teinocoptes domrowi Fain, 1961

Teinocoptes domrowi Fain, 1961a: 269.

Diagnosed in the larva by the loss of spines (reversal) (19); in the tritonymph by the presence of distinct setae *cp* (87) and *pR* I (170) (reversals); in the female by the presence of membranous perianal setae (97), and the presence of setae *vF* I (reversal) (168).

The larva of *T. domrowi* is characterized by the presence of partly sclerotized undulations of the dorsal striations, giving it a scale-like aspect (Fain, 1961a). The female is characterized by the membranous, tripartite perianal and *d* setae. The distance between setae *d 1* and *d 2* exceeds that between setae *d 2* and *e 2*.

The majority of the immatures and females attach at, or very close to, the posterior edge of the wing but immatures may also attach on the wing surface (Fain, 1963a; present study).

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Pteropodidae) and localities: *Acerodon jubatus* (Eschscholtz, 1831). PHILIPPINES: LEYTE, Maripipi Is., 1 km N, 1 km W Maripipi, 11°47'N 124°20'E, elev. 350 m, 26 April 1987, P.D. Heideman (PDH 3479), NMNH #457999, HK 87–0426–1; same locality and date, PDH 3481, NMNH #458985, HK 87–0426–2.

Pteropus hypomelanus Temminck 1853. MALAYSIA: Pulau Tioman, 1 May 1966 (specimen in collection BME); PHILIPPINES: LEYTE, Maripipi Is., 3 km N, 3 km W Maripipi, 11°47'N 124°19'E, elev. 50 m, 23 April 1987, PDH 3441, NMNH #458434, HK 87–0423–1; same locality and date, PDH 3444, NMNH #459239, HK 87–0423–2; NEGROS ORIENTAL, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 10 May 1987, E.A. Rickart (EAR 1557), NMNH #459245, HK 87–0510–3.

Pteropus speciosus Andersen, 1908. PHILIPPINES: SULU, Sibutu Is., 4°45'N 119°25'E, 26 May 1988, E. Mendez, NMNH, HK 88–0822–7.

Melonycteris melanops Dobson, 1877. PAPUA NEW GUINEA: NEW IRELAND, 4 km S Hilalon, 18 July 1979, J.D. Smith (JD5 4829) (specimens in collection OSU).

Literature records: on *Pteropus conspicillatus* Gould, 1850 from AUSTRALIA: QUEENSLAND, near Innisfail, Mundoo (Fain, 1961a [Type series]; Domrow, 1962); on *Pteropus alecto* Temminck, 1837 (= *P. gouldi*) from AUSTRALIA (Domrow, 1962); on *Pteropus giganteus* (Brunnich, 1782) from INDIA (Mitchell, 1970); on *Pteropus scapulatus* Peters, 1862 from AUSTRALIA (Domrow, 1962); on *Pteropus speciosus* from INDONESIA (Java Sea, Pulo Sulombo) (Fain, 1963a); on *Syconycteris australis* (Peters, 1867) (= *S. crassa*) from INDONESIA: IRIAN BARAT (Mitchell & Fain, 1963).

Deposition of specimens: CUIC, FMNH, MAK, NMNH, PNC, UMMZ, WAM, ZIAC, and ZIZM.

The next two species, *T. auricularis* and *T. ituriensis*, are very similar. *Teinocoptes ituriensis* was not included as a terminal taxon in the analysis, since all character states that could be determined were the same in both species (see p. 3). The assemblage of both species is diagnosed in the female by the arrangement of the lateral spines in a field (42).

Teinocoptes auricularis Fain, 1959

Teinocoptes auricularis Fain, 1959j: 336.

The female is characterized by the absence of scales, and the minute size of setae *d 2*. The distance between setae *d 1* and *d 2* is at least three times as great as that between setae *d 2* and *e 2*. All stages have been described previously (Fain, 1959j). Comparative measurements of the male are included in Table 11.

Immatures and females occur in or on the ears (Fain, 1959j; present study), and on the nipple (present study).

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Epomophorus wahlbergi* (Sundevall, 1846). Type host. TANZANIA: ZANZIBAR (paratype male, specimen in collection IRSN).

Epomophorus gambianus (Ogilby, 1835). SENEGAL: CASAMANCE, 20 km E Zinguinchor, Diabane, 12°33'N 16°05'W, 27 December 1982, P.L. Ames (2276), FMNH, HK 86-0226-1.

Hypsignathus monstrosus Allen, 1861. ANGOLA: LUNDA, Dundo, July 1948, A. Barros Machado, FMNH #66435, BMOC 86-0224-16.

Literature records: on *Epomophorus wahlbergi* from TANZANIA (Fain, 1959j [Type series]); on *Hypsignathus monstrosus* from ZAIRE (Fain, 1967); on *Micropteropus pusillus* (Peters, 1867) from ZAIRE (Fain, 1959j).

Teinocoptes ituriensis Fain, 1967

Teinocoptes ituriensis Fain, 1967: 363.

This species differs from *T. auricularis* by the larger body size and the smaller width of the perianal setae (respectively 480 by 420 vs. less than 400 by 390 μm, and < 3.5 vs. 5–6 μm [measurements based on Fain, 1959j and 1967]). The distinct possibility that these species are identical cannot be tested until more material of *T. ituriensis* becomes available.

The type nymph and female were collected from the "body" (Fain, 1967).

Material examined: None.

Literature records: on *Rousettus angolensis* from ZAIRE: HAUT-ZAIRE, N Kasenyi, Saliboko (Fain, 1967 [Type series]).

Teinocoptes harpyionycteris (Klompen & OConnor, 1987), new combination

Chirobia harpyionycteris Klompen & OConnor, 1987: 153.

Diagnosed in the larva by vestigial or absent setae *cp* (84); in the nymphs by not adding legs IV (reversal) (213, 214); in the nymphs and female by the reduction in the height of the body (reversal) (3, 5); in the female by the complete absence of spines or scales (reversal) (32, 33, 41), and the loss of setae *sR* III (200); in the male by the presence of spines on the dorsum (46), and the presence of setae *e* and *w* IV (reversals) (190, 192).

This species was placed in the genus *Chirobia* based on the reduction of coxal apodemes III and the non-tarsal leg setation in the nymphs and female, and the loss of fusion between coxal apodemes III and IV in the male (Klompen & OConnor, 1987). However, based on all characters examined for this study, it is more parsimonious to include it in the genus *Teinocoptes* (see comments in "Phylogenetic Analysis" section). Upon description the association of the single, allotype, male with the immatures and female was indicated as tentative (Klompen & OConnor, 1987). Even though several more males resembling the allotype have been collected, the evidence remains circumstantial, since molting stages have not yet been found. Comparative measurements of the newly collected males are included in Table 11.

All stages occur exclusively on the wing membrane, most often attached to the hairy part of the wing close to the body (Klompen & OConnor, 1987; present study).

Material examined: All stages.

Hosts (Chiroptera: Pteropodidae) and localities: *Harpyionycteris whiteheadi* Thomas, 1896. PHILIPPINES: CAMARINES SUR, 4 km N, 18 km E Naga, Mt. Isarog, 13°40'N 123°20'E, elev. 475 m, 5 May 1988, E.A. Rickart (EAR 2052), NMNH #573660, HK 88-0822-12; LEYTE, Biliran Is., 11°32'N 124°32'E, elev. 920 m, 1 May 1984, P.D. Heideman (PDH 2514), UMMZ #161303, HK 84-0621-8; LEYTE, 8 km N, 2 km E Baybay, 10°46'N 124°49'E, elev. 500 m, 24 May 1984, L.R. Heaney (LRH 2667), UMMZ #161306, HK 84-0730-1; same locality, 23 March 1987, LRH 3030, NMNH, HK 87-0323-1; LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 21 March 1987, PDH 3214, NMNH #459113, HK 87-0321-3; same locality, 22 March 1987, PDH 3228, NMNH #459114, HK 87-0322-5; NEGROS ORIENTAL, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 28 August 1982, PDH 820, UMMZ #158903, BMOC 83-1600-28; same locality, 1 September 1982, PDH 853, UMMZ #162376, BMOC 83-1600-34; 2 September 1982, PDH 857, FMNH, BMOC 83-1600-35; 4 October 1982, PDH 921, PNM, BMOC 83-1600-40; 8 February 1984, R.B. Utzurrum (RBU 252), UMMZ #161302, HK 84-0621-10.

Harpyionycteris celebensis Miller & Hollister, 1921. INDONESIA: SULAWESI, Lake Lindu, Tomado, 1°18'S 120°05'E, elev. 950 m, 25 January 1972, G.G. Musser, AMNH #240483, HK 86-0813-3.

Literature records: on *Harpyionycteris whiteheadi* from PHILIPPINES (Klompen & OConnor, 1987 [Type series]).

Deposition of specimens: AMNH, BMNH, CUIC, FMNH, NMNH, OSU, PNC, UMMZ, WAM, ZIAC, and ZIZM.

In addition to the species discussed above, a few more undescribed species were found during this study. However, the available material is insufficient for complete description.

Teinocoptes sp. 1

Material examined: 2 females.

Hosts (Chiroptera: Pteropodidae) and localities: *Balionycteris maculata* (Thomas, 1893). MALAYSIA: SELANGOR, Gombak Forest, 4 November 1982, F.S. Lukoschus.

Chironax melanocephalus (Temminck, 1825). MALAYSIA: PAHANG, Genting Sempah, 3°21'N 101°47'E, elev. 700 m, 8 March 1969, Yong Ghong Chong, AMNH #216740, HK 86-0815-9.

Teinocoptes sp. 2

Material examined: 1 tritonymph and 1 female.

Host (Chiroptera: Pteropodidae) and locality: *Rousettus lanosus* Thomas, 1906. ETHIOPIA: KEFA, Ghera Region, Afallo, 7°41'N 36°20'E, 2 May 1971, M. Desfayes, FMNH #105409, HK 86-0226-4.

Teinocoptes sp. 3

Material examined: 1 protonymph, 1 tritonymph, and 3 females.

Host (Chiroptera: Pteropodidae) and locality: *Ptenochirus minor* Yoshiyuki, 1979. PHILLIPINES: LEYTE, 10 km N, 4 km E Baybay, 10°47'N 124°50'E, elev. 700 m, 20 March 1987, J.S.H. Klompen (JSHK 30), NMNH #459215, HK 87–0320–4.

The sister group of the *Nycteridocoptes-Teinocoptes* lineage (node 47, Fig. 48) is diagnosed in all stages by the transformation of leg setae *r* III to spines (196); in the immatures and female by the loss of solenidia σ I (172); in the female tritonymph by the loss of spines and/or scales (reversal) (29); in the female by the loss of spines and/or scales in the area posterior to the *d 1* setae (reversal) (37, 38); in the male by the presence of a transverse apodeme (150), and the medial fusion of coxal apodemes III (157).

All taxa in the *Chirophagoides-Notoedres* lineage are ancestrally associated with bats in the suborder Microchiroptera, with some colonization to non-volant mammals. The first dichotomy involves the genus *Chirophagoides* and the remaining Teinocoptinae.

Chirophagoides Fain, 1963
(Figs. 42, 43)

Chirophagoides Fain, 1963b: 159.

Diagnosed in the female by the transformation of setae *sci* into broad, short spines (64) and setae *c 1* and *c 2* from filiform or spine-like to short, broad spines (75, 81), parallel but not fused coxal apodemes I (139), and the presence of ambulacra on legs III–IV (204); in the male by the presence of a lateral notch in the posterior median shield (16), poorly developed posterior lateral shields (18.2), and the transformation of setae *f* IV (188) and *r* IV (198) into spines. *Chirophagoides* is also characterized by the absence of setae *g* in the male (present in the female and tritonymph), and a unique modification of trochanteral setae *pR* I–II. These setae consist of a filiform part projecting from a bulbous base.

Type species *Chirophagoides mystacopis* Fain, 1963.

Chirophagoides mystacopis Fain, 1963
(Figs. 42, 43)

Chirophagoides mystacopis Fain, 1963b: 159.
Chirophagoides mystacops Fain, 1968: 156.

With the characters of the genus. The species has been described for the tritonymph and adults, with a brief note on the protonymph (Fain, 1963b). Information on site choice is limited; all stages were embedded in host tissue (Fain, 1963b).

Material examined: Female tritonymph, female, and male.

Host (Chiroptera: Mystacinidae) and locality: *Mystacina tuberculata* Gray, 1843. NEW ZEALAND: Southland, Stewart Is. (paratypes, specimens in collections IRSN and BMNH).

Literature records: on *Mystacina tuberculata* (= *Mystacops velutinus*) from NEW ZEALAND (Fain, 1963b [Type series]).

The sister group of *Chirophagoides* is the *Chirnyssoides/Notoedres* lineage (node 48, Fig. 48). This lineage is diagnosed by numerous characters: in all stages by never adding setae *f2* (101, 102, 103), *g* (123, 124), *3 a* (127, 128), and *f* III–IV (185, 186, 187); in the eggs by the presence of well developed stalks (138); in the immatures and female by the loss of the anterior median shield (8); in the female by a relative increase in the height of the body (4), the absence of dorsal spines and/or scales (reversal) (32, 35, 36), and the transformation from spines to filiform of setae *sci* (63) and *c 2* (79) (reversals); in the male by the presence of a well developed anterior median shield (10), the transformation from spines to filiform of setae *c 2* (reversal) (80), and the loss of setae *e* III (190).

The genera *Chirnyssoides* and *Notoedres* diverge at node 48.

Chirnyssoides Fain, 1959

Chirnyssoides Fain, 1959h: 2.

Diagnosed in the immatures and female by coxal apodemes III with a well developed and bifurcate basal branch (146); in the male by the strong elongation of the aedeagus (134), the loss of solenidia σ I (173), and the transformation of setae *sR* III into spines (202). In addition males of *Chirnyssoides* never add setae *4 a*.

Type species *Chirnyssoides caparti* Fain, 1959.

Existing classifications of *Chirnyssoides* recognize three subgenera. Two, *Noctiliocoptes* Fain & Lukoschus, 1971 and *Carollicoptes* Fain & Lukoschus, 1971, are monobasic and the third, *Chirnyssoides* (*s.s.*), includes the eight remaining species (Fain & Lukoschus, 1971, 1975). *Carollicoptes* (= *C. surinamensis*) is synonymized with *Chirnyssoides* (*s.s.*) since recognition of *Carollicoptes* would render *Chirnyssoides* (*s.s.*) paraphyletic (Fig. 55). Possible paraphyly is not a problem with regard to the subgenus *Noctiliocoptes; Chirnyssoides noctilionis*, the only species in this subgenus, is the sister group of all other species (node 50, Fig. 55). In order to minimize changes in existing classifications I will retain this subgenus. The division of *Chirnyssoides* into two subgenera also reflects a dichotomy in host associations: *C.* (*Noctiliocoptes*) occurs exclusively on Noctilionidae, and *C.* (*Chirnyssoides*) on Phyllostomidae.

Chirnyssoides (*Noctiliocoptes*) Fain & Lukoschus, 1971

Chirnyssoides (*Noctiliocoptes*) Fain & Lukoschus, 1971: 299.

Diagnosed in all stages by not adding setae *4 a* (130); in the immatures by the strongly increased height of the body (5); in the female by the elongation of setae *sci* (61), and the bifurcation of the distal end of the sternum (141); in the male by the loss of the anterior lateral shields (reversal) (11).

Type species *Notoedres* (*Bakeracarus*) *noctilionis* Dusbabek, 1970.

Chirnyssoides (*Noctiliocoptes*) *noctilionis* (Dusbabek, 1970)

Notoedres (*Bakeracarus*) *noctilionis* Dusbabek, 1970: 275.
Chirnyssoides (*Noctiliocoptes*) *noctilionis* (Dusbabek), Fain & Lukoschus, 1971: 300.

With the diagnostic characters of the subgenus.

The species is characterized by the unique morphology of coxal apodemes III in the immatures and females: the anterior tine of the basal branch of each apodeme bends back to fuse with the main branch.

The attachment site of the various stages has not been reported.

Material examined: All stages.

Hosts (Chiroptera: Noctilionidae) and localities: *Noctilio leporinus* (Linnaeus, 1758). Type host. CUBA: LA HABANA, Isla de Piños, Los Almacigos, 24 January 1966, Dusbabek & de la Cruz (paratype, specimen in collection NNML); SURINAM: Weg naar Zee, 11 September 1971, Lukoschus & Kok 455.

Noctilio albiventris Desmarest, 1818 (= *N. labialis*). SURINAM: Lelydorp, 23 January 1970, Kok 110 and 234; Meerzorg, 15 August 1971, Lukoschus & Kok 249; Weg naar Zee, 11 September 1971, Lukoschus & Kok 448 and 449.

Literature records: on *Noctilio leporinus* from CUBA (Dusbabek, 1970 [Type series]), and SURINAM (Fain & Lukoschus, 1971, 1975); on *Noctilio albiventris* from SURINAM (Fain & Lukoschus, 1971, 1975).

Chirnyssoides (*Chirnyssoides*) Fain, 1959

Chirnyssoides (*Chirnyssoides*) Fain, 1959h: 2.
Chirnyssoides (*Carollicoptes*) Fain & Lukoschus, 1971: 300, new synonymy.

Diagnosed in all stages by the loss of setae *la* I–II (164, 165); in the larva by the vestigial aspect of setae *cp* (84); in the immatures and female by minute setae *c 1* (72, 73); in the nymphs and female by minute setae *sci* (62) and *c 2* (78); in the female by the minute or vestigial aspect of setae *c 3* (90); in the male by the transformation of setae *sce* (71) into elongate spines, and setae *gT* I–II (166) into large spines.

Type species *Chirnyssoides caparti* Fain, 1959.

The next dichotomy involves the assemblage of *C. amazonae* and *C. caparti* and a lineage including the remaining species. The assemblage of *C. amazonae* and *C. caparti* (Fig. 55, node 51) is diagnosed in the nymphs and female by coxal apodemes IV with the distal end bifurcate (148); in the male by the transformation of setae *r* IV into spines (198).

Chirnyssoides (*Chirnyssoides*) *amazonae* Fain, 1959
(Figs. 5, 30, 31)

Chirnyssoides amazonae Fain, 1959h: 14.
Chirnyssoides carolliae Fain, 1962a: 400.

Chirnyssoides amazonae retains the ancestral addition sequence of the perianal setae. In the nymphs and female the anterior four pairs of perianal setae are filiform, the posterior four pairs have an inflated base. Coxal apodemes III in these stages with a bifurcate basal branch. The male can be distinguished by a combination of filiform setae *cp* (the ancestral condition) and a relatively long, and medially swollen aedeagus. All stages have been described previously (Fain, 1959h, 1962a; Fain & Lukoschus, 1975).

The immatures and males occur on the wing membrane, the females were found almost exclusively on the anterior or posterior edge of the wing (Fain, 1959h; present study).

Material examined: All stages.

Hosts (Chiroptera: Phyllostomidae) and localities: *Carollia brevicauda* (Schinz, 1821). Type host. ECUADOR: PASTAZA, Mera, 22 February 1984, L.S. Cushman (LSC 204), UMMZ, HK 84–0508–2; MEXICO: CHIAPAS, 2 km S, 5 km W Palenque, 17°31'N 91°58'W, 19 February 1985, B.M. OConnor, BMOC 85–0219–11; same data, UMMZ #163577, HK 85–0313–1; UMMZ #163579, HK 85–0305–3.

Carollia castanea Allen, 1890. ECUADOR: NAPO, Rio Bununo, S Venecia, 1 March 1984, LSC 707, UMMZ #164876, HK 84–0504–1.

Carollia perspicillata (Linnaeus, 1758). SURINAM: Zanderij, 2 January 1970, Kok 74, 211, and 212; Brownsberg, 20 October 1971, Lukoschus & Kok 714.

Carollia subrufa (Hahn, 1905). MEXICO: CHIAPAS, 6 km N, 2 km W Ocosingo, 17°04'N 92°15'W, 21 February 1985, B.M. OConnor, UMMZ #163599, HK 85–0319–5.

Glossophaga soricina (Pallas, 1766). MEXICO: CHIAPAS, 2 km S, 5 km W Palenque, 17°31'N 91°58'W, 19 February 1985, B.M. OConnor, BMOC 85–0219–10; same data, UMMZ #163581, HK 85–0320–2; UMMZ #163585, HK 85–0320–1; CHIAPAS, 6 km N, 2 km W Ocosingo, 17°04'N 92°15'W, 21 February 1985, B.M. OConnor, UMMZ #163593, HK 85–0327–1; PERU: CUZCO, Kiteni, elev. 650 m, 28 May 1984, P. Myers (PM 5141), UMMZ #160894, HK 84–0615–3; same locality, 29 May 1984, PM 5159, UMMZ #160897, HK 84–0615–2; May 1984, J.L. Patton (JLP 11198), MVZ #170030, HK 84–0612–1.

Literature records: on *Carollia brevicauda* (= *Hemiderma brevicauda*) from BRAZIL (Fain, 1959h [Type series]); on *Carollia perspicillata* from PANAMA (Fain, 1962a) and SURINAM (Fain & Lukoschus, 1971, 1975); on *Carollia subrufa* from PANAMA (Fain, 1962a); on *Glossophaga soricina* from SURINAM (Fain & Lukoschus, 1971, 1975).

Deposition of specimens: BMNH, NMNH, and UMMZ.

Chirnyssoides (*Chirnyssoides*) *caparti* Fain, 1959

Chirnyssoides caparti Fain, 1959h: 4.

Diagnosed in the immatures and female by the loss of the bifurcation of the basal branch of each coxal apodeme III (reversal) (146); in the male by the transformation of setae *cp* to long, spine-like rods (89).

Chirnyssoides caparti differs from *C. amazonae* by the diagnostic characters mentioned above. All stages have been described previously (Fain, 1959h; Fain & Lukoschus, 1975). This species was found exclusively on the wing (Fain, 1959h; present study).

Material examined: All stages.

Hosts (Chiroptera: Phyllostomidae) and localities: *Artibeus cinereus* (Gervais, 1856). SURINAM: Brownsberg, 21 October 1971, Lukoschus & Kok 725.

Artibeus lituratus (Olfers, 1818). MEXICO: CHIAPAS, 2 km S, 5 km W Palenque, 17°31'N 91°58'W, 19 February 1985, B.M. OConnor, UMMZ #163580, HK 85–0329–1; PARAGUAY: ALTO PARAGUAY, West bank Rio Paraguay, Estancia Puerto Ramos, ca 20°S 58°W, 30 September 1988, M.W. Nachman (MWN 439), UMMZ, HK 89–0321–11; same locality and date, MWN 440, UMMZ, HK 89–0321–12; 2 October 1988, MWN 444, UMMZ, HK 89–0309–2; PERU: CUZCO, Kiteni, elev. 650 m, 29 May 1984, P. Myers (PM 5156), UMMZ #160864, HK 84–0615–1; SURINAM: Santo Boma, 6 August 1971, Lukoschus & Kok 173; Wageningen, 26 September 1971, Lukoschus & Kok 560.

Uroderma bilobatum Peters, 1866. SURINAM: Weg naar Zee, 11 September 1971, Lukoschus & Kok 458.

Literature records: on *Artibeus jamaicensis* Leach, 1821 from BRAZIL: AMAZONAS, Rio Curiay (Fain, 1959h [Type series]), MEXICO (Webb & Loomis, 1977), and PANAMA (Fain, 1962a); on *Artibeus cinereus* from PANAMA (Fain, 1962a) and SURINAM (Fain & Lukoschus, 1975); on *Artibeus lituratus* from SURINAM (Fain & Lukoschus, 1975); on *Artibeus toltecus* (Saussure, 1860) from MEXICO (Webb & Loomis, 1977), and PANAMA (Fain, 1962a); on *Chiroderma salvini* Dobson, 1878, *Desmodus rotundus* (Geoffroy, 1810), *Vampyressa pusilla* (Wagner, 1843), *Vampyrodes caraccioli* (Thomas, 1889), and *Vampyrops vittatus* (Peters, 1860) from PANAMA (Fain, 1962a); on *Uroderma bilobatum* from SURINAM (Fain & Lukoschus, 1975); on an unidentified bat from DOMINICAN REPUBLIC (Fain, 1960b).

Deposition of specimens: BMNH, NMNH, and UMMZ.

The lineage including the remaining species (Fig. 55, node 52) is diagnosed in all stages by not adding setae *4 a* (130); in the female by the decrease in height of the body (reversal) (4). *Chirnyssoides vampyrops* diverges from a lineage (node 53) diagnosed by a delay in addition of the *ps* setae to the adult (116, 117); in the female by the strong reduction of setae *cG* I–II (167). The next dichotomy is between *C. surinamensis* and a lineage (node 54) diagnosed by the delay in addition of setae *h 1* and *h 2* to the protonymph (104, 106). *Chirnyssoides stenoderma* diverges from a lineage (node 55) diagnosed in the tritonymph by the vestigial aspect of setae *cp* (87). This lineage may also be diagnosed by a similar reduction of setae *cp* in the protonymph (86). However, the condition of this character for *C. stenoderma* is unknown, and it may diagnose a larger group, the sister group of *C. surinamensis* (node 54). *Chirnyssoides parvisuctus* diverges from a lineage (node 56) diagnosed by a delay in the addition of setae *h 2* to the tritonymph (107); in the immatures and female by the loss of the bifurcation of the basal branch of each coxal apodeme III (reversal) (146); in the female by not adding setae *sR* III (200). Finally, the sister group relationship between *C. phyllostomus* and *C. venezuelae* (node 57) is supported by the delay in addition of setae *h 2* to the adults (108).

Chirnyssoides (*Chirnyssoides*) *vampyrops* Fain & Lukoschus, 1975

Chirnyssoides (*C.*) *vampyrops* Fain & Lukoschus, 1975: 108.

Diagnosed in the immatures and female by the loss of bifurcation of the basal branch of each coxal apodeme III (reversal) (146).

The shape of the perianal setae in the immatures and female, more or less spatulate apically, is unique within the genus. The immatures and female have been described previously (Fain & Lukoschus, 1975). The male is still unknown.

The immatures and females occur on the wing membrane.

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Phyllostomidae) and localities: *Vampyrops lineatus* (Geoffroy, 1810). PARAGUAY: ALTO PARAGUAY, West bank Rio Negro, Estancia Inmaculado Concepcion, 20°05'S 58°10'W, 26 September 1988, M.W. Nachman (MWN 342), UMMZ, HK 89–0309–1; ALTO PARAGUAY, West bank Rio Paraguay, Estancia Puerto Ramos, ca 20°S 58°W, 2 October 1988, MWN 442, UMMZ, HK 89–0315–2.

Uroderma bilobatum Peters, 1866. SURINAM: Weg naar Zee, 11 September 1971, Lukoschus & Kok 458.

Literature records: on *Vampyrops helleri* (Peters, 1867) from SURINAM (Fain & Lukoschus, 1975 [Type series]); on *Uroderma bilobatum* from SURINAM (Fain & Lukoschus, 1975).

Deposition of specimens: UMMZ.

Chirnyssoides (*Chirnyssoides*) *surinamensis*
Fain & Lukoschus, 1971

C. (*Carollicoptes*) *surinamensis* Fain & Lukoschus, 1971: 305.
C. (*Carollicoptes*) *zanderyensis* Fain & Lukoschus, 1971: 309.

Diagnosed in all stages by not adding setae *ps 1* and *ps 2* (118, 119, 120); in the female by the loss of dorsoventral elongation (reversal) (3).

The nymphs and female are characterized by a unique modification of setae *h 2* (in the female also setae *h 1*), from filiform or spine-like to ovoid and membranous. All stages have been described previously (Fain & Lukoschus, 1971). The synonymy between *C. surinamensis* and *C. zanderyensis*, tentatively proposed by Fain & Lukoschus (1975), is confirmed based on molting stages in the new collections.

Development is characterized by paedomorphosis in various aspects of morphology (Klompen & OConnor, 1989) and behavior. The female retains the nymphal body shape (more or less flattened), instead of becoming dorsoventrally elongated (a process observed in all other *Chirnyssoides*). *Chirnyssoides surinamensis* retains the ancestral setal complement in the larva, but unlike other *Chirnyssoides*, it never adds to this complement. This results in a condition unique within the genus of adults without the *ps* setae. Unlike most other *Chirnyssoides* species, the females do not move to the edge of the wing but remain attached to the wing surface, the attachment site of the immatures. The above characteristics led Fain & Lukoschus (1971) to propose a new subgenus, *Carollicoptes*, to accommodate this species. However, as noted in the discussion of the genus, recognition of *C.* (*Carollicoptes*) would leave *C.* (*Chirnyssoides*) paraphyletic, and these subgenera are therefore synonymized.

Material examined: All stages.

Hosts (Chiroptera: Phyllostomidae) and localities: *Carollia perspicillata* (Linnaeus, 1758). Type host. PERU: MADRE DE DIOS, Hacienda Erika, Rio Alto, 1 May 1984, P. Myers (PM 4848), UMMZ #160882, HK 84–0613–2; CUZCO, Kiteni, elev. 650 m, 28 May 1984, PM 5144, UMMZ #160886, HK 84–0614–1; same locality and date, PM 5145, UMMZ #160887, HK 84–0614–3; SURINAM: Zanderij, 2 January 1970, Kok 73 and 74; Moeroekreek, 15 September 1971, Lukoschus & Kok 471; same locality, 16 September 1971, Lukoschus & Kok 478 and 480; Brownsberg, 20 October 1971, Lukoschus & Kok 718.

Carollia brevicauda (Schinz, 1821). ECUADOR: PASTAZA, Mera, 22 February 1984, L.S. Cushman (LSC 204), UMMZ, HK 84–0508–2; MEXICO: CHIAPAS, 2 km S, 5 km W Palenque, 17°31'N 91°58'W, 19 February 1985, B.M. OConnor, UMMZ #163576, HK 85–0305–1; same data, UMMZ #163577, HK 85–0313–1; UMMZ #163579, HK 85–0305–

3; PERU: MADRE DE DIOS, Hacienda Erika, Rio Alto, 1 May 1984, PM 4845, UMMZ #160879, HK 84–0613–1.

Carollia subrufa (Hahn, 1905). MEXICO: CHIAPAS, 6 km N, 2 km W Ocosingo, 17°04'N 92°5'W, 21 February 1985, B.M. OConnor, UMMZ #163595, HK 85–0319–7; same data, UMMZ #163598, HK 85–0319–3; UMMZ #163599, HK 85–0319–5.

Glossophaga soricina (Pallas, 1766). MEXICO: CHIAPAS, 2 km S, 5 km W Palenque, 17°31'N 91°58'W, 19 February 1985, B.M. OConnor, UMMZ #163585, HK 85–0320–1; PERU: CUZCO, Kiteni, elev. 650 m, 29 May 1984, PM 5159, UMMZ #160897, HK 84–0615–2.

Literature records: on *Carollia perspicillata* from SURINAM (Fain & Lukoschus, 1971 [Type series]; Fain & Lukoschus, 1975).

Deposition of specimens: BMNH, CUIC, NMNH, and UMMZ.

Chirnyssoides (*Chirnyssoides*) *stenoderma*
Fain & Lukoschus, 1975

Chirnyssoides (*C.*) *stenoderma* Fain & Lukoschus, 1975: 110.

This species differs from all others in the genus by a combination of the addition sequence of the perianal setae and the morphology of the coxal apodemes. Setae *h 1* and *h 2* are absent in the larva but present in the tritonymph, setae *ps 1* and *ps 2* are not added until the adult stages. Coxal apodemes III in the nymphs and female with a bifurcate basal prolongation but the anterior tine is very poorly developed. The distal end of each coxal apodeme IV is not bifurcate.

The larva, tritonymph, and female have been described, with brief notes on the morphology of the male (Fain & Lukoschus, 1975).

Material examined: None.

Literature records: on *Stenoderma* sp. from SURINAM (Fain & Lukoschus, 1975 [Type series]).

Chirnyssoides (*Chirnyssoides*) *parvisuctus*
Fain & Lukoschus, 1975

Chirnyssoides (*C.*) *parvisuctus* Fain & Lukoschus, 1975: 107.

Diagnosed by the addition of setae *ps 1* and *ps 2* in the tritonymph (reversal) (117); in the nymphs and female by coxal apodemes IV with the distal end bifurcate (148).

The larva, nymphs, and female have been described previously (Fain & Lukoschus, 1975). The male is unknown.

Material examined: Nymphs and female.

Hosts (Chiroptera: Phyllostomidae) and locality: *Micronycteris brachyotis* (Dobson, 1879). SURINAM: Gros Gold Mine, 23 August 1971, Lukoschus & Kok 338 and 342 (paratypes).

Literature records: on *Micronycteris brachyotis* from SURINAM (Fain & Lukoschus, 1975 [Type series]).

Chirnyssoides (*Chirnyssoides*) *brasiliensis* Fain, 1959

Chirnyssoides (*C.*) *brasiliensis* Fain, 1959h: 11.

Diagnosed in the male by the transformation of setae *cp* into long spine-like rods (89).

The morphology of the *h* setae in the tritonymph is unique: one pair is minute, the other has an inflated base and is subequal in length to the other perianal setae. The nymphs and adults have been described previously (Fain, 1959h; Fain & Lukoschus, 1975). All stages have been recovered from the wing membrane and the ears (Fain, 1959h).

Material examined: Tritonymph and female.

Hosts (Chiroptera: Phyllostomidae) and localities: *Sturnira lilium* (Geoffroy, 1810). Type host. SURINAM: Brownsberg, Lukoschus & Kok 702.

Phylloderma stenops Peters, 1865. VENEZUELA: BOLIVAR, SE El Manteco, 3 February 1981, M.W. Haiduk, CMNH #78306, HK 86–0703–9.

Literature records: on *Sturnira lilium* from BRAZIL: AMAZONAS, Rio Curiay and Pernambuco (Fain, 1959h [Type series]), and SURINAM (Fain & Lukoschus, 1975).

Deposition of specimens: UMMZ.

Chirnyssoides (*Chirnyssoides*) *phyllostomus*
Fain & Lukoschus, 1975

Chirnyssoides (*C.*) *phyllostomus* Fain & Lukoschus, 1975: 105.

This species is characterized in the female by the combination of long setae *c 1* and minute setae *sci* and *c 2*. The larva, tritonymph, and female have been described (Fain & Lukoschus, 1975). The previously undescribed protonymph resembles the tritonymph. Setae *h 1* are very small and setae *h 2*, *ps 1*, and *ps 2* are absent. Setae *cp* of the male are short and filiform, and the aedeagus is relatively thin (about 9 μm), parallel sided, and with a relatively small posterior fork. The male differs from that of *C. venezuelae* by a slightly longer aedeagus (respectively 44–50 vs. 40 μm).

Females and some immatures were found on the anterior edge of the wing and on the ears (both pinnae and tragus); most of the immatures occurred on the wing membrane.

Material examined: All stages.

Hosts (Chiroptera: Phyllostomidae) and localities: *Phyllostomus hastatus* Pallas, 1767. Type host. SURINAM: Moeroekreek, 17 September 1971, Lukoschus & Kok 495.

Tonatia carrikeri (Allen, 1910). BRAZIL: PARA, Belém, Utinga, 24 January 1977, W.L. Overall, FMNH #126251, HK 86–0224–9.

Tonatia silvicola (d'Orbigny, 1836). SURINAM: Brokopondo, Brownsberg Nature Reserve, 24 September 1979, S.L. Williams et al., CMNH #64046, HK 86–0702–12.

Literature records: on *Phyllostomus hastatus* from SURINAM (Fain & Lukoschus, 1975 [Type series]).

Deposition of specimens: BMNH, FMNH, NMNH, and UMMZ.

Chirnyssoides (*Chirnyssoides*) *venezuelae* Fain, 1959

Chirnyssoides (*C.*) *venezuelae* Fain, 1959h: 10.

Diagnosed in the female by the presence of well developed setae *sci* (reversal) (62).

Chirnyssoides venezuelae shares with *C. phyllostomus* the delay in addition of setae *h 2* to the tritonymph, and the presence of long setae *c 1* in the female. It differs by the presence of long (not minute) setae *sci* and *c 2* in the female. All stages have been described previously (Fain, 1959h; Fain & Lukoschus, 1975). Females and nymphs were collected from the wings and the ear (Fain, 1959h).

Material examined: Female.

Host (Chiroptera: Phyllostomidae) and locality: *Tonatia silvicola* (d'Orbigny, 1836). SURINAM: Brownsberg, 20 October 1971, Lukoschus & Kok 719.

Literature records: on *Tonatia brasiliense* (Peters, 1866) from VENEZUELA: San Esteban (Fain, 1959h [Type series]); on *Tonatia silvicola* from SURINAM (Fain & Lukoschus, 1975).

The sister group of *Chirnyssoides* is the genus *Notoedres* new concept (Fig. 48).

Notoedres Railliet, 1893

Notoedres Railliet, 1893: 660.
Chirnyssus Fain, 1959a: 119, new synonymy.
Bakeracarus Fain, 1959i: 162.
Notoedres (*Metanotoedres*) Fain, 1959i: 133, new synonymy.
Mysarcoptes Lawrence, 1960: 724.
Notoedres (*Neonotoedres*) Fain, 1963c: 257, new synonymy.
Notoedres (*Jansnotoedres*) Fain, 1965b: 332, new synonymy.
Suncicoptes Fain & Lukoschus, 1976: 1, new synonymy.

Diagnosed by the delay in addition of setae *h 2* to the protonymph (106); in all stages by the absence of setae *ps 1* and *ps 2* (116–120); in the male by the presence of genital apodemes (154), and the transformation of setae *kT* III–IV from large spines to thin spines or filiform (reversal) (199).

Type species *Sarcoptes cati* Hering, 1838.

The history of classification in this lineage is quite complex. In addition to the genus *Notoedres*, four genera, *Chirnyssus* Fain, 1959 (including *myoticola* and *africanus*), *Bakeracarus* Fain, 1959i, *Mysarcoptes* Lawrence, 1960 (*paucipilis*), and *Suncicoptes* Fain & Lukoschus, 1976 (*indicus*) have been described. In the latest revision of the genus *Notoedres*, Fain (1965b) relegated *Bakeracarus* to subgeneric status and synonymized *Mysarcoptes* with *Notoedres*. In a series of papers Fain (1959i, 1963c, 1965b) also described three new subgenera of *Notoedres*, *Metanotoedres* Fain, 1959 (including *miniopteri* and *verheyeni*), *Neonotoedres* (*elongatus*),and *Jansnotoedres* (*centrifera*).

The results of the phylogenetic analysis require some changes in this classification. Two monophyletic groupings can be recognized within the lineage (Figs. 56, 57): one including *N.* (*B.*) *lasionycteris*, the type species of *Notoedres* (*Bakeracarus*), the other including *N.* (*N.*) *cati*, the type species of *Notoedres*. I propose to recognize both lineages as subgenera (*Bakeracarus* and *Notoedres*). All other supraspecific taxa that are currently recognized are synonymized with the subgenus *Notoedres*. These groupings, as currently defined, are either paraphyletic (*Chirnyssus*, *N.* [*Metanotoedres*]), or monobasic (*Suncicoptes*, *N.* [*Neonotoedres*], and *N.* [*Jansnotoedres*]). Recognition of one or more of these groupings would involve proposing many additional supraspecific taxa to preserve monophyly for each recognized lineage, a procedure which is considered inappropriate given the poor resolution of relationships in *Notoedres*.

The following discussion is based on the analysis of relationships in *Notoedres* excluding *Notoedres indicus* (Fig. 57), and not on the analysis including all species of *Notoedres* (Fig. 56) (see comments in the "phylogenetic analysis" section). The first dichotomy in this lineage is between the subgenera *Bakeracarus* (node 59) and *Notoedres* (node 63).

Notoedres (*Bakeracarus*) (Fain, 1959)

Bakeracarus Fain, 1959i: 162.
Notoedres (*Bakeracarus*) (Fain), Fain, 1965b: 331.

Diagnosed in the immatures by the strong dorsoventral elongation of the body (5); in the female by parallel but not fused coxal apodemes I (139).

The coxal apodemes I in the male are usually relatively short. They usually do not extend posterior to the distal tip of coxal apodemes II.

Type species *Sarcoptes lasionycteris* Boyd & Bernstein, 1950.

Resolution within *Bakeracarus* is poor, due to a number of species described for only a single life stage. The polychotomy at node 59 involves four lineages. The first includes *N.* (*B.*) *paraguayensis* and *N.* (*B.*) *plecoti* (*N.* [*B.*] *plecoti* was not included as a terminal taxon, see p. 3). This lineage is diagnosed in the female by the large bare area on the dorsum (58). In addition, both species share a very unusual, dense pattern of striation in the female (Fig. 220).

Notoedres (*Bakeracarus*) ***paraguayensis*** nov. spec.
(Figs. 220–223)

Diagnosed in the male by the transformation of setae *kT* III–IV from spine-like or filiform to large spines (199).

This species closely resembles *N.* (*B.*) *plecoti*. Differences include: the female is larger (300 vs. 225 μm [the single female of *B. plecoti* was a pharate, which might account for smaller body size]), the *d 1*, *e 1*, *h 1*, and *c 3* setae are much longer (respectively 19 vs. 11 μm for setae *d 1*, *e 1*, and *h 1*, 37 vs. less than 10 μm for setae *c 3*), and the relative sizes of the setae differ. In *N.* (*B.*) *paraguayensis* setae *d 1* and *e 1* are distinctly longer than setae *d 2* and *e 2*, but in *N.* (*B.*) *plecoti* these setae are subequal in length.

Nymphs: Dorsum completely covered by widely spaced striations (no bare areas). Dorsal setal pattern as in the female (Fig. 220) but setae much shorter. Setae *h 2* added in the protonymph. Setae *4 a* added (but very small) in the tritonymph.

Female (Figs. 220, 221): Striation pattern very dense, with a large bare area anterior to the anus. All body setae well developed. Measurements in Table 12.

Male (Figs. 222, 223): Sclerotization of the dorsal shields moderately well developed. Posterior median and anal shields completely fused. Coxal apodemes I and II not reaching the transverse apodeme. Measurements in Table 13.

All stages occur on the wing, embedded in the skin overlying the arm bones, or attached to the wing membrane close to the arms. Remnants of the cuticle of all immature stages can be found in the adult cysts indicating that these mites do not change attachment site through ontogeny.

Material examined: Nymphs, female, and male.

Hosts (Chiroptera: Vespertilionidae) and locality: *Myotis nigricans* (Schinz, 1821). PARAGUAY: ALTO PARAGUAY, West bank Rio Negro, Estancia Inmaculado Concepcion, 20°05'S 58°10'W, 26 September 1988, M.W. Nachman (MWN 425), UMMZ, HK 89–0315–6 (holotype female); same locality and date, MWN 412, UMMZ, HK 89–0315–3; MWN 420, UMMZ, HK 89–0323–18; MWN 421, UMMZ, HK 89–0323–36 (allotype male); MWN 424, UMMZ, HK 89–0321–7; MWN 426, UMMZ, HK 89–0321–6; MWN 429, UMMZ, HK 89–0321–3; 25 September 1988, MWN 404, UMMZ, HK 89–0323–37; same date, MWN 406, UMMZ, HK 89–0323–21.

Etymology: The specific name is derived from the name of the country, Paraguay, in which the type series was collected.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, OSU, and UMMZ.

Notoedres (*Bakeracarus*) *plecoti* Fain, 1959, new combination

Notoedres (*Notoedres*) *plecoti* Fain, 1959i: 150.

The differences with *N.* (*B.*) *paraguayensis* are listed in the discussion of that species. The nymphs and female, the only stages described, were attached to the wing, close to the posterior edge (Fain, 1959i).

Material examined: None.

Literature records: on *Plecotus auritus* (Linnaeus, 1758) from BELGIUM: Brussels (Fain, 1959i [Type series]), and BULGARIA (Beron, 1970).

The next two lineages are monobasic. Each of the two species is known from a single collection only.

Notoedres (*Bakeracarus*) *coreanus* Ah, 1975

Notoedres (*B.*) *coreanus* Ah, 1975: 722.

The species has been described from a single female removed from the nose of its host. The species can be distinguished from all other *Bakeracarus* by the short setae *d* III–IV (< 50 μm) (Ah, 1975).

Material examined: None.

Literature records: on *Pipistrellus savii* (Bonaparte, 1837) from SOUTH KOREA: near Seoul (Ah, 1975 [Type series]).

Notoedres (*Bakeracarus*) *helicothrix* Fain & Lukoschus, 1975

Notoedres (*B.*) *helicothrix* Fain & Lukoschus, 1975: 116.

Diagnosed in the larva by having setae *h 1* distinctly longer than the other opisthosomal setae (105).

The female differs from those of other *Bakeracarus* species by the long, filiform setae *d 1, e 1,* and *h 1* (> 40 μm). Site information is not available for this species.

Material examined: Larva and female.

Host (Chiroptera: Molossidae) and locality: *Molossops planirostris* (Peters, 1865). SURINAM: Meerzorg, August 1971 (paratypes, specimens in collection NNML).

Literature records: on *Molossops planirostris* from SURINAM (Fain & Lukoschus, 1975 [Type series]).

The fourth and last lineage originating at node 59 (node 60) includes all species of the *lasionycteris* group. Most of these were described as subspecies of *N.* (*B.*) *lasionycteris* but since they are quite distinct it is more consistent to recognize them as separate species.

The lineage is diagnosed in all stages by not adding setae *4 a* (130); in the immatures and female by the spoon-shaped tip of setae *d 1, e 1,* and *h 1* (96); in the tritonymph by the vestigial aspect of setae *cp* (87); in the nymphs and female by the minute setae *sce* (70) and *c 2* (78); in the female by the strong reduction of setae *c 3* (90), and the extreme reduction or loss of setae *cG* I–II (167).

Within the *lasionycteris* group basal relationships remain unresolved, as illustrated by the trichotomy between *N.* (*B.*) *anisothrix, N.* (*B.*) *lasionycteris,* and a lineage including the three remaining taxa (Fig. 57, node 61).

Notoedres (*Bakeracarus*) *anisothrix* (Fain & Lukoschus, 1975)

Notoedres (*B.*) *lasionycteris anisothrix* Fain & Lukoschus, 1975: 116.

The very short setae *e 1* (4–6 μm) of the female are unique within the *lasionycteris* group. Only the female has been described (Fain & Lukoschus, 1975), and site information is not available.

Material examined: None.

Literature records: on *Molossus molossus* (Pallas, 1766) from SURINAM: Weg naar Zee and Wageningen (Fain & Lukoschus, 1975 [Type series]).

Notoedres (*Bakeracarus*) *lasionycteris* (Boyd & Bernstein, 1950)

Sarcoptes lasionycteris Boyd & Bernstein, 1950: 95.
Teinocoptes lasionycteris (B. & B.), Yunker, 1958: 34.
Bakeracarus lasionycteris (B. & B.), Fain, 1959i: 162.
Notoedres (*B.*) *lasionycteris* (B. & B.), Fain, 1965b: 331.

Diagnosed in the male by the loss of fusion between the posterior median and anal shields (15).

This species includes the type form, as well as *N.* (*B.*) *lasionycteris minimus* (Dusbabek, 1970) and *N.* (*B.*) *lasionycteris intermedius* (Dusbabek, 1970). Given the information currently available (both specimens and literature) these forms cannot be distinguished. However, it is conceivable that as more material becomes available this assemblage will prove to include more than one species. All stages have been described previously (Boyd & Bernstein, 1950; Dusbabek, 1970), although the male is known only for *N. lasionycteris minimus.*

Females occur on the ears and the arm of their hosts (Boyd & Bernstein, 1950). Site choice of the immatures and males has never been reported.

Material examined: Larva and female.

Hosts (Chiroptera: Molossidae) and localities: *Molossus molossus* (Pallas, 1766). SURINAM: Meerzorg, 14 August 1971, Lukoschus & Kok 242; same locality, 25 August 1971, Lukoschus & Kok 355.

Molossus ater Geoffroy, 1805. SURINAM: Moeroekreek, 19 September 1971, Lukoschus & Kok 499 and 500.

Literature records: *Notoedres* (*B.*) *lasionycteris lasionycteris:* on *Lasionycteris noctivagans* (LeConte, 1831) (Chiroptera:

FIGS. 220, 221. *Notoedres* (*Bakeracarus*) *paraguayensis*, female, dorsal (220) and ventral (221) view.

Vespertilionidae) from USA: PENNSYLVANIA (Boyd & Bernstein, 1950 [Type series]), and NORTH CAROLINA (Whitaker et al., 1975).

Notoedres (*B.*) *lasionycteris minimus* on *Molossus molossus* from CUBA (Dusbabek, 1970 [Type series]), and SURINAM (Fain & Lukoschus, 1975); on *Molossus ater* Geoffroy, 1805 from SURINAM (Fain & Lukoschus, 1975); on *Nyctinomops laticaudatus* (Geoffroy, 1805) (= *Tadarida yucatanica*) (Molossidae) from CUBA (Dusbabek, 1970).

Notoedres (*B.*) *lasionycteris intermedius* on *Mormopterus minutus* (Miller, 1899) (Molossidae) from CUBA (Dusbabek, 1970 [Type series]); a single specimen each on *Tadarida brasiliensis* (Geoffroy, 1824) (Molossidae), *Pteronotus macleayii* (Gray, 1839) (= *Chilonycteris macleayii*) (Mormoopidae) and *Eptesicus fuscus* (Beauvois, 1796) (Vespertilionidae), from CUBA (Dusbabek, 1970).

The lineage including the remaining taxa in the *lasionycteris* group (Fig. 57, node 61) is diagnosed by the delay in addition of setae *h 2* to the adult (107, 108); in the female by the minute setae *sci* (69). Within this lineage, the sister group relationship between *N.* (*B.*) *eptesicus* and *N.* (*B.*) *americanus* (node 62) is supported in all stages by the failure to add setae *h 2* (109); in the male by the loss of the transverse and median apodemes (reversals) (150, 151), and the free coxal apodemes III (reversal) (156, 157).

Notoedres (*Bakeracarus*) *corynorhini* (Fain, 1961)

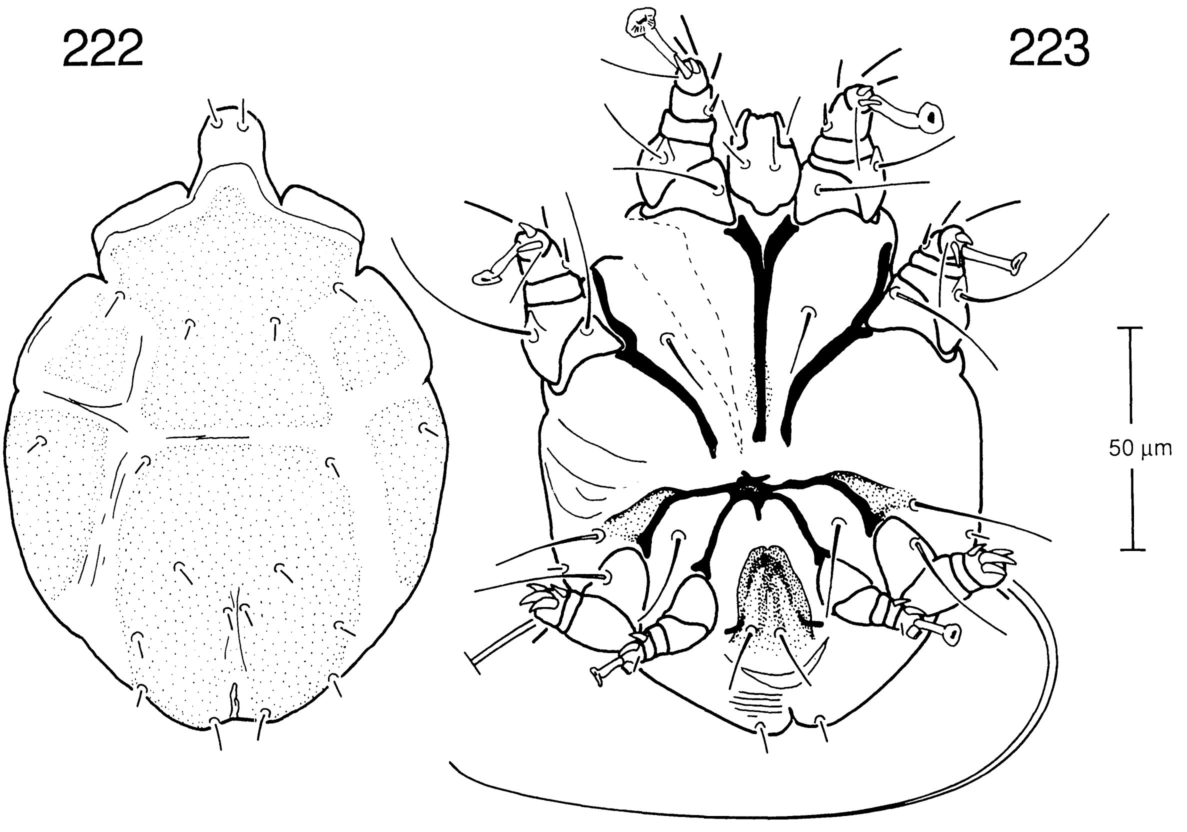
Bakeracarus lasionycteris corynorhini Fain, 1961b: 73.
Notoedres (*B.*) *lasionycteris corynorhini* (Fain), Fain, 1965b: 331.

Diagnosed in the larva by the minute setae *sci* (72).

The female closely resembles that of *N.* (*B.*) *lasionycteris* but differs by the smaller length of the perianal setae (see Fain, 1961b; Fain & Lukoschus, 1971). Both adult stages have been described (Fain, 1961b) but the description of the male is incomplete. Females and eggs were collected from the edges of the ear pinnae (B.M. OConnor, pers. comm.)

Material examined: Larva, tritonymph, and female.

Host (Chiroptera: Vespertilionidae) and locality: *Plecotus townsendii* Cooper, 1837. USA: ARIZONA, Cochise Co., 5 mi



FIGS. 222, 223. *Notoedres (Bakeracarus) paraguayensis,* male, dorsal (222) and ventral (223) view.

W Portal, Southwest Research Station, 11 June 1972, G. Dingerkus, BMOC 78-0501-3.

Literature records: on *Plecotus rafinesquei* Lesson, 1827 (= *Corynorhinus rafinesquei*) from USA: VIRGINIA (Fain, 1961b [Type series]; Yunker, 1958). Specimens reported by Whitaker et al. (1983) from *Plecotus townsendii* (USA: OREGON) may belong to this species.

Deposition of specimens: UMMZ.

Notoedres (Bakeracarus) eptesicus (Fain & Lukoschus, 1971)

Notoedres (B.) lasionycteris eptesicus Fain & Lukoschus, 1971: 310.

Diagnosed in the protonymph by the vestigial aspect of setae *cp* (86). This character may diagnose the entire *lasionycteris* group but this is the only species in the group for which the character state could be determined.

The female can be distinguished from all others in the *lasionycteris* group by the great length of setae *sci* (27–31 µm). All stages have been described briefly. The immatures and males attach to the wing membrane, the females to the posterior edge of the wing (Fain & Lukoschus, 1971).

Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Vespertilionidae) and localities: *Eptesicus brasiliensis* (Desmarest, 1819). SURINAM: Lelydorp, 24–27 February 1970, Lukoschus 186, 187, and 190 (all paratypes); Welgedacht, 1 August 1971, Lukoschus & Kok 126; same locality, 9 August 1971, Lukoschus & Kok 196; Paramaribo, August 1971, Lukoschus & Kok 216; Tawajariweg, 5 September 1971, Lukoschus & Kok 406.

Literature records: on *Eptesicus brasiliensis* (= *E. melanopterus*) from SURINAM (Fain & Lukoschus, 1971 [Type series]; Fain & Lukoschus, 1975). The specimens reported by Whitaker et al. (1983) from *Eptesicus fuscus* (USA: OREGON) may belong to this species.

Notoedres (Bakeracarus) ***americanus*** nov. spec.
(Figs. 225, 227–230)

Diagnosed in the male by the transformation of setae *ra* I–II from spines to filiform (reversal) (163), and setae *r* IV from filiform to spines (——198).

Immatures (Fig. 225): resembling the female in general morphology, striation pattern, and setal pattern but perianal setae relatively shorter.

Female (Figs. 227, 228): Setae *d 1*, *e 1*, and *h 1* well developed spine-like rods with a spoon-shaped tip. Posterior legs small. Measurements in Table 12.

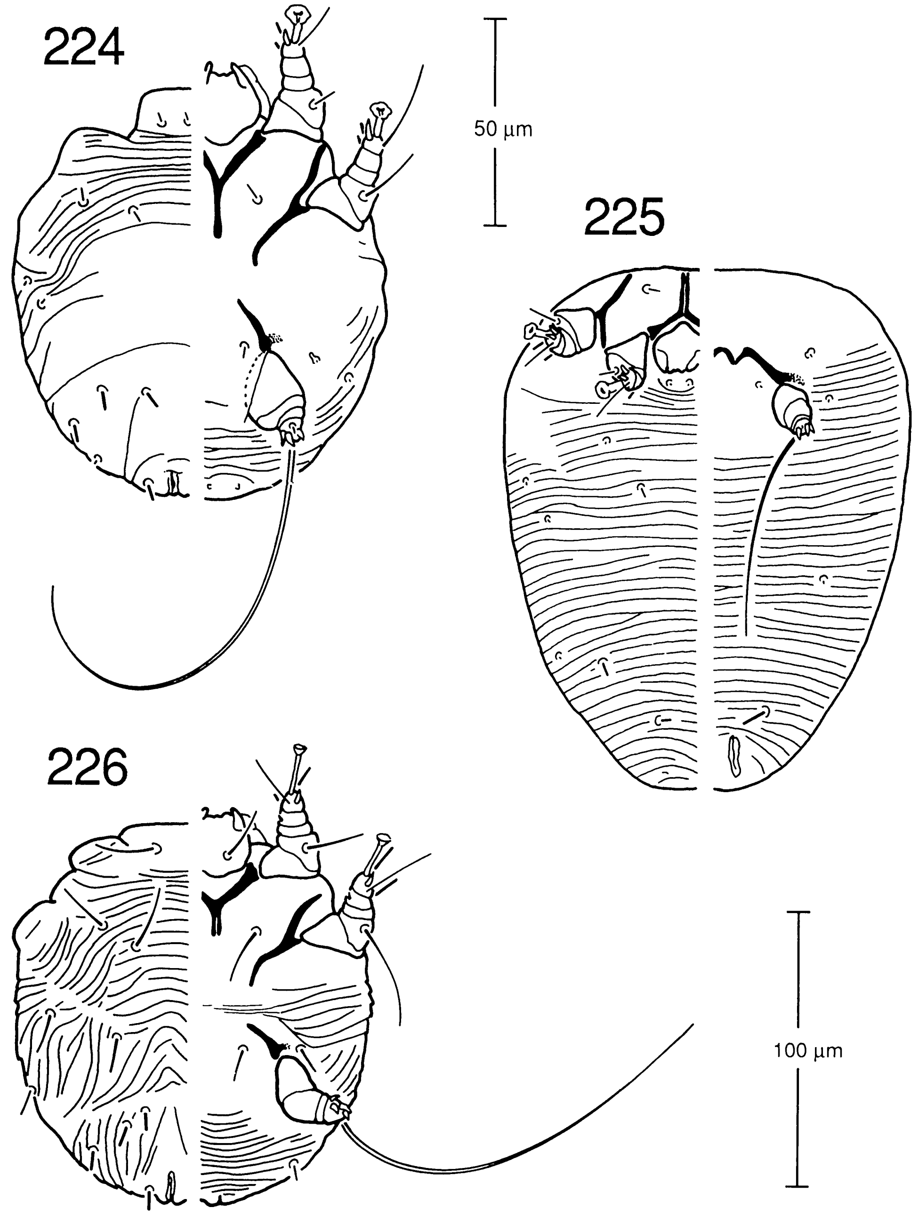
Male (Figs. 229, 230): Only a single male available. Dorsal shields very poorly sclerotized. Posterior median and anal shields fused. Genital area relatively large. Coxal apodemes I and II short. Measurements in Table 13.

Table 12. Comparative measurements of female *Notoedres*. 1.

	paraguayensis N=6			*americanus* N=5			*philippinensis* N=11			*miniopteri* N=3	
	av	SD	range	av	SD	range	av	SD	range	av	range
gnathosoma											
length	53	3	49–57	41	5	37–46	57	2	54–62	52	43–58
width	40	2	37–43	32	1	32–33	43	2	39–47	43	39–46
subcapitular seta	13	8	6–25	16	1	15–16	11	2	9–14	10	7–13
palpal seta α *l*											
length	15	1	13–17	10	1	9–10	19	3	16–25	17	14–20
width	0.7	0.2	0.4–0.9	0.6	0.1	0.5–0.7	1.6	0.3	1.1–1.9	2.3	2.0–2.8
body											
length	301	16	286–330	329	47	283–377	371	49	310–478	427	417–440
width	204	15	186–228	206	20	184–221	324	68	242–457	383	358–402
seta *vi*	14	1	13–15	4	1	3–5	4	1	3–4	3	–
seta *sci*	5	1	4–7	7	1	6–9	3	1	2–4	13	10–15
seta *sce*	13	1	12–15	4	1	3–5	5	1	4–6	7	6–7
seta *c 1*	5	1	4–6	5	1	4–6	3	1	2–4	11	8–13
seta *c 2*	5	1	5–6	1	–	–	3	1	2–5	8	8–9
seta *cp*	6	1	5–8	2	1	1–4	4	1	3–5	6	6–7
seta *c 3*	40	5	35–47	1	–	1–2	5	1	4–6	6	5–7
seta *d 1*	19	2	16–21	19	2	16–21	6	1	4–8	37	34–42
seta *d 2*	13	1	11–14	4	2	1–7	3	1	2–5	37	33–40
seta *e 1*	19	1	17–21	17	2	13–19	7	1	5–9	36	32–42
seta *e 2*	13	2	10–14	6	2	4–8	3	1	1–3	23	20–25
seta *h 1*	19	1	18–20	26	3	22–31	11	3	9–17	38	35–39
seta *h 2*	17	2	14–19	–			6	3	3–14	39	34–43
width seta *d 1*	1.5	0.2	1.3–1.8	1.2	0.3	0.8–1.5	0.5	0.2	0.2–0.7	3.8	3.5–4.2
width seta *d 2*	0.6	0.1	0.5–0.8	0.4	0.2	0.3–0.7	0.2	0.1	0.1–0.3	3.5	3.4–3.5
width seta *e 1*	1.4	0.2	1.2–1.8	1.1	0.2	0.9–1.4	0.6	0.2	0.4–1.0	4.0	3.8–4.3
width seta *e 2*	0.8	0.2	0.6–1.1	0.4	0.1	0.3–0.6	0.2	0.1	0.1–0.3	2.9	2.8–3.2
width seta *h 1*	1.6	0.2	1.4–1.8	1.5	0.2	1.3–1.6	0.8	0.1	0.6–1.0	3.6	3.3–3.9
width seta *h 2*	1.1	0.2	0.9–1.3	–			0.4	0.2	0.1–0.7	3.6	3.1–4.2
seta *1 a*	25	4	19–30	7	1	6–7	10	1	9–12	7	6–8
seta *3 b*	18	1	15–21	4	1	3–5	6	1	5–7	5	3–6
seta *4 a*	12	1	10–14	–			4	1	1–6	4	3–5
copulatory cone	2	1	2–3	4	2	2–7	5	1	4–6	3	2–3
bursa copulatrix	54	8	44–66	72	9	60–80	59	5	52–69	49	–
coxal apodemes I	63	3	59–67	47	2	45–49	77	3	73–82	59	56–64
coxal apodemes II	87	10	74–95	60	4	55–65	101	8	93–117	88	87–90
coxal apodemes III	39	1	37–40	25	2	22–28	41	2	38–45	36	33–39
coxal apodemes IV	36	2	33–39	23	2	22–27	41	3	35–46	36	33–40
leg I	62	5	57–69	49	6	40–54	66	5	55–72	50	48–52
leg II	64	4	56–67	49	7	42–59	79	11	61–100	50	46–55
leg III	51	4	46–54	33	3	30–37	63	4	57–68	52	48–58
leg IV	49	2	45–51	32	3	29–37	60	2	57–63	50	50–52
seta *pR* I	41	9	30–51	6	1	5–8	14	2	10–18	7	6–8
seta *pR* II	53	9	40–67	6	1	5–7	25	8	12–36	7	6–9
seta *sR* III	55	7	42–61	5	1	4–5	7	1	6–8	7	7
seta *vF* I	31	3	28–36	18	3	14–21	10	1	9–12	7	5–8
seta *vF* II	62	5	57–68	35	6	26–41	45	6	37–57	29	–
seta *cG* I	62	7	51–68	–			7	1	6–9	1	–
seta *cG* II	9	2	6–11	–			6	1	6–7	3	–
seta *d* III	240	16	214–255	115	5	110–119	235	18	206–260	84	57–99
seta *d* IV	234	18	207–247	110	11	102–127	254	23	209–285	78	64–105
solenidion φ I	20	1	19–22	12	3	8–15	13	1	11–15	6	5–6
solenidion φ II	20	1	18–22	13	2	10–16	16	4	13–25	7	6–8
solenidion φ III	9	1	8–10	6	1	5–6	8	2	5–10	7	6–7
solenidion φ IV	7	1	5–7	3	–	–	6	1	4–7	4	4–5
solenidion ω-1 I	20	2	18–22	11	1	9–12	12	1	10–14	7	7
solenidion ω-3 I	14	1	13–16	3	–	3–4	11	1	10–11	6	4–7
solenidion ω II	28	1	27–30	13	1	12–14	16	2	13–19	9	8–10
ambulacral stalk I	18	1	17–20	13	1	11–15	18	1	17–21	10	10
ambulacral stalk II	19	2	17–21	11	1	10–12	20	1	19–21	12	12

Table 13. Comparative measurements of male *Notoedres*. 1.

	paraguayensis			*americanus*	*philippinensis*			*miniopteri*	
	N = 5			N = 1	N = 10			N = 2	
	av	SD	range		av	SD	range		
gnathosoma									
length	32	2	30–35	30	46	2	44–50	33	31
width	26	1	25–27	24	32	1	31–34	26	28
subcapitular seta	9	1	8–12	9	9	3	7–13	7	10
palpal seta α *l*									
length	12	3	9–16	–	18	2	14–22	12	14
width	0.7	0.1	0.6–0.7	–	1.0	0.2	0.7–1.3	0.5	0.5
body									
length	205	13	185–220	191	261	16	228–284	182	192
width	139	5	133–145	119	205	11	194–229	166	156
seta *vi*	8	2	6–11	14	2	1	1–3	2	2
seta *sci*	4	1	4–5	4	4	1	2–5	7	8
seta *sce*	7	1	6–9	4	6	1	5–8	7	7
seta *c 1*	5	1	3–6	4	5	1	4–7	8	9
seta *c 2*	5	1	4–5	2	5	1	4–6	8	9
seta *cp*	6	1	5–7	6	8	1	7–8	6	7
seta *c 3*	36	3	32–39	–	17	1	15–18	12	12
width seta *c 3*	1.4	0.1	1.3–1.5	0.6	5.3	0.5	4.5–6.4	4.5	4.9
seta *d 1*	7	1	6–7	7	4	1	2–4	9	7
seta *d 2*	6	1	5–7	5	2	1	1–3	6	7
seta *e 1*	7	1	6–8	8	5	1	3–6	10	9
seta *e 2*	6	1	5–7	4	1	1	1–3	4	3
seta *h 1*	9	1	8–10	8	6	1	5–7	8	8
seta *h 2*	8	1	7–8	–	2	1	2–3	4	6
seta *1 a*	22	4	17–27	12	15	1	13–16	13	16
seta *3 b*	30	5	23–34	20	16	1	14–17	12	12
width seta *3 b*	1.3	0.2	1.1–1.5	1.2	3.9	0.5	3.5–4.7	4.8	4.2
seta *4 a*	21	2	19–23	–	7	1	6–10	5	6
genital area									
length	43	2	41–45	52	61	5	54–68	42	36
width	28	4	24–35	33	43	5	36–54	23	23
coxal apodemes I	66	4	61–71	54	98	6	91–105	74	69
coxal apodemes II	72	1	70–74	73	103	7	91–112	73	81
coxal apodemes III	22	2	20–24	16	31	1	30–34	19	21
coxal apodemes IV	27	1	26–28	24	35	2	31–38	26	24
leg I	51	4	46–56	56	76	8	62–83	53	58
leg II	56	6	20–24	16	86	8	72–96	50	59
leg III	48	4	43–52	45	68	4	62–73	50	55
leg IV	35	3	31–39	39	57	5	48–62	47	35
seta *pR* I	36	3	32–39	31	32	5	27–41	28	30
seta *pR* II	44	5	39–49	36	50	9	34–59	36	50
seta *sR* III	42	5	34–48	24	9	1	8–10	7	9
width seta *sR* III	1.2	0.2	1.1–1.5	0.8	3.9	0.5	3.4–5.0	3.6	3.9
seta *vF* I	25	5	18–33	19	15	4	11–26	9	17
seta *vF* II	54	5	47–58	47	60	8	49–73	56	56
seta *cG* I	35	4	30–41	43	28	4	22–32	24	30
seta *cG* II	7	1	5–9	11	5	1	4–7	4	4
seta *mG* I	28	4	20–32	35	11	2	7–13	–	21
seta *d* III	248	4	244–251	–	310	37	258–357	308	–
solenidion σ I	3	1	2–4	4	3	1	2–4	1	3
solenidion ϕ I	16	2	14–19	17	21	1	19–22	10	18
solenidion ϕ II	16	2	15–19	16	24	1	22–25	12	15
solenidion ϕ III	11	2	8–14	6	8	1	6–10	6	8
solenidion ϕ IV	9	1	7–10	6	16	1	13–17	11	13
solenidion ω-1 I	20	2	18–23	17	16	1	15–18	15	19
solenidion ω-3 I	12	2	10–15	15	15	1	14–16	15	14
solenidion ω II	27	2	24–29	24	22	2	18–25	30	27
ambulacral stalk I	17	1	16–19	21	20	1	18–22	14	22
ambulacral stalk II	17	1	16–19	19	23	1	21–24	16	19
ambulacral stalk IV	12	1	11–12	11	19	1	17–21	14	20



Figs. 224–226. *Notoedres*, larvae, dorsal (left) and ventral (right) view: *N.* (*N.*) *namibiensis* (224), *N.* (*Bakeracarus*) *americanus* (225), *N.* (*N.*) *centrifera* (226). Figs. 225–226 same scale.

All stages were collected from the posterior trailing edge of the wing. The cysts of the adults contained remnants of the cuticle of all immature stages, indicating that the mites do not change site after molting.

Material examined: All stages.

Hosts (Chiroptera: Vespertilionidae) and localities: *Myotis nigricans* (Schinz, 1821). Type host. PARAGUAY: Alto Paraguay, West bank Rio Negro, Estancia Inmaculado Concepcion, 20°05'S 58°10'W, 25 September 1988, M.W. Nachman (MWN 409), UMMZ, HK 89–0323–20 (holotype female); same locality and date, MWN 407, UMMZ, HK 89–0323–33; MWN 411, UMMZ, HK 89–0323–26; 26 September 1988, MWN 413, UMMZ, HK 89–0323–29; same date, MWN 414, UMMZ, HK 89–0323–30; MWZ 431, UMMZ, HK 89–0321–1 (allotype male).

Myotis velifer (Allen, 1890). USA: Kansas, 25 July 1952, P.H. Krutzsch, MVZ #168010, HK 86–0521–9; same data, MVZ #168011, HK 86–0521–6; MVZ #168014, HK 86–0521–8; MVZ #168016, HK 86–0521–7; MVZ #168018, HK 86–0521–10.

Literature records: The specimens collected by Yunker (1958) from *Myotis lucifugus* (LeConte, 1831) (USA: Virginia), and by Whitaker et al. (1983) from *Myotis yumanensis* and *M. volans* (USA: Oregon) may belong to this species.

Etymology: The specific name is derived from the name of the region, North and South America, from which the species has been collected.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, OSU, and UMMZ.

The sister group of the subgenus *Bakeracarus* is the nominate subgenus *Notoedres* (new concept) (node 63, Fig. 57).

Notoedres (*Notoedres*) Railliet, 1893

Notoedres (*Notoedres*) Railliet, 1893: 660.
Notoedres (*Metanotoedres*) Fain, 1959i: 133, new synonymy.
Notoedres (*Neonotoedres*) Fain, 1963c: 257, new synonymy.
Notoedres (*Jansnotoedres*) Fain, 1965b: 332, new synonymy.

Diagnosed in the female by a change in the body shape (height not exceeding the width) (reversal) (3, 4).

Type species *Sarcoptes cati* Hering, 1838.

Within the subgenus *Notoedres* resolution of the basal relationships is very poor, as demonstrated by the eleven lineages arising at node 63. As mentioned previously (p. 25), this is caused largely by the numerous species known for only a single or a few life stages. Future collections of additional stages should help resolve this polychotomy.

The first lineage at node 63, the *myoticola* group, includes among others species formerly included in the genus *Chirnyssus* and the subgenus *N.* (*Metanotoedres*). The lineage (node 64) is diagnosed in the larva and male by the transformation of setae *3 b* into spines (122); in the female by the inflated base of palpal setae α *l* (1), parallel but not fused coxal apodemes I (139), the loss of setae *la* I–II (164), and the transformation of setae *sR* III into spines (201); in the male by the fusion of the anterior lateral and anterior median shields (12 state 1), and the transformation of setae *c 3* (93), setae *gT* I–II (166), setae *kT* III–IV (199), and setae *sR* III (202) into spines.

The first dichotomy in the *myoticola* group is between *N. philippinensis* and a lineage (node 65) diagnosed in the female by the transformation of setae *sci* (63), *c 1* and *c 2* (79) into spines; in the male by the loss of fusion between the posterior median and the anal shields (15), and the transformation of setae *4 a* into spines (132). *Notoedres miniopteri* diverges from the assemblage of *N. verheyeni* and the species associated with *Myotis* (node 66), an assemblage diagnosed in the male by the loss of fusion between the anal shields (14).

Notoedres (*Notoedres*) ***philippinensis*** nov. spec.
(Figs. 231–251)

Diagnosed in the female by the presence of a large bare zone on the dorsum (58), and the minute size of setae *sci* (62), *c 1* (73), and *c 2* (78).

Larva (Fig. 231): Striation limited to the anterior and lateral parts of the dorsum. Perianal setae short, setae *d 2* and *e 2* minute. Ventral setae *c 3* and *3 b* well developed spines in most specimens (Fig. 231), distinctly thinner in other specimens.

Nymphs (Figs. 232, 233): Resembling the larva. Legs IV and setae *h 2* added in the protonymph. Setae *4 a* and trochanteral setae added in the tritonymph. Setae *sR* III in the tritonymph spine-like. Length of the perianal setae of both nymphal stages variable: very short in some specimens (see Fig. 232), longer in others (Fig. 233). Intermediate forms occur, although infrequently.

Female (Figs. 234–241): Bare area on the dorsum smaller than in the nymphs. Perianal setae short or minute (setae *d 2, e 1*). Tibial setae *gT* I–II and *kT* III–IV large spines. Genual setae *cG* II reduced in length and spine-like. Trochanteral flaps I–II poorly developed. Trochanteral setae *sR* III spine-like. Measurements in Table 12.

Male (Figs. 242–251): Dorsal shields well developed, covering nearly the entire dorsum. Dorsal setae very small to minute. Setae *c 3, 3 b,* and *sR* III big spines, setae *4 a* filiform. Coxal apodemes I and II touching or nearly touching the transverse apodeme. Tarsal setae *la* I–II present. Setae *cG* II as in the female. Measurements in Table 13.

The variability in morphology of the immatures does not appear to indicate host races; the two forms can co-occur on the same host and occurred on all three host species. Sexual dimorphism can also be excluded, since developing females were found in both kinds of tritonymphs.

Nearly all specimens were collected from juvenile, largely hairless bats. On these hosts the mites occurred most often on the forearm and head, but some specimens were found on the body and uropatagium.

Material examined: All stages.

Hosts (Chiroptera: Vespertilionidae) and localities: *Miniopterus tristis* (Waterhouse, 1845). Type host. PHILIPPINES: NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 10 June 1984, P.D. Heideman (PDH 2806), UMMZ #160368, HK 84–0620–2 (holotype female, allotype male); same locality and date, PDH 2807, UMMZ #160369, HK 84–0727–5; PDH 2836, UMMZ #160371, HK 84–0810–1.

Miniopterus australis Tomes, 1858. PHILIPPINES: NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 14 June 1987, LRH 3643, NMNH, HK 87–0614–17; same locality and date, several juveniles, NMNH, HK 87–0614–18.

Miniopterus schreibersi (Kuhl, 1819). PHILIPPINES: NEGROS ORIENTAL, 4 km N Manjuyod, 9°43'N 123°10'E, elev. 50 m, 10 June 1984, PDH 2835, UMMZ #160367, HK 84–0810–2; same locality, 14 June 1987, L.R. Heaney (LRH 3603), NMNH, HK 87–0614–14; same date, LRH 3621, NMNH, HK 87–0614–15; several juveniles, NMNH, HK 87–0614–16.

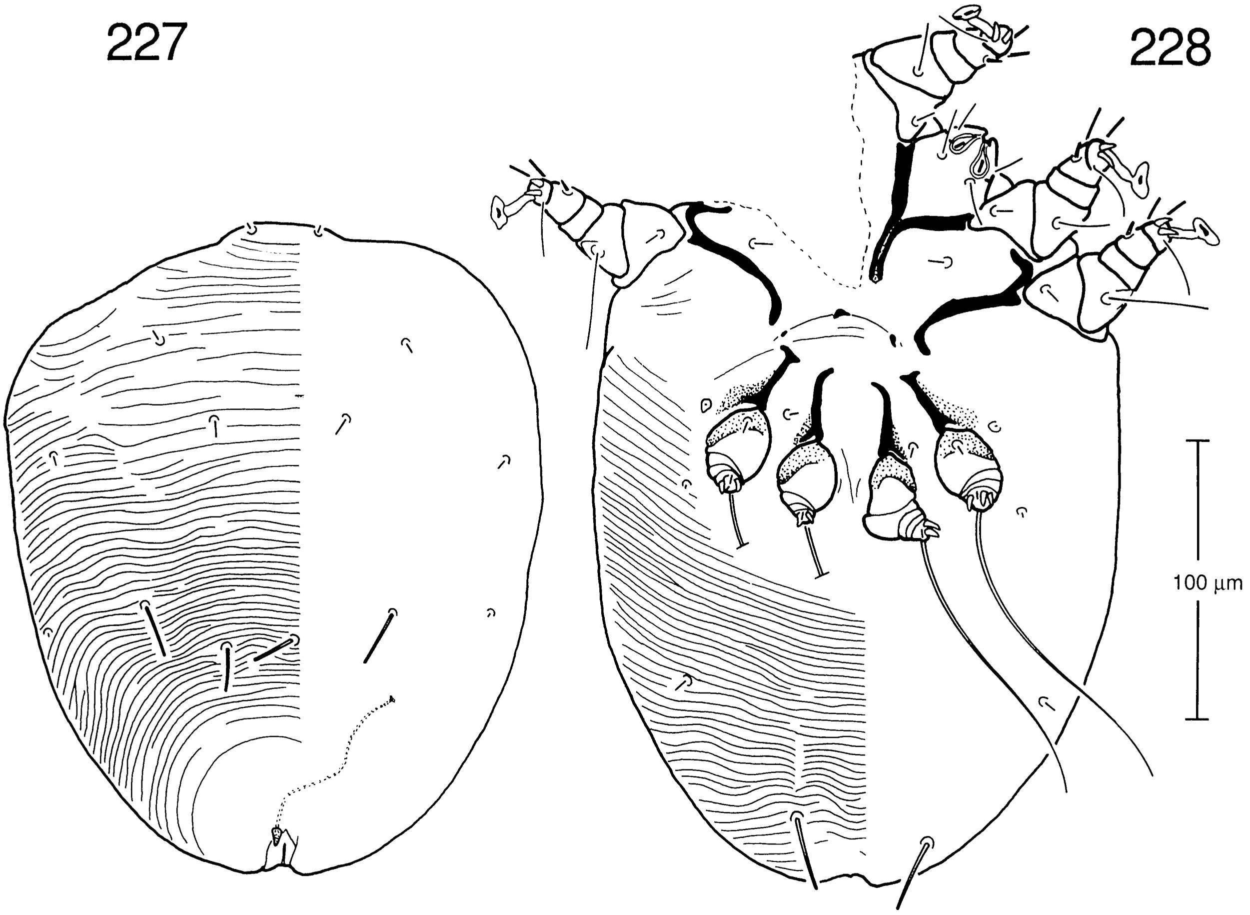
Etymology: The specific name is derived from the name of the country, the Philippines, in which the type series was collected.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, IRSN, NMNH, OSU, PNC, and UMMZ.

Notoedres (*Notoedres*) *miniopteri* Fain, 1959, new combination

Notoedres (*Metanotoedres*) *miniopteri* Fain, 1959i: 155.

The female and male have been described previously (Fain, 1959i). One correction needs to be made regarding



Figs. 227, 228. *Notoedres* (*Bakeracarus*) *americanus*, female, dorsal (227) and ventral (228) view.

the shield structure in the male. The anal shields were partially fused in the two males examined, not free as indicated in the description. The immatures strongly resemble those of *N. philippinensis*. Both larva and nymphs have a bare area on the dorsum (less extensive than in *N. philippinensis*) and the perianal setae are small. By contrast, the female of *miniopteri* has no bare area and the perianal setae are very long (35–45 µm) and spine-like. Comparative measurements of the adults are included in Tables 12 and 13.

Immatures and males occur on the skin over the arm bones, but females encyst in the lower lip. Fain (1959i) reported some trunk formation near a female cyst but this was not observed in the present study. Fain (1959i) also found specimens (females and males) on the ear.

Material examined: All stages.

Hosts (Chiroptera: Vespertilionidae) and localities: *Miniopterus schreibersi* (Kuhl, 1819). Type host. FRANCE: Jura, 17 km NE Lons-le-Saunier, Beaune les Messiers, ca 46°45'N 5°45'E, 27 June 1956, D.E. Russell, MVZ #129659, HK 86–0520–5; MADAGASCAR: Fianarantsoa, 1 km N Kianjavato, 21°23'S 47°52'E, elev. 300 m, 12 August 1987, L.H. Emmons (LHE 662), NMNH #448889, HK 87–1214–1; Fianarantsoa, 2 km NE Andrambovato, ca 21°30'S 47°27'E, elev. 550 m, 19 August 1988, G.K. Creighton (GKC 2806), NMNH #449306, HK 88–1009–3; USSR: Turkmen, Bakhardeu, 38°26'N 57°25'E, 18 August 1927, V.G. Geptner, MVZ #135286, HK 86–0522–2; same data, MVZ #135287, HK 86–0522–1.

Miniopterus inflatus Thomas, 1903. ETHIOPIA: Eritrea, 10 km N Asmera, Sciumagalle Mine, 16°35'N 38°30'E, 28 February 1943, Ihane Riney, MVZ #100990, HK 86–0522–7; same data, MVZ #100992, HK 86–0522–6.

Literature cited: on *Miniopterus schreibersi* from ITALY: Toscana (Fain, 1959i [Type series]), and SPAIN (Fain & Lukoschus, 1969); on *Miniopterus inflatus* from ZAIRE (Fain, 1959i); on *Pipistrellus nanus* (Peters, 1852) from ZAIRE (Fain, 1959i).

Deposition of specimens: NMNH and UMMZ.

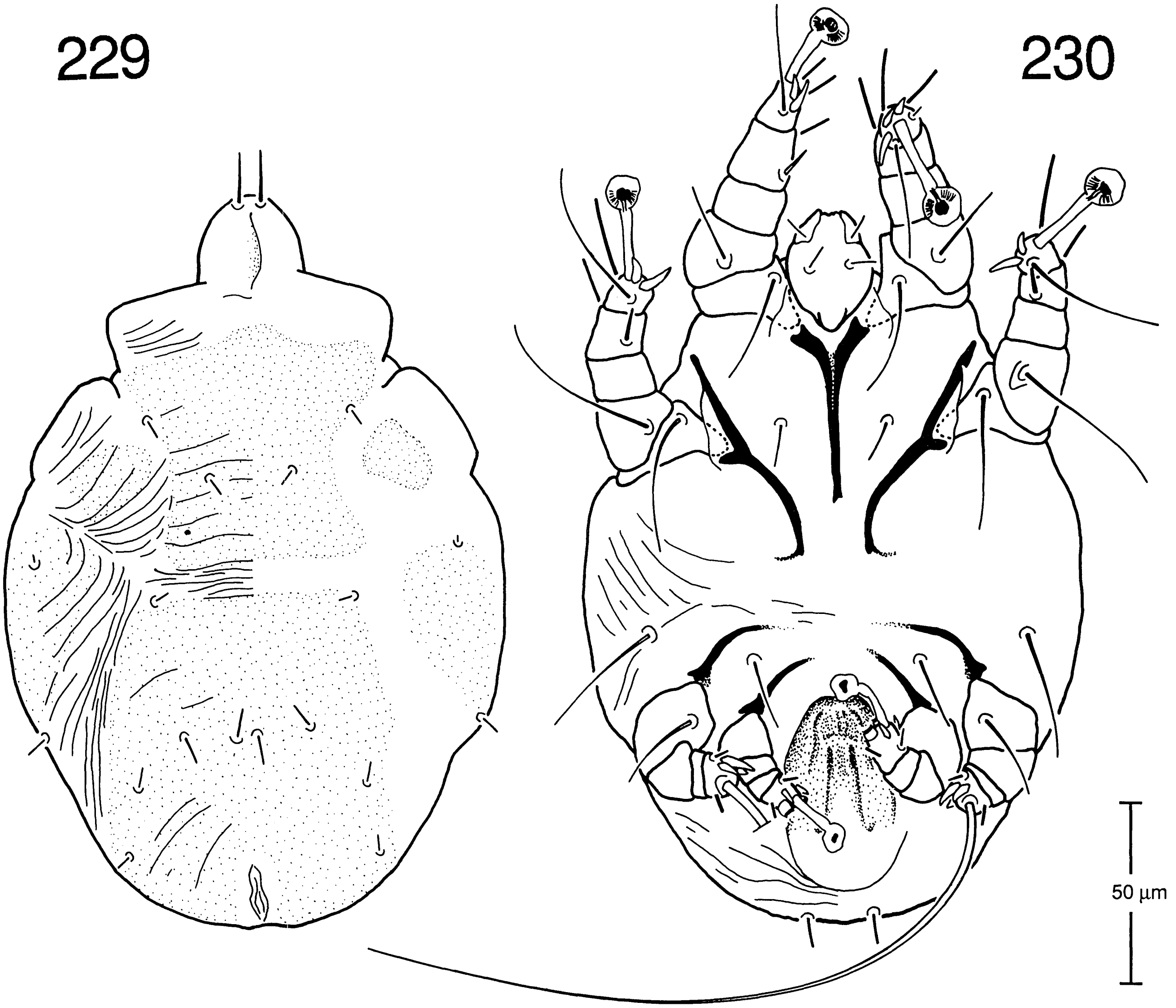
Notoedres (*Notoedres*) *verheyeni* Fain, 1959, new combination

Notoedres (*Metanotoedres*) *verheyeni* Fain, 1959i: 157.

Diagnosed in the tritonymph by the minute setae *c 2* (78). The other propodosomal setae are also very small to minute in the tritonymph.

Only the nymphs and male have been described (Fain, 1959i). The nymphs have a large bare area on the dorsum. Both nymphs and male were collected on the wings (Fain, 1959i).

Material examined: None.

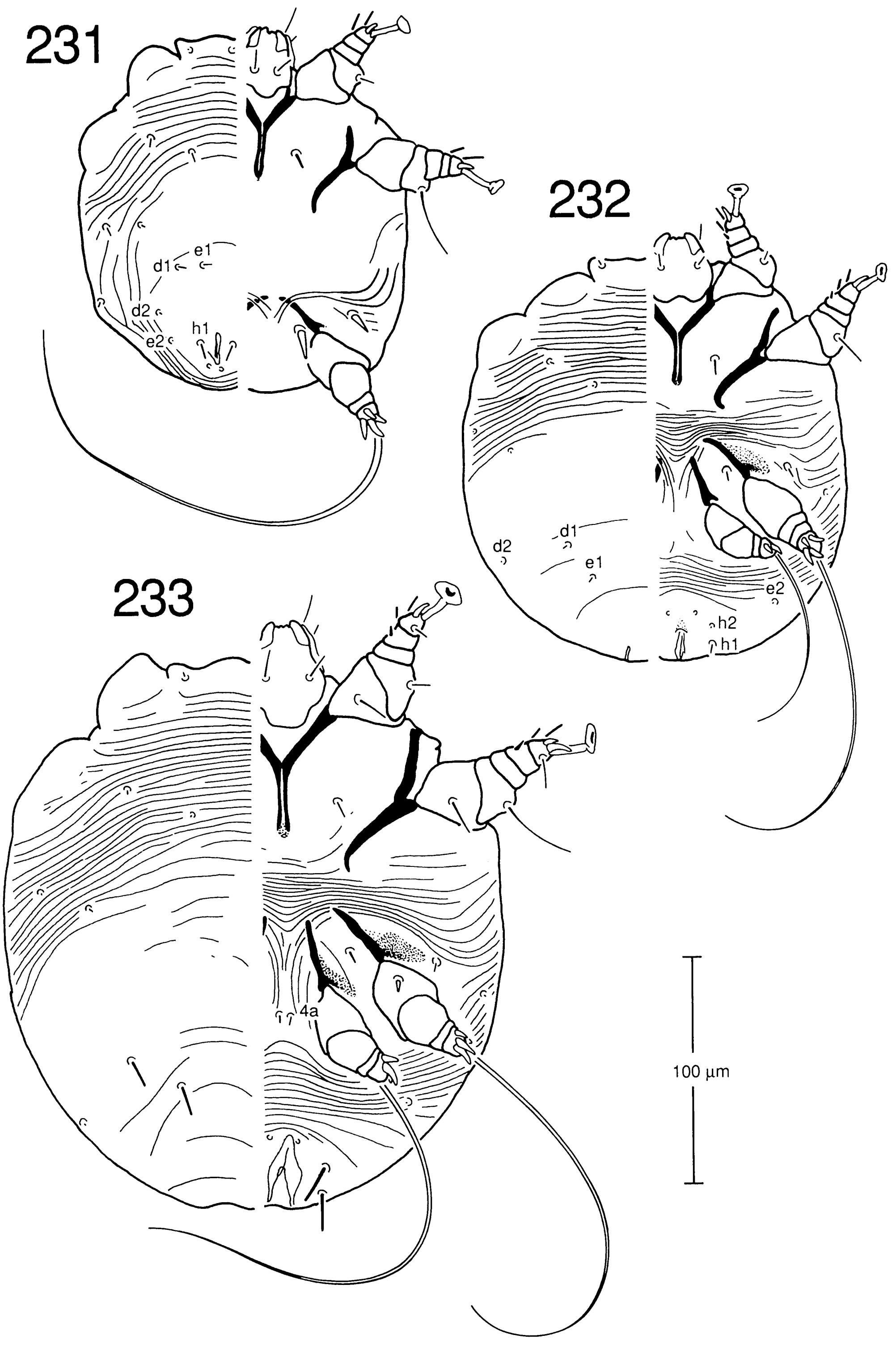


FIGS. 229, 230. *Notoedres* (*Bakeracarus*) *americanus*, male, dorsal (229) and ventral (230) view.

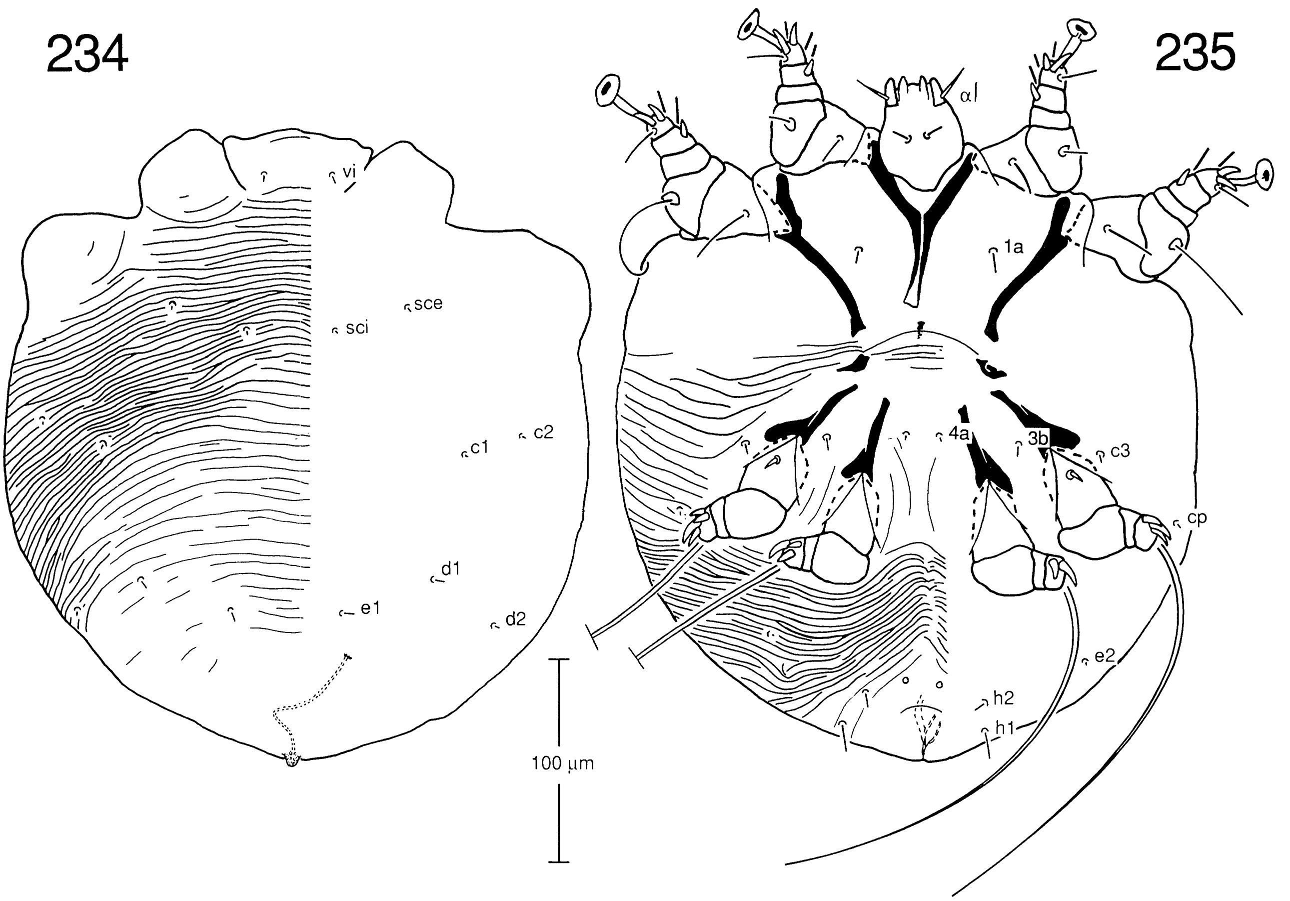
Literature records: *Coleura afra* (Peters, 1852) (= *C. gallorum*) (Chiroptera: Emballonuridae) from ZAIRE: SHABA, Moba (Fain, 1959i [Type series]).

The four remaining species in the *myoticola* group are all associated with hosts in the genus *Myotis* (Vespertilionidae). They are highly similar in morphology and habitat choice. Differences are largely limited to measurements of the propodosomal and perianal setae in the female (Table 14). In *N. myoticola* and *N. nigricans* setae *sci*, *c 1*, and *c 2* are relatively long (11–18 µm); in *N. roesleri* and *N. myotis* these setae are much shorter (5–9 µm). In *N. myotis*, *N. nigricans*, and *N. roesleri* palpal setae α *l* are much wider than in *N. myoticola* (3.7–4.5 vs. 2.6 µm). In *N. myotis* setae *e 2* are about 1/4 the length of the other perianal setae (7 vs. 26–29 µm), while in *N. roesleri* this ratio is 1/2 to 1/3 (11 vs. 24–28 µm). Although these differences are small, there is some evidence that they are consistent over the range of these species. The setal length ratio for *N. roesleri* is the same in the specimens described by Vitzthum (1932) from Venezuela as in the specimens from Guatemala and Honduras collected during this study. Only one species, *N. nigricans*, has been included in the phylogenetic analysis (see p. 3).

The observed host specificity of these species casts some doubts on a few older records of mite species in this group. *Notoedres myotis* was described from *Myotis velifer*, but has also been reported from *Myotis yumanensis* from California (Beck, 1966) and Texas (Whitaker & Easterla, 1975), and *Antrozous pallidus* from California (Beck, 1966). Reexamination of some of the specimens from these new host species collected by Beck revealed small but consistent differences with *N. myotis*, indicating at least two new species. The scarceness of the material does not allow their description.



Figs. 231–233. *Notoedres* (*Notoedres*) *philippinensis*, immatures, dorsal (left) and ventral (right) view: larva (231), protonymph (232), tritonymph (233).



FIGS. 234, 235. *Notoedres* (*Notoedres*) *philippinensis*, female, dorsal (234) and ventral (235) view.

Notoedres (*Notoedres*) ***nigricans*** nov. spec.
(Figs. 252–255)

Diagnosed in the male by the loss of solenidia σ I (173).

Female (Figs. 252, 253): Dorsum completely striated. Propodosomal and perianal setae well developed. Setae *e 2* about half the length of the other perianal setae (14 vs. 24–29 µm). Genual setae *cG* I–II short and spine-like. Measurements in Table 14.

Male (Figs. 254, 255): Resembling the male of *N. myoticola*. It differs by much smaller dorsal setae (5–8 vs. about 12 µm in *N. myoticola*), and the fusion of coxal apodemes III to the junction of the transverse and median apodemes, instead of to the transverse apodeme. Genual setae *cG* I and *mG* I–II long and filiform; setae *cG* II short, thin spines. Measurements in Table 15.

The females occur on the lips of their hosts. They are deeply embedded in the skin, with a trunk-like structure of host tissue projecting outward from the attachment site. The eggs are attached to the inside wall of the trunk. This type of habitat has been described for all species in the *myoticola* group associated with *Myotis* spp., and may be characteristic of this assemblage (Roesler, 1932; Hedeen, 1953; Fain & Aellen, 1961; present study). The only male collected was attached dorsally on the wrist.

Material examined: Female and male.

Host (Chiroptera: Vespertilionidae) and locality: *Myotis nigricans* (Schinz, 1821). PARAGUAY: ALTO PARAGUAY, West bank Rio Negro, Estancia Inmaculado Concepcion, 20°05'S 58°10'W, 26 September 1988, M.W. Nachman & S.M. Goodman (MWN 417), UMMZ, HK 89–0323–17 (holotype female); same locality and date, MWN 429, UMMZ, HK 89–0321–3 (allotype male); MWN 430, UMMZ, HK 89–0321–9; 25 September 1988, MWN 406, UMMZ, HK 89–0323–21; same date, MWN 411, UMMZ, HK 89–0323–26.

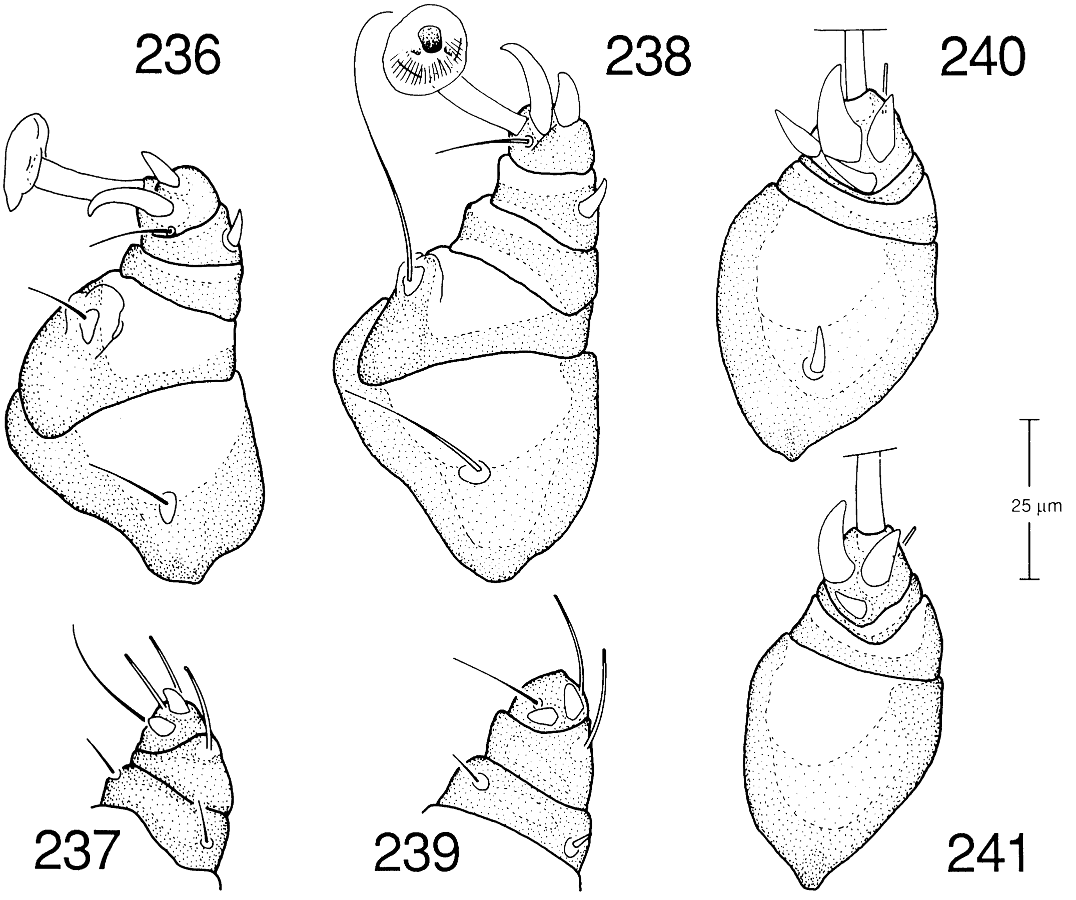
Etymology: The specific name is derived from the specific name of the type host, *Myotis nigricans*.

Deposition of specimens: Holotype female and allotype male in collection UMMZ. Paratypes in BMNH, OSU, and UMMZ.

Notoedres (*Notoedres*) *myoticola* (Fain, 1959), new combination

Chirnyssus myoticola Fain, 1959a: 120.

The tritonymph differs from those of *N. philippinensis* and *N. verheyeni* by the absence of a bare area on the dorsum and the transformation of setae *c 3, 3 b, 4 a,* and *sR* III to large spines (Fain, 1959a). These setae are very small spines in the



Figs. 236–241. *Notoedres* (*Notoedres*) *philippinensis*, female: ventral (top) and dorsal (bottom) view of legs I (236, 237) and II (238, 239), ventral view of legs III (240) and IV (241).

female. The type series of four males, one tritonymph, and a larva was found in the mouth of the host (Fain, 1959a), but this habitat yielded no specimens during this study. The habitat of the female is similar to that described for *N. nigricans* (Fain & Aellen, 1961; Fain & Lukoschus, 1969; present study).

Material examined: Larva and female.

Hosts (Chiroptera: Vespertilionidae) and localities: *Myotis blythii* (Tomes, 1857). USSR: Uzbek, Samarkandskaya Oblast, ca 40°N 67°E, July 1966, O. Bogdanov, MVZ #135282, HK 86–0523–2.

Myotis capaccinii (Bonaparte, 1837). TURKEY: Istanbul, Kucukcekmece, 40°59′N 28°46′E, 15 May 1971, F.W. Maurer, FMNH #105621, HK 87–0904–8.

Myotis daubentoni (Kuhl, 1819). GREAT BRITAIN: Norfolk, Ormesby colony, 12 October 1979 (specimen in collection BMNH).

Literature records: on *Myotis myotis* (Borkhausen, 1797) from BELGIUM (Fain, 1959a [Type series]; Fain & Lukoschus, 1969), SWITZERLAND (Fain & Aellen, 1961), and GERMANY (Fain & Lukoschus, 1969).

Deposition of specimens: FMNH and UMMZ.

Notoedres (*Notoedres*) *myotis* (Hedeen, 1953)

Sarcoptes myotis Hedeen, 1953: 334.

Notoedres (*N.*) *myotis* (Hedeen), Fain, 1959i: 138.

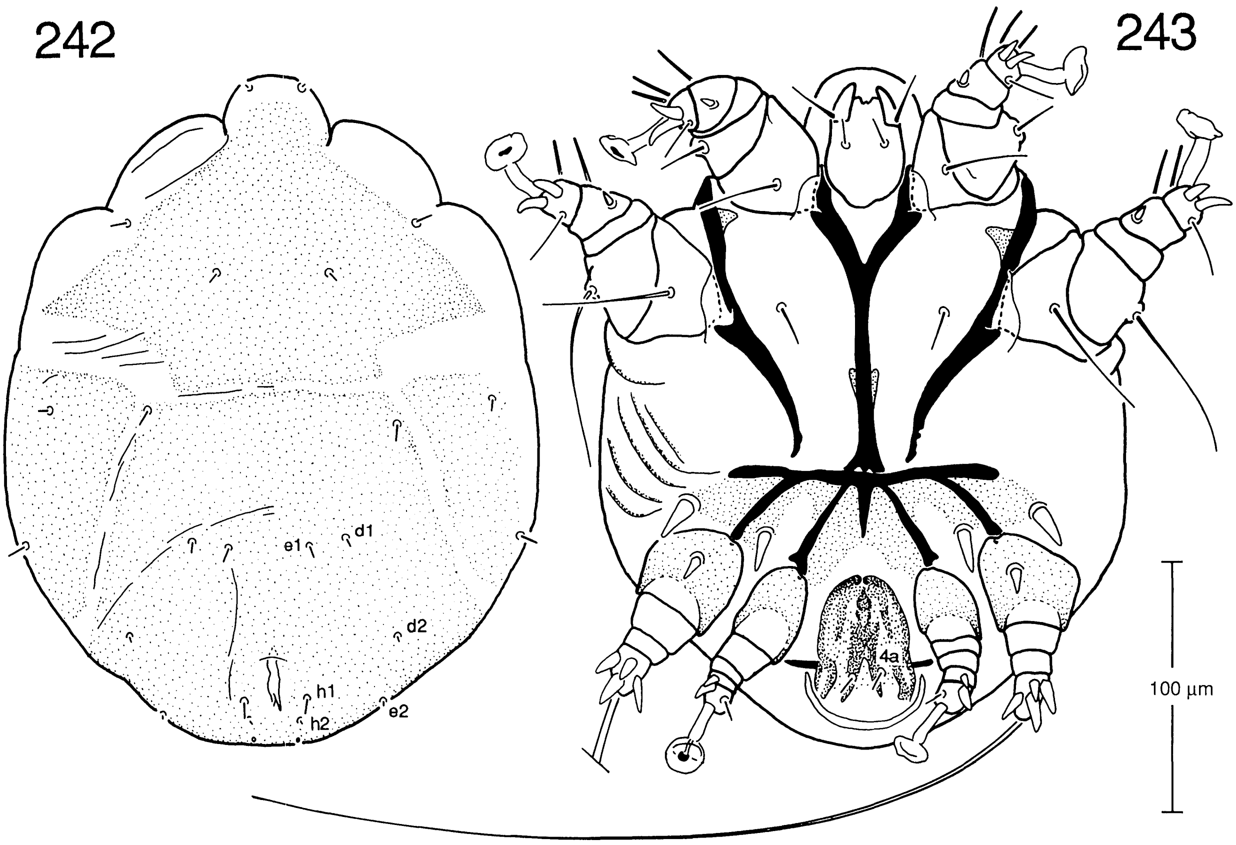
The species is known only from the female (Hedeen, 1953; Fain, 1959i). The site choice of the female and the pathology are identical to those described for *N. nigricans* (Hedeen, 1953; present study), although trunk formation is not always distinct (Bradshaw & Ross, 1961).

Material examined: Female.

Host (Chiroptera: Vespertilionidae) and locality: *Myotis velifer* (Allen, 1890). USA: Kansas, 25 July 1952, P.H. Krutzsch, MVZ #168010, HK 86–0521–9; same data, MVZ #168011, HK 86–0521–6; MVZ #168014, HK 86–0521–8; MVZ #168016, HK 86–0521–7.

Literature records: on *Myotis velifer* from USA: Texas (Hedeen, 1953 [Type series]; Fain, 1959i, 1960b), and Arizona (Bradshaw & Ross, 1961).

Deposition of specimens: BMNH and UMMZ.



FIGS. 242, 243. *Notoedres (Notoedres) philippinensis,* male, dorsal (242) and ventral (243) view.

Notoedres (Notoedres) roesleri Vitzthum, 1932

Notoedres roesleri Vitzthum, 1932: 400.

The female is the only previously described life stage (Vitzthum, 1932). The larva strongly resembles *N. myoticola.* Its dorsum is largely unstriated (bare area more extensive than in *N. myoticola*), and setae *3 b* are transformed into large spines. Setae *c 3* are filiform in the larvae of the *Myotis* associates, not spines as in *N. philippinensis.* The perianal setae are very small to minute. Site choice of the female and pathology as in *N. nigricans* (Roesler, 1932; Vitzthum, 1932).

Material examined: Larva and female.

Host (Chiroptera: Vespertilionidae) and localities: *Myotis nigricans* (Schinz, 1821). GUATEMALA: CHIMALTENANGO, Los Chocoyos, 14°42′N 91°03′W, 6 February 1934, F.J.W. Schmidt, FMNH #41849, HK 86–0225–13; same data, FMNH #41851, HK 86–0225–14; HONDURAS: Gracias, 14°35′N 88°35′W, 6 December 1937, P.A. McGraw, FMNH #47620, HK 86–0225–12.

Literature records: on *Myotis nigricans* from VENEZUELA (Vitzthum, 1932 [Type series]; Roesler, 1932).

Deposition of specimens: FMNH and UMMZ.

The next two lineages at node 63 (Fig. 57) are monobasic, including respectively *N. africanus* and *N. benoiti.*

Notoedres (Notoedres) africanus (Fain, 1959), new combination

Chirnyssus africanus Fain, 1959g: 251.

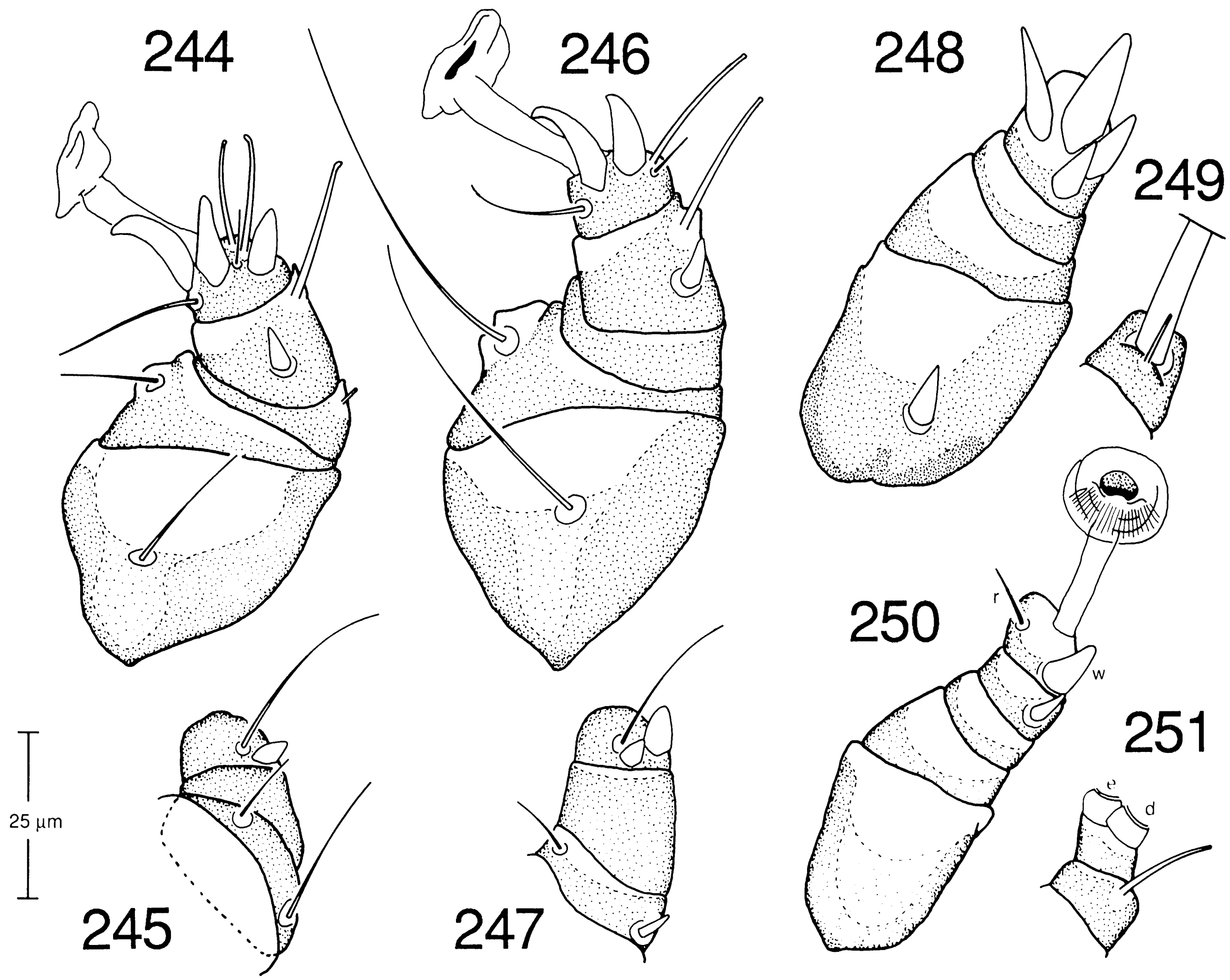
Diagnosed in the larva and male by the transformation of setae *3 b* into spines (122); in the female by the presence of a large non-striated zone on the dorsum (58); in the male by the transformation of setae *c 3* (93), setae *gT* I–II (166), and setae *sR* III (202) into spines, and the loss of solenidia σ I (173).

The nymphs and adults have been described previously (Fain, 1959g). The shape of setae *c 3, 1 a, 3 b,* and *sR* III in the male is unique within the genus. These setae have a well developed spine-like base and a long and filiform distal portion (comparative measurements in Table 15). The immatures and males embed in the wing membrane, the females attach near the posterior edge of the wing and uropatagium (Fain, 1959g).

Material examined: Tritonymph and male.

Host (Chiroptera: Emballonuridae) and locality: *Coleura afra* (Peters, 1852). ZAIRE: HAUT-ZAIRE, Mont Wago and Boma (paratypes, specimens in collection IRSN).

Literature records: on *Coleura afra* (= *C. gallorum*) from ZAIRE (Fain, 1959g [Type series]), KENYA (Fain, 1961c), and TANZANIA (Fain, 1961c).



Figs. 244–251. *Notoedres* (*Notoedres*) *philippinensis*, male, ventral (top) and dorsal (bottom) views of legs I (244, 245), II (246, 247), III (248, 249), and IV (250, 251).

Notoedres (*Notoedres*) *benoiti* Fain, 1959

Notoedres (*N.*) *benoiti* Fain, 1959i: 149.

Diagnosed in the nymphs and female by minute setae *c 2* (78); in the female by the transformation of setae *sci* into spines (reversal) (63), and the reduction of setae *c 1* (73).

The tritonymph and female have been described previously (Fain, 1959i). All specimens collected were attached to the wing membrane.

Material examined: Female.

Host (Chiroptera: Emballonuridae) and locality: *Coleura afra* (Peters, 1852). ZAIRE: Haut-Zaire, Mont Wago and Moba (paratype, specimen in collection OSU).

Literature records: on *Coleura afra* (= *C. gallorum*) from ZAIRE (Fain, 1959i [Type series]).

The next lineage includes *N. alexfaini* and *N. cheiromeles*. The latter species was not included as a terminal taxon (see p. 3). The lineage is diagnosed in the larva by having setae *h 1* longer than the other perianal setae (105); in the female by the presence of a large bare area on the dorsum (58).

Notoedres (*Notoedres*) *alexfaini* Lavoipierre, 1968
(Figs. 38, 39)

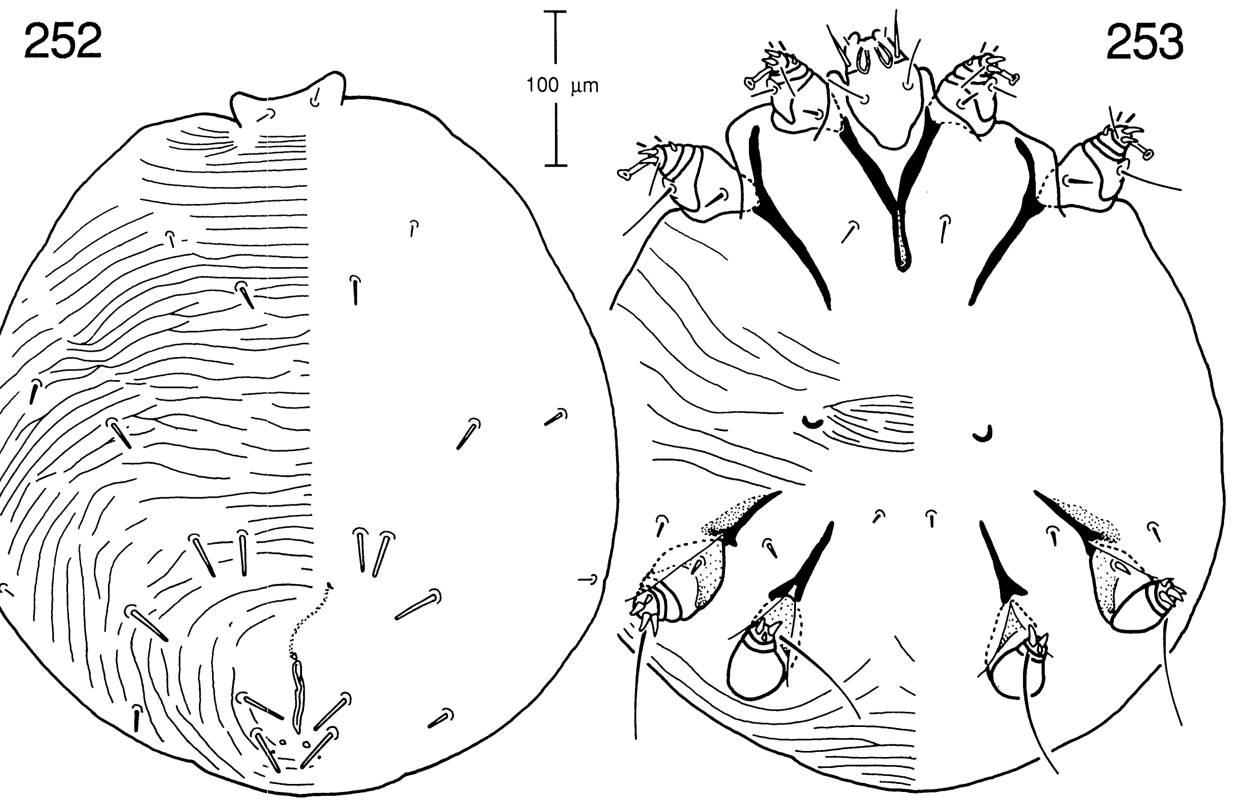
Notoedres alexfaini Lavoipierre, 1968: 314.
Notoedres longisetosus Lavoipierre, 1968: 314.

Diagnosed in the male by the loss of the genital apodemes (reversal) (154), and the presence of setae *f* III–IV (reversal) (186, 187).

The female tritonymph and female have been described by Lavoipierre (1968), the other stages by Klompen et al. (1983). The mites occur on the trunk of their host, burrowing into the stratum corneum (Lavoipierre & Rajamanickam, 1968). When present in some number they produce severe dermatological changes manifested as scabby lesions (Lavoipierre & Rajamanickam, 1968).

Material examined: All stages.

Hosts (Chiroptera: Molossidae) and localities: *Cheiromeles torquatus* Horsfield, 1824. Type host. INDONESIA: Riau Isl., Pulau Galang, 0°45'N 104°14'E, March 1926, FMNH #66191, HK 87–0904–7; Sumatra, Simeulue Is., Sinabang, July 1913, E. Jacobson 1793, NNML #28053; MALAYSIA:



Figs. 252, 253. *Notoedres* (*Notoedres*) *nigricans*, female, dorsal (252) and ventral (253) view.

Selangor, Gombak Forest, 4 May 1979, M. Nadchatram 80; Selangor, Kepong, Bukit Lagong Forest Reserve, 3°15′N 101°37′E, 10 March 1953, Lim Boo Liat, FMNH #110769, HK 86–0225–3; same data, FMNH #110770, HK 86–0225–2; Negeri Sembilan, Simpang Pertang, Durian Tawak, 2°56′N 102°12′E, 20 April 1972, Lim Boo Liat, AMNH #247588, HK 86–0814–11.

Cheiromeles parvidens Miller & Hollister, 1921. INDONESIA: Sulawesi, Pinedapa, J.C. Raven, NMNH #219360, HK 87–0729–4; same data, NMNH #219361, HK 87–0729–8.

Literature records: on *Cheiromeles torquatus* from SINGAPORE (Lavoipierre, 1968 [Type series]; Lavoipierre & Rajamanickam, 1968), INDONESIA: Sumatra (Klompen et al., 1983), and MALAYSIA (Klompen et al., 1983).

Deposition of specimens: AMNH, FMNH, NMNH, PNC, and UMMZ.

Notoedres (*Notoedres*) *cheiromeles* Fain, 1959

Notoedres (*N.*) *cheiromeles* Fain, 1959i: 151.

The larva (Klompen et al., 1983) and female (Fain, 1959i) have been described previously. The immatures and female of *N. cheiromeles* are characterized by the setal pattern: setae *e 2* are much longer than the other perianals, a unique condition within the genus. As in *N. alexfaini* sexual dimorphism in the tritonymphs is pronounced. The relative size distribution of the dorsal setae is the same in all immatures and the female but the absolute size of the setae in the female tritonymph is much larger. The length of setae *e 2* in this stage exceeds that of the anterior legs. All stages occur on the trunk, limbs, and wing membrane. *Notoedres cheiromeles* produces shallow epidermal craters on the stratum corneum (Lavoipierre & Rajamanickam, 1968). Host reactions include strong hyperkeratinization of the epidermis but no dermal hyperplasia (Lavoipierre & Rajamanickam, 1968).

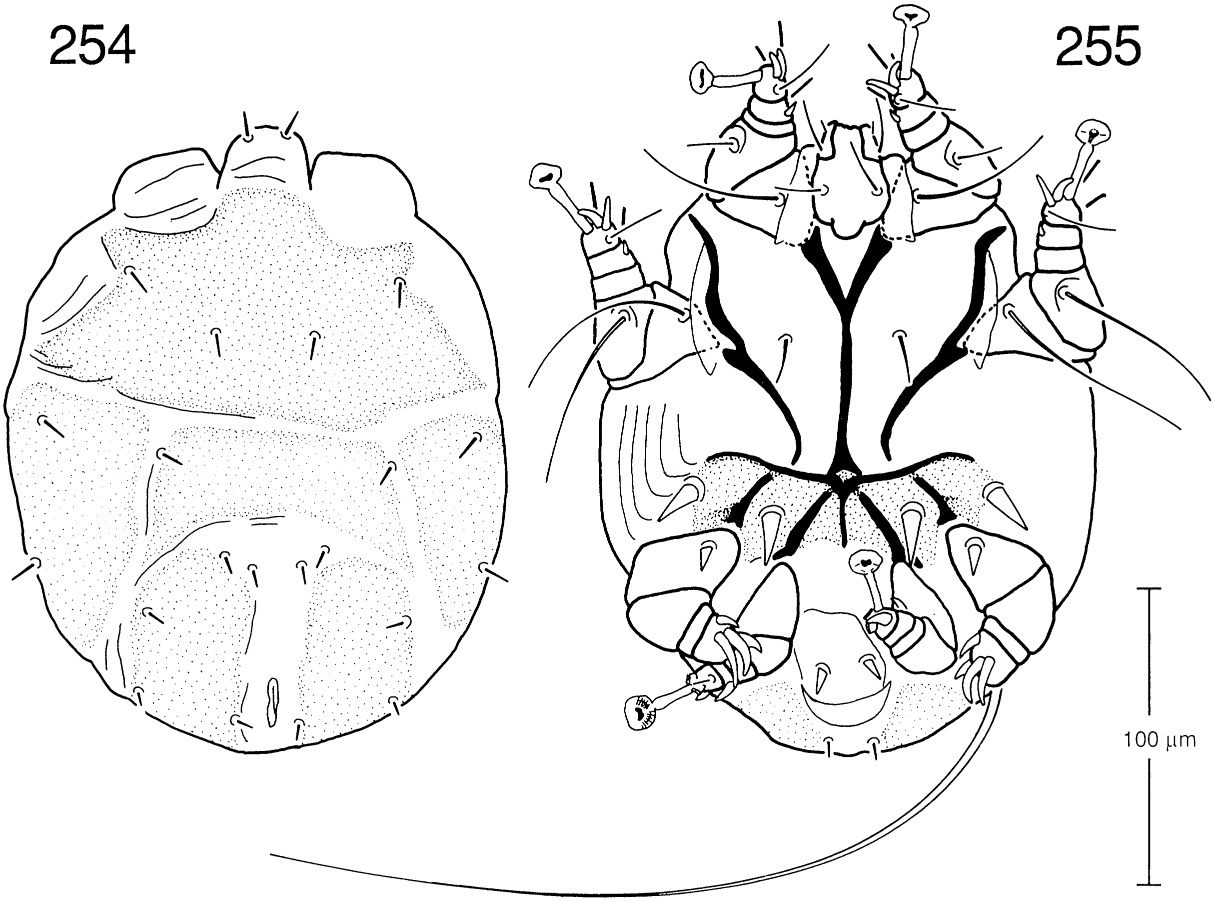
Material examined: Larva, nymphs, and female.

Hosts (Chiroptera: Molossidae) and localities: *Cheiromeles torquatus* Horsfield, 1824. INDONESIA: Sumatra, Simeulue Is., Sinabang, July 1913, E. Jacobson 1793, NNML #28053; MALAYSIA: Selangor, Kepong, Bukit Lagong Forest Reserve, 3°15′N 101°37′E, 10 March 1953, Lim Boo Liat, FMNH #110769, HK 86–0225–3; same data, FMNH #110770, HK 86–0225–2; Negeri Sembilan, Simpang Pertang, Durian Tawak, 2°56′N 102°12′E, 20 April 1972, Lim Boo Liat, AMNH #247588, HK 86–0814–11.

Literature records: on *Cheiromeles torquatus* from INDONESIA: “Giesting” (Fain, 1959i [Type series]; Klompen et al., 1983), MALAYSIA (Lavoipierre & Rajamanickam, 1968; Klompen et al., 1983), and SINGAPORE (Lavoipierre, 1968; Lavoipierre & Rajamanickam, 1968).

Deposition of specimens: AMNH, FMNH, PNC, and UMMZ.

The next lineage at node 63, the assemblage of *N. elongatus* and *N. rajamanickami* (Fig. 57, node 67), is diagnosed in the larva by having setae *h 1* longer than the other perianal



FIGS. 254, 255. *Notoedres* (*Notoedres*) *nigricans*, male, dorsal (254) and ventral (255) view.

setae (105); in the female by the presence of a sclerotized flange on coxal apodemes II (143).

Notoedres (*Notoedres*) *elongatus* Fain, 1963, new combination

Notoedres (*Neonotoedres*) *elongatus* Fain, 1963c: 257.

This species was placed in its own subgenus based on the elongation of the female. However, a certain degree of elongation is most probably also a feature of *N. rajamanickami* in its natural state (Lavoipierre, 1968). In addition, recognition of *Neonotoedres* would leave *Notoedres* as a paraphyletic grouping. Only the female has been described (Fain, 1963c). The previously undescribed larva strongly resembles that of *N. rajamanickami* in setal morphology and striation pattern. Setae *cp* are minute and all perianal setae are long spine-like rods with bifurcate tips. Setae *h 1* are distinctly longer than the other perianal setae (35 vs. 22–28 µm). Females and larvae occur in cysts on the wing and uropatagium, usually near the finger bones. The mites burrow into the dermis and the burrow is lined with epidermal tissue (Lavoipierre & Rajamanickam, 1968). Dermal hyperplasia is extensive but hyperkeratinization is moderate (Lavoipierre & Rajamanickam, 1968).

Material examined: Larva and female.

Hosts (Chiroptera: Molossidae) and locality: *Cheiromeles parvidens* Miller & Hollister, 1921. INDONESIA: SULAWESI, Pinedapa, J.C. Raven, NMNH #219360, HK 87–0729–4.

Literature records: on *Cheiromeles torquatus* Horsfield, 1824 from INDONESIA: SUMATRA, Simeulue Is., Sinabang (Fain, 1963c [Type series]), MALAYSIA and SINGAPORE (Lavoipierre, 1968; Lavoipierre & Rajamanickam, 1968).

Deposition of specimens: UMMZ.

Notoedres (*Notoedres*) *rajamanickami* Lavoipierre, 1968

Notoedres rajamanickami Lavoipierre, 1968: 315.

The larva and female have been described previously (Lavoipierre, 1968; Klompen et al., 1983). The female differs from that of *N. elongatus* by the more rounded body shape (the body is distinctly elongate in *N. elongatus*) and by the much shorter setae *d* III–IV (130–140 µm vs. 275–325 µm in *N. elongatus*). *Notoedres rajamanickami* occurs only on the head in deep (up to 0.9 mm) burrows near the stout vibrissae of the cheek and chin (Lavoipierre & Rajamanickam, 1968). As in the previous species, the mites burrow into the dermis. The host skin reaction is similar to that described for *N. elongatus* (Lavoipierre & Rajamanickam, 1968).

Material examined: Larva and female.

Hosts (Chiroptera: Molossidae) and locality: *Cheiromeles*

Table 14. Comparative measurements of female *Notoedres*. 2.

	nigricans N=6			*myoticola* N=4		*myotis* N=4		*roesleri* N=3		*namibiensis* N=5		
	av	SD	range	av	range	av	range	av	range	av	SD	range
gnathosoma												
length	77	4	75–86	64	59–71	65	57–74	56	55–58	47	2	44–50
width	53	5	48–59	46	44–49	57	51–60	48	47–49	38	3	36–42
subcapitular seta	23	3	20–27	16	15–17	18	16–21	15	14–15	10	1	8–11
palpal seta α *l*												
length	31	2	28–34	19	16–22	29	21–35	22	21–22	10	2	8–13
width	4.0	0.2	3.7–4.2	2.6	2.3–2.9	4.5	3.8–5.0	3.7	3.4–4.1	0.4	0.1	0.3–0.6
body												
length	487	38	445–538	446	349–548	477	–	450	447–453	295	23	270–327
width	428	45	376–501	388	321–491	466	464–468	403	380–425	288	59	248–375
seta *vi*	8	1	7–9	6	5–7	7	6–8	5	3–6	6	1	5–7
seta *sci*	15	2	11–16	11	6–14	7	6–8	9	8–9	9	1	8–9
seta *sce*	8	2	5–10	7	6–10	7	6–8	6	5–7	7	1	6–8
seta *c 1*	18	2	14–19	11	5–15	6	4–7	6	5–7	6	1	6–7
seta *c 2*	13	2	10–15	11	5–14	7	5–8	7	6–8	6	1	5–6
seta *cp*	8	1	6–9	5	5–7	6	6	8	7–8	4	1	3–5
seta *c 3*	8	1	7–9	5	4–6	7	6–8	6	5–7	6	1	4–7
seta *d 1*	26	4	20–29	28	22–34	27	24–30	25	25–26	23	3	18–27
seta *d 2*	29	3	23–31	34	31–36	26	22–31	24	22–27	27	2	25–31
seta *e 1*	24	2	21–27	26	22–30	27	26–28	27	26–28	17	2	15–19
seta *e 2*	14	2	12–17	14	11–18	7	5–8	11	10–12	13	2	10–15
seta *h 1*	28	1	26–29	30	27–35	29	27–31	28	25–29	24	2	21–26
seta *h 2*	27	2	25–31	31	27–39	28	25–29	28	27–30	23	4	19–29
width seta *d 1*	3.4	0.1	3.2–3.6	3.8	3.3–4.2	3.6	3.2–4.3	3.3	2.9–3.6	2.4	0.3	2.1–2.7
width seta *d 2*	3.6	0.3	3.2–4.2	4.0	3.1–4.6	3.8	3.4–4.5	3.2	3.0–3.3	2.7	0.3	2.3–3.0
width seta *e 1*	3.2	0.2	2.9–3.5	3.0	2.8–3.2	3.8	3.5–4.4	2.9	2.8–3.0	1.8	0.2	1.6–2.1
width seta *e 2*	2.0	0.2	1.7–2.3	2.2	2.0–2.5	1.2	1.1–1.2	1.6	1.4–1.6	1.0	0.1	0.7–1.1
width seta *h 1*	3.1	0.2	2.9–3.4	3.5	3.1–4.0	3.4	2.8–4.1	3.3	3.0–3.7	2.3	0.4	1.8–2.8
width seta *h 2*	2.9	0.2	2.5–3.2	3.3	3.1–3.4	3.4	2.6–4.1	3.0	2.8–3.2	2.1	0.3	1.8–2.6
seta *1 a*	12	1	11–13	9	7–10	10	7–12	9	8–9	10	1	9–10
seta *3 b*	9	1	7–10	6	5–8	6	5–7	6	5–6	8	1	7–9
seta *4 a*	7	1	6–8	5	3–6	6	5–7	5	4–5	4	1	4–6
copulatory cone	3	1	3	7	–	–		5	4–5	4	1	3–5
bursa copulatrix	54	–	51–57	51	41–60	82	77–91	55	–	45	–	45
coxal apodemes I	93	4	86–97	78	73–84	90	84–97	77	68–83	67	2	64–68
coxal apodemes II	130	6	125–141	103	86–117	123	115–131	101	96–105	91	3	89–95
coxal apodemes III	53	4	48–61	43	42–45	54	46–60	47	41–50	33	2	32–36
coxal apodemes IV	55	4	48–60	45	44–48	57	53–61	44	41–47	31	2	29–33
leg I	70	6	61–76	52	44–61	61	55–65	45	40–50	46	5	40–52
leg II	79	6	68–85	56	49–67	64	61–66	54	53–54	53	5	49–59
leg III	71	9	55–83	53	48–58	68	63–70	54	52–55	44	3	40–47
leg IV	70	8	60–77	53	49–57	66	57–76	53	49–58	45	3	41–50
seta *pR* I	11	1	9–12	10	10	12	11–15	6	–	15	3	11–17
seta *pR* II	14	2	11–17	10	9–13	14	11–17	10	9–10	29	6	23–37
seta *sR* III	9	1	8–10	6	6	8	8–9	6	6–7	6	1	4–6
seta *vF* I	15	3	10–18	13	11–15	18	–	8	–	15	3	12–20
seta *vF* II	38	4	33–45	34	32–36	36	27–43	34	28–41	40	9	27–51
seta *cG* I	6	2	4–8	9	–	19	–	10	–	4	1	4
seta *cG* II	4	1	4–6	4	3–5	16	–	8	7–8	5	1	5–6
seta *d* III	76	8	69–87	93	66–113	62	57–67	69	63–73	157	14	142–171
seta *d* IV	79	8	71–91	105	78–136	77	71–82	63	56–67	191	13	175–204
solenidion φ I	11	1	10–13	12	10–14	12	11–13	10	9–10	13	1	11–14
solenidion φ II	13	2	11–17	13	12–15	11	11–12	13	11–17	14	1	12–15
solenidion φ III	8	1	5–9	8	7–10	7	6–8	7	6–8	7	2	5–8
solenidion φ IV	8	1	6–10	8	8–10	7	6–10	6	5–7	5	2	3–7
solenidion ω-1 I	11	1	10–13	9	6–11	10	8–10	12	11–13	10	1	10–11
solenidion ω-3 I	7	1	7–8	8	7–8	6	6–7	8	6–10	6	1	5–7
solenidion ω II	12	1	11–13	14	12–16	11	9–13	12	10–13	15	1	13–17
ambulacral stalk I	16	1	15–17	13	10–15	15	–	14	13–14	14	1	13–14
ambulacral stalk II	17	1	16–18	16	13–18	16	–	–		14	1	13–15

Table 15. Comparative measurements of male *Notoedres*. 2.

	nigricans	*africanus*	*namibiensis*	*dewitti*	*chiropteralis*		*centrifera*	
	N = 1	N = 1	N = 1	N = 1	N = 1		N = 10	
						av	SD	range
gnathosoma								
length	36	33	33	30	29	30	2	26–33
width	28	23	26	21	26	24	2	22–28
subcapitular seta	13	17	7	21	11	13	2	11–17
palpal seta α *l*								
length	18	–	8	–	13	7	1	4–9
width	0.4	–	0.2	–	0.2	0.4	0.2	0.3–0.7
body								
length	208	193	199	155	163	169	20	130–202
width	167	152	160	132	136	133	15	106–160
seta *vi*	8	6	8	8	18	30	3	22–33
seta *sci*	7	4	9	8	9	22	4	17–29
seta *sce*	8	6	9	10	8	18	3	13–22
seta *c 1*	7	3	11	7	7	18	1	17–21
seta *c 2*	8	4	9	8	6	20	3	15–25
seta *cp*	8	7	13	10	4	13	2	8–16
seta *c 3*	18	12	35	16	37	26	4	18–32
width seta *c 3*	6.1	2.0	0.8	0.6	1.0	0.9	0.1	0.6–1.1
seta *d 1*	6	3	10	8	7	15	2	13–18
seta *d 2*	6	3	9	7	8	9	1	8–10
seta *e 1*	6	3	9	8	8	15	2	11–18
seta *e 2*	6	4	7	8	–	8	1	7–9
seta *h 1*	5	4	6	6	6	8	1	7–9
seta *h 2*	5	5	4	8	6	7	1	6–8
seta *1 a*	15	–	11	10	10	30	4	23–36
seta *3 b*	18	12	16	18	15	25	2	22–28
width seta *3 b*	6.7	2.6	1.1	0.8	0.7	0.9	0.2	0.6–1.2
seta *4 a*	9	5	–	–	4	29	6	18–37
genital area								
length	–	34	26	36	37	28	3	23–31
width	29	22	–	29	30	21	2	18–23
coxal apodemes I	78	81	68	59	52	38	3	34–42
coxal apodemes II	85	76	146	59	65	60	5	53–69
coxal apodemes III	21	20	25	20	22	21	4	17–29
coxal apodemes IV	24	19	41	17	20	21	2	19–25
leg I	57	74	64	73	56	43	4	34–48
leg II	58	76	67	67	55	45	6	34–55
leg III	57	46	53	45	39	40	4	31–45
leg IV	49	33	36	36	42	29	3	22–31
seta *pR* I	49	43	36	32	30	34	6	27–42
seta *pR* II	66	24	43	34	32	37	6	29–48
seta *sR* III	9	15	27	16	18	27	2	23–31
width seta *sR* III	3.8	1.7	–	0.7	0.7	0.6	0.1	0.4–0.8
seta *vF* I	14	18	14	25	19	25	3	22–33
seta *vF* II	61	44	52	45	33	42	5	37–49
seta *cG* I	28	18	22	32	26	15	4	7–18
seta *cG* II	4	–	6	5	–	8	3	5–11
seta *mG* I	22	14	14	15	33	24	6	18–39
seta *d* III	297	289	250	299	180	183	10	166–198
solenidion σ I	–	–	3	–	–	2	–	–
solenidion φ I	14	15	14	14	16	17	1	16–19
solenidion φ II	18	22	19	17	14	15	1	13–18
solenidion φ III	8	9	9	7	7	7	1	6–9
solenidion φ IV	7	13	11	11	14	8	1	6–10
solenidion ω-1 I	17	19	14	24	15	17	1	15–19
solenidion ω-3 I	10	11	9	10	14	14	1	12–15
solenidion ω II	18	34	20	34	21	22	2	20–26
ambulacral stalk I	18	33	18	27	15	19	2	15–21
ambulacral stalk II	21	24	18	27	12	19	1	18–21
ambulacral stalk IV	14	15	12	15	11	2	1	1–2

torquatus Horsfield, 1824. MALAYSIA: SELANGOR, Gombak Forest, 4 May 1979, M. Nadchatram.

Literature records: on *Cheiromeles torquatus* from MALAYSIA: SELANGOR, Bukit Lagong Forest Reserve (Lavoipierre, 1968 [Type series]); MALAYSIA (Lavoipierre & Rajamanickam, 1968; Klompen et al., 1983), and INDONESIA (Klompen et al., 1983).

The next three lineages originating at node 63 (Fig. 57) are monobasic.

Notoedres (*Notoedres*) ***namibiensis*** nov. spec.

(Figs. 12, 13, 20, 21, 224, 256–259)

Diagnosed in the nymphs by well developed (not minute) setae *cp* (reversal) (85); in the male by the loss of fusion between the posterior median and the anal shields (15).

Larva (Fig. 224): Striation restricted to the anterior and lateral parts of the dorsum. Perianal setae spine-like. Setae *e 2* strongly reduced, the other perianal setae subequal in length. Setae *c 3* minute.

Tritonymph (the protonymph is unknown): Bare area on the dorsum smaller than in the larva. Relative size of the perianal setae similar, absolute size longer. Setae *c 3* slightly longer.

Female (Figs. 256, 257): Dorsum completely striated. All setae considerably longer than in the tritonymph. Setae *e 2* also relatively longer. Tibial setae spine-like. Measurements in Table 14.

Male (Figs. 12, 13, 20, 21, 258, 259): Dorsal shields well sclerotized. Coxal apodemes I and II long, fused to the transverse apodeme. Genual setae *cG* II much smaller than *cG* I. Presence or absence of setae *r* IV could not be determined due to the poor condition of legs IV of the single available male. Measurements in Table 15.

Females and egg masses were collected from the ear pinnae, with additional females and immatures on the wing membrane, close to the wrist.

Material examined: Larva, tritonymph, female, and male.

Host (Chiroptera: Molossidae) and locality: *Tadarida aegyptiaca* (Geoffroy, 1818). NAMIBIA: KAOKOVELD, Orumana, 26 February 1975, H. Roer, MAK #77789, HK 85–0620–1 (holotype female, allotype male).

Etymology: The specific name is derived from the name of the country, Namibia, where the type series was collected.

Deposition of specimens: Holotype female and allotype male in MAK. Paratypes in MAK, UMMZ.

Notoedres (*Notoedres*) *yunkeri* Fain, 1962

Notoedres yunkeri Fain, 1962a: 392.

Diagnosed in the female by the long setae *c 1* (short in the immatures) (74); in the male by the loss of fusion between the posterior median and the anal shields (15).

The immatures and females are characterized by the shape of the dorsal setae: spine-like with bifurcate tips and a lateral notch. All stages have been described previously (Fain, 1962a). Females occur in cysts on the uropatagium. The eggs are contained within structures reminiscent of the trunks found in the *myoticola* group (Fain, 1962a).

Material examined: None.

Literature records: on *Molossus molossus* (Pallas, 1766) (= *M. coibensis*) (Chiroptera: Molossidae) from PANAMA (Fain, 1962a [Type series]).

Notoedres (*Notoedres*) *tadaridae* Fain, 1959

Notoedres (*N.*) *tadaridae* Fain, 1959i: 146.
Notoedres dohanyi Klompen et al., 1983: 290, new synonymy.

Diagnosed in the larva and nymphs by well developed setae *cp* (reversal) (83, 85).

Examination of several new collections allowed a reevaluation of the differences between *N. tadaridae* and *N. dohanyi.* Both differences listed in the original description of *N. dohanyi* (shape and length of the perianal setae, and presence/absence of setae *4 a*) proved to be inconsistent. Measurements of both length and width of the perianal setae in African and Asian populations show comparable ranges of variation. Furthermore, the absence of setae *4 a* in the description of *N. tadaridae* was an omission; the setae are present in some paratypes. Based on these observations *N. dohanyi* is synonymized with *N. tadaridae.*

The larva and female have been described previously (Dusbabek, 1980; Fain, 1959i; Klompen et al., 1983). During this study two tritonymphs were found on *Chaerophon* and *Mops* in addition to females of *N. tadaridae* and *N. dewitti.* Based on the presence of setae *4 a* in one of these tritonymphs, I tentatively associate that nymph with *N. tadaridae* (setae *4 a* are absent in *N. dewitti*). Setae *d 2, e 2,* and *h 2* of this tritonymph are minute; setae *d 1, e 1,* and *h 1* are spine-like rods, 7–8 μm in length. In the female setae *d 1, d 2, e 1, h 1,* and *h 2* are longer and subequal in length (7–12 μm). Comparative measurements of the female in Table 16. Females produce large cysts on the ears (especially on the tragus) and in the skin overlying the wing bones.

Material examined: Larva, tritonymph, and female.

Hosts (Chiroptera: Molossidae) and localities: *Chaerophon pumila* (Cretzschmar, 1826). Type host. MADAGASCAR: MAHAJANGA, 40 km S Marovoay, Ampijoroa, 16°14′S 46°28′E, 11 March 1963, Ken Lange 443, NMNH #341771, HK 88–0901–2.

Chaerophon jobensis (Miller, 1902). AUSTRALIA: WESTERN AUSTRALIA, Mount Hart, 18 September 1976, Kimberley Exp. 2723.

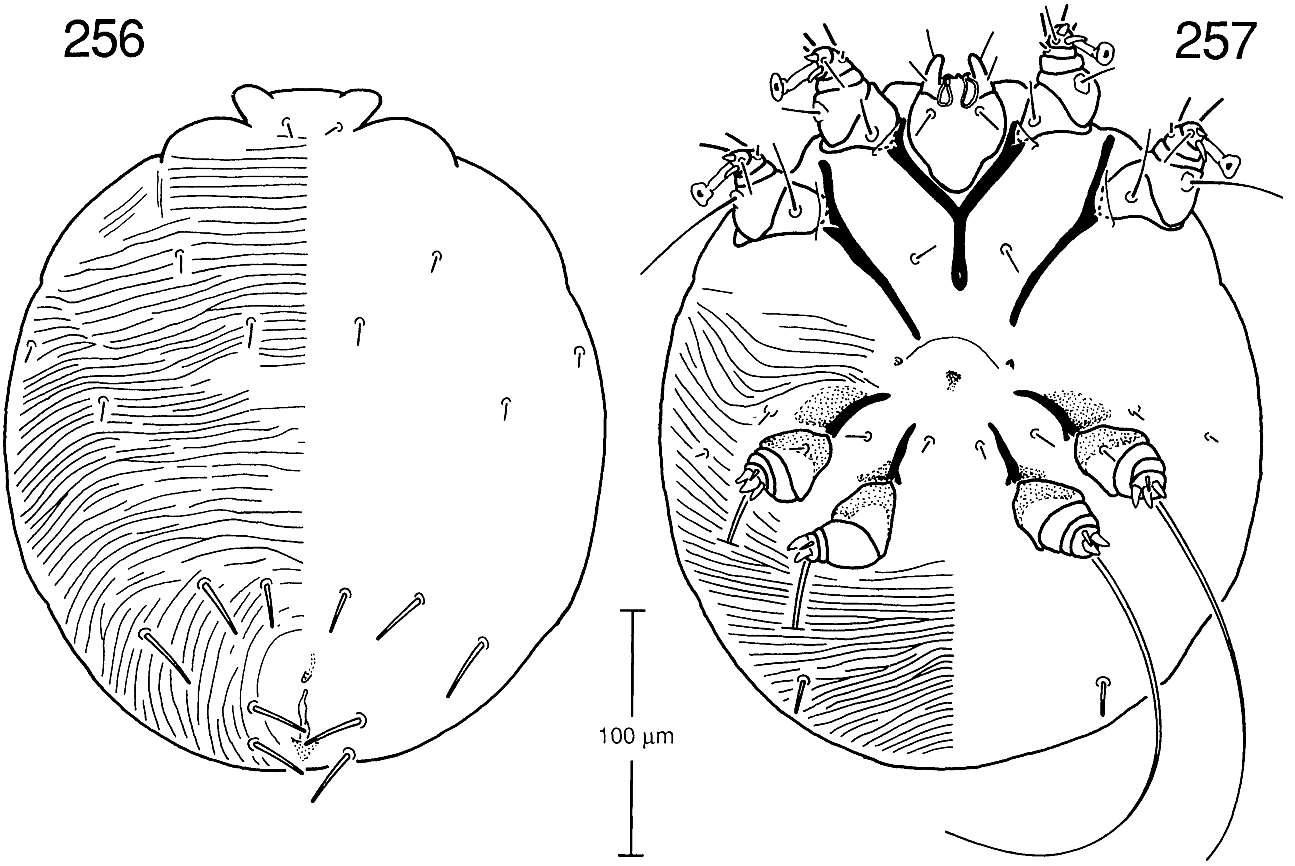
Chaerophon plicata (Buchanan, 1800). INDONESIA: SUMBAWA, Batu Tering, 8°48′S 117°22′E, 24 May 1988, D. Kitchener (S 319), WAM, HK 89–0120–1; same locality and date, S 327, WAM, HK 89–0301–2.

Mops condylurus (Smith, 1833). GHANA: EASTERN, Teshi, 5°35′N 0°06′W, J.W. Leduc 305, NMNH #479647, HK 88–0902–2; MADAGASCAR: FIANARANTSOA, 1 km N Kianjavato, 21°23′S 47°52′E, elev. 300 m, 12 August 1987, L.H. Emmons (LHE 659), NMNH #448890, HK 87–1210–1.

Mops midas (Sundevall, 1843). MADAGASCAR: S. Amboasary, 16 November 1931, Dr. Bluntschli, AMNH #170624, HK 86–0814–12.

Mops mops (De Blainville, 1840). MALAYSIA: SELANGOR, Gombak Forest, Rudnick, IMR #83.

Literature records: on *Chaerophon pumila* (= *C. faini*) from ZAIRE (Fain, 1959i [Type series]) and UGANDA (Dusba-



FIGS. 256, 257. *Notoedres* (*Notoedres*) *namibiensis*, female, dorsal (256) and ventral (257) view.

bek, 1980); on *Chaerophon plicata* from MALAYSIA (Klompen et al., 1983); on *Mops condylurus* from ANGOLA (Fain, 1965b) and UGANDA (Dusbabek, 1980); on *Mops mops* from MALAYSIA (Klompen et al., 1983).

Deposition of specimens: AMNH, NMNH, UMMZ, and WAM.

The ninth lineage at node 63 includes four species associated with molossid bats in the genera *Chaerophon* and *Mops*. The lineage is diagnosed in all stages by not adding setae *4 a* (130); in the larva by well developed setae *cp* (reversal) (83); in the female by dorsoventral elongation of the body (reversal) (3), elongation of setae *sci* (61) and *c 1* (74), and the bifurcate condition of the distal end of the sternum (141). Only *N. dewitti* has been included as a terminal taxon in the analysis (see p. 3).

Notoedres (*Notoedres*) *dewitti*
Klompen, Lukoschus, Fain, & Nadchatram, 1983
(Figs. 260, 261)

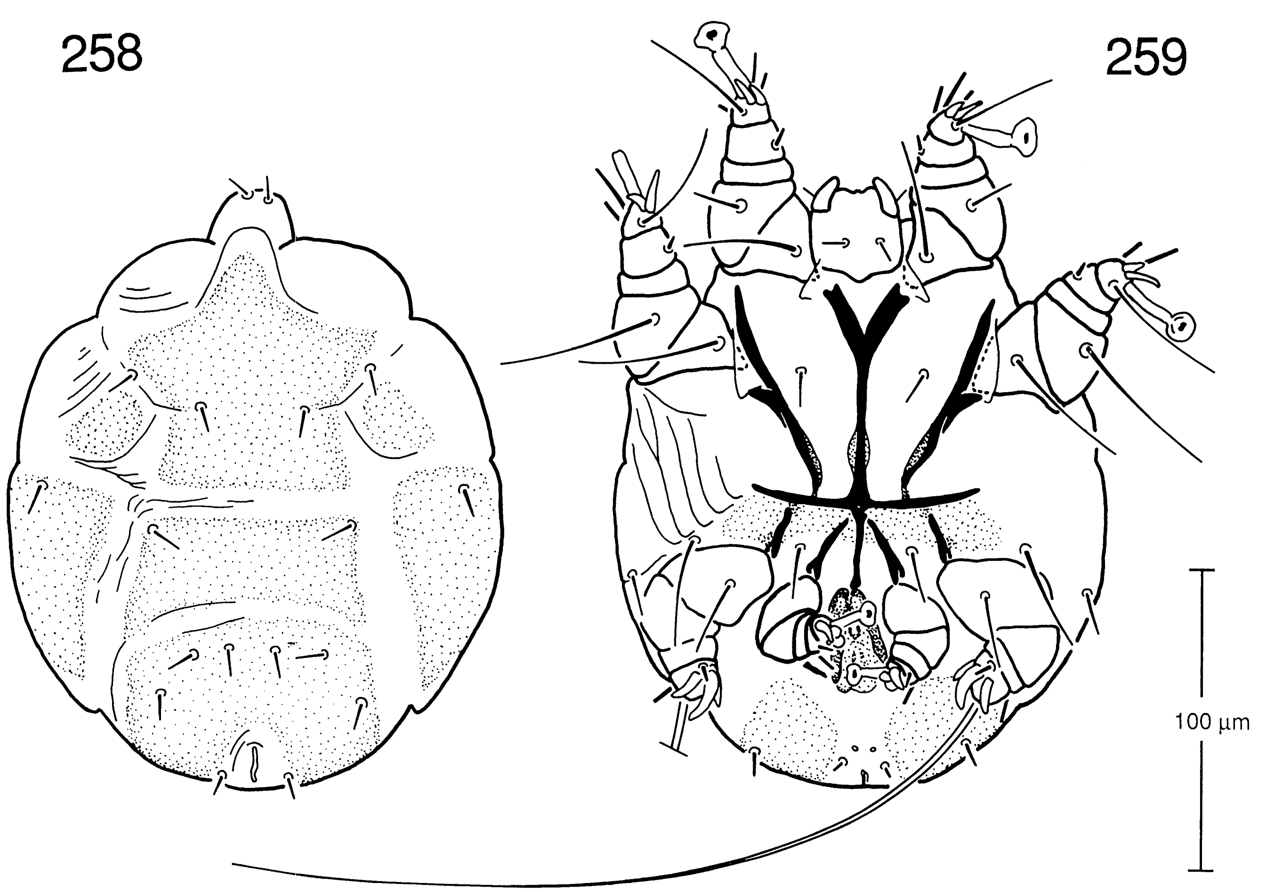
Notoedres dewitti Klompen et al., 1983: 294.

Diagnosed in the nymphs by well developed setae *cp* (reversal) (85); in the male by the loss of fusion between the posterior median and the anal shields (15), the transformation of setae *ra* I–II from spines to spine-like/filiform (reversal) (163), the loss of solenidia σ I (173), and the loss of setae *r* IV (195).

The larva and female have been described previously (Klompen et al., 1983). The association of a tritonymph and male with this species is tentative, since it is not supported by evidence from pharates. It is based on the shared absence of setae *4 a* in the tritonymph, male, and known *N. dewitti* females (see comments for *N. tadaridae*). The morphology of the tritonymph differs distinctly from that of the larva and female. The anterior dorsal setae are short (about 6 µm) and filiform. Most perianal setae are spine-like rods (12–15 µm) with setae *e 2* less than 5 µm long. By contrast, in the larva and female (Table 16) the dorsal setae are long and filiform (setae *c 1* of the larva are minute). The male (Figs. 260, 261) is very small with relatively long, well developed anterior legs. The dorsal shield pattern and coxal apodemes resemble those of *N. namibiensis*. Setae *cG* II are much smaller than *cG* I. Measurements in Table 15. All stages occur on the wing membrane, relatively close to the finger bones. The preferred attachment site appears to be the area between the second and third finger.

Material examined: Larva, tritonymph, female, and male.

Hosts (Chiroptera: Molossidae) and localities: *Chaerophon plicata* (Buchanan, 1800). Type host. INDONESIA: SUMBAWA, Batu Tering, 8°48′S 117°22′E, 24 May 1988, D. Kitchener (S 319), WAM, HK 89–0120–1; same locality and date,



FIGS. 258, 259. *Notoedres* (*Notoedres*) *namibiensis*, male, dorsal (258) and ventral (259) view.

S 327, WAM, HK 89–0301–2; MALAYSIA: NEGERI SEMBILAN, Kuala Pilah, 9 May 1979, F.S. Lukoschus (paratypes).

Chaerophon jobensis (Miller, 1902). AUSTRALIA: WESTERN AUSTRALIA, Mount Hart, 13 September 1976, Kimberley Exp. 2704; same locality, 18 September 1976, Kimberley Exp. 2723.

Mops condylurus (Smith, 1833). GHANA: EASTERN, Teshi, 5°35′N 0°06′W, 27 May–1 June 1971, J.W. Leduc 305, NMNH #479647, HK 88–0902–2; same locality and date, J.W. Leduc 306, NMNH #479648, HK 88–0901–9; J.W. Leduc 307, NMNH #479649, HK 88–0902–3; J.W. Leduc 310, NMNH #479652, HK 88–0902–5; MADAGASCAR: FIANARANTSOA, 1 km N Kianjavato, 21°23′S 47°52′E, elev. 300 m, 12 August 1987, L.H. Emmons (LHE 660), NMNH #448891, HK 88–0117–4.

Mops mops (De Blainville, 1840). MALAYSIA: SELANGOR, Gombak Forest, Rudnick, IMR #83.

Literature records: on *Chaerophon plicata* and *Mops mops* from MALAYSIA (Klompen et al., 1983 [Type series]); on *Chaerophon jobensis* from AUSTRALIA (Klompen et al., 1983).

Deposition of specimens: NMNH, PNC, UMMZ, and WAM.

Notoedres (*Notoedres*) *ismaili*
Klompen, Lukoschus, Fain, & Nadchatram, 1983

Notoedres ismaili Klompen et al., 1983: 292.

This species differs from *N. dewitti* in the larva by the long, spine-like (not filiform) shape of setae *c 1*, and in the female by the spine-like (not filiform) shape of setae *h 1* and *h 2*. It has been described for the larva and female (Klompen et al., 1983). Site information is not available.

Material examined: Larva and female.

Host (Chiroptera: Molossidae) and locality: *Chaerophon plicata* (Buchanan, 1800). Type host. MALAYSIA: NEGERI SEMBILAN, Kuala Pilah, 9 May 1979 (paratype, specimen in collection NNML).

Literature records: on *Chaerophon plicata* and *Mops mops* (de Blainville, 1840) from MALAYSIA (Klompen et al., 1983 [Type series]).

Notoedres (*Notoedres*) *ovatus* Dusbabek, 1980

Notoedres ovatus Dusbabek, 1980: 93.

The larva differs from that of *N. dewitti* by the much shorter perianal setae (the anterior dorsal setae are highly similar). The female is characterized by the unique shape of setae *sci* and *c 1:* spine-like, relatively thin near the base and

Table 16. Comparative measurements of female *Notoedres*. 3.

	tadaridae			*dewitti*			*chiropteralis*			*centrifera*		
	N=9			N=11			N=9			N=23		
	av	SD	range	av	SD	range	av	SD	range	av	SD	range
gnathosoma												
length	34	1	32–35	38	6	30–53	43	5	33–48	39	3	35–48
width	25	1	24–27	29	5	24–39	36	2	30–38	36	3	31–43
subcapitular seta	8	2	6–10	18	9	12–40	15	5	9–22	–		
palpal seta α *l*												
length	14	4	10–18	15	3	11–21	16	2	13–19	5	1	4–6
width	0.3	0.1	0.2–0.4	0.5	0.1	0.3–0.6	0.8	0.3	0.4–1.4	1.0	0.2	0.6–1.5
body												
length	294	123	203–499	263	57	198–393	334	86	346–497	275	28	238–344
width	254	116	185–428	214	45	160–315	263	47	207–338	232	27	199–308
seta *vi*	8	4	4–14	18	6	9–31	11	2	6–14	37	5	27–45
seta *sci*	5	2	1–8	55	6	50–64	36	8	22–47	28	4	21–35
seta *sce*	5	2	1–8	23	5	17–35	20	3	15–25	24	3	17–31
seta *c 1*	5	2	3–8	46	6	37–59	4	1	3–5	23	3	15–28
seta *c 2*	5	1	3–7	22	2	19–27	7	2	3–10	24	4	17–30
seta *cp*	3	2	1–7	22	6	14–35	5	1	2–6	9	2	7–13
seta *c 3*	4	3	2–9	20	8	11–36	6	2	3–8	31	4	19–38
seta *d 1*	12	3	8–18	39	6	31–54	25	4	18–28	16	2	12–22
seta *d 2*	7	7	2–19	37	7	17–50	26	4	16–32	12	2	10–21
seta *e 1*	10	2	7–14	34	5	26–42	22	3	17–27	15	2	12–20
seta *e 2*	4	2	1–8	30	6	21–39	9	5	5–19	11	1	8–15
seta *h 1*	11	2	8–13	25	4	20–32	23	4	16–28	10	1	8–12
seta *h 2*	10	3	6–14	25	4	21–31	22	3	13–24	10	2	7–14
width seta *d 1*	1.5	0.5	1.0–2.4	1.6	0.5	1.0–2.5	1.8	0.1	1.5–2.0	1.3	0.2	0.9–1.8
width seta *d 2*	1.2	0.7	0.4–2.2	1.5	0.3	0.9–1.9	1.7	0.3	1.0–2.1	1.2	0.2	1.0–1.8
width seta *e 1*	1.3	0.3	1.0–2.0	1.4	0.3	1.0–1.8	1.6	0.4	0.9–2.0	1.3	0.3	1.0–1.9
width seta *e 2*	0.5	0.1	0.4–0.7	1.2	0.3	0.9–1.6	0.7	0.2	0.3–1.1	1.1	0.2	0.6–1.5
width seta *h 1*	1.3	0.4	0.8–2.1	0.9	0.3	0.7–1.8	1.6	0.3	1.0–2.0	1.1	0.2	0.7–1.4
width seta *h 2*	1.2	0.6	0.7–2.4	1.1	0.5	0.7–2.7	1.5	0.3	1.0–1.9	1.0	0.2	0.4–1.4
seta *1 a*	9	2	6–12	23	4	18–44	13	2	9–15	38	4	27–46
seta *3 b*	7	2	3–10	15	7	10–34	12	3	7–14	29	4	18–36
seta *4 a*	3	1	2–5	–			6	1	5–8	22	3	15–26
copulatory cone	2	1	1–3	3	1	2–6	3	1	3–4	5	1	4–7
bursa copulatrix	43	22	22–92	68	8	57–81	48	5	41–52	38	6	29–50
coxal apodemes I	45	5	40–56	46	9	41–73	59	6	49–65	51	3	48–59
coxal apodemes II	66	8	58–81	56	19	41–109	85	12	64–99	77	5	65–86
coxal apodemes III	24	3	21–28	27	10	20–57	33	3	27–36	31	3	28–41
coxal apodemes IV	23	4	17–29	23	11	15–56	28	3	22–31	29	4	24–46
leg I	40	7	32–52	44	12	28–77	48	8	35–60	51	3	45–57
leg II	42	7	33–56	41	11	30–71	56	7	47–68	55	4	45–61
leg III	34	4	29–39	26	6	20–44	45	5	37–52	52	3	46–58
leg IV	35	3	30–41	25	7	20–45	43	4	39–50	50	3	41–56
seta *pR* I	18	4	14–22	27	13	17–62	31	4	25–36	46	5	38–56
seta *pR* II	31	–	30–32	31	10	23–56	38	9	26–52	50	7	36–62
seta *sR* III	6	3	2–10	12	8	3–32	6	1	3–8	30	4	22–38
seta *vF* I	11	5	6–18	17	5	11–30	31	4	22–35	33	2	29–38
seta *vF* II	37	11	21–46	37	14	26–77	57	11	35–72	52	4	41–59
seta *cG* I	11	2	9–13	33	11	12–55	42	6	31–51	15	4	6–24
seta *cG* II	5	1	5	31	7	21–48	10	3	7–14	12	3	7–18
seta *d* III	145	30	111–179	115	17	87–145	166	16	141–183	178	13	157–203
seta *d* IV	177	57	115–245	136	6	126–142	185	19	160–208	185	14	160–215
solenidion ϕ I	11	3	7–15	14	5	10–29	18	2	14–20	21	1	19–24
solenidion ϕ II	10	4	6–16	13	2	10–17	19	4	10–24	21	1	18–23
solenidion ϕ III	7	2	4–8	7	2	4–12	6	1	5–9	10	1	6–12
solenidion ϕ IV	6	2	4–8	6	2	4–13	5	1	3–6	8	2	5–10
solenidion ω-1 I	11	2	8–13	14	2	11–18	16	3	12–21	23	1	20–26
solenidion ω-3 I	7	2	5–10	7	1	6–10	13	2	10–15	16	1	14–17
solenidion ω II	12	3	10–17	14	1	12–17	22	4	14–26	25	2	19–28
ambulacral stalk I	14	3	11–18	15	5	11–29	15	2	12–17	22	1	19–24
ambulacral stalk II	14	2	11–18	13	5	9–28	15	2	11–18	23	1	20–25

tip but wider near the middle, and with a lateral tooth (Dusbabek, 1980). The nymphs and male have not been described. The new material was collected from the wing membrane, close to the posterior edge of the wing.

Material examined: Larva and female.

Hosts (Chiroptera: Molossidae) and locality: *Mops condylurus* (Smith, 1833). MADAGASCAR: FIANARANTSOA, 1 km N Kianjavato, 21°23'S 47°52'E, elev. 300 m, 12 August 1987, L.H. Emmons (LHE 660), NMNH #448891, HK 88–0117–4.

Literature records: on *Mops condylurus* (Smith, 1833) from UGANDA: TORO, Toro Game Reserve (Dusbabek, 1980 [Type series]).

Deposition of specimens: UMMZ.

Notoedres (*Notoedres*) *tristis* Fain & Marshall, 1977

Notoedres tristis Fain & Marshall, 1977: 38.

The presence of sclerotized dorsal patches in the larva is unique in the family. The setae in the larva are shorter than in *N. dewitti* or *N. ismaili* (Klompen et al., 1983). Although the female is much larger than that of *N. dewitti* (length > 750 vs. 200–400 µm), the setae are on average a little shorter (most perianal setae 23–29 µm, setae *e 2* 15 µm).

Material examined: Larva and female.

Host (Chiroptera: Molossidae) and locality: *Chaerophon jobensis* (Miller, 1902). AUSTRALIA: WESTERN AUSTRALIA, Mount Hart, 10 September 1976, Kimberley Exp. 2678; same locality, 14 September 1976, Kimberley Exp. 2717.

Literature records: on *Chaerophon jobensis* from VANUATU: Malo Is. (Fain & Marshall, 1977 [Type series]), and AUSTRALIA (Klompen et al., 1983).

The remaining two lineages arising at node 63 (Fig. 57) include all *Notoedres* species parasitizing hosts other than bats. Relationships within the first of these two, the *muris-musculi* lineage, are well resolved. The lineage (node 68) is diagnosed in the eggs by the loss or extreme reduction of the stalks (reversal) (138); in the nymphs by well developed setae *cp* (reversal) (85); in the male by the loss of the anterior lateral shields (reversal) (11, 12 state 0), the loss of fusion between the anal shields (15), the loss of solenidia σ I (173), and the spine-like shape of setae *kT* III–IV (199).

Notoedres muris diverges from a lineage (node 69) diagnosed in the female by the elongation of setae *sci* (61), and parallel but not fused coxal apodemes I (139); in the male by the loss of the posterior lateral shields (reversal) (17, 18 state 0). A lineage including three species associated with bats (node 70) diverges from the remaining species, all associated with non-volant mammals. The first lineage is diagnosed in the egg by the presence of a well developed stalk (138); in the nymphs by minute, vestigial, or absent setae *cp* (85); in the immatures and female by minute setae *c 1* (72, 73). The grouping of *N. chiropteralis* and *N. schoutedeni* is diagnosed in the nymphs and female by the strong increase in height of the body (3, 4, 5).

Notoedres (*Notoedres*) *muris* Megnin, 1877

Notoedres muris Megnin, 1877: 71.
Notoedres alepis Railliet & Lucet, 1893: 404–405.

Diagnosed in the male by the loss of the genital apodemes (reversal) (154).

All life stages have been described previously (Lavoipierre, 1964; Oudemans, 1926; Watson, 1962). *Notoedres muris* usually burrows into the ear pinnae, eyelids, nose, and tail (Flynn, 1973; Klompen & Nachman, 1990; Lavoipierre, 1964; Watson, 1962). Less frequently it also affects the limbs and anal region (Flynn, 1973; Lavoipierre, 1964). The mite burrows are usually restricted to the stratum corneum (Gordon et al., 1943; Watson, 1962). Pathology includes strong proliferation of epidermal cells which tend to cornify into scabs, and a thickening of the stratum corneum (McKenzie et al., 1976; Watson, 1962). Reported pathology is similar in the various hosts affected.

Material examined: All stages.

Hosts (Rodentia: Muridae) and localities: *Rattus norvegicus* (Berkenhout, 1769). Type host. NETHERLANDS: OVERIJSEL, Oldenzaal, 18 May 1967, F.S. Lukoschus 303.

Rattus niobe (Thomas, 1906). PAPUA NEW GUINEA: SOUTHERN HIGHLANDS, Kagoba, 19 May 1968, N. Wilson (specimen in collection BME).

Holochilus brasiliensis (Desmarest, 1819). ARGENTINA: ENTRE RIOS, 6 km S. Puerto Ibicuy, 33°47'S 59°10'W, 1–7 November 1988, M.W. Nachman, HK 88–1117–1.

Praomys natalensis (Smith, 1834). SOUTH AFRICA: TRANSVAAL, Johannesburg, 27 March 1957, F. Zumpt.

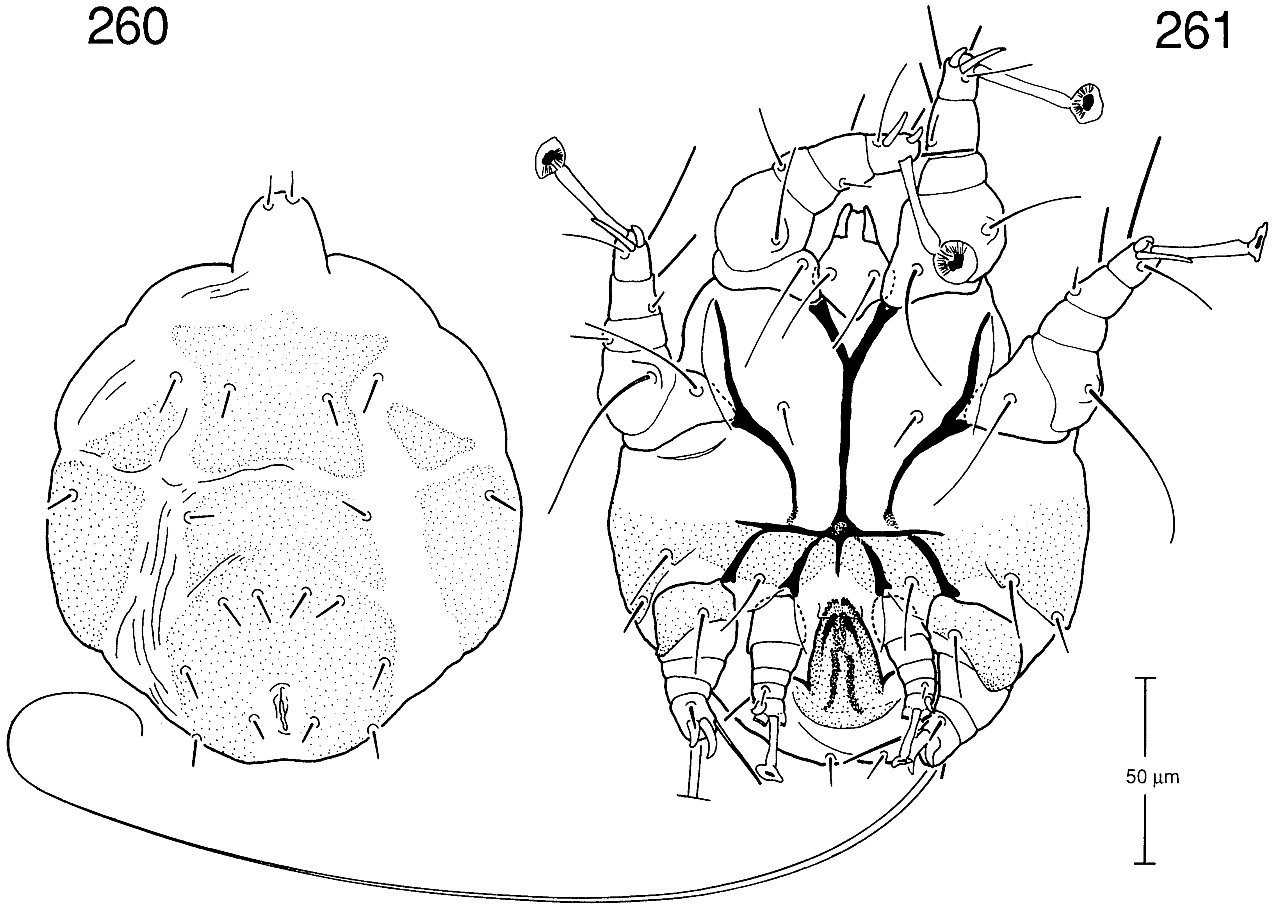
Literature records (Rodentia: Muridae): on *Rattus norvegicus* from FRANCE (Megnin, 1877 [Type series]), various sites in Europe (Fain, 1965b), AUSTRALIA (Domrow, 1954); NEW ZEALAND (Whitten, 1962), and the USA (DeGiusti & Hartley, 1965); on *Rattus rattus* (Linnaeus, 1758) from various sites in Europe (Fain, 1965b), and SOUTH AFRICA (Zumpt, 1961); on *Rattus tunneyi* Thomas, 1904 (= *R. culmorum*) from AUSTRALIA (Domrow, 1955); on *Arvicola sapidus* Miller, 1908 from SPAIN (Zapatero Ramos et al., 1978); on *Arvicola terrestris* (Linnaeus, 1758) from FRANCE (Railliet & Lucet, 1893); on *Cricetus cricetus* (Linnaeus, 1758) from BELGIUM (Fain, 1965b); on *Holochilus brasiliensis* from ARGENTINA (Klompen & Nachman, 1990); on *Melomys cervinipes* (Gould, 1852) from AUSTRALIA (Domrow, 1974; McKenzie et al., 1976); on *Microtus californicus* (Peale, 1848) from USA (Lavoipierre, 1964).

Records from other host groups: on *Isoodon macrourus* (Gould, 1842) (Marsupialia: Peramelidae) and *Trichosurus vulpecula* (Kerr, 1792) (Marsupialia: Phalangeridae) from AUSTRALIA (Domrow, 1974); on *Erinaceus europaeus* Linnaeus, 1758 (Insectivora: Erinaceidae) from NEW ZEALAND (Heath et al., 1971).

Deposition of specimens: UMMZ.

Notoedres (*Notoedres*) *chiropteralis* (Trouessart, 1896)

Sarcoptes chiropteralis Trouessart, 1896: 747.
Prosopodectes chiropteralis (Trouessart), Canestrini, 1897: 911.
Notoedres vanschaiki Van Eyndhoven, 1946: 30.
Notoedres chiropteralis (Trouessart), Fain, 1959d: 330.
Notoedres (*N.*) *chiropteralis* (Trouessart), Fain, 1959i: 138.
Bakeracarus schoutedeni hyatti Fain, 1963d: 222, new synonymy.



Figs. 260, 261. *Notoedres* (*Notoedres*) *dewitti*, male, dorsal (260) and ventral (261) view.

A reexamination of the descriptions of *N. chiropteralis*, *N. schoutedeni* and *N. schoutedeni hyatti* in conjunction with examination of new material collected from *Pipistrellus* and *Scotophilus* in Southeast Asia, revealed a moderate variability in measurements. Based on these measurements and some qualitative characters, two distinct forms could be recognized: in the first setae *e 1* are about 2–3 times the length of setae *e 2*, in the second both pairs of *e* setae are subequal in length. The first group corresponds to *N. chiropteralis* and *N. schoutedeni hyatti* and occurs in Eurasia. The second corresponds to *N. schoutedeni* (*s.s.*) and occurs in Africa. I could not establish consistent differences between *N. chiropteralis* and *N. schoutedeni hyatti* and therefore synonymize them. The various stages of *N. chiropteralis* have been described by van Eyndhoven (1947) and Fain (1959d, 1959i, 1963d). Comparative measurements are included in Tables 15 and 16.

Females attach to the ear pinnae or to the wing. On the wing the preferred sites are the skin over the arm bones and the anterior and posterior edges of the wing (van Eyndhoven, 1941, 1947). Observations on site choice of the immatures and males are rare but they appear to occur in the same sites. Females of "*hyatti*" attach to the skin "in the depth of the ear" (Fain, 1963d).

Material examined: All stages.

Hosts (Chiroptera: Vespertilionidae) and localities: *Nyctalus noctula* (Schreber, 1774). NETHERLANDS: Noord Brabant, Oss, 29 August 1973, F.S. Lukoschus.

Pipistrellus javanicus (Gray, 1838). PHILIPPINES: Negros Oriental, 9 km N, 4 km W Dumaguete, 9°23'N 123°11'E, elev. 600 m, 30 April 1987, L.R. Heaney (LRH 3406), NMNH, HK 87–0505–1; Negros Oriental, 3 km N, 14 km W Dumaguete, Lake Balinsasayao, 9°21'N 123°11'E, elev. 850 m, 29 June 1987, J.S.H. Klompen (JSHK 124), NMNH, HK 87–0629–1; same locality, 2 July 1987, JSHK 132, NMNH, HK 87–0702–4.

Scotophilus kuhli Leach, 1822. MALAYSIA: Kuala Lumpur, Thai Embassy, 28 September 1965, bat 22 (specimens in collection BME).

Literature records: on *Eptesicus serotinus* Schreber, 1778 from FRANCE (Trouessart, 1896 [Type series]), GERMANY (Fain, 1959d; Fain & Lukoschus, 1969), the NETHERLANDS (van Eyndhoven, 1941, 1946, 1947; Fain, 1959d), and SPAIN (Fain & Lukoschus, 1969); on *Nyctalus noctula* from the NETHERLANDS (van Eyndhoven, 1947; Fain & Lukoschus, 1969), and GERMANY (Fain & Lukoschus, 1969); on *Pipistrellus pipistrellus* (Schreber, 1774) from GERMANY (Fain, 1959d; Fain & Lukoschus, 1969); on *Tylonycteris pachypus* (Temminck, 1840) from NEPAL (Fain, 1963d [as *B. schoutedeni hyatti*]).

Deposition of specimens: NMNH, PNC, and UMMZ.

Notoedres (*Notoedres*) *schoutedeni* Fain, 1959

Notoedres (*Notoedres*) *schoutedeni* Fain, 1959i: 143.
Bakeracarus schoutedeni (Fain), Fain, 1963d: 222.
Notoedres (*Bakeracarus*) *schoutedeni* (Fain), Fain, 1965b: 331.

This species differs from *N. chiropteralis* by the subequal length of the *e* setae in the female. The males may differ by having separate anal shields (14), but the condition for this character could not be determined in the single overcleared male of *N. chiropteralis* available. All stages have been described previously (Fain, 1959i). Immatures and males were found on the wing surface; females attached near the anterior edge of the wing or near the arm bones (Fain, 1959i).

Material examined: None.

Literature records: on *Eptesicus tenuipinnis* (Peters, 1872) from ZAIRE: HAUT-ZAIRE, Buta (Fain, 1959i [Type series]); on *Eptesicus "ater"* from ZAIRE (Fain, 1959i).

Notoedres (*Notoedres*) *mimetilli* Fain, 1959

Notoedres (*N.*) *mimetilli* Fain, 1959i: 153.

This species has been described from the nymphs and female (Fain, 1959i, 1963c). It is characterized by the long *sci*, *d 1*, and *e 1* setae, contrasting with the remaining perianal setae, which are much shorter and spine-like.

Material examined: None.

Literature records: on *Mimetillus moloneyi* (Thomas, 1891) (= *M. thomasi*) (Chiroptera: Vespertilionidae) from ZAIRE: SHABA (Fain, 1959i [Type series]), and SIERRA LEONE (Fain, 1963c).

The lineage including the remaining species of the *murismusculi* lineage (Fig. 57, node 71) is diagnosed in the male by the strong reduction of the posterior median shield (13), the loss of setae *e* IV (191), and the fusion of the tibia and tarsus of legs IV (209). Within this assemblage *N. centrifera* diverges from a lineage (node 72) diagnosed in all stages by rarely or never adding setae *4 a* (130), and in the larva and female by scale-like striations on the dorsum (56, 57).

Notoedres (*Notoedres*) *centrifera* Jansen, 1963
(Figs. 44, 45, 226, 262–265)

Notoedres centrifera Jansen, 1963: 259.
Notoedres douglasi Lavoipierre, 1964: 6, new synonymy.
Notoedres (*Jansnotoedres*) *centrifera* Jansen, Fain, 1965b: 332.

Diagnosed in the larva by the presence of well developed setae *cp* (reversal) (83); in the female by the elongation of setae *c 1* (74); in the male by the loss of all dorsal shields (9, 10), and the extreme reduction of the ambulacra on legs IV (Fig. 44).

Extensive comparisons of both qualitative characters and measurements (Tables 15, 16) for females and males revealed no consistent differences between the North American populations (*N. douglasi*) and the Southeast Asian one (*N. centrifera*). The proposed synonymy confirms earlier suggestions (Fain, 1965b). All stages of this mite have been described previously (Jansen, 1963; Lavoipierre, 1964). *Notoedres centrifera* can cause severe mange in squirrels, characterized by alopecia and extensive scaling and scabbing (Allen, 1943; Evans, 1984), occasionally resulting in death. This mite may have contributed to the decline of the western grey squirrel (*Sciurus griseus*) in parts of California (Bryant, 1921, 1926).

Material examined: All stages.

Hosts (Rodentia: Sciuridae) and localities: *Ratufa bicolor* (Sparrman, 1778). Type host. Private collection in the NETHERLANDS (paratypes).

Glaucomys volans (Linnaeus, 1758). USA: PENNSYLVANIA, Huntingdon Co., Juniata Field Station, 28 August 1981, J.O. Whitaker, Jr. 223.

Sciurus carolinensis Gmelin, 1788. USA: NEW YORK, Tompkins Co., Ithaca, Cornell Univ. campus, 4 April 1974, B.M. OConnor, BMOC 74–0404–10; same locality, 28 May 1975, BMOC 75–0528–1; NEW YORK, Tompkins Co., 7 mi S Ithaca, 26 April 1975, BMOC 75–0426–1; NEW YORK, Livingston Co., 2.5 km N Dansville, 3 June 1982, #709, E.J. Spicka.

Sciurus griseus Ord, 1818. USA: OREGON, Hood River Co., Hood River, 25 February 1971, H.C. Morse, J. Wernz.

Sciurus niger Linnaeus, 1758. USA: KANSAS, 1957, #43, K.H. Wilson; INDIANA, Elkhart Co., Elkhart, T.W. Schillhorn van Veen, BMOC 79–1205–1; MICHIGAN, St. Joseph Co., 27 May 1983, N. Wells Gosling, BMOC 83–0606–2.

Tamias striatus (Linnaeus, 1758). USA: MICHIGAN, Cheboygan Co., University of Michigan Biological Station, 22 August 1965, R. Beer, WJW 650822–1.

Literature records: on *Ratufa bicolor* from the NETHERLANDS (captivity) (Jansen, 1963 [Type series]); on *Sciurus griseus* from USA: CALIFORNIA (Bryant, 1921, 1926; Lavoipierre, 1964 [type host of *N. douglasi*]); on *Sciurus niger* from USA: ILLINOIS, INDIANA (Evans, 1984), and MICHIGAN (Allen, 1943).

Deposition of specimens: UMMZ.

Notoedres (*Notoedres*) *cati* (Hering, 1838)

Sarcoptes cati Hering, 1838: 605.
Notoedres cati (Hering), Canestrini & Kramer, 1899: 11.
Notoedres caniculi Gerlach, 1857: 29.

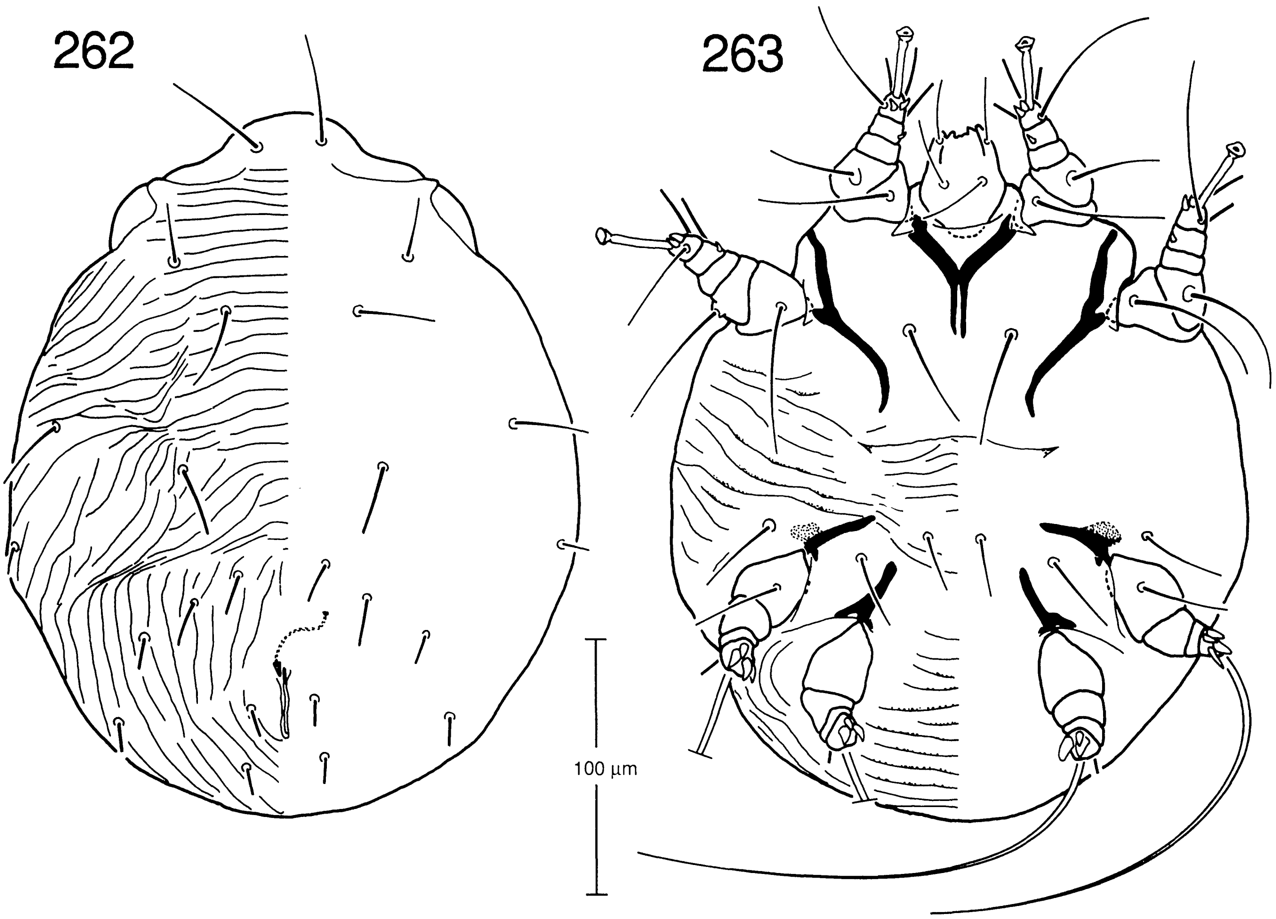
Diagnosed in the nymphs by a strong reduction of setae *cp* (85); in the female by the elongation of setae *c 1* (74), and fused coxal apodemes I (139); in the male by the loss of fusion between the anal shields (14), the loss of the genital apodemes (reversal) (154), the transformation of setae *r* IV to spines (198), and the transformation of setae *kT* III–IV from large spines to thin spines or filiform (reversal) (199).

All stages have been described previously (Grandjean, 1938a, 1938b; Oudemans, 1926). The infestation site may vary between host species. In the most common host, the domestic cat, the mites tend to burrow into the epidermis of the ears, face, neck, and sometimes the legs and genital region (Flynn, 1973). On the civet cat, examined during this study, the mites were concentrated on the tail.

Material examined: All stages.

Hosts and localities: *Felis silvestris* Schreber, 1777 (Carnivora: Felidae). Type host. USA: NEW YORK, Tompkins Co., Ithaca, 1967, New York State Vet. College, NYSVC 67–171.

Paradoxurus hermaphrodites (Pallas, 1777) (Carnivora: Viv-



FIGS. 262, 263. *Notoedres* (*Notoedres*) *centrifera*, female, dorsal (262) and ventral (263) view.

erridae). PHILIPPINES: LEYTE, 7 km N Baybay, VISCA, 10°45′N 124°47′E, elev. 10 m, 9 April 1987, L.R. Heaney (LRH 3167), NMNH #458891, HK 87-0409-3.

Literature records: The majority of the records of this mite are from Carnivora. On Felidae: *Felis silvestris* from GERMANY (Hering, 1838 [Type series]), various sites in Europe (Fain, 1965b), FIJI (Munro, 1978) and SOUTH AFRICA (Zumpt, 1961) (*N. cati* appears to be a cosmopolitan parasite of domestic cats); *Felis serval* from POLAND (captivity) (Ramisz & Pietrak, 1985); *Acinonyx jubatus* (Schreber, 1776) from SOUTH AFRICA (Young et al., 1972); *Lynx rufus* (Schreber, 1776) from USA: CALIFORNIA (Holdenreid et al., 1951), MASSACHUSETTS and CONNECTICUT (Penner & Parke, 1954); *Panthera uncia* (Schreber, 1775) from USA (captivity) (Fletcher, 1978). On Procyonidae: *Nasua nasua* (Linnaeus, 1766) from MEXICO (captivity) (Lavoipierre, 1964). On Herpestidae: *Herpestes auropunctatus* (Hodgson, 1836) from USA: HAWAII (Garrett & Haramoto, 1967) and the VIRGIN ISLANDS (Nellis & Everard, 1983).

Additional records from *Oryctolagus cuniculus* (Linnaeus, 1758) (Lagomorpha: Leporidae) (captivity) from Europe, ZAIRE (Fain, 1965b), PHILIPPINES (Cariaso & Rueda, 1986), and SOUTH AFRICA (Zumpt, 1961).

Deposition of specimens: NMNH, PNC, and UMMZ.

Notoedres (*Notoedres*) *musculi* (Krämer, 1865)

Sarcoptes musculi Krämer, 1865: 225.
Notoedres musculi Oudemans, 1926: 193.

Diagnosed in the female by the short setae *sci* (reversal) (61).

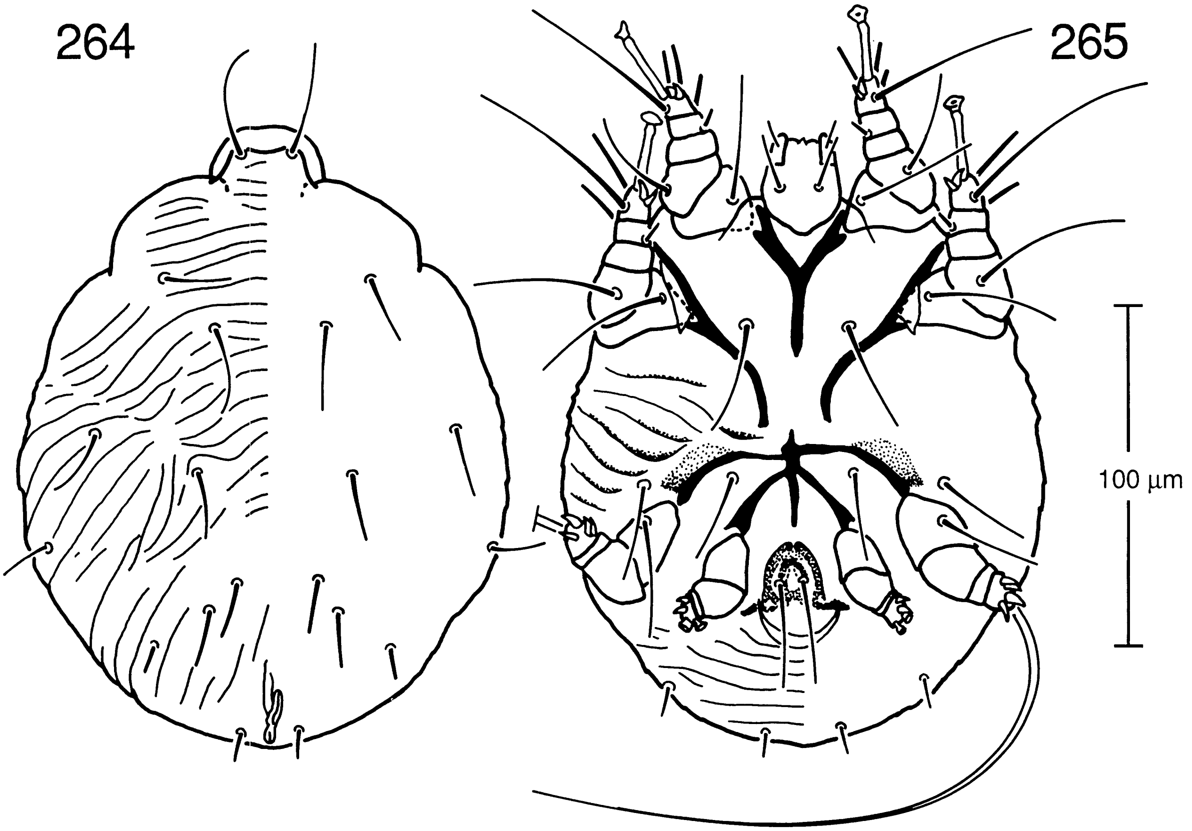
Setae *4 a* are absent in most females of *N. musculi*. If at all present, this setal pair is usually represented by only one of the two setae. The immatures and female have been described previously (Klompen et al., 1983; Oudemans, 1926). The single male collected during this study is still contained within the tritonymph, and is very poorly sclerotized, not allowing an adequate description. *Notoedres musculi* has been recovered from the tail region of *Apodemus* (Klompen et al., 1983).

Material examined: All stages (male in very poor condition).

Hosts (Rodentia: Muridae) and localities: *Apodemus agrarius* (Pallas, 1771). SOUTH KOREA: Seoul, 30 May 1952, US Army, NMNH #297310.

Apodemus flavicollis (Melchior, 1834). GREECE: Evros Delta, 9 May 1986, H. Strijbosch.

Literature records: on *Mus domesticus* Rutty, 1772 from GERMANY: NIEDERSACHSEN, Göttingen (Krämer, 1865 [Type series]), and the NETHERLANDS (Oudemans,



FIGS. 264, 265. *Notoedres* (*Notoedres*) *centrifera*, male, dorsal (264) and ventral (265) view.

1926); on *Apodemus agrarius* from SOUTH KOREA (Klompen et al., 1983).

Deposition of specimens: UMMZ.

The last lineage at node 63 (node 73, Fig. 57) is diagnosed in the eggs by the loss or extreme reduction of the stalks (reversal) (138); in the nymphs by well developed setae *cp* (reversal) (85); in the male by the fusion of tibia and tarsus IV (209). The sister group of *N. oudemansi* (node 74) is diagnosed in the female by the presence of a large bare zone on the dorsum (58); in the male by the loss of solenidia σ I (173), and the loss of setae *e* and *r* IV (191, 195).

Notoedres (*Notoedres*) *oudemansi* Fain, 1965

Notoedres (*Notoedres*) *oudemansi* Fain, 1965b: 327.

Diagnosed in the female by the scale-like striations on the dorsum (57) (these striations are absent in the larva).

The female and larva (Fain, 1965b) as well as the male (Gregory, 1981) have been described. *Notoedres oudemansi* has been associated with severe mange in an African hedgehog, causing alopecia and encrustations in the hairy (not spiny) part of the body and in the face (Gregory, 1981). The infestation described by Gregory was fatal.

Material examined: None.

Literature records: on *Rattus rattus* (Linnaeus, 1758) (Rodentia: Muridae) from RUANDA: near Butare (Fain, 1965b [Type series]); on *Erinaceus albiventris* Wagner, 1841 (Insectivora: Erinaceidae) from KENYA (Gregory, 1981).

Notoedres (*Notoedres*) *pseudomuris* Lavoipierre, 1968

Notoedres pseudomuris Lavoipierre, 1968: 316.

Diagnosed in the female by parallel, not fused, coxal apodemes I (139).

The female (Lavoipierre, 1968), male, and larva (Klompen et al., 1983) of *Notoedres pseudomuris* have been described. The mites burrow into the ear pinnae, snout, tail, and limbs, causing a skin reaction superficially resembling that caused by *N. muris*.

Material examined: All stages.

Hosts (Rodentia: Muridae) and localities: *Mus musculus* Linnaeus, 1766. EGYPT: BEHEIRA, between El Beida and El Zugm, Wadi el Natrom, 4 March 1989, S.M. Goodman (SMG 2819), UMMZ, BMOC 89-0509-6; PHILIPPINES: ILOILO, Iloilo, September 1912, C. Fox, NMNH #175766.

Apodemus sylvaticus (Linnaeus, 1758). TAIWAN: Chueifeng, R.F. Kuntz, NMNH #334382.

Microtus transcaspicus Satunin, 1905. USSR: Kopet-Dag Mts., May 1974, Moljukov, SMF.

Literature records: on *Mus musculus* (= *M. formosanus*) from TAIWAN (Lavoipierre, 1964 [Type series]); on *Apodemus sylvaticus* from TAIWAN and *Mus musculus* from the PHILIPPINES (Klompen et al., 1983).

Deposition of specimens: UMMZ.

Notoedres (*Notoedres*) *pahangi*
Klompen, Lukoschus, Fain, & Nadchatram, 1983
(Figs. 46, 47)

Notoedres pahangi Klompen et al., 1983: 276.

Diagnosed in the male by the transformation of setae *kT* III–IV to spines (199).

This species has been described for all stages (Klompen et al., 1983). Information on site choice and pathology is not available.

Material examined: All stages.

Hosts (Rodentia: Muridae) and localities: *Rattus tiomanicus* (Miller, 1900). Type host. MALAYSIA: SELANGOR, Bukit Lanjan, 7 May 1979, F.S. Lukoschus (FSL) (paratypes); SELANGOR, Subang Forest, 7 May 1979, IMR #121 (paratypes); Gombak Forest, 4 November 1982, FSL; Bukit Fraser, 17 October 1982, FSL.

Rattus argentiventer (Robinson & Kloss, 1916). MALAYSIA: SELANGOR, 1 June 1979, IMR #180, (paratypes).

Rattus exulans (Peale, 1848). PHILIPPINES: BUKIDNON, Katanglad Mts, October 1965, Bregulla, SMF #30945 (paratypes).

Rattus hoffmanni (Matschie, 1901). INDONESIA, Van Peenen, NMNH #502095 (paratypes).

Aethomys namaquensis (Smith, 1834). SOUTH AFRICA: Sturder Pass, 4 October 1980, Misonne #53851.

Arvicanthus niloticus (Desmarest, 1822). KENYA: S Guaso Nyiro, 1909, Loring.

Berylmys bowersi (Anderson, 1879). MALAYSIA: Bukit Fraser, 17 October 1982, F.S. Lukoschus.

Bunomys penitus (Miller & Hollister, 1921) (= *Rattus penitus*). INDONESIA, Van Peenen, NMNH #502099 (paratypes).

Niviventer fulvescens (Gray, 1847) (= *Rattus yerdoni*). MYANMAR: Mt. Carin, 1885, Fea, ZIZM (paratypes).

Literature records: on *Rattus tiomanicus* from MALAYSIA: SELANGOR (Klompen et al., 1983 [Type series]). Other hosts and localities as listed above under paratypes (Klompen et al., 1983).

The following three species are provisionally aligned with *N. pahangi*, a species from which they did not differ in the characters examined (see p. 3). They share with *N. pahangi* the presence of a large non-striated area on the dorsum of the female (58) and fused coxal apodemes I (ancestral at this level). *Notoedres galagoensis* and *N. paucipilis* are poorly known species, and a majority of the character states for these species could not be determined in the absence of material.

Notoedres (*Notoedres*) *jamesoni* Lavoipierre, 1964

Notoedres jamesoni Lavoipierre, 1964: 8.

This species has been described from the female (Lavoipierre, 1964) and the larva (Klompen et al., 1983). The female differs from that of *N. pahangi* by the presence of a single pair of scale-like structures on the dorsum; the larva differs by the unequal size of the anterior and perianal dorsal setae (subequal in *N. pahangi*).

Information on site choice and pathology is not available.

Material examined: Larva and female.

Hosts (Rodentia: Muridae) and localities: *Rattus annandalei* (Bonhote, 1903). MALAYSIA: SELANGOR, Subang Forest, 7 May 1979, IMR #117.

Rattus tiomanicus (Miller, 1900). MALAYSIA: SELANGOR, Subang Forest, 7 May 1979, IMR #121.

Literature records: on an unidentified rat from VIETNAM (Lavoipierre, 1964 [Type series]); on *Bandicota bengalensis* (Gray & Harwicke, 1833) from INDIA (Mitchell, 1970); on *Rattus annandalei, Rattus argentiventer* (Robinson & Kloss, 1916) and *Rattus tiomanicus* from MALAYSIA (Klompen et al., 1983).

Notoedres (*Notoedres*) *paucipilis* (Lawrence, 1960)

Mysarcoptes paucipilis Lawrence, 1960: 724.

Notoedres (*Notoedres*) *paucipilis* (Lawrence), Fain, 1965b: 331.

This species is known only from an inadequate description of the female (Lawrence, 1960). The female shares with the female of *N. pahangi* the presence of interrupted striation of the posterior dorsum. It differs by the greater relative length of the anterior dorsal setae (compared to the perianal setae).

Material examined: None.

Literature records: on *Pelomys fallax* (Peters, 1852) (Rodentia: Muridae) from ZAIRE: KIVU, Bukavu (Lawrence, 1960 [Type series]).

Notoedres (*Notoedres*) *galagoensis* Fain, 1963

Notoedres galagoensis Fain, 1963e: 109.

The female differs from that of *N. pahangi* by the presence of (widely spaced) striations in the area anterior to the anus. Setae *h 1* are twice the length of setae *h 2* (subequal in *N. pahangi*). Both immatures and female have been described (Fain, 1963e). All specimens were recovered from a cyst on the ear pinnae of a galago (Fain, 1963e).

Material examined: None.

Literature records: on *Galago demidovii* (Fischer, 1806) (Primates: Galagidae) from ZAIRE (Fain, 1963e [Type series]).

The exact affinities of *N. indicus* within *Notoedres* are unclear, due to the large amount of missing data for this species. Based on the analysis including all species of *Notoedres* (Fig. 56), it is classified as *incertae sedis* within *Notoedres* (*s.s.*).

Notoedres (*Notoedres*) *indicus* (Fain & Lukoschus, 1976)
new combination

Suncicoptes indicus Fain & Lukoschus, 1976: 1.

Diagnosed in all stages by the loss of setae *4 a* (130); in the female by the presence of a large non-striated area on the dorsum (58), parallel, not fused, coxal apodemes I (139), and the absence of setae *c 1* and four pairs of perianal setae.

Described as the type species of a new genus, *Suncicoptes* Fain & Lukoschus, 1976, this species shares the derived characters of some but not all *Notoedres*. Recognition of *Suncicoptes* would make *Notoedres* paraphyletic and is rejected. The species is known only from the female. All specimens were collected from small lesions near the base of the tail (Fain & Lukoschus, 1976).

Material examined: None.

Literature records: on *Suncus murinus* (Linnaeus, 1766) (Insectivora: Soricidae) from INDIA: MAHARASHTRA, Bombay (Fain & Lukoschus, 1976 [Type series]).

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APPENDIX 1. KEYS TO THE GENERA AND SPECIES

The identification of specimens in a collection of Sarcoptidae can be a problem since up to seven different species of Sarcoptidae may occur on a single host specimen. This phenomenon is most common among the bat associated species, but it also occurs on hosts other than bats (e.g. rodents, hedgehogs). It is therefore recommended to examine each specimen individually. In addition, the different life stages in some Sarcoptidae may have distinctly different morphologies (e.g. many Teinocoptinae). In order to encompass this variation, separate keys for each life stage are presented for some genera. The life stages of most species can be identified using the following key.

1. Three pairs of legs .... larva
Four pairs of legs 2

2. Setae *3 a, 4 a, f 2, h 3*, and the *ps* and trochanteral setae absent; solenidia ω-3 I absent .... protonymph
Any or all of these structures present 3

3. Genital structures absent .... tritonymph
Genital structures present .... adults 4

4. Oviporus present anterior to coxae III; bursa copulatrix present, terminating in a copulatory cone (Fig. 59, cc) situated near the anus .... female
Aedeagus present, usually posterior to coxae IV .... male

Some of the characters used in the above key are not valid for all taxa, due to the extensive ontogenetic changes occurring in some derived genera (e.g. legs IV are absent in the nymphs and females of many taxa in the *Teinocoptes* group), and additional comments regarding the identification of life stages are listed with the individual keys. Host and locality information may aid in the identification of some species and notes on host associations are therefore included. In keys that consist of several partial keys, host associations are listed in the key to the females only.

KEY 1. GENERA AND SPECIES IN THE SMALLER GENERA

Based on the morphology of the adults. Characters specific for the immatures are included when available. The males of *Satanicoptes armatus, Rousettocoptes mammophilus* and *Tychosarcoptes amphipterinon*, and the female of *Tychosarcoptes orphanus*, have not been described. Immatures have not been described for several of the species included in this key.

1. Dorsal shields absent in all stages; tarsus I with 0–1 spine-like setae (Figs. 6, 7); all segments of the posterior legs free. Associated with Dasyuridae (Marsupialia) .... Diabolicoptinae 2
Dorsal shields usually present in the male, sometimes also in the immatures and female; tarsus I with at least 2 spine-like setae (Figs. 8–13); tibia and tarsus of legs III in the immatures and female fused 4

2. Coxal apodemes I parallel but not fused together; bifurcate hooks or spines on trochanter II absent .... *Diabolicoptes sarcophilus*
Coxal apodemes I fused together to form a sternum; with a bifurcate hook or spine on trochanter II ..... *Satanicoptes* 3

3. Setae *ps 1* and *ps 2* present in the female; bifurcate hooks on femora I–II absent .... *Satanicoptes phascogale*
Setae *ps 1* and *ps 2* never added; bifurcate hooks on femora I–II present .... *Satanicoptes armatus*

4. Tarsi I–II with 2 spine-like setae (Figs. 8, 9); tibia and tarsus IV in the male fused. Associated with a variety of non-volant mammals .... Sarcoptinae 5
Tarsi I–II with 3–4 spine-like setae (Figs. 10–13); tibia and tarsus IV in the male may or may not be fused. Primarily associated with Chiroptera, secondarily with other orders .... Teinocoptinae 12

5. Setae *sci, c 1*, and *c 2* long (> 20 μm) and filiform in the adults (filiform or spine-like rods in the immatures); setae *g* added in the protonymph. Associated with Rodentia . . *Trixacarus* 6

Setae *sci, c 1,* and *c 2* much shorter and broad in all stages; setae *g* never added. Primarily associated with Primates, secondarily with other orders 8

6. Setae *sci, c 1,* and *c 2* layered (Fig. 59); setae *e 2* and *f 2* present in the nymphs and adults. Associated with Muridae .... *Trixacarus eliurus*
Setae *sci, c 1,* and *c 2* simple, not layered (Fig. 66); setae *e 2* and *f 2* never added 7

7. Dorsal spines in the adults short, broad; no spines lateral to the anus in the female; anal shields in the male fused to the posterior median shield. Associated with Muridae .... *Trixacarus diversus*
Dorsal spines in the adults elongated; spines present lateral to the anus in the female; anal shields in the male not fused to the posterior median shield. Associated with Caviidae .... *Trixacarus caviae*

8. Anterior median shield in the immatures and female absent; median apodeme in the male not fused to the apodemes of the genital area (see discussion characters 151–153). Associated with Cebidae .... *Kutzerocoptes grunbergi*
Anterior median shield in the immatures and female present; median apodeme in the male fused to the apodemes of the genital area 9

9. Posterior ventral tubercles in the female poorly developed (see discussion characters 47, 48); anal shields in the male not fused to the posterior median shield; posterior lateral shields in the male present. Primarily associated with Hominoidea and domesticated animals .... *Sarcoptes scabiei*
Posterior ventral tubercles in the female well developed; anal shields in the male fused to the posterior median shield; posterior lateral shields in the male absent. Associated with Cercopithecidae .... *Prosarcoptes* 10

10. Ambulacra of legs III–IV absent .... *Prosarcoptes talapoini*
Ambulacra of legs III–IV present in the tritonymph and adults 11

11. Setae *3 a* added in the tritonymph and female .... *Prosarcoptes pitheci*
Setae *3 a* not added in the tritonymph and female .... *Prosarcoptes scanloni*

12. Anterior median shield in the immatures and female present; setae *sci, c 1,* and *c 2* short, broad spines; trochanteral setae *pR* I–II consisting of a filiform part projecting from a bulbous base. Associated with Mystacinidae .... *Chirophagoides mystacopis*
Anterior median shield in the immatures and female absent; setae *sci, c 1,* and *c 2* small, thin spines, spine-like rods or filiform; trochanteral setae *pR* I–II, if present, filiform or spine-like, simple.................................. 13

13. Ambulacral disc of legs I–II of the female absent; setae *3 a* and *g* added, at least in the male; eggs never anchored by stalks. Primarily associated with Pteropodidae 14
Ambulacral disc of legs I–II of the female present; setae *3 a* and *g* never added; eggs usually anchored by stalks. Never associated with Pteropodidae............................ 20

14. Anus of ovigerous females projecting on a dorsal "tube" (Fig. 3); coxal apodemes III of the larva without an anterolateral projection; ambulacra present on legs III–IV of the female tritonymph and male .... *Nycteridocoptes* (key 2)
Body of the ovigerous females differently shaped; coxal apodemes III of the larva with an anterolateral projection (Fig. 2); ambulacra on legs III–IV absent in all stages 15

15. Setae *f 2* and *h 3* added in the protonymph; legs IV with 4 well developed segments. Associated with cynopterine Pteropodidae .... *Cynopterocoptes heaneyi*
Setae *f 2* and *h 3* never added; legs IV in the immatures and females reduced to 1–2 segments (Figs. 164, 175)....... 16

16. Setae *c 1* in the nymphs and female short but distinct; height of the body in the nymphs and female less than the width; with a large internal spur on trochanter III of the female (Fig. 159). Associated with *Rousettus* and *Eonycteris* .... *Rousettocoptes mammophilus*
Setae *c 1* in the nymphs and female minute (< 5 μm); height of the body in the nymphs and female usually exceeding the width; internal spur on trochanter III absent........... 17

17. Most posterior spine in the lateral spine group of the female very large (> 10 μm) (Figs. 167, 169); median ventral outgrowths in the male absent (see discussion of characters 53–55).................................. *Tychosarcoptes* 18
Posterior spine in the lateral spine group of the female small; median ventral outgrowths in the male present (Figs. 191, 210, 219).. 19

18. Scales present lateral to the anus of the female; legs IV in the female present; coxal apodemes III and IV in the male not fused to each other. Associated with *Ptenochirus* .... *Tychosarcoptes ptenochirus*
Scales absent lateral to the anus of the female; legs IV in the female absent. Associated with *Cynopterus* .... *Tychosarcoptes amphipterinon*
Coxal apodemes III and IV in the male fused to each other. Host unknown .... *Tychosarcoptes orphanus*

19. Coxal apodemes II in the immatures and female elongated, with an anterolateral projection (Fig. 189); legs IV in the female absent; coxal apodemes III and IV in the male never fused .... *Chirobia* (key 3)
Coxal apodemes II in the immatures and female not present; coxal apodemes III and IV in the male usually fused............................... *Teinocoptes* (key 4)

20. Setae *ps 1* and *ps 2* present in the adults; aedeagus of the male elongate. Associated with Noctilionidae and Phyllostomidae............................... *Chirnyssoides* (key 5)
Setae *ps 1* and *ps 2* never added; aedeagus of the male short. Primarily associated with Vespertilionidae and Molossidae, one lineage on hosts other than bats ...... *Notoedres* (key 6)

Key 2. *Nycteridocoptes*

The life stages in this genus have distinctly different morphologies, but can be identified using the general key to the stages. One addition concerns sexual dimorphism in the tritonymphal stage. The female tritonymph is characterized by well developed ambulacra on legs III–IV and often by spines on the dorsum. These structures are absent in most male tritonymphs (present in the male tritonymph of *N. heidemanni*). Development in *N. cynopteri* is unusual since neither legs IV nor any setae are added during ontogeny. Differentiation of the immatures of this species is extremely difficult (see species discussion), but this may not be a problem since these stages are rarely collected outside of the cyst containing a female. Most species in this genus are associated with bats in the family Pteropodidae, but a few species are associated with other families of bats (Vespertilionidae, Rhinolophidae).

2a. Female

1\. Legs IV absent. Associated with *Cynopterus* and *Ptenochirus* .... *cynopteri*
Legs IV present 2

2\. Small spines present in the zone between setae *d 1* and the anus (Fig. 93) 3
Small spines absent in that zone (Fig. 124) 6

3\. Small spines restricted to a zone anterior to the anus; spines may be transformed to scales 4
Small spines present in a continuous transverse band between setae *sci* and *c 1* 5

4\. Associated with a variety of Pteropodidae; restricted to Australasia .... *microphallus*
Associated with *Rousettus;* restricted to Africa .... *rousetti*

5\. Small spines present in the zone lateral to the anus. Associated with *Aethalops* .... *malayi*
Small spines absent in that zone. Associated with *Cynopterus, Haplonycteris,* and *Ptenochirus* .... *heidemanni*

6\. Small spines present in an isolated ventrolateral patch (see discussion of characters 44, 45; Figs. 131, 132, 136, 137) 7
Isolated ventrolateral patch of spines absent 11

7\. Small spines in the ventrolateral patch arranged linearly. Associated with *Pteropus* .... *orientalis*
Ventrolateral spine patch more or less oval. Associated with Microchiroptera 8

8\. Ventrolateral spine patch roughly oval (Figs. 136, 137). Associated with Rhinolophidae 9
Ventrolateral spine patch oval with a distinct notch (Figs. 131, 132). Associated with Vespertilionidae 10

9\. Associated with *Rhinolophus* .... *eyndhoveni*
Associated with *Triaenops* .... *hoogstraali*

10\. Associated with *Miniopterus* .... *miniopteri*
Associated with *Myotis, Vespertilio, Eptesicus, Plecotus* ...... *poppei*

11\. Small spines absent in the zone between setae *c 1* and the anus. Associated with *Notopteris* .... *notopteris*
Small spines present in that zone 12

12\. Setae *cp* and *c 3* short (< 15 μm); dorsal spines in the area near the anus poorly developed (Fig. 124). Associated with *Rousettus* and *Eonycteris* .... *macrophallus*
Setae *cp* and *c 3* longer (> 20 μm); all dorsal spines well developed (Fig. 122) 13

13\. Perianal setae unequal in size. Associated with *Eidolon*... *pteropi*
Perianal setae subequal in size. Primarily associated with *Rousettus* and *Eonycteris* 14

14\. Spine zone lateral to the anus small, not extending posteriorly beyond the anus; setae *sce* long (25 μm). Restricted to Australasia .... *asiaticus*
Spine zone lateral to the anus larger, extending beyond the anus; setae *sce* short (11–12 μm). Restricted to Africa .... *lavoipierrei*

2b. Male

The male of *malayi* has not been described.

1\. Legs IV absent .... *cynopteri*
Legs IV present 2

2\. Ambulacra of the posterior legs similar to those of the anterior legs 3
Ambulacra of legs IV modified, with a short stalk and unguinal sclerites in the disc (Fig. 26) 4

3\. Setae *3 a* and *g* spine-like .... *heidemanni*
Setae *3 a* and *g* filiform .... *orientalis*

4\. Solenidia σ I thick, spine-like (Fig. 11) 5
Solenidia σ I thin, rod-shaped (Fig. 106) 9

5\. Setae *3 a* and *g* spine-like .... *pteropi*
Setae *3 a* and *g* filiform 6

6\. Setae *cp* short (16 μm) .... *notopteris*
Setae *cp* long (> 30 μm) 7

7\. Aedeagus elongated (50–60 μm) .... *macrophallus*
Aedeagus shorter (< 30 μm) 8

8\. Posterior median shield with a lateral notch .... *asiaticus*
Posterior median shield without a lateral notch ..... *lavoipierrei*

9\. Setae *cp* short (14–19 μm) 10
Setae *cp* long 11

10\. Posterior median shield with a lateral notch .... *microphallus*
Posterior median shield without a lateral notch .... *rousetti*

11\. Setae *h 2* and *ps 2* long, thin spines (14 μm) .... *eyndhoveni, hoogstraali*
Setae *h 2* and *ps 2* short, thin spines (7–10 μm) 12

12\. Setae *c 1* elongate (2 X setae *c 2*) .... *poppei*
Setae *c 1* short .... *miniopteri*

2c. Female tritonymph

The female tritonymphs of *malayi, lavoipierrei,* and *hoogstraali* have not been described.

1\. Legs IV absent .... *cynopteri*
Legs IV present 2

2\. Ambulacra of the posterior legs similar to those of the anterior legs 3
Ambulacra of legs III–IV modified, with a short stalk and unguinal sclerites (Figs. 26, 117) 4

3\. Setae *3 a* and *g* spine-like .... *heidemanni*
Setae *3 a* and *g* filiform .... *orientalis*

4. Setae *g* spine-like 5
   Setae *g* filiform 7

5. Setae *3 a* filiform .... *notopteris*
   Setae *3 a* spine-like 6

6. Setae *cp* long; spines present on the dorsum .... *pteropi*
   Setae *cp* short; no spines on the dorsum ... *microphallus, rousetti*

7. Ambulacra of legs III–IV very small (diameter of the disc 6–8 μm), smaller than the ambulacra of the anterior legs .... *miniopteri*
   Ambulacra of legs III–IV well developed, subequal in size or larger than those of the anterior legs 8

8. Spines absent from the area anterior to setae *c 1* .... *eyndhoveni*
   Spines present in that zone ...... *macrophallus, asiaticus, poppei*

2d. Protonymph and male tritonymph

The protonymph of *malayi*, and the male tritonymph of *malayi* and *pteropi* have not been described.

1. Legs IV absent .... *cynopteri*
   Legs IV present 2

2. Setae *sci* thin spine-like rods with bifurcate tips 3
   Setae *sci* small, thin spines, or filiform 6

3. Setae *f 2* present in the protonymph, well developed in the male tritonymph 4
   Setae *f 2* absent in the protonymph, minute in the male tritonymph 5

4. Setae *h 3* present in the protonymph .... *pteropi*
   Setae *h 3* absent in the protonymph .... *asiaticus, lavoipierrei*

5. Setae *3 a, g,* and *4 a* absent .... *orientalis*
   Setae *3 a, g,* and *4 a* vestigial or minute .... *macrophallus*

6. Ambulacra present on legs III–IV of the male tritonymph; setae *cp* long .... *heidemanni*
   Ambulacra on legs III–IV of the male tritonymph absent; setae *cp* short, minute or absent 7

7. Setae *f 2* vestigial or absent in both stages 8
   Setae *f 2* present in both stages 9

8. Setae *ps 2* minute in both stages .... *miniopteri*
   Setae *ps 2* subequal to the other perianal setae, well developed .... *microphallus, rousetti*

9. Setae *h 3* minute, vestigial, or absent in both stages 10
   Setae *h 3* well developed in both stages 11

10. Setae *c 3* minute in the protonymph .... *notopteris*
    Setae *c 3* well developed .... *eyndhoveni*

11. Setae *cp* absent in the protonymph, minute or vestigial in the male tritonymph .... *poppei*
    Setae *cp* minute but distinct in both stages .... *hoogstraali*

2e. Larva

The larva of *pteropi* has not been described.

1. Setae *cp* well developed, long .... *heidemanni*
   Setae *cp* minute, vestigial, or absent 2

2. Setae *sci* strongly elongate (length > 4 X width) 3
   Setae *sci* shorter 4

3. Setae *h 1* minute, much smaller than the other perianal setae .... *orientalis*
   All perianal setae subequal in length .... *malayi*

4. Setae *d 2* and *e 2* minute .... *miniopteri*
   All perianal setae well developed .... *cynopteri, microphallus, rousetti, notopteris, asiaticus, lavoipierrei, macrophallus, poppei, eyndhoveni, hoogstraali*

KEY 3. *CHIROBIA*

The posterior legs of the nymphs and females of *Chirobia* and *Teinocoptes* (Key 4) are strongly regressed. Legs IV in particular are extremely small (most *Teinocoptes*) or never added (female *Chirobia*). Setae *3 a, f 2,* and *h 3* are never added and all leg structures are extremely small and difficult to observe. Nymphs and females can be differentiated most easily from larvae by the addition of a fourth pair of perianal setae (setae *ps 1*). Females can be identified by the presence near the anus of the bursa copulatrix and a well developed copulatory cone (Figs. 188, 207). All species in this genus are associated with Pteropodidae (Chiroptera).

3a. Female

1. Setae *d 1* and *d 2* filiform 2
   Setae *d 1* and *d 2* spine-like rods 6

2. Scales in the zone posterior to the anus 3
   Scales absent in that zone 5

3. Setae *d 2* longer than setae *d 1;* setae *d* III distinct. Associated with *Haplonycteris fischeri* .... *haplonycteris*
   Setae *d 2* shorter than setae *d 1;* setae *d* III minute or absent . 4

4. Setae *d 1* on average 30 μm, setae *d 2* 15 μm, perianal setae 36–38 μm. Associated with *Ptenochirus jagori* .... *jagori*
   Setae *d 1* 18 μm, setae *d 2* 8 μm, perianal setae 28–31 μm. Associated with *Ptenochirus minor* .... *minor*

5. Perianal and *d* setae long (respectively 30–32 and 45 μm). Associated with *Thoopterus* .... *thoopterus*
   Perianal and *d* setae shorter (23–24 and 35 μm). Associated with *Chironax* and *Rousettus celebensis* .... *brevior*

6. Height of the body exceeding the width; scales present posterior to the anus. Associated with *Cynopterus* .... *cynopteri*
   Height of the body not exceeding the width; development of the scales variable 7

7. Scales posterior to the anus 8
   Scales posterior to the anus absent 9

8. Setae *d 2* shorter than setae *d 1;* in the nymphs scales posterior to the anus. Associated with *Rousettus angolensis* ... *angolensis*
   Setae *d 1* and *d 2* subequal in length; no scales posterior to the anus in the nymphs. Associated with *Eonycteris* .... *eonycteris*

9. Scales lateral to the anus. Associated with *Rousettus amplexicaudatus* .... *rousettus*
   Scales lateral to the anus absent 10

10\. Scales in the zone between setae *c 1* and *d 1*. Associated with *Rousettus lanosus* and *R. madagascariensis* .... *squamata*
No scales in that zone.................................. 11

11\. Scales in the zone directly anterior to the anus. Associated with *Epomophorus* and *Hypsignathus*.................... *otophaga*
No scales in that zone. Associated with *Rousettus aegyptiacus* and *R. leschenaulti*................................ *congolensis*

3b. Male

The male of *angolensis* has not been described.

1\. Genu and femur IV fused...... *congolensis, eonycteris, otophaga, rousettus, squamata*
Genu and femur IV not fused............................ 2

2\. Genital area rounded or oval, small (29–36 μm long)................................. *thoopterus, brevior*
Genital area elongate, larger (44–48 μm long).............. 3

3\. With a translucent flap covering the anterior portion of the sternum (Figs. 191, 202); lateral shields present... *cynopteri, jagori, minor*
Translucent flap absent; lateral shields very poorly developed or absent.................................. *haplonycteris*

3c. Larva

1\. Pointed scales present (Fig. 185).......................... 2
Pointed scales absent..................................... 5

2\. No scales posterior to the anus....................... *brevior*
Scales posterior to the anus present....................... 3

3\. No spine-like structures between setae *c 1*........... *cynopteri*
Spine-like structures in that zone present (Fig. 185)......... 4

4\. Total of 5–10 spine-like structures between setae *c 1* .... *jagori*
Total of 15–20 spine-like structures between setae *c 1* ... *minor*

5\. Scales posterior to the anus .... *haplonycteris*
Scales posterior to the anus absent 6

6\. Scales extending to the anus.............................. 7
Scales restricted to two separate patches near setae *c 1*....... 8

7\. Scales near the anus small, dense, and well delimited. *thoopterus*
Scales near the anus large, poorly defined, and merging into striations..................... *eonycteris, rousettus, squamata*

8\. Setae *e 2* subequal to the *d* setae................... *congolensis*
Setae *e 2* much smaller than the *d* setae.................... 9

9\. Patches of scales near setae *c 1* each with only 5–10 scales... *otophaga*
Patches of scales each with over 20 scales .... *angolensis*

KEY 4. *TEINOCOPTES*

Nymphs and females of this genus can be differentiated using the characters given for *Chirobia* (Key 3). In general, the morphology of the nymphs resembles that of the females. Differences are usually expressed in the extent of the area covered with scales (smaller in the nymphs) and the morphology of the dorsal setae (never membranous and often spine-like instead of filiform in the nymphs). All species in this genus are associated with Pteropodidae (Chiroptera).

4a. Female

1\. Scales absent... 2
Scales present.. 6

2\. Height of the body over twice the width. Associated with *Eidolon*.. *eidoloni*
Height/width ratio less than two.......................... 3

3\. Perianal setae membranous and trilobed. Associated with *Pteropus* and *Acerodon*.............................. *domrowi*
Perianal setae not membranous or trilobed................. 4

4\. Height of the body not exceeding the width; lateral spine series absent. Associated with *Harpyionycteris* .... *harpyionycteris*
Height of the body exceeding the width; lateral spine series present (see Figs. 167, 169)........................... 5

5\. Width of the perianal setae < 3.5 μm; body height about 400 μm. Associated with epomophorine Pteropodidae .... *auricularis*
Width of the perianal setae 5–6 μm; body height about 480 μm. Associated with *Rousettus angolensis*.......... *ituriensis*

6\. Scales restricted to separate patches...................... 7
Scales in a continuous transverse band between setae *sci* and *c 1*... 13

7\. Well developed sclerotized zone present posterior to the genital area (Fig. 215)..................................... 8
Postvulvar sclerotization absent.......................... 12

8\. Perianal setae membranous................................ 9
Perianal setae filiform or spine-like, not membranous...... 10

9\. Verrucous zone anterolateral to legs III (Fig. 208); scales not pointed. Associated with *Rousettus* and *Eonycteris*... *eonycteris*
Verrucous zone absent; scales spine-like. Associated with *Dobsonia* .... *strandtmanni*

10\. Setae *d 2* distinctly longer than setae *d 1; d* setae with rounded tips. Associated with *Notopteris*.................... *haymani*
Setae *d 1* and *d 2* subequal in length, filiform.............. 11

11\. Perianal setae very small (3–6 μm). Associated with *Nyctimene* .... *aingworthi*
Perianal setae long (62–65 μm), filiform. Associated with *Harpyionycteris*............................. *philippinensis*

12\. All four pairs of perianal setae arranged linearly; scaled area narrow near the midline of the body. Associated with *Dobsonia*....................................... *katherinae*
Only three pairs of perianal setae arranged linearly; scaled area broad near the midline. Associated with *Dobsonia*.... *wilsoni*

13\. Scales covering the anterior dorsum from setae *c 1* to the anus.. 14
No scales in the area directly anterior to the anus.......... 15

14\. Scales lateral to the anus; height of the body less than twice the width. Associated with *Thoopterus*................ *johnsoni*
No scales lateral to the anus; height of the body over twice the width. Associated with *Cynopterus* and *Ptenochirus*... *asiaticus*

15. Well developed sclerotized zone posterior to the genital area present..16
    Postvulvar sclerotization absent..........................18

16. Verrucous zone anterolateral to legs III. Associated with *Eonycteris* and *Macroglossus*.......................... *malayi*
    Verrucous zone absent..................................17

17. Lateral spines arranged linearly. Associated with *Rousettus* and *Eonycteris* .... *pahangensis*
    Lateral spines arranged in a field. Associated with epomophorine Pteropodidae............................ *epomophori*

18. Distance between setae *d 1* and *d 2* distinctly exceeding the distance between setae *d 2* and *e 2*. Associated with *Rousettus amplexicaudatus*.............................. *vandeuseni*
    Distance between setae *d 1* and *d 2* subequal to or less than the distance between setae *d 2* and *e 2*....................19

19. Perianal setae thick (6 μm). Associated with *Rousettus aegyptiacus*... *rousetti*
    Perianal setae thinner (4 μm). Associated with *Rousettus madagascariensis*.................................. *astridae*

4b. Male

The males of *pahangensis, asiaticus, rousetti, katherinae, wilsoni, aingworthi, johnsoni, haymani, eidoloni, domrowi,* and *ituriensis* have not been described.

1. Median ventral outgrowths pointed (Fig. 210)..............2
   Median ventral outgrowths blunt (Fig. 217)................7

2. Median ventral outgrowths elongate (Fig. 219).............3
   Median ventral outgrowths short..........................5

3. A single pair of relatively large spines present on the propodosoma (Fig. 218); genu and femur IV fused... *eonycteris*
   A number of small spines present on the propodosoma; genu and femur IV not fused..............................4

4. Numerous small spines between the anterior and posterior median shields; very large (404–465 μm)....... *harpyionycteris*
   Spines between the anterior and posterior median shields absent; small (223 μm).......................... *auricularis*

5. Small spines present between the anterior and posterior median shields.................................... *strandtmanni*
   Small spines absent.....................................6

6. Large body size (346 μm); setae *3 a* relatively short (8 μm).................................... *epomophori*
   Smaller (145–227 μm); setae *3 a* longer (11–15 μm)......................... *vandeuseni, astridae*

7. Setae *sci* longer than setae *sce*........................ *malayi*
   Setae *sci* shorter than setae *sce*.................. *philippinensis*

4c. Larva

The larva of *ituriensis* has not been described.

1. Dorsum without spines..................................2
   Dorsum with spines.....................................3

2. Dorsum with a scaly aspect........................ *domrowi*
   Dorsum striate................ *malayi, philippinensis, aingworthi*

3. At least 20 scales present near setae *c 1*............ *epomophori*
   Only a few scales present, or scales absent.... *asiaticus, astridae, auricularis, eidoloni, eonycteris, harpyionycteris, haymani, katherinae, pahangensis, rousetti, strandtmanni, vandeuseni, wilsoni*

KEY 5. *CHIRNYSSOIDES*

The life stages can be identified using the general key to the stages. Problems may occur since setae *3 a, g, f 2,* and *h 3* are never added, and the ontogenetic addition patterns of setae *4 a, h,* and *ps,* as well as setae *sR* III are variable within the genus. Moreover, the bursa copulatrix may be present in the nymphal stages (Fain, 1959h). The presence/absence of the trochanteral setae of the anterior legs should be used to identify tritonymphs.

5a. Female (adapted from Fain & Lukoschus, 1975)

1. Setae *sci* long (> 20 μm); the anterior tine of the basal branch of each coxal apodeme III curved backward to fuse to the main branch. Associated with Noctilionidae; subgenus *Noctiliocoptes*.................................... *noctilionis*
   Setae *sci* short or minute (< 10 μm); basal branch of each coxal apodeme III ending free. Associated with Phyllostomidae; subgenus *Chirnyssoides*...............................2

2. Setae *ps 1* and *ps 2* absent; setae *h 1* and *h 2* ovoid, all other perianal setae filiform. Associated with *Carollia* and *Glossophaga*.................................... *surinamensis*
   Setae *ps 1* and *ps 2* present; all perianal setae similar in shape...3

3. Height of the body over twice the width; setae *4 a* present...4
   Height of the body less than twice the width; setae *4 a* absent...5

4. Basal branch of each coxal apodeme III bifurcate (Fig. 5). Associated with *Carollia* and *Glossophaga*.............. *amazonae*
   Basal branch of each coxal apodeme III not bifurcate. Associated with a variety of Stenodermatini.............. *caparti*

5. Setae *c 1* spine-like rods (27–30 μm)......................6
   Setae *c 1* filiform, short (< 8 μm)........................7

6. Setae *sci* and *c 2* minute (< 5 μm). Associated with *Phyllostomus* and *Tonatia*............................... *phyllostomus*
   Setae *sci* and *c 2* well developed (9–10 μm). Associated with *Tonatia*..................................... *venezuelae*

7. Basal branch of each coxal apodeme III bifurcate (Fig. 5)....8
   Basal branch of each coxal apodeme III not bifurcate.......9

8. Distal end of each coxal apodeme IV bifurcate (Fig. 5). Associated with *Micronycteris*......................... *parvisuctus*
   Distal end of each coxal apodeme IV simple. Associated with *Stenoderma*................................. *stenoderma*

9. Perianal setae spatulate. Associated with *Vampyrops* and *Uroderma*....................................... *vampyrops*
   Perianal setae attenuate. Associated with *Sturnira* (and *Phylloderma*).. *brasiliensis*

5b. Male (adapted from Fain & Lukoschus, 1975)

The males of *parvisuctus* and *vampyrops* have not been described. The male of *stenoderma* has been described from a very poorly sclerotized specimen and is not included in this key.

1. Anterior lateral shields absent; setae *sce* short and filiform.. *noctilionis*
   Anterior lateral shields present; setae *sce* well developed spine-like rods.. 2

2. Setae *cp* long (25–30 μm), spine-like rods.................. 3
   Setae *cp* shorter (about 6 μm), filiform..................... 4

3. Aedeagus long (75 μm) and narrow (6–7 μm) .... *caparti*
   Aedeagus shorter (50 μm) and wider (10 μm)....... *brasiliensis*

4. Setae *ps 1* and *ps 2* absent .... *surinamensis*
   Setae *ps 1* and *ps 2* present.............................. 5

5. Setae *r* IV spines; aedeagus medially inflated and with very broad posterior arms .... *amazonae*
   Setae *r* IV filiform; aedeagus parallel-sided and with smaller posterior arms 6

6. Aedeagus relatively short (about 40 μm)........... *venezuelae*
   Aedeagus longer (45–50 μm).................... *phyllostomus*

5c. Immatures

The larva of *brasiliensis* and the protonymph of *stenoderma* have not been described.

1. Height of the body exceeding the width .... *noctilionis*
   Height of the body less than the width..................... 2

2. Basal branch of each coxal apodeme III bifurcate (Fig. 5).... 3
   Basal branch of each coxal apodeme III not bifurcate 6

3. Posterior perianal setae in the nymphs with an inflated base; setae *ps 1* and *ps 2* present in the protonymph .... *amazonae*
   Posterior perianal setae in the nymphs simple rods or filiform; setae *ps 1* and *ps 2* absent in the protonymph 4

4. Setae *h 1* and *h 2* present in the larva; setae *h 2* ovoid .... *surinamensis*
   Setae *h 1* and *h 2* absent in the larva; setae *h 2* simple rods or filiform 5

5. Setae *ps 1* and *ps 2* present in the tritonymph....... *parvisuctus*
   Setae *ps 1* and *ps 2* absent in the tritonymph........ *stenoderma*

6. Setae *h 1* and *h 2* present in the larva; setae *ps 1* and *ps 2* present in the nymphs 7
   Setae *h 1* and *h 2* absent in the larva; setae *ps 1* and *ps 2* absent in the nymphs 8

7. All perianal setae spatulate apically .... *vampyrops*
   Perianal setae attenuate apically; posterior perianal setae in the nymphs basally inflated.......................... *caparti*

8. Setae *h 2* present in the tritonymph................ *brasiliensis*
   Setae *h 2* absent in the tritonymph...... *venezuelae, phyllostomus*

KEY 6. *NOTOEDRES*

The life stages can be differentiated using the general key to the stages. Setae *3 a, g, f 2, h 3,* and the *ps* setae are never added, and the addition of setae *h 2* is delayed to the protonymph. The trochanteral setae are always added in the tritonymph. The nymphs generally resemble the female in morphology. However, distinctly different morphologies of the nymphs are found among several species associated with Molossidae. The majority of the species in this genus are associated with Chiroptera. The remaining species are associated with Rodentia, Insectivora, Primates, Carnivora, and Lagomorpha.

6a. Females

The female of *verheyeni* has not been described.

1. Setae *d 1, e 1,* and *h 1* spine-like with a thickened, rounded tip; setae *4 a* absent 2
   Setae *d 1, e 1,* and *h 1* spine-like or filiform, never with a thickened tip; setae *4 a* usually present...................... 6

2. Setae *e 1* short (4–6 μm for the female). Associated with *Molossus* (Molossidae) .... *anisothrix*
   Setae *e 1* long (14–43 μm)................................ 3

3. Setae *h 2* never added.................................... 4
   Setae *h 2* added 5

4. Setae *sci* elongate (27–31 μm for the female). Associated with *Eptesicus* (Vespertilionidae) .... *eptesicus*
   Setae *sci* short (6–9 μm). Associated with *Myotis* (Vespertilionidae).................................... *americanus*

5. Setae *sce* in the female minute (2–3 μm); setae *h 2* not added until the adult stages. Associated with *Plecotus* (Vespertilionidae).................................... *corynorhini*
   Setae *sce* in the female longer (5–8 μm); setae *h 2* present in the nymphs. Associated with Vespertilionidae and Molossidae.. *lasionycteris*

6. Base of palpal setae α *l* inflated (Figs. 235, 253); setae *sR* III spines.. 7
   Base of setae α *l* not inflated; setae *sR* III filiform.......... 12

7. Setae *sci, c 1,* and *c 2* minute (< 5 μm) (Fig. 234). Associated with *Miniopterus* (Vespertilionidae) .... *philippinensis*
   Setae *sci, c 1,* and *c 2* well developed spines................. 8

8. Perianal setae (with the exception of setae *e 2*) long (36–39 μm). Associated with *Miniopterus*................ *miniopteri*
   Perianal setae shorter (24–34 μm). Associated with *Myotis*.... 9

9. Setae *sci, c 1,* and *c 2* relatively long (11–18 μm) 10
   Setae *sci, c 1,* and *c 2* shorter (5–9 μm).................... 11

10. Palpal setae α *l* wide (4.0 μm) .... *nigricans*
    Palpal setae α *l* less wide (2.6 μm).................. *myoticola*

11. Setae *e 2* about 1/4 the length of the other perianal setae (7 vs. 26–39 μm)...................................... *myotis*
    Setae *e 2* 1/3 to 1/2 the length of the other perianal setae (11 vs. 24–28 μm)...................................... *roesleri*

12. Setae *c 1* minute (< 5 μm) and setae *sci* elongate (> 15 μm); dorsum completely striate........................... 13

Setae *c 1* well developed and/or setae *sci* short; dorsum with or without bare areas 16

13. Height of the body in the nymphs and female exceeding the width. Associated with *Eptesicus* and related genera (Vespertilionidae) 14
Height of the body not exceeding the width 15

14. Setae *e 1* 2–3 times as long as setae *e 2* .... *chiropteralis*
Setae *e 1* subequal in length to setae *e 2* .... *schoutedeni*

15. Setae *sci, d 1,* and *e 1* filiform. Associated with *Mimetillus* (Vespertilionidae) .... *mimetilli*
Setae *sci, d 1,* and *e 1* spine-like. Associated with *Coleura* (Emballonuridae) .... *benoiti*

16. Distal end of the sternum bifurcate; height of the body exceeding the width; setae *4 a* not added. Associated with *Chaerophon* and *Mops* (Molossidae) 17
Distal end of the sternum not bifurcate; height of the body usually not exceeding the width; setae *4 a* usually added. 20

17. Setae *h 1* and *h 2* spine-like rods with bifurcate tips ..... *ismaili*
Setae *h 1* and *h 2* filiform 18

18. Setae *sci* and *c 1* spine-like with a lateral tooth, relatively thin near the base and tip but wider in the middle .... *ovatus*
Setae *sci* and *c 1* filiform to spine-like 19

19. Large (> 750 μm); setae *d 1, d 2, h 1,* and *h 2* subequal in length (23–29 μm) .... *tristis*
Much smaller (200–400 μm); setae *d 1* and *d 2* distinctly longer than setae *h 1* and *h 2* (37–39 vs. 25 μm) .... *dewitti*

20. Height of the body exceeding the width; setae *3 b* spines. Associated with *Pipistrellus* (Vespertilionidae) .... *coreanus*
Body usually rounded; setae *3 b* filiform 21

21. Dorsum completely or almost completely striated (e.g. Fig. 252) 22
At least 20% of the dorsum bare (e.g. Figs. 220, 234) 32

22. All perianal setae inserted close to the anus; coxal apodemes II with a sclerotized flange. Associated with *Cheiromeles* (Molossidae) 23
Arrangement of the perianal setae different; sclerotized flange absent 24

23. Body elongate; setae *d* III–IV long (275–325 μm) .... *elongatus*
Body more rounded; setae *d* III–IV short (132–140 μm) .... *rajamanickami*

24. Perianal setae spine-like rods, each with a bifurcate tip and a lateral tooth. Associated with *Molossus* (Molossidae) . . *yunkeri*
Perianal setae spine-like or filiform, never with a lateral tooth 25

25. Setae *d 1, e 1,* and *h 1* very long (> 40 μm) and setae *d 2, e 2,* and *h 2* short. Associated with *Molossops* (Molossidae) .... *helicothrix*
Pattern of setal lengths different 26

26. Dorsum with scale-like striations 27
Dorsum without scale-like striations 29

27. Setae *sci* and *c 1* elongate (> 20 μm). Associated with small Carnivora and domestic rabbits (Lagomorpha) .... *cati*
Setae *sci* and *c 1* short 28

28. Coxal apodemes I fused into a sternum; setae *4 a* present. Associated with Muridae (Rodentia) and Erinaceidae (Insectivora) .... *oudemansi*
Coxal apodemes I parallel, but not fused; setae *4 a* rarely added. Associated with Muridae .... *musculi*

29. Anterior dorsal setae long (23–28 μm), longer than the perianal setae. Associated with Sciuridae (Rodentia) .... *centrifera*
Anterior dorsal setae relatively short, not longer than the perianal setae 30

30. Perianal setae subequal in length to the anterior dorsal setae. Primarily associated with Muridae (secondary associations with Marsupialia and Insectivora) .... *muris*
Perianal setae at least twice the length of the anterior dorsal setae 31

31. Perianal setae long and stout (setae *d 1, d 2, h 1,* and *h 2* 23–27 μm). Associated with *Tadarida* (Molossidae) ..... *namibiensis*
Perianal setae shorter and more slender (setae *d 1, d 2, h 1,* and *h 2* 7–12 μm). Associated with *Chaerophon* and *Mops* (Molossidae) .... *tadaridae*

32. Dorsal striation of the female very dense (Fig. 220); height of the body exceeding the width 33
Striations widely spaced; height of the body not exceeding the width 34

33. Setae *d 1* and *e 1* subequal in length to setae *d 2* and *e 2;* setae *c 3* short (10 μm). Associated with *Plecotus* (Vespertilionidae) .... *plecoti*
Setae *d 1* and *e 1* longer than setae *d 2* and *e 2* (19 vs. 13 μm); setae *c 3* long (37 μm). Associated with *Myotis* (Vespertilionidae) .... *paraguayensis*

34. Setae *d 2* and *e 2* extending half the length of the other perianal setae; a narrow bare zone on the dorsum extending from setae *sci* to setae *h 1.* Associated with *Coleura* (Emballonuridae) .... *africanus*
Striation and/or setal pattern different 35

35. Setae *e 2* twice as long as the other perianal setae. Associated with *Cheiromeles* (Molossidae) .... *cheiromeles*
Setal pattern different 36

36. Large (410–490 μm); perianal setae long (28–43 μm), setae *h 2* very long (41–53 μm). Associated with *Cheiromeles* (Molossidae) .... *alexfaini*
Body smaller; perianal setae shorter (5–15 μm) 37

37. Setae *d 1, e 1,* and *4 a* absent; striation limited to the area anterior to setae *sce.* Associated with *Suncus* (Insectivora) .... *indicus*
Setae *d 1, e 1,* and *4 a* present; striation more extensive 38

38. Striations of the posterior dorsum interrupted. Associated with Muridae 39
Striations continuous 40

39. Anterior dorsal setae subequal in length to the posterior dorsal setae .... *paucipilis*

Anterior dorsal setae shorter than the posterior dorsal setae (6 vs. 8–10 μm) .... *pahangi*

40. Striations in the zone between setae *sci* and *e 2* very widely spaced, lateral striation dense; length of setae *h 1* exceeding that of all other perianal setae. Associated with *Galago* (Primates) .... *galagoensis*
Striation and setal pattern different. Associated with Muridae 41

41. Bare zone restricted to the posterior half of the dorsum; lateral striations dense .... *pseudomuris*
Bare zone encompassing most of the dorsum; lateral striations widely spaced .... *jamesoni*

6b. Male

The males of *plecoti, helicothrix, coreanus, anisothrix, myotis, roesleri, benoiti, cheiromeles, elongatus, rajamanickami, tadaridae, ismaili, ovatus, tristis, mimetilli, galagoensis, jamesoni, paucipilis, musculi*, and *indicus* have not been described. The descriptions of the males of *corynorhini* and *eptesicus* are incomplete.

1. Setae *c 3, 3 b*, and *sR* III spines or with a thickened base 2
Setae *c 3, 3 b*, and *sR* III filiform 6

2. Anterior lateral shields not fused to the anterior median shield; setae *c 3, 3 b*, and *sR* III with a thickened base and a filiform tip .... *africanus*
Anterior lateral shields fused to the anterior median shield; setae *c 3, 3 b*, and *sR* III spines, without a filiform tip (Figs. 243, 255) 3

3. Anal shields fused to the posterior median shield (Fig. 242); setae *4 a* filiform .... *philippinensis*
Anal shields not fused to the posterior median shield; setae *4 a* spines 4

4. Anal shields fused together .... *miniopteri*
Anal shields not fused together 5

5. Solenidia φ IV very long (25 μm) .... *verheyeni*
Solenidia φ IV shorter (5–10 μm), subequal to solenidia φ III .... *myoticola, nigricans*

6. Setae *4 a* absent .... *lasionycteris, corynorhini, eptesicus, americanus*
Setae *4 a* present 7

7. Anterior and posterior lateral shields absent 8
At least posterior lateral shields present 10

8. Tibia and tarsus IV not fused; posterior median shield well developed .... *chiropteralis, schoutedeni*
Tibia and tarsus IV fused; posterior median shield reduced, not encompassing the bases of setae *d 1* 9

9. All dorsal shields absent; ambulacrum of legs IV with a very short stalk (1–2 μm) (Fig. 44) .... *centrifera*
Dorsal shields present; ambulacrum of legs IV with a well developed stalk .... *cati*

10. Tibia and tarsus of legs IV not fused 11
Tibia and tarsus of legs IV fused 16

11. Anterior lateral shields absent .... *muris*
Anterior lateral shields present 12

12. Anal shields fused to the posterior median shield 13
Anal shields not fused to the posterior median shield 14

13. Genital apodemes absent; setae *cp* 1/2 to 2/3 the length of setae *c 3* .... *alexfaini*
Genital apodemes present; setae *cp* about 1/6 the length of setae *c 3* .... *paraguayensis*

14. Setae *d 1* inserted anterior to setae *e 1* .... *yunkeri*
Setae *d 1* inserted at the same level or posterior to setae *e 1* ... 15

15. Solenidia σ I absent; ambulacral stalks I–II long (27 μm) .... *dewitti*
Solenidia σ I present; ambulacral stalks I–II short (18 μm) .... *namibiensis*

16. Setae *e* IV present, tibiotarsi IV each with 2 setae transformed to small suckers .... *oudemansi*
Setae *e* IV absent, tibiotarsi IV each with only one small sucker (Figs. 46, 47) 17

17. Setae *kT* III–IV large spines; transverse apodeme poorly developed, barely extending beyond the junction with coxal apodemes III .... *pahangi*
Setae *kT* III–IV smaller; transverse apodeme extending beyond the junction with coxal apodemes III .... *pseudomuris*

6c. Larva and eggs

The larvae of *paraguayensis, plecoti, anisothrix, coreanus, nigricans, myotis, verheyeni, africanus, benoiti, mimetilli, paucipilis*, and *indicus* have not been described. The larva of *galagoensis* is incompletely described and is not included in this key.

1. Setae *3 b* spines (Fig. 231) 2
Setae *3 b* filiform 4

2. Setae *d 2* and *e 2* well developed, subequal in length to setae *d 1* and *e 1* .... *myoticola, roesleri*
Setae *d 2* and *e 2* minute 3

3. Setae *c 3* thick spines (Fig. 231) .... *philippinensis*
Setae *c 3* thin, spine-like or filiform .... *miniopteri*

4. Setae *d 1, e 1*, and *h 1* long and well developed, setae *d 2* and *e 2* minute; height of the body exceeding the width (Fig. 225) 5
Arrangement of the perianal setae different; body shape usually rounded 8

5. Setae *h 1* much longer than setae *d 1* and *e 1* (40–45 vs. 25-35 μm); setae *d 1, e 1*, and *h 1* filiform .... *helicothrix*
Length difference much smaller or absent; setae *d 1, e 1*, and *h 1* spine-like 6

6. Setae *sci* long (about 15 μm) .... *eptesicus*
Setae *sci* short (about 5 μm) 7

7. Setae *c 1* minute (< 3 μm) .... *corynorhini*
Setae *c 1* small, but distinct .... *lasionycteris, americanus*

8. Setae *h 1* longer than the other perianal setae 9
Setae *h 1* subequal to or shorter than the other perianal setae 11

9. Setae *h 1* long (15–20 μm), all perianal setae spine-like rods with bifurcate tips .... *elongatus, rajamanickami*
   Setae h 1 shorter (7–8 μm), perianal setae spine-like or filiform with rounded tips 10

10. Setae *e 2* shorter than setae *e 1* .... *alexfaini*
    Setae *e 2* longer than setae *e 1* .... *cheiromeles*

11. Eggs with a well developed stalk; parasitic on bats 12
    Eggs without a stalk, or stalk very poorly developed; parasitic on hosts other than bats 20

12. Height of the body exceeding the width; setae *sci* well developed (10–20 μm) 13
    Body rounded; setae *sci* variously well developed 14

13. Setae *sci* long (19–20 μm); perianal setae short (3–5 μm) .... *schoutedeni*
    Setae *sci* shorter (10–12 μm); perianal setae longer (about 7–9 μm) .... *chiropteralis*

14. Setae *sci* long (> 20 μm) 15
    Setae *sci* shorter (< 10 μm) 18

15. Dorsal shields present .... *tristis*
    Dorsal shields absent 16

16. Setae *c 1* spine-like rods, 11–13 μm long .... *ismaili*
    Setae *c 1* minute (< 3 μm) 17

17. Perianal setae relatively small (10–15 μm) .... *ovatus*
    Perianal setae long (> 25 μm) .... *dewitti*

18. Setae *d 1* and *e 1* spine-like rods, each with a lateral tooth .... *yunkeri*
    Perianal setae without a lateral tooth 19

19. Setae *e 2* less than half the length of the remaining perianal setae .... *namibiensis*
    Setae *e 2* subequal in length to the remaining perianal setae .... *tadaridae*

20. Dorsum with wave-like/scale-like striations 21
    Dorsum without such striations 22

21. Setae *sci* spine-like, well developed .... *cati*
    Setae *sci* filiform, short (6 μm) .... *musculi*

22. Setae *sci* long (> 20 μm) (Fig. 226) .... *centrifera*
    Setae *sci* shorter (< 10 μm) 23

23. Setae *d 2* and *e 2* distinctly shorter than setae *d 1* and *e 1* .... *oudemansi*
    All perianal setae subequal in length 24

24. Anterior dorsal setae filiform, short, perianal setae distinctly longer, spine-like .... *pseudomuris, jamesoni*
    Anterior dorsal and perianal setae subequal in size and shape 25

25. Bare zone on the dorsum large, extending from setae *sci* to the anus; perianal setae short (3–5 μm) .... *pahangi*
    Bare zone small, restricted to the posterior half of the dorsum; perianal setae longer (> 10 μm) .... *muris*

APPENDIX 2. DATA MATRIX

The ancestral states for the hypothetical ancestor of the entire family are all zero. The states for the hypothetical ancestors of *Nycteridocoptes*, *Cynopterocoptes* + the *Teinocoptes* group, *Chirnyssoides*, and *Notoedres*, as used in the partial analyses, are added at the end of this matrix.

Rhyncoptidae

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Diabolicoptes sarcophilus

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Satanicoptes phascogale

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Satanicoptes armatus

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Trixacarus eliurus

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Trixacarus diversus

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Trixacarus caviae

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0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 0 0 0 0 0 1 0 1 0 1 0 0 1 0 0 1 1 1 1 1 0 0 0
0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 ? 0 1 0 ? 0 0 0 0 0 0 0 0
? ? ? 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 0 0 0 ? ? 0 0 0 0 ? ? 1 ? ? 0 0 0 1 0 0 0 ? 0 0
0 ? 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 1 0 ? 1 0 0 ? 0 0 0 0 ? ? 0 0 ? 0 1 1 ? 0 1 ? ? 0 0 0 ? 0 0 0 0 1 1 0 0 0
? ? 0
```

Kutzerocoptes grunbergi

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0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 2 1 0 0 0 0 0 1 0 1 0 1 0 0 1 0 0 1 1 1 1 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 0 1 0 1 0 1 1 1 1 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1 1 1 1 1 0 0 0 1 1 1 0 0
0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 1 ? 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 1 1 1 0 1 1 0
0 0 0 0 0
```

Sarcoptes scabiei
0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 1 2 1 0 0 0 0 0 1 0 1 0 1 0 0 1 0 0 1 1 1 1 0 0 0 0
0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 0 1 0 1 0 1 1 1 1 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 1 1 1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 1 0 1 1 0
0 0 0 0 0

Prosarcoptes talapoini
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 0 0 1 1 1 1 1 0 0 0 0 0
0 1 1 1 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 1 1 ? ? 0 1 0 ? 0 ? 0 0 1 ? 1 0 1 1 1 1 ? ? ? ? ?
0 0 0 0 0 0 0 0 0 0 0 ? ? ? ? 0 0 0 ? ? ? 0 0 0 0 ? ? 1 ? ? 0 0 0 1 0 1 1 ? ? 0 0 ? 0 0
0 1 0 1 1 ? ? 0 0 0 0 0 ? 0 0 0 0 0 0 1 1 1 1 0 1 0 1 1 1 0 0 0 ? ? 0 ? 0 0 0 0 ? ? ?
? ? 0 ? 1 0 0 ? 0 0 0 0 ? ? ? ? 0 0 1 1 0 0 1 0 0 0 0 0 ? 0 0 0 0 1 1 0 0 0 ? ? 0

Prosarcoptes pitheci
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 1 0 0 1 0 0 1 1 1 1 0 0 0 0
0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 ? 0 0 0 0 0 0 1 0 ? 0 1 1 1 ? 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 ? ? ? ? ? ? ? ? 0 0 0 0
0 0 ? ? ? ? ? 0 0 1 0 0 0 0 0 ? 0 ? ? ? ? ? 0 1 1 ? 0 1 ? 0 0 0 0 1 1 1 1 0 1 1 0 0 0 0
0 0

Prosarcoptes scanloni
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 1 0 0 1 0 0 1 1 1 1 0 0 0 0
0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 0 1 0 1 0 1 1 1 1 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
1 0 ? 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 1 1 1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 1 0 1 1 0
0 0 0 0 0

Nycteridocoptes heidemanni
0 1 1 0 0 1 1 1 0 1 1 1 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 1 1 1 1 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1
0 0 1 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 1 1 0 1 1 1 0 1 ? 1 0 0 0 1 0 1 1 0 1 0 0
0 0 0 0 0

Nycteridocoptes microphallus
0 1 1 0 0 1 0 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 0
1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 1 1 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 1 1
0 0 1 0 0 0 1 0 1 1 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 1 1 0 1 1 0 0 1 0 1 0 0 0 1 0 1 1 1 1 0 0
0 0 0 0 0

Nycteridocoptes rousetti
0 1 1 0 0 1 0 1 0 1 1 1 0 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 0
1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 1 1 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 1 1
0 0 1 0 0 0 1 0 1 1 0 0 1 0 ? 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 1 1 0 1 1 0 0 1 0 1 0 0 0 1 0 1 1 1 1 0 0
0 0 0 0 0

Nycteridocoptes malayi
0 1 1 0 0 1 1 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? ? ? ? 1 1 0 1 1 1 1 1 0 1 0 0 0
0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 0 1 0 1 ? ? 0 0 0 ? 0 0 0 0 ? 0 0 1 ? 0 0 1 1 ? ? ? 0
? 0 0 0 ? 0 ? 0 0 0 ? ? ? ? 0 0 0 0 ? ? 0 ? ? ? ? ? 0 ? ? 0 0 0 1 0 0 0 ? ? 0 0 ? 0 0 ? 1
? 1 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 1 ? ? ? 0 0 0 0 0 ? ? 1 ? 1 ?
1 0 0 ? 0 ? 0 ? ? ? 1 ? ? ? 1 ? ? 0 1 ? ? 0 0 ? ? 0 ? ? ? 1 ? 0 ? 0 ? ? 0

Nycteridocoptes orientalis
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 ? 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 1 0
0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 0 0 1 0 1 0 0 0 1 0 1 1 0 1 0 0
0 0 0 0 0

Nycteridocoptes miniopteri
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 1 1 0 0 0 0 1 0
0 1 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 1 0 1 1 0 0 ? 0 ? 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 ? 0 1 ? 0
0 0 0 ? 0 0 ? 1 1 0 1 0 0 0 0 1 0 0 0 1 ? 0 1 0 ? 1 1 0 ? ? 1 0 0 0 1 0 1 1 1 1 0 0 0
0 0 0 0

Nycteridocoptes poppei
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 1 1 0 0 0 0 1 0
0 1 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 1 1 1 1 0 1 1 1 0 1 ? 1 0 0 0 1 0 1 1 1 1 0 0
0 0 0 0 0

Nycteridocoptes eyndhoveni
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 1 1 0 0 0 0 1 0
0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 1 0 1 1 0 0 ? 0 ? 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 ? 1 1 ? ? ? 1 0 0 0
0 0 0 ? ? 1 ? 1 0 1 0 0 0 0 ? 0 ? ? ? 0 ? ? ? 1 ? ? 0 1 ? 1 0 0 0 1 0 1 1 1 1 0 0 0 0 0
0 0

Nycteridocoptes hoogstraali
0 1 1 0 0 1 1 1 0 1 1 1 0 ? ? 1 1 1 0 0 0 0 0 0 0 0 0 0 ? ? ? 1 1 0 1 1 0 0 0 0 1 0 0
1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 0 1
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 1 0 1 0 ? 0 0 0 0 0 0 1 0 0 0 ? 0 0
0 ? 0 0 0 1 0 1 1 0 0 ? 0 ? 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 ? 1 1 1 1 1 1 ? 0 1 ? 0 0 0
0 ? 0 0 ? 1 1 0 1 0 0 0 0 1 ? 0 0 1 ? 1 ? ? ? 1 ? 0 ? ? 1 0 0 0 ? 0 1 1 1 1 0 0 0 0 0
0 0

Nycteridocoptes notopteris
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 ? 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 1 0
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 1 1 1 1 0 1 0 0 ? 0 1 0 0 0 1 1 1 1 0 1 1 1 0 1 ? 1 0 0 0 1 0 1 1 1 1 0 0
0 0 ? 0 0

Nycteridocoptes lavoipierrei
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0 ? ? ? 1 1 0 1 1 1 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 ? 0
0 0 ? 0 0 0 1 0 1 1 0 0 ? ? ? 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 ? 0 1 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 1 1 1 0 1 ? 1 0 0 0 ? 0 1 1 1 1 0 0
0 0 0 0 0

Nycteridocoptes asiaticus
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 1 1 1 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 1 1 1 0 1 ? 1 0 0 0 1 0 1 1 1 1 0 0
0 0 0 0 0

Nycteridocoptes macrophallus
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 1 1 1 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 1 0 0 0 0 1 0 0 1 1 0 0 1 1
1 1 1 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 1 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 1 1 1 0 1 ? 1 0 0 0 1 0 1 1 1 1 0 0
0 0 0 0 0

Nycteridocoptes pteropi
0 1 1 0 0 1 1 1 0 1 1 1 0 1 1 1 1 1 ? ? ? ? ? ? 0 0 0 0 1 1 0 1 1 0 1 1 1 0 1 0 1 0 0
0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 1 0 ? 1 1 0 0 0 1 ? 0 0 0 ? 0 0 1 1 0 0 ? ? 1 1
? 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 ? ? ? 0 0 0 1 1 0 ? 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 1
0 0 0 1 0 1 1 0 0 ? 0 ? 0 0 ? 0 0 0 0 0 0 1 0 0 0 ? 1 0 1 1 1 1 1 1 ? 0 1 ? 0 0 0 0 ?
0 1 ? 1 1 0 1 0 0 ? 0 1 ? 0 0 0 ? 0 1 0 ? 1 1 0 ? ? 1 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 0

Cynopterocoptes heaneyi
0 1 0 0 0 0 0 1 0 1 1 2 0 1 0 0 1 1 1 0 1 1 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 0 0 0 1 0
1 0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 1 ? ? 1 0 1 1 1 0 0 1 0 0 0 1 0 0 0 0 0 0 1 0 0 0 0 1 0 1 1 1 1 1 1 1 0 0 0 1
1 0 0 1 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0
0 0 0 0 0

Rousettocoptes mammophilus
0 1 0 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 1 0 0 0 0 0 1 1 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0
0 0 ? 0 0 0 1 0 0 ? ? ? 0 0 0 0 0 0 1 1 0 0 0 ? 0 1 1 ? 0 0 0 0 ? 0 1 1 ? 0 0 1 0 1 0
0 0 ? 0 0 0 ? 0 ? 0 1 0 1 1 1 1 1 0 0 0 0 0 0 ? ? ? 1 1 1 0 0 0 0 0 1 0 0 0 0 ? 0 ? 0
1 ? ? 1 ? 1 ? 1 0 0 1 0 0 0 1 0 0 0 0 1 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 1 ? ? 0 1 1 1 0 1 ?
? 1 ? 1 1 1 0 0 ? 1 ? 0 ? ? ? 1 ? ? ? 1 ? ? 0 ? ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 1 1 0 0

Tychosarcoptes amphipterinon
0 1 1 0 1 0 0 1 ? ? ? ? ? ? ? ? ? ? 1 1 0 0 0 0 1 1 0 0 1 1 1 1 1 1 1 1 1 1 0 1 1 0 1
0 0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 1 0 0 1 1 0 0 0 ? 0 1 1 ? 0 1 0 0 0 0 1 1 ? 0 0 1 0 1 1
0 0 ? 0 0 0 ? 0 ? 0 1 0 1 1 1 1 1 0 0 0 0 0 0 ? ? ? 1 1 1 0 0 0 0 0 1 0 0 0 0 ? 0 ? 0
1 ? ? 1 ? 1 ? 1 0 0 1 0 0 0 1 0 0 0 0 1 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 1 ? ? 0 0 0 0 0 1 ?
? 1 ? 1 1 1 0 0 0 1 0 0 ? ? ? 1 ? ? ? 1 ? ? 0 ? ? ? 1 ? ? 0 0 ? ? ? 1 ? 0 ? 1 1 0 1

Tychosarcoptes orphanus
? ? ? ? ? ? ? ? 0 1 1 2 1 1 1 0 1 1 ? 1 ?
? ? ? ? ? 0 0 0 ? ? ? ? 0 ? ? ? 0 ? ? 0 0 ? ? 0 ? ? ? ? ? 0 ? ? 0 0 ? ? ? ? ? ? ? 0 ? ? ? 0
0 0 ? ? 0 ? ? ? ? 1 ? ? ? ? ? 0 0 0 0 ? ? 1 ? ? 0 ? ? 1 0 ? 0 ? 0 ? 0 ? ? ? ? ? 0 1 1 ? ? ?
? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 1 0 1 ? 1 1 ? 0 ? 0 0 ? ? ? ? ? ? 0 0 ? 0 ? ? 1 0 ? ? ? 0 ?
0 1 ? ? 1 0 0 ? 1 1 0 ? ? 0 ? ? 0 ? ? 0 0 0 1 1 ? 0 ? ? ? ?

Tychosarcoptes ptenochirus
0 1 1 0 1 0 0 1 0 1 0 0 1 1 ? 0 ? ? 1 1 1 0 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0
1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 0
1 1 1 0 0 0 0 0 0 0 0 0 1 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 0 0
0 0 0 1 ? ? 1 0 1 1 1 0 0 1 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
0 1 1 1 0 0 1 0 1 1 1 0 0 0 1 0 0 0 1 ? 1 1 0 0 1 1 1 0 ? ? 0 0 0 0 0 0 0 0 0 1 1 0
0 1 1 0 0

Chirobia thoopterus
0 1 1 0 1 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 ? 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 1 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
0 1 1 0 1

Chirobia brevior
0 1 1 0 1 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 ? 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 1 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
0 1 1 1 1

Chirobia cynopteri
0 1 1 0 1 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0
0 0 0 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 1 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
0 1 1 0 1

Chirobia haplonycteris
0 1 1 0 1 0 0 1 0 1 0 0 0 0 0 0 ? ? 1 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 0 0
0 0 0 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 0 1 1 0 1 0 1 ? 1 0 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
0 1 0 0 1

Chirobia jagori
0 1 1 0 1 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 1 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
0 1 0 0 1

Chirobia eonycteris
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 0 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 1 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 0 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
1 1 1 1 1

Chirobia rousettus
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 1 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 0 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
1 1 1 1 1

Chirobia squamata
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 1 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 1 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
1 1 1 1 0 0 1 0 1 1 1 0 0 1 1 0 1 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1
1 1 1 1 1

Chirobia angolensis
0 1 0 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 1 0 1 0 0 0 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0
0 0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 1 0 0 1 1 0 0 0 ? 0 1 1 ? 0 1 0 0 0 0 1 1 ? 0 0 1 1 1 1
1 1 ? 1 1 ? ? 0 ? 0 0 0 1 1 1 1 1 0 0 0 0 0 0 ? ? ? 1 1 1 0 0 0 0 1 1 0 1 ? ? ? 1 ? ? 1
? ? 1 ? 1 ? 1 0 0 1 0 1 0 1 0 0 1 0 1 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 1 ? ? 0 1 1 1 1 1 ? ?
1 ? 1 1 1 0 0 1 1 ? 1 ? ? ? 1 ? ? ? 1 ? ? 0 ? ? ? 1 ? ? 0 0 ? ? ? 1 ? 1 ? 1 1 1 1

Chirobia congolensis
0 1 0 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 1 0 1 0 0 0 1 1 0 0 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1 1
1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 1 0 ? 0 1
0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1 1
1 1 1 ? ? 1 ? 1 1 1 0 0 1 1 0 1 ? ? ? 1 ? ? ? 1 ? 1 0 ? ? 0 1 ? 0 0 0 0 0 0 1 1 1 ? 1 1
1 1

Chirobia otophaga
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 1 0 0 0 1 1 0 0 1 1 1 1 1 1 1 1 0 1 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 1 1 ? 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 1 1 1 0 1 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 1
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1 1 1 1 1

Teinocoptes vandeuseni
0 1 1 1 1 0 0 1 0 1 1 2 0 0 0 0 1 1 1 0 0 0 0 0 1 1 0 0 1 1 1 1 1 1 1 1 0 0 0 0 1 1
0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 1 1 1 0 1 0 0 0 1
0 0 0 1 0 0 1 0 1 1 1 0 0 1 1 0 0 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 0 0 0 0 0 0 0 0 1 1 0
1 1 1 1 0

Teinocoptes malayi
0 1 1 1 1 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 1 1 0 0 1 1 1 1 1 1 1 1 0 0 0 0 1 0
0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 1 0 0 1 0 0 0 0 1 1 0 0 0 1 1
1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 0 ? 0
1 0 ? 1 ? ? 1 0 1 1 1 0 0 1 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 1 1 1 0 1 0 0 0 0
1 1 0 1 0 0 1 0 1 1 1 0 0 1 1 0 0 0 1 ? 1 1 0 1 1 1 1 0 ? ? 0 0 0 0 0 0 0 0 0 1 1 0
1 1 0 0 0

Teinocoptes pahangensis
01111001??????????1000001100111111110000100
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10?000?0?00011111000000???11100000101???1??
1??1?1?1001000100001????????11?11?1??010001?
?1?1110011?0???1???1??0???00?00???1?0?1000

Teinocoptes epomophori
011110010112000011101000????111111111000011
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1?100000000000111110000000000111000001010?0
10?1??1011100100010000100000010111111010001
0001001011100110001?11011110??0000000000110
11?00

Teinocoptes asiaticus
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00?000?0?00011111000000???1110000010000?1??
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Teinocoptes astridae
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1110000000000011111000000000011100000100000
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0101001011100110001?11011110??0000000000110
11000

Teinocoptes strandtmanni
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11110?0000001011111000000000011100000100000
10?1??10111001000100001000000000111110??0???
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10

Teinocoptes katherinae
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0?1?0???1???1??0???00??0???1?0?1??0

Teinocoptes wilsoni
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Teinocoptes aingworthi
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Teinocoptes philippinensis
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0101001011100110001?11011110??0000000000110
11100

Teinocoptes eonycteris
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0111001011100110001?11011110??0000000000110
11000

Teinocoptes johnsoni
0110?001??????????100000???????1111111101000
0?001110????000001100??01???100?011?00?????1
?000?0?000????1?????0?????1??0001?1???1??1??1?
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Teinocoptes haymani
0111?001??????????100000???????1111000001000
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Teinocoptes eidoloni
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00?1?0???1???1??????00??0???1?0?1??0

Teinocoptes domrowi
01101001??????????00000000000000110000000100
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1??1?1?1001000100001????????11?11?1??000001?
?1?11100?1?0???1???1??0???00?00???1?0?1000

Teinocoptes auricularis
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000000100011100010011000001100100001100010
11100100000000111110000000000111000001010?0
10?1??1011100100010000100000000011111010001
1111??1?11100110001?11011110??00000000001100
1000

Teinocoptes harpyionycteris
0100000101120000111000000000000000000000000
000100100011100010011000001100100001100011
11100100000000111110000000000111000001010?0
10?1??1011100100010000100000000011111010001
1111001011100?10001?10001110??01?0000001100
1110

Chirophagoides mystacopis
0??0000000012000112??????????0001001100000000
00000000000?00000011??00000?0010001110?????
00000000000???00??0000000?11?00001000000000
001011??10?00?0000011000011111111?00?000010
011001000000001?0001101?110000101010000?00

Chirnyssoides (Noctiliocoptes) noctilionis
0111100101000000110000000000000000000000000
0000000000000000001000000000000000000000010
10000000000000111110000000000111000001011??
11?1??111101001000010001100001111111100000
00011?1100100000111?11?0110110100100010100
00000

Chirnyssoides (*Chirnyssoides*) *amazonae*
0 1 1 1 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 1 1
1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
1 1 ? 0 0 0 1 1 1 1 0 1 0 0 0 0 0 0 0 1 1 0 1 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 1 1 0 0 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Chirnyssoides (*C.*) *caparti*
0 1 1 1 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 1 1
1 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
1 1 ? 0 0 0 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 0 1 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 1 1 0 0 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Chirnyssoides (*C.*) *vampyrops*
0 1 1 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 1 0 0 0 0 ? 0 0 0 ? 1 1 0 0 0 0 1 0 ? 0 0 1 1 1 0
0 0 ? 1 0 0 ? 0 ? 0 0 0 1 1 1 1 1 0 0 0 0 0 0 ? ? ? 1 1 1 0 0 0 0 0 1 0 1 ? ? ? 1 ? ?
1 ? ? 1 ? 1 ? 0 1 0 0 0 0 0 0 1 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 1 ? ? 0 0 0 0 0 1 ?
? 1 ? 0 0 1 0 0 0 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 0 0 0 0

Chirnyssoides (*C.*) *surinamensis*
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 1 1
1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 1 ? ? 1 1 1 1 0 1 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 0 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Chirnyssoides (*C.*) *stenoderma*
0 1 1 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 1 0 0 0 ? 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 ? ? 1 ? 0
0 0 1 0 0 0 0 0 0 0 0 ? 1 1 1 1 1 ? 1 ? 0 0 0 0 0 1 1 1 1 1 0 0 0 1 0 1 1 ? ? 1 1 ? ?
? ? 1 1 1 1 0 1 ? ? ? ? ? 0 1 1 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ?
? 0 0 1 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 1 0 1 0 0 0 0 ? 0 0

Chirnyssoides (*C.*) *parvisuctus*
0 1 1 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 1 0 0 0 0 ? 0 0 0 ? 1 1 0 0 0 0 1 0 ? 0 0 ? ? 1 1
1 0 ? 1 0 0 ? 0 ? 0 0 0 1 1 1 1 1 1 ? 1 0 0 0 ? ? ? 1 1 1 1 0 0 0 0 1 0 1 ? ? ? 1 ? ? 1
? ? 1 ? 1 ? 0 1 0 0 0 0 0 0 1 1 0 1 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 1 ? ? 1 0 0 0 0 1 ? ?
1 ? 0 0 1 0 0 0 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 0 0 0 0

Chirnyssoides (*C.*) *brasiliensis*
0 1 1 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 1 0 0 ? 0 0 0 0 0 1 ? 1 0 0 0 0 1 0 0 0 0 ? ? 1 1
1 0 1 1 0 0 0 0 0 0 0 0 1 1 1 1 1 ? ? 1 1 0 0 0 0 0 1 1 1 1 1 0 0 0 1 0 1 1 ? ? 1 1 ?
1 ? ? 1 1 1 1 0 1 0 0 0 0 0 ? 1 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 ? ? 1 0 0 0 0 1
? ? 1 ? 0 0 1 0 0 0 0 0 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 1 ? ? 0 0 0 1 0 1 0 0 0 0 0 0 0

Chirnyssoides (*C.*) *phyllostomus*
0 1 1 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 1 1
1 1 1 0 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 1 ? 1 1 1 0 0 0 0 1 1 1 1 1 0 0 0 1 0 1 1 ? ?
1 1 ? 1 ? ? 1 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 ? 1 1 ? 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Chirnyssoides (*C.*) *venezuelae*
0 1 1 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 0 0 ? ?
? ? ? 0 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 1 ? 1 1 1 0 0 0 0 1 1 1 1 1 0 0 0 1 0 1 1 ? ? 1
1 ? 1 ? ? 1 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 1 ? ? 1 0 0 0
0 1 ? ? 1 ? 0 0 1 0 0 0 0 0 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 1 ? ? 0 0 0 1 0 1 0 0 0 0 0 0 0

Notoedres (*Bakeracarus*) *paraguayensis*
0 1 1 1 1 0 0 1 0 1 1 2 0 0 0 0 1 1 ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 ? 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 ? ? 1
0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 ? ? ? 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ? 1 1
? 0 0 0 1 0 1 1 0 1 1 0 ? 0 0 ? 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0
0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 0 0 0 0 0 1 0 1 0 0 0 0
0 0 0

Notoedres (*B.*) *coreanus*
0 1 1 1 ? 0 0 1 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0
? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 ? ? ? 0 0 ? ? ? 0 0 0 ? 0 0 0 ? 0 0 ? ? ? ? ? 0 ? 0
0 0 ? 0 ? 0 0 0 ? ? ? ? 1 ? ? ? ? ? 0 ? ? ? ? ? 1 ? ? 1 1 1 1 ? 1 ? ? ? 1 ? ? 0 0 ? 1 ? 1 ?
? ? 1 0 ? 0 0 ? 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? 1 ? 1 1 ? ? ? ? 0 0 0 0 0 1 ? ? 1 ? 0 ? 1 0 0
? 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? ? 0 ? ? ? 1 ? 0 ? 0 ? ? 0

Notoedres (*B.*) *helicothrix*
0 1 1 ? 1 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 ? 0 0 0 0 0 0 0 0 ? 0 0 1 0 1 ? 0
0 ? 0 0 0 ? 0 ? 0 0 0 ? 1 1 1 1 0 1 1 ? 0 0 ? ? ? 1 1 1 1 1 1 1 1 1 0 1 ? ? ? 1 ? ? 0 0
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0 1 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? 0 ? ? ? 1 ? 0 ? 0 ? 0 0

Notoedres (*B.*) *anisothrix*
? 1 1 ? ? 0 0 1 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ?
0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 ? ? ? 0 0 ? ? ? 0 0 0 ? 0 1 0 ? 0 0 ? ? ? ? ? 0 ? ? 0
0 ? 0 ? 1 0 0 ? ? ? ? 1 ? ? ? ? ? 0 ? ? ? ? ? 1 ? ? 1 1 1 1 ? 1 ? ? ? 1 ? ? ? ? ? 1 ? 1 ? ?
? ? 0 ? 0 0 ? 0 0 0 0 0 ? 0 ? 1 0 0 ? 0 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? 0 ? ? ? 1 ? 0 ? 0 ? ? 0

Notoedres (*B.*) *lasionycteris*
? 1 1 1 1 0 0 1 0 1 ? ? 0 0 1 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 ? ? 0 0 0 ? 0 ? 0 0 0 ? 0 1 0 0 0 0 ? ? ? ? ?
0 0 1 0 0 0 0 0 1 0 0 ? ? ? ? 1 ? ? ? ? ? 0 0 0 0 ? ? 1 ? ? 1 1 1 1 0 1 1 ? ? 1 1 ? 1 ?
? 1 0 1 1 ? ? 1 0 ? 0 0 ? 0 0 0 0 0 1 1 0 0 ? 0 1 1 ? ? ? 1 1 ? ? ? 0 1 0 0 0 0 1 ? ? 1
? 0 ? 1 0 0 ? 0 0 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? 0 0 0 0 ? 0 0 1 0 1 ? 0 0 0 ? ? 0

Notoedres (*B.*) *corynorhini*
0 1 1 1 1 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 0 0 0 0 0 ? 0 1 1 ? 1 0 0 0 0 0 1 0 ? 0 0 ? ? 1 ?
1 0 ? 1 0 0 0 0 ? 1 0 0 1 1 1 1 1 0 0 1 ? 1 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 ? ? ? 1 ? ?
1 ? ? 1 ? 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 ? ? ? ? ? 0 ? ? 1 1 ? 1 1 ? 0 ? 0 1 0 0 0 0 1 ?
? 1 ? 0 0 1 0 0 0 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 0 0 0 0 1 0 1 ? 0 ? 0 0 0 0

Notoedres (*B.*) *eptesicus*
0 1 1 1 1 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 1 ? 1
1 1 0 0 1 0 0 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 1 ? ? ? 1 1 1 1 1 1 1 1 1 0 1 1 ? ? 1 1
? 1 ? ? 1 0 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 ? 1 1 ? 0 ? ? 1 0 0 0 0
1 ? ? 1 ? 0 0 1 0 0 0 0 0 1 ? ? ? 1 ? ? 0 1 ? ? 1 1 ? 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0

Notoedres (*B.*) *americanus*
0 1 1 1 1 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0
1 ? 1 0 0 1 0 0 0 0 0 1 0 0 1 1 1 1 1 0 0 1 1 1 1 ? ? ? 1 1 1 1 1 1 1 1 1 0 1 1 ? ? 1
1 ? 1 ? ? 1 0 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 1 1 1 0 0 0 0 1 0 0
0 0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 1 0 0 0 0 0 0 0 1 0 1 0 0 0
0 0 0 0

Notoedres (*Notoedres*) *africanus*
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 ? 0 1 0 0 0 0 0 0 ? 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 ? ? ? ?
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0 0 0 1 0 1 1 0 1 0 0 0 0 0 ? 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 ? 0 1 ? 0 0 0 0
? 1 ? 1 ? 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0
0 0

Notoedres (N.) philippinensis
1 1 0 0 0 0 0 1 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0
1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 1 0 1 0 0
0 0 0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 1 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Notoedres (N.) miniopteri
1 1 0 0 0 0 0 1 0 1 1 1 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0
1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 ? ?
1 1 ? 0 0 1 1 0 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 1 0 1 0 0
0 0 0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 1 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Notoedres (N.) verheyeni
? 1 0 0 0 0 0 1 0 1 1 1 0 1 1 0 1 1 ? ? ? ? ? ? 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ?
0 0 0 ? ? ? ? 0 0 0 0 ? ? 0 0 ? ? ? 0 ? 0 0 0 ? 0 0 ? ? 0 ? 0 0 1 ? 0 0 0 ? ? 1 ? ? ? 0 ?
? ? 1 0 ? 0 0 0 1 1 1 1 1 ? ? ? 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 ? ? 1 1 ? 0 0 ? ?
0 1 1 ? ? ? ? ? 0 0 ? 0 0 0 0 0 1 1 0 0 1 0 1 1 ? ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? ? ? ? ? 0
1 0 0 0 0 0 ? ? ? ? ? ? ? 0 1 1 ? 1 1 ? 1 0 1 1 0 ? 0 1 0 1 0 0 0 0 0 0 ?

Notoedres (N.) nigricans
1 1 0 0 0 0 0 1 0 1 1 1 0 1 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0
1 ? 0 0 0 0 0 0 1 0 0 0 0 0 ? 1 1 1 1 0 0 1 0 0 0 0 0 0 ? 1 1 ? 1 1 1 1 1 1 1 1 ? ? 1
1 ? 0 0 1 1 0 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 1 0 1 0 0 0
0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 1 1 0 0 0 1 0 1 0 0 0
0 ? 0 0

Notoedres (N.) chiropteralis
0 1 1 1 1 0 0 1 0 1 0 0 0 ? 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 1 1 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 ? 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 ? 1 1 ? 1 0 0 0 0 0 0 1 0 1 0 0
0 0 0 0 0

Notoedres (N.) benoiti
0 1 0 0 0 0 0 1 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 1 0 ? 0 ? 0 0 0 ? ? 1 0 0 0 0 1 0 ? 0 0 ? ? 1 ? 0 0 ?
0 0 0 ? 0 ? 0 0 0 ? 1 1 1 1 ? ? ? ? 0 0 ? ? ? 1 1 1 1 1 1 1 1 1 ? 1 ? ? ? 1 ? ? 0 0 ? 1
? 1 ? 0 ? 0 0 0 0 0 ? 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? ? ? ? ? 0 0 0 0 1 ? ? 1 ? 0 0
1 0 0 ? 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 0 ? 0 0

Notoedres (N.) mimetilli
0 1 0 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
0 0 ? ? ? ? ? ? ? ? 0 ? 0 0 1 0 ? 0 ? 0 ? 0 ? 0 ? ? 1 0 0 0 0 0 0 ? 0 0 ? ? 1 0 0 0 ? 0 0
0 ? 0 ? 0 0 0 1 1 1 1 1 ? ? ? 0 0 0 ? ? ? 1 1 1 1 1 1 1 1 1 ? 1 ? ? ? 1 ? ? 0 0 ? 1 ? 1
? ? ? ? 0 ? 0 0 ? 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 ? ? ? ? ? ? 0 1 0 0
0 0 ? ? ? ? ? ? ? ? ? 1 ? ? 1 1 ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 0 0 0 ?

Notoedres (N.) alexfaini
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 0 0 0 1 1 0 0 1 1 0 1 1 0 0 0 0 0 0 0 0 1 0 1 0 0
0 0 0 0 0

Notoedres (N.) elongatus
0 1 0 0 ? 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 ? ? 0 0 0 0 ? 0 0 0 ? 0 0 1 0 ? ? ? 0
? 0 0 0 ? 0 ? 0 0 0 ? ? ? ? 1 0 1 1 ? ? 0 ? ? ? ? ? 1 ? ? 1 1 1 1 0 1 ? ? ? 1 ? ? 0 0 ? 1
? 1 ? 0 1 0 0 0 0 1 0 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 0 ? ? 0 0 0 0 0 1 ? ? 1 ? 0
? 1 0 0 ? 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? ? 0 ? ? ? 1 ? 0 ? 0 ? ? 0

Notoedres (N.) rajamanickami
0 1 0 0 ? 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 0 0 0 0 ? ? 0 0 ? ? 0 0 0 0 ? 0 0 0 ? 0 0 1 0 ? ? ? 0
? 0 0 0 ? 0 ? 0 0 0 ? ? ? ? 1 0 1 1 ? ? 0 ? ? ? ? ? 1 ? ? 1 1 1 1 0 1 ? ? ? 1 ? ? 0 0 ? 1
? 1 ? 0 1 0 0 0 0 1 0 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 0 ? ? 0 0 0 0 0 1 ? ? 1 ? 0
? 1 0 0 ? 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? ? 0 ? ? ? 1 ? 0 ? 0 ? ? 0

Notoedres (N.) namibiensis
0 1 0 0 0 0 0 1 0 1 1 2 0 0 1 0 1 1 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 ? 0 0 0 0 0 0 0 0 0 0 0 0 ? 1 1 1 1 0 0 1 ? 0 0 0 0 0 ? 1 1 ? 1 1 1 1 1 0 1 1 ? ? 1
1 ? 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0
0 0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 ? 1 1 ? 0 0 0 0 0 0 0 1 0 1 0 0 0
0 ? 0 0

Notoedres (N.) yunkeri
0 1 0 0 0 0 0 1 0 1 1 2 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0
? ? ? 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ? 1
1 ? 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 ? 0 1 1 ? ? ? ? ? ? ? ? 0 ? 0 0 0
0 ? ? ? ? ? 0 0 1 0 0 0 0 0 ? ? ? ? ? ? ? 0 1 1 0 1 1 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0
0

Notoedres (N.) tadaridae
0 1 0 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 ? 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 ? 0
0 ? 0 0 0 ? 0 ? 0 0 0 ? 1 1 1 1 0 0 1 ? 0 0 ? ? ? ? 1 1 ? 1 1 1 1 1 0 1 ? ? ? 1 ? ? 0 0
? 1 ? 1 ? 0 1 0 0 0 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 0 ? ? 0 0 0 0 0 1 ? ? 1
? 0 0 1 0 0 0 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 0 ? 0 0

Notoedres (N.) dewitti
0 1 1 0 0 0 0 1 0 1 1 2 0 0 1 0 1 1 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 0 0 0 0 0 0 0 0 0 0 ? 1 1 1 1 0 0 1 ? 0 0 0 0 0 ? 1 1 ? 1 1 1 1 1 0 1 1 ? ? 1
1 ? 1 ? ? 1 0 1 1 0 1 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0
0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 1 1 1 ? 0 0 0 0 0 0 0 1 0 1 0 0 0
0 ? 0 0

Notoedres (N.) cati
0 1 0 0 0 0 0 1 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 1 ? ? 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 1 0 1 1 0 1 1 1 0 0 0 0 0 0 0 1 0 1 1 0
0 0 0 0 0

Notoedres (N.) centrifera
0 1 0 0 0 0 0 1 1 0 0 0 1 ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 0 1 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 1 0 1 1 0 1 1 0 1 0 0 0 0 0 0 1 0 1 1 0
0 0 0 0 0

Notoedres (N.) muris
0 1 0 0 0 0 0 1 0 1 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 0 0 0 0 0 1 0 1 0 0
0 0 0 0 0

Notoedres (N.) oudemansi
? 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 0 ? 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 ? 0 1 1 ? ? ? ? ? ? ? ? ? 0 0 0 0
0 ? ? ? ? ? 0 0 1 0 0 0 0 0 ? ? ? ? ? ? 0 0 1 1 ? 1 1 ? 0 0 0 0 0 0 0 1 0 1 1 0 0 0 0 0
0

Notoedres (*N.*) *pahangi*
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 1 0 1 1 1 1 1 ? 1 0 0 0 0 0 0 1 0 1 1 0
0 0 0 0 0

Notoedres (*N.*) *pseudomuris*
0 1 0 0 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 0 1 0 ? 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 1 0 1 1 1 1 1 ? 0 0 0 0 0 0 0 1 0 1 1 0
0 0 0 0 0

Notoedres (*N.*) *musculi*
0 1 0 0 0 0 0 1 0 ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 ? 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 1 0 0 ?
0 0 ? 0 0 0 ? 0 ? 0 0 0 ? 1 1 1 1 0 0 1 ? 0 0 ? ? ? ? 1 1 ? 1 1 1 1 1 0 1 1 ? ? 1 1 ? 1
? ? 1 0 1 1 0 0 1 0 ? 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 1 1 1 1 0 ? ? 0 0 0 0 0 1 1 ?
1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 1 0 1 1 ? 1 1 ? ? 0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0

Notoedres (*N.*) *indicus*
0 1 0 0 ? 0 0 1 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0
? 0 0 0 0 0 0 ? ? ? ? 0 1 0 0 0 0 ? ? ? ? ? ? 0 ? ? ? 0 0 0 ? ? 0 0 ? 0 0 ? ? ? ? ? 0 ? 0
0 0 ? 0 ? 0 0 0 ? ? ? ? 1 ? ? ? ? ? 0 ? ? ? ? ? 1 ? ? 1 1 1 1 ? 1 ? ? ? 1 ? ? 1 ? ? 1 ? 1 ?
0 ? 1 0 ? 0 0 ? 0 0 0 0 0 ? ? ? ? ? ? ? ? 1 1 ? 1 1 ? 0 ? ? 0 0 0 0 0 1 ? ? 1 ? 0 ? 1 0 0
? 0 ? 1 ? ? ? 1 ? ? ? 1 ? ? 1 1 ? ? 0 0 ? 0 0 ? ? ? 1 ? 0 ? 0 ? ? 0

Hypothetical ancestors:

Nycteridocoptes
0 1 1 0 0 1 1 1 0 1 1 1 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 1 1 1 1 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 1 0
1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 0 1 0 0 0 1 1
0 0 1 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0
0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 0 1 1 1 0 1 1 0 0 1 0 1 0 0 0 1 0 1 1 0 1 0 0
0 0 0 0 0

Cynopterocoptes + the *Teinocoptes* group
0 1 1 0 0 0 0 1 0 1 1 2 0 1 0 0 1 1 1 0 0 0 0 0 1 1 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 0 0 0 1 0
1 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0
0 0 0 1 ? ? 1 0 1 1 1 0 0 1 0 0 0 1 0 0 0 0 0 0 1 0 0 0 0 1 0 1 1 1 1 1 1 1 0 0 0 1
0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0
0 0 0 0 0

Chirnyssoides
0 1 1 1 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 1 ? ?
1 1 ? 0 0 0 1 1 1 1 0 1 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 0 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 1 ? 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 1 0 0 1 0 0 0 1 0 1 0 0
0 0 0 0 0

Notoedres
0 1 1 1 0 0 0 1 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 1 1 ? ?
1 1 ? 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0
0 0 0 1 0 0 1 1 0 0 1 0 0 0 0 0 1 1 1 ? 1 1 0 0 1 1 0 1 1 0 0 0 0 0 0 0 0 1 0 1 0 0
0 0 0 0 0