Heteromorphism among selected feather mite species (Analgoidea: Freyanidae) of the genus Freyana Haller, 1877

by

Julio Eduardo Budde

Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in the

Department of

Biological Sciences

Paul C Peterson 12/6/91

Advisor Date

Sally M. Hotchkiss December 16, 1991

Dean of the Graduate School Date

Youngstown State University

December, 1991

y-10-5

THESIS APPROVAL FORM

THESIS TITLE: Heteromorphism among selected feather mite species (Analogoidea: Freyanidae) of the genus *Freyana* Haller,187

AUTHOR: Julio Eduardo Budde

DEGREE: Master of Science in the Department of Biological Sciences

ADVISOR: Dr. Paul C. Peterson

COMMITTEE MEMBERS:	ACCEPT	REJECT
David B. MacLean	✓	
[illegible]	✓	
Dale W. Fishbeck	✓	
Paul C. Peterson	✓	

DATE December 6, 1991

1 copy to accompany library copy

1 copy to advisor

1 copy to Departmental Files

ABSTRACT

Heteromorphism among selected feather mite species (Analgoidea: Freyanidae) of the genus Freyana Haller, 1877

Julio E. Budde
Master of Science
Youngstown State University, 1991

Morphology and ontogeny of two species of freyanids (*Freyana largifolia* Megnin et Trouessart, 1884, and *Freyana reticulata* n. sp.) inhabiting *Pteronetta hartlaubi* Cassin, 1859, (Aves: Anatidae) were investigated and compared with the type species, *Freyana anatina* Haller 1877. Two new morphological characters are described, the propodosomal projection and seta $\mathcal{E}$. The mites are illustrated using diagramatic representations and scanning electron micrographs. All mites were obtained from museum study skins. Observations were made to elucidate if there is niche partitioning in *Freyana anatina* heteromorphic males in the primary feathers of *Anas platyrhynchos* Linnaeus (Aves: Anatidae).

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to Dr. Paul C. Peterson, Youngstown State University, for the guidance and support he generously provided me during the preparation of this thesis. Invaluable advice was also provided by Dr. David MacLean, Youngstown State University; Dr. Dale Fishbeck, Youngstown State University; Dr. Paul VanZandt, Youngstown State University, and Dr. Anthony Sobota, Youngstown State University. A special thanks goes to Dr. Warren T. Atyeo, University of Georgia, and Dr. Richard Zuci, U.S. Museum of Natural History, for lending me the materials to do this study. Finally, I wish to thank Andrea Justine for the many hours she spent helping me with the computer work.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF SCANNING ELECTRON MICROGRAPHS

LIST OF TABLES

INTRODUCTION

Feather mites (Acarina: Analgoidea) are a group of obligatory ectoparasites inhabiting the feathers of their avian hosts. Currently, there are twenty-five recognized families containing over 1400 described species (Gaud and Atyeo, 1978). Indications from field collected birds and museum study skins seem to suggest that there are perhaps an equal or greater number of feather mites that are undescribed. This study focuses on the family Freyanidae, the species of which are parasitic on birds closely associated with water (Anseriformes, Ciconiiformes, and Procellariiformes). Species of the Freyanidae have been assigned to four subfamilies: the Michaeliinae Gaud and Mouchet 1959, the Diomedacarinae Gaud and Atyeo 1981, the Burhinacarinae Gaud and Atyeo 1981, and the Freyaninae Gaud and Atyeo 1981. The subfamily Freyaninae is further divided into eight genera: <u>Freyana</u> Haller, 1877; <u>Halleria</u> Megnin and Trouessart, 1844; <u>Pavlovskiana</u> Dubinin, 1950; <u>Freyanopsis</u> Dubinin, 1950; <u>Parafreyana</u> Cerny, 1969; <u>Allofreyana</u> Gaud and Atyeo, 1975; <u>Dobyella</u> Gaud and Atyeo, 1975; and <u>Pelycymerus</u> Gaud and Atyeo, 1975. The largest in terms of numbers of species is the genus <u>Freyana</u>, to which are currently being assigned thirty-six described species of mites, all parasitic on birds belonging to the family Anatidae (ducks, geese, and swans). The currently recognized species and subspecies of the genus Freyana are listed in table 1 along with their hosts.

This study focuses on species of freyanids found on the duck *Pteronetta hartlaubi* Cassin, 1859. Morphology and ontogeny are investigated for two species of freyanids (*Freyana largifolia* Megnin et Touessart and *Freyana reticulata* n. sp.) co-inhabiting Hartlaub's duck, and also for *Freyana anatina* Haller, the type species for the genus. *Freyana reticulata* is species specific on *Pteronetta hartlaubi*. *Freyana largifolia* has been recorded on *Pteronetta hartlaubi*, *Anas platyrhynchos* Linnaeus, and numerous other ducks of the genus *Anas* Linnaeus. *Freyana anatina* also parasitizes *Anas platyrhynchos* as well as several other ducks belonging to the genus *Anas*. The morphology and ontogeny of *Freyana reticulata*, as well as the ontogeny of *Freyana largifolia*, are presented here for the first time. Two morphological characters, the propodosomal projection and seta ε, are also described and illustrated for the first time. Descriptions of the nymphal stages as well as the adult forms are presented. Like the genus *Freyana* in general, these species are characterized by dimorphism in the adult male forms. The form superficially resembling the female is termed the homeomorph. Conversely, the form deviating from the "normal" type, characterized by heavy sclerotization and enlarged tibial expansions, is termed the heteromorph. Since these two forms may represent an example of adaptive radiation and niche partitioning along feather zone microhabitats, the phenomenon of heteromorphy is afforded additional treatment in this paper.

Accordingly, observations were made to elucidate if heteromorphic males of the species Freyana anatina tended to restrict themselves to a certain microhabitat on the primary feathers of Anas platyrhynchos.

Feather mites were first described as living on bird feathers by de Geer in 1788. Nitzch (1818) later classified them into a separate taxon. Subsequently, a plethora of descriptive studies have been conducted by numerous authors. However, it was not until V.B. Dubinin's extensive studies on the ectoparasitic avifauna of Russia that the family Freyanidae was recognized. In addition to morphological studies and systematics, Dubinin recognized the need to extend research into areas that have been largely neglected. Much research needs to be conducted on ecological aspects of feather mites. To date, no one has determined the nutritional needs of feather mites, nor their reproductive aspects, behavior, or life histories. Instead, extensive revisions of higher taxa have kept systematists occupied. With the advent of sophisticated numerical taxonomy methodologies, Moss, Peterson, and Atyeo (1977) advanced analgoid systematics beyond mere conjecture. Today, methods used by evolutionary phylogeneticists may further clarify evolutionary relationships among feather mites. Griffiths, et al. (1990), working with free-living mites, presented a theory on metameric and setal changes during ontogeny. Consequently, it may now be possible to infer homologies among setae on mites of diverse taxa, further illuminating phylogenetic relationships.

Feather mites (Superfamily Analgoidea) are members of a diverse assemblage of organisms belonging to the order Acarina. Since the period between the Cenozoic and Mesozoic Eras, the acarina have radiated into a multitude of niches, leaving behind their predatory ancestry (Lindquist, 1975). For example, different groups of mites infest grains, soil, fungus, or lead scavenging or commensal lifestyles. Analgoid mites became restricted to a parasitic lifestyle on avian hosts. They have been isolated from all avian taxa with the single exception of the penguins. Presumably, feather mites must have been subjected to a wide variety of ecological pressures, judging by their incredible diversity in terms of morphology, habitat, and numbers of species. Analgoids most probably evolved from nidicolous mites, the tyroglyphids (Dubinin, 1951). Dubinin (1951) postulated that feather mites have been associated with their avian hosts and diverged from their tyroglyphoid ancestry at about the time between the Cretaceous and Tertiary Periods. Intensive evolutionary radiation has occurred in this group since the Oligocene (Cerny, 1971).

Dubinin (1950) believed that host specificity was a function of the unique environmental conditions in which each mite species evolved and co-evolved with the host species. Thus, phylogenetically older host groups presumably have had a long association with their parasites. This long period of co-evolution may have reached the point where the parasites eventually became restricted to a single host or group of related hosts and are subsequently unable to colonize phylogenetically newer host groups. However, certain mite groups are characteristically much less host-specific and are able to parasitize a wide variety of hosts. These taxa may have had a shorter association with their avian hosts to the extent that recolonization may occur frequently between phylogenetically disparate avian hosts. Kethly and Johnston (1975) advanced a further mechanism whereby parasites may evolve independently from their hosts. If mites are specifically preadapted to living in a particular microhabitat, they may be able to colonize distantly related host groups as long as this microhabitat (resource) is the same. Thus, the parasite tracks a resource and evolves independently of the host's evolution. However, most authors, including Atyeo and Gaud (1979), suggest that co-evolution between parasite and host is the norm among feather mite superfamilies Freyanoidea and Pterolichoidea. In a study on cuckoos, it was found that transfer of feather mites from passerine foster parents to cuckoo chicks in the nest was not successful (Atyeo and Gaud, 1983). Additionally, contact between disparate avian groups is unlikely due to geographical,behavioral, and morphological isolating mechanisms.

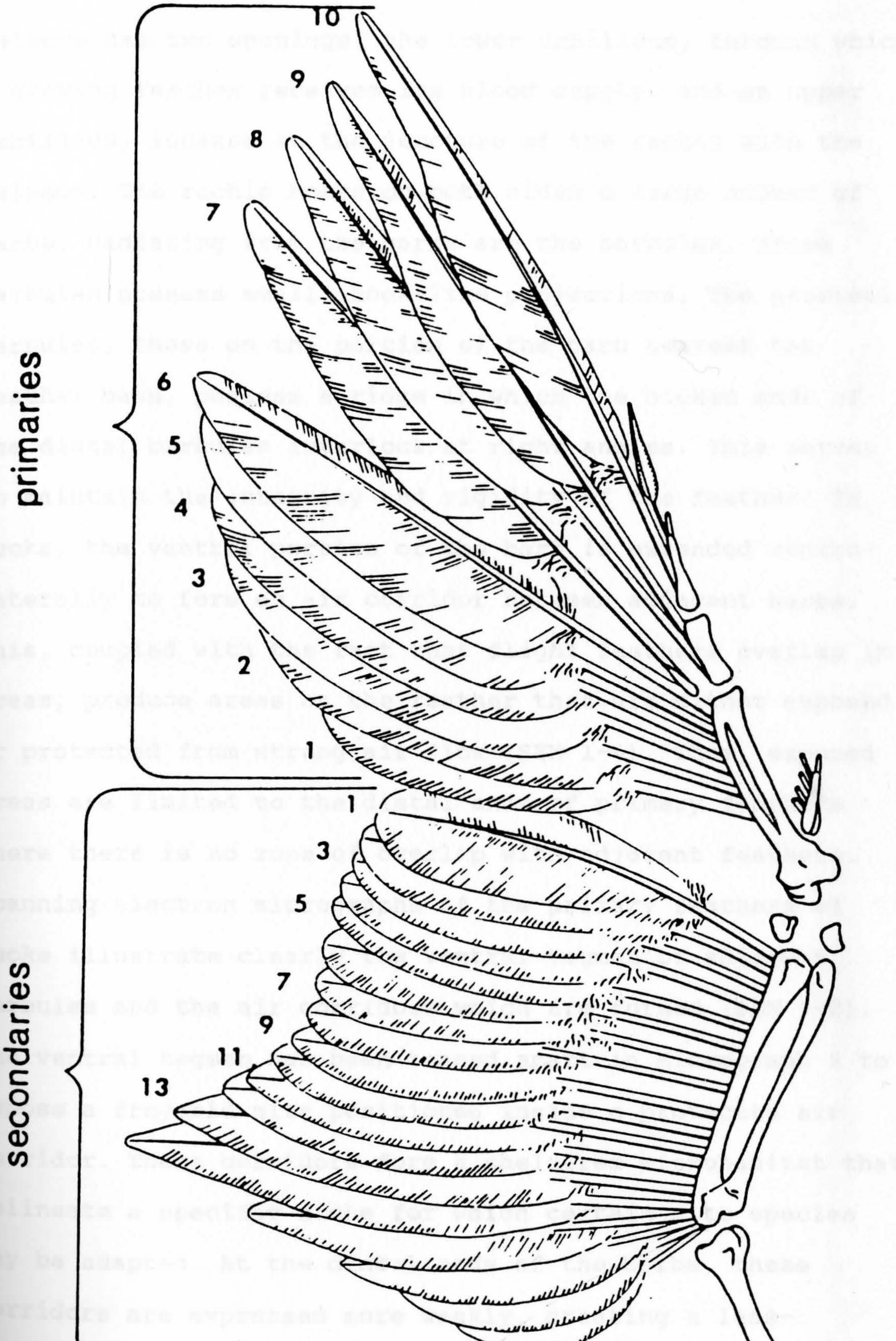
In order to understand the co-evolution of feather mites with their hosts, it is important to investigate the feather microhabitats. There are five types of feathers found on birds: 1) the large stiff feathers of the wings and tail (remiges and retrices, respectively); 2) contour feathers that cover most of the body, firm-vaned distally but loose webbed proximally; 3) filoplumes, specialized, hair-like feathers; and 5) bristles, small soft feathers lacking a vane. The primary feathers are those feathers attached to the carpo-metacarpus and digits II and III. Secondary flight feathers are those feathers attached to the dorsal side of the ulna. Figure 1 illustrates the feather positioning and numbering system in a typical avian wing. Feather mites, including Freyana spp., usually occupy positions along the rachis of primary feathers 1-6 and secondary feathers 1-13 (Peterson, 1975). Micrograph 2 shows a freyanid mite positioned at the juncture of the rachis with the feather barbs.

New feathers must form each time a bird undergoes a molt. After a feather is shed, the papilla (or feather follicle), is reactivated. Thereafter, a pinfeather emerges covered in a horny cutaneous sheath. After the feather has grown to a certain length, the tip of the growing feather eventually pierces the apex of the sheath. The feather continues to grow and the sheath is normally removed through preening activities of the bird.

The remiges of the wing consist of a central shaft and adjacent vane. The shaft is composed of two parts: the cylindrical and hollow calamus whose base is imbedded in the feather follicle in the skin, and the distal rachis. The

Figure 1

Diagram of a wing showing primary and secondary feathers (after Lucas and Stettenheim, 1972).

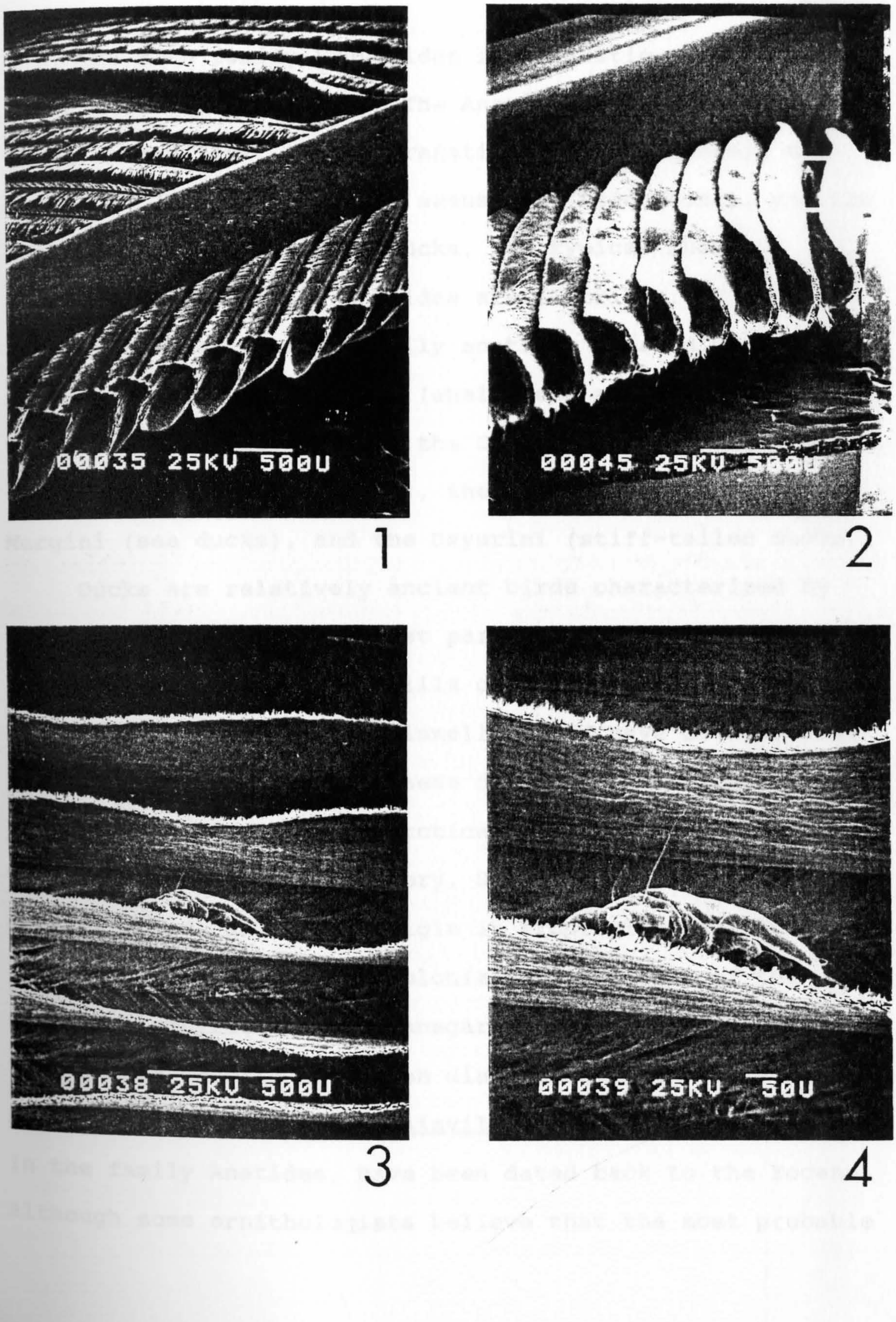


1

calamus has two openings: the lower umbilicus, through which a growing feather receives its blood supply, and an upper umbilicus, located at the juncture of the rachis with the calamus. The rachis bears on both sides a large number of barbs. Radiating from the barbs are the barbules. These barbules possess small, hook-like projections. The proximal barbules, those on the portion of the barb nearest the feather base, possess a ridge in which the hooked ends of the distal barbules interlock at right angles. This serves to maintain the integrity and rigidity of the feather. In ducks, the ventral portion of the barb is extended ventro-laterally to form an air corridor between adjacent barbs. This, coupled with the fact that flight feathers overlap in areas, produce areas on the feather that are either exposed or protected from strong air flow (SEM 1-4). Thus, exposed areas are limited to the distal ends of primary feathers where there is no zone of overlap with adjacent feathers. Scanning electron micrographs of the primary feathers of ducks illustrate clearly the ventral tegmen of adjacent barbules and the air corridors which are formed (SEM 1-2). The ventral tegmen has been teased apart in Micrograph 2 to expose a freyanid mite positioned inside a protected air corridor. These corridors form a sheltered microhabitat that delineate a specific niche for which certain mite species may be adapted. At the distal ends of the barbs, these corridors are expressed more weakly, creating a less-sheltered habitat that may be exploited by a different species of mite. The exposed areas of a typical anatid feather are shown in Micrographs 3 and 4. These photos also reveal the position of a freyanid mite located at the distal ends of the barbs.

SEM Micrographs 1-4

1,Primary feather from anatid showing characteristic air corridors (28X). 2,freyanid mite (in box) located within protected corridor (40X). 3,freyanid mite situated in exposed section of feather (72X). 4,close-up of SEM microgaph 3 showing position of tactile setae (140X).


00035 25KV 500U
1
00045 25KV 500U
2
00038 25KV 500U
3
00039 25KV 50U
4

HOST

The mite family Freyanidae is parasitic only on the waterfowl family Anatidae. The Anatidae are subdivided into three subfamilies: the Anseranatinae (magpie goose), the Anserinae (whistling ducks, swans, and true geese), and the anatinae (sheldgeese, shelducks, and typical ducks). Included in the family Anatidae are 11 tribes, 43 genera, and 146 species. The subfamily anatinae is subdivided into seven tribes: The Tadornini (sheldgeese and shelducks), the Tachyerini (steamer ducks), the Cairinini (perching ducks), the Anatini (dabbling ducks), the Aythyini (pochards), the Mergini (sea ducks), and the Oxyurini (stiff-tailed ducks).

Ducks are relatively ancient birds characterized by having feet that are at least partially webbed to increase swimming efficiency, have bills of various shapes with specialized development of lamellae, and have down-covered young. Zoogeographically, these ducks are distributed on every continent except Antarctica, and many of these waterfowl are highly migratory. Some ornitholgists believe that waterfowl had their origin in tropical areas, but radiated and succeeded in colonizing grasslands of the northern temperate zone (Johnsgard, 1968).

Anatid fossils have been discovered that are over 50 million years old. Both Romainvilla and Eonessa, classified in the family Anatidae, have been dated back to the Eocene. Although some ornithologists believe that the most probable waterfowl ancestor was related to the flamingoes and storks, the consensus is that a gallinaceous ancestor related to birds such as chachalacas gave rise to the Anatidae (Johnsgard, 1968).

The duck investigated in this study is Hartlaub's duck, Pteronetta hartlaubi Cassin, 1859, a perching duck belonging to the Cairinini. Inhabiting equatorial Africa from Sierra Leone and Liberia, south to northern Angola, east to southern Sudan, Cameroun, Gabon, and Zaire, this species does not migrate to distant breeding or wintering grounds (Soothill, 1988). It is described as being rather sedentary, preferring to shelter around heavily overgrown riverbanks. In addition, Soothill (1988) reports that this duck does not fly long distances. Daily flights are usually limited to nearby feeding grounds. Hartlaub's duck is basically a brownish bird, with chestnut shading on its chest, fading into an olive-brown rump. The upper wing coverts are distinctively blue. The head and neck are black in males and brown in females. The bill is colored black with a light-colored band at its tip. Overall size of this species is about 55-60 cm., about the size of a mallard. Like other members of the Cairinini, Hartlaub's duck is a cavity nester in trees. Incubation of the eggs takes approximately 32 days and the young are fledged in about eight weeks. The duck is omnivorous in that it consumes both plant and animal matter with worms, spiders, snails, and aquatic insects and their larvae making up a substantial portion of its diet.

A thorough analysis of the ectoparasites of Pteronetta hartlaubi reveals two species of freyanids commonly found on it. Freyana largifolia and Freyana reticulata n. sp. have been recorded on the primary feathers of this duck.

THE GENUS <u>Freyana</u> HALLER, 1877

The earliest taxonomic studies on the genus Freyana was carried out by Haller (1877), in which he described Freyana anatina. Megnin and Trouessart (1884) conducted further research which led to the recognition of five subspecies of Freyana anatina. Canestrini (1899) did not recognize the trinomial designation as legitimate and regarded the subspecies as synonymous with the type. Berlese (1898) did further systematic revisions on the genus but added to the confusion by publishing a species description of Freyana anatina that erroneously contained F. largifolia characters. Dubinin (1950, 1953) described 12 additional species 11 subspecies of Freyana anatina, and 8 subspecies of Freyana largifolia. Currently, these subspecies are being elevated to the rank of full species. The recognized species and subspecies of the genus Freyana are listed along with their hosts in Table 1 (pg. 3).

The preceding species descriptions were limited to a discussion of adult morphology. This study includes detailed descriptions of all nymphal stages and adult morphotypes of Freyana anatina, Freyana largifolia, and Freyana reticulata n. sp. The life history of freyanids is uniform throughout the genus. Females may be either oviparous or ovoviviparous. Eggs are usually laid where the feather barb meets the rachis. The larvae contain only three pairs of legs, in contrast to the normal four pairs found in adults and nymphs. There are characteristically fewer setae than in the adult condition (Fig. 29-30, Table 3). Sclerotization is minimal, usually limited to small areas of the propodosomal and hysterosomal shields. There are no external sexual organs present.

Protonymphs have four pairs of legs, and possess most of the setae present in the adult condition (Fig. 23-24, Table 3). There is one pair of genital discs present, but no copulatory opening. The protonymph is larger and is slightly more sclerotized than the larvae.

The tritonymph possesses the full complement of setae present as in adults (Fig. 17-18, Table 2), and has two pairs of genital discs. Although not as fully sclerotized as the adults, tritonymphs show greater sclerotization than previous instars. Still, there is no development of external sexual organs, and sexual dimorphism is slight. However, the female does possess a copulative opening (genital pore) on the terminal end of the dorsal hysterosoma. Female tritonymphs are able to copulate at this stage.

Adults are characterized by a heavy sclerotization and a complete complement of sexual organs. Males possess adanal discs for adhering to the female during copulation. A unique character among males of the genus <u>Freyana</u> is a consistent pattern of dimorphism. The homeomorphic male resembles the female superficially. The degree of sclerotization of the coxal-sternal skeleton and the tibial expansions on legs II of homeomorphs (Fig. 10, 42, 74, SEM 10, 37, 52) parallel the female condition (Fig. 14, 46, 78, SEM 14, 41, 56) . Conversely, heteromorphic males are distinguished by their pronounced degree of sclerotization (Fig. 3, 35, 67). The coxal-sternal skeleton displays a greater degree of fusion of the epimerites (Fig. 9, 41, 73) than in the homeomorphic form. The tibia of legs II are hypertrophied with characteristic "horns" located at the dorsal terminus of this segment (Fig. 5, 37, 69, SEM 6, 33, 48). Terminal setae and lateral lamellae (chitinous expansions extending from the lateral edge of the hysterosoma) may also be enlarged and elongated (Fig. 34-35, SEM 34).

The evolutionary significance of heteromorphy remains obscure. Dubinin (1951) suggested that enlarged tibial expansions and elongated terminal setae serve to attach a copulating male to the female and/or the feather. Supposedly, males must not only remain affixed to the feather, but must grasp the female during copulation. However, this hypothesis seems inadequate considering the fact that homeomorphic males have a fully developed complement of reproductive organs and lack such expansions. There is no evidence to date to suggest that only heteromorphic males mate, and homeomorphic males do not. Furthermore, it seems improbable that the long, slender terminal setae of heteromorphic males could function as an effective anchoring mechanism.

A study conducted by Dubinin (1951) on the feather mites parasitic on <u>Anas platyrhynchos</u>, the mallard duck, may provide some insight into the adaptive significance of enlarged tibia and terminal setae of freyanids. Freyana anatina and F. largifolia co-inhabit the primary feathers of this duck. Dubinin postulated that Freyana anatina is adapted to those portions of the wings where air-corridors are prominent (SEM 1-2), while F. largifolia inhabits the exposed distal portions of the primaries (SEM 3-4). If this is true, these two species have undergone niche partitioning in their respective feather microhabitats. This hypothesis may pertain to heteromorphy as well. Freyana largifolia has large tibial expansions on legs II (Fig,37, SEM 33), supposedly serving as anchoring mechanisms in areas exposed to turbulent air flow. In this regard, F. anatina heteromorphic males (Fig. 5, SEM 10) are very similar to F. largifolia homeomorphic males. If enlarged tibial expansions are adaptations for attachment in exposed feather areas, then it follows that perhaps the heteromorphic form of F. anatina likewise occupies this niche, whereas the homeomorphic form would be expected to occupy the protected air corridors.

Bird migration may be associated with freyanid dimorphism if increased feather attachment is indeed a major function of heteromorphic characters. Most anatids undergo substantial annual migrations from breeding grounds to wintering areas. Prolonged flights may expose ectoparasites to unusually strong and protracted air currents threatening to dislodge them. Under these circumstances, one would expect heteromorphic forms to be able to adhere better, especially in distal feather zones. Some ducks, however, such as Pteronetta hartlaubi, do not exhibit migratory behavior. If heteromorphy is an adaptation for fixation during migration, one might expect heteromorphism to be absent or reduced in non-migratory ducks.

Timms (1981) suggested that environmental conditions, specifically crowding, induced decreased incidence of heteromorphy. However, it is not clear at what stage heteromorphic development is induced. Whether eggs are predetermined to develop their designated morphotype, or whether the larvae and nymphal instars are subject to change during ontogeny because of environmental stress, remains unknown. In a cross-rearing study of the astigmatid mite Sancassania berlesei, which exhibits varying degrees of andropolymorphism, it was determined that the ratios of male morphotypes was independent of the morphotype of the male parent (Timms, 1981).

If crowding significantly affects the development of heteromorphic characters in mites, then it is plausible that the molting period of the bird presents a significant environmental stress on its associated mites to affect heteromorphy. Ginetzinskaya (1942) reported that F. anatina moved from the usual place of habitation on the feather vane during the moult of the host. Some stimulus apparently caused the mites to reposition their site of localization to a developing pinfeather. They amass at the base of the apical horny sheath of the pinfeather. During this stage the mites are subjected to extreme crowding conditions. As the feather continues to grow, the mites migrate along the feather shaft and presumably position themselves along the barbs of the mature flight feathers (Ginetzivskaya, 1942).

MATERIALS AND METHODS

Feather mites for this study were obtained from the collection at the University of Georgia, Athens, Georgia (UGA) and the United States National Museum, Smithsonian Institution, Washington D.C. (USNM). Previously collected mites from UGA were stored in 70% ethanol. Specimens from USNM were collected by scraping museum study skins according to specific feather zonation. For morphometric analysis, mites were cleared in lactophenol, heated to 100 degrees C for twenty minutes, and subsequently mounted on microscope slides using Hoyer's mounting media. Specimens were examined using a Wild-Heerbrug phase contrast microscope equipped with a drawing tube.

Detailed morphological analysis was conducted using a Hitachi S-450 scanning electron microscope. Specimens were prepared by washing in Markson detergent and sonicating for one minute to remove debris. Mites were then subjected to dehydration with alcohol using concentrations of 70%, 90%, 95%, and 100% ethanol. After drying, the specimens were sputter-coated with gold to a thickness of 18 angstroms using a Polaron E5100 sputter-coater. Accelerating voltage was maintained at 25 kV. Photographs were taken using type 52 and 55 Polaroid film. The chaetotaxal designations used in this paper are from Atyeo and Gaud (1966).

EXTERNAL MORPHOLOGY
(Fig. 2-7)

The external morphology of freyanids shall be summarized by examining the adult condition in Freyana anatina. Dorsal Idiosoma: The propodosoma is generally triangular in shape, with an extended tectum partially covering the dorsal aspect of the gnathosoma. There are four pairs of setae located on the propodosoma: the long, setiform external scapular (sce), the short internal scapular (sci), and the very small vertical internal (vi) and vertical external (ve) setae (Fig.2). In some freyanids, as demonstrated by electron microscopy, there exists a small sclerotized projection which extends from the lateral margin of the propodosomal shield at the level of the articulation of leg I (SEM 24-27). This character has not been previously described and may have taxonomical significance.

A transverse suture separates the propodosoma from the hysterosoma. This suture may be very narrow, form a deep furrow, or consist of striated tissue. The dorsal hysterosoma bears 10 pairs of setae (Fig.2): dorsal setae d1-d5, and lateral setae l1-l5. Setae dI-d3 are short and setiform. Setae d4 and d5 are usually long and may have leaf-like lateral extensions at their base. Setae l1-l3 are short and setiform. Setae l4 and l5 are variable in shape and are usually very long. A pair of ventral post-anal external setae (pae) are present as well as a pair of postanal internal (pai) setae. The latter are situated medially on the terminal end of the hysterosoma and are of diagnostic significance in differentiating between species, sexes, and morphs.

Ventral Idiosoma: The coxal-sternal skeleton and associated epimerites are primary characters in distinguishing among species of freyanids. Epimerites IA and II fuse to form coxal field I. Epimerites II and IIA form a well-defined coxal field II. Coxal fields III and IV are likewise delineated by their respective epimerites. According to the degree of sclerotization, the coxal fields may be open or closed. This is an important distinguishing feature among freyanid species and their morphotypes.

There are 9 pairs of setae associated with the ventral idiosoma (Fig. 3). The humeral (h) and subhumeral (sh) setae are located on the lateral margins of the hysterosoma, posterior to the transverse suture. The humerals are much longer than the subhumerals. Coxal field I incorporates sternal seta (s), which is uniformly small and setiform. Coxal seta (cx3) is located within coxal field III. Additionally, there are three pairs of central setae: c1, c2, and c3. Adanal seta (a) is located anterior to seta pai. Thus, in males, the adanal setae are positioned directly anterior to the adanal discs.

Leg Chaetotaxy (Fig. 4-7): In feather mites, larvae possess three pairs of legs, while adult mites and nymphs have four pairs. The legs are composed of seven segments:

coxa, trochanter, femur, genu, tibia, tarsus, and pretarsus. The pretarsus is modified into a rounded ambulacrum. Some setae are lacking in the larvae and protonymphs that are found in the adults (Table 2). The discussion of leg chaetotaxy will focus on the full complement of setae on each segment, as observed in the adult (Fig.4-7). The leg chaetotaxy of larvae and protonymphs can be compared with the adult using table 3.

In leg I the trochanter contains one seta, pR. Likewise, seta vF is the single seta associated with the femur. The genu bears two setae, cG and mG, as well as two solenidia, σ_1 and σ_2. Positioned on the tibia is seta gT, a short tactile seta, as well as a long solenidion, φ. The tarsus of leg I of <u>Freyana</u> spp. bears 9 setae: ba, d, ε, f, e, s, ra, la, and wa (Fig. 4, SEM 30). Seta   has not been described in previous literature, presumably because of its very small size (<5 microns). The seta is positioned between setae ba and d (SEM 28-29). Two solenidia are also located here: ω_1 and ω_3 (SEM 31). Finally, the pretarsus is modified into an ovoid ambulacrum that usually possesses an apical process.

On leg II all setae are present as in leg I except for the absence of σ_2 and ω_3, on the genu and tarsus, respectively. Many setae, however, are repositioned due to the hypertrophy of the tibia in heteromorphic males.

The seta on leg III on the trochanter is designated sR. Seta vF is absent, as well as σ_2, cG and mG. Tibia III bears the solenidion θ and setae kT. The tarsus contains six setae: d, f, e, r, w$'$, and w$''$.

On leg IV, no setae are located on the trochanter, femur, or genu. The tibia and tarsus have the same chaetotaxy as found in the corresponding segments of leg III.

TABLE 2. LEG CHAETOTAXY OF ADULTS AND TRITONYMPH OF F. ANATINA

	Leg							
Segment	I		II		III		IV	
	Seta	Sol	Seta	Sol	Seta	Sol	Seta	Sol
Trochanter	1	0	1	0	1	0	0	0
Femur	1	0	1	0	0	0	0	0
Genu	2	2	2	1	0	1	0	0
Tibia	1	1	1	1	1	1	1	1
Tarsus	9	2	8	1	6	0	6	0

TABLE 3. LEG CHAETOTAXY OF PROTONYMPH AND LARVA OF *F*. *ANATINA*

Segment	Leg							
	I		II		III		IV	
	Seta	Sol	Seta	Sol	Seta	Sol	Seta	Sol
Trochanter	0	0	0	0	0	0	0	0
Femur	1	0	1	0	0	0	0	0
Genu	2	2	2	1	0	1	0	0
Tibia	1	1	1	1	1	1	1	0
Tarsus	9	1	8	1	6	0	4	0

Freyana anatina Haller

(Figs.2-33,SEM 5-19)

Haller, 1877, Zwei. neue Millbengattungen. Z. wiss. Zool., 30: 98-99.

Megnin et Trouessart, 1884, Journ. Microgr., 8 (2) : 99-100.

Trouessart et Megnin, 1885, Bull. Soc. Angers, 14 : 37, fig. 5.

Ginetzinskaya, 1942, Acad. Sciences USSR, 37(4) : 170-173.

Ginetzinskaya, 1949, Scientific Notes of Leningrad State Univ., Problems of Ecol. Parasit., 19(4) : 92, 103-107.

Dubinin, 1950, Akad. Nauk. USSR, 6(5) : 1-363, fig 10.

Dubinin, 1951, Parazit. Sb., 13 : 211, 214.

Radford, 1953, Parasitology, 42 (3-4) : 199.

Dubinin, 1953, Fauna of the USSR, 6(6) : 251-252, fig.100.

This species parasitizes a number of ducks belonging to the genus Anas. Dubinin (1951) stated that F. anatina, along with Freyana largifolia, parasitize the common mallard, Anas platyrhynchos. Adults are easily distinguished from other freyanids by the size and shape of the terminal setae (l3, l4, l5, d4, d5, and pai). Additional distinguishing characters include the presence of seta ve, absence of the propodosomal projection, shape and size of tibial expansions of legs II, development of the coxal-sternal skeleton, and pattern on the hysterosomal shield. The following is a re-description of F. anatina including both morphotypes of the male. Specimens were collected from the type host, Anas platyrhynchos, as well as from other ducks in the genus.

Heteromorphic Male (Fig.2-7, SEM 5-8): Length 654 μ,c.v.=4%. Width 408 μ.c.v.=5%. Dorsal Idiosoma: Propodosomal shield well developed, with fine "granulated" appearance. Seta vi small, setiform; located on anterior margin of propodosomal shield. Seta ve small, setiform; positioned within shallow depression medial to leg I. Propodosomal projection absent. Setae sce and sci on posterior margin of propodosomal shield. Seta sce long, setiform. Seta sci short, setiform, located at same level as seta sce. The transverse suture is prominent, relatively narrow. Hysterosomal shield well developed, with a fine granulated appearance superimposed by numerous small lacunae. Lateral lamellae well developed, extending from insertion of setae d2 to l4. Setae d1-d3 as microsetae. Seta d4 medium length, positioned on dorsum between insertions of setae l5 and d5. Lateral setae l1 and l2 short, setiform. Seta l3 long, setiform; seta l4 lanceolate. Seta l5 long, setiform. Seta d5 long, setiform with expanded leaf-like lateral extensions at insertion. Seta pai characteristically boot-shaped (Fig. 2, SEM 8).

Ventral Idiosoma: Coxal-sternal skeleton strongly fused, forming closed coxal fields I-IV. Genital organ positioned between setae c2 and c3 at level of legs IV. Large adanal discs present. Sternal seta (s) located within coxal field I. Subhumeral seta (sh) positioned at same level as humeral seta (h). Coxal field III with coxal seta cx3. Three pairs of medial setae: c1, c2, c3. Adanal seta (a) anterior to adanal discs. External postanal seta (pae) anterior to insertion of seta 14. Gnathosoma: Chelicerae placed medially. Short, movable digit located ventrally. Palpi lateral, closely appressed to chelicerae (SEM 20-23). Palps with two segments bearing three setae : ventral (V), dorsal (d), and supracoxal setae (elc p) (SEM 21). A single short apical solenidion ω_3 positioned distally. Ventrally, gnathosoma composed of subcapitulum with hypostome. Pseudorutellar process located lateral to hypostome. Legs: (Fig.4-7, SEM 6). Typical leg setation as found in all Freyana spp. Note solenidia σ_2 in the genu, which has been omitted from most descriptions, as well as newly discovered seta ε on the tarsus. Dorsal horn on tibia of legs II characteristic of heteromorphic male.

Homeomorphic Male: (Fig. 8-10, SEM 9-12): Length 630 μ, c.v.=9%. Width 375 μ, c.v.=6%. Can be distinguished from heteromorphic male by the coxal-sternal skeleton, the tibial expansions of legs II, and the size and shape of terminal setae. Dorsal Idiosoma: Propodosomal shield heavily sclerotized, with setae ve and vi as in heteromorphic male. Hysterosomal shield well-developed, with a granular texture, marked by numerous small lacunae. Lateral lamellae narrower than in heteromorph. Terminal hysterosomal setae (l5, d4, d5) similar to heteromorph. Seta pai boot-shaped (SEM 12), broader than in heteromorph. Ventral Idiosoma: Coxal-sternal skeleton not as strongly fused as in heteromorph. Epimerites I fused; with coxal field I open. Epimerites II and IIA not fused; with coxal field II open. Epimerites III and IIIA fused forming closed coxal field III. Genital organ positioned between setae c2 and c3, at level of leg IV. Seta pae short, setiform, located anterioventral to insertion of seta 14. Legs: As in heteromorph, except tibial expansion on legs II not as pronounced (Fig. 10, SEM 10).

Female (Fig. 11-16, SEM 13-16): Length 583 µ, c.v.=5%. Width 386 µ, c.v.=5%. Female with more pronounced rectangular shape than males. Dorsal Idiosoma: Propodosomal shield as in homeomorphic male. Hysterosomal shield well developed, with granular texture and marked by very small lacunae. Posterior portion of hysterosoma with prominent oval lacunae. Lateral lamellae as in homeomorphic male. Seta 14 lanceolate, shorter than in males. Seta 15 long, setiform. Seta d5 long, setiform, with small membranous expansions at the base. Seta pai is characteristically oar-shaped (Fig.11, SEM 16). Ventral Idiosoma: Coxal-sternal skeleton weakly sclerotized. Coxal fields I, II, and III open. Prominent semilunar pregenital apodeme at level of epimerites II. Legs (Fig. 13-16, SEM 14): as in homeomorphic male.

Tritonymph (Fig. 17-22, SEM 17): Length 544 µ, c.v.=3%, Width 329 µ, c.v.=4%. Tritonymph with the same leg chaetotaxy, idiosomal setae, and number of genital discs as the adult.

Tritonymph weakly sclerotized. No external genitalia present in males. Dorsal Idiosoma: Propodosomal shield weakly sclerotized, with setae ve and vi present. Propodosomal projection absent. Setae sce and sci located posterior to propodosomal shield at anterior margin of band of striated, unsclerotized tissue. Lateral lamellae narrow, extending from level of seta l2. Setae d1-d4, l1-l2, short, setiform. Seta l3 long, setiform. Seta l4 short, lanceolate. Terminal setae d5, l5 long, setiform. Seta pai short, lanceolate. Hysterosomal shield not as heavily sclerotized, and shorter in length than in the adult condition, marked with many very small lacunae. Ventral Idiosoma: Chaetotaxy as in adults. Coxal-sternal skeleton weakly formed with coxal fields I, II, and III open. Two pairs of genital discs located between setae c2 and c3 at level of insertions of legs IV. Female tritonymph has dorsal copulative opening. No external genitalia in male tritonymph.

Protonymph (Fig. 23-28, SEM 18): Length 474 µ,c.v.=3%, Width 266 µ,c.v.=4%. This instar is distinguished from the tritonymph by overall size, sclerotization, leg chaetotaxy, and number of genital discs present. Dorsal Idiosoma: Propodosomal shield less sclerotized than in tritonymph. Setae ve and vi present. Propodosomal projection absent. Setae sce and sci located directly posterior to posterior margin of propodosomal shield. Transverse suture separating propodosomal and hysterosomal shields. Band of striated, unsclerotized tissue between propodosomal and hysterosomal shields broader than in tritonymph. Hysterosomal shield smaller than in tritonymph, granular, and marked with many small lacunae. Lateral lamellae absent. Setae d1-d4 short, setiform. Setae l1, l2, and l4 short, setiform; l3 slightly longer, setiform. Setae d5 and l5 long, setiform. Seta pai short, lanceolate. <u>Ventral</u> <u>Idiosoma</u>: Coxal-sternal skeleton less-heavily sclerotized than in tritonymph. All coxal fields open. One pair of genital discs present. No genitalia present. Ventral idiosoma with seven pairs of setae; two central setae missing from adult condition. Legs: Setae on trochanters absent. Solenidion σ_2 absent. Tibial solenidion ϑ absent. On tarsus, seta f absent as well as seta w. Tibial expansions on legs II absent.

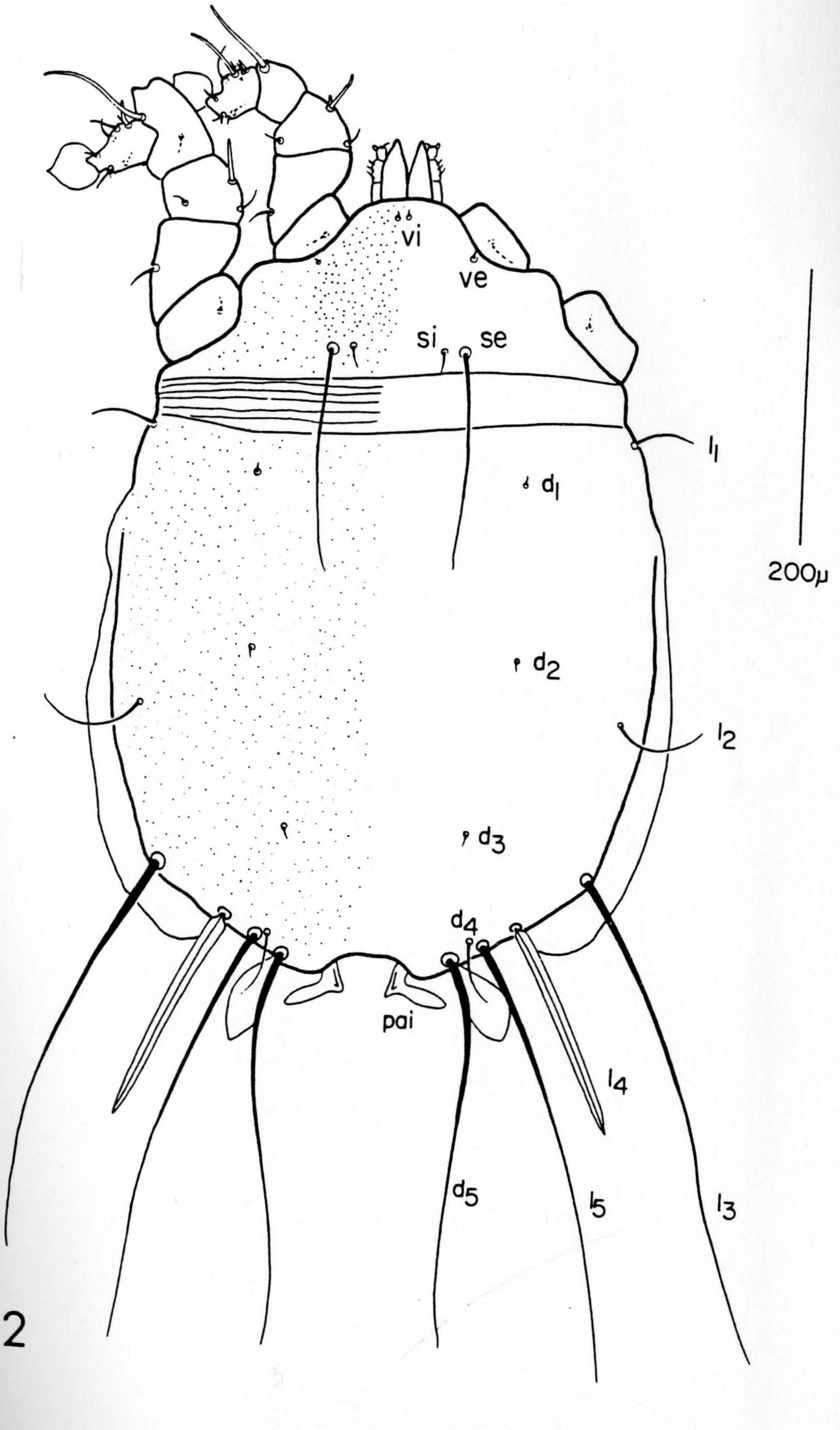
<u>Larvae</u> (Fig. 29-33, SEM 19): Length 398 , Width 203 ,(n=4, c.v.=n.a.) <u>Dorsal</u> <u>Idiosoma</u>: Propodosomal shield weakly sclerotized, granular, bearing setae ve, vi . Propodosomal projection absent. Setae sce and sci positioned on broad band of striated, unsclerotized tissue directly posterior to propodosomal shield. Hysterosomal shield weakly sclerotized, not extending to lateral margin of idiosoma. Hysterosomal shield with granular appearance, bearing numerous small lacunae. Setae d1-d3 short, setiform, with setae l4, l5, pai absent. Terminal seta d4(?) setiform. Seta d5(?) long setiform. Legs: As in protonymph, but lacking leg IV.

Materials examined: From Anas platyrhynchos: 3 heteromorphic males, 2 homeomorphic males, Hunting Creek and Potomac River, Va., 7-X-1989 (USNM 388711). 4 heteromorphic males, 1 homeomorphic male, Mobile Bay, Alabama, 3-XII-1915 (USNM 260170). 1 homeomorphic male, Mt. Vernon, Indiana, 9-II-1922 (USNM 286928). 7 heteromorphic males, Talbot Co., Maryland, 10-IV-1981 (USNM 598532). 1 heteromorphic male, 21 females, 16 tritonymphs, 15 protonymphs, 5 larvae, composite from Bayouha Botre, Alabama, 26-XI-1915 (USNM 260164), Nigger Lake, Alabama, 1-XII-1915 (USNM 260169), Mobile Bay, Alabama, 3-XII-1915 (USNM 260171), 2 heteromorphic males, 5 homeomorphic males, 6 females, Nagykanizsa, Hungary, 4-II-1954 (UGA 7726), 1 homeomorphic male, 2 tritonymphs, Varaszlo, Hungary, 24-VIII-1952 (UGA 7727), 1 heteromorphic male, 1 homeomorphic male, Tornyiszentmilos, Hungary, 7-II-1952 (UGA 7728).

Additional material: From Anas erythrorhyncha: 2 homeomorphic males, Cephepe, Bechuanaland Province, South Africa, 18-I-1956 (NU 2106). From Anas diazi: 3 homeomorphic males, 5 females, near Mexico City, Mexico, 27-VIII-1910 (AMNH 54124), 1 female, 15 mi. S. Hatch, New Mexico, 13-III-1933 (AMNH 749712).

Figure 2

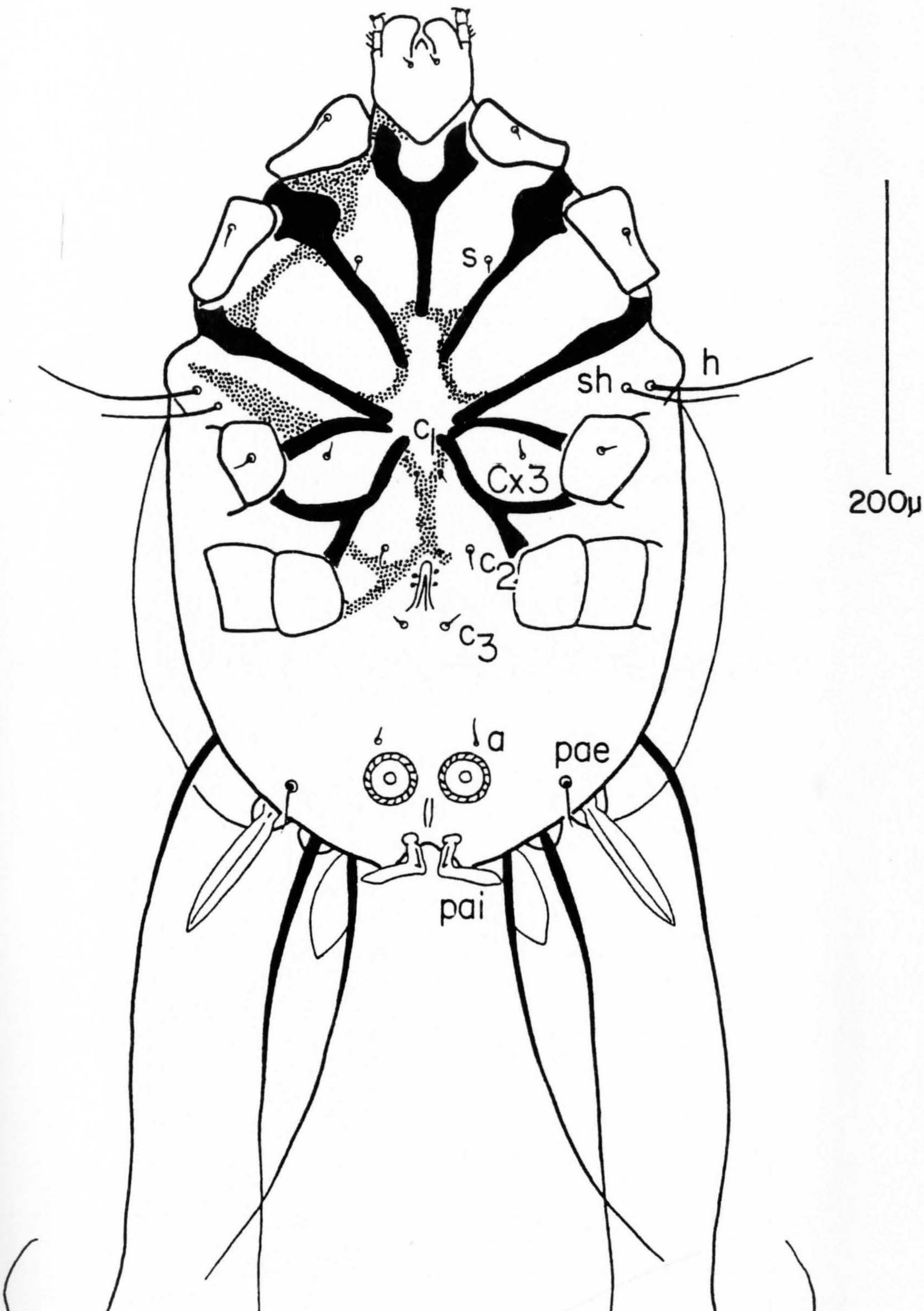
Freyana anatina heteromorphic male, dorsal aspect



2

Figure 3

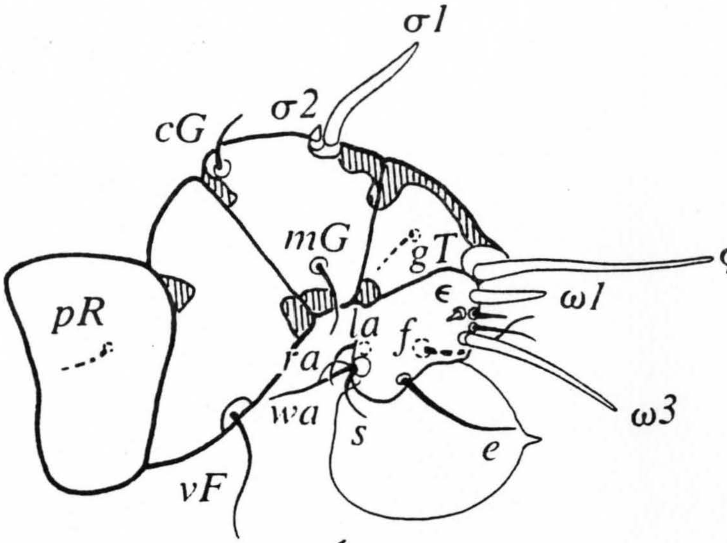
Freyana anatina heteromorphic male, ventral aspect



3

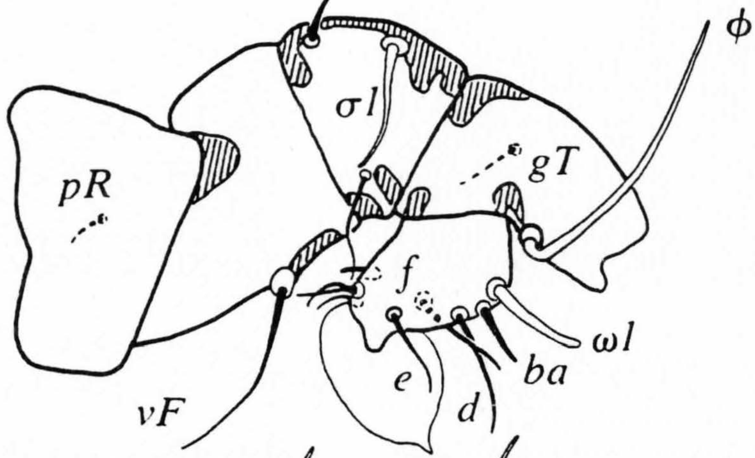
Figure 4-7

Freyana anatina heteromorphic male, antaxial aspects of legs. 4, leg I. 5, leg II. 6, leg III. 7, Leg IV.

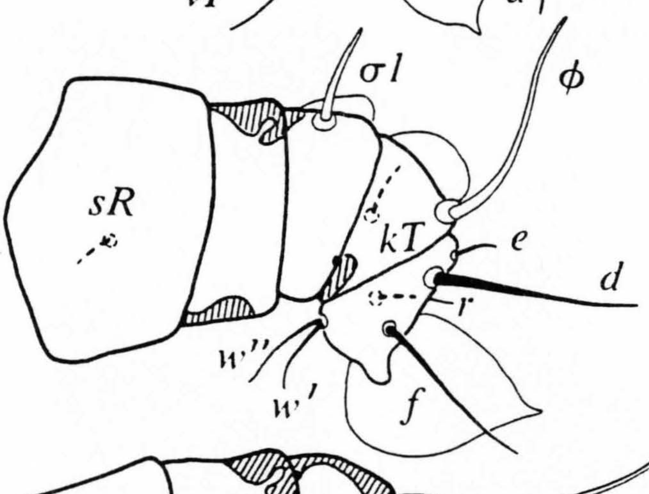
4


I

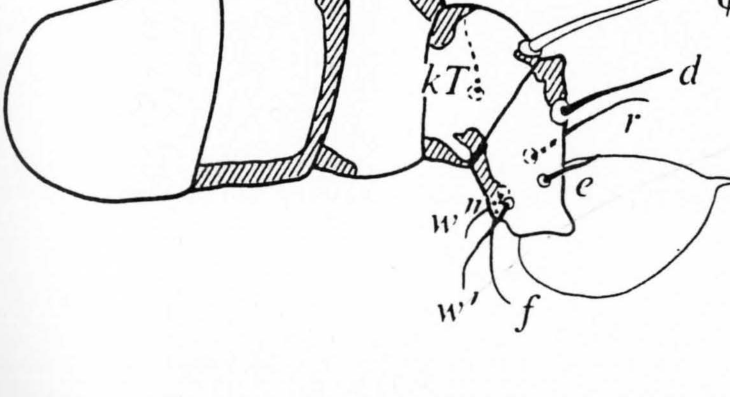
100µ

5


II

6


III

7


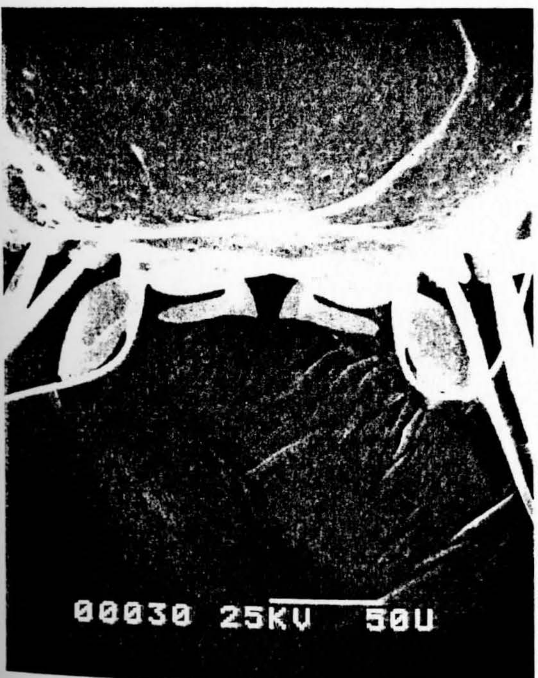
IV

SEM Micrographs 5-8

Freyana _anatina_ Haller, 1844 heteromorphic male. 5,dorsal aspect (180X). 6,leg II (1000X). 7,terminal setae (420X). 8,seta pai (1600 X).

5

6

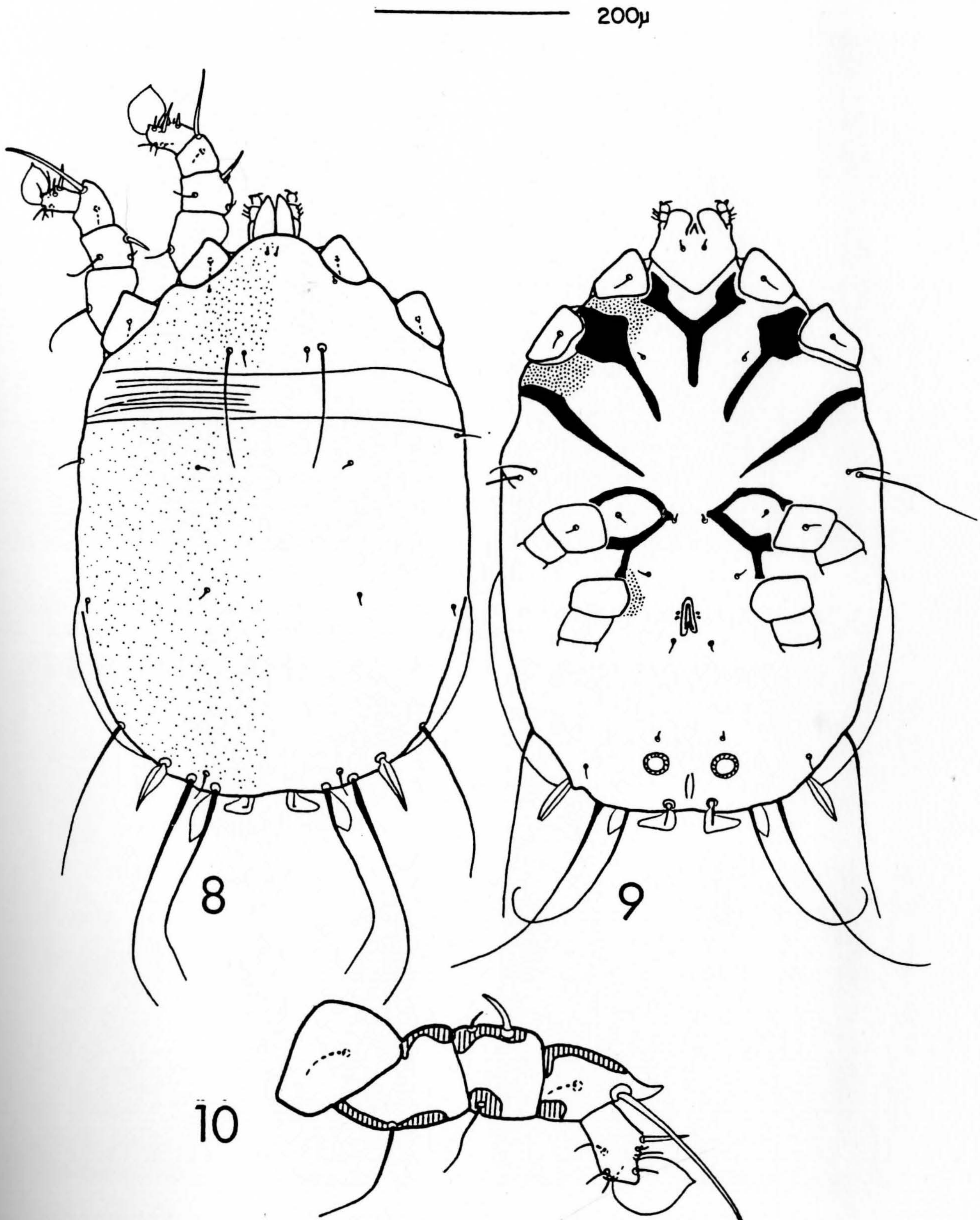


7

8

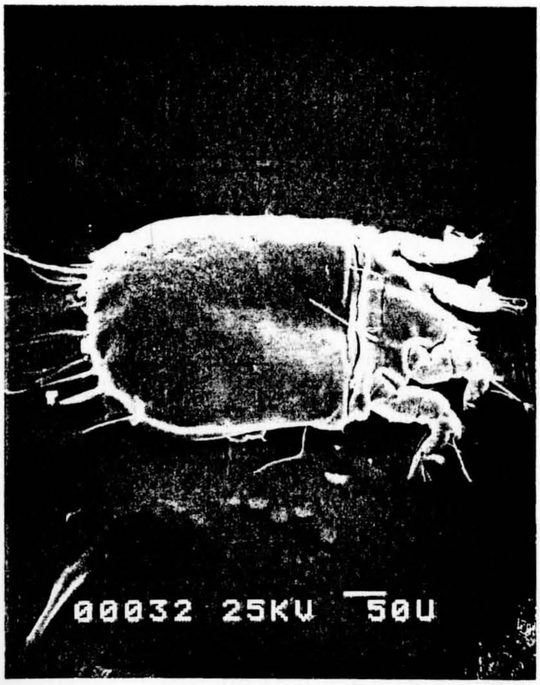
Figures 8-10

Freyana anatina homeomorphic male
8, dorsal aspect. 9, ventral aspect. 10, leg II.

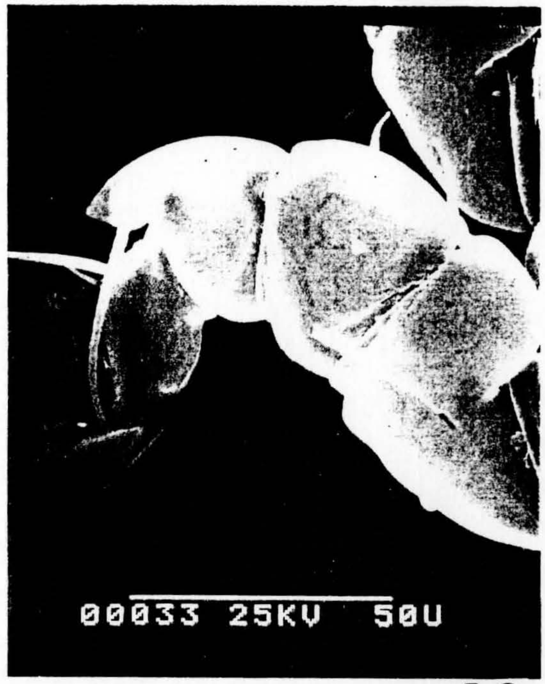

200µ
8
9
10
200µ

SEM Micrographs 9-12

<u>Freyana</u> <u>anatina</u> homeomorphic male. 9,dorsal aspect (140X). 10,leg II (920X). 11,terminal setae (300X). 12,seta pai (2500X).

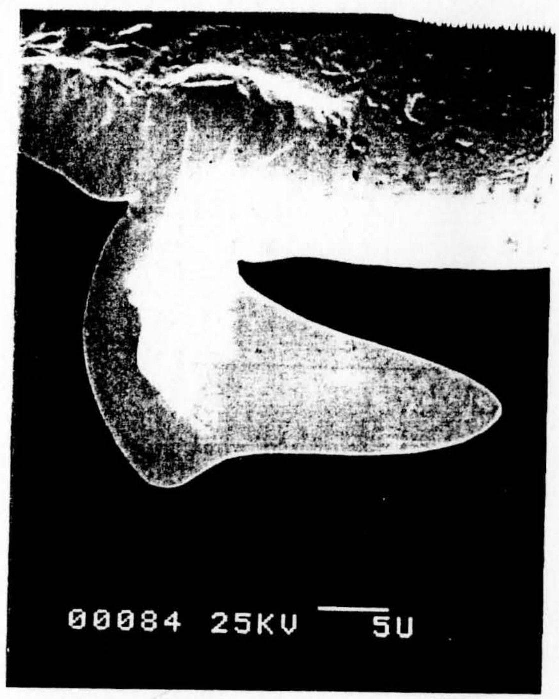


9



10

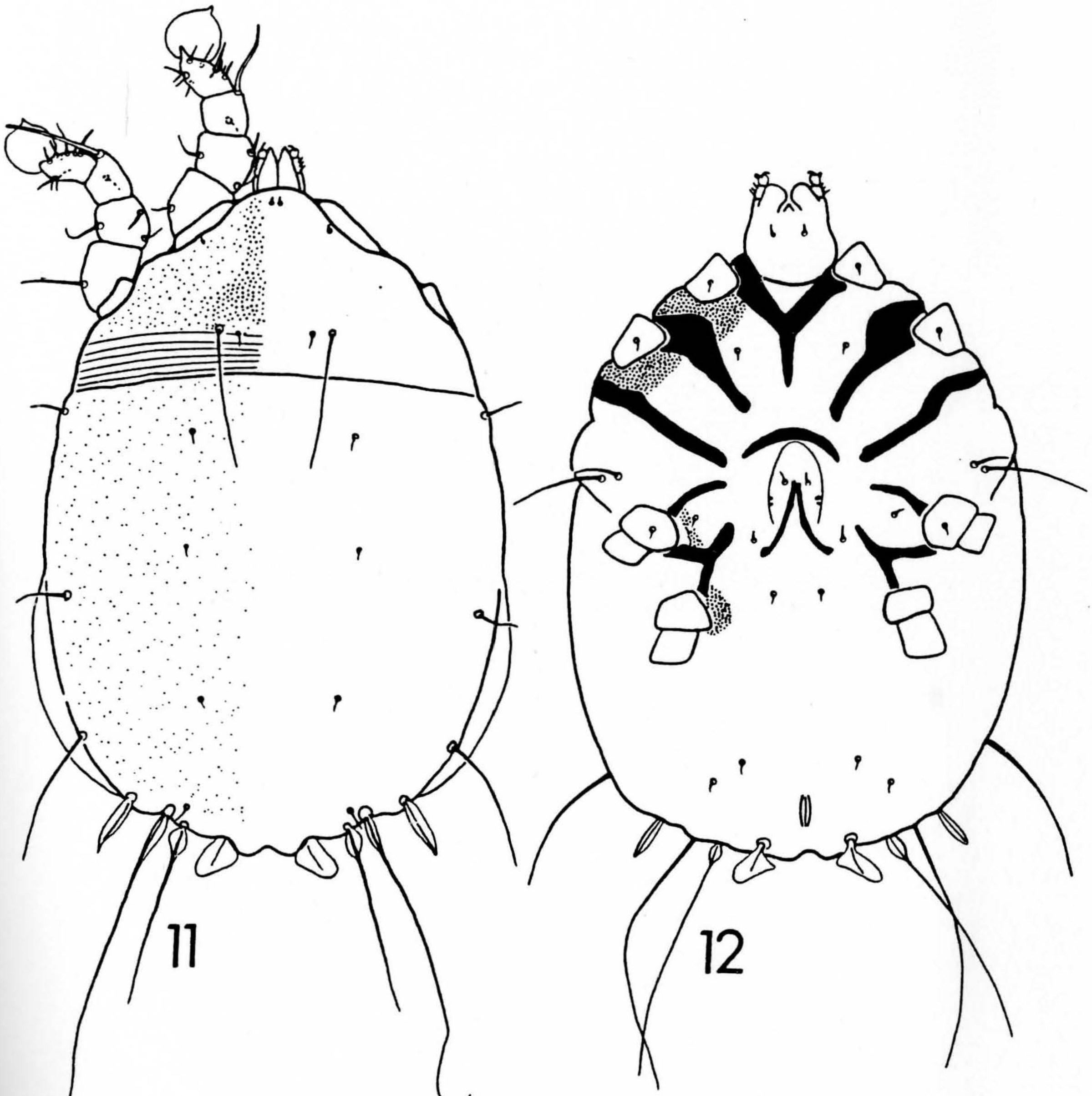
11



12

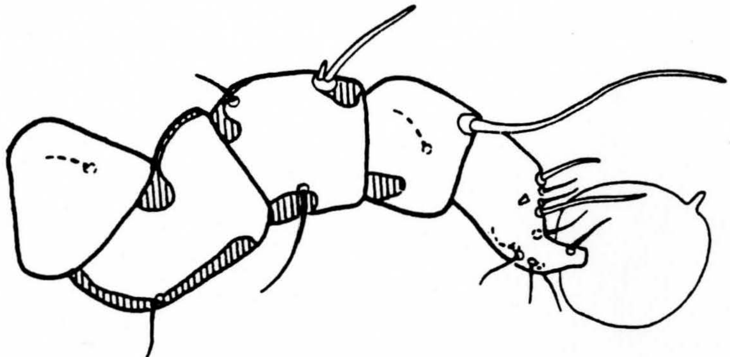
Figures 11-12

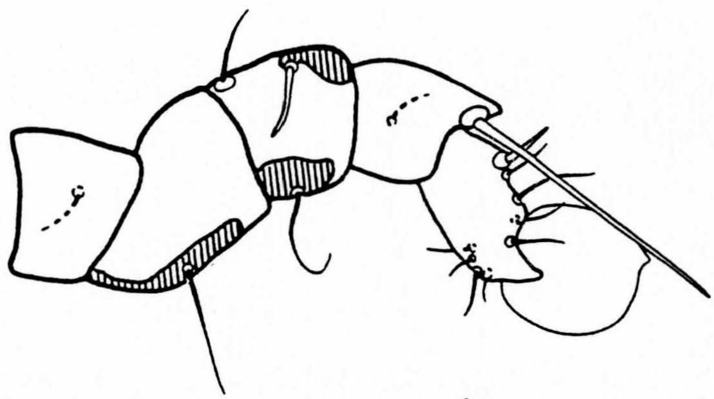
Freyana anatina female
11, dorsal aspect. 12, ventral aspect


11
12
200μ

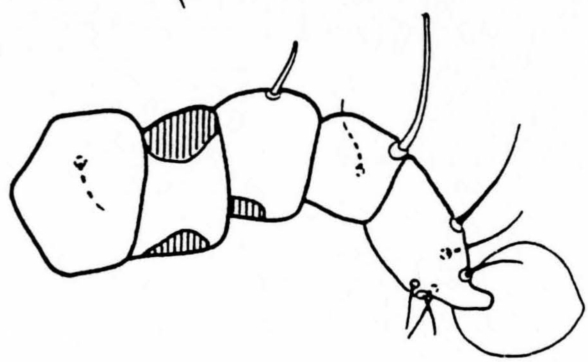
Figures 13-16

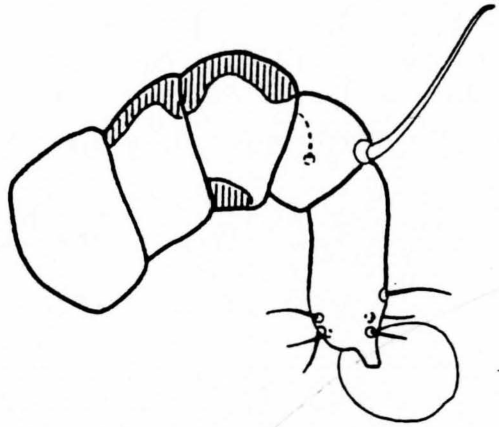
Freyana anatina female, antaxial aspects of legs. 13, leg I. 14, leg II. 15, leg III. 16, leg IV.

13

I

14

II

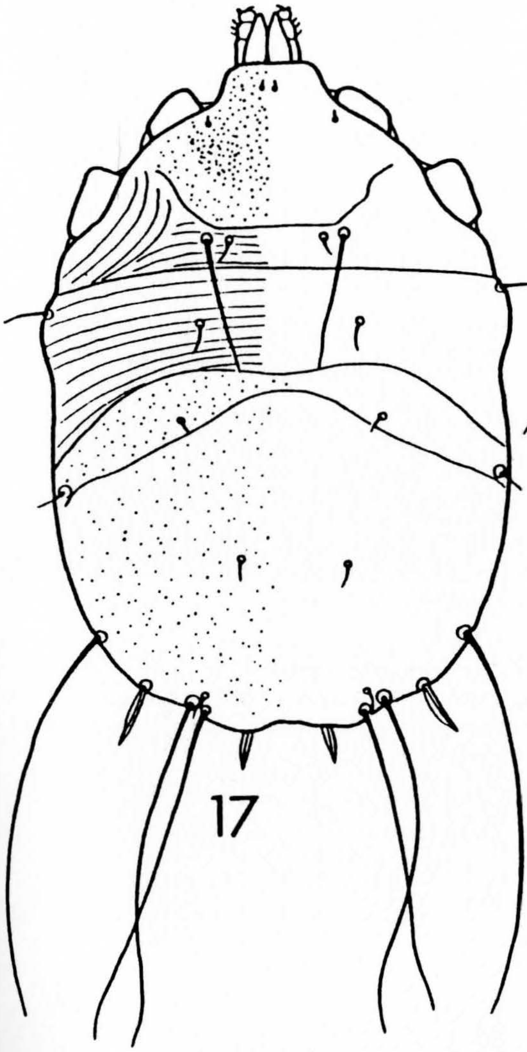
100µ

15

III

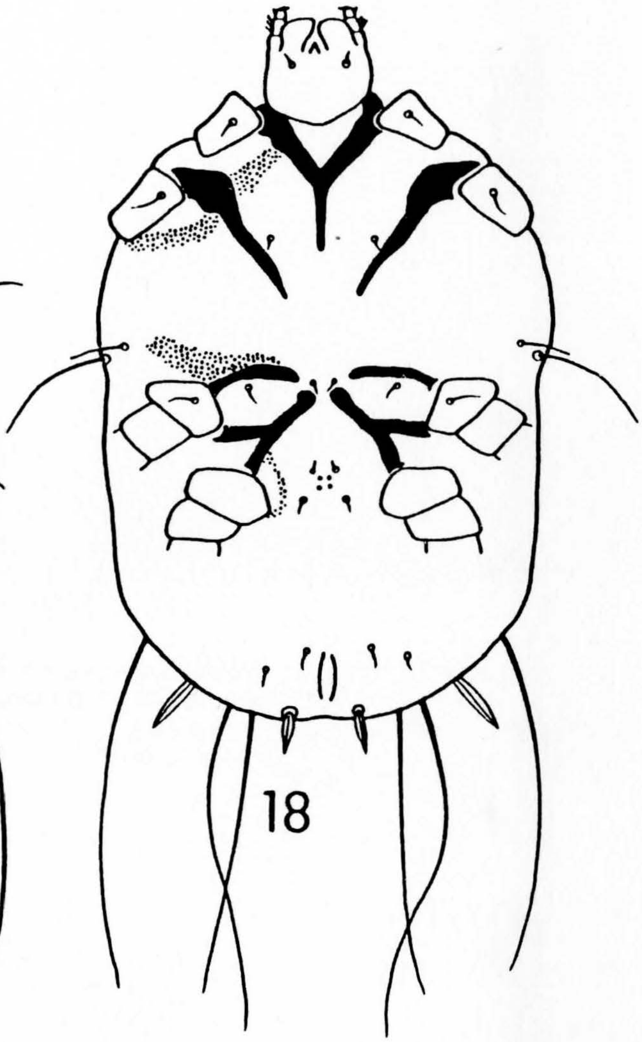
16

IV

Figures 17-18

Freyana anatina tritonymph
17, dorsal aspect. 18, ventral aspect



17

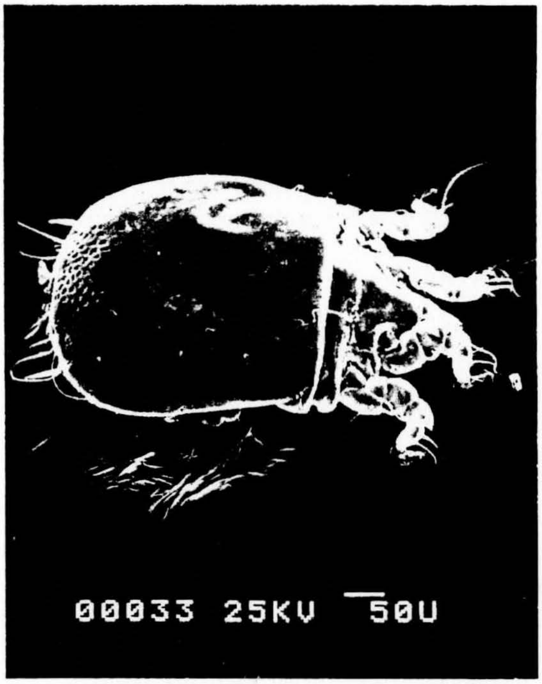


18

200μ

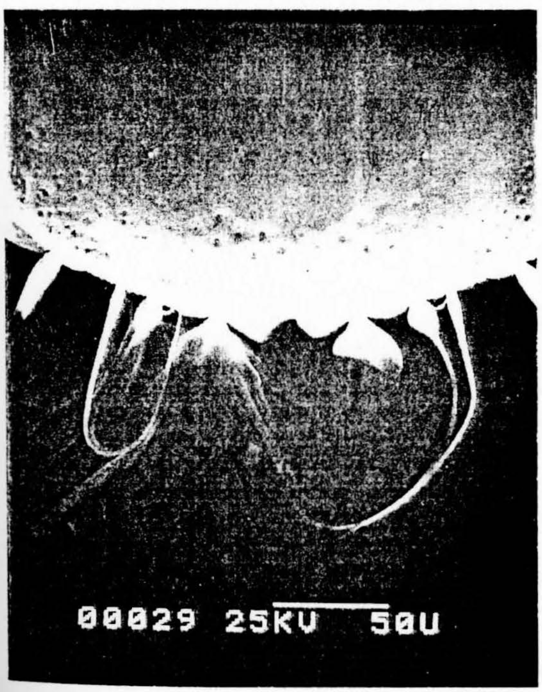
SEM Micrographs 13-16

Freyana anatina adult female. 13,dorsal aspect (140X). 14,leg II (1000X). 15,terminal setae (420X). 16, seta pai (2600X).



13

14



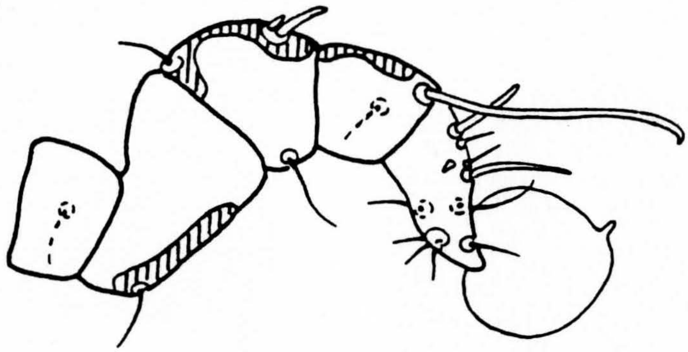
15

16

Figures 19-22

Freyana anatina tritonymph, antaxial aspects of legs 19, leg I. 20, leg II. 21, leg III. 22, leg IV.

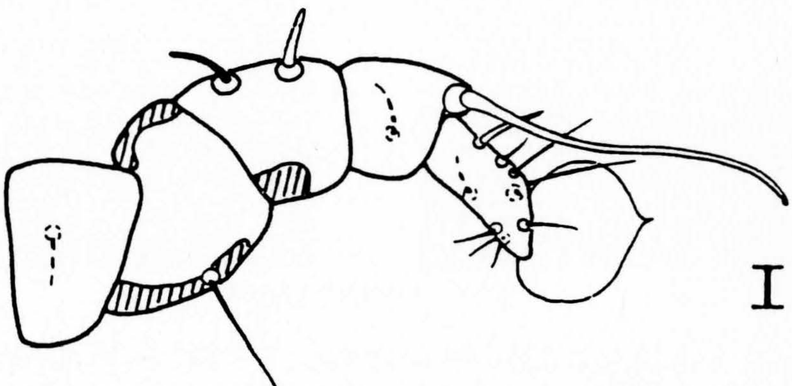
19



I

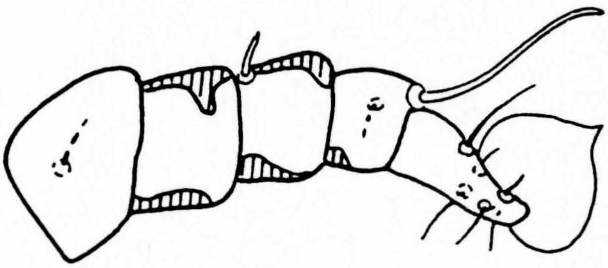
100µ

20



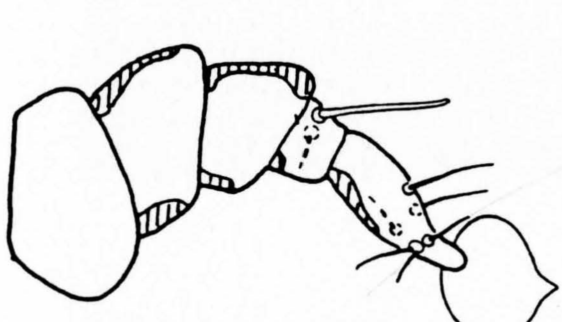
II

21



III

22



IV

SEM Micrographs 17-19

<u>Freyana</u> <u>anatina</u>. 17,tritonymph (170X). 18,protonymph (190X). 19,larvae (280X).

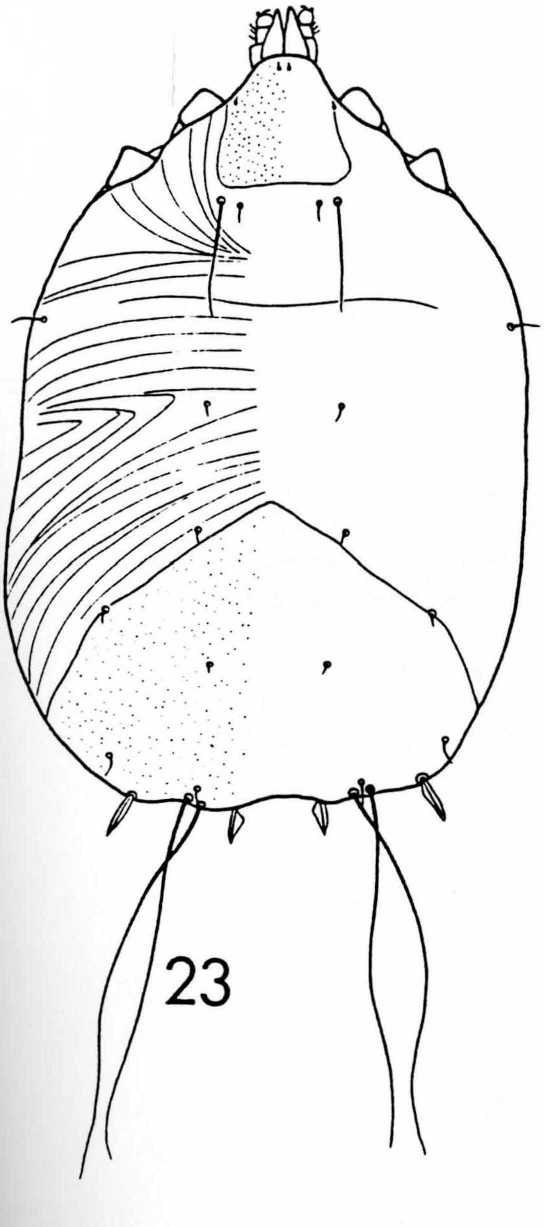
17

18

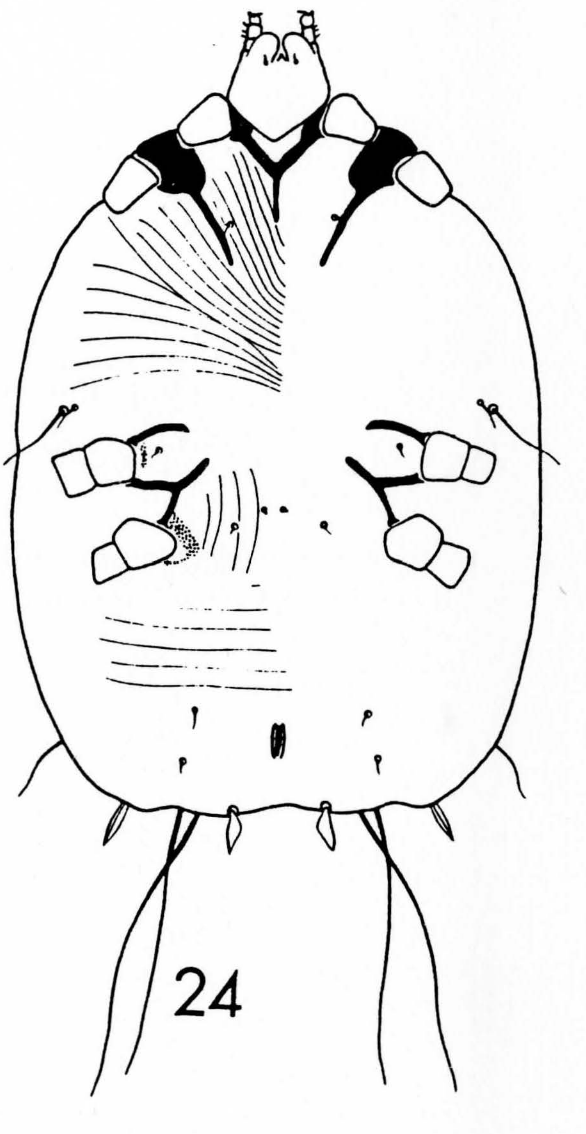
19

Figures 23-24

Freyana anatina protonymph
23, dorsal aspect. 24, ventral aspect.



23

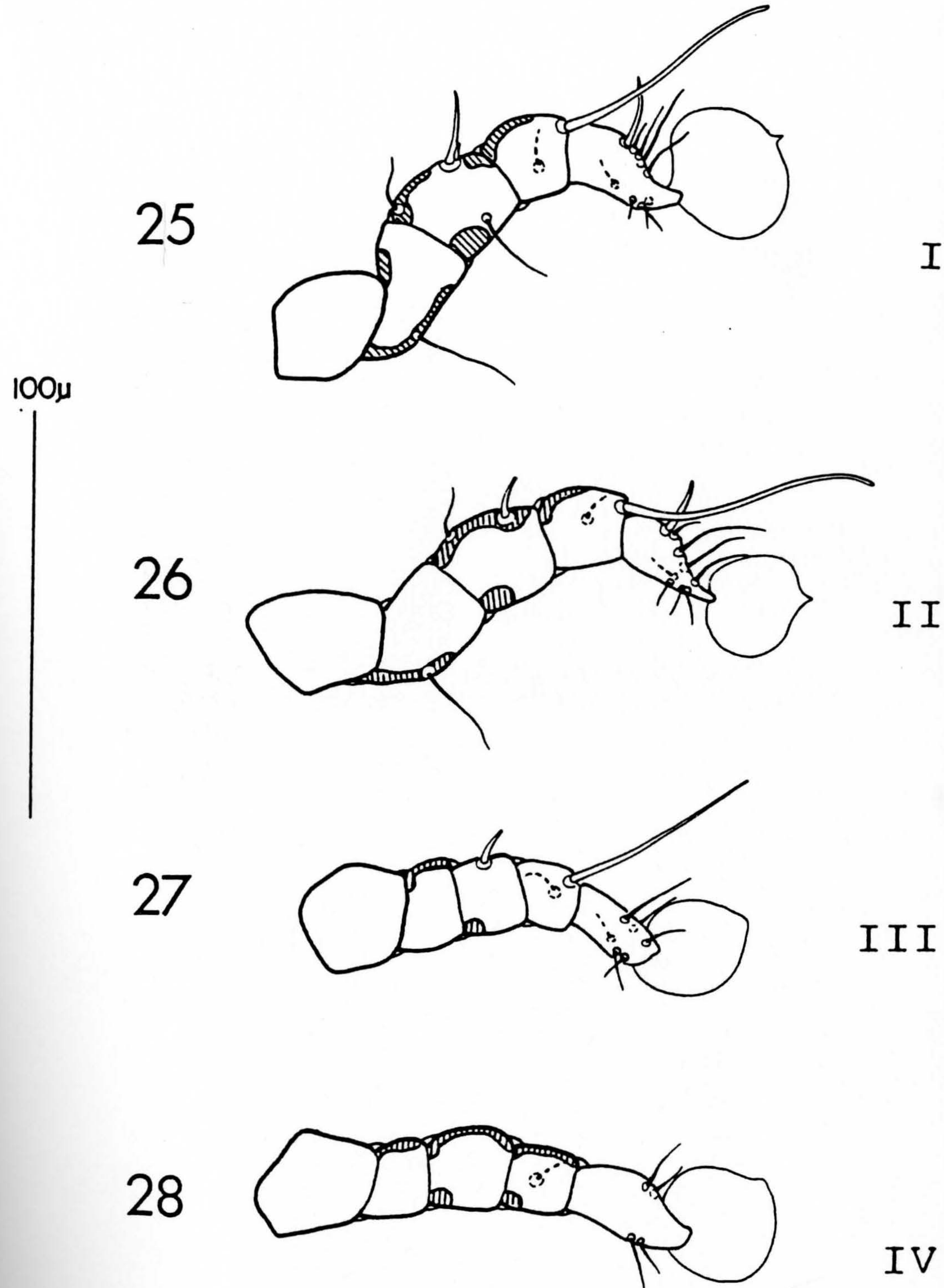


24

100μ

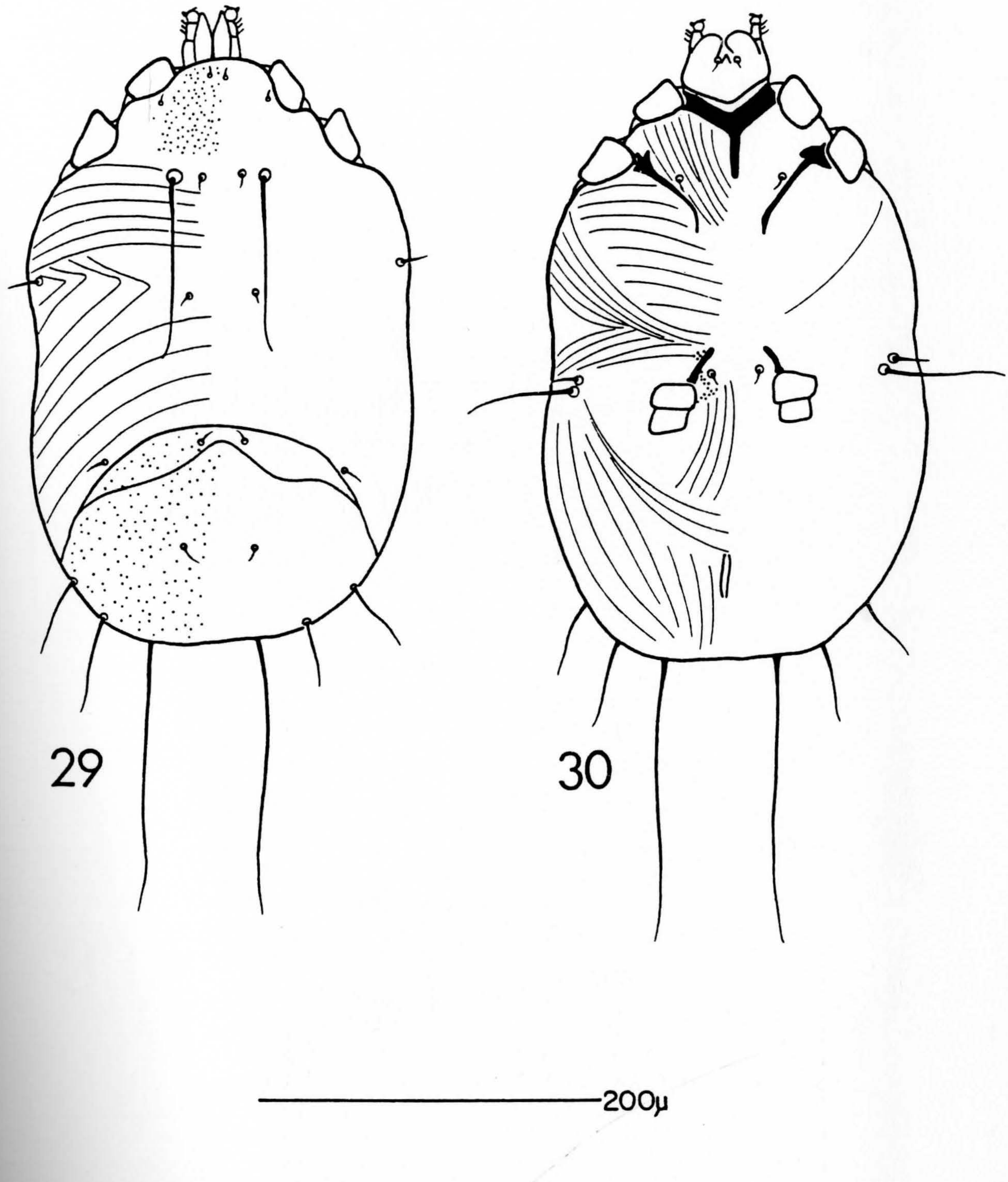
Figures 25-28

Freyana anatina protonymph, antaxial aspects of legs 25, leg I. 26, leg II. 27, leg III. 28, leg IV.


25
I
100µ
26
II
27
III
28
IV

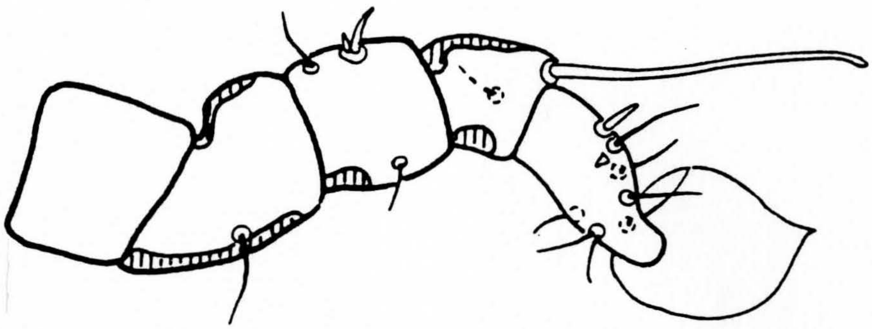
Figures 29-30

Freyana anatina larvae
29, dorsal aspect. 30, ventral aspect

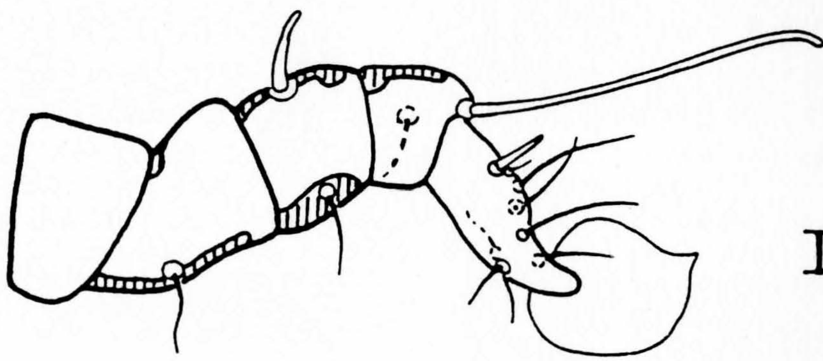

29
30
200µ

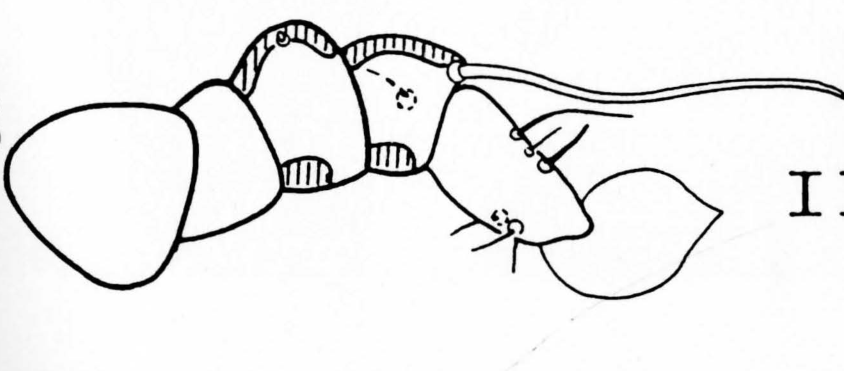
Figures 31-33

Freyana anatina larvae, antaxial aspects of legs. 31, leg I. 32, leg II. 33, leg III.

31  I

100µ

32  II

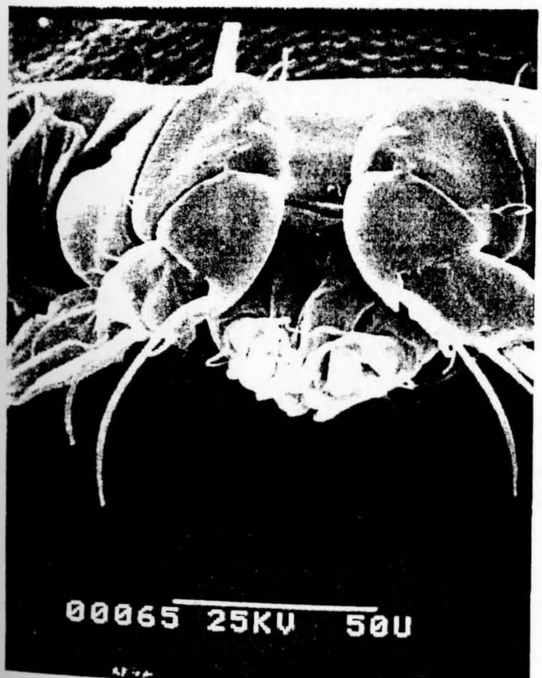
33  III

SEM Micrographs 20-23

20,Anterior aspect of Freyanid showing position of gnathosoma (in box) (310X). 21, close-up of box in SEM 20 (arrow indicates seta elc p) (1500X). 22, gnathosoma showing position relative to legs I (740X). 23, gnathosoma, dorsal aspect (2000X).

20

21

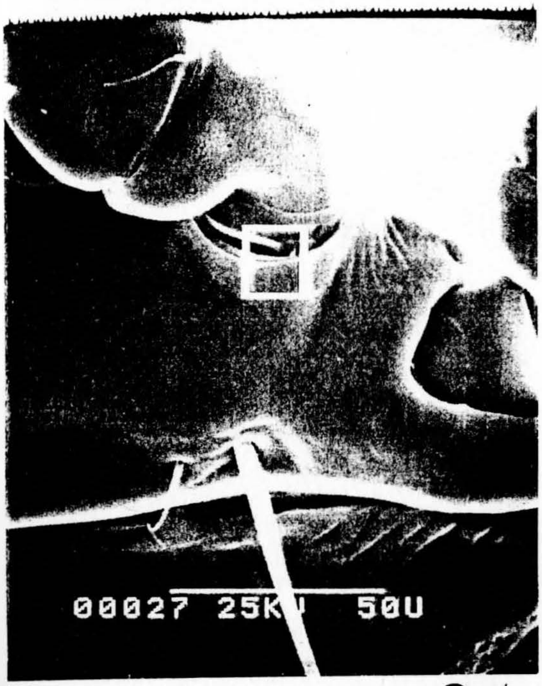


22

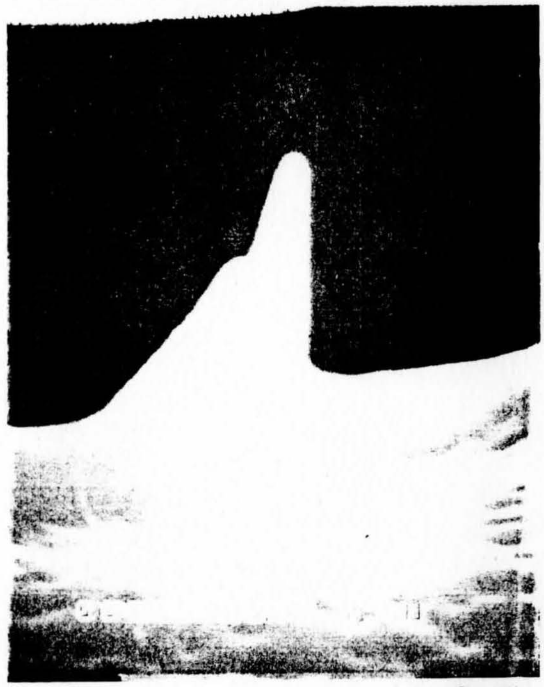
23

SEM Micrographs 24-27

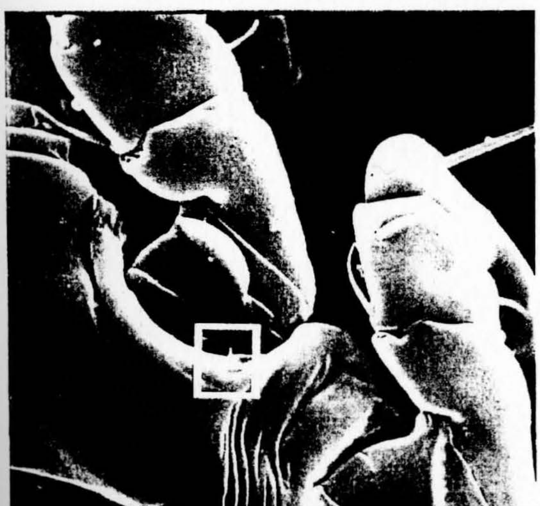
24, Position of propodosomal projection on female Freyana largifolia (800X). 25, close-up of box in SEM 24 (2300X). 26, position of propodosomal projection on freyanid nymph (1000X). 27, close-up of box in SEM 26.



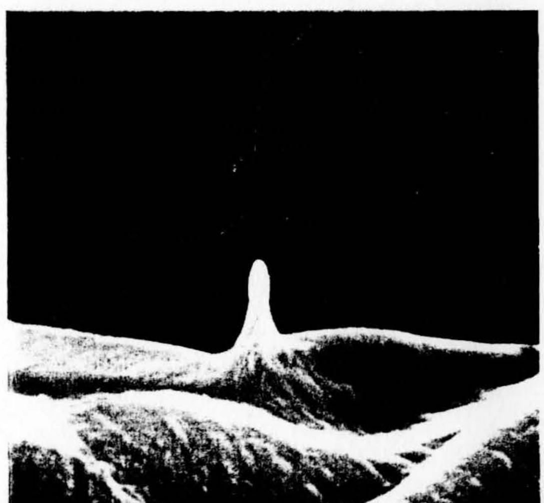
24



25



26



27

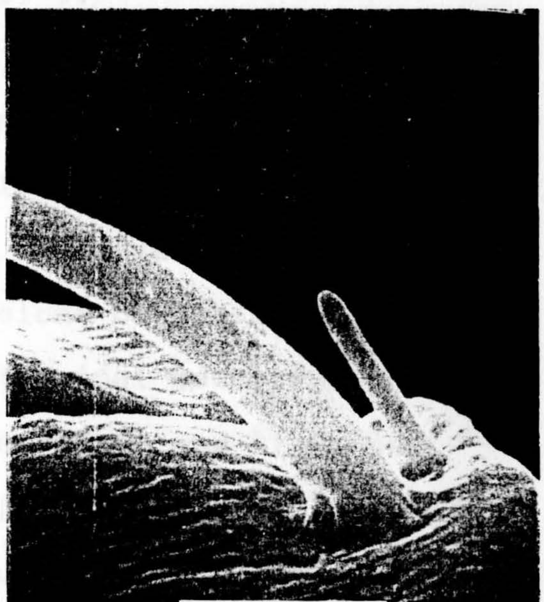
SEM Micrographs 28-31

28,Freyana largifolia heteromorphic male, leg I (1000X). 29, close-up of box in SEM micrograph 28 with arrow pointing to (8000X). 30,Freyana sp. male, leg I (920X). Freyana sp. adult female, setae and (7600X).

28

29

30



31

Freyana largifolia Megnin et Trouessart

(Figs.34-65, SEM 32-46)

Megnin et Trouessart, 1884. Journ. Microgr., 8(2):100.

Trouessart et Megnin, 1885, Bull. Soc. Angers, 14: 37.

Berlese, 1886, A. M. S. ital., fasc. 24, No. 1.

Ginetzinskaya, 1942, Acad. Sciences USSR, 37 (4) :170-73. fig 1.

Ginetzinskaya, 1949, Scientific Notes of Leningrad Stae Univ., Prob. of Ecol. Parasit., 19 (4) : 92, 103-107.

Dubinin, 1950, Akad. Nauk USSR, Zool. Inst., Parazit. Sb., 12 : 33-35, fig.5.

Dubinin,1951 Parazit., Sb., 13 :214.

Dubinin, 1953, Fauna of the USSR, 6 (6) :264-67, fig.77, 85, 87,9,91,94,99,107-9.

Freyana largifolia is distinguished from F. anatina and other related species by the following characteristics: 1) overall shape and size, 2) shape and size of lateral lamellae, 3) structure and dimensions of tibial expansions on leg II, 4) shape and size of terminal setae, 5) dorsal idiosomal pattern, 6)absence of seta ve, and 7) presence of propodosomal projection. F. largifolia has been recorded from numerous species of the genus Anas. This species, along with F. anatina, is known to inhabit the primary feathers of Anas platyrhynchos.

Heteromorphic Male (Fig.34-39, SEM 32-35): Length (including gnathosoma) 642µ,c.v.=3%, Width 437µ,c.v.=4%.

Dorsal Idiosoma: Propodosomal shield well developed with setae sce and sci positioned on posterior margin. Seta vi located inside small depression located on anterior margin of propodosoma. Seta ve absent. Lateral protuberance on propodosomal shield at level of insertion of legs I. Prominent transverse furrow separating propodosoma from hysterosoma. Hysterosomal shield well developed, bearing numerous small lacunae. Lateral lamellae well developed, extending from insertion of seta d1 to seta l4, with a prominent groove at the level of seta l3. Setae d1, d2, and d3 as microsetae. Seta l3 long, setiform. Seta d4 small, setiform, located between setae l4 and l5. Seta l4 large, oval shaped. Seta l5 long, setiform. Seta d5 long, setiform, with oval extension at base. Seta pai boot-shaped, larger than in homeomorphic male (SEM 35). Ventral Idiosoma: Epimerites I fused. Epimerites II and IIA fused to form closed coxal field II. Epimerites III and IIIA fused to form closed coxal field III. Small scerite extending from level of seta c1 to slightly anterior of seta c2. Genital organ positioned at level of leg III, flanked by two pairs of genital discs. Seta pae anterior to insertions of setae l4 and l5. Ventral setae (s, h, sh, c1-c3, a) present. Gnathosoma: All setae present as in F. anatina. Leg chaetotaxy: All setae present as in F. anatina with large triangular tibial expansions on legs II. (Fig.37, SEM 33). Homeomorphic Male (Fig.40-42, SEM 36-39): Length 569μ, Width 314μ, (n=4, c.v.=n.a.). Dorsal Idiosoma: Propodosomal shield well-developed. Seta ve absent. Propodosomal projection present. Hysterosomal shield covered with small lacunae. Lateral lamellae not as prominent as in heteromorphic male, extending from level of seta d2 to seta l4. Lateral lamellae with groove at insertion of seta l3. Dorsal setae (d1, d2, and d3) small, setiform. Seta d5 as in heteromorphic male but with smaller oval extension at base. Seta pai boot-shaped (SEM 39), not as elongate as in heteromorphic male. Ventral Idiosoma: Epimerites I fused, coxal field I open. Epimera II and IIA fused forming closed coxal field II. Medial sclerite at junction of epimera II and IIA not fused with epimerite III. Epimerites III and IIIA fusing to form closed coxal field III. Genital organ as in heteromorphic male, positioned at level of legs III. Adanal discs smaller than in heteromorphic male. All ventral setae present. Leg chaetotaxy as in typical Freyana spp. Dorsal tibial expansions on legs II not as large as in heteromorphic male (Fig.42, SEM 37).

Female (Fig. 43-48, SEM 40-43): Length 584 μ, c.v.=3%, Width 388 μ, c.v.=4%. Dorsal Idiosoma: Ovoid shape with propodosomal shield similar to adult homeomorphic male. Prominent transverse suture separating propodosomal shield from hysterosoma. Lateral lamellae as in homeomorphic male. Setae d1, d2, d3, l1, l2 small, setiform. Seta l3 long, setiform. Seta d4 small, setiform, positioned anterior to insertion of seta l5. Seta l4 short, lanceolate. Seta l5 long, setiform. Seta d5 long, setiform with narrow membranous lateral expansions at insertion. Seta pai short, with two pointed apices (SEM 43). Ventral Idiosoma: All ventral setae present. Coxal field 1 open. Epimera II and IIA in close proximity to each other but not fused. Coxal field III closed. Pregenital apodeme prominent, semilunar in shape, positioned at level of junction of epimera II and IIA. Leg Chaetotaxy: All setae present. Dorsal tibial expansions of legs II greatly reduced (SEM 41).

Tritonymph (Fig. 49-54, SEM 44): Length 530 μ,c.v.=6%, Width 345 μ,c.v.=8%. The tritonymph resembles adult in leg chaetotaxy, but lacks external genitalia, lateral lamellae, and is less-heavily sclerotized than adult. Dorsal Idiosoma: Propodosomal shield well developed; seta ve absent, seta vi present. Setae sce and sci located on weakly sclerotized region between transverse suture and propodosomal shield. Transverse suture well defined. Propodosomal projection present. Hysterosomal shield weakly sclerotized, bearing numerous small lacunae. Band of unsclerotized, striated tissue extending from transverse suture posteriorly to level between setae d1 and d2. Seta l3 short, setiform (unlike F. anatina). Seta l4 short, lanceolate. Seta d4 short, setiform. Setae d5 and l5 long, setiform. Seta pai short, lanceolate. Ventral Idiosoma: Chaetotaxy as in homeomorphic male. Coxal fields I and II open, epimera III and IIIA not fused. Coxal field III open. Two pairs of genital discs positioned between setae c2 and c3. Female tritonymph has dorsal copulative opening, the bursa copulatrix. No genital organ in male tritonymph present.

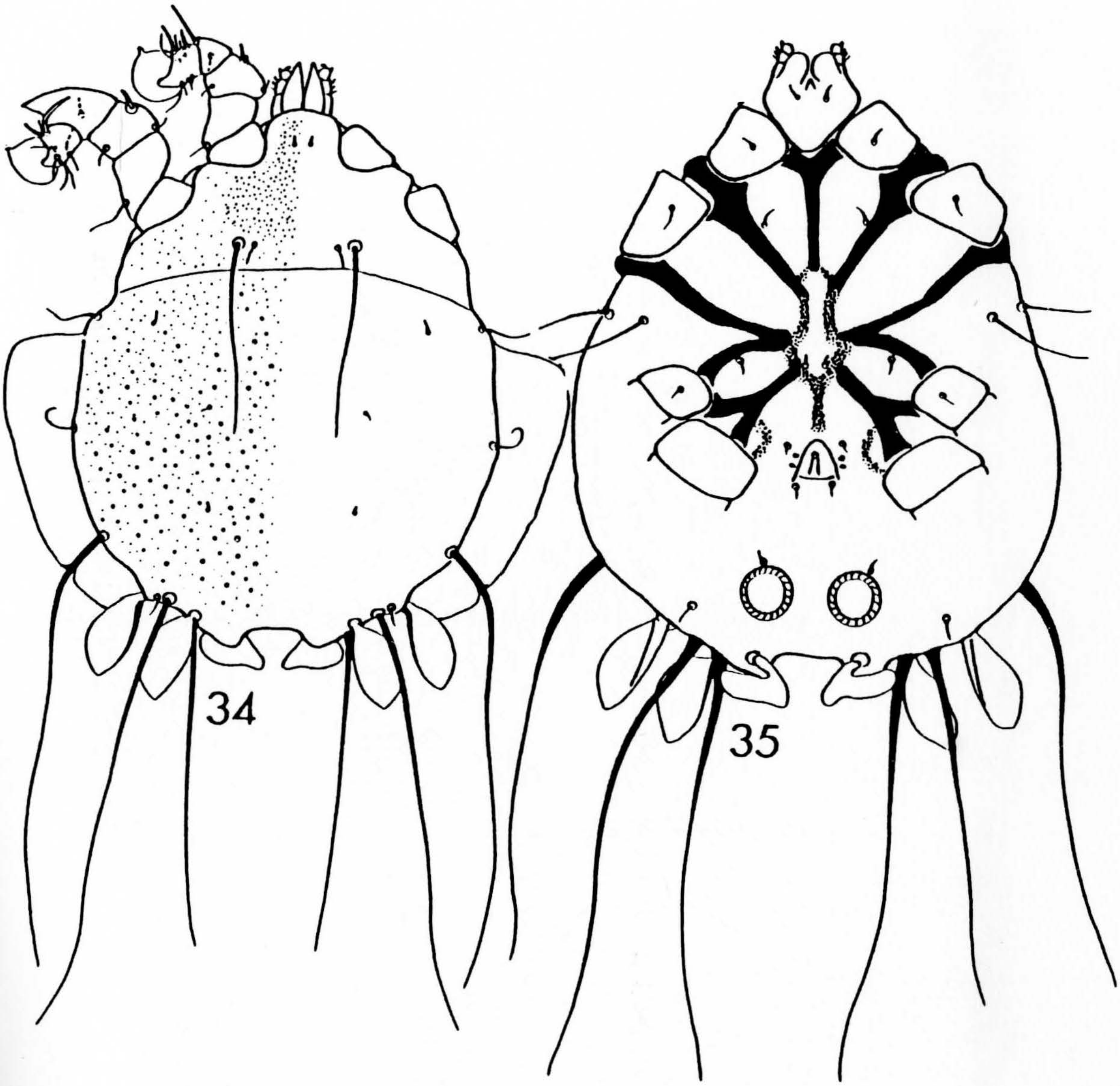
Protonymph (Fig. 55-60, SEM 45): Length 412μ, c.v.=9%, Width 257μ, c.v.=8%. Distinguished from tritonymph by size, degree of sclerotization, leg chaetotaxy, and single pair of genital discs. Dorsal Idiosoma: Propodosomal shield not as heavily sclerotized as in tritonymph, and smaller. Seta vi present, seta ve absent, and propodosomal projection present. Prominent transverse suture separating propodosomal shield from hysterosoma. Unsclerotized, striated tissue between shields broader than in tritonymph. Hysterosomal shield like tritonymph but smaller. Small lacunae covering hysterosomal shield. Lateral lamellae absent. Seta l3 short, setiform, with seta pai short, lanceolate. Setae d1 and d2 situated anterior to hysterosomal shield. Ventral Idiosoma: coxal fields I-IV open. One pair of genital discs at level of seta c2. Setae pR and sR on trochanters of legs absent. Solenidion W3 on tarsus of leg I absent; tibia of leg IV lacking solenidion theta.

Larvae (Fig. 61-65, SEM 46): Length 326μ, c.v.=5%, Width 189 μ, c.v.=5%. Larvae distinguished by six legs, size, and degree of sclerotization. Lateral lamellae absent, with idiosoma weakly sclerotized. Seta vi present. Seta ve absent. Propodosomal projection present at lateral margin of propodosoma at level of leg II. Leg chaetotaxy as in protonymph, but lacking leg IV. Setae d1-d3, l1-l3 short, setiform. Seta d4? short, setiform. Seta d5? long, setiform. All other setae as in protonymph.

Materials examined: From Anas cyanoptera: 3 he, 4 ho males, 7 females, Yakima County, Washingtom, 4-V-1942 (NU 1711). From Anas discors: 5 he, 2 ho males, 7 females, White Rock Lake, Dallas County, Texas, 14-IV-1936 (NU 1036). From Pteronetta hartlaubi: 7 he, 2 ho males, 17 females, 10 tritonymphs, 9 protonymphs, 4 larvae, Anguanamo, Ngoui, W. Chad Terr., French Equatorial Africa, 13-VIII-1918 (USNM 255278); 3 he, 1 ho male, 22 females, 8 tritonymphs, 2 protonymphs, Anguanamo, Ngoui, W. Chad Terr., French Equatorial Africa, 13-VIII-1918 (USNM 255279); 2 he, 1 ho male, 1 female, 4 tritonymphs, Mpivia, Fernan Vaz, West Gabon, French Equatorial Africa, 13-IV-1918 (USNM 255280); 16 heteromorphic males, 2 homeomorphic males, 19 females, 5 tritonymphs, 10 protonymphs, 9 larvae, Niangara, Uele Province, Zaire, 18-IV-1913 (AMNH 157645).

Figures 34-35

Freyana largifolia heteromorphic male
34, dorsal aspect. 35, ventral aspect

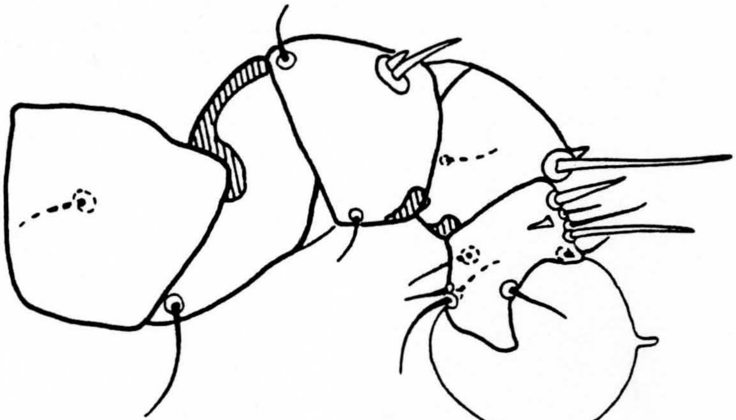

34
35
100µ

Figures 36-39

Freyana largifolia heteromorphic male, antaxial aspects of legs. 36, leg I. 37, leg II. 38, leg III. 39, leg IV.

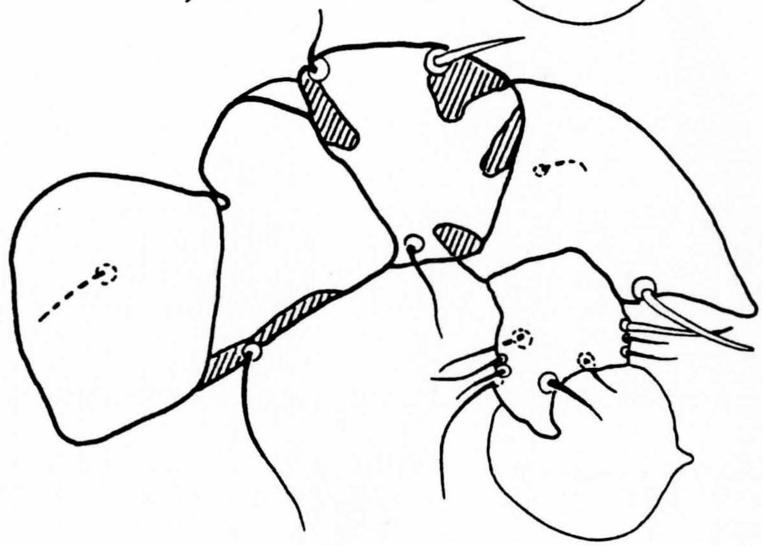
100µ

36



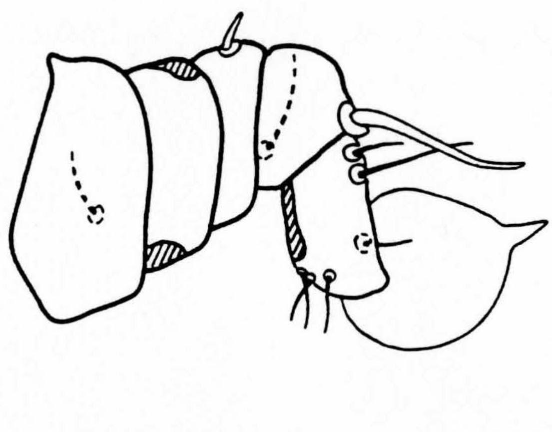
I

37



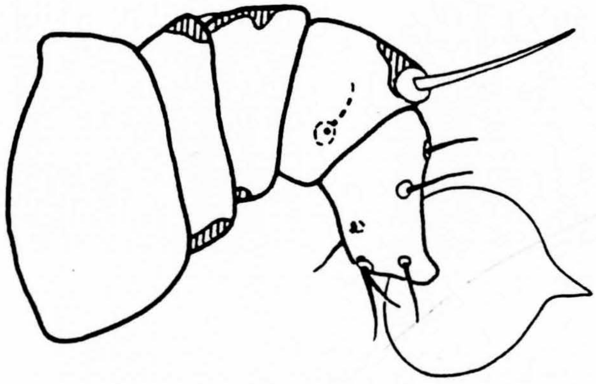
II

38



III

39

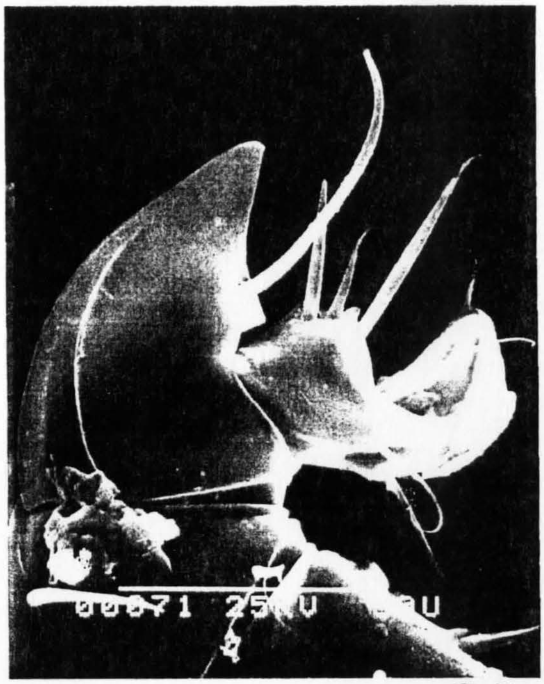


IV

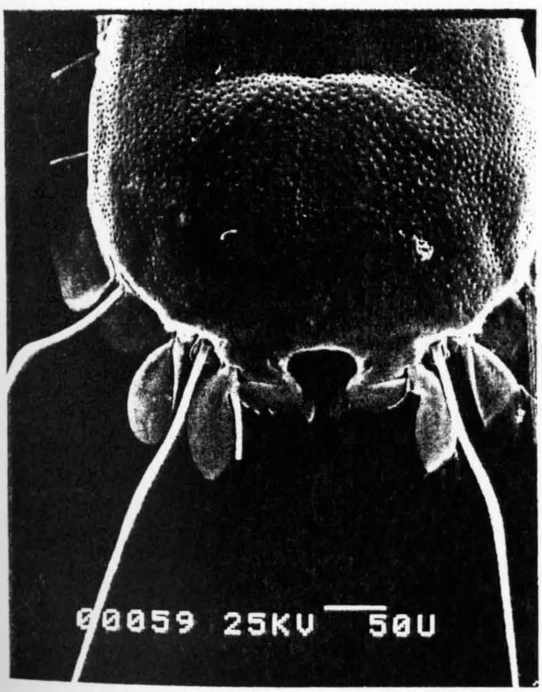
SEM Micrographs 32-35

Freyana largifolia heteromorphic male. 32, Dorso-lateral aspect (100X). 33, leg II (980X). 34, terminal setae (220X). 35, seta pai (1500X).

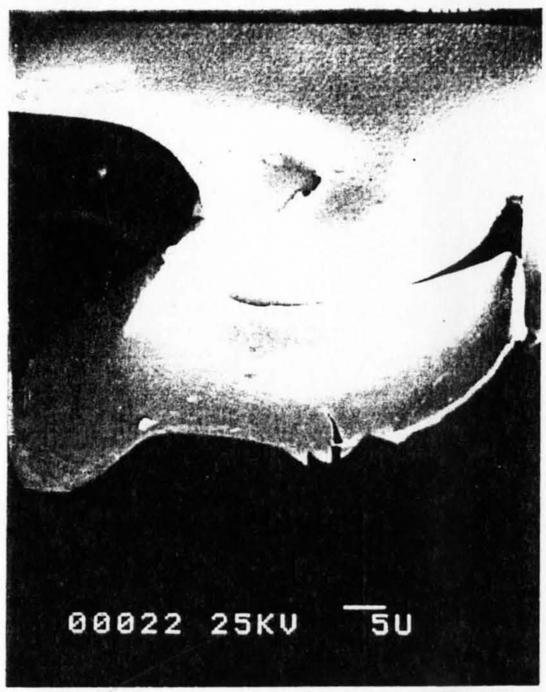
32



33



34

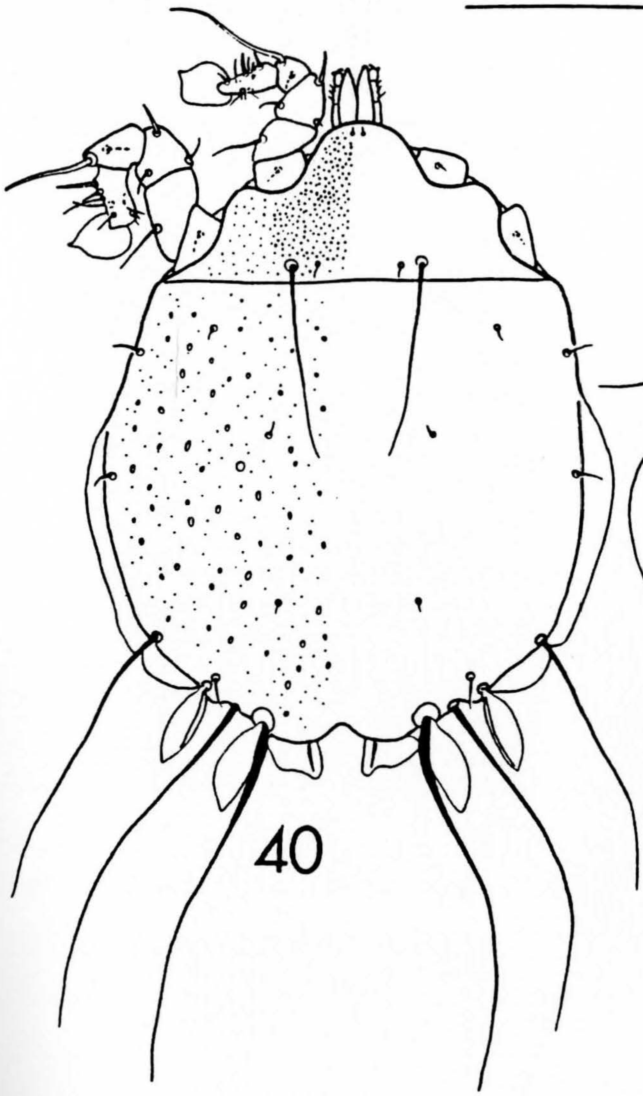


35

Figures 40-42

Freyana largifolia homeomorphic male
40, dorsal aspect. 41, ventral aspect. 42, leg II.

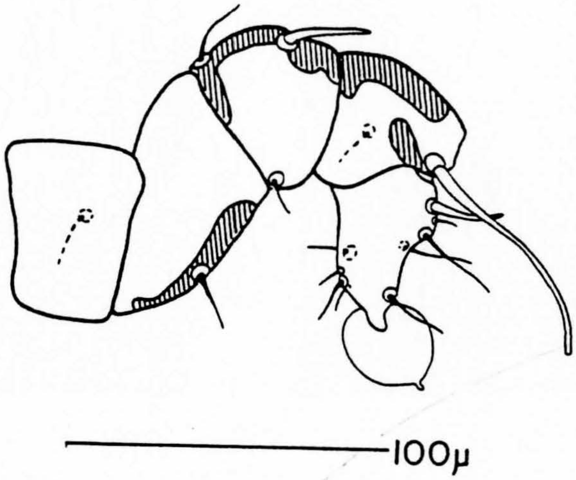
200µ



40

41

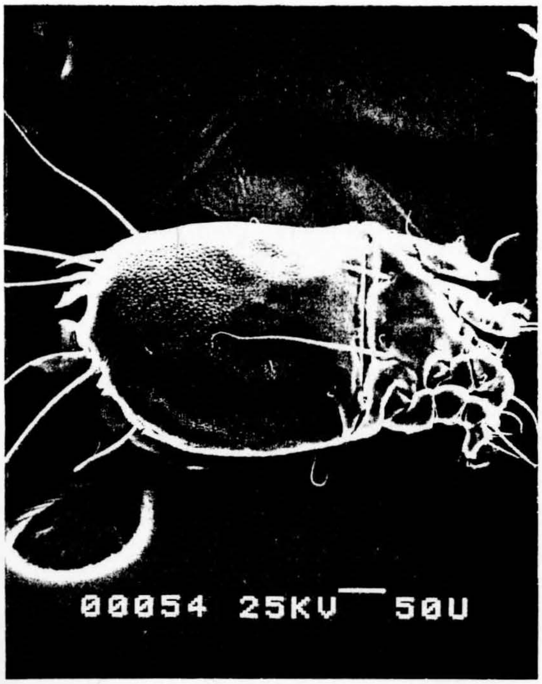
42



100µ

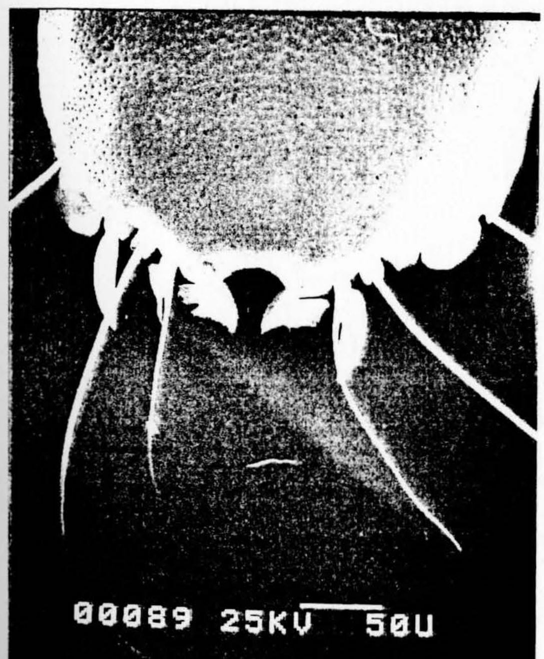
SEM Micrographs 36-39

Freyana largifolia homeomorphic male. 36,dorso-lateral aspect (160X). 37,leg II (1000X). 38,terminal setae (920X). 39, seta pai (1200X).



36

37

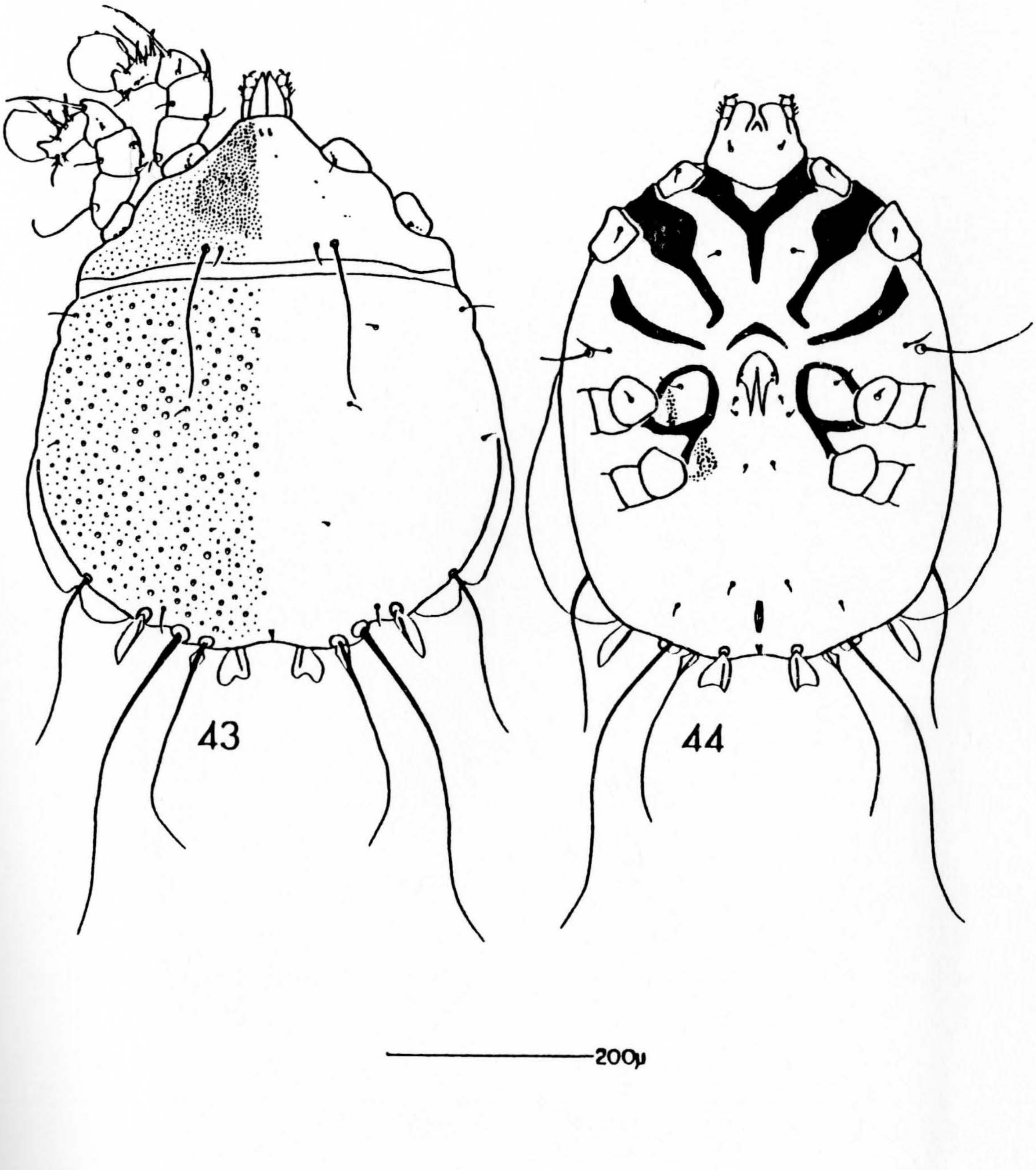


38

39

Figures 43-44

Freyana largifolia female
43, dorsal aspect. 44, ventral aspect.



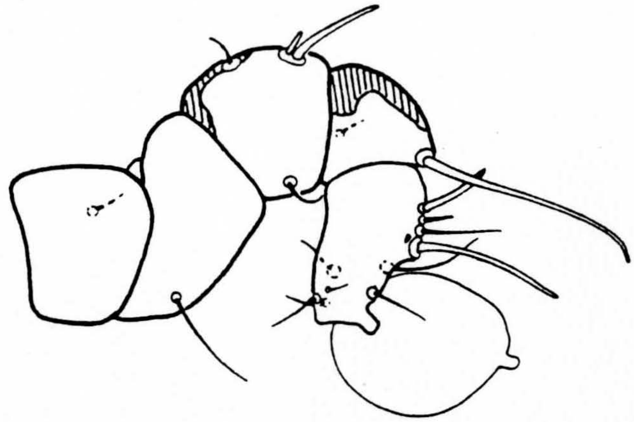
43

44

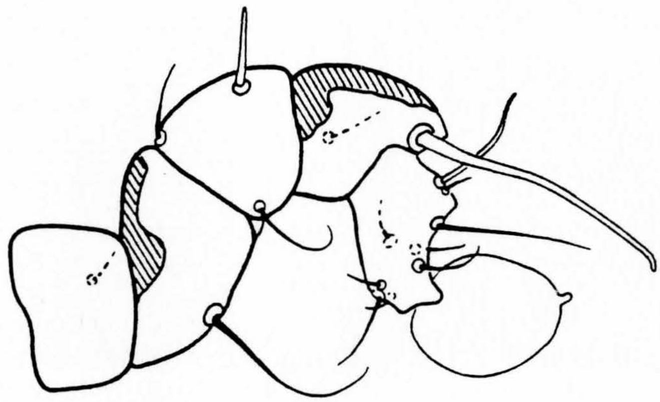
200µ

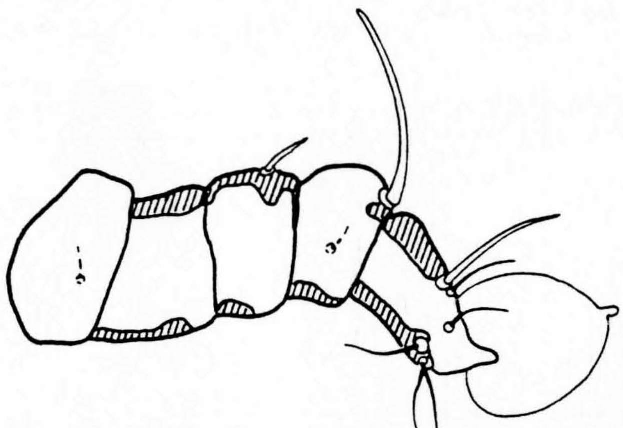
Figures 45-48

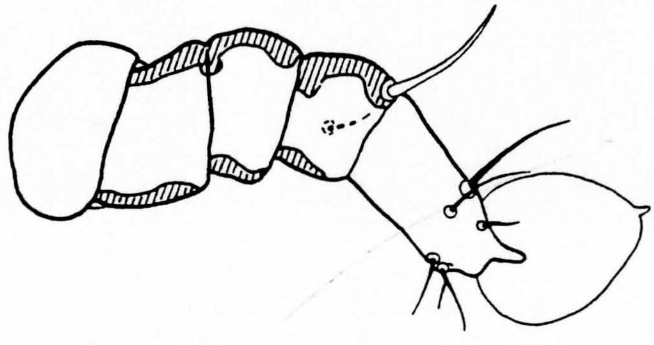
Freyana largifolia female, antaxial aspects of legs 45, leg I. 46, leg II. 47, leg III. 48, leg IV.

45

I

100µ

46

II

47

III

48

IV

SEM Micrographs 40-43

Freyana largifolia adult female. 40,dorso-lateral aspect (140X). 41,leg II (960X). 42,terminal setae (310X). 43, seta pai (2300X).

40

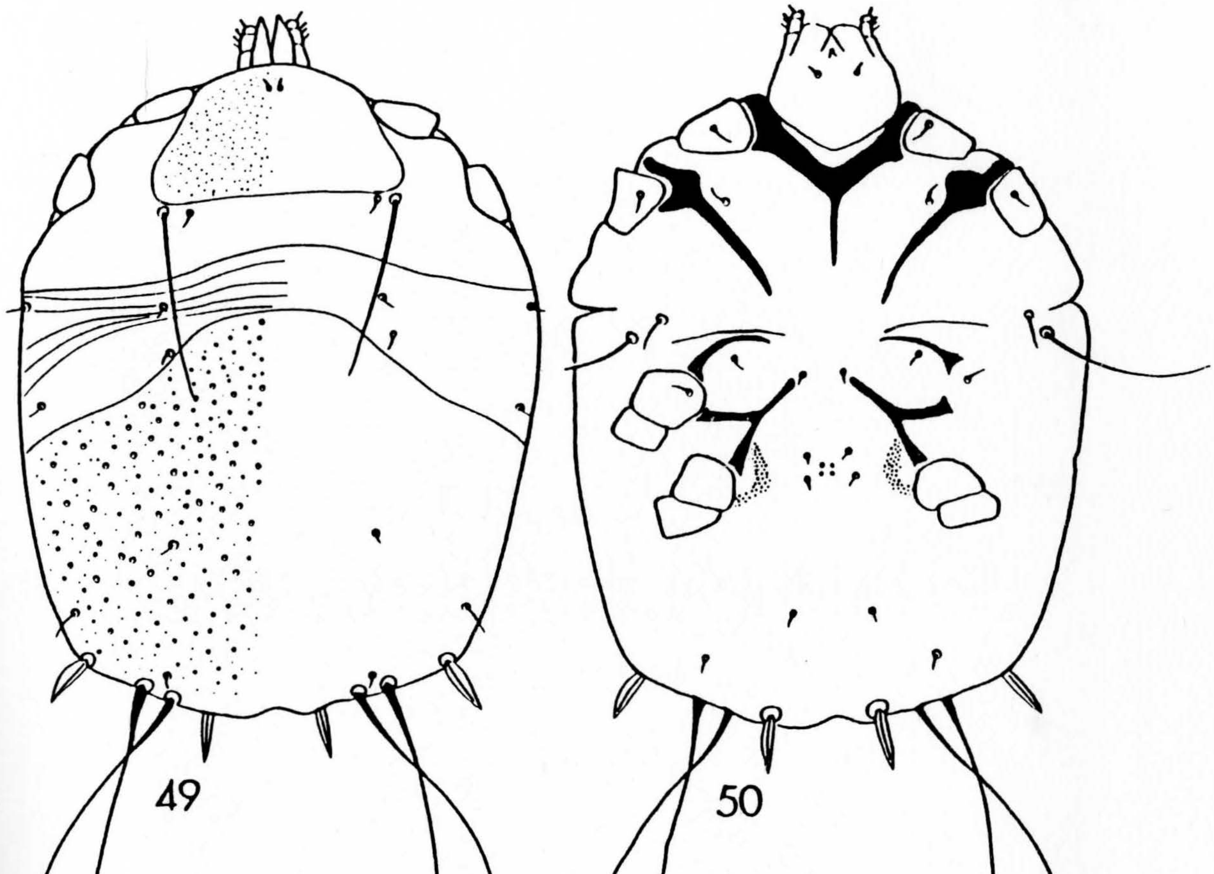
41

42

43

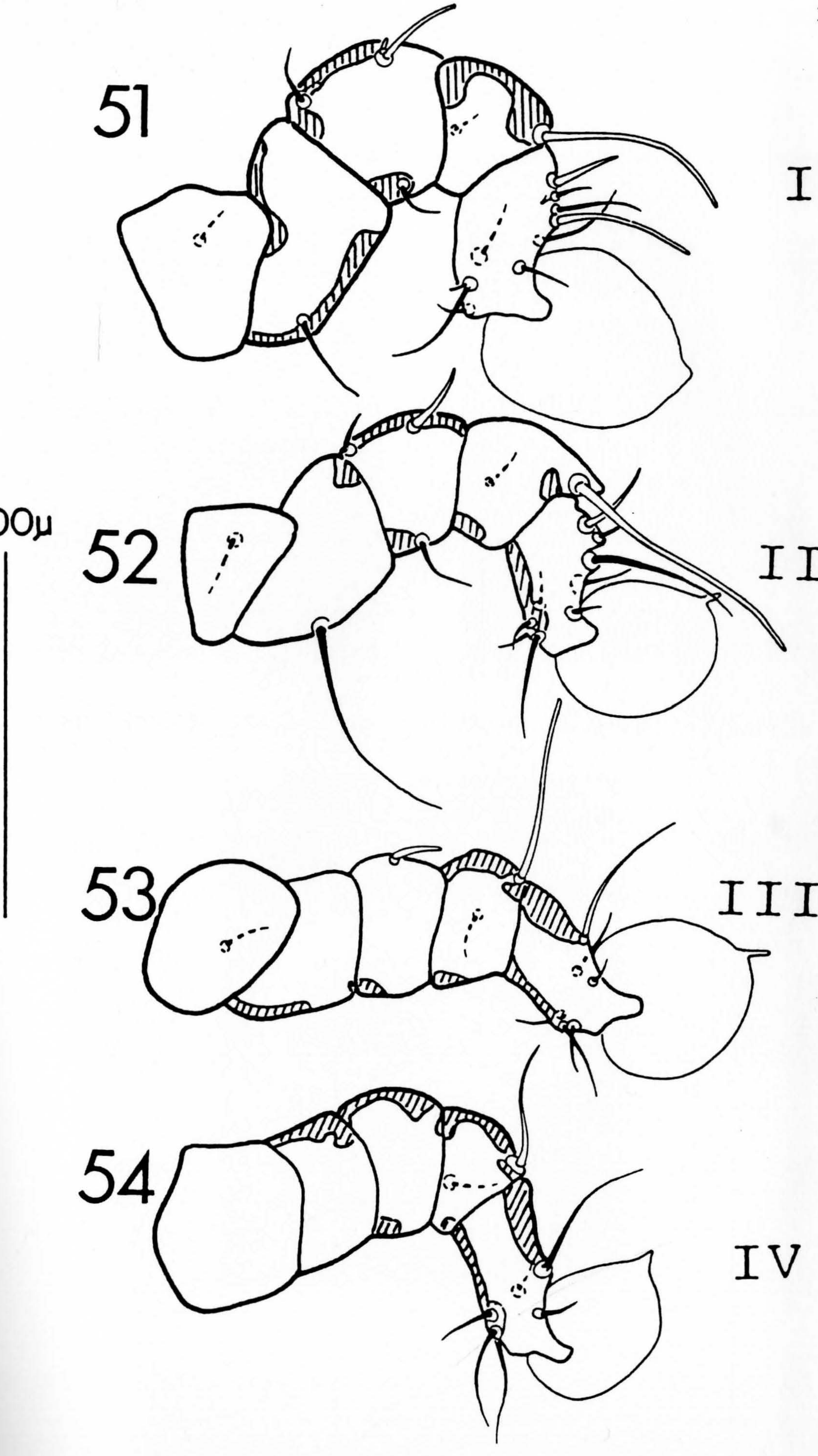
Figures 49-50

Freyana largifolia tritonymph
49, dorsal aspect. 50, ventral aspect


49
50
200µ

Figures 51-54

Freyana largifolia tritonymph, antaxial aspects of legs. 51, leg I. 52, leg II. 53, leg III. 54, leg IV.


51
I
100µ
52
II
53
III
54
IV

SEM Micrographs 44-46

Freyana largifolia. 44,tritonymph (210X). 45,protonymph (200X). 46,larvae (260X).

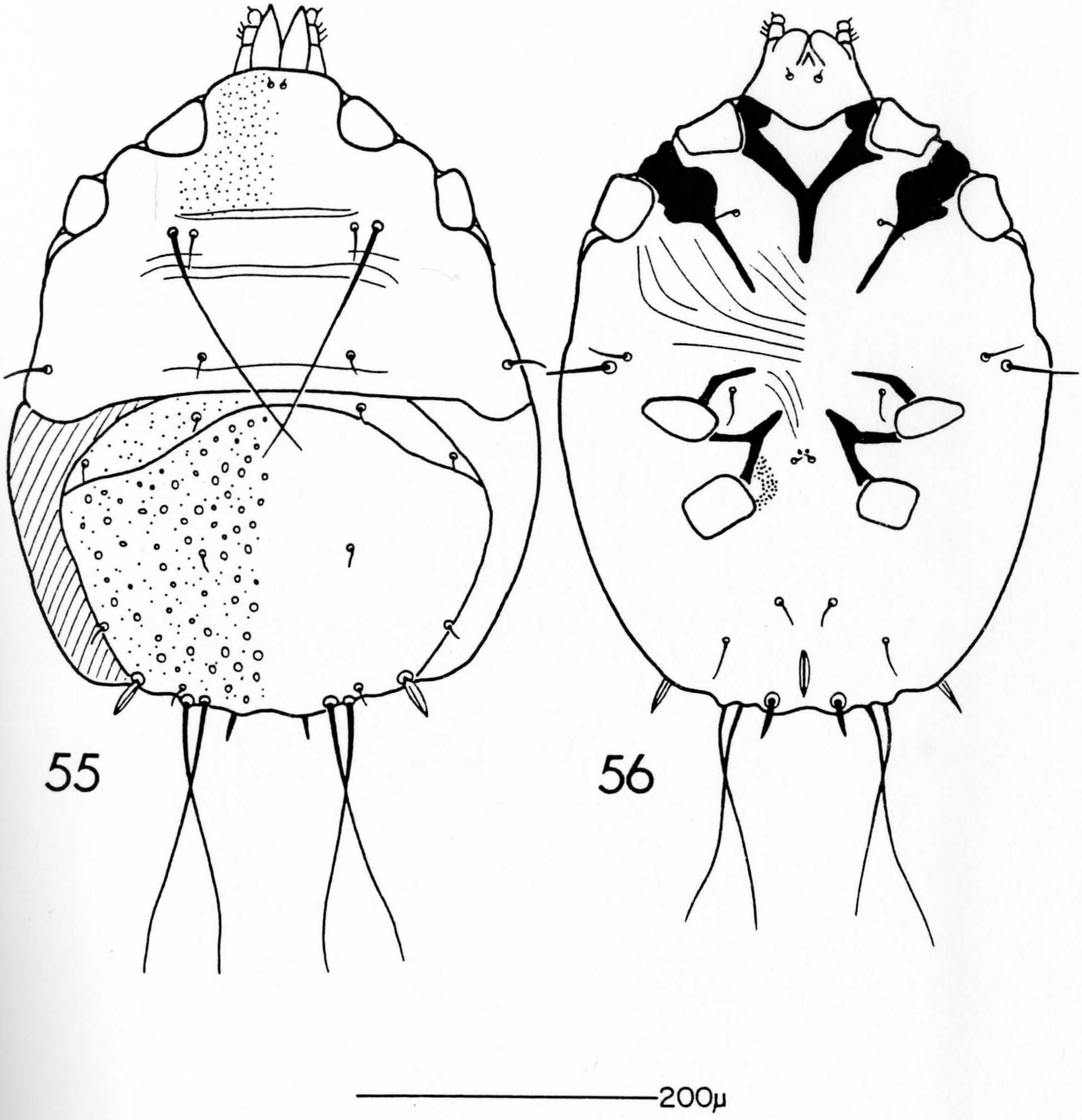
44

45

46

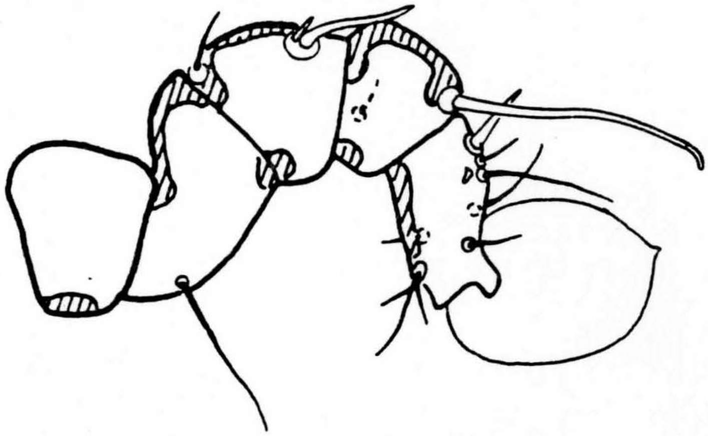
Figures 55-56

<u>Freyana</u> <u>largifolia</u> protonymph
55, dorsal aspect. 56, ventral aspect.

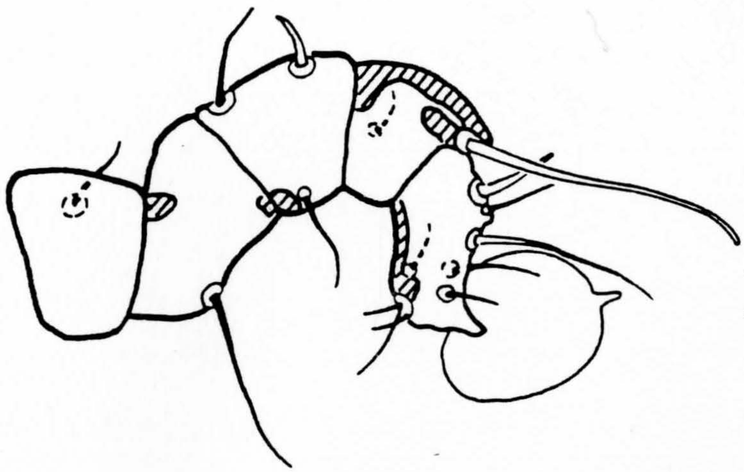

55
56
200µ

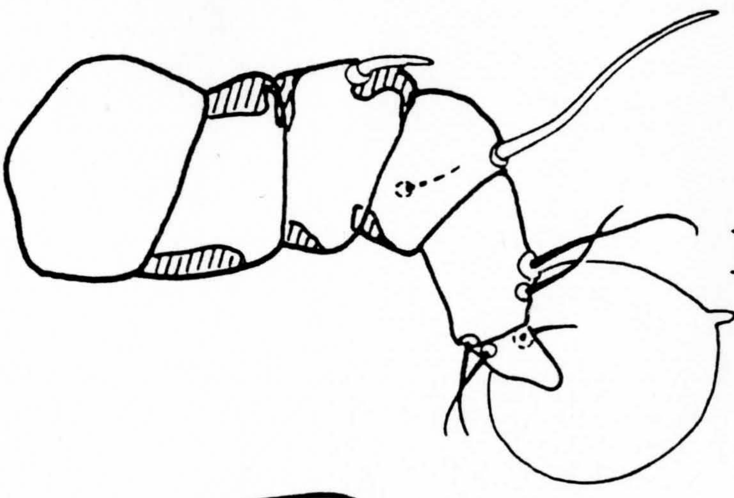
Figures 57-60

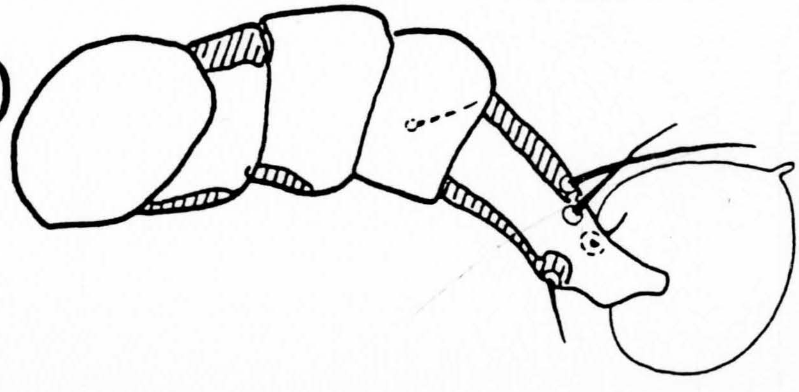
Freyana largifolia protonymph, antaxial aspects of legs. 57, leg I. 58, leg II. 59, leg III. 60, leg IV.

57

I

100µ

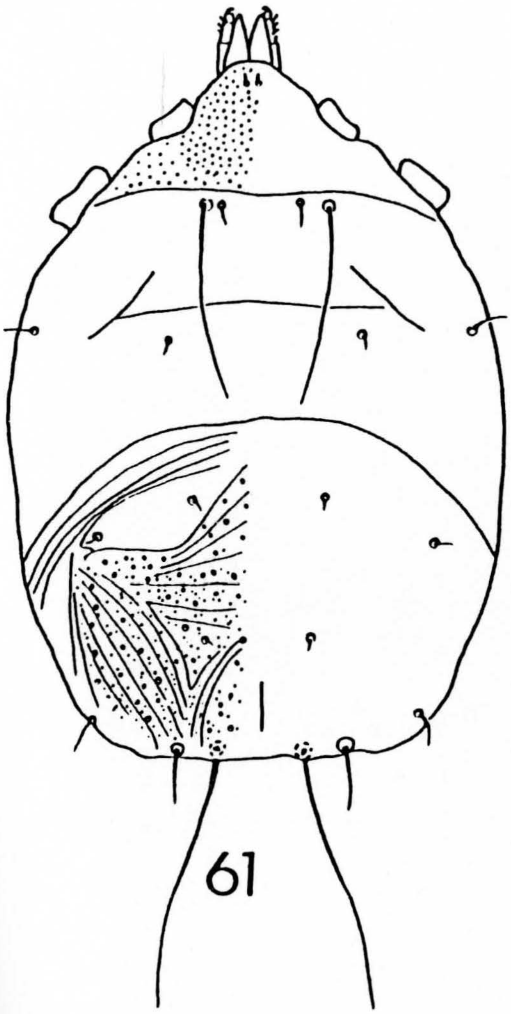
58

II

59

III

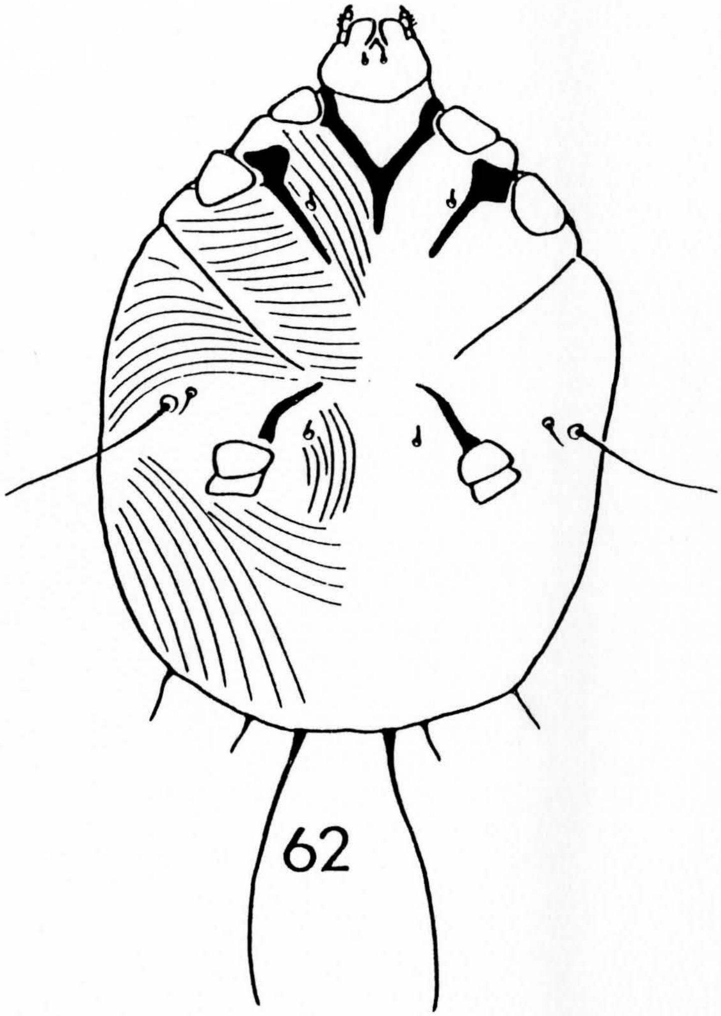
60

IV

Figures 61-62

<u>Freyana</u> <u>largifolia</u> larvae
61, dorsal aspect. 62, ventral aspect.



61



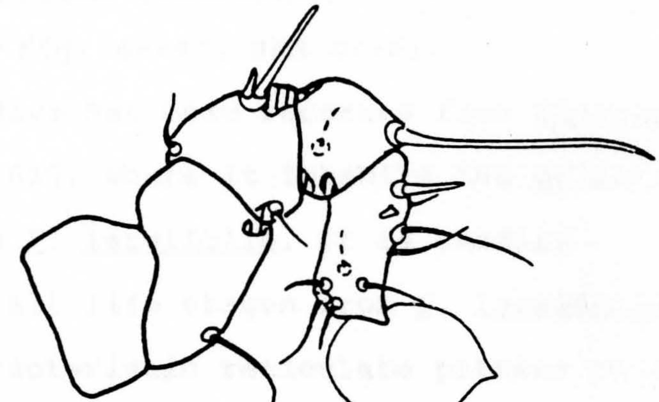
62

200µ

Figures 63-65

Freyana largifolia larvae, antaxial aspects of legs. 63, leg I. 64, leg II. 64, leg III.

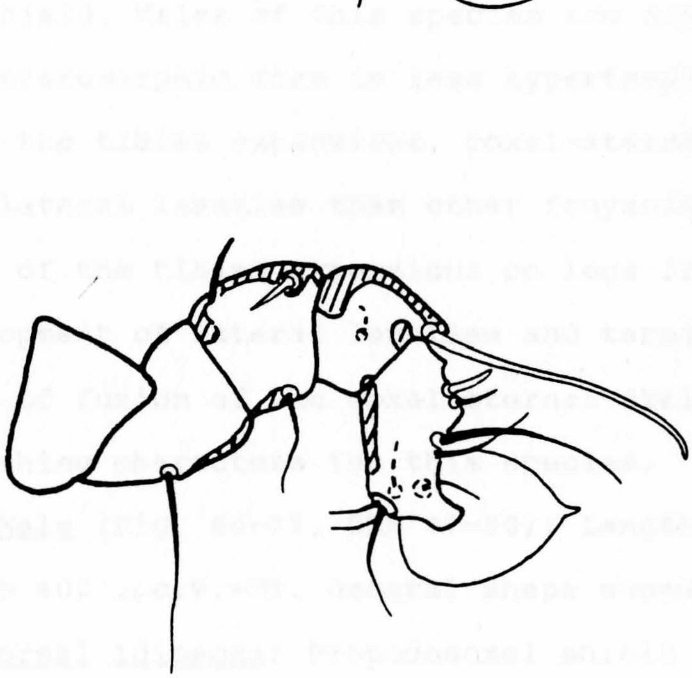
63



I

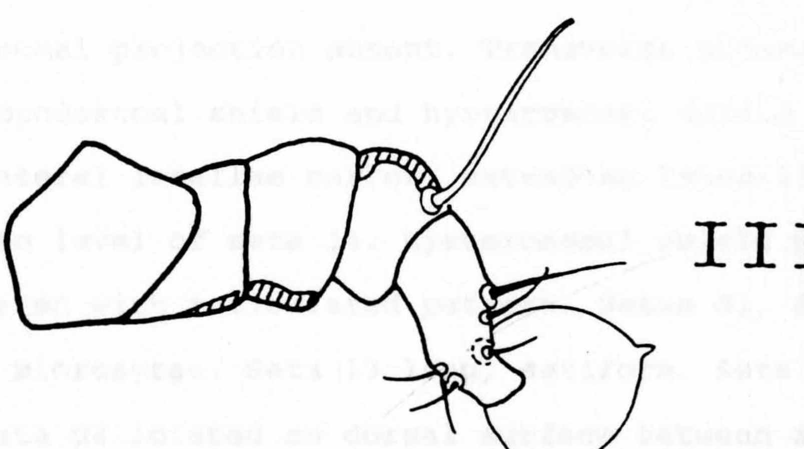
100µ

64



II

65



III

Freyana reticulata n. sp.

Fig. 66-97, SEM 47-61

This new species has been recorded from Pteronetta hartlaubi Cassin, 1859, where it inhabits the primary feathers along with F. largifolia. It is readily distinguishable in all life stages from F. largifolia and F. anatina by the characteristic reticulate pattern on the hysterosomal shield. Males of this species are dimorphic, although the heteromorphic form is less hypertrophied in the development of the tibial expansions, coxal-sternal skeleton, and lateral lamellae than other freyanids. The size and shape of the tibial expansions on legs II, along with the development of lateral lamellae and terminal setae, and the degree of fusion of the coxal-sternal skeleton are also distinguishing characters for this species.

Heteromorphic Male (Fig. 66-71, SEM 47-50): Length 603 µ, c.v.=4%. Width 400 µ, c.v.=2%. General shape somewhat rectangular. Dorsal Idiosoma: Propodosomal shield well developed. Setae vi, ve both present. Setae sce and sci located anterior to transverse suture in deeply sclerotized area. Propodosomal projection absent. Transverse suture separating propodosomal shield and hysterosomal shield as a deep cleft. Lateral lamellae narrow, extending laterally from seta sh to level of seta l4. Hysterosomal shield well developed, marked with reticulated pattern. Setae d1, d2, d3, l1, l2 as microsetae. Seta l3 long, setiform. Seta l4 lanceolate. Seta d4 located on dorsal surface between setae d5 and l5. Seta l5 long, setiform. Seta d5 long, setiform with expanded oval membranous expansion at base. Seta pai extending posteriorly to a pointed tip with a lateral expansion, forming another pointed tip (Fig.66, SEM 50). Ventral Idiosoma: Epimerites I fused into a thick sternum. Epimerites I, II, and IIA not fused, forming open coxal fields I and II. Epimerites IIA nearly fused with epimerites III. Epimera III and IIIA fused. Coxal field III closed. Sternal seta small, setiform. Seta sh small, setiform. Lateral to seta sh, seta h long, setiform. Setae c1, c2, c3, cx3 small, setiform. Genital organ located between setae c2 and c3. Two pairs of genital discs flank genital organ. Small setiform adanal seta positioned anterior to adanal discs. Seta pae located anterioventral to seta l4. Gnathosoma: chaetotaxy as in *F. anatina*. Legs: chaetotaxy as in *F. anatina*. Tibial expansions of legs II (Fig.69, SEM 48) not noticeably larger than in homeomorphic male.

Homeomorphic Male (Fig.72-74, SEM 51-54): Length 588μ, c.v.=6%. Width 376μ,c.v.=4%. Dorsal Idiosoma: Propodosomal shield well developed. Setae ve, vi present. Transverse suture well defined. Lateral lamellae extending from level of seta d2 to level of seta l4. Seta pai boot-shaped (Fig.72, SEM 54). Dorsal setae as in heteromorphic male. Hysterosomal shield well developed, with reticulated pattern. Ventral Idiosoma: Epimerites I fused. Coxal fields I, II, and III open. Distance between epimera IIA and III greater than in heteromorphic male. All ventral setae as in heteromorphic male. Seta pae slightly anteriomesal to seta l4. Legs: Leg chaetotaxy as in F. anatina. Tibial expansions of legs II (Fig. 74, SEM 52) slightly smaller than in heteromorphic male.

Female (Fig. 75-80, SEM 55-58): Length 592μ ,c.v.=2%. Width 392 μ, c.v.=3%. Body very oval in overall shape. Dorsal Idiosoma: Propodosomal chaetotaxy as in males. Lateral lamellae extend from area anterior to level of seta d2, posteriorly to level of seta l4. Lateral lamellae very narrow. Well developed hysterosomal shield with large prominent lacunae on posterior region. Hysterosomal shield marked by reticulated pattern. Seta l3 long, setiform. Seta l4 lanceolate. Seta d4 short, setiform; seta l5 long, setiform; seta d5 elongate with small lateral membranous expansions at insertion. Seta pai paddle-shaped (Fig.75, SEM 58). Ventral idiosoma: Coxal fields I, II, and III open. Ventral setae as in males. Seta pae positioned between setae d5 and l5. Leg chaetotaxy as in F. anatina. Prominent semilunar pregenital apodeme positioned at level of epimerites IIA.

Tritonymph (Fig. 81-86, SEM 59): Length 534μ , c.v.=7%. Width 334μ , c.v.=8%. Body rectangular in shape. Dorsal Idiosoma: Propodosomal shield well developed, smaller than in adults. Setae ve, vi present. Propodosomal projection absent. Transverse suture well defined. Hysterosomal shield not as heavily sclerotized as in adults. Setae sce, sci, d1, and l1 positioned on band of unsclerotized striated tissue between propodosomal and hysterosomal shields. Hysterosomal shield marked by reticulated pattern. Setae d1-d4 short, setiform. Setae l1 and l2 short, setiform. Seta l3 long, setiform. Seta l4 short, lanceolate. Setae d5 and l5 long, setiform. Seta pai short, lanceolate. Ventral idiosoma: Epimerites I fused into sternum. Epimerites II-IV not fused, with coxal fields I-IV open. Two pairs of genital discs present, positioned at level of leg IV. All ventral setae present. Seta sh located slightly anteriomesal to seta h. Seta c2 at positioned at level of genital discs. Female tritonymph has dorsal copulative opening. Male tritonymph has no external genitalia.

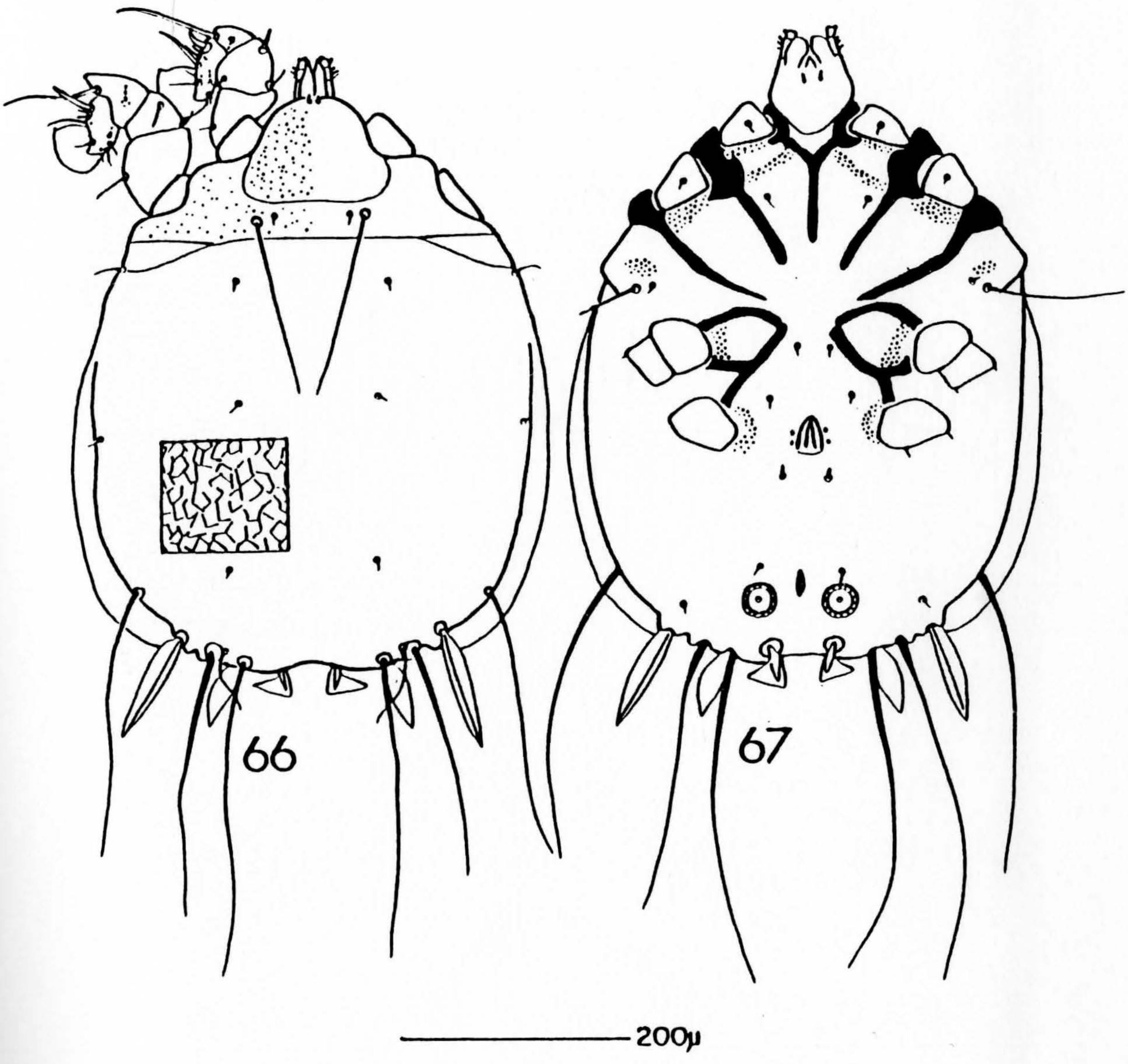
Protonymph (Fig. 87-92, SEM 60): Length 427μ, c.v.=7%, Width 261μ, c.v.=9%. Distinguished from tritonymph by smaller size, degree of sclerotization, leg chaetotaxy, and single pair of genital discs. Body shape more oval than in tritonymph. Dorsal Idiosoma: Propodosomal shield not as heavily sclerotized as in tritonymph. Setae ve and vi present. Propodosomal projection absent. Band of unsclerotized, striated tissue broader than in tritonymph. Hysterosomal shield not as large as in tritonymph, containing reticulated pattern. Lateral lamellae absent. Seta l3 short, setiform. Seta pai short, lanceolate. Other setae as in F. anatina protonymph. Ventral Idiosoma: Coxal-sternal skeleton weakly scerotized. Epimerites I fused into short sternum. Epimerites II-IV not fused, with open coxal fields I-IV. One pair of genital discs positioned at level of leg IV.

Larvae (Fig. 93-97, SEM 61): Length 301 μ, Width 168 μ, (n=8, c.v.=n.a.). Leg chaetotaxy as in protonymph but lacking leg IV. Dorsal Idiosoma: Propodosomal shield weakly sclerotized, bearing setae ve and vi. Propodosomal projection absent. Lateral lamellae absent. Large region of unsclerotized, striated tissue between propodosomal and hysterosomal shields. Hysterosomal shield weakly sclerotized, not extending to margin of idiosoma, with well-defined reticular pattern. Ventral Idiosoma: All coxal fields open. Setation as in *F. anatina* larvae.

Materials examined- From *Pteronetta hartlaubi*: 1 heteromorphic male, 4 homeomorphic males, 16 females, 8 tritonymphs, 2 protonymphs, 6 larvae, Niangara, Uele Prov., Zaire (=Belgian Congo), 18-IV-1913 (AMNH 157645). 8 females, 5 tritonymphs, 2 protonymphs, 3 larvae, Anguanamo, Ngoui, W. Chad Terr., French Equatorial Africa, 13-VIII-1918 (USNM 255278), 1 tritonymph, 1 protonymph, Mpivia, Fernan Vaz., W. Gabon, French Equatorial Africa, 13-IX-1918 (USNM 255280), 5 heteromorphic males, 7 females, 8 tritonymphs, 3 protonymphs, Anguanamo, Ngoui, W. Chad Terr., French Equatorial Africa, 13-VIII-1918 (USNM 255279), 14 females, 7 tritonymphs, 7 protonymphs, Anguanamo, Ngoui, W. Chad Terr., French Equatorial Africa, 13-VIII-1918 (USNM 255279).

Figures 66-67

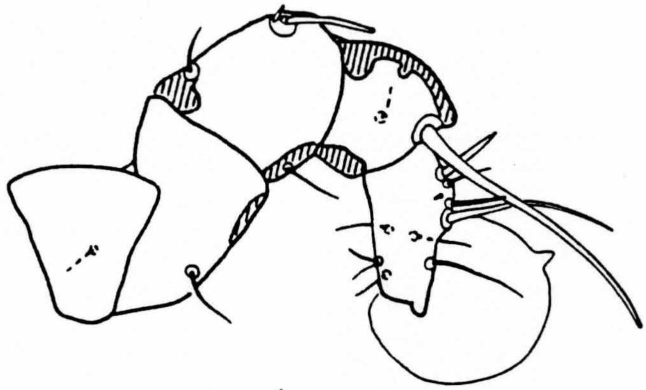
<u>Freyana</u> <u>reticulata</u> n. sp. heteromorphic male
66, dorsal view. 67, ventral view.


66
67
200µ

Figures 68-71

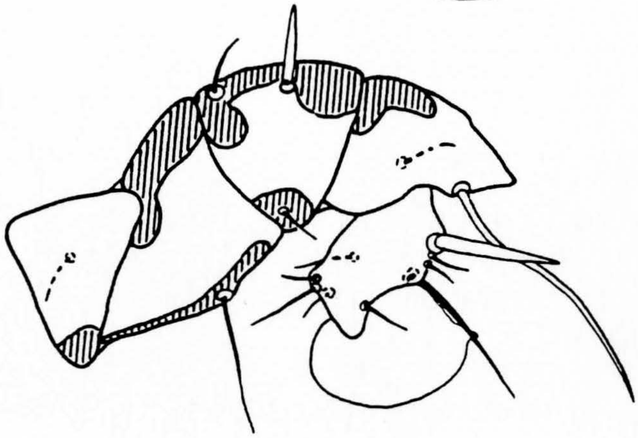
Freyana reticulata n. sp. heteromorphic male, antaxial aspects of legs. 68, leg I. 69, leg II. 70, leg III. 71, leg IV.

68



I

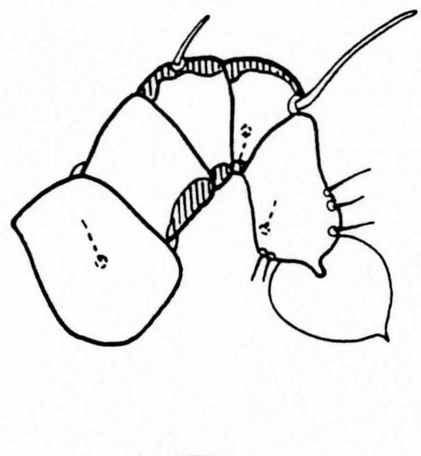
69



II

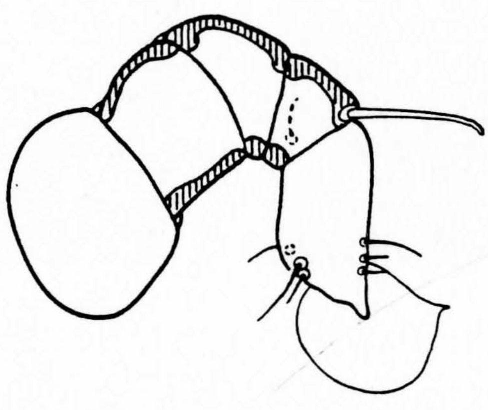
100µ

70



III

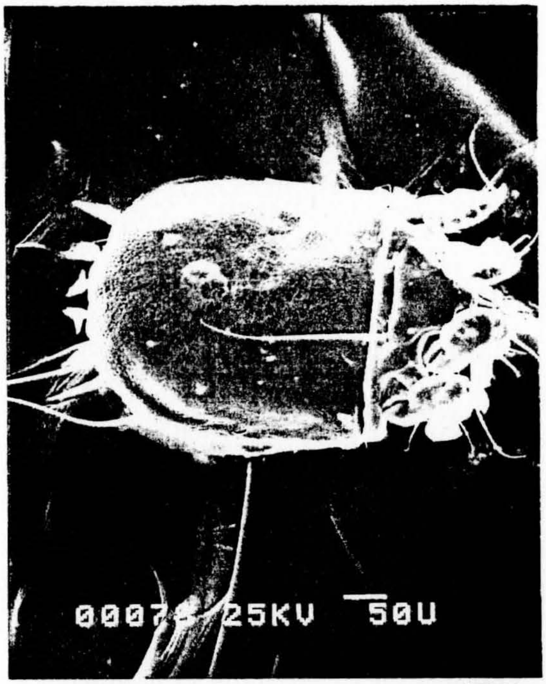
71



IV

SEM Micrographs 47-50

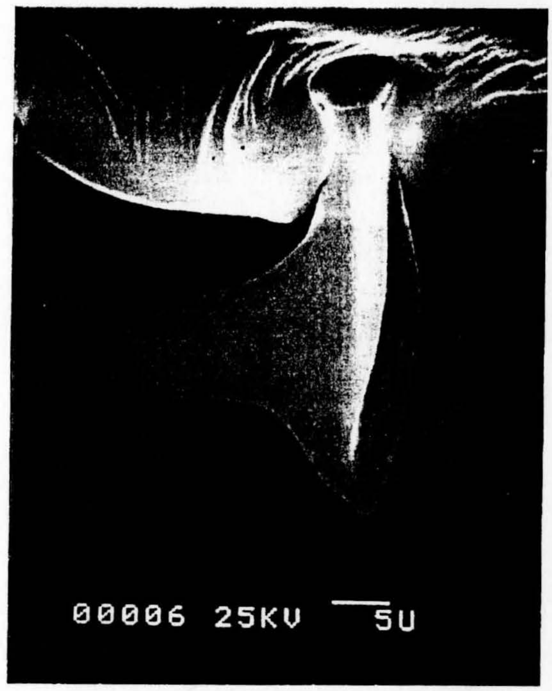
Freyana reticulata n.sp. heteromorphic male. 47, dorso-lateral aspect (150X). 48, leg II (1400X). 49, terminal setae (370X). 50, seta pai (2700X).



47

48

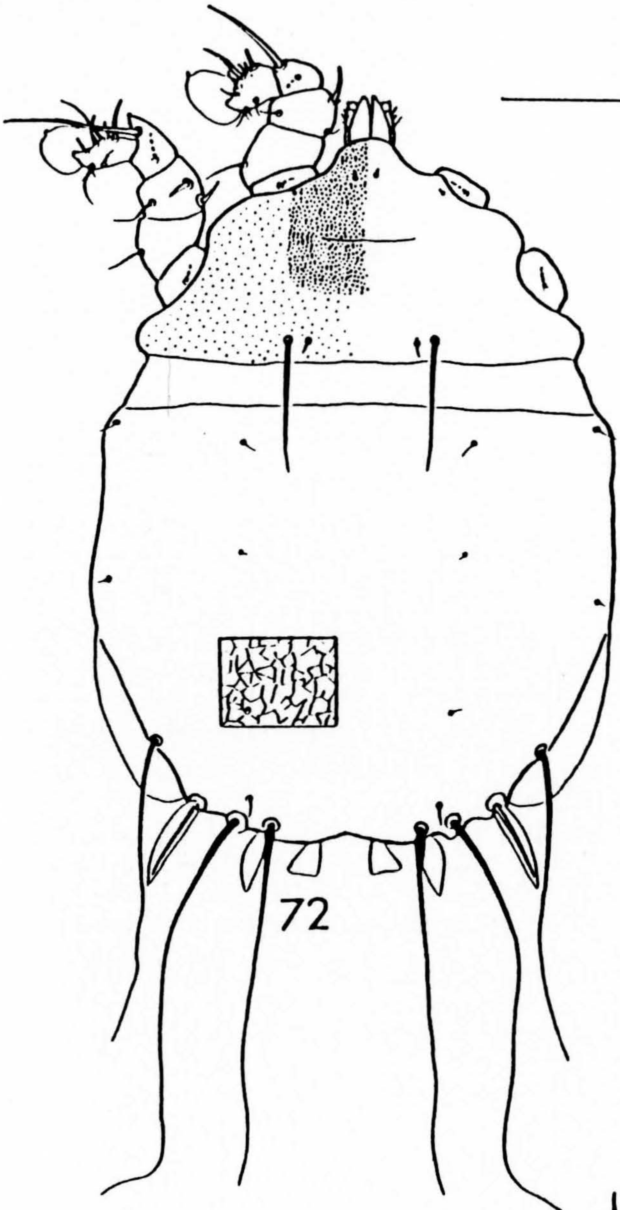
49



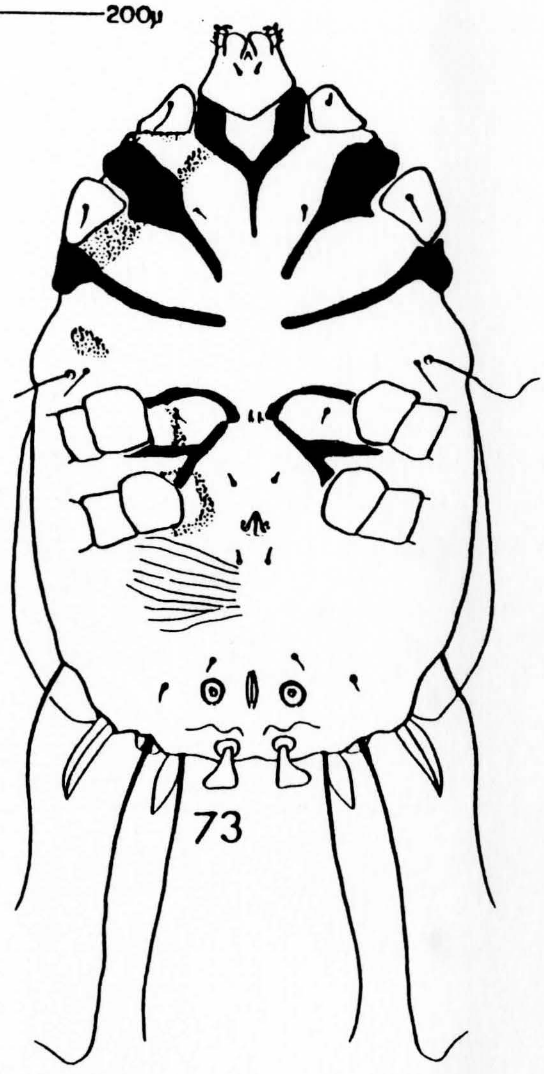
50

Figures 72-74

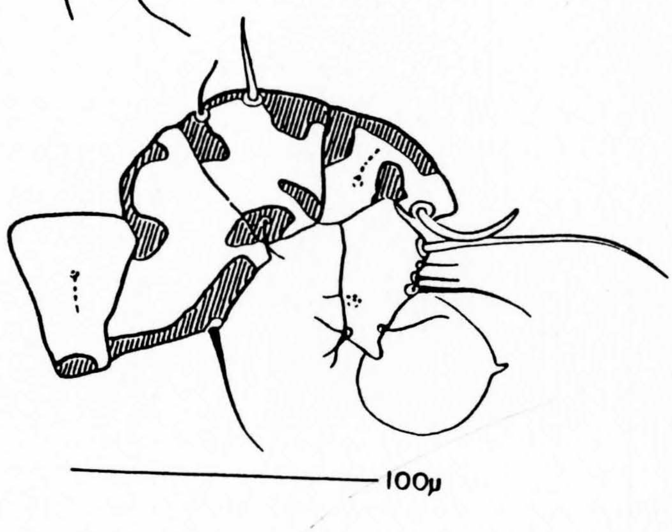
Freyana reticulata n. sp. homeomorphic male
72, dorsal aspect. 73, ventral aspect. 74, leg II.



72



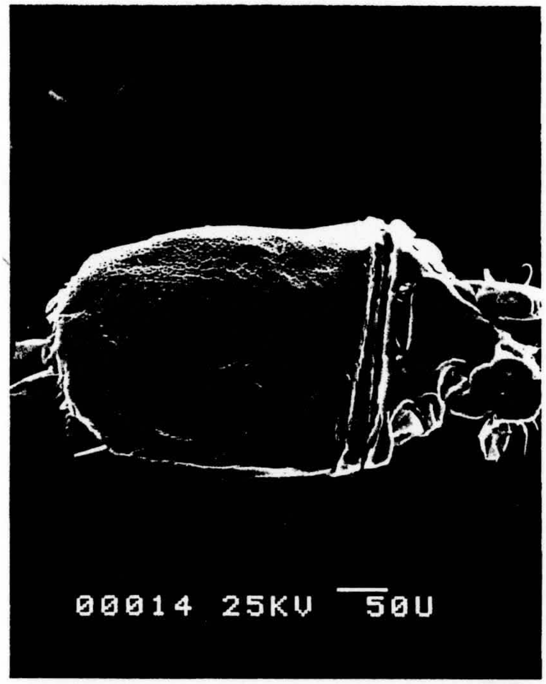
73



74

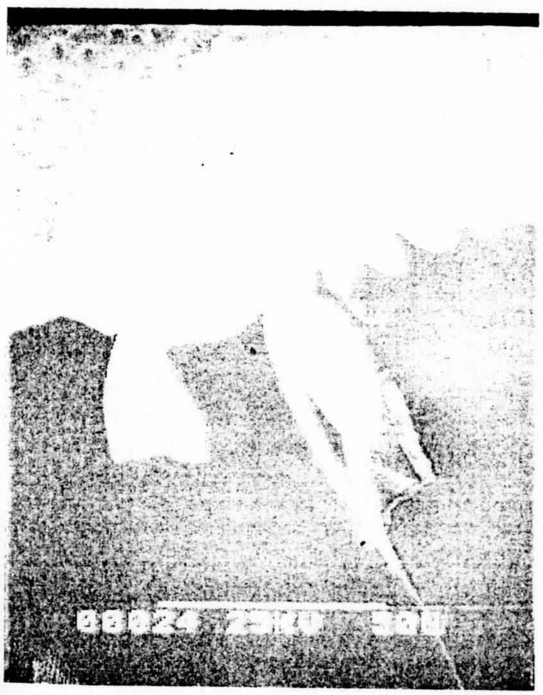
SEM Micrographs 51-54

Freyana *reticulata* n.sp. homeomorphic male. 51, dorso-lateral aspect (180X). 52, leg II (820X). 53, terminal setae (840X). 54, seta pai (2100X).



51

52

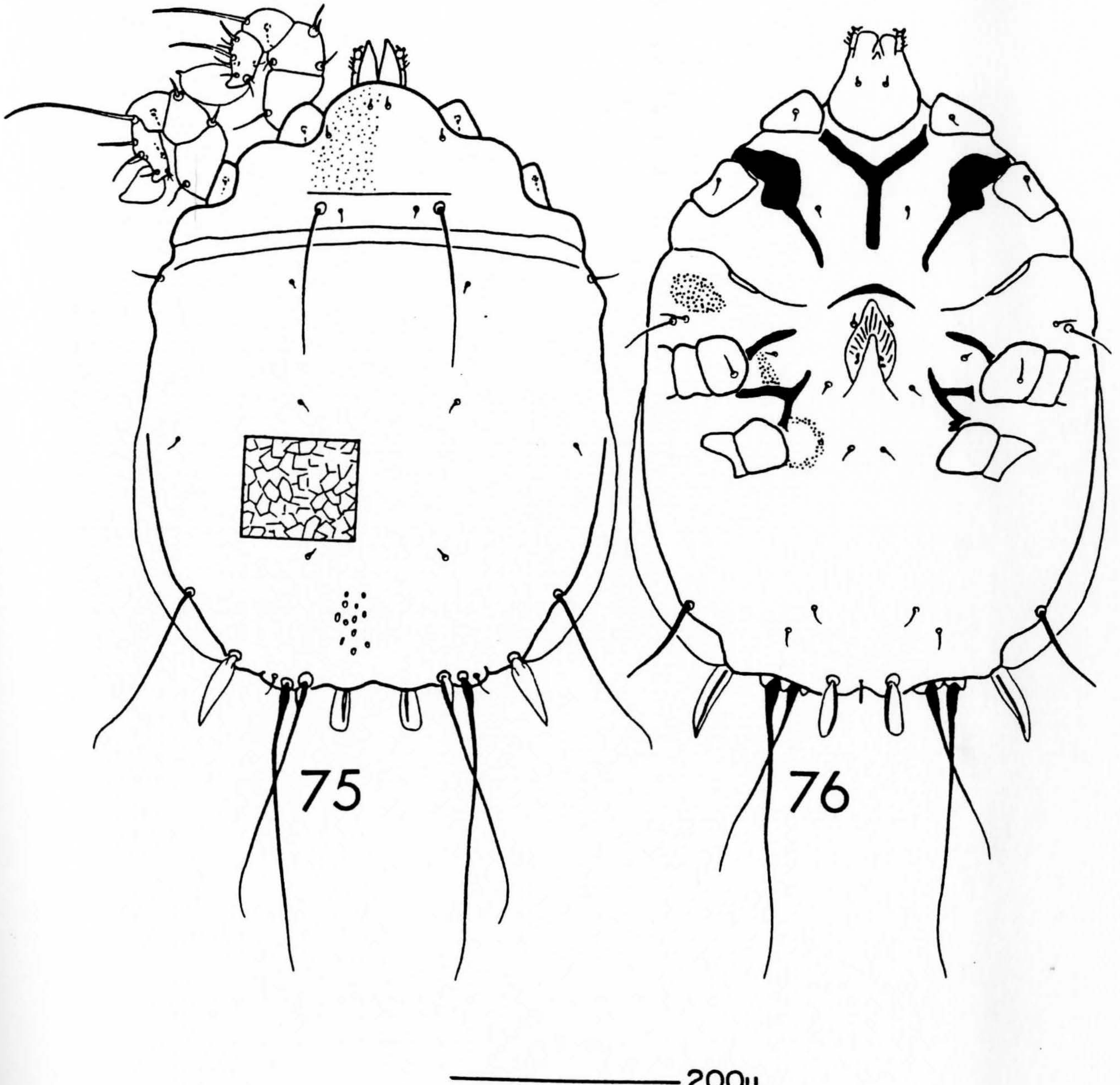


53

54

Figures 75-76

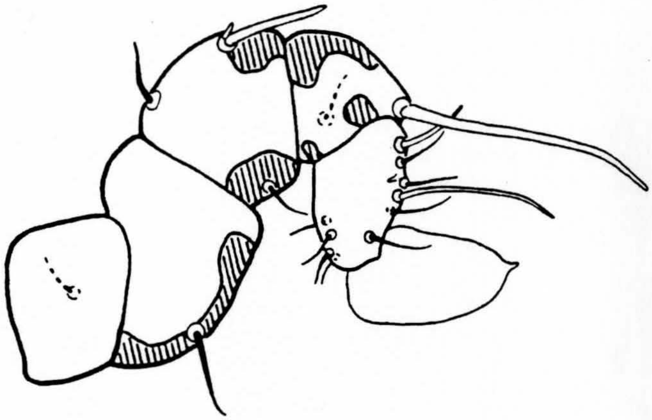
Freyana *reticulata* female
75, dorsal view. 76, ventral view.


75
76
200µ

Figures 77-80

<u>Freyana</u> <u>reticulata</u> n. sp. female, antaxial aspects of legs. 77, leg I. 78, leg II. 79, leg III. 80, leg IV.

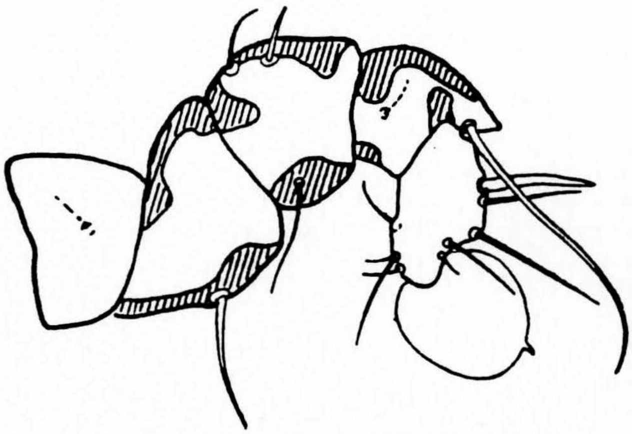
77



I

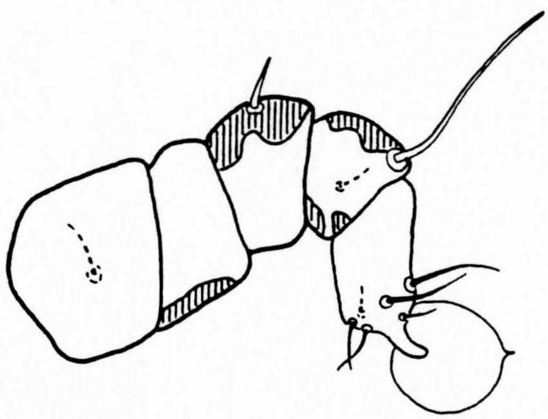
78

100µ



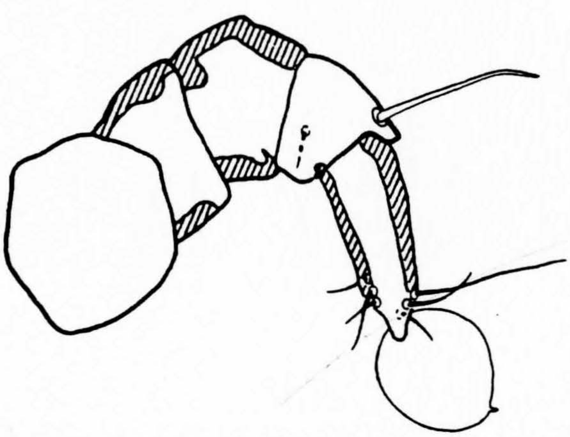
II

79



III

80

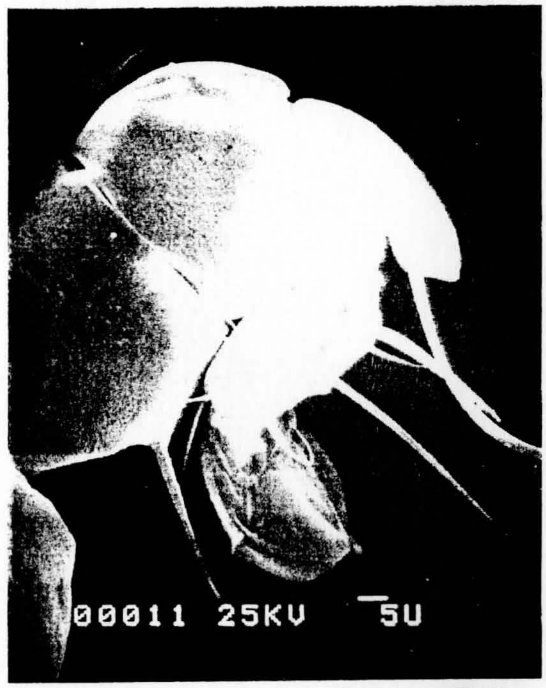


IV

SEM Micrographs 55-58

Freyana reticulata n.sp. adult female. 55, Dorso-lateral aspect (140X). 56, leg II (1000X). 57, terminal setae (240X). 58, seta pai (1700X).

55



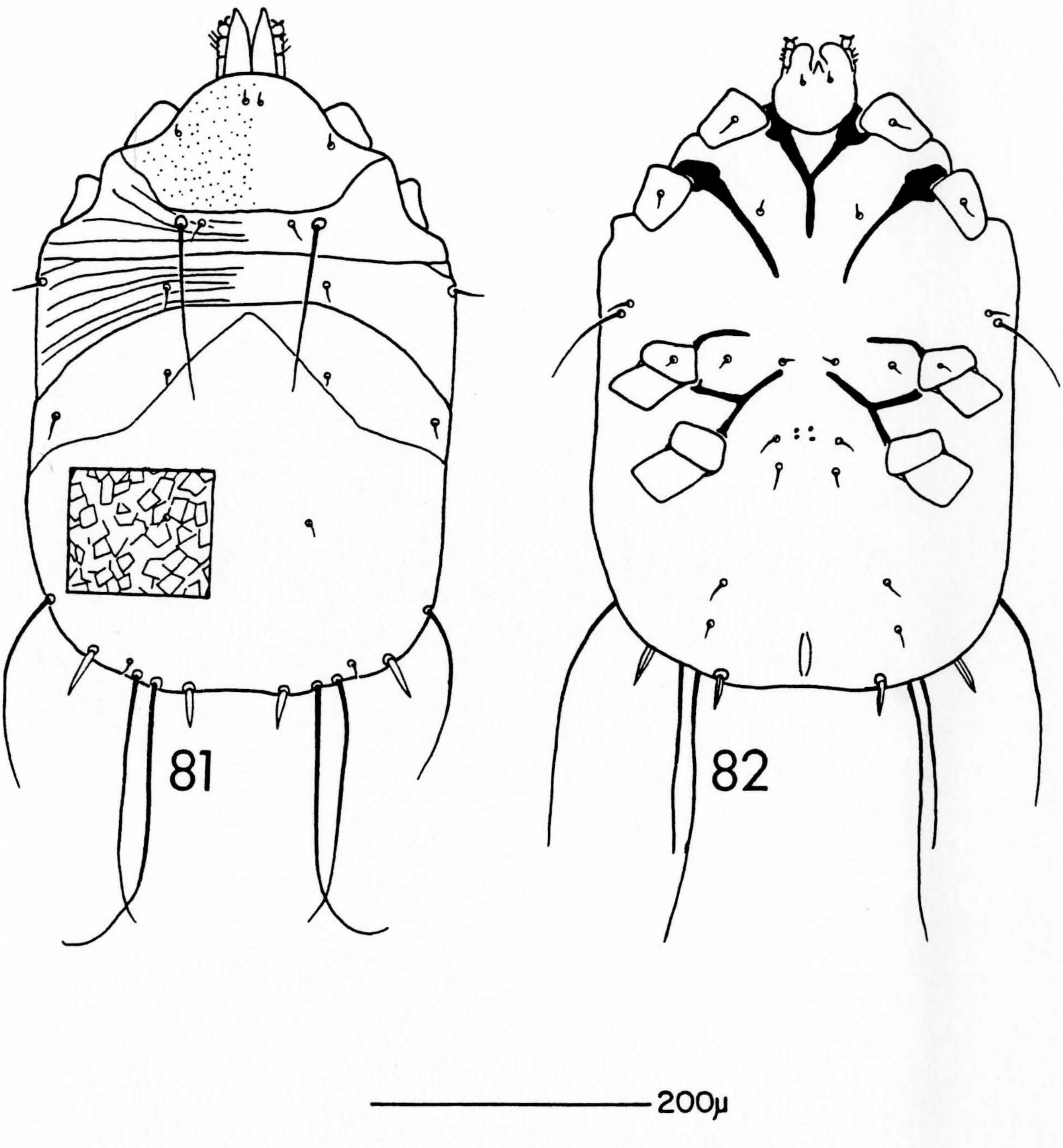
56

57

58

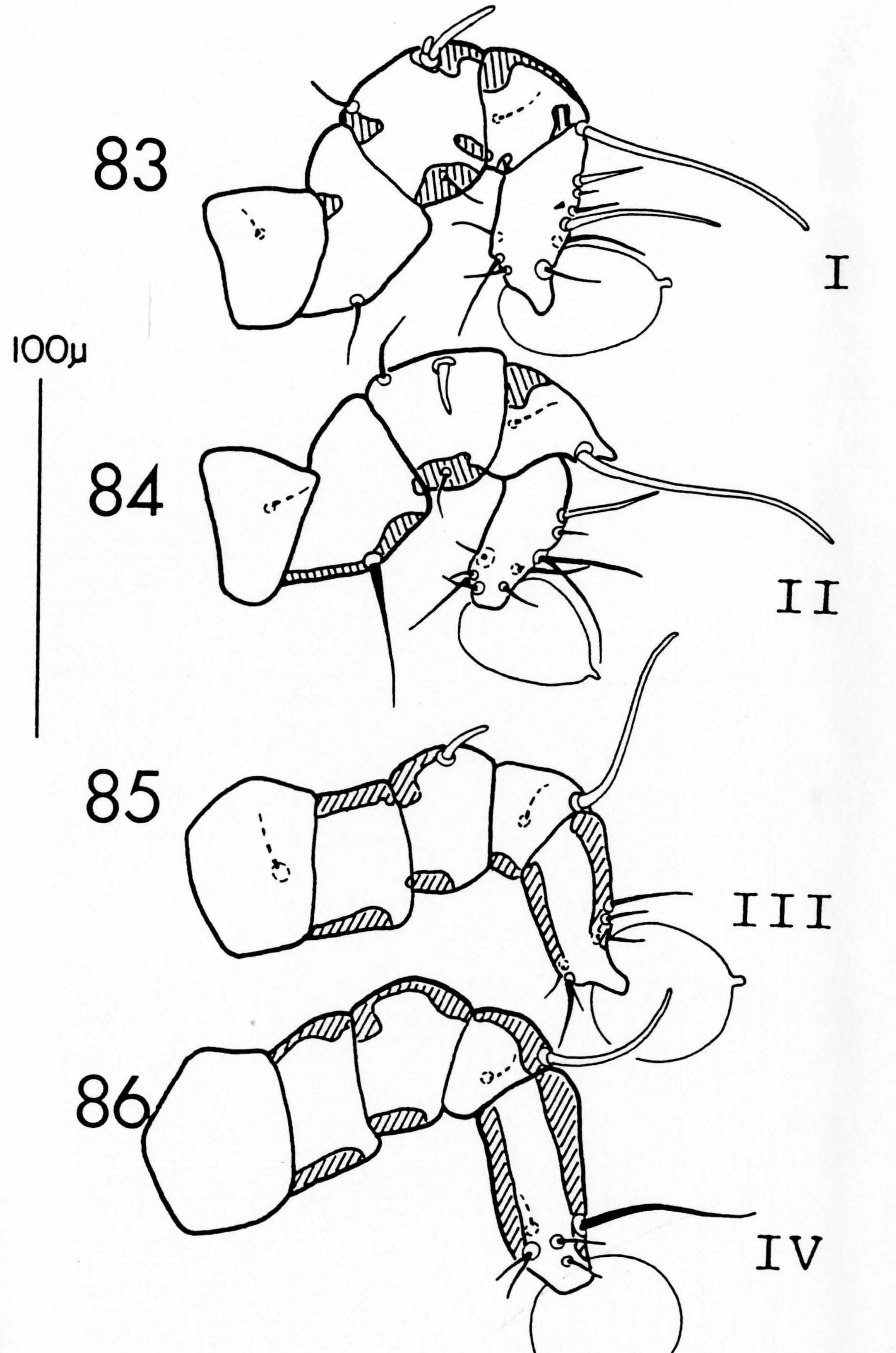
Figures 81-82

Freyana reticulata tritonymph
81, dorsal view. 82, ventral view.


81
82
200µ

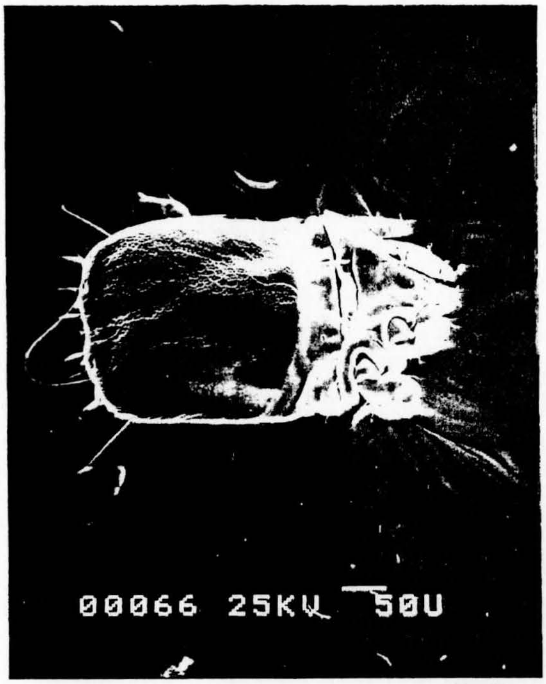
Figures 83-86

Freyana reticulata tritonymph, antaxial aspects of legs 83, leg I. 84, leg II. 85, leg III. 86, leg IV.

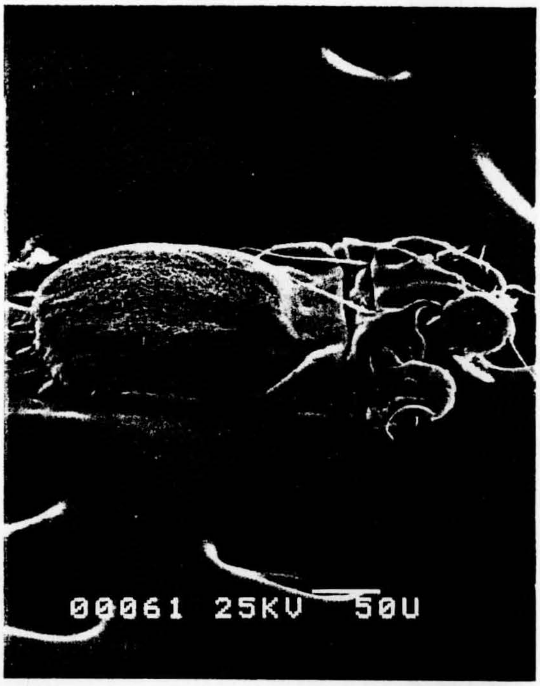

83
I
100µ
84
II
85
III
86
IV

SEM Micrographs 59-61

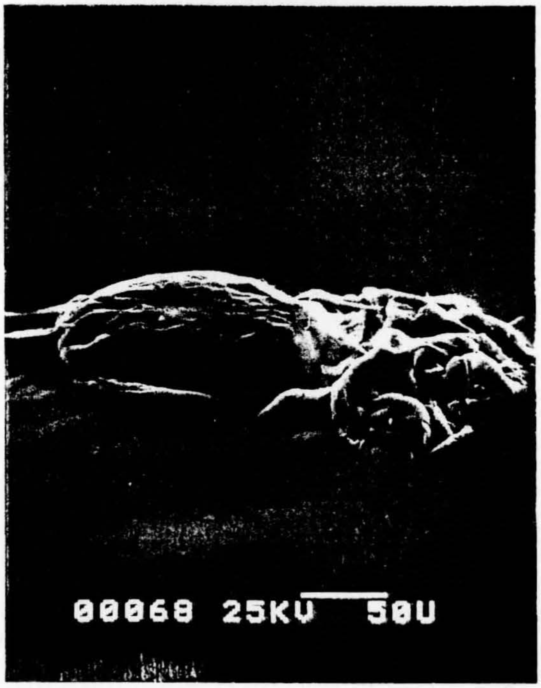
Freyana reticulata n.sp. 59, tritonymph (160X). 60, protonymph (240X). 61, larvae (310X).



59



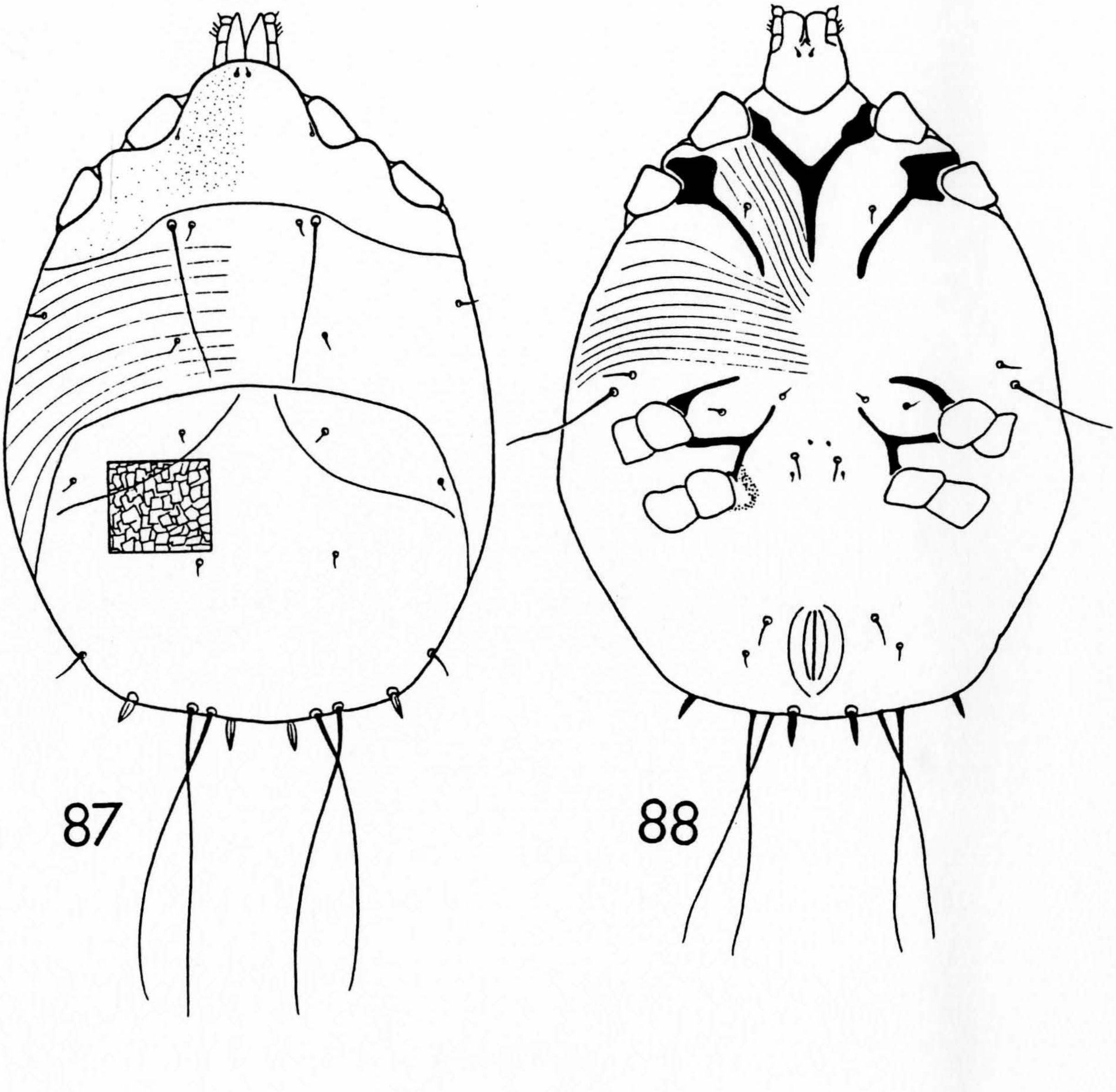
60



61

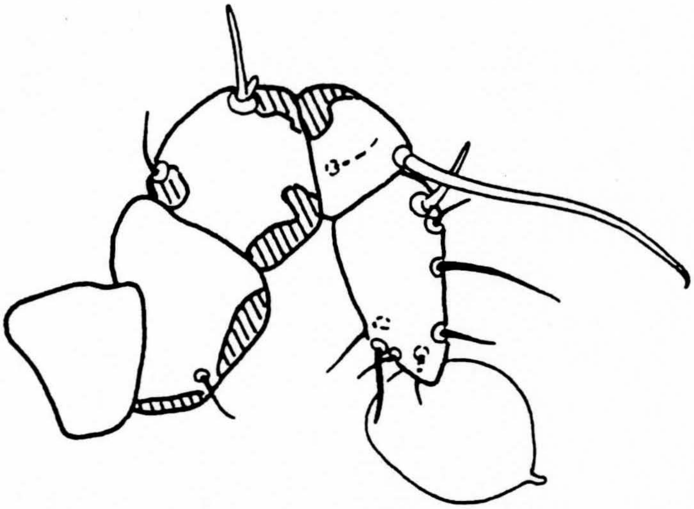
Figures 87-88.

Freyana reticulata n. sp. protonymph
87, dorsal aspect. 88, ventral aspect.

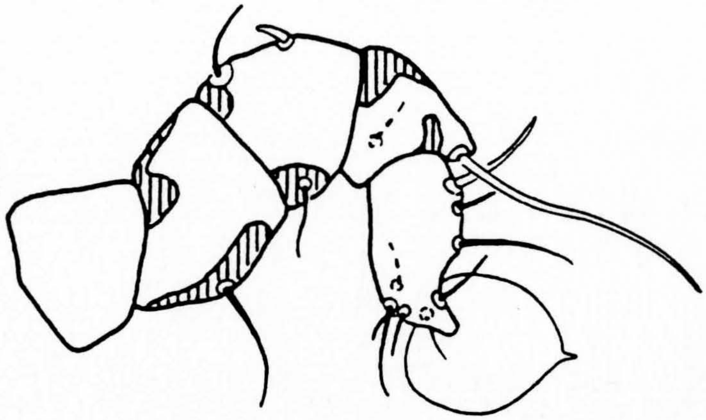

87
88
200µ

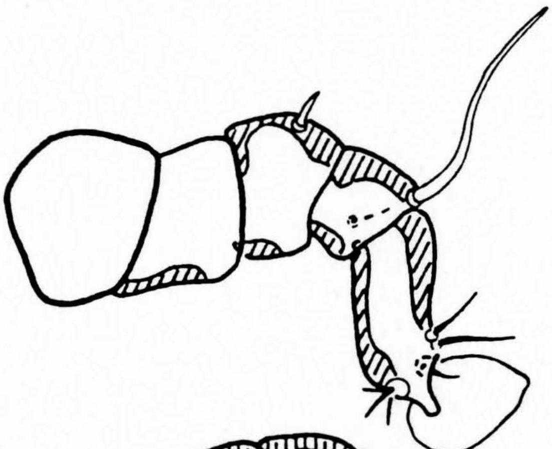
Figures 89-92

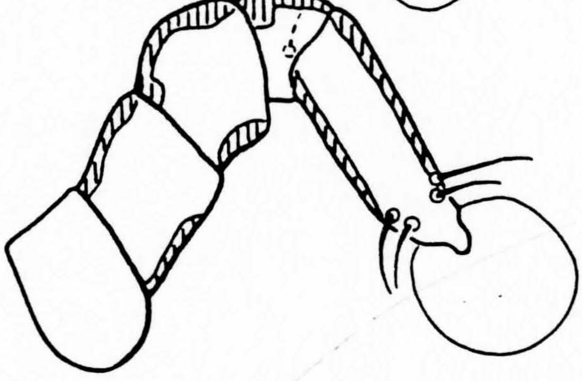
Freyana reticulata n. sp. protonymph, antaxial aspects of legs. 89, leg I. 90, leg II. 91, leg III. 92, leg IV

89

I

100µ

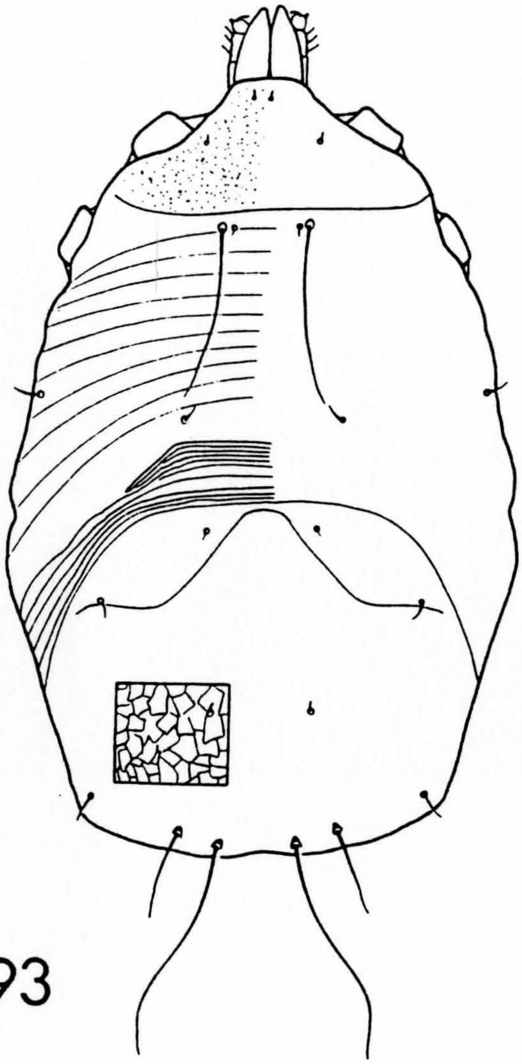
90

II

91

III

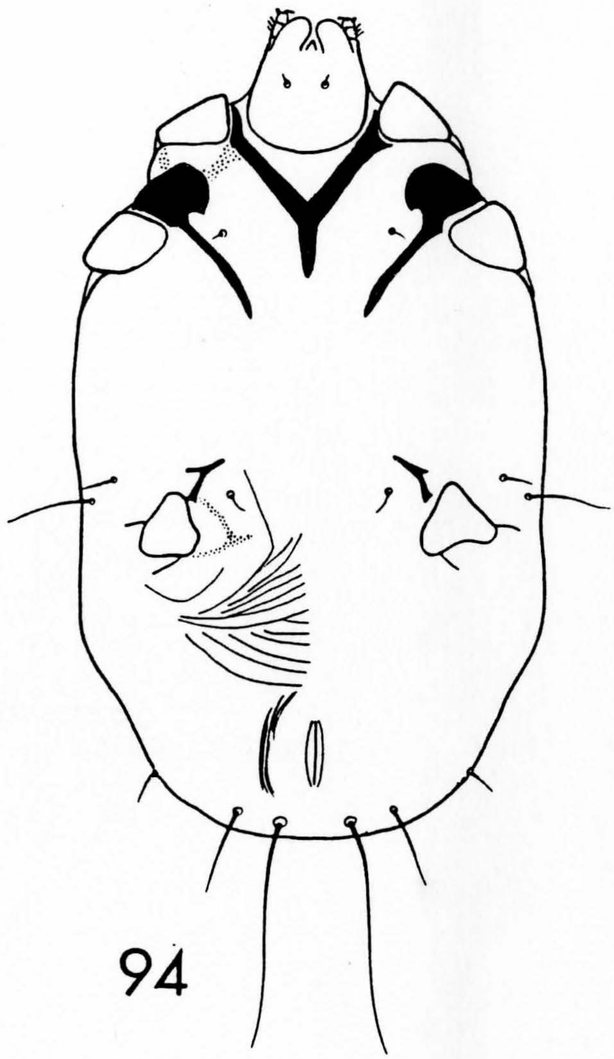
92

IV

Figures 93-94

Freyana reticulata larvae
93, dorsal aspect. 94, ventral aspect.



93



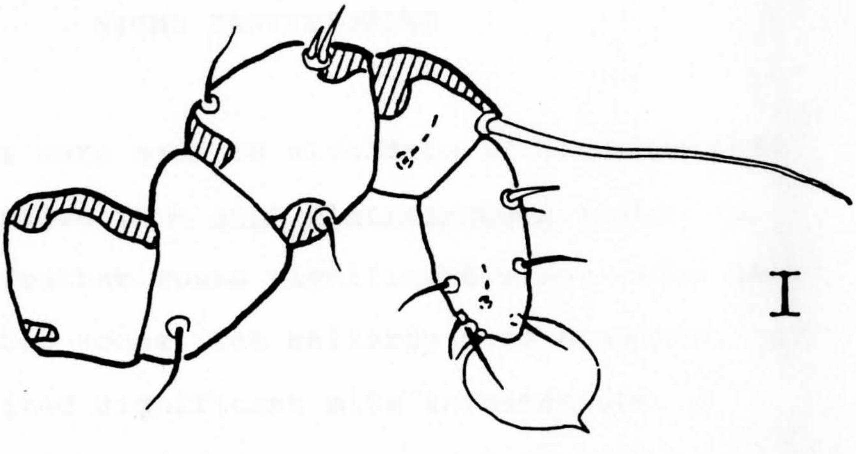
94

200μ

Figures 95-97

Freyana reticulata larvae, antaxial aspects of legs. 95, leg I. 96, leg II. 97, leg III.

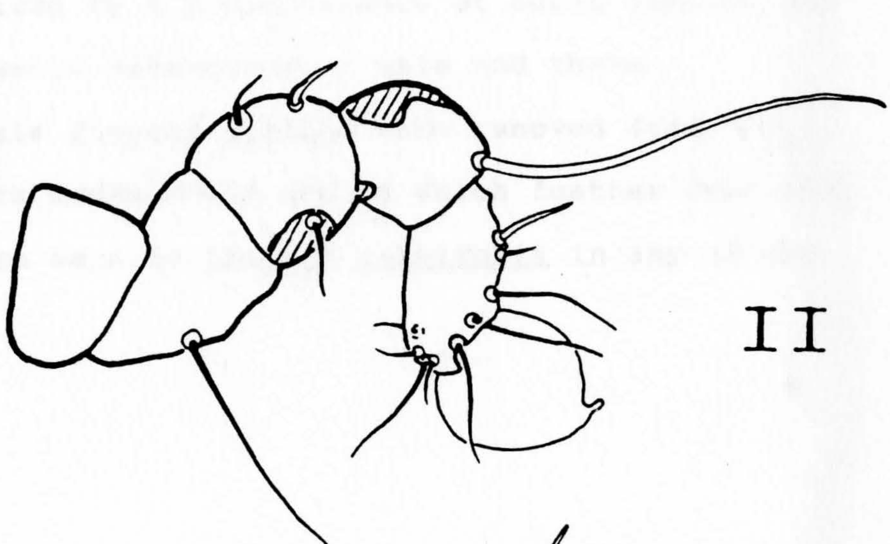
95



I

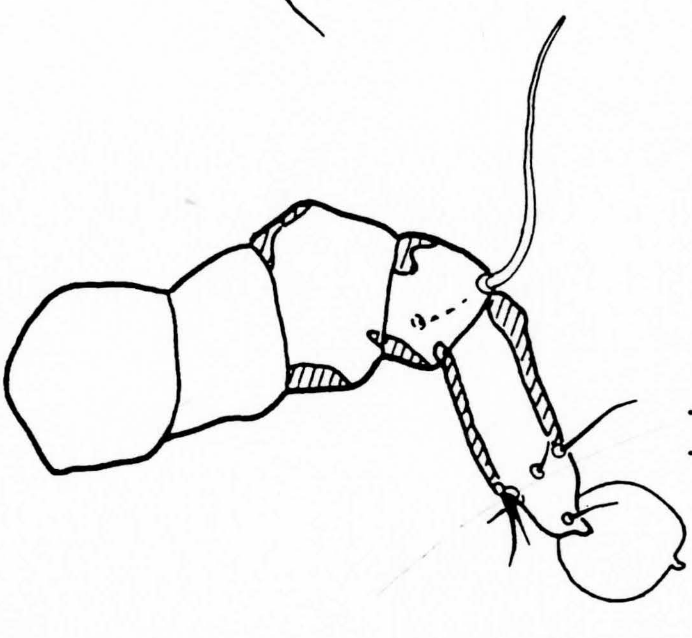
100µ

96



II

97



III

NICHE PARTITIONING

Observations were made to elucidate if heteromorphic *Freyana anatina* males from *Anas platyrhynchos* tended to inhabit exposed feather zones significantly more than they inhabited protected zones. Ten mallards were examined, but only three exhibited significant mite infestations. A similarity shared among all ducks observed in this study was the scarcity of adult male mites found on them. Infestations were characterized by a preponderance of adult females and tritonymphs. Twelve heteromorphic male and three homeomorphic male *Freyana anatina* were removed from the primary feathers ducks while noting which feather zone they came from. There were no *Freyana largifolia* in any of the samples.

RESULTS

Eleven specimens were positioned in the protected air corridors, while only a single specimen was located in an exposed region. The mites probably did not inhabit exposed feather zones significantly more than they inhabited air corridors.

DISCUSSION

The study suggests that heteromorphic males of Freyana anatina are not present in protected versus exposed areas of a feather in a 1:1 ratio. The majority of these males were located in the protected corridors. Thus, for the representative population of this study, the hypothesis that heteromorphy is an adaptation to utilize exposed feather zones is most likely invalid. It is not probable that the evolutionary significance of heteromorphic characters in Freyana anatina is linked to feather microhabitat niche partitioning for the sample population. Considerably larger sample sizes would reveal vital information concerning heteromorphic/ homeomorphic male ratios and its relationship to intrapsecific competition. Other factors not studied, such as interspecific competition, may play a more important role in niche partitioning in feather zone microhabitats. Further studies need to be conducted to determine the significance of niche partioning, competitive exclusion, and androheteromorphism. Cross-rearing studies may prove valuable in discerning the heritability of freyanid heteromorphism. Similarly, the genetic basis of heteromorphy may be elucidated by employing electrophoretic analysis.

BIBLIOGRAPHY

Atyeo,W.T., 1979. Feather mites and their hosts. Recent Advances in Acarology. Academic Press, 2: pp. 355-361.

Atyeo,W.T. and J. Gaud, 1966. The chaetotaxy of sarcoptiform feather mites (Acarina, Analgoidea). J. Kansas ent. Soc., 39 (2) : pp. 337-346.

----------------------, 1983. Feather mites of obligate brood parasites. J. Parasit. 69: 455-458.

Berlese, A., 1898. Acari, Myriopoda et Scorpiones hucusque in Italia reperta, Padova, fasc. 85, No. 1.

Canestrini, G., and P. Kramer, 1899. Demodicidae und Sarcoptidae. Das Tierreich, 7: pp.1-193.

Cerny, V. 1971. Parasite- host relationships in feather mites. Proc. 3rd. Intl. Congr. Acarology : pp. 761-764.

Dabert, Jacek, 1987. Morphological analysis of Freyana anatina (Koch,1844), feather mites (Acari, Freyanoidea). Acta Parasitologica Polonica, 32(3) : pp.239-262.

DeGeer, C., 1778. Memoires pour servir a l'histoire des Insects. Stockholm. 7: pp.100-115.

Dubinin,V.B. 1950. Systematic analysis of species of feather mites (Sarcoptiformes, Analgesoidea), parasites of anatids. Parazit. Sb.,12: pp. 17-22.

------------, 1951a. Feather mites (Analgesoidea). Part I. Introduction to their study. Fauna USSR, Paukoobraznye, 6(5) : pp.1-363.

------------, 1951b. Feather mites of the Baraba Steppe. Report I. Feather mites of Waterfowl and wading birds of the orders of rails, grebes, palmipedes, anserines, herons, gulls, and limicoles. Parazit. Sb., 13 :pp. 120-256.

------------, 1953, Feather mites (Analgesoidea). Part II. Families Epidermoptidae and Freyanidae. Fauna USSR, Paukobraznye, 6(6) :pp. 1-411.

Gaud, J., and W. T. Atyeo, 1985. La famille Freyanidae, Dubinin (Sarcoptiformes plumicoles, Freyanoidea) III. Sous- famille Freyaninae. Acarilogica, 26 (4) : pp. 385-392.

Ginetzinskaya, T.A., 1942. A new form of adaptation of feather mite Freyana anatina Koch to the molt of the host. Dokl. Akad. Nauk. USSR, 37(4): pp. 146-149.

Ginetzinskaya, T.A., 1949. Parasite fauna of the anatinae of the Volga Delta. Uchen. Zap. Leningr. gos. Univ. 101, ser. Biol., 19 (4) : pp. 89-101.

Griffiths. P.A., W.T. Atyeo, R.A. Norton, and C.A. Lynch. 1990. The idiosomal chaetotaxy of astigmatid mites. J. Zool., London. 220: pp.1-32.

Haller, G., 1877. Freyana und Picobia. Zwei. neue Milbengattugen. Z. wiss. Zool., 30: pp.81-998.

Johnsgard, P.A. 1968. Waterfowl: Their Biology and Natural History. Univ. Neb. Press. pp.1-26.

Kethley, J.B. and D.E. Johnston. 1975. Resource tracking patterns in bird and mammal ectoparasites. Misc. Publs. ent. Soc. Am. 9: 231-236.

Lucas, A.M., and P.R. Stettenheim. 1972. Avian Anatomy, Part I. Agriculture Handbook 362. U.S. Government Printing Office, Washington D.C., fig. 2.

Lindquist, E.E. 1975. Associates between mites and other arthropods in forest floor habitats. Can. Ent. 107: 425-437.

Megnin, P., and E.L. Trouessart. 1884. Les Sarcoptides plumicoles. J. Micrograr. 8(2): pp. 92-101.

Moss, Wayne W., Paul C. Peterson, and Warren T. Atyeo. 1977. A multivariate assessment of phenetic relationships within the feather mite family Eustathiidae (Acari). Systematic Zoology. 26 (4):pp. 386-409.

Peterson, Paul C., 1975. An analysis of host-parasite associations among feather mites (Acari: Analgoidea). Misc. Publs. ent. Soc. Am., 9(5) : pp. 237-242.

Radford, C.D., 1950. Systematic checklist of mite genera and type species. Un. int. Sci. biol., Ser. C (Sec. Ent.) (1) : pp. 1-232.

Soothill, E. and P. Whitehead, 1978. Wildfowl of the World. Blanford books Ltd. pp.1-5,248.

Timms, S., and D.N. Ferro, and R.M. Emberson, 1981. Andropolymorphism and its heritability in Sancassania berlesei. Acarilogica, 22 (4) : pp. 391-398.

Trouessart, E.L. and M. P. Megnin, 1885. Monographie dugenre Freyana et description des especes nouvelles du Musee d'Angers., 16 : pp.85-156.