AN ABSTRACT OF THE THESIS OF

David Evans Walter for the degree of Doctor of Philosophy in the Department of Entomology presented on December 3, 1984.

Title A revision of the Macrocheles glaber species group (Acari:Macrochelidae) using phylogenetic systematics.

Redacted for privacy

Abstract approved:

The *Macrocheles glaber* species group contains many of the common mites which are associated with the dung of domestic animals. Species in the *glaber* group have been investigated for their use as biological control agents of synanthropic flies.

Over 10,000 slide-mounted specimens of *Macrocheles* in the OSU Acarology Collection and numerous other specimens loaned from around the world, were examined. Twenty-one species described in the literature were reviewed for inclusion in the *glaber* group. As a result, eight previously described species are redescribed, 11 new species are proposed, and one species is excluded. One misidentification in the

literature is corrected. One new synonymy is proposed. The 30 resultant species in the glaber group are divided into ten species complexes arranged in three subgroups defined by shared derived characters.

The distributions and phoriont hosts of these 30 species are tabulated and anaylzed. The glaber group has its center of diversity in the Old World Tropics and is distributed in all biogeographic realms except the Neotropical and Antarctic. Populations of Macrocheles perglaber from Oregon and France are interfertile.

The species of the glaber group occupy an intermediate position between the primitive free-living members of Macrocheles and the extensive radiation of derived phoretic species. Most species in the glaber group show no specificity in their phoresy on scarab beetles. The paganus-rhodesi cluster, however, is restricted to the tribe Scarabaeini. The dominant morphological trend in the glaber group is the reduction in the degree of sclerotization and ornamentation.

A revision of the *Macrocheles glaber* species group (Acari:Macrochelidae) using phylogenetic systematics.

by

David Evans Walter

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed December 3, 1984

Commencement June 1985

APPROVED: Redacted for privacy

Professor of Entomology in charge of major

Redacted for privacy

Head of Department of Entomology

Redacted for privacy

Dean of Graduate School

Date thesis is presented 3 December 1984

Typed by the author, David Evans Walter

ACKNOWLEDGEMENTS

I would like to express my deep appreciation to Gerald W. Krantz my major professor, my mentor and my friend. Whatever good comes of this thesis, is due to Jerry Krantz's wisdom and tolerance.

Thanks are also due to the remainder of my committee, Norm Anderson, Bill Denison, Tim Schowalter, and William Proebsting for maintaining interest in the arcane field of acarine systematics, providing guidance, and producing an intellectual gauntlet between my ego and my doctorate.

Numerous others were helpful in the research and writing of this thesis. I'd especially like to thank Stuart Sloan for his technical help, and Paul Oman and Chris Darling for their theoretical help. Bruce Halliday (CSIRO) provided live Macrocheles perglaber from Europe and Australia. Thanks to Bill Redmond (SUNY, New Paltz), Al Soeldner, and Andy Moldenke for their help with the SEM. Bill Stephen helped with the word processing. Dan Bean helped in the darkroom. Geraldine Bodine facilitated numerous matters. C.A. Macdonald helped with the articles. S. Bag helped with the humor. The National Science Foundation helped with the money (DEB - 8120986-01). I am indebted to them all.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

A REVISION OF THE MACROCHELES GLABER SPECIES GROUP (ACARI:MACROCHELIDAE) USING PHYLOGENETIC SYSTEMATICS.

> "All organic beings are found to resemble each other in descending degrees, so that they can be classified in groups under groups. This classification is evidently not arbitrary, like the grouping of stars in a constellation." C. Darwin (1859:411).

INTRODUCTION

Of the 15 genera in the family Macrochelidae (Acari:Mesostigmata), the genus Macrocheles is by far the largest with approximately 300 described species and another 300 forms which await description (G.W.Krantz, pers. comm.). The problems inherent in dealing with a taxon of this magnitude have led to the creation of a number of species groups in past years (Berlese 1918, Evans & Hyatt 1963, Filipponi & Pegazzano 1962, 1963, Costa 1967, Johnston 1970, Krantz 1981a, b, and in progress). Species of Macrocheles are predators of nematodes, enchytraeids and arthropods associated with moist organic substrates. The basic lineages of the genus are thought to be free-living associates of stable habitats such as moist litter or animal nests: however, most of the species radiation in Macrocheles appears to have occurred in conjunction with the diversification of

the Scarabaeidae (Insecta:Coleoptera) associated with the dung of large vertebrates. The glaber species group appears to lie near the base of this great radiation in species of Macrocheles that have become phoretic on insects associated with transient dung habitats.

At present, the species groups in the genus Macrocheles are indistinctly defined. The glaber species group sensu latu may include ten percent of all the species in Macrocheles . This thesis is an attempt to use phylogenetic analysis to define the limits of the glaber species group, differentiate it from other species groups in the genus, catalogue the described species that belong to the group, and to provide descriptions of new species.

Importance of the glaber group

Species in the glaber group are among the most common fimicolous mites in the northern temperate zone. They are often associated with cattle pastures and dung, as well as with poultry houses and other sites where there are accumulations of dung. Their synanthropic habits led to the their early description (Muller, 1860) and stimulated the research which

culminated in the experimental taxonomy of Filipponi & Pegazzano (1962).

More recently, interest in the glaber group has intensified because of their potential use as biological control agents against flies breeding in dung (Krantz 1983). This interest led to extensive new research into the systematics of the glaber group (Krantz 1981, Halliday 1982-1984) and the introduction of exotic species in the glaber group for biological control of pest flies in Australia (Wallace et al. 1979, and see papers in Wallace 1982).

Systematic rationale

At its basic level, taxonomy is concerned with ordering the relationships among organisms. The resulting inventory, however, should do more than list taxa. A taxonomic scheme should index knowledge about a group of organisms, and have "high predictive value and ... maximum information retrieval." (Mayr 1969). To be useful the order achieved by a taxonomic arrangement must reflect the theory that describes how this ordering has come into being (Hennig 1966). This study is based on the principles of phylogenetic systematics (Hennig 1966, Wiley 1981, Eldredge and Cracraft 1980) and

attempts to show relationships among species of Macrocheles based on shared derived characteristics.

While taxonomy is concerned with the ordering of organisms, systematics is the study of the diversity that is inherent within that ordering (Mayr 1969, Wiley 1981). Phylogenetic systematics constructs a hierarchical taxonomy that attempts to reconstruct the history of speciation events within a lineage. The "community of similarity" among organisms is used to infer "community of descent" (Hennig 1966) and so to serve as a basis for construction of an evolutionary classification of a group.

The branching sets of nested relationships (cladograms) which result from a phylogenetic analysis often require more taxa than the traditional Linnean hierarchy. This problem can be reduced by using the phylogenetic sequencing convention (Wiley 1981) or constructing paraphyletic groups. The term 'species group' is an informal term (or neutral term in the language of Mayr 1969) for a cluster of closely related species that has no standing under the International Code of Zoological Nomenclature. In order to provide a taxonomic structure for the analysis, I will use the following terms to describe clusters of species: the species group for the assemblage of species related to Macrocheles glaber, the subgroup for the major divisions

of the species group, and the species complex for clusters of very similar species. If two very similar complexes form a common sister group to another complex, then the paired complexes are referred to as a cluster.

Since the nested sets of taxa which are produced by a phylogenetic analysis are based on shared derived similarities rather than on overall similarity, there may be morphological gaps between primitive and derived members of a taxon which would prompt their placement in separate taxa in more traditional classifications. The taxa that result from a phylogenetic analysis reflect the lineage of a group of animals. There is no attempt to produce taxa which are of similar size or composition. Thus, clusters of species produced by recent radiations may have the same taxonomic level as a single relict species from another cluster.

Problems in Macrocheles systematics

The major trend in the evolution of the Acari has been toward small size and the reduction of characters. The species of the Macrocheles glaber group conform to this trend. Most adult female macrochelids range in size from 500 to 1200 um, and exhibit a limited number of morphological characters. Along with a reduction in characters, there is a reduction in variance of the

remaining characters. For example, all of the members of the Macrocheles glaber group have 28 pairs of setae on the dorsal shield, the same compliment of dorsal and ventral shields, the same number of setae on those shields, similar integumental patterns and setation, and similar phoretomorphic chelicerae. One of the few places where some variation in structure does occur is on genua IV, which may have either 6 or 7 setae.

Most of the observable morphological differences among species, therefore, depends on ornamentation of the various shields and setae. This ornamentation is difficult to quantify and, in general, has been poorly illustrated in previous works. Berlese (1918) first noted the importance in macrochelid systematics of the pattern of lines and punctations on the sternal shield. Succeeding authors have used these patterns, although often in an amorphous manner, such as stating "with a distinctive pattern of lines on the sternal shield". The use of phase contrast, interference contrast and, more recently, scanning electron microscope (SEM) photography (Figure 1) has greatly aided in the identification of species of Macrocheles, since the sternal shield patterns often are diagnostic for complexes of closely related species.

Along with the ornamentation of the shields, the kind and degree of plumosities of the setae (Figure 2)

have been used for taxonomic discrimination. These plumosities, however, have been poorly differentiated by various authors. In addition, setae often are broken off, even in type specimens. Furthermore, many types of plumosities may not be observable in some orientations of slide mounted specimens.

The members of the Macrocheles glaber group are generally adapted for phoresy on insects which visit dung. This dependence on other organisms for transportation is correlated with the reduction in sclerotization of the shields and reduction in the degree of ornamentation of those shields and setae. Presumably, shield reduction reflects the reduced importance of heavy armor and elaborate sensory setae a circumscribed habitat. By the same token, developmental time required by dung inhabiting macrochelids is extremely short (Cicolani 1979) and shield reduction may be an incidental result of rapid development. It is interesting to note that reduction in characters in female glaber group members has not been matched by any apomorphies related to phoresy. Except for the presence

of a bidentate cheliceral tooth (which is plesiomorphic [=primitive] in the Macrocheles glaber group) all adaptations for phoresy in females of the glaber group are behavioral rather than morphological.

The glaber group males lack both the bidentate cheliceral tooth and the phoretic behavior, but has elaborately ornamented setae and well developed leg spurs and tubercles all of which aid in which aid in locating, guarding and mating with the females. However, since most collections are from phorionts, and since only the adult female is phoretic, the taxonomy of the glaber group has been based almost entirely on the character-poor female semaphoront (that is, on the adult female subset of morphological characters, within the set of characters which defines the species as a whole, in the sense of Hennig 1966). This greatly complicates the identification of reproductively isolated, but morphologically indistinguishable, sibling species (Filipponi 1959, Filipponi and Pegazzano 1963, Cicolani *et al.* 1981, Halliday 1983).

Figure 1. Composite SEM of ventral surface of *Macrocheles peregrinus* [female paratype, South Africa]: P = palp; CH = chelicera; D = deutosternal groove with denticles; T = tritosternum; S = sternal shield; M = metasternal shield; E = episternal shield; VA = ventrianal shield; I - IV = coxae of legs I - IV.

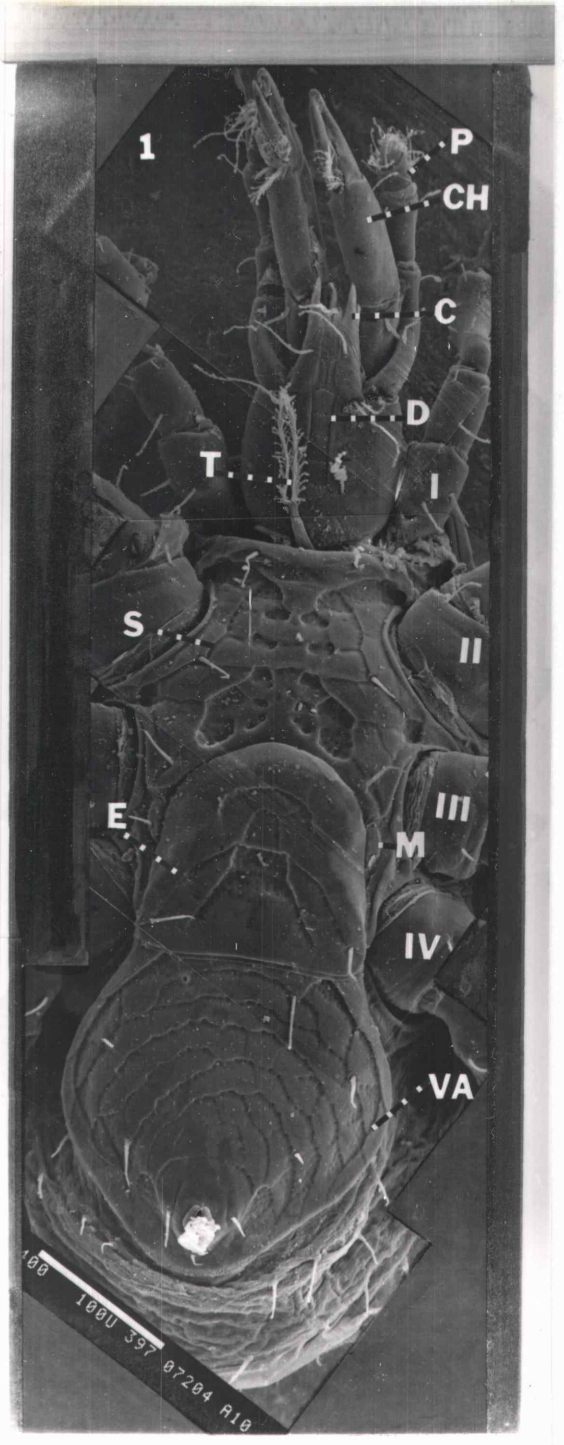


Figure 1.

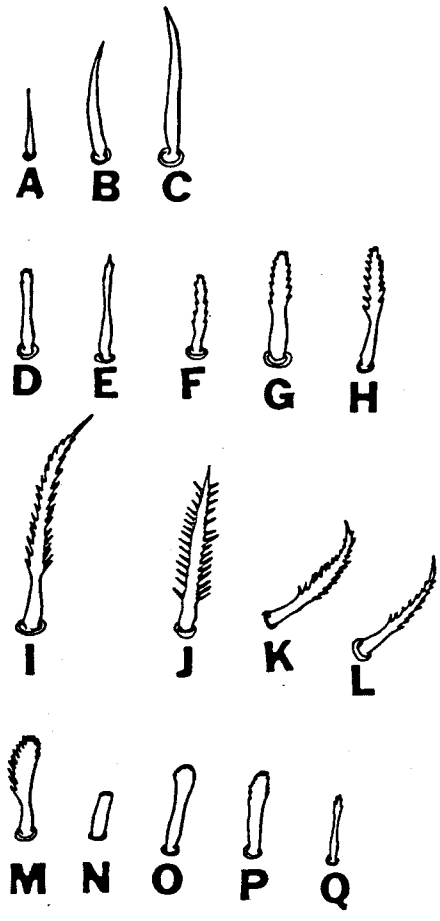


Figure 2. Setal ornamentation in the Macrocheles glaber group.

A-C) smooth acicular; D, E) distally pilose; F) pectinate; G, H) distally pectinate; I-L) strongly bipectinate; M) plumose; N) terminally flat pilose; O-Q) distally pilose.

MATERIALS AND METHODS

The OSU Acarology collection has provided the bulk of the material used in this study. Over 10,000 slide-mounted Macrocheles from throughout the world were studied and approximately 1,000 of these were determined to meet within the provisional definition of the glaber group sensu Krantz (1981). Extensive collections of macrochelids from scarabs and other dung insects, alcohol collections, and slide preparations were obtained from the British Museum (Natural History), London; the Museum National d'Histoire Naturelle, Paris; the Canadian National Collection, Ottawa; the Field Museum of Natural History, Chicago; the Acarology Institute, The Ohio State University, Columbus; the Museum of Comparative Zoology, Harvard; the California Academy of Sciences, San Francisco; the U. S. National Museum, Washington, D.C.; the Rijksmuseum Naturalijke Historie, Leiden; and numerous other museums and individuals from around the world.

Type material was borrowed from the Koninklijk Museum Voor Midden-Afrika, Tervuren; the Czechoslovakian Academy of Sciences, Prague; Potchefstroom University, South Africa; the Zoological Museum of the University of Hamburg; and the British Museum (Natural History). Series from the cultures

used to describe Macrocheles perglaber Filipponi and Pegazzano, and to redescribe Macrocheles glaber (Muller) and M. scutatus (Berlese) were obtained from the Istituto Sperimentale per la Zoologia Agraria, Florence. G.W. Krantz made his extensive notes and drawings of the Berlese collection available.

Cultures of Macrocheles perglaber were started from mites collected from cow dung at several sites in Oregon (Benton, Jackson and Klamath Counties). Cultures of Macrocheles perglaber and Macrocheles glaber from mites collected in cow pastures in France were obtained from CSIRO, Canberra, Australia. Mites used to initiate cultures of Macrocheles praedafimetorium Richards and Richards, were obtained from Lynn Richards, University of Lethbridge, Alberta, Canada. Cultures of M. muscaedomesticae (Scopoli) from poultry house manure and M. merdarius (Berl.) from cow dung in Corvallis also were maintained for comparative purposes.

A Zeiss photomicroscope equipped with interference contrast was used for light microscopic observations and photography. Microscopic mounts were made on glass slides in Hoyer's mounting medium ringed with Glyptal, after clearing in lactophenol or Nesbitt's solution (Krantz 1978). Mites were mounted whole or with the dorsal plate removed. Drawings were made with a drawing tube under interference contrast of mounted specimens or

of mites mounted in lactic acid in depression slides. Measurements were made with a stage-calibrated ocular micrometer. Scanning electron micrographs were made from gold-palladium coated specimens on a Amray 1000 SEM by Alfred Soeldner (OSU) and William Redmond (SUNY, New Paltz).

Cladistic programs were used for both outgroup and ingroup analysis. The Wagner 78 Cladistic Program (Farris) and the Phylogenetic Analysis Under Parsimony (PAUP 2.1, 2.2)(Swofford) programs were made available through the Computer Center, Oregon State University. Results obtained from the two programs were generally similar; however, more trees of greater parsimony were produced by the PAUP programs. In addition, a variety of manipulations are available on the PAUP programs which are not available on the Wagner. Consequently, the PAUP program became the preferred analytical tool.

LITERATURE REVIEW

Macrocheles glaber was first described in 1860 as Holostaspis glabra Julius Muller. Species referred to glaber are the most common coprophilous macrochelids in Europe (Evans & Browning 1956). Berlese (1918) used glaber as the type species for Coprholaspis, a new subgenus of Macrocheles and described and illustrated the distinctive sternal shield ornamentation of glaber. Evans & Hyatt (1963) divided Macrocheles into three species groups. Macrocheles sensu stricto (i.e. those with 28 pairs of dorsal setae) were referred to as the glaber-group. Machado-Allison (1964) and Mendez Olivo (1966) followed this broad definition of the glaber-group. Filipponi (1959, 1962) and Filipponi and Pegazzano (1962) used what has been termed the experimental taxonomic approach (Filipponi 1964) that involved culturing and attempting crosses between different morphotypes referred to glaber, and found that glaber included three closely related species, glaber (Muller), scutatus (Berlese), and a new species, perglaber Filipponi & Pegazzano. Males of all three species are distinctive, but the females of glaber and perglaber are extremely close sibling species which are difficult to distinguish. Krantz (1981) described two new species that he considered closely related to

glaber, and redefined the characteristics of the group. A review of the literature suggests that approximately 30 described species fit the Krantz (1981) concept of glaber.

Life history and habitat data for members of the glaber group may be found in Evans & Browning (1956), Bregetova & Koroleva (1960), Filipponi & Pegazzano (1962), Filipponi & diDelupis (1963), Filipponi & Francavigilia (1963) (larviparity), Krauss (1970), and Wallace (1982). Phoretic relationships in the glaber group have been documented in Ryke & Meyer (1958), Bregetova & Koroleva (1960), Axtell (1962), Evans & Hyatt (1963), Petrova (1964), Sychevskaya (1964), Krantz & Filipponi (1964), Cicolani (1979b), Wallace et al. (1979), and Krantz (1981a). North American records for members of the glaber group include Axtell (1962,1963), Macqueen & Beirne (1974), Norton 1973 and Richards & Richards (1977). The use of macrochelids in the glaber group as agents of biological control has been reviewed by Axtell (1969) and Krantz (1983).

Figure 3. Dorsal and lateral views of Macrocheles. (A) lateral view of the gnathosoma, (B) dorsal view of the gnathosoma, (C) lateral view of the gnathosoma and palps, (D) lateral view of peritrematic shield and peritreme, (E) and, lateral view of the ventrianal shield of Macrocheles perglaber, female (Klamath Co., OR), (F) posterior dorsal opisthosoma showing narrowing dorsal shield in Macrocheles nr. transmigrans (North Burma).

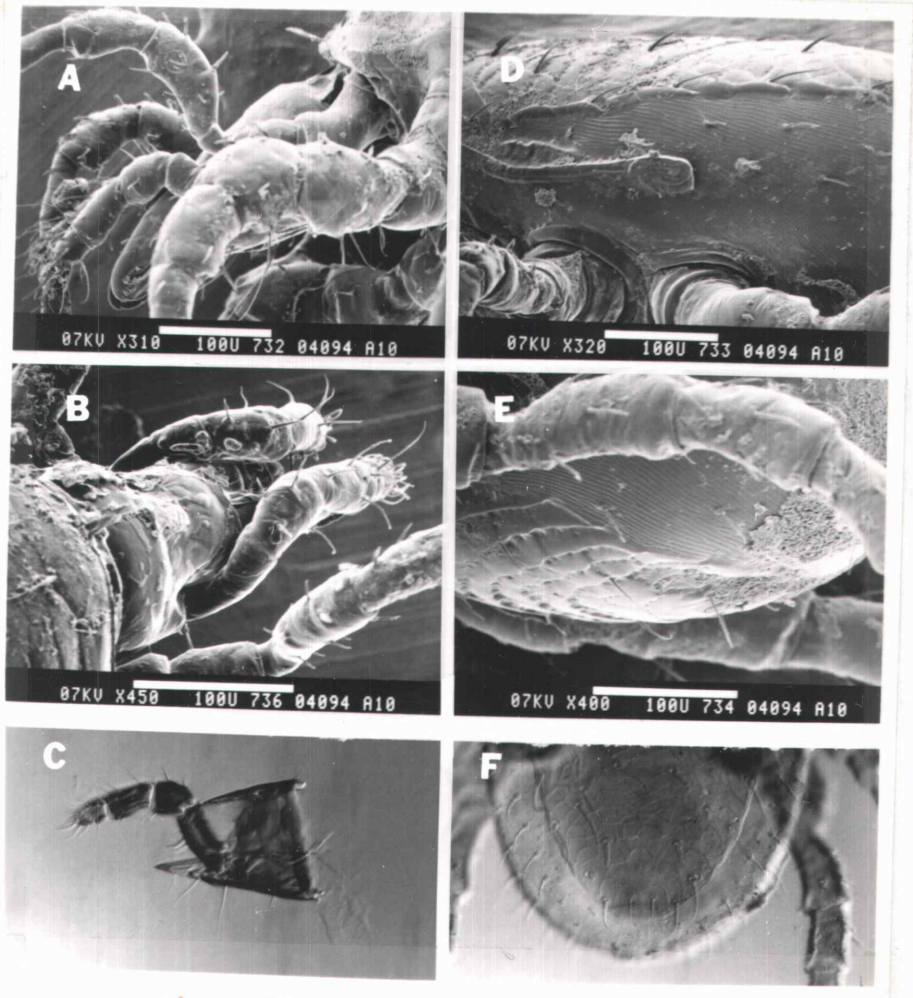

A
07KV X310 100U 732 04094 A10
D
07KV X320 100U 733 04094 A10
B
07KV X450 100U 736 04094 A10
E
07KV X400 100U 734 04094 A10
C
F

Figure 3.

AN ATLAS OF THE GLABER GROUP

The following diagnosis and discussion of the morphology of the glaber species group is based on specimens of Macrocheles perglaber Filipponi & Pegazzano, the larger sibling species of M. glaber, produced in colonies cultured from females collected from cow dung in Klamath County, Oregon. Numerous slide mounted specimens of M. glaber (Muller), eurygaster Krantz, peregrinus Krantz, praedafimetorium Richards & Richards, and kraepilini (Berlese) from the OSU Acarology Collection also were examined. Special consideration was given to the composite SEM photographs of perglaber from Klamath County, Oregon (fig.6) and of peregrinus (paratype) from Natal, South Africa (fig.1).

Adult Female

Dorsum: The gnathosoma (figs. 1, 3 A-C) is a tubular structure which encloses the chelicerae and the bases of the palps (van der Hammen 1964). The dorsal surface of the gnathosoma begins under the dorsal shield between the coxae of legs I and extends anteriorly over the chelicerae. The anterior margin of the roof of the gnathosoma is denticulate and prolonged medially into a tripartite structure, the epistome, which traps fluids

during feeding (Wernz & Krantz 1976). The epistome in the glaber group is composed of lateral flags which extend over the chelicerae and a median bifurcate element which extends between the chelicerae (fig. 3 B).

The dorsal shield (fig. 4) arises behind the gnathosoma and is fused laterally to the peritrematic shields over coxae I. The peritrematic shields diverge laterally (fig. 3 D), and the dorsal shield flares to its maximum width at the humeral angles and is extended posteriorly to broadly cover the opisthosoma (fig. 4) or it becomes narrowed, exposing the opisthosoma (fig. 3 E). The dorsal shield (fig. 4) is a heavily sclerotized reddish brown sclerite which is reticulated with a cell-like pattern formed by punctate depressions. The punctae are small ovals separated by 1-2 diameters along the cell lines. A punctate procurved line (actually a ridge) occurs at the level of setae z6 - r4. Setal designations follow Lindquist and Evans (1965) (fig. 4). Small punctate fields occur posterior to setae r4 at the lateral margins of the procurved line. Scattered punctations occur in the fields of the cellular reticulations posterior to the procurved line, between the marginal (S series) and the lateral (Z series) setae.

Interior muscle attachments give rise to troughs in the region of setae j6, z6 and J2 that often are

marked by distinctive elliptical to reniform sigillary scar patterns which show up under transmitted light microscopy . The sigillary depressions cause the median portion of the dorsal shield to appear hump-like. Posterior to the sigillary area, a pair of punctate depressions (posterior rami) diverge at an angle of 45 degrees from the procurved line. The posterior rami of the procurved line probably mark further muscle attachments. The margin of the shield is slightly raised and scalloped. A slight triangular declivity may be seen around the clunal (J5) setae.

There are 28 pairs of setae on the dorsal shield. These setae may be tapering and pilose for part of their length (figs. 2 F, 5 C), thickened and distally pilose (typical condition for setae j4, z4) (figs. 2 D-E, 19 E) acicular and smooth (figs. 2 A-C, 5 A, 13 H, 19 E), expanded and smooth, weakly bipectinate (fig. 2 F-G), distally bipectinate (figs. 2 H, 20 B) expanded and bipectinate (figs. 2 I-L, 5 B, D-E), biserrate (J5 setae only)(fig. 5 D-E), or plumose (figs. 5 J, 15 F). Most setae have a scimitar-like curve and follow the body line; however, the vertical setae (j1) typically project over the gnathosoma as a unit from adjacent bases (fig. 1 A, B; the anterior humeral seta (r2) often projects at a right angle from the body axis and the clunal setae are always biserrate and situated in a

slight to moderate declivity. The humeral (r2, r3), marginal (r4, s6, S1, S2, S4), and posterior (S5, Z5) setae occur along the margin of the shield and are typically tapering and often pilose. Losses of pilosity from the setae on the margin of the shield seem to occur in a definite progression, with the marginals becoming smooth before the posterior or humeral setae. In the glaber group, the posterior setae (S5, Z5) are usually pilose or pectinate and the vertical setae (j1) are always pilose, at least distally. A hexagonal array of typically short smooth setae (j6, z6, J2) in the sigillary depressions, bisected by the procurved line, is referred to as the dorsal hexagon.

There are 22 pairs of pore-like structures on the dorsal shield. Six pairs (pj3, pz4, pz5, pz6, pZ3, pS5) are gland openings, and the remainding 16 pairs are cuticle covered structures resembling proprioreceptors (Krantz and Redmond *in press*).

The peritrematic groove extends ventrad from seta z1 and runs along the anterior ventral margin of the dorsal shield to the humeral region between setae r2-r3 (fig. 3 D), where the peritrematic shield diverges from the dorsal shield. The narrow peritrematic shield continues laterally in the integument to the level of s6 (between coxae 3-4),where it recurves and enters the stigma. The peritrematic shield contains four pore-like

structures (van der Hammen 1964), one of which (pp2) appears to be secretory (Krantz & Redmond *in press*) and opens into the peritrematic groove at the level of s4.

Venter: The venter of the gnathosoma (fig. 1) is composed of an anterior hypostome formed from the palpcoxal endites, and a posterior basis capituli formed from palpcoxal and deutosternal elements. The hypostome terminates in a pair of lateral corniculi and a pair of medial internal malae. Dorsal to the hypostome are a number of processes - the labrum, patrocinia, paralabral flaps, fimbrilla and the siphunculi (see van der Hammen 1964 for details). The first pair of hypostomatic setae are long and hypostomatic setae 2,3 occur as a pair of long (medial, seta 3) and short (lateral, seta 2) bristles at the beginning of the basis capituli. A median deutosternal groove bisects the basis capituli and hypostome to terminate at the internal malae. Five transverse rows of deutosternal denticles are evenly arranged along the groove from the level of the deutosternal setae anteriorly to the base of the hypostome. Within the hypostomatic portion of the deutosternal groove, at the level of the first hypostomatic setae, is another series of deutosternal denticles which are not transverse, but separate reflexed parallel lines. The deutosternal groove and denticles function in feeding (Wernz & Krantz

1976). The coxae of legs I and the tritosternum arise from sclerotized integument posterior to the gnathosoma. The tritosternum is produced anteriorly as a base with heavily plumose biflagellate laciniae that lie under the deutosternal groove and function in retaining fluids during feeding (Wernz & Krantz 1976). Posterior to the tritosternum is a series of sclerotized plates that runs between the coxal insertions and onto the ventral opisthosoma.

The sternal shield (figs. 1, 6, 7) forms the ventral surface of the body between the coxae of legs I-III. The original terminology for the various 'lines' and punctations was developed by Berlese (1918), and it has been followed in this thesis except where the SEM indicates a different interpretation or a new structure.

The anterior margin of the sternal shield is a raised lip which extends laterally to the anterior angles which join the exites of coxae I. The posterior margin of the ridge appears to be a line in transmitted light microscopy, and contains the insertions of the first pair of sternal setae (st 1). This has been named the linea anterior transversa by Krantz and Filipponi (1964). Posterior to st 1, the sternal shield is produced medially as a tongue-shaped plateau, which drops off laterally towards the anterior corners of the shield. The resulting ridge, which again appears as a

line, is the linea angulata (l. ang.). The l. ang. contains the first pair of sternal pores (sp 1) in the wall of the ridge posterior to the insertions of st 1. The l. ang. is strongly punctate at its base and is bordered by punctate fields from the anterior angle of the sternal shield to a deeply punctate median ridge at the posterior median convergence of the l. ang.. This posterior median convergence may be narrowed in some species (fig. 14), or become obsolete in advanced groups (figs. 19, 20). The posterior median ridge between the l. ang. and the l.m.t. is referred to as the linea arcuata (l. arc.) . In the glaber and praedafimetorium subgroups, the l. arc. has large deep areolations. The lateral edges of these punctae cause the l. arc. to appear to be reflexed (figs. 1, 6, 13). In many species of the glaber subgroup, there is a second areolate ridge anterior to the l. arc. at the median convergence of the l. ang.. When this ridge is strongly developed, it is considered the first l. arc. (Filipponi & Pegazzano 1962). In the scutatus subgroup, there is a single l. arc. that is not deeply punctate, and is produced laterally to form a procurved loop which recurves to join a pair of lateral punctate ridges, the lineae obliquae anteriores (l.o.a.) (figs. 17-20). The l.o.a. arise at st 2 and arch anteriorly to join the l. ang. as a faint line in some species, but this is often obscure.

The sternal shield is bisected by the linea media transversa (l.m.t.), a transverse ridge arising in the median angles of the shield and running along the base of the insertions of st 2. A circular, evenly punctate pit-like depression in each median angle is here designated the area punctata laterales (a.p.l.). The anterior border of each a.p.l. is formed by the deflected lateral extension of the l.m.t.. A pair of forked ridges which define a posteromedian recessed area of the sternal shield arise posterolaterally from the l.m.t.. These ridges are referred to collectively as the linea oblique posteriores (l.o.p.). The laterally curved section, which runs to the a.p.l. and includes sp 2, is referred to as the l.o.p. proper, while the segment which runs to st 3 is referred to as the ramus.

Within the recessed area defined by the l.m.t. and the l.o.p. are punctate structures of taxonomic importance, but of unknown function. A poorly defined series of scattered deep punctations occupies the median area between the l.m.t. and the posterior margin of the sternal shield, and was referred to by Berlese (1918) as the areae punctiformes (a.pf.). Lateral to the a.pf. are pairs of contiguous elliptical evenly punctate depressions, the areae punctatae posteriores (a.p.p.).

The lateral walls of the a.p.p. are formed by the l.o.p..

The posterior angles of the sternal shield contain the last pair of sternal setae (st 3). The lateral borders of the sternal shield have a thickened rim which appear as marginal lines in light microscopy. The posterior border of the sternal shield is arched to accommodate the anterior membranous extension of the epigynial shield.

The epigynial shield (figs. 1, 6) is roughly trapezoidal in shape with a membraneous anterior margin and a truncate posterior border. A single seta (st 5) occurs at each posterior corner. When the base of the epigynial shield is broadened, it is referred to as flared (fig. 6). If the length and width are approximately equal, the shield is considered to be squared (fig. 1).

The ornamentation of the epigynial shield consists of punctations and ridges that have not previously been named. Anteriorly there is a curved punctate depression, and below it there is a dome-shaped cell. The base of the dome cell is formed by an arched ridge that joins the epigynial setae (st 5). This arch is often the last epigynial ornamentation to disappear in regressive groups. The ridge forms the top of the trapezoidal the central cell, which may or may not be

centrally punctate. Finally a curved ridge forms the base of the central cell. A pair of accessory sclerites join the parapodal sclerites internally and are easily visible under light microscopy. The sacculus foemineus has small paired and unstalked sacculi.

The metasternal shields (figs. 1, 6) lie in the integument lateral to the epigynial shield and behind the posterior angles of the sternal shield . The metasternal shields are small rounded, narrowed, or teardrop-shaped sclerites which have a cuticle-covered pore (sp3) at the anterior end, and a single seta (st 4) inserted near the posterior margin.

Lateral to the median complex of shields are the insertions of coxae II - IV. A narrow sclerite, the endopodal shield (fig. 1), is produced internally between coxal bases III-IV. The endopodal elements of coxae II-III are fused insensibly to the sternal shield; coxae I lack endopodal elements. The outer angles of coxal insertions I-III are flanked by narrow curved exopodal sclerites, while coxae IV are bordered by parapodal sclerites. These sclerites join the endopodal elements or sternal shield to form scleritic rings around the coxae. A small subdermal metapodal sclerite is located posterior to each of the parapodal shields. The integument posterior to coxae IV also supports the sclerotized opening of a secretory gland, the postcoxal

pore (or solenostome). A similar gland opening occurs above coxa IV and posterior to the peritrematic shield, and is referred to as the postperitrematic pore.

Posterior to the epigynial shield is the ventrianal shield (figs. 1, 6) on which are inserted three pairs of ventral setae (Jv1, Zv2, Jv3), a pair of paranal setae, and the postanal seta. The postanal seta may be smooth or plumose, while the other ventrianal setae are invariably smooth. The ventrianal shield is ornamented with recurved punctate ridges. The ventral setae lie on the first (Jv1), second (Zv2), and fifth (Jv3) of these ridges, although some variation occurs with the insertions of Jv3. When the punctations of the ventrianal shield cause the ridges to appear to have small emarginations, the ventrianal shield is said to be dimpled (fig. 1). In the limue complex, the dimples are strongly produced (fig. 14 B, D).

The anal opening occurs within the fields of the paranal-postanal setae, in a triangular area which is elevated above the surface of the shield (fig. 6). The anal and postanal valves guard the anal opening. Lobe-like cells form the lateral margins of the elevated anal protrusion. These cells are often freely punctate in their fields. The punctations may continue up the lateral margins of the shield. A thin terminal band of

microvillae, the cribrum, runs between a pair of gland openings at the posterior edge of the ventrianal shield.

The general shape of the ventrianal shield is subcordate. The anterior margin is truncated where it comes into contact with the epigynial shield. The shield flares to its widest point between the levels of Zv2 and Jv3, and then tapers to the cribral area. The integument surrounding the ventrianal shield is plicate and carries numerous short setae.

Appendages: The chelicerae (fig. 10) are three segmented. The basal segment is tubular and gives rise proximally to the cheliceral retractor muscle. The second cheliceral segment articulates with the distal end of the basal segment and terminates in the third, or fixed digit. The fixed digit bears a dorsal seta, an antiaxial lyrifissure at the base of the movable digit, another on the proximal aspect of the fixed digit, and a subterminal sensory structure of unknown function (Evans 1984). The fixed digit is hooked terminally and bears a subterminal recess which receives the tip of the movable digit. Basal to the terminal hook is a large tooth which carries a specialized seta, the pilus dentilis. Proximal to the pilus is a ridged surface which opposes the bidentate tooth of the movable digit, and a gland opening (van der Hammen 1964). A long internal and a short internal arthrodial brush arise ventrally at the

articulation of the movable digit. The movable digit, which is considered a modified apotele by van der Hammen (1964), bears a terminal hooked tip, a small subterminal tooth and a more proximal bidentate tooth.

The coxae of the palps (=pedipalps of other Arachnida) are modified to form the gnathosoma. The trochanter is elongate and paraxially bowed. The femur forms a short segment which produces the genu and tibiotarsus. The paraxial surface of the genu has modified setae, and the tarsus supports a number of setae, some of which appear to be chemosensory (see Farish and Axtell 1966, Coons and Axtell 1973).

The first pair of legs are modified as sensory organs and are used to tap the substrate in advance of the mite. The ambulacra and claws of tarsi I are lost and the tarsi terminate in a crown of setae, some of which appear to be chemosensory (see Farish and Axtell 1966, Coons and Axtell 1973). Legs II - IV are ambulatory structures and have the claws, ambulacra, and divided paradactyli typical of Macrocheles. Leg II is stouter than the others, and all have the six segments (coxa, trochanter, femur, genu, tibia, tarsus, and pretarsus) typical for parasitiform mites. Coxa III bears the sperm induction pore posterodorsally. Leg chaetotaxy appears to be fixed in number throughout the glaber group with the exception of genu IV which may

have six or seven setae (types VI and VII of Evans 1963, depending on the presence or absence of the posterolateral seta). A complete leg chaetotaxy for glaber group species may be found in Krantz (1981).

Figure 4. Setal types in Macrocheles: A) long, smooth acicular [oigru, n.sp., India, humeral region]; B) enlarged and strongly bipectinate [transmigrans, Szechuan, humeral region]; C) distally pectinate [muscaedomesticae, Z5, Oregon]; D) serrate clunal (J5) and bipectinate Z5 [kraepilini, SE Asia]; E) long curled clunal (J5) seta [macroscatophilus, n.sp., Zaire]; F) distally pilose vertical (j1) setae [perglaber, Oregon]; G) distally pilose vertical (j1) setae [peregrinus, paratype, South Africa]; H) slender, distally pilose vertical (j1) setae [scutatus, Israel]; I) short, thick, terminally pilose vertical (j1) setae [glaber tsaii, holotype, Canton]; J) plumose [longipes, Z5 and integumental setae (i), Africa].

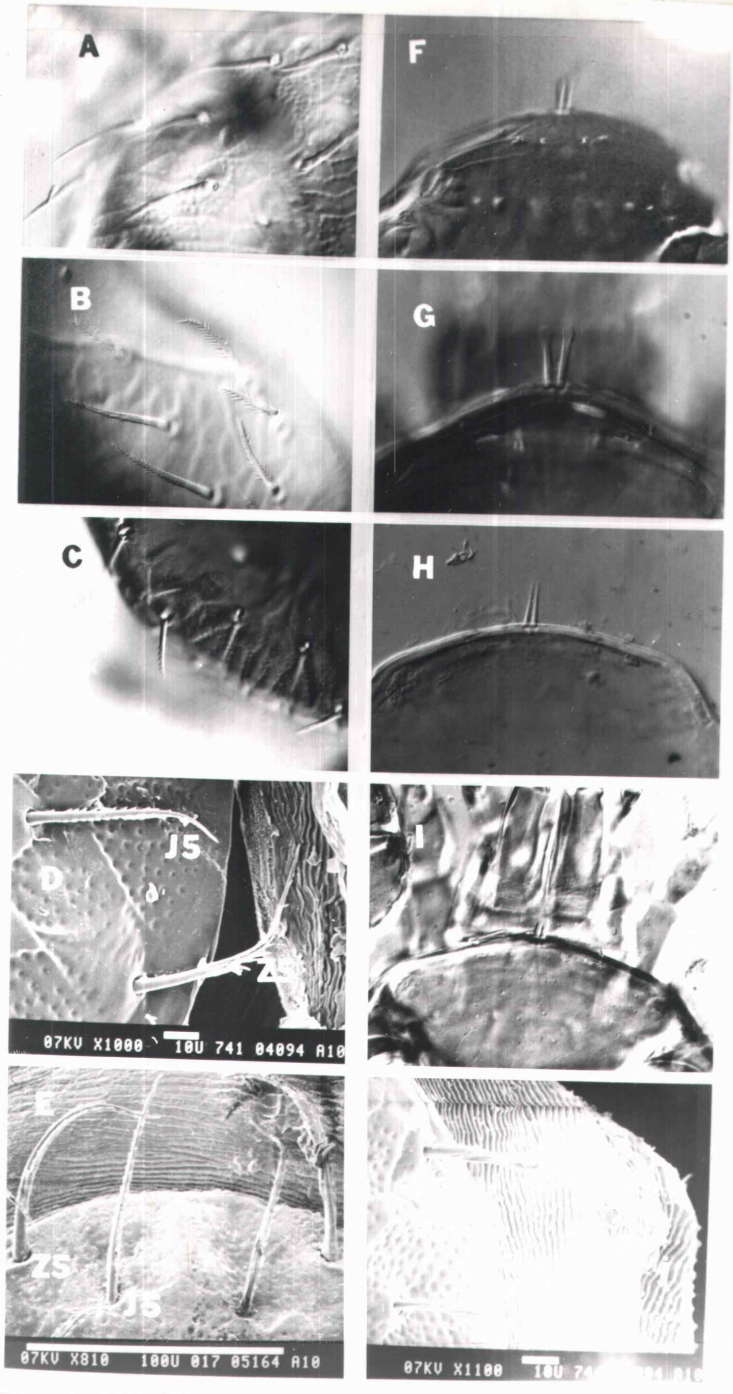

A
F
B
G
C
H
J5
D
I
07KV X1000 10U 741 04094 A10
E
Zs
J5
07KV X810 100U 017 05164 A10
07KV X1100

Figure 4.

Fig. 5. Dorsal shield of Macrocheles perglaber F&P (after Filipponi & Pegazzano 1962). Setal notation follows Lindquist & Evans 1963.

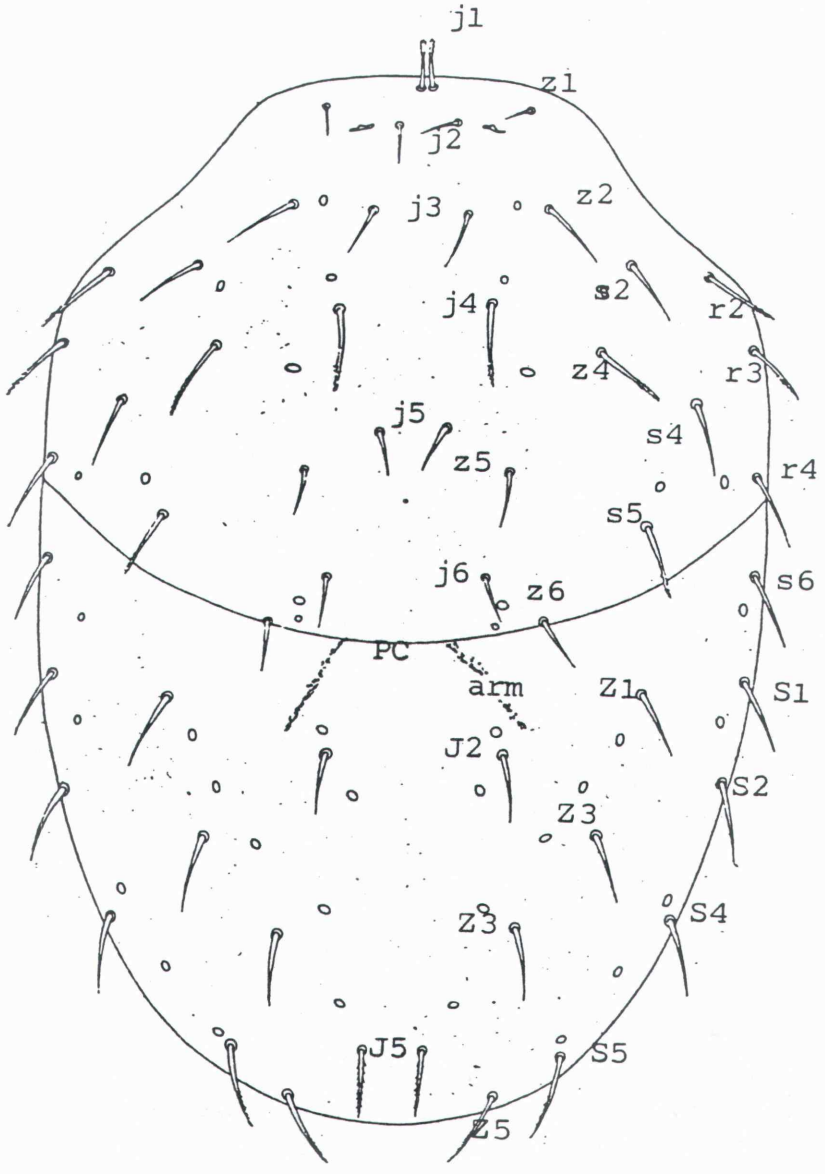
PC = procurved line

j1 = vertical setae

r2, r3 = humeral setae

S5, Z5 = posterior setae

J5 = clunal setae



Macrocheles perglaber

Figure 5.

Figure 6. Composite SEM of ventral shields of *Macrocheles perglaber* (female, Klamath Co., OR): S = sternal shield; AP = area punctatae posterior; EP = endopodal plate; E = epigynial shield; M = metasternal plate; VA = ventrianal shield; A = anal plates; C = cribrum.

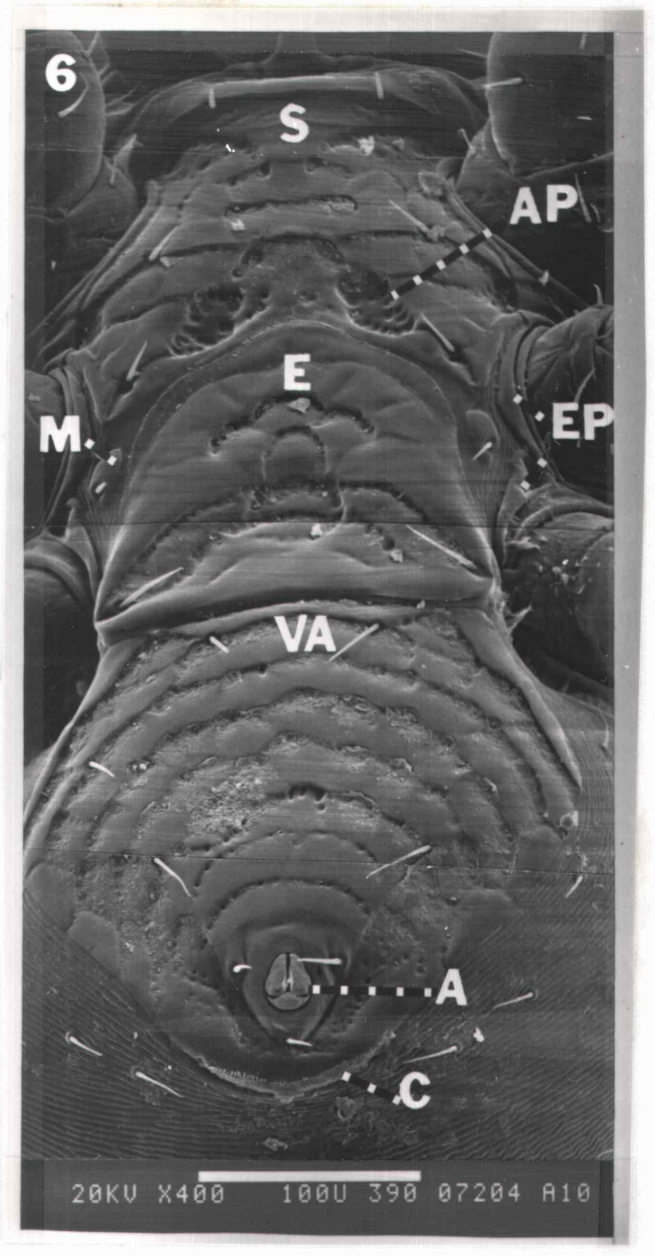
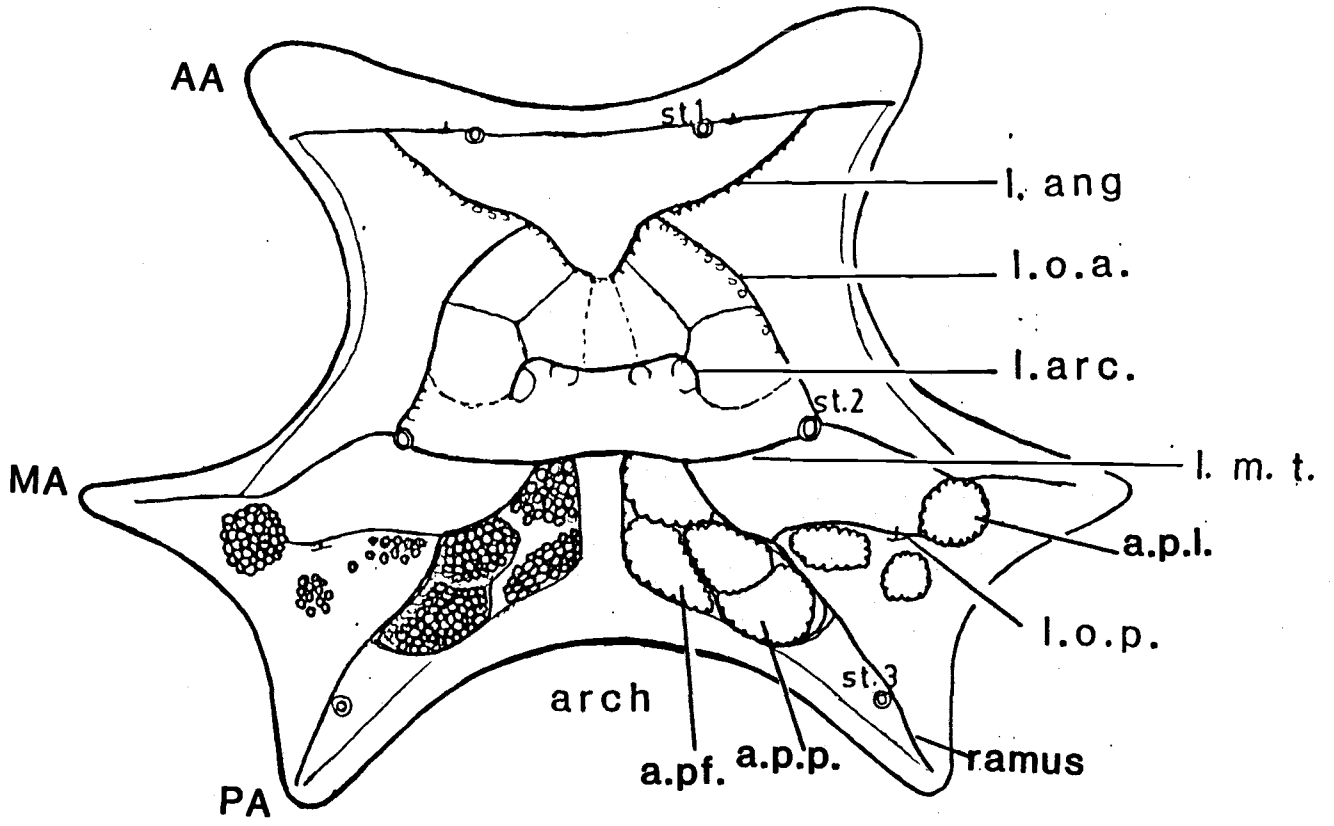


Figure 6.

Figure 7. The lines and punctations of taxonomic importance on the sternal shield in the glaber group: st1-3 (sternal setae 1-3); l.ang. (linea angulata); l.arc. (linea arcuata); l.o.a. (linea oblique anteriores); l.m.t. (linea media transversa); l.o.p. (linea oblique posteriores) and ramus (posterior branch of bifurcate l.o.p.); a.p.l. (area punctatae laterales); a.p.p. (area punctatae posteriores 1 and 2); a.pf. (area punctiformes); PA = posterior angle of sternal shield; MA = median angle of the sternal shield; AA = anterior angle of sternal shield.



STERNAL SHIELD

Figure 7.

The Adult Male

Males in the glaber group are haploid and arrhenotokous (Filipponi & Pegazzano 1962) and illustrate strong sexual dimorphism. In general, males are smaller and more heavily sclerotized than are the females and the setae are more ornamented. Males are immediately distinguishable by size, shape of the opisthosoma, fusion of ventral plates, spurs on legs, and the spermatodactyl on the chelicerae. While differing in these details, much of the background ornamentation of reticulations and punctations is similar in males and females. The following description of male characters emphasizes the differences. Structures similar in both sexes are more completely described for the female.

Dorsum: With the same complement of setae, gland openings, and pores (28, 6, and 16 pairs respectively) as in the female, but with the setae typically more often and more strongly ornamented (fig. 8 A) . The peritrematic shield is fused with the dorsal shield for its entire length and often incorporates setae in the r-R series, as well as the normal complement of pores. The median sigillary area is strongly produced, with typically smooth setae in the dorsal hexagon. The

Figure 8. Macrocheles perglaber, male (Klamath Co., OR): A) dorsal surface; B) venteral view of spurs on trochanter and femur of leg IV; C) the chelicera and spermatodactyl of Macrocheles tantalus (Honolulu); D) Ventral shields, perglaber ; E) chelicera and spermatodactyl, perglaber.

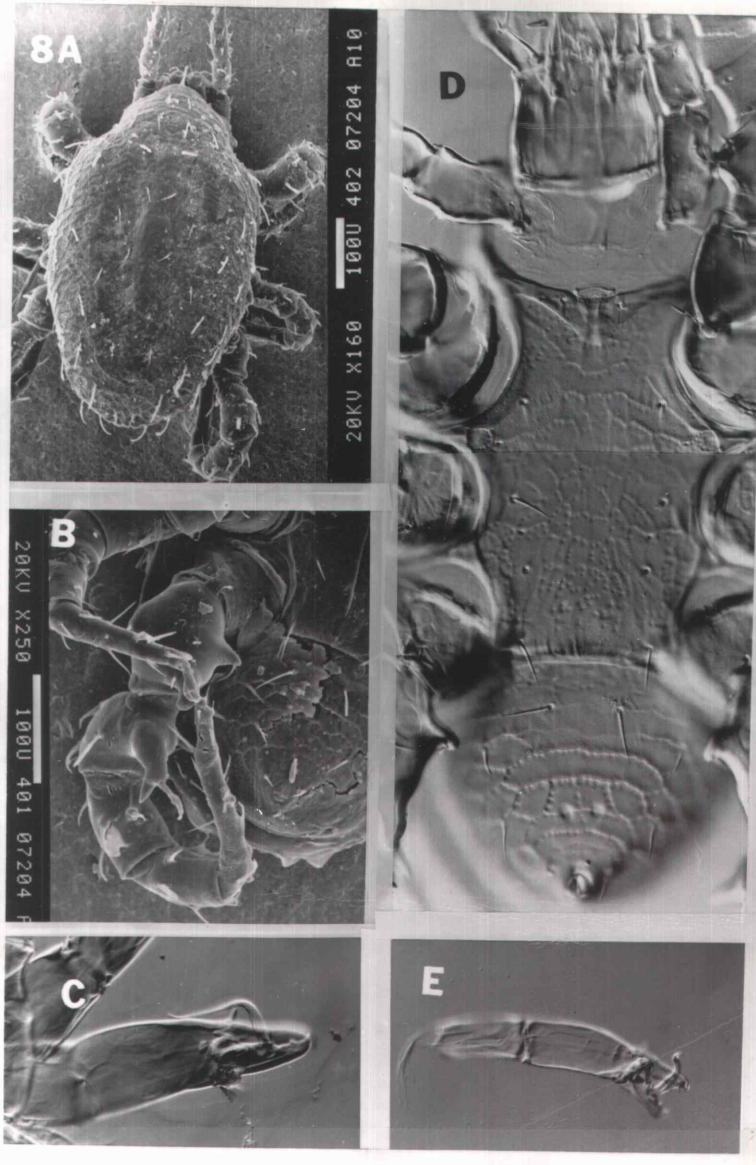


Figure 8.

procurved line and its attendant rami are usually but not always lost.

Posteriorly, the dorsal shield is narrower than that of the female, exposing the loop of the peritreme to dorsal view. The posterior lateral and posterior margins of the dorsal shield are ornamented with small tubercles. The median posterior portion of the dorsal shield is strongly deflected and contains numerous tubercles, especially in the area of the clunal setae.

Venter: The ventral gnathosoma is similar in form and structure in the male and female, as is the tritosternum. Posterior to the tritosternum is the anteromarginal genital aperture and its associated internal apodemes characteristic of podospermous Gamasina.

The intercoxal area supports a single plate, the sternitigenital shield (fig. 8 D), which represents the fusion of the sternal, epigynial, metasternal, and endopodal shields. The sternitigenital shield carries the sternal setae (st1-5) and pores (sp1-3). Except for the linea angulata which carries sp2 and the areae punctatae laterales, the lineae and punctations which are characteristic of the female shields are obscure or lacking. The sternitigenital shield connects to the exopodal and parapodal shields, and is truncate at its posterior margin.

Posterior to the sternitigenital shield is a free ventrianal shield with a recurved pattern of lines and punctations. The ventrianal shield may be subcordate in shape and carry the same compliment of setae as the female, or it may be expanded laterally into a peltate shape (*sensu* Krantz 1981) and incorporate more of the ventral setae. The terminal cribrum is usually wider in the male and typically has a pair of strap-like paranal extensions on either side of the postanal seta. The remaining integumental setae and pores are similar to those of the female. The postcoxal pore tends to be closer to the parapodal shield in the male, than in the female.

Appendages: The chelicerae (fig. 8 C, E) each support an antiaxial spermatodactyl on the movable digit. The spermatodactyl typically tapers to a blunt tip, and is strongly elbowed medially. The spermatodactyl appears to replace the bidentate tooth of the female. The tooth distal to the spermatodactyl is larger in the male than is the homologous tooth in the female. The ridged area of the immoveable digit is lacking, and the pilus dentilis is short, thick, and triangular. The mechanics of sperm transfer in macrochelids have been described in Krantz & Wernz (1979).

The palps and legs I are not noticeably modified in the males; however, legs II-IV may bear small to large spurs. Femur II typically bears a thick hooked spur ventrally. The genu and tibia of legs II each have a small bump-like spur ventrally. Legs III may bear small triangular spurs ventrally on the trochanter and femur. Legs IV are strongly ornamented with a variety of spurs (fig. 8 B). Trochanter IV has up to three triangular setiferous or hooked spurs. Femur IV has a large setiferous spur ventrally that varies from a simple column with a terminal seta to a stout complex of hooks and projections. More rarely, genu and tibia IV may have spurs. Tarsus IV is weakly curved in an S-shape and often bears a median dorsal spur. The degree of development of the spurs on the legs is highly variable. Some males may have little or no development of spurs. This considerably lessens the taxonomic usefulness of the armature of the male legs.

Developmental Stages

Egg: Oval and pearly white, surface appears smooth and unornamented.

Larva: With numerous setal deficiencies. Chaetotaxy of the legs as in Krantz (1981). Leg IV absent, leg I sensory. The ambulacrae are not unusually

developed. Palp apotele appearing two tined due to failure of proximal tine to elongate. Chelicerae with fixed digit armed with teeth, moveable digit with a single small tooth. Epistome with short broad stipe and bifurcate tip, lateral elements absent. Hypostomatic setae 3 and deutosternal setae absent. Laterally the peritreme is short, sinuous and recurved into a prominent stigma dorsal to coxae II - III.

Dorsally there are 14 pairs of setae, but no well defined shield. The vertical setae are separated, smooth, straight and divergent. The humeral seta is long distally pilose, and projects from the body. A dorsal hexagon of short smooth setae (j5, z5, j6) is present. The clunal setae are remote from each other, long and smooth. Setae Z3, Z4, and S4 are long, slightly curled, and project posteriorly.

Ventrally the intercoxal area bears three pairs of setae (st1-3) with gland openings lateral to st1 and posterior to st3. Two pairs of setae (st4-5) occur in the postcoxal area with st4 being very short. The paranals are > twice the length of the postanal. The anal opening is poorly defined.

Protonymph: With the chaetotaxic deficiencies noted in Krantz (1981). The ambulacrae have strongly developed acuminate lateral pulvillar lobes. The median lobe is rounded and the operculi are setate, undivided

and longer than the claws. The proximatal tine of the palp apotele is weakly developed, but the fixed and movable digits are more developed than in the larva and have hooked tips and small teeth. The epistome is stipitate with a bifurcate tip and denticulate posterior margins, but lacks lateral processes. The hypostomatic setation is complete.

The dorsal shield is divided behind j6 at the level of what would be the procurved line in the adult (fig. 9 B). The podonotal shield is weakly punctate-reticulate, has a pattern of sigillary scars, and bears 11 pairs of setae and at least five pairs of pore openings. The vertical setae are distant from each other but parallel (fig. 9 E), setae j4 and z4 are thick and distally pilose, and the dorsal hexagon is as in the larva. The posterior margin of the podonotal shield is incised behind z6 at the site of a gland opening; another pair of gland openings occurs in the integument behind the posterior corners of the podonotal shield and mesal of setae s6 which are free in the integument. The opisthonotal shield is more strongly sclerotized (especially in the pygidial area) and more strongly punctate-reticulate than is the podonotal shield. Eight pairs of setae and at least seven pairs of pores occur on the opisthonotal shield. The posterior portion of this shield is decurved and has a strong declivity

appearing as an arch between setae Z4's. Setae Z4, S4, Z5, and S5 setae are on small tubercles and all are strongly bipectinate. The clunal setae are biserrate. The stigma is dorsal to legs III and IV.

Ventrally, an elongate sternal shield bears st1-3 and sp1-2 marginally in the intercoxal region. A pair of pores occurs in the integument between coxae IV, followed by short st4 and long st5 setae. The anal shield is rounded with paranal setae, a postanal seta, anal valves, and a U-shaped cribrum bordering the anal valves (fig. 9 C). Three pairs of smooth setae surround the anal shield.

Deutonymph: The deutonymph carries the same chaetotaxic complement as the adult. The epistome is tripartite and the proximal tine of the palp apotele is developed to one-third the length of the more distal tines (fig. 9 F). The chelicerae are similar to those of the protonymph, rather than those of the adult, i.e. not phoretomorphic and attenuated. Both digits have a terminal hook and two small teeth. The ambulacrae are developed similarly to those of the protonymph.

Dorsally, there is a single shield deeply incised at the level of setae z6 (fig. 9 A) (where the procurved line appears in the adult female), and has a strong punctate-reticulate pattern and numerous sigillary scars. The anterior portion of the dorsal shield bears

18 pairs of setae and the posterior portion bears 10 pairs. The vertical setae are distant, parallel and distally pilose. Setae j4 and z4 are thick and distally pilose. Setae r2 and r3 are distally pilose and project from the humeral area. There is a slight declivity and a strong pattern of ornamentation posteriorly at the level of setae S4. Setae S4, Z4, S5, and Z5 are strongly pectinate, and the clunal setae are biserrate. The peritremes are free in the integument from the level of z1 to the prominent stigmata.

Ventrally the sternal shield (fig. 9 D) bears four pairs of setae (st1-4) and three pairs of pores (sp1-3). Setae st5 ,two pairs of scutellae, Jv1, Zv2, and Zv3 occur in the integument posterior to the sternal shield. The anal shield is round and bears the paranal and postanal setae, along with a terminal cribrum with paranal lobes. The postperitrematic and postcoxal pores occur free in the integument as do the (inguinal ?) pores which open between the postcoxal pores and setae Jv1.

Figure 9. Developmental stages of *Macrocheles perglaber* from Klamath County, Oregon: A) dorsal shield of deutonymph; B) dorsal shield of protonymph; C) ventrianal shield of protonymph; D) sternal shield of deutonymph; E) vertical setae and palp of protonymph; F) palp of deutonymph.

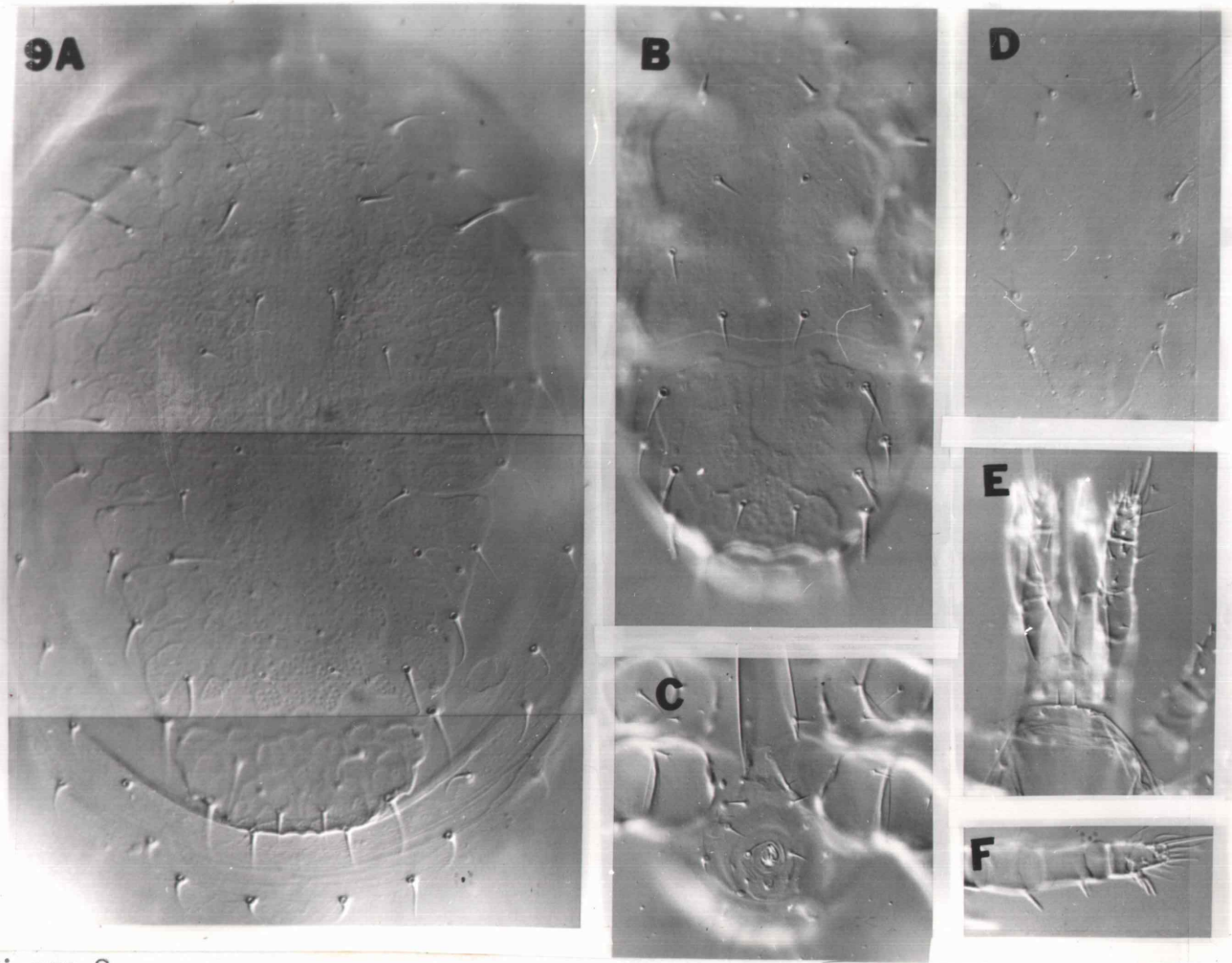


Figure 9.

Figure 10. Cheliceral types in the Macrochelidae: A) *Longicheles* sp.; B) *Macrolaspis* sp.; C) *Machrocheles mammifer*; D) *Machrocheles* near *neovernalis*, with bidentate tooth on movable digit.

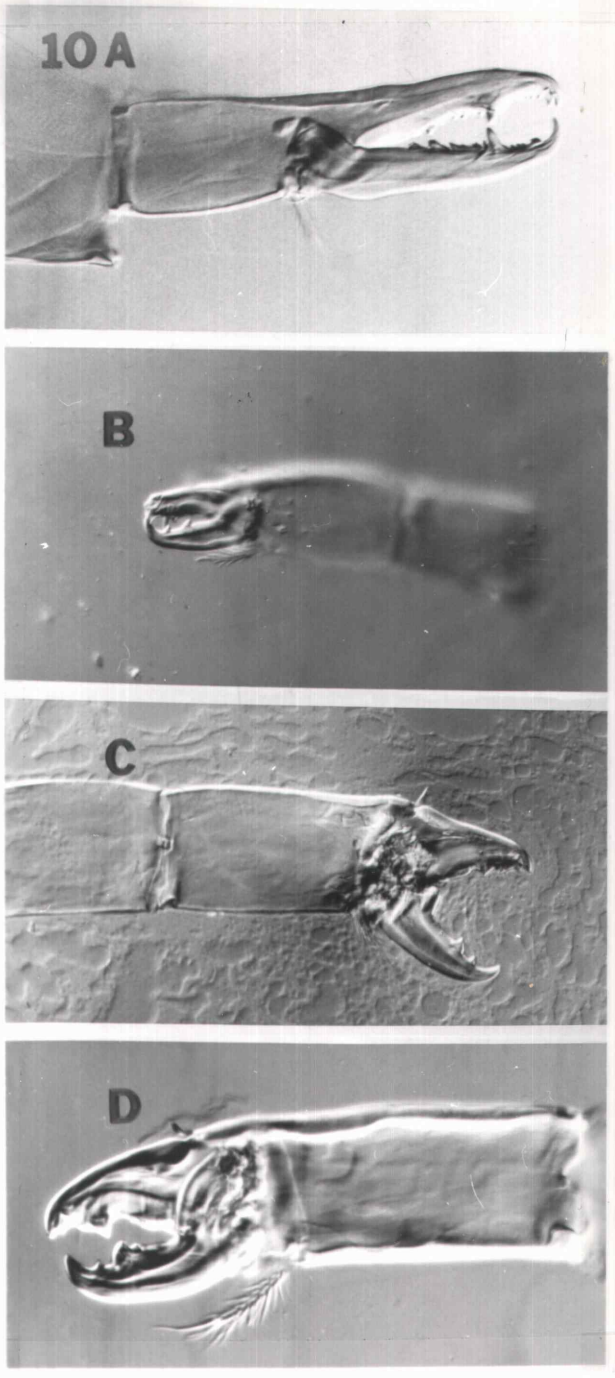


Figure 10.

OUTGROUP ANALYSIS

The taxonomic attributes or characters used in a cladistic analysis must have at least two character states: a primitive (plesiomorphic) condition or generally occurring state which does not help to define a group of related organisms, and an advanced condition (apomorphic) or character state of restricted occurrence which delineates a set of related taxa. The direction of change (primitive to derived) in the states of a character is termed polarity. The most useful method for determining polarity is by out-group comparison (Wiley 1981). The out-group method has been cogently discussed by Watrous & Wheeler (1981), and their method is followed here.

In order to better define the position of the glaber species in the genus Macrocheles, a series of cladistic analyses using the Farris/Wagner 78 algorithm were performed on the Macrocheles species groups (*sensu* Krantz) using the primitive free-living genus Geholaspis (Macrochelidae) as an out-group. Geholaspis was not an altogether satisfactory choice since certain key characters present in Macrocheles are absent in Geholaspis, making it impossible to establish polarities in these characters. Therefore, the least derived

assemblage within the genus Macrocheles - the free-living opacus group - was considered the outgroup in a subsequent series of Wagner analyses. This is the stepwise movement from taxonomic out-groups to functional out-groups recommended by Watrous & Wheeler (1981). These analyses indicated that the glaber group occupies a position near the base of the radiation of the phoretic Macrocheles.

After the acquisition of PAUP, the Wagner analyses were confirmed and the functional in-group was advanced in a series of analyses to Macrocheles penicilliger (Berl.). Although penicilliger would have been a felicitous choice as an out-group since a long series of immatures and adults are available in the OSU Acarology Collection, a number of autapomorphies of the dorsal and sternal shields would make it necessary to postulate several reversals in establishing polarities. This would also have been true for the matrius and punctoscutatus groups, which are even more closely related to the glaber group than is penicilliger.

Finally, Macrocheles mammifer Berlese was chosen as the out-group for a cladistic analysis of Macrocheles species groups using the PAUP program. The results of the mammifer analysis are given in Figure 11A. Ventral SEM's of mammifer and sternal shield interference contrast photographs of other macrochelids outside of

the glaber group are shown in Figure 12. The characters used in this out-group analysis and their plesiomorphic and derived states are listed in Table 1.

A number of interesting ecological points have been produced by this out-group analysis. Although species in the mammifer group are often found in association with dung (Bregetova & Koroleva 1960), the chelicerae are not phoretomorphic (see fig. 10). A number of mammifer specimens in the OSU Acarology Collection were collected from rodents. Other common phorionts include scarabs (Turk 1948) and passalid beetles (Delfinado & Baker 1975).

Species in the penicilliger group are commonly associated with nests of birds and mammals. Although, lacking a bidentate tooth on the chelicera to facilitate gripping the hairs of their phoriont, M. penicilliger is often a close phoretic associate with primitive scarab beetles of the genus Trox (Philips 1984).

The species groups above penicilliger have developed the bidentate cheliceral tooth. The species in the matrius group again are commonly found associated with mammals and mammal nests (Bregetova & Koroleva 1960), as are some species in the glaber group (especially in the glaber and praedafimetorium complexes) (OSU Acarology Collection). Most species in the glaber and other more highly derived groups have

Table 1. The polarity of character state changes for the *glaber* out-group analysis in fig. 11A.

Character	Out-group state	Derived states
Chelicera, shape	slender	stout
Bidentate tooth	absent	present
Vertical setae (j1)		
a) bases	near	adjacent, displaced
b) orientation	divergent	parallel
c) ornamentation	plumose	distally pilose, smooth
Dorsal setae	plumose	smooth, pilose, pectinate
Dorsan hexagon	smooth	ornamented
Dorsal shield		
a) margin	scalloped	toothed
b) posterior	broad	narrowed
c) procurved line	none	present, lost
Clunal setae (J5)	smooth	biserrate, palmate, triangular
Sternal shield		
a) l/w	l > w	l = w, w > l
b) arch	developed	reduced, extreme

Table 1. (Continued)

c) ornamentation	punctate-reticulate	reduced, smooth, neoreticulate
Lineae		
a) l. ang.	developed, open	closed, reduced
b) l.o.a.	not well defined	strong arch, lost completely
c) l. arc.	flat loop	plunging, lost, flat, lineate
d) l.o.p.	not developed	Y-shaped, reduced, parallel, lost
e) l.m.t.	strong ridge	lost
f) a.p.p	present	grape-like, reduced, lost
g) a.pf.	distinct	reduced, lost
Metasternal shield	elongate	reduced, teardrop, narrowed
Epigynial shield		
a) shape	squared	flared , reduced
b) ornamentation	punctate-reticulate	evenly or centrally punctate, reduced

Table 1. (Continued)

Ventrianal shield		
a) shape	subcordate	expanded, narrow, angular
b) ornamentation	punctate-reticulate	dimpled, reduced
c) cribrum	paranal	terminal
Postcoxal pore		
a) shape	small circle	enlarged triangle
b) position	in integument	adjacent or fused to parapodal plate
Ventral setae	ornamented	smooth

restricted their association with vertebrates to living in their dung, but have expanded their relationship with the Scarabaeidae and other dung inhabiting insects to become some of our most common phoretic mites.

The out-group analysis (fig. 11A) indicates that the glaber species group is a paraphyletic assemblage near the base of the radiations of the phoretic groups of Macrocheles. A monophyletic taxon that included the species considered to be in the glaber group would also include the more derived species groups (dimidiatus, vernalis, and pisentii in fig. 11A, as well as other species groups not included in the analysis). As mentioned in the introduction, relationships in Macrocheles are confounded by the trends towards reduction in morphology. A number of morphological inovations, such as the bidentate cheliceral tooth, and to a lesser extent the linea media transversa and biserrate clunal setae, link the majority of the phoretic species groups in Macrocheles. The few striking inovations, such as added dorsal setae, enlarged bipectinate dorsal setae (of unknown function) or regression of the dorsal shield (probably to allow greater expansion of the opisthosoma of the female during feeding or gestation) have occurred convergently numerous times in very different species groups. The majority of morphological characters - the size, shape

and ornamentation of the shields and setae - seem to have been reduced in parallel in many species groups. It has recently been suggested that developmental constraints may cause nonrandom parallel morphological evolution (Alberch et al. 1979, Alberch 1980). It has also been suggested that parallel evolution, especially in regard to loss of characters, represents a serious challange to the minimum step (most parsimonious) cladogram as a true indicator of geneological relationships (Gosliner & Ghiselin 1984). However, while awaiting the revision of the entire genus Macrocheles (Krantz & Walter, in progress), I intend to follow the current taxonomic tradition, and recognise the glaber species group.

I have divided the species in the glaber group into ten complexes of closely related species. These species complexes and their distinguishing apomorphies are given in Table 2. Macrocheles matrius was chosen as an out-group for the ten complexes in the glaber group, and a cladistic analysis using the PAUP program (fig. 11B) indicates that these complexes may be conveniently grouped into three subgroups.

Figure 11. Out-group analyses for the glaber group generated by Phylogenetic Analysis Using Parsimony (PAUP), Version 2.1 (Swofford 1983). All characters are unweighted and unordered. Taxa were added using CLOSEST with ROOT=ANCESTOR. A) the relationship of some glaber group species to other species of Macrocheles - mammifer=ancestor, characters in Table 1; B) the unresolved cladogram of the glaber group complexes - matrius=ancestor, apomorphies in Table 2 used as characters.

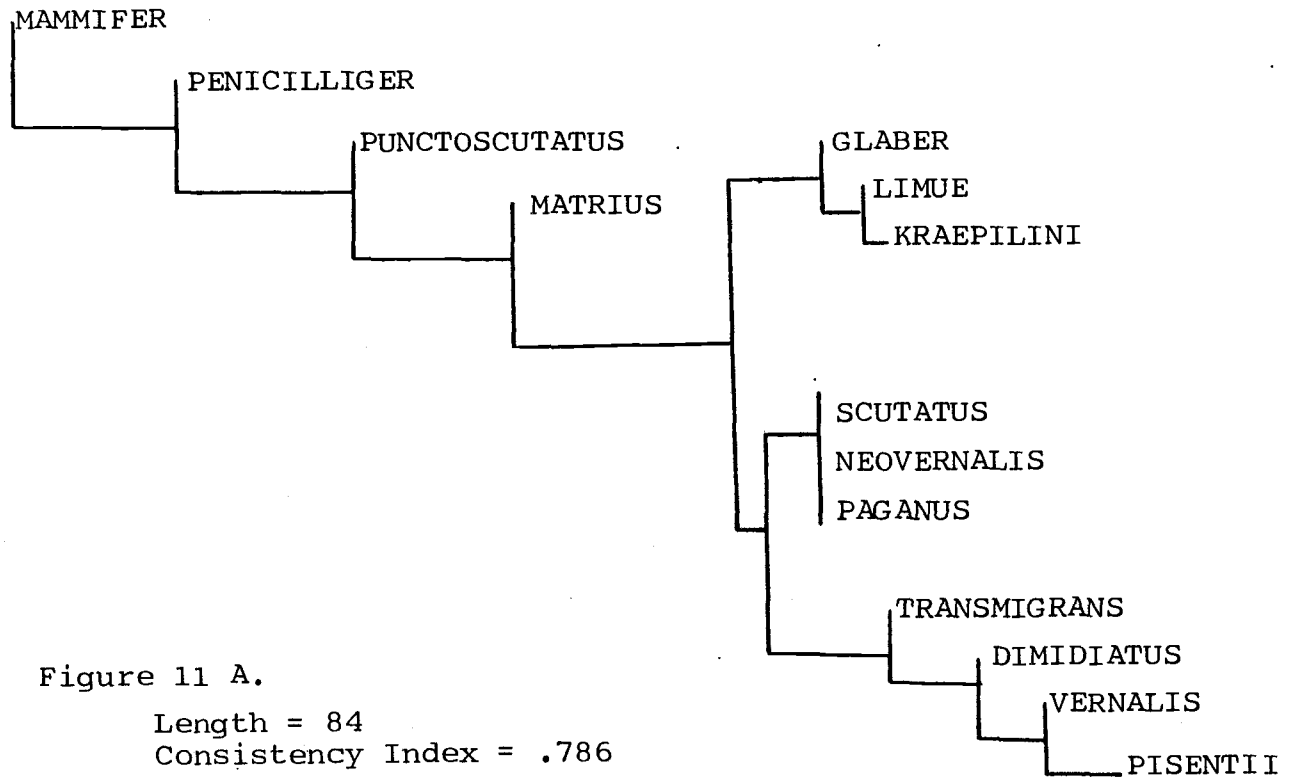


Figure 11 A.

Length = 84
Consistency Index = .786

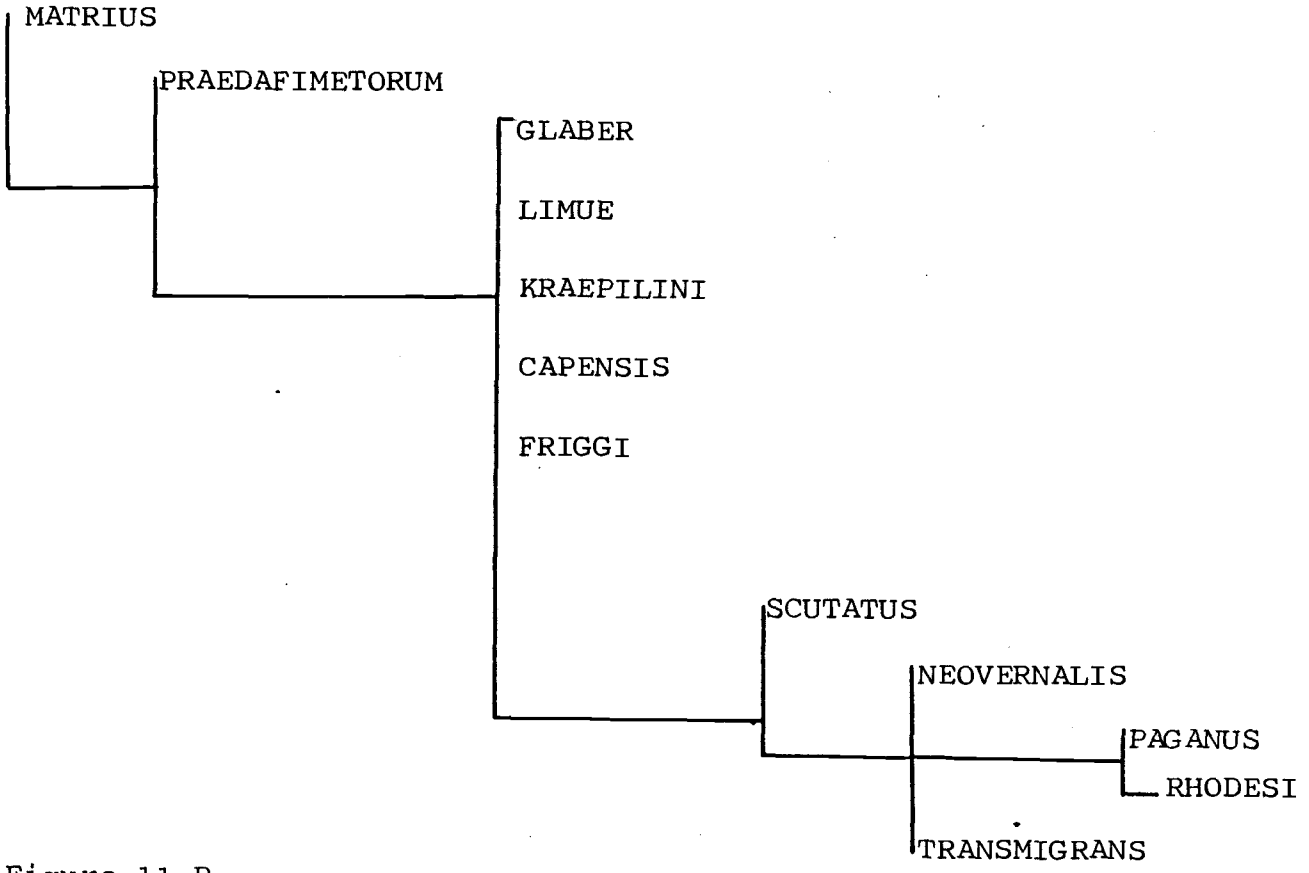


Figure 11 B.

Length = 17
Consistency Index = .882

Table 2. The apomorphies and important plesiomorphies of the subgroups defined in fig. 11B.

praedafimetorum subgroup - [*praedafimetorum* complex]

cribrum terminal only

linea angulata punctate and open

linea arcuata punctate and reflexed

linea oblique posteriores well developed with distinct ramus

sternal st 2 not reaching insertions of st 3

(retains holoventral shield in male, restricted phoretic behavior and area punctatae posteriores-area punctiformes of *matrius*)

glaber subgroup - [*glaber*, *limue*, *kraepilini*, *capensis*, and *friggi* complexes]

with the apomorphies of the *praedafimetorum* subgroup and :

male ventrianal shield free

phoretic behavior well developed including occassional use of Scarabaeini

area punctatae of two depressed clusters of punctations

area punctiformes not acinous

ventrianal lines dimpled

tropical and temperate distribution

scutatus subgroup - [*scutaus*(including *neovernalis*), *paganus*, *rhodesi*, and *transmigrans* complexes]

reduction or loss of the linea oblique posteriores

reduction or loss of the area punctatae and area punctiformes

reduction of ornamentation of ventrianal shield

length of ventrianal shield $\geq$ width

linea angulata reduced

linea arcuata without deep punctae

A KEY TO DIFFERENTIATE THE *MACROCHELES GLABER* SPECIES GROUP FROM OTHER *MACROCHELES*.

1. Chelicerae phoretomorphic, stout with bidentate tooth and opposed rasp; clunal setae biserrate,triangular or palmate.....2

1'. Chelicerae without bidentate tooth; clunal setae long and smooth.....Group A

2(1). Sternal shield with well developed punctate lines including the l.m.t. and l.o.p., and often the l. ang. and l.o.a.; procurved line usually present.....3

2'. Sternal shield lacking punctate lines; procurved line lost.....Group B

3(2). L.o.a. forming a strong arch from the l.m.t. at st2 to the l. ang. (which may be obsolete); l.o.p. at most a disjunct ridge parallel to l.m.t.; the sternal shield may have deep rectangular punctae posterior to l.m.t. .....Group C

3'. L.o.a. not arched to to l.ang., l.o.p. approaching or joined to l.m.t., no large rectangular punctae behind l.m.t. but elliptical punctate depressions may be present.....4

4(3'). Cribrum with paranal extensions; vertical (j1) setae bushy plumose; male ventrianal shield subcordate and fused to sternitigenital shield; ventral shields evenly punctate; often associated with mammal nests.....Group D

4'. Cribrum terminal; dorsal setae not bushy plumose.....5

5(4'). Sternal shield as wide or wider than long.....6

5'. Sternal shield longer than wide.....glaber group

6(5). Ventrianal shield rounded and punctate-reticulate; procurved line present; remnants of punctate l.arc. present.....friggi complex (glaber group)

6(5). Ventrianal shield narrowed, often angular; sternal shield glossy, lineae of sternal shield reduced and lacking strong punctate

depressions other than a.p.l.;
.....*vernalis* species group.

Group A (1'). Free-living potpourri e.g. *terreus*, *carinatus*, *penicilliger*, and *mammifer* groups.

Group B (2'). Phoretic species groups with strong reduction in characters e.g. *robustulus*, *mycotrupetes*, *grossipes*, *hamadryas*, *krantzi*, *pisentii*, *vernalis* (*pars*), and *sternalis* groups.

Group C (3). The *muscaedomesticae*-*subbadius*-*dimidiatus* groups, a closely related assemblage.

Group D (4). The *matrius*-*punctoscutatus* groups.

DIAGNOSIS OF THE *GLABER* SPECIES GROUP

The members of the glaber species group have the following characteristics:

Developmental stages: Setae j4 and z4 thickened and distally pilose in the protonymph and deutonymph (z4 only in larva). Ambulacrae with broad membranous acuminate operculi and narrow elongate lateral pulvillar lobes.

Male: Holodorsal shield with procurved line suppressed (retained in limue) , j4 and z4 thickened and distally pilose, and posterior margin and pygidial region tuberculate. Ventrianal shield separate from sternitigenital shield and either subcordate in shape with three pairs of ventral setae, or peltate in shape with up to six pairs of setae (the ventrianal shield is fused to the sternitigenital shield in praedafimetorum). Peritrematic shield fused to dorsal shield and including part of the r-R series. Tarsus IV sinuate and tuberculate. Femur IV with a complex setiferous spur (not well developed in minor males or in limue). Legs II and IV with numerous spurs and tubercles.

Female: Dorsal shield with vertical setae adjacent, parallel and distally pilose, j4 and z4 thickened and distally pilose (occasionally smooth or bipectinate), with a well developed procurved line with

posterior arms. Sternal shield longer than wide (with exceptions in the friggi subgroup) with a well developed pair of converging ridges (linea angulata) containing sp1 above punctate fields which extend to the anterior angles of the shield. With one or two short median transverse punctate ridges (linea arcuata), . A well developed transverse ridge (the linea media transversa) from which a pair of Y-shaped punctate ridges (lineae obliquae posteriores) diverges toward the posterior angle of the shield and encompass a depressed postero-median area of the sternal shield. The anterior arm of the l.o.p. bears sp2, and the posterior ramus (which may be lost) forms the lateral edge of the area punctatae. The postero-median depression contains two pairs of recessed elliptical acinous (grape-like) clusters of punctae (areae punctatae posteriores) and a median punctate area (area punctiformes), both of which may be reduced to a few scattered punctae. The ventrianal shield is subcordate, expanded or rounded in shape, and either strongly ornamented with emarginate punctate ridges (dimpled) or smoothly punctate. There is a narrow terminal cribrum.

The glaber species group is closely related to its plesiomorphic sister-group, the matrius species group, through the species of the praedafimetorium complex. These appear to be regressive species which have

achieved a glaber level of morphology from a matrius-like ancestor. Clearly, the morphologies represented in the glaber species group are diverse and are best treated as a number of subgroups.

Figure 12. Some species of Macrocheles outside of the glaber group: A) mammifer Berlese, ventral SEM; B) mammifer Berlese, sternal shield SEM; C) matrius matrius Hull, sternal shield; D) vernalis (Berlese), sternal shield; E) subbadius (Berlese), sternal shield; F) pisentii (Berlese), sternal shield; G) robustulus (Berlese), sternal shield.

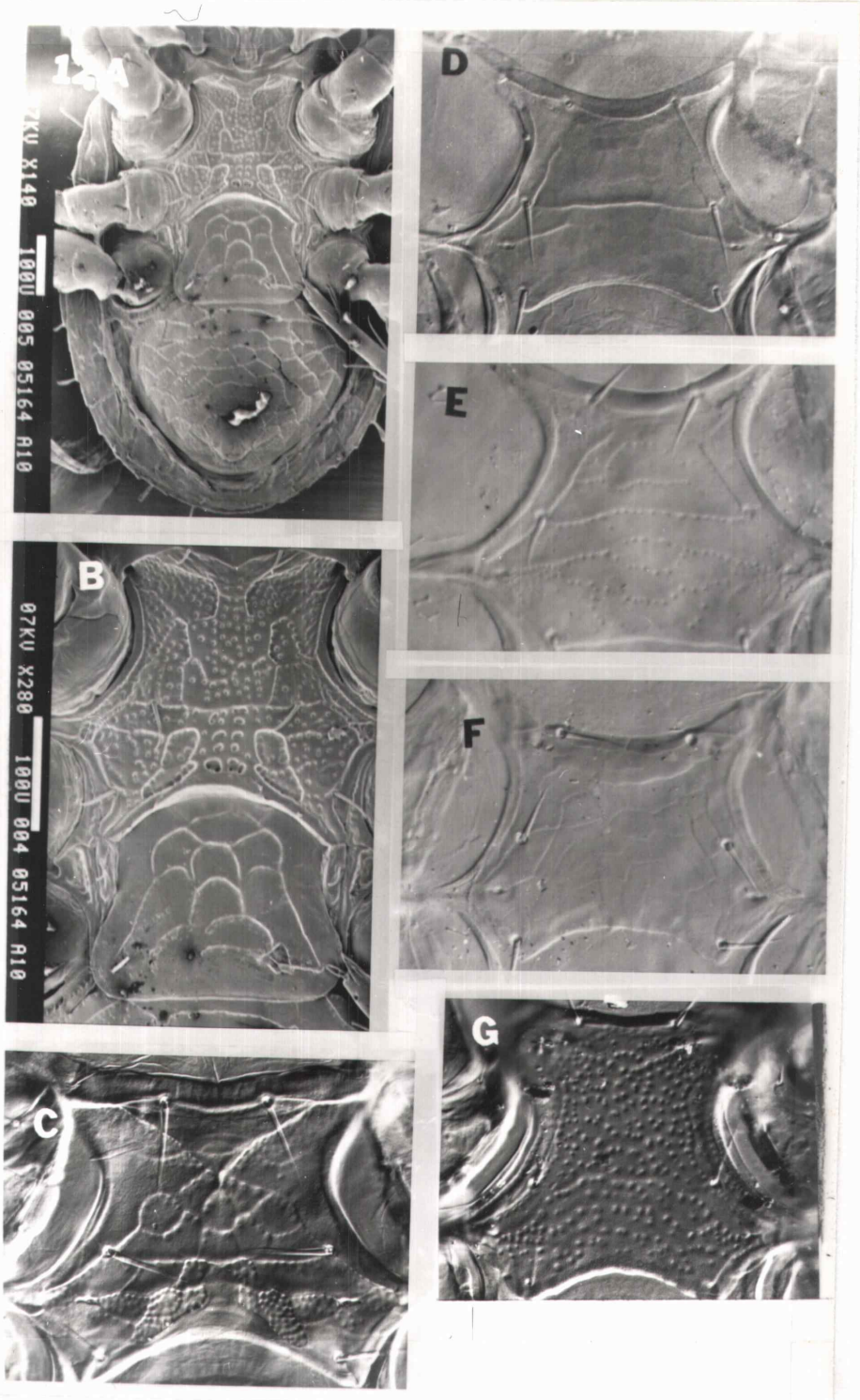

D
E
F
G
B
07KU X280 100U 004 05164 A10
C
12.4
7KU X140 100U 005 05164 A10

Figure 12.

KEY TO THE SUBGROUPS OF THE GLABER SPECIES GROUP

1. Sternal shield with lineae angulatae forming a converging pair of elevated ridges opening medially, a deeply areolate, often reflexed, linea arcuata, areae punctatae posteriores an acinous (grape-like) depression, deeply areolate area punctiformes, and well developed, branched linea oblique posteriores; ventrianal shield subcordate, width ≥ length, with strongly punctate-reticulate emarginate (dimpled) lines 2

1' Sternal shield with lineae angulatae weakly produced and not open medially, linea arcuata not deeply areolate, either a flat weakly punctate loop or obsolete, linea oblique posteriores weakly produced, often disjunct and/or without ramus, areae punctatae posteriores and area punctiformes obsolescent; ventrianal shield weakly punctate-reticulate, length ≥ width.....3

2. Male ventrianal shield fused to sternitigenital shield; female sternal shield with area punctiformes acinous and posterior angles extended towards metasternal shields; western North America;.....praedafimetorum subgroup

2' Without the above characteristics; worldwide distribution.....*glaber* subgroup

3. Sternal shield wider than long with medially open lineae angulatae.....*friggi* complex of *glaber* subgroup

3' Sternal shield as long or longer than wide, lineae angulatae reduced and closed medially.....*scutatus* subgroup

THE GLABER SUBGROUP

Diagnosis: The paraphyletic assemblage of complexes of species that represent glaber in a narrow sense. The linea angulata is strongly produced and open medially. The linea arcuata is deeply areolate and reflexed. The linea oblique posteriores is well developed, attached to the linea media transversa and has a distinct ramus. The area punctatae is an acinous depression and the area punctiformes is deeply areolate. Reduction of characters occur in two complexes in the glaber subgroup. In the friggi complex, the sternal shield is compressed, the width becoming greater than the length, and the ornamentation becomes reduced. In the capensis complex, the dorsal shield narrows over the opisthosoma. However, most species in the glaber subgroup have characteristically strong ornamentation of the dorsal and ventral shields. The members of the glaber subgroup are phoretic on a broad range of scarab species and occur in all biogeographic realms except the Neotropical.

KEY TO THE SPECIES COMPLEXES OF THE *GLABER* SUBGROUP

1. Sternal shield compressed, width ≥ length; linea arcuata, linea oblique posteriores, and area punctatae obsolescent to obsolete.....*friggi* complex

1' Sternal shield longer than wide, ornamentation not reduced.....2

2. At least some dorsal setae bipectinate for their entire length.....3

2' Dorsal setae smooth or distally pilose.....4

3. Dorsal shield narrowing over opisthosoma; from the Ethiopian realm.....*capensis* complex

3' Dorsal shield broad posteriorly; Oriental, Australasian, Oceanian.....*kraepilini* complex

4. Linea angulata very narrow medially; posterior arms of sternal shield produced toward metasternal shields; postcoxal pore heavily sclerotized.....*limue* complex

4' Not as above.....*glaber* complex

THE GLABER SPECIES COMPLEX

(figs. 1, 3, 6, 13)

Diagnosis: With the characteristics of the subgroup but lacking expanded strongly bipectinate setae or a compressed sternal shield or a sternal shield with strongly produced posterior sternal angles or a medially narrow linea arcuata. This is the largest complex of species in the glaber group.

Macrocheles glaber (Muller, 1860)

(fig. 13 A)

Holostaspis glabra Muller, 1860
Gamasus stercorarius Kramer, 1876
Holostaspis marginatus (Hermann), 1882
Holostaspis badius, Foa [not Koch, 1839], 1900
Macrocheles badius, Oudemans, 1904
Macrocheles vulgaris, Oudemans, 1914
Macrocheles marginatus littoralis Halbert, 1915
Macrocheles (Coprholaspis) alecto Berlese, 1918
Macrocheles (Coprholaspis) a. aegyptius Berlese, 1918
Macrocheles (Coprholaspis) a. aethiopicus Berlese, 1918
Macrocheles (Coprholaspis) a. australis Berlese, 1918
Macrocheles (Monoplites) oudemansii Hull [in part], 1925
Macrocheles veterrimus Sellnick, 1940
Coprholaspis glaber (Muller), Witzthum, 1943
Coprholaspis anglicus, Turk, 1946
Macrocheles stercorarius Sellnick, 1955
Macrocheles subglaber Filipponi, 1959
Macrocheles glaber (Muller), Evans & Browning 1956, Bregetova & Koroleva 1960, Krauss 1970, Bregetova 1977
Macrocheles alecto Berlese, Krauss 1970

The slides in the OSU Acarology Collection which represent members of the glaber sibling species cluster were divided between glaber *sensu latu* and perglaber. Those specimens which could not be ascribed to either species were delegated to a "glaber" category for distributional and phoretic information along with literature records from before Filipponi & Pegazzano (1962).

Diagnosis: A medium size species with a single linea arcuata. Macrocheles glaber may be differentiated from M. perglaber F. & P. by its smaller size, triangular-cordate ventrianal shield, single linea arcuata, and fewer pilose dorsal setae.

The collections which were unequivocally not perglaber represented a broad variation in degree of ventral sclerotization, setal pilosity, and size. The collections from the northern Palearctic seem to represent glaber *sensu stricto*, as does the material from Australia. In the Nearctic, a single specimen from Florida and a single collection from Corvallis, Oregon seem to represent glaber *sensu stricto*.

The collections of glaber from southern Asia are quite variable morphologically, and may represent a cluster of species. I think it is inadvisble to nominate new species in this cluster without access to associated males. Two nominate forms near glaber from

Figure 13. The species in the glaber complex: A) glaber (culture, Rome); B) glaber tsaii, (holotype, Canton); C) perglaber (culture, Rome); D) helenaensis (paratype, St. Helene); E) hyatti (holotype, New Zealand); F) peregrinus (paratype, South Africa); G) oigru, n.sp. (holotype, India); H) posterior dorsal setae, oigru, n.sp. (Holotype, India); I) medialis (Namibia); J) caligynus (Java).

Figure 13. A-F

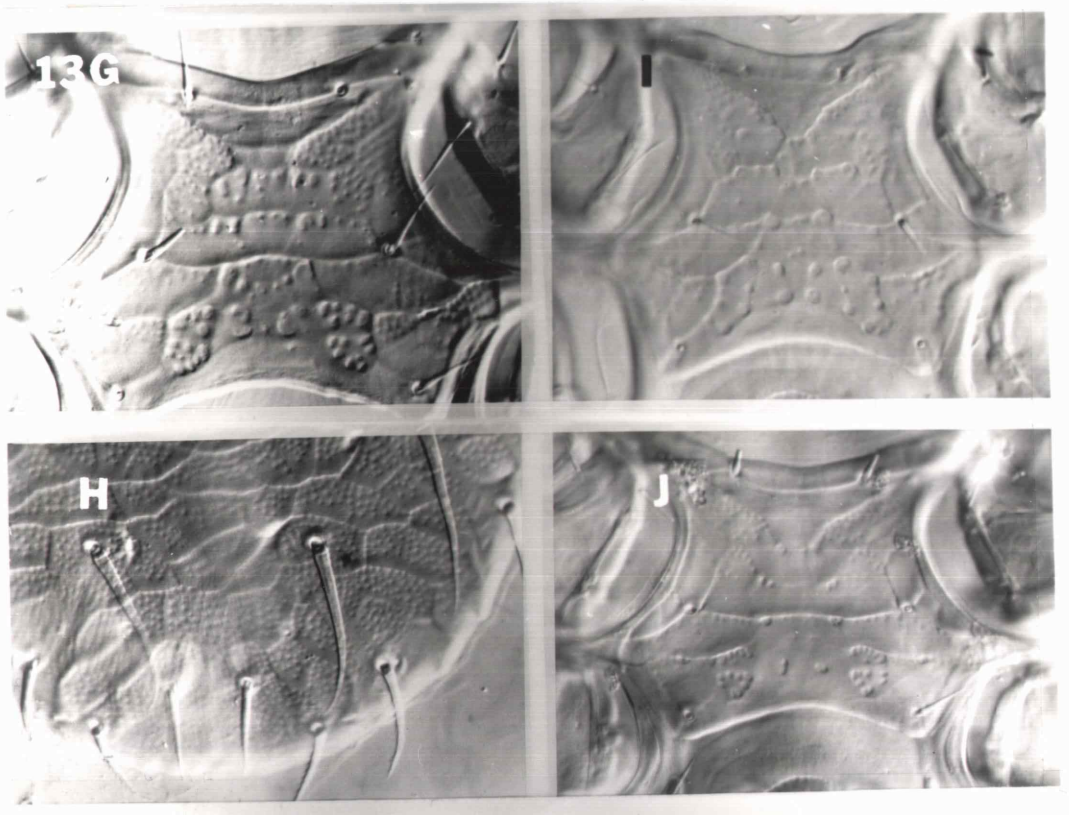


Figure 13. G-J

Table 3. Variation in dorsal shield lengths of some populations of *Macrocheles glaber*.

Locality	Range in um	Mean(+1S.D.)	N
Italy	722 - 907	802.7(±50.5)	50
Morocco	748 - 863	811.2(±29.6)	12
Mongolia	713 - 897	788.7(±56.6)	9
Australia	725 - 851	800.9(±46.0)	12
Sinkiang	651 - 805	746.3(±46.1)	16
Japan	713 - 805	769.3(±31.5)	8
Formosa	759 - 806	793.2(±19.3)	6
SE Asia	725 - 770	747.6(±17.9)	5

this region are discussed below. Table 3 contains some comparisons of dorsal shield lengths and morphological variation for collections of glaber.

Macrocheles glaber tsaii Samsinak 1962

(figs. 5 I, 13 B)

This subspecies of glaber was described from Canton, China and may be distinguished from glaber *sensu stricto* by the short vertical (j1) setae, pilose only at the tips, acuminate smooth j4, z4 setae, pilose Z5 setae, and reduced ornamentation of the sternal shield. These characteristics show up in several of the OSU Acarology Collection series from southeastern Asia; however, they are not always linked. The short vertical setae, which are the most striking variation in glaber tsaii, appear to be a developmental anomoly. Individuals in collections from Japan, India, Vietnam, and Malasia have short vertical setae, while others in the same collections have vertical setae of normal length.

Macrocheles calyginus (Berlese, 1910)

(figs. 13 J)

Holostaspis calyginus Berlese, 1910
Macrocheles (Coprholaspis) calyginus Berlese, 1918

The type, from Java, is very similar to glaber (G.W. Krantz, personal communication), but smaller (690 x 440 um) and with reduced ventral ornamentation, a distinctive l. arc., disjunct l.o.p. and reduced epigynial ornamentation. The following diagnosis is based on two specimens in the OSU Acarology Collection from Java, Croisiere du "Nirvana", Palaboehan Ratoe, E. Cordier, ex Onitis falcatus Wulfen, coll. C. de Bearn, 31 May 1908.

Diagnosis: A small, glaber-like species from southeast Asia, with reduced ventral ornamentation, a punctate, but reflexed l.arc., a bifurcate but disjunct l.o.p., and a.p.p. reduced to elliptical perimeters of punctae. Dorsal setae j4, r2 and r3 are distally pilose.

Description: Smaller on the average than glaber (679 x 441 um, n=3), with short distally pilose vertical setae (j1), j4, and humeral (r2, r3) setae pilose distally, clunal (J5) setae serrate, others acicular and smooth. The ventral ornamentation is reduced with a punctate l. arc. which joins the l.o.a. in a scutatus-like loop after the faint reflextion. The l.m.t. is distinct, the l.o.p. is disjunct and the ramus is evanescent, and the a.p.p. is represented by an pair of elliptical perimeters of punctae. The ventrianal shield is gently

rounded cordate and about as wide as long. The postcoxal pore is distant from the parapodals.

Size and Distribution: Berlese's notebook reports caligynus from Java (ex Copris [=Catharsius] molossus) and India (ex Catharsius ajax). Another specimen from the OSU Acarology Collection from Vietnam (ex scarab), resembles calyginus but is larger (length= 771 um).

Macrocheles perglaber Filipponi & Pegazzano 1962
(figs. 3, 6, 13 C)

This larger sibling species of glaber is more discrete morphologically than its relative. Macrocheles perglaber is broadly holartic in distribution, and occurs in Australia and Northern Africa. A slightly different form occurs in Zaire, and may be a new species. However, males are lacking in the collection. The North American and Australian populations may have been introduced by man recently, and they freely interbreed with the European forms (Halliday 1983, Walter, in this thesis). Table 4 lists some size variations in perglaber.

Table 4. Variation in the lengths of the dorsal shield in some populations of *Macrocheles perglaber*.

Locality	Range in um	Mean(+1 S.D.)	N
Italy	833 -1018	925.2(±43.9)	50
Morocco	851 - 979	916.3(±63.6)	3
Australia	817 - 943	906.3(±57.4)	6
Szechuan	978 -1035	1014.0(±31.3)	3
Zaire	851 - 963	892.8(±44.5)	9
South Dakota	792 - 972	891.6(±55.4)	8
New York	882 - 972	923.4(±34.6)	5
Oregon	864 - 963	912.6(±30.8)	15

Macrocheles jaliscensis Mendez-Olivo 1966

It is questionable whether this species is a member of the glaber group. If it does belong here, then it is the only known species of the glaber species complex endemic to North America. The original collection was from Dichotomius carolinus in Mexico. The type specimen has been unavailable for examination. The only glaber group specimen from Central or South America in the OSU Acarology Collection is a single "glaber" (probably glaber) from Vera Cruz, Mexico. The species description of jalisciensis indicates that it has some of the plesiomorphies of a member of the glaber group. However, the illustration, although poor, indicates that jalisciensis may be a member of the mammifer species group. The shape and indications of ornamentation on the sternal and epigynial shields are similar to those of mammifer.

Macrocheles peregrinus Krantz 1981

(figs. 1, 5 G, 13 F)

This is a distinctive African species in the glaber complex. It is the only species with a postcoxal pore which appears fused and compressed to the parapodal plates. Series of specimens in the OSU Acarology Collection representing peregrinus are from the

following countries: South Africa, Kenya, Tanzania, Ethiopia, Aden, Egypt, North Africa, Zaire, Cameroons, Rwanda, and Namibia. The size and morphology is reasonably constant. Collections from Zaire had dorsal shield lengths which averaged 792. 1 um [±35.4, range = 747-873 um, n=20] while South African collections (including the paratype series) averaged 802.6 um [± 35.8, range = 748-860 um, n=15].

Macrocheles medialis Berlese 1918

(figs. 13 I)

This species is a scaled down version of peregrinus which appears to be commonly distributed throughout subsaharan Africa. The original description (Berlese 1918) and Berlese notebook drawings adequately define this species. The following diagnosis is based on specimens in the OSU Acarology Collection.

Diagnosis: A small glaber-like species from subsaharan Africa, with two punctate l.arc., bifurcate l.o.p. and distinct a.p.p. and a.pf.. Dorsal setae j4 and z4 are distally pectinate.

Description: The dorsal shield is strongly reticulated, broadly rounded posteriorly, about 650 um long (type) [x=655.6±52.2, range = 529-771 um, n=32] and the procurved line is strongly produced. The vertical setae

(j1) are long, slender and distally pilose. The clunal (J5) setae are acicular and serrate. The j4 and z4 setae are distally pectinate. The other 24 pairs of setae are smooth, not inflated, and pointed. The sternal shield is longer than wide and ornamented with distinct lines and punctae. The l. ang. has punctate margins, one or two deeply punctate reflexed l. arcuatas are present. The l.m.t. is well developed. The l.o.p. is strongly produced and bifurcate. The a.p.p. is somewhat reduced, but represented but large deep punctae, as is the a. pf.. The epigynial shield is ornamented with a complete set of punctate lines. The ventrianal shield is as wide or wider than long and evenly punctate reticulate. The postcoxal pore is adjacent, but does not appear fused to the parapodal plates.

Size and Distribution: Collections representing <u>medialis</u> in the OSU Acarology Collection come from Chad, the Central African Republic, Cameroons, Zaire, Southwest Africa and Kenya. The average size of the dorsal shield varies somewhat from place to place: Kenya, x= 676.0 um (±53.6), range = 621-748 um, n=4; Namibia, x= 668.4 (±34.7) um, range = 627-707 um, n=12; Zaire, x= 643.8 (±68.0) um, range= 529-771 um), n=12.

Macrocheles hyatti Krantz & Filipponi 1964

(figs. 13 E)

This mite has been reported only from New Zealand (Emberson 1973). Macrocheles hyatti has the distinction of being the only species in the glaber group for which a fossil (7-8000 B.P.) has been identified (Emberson 1973). The heavily sclerotized and punctate sternal shield is similar to another island species, Macrocheles helenaensis van Driel.

Macrocheles helenaensis van Driel 1977

(figs. 13 D)

This mite was described from Sainte Helene, an island 2000 km west of the African mainland. The drawings and photographs in the description of Macrocheles helenaensis represent a distinctive species in the glaber complex. The holotype slide deposited in the Central African Museum, Teruven, Belgium, however, is an individual of Macrocheles penicilliger (Berlese). This is an unfortunate complication, since the paratypes which I have obtained in alcohol and have since mounted in Hoyer's, represent the described species. Pending clarification by the author of the species, I have assumed that the holotype has been misplaced, and have

used the concept of helenaensis contained in the description and illustrated by the paratypes.

Macrocheles oigru, new species

(figs. 5 A, 13 G, H)

This is a distinctive new species near glaber from Asia with greatly elongate dorsal setae. The name is derived from a children's nonsense word used in Cape Cod to mean someone whose head is too big for their body, in reference to the oversized setae.

Diagnosis: A medium sized species from southern Asia with a strongly ornamented sternal shield, rounded ventrianal shield and very long, smooth dorsal setae.

Description: The dorsal shield is strongly punctate-reticulate with a well developed procurved line. The vertical (j1) setae are adjacent, thick and distally plumose. The clunal setae (J5) are serrate. The j4 setae is thickened and distally pilose, and the posterior setae (S5, J5) are pectinate. The z1 is short and smooth, but the other dorsal setae are elongate, smooth and acicular and reach or pass the insertion of the next seta. The sternal shield is strongly ornamented along the l.ang., with two deeply punctate l. arc., a l.m.t. a bifurcate l.o.p. with punctate ornamentation. The a.p.p. are grape-like and the a.pf.

are deeply punctate. The metasternal plates are rounded. The epigynial shield is strongly ornamented. The ventrianal shield is wider than long and rounded with strong punctate-reticulate ornamentation.

Size and Distribution: The holotype and three paratypes were collected at 1400' in Coimbatore, Madras State, India from Onitis philemon collected by T.R.S. Nathan in 1977. The lengths of the dorsal shields of the type series ranged from 693 to 747 um (x= 713.3±25.9 um). An additional collection from the Pulney Hills, Kodaikamal, India at 2000m from a beetle (unidentified) collected by P.S. Nathan in November, 1953 had dorsal shield lengths from 675 to 774 um (x=716.1±34.8 um, n= 7). An additional collection of two specimens from Onitis falcatus, identical to the type series except for a reduction of the punctations along the l. ang., ranged from 648 to 720 um. This last collection was from Java, Croisiere du "Nirvana", Palaboen Ratoe, E. Corier, by C. de Bearn 31 May 1908.

THE LIMUE COMPLEX

(fig. 14)

Diagnosis: Large African and southeast Asian members of the glaber subgroup with the l.ang. produced as a a narrow median tongue and a broadly expanded ventrianal shield with strongly dimpled reticulations. The postcoxal pore is appressed to the parapodal plates and usually enlarged.

KEY TO THE SPECIES IN THE LIMUE COMPLEX

1. Ventrianal shield with smoothly dimpled, rectangular cells, l.arc. flat.....2

1' Ventrianal shield coarsely punctate-reticulate, l. arc. punctate and procurved.....caelatus

2. Dorsal setae smooth.....limue

2' Marginal dorsal setae distally pilose, ex goliath beetles.....witcoskyanus

Macrocheles limue Samsinak 1962

(figs. 14 D)

Macrocheles eurygaster Krantz 1981, new synonomy

Macrocheles limue is a large almost round mite that is phoretic on a large number of beetles in tropical

Africa, southeast Asia and the Philippines. The African populations have been referred to as eurygaster by Krantz (1981), however, although the holotype of limue is somewhat less punctate along the l. ang., it is otherwise morphologically identical to eurygaster. Males of limue reared from females collected in Bogor, Java are similarly indistinguishable from males of

Figure 14. The species in the *limue* complex: A) sternal shield of *caelatus* (Zaire); B) ventrianal shield of *caelatus*; C) sternal shield of *witcoskyanus*, n.sp., (holotype, Cameroons); D) Ventral shields of *limue* (holotype, Canton).

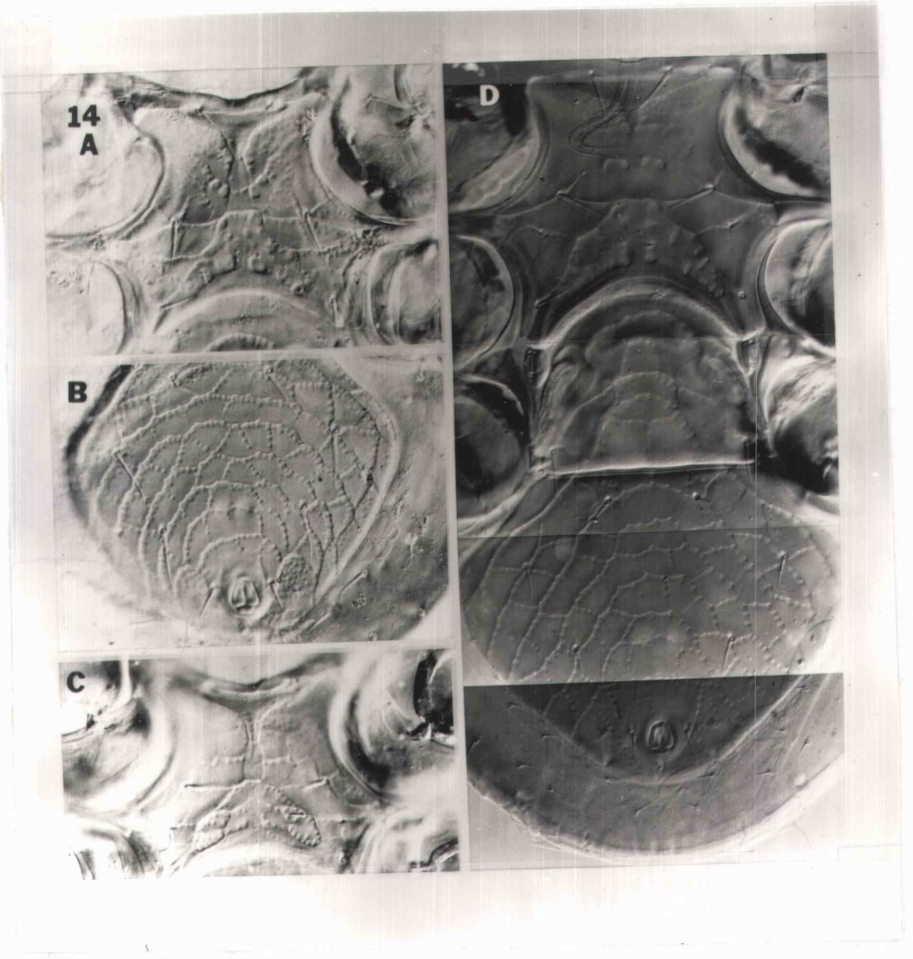


Figure 14.

Table 5. Variations in the lengths of the dorsal shields in *Macrocheles limue* from Africa and Asia.

Locality	Range in um	Mean(+1 S.D.)	N
Zaire	955 -1107	1003.1(±46.4)	17
South Africa	891 -1026	969.0(+46.9)	9
Indonesia	863 -1008	937.0(+53.9)	7
India	874 - 909	893.5(+14.0)	6
Philippinies	805 - 932	887.2(+37.2)	15

eurygaster. Table 5 contains some dorsal shield measurements of various populations of limue.

Macrocheles caelatus Berlese 1918

(figs. 14 A, B)

This obscure Berlese species is represented in the OSU Acarology Collection by a few specimens from central Africa. It is placed in the limue complex because of the narrow l. ang. (clearly visible in the Berlese drawing) and the expanded and strongly dimpled ventrianal shield visible on a specimen identified as caelatus by G.W. Krantz. The following diagnosis is based on the specimens in the OSU Acarology Collection.

Diagnosis: A medium sized mite from central Africa, with a strongly ornamented ventral shields including a narrow l.ang., deeply punctate and reflexed l.arc., and strongly punctate-reticulate ventrianal shield. Dorsal setae j4 and z4 are thickened and distally pilose.

Description: Dorsal shield broadly oval with strongly punctate-reticulate and evenly punctate ornamentation. The vertical (j1) setae are adjacent and distally plumose. The j4, z4 setae are thickened and distally pilose. The clunal (J5) setae are serrate. The other dorsal setae are long and acicular. The sternal shield is longer than wide and heavily sculptured. The l. ang.

is produced in a narrow tongue and strongly punctate fields are produced along its margin. The l. ang. is deeply punctate, reflexed and strongly procurved in some specimens (flat in others) and may appears to bisect the l.o.a.. The l.m.t. is distinct with the bifurcate l.o.p. diverging into a strong sternal arch. The a.p.p. and a.pf. are strongly punctate. The metasternal plates are rounded. The epigynial shield is flared and punctate-reticulate. The ventrianal shield is expanded laterally, wider than long, and punctate-reticulate with strong dimples. The postcoxal pore is enlarged and appressed to the parapodal plates.

Size and Distribution: The average length of the dorsal shields of seven specimens is 753.6 um (±82.8, range= 623-855 um). The distribution of the specimens in the OSU Acarology Collection is Zaire and Rwanda on species of Onitis and Copris. The Berlese type was collected in East Africa.

Macrocheles witcoskyanus, new species

(figs. 14 C)

This is an undescribed species with the l. ang. and ventrianal shield characteristic of the limue complex, that was collected from a goliath beetle from the Cameroons. The species is named in honor of Jeff

Witcosky, a lapsed acarologist [name + *-anus*, (L.) belonging to].

Diagnosis: A moderate-sized species phoretic on goliath beetles in central Africa, with a strongly ornamented sternal shield including a narrow l.ang. and strongly punctate a.p.p. and a.pf.. The ventrianal shield is ornamented with smoothly dimpled rectangular cells. The dorsal setae are distally pilose.

Description: Dorsal shield broadly elliptical and evenly reticulate with the procurved line faint. The vertical (j1) setae are adjacent or separate, long, and distally pilose. The j2 setae are sparsely pilose distally and the setae on the margin of the dorsal shield are also sparsely pilose distally. The clunal (J5) setae are serrate. The sternal shield is longer than wide with long heavy setae. The l. ang. is narrowly produced and punctate. There are two l. arc., the second of which is deeply punctate and reflexed. The l.o.p. is bifurcate and the a.p.p. and a.pf. are strongly punctate. The metasternal shields are rounded, the epigynial shield is squared and evenly punctate-reticulate. The ventrianal shield is broadly expanded laterally, wider than long and ornamented with deeply dimpled rectangular cells. The postcoxal pore is appressed to the parapodal plates.

Size and Distribution: The holotype female and six paratype females were collected from a <u>Goliathus</u>

goliathus from the Cameroons, Sanaga, April 1974. The series had dorsal shield lengths that ranged from 783 to 878 um (x= 834.1±33.4 um, n=7).

THE KRAEPILINI-CAPENSIS CLUSTER

The kraepilini and capensis complexes are sister groups which are united by their strongly bipectinate setae. The capensis complex is restricted to the Ethiopian realm, while the kraepilini complex is distributed throughout the tropical portions of the Oriental, Australasian and Oceanian realms. This could indicate a vicariant splitting of this cluster, or a dispersal event. The species in the kraepilini complex have successfully dispersed across the Pacific as far as Hawaii.

THE KRAEPILINI COMPLEX

(fig. 15 A-B,D-E)

Diagnosis: Large members of the glaber subgoup with enlarged bipectinate setae. Genu IV may have six or seven (postero-lateral seta present) setae.

KEY TO THE SPECIES IN THE KRAEPILINI COMPLEX

1. Genu IV with six setae.....kraepilini
1' Genu IV with seven setae.....2
2. Setae z1 longer than j1, j2 bipectinate; from Hawaiian Islands.....tantalus
2' Setae z1 short, j2 not strongly bipectinate; southeast Asia.....hallidayi

Macrocheles kraepilini (Berlese, 1905)

(figs. 5 D, 15 A, B)

Holostaspis kraepilini Berlese 1905
Macrocheles (Coprholaspis) kraepilini Berlese 1918
Macrocheles multihamatus Vitzthum 1926
Macrocheles kraepilini (Berlese), Krantz & Filipponi 1964

Macrocheles kraepilini has been redescribed by Krantz & Filipponi (1964) and I am following their

concept of kraepilini. It is the only member of the kraepilini complex with only six setae on genu IV.

Size and Distribution: Macrocheles kraepilini is represented in the OSU Acarology Collection by collections from Pakistan, India, Thailand, Vietnam, Malaya, Java, Singapore, the Philippines, Samoa, and Western Samoa. Krantz & Filipponi (1964) report kraepilini from Fiji and New South Wales (possibly mislabeled collection from Queensland?). The dorsal shield lengths of 31 specimens ranged from 863 to 1173 um ($x=1020.0\pm72.0$ um).

Macrocheles tantalus, new species

(fig. 8 C, 15 D)

The species is named for Mt. Tantalus in Honolulu where a series was collected under a rotting avocado.

Diagnosis: A large species similar to kraepilini but having seven setae on genu IV and restricted to the Hawaiian Islands. Setae z1 are long and smooth and setae j2 are strongly bipectinate.

Description: Dorsal shield punctate-reticulate with well developed procurved line. Vertical (j1) setae adjacent and pilose for greater than half their length. Setae z1 longer than j1 and thin. Seta j2 and other dorsal setae excepting the hexagon and z5 are

bipectinate. The clunal (J5) setae are serrate. The sternal shield is longer than wide with two deeply punctate l. arc. and well developed l.m.t., l.o.p., l. ang., a.p.p. and a.pf.. The metasternal plates are rounded. The epigynial shield is flared and smoothly punctate-reticulate. The ventrianal shield is broadly cordate and smoothly punctate-reticulate. The postcoxal pore is enlarged. Genu IV has seven setae, including a postero-lateral.

The male has a dorsal shield strongly ornamented with ridged polygonal cells, and is narrowed and denticulate posteriorly. The procurved line is lost. The posterior setae (S5, Z5) are bipectinate. The sternitigentital shield is irregularly punctate-reticulate and truncate posteriorly. The ventrianal shield is broadly peltate and carries 4 or 5 ventral setae and paranal cribral extensions. Femur IV carries a short spur and a longer setiferous spur. Femur II has a large spur ventrally. Genu IV has seven pectinate setae.

Size and Distribution: Collections of tantalus are restricted to the Hawaiian Islands of Oahu and Maui. A series of seven specimens of Macrocheles tantalus had dorsal shield lengths ranging from 1001 to 1208 um ($x = 1174.9 \pm 82.7$). Macrocheles tantalus has been collected in leaf litter, under rotting avocados, and has been

found phoretic on Rattus exulans and R. rattus, Copris incertus procidius, and Onthophagus curicorius incensus.

Macrocheles hallidayi, new species

(fig. 15 E)

The mite is named for the perspicacious Australian acarologist, Bruce Halliday.

Diagnosis: This is the robust southeast Asian mite in the glaber subgroup with seven setae on genu IV. The dorsal setae are sparsely to strongly bipectinate. Setae z1 are short and smooth.

Description: Dorsal shield broadly oval, strongly reticulated with a well developed procurved line. The vertical (j1) setae are adjacent, long, stout and distally pilose. The dorsal setae are long, acicular and the setae on the margin of the dorsal shield and on the opisthonotum are sparsely bipectinate. The clunal (J5) setae are strongly serrate. The posterior setae (Z5, S5) are short, curled and strongly bipectinate. The sternal shield is longer than wide with a strongly punctate margin along the l. ang., a well developed l.o.a., two deeply punctate l. arc., a strong l.m.t., distinct and bifurcate l.o.p., well developed a. pf. and grape-like a.p.p.. The metasternal plates are rounded. The epigynial shield is flared and punctate-reticulate. The ventrianal shield is broadly cordate and evenly

punctate-reticulate. The postcoxal pore is somewhat enlarged and genu IV has seven setae including a postero-lateral seta.

Size and Distribution: The OSU Acarology Collection has series of Macrocheles hallidayi from India, Thailand, Cambodia, Java, and Sarawak. Macrocheles hallidayi has also been reported from Queensland (B. Halliday, personal communication). Fifteen specimens from southeast Asia had dorsal shields which ranged in length from 955 to 1231 um (x= 1078.0±89.1). Macrocheles hallidayi has been collected as a phoretic on Onitis falcatus, O. philemon, O. subopacus, Heliocopris bucephulas, and Catharsius sagax.

Figure 15. The species in the *kraepilini* and *praedafimetorum* complexes: A) dorsal shield SEM, *kraepilini*; B) ventral shield SEM composite of *kraepilini*; C) sternal shield, *praedafimetorum*, paratype, Alberta, Canada. D) sternal shield of *hallidayi*, n.sp., holotype; E) sternal shield of *tantalus*, n.sp., holotype; F) dorsal shiled and plumose dorsal setae of *Macrocheles penicilliger*; G) ventral SEM of sp. nr. *praedafimetorum* from nest of *Aplodontia rufa*, Mary's Peak, Oregon.

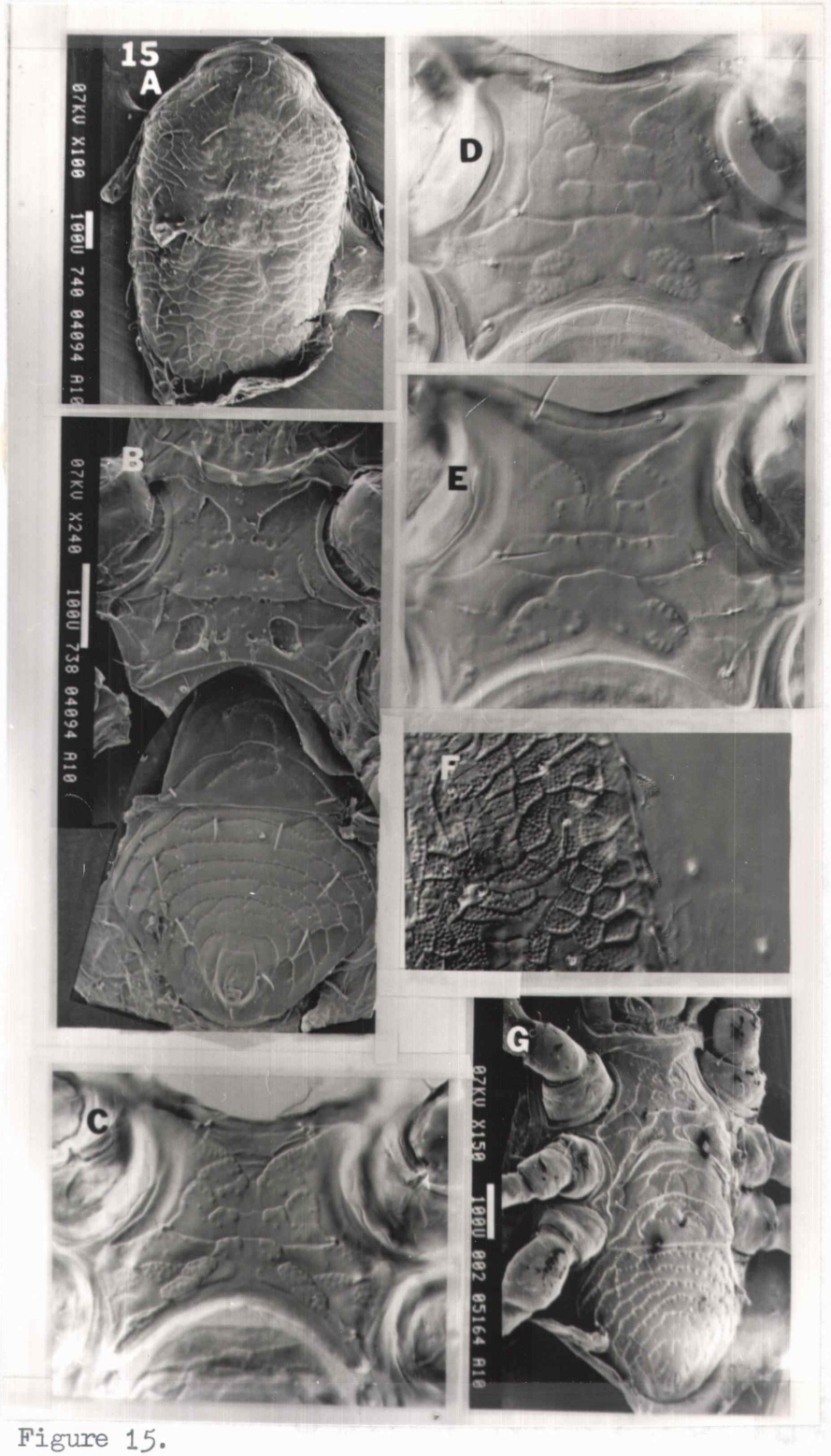

15
A
07KV X100 100U 740 04094 A10
B
07KV X240 100U 738 04094 A10
C
D
E
F
G
07KV X150 100U 002 05164 A10

Figure 15.

THE CAPENSIS COMPLEX

(figs. 5 E, 16)

This subgroup consists of a single complex of two species restricted to subsaharan Africa and named for the new species, capensis.

Diagnosis: The dorsal shield is reticulated and narrows over the opisthosoma and has a heavily punctate procurved line and posterior arms. The vertical (j1) setae are adjacent, long and plumose. The clunal (J5) setae are serrate, long and curled. The z1 setae are short and smooth. The median dorsal setae are long and smooth but the other dorsal setae are elongate and strongly bipectinate as are the integumental setae. The sternal shield is longer than wide and strongly punctate along the margins or across its entire field. At least the tips of the first pair of sternal setae are pilose.

KEY TO THE CAPENSIS COMPLEX

1. Sternal shield evenly punctate, a.pf. obscure, setae on ventral plates strongly pectinate, dorsal shield 700 to 1060 um long.....capensis

1' Background punctation reduced, a.pf. deeply punctate, st1 distally pilose, other ventral

setae at most weakly pilose, dorsal shield 875 to 1270 um long.....macroscatophilus

Macrocheles capensis, new species

(fig. 16 A, B)

This is the name suggested by van Driel in his doctoral thesis (1973) for a collection of this species from Port Elizabeth by C.D. van Driel.

Diagnosis: A large species from subsaharan Africa with large, bipectinate dorsal and ventral setae, a tapering dorsal shield, a small, triangular ventrianal shield and heavy background punctation on the ventral shields.

Description: The sternal shield is heavily punctate throughout with a strong medially punctate l.ang., punctate l.arc., l.m.t., a bifurcate l.o.p., and deeply recessed a.p.p.. The a.pf. are obscured by the punctate ornamentation. The epigynial shield is punctate-reticulate as is the small triangular ventrianal shield. All of the ventral setae are strongly bipectinate. The dorsal shield narrows posteriorly and has plumose vertical (j1) setae, long, curled, serrate clunal (J5) setae, smooth z1, z5, j6, and J2 setae and the rest of the setae are elongate and strongly bipectinate.

Size and Distribution: Macrocheles capensis has been collected in South Africa, Kenya, Ethiopia, Rwanda and

Zaire. It is occassionally phoretic on beetles in the genera Onitis, Heliocopris, and Diastellopalpus. The holotype and a paratype were collected in Garamba National Park, Zaire by H. DeSaeger (coll. 1609) from elephant dung on 23 April 1951. A collection of 19 capensis from Zaire had dorsal shield lengths that ranged from 702 to 1018 um ($\bar{x}$= 887.8±78.1).

Macrocheles macroscatophilus, new species

(figs. 5 E, 16 C, D)

This is a larger sibling species of capensis that has been collected in Zaire and Ethiopia. The name is in reference to its size and habitat.

Diagnosis: This is a very large subsaharan Africa species with large, bipectinate dorsal setae, a tapering dorsal shield, and smooth to weakly pilose ventral setae.

Description: The dorsal setae are bipectinate as in capensis. The sternal shield is punctate around the margins. There are two deeply punctate l.arc.. The a.p.p. is deeply recessed and the a.pf. are deep punctae. The st1 are distally pilose, but the remaining setae of the ventral plates are smooth or at most sparsely pilose distally. The ventrianal shield is rounded subcordate and larger than in capensis.

Size and Distribution: The holotype of Macrocheles macroscatophilus and three paratypes were collected from an unidentified coprophagic insect by H. DeSaegar from a grassy savana in Garamba National Park, Zaire on 26 August 1952.

A collection of 29 Macrocheles macroscatophilus from Zaire had dorsal shield lengths which ranged from 874 to 1269 um (x= 1002.3±81.3). This species has been collected from beetles in the genera Onitis and Heliocopris from Zaire and Ethiopia.

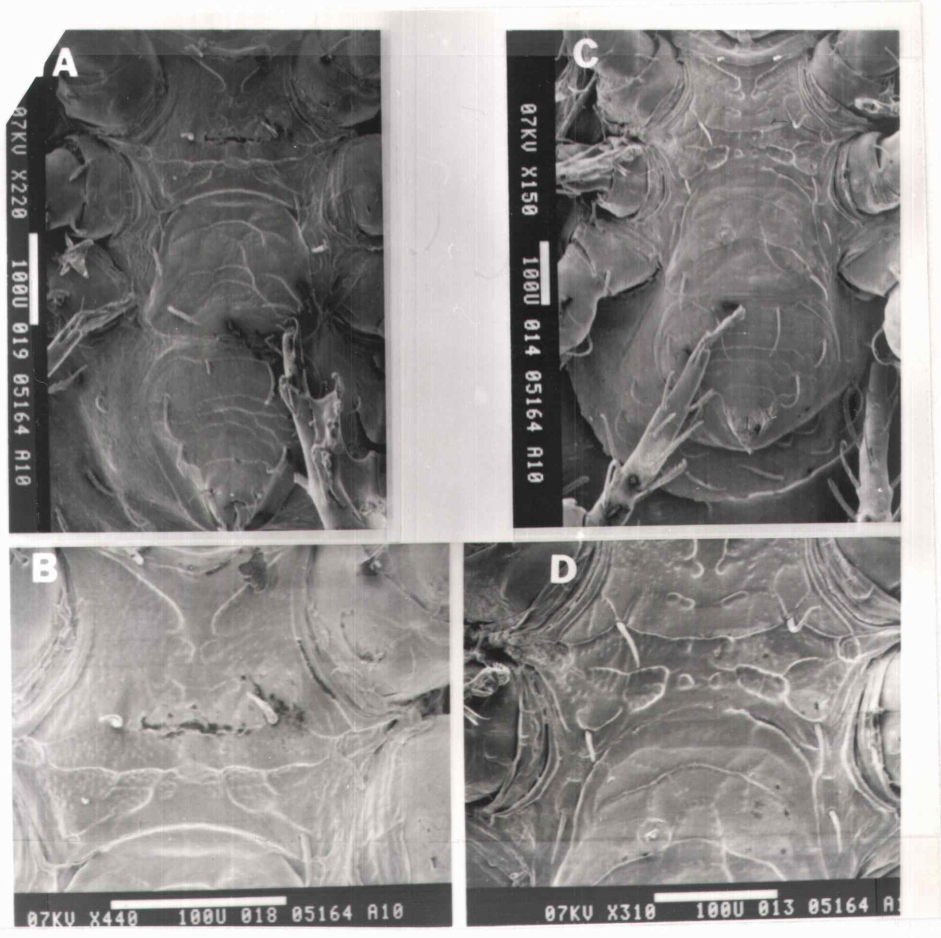


Figure 16. The species in the capensis complex: A) capensis, n.sp. (ventral SEM, Zaire); B) capensis, n.sp. (sternal shield SEM, Zaire); C) macroscatophilus, n.sp. (ventral SEM, Zaire); D) macroscatophilus, n.sp. (sternal shield SEM, Zaire).

THE FRIGGI COMPLEX

(fig. 17)

This complex is named for the new species, Macrocheles friggi.

Diagnosis: Sternal shield compressed such that the length is equal to or less than the width, and with a corresponding reduction in ornamentation. The l.ang. is open medially and obsolete. There is a single l. arc. which is faint but punctate. The l.m.t. is strongly developed. The l.o.p. is disjunct and the ramus is evanescent or lost. The a.p.p. and a.pf. are reduced to scattered punctae or lost. Distributed in subsaharan Africa and Thailand.

KEY TO THE SPECIES IN THE FRIGGI COMPLEX

1. Posterior dorsal shield setae and integumental setae bipectinate .....nalani

1' Dorsal shield setae (except vertical and clunal setae) and integumental setae smooth.....2

2. Sternal shield about as long as wide, l.arc. deeply punctate.....friggi

2' Sternal shield wider than long, l.arc. lost, vertical setae flat pilose.....pumiliosternus

Macrocheles friggi, new species

(fig. 17 A, B)

This species name was proposed by van Driel (1973) in his doctoral thesis and in an unpublished manuscript for specimens collected in Zaire.

Diagnosis: A medium sized species from subsaharan Africa with a sternal shield about as wide as long with reduced, but deeply punctate lines. The dorsal setae are smoothly acicular.

Description: The dorsal shield is evenly reticulate with a procurved line and broad over the opisthosoma. The vertical (j1) setae are adjacent and distally pilose and the clunal (J5) setae are weakly serrate. The other dorsal setae are smooth and acicular. The sternal shield is about as wide as long, with an open punctate l. ang., an evanescent l.arc. with deep punctae, a strong l.m.t., and a disjunct l.o.p. with evanescent ramus. There are deep punctae on the l.m.t. at the point at which the l.o.p. would join. The a.p.p. and a.pf. are reduced to scattered deep punctae. The epigynial shield has reduced reticulations and a strong arch. The metasternal plates are narrow. The ventrianal shield is roundly cordate with the width is

greater than the length and evenly punctate-reticulate. The postcoxal pore is adjacent to the parapodals.

Size and Distribution: The holotype and three paratypes are from a Heteronitis castelnaui collected by A. Boucomont in 1936 at Stanley Pool, Zaire. The lengths of the dorsal shields of 25 specimens form Zaire ranged from 648 to 810 um (x= 722.6±48.2 um). The dorsal shield lengths of 42 specimens from Zaire, Kenya, Ethiopia and Uganda fell within the above range and averaged 731.4 um (±44.6).

Macrocheles friggi has been collected from beetles in the genera Oniticellus, Catharsius, Heliocopris, Scarabaeus, Heteronitis, and Onitis in the Cameroons, the Central African Republic, Zaire, Kenya and Ethiopia.

Macrocheles pumiliosternus, new species

(fig. 17 C, F)

Macrocheles neovernalis Ryke & Meyer, [misidentified by Costa, 1975]

Diagnosis: This interesting little mite from central and southern Africa may be readily told from neovernalis by the squat sternal shield that is much wider than long for which it is named (*pumilio*, (L) a dwarf, *stern-*, (L) breast). The short, thick, terminally pilose vertical

setae in pumiliosternus are a good diagnostic character. In neovernalis, the vertical setae are variable in size and usually pilose in the distal one-fifth. The long thick- walled cornu sacculus illustrated in Costa (1975) is also quite different from neovernalis.

Description: Dorsal shield with a reticulate pattern, strong procurved line and reduced laterally over the opisthosoma. The vertical (j1) setae are short, thick and pilose terminally. The clunal (J5) setae are weakly serrate. All other dorsal setae are smoothly acicular. The sternal shield is squat, much wider than long, with an obsolete l.ang. and l.arc., a strong shelf-like l.m.t., and a disjunct subparallel l.o.p.. The a.p.p. and a.pf. are reduced to a few deep punctae. The ornamentation of the epigynial shield is reduced to the arch. The metasternals are small and narrow. The ventrianal shield is small, roundly cordate, wider than long and evenly punctate-reticulate. The postcoxal pore is adjacent to the parapodal shield. The chelicerae have strong teeth and are rather large in comparison to the small body.

Size and Distribution: The holotype and five paratypes were collected on Onitis inversidius Lansb. by J. Surcouf in December 1929 at Chamba on the Zambeze River, Zaire. The length of the dorsal shield of the type series ranged from 495 to 540 um (x= 522.8±15.2). A

series of twenty specimens from around Africa ranged from 495 to 576 um (x= 524.3±17.3). The Costa (1975) specimen was 520 um long.

Macrocheles pumiliosternus has been collected from Gabon, the Cameroons, Chad, Zaire, Uganda, Kenya and South Africa. Phorionts of Macrocheles pumiliosternus include beetles in the genera Onitis, Heteronitis, Catharsius, Heliocopris, Scarabaeus and Pritophilus.

Macrocheles nalani, new species

(fig. 17 D, E)

Diagnosis: This is a distinctive species with enlarged distally bipectinate posterior opisthonotal setae and a squat sternal shield. This new species is described from two collections off Heliocopris tyrannus in Thailand. The name is from the Hawaiian, *nalani*, which means heavenly.

Description: Sternal shield much wider than long with an open, evanescent l.ang., a punctate-reflexed, but strongly faded l.arc., the l.m.t. is in the form of a strong median shelf, the l.o.p. is disjunct and parallel to the l.m.t. with the ramus evanescent and the a.p.p. and a.pf. reduced to a few faint scattered spots. The ornamentation of the epigynial shield is very reduced except for the arch. The metasternal plates are narrow.

The ventrianal shield is rounded cordate, wider than long and evenly punctate-reticulate. The posterior integumental setae are elongate and bipectinate. The dorsal shield is reticulate with a well developed procurved line. The vertical (j1) setae are adjacent and distally pilose. The clunal (J5) setae are serrate. The j4 setae are distally pilose and the z4 setae are long and smoothly acicular. On the opisthonotal plate, the S4, S5 and Z4, Z5 setae are long, thick and distally pectinate. The other dorsal setae are smoothly acicular.

Size and Distribution: The holotype of Macrocheles nalani and six paratypes were collected on Heliocopris tyrannus Thomas by Willoughby Lowe on the Toak Plateau, Tenaserim, Thailand in January 1924. The lengths of the dorsal shields of the type series ranged from 603 to 644 um ($x= 628.1 \pm 13.3$). A second collection by H.M. Simth in Bankiriwong, Thailand, 14 July 1929, on the same phoriont ranged from 630 to 675 um ($x= 656.7 \pm 17.0$, $n=12$).

Figure 17. The species in the *friggi* complex: A) *friggi* (SEM, Zaire); B) *friggi* (Zaire); C) *pumiliosternus*, n.sp. (holotype, Zaire); D) *nalani*, n.sp. (SEM, Bankiriwong); E) *nalani*, n.sp. (holotype, Toak Plateau, Thailand); ventrianal shield of *pumiliosternus*, n.sp. (holotype, Zaire).

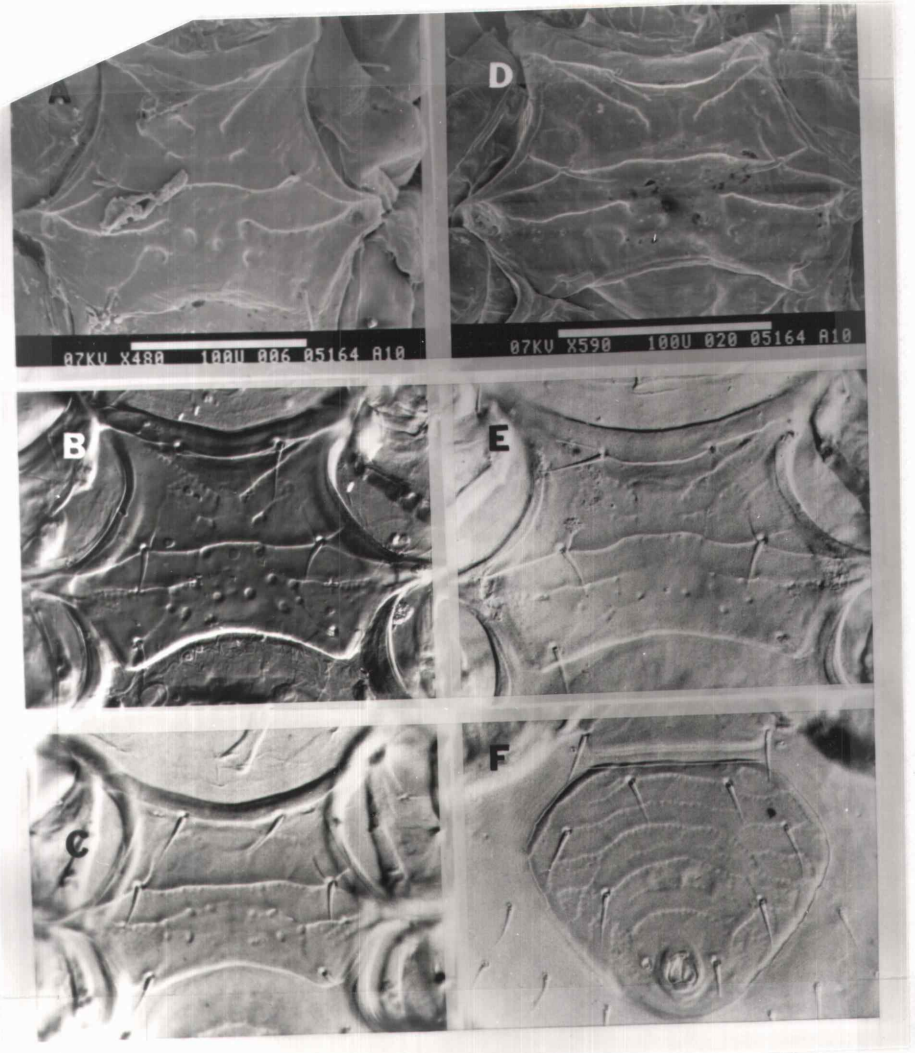

A
07KV X480 100U 006 05164 A10
D
07KV X590 100U 020 05164 A10
B
E
C
F

Figure 17.

THE PRAEDAFIMETORUM SUBGROUP

(fig. 15 C, G)

It is arguable whether or not the species in the praedafimetorum complex belong in the glaber species group. The morphology of praedafimetorum is very similar to that of species in the matrius species group (fig. 14 C). Especially striking are the fused ventral shield complex in the males, and the structure of the sternal shield ornamentation. The primary differences are reduction characters, especially the lack of plumose dorsal setae, the reduced punctation of the sternal shield, and the loss of the perianal cribral extension.

The ecological characteristics of the praedafimetorum group are also very similar to the matrius species. Macrocheles praedafimetorum is rarely phoretic on beetles, but commonly associated with the nests of birds, mammals and bumblebees.

However, since praedafimetorum has reached the glaber grade of morphology by sharing the important apomorphies (l. arc., l.o.p., a.p.p.) of the sternal shield, I am provisionally including praedafimetorum as a subgroup in the glaber species group.

Diagnosis: Large, strongly sclerotized macrochelids common in moist litter habitats, dung, dead animals and animal and bird nests in western North America and one

collection from Irkutsk, U.S.S.R.. The sternal shield has strongly arched posterior angles and is strongly ornamented with lines and punctae including acinous a.p.p. and a.pf., two deeply punctate l.ang., the second of which is reflexed and contiued in a procurved loop to join the well developed l.o.a.. The ventrianal shield is wider than long and strongly sclerotized, and the cribrum is terminal and does not have perianal extensions. The j4, z4, humeral (r2, r3), and posterior (S5, Z5) setae are often pectinate for more than half their length.

Macrocheles praedafimetorum Richards & Richards 1977

(fig. 15 C, G)

This is the only nominate species in the praedafimetorum complex. It is associated with decaying vegetation in nests of Bombus bifarius, flavifrons, frigidus, mixtus, occidentalis and ternarius in Alberta, Canada (Richards & Richards 1977). The type series had dorsal shield lengths of 900 to 1156 um (x= 1007.5, n=13), but included some misidentified Macrocheles perglaber.

Size and Distribution: Specimens which vary only in the degree of plumosity in the dorsal setae occur throughout western North America. Several similar

species in the matrius species group may be differentiated from praedafimetorum by their possession of a perianal cribrum. Macrocheles praedafimetorum may be found in dung, wet, marshy litter, riparian litter, beach litter, gull nests, petrel burrows, the nests of Aplodontia rufa and bumblebees. Macrocheles praedafimetorum is phoretic on millipedes, Aphodius fossor, Nicrophorus defodiens and N. pustulatus, Eutamias sp., and Zapus trinotatus. Specimens in the OSU Acarology Collection were collected in British Columbia and Alberta, Canada, Wyoming, Washington, Oregon and coastal California (as far south as Stinson Beach). Forty specimens from Oregon had dorsal shield lengths which ranges from 828 to 1150 um ($x = 1020.8 \pm 60.9$ um). Fifty-nine specimens from the U.S. and Canada fell within the above range and averaged 1005.0 um, very close to the type series.

Three specimens that are similar to praedafimetorum were collected from Geotrupes baikalicus near Irkutsk on Lake Baikal. Since Bregetova & Koroleva (1960) have named several subspecies of matrius from the Soviet Far East, and praedafimetorum is very close to matrius, I will defer description of these specimens until a thaw in U.S.-Soviet relations allows a response to our request for type specimens, or a nuclear holocaust disposes the question.

THE *SCUTATUS* SUBGROUP

Diagnosis: This subgroup is composed of four complexes of species united by similar trends in reduction of ventral shield ornamentation. The linea angulata is weakly produced. The linea arcuata is flat, minutely punctate, and extended as lateral loops to join the linea oblique anteriores, or the linea arcuata is obsolete. The linea oblique posteriores is often disjunct from the linea media transversa, and the ramus is obsolescent to obsolete. The area punctatae posteriores and area punctiformes are reduced to scattered punctations or obsolete. The ornamentation of the epigynial shield is obsolescent except for the arch. The metasternal shields are narrow. The ventrianal shield is small and weakly ornamented with the length $\geq$ the width.

KEY TO THE COMPLEXES OF THE *SCUTATUS* SUBGROUP

1. Dorsal setae enlarged and strongly bipectinate for their entire length; dorsal shield narrowed over opisthosoma; phoretic on *Enoplotrupes*.....*transmigrans* complex

1' Dorsal setae smooth, distally pilose or at most bipectinate distally; dorsal shield broad posteriorly.....2

2. All dorsal setae (except vertical and clunal setae) smooth; a line of punctae connecting l.o.ps.; phoretic on Scarabaeini in southern Africa.....<u>rhodesi</u> complex

2' At least dorsal seta j4 distally pilose.....3

3. Sternal setae long and stout; phoretic on Scarabaeini; sternal ornamentation very reduced; ventrianal shield longer than wide and weakly ornamented; dorsal setae may be distally bipectinate (fig. 20 A-C, F-G).....<u>paganus</u> complex

3' Sternal setae not enlarged; phoretic on a variety of beetles; distinct to very reduced; ventrianal shield rounded subcordate, about as wide as long; postcoxal pore appressed to parapodal plate (fig. 19).....<u>scutatus</u> complex

THE TRANSMIGRANS COMPLEX

(figs. 3 F, 5 B, 18)

The transmigrans complex has a single nominate species.

Diagnosis: The dorsal shield is reticulate with a procurved line and strongly narrowed over the opisthosoma. The vertical (j1) setae are adjacent, inflated and plumose for their entire length. The clunal (J5) setae are serrate. The remainder of the dorsal setae are enlarged and strongly bipectinate for their entire length. The integumental setae are similarly bipectinate. The sternal shield is longer than wide with a well developed l.ang., a strongly looping l.arc. which joins the l.o.a., a l.m.t., and a disjunct l.o.p. without a ramus. The a.p.p. is reduced to scaterred fine punctations and the a.pf. is smooth. Punctate fields continue along the l.o.p. towards the a.p.l.. The epigynial ornamentation is reduced. The metasternal plates are small. The ventrianal shield is longer than wide with ligthly punctate lines. The terminal cribrum is wide. The male has most of the dorsal setae bipectinate and a separate subcordate ventrianal shield.

Macrocheles transmigrans Petrova & Taskaeva 1964

(figs. 5 B, 18)

This species was described from a scarab beetle from Hunan, China. The specimens in the OSU Acarology Collection were all collected from *Enoplotrupes* spp. from India, Burma, and Szechuan, China or from *Helictopleurus giganteus* in Madagascar.

Figure 18. The transmigrans complex: A) anterior dorsal setae of transmigrans (Szechuan); B) sternal shield of transmigrans (Szechuan); venrianal shield of transmigrans (Szechuan).

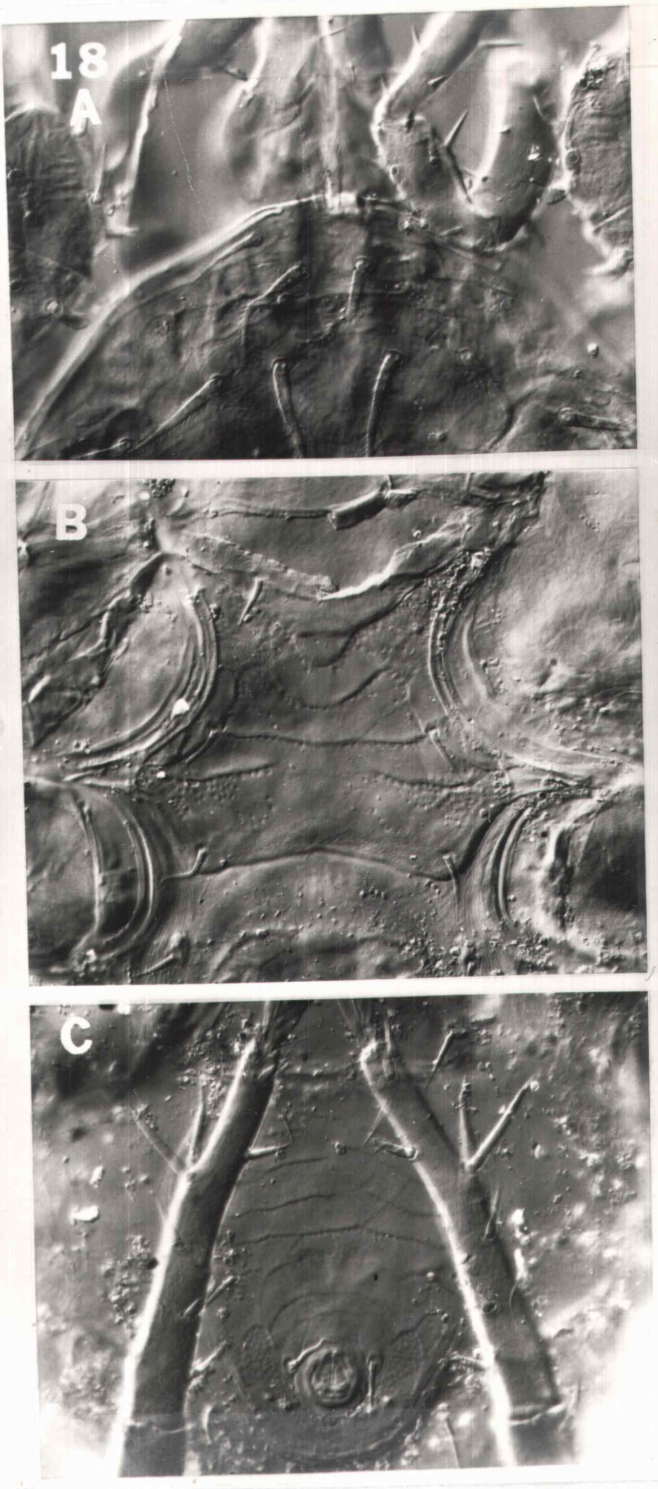


Figure 18.

THE SCUTATUS COMPLEX

(figs. 5 H, 19)

The scutatus complex is composed of four nominate and one new species from the Old World.

Diagnosis: The scutatus complex is a poorly defined collection of smallish species which resemble Macrocheles scutatus (Berl.), the smallest, least ornamented of the three species in Filipponi & Pegazzano's glaber group. The sternal shield is longer than wide and the ornamentation is reduced. The l.arc. is not reflexed nor deeply punctate. It is often procurved to join the l.o.a. but may be evanescent or lost. The l.m.t. is distinct. The l.o.p. is evanescent and the ramus may be lost. The a.p.p. and a.pf. are reduced to scattered punctations or lost. The epigynial shield is squared and punctate-reticulate to nearly smooth except for the arch. The metasternal plates are small. The ventrianal shield is small and roundly subcordate with the length about the same as the width and evenly punctate-reticulate. The postcoxal pore is adjacent to the parapodal plates. The dorsal shield is reticulate with adjacent, distally pilose vertical (j1) setae, a procurved line and serrate clunal (J5) setae. The j4, z4 setae are usually thickened and distally pilose.

KEY TO THE SPECIES IN THE *SCUTATUS* COMPLEX

1. Setae j3 distally pectinate (as well as j4, z4, r2, r3); southern Africa.....*subscutatus*

1' Setae j2 smooth 2

2. L.o.p. disjunct from l.m.t. and without ramus, a.p.p. and a.pf. reduced to a few punctae or lost.....3

2' L.o.p. reduced but united to l.m.t. and with ramus, a.p.p. reduced but distinct.....4

3. L.arc. lost, dorsal setae except j4 smooth; southeast Africa.....*neovernalis*

3' L.arc. evanescent, j4, z4, r2, r3 often distally pectinate, S5, Z5 always distally pectinate; Asia, Philippines.....*dispar*

4. L.arc. forming the base of a line of cells, a.p.p. finely punctate; Northern Europe...*neoscutatus*

4' L.arc. a procuved loop joined to l.o.a., a.p.p. coarsely punctate.....*scutatus*

Macrocheles scutatus (Berlese, 1904)

(figs. 5 H, 19 A)

Holostaspis subbadius scutatus Berlese, 1904
Macrocheles vicinus Leitner, 1946
Macrocheles subbadius, Evans & Browning 1956, Bregetova & Koroleva 1960
Macrocheles scutatus (Berlese), Filipponi & Pegazzano (1962)
Macrocheles willmanni Kraus, 1970
Macrocheles scutatus (Berlese), Bregetova 1977

This species was redescribed by Filipponi & Pegazzano (1962). It is broadly distributed but of reasonably conservative morphology.

Size and Distribution: A series of fifty individuals from Italy had dorsal shield lengths of 463 to 703 um (x=622.1±38.1)(Filipponi & Pegazzano 1962), while a collection from Sinkiang, China ranged from 598 to 656 um (x= 632.8±19.4, n= 6) and a collection from India ranged from 667 to 707 um (x= 684.3±13.4, n= 6).

Specimens in the OSU Acarology Collection are from throughout Europe, North Africa, Morocco, Israel, India, Sinkiang, and the Philippines. Bregetova & Koroleva report scutatus from all across European Russia and Central Asia. Emberson (1973) reports scutatus from Rattus exulans in New Zealand. The collections in the OSU Acarology Collection were phoretic on species of Geotrupes, Onitis, Copris, and Onthophagus.

Macrocheles neoscutatus Krantz 1972

(fig. 19 B)

Diagnosis: The pattern of cells between the l.ang. and l.arc. and the finely punctate a.p.p. are distinctive for this species which has been collected once in a woods in Hamburg.

Macrocheles neovernalis Ryke & Meyer 1958

(fig. 19 F)

Macrocheles neovernalis, Ryke & Meyer, Costa 1975

[misidentified pumiliosternus as neovernalis]

Diagnosis: With the exception of the distally pilose vertical (j1) setae, serrate clunal setae (J5), and sparsely pilose j4 setae the dorsal setae of neovernalis are smooth. The sternal shield is distinctive, the l.arc. has been lost (or is extremely faint), the l.o.p. is disjunct and has lost the ramus, and the a.p.p. and a.pf. are lost or extremely faint.

Size and Distribution: Specimens in the OSU Acarology Collection are from South Africa, Mozambique, East Africa, and Zaire and were phoretic on Heliocopris spp. or Catharsius sp.. A series of fifteen specimens of neovernalis from southern Africa had dorsal shield

lengths of 621 to 719 um (x=671.0±30.3). The holotype has a dorsal shield length of 650 um..

Macrocheles dispar Berlese 1918

(fig. 19 D)

Diagnosis: This is a small to moderate sized Asian species with distally pectinate podonotal (j4, z4, r2, r3) and posterior (S5, Z5) setae. The ventral ornamentation is reduced, the l.arc. is obsolete, the l.o.p. is disjunct and lacks a ramus, and the a.p.p. and a.pf. are reduced to a few scattered punctae.

Description: The dorsal shield is punctate-reticulate with a procurved line, long, distally pilose vertical (j1) setae, serrate clunal (J5) setae, distally pectinate j4, z4, r2, r3, Z5 and S5 setae. The sternal shield is longer than or about as long as wide. The l.arc. is a faint loop, the l.o.p. is disjunct and the ramus is lost. The a.p.p. and a.pf. are reduced to a few scattered punctations. The epigynial ornamentation is reduced. The metasternal plates are narrow. The ventrianal shield is longer than wide and has evenly punctate lines. The male has a separate subcordate ventrianal shield a large spur on femur II, and a pair of spurs, one of which is setiferous, on femur IV.

Size and Distribution: A series of 21 specimens of Macrocheles dispar from southeast Asia ranged from 644 to 886 um (x=752.7±63.4). The original description from Java included two specimens with dorsal shields 760 and 900 um in length. The collections of Macrocheles dispar in the OSU Acarology Collection are from Szechuan, China, Vietnam, Taiwan, and the Philippines and were collected from beetles in the genera Catharsius, Enoplotrupes, and Paragymnopleurus.

Macrocheles subscutatus, new species

(fig. 19 C, E)

This new species is a distinctive relative of scutatus from southern Africa. The specific name is a reference to its similarity to scutatus.

Diagnosis: A small scutatus-like species from southern Africa with distally pectinate podonotal setae (j3, j4, z4, r2, r3) and smooth posterior (S5, Z5) setae. The sternal shield ornamentation is evanescent.

Description: The dorsal shield is punctate-reticulate with adjacent, distally pilose vertical (j1) setae, serrate clunal setae (J5), distally pectinate j3, j4, z4, r2, and r3 setae. The other dorsal setae are short, smooth and acicular. The sternal shield is longer than wide with a faintly punctate looping l.arc., a l.m.t.,

l.o.p. without a ramus, and a.p.p. and a.pf. reduced to a few small scattered punctae. The epigynial ornamentation is reduced. The metastrnal plates are small. The ventrianal shield is rounded subcordate and evenly punctate-reticulate, with the length about equal to the width. The post anal seta is long and smooth and the postcoxal pore is adjacent to the parapodal plate.

Size and Distribution: The holotype and four paratypes were collected from scarabs in a trap in Hluhluwe, Natal, South Africa by G. Flanagan on 16 November 1980. The type series have dorsal shields that range from 725 to 828 um in length (x= 777.6±38.5). Ten specimens from South Africa range from 690 to 828 um (x= 764.3±45.1). Specimens of Macrocheles subscutatus in the OSU Acarology Collection were collected from beetles in the genera Copris, Heliocopris, Catharsius, and Scarabaeus in Tanzania, Zimbabwe, and South Africa.

THE PAGANUS-RHODESI CLUSTER

The paganus and rhodesi complexes are closely related groups of species phoretic on beetles in the Scarabaeini in southern Africa. Distinguishing characters include very reduced ventral ornamentation and enlarged sternal setae. Sternal setae 2 extend past the insertions of st 3.

Figure 19. The species in the *scutatus* complex: A) *scutatus* (culture, Italy); B) *neoscutatus* (holotype, Germany); C) *subscutatus*, n.sp. (holotype, South Africa); D) *dispar* (Szechuan); E) *subscutatus*, n.sp. (SEM anterior dorsal setae j1 - 3, Zaire); F) *neovernalis* (ventral shields, South Africa).

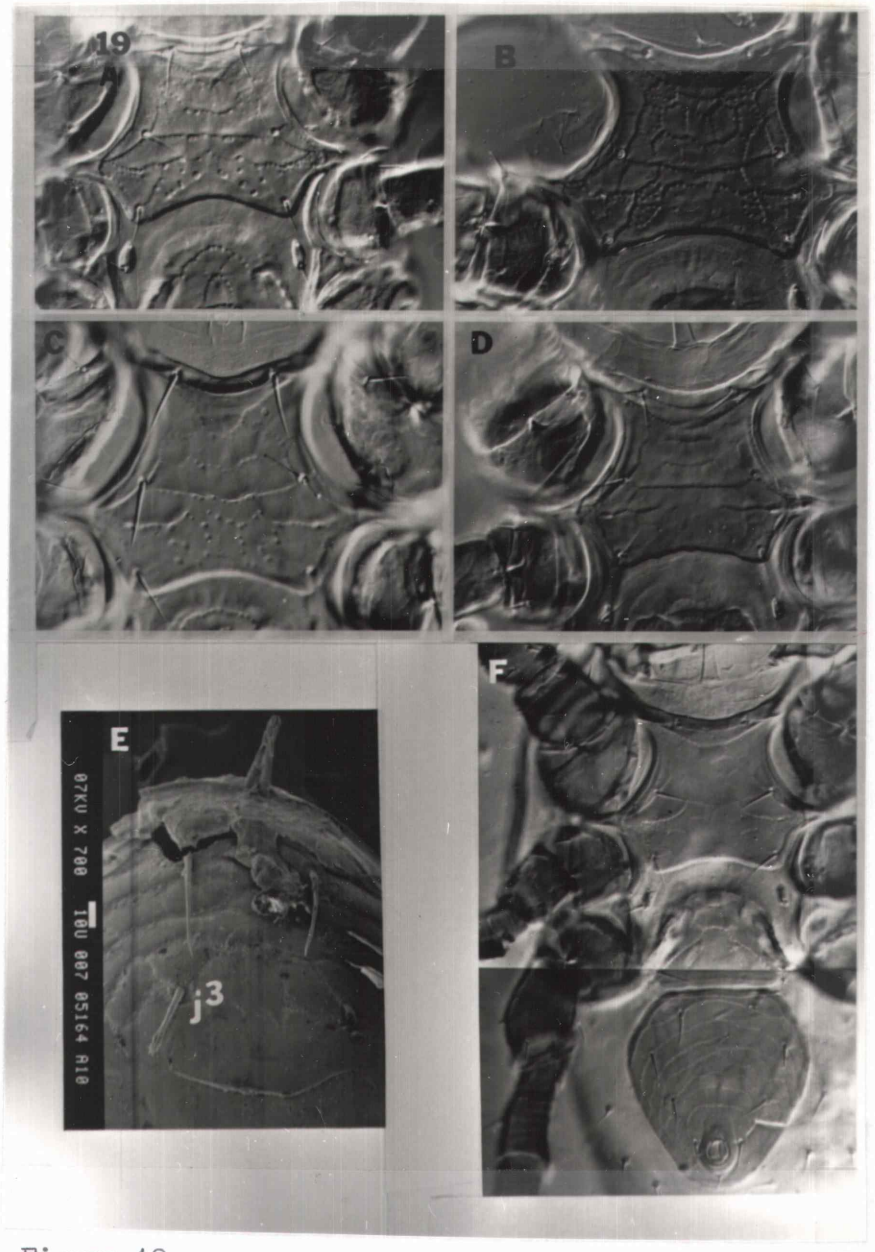


Figure 19.

THE PAGANUS COMPLEX

(fig. 20 A-C, F-G)

Diagnosis: The paganus complex is a small collection of species from southern Africa that are associated with beetles in the Scarabaeini. The sternal setae are long, stout, straight and smooth. The ornamentation of the sternal shield is reduced in most species, with the ramus of the l.o.p. lost. The l.arc. is a faintly punctate, flatened loop.

KEY TO THE SPEICES IN THE PAGANUS COMPLEX

1. Most dorsal setae smooth.....paganus

1' Most dorsal setae pilose-pectinate.....agnosticus

Macrocheles paganus Berlese 1918

(fig. 20 C, F, G)

The following diagnosis is based on a series of paganus collected on the type phoriont, Scarabaeus paganus, from the type locality, Angola.

Diagnosis: A moderate sized species from subsaharan Africa with thickened, distally pilose j4, z4 and r2 setae and other dorsal setae long, smooth and acicular. The ornamentation of the ventral shields is reduced, with a looping l.arc. and disjunct l.o.p. without a ramus.

Description: The dorsal shield is lightly punctate-reticulate with a procurved line that lacks posterior punctate arms. The vertical (j1) setae are adjacent and distally pilose, and the clunal (J5) setae are serrate. The j4, z4 setae are thick and distally pilose, and the r2 is usually distally pilose. The remainder of the setae are large, smooth and acicular. The sternal shield is longer than wide and has long heavy sternal setae. St2 extends beyond the insertion of st3. The l.ang. is faintly punctate, the l.arc. a faint flat loop, the l.m.t. is wavy, the l.o.p. is disjunct and the ramus is lost. The a.pf. is lost and only a few minute punctae remain of the a.p.p.. The metasternal plates are narrow. The epigynial shield has a distinct arch, but the other ornamentation is reduced. The ventrianal shield is longer than wide and has smoothly punctate lines. Leg IV has three long spur-like ventral setae.

Size and Distribution: Macrocheles paganus is widely distributed throughout subsaharan Africa. The northern, tropical populations have variations in the shape of the ventrianal shield which are distinctive. Table 5 documents some of the dorsal shield length variations in the OSU Acarology Collection. The collections are from scarabs, primarily members of the Scarabaeini such as Scarabaeus spp. and Pachylomera, but also Catharsius fastidiosus. The range documented in the OSU Acarology

Collection includes the Ivory Coast, Ghana, the Congo, Zaire, Angola, South Africa, Mozambique, and Kenya.

Macrocheles agnosticus, new species

(fig. 20 A, B)

This new species is very similar to paganus, however, the dorsal setae are thickened and distally pilose. The specific name is an oblique reference to its close relative inspired by the prevaling political climate.

Diagnosis: A moderate sized species from southern Africa with thickened and distally pilose-pectinate dorsal setae. The ventral shields have reduced ornamentation. The l.arc. is faint and looping, the l.o.p. is disjunct and without a ramus, and the a.p.p. and a.pf. are gone.

Description: The dorsal shield is lightly punctate-reticulate with a procurved line. The vertical (j1) setae are adjacent and distally pilose, and the clunal (J5) setae are serrate. The z1 setae are short and distally pilose. The remainder of the dorsal setae are thickened and distally pilose-pectinate, as are the integumental setae. The sternal setae are long, the sternal shield is longer than wide with a faint, flat l.arc., the l.o.p. is disjunct and without a ramus.

The a.pf. is gone and the a.p.p. is reduced to a few scattered punctae. The epigynial shield ornamentation is reduced to the arch. The metasternal plates are narrow. The ventrianal shield is small, longer than wide and has lightly punctate lines.

Size and Distribution: The holotype and seven paratypes were collected in South Africa from Scarabaeus savigni and had dorsal shields which ranged in length from 667 to 759 um (x= 727.5±35.2). Another individual of Macrocheles agnosticus was collected from Scarabaeus convexus in Capetown, South Africa.

Table 6. Variations in the lengths of the dorsal shield in Macrocheles paganus *sensu latu* in Africa.

Locality	Range in um	Mean(+1 S.D.)	N
Angola/S.Africa	598 - 863	746.0(±54.8)	20
Mozambique	659 - 690	664.5(±17.0)	4
Kenya	656 - 713	687.5(±25.3)	4
Congo	690 - 771	740.0(±43.7)	3
Ghana	667 - 748	734.5(±36.1)	6
Ivory Coast	664 - 759	721.6(±51.2)	5

Figure 20. The species in the paganus subgroup: A) agnosticus, n.sp. (paratype, South Africa); B) agnosticus, n.sp. (posterior dorsal setae, paratype, South Africa); C) paganus (ex Scarabaeus paganus, Angola); D) rhodesi (South Africa); E) natalensis (South Africa); F) nr. paganus (ventral SEM, ex Scarabaeus festivus, Congo); G) sternal shield SEM of specimen in F).

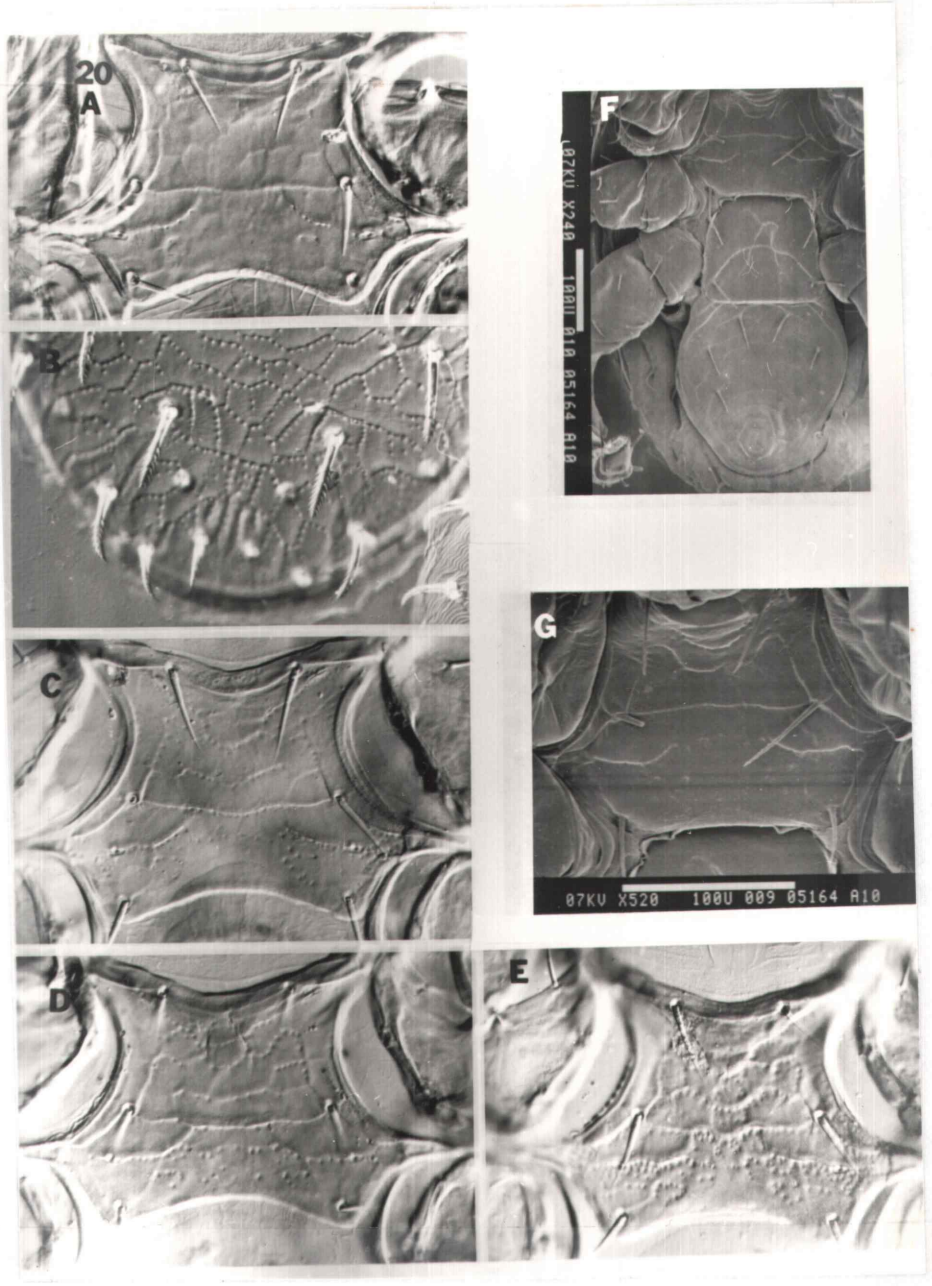

20
A
B
C
D
E
F
07KV X240 100U 010 05164 A10
G
07KV X520 100U 009 05164 A10

Figure 20.

THE RHODESI SPECIES COMPLEX

Diagnosis: The rhodesi complex is a small assemblage of macrochelids phoretic on the Scarabaeini in southern Africa. The sternal setae are heavy and the sternal shield is nearly as wide as long. The l.o.p. is attached to the l.m.t., but the ramus is lost. A line of punctae connects the l.o.p. and the a.p.p. is represented by a pair of elliptical perimeters of punctae.

KEY TO THE SPECIES IN THE RHODESI COMPLEX

1. Ventral shields strongly ornamented, ventrianal shield rounded.....natalensis

1' Ventral shield ornamentation reduced, ventrianal shield subcordate.....rhodesi

Macrocheles rhodesi Evans & Hyatt 1963

(fig. 20 D)

Diagnosis: A moderate sized species from southern Africa with most of the dorsal setae long, smooth and acicular. The sternal shield is about as long as wide and has reduced ornamentation, including the l.o.p.

without a ramus, but connected by a median punctate line.

Description: Dorsal shield reticulate with a procurved line. The The vertical (j1) setae are adjacent and distally pilose, and the clunal (J5) setae are serrate. In some collections the j4, z4 setae are distally pilose, or the z4 setae or both pairs may be smooth. The original description indicates that the dorsal setae are smooth. The remainder of the dorsal setae are always large, smooth and acicular. The sternal shield is nearly as wide as long and the sternal setae are long. The l.arc. is a flattened loop, the l.o.p. is attached, and connected by a line of punctae, but lacks a ramus. The a.p.p. are a pair of elliptical arrangements of small punctae. The metasternal plates are narrow, and the epigynial shield has a distinct arch. The ventrianal shield is longer than wide and has smoothly punctate lines.

Size and Distribution: A series of 22 Macrocheles rhodesi from South Africa had dorsal shields which ranged from 633 to 805 um (x= 732.6±43.8) in length. Phorionts include species of Scarabaeus, Gymnopleurus, and Sebasteos in South Africa, Botswana, Zimbabwe, and Mozambique.

Macrocheles natalensis Evans & Hyatt 1963

(fig. 20 E)

Diagnosis: This species is similar to rhodesi, but the dorsal and ventral shields are strongly sclerotized and punctate-reticulate. The ventrianal shield is rounded rather than subcordate.

Size and Distribution: A series of nine specimens of Macrocheles natalensis from South Africa had dorsal shield lengths which ranged from 633 to 782 um (x= 724.6±51.9). The OSU Acarology Collection has collections of natalensis only from South Africa, phoretic on species of Scarabaeus, Sisyphus and Sarophorus.

ANALYSIS OF PHORIONTS

The plesiomorphic sister groups of Macrocheles glaber are often associated with mammals and their nests. Phoresy on mammals is considered the plesiomorphic phoretic habit for the glaber group in this thesis. Only two subgroups, glaber and scutatus, have species that have been collected as phoretic associates of mammals, primarily rodents. Both Macrocheles glaber and perglaber in the glaber complex have been reported in association with numerous mammal species (Bregetova & Koroleva 1960, Farish 1965, and see Appendix I). Macrocheles tantalus, in the kraepilini complex, has been taken on two species of Rattus in Hawaii. Macrocheles scutatus has been occassionally reported as phoretic on a rodent (Emberson 1973). The members of the praedafimetorum complex are often associated with vertebrate nests, as are their close relatives in the matrius species group.

In Europe, where extensive surveys have been made of mites phoretic on synanthropic flies, Macrocheles glaber, perglaber, and scutatus have also been reported from muscid flies on occasion (Bregetova & Koroleva 1960, Petrova 1964, Sychevskay 1964,and Farish 1965). The numbers of individuals collected from Diptera is typically very low, and probably represents

opportunistic attachment to whatever insect is available in a declining habitat. It might be expected that other members of the glaber group will be found on flies.

The primary phoriont taxon in the glaber group is the beetle family Scarabaeidae (*sensu* Richter 1958). The species in the glaber group are phoretic on scarabs in four subfamilies of the Scarabaeidae, primarily the dung inhabiting subfamilies Geotrupinae, Aphodiinae and Coprinae (=Scarabaeinae) (see Table 7). The African species, witcoskianus, n.sp., is unusual in that it is phoretic on the goliath beetle in the subfamily Cetoniinae. The OSU Acarology Collection has numerous glaber group collections by the H. DeSaegar Expedition to Garamba National Park in Zaire that are labeled as "*avec insect xylophage*". These xylophagous insects may turn out to be scarabs in currently unrepresented subfamilies and tribes.

The genera and tribes of the Scarabaeidae used in this paper follow Junk (1912). The only members of the glaber group which are phoretic on scarabs in the Aphodiinae belong to the glaber subgroup, in the glaber, limue, and praedafimetorum complexes (Tables 7, 8). The Aphodiinae reaches its greatest diversity in the Neotropical Realm from which the glaber group is absent. The Geotrupinine scarabs may carry glaber group species in the praedafimetorum, glaber, scutatus, and

transmigrans complexes (Tables 7, 8). Macrocheles glaber, perglaber, and scutatus are typical phoretic mites on Palearctic species of Geotrupes (see Appendix I). Macrocheles transmigrans is typically phoretic on species of Enoplotrupes.

The main source of phoretic transport used by the glaber group species is the scarab subfamily Coprinae (=Scarabaeinae). Two dozen genera in the five tribes of the Scarabaeinae are recorded as phorionts for glaber species in the OSU Acarology Collection (Table 7).

Species in the glaber subgroup appear to be opportunistic phoretics on whatever dung beetle is available. The phorionts recorded in the OSU Acarology Collection for Macrocheles glaber (Muller, 1860) include forty species of scarabs in eleven genera (see Appendix I). Macrocheles peregrinus Krantz 1981 is recorded from sixty species in fifteen scarab genera. And in the limue complex of the glaber subgroup, Macrocheles limue Samsinak 1962 is recorded from fifty-seven species in twelve genera of scarabs. The African species in the friggi subgroup also tend to be generally phoretic with friggi having been collected from twenty-four species of scarabs in seven genera and pumiliosternus represented by collections from nine species in six scarab genera.

The members of the scutatus subgroup show little specificity in their phoretic habits, although they are

not as widely phoretic as the members of the glaber and friggi subgroups. Macrocheles scutatus, subscutatus, and dispar are each recorded from four genera in two to four tribes of the Scarabaeidae. Macrocheles neovernalis has been recorded from only two genera in a single tribe, the Coprini. Outside of Madagascar, where they are phoretic on Helictopleurus, a member of the Oniticellini, the transmigrans subgroup has been collected entirely from species of Enoplotrupes, a member of the Geotrupinae.

The members of the paganus subgroup are the only other members of the glaber group which exhibit apparent phoretic specificity. The paganus subgroup, four species species in two complexes restricted to subsaharan Africa, are almost exclusively phoretic on members of the tribe Scarabaeini. With a few exceptions (peregrinus and limue), the species in the other subgroups are rarely found members of the Scarabaeini. With the exceptions of a single collection of paganus on Cathrsius fastidiosus (Coprini) and natalensis on Sarophorus castatus (Coprini), the members of the paganus subgroup are reported only from seventeen species in five genera of the Scarabaeini.

Records for phoresy on beetles outside of the Scarabaeidae are rare. Macrocheles perglaber and praedafimetorum have been collected a number of times

from carrion beetles in the genus Nicrophorus (Silphidae) (Appendix I). Farish (1965) reports literature records for "glaber" (=glaber-perglaber) from Hister impressus (Histeridae), Chrysomela staphylea (Chrysomelidae), and Ips typographus (Scolytidae). Finally, there are two recorded beetle phorionts which I have been unable to place taxonomically. Macrocheles kraepilini is reported as phoretic on Pachylistes chinensis [?Scarabaeini] (Krantz &Filipponi 1964), and the OSU Acarology Collection has a specimen of pumiliosternus collected from Pristophilus passaloides [?family].

Table 7. Genera of the Scarabaeidae used as phorionts by species in the *glaber* group.

SUBFAMILY	GEOTRUPINAE			APHODIINAE	CETONINAE	COPRINAE	
TRIBE	Geotrupini					Onthophagini	
GENUS / COMPLEX	*Geotrupes*	*Ceratophyus*	*Enoplotrupes*	*Aphodius*	*Goliathus*	*Onthophagus*	*Phalops*
glaber	X	X		X		X	X
limue				X	X	X	
kraepilini						X	
praedafimetorum	X			X			
friggi							
capensis						X	
transmigrans			X				
scutatus	X		X			X	
paganus							
rhodesi							

Table 7. (continued)

SUBFAMILY	COPRINAE								
TRIBE	Onitini					Coprini			
GENUS	*Allonitis*	*Bubas*	*Chironitis*	*Heteronitis*	*Onitis*	*Sarophorus*	*Heliocopris*	*Catharsius*	*Copris*
COMPLEX									
glaber		X	X	X	X	X	X	X	X
limue	X			X	X		X	X	X
kraepilini					X		X	X	X
praedafimetorum									
friggi	X			X	X		X	X	
capensis					X		X		
transmigrans									
scutatus					X		X	X	X
paganus								X	
rhodesi						X			

Table 7. (continued).

SUBFAMILY	COPRINAE									
TRIBE	Oniticellini			Scarabaeini						
GENUS / COMPLEX	*Oniticellus*	*Helictopleurus*	*Liatongus*	*Allogymnopleurus*	*Garreta*	*Gymnopleurus*	*Pachylomera*	*Scarabaeus*	*Sebastos*	*Sysyphus*
glaber	X		X	X	X			X		X
limue	X		X		X			X		
kraepilini										
praedafimetorum	X									
friggi	X							X		
capensis										
transmigrans		X								
scutatus								X		
paganus							X	X		
rhodesi						X		X	X	X

BIOGEOGRAPHY

The center of diversity for the glaber species group is the Old World Tropics (fig. 21). The Ethiopian Realm is especially rich in species and has a high rate of endemism. Seventeen glaber group species occur in the Ethiopian Realm and 14 of these (82%) are known from nowhere else. These 14 endemic species represent nearly one-half of the species in the glaber group. The Oriental Realm contains 11 species of which 5 (46%) are endemic. Of the ten species complexes in the glaber group, only the praedafimetorum complex does not have representative species in the paleotropics (Table 7).

The praedafimetorum complex is the primitive sister-group of the remainder of the glaber group (see fig. 11B), and it shares many similarities with the matrius species group. Of the nine advanced complexes of the glaber group, only the kraepilini complex is not represented in the Ethiopian Realm. The kraepilini and capensis complexes form a sister-group cluster (see fig. 27 in Phylogeny section). The capensis complex is restricted to the Ethiopian Realm, while the kraepilini complex is distributed across the Oriental, Australasian and Oceanian Realms (fig. 24). This distribution pattern could be explained by a vicarient event separating the capensis and kraepilini complexes, and

the dispersal and speciation of the kraepilini species across southeast Asia and the Pacific. In the kraepilini complex, Macrocheles tantalus, n. sp., is endemic to the Hawaiian Islands and Bruce Halliday (personal commuication) reports that an undescribed species with seven setae on genu IV is endemic to tropical Australia.

Although the paleotropics represent the center of diversity of the glaber group, this does not necessarily mean that the center of origin of the glaber group is also the Old World tropics. The latitudinal gradient in diversity of arthropods is well documented. The primitive species groups (penicilliger, punctoscutatus, matrius, and praedafimetorum) in the lineage that produced the glaber group are broadly temperate in distribution (Evans & Browning 1956). The glaber and scutatus subgroups both have species with broad temperate distributions (figs. 22, 26). An alternative to a paleotropical origin of the glaber group, would be a Palearctic origin with subsequent dispersal (or vicariance) to the tropics. In general, arguments about center of origin have limited heuristic value. This is especially true for the glaber group, since there is essentially no fossil record for Macrocheles.

In the Nearctic, Macrocheles praedafimetorum is endemic to western North America, except for a questionable record from near Lake Baikal in Russia. As

discussed in the text, praedafimetorum is closely related to the matrius species group and is included in the glaber group because it appears to have convergently derived the key characteristics of that group. If we assume, for the sake of argument, that praedafimetorum belongs to the plesiomorphic sister group of glaber, then Nearctic representatives of the glaber group are represented by Macrocheles perglaber, with a broad distribution across the northern United States and southern Canada (fig. 22), two single specimen collections that appear to be Macrocheles glaber from Florida and Mexico, and a single collection of a species that appears to be glaber from Corvallis, Oregon.

Macrocheles jalisciensis was described from Mexico. No response was received to the requests for the type of jalisciensis. However, from the description and accompanying illustration, jalisciensis is probably not a member of the glaber group. The structure of the sternal and epigynial shields, and the dorsal chaetotaxy indicate that jalisciensis is probably a member of the mammifer or muscaedomesticae species group.

The Nearctic glaber fauna, therefore, is represented by the two species most closely associated with man and his domestic animals; viz. glaber and perglaber. It seems probable that glaber has been introduced into North America, and that the glaber group

arose in the Old World. If the jalisciensis type should represent a new species in the glaber group, however, this would tend to falsify the above hypothesis.

The glaber subgroup is the most widely distributed of the three subgroupings. Within the glaber subgroup, the glaber complex is very broadly distributed (fig. 22). The limue complex and the kraepilini complexes are both restricted to the Old World tropics (figs. 24, 25). The limue species are Ethiopian and Oriental, while the kraepilini species are southeast Asian, with a few records from tropical Australia and some Oceanian islands.

The scutatus subgroup is broadly distributed across the Palearctic, Ethiopian, Oriental, and Australian Realms (fig. 26), with endemic species in each realm except the Australian. The Australian Realm record involves a collection of scutatus from a rat (Emberson 1973).

The remaining subgroups have more restricted distributions. The capensis, paganus, rhodesi, (figs. 24, 26) and, to a large extent, friggi (figs. 23) complexes are endemic to subsaharan Africa. Macrocheles nalani, a member of the the friggi complex also occurs in Thailand. The transmigrans subgroup is distributed across southeast Asia and Madagascar (fig. 25).

Table 8. The distribution of the species complexes in the *glaber* group by realm.

COMPLEX	NEARCTIC	PALEARCTIC	ETHIOPIAN	ORIENTAL	AUSTRALASIAN	OCEANIAN
glaber	X	X	X	X	X	X
limue			X	X		
kraepilini				X	X	X
praedafimetorum	X	(X)				
friggi			X	X		
capensis			X			
transmigrans			X	X		
scutatus		X	X	X	X	
paganus			X			
rhodesi			X			

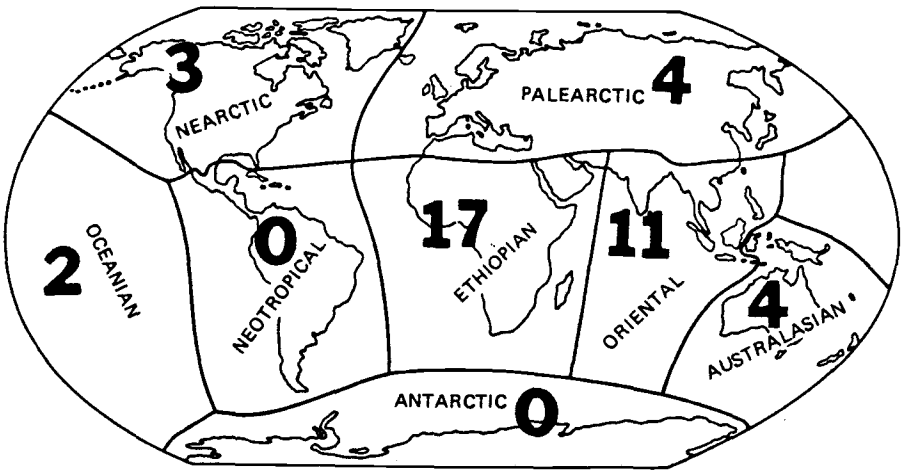


Figure 21. The number of species in the Macrocheles glaber group in each biogeographic realm.

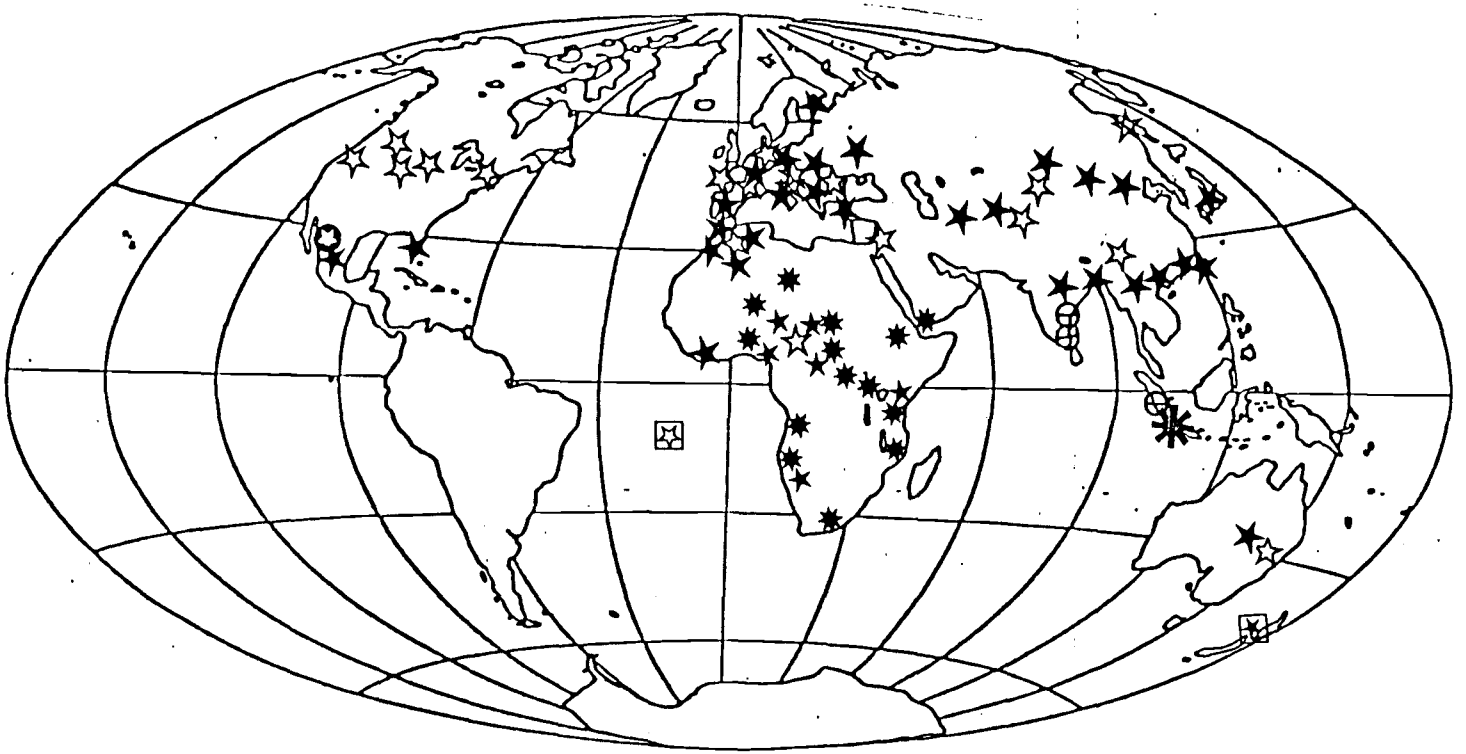


Figure 22. The world distribution of the glaber species complex.

glaber ★
caligynus ✱
perglaber ☆
jalisciensis ✪
peregrinus ✸
medialis ★
hyatti ⊠
helenaensis ⊠
oigru ⊖

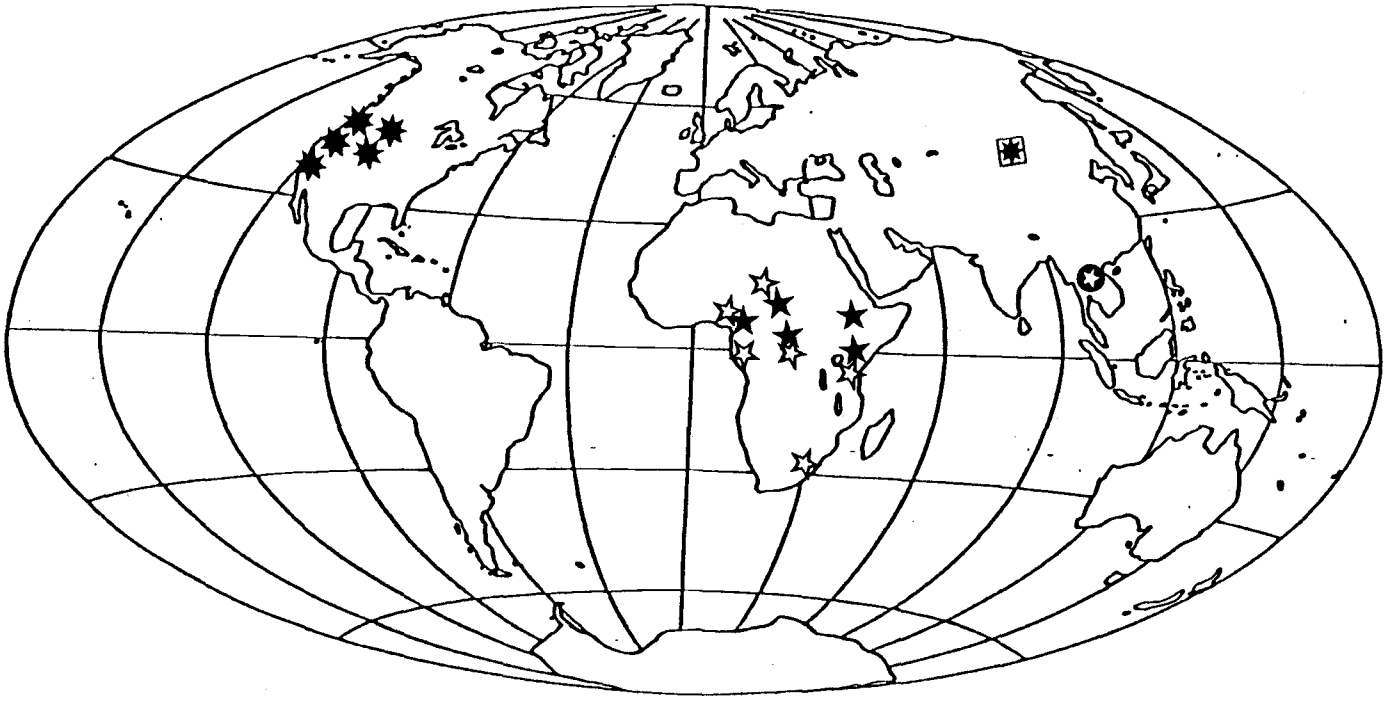


Figure 23. The world distribution of the *friggi* and *praedafimetorum* complexes.

FRIGGI COMPLEX	*PRAEDAFIMETORUM* COMPLEX
friggi ★	*praedafimetorum* ✸
pumiliosternus ☆	? new species ✱
nalani ✪	

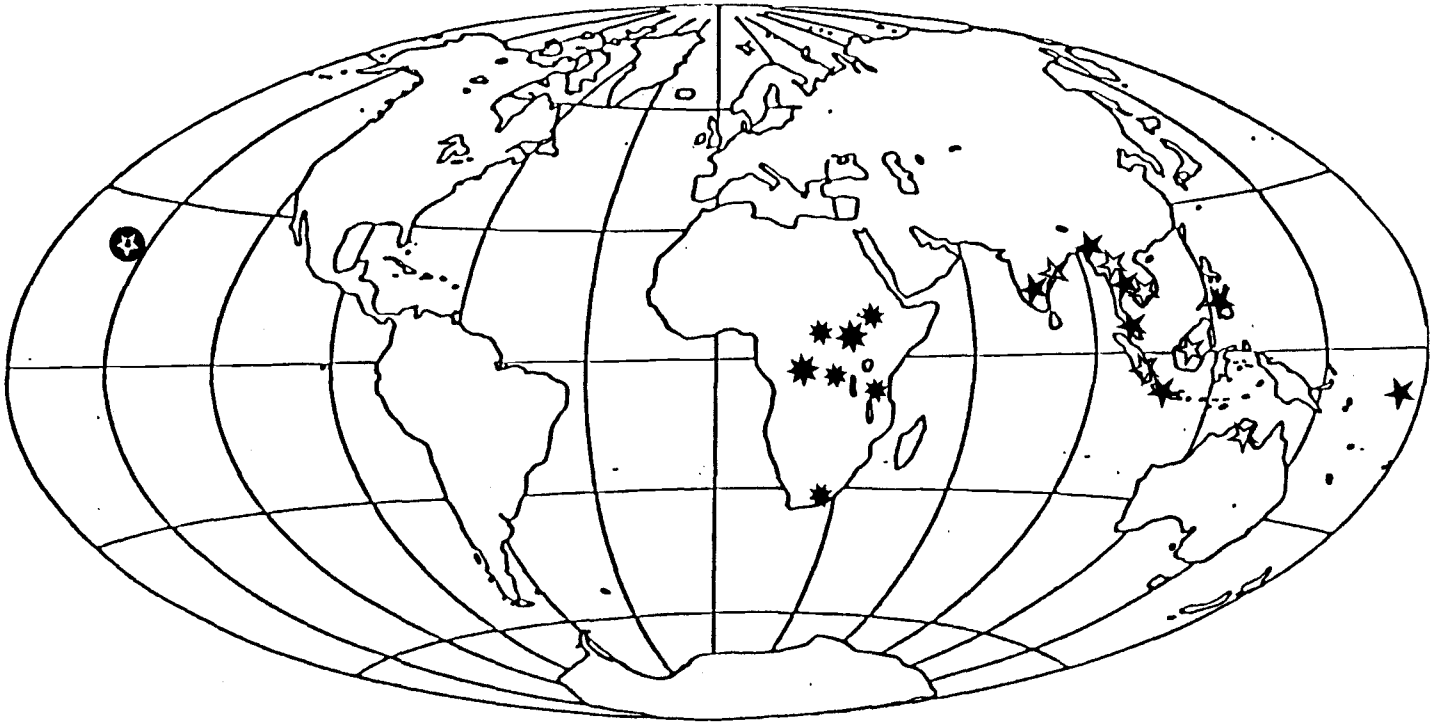


Figure 24.

The world distribution of the kraepilini and capensis complexes.

Kraepilini Complex	Capensis Complex
kraepilini ✦	capensis ✸
tantalus ✪	macroscatophilus ✸
hallidayi ☆	

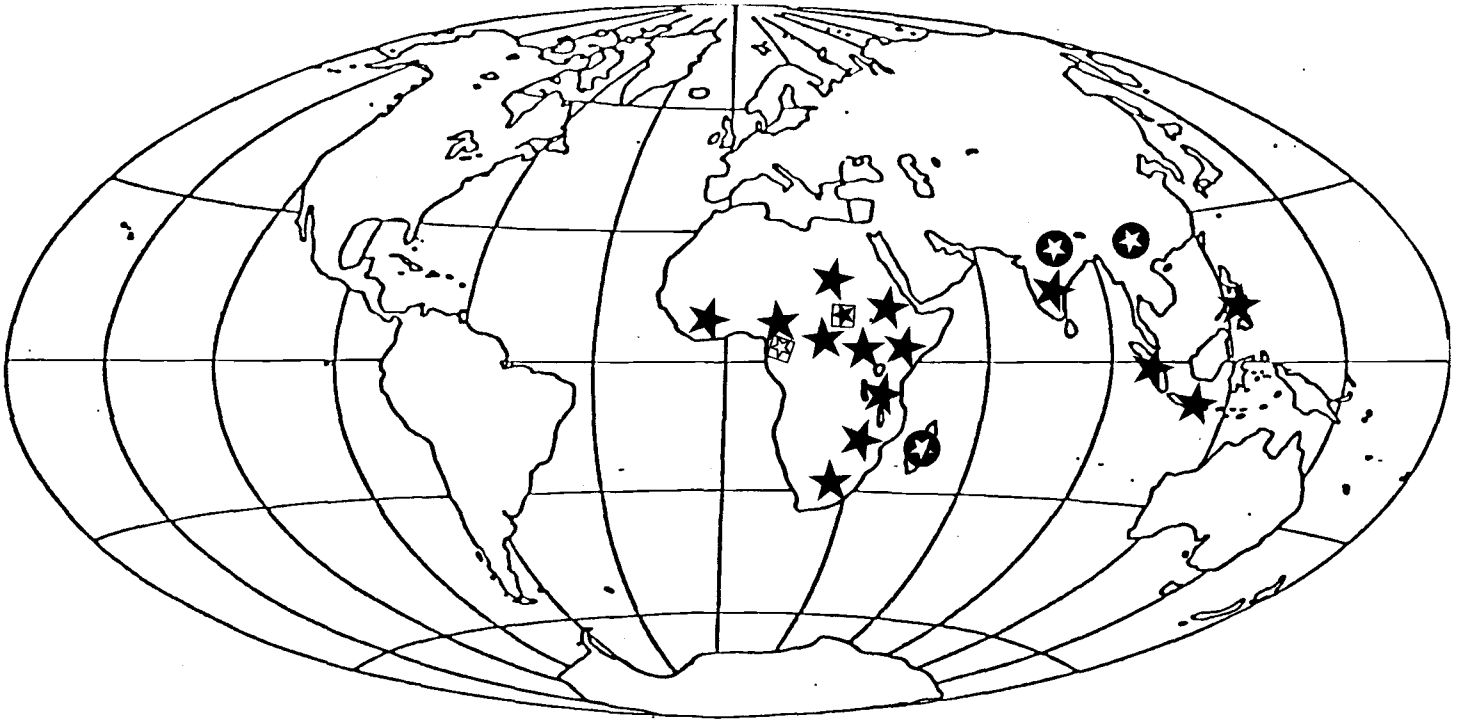


Figure 25. The world distribution of the limue and transmigrans complexes.

LIMUE COMPLEX

limue ★
caelatus ⊠
witcoskianus ⊠

TRANSMIGRANS COMPLEX

transmigrans ✪

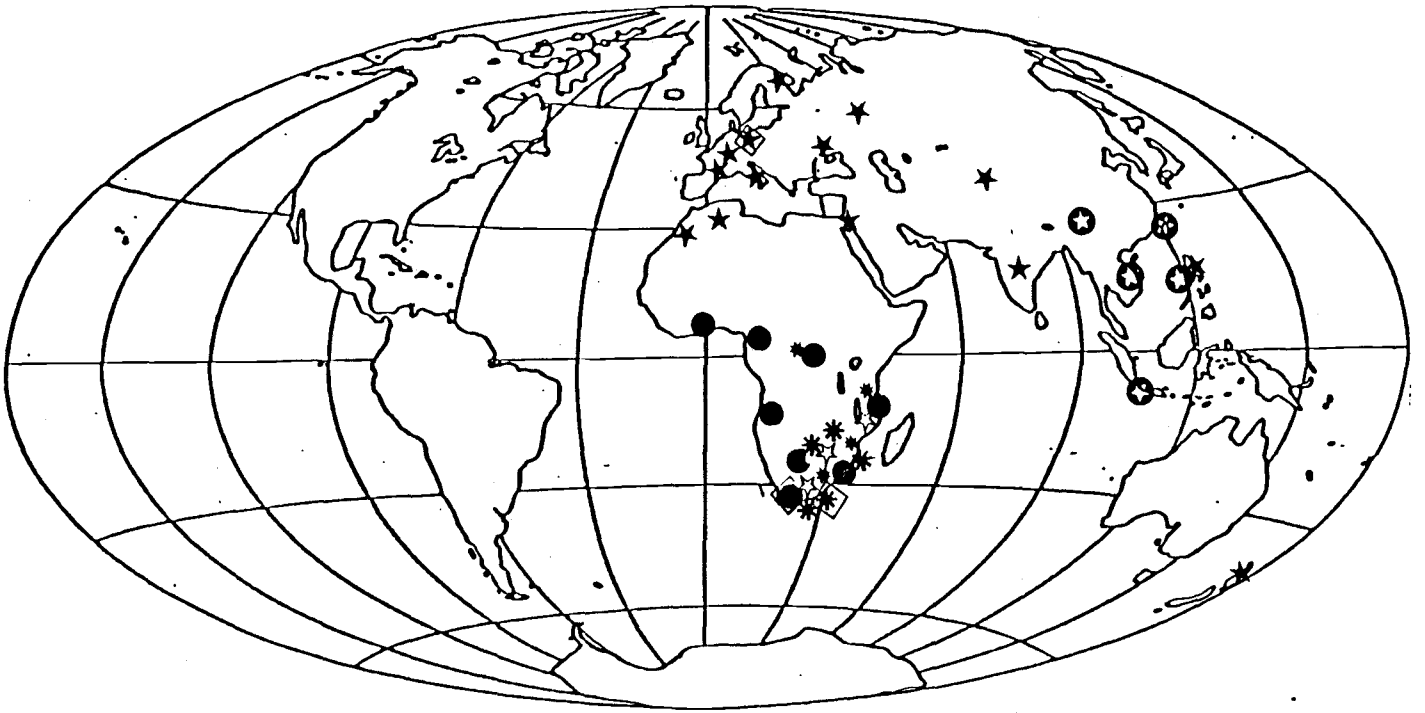


Figure 26. The world distribution of the scutatus, paganus and rhodesi complexes.

SCUTATUS COMPLEX
- scutatus ★
- neoscutatus ◈
- subscutatus ☆
- neovernalis ✸
- dispar ✪

PAGANUS COMPLEX
- paganus ●
- agnosticus ◆

RHODESI COMPLEX
- rhodesi ✱
- natalensis ❋

PHYLOGENY

Cladistic Analysis

Krantz (1981) listed 16 morphological characters that were characteristic of females in the glaber group. Fifteen of these characters occur outside of the glaber group, and are therefore plesiomorphies and cannot be used to define the glaber group. The bifurcate linea oblique posteriores is diagnostic for most species in the glaber and praedafimetorum subgroups, however, it is absent in eight of the ten species in the scutatus subgroup.

The outgroup analysis (fig.11) indicated that the species of Macrocheles which were delegated to the glaber group (*sensu* Krantz) represented several clusters of species that were intermediate in character between the generally free living species in Macrocheles and the derived higher phoretic Macrocheles.

The free-living Macrocheles that precede glaber in the cladogram in Figure 11A have similar ecologies, but fall into two morphological groupings. Species such as mammifer and penicilliger have smooth clunal setae and slender chelicerae which lack the bidentate tooth (fig. 10, 27). The species such as punctoscutatus and matrius have derived the serrate clunal setae and bidentate cheliceral tooth characteristic of the remainder of the

genus, but have retained the free living habit, association with vertebrate nests, cribrum with perianal extensions, and ornate, bushy-plumose dorsal setae (fig. 15F) of the less derived species of Macrocheles.

The a priori assumption of this analysis has been that the ancestor of the glaber group was a free-living, heavily sclerotized mite associated with a concentrated organic substrate, such as dung, which would have attracted scarab beetles. Macrocheles matrius is intermediate in both morphology and ecology between the free-living species of Macrocheles and the members of the glaber group. Macrocheles matrius matrius is often collected in litter and vertebrate nests as well as in manure, and may be phoretic on dung beetles (Bregetova and Koroleva 1960). The sternal shield of matrius approaches the glaber level of organization (fig. 12C).

Macrocheles praedafimetorum also represents a transitional element between the free-living vertebrate associates and the coprophilous scarab associates in the glaber group. The majority of collections of members of the praedafimetorum complex in the OSU Acarology Collection are from litter habitats or vertebrate nests (see Appendix I). A few specimens have been collected as phoretics on beetles, primarily carrion beetles (Nicrophorus), and generalized geotrupine and aphodiine dung beetles. The morphology of the dorsal and ventral

shields of praedafimetorum also is very similar to that of undescribed species in the matrius complex from North America in the OSU Acarology Collection. Finally, the subcordate ventrianal shield that is fused to the sternitigenital shield of the male in praedafimetorum is the apomorphous condition in the punctoscutatus-matrius species groups. The outgroup PAUP analysis of the glaber complexes (fig. 11) places the praedafimetorum complex between matrius and glaber.

Members of the glaber subgroup are somewhat less strongly sclerotized than praedafimetorum, more restricted to dung habitats, and phoretic on a broad variety of dung beetles in the Geotrupinae, Aphodiinae, and Coprinae. Within the glaber subgroup, the species near glaber in southeast Asia (including caligynus and glaber tsaii fig. 13B, J) have reduced sclerotization and obsolescent ornamentation of the sternal shield. The species of the friggi complex (fig. 16) are also reduced in sclerotization and ornamentation of the sternal shield. These species retain the open linea angulata and the deep punctae of the linea angulata and linea arcuata characteristic of the glaber subgroup. In addition, the friggi complex has a unique reduction of the sternal shield anterior to the linea media transversa.

In contrast to this, the members of the scutatus subgroup do not retain the deep median sternal punctae, and have similar fading of the linea arcuata, linea angulata, linea oblique posteriores, areae punctatae, and area punctiformes (figs. 18, 19, 20). The palearctic members of the scutatus complex (scutatus and neoscutatus) retain more sternal ornamentation than the remaining species in the scutatus subgroup (compare fig. 19A, B to 19C, D, F and 20A, C-E). Macrocheles dispar and neovernalis resemble scutatus in general aspect, while having extreme reduction of the sternal ornamentation similar to the paganus-rhodesi cluster. When these species were included in the cladistic analysis as a separate complex, they could not be resolved, since they lack the derived apomorphies of the paganus-rhodesi cluster or the transmigrans complex. I believe that they represent species related to scutatus that have undergone reduction in sternal ornamentation independent of the more advanced complexes in the scutatus subgroup and, therefore, they have been retained as species in the scutatus complex. Some possible patterns of reduction in sternal shield ornamentation are presented in Figure 28.

The final cladistic analysis is based on changes in 16 morphological characters, two distributional characters, and two behavioral characters (Table 9).

The character states were polarized using Macrocheles matrius as the outgroup, following the Watrous & Wheeler (1981) proceedure. All of the characters were analyzed as ordered transformation series. The resulting cladogram (fig. 29A) supports the construction of three monophyletic subgroupings of the glaber group. It must be remembered, however, that the original outgroup analysis (fig. 11A) indicates that some of the more derived species groups in the genus Macrocheles are part of the same lineage as the scutatus subgroup, and therefore the glaber group *sensu latu* is paraphyletic. Until the revision of the genus Macrocheles has been completed (Krantz & Walter, in progress), I do not wish to split-out an excessive number of very similar species groups (praedafimetorum, scutatus, paganus-rhodesi and transmigrans would all be elevated to the species group level). It is quite possible that different characters may resolve the higher phoretic Macrocheles into several distinct lineages.

The kraepilini and capensis complexes are similar sister-groups. The areae punctatae tend to be produced as a single circular depression (figs. 15B, 17D), rather than as a pair of partially contiguous depressions (figs. 1, 6). More strikingly, but less importantly, both have species which have enlarged and strongly bipectinate dorsal setae and inflated plumose vertical

setae. This setal condition has been evolved numerous times in unrelated species of Macrocheles, for example in the transmigrans complex and in several species of the dimidiatus species group.

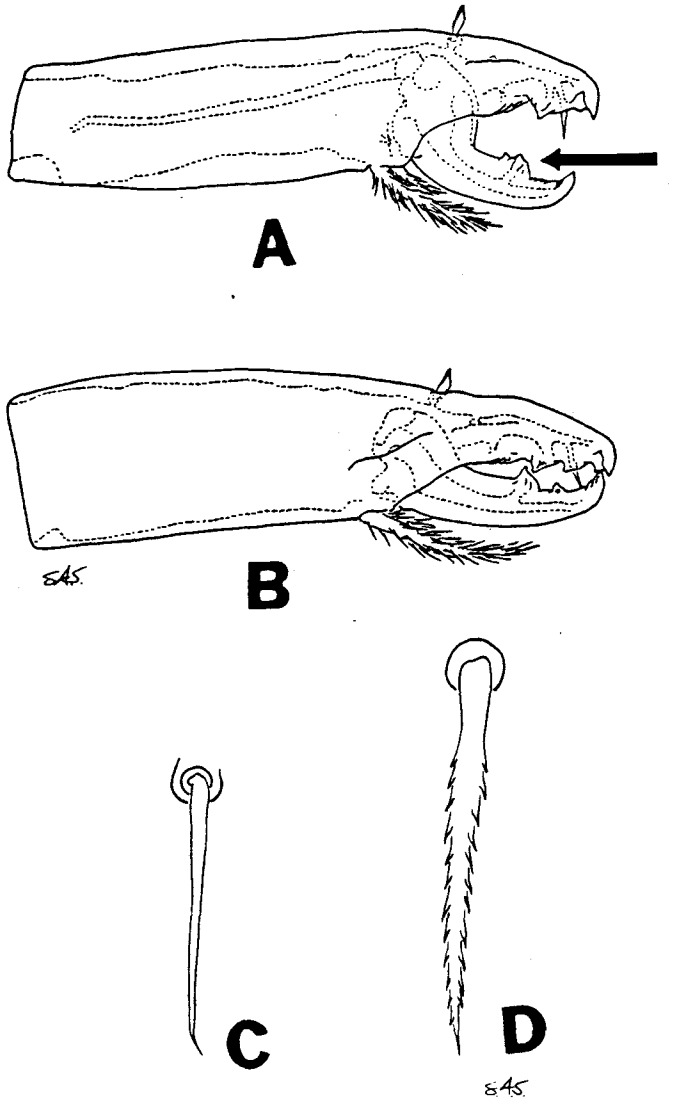


Figure 27. The chelicerae and clunal setae. (A) Macrocheles perglaber with the bidentate tooth (arrow) of the phoretic Macrochelidae, (B) M. mammifer, a free-living macrochelid without a bidentate tooth, (C) clunal seta of mammifer, (D) clunal seta of perglaber.

Figure 28. Phylogenetic trends in the sternal shield. A suggested sequence for the reduction of ornamentation of the sternal shields in the glaber group. Sternal setae are not shown.

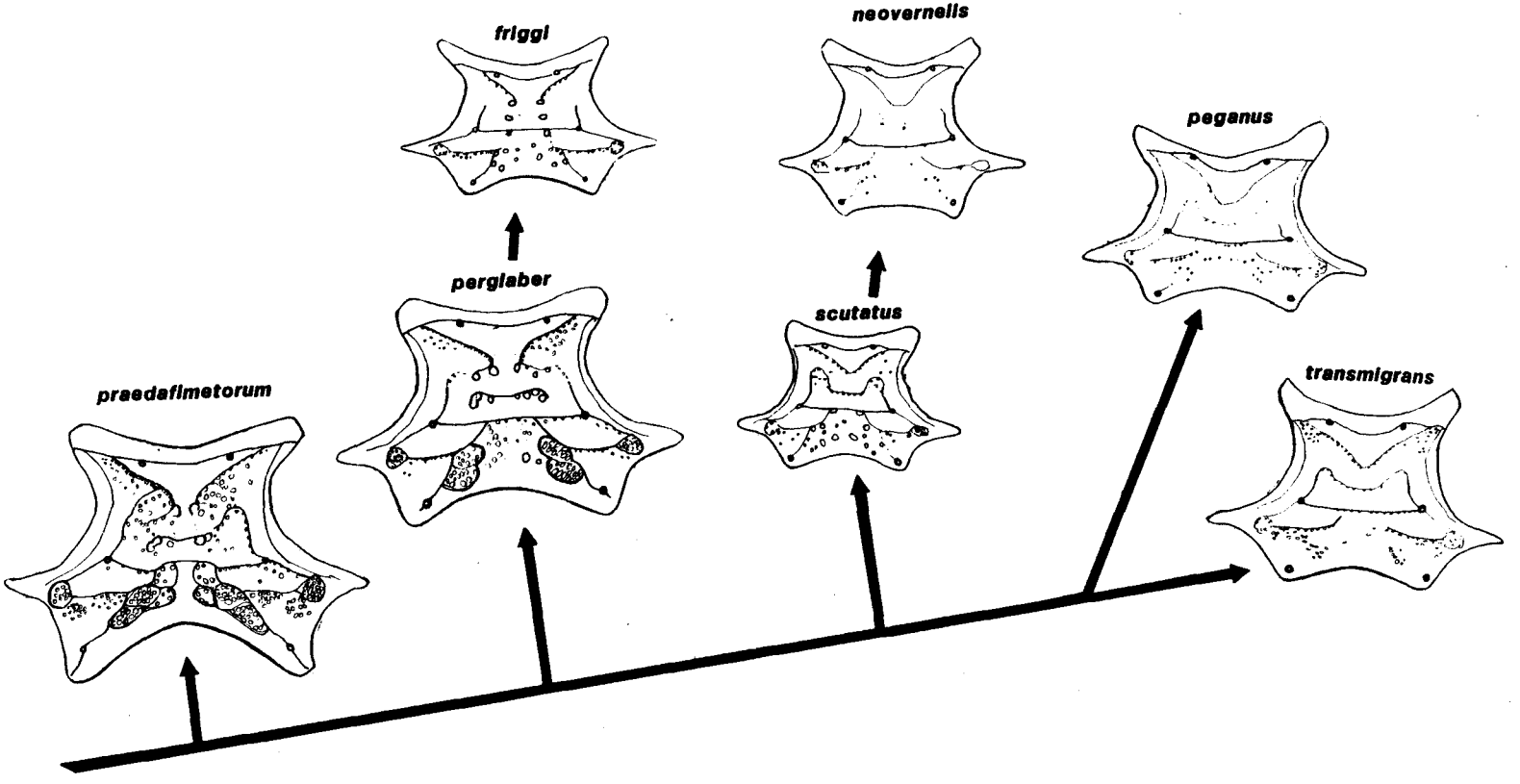

friggi
neovernelis
peganus
perglaber
scutatus
transmigrans
praedafimetorum

Figure 28

Table 9. The characters used in the cladistic analysis of the relationships of the species complexes in the glaber group (fig. 29). Character state changes were polarized using Macrocheles matrius Hull.

CHARACTER	PRIMITIVE	DERIVED
1. male ventri-anal shield	fused	free
2. area punctiformes	acinous	punctate, fading
3. area punctatae	acinous	fading
4. area punctatae	not depressed	depressed
5. linea angulata	closed	open
6. linea arcuata	not areolate	areolate
7. linea oblique posteriores	not distinct	distinct, fading
8. linea oblique posteriores	no ramus	bifurcate, fading
9. epigynial shield	ornamented	reduced
10. ventrianal shape	broadly cordate	rounded, subcordate, angular
11. ventrianal ornamentation	coarse lines	dimpled, reduced
12. sternal length/width	length>width	length reduced
13. sternal setae	not enlarged	enlarged
14. sternal arch	developed	not developed

(Table 9. continued)

15. dorsal shield	broad posteriorly	narrowed
16. dorsal setae	not bipectinate	bipectinate
17. phoretic	not commonly	typically
18. Scarabaeini	not used as phorionts	sometimes, exclusively
19. Temperate distribution	yes	no
20. Tropical distribution	no	Ethiopian, Oriental or both

Experimental Taxonomy

The experimental taxonomic approach to Macrocheles pioneered by Filipponi (Filipponi 1959, 1964, Filipponi & Pegazzano 1962) has been of special importance in clarifying the taxonomy of macrochelid mites. The demonstration of sympatry in sibling species with morphologically similar females has led to an increased emphasis on culturing these forms. Cultures have provided information on life cycles and ecology as well as allowing for the production of large series for documentation of morphological variation. Generation of normally unavailable males and immatures in culture provides an important and oftentimes necessary source for characters useful for sibling species discrimination.

The theoretical basis for the experimental taxonomic approach is the concept of the biological species. However, the idea that there is a single, monolithic species concept, into which all sexually reproducing species will naturally fall, has retreated since Filipponi pioneered experimental crossings among species of Macrocheles. Similarly, the intense investigations of Drosophila, with over 2,000 species worldwide, have demonstrated that reproductive isolation may follow or precede adaptive divergence and that,

although there are many good biological species, there are also many superspecies or semispecies complexes (Dobzhansky 1972). Indeed, in Drosophila, distinct species have been demonstrated to maintain natural hybrid populations, and to exchange genetic material while remaining good species (Carson *et al.* 1975).

According to the experimental taxonomic approach, species isolation is considered absolute only if mating with congeners will not take place, or if fertile offspring cannot be produced. If crossing does takes place and the resulting offspring are fertile, then the populations in question may be either the same species, or different species which are genetically compatible, but whose isolating mechanisms either do not exist, or have broken down under the conditions of the culture.

Populations of Macrocheles 'perglaber' from cow pastures in Corvallis, Benton County, Oregon (moist, moderate temperature climate) were cultured and crossed with cultures of 'perglaber' collected on pine-sagebrush cattle ranges in Klamath County, Oregon (dry, extreme temperature variation). Males from both populations vigorously courted and mated with females from the other population, and a hybrid culture was maintained for several generations.

Cultures of the arrhenotokous Macrocheles glaber and perglaber derived from collections in Montpellier,

France were obtained from Dr. R.B. Halliday at Canberra, Australia. Halliday has successfully crossed the Australian '*perglaber*' with the Montpellier strain. I have had problems with fungal contaminants overrunning the Montpellier cultures, resulting in low population numbers. I have, however, placed seven female deutonymphs from the Klamath culture with seven males from Montpellier in individual culture. One female died but the remaining six females all produced numerous female offspring indicating that mating had taken place. Nine of the F1 females from two individual cultures were backcrossed to Montpellier males, and successfully produced offspring, indicating that the Oregon *perglaber* is, within the limits of the experimental taxonomic approach, acting as the same species as the European and Australian *perglaber*.

As mentioned in the text, I have not been able to collect live *glaber* in Oregon.

Evolutionary Trends

A number of generalized patterns summarize the broad evolutionary trends in the *glaber* species group. The most widely distributed species are in the plesiomorphic groups. Collections of *Macrocheles matrius matrius* that are morphologically

indistinguishable are known from the Holarctic and Australia. Macrocheles glaber and perglaber also are present in these reagions as well as in the Ethiopian and Oriental Realms. Macrocheles scutatus has been collected from the Palearctic, Oriental and Australian Realms. Each of these species is closely associated with the manure of farm animals. Thus perhaps the most noteworthy evolutionary trend in the glaber group is a tendency to achieve a broad distribution through association with man. The introduction of Macrocheles peregrinus into Australia in the last decade as a biological control agent for synanthropic flies is a less stochastic example of the selective advantages that species in the glaber group accrue by association with man.

The trend in the glaber group from free-living or vertebrate nest associates to primarily dung-inhabiting species is correlated with certain morphological and behavioral changes. Members of the plesiomorphic praedafimetorum complex are heavily sclerotized with broad dorsal and ventral shields covered with strong ridges and deep punctae, and are rarely phoretic on beetles . The intermediate complexes in the glaber subgroup have somewhat reduced sclerotization and smaller shields, and are indiscriminately phoretic on a broad spectrum of beetles. The scutatus subgroup has

reductions in the size and the degree of sclerotization of the shields. The more reduced complexes, also tend to be more restricted in their choice of phorionts. Members of the paganus-rhodesi cluster are primarily phoretic on members of the Scarabaeini.

The ornamentation of the dorsal setae does not follow any clear evolutionary trend. The bushy-plumose setae characteristic of free-living species are lost in phoretic species, and some trend toward smooth acicular setae is apparent. However, except for the glaber and rhodesi complexes, each of the other complexes has at least one species with highly ornamented dorsal setae, or at least a profusion of pilose setae. Three of the complexes are characterized by enlarged and strongly bipectinate setae (transmigrans, capensis, and kraepilini).

Of course, all of the a priori assumptions about evolutionary reduction of sclerotization and ornamentation, could be wrong. If one assumes that, in fact, the evolutionary trend has been from a poorly sclerotized, phoretic, tropical species to a heavily sclerotized, free-living, temperate species then a cladogram such as Figure 29B can be generated. In this cladogram the most derived complex, transmigrans, has been used as the outgroup. The results are not radically different from Figure 29A. The glaber

subgroup is still a monophyletic assemblage, however, it forms a sister-group cluster with a combined *matrius-praedafimetorum* subgroup. The *scutatus* and *paganus-rhodesi* complexes form groups of equal rank.

Figure 29. The PAUP ingroup cladistic analysis of the species complexes in the glaber group. Rooted (A) using Macrocheles matrius as the designated outgroup, and (B) using M. transmigrans as the designated outgroup; Both cladograms were generated using Farris optimization, Closest addition sequence, and the unweighted characters in Table 9. Both trees had length = 48, consistency index = .708.

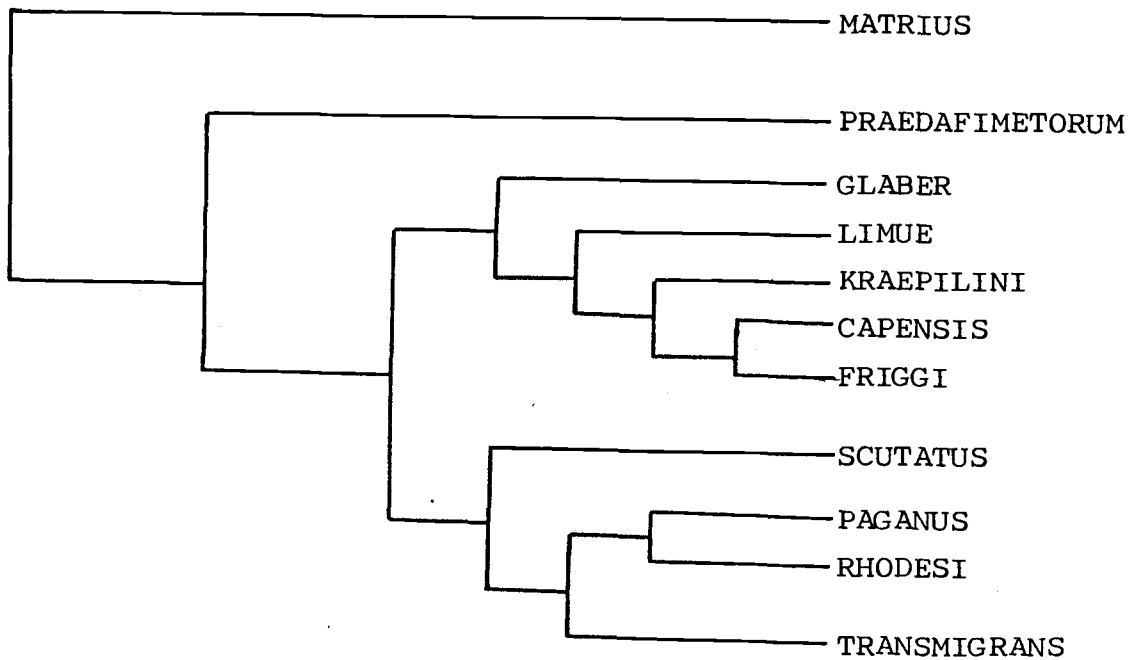

MATRIUS
PRAEDAFIMETORUM
GLABER
LIMUE
KRAEPILINI
CAPENSIS
FRIGGI
SCUTATUS
PAGANUS
RHODESI
TRANSMIGRANS

Figure 29 A.

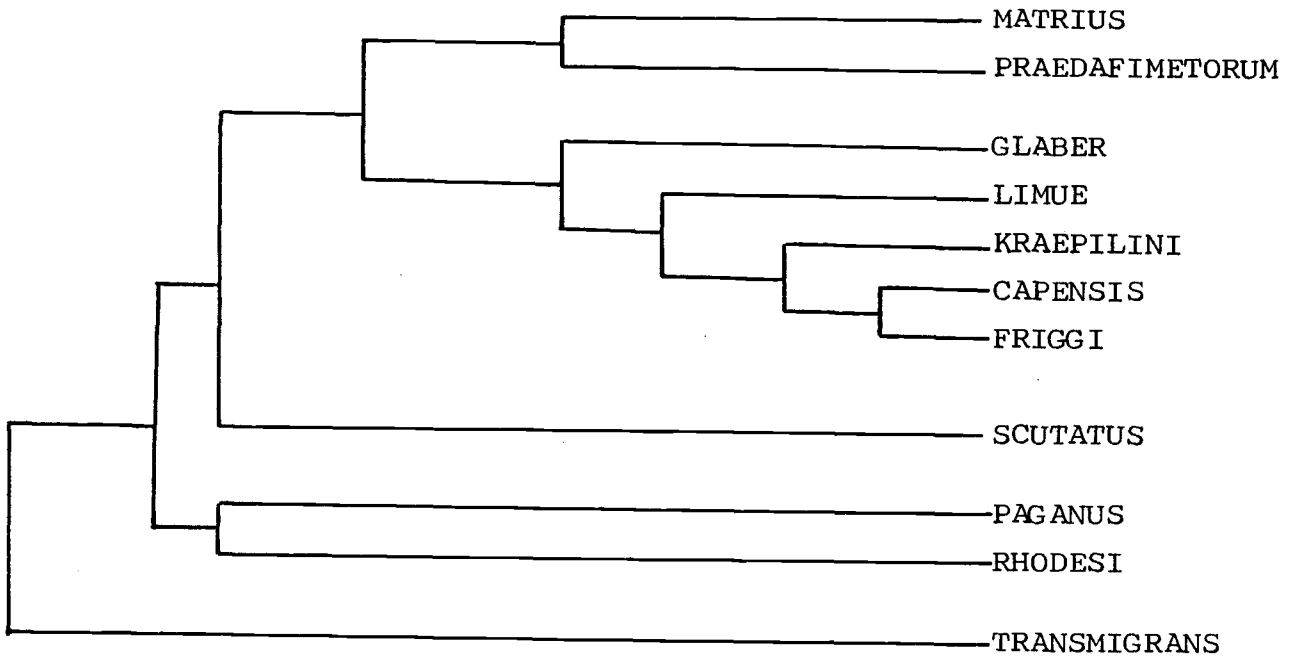

MATRIUS
PRAEDAFIMETORUM
GLABER
LIMUE
KRAEPILINI
CAPENSIS
FRIGGI
SCUTATUS
PAGANUS
RHODESI
TRANSMIGRANS

Figure 29 B.

BIBLIOGRAPHY

Alberch, Pere 1980. Ontogenesis and morphological diversification. Amer. Zool. 20: 653-667.

Alberch, P., S.J. Gould, G.F. Oster, and D.B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5: 296-317.

Axtell, R.C. 1962. Macrochelidae (Acari: Mesostigmata) inhabiting manure and their effect on house fly production. Ph.D. Thesis, Cornell University, Ithaca, New York, 151 pp.

Axtell, Richard C. 1963. Acarina occurring in domestic animal manure. Ann. Ent. Soc. Amer. 56: 628-633.

Axtell, R.C. 1969. Macrochelidae (Acarina:Mesostigmata) as biological control agents for synanthropic flies. W.H.O./VBC/69.119, 17pp.

Berlese, A. (1889). Acari, myriapoda et scorpiones hucusque in Italia reperta. Padova 52(1),(6).

Berlese A. (1904). Acari nuovi. Manipulus II. Redia 1:258-280.

Berlese, A. (1905). Acari nuovi. Redia 2: 154-176.

Berlese, A. (1908). Elenco di generi e species nuove di Acari. Redia 5: 1-15.

Berlese, A. (1910). Liste di nuove species e nuovi generi di Acari. Redia 6: 242-271.

Berlese, A. (1918). Centuria quarta di acari nuovi. Redia 13: 115-192.

Bregetova, N. (1977). Macrochelidae. pp.346-411 In: Mesostigmata. M. C. Gilarova and N. G. Bregetova (eds.). Leningrad.

Bregetova, N.G. and E.G. Koroleva. (1960). The macrochelid mites (Gamasoidea, Macrochelidae) in the USSR. Sborn. Akad. Nauk SSSR Zool. Inst. 19: 32-154.

Carson, H.L., P.S. Nair and F.M. Sene. (1975). Drosophila hybrids in nature: Proof of gene exchange between sympatric species. Science 189: 806-807.

Cicolani, B. (1979a). The intrinsic rate of natural increase in dung macrochelid mites, predators of Musca domestica eggs. Boll. Zool. 46:171-178.

Cicolani, B. (1979b). Osservazioni faunistiche ed ecologiche sughi Acari coprobionti il genere Macrocheles Latr. (Mesostigmata) in Abruzzo. Biologia Contemporanea 6: 116-126.

Cicolani, B., A.P. Bianchi Bullini and L. Bullini. (1981). Morphological and genetic differentiation between Macrocheles glaber and Macrocheles perglaber (Acarina:Macrochelidae). Internat. J. Acarol. 7:221-224.

Coons, L.B. and R.C. Axtell. (1973). Sensory setae of the first tarsi and palps of the mite Macrocheles muscaedomesticae. Ann. Ent. Soc. Amer. 66: 539-544.

Costa, M. (1967). Notes on macrochelids associated with manure and coprid beetles in Israel. II. Three new species of the Macrocheles pisentii complex, with notes on their biology. Acarologia 9(2): 304-329.

Costa, M. (1974). A note on mites associated with Heliocopris japetus Klug from Kenya. Entomol. Mitt. Zool. Mus. Hamburg 4 Band. Nr. 86 : 481-497.

Costa, M. (1975). Further notes on mites associated with Heliocopris japetus Klug from Kenya. Mitt. Hamburg Zool. Mus. Inst. 72: 119-136.

Delfinado, M.D. and E.W. Baker. (1975). Mites (Acarina) associated with Popilius disjunctus (Illiger) (Coleoptera:Passalidae) in the Eastern United States. J. N.Y. Ent. Soc. 83: 49-59.

Dobzhansky, T. (1972). Species of Drosophila. Science 177: 644-669.

Eldredge, N. and J. Cracraft. (1980). Phylogenetic patterns and the evolutionary process. Columbia University Press, New York, 349pp. .

Emberson, R. M. (1973). Macrochelid mites in New Zealand (Acarina :Mesostigmata:Macrochelidae). New Zealand Entomol 5(2): 118-127.

Emberson, R.M. (1973). Additions to the macrochelid mites in New Zealand (Acarina:Mesostigmata:Macrochelidae). : 294-302.

Evans, G.O. (1963). Observations on the chaetotaxy of the legs in free-living Gamasina (Acari: Mesostigmata). Bull. Brit. Mus. (Nat. Hist.), Zool. 10: 513-527.

Evans, G.O. and E. Browning. (1956). British mites of the subfamily Macrochelinae Tragardh (Gamasina-Macrochelidae). Bull. British Mus. (Nat. Hist.) Zool. 4(1): 55pp.+ plates.

Evans, G.O. and K.H. Hyatt. (1963). Mites of the genus Macrocheles Latr. (Mesostigmata) associated with coprid beetles in the collections of the British Museum (Natural History). Bull. British Mus. (Nat. Hist.) Zool. 9(9): 325-401.

Falconer, W. 1923. Two British mites new to science and a new subgenus of Macrocheles Latr. Naturalist, Lond. : 151-153.

Farish, D.J. (1965). Some aspects of the sensory and phoretic behavior of Macrocheles muscaedomesticae (Scopoli, 1772) (Acarina:Mesostigmata) with a consideration of phoresy as a phenomenon. Ph. D. thesis, Raleigh, N.C.

Farish, D.J. and R.C. Axtell. (1966). Sensory functions of the palps and first tarsi of Macrocheles muscaedomesticae (Acari:Macrochelidae), a predator of the house fly. Ann. Ent. Soc. Amer. 59: 165-170.

Filipponi, A. (1959). Due specie riproduttivamente isolate sotto il nome di Macrocheles glaber

(Muller) (Acarina:Macrochelidae). Riv. Parassit. 20: 199-212.

Filipponi, A. (1964). Experimental taxonomy applied to the Macrochelidae (Acari:Mesostigmata). Acarologia h.s. (1st Int. Congr.) 6: 92-100.

Filipponi, A. and F. Pegazzano. (1960). Acari del genera Glyptholaspis nom. nov. pro Macrocheles (Macrocheles) Berl. 1918 (Mesostigmata, Macrochelidae). Redia 45: 133-171.

Filipponi, A. and F. Pegazzano. (1962). Specie italiane del gruppo-glaber (Acarina, Mesostigmata, Macrochelidae, Macrocheles). Redia 47: 211-238.

Filipponi, A. and F. Pegazzano. (1963). Specie italiane del gruppo-subbadius (Acarina, Mesostigmata, Macrochelidae). Redia 48: 69-91.

Gosliner, T.M. and M.T. Ghiselin. 1984. Parallel evolution in opisthobranch gastropods and its implications for phylogenetic methodology. Syst. Zool. 33: 255-274.

Ghilyarov, M.S. and N.G. Bregetova (Eds.). (1977). Family Macrochelidae Vitzthum 1930. *In* A key to the soil-inhabiting mites, Mesostigmata. Akad. Nauk SSSR, Zool. Inst., Leningrad: 346-411.

Halliday, R.B. (1982). Taxonomic background to the use of macrochelid mites in the dung beetle program. The biological control of dung in Australia. A.M.R.C. Workshop, Canberra.

Halliday, R.B. (1983). Taxonomy and biology of macrochelid mites. Progress Report , Aust. Meat Res. Council

Halliday, R.B. (1984). Taxonomy and biology of macrochelid mites. Prog. Rep. Suppl. January.

Hull, J.E. (1925). Acari of the family Gamasidae : new and rare British species. Ann. & Mag. Nat. Hist. pp. 201-219, plates XVI-XIX.

Johnston, D.E. (1970). Notes on a collection of Australian Macrochelidae with the description

of Macrocheles beieri, n. sp. . Ann. Naturhistor. Mus. Wien 74: 145-150.

Junk, W. (ed.) (1912). Coleopterorum catalogus. Berlin.

Koyumdjieva, M.I. (1981). Gamasid mites (Gamasoidea, Parasitiformes) associated with scarabaeid beetles (Coleptera, Scarabaeidae) in Bulgaria. Acta Zool. Bulg. 17: 17-26.

Krantz, G.W. (1962). A review of the genera of the family Macrochelidae Vitzthum 1930 (Acarina:Mesostigmata). Acarologia 4(2): 143-173.

Krantz, G.W. (1965). A new species of Macrocheles (Acarina:Macrochelidae) associated with bark beetles of the genera Ips and Dendroctonus. J. Kansas Entomol. Soc. 38(2): 145-153.

Krantz, G.W. (1972). Macrochelidae from Hamburg (Acari:Mesostigmata), with descriptions of two new species. Entomol. Mitteilungen 78: 263-274.

Krantz, G.W. (1978). A manual of acarology. Second Ed., Oregon State Univ. Bookstore: 509pp. + viii.

Krantz, G.W. (1981a). Two new glaber group species of Macrocheles (Acari:Macrochelidae) from southern Africa. Int. J. Acarol. 7: 3-16.

Krantz, G.W. (1981b). A review of mites of the genus Macrocheles Latreille 1829 (Acari:Gamasida:Macrochelidae). Proposal to Nat. Science Found., Systematic Biology, 64pp.

Krantz, G.W. (1983). Mites as biological control agents of dung-breeding flies, with special reference to the Macrochelidae. *In:* Biological control of pests by mites. M.A. Hoy, G.L. Cunningham, and L. Knutson (eds.). University of California Special Publication 3304: 91-98.

Krantz, G.W. and A. Filipponi. (1964). Acari della famiglia Macrochelidae (Mesostigmata) nella collezione del South Australian Museum. Riv. Parassitol. 25(1): 35-54.

Krantz, G.W. and J.L. Mellott. (1968). Two new species of Macrocheles (Acarina:Macrochelidae) from Florida, with notes on their host-specific relationships with geotrupine beetles (Scarabaeidae:Geotrupinae). J. Kansas Ent. Soc. 41(1): 48-56.

Krantz, G.W. and J.L. Mellott. (1972). Studies on phoretic specificity in Macrocheles mycotrupetes and M. peltotrupetes Krantz and Mellott (Acari: Macrochelidae), associates of geotrupine Scarabaeidae. Acarologia 14(3): 317-344.

Krantz, G.W. and W. Redmond. *In press*

Krantz, G.W. and J.G. Wernz. (1979). Sperm transfer in Glyptholaspis americana. Rec. Adv. Acarol. 2: 441-446.

Krauss, W. (1970). Die europaischen Arten der Gattungen Macrocheles Latreille 1829 und Geholaspis Berlese 1918. Acarologie, Schrift. Vergleich. Milbenkunde (Furth/Bayern) 14: 60pp. + plates.

Lindquist, E.E. and G.O. Evans (1965). Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina:Mesostigmata). Mem. Ent. Soc. Canada 47: 64pp..

Machado-Allison, C.E. (1964). Tres nuevos acaros (Mesostigmata) entomofilos de Mexico (Diplogyniidae y Macrochelidae). Ciencia Mex. 23(4): 152-158.

Macqueen, A. and B.P. Beirne. (1974). Insects and mites associated with fresh cattle dung in the southern Interior of British Columbia. J. ent. Soc. Br. Columb. 71: 5-9.

Mayr, E. (1969). Principles of systematic zoology. McGraw-Hill Book Company, New York, 428pp. .

Mendez Olivo, C. (1968). Notas sobre Macrocheles de Mexico (Acari:Macrochelidae). Ann. Esc. Nac. Cienc. Biol. Mex. 15: 135-183.

Muller, J. (1860). K.K. mahr. Schles. Ges. Bunn: 178.

Norton, R.A. (1973). Macrocheles ontariensis n. sp., a new mite (Acarina: Macrochelidae) from freshwater beach debris in New York. J. Kan. Ent. Soc. 46: 101-107.

Oudemans, A.C. (1928). Fauna Buruana. Acari. Treubia 7, Suppl. 37-43.

Petrova, A.D. (1960). Materialien uber den Bau des inneren Sackchens des Receptaculum seminis der gamasoiden Milben Macrochelidae Vitzt. pp. 393-400.

Petrova, A.D. (1964). The part played by synanthropic flies in the spread of Macrochelidae Vitzt. Med. Parazit. Bolezn. 5: 553-557.

Petrova, A.D. (1967). New species of mites of the family Macrochelidae Vitz., 1930. Zool. Jour. 46(7): 1037-1047. (in Russian).

Petrova, A.D. (1979). On a special feature of Malpighian tubules function in the macrochelid mite Macrocheles glaber Mull. (Mesostigmata:Macrochelidae). Proc. IV Int. Congr. Acarol. :493-494.

Petrova, A.D. and E. Z. Taskaeva. (1964). Gamasoid mites (Parasitiformes, Gamasoidea) from southern China. Bull. Prep. Biol. 69(5): 47-61. (in Russian).

Philips, J.R. (1984). Acarine symbionts of trogid beetles. pp. 552-556, *In*: Acarology VI (Vol. 1). D.A. Griffiths and C.E. Bowman (eds.), John Wiley & Sons, New York, 645 pp.

Richards, K.W. and L.A. Richards. (1977). A new species of Macrocheles (Acarina:Macrochelidae) found in bumblebee nests (Hymenoptea:Apidae). Can. Ent. 109: 711-719.

Ritcher, P.O. (1958). Biology of the Scarabaeidae. Ann. Rev. Entomol. 3: 311-334.

Ryke, P.A.J. (1959). Some parasitoid mites (Acarina: Mesostigmata: Parasitoidea) symbiotic on a carpenter bee and a scarabaeid beetle from Mozambique. Coimbra Editora, Limitada 19 pp.

Ryke, P.A.J. and M. K. P. Meyer. (1958). Some parasitoid mites (Mesostigmata:Acarina) associated with Coleoptera in the western Transvaal. J. Ent. Soc. S. Africa 21(1): 139-161.

Samsinak, K. (1962). Neue entomophile Acari aus China. Acta Soc. Ent. Cechoslov. 59(2): 186-204.

Sellnick, M. (1940). Die Milbenfauna Islands. Goteborgs Kungl. Vetenskaps-Vitt.-Samh. Handl. Ser. B. 6(14): 3-129.

Sychevskaya, V.I. (1964). Mites found on synanthropic flies in Uzbekistan. Med. Parazit. (Moscow) 33: 557-560.

Turk, F.A. (1945). Studies of Acari, V. -Notes on and descriptions of new and little-known British Acari. Ann. & Mag. of Nat. Hist. (ser. 11) 96: 785-820.

van der Hammen, L. (1964). The morphology of Glyptholaspis confusa (Foa, 1900)(Acarida, Gamasina). Zool. Verhandelingen 71: 55pp.

Van Driel, C.D. (1973). 'n Taksonomiese ondersoek van die families Macrochelidae Vitzthum en Parholaspidae Krantz (Mesostigmata: Acari) in die etiopiese wyk. M.S. thesis, Potchefstroomse University, South Africa.

Van Driel, C.D. van, G.C. Loots and J.F. Marais. (1977). Freeliving Mesostigmata. In: La faune terrestre de l'ile de Saint-Helene. Kon. Mus. Roy. l'Afrique Cent. 22: 305-336.

Wallace, M. M. H. (ed.) (1982). The biological control of dung in Australia. A.M.R.C. Workshop, Canberra.

Wallace, M.M.H., M. Tyndale-Biscoe and E. Holm. (1979). The influence of Macrocheles glaber on the breeding of the Australian bushfly, Musca vetustissima in cow dung. Rec. Advances Acarol. II: 217-222.

Watrous, L.E. and Q.D. Wheeler. (1981). The out-group comparison method of character analysis. Syst. Zool. 30(1): 1-11.

Wernz, J.G. and G.W. Krantz (1976). Studies on the function of the tritosternum in selected Gamasida (Acari). Can. J. Zool. 54(2): 202-213.

Wiley, E.O. (1981). Phylogenetics. John Wiley & Sons, New York, 439pp. .

APPENDIX

I. LIST OF PHORIONTS

THE GLABER SPECIES COMPLEX

Macrocheles glaber (Muller, 1860)

Aphodius fossor Netherlands, Br. Columbia (Macqueen & Beirne 1974)
rufipes Netherlands

Geotrupes amoenus Manchuria
auratus Japan
baikalicus Irkutsk
cornithius Sinkiang, Tibet
corruscans Spain
deblockii Manchuria
douei Malta, Morocco, Tunisia
hypocrita Gibralta
intermedius Algeria
laevigatus Europe
jacoueri Sinkiang
jakowlevi E. Europe, Turkey, Liberia
mutator Switz., France
niger France, N. Africa
selengae Mongolia
silvaticus Netherlands
spiniger Greece, Corsica, Romania
stercorarius Netherlands, Switz.
substriatellus Formosa
vernalis Poland, Yugoslavia
sp. Nepa

Ceratophyus polyceros dauricus USSR

Heliocopris bucephalas India

Copris lunaris Prussia, Central Asia
ochus Japan
magicus Burma

Oniticellus cinctus Canton

Onitis belial Morocco
damoetas Greece
humerosus Morocco
numida Morocco
subopacus India

Chironitis moeris Kirghiz

Bubas bison Majorca, Algeria
bubalus (Costa 1966)

Onthophagus blatchley Florida?
gladiator Fukien
sp. Australia

scarab Germany, Pakistan

rhinoceras beetle India

Mammals

Hystrix cristata Netherlands

Rattus norvegicus Netherlands

Macrocheles caligynius (Berlese, 1910)

Copris sp. Java (Vitzthum 1943)

Macrocheles perglaber Filipponi & Pegazzano 1962

Aphodius fossor Br.Columbia, Oregon
rufipes Netherlands

Geotrupes baikalicus Irkutsk
genestiericus Szechuan
niger France
spiniger France, Greece
stercorarius Switzerland

Copris fricator Michigan, New York
lunaris Prussia
tripartitus Szechuan
hispanus Sardinia

Oniticellus californicus Oregon

Onitis belial Morocco
humerosus Israel, Sinkiang

Onthophagus graniculatus Australia
hecate Mich.
sp. Australia

Nicrophorus germanica Europe
hecate Oregon
sepulta Austria

Mammals

Microtus pennsylvannicus nest New York

Rattus norvegicus New Zealand

Bombus nests
Bombus appositus & ternarius nests Alberta
B. terrestris nest New Zealand

Other habitats

bark of Dendroctonus infested pine (Br.Columbia), dead deer (New York), leaf litter, freshwater beach debris, rotting mushrooms, cow, horse, and bison dung

Oregon, Washington, South Dakota, Minnisota, Michigan, Nebraska, New York

British Columbia, Alberta, Mannnitoba, Ontario, New Brunswick

M. "glaber" before F&P

flies - ex Farish 1965, Petrova 1964

Musca domestica
autumnalis
Lucilia sericata
illustria
Morellia hortorum
Phormia regina
Calliphora erythrocephala
uralensis

Microchrysa polita
Ophyra leucostoma
Fannia incisurata
canicularis
Sarcophaga carnaris

mammals ex Farish 1965

Sciurus vulgaris
Rattus turkestanicus
Mus musculus
Apodemus agrarius
speciosus
Meriones erythrourus
Lemmus lemmus
Clethrionomys glareolus
rufocanus
Arvicola terrestris

(other beetles - Farish 1965, Krauss 1970, Wallace et al. 1979

Nicrophorus vespilloides

Hister impressus
latipes
stercorarius
unicolor

Onthophagus ovatus
granulatus Australia
australis Australia

Aphodius tasmaniae Australia
fimentarius
prodromus

Geotrupes stercorosus

Chironitis pamphilius

Chrysomela staphylea

Ips typographus

Macrocheles jalisciensis Mendez-Olivo 1966

Dichotomius carolinus Mexico

Macrocheles peregrinus Krantz 1981

Aphodius maculicollis South Africa
sp. South Africa

Allogymnopleurus thalassinus South Africa

Catharsius mirabilis Kenya
tricornutus South Africa
ulysses South Africa

Chironitis furcifer North Africa
scabrosus South Africa
spicticollis South Africa
stuhlmanni Kenya

Copris anceus South Africa
elephenor Namibia, South Africa
fallaciosus South Africa
laioides South Africa

Oniticellus africanus South Africa
intermedius South Africa
triangulatus South Africa

Garreta malleolus South Africa

Heliocopris andersoni Kenya, South Africa
colossus Zaire, South Africa
dilloni Kenya, South Africa
midas Zaire, South Africa
sp. Angola

Liatongus militaris South Africa

Onitis adelphus Rwanda
aeruginosus South Africa
aethiops Ethiopia
alexis South Africa
artuosus South Africa
aygulus South Africa
caffer South Africa
cryptodus Zaire
deceptor South Africa
inflaticollus Tanzania
picticollis South Africa

reichei rhodesianus Zaire
sphinx Ethiopia
spinicrus Kenya
subcrenatus Rwanda
tygulus Central African Republic
viridulus South Africa
westermanni South Africa

Onthophagus aciculatus South Africa
alcyon South Africa
auriceps South Africa
binodus South Africa
blanchardi Zaire
brucei South Africa
confusus South Africa
gazella South Africa
minutus South Africa
tersidorus South Africa
sp. 1 South Africa
sp. 2 South Africa

Phalops smaragdinus South Africa

Sarophorus costatus South Africa

Scarabaeus goryi South Africa
rugosus South Africa
nigreneous South Africa

Sisyphus rubrus South Africa
spinipes South Africa

Macrocheles medialis Berlese 1918

Heliocopris andersoni Namibia, Zaire
atropos Zaire
dilloni Kenya
hamadryas Zaire

Catharsius mirabilis Kenya

Onitis sphinx Zaire
reichei Cameroons
tygulus Central African Republic
viridulus Zaire
mniszechianus Zaire

Heteronitis pauliani Chad

Macrocheles hyatti Krantz & Filipponi 1964

litter in New Zealand

Macrocheles helenaensis van Driel 1977

litter on St. Helene

Macrocheles oigru, new species

Onitis philemon India
falcatus Java

THE LIMUE SPECIES COMPLEX

Macrocheles limue Samsinak 1962

Aphodius maculicollis South Africa

Onitis abyssinicus Zaire
adelphus Rwanda, Zaire
aeruginosus Kenya
alexis Zaire, South Africa
artuosus Zaire, Cameroon
aygulus South Africa
caffer South Africa
castaneus India
cupressus Guinea
deceptor South Africa
fabricii Zaire
falcatus Java
inversidens Zambeze
monstrosus Zaire
nemoralis Zaire
oxulis India
philemon Philippines
reichei Zaire
senegalensis Chad
sphinx Zaire
spinicrus Kenya
subcrenatus Zaire
subopacus India
uncinatus Zaire
vanderkelleri Zaire

viridulus Zaire, Burundi, Rwanda, South Africa
westermanni South Africa
sp. Bali

Allonitis nasutus Zaire

Heteronitis castelmaui Zaire
paulioni Chad

Oniticellus intermedius South Africa
nasicornis Zaire
planatus Zaire

Liatongus militaris South Africa

Copris atropolitis Zaire
elephenor South Africa
fallaciosus South Africa

Heliocopris andersoni Kenya, Zaire
colossus Zaire
dilloni Kenya
haroldi Zaire
japetus Kenya
samson Zaire
tyrannus Sumatra
sp. India

Catharsius chinai Ethiopia
mirabilis Kenya
obtusicornis Zaire
polynices Zaire
tricornutus South Africa
sp. South Africa

Onthophagus tridens Zaire

Scarabaeus gangeticus Zaire
intermedius South Africa

Garreta malleolus South Africa

unknown scarab - Uganda

Macrocheles caelatus Berlese 1918

Copris wiesei Zaire

Onitis alexis Zaire
reichei Zaire
sulepennis Rwanda
vanderkellini Zaire
viridulus Zaire

Macrocheles witcoskianus, new species

Goliathus goliathus Cameroons

THE KRAEPILINI SPECIES COMPLEX

Macrocheles kraepilini (Berlese)

Copris incertis (F&P)

Catharsius molossus Java

Onitis falcatus Java

Pachylistes chinensis (F&P)

also Malaya, Singapore, Philippines, Samoa, W. Samoa, Vietnam, Thailand, India, Pakistan, Queensland?

Macrocheles hallidayi, new species

Onitis falcatus Java
philemon India
subopacus Cambodia

Heliocopris bucephulas India
sp. India

Catharsius sajax India

also Thailand, Borneo(Sarawak)

Macrocheles tantalus, new species

Copris incertus procidius Hawaii

Onthophagus curircorius incensus Hawaii

Rattus exulans Hawaii
rattus HA

THE PRAEDAFIMETORUM SPECIES COMPLEX

Macrocheles praedafimetorum Richards & Richards

in nests of Bombus bifarius, flavifrons, frigidus, mixtus, occidentalis, ternarius

Nicrophorus defodiens Washington
pustulatus Oregon

Aphodius fossor Oregon

marshy litter, dead raccoon, beach litter, forest litter, gull nest, aplodontia nest, Eutamias sp., millipede, Zapus trinotatus, petrel burrow, rotting mushrooms

British Columbia, WASHINGTON, Oregon, California, Wyoming, Alberta

THE FRIGGI SPECIES COMPLEX

Macrocheles friggi, new species

Catharsius bradshawi Cameroons
obtusicornis Zaire
polynices Zaire

Scarabaeus festuvus paganus Zaire

Heliocopris colossus Central African Republic
haroldi Zaire
minos Zaire
samson Zaire

Heteronitis castelmaui Zaire
abyssinicus Zaire

Allonitis nasutulus Zaire

Onitis adelphus Zaire
artuosus Cameroons, Zaire
fabricii Zaire
meyeri Kenya
monstrosus Zaire
reichei Zaire
robustus Zaire

sphinx Zaire
subcrenatus Zaire
uncinatus Zaire
vicinus Ethiopia

Oniticellus planatus Zaire
tibatensis Zaire

Macrocheles nalani, new species

Heliocopris tyrannus Thailand

Macrocheles pumiliosternus, new species

Onitis inversidens Zaire
reichei Zaire, Cameroons

Heteronitis peculiani Chad

Heliocopris japetus Kenya (Costa 1975)
dilloni Kenya
andersoni South Africa

Catharsius mirabilis Kenya

Sacarbaeus gangeticus Zaire

Pritophilus passaloides Gabon

THE CAPENSIS SPECIES COMPLEX

Macrocheles capensis, new species

Onitis aethiops Ethiopia
artuosus Zaire
subcrenatus Zaire
vanderkelleni Zaire

Heliocopris colossus Rwanda

Diastellopalpus lamellicornis Kenya

Macrocheles macroscatophilus, new species

Onitis aethiops Ethiopia
artuosus Zaire
monstrosus Zaire
subcrenatus Zaire

Heliocopris colossus Zaire
haroldi Zaire

THE TRANSMIGRANS COMPLEX

Macrocheles transmigrans Petrova & Taskeva 1964

Enoplotrupes sinensis Szechuan
varicolor Szechuan
serricornis Burma
splendens India

Helictopleurus gigateus Madagascar

THE SCUTATUS SUBGROUP

Macrocheles scutatus (Berlese, 1904)

Rattus exulans New Zealand (Emberson 1973)

Geotrupes fossor E. Europe
mutator Italy, Switz.
niger N. Africa

Onitis belial France, Marocco
humerosus Sinkiang
philemon Philippines, India

Copris hispanus Israel

Onthophagus sp. S. India

Macrocheles neoscutatus Krantz 1972

litter in Germany

Macrocheles neovernalis Ryke & Meyer 1958

Heliocopris hamadryas South Africa
hunteri South Africa
erycoides Zaire
neptunus East Africa

Catharsius tricornutus South Africa, Mozambique (Ryke 1959)
dux Zaire

Macrocheles subscutatus, new species

Copris elphenor South Africa

Heliocopris neptunus South Africa

Catharsius marcellus Tanzania

Scarabaeus cupreus Zimbabwe
savigni South Africa

Macrocheles dispar Berlese

(Copris molossus, Copris sp. and Aphodius sp.,Java)

Catharsius molossus Philippines

Enoplotrupes sinensis Szechuan
varicolor Szechuan

Paragymnopleurus rudis Taiwan

scarab Vietnam

Macrocheles paganus Berlese

Scarabaeus paganus Angola
deludens South Africa
festivus Zaire, Ghana, Congo, Ivory Coast
intermedius Zaire

Pachylomera femoralis Mozambique

Catharsius fastidiosus Kenya

Macrocheles agnosticus, new species

Scarabaeus savigni South Africa
convexus South Africa

Macrocheles rhodesi Evans & Hyatt

Scarabaeus palemo Botswana
lamarcki South Africa
nigroaneus Mozambique
subaeneus South Africa
bonelli South Africa

paganus South Africa

Gymnopleurus azureus Zimbabwe (E&H)

Sebasteos laticepes South Africa (E&H)
galenus Zimbabwe (E&H)

Macrocheles natalensis ***Evans & Hyatt***

Scarabaeus cuvieri (E&H)
lamarcki South Africa

Sisyphus rubrus South Africa
Sarophorus castatus South Africa