A review of the parasitic mite family Psorergatidae (Cheyletoidea: Prostigmata: Acari) with hypotheses on the phylogenetic relationships of species and species groups

K.M.T. Giesen

Giesen, K.M.T., 1990. A review of the parasitic mite family Psorergatidae (Cheyletoidea: Prostigmata: Acari) with hypotheses on the phylogenetic relationships of species and species groups.

Zool. Verh. Leiden 259, 15.x.1990: 1-69, figs. 1-29, tables 1-10.— ISSN 0024-1652.

Key words: Acari; Prostigmata; Cheyletoidea; Psorergatidae; *Psorergates*; *Psorergatoides*; *Psorobia*; general morphology; keys; tables of measurements; tables of hosts and parasites; phylogenetic relationships; co-evolution.

Extensive description of the mite family Psorergatidae starting with general morphology, a redescription of the type species of the family (*Psorergates simplex* (Tyrrell, 1883)), and keys to the genera (*Psorergates, Psorergatoides, Psorobia*) and all known species. Phylogenetic analyses, hypotheses of hosts and parasites are given. The last section contains tables of measurements and lists of psorergatic mite species and their hosts.

K.M.T. Giesen, Department of Aquatic Ecology, Catholic University Nijmegen, Toernooiveld, 6525 ED Nijmegen, The Netherlands.

Contents

Introduction

The purpose of this paper is to present a review of the parasitic mite family Psorergatidae (Dubinin, 1957). Numerous papers have been published with descriptions of new psorergatic mites, but never has been attempted to arrange these species in a phylogenetic rank order. The author has tried to construct a consistent phylogenetic tree and shows some difficulties which can arise in doing so.

Since the description of the first *Psorergates* species by Tyrrell, 1883, numerous new species have been described. After establishment by Dubinin (1957) of a separate family Psorergatidae, Fain (1959 a,b) named two new genera. The genus *Psorergatoides*, infesting Chiroptera hosts, and the genus *Psorobia* on several different host orders.

Mites of the family Psorergatidae are small, dorso-ventrally flattened, disc-shaped mites. The first species, *Psorergates simplex* was described by Tyrrell in 1883 from the house mouse *Mus musculus*, from Canada. He enumerated the following characteristics for this new genus: "General shape of the male and female quite different, the male being provided with legs which are terminated by a spine and claw, in the female the legs are very small and without terminal appendage, mandibles styliform. The nymph and larva resemble the female rather than the male. "

Figures in the original publication show that Tyrrell took a nymph for a female and the female for a male specimen. Tyrrell did not consider the chaetotaxy of the body, gnathosoma and legs, and the legs were to be four-segmented (tibia-genu fused). He added drawings of the dorsal and ventral side of the male (really the female), the female (in reality a nymph), a nymph, larva, egg, and the gnathosoma. *P. simplex* was to be closely related to the genus *Myobia*.

Following you will find an update of the knowledge of the family Psorergatidae with tables of measurements, host tables and phylogenetic hypotheses.

Material used for this study belongs to the Lukoschus' collection, which contains a very large collection of almost all described species from Psorergatidae besides a number of undescribed species. The collection is now transferred to the Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie) in Leiden after his untimely demise in August 1987. Data from species not present in the Lukoschus' collection were drawn from literature.

Systematic position of the family Psorergatidae

Historically the species of Psorergatidae have been placed in several families and

superfamilies. Tyrrell, describing the first species, relegated the new genus under the family Myobiidae. Vizthum (1929), however, considered the genus *Psorergates* to be part of the family Cheyletidae. Next, the genus was placed in the family Myobiidae again by Baker & Wharton (1964). Before this Dubinin (1957) considered the genus *Psorergates* to be forming a separate family Psorergatidae belonging to the superfamily Demodicoidea together with the family Demodicidae. Probably because of being unfamiliar with the Russian literature Baker & Wharton did not know about the new status of the genus.

More recent classifications by Krantz (1978) and Kethley (1982) show relationships of the family Psorergatidae with eight other families in the superfamily Cheyletoidea. Krantz gives a brief description of the family with enumeration of the pathological effects (mange, dermatitis, follicular infection), infested host orders, and a sample drawing of one of the species. Also a key is given to the family. Krantz places the family Psorergatidae in the superfamily Cheyletoidea together with the families Cheyletidae, Cheyletiellidae, Myobiidae, Harpyrhynchidae, Syringophilidae, Ophioptidae, Demodicidae and Cloacaridae. The superfamily Cheyletoidea belongs to the subcohort Raphignathae and the cohort Eleutherengonina, suborder Actinedida, order Acariformes.

Kethley (1982) largely follows the classification of Krantz (1978), except for the name of the suborder for which he uses the older name Prostigmata (also used by Krantz in 1970).

In Moss et al. (in prep.) phylogenetic relationships of the family Harpyrhychidae are elucidated. Here we find a phylogenetic analysis of the superfamily Cheyletoidea with 65 different characters. It appears to be that the families Demodicidae, Cloacaridae and Psorergatidae belong to a monophyletic group characterized by a number of apomorphies. The family Psorergatidae is the sistergroup of the Demodicidae and Cloacaridae and shows the apomorphic characteristic of having retrorse spurs on femora I-IV. Sister group of latter three families is the branch of the cladogram formed by the families Harpyrhynchidae and Ophioptidae.

Morphology of the mites of the family Psorergatidae*

Adults. Body shape and body formation

Psorergatidae are tiny, dorso-ventrally flattened mites. The body outline (figs. 1, 4, 5) is slightly oval with a length from the tip of the gnathosoma to the end of the opisthosoma ranging from 90 to 220 microns, and a width ranging from 80 to 170 microns. The legs are inserted ventro-laterally and are regularly distributed over the idiosoma. The dorsal shield (figs. 4, 5) is striated at its margins, where the cuticula is soft, and the outer borders of the shield are often undulated. The sclerotized part of the shield is punctated. Males have a dorso-anterior, elongated penis. The female,

*For reasons of comparison and a more uniform nomenclature of the chaetotaxy of body and legs I followed the nomenclature setae given in Moss et al. (in prep.). If old names are different from the ones given in Moss et al. (in prep.) these will be given in parentheses in this section. Throughout the manuscript mostly old names will be used to make comparison with the original literature easier.

genital opening (fig. 1, GO) lies postero-ventrally between two adanal lobes. The male possesses only one postero-ventral adanal lobe (fig. 6). The venter of both males and females shows four pairs of more or less well sclerotized epimera, projecting inwards from the bases of the legs. In most species the first pair of epimera is recurved laterally. In both sexes the anus is absent.

Gnathosoma

The gnathosoma (figs. 3, 4, 5, 7, 8) consists of a basal part, the hypostome, and a pair of two-segmented palps. The dorso-anterior part of the hypostome is the stylophore capsule (*stc*) flanked by the palps. The two-segmented (gnathosomal) supracoxal setae (*ep*) are situated dorso-laterally on the hypostome. The proximal part of these setae is dentated apically and more or less enfolds the distal part. The supracoxal setae are basically the same in all species except in *Psorergates* species from Sciuridae hosts. In the latter species the supracoxal setae are enwrapped in a part of the epidermis and the setae are one-segmented (Giesen & Lukoschus, 1982; Giesen et al., 1982). The palps flank the stylophore capsule and are inserted antero-laterally on the hypostome. The dorso-basal part of the palps consists of the fused trochanter-femur-genu segments (Moss et al., in prep.). The other segment of the palps is situated ventrally of the basal segment and is a fusion of the tibia-tarsus segments (Moss et al., in prep.). The trochanter-femur-genu segment bears three setae. The (palpal tibial) dorsal femoral seta (*dF*) is serrate in the genera *Psorobia* and *Psorergatoides.* In the genus *Psorergates* the *dF* seta is smooth and variable in length. The latter seta shows consistent differences between genera and groups within genera and therefore is an important diagnostic character. Right next to the dorsal femoral seta is the, always very small, antiaxial seta (*vG*). Both setae, *vG* and *dF*, are so close-set that the hair rings are fused. Apically the spine-like, distal, dorsal seta (*dG*) is present. The tibia-tarsus segment of the palps has four setae. Dorso-laterally is a thin, tactile seta, probably *ats* if we compare the topology in the Psorergatidae and Harpyrhynchidae (Moss et al., in prep.). Medio-apically are present three strong, spine-like setae (fig. 3). Comparison with the related family Harpyrhynchidae could not resolve homology between these setae and any of the setae present in Harpyrhynchidae. One of the setae in Psorergatidae might be homologous with the tarsal hook (*thk*) in Harpyrhynchidae. The morphology of two of these setae shows sawed, bended, apical parts, the third seta is pointed, spine-like and straight.

The chelicerae are partially contained in the stylophore capsule and consist of two parts. The sclerotized cheliceral condyle is the median structure with dorsally directed teeth. The number and shape of these teeth can vary in the different species of the family, but because exact morphology (fig. 8) can only be observed in very heavily squashed specimens, this character is not used in the keys to the species. The movable digits of the chelicerae are connected to the condyle as figured (fig. 8) and project between the cheliceral condyle. Scanning Electron Microscope (SEM) photographs of the cheliceral condyle, the setae of the palpal tibia-tarsus segment, and the supracoxal (*ep*) seta are shown in Giesen & Lukoschus (1982).

Ventrally on the stylophore a pair of small (subgnathosomal) setae are present. These setae are homologes of the internal subcapitulars (*pmc* 1) in the family Harpyrhynchidae.

Legs

The legs (figs. 1, 2) have five segments and are slightly tapering towards the end. The trochanter segments have an anterior, proximal spur directed towards the venter middle. Apparently these spurs are used for fixation to the host and are equivalent in function to the coxal lobes of Harpypalpinae mentioned in Moss et al. (in prep.). Also the femur segments have a proximal, posterior spur directed to the venter middle and probably with the same function as the trochanter spurs.

Chaetotaxy of the legs.— The chaetotaxy is based on the nomenclature of leg setae of Stigmatidae by Grandjean (1944), and of Harpyrhynchidae by Moss et al. (in prep.), and homologies are hypothesized on grounds of topology and general reduction trends of setae.

Trochanter with one ventral seta (*v*) in all species of the family. The length of this seta may vary and can be a diagnostic character on the species level. Femora I-IV at least with one postero-lateral seta (*v*). In a number of species groups in the different genera a second seta, proximal of the *v* seta may be present. The latter seta is hypothesized to be the *v"* seta of femora I-IV. Because of the consistent differences between different species groups in number and in length of the femoral setae these are considered to be important diagnostic characters. Genu I to IV only has one seta (*v"*) postero-laterally on the ventral side. The genual seta can be absent in species of the genus *Psorergatoides*. In species of the other two genera of the family Psorergatidae, the genual seta of leg IV can be much longer and stronger than the genual seta of legs I-III or it can be subequal. Because of the consistent differences in absence/presence and length of this seta between species groups this seta is considered to be an important diagnostic character. The tibia always has a short spine-like seta ventro-laterally on the anterior side. The shape of this spine may vary between species groups. It is hypothesized that this spine is homologuous to the *v'* in Harpyrhynchidae. Medio-dorsally a seta (*d*) is present in all known species.

Tarsi with a bilobed pad-like empodium and two apical claws. The claws in the genera *Psorergates* and *Psorergatoides* may be one-pointed, bifurcated of trifurcated. Because of consistent differences in the number of claw points between species groups in the two genera mentioned above this character is considered to be of taxonomic importance. Ventrally legs I-III always have an antero-lateral spine. This spine, hypothesized to be the *u'* homologe, may vary in shape between species and species groups. The presence of *u'* on leg IV is an important diagnostic character for distinguishing major groups within the different genera. Dorso-laterally mostly two setae are present, *tc'* and *tc"*. These setae are in general equally long, but the species of the *"insectivora"* group of the genus *Psorergates* exhibit a reduced *tc'* seta, which is never longer than 5 micrometers. In addition to this the posterior *tc"* seta can be absent or present in the *"insectivora"* group. Medio-dorsally a third, small, mostly enveloped by a skin fold, rounded seta is present on legs I and II. This little seta is hypothesized to be homologuous with the *p"@* seta of Harpyrhynchidae and is probably not a solenidion as indicated in previous literature. Because this seta is so extremely small, the method to distinguish solenidia with the help of polarized light mentioned by Grandjean (1973) is not applicable here. Next to the *p"@* seta a solenidion (omega) is present on legs I and II.

Idiosoma

Dorsally the idiosoma is covered by a circular to oval, punctated shield. The only known deviation from this is in the male of *Psorergates quercinus*, which has a shield divided into a posterior and an anterior part. The outline of the idiosoma is mostly undulating with the soft parts between the edge of the shield and the borders of the idiosoma being striated. At the edge of the shield three or four pairs of setae are present (figs. 4, 5). Antero-laterally the *sc i* setae, laterally between the level of legs II and III a seta of the *c*-series and between the level of legs III and IV a setae of the *d*-series is present. Two genera of the family Psorergatidae have a fourth seta on the dorsal shield. This seta of the *e*-series is situated postero-laterally behind the level of legs IV. Dorsal setae in the genera *Psorergates* and *Psorobia* are thin, mostly short, but distinct. In the genus *Psorergatoides* however, the dorsal setae are reduced to point-like setae, or often only the alveoli remain. In some specimens and species even these hair rings are hardly distinguishable any more.

In females one more pair of dorsal setae is present antero-medially on the dorsal shield. These *ve* setae are also present in males along with a pair of genito-anal setae (*ps*) laterally of the genital opening. Relative position of *ve* and *ps* setae in males may vary and is an useful diagnostic character.

Venter of idiosoma (fig. 1). Laterally four pairs of legs are inserted, equally spaced along the idiosoma. The opisthosoma is greatly reduced and in females the genital opening is situated median at the level of legs IV. The two pairs of opisthosomal setae are shifted along with the genital opening and are situated on two adanal lobes alongside the genital opening. Generally these setae (*h 1* and *h 2*) are subequal, but one of each pair may be reduced in length. In males only one median adanal lobe is present, bearing one pair of setae (*h*). In males these setae can be completely reduced as in a number of species of the genus *Psorergatoides*. Because of consistent variation in the length of the *h* setae between species and between species groups, these setae are considered to be an important diagnostic character.

From the legs projecting to the venter middle, are subcutaneously the sclerotized epimera. The epimera of legs I are mostly recurved laterally, the other three pairs are straight. At the level of legs III is the only remaining pair of coxal and intercoxal setae. These intercoxal setae of legs III (*ic III*) are an important diagnostic character. The distance between these setae may vary between species groups of the genus *Psorergates*, or these setae may be totally absent as in some species of the genus *Psorergatoides*.

Morphology of the male genital region

The genital opening in males is situated dorsally, approximately at the level of the *sc i* setae. In comparison to the related Harpyrhynchidae, the genital opening has shifted much more dorso-anteriorly. The penis and penis sheath of Psorergatidae males are usually straight, but may vary greatly in length between different species. For comparison of species groups this character is not very useful, but for species distinction it can be helpful.

Developmental stages

Almost no morphological differences in the developmental stages of the different

species of the family Psorergatidae can be found. Larvae and nymphs of the genus *Psorergates* can be distinguished by their different gnathosomal setae, but otherwise no clear differentiating characteristics exist.

Egg.— The eggs (fig. 10) are circular to slightly oval without any appendices or protrudings as for instance in Demodicidae. The size of the egg is relatively very large in comparison to the female; it fills almost half of the idiosoma (fig. 9). Like in most obligate parasites numbers of eggs are very low.

Praelarva.—The praelarva (fig. 11) develops within the egg without hatching. Two small, sclerotized, sickle-shaped structures (the pharyngeal bulb?) are visible inside, and a first differentiation in gnathosoma and idiosoma takes place. In this praelarva subsequently a larva develops (fig. 12).

Larva.—The larvae (fig. 13) are disc-shaped and relatively big in comparison to the adults. The gnathosoma is very alike that of the adults, but the setation is somewhat shorter (fig. 14). The three pairs of two-segmented legs possess two, three-pointed claws on the apical segment. The first and second pair of legs also show a small solenidion (*so*) on the apical segment. The proximal segments of the three pairs of legs have a ventro-median directed, basal spur, varying in size and degree of sclerotization. The epimera, when visible, are weakly sclerotized. Setae are absent on legs and idiosoma.

Protonymph.— The protonymph (fig. 15) has a fourth pair of legs added, and is a little bigger as the larva. Setation of the gnathosoma (fig. 16), and leg claws are stronger. The pronounced sexual dimorphism of the "dissimilis " group of the genus Psorergates already shows in the protonymphs. The gnathosomal setation of the female protonymphs is longer and stronger.

Deutonymph.— Only very small differences can be found between protonymphs and deutonymphs of a species of the family Psorergatidae. Deutonymphs (fig. 17) are a little bit bigger, and the fourth pair of legs is slightly shifted posteriorly. Also the setation of the gnathosoma is somewhat stronger (fig. 18).

The genera of the family Psorergatidae

Since the description of *Psorergates simplex* by Tyrrell in 1883 very few species have been described until 1959, when Fain divided the family Psorergatidae into three genera. Only 11 species were known (Fain added 7 new species in his publications 1959a,b). Since than 59 new species are described, mainly by Lukoschus and coworkers. The genus *Psorergates* is characterized by the apomorphies of having smooth palp-tibial (*dF*) setae, and the presence of three pairs of dorso-lateral shield setae (*sci, c, d*). Hosts are from the orders Scandentia, Rodentia and Insectivora. Infested families are Tupaiidae, Cricetidae, Muridae, Sciuridae, Gliridae, Talpidae and Soricidae (see also tables 9 and 10). The genus *Psorergatoides* is characterized by the apomorphy of having four pairs of strongly reduced dorso-lateral shield setae (*sci, c, d, e*). These setae are reduced to point-like structures, and sometimes only the alveoli remain. *Psorergatoides* species have the serrate palp-tibial setae (*dF*) in common with *Psorobia*. Hosts are members of the order Chiroptera. No other genera of the family Psorergatidae are known from this host order.The genus *Psorobia* does not

have any apomorphies. This genus appears to be para- or polyphyletic as will be discussed on page 35. Also the host group is not homogeneous. Host orders are Rodentia, Artiodactyla, Primates, Insectivora, Carnivora, and Lagomorpha.

Psorergates (Tyrrell, 1883)
Psorergates simplex (Tyrrell, 1883)
(figs. 18-22, table 1)

Introduction.— As already mentioned in the general introduction Tyrrell (1883) described the type species of the genus *Psorergates*, giving this new species the following characteristics: "General shape of the male and female quite different, the male being provided with legs which are terminated by a spine and claw, in the female the legs are very small and without terminal appendage, mandibles styliform. The nymph and larva resemble the female rather than the male, oviparous." Figures of dorsal and ventral sides of the male, female, nymph, larva, egg and gnathosoma were added. Piana (1886) found *P. simplex* in cysts on the house mouse. He thought *Psorergates* was most closely related to the genus *Sarcoptes*. Michael (1889) described a mite, *Goniomerus musculinus* (*Psorergates musculinus*), from the ear conches of *Arvicola agrestis*. Neumann (1893) described *P. simplex* from subcutanous cysts and from scabs of the ear of *Mus musculus*. He added drawings of the male, and mentioned that Tyrrell had taken the female for a male and a nymph for a female. Neumann also pointed out that male and female are very much alike, the male only differing through the presence of a long dorsal penis. He incorporated the genus *Psorergates* in the subfamily Cheyletinae.

Canestrini (1894) gave a redescription of *P. simplex* from *Mus musculus* and *Arvicola agrestis* with drawings of the female, male and penis, larva, egg and cyst. In the discussion Canestrini mentioned that Gerlach (1857) had made some drawings of an unknown mite. Although there were quite considerable differences between these drawings and the ones made by himself, Canestrini thought the two species to be conspecific, because of the shape of the body, the place of the epimera, the form and direction of the legs, the presence of terminal setae and the host species.

The type specimens of *Psorergates simplex* are lost, and the rather poor descriptions of Tyrrell and later authors were always felt as a lack in the documentation of the family. A new series of specimens was collected from the same host (*Mus musculus*), from the same locality (Canada), and in the same niche (the ear concho). Based on above identical host specifications and comparison with existing descriptive material of the original type specimen redescription seems justifiable, although Fain et al. (1966) did not want to come to the same conclusion.

Diagnosis.— *Psorergates simplex*, with characteristics of the family Psorergatidae, genus *Psorergates*. Belonging to the "*muricola*" species group with short (2-6 microns), strong, smooth palpal tibial (*dF*) setae; short, subequal, genual setae I-IV; sclerotized ducts in females; and the formation of a.m. (*v e*) and genital (*ps*) setae in males quadrangle-like. Differing from the most closely related species by the size of the dorsal shield in females, length of gnathosomal (*ep*) setae in females, and length of penis (see also tables 7 and 8).

Description.— Female shape and body formation like in other species of the genus. Measurements of 10 specimen (in micrometers) in table 1.

Venter (fig. 18). Epimera I recurved, not fused with epimera II. Epimera II-IV linear, weakly sclerotized, directed ventro-median. Genital opening a longitudinal slit between legs IV, flanked by a pair of adanal lobes, each with a pair of strong, long, filiform setae (*h 1, h 2*). Anterior of the genital opening two sclerotized ducts, which are strongly sclerotized proximally, lead into the corps inner. Ventral setae (*ic III*) situated medially at the level of legs III.

Legs with five free segments: trochanters each with a prominent, well sclerotized, acute, proximal spur, and a single, filiform seta (*v*) at the base of this spur. Femoral spur medio-caudad directed with at its base two postero-lateral, subequal setae (*v, v"*). Genual setae (*v"*) subequal on all legs. Tibiae I-III with ventrally a short, setiform, antero-lateral spine (*l'*), and medio-dorsally a filiform seta (*d*, fig. 21). Tarsi (figs. 18, 21) I-IV with a small, antero-lateral, ventral spine (*u'*), and dorsally an anterior (*tc'*), and posterior (*tc"*), filiform seta. The posterior seta is lacking on tarsus IV. Tarsi I-II dorsally with solenidion omega, and a very small seta (*p"@*) enveloped by a fold of the epidermis. Apically two one-pointed claws, and a bilobed empodium are present on tarsi I-IV.

Dorsum (fig. 19) with sclerotized , punctated shield and lateral, weak parts striated as figured. Three pairs of setae (*sc i, c, d*) at the margins of the sclerotized shield, and a pair of point-like antero-median setae (*v e*) at a distance of 13-16 microns from the anterior shield border.

Gnathosoma (figs. 18, 19) ventrally with a pair of thin setae (*pmc 1*) at the base of hypostome, anteriorly of the pharyngeal bulb. Dorsally on the hypostome the gnathosomal (*ep*) setae, inserted directly beneath the palps. The bipartite gnathosomal setae have a dentated basal part, and a smooth apical part. The basal, palpal trochanter-femur-genu segment has a posterior, short, strong seta (*dF*), and a minute seta (*vG*) directly in front of the *dF* seta with fused alveoli. Apically a weakly sclerotized spur (*dG*) is present, and ventro-laterally (fig. 18) a small seta (*v'*) can be observed on the basal, palpal segment. Ventrally is the apical, palpal tibia-tarsus segment. No specimens were available with clearly visible structures on this palp segment. For reference to the possible structures present see general description in chapter III. Sclerotized, fixed part of chelicerae three-dentated.

Male shape and body formation as in female. Measurements of 5 specimens (in micrometers) in table 1.

Venter (fig. 20). Epimera I recurved, more strongly sclerotized in the middle. Epimera II-IV weakly sclerotized, straight. At the level of epimera III a pair of ventral, median setae (*ic III*). A single, small, adanal lobe gives rise to a pair of long, filiform setae (*h*). Anus absent.

Legs like in female, setal length corresponding with female, except femoral setae somewhat shorter.

Dorsum (fig. 22) with sclerotized, punctate shield, except the region of the genital opening. Three pairs of lateral shield setae (*sc i, c, d*). Antero-medially the genital opening flanked by two pairs of setae (*v e, ps*), with distinct alveoli. The formation of these setae is quadrangle-like. Penis simple, penis sheath a sclerotized rod with posteriorly a deep incision.

Gnathosoma as in female.

Developmental stages like in other species of the genus.

Type host and locality.— *Mus musculus* L. (Muridae, Rodentia). Canada. *Psorergates* specimens from *M. musculus* from Europe appear to be conspecific with the described specimens from Canadian host.The mites were found under a thin layer of the stratum corneum at the inside base of the ear concho.

Table 1. Measurements of *Psorergates simplex* (Tyrrell, 1883) (females and males)

	females (N=10) min-max	males (N= 5) min-max
body length	146 (143-150)	120 (108-126)
body width	116 (114-119)	96 (91-101)
shield length	106 (101-108)	78 (74-85)
shield width	100 (96-102)	74 (72-84)
length setae		
terminal	76 (72-82)	59 (55-62)
trochanter	8 (8-10)	8
femora I-III	17 (16-17)	13 (13-14)
femur IV	17 (17-18)	15 (14-16)
genua I-III	4 (4-5)	4 (2-4)
genu IV	4 (4-5)	4 (2-4)
lateral shield	6 (5-6)	5 (5-6)
palpal tibial	5 (5-6)	5
gnathosomal	4 (4-5)	5 (4-5)
ventral	7	6 (6-7)
distance between		
ventral setae	11 (8-11)	11 (8-14)
a.m. setae		11 (11-12)
genital setae		8
length penis		44 (42-47)
length penis sheath		26 (24-29)

Subdivision of the genus

The genus *Psorergates* can be divided into six groups with characteristics as described in several publications. They are known under the names *"dissimilis"*, *"muricola"*, *"apodemi"*, *"gliricola"*, *"sciuricola"* and *"insectivora"* groups. The groups with their included species are given below followed by a description with definitions of each group.

"dissimilis" group: *P. canadensis, P. watsoni, P. micromydis, P. auricola, P. zibethicalis, P. dissimilis, P. oeconomi, P. townsendi.*

"muricola" group; *P. muricola, P. oettlei, P. simplex, P. hispanicus, P. agrestis, P. rattus.*

"apodemi" group: *P. apodemi, P. deomydis, P. arvalis, P. pitimydis, P. microti, P. neerlandicus, P. callipidis, P. peromysci, P. pinetorum, P. alleni.*

"gliricola" group: *P. muscardinus, P. quercinus, P. eliomydis.*

"sciuricola" group: *P. paraxeri, P. dremomydis, P. glaucomys, P. tupaiae, P. ramai.*

"insectivora" group: *P. talpae, P. desmanae, P. urotrichi, P. sorici, P. cinereus, P. squamipes, P. cryptotis, P. baueri, P. mexicanus, P. crocidurae, P. doriae, P. etruscus.*

The *"dissimilis"* group is defined by Lukoschus et al. (1967) by the following characteristics. Large distance between the ventral (*ic III*) setae, and sexual dimorphism in the length of the palpal tibial (*dF*) setae. Females having long (25-36 μ) whip-like palpal tibial setae, and males very short setae (never longer than 5 μ). Genital setae of the males are situated on larger sclerotized shields. In the phylogenetic analysis of this paper the characteristic of sexual dimorphism with unequal palpal tibial (*dF*) setae in females and males is apomorphic for the *"dissimilis"* group including *P. musculinus*. Additional apomorphies for the *"dissimilis"* group are the large distance between the ventral setae (more than 30 μ), a wider than long shield, and unequal setae on femora I-V. *P. musculinus* is characterized by the very short distance between the ventral setae. With a somewhat restricted definition of the *"dissimilis"* group latter species is included and like in Giesen & OConnor (in press) I would like to add this species.

The *"muricola"* group is defined in Lukoschus et al. (1967) by the distance between the ventral (*ic III*) setae (between 5 and 20 μ), sclerotized ducts running from the genital opening to the body inner in females (fig. 23), equally short setae on genu I-IV, short palpal tibial (*dF*) setae in males and females, and the genital (*ps*) and antero-median (*v e*) setae in males are arranged in a quadrate form. Here the *"muricola"* group is defined by palpal tibial (*dF*) setae less than 6 μ, and the subequally short genual setae of legs I-IV.

The *"apodemi"* group is also defined by Lukoschus et al. (1967) and shows the following characteristics. Like the *"muricola"* group it has sclerotized genital ducts in females, and the same range of distances for the ventral (*ic III*) setae. The group is additionally defined by the different lengths of genual setae on legs I-III and IV, by the truncate palpal tibial (*dF*) setae with length (10-18 μ), and the arrangement of the genital (*ps*) and antero-median (*v e*) setae in males is trapezoid. In the analysis used in this paper no apomorphies are found which could be uniquely ascribed to the *"apodemi"* group. The sclerotized ducts in females are shared with the *"muricola"* and *"sciuricola"* groups, and the trapezoid formation of the genital (*ps*) and antero-median (*v e*) setae is shared with the *"sciuricola"* group. The character of truncate palpal tibial (*dF*) setae is not used in this analysis.

The *"gliricola"* group (new group) is first mentioned as three species more closely related to each other than each of them is to any other species of the genus by Lukoschus et al. (1971), but they give no definition of this group. Lukoschus et al. (1967) put the, at that time, described species *P. eliomydis* together with *P. musculinus* in the *"musculinus"* rest group. In the analysis of this publication the group is defined by a single apomorphy, which is the sclerotized genital atrium (fig. 1) in females.

The *"sciuricola"* group is defined by Giesen & Lukoschus (1982) with the following characteristics. Tibial spine on legs IV present, tarsal spines strong, gnathosomal (*ep*) setae short, bilobed, with subequal length of lobes, and dorsal setae on tibiae I-IV relatively long. In the analysis in this paper no apomorphies could be found, but it is the single group within the genus Psorergates which retains the tibial spine on legs IV, and which shows no sclerotized genital ducts as the *"muricola"* and *"apodemi"* groups do.

The last group is the *"insectivora"* group defined by Lukoschus (1968). This is a large group containing almost all psorergatid species from Insectivora hosts, except one species from a macroscelidid host, which belongs to the genus *Psorobia*. Def-

initions given by Lukoschus (1968 a,b) are dorso-anterior (*tc'*) and dorso-posterior (*tc"*) setae of tarsi I-III strongly differing in length, the anterior seta being very short; strongly anteriorly recurved dorsal shield; dorsal shield setae clearly seperated from shield border; gnathosomal (*ep*) setae lobed; terminal (*h*) setae of males on a longer, stronger sclerotized shield; very long setae on genua IV. Apomorphies from phylogenetic analysis are short palpal tibial (*dF*) setae (less than 6 μ); femoral setae (on each femur) unequal, the distal seta being half to two-thirds the length of the distal seta; short (less than 6 μ) dorso-anterior (*tc'*) seta on tarsi.

Key to the species (based on females)

1. Palpal tibial setae short (never more than 6 μ); dorso-anterior and dorso-posterior setae of tarsi strongly differing in length, sometimes dorso-posterior seta absent. Seta of genu IV relatively very long and strong (seta always longer than seta femur IV). *"insectivora"* group 34
- Palpal tibial setae longer (except in *P. deomydis*); dorso-lateral setae of tarsi subequal; genual setae subequal or not so pronounced as in the *"insectivora"* group (seta always shorter than femur IV seta) 2
2. Tibial spine IV present 3
- Tibial spine IV absent 7
3. Genual setae I-IV setiform; length of proximal seta of femora I-IV at least half of distal seta; gnathosomal setae short with subequal lobes. *"sciuricola"* group 5
- Genual setae I-IV reduced to short spines; proximal setae of femora I-IV reduced to short spines 4
4. Dorsal shield length 78-84 μ; lateral shield setae 4-5 μ; distance between ventral setae 10-12 μ ..... ***P. tupaiae***
- Dorsal shield length 71-76 μ; lateral shield setae 5-7 μ; distance between ventral setae 5-10 μ ..... ***P. ramai***
5. Tibial spine strong; femoral spur acute; tarsal spine strong, two-pointed; genu IV seta short 5-9 μ ..... ***P. paraxeri***
- Genu IV seta longer than 10 μ 6
6. Tibial spine strong; femoral spur blunt; tarsal spine strong, truncate; genu IV seta long 17-22 μ ..... ***P. dremomydis***
- Tibial spine thin, hair-like; femoral spur acute; tarsal spine strong, one-pointed; genu IV seta long c. 15 μ ..... ***P. glaucomys***
7. Setae genua I-III and genu IV subequal 4-5 μ; palpal tibial setae shorter than 10 μ, strong, like broken off. *"muricola"* group 8
- Setae genua I-III and genu IV of different length; palpal tibial setae filiform, longer than 10 μ (except *P. deomydis*) 13
8. Gnathosomal setae short 2 μ 9
- Gnathosomal setae longer than 4 μ 10
9. Shield distinctly oval shaped, length c. 84 μ, width c. 75 μ ..... ***P. muricola***
- Shield circular, length c. 96 μ, width c. 93 μ ..... ***P. oettlei***
10. Gnathosomal setae c. 9 μ; palpal tibial setae 1-2 μ ..... ***P. rattus***
- Gnathosomal setae 4-5 μ; palpal tibial setae 4-6 μ 11
11. Shield length 101-108 μ; shield width 96-102 μ ..... ***P. simplex*** (neotype)

- Shield length smaller than 95 µ; shield width smaller than 85 µ; palpal tibial setae 4-6 µ 12
12. Body length 117-129 µ; body width 99-105 µ ..... *P. hispanicus*
- Body length 129-150 µ; body width 105-120 µ; lateral shield setae 3-4 µ; setae femur IV 12-15 µ; trochanter setae 7-8 µ ..... *P. agrestis*
13. Distance between ventral setae very small c. 2 µ; shield long and oval shaped; lateral shield setae very long 33-42 µ ..... *P. musculinus*
- Distance between ventral setae more than 5 µ 14
14. Distance between ventral setae more than 20 µ; palpal tibial setae longer than 25 µ; dorsal shield more oval shaped; *"dissimilis"* group 15
- Distance between ventral setae less than 20 µ; palpal tibial setae shorter than 20 µ 22
15. Ventral setae longer than 8 µ 16
- Ventral setae shorter than 8 µ 18
16. Distance between ventral setae 20-24 µ; gnathosomal setae c. 2 µ; palpal tibial setae 26-29 µ. ..... *P. watsoni*
- Distance between ventral setae more than 30 µ 17
17. Distance between ventral setae 34-36 µ; gnathosomal setae 8-9 µ; palpal tibial setae 34-37 µ ..... *P. canadensis*
- Distance between ventral setae 37-42 µ; gnathosomal setae 6-7 µ; palpal tibial setae 27-35 µ ..... *P. townsendi*
18. Setae genua I-III and genu IV subequal c. 5 µ; setae femora I-III c. 15 µ; setae femur IV c. 20 µ ..... *P. micromydis*
- Setae genua I-III and genu IV of different length; setae femora I-III 20-30 µ; seta femur IV 25-45 µ 19
19. Very long setae on femora and genua, femora I-III 25-30 µ, femur IV 30-45 µ, genua I-III 8-10 µ, genu IV 24-30 µ ..... *P. auricola*
- Setae on femora and genua shorter than above 20
20. Body length 159-168 µ; body width 120-142 µ; distance between ventral setae 20-27 µ; seta genu IV c. 18 µ; setae femora I-III c. 20 µ, setae femur IV c. 25 µ ..... *P. dissimilis*
- Setae femora I-III c. 25 µ; setae femur IV c. 30 µ 21
21. Body length 174-207 µ; body width 144-174 µ; distance between ventral setae 27-36 µ; setae genu IV c. 12 µ; setae femora I-III c. 25 µ; setae femur IV c. 30 µ ..... *P. zibethicalis*
- Body length 142-174 µ; body width 119-145 µ; distance between ventral setae 26-30 µ; seta genu IV c. 18 µ; setae femora I-III c. 25 µ; setae femur IV c. 30 µ ..... *P. oeconomi*
22. Genital sclerotized rods running inside body (fig. 19); dorsal shield circular or wider than long; length ventral setae 5-7 µ; *"apodemi"* group 25
- Dorsal shield oval, longer than wide 23
23. No genital rods present; dorsal shield oval shaped; length ventral setae more than 10 µ; *"gliricola"* group 32
- Genital rods present; dorsal shield oval shape 24
24. Length ventral setae 8-11 µ; shield length 88-91 µ; shield width 78-81 µ ..... *P. peromysci*
- Length ventral setae 5-7 µ; shield length 113-132 µ; shield width 106-115 µ .....

..... ***P. alleni***

25. Palpal tibial setae very short 2-3 μ; distance between ventral setae 14-19 μ; body length 132-150 μ; body width 111-123 μ ..... ***P. deomydis***
- Palpal tibial setae longer than 10 μ 26
26. Shield length shorter than shield width 27
- Shield length c. equal or longer than shield width 28
27. Body length 126-141 μ; body width 111-123 μ; terminal setae 60-66 μ; setae femora I-III c. 15 μ; lateral shield setae 5-6 μ ..... ***P. arvalis***
- Body length 117-135 μ; body width 105-120 μ; terminal setae c. 75 μ; setae femora I-III 20-25 μ; lateral shield setae 4-5 μ ..... ***P. pitimydis***
28. Shield width smaller than 80 μ 29
- Shield width longer than 80 μ 31
29. Body length 105-143 μ; body width 90-114 μ; terminal setae 60-75 μ; gnathosomal setae 4-5 μ; setae femora I-III c. 15 μ; setae femur IV c. 20 μ ..... ***P. microti***
- Setae femora I-III longer than 15 μ; setae femora IV longer than 20 μ 30
30. Setae femora I-III c. 19 μ; setae femur IV c. 24 μ; distance between ventral setae c. 9 μ ..... ***P. neerlandicus***
- Setae femora I-III 22-26 μ; setae femur IV 22-30 μ; seta genua I-III 6-8 μ; seta genu IV 16-22 μ ..... ***P. pinetorum***
31. Palpal tibial setae 10-13 μ; seta genu IV 10-15 μ ..... ***P. apodemi***
- Gnathosomal setae c. 5 μ; palpal tibial setae 15-18 μ; seta genu IV c. 18 μ; shield length 87-105 μ; shield width 78-105 μ ..... ***P. callipidis***
32. Distance between ventral setae 14-18 μ; setae femora I-III 18-22 μ; shield length 109-118 μ; gnathosomal setae c. 5 μ; palpal tibial setae 17-19 μ ..... ***P. quercinus***
- Shield length 96-106 μ 33
33. Distance between ventral setae 7-14 μ; setae femora I-III 23-27 μ; shield length 96-106 μ; gnathosomal setae 5-7 μ; palpal tibial setae 12-14 μ ..... ***P. muscardinus***
- Distance between ventral setae c. 15 μ; setae femora I-III c. 30 μ; shield length c. 102 μ; gnathosomal setae c. 3 μ; palpal tibial setae c. 18 μ ..... ***P. eliomydis***
34. Tarsal claws one-pointed; dorso-posterior seta of tarsi I-III present; two setae on femur IV; *"talpidae"* group 37
- Tarsal claws two- or three-pointed 35
35. Tarsal claws two-pointed 36
- Tarsal claws three-pointed; dorso-posterior seta of tarsi I-III absent; two setae on femur IV; *"crocidurini"* group 43
36. Tarsal claws two-pointed; dorso-posterior seta of tarsi I-III present; one seta on femur IV; ventral part of empodium rounded; *"soricini"* group 39
- Tarsal claws two-pointed; dorso-posterior seta of tarsi I-III present; one seta on femur IV; ventral part of empodium acute; *"blarinini"* group 41
37. Seta trochanter shorter than 5 μ; seta genua I-III 1 micron; seta tibia 4-5 μ; shield length 70-78 μ; shield width 65-71 μ ..... ***P. urotrichi***
- Seta trochanter longer than 8 μ; seta genua I-III 3-5 μ; seta tibia 10-15 μ; shield length more than 79 μ; shield width more than 70 μ 38
38. Proximal seta of femoral setae distinctly shorter and thinner than distal seta, distal seta 20-28 μ; terminal setae 78-98 μ; shield length 87-96 μ; shield width 75-90 μ ..... ***P. desmanae***
- Proximal seta of femoral setae somewhat shorter but equally strong as distal one,

distal seta 28-36 µ; shield length 80-96 µ; shield width 70-76 µ; terminal setae 60-72 µ ..... ***P. talpae***

39. Dorso-posterior seta of tarsi I-III shorter than 10 µ; trochanter seta shorter than 5 µ ..... ***P. squamipes***
- Dorso-posterior seta of tarsi I-III longer than 13 µ; trochanter seta longer than 5 µ 40
40. Body length 117-135 µ; body width 93-99 µ; seta femur IV 28-33 µ; ventral setae 4 µ; gnathosomal setae 8-9 µ ..... ***P. sorici***
- Body length 138-159 µ; body width 112-131 µ; seta femur IV 19-25 µ; ventral setae 8 µ; gnathosomal setae 11-13 µ ..... ***P. cinereus***
41. Seta genu IV 22-31 µ; epimeron I not circularly closed, strongly sclerotized prolongations of epimera II-IV along the trochanters ..... ***P. cryptotis***
- Seta genu IV 33-48 µ 42
42. Seta genu IV 33-45 µ; epimeron I circularly closed, no sclerotizations along trochanters II-IV ..... ***P. baueri***
- Seta genu IV 37-48 µ; large distance between ventral setae 13-21 µ; long terminal setae 60-75 µ; shield length 89-95 µ; dorso-posterior seta of tarsus 20-25 µ ..... ***P. mexicanus***
43. Shield length 72-78 µ; shield width 58-60 µ; terminal setae 36-43 µ; distance between ventral setae 6-7 µ; ventral part of empodium acute ..... ***P. etruscus***
- Shield width 66-75 µ 44
44. Shield length 78-85 µ; shield width 66-72 µ; terminal setae 49-58 µ; distance between ventral setae 13-18 µ; ventral part of empodium rounded . ***P. crocidurae***
- Shield length 86-93 µ; shield width 70-75 µ; distance between ventral setae 17-24 µ; ventral part of empodium rounded ..... ***P. doriae***

Key to the species (based on males)

1. Palpal tibial setae short (never more than 6 µ); dorso-anterior and dorso-posterior setae of tarsi strongly differing in length, sometimes dorso-posterior seta absent. Seta of genu IV relatively very long and strong (seta always longer than seta femur IV); *"insectivora"* group 33
- Palpal tibial setae longer (except in P. deomydis); dorso-lateral setae of tarsi subequal; genual setae subequal or not so pronounced as in the *"insectivora"* group (seta always shorter than femur IV seta) 2
2. Tibial spine on leg IV present 3
- Tibial spine on leg IV absent 7
3. Genual setae I-IV setiform; length of proximal seta of femora I-IV at least half of distal seta; gnathosomal setae short with subequal lobes.."sciuricola" group 5
- Genual setae I-IV reduced to short spines; proximal femoral seta reduced to short spine 4
4. Length penis 36-39 µ; length penis sheath 24-28 µ; distance between ventral setae 9-12 µ, between a.m. setae 25-28 µ ..... ***P. tupaiae***
- Length penis 20-28 µ; length penis sheath 15-21 µ; distance between ventral setae 6-9 µ, between a.m. setae 23-25 µ ..... ***P. ramai***
5. Tibial spine strong; femoral spur acute; tarsal spine strong, two-pointed; genu IV

seta short 6-7 µ; penis sheath very long 38-45 µ; distance between a.m. setae 29-32 µ ..... ***P. paraxeri***

- Penis sheath 10-18 µ 6

6. Tibial spine strong; femoral spur blunt; tarsal spine strong, truncate; genu IV seta long 17-19 µ; penis sheath c. 18 µ; distance between a.m. setae 20-23 µ ..... ***P. dremomydis***

- Tibial spine thin, hair-like; femoral spur acute; tarsal spine strong, one-pointed; genu IV seta long c. 23 µ; penis sheath c. 10 µ; distance between a.m. setae c. 20 µ ..... ***P. glaucomys***

7. Setae genua I-III and genu IV subequal long 4-5 µ; palpal tibial setae strong, like broken off, shorter than 10 µ; *"muricola"* group 8

- Setae genua I-III and genu IV of different length; palpal tibial setae filiform, longer than 10 µ (except in *P. deomydis*) 13

8. Terminal setae absent ..... ***P. oettlei***

- Terminal setae present 9

9. Dorsal shield oval, length and width differing 10 µ or more 10

- Dorsal shield approximately circular 11

10. Shield width 66 µ; length penis 28 µ; length penis sheath 19 µ; femoral setae 15-18 µ ..... ***P. rattus***

- Shield width 75 µ; length penis 42 µ; length penis sheath 27 µ; femoral setae 10-12 µ ..... ***P. agrestis***

11. Body length 99-105 µ; body width 81-90 µ; terminal setae 70-80 µ; lateral shield setae c. 3 µ; penis length 39-42 µ ..... ***P. hispanicus***

- Lateral shield setae 5-7 µ 12

12. Body length 108-126 µ; body width 91-101 µ; terminal setae 55-62 µ; lateral shield setae 5-6 µ; penis length 42-47 µ ..... ***P. simplex*** neotype

- Body length 105-111 µ; body width 93-94 µ; terminal setae 60-65 µ; lateral shield setae 6-7 µ; penis length 34-38 µ ..... ***P. muricola***

13. Distance between ventral setae very small 2-5 µ; ventral setae 12 µ; lateral shield setae 8-12 µ ..... ***P. musculinus***

- Distance between ventral setae more than 5 µ 14

14. Distance between ventral setae more than 20 µ; length ventral setae 4-5 µ; lateral shield setae 3-5 µ; *"dissimilis"* group 15

- Distance between ventral setae 5-20 µ 22

15. Genual setae I-III and genual seta IV subequal long c. 4 µ; setae femora I-III c. 10 µ; setae femur IV c. 12 µ ..... ***P. micromydis***

- Genual setae I-III and genual seta IV of different length; femoral setae I-III 15 µ or more; femoral setae IV 16 µ or longer 16

16. Length penis sheath more than 30 µ 17

- Length penis sheath less than 30 µ 19

17. Distance between ventral setae 24 µ; length penis 36-40 µ; length penis sheath 33-35 µ; shield width 56-62 µ; terminal setae 37-48 µ ..... ***P. watsoni***

- Distance between ventral setae more than 30 µ 18

18. Distance between ventral setae 32 µ; length penis 40-44 µ; length penis sheath 34-38 µ; shield width 63-68 µ; terminal setae 16-38 µ ..... ***P. canadensis***

- Distance between ventral setae 40-49 µ; length penis sheath 35-0 µ; shield width 71-98 µ; terminal setae 13-32 µ ..... ***P. townsendi***

19. Length penis 45-50 µ; shield length 100-111 µ; shield width 90-96 µ *P. zibethicalis*
- Penis shorter than 45 µ; shield length less than 100 µ; shield width less than 85 µ 20
20. Seta genua I-III 5 µ; seta genu IV 14 µ; length penis 38 µ; palpal tibial setae 3-4 µ; length penis sheath 20 µ; gnathosomal setae 4-5 µ ..... *P. oeconomi*
- Length penis sheath 24-29 µ 21
21. Seta genua I-III 4-6 µ; seta genu IV 12-13 µ; length penis 39-42 µ; palpal tibial setae 1-2 µ; length penis sheath 24-29 µ; gnathosomal setae 2-3 µ ..... *P. dissimilis*
0- Seta genua I-III 8 µ; seta genu IV 15-20 µ; length penis 33-38 µ; palpal tibial setae 4-5 µ; length penis sheath 24-27 µ; gnathosomal setae 5-6 µ ..... *P. auricola*
22. Dorsal shield approximately circular, or sometimes wider than long; length ventral setae 6 µ or less; palpal tibial setae longer than 8 µ (except P. deomydis) "apodemi" group 26
- Dorsal shield oval, longer than wide 23
23. Length ventral setae 6 µ or more; palpal tibial setae shorter than 8 µ *"gliricola"* group 25
- Length ventral setae 5-8 µ, palpal tibial setae 10-15 µ 24
24. Shield length 78-86 µ; shield width 66-70 µ; trochanter setae 8-9 µ; femoral setae 11-19 µ ..... *P. peromysci*
- Shield length 103-113 µ; shield width 96-98 µ; trochanter setae 14-18 µ; femoral setae 23-35 µ ..... *P. alleni*
25. Length penis 29-34 µ; length penis sheath 18-24 µ; distance between a.m. setae 8-9 µ; distance between genital setae 3-5 µ; genital and a.m. setae very close-set .... *P. muscardinus*
- Length penis 46-52 µ; length penis sheath 28-31 µ; distance between a.m. setae 24-25 µ; distance between genital setae 19-20 µ ..... *P. quercinus*
26. Palpal tibial setae very small 1-2 µ; length penis sheath 24-25 µ; distance between a.m. setae 18 µ; distance between genital setae 10 µ ..... *P. deomydis*
- Palpal tibial setae longer than 8 µ 27
27. Length penis sheath more than 30 µ 28
- Length penis sheath less than 30 µ 29
28. Palpal tibial setae 15-18 µ; shield length 84-90 µ; shield width 78-87 µ .... *P. callipidis*
- Palpal tibial setae 10-13 µ; shield length 75-85 µ; shield width 76-78 µ *P. apodemi*
29. Length penis sheath 24-26 µ 30
- Length penis sheath 20-23 µ 31
30. Dorsal shield wider than long, shield length 69 µ, shield width 75 µ; terminal setae c. 66 µ ..... *P. arvalis*
- Dorsal shield circular, shield length 65-70 µ, shield width 65-73 µ; terminal setae 45-55 µ ..... *P. microti*
31. Length penis 33-36 µ; lateral shield setae 5-7 µ; length femur IV setae 15 µ .... *P. pitimydis*
- Length femur IV setae 19-25 µ 32
32. Length penis 24-30 µ; lateral shield setae 4 µ; length femur IV setae 19-20 µ .... *P. neerlandicus*
- Genua I-III seta 6-7 µ; genu IV seta 17-20 µ; femur IV setae 20-25 µ . *P. pinetorum*
33. Tarsal claws one-pointed; dorso-posterior seta of tarsi I-III present; two setae on

femur IV; rectangular formation of a.m. and genital setae; *"talpidae"* group 36
- Tarsal claws two- or three-pointed 34
34. Tarsal claws two-pointed 35
- Tarsal claws three-pointed; dorso-posterior seta of tarsi I-III absent; two setae on femur IV; rectangular formation of a.m. and genital setae; *"crocidurini"* group . 40
35. Tarsal claws two-pointed; dorso-posterior seta of tarsi I-III present; one seta on femur IV; ventral part of empodium rounded; linear formation of a.m. and genital setae; *"soricini"* group 38
- Tarsal claws two-pointed; dorso-posterior seta of tarsi I-III present; one seta on femur IV; ventral part of empodium acute; linear formation of a.m. and genital setae; shield length 67-72 µ; shield width 50-55 µ ..... ***P. cryptotis***
36. Seta trochanter 4 µ; shield length c. 75 µ; shield width c. 65 µ .....***P. urotrichi***
- Seta trochanter longer than 8 µ; seta genua I-III 3-4 µ; seta tibia 8-12 µ 37
37. Terminal setae 72-89 µ; setae femora I-III 15-20 µ; shield length 84-90 µ; shield width 75-81 µ ..... ***P. desmanae***
- Terminal setae 51-54 µ; setae femora I-III 25-28 µ; shield length 72-74 µ; shield width 62-66 µ ..... ***P. talpae***
38. Penis very long 50-51 µ; dorso-posterior seta of tarsi I-III c. 7 µ; seta trochanter 3 µ ..... ***P. squamipes***
- Penis shorter than 40 µ; dorso-posterior seta of tarsi longer than 11 µ; seta trochanter longer than 5 µ 39
39. Penis sheath 20-23 µ; setae femora I-III 12-16 µ; seta femur IV 14-19 µ; shield length 75-78 µ; shield width 63-70 µ ..... ***P. cinereus***
- Penis sheath 11-14 µ; setae femora I-III 20-25 µ; seta femur IV 20-25 µ; shield length 70-78 µ; shield width 57-62 µ ..... ***P. sorici***
40. Shield length 76 µ; shield width 56 µ; distance between first and second pair of lateral shield setae smaller than distance between second and third pair ..... ***P. etruscus***
- Subequal distances between lateral shield setae 41
41. Shield length 75-84 µ; shield width 64-70 µ; distance between ventral setae 12-14 µ; trochanter setae 8-9 µ; distance between a.m. setae 12-13 µ ..... ***P. crocidurae***
- Shield length 79-92 µ; shield width 61-73 µ; distance between ventral setae 11-19 µ; trochanter setae 3 µ; distance between a.m. setae 15-16 µ ..... ***P. doriae***

N.B. Males of *Psorergates baueri* and *Psorergates mexicanus* are unknown.

Psororbia Fain, 1959
(fig. 27, tables 2-4)

Fain (1959) formed a new genus *Psorobia* for the single species *P. ovis* with the differentiating character of fused epimera I. Although *P. cercopitheci* was already described at that time he did not include this species in the new genus, because it did not have fused epimera I. After reexamining paratypes of *P. ovis* Fain (1961) concluded that the fused epimera I were an artifact of the previously examined specimen. He redefined *Psorobia* and reduced it to a subgeneric status with the new definition: there are 5 pairs of dorsal shield setae, the 4 lateral pairs (*sc i, c, d, e*) well measurable

Table 2. Measurements and numerical data of the genus *Psororbia*, females; n.o. = not observed.

	bos (N= *) min-max	*ovis* (N= *) min-max	*castoris* (N= *) min-max	*foinae* (N= *) min-max	*mustelae* (N= *) min-max
body length	135-145	177-220	161-187	153-160	141-159
body width	113	126-170	134-166	132-135	114-134
shield length	105	153	117-129	103	93-105
shield width	95	142	108-120	105	
length setae					
terminal	100	140-160	113-12	120-130	100-120
trochanter	n.o.	20	11-18	16	7-10
femora I-III	25	25	11-18	20-25	18-25
femur IV	25	25	15-19	20-25	20-25
genua I-III	n.o.	8	3	4	3
genu IV	45	60	14-21	50-60	48-61
lateral shield	12-14	15-18	5-6	6-8	5-6
palpal tibial	28	25	14-21	18-20	18-22
gnathosomal	n.o.	6	5-6	5-6	5-6
ventral	n.o.	10	5-6	5-6	5-6
distance between.					
ventral setae	n.o.	11	6-9	12	15-21
no setae femur I-III	2	2	2	2	2
no setae femur IV	2	2	2	2	2
tibial spine IV	present	present	absent	absent	absent

Table 3. Ditto: females of the genus*Psorobia* (continued); * = number of measured specimens unknown.

	zumpti (N= *) min-max	*hystrici* (N= *) min-max	*elephantuli* (N=4) min-max	*lagomorphae* (N=18) min-max	*cercopitheci* (N= *) min-max
body length	120-138	140-150	135-149	111-131	117-132
body width	105-126	120-150	108-122	107-119	100-115
shield length	105	90-100	95-105	97-101	78
shield width	100	90-100	82-90	93-101	84
length setae					
terminal	100	90	105-112	99-123	60
trochanter	20	12	22-24	19- 26	12
femora I-III	22	15-18	24-29	21-27	12-15
femur IV	30	15-18	34-46	20-30	12-15
genua I-III	5	6	5-6	9-13	absent
genu IV	60	6	56-73	62- 78	absent
lateral shield	5-6	5-6	6-8	4-5	6
palpal tibial	14-16	25-32	17-21	14-15	18
gnathosomal	5	30	7-8	8-10	8
ventral	5-6	5	6-7	8-11	6
distance between					
ventral setae	13	6	11-15	7-15	9
no setae femur I-III	2	2	2	1	1
no setae femur IV	1	1	2	1	1
tibial spine IV	absent	present	present	absent	present

(4-18 μ), the antero-median (*v e*) pair short and spine-like; posterior palpal tibial (*dF*) setae serrated and long. Up till now the definition has not changed, but the phylogenetic analysis learns that the genus *Psorobia* is not a monophyletic group. Clear relationships with unequivocal apomorphic characteristics could not be defined though and therefore I suggest to retain the genus with the definition given by Fain (1961).

Table 4. Measurements and numerical data of the genus *Psorobia*, males; * = number of measured specimens unknown; n.o. = not observed.

	bos (N=1)	*ovis* (N= *) min-max	*castoris* (N= *) min-max	*foinae* (N= *) min-max	*mustelae* (N= *) min-max
body length	159	153-186	168-175	144	126-147
body width	127	111-135	136-144	117-120	111-122
shield length	113	129	125-127	30 & 66-72	90-104
shield width	98	120	106-110	63-71 & 92-93	85-97
length setae					
terminal	190	150	107-127	120-130	100-125
trochanter	14	16	10-13	16	7-8
femora I-III	28	20	16-19	20-25	18-20
femur IV	24	20	16-19	20-25	16-18
genua I-III	6	5	4	4	2-3
genu IV	50	42-53	20-24	50-60	51-63
lateral shield	16	16	7	6-8	5-6
palpal tibial	27	20	17-22	17	18-21
gnathosomal	14	5-6	5	7	5-6
ventral	9	9	5	6	5-6
distance between					
ventral setae	7	11	10-11	7	10-16
a.m. setae	41	9	17	11	12-14
genital setae	7	36	24-25	21	19- 26
length penis	47	57	31-33	42	42-45
length penis sheath	n.o.	30	19-24	26-30	30-33
no setae femur I-III	2	2	2	2	2
no setae femur IV	2	2	2	2	2
tibial spine IV	present	present	absent	absent	absent

Key to the species (based on females)

1. Two setae present on femur IV. 2
- One seta present on femur IV. 7
2. Spine on tibia IV present 4
- Spine on tibia IV absent 5
3. Tarsal spine bifid 4
- Tarsal spine one-pointed; femur IV setae 34-46 μ; lateral shield setae 6-8 μ ..... ***P. elephantuli***
4. Terminal setae 140-160 μ; shield length 153 μ; shield width 142 μ ..... ***P. ovis***
- Terminal setae 100 μ; shield length 105 μ; shield width 95 μ ..... ***P. bos***
5. Seta genu IV longer than 45 μ 6

Table 4. Measurements and numerical data of the genus *Psorobia* males (continued); ~ = approximately.

	zumpti (N= *) min-max	*hystrici* (N= *) min-max	*elephantuli* (N=1)	*cercopitheci* (N= *) min-max
body length	117-126	118-132	132	105-125
body width	105-110	110-122	95	90-107
shield length	95	90-98	95	66
shield width	95	88-90	83	78
length setae				
terminal	120	60	123	50
trochanter	12-14	n.o.	22	8
femora I-III	18-20	n.o.	23	9-10
femur IV	27-30	n.o.	37	9
genua I-III	4-6	n.o.	5	absent
genu IV	50-60	n.o.	55	absent
lateral shield	5-6	5	6	6
palpal tibial	18	25	18	15
gnathosomal	5	25	8	7
ventral	5	n.o.	6	5
distance between				
ventral setae	12	n.o.	12	13
a.m. setae	11	n.o.	16	17
genital setae	23	n.o.	23	5
length penis	35	~47	83	24
length penis sheath	30	~42	23	10
no setae femur I-III	2	2	2	1
no setae femur IV	1	1	2	1
tibial spine IV				

- Seta genu IV 14-21 µ ..... ***P. castoris***
6. Trochanter seta c. 16 µ; distance between ventral setae c. 12 µ ..... ***P. foinae***
- Trochanter seta 7-10 µ; distance between ventral setae 15-21 µ ..... ***P. mustelae***
7. Two setae present on femora I-III 9
- One seta present on femora I-III 8
8. Tibial spine present; genual setae absent ..... ***P. cercopitheci***
- Tibial spine absent; genual setae I-III 9-13 µ; genu IV seta 62-78 µ ..... ***P. lagomorphae***
9. Tibial spine on leg IV absent; genual seta IV very long c. 60 µ ..... ***P. zumpti***
- Tibial spine on leg IV present; genual seta IV short c. 6 µ ..... ***P. hystrici***

Key to the species (based on males)

1. Two setae present on femur IV 2
- One seta present on femur IV 7
2. Spine on tibia IV present 3
- Spine on tibia IV absent 5
3. Tarsal spines bifid 4

- Tarsal spines one-pointed; shield length 95 μ; shield width 83 μ; length penis 83 μ; length penis sheath 23 μ ..... ***P. elephantuli***
4. Terminal setae c. 150 μ; shield length c. 129 μ; shield width c. 120 μ ..... ***P. ovis***
- Terminal setae at least 190 μ; shield length c. 113 μ; shield width c. 98 μ ..... ***P. bos***
5. Penis length 31-33 μ; seta genu IV 20-24 μ ..... ***P. castoris***
- Penis length more than 35 μ; seta genu IV longer than 50 μ 6
6. Two dorsal shields; distance between ventral setae c. 7 μ ..... ***P. foinae***
- One dorsal shield; distance between ventral setae 10-16 μ ..... ***P. mustelae***
7. Two setae present on femora I-III 8
- One seta present on femora I-III; tibial spine present on leg IV ..... ***P. cercopitheci***
8. Tibial spine on leg IV present; terminal setae c. 60 μ; gnathosomal setae c. 25 μ ..... ***P. hystrici***
- Tibial spine on leg IV absent; terminal setae c. 120 μ; gnathosomal setae c. 5 μ ..... ***P. zumpti***

N.B. The male of *Psorobia lagomorphae* is unknown.

Psorergatoides Fain, 1959
(tables 5, 6)

The genus *Psorergatoides* was first described as a subgenus by Fain (1959) defined by the very short (point-like) dorsal shield setae. The female having four pairs of lateral shield setae (*sc i, c, d, e*) and one pair of antero-median (*v e*) setae, and the male having four pairs of lateral shield setae (*sc i, c, d, e*), a pair of antero-median (*v e*) setae and a pair of genital (*ps*) setae. The genus was redefined by Fain (1961) with the same characteristics described above and the additional character of having serrated posterior palpal tibial (*dF*) setae. This monophyletic genus is still defined by the same characteristics. Phylogenetic relationships of the many lower taxa are equivocal and therefore no attempt is made to formate groups as has been done with the genus *Psorergates*.

Key to the species (based on females)

1. Two setae on femora I-III, one seta of femur IV present 2
- One seta on all femora 5
2. Terminal setae longer than 75 μ 3
- Terminal setae shorter than 50 μ 4
3. Shield length 105-112 μ; shield width 100-110 μ; setae femora I-III 20-27 μ, seta genu IV 17-29 μ ..... ***P. australiensis***
- Shield length 130 μ; shield width 126 μ; setae femora I-III 15-20 μ; seta genu IV 15-18 μ ..... ***P. kerivoulae***
4. Setae femora I-III 4-6 μ; seta genu IV 1-2 μ; shield length 135 μ; shield width 130 μ ..... ***P. nycteris***
- Setae femora I-III 13-18 μ; seta genu IV 19-23 μ; shield length 75-81 μ; shield width 70-79 μ ..... ***P. tadaridae***

5. Ventral setae absent 6
- Ventral setae present 8
6. Tarsal claws two-pointed, seta femora I-III shorter than 5 µ 7
- Tarsal claws one-pointed; seta femora I-III c. 10 µ ..... *P. emballonurae*
7. Terminal setae 5 µ; shield length 112 µ; shield width 94 µ ..... *P. indicicola*
- Terminal setae 20-39 µ; shield length 76-88 µ; shield width 70-83 µ *P. peropteryx*
8. Seta femora I-III 1-12 µ 9
- Seta femora I-III 12-20 µ 14
9. Terminal setae longer than 55 µ 10
- Terminal setae shorter than 45 µ 11
10. Tarsal claws two-pointed; shield length 104 µ; shield width 99 µ . ..... *P. artibei*
- Tarsal claws one-pointed; shield length 94 µ; shield width 85 µ ..... *P. guyanensis*
11. Seta femora I-III 12 µ; shield length 118 µ; shield width 103 µ.....*P. glossophagae*
- Seta femora I-III 1-4 µ; shield length less than 100 µ; shield width less than 95 µ 12
12. Shield length 80 µ; shield width 80 µ; terminal setae 32-40 µ .....*P. molossi*
- Shield length 88-94 µ; shield width 77-90 µ; terminal setae 20-30 µ 13
13. Body length 102-118 µ; shield width 78 µ; genual setae present 1-2 µ; gnathosomal setae 2 µ ..... *P. lonchorhina*
- Body length 132-146 µ; shield width 77-90 µ; genual setae absent; gnathosomal setae 5-6 µ ..... *P. surinamensis*
14. Tarsal spine one-pointed; shield length 84 µ; shield width 85 µ ... *P. hipposideros*
- Tarsal spine bifid; shield length and shield width different 15
15. Genual seta IV 17 µ; seta femora I-III 20 µ; palpal tibial seta 15 µ ..... *P. desmodus*
- Genual seta IV less than 5 µ; seta femora I-III 12-15 µ; palpal tibial setae 20-21 µ 16
16. Genual seta I-IV absent; shield length 79 µ; shield width 72 µ ..... *P. rhinolophi*
- Genual seta I-IV c. 4 µ; shield length 120 µ; shield width 116 µ ..... *P. laviae*

Key to the species (based of males)

1. Two setae on femora I-III, one seta on femur IV present 2
- One seta on all femora present 4
2. Shield length 69-74 µ; shield width 59-65 µ; palpal tibial seta 6-8 µ .. *P. tadaridae*
- Shield length more than 85 µ; shield width more than 80 µ; palpal tibial seta 12-14 µ 3
3. Shield length 90-102 µ; shield width 84-98 µ; genu IV seta 16-18 µ *P. australiensis*
- Shield length c. 120 µ; shield width c. 90 µ; genu IV seta 8-9 µ .....*P. kerivoulae*
4. Ventral setae absent 5
- Ventral setae present 7
5. Tarsal claws one-pointed; distance between a.m. setae 11 µ; distance between genital setae 11 µ ..... *P. emballonurae*
- Tarsal claws bifid; distance between a.m. setae 2-3 µ 6
6. Shield length 103 µ; penis sheath 18-22 µ; terminal setae 5-10 µ ..... *P. indicicola*
- Shield length 72-81 µ; penis sheath 10 µ; terminal setae 18-34 µ ..... *P. peropteryx*
7. Terminal setae absent 8

- Terminal setae present 12
8. Tarsal claws bifid; shield length 97 μ; shield width 83 μ; distance between ventral setae 15-35 μ ..... ***P. artibei***
- Tarsal claws one-pointed 9
9. Dorsal shield length and width c. 69 μ 10
- Shield length and shield width different, more ovally shaped 11
10. Distance between ventral setae 12 μ; distance between genital setae 5 μ ..... ***P. molossi***
- Distance between ventral setae c. 5 μ; distance between genital setae 9-10 μ ..... ***P. lonchorhina***
11. Body length 156-179 μ; body width 117-140 μ; shield length 101 μ; shield width 79 μ ..... ***P. glossophagae***
- Body length c. 121 μ; body width 94-98 μ; shield length 74-76 μ; shield width 67-68 μ ..... ***P. surinamensis***
12. Tarsal spine bifid 13
- Tarsal spine one-pointed; distance between a.m. setae 6-7 μ; length penis 42 μ..... ***P. hipposideros***
13. Distance between genital setae 14-15 μ; body width 81-86 μ ..... ***P. rhinolophi***
Distance between genital setae 8 μ; body width 85-105 μ ..... ***P. desmodus***

N.B. The males of *P. guyanensis*, *P. nycteris* and *P. laviae* are unknown.

Pathology

Three types of infections can be observed when a host is parasitized by psorergatic mites (Lukoschus, 1967). Some species live between the stratum lucidum and stratum corneum, mostly in the inner ear concho. The mites are nestled in shallow pits of the epidermis in the shape of the mites (see also Giesen et al., 1989). Beneath the parasites the stratum granulosum lacks the nuclei, or they are sickle-shaped towards the epidermis surface. The affected cells show at the side of the mite a larger vacuole, an effect of the sucking of the psorergatic mite after piercing the cell wall with its stylet-shaped movable digits of the chelicerae. At the sides of the mite's nestling a clear outgrowing of the stratum germanitivum is visible. The epidermis at infected places is thicker than normal. Between the stratum germanitivum and the stratum granulosum another one to three cell layers are visible due to cell divisions of the stratum germanitivum. Furthermore the stratum corneum is more than twice as thick (hyperkerastosis). Females without eggs mostly nestle in shallow pits of the epidermis (see also Downing & Mort (1962), Murray (1961), Carter (1941) and Sheldon (1966)). Females with eggs lie in very superficial pits of the epidermis. Here mostly the stratum corneum is loosened in a greater area of the epidermis. The females wander around and deposit their eggs on the surface of the skin under the fine scurf.

A second kind of infection is found at the tibia of the legs of the hosts, where the hair implantation is scarce. This same type of infection is also found around the genital region of hosts where hair implantation is also scarce. The mites are nestled in pits of the epidermis. The pathological phenomena beneath the mites are the same as

described above, but the stratum corneum shows a much stronger hyperkerastosis. The connective tissue sidewards of the mites is hypertrophying. In this case the egg laying female is staying in one place (pit) of the epidermis, and all the descendants are staying too. So the infection is much more rigorous, and morbid growth of the epidermis is shown.

The third kind of infection concerns hair follicles in regions of the femur of the legs of hosts, where the hair implantation is thicker. The mites nestle in pits in the hair follicle in the hair root sheath. They feed on the nuclei of the root sheath and cause hypertrophy of the cells between the different parasites in the hair follicles. The nuclei of the root sheath are strongly enlarged and strongly increased in number. The hair follicles which are parasitized show strong hyperkerastosis. In one hair follicle mostly more females with eggs are present. In strong infections the root sheath is often disrupted to neighbouring infested hair follicles thus forming big cysts, which enclose more hairs.

Phylogenetic relationships of the species groups of the family Psorergatidae

Character state polarities

1. Number of lateral shield setae. The genera *Psorobia* and *Psorergatoides* exhibit 4 pairs of lateral shield setae (*sc i, c, d, e*). The genus *Psorergates* shows 3 pairs of setae on the dorsal shield (*sc i, c, d*). Comparison with the outgroup learns that 4 pairs of lateral shield setae as in the first two genera mentioned should be considered the ancestral state. 1a. Four pairs of lateral shield setae present; 2a. Three pairs of lateral shield setae present.

2. Length of lateral shield setae. In the genus *Psorergatoides* the lateral shield setae are very reduced. Only point-like setae remain, and sometimes even these are reduced leaving the alveoli as the indicators of setae. The genera *Psorobia* and *Psorergates* always have good measurable setae on the dorsal shield, ranging from a little longer than 2 µ to well over 30 µ. The totally reduced setae of the genus *Psorergatoides* are considered apomorphic. 2 a. Lateral shield setae longer than 2 µ. 2 b. Lateral shield setae point-like, or sometimes totally absent.

3. Form of palpal tibial setae (*dF*). In the outgroup and the genera *Psorobia* and *Psorergatoides* the palpal tibial setae are serrated. In the genus *Psorergates* these setae are smooth. The latter state is considered to be the derived one.3 a. Palpal tibial setae serrated. 3 b. Palpal tibial setae smooth.

4. Sexual dimorphism in the palpal tibial setae (*dF*). The only species of the family which show sexual dimorphism in the palpal tibial setae are the "dissimilis" group of the genus *Psorergates* and *Psorergates musculinus*. This last species is considered to be the sistergroup of the "*dissimilis*" group according to Giesen & OConnor (1987) with the synapomorphy of this very character state. No sexual dimorphism of the palpal tibial setae is considered to be the ancestral state. 4 a. No sexual dimorphism of the palpal tibial setae. 4 b. Sexual dimorphism of palpal tibial setae present.

5. Distance between ventral setae (*ic III*). Three different character states can be distinguished. The ventral setae can be very close-set (less than 3 µ apart) as in the species *Psorergates musculinus*, they can be further apart over a broad range between 3 and 25 µ as in most species of the family, and they can be very wide-set (over 30 µ

apart) as in the *"dissimilis"* group of the genus *Psorergates*. The median range of distances between the ventral setae is considered to be ancestral. The other states are both apomorphic. 5 a. Distance between ventral setae ranging from 3 to 25 μ. 5 b. Distance between ventral setae less than 3 μ. 5 c. Distance between ventral setae more than 30 μ.

6. Length palpal tibial setae (*dF*). Besides being smooth or serrated the palpal tibial setae exhibit different lengths and strengths. Some setae are very short (less than 6 μ), and truncate. This character state is shown by the *"muricola"* and *"insectivora"* groups of the genus *Psorergates*. Others are of a median range between 7 and 25 μ and show the same truncate form as the short and stout palpal tibial setae. Lastly these setae can be very long (more than 25 μ) and filiform as in *Psorobia bos, Psorobia hystrici,* the *"dissimilis"* group (females) of the genus *Psorergates,* and *Psorergates musculinus*. The outgroup exhibits truncate, medium sized, truncate palpal tibial setae (*dF*). Therefore the medium-sized palpal tibial setae is considered to be the ancestral state and the other two states to be derived. 6 a. Length palpal tibial setae between 7 and 25 μ. 6 b. Length palpal tibial setae less than 6 μ. 6 c. Length palpal tibial setae more than 25 μ.

7. Ventral setae (*ic III*). In three species of the genus *Psorergatoides (P. peropteryx, P. emballonurae, P. indicicola)* the ventral setae are absent. In all other species of the family these setae are present, which is considered to be ancestral. 7 a. Ventral setae present. 7 b. Ventral setae absent.

8. Sclerotized genital ducts. These ducts are present in the *"apodemi"* and *"muricola"* groups of the genus *Psorergates*. All other species of the family and the outgroup do not possess these ducts. The presence of these ducts is considered to be the derived state. 8 a. Sclerotized genital ducts absent. 8 b. Sclerotized genital ducts present.

9. Sclerotized genital atrium. An unsclerotized atrium is present in all species of the family except in the species of the *"gliricola"* group of the genus *Psorergates* and the species *Psorergates glaucomys* and *P. paraxeri* of the *"sciuricola"* group. The unsclerotized atrium is considered to be ancestral. 9 a. Unsclerotized genital atrium. 9 b. Sclerotized genital atrium.

10. Shape dorsal shield. In some species and species groups of the family the dorsal shield is longer than wide (oval) as in the genus *Psorergates* the *"gliricola"* group, *P. musculinus, P. alleni, P. peromysci,* and the *"insectivora"* group. In the genus *Psorobia* the species *P. bos, P. ovis, P. elephantuli* have a longer than wide shield. All other species of the family have a circular or wider than long shield. The character state polarity of this character could not be determined. Also the not very coherent distribution of this character among the species of the family makes it a less valuable character. Although it could be used for species and species group definition the shape of the dorsal shield only contributes to the formation of a number of paraphyletic or polyphyletic groups. This character is mentioned here in order to be as elaborate as possible in the character analysis, but will not be used in the analyses themselfs. 10 a. Dorsal shield longer than wide. 10 b. Dorsal shield wider than long, or circular.

11. Relative position of antero-median (*v e*) and genital (*ps*) setae in males. Within the genus *Psorergates* this character has been used to diagnose some groups. This has been done for the *"apodemi"*, *"muricola"*, and *"dissimilis"* groups by Lukoschus et al. (1967) and for the *"insectivora"* group by Giesen & Lukoschus (1983). In the *"dissim-*

ilis", *"muricola"*, *"gliricola"* groups, some species of the *"insectivora"* group, and *P. musculinus* the distance between the genital and the antero-median setae differs at the most a factor 1.7. In the *"apodemi"* and *"sciuricola"* groups, two subgroups of the *"insectivora"* group, and in *P. tupaiae* and *P. ramai* the distances between these setae differ at least 1.8. *Psorobia cercopitheci* and *Psorobia castoris* show a ratio smaller than 1.7 for the distances between these setae. In the other species of this genus the distances between these setae differ at least 1.8. All species of the genus *Psorergatoides* except *P. surinamensis, P. tadaridae* and *P. indicicola* have distances between the a.m. and genital setae which differ at the most 1.7. 11a. Ratio between distance of antero-median and distance of genital setae more than 1.8. 11b. Ratio between distance of antero-median and distance of genital setae less than 1.7.

12. Length of genual (*v"*) setae. The genual setae can exhibit two different states. The setae of all four genua can be subequal in length as in the *"muricola"* group, *P. paraxeri, P. glaucomys, P. tupaiae* and *P. ramai* of the genus *Psorergates; Psorobia hystrici* and *Psorobia cercophitheci*, and in the genus *Psorergatoides P. peropteryx, P. nycteris, P. hipposideros, P. glossophagae, P. lonchorhina, P. molossi, P. emballonurae* and *P. laviae*. The other state shows a genual seta IV which is much longer than the genual seta on legs I-III. The latter is the case in all other species of the family, and is considered to be the ancestral state. 12a. Genual seta of leg IV much longer than setae of genua I-III. 12b. Genual setae of legs I-IV subequal.

13. Number of setae on femora I-IV. It is hypothesized that ancestrally two setae (v, v") are present on all femora. The species of the genus *Psorergatoides* show only one seta on femur IV, and all species except *P. australiensis, P. kerivoulae, P. tadaridae* and *P. nycteris* also have only one seta on femora I-III. A number of species of the "insectivora" group of the genus *Psorergates*, and *Psorobia zumpti, P. hystrici, P. cercopitheci* and *P. lagomorphae* also have only one seta on femur IV. More-over *Psorobia lagomorphae* and *Psorobia cercophitheci* have one seta on femora I-III. 13a. Two setae present on all femora.13b. Two setae present on femora I-III and one seta on femur IV. 13c. One seta present on all femora.

14. Loss of genual setae (*v"*). *Psorobia cercopitheci* has lost the genual seta on legs I-IV. In the genus *Psorergatoides* the species *P. surinamensis, P. indicicola and P. rhinolophi* the genual setae are also absent. In all other species of the family these setae are present. The latter state is considered to be ancestral. 14a. Genual setae I-IV present. 14 b. Genual setae I-IV absent.

15. Tibial spine IV (*l'*). In most species of the genus *Psorergates* this spine is absent, except in the species of the *"sciuricola"* group and *P. tupaiae* and *P. ramai*. This spine is present in all species of the genus *Psorergatoides* and in a number of species of the genus *Psorobia: P. bos, P. ovis, P. hystrici, P. cercopitheci* and *P. elephantuli* exhibit a tibial spine IV. The absence of the tibial spine IV is the derived character state. 15a. Tibial spine IV present. 15b. Tibial spine IV absent.

16. Shape of tarsal spines (*v'*). Spines are hypothesized to be derived from normal filiform setae. A further derivation of the setal shape could be imagined in the form of different shapes of the reduced setae. In the family Psorergatidae the spines of the tarsi normally are one-pointed and simple. Sometimes however a bifid spine is seen. This is the case in two of the three species of *"sciuricola"* group of the genus *Psorergates*, and in most species of the genus *Psorergatoides* except in *P. hipposideros, P. indicicola* and *P. peropteryx*. 16a. Tarsal spine simple, one-pointed. 16b. Tarsal spine bifid.

17. Shape of empodium. In the family Psorergatidae the empodium consists of two lobes. These lobes are semi-circular and inserted between the claws on the praetarsi. The bigger, ventral lobe of this empodium exhibits a different shape in a number of species in the *"insectivora"* group of the genus *Psorergates*. The ventral part of the empodium is pointed in the species *P. doriae, P. etruscus, P. cryptotis, P. baueri,* and *P. mexicanus*. 17a. Shape of empodium rounded. 17b. Shape of empodium acute.

18. Shape of tarsal claws. In the outgroup and in most species of the family the tarsal claws are one-pointed. In some species of the *"insectivora"* group namely *P. cryptotis, P. baueri, P. mexicanus, P. sorici, P. cinereus, P. squamipes, Psorobia castoris, Psorergatoides artibei, Psorergatoides indicicola* and *Psorergatoides peropteryx* the tarsal claws are two-pointed. In the species *P. crocidurae, P. doriae and P. etruscus* of the *"insectivora"* group of the genus *Psorergates* even three points are present. The evolutionary sequence is hypothesized to be one-pointed, two-pointed, three-pointed. 18a. Tarsal claws one-pointed. 18b. Tarsal claws two-pointed. 18c. Tarsal claws three-pointed.

19. Terminal setae (*h* 1, *h* 2) in females. Normally the terminal setae are subequal in the species of the family. There is one exception for this: *Psorobia lagomorphae* shows strongly unequal *h 1* and *h 2* setae, in which the *h 1* seta is much shorter and thinner than the *h 2* seta. The strongly unequal terminal setae are considered to be derived. 19a. Terminal setae subequal. 19b. Terminal setae strongly differing in length and strength.

20. Relative length of femoral setae. In the species of Psorergatidae which possess two femoral setae on at least legs I-III a general reduction can be seen in the length of distal seta (*v"*). It is hypothesized that the subequal length of the femoral setae is ancestral. The first step is visible in the reduction of the distal setae to two-thirds or half the length of the proximal seta. Next a further reduction occurs to a spine-like seta of as in the species *Psorergates tupaiae* and *Psorergates ramai*. Finally the distal seta is totally reduced and only one seta is left on the femora (see character 13). A partly reduction of the distal seta occurs in the *"dissimilis"* group of the genus *Psorergates, Psorergates paraxeri,* most species of the *"insectivora"* group, and all species of the genus *Psorergatoides* with two setae on femora I-III. 20a. Femoral setae subequal. 20b. Femoral setae unequal, the distal seta being half to two-thirds the length of the distal seta. 20c. Distal seta reduced to spine-like seta.

21. Shape tibial spines (*l'*). Like the tarsal spines the tibial spines can exhibit different morphologies. Normally a single pointed spine is present, but in one species this spine is transformed and now has a two-pointed shape. This is the case in *Psorobia bos*. From a number of species no good descriptive material is present, or I did not have the possibility to examine material myself. For these species no definite answers could be given ofcourse and character state decisions remain open. 21a. Tibial spines one-pointed. 21b. Tibial spines two-pointed.

22. Dorso-anterior seta (*tc'*) of tarsi I-IV. Normally the two apical setae of the tarsi (*tc', tc"*) are subequal in length. In the *"insectivora"* group of the genus *Psorergates* however these two setae are strongly differing in length. For all these species applies that the dorso-anterior seta is reduced to a length of 1 to 5 μ. The dorso-posterior (*tc"*) seta can be normally developed or absent. The subequal length of the tarsal setae is considered to be the ancestral state. 22a. Dorso-anterior and dorso-posterior seta of tarsi subequal; dorso-anterior seta at least 5 μ long. 22b. Dorso-anterior seta

reduced to a length of 1-5 μ.

23. Dorso-posterior (*tc"*) seta of tarsi I-III. As already mentioned above the dorso-posterior and dorso-anterior setae of the tarsi are normally subequal. The dorso-posterior seta is absent in one subgroup of the *"insectivora"* group of the genus *Psorergates*. This applies to the species *P. crocidurae, P. doriae* and *P. etruscus*. In all other species of the family this seta is normally developed. The latter state is considered to be ancestral. 23a. Dorso-posterior seta of tarsi I-III normally developed. 23b. Dorso-posterior seta of tarsi I-III absent.

24. Length of femoral seta (*v*). As described in character 20 the distal seta of the femora shows a reduction in length and finally is totally absent. This trend in reduction of leg and body setae pursues in the proximal seta of femora I-IV. After total reduction of the distal seta a reduction in length of the proximal seta follows in a number of species of the genus *Psorergatoides*. The species *P. surinamensis, P. lonchorhina, P. molossi, P. indicicola*, and *P. peropteryx* show a femoral seta which is shorter than 5 μ. Setae of a length more than 5 μ are considered to be ancestral. 24a. Femoral setae longer than 5 μ. 24b. Femoral setae less than 5 μ.

25. Terminal setae (*h*) in males. The outgroup as well as most of the species of the family show at least two h setae. These setae are absent in one species of *Psorergates, P. oettlei*, and in a number of species of the genus *Psorergatoides, P. australiensis, P. kerivoulae, P. tadaridae, P. surinamensis, P. lonchorhina* and *P. molossi*. The presence of terminal setae is considered to be ancestral. 25a. Terminal setae present in males. 25b. Terminal setae absent in males.

26. Length terminal setae (*h 1, h 2*) in females. Normally the terminal setae are very well developed and relatively very long. In a few species of *Psorergatoides* these setae are reduced to a length shorter than 40 μ. This is the case in *P. nycteris, P. glossophagae, P. surinamensis, P. lonchorhina, P. molossi, P. emballonurae, P. indicicola*, and *P. peropteryx*. The reduction of the terminal setae is considered to be derived. 26a. Terminal setae longer than 40 μ. 26b. Terminal setae shorter than 40 μ.

27. Gnathosomal setae (*ep*). In all species except the *"sciuricola"* group of the genus *Psorergates* the gnathosomal setae are two-segmented. In the *"sciuricola"* group these setae are one-segmented, bilobed and enfolded by a pouch-like structure. The latter structure is considered to be derived. 27a. Gnathosomal setae two-segmented. 27b. Gnathosomal setae one-segmented, undivided.

Character analysis

The data for 35 different species and species groups (OTU's) were analyzed using the computer program Phylogenetic Analysis Using Parsimony (PAUP) version 2.4 for IBM-PC and compatibles developed by David L. Swofford. The analysis yielded one tree (fig. 23) with a length of 68 character state changes and a consistency index of 0.457. First I elucidate the tree generated by the PAUP program. Then I discuss some different arrangements with somewhat different hypotheses and abandoning the principle of parsimony.

Most of the characters and character states mentioned in the chapter about character state polarities are not recognizable in this form in any outgroup. An apomorphy for the entire family Psorergatidae is given by Moss et al. (in prep.). For polarity decissions and rooting of the trees a hypothetical ancestor is chosen with all characters in a plesiomorph condition. Here the first difficulty occurs, because one of the

species of the ingroup, *Psorobia elephantuli*, shows all characters in the hypothesized plesiomorphic condition too. It could be hypothesized that *P. elephantuli* is the ancestor of the family Psorergatidae (Wiley, 1981: 222-225). I could not find more usefull morphological characters to include in this analysis, but maybe ecological, genetic, physiological or geographical characters should be included too in inferring phylogenetic relationships of this family.The tree (fig. 23) shows that the genus *Psorergates* is monophyletic, the genus *Psorobia* clearly paraphyletic, and the genus *Psorergatoides* probably monophyletic. I will resume to latter genus in my discussion about different configurations of the tree found by the PAUP program.

Descending from the hypothetical ancestor are three groups. These sistergroups are the monophyletic *Psorobia elephantuli* with no apomorphic characters as already mentioned above; the also monophyletic species *Psorobia bos* and *P. ovis* with the apomorphies of having very long (more than 25 μ) palpal tibial setae, the ratio between distance of antero-median and distance of genital setae more than 1.8, and tibial spines two-pointed; and the last group consisting of all other species of the family with the apomorphy of lacking tibial spine IV. Within this last group the monophyletic genus *Psorergates*, characterized by the presence of three lateral shield setae and smooth palpal tibial setae, is the sistergroup of the genus *Psorergatoides* and all species of the genus *Psorobia*, except the three species mentioned above. The latter group is characterized by the presence of a circular or wider than long dorsal shield. The genus *Psorergates* falls into four groups with unclear relationships. The first of these four sistergroups, enclosing *P. musculinus* and the *"dissimilis"* group, is characterized by a sexual dimorphism of the palpal tibial setae, and very long palpal tibial setae in females. Within this group the *"dissimilis"* group with the apomorphic characters of the distance between the ventral setae more than 30 μ, a circular or wider than long dorsal shield and partly reduced proximal setae on femora I-IV, is the sistergroup of *P. musculinus* with ventral setae which are very close-set (distance less than 3 μ). The *"dissimilis"* group consists of eight species all with minor meristic differences. The second group of the genus *Psorergates* contains the species of the *"gliricola"* group with three species and the shared apomorphy of the presence of a sclerotized atrium. The third group is the *"insectivora"* group with members parasitizing Insectivora hosts. This group has palpal tibial setae which are shorter than 6 μ, the proximal seta on femora I-IV is two-thirds to half the length of the distal seta and the dorso-anterior seta of tarsi I-IV is less than 5 μ long. Within this group the species *P. desmanae*, *P. talpae* and *P. urotrichi*, all parasitizing hosts of the family Talpidae, are not characterized by any apomorphies. Latter species group is the sistergroup of the rest of the *"insectivora"* group, which shows the apomorphy of two- or three-pointed claws contrary to the single-pointed claws of the first group. Within this group the species *P. doriae*, *P. crocidurae* and *P. etruscus* from hosts of the Crocidurini (Soricidae) with the characteristics of an acute shaped ventral part of the empodia, three-pointed tarsal claws and the dorso-posterior seta of tarsi I-III absent are the sistergroup of two species groups from Blarinini and Soricini/Anourosoricini (Soricidae). The sister group of the *"crocidurini"* group has only one seta present on femur IV and the ratio of the distances between antero-median and genital setae in males is more than 1.8. Within this group the *Psorergates* species parasitizing Blarinini hosts with the apomorphy acute empodium is the sistergroup of the species group with *P. sorici*, *P. cinereus* and *P. squamipes* from Soricini/Anourosoricini hosts with the reversal of the

length of the proximal seta of femoral setae to a subequal length with the distal seta. The fourth group of the genus *Psorergates* consists of the *"gliridae"* group, the species parasitizing Tupaiidae, the *"muricola"* group, the *"apodemi"* group and the species *P. alleni* and *P. peromysci* showing the presence of sclerotized ducts as a derived character. Within latter group the species *P. alleni* and *P. peromysci* are the sister group of all the others with a circular shield as distinghuishing character. The sistergroup of these two species exhibits the characteristic of having a ratio between the distances of antero-median and genital setae in males being more than 1.8. Within latter group the *"muricola"* group with short palpal tibial setae and subequal short genual setae on legs I-IV is the sistergroup of the *"apodemi"* group, *"sciuricola"* group and the species from tupaiid hosts characterized by a ratio more than 1.8 of antero-median and genital setae. The *"apodemi"* group with no apomorphies is the sistergroup of the *"sciuricola"* group and *P. tupaiae* and *P. ramai* exhibiting reversals of sclerotized genital ducts in females (no such ducts visible), and the tibial spine on legs IV. Within latter group *P. dremomydis* is the sistergroup of *P. paraxeri* / *P. glaucomys* and *P. tupaiae* / *P. ramai* with undivided gnathosomal setae as apomorphy. The latter two groups are characterized by subequal genital setae on legs I-IV, and a reduction of the proximal femoral setae. This reduction of the proximal femoral setae is even more pronounced in the species from Tupaiidae where this seta is reduced to a short, strong spine. This and the short palpal tibial setae (less than 6 μ) are the apomorphies of *P. tupaiae* and *P. ramai*. Their sistergroup are the species *P. paraxeri* and *P. glaucomys* with a sclerotized genital atrium present, two-pointed tarsal spines and an undivided gnathosomal seta.

The sistergroup of the genus *Psorergates* is characterized by a circular or wider than long dorsal shield. Within this group the species group infesting Carnivora (*Psorobia foinae* and *P. mustelae*), exhibiting no apomorphic characteristics, is the sistergroup of all other species, showing a reduction of the proximal femoral setae to two-thirds or half the length of the distal setae. In this latter group *Psorobia castoris* with the derived character of having two-pointed tarsal claws is the sistergroup of the clade characterized by two setae on femora I-III and one seta on femur IV. At this point the tree shows another multifurcation. The clade splices in three sistergroups; one containing *Psorobia zumpti* with no derived character states; one containing *Psorobia lagomorphae* with one seta on all femora, and strongly unequal terminal setae in females; the third group consists of the genus *Psorergatoides, P. hystrici* and *P. cercophitheci* with the apomorphies subequal, short genual setae, and the reversal of tibial spine IV, which is present in these species. Sistergroup of the genus *Psorergatoides* with *P. cercopitheci* is *P. hystrici* characterized by very long palpal tibial setae (more than 25 μ). The genus *Psorergatoides* (with *P. cercopitheci*) is characterized by the reduction of the lateral shield setae to point-like structures, and one seta on all femora. *Psorergatoides hipposideros* is the sistergroup of the rest of the genus and shows no derived character states. The sistergroup of *P. hipposideros* has two-pointed tarsal spines. Latter group shows a multifurcation of four branches. The first branch with *Psorobia cercopitheci* and *Psorergatoides rhinolophi* is characterized by the total absence of genual setae; the latter species and sistergroup of *P. cercophitheci* cannot be distinghuished by any apomorphy, the *Psorobia* species has a reversal in character 2, which means that four pairs of more than 2 μ long, lateral shield setae are visible. The second branch of the multifurcation is also characterized by a reversal. The ratio

of the antero-median and genital setae is less than 1.7 in this group of six species. *P. desmodus* and *P. guyanensis* are forming a group with no apomorphies. The sistergroup of latter group has males in which the terminal setae are absent. *P. artibei* and the three species group *P. australiensis, P. kerivoulae* and *P. tadaridae* are sistergroups. The latter characterized by a reversal of the second seta on femora I-III, and the first by the presence of two-pointed claws. The third branch of the multifurcation is characterized by a reduction of the terminal setae in females (shorter than 40 μ) and contains two bigger sistergroups. One group with males having lost their terminal setae, and one group without ventral setae. The sistergroup with reduction of the male terminal setae gives rise to three groups; *P. glossophagae* without apomorphies, *P. nycteris* with a reversal of the second seta on femora I-III, and another species group characterized by very short (less than 4 μ) setae on all femora. Within latter group *P. surinamensis*, without genual setae, is the sistergroup of *P. lonchorhina* and *P. molossi*, exhibiting no apomorphies. The sistergroup of above described group of five species is characterized by the absence of ventral setae as mentioned before. Within this group of three species the sistergroup of *P. emballonurae*, without derived characters, is *P. indicicola* and *P. peropteryx* with a reversal of the tarsal spine from two-pointed to one-pointed, with tarsal claws two-pointed and with very short femoral setae (less than 4 μ). *P. peropteryx*, also without apomorphic characters, is the sistergroup of *P. indicicola* with absent genual setae I-IV. The fourth branch of the multifurcation is formed by the single species *P. laviae* and shows no apomorphies.

The complete tree shows only 12 unique characters (out of 27 used characters) assigned to 6 higher order taxa and 6 terminal taxa. Also 7 characters showing reversals in 5 higher order taxa and 4 terminal taxa are found. Altogether this yields a highly unsatisfactory tree with no clear groupings of genera (except the genus *Psorergates)* and within genera. Because of the strongly reductive trends in the evolution of characters of these parasites a strong homoplasy is inevitable. A consensus tree would show a multifurcation of about as many branches as there are terminal taxa, and any hypothesis about possible phylogenetic relationships and co-evolutionary patterns would be impossible. I would like to show that remarkably better results can be accomplished by hypothesizing that no reversals occur. I do not want to adhere to Dollo's rule, but in this case, concerning parasites of the family Psorergatidae, this rule might indeed be applicable. Trying to avoid this issue I can also argue that character weighting can be advocated (Wheeler, 1986). By simply giving extra weight to the reversed characters the same results appear.

Phylogenetic relationships of the genus *Psorergatoides*

To examplify my hypothesis about character weighting (or Dollo's rule) I would first like to reexamine the relationships of the genus *Psorergatoides*. The original tree shows this genus with the taxon *Psorobia cercopitheci* as the sistergroup of *P. rhinolophi*. Using the algorithm suggested by Farris (1974) for distinghuishing paraphyletic groups it appears that the genus *Psorergatoides* is paraphyletic, because of the presence of this *Psorobia* species within latter genus. Fig. 24 shows a subtree (consistency index 0.518) in which no reversals occur. *Psorobia cercopitheci* disappears and the genus *Psorergatoides* becomes monophyletic. But also the groupings within latter genus make more sense now. Looking at the host families of the species in the original tree (fig. 23) it occurs that the family Hipposideridae is the sistergroup of all

other bat families in this analysis, and the *Psorergatoides* species from the family Phyllostomidae do not cluster together. Of course it could be hypothesized that colonization events took place several times, but with different clustering of the species in the original tree a more coherent picture appears. In this case I have used the relationships of the hosts to argument for phylogenetic relationships of the parasites. Of course you cannot use this argument reversed and hypothesize that because of certain affinities of psorergatid species host species or species groups are related. Latter would be a nice example of circular reasoning. Results of this analysis are tentative, moreover because more equally parsimonious trees can be constructed. If I would strictly adhere to constructing a phylogenetic tree using only apomorphies and the rule of parsimony, without admitting reversals, and parallel developments (homoplasy) no tree could be constructed, or a consensus tree would result with a multifurcation at its base and as many branches as OTU's present. Formally there should be no difference between a parallel development of a certain character and the reversal of this same character. As far as I know it cannot be proven that it is more likely for a character to occur more than once instead of being reversed. One should consider though that most of the characters in this group are reductive, and empirically it can be concluded that in a most parsimonious tree (fig. 23) far more parallel developments occur than reversals. Is it an extra assumption to suppose that instead of a reversal the character shows one more parallel development, and resulting the tree becomes successively longer? Also a reversal is an assumption, and hypothesizing no reversals occur a (tentative) tree results in which sistergroup relationships are more clearly elucidated. At least the original analysis learns that strictly adhering to the principle of parsimony (without considering homoplasy, which is also restricted in most mathematical models) no workable hypothesis results. Or should I say here is the result and leave the interpretation to the reader? In the following chapter I will discuss the possible co-evolutionary patterns of parasites and hosts.

Phylogenetic relationships of the genus *Psorergates*

Phylogenetic relationships of the genus *Psorergates* are shown in the top half of figure 23. Here too reversals occur. Hypothesizing no reversals occur, like in the genus *Psorergatoides*, trees result in which the species from sciurid and tupaiid hosts are the sistergroup of all other species of the genus. figure 25 shows a tree with sistergroup relations for the *"muricola"* group and the *"insectivora"* group, figure 26 with sistergroup relations for the "muricola" group with the *"apodemi"* group and *P. alleni/P. peromysci*. Results of this analysis are largely in congruence with those found by Giesen & OConnor (1987). Discrepancies can be found in the character state polarity of the ratio between the distance of the antero-median and genital setae in males, and the use of the character of the shape of the dorsal shield, resulting in slightly different tree topologies. Apparently the *Psorergates* species radiated into several groups all infesting Muridae, Cricetidae and Gliridae. Early colonization of Insectivora hosts took place, or otherwise this group was also part of the radiation from the hypothesized ancestor of this large group. Within the *"insectivora"* group equally parsimonious phylogenetic relationships can be hypothesized between the group infesting Talpidae hosts and the sistergroup of Soricidae parasites, or that *Psorergates* species from Soricini/Anourosoricini hosts are the sistergroup of the other members of the *"insectivora"* group. In latter case the species from Talpidae hosts are the sistergroup

of the parasites from Blarinini and Crocidurini. Using the same argument, being less colonization events, as for the genus *Psorergatoides* I would hypothesize that the tree topology in which the parasites from Talpidae are the sistergroup of the species from Soricidae is more likely.

Phylogenetic relationships of the genus *Psorobia*

Finally the genus *Psorobia* is analysed. Admitting no reversals yields a great number of different trees with virtually every sistergroup relationship possible. An example of one of the trees is given in figure 27. Unfortunately argumenting that hostgroup relationships will help to hypothesize true relationships of this genus are not valid, because the hosts are from very different families and even very different orders. The phylogeny of these host groups is unknown and, as with the genus *Psorobia*, shows radiation from the basis of the tree. One thing can be concluded from all hypothetical trees: the genus *Psorobia* is a nonnatural group.

Coevolutionary patterns of Psorergatidae and their host

Host cladograms for the genera *Psorergates* and *Psorergatoides* are constructed by substitution of the parasite species by the host species or species groups. Figure 28 shows a host cladogram derived from figure 24, and figure 29 shows a host cladogram derived from figure 25.

Normally coevolutionary patterns can be hypothesized because of congruent or nearly congruent cladograms of hosts and parasites. Incongruencies can be explained by hypothesizing extinction, colonization or sympatric speciation. But I used the gross phylogenetic relationships of the hosts already to hypothesize certain tree configurations. By reversing the argument I would proof nothing, but only show a lot of "wishfull thinking" in trying to show a nice coevolution of hosts and parasites.

It can be concluded that the family Psorergatidae is not a good indicator for host relationships.

Table 5. Measurements and numerical data of the genus *Psorergatoides*, females; * = number of specimens unknown; n.o. = not observed.

	australiensis (N=10) min-max	*kerivoulae* (N= 5) min-max	*nycteris* (N= 5) min-max	*tadaridae* (N=10) min-max	*hipposideros* (N= *) min-max	*desmodus* (N=20) min-max	*artibei* (N=17) min-max	*guyanensis* (N= 2) min-max
body length	159-167	170-186	175-205	102-117	117-150	118-139	133-179	137-146
body width	140-152	148-162	160-180	96-105	108-142	105-121	108-143	125-132
shield length	105-112	130	135	75-81	84	74-81	104	94
shield width	100-110	126	130	70-79	85	68-75	99	85
length setae								
terminal	78-108	75-80	8-10	45-50	45-60	48-70	60-70	60
trochanter	10-16	12-18	4-6	5-8	n.o.	6	10	7
femora I-III	20-27	15-20	4-6	13-18	15-18	20	11	10
femur IV	14-25	12-15	4- 5	10-13	n.o.	10	12	9
genua I-III	2-3	1-2	1-2	1-2	1	1	6-8	3
genu IV	17-29	15-18	1-2	19-23	1	17	15	15
lateral shield	0	0	0	0	0	0	0	0
palpal tibial	15-18	13-17	8-10	5-8	15-18	15	19	17
gnathosomal	6-8	3-4	2-4	4-6	5	6	6-8	6
ventral	4-8	6-7	3	4-5	n.o.	4-5	4-5	5
distance between								
ventral setae	14-20	16-18	12	16-18	12	14	15-50	20-23
no setae femur I-III	2	2	2	2	1	1	1	1
points tarsal spine	2	2	2	2	1	2	2	2
no of clawpoints	1	1	1	1	1	1	2	1

Table 5. Measurements and numerical data of the genus *Psorergatoides*, females (continued).

	glossophagae (N=20) min-max	*surinamensis* (N= 7) min-max	*lonchorhina* (N= 5) min-max	*molossi* (N=20) min-max	*emballonurae* (N= 4) min-max	*indicicola* (N=20) min-max	*peropteryx* (N=20) min-max	*rhinolophi* (N= 5) min-max	*laviae* (N= 3) min-max
body length	166-191	132-146	102-118	115-124	138-153	156-186	118-143	120-138	166-190
body width	143-179	107-123	80-112	92-117	135-150	136-154	100-137	110-125	140-165
shield length	118	85-94	88	80	107	112	76-88	79	120
shield width	103	77-90	78	80	91	94	70-83	72	116
length setae									
terminal	20-25	24-30	20-30	32-40	8-10	5	20-39	45-60	50
trochanter	11	5	2-3	5	3-4	4	2	2-3	3
femora I-III	12	4	1-2	2	10	3	2	12-15	15
femur IV	11-18	4	1-2	2	n.o.	3	2	12- 15	15
genua I-III	2	absent	1-2	2	1-2	absent	1-2	absent	4
genu IV	2	absent	1-2	2	1-2	absent	1-2	absent	4
lateral shield	0	0	0	0	0	0	0	0	0
palpal tibial	16	14-15	12	14	12	18	14	20	21
gnathosomal	5-6	5-6	2	6	4	6	5	3	4
ventral	5	4	2	4	absent	absent	absent	n.o.	2
distance between									
ventral setae	15-20	7	9	12 16	-	-	-	15-18	15
no setae femur I-III	1	1	1	1	1	1	1	1	1
points tarsal spine	2	2	2	2	2	1	1	2	2
no of clawpoints	1	1	1	1	1	2	2	1	1

Table 6. Measurements and numerical data of the genus *Psorergatoides*, males.

	australiensis (N= 4) min-max	*kerivoulae* (N= 2) min-max	*tadaridae* (N= 5) min-max	*hipposideros* (N= *) min-max	*desmodus* (N=16) min-max	*artibei* (N= 8) min-max	*glossophagae* (N=20) min-max
body length	146-159	185-186	93-105	100	98-121	127-161	156-179
body width	115-129	145-147	75-90	84	85-105	99-122	117-140
shield length	90-102	120	69-74	78	76-80	97	101
shield width	84-98	90	59-65	61	72-73	83	79
length setae							
terminal	absent	absent	absent	25-30	30-76	absent	absent
trochanter	11-12	9-13	5-6	4-5	5	6	15
femora I-III	17-9	12-15	9-11	11	7	7	8
femur IV	13-16	10	8-9	7	6	7-9	10
genua I-III	2	1-2	1	absent	1	6-8	2
genu IV	16-18	8-9	13-16	absent	9	15	2
lateral shield	0	0	0	0	0	0	0
palpal tibial	12-14	13	6-8	10	16	19	14
gnathosomal	4	4	4-8	4	4	8	6
ventral	5-6	5-7	4	1	4	4	5
distance between							
ventral setae	16-21	18	19-26	4-5	14-15	15-35	18
a.m. setae	11-12	4- 5	9-11	6-7	12	12	7-8
genital	8-9	4-5	6	10-11	8	12	7-8
length penis	15-22	18-21	25-29	42	22	26-32	19-29
length penis sheath	16	22	11-13	14	13-14	16-20	13-16
no setae femur I-III	2	2	2	1	1	1	1
points tarsal spine	2	2	2	1	2	2	2
no of clawpoints	1	1	1	1	1	2	1

Table 6. Measurements and numerical data of the genus *Psorergatoides*, males (continued).

	surinamensis (N= 2) min-max	*lonchorhina* (N= *) min-max	*molossi* (N=20) min-max	*emballonurae* (N= *) min-max	*indicicola* (N=20 min-max	*peropteryx* (N=20) min-max	*rhinolophi* (N= 3) min-max
body length	121	99	92-117	111	143-166	98-125	96-105
body width	94-98	90	80-105	99	105-140	82-112	81- 86
shield length	74-76	69	69	88	103	72- 81	78
shield width	67-68	69	69	81	96	61-74	70
length setae							
terminal	absent	absent	absent	15-20	5-10	18-34	60-70
trochanter	3	2-3	4	n.o.	5	4	6-7
femora I-III	2-3	1-3	2	13	3	2	10
femur IV	2	1-3	2	n.o.	4	2	7
genua I-III	absent	absent	1	absent	absent	1	absent
genu IV	absent	absent	1	absent	absent	1	absent
lateral shield	0	0	0	0	0	0	0
palpal tibial	14-15	12	10-12	8	13	12-15	12
gnathosomal	5-6	4	5-6	3	6	4-5	3
ventral	3	2	3	absent	absent	absent	2
distance between							
ventral setae	10	5	12	-	-	-	5
a.m. setae	9	8-9	8	11	2-3	3	10-11
genital setae	5	9-10	5	11	7	5	14-15
length penis	26	29	18-25	50	34-51	30	26
length penis sheath	14	14	10-15	22	18-22	10	12
no setae femur I-III	1	1	1	1	1	1	1
points tarsal spine	2	2	2	2	1	1	2
no of clawpoints	1	1	1	1	2	2	1

Table 7. Measurements and numerical data of the genus *Psorergates*, females.

	canadensis (N=12) min-max	*watsoni* (N=10) min-max	*micromydis* (N=49) min-max	*auricola* (N=16) min-max	*zibethicalis* (N=14) min-max	*dissimilis* (N= *) min-max	*oecomomi* (N=17) min-max	*townsendi* (N=10) min-max
body length	160-179	120-138	136-171	144-162	174-207	159-168	142-174	157-169
body width	126-152	92-101	107-150	114-138	144-174	120-142	119-145	137-149
shield length	103-106	90-92	93-110	99-108	111-120	91-104	99-125	100-108
shield width	69-92	58-69	78-93	78-90	100-108	81-98	81-93	91-96
length setae								
terminal	76-97	67-74	70	90-100	75-90	75-80	70-87	73-93
trochanter	15-17	16-18	12	18	15	15	15	10-15
femora I-III	28-32	19-21	15	25-30	25	20	25	27-33
femur IV	34- 42	21- 24	20	30-45	30	25	30	29- 37
genua I-III	8-10	8-9	5	8-10	8	8	6	9-12
genu IV	20-24	18-21	5	24-30	12	18	18	18-23
lateral shield	8	9	8	9	6-7	7-8	8	8-10
palpal tibial	34- 37	26-29	25-32	30-36	27-36	27-30	26-30	27-35
gnathosomal	8-9	2	6	8-10	7	7	8-9	6-7
ventral	9-10	10	6	6	6-7	4-5	5	7-10
distance between								
ventral setae	34-36	20-24	22-27	27-36	27-36	20-27	26-30	37-42

Table 7. Measurements and numerical data of the genus *Psorergates*, females (continued).

	deomydis (N= 9) min-max	*arvalis* (N= 5) min-max	*pitymidis* (N=10) min-max	*microti* (N=32) min-max	*neerlandicus* (N= *)	*apodemi* (N=53) min-max	*callipidis* (N=23) min-max	*peromysci* (N=10) min-max	*pinetorum* (N=10) min-max
body length	132-150	126-141	117-135	105-143	132	123-157	126-156	142-153	123-140
body width	111-123	111-123	105-120	90-114	115	105-132	99-132	116-126	108-122
shield length	90-99	72-75	72-84	67-75	77	84-99	87-105	88-91	73-78
shield width	84-93	81-84	78-93	69-78	77	78-96	78-105	78-81	76-81
length setae									
terminal	66	60- 66	75	60-75	79	75-90	75-90	66-79	66-88
trochanter	7	8-10	8-9	8	9	12	10	8-11	10-14
femora I-III	15	15	20-25	15	19	20	20	16-25	22-26
femur IV	18-20	20-25	20-25	20	24	20	25	16-29	22-30
genua I-III	4	8	6	6	5	3-5	5	4-6	6-8
genu IV	15	12-15	12-15	15	16	10-15	18	15-18	16-22
lateral shield	4-5	5-6	4-5	4-5	5	5	6	6-8	4-6
palpal tibial	2-3	10-14	12	12	12	10-13	15-18	15-16	10-14
gnathosomal	4-5	3-4	3	4-5	4	5-6	5	5-7	4-6
ventral	6	6	5-6	5-6	7	7	7	8-11	6-8
distance between									
ventral setae	14-19	11-15	9-12	9-13	9	9-13	9-12	8-13	11-14

Table 7. Measurements and numerical data of the genus *Psorergates*, females (continued).

	alleni (N=13) min-max	*muricola* (N= *) min-max	*oettlei* (N= *)	*rattus* (N= 6) min-max	*simplex* (N=10) min-max	*hispanicus* (N=10) min-max	*agrestis* (N=13) min-max
body length	154-175	120-135	135	123-139	143-150	117-129	129-150
body width	130-149	93-110	117	110-117	114-119	99-105	105-129
shield length	113-132	84	96	88-93	101-108	78-85	81-87
shield width	106-115	75	93	82-90	96-102	78-82	78-84
length setae							
terminal	93-118	70- 80	75	60-70	72-82	75-90	65-80
trochanter	18-20	8	10	8-9	8-10	8-9	7-8
femora I-III	26-35	15	15	15-18	16-17	15	12-15
femur IV	28-45	15	15	15-18	17-18	18-20	12-15
genua I-III	9-11	4	5	3-4	4-5	4	4
genu IV	16-20	4	5	3-4	4-5	4	4
lateral shield	6-8	5-6	5	4-5	5-6	4-5	3-4
palpal tibial	17-22	5	5	1-2	5-6	4-5	5-6
gnathosomal	6-7	2	2	9	4-5	4-5	5
ventral	5-7	6	7	6-7	7	6	5-6
distance between							
ventral setae	13-20	12	10	13	8-11	10-12	9-13

Table 7. Measurements and numerical data of the genus *Psorergates*, females (continued).

	musculinus (N= *) min-max	*muscardinus* (N=18) min-max	*quercinus* (N=10) min-max	*eliomydis* (N= 1)	*paraxeri* (N= 8) min-max	*dremomydis* (N=11) min-max	*glaucomys* (N= 1)	*tupaiae* (N=10) min-max	*fritzi* (N=10) min-max
body length	159	145-186	157-179	153	113-137	110-124	122	122-137	101-129
body width	114	124-152	118-151	132	100-113	98-122	106	103-122	102-112
shield length	111	96-106	109-118	102	76-93	70-75	83	78-84	71-76
6shield width	78	74-83	76-87	78	81-93	76-78	79	74-81	70-77
length setae									
terminal	100	69-88	72-84	90	55-63	67-80	60	38-56	49-59
trochanter	18	12	12-16	12	11-15	10-12	8	6-10	6-9
femora I-III	25	23-27	18-22	30	15-17	17-22	11	8-11	7-10
femur IV	30-35	23-27	22-24	30	13-20	19-25	11	7-10	6-8
genua I-III	15	5	5	4	5-7	8-9	6	3	3
genu IV	30	17-29	16-18	15	5-9	17-22	15	3	3
lateral shield	33-42	8-9	7-8	7	10-12	7-10	5	4-5	5-7
palpal tibial	25-30	12-14	17-19	18	13-15	12-13	10	4-5	5-7
gnathosomal	15-20	5-7	5	3	4-5	4-6	4	5	7-9
ventral	12	8-12	11	15	5-6	5-6	8	3-4	4-5
distance between									
ventral setae	2	7-14	14-18	15	9-14	12-16	14	10-12	5-10

Table 7. Measurements and numerical data of the genus *Psorergates*, females, (continued).

	urotrichi (N=10) min-max	*desmanae* (N=12) min-max	*talpae* (N=13) min-max	*crocidurae* (N=10) min-max	*doriae* (N= 6) min-max	*etruscus* (N= 9) min-max
body length	117-132	135-168	126-144	123-138	111-122	97-120
body width	88-108	108-140	99-117	96-112	98-110	78-97
7shield length	70-78	87-96	80-96	78-85	86-93	72-78
8shield width	65-71	75-90	70-76	66-72	70-75	58-60
length setae						
terminal	62-76	78-98	60-72	49-58	44 -49	31-43
trochanter	3-4	10-12	9-11	8	4-5	4-10
femora I-III	18-24	20-28	28-36	20-35	9-20	13-18
femur IV	26-44	36-45	33-39	25-33	14-29	16-20
genua I-III	1	5	3	3	1	1
genu IV	40-52	51-60	50-55	30-35	21-29	22
tarsus d.a.	2-4	6	4	3	4-6	1-2
tarsus d.p.	15-23	15-18	16-20	absent	absent	absent
lateral shield	3-5	5-6	4-5	4	3-4	2-3
palpal tibial	3-4	5-6	4	3	4-5	4
gnathosomal	5-8	9-10	6	7	6-8	5-7
ventral	3-4	5-6	3-4	2	3-	4 4
distance between						
ventral setae	9-11	9-11	7-11	13-18	17-24	6-7
no of clawpoints	1	1	1	3	3	3
no setae femur IV	2	2	2	2	2	2
shape empodium	rounded	rounded	rounded	rounded	acute	acute

Table 7. Measurements and numerical data of the genus *Psorergates*, females (continued).

	cryptotis (N=13) min-max	*baueri* (N=12) min-max	*mexicanus* (N=15) min-max	*sorici* (N=10) min-max	*cinereus* (N=10) min-max	*squamipes* (N=20) min-max
body length	98-120	99-129	123-135	117-135	138-159	121-139
body width	78-98	78-101	103-113	93-99	112-131	91-112
shield length	71-76	67-81	89-95	76-87	85-92	81-89
shield width	58-65	53-68	78-84	63-72	68-77	63-70
length setae						
terminal	43-62	48-58	60-75	52-60	51-77	53-77
trochanter	5-11	5-8	7-10	9-10	10-13	4
femora I-III	15-23	20-27	23-28	20-25	16-23	15
femur IV	14- 23	20-27	19-25	28-33	19-25	20
genua I-III	1	1	2-3	2	2	1
genu IV	22-31	33-45	37-48	30-35	32-36	36-45
tarsus d.a.	2-3	2-3	3-5	3-4	4	2
tarsus d.p.	14-20	14-18	20-25	14-18	16-18	9
lateral shield	4-7	3-5	4-5	4-5	5	4
palpal tibial	1-3	2	2-3	2-3	3	2
gnathosomal	6-9	5-8	4-7	8-9	11-13	7-9
ventral	5-8	4-6	4-7	4	8	5
distance between						
ventral setae	9-13	5-10	13-21	9-11	11-13	10-30
no of clawpoints	2	2	2	2	2	2
no setae femur IV	1	1	1	1	1	1
shape empodium	acute	acute	acute	rounded	rounded	rounded

Table 8. Measurements and numerical data of the genus *Psorergates*, males.

	canadensis (N= 5) min-max	*watsoni* (N= 9) min-max	*micromydis* (N=12) min-max	*auricola* (N=21) min-max	*zibethicalis* (N=10) min-max	*dissimilis* (N= *) min-max	*oeconomi* (N= 3) min-max	*townsendi* (N=10) min-max
body length	131-158	115-136	139-160	135-153	150-201	145-160	145-161	137-149
body width	110-133	92-104	99-144	108-135	129-165	124-126	125-139	123-135
shield length	83-87	72-85	87-98	81-93	100-111	78-98	90	87-98
shield width	63-68	56-62	64-84	69-81	90-96	70-75	73	71-98
length setae								
terminal	16-38	37-48	35-44	10-54	25-39	0-36	26	13-32
trochanter	10-11	9-10	8	10	12	8	8	8-11
femora I-III	19-22	16-20	10	15-20	15	15	15	21-26
femur IV	24-29	19-23	12	18-25	20	20	23	24-34
genua I-III	7	5	4	8	5-6	4-6	5	8-10
genu IV	18	16-18	4	15-20	10-12	12-13	14	10-17
lateral shield	6	5	4-5	4-5	5	3-5	4-5	5-6
palpal tibial	3	3	3-4	4-5	3	1-2	3-4	2-3
gnathosomal	3	2	4-5	5-6	3-4	2-3	4-5	3-4
ventral	6	5	4	5	5	5	4	5-7
distance between								
ventral setae	32	24	22-26	27-36	27-33	22-36	35-38	40-49
a.m. setae	15	14	16	18	17	18	16	16- 18
genital setae	13	13	13	15	11	15	13	15-17
length penis	40-44	36-40	35-42	33-38	45-50	39-42	38	35-42
length penis sheath	34-38	33-35	24	24-27	23	24-29	20	35-40

Table 8. Measurements and numerical data of the genus *Psorergates*, males (continued); ~ = approximately.

	deomydis (N= 4) min-max	*arvalis* (N= 1) min-max	*pitymydis* (n=10) min-max	*microti* (N=18) min-max	*neerlandicus* (N= *) min-max	*apodemi* (N=21) min-max	*callipidis* (N=15) min-max	*peromysci* (N= 6) min-max	*pinetorum* (N=10) min-max
body length	117-123	115	100-123	97-119	104-119	114-141	117-135	120-135	103-130
body width	99-102	94	87-111	85-102	82-101	91-117	99-108	102-114	88-120
shield length	75-84	69	63-72	65-70	70-78	75-85	84-90	78-86	69-79
shield width	68-81	75	69-78	65-73	67-73	76-78	78-87	66-70	67-73
length setae									
terminal	54-60	66	60-70	45-55	62-67	~60	~75	34-65	62-95
trochanter	5-6	9	6-7	7	7-9	12	10	8-9	7-9
femora I-III	10	15	15	15	16-20	15	15-20	14-15	16-20
femur IV	15	20	15	20	19- 20	15-20	20-25	11-19	20-25
genua I-III	3-4	8	5-6	6	4-5	5	5	4-6	6-7
genu IV	8-10	15	10-12	12-15	12-14	12-15	15-18	10-16	17-20
lateral shield	4-5	4-5	5-7	5	4	5-6	6	5-6	5-7
palpal tibial	1-2	12	12	12	8-11	10-13	15-18	10-15	10-11
gnathosomal	3	3-4	3	4-5	4	5-6	4-5	5-6	5
ventral	6	6	5-6	5-6	5-6	5-6	6-7	5-8	5-7
distance between									
ventral setae	14-16	11	7-9	8-15	7-10	9-15	9-12	13-15	8-14
a.m. setae	18	16	20	16	18-19	15	17	17-19	19-22
genital setae	10	5	7	7	7	7	7	7-8	8-9
length penis	30-33	28	33-36	24-27	24-30	45-51	45-51	32-38	28-34
length penis sheath	24-25	26	20	24-26	20-23	37-40	35-38	19-24	21-23

Table 8. Measurements and numerical data of the genus *Psorergates*, males (continued).

	alleni (N= 4) min-max	*muricola* (N= *) min-max	*rattus* (N= 1) min-max	*oettlei* (N= *) min-max	*simplex* (N= 5) min-max	*hispanicus* (N= 9) min-max	*agrestis* (N= 1) min-max
-body length	130-156	105-111	102	120-135	108-126	99-105	126
body width	120-125	93-94	88	100-108	91-101	81-90	99
shield length	103-113	76	80	75-86	74-85	70-75	84
shield width	96-98	72	66	73-81	72-84	66-72	75
length setae							
terminal	64-92	60-65	50-60	absent	55- 62	70-80	65
trochanter	14-18	7	8-9	8	8	6	7
femora I-III	23-35	15	15-18	15	13-14	10	10-12
femur IV	26-32	15	15-18	18	14-16	12	10-12
genua I-III	8-10	4-6	3-4	2-3	2-4	4	3
genu IV	17-18	4-6	3-4	2-3	2-4	4	3
lateral shield	5-7	6-7	4-5	4	5-6	3	3
palpal tibial	17-18	4	1-2	2	5	3- 4	4
gnathosomal	5-7	2	n.o.	2-3	4-5	4-5	4
ventral	6-7	5-7	8	6	6-7	5	5
distance between							
ventral setae	11-14	13	7	9	8-14	9-12	9
a.m. setae	23-24	10	15	12	11-12	10	12
genital setae	9-10	8	7	10	8	7	10
length penis	39-46	34-38	28	48-52	42-47	39-42	42
length penis sheath	22-24	24-30	19	39-45	24-29	27-30	27

Table 8. Measurements and numerical data of the genus *Psorergates*, males (continued).

	musculinus (N= *) min-max	*muscardinus* (N=16) min-max	*quercinus* (N= 9) min-max	*paraxeri* (N= 8) min-max	*dremomydis* (N=10) min-max	*glaucomys* (N= 1)	*tupaiae* (N= 9) min-max	*fritzi* (N=10) min-max
body length	138-147	131-154	129-154	113-135	89-107	121	106-122	97-122
body width	114-132	115-138	109-134	91-108	74-95	101	91-106	90-109
shield length	102	79-99	98	81-92	67-74	84	69-80	71-77
shield width	82	63-74	66	75-90	64-75	78	69-74	65-74
length setae								
terminal	30-50	32-38	46-49	78-94	77-80	91	41-60	60-70
trochanter	11-13	7-9	6-9	11-13	9-10	8	8-10	6-8
femora I-III	20	14-16	12-14	15-18	14-20	12	9-12	7-10
femur IV	20	17-22	13-16	16-22	19-23	12	8-9	6-8
genua I-III	6-8	4	2-4	5-7	6-9	8	3	2-3
genu IV	12-13	13-18	8-13	6-7	17-19	23	3	2-3
lateral shield	8-12	8-10	5	8-14	9	5	5	5-6
palpal tibial	7-10	3-5	6-8	11-16	9-13	12	3-6	4-6
gnathosomal	12-16	3-5	4	4	4	4	4-6	6-7
ventral	12	6-10	7	4-8	5-6	8	4	3-4
distance between								
ventral setae	2-5	13-20	16-19	9-13	12-16	15	9-12	6-9
a.m. setae	10	8-9	24-25	29-32	20-23	20	25-28	23-25
genital setae	11	3-5	19-20	12-14	9	10	14	13-15
length penis	29-34	29-34	46-52	40-45	24-26	35	36-39	20-28
length penis sheath	18-21	18-24	28-31	38-45	18	10	24-28	15-21

Table 8. Measurements and numerical data of the genus *Psorergates*, males (continued).

	urotrichi (N= 2)	*desmanae* (N= 5)	*talpae* (N= 7)	*crocidurae* (N=10)	*doriae* (N=10	*etruscus* (N= 1)	*cryptotis* (N= 3)	*sorici* (N=10)	*cinereus* (N= 6)	*squamipes* (N= 5)
body length	116-119	132-146	108-120	105-114	103-113	103	98-105	102-115	110-129	100-121
body width	88-91	105-120	90-99	85-93	81-93	79	76-98	84 93	86-113	85-100
shield length	75-76	84-90	72-74	75-84	79-92	76	67-72	70-78	75-78	77-85
shield width	65-66	75-81	62-66	64-70	61-73	56	50-55	57-62	63-70	60-67
length setae										
terminal	56-58	72-89	51-54	42-48	26-38	32-36	45-50	52-60	41-50	45-60
trochanter	4	9-10	7-8	8-9	3	4-8	6-7	7	6	3
femora I-III	18-25	15-20	25-28	18-23	7-14	16	13-16	20-25	12-16	12
femur IV	24	25-36	30-33	20-25	10-21	21	18	20-25	14-19	13-27
genua I-III	1	4	3	3	1	1	1	2	2	1
genu IV	33-38	35-40	40-45	30-33	18-27	18	24-26	27-34	29	25-30
tarsus d.a.	2-3	5	3	2	2-3	1	2-3	3	3	2
tarsus d.p.	15-18	14-15	14-16	absent	absent	absent	11-13	14-18	14	7
lateral shield	4	4-5	4	3-4	3	3	4-5	3-4	5	4
palpal tibial	4	5	3-4	3	2-3	3	2	2	2-3	2
gnathosomal	6	9-10	6	7-8	5-6	6	11-13	7-8	11	7-8
ventral	4	4-5	3	2-3	3-4	2-3	6	3-4	6	5
distance between										
ventral setae	8-9	7-8	7-10	12-14	11-19	7	8-11	10-14	10	10
a.m. setae	11	9-10	10-11	12-13	15-16	9	11	12-14	13-15	13
genital setae	9-11	10-11	9	7-8	9-10	7	4	5	4	8
length penis	30-33	28-31	25-29	24-27	27-30	21	31-36	36-38	36-39	50-51
length penis sheath	19-20	23-24	18	15-16	14-21	14	18-19	11-14	20-23	32-34
no of clawpoints	1	1	1	3	3	3	2	2	2	2
no setae femur IV	2	2	2	2	2	2	1	1	1	1
shape empodium	rounded	rounded	rounded	rounded	acute	acute	acute	rounded	rounded	rounded

Table 9. Mite species list of the family Psorergatidae

Mite species	Reference	Host family	Host species
Genus *Psorobia* Fain, 1959			
bos	Johnston, 1964	Bovidae	*Bos taurus*
castoris	Kok, Lukoschus & Clulow, 1970	Castoridae	*Castor canadensis*
cercopitheci	Zumpt & Till, 1955	Cercopithecidae	*Cercopithecus aethiops pygerythus*
	Sheldon, 1966	Cercopithecidae	*Cercocebus torquates* atys
elephantuli	Giesen, Spicka &Whitaker,1985	Macroscelididae	*Elephantulus rozeti*
foinae	Fain & Lukoschus, 1968	Mustelidae	*Martes foinae*
hystrici	Till, 1957	Hystricidae	*Hystrix africae australis*
lagomorphae	Giesen, Spicka & Whitaker,1985	Leporidae	*Sylvilagus floridanus*
mustelae	Lukoschus, 1969	Mustelidae	*Mustela erminea*
			Mustela nivalis
ovis	Womersley, 1941; Fain, 1959	Bovidae	*Ovis aries*
zumpt	Fain, 1965	Bathyergidae	*Cryptomys hottentotus*
Genus *Psorergatoides* Fain, 1959			
artibei	Lukoschus, Rosmalen & Fain, 1973	Phyllostomidae	*Artibeus literatus fallax*
australiensis	Giesen, Lukoschus & Fain, 1982	Vespertilionidae	*Eptesicus pumilus*
			Eptesicus douglasi
			Nyctophilus arnhemensis
			Nyctophilus walkeri
desmodus	Lukoschus, Louppen &Fauran,1979	Desmodontidae	*Desmodus rotundus*
emballonurae	Fain, 1959b	Emballonuridae	*Emballonura nigrescens*
glossophagae	Lukoschus, Rosmalen & Fain, 1973	Phyllostomidae	*Glossophagae soricina*
guyanensis	Lukoschus, Louppen& Fauran,1979	Phyllostomidae	*Rhinophylla pumilio*
hipposideros	Fain, 1959b	Hipposideridae	*Hipposideros abae*
			Hipposideros caffer centralis
indicicola	Lukoschus, Rosmalen & Fain, 1973	Emballonuridae	*Saccopteryx canescens*
			Saccopteryx billineata
kerivoulae	Fain, 1959a	Vespertilionidae	*Kerivoula cuprosa*
			Kerivoula harrisoni bellula
	Fain, 1959b		*Myotis muricola*
			Myotis bocagei
			Plecotus auritus
	in collection Lukoschus		*Myotis mysticinus*
laviae	Fain, 1959a	Megadermatidae	*Lavia frons*
lonchorhina	Fain, 1959b	Phyllostomidae	*Lonchorhina aurita*
		Emballonuridae	*Saccopteryx canina*
molossi	Lukoschus, Rosmalen & Fain, 1973	Molossidae	*Molossus ater*
			Molossus molossus
nycteris	Fain, 1959a	Nycteridae	*Nycteris macrotis*
			Nycteris spec.
peropteryx	Lukoschus,Louppen & Fauran,1979	Emballonuridae	*Cormura brevirostris*
			Peropteryx macrotis
rhinolophi	Fain, 1959a	Rhinolophidae	*Rhinolophus hildebrandti*
			Rhinolophus aethiops
	Fain, 1959a,b		*Rhinolophus clivosus zuluensis*
	Fain, 1959b		*Rhinolophus hipposideros*
			Rhinolophus affinis
			Rhinolophus ferrum-equinum
	in collection Lukoschus		*Rhinolophus mehelyi*

surinamensis	Lukoschus,Louppen & Fauran,1979 in collection	Phyllostomidae	*Tonatia nicaraguae* *Tonatia carrikeri*
tadaridae	Giesen, Luk. & Nadchatram, 1982	Molossidae	*Tadarida mops*
Genus *Psorergates* Tyrrell, 1883			
agrestis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Microtus agrestis bailloni*
apodemi	Fain,Lukoschus & Hallmann,1966	Cricetidae	*Apodemus sylvaticus*
arvalis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Microtus arvalis meridianus*
auricola	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Pitymys duodecimcostatus flavescens*
baueri	Lukosch.,de Cock & Driessen,1971	Soricidae	*Neomys fodiens*
callipidis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Apodemus callipides*
canadensis	Kok, Lukoschus & Clulow, 1971	Cricetidae	*Microtus pennsylvanicus*
cinereus	Kok, Lukoschus & Clulow, 1971	Soricidae	*Sorex cinereus*
crocidurae	Lukoschus, 1968	Soricidae	*Crocidura russula russula*
cryptotis	Giesen & Lukoschus, 1983	Soricidae	*Cryptotis nigrescens*
deomydis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Deomys ferrugineus chrystyi*
desmanae	Lukoschus, 1968	Talpidae	*Galemys pyrenaicus*
dissimilis	Fain, Lukoschus & Hallmann, 1966	Cricetidae	*Clethrionomys glareolus*
doriae	Giesen, Lukoschus & Nadch., 1982	Soricidae	*Crocidura doriae*
dremomydis	Giesen, Lukoschus & Nadch., 1982	Sciuridae	*Dremomys rufigenis*
eliomydis	Lukoschus, Fain & Beaujean, 1967	Gliridae	*Eliomys quercinus ophiusae*
etruscus	de Cock, Lukoschus & Ariani, 1970	Soricidae	*Suncus etruscus*
glaucomys	Ah, Peckham & Atyeo, 1973	Sciuridae	*Claucomys v. volans*
hispanicus	Lukoschus, Fain & specimens in collection Lukoschus	Cricetidae	*Mus musculus spretus* *Mus musculus commissarius*
mexicanus	Giesen, Lukoschus, Whitaker & Gettinger, 1983	Soricidae	*Notiosorex crawfordi*
micromydis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Micromys minutus soricinus*
microti	Fain, Lukoschus & Hallmann, 1966	Cricetidae	*Clethrionomys glareolus* *Microtus agrestis*
muricola	Fain, Lukoschus & Hallmann, 1966	Cricetidae	*Hybomys univattus* *Mus musculus* *Apodemus sylvaticus*
	Fain, 1961		*Lophuromys aquilus* *Otomys irroratus elgonis*
muscardinus	Lukosch., de Cock & Driessen,1971	Gliridae	*Muscardinus avellanarius*
musculinus	Michael, 1889	Cricetidae	*Clethrionomys glareolus*
	Fain, Lukoschus & Hallmann, 1966		*Arvicola agrestis*
	Rioux & Golvan, 1961		*Apodemus sylvaticus*
neerlandicus	Lukosch., de Cock & Driessen,1971	Cricetidae	*Microtus oeconomus*
oeconomi	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Microtus oeconomus arenicola*
oettlei	Till, 1960	Cricetidae	*Rattus natalensis*
paraxeri	Giesen & Lukoschus, 1982	Sciuridae	*Paraxerus cepapi*
peromysci	Giesen, Lukoschus, Whitaker & Gettinger, 1983	Cricetidae	*Peromyscus maniculatus* *Peromyscus leucopus*
pinetorum	Giesen, Lukoschus, Whitaker & Gettinger, 1983	Cricetidae	*Microtus pinetorum*
pitymydis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Pitymys duodecimcostatus flavescens*
quercinus	Lukosch.,de Cock & Driessen,1971	Gliridae	*Eliomydis quercinus*
simplex	Tyrrell, 1883	Cricetidae	*Mus musculus*
	Canestrini, 1894		
	Neumann, 1893		

	Fain, Lukoschus & Hallmann, 1966		
	Canestrini, 1894		*Arvicola agrestis*
	Neumann, 1893		*Arvicola arvalis*
sorici	Lukoschus, 1968	Soricidae	*Sorex araneus araneus*
squamipes	Lukoschus, Louppen & Maa, 1974	Soricidae	*Anourosorex squamipes*
talpae	Lukoschus, 1968	Talpidae	*Talpa europaea europaea*
townsendi	Giesen, Lukoschus, Whitaker & Gettinger, 1983	Cricetidae	*Microtus townsendi*
tupaiae	Giesen & Lukoschus, 1982	Tupaiidae	*Tupaia dorsalis*
urotrichi	Giesen & Lukoschus, 1983	Talpidae	*Urotrichus talpoides*
watsoni	Kok, Lukoschus & Clulow, 1971	Cricetidae	*Peromyscus maniculatus*
zibethicalis	Lukoschus, Fain & Beaujean, 1967	Cricetidae	*Ondatra zibethica*

Table 10. List of host species of the family *Psorergatidae*

Host family	Host species	Locality	Mite species
		Insectivora	
Tenrecidae	*Echinops telfairi*	Madagascar	Psorergatidae spec.
Macroscelididae	*Elephantulus*	Tunis	*Psorobia elephantuli*
Soricidae			
Soricini	*Sorex cinereus*	Canada	*Psorergates cinereus*
	Sorex araneus araneus	Netherlands	*Psorergates sorici*
	Microsorex koyi	Canada	*Psorergates* spec.
Blarinini	*Neomys fodiens*	Austria	*Psorergates baueri*
	Cryptotis nigrescens	Panama	*Psorergates cryptotis*
	Notiosorex crawfordi	Mexico	*Psorergates mexicanus*
Crocidurini	*Crocidura doriae*	Malaysia	*Psorergates doriae*
	Crocidura lasiura	China	*Psorergates crocidurae*
	Crocidura russula russula	Netherlands, Spain	*Psorergates crocidurae*
	Suncus etruscus	Italy	*Psorergates etruscus*
Anourosoricini	*Anourosorex squamipes*	Taiwan	*Psorergates squamipes*
Talpidae	*Galemys pyrenaicus*	France	*Psorergates desmanae*
	Talpa europaea europaea	Netherlands, Spain	*Psorergates talpae*
	Urotrichus talpoides	Japan	*Psorergates urotrichi*
	Neurotrichus gibbsii	Washington (USA)	*Psorergates* spec.
		Chiroptera	
Emballonuridae	*Emballonura nigrescens*	New Guinea	*Psorergatoides emballonurae*
	Saccopteryx canina	Venezuela	*Psorergatoides lonchorhina*
	Saccopteryx canescensi	Surinam	*Psorergatoides ndicicola*
	Saccopteryx billineata	Surinam	*Psorergatoides indicicola*
	Cormura brevirostris	French Guyana	*Psorergatoides peropteryx*
	Peropteryx macrotis	French Guyana	*Psorergatoides peropteryx*
Nycteridae	*Nycteris macrotis*	Zaire	*Psorergatoides nycteris*
	Nycteris spec.	Ruanda-Urundi	*Psorergatoides nycteris*
Megadermatidae	*Lavia frons*	Ruanda-Urundi	*Psorergatoides laviae*
Rhinolophidae	*Rhinolophus euryale*	Italy, Spain	*Psorergatoides rhinolophi*
	Rhinol. clivosus zuluensi s	Zaire	*Psorergatoides rhinolophi*
	Rhinolophus hildebrandti	Zaire	*Psorergatoides rhinolophi*
	Rhinolophus eathiops	Angola	*Psorergatoides rhinolophi*
	Rhinolophus hipposideros	Belgium	*Psorergatoides rhinolophi*

	Rhinolophus affinis	Birma	*Psorergatoides rhinolophi*
	Rhinol. ferrum-equinum	Belgium, France	*Psorergatoides rhinolophi*
	Rhinolophus mehelyi	Italy	*Psorergatoides rhinolophi*
Hipposideridae	*Hipposideros abae*	Zaire	*Psorergatoides hipposideros*
	Hipposideros caffer centralis	Zaire	*Psorergatoides hipposideros*
Phyllostomidae	*Lonchorhina aurita*	Venezuela	*Psorergatoides lonchorhina*
	Tonatia nicaraguae	unknown	*Psorergatoides surinamensis*
	Tonatia carrikeri	Surinam	*Psorergatoides surinamensis*
	Glossophaga soricina	Surinam	*Psorergatoides glossophagae*
	Rhinophylla pumilio	French Guyana	*Psorergatoides guyanensis*
	Artibeus lituratus	Surinam	*Psorergatoides artibei*
Desmodontidae	*Desmodus rotundus*	French Guyana	*Psorergatoides desmodus*
Vespertilionidae	*Myotis muricola*	Borneo	*Psorergatoides kerivoulae*
	Myotis bocagei	Ivory Coast	*Psorergatoides kerivoulae*
	Myotis mysticinus	Malaysia	*Psorergatoides kerivoulae*
	Plecotus auritus	Belgium	*Psorergatoides kerivoulae*
	Kerivoulae cuprosa	Zaire	*Psorergatoides kerivoulae*
	Kerivoulae harrisoni bellula	Zaire	*Psorergatoides kerivoulae*
	Eptesicus pumilus	Australia	*Psorergatoides australiensis*
	Eptesicus douglasi	Australia	*Psorergatoides australiensis*
	Nyctophilus arnhemensis	Australia	*Psorergatoides australiensis*
	Nyctophilus walkeri	Australia	*Psorergatoides australiensis*
Molossidae	*Tadarida mops*	Malaysia	*Psorergatoides tadaridae*
	Molossus ater	Surinam	*Psorergatoides molossi*
	Molossus molossus	Surinam	*Psorergatoides molossi*
		Primates	
Cercopithecidae	*Macaca arctoides*	USA (captured)	*Psorobia* spec.
	Cercopithecus aethiops pygerythus	South Africa	*Psorobia cercopitheci*
	Cercophithecus mona mona	Africa	*Psorobia* spec.
	Cercophithecus	Western Africa (captured)	*Psorobia cercophitheci*
		Lagomorpha	
Leporidae	*Sylvilagus floridanus*	Indiana (USA)	*Psorobia lagomorphae*
		Scandentia	
Tupaiidae	*Tupaia dorsalis*	Borneo	*Psorergates tupaiae*
		Rodentia	
Sciuridae	*Glaucomys volans volans*	USA	*Psorergates glaucomys*
	Dremomys rufigenis	Malaysia	*Psorergates dremomydis*
	Paraxerus cepapi	South Africa	*Psorergates cepapi*
Heteromyidae	*Heteromys anomalus*	Venezuela	*Psorergates* spec.
Castoridae	*Castor canadensis*	Canada	*Psorobia castoris*
Cricetidae	*Reithrodontomys megalotis*	Canada	*Psorergates* spec.
	Peromyscus maniculatus	Canada	*Psorergates peromysci* *Psorergates watsoni*
	Peromyscus leucopus	Canada	*Psorergates peromysci*
	Sigmodon hispidus	Georgia (USA)	*Psorergates* spec.
	Dicrostonyx groenlandicus	Groenland	*Psorergates* spec.
	Clethrionomys gapperi proteus	Labrador (USA)	*Psorergates* spec.
	Clethrionomys gapperi	Alberta (USA)	*Psorergates* spec.

	athabascae		
	Clethrionomys glareolus	Netherlands	*Psorergates microti*
			Psorergates musculinus
			Psorergates dissimilis
	Clethrionomys rucanus	Sweden	*Psorergates* spec.
	Clethrionomys rutilus	Sweden	*Psorergates* spec.
	Arvicola agrestis	unknown	*Psorergates simplex*
		unknown	*Psorergates musculinus*
		Netherlands	*Psorergates* spec.
	Arvicola arvalis	unknown	*Psorergates simplex*
	Ondatra zibethica	Germany	*Psorergates zibethicalis*
	Pitymys savil	Italy	*Psorergates* spec.
	Pitymys duodecimcostatus	Spain	*Psorergates pitymydis*
	flavescens	Spain	*Psorergates auricola*
	Pitymus subterraneus	Netherlands	*Psorergates* spec.
	Pitymys pinetorum	Indiana (USA)	*Psorergates pinetorum*
	Microtus arvalis meridianus	Spain	*Psorergates arvalis*
	Microtus arvalis	Spain, Netherlands	*Psorergates* spec.
	Microtus agrestis	England	*Psorergates musculinus*
		Netherlands	*Psorergates microti*
		Netherlands	*Psorergates* spec.
	Microtus agrestis bailloni	Netherlands	*Psorergates agrestis*
	Microtus oeconomus	w. Mongolia	*Psorergates* spec.
		Netherlands	*Psorergates neerlandicus*
	Microtus oeconomus arenicola	Netherlands	*Psorergates oeconomi*
	Microtus nivalis	Switzerland	*Psorergates* spec.
	Microtus pennsylvanicus	Canada	*Psorergates canadensis*
	Micromys minutus soricinus	Netherlands	*Psorergates micromydis*
	Apodemus sylvaticus	Spain	*Psorergates callipidis*
	callipides	Spain	*Psorergates meati*
	Apodemus sylvaticus	Netherlands	*Psorergates apodemi*
		France	*Psorergates musculinus*
	Hybomys univattus	Zaire	*Psorergates muricola*
	Rattus norvegicus	Japan	*Psorergates* spec.
	Rattus natalensis	South Africa	*Psorergates oettlei*
	Mus musculus	Canada	*Psorergates simplex*
		Indiana (USA)	
		Netherlands	
		Netherlands	*Psorergates muricola*
	Mus musculus spretus	Spain	*Psorergates hispanicus*
	Mus commissarius	Phillipines	*Psorergates hispanicus*
	Lophuromys aquilus	Zaire	*Psorergates muricola*
	Deomys ferrugineus chrystyi	Zaire	*Psorergates deomydis*
	Otomys irroratus elgonis	Zaire	*Psorergates muricola*
Gliridae	*Muscardinus avellanarius*	Germany	*Psorergates muscardinus*
	Eliomys quercinus	Spain	*Psorergates quercinus*
	Eliomys quercinus ophiusae	Spain	*Psorergates eliomydis*
Hystricidae	*Hystrix africae-australis*	South Africa	*Psorobia hystrici*
Bathyergidae	*Cryptomys hottentotus*	South Africa	*Psorobia zumpti*
		Carnivora	
Mustelidae	*Mustela nivalis*	Netherlands	*Psorobia mustelae*
	Mustela erminea	Netherlands	*Psorobia mustelae*
	Martes foinae	Belgium	*Psorobia foinae*

		Artiodactyla	
Bovidae	*Bos taurus*	USA	*Psorobia bos*
	Ovis aries	Australia, USA South Africa	*Psorobia ovis*

Acknowledgements

I would like to thank the late Dr. Lukoschus, who was my tutor for the research field of systematic parasitology, and who initiated my special interest for the mite family Psorergatidae. John Kethley, Field Museum Chicago, and Barry OConnor, The University of Michigan, helped me a lot with their knowledge on phylogenetic systematics of prostigmatic and astigmatic mites. Discussions with Barry OConnor and Hans Klompen helped me to develop my own view on the phylogenetic relationships of Psorergatidae and co-evolutionary patterns of mites and hosts.Special thanks to Prof. C. den Hartog for giving me possibilities to use laboratory facilities, and cooperation in publication of this thesis.

References

Ah H-S., Peckham J.C. & Atyeo W.T., 1973. *Psorergates glaucomys* sp.n. (Acari: Psorergatidae), a cystogenous mite from the southern flying squirrel (*Glaucomys v. volans*), with histopathologic notes on a mite-induced dermal cyst.— J. Parasit., 59: 369-374.

Baker E.W. & Wharton G.W., 1964. An introduction to acarology.— The MacMillon Company, New York, 4th ed.

Beresford-Jones W.P., M.A., 1965. Occurrence of the mite *Psorergates simplex* in mice.— Austral. Vet. J., 41: 289-290.

Canestrini G., 1894. Varia. *Psorergates, Hemisarcoptes, Histiogaster.* Appendice ai psoroptidi.— Prospetto dell'Acarofauna Italiana: 809-812.

Carter H.B., 1941. A skin disease of sheep due to an ectoparasitic mite, *Psorergates ovis*, Womersley 1941.— Austral. Vet. J., 17: 193-201.

Cock A.W.A.M. de, Lukoschus F.S. & Ariani A.P., 1970. *Psorergates etruscus* spec. nov. (Acari: Psorergatidae), a new itch mite from *Suncus etruscus* (Soricidae).— Ann. Ist. e Mus. Zool. Univ. Napoli, 19 (4): 1-9

Downing W. & Mort P., 1962. Experiments in the control of the itch mite, *Psorergates ovis*, Womersley, 1941. Part 1 and 2.— Austral. Vet. J., 38: 77-85 and 269-274.

Dubinin V.B., 1957. New classification of the mites of the superfamilies Cheyletoidea W. Dub. and Demodicoidea W. Dub. (Acariformes, Trombidiformes).— Mag. Parasit., 17: 103-131.

Dubinin W., 1955. Acariens des rongeurs d'U.R.S.S. II. Psorergatidae.— Trav. Acad. Sci. U.R.S.S. (Zool.), 59: 150-152.

Fain A., 1959a. Les acariens psoriques parasites des Chauves-souris. III. Le genre *Psorergates* Tyrrell (Trombidiformes - Psorergatidae).— Bull. Ann. Soc. Roy. Ent. Belg. 95, I-IV: 54-69.

Fain A., 1959b. Les acariens psoriques parasites des Chauves-souris, IX. Nouvelles observations sur le genre *Psorergates* Tyrrell.— Bull. Ann. Soc. Roy. Ent. Belg., 95, VII-VIII: 232-248.

Fain A., 1961. Notes sur le genre *Psorergates* Tyrrell. Description de *Psorergates ovis* Womersley et d'une espece nouvelle.— Acarologia, 3 (1): 60-71

Fain A., 1965. Sur un cas de gale chez un rat-taupe (*Cryptomys hottentotus*) produite par un acarien du genre *Psorergates* (Psorergatidae: Trombidiformes).— Acarologia, 7: 295-300.

Fain A., Lukoschus F.S. & Hallmann P., 1966. Le genre *Psorergates* chez les murides. Description de trois especes nouvelles (Psorergatidae: Trombidiformes).— Acarologia, 8: 251-274.

Fain A. & Lukoschus F.S., 1968. *Psorergates* (*Psorobia*) *foinae* sp.n., acarien producteur de gale chez la fouine en belgique.— Bull Inst. r. Sci. nat. Belg., 44 (14): 1-6.

Farris J.S., 1974. Formal definitions of paraphyly and polyphyly—. Syst. Zool. 23: 548-554.

Gerlach A.C., 1857. Kratze und Raude, entom. und klin. bearbeitet.— Berlin 1 (I), Plate 8, fig. 44.

Giesen K.M.T. & Lukoschus F.S., 1982a. A new species of the genus *Psorergates* Tyrell, 1883 (Acarina:

Prostigmata: Psorergatidae) parasitic on the tree-shrew *Tupaia dorsalis* (Mammalia: Scandentia) from Borneo.— Zool. Med. Leiden 56: 259-266.

Giesen K.M.T. & Lukoschus F.S., 1982b. A new itch mite (Acarina: Prostigmata: Psorergatidae) from the South African bush squirrel *Paraxerus cepapi*.— Bull. Inst. r. Sci. nat. Belg., 53: 1-9.

Giesen K.M.T. & Lukoschus F.S., 1983. Two new species of the genus *Psorergates* Tyrell, 1883 (Acarina: Prostigmata: Psorergatidae) parasitic on insectivores, with a key to the known species from Insectivora hosts.— Acarologia 24: 403-415.

Giesen K.M.T., Lukoschus F.S. & Fain A., 1982. Parasites of Western Australia XV. A new species of *Psorergatoides* (Acarina: Psorergatidae) from Australian bats.— Rec. West. Aust. Mus., 9: 315-323.

Giesen K.M.T., Lukoschus F.S. & Nadchatram M., 1982. Three new itch mites of the family Psorergatidae (Acari, Prostigmata) from Malaysian small mammals.— Malay. Nat. J., 35: 315-328.

Giesen K.M.T., Lukoschus F.S., Whitaker J.O. Jr. & Gettinger D., 1983. Four new species of itch mites (Acari: Psorergatidae: Prostigmata) from small mammals in North America.— J. Med. Entomol., 20: 164-173.

Giesen K.M.T., Nutting W.B. & Nadchatram M., 1989. A new mite species of the genus *Psorergates* Tyrrell (Acari: Prostigmata: Psorergatidae) parasitic on the tree shrew *Tupaia glis* , with notes on pathology.— Raffles Bull. Zool. 37: 132-141.

Giesen K.M.T. & OConnor B.M. (in press). Phylogenetic and coevolutionary patterns in the genus *Psorergates* (Acari: Psorergatidae), with description of a new species from *Hodomys alleni* (Rodentia: Muridae).Submitted to Systematic Parasitology.

Giesen K.M.T., Spicka E.J. & Whitaker J.O. Jr., 1985. Two new species of the genus *Psorobia*, Fain, 1959 (Psorergatidae: Prostigmata) from two new host orders, Lagomorpha and Insectivora.— Acarologia 26: 147-153.

Giesen K.M.T. & Yunker C.E., 1985. *Psorobia bos* Johnston, 1964, the cattle itch-mite. Description of the male (Acari: Psorergatidae).— Acarologia 26: 37-41.

Grandjean, F., 1973. In: L. v.d. Hammen (ed.) Oeuvres acarologiques complètes.— Dr. W. Junk B.V. Publishers, The Hague.

Johnston D.E., 1964. *Psorergates bos*, a new mite parasite of domestic cattle. (Acari - Psorergatidae).— Wooster Ohio Research Note, 129: 1-7.

Kethley J., 1982. Acariformes.In: S. P. Parker (ed.) Synopsis and classification of living organisms, 2: 117-146.— McGraw-Hill, Inc.

Kok N.J.J., Lukoschus F.S. & Clulow F.V., 1970. *Psorobia castoris* spec. nov. (Acarina: Psorergatidae), a new itch mite from the beaver, *Castor canadensis*.— Can. J. Zool., 48: 1419-1423.

Kok N.J.J., Lukoschus F.S. & Clulow F.V., 1971. Three new itch mites from Canadian small mammals (Acarina: Psorergatidae).— Can. J. Zool., 49: 1239-1248.

Krantz G.W., 1970. A manual of Acarology: 1-335.— Oregon State Univ. Bookstores, Corvallis.

Krantz G.W., 1978. A manual of Acarology, Second Edition.— OSU Book Stores, inc. Corvallis, Oregon.

Lavoipierre M.M.J. & Crewe W., 1955. The occurrence of a mange-mite, *Psorergates* sp. (Acarina), in a West African monkey.— Ann. Trop. Med. & Parasitol., 49: 351.

Lee J., Yunker C.E., Lang C.M., Hartshorn R.D. & Hughes H.C., (manuscript). A new species of psoric mange mite (Acari: Psorergatidae) on stumptail macaques (*Macaca arctoides*).

Lukoschus F.S., 1967. Kratzmilben an Spanischen Kleinsaugern (Psorergatidae: Trombidiformes).— Rev. Iber. Parasitol., 27: 203-228.

Lukoschus F.S., 1968a. *Psorergates desmanae* sp. nov., eine neue Kratzmilbe von *Galemys pyrenaicus* (Psorergatidae: Trombidiformes).— Bull. Mus. nat. Hist. natur. Paris, 2 (40): 125-131.

Lukoschus F.S., 1968b. Neue Kratzmilben von einheimischen Insektivoren (Psorergatidae: Trombidiformes).— Tijdschr. Ent. 111: 75-88.

Lukoschus F.S., 1969. *Psorergates* (*Psorobia*) *mustelae* spec. nov.. Eine neue Kratzmilbe von *Mustela nivalis* L. (Acarina: Psorergatidae).— Zool. Anz., 183: 111-118.

Lukoschus F.S., Cock A.W.A.M. de & Driessen F.M., 1971. Four new species of the genus *Psorergates* Tyrrell from European hosts (Acarina: Psorergatidae).— Tijdschr. Ent., 114: 185-200.

Lukoschus F., Fain A. & Beaujean M.M.J., 1967. Beschreibung neuer *Psorergates*-Arten (Psorergatidae: Trombidiformes).— Tijdschr. Ent. 110: 133-181.

Lukoschus F.S., Louppen J.M.W. & Fauran P., 1979. Parasitic mites of Surinam XIV. New observations

on the genus *Psorergatoides* Fain, 1959 (Psorergatidae: Trombidiformes), with a key to the known species.— Intl. J. Acar., 5: 311-324.

Lukoschus F.S., Louppen J.M.W. & Maa T.C., 1974. *Psorergates squamipes* n. sp. (Acari: Psorergatidae), a skin mite from *Anourosorex squamipes* (Insectivora) in Taiwan.— Pacific Insects, 16: 51-56.

Lukoschus F.S., Rosmalen P.G. & Fain A., 1973. Parasitic mites of Surinam XI. Four new species of the genus *Psorergatoides* Fain, 1959, (Psorergatidae: Trombidiformes).— Tijdschr. Ent., 116: 63-81.

Michael A.D., 1889. On some unrecorded parasitic Acari found in Great Britain.— J. Linn. Soc. (Zool.) London, 20: 400-406.

Moss W.W., Kethley J. & Lukoschus F.S., (in prep.). Phylogenetic relationships of the mite family Harpyrhynchidae, with a revision of the subfamily Harpypalpinae (Acari: Cheyletoidea) skin parasites of passeriform birds.

Murray M.D., 1961. The life cycle of *Psorergates ovis* Womersley, the itch mite of sheep.— Austral. J. Agr. Res., 12: 965-973.

Neumann M.G., 1893. Note preliminaire sur le *Psorergates simplex*, acarien parasite de la souris.— Compt. rend. Soc. Biol., 330.

Neumann M.G., 1893. Sur un acarien (*Psorergates simplex* Tyrrell) de la souris.— Bull. Soc. Hist. Natur. Toulouse., 27: 13-22.

Piana G.P., 1886. Cisti cutanee contenenti acari nei topi. Annuario p. anno scolastico 1885-86.— R. Scuola Sup. di Med. Veterin. Milano: 122, tav. I.

Rioux J.A. & Golvan Y.J., 1961. Gale a *Psorergates musculinus* (Michael, 1889) (Acari: Myobiidae) chez les mulots *Apodemus sylvaticus* (Linne 1758) de massif de caroux (Herault).— Ann. Parasitol. Hum. pom., 36: 785-787.

Sheldon W.S., 1966. Psorergatic mange in the sooty mangabey (*Cercocebus torquatus atys*) monkey.— Lab. Animal. Care., 16: 276-279.

Spicka E.J., 1976. First report of *Psorergates simplex* Tyrrell, 1883 (Acari: Psorergatidae) from wild house mouse, *Mus musculus*, in the United States.— Proc. Indiana Acad. Science 1975., 85: 418-422.

Till W.M., 1957. Two new parasitic mites (Acarina) from the South African porcupine.— Parasitology., 47: 329-334.

Till W.M., 1960. *Psorergates oettlei* n.sp., a new mange-causing mite from the multimammate rat (Acarina: Psorergatidae).— Acarologia., 2: 75-79.

Tyrrell J.B., 1883. On the occurrence in Canada of two species of parasitic mites.— Proc. Canad. Inst. N.S., I: 332-342.

Vitzhum H., 1929. Acari. Die Tierwelt Mitteleuropas. III (7).

Walker E.P., 1975. Mammals of the world, third edition, vols. 1-2.— The Johns Hopkins University Press, Baltimore and London.

Wassel M.E., Whitaker J.O. Jr. & Spicka E.J., 1980. The ectoparasites and other associates of the cottontail rabbit *Sylvilagus floridanus*, in Indiana.— Proc. Indiana Acad. Science .1979., 89: 418-420.

Wheeler Q.D., 1986. Character weighting and cladistic analysis.— Syst. Zool., 35: 102-109.

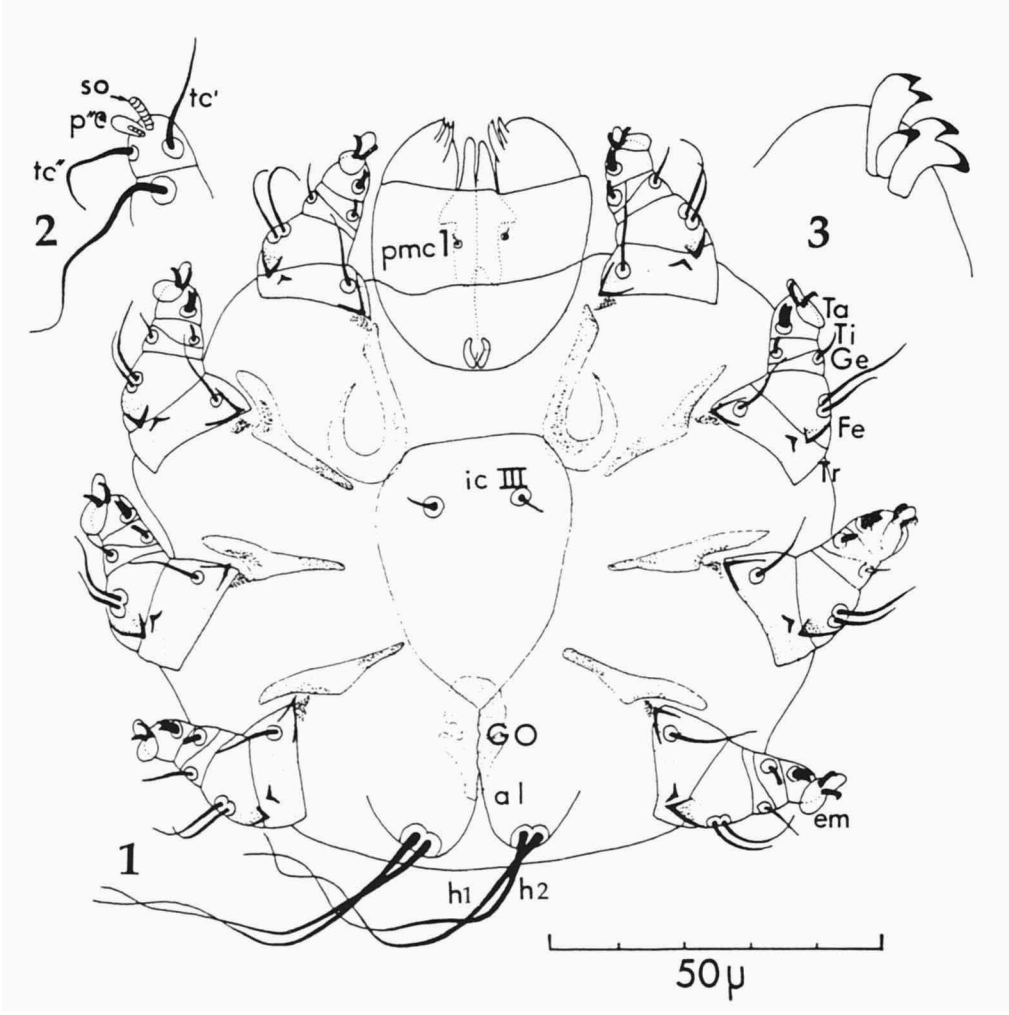
Wiley E.O., 1981. Phylogenetics. The theory and practice of phylogenetic systematics: 1-439.— John Wiley & sons, New York.

Womersley H., 1941. Notes on the Cheyletidae of Australia and New Zealand, with descriptions of new species.— Rec. S. Austral. Mus., 7: 51-64.

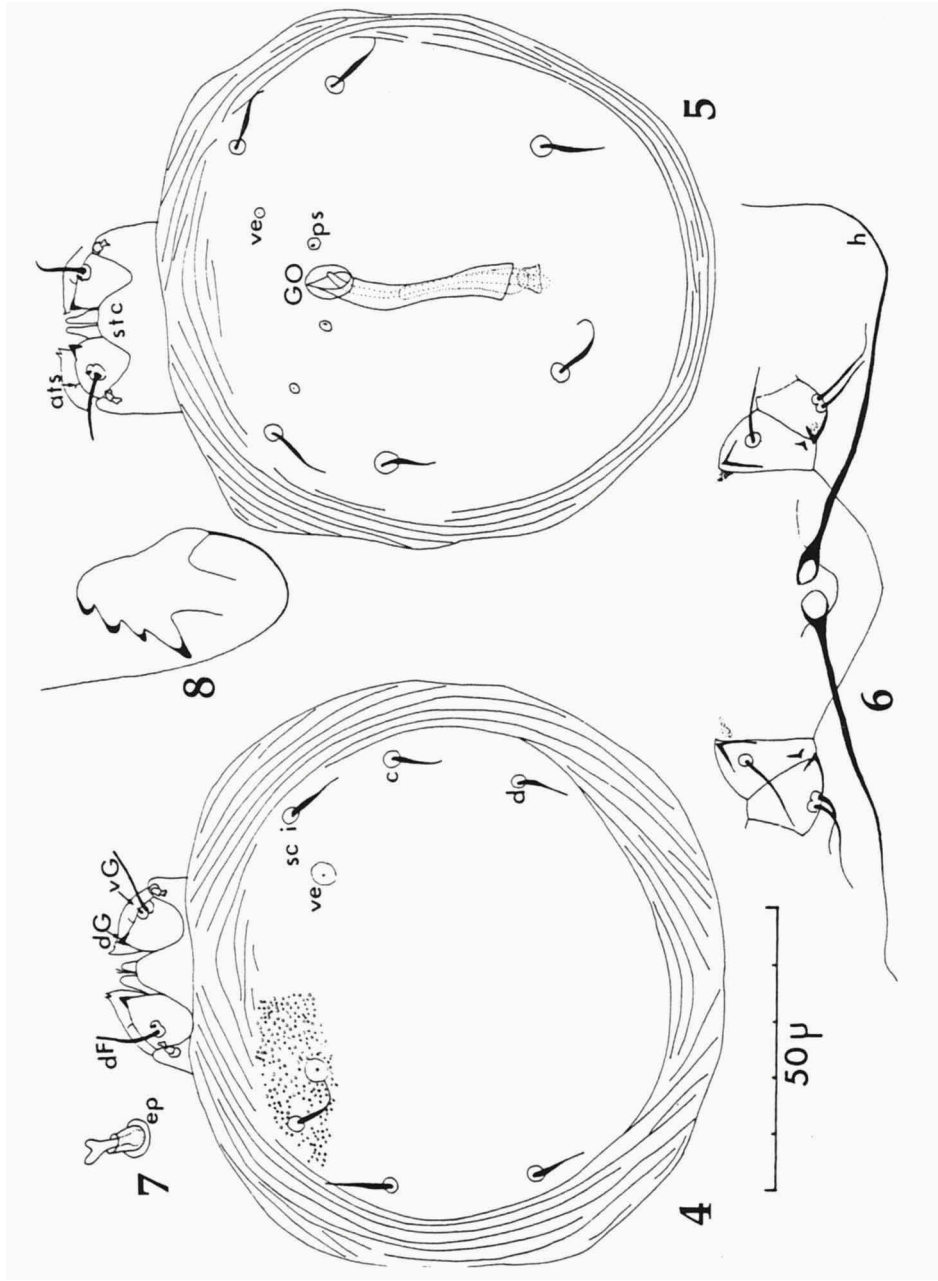
Wood, 1955. from DeBlase A.F. & Martin R.E., 1974. A manual of mammology: 218-219.— WM. C. Brown Company Publishers.

Zumpt F. & Till W., 1955. The mange-causing mites of the genus *Psorergates* (Acarina: Myobiidae) with description of a new species from a South African monkey.— Parasitology, 45: 269-274.

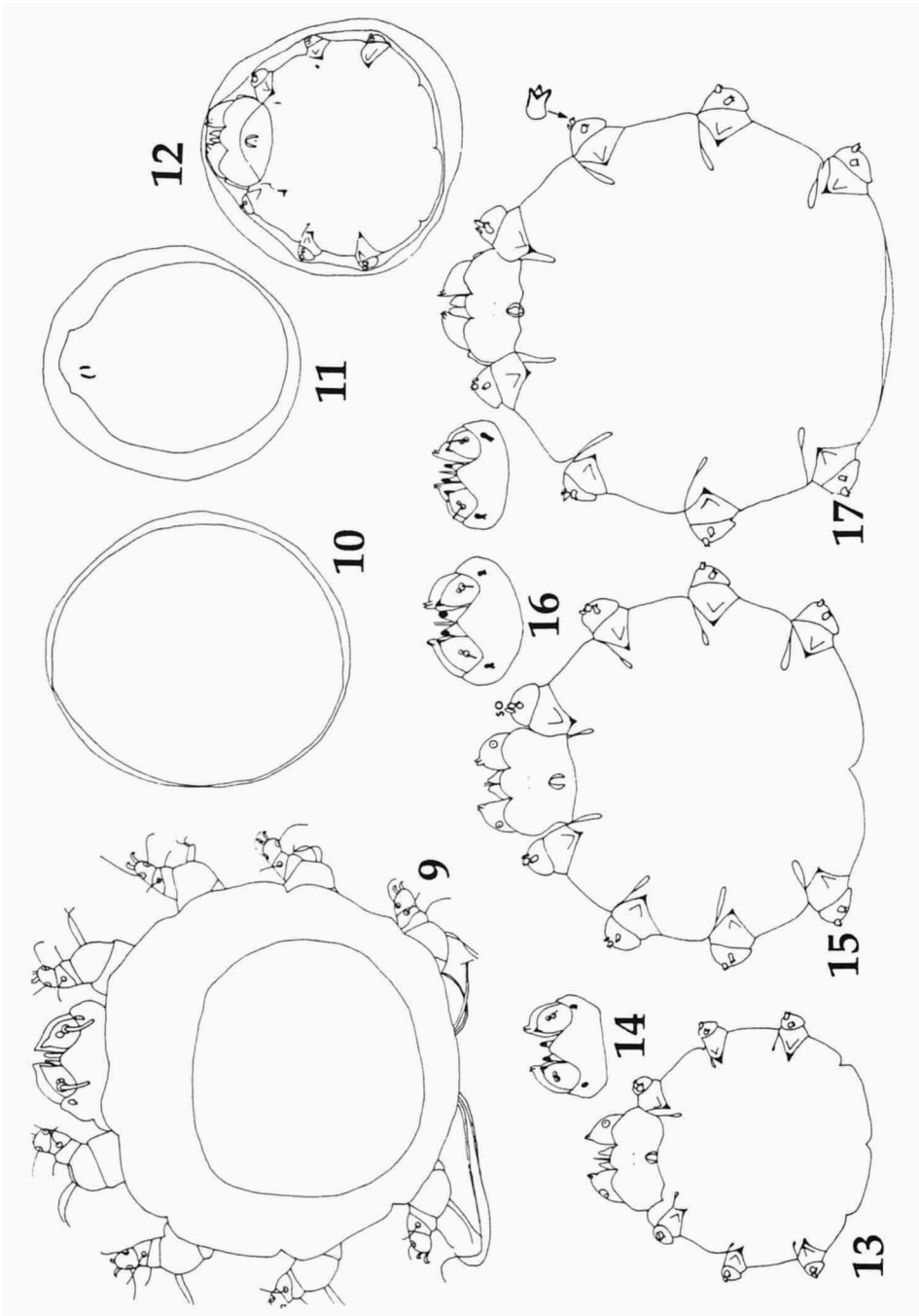
Received: 4.iv.1988
Accepted: 19.i.1990
Edited: J. Krikken



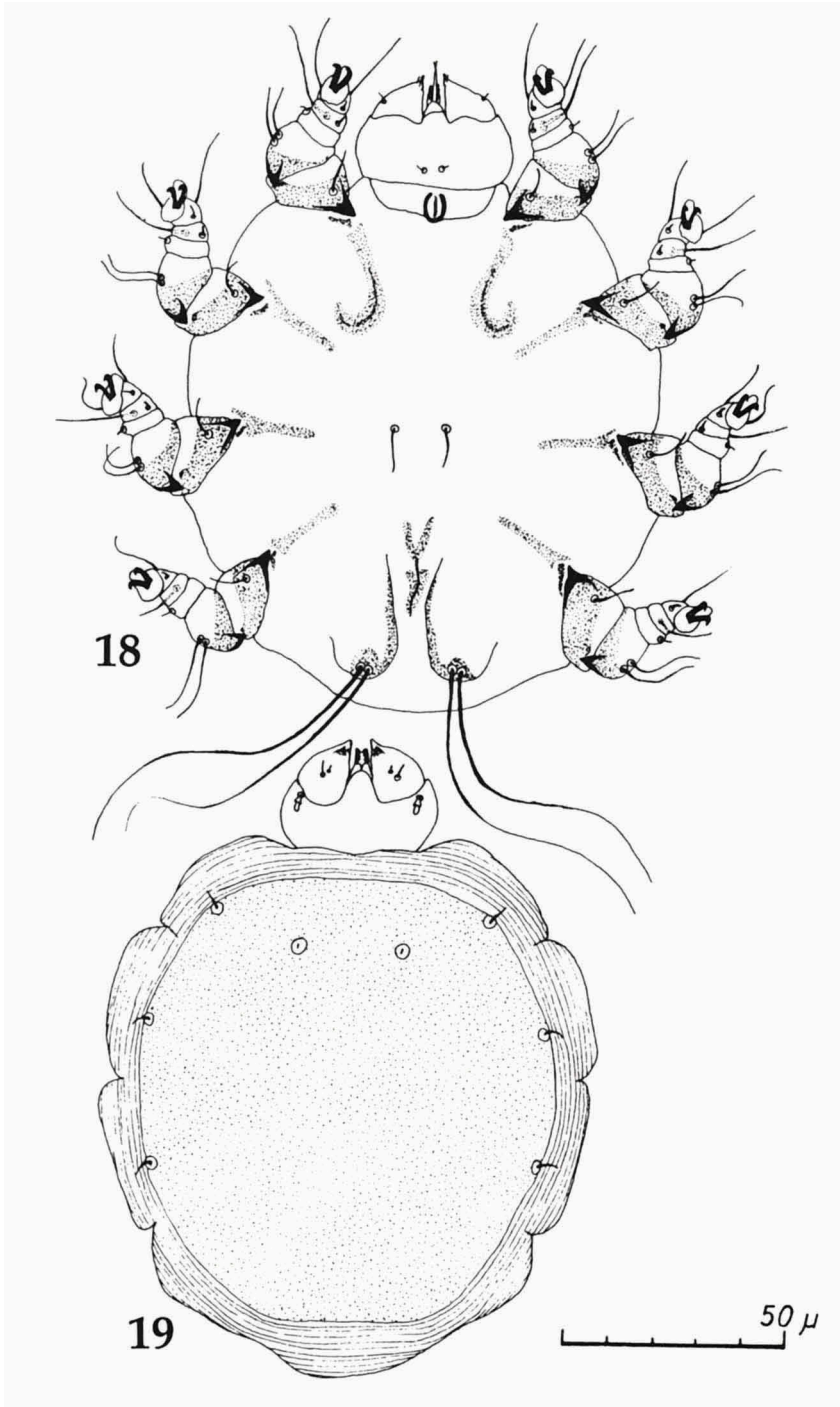
Figs. 1-3. *Psorergates cepapi* Giesen & Lukoschus, 1982. 1) female venter. (a l: adanal lobe; em: empodium; Fe: femur; Ge: genu; GO: genital opening; *h 1, h 2*: terminal setae; *ic III*: intercoxal or ventral setae; *pmc 1*: internal subcapitular or subgnathosomal setae; Ta: tarsus; Ti: tibia; Tr: trochanter). 2) tibia and tarsus of leg I, ventral side. (*p"@*: enveloped seta of tarsus I-II; so: solenidion omega; *tc'*: dorso-anterior seta; *tc"*: dorso-posterior seta). 3) Tibia-tarsus segment of palps (formerly tarsus-segment) with three spine-like setae.



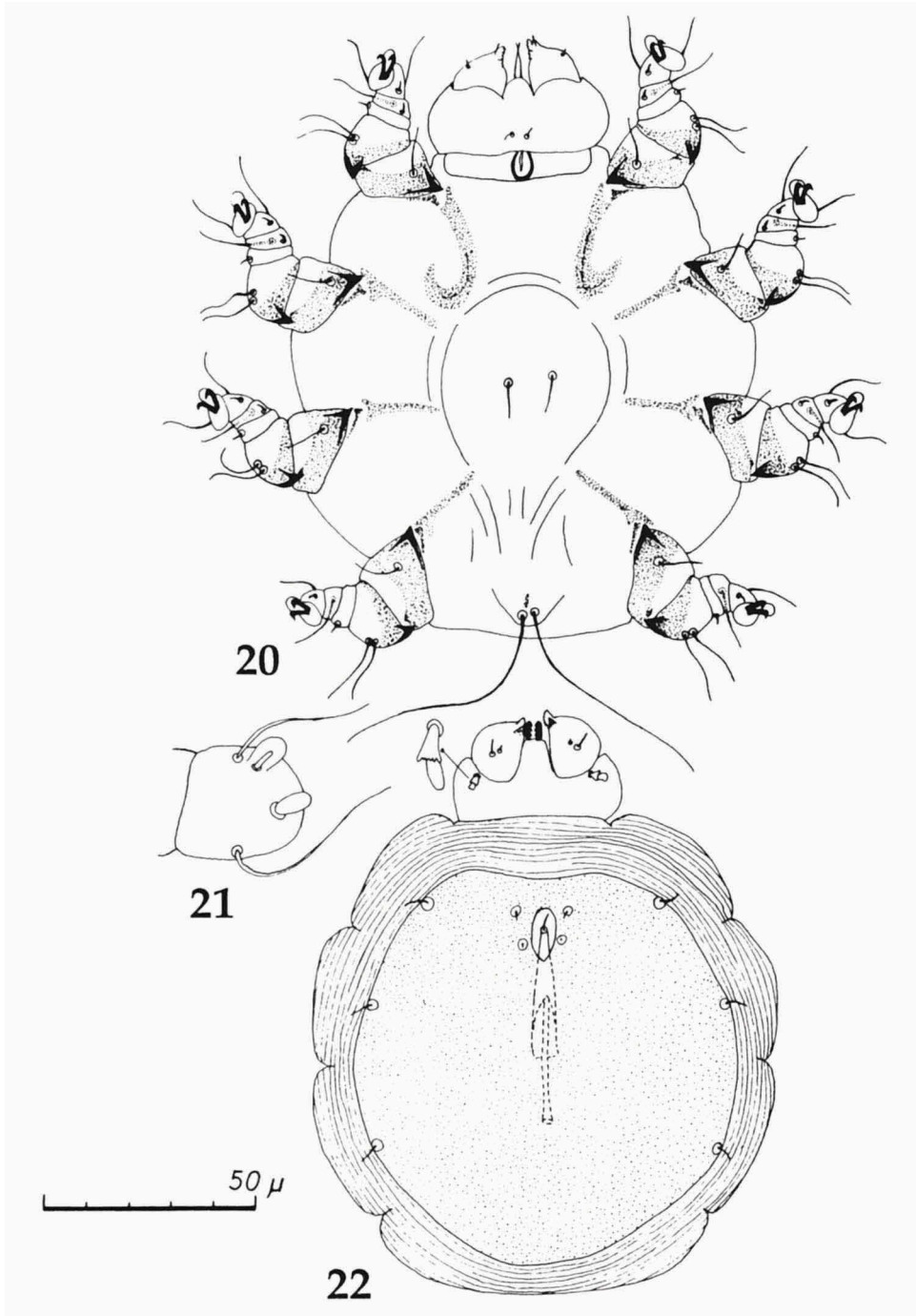
Figs 4-8. *Psorergates cepapi* Giesen & Lukoschus, 1982. 4) female dorsum. (*c, d*: lateral shield setae; *dF*: dorsal femoral or palpal tibial seta; *dG*: dorsal genual seta or apical spur; *sc i*: lateral shield seta; *v e*: antero-median seta; *vG*: antiaxial seta). 5) male dorsum. (*ats*: dorso-lateral seta on tibia-tarsus (formerly tarsus) segment of palps; GO: genital opening; *ps*: genito-anal (genital) setae; stc: stylophore capsule; *v e*: antero-median seta). 6) terminal part of male venter (*h*: terminal seta). 7) *ep*: supracoxal (gnathosomal) seta. 8) chelicera.



Figs. 9-17. Developmental stages of the family Psorergatidae. 9) female with egg; 10) egg; 11) egg with praelarva; 12) larva enveloped by praelarva and egg; 13) larva; 14) gnathosoma larva, dorsally; 15) protonymph; 16) gnathosoma deutonymph, dorsally; 17) deutonymph with gnathosoma dorsally, and three-pointed claw.



Figs. 18-19. *Psorergates simplex* (Tyrrell, 1883); 18, female venter; 19, female dorsum.



Figs. 20-22. *Psorergates simplex* (Tyrrell, 1883); 20, male venter; 21, tarsus of leg I, ventrally; 22, male dorsum.

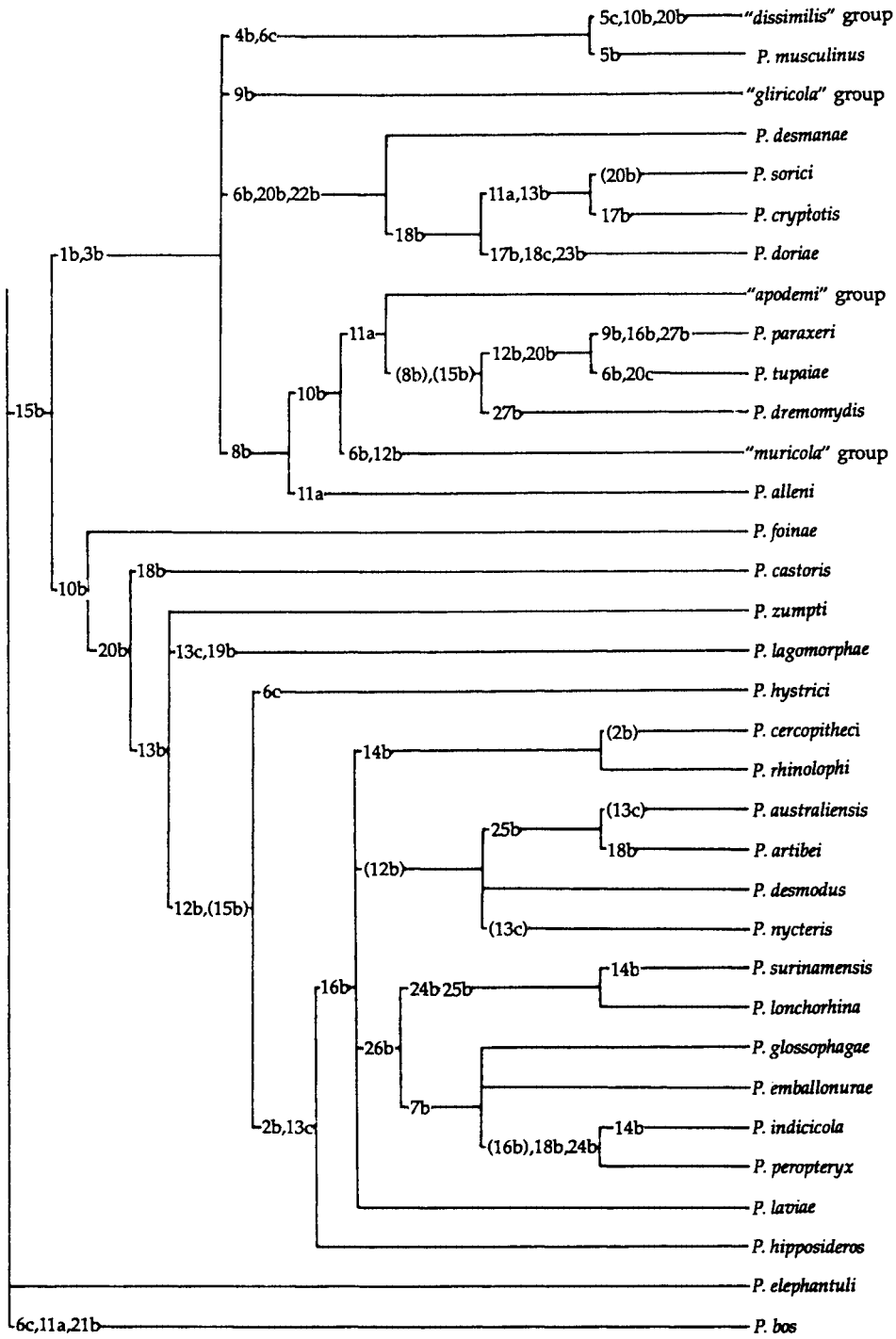
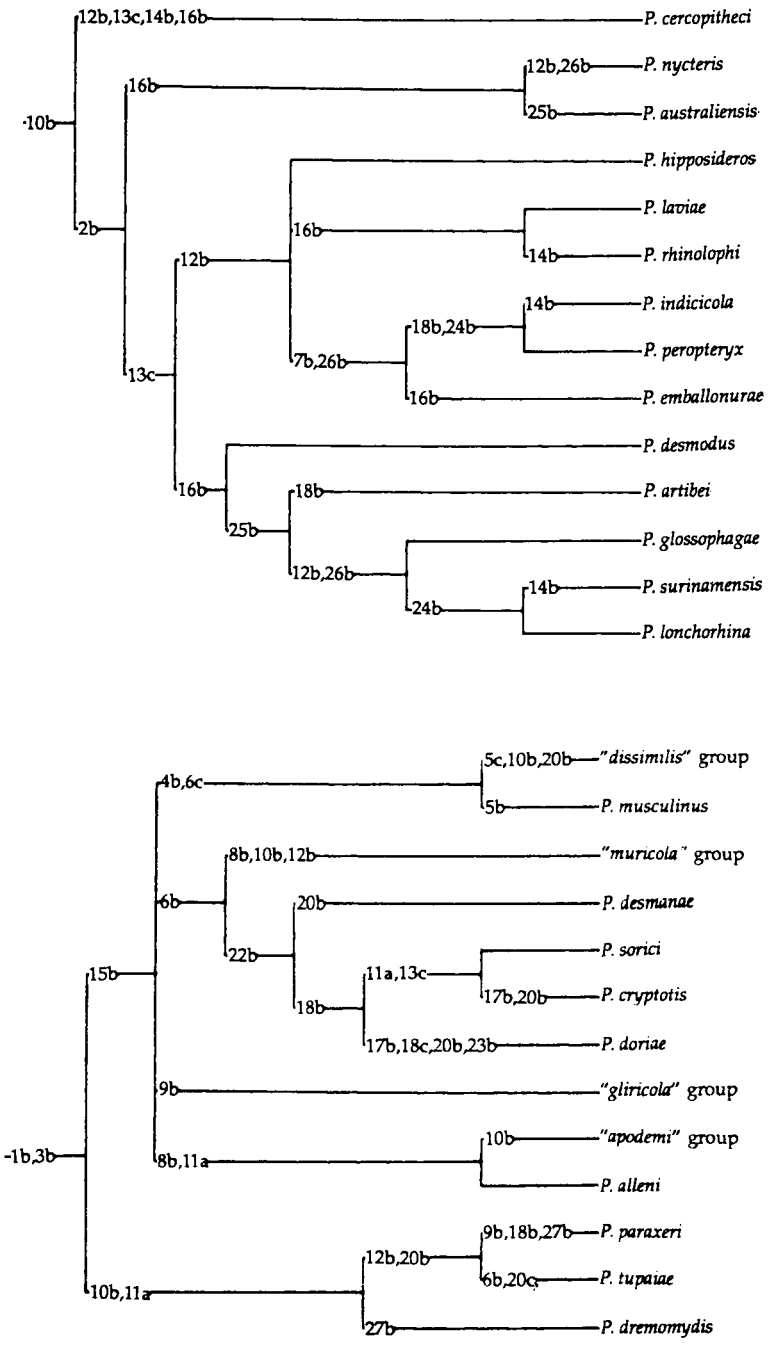
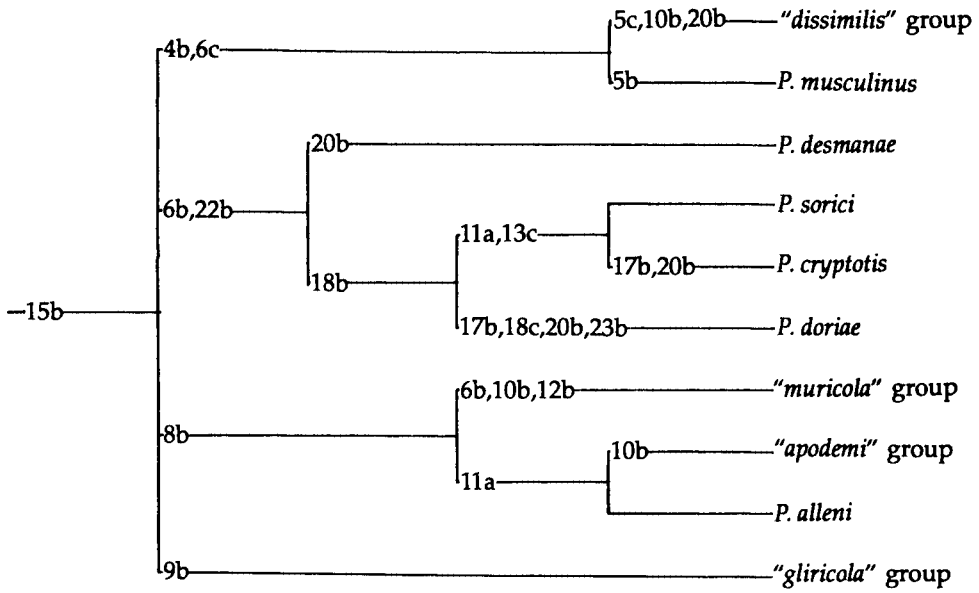
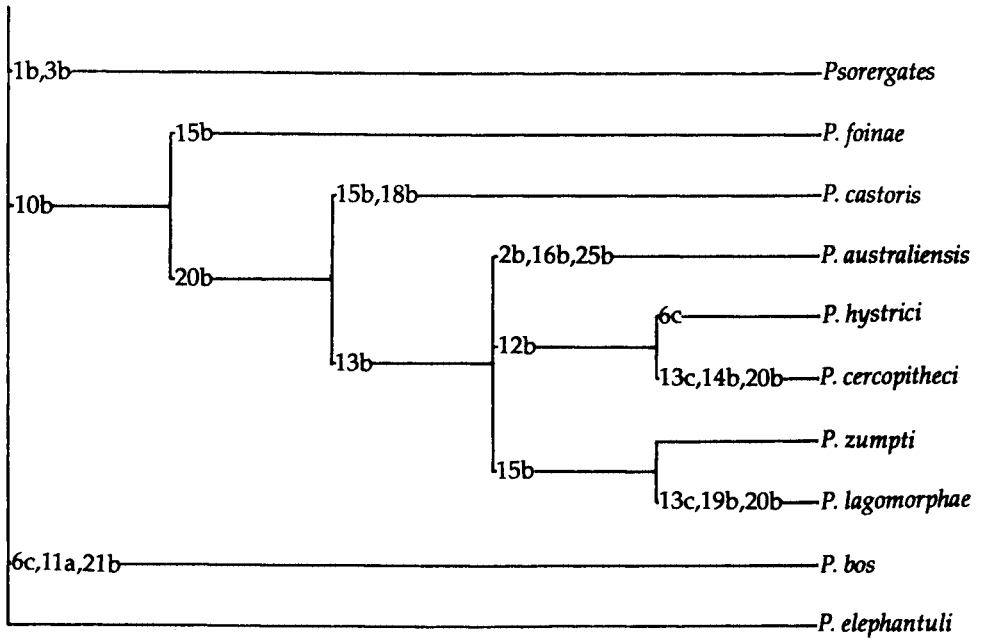


Fig. 23. Cladogram of the species and species groups of the family Psorergatidae constructed with the aid of computer program PAUP. (): reversal.



Figs. 24 (upper), 25. Cladograms of the genera *Psorergatoides*, and *Psorergates*. For explanation see text.





Figs. 26 (upper), 27. Cladograms of the genera *Psorergates*, and *Psorobia*. For explanation see text.

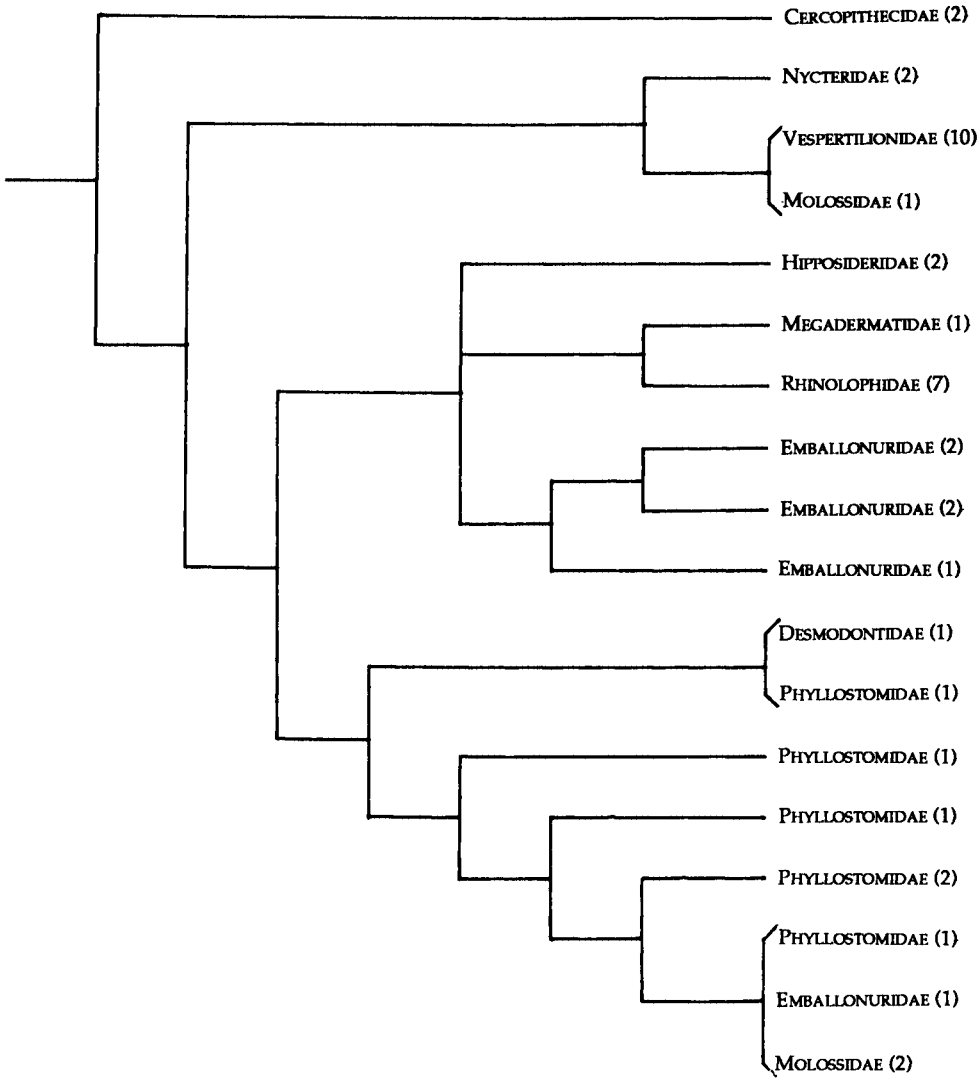


Fig. 28. Host cladogram of the families parasitized by Psorergatidae derived from figure 24. The numbers between parentheses represent the number of infested host species). For further explanation see text.

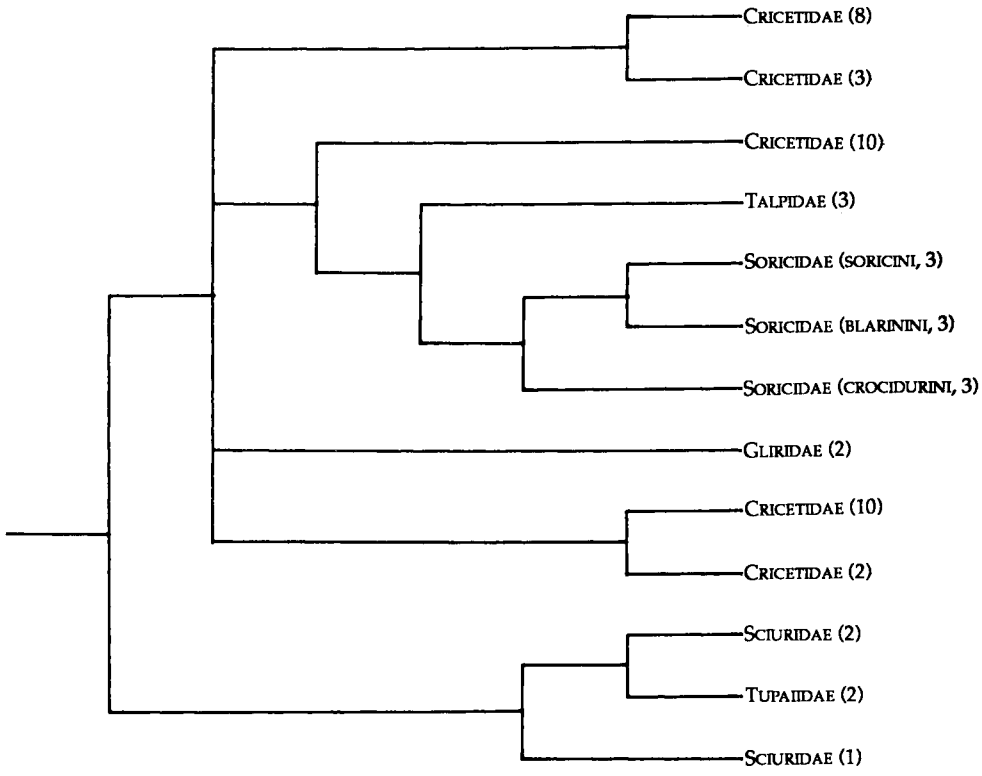


Fig. 29. Host cladogram of the families parasitized by Psorergatidae derived from figure 25. The numbers between parentheses represent the number of infested host species). For further explanation see text.