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PATHOGENS AND PARASITES OF OPILIONES (ARTHROPODA: ARACHNIDA)

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ABSTRACT. This is the first paper to review the literature records on all pathogens and parasites of Opiliones on a global level. These organisms (bacteria, fungi, protozoans, cestodes, trematodes, nematodes, arthropods) are listed in phylogenetic order along with available information on hosts, collection localities, life history, and taxonomic history. The opilion hosts are also listed (by their currently accepted names) along with the names of their known pathogens and parasites. Diagnostic characters and some taxonomic keys are provided for taxa which are relatively well know. Citations to other available keys are provided. Many new host and distribution records are provided.

Two fungi [*Engyodontium aranearum* (Cavara), *Torrubiella pulvinata* Mains] are removed from the list of pathogens of opilions and it is suggested that the original hosts were misidentified spiders.

Two new combinations are recorded in the Mermithidae: *Agamomermis phalangii* (Haldeman 1851), *Agamomermis truncatula* (Rudolphi 1819). *Agamermis incerta* Steiner in Stipperger 1928 is regarded as a *nomen nudum*.

The type locality of the mite *Leptus lomani* (Oudemans 1903b) is restricted to Corral (39°53'S, 73°25'W), Valdivia, Chile.

Unlike many arachnids, Opiliones or harvestmen lack a pumping stomach and therefore they chew their food and often consume oocysts and spores. Examination of their feces reveals a variety of chitinous fragments from their arthropod prey as well as plant pieces. Some saprophytic fungi and yeast spores can be observed as well as gametocytes of internal parasites. The frequent grooming of the legs by the harvestmen may also lead to the ingestion of oocysts and spores. While ingestion is the common entrance pathway for some opilion pathogens, fungi infect their host through penetration of the cuticle. Although gregarines and mites are frequently encountered when observing harvestmen, relatively few researchers have documented their occurrences.

Harvestmen are unique among arthropods by possessing bilateral exocrine glands which open onto the dorsal surface of the cephalothorax near the base of the second pair of legs. These glands produce a variety of volatile secretions (Ekpa *et al.* 1984, 1985) that have been generally considered to be defensive in nature. The glands have also been proposed to function in a variety of other behaviors including protection from external pathogens and parasites (see Holmberg 1986, and citations therein). To date, only defense against predators and harvestman aggregation formation have been demonstrated.

While working with a South America harvestman, Estable *et al.* (1955) discovered that the exocrine gland secretion was a remarkably effective antibiotic, *in vitro*, against 18 genera of bacteria (Gram positive and negative) and protozoa. Their work revealed that the secretion was also active when given orally to mice infected with intestinal parasites. The substance was tolerated perfectly by the mice but destroyed giardias, trichomonas and hexamites. The components of the secretion were later determined to be a composed of a variety of quinones (Fieser & Ardao 1956).

The major components of the exocrine secretions of harvestmen differ between the two suborders, Laniatores and Cyphopalpatores. Minor components and ratios of components differ among congeneric species (Ekpa *et al.* 1985). The few chemical analyses thus far reported (see Ekpa *et al.* 1984, and citations therein) from Laniatores reveal a variety of alkylated benzoquinones, phenols, N,N-dimethyl-β-phenylethylamine and bornyl esters. Only the Palpatore section of the suborder Cyphopalpatores has been chemically investigated. Those analyses reve

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members of this group secrete short-chained acyclic ketones, alcohols and naphthoquinones (see Ekpa *et al.* 1985, and citations therein).

Even though harvestmen are abundant in warm moist situations, few records are available of fungi infecting these animals. Because the major components of harvestman exocrine secretions are members of chemical classes known to be fungicides (see Torgeson 1969; Cole *et al.* 1975), it is likely these secretions are used to protect harvestmen from infection. The use of these secretions in defense and grooming needs further study.

While there are several world-wide taxonomic revisions of harvestmen, no similar treatment for their parasites has been undertaken. This is in part due to the incorrect view that harvestmen are not of economic importance. Mounting evidence demonstrates that harvestmen are beneficial and that they consume considerable quantities of pest insects and mites. Because of this beneficial status, no one has investigated parasites for controlling opilions. Experiments involving insect pathogens on harvestmen reveal opilions are susceptible. Like conventional insecticides, insect pathogens and parasites could have a severe impact on the beneficial harvestmen.

Many of the records of parasites from harvestmen are incomplete. In some cases the host, but not the parasite, is identified to species. In other cases, the parasite but not the host is identified to species. The purpose of this contribution is to bring together the limited information on this topic so that a foundation can be built for future research.

Because of the lack of good characters in some groups (*i. e.*, Microsporida and juveniles of Mermithidae) collective groups have been named. Such groups or genera often include species which probably are not related. This group name is used simply for "taxonomic convenience" and includes species not readily placed in known genera (possibly because a particular life stage is unknown) and species *incertae sedis*. Some taxonomically convenient groups also occur at higher levels in fungi. In fungi, the sexual stage (teleomorph of ascomycetes and basidiomycetes) and their asexual stages (anamorphs or conidial stages) are sometimes placed in separate genera and classes. In some cases, two or more ascomycetes may be identified as having the same form species for an anamorph.

When one discusses parasites of opilions, the topic of phoresy arises. Phoresy is not parasitism but rather a form of symbiotic relationship in which the smaller organism associates with the harvestman in order to obtain transportation. Phoresy as well as passive transport of fungal and plant spores will not be examined here.

Superkingdom Prokaryotae
Kingdom Monera
Division Gracilicutes
Family Enterobacteriaceae

Xenorhabdus Thomas & Poinar contains five described species and other undescribed species (Akhurst & Boemare 1990). They typically inhabit nematodes and their host arthropods (insects and arachnids). See under Nematoda (Rhabditoidea) for further details on this relationship. Pertinent taxonomic papers are cited with a review of the taxonomic problems in Akhurst & Boemare (1990).

Xenorhabdus luminescens Thomas & Poinar (1979) is introduced into the arthropod host by a Heterorhabditidae [*Heterorhabditis bacteriophora* Poinar]. Poinar & Thomas (1985) demonstrated this bacterium could kill a Phalangiidae (*Phalangium opilio* Linn., reported as *P.* sp.) if introduced by the correct nematode.

Xenorhabdus nematophilus (Poinar & Thomas 1965) was originally described in combination with *Achromobacter* Bergey, Breed & Murray. This bacterium is introduced into the arthropod host by a Steinernematidae [*Steinernema carpocapsae* (Weiser)]. Poinar & Thomas (1985) demonstrated that this bacterium could kill a Phalangiidae, *Phalangium opilio* (reported as *P.* sp.), if introduced by the proper nematode.

Superkingdom Eukaryotae
Kingdom Fungi
Division Eumycota

At least one species of fungus successfully kills a Gonyleptidae (see under *Torrubiella gonylepticida* and unidentified fungi). Gonyleptoidea are known to have phenols which are antagonistic to fungal growth in their exocrine secretions. Either *T. gonylepticida* and another unidentified fungus from Panama are not retarded by phenols, or the hosts were unable to produce phenols in sufficient quantity. The extent of phenol production in various gonyleptid genera and its use in controlling fungi have not been investigated. Likewise, the effects of age and health of the har-

vestman on phenol production have not been examined.

Unidentified Fungi

Griffiths (1978) illustrated a harvestman [not identified, but almost certainly *Nelima paessleri* (Roewer)] covered by mycelia of soil microfungi. The fungi are reported not to be pathogenic, but simply use the harvestman corpse as a substrate.

Mora (1987, fig. 8) reported mortality in adult males of a Gonyleptidae (*Zygopachylus albomarginis* Chamberlin) by an unidentified fungus on Barro Colorado Island, Panama. Males of this nest-building harvestman eat all fungus appearing in the nest, thus preventing the proliferation of mycelia. Mora (1987) suggested the males ingested the fungi (spores) which eventually killed them. This is probably incorrect because nearly all other fungal pathogens of invertebrates infect their host through the cuticle (Samson *et al.* 1988). Ten fatalities were observed from 199 nest-guarding males examined by Mora.

Subdivision Ascomycotina
Class Pyrenomycetes
Order Clavicipitales
Family Clavicitaceae

Torrubiella Boudier is a genus with primary host affinities for spiders (Araneae), although several species are also known from insects, especially Coccidae (Kobayasi & Shimizu 1982; Humber & Rombach 1987). Two species have been reported from harvestmen, but only one report appears to be valid.

Torrubiella gonylepticida (Möller 1901) was originally described in combination with *Cordyceps* Fries. Petch (1937) transferred the species to its present combination and redescribed the species. Möller (1901), when describing the host, referred to it as a spider ('Die Spinnen', not 'Weberknechte'). Subsequent authors (Petch 1937; Koval 1974; Kobayasi & Shimizu 1982) have continued to list the only host as a spider. Fortunately, the specific name refers to the true type host, a Gonyleptidae harvestman. Möller (1901, taf. 6, fig. 89) clearly illustrated the gonyleptid host, but not in sufficient detail to determine to which genus it belongs. Kobayasi & Shimizu (1982) reprinted Möller's illustration and stated the type locality was Brazil.

Petch (1937) described the conidial stage as *Spicaria longipes*; which is now recognized as *Paecilomyces farinosus* (Holm *ex* S. F. Gray) (Brown & Smith 1957). Petch recorded *T. gonylepticida* and the conidial stage from various spiders from Trinidad. Koval' (1974) listed the conidial stage from spiders collected on *Magnolia* Linné leaves in Russia (formerly Russian Soviet Federative Socialist Republic, USSR). In the key to *Torrubiella* spp. by Koval', two varieties of *T. gonylepticida* are differentiated on the basis of perithecia and ascus lengths. However, the two taxa should be attributed to another species: the third taxa in the key should be *T. arachnophila* var. *pleiopus* Mains and the fourth should be *T. arachnophila* var. *pulchra* Mains.

Torrubiella pulvinata Mains (1949) was described from "Opilionoidea" collected on Oahu, Hawaii. *Paecilomyces* (reported as *Spicaria*) *pulvinata* (Mains 1949) was the name given to the conidial stage. Samson (1974) listed *S. pulvinata* as a synonym of *P. farinosus*, thus regarding the anamorph for both *T. gonylepticida* and *T. pulvinata* to be the same species. Mains (1949, p. 303) stated "The hosts of this collection are so severely parasitized that accurate determination is difficult. They appear to be arachnids belonging to the Opilionoidea." Because opilions appear to be absent from the Hawaiian Islands (F. G. Howarth pers. commun.), the host is more likely a long-legged, pholcid spider. The setae-spines on the legs illustrated by Mains (1949, fig. 1A) are long and unlike those on harvestmen. They are similar to those found on spiders. There are five adventive cosmopolitan Pholcidae (Araneae) established in the islands that could be confused as opilions by non-specialists. The opilion host records are considered here to be incorrect.

Subdivision Deuteromycotina
Class Hyphomycetes

The Hyphomycetes is an artificial class representing the asexual states of Ascomycetes and Basidiomycetes, or fungi for which sexual states are unknown. Orders and families do not exist in current classifications of these fungi.

Hymenostilbe Petch is comprised of seven described species. Species are known to infect a variety of insect hosts, spiders (Mains 1950; Evans & Samson 1987) and harvestmen. Mains (1950) stated members of this genus are the conidia (anamorph) state of *Cordyceps* spp.; whereas

Evans & Samson (1987) reported the teleomorph connection remains unproven. Specific identifications are best made by consulting the diagnoses provided by Mains (1950). *Hymenostilbe verrucosa* Mains (1950) was originally described from spiders collected in Maine, USA. Other records are from spiders in England and a "Phalangiidae" in England (Leatherdale 1970).

Engyodontium de Hoog is comprised of seven species, two of which are reported to infect spiders and one on "opilionids". A key to the species is provided by Gams *et al.* 1984. *Engyodontium aranearum* (Cavara) was originally described in the genus *Sporotrichum* Link *ex* Fries and was transferred to its present combination by Gams *et al.* (1984). A redescription and synonymy are provided by Gams *et al.* (1984). The teleomorph state is unknown, but other members of the genus have a *Torrubiella* teleomorph. Those same authors reported hosts as a fly, spiders and opilions. The specimen in their photograph (fig. 3), as well as those of Samson *et al.* (1988, pl. 68a,b), superficially resembles opilions, but judging from the dense placement and morphology of the setae on the host legs (figs. 3, 68b) they are not harvestmen. They are more likely pholcid spiders (Araneae: Pholcidae). The opilion host record for this species of fungus is considered herein incorrect.

Nomuraea Maublanc is composed of three described species (Ignoffo *et al.* 1989; Greenstone *et al.* 1988). *Nomuraea rileyi* (Farlow) Samson is a well-known pathogen of insects. *Nomuraea atypicola* (Yasudo) Samson is reported to infect spiders, harvestmen and insects. *Nomuraea anemonoides* Hocking was originally isolated from soil and, in high doses in the laboratory, can cause mortality in insects.

Nomuraea atypicola (Yasuda 1915) was originally described as a member of the genus *Isaria* J. Hill *ex* E. M. Fries. It was found on an Atypidae spider in Japan. It was transferred to its present combination by Samson (1974). The teleomorph or sexual state is *Cordyceps cylindrica* Petch (1937). Greenstone *et al.* (1988) reported the infection of a harvestmen by this fungus under laboratory conditions. The infected Sclerosomatidae, *Leiobunum vittatum* (Say), was collected in Missouri, USA. This species of fungus is commonly found infecting spiders (Greenstone *et al.* 1988) and under laboratory conditions was also found to be infective to Lepidoptera larvae (Ignoffo *et al.* 1989).

Subdivision Zygomycotina
Class Zygomycetes
Order Entomophthorales
Family Entomophthoraceae

Pandora Humber (1989) is comprised of 16 species of obligately pathogenic fungi. Hosts include members of insects and arachnids. A single species is recorded from opilions. *Pandora phalangicida* (Lagerheim 1898) was originally described from Phalangiidae collected in Sweden as a species of *Empusa* Cohn (*Entomophthora*). Batko (1966) transferred the species to *Zoophthora* Batko 1964, and placed it in the subgenus *Pandora* Batko 1966. Humber (1989) placed it in his new genus *Pandora*. Ellis (1956) and Leatherdale (1958, 1970) recorded this fungus from a Phalangiidae, *Phalangium opilio*, in England.

Entomophaga Batko includes 10 described species (Humber 1989). All are obligate pathogens of insects and arachnids. A single species is recorded from opilions. A key for identification of members of this genus is provided by Keller (1987). Comparisons to original descriptions (species and citations are listed in Humber 1989) are required for positive identifications. *Entomophaga batkoi* (Bałazy 1978) was originally described in the genus *Entomophthora* Fresenius. Later, Remaudière & Keller (1980) transferred the species to *Conidiobolus* Brefeld (Family Ancylistaceae), but the current combination with *Entomophaga* was made by Keller (1987). Bałazy (1978) described this fungus from harvestmen collected near Poznań, Poland. Phalangiidae [*Oligolophus tridens* (C. L. Koch)] and rarely Sclerosomatidae (*Leiobunum rotundum* Latreille and *Leiobunum blackwalli* Meade) were infected. An epizootic (temporary increase in the incidence of infections) was observed during late summer.

Keller (1987) reported this species of fungus was rather common and often caused epizootics in open woods, along the borders of forests and hedges. From late July to the middle of September it was collected from *Oligolophus tridens* in Switzerland.

Kingdom Animalia
Subkingdom Protozoa

Although seldom reported, Protozoa are common parasites of Opiliones. To date, all records of Protozoan parasites of Opiliones are from USA,

Europe and India. Their reported absence from other localities is likely due to lack of study. While dissecting gonads for anatomical and chromosomal studies, I have often observed gregarines from North and Middle America species (especially from Phalangiidae and Cosmetidae). Ellis (1913, p. 280) reported that he was unable to locate gregarines in the "alimentary canal of perhaps two hundred Phalangidea" from Michigan and Colorado. His failure to locate parasites may have been caused by the time of year he examined the opilions or possibly the taxa he examined do not harbor gregarines (these taxa are unknown, but probably are members of the Sclerosomatidae: Leiobuninae as they are the dominate forms in the two mentioned areas). Only two studies have been published on opilion hematocytes, one of which resulted in the discovery of a blood parasite.

Phylum Microspora
Class Microsporea
Order Microsporida
Collective Group *Microsporidium*

Species that cannot be readily placed to genus, as well as species *incertae sedis*, are lumped into *Microsporidium* sensu Sprague (1977). *Microsporidium weiseri* (Šilhavý 1960) was originally described in the genus *Stempellia* Léger & Hesse (Family Thelohaniidae). Sprague (1977) transferred this species to its present combination with *Microsporidium* because the species did not fit any of the known genera. This parasite was found in smear-preparations of hemolymph of a Phalangiidae, *Opilio parietinus* (De Geer). The harvestmen was collected in Třebíč, Czechoslovakia. The plasmodium have 2, 4, 8 and 16 spores and are found in the hemolymph and hemocytes (plasmatocytes) of its host.

Phylum Apicomplexa

All known Apicomplexa parasites of opilions are septate eugregarines and as such have several features in common. Both sexual and asexual stages occur (gametogony and sporogony), but merogony is absent. The mode of infection is ingestion of oocysts. The trophozoites attach to the lining of the gut and divide to form merozoites and gamonts. Gametocytes are passed in the feces, and no intermediate host or vector is needed. Because most species are believed to attach to intestinal epithelial cells, gregarines in opilions probably are not pathogenic.

The gregarine genera and some species known from harvestmen can be identified by the following taxonomical key. Because some species are inadequately described (some life-stages unknown) identifications to species are difficult. Useful keys or tables of characters are mentioned under specific genera in the following account.

Class Sporozoasida
Subclass Gregarinasina

Tsurusaki (1986) found gregarines in Sclerosomatidae harvestmen, *Leiobunum manubriatum* Karsch and *Leiobunum globosum* Suzuki, from numerous localities in Japan. He also provided data on parasitism rates as related to species, locality and season. His gregarines have not been identified.

Hunt (1979) found numerous gregarines in the midgut diverticula of Triaenonychidae harvestmen, *Equitius doriae* Simon, from southeastern Australia. His gregarines were never identified.

Mitov reported (pers. commun.) that he had discovered gregarines in preserved material of the following harvestmen from Vitosha Mountain and West Rodopy, Bulgaria: Nemastomatidae [*Carinostoma ornatum* (Hadži), *Paranemastoma radewi* (Roewer), *Pyza bosnica* (Roewer)]; Sclerosomatidae [Leiobunum rumelicum Šilhavý]; Phalangiidae [*Lacinius ephippiatus* (C. L. Koch), *L. horridus* (Panzer), *L. dentiger* (C. L. Koch), *Lophopilio palpinalis* (Herbst), *Mitopus morio* (Fabricius), *Odiellus lendli* (Sørensen), *Opilio dinaricus* Šilhavý, *O. ruzickai* Šilhavý, *O. saxatilis* (C. L. Koch), *Phalangium opilio, Zacheus anatolicus* (Kulczyński), *Z. crista* (Brullé)].

Other new records include unidentified gregarines from a Phalangiidae, *Odiellus pictus* Wood, collected in the West Virginia University Forest, Chestnut Ridge, Preston County, West Virginia, USA and an unidentified gregarine from a Sclerosomatidae, *Leiobunum politum* Weed, collected in Columbus, Ohio, USA. This latter series is remarkable as the parasites were only discovered after a hundred years of storage.

Key For Identification Of Gregarines Found In Harvestmen

1a. Oocysts without spines or thickening at poles 2
1b. Oocysts with spines or thickenings at poles, sometimes at equator and also along edges ..... (Family Actinocephalidae) 5

Subfamily Acanthosporinae

2a. Epimerite simple, spherical; oocysts biconical, with truncate ends, released unchained by simple dehiscense of the gametocyst ..... Family Hirmocystidae
Arachnocystis arachnoidea (Devdhar & Gourishankar)

2b. Epimerite complex and varied; oocysts biconical orcylindroconical, united as a string of beads ..... Family Actinocephalidae 3

Subfamily Actinocephalinae

3a. Epimerite sessile, with short neck having 8–10 simple digitform processes at apex; neck persists more or less in sporont, but digitform processes (tentacles) disappear; gametocysts dehisce by formation of hole in wall through which oocysts are extruded in a single thread; oocysts biconical or lemon-shaped ..... *Actinocephalus megabuni* Ormières & Baudoin

3b. Epimerite without digitform process at apex, gametocysts rupture by simple dehiscence 4

4a. Epimerite a large, flattened and fluted disk, oocysts ovoid to biconical, in lateral chains. . . *Anthorhynchus*
Anthorhynchus longispora Ormières & Baudoin
Anthorhynchus sophiae (Schneider)

4b. Epimerite a large flattened centrally indented papilla with crenulate border, lost early. Protomerite with numerous vertical laminations, broadening to an umbrella in the mature sporont, each costule curved to form a spine pointing backward; oocysts biconical or ovoid, united as a string of beads . . . . *Sciadiophora*
Sciadiophora caudata (Rössler)
Sciadiophora fissidens (Rössler)
Sciadiophora gagrellula Devdhar & Amoji
Sciadiophora geronowitschi (Johansen)
Sciadiophora phalangii (Léger)
Sciadiophora claviformis Ormières & Baudoin

5a. Epimerite a conical knob, dentated at the base with a series (about 20) of vertical lamelle. Oocysts cylindrical with pointed ends, a tuft of spines at each pole ..... *Contospora opalniae* Devdhar & Amoji

5b. Epimerite simple, globular, without ornamentation 6

6a. Oocysts barrel-shaped, asymmetrical, without terminal tufts, with two equatorial (lateral) thickenings on longitudinal cordons ..... *Doliospora*
Doliospora repelini (Léger)
Doliospora troguli (Geus)

6b. Oocysts biconical and symmetrical 7

7a. Oocysts with 8 to 10 slender spines at each pole and released in chains of 2 to 3 or more from the gametocyst ..... *Echinoocysta phalangii* (Amoji & Devdhar)

7b. Oocysts with slender spines on poles and sides; released unattached from the gametocyst ..... *Cosmetophilus vonones* Cokendolpher

Order Eugregarinorida
Suborder Septatorina
Superfamily Gregarinicae
Family Hirmocystidae

Arachnocystis Levine is restricted to Oribatei mite and opilion hosts. Four species are known, of which one (the type species) occurs in opilions (Levine 1979, 1985). *Arachnocystis arachnoidea* (Devdhar & Gourishankar 1971) was originally described in the genus *Sycia* Léger (Family Lecudinidae). Levine (1979) transferred the species to his new genus *Arachnocystis,* where it was designated the type species. This species was found in the intestinal ceca of an Assamidae, *Oppalnia* sp. (reported as *Opalnia* sp., see Cokendolpher 1991), from Someshwar near Dharwar, Karnataka State, India (Devdhar 1962).

Superfamily Stenophoricae
Family Actinocephalidae
Subfamily Actinocephalinae

Actinocephalus Stein is a relatively large genus with about 40 described species in insects and one in an opilion (Levine 1985). *Actinocephalus megabuni* Ormières & Baudoin (1973) was discovered in the intestine of a Phalangiidae, *Megabunus diadema* (Fabricius). It was collected in Besse, France.

Anthorhynchus Labbé are found in a termite (Kalavati & Narasimhamurti 1978) and opilion hosts. Two species are described from harvestmen. The type species, by monotypy, is *Anthorhynchus sophiae* Schneider; an opilion parasite.

Anthorhynchus longispora Ormières & Baudoin (1973) was described from the guts of two

families of harvestmen: Sclerosomatidae [*Leiobunum* (reported as *Liobunum*) *rotundum*] and Phalangiidae [*Mitopus morio*, *Opilio parietinus*, *Platybunus bucephalus* (C. L. Koch)]. All harvestmen were collected near Besse-en-Chandesse, France.

Anthorhynchus sophiae (Schneider 1887) was originally described in the genus *Anthocephalus* Schneider. Because that generic name is preoccupied, Labbé (1899) provided the replacement name and transferred the species to its present combination. The original collection of this parasite was from the intestine of a Phalangiidae, *Phalangium opilio*, captured in Poitiers, France. This species is also reported by Pfeifer (1956, from Germany) and Ormières & Baudoin (1973, from France) from the Sclerosomatidae [*Leiobunum blackwalli* (reported as *L. hassiae* Müller), *Leiobunum* (=*Liobunum*) *rotundum*] and the Phalangiidae [*Lacinius ephippiatus*, *Mitopus morio*, *Oligolophus tridens*, *Phalangium opilio*, *Rilaena* (reported as *Platybunus*) *triangularis* (Herbst)].

Sciadiophora Labbé are restricted to opilion hosts. There are five described species. Devdhar & Amoji (1978a) provided a table of characters which is useful in making identifications.

Sciadiophora caudata (Rössler 1882) was originally described in the genus *Stylorhynchus* Stein. Because that name was preoccupied, Ellis (1912) provided the new generic name *Stylocephalus*. Watson Kamm (1922) transferred the species to its present combination with *Sciadiophora*. This species was originally found in the intestines of Phalangiidae [*Mitopus morio*, *Odiellus* (reported as *Odius*) *spinosus* (Bosc), *Phalangium opilio*, Phalangiidae gen. sp.] from Germany. Ormières & Baudoin (1973) reported collections from the same three hosts from Besse and Tamarissière, France.

Sciadiophora fissidens (Rössler 1882) was first described in the genus *Actinocephalus* and was later transferred by Labbé (1899) to *Sciadiophora*. This species was found in intestines of Phalangiidae [*Lophopilio* (reported as *Odiellus*) *palpinalis*, *Phalangium opilio*, Phalangiidae gen. sp.] from Germany.

Sciadiophora gagrellula Devdhar & Amoji (1978b) was described from a Sclerosomatidae, *Gagrellula saddlana* (Roewer), which were collected in Dharwar and Kumta, Karnataka State, India (Devdhar 1962). This gregarine is found in the intestine and intestinal ceca. Unlike most described opilion parasites, this species is known (and illustrated) by all life stages.

Sciadiophora geronowitschi (Johansen 1894) was described in the genus *Actinocephalus* and was transferred to its present combination by Labbé (1899). This protozoa was discovered in the intestines of a Phalangiidae, *Phalangium opilio*, from Russia (formerly Russian Soviet Federative Socialist Republic, USSR).

Sciadiophora phalangii (Léger 1897) was first described in combination with *Lycosella* Léger. It was the type and only species in the genus. Because *Lycosella* was preoccupied, Labbé (1899) proposed the new name *Sciadiophora*, with *S. phalangii* being the type-species. This species has been recorded, redescribed and illustrated by numerous authors (Minchin 1903; Wellmer 1911; Ellis 1913; Watson Kamm 1922; Stipperger 1928; Pfeifer 1956; Šilhavý 1961; Geus 1969; Kudo 1971; Ormières & Baudoin 1973). Two families of harvestmen have been reported as hosts (all European): Sclerosomatidae [*Leiobunum rotundum*] and Phalangiidae [*Lacinius dentiger*, *Mitopus morio* (reported as *Opilio grossipes*), *Opilio parietinus*, *Phalangium* sp., *Phalangium opilio* (reported as *Phalangium cornutum*), *Platybunus bucephalus*, *Platybunus pinetorum* (C. L. Koch), *Rileana* (=*Platybunus*) *triangularis*]. The original collection of this species was recorded from two hosts, *Phalangium crassum* Dufour and *P. cornutum* from Vallée de la Loire (where it was rare) and Provence (where it was common), France. As noted above, the latter species is now known as *P. opilio* but the identification of the former species is uncertain (Roewer 1923). Records of this parasite are from France, Austria, Germany and Czechoslovakia.

Sciadiophora claviformis Ormières & Baudoin (1973) was found in the intestine of a Phalangiidae, *Mitopus* sp. (based on the collection locality the species is probably *M. morio*). The collection locality was Vallée de Chaudefour, France.

Subfamily Acanthosporinae

Contospora Devdhar & Amoji are known only from opilions. The single species, *Contospora opalniae* Devdhar & Amoji (1978a), was described from the midgut and cecum of an Assamidae, *Oppalnia* sp. (reported as *Opalnia* sp., see Cokendolpher 1991). It is known from Someshwar and Kalghatgi, Dharwar District, India (Devdhar 1962).

Cosmetophilus Cokendolpher is a monotypic genus restricted to an opilion host. It is the only genus of gregarines positively identified from harvestmen in the New World. *Cosmetophilus vonones* Cokendolpher (1991) was described from the intestine and intestinal ceca of the cosmetid harvestman *Vonones sayi* (Simon) from Texas, USA. Other samples presumably of this species were recorded from the same host collected in Tennessee, USA. Unlike most described opilion gregarines, this species is known (and illustrated) by all life stages.

Doliospora Ormières & Baudoin (1969) are restricted to opilion hosts. There are two described species. *Doliospora repelini* (Léger 1897) was originally described in the genus *Acanthospora* Léger (1892). It was designated the type-species of the new genus, *Doliospora*, by Ormières & Baudoin (1969). This species has been reported by Léger (1897) and Ormières & Baudoin (1973) from France from the intestines of the Sclerosomatidae [*Leiobunum* (=*Liobunum*) *rotundum*] and the Phalangiidae [*Oligolophus tridens*, *Opilio parietinus*, *Megabunus diadema*, *Mitopus morio* (=*O. grossipes*), *Phalangium opilio* (=*P. cornutum* - type host), *Platybunus bucephalus*].

Doliospora troguli (Geus 1969) was originally described in the genus *Acanthospora* and transferred to its current combination by Levine (1980). It was found in the intestine of a Troguloidae, *Trogulus tricarinatus* (Linné), in Rathsberg, Germany. Neither its gametocysts nor its oocysts are described.

Echinoocysta Levine (1984) is composed of a single species that is restricted to an opilion host. *Echinoocysta phalangii* (Amoji & Devdhar 1979) was originally described in the genus *Echinospora* Amoji & Devdhar (1979). Because that genus was preoccupied, Levine (1984) proposed the new name *Echinoocysta* and transferred the species to its current combination. This protozoa is found in the intestine and intestinal ceca of an Assamidae, *Oppalnia* sp. (reported as *Opalnia* sp., see Cokendolpher 1991) from Someshwar, near Dharwad, Karnataka State, India.

Subkingdom Eumetazoa
Phylum Platyhelminthes
Class Cestoda (Cestoidea)
Order Cyclophyllidea
Subclass Eucestoda
Family Hymenolepididae

Pseudhymenolepis Joyeux & Baer (1935) is monotypic. *Pseudhymenolepis redonica* Joyeux & Baer (1935) was described from the shrew *Crocidura russula* Herm. (Insectivora: Soricidae). A flea, *Ctenophtalmus arvernus* (Hystrichopsyllidae), is known to be an intermediate host of this cestode. Gabrion (1977) reported finding cysticercoides in a Phalangiidae, *Phalangium opilio*, collected during early July. The harvestman was found in a shrew nest (previously named species). Shrews in the general area of the nest revealed proglotids of this cestode as well. It has been proposed that *P. opilio* will serve as the intermediate host when fleas are absent.

Class Trematoda
Order Digenea

Creplin (1846, p. 156) reported finding an unidentified larval fluke in a Phalangiidae (*Phalangium opilio*). The fluke was listed as "*Distomum Cystidicola* Cr. sp. n." As no illustration or description was provided this name must be considered a *nomen nudum*.

Family Dicrocoeliidae

Brachylecithum Ström was originally described as a subgenus of *Lypersomum* Looss. Adult flukes of this genus are found in the liver and gall bladder of birds and rarely in mammals. Data are available on the life cycles of six (incomplete data for five species) *Brachylecithum* spp. (see Carney 1970, 1972). In a typical lifecycle the eggs are passed in the feces of the definitive host, a bird or mammal. The eggs are eaten by a terrestrial snail, the intermediate molluscan host, where they develop into miracidia and sporocysts. The cecariae emerge from the snail as a slime ball and are eaten by a second intermediate host (usually an arthropod). The cecariae encyst in the arthropod hemocoel and infect the vertebrate host upon eating the intermediate host. In some arthropod hosts, the metacercariae lodge in or near the host brain causing behavioral and morphological changes (Hohorst & Graefe 1961; Carney 1969). These changes appear to increase the chances of predation upon the arthropod host (Carney 1969).

Brachylecithum sp. cysts and metacercaires were reported from a Phalangiidae, *Phalangium opilio*, by Gabrion & Ormières (1973). The trematodes were found in the muscles and adipose tissue of the body. The infected harvestman was collected in Sète and Montpellier, France. *Brachylecithum* adults are known from Passeriformes birds in the south of France. Because *Brachlecithum* spp. appear to be relatively host-

specific in the arthropod stage of development (Carney 1970), the record in *Phalangium* is probably of an undescribed species.

Phylum Nematoda (Nemata)
Unidentified Class

Laniatores (Triaenonychidae and/or Synthetonychidae) from New Zealand are reported by Forster (1954) to be infested by unspecified nematodes. Dr. V. Tood (in Sankey 1949a) recorded nematodes from *Rilaena* (=*Platybunus*) *triangularis*.

Class Secernentia
Subclass Rhabditia
Order Rhabditida
Suborder Rhabditin
Superfamily Rhabditoidea
Family unidentified

Pfeifer (1956) reported "rhabditid" nematodes from Phalangiidae (*Lacinius horridus* and *Phalangium opilio*) that were captured in Berlin, Germany.

Family Steinernematidae

Steinernema Travassos is comprised of nine distinct species (Poinar 1990). Until recently, most species were referred to *Neoaplectana* Steiner. Others referred to *Neoaplectana* are either synonyms, misidentified or insufficiently described (Poinar & Welch 1981). Keys and other descriptive data needed for identification of the various species can be located in Poinar (1990). Only one species is known from a phalangid host. All species thus far discovered carry a single species of symbiotic bacterium in the alimentary tract of the third-stage juvenile. The infective stage nematodes occur on soil and have the ability to locate and enter arthropod hosts. To reach the hemolymph of the host, the nematodes enter via a natural opening and then penetrate through the gut or tracheal walls. Once inside the host, the nematode releases its associated bacterium which kills the host within 48 hours. The nematodes mature into males and females inside the arthropod and the females release eggs within the cadaver (Poinar 1983).

Steinernema carpocapsae (Weiser 1955) was originally described in combination with *Neoaplectana* from codling moth larvae collected in Czechoslovakia. Poinar & Thomas (1985) demonstrated this nematode could infect and successfully reproduce in a Phalangiidae, *Phalangium opilio* (reported as *P.* sp.). Its symbiotic bacterium *Xenorhabdus nematophilus* (Poinar & Thomas) killed the above mentioned arthropod host. This nematode has a wide host range of insects and arachnids (Poinar 1979; Poinar & Thomas 1985; Poinar *et al.* 1985). A thorough description and review of this nematode and its relationship with *X. nematophilus* are provided by Poinar (1979).

Family Heterorhabditidae

Heterorhabditis Poinar is the only genus in the family. It is known by three described species (Poinar & Welch 1981; Poinar 1990), one of which is known to infect harvestmen. Keys to the infective juveniles of the three species is found in Poinar (1990). Adults are identified by electrophoretic analysis of enzymes (Akhurst 1987), DNA fingerprinting and morphology (Poinar *et al.* 1987). The mode of entry into the host and general life cycle follow that listed under *Steinernema*, except that *Heterorhabditis* have a heterogenic life cycle. Maturing females can either be hermaphroditic or amphimictic. The first hermaphroditic generation is usually followed by one or more amphimictic generations in a single cadaver. Juveniles of *Heterorhabditis* can enter host via natural openings, or in smaller, more fragile host by breaking the cuticle with a dorsal (and sometimes ventral) hook.

Heterorhabditis bacteriophora Poinar 1975, is a well-known insect parasite. Considerable literature on this species is listed under a synonym *Heterorhabditis heliothidis* (Khan *et al.* 1976); which was originally described in combination with the new genus *Chromonema* (Khan *et al.* 1976). Poinar & Thomas (1985) demonstrated this nematode could infect and successfully reproduce in the Phalangiidae *Phalangium opilio* (reported as *P.* sp.). Its symbiotic bacterium *Xenorhabdus luminescens* killed the above mentioned host. This nematode has a wide host range of insects and arachnids (Poinar 1979; Poinar & Thomas 1985; Poinar *et al.* 1985). A thorough review of this nematode is provided by Poinar (1979).

Class Adenophorea
Subclass Enoplia
Order Mermithida
Superfamily Mermithoidea
Family Mermithidae

All known mermithid records from harvestmen are based on juvenile nematodes. Consequently, none can be accurately assigned to a

genus (see below under *Agamomermis*). Researchers fortunate enough to obtain adult material should consult the key provided by Poinar (1977).

Matthiesen (1974) reported the discovery of a Gonyleptidae (*Gonyleptes fragilis* Mello-Leitão) which was infested by a internal parasite. Preliminary observations through the harvestman's body (the parasite was apparently not dissected from the host) suggested the parasite to be either a Nematomorpha or mermithid. Because there are no other recorded cases of the former attacking Opiliones, I assume the parasite was a juvenile mermithid.

Unknown species were reported by Poinar (1985) from a Sclerosomatidae [*Togwoteeus* (reported as *Homolophus*) *biceps* (Thorell) from western Canada], a Cosmetidae [*Paecilaemana quadripuncta* Goodnight & Goodnight from Costa Rica] and a Protolophidae [*Protolophus* sp. from the southwestern USA]. Pfeifer (1956) also reported an unknown species from a Phalangiidae, *Phalangium opilio*, from Berlin, Germany.

Tsurusaki (1986) found unidentified mermithids in two species of Sclerosomatidae (*Leiobunum globosum*, *Leiobunum manubriatum*) in Japan.

Mitov reported (pers. commun.) that he had discovered larval mermithids in preserved material of the following harvestmen from Vitosha Mountain and West Rodopy, Bulgaria: Nemastomatidae (*Paranemastoma radewi*), Phalangiidae (*Lacinius ephippiatus*, *L. horridus*, *L. dentiger*, *Lophopilio palpinalis*, *Mitopus morio*, *Phalangium opilio*, *Zacheus crista*).

Agamomermis Stiles is a collective group erected to receive species which were described from larvae (which lack meaningful taxonomic characters) [see Poinar & Welch (1981)]. When diagnosing *Agamomermis*, Stiles (1903) stated the group was artificial and therefore should have no type species. All of the mermithids thus far recorded from harvestmen are considered *incertae sedis* and therefore those species that were originally described from harvestmen should be transferred to *Agamomermis*. This action was indicated but not formally performed by Poinar (1985).

Agamomermis phalangii (Haldeman 1851), new combination, was originally described in combination with *Filaria* Mueller from a Phalangiidae, *Phalangium opilio* (reported as *P. cornutum*). *Agamomermis truncatula* Rudolphi (1819), new combination, was originally described in combination with *Filaria*. Steiner (1922) transferred the species to *Mermis*. The original specimens were from the abdomens of Phalangiidae, *Phalangium opilio* and *Opilio* (reported as *Phalangii cornuti* and *Opilionis*). Diesing (1851) listed the species as "*Gordius truncatulus* Diesing," but it is unclear if he had additional material.

Agamermis incerta was reported by Stipperger (1928) from *Mitopus morio* collected in Tirol, Austria. Stipperger (1928, p. 60) stated that he had sent the specimen to Dr. G. Steiner for identification and that he had received an identification as "*Agamermis incerta* n. sp." Pfeifer (1956) and Poinar (1985) referred to this species as *Agamermis incerta* (Steiner), indicating that it had been described in some other genus. I have been unable to locate the description of this species (in combination with *Agamermis* Cobb, Steiner & Christie; *Hexamermis* Steiner, or *Mermis* Dujardin) in Zoological Record (1918–1940) and presume it is a *nomen nudum*. Apparently, Poinar (1985) also was unable to locate Steiner's description of *incerta* (in combination with *Agamermis* or otherwise) from a spider, as this species of mermithid does not occur in his table except associated with Stipperger's 1928 paper.

Hexamermis sp., *incertae sedis*, juveniles were reported (Unzicker & Rotramel 1970) from an immature Phalangiidae harvestman (*Opilio* sp.–only species in region is *O. parietinus*) from Illinois, USA. Because of the uncertainty of the identification, this species is best retained as *Agamomermis* sp.

Mermis sp. was reported by Kästner (1928). He stated Julius Rühm of Nernberg saw a "Mermis" emerge from a "Phalangiidaen." This record was later cited as Phalangiidae, *Opilio* sp., by Poinar (1985). The only paper by Rühm cited by Kästner was published in 1926 and contained no mention of a *Mermis*. Apparently, there has been some miscommunication regarding this record. Probably, Rühm verbally communicated this observation to Kästner and used "Mermis" as a general term for a mermithid nematode. Furthermore, because the record is of a postparasitic juvenile, the record is correctly attributed to *Agamomermis* sp.

Phylum Nematomorpha

Hairworms are free-living as adults and parasitic as juveniles in insects, spiders and crustaceans. Some early records of mermithid nem-

atodes were incorrectly assigned to two genera (*Filaria* and *Gordius* Linné) belonging to this phylum. Those species are listed herein as *Agamomermis* spp. (see this group under the Nematoda).

Phylum Arthropoda
Class Insecta
Order Diptera
Suborder Cyclorrhapha

The Cyclorrhapha is comprised of many families of flies, each having a different life cycle – most are not parasitoides. Without knowing the identification of the fly, little can be written other than a notice of the single reported occurrence.

Soares (1945) reported the discovery of a fly pupa inside an adult of a Gonyleptidae (*Discocyrtus invalidus* Piza). The gonyleptid was collected at Porto Cabral, Estado de São Paulo, Brazil.

Suborder Nematocera
Family Ceratopogonidae

Tsurusaki (pers. commun.) reported finding adult flies of this family, subfamily Forcipomyiinae, settled on the leg femora of *Nelima nigricoxa* and *Gagrellula ferruginea* in Japan. When he disturbed the flies they would hover around the host. He suspected they were sucking blood from the harvestmen.

Order Hymenoptera
Family Chalcidae

Laniatores (Triaenonychidae and/or Synthetonychidae) from New Zealand are reported by Forster (1954) to be infested by chalcid wasps. No specific identifications were provided.

Family Pompilidae

Anoplius Dufour is a large, diverse group of wasps which prey almost exclusively upon spiders (Evans & Yoshimoto 1962). The female wasps sting and paralyze spiders which are individually entombed with a wasp egg. The wasp young will then devour the spider as it grows. Some of the species permanently paralyze their prey while others only paralyze them temporarily. Some adult wasps feed upon spiders while others feed upon nectar of flowers. Only a single species has been recorded to prey upon a harvestman.

Anoplius (*Pompilinus*) *marginatus* (Say 1824) is found over most of temperate North America east of the Rocky Mountains. It is often common and unlike other pompilids is not very selective as to the prey it takes. Prey items include at least 22 species of spiders from seven different families (Evans & Yoshimoto 1962). Evans (1948) recorded a female wasp taking a Phalangiidae (*Odiellus pictus*) in East Hartford, Connecticut, USA. Because the harvestman was taken away from the wasp before it dug a nest it is uncertain if it would use the *O. pictus* to provision the nest. Evans (pers. commun.) recalled that the wasp was captured while it was dragging the opilion across the ground but he could not determine whether the opilion was used in provisioning the wasp nest. Pompilids often take prey and then abandon it, sometimes after feeding on it.

Class Arachnida
Order Acarina
Suborder Prostigmata

Mites known to be parasitic on harvestmen belong to the families Thrombidiidae and Erythraeidae. Only the larval forms are parasitic (protelean parasites) while the nymphs and adults are predaceous on small insects. Because the larval and post-larval stages of these two families are heteromorphic, systematists have long used different scientific names for each (Southcott 1961). Only after the larval and post-larval stages are associated by rearings can any meaningful classifications be constructed.

Laniatores (Triaenonychidae and/or Synthetonychidae) from New Zealand are reported by Forster (1954) to be often heavily infested by mites. Hunt (1979) found a species of parasitic mite on Triaenonychidae harvestman, *Equitius doriae* Simon, from southeastern Australia. Burton & Burton (1984, pp. 218 and 226) published a color photograph of a harvestman with numerous parasitic red mites. The harvestman is clearly *Mitopus morio*. The mites are probably members of the genus *Leptus*, although this can not be stated for certain. Elliott & Reddell (1987) reported that many of the *Leiobunum townsendi* occurring in caves in central Texas carried red chiggers on their legs. The mites are probably not chiggers but more likely the larvae of *Leptus*. Eaton (1985) stated in a report on some harvestmen from a cave in southeastern, New Mexico that the "The [harvestmen] spiders all had one or more small, shiny, bright red, oval bumps on their legs which appeared to be some kind of parasite." These parasites are likewise probably *Leptus* sp. and the hosts are almost certainly *L. townsendi*.

Other unidentified mites from my collection include: Cosmetidae (*Vonones sayi*) from Sam Houston National Forest, Lake Stubblefield, Walker County, and Lake Kirby, Taylor County, Texas, USA (mites found on dorsa of abdomens); Phalangiidae [*Zacheus hebraicus* (Simon)] from Beith Shemesh, Israel (mite from tibia I); Sclerosomatidae: Leiobuninae (*Leiobunum townsendi* Weed) from near Cloudcroft, New Mexico, USA; [*Leiobunum ventricosum* (Wood)], West Virginia University Forest, Chestnut Ridge, Monongalia County, West Virginia, USA.; (*Nelima paessleri* Roewer) from Moose Creek Research Station, Idaho, USA; Sclerosomatidae: Gagrellinae (*Gagrellopsis nodulifera* Sato & Suzuki) from Mt. Daisen, Tottori Pref., Japan (mite found on dorsum of abdomen); (*Trachyrhinus rectipalpus* Cokendolpher) from 2 km W. of Cuevitas, Starr County and Buffalo Gap, Taylor County, Texas, USA; (*Prionostemma panama* Goodnight & Goodnight) from Orillas de Rio Mata Ahogado el Vallo de Antón, Prov. Coclé, Panama (mite was found on the abdomen); Sclerosomatidae: Metopilio Group (*Globipes* sp.) from near Cloudcroft, New Mexico, USA.

Family Thrombidiidae

Known as the velvet mites, adults of this family are among the largest and most conspicuous families of mites.

Allothrombium Berlese is a small genus with seven described species. Its members are parasitic on harvestmen, spiders, several orders of insects and isopods (Welbourn 1983). Mégnin (1876) described the larva of a mite reared from opilions. He identified the mite as either *Trombidium fuliginosum* Herman or *Trombidium gymnopterorum* Berlese. Based on the structure of the tarsal claws, Southcott (1961) identified Mégnin's specimen (which was illustrated) as an *Allothrombium* sp.

Allothrombium chanaanense Feider (1977) was described from an "Opilionida" from Jerusalem, Israel. This species of mite is only known from the larval forms. Host records also include insects: an Acrididae [*Prionsosthenus galericulatus* (Stål)] and an unidentified Aphidae from Israel (Feider 1977).

Allothrombium neapolitum Oudemans (1910a) was described from a Phalangidae (*Phalangium* sp.) from Portici, Campania, southern Italy. Oudemans (1913) redescribed and illustrated this species. Specimens identified from my collection were found attached to the edges of the abdominal spiracles of a Phalangiidae, *Zacheus crista* Brullé. The collections were from Lindos, Rhodos.

Trombidium Fabricius is a relatively large genus of conspicuous mites with about 20 species. Member species have been observed and recorded since the first record in about 300 B.C. by Apollodorus. About half of the described species are known only by adults. Juveniles are known to feed on numerous orders of insects as well as spiders, a pseudoscorpion and harvestmen (Welbourn 1983).

Yokogawa (1940) described and illustrated a Sclerosomatidae (*Nelima* sp.) parasitized by a mite from Japan. The mite was identified as a "*Trombidinium*" [*sic*]. *Trombidium hungarium* Kobulej (1957) is recorded from a Phalangiidae (*Egaenus convexus* Koch) from Mátraszentimre, Hungary. Both the larva and the nymph of this species were described by Kobulej (1957).

Family Erythraeidae

The first record of a harvestman parasite was probably an erythraeid mite. Lister (1678) reported scarlet-colored "bugs" attached and feeding from what is now known to be Phalangiidae *Phalangium opilio* in England. Sankey (1949b) reported mites of this family from numerous species of harvestmen collected in England. Specifically, he recorded hosts as: Sclerosomatidae [*Leiobunum blackwalli*, *L. rotundum*, *Nelima silvatica* (Simon)] and Phalangiidae [*Mitopus morio*, *Oligolophus hansenii* (Kraepelin), *O. tridens*, *Opilio parietinus*, *Paroligolophus agrestis* (Meade), *Phalangium opilio*, *Rilaena triangularis* (=*Platybunus triangularis*)]. Sankey (1949a) stated that he had records of 10 species of harvestmen (presumably those listed above) being used as carriers by the larvae of *Erythraeus phalangioides* (De Geer 1778). This identification is probably incorrect as this species is not otherwise known to feed on harvestmen and there is some question regarding the true identity of larval *E. phalangiodes* (see Southcott 1961). Possibly, Sankey confused the names *phalangii* and *phalangiodes*; both of which were described by De Geer. Martínez Crespo & Morales Soto (1979) reported that mites of the family Erythraeidae were parasitic on Opiliones from Mexico.

There are over 50 species of *Charletonia* Oudemans described as larvae and 22 species described originally as adults. Species are recorded from every continent except Antarctica (Southcott 1991). Larvae of two species are par-

asitic on harvestmen (Kawashima 1961; Southcott 1961, 1965, 1991). The other species are common parasites as juveniles on locusts (Acrididae) and less commonly encountered on jumping plant lice (Psyllidae: Homoptera), true bugs (Lygaeidae and Miridae: Hemiptera), wasps (Braconidae: Hymenoptera), Lepidoptera, dragonflies (Libellulidae: Odonata), flies (Tabanidae, Dolichopodidae and Bombylidae: Diptera), mantis (Mantidae: Mantodea), walking sticks (Phasmatidae: Phasmida), katydids (Tettigoniidae: Orthoptera), beetles (Curculionidae, Melyridae, Tenebrionidae: Coleoptera), mites (Erythraeidae: Acarina) and spiders (Theridiidae, Philodromidae: Araneae). Keys to the species are provided by Southcott (1991).

Charletonia enghoffi Southcott (1991) is known by four larvae recovered from the dorsum and femora of the Phalangiidae, *Bunochelis canariana* (Strand). The species were obtained in February in Teno Barranco de las Cuevas, Tenerife, Canary Islands.

Charletonia southcotti Kawashima (1961) is recorded from a Sclerosomatidae, *Metagagrella tenuipes* (L. Koch) (reported as *Gagrella japonica* Roewer), that was collected at the seashore of Kasumigaoka, Fukuoka City, Fukuoka-Prefecture, Kyushu, Japan. This species of mite is only known from the single collection on 12 July. Thirty-five mites were recovered from 20 opilions. It is known only by the larval stage, which was redescribed by Southcott (1965).

Leptus Latreille is a large genus and its members are widespread. Over 60 *Leptus* spp. have been described from larvae. Many adults have also been described, but only in a few cases have correlations been made between larval and post-larval forms. Only in a single case is a species described from larval and all post-larval stages (Welbourn & Jennings 1991). Many species remain undescribed. Member species are generally parasitic on spiders, scorpions, harvestmen, diplopods, Collembola, and insects. Many of the early reports and even some more recent are suspect as the true identity of the mites identified is uncertain. Southcott (1961, 1991, 1992) reviewed some of the problems regarding the European mites (*phalangii, ignotus, nemorum, coccineus*) which had been referred to various genera. Southcott (1989) provided a key to the parasitic larval forms that were recognizable (most early descriptions are inadequate to recognize the species) in the New World. Welbourn & Jennings (1991) added a new species (from Lepidoptera host) from the USA and provided some additional comments on members of the genus. Southcott (1992) described numerous new species and provided a key to the taxa from North America and Europe. He also resolved the identity of *L. ignotus* and found the type species, *Acarus phalangii*, to be an illegitimate name. Kawashima (1958) and Haitlinger (1990) provided keys to the parasitic larval forms from Japan and northern Africa, respectively.

Leptus spp. have been reported from a variety of hosts and localities. The mode of attachment was described in *Leptus* sp. on two species of Phalangiidae (*Mitopus morio, Phalangium opilio*) by Åbro (1988). Åbro (1991) described unsuccessful parasitic attachments of larval *Leptus* spp. to the ocular tubercle of *Phalangium*. Evans *et al.* (1961, fig. 211) illustrated a Phalangiidae (*Mitopus morio*) infested with *Leptus* sp. larvae from the British Isles. Welbourn (1983) reported *Leptus* spp. from unidentified Opiliones collected in Ohio and Arkansas.

Robert G. Holmberg reported (pers. commun.) that he had found 39 vials of harvestmen infested with 78 mites, all of which have been identified as *Leptus* spp. by I. M. Smith (Biosystematic Research Center, Ottawa, Canada). Dr. Holmberg's collections were from: "*Togwoteeus biceps* from Canada and the USA, *Mitopus morio* from England, *Odiellus pictus* from Canada, *Oligolophus tridens* from Canada, *Paroligolophus agrestis* from Wales, *Phalangium opilio* from Canada and England, and *Leiobunum townsendi* from U.S.A."

Mullen (1988) reported "opilionids" commonly serve as the host to *Leptus* mites. Savory (1938) recorded *Belaustium* [sic] (*Ritteria*) *nemorum* (Koch) from harvestmen in England. This observation was later cited on several occasions in general works about arachnids by Savory and Cloudsley-Thompson. The original observations were most likely based on a misidentification and probably were representatives of the genus *Leptus*. Not only is *Leptus* widely known as a harvestman parasite, but members of the Balaustiinae are generally considered not to be parasitic on arthropods (Southcott 1961).

Cox *et al.* (1921) found an immature *Erythaeus* [sic] sp. on a "phalangid" in California, USA. This mite is probably a *Leptus* sp. Mites from almost every genus of the Erythraeidae have been misidentified as *Erythraeus* Latreille (see Southcott 1961).

Leptus phalangii (De Geer 1778) was originally described in combination with *Acarus* Linné. When erecting the genus *Leptus*, Latreille (1796) designated (by monotypy) *Acarus phalangii* as the type species. The type specimens were from a Phalangiidae (*Phalangium* sp.) collected in Sweden. Apparently, none of De Geer's specimens were preserved. There has been considerable confusion over the identity of this species. Furthermore, as noted by Southcott (1992) the specific name is not available under the International Code of Zoological Nomenclature as De Geer did not treat it consistently as a binomen. Only in a few cases can specimens that have been previously referred to in the literature as *Leptus phalangii* be assigned currently recognized names.

Leptus ignotus (Oudemans 1903a) was originally described in combination with *Erythraeus*. The type locality is Borkum, Holland. Southcott (1991) redescribed the species and limited the species diagnosis to specimens which had not been recorded from opilion hosts. Therefore all records of this species from opilion host can be assumed to be misidentified and are referred to in Table 1 as *Leptus* sp. Evans *et al.* (1961) recorded a mite (identified as *L. ignotus*) parasitic on *Opilio parietinus* in the British Isles. Other records are also from the Phalangiidae: *Mitopus morio* from Tirol, Austria (Stipperger 1928) and Bulgaria (Beron 1975); *Opilio ruzickai* from Bulgaria (Beron 1975); and *Phalangium opilio*, *R. triangularis*, *Lophopilio* (reported as *Odiellus*) *palpinalis* from Poland (Haitlinger 1987). Southcott (1992) suggested that some of the specimens identified by Beron and Haitlinger were *Leptus holmiae* Southcott.

Mites reported as *Leptus phalangii* have been reported by Pfeifer (1956) and Evans (1910) on Phalangiidae (*Phalangium opilio*) in Berlin, Germany, and Midlothian, Scotland, respectively. Spoek (1964) also recorded this mite to be parasitic on harvestmen from the Netherlands. None of these mites can be accurately identified at present and are best referred in Table 1 as *Leptus* sp. Meade (1855) reported "harvest-men" from England were frequently infested by a bright red parasitic mite, which he identified as *Trombidium phalangii* (=*Leptus phalangii*). He further specified that the mite occurred on *Leiobunum rotundum*.

Sellnick (1940) recorded both *Achorolophus ignotus* and *Leptus* (reported elsewhere in the paper as *Erythraeus*) *phalangioides* (De Geer) from Phalangiidae (*M. morio*) on Iceland. He not only recorded both mites from a single species of harvestmen, but in two cases he recorded what he felt were these species from individual harvestmen. Although these cannot be identified with certainty at this time, they are probably *L. holmiae*. Until specimens can be studied I am referring to them in Table 1 as *Leptus* sp.

Numerous mites from opilions in my collection represent new records and include: Sclerosomatidae: *Eumesosoma roeweri* (Goodnight & Goodnight) from Alma, Nebraska, USA.; *Krusa* sp. from 10 mi. W. Aquismon, San Luis Potosí, México; *Leiobunum aldrichi* Weed from Tishomingo State Park, Tishomingo County, Mississippi, USA; *Leiobunum flavum* Banks from Beaver's Bend State Park, McCurtain County, Oklahoma; Merrymount Campground, 18 miles SW Nashville, Davidson, Tennessee, USA; *Leiobunum montanum montanum* Suzuki from Mt. Ischizuchi, 1490-1745 m., Ehime Prefecture, Japan; *Leiobunum* sp. from 2 km. N. Tasquillo, Rio Tula, Hidalgo, México; *Leiobunum* sp. nr. *depressum* Davis from 7.5 miles S. George West, Live Oak County, Texas, USA.; *Leiobunum townsendi* from East Turkey Creek, Chiracahua Mountains, Cochise County, Arizona; outside Hidden Cave (reared to deutonymph) and Hermit Cave, Eddy County, New Mexico, USA.; *Leiobunum vittatum* (Say) from Homesville, Nebraska, USA.; *Trachyrhinus marmoratus* Banks from Pecos River, east of Pecos, Pecos County, and Indio Mountains, 25 km S Van Horn, Hudspeth County, Texas, USA. Phalangiidae: *Odiellus pictus* from Garland, Penobscot County, Maine, USA.; *Phalangium opilio* from Bowdoinham, near Cathance River, Sagahahoc County, Maine, USA.

Additional mites from my collection have been identified by W. Calvin Welbourn as *Leptus* spp. 1–11. They are as follows: *Leptus* sp. 1 is known from a Sclerosomatidae (*Leiobunum townsendi*) and a Protolophidae (*Protolophus singularis* Banks) from Fort Bayard, Grant County, New Mexico, USA. *Leptus* sp. 2 is known from several species of Sclerosomatidae: *Eumesosoma roeweri* from 14 miles E. Burnet, Burnet County, Texas; 7.5 miles ESE Bandera, Bandera County, Texas; Texas Tech University Center, Junction, Kimble County, Texas, USA; *Leiobunum flavum* Banks from Graham Creek, 5 miles SSE Zavalla, Angelina County, Texas, USA; *Leiobunum townsendi* from Montague County, Texas, USA. *Leptus* sp. 3 is known from two species of Scle-

rosomatidae (*Leiobunum aldrichi*, *L. nigripes* Weed) from the W. Bank of J. Percy Priest Lake, Elm Hills Park, Davidson County, Tennessee, USA. *Leptus* sp. 4 is known from a Phalangiidae (*Egaenus convexus*) from Bürgenland, Ruster Hügelland, Austria. *Leptus* sp. 5 is known from a Sclerosomatidae (*Trachyrhinus marmoratus* Banks) from 39.6 miles SW Marfa, Presidio County, Texas, USA. *Leptus* sp. 6 is known from a Sclerosomatidae [*Marthana nigerrima* (Müller)] from Tuba Mountains, S. Palawan Cabar, Palawan, Philippines. *Leptus* sp. 7 is known from a Sclerosomatidae (*Eumesosoma*? sp.) from Joya de Juan Mesa (outside), near La Laguna, Tamaulipas, Mexico. *Leptus* sp. 8 is known from a Sclerosomatidae (*Leiobunum* sp.) from km 120 marker on Highway 70, San Luís Potosí, México. *Leptus* sp. 9 is known from a Sclerosomatidae (*Leiobunum* sp.) from roadcut at Gomez Farias, Tamaulipas, México. *Leptus* sp. 10 is known from a Sclerosomatidae (*Lacinius ephippiatus*) from Wr. Wald, Latisberg (Cobenze) E-Mg *ca.* 380–400 m, Wien XIX, Austria. *Leptus* sp. 11 is known from a Phalangiidae (*Mitopus morio)* from Wr. Wald, Rekawiokel, near Bldf., N. G., Austria.

Leptus bicristatus Fain & Elsen (1987) was described from a larva on an "Opilion" from Chowo Rocks, Plateau de Nyika, Malawi (6–8 December 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Roewer) (Kauri, pers. commun.).

Leptus gagrellae (Oudemans 1910b) was originally described in combination with *Achorolophus* Berlese. It was described from a Sclerosomatidae (*Gagrella* sp.) from Tjibodas, West Java Prov., Indonesia. This species was redescribed and illustrated by Oudemans (1913).

Leptus hidakai Kawashima (1958) was described from larvae collected on a Clubionidae spider (*Chiracanthium* sp.) and a Phalangiidae (*Opilio pentaspinulatus* Suzuki). All specimens were obtained on 24 June at Tachibana-yama, Kasuya-gun, Fukuoka Prefecture, Japan. A harvestmen is illustrated in the original description with eight mites attached to its legs and abdomen.

Leptus holmiae Southcott (1992) is a wide-ranging species in the Holarctic region. It is recorded (Southcott 1992) from a free living-example collected in the Burzyanskij region, Bashkir ASSR; and as ectoparasites on Phalangiidae: *Mitopus morio* from Denmark, Iceland, Poland, Sweden; *Opilio* sp. from Sweden; *Opilio canestrinii* (Thorell) from Denmark; *Phalangium opilio* from England; *Rileana* (reported as *Platybunus*) *triangularis* from England. Southcott (1992) stated that he felt some additional specimens reported in the literature might be this species but that he could not be certain because he had not studied any samples of the series reported. These questionable records are Phalangiidae: *Mitopus morio* and *Opilio ruzickai* from Bulgaria (Beron 1975); and *Phalangium opilio*, *R. triangularis*, *Lophopilio* (reported as *Odiellus*) *palpinalis* from Poland (Haitlinger 1987).

Leptus indianensis Fain *et al.* (1987) was described from larvae collected on several species of Sclerosomatidae: *Leiobunum aldrichi* (reported as *L. longipes*) and *Leiobunum calcar* (Wood) from 2 miles northwest Brazil, Clay County, Indiana, USA.; *Leiobunum* sp., *L. nigripes, L. speciosum* Banks and *L. ventricosum* from 9 miles southwest of Crawfordsville, Montgomery County, Indiana, USA. New records from my collection include *L. nigripes* Weed from 4 miles ESE Morris on Pine Bluff Road, Grundy County, Illinois, USA.; *L. formosum* (Wood) from Potomac River and Chesapeake Bay junction, Wakefield, Virginia, USA.

Leptus jocquei Fain & Elsen (1987) was described from nine larvae taken from "Opilions" collected in Dembo, Plateau Nyika, Malawi (5–20 December 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Kauri, pers. commun.).

Leptus kalaallus Southcott (1992) is thus far known only from the Phalangiidae, *Mitopus morio*, collected in Greenland. The larval mites were found attached to the opilion abdomens.

Leptus lomani (Oudemans 1903b) was described from a Gonyleptidae, *Lycomedicus* (reported *Discocyrtus*) *funestus* (Butler), from Chile. This species was redescribed and illustrated by Oudemans (1913). The original series of 10 mites was reported to have been collected by J. C. C. Loman in 1900. Other sources indicate that Jan C. C. Loman, of Amsterdam, did not collect the specimens himself. The harvestmen were probably collected by Prof. Dr. Ludwig Plate and forwarded to Oudemans by Loman. The only examples of this harvestman reported in the literature from Chile during the same time period was by Loman (Cekalovic K. 1985). Loman (1899) stated that there were several specimens of *L. funestus* from Corral that were in the Plate collection. Therefore, I am herein restricting the type locality of *L. lomani* to Corral (39°53′S, 73°25′W), Valdivia, Chile.

Leptus nearcticus Fain *et al.* (1987) was described from larvae collected off three species of

Sclerosomatidae: *Leiobunum aldrichi* (reported as *L. longipes*), *L. nigripes* and *L. vittatum* from 2 miles northwest Brazil, Clay Co., Indiana (1–18 September 1986). Fain *et al.* (1987) reported other samples from the type locality from *Leiobunum* sp. (females). These have now been identified as *L. aldrichi*.

Leptus oudemansi (Karppinen 1958) was original proposed as a replacement name in the genus *Achorolophus*. This name was provided because *Achorolophus gracilipes* Oudemans 1910a, was preoccupied by *Rhyncholophus gracilipes* Kramer 1897; both were considered by Karppinen (1958) to belong to *Achorolophus*. Both are now considered by Southcott (1992) to belong to *Leptus* and are thus still homonyms. Oudemans' (1910a) original specimens were found on a Cosmetidae (*Cynorta* sp.) from Surinam. This species was redescribed and illustrated by Oudemans (1913).

Leptus puylaerti Fain & Elsen (1987) is known by five larvae found attached to "Opilions" collected at Chowo Rocks, Nyika Plateau, Malawi (6–18 Dec. 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Kauri, pers. commun.).

Leptus polythrix Fain & Elsen (1987) is known by eight larvae found attached to "Opilions" collected at Dembo, Nyika Plateau, Malawi (5–20 December 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Kauri, pers. commun.).

Leptus stieglmayri (Oudemans 1905) was described from Opiliones collected in Santa Cruz, Rio Grande do Sul, Brazil. Oudemans (1913) redescribed this species and recorded a specimen that was collected from a beetle (Cleridae) collected in Brazil.

A probable new genus (near *Leptus*) is under study by W. Calvin Welbourn. Thus far, members are only known from harvestmen from my collection obtained in Chile. The new specimens are known from two species of Neopilionidae (*Thrasychirus modestus* Simon, *Thrasychirus dentichelis* Simon) from Isla Deceit Caleta Toleda, archipiélago Cabo de Hornos, Magallanes, Chile. This is the southern most record for a harvestman parasite. Other host records include species of Gonyleptidae: *Eubalta meridionalis* (Sörensen) from Reserva Forestal Magallanes, 8 km west Punta Arenas, Magallanes, Chile; *Metagyndes pulchella* (Loman); Niebla, near Valdivia, Chile; *Acanthoprocta pustulata* Loman from Cerro Nielol, Temuco, Chile.

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Table 1.—List of pathogens and parasites grouped by opilion host.

Host	Parasite	Source
Family? *incertae sedis*		
harvestmen, England	?*Leptus* sp.	Evans 1910; Savory 1938
harvestmen, Netherlands	*Leptus* sp.	Spoek 1964
Opliones, Brazil	*Leptus stieglmayri*	Oudemans 1905
Opiliones, Mexico	Erythraeidae	Martínez Crespo and Morales Soto 1979
Opiliones, U.S.A	*Leptus* spp.	Welbourn 1983
Opilionidé, Israel	*Allothrombium chanaanense*	Feider 1977
opilionids	*Leptus* sp.	Mullen 1988
phalangid, U.S.A	?*Leptus* sp.	Cox et al. 1921
Phalangium crassum, France	*Sciadiophora phalangii*	Léger 1897
Suborder Laniatores		
Family Triaenonychidae and/or Synthetonychidae		
gen. sp., New Zealand	Acarina, gen. sp.	Forster 1954
	Chalcidae, gen. sp.	Forster 1954
	Nematoda, gen. sp.	Forster 1954
Family Triaenonychidae		
Equitius doriae	Acarina, gen. sp.	Hunt 1979
	Gregarinasina, gen. sp.	Hunt 1979
Family Assamidae		
Oppalnia sp., India	*Arachnocystis arachnoidea*	Devdhar 1962; Devdhar and Gourishankar 1971
	Contospora opalniae	Devdhar 1962; Devdhar and Amoji 1978a
	Echinoocysta phalangii	Amoji and Devdhar 1979
Family Gonyleptidae		
gen. sp. Brazil	*Torrubiella gonylepticida*	Möller 1901
Acanthoprocta pustulata	N. gn. nr. *Leptus* sp.	herein
Discocyrtus invalidus	Cyclorrhapha, gen. sp.	Soares 1945
Eubalta meridionalis	N. gn. nr. *Leptus* sp.	herein
Gonyleptes fragilis	*Agamomermis* sp.	Mattheisen 1974
Lycomedicus funestus	*Leptus lomani*	Oudemans 1903b
Metagyndes pulchella	N. gn. nr. *Leptus* sp.	herein
Zygopachylus albomarginis	Eumycota, gen. sp.	Mora 1987
Family Cosmetidae		
Cynorta sp.	*Leptus oudemansi*	Oudemans 1910a
Paecilaemana quadripuncta	*Agamomermis* sp.	Poinar 1985
Vonones sayi	Acarina, gen. sp.	herein
	Cosmetophilus vonones	Cokendolpher 1991
Suborder Cyphopalpatores		
Superfamily Troguloidea		
Family Troguloidae		
Trogulus tricarinatus	*Doliospora troguli*	Geus 1969
Family Nemastomatidae		
Carinostoma ornatum	Gregarinasina, gen. sp.	herein
Paranemastoma radewi	Gregarinasina, gen. sp.	herein

Table 1.—Continued.

Host	Parasite	Source
	Agamomermis sp.	herein
Pyza bosnica	Gregarinasina, gen. sp.	herein
Superfamily Phalangioidea		
Family Neopilionidae		
Thrasychirus dentichelis	N. gn. nr. *Leptus* sp.	herein
Thrasychirus modestus	N. gn. nr. *Leptus* sp.	herein
Family Protolophidae		
Protolophus sp., U.S.A.	*Agamomermis* sp.	Poinar 1985
Protolophus singularis	*Leptus* sp. #1	herein
Family Sclerosomatidae		
Metopilio group		
Globipes sp.	Acarina, gen. sp.	herein
Subfamily Leiobuninae		
Eumesosoma? sp.	*Leptus* sp. #7	herein
Eumesosoma roeweri	*Leptus* sp.	herein
	Leptus sp. #2	herein
Leiobunum sp., U.S.A.	*Leptus indianensis*	Fain et al. 1987
Leiobunum sp. near *depressum*, U.S.A.	*Leptus* sp.	herein
Leiobunum sp., Hidalgo, Mexico	*Leptus* sp.	herein
Leiobunum sp., San Luis Potosí, Mexico	*Leptus* sp. #8	herein
Leiobunum sp., Tamaulipas, Mexico	*Leptus* sp. #9	herein
Leiobunum aldrichi	*Leptus* sp.	herein
(=*Leiobunum longipes*)	*Leptus* sp. #3	herein
	Leptus indianensis	Fain et al. 1987
	Leptus nearcticus	Fain et al. 1987
Leiobunum blackwalli (=*L. hassiae*)	*Anthorhynchus sophiae*	Pfeifer 1956
	Entomophaga batkoi	Bałazy 1978
	Erythraeidae, gen. sp.	Sankey 1949b
Leiobunum calcar	*Leptus indianensis*	Fain et al. 1987
Leiobunum globosum	*Agamomermis* sp.	Tsurusaki 1986
	Gregarinasina, gen. sp.	Tsurusaki 1986
Leiobunum flavum	*Leptus* sp.	herein
	Leptus sp. #2	herein
Leiobunum formosum	*Leptus indianensis*	herein
Leiobunum manubriatum	*Agamomermis* sp.	Tsurusaki 1986
	Gregarinasina, gen. sp.	Tsurusaki 1986
Leiobunum montanum montanum	*Leptus* sp.	herein
Leiobunum nigripes	*Leptus* sp. #3	herein
	Leptus indianensis	Fain et al. 1987; herein
	Leptus nearcticus	Fain et al. 1987
Leiobunum politum	Gregarinasina, gen. sp.	herein
Leiobunum rotundum	*Anthorhynchus longispora*	Ormières and Baudoin 1973
	Anthorhynchus sophiae	Pfeifer 1956
	Doliospora repelini	Ormières and Baudoin 1973

Table 1.—Continued.

Host	Parasite	Source
	Entomophaga batkoi	Batazy 1978
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	Meade 1855
	Sciadiophora phalangii	Pfeifer 1956
Leiobunum rumelicum	Gregarinasina, gen. sp.	herein
Leiobunum speciosum	*Leptus indianensis*	Fain et al. 1987
Leiobunum townsendi	Acarina, gen. sp.	Elliott and Reddell 1987; herein
	Leptus sp.	herein
	Leptus sp. #1	herein
	Leptus sp. #2	herein
Leiobunum ventricosum	Acarina, gen. sp.	herein
	Leptus indianensis	Fain et al. 1987
Leiobunum vittatum	*Leptus* sp.	herein
	Leptus nearcticus	Fain et al. 1987
	Nomuraea atypicola	Greenstone et al. 1988
Nelima sp., Japan	*Trombidium* sp.	Yokogawa 1940
Nelima nigricoxa	Forcipomyiinae, gen. sp.	herein
Nelima paessleri	Acarina, gen. sp.	herein
Nelima silvatica	Erythraeidae, gen. sp.	Sankey 1949b
Togwoteeus biceps	*Agamomermis* sp.	Poinar 1985
	Leptus sp.	herein
Subfamily Gagrellinae		
Gagrella sp., Indonesia	*Leptus gagrellae*	Oudemans 1910b
Gagrellopsis nodulifera	Acarina, gen. sp.	herein
Gagrellula ferruginea	Forcipomyiinae, gen. sp.	herein
Gagrellula saddlana	*Sciadiophora gagrellula*	Devdhar 1962; Devdhar and Amoji 1978b
Krusa sp., Mexico	*Leptus* sp.	herein
Marthana nigerrima	*Leptus* sp. #6	herein
Metagagrella tenuipes	*Charletonia southcotti*	Kawashima 1961
Prionostemma panama	Acarina, gen. sp.	herein
Trachyrhinus marmoratus	*Leptus* sp.	herein
	Leptus sp. #5	herein
Trachyrhinus rectipalpus	Acarina, gen. sp.	herein
Family Phalangiidae		
gen. sp., England	*Hymenostilbe verrucosa*	Leatherdale 1970
	Pandora phalangicida	Leatherdale 1970
gen. sp., Germany	*Sciadiophora caudata*	Rössler 1882
	Sciadiophora fissidens	Rössler 1882
gen. sp., Sweden	*Pandora phalangicida*	Lagerheim 1898
Subfamily Phalangiinae		
Bunochelis canariana	*Charletonia enghoffi*	Southcott 1991
Cristina lettowi	*Leptus bicristatus*	Fain & Elsen 1987
	Leptus jocquei	Fain & Elsen 1987
	Leptus polythrix	Fain & Elsen 1987
	Leptus puylaerti	Fain and Elsen 1987
Phalangium sp., Italy	*Allothrombium neapolitum*	Oudemans 1910a

Table 1.—Continued.

Host	Parasite	Source
Phalangium sp., Sweden	*Leptus* sp.	De Geer 1778
Phalangium sp., Europe	*Sciadiophora phalangii*	Geus 1969
Phalangium opilio (=*Phalangium cornutum*)	*Agamomermis* sp.	Pfeifer 1956; herein
	Agamomermis phalangii	Haldeman 1851
	Agamomermis truncatula	Rudolphi 1819
	Anthorhynchus sophiae	Schneider 1887; Ormières and Baudoin 1973
	Brachylecithum sp.	Gabrion and Ormières 1973
	Digenea, gen. sp.	Creplin 1846
	Doliospora repelini	Léger 1897; Ormières and Baudoin 1973
	Erythraeidae, gen. sp.	Sankey 1949b
	Gregarinasina, gen. sp.	herein
	Heterorhabditis heliothidis	Poinar and Thomas 1985
	Leptus sp.	Evans 1910; Pfeifer 1956; Åbro 1988, 1991; herein
	Leptus holmiae	Southcott 1992
	Leptus holmiae?	Haitlinger 1987
	Pandora phalangicida	Ellis 1956; Leatherdale 1958, 1970
	Pseudhymenolepis redonica	Gabrion 1977
	Rhabditida, gen. sp.	Pfeifer 1956
	Sciadiophora caudata	Rössler 1882; Ormières and Baudoin 1973
	Sciadiophora fissidens	Rössler 1882
	Sciadiophora geronowitschi	Johansen 1894
	Sciadiophora phalangii	Léger 1897; Geus 1969
	Steinernema carpocapsae	Poinar and Thomas 1985
	Xenorhabdus luminescens	Poinar and Thomas 1985
	Xenorhabdus nematophilus	Poinar and Thomas 1985
Rilaena triangularis (=*Platybunus triangularis*)	*Anthorhynchus sophiae*	Pfeifer 1956
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus holmiae	Southcott 1992
	Leptus holmiae?	Haitlinger 1987
	Nematoda, gen. sp.	Sankey 1949a
	Sciadiophora phalangii	Pfeifer 1956
Zacheus anatolicus	Gregarinasina, gen. sp.	herein
Zacheus crista	*Agamomermis* sp.	herein
	Allothrombium neapolitum	herein
	Gregarinasina, gen. sp.	herein
Zacheus hebraicus	Acarina, gen. sp.	herein
Subfamily Oligolophinae		
Lacinius ephippiatus	*Agamomermis* sp.	herein

Table 1.—Continued.

Host	Parasite	Source
	Anthorhynchus sophiae	Pfeifer 1956
	Gregarinasina, gen. sp.	herein
	Leptus sp. #10	herein
Lacinius dentiger	*Agamomermis* sp.	herein
	Gregarinasina, gen. sp.	herein
	Sciadiophora phalangii	Šilhavý 1961
Lacinius horridus	*Agamomermis* sp.	herein
	Gregarinasina, gen. sp.	herein
	Rhabditida, gen. sp.	Pfeifer 1956
Mitopus morio	Acarina, gen. sp.	Burton and Burton 1984
(=*Opilio grossipes*)	*Agamomermis* sp.	Stipperger 1928; herein
	Anthorhynchus longispora	Ormières and Baudoin 1973
	Anthorhynchus sophiae	Pfeifer 1956
	Doliospora repelini	Ormières and Baudoin 1973
	Erythraeidae, gen. sp.	Sankey 1949b
	Gregarinasina, gen. sp.	herein
	Leptus sp.	Stipperger 1928; Evans et al. 1961; Åbro 1988; herein
	Leptus sp. #11	herein
	Leptus holmiae	Southcott 1992
	Leptus holmiae?	Sellnick 1940; Beron 1975
	Leptus kalaallus	Southcott 1992
	Sciadiophora caudata	Rössler 1882; Ormières and Baudoin 1973
	Sciadiophora phalangii	Stipperger 1928; Pfeifer 1956; Ormières and Baudoin 1973
Mitopus sp., France	*Sciadiophora claviformis*	Ormières and Baudoin 1973
Odiellus lendli	Gregarinasina, gen. sp.	herein
Odiellus pictus	*Anoplius marginatus*	Evans 1948
	Gregarinasina, gen. sp.	herein
	Leptus sp.	herein
Odiellus spinosus (=*Odius spinosus*)	*Sciadiophora caudata*	Rössler 1882; Ormières and Baudoin 1973
Oligolophus hansenii	Erythraeidae, gen. sp.	Sankey 1949b
Oligolophus tridens	*Anthorhynchus sophiae*	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
	Entomophaga batkoi	Bałazy 1978; Keller 1987
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	herein
Paroligolophus agrestis	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	herein
Subfamily Opilioninae		
Egaenus convexus	*Leptus* sp. #4	herein
	Trombidium hungarium	Kobulej 1957
Opilio sp., Europe	*Agamomermis* sp.	Kastner 1928
	Agamomermis truncatula	Rudolphi 1819

Table 1.—Continued.

Host	Parasite	Source
	Leptus holmiae	Southcott 1992
Opilio canestrinii	*Leptus holmiae*	Southcott 1992
Opilio dinaricus	Gregarinasina, gen. sp.	herein
Opilio parietinus	*Agamomermis* sp.	Unzicker and Rotramel 1970
	Anthorhynchus longispora	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	Evans et al. 1961
	Microsporidium weiseri	Šilhavý 1960
	Sciadiophora phalangii	Pfeifer 1956
Opilio pentaspinulatus	*Leptus hidakai*	Kawashima 1958
Opilio ruzickai	Gregarinasina, gen. sp.	herein
	Leptus holmiae?	Beron 1975
Opilio saxatilis	Gregarinasina, gen. sp.	herein
Subfamily Platybuninae		
Lophopilio palpinalis (=*Odiellus palpinalis*)	*Agamomermis* sp.	herein
	Gregarinasina, gen. sp.	herein
	Leptus sp.	Haitlinger 1987
	Leptus holmiae?	Haitlinger 1987
	Sciadiophora fissidens	Rössler 1882
Megabunus diadema	*Actinocephalus megabuni*	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
Platybunus bucephalus	Anthorhynchus *longispora*	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
	Sciadiophora phalangii	Ormières and Baudoin 1973
Platybunus pinetorum	*Sciadiophora phalangii*	Pfeifer 1956

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