

Mesostigmatic Mites (Acari) Associated with Ground, Burying, Roving Carrion and Dung Beetles (Coleoptera) in Sapporo and Tomakomai, Hokkaido, Northern Japan

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ABSTRACT—A total of 19 species belonging to 5 families of mesostigmatic mites were collected in Sapporo and Tomakomai, northern Japan, on four groups of beetles, i.e., ground beetles (Carabinae, Carabidae), burying beetles (Nicrophorini, Silphinae, Silphidae), roving carrion beetles (Silphini, Silphinae, Silphidae) and dung beetles (Scarabaeidae and Geotrupidae), all of which mainly forage on the ground surface. No mite species was found on more than one group of beetles except for *Poecilochirus carabi*, which was found almost exclusively on burying beetles and rarely on ground beetles. Mites also seemed to be specific to particular beetle group(s) at the family level. Thus, the “phoretic” mite faunas were distinctly different between the beetle groups: ground beetles (seven species) were characterized by carrying only one mite species, *Iphidosoma fimetarium*, burying beetles (two species) by two mite species (*Alliphis necrophilus*, *P. carabi*), roving carrion beetles (three species) by one mite species, *Rhodacaridae* sp., and dung beetles (11 species) by 15 mite species that included 8 species of *Macrocheles*. Mites associated with dung beetles included specialist species such as *Holostaspella* sp. 1 which was specific to subsocial *Copris ochus*, and generalist species like *Macrocheles* sp. aff. *glaber* that was found on nine dung beetle species.

INTRODUCTION

Various species of mites are found clinging to or moving on the body surface of other organisms, particularly insects. Although such an association between mites and insects sometimes involves complex relationships such as mutualism [37, 41, 42], the association is usually called phoretic on the assumption that the mites use the beetles as vehicles. The majority of larger species of phoretic mites belong to the suborder Mesostigmata [8, 13, 15, 16]. There are a lot of carrier records of these mesostigmatic mites, and carrier specificity of some species has been investigated [5, 9, 10, 12, 27, 28, 30, 34, 40]. Phoretic mesostigmata are also known as an important control agent of house flies [1, 7, 29].

In Japan, too, phoretic mesostigmatic mites are common, and so far 26 species have been recorded on various insect species [21–25]. However, these studies dealt with the mites in the middle and the southern parts of Japan, and no comprehensive study has been undertaken on the mites of the northern part. Furthermore, we know very little on the biology of the Japanese species, except for the carrier records of some species.

Since 1989, we have studied relationships between mesostigmatic mites and various groups of beetles in Hokkaido, northern Japan. As an outcome of this study, we will present below a list of mesostigmatic mites so far confirmed by us on four taxonomically and ecologically different groups of beetles, i.e., ground beetles (Carabidae), burying beetles (Nicrophorini, Silphinae, Silphidae), roving carrion beetles

(Silphini, Silphinae, Silphidae), and dung beetles (Geotrupidae and Scarabaeidae). We will also summarize suggested relationships between mesostigmatic mites and carrier beetles.

MATERIALS AND METHODS

We collected beetles with the aid of pitfall traps set at forest margins and in the forests in the vicinity of Sapporo, and Hokkaido University Tomakomai Experiment Forest, Tomakomai, Hokkaido, northern Japan. The pitfall traps were baited with meat or without any bait. We also collected beetles from cattle dung by hand in pastures of Hokkaido Agricultural Experiment Station in Sapporo. Beetles collected on other occasions were also examined for their phoretic mites. No quantitative sampling of beetles was undertaken. Beetles were anesthetized with chloroform or ethyl-ethyl. Mites detached from the anesthetized beetles were fixed in 70% ethanol, softened and cleared in lactophenol and mounted with a gum-chroral medium on a glass slide [27, 36]. Observation and identification of mites were made on these mounted specimens under a phase-contrast microscope.

RESULTS

Beetles examined and those bearing mesostigmatic mites

We examined 33 species of beetles during the course of this study. Mesostigmatic mites were obtained from 23 beetle species, which are asterisked in the following list (scientific names of the beetles followed Hirashima [17], except those of *Aphodius* dung beetles for which we follow Masumoto *et al.* [33]):

Ground beetles (Carabinae, Carabidae, 12 species):
Cychrus morawitzi Géhin, 1885, *Calosoma maximowiczii*

(Morawitz, 1863), *Cl. inquisitor cyanescens* Motschulsky, 1858, *Campalita chinense* (Kirby, 1818), **Carabus granulatus yezeensis* Bates, 1883, **C. conciliator hokkaidensis* Lapouge, 1924, **C. albrechti albrechti* Morawitz, 1862, **Leptocarabus arboreus arboreus* (Lewis, 1882), **L. opaculus opaculus* (Putzeys, 1875), *Procrustes kolbei aino* (Rost, 1908), **Damaster gehinii gehinii* (Fairmaire, 1876), **D. blaptoides rugipennis* (Motschulsky, 1861).

Burying beetles (Nicrophorini, Silphinae, Silphidae, 5 species): **Nicrophorus maculifrons* Kraatz, 1877, **N. quadripunctatus* Kraatz, 1897, *N. investigator investigator* Zetterstedt, 1824, *N. vespilloides* (Herbst, 1784), *Ptomascopus morio* (Kraatz, 1877).

Roving carrion beetles (Silphini, Silphinae, Silphidae, 4 species): **Silpha perforata venatoria* Harold, 1877, **Eusilpha japonica* (Motschulsky, 1860), **Phosphuga atrata* (Linnaeus, 1758), *Dendroxena sexcarinata* (Motschulsky, 1866).

Dung beetles (Geotrupidae and Scarabaeidae, 12 species): **Geotrupes auratus* Motschulsky, 1857, **G. laevistriatus* Motschulsky, 1857, **Coprins ochus* Motschulsky, 1860, **Liatongus phanaeoides* (Westwood, 1840), **Caccobius jessoensis* Harold, 1867, **Onthophagus ater* Waterhouse, 1875, **O. atripennis atripennis* Waterhouse, 1875, **Aphodius elegans* Allibert, 1847, **A. haemorrhoidalis* (Linnaeus, 1758), **A. quadratus* Reiche, 1847, **A. pusillus* (Herbst, 1789), *A. rectus* (Motschulsky, 1866).

List of mesostigmatic mites collected

A total of nineteen species of mites were collected from 23 species of beetles. They are enumerated below with some notes. Full taxonomic accounts of these mites will be published elsewhere by the first author ([38]; in preparation). Mites referred to by the combinations of the generic name and the species code number are undescribed species. Asterisked species are those recorded from Japan for the first time. For each species, a) stages of mites collected; b) carrier beetles confirmed by us; c) attaching site and d) known geographic distribution, are given.

Superfamily Eviphidoidea

Family Eviphididae

1) *Eviphis cultratellus* (Berlese, 1910)*: a) female, male, deutonymph; b) *Coprins ochus*; c) ventral surface of body, mainly intersegmental membrane between prothorax and mesothorax; d) Japan (Hokkaido), Java, Egypt, India, South Africa.

This species has been collected on the dung beetles *Onitis* spp. [35], *Coprins* sp. [2], and from cattle dung [3].

2) *Eviphis* sp. 1*: a) female; b) *Coprins ochus*; c) ventral surface of body, mainly intersegmental membrane between prothorax and mesothorax; d) Japan (Hokkaido).

3) *Alliphis halleri* (G. & R. Canestrini, 1881): a) female, male, deutonymph; b) *Coprins ochus*, *Caccobius jessoensis*, *Aphodius elegans*; c) mainly around the mouthparts; d) Japan (Hokkaido, Shikoku), Europe, Israel.

This species has so far been collected on the dung beetle

Geotrupes laevistriatus and on the burying beetle *Nicrophorus quadripunctatus* in southern Japan [21], and on five species of dung beetles (*Coprins* [8], *Geotrupes* [6, 18, 26]) in Europe and Israel.

4) *Alliphis necrophilus* Christie, 1983*: a) female, male, deutonymph; b) *Nicrophorus maculifrons*, *N. quadripunctatus*; c) specifically found on the ventral membranous portion connecting prothorax and mesothorax; d) Japan (Hokkaido), UK.

Unlike *A. halleri*, the present species was exclusively found on burying beetles of the genus *Nicrophorus*. *A. necrophilus* also has been collected on several species of *Nicrophorus* beetles in the UK [6].

5) *Scarabaspis spinosus* Ishikawa, 1968: a) female, male, deutonymph; b) *Geotrupes laevistriatus*; c) ventral surface of body, mainly prothorax; d) Japan (Hokkaido, Shikoku).

This species seems to be specific to the dung beetle *G. laevistriatus* [21, present study].

6) *Pelethiphis hogai* Ishikawa, 1984: a) female, male; b) *Geotrupes auratus*; c) specifically found on the ventral side of the prothorax; d) Japan (Hokkaido, Honshu).

This species is thus far known only on *G. auratus* ([25]; present study).

Family Macrochelidae

7) *Macrocheles insignitus* Berlese, 1918: a) female; b) *Liatongus phanaeoides*, *Aphodius quadratus*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido, Honshu, Shikoku), Europe, USA.

This species has been found in a variety of habitats including beetles, a rodent, compost, cattle dung, grassland soil, wet mosses, and nests of bumble bees (*Bombus* sp.) [20, 24, 31].

8) *Macrocheles serratus* Ishikawa, 1968: a) female, male, deutonymph; b) *Geotrupes laevistriatus*, *Aphodius quadratus*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido, Shikoku).

9) *Macrocheles* sp. aff. *glaber* (Müller, 1860)*: a) female; b) *Geotrupes auratus*, *G. laevistriatus*, *Coprins ochus*, *Liatongus phanaeoides*, *Caccobius jessoensis*, *Aphodius quadratus*, *A. haemorrhoidalis*, *A. pusillus*, *A. elegans*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido); *M. glaber* is nearly cosmopolitan, being distributed in Europe, Mediterranean areas, Russia, USA, Australia and New Zealand.

Although this species can be identified with *M. glaber* we could not obtain deutonymphs which are indispensable for exact identification. *M. glaber* has so far been collected on various groups of coprophagous scarabaeid beetles (*Geotrupes*, *Typhaeus*, *Aphodius*, *Onthophagus*, *Coprins*) in Europe, Australia and Japan. Also collected on burying beetles (*Nicrophorus*), bumble bees (*Bombus*), small mam-

imals and their nests, and in a variety of manure and rotting vegetation habitats [11, 20].

10) *Macrocheles* sp. aff. *monchadskii* Bregetova & Koroleva, 1960*: a) female; b) *Geotrupes laevistriatus*, *Onthophagus ater*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido); *M. monchadskii* was described from Adzhar (Russia).

Macrocheles monchadskii was recorded from leaf litter [4].

11) *Macrocheles* sp. aff. *hallidayi* Walter & Krantz, 1986*: a) female; b) *Geotrupes auratus*, *Onthophagus ater*, *O. atripennis atripennis*, *Copris ochus*, *Liatongus phanaeoides*, *Aphodius quadratus*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido); *M. hallidayi* is widespread in SE Asia, covering India, Thailand, Cambodia, Java and Sarawak.

Macrocheles hallidayi has been found on dung beetles of the genera *Onitis*, *Heliocopris*, and *Catharsius* [39].

12) *Macrocheles* sp. aff. *moneronicus* Bregetova & Koroleva, 1960*: a) female; b) *Geotrupes laevistriatus*, *Liatongus phanaeoides*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido); *M. moneronicus* was described from Moneron Island (Russia) [4].

13) *Macrocheles* sp. 1*: a) female; b) *Geotrupes laevistriatus*, *Onthophagus ater*, *O. atripennis atripennis*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido).

14) *Macrocheles* sp. 2*: a) female; b) *Copris ochus*, *Liatongus phanaeoides*, *Onthophagus ater*, *Aphodius quadratus*, *A. elegans*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido).

15) *Holostaspella* sp. 1*: a) female, male, deutonymph, protonymph; b) *Copris ochus*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido).

This species was found exclusively on the subsocial dung beetle *C. ochus*. Not only adults, but also deutonymphs and protonymphs were collected on beetle body surface and from dung balls which were made by the parental beetles as the larval food [38].

Family Pachylaelapidae

16) *Pachylaelaps copris* Ishikawa, 1984: a) female, male; b) *Copris ochus*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido, Kyushu).

Thus far collected only on *C. ochus* ([25]; present study).

Superfamily Parasitoidea

Family Parasitidae

17) *Poecilochirus carabi* G. & R. Canestrini, 1882*: a)

deutonymph; b) *Nicrophorus maculifrons*, *N. quadripunctatus*, *Carabus albrechti albrechti*, *Damaster gehinii gehinii*; c) mainly found on the ventral surface of body, in particular the membranous portion between prothorax and mesothorax; d) Japan (Hokkaido), Europe, Russia, China, USA.

P. carabi has been collected on various species of burying beetles (*Nicrophorus*) and carcasses of birds and small mammals, and has been said to be mutualistic with *Nicrophorus* beetles [5, 37, 41, 42]. In the present study, too, this species was mainly collected on *Nicrophorus* beetles. In addition, *P. carabi* has been collected on dung beetles (*Aphodius*) and ground beetles (*Carabus*, *Pterostichus*) ([19, 34, 37, 40]; present study). The nature of association between *P. carabi* and beetles other than burying beetles is yet unknown.

Superfamily Rhodacaroidea

Family Rhodacaridae

18) *Iphidosoma fimetarium* (Müller, 1859)*: a) female; b) *Carabus granulatus yezoensis*, *C. conciliator hokkaidensis*, *C. albrechti albrechti*, *Leptocarabus arboreus arboreus*, *L. opaculus opaculus*, *Damaster gehinii gehinii*, *D. blaptoides rugipennis*; c) mainly attached to the dorsal side of mesothorax, metathorax and abdomen covered by elytra; d) Japan (Hokkaido), Russia, Europe.

We collected *I. fimetarium* on seven species of carabid beetles. In Russia and Europe, too, this species has been collected on ground beetles of the genera *Carabus*, *Pterostichus* and *Nebria* [14, 32].

19) Rhodacaridae sp. a) deutonymph; b) *Silpha perforata venatoria*, *Eusilpha japonica*, *Phosphuga atrata*; c) mainly attached to the dorsal side of mesothorax, metathorax and abdomen covered by elytra. d) Japan (Hokkaido).

The genus, to which this species belongs, is difficult to determine since only deutonymphs are available.

REMARKS

Summarizing the above findings, we prepared a synoptic list of mesostigmatic mites and carrier beetles (Table 1). Some ecological properties of examined beetles were summarized in Table 2, together with associated mite families. Recent studies have shown that carrier specificity may be different between populations of a single mite species [5, 34, 40]. Furthermore, there may be seasonal difference in mite frequencies on beetles. Since we did not make any quantitative sampling of beetles, our data is not appropriate to analyze such spatio-temporal variation of beetle-mite interaction. However, our results suggest certain noteworthy aspects of mite-beetle associations as shown below.

First, mesostigmatic mites were never collected on the beetles foraging on tree foliage; all the beetles that carried mesostigmatic mites forage on the ground (Table 2), or forage on the foliage of undergrowth plants (*Phosphuga atrata*). Secondly, except for *P. carabi*, which was almost exclusively found on burying beetles but rarely on ground beetles, no mite species were found on more than one beetle

TABLE 1. Synopsis of carrier beetles and associated mesostigmatic mites examined in the present study

Groups and species of carrier beetles	Families and species of mesostigmatic mites													
	Eviphididae	<i>Eviphis cultratus</i>	<i>E. sp. 1</i>	<i>Alliphis halleri</i>	<i>A. necrophilus</i>	<i>Scarabaspis spinosus</i>	<i>Pelethiphis hogai</i>	Macrochelidae	<i>Macrocheles insignitus</i>	<i>M. serratus</i>	<i>M. sp. aff. glaber</i>	<i>M. sp. aff. monchadskii</i>	<i>M. sp. aff. hallidayi</i>	<i>M. sp. aff. moneronicus</i>
Ground beetles														
<i>Carabus glanulatus yesoensis</i>														+
<i>C. conciliator hokkaidensis</i>														+
<i>C. albrechti albrechti</i>														+
<i>Leptocarabus arboreus arboreus</i>														+
<i>L. opaculus opaculus</i>														+
<i>Damaster gehinii gehinii</i>														+
<i>D. blaptoides rugipennis</i>														+
Burying beetles														
<i>Nicrophorus maculifrons</i>					+									+
<i>N. quadripunctatus</i>					+									+
Roving carrion beetles														
<i>Silpha perforata venatoria</i>														+
<i>Eusilpha japonica</i>														+
<i>Phosphuga atrata</i>														+
Dung beetles														
<i>Geotrupes auratus</i>						+					+	+		
<i>G. laevistriatus</i>					+					+	+	+	+	+
<i>Copris ochus</i>		+	+	+							+			+
<i>Liatongus phanaeoides</i>								+		+	+	+	+	+
<i>Caccobius jessoensis</i>				+						+				
<i>Onthophagus ater</i>											+	+	+	+
<i>O. atripennis atripennis</i>												+	+	
<i>Aphodius quadratus</i>								+	+	+	+			+
<i>A. haemorrhoidalis</i>										+				
<i>A. pusillus</i>										+				
<i>A. elegans</i>				+						+				+

group (Table 1). Such strong associations with particular groups of beetles are also noticed at the family level of mites (Table 2). We briefly examine below these mite-beetle associations for each mite family.

Eviphididae: Five eviphidid species were collected on five species of dung beetles, and one eviphidid species on two species of burying beetles. Since all these beetle species are either presocial or subsocial and bury food under the ground for their larvae, eviphidid mites might be specific to beetles that share this particular behavioral characteristic. Carrier specificity of eviphidid mites seems to be intense. Two closely related *Alliphis* species differ in their carriers, *A. halleri* on dung beetles and *A. necrophilus* on burying beetles (*Nicrophorus*). Furthermore, *Scarabaspis spinosus* and

Pelethiphis hogai were found to be specific to different species of *Geotrupes* dung beetles, the former to *G. laevistriatus* and the latter to *G. auratus*.

Macrochelidae: About half of the mite species reported in the present paper are macrochelids, and they belong to a single genus *Macrocheles*, except for *Holostaspella* sp. 1. All the species were collected on dung beetles. Some *Macrocheles* species, in particular *M. sp. aff. glaber*, are generalists and were found on various species of dung beetles, whereas *Holostaspella* sp. 1 was a specialist and found only on the subsocial *Copris ochus* and in the dung balls prepared by the beetles.

Pachylaelapidae: Only one species, *Pachylaelaps copris*, was collected. Like *Holostaspella* sp. 1, *P. copris* was spe-

TABLE 2. Some ecological properties of beetles examined and associated mite families.

Beetle group and genus	Food type	Foraging at	Flight ability	Sociality	Associated mite family***				
					EV	MA	PC	PR	RD
Ground beetles									
<i>Cychrus</i> *	Live invertebrates	Ground	—	None					
<i>Calosoma</i> *	Live invertebrates	Tree foliage	+	None					
<i>Campalita</i> *	Live invertebrates	Tree foliage	+	None					
<i>Carabus</i>	Live invertebrates	Ground	—	None				(+)	+
<i>Leptocarabus</i>	Live invertebrates	Ground	—	None					+
<i>Procrustes</i>	Live invertebrates	Ground	—	None					
<i>Damaster</i>	Live invertebrates	Ground	—	None				(+)	+
Burying beetles									
<i>Nicrophorus</i>	Small vertebrate carcasses	Ground	+	Subsocial	+			+	
<i>Ptomascops</i> *	Vertebrate carcasses	Ground	+	None (?)					
Roving carrion beetles									
<i>Silpha</i>	Live and dead organic matter	Ground	—	None					+
<i>Eusilpha</i>	Live and dead organic matter	Ground	—	None					+
<i>Phosphuga</i>	Live invertebrates	Foliage of undergrowth	—	None					+
<i>Dendroxena</i> *	Live invertedrates	Tree foliage	+	None					
Dung beetles									
<i>Geotrupes auratus</i>	Vertebrate dung	Ground	+	Presocial	+	+			
<i>G. laevistriatus</i>	Vertebrate dung, dead organic matter	Ground	+(?)	Presocial	+	+			
<i>Copris</i>	Vertebrate dung	Ground	+	Subsocial	+	+	+		
<i>Liatongus</i>	Vertebrate dung	Ground	+	Presocial		+			
<i>Caccobius</i>	Vertebrate dung	Ground	+	Presocial	+	+			
<i>Onthophagus</i>	Vertebrate dung	Ground	+	Presocial		+			
<i>Aphodius</i> I**	Vertebrate dung	Ground	+	Presocial	+	+			
<i>Aphodius</i> II**	Vertebrate dung	Ground	+	None		+			

* No mesostigmatic mites were found on these beetles

** *Aphodius* I: *A. quadratus*, *A. elegans*; *Aphodius* II: *A. haemorrhoidalis*, *A. rectus*, *A. pusillus*.

*** EV, Eviphididae; MA, Macrochelidae; PC, Pachylaelapidae; PR, Parasitidae; RD, Rhodacaridae.

cific to *Copris ochus*.

Parasitidae: Only one species, *Poecilochirus carabi*, was collected. This is the only species that was collected on two different groups of beetles, the ground beetles and burying beetles. In USA and Europe, this species is known to be mutualistic with burying beetles [5, 37, 41, 42], but nothing is known about the association with ground beetles as mentioned before.

Rhodacaridae: Rhodacarid mites in the surveyed habitats may be specific to beetles that forage exclusively on the ground. All the beetle species bearing rhodacarids are either ground beetles or roving carrion beetles that cannot fly, whereas burying beetles and dung beetles, which were rhodacarid-free, can fly well (with the possible exception of *G. laevistriatus* which rarely flies as far as we know). *Iphidosoma fimetarium* was specific to ground beetles but did not show preference to particular species of ground beetles. Likewise, Rhodacaridae sp. was specific to roving carrion beetles

but did not show species specificity.

Reflecting these carrier specificities of mesostigmatic mites, the "phoretic mite" faunas of the four beetle groups were distinctly different (Tables 1, 2). Ground beetles (seven species) were characterized by only one mite species (*Iphidosoma fimetarium*), burying beetles (two species) by two species (*Alliphis necrophilus*, *Poecilochirus carabi*), roving carrion beetles (three species) by one species (Rhodacaridae sp.), and dung beetles (11 species) by 15 species, including 8 species of *Macrocheles*.

Thus, most mite species, or mite families, showed definite preference for a particular group of beetles. The reason is not yet clear. Since the four beetle groups treated in the present study differ phylogenetically and ecologically, both phylogenetic constraints and ecological factors could affect the carrier specificity. Future studies will clarify which factor is most important in shaping the carrier preference of these mites.

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REFERENCES

- 1 Axtell RC (1964) Phoretic relationship of some common manure-inhabiting Macrochelidae (Acarina: Mesostigmata) to the house fly. *Ann Entomol Soc America* 57: 584–587
- 2 Berlese A (1910) Lista di nuove specie e nuovi generi di Acari. *Redia* 6: 242–271
- 3 Bhattacharyya SK (1971) The genus *Eviphis* in India (Acarina: Mesostigmata: Eviphididae). *Acarologia* 13: 266–271
- 4 Bregetova NG, Koroleva EV (1960) The macrochelid mites (Gamasoidea, Macrochelidae) in the USSR. *Parazit Sb* 19: 32–154
- 5 Brown JM, Wilson DS (1994) *Poecilochirus carabi*: Behavioral and life-history adaptations to different hosts and the consequences of geographical shifts in host communities. In “Mites: Ecological and Evolutionary Analyses of Life-History Patterns” Ed by MA Houck, Chapman & Hall, pp 1–22
- 6 Christie JE (1983) A new species of *Alliphis* (Mesostigmata: Eviphididae) from Britain. *Acarologia* 24: 231–242
- 7 Cicolani B (1992) Macrochelid mites (Acari: Mesostigmata) occurring in animal droppings in the pasture ecosystem in central Italy. *Agri Ecosys Environ* 40: 47–60
- 8 Costa M (1963) The mesostigmatic mites associated with *Copris hispanus* (L.) (Coleoptera, Scarabaeidae) in Israel. *J Linn Soc Zool* 45: 25–45
- 9 Costa M (1967) Notes on macrochelids associated with manure and coprid beetles in Israel. II. Three new species of the *Macrocheles pisentii* complex, with notes on their biology. *Acarologia* 9: 304–329
- 10 Costa M (1969) The association between mesostigmatic mites and coprid beetles. *Acarologia* 11: 411–426
- 11 Evans GO, Browning E (1956) British mites of the subfamily Macrochelinae Tragardh (Gamasina - Macrochelidae). *Bull Br Mus nat Hist (Zool)* 4: 1–55.
- 12 Evans GO, Hyatt KH (1963) Mites of the genus *Macrocheles* Latr (Mesostigmata) associated with coprid beetles in the collections of the British Museum (Natural History). *Bull Br Mus nat Hist (Zool)* 9: 327–401
- 13 Evans GO, Sheals JG, Macfarlane D (1961) The Terrestrial Acari of the British Isles. An Introduction to their Morphology, Biology and Classification. 1. Introduction and Biology. British Museum, London
- 14 Ghilarov MS, Bregetova NG (1977) A Key to the Soil-Inhabiting Mites. Mesostigmata. *Zool Inst Akad Sci USSR, Leningrad*, 718 pp
- 15 Halffter G., Matthews GE (1971) The natural history of dung beetles. A supplement on associated biota. *Rev lat amer Microbiol* 13: 147–164
- 16 Halliday RB (1986) Mites of the *Macrocheles glaber* group in Australia (Acarina: Macrochelidae). *Aust J Zool* 34: 733–752
- 17 Hirashima Y (Ed) (1989) A Check List of Japanese Insects I. xi + 540 pp. Published by Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka.
- 18 Hyatt KH (1959) Mesostigmatic mites associated with *Geotrupes stercorarius* (L.) (Col., Scarabaeidae). *Entomologist's Mon Mag* 95: 22–23
- 19 Hyatt KH (1980) Mites of the subfamily Parasitinae (Mesostigmata: Parasitidae) in the British Isles. *Bull Br Mus nat Hist (Zool)* 38: 237–378
- 20 Hyatt KH, Emberson RM (1988) A review of the Macrochelidae (Acari: Mesostigmata) of the British Isles. *Bull Br Mus nat Hist (Zool)* 54: 63–125
- 21 Ishikawa K (1968) Studies on the mesostigmatid mites associated with the insects in Japan (I). *Rep Res Matsuyama Shinonome Jr Coll* 3: 197–218
- 22 Ishikawa K (1977) On the mesostigmatid mites associated with the cerambycid beetle, *Monochamus alternatus* Hope (I). *Annot Zool Japon* 50: 99–104
- 23 Ishikawa K (1977) On the mesostigmatid mites associated with the cerambycid beetle, *Monochamus alternatus* Hope (II). *Annot Zool Japon* 50: 182–186
- 24 Ishikawa K (1980) *Macrocheles insignitus*. In “Illustrations of the Mites and Ticks of Japan” Ed by S Ehara, Zenkoku Nōson Kyōiku Kyōkai, Tokyo, pp 90–91 (In Japanese)
- 25 Ishikawa K (1984) Studies on the mesostigmatid mites associated with the insects in Japan (II). *Rep Res Matsuyama Shinonome Jr Coll* 15: 89–102
- 26 Koyumdjieva MI (1981) Gamasid mites (Gamasoidea, Parasitiformes) associated with scarabaeid beetles (Coleoptera, Scarabaeidae) in Bulgaria. *Acta Zool Bul* 17: 17–26
- 27 Krantz GW (1978) A Manual of Acarology, Second Edition. Oregon State Univ. Book Stores, Inc., Corvallis, 509 pp
- 28 Krantz GW (1981) Two new *glaber* group species of *Macrocheles* (Acari: Macrochelidae) from southern Africa. *Int J Acarol* 7: 3–16
- 29 Krantz GW (1983) Mites and biological control agents of dung-breeding flies, with special reference to the Macrochelidae. In “Biological Control of Pests by Mites” Ed by MA Hoy, GL Cunningham, L Knutson, University of California, Special Publication 3304, Berkley, pp 91–98
- 30 Krantz GW, Mellott JL (1972) Studies on phoretic specificity in *Macrocheles mycotropetes* and *M. peltotropetes* Krantz and Mellott (Acari: Macrochelidae), associates of geotrupine Scarabaeidae. *Acarologia* 14: 317–344
- 31 Krantz GW, Whittaker JO Jr (1988) Mites of the genus *Macrocheles* (Acari: Macrochelidae) associated with small mammals in North America. *Acarologia* 29: 225–259
- 32 Lundqvist L (1991) Rearing deutonymphs of *Iphidosoma fimetarium* (J. Müller), a mesostigmatic mite associated with carabid beetles. In “The Acari: Reproduction, Development and Life-history Strategies” Ed by R Schuster, PW Murphy, pp 445–452
- 33 Masumoto K., Dellacasa G, Kiuchi M (1990) On the *Aphodius* species of Japan. *Ent Rev Japan* 45: 145–156
- 34 Müller JK, Schwarz HH (1990) Differences in carrier preference and evidence of reproductive isolation between mites of *Poecilochirus carabi* (Acari, Parasitidae) living phoretically on two sympatric *Necrophorus* species. *Zool Jb Syst* 117: 23–30
- 35 Ryke PAJ, Meyer MKP (1957) Eviphidinae Berlese 1913 (Mesostigmata: Acarina) associated with South African beetles. *Ann Mag Nat Hist (Ser 12)* 10: 593–618
- 36 Shirasaka A, Ito Y (1980) Technique for the collecting and preparation of mites. In “Illustrations of the Mites and Ticks of Japan” Ed by S Ehara, Zenkoku Nōson Kyōiku Kyōkai, Tokyo, pp 511–520 (In Japanese)
- 37 Springett BP (1968) Aspects of the relationship between burying beetles, *Necrophorus* spp. and the mite, *Poecilochirus necrophori* Vitz. *J Anim Ecol* 37: 417–427
- 38 Takaku G (1994) A new species of the genus *Holostaspella* (Acari: Macrochelidae) from northern Japan. *Acarologia* 35 (In press)
- 39 Walter DE, Krantz GW (1986) Description of the *Macrocheles*

- kraepelini* species complex (Acari: Macrochelidae) with two new species. Can J Zool 64: 212-217
- 40 Wilson DS (1982) Genetic polymorphism for carrier preference in a phoretic mite. Ann Entomol Soc America 75: 293-296
 - 41 Wilson DS (1983) The effect of population structure on the evolution of mutualism: a field test involving burying beetles and their phoretic mites. Amer Nat 121: 851-870
 - 42 Wilson DS, Knollenberg WG (1987) Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites. Evol Ecol 1: 139-159