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Tiny mites on a great journey – a review on scutacarid mites as phoronts and inquilines (Heterostigmatina, Pygmephoroidea, Scutacaridae)

Julia Baumann

Abstract

The members of the family Scutacaridae (Acari, Heterostigmatina, Pygmephoroidea) are soil-living, fungivorous mites, and some of them are known to be associated with other animals. After reviewing the mites’ behavioural and morphological adaptations to their animal-associated lifestyle, the present publication shows the result of a thorough literature research on scutacarids living in different kinds of associations with other animal taxa. It revealed that within the more than 800 scutacarid species that have been described so far, about the half of them can be found together with various animal taxa. The respective scutacarid species can be phoretic using their hosts for dispersal, they can be inquilines of their hosts benefiting from favourable conditions in the hosts’ nests, or they can be both. The highest number of scutacarid species, by far, (n = 214) is associated with ants. The second highest number can be found on beetles (94; mainly on ground beetles, Carabidae), followed by mammals (52), bees and wasps (35) and other insect taxa (39), and some species can be found together with birds (10) and arachnids (6). The most frequent genera Scutacarus, Imparipes and Archidispus show host preferences: Scutacarus and Imparipes tend to prefer ants, while Archidispus prefers beetles. Usually, scutacarid species are rather specialised on one host genus or one host family, but some seem to be host generalists. The possible influence of scutacarids on their hosts is not known yet, but they could play a sanitary role in their hosts’ nests.

Keywords phoresy, associations, inquilines, Formicidae, Carabidae, Scutacarus, Imparipes, Archidispus

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Introduction

Phoresy is a phenomenon that can be found all over the animal kingdom. There are several definitions for this behavioural trait, ranging from strict to relatively loose interpretations. What they all agree about is that it is about a small individual, the phoront, being transported by a larger animal, the host. In contrast to parasitism, the phoront does not feed on its host. In fact, in strict definitions of phoresy like that stated by Farish and Axtell (1971), the phoront does not feed at all while it is attached to its host and does also cease any other activities. According to them, the only aim of phoresy is dispersal in order to reach new habitats which are favourable for reproduction (either for the phoront’s own reproduction or that of its progeny). More recent and loose definitions of phoresy like that of Walter and Proctor (1999) don’t exclude feeding during the phoretic stage anymore.

As phoresy is about dispersal, it is no wonder that this phenomenon gets more frequent the smaller the studied species are: small animals naturally don’t have the ability to move for large distances on their own, instead they have to rely on other dispersal mechanisms like...
anemochory (transport by air currents), hydrochory (transport by water) or said phoresy. Mites (Acari) are characterized by consistently small body sizes (Krantz and Walter 2009), and several groups of mites have indeed developed different strategies for dispersing through phoresy. In all these mites phoresy is restricted to one stage, either the (gravid) females or deutonymphs (Krantz and Walter 2009). Some mites, like gamasid deutonymphs, do not have any special morphological adaptations to phoresy at all, but freely move on their host’s body surface. Almost all other phoretic mites possess adaptations for attaching to their hosts, like ventral sucker plates in astigmatid deutonymphs or anal pedicels secreted by uropodid deutonymphs, both allowing the mites to adhere to smooth body surfaces (Ebermann 2004). Scutacarid mites, which are the main protagonists of the present paper, cling to their host by using enlarged claws on leg I.

The mite family Scutacaridae belongs to the superfamliy Pygmephoroidea, Heterostigmatina, and is characterized by remarkably small body sizes of about 200 μm, a strong sexual dimorphism and a shortened generation cycle with larvae being the only juvenile stage (Walter and Proctor 1999). All members of the family are fungivorous (Binns 1979; Ebermann 1991a; Ebermann and Goloboff 2002; Jagersbacher-Baumann and Ebermann 2013), and most of them are soil inhabiting mites occurring predominantly in decaying material, often in ephemeral habitats like manure or compost (Ebermann 1991a). Following the current taxonomy, the family Scutacaridae comprises some 24 genera (Zhang et al. 2011). In almost the half of these genera, species associated with other animals can be encountered, and the host taxa range from arachnids to insects and finally to mammals (e.g. Ebermann and Palacios-Vargas 1988, Eickwort 1990, Jagersbacher-Baumann and Ebermann 2012a). Most of the respective species have been encountered phoretic on their hosts, but there are also many species which only have been found as inquilines in the nests of their hosts. These inquilines are also included in the present review.

Although several studies about scutacarids associated with different host taxa have been published, a comprehensive overview about the known associations and all involved taxa was lacking until today and will be given in the present paper. Moreover, the morphological and behavioural adaptations of scutacarids to phoresy will be described.

**Morphological adaptations of scutacarid mites to phoresy and phoretomorphism**

Phoretic behaviour is presumably always induced by a reduction of the quality of food in the current habitat (Ebermann 2004). As soon as conditions get worse, mites have to be prepared to take action. In order to successfully perform phoresy, every phoretic mite instar, irrespective of the mite taxon, must fulfil two prerequisites: it has to 1) possess the sensory capability to identify suitable hosts and 2) have the mechanical ability to attach to the host (Eickwort 1994). While the sensory equipment responsible for host identification in scutacarids is not really known yet (see below, “Mounting and dismounting of hosts”), the morphological adaptations are well understood.

In Scutacaridae, only adult females perform phoresy, and their habitus is indeed predestined for this mode of dispersal (Figure 1). Their body is covered by curved dorsal tergits, which give them a tortoise-like appearance, and when attached to their hosts, their characteristic habitus offers practically no point of attack and thus it is difficult for the hosts to remove the mites (Ebermann 1991a). In regard of their general body shape, scutacarids are very similar to astigmatid hypopi (Aneotida, Acarida), and that is exactly what they had been mistaken for shortly upon their discovery in the 18th century (Michael 1884). In fact, a body plan similar to that described above can not only be found in Scutacaridae and astigmatid hypopi, but also in Tarsonemidae, Pyemotidae and some Uropodina (Lindquist 1975, Ebermann 2004). Scutacarids attach to their hosts by using large claws on leg I (Figure 2a) which can grasp setae or soft intersegmental skin (Ebermann 1991a). There are scutacarid species without these large
Figure 1. Fronto-dorsal view of a typical scutacarid adult female (*Imparipes (Sporichneuthes) dispar* Rack, 1964) moving on a carpet of fungi, scanning-electron micrograph. The curved tergites give the mite a tortoise-like habitus.

Figure 2. Differences between the tarsi and the claws on leg I of a) a phoretic and b) a nonphoretic morph of a female scutacarid (*Scutacarus acarorum* Goeze 1780).
claws, and these species are generally supposed not to perform phoresy. As will be seen below, there are also species in which both occur, morphs with and morphs without large claws on leg I. The detailed structure of the claws can also differ between scutacarid genera: for example, the claws of phoretic Lamnacarus females have long, thin tips which are not present in other genera (Ebermann 1991a).

In addition to their characteristic morphology, scutacarid mites can also avoid being removed by their hosts by choosing attachment sites which are difficult to reach for the (grooming) host, like under the elytra of beetles (e.g. Karafiat 1959). It is a general trend that phoretic mite taxa are not distributed randomly on their host, but gather highly localised in places that are not groomed (Eickwort 1994, Ebermann 2004). However, some scutacarid species on the contrary attach to exposed body parts of their hosts: for example, Thaumatopelvis reticulatus Ebermann, 1980 clings to setae on the head of ants (Ebermann 1980b). The exposed location demonstrates that the claws are powerful attachment structures as the mites can even withstand the grooming of the host.

**Phoretomorphism**

In the genera Archidispus, Lamnacarus and Scutacarus, dimorphic species characterized by the occurrence of phoretic and non-phoretic females exist. This female dimorphism, which is also referred to as phoretomorphism, had firstly been suggested by Norton (1977) for Scutacaropsis baculitarsus agaricus (Norton and Ide, 1974) and had thereafter been demonstrated in other scutacarid species belonging to the genera Archidispus, Lamnacarus and Scutacarus through laboratory cultures by Ebermann (1991a,b). A similar dimorphism in connection with phoresy is also known from other mite taxa, either in deutonymphs or in adult females (Krantz and Walter 2009). To date, 11 scutacarid species are known to be dimorphic (Table 1). The main difference between the two morphs is the size of the claw on the tarsus of leg I, which is large in the phoretic morph and small or even absent in the non-phoretic morph (Figure 2). Moreover, the sclerotisation of phoretic females appears to be stronger (Ebermann 1991a). In the genus Archidispus, there are also distinct differences in the shape of particular setae between the two morphs (Ebermann 1991a,b; Figure 3). The large claws on leg I and the stronger sclerotization can easily be interpreted as adaptations to phoretic behaviour because they allow attachment and also protect the mites during their journey. The possible adaptive value of the differently shaped body setae in the genus Archidispus on the other hand remains unclear.

Laboratory cultures showed that females of both morphs can also produce female offspring belonging to both morphs. The mechanisms for morph determination are not totally clear yet, but Ebermann (1991a) convincingly hypothesized that the quality of nutrition of larvae might

<table>
<thead>
<tr>
<th>species (phoretic morph)</th>
<th>non-phoretic morph</th>
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<tr>
<td>Archidispus amarae (Kurosa, 1970)</td>
<td>described by Ebermann (1991a)</td>
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<tr>
<td>Archidispus armatus (Karafiat, 1959)</td>
<td>A. soosi (Mahunka); synonymized by Ebermann (1991a)</td>
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<td>Archidispus bembidii (Karafiat, 1959)</td>
<td>described by Ebermann (1991a)</td>
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<tr>
<td>Archidispus magnificus (Karafiat, 1959)</td>
<td>described by Ebermann (1991b)</td>
</tr>
<tr>
<td>Archidispus minor (Karafiat, 1959)</td>
<td>described by Ebermann (1991b); very similar to A. haarloevi Karafiat</td>
</tr>
<tr>
<td>Lamnacarus ornatus Balogh &amp; Mahunka, 1963</td>
<td>L. coprophilus Mahunka; synonymized by Ebermann (1990)</td>
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<tr>
<td>Scutacarus acarorum (Gozeze, 1780)</td>
<td>reported by Ebermann (1992)</td>
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<td>Scutacarus australiensis Mahunka, 1967</td>
<td>reported by Greenslade &amp; Clift 2004</td>
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<tr>
<td>Scutacarus baculitarsus agaricus (Norton &amp; Ide, 1974)</td>
<td>reported by Norton (1977)</td>
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<td>Scutacarus deserticolus Mahunka, 1969</td>
<td>reported by Ebermann (1991a)</td>
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<tr>
<td>Scutacarus longitarsus (Berlese, 1905)</td>
<td>S. subfimetarius Momen &amp; El-Bagoury; synonymized by Ebermann (1990)</td>
</tr>
<tr>
<td>Scutacarus mendax Karafiat, 1959</td>
<td>reported by Jagersbacher-Baumann (2014)</td>
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most likely be the determining factor. Behavioural experiments proofed that phoretic females readily attach to offered hosts, while non-phoretic females mount hosts only in exceptional cases (Ebermann 1991a).

**Adaptivity of phoretomorphism**

Ebermann (1991a, 2004) stated that phoretomorphism most likely can be regarded as an adaptation to ephemeral or heterogeneous habitats. Accordingly, the phoretic morph is considered to be responsible for dispersal, and the usually smaller and weakly sclerotized non-phoretic morph is seen as an “energy saving version” specialized on reproduction: As long as conditions in the habitat are favourable, the non-phoretic females predominate and procreate quickly. Worsening conditions induce the increased development of phoretic females which mount on suitable hosts and thus disperse to new habitats. Ebermann (1992) hypothesized that differences in the degree of phoretomorphism reflect the selective pressure towards phoresy in scutacarids. This means that species with a strong degree of phoretomorphism depend on phoresy because they are specialized on certain habitat conditions, while species with a low degree of phoretomorphism do not exclusively rely on phoresy because they are also able to reproduce and thrive in suboptimal habitat conditions.

**Taxonomical consequences of phoretomorphism**

The detection of phoretomorphism had important consequences for scutacarid taxonomy as some taxa, which had been treated as separated species before, had to be merged into one single species. Accordingly, Ebermann (1990) demonstrated that *Archidispus soosi* (Mahunka, 1967) is the non-phoretic morph of *A. armatus* (Karafiat, 1959), *Lamnacarus coprophilus* Mahunka,
1968 is the non-phoretic morph of \textit{L. ornatus} Balogh & Mahunka, 1963 and \textit{Scutacarus subfimetarius} Momen & Bagoury, 1989 is the non-phoretic morph of \textit{S. longitarsus} (Berlese, 1905). In the same work, Ebermann also discouraged from using \textit{Variatipes}, a subgenus of the genus \textit{Scutacarus} that is defined by the absence of claws on leg I. This absence of claws could indeed be a “good” character evolved by a gradual reduction of the claws, but specimens without claws could also be non-phoretic morphs of other species.

Most taxonomic problems caused by phoretomorphism arise in the genus \textit{Archidispus} as the two female morphs differ extremely in this taxon. For several \textit{Archidispus} species, only the non-phoretic or the phoretic morph have been described so far (Ebermann 1990), and further analyses may reveal that many of these species in reality represent the two morphs of one single species. Until now, cumbersome rearing experiments have been the only way to unequivocally identify the two morphs of a phoretomorphic species (Ebermann 1991a). Nowadays, molecular genetic methods are also available for investigating the status of different morphs, but so far no studies on the topic have been performed.

**Mounting and dismounting of host**

**Mounting**

The detailed act of identifying and mounting hosts is unclear for most phoretic scutacarids. Most species that could be observed alive didn’t show any recognisable searching or appetite behaviour, but simply “adhered” to host individuals when being put together with them in plastic boxes in behavioural experiments (Schousboe 1986, Ebermann 1991a). Some scutacarids, however, display appetite behaviour: In order to locate potential new hosts, females of these species move to exposed positions and put themselves in an upright position, the “perching stance”: The first legs are held out with or without questing movements similar to what can be observed in ticks (Binns 1979). The mites stand on their extended legs IV which are normally trailed during locomotion, and they are apparently backed by their dorsal setae. The appetite behaviour described above has been reported for \textit{Scutacaropsis baculitarsus} (Mahunka, 1968) by Binns (1979), for \textit{Archidispus amarae} (Kurosa, 1970), \textit{A. armatus}, \textit{A. bembidii} (Karafiát, 1959), \textit{A. magnificus} (Karafiát, 1959) and \textit{A. minor} (Karafiát, 1959) by Ebermann (1991a,b), for \textit{Imparipes} (\textit{Sporichneuthes}) \textit{dispar} Rack, 1964 by Ebermann (1995) and for the genus \textit{Lophodispus} by Schlagbauer (1997) and Ebermann and Krisper (2014), and it has moreover been observed in \textit{Imparipes (I.) histricinus} Berlese, 1903, \textit{Scutacarus longipes} Rack, 1975 and \textit{S. longitarsus} (Berlese, 1905) (Ebermann pers. comm.). In the genus \textit{Archidispus}, Ebermann (1991a) noted that only phoretomorph females performed appetite behaviour, while non-phoretomorph females always fled whenever potential hosts approached.

\textit{Imparipes (S.) dispar}, \textit{Lophodispus bulgaricus} Dobrev, 1992 and \textit{L. irregularis} (Mahunka, 1971) are the only scutacarid species which are known to mount its hosts by jumping, as has been reported by Ebermann (1995) for \textit{Imparipes} and by Schlagbauer (1997) in his master thesis for \textit{Lophodispus}. The jumping behaviour of \textit{I. dispar} is provoked by tactile stimuli of the mite’s dorsal setae or even by air currents, and three types of jumping have been demonstrated: the aimed jump, the sideward jump and the high-and-long jump. While the latter two are interpreted as escape mechanisms for evading predators, the aimed jump is part of the mite’s phoretic behaviour as it permits \textit{I. dispar} to jump onto fast-moving hosts. The two \textit{Lophodispus} species show the same jumping types as \textit{I. dispar} and additionally are able to jump backwards, but it is more difficult to provoke the jumping behaviour in them. Although observations indicate that leg IV in all cases plays the most important role in jumping, the detailed mechanisms of the movement are unknown: neither \textit{I. dispar} nor the two \textit{Lophodispus} species show clear (external) morphological differences compared to non-jumping scutacarids.

Generally speaking, for successful host finding and identification, both mechanical as well as chemical stimuli are necessary. Mechanosensitive setae are located on the mites’ dorsal side as well as on their legs (Jagersbacher-Baumann 2007), and chemosensitive setae
(solenidia) can be found on the legs, with legs I possessing the highest number of solenidia. The perching stance of some scutacarids, where legs I are outstretched, strongly points to a great importance of chemical cues, whereas experiments with *I. dispar* showed positive reactions to tactile stimuli (Ebermann 1995), suggesting that mechanical stimuli are more important here (Ebermann 2004). Different scutacarid species presumably follow different strategies in the act of host finding and identification, but detailed studies on this issue are lacking to date.

**On the host**

On their host, the mites usually are motionless (Karafiat 1959; pers. obs.). There is only one observation by Travis (1941) describing scutacarid mites (“Disparipedidae”) riding fire ants while standing “rather erect, bobbing up and down and tapping the ant with the first pair of legs”. Travis further describes that the mites feed on liquids on the mouthparts and occasionally also on the anal opening of the ants. The described behaviour rather resembles the appetite behaviour described above and does not fit to what is known about the feeding habits (fungivory) of scutacarids at all. As his descriptions are extraordinary, it is possible that Travis either misinterpreted the observations he made in the artificial environment of a laboratory or in fact saw mites of the family Antennophoridae (Mesostigmata) and mistook them for Scutacaridae. Another remarkable report is that of Schousboe (1986) who noted that *Scutacarus acarorum* (Goeze, 1780) specimens on overwintered *Bombus* queens discharged dark fecal pellets, something that has never been observed by other researchers afterwards.

Scutacarid mites are no parasites of their hosts, although this assumption had been stated at least in the case of the bumble bee associated *S. acarorum* (Chmielewski 1971) and since then has been circulating like an urban legend (Chmielewski and Baker 2008, Kontschán 2015, Kontschán et al. 2016). Indeed, Chmielewski never really observed parasitic behaviour (pers. comm. between Chmielewski and Ebermann). Experiments by Karafiat (1959) and Schousboe (1986) proved that scutacarids are not parasitic, and the morphology of their gnathosoma with its delicate, stylet-like chelicerae also shows that they hardly could be parasites (Schousboe 1986).

The number of scutacarids phoretic on one host specimen usually is low and ranges around 10 mites per host individual (eg. Ebermann and Hall 2003, Hall and Ebermann 2005, Kurosa 2005). Some species, however, can also be found in higher numbers. Mites belonging to the genus *Archidispus* associated with different carabid beetles for example frequently occur in abundances of around 40 mite individuals per host specimen (e.g. Kurosa 1983, 1991, 2003). The highest numbers of scutacarids are known for *A. bembidii*: more than 100 individuals have been reported from under the elytra of different carabid species (Karafiat 1959, Ebermann 1991a). Generally, reports of more than 50 scutacarids on one host specimen are rather rare (e.g. 115 *Scutacarus acarorum* on *Bombus terrestris* queen (Schousboe 1986), 71 *Imparipes apicola* (Banks, 1914) on *Andrena flavigipes* (Ebermann and Hall 2005)).

**Dismounting**

Dismounting of hosts has rarely been observed. Karafiat (1959) reported that *Archidispus bembidii* dismounted from beetles if the host was dead or if the mite was disturbed, and Binns (1979) noted that *Scutacaropsis baculitarsus* detached from anesthetized, decapitated flies. On the other hand, Schousboe (1986) was only in one exceptional case able to observe detachment of *S. acarorum* from bumble bees. He reported that apart from this case, the mites never dismounted, even if the host was dead. It is not clear which factors induce dismounting, but most probably the mites detect new habitats by chemical stimuli. “Negative stimuli” like disturbance or even death of the host seem to play a minor role in inducing dismounting. This assumption is supported by the fact that phoretic scutacarid mites can often be encountered on pinned, dried insects and also on animal material stored in ethanol (Ebermann pers. comm., pers. obs.).
Apparently the act of phoresy is risky for the mites because suitable environments cannot always be reached. Indeed, it is not too uncommon to find dead scutacarids on their host which obviously never arrived at their desired destination (Karafiat 1959, Ebermann 1991a).

**Sporothecae**

As mentioned above, presumably all scutacarids are fungivorous. Only species of the subgenus *Sporichneuthes* of the genus *Imparipes* are known to feed on spores, all others suck the content of fungal hyphae (Ebermann 1998). While some species apparently are food generalists, others seem to be rather selective, feeding on only a few or even only on one fungal species (Ebermann *et al.* 2013). Some of the scutacarids with a constricted food spectrum developed a very rare phenomenon: they possess sporothecae. Sporothecae are defined as repositories inside the mites’ body which are used for storage and transport of fungal spores (Suski 1973, Ebermann and Hall 2003), and Jaggersbacher-Baumann and Ebermann (2012a) moreover suggested that these repositories have to be filled actively by the mites. By transporting the spores of their preferred fungal species, the mites can secure food for their offspring: the spores are released and fungal hyphae start to grow as soon as the mites reach suitable habitats. Using this strategy, the mites avoid the risk of not finding their nutritional fungi when colonizing new environments (Ebermann *et al.* 2013).

Presumed sporothecae have been identified in four species belonging to the genera *Heterodispus* and *Imparipes*, and the two genera use different anatomical structures for transporting fungal spores ([Figure 4](#fig4)): The African mite *Heterodispus foveatus* Jaggersbacher-Baumann & Ebermann, 2012, associated with coleoptera and small mammals, possesses characteristic cavities in its posterior sternal plate which frequently are filled with spores and thus are interpreted as sporothecae (Jaggersbacher-Baumann and Ebermann 2012a). *Imparipes apicola*, *I. breganti* Ebermann & Hall, 2004 and *I. haeseleri* Ebermann & Hall, 2003, all three phoretic on sphecids and wild bees, on the other hand use their genital atrium for fungal spore transfer (Ebermann and Hall 2003, 2004). So far it has not been possible to identify the fungal species transported in the sporothecae (Ebermann and Hall 2003, Ebermann *et al.* 2013).

Transport of fungal spores by scutacarids can also happen occasionally as the spores tend to adhere on the mites’ surface (Jaggersbacher-Baumann and Ebermann 2012a), which can

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**Figure 4** Schematic illustration of the sporothecae of a) *Imparipes haeseleri* and b) *Heterodispus foveatus*. Ventral view. Arrows point to the spores inside the sporothecae.
frequently be observed in microscopic slides. Of course, this mode of transport does neither include specialised anatomical structures nor active collection of spores on the part of the mites, so this random occurrence of spores on the mites should not be confused with real sporothecae.

**Scutacarid species and their hosts**

Scutacarid mites occur in associations with other animal taxa because it is beneficial for them. Either the mites find favourable environmental conditions in the nests of their hosts (most likely, these conditions simply mean “availability of appropriate nutritional fungi”), or they mount their hosts in order to take advantage of their dispersal abilities so that they can reach new habitats, or both factors are true.

The following chapter will give an overview on (to my knowledge) all reports of associations between scutacarids and other animal taxa published until May 2017. In total, 414 species and subspecies in 17 genera have been reported from some kind of associations with other animals (reports of species listed as “near” or “cf” have been counted as separate species and are thus included in this number). Most species (n = 162) belonged to the genus *Scutacarus*, followed by *Imparipes* (125) and *Archidispus* (76; Figure 5). In the last published comprehensive summary of the taxonomic richness within the order Trombidiformes by Zhang et al. (2011), the family Scutacaridae is indicated to contain about 800 species in 24 genera, so it seems safe to estimate that approximately the half of all scutacarid species live in some kind of association with other animal taxa.

The following subchapters are divided into the reported host taxa, starting with Arachnida, moving to various taxa within the large group of Hexapoda, then to Aves and finally to Mammalia. Due to clarification reasons, the groups of hosts that are used in the graphs do not represent consistent taxonomic taxa, they rather are groups which combine hosts of different taxonomic levels using their common names (e.g., “ants” only describes members of one family while “mammals” covers the members of one whole class).

![Figure 5](image_url)

*Figure 5* Number of scutacarid species found in associations with other animals, grouped according to their genus.
Anticipatory it can be stated that by far most scutacarid species can be encountered in association with ants (Formicidae) (Figure 6) and that the prevailing types of associations vary between the different host groups (Figure 7). The subchapters give information on the number of associated scutacarid species of the host taxa and, if available, details on the associations and possible biological backgrounds. The included annex is ordered according to the hosts, giving information on the associated scutacarid species, the type of association (inquiline, phoront, or both), the geographic range and occasionally other interesting remarks (for example, other known habitats of the mites, like soil or moss). In another table available in the online supplementary material, the same information is organized the other way round, listing the scutacarid species first and adding the reported host taxa for each species afterwards.

**Arachnida**

Associations between mites and other arachnids in general are rare (Ebermann 2004), thus it is no surprise that scutacarid mites also can only rarely be found in association with other arachnids (Annex I). So far, two *Scutacarus* species have been reported phoretic on spiders, *Araneae*, of the family Nemesiidae from Argentina (Ebermann and Goloboff 2002). Another species, the usually soil inhabiting *Imparipes tocatphi*lus Ebermann & Palacios-Vargas, 1988 from Central and South America, has also been found phoretic on *Ricinulei* (Ebermann and Palacios-Vargas 1988). On spiders and ricinuleids, the scutacarids attach to the soft integument of the legs (Ebermann and Palacios-Vargas 1988, Ebermann and Goloboff 2002).

Even other mites, *Acari*, have been reported as phoresy hosts for scutacarids. *Scutacarus talpae* (Oudemans, 1913) was found by Oudemans (1913) inside of a mole’s nest, and all five encountered individuals were attached to deutonymphs of the mesostigmatid *Haemogamasus ambulans*. In the respective publication, Oudemans expressed his surprise as the scutacarids could neither be found on protonymphs or adults of *H. ambulans* nor on any other gamasid genus, all of which were available in enormous numbers. Other scutacarid species using mites as phoresy host are *S. acarorum* and *S. deserticolus* Mahunka, 1969. Both are common
phoronts on gamasid Parasitellus deutonymphs (mostly P. fucorum), which are in turn phoretic on various bumble bee (Bombus) species (Rack 1964, Chmielewski 1971, Schousboe 1986, Ebermann 1991a, 2004, Schwarz and Huck 1997, Khaustov 2008). On the Parasitellus deutonymphs, the scutacarids cling to setae on body and legs (e.g. Schousboe 1986). The association between S. acarorum/S. deserticolus and Parasitellus sp. is the only example of frequent hyperphoresy in Scutacaridae. Hyperphoresy generally is an uncommon phenomenon that has apart from this example been demonstrated in mesostigmatid mites (Bajerlein and Błoszyk 2003, Szymkowiak et al. 2007) and accidentally in astigmatid hypopi (Athias-Binche 1994). Ebermann (2004) described one exceptional finding of hyper-hyperphoresy from a bumble bee: he found a scutacarid phoretic on a Parasitellus deutonymph, and the scutacarid in turn also had a hypopus of Aneotidae (Astigmata) attached.

**Hexapoda**

**Entognatha**

Only one scutacarid species, Imparipes intentatus Khaustov, 2008, has been reported from Entognatha, all other hexapod hosts belong to Ectognatha. The respective host is a member of the Diplura, genus Campodea (Khaustov 2008; Annex 1). As diplurans occur frequently in soil and don’t have strong dispersal abilities due to their small size, the found association between mite and diplurans may have been by chance. When extracted through Berlese-Tullgren funnels and kept alive in boxes filled with plaster of Paris, some scutacarids appear to be stressed and for short periods of time tend to attach to whatever host available (pers. obs.). In these artificial environments scutacarid individuals have even been observed to “desperately” cling to other conspecifics. Bearing this behaviour in mind, unusual reports of phoresy like that on diplurans should be taken with a grain of salt.

![Figure 7](https://example.com/figure7.png)

**Figure 7** Percentages of differently associated scutacarid species and subspecies according to their different host groups. Types of associations: p, phoretic; i, inquilines; ip, inquilines and phoretic, n.k., not known (not given in literature). The group “insects” comprises Entognatha, Dermaptera, Diptera, Heteroptera, Isoptera and Orthoptera as well as hosts that have not been defined further in literature.
Coleoptera

In the taxon Coleoptera, by far the most scutacarid species (62 spp.) can be detected on ground beetles, Carabidae (Figures 8-9, Annex II). All of the mites associated with Carabidae belong to the genus Archidispus, no other scutacarid genera have been found so far (e.g. Karafiat 1959, Kurosa 1977, 1980, 1989, 2005, Khaustov 2008; for other references see Annex II). Moreover, Archidispus can only rarely be seen on beetles belonging to families other than Carabidae. Only two species, A. armatus and A. bembidii, can apart from Carabidae also be encountered on Heteroceridae, Hydrophilidae and Staphylinidae (Karafiat 1959, Mahunka 1972b, Khaustov 2008), and A. irregularis Katlav & Hajinqanbar, 2016 was found only on Staphylinidae. Generally speaking, different scutacarid genera can be found on other beetle families, but among them, the genus Scutacarus is the most prominent (Figure 10).

In the following, the beetle families reported to be hosts for scutacarids will be discussed. Within the family Carabidae, most associated Archidispus species are rather opportunistic regarding their host choice: the majority of the reported species have been found on different species of one carabid genus, and about the half of the scutacarids occurred on several different carabid genera. The scutacarids have only been reported from imagines, they have never been found on the beetles’ soil living larvae or pupae (Karafiat 1959). On their carabid hosts, the mites can be found on four typical attachment locations: the cervical membrane between head and prothorax, the intersegmental membrane between pro- and mesothorax, between thorax and abdomen, and finally under the beetle’s elytra (e.g. Karafiat 1959, Kurosa 1970, 1972a, Khaustov 2008). Some Archidispus species show no preference for special attachment sites (Kurosa 1984), while others prefer certain regions. For example, A. magnificus preferably attaches on the anterior part of the prothorax of its carabid hosts and A. sugiyamai Kurosa, 1991 on the posterior part of the prothorax (Ebermann et al. 2011). These two species can also simultaneously be found on the same host, each one on its preferred attachment site. It is common to encounter more than one Archidispus species on one host (e.g. Kurosa 2009). Only five Archidispus species found on Carabidae have also been reported from soil samples, and all of them display phoretomorphism (Table 1). The carabid beetles used for phoresy usually

![Figure 8](https://example.com/figure8.png)
occur in moist environments, which are often inhabited by scutacarid species as they favour the growth of fungi. The moist habitats don’t offer stable environmental conditions as they are prone to frequent flooding, and thus the respective scutacarids strongly depend on phoresy in order to escape from flooded regions (Ebermann 1991a).

Additional to Carabidae, scutacarids in moist habitats also use ripicolous Heteroceridae and Hydrophilidae as hosts (Annex III). On these two beetle families, species belonging to the genera Archidispus, Imparipes, Pygmodisus and Scutacarus can be found (Karafiat 1959, Kurosa 1980, Messner 2001, Khaustov 2008, Ebermann et al. 2016). The respective mites have been reported from under the elytra or attached randomly on the beetles’ surface (Karafiat...
Members of **Staphylinidae** also often occur in moist habitats, moreover on dung and on carcasses (Zahradník 1985). Mites belonging to five scutacarid genera have been found phoretic on staphylinid beetles from the Holarctic and from Sudan: *Archidispus armatus*, *A. irregularis*, *Imparipes dispar*, *I. histricinus*, *Lamnacarus ornatus* and 3 *Scutacarus* species (e.g. Karafiat 1959, Ebermann 1991a, Khaustov 2008, Truck 2012, Ebermann et al. 2016; for other references see **Annex III**). Most of these scutacarid species have also been recorded from other habitats like soil, moss, manure or *Fragaria* plants. On their host, the mites can be found rather randomly on different attachment sites like the legs, the lateral abdomen or between caput and prothorax (Karafiat 1959, Ebermann 1991a).

Scutacarids can also be found on beetle families which occur in other than moist habitats which may be suitable for the mites as well: fungus-infested wood, manure, carcasses and different types of decaying material in general.

**Beetle species with an affinity to fungus-infected wood** can be found in the families Curculionidae and **Cupepidae** (**Annex III**). In **Curculionidae**, *Scutacarus scolyti* Mahunka & Moser, 1980 and *S. cf. culmusphilus* Sevastianov, 1975 have been reported from four species of wood borer and bark beetles from Eurasia (Mahunka and Moser 1980, Khaustov 2008, Knapp 2008). The mite occurs in the galleries made by the beetles (Khaustov 2008) and also phoretic on setae on the base of the coxae (Mahunka and Moser 1980). As the galleries made by these beetles are known to contain fungi (e.g. Vega & Blackwell 2005, Okabe 2013), it is probable that the scutacarids feed on them. Moreover, dead wood and microorganisms are available as possible food sources (Okabe 2013). The red palm weevil *Rhynchophorus ferrugineus* is another curculionid beetle which has been reported as host for a not nearer identified species of the genus *Scutacarus* in Egypt (El-Sharabasy 2010). The beetle is an important pest of palms in Asia and Europe which is known to be a host to several mite species (Al-Deeb et al. 2011), but associated scutacarids had never been reported before.

One species of **Cupepidae**, the North American *Tenomerga cinerea* has been given as host of the scutacarid *Imparipes cupes* Delfinado&Baker, 1978 (Delfinado and Baker 1978). Larvae of *T. cinerea* are known to thrive in fungus-infested wood (Hörnschemeyer 2005), which probably is a suitable habitat for the scutacarids as well.

**Scarabaeidae**, which often are coprophilous and as such visit habitats that are commonly used by scutacarid species, have also been reported as phoresy hosts for several scutacarids: *Archidispus sacculiger* (Mahunka, 1968), *Heterodispus near elongatus* (Trägardh, 1904), two *Pygmodispus* species and three *Scutacarus* species have been found phoretic on Scarabaeidae from Brazil, Canada, Chile, Iran, Java and the USA (Paoli 1911, Mahunka 1968a, Norton 1973, Ebermann and Rodrigues 2001, Rodrigues et al. 2001, Ebermann et al. 2003, Loghmani et al. 2014; **Annex III**). Not all of the scarabaeid species used as hosts are dung beetles: imagines of *Osmoderma eremicola* feed on sap and damaged fruits, but the juvenile stages thrive in decaying wood (Norton 1973), and the juveniles of *Bothynus striatellus* are crop pests in South America (SiNAViMo 2015). As attachment sites on the beetles, the underside of the elytra, hairs on the ventral side and the suture between forelegs and head have been reported (Mahunka 1968a, Ebermann and Rodrigues 2001, Ebermann et al. 2003).

Another family of beetles occurring in different types of decaying material is the family **Ptiliidae**. These mycophagous beetles are characterized by very small body sizes (Zahradník 1985), still three different *Scutacarus* species have been reported from one single specimen of Ptiliidae which has not been identified to genus- or species level (Mahunka and Zaki 1992, Truck 2012; **Annex III**). The mites attach to thick hairs on the abdomen or legs of the beetles (Truck 2012).

Members of the family **Tenebrionidae** also are used as hosts by scutacarids (**Annex III**). Beetles of this family are generalists (Zahradník 1985), and thus it is very likely that they often visit habitats that are suitable for scutacarids, too. Two *Heterodispus* species from Ukraine and Africa have been reported phoretic on tenebrionid beetles, whereas the concrete attachment sites are unknown (Khaustov 2008, Jagersbacher-Baumann and Ebermann 2012a).
The last family of Coleoptera which has been reported as host for Scutacaridae is the Pselaphidae. Only one scutacarid species phoretic on Pselaphidae is known to date, namely *Imparipes pselaphidorum* Ebermann, 1988 from individuals of the genus *Centrophthalmus* in Tanzania (Ebermann 1988; Annex III). Many Pselaphidae are known to be myrmecophilous (Zahradník 1985), which could be an explanation for why the scutacarids can be found on them: the mites could be primarily commensals of ants which also can move to the syntopically occurring beetles. However, the pselaphids found to bear *I. pselaphidorum* are not myrmecophilous and thus the reasons for the associations between mites and beetles remain unclear (Ebermann 1988).


**Hymenoptera: bees and wasps**

In addition to beetles, different *Hymenoptera* belonging to the suborder Apocrita are important hosts for Scutacaridae. Apocrita divide into the monophyletic subclade Aculeata (containing ants, bees and wasps) and the artificial, paraphyletic group Terebrantia/“Parasitica”. Members of Terebrantia have only been reported as hosts of Scutacaridae in one case: *Imparipes dispar* has been found phoretic on specimens of Eucoilidae, Proctotrupoidea and Pteromalidae (Ebermann et al. 2016; Annex I). On the other hand, a larger number of scutacarids (35 spp.) is associated with different social, but also with solitary Aculeata, as will be described below.

**Bees**

In the superfamly *Apoidea*, scutacarid mites occur together with Apidae, Andrenidae, Colletidae, Crabronidae, Halictidae and Sphecidae (Annex IV). In fact, Scutacaridae are amongst the most frequent and diverse associates of bees (Eickwort 1994). Most of the associated scutacarids belong to the genera *Imparipes*, followed by *Scutacarus* (Figure 10).

In the Apidae, scutacarid mites play no large role as inquilines of the economically important honey bee *Apis mellifera*; only two species, *Imparipes apicola* and *Scutacarus acarorum*, have been reported from nests of honey bees, and neither of them is a frequent associate (Banks 1914, Schousboe 1986). More scutacarids can be found as common inquilines and phoronts of bumble bees (genus *Bombus*). The scutacarid acarofauna of bumble bees consists of 6 *Scutacarus* species, *Parascutacarus indicus* Baker & Delfinado, 1975 and *Imparipes degenerans* Berlese, 1904 (e.g. Karafiat 1959, Cross and Bohart 1969, Larsson 2007, Jagersbacher-Baumann 2015; for other references see Annex IV). *Imparipes degenerans*, however, has only been reported once from *Bombus* and can normally be found on ants and in their nests and also in rodents’ nests. Among the *Scutacarus* species associated with bumble bees, *S. acarorum* is particularly worth mentioning as it is one of the most common “bumble bee mites” (Chmielewski 1971), as it performs hyperphoresy on phoretic mesostigmatid deutonymphs (e.g. Schousboe 1986) and as it was one of the first mite species to be described in history by Goeze in 1780 (Goeze 1780). On bumble bees, scutacarid mites can be found on the base of the forewings, on the thorax or between thorax and abdomen, and they are most frequent on hibernated queens (e.g. Chmielewski 1971, Schousboe 1986). In the nests, the scutacarids can mostly be found in the outer portions, and they are much less frequent in artificial hives than in natural nests (Chmielewski 1971). As workers emerge constantly in bumble bee nests, the life cycles of most associated mites are expected not to be well synchronized with that of their hosts (Okabe 2013).
Indeed, the developmental cycle of *S. acarorum* takes around 9 days (Jagersbacher-Baumann and Ebermann 2013), being much shorter than that of its host.

In nests of Apidae, flower nectar, pollen, microorganisms and nest debris are present, although microorganisms and nest debris lack in honey bees (Okabe 2013). Dead brood, provisions and parts of the debris can become moldy and then offer suitable food for saprophagous mites like Scutacaridae (Eickwort 1994). As there is not much substrate which can become moldy in the nests of honey bees (Okabe 2013), this may explain the scarceness of associated scutacarids.

Solitary bees belonging to the families *Andrenidae* and *Colletidae* generally have few associated mite genera (Eickwort 1994). However, they serve as hosts for four scutacarid species of the genus *Imparipes* (e.g. Eickwort 1979, Ebermann and Hall 2003, 2004, Ebermann et al. 2013; for other references see *Annex IV*). The two bee families offer different habitat conditions: members of Andrenidae are ground-nesting, while Colletidae nest in dead wood. *Imparipes breganti* and *I. burgeri*, which use bees of both families as hosts, are thus considered to be pronounced generalists (Ebermann and Hall 2004, Ebermann et al. 2013).

*Imparipes apicola* is associated with different species of Andrenidae, but also with *Halictidae*, which are another family of soil-nesting and rather primitive bees that exhibit a great diversity of mite associates (Eickwort 1979, 1994). Eickwort (1979) gives a thorough description of the life history of *I. apicola* inside the cells of a laboratory reared *Lasioglossum* host, showing that, in contrast to species associated with bumble bees (see above), the mite’s life cycle follows that of its host. Halictid bees are also hosts for 15 other *Imparipes* species, moreover for two *Nasutiscutacarus* and two *Scutacarus* species (e.g. Beer and Cross 1960, Delfinado and Baker 1976, Ebermann and Hall 2005; for other references see *Annex IV*). Most of these scutacarids have been found phoretic on the bees, but some have also been reported from their nests. Like in Apidae, nests of Halictidae provide flower nectar, pollen, microorganisms and nest debris as potential food sources for different mites (Okabe 2013). Accordingly, Ordway (1964) reported mites of the genus *Imparipes* from halictid nest cells containing pupae, near or on the fecal deposit, and Eickwort and Eickwort (1971) also found larvae of *I. eickworti* Mahunka in cell contents of its halictid host.

Sphecoid wasps of the families *Crabronidae* and *Sphecidae* have been identified as phoresy hosts for five scutacarids, one *Archidispus* (*A. sphecis* Mahunka, 1977) and four *Imparipes* species (e.g. Kuhlmann 1998, Ebermann and Hall 2003, 2004, Ebermann et al. 2013; for other references see *Annex IV*). Among these mites, only *A. sphecis* (Lang and Mahunka 1977) is exclusively known from sphecids. The reported host species build nests in different substrates like sand, mud, dead wood or stalks. After deposition of the eggs, the nests are supplied with different paralyzed insects or spiders which serve as food for the offspring (Witt 1998). The nests probably are suitable habitats for mites as they contain enough material which could become moldy. However, no scutacarids have been reported from nests so far, all of the reported species were phoretic on the sphecoid wasps. Lang and Mahunka (1977) described the coxal region as favored attachment site on the hosts.

**Wasps**

Associations between *Vespoidea* (exclusive Formicidae!) and Scutacaridae are extremely rare. Species of *Mutilidae* and *Pompilidae* have been found to carry phoretic specimens of *Imparipes burgeri* Ebermann & Jagersbacher-Baumann, 2013 (Ebermann et al. 2013) and *Scutacarus subquadratus* Khaustov & Chydyrov, 2004 (Loghmani et al. 2014). Wasps of these families build their nests in sand, are kleptoparasites of other wasps or parasitoids on halictid bees (Witt 1998). Another scutacarid, *I. haeseleri*, has been reported from a member of *Vespidae* (Ebermann and Hall 2003, Hall and Ebermann 2005). The respective host species, *Symmorphus bifasciatus*, builds its nests in stalks, reed or dead wood (Witt 1998) and animal meat, microorganisms, nest debris and dead larvae are available as food in its nests (Okabe 2013). Finally, Vitzthum (1927) reported random findings of *S. acarorum* on wasps, not without
hypothesizing that these associations may be the rare results of occasional contact between wasps and bumble bees on flowers.

Hymenoptera: ants

The majority of scutacarid mites living in associations with other animals can be found with another family of Vespoidae, the Formicidae, or ants (214 spp.). Most associated scutacarids belong to the genera *Scutacarus* and *Imparipes* (Figures 11, 12; Annex V-VII). A great variety of different mite taxa can be found as guests of ants (e.g. Vitzthum 1919, Campbell et al. 2013), and it is also common to encounter more than one scutacarid species within one single ant nest (e.g. Friedl 2000). Scutacarids are either phoretic on the ants or they live in ant nests, or both. Inside the ants’ nests, nest debris and (in army ants) temporary provisions are available (Okabe 2013), both of which can become moldy and then serve as food sources for scutacarids. On the ants, scutacarids can be found on the thorax, between the coxae, but also on rather exposed parts like the ant’s legs or on the head (e.g. Paoli 1911, Rettenmeyer 1961a, Ebermann 1982, Elbadry et al. 1976).

From not further determined “ants”, 51 scutacarid species have been reported: *Archidispus haarloevi* (Karafiat, 1959), 13 *Imparipes* species, *Pygmodispus calcaratus* Paoli, 1911 and 36 *Scutacarus* species (e.g. Karafiat 1959, Mahunka 1981, 1986, Dobrev 1992; for other references see Annex V). For all other reports of associations between ants and Scutacaridae, at the least the subfamily of the host was given. Most scutacarid species occur together with Formicinae and Myrmicinae (Figure 12; Annex VI, VII).

In the subfamily *Formicinae*, *Archidispus intermissus* (Karafiat, 1959), 28 *Imparipes* species, 2 *Lophodispus* species, 58 *Scutacarus* species and *Thaumatopelvis reticulatus* are present as associates (e.g. Karafiat 1959, Mahunka 1972b, 1977c, Khustov 2008, Ebermann and Krisper 2014; for other references see Annex VI). The scutacarids could be detected in 5 ant genera, and the majority of all mite species (52 species) was present in the genus *Lasius*. Ants of this genus can occur in high population densities (e.g. *L. alienus* or *L. niger*), they frequently are social parasites of other ants and often feed through trophobiosis in symbiosis with aphids (Seifert 1996). Scutacarids can also often be found in associations with zoophagous *Formica* ants, further with the genera *Camponotus* and *Paratrechina*. There are even species

**Figure 11** Number of scutacarid species belonging to different genera associated with ants (Formicidae). “Other genera” combine *Diversipes, Lamnacarus, Lophodispus, Nasutiscutacarus, Parascutacarus, Reuctacarus, Rettenmeyerella, Scutacaropsis, Symbolacrasis* and *Thaumatopelvis*. 

associated with desert ants of the genus *Cataglyphus*, which are highly thermophilic scavengers feeding mostly on dead arthropods (Lenoir *et al.* 2009).

Thirty-four Imparipes species, *Lophodispus irregularis* and 38 Scutacarus species have been reported from the subfamily *Myrmicinae* (*e.g.* Ebermann 1979, 1980a, b, Khaustov 2008, Ebermann and Krisper 2014; for other references see *Annex VII*). The mites have been found in association with ants belonging to 10 genera, and the largest number of mites (25 species) was present in the genus *Myrmica*. The genera accepted as hosts are characterized by different life styles, ranging from harvester ants feeding on seeds (*e.g.* *Messor*) to zoophagous (*e.g.* *Myrmica*) and omnivorous ants (*e.g.* *Solenopsis*). The colony sizes of the hosts also vary, ranging from 40-120 workers in *Stenamma* to some thousand workers in *Aphenogaster* (Seifert 1996).

Scutacarids can also be associated with army ants of the subfamily *Dorylinae* (following the taxonomic classification by Brady *et al.* 2014). These ants are carnivorous, they raid for food in large groups, build extremely large colonies and the whole colonies emigrate periodically (Rettenmeyer *et al.* 2011, Okabe 2013). Colonies of Dorylinae are home to several animals belonging to a variety of taxa, but their most abundant guests are mites (Gotwald 1996, Rettenmeyer *et al.* 2011). Accordingly, Dorylinae also serve as hosts for scutacarids: 39 scutacarid species belonging to seven genera have been reported from five army ant genera (*Annex V*). The respective mites are 4 *Archidispus* species, 24 *Imparipes* species, *Pygmodispus dorylini* Mahunka, 1977, *Rettenmeyerella petropolitana solenifera* Mahunka, 1977, 2 *Scutacaropsis* species, 5 *Scutacarus* species and 2 *Thaumatopelvis* species (Rettenmeyer 1961a, Mahunka 1977a,b, Ebermann 1980b, Berghoff and Franks 2007, Berghoff *et al.* 2009, Rettenmeyer *et al.* 2011). Within ants, Dorylinae display the highest diversity of scutacarids on genus level.

Six scutacarid species (*3 Imparipes, Lophodispus tapinoma* Sobhi & Hajiqanbar, 2017 and 2 *Scutacarus*) were found in association with ants of the subfamily *Dolichoderinae*, either with members of the genus *Tapinoma* or with members of *Liometopum* (Mahunka 1977c, 1982, Khaustov 2008; *Annex V*). *Tapinoma* ants are omnivorous and not sedentary, instead they often

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**Figure 12** Number of scutacarid species belonging to different genera associated with different subfamilies of ants (*Formicidae*).
change the location of their nests, while *Liometopum* ants are sedentary, associated with trees and shrubs and they can also be minor pests in housing areas (Hoey-Chamberlain *et al.* 2013).

Only one scutacarid, *Imparipes malus* Khaustov, 2008, has been reported from *Ponera coarctata* of the subfamily *Ponerinae* (Khaustov 2008; *Annex V*). The concealed life style of this thermophile ant species makes it difficult to sample (Seifert 1996, Wagner 2014), so intensified collections may reveal a higher number of associated scutacarids.

**Other insect taxa**

Different other insect taxa beside Coleoptera and Aculeata also serve as hosts for a variety of Scutacaridae (*Annex I, Figures 6, 7, 13*). There are unique reports of scutacarid species found on earworms (*Dermaptera*) and on bugs (*Heteroptera*), respectively (Trägårdh 1905, Paoli 1911, Khaustov 2008). The mite species reported from earworms is *Imparipes histricus*, which is a pronounced generalist and which has been reported from ants and beetles, from mammals’ nests and from soil (*Table 2*). As will be discussed below, *I. histricus* might in fact be a cryptic species complex. On the other hand, the scutacarid associated with the heteropteran family Reduviidae, *Imparipes nikitensis* Khaustov, 2005, has not been reported from any other host (Khaustov 2008).

Reports of Scutacaridae associated with *Orthoptera* are quite rare (*Annex I*). Two *Heterodispus* species have been found on crickets (Mahunka 1964a, Khaustov 2008), and *Imparipes rectangulatus* Mahunka, 1977 has been reported from grasshoppers (Mahunka 1977a). The latter species is another generalist, occurring also together with South American army ants (e.g. Berghoff *et al.* 2009).

Nine scutacarid species and subspecies can be found phoretic on 12 families of flies (*Diptera*) from the Holarctic and South America (*Annex I*): 2 *Imparipes* species, *Scutacaropsis baculitarsus, Scutacaropsis baculitarsus agaricus*, 3 *Scutacarus* species, *Rettenmeyerella petropolitana* Vitzthum, 1928 and *Rettenmeyerella petropolitana solenifera*. Most of these scutacarids have also been reported from other environments like soil or from other hosts (e.g. Norton and Ide 1974, Binns 1979). On their host, the scutacarids can be found on caput, thorax, abdomen, wings or on the metacoxae (Norton and Ide 1974, Binns 1979, Zaki *et al.* 1987, Ebermann *et al.* 2016).

*Figure 13* Number of scutacarid species belonging to different genera associated with various “insects” (insecta). The group “insects” comprises Entognatha, Dermaptera, Diptera, Heteroptera, Isoptera and Orthoptera as well as hosts that have not been defined further in literature. “Other genera” combine Coronipes, Diversipes, Reductacarus, Rettenmeyerella, Scutacaropsis and Thaumatopelvis.
Table 2 Scutacarid species with a considerable broad host range.

<table>
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<tr>
<th>Scutacarid species</th>
<th>Host taxa</th>
<th>References</th>
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<tr>
<td><em>Heterodispus foveatus</em></td>
<td>Coleoptera (Carabidae), small mammals (rodents)</td>
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<td><em>Rettenmeyerella petropolitana</em> (Vitzthum, 1928)</td>
<td>Ants, diptera</td>
<td>Vitzthum 1928, Mahunka 1977a</td>
</tr>
<tr>
<td><em>Scutacarus deserticolus</em></td>
<td>Acari, bees, small mammals (rodents)</td>
<td>Mahunka 1969a, 1972b, Ebermann 1991a</td>
</tr>
<tr>
<td>Mahunka, 1969</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. eucomus</em> (Berlese, 1908)</td>
<td>Ants, small mammals (rodents)</td>
<td>Mahunka 1970b, Sevastyanov &amp; Uzhevskaya 2003</td>
</tr>
<tr>
<td><em>S. imitans</em></td>
<td>Birds, small mammals (rodents)</td>
<td>Delfinado &amp; Baker 1976</td>
</tr>
<tr>
<td>Delfinado &amp; Baker, 1976</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mahunka, 1965</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. mendax</em></td>
<td>Bees, small mammals (Eulipotyphla)</td>
<td>Kalüz 2001, Jagersbacher-Baumann 2014</td>
</tr>
<tr>
<td>Karafiat, 1959</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sevastianov, 1975</td>
<td></td>
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</tr>
<tr>
<td><em>S. palustris</em></td>
<td>Ants, small mammals (rodents)</td>
<td>Mahunka 1968b, Sevastyanov &amp; Uzhevskaya 2003</td>
</tr>
<tr>
<td>Rack, 1966</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
As has been shown above, a vast number of scutacarids can be found in the nests of social hymenopterans. One could assume that the abundance of scutacarid species in another taxon of social insects, namely termites (Isoptera), should be high as well. After all, fungal cultures and microorganisms are available as food sources in their nests (Okabe 2013). However, a surprisingly low number of scutacarids has been reported in association with termites so far (Annex I). The respective species are Archidispus brevisetus (Mahunka, 1964) from Africa, Coronipes samsinaki (Mahunka, 1966) from China (Mahunka 1966) and C. sperati Khaustov et al., 2016 from South Korea, Gerdalbertia elongata Khaustov, Hugo-Coetzee & Ermilov, 2017 from South Africa, 4 Imparipes species from Africa, Europe and the USA, and Scutacarus mirabilis Mahunka, 1964 also from Africa (Mahunka 1964a, Delfinado and Baker 1976, Khaustov et al. 2016, 2017, Baumann and Ferragut unpubl.). Moreover, not nearer identified Scutacaridae have been reported by Wang et al. (2002) from China.

**Birds, Aves**

Some Scutacaridae have been found in fecal pellets of eagles (Accipitridae) and owls (Strigiformes), in the debris of mutton bird (Procellariidae) nests, on the feathers of “Antarctic birds” and in the nests of other not identified birds (Annex VIII). Strictly speaking, the occurrence of scutacarid mites in birds’ fecal pellets does not indicate any further association between the two animals; the respective mites have still been included in the present review because reports of scutacarids in connection with birds are scarce. The mites reported in association with birds (Figure 14) comprise 7 Scutacarus species, Heterodispus longisetosus (Womersley, 1955), Imparipes obsoletus Rack, 1966 and Pygmodispus abestus Mahunka & Philips, 1978 and unidentified Scutacaridae (Womersley 1955, Delfinado et al. 1976, Delfinado and Baker 1976, 1978, Mahunka and Philips 1978, Philips et al. 1988, Krivolutsky et al. 2004). Curiously, one of the Scutacarus species, S. meansi Delfinado & Baker, 1978, has not only been found in bird’s nests’ debris, but also in dog food (Delfinado and Baker 1978). Another species, S. imitans Delfinado & Baker, 1976, has been reported from bird’s nests, but also from nests of...
shrew and from the coat of grey squirrels (Delfinado and Baker 1976), suggesting that this mite is a pronounced generalist. Apart from the mites from Antarctic birds, all scutacarids associated with birds have been reported from North America.

Mammals, Mammalia

Scutacarids have been reported from several “small mammals” (52 spp.), and in all cases where host species have been nearer identified in literature, they turned out to be soil dwelling and to belong either to the group of Eulipotyphla or Rodentia. Apparently, the nests of these mammals offer a favourable environment for mites (Ebermann 2004). Like in birds, most associated scutacarids belong to the genus Scutacarus (Figure 15). All in all, the following scutacarids have been reported: Diversipes exhamulatus (Michael, 1886), 5 Heterodispus species, 15 Imparipes species, Lophodispus irregularis, Pygmodispus ziczii Mahunka, 1964, 28 Scutacarus species and Reductacarus singularis Mahunka, 1963 (e.g. Mahunka 1967a, 1972b, 1975b, Sosnina and Sevastianov 1975, Sevastyanov and Uzhevskaya 2003; for more references see Annex VIII). Most species occur in the nests of rodents, only 12 Scutacarus species and Reductacarus singularis were found in the nests of Eulipotyphla.

While most scutacarids live inside their mammal hosts’ nests, five species, namely H. foveatus, I. cupes, I. spickai Mahunka, 1977, S. geomyi Mahunka, 1977, S. imitans and S. missourensis Mahunka, 1977, were found phoretic on their hosts (Drummond 1957, Basolo and Funk 1974, Delfinado and Baker 1976, Mahunka 1977d, Spicka 1981, Estébanes-González and Cervantes 2005, Jaggersbacher-Baumann and Ebermann 2012a). Amongst these, only I. cupes has not been reported from the coat of its host, the pocket mouse Chaetodipus spinatus lambi, but from its dorsal skin, where the mite apparently lives in small cavities that appear as scabs (Estébanes-González and Cervantes 2005). This report is extraordinary as it is the only one describing the occurrence of scutacarid mites “inside” its host and not attached to external structures like setae, hairs or feathers.

All of the scutacarids associated with mammals except the African H. foveatus and the Mexican I. cupes have been reported from the Holarctic. Unidentified scutacarids have also been reported from mammal carion (Early and Goff 1986) and scutacarid mites can frequently be found in mammal dung (e.g. Mahunka 1964b, Truck 2012). It would have exceeded the scope of the present review to include all of these dung inhabiting species as, in contrast to...
scutacarids in bird’s faeces, there is a high number of them and as they cannot be regarded as real associates of mammals.

Last but not least, there are even studies in which Scutacaridae have been found in connection with humans. Of course these encounters are no examples of associations and should only be considered as random or accidental, but they still are worth mentioning in this paper: Paik et al. (1992) found not identified Scutacaridae in low numbers in house dust in Seoul, Korea, and Modak (1991) found members of the genera Imparipes and Scutacarus in house dust in West Bengal, India. Modak even described a new species “Imparipes tropicus” from house dust, but as the description is only available in a PhD thesis and has not been published properly, it has to be considered a nomen nudum.

**Genus specific trends**

Some scutacarid genera show clear preferences towards special host taxa, while other genera are evenly distributed amongst a variety of hosts (Figure 16). Strong preferences can be detected in the genera Archidispus, Imparipes and Scutacarus.

The vast majority of all known Archidispus species (85%) occurs phoretic on beetles, and within this taxon predominately on ground beetles (Carabidae). Less than 10% of the known Archidispus species have been reported in association with other hosts- ants, “insects”, bees and termites. The term “insects” has been adopted from the original literature and indicates that the hosts had not been identified in detail. “Insects” might therefore also include beetles, meaning that the number of Archidispus associated with Coleoptera may even be higher than given here. There are no reports of Archidispus in association with birds or mammals.

Both Imparipes and Scutacarus clearly prefer ants as hosts: 63% of all known Imparipes and 58% of all known Scutacarus species have been found on ants or in ant nests. Both genera have also been reported from associations with beetles, bees, termites, other insects, small mammals and birds. Within these other host taxa, most species of both genera can be found on mammals and bees (or in their nests), with Imparipes showing a trend towards preferring bees and Scutacarus preferring mammals as host. Scutacarus is, moreover, the only scutacarid genus occurring in associations with other acari.
In the genus *Heterodispus*, no comparable clear trend towards host preference is recognizable. However, most species of this genus have been reported as inquilines of small mammals (42%), 25% were found on beetles and “insects”, respectively, and less than 10% as inquilines of birds.

*Pygmodispus* can be found on ants, beetles, other insects, small mammals and birds, and there is a tendency towards “insects” as hosts since most species (63%) were found phoretic on this taxon.

The genera *Diversipes, Lamnacarus, Lophodispus, Nasutiscutacarus, Parascutacarus, Reductacarus, Rettenmeyerella, Scutacaropsis, Symbolacrasis* and *Thaumatopelvis* are poor in species, so it does not make much sense to talk about “trends” regarding their host taxa. However, some of these genera have been reported from diverse hosts: *Diversipes* (3 species) can be found together with beetles, bees and small mammals; *Reductacarus* (2 species) with “insects” and mammals; *Rettenmeyerella* (2 subspecies) with ants and diptera; and finally *Thaumatopelvis* (6 species) with beetles, ants and other “insects”. The other genera apparently

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**Figure 16** Percentage distribution of scutacarid genera along different host taxa. “Other genera” combine *Diversipes, Lamnacarus, Lophodispus, Nasutiscutacarus, Parascutacarus, Reductacarus, Rettenmeyerella, Scutacaropsis, Symbolacrasis* and *Thaumatopelvis*. 
are restricted to one host taxon: *Lamnacarus* (2 species) and *Symbolacrasis* (3 species) have been reported from beetles, *Nasutiscutacarus* (2 species) and *Parascutacarus* (1 species) from bees, and *Lophodispus* (2 species) and *Scutacaropsis* (2 species) from ants.

**Generalists and specialists**

In most of cases, the host range of single scutacarid species apparently is rather narrow. One species usually uses hosts belonging to one genus or family, and several species have been reported from only one host species (Annex). A similar trend can also be recognized in other phoretic mite taxa. For example, when analyzing mites associated with bees, Eickwort (1994) reported that few mite species can be found on only one host species, but that there also few occurring on hosts belonging to more than one subfamily; the majority of mite species are in association with many congeneric host species which are available in the range of the mite.

Examples for scutacarids that have been reported only from one host species are *Imparipes adleri* Delfinado & Baker, 1976 found on the termite *Reticulitermes virginicus* (Delfinado and Baker 1976), *Pygmodispus zicsii* from the rodent *Cricetulus migratorius* (Sevastyanov and Uzhevskaya 2003) or *Scutacarus sabinaesimilis* Khaustov & Chydyrov, 2004 from the ant *Tapinoma simrothy* (Khaustov 2008). However, Scutacaridae in general are weakly studied and several reports of phoretic scutacarids are random findings. Comprehensive or more focused studies on the mites’ hosts like the one by Ebermann et al. (2016) on *I. dispers* might thus reveal more host species.

Some scutacarid species, however, already seem to be pronounced generalists and can be found on a variety of hosts belonging to very different taxa (Table 2). For most of these host taxa, one important ecological similarity can be encountered: a lifestyle strongly connected to the substrate “soil”. Because of this shared habitat, it probably is rather easy for mites with a generalist life style to switch between different hosts. For other host taxa, like flies and ants, it is more difficult to find clear points of contact between them and thus to explain the occurrence of a mite species on both groups.

While some of the presumed generalists have been investigated thoroughly and thus their species status is quite certain (e.g. Jagersbacher-Baumann and Ebermann 2012a, Ebermann et al. 2016), the status of other generalists is questionable. As will be discussed below, the respective species could have been misidentified or might be complexes of cryptic species.

**Discussion and future perspectives**

The present work shows that most animal taxa that are accepted as host by scutacarid mites have a strong connection to the habitat “soil”: either they are highly mobile, epigaeic species, or they are endogaecic species building nests in the ground. As Scutacaridae are also soil inhabiting mites, it seems probable that associations between them and their host evolved through the shared habitat. The genus specific trends towards different taxa also indicate that the associations between scutacarids and their hosts evolved independently several times within the family, and most probably also within the genera.

Exceptions from typical soil living hosts are bark beetles and some Apoidea and Vespoida that thrive in dead wood, reeds and stall; moreover not ground dwelling birds which can harbour scutacarids in their nests. These hosts, however, still offer favourable conditions in form of mouldy debris in their dwellings which contains the mites’ nutritional fungi.

Based on the compiled information on scutacarids and their hosts given in the present review, their associations can be grouped into three categories with typical ecological characteristics:

1. Phoresy only

Host within this group have high dispersal abilities and are only used for phoresy. They can transport the scutacarids to new, suitable habitats, but they themselves do not provide theses respective habitats (that is, they do not build nests that offer favourable conditions for the
mites). Typical for this group are epigaeic, fast running Carabidae and several other beetles like Staphylinidae or Hydrophilidae, moreover flying insects like Orthoptera and Diptera.

2. Shared habitat only
This group includes soil-dwelling hosts whose nests have been invaded randomly by the scutacarid mites through the surrounding soil (as described by Okabe 2013). The mites live in the dwellings of their hosts as facultative commensals, or, if the association is already more evolved, as obligate inquilines. In this category, hosts are not used for dispersal. This type of association is not very common; typical hosts are mammals and ant species with large and temporarily stable nests, like some members of the genus Crematogaster.

3. Shared habitat and phoresy
In this category, the hosts build nests which are more or less temporary. The scutacarids live in the hosts’ nest as obligatory commensals and when the time is right they use their hosts for phoresy in order to reach new habitats, that is, new nests. Examples for hosts in this group are ant species with fissioning colonies, bumble bees with annual colonies or wild bees which build single brood cells. In fact, the majority of associations between scutacarid mites and their hosts belong to this category.

Future perspectives

Behavioural aspects
Although many associations between various species of Scutacaridae and other animals have been reported, most times also including information about the type of association (inquilinism, phoresy, or both), few details are known about the behaviour of the mites and the interactions with their hosts. At has been mentioned in the introduction, the mechanisms of host finding, host identification, host switch and identification of suitable habitats are only speculative today and should be subject of future studies. Behavioural experiments which could shed a light on this issue can, however, be rather complicated because of the mites’ extremely small size which makes them more difficult to handle.

The cohabitation of mites and their hosts also raises questions: What fungi exactly do the mites feed on in the shared habitat, are they food specialists or generalists? The nutritional fungal species have only been identified for very few scutacarid species (Jagersbacher-Baumann and Ebermann 2013). Have the scutacarids any influence, positive or negative, on their hosts? Most likely, the tiny mites do not bother or harm their hosts in any way. A strong support for this assumption is the fact that hosts usually do not remove their mites (Eickwort 1994). It is possible that Scutacaridae even have a positive effect on their hosts as they could play a sanitary role by feeding on potentially harmful fungi. Such sanitary roles have been hypothesized for other mite taxa before (Okabe 2013), but so far only one study provides statistically supported evidence for it: Biani et al. (2009) observed significant correlations between the presence of Laelaspeoides mites (Mesostigmata) in a bee nest, the absence of fungi in brood cells and a decrease in bee mortality. Studies on scutacarids about this topic are still lacking to date. Preliminary observations revealed that scutacarid mites can consume considerable amounts of fungal hyphal in laboratory cultures (Baumann unpublished), so a sanitary effect indeed seems probable.

Cryptic species complexes?
In scutacarid species with a broad host spectrum and/or a wide geographical distribution, doubts about the status of the respective species should arise for two reasons, as has already been discussed in Ebermann et al. (2016).

(1) The frequent occurrence of a species on certain hosts tempts to neglect a proper identification. For example, S. acarorum is widely distributed and is also the most common scutacarid associated with bumble bees. Comparisons between presumed S. acarorum individuals from spatially distinct populations (European localities and New York) confirmed
their conspecificity even after thorough morphometric analyses (Jagersbacher-Baumann 2015). Because of its abundance, apparently all scutacarids encountered on bumble bees often are being identified as *S. acarorum* without any closer inspection. However, there are at least three other morphologically similar scutacarid species associated with bumble bees: *S. deserticolus*, *S. mendax* and *S. occultatus* Sevastianov, 1975. They all belong to the *acarorum* species-complex as they share a very similar phenotype and can also be encountered syntopically in the nests of large bumble bee species (Jagersbacher-Baumann 2014). Re-inspections of presumed *S. acarorum* individuals thus already revealed incorrect classifications: for example, specimens of “*S. acarorum*” from Hamburg, Germany, were identified as *S. deserticolus* (Ebermann 1991a), and “*S. acarorum*” reported from bumble bees in Argentina turned out to be *S. mendax* or a new species close to *S. mendax* (Revainera et al. 2014 and pers. comm.). A not nearer identified scutacarid from Brazilian bumble bees (Guerra et al. 2012) also turned out to be a variation of *S. mendax* (Baumann unpublished).

(2) Thorough morphological and molecular genetic analyses of scutacarids will most likely reveal the existence of several “cryptic” species. The term cryptic species describes species which are impossible or extremely difficult to distinguish by traditional (morphological) means, and due to advanced techniques, many of them have been described in the recent years in mites (Knee et al. 2012, Skoracka et al. 2015). Although it had been stated before that host-race formation of mites might be a main driving force for cryptic speciation, this hypothesis could not be supported by Skoracka et al. (2015). They showed that not only strong host relationships can induce speciation, but also abiotic or other host-independent environmental factors can do so. An example for a cryptic species complex could be present in the scutacarid *I. histricinus*, which apparently is one of the most frequent guests of ants (Annex V-VII; Karafiat 1959, Okabe 2013). Closer inspections of the mites identified as *I. histricinus* might reveal the existence of several new species with a similar phenotype. In fact, there are already several reports of scutacarids only being similar to *I. histricinus*: for example, Mahunka (1967b, 1970b) reported *I. cf. histricinus* from ants of the genus *Formica*. The respective specimens have not yet been described as separate species.

Additional, all other scutacarid species with a broad host spectrum (Table 2) or species with a wide geographic distribution also could in reality be complexes of cryptic species.

**Phoretomorphism**

The factors determining the morphs in dimorph/phoretomorph scutacarid genera like *Archidisparus* or *Scutacarus* are another point which needs further clarification. Ebermann (1991a) already showed that morph determination might happen in the larval stage and might be induced by the quality and/or quantity of available food, but detailed and statistically supported studies are still pending.

**Scutacarid fauna**

Last but not least, the knowledge of the scutacarid fauna in different countries is very fragmentary, depending on the individual interests of different researchers and made difficult by the generally low abundance and small size of the scutacarids. While some countries like Austria, Hungary, Iran or Russia have been and/or are still investigated intensely by researchers like Ebermann, Hajiqanbar, Khaustov, Loghmani and Mahunka, others, like Spain or Portugal (Ferragut 2015) are practically “terra incognita” when it comes to Scutacaridae. From other countries, soil living scutacarids have been reported, but few or no associations with other animals are known yet. For example, although several scutacarid mites are known from Australia (e.g. Mahunka 1967c, 1974d), only three species have been reported from associations with other animals (Womersley 1955, Mahunka 1975c, Seastedt et al. 1986). Investigating Scutacaridae from new geographical areas as well as closer looks on other possible host taxa will most likely bring more associated/phoretic scutacarid species to light, several of which might be new to science.
Because of their size, scutacarids may often simply be overlooked, and moreover, they can easily be mistaken for astigmatid deutonymphs (hypopi) by non-specialists when they are attached to their hosts. With the present review, the awareness of Scutacaridae and their manifold associations with other animals will hopefully rise.

Acknowledgements

I am forever indebted to my “Doktorvater” (doctoral supervisor) Ernst Ebermann for introducing me to the fascinating family Scutacaridae, for passing on his invaluable collection of mites and literature to me and for still supporting me even after his retirement. “Muito obrigada” to Carlos Flechtmann for sharing his information of associations between mites and other arthropods with me.

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ANNEX: LIST OF SCUTACARID SPECIES ASSOCIATED WITH DIFFERENT HOSTS

I. Scutacarid species associated with Arachnida, Entognatha and Ectognatha (excl. Coleoptera and Aculeata)

II. Scutacarid species associated with Carabidae (Hexapoda, Ectognatha, Coleoptera)

III. Scutacarid species associated with Coleoptera excl. Carabidae (Hexapoda, Ectognatha)

IV. Scutacarid species associated with Apoidea and Vespoidae excl. Formicidae (Hexapoda, Ectognatha, Aculeata)

V. Scutacarid species associated with Formicidae excl. Formicinae and Myrmicinae (Hexapoda, Ectognatha, Aculeata, Vespoidae)

VI. Scutacarid species associated with Formicinae (Hexapoda, Ectognatha, Aculeata, Vespoidae)

VII. Scutacarid species associated with Myrmicinae (Hexapoda, Ectognatha, Aculeata, Formicidae)

VIII. Scutacarid species associated with Aves and Mammalia

The following information will be given for each host in telegraphic style: associated scutacarid species; distribution area; type of association (i = inquiline, ip = inquiline and phoretic, nk = not known, p = phoretic); references and remarks (if available)

I. SCUTACARID SPECIES ASSOCIATED WITH ARACHNIDA, ENTOGNATHA AND ECTOGNATHA (EXCL. COLEOPTERA AND ACULEATA)

Arachnida

Acari

Haemogamasidae: Haemogamasus ambulans
- Scutacarus talpae (Oudemans, 1913); Netherlands; p; Oudemans 1913; in nest of Talpa europea

Parasitidae: Parasitellus fucorum
- Scutacarus acarorum (Goethe, 1780); Holarctic; p; Rack 1964, Chmielewski 1971, Schousboue 1986, Schwarz & Hück 1997, Khausov 2008, Baumann unpubl.; on Bombus spp. (→ hyperphoresy!) or in nests of Bombus spp.
- Scutacarus deserticolus Mahunka, 1969; Austria; p; Ebermann 1991a; on Bombus spp. (→ hyperphoresy!) or in nests of Bombus spp.

Aranaea

Nemesiidae: Stenoteromma igna, S. platense, S. uruguay
- Scutacarus adgregatus Ebermann & Goloboff, 2002; Argentina; p; Ebermann & Goloboff 2002
- Scutacarus araneophilus Ebermann & Goloboff, 2002; Argentina; p; Ebermann & Goloboff 2002

Ricinulei

Ricinoididae: Cryptocellus boneti
- Imparipes (Imparipes) tocatlphilus Ebermann & Palacios-Vargas, 1988; Brazil, Mexico; p; Ebermann & Palacios-Vargas 1988; also in soil, guano from caves

Hexapoda: Entognatha

Diplura

Campodeidae: Campodea sp.
- Imparipes (Imparipes) intentatus Khausov, 2008; Ukraine; p; Khausov 2008

Hexapoda: Ectognatha

Dermaptera

Forficulidae
- Imparipes (Imparipes) hirricinus Berlese, 1903; Italy, Sudan; p; Trägårdh 1905, Paoli 1911; also in soil, moss; is Imparipes forficulae sensu Trägårdh.
Diptera

Anisopodidae, Ceratopogonidae, Chironomidae, Conopidae, Dolichopodidae, Mycetophilidae, Psychodidae, Scatopsidae

*Imparipes (Sporichneuthes) dispar* Rack, 1964; Austria; p; Ebermann *et al.* 2016

Muscidae: *Musca domestica*

*Scutacarus* sp.; India; p; Roy *et al.* 2016

Phoridae: *Aphiochaeta enderleini*

*Rettenmeyerella petropolitana* (Vitzthum, 1928); Brazil; p; Vitzthum 1928

Phoridae: *Megaselia dakotensis*

*Scutacaropsis bacillurars agaricus* (Norton & Ide, 1974); USA (Delaware, Pennsylavania); p; Norton & Ide 1974; also in mushroom-bedding compost

Phoridae: *Megaselia halterata*

*Scutacaropsis bacillurars* (Mahunka, 1968); Chile, Europe; p; Binns 1979; also in debris

Phoridae

*Rettenmeyerella petropolitana solenifera* Mahunka, 1977; Costa Rica; p; Mahunka 1977a; Phoridae associated with *Éciton hamatum*

*Scutacarus australiensis* Mahunka, 1967; Australia; p; Greenslade & Clift 2004; also in compost

Sciariidae

*Imparipes (Sporichneuthes) dispar* Rack, 1964; Austria; p; Ebermann *et al.* 2016

*Scutacarus australiensis* Mahunka, 1967; Australia; p; Greenslade & Clift 2004; also in compost

Sphaeroceridae: *Leptocera nigra*

*Scutacarus longitarsus* (Berlese, 1905); cosmopolitic; p; Zaki *et al.* 1987, Khaustov 2008; also in banks of rivers and lakes

Sphaeroceridae: *Leptocera fontinalis*

*Scutacaropsis bacillator agaricus* (Norton & Ide, 1974); USA (Delaware, Pennsylavania); p; Norton & Ide 1974; also in mushroom-bedding compost

Phoridae

*Rettenmeyerella petropolitana solenifera* Mahunka, 1977; Costa Rica; p; Mahunka 1977a; Phoridae associated with *Éciton hamatum*

*Scutacarus australiensis* Mahunka, 1967; Australia; p; Greenslade & Clift 2004; also in compost

Sphaeroceridae

*Imparipes (Sporichneuthes) dispar* Rack, 1964; Austria; p; Ebermann *et al.* 2016

*Scutacarus australiensis* Mahunka, 1967; Australia; p; Greenslade & Clift 2004; also in compost

Sphaeroceridae

*Scutacaropsis bacillator agaricus* (Norton & Ide, 1974); USA (Delaware, Pennsylavania); p; Norton & Ide 1974; also in mushroom-bedding compost

Heteroptera

Reduviidae: *Pasira mediterranea*

*Imparipes (Imparipes) nikitensis* Khaustov, 2005; Crimea; p; Khaustov 2008

Hymenoptera: Terebrantia/Parasitica

Eucolliidae, Proctotrupoidea, Pteromalidae

*Imparipes (Sporichneuthes) dispar* Rack, 1964; Austria; p; Ebermann *et al.* 2016

Isoptera

Rhinotermitidae: *Coptotermes formosanus*

*Coronipes samsinaki* (Mahunka, 1966); China; i; Mahunka 1966

“Scutacaridae”; China; ip; Wang *et al.* 2002

Rhinotermitidae: *Reticulitermes flavipes*

“Scutacaridae”; China; ip; Wang *et al.* 2002

Rhinotermitidae: *Reticulitermes speratus kyushuensis*

*Coronipes sperati* Khaustov *et al.* 2016; South Korea; p; Khaustov *et al.* 2016

Rhinotermitidae: *Reticulitermes virginicus*

*Imparipes (Imparipes) adleri* Delfinado & Baker, 1976; USA; i; Delfinado & Baker 1976

Rhinotermitidae: *Reticulitermes* sp.

*Imparipes (Imparipes) cf. adleri* Delfinado & Baker, 1976; Spain; ip; Baumann & Faggart unpubl.

Termitidae: *Odontotermes nolaiensis*

*Archidispus brevisetus* (Mahunka, 1964); Angola; i; Mahunka 1964a

Termitidae: *Pericapritermes spp.*

*Imparipes (Imparipes) termiophilus* Silvestri, 1918; Western Africa; n.k.; Khaustov *et al.* 2016

Termitidae: *Pseudacanthotermes spiniger*

*Imparipes (Imparipes) angolensis* Mahunka, 1964; Angola; p; Mahunka 1964a

*Scutacaropsis mirabilis* Mahunka, 1964; Angola; p; Mahunka 1964a

Termitidae: *Trinervitermes trinervoides*

*Gerdaalbertia elongata* Khaustov, Hugo-Coetze & Ermilov, 2017; South Africa; ip; Khaustov *et al.* 2017
Orthoptera
Caelifera

Imparipes (Imparipes) rectangulatus Mahunka, 1977; Costa Rica, Ecuador, USA (Kansas); p; Mahunka 1977a

Gryllidae: Brachytrupes membranaceus
Heterodispus pilosus Mahunka, 1964; Angola; p; Mahunka 1964a

Gryllotalpidae: Gryllotalpa gryllotalpa
Heterodispus severus Khaustov, 2008; Ukraine; p; Khaustov 2008

“Insecta” (not further classified in literature)

Archidispus certus Mahunka, 1974; Ghana; p; Mahunka 1974b
Archidispus magyari Mahunka, 1974; Ghana; p; Mahunka 1974b
Archidispus teleki Mahunka, 1974; Ghana; p; Mahunka 1974b
Diversipes pygmodispoides Mahunka, 1973; Tanganyika; p?, Mahunka 1973a; found in soil traps together with insects
Heterodispus (Teherodispus) konrathi Mahunka, 1974; Ghana; p; Mahunka 1974b
Pygmodispus (Allodispus) angulosus Mahunka, 1979; South Africa; p; Mahunka 1979
Pygmodispus (Allodispus) brachiosus Paoli, 1911; Tanganyika; p?, Mahunka 1973a; found in soil traps together with insects
Pygmodispus (Allodispus) pseudocoprophilus Mahunka, 1979; Ghana; p; Mahunka 1979
Reductacarus africanus Mahunka, 1975; Ghana; p; Mahunka 1975a
Scutacarus appropinquatus Mahunka, 1979; Tanzania; p; Mahunka 1979
Scutacarus endroedi Mahunka, 1979; South Africa; p; Mahunka 1979
Scutacarus ghanensis Mahunka, 1974; Ghana; p; Mahunka 1974a
Scutacarus parapelvus Mahunka, 1974; Ghana; p; Mahunka 1974a
Scutacarus perlatus Mahunka, 1974; Ghana; p; Mahunka 1974a
Scutacarus soosi Mahunka, 1974; Nigeria; p; Mahunka 1974a
Scutacarus undulomarginatus Mahunka, 1979; Tanzania; p; Mahunka 1979
Thaumatopelvis gracilis Mahunka, 1974; Ghana; p; Mahunka 1974a

II. SCUTACARID SPECIES ASSOCIATED WITH CARABIDAE (HEXAPODA, ECTOGNATHA, COLEOPTERA)

Brachyninae
Brachinus stenoderus

Archidispus riparius Kurosa, 1989; Japan; p; Kurosa 1989

Brosicinae
Broscus cephalotes

Archidispus carabidiophilus Sevastianov, 1974; Crimea, Russia, Ukraine; p; Khaustov 2008
Crasedonotus tibialis

Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983

Carabinae
Carabus opacus

Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983

Elaphrinae

Elaphrus spp.

Archidispus bembidii (Karafiat, 1959); Belgium, Germany, Japan; p; Karafiat 1959, Kurosa 1980, Fain et al. 1995
Harpalinae

**Acupalpus** spp.

Archidispus acupalpi Kurosa, 2009; Japan; p; Kurosa 2009

Archidispus bembidii (Karafiat, 1959); Germany, Iran, Japan; p; Karafiat 1959, Kurosa 1980, Katlav et al. 2015

Archidispus conspicuus Kurosa, 1978; Japan; p; Kurosa 1978, 1980

Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus f oliatus (Kurosa, 1978); Japan; p; Kurosa 1978, 1980

Archidispus insolitus (Kurosa, 1974); Japan; p; Kurosa 1974, 1977, 1980

Archidispus longicaudatus (Kurosa, 1978); Japan; p; Kurosa 1978, 1980

Archidispus masatakai Kurosa, 2003; Japan; p; Kurosa 2003

Archidispus minor (Karafiat, 1959); Germany; p; Karafiat 1959

Archidispus ohtanii Kurosa, 1989; Japan; p; Kurosa 1989


Archidispus triangularis (Kurosa, 1974); Japan; p; Kurosa 1974, 1977, 1980

Archidispus yanoi Kurosa, 1984; Japan; p; Kurosa 1984

Anisodactylus** spp.

Archidispus amarae (Kurosa, 1970); Austria, Japan, Moldavia, Ukraine; p; Kurosa 1970, 1972b, 1977, 1980, Khaustov 2008

Archidispus bembidii (Karafiat, 1959); Germany, Japan; p; Karafiat 1959, Kurosa 1980

Archidispus chujoi Kurosa, 2005; Japan; p; Kurosa 2005

Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus minor (Karafiat, 1959); Germany; p; Karafiat 1959

Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983

Harpalus** spp.

Archidispus amarae (Kurosa, 1970); Austria, Japan, Moldavia, Ukraine; p; Khaustov 2008

Archidispus carabidophilus Sevastianov, 1974; Russia, Ukraine; p; Khaustov 2008

Archidispus chujoi Kurosa, 2005; Japan; p; Kurosa 2005

Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus curtonoti (Kurosa, 1972); Japan; p; Kurosa 1980, 1977

Archidispus longicaudatus (Kurosa, 1978); Japan; p; Kurosa 1980

Archidispus minor (Karafiat, 1959); Germany, Hungary; p; Karafiat 1959, Mahunka 1972b

Archidispus ophoni (Kurosa, 1972); Japan; p; Kurosa 1980, 1977

Archidispus sellnicki (Mahunka, 1964); Hungary, Moldavia, Russia, Ukraine; p; Khaustov 2008

Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983

Archidispus tauricus Khaustov, 2002; Crimea; p; Khaustov 2002, 2008

Loxoncus** spp. (syn., Anoplogenius)

Archidispus acupalpi Kurosa, 2009; Japan; p; Kurosa 2009

Archidispus anoplogenii (Kurosa, 1974); Japan; p; Kurosa 1974, 1977, 1980

Archidispus bembidii (Karafiat, 1959); Japan; p; Kurosa 1980

Archidispus chujoi Kurosa, 2005; Japan; p; Kurosa 2005

Archidispus conspicuus Kurosa, 1978; Japan; p; Kurosa 1978, 1980

Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus foliatus (Kurosa, 1978); Japan; p; Kurosa 1978, 1980

Archidispus fusiformis Kurosa, 1976; Japan; p; Kurosa 1976, 1977

Archidispus insolitus (Kurosa, 1974); Japan; p; Kurosa 1970, 1974, 1980

Archidispus longicaudatus (Kurosa, 1978); Japan; p; Kurosa 1978, 1980

Archidispus masatakai Kurosa, 2003; Japan; p; Kurosa 2003

Archidispus ohtanii Kurosa, 1989; Japan; p; Kurosa 1989

Archidispus okumurai Kurosa, 1983; Japan; p; Kurosa 1983

Archidispus papillosus Kurosa, 1978; Japan; p; Kurosa 1978
Archidispus proximus Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus pseudomega Kurosa, 1984; Japan; p; Kurosa 1984
Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983
Archidispus triangularis (Kurosa, 1974); Japan; p, Kurosa 1974, 1977, 1980

Ophonus spp.
Archidispus ophoni (Kurosa, 1972); Japan; p; Kurosa 1972b

Oxycentrus argutoroides
Archidispus similis Kurosa, 1989; Japan; p, Kurosa 1989

Stenolophus spp.
Archidispus acupalpi Kurosa, 2009; Japan; p; Kurosa 2009
Archidispus americanus Khaustov & Husband, 2004; USA (Arkansas); p, Khaustov & Husband 2004
Archidispus anoplogenii (Kurosa, 1974); Japan; p; Kurosa 1974
Archidispus arakawanus Kurosa, 1990; Japan; p; Kurosa 1990
Archidispus bembidii (Karafiat, 1959); Germany, Hungary; p; Karafiat 1959, Mahunka 1972b, Kurosa 1980
Archidispus chujoi Kurosa, 1965; Japan; p; Kurosa 1965
Archidispus insolitus (Kurosa, 1974); Japan; p; Kurosa 1974, 1977, 1980
Archidispus iriomotensis Kurosa, 1990; Japan; p, Kurosa 1990
Archidispus kazuyoshikurosai Khaustov, 2004; Moldavia, Ukraine; p; Khaustov 2004
Archidispus longicaudatus (Kurosa, 1978); Japan; p; Kurosa 1978
Archidispus longisolenidiatus Khaustov, 2008; Ukraine; p; Khaustov 2008
Archidispus masatakai Kurosa, 2003; Japan; p; Kurosa 2003
Archidispus minor (Karafiat, 1959); Germany, Hungary; p; Karafiat 1959
Archidispus missouriensis Khaustov & Husband, 2004; USA (Missouri); p; Khaustov & Husband 2004
Archidispus nickelli (Mahunka, 1969); USA (Kansas); p, Mahunka 1969c
Archidispus ocellatus Khaustov & Husband, 2004; USA (Missouri); p; Khaustov & Husband 2004
Archidispus papillosus Kurosa, 1978; Japan; p; Kurosa 1978
Archidispus pseudomega Kurosa, 1984; Japan; p; Kurosa 1984
Archidispus similis (Kurosa, 1974); Japan; p; Kurosa 1974, 1977, 1980
Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983

Trichotichnus spp.
Archidispus jezoensis Kurosa, 1983; Japan; p; Kurosa 1983
Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983
Licininae

*Chlaenius* spp.
- *Archidispus conciliatus* Khaustov, 2008; Crimea; p; Khaustov 2008
- *Archidispus crassiradix* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus ohtani* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus proximus* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus riparius* Kurosa, 1989; Japan; p; Kurosa 1989

*Lachnocrepis* spp.
- *Archidispus crassiradix* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus proximus* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus similis* Kurosa, 1989; Japan; p; Kurosa 1989

Oodes spp.
- *Archidispus proximus* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus similis* Kurosa, 1989; Japan; p; Kurosa 1989

Nebrinae

*Nebria* spp.
- *Archidispus diploei* Kurosa, 1991; Japan, Russia (far east); p; Kurosa 1991, Khaustov 2008

Omophroninae

*Omophon aequalis aequalis*
- *Archidispus riparius* Kurosa, 1989; Japan; p, Kurosa 1989

Platyninae

*Agonum* spp.
- *Archidispus bembidi* (Karafiat, 1959); Belgium, Germany, Hungary, Japan; p, Karafiat 1959, Mahunka 1972b, Kurosa 1980, Fain *et al.* 1995
- *Archidispus magnificus* (Karafiat, 1959); Austria, France, Germany, Hungary, Russia, Ukraine; p; Karafiat 1959, Mahunka 1972b, Ebermann 1991b, Khaustov 2008, also in soil
- *Archidispus minor* (Karafiat, 1959); Germany, Hungary; p; Karafiat 1959, Mahunka 1972b

*Calathus* sp.
- *Archidispus minor* (Karafiat, 1959); Germany; p; Karafiat 1959

*Colpodes japonicus, Platynus* spp.
- *Archidispus chujoi* Kurosa, 2005; Japan; p; Kurosa 2005
- *Archidispus crassiradix* Kurosa, 1989; Japan; p; Kurosa 1989

*Synuchus arcaucicollis*
- *Archidispus similis* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus subintermissus* Kurosa, 1983; Japan; p; Kurosa 1983

Pterostichinae

*Amara* spp.
- *Archidispus carabidophilus* Sevastianov, 1974; Russia, Ukraine, p; Khaustov 2008
- *Archidispus celiae* (Kurosa, 1972); Japan; p; Kurosa 1972b, 1977, 1980
- *Archidispus crassiradix* Kurosa, 1989; Japan; p; Kurosa 1989
- *Archidispus curtonoti* (Kurosa, 1972); Japan; p; Kurosa 1972b, 1977, 1980
- *Archidispus minor* (Karafiat, 1959); Germany, Hungary, Iran; p; Karafiat 1959, Mahunka 1972b, Loghmami *et al.* 2014
- *Archidispus ophoni* (Kurosa, 1972); Japan, Moldavia; p; Khaustov 2008
- *Archidispus riparius* Kurosa, 1989; Japan; p, Kurosa 1989
- *Archidispus sellnicki* (Mahunka, 1964); Hungary, Moldavia, Russia, Ukraine; p; Khaustov 2008
- *Archidispus subintermissus* Kurosa, 1983; Japan; p; Kurosa 1983
Archidispus tauricus Khaustov, 2002; Ukraine; p; Khaustov 2002, 2008

Chlaeminus annamensis
Archidispus chujoi Kurosa, 2005; Japan; p; Kurosa 2005

Lesticus magnus
Archidispus ohtanii Kurosa, 1989; Japan; p, Kurosa 1989
Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989

Poecilus spp.
Archidispus carabidophilus Sevastianov, 1974; Russia, Ukraine; p; Khaustov 2008
Archidispus minor (Karafiat, 1959); Germany; p; Karafiat 1959
Archidispus tauricus Khaustov, 2002; Ukraine; p; Khaustov 2002, 2008

Pterostichus spp.
Archidispus belorussicus Khaustov, 2002; Belarus; p; Khaustov 2002, 2008
Archidispus bembidii (Karafiat, 1959); Iran; p; Katlav et al. 2015
Archidispus carabidophilus Sevastianov, 1974; Russia, Ukraine; p, Khaustov 2008
Archidispus chujoi Kurosa, 2005; Japan; p; Kurosa 2005
Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus jezoensis Kurosa, 1983; Japan; p; Kurosa 1983
Archidispus minor (Karafiat, 1959), Germany, Hungary; p; Karafiat 1959, Mahunka 1972b
Archidispus ohtanii Kurosa, 1989; Japan; p, Kurosa 1989
Archidispus pseudoctarotenot Khaustov, 2008; Belarus; p; Khaustov 2008
Archidispus quietus Khaustov, 2008; Belarus; p; Khaustov 2008
Archidispus riparius Kurosa, 1989; Japan; p, Kurosa 1989
Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983
Archidispus tonegawanus Kurosa, 2005; Japan; p; Kurosa 2005

Trechinae

Bembidion spp.
Archidispus chujoi Kurosa, 2005; Japan; p; Kurosa 2005
Archidispus cnemidot Kurosa, 1991; Japan; p, Kurosa 1991
Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus magnificus (Karafiat, 1959); Austria; Ebermann et al. 2011
Archidispus nobukoa Kurosa, 1991; Japan; p; Kurosa 1991
Archidispus riparius Kurosa, 1989; Japan; p, Kurosa 1989

Diplous caligatus
Archidispus diploi Kurosa, 1991; Japan, Russia (far east); p; Kurosa 1991, Khaustov 2008
Archidispus riparius Kurosa, 1989; Japan; p, Kurosa 1989

Diplous depressus
Archidispus riparius Kurosa, 1989; Japan; p, Kurosa 1989

Elaphropus diabrachys
Archidispus esfarayenicus Hajiqanbar & Khaustov, 2014; Iran; p, Hajiqanbar & Khaustov 2014

Patrobus flavipes
Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989

Pogonistes rufaeneus
Archidispus szaboi (Mahunka, 1977); Hungary, Ukraine, p; Khaustov 2008
“Carabidae” (not further classified in literature)

Archidipsus amarae (Kurosa, 1970); Austria; p; Ebermann 1991a, also in soil
Archidipsus armatus (Karafiat, 1959); Hungary; p; Mahunka 1981; also in soil
Archidipsus bembidii (Karafiat, 1959); Germany; p; Karafiat 1959, Khaustov 2008; up to 100 specimens/beetle; near water
Archidipsus conspicuus Kurosa, 1978; Iran; p; Katlav et al. 2015
Archidipsus minor (Karafiat, 1959); Asia, Europe; p; Karafiat 1959, Mahunka 1981, Ebermann 1991b, Khaustov 2008, also in soil
Archidipsus ohtanii Kurosa, 1989; Japan, Moldavia, Ukraine; p; Khaustov 2008
Archidipsus truncatus (Delfinado & Baker, 1976); USA (Florida); p; Delfinado & Baker 1976

III. SCUTACARID SPECIES ASSOCIATED WITH COLEOPTERA EXCL. CARABIDAE (HEXAPODA, ECTOGNATHA)

Cupepidae

Cupes concolor

Imparipes (Imparipes) cupes Delfinado & Baker, 1978; USA; p; Delfinado & Baker 1978

Curculionidae

Hylurgops palliatus

Scutacarus scolyti Mahunka & Moser, 1980; Germany; p; Mahunka & Moser 1980
Ips typographus

Scutacarus cf. culmusophilus Sevastianov, 1975; Austria; p; Knapp 2008
Scutacarus scolyti Mahunka & Moser, 1980; Germany, Russia, Sweden, ip; Mahunka & Moser 1980, Moser et al. 1989, Khaustov 2008
Pityogeneschalcographus

Scutacarus cf. culmusophilus Sevastianov, 1975; Austria; p; Knapp 2008
Scutacarus scolyti Mahunka & Moser, 1980; Austria, Russia; ip; Khaustov 2008, Schäffer & Baumann unpubl.
Rhynchophorus ferrugineus

Scutacarus sp.; Egypt; n.k.; El-Sharabasy 2010
Trypodendron lineatum

Scutacarus scolyti Mahunka & Moser, 1980; Germany; p; Mahunka & Moser 1980

Heteroceridae

Augyles hispidulus

Scutacarus sphaeroideus Karafiat, 1959; Russia; p, Khaustov & Sazhnev 2016
Heterocerus fenestratus

Scutacarus longitarsus (Berlese, 1905); Germany, Italy; p, Karafiat 1959, also in moss
Scutacarus sphaeroideus Karafiat, 1959; Russia; p, Khaustov & Sazhnev 2016
Heterocerus flexuosus

Scutacarus sphaeroideus Karafiat, 1959; Russia; p, Khaustov & Sazhnev 2016
Heterocerus marginatus

Scutacarus longitarsus (Berlese, 1905); Germany, Italy; p, Karafiat 1959, also in moss
Heterocerus sp.

Archidipsus bembidii (Karafiat, 1959); Holarctic; p; Khaustov 2008
Scutacarus sphaeroideus Karafiat, 1959; Japan; p; Kurosa 1980
Hydrophilidae

Cercyon lateralis
Imparipes (Sporichneuthes) dispar Rack, 1964; Austria; p; Ebermann et al. 2016

Cercyon ustulatus
Pygmodispus equestris Paoli, 1911; Austria, Germany, Hungary, Italy, Ukraine; p; Karafiat 1959, Khaustov 2008; also in moss, forest litter

Coelostoma sp.
Archidispus bembidii (Karafiat, 1959); Holarctic; p; Khaustov 2008

Pselaphidae

Centrophthalmus sp.
Imparipes (Imparipes) pselaphidorum Ebermann, 1988; Africa; p; Ebermann 1988

Ptiliidae

Scutacarus emadi Mahunka & Zaki, 1992; Egypt; p; Mahunka & Zaki 1992
Scutacarus longitarsus (Berlese, 1905); Egypt; p; Mahunka & Zaki 1992
Scutacarus pugillator (Paoli, 1911); Austria, Egypt; p; Mahunka & Zaki 1992, Truck 2012; also in manure, soil

Scarabaeidae

Aphodius lividus
Pygmodispus bicornatus Ebermann & Rodrigues, 2001; Brazil; p; Ebermann & Rodrigues 2001; also in soil
Scutacarus longitarsus (Berlese, 1905); Brazil; p; Rodrigues et al. 2001

Ataenius spp.
Pygmodispus bicornatus Ebermann & Rodrigues, 2001; Brazil; p; Ebermann & Rodrigues 2001, Rodrigues et al. 2001; also in soil
Scutacarus sp.; Brazil; p; Rodrigues et al. 2001

Bothynus striatellus
Archidispus sacculiger (Mahunka, 1968); Chile; p; Mahunka 1968a

Copris sp.
Pygmodispus (Allodispus) brachiosus Paoli, 1911; Java; p; Paoli 1911

Digitonthophagus gazella
Pygmodispus bicornatus Ebermann & Rodrigues, 2001; Brazil; p; Rodrigues et al. 2001; also in soil

Osmoderma eremicola
Heterodispus near elongatus (Trägardh, 1904); USA (New York); p; Norton 1973

Pleurophorus anatolicus, Rhysemodes orientalis
Scutacarus iranicus Ebermann et al., 2003; Iran; p, Ebermann et al. 2003, Loghmani et al. 2014

Staphylinidae

Archidispus armatus (Karafiat, 1959); Iran; p; Katlav et al. 2015
Lamnacarus ornatus Balogh & Mahunka, 1963; Austria; p; Truck 2012

Atheta malleus
Lamnacarus ornatus Balogh & Mahunka, 1963; Austria, Hungary, Lithuania, Mongolia, Russia; p; Ebermann 1991a, Khaustov 2008, also in dung

Bledius sp.
Archidispus irregularis Katlav & Hajianbar, 2016; Iran; p; Katlav et al. 2016
Boopinus fuliginosus
Scutacarus spheroideus Karafiat, 1959; Germany; p; Karafiat 1959; also in moss

Lithocharis nigriceps
Imparipes (Sporichneuthes) dispar Rack, 1964; Austria; p; Ebermann et al. 2016
Philonthus fulvipes, P. micans
Archidispus armatus (Karafiat, 1959); Germany, Hungary; p; Karafiat 1959, Mahunka 1972b

Stenus spp.
Scutacarus longipes Rack, 1975; Austria, USA; p; Ebermann 1978; also on Fragaria plants
Scutacarus sphæroideus Karafiat, 1959; cosmopolitan; p; Karafiat 1959, Khaustov 2008; on shores of rivers and lakes; also in moss

Trogophloeus corticinus
Scutacarus longitarsus (Berlese, 1905); Austria; p; Ebermann 1991a; also in manure

Tychus mutinensis
Imparipes (Imparipes) histrionicus Berlese, 1903; Italy; p; Paoli 1911; also in soil, moss

Tenebrionidae
Anomalipus elephas
Heterodispus foveatus Jagersbacher-Baumann & Ebermann 2012; Botswana; p; Jagersbacher-Baumann & Ebermann 2012a
Blaps halophila
Heterodispus temperatus Khaustov, 2008; Ukraine; p; Khaustov 2008

“Coleoptera” (not further classified in literature)
Archidispus cornutus (Mahunka, 1973); Ghana; p; Mahunka 1973a
Diversipes horridolatus Mahunka, 1975; Australia; p; Mahunka 1975c
Lamnacarus expansus Mahunka, 1973; Ghana; p; Mahunka 1973b
Scutacarus elacatus Mahunka, 1973; Ghana; p; Mahunka 1973b
Scutacarus rhödiformis Mahunka, 1973; Ghana; p; Mahunka 1973b
Symbolocrasis acutimera Mahunka, 1973; Ghana; p; Mahunka 1973b
Symbolocrasis hypostigma Mahunka, 1973; Ghana; p; Mahunka 1973b
Symbolocrasis synmixta Mahunka, 1973; Ghana; p; Mahunka 1973b
Thaumatopelvis gracilis Mahunka, 1974; Ghana; p; Ebermann 1980b
Thaumatopelvis sellata Mahunka, 1973; Ghana; p; Mahunka 1973b, Ebermann 1980b

IV. SCUTACARID SPECIES ASSOCIATED WITH APOIDEA AND VESPOIDEA EXCL. FORMICIDAE (HEXAPODA, ECTOGNATHA, ACULEATA)

Apoidea: Apidae
Apis mellifera
Imparipes (Imparipes) apicola (Banks, 1914); Canada; n.k.; Banks 1914
Scutacarus acarorum (Goeze, 1780); n.k.; i; Schousboe 1986

Bombus spp.
Imparipes (Imparipes) degenerans Berlese, 1904; Florida, Germany, Italy, Russia; p; Karafiat 1959; also in moss; only 1 finding on B. terrestris!
Parascutacarus indicus Baker & Delfinado, 1975; India; p; Baker & Delfinado 1975
Scutacarus acarorum (Goeze, 1780) (?); Argentina; p; Maggi et al. 2011, Revainera et al. 2014; could be S. mendax (pers. comm. Revainera)

Scutacarus cf. mendax Karafiat, 1959; Brazil, p; Guerra et al. 2012; det. Baumann (unpubl.)

Scutacarus deserticolus Mahunka, 1969; Austria; ip; Ebermann 1991a, Baumann unpubl.

Scutacarus mendax Karafiat, 1959; Austria; i; Jagersbacher-Baumann 2014b

Scutacarus occultatus Sevastianov, 1975; Austria, Hungary, Ukraine; ip; Khaustov 2008, Jagersbacher-Baumann 2014b

Scutacarus pygmeophoroides Mahunka, 1967, Hungary, Mongolia; i; Mahunka 1967a, 1972b

Scutacarus spinosus Storkan, 1936; Mongolia; i; Mahunka 1967a, 1968a

Dasypodaplumipes

Imparipes (Imparipes) rafalskii Dastych, 1978, Poland; p; Dastych 1978

“Bees” (not further classified in literature)

Diversipes zweelferi Karafiat, 1959; Germany, Poland; i; Karafiat 1959, also in meadow soil

Scutacarus acarorum (Goeze, 1780); Germany; p; Karafiat 1959; in detritus of nest of “wild bees”, attached to wings

Scutacarus unicus Delfinado & Baker, 1976; USA, New York; n.k.; Delfinado & Baker 1976; also in leaf litter

Apoidea: Halictidae

Augochlorella spp.

Imparipes spp.; USA (Kansas); i; Ordway 1964

Halictus spp.

Imparipes spp; USA; n.k.; Banks 1904

Imparipes (Apidae) paulyi Ebermann & Fain, 2002; Algeria, Namibia, Uganda, Iran; p; Ebermann & Fain 2002, Loghmani et al. 2014

Imparipes (Imparipes) apicola (Banks, 1914); Austria, Belgium, Germany, Mexico, Poland, USA; n.k.; Cross & Bohart 1969, 1992, Delfinado & Baker 1976, Kuhlmann 1998, Ebermann & Hall 2005

Imparipes (Imparipes) apidophilus Mahunka, 1974, Hungary; p; Mahunka 1974c

Imparipes (Imparipes) americanus (Banks, 1904); Canada (British Columbia); n.k.; Banks 1906

Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013

Imparipes (Imparipes) floridensis Delfinado & Baker, 1976; USA (Florida); i; Delfinado & Baker 1976

Scutacarus acarorum (Goeze, 1780); Belgium; p; Fain & Baugnèe 1996

Lasiosglossum spp.

Imparipes (Imparipes) apicola (Banks, 1914); Austria, Belgium, Germany, Mexico, Poland, USA; ip; Cross & Bohart 1969, 1992, Delfinado & Baker 1976, Eickwort 1979, Kuhlmann 1998, Ebermann & Hall 2005

Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Iran, Poland, Slovakia; p; Ebermann et al. 2013, Bakiani et al. 2016

Imparipes (Imparipes) eickworti Mahunka, 1969; Costa Rica; ip; Mahunka 1969b, Eickwort & Eickwort 1971

Imparipes (Imparipes) ithacensis Delfinado & Baker, 1976; USA (New York); n.k.; Delfinado & Baker 1976

Imparipes (Imparipes) mexicanus Delfinado & Baker, 1976; Mexico; p; Delfinado & Baker 1976

Imparipes (Imparipes) neotropicus Delfinado & Baker, 1976; Chile; p; Delfinado & Baker 1976

Imparipes (Imparipes) vulgaris Delfinado & Baker, 1976; USA (California); ip; Delfinado & Baker 1976

Scutacarus eickworti Delfinado & Baker, 1976; USA (New York); p; Delfinado & Baker 1976

Nomia spp.

Imparipes (Imparipes) apicola (Banks, 1914); USA (Idaho, Nevada, Utah, Wyoming); ip; Cross & Bohart 1969, 1992; in Cross & Bohart 1969 handled as Imparipes americanus

Imparipes (Imparipes) texanus (Cockerell, 1910); USA; n.k.; Cockerell 1910

Nasutiscutacarus ampliatus Beer & Cross, 1960; Philippines; p; Beer and Cross 1960

Nasutiscutacarus anthrenae Beer & Cross, 1960; Indonesia; p; Beer and Cross 1960
Nomiapis sp.
Imparipes (Apidacarus) paulyi Ebermann & Fain, 2002; Iran; Loghmani et al. 2014

Sphecodes spp.
Imparipes (Imparipes) apicola (Banks, 1914); Austria, Belgium, Germany, Mexico, Poland, USA; n.k.; Cross & Bohart 1969, 1992, Delfinado & Baker 1976, Kuhlmann 1998, Ebermann & Hall 2005
Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004
Imparipes (Imparipes) burgeri Ebermann & Jagensbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013

“Halictidae” (not further classified in literature)
Imparipes (Imparipes) apicola (Banks, 1914); Belgium; p; Fain et al. 1992; given as Imparipes hystricinus dispar; later determined as Imparipes apicola by Ebermann (pers. comm.)

Apoidea: Sphecidae

Cerceris spp., Crossocerus spp., Lestica spp.
Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004
Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005

Diodontus spp., Gorytes spp.
Imparipes (Imparipes) apicola (Banks, 1914); Austria, Belgium, Germany, Mexico, Poland, USA; n.k.; Cross & Bohart 1969, 1992, Delfinado & Baker 1976, Kuhlmann 1998, Ebermann & Hall 2005
Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004

Ectemnius spp.
Imparipes (Imparipes) apicola (Banks, 1914); Austria, Belgium, Germany, Mexico, Poland, USA; n.k.; Cross & Bohart 1969, 1992, Delfinado & Baker 1976, Kuhlmann 1998, Ebermann & Hall 2005
Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005

Larra spp., Sphex spp.
Archidisopus sphecis Mahunka, 1977; Vietnam; p; Lang & Mahunka 1977

Pemphredon spp., Stigmus solskyi
Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005

“Sphecidae” (not further classified in literature)
Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Ukraine; n.k.; Khaustov 2008

Apoidea: Andrenidae

Andrena spp.
Imparipes (Imparipes) apicola (Banks, 1914); Austria, Belgium, Germany, Mexico, Poland, USA; n.k.; Cross & Bohart 1969, 1992, Delfinado & Baker 1976, Ebermann & Hall 2005
Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004
Imparipes (Imparipes) burgeri Ebermann & Jagensbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013

“Andrenidae” (not further classified in literature)
Imparipes (Imparipes) apicola (Banks, 1914); USA; ip; Eickwort 1979
Imparipes (Imparipes) cf. parapicola Delfinado, Baker & Abbatienlo, 1976; Iran; p; Kamali et al. 2001
Apoidea: Colletidae

Hylaeus spp.

Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013
Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004
Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005

Apoidea: Megachilidae

Megachile lapponica

Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005

Osmia papaveris

Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004

Apoidea: Crabronidae

Bembix tarsata, Mimesae equestris, Psenulus concolor, Trypoxylon minus

Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013

Lindeniusspp.

Imparipes (Imparipes) breganti Ebermann & Hall, 2004; Austria, Belgium, Germany; p; Ebermann & Hall 2004
Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany; p; Ebermann et al. 2013

Mimumesadahlbomi

Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005
Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013

Vespoidea: Vespidae

Symmorphusbifasciatus

Imparipes (Imparipes) haeseleri Ebermann & Hall, 2003; Austria, Belgium, Germany, India, Italy, Poland, Ukraine; p; Ebermann & Hall 2003, Hall & Ebermann 2005

Vespasp.

Scutacarus acarorum (Goeze, 1780); Germany; p; Vitzthum 1927; extremely rare

Vespoidea: Mutillidae

Myrmilla calva

Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013

Tricholabiodes sp.

Scutacarus subquadratus Khaustov & Chydyrov, 2004; Iran; p; Loghmani et al. 2014

Vespoidea: Pompilidae

Anopliusinfuscatus, Caliarius fasciatus, Evagates proximus

Imparipes (Imparipes) burgeri Ebermann & Jagersbacher-Baumann, 2013; Austria, Belgium, Germany, Poland, Slovakia; p; Ebermann et al. 2013
V. SCUTACARID SPECIES ASSOCIATED WITH FORMICIDAE EXCL. FORMICINAE AND MYRMICINAE (HEXAPODA, ECTOGNATHA, ACULEATA, VESPOIDEA)

Dolichoderinae

Tapinoma erraticum
Imparipes (Imparipes) comatus Mahunka, 1970; France, Hungary, Ukraine; i; Mahunka 1977c, Khausov 2008 Imparipes (Imparipes) pennatus Karafiat, 1959; France; n.k.; Mahunka 1977c

Tapinoma simrothi
Scutacarus sabinaesimilis Khausov & Chydyrov, 2004; Turkmenistan; i, Khausov 2008

Tapinoma sp.
Lophodispus tapinoma Sobhi & Hajiqanbar 2017; Iran; p; Sobhi et al. 2017

Liometopum apiculatum
Imparipes (Imparipes) liometopi Mahunka, 1982; Mexico; p; Mahunka 1982; nom. nov. (Mahunka & Rack 1984), i. (i.) mexicanus
Scutacarus athiashenriotae Mahunka, 1982; Mexico; p; Mahunka 1982

Dorylinae

Cheliomyrmex morosus
Imparipes (Imparipes) lapillatus Mahunka, 1977; Panama; p; Berghoff & Franks 2007; also in soil and litter

Eciton spp.
Imparipes (Imparipes) crudelatus Mahunka, 1977; Ecuador, Panama; i.p; Mahunka 1977b, Rettenmeyer et al. 2011
Imparipes (Imparipes) cf. crudelatus Mahunka, 1977; Panama; p; Berghoff et al. 2009
Imparipes (Imparipes) egisetus Mahunka, 1977; Costa Rica; i; Mahunka 1977b
Imparipes (Imparipes) lapillatus Mahunka, 1977; Ecuador, Panama; i.p; Mahunka 1977b, Berghoff et al. 2009
Imparipes (Imparipes) marianae Mahunka, 1977; Costa Rica, Ecuador; p; Mahunka 1977a, Rettenmeyer et al. 2011
Imparipes (Imparipes) officius Mahunka, 1977; Costa Rica, i; Mahunka 1977b
Imparipes (Imparipes) recisus Mahunka, 1977; Panama; i; Mahunka 1977b
Imparipes (Imparipes) rectangulatus Mahunka, 1977; Costa Rica, Ecuador, Panama, USA (Kansas); p; Mahunka 1977a, Berghoff et al. 2009, Rettenmeyer et al. 2011
Imparipes (Imparipes) suboletus Mahunka, 1977; Panama; i.p; Mahunka 1977b, Berghoff et al. 2009, Rettenmeyer et al. 2011
Imparipes sp.; Panama; p; Berghoff et al. 2009
Imparipes (Telodispus) opusculus Mahunka, 1977; Brazil, Costa Rica, Mexico, i.p; Mahunka 1977b, Rettenmeyer et al. 2011
Imparipes (Telodispus) rationis Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a
Pygmodispus (Pygmodispus) dorylini Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a
Rettenmeyerella petropolitana solenifera Mahunka, 1977; Costa Rica, Ecuador, i; Mahunka 1977a, also from refuse deposit with Phoridae, Staphylinidae
Scutacaropsis problematicus Mahunka, 1977; Costa Rica, Ecuador, p; Mahunka 1977a, Rettenmeyer et al. 2011
Scutacaropsis scutacaroides Mahunka, 1977; Ecuador, n.k.; Mahunka 1977a
Scutacarus andreassi Mahunka, 1968; Panama; p; Berghoff et al. 2009
Scutacarus omittatus Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a
Scutacarus pseudocomus Mahunka, 1977; Panama; i.p; Mahunka 1977b, Rettenmeyer et al. 2011
Scutacarus setarius Mahunka, 1977; Costa Rica; i; Mahunka 1977b
“Scutacaridae”; Central America; i; Rettenmeyer 1961b

Labidus spp.
Archidispus calcarifer (Mahunka, 1977); Costa Rica, Panama, i; Mahunka 1977b
Archidispus repus Mahunka, 1977; Costa Rica, Panama; i; Mahunka 1977b
Imparipes (Imparipes) compensatus Mahunka, 1977; Costa Rica, Ecuador; i; Mahunka 1977b
Imparipes (Imparipes) convexus Mahunka, 1977; Costa Rica, Ecuador; n.k.; Mahunka 1977a
Imparipes (Imparipes) rettenmeyeri Mahunka, 1977; Costa Rica, Ecuador; n.k.; Mahunka 1977a
Imparipes (Telodispus) nabilatus Mahunka, 1977; Costa Rica; i, Mahunka 1977b
Imparipes (Telodispus) opacusculus Mahunka, 1977; Brazil, Costa Rica, Mexico; i, Mahunka 1977b
Scutacaropsis problematicus Mahunka, 1977; Costa Rica, Ecuador; n.k.; Mahunka 1977a
Thaumatopelvis minutissimus Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a, Ebermann 1980b
Thaumatopelvis rugosus Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a, Ebermann 1980b

Neivamyrmex spp.

Archidispus statitus (Mahunka, 1977); Brazil; i; Mahunka 1977b
Archidispus willmanni Mahunka, 1977; Costa Rica; n.k.; Mahunka 1977a
Imparipes (Imparipes) cassovaricus Mahunka, 1970; Costa Rica; n.k.; Mahunka 1977a
Imparipes (Imparipes) compensatus Mahunka, 1977; Costa Rica, Ecuador; i; Mahunka 1977b
Imparipes (Imparipes) dimidiatus Mahunka, 1977; Costa Rica; n.k.; Mahunka 1977a
Imparipes (Imparipes) egisetus Mahunka, 1977; Costa Rica; i; Mahunka 1977b
Imparipes (Imparipes) rectangulatus Mahunka, 1977; Costa Rica, Ecuador, USA (Kansas); n.k.; Mahunka 1977a
Imparipes (Imparipes) saevus Mahunka, 1977; Costa Rica; i; Mahunka 1977b
Imparipes (Telodispus) elzingai Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a
Imparipes (Telodispus) moralesi Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a
Imparipes (Telodispus) moricus Mahunka, 1977; USA; i; Mahunka 1977b
Imparipes (Telodispus) retrosus Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a
Thaumatopelvis minutissimus Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a, Ebermann 1980b

Nomamyrmex esenbeckii

Archidispus repus Mahunka, 1977; Costa Rica, Panama; i; Mahunka 1977b
Scutacaridae; Brazil, Panama; p; Rettenmeyer 1961a; “20 different species”

Ponerinae

Ponera coarcta
ta

Imparipes (Imparipes) malus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

“Ants” (not further classified in literature)

Archidispus haarloevi (Karafiat, 1959); Denmark, Hungary; i; Karafiat 1959, Mahunka 1981; also in meadow soil, oak litter
Genus Imparipes; USA; n.k.; Banks 1904
Imparipes (Imparipes) degenerans Berlese, 1904; Germany, Italy, Russia, USA (Florida); ip; Karafiat 1959; also in moss
Imparipes (Imparipes) hortobagynsis Mahunka, 1981; Hungary; i; Mahunka 1981
Imparipes (Imparipes) histrinclus Berlese, 1903; Germany, Hungary, Italy, Russia, Sudan; ip; Karafiat 1959, Mahunka 1981; also in forest litter
Imparipes (Imparipes) imagininus Mahunka, 1981; Hungary; i; Mahunka 1981
Imparipes (Imparipes) intermissus Karafiat, 1959; Hungary; i; Mahunka 1965b
Imparipes (Imparipes) longisetosus Willmann, 1951; Germany, Hungary; i; Mahunka 1981; also in saline turf
Imparipes (Imparipes) myrmecophilus Mahunka, 1972; Hungary; i; Mahunka 1981; also in forest litter, rotten debris of oak wood
Imparipes (Imparipes) obsoletus Rack, 1966; Europe; i; Mahunka 1981; also in soil
Imparipes (Imparipes) pennatus Karafiat, 1959; Germany, Hungary; i; Mahunka 1970b
Imparipes (Imparipes) robustus Karafiat, 1959; Bulgaria, Germany; ip; Karafiat 1959, Dobrev 1992; also in moss
Imparipes (Imparipes) steinmanni Mahunka, 1971; Korea; i; Mahunka 1971
Imparipes (Imparipes) tenuis Mahunka, 1981; Hungary; i; Mahunka 1981
Imparipes (Imparipes) vasarhelyii Mahunka & Mahunka-Papp, 1980; Romania; i; Mahunka & Mahunka-Papp 1980

Pygmodispus calcaratus Paoli, 1911; Hungary; i; Mahunka 1986; also in horse manure
Scutacarus bugacensis Mahunka, 1986; Hungary; i; Mahunka 1986
Scutacarus bursula (Berlese, 1903); Germany; Italy; n.k.; Karafiat 1959
Scutacarus calcaratus Storkan, 1936; Bulgaria; n.k.; Štorkán 1936
Scutacarus carsticus Mahunka & Mahunka-Papp, 1980; Hungary; i; Mahunka & Mahunka-Papp 1980
Scutacarus concinnus Mahunka, 1964; Hungary; i; Mahunka 1970b
Scutacarus echidna (Berlese, 1905); Palaearctic; i; Mahunka 1981; also in turf, soil
Scutacarus ellipticus Karafiat, 1959; Europe; i; Mahunka 1981, 1986; also in soil, moss
Scutacarus exspectatus Karafiat, 1959; Hungary; i; Mahunka 1981
Scutacarus gratus hortobagyiensis Mahunka, 1981; Hungary; i; Mahunka 1981, 1986; also in litter
Scutacarus kassaii Mahunka, 1965; Hungary; i; Mahunka 1986
Scutacarus laetificus Rack, 1966; Bulgaria; i; Dobrev 1992
Scutacarus latifrons Mahunka, 1964; Hungary, Italy; i; Mahunka 1970b
Scutacarus longisetus (Berlese, 1904); Germany, Hungary; i; Karafiat 1959, Mahunka 1981, 1986; also in oak litter, earth from under carcasses, grassy samples
Scutacarus longisetus bucephalos Balogh & Mahunka, 1963; Hungary; i; Mahunka 1986
Scutacarus molnari Mahunka, 1981; Hungary; i; Mahunka 1981; in saline habitat
Scutacarus ovoideus Karafiat, 1959; Germany, Hungary; i; Karafiat 1959, Mahunka 1981; also in moss
Scutacarus peractus Karafiat, 1959; Hungary; i; Mahunka 1981; also in oak litter, rotten debris
Scutacarus pleurotricha Mahunka, 1970; Hungary; i; Mahunka 1970d, 1981
Scutacarus pygmephoroides Mahunka, 1967; Hungary; i; Mahunka 1986; also in litter of Populus
Scutacarus quadrangularis (Paoli, 1911); Hungary; i; Balogh & Mahunka 1962; also in litter, meadow soil, moss; “Variatipes”- group: no claw on leg I
Scutacarus rakonczayi Mahunka, 1981; Bulgaria, Hungary; i; Mahunka 1981, Dobrev 1992
Scutacarus rotundatus [sic]; Bulgaria; n.k.; Štorkán 1936; should be S. rotundus (Berlese, 1903)
Scutacarus silvestri (Berlese, 1903); Hungary; i; Mahunka 1986; also in soil, moss; in text “S. silvestris”
Scutacarus sphæroideus Karafiat, 1959; Hungary; i; Mahunka 1981
Scutacarus spinipars Mahunka, 1986; Hungary; i; Mahunka 1986; also in litter, manure
Scutacarus spinosus Storkan, 1936; Hungary; i; Mahunka 1963, 1981; also in meadow soil, mossy turf
Scutacarus stammeri Karafiat, 1959; Hungary; i; Mahunka 1981, 1986
Scutacarus striatamarginatus Mahunka, 1986; Hungary; i; Mahunka 1986
Scutacarus subcomosus Mahunka, 1970; Hungary; i; Mahunka 1970d
Scutacarus subellipticus Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976
Scutacarus subterraneus spinosus Storkan, 1936; Bulgaria; n.k.; Štorkán 1936
Scutacarus tacei Willmann, 1942; Europe; i; Mahunka 1981; also in rotten straw
Scutacarus tacei suborbiculatus Rack, 1964; Europe; i; Mahunka 1981; also in mossy turf, meadow litter
Scutacarus terrenus Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976
Scutacarus transfusionis Mahunka & Mahunka-Papp, 1980; Hungary; i; Mahunka & Mahunka-Papp 1980
VI. SCUTACARID SPECIES ASSOCIATED WITH FORMICINAE
(HEXAPODA, ECTOGNATHA; ACULEATA, FORMICIDAE)

**Camponotus spp.**

- *Imparipes (Imparipes) robustus* Karafiat, 1959; Austria, Bulgaria, France, Germany, Hungary, Japan, Mongolia, Russia, Ukraine (Palaearctic?); n.k.; Khaustov 2008; also in soil, litter
- *Scutacarus circularis* (Berlese, 1903); Italy; p; Berlese 1903, Paoli 1911
- *Scutacarus echidna* (Berlese, 1905); Germany; i; Rack 1966
- *Scutacarus kassaii* Mahunka, 1965; Austria, Czechoslovakia, Hungary, Russia; p; Mahunka 1967b, 1968a, Ebermann 1978
- *Scutacarus novellus* Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
- *Scutacarus rarissimus* Sevastianov, 1983; Ukraine; p; Sevastianov 1983
- *Scutacarus rotundulus* Khaustov & Chydyrov, 2004; Turkmenistan; i; Khaustov & Chydyrov 2004, Khaustov 2008
- *Scutacarus tyrrenicus* Ebermann, 1986; Italy, Ukraine; n.k.; Khaustov 2008

**Cataglyphis aeneascens**

- *Scutacarus berdyevi* Chydyrov 2007; Turkmenistan; p; Chydyrov 2007

**Cataglyphis bicolor**

- *Scutacarus aegypticus* Yousef & Metawally, 1973; Egypt; p; Yousef & Metawally 1973, Elbadry et al. 1976
- *Scutacarus unicosimilis* Metwali, 1984; Egypt; i; Metwali 1984
- *Scutacarus wisniewskii* Metwali, 1984; Egypt; i; Metwali 1984

**Cataglyphis emery**

- *Imparipes (Imparipes) kaglyphi* Khaustov & Chydyrov, 2004; Turkmenistan, i; Khaustov & Chydyrov 2004, Khaustov 2008

**Cataglyphis cf. nodus**

- *Imparipes (Imparipes) histicinus* Berlese, 1903; Iran; p; Loghmani et al. 2014
- *Scutacarus subquadratus* Khaustov & Chydyrov, 2004; Iran; p; Loghmani et al. 2014

**Lasius spp.**

- *Archidispus intermissus* (Karafiat, 1959); Austria, Belarus, Germany, Hungary, Japan, Kazakhstan, Poland, Ukraine; p; Karafiat 1959, Mahunka 1972b, Khaustov 2008
- *Imparipes (Imparipes) bisetus* Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
- *Imparipes (Imparipes) brevibasis* (Sevastianov, 1983); Russia, Ukraine; i; Sevastianov 1983, Khaustov 2016a
- *Imparipes (Imparipes) brevitarsus* Ebermann, 1981; Austria, Russia; ip; Ebermann 1981, Friedl 2000, Ebermann & Krisper 2014, Khaustov 2015d
- *Imparipes (Imparipes) cf. histicinus* Berlese, 1903; Austria; p; Ebermann 1978
- *Imparipes (Imparipes) comatus* Mahunka, 1970; France, Hungary, Ukraine; i; Khaustov 2008
- *Imparipes (Imparipes) extremiorientalis* Khaustov, 2017; Russia; p; Khaustov 2017
- *Imparipes (Imparipes) fuliginosophilus* Khaustov, 2016; Russia; p; Khaustov 2016a
- *Imparipes (Imparipes) histicinus* Berlese, 1903; Austria, Czech Republic; i; Štorkán 1940, Ebermann 1980a, 1982; also in moss
- *Imparipes (Imparipes) histicinus var. vimariensis* Vitzthum, 1919; Germany; p; Vitzthum 1919
- *Imparipes (Imparipes) imaginatus* Mahunka, 1981; Austria; p; Friedl 2000, Ebermann & Krisper 2014
- *Imparipes (Imparipes) lasii* Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
- *Imparipes (Imparipes) mordax* Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
- *Imparipes (Imparipes) obsoletus* Rack, 1966; holarctic; ip; (Paoli 1911), Mahunka 1977c, Ebermann 1979, Friedl 2000, Khaustov 2008, Ebermann & Krisper 2014, Khaustov 2016a, 2016c; also in decaying material; Paoli (1911) published a species identified as *I. degenerans* - however, the drawings and description strongly indicate that the species was *I. obsoletus* (Ebermann, pers. comm.)
- *Imparipes (Imparipes) robustus* Karafiat, 1959; Austria, Bulgaria, France, Germany, Hungary, Japan, Mongolia, Russia, Ukraine (Palaearctic?); n.k.; Mahunka 1972b, Khaustov 2008
- *Imparipes (Imparipes) sevastianovi* Khaustov, 2008; Russia, Ukraine; n.k.; Khaustov 2008, 2016a
- *Imparipes (Imparipes) sklyari* Khaustov, 2008; Russia, Ukraine; ip; Khaustov 2008, 2016c
- *Imparipes (Imparipes) tomentosus* Khaustov, 2016; Russia; p; Khaustov 2016b
Imparipes (Imparipes) sp. A (sensu Friedl 2000); Austria; p; Friedl, Ebermann & Krisper 2014

Imparipes (Imparipes) sp. B (sensu Friedl 2000); Austria; p; Friedl 2000, Ebermann & Krisper 2014

Imparipes (Sporichneuthes) dispar Rack, 1964; Austria; p; Messner 2001

Lophodispus bulgaricus Dobrev, 1992; Austria; p; Friedl 2000, Ebermann & Krisper 2014


Scutacarus acarorum (Goeze, 1780); Gocece, 1780; Belgium; p; Fain & Baugnée 1996

Scutacarus aequalis Khaustov, 2016; Russia; p; Khaustov 2016b

Scutacarus bucephalus Balogh & Mahunka, 1963; Austria; p; Friedl 2000, Ebermann & Krisper 2014

Scutacarus carsticus Mahunka & Mahunka-Papp, 1980; Hungary, Ukraine, ip; Khaustov 2008

Scutacarus crinitus Khaustov, 2015; Russia; p; Khaustov 2015c

Scutacarus ellipticus Karafiat, 1959; Austria, Germany, Hungary, Russia, Switzerland, Ukraine; former Yugoslavia; p; Mahunka 1977c, Friedl 2000, Khaustov 2008, Ebermann & Krisper 2014; also in soil

Scutacarus exspectatus Karafiat, 1959; Austria, Germany, Hungary, Japan, Ukraine; ip; Karafiat 1959, Friedl 2000, Khaustov 2008, Ebermann & Krisper 2014

Scutacarus flexisetosimilis Khaustov, 2016; Russia; p; Khaustov 2016b

Scutacarus flexisetus Karafiat, 1959; Austria, Germany, Hungary, Japan, Russia, Ukraine; ip; Karafiat 1959, Sevastianov 1965, Ebermann 1979a, 1980a, Mahunka 1972b, Khaustov 2008, 2016a, Ebermann & Krisper 2014

Scutacarus gratus Karafiat, 1959; Germany, Hungary, Ukraine; n.k.; Karafiat 1959, Sevastianov 1965, Mahunka 1972b

Scutacarus gratus hortobagyensis Mahunka, 1981; Austria; p; Ebermann & Krisper 2014

Scutacarus hauseri Mahunka, 1977; Austria, Switzerland; p; Ebermann 1979, Friedl 2000, Ebermann & Krisper 2014

Scutacarus heterotrichus Khaustov, 2015; Russia; ip; Khaustov 2015d

Scutacarus hystrichocentrus Sevastianov, 1983; Ukraine; n.k.; Sevastianov 1983, Khaustov 2008

Scutacarus insolitus Khaustov, 2015; Russia; ip; Khaustov 2015d

Scutacarus kassaii Mahunka, 1965; Russia; ip; Khaustov 2015a

Scutacarus lasiophilus Khaustov, 2015; Russia; p; Khaustov 2015c

Scutacarus longisetus (Berlese, 1904); Austria, Bulgaria, Crimea, Hungary, Italy, Poland, Russia, Switzerland, Ukraine, former Yugoslavia; ip; Paoli 1911, Ebermann 1978, 1979, Mahunka 1977c, 1986, Friedl 2000, Khaustov 2008, 2016a, 2016c, Ebermann & Krisper 2014

Scutacarus molnari Mahunka, 1981; Russia; ip; Khaustov 2015d

Scutacarus moseri Khaustov, 2015; Russia; ip; Khaustov 2015d

Scutacarus nudus (Berlese, 1886); Germany, Italy, Netherlands; i; Paoli 1911, Parmentier et al. 2015; “Varietipes”- group: no claw on leg I

Scutacarus nudus bisetus Karafiat, 1959; USA (Maryland); i; Ebermann 1980b; “Varietipes”- group: no claw on leg I

Scutacarus ovoideus Karafiat, 1959; Austria, Germany, Greece, Hungary, Poland, Switzerland, Ukraine; ip; Mahunka 1977c, Khaustov 2008

Scutacarus ponticulus Mahunka, 1981; Austria, Hungary, Russia, Ukraine; ip; Friedl 2000, Khaustov 2008, 2016c, Ebermann & Krisper 2014

Scutacarus pseudospinosus Khaustov, 2008; Russia, Ukraine; ip; Khaustov 2008, 2016c, on alates

Scutacarus rotundatus [sic]; Czech Republic; n.k.; Storkán 1940; should be S. rotundus (Berlese, 1903)

Scutacarus rotundus (Berlese, 1903); Germany, Italy; n.k.; Karafiat 1959

Scutacarus rusticus Sevastianov, 1983; Ukraine; p; Sevastianov 1983

Scutacarus sibirienensis Khaustov, 2015; Russia; ip; Khaustov 2015d

Scutacarus spinosus Storkán, 1936; cosmopolitan; ip; Khaustov 2008, 2016c; common in soil

Scutacarus suavis Khaustov, 2008; Crimea; n.k.; Khaustov 2008

Scutacarus subcomosus Mahunka, 1970; Switzerland; n.k.; Mahunka 1977c

Scutacarus subterraneus (Oudemans, 1913); Carpathians, Germany, Hungary, Lithuania, Netherlands, Poland, Russia, Ukraine; ip; Vitzthum 1919, Storkán 1940, Sevastianov 1965, Sosnina & Sevastianov 1975, Ebermann 1979, Khaustov 2008, 2016a, Ebermann & Krisper 2014
Scutacarus subtilis Rack, 1966; Austria; i; Friedl 2000, Ebermann & Krisper 2014; “Variatipes”-group: no claw on leg

Scutacarus tacei Willmann, 1942; Austria, Czechoslovakia, France, Germany, Hungary, India, Switzerland, former Yugoslavia; p; Ebermann 1978

Scutacarus tutus Khaustov, 2008; Russia, Ukraine, i; Khaustov 2008, 2016c

Scutacarus velutinosus Sevastianov, 1983, Ukraine; p; Sevastianov 1983

Thaumatopelvis reticulatus Ebermann, 1980; USA (Maryland); p; Ebermann 1980b

Formica spp.

Imparipes (Imparipes) cf. histrionicus Berlese, 1903; Austria; i; Mahunka 1970b

Imparipes (Imparipes) cf. histrionicus Berlese, 1903; Czechoslovakia; n.k.; Mahunka 1967b

Imparipes (Imparipes) circinnatus Mahunka, 1980; Austria; p; Ebermann & Krisper 2014

Imparipes (Imparipes) comatus Mahunka, 1970; Hungary; i; Mahunka 1970b, 1980

Imparipes (Imparipes) cunicularius Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Imparipes (Imparipes) gagati Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Imparipes (Imparipes) nescius Khaustov, 2008; Russia, Ukraine; ip; Khaustov 2008, 2015b

Imparipes (Imparipes) nugax Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Imparipes (Imparipes) pennisus Karafiat, 1959; Germany, Hungary; n.k.; Karafiat 1959, Mahunka 1972b

Imparipes (Imparipes) robustus Karafiat, 1959; Austria, Bulgaria, France, Germany, Hungary, Japan, Mongolia, Russia, Ukraine (Palaearctic?); p; Mahunka 1967b, 1972b, Friedl 2000, Khaustov 2008, 2015, Ebermann & Krisper 2014, also in soil, litter

Imparipes (Imparipes) sp.B (sensu Friedl 2000); Austria; p; Friedl 2000; only 1 specimen

Imparipes (Imparipes) tenuis Mahunka, 1981; Austria; i; Friedl 2000

Scutacarus atypicus (Karafiat, 1959); Austria, Germany, Hungary, Russia; p; Karafiat 1959, Mahunka 1972b, Friedl 2000, Ebermann & Krisper 2014, Khaustov 2015b

Scutacarus avarus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Scutacarus carsticus Mahunka & Mahunka-Papp, 1980; Hungary, Ukraine; ip; Khaustov 2008

Scutacarus concinnus Mahunka, 1964; Hungary; i; Nemestöthy & Mahunka 1981

Scutacarus hungaricus Mahunka, 1965; Hungary; i; Nemestöthy & Mahunka 1981

Scutacarus karafiati Khaustov, 2015; Russia; p; Khaustov 2015b

Scutacarus kassai Mahunka, 1965; Austria, Hungary, Russia; p; Ebermann 1978

Scutacarus nudus (Berlese, 1886); Germany; n.k.; Parmentier et al. 2015; “Variatipes”-group: no claw on leg

Scutacarus palustris Rack, 1966, Hungary; i; Mahunka 1968b

Scutacarus pilatus Khaustov, 2008; Russia, Ukraine, ip; Khaustov 2008, 2015b

Scutacarus ponticus Mahunka, 1981; Hungary; i; Nemestöthy & Mahunka 1981

Scutacarus pseumphoroides Mahunka, 1967; Russia; i; Khaustov 2015a

Scutacarus rotundatus [sic]; Czech Republic; n.k.; Štorkán 1940; should be S. rotundus (Berlese, 1903)

Scutacarus rotundus (Berlese, 1903); Austria, Germany, Hungary, Italy, Russia; ip; Berlese 1903, Paoli 1911, Karafiat 1959, Mahunka 1970a, 1970b, 1972b, Khaustov 2015b

Scutacarus silvestri (Berlese, 1903); Austria; p; Friedl 2000, Ebermann & Krisper 2014

Scutacarus stammeri Karafiat, 1959; Germany, Hungary, Italy, Ukraine; i; Karafiat 1959, Mahunka 1972b, Khaustov 2008

Scutacarus tacei Willmann, 1942; Austria; p; Ebermann & Krisper 2014

Paratrechinaja jaegerskioeldi

Scutacarus gouheri Metwali & Ahmed, 1987; Egypt; p; Metwali & Ahmed 1987

Scutacarus notabilosimillis Metwali & Ahmed, 1987; Egypt; p; Metwali & Ahmed 1987
VII. SCUTACARID SPECIES ASSOCIATED WITH MYRMICINAE (HEXAPODA, ECTOGNATHA; ACULEATA, FORMICIDAE)

Acromyrmex lundi

Imparipes (Telodispu) formicarum Lombardini, 1960; Argentina; n.k.; Lombardini 1960

Aphenogaster spp.

Imparipes (Imparipes) obstinatus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) ursus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Scutacarus amoenus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Scutacarus ellipticus Karafiát, 1959; Austria; p; Ebermann & Krisper 2014
Scutacarus ovoideus Karafiát, 1959; Austria; p; Ebermann & Krisper 2014
Scutacarus sp.; Austria; p; Ebermann & Krisper 2014
Scutacarus tacitus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Atta cephalotes

Imparipes (Imparipes) atta Delfinado & Baker, 1976; Panama; n.k.; Delfinado & Baker 1976

Crematogaster spp.

Lophodispu irregularis (Mahunka, 1971); USA (Maryland); i; Ebermann 1980b
Scutacarus nudus bisetus Karafiát, 1959; USA (Maryland); i; Ebermann 1980b; “Variatipes”-group: no claw on leg I
Scutacarus rapoporti Mahunka, 1968; USA (Alabama); i; Ebermann 1980b

Messor spp.

Imparipes (Imparipes) histricinus Berlese, 1903; Angola, Australia, Austria, Brazil, Hungary, Italy, Mongolia, Tunisia, Ukraine, former Yugoslavia; i; also in soil
Imparipes (Imparipes) ignotus Khaustov & Chydyrov, 2004; Turkmenistan; i; Khaustov & Chydyrov 2004, Khaustov 2008
Imparipes (Imparipes) longicaudus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) messori Metwali & Ahmed, 1987; Egypt; p; Metwali & Ahmed 1987
Imparipes (Imparipes) moderatus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) morosus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) obsoletus Rack, 1966; holarctic; n.k.; Khaustov 2008; also in soil
Imparipes (Imparipes) placidus Khaustov & Chydyrov, 2004; Turkmenistan; i; Khaustov & Chydyrov 2004, Khaustov 2008
Scutacarus fimbrillatosimilis Metwali & Ahmed 1987; Egypt; p; Metwali & Ahmed 1987
Scutacarus quaesitus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Monomorium salmonis

Imparipes (Imparipes) messori Metwali & Ahmed, 1987; Egypt; p; Metwali & Ahmed 1987

Myrmica spp.

Imparipes (Imparipes) charkoviensis Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) circinnatus Mahunka, 1980; Austria; p; Friedl 2000, Ebermann & Krisper 2014
Imparipes (Imparipes) comatosimilis Metwali, 1981; Austria, Poland; p; Metwali 1981, Friedl 2000, Ebermann & Krisper 2014
Imparipes (Imparipes) comatus Mahunka, 1970; France, Hungary, Ukraine; i; Khaustov 2008
Imparipes (Imparipes) histricinus Berlese, 1903; Austria; i; Ebermann 1980a; also in moss
Imparipes (Imparipes) quaesitus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) sp.B (sensu Friedl 2000); Austria; p; Friedl 2000, Ebermann & Krisper 2014
Imparipes (Imparipes) sp. C (sensu Friedl 2000); Austria; p; Friedl 2000, Ebermann & Krisper 2014
Scutacarus angustus Mahunka, 1970; Austria, Hungary, Russia, Ukraine; i; Mahunka 1970b, 1972b; “Variatipes”-group: no claw on leg I
Scutacarus atypicus (Karafiát, 1959); Austria, Germany; i; Ebermann 1980a
Scutacarus crassissetus (Paoli, 1911); Austria; i; Mahunka 1970b; also in moss
Scutacarus ellipticus Karafiát, 1959; Austria, Germany, Hungary, Russia, Switzerland, Ukraine, former Yugoslavia; ip; Karafiát, Mahunka 1972b, 1977c, Friedl 2000, Khaustov 2008, Ebermann & Krisper 2014; also in soil
Scutacarus eucomus (Berlese, 1908); Austria; i; Mahunka 1970b; also in soil; “Variatipes”- group: no claw on leg I
Scutacarus hauseri Mahunka, 1977; France; n.k.; Mahunka 1977c
Scutacarus kassaii Mahunka, 1965; Russia; i; Khaustov 2015a
Scutacarus latus Karafiat, 1959; Austria; p; Friedl 2000, Ebermann & Krisper 2014
Scutacarus longisetus (Berlese, 1904); Austria, Bulgaria, Hungary, Italy, Poland, Switzerland, Ukraine, former Yugoslavia; i; Mahunka 1977c, Ebermann 1978, Khaustov 2008
Scutacarus myrmecophilus Metwali, 1981; Poland, Ukraine; i; Metwali 1981, Khaustov 2008
Scutacarus myrmicus Khaustov, 2015; Russia; i; Khaustov 2015c
Scutacarus ovoides Karafiat, 1959; Austria, Germany, Greece, Hungary, Poland, Switzerland, Ukraine; i; Mahunka 1977c, Ebermann 1979, Friedl 2000, Khaustov 2008, Ebermann & Krisper 2014
Scutacarus pegazzanoae Ebermann, 1986; Austria; p; Friedl 2000, Ebermann & Krisper 2014
Scutacarus plumosus (Paoli, 1911); Austria; i; Mahunka 1970b; also in soil; “Variatipes”- group: no claw on leg I
Scutacarus subtilis Rack, 1966; Austria; i; Mahunka 1970b; also in moss; “Variatipes”- group: no claw on leg I
Scutacarus tactei Willmann, 1942; Austria, Czechoslovakia, France, Germany, Hungary, India, Switzerland, former Yugoslavia; p; Ebermann 1978, Ebermann & Krisper 2014; also in soil
Scutacarus yuliae Khaustov, 2006; Ukraine; p; Khaustov 2006, 2008

Pheidole pallidula
Imparipes (Imparipes) kugitangensis Khaustov & Chydyrov, 2004; Turkmenistan; i; Khaustov 2008
Scutacarus magyarosimilis Metwali & Ahmed, 1987; Egypt; p; Metwali & Ahmed 1987

Pogonomyrmex occidentalis
Imparipes (Imparipes) latispinus Mahunka, 1970; USA (Nebraska); n.k.; Mahunka 1970c
Scutacarus wranoskyi Mahunka, 1970; USA (Nebraska); n.k.; Mahunka 1970c

Solenopsis spp.
Imparipes (Imparipes) histicinus Berlese, 1903; Italy; p; Berlese 1903
Imparipes (Imparipes) cf. parapicolosimilis Metwali, 1981; Austria; p; Friedl 2000, Ebermann & Krisper 2014
Imparipes (Imparipes) louisianae Ebermann & Moser, 2008; USA (Louisiana); p; Ebermann & Moser 2008, Moser & Blomquist 2011; on alates
Scutacarus andrassyi Mahunka, 1968; USA (Louisiana); n.k.; Ebermann & Moser 2008, Moser & Blomquist 2011
Scutacarus n.sp. near deserticolus Mahunka, 1969; USA (Louisiana); n.k.; Ebermann & Moser 2008, Moser & Blomquist 2011
Scutacarus natus Ebermann & Moser, 2008; USA (Louisiana); n.k.; Ebermann & Moser 2008, Moser & Blomquist 2011
Scutacarus tertius Ebermann & Moser, 2008; USA (Louisiana); n.k.; Ebermann & Moser 2008, Moser & Blomquist 2011

Temnothorax spp.
Imparipes (Imparipes) histicinus Berlese, 1903; Iran; p; Loghmani et al. 2014
Scutacarus claviger (Paoli, 1911); Iran; p; Loghmani et al. 2014

Tetramorium spp.
Imparipes (Imparipes) cf. imaginatus Mahunka, 1981; Austria; p; Friedl 2000, Ebermann & Krisper 2014
Imparipes (Imparipes) cf. tenuis Mahunka, 1981; Austria; p; Friedl 2000, Ebermann & Krisper 2014
Imparipes (Imparipes) comatus Mahunka, 1970; France, Hungary, Ukraine; i; Khaustov 2008
Imparipes (Imparipes) hortobagensis Mahunka, 1981; Hungary, Ukraine; i; Khaustov 2008
Imparipes (Imparipes) histicinus Berlese, 1903; Austria, Czech Republic, Italy; ip; Berlese 1903, Štorkán 1940, Ebermann 1980a; also in moss
Imparipes (Imparipes) lentus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) parapicolosimilis Metwali, 1981; Poland; i; Metwali 1981
Imparipes (Imparipes) paucus Khaustov, 2008; Ukraine; n.k.; Khaustov 2008
Imparipes (Imparipes) robustus Karafiat, 1959; Austria, Bulgaria, France, Germany, Hungary, Japan, Mongolia, Russia, Ukraine (Palaearctic?); n.k.; Khaustov 2008; also in soil, litter

Imparipes (Imparipes) sklyari Khaustov, 2008; Ukraine; n.k.; Khaustov 2008

Scutacarus bursula (Berlese, 1903); Germany, Italy, Ukraine; ip; Paoli 1911, Khaustov 2008

Scutacarus cf. paolii Mahunka, 1965; Austria; p; Ebermann & Krisper 2014

Scutacarus ellipticus Karafiat, 1959; Austria; p; Ebermann & Krisper 2014

Scutacarus longisetus (Berlese, 1904); Austria, Bulgaria, Hungary, Italy, Poland, Switzerland, Ukraine, former Yugoslavia; i; Khaustov 2008

Scutacarus paolii Mahunka, 1965; Austria, Hungary; i; Ebermann 1980a; also in soil

Scutacarus rakonczayi Mahunka, 1981; Austria; p; Ebermann & Krisper 2014

Scutacarus subquadratus Khaustov & Chydyrov, 2004; Turkmenistan; n.k.; Khaustov 2008

Imparipes (Imparipes) cf. imaginatus Mahunka, 1981; Austria; p; Ebermann & Krisper 2014

Imparipes (Imparipes) cf. parapicolosimilis Metwali, 1981; Austria; p; Ebermann & Krisper 2014

“Myrmicinae” (not further classified in literature)

Imparipes (Imparipes) rectangulatus Mahunka, 1977; USA (Kansas); n.k.; Mahunka 1977a

Scutacarus rettenmeyeri Mahunka, 1977; USA (Kansas); n.k.; Mahunka 1977a

VIII. SCUTACARID SPECIES ASSOCIATED WITH AVES AND MAMMALIA

Aves: Accipitridae

Scutacarus ameropannonicus Mahunka & Philips, 1978; USA (New York); i; Mahunka & Philips 1978; in fecal pellet

Aves: “Antarctic birds”

Scutacaridae; Antarctica; p; Krivolutsky et al. 2004

Aves: Procellariidae

Puffinus tenuirostris

Heterodispus longisetosus (Womersley, 1955); Australia; i; Womersley 1955

Aves: Strigiformes

Pygmodispus (Pygmodispus) abestus Mahunka & Philips, 1978; USA (New York); i; Mahunka & Philips 1978; in fecal pellet

Scutacarus subsphaeroides Mahunka & Philips, 1978; USA (New York); i; Mahunka & Philips 1978; in fecal pellet

Scutacaridae; USA (Massachusetts); i; Philips et al. 1988

Aves: “birds” (not further classified in literature)

Imparipes (Imparipes) obsoletus Rack, 1966; USA (New York); i; Delfinado et al. 1976

Scutacarus imitans Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976

Scutacarus meansi Delfinado & Baker, 1978; USA (New York); i; Delfinado & Baker 1978; also in dog food (sic!)

Scutacarus subaffinis Delfinado & Baker, 1978; USA (New York); i; Delfinado & Baker 1978

Scutacarus unicus indefinitus Delfinado & Baker, 1978; USA (New York); i; Delfinado & Baker 1978

Scutacarus uniformis Delfinado et al., 1976; USA (New York); i; Delfinado et al. 1976
**Mammalia: Eulipotyphla**

**Soricidae: Blarinabrevicauda**

*Scutacarus impar* Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976; in wet habitats

*Scutacarus subspinosis* Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976

**Soricidae: Crocidura suaveolens**

*Reductacarus singularis* Mahunka, 1963; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Scutacarus eucomus* (Berlese, 1908); Ukraine; i; Sevastyanov & Uzhevskaya 2003; “Variatipes”-group: no claw on leg I

**Soricidae: Sorex sp.**

*Scutacarus apodemi* Mahunka, 1963; Hungary; i; Mahunka 1963

*Scutacarus ornaiyri* Mahunka, 1963; Hungary; i; Mahunka 1972b

*Scutacarus spinosus* Storkan, 1936; Hungary; i; Mahunka 1963; in meadow soil

**“Soricidae” (not further classified in literature)**

*Scutacarus imitans* Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976

*Scutacarus subspinosis* Delfinado & Baker, 1976; USA (New York); i; Delfinado & Baker 1976

**Talpidae: Talpa europea**

*Scutacarus acarorum* (Goeze, 1780); Europe; n.k.; Oudemans 1913

*Scutacarus mahnerii* Mahunka, 1972; Austria; i; Mahunka 1972a

*Scutacarus mendax* Karafiát, 1959; Slovakia; i; Kalúz 2001

*Scutacarus talpae* (Oudemans, 1913); Netherlands; i; Oudemans 1913; phoretic on gamasids in nest!

**“Talpidae” (not further classified in literature)**

*Scutacarus subterraneus* (Oudemans, 1913); Balkans, Germany; i; Karafiát 1959; also in meadow soil

**Mammalia: Rodentia**

**Cricetidae: Clethrionomys glareolus**

*Scutacarus subterraneus* (Oudemans, 1913); Ukraine; i; Sevastyanov & Uzhevskaya 2003

**Cricetidae: Cricetulus migratorius**

*Heterodipsis elongatus* (Paoli, 1911) (?); Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) comatus* Mahunka, 1970; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) obsoletus* Rack, 1966; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Lophodipsis irregularis* (Mahunka, 1971); Ukraine; i; Sevastyanov & Uzhevskaya 2003; syn. *Imparipes (I.) taurensis* Sevastianov, 1975

*Pygmodispus (Pygmodispus) zicsii* Mahunka, 1964; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Scutacarus eucomus* (Berlese, 1908); Ukraine; i; Sevastyanov & Uzhevskaya 2003; “Variatipes”-group: no claw on leg I

*Scutacarus kassaii* Mahunka, 1965; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Scutacarus quadrangularis* (Paoli, 1911); Ukraine; i; Sevastyanov & Uzhevskaya 2003; “Variatipes”-group: no claw on leg I

*Scutacarus spinosus* Storkan, 1936; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Scutacarus tacensis* Mahunka, 1964; Ukraine; i; Sevastyanov & Uzhevskaya 2003

**Cricetidae: Microtus arvalis**

*Heterodipsis elongatus* (Paoli, 1911); Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) carabidophilus* Sevastianov, 1974; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) cavernophilus* Sevastianov, 1974; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) crassimerus* Mahunka, 1968; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) degenerans* Berlese, 1904; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) hungaricus* Balogh & Mahunka, 1962; Ukraine; i; Sevastyanov & Uzhevskaya 2003

*Imparipes (Imparipes) kossensis* Sevastianov, 1975; Ukraine; i; Sosnina & Sevastianov 1975

*Imparipes (Sporichneuthes) kaszabi* Mahunka, 1967; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Lophodispus irregularis (Mahunka, 1971); Ukraine; i; Sosnina & Sevastianov 1975, Sevastyanov & Uzhevskaya 2003; syn. Imparipes (I.) taurensis Sevastianov, 1975
Scutacarus culmusophilus Sevastianov, 1975; Ukraine; i; Sosnina & Sevastianov 1975
Scutacarus occultatus Sevastianov, 1975; Ukraine; i; Sosnina & Sevastianov 1975

**Cricetidae: Microtus brandti**
Imparipes (Imparipes) mongolicus Mahunka, 1967; Hungary, Mongolia; i; Mahunka 1967a, 1972b
Imparipes (Sporichneuthes) kaszabi Mahunka, 1967; Mongolia; i; Mahunka 1967a
Reductacarus singularis Mahunka, 1963; Mongolia; i; Mahunka 1967a
Scutacarus sphaeroideus Karafiát, 1959; Mongolia; i; Mahunka 1967a
Scutacarus tacensis Mahunka, 1964; Hungary, Mongolia; i; Mahunka 1967a, 1972b

**Cricetidae: Microtus pennsylvanicus**
Scutacarus spinosus Storkan, 1936; USA (New York); i; Delfinado & Baker 1976; also in leaf litter

**Cricetidae: Microtus sp.**
Reductacarus singularis Mahunka, 1963; Hungary; n.k.; Mahunka 1972b
Scutacarus deserticolus Mahunka, 1969; Hungary, Mongolia; i; Mahunka 1969a, 1972b

**Cricetidae: Peromyscus leucopus**
Scutacaridae; USA (Illinois); p; Drummond 1957, Basolo & Funk 1974

**Geomyidae: Geomys bursarius**
Imparipes (Imparipes) spickai Mahunka, 1977; USA (Illinois); p; Mahunka 1977d
Scutacarus geomyi Mahunka, 1977; USA (Illinois); p; Mahunka 1977d
Scutacarus missouriensis Mahunka, 1977; USA (Missouri); p; Mahunka 1977d

**Geomyidae: Geomys bursarius illinoensis**
Imparipes (Imparipes) spickai Mahunka, 1977; USA (Illinois); p; Spicka 1981
Scutacarus geomyi Mahunka, 1977; USA (Illinois); p; Spicka 1981

**Geomyidae: Geomys bursarius missouriensis**
Scutacarus missouriensis Mahunka, 1977; USA (Missouri); p; Spicka 1981

**Heteromyidae: Chaetodipus spinatus lambi**
Imparipes (Imparipes) cupes Delfinado & Baker, 1978; Mexico; p; Estébanes-González & Cer-vantes 2005, skin of dorsal region; in small cavities that appear as scabs

**Heteromyidae: Dipodomys spectabilis**
Scutacaridae; Australia; i; Seastedt et al. 1986

**Muridae: Apodemus agrarius**
Heterodispus elongatus (Paoli, 1911) (?); Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) obsoletus Rack, 1966; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus euconus (Berlese, 1908); Ukraine; i; Sevastyanov & Uzhevskaya 2003; “Variatipes”-group: no claw on leg I

**Muridae: Apodemus flavicollis**
Imparipes (Imparipes) degenerans Berlese, 1904; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) histricinus Berlese, 1903; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Lophodispus irregularis (Mahunka, 1971); Ukraine; i; Sosnina & Sevastianov 1975, Sevastyanov & Uzhevskaya 2003; syn. Imparipes (I.) taurensis Sevastianov, 1975
Scutacarus culmusophilus Sevastianov, 1975; Ukraine; i; Sosnina & Sevastianov 1975, Sevastyanov & Uzhevskaya 2003
Scutacarus indistinctus Sevastianov, 1975; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus palustris Rack, 1966; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus tener Sevastianov, 1975; Ukraine; i; Sevastyanov & Uzhevskaya 2003

**Muridae: Apodemus sylvaticus**
Heterodispus citelli Mahunka, 1970; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Heterodispus elongatus (Paoli, 1911); Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Apidacarus) platycephalus Sevastianov, 1974; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) carabidophilus Sevastianov, 1974; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) cavernophilus Sevastianov, 1974; Ukraine; i; Sevastyanov & Uzhevskaya 2003

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Imparipes (Imparipes) comatus Mahunka, 1970; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) crassimerus Mahunka, 1968; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) histrionicus Berlese, 1903; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Imparipes) penicillatus Mahunka, 1967; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Imparipes (Sporichneuthes) kaszabi Mahunka, 1967; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus apodeni Mahunka, 1963; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus culmusphilus Sevastianov, 1975; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus eucosmus (Berlese, 1908); Ukraine; i; Sevastyanov & Uzhevskaya 2003; “Variatipes”-group: no claw on leg I
Scutacarus kassaii Mahunka, 1965; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus quadrangularis (Paoli, 1911); Ukraine; i; Sevastyanov & Uzhevskaya 2003; “Variatipes”-group: no claw on leg I
Scutacarus sphaeroideus Karafiat, 1959; Ukraine; i; Sevastyanov & Uzhevskaya 2003
Scutacarus spinosus Storkan, 1936; Hungary; Ukraine; i; Sevastyanov & Uzhevskaya 2003, Mahunka 1963

Muridae: Apodemus sp.
Scutacarus apodeni Mahunka, 1963; Hungary; Ukraine; i; Mahunka 1963, Sosnina & Sevastianov 1975
Scutacarus ormayi Mahunka, 1963; Hungary; i; Mahunka 1972b
Scutacarus spinosus Storkan, 1936; Hungary; i; Mahunka 1963; also in soil

Muridae: Desmodillus auricularis, Dipodillus harwoodi, Gerbilliscus (= Tatera) leucogaster, Rhadomys pumila
Heterodipsus foveatus Jaggersbacher-Baumann & Ebermann, 2012; Kenya, Namibia, Rwanda, South Africa; ip; Jaggersbacher-Baumann & Ebermann 2012a

“Muridae” (not further classified in literature)
Diversipes exhamulatus (Michael, 1886); Germany; i; Rack 1966; also in soil, decaying material
Imparipes (Imparipes) obsoletus Rack, 1966; Germany; i; Rack 1966
Scutacarus peractus Karafiat, 1959; Germany; i; Rack 1966; also in soil, decaying material

Sciuridae: Citellus citellus
Heterodipsus cielli Mahunka, 1970; Hungary; i; Mahunka 1970a
Heterodipsus elongatus (Paoli, 1911); Hungary; i; Balogh & Mahunka 1962
Heterodipsus pannonicus Mahunka, 1963; Hungary; i; Mahunka 1963, Jaggersbacher-Baumann & Ebermann 2012b
Reductacarus singularis Mahunka, 1963; Hungary; i; Mahunka 1963
Scutacarus spinosus Storkan, 1936; Hungary; i; Mahunka 1963; also in meadow soil

Sciuridae: Sciurus carolinensis
Scutacarus imitans Delfinado & Baker, 1976; USA (New York); p; Delfinado & Baker 1976

Sciuridae: Xerus inauris
Heterodipsus foveatus Jaggersbacher-Baumann & Ebermann, 2012; South Africa; i; Jaggersbacher-Baumann & Ebermann 2012a

Mammalia: “rodents” (not further classified in literature)
Heterodipsus tragardhi (Delfinado & Baker, 1976); USA (New York); i; Delfinado & Baker 1976
Scutacarus kassaii Mahunka, 1965; Ukraine; i; Sklyar & Sevastianov 1997

Mammalia: “small mammals” (not further classified in literature)
Scutacarus longisetus (Berlese, 1904); Slovenia; i; Mahunka 1975b; also in ant nests
Scutacarus major (Paoli, 1911); Slovenia; i; Mahunka 1975b
Scutacarus plumosus (Paoli, 1911); Slovenia; i; Mahunka 1975b
Scutacarus quadrangularis (Paoli, 1911); Slovenia; i; Mahunka 1975b; “Variatipes”-group: no claw on leg I
Scutacarus sphaeroideus Karafiat, 1959; Slovenia; i; Mahunka 1975b
Scutacarus spinosus Storkan, 1936; Slovenia; i; Mahunka 1975b

Mammalia: carrion of Felis silvestris catus
Scutacaridae; USA (Hawaii); n.k.; Early & Goff 1986