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

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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

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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 superfamily Pygmephoroidea, Heterostigmatina, and is characterized by remarkably small body sizes of about 200µm, 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 (Anoetida, 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

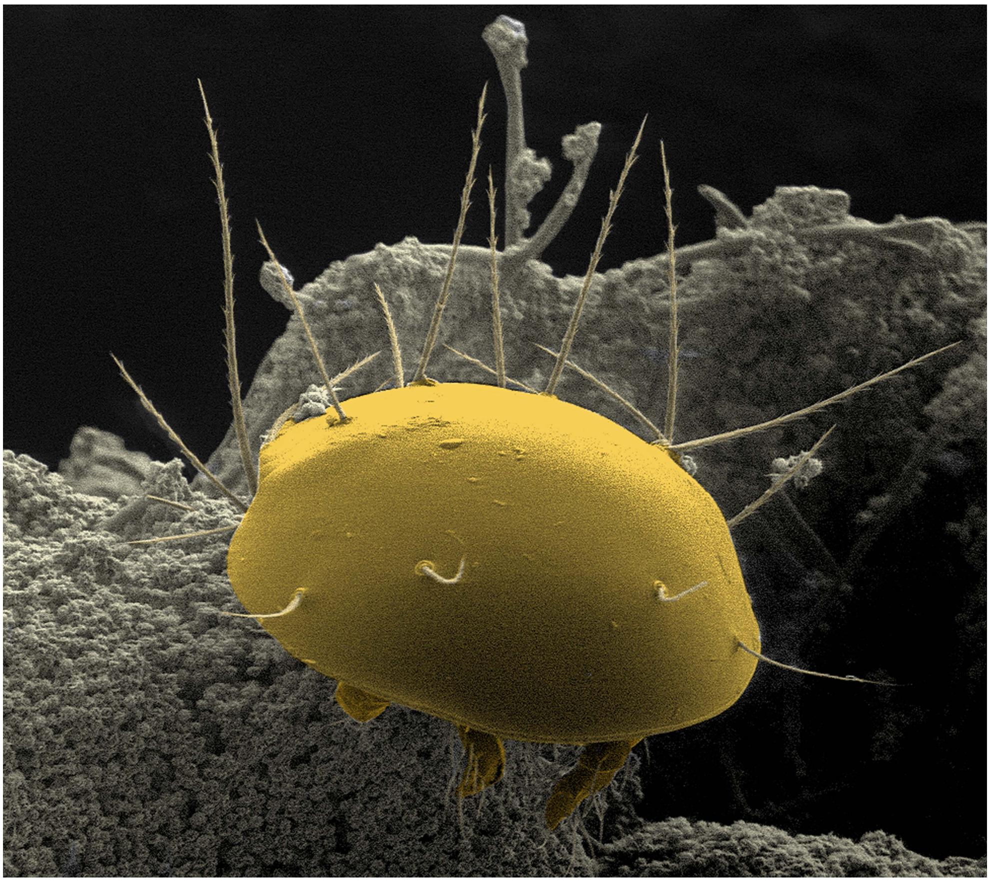

Figure 1 Fronto-dorsal view of a typical scutacarid adult female (*Imparipes* (*Sporichneuthes*) *dispar* Rack, 1964) moving on a carpet of fungi, scanning-electron micrograph. The curved tergites give the mite a tortoise-like habitus.

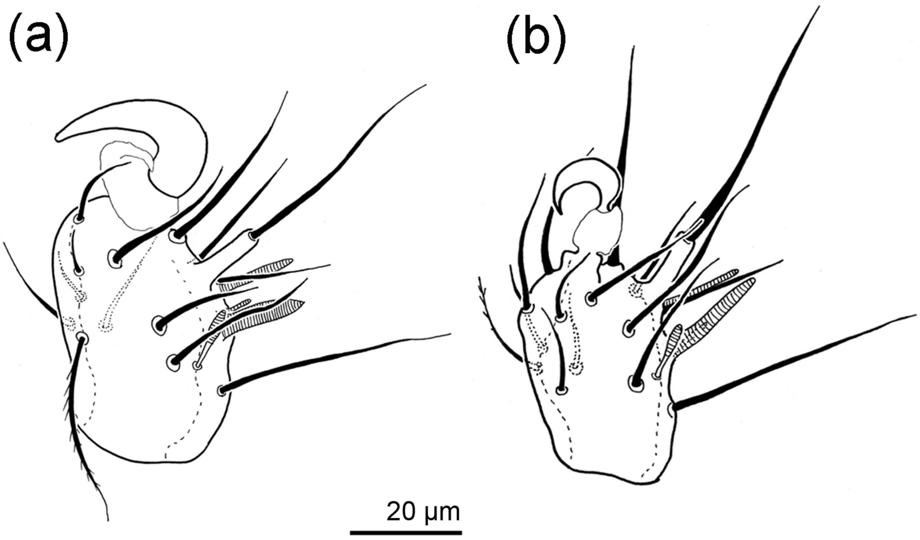

Figure 2 Differences between the tarsi and the claws on leg I of a) a phoretic and b) a nonphoretic morph of a female scutacarid (*Scutacarus acarorum* Goeze 1780).

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 1 Scutacarid species for which phoretomorphism has been reported.

species (phoretic morph)	non-phoretic morph
Archidispus amarae (Kurosa, 1970)	described by Ebermann (1991a)
Archidispus armatus (Karafiat, 1959)	*A. soosi* (Mahunka); synonymized by Ebermann (1991a)
Archidispus bembidii (Karafiat, 1959)	described by Ebermann (1991a)
Archidispus magnificus (Karafiat, 1959)	described by Ebermann (1991b)
Archidispus minor (Karafiat, 1959)	described by Ebermann (1991b); very similar to *A. haarloevi* Karafiat
Lamnacarus ornatus Balogh & Mahunka, 1963	*L. coprophilus* Mahunka; synomnyized by Ebermann (1990)
Scutacarus acarorum (Goeze, 1780)	reported by Ebermann (1992)
Scutacarus australiensis Mahunka, 1967	reported by Greenslade & Clift 2004
Scutacarus baculitarsus agaricus (Norton & Ide, 1974)	reported by Norton (1977)
Scutacarus deserticolus Mahunka, 1969	reported by Ebermann (1991a)
Scutacarus longitarsus (Berlese, 1905)	*S. subfimetarius* Momen & El-Bagoury; synonymized by Ebermann (1990)
Scutacarus mendax Karafiat, 1959	reported by Jagersbacher-Baumann (2014)

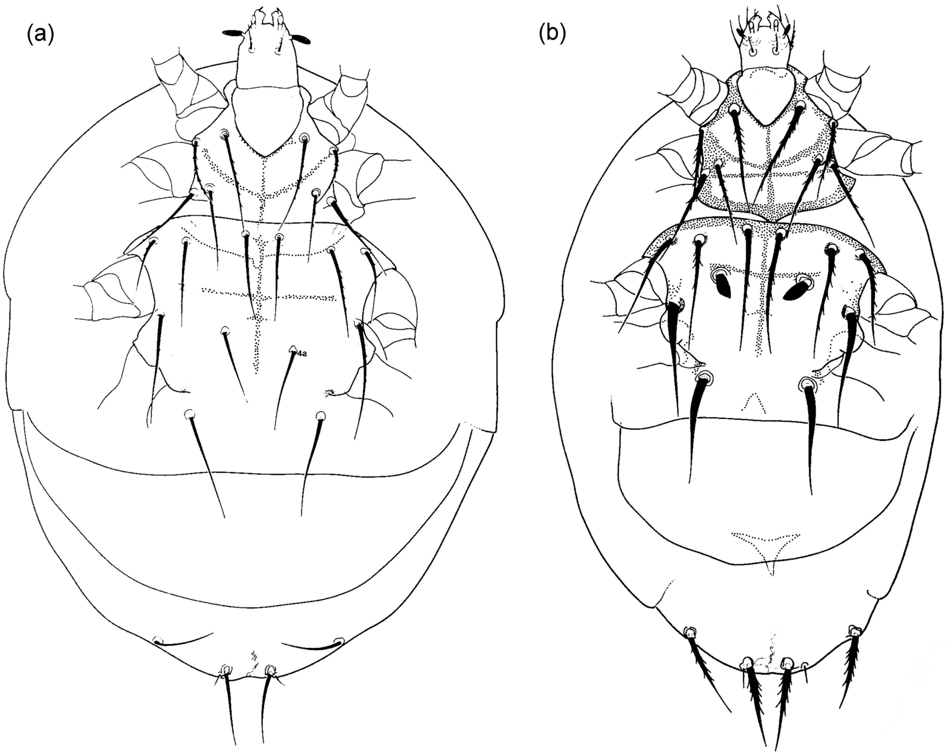

Figure 3 a) Non-phoretic and b) phoretic female of *Archidispus armatus* Karafiat 1959, ventral view. The body setae differ distinctly between the two morphs (modified after Ebermann 1991a).

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 *L. ornatus* Balogh & Mahunka, 1963 and *Scutacarus subfimetarius* Momen & Bagoury, 1989 is the non-phoretic morph of *S. longitarsus* (Berlese, 1905). In the same work, Ebermann also discouraged from using *Variatipes*, a subgenus of the genus *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 *Archidispus* as the two female morphs differ extremely in this taxon. For several *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 appetence 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 appetence 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 appetence behaviour described above has been reported for *Scutacaropsis baculitarsus* (Mahunka, 1968) by Binns (1979), for *Archidispus amarae* (Kurosa, 1970), *A. armatus*, *A. bembidii* (Karafiat, 1959), *A. magnificus* (Karafiat, 1959) and *A. minor* (Karafiat, 1959) by Ebermann (1991a,b), for *Imparipes* (*Sporichneuthes*) *dispar* Rack, 1964 by Ebermann (1995) and for the genus *Lophodispus* by Schlagbauer (1997) and Ebermann and Krisper (2014), and it has moreover been observed in *Imparipes (I.) histricinus* Berlese, 1903, *Scutacarus longipes* Rack, 1975 and *S. longitarsus* (Berlese, 1905) (Ebermann pers. comm.). In the genus *Archidispus*, Ebermann (1991a) noted that only phoretomorph females performed appetence behaviour, while non-phoretomorph females always fled whenever potential hosts approached.

Imparipes (S.) dispar, *Lophodispus bulgaricus* Dobrev, 1992 and *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 *Imparipes* and by Schlagbauer (1997) in his master thesis for *Lophodispus*. The jumping behaviour of *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 *I. dispar* to jump onto fast-moving hosts. The two *Lophodispus* species show the same jumping types as *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 *I. dispar* nor the two *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 appetence 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) proofed 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 flavipes* (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 hyphe (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 Jagersbacher-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**): The African mite *Heterodispus foveatus* Jagersbacher-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 (Jagersbacher-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 (Jagersbacher-Baumann and Ebermann 2012a), which can

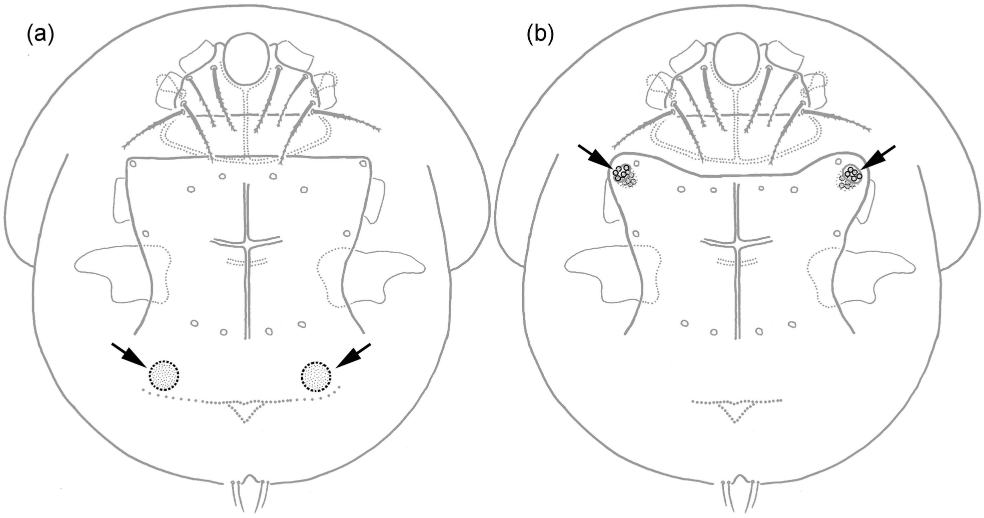

Figure 4 Schematic illustration of the sporothecae of a) *Imparipes haeseleri* and b) *Heterodispus foveatus*. Ventral view. Arrows point to the spores inside the sporothecae.

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).

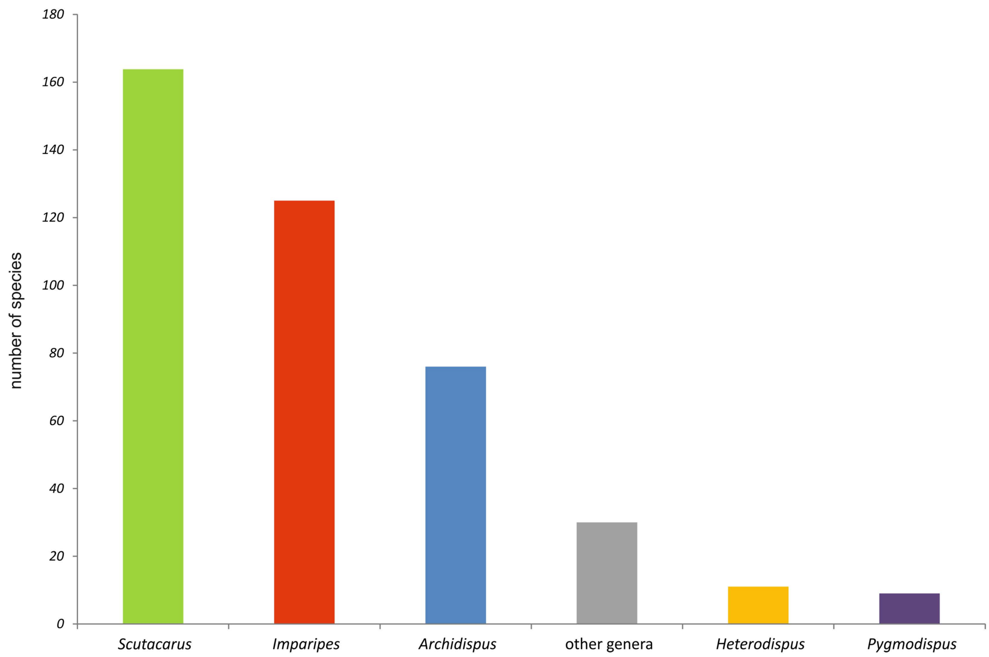

Figure 5 Number of scutacarid species found in associations with other animals, grouped according to their genus.

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 tocatlphilus* 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

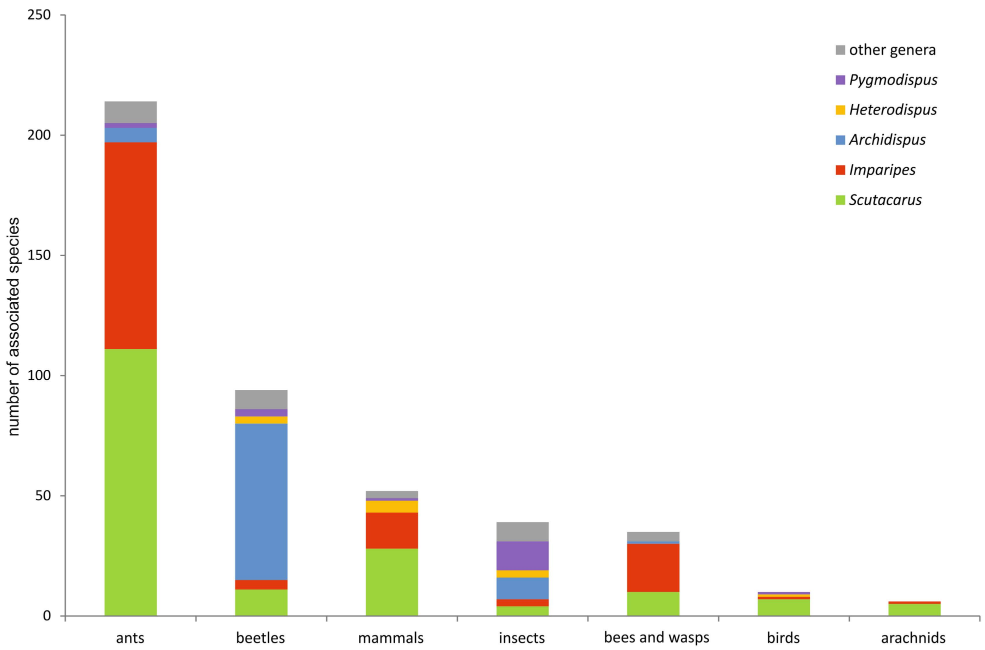

Figure 6 Number of scutacarid species and subspecies, genera marked by colour, associated with different host groups. The group "insects" comprises Entognatha, Dermaptera, Diptera, Heteroptera, Isoptera and Orthoptera as well as hosts that have not been defined further in literature.

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 Anoetidae (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 I**). 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.

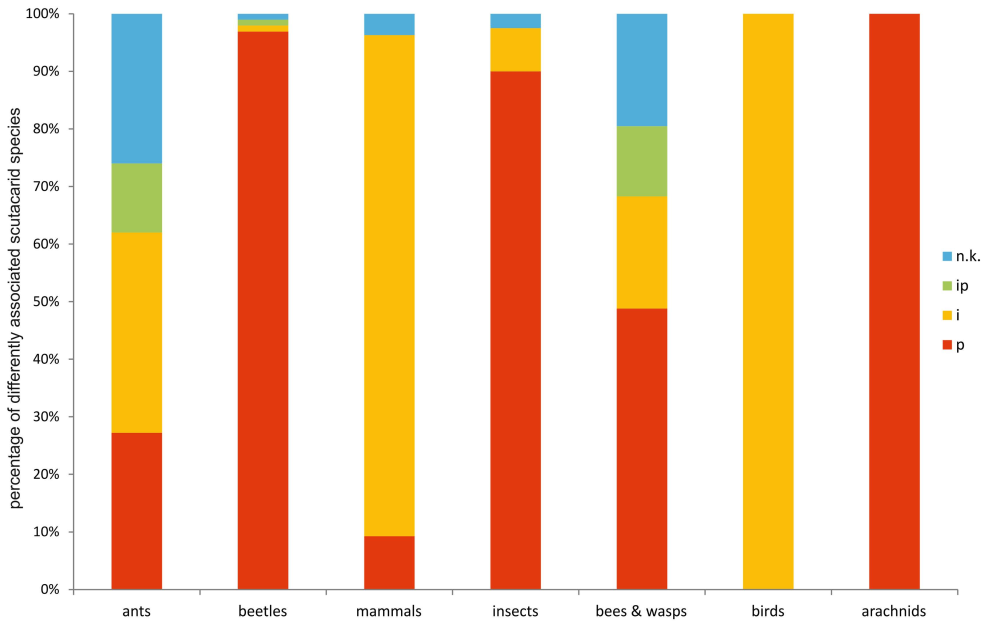

Figure 7 Percentages of differently associated scutacarid species and subspecies according to their different host groups. Types of associations: p, phoretic; i, inquilines; ip, inquilines and phoretic, n.k., not known (not given in literature). The group "insects" comprises Entognatha, Dermaptera, Diptera, 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

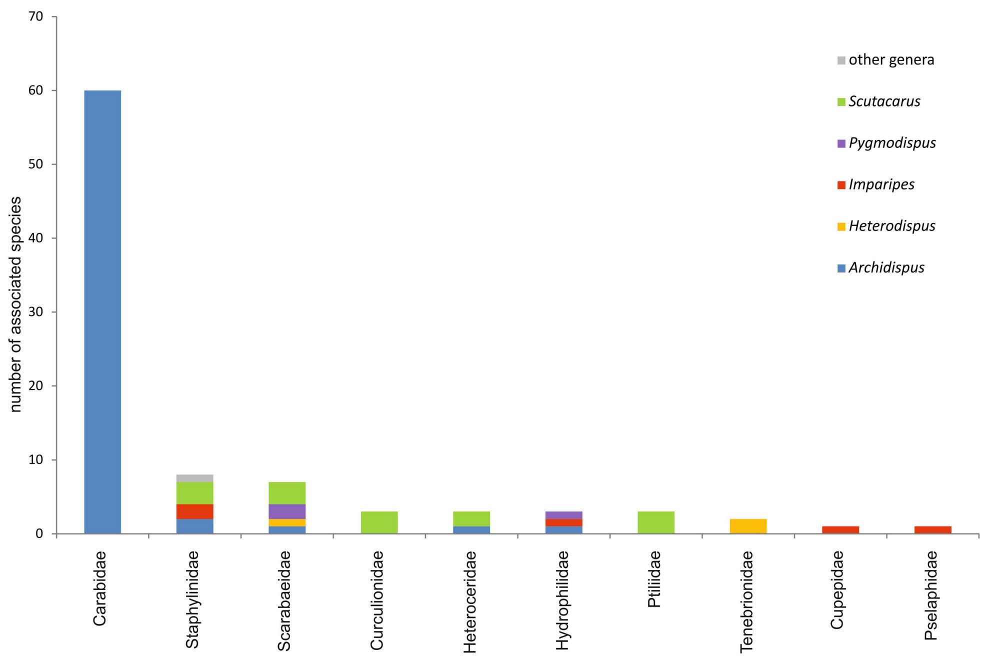

Figure 8 Number of scutacarid species associated with different families of beetles (Coleoptera)

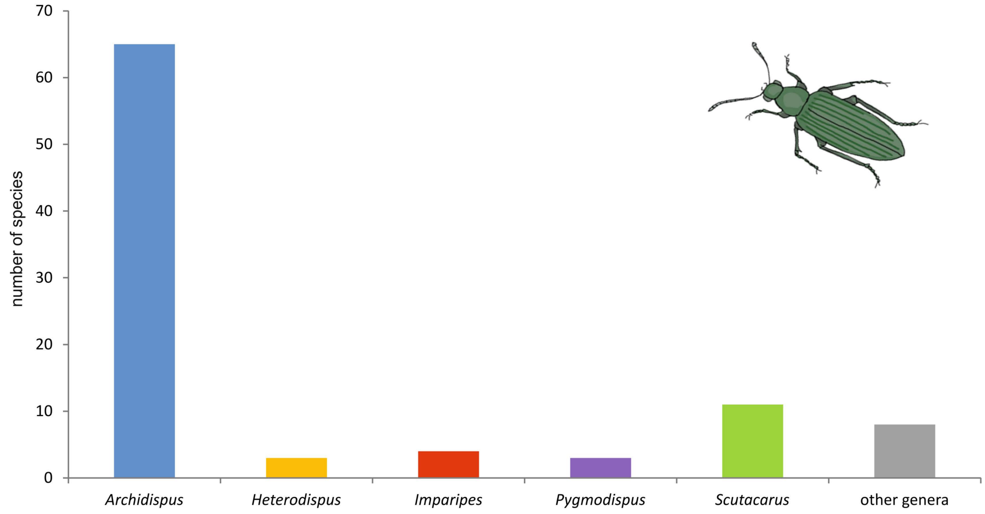

Figure 9 Number of scutacarid species belonging to different genera associated with beetles (Coleoptera). "Other genera" combine *Diversipes*, *Lamnacarus*, *Symbolacrasis* and *Thaumatopelvis*.

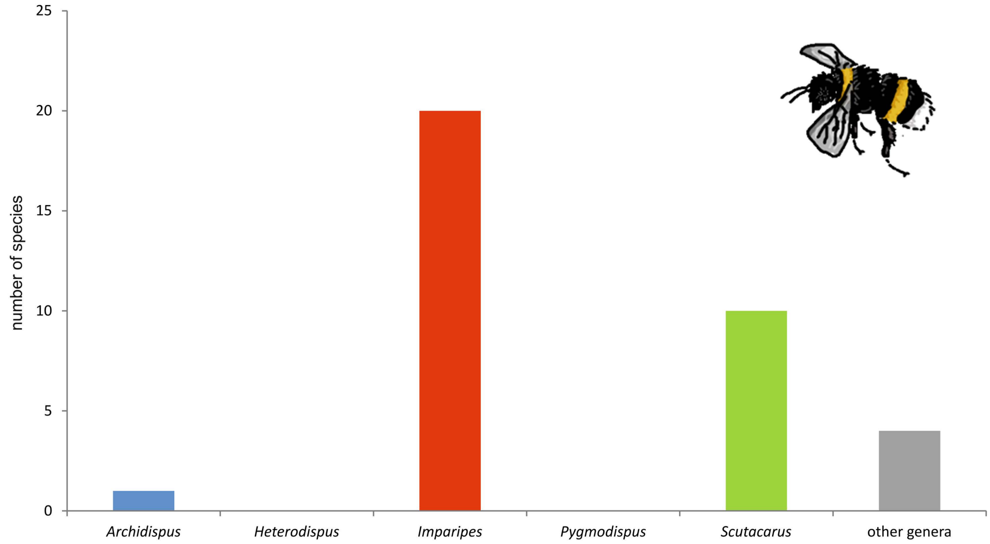

Figure 10 Number of scutacarid species belonging to different genera associated with bees and wasps (Apoidea and Vespoidea excl. Formicidae). "Other genera" combine *Diversipes*, *Lamnacarus*, *Lophodispus*, *Nasutiscutacarus*, *Parascutacarus*, *Reductacarus*, *Rettenmeyerella*, *Scutacaropsis*, *Symbolacrasis* and *Thaumatopelvis*.

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*, *Pygmodispus* 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

1959).

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. *culmusophilus* 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 with 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).

Finally, there are also reports of scutacarid mites phoretic on not nearer identified "coleoptera" from Australia and Ghana (**Annex III**). They comprise *Archidispus cornutus* (Mahunka, 1973), *Diversipes horridolatus* Mahunka, 1975, *Lamnacarus expansus* Mahunka, 1973, 2 *Scutacarus* species, 3 *Symbolacrasis* species and two species of *Thaumatopelvis* (Mahunka 1973a, 1973b, 1975c, Ebermann 1980b). The three species *Symbolacrasis acutimera* Mahunka, 1973, *S. hypostigma* Mahunka, 1973 and *S. synmixta* Mahunka, 1973 are the only known members of *Symbolacrasis*, which means that the entire genus is known exclusively phoretic on coleopterans.

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 superfamily **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 **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 Vespoidea, 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, Khaustov 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

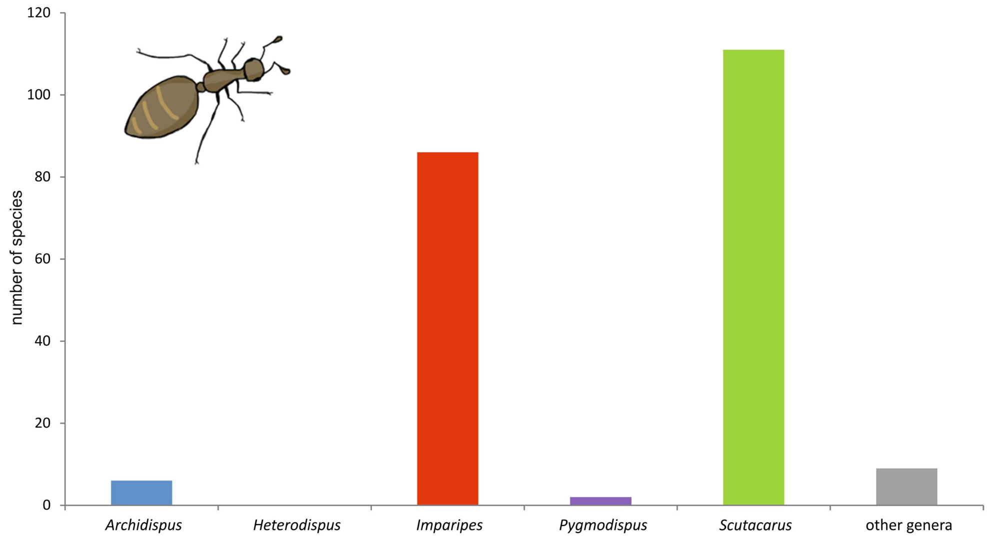

Figure 11 Number of scutacarid species belonging to different genera associated with ants (Formicidae). "Other genera" combine *Diversipes*, *Lamnacarus*, *Lophodispus*, *Nasutiscutacarus*, *Parascutacarus*, *Reductacarus*, *Rettenmeyerella*, *Scutacaropsis*, *Symbolacrasis* and *Thaumatopelvis*.

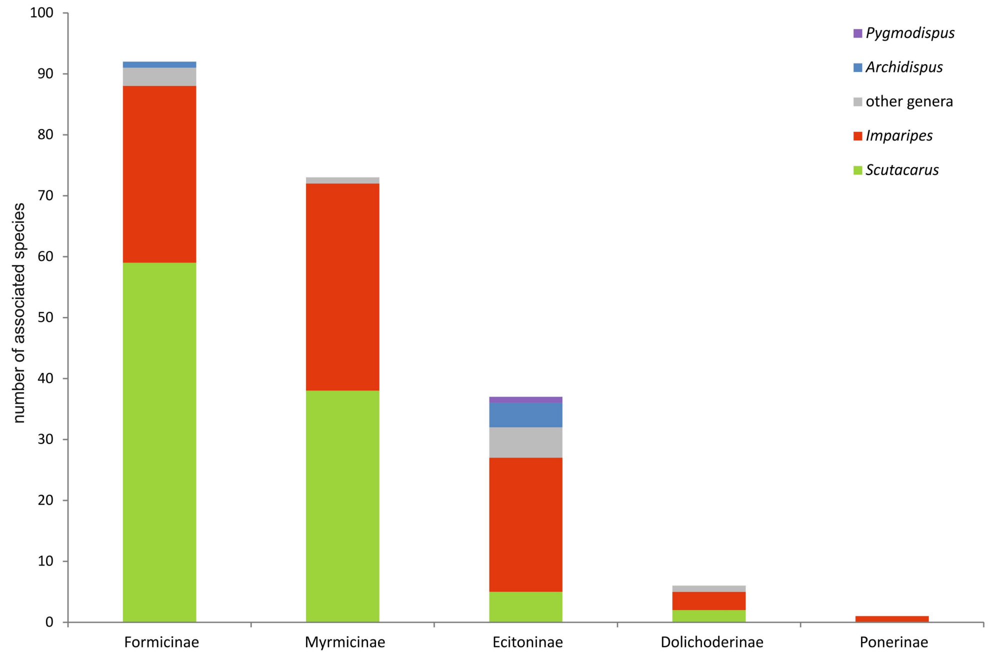

Figure 12 Number of scutacarid species belonging to different genera associated with different subfamilies of ants (Formicidae).

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 classifaction 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 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 histricinus*, 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. histricinus* 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).

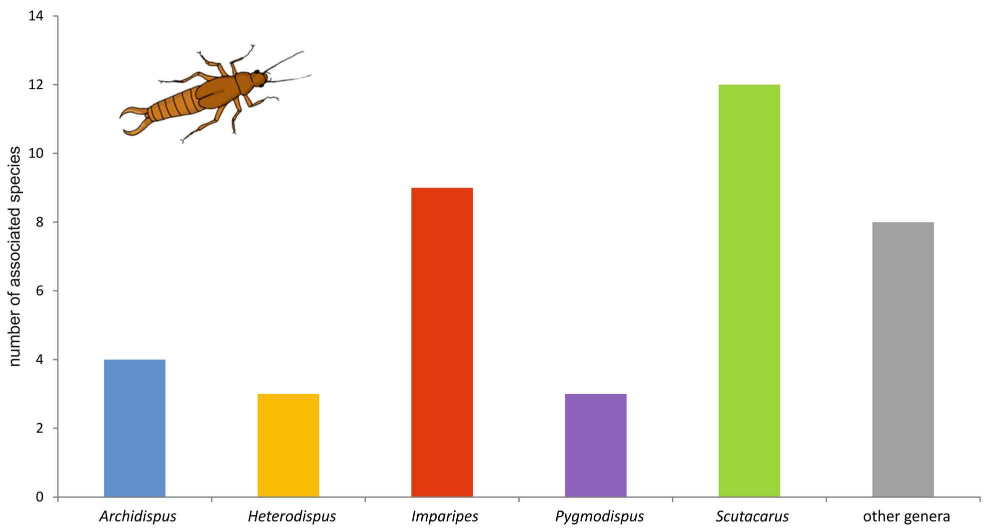

Figure 13 Number of scutacarid species belonging to different genera associated with various "insects" (insecta). The group "insects" comprises Entognatha, Dermaptera, Diptera, Heteroptera, Isoptera and Orthoptera as well as hosts that have not been defined further in literature. "Other genera" combine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

Table 2 Scutacarid species with a considerable broad host range.

Scutacarid species	Host taxa	References
Heterodispus foveatus Jagersbacher-Baumann & Ebermann 2012	Coleoptera (Carabidae), small mammals (rodents)	Jagersbacher-Baumann & Ebermann 2012a
Imparipes (Imparipes) comatus Mahunka, 1970	Ants, small mammals (rodents)	Mahunka 1970b, 1977c, Sevastyanov & Uzhevskaya 2003, Khaustov 2008
I. (I.) cupes Delfinado & Baker, 1978	Coleoptera (Cupepidae), small mammals (rodents)	Delfinado & Baker 1978, Estébanes-González & Cervantes 2005
I. (I.) degenerans Berlese, 1904	Ants, bees, small mammals (rodents)	Karafiat 1959, Sevastyanov & Uzhevskaya 2003
I. (I.) histricinus Berlese, 1903	Ants, Coleoptera, Dermaptera, small mammals (rodents)	Trägårdh 1905, Paoli 1911, Štorkán 1940, Karafiat 1959, Ebermann 1980a, 1982, Mahunka 1981, Sevastyanov & Uzhevskaya 2003, Khaustov 2008
I. (I.) obsoletus Rack, 1966	Ants, birds, small mammals (rodents)	Rack 1966, Delfinado et al. 1976, Mahunka 1981, Sevastyanov & Uzhevskaya 2003, Khaustov 2008
I. (I.) penicillatus Mahunka, 1967	Diptera, small mammals (rodents)	Mahunka 1973c, Sevastyanov & Uzhevskaya 2003
I. (I.) rectangulatus Mahunka, 1977	Ants, Caelifera	Mahunka 1977a
I. (Sporichneuthes) dispar Rack, 1964	Ants, coleoptera, diptera, hymenoptera	Messner 2001, Ebermann et al. 2016
Rettenmeyerella petropolitana (Vitzthum, 1928)	Ants, diptera	Vitzthum 1928, Mahunka 1977a
Scutacarus deserticolus Mahunka, 1969	Acari, bees, small mammals (rodents)	Mahunka 1969a, 1972b, Ebermann 1991a
S. eucomus (Berlese, 1908)	Ants, small mammals (rodents)	Mahunka 1970b, Sevastyanov & Uzhevskaya 2003
S. imitans Delfinado & Baker, 1976	Birds, small mammals (rodents)	Delfinado & Baker 1976
S. kassaii Mahunka, 1965	Ants, small mammals (rodents)	Mahunka 1967b, 1968a, 1986, Ebermann 1978, Sevastyanov & Uzhevskaya 2003
S. longisetus (Berlese, 1904)	Ants, small mammals	Paoli 1911, Karafiat 1959, Ebermann 1978, 1979, Mahunka 1977c, 1986, Khaustov 2008, Ebermann & Krisper 2014
S. longitarsus (Berlese, 1905)	Coleoptera, diptera	Karafiat 1959, Zaki et al. 1987, Samšiňák 1989, Ebermann 1991a, Mahunka & Zaki 1992, Rodrigues et al. 2001, Khaustov 2008
S. mendax Karafiat, 1959	Bees, small mammals (Eulipotyphla)	Kalúz 2001, Jagersbacher-Baumann 2014
S. occultatus Sevastianov, 1975	Bees, small mammals (rodents)	Sosnina & Sevastianov 1975, Khaustov 2008, Jagersbacher-Baumann 2014
S. palustris Rack, 1966	Ants, small mammals (rodents)	Mahunka 1968b, Sevastyanov & Uzhevskaya 2003

Table 2 Continued.

Scutacarid species	Host taxa	References
S. plumosus (Paoli, 1911)	Ants, small mammals	Mahunka 1975b, Ebermann & Krisper 2014
S. quadrangularis (Paoli, 1911)	Ants, small mammals (rodents)	Balogh & Mahunka 1962, Mahunka 1970b, 1975b, Sevastyanov & Uzhevskaya 2003
S. sphaeroideus Karafiat, 1959	Ants, coleoptera, small mammals	Karafiat 1959, Mahunka 1967a, 1975b, 1981, Kurosa 1980, Sevastyanov & Uzhevskaya 2003, Khaustov 2008
S. spinosus Storkan, 1936	Ants, bees, small mammals	Mahunka 1963, 1967a, 1968a, 1975b, 1981, Delfinado & Baker 1976, Sevastyanov & Uzhevskaya 2003, Khaustov 2008
S. subterraneus (Oudemans, 1913)	Ants, small mammals (Eulipotyphla)	Vitzthum 1919, Štorkán 1940, Karafiat 1959, Sevastianov 1965, Sosnina & Sevastianov 1975, Ebermann 1979, Sevastyanov & Uzhevskaya 2003, Khaustov 2008, Ebermann & Krisper 2014

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

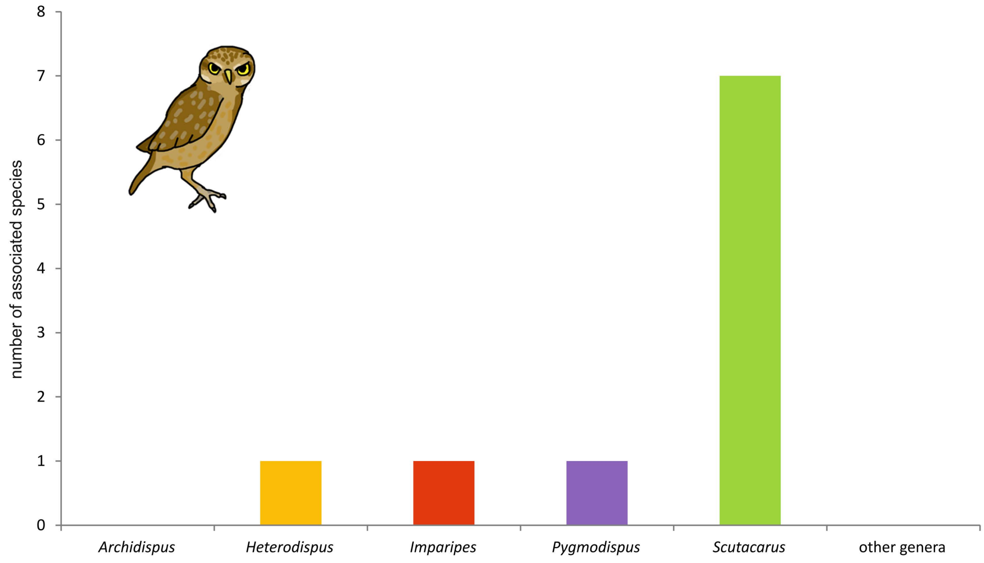

Figure 14 Number of scutacarid species belonging to different genera associated with birds (Aves).

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 zicsii* Mahunka, 1964, 28 *Scutacarus* species and *Reductacarus singularis* Mahunka, 1963 (e.g. Mahunka 1967a, 1972b, 1975b, 1977d, 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, Jagersbacher-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 carrion (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

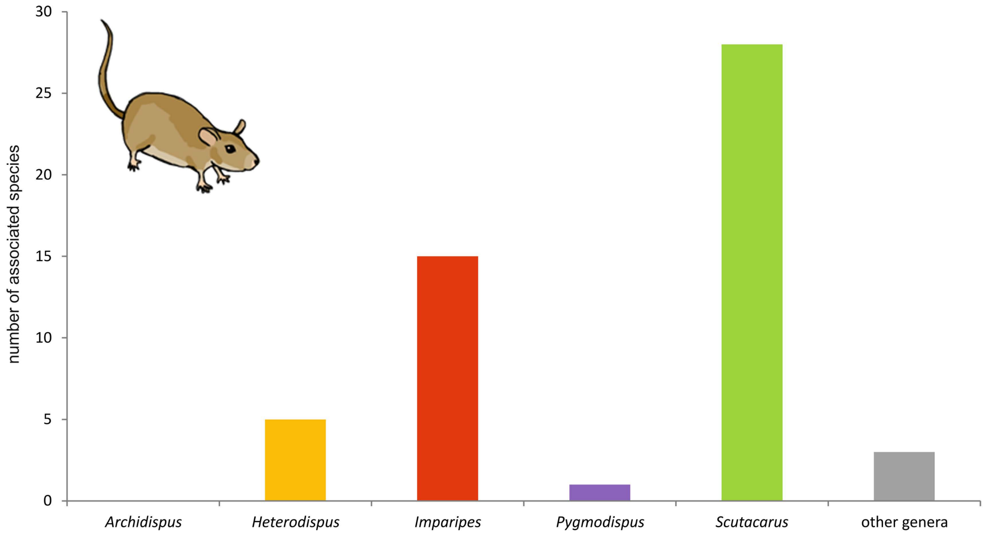

Figure 15 Number of scutacarid species belonging to different genera associated with mammals (Mammalia). "Other genera" combine *Diversipes*, *Lamnacarus*, *Lophodispus*, *Nasutiscutacarus*, *Parascutacarus*, *Reductacarus*, *Rettenmeyerella*, *Scutacaropsis*, *Symbolacrasis* and *Thaumatopelvis*.

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.

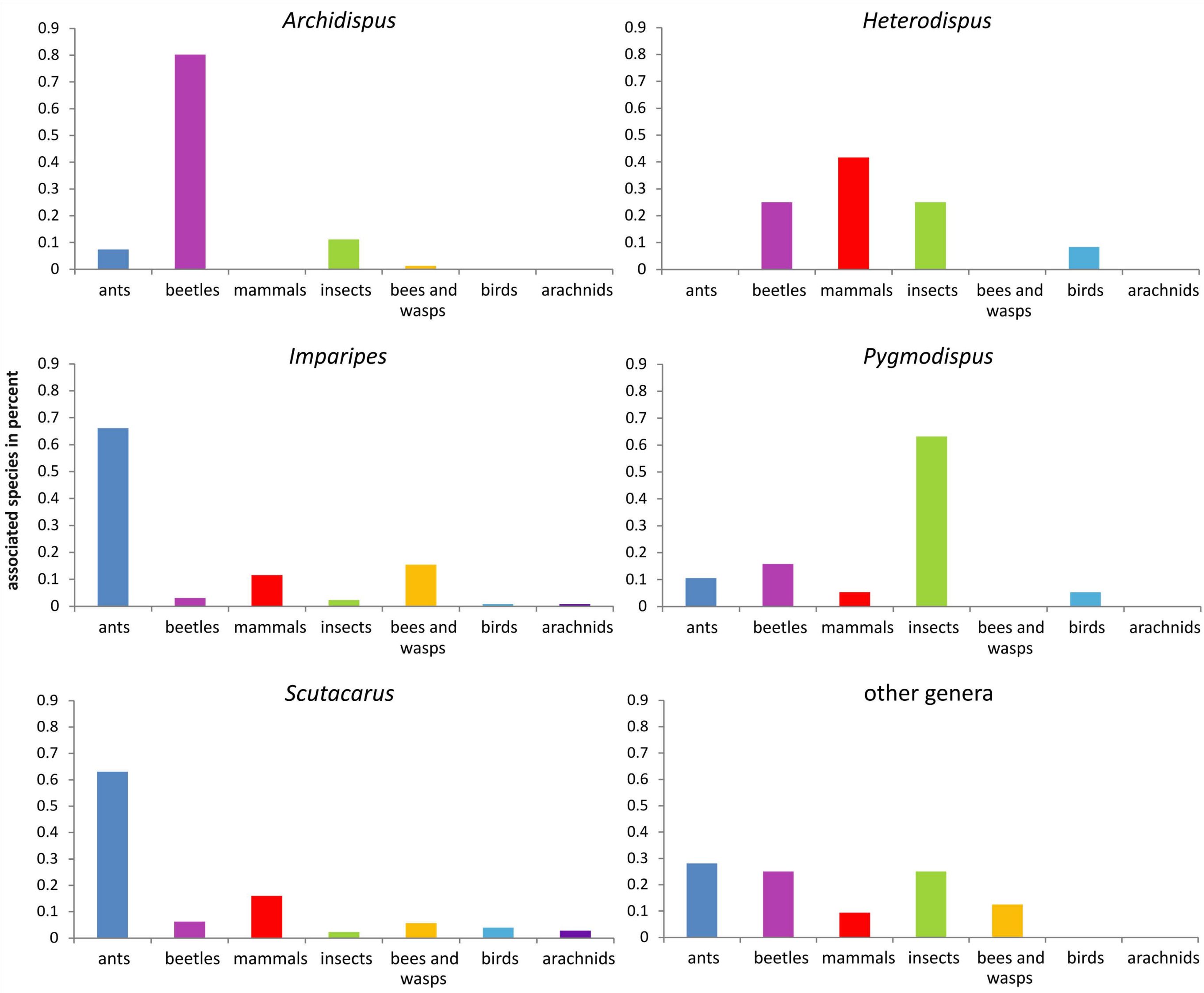

Figure 16 Percentage distribution of scutacarid genera along different host taxa. "Other genera" combine *Diversipes*, *Lamnacarus*, *Lophodispus*, *Nasutiscutacarus*, *Parascutacarus*, *Reductacarus*, *Rettenmeyerella*, *Scutacaropsis*, *Symbolacrasis* and *Thaumatopelvis*.

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 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. dispar* 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 endogaeic 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 Vespoidea that thrive in dead wood, reeds and stalk; 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 *Laelaspoides* 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 hyphe 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 *Archidispus* 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

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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 **Vespoidea** excl. Formicidae (Hexapoda, Ectognatha, Aculeata)
V. Scutacarid species associated with **Formicidae** excl. Formicinae and Myrmicinae (Hexapoda, Ectognatha, Aculeata, Vespoidea)
VI. Scutacarid species associated with **Formicinae** (Hexapoda, Ectognatha, Aculeata, Formicidae)
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 (Goeze, 1780); Holarctic; p; Rack 1964, Chmielewski 1971, Schousboue 1986, Schwarz & Huck 1997, Khaustov 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: *Stenoterommata iguazu, S. platense, S. uruguai*

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 Khaustov, 2008; Ukraine; p; Khaustov 2008

Hexapoda: Ectognatha

Dermaptera

Forficulidae

Imparipes (Imparipes) histricinus 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 baculitarsus agaricus (Norton & Ide, 1974); USA (Delaware, Pennsylvania); p; Norton & Ide 1974; also in mushroom-bedding compost

Phoridae: *Megaselia halterata*

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

Phoridae

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

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

Sciaridae

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*

Scutacarus longitarsus (Berlese, 1905); USA (Arizona); p; Samšiňák 1989

Sphaeroceridae: *Copromyza costalis, Copromyza acutangula, Coproica pseudolugubris*

Imparipes (Imparipes) penicillatus Mahunka, 1967; Mongolia; p; Mahunka 1973c; also in soil

Heteroptera

Reduviidae: *Pasira mediterranea*

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

Hymenoptera: Terebrantia/Parasitica

Eucoilidae, 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 & Ferragut unpubl.

Termitidae: *Odontotermes nolaensis*

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

Termitidae: *Pericapritermes appellans*

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

Termitidae: *Pseudacanthotermes spiniger*

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

Scutacarus mirabilis Mahunka, 1964; Angola; p; Mahunka 1964a

Termitidae: *Trinervitermes trinervoides*

Gerdalbertia elongata Khaustov, Hugo-Coetzee & 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 telekii 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 endroedii 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

Broscinae

Broscus cephalotes

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

Craspedonotus tibialis

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

Carabinae

Carabus opaculus

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 foliatus (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 rostratus Kurosa, 1976; Japan; p, Kurosa 1976, 1977, 1980

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 omega Kurosa, 1976; Japan; p; Kurosa 1976, 1977, 1980

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 rostratus Kurosa, 1976; Japan; p; Kurosa 1976, 1977, 1980
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, 2005; Japan; p; Kurosa 2005
Archidispus conspicuus Kurosa, 1978; Japan; p; Kurosa 1978, 1980
Archidispus crassiradix Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus difficilis Kurosa, 1983; Japan; p, Kurosa 1983
Archidispus dubinini Khaustov, 2003; Ukraine; p; Khaustov 2003, 2008
Archidispus foliatus (Kurosa, 1978); Japan; p; Kurosa 1978, 1980
Archidispus fukudai Kurosa, 1984; Japan; p; Kurosa 1984
Archidispus fusiformis Kurosa, 1976; Japan; p, Kurosa 1976, 1977, 1980
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 2008
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 omega Kurosa, 1976; Japan; p, Kurosa 1976, 1977, 1980
Archidispus papillosus Kurosa, 1978; Japan; p; Kurosa 1978, 1980
Archidispus pseudomega Kurosa, 1984; Japan; p; Kurosa 1984
Archidispus rostratus Kurosa, 1976; Japan; p; Kurosa 1976, 1977, 1980
Archidispus satoui (Kurosa, 1983); Japan; p, Kurosa 1983
Archidispus similis Kurosa, 1989; Japan; p; Kurosa 1989
Archidispus stenolophi Kurosa, 1990; Japan; p, Kurosa 1990
Archidispus subintermissus Kurosa, 1983; Japan; p; Kurosa 1983
Archidispus triangularis (Kurosa, 1974); Japan; p, Kurosa 1974, 1977, 1980
Archidispus ukrainicus Khaustov, 2004; Ukraine; p; Khaustov 2008
Archidispus undulatus Kurosa, 2003; Japan; p; Kurosa 2003

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 ohtanii 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 tonegawanus Kurosa, 2005; Japan; p; Kurosa 2005

Oodes spp.

Archidispus proximus Kurosa, 1989; Japan; p; Kurosa 1989

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

Nebriinae

Nebria spp.

Archidispus diploi Kurosa, 1991; Japan, Russia (far east); p; Kurosa 1991, Khaustov 2008

Omophroninae

Omophron aequalis aequalis

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

Platyninae

Agonum spp.

Archidispus bembidii (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 arcuaticollis

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

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

Pterostichinae

Amara spp.

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

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, Loghmani *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 pseudocurtonoti Khaustov, 2008; Belarus; p; Khaustov 2008

Archidispus pterostichi Rack, 1973; Hungary, Netherlands, Ukraine; p, Rack 1973, 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 bembidii (Karafiat, 1959); Asia, Africa, Europe, North America; p; Karafiat 1959, Mahunka 1972b, Kurosa 1980, Ebermann 1991a, Fain *et al.* 1995, Fain & Miessen 1997

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

Archidispus cnemidoti Kurosa, 1991; Japan; p, Kurosa 1991

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

Archidispus magnificus (Karafiat, 1959); Austria; Ebermann *et al.* 2011

Archidispus nobukoae Kurosa, 1991; Japan; p; Kurosa 1991

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

Archidispus sugiyamai Kurosa, 1991; Austria, Japan, Ukraine; p, Kurosa 1991, Khaustov 2008, Ebermann *et al.* 2011

Diplous caligatus

Archidispus diploi Kurosa, 1991; Japan, Russia (far east); p; Kurosa 1991, Khaustov 2008

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

Archidispus sugiyamai Kurosa, 1991; Japan, Ukraine; p, Kurosa 1991, Khaustov 2008

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 rufoaeneus

Archidispus szaboi (Mahunka, 1977); Hungary, Ukraine, p; Khaustov 2008

“Carabidae” (not further classified in literature)

Archidispus amarae (Kurosa, 1970); Austria; p; Ebermann 1991a, also in soil

Archidispus armatus (Karafiat, 1959); Hungary; p; Mahunka 1981; also in soil

Archidispus bembidii (Karafiat, 1959); Germany; p, Karafiat 1959, Khaustov 2008; up to 100 specimens/beetle; near water

Archidispus conspicuus Kurosa, 1978; Iran; p, Katlav *et al.* 2015

Archidispus minor (Karafiat, 1959); Asia, Europe; p; Karafiat 1959, Mahunka 1981, Ebermann 1991b, Khaustov 2008, also in soil

Archidispus ohtanii Kurosa, 1989; Japan, Moldavia, Ukraine; p, Khaustov 2008

Archidispus 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

Pityogenes chalcographus

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.

Archidispus 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 bicornutus Ebermann & Rodrigues, 2001; Brazil; p; Ebermann & Rodrigues 2001; also in soil

Scutacarus longitarsus (Berlese, 1905); Brazil; p; Rodrigues *et al.* 2001

Ataenius spp.

Pygmodispus bicornutus 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 bicornutus 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, Rhyssemodes 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 & Hajiqanbar, 2016; Iran; p; Katlav *et al.* 2016

Boopinus fuliginosus

Scutacarus sphaeroideus 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 sphaeroideus Karafiat, 1959; cosmopolitic; 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) histricinus 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 rhabdiformis 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); Austria, Belgium, Czechoslovakia, Denmark, Germany, Great Britain, Greece, Hungary, Japan, Korea, Mongolia, New York, North America, Poland, Russia, Sweden, Switzerland, Turkey; ip; Michael 1884, Paoli 1911, Karafiat 1959, Mahunka 1965a, 1967a, 1967b, 1972b, Cross & Bohart 1969, Chmielewski 1971, Delfinado *et al.* 1976, Kurosa 1980, Schousboe 1986, Ebermann 1992, Fain *et al.* 1992, Fain & Baugnée 1996, Schwarz & Huck 1997, Çankaya & Kaftanoglu 2006, Larsson 2007, Chmielewski & Baker 2008, Khaustov 2008, Jagersbacher-Baumann 2014a, Kontschán 2015, Kontschán *et al.* 2016; also in moss, soil

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 pygmephoroides Mahunka, 1967; Hungary, Mongolia; i; Mahunka 1967a, 1972b

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

Dasypoda plumipes

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

"Bees" (not further classified in literature)

Diversipes zwoelferi 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 (Apidacarus) 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 & Baugnée 1996

Lasioglossum 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; p; 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 & Jagersbacher-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.**

Archidispus 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 & Jagersbacher-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 & Abbatiello, 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, Mimesa equestris, Psenulus concolor, Trypoxylon minus

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

Lindenius spp.

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

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

Mimumesa dahlbomi

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

Symmorphus bifasciatus

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

Vespa sp.

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

Anoplius infuscatus, Caliadurgus fasciatellus, Evagetes 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, Khaustov 2008 *Imparipes (Imparipes) pennatus* Karafiat, 1959; France; n.k.; Mahunka 1977c

Tapinoma simrothi

Scutacarus sabinaesimilis Khaustov & Chydyrov, 2004; Turkmenistan; i, Khaustov 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; ip; 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; ip; 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; ip; 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, ip; 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 andrassyi Mahunka, 1968; Panama; p; Berghoff *et al.* 2009

Scutacarus omittatus Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a

Scutacarus pseudocomus Mahunka, 1977; Panama; ip; Mahunka 1977b, Rettenmeyer *et al.* 2011

Scutacarus setarus 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) opusculus 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

Scutacarus chadabi Mahunka, 1977; Ecuador; n.k.; Mahunka 1977a

"Dorylinae" (not further classified in literature)

Scutacaridae; Brazil, Panama; p; Rettenmeyer 1961a; "20 different species"

Ponerinae

Ponera coarctata

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) hortobagyensis Mahunka, 1981; Hungary; i; Mahunka 1981

Imparipes (Imparipes) histricinus Berlese, 1903; Germany, Hungary, Italy, Russia, Sudan; ip; Karafiat 1959, Mahunka 1981; also in forest litter

Imparipes (Imparipes) imaginatus 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 hortobagyensis Mahunka, 1981; Hungary; i; Mahunka 1981, 1986; also in litter

Scutacarus hauseri Mahunka, 1977; Hungary, Switzerland; ip; Mahunka 1981, 1986, Dobrev 1992

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 sphaeroideus Karafiat, 1959; Hungary; i; Mahunka 1981

Scutacarus spinitarsus 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 striatomarginatus 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 tackei Willmann, 1942; Europe; i; Mahunka 1981; also in rotten straw

Scutacarus tackei 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 tyrrhenicus Ebermann, 1986; Italy, Ukraine; n.k.; Khaustov 2008

Cataglyphis aenescens

Scutacarus berdyevi Chydyrov 2007; Turkmenistan; p; Chydyrov 2007

Cataglyphis bicolor

Scutacarus agypticus 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) kataglyphi Khaustov & Chydyrov, 2004; Turkmenistan, i; Khaustov & Chydyrov 2004, Khaustov 2008

Cataglyphis cf. nodus

Imparipes (Imparipes) histricinus 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. *histricinus* 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) histricinus Berlese, 1903; Austria, Czech Republic; i; Štorkán 1940, Ebermann 1980a, 1982; also in moss

Imparipes (Imparipes) histricinus 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

Lophodispus irregularis (Mahunka, 1971); Austria, Hungary, Japan, Korea, Ukraine, USA; ip; Kurosa 1972a, Ebermann 1978, 1979, 1980a, 1980b, 1982, Friedl 2000, Khaustov 2008, Ebermann & Krisper 2014; also in soil, rotten wood

Scutacarus acarorum (Goeze, 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 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, 1993; Ukraine; n.k.; Sevastianov 1983, Khaustov 2008

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

Scutacarus kassaii Mahunka, 1965; Russia; i; 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; "Variatipes"- group: no claw on leg I

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

Scutacarus ovoideus Karafiat, 1959; Austria, Germany, Greece, Hungary, Poland, Switzerland, Ukraine; i; 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.; Štorkán 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 sibiriensis Khaustov, 2015; Russia; ip; Khaustov 2015d

Scutacarus spinosus Storkan, 1936; cosmopolitic; 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, Štorkán 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 I

Scutacarus tackei 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. *histricinus* Berlese, 1903; Austria; i; Mahunka 1970b

Imparipes (Imparipes) cf. *histricinus* 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) pennatus 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, 2015b, 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; Nemestóthy & Mahunka 1981

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

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

Scutacarus kassaii 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 I

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

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

Scutacarus ponticulus Mahunka, 1981; Hungary; i; Nemestóthy & Mahunka 1981

Scutacarus pygmephoroides 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 tackei Willmann, 1942; Austria; p; Ebermann & Krisper 2014

Paratrechina 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 (Telodispus) 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 Karafiat, 1959; Austria; p; Ebermann & Krisper 2014

Scutacarus ovoideus Karafiat, 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.

Lophodispus irregularis (Mahunka, 1971); USA (Maryland); i; Ebermann 1980b

Scutacarus nudus bisetus Karafiat, 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 salomonis

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 (Karafiat, 1959); Austria, Germany; i; Ebermann 1980a

Scutacarus crassisetus (Paoli, 1911); Austria; i; Mahunka 1970b; also in moss

Scutacarus ellipticus Karafiat, 1959; Austria, Germany, Hungary, Russia, Switzerland, Ukraine, former Yugoslavia; ip; Karafiat 1959, 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 myrmicinus Khaustov, 2015; Russia; i; Khaustov 2015c

Scutacarus ovoideus Karafiat, 1959; Austria, Germany, Greece, Hungary, Poland, Switzerland, Ukraine; ip; 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; p; Friedl 2000, Ebermann & Krisper 2014

Scutacarus quadrangularis (Paoli, 1911); Austria; i; Mahunka 1970b; also in moss, litter, 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 tackei 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) histricinus 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 nanus 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) histricinus 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) hortobagyensis Mahunka, 1981; Hungary, Ukraine; i; Khaustov 2008

Imparipes (Imparipes) histricinus 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

Stenamma debile

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 subsphaeroideus 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: Blarina brevicauda

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

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

Talpidae: Talpa europea

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

Scutacarus mahnerti Mahunka, 1972; Austria; i; Mahunka 1972a

Scutacarus mendax Karafiat, 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; Karafiat 1959; also in meadow soil

Mammalia: Rodentia

Cricetidae: Clethrionomys glareolus

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

Cricetidae: Cricetulus migratorius

Heterodispus 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

Lophodispus 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

Heterodispus 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 Karafiat, 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 & Cervantes 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 eucomus (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

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

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

Imparipes (Imparipes) histricinus 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

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

Scutacarus apodemi Mahunka, 1963; Ukraine; i; Sevastyanov & Uzhevskaya 2003

Scutacarus culmusophilus Sevastianov, 1975; 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 sphaeroideus Karafiat, 1959; Ukraine; i; Sevastyanov & Uzhevskaya 2003

Scutacarus spinosus Storkan, 1936; Hungary, Ukraine; i; Sevastyanov & Uzhevskaya 2003, Mahunka 1963

Muridae: Apodemus sp.

Scutacarus apodemi 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, Rhabdomys pumilio

Heterodispus foveatus Jagersbacher-Baumann & Ebermann, 2012; Kenya, Namibia, Rwanda, South Africa; ip; Jagersbacher-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

Heterodispus citelli Mahunka, 1970; Hungary; i; Mahunka 1970a

Heterodispus elongatus (Paoli, 1911); Hungary; i; Balogh & Mahunka 1962

Heterodispus pannonicus Mahunka, 1963; Hungary; i; Mahunka 1963, Jagersbacher-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

Heterodispus foveatus Jagersbacher-Baumann & Ebermann, 2012; South Africa; i; Jagersbacher-Baumann & Ebermann 2012a

Mammalia: "rodents" (not further classified in literature)

Heterodispus 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