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An update on the knowledge about scutacarid mites as phoronts and inquilines

Julia Baumann ^a^aInstitute of Biology, Department of Biodiversity and Evolution, University of Graz, Universitätsplatz 2, 8010 Graz, Austria.

Original research

ABSTRACT

Scutacarid mites are known to be associated with various other animal taxa, either as inquilines or as phoronts (or both). The present publication is an update of a review article about inquilinism and phoresy in Scutacaridae from 2018, and it deals with the respective literature from 2017 to 2023. Seventeen new scutacarid species associated with other animals have been described in the respective timespan, seven other species have been newly reported as phoretic and several new host species for scutacarids have been encountered. Whenever possible, attachment sites of the mites, behavioural observations and/or remarks about the presumed habitat of hosts and mites are given.


Keywords Scutacaridae; phoresy; commensals; literature review

Introduction

Scutacarids (Scutacaridae, Pygmephorioidea, Heterostigmata) are mostly soil-inhabiting, fungivorous mites which are often associated with various other animal taxa: about half of the more than 800 described species (most recent number published by Rahiminejad *et al.* (2023)) can be found as phoronts or inquilines of other animals. In my review article from 2018 (Baumann 2018), I gave an overview about all associations between scutacarids and other animal taxa published until May 2017, and the aim of the present work is to update this information by including all new articles released between May 2017 and September 2023 (and the occasional publication that had slipped my attention in my previous review article). Following the structure of Baumann (2018), new information about either new scutacarid species and/or new hosts is given in the text; further reports that simply list new combinations of scutacarid species and hosts and/or new geographical localities are listed only in the Annex. The 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).

The online supplementary material consists of a table listing the scutacarid species first and adding the reported host taxa for each species afterwards. While the Annex only contains the new information published between 2017 and 2023, the table in the supplementary material is an updated version of the one from 2018, thus containing all information about scutacarids and their hosts available to date.

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Corresponding author
Julia Baumann 
julia.baumann@uni-graz.at

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Methods

The articles were gained by searching the term 'Scutacaridae' for the period 2017-2023 in Google Scholar and Web of Science in September 2023, and by scanning the references in the respective articles for publications that I had missed before. In order to maintain clarity and to keep focus on the mites, author names are only provided for scutacarid species but not for their hosts.

Results and Discussion: New information about scutacarid species and their hosts

Between May 2017 and September 2023, 27 articles containing information about scutacarids as phoronts or inquilines have been published, dealing with mites from 15 countries (Algeria, Australia, Brazil, Chile, Egypt, India, Iran, Mexico, Papua New Guinea, Russia, South Africa, Spain, Sri Lanka, Ukraine and Uruguay). As result of the present literature study, 17 new scutacarid species described since 2017 and one species already described in 1975 can be added to the scutacarids found in association with other animal taxa (**Table 1**). Moreover, seven species already known to science have been recorded as phoronts or inquilines for the first time since 2017 (**Table 2**). Eight animal (sub)families, 18 genera and 28 species have been found as new host taxa for scutacarid mites.

Arachnids (Annex I)

Until now, only two species of *Scutacarus* had been reported in association with (nemesiid) spiders, and both had been encountered in South America (Baumann 2018). There has now been an interesting new finding of a scutacarid species phoretic on spiders: a member of *Imparipes*, most probably a new species, attached between coxae III and IV of the Australian cave-inhabiting anamid spider *Trogloidiplura beirutpakbarai* (Marsh *et al.* 2023).

Table 1 New scutacarid species associated with other animal taxa described since 2017 (and one species already described in 1975 that was missing in Baumann (2018)).

Scutacarid species	Host	Reference
<i>Archidispus hydrophilus</i>	<i>Coleostoma fabricii</i>	Khadem-Safdarkhani <i>et al.</i> 2022
<i>Imparipes (I.) bengalensis</i>	<i>Labidura bengalensis</i>	Radhakrishnan and Ramaraju 2017
<i>Imparipes (I.) clementis</i>	<i>Reticulitermes banyulensis</i>	Baumann and Ferragut 2019
<i>Imparipes (I.) hajiyanbari</i>	<i>Lasius</i> sp.	Rahiminejad <i>et al.</i> 2022
<i>Nasutiscutacarus latisetus</i>	<i>Hoplonomia westwoodi</i>	Khaustov and OConnor 2019
<i>Nasutiscutacarus longicaudus</i>	<i>Mellitidia gressitti</i>	Khaustov and OConnor 2019
<i>Pygmodispus (P.) odontotarsus</i>	Cricetidae	Sosnina and Sevastianov 1975
<i>Scutacarus camponoti</i>	<i>Camponotus distinguendus</i>	Khaustov 2017a
<i>Scutacarus cingulatus</i>	<i>Camponotus cingulatus</i>	Silva <i>et al.</i> 2019
<i>Scutacarus ebermanni</i>	<i>Messor</i> sp.	Sobhi <i>et al.</i> 2017b
<i>Scutacarus neotropicus</i>	<i>Lasiophanes picinus</i>	Khaustov 2017a
<i>Scutacarus olszanowskii</i>	<i>Anoplolepis</i> sp.	Khaustov <i>et al.</i> 2020
<i>Scutacarus pseudoapodemi</i>	<i>Camponotus oasisium</i>	Navabi <i>et al.</i> 2018a
<i>Scutacarus pseudoplurisetus</i>	<i>Ips typographus</i>	Khaustov 2017b
<i>Scutacarus shajariani</i>	<i>Tetramorium</i> sp.	Sobhi <i>et al.</i> 2017b
<i>Scutacarus termitophilus</i>	<i>Trinervitermes trinervoides</i>	Khaustov <i>et al.</i> 2018a
<i>Scutacarus variabilis</i>	<i>Anoplolepis</i> sp.	Khaustov <i>et al.</i> 2020
<i>Thaumatopelvis lorasiacus</i>	<i>Formica</i> sp., <i>Pheidole</i> sp.	Navabi <i>et al.</i> 2018b

Table 2 Species already known to science that have been recorded as phoronts or inquilines of other animal taxa for the first time since 2017.

Scutacarid species	Host	Other known habitat	Reference
<i>Heterodispus turkmenistaniensis</i> Khaustov & Chydyrov, 2005	<i>Scarites (Scarites) procerus eurytus</i>	soil under cucumbers	Sobhi et al. 2017a
<i>Imparipes (Imparipes) lituanicus</i> Lazauskene & Sevastianov, 1974	<i>Lasius</i> spp.	forest litter	Rahiminejad et al. 2022
<i>Imparipes (Sporichneuthes) intermedius</i> Paoli, 1911	"Scarabaeidae", <i>Onthophagus</i> sp.	soil and litter	Rahiminejad et al. 2020a
<i>Scutacarus evansi</i> Momen & Curry, 1987	<i>Apis mellifera</i>	grassland on reclaimed peat	Abd El Hady & Mahfouz 2021
<i>Scutacarus levis</i> Mahunka, 1981	<i>Lasius umbratus</i>	meadow	Khaustov & Tolstikov 2016
<i>Scutacarus muscocicola</i> Sevastianov, 1983	<i>Ips typographus</i>	moss	Khaustov 2017b, Khaustov et al. 2018b
<i>Scutacarus shivicki</i> Lazauskene & Sevastianov, 1974	<i>Messor</i> sp.	soil and litter	Sobhi et al. 2017a

Hexapoda

Isoptera (Annex I)

Two new scutacarid species associated with termites have been described since Baumann (2018): *Scutacarus termitophilus* Khaustov, Hugo-Coetzee & Ermilov, 2018 on *Trinervitermes trinervoides* (Khaustov et al. 2018a), which is the first species of the genus *Scutacarus* found in association with termites, and *Imparipes clementis* Baumann, 2019 (Baumann and Ferragut 2019). The latter was found attached to the coxae of *Reticulitermes banyulensis* (Baumann et al. 2018, Baumann and Ferragut 2019). Termites could never be seen removing attached mites of *I. clementis*, even when they were self- or allogrooming. Attachment didn't happen by claws on leg I, as is typical for Scutacaridae (Baumann 2018), but by large empodia on legs II and III (Baumann et al. 2018). This species was thus the first example of a scutacarid without claws on leg I that still can attach to a phoresy host, which indicates that -contrary to previous opinion- all other species without claws I might also be able to perform phoresy using their empodia. The attachment of the mites seemed to be weak as the mites detached after the slightest external disturbance, which might indicate that phoresy is restricted to the inside of the termite nest (Baumann et al. 2018).

Inside the termites' nests, *I. clementis* was found either on the termites or inside the tunnels that the termites created in dead wood, and they were located preferably near termite carcasses (Baumann et al. 2018, Baumann and Ferragut 2019). Only few scutacarid specimens could be found in the soil surrounding the nests. *Imparipes clementis* turned out to be easy to rear in the laboratory: lab cultures of the mites thrived on different substrates and larvae and males could be gained and described through those cultures (Baumann and Ferragut 2019). During those rearings, it became also clear that the number of phoretic scutacarids rose when the termite colony was in a bad state (identified as such by an increasing number of dead termites). In one instance, one female of *I. clementis* was observed performing appetite behavior (Baumann et al. 2018), being now the twelfth scutacarid species reported to show this behavioral trait.

Coleoptera (Annex II and Annex III)

Within Coleoptera, the by far largest number of associated scutacarids can be found in the family **Carabidae** (Baumann 2018). However, since 2017, only three scutacarid species have been reported from carabid beetles (see Annex II), and only one of these reports is worth mentioning here: *Heterodispus turkmenistaniensis* Khaustov & Chydyrov, 2005 was encountered in Iran on the beetle *Scarites (Scarites) procerus eurytus* (Sobhi et al. 2017a), and this is the first report of the carabid subfamily Scaritinae as hosts for Scutacaridae. The authors found *H. turkmenistaniensis* also on beetles belonging to the family **Tenebrionidae**, and it was also reported on Scarabaeidae (see below). Until now, this scutacarid species was only known from soil samples.

Two new species of Scutacaridae associated with two other beetle families have been described: *Archidispus hydrophilus* Khadem-Safdarkhani & Hajiqaanbar, 2022 was found attached to *Coleostoma fabricii* (**Hydrophiliidae**; see Annex III) on its hosts sternite between the coxae (Khadem-Safdarkhani et al. 2022). This beetle feeds on decomposing material below

wet rocks or among grass roots. This material supposedly is an ideal substrate for the growth of fungal mycelia, which in turn are a likely food source for the mite (Khadem-Safdarkhani *et al.* 2022). In the family **Curculionidae** (see Annex III), *Scutacarus pseudophurisetus* Khaustov, 2017 was described from the wood borer *Ips typographus* (Khaustov 2017b and Khaustov *et al.* 2018b), a species which has already been noted as host for two scutacarid species before (Baumann 2018). The total number of scutacarid species associated with *I. typographus* now went up to five as Khaustov (2017b), and Khaustov *et al.* (2018b) also reported *Scutacarus palustris* Rack, 1966, a species also associated with ants and rodents (Baumann 2018), and *Scutacarus muscocicola* Sevastianov, 1983, which had until now only been reported from moss and litter, on this beetle. All five species associated with *I. typographus* belong to the genus *Scutacarus*.

In the family **Scarabaeidae**, three new genera have been reported as a new host for scutacarids: the genus *Adoretus* for *Heterodispus turkmenistaniensis*, the genus *Hybalus* for *Pygmodispus odontotarsus* Sevastianov, 1975 (Khaustov and Frolov 2018), and the genus *Oryctes* for *Scutacarus longitarsus* (Berlese, 1905) (Rahiminejad *et al.* 2020a, 2023).

All three scutacarid species appear to be generalists in terms of habitat and/or host range, as *P. odontotarsus* has already been reported from the nest of a small mammal and from soil, *S. longitarsus* has been found on dipterans and various families of coleoptera (Baumann 2018 and this publication) and *H. turkmenistaniensis* on different coleoptera families and from soil (this publication).

Imparipes (Sporichneuthes) intermedius Paoli, 1911, a species until now only known from soil and litter, has now also been encountered on different scarab beetles (Rahiminejad *et al.* 2020a)

Furthermore, six new beetle families have been identified as hosts for Scutacaridae: Cerambycidae, Dryopidae, Elateridae, Geotrupidae, Lucanidae and Meloidae (see Annex III).

In **Cerambycidae**, *Scutacarus hystrichocentrus* Sevastianov, 1983 was encountered on the beetle *Paranda caspia* by Hajiqanbar and Arjomandi (2019). This beetle attacks dead host plants which had already been infested by wood boring insects, and the authors conclude that the dead wood presumably is a suitable habitat for scutacarid mites. Until now, *S. hystrichocentrus* was only known as associate of ants of the genus *Lasius* (see Baumann 2018).

In the family **Dryopidae**, the genus *Dryops* has been reported as new host for *Scutacarus sphaeroideus* Karafiat, 1959 (Rahiminejad *et al.* 2020b, 2023). About 75% of dryopid species are aquatic (Khagani *et al.* 2022), but although no nearer information was available, it is most probable that *S. sphaeroideus* was attached to one of the remaining riparian or terrestrial species.

Beetles of the family **Elateridae** were identified as new hosts for *Archidispus insolitus* (Kurosa, 1974) and *Imparipes (I.) moderatus* Khaustov, 2008. *Archidispus insolitus*, until now only known from Carabidae (Baumann 2018), has also been found on Meloidae (see below), Tenebrionidae and Scarabaeidae (Rahiminejad *et al.* 2023). *Imparipes (I.) moderatus* was encountered on *Drasterius bimaculatus* by Navabi *et al.* (2018a). This scutacarid species was until now only known as associate of ants (Baumann 2018). *Drasterius bimaculatus* adults live on the ground of many different terrestrial habitats including riverside alluvial soils, whereas their larvae are rhizophagous (Gradinarov 2003, Hardersen *et al.* 2012). The high mobility of the adults as well as the rhizophagous lifestyle of the larvae most likely make these beetles an attractive host for scutacarids.

In **Geotrupidae**, *Geotrupes spiniger* was determined as host for *Scutacarus longitarsus* by Rahiminejad *et al.* (2020a). This species builds brood chambers that are filled with dung (Klemperer 1979), which most likely facilitates the growth of fungi and thus allows scutacarids to thrive there.

Lucanus ibericus of the family **Lucanidae** has also been newly reported as host for *Scutacarus longitarsus* (Rahiminejad *et al.* 2020a, 2023). The larvae of lucanid beetles live in decayed wood, a suitable habitat for scutacarids.

Finally, the family **Meloidae** has been listed as a new host for *Archidispus insolitus* (Rahiminejad *et al.* 2023). Adult beetles are mostly phytophagous, but their juvenile stages are often associated with solitary hymenopterans and complete their metamorphosis in soil (Ghahari & Campos-Soldini 2019), which could explain the association of the scutacarids with these beetles.

Hymenoptera: Bees (Annex IV)

Scutacaridae don't play an important role as associates of the honey bee *Apis mellifera* (family **Apidae**). Still, the third scutacarid species after *Imparipes apicola* (Banks, 1914) and *Scutacarus acarorum* (Goeze, 1780) (Baumann 2018) was now encountered as inquiline of *A. mellifera* by Abd El Hady and Mahfouz (2021). They found *Scutacarus evansi* Momen & Curry, 1987 in bee hives in Egypt, albeit only in low abundance.

In different *Bombus* species (also family Apidae), *Scutacarus acarorum* can be found as a frequent associate. This mite species generally prefers hibernated queens as phoresy host (Baumann 2018). It has now also been found associated with *Bombus bellicosus* and *B. pauloensis* in Uruguay (Revainera *et al.* 2019), and although authors state that the associated acarofauna in general preferred queens as host, the prevalence of *S. acarorum* was highest in males of both *Bombus* species in the respective study. Another species, *Imparipes (I.) rafalskii* Dastych, 1978, was newly found associated with *B. terrestris* and also with the genus *Andrena* of the family **Andrenidae** (Sobhi *et al.* 2017a). This scutacarid was until now only known phoretic on the apid *Dasygaster plumipes* (Baumann 2018).

Nazari *et al.* (2019) found an *Imparipes* species phoretic on either the genus *Andrena* (Andrenidae) or on *Antophora* (Apidae); the real host is unclear because the text and table 2 of the respective publication are inconsistent with one another. If the host in fact is *Antophora*, this would be the first report of this genus as host for Scutacaridae.

Until now, only two species of the scutacarid genus *Nasutiscutacarus* were known, *N. ampliatus* Beer & Cross, 1960 and *N. anthrenae* Beer & Cross, 1960, both of which are phoretic on bees of the soil nesting family **Halictidae** (Baumann 2018). This number was now doubled by Khaustov and OConnor (2019), who described two new scutacarids associated with halictid bees: *N. latisetus* Khaustov & OConnor, 2019 from Sri Lanka and *N. longicaudus* Khaustov & OConnor, 2019 from Papua New Guinea. *Nasutiscutacarus* is characterized by an elongated gnathosoma which implies a highly specific, albeit still unknown, feeding source (Khaustov and OConnor 2019). Since all known species of *Nasutiscutacarus* are associated with Halictidae, the elongated gnathosoma most likely is an adaptation to special conditions in the hosts' nests. However, other scutacarid genera possessing typical scutacarid gnathosomata can also be encountered in association with Halictidae (Baumann 2018), which indicates that it must be a unique niche within halictid nests that is exploited by *Nasutiscutacarus*.

Hymenoptera: Ants (Annex V, Annex VI and Annex VII)

Most scutacarids in associations with other animals are associated with ants (Baumann 2018), therefore it is not surprising that 10 of the 18 new phoretic scutacarid species (given in **Table 1**) also are associated with ants. Scutacaridae belong to the superfamily Pygmephoroidae, and within the superfamily they might be best adapted to the association with ants, as can be concluded based on a study of the myrmecophilous pygmephoroid species in Western Siberia by Khaustov and Tolstikov (2016). The respective work revealed that more than 70% of the found species indeed belonged to the family Scutacaridae (the remaining species belonged to Neopygmephoridae and Microdispidae). The authors also found highly specific mite communities for most ant species, indicating a coevolution between mite lineages and ants.

Dolichoderinae, Ponerinae (Annex V)

In the subfamily Dolichoderinae, two new *Tapinoma* species have been reported as hosts for Scutacaridae. A not nearer identified *Scutacarus* species has been found associated with *Tapinoma sessile*, an invasive species occurring in natural and urban areas all over North America (Uppstrom 2010, Blumenfeld *et al.* 2021), and *Imparipes comatus* Mahunka, 1970 has been reported on *Tapinoma tauridis* from Iran (Sobhi *et al.* 2017a). However, *T. tauridis* is currently considered to be a junior synonym of *T. erraticum* (Bolton 1995, updated online 2020) which has been listed as host for *I. comatus* before (see Baumann 2018).

Until now, only one ant species (*Ponera coarctata*) of the subfamily Ponerinae has been known as host for Scutacaridae, and it has already been stated that intensified collection effort of these ants should increase the number of associated mites (Baumann 2018). Uppstrom (2010) effectively reported two not nearer identified *Imparipes* species and one *Scutacarus* species from *Ponera pennsylvanica* from North America, and Lopes *et al.* (2015) cite a Japanese book by Maruyama *et al.* (2013) who report a *Scutacarus* species attached to *Brachyponera chinensis*.

Rocha *et al.* (2020) also reported scutacarid mites phoretic on *Neoponera villosa* from Mexico; however, I was able to study the respective mites in December 2022 and they turned out not to be scutacarids, but members of the morphologically similar neopygmephorid genus *Petalomium* (Baumann unpublished).

The following new scutacarids have been described as associates of ant species belonging to the subfamily **Formicinae (Annex VI)**: six *Scutacarus* species *Thaumatopelvis lorasiacus* Navabi & Hajiqanbar, 2018 and *Imparipes hajiqanbari* Rahiminejad *et al.*, 2022. Moreover, *I. lituanicus* Lazauskene & Sevastianov, 1974, which was until now only known from forest litter, has been reported associated with *Lasius* sp. (Rahiminejad *et al.* 2022).

The genus *Anoplolepis* was reported as host for scutacarids for the first time, specifically for *Scutacarus olszanowskii* Khaustov *et al.*, 2020 and *S. variabilis* Khaustov *et al.*, 2020. This case is interesting as the host ants were found in old termite nests of *Trinervitermes trinervoides* (Khaustov *et al.* 2020). Another new host genus was *Lasiophanes*, an endemic genus of Patagonia. *Lasiophanes picinus*, a terrestrial species that lives in relatively humid soils (Fergnani *et al.* 2008), was found as host species for *S. neotropicus* Khaustov, 2017 (Khaustov 2017b).

Thaumatopelvis lorasiacus was not only found on Formicinae, but also phoretic on ants of the genus *Pheidole* (Rahiminejad *et al.* 2022), which belongs to the subfamily **Myrmicinae (Annex VII)**. Two more new *Scutacarus* were described associated with this subfamily: *S. ebermanni* Sobhi & Hajiqanbar, 2017 and *S. shajariani* Sobhi & Hajiqanbar, 2017 (Sobhi *et al.* 2017b).

Khaustov and Tolstikov (2016) and Silva *et al.* (2019) mentioned the attachment sites of several of the found scutacarid species in their papers (for details, see Annex V - VII). These authors also reported that the scutacarids could be found on workers of various ant species and also on winged ants (that is, sexual forms). In accordance with this finding, *Imparipes hajiqanbari* was also collected from alates of *Lasius* sp. (Rahiminejad *et al.* 2022).

Conclusion/closing remarks

As this review shows, knowledge about the scutacarid fauna associated with other animals has considerably increased through various publications since May 2017. However, almost all papers are restricted to describing new species or reporting associations between mites and their hosts, but rarely investigating further. This means that three of the four “future perspectives”-behavioural aspects, cryptic species complexes, phoretomorphism, and scutacarid fauna-commented in my previous work (Baumann 2018) still have to be dealt with.

Regarding behavioural aspects, the studies about *Imparipes clementis*, which is associated with termites (Baumann *et al.* 2018, Baumann and Ferragut 2019), gave some new insights

as they demonstrated that phoretic attachment is possible even without claws on leg I, that the hosts never tried to remove attached mites, that mites can be found in areas inside the termite nests where termite corpses are buried and that the number of phoretic mites increases when a colony is in a bad state (presumably so that the mites have a chance to leave the “sinking ship”, the moribund nest). There is still a lot of information about behavioral aspects lacking, for example: How exactly is the phoretic behavior initiated, how is it stopped? What influence, if at all present (e.g. sanitary role), do the mites have on their hosts?

There haven't been any new studies dealing with cryptic species complexes or phoretomorphism in Scutacaridae, but there was a study investigating the influence of the dispersal ability on phenotypic patterns. By comparing populations of a phoretic scutacarid species (with supposed high dispersal ability) with those of a presumed non-phoretic species (with supposed low dispersal ability), it was revealed that the non-phoretic species shows a clear phenotypic population structure compared to the homogenous phoretic species, caused most likely by differences in their gene-flow (Baumann 2021). This result supports the assumption that phoresy does not promote (allopatric) speciation as it, on the contrary, allows for panmixis of geographically separated populations (Seeman and Walter 2023).

Molecular genetic studies could further shed a light on questions regarding the population structures of phoretic scutacarids, possible cryptic species complexes and the mechanisms determining the phoretomorphism which is present in some species. However, molecular genetic analyses including scutacarids are still scarce and the respective studies don't focus on Scutacaridae but only include them in comprehensive phylogenetic trees or studies on the diversity of acarofauna (e.g. Young *et al.* 2012, Klimov *et al.* 2018). The respective publications show that DNA extraction of scutacarids is feasible, but may require special handling (like the application of semidestructive methods) due to the small size of the mites.

ORCID

Julia Baumann  <https://orcid.org/0000-0002-4486-4121>

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ANNEX: LIST OF SCUTACARID SPECIES ASSOCIATED WITH DIFFERENT HOSTS

- I. Scutacarid species associated with 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 (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 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); reference(s) and remarks (if available)

* indicates that taxon is recorded for the first time as host for Scutacaridae

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

Arachnida

Aranacea

Anamidae*: *Trogloidiplura** *beirutpakbarai**

Imparipes sp.; Australia; p; Marsh *et al.* (2023)

Dermaptera

Forficulidae: *Labidura** *bengalensis**

Imparipes (I.) bengalensis Radhakrishnan & Ramaraju, 2017; India; p; Radhakrishnan & Ramaraju (2017); on the forewing

Isoptera

Rhinotermitidae: *Reticulitermes banyulensis**

Imparipes (I.) clementis Baumann, 2019; Spain; ip; Baumann & Ferragut (2019); males and larvae were gained through laboratory cultures; between termites' coxae

Termitidae: *Trinervitermes trinervoides*

Scutacarus termitophilus Khaustov, Hugo-Coetzee & Ermilov, 2018; South Africa; ip; Khaustov *et al.* (2018a); phoretic on workers of termites

“Insecta”

Scutacarus sphaeroideus Karafiat, 1959; Iran; p; Hajizadeh & Hosseini (2022); found on insects attracted by light traps

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

Harpalinae

Harpalus sp.

Archidispus minor Karafiat, 1959; Iran; p; Hajiqanbar & Arjomandi (2019)

Pterostichinae

Amara sp.

Archidispus szabo Mahunka, 1977; Iran; p; Rahiminejad & Hajiqanbar (2020)

Scaritinae*

*Scarites** (*Scarites*) *procerus eurytus**

Heterodispus turkmenistaniensis Khaustov & Chydyrov, 2005; Iran; p; Msc thesis of Mortazavi (2010), cited in Sobhi *et al.* (2017a); new record as phoretic species (so far only recorded from soil under cucumbers)

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

Cerambycidae*

*Parandra** *caspia**

Scutacarus hystrichocentrus Sevastianov, 1983; Iran; p; Hajiqanbar & Arjomandi (2019)

Curculionidae

Ips typographus

Scutacarus muscocola Sevastianov, 1983; Russia; p; Khaustov (2017b), Khaustov *et al.* (2018b); new record as phoretic species (so far recorded from moss)

Scutacarus palustris Rack, 1966; Russia; p; Khaustov *et al.* (2018b)

Scutacarus pseudoplurisetus Khaustov, 2017; Russia; p; Khaustov (2017b), Khaustov *et al.* (2018b)

Scutacarus scolyti Mahunka & Moser, 1980; Russia; p; Khaustov (2017b), Khaustov *et al.* (2018b); attached between the coxae of the beetle

Elateridae*

Archidispus insolitus (Kurosa, 1974); Iran; p; Rahiminejad *et al.* (2023); under elytra or on mesothorax

*Drasterius** *bimaculatus**

Imparipes (I.) moderatus Khaustov, 2008; Iran; p; Navabi *et al.* (2018a)

Dryopidae*

*Dryops** sp.

Scutacarus sphaeroideus Karafiat, 1959; Iran; p; Rahiminejad *et al.* (2020b, 2023)

Geotrupidae*

*Geotrupes** *spiniger**

Scutacarus longitarsus (Berlese, 1905); Iran; p; Rahiminejad *et al.* (2020a)

Hydrophilidae

Scutacarus sphaeroideus Karafiat, 1959; Iran; p; Rahiminejad *et al.* (2020b, 2023)

*Coleostoma** *fabricii**

Archidispus hydrophilus Khadem-Safdarkhani & Hajiqanbar, 2022; Australia; p; Khadem-Safdarkhani *et al.* (2022)

Lucanidae*

*Lucanus** *ibericus**

Scutacarus longitarsus (Berlese, 1905); Iran; p; Rahiminejad *et al.* (2020a, 2023)

Meloidae*

Archidispus insolitus (Kurosa, 1974); Iran; p; Rahiminejad *et al.* (2023); under elytra or on mesothorax

Scarabaeidae

Imparipes (Sporichneuthes) intermedius Paoli, 1911; Iran; p; Rahiminejad *et al.* (2020a); new record as phoretic species (so far collected from forest soil and litter)

*Adoretus** *persicus**

Heterodispus turkmenistaniensis Khaustov & Chydyrov, 2005; Iran; p; Rahiminejad *et al.* (2023)

*Hybalus** sp.

Pygmodispus odontotarsus Sevastianov, 1975; Algeria; p; Khaustov & Frolov (2018);

Onthophagus sp.

Imparipes (Sporichneuthes) intermedius Paoli, 1911; Iran; p; Rahiminejad *et al.* (2020a); new record as phoretic species (so far collected from forest soil and litter)

*Oryctes** *nasicornis**

Scutacarus longitarsus (Berlese, 1905); Iran; p; Rahiminejad *et al.* (2020a, 2023)

Tenebrionidae

Archidispus insolitus (Kurosa, 1974); Iran; p; Rahiminejad *et al.* (2023); under elytra or on mesothorax

*Blaps mortisaga**

Heterodispus turkmenistaniensis Khaustov & Chydyrov, 2005; Iran; p; Sobhi *et al.* (2017a); new record as phoretic species (so far only recorded from soil under cucumbers)

Gonocephalum pubiferum

Heterodispus turkmenistaniensis Khaustov & Chydyrov, 2005; Iran; p; Msc thesis of Loghmani (2013), cited in Sobhi *et al.* (2017a); new record as phoretic species (so far only recorded from soil under cucumbers)

IV. SCUTACARID SPECIES ASSOCIATED WITH APOIDEA (HEXAPODA, ECTOGNATHA, ACULEATA)

Apoidea

Andrena sp. (Andrenidae) or *Anthophora* sp.* (Apidae)

Imparipes sp.; Iran; p; Nazari *et al.* (2019); not clear if mites were found on *Andrena* sp. (as given in the text) or on *Anthophora* (as given in table 2); *Anthophora* would be first record of the genus as host for Scutacaridae

Apoidea: Apidae

Apis mellifera

Scutacarus evansi Momen & Curry, 1987; i (?); Egypt; Abd El Hady & Mahfouz (2021); Soliman & Kandil are given as authors of *S. evansi* in the respective paper; new record as phoretic species (so far only recorded from grassland on reclaimed peat)

Bombus sp.

Scutacarus acarorum (Goeze, 1780); Iran; p; Hajiqanbar & Arjomandi (2019)

*Bombus bellicosus**

Scutacarus acarorum (Goeze, 1780); Uruguay; p; Revainera *et al.* (2019)

*Bombus pauloensis**

Scutacarus acarorum (Goeze, 1780); Uruguay; p; Revainera *et al.* (2019)

Bombus terrestris

Imparipes (I.) rafalskii Dastych, 1978; Ukraine; p; Sobhi *et al.* (2017a), citing an article in Russian by Zaloznaya & Khaustov (2007)

Apoidea: Andrenidae

Imparipes sp. nr. *parapicola* Delfinado Baker & Abatiello, 1976; Iran; p(?); Rahiminejad *et al.* (2023); listed as “parasitic on mining bees”

Andrena sp.

Imparipes (I.) rafalskii Dastych, 1978; Iran; p; Sobhi *et al.* (2017a)

Apoidea: Halictidae

*Hoplonomia** *westwoodi**

Nasutiscutacarus latisetus Khaustov & OConnor, 2019; Sri Lanka; p; Khaustov & OConnor (2019)

*Mellitidia** *gressitti**

Nasutiscutacarus longicaudus Khaustov & OConnor, 2019; Papua New Guinea; p; Khaustov & OConnor (2019)

V. SCUTACARID SPECIES ASSOCIATED WITH FORMICIDAE EXCL. FORMICINAE AND MYRMICINAE (HEXAPODA, ECTOGNATHA, ACULEATA, VESPOIDEA)

Dolichoderinae

*Tapinoma sessile**

Scutacarus sp.; USA; p; Uppstrom (2010)

*Tapinoma tauridis**

Imparipes (I.) comatus Mahunka, 1970; Iran; p; Sobhi *et al.* (2017a); the ant species is currently considered a synonym of *T. erraticum* (Bolton 1995, updated online 2020)

Ponerinae

*Brachyponera** *chinensis**

Scutacarus sp.; Japan; p; Lopes *et al.* (2015), citing Maruyama *et al.* (2013); attached to the head of the ant

*Ponera pennsylvanica**

two not further identified *Imparipes* species; USA; p; Uppstrom (2010)
one not further identified *Scutacarus* species; USA; p; Uppstrom (2010)

VI. SCUTACARID SPECIES ASSOCIATED WITH FORMICINAE (HEXAPODA, ECTOGNATHA, ACULEATA, FORMICIDAE)

*Anoplolepis** sp.

Scutacarus olszanowskii Khaustov *et al.*, 2020; South Africa; p; Khaustov *et al.* (2020); ants in an old nest of *Trinervitermes trinervoides* termites

Scutacarus variabilis Khaustov *et al.*, 2020; South Africa; p; Khaustov *et al.* (2020); ants in an old nest of *Trinervitermes trinervoides* termites

Camponotus sp.

Imparipes (I.) ignotus Khaustov & Chydyrov, 2004; Iran; p; Navabi *et al.* (2018a)

Imparipes (I.) malus Khaustov, 2008; Iran; p; Navabi *et al.* (2018a)

*Camponotus chromaiodes**

Scutacarus sp.; USA; p; Uppstrom (2010)

*Camponotus cingulatus**

Scutacarus cingulatus Silva, Khaustov & Oliveira, 2019; Brazil; ip; Silva *et al.* (2019); females found phoretic on ants, males and larvae (but no females) found in the nest

*Camponotus distinguendus**

Scutacarus camponoti Khaustov 2017; Chile; ip; Khaustov (2017a); males found in the nest

*Camponotus oasisium**

Scutacarus pseudoapodemi Navabi & Hajiqanbar, 2018; Iran; p; Navabi *et al.* (2018a)

Imparipes (I.) morosus Khaustov, 2008; Iran; p; Navabi *et al.* (2018a)

Cataglyphis sp.

Scutacarus subquadratus Khaustov & Chydyrov, 2004; Iran; p; Sobhi *et al.* (2017a)

Formica sp.

- Scutacarus avarus* Khaustov, 2008; Iran; p; Navabi *et al.* (2018a)
Thamatopelvis lorasiacus Navabi & Hajiqanbar, 2018; Iran; p; Navabi *et al.* (2018b)
- Formica* spp.
Imparipes sp.; USA; p; Uppstrom 2010
Imparipes (I.) obsoletus Rack, 1966; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) nescius Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) robustus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus atypicus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016); attached to the anterior surface of ant abdomen
 3 not nearer identified *Scutacarus* spp.; USA; p; Uppstrom (2010)
Scutacarus carsticus Mahunka & Mahunka-Papp, 1980; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus pilatus Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus rotundus (Berlese, 1903); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus subterraneus (Oudemans, 1913); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
- Formica fusca*
Scutacarus karafiatii Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
- Formica rufa*
Scutacarus (tackei?) suborbiculatus Rack, 1964; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)**Formica sanguinea*
Scutacarus pseudospinosus Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Lasiophanes picinus**
Scutacarus neotropicus Khaustov, 2017; Chile; p; Khaustov (2017a)
- Lasius* sp.
Imparipes (I.) hajiqanbari Rahiminejad *et al.*, 2022; Iran; p; Rahiminejad *et al.* (2022); found on alates
- Lasius* spp.
 5 not nearer identified
Imparipes spp.; USA; p; Uppstrom (2010)
Imparipes (I.) histricinus Berlese, 1903; Iran; p; Rahiminejad *et al.* (2022)
Imparipes (I.) lituanicus Lazauskene & Sevastianov, 1974; Iran; p; Rahiminejad *et al.* (2022); new record as phoretic species (so far only found in forest litter)
Imparipes (I.) obsoletus Rack, 1966; Russia, Iran; p; Khaustov & Tolstikov (2016), Rahiminejad *et al.* (2022)
Imparipes (I.) sklyari Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
 17 not nearer identified
Scutacarus spp.; USA; p; Uppstrom (2010)
Scutacarus heterotrichus Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus lasiophilus Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016); on lateral parts of ant abdomen
Scutacarus longisetus (Berlese, 1903); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus pseudospinosus Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016); attached to tibia of leg I of *Lasius niger*
Scutacarus spinosus Štorkán, 1936; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
- Lasius alienus*
Diveripes sp.; USA; p; Uppstrom (2010); attached to the ant head
Pygmodispus sp.; USA; p; Uppstrom (2010); attached to the ant head
- Lasius flavoniger**
Imparipes (I.) sevastianovi Khaustov, 2008; Iran; p; Hajiqanbar & Arjomandi (2019)
- Lasius flavus*
Imparipes (I.) brevitarsus Ebermann, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus insolitus Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus molnari Mahunka, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016); on lateral parts of ant abdomen
Scutacarus moseri Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus ponticulus Mahunka, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus sibiriensis Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016); attached to the ant head
Scutacarus tutus Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
- Lasius fuliginosus*
Imparipes (I.) brevbasis (Sevastianov, 1983); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) fuliginophilus Khaustov, 2016; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) sevastianovi Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus flexisetus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus heterotrichus Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
- Lasius niger*
Lophodispus irregularis (Mahunka, 1971); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)

- Scutacarus carsticus* Mahunka & Mahunka-Papp, 1980; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus crinitus Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus ellipticus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus expectatus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus hauseri Mahunka, 1977; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus hystrichocentrus Sevastianov, 1983; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus (gratus?) hortobagvensis Mahunka, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus kassaii Mahunka, 1965; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus velutinosus Sevastianov, 1983, Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
*Lasius obscuratus**
Imparipes (I.) placidus Khaustov & Chydyrov, 2004; Iran; p; Sobhi *et al.* (2017a)
Lasius umbratus
Scutacarus aequalis Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus flexisetosimilis Khaustov, 2016; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus levis Mahunka, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016); new record as phoretic species (so far reported from grass sample)
Scutacarus velutinosus Sevastianov, 1983; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)

VII. SCUTACARID SPECIES ASSOCIATED WITH MYRMICINAE (HEXAPODA, ECTOGNATHA, ACULEATA, FORMICIDAE)

Aphaenogaster spp.

- 2 not nearer identified *Imparipes* spp.; USA; p; Uppstrom (2010)
 4 not nearer identified *Scutacarus* spp.; USA; p; Uppstrom (2010)
Messor sp.
Imparipes (I.) histricinus Berlese, 1903; Iran; p; Sobhi *et al.* (2017a)
Scutacarus ebermanni Sobhi & Hajiqanbar, 2017; p; Iran; Sobhi *et al.* (2017b)
Scutacarus remissus Khaustov, 2008; Iran; p; Sobhi *et al.* (2017a)
Scutacarus shivicki Lazauskene & Sevastianov, 1974; Iran; p; Sobhi *et al.* (2017a); new record as phoretic species (so far reported from soil and litter)

*Messor caducus**

- Imparipes (I.) gagati* Khaustov, 2008; Iran; p; Navabi *et al.* (2018a)

Myrmica ruginodis

- Imparipes (I.) charkoviensis* Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) comatosimilis Metwali, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus ellipticus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus hystrichocentrus Sevastianov, 1983; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus kassaii Mahunka, 1965; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus latus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus myrmecophilus Metwali, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus myrmicinus Khaustov, 2015; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus ovoideus Karafiat, 1959; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus pseudospinosus Khaustov, 2008, Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus spinosus Štorkán, 1936, Russia; nk (presumably ip); Khaustov & Tolstikov (2016); on lateral parts of ant abdomen
Scutacarus subterraneus (Oudemans, 1913); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)

Pheidole sp.

- Thaumatopelvis lorasiacus* Navabi & Hajiqanbar, 2018; Iran; p; Navabi *et al.* (2018b)

*Solenopsis molesta**

- 2 not nearer identified *Imparipes* spp.; USA; p; Uppstrom (2010)

Tetramorium sp.

- Imparipes (I.) imaginatus* Mahunka, 1981; Iran; p; Sobhi *et al.* (2017a)
Imparipes (I.) lentus Khaustov, 2008; Iran; p; Sobhi *et al.* (2017a)
Imparipes (I.) malus Khaustov, 2008; Iran; p; Navabi *et al.* (2018a)
Imparipes (I.) placidus Khaustov & Chydyrov, 2004; Iran; p; Sobhi *et al.* (2017a)
Imparipes (I.) tenuis Mahunka, 1981; Iran; p; Sobhi *et al.* (2017a)
Scutacarus shajariani Sobhi & Hajiqanbar, 2017; Iran; p; Sobhi *et al.* (2017b)

Tetramorium caespitum

- Imparipes* sp.; USA; p; Uppstrom (2010)
Imparipes (I.) parapicosimilis Metwali, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) histricinus Berlese, 1903; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) imaginatus Mahunka, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Imparipes (I.) lentus Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)

Imparipes (I.) hortobagyensis Mahunka, 1981; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Lophodispus irregularis (Mahunka, 1971); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus claviger (Paoli, 1911); Russia; nk (presumably ip); Khaustov & Tolstikov (2016)
Scutacarus pseudospinosus Khaustov, 2008; Russia; nk (presumably ip); Khaustov & Tolstikov (2016)

VIII. SCUTACARID SPECIES ASSOCIATED WITH MAMMALIA

Cricetidae

Pygmodispus odontotarsus Sevastianov, 1975; Ukraine; i; Sosnina & Sevastianov (1975)