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Mesostigmatid mites associated with the dung beetle *Copris lunaris* (Coleoptera: Scarabaeidae)

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Abstract. We examined the mesostigmatid mites found in four nest chambers of the dung beetle *Copris lunaris* (Scarabaeidae) in Slovakia. A total of 763 mites was found, belonging to ten species. The most frequent and abundant species were *Pelethiphis opacus*, *Macrocheles copridis*, *Parasitus copridis*, *Uropoda copridis*, *Copriphis pterophilus*, and *Onchodellus hispani*. The nests contained 19 dung balls, each enclosing a beetle pupa. Altogether 472 mites were found in these brood balls. A further 291 mites were found on the parental beetles in the nests. Three mite species were clearly more abundant in brood balls than on parental beetles, and these belonged to the life cycle stage that disperses by phoresy. The mites found in brood balls apparently disperse on the young adult beetles when they emerge. Only *Parasitus copridis* was more abundant on parental beetles than in brood balls. Different species of mites have developed different strategies for dispersal, as shown by their preferential attachment to either the parental or progeny generations of beetles.

INTRODUCTION

The adults and larvae of dung beetles of the family Scarabaeidae are coprophagous, feeding on the excrement of various mammals, mainly large herbivores. Many groups of predatory mites have also evolved a specialised habitat association with mammalian dung. Because of the temporally and spatially isolated nature of dung pads, these mites often disperse by phoresy on coprophilous insects that have similar habitat requirements (Krantz, 1983). Phoresy of this type requires behavioural and life history adaptations to ensure that the dispersal stage of the mite is available and active at the time when the carrier insect is ready to leave a local habitat patch. These adaptations have become especially complex in the case of mites associated with dung beetles of the subfamily Coprinae, which demonstrate a high level of parental brood care. In these beetles the female, sometimes together with the male, remains in the underground nest chamber caring for the brood until the emergence of the progeny (Halffter & Edmonds, 1982). Many species of mites that breed in these nest chambers disperse by phoresy on the beetles, as is common for other taxa of dung beetles, but the existence of brood care in the Coprinae means that the mites have the unusual opportunity of access to both the parental and progeny generations of beetles.

Among the Coprinae, only *Copris lunaris* (Linnaeus, 1758) occurs in Central Europe. Its nesting behaviour has been described by several authors, including Lengerken (1952), Teichert (1960), Rommel (1967) and Klemperer (1982a, b). The female excavates a chamber under a cow dung pad and, together with the male, fills it with dung. These two parental beetles bring with them a community of phoretic mites. The dung is formed into a loaf-like mass and allowed to ferment for a time. The female then forms 4–8 pear-shaped brood balls and lays one egg into a small cavity on the top of each. The female, sometimes together with the male, stays in the subterranean chamber until hatching of the adult progeny, and protects the brood balls containing larvae or pupae. Finally, the parent female leaves the subterranean nest chamber together with her adult progeny.

When a pair of *Copris lunaris* beetles first build and provision a breeding chamber, the dung is fresh and wet, and it undergoes an initial period of fermentation. The beetles then break up the dung mass and form it into four or five pear-shaped brood balls, and the female lays one egg in each. When the brood balls are fully formed and the beetle larva is developing, the dung gradually dries out and is consumed from within by the larva, and by the time the larva has pupated, the nest is relatively dry, without actively decaying organic material. Shortly before the pupa ecloses to an adult, the walls of the brood ball are so dry and hard that migration of mites into or out of the brood balls becomes impossible. The entry of mites into the brood balls must start early, shortly after the beetle egg is laid, and can only continue until the walls of the brood ball have hardened. The brood ball of *Copris lunaris* has a small area where the wall is thin and porous, apparently to allow ventilation (Klemperer, 1982a, b). It is not known whether mites can pass through this porous area, but the presence of different mite species assemblages inside versus outside the brood ball suggests that they do not (see results below). When the beetle pupae have completed their development, the young adult beetles emerge, and both the female parent and the newly-emerged offspring beetles break out of the brood chamber and escape. When the young adult progeny emerge from the pupae, there is a short period when both the parental and progeny generations of adult beetles are present in the nest at the same time (Klemperer, 1982a, b).

Many papers have been published on the mesostigmatid mites that live in association with species of *Copris*, but few of them have paid special attention to the behavioural relationship between the mites and their beetle hosts. Most are faunistic or taxonomic papers based on mites collected from adult beetles in France (Théodoridès, 1955), Israel (Costa, 1963), Bulgaria (Koyumdjieva, 1981), Poland (Haitlinger, 1987), Slovakia (Mašán, 1994a, b), Japan (Takaku et al., 1994) and Russia (Makarova, 1996). Only the papers of Costa (1964, 1965, 1969) deal with details of the biology of the mites and their ecological relationships with the beetles. The purpose of this paper is to review the diversity of Mesostigmata obtained from subterranean nests of *Copris lunaris* in Slovakia, and to examine how the dispersal behaviour of different species of mites is related to the reproductive behaviour of their host beetles.

MATERIAL AND METHODS

Mites were obtained from four subterranean nests of *Copris lunaris* excavated from warm lowland pasture (180 m a.s.l.) near Brunovce village in Southwest Slovakia (17°51′E, 48°40′N) on August 3rd, 1994. In Slovakia, *Copris lunaris* begins to excavate nest chambers in late spring (May, June) and the new generation hatches in late summer (August, September). Each nest chamber is about 12–15 cm long and 6–8 cm high, usually immediately under a fresh cow dung pad.

In suitable habitats, it is not difficult to find a vertical gallery occupied by burrowing beetles during the early stages of nest construction. The presence of burrowing beetles is usually revealed by disturbed soil lying around the margins of the dung pad. Later, when the beetles move into the nest chamber, the gallery opening is gradually filled by dung and soil, it becomes overgrown by vegetation, and the old dung pad is washed away by rain and destroyed by grazing cattle. Therefore it is very difficult to detect nests 2–3 months after their construction.

The nests examined in this study were built in light sandy soil in a cattle resting area, where the vegetation had been destroyed by the cattle. The small remnants of dried dung together with the upper soil layer were removed from the soil surface using a flat hoe, to reveal the tunnel opening, about 2 cm in diameter, filled with various material. In *Copris lunaris*, the tunnel mostly passes into a short gallery about 5 cm deep, which leads into the nest chamber. Each excavated nest contained one parental female beetle and four or five brood balls, each containing a beetle pupa. The brood balls taken from individual nests were stored separately on damp cotton wool in glass jars at room temperature until their contents were examined (nest number 1, 5 brood balls, opened 3 August 1994; nest number 2, 5 brood balls, 7 August 1994; nest number 3, 5 brood balls, 17 August 1994; nest number 4, 4 brood balls, 21 August 1994). All brood balls contained a live beetle pupa and live mites. The parental female beetles were each preserved separately in alcohol. The mites that were found inside brood balls and those that were found on the bodies of the parental beetles were recorded separately. Small remnants of old cattle excrement mixed with soil detritus occurring in nest chambers were not examined.

Using forceps, mites were collected from the bodies of the parental beetles and under the beetles' elytra (if not found in the sediment in the vial), and collected separately from the living pupae and inner surface of the brood balls. For identification, individual mites were mounted onto permanent slides using gum-chloral medium (Swan's Medium). The material is deposited at the Institute of Zoology, Slovak Academy of Sciences.

RESULTS

Altogether 763 mites were collected from the nests of *Copris lunaris*, including members of six families (Eviphididae, Macrochelidae, Melicharidae, Pachylaelapidae, Parasitidae, Uropodidae). These are listed in Table 1, and compared with the mites collected in previous European studies of *Copris lunaris*. A total of 27 species of Mesostigmata has been found associated with *C. lunaris*, ten of which were collected in the present study. The mite species listed in Table 1 are *Alliphis halleri* (G. & R. Canestrini, 1881); *Alliphis montanus* Koroleva, 1968 = *Alliphis rotundianalis* Mašán, 1994b, = *Alliphis* sp. 2 of Mašán (1994a); *Alliphis phoreticus* Mašán, 1994b = *Alliphis* sp. 1 of Mašán (1994a); *Alliphis scarabaeorum* Ogandzhanyan, 1969; *Copriphis pterophilus* (Berlese, 1882), often referred to as *Eviphis pterophilus* (Berlese, 1882), see Mašán & Halliday (2009); *Halolaspis hypedon* Mašán & Halliday, 2009 = *Iphidosoma pratensis* Karg *sensu* Mašán (1994a) [misidentification]; *Macrocheles copridis* Mašán, 2003; *Macrocheles glaber* (Müller, 1860) = *Macrocheles veterrimus* Sellnick, 1940, [synonymy by Filipponi & Pegazzano (1962)]; *Macrocheles lumareti* Niogret & Nicot, 2008, this date because *Macrocheles lumareti* in Niogret et al. (2006) is a nomen nudum; *Macrocheles merdarius* (Berlese, 1889); *Macrocheles perglaber* Filipponi & Pegazzano, 1962; "*Nothrholaspis pseudoterreus*" attributed to Turk (in litt.) by Théodoridès (1955) is a nomen nudum, and the name is used here for bibliographic reference only; *Onchodellus hispani* (Berlese, 1903); *Onchodellus reticulatus* (Berlese, 1904) = *Pachylaelaps karawaiewi* Berlese, 1920 sensu Mašán (1994a) [misidentification, see Mašán (2007)]; *Pachylaelaps pectinifer* (G. & R. Canestrini, 1881); *Parasitus coleoptratorum* (Linnaeus, 1758); *Parasitus copridis* Costa, 1963; *Parasitus fimetorum* (Berlese, 1903); *Parasitus heliocopridis* Oudemans, 1910; *Parasitus lunariphilus* Makarova, 1996; *Parasitus mustelarum* Oudemans, 1903; *Pelethiphis opacus* Koyumdjieva, 1981; *Proctolaelaps ventrianalis* Karg, 1971; *Scarabaspis inexpectatus* Oudemans, 1903; *Uropoda copridis* (Oudemans, 1916).

Details of the mites found on beetles and in brood balls are summarised in Table 2. Each nest contained one adult parental female beetle. The mites collected from the four parental beetles comprised 291 specimens belonging to nine species. Mites occurred on all four parental beetles, and the average number of mites per parental beetle was 72.8 individuals (range 16–101). The most abundant species were *Parasitus copridis*, *Macrocheles copridis* and *Pelethiphis opacus*. These three species made up 91% of all the mites collected on beetles.

The 19 brood balls that were examined contained a total of 472 mites belonging to seven species. These mites were found inside the brood balls, sometimes on the surface of the beetle pupa. The number of mites in each brood ball ranged from 5 to 69 (mean 24.8), and the number of mite species per brood ball varied from two to

TABLE 1. Mesostigmatid mites associated with *Copris lunaris*. * = collected in present study

Mite species	Family	Location	Reference
Alliphis halleri	Eviphididae	Slovakia	Mašán (1994a)
Alliphis montanus *	Eviphididae	Slovakia	Mašán (1994b)
Alliphis phoreticus *	Eviphididae	Slovakia	Mašán (1994a, b)
Alliphis scarabaeorum	Eviphididae	Armenia	Ogandzhanyan (1969)
Copriphis pterophilus *	Eviphididae	Bulgaria France Slovakia	Koyumdjieva (1981) Théodoridès (1955) Mašán (1994a)
Halolaspis hypedon	Eviphididae	Slovakia	Mašán (1994a) Mašán & Halliday (2009)
Macrocheles copridis *	Macrochelidae	Slovakia	Mašán (2003)
Macrocheles glaber	Macrochelidae	France Poland Slovakia	Niogret et al. (2006) Théodoridès (1955) Haitlinger (1987) Mašán (1994a)
Macrocheles lumareti	Macrochelidae	France	Niogret et al. (2006) Niogret & Nicot (2008)
Macrocheles merdarius	Macrochelidae	Poland Slovakia	Haitlinger (1987) Mašán (1994a)
Macrocheles perglaber	Macrochelidae	Bulgaria France	Koyumdjieva (1981) Niogret et al. (2006)
"*Nothrholaspis pseudoterreus*"	Macrochelidae	France	Théodoridès (1955)
Onchodellus hispani *	Pachylaelapidae	Bulgaria Poland Slovakia	Koyumdjieva (1981) Haitlinger (1987) Mašán (1994a)
Onchodellus reticulatus	Pachylaelapidae	Slovakia	Mašán (1994a, 2007)
Pachylaelaps pectinifer	Pachylaelapidae	France	Théodoridès (1955)
Parasitus coleoptratorum	Parasitidae	Bulgaria Slovakia	Koyumdjieva (1981) Mašán (1994a)
Parasitus copridis *	Parasitidae	Bulgaria Poland Slovakia	Koyumdjieva (1981) Haitlinger (1987) Mašán (1994a)
Parasitus fimetorum	Parasitidae	Slovakia	Mašán (1994a)
Parasitus heliocopridis	Parasitidae	France	Théodoridès (1955)
Parasitus lunariphilus	Parasitidae	Russia	Makarova (1996)
Parasitus mustelarum	Parasitidae	Slovakia	Mašán (1994a)
Parasitus sp.	Parasitidae	Bulgaria	Koyumdjieva (1981)
Pelethiphis opacus *	Eviphididae	Bulgaria Poland Slovakia	Koyumdjieva (1981) Haitlinger (1987) Mašán (1994a, b)
Proctolaelaps ventrianalis *	Melicharidae	Slovakia	Mašán (1994a)
Scarabaspis inexpectatus *	Eviphididae	Poland	Haitlinger (1987)
Uropoda copridis *	Uropodidae	Poland Slovakia	Wiśniewski (1982) Haitlinger (1987) Mašán (1994a, 1998)
Uropoda sp.	Uropodidae	Slovakia	Mašán (1994a)

seven. The most frequent species were *Macrocheles copridis* (found in 18 of the 19 brood balls), *Copriphis pterophilus* and *Pelethiphis opacus* (both 14/19), *Uropoda copridis* (11/19), *Onchodellus hispani* (9/19) and *Parasitus copridis* (7/19). Overall the most abundant species in brood balls were *Pelethiphis opacus*, *Macrocheles copridis*, *Uropoda copridis*, and *Copriphis pterophilus*. Together these four species made up 86% of the mites found in brood balls.

DISCUSSION

When our results are combined with those of previous authors, a total of 27 species of Mesostigmata has been found in association with *Copris lunaris*. For comparison, Costa (1963) found 17 species on *Copris hispanus* in Israel. Haitlinger (1999) suggested that the mite fauna associated with *C. lunaris* in Slovakia (16 species) was richer than that of Poland (10 species), but this may simply reflect the intensity of the collecting effort.

All the mites in a particular beetle nest are the descendants of colonising mites that were brought in phoreti-

TABLE 2. Numbers of mites found in four nest chambers of *Copris lunaris*.

Nest number	On parental beetles (n = 4)						In brood balls (n = 19)					
	1	2	3	4	Total	Mean	1	2	3	4	Total	Mean
Proctolaelaps ventrianalis	0	0	0	0	0	0	0	0	0	1	1	0.1
Uropoda copridis	0	0	1	1	2	0.5	29	0	50	5	84	4.4
Alliphis montanus	2	0	0	0	2	0.5	0	0	0	0	0	0
Scarabaspis inexpectatus	2	0	0	0	2	0.5	0	0	0	0	0	0
Copriphis pterophilus	0	0	3	0	3	0.8	24	0	14	30	68	3.6
Alliphis phoreticus	2	2	1	3	8	2.0	0	0	0	0	0	0
Onchodellus hispani	0	1	7	2	10	2.5	0	0	21	24	45	2.4
Pelethiphis opacus	2	0	41	31	74	18.5	62	0	35	55	152	8.0
Macrocheles copridis	2	41	16	19	78	19.5	20	40	32	12	104	5.5
Parasitus copridis	6	55	32	19	112	28.0	2	11	0	5	18	1.0
Totals	16	99	101	75	291	72.8	137	51	152	132	472	24.8

cally by the two parental beetles. This original mite population has produced two derived populations – some mites associated with the parental beetles, and some in the brood balls. In terms of a simple inventory of the species present, the mite species found on parental beetles and in brood balls were generally similar (Table 2). However, the relative abundance of individual species in the two types of collection was strongly heterogeneous (2 × 10 contingency table analysis, Chi-squared = 244, d.f. = 9, $P < 0.001$). Four species of mites were rare in the present study – *Alliphis phoreticus*, *Alliphis montanus*, *Scarabaspis inexpectatus*, *Proctolaelaps ventrianalis*. According to Mašán (1994a) and the present results, these species are very rare or absent in the maternal brood balls. They are more abundant in the subterranean nests when fresh dung is present, in the initial phase of nesting, before brood balls are formed. They do not have a close specific relationship with species of *Copris*, and are not considered further. The other six species differ in their preferences for attachment to the parental and progeny generations of beetles. Two species occurred almost exclusively in brood balls (*Copriphis pterophilus*, *Uropoda copridis*). *Macrocheles copridis*, *Onchodellus hispani* and *Pelethiphis opacus* also occurred more commonly in brood balls than on the parental beetles, although less strongly. In contrast, *Parasitus copridis* was much more common on parental beetles than in brood balls.

Parasitus copridis is the largest and most active of the mites found on *Copris lunaris*. It was the only species that occurred more abundantly on the parental beetles (112 specimens) than in the brood balls (18 specimens). The specimens of *Parasitus copridis* found in this study were all deutonymphs, the dispersing stage of this species. Costa (1964) has shown that deutonymphs of *Parasitus copridis* eclose to adults and complete their life cycle when dung beetles (*Copris hispanus*) are present. In the present study, it appears likely that this species developed up to the deutonymph stage in the brood chambers before they were excavated, and these deutonymphs were waiting to disperse. The high mobility of *Parasitus copridis* deutonymphs should allow them to locate the newly-hatched beetles in the nest chamber as they emerge from their brood balls, and attach to them when they leave, but most were found attached to the parental beetles. The behaviour of *Parasitus copridis* appears to be similar to that of species of *Poecilochirus* (Parasitidae) that breed in the brood chambers of carrion-feeding beetles (Silphidae). Most deutonymphs of *Poecilochirus* spp. disperse by attachment to the parental beetles, while a minority wait in the brood chamber until the new generation of young beetles emerges (Schwarz & Koulianos, 1998), and the same appears to be true for *Parasitus copridis*.

In contrast, *Uropoda copridis* is a strongly sclerotised slow-moving uropodine with very low mobility. In this species, 84 of the 86 specimens were found within brood balls. Once again, all the specimens of this species were the phoretic stage, the deutonymph. The interesting finding of the only known female specimen of *Uropoda copridis*, originally discovered on the larva in a maternal brood ball of *Copris lunaris* and described by Mašán (1998), has not been repeated in this study. This suggests a different type of dispersal strategy, in which the deutonymphs of *Uropoda copridis* attach to the newly-emerged beetle before it breaks out of its brood ball. Deutonymphs of *U. copridis* attach themselves to phoronts using an adhesive anal pedicel, as found in many species of Uropodina (Athias-Binche, 1984). This attachment appears to make it impossible for a mite to transfer from one beetle to another.

Copriphis pterophilus was also found almost exclusively in brood balls (68 of the 71 specimens collected). However, in this case all the mite specimens collected were adults, both males and females. No larval or nymphal stages were found during the present study, either on parental beetles or in brood balls. Adult males and females of this mite are phoretic, and can be found clustered under the elytra of *Copris lunaris* collected in dung outside of brood chambers (PM, personal observations). Within the subelytral cavity, mites attach to the beetle by grasping its soft intersegmental and pleural membranes. This probably limits their ability to transfer from one beetle to another. It appears that they are phoretic on the progeny generation of beetles much more than on the parental generation. This behaviour is similar to that of *Alliphis necrophilus* Christie, 1983, which disperses by phoresy under the elytra of carrion beetles, and strongly favours the progeny generation of hosts (Schwarz & Koulianos, 1998). We believe that *Copriphis pterophilus* reproduces in the brood chambers of *Copris lunaris*. Deutonymphs have occasionally been found in newly-formed nests during previous studies (PM, pers. observ.), but the details of its life cycle have not yet been worked out.

Macrocheles copridis appears to adopt a mixed strategy, with the phoretic stage, adult females, occurring in brood balls and on parental beetles in roughly equal numbers. This species appears to disperse on both parental and progeny generations of beetles, as does its counterpart *Macrocheles nataliae* Bregetova & Koroleva on carrion beetles (Schwarz & Koulianos, 1998).

Onchodellus hispani appears to adopt a similar strategy to that of *Macrocheles copridis*. Most specimens were found inside brood balls (45 specimens), but some were found on the parental beetles (10 specimens), and all were adults. Adult males and females of this mite are phoretic on *Copris hispanus* and *Copris lunaris* (Costa, 1963; Koyumdjieva, 1981) and our observations suggest that it is phoretic on both parental and progeny generations of beetles.

The life cycle of *Pelethiphis opacus* is not well understood. It was abundant in our collections, both in brood balls and on parental beetles. The 74 specimens collected on beetles included only males and deutonymphs, and the 152 specimens found in brood balls were all deutonymphs. The female of this species remains unknown, so its taxonomic placement cannot be determined with complete confidence, and the location and timing of its breeding also remain unknown.

Schwarz & Koulianos (1998) noted that mites breeding in the brood chambers of carrion-burying beetles (Silphidae) must choose whether to leave the brood chamber by attaching to the parental beetles, or wait until the progeny beetles emerge and depart. This situation is a direct consequence of the brood care practised by these beetles, which means two generations of beetles are present in the brood chambers at the same time. The same is true of the dung beetle associated mites reported here. Among the mite species associated with *Copris lunaris*, the phoretic stages of three species show a strong preference to wait in the brood ball and disperse on the progeny beetles (*Uropoda copridis*, 98% in brood balls), *Copriphis pterophilus* (96%), and *Onchodellus hispani* (82%), and two show no clear preference, *Pelethiphis opacus* (67%) and *Macrocheles copridis* (57%). Only the most mobile and active species, *Parasitus copridis*, showed a strong preference for the parental beetles (86%) instead of brood balls. However, we have only recorded the location of mites at a time when the parental beetles are present in the brood chamber, and the brood ball contains a beetle pupa, not an active young progeny beetle. We do not yet know whether any mites transfer from parental beetle to progeny beetle after the latter has eclosed and broken out of its brood ball.

The mites discussed here all belong to the Order Mesostigmata. *Copris lunaris* also supports a diverse community of other phoretic mites, including *Acotyledon abnormis* Samšiňák, 1966 (Acaridae), *Pavania riparia* Sevastianov, 1980 (Dolichocybidae) and *Spatulaphorus copridis* Khaustov, 2007 (Pygmephoridae). Haitlinger (1987) reported some Astigmatid mites associated with *Copris lunaris*, including *Sancassania geotruporum* (Zachvatkin, 1941) and three species of Histiostomatidae. Species of *Sancassania* Oudemans, 1916 (= *Caloglyphus* Berlese, 1922) have been reported as attacking the immature stages of several groups of insects, including cockroaches (Li et al., 2003), flies (Park & Kim, 1997) and dung beetles (Veenakumari & Veeresh, 1996). Hughes (1976) reported that *Sancassania berlesei* (Michael, 1903) is often found in insect cultures, causing considerable damage to insect eggs and larvae.

Lindquist et al. (2009) summarised data showing that Mesostigmata in the families Eviphididae, Macrochelidae, Melicharidae, Pachylaelapidae, Parasitidae, and Uropodidae are predatory. Direct observations of the feeding behaviour of the species collected in the present study are lacking, but evidence from related species shows that they are likely to feed on nematodes, small insect eggs, and other mites. The presence of these predatory mites in *Copris lunaris* brood balls could therefore be beneficial to the beetles, by preventing the build-up of Astigmata that could threaten the beetle egg and larva. An unsuccessful attempt was made to introduce *Copris lunaris* into Australia to aid in the control of dung-breeding flies (Edwards, 2007). During the introduction of European and African dung beetles into Australia, all mites and other associated fauna were rigorously excluded (Waterhouse, 1974), when the complexity of their ecological roles was not fully understood. It is now known that some of these predatory mites are beneficial in contributing to the control of dung-breeding flies (Wallace et al., 1979). It is also conceivable that they could be beneficial through a symbiotic relationship with the dung beetles themselves. Wilson & Knollenberg (1987) showed that predatory mites (Parasitidae) are usually beneficial to the carrion beetles (Silphidae) on which they are phoretic, but could be harmful at high densities by directly attacking the beetles' eggs. The eggs of *Copris lunaris* are large (ca. 5 mm long) and have a strongly sclerotised outer surface (PM, pers. observ.). We consider it unlikely that the predatory Mesostigmata we report here could damage these eggs, but the possibility can not be excluded.

The results presented here point to an unexpected level of complexity in the relationships between dung beetles and phoretic mites. A more detailed study of the life cycles and behaviour of these mites would be a valuable addition to our understanding of the ecology of dung-breeding arthropods, with implications for both practical applications and biodiversity conservation.

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