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Subscriptions: Year 2021 (Volume 61): 450 €
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Previous volumes (2010-2020): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIÉ-sur-LEZ Cedex, France
ISSN 0044-586X (print), ISSN 2107-7207 (electronic)

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

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THE ASSOCIATION BETWEEN MESOSTIGMATIC MITES
AND COPRID BEETLES

BY

Michael Costa

Kibbutz Mishmar Haemek, Israel.

Although a number of papers are devoted to the relations between mites and insects (Sellnick, 1939; Vitzthum, 1940-43; Travårdh, 1943; Cooreman, 1961; Samsinák, 1965) none are devoted to mesostigmatic mites exclusively. There are many taxonomic papers devoted to insecticolous mites (e.g. Turk, 1948; Ryke, 1959; Ryke & Meyer, 1957, 1958; Samsinák, 1957, 1960, 1962; Womersley, 1958, 1960, 1961; Evans & Hyatt, 1963; Hyatt, 1964), but only few papers are concerned with mite-fauna surveys of single insect species or groups (e.g. Berlese, 1903; Vitzthum, 1926, 1930; Hyatt, 1959; Costa, 1963). In only a few cases the biology of the host, as well as that of the mite, has been studied and related (Neumann, 1943; Skaife, 1952; Rapp, 1959; Mollin & Hunter, 1964).

In an attempt to understand the relationships between the mites and their insect hosts, I have tried to prepare a list of gamasine mites that are associated with insects. This list is a preliminary attempt, prepared only from the literature available to me, and by no means exhaustive. No attempt has been made at this stage to clear up the many possible synonyms (except those that have been already accepted in the literature). It seems to me that a complete investigation of this type will be profitable. The preliminary results are summarized in table 1 and comprise 435 mite species.

An analysis of the table shows immediately that the gamasine mites are distributed very unevenly between the various orders of insects. Provision for the brood, brood-care and some sort of nesting for inhabiting of closed spaces (e.g. the galleries of wood-boring beetles) seem to be important conditions for establishing stable relationships between the mites and their hosts. The insect groups in which these characteristics are developed to their highest degree, namely the

1. This study was supported by the Israel Academy of Sciences and Humanities.
2. State Teacher's College "Seminar Hakibbutzim Oranim", P.O. Kiryat Tivon, Israel.

Acarologia, t. XI, fasc. 3. 1969.
social insects, are therefore the optimal host and show an abundance of mite symbionts.

For different mites different stadia may be associated with the adult insect host, usually the phoretic stage is only one stage out of the whole life-cycle of the mite, e.g. the deutonymph or the female. In rare cases only, the whole life-cycle of the mite is completed on the adult insect, this actually occurs in the parasitic mites of the family Otopheidomenidae. The type of phoretic stadium that is associated with the adult insect, seems to be characteristic at the generic or even the family level. The situation is summarized for some groups in fig. 1.

Another criterion for the closeness of the mite—insect association is the degree of host specificity. It may be assumed a priori that strict host specificity is a reliable indication of a very close relationship, even if one mite stadium only is found regularly on the adult host. A very good illustration for this are the relations between the various species of Dinogamasus Kramer and bees of the genus Mesotrichia (Xylocopidae). The bees have on the first abdominal tergite a small pouch that opens to the exterior and this harbours usually half a dozen or more female mites. The relationship between the mite and its host are very specific and are an interesting example of parallel evolution of mite and host. SKAIFE (1952) has investigated the biology of both Mesotrichia (Xylocopa) caffra L. and its symbiotic mite Dinogamastis braunsi Vitzt. His investigation has shown a very close relationship between the two animals. Mature females (males have never been found in this apparently completely thelykotokous genus) remain in the bee’s pouch until egg-laying is commenced by the bee. The bee lays single eggs in chambers provided with pollen, at the same time one or two mites leave the pouch and cling to the pollen store. The mites remain fairly inactive (and are apparently non-feeding) during the time of development of the bee larva. Only when the quiescent prepupal stage has been reached by the bee larva do the mites become active. They run about on the surface of the prepupa, feeding apparently on exudates, swelling and becoming almost globular. The mites invariably die if they are separated from their host during this period. When the bees start to pupate each mite lays 5-10 large eggs. Then, during the four-five weeks of pupal development, the mite completes its whole life-cycle and the newly emerged young bees leave the nest with mites in their pouch.

Mites of the genus Coleolaelaps Berl. have similar, though less specific, relations with the phytophagous scarabaeids. Usually only female mites are carried by the adult host, whereas males and the immature stages may be found associated with the beetle grub in its subterranean crypt. The mites feed on the exudates of the beetle grub, apparently whithout harming the host.

In both cases we find that the mite has adapted its biological cycle completely to the annual breeding cycle of its host. This synchronization of life cycles is extremely interesting and the problem that remains to be solved is the means by which the mite is influenced by its host.

The simplest association between mite and host is undoubtedly pure phoresy
in which the mite is carried by its more mobile host to a specific habitat which is optimal for both host and mite. Often, cases of this nature display an "ecological specificity" only, *Macrocheles glaber* (Müller) for instance, may be phoretic on both coprid beetles and muscid flies that visit dung heaps. Great care must be taken in the identification of both host and mite, because apparently non-specific relations may be actually simulated by a group of closely related and similar species (see below, the *Macrocheles pisentii* complex).

Table 1 shows that mesostigmatic mites are associated with four beetle families: Passalidae, Ipidae (= Scolytidae), Silphidae and Scarabaeidae. The widespread success of these families is due to their social organization and brood-care as well as their habitats, and in this way they are outstanding among the many families of the Coleoptera. The Passalidae inhabit decaying wood in the moist, warm, forests of the world, and their abundant mite fauna is recruited mainly from non-gamasine mesostigmatic mites (Diplogyniidae, Schizogyniidae, Diarthrofalloidae etc.). It is surprising that in spite of this, only the biology of *Cosmolaelaps passali* Hunter & Mollin, 1964, a hypoaspid mite, has been investigated (MOLLIN & HUntER, 1964). Usually only female mites are found on the host *Popilius disjunctus*. Males and the immature stages live in frass in and near the beetle tunnels. The most important results of the study show that reproduction of the mite occurred only when the female was in direct contact with the host.

The Ipidae show associations mainly with mites of the genera *Digamasellus* Berl. and *Proctolaelaps* Berl. In the last mentioned species both males and females are phoretic, though males are rarer. HIRSCHMANN & RÜHM (1955) report on the association between *Digamasellus quadrisetus* Berl. and *Ips typographicus*. At springtime, deutonymphs of *D. quadrisetus* are often found beneath the elytra of young beetles. These form new galleries where the mites resume their development, the nymphs moulting into males or females and the biological cycle of the mite starts anew. *D. quadrisetus* is omnivorous but its staple food is formed by tiny nematodes which are also carried by the beetle into its habitat. The deutonymphs of many *Digamasellus* species are adapted to phoresy by being more heavily sclerotized than the remaining stages.

The Silphidae are known for their common association with deutonymphs of various species of the genus *Poecilochirus* Berl. NEUMANN'S (1943) work on the biology of *Poecilochirus necrophorus* Vitzt. and *Necrophorus humator* F. has shown that the mites are paraphages. He has succeeded in rearing the mites on fresh fly larvae, in petri dises and in the absence of the host. NEUMANN found that the biological cycle of the mite can be completed within 8-9 days. According to him three or four different species of *Poecilochirus* may occur on the same species of *Necrophorus*.

In this paper I shall mainly report on the work done on the associations between mesostigmatic mites and coprid beetles, especially *Copris hispanus* L. and *Scarabaeus* spp. (COSTA, 1963, 1964, 1966a, 1966b, 1967a, 1967b).

In the temperate zone the scarabaeids are the most important beetle hosts for
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**Table 1**: The number of species in the gamasine families which are associated with the various orders of insects (Parasitidae including *Pectinobius*, Rhodacaridae including Digamasellidae).
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Fig. 1: The stages occurring on the adult insect host in several gamasine mites. (circle — rare occurrence).
coleopterous mesostigmatic mites. Theodorides (1955) has collected 36 species of mesostigmatic mites from about 2000 beetles (169 beetle species from 18 families, Ipidae not collected), of these a total of 22 species were collected from scarabaeids. In my own work I have concentrated largely on the mite fauna of Copris hispanus (L.) and not less than 19 species of mesostigmatic mites have been found associated with it. However, only eight species show a definite association with the beetle and account for 99.3% of the collected specimens (Costa, 1963). Three species (Pachylaelaps hispani Berl., Neopodocimn um caputmedusae (Berl.) and Alliphis gurei Costa) seem to be strictly host specific. A fourth species, Parasitus copridis Costa, is practically host specific but has been collected occasionally in small numbers from other beetles. P. copidis has been collected also in Great Britain (G. O. Evans personal communication).

Copris hispanus (L.), like other beetles of the subfamily Coprinae, has a well developed system of brood-care. In Israel the beetles start to be active with the beginning of the rainy season in November. During this season they are easily attracted to light traps, especially on rainy nights. Activity preparatory to egg-laying starts in March and egg-laying reaches its peak in April. Fresh cattle manure is buried into the ground by both the male and female beetle. After about a week the female starts to shape four to five large pills and a single egg is deposited into each of the pills. The female remains with the developing eggs until the young beetles hatch. The beetles, because of the external hardening of the pills, can emerge only after rain has been soaked into the ground to a depth of about 30-40 cm. Rommel (1962) has reported briefly on the mites associated with Copris hispanus (L.) and Copris lunaris (L.) and its egg pills.

Parasitus copridis occurs on the beetle in its deutonymphal stage only, a fact which is characteristic for the genus. Relationships in various degrees of closeness exist between mites of the genus Parasitus and its host beetles. Parasitus fimatorum Berl. and Parasitus consanguineus Oudemans & Voigts have been collected frequently from C. hispanus (the former often in very large numbers), but the various stages of these mites have been collected on many occasions in litter, compost heaps etc., without being associated with beetles at all. Rapp (1955) has worked extensively on the biology and ethology of Parasitus coleoptratorum L. which is associated mainly with beetles of the species Geotrupes stercorarius, and all the information on this species are from his paper. He has shown that the deutonymphs of P. coleoptratorum are adapted to phoresy by a high resistance to desiccation. Larvae and protonymphs die in a dry atmosphere (0% R.H., 21°C) after 20 and 37 minutes respectively, adults remain alive in these conditions for 2.5 hours whereas deutonymphs succumb only after 9.5 — 10 hours. The deutonymphs are also very resistant to starvation and remain alive without food for many weeks. After continuously starving for 2 months, only 40% of the deutonymphs of P. coleoptratorum died, the remaining 60% withstood this hardship without any apparent damage.

In contrast to the quickly developing nymphs of Poecilochirus necrophori only
20-40% of the deutonymphs of *P. coleoptratorum* moulted spontaneously into adults during 5-6 months in which they were kept in dishes with abundant food and high humidities. Rapp's experiment led to the conclusion that fresh horse droppings contain a factor which removes the barrier to moulting. If fresh horse droppings are added to the deutonymphs of *P. coleoptratorum*, nearly all of them (95%) moult within 1.25 days into adults. Droppings aged for eight days also induced moulting in the deutonymphs but was less effective. Rapp has also shown that filter paper wetted with the pressed filtrated fluid of fresh horse droppings induced the moultng of deutonymphs into adults with a success of 85%.

![Graph showing the development of the population of deutonymphs of *Parasitus copridis* on *Copris hispanus* (average for 3 years and 10 beetles; further explanation in text).](image)

**Fig. 2**: The development of the population of deutonymphs of *Parasitus copridis* on *Copris hispanus* (average for 3 years and 10 beetles; further explanation in text).

I was able to repeat this with a dozen deutonymphs of *P. coleoptratorum* collected from *Copris hispanus* in the northern part of Israel. I should like to point out, however, that many adults, deutonymphs and the remaining juvenile stages of this species have been collected by me from funnel extracts of mounds of *Gazella* droppings and possibly all kinds of droppings should be examined for their influence on moulting.

In *Parasitus copridis* an arrest of moulting in the deutonymph is even more marked. I was able to keep actively feeding deutonymphs for periods exceeding 6 months and only very few individuals, never more than 5% of the population, moulted into adults. Actually the first adults were obtained by chance. I happened to collect a *Copris* beetle with about two dozen deutonymphs adhering to it. The beetle was put into a small jar with fresh cattle manure. When I opened the jar three days later I found not only adults but also quickly running whitish...
larvae. This was for a long time the only procedure by which I could induce about 60-70% of the deutonymphs to moult into adults (Costa, 1964).

Horse droppings of the same batch that had induced the nymphs of P. coleoptratorum to moult, had no effect at all upon the deutonymphs of P. copridis, and usually neither did fresh cow dung. However, in one case I obtained within five days 3 ♂ and 4 ♀ from ten deutonymphs that were kept in a small jar with fresh cow dung.

![Graph](image)

**Fig. 3:** The deutonymph populations of *Parasitus copridis* on ten *Copris hispanus* beetles, including a single female in breeding activity.

It is relevant to note here that the activity of *Copris* beetles in the manure has a distinct depressing activity on moulds. Dung in which beetles had been active for several days did not turn mouldy for over a week even after the removal of the beetles. During the rearing experiments the development of moulds was detrimental to the development of the mites and many of them died, mould being the only apparent cause.
At this stage I has started to rear mites in small plaster cells (Costa, 1966a). Ten deutonymphs were crowded into a small cell of one square cm with a depth of 2 mm. As a control, ten deutonymphs of the same batch were put on a female C. hispanicus that was then put into a jar with fresh cow manure. Within 20 days I obtained a single male and a single female in the cell (they emerged on the 6th day and no additional nymphs moulted for a further 14 days) compared with 5 ♂ and 2 ♀ from the jar containing the beetle (Costa, 1964).

To find out the possible influence of population density on moultng, 200 deutonymphs of P. copridis were divided into groups of ten nymphs each. Ten of the groups were reared in cells of one square cm and ten groups were reared in cells of 5 square cm. If an adult appeared in one of the cells, it was taken out and replaced by a nymph. During the 30 days of the experiment, 10 ♂ and 7 ♀ were obtained from the small cells with a high population density, and 4 ♂ plus 2 ♀ from the large cells with only a fifth of the density. In eight out of ten of the small cells adults appeared, whereas only in three of the large cells did adults develop. Although this is still inconclusive, there is a strong indication that high population density induces the nymphs to moult into adults. The adaptive value of this is also obvious as it ensures the meeting of males with females.

During the rearing experiments some additional biological data were collected. In several cases females emerged before males and males were not observed to follow female deutonymphs in wait for their moult. This behaviour, however, has been described for P. coleoptratorum. Two males never hatched simultaneously in the same cell, on the contrary, on several occasions males were seen to kill male deutonymphs (pharate males) a behaviour which has also been observed in Neo- podocinum caputmedusae and Macrocheles spp. (Costa, 1966b, 1967b).

In a few cases, direct development from egg to adult took place and the minimal time of development for the male and the female was 13 and 15 days respectively. The adults of the genus Parasitus seem to have a relatively short span of life. For the female of P. coleoptratorum it is 6-10 days (exceptionally 14 days) and for P. copridis 18-24 days. In P. copridis the males live longer than the females and life spans of over 35 days have been observed.

The number of eggs is 100-130 per female in P. coleoptratorum and only about 40 in P. copridis. In both cases the number of eggs per unit time is strongly influenced by the ambient temperature. P. coleoptratorum lays an egg every 45-60 minutes at 25°C and only every two hours at 17°C. At room temperatures during January, P. copridis laid a maximum of five eggs within 24 hours, whereas in June 25 eggs were laid during the same period of time. It is interesting to compare these observations with the behaviour of Macrocheles species in which the adult female is phoretic and has a long span of life (see below).

The rearing of P. copridis from egg to deutonymph is very easy in small cells and the mites feed readily on small nematodes (Panagrellus sp.). The rearing of P. coleoptratorum under the same conditions, however, proved to be very difficult. The juveniles of this species show, under these conditions, strong canni-
ballistic tendencies and often only a single mite remained from an initial batch of twelve or more larvae.

The reproductive activity of the host, *Copris hispanus* seemed to have a big influence on the reproduction of the mites. In order to investigate this further, the following experiment was carried out. Ten beetles, males and females in equal numbers, were reared separately in large glass jars filled with soil. Ten deutonymphs were put on each of the beetles which were then returned to their respective jars after fresh cow dung had been added. After a month the beetles were recovered and the nymphs were removed and counted. Each beetle received again its complement of ten deutonymphs and was put back into its jar with fresh cow dung. The experiment was continued for three years and the results are shown in the curve of fig. 2. Only the positive standard deviation is indicated in the curve, because negative values were meaningless in many cases because the high deviation is mainly caused by especially high (positive) infestation rates in single beetles, as can be seen in table 2.

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<td>8.9</td>
<td>13.1</td>
</tr>
<tr>
<td>B</td>
<td>±4.6</td>
<td>±18.3</td>
<td>±21.5</td>
<td>±28.5</td>
<td>±11.5</td>
<td>±19.7</td>
<td>±5.7</td>
<td>±5.2</td>
<td>±1.8</td>
<td>±4.3</td>
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<td>80</td>
<td>106</td>
<td>142</td>
<td>49</td>
<td>109</td>
<td>16</td>
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**Table 2.** The development of the population *P. copridis* on *C. hispanus*, average for three years (further explanation in text). A. — Mites per beetle. B. — Standard deviation. C. — Maximal count. D. — Minimal count.

The curve of the mite population closely follows the activity rhythm of the beetles which start to be active after the November rains and whose reproductive activity reaches its peak in April. An outstanding, though not unique, example was provided by the mite population of a single female which bred during June, after all the other beetles had already entered into a period of quiescence. On the active beetle 109 deutonymphs of *P. copridis* were counted, on the remaining beetles the count was only 8.9 deutonymphs per beetle (fig. 3).

Opening the brood pills of *C. hispanus* often reveals a large number of mites enclosed within the pill with the large egg or grub of the beetle. Many of the pills harbour up to a dozen deutonymphs of *P. copridis*, which had entered it at the time the egg was laid. The nymphs remain in the pill with the egg and the developing stages of the beetle until emergence of the latter. The "captivity" of the nymphs may last as long as eight to nine months (April-November) and, during this time, the nymphs remain in a state of arrested development, they do not seem to feed, except possibly on the exudates of the developing beetle larva.

The adaptive significance of this relationship is obvious: the mite is protected in the brood-pills during the hot, arid summer months and is brought into a suitable environment by the emerging beetle. This explains also the adaptive significance of the longevity of the deutonymphal stage. All this points to the regula-
tion of the development of *P. copridis* by internal factors as well as by external factors provided by the beetle.

*Neopodocinum caputmedusae* approaches the conditions found in the parasitic mites of the family Otopheidomenidae, and all the stages, except the transient, non-feeding larvae, were found on the beetle. Deutonymphs, however, were rarely found and the various stages were collected at the following rate: protonymphs — 49.2 %, deutonymphs — 3.4 %, males — 8.8 %, females — 38.5 % (a total of 694 specimens collected from 80 beetles).

*N. caputmedusae* is strongly dependent on its host for the completion of its development. Females stop egg laying, or the production of larvae, shortly after becoming separated from the host. Females which had been reared from deutonymphs and which never had any contact with the host never reproduced although copulation was observed repeatedly. In the rearing cell usually not more than a moult into the consecutive stage occurred and then development was arrested. This is partly similar to the conditions found in *Cosmolaelaps passali* (see above). In both cases the mite needs for its normal development some factor provided by direct contact with the host.

An examination of the brood-pills of *Copris hispanus* showed that they may harbour large numbers of deutonymphs of *N. caputmedusae*. From two brood-pills, collected in the field at the beginning of April and containing a large beetle egg each, 43 deutonymphs were collected. These nymphs were completely different in external appearance from those collected off the beetles. They were large and globular in shape, weakly sclerotized and had shorter setae (fig. 4). On emergence of the adults, 37 females and 3 males were obtained. Three deutonymphs were killed by the males and on examination turned out to be pharate males. In addition to arrhenotoky this might be a factor to account for the scarcity of males in the Macrochelidae (Costa, 1966b). The deutonymphs moult regularly into adults within the pills.

*N. caputmedusae* is extremely interesting in having polymorphic males. Most males (about 90 %) are feminine in appearance in their sclerotization and chaetotaxy, about 10 % are strongly heteromorphic. The heteromorphic males are heavily sclerotized and show an exaggeration of the secondary male sex characters. On the other hand the dorsal chaetotaxy is reduced in contrast with the neosetous condition prevailing in the common males and females. Several males of an intermediate condition have also been found. All the three forms have been raised from the same group of deutonymphs. Nothing is known about the significance or the cytological background of the male polymorphism.

An interesting, though still unsolved, problem is posed by *Alliphis gurei*. Only deutonymphs and males (69δn, 99 ζ from 43 beetles) of this species have been collected. An attempt was made to rear the mites in order to obtain females. Although the mites remained alive in the cells for about two months, no development took place. It is conceivable that in this species too the brood-pill of its host is the main site for its reproductive activity.
Fig. 4: The two different forms of the deutonymph of *Neopodocinum capitamedusae* (left — phoretic on adult *Copris hispanus*; right — from brood pill of *C. hispanus*).
Although the whole developmental cycle of *Pachylaelaps hispani* was obtained in the laboratory, it does not seem to be normal under laboratory conditions. Four females produced only 15 eggs within five weeks. In a second attempt 2 ♂ and 5 ♀ were introduced into a rearing cell and they produced 17 eggs within four weeks. This reproductive rate seems to be below the natural rate of increase.

In conclusion it can be said that the association between *Copris hispanus* and its mites exceeds by far the simple states of symphorium or paraphagium. Various degrees of dependence upon the host are attained by different species of mites. Entering the brood-pills of the hosts is of great survival value to the mites, protecting them from heat, desiccation and enemies during the hot months of the arid summer, and ensuring dispersal to suitable habitats with the emergence of the hosts.

An examination of three species of *Scarabaeus*, namely *S. puncticollis*, *S. sacer* and *S. cristatus* has shown that each of them is host to a different species of the *Macrocheles pisentii* complex (Costa, 1967b). The high incidence of host-mite specificity shows that the relations probably exceed mere phoresy. Indications are that the mites have differing heat-humidity requirements in accordance with the ecological requirements of their hosts.

Attempts were made to crossbreed the three species but in most cases the females were killed by the males. In one case (♂ of *M. parapisentii* × ♀ of *M. sacer*) the male was "outsized" by the female which stayed alive. Although normal copulation was observed, no impregnation took place. Impregnation was not achieved in similar cases in which the mites went through all the normal movements of copulation and were separated after that. Success or failure of fertilization is easily demonstrated in arrhenotokous species which produce only male offspring if not fertilized.

The breeding of *Scarabaeus* species in captivity is difficult and mostly unsuccessful. However, several adult females of *M. parapisentii* were collected from brood-pills (obtained in captivity) of *S. puncticollis*.

In species of the genus *Macrocheles* the adult female is the stage of longevity and phoresy. The egg laying schedule of *Macrocheles* is very different from that of *Parasitus*. Two eggs of *M. parapisentii* were isolated, a male and female developed and were put into one cell. Copulation took place, the male died after 36 days and the female lived for 163 days. During this time a total of 78 eggs or larvae were produced. No change occurred in the rate of egg laying during this long period despite ample changes in the ambient temperature. However, during the hot season of July-August complete stoppage of egg laying took place for about 30 days and was then resumed at the former rate. From the larvae 68 were reared to maturity. Several juveniles died and the last six eggs were not viable. The 68 adult thus obtained comprised 18 males and 50 females. The males appeared only at the begin and the end of the female's oviposition period. This indicates how a single impregnated female can colonize new habitats, especially as the developmental cycle is very speedy and took not more than 3-4 days for males and
4-5 days for females in *M. parapisentii*. According to my observations only freshly hatched females can be successfully impregnated and the fertilization of old, well hardened females cannot take place. It seems, therefore, inconceivable that male offspring can fertilize their mother which in consequence would turn into the founder of a new generation (SAMSINAK, 1965, quoting FILIPPONI, 1955). The problem of the settlement of new habitats by a single female mite is highly artificial, usually many beetles are attracted to any one fresh dung heap and each beetle generally carries many mites.

Although the males of *Macrocheles* species are found only in extremely rare cases on the insect host (I once recorded a male *Macrocheles saceri* on the beetle, the only example of a male insecticolous *Macrocheles I have found*), the potency of the production of males is apparently very high in wild populations of females carried by the host. Seven females of *M. parapisentii* were collected from a single *Scarabaeus puncoticollis* and a total of 77 adult offspring was obtained from them. These comprised 48 males and 29 females.

In spite of the high host-specificity of these macrochelids they have been cultivated successfully in the laboratory through many generations (over a year) in the complete absence of their hosts. If one takes into consideration the sympatric distribution of the three species of *Scarabaeus* that have been mentioned (all three have been collected by me in the same area of dunes near Acre), it makes the problem of this case of mite-host specificity even more intriguing.

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DISCUSSION.

RADOVSKY (U.S.A.).

With respect to mites on Xylocopa, is it likely that this is a mutualistic relation­
ship? I know that there are other mites, Astigmata, in pouches of Hyme­
noptera.

COSTA.

As far as I know, the bee does not benefit from the association because it is
fairly easy to breed the bees without the presence of mites. Xylocopine bees
form a large group but only a small number of subgenera are parasitized by Dinog­
gamasus.

RADOVSKY.

Is there any species of Xylocopa known in which there is a pouch but no asso­
ciated species of mites?

COSTA.

No. As far as I know the pouch has no other function than harbouring the
mites.

SOLomon (U.K.).

Is it possible that the mites for which Xylocopa develops sacs in her abdomen,
play a useful part in the breeding cells by, for example, feeding on fungi or waste
material that might harbour bacteria?
The bees grow perfectly well in the absence of mites. Actually Skaife thought that the bees may carry acarid mites, for example, *Sennertia*, and that the *Dinogamasus* would feed on them but this is not so. The chelicerae are essentially scraping organs and Skaife found that the mite feeds only at the stage of pupation of the bee. It is possible that certain exudates are produced during pupation and that the mite feeds on these.

**Ryke (S. Africa).**

I would like to ask Dr. Costa about the relative numbers of male and female mites occurring on the beetles. We have found on one species of beetle, hundreds of males but no females.

**Costa.**

In *Macrocheles* only females are present whereas in a species which I have called *Alliphis halleri* I have found males, females and deutonymphs on the beetle. *Alliphis gurei*, on the other hand, is represented by males and deutonymphs and I have not succeeded in breeding the female.

**Hobart (U.K.).**

Some ants are known to carry mites disposed in a symmetrical fashion and some Ipinidae carry hypopi in the elytral declevity. It is surprising to note that in some coprids, groups of parasites sit on the top of the elytra from which it might be thought they would be easily removed during burrowing. Comments, please.

**Costa.**

There are certain interesting differences in the distribution of the various species of mites on the beetles. The *Macrocheles* group hold on to the setae of the host by means of their chelicerae and are found on the underside of the beetle, especially around the mouth parts. *Parasitus* species are more agile and cluster between the mouth parts, and legs I and legs II. While the beetle is burrowing they move actively over its body surface. One species of *Eviphis* is found only on the intersegmental membrane where the head retracts into the pronotum. There is obviously some kind of specificity in the place of attachment of the mite on the beetle.

**Dean (U.K.).**

You referred to the rich nematode fauna at the dung interface and to culturing experiments using nematodes. Do you have any comments on the feeding preference of these mites and the influence they could have on the nematode fauna, and on the phoretically associated nematodes of beetles?

**Costa.**

I use *Panagrellus* because it is easy to culture. There is a wide variety of nematode species present at the dung-litter-soil interface where the beetles live.
but I do not know the species represented. I have often observed phoretic nematodes but I know very little about them.

Olivier (U.S.A.).

Since the species of macrochelids you work on are arrhenotokous, it would be quicker and easier to determine whether a female is a virgin by the chromosome number of the eggs, that is, embryonic tissue, rather than having to rear the progeny to determine their sex.

Rodriguez (U.S.A.).

In our work with *Macrocheles muscaedomesticae*, we find that a rhabditid nematode is acceptable to the mite but *Panagrellus* is not at all acceptable.

Costa.

Thank you for the information. I have not tried to feed *M. muscaedomesticae* but I have been unsuccessful in rearing some other species. There must be some difference between the nematodes, such as the strength of the cuticle which would affect the feeding of the mites.

Axtell (U.S.A.).

I would like to comment on the specificity of *Macrocheles*. In our work with phoretic Macrochelids on flies we have shown that the mite will attach to a variety of fly species. The regulating factor is the condition of the substrate. The attractiveness of the manure to the mites decreases as the manure ages. The flies are also attractive, but this is at a constant level. The mites attach to the flies that visit when the attractancy of the manure has decreased below the level of attractancy of the fly. In species such as *Macrocheles muscaedomesticae* and *M. subbadius* there is certainly no host specificity and this is probably true for many species.

Costa.

I certainly agree with your statement but I was trying to point out the more specific associations in which the relationships are more intimate.

Solomon.

Do the phoretic mites ever harm the beetles, for example, by hindering their movements?

Costa.

No. The Hon. Miriam Rothschild recently sent me a photograph of a *Necrophorus* covered with *Poecilochirus*. She counted 475 deutonymphs on the beetle. In rearing the beetles I have never noticed any difference in behaviour which might be correlated with the number of mites which are present on them.