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DIGAMASELLUS FALLAX LEITNER (MESOSTIGMATA : DIGAMASELLIDAE)
PHORETIC ON MUSHROOM SCIARID FLIES

BY

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Sciarid flies, Lycoriella auripila Winn. (Diptera : Lycoriidae), from mushroom houses frequently carry mites. A previous paper (BINNS, 1972), which examined phoresy in Arctoseius cetratus (Sellnick) (Mesostigmata : Ascidae), referred briefly to similar behaviour in deutonymphs of a digamasellid. The present work examines the association between Digamasellus fallax Leitner and its sciarid host and attempts to clarify its ecological role.

The type locality of D. fallax is given as rotting organic material containing pine-needles or straw (LEITNER, 1949). Other species have been described from similar situations (LEITNER, 1949), from agricultural soils (LEITNER, 1949; SHEALS, 1956) and litter (HURLBUTT, 1957). On the basis of cheliceral dentition, HIRSCHMANN (1960) distinguished multidentate species of digamasellid, including D. fallax, associated with coniferous woodland, from the more ecologically diverse quadridentate group. Phoresy is common in the deutonymphs of the many species associated with bark-beetles and their galleries (HIRSCHMANN, 1960; HURLBUTT, 1967), though the mites tend to be habitat-rather than host-specific (LINDQUIST, 1969). HIRSCHMANN (1960) also described phoretic association with “Schnellkäfer” (Coleoptera : Elateridae).

OBSERVATIONS.

Habitat of D. fallax. D. fallax has been found in both spawned and unspawned mushroom compost. The present observations were made during the early summer of 1972 on a continuous culture of sciarid flies in unspawned compost. The culture was housed in an unheated room with a north-facing window. Each week, two shallow boxes containing c. 2.5 kg of freshly pasteurised compost were placed, at random, on a rack where they remained for 8 wk. Sciarid infestation was encouraged by the addition of cotton-seed meal at the rate of c. 125 g per box of compost which was kept moist throughout. A continuous supply of adult insects was thus ensured which were most easily collected from the window using an aspirator.

Phoretic association. Insects were killed quickly by refrigeration at -30°C. Examination of large numbers of sciarids then showed that males carried very few mites. Thus, two out of a catch of 75 males carried a single deutonymph each. In samples of female flies, the infestation rate was high and burdens of over 20 mites per fly were seen. Counts of mites per fly were made on two occasions with an interval of 2 days. From totals of 173 and 216 female flies respectively,

30 (17%) and 85 (46%) carried mites with means of 0.99 and 1.89 mites per fly. The numerical distribution of mite attachments observed was then compared with Poisson and negative binomial distributions (Southwood, 1966). The figures given below show the goodness of fit of the observed values in each sample to these distributions as expressed by their $\chi^2$ values and the probabilities ($P$) with which the recorded values could be expected to diverge from these theoretical distributions by chance variation alone. Clearly, neither distribution gave a good correlation with the counts.

<table>
<thead>
<tr>
<th>sample</th>
<th>Fitted Poisson</th>
<th>Fitted negative binomial</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\chi^2$</td>
<td>184</td>
<td>13.1</td>
</tr>
<tr>
<td>degrees of freedom</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>$P$</td>
<td>$&lt;0.0005$</td>
<td>$&lt;0.0005$</td>
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In Figures 1 and 2, the mite distribution obtained in each count is plotted against a negative binomial curve which gave the better fit. This shows that the divergence, in each sample, was towards excessive “clumping” (area above curves) with deficient numbers of flies carrying between one and three mites.

Attachment. Irrespective of their number, deutonymph always gathered round the anterior of the host abdomen forming a tight cluster. Where many mites attached, some overlapped and lay on the backs of others. The dorsum of the host seemed to be avoided but, otherwise, no precise orientation was apparent. However, where fewer mites attached, a slight preference for the sides of the abdomen was evident, the mites lying with their sagittal planes at right angles to that of the host, though the gnathosoma was directed either upwards or downwards. Deutonymphs attached by the ambulacral claws and only rarely by their mouthparts. Legs II and IV, which are somewhat stouter, were mainly employed, as could clearly be seen in the many individuals which grasped the pleuron and/or the soft cuticle between adjacent sclerites.

Experimental observations suggested that attachment occurs at eclosion of the host. Thus, c. 30 deutonymphs were brushed from their hosts into each of two small pots, containing only moist plaster of Paris, to which ten sciarid pupae were added after 24 h. Approximately 24 h later, one pupa in each pot was found to be attended by two and four deutonymphs respectively. Their position on the pupae, which corresponded with that of phoretic mites, was maintained without movement for several hours. If the pupa was disturbed, they quickly moved round to a new position at the side of the abdomen with their bodies in the vertical plane but oriented without reference to the anatomy of the pupa. They therefore showed only a weak preference for attachment sites but displayed their readiness, under conditions unfavourable for feeding, to attach for a second time.

Observations at several sites suggested that only a single species of phoretic mite was carried at one time. *D. fallax* and *A. cetratus* have been found on different host individuals collected simultaneously from the same mushroom house. However, no mites other than *D. fallax* were found on the sciarids examined above. Similarly, flies carrying *A. cetratus* (Bins, 1972) carried only this species. While the females of *A. cetratus* often carried up to six hypopi of *Caloglyphus sp.* (Astigmata: Glycyphagidae), the deutonymphs of *D. fallax* were invariably clean. *D. fallax* did not attach to either *Scatops fuscipes* Mg. (Diptera: Scatopsidae) or to *Limosina heteroneura*.
SAMPLE 1.

Total flies 173
Total mites 171
Mean mites/fly 0.99

Figs. 1 & 2. — Frequency of mite attachments in two populations of sciarid flies (histograms) plotted against a negative binomial curve.
Hal. (Diptera: Spaeroceridae) which collected on the window of the rearing room in large numbers along with mite-bearing sciarids. More than 100 of each species were examined and found free of mites. However, deutonymphs of Gamasodes spiniger (Tragd.) (Mesostigmata: Parasitidae) were found attached to the sphaerocerid; an additional host for this mite (Binns, 1972).

**Culture and feeding.** Cultures of D. fallax were maintained at 16°C for several months in 60 ml polythene containers half-filled with moist plaster of Paris and supplied only with saprophagous nematodes. These were extracted from the compost and reared on porridge oats over moist sand as described by Singer and Krantz (1960), though invasion by fungus caused frequent failures. This difficulty was removed by rearing on Carolina Instant Drosophila Medium (Gerrard and Haig, Littlehampton, Sussex).

Deutonymphs were very mobile when brushed from their hosts and their constant activity, apparently due to an absence of thigmotactic stimulation, precluded accurate feeding-preference experiments (cf. Ito, 1971). In four such observations over a period of 5 h, twenty-two mites in rearing pots were found associated with sand carrying nematodes but only nine around clumps of peat carrying sciarid eggs placed in the same containers. However, a high proportion of deutonymphs were seen to feed within a few minutes of leaving their host when provided with nematodes. Prey selection appeared to be by chance encounter but recognition was instantaneous. Similar mites did not feed on insect material presented either in the same or separate containers. Neither fresh nor frozen sciarid eggs nor live first-instar larvae were accepted despite repeated encounters.

Deutonymphs placed in individual cells — shallow depressions, 1 cm diameter, drilled in a block of plaster of Paris and enclosed beneath a microscope cover-glass (cf. Schaller, 1953) — fed on nematodes as described. The idiosoma became distended and opaque within a few hours and, at 16°C, all had moulted within 7 days of collection. By contrast, deutonymphs given only sciarid eggs, which had been stored in a refrigerator, did not feed and maintained throughout the flattened, translucent appearance of the phoretic mite. Some died and none had moulted within 10 days of encapsulation.

The chelicerae of female D. fallax, extracted from compost or reared in the laboratory, corresponded to those figured by Leitner (1949), though they appeared more slender than those shown by Hirschmann (1960). They also closely resembled the multidentate dentition attributed by Hirschmann (1960) to D. comatus Hirschmann and D. quadrisetus (Berlese), both of which are predators of nematodes frequenting bark-beetle galleries (Ruhn, 1956). However, in the females of D. reticulatus Sheals, which preys on small collembola and their eggs (Sheals, 1956), and in A. cetratus, which takes the eggs and larvae of sciarids as well as nematodes (Binns, 1972), the digitus mobilis has fewer and larger teeth. Thus the chelicerae of these latter species resemble more closely the “nematophagous” type of Karg (1961) than do the chelicerae of those digamasellids shown to feed on nematodes.

Some cannibalism was observed in cultures; in one case one adult appeared to attack another. An adult A. cetratus was similarly consumed. Very occasionally, mites in cultures were seen manipulating insect material, but their main food material was clearly nematodes.

**Compost extractions.** To complement direct observations on phoresy the fauna of the sciarid rearing-medium was also examined to follow the relative changes in the populations of the inhabitants with increasing age of the compost. Samples were examined, simultaneously, by two extraction techniques: by Tullgren funnel and by a modified Steinhorst nematode-extractor using water-mist percolation. The latter method employed apparatus built by Wyatt (1963).
for the extraction of dipterous larvae and used a sample of 200 cc compost compared with the Tullgren sample of 120 cc. Three samples, amassed from pairs of boxes containing compost of the same age, were examined by each extraction method. Samples were taken, between 2 and 5 cm below the compost surface, from material aged 1, 2, 3, 4, 5 and 7 wk after introduction to the rearing room. The initial sampling, which was simultaneous with the first mite-fly count (Fig. 1), was repeated after 1 wk; the 1 wk compost in the first samples becoming 2 wk in the second and so on. For convenience 6 and 8 wk compost, held in the room, was not examined. The results obtained are summarised in Fig. 3 which indicates the populations of insect larvae and mites in 600 cc compost or three mist-extraction samples. In practice, the totals obtained varied between samples but the results obtained from the two sets of extractions were broadly similar and have been presented together. However, where large numbers of individuals were present, assessments were based on estimates rather than accurate counts.

![Graph](image-url)  
**Fig. 3.** - Estimated populations of nematodes, mites and larval diptera in ageing compost.

Mist-extraction showed that 1 wk compost had already been colonised by approximately 100 early-instar sciarid larvae. A maximum of c. 1,000 sciarid larvae occurred in 2 and 3 wk compost declining to only 200 after 5 to 7 wk. Although large numbers of adult scatopsids were found in the rearing room, the compost contained few larvae until 5 to 7 wk when they reached a peak of 50 larvae. None was found until compost was 3 wk old. Scatopsid larvae were also
found in Tullgren extracts in comparable numbers. Collembola were extracted by both systems in approximately the same numbers as the scatopsids.

An accurate count of nematodes was not attempted since it was clear, on each occasion, that an enormous peak was reached at 1 wk after which only a small fraction remained, until the 7 wk compost was virtually nematode-free.

While the Tullgren extractions confirmed the distribution of scatopsids, they were disappointing in respect of mite recoveries. In the first test, very few digamasellids were found and, in the second, only a few more. On each occasion, 1 and 2 wk compost yielded c. 50 Tyrophagus putrescentiae Schrank (Astigmata : Acaridae) and a similar number in the mist extracts. The latter contained large numbers of *D. fallax* and estimates of this mite were therefore based on this method. Again, accurate counts were impossible since large amounts of organic debris made the extract increasingly opaque with older compost. Many of the mites, the majority of which were adult, either clung to or buried themselves in the debris. Their absence from extracts of 1 wk compost may have been due to the lack of such refuges (though some were found in the corresponding Tullgren extractions and have been included in the population graph). In practice an estimate of 100 mites was made for a single 200 cc sample of 4 wk compost, in which the peak population seemed to occur, and other values were obtained by comparison with this. These figures should therefore be treated with more caution than those for either the insects or the nematodes but they give an indication of the distribution of adult *D. fallax* in compost of different ages. Both males and females were found, many of the latter containing a well-developed egg.

**DISCUSSION.**

Nearly all the mite species associated with scolytid beetle galleries are phoretically dependent (Lindquist, 1969). Of these, the digamasellids are the main predators of nematodes (Rüm, 1956). Feeding experiments and comparison with the chelicerae of species with known feeding habits suggest that *D. fallax* is primarily nematophagous and unlikely to affect the numbers of the host. Its phoretic behaviour could, therefore, be expected to contrast with that of *A. cetratus* which preys on the eggs and larvae of the sciarid (Binns, 1972). However, the association of *D. fallax* with *L. auripila* appears to be less "casual" than was previously suggested (Binns, 1972) and is probably determined by the large number of nematodes which develop in the compost in which the sciarid lays its eggs.

Nematodes were most numerous in extracts of 1 wk compost. In more detailed studies, Hesling (personal communication) has shown that saprophagous nematodes, introduced immediately following pasteurising, reach their maximum population after approximately 9 days and then rapidly decline. A similar but more rapid cycle occurred in laboratory, sand-oat cultures of nematodes. Since the larval stages of the sciarid occupy 23 days at 16°C, the large numbers of their larvae extracted from 2 and 3 wk old compost must have developed from eggs laid in fresh compost. As the female sciarid is responsible for colonising new sites, the deutonymphs of *D. fallax* (as in *A. cetratus*) associate mainly with this sex. The introduction of phoretic deutonymphs at oviposition of the host is therefore synchronised with the rapid increase in their nematode prey. *Scatopse fuscipes* is clearly an unsuitable host in preferring much older compost.

The numerical distribution of mite attachments is puzzling. In neither of the sciarid fly populations examined (Fig. 1 and 2) did mite frequency coincide with a Poisson distribution, such as might result from chance encounters between randomly distributed mites and their host (cf. Disney, 1971 a, b), nor did it correspond with a "clumped", negative binomial distri-
bution which might result from encounters with aggregations of mites (cf. Binns, 1972). In each of the counts, the mite burdens diverged from a negative binomial distribution by excessive “clumping”. The observed distribution could have been generated by the interaction of two, randomly distributed populations having a low and a relatively high frequency of mite attachments. However, this possibility is not supported by the results of the compost extractions.

The estimates of mite numbers in compost samples were the least reliable and refer, mainly, to adults. However, the mist extractions indicated no major discrepancy between the distribution of mites and the larvae of the host. Whatever the age of the compost, mites were invariably fewer than sciarid larvae which were, in fact, ten times as numerous as mites after 2 wk. It is difficult, therefore, to account for the mean of nearly two deutonymphs per fly in the second count. However, in a population containing sciarid larvae of all stages at 16°C, larvae should outnumber pupae by three to one while pupae may attract mites for a relatively short period. Similarly, although the smaller Tullgren samples yielded totals of between 0 and 30 mites from samples of compost from one box, the proportion of flies with large mite burdens is surprisingly high.

The preference of both *D. fallax* and *A. cetratus* for the anterior abdomen may relate to the grooming movements of the host which appear to be limited to brushing of the ovipositor and the hind abdomen. Disney (1971, a, b) showed that, in larvae of black-flies (Diptera: Simuliidae), “niche-separation” i.e. localised attachment sites, occurred where there was inter-specific competition for the same host. This suggests that *D. fallax* and *A. cetratus*, which share the same attachment site but have not been on the same host individual, do not compete directly for phoretic dispersal. However, the more predictable distribution pattern and orderly attachment in *A. cetratus* (Binns, 1972) suggest a need to limit the number of potential predator mites carried by each fly. This is unnecessary in *D. fallax* where the association appears to be purely phoretic.

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**Summary.**

Deutonymphs of *Digamasellus fallax* Leitnér, phoretic on the females of the sciarid *Lycoriella auripila* Winn., fed and developed on saprophagous nematodes but not on eggs or larvae of the host. Extraction of compost in which sciarids develop showed a high initial population of nematodes. The introduction of phoretic nymphs at oviposition of the host would therefore synchronise with the rapid increase in their prey. Comparison is made with phoresy in *Arctoseius cetratus* (Sellnick) which is a predator of the sciarid host.

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