MITES FROM NOCTUID MOTHS

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My purpose in this paper is to introduce some of the mites that I have found on noctuid moths, and to enlist the help of lepidopterists in learning more about them. Until recently most of these mites were undiscovered or undescribed. Little or nothing is known about the biology of most of the species, and it is possible that when we know more, the mites may provide some interesting information about the moths that are their hosts.

One of the oldest names in acarology is that of a mite first found adhering to the wing of an unidentified moth. It was figured and described in *The Naturalists's* [sic!] *Miscellany* in 1794, as *Acarus lepidopterorum*. "This remarkable insect," as its discoverers described it, is now known as *Cheletomorpha lepidopterorum* (Shaw and Nodder). As far as I know, it has never again been found upon a moth, though it is a well known predator upon mites of other species.

Almost every collector of Lepidoptera has seen moths or butterflies bearing one or more tiny, orange-red, sack-like objects upon their bodies or appendages. Magnification of these objects shows three pairs of long, setose legs, often extended posteriorly and free of contact with the host. Attachment is by a set of mouthparts firmly implanted in the host's body. These parasites are the larvae of mites belonging to the trombidiform family Erythraeidae, distantly related to the chiggers. In a few days, the larvae become engorged with the hemolymph of the moth. They then drop off and complete their complex development amid low vegetation at or near the soil surface. The Nearctic species of erythraeids have been little studied and are not well known. They do not seem to be specific with regard to host species or site of attachment. One may find them on any part of the insect's body—on a wing vein, on an antenna, or even on the surface of a compound eve. As a rule there are only one or a few on a single host, but I have taken a female of Eurois astricta Morrison carrying at least 32 of them.

Unlike the larval erythraeids, which are conspicuous because of their exposed position, most moth mites are well hidden and seldom seen. There are very few published records of them. Except for one species which I shall mention later, their incidence on a given species of host, in my experience, is lower than ten percent. Yet, not counting the al-

 $^{^1}$ With minor modifications, this is a paper that was presented at the 17th Annual Meeting of The Lepidopterists' Society at Ottawa, Canada, on 31 May 1966.

most ubiquitous erythraeid larvae, mites have been found on moths of more than 135 species belonging to many different families. The mites are easiest to find on fresh or living moths and on relaxed specimens, but can also be discovered on specimens long since spread and dried. Some species move about on their hosts. One may discover them on the neck, behind the front leg bases, under the tegulae, or where the thorax joins the abdomen. Other species prefer certain definite sites on the host. I shall discuss some of the mites that I have found on adult noctuids in three of the most favored locations: under the base of the proboscis, on the collar, and in the ears.

The proboscis of a noctuid moth is virtually a retractable gangplank. Flanked by the palpi, its base is also an ideal hideout for a stowaway mite. It is not surprising, then, to find that this spot may be occupied, sometimes by a single mite, sometimes by several. The search for mites on a freshly collected noctuid is best preceded by brief exposure of the insect to carbon dioxide or sublethal exposure to a killing agent which will leave the moth in complete relaxation. The insect is then grasped by the upraised wings with light, self-closing forceps (a trimmed-down spring clothespin will do), and placed under the low power of an entomological microscope. Passive extension of the tongue exposes any interpalpal mites that may be present. These can be picked up and transferred to alcohol by means of an insect pin which has been moistened or coated with petroleum jelly at its tip.

In twelve moths out of thousands examined in this way, I have found between the palpi the peculiar, non-feeding and mouthless nymphal stages of mites representing various species of the suborder Acaridei. These immature forms are variously known as travellers, wandernymphs, or "hypopi." They are strictly phoretic; that is, they use the moth as a vehicle only, rather than as a source of food. They are usually inactive, and may be attached to the host by ventral suckers. Many kinds of insects carry hypopodal mites, some more or less regularly. Under conditions favorable to further development, the travellers leave the host and eventually transform into adults. My specimens have not yet been determined, but among their hosts were four species of *Acronycta*, two of *Charadra*, one of *Graphiphora*, one of *Catocala*, and one of *Zale*, all from eastern United States. The mites are probably not restricted to noctuids as hosts, and perhaps not even to Lepidoptera.

The palpal bases of noctuids sometimes conceal larger mites of various species representing the more primitive suborder Mesostigmata. For some of these mites, to be mentioned later, the interpalpal region is merely a place to wait until the gangplank is lowered for debarkation; their main quarters on the moth are elsewhere. The other species that



Fig. 1. Blattisocius patagiorum Treat, an ascid mite found on the thorax of *Pseudospaelotis haruspica* (Grote) and other noctuid moths. Phase contrast photomicrographs of cleared and mounted specimens. Left, male; right, female. Magnification (as printed) about $80 \times$.

I have found between the palpi have usually not been seen on any other part of the insect. Such mites have appeared on 19 moths of 13 species: six of *Acronycta*, one of *Amphipyra*, three of *Catocala*, two of *Zale*, and one of *Zaleops*. One of these, *Zaleops*, was collected in Tucson, Arizona, the remainder in Massachusetts and New York. There are probably about seven species of mites in my series, at least six of which appear to be undescribed. All of the specimens are adult females of the family Ascidae, representing the genera *Lasioseius* and *Proctolaelaps*. Known species of *Proctolaelaps* have been found on insects of many kinds. One was described by Lyonet in 1760, from the caterpillar of the goat moth, but so far as I know none has previously been reported from adult moths of any species.

It is an open question whether these interpalpal ascids are to be considered as parasites or as phoretics. I have never caught one in the act of feeding, but in the soft cuticle of the moth's neck or in the retrocoxal region of the prothorax there are often small punctures, plugged with black, coagulated hemolymph. Punctures of this kind are characteristic feeding scars of mites that are known ectoparasites. Lindquist and Evans (1965) state that "No ascid mites are known to be truly parasitic." Many are believed to be predators on other mites and small arthropods, or upon their eggs, larvae, or nymphs. It should be noted that the moths listed above as hosts include several that probably rest during the day on or under the bark of trees, a habitat often rich in mites of many kinds, including ascids. It may be that for the mites in question, phoresy on moths is only occasional or even accidental rather than obligatory. Against this view is the apparent preference of the *Lasioseius* and *Proctolaelaps* species for the interpalpal region, which suggests some degree of regularity in the association.

In contrast with the interpalpal mites in its choice of residence is another ascid, of the genus Blattisocius (Fig. 1). It occupies the dorsal surface of the thorax, on or near the patagia (Treat, 1966). It has appeared on five specimens of Spaelotis clandestina Harris, on two of Graphiphora haruspica (Grote), and on one each of Apamea lignicolora (Guenée) and Amphipyra pyramidoides Guenée, all common noctuids that typically hide under loose bark or in the crevices of buildings. Three of the hosts (S. clandestina) were taken in Giles County, Virginia, the others in Tyringham, Massachusetts. The adult mites are easy to spot. Their yellow posterior portions protrude from among the hairs and scales on or behind the host's patagia or on the anterior portion of the thoracic disc. In the summer of 1965 I was lucky enough to find some of these mites on a moth that subsequently lived for more than two months in a plastic petri dish where I was able to watch the mites under the microscope. I saw them mate and lay their eggs, and I followed their development through all stages. One of the hosts of this mite, Graphiphora haruspica, holds the record for harboring the greatest variety of stowaways of any noctuid. Mites of eleven species have been taken from various specimens of this moth.

The interpalpal and patagial mites already mentioned were regularly found in the places indicated, and not elsewhere. Some species of noctuid stowaways seem to be less selective. These include three known species of *Blattisocius*, the laelaptid mite *Androlaelaps casalis* (Berlese), and a few others. I shall not take time to discuss them here.

The most interesting mites of all are those that live in the ears. The noctuid ear or tympanic organ is a fascinating and beautiful thing in itself. Unknown until 1877, and almost completely neglected until its rediscovery by Eggers in 1911, it remained a puzzle to entomologists until recent years. It is now recognized as a superbly sensitive detector of the ultrasonic voices of insect-eating bats and perhaps of other predators (Payne et al., 1966). It has also gained attention, chiefly through the work of Kenneth Roeder, as an ideal subject for the study of the



Fig. 2. Lacinipolia m. meditata (Grote). Left tympanic area. The pale, antlerlike objects to the right of center are cuticular outgrowths of the nodular sclerite or epaulette, which forms the lateral border of the tympanic frame. They screen the tympanic membrane (dark areas between the "antlers"), and at least in some instances protect it from mites.

nervous mechanism in a simple form of acoustically activated behavior (Roeder, 1966).

The essential part of the tympanic organ is a thread-like sensillum, attached at one end to a thin cuticular membrane and containing a single pair of sensory neurons. This sensillum is suspended in hammock fashion within the tympanic air sac. Two round, membranous windows bear upon the air sac from the exterior. These are the tympanic membrane with its attached sensillum, and the countertympanic membrane, which apparently is not innervated. The tympanic membrane is set in a deep, scale-free recess in the metathorax at the base of the hind wing. The countertympanic membrane is roofed by an eggshell-shaped countertympanic cavity, which extends rearward into the first abdominal segment and has an oval or slit-like opening to the exterior just above the tympanic recess. The hood, a lateral projection of the first abdominal pleura, forms the posterolateral border of the tympanic recess and is anatomically analogous to the pinna of the human ear.



Fig. 3. Living colony of the moth ear mite *Dicrocheles phalaenodectes* in the right tympanic area of a female armyworm moth, *Pseudaletia unipuncta* (Haworth). Several gravid females are visible, together with larvae, nymphs, and eggs. The upraised hind wing of the moth appears at the upper right of the photograph, the abdomen at the left. Photo by Dr. A. B. Klots, reprinted with permission of the Journal of the New York Entomological Society.

In many noctuids the tympanic recess is more or less hidden from view by long, hair-like scales projecting rearward from above the hind leg base. In a few species, unrelated to one another (*e.g.*, *Acronycta* hamamelis Guenée, and Lacinipolia olivacea (Morrison)), the lateral border of the tympanic membrane bears a heavily sclerotized, thorny, hedge-like outgrowth (Fig. 2) screening the tympanic membrane (Treat, 1956). Eggers (1936) referred to this structure as "das Trommelfellschutzgitter," literally, "the drum membrane protection screen," and speculated that it could serve as a barrier to foreign objects. This structure is not of common occurrence, and in most species the tympanic membrane is screened only by easily displaceable hairs.

Except for the interpalpal, post-patagial, and subtegular areas, the tympanic recesses and the countertympanic cavities are the only readily accessible, scale-free parts of the body surface. Like the ears of hairy mammals and the nasal passages of birds, they offer attractive berths for stowaways, and they can be made to yield a free meal as well.

Three kinds of mites are known to take advantage of these accommodations more or less regularly (Treat, 1954, 1955b, 1961). Their discovery was the chance result of my rather clumsy efforts, in the early 1950's, to learn something about the function of the tympanic organ. For this purpose I had to examine the ears of a great many moths, both living and dead. It was almost inevitable that in this process I should eventually come upon some ear-dwelling mites.

The first species that I shall mention, though the latest to be described. is a minute red mite belonging to the family Tydeidae. This species was originally described as Pronematus pyrrohippeus, but it seems to belong to a new genus, Pronematulus, proposed by E. W. Baker (1965). This mite is so small that it would be possible to pack a thousand of them into one ear of a moth, although five or six are the most I have found there, and usually only one or two. So far, only 43 specimens have been discovered, and of these, seven were lost in experimental procedures. Their hosts, all collected at Tyringham, Massachusetts, comprised 23 moths of 11 species, the most frequent being Apamea lignicolora and Graphiphora haruspica, each with five cases of infestation. With one or two exceptions, all of these mites, when first seen, were resting quietly in the tympanic recess, often on the tympanic membrane itself. Sometimes they seem to be unattached, while in other instances they adhere to the moth's cuticle as though by a posterior ventral sucker. They are not readily disturbed, but once aroused they move rapidly and may quickly lose themselves in the vestiture bordering the ear. Some specimens have stayed for several days in the same position within the ear. Twice I have found single eggs of this mite on a tympanic membrane, and from one of these eggs, after six days, there emerged a living larva, the only one so far known. One or both ears may harbor the mites, but so far no sign of damage to the host has been seen.

The nearest relatives of *P. pyrrohippeus* are known to be predators of other species of mites or their eggs, and this, of course, suggested phagophily as a possible type of association in *P. pyrrohippeus*. As phagophiles, these little tydeids might be awaiting a chance to attack some other kind of stowaway on the same moth. Yet despite one appearance of a *P. pyrrohippeus* among ear-dwelling mites of another species, I am inclined to think that their usual relationship to their host is merely phoretic, and that they probably spend most of their lives as free-living predators.

The story is quite different with the moth ear mite, Dicrocheles phalaenodectes (Treat, 1954). Of the three ear-dwelling species now described, this was the first to be discovered, and is in many ways the most interesting. It was at first provisionally assigned to the laelaptid genus Myrmonyssus Berlese, but later became the type of a new genus, Dicrocheles Krantz and Khot (1962). Its family status, like that of many laelaptoids, is now in doubt. The first specimen came to me on a moth that flew into my attic laboratory in Tyringham in 1952 and practically presented its ears for inspection. It was one of those furry insects called "False Wainscots," Leucania pseudargyria Guenée. The moth's right ear was normal, but in its left ear were several round, white eggs looking like tiny pearls. When one of these eggs produced a living larval mite, I became interested. Soon another infested moth appeared, and before long it was evident that in moths of the genus Leucania and related genera, these mites were fairly common. The question was, were they of strictly local distribution? Moths in the study collection of The American Museum of Natural History soon gave the answer: the mites, or very similar ones are to be found around the world (Treat, 1955a). If they had not been discovered previously, why not? Was it because lepidopterists had rarely concerned themselves with moth ears, or because, having seen the mites, perhaps many times, they thought them not worth reporting? I do not know. At any rate the mites are there, and during midsummer of a favorable year as many as 90 percent of the moths of a favored species may harbor them. In Tyringham, during the five-year period from 1953 through 1957. I found 569 infested moths. In the three genera, Leucania, Aletia, and Pseudaletia, this total represented an overall incidence of 31.3 percent for the moths examined (Treat, 1958b).

Unlike the mites mentioned earlier, *Dicrocheles* develops large colonies on its host, destroying the occupied ear as a sense organ (Fig. 3). A mature colony may comprise more than one hundred active mites and nearly as many eggs. During midsummer, the entire life cycle may take as little as five days. The eggs hatch in about 48 hours, and the sixlegged larvae soon begin feeding through the delicate tracheal epithelium of the tympanic air sac. Their mother has prepared the way for them by perforating the tympanic and countertympanic membranes. She may lay her eggs in the air sac itself, or in the outer recess, or in both places. The first eggs often develop into males, which do not undergo the second nymphal stage and are ready to copulate with unmated females as they become available (Treat, 1965). In a large colony, all three chambers of the ear are filled to overflowing with mites and their eggs.

Such a colony has social problems. Defecation is restricted to two places: the rearmost end of the countertympanic cavity, and the outer rim of the external tympanic recess. In the latter place the liquid fecal droplets are deposited on the screening hairs and scales, which gradually become matted into a sort of thatch that loosely covers the recess. In the countertympanic cavity, the feces, as they dry, form a waxy or gummy plug with which are mingled many cast skins.

Copulation takes place chiefly in the countertympanic cavity, where mating pairs often can be found. Males comprise fewer than ten percent of the inhabitants. Even if the host dies they usually do not leave the ear. Several adult females may contribute to the colony, either from its initiation or after the first brood has developed. As the population pressure increases, some of the maturing and fertile females must find a new home.

Here is one of the most remarkable things about these mites. An easily available home—the contralateral ear—is ready and waiting only a short distance away, but it is almost never occupied. Experimentally, one can induce the mites to form bilateral colonies, but in nature this does not happen once in a thousand times. Instead, the young females make their way to the collar and dorsal side of the moth's neck, where, temporarily, they may do some feeding. As the moth's evening flight period approaches, the mites assemble a few at a time between the palpi, and when a flower is visited they disembark, using the tongue as a gangplank or sometimes just going "over the rail." From the flower, these wanderers may board another, less crowded moth, but no matter how many *Dicrocheles* re-embark on a single insect, all proceed, apparently by a more or less fixed route, to a single ear, and however large the colony may become, the opposite ear is left unoccupied and undamaged (Treat, 1957, 1958a, 1962).

Such one-sidedness is obviously not out of consideration for the moth. The mites, too, have something to gain by it. To a hungry bat, a fat noctuid is no less attractive for having an earful of *Dicrocheles*, and a totally deafened moth has less than an even chance of escaping capture. Plainly there is adaptive value for the mites in their habit of unilaterality.

The social life and behavior of the moth ear mites make a fascinating

study. At times a mature female in the presence of others exhibits a peculiar side-to-side shaking movement, curiously reminiscent of the wagging dance of the honey bees. The significance of this dance is not quite clear; it may be a signal of some kind, perhaps to bring about the dispersal of the young females.

There are other problems. Where are the moth ear mites during a northern winter when few if any adult moths of the host species are about? Why is it that at least in the type locality, the incidence of infestation drops so sharply from its peak in mid-July to a mere trickle through most of August and September, although available hosts are still on the wing? Despite its apparent preference for hadenines of the *Leucania* group, *Dicrocheles* has been taken from moths of no fewer than 74 species representing at least five noctuid subfamilies, chiefly the Agrotinae, the Hadeninae, and the Cuculliinae, with occasional records from the Plusiinae and very rarely from the Acronyctinae. Other groups seem to be immune.

There is one more mite that I should like to mention briefly. Its name is *Otopheidomenis zalelestes* (Treat, 1955b). It was discovered during a search of museum specimens in quest of ear-dwelling mites. As its specific name suggests, it was found on moths of the genus *Zale*, and has so far appeared nowhere else. I have seen 43 infested moths, representing nine species of this genus. The known distribution includes eastern United States, Central America, and the Antilles. The incidence in most of the museum series examined was not above five percent. Only one adult mite of this species has been seen alive; to my surprise, it was bright green, no doubt the color of its host's hemolymph. This mite became the type of a new genus and family, the Otopheidomenidae, now regarded by many acarologists as a subfamily of parasitic phytoseiids, which are normally plant-dwelling predators or general feeders.

The name Otopheidomenis means "one who spares the ear." It alludes to the mites' habit of laying eggs in the tympanic recess and under the hood, but leaving the sensory structures uninjured. The larvae, upon hatching, evidently creep out of the ear and up to the crested vestiture of the thoracic notum, where their remains and cast skins can be seen even on long-dried specimens. The later stages, including adult males and females, are most often found under the tegulae. The colonies are never very large, perhaps 20 at the most. The point of special interest is that in contrast with Dicrocheles, which is destructive but unilateral, Otopheidomenis injures neither ear, but occupies both!

The spectrum of mites inhabiting moths presents all shades of host dependency, from the occasional, probably temporary, and perhaps chance association of, say, a *Blattisocius*, to the obligatory, semi-internal, and

host-selective parasitism of *Dicrocheles*. Here is a garden of wonders for the inquiring lepidopterist, a garden that is virtually unexplored. I have only hinted at some of the problems that invite attention. Some of these can be illuminated only by the collective experience of many observers, both here and abroad. I invite you to join in this coöperative venture, and welcome your questions, criticism, and correspondence.

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