

The Biology of Allergenic Domestic Mites

An Update

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Introduction

With the incidence of allergic disease, particularly asthma, continuing to rise, it is timely to review our knowledge of allergenic mites with a view to their control. It is now well established that in many parts of the world, sensitization is often to allergenic mites, which comprise a number of species. In this article emphasis is given to pyroglyphid house dust mites, primarily because our knowledge of these mites is most comprehensive. Storage mites in the families Acaridae and Glycyphagidae, which are also found in house dust, are mentioned where appropriate, however, our understanding of these mites is much less complete. The term "domestic mites" is now used to include both the pyroglyphid mites and storage mite species that are found in house dust and cause the development of IgE antibody responses (1). A comprehensive review of all of these mites has not been published since 1990 (2). This article therefore aims to update this information with recently published data.

Taxonomy and Identification

Pyroglyphidae

The family Pyroglyphidae contains 18 genera and 46 species, of which 28 species have been found on birds or in their nests and 5 in stored products or on mammals. The remaining 13 species are those of greatest importance in allergic disease, as these are found in house dust. Only 3 of these 13 species are found routinely in house dust in various parts of the world, and these species have therefore been studied in tremendous detail with respect to their biology, allergenicity, and control.

Dermatophagoides pteronyssinus was the first mite species to be identified as a source of allergens in house dust (3), and in the numerous investigations that followed, *D. farinae* and *Euroglyphus maynei* were also found to be common inhabitants of house dust and important sources of mite allergens. The *Dermatophagoides* species are placed in the subfamily Dermatophagoidinae, whereas *Euroglyphus* is placed in the subfamily Pyroglyphinae. According to their morphology, therefore, these two subfamilies are considered to be phylogenetically distant. However, recent work by Dilworth et al. (4), Hill et al. (5), and Kent et al. (6) comparing the cDNA sequence of the group I allergen produced by these mites indicates that, in this respect at least, *E. maynei* is more closely related to *D. pteronyssinus* and *D. farinae* than *D. pteronyssinus* and *D. farinae* are to each other. There is 82% sequence homology between *Der p I* and *Der f I* and 85% sequence homology between *Der p I*, *Der f I*, and *Eur m I*.

The key features of these mites that are used in identification include the shape of the bursa copulatrix, shape of the tegmen, shape of the hysteronotal shield, and orientation of the dorsal striations. It would be inappropriate to reproduce keys for the identification of these species in this article, as detailed keys have already been published. Fain et al. (2) reviewed the systematics of all known species of the family Pyroglyphidae and included excellent drawings of all species. Colloff and Spieksma (7) recently published a very useful pictorial key to facilitate identification of these mites by nonacarologists. Coherent publications therefore now exist for the identification of pyroglyphid mites, however, the immature stages of these mites remain more difficult to differentiate as few keys other than that of Mumouoglu (8) cover this subject.

Acaridae and Glycyphagidae

The families Acaridae and Glycyphagidae contain a number of species that are commonly found in stored products, but may occasionally be found in house dust. As well as their economic importance, they are an important factor in asthma suffered by those working with stored products and may also contribute to domestic allergens. The Acaridae that are most commonly found in these habitats are *Acarus siro* and *Tyrophagus putrescentiae*, whereas of the Glycyphagidae, *Glycyphagus domesticus*, *Lepidoglyphus destructor*, and *Blomia tropicalis* are most widespread.

These species can be differentiated from the Pyroglyphidae by the cuticle, which lacks the striations found in the latter family. The cuticle also distinguishes the Acaridae and Glycyphagidae, being smooth in the former and densely covered with small spines in the latter. Within the Acaridae the hairs *sc i* and *ve* are the most obvious features sepa-

rating *Tyrophagus* and *Acarus* species, whereas within the Glycyphagidae, the crista metopica and tarsal scales are usually adequate to identify between *Glycyphagus* and *Lepidoglyphus* species. Fain et al. (2) and Colloff and Spieksma (7) provided recently published keys and diagrams for these families and Hughes (9) and Ottoboni and Piu (10) published keys to the species level. Comprehensive publications therefore are now available for the identification of acarid and glycyphagid adult mites; however, no keys are available for differentiation of the immature stages of these mites.

Geographical Distribution

The Pyroglyphidae, Acaridae, and Glycyphagidae are all cosmopolitan in their distribution, however, certain species may predominate in different countries. It has been well documented that *D. pteronyssinus* predominates over the other species in most countries and this is particularly evident in coastal areas; a reflection of the high humidity requirements of this species. In the United States, however, *D. farinae* predominates in states that are far from the coast, owing to lower humidity requirements of this species. Similarly, in Europe this species is rare in all countries close to the coast (e.g., Holland, England, Scotland, Belgium), but is abundant in countries that are inland (e.g., Czechoslovakia, Eastern France). A comprehensive table of geographical distribution of the domestic Pyroglyphidae features in Fain et al. (2) in which over 100 house dust surveys are cited. From this table and also an excellent review by Colloff (11), the distribution of *E. maynei* is now better understood.

E. maynei, like *D. pteronyssinus*, appears to have high humidity requirements, therefore, these two species are frequently found together in coastal localities. As a result, *E. maynei* constitutes the second most important species (after *D. pteronyssinus*) in coastal areas of Europe, including the United Kingdom, Holland, Belgium, and Italy where allergic asthma is prevalent. In more inland regions (central United States, Central Russia) and in the tropics (e.g., Brazil) *E. maynei* is less frequent or rare. This is supported by recent analysis of climatic data from the localities where this species has been recorded, which shows a preference for areas of a mean annual humidity >62% (11). As recently as 1991, *E. maynei* was found in Australia for the first time (12). Although we now realize that *D. pteronyssinus* and *E. maynei* tend to have a similar geographical distribution, the reason why *E. maynei* is usually found in lesser numbers than *D. pteronyssinus* may be explained by differences in their reproductive biology. This question is explored in the section on reproduction and development.

The geographical distribution of Pyroglyphid mites may also be influenced by altitude, although information on this has been conflicting (13–15). Colloff (11) clarified the discrepancy for *E. maynei* when he statistically analyzed findings from altitudes below and above 100 m altitude and found that this species was found more frequently and constituted a greater percentage of the total mite fauna at altitudes below 100 m. This can probably be accounted for by the higher humidities found at low altitudes. The same is likely to be true for *D. pteronyssinus* and *D. farinae*, although similar statistical analysis has not been done for these species. Nevertheless, the general concept of Pyroglyphid mites occurring in areas of high relative humidity should be treated with some caution as this is probably related to the distribution of house dust mite surveys done to date, having been carried out mainly in maritime Europe (11).

The occurrence of the Acaridae and Glycyphagidae has been reported in numerous house dust surveys. They appear to have a worldwide distribution, but these species tend to be found rather sporadically and in low numbers in house dust (16). These mites are primarily storage mites and are thus not truly associated with humans to the same extent as the Pyroglyphidae. The Acaridae and Glycyphagidae do not feed on skin scales, but on a variety of carbohydrate and protein food sources. These species therefore tend to be more common in floor dust where such food particles may accumulate, than in mattresses, upholstered furniture, and so on (12; and Hart, unpublished observations). The sporadic occurrence of these mites in these niches may therefore relate to cleanliness or humidity of the home. Indeed there are reports of explosions in populations of *G. domesticus* in damp homes (17,18).

One exception to this sporadic occurrence is *B. tropicalis*, a glycyphagid mite that has been found to be abundant in homes in Brazil (19), Venezuela (20), Florida (21,22), Hong Kong (23), and also in Puerto Rico (Montealegre and Hart, unpublished observations). This species appears to be better adapted to climatic conditions in the tropics and subtropics and is likely to be an important source of domestic allergens in the countries where it is common (19,21,22,24).

The Habitat of Dust Mites

Mite Habitats

The majority of mites of the family Pyroglyphidae inhabit the nests of various birds and mammals. The mites of this group that inhabit house dust have probably evolved from nest inhabiting mites, having become adapted to the environment or “nest” of humans. In this environment, pyroglyphid mites do not normally come into direct contact

with humans, but rather, they survive, develop, and feed in house dust. The main constituent of the diet of house dust mites is human skin scales and thus pyroglyphid dust mites are usually most abundant in mattresses, sofas, and other upholstered furniture, since these are the areas where humans spend prolonged resting periods, allowing skin scales to accumulate therein. There is some evidence to suggest that the type of mattress may influence the development of mite populations, spring mattresses harboring larger mite populations than foam mattresses (25; Cookson et al., unpublished observations). Furthermore, the use of blankets rather than duvets may favor mite populations (Cookson et al., unpublished observations).

Some house dust surveys have, however, reported higher numbers of pyroglyphid mites in carpets than in mattresses (26), although, since dust from mattresses and floors differs in physical density, one cannot easily compare numbers of mites from these two substrata. The influence of carpet fiber type on mite populations has received some attention, but results are contradictory. Jorde et al. (27) suggested that nylon carpets support greater populations than wool carpets, whereas Price et al. (28) found more aeroallergen and Brown (29) observed more mites in rooms with wool carpets compared to those with nylon carpets.

Soft toys have also been observed to harbor large populations of pyroglyphid mites (26,30; Hart and Young, unpublished observations) and are likely to be an important source of mite allergens in childhood asthma.

The house dust mite habitat distribution outlined is consistent for *D. pteronyssinus*, *D. farinae*, and *E. maynei*, but there are indications that *E. maynei* may be more restricted to mattresses than *Dermatophagoides* (31–35).

The Acaridae and Glycyphagidae are more common in floor dust, than in mattresses, upholstered furniture, and so on (12; Hart, unpublished observations), however, in areas where *B. tropicalis* is abundant, this species is routinely found in mattresses (20,22).

Sampling Techniques

Some fundamental problems of sampling house dust for mites have not been resolved, despite nearly 30 years of intensive work. Vacuum sampling is used in the majority of studies, and other methods, e.g., heat escape and the mobility test (36) and monitoring of airborne allergens (37) have not been widely accepted. In vacuum sampling, differences in physical density of dust from different substrata, variations in extraction efficiency of live and dead mites, and the topography of various substrata may result in misleading data where comparing mites from different habitats in the home. For

example, since floor dust contains a high proportion of heavy particles, e.g., grit, sand, in comparison to lighter, more fibrous mattress dust, unit weight expressions of mite abundance are likely to underestimate the number of mites in carpets.

The expression of mite densities in most studies as number of individuals per unit weight of dust is another problem, since this does not take into consideration the total weight of dust collected, which is related to the quantity of dust in the substrate. Various workers have shown that this can overemphasize the importance of a few mites living in a low-dust environment, whereas high mite abundance in dusty habitats will be underemphasised (38–40). A further important aspect is the use of unit weight for studies involving repeated sampling, e.g., clinical trials of house dust mite control. In such studies addition of acaricidal powders to substrates may increase the weight of dust collected and thus have a diluting effect on mite density. On the other hand, repeated vacuuming is likely to deplete the amount of dust in the substratum, thus having a concentrating effect on mite density. Expression of mite density per unit area can overcome some of these problems, but has not been widely adopted. Colloff (41) provided a comprehensive review of these aspects of sampling for domestic mites and their allergens.

The Mattress Microhabitat

Within mattresses, the distribution of house dust mites has been the subject of debate. Some workers (38,42–44) suggest that the superficial layers of the mattress are richest in mites and that mites may accumulate around seams, buttons, and so on, whereas other workers (45–47) argue that most mites occur at the sides of the mattress. More recently, Hay (26,48) using an *in situ* core sampling technique found a patchy distribution of *D. pteronyssinus* within a single mattress and explains this by localized variation in microclimate, particularly humidity. Hay's work questions the traditional image of house dust mites living in an environment rich in nutrients, and suggests that in contrast the house dust habitat is a sparsely populated, desert-like environment containing small isolated patches of mites.

Colonization of Homes

The colonization of new houses, mattresses, or furnishings by mites is still not understood completely. Mites themselves are relatively immobile, being incapable of moving long distances, and therefore populations in different homes are effectively geographically isolated from one another. They can, however, be transported to new habitats on human clothing or in furnishings moved from one home to another. This was seen in Papua New Guinea when blankets were introduced into

the homes of tribespeople, the mite populations in these homes soared and many of the occupants developed mite-mediated asthma (49).

In a study of homes in Oxfordshire, UK, Hart and Whitehead (35) found significantly larger populations of *D. pteronyssinus* in houses more than 10 yr old. In Holland, however, a recent study attempted to assess the relationship between the occupation time of houses and numbers of mites or allergen levels in carpet dust (50). Homes aged 2 wk to 2 yr, with new carpets at the start of occupation, were studied, however, no relationship was found between the age of the houses and average levels of the mite allergens *Der p* I and *Der p* II or mite numbers.

Microclimate of House Dust

The major limiting climatic factor for dust mite populations is thought to be indoor air humidity of the house (44,51). Temperature appears to be of less direct importance, but does act indirectly via its influence on relative humidity. Dust mites osmoregulate through their cuticle and therefore require a high ambient humidity to prevent an excessive water loss. They will therefore proliferate at an absolute indoor air humidity of 7 g/kg (equivalent to a relative humidity of 45% at 20°C) (52). However, indoor humidity rarely reaches such high values, except in areas with excessively high outdoor humidities or in homes that are tightly insulated to preserve energy (53). This apparent contradiction can be explained by examining the microclimate of the main niche of these mites, i.e., the mattress.

During the approx 8 h when a mattress is occupied, within 2 h the heat and transpiration of the occupant cause the temperature to rise to between 25 and 30°C, regardless of ambient temperature, and the relative humidity increases to 80–95% (54–57). Thus for up to 8 h a day mites in mattresses experience favorable conditions. Furthermore, if the bed is made immediately on rising, it can take up to 16 h for the temperature and humidity of the mattress to fall and come into equilibrium with the dryer, cooler bedroom air (58). Corresponding with this diurnal fluctuation in the humidity of the mattress, de Boer (59) observed a diurnal vertical migration of mites within the mattress.

Nevertheless, whatever the level of humidity during occupation, the minimum humidity of the bedroom while the mattress is unoccupied will be the limiting factor on the mite population. Each house has its own level of indoor humidity (influenced by number of occupants, heating, construction of house, altitude, etc.) that will thus create between-house differences in numbers of mites present.

Unlike mattresses that are occupied daily, carpets do not have a regular increase in temperature or humidity. They are therefore more influenced by the indoor air humidity of the house and are less able to

support large mite populations if the indoor humidity is low. In support of this, Bronswijk (44), in a study of mite population dynamics in mattresses and living room carpets, reported a constant, fluctuating population in mattresses, but found live mites in living room carpets only during the summer months when indoor humidity is at its highest.

Several other factors may influence the microclimate of the mattress. The effects of using an electric blanket as a means of mite control have been investigated (59–62). From these studies it has been suggested that the number of mites in mattresses are reduced by 19–50% using electric blankets in comparison to controls, however, the blankets were left on for abnormally long periods in these studies. de Boer and van der Geest (61) found that mites migrate away from the heat of electric blankets. Since these mites are therefore unaffected by the heat, the use of electric blankets as a means of control is unlikely to completely eliminate mites from mattresses.

Central heating is another vital factor in both microclimate of the mattress and carpets. In houses with good ventilation this may result in conditions that are too dry and warm for efficient mite survival (54,55,63,64), whereas in homes with tight insulation it may actually increase indoor relative humidity by increasing condensation (64–67). Lintner and Brame (68) showed that in the United States, air-conditioned houses do not show any seasonal rise in house dust mite allergen levels and remain overall lower than houses without air conditioning. In relation to this, building construction and ventilation are now under investigation as a means of controlling domestic mites, with promising results to date (64,69). The fact that mite allergen levels are lower in public places that are air conditioned supports these findings (70). In a recent German study, houses with subfloor heating were found to contain substantially lower numbers of mites compared to houses with radiative heating (71).

Nonclimatic factors may also influence the microclimate of the mattress. Walshaw and Evans (72) suggested a weak relationship between decreasing social class, increasing ionic sodium concentrations in beds and increasing density of *E. maynei*. It has been shown that, in the United States, children of lower socioeconomic groups have a higher morbidity and mortality from asthma than middle class children, regardless of race or ethnic status (73). A positive relationship also has been suggested to exist between the age of the house furnishings and mite abundance (74).

The humidity requirements of storage mites are even higher than those for pyroglyphid house dust mites. The environmental humidity limit for storage mite survival is more than 60% RH at 21°C and they will therefore only occur in very damp environments such as damp food stores or damp homes (75). Since their main habitat in homes is

the carpet rather than mattresses (owing to dietary requirements), they cannot benefit from the diurnal increase in mattress humidity and therefore will survive only when conditions in the house are extremely damp. This probably explains the sporadic occurrence of storage mites in the home environment.

Seasonality of Dust Mite Populations

In temperate climates seasonal fluctuations in the numbers of mites found in house dust are evident, being low at the beginning of the summer and reaching a peak in late summer before dropping again in late autumn to low winter levels. This fluctuation results from a combination of outdoor temperature and humidity along with the use of central heating. In the summer months, windows and doors are open for prolonged periods and no heating is used, thus indoor humidity equilibrates with the high outdoor humidity at this time and mite populations increase. During the winter, however, doors and windows are less frequently opened and this together with the use of central heating creates a very warm but very dry atmosphere in the home. Since mites require a high relative humidity to thrive, these conditions are unfavorable and result in a decline in mite numbers. Thus, in winter, populations of dust mite decrease, but the temporary increase in humidity of mattresses when occupied, enables pyroglyphid mites in mattresses to survive these detrimental conditions better than mites in carpets, which may include Acaridae and Glycyphagidae.

In subequatorial and southern latitudes, populations of *Dermaphagoides* species reach a maximum in February (76) or March (77), reflecting the highest temperatures and rainfall that occur in these regions between December and March.

Despite the seasonality of mite numbers, the allergenic feces produced by these mites remain in the environment and fluctuate less obviously (78,79). Thus, although mite numbers show seasonal trends, allergic symptoms to mite allergens are nonseasonal, as seen in perennial rhinitis.

Most of these studies on seasonality have involved only *Dermaphagoides* mite species and therefore the situation with *E. maynei* or the Acaridae and Glycyphagidae is unclear. Charlet et al. (32) found two population peaks in October and April and likewise Carswell et al. (30) found an increase in *E. maynei* populations between October and December. Walshaw and Evans (72), however, stated that numbers of this species were lowest in the autumn (August to October). Storage mites tend to be found in carpets in dwellings during the humid summer months, since this is the only time of year when conditions in this habitat are suitable for survival of these mites. Seasonality of *B. tropicalis* has not been investigated.

Anatomy and Physiology of Dust Mites

Although the anatomy and physiology of domestic mites may be considered as a separate subject from their biology, these features may have an important influence on the aetiology of allergic disease. The features that are considered here because of their bearing on allergic disease are feeding and digestion, excretion, and osmoregulation.

Feeding, Digestion, and Excretion

The feeding process of dust mites has been described in detail by Fain et al. (2). Briefly, mites use their mouthparts (chelicerae) to break up food and pass it into the oral region from which it is moved into the alimentary canal by a muscular pharyngeal pump. During passage through the alimentary canal (by peristalsis), digestion and absorption of the food occur by means of secretory and digestive cells lining the canal. Waste products are engulfed in a peritrophic membrane which is formed in the colon or posterior midgut and surrounds the feces when excreted. Various points in this digestive process have been suggested to be important in the allergenicity of house dust mites, and recently the digestive system of house dust mites has received a great deal of attention.

The first evidence for the importance of the digestive system of house dust mites in allergen production was from the work of Tovey et al. (80) in which feces were implicated as a major source of mite allergens. In 1988 Chua et al. (81) published the cDNA sequence for the major house dust mite allergen *Der p* I that was found to be highly homologous to and have similar enzymatic activity to the cysteine proteases papain and actinidin (82–85). In addition, the group III house dust mite allergens have been shown to have a similar physiologic function as the serine proteases trypsin and chymotrypsin (86,87). This enzymatic activity may be important in allergic disease via its influence on bronchial permeability (85) or by disrupting the immune system, by for example proteolysis of IgG (88). Stewart et al. (89) also found alpha amylase, glucoamylase, lipase, and lysozyme enzymes in *D. pteronyssinus* fecal extracts; amylase is known to be allergenic and may be homologous to the group II allergens (83,90). In 1992, Stewart et al. (91) further reported these enzymes in *D. pteronyssinus*, *D. farinae*, and *E. maynei* mites, and in the same study reported the occurrence of aminopeptidase, carboxypeptidase B, alkaline phosphatase, phosphoamidase, B-galactosidase, esterase, and acid phosphatase in mite and fecal extracts of all three species.

These enzymes are present in mite feces and are therefore likely to represent digestive enzymes. Indeed, all of the enzymes found so far in

mite fecal extracts correspond to hydrolytic enzymes often associated with digestive processes in both invertebrates and vertebrates. It is likely that these enzymes are present within material bound by the peritrophic membrane or attached to it (91), and this is supported by studies using immunohistochemistry that have shown *Der p* I to be located in the midgut epithelium (92,93). It may therefore eventually be possible to culture midgut epithelial cells in vitro for mite allergen production.

The acarid and glycyphagid mites appear to produce species specific allergens and also allergens that are crossreactive to pyroglyphid mite allergens (94–100). It is likely that these allergens will have enzymatic activity, since it is known that the house dust and storage mites have similar enzyme repertoires (101). In support of this, Hage Hamsten (102), using immunohistochemistry, demonstrated the presence of allergens on the gut wall and in fecal pellets of *Lepidoglyphus destructor*. However, Hage-Hamsten et al. (103) found that the N-terminal amino acid sequence of a 15-kDa allergen in *L. destructor* showed no homology with either cysteine or serine proteases or with mite amylase.

From a biological point of view, Colloff (101) questioned the biological function of species-specific allergens or enzymes that may not occur in closely related mite species. From a clinical point of view, if the allergens from both house dust and storage mites are similar, the diagnosis, management, and epidemiology of mite-mediated allergic disease could be simplified by cocktailing the relevant allergen peptides for use in IgE assays, immunotherapy, and mite allergen quantification.

Immunochemical assays that currently exploit the excretory products of mites for measurement of mite allergen levels in dust samples include enzyme-linked immunosorbent assay (ELISA), radioallergosorbent test (RAST), and inhibition radioimmunoassay (RIA) (104–106). The most widely used of these assays is the ELISA that currently uses species-specific monoclonal antibodies to provide accurate measurements of group I and II allergens from pyroglyphid mites (107,108).

An alternative assay developed to quantify dust mites and their allergens in house dust is based on measuring the dose of guanine in dust samples (109,110). Guanine represents the major final product of nitrogenous waste excretion of mites, and the quantity of guanine in dust samples appears to give an indication of the presence of mites. The guanine in dust samples is visualized in this method using a chemical coloration reaction and the method is simple enough to be carried out by patients themselves. Nevertheless, no indication of the species of mites present in dust is given and this method is not accurate enough for use in clinical investigations (111).

Osmoregulation

Because of the importance of humidity in the survival of domestic mites, their osmoregulation has been the subject of extensive study (112). Domestic mites are 70–75% water by weight, but significant amounts of water are obtained neither from feeding nor metabolic production. To maintain their water balance, mites rely primarily on water vapor that is actively extracted from unsaturated air by ingestion of a hyperosmotic solution that is secreted by the supra coxal glands. At relative humidities >65–70%, adequate amounts of water can be extracted from unsaturated air using this mechanism. At humidities ≤50% (found indoors in temperate climates over a period of several months) insufficient water is absorbed and mites will survive for only 6–11 d. They can, however, survive for longer periods at such low humidities by forming a desiccation-resistant quiescent protonymphal stage that can survive for a period of months. It is likely that these quiescent protonymphs survive dry periods—they are firmly glued to the substrate and are therefore not removed by vacuuming carpets—and serve as the source of breeding mites when the relative humidity in homes is optimal (113). However, the factors that induce formation of the quiescent protonymph have not yet been elucidated.

Mites of the families Acaridae and Glycyphagidae are more sensitive to desiccation than the Pyroglyphidae (75), however, these mites can survive prolonged dry conditions by the production of nonfeeding hypopi which may survive for more than 1 yr in drought conditions (114–116). The length of time required for formation of the diapausing hypopus is genetically determined, but the length of time that these mites remain in the diapausing hypopus is influenced by environmental factors. Low environmental humidities and high temperatures trigger hypopus formation, whereas completion of the hypopus stage and molting to the tritonymph is triggered by high humidities at moderate temperatures. This genetic polymorphism in hypopus formation means that a variety of genotypes are always ready to meet adverse environmental conditions and provides a fail safe device for survival and development in the irregularly fluctuating environments occupied by these mites (115).

Reproduction and Development

Only sexual reproduction occurs in the Pyroglyphidae, Acaridae, and Glycyphagidae, involving the adult males mating with female tritonymphs or adult females. After mating, adult females lay eggs singly on the substrate. The reproduction and development of these mites has been reviewed (2,117), and recently more information has become

available on the ultrastructure of the reproductive system of *D. pteronyssinus* and *D. farinae* using light microscopy, scanning, and transmission electron microscopy (118). These studies have provided a detailed insight into the structure and functioning of the reproductive system of male and female mites of these species. Furthermore, our understanding of the population dynamics of house dust mite populations and the influence of fungi on dust mites has been significantly enhanced by recent studies.

Population Dynamics

Colloff (119) used previously available in vitro data on fecundity and survivorship rates and hypothetical values based on means from a number of studies to calculate the stable age distributions of *D. pteronyssinus* and *E. maynei*. It was found that the stable age structure for *D. pteronyssinus* was one in which immatures were dominant, eggs were second in abundance, and then adults. This was similar to the stable age distribution found in natural populations of this species. For *E. maynei* the calculated stable age distribution was also one in which immatures dominated, followed by eggs, and then adults. This, however, differs from that found in natural populations sampled in this study, where adults were dominant, then immatures, and then eggs. This suggests that the natural population of *E. maynei* was in decline at the time of sampling, since as population growth rate declines, populations become more elderly. This agrees with reports in the literature (11) of *D. pteronyssinus* having a more frequent occurrence, higher density, and shorter life cycle than *E. maynei*.

The age structure of house dust mite populations has an important potential influence on the recovery of mite populations following acaricide treatment. If the acaricide is nonovicidal, populations with a higher proportion of eggs will survive treatment better than populations with a low proportion of eggs. Indeed, the age-structure of mite populations shows seasonal variations (113) that may therefore influence the efficacy of acaricides at different times of year. Clearly, more information on the population dynamics of domestic mites would enhance our understanding of mite control.

Mite-Fungal Relations

Until recently, the traditional view of house dust mite-fungal relations was that fungi enhance rates of mite population increase. The fungus *Aspergillus amstelodami* was thought to render the diet more suitable for mites by predigestion of lipids (120). A further suggestion was that *A. penicilliioides* provided a rich source of dietary vitamins and sterols (120,121). Hay (122), however, refuted these ideas in his studies that

were among the first to compare mites reared on a diet containing fungus with fungus-free controls. Hay found that *D. pteronyssinus* reared over two generations on diets with fungi (*A. penicillioides* and *Wallemia sebi*) had reduced survival (owing to increased preadult mortality), prolonged development time, and shorter adult length when compared to mites reared on diets without fungi, and suggested that the antagonistic effects of the fungi were owing to changes in the physical nature of the substratum. These results support previous tentative suggestions that fungi could be antagonistic to mites by altering the physical structure of the substratum as a result of dense fungal growth (123) or owing to the presence of toxic fungal metabolites (124).

It is now therefore well established that fungi are of no nutritional significance to house dust mites; and neither does the presence of mites influence the growth of fungi (26). This explains the poor to moderate results obtained in clinical studies of house dust mite control using the antifungal antibiotic natamycin (125–128), despite this product having ovicidal properties (123). This approach to house dust mite control can now be discounted.

In stored products, fungi are thought to be more beneficial to mites (129). Indeed, *Acarus* and *Tyrophagus* can be reared on a diet exclusively of stored product fungi (130–132).

Fungi are an important source of dust allergens (133) and since they are ingested by mites, it is possible that fungi could contribute to mite allergenicity if allergenic spores, mycelium, or fungal enzymes are present in mites or their feces in sufficient concentrations to elicit an allergic response in asthmatics. This does not, however, appear to be the case in house dust mites. Hay et al. (134) demonstrated that larval *D. pteronyssinus* which lack fungi have allergen profiles indistinguishable from fungus-bearing adult mites. In addition, laboratory reared fungus-free *D. pteronyssinus* and mites fed with either *A. penicillioides* or *W. sebi* had identical allergen profiles. Whether a similar situation exists for storage mites is not known and would merit investigation.

Conclusion

Since 1990 our knowledge of the biology of domestic mites has increased in a number of areas. Taxonomically, keys that are easier to use by nonacarologists have been made available and should help in clinical studies of mite populations in the home environment. From house dust surveys our understanding of the geographical distribution of *E. maynei* and *B. tropicalis* has progressed. Detailed studies of mite populations in mattresses has clarified the distribution of mites within this habitat, which may eventually aid in targeting control of mites in mattresses. In relation to this, a clearer understanding of the influence

of climatic factors on the mattress microhabitat has led to investigations into the potential use of ventilation as a means of domestic mite control. Our increased understanding of the survival of desiccation resistant protonymphs is important in this regard. More information on the biochemistry of mite enzymes has been obtained from studies to characterize potentially allergenic mite enzymes. Finally, the relationship between house dust mites and fungi has been resolved with respect to both nutritional ecology and allergen production. Our progress in all of these areas serves to demonstrate the invaluable contribution that biological research can make to clinical studies of domestic mite epidemiology, allergen production, and control.

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