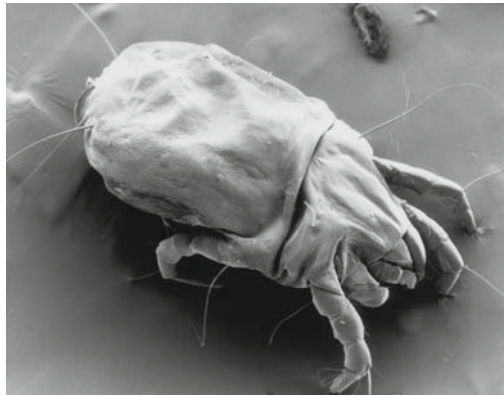


DUST MITES

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MATTHEW J. COLLOFF



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National Library of Australia Cataloguing-in-Publication entry

Colloff, Matthew, 1958–
Dust mites / Matthew Colloff.
9780643065895 (hbk.)
Includes index.
Bibliography.
House dust mites – Ecology.
House dust mites – Control.

595.42

Published exclusively in Australia and New Zealand by

CSIRO PUBLISHING

150 Oxford Street (PO Box 1139)

Collingwood VIC 3066

Australia

Telephone: +61 3 9662 7666

Local call: 1300 788 000 (Australia only)

Fax: +61 3 9662 7555

Email: publishing.sales@csiro.au

Web site: www.publish.csiro.au

Published exclusively throughout the world (excluding Australia and New Zealand),

by Springer, with ISBN 978-90-481-2223-3.

Springer

Van Godewijkstraat 30

3311 GX Dordrecht

The Netherlands

Tel: +31 78 657 60 00

Fax: +31 78 657 65 55

Web site: www.springer.com

Front cover: photograph by Matthew J. Colloff; background woodcut by August Hauptmann.

Back cover: illustration by Antony van Leeuwenhoek.

Set in 10/13 Minion

Edited by Anne Findlay

Cover and text design by James Kelly

Typeset by Planman Technologies

Index by Russell Brooks

Printed in Australia by Ligare

The book has been printed on paper certified by the Programme for the Endorsement of Forest Chain of Custody (PEFC). PEFC is committed to sustainable forest management through third party forest certification of responsibly managed forests.

CSIRO PUBLISHING publishes and distributes scientific, technical and health science books, magazines and journals from Australia to a worldwide audience and conducts these activities autonomously from the research activities of the Commonwealth Scientific and Industrial Research Organisation (CSIRO).

The views expressed in this publication are those of the author(s) and do not necessarily represent those of, and should not be attributed to, the publisher or CSIRO.

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Acknowledgements

I owe a great debt of gratitude to those research scientists who have worked on dust mites and allergy. Their discoveries shaped my thoughts, and form the subject matter of this book. I thank the following people for their interest, wit, insight and for sharing their knowledge of dust mites, acarology, allergy and related issues over the last 20 years or so: John Andrews, Larry Arlian, Rob de Boer, Harry Morrow Brown, Martin Chapman, Julian Crane, Roy Crowson, Alex Fain, Enrique Fernández-Caldas, Malcolm Cunningham (who also gave permission to use his figures of thermohygrographic recordings), Peter Friedman, Barbara Hart, David Hay, Mike Hill, Stephen Holgate, Willi Knülle, Jens Korsgaard, Peter McGregor, Charlie McSharry, Terry Merrett, Bruce Mitchell, Roy Norton, Tom Platts-Mills, Heather Proctor, Rob Siebers, Frits Spieksma, Richard Sporik, Geoff Stewart, Wayne Thomas, Walter Trudeau, David Walter, Manfred Walzl (who gave permission to use his figures of the gut and reproductive organs of dust mites), and Ann Woolcock (who persuaded me to compile global datasets on distribution and abundance of dust mites and their allergens).

I owe a particular debt of gratitude to two people. Euan Tovey (Woolcock Institute for Medical Research, Sydney) contributed to this book in many ways. He has provided continued support and enthusiasm, sent me copies of numerous papers and manuscripts, tolerated dozens of queries over the years, and allowed me to reproduce several of his figures. Christina Luczynska (King's College, London) maintained a regular correspondence with me on many aspects of dust mites, allergy and epidemiology of asthma from the early 1990s until her death in October, 2005. I thank her for her friendship, critical insight and honesty. During her short life she inspired and motivated many of her scientific colleagues and friends. I am privileged to have been one of them.

Kevin Jeans, latterly commissioning editor of CSIRO Publishing, was a source of inspiration and a pleasure to work with. His successor, Anne Crabb, wisely left me alone to get on with it. John Manger and Briana Elwood did likewise, and saw the book

through to completion with humour, tolerance and goodwill. Tracey Millen, Anne Findlay and James Kelly provided efficient, sensitive editorial and design support and encouragement. I thank them all.

For providing me with climate data used in Chapter 4, I thank Peter Jones (Centro Internacional de Agricultura Tropical, Cali, Colombia), Amos Porat (Climatology Branch, Israel Meteorology Service, Bet Dagan, Israel), and William Brown (Climate Services Division, National Climatic Data Centre, Asheville, NC, USA). I am grateful to Richard Brenner, Martin Chapman and Kosta Mumcuoglu for permission to reproduce illustrations. Photographs from Papua New Guinea were taken by Yvon Perouse, and supplied courtesy of Geoff Clarke (CSIRO). Of my other CSIRO colleagues, I am very grateful to Bob Sutherst, Anne Bourne and Ric Bottomly, for their assistance in databasing the global distribution of dust mite species. Andrew Whiting, at short notice and with a high degree of professional skill, translated these records into elegant distribution maps. Saul Cunningham patiently helped with queries on statistics and data analysis, Kim Pullen let me run ideas and numbers past him and gently corrected me when they were wrong, and Anne Hastings provided Figures 3.4 and 4.2. Mike Lacey gave me unstinting assistance with the chemistry of pheromones, lipids and cuticular hydrocarbons. His cheerful encouragement helped me think deeper about how the chemical properties of these compounds influence the biology of the mites. I thank the staff of CSIRO Library Services for their ever-prompt and efficient assistance in obtaining many obscure, hard-to-find publications.

I am grateful to Roy Norton and Tomoyo Sakata for editing the pheromone section and Frank Radovsky generously answered my queries about mites associated with ancient human remains. Sam Killen helped me with maths problems when I got stuck, and Alison Killen provided support, encouragement and generally put up with me.

My research on dust mites would not have been possible without the facilities, support and funding provided by The University of Glasgow, The Medical

Research Council, The Wellcome Trust, The Royal Society, The Stobhill Hospital Trust, Glasgow, and CSIRO Entomology, Canberra. I am especially grateful to Ron Dobson for his many kindnesses and years of wise counsel while I was at the Department of Zoology, University of Glasgow.

I thank those volunteers who have allowed me into their homes in search of mites. It is to them and the

many thousands like them that this book is dedicated. Lastly, Huw Smith and Tony Girdwood of the Scottish Parasite Diagnostic Laboratory, Stobhill Hospital Trust, Glasgow, I thank for their friendship over the years. They provided support, inspiration and instilled in me the unabashed joy of doing science.

Preface

Research on mites and allergies has grown enormously since 1964 when dust mites were confirmed as the source of allergens capable of inducing allergic reactions. Studies have become multidisciplinary, drawing on the skills of molecular biologists, clinicians, immunologists, acarologists, architects and engineers, epidemiologists, hygienists and pest controllers. It has become rather difficult for practitioners of one speciality to become familiar with the literature generated by another.

In 1987 a group of scientists and clinicians met in Bad Kreuznach, Germany, to discuss the state of the house dust mite allergy problem. They made recommendations about research collaboration, standardisation of methods, and set guidelines on the level of allergen exposure that was perceived to represent a risk for the development of asthma. It was evident from those discussions that knowledge gaps existed between the clinical and allergological researchers and those working on dust mite biology and ecology. That gap still exists today, though people are more aware of it and doing more to bridge it. The purpose of this book is to provide a reference work for all those with an involvement or interest in house dust mite research, incorporating in a single volume the topics of systematics, physiology, ecology, epidemiology, allergen biochemistry and mite control and allergen avoidance. This task has been a little overwhelming at times, especially since the book was written in my spare time. I make no apologies for a rather basic treatment of some of the clinical and immunological aspects. A detailed review is beyond my scope. I hope I have demonstrated that research on the biology and ecology of house dust mites is most useful when integrated

within the broader context of epidemiology and management of disease, rather than as an end in itself, and that the control of dust mites is subject to the same ecological principles as any other problem in pest management.

One reason for writing this book was to tackle some of the myths and misconceptions about house dust mites that have appeared in the literature and on the Internet, some of which have generated misunderstanding of what these animals do and how they live. Most are harmless generalisations, but inaccuracies tend to be cumulative and lead to bias. The control of dust mites is a significant area where the need for high-quality objective data has been downplayed, partly due to interests related to commercial anti-mite products, but also due to a lack of appreciation about the manner in which dust mite populations behave in response to environmental variables.

I have attempted to make this book as comprehensive as possible. The intention is, first and foremost, that it is a work both of reference and synthesis. I have tried to explain basic biological and ecological phenomena for the benefit of medical researchers who may not be familiar with them. More experienced biologists can skip these sections. Putting dust mite research into an historical context is important to me because the first point-of-contact for the advance of knowledge is what has already been written. The sections on the history of research show what has been done, how the subject has progressed and therefore what is likely to be productive for future investigators.

*Matthew J. Colloff
Canberra, December 2008*

Introduction

What are dust mites and why are they important?

House dust mites are arachnids, not insects, and are related to ticks, spiders and harvestmen. They are found in almost every home, where they live in dust which accumulates in carpets, bedding, fabrics and furniture. As well as providing a habitat for the mites, house dust also contains their food source: shed human skin scales which become colonised by moulds, yeasts and bacteria. The principal dust mite species belong to the family Pyroglyphidae, with *Dermatophagoides pteronyssinus*, *D. farinae* and *Euroglyphus maynei* being the top three pyroglyphid species in terms of global frequency and abundance. *D. farinae*, though common in continental Europe and North America, is rare in the UK and Australia. *Blomia tropicalis* (family Echimyopodidae) has emerged as a particularly important species in the tropics and subtropics. In rural homes in temperate latitudes, species of *Glycyphagus* and *Lepidoglyphus* (family Glycyphagidae) may be very abundant. Traditionally, the common name 'house dust mite' has been used to include those members of the family Pyroglyphidae that live permanently in house dust. Terms such as 'domestic mites' have been used to include pyroglyphid mites as well as stored products species such as *Lepidoglyphus destructor*.

Allergens from dust mites and other indoor allergens – those from domestic pets and cockroaches are the most common – are ubiquitous allergens to which people are exposed and become sensitised. They have been found at an Antarctic research station (Siebers *et al.*, 1999) and on the Mir Space Station (Ott *et al.*, 2004). An association between mites and asthma has long been suspected and because of this, dust mites have been the subject of intense study for more than three decades. A considerable body of data on dust mite ecology, physiology, allergy, allergen chemistry and molecular biology has now been collected, and a

more complete understanding of the principal dust mite species and their allergens has emerged.

As a result of dusting, vacuuming, bed-making, or any other activity that causes settled dust to become airborne, the faecal pellets and smaller allergen-bearing particles become temporarily suspended in the air – the faecal pellets are too large to stay there for very long – and may become inhaled. Those people who are atopic (i.e. are genetically predisposed to develop allergic reactions to common allergens like those derived from pollens, dust mite and animal skin scales) respond to this exposure either by making IgE antibodies, which then bind with immunologically active cells to cause the release of mediators such as histamine, and the development of localised inflammation. The allergic reactions are manifest as symptomatic asthma, eczema, rhinitis and conjunctivitis. Although the estimate is by no means reliable, and probably conservative, roughly 1–2% of the world population (65–130 million people) suffer from allergy to house dust mites.

In this book I attempt to cover some major issues of house dust mite biology that have relevance to allergy and asthma *per se*. Specifically, I address the theme of the biological properties of dust mites that make them such important agents of human disease. This approach is somewhat different from that of other reviews of dust mite biology (van Bronswijk and Sinha, 1971; Wharton, 1976; Arlian, 1989; Spiekma, 1991; Hart, 1995), which have presented the basic facts of dust mite biology. We can only go some way toward answering this question by looking at the physiology, reproduction, ecology and evolution of other, related, mite taxa. Dust mites should not be studied in isolation or their study viewed as a discrete discipline. The major biological attributes that have contributed to the success of dust mites are their body water balance, digestive physiology and population dynamics.

Life cycle

Mites are poikilothermic (they cannot control their body temperature) so the length of their life cycle varies with the temperature of their habitat. The stages in the life cycle are the egg, a six-legged larva, two eight-legged nymphal stages and adult males and females. In the laboratory, at optimum conditions (75–80% RH at 25–30°C), egg-to-adult development of *D. pteronyssinus* takes 3–4 weeks. The adults live for about 4–6 weeks, during which time the females each produce 40–80 eggs.

Ecology

Nobody has estimated accurately the total numbers of mites in mattresses or carpets. To do this, the item would have to be cut up, washed thoroughly and each mite removed and counted – an almost impossible task. Instead, estimates of mite population size are made by sampling small areas with a vacuum cleaner or sticky trap. Numbers of mites fluctuate according to season. In northern Europe, populations are generally largest in late summer and autumn and smallest in winter. The autumn increase correlates with greater production of allergens and some indication in some studies of a worsening of allergic symptoms. Larger mite populations tend to be found at places with damper climates than dry ones, thus allergy to mites tends to be rarer among people living in continental interiors or mountainous regions than among people living at low-altitude maritime localities, although there are many exceptions.

Water balance – the key to survival

Mite body water loss constrains colonisation and population growth. It is the ability of house dust mites to survive at humidities well below saturation that accounts for their successful colonisation of human dwellings worldwide. Dust mites live in conditions where temperature and humidity is far from constant. Fluctuations occur in beds due to body heat and sweating by the occupant, and when the bed is vacated, temperature and humidity fall until they match those of the ambient air. Dust mites survive these large fluctuations in microclimate by burrowing down into areas of the mattress where moisture may be retained, or they can cluster together and remain still to minimise body water loss. Additionally, they possess a simple mechanism that extracts water from unsaturated air. At the base of the first pair of legs are glands full of a solution

of sodium and potassium chloride. This fluid absorbs water from the air and, as humidity falls, water evaporates from the glands and the salts crystallise, blocking the entrance of the gland and reducing further water loss. As humidity increases again, the salts re-dissolve and water is absorbed by the hygroscopic salts to replenish that lost during the dry period.

Allergens

During digestion, cells bud off from the wall of the midgut, engulf food particles and travel along the gut lumen breaking down the food as they go. The products of digestion are absorbed throughout the gut epithelium into the haemolymph. By the time they reach the hindgut, the cells start to dehydrate and die, packaging themselves into faecal pellets surrounded by a peritrophic membrane that protects the delicate hindgut from damage by abrasion. This mode of digestion results in relatively large quantities of enzymes accumulating in the faecal pellets. The pellets, some 20–50 µm in diameter, are egested and accumulate in the textiles which the mites inhabit. The enzymes, being proteins, are immunogenic – capable of eliciting an immune response when humans are exposed to them. The first mite allergen that was identified and purified is called Der p 1, and is found mainly in the faeces. Many more are now known, from many more species.

Why do house dust mites make allergens? Clearly allergens are biologically functional proteins within the mites and the allergenic activity is incidental; an unfortunate consequence of their ubiquity and abundance in human dwellings. The association of Der p 1 with the gut and faecal pellets strongly indicates a digestive function, as does the sequence of their amino acids. Several other allergens of mites are also functional enzymes, including amylase (group 4 allergens). These allergenic enzymes have been found in extracts enriched with mite faecal pellets, suggesting they are associated with digestion. Group 2 allergens are not found in large concentrations in faecal pellets and are probably derived from a source other than the gut. Other allergens have no known functional role and database searches for comparisons of their amino acid sequences yield few clues. Tovey *et al.* (1981) estimated that *D. pteronyssinus* in laboratory cultures produced about 20 faecal pellets per mite per day, each containing an average of 100 picograms of Der p 1. Faecal pellets and Der p 1 are relatively stable at room temperature and therefore accumulate in house dust. Group 1 allergens are highly water-soluble

and become denatured at temperatures above 75°C, whereas group 2 allergens are heat-resistant.

Epidemiology

Dust mite allergy has been shown to be an independent risk factor for the development of asthma (reviewed by Platts-Mills *et al.*, 1987; International Workshop Report, 1988; Platts-Mills *et al.*, 1989). Allergy to house dust mites and other indoor allergens is a major cause of ill health worldwide. The prevalence of asthma in Australia is among the highest in the world. In 1993, approximately 23% of children in the 7–11-year-old age group had asthma, compared with 17% from New Zealand and about 15% from the UK. A significant proportion of cases, perhaps between a third and a half, can be attributed to allergens of dust mites. Globally, the prevalence of asthma has been increasing markedly since the 1960s, and had risen about 1.5–2 times in Australia by 2000. Are more people being exposed to dust mite allergens than previously and are greater concentrations present within their homes? What else might be going on that could explain this phenomenon?

The distribution and abundance of dust mites is not uniform – houses next door to each other and of the same design can have vastly different mite population densities and species-composition. Thus patterns of exposure to the allergens will vary also. These differences, extended regionally and globally, translate into epidemiological variables such as the proportion of people who develop mite-mediated allergies, the age at which symptoms are manifest, the severity of symptoms and their morbidity, and the risk of development of allergic diseases in newborn children. Furthermore, there is evidence to suggest that the symptoms and pathology of allergic disease can influence the nutrition, reproductive physiology and population dynamics of the mites. For example, people with atopic dermatitis tend to have very dense dust mite populations in their beds compared with those of healthy non-atopics. They also have lower levels of certain lipids in their skin scales, which probably more closely match lipid dietary optima for dust mites than fresh scales from non-atopics. They shed more scales and lose more body water at night through sweating and transcutaneous transpiration. All these factors result in microhabitat changes that are potentially advantageous to dust mites.

In recent years it has been shown that reduction in allergen exposure can result in improvement of

clinical symptoms of allergy. As this implies that the condition is avoidable, it would seem reasonable to use allergen avoidance measures in clinical management, although such intervention is by no means reliable or reproducible. Furthermore, acquisition of sensitivity to allergens of mites and pets during infancy may increase the risk of developing asthma, and it has been suggested that allergen eradication be directed toward infants at high risk to attempt to prevent sensitisation and symptoms. However, recommendation of allergen avoidance has been constrained by conflicting results of published clinical trials, a bewildering profusion of different methods and products, with little clear information about where and how often to use them or which patients are likely to benefit. Additionally, there is no universal agreement on how to monitor allergen exposure that may be relevant both to primary sensitisation and to triggering of symptoms.

The association between dust mites and humans has, I suspect, been a very long one, probably commencing with human settlement and the development of agricultural systems and food storage. But there is no way of knowing whether early human communities harboured dust mites in their homes and suffered mite-induced asthma and allergies. Stored products mites have been found in Neolithic remains from archaeological sites in Europe and even in the gut contents of mummified human remains. Dust mites have been found in low densities in dwellings of isolated tribal societies in Amazonia and Papua New Guinea, though in the latter case the mite populations only really took off after the tribespeople started using blankets and Western-style clothing. Why should the early association between dust mites and humans be of any consequence? Apart from the fact that historical problems have a curious attractiveness to many biologists (myself included) that vastly outweighs the likelihood of their solubility, it would make a tremendous difference to our understanding of the biology of dust mites to know if they evolved in tandem with Neolithic societies or whether mite allergy is a 20th-century phenomenon brought about by favourable (for the mites) changes in housing design and construction. Both hypotheses have been made, and both are somewhat difficult to test. There is little doubt that in many parts of the world houses are warmer, moister and less well-ventilated than they used to be, partly due to double-glazing, central heating and insulation.

Mite control and allergen avoidance

A number of products aimed at reducing exposure to allergens of mites and pets are currently available for sale direct to the public, without medical supervision of their use, and, in several instances, without independent evaluation of their efficacy or safety. This is a matter of concern. It is also worrying that these products can be purchased and used by people who may have symptoms that are not attributable to mite and pet allergens. Reduction in exposure to allergens can improve symptoms of asthma and reduce the need for drugs. Although well-designed trials have demonstrated clinical benefit, and several control treatments are available commercially, relatively few physicians give patients advice on mite and allergen control.

Allergen exposure in bedrooms can be reduced by using a mattress cover, replacing old pillows and, if possible, removing the carpet. Mites can be killed in all manner of ways, but standardised, routine methods for reproducibly and reliably controlling mites and their allergens and consistently alleviating allergic asthma have yet to be designed. This objective requires better knowledge of the biology and ecology of these extraordinary creatures than we have at present.

Perceptions of dust mites and allergic diseases

In the 1970s nobody had heard about dust mites apart from a few scientists and doctors and a handful of asthma patients. As an undergraduate reading zoology in the late 1970s and early 1980s, I cannot recall myself or my fellow students having any awareness through our course work or reading of these minute, blind arachnids that shared our lodgings. Dust mites may have merited half a page or so in the medical entomology textbooks, whereas ticks and chigger mites had entire chapters devoted to them. And the term allergy evoked no association with asthma, but with 'Total Allergy Syndrome' and a generally held view that this disorder, as with other allergies, was partially or wholly psychosomatic. At school, there were a few asthmatic children but rarely more than one in a class of 30 pupils.

Since the early 1990s, public perceptions about asthma, allergy and dust mites have changed completely. Articles on these topics in the media have been largely responsible for educating people that asthma is a major public health issue, that it can be fatal, and that its

prevalence has increased considerably. Schoolteachers are versed in first aid provision for sufferers and are aware of symptoms and medication use. Their classrooms may each now contain four or more asthmatics. It is accepted that a sizeable proportion of asthma cases have an allergic basis and that allergic reactions are not 'all in the mind'. Many people have heard of dust mites and know they live in their beds and carpets and produce allergens in their faecal pellets. Publicity campaigns by medical charities, fundraising events to support research and the publication of new research findings have formed the basis for the rise in media interest, together with the unending public fascination with human disease and the life that cohabits their homes.

Attitudes within the medical profession have changed too. In the preface to their book explaining the discovery of dust mites and their role in asthma and allergy, *House Dust Atopy and the House Dust Mite*, Voorhorst and colleagues (1969) stated starkly that they had been unable to persuade their professional colleagues of the connection between mites and disease, because many of them were not acquainted with the frame of reference within which the discovery of dust mites in homes had taken place. At the time, the notion that dust mites cause asthma was perceived as not biologically plausible and regarded with suspicion or derision (Spieksma, 1992; Spieksma and Dieges, 2004). This attitude persisted throughout much of the 1970s and 1980s. Nowadays there can be few medical practitioners who do not take seriously the role of mites in allergic disease. However, it would be wrong to assume that dust mites were *the* most important source of allergens in relation to diseases with an atopic basis, or that the relationship between allergen exposure, development of allergy and appearance of disease is anything other than complex and multi-factorial.

Allergy has received recognition as a medical discipline in its own right rather than being regarded as a branch of clinical immunology, and postgraduate specialist training courses exist. Allergy and asthma clinics have become more common and widespread, and there are doctors and nurses in general practice with specialist knowledge and training. Professional and learned societies such as the British Society of Allergy and Clinical Immunology and the American Academy of Allergy and Immunology have campaigned hard and successfully to rid the discipline of its former public image of pseudoscience and overtones of alternative medicine.

1. Identification and taxonomy, classification and phylogeny

The main service which the present day world expects of its systematists remains ... the speedy and reliable identification of organisms.

R.A. Crowson, 1970

Discrimination and identification have value beyond the obvious separation of edible from poisonous, valuable from worthless, or safe from dangerous. This is a means to gain an appreciation of the richness of the environment and our human place within it ... We start to understand our history by seeking to collect and classify.

Richard Fortey, 1997

1.1 What is the use of taxonomy?

The subclass Acari – the mites – contains about 45 000 species that have been formally named and described. This is a small percentage of the total global diversity of mites, estimated to be between 540 000 and 1 132 000 species (Walter and Proctor, 1999), making it the most diverse group of arthropods after the insects. The science dealing with the study of mites is called Acarology. To make sense of the enormous diversity of living organisms a system of description and ordering is required.

Taxonomy (literally, the naming of taxa, or groups of phylogenetically related organisms – subspecies, species, genera, families and so forth: see Table 1.1) is the science that deals with the recognition, description

and defining of organisms. It involves providing taxa with an ‘identity’ that allows them to be recognised, hopefully in a reliable and repeatable manner. For practical purposes, the identity of a species is defined by comparing it with related species and by characters that are unique to that taxon. In the majority of animal taxa, and especially arthropods, such characters have been mostly morphological ones because traditionally the vast bulk of taxonomic work was done using dead specimens from museum collections. However, characters based on behaviour, ecology, biochemistry, gene sequences, protein characteristics and biogeography are also used by taxonomists to great effect. Nevertheless, most newly described species are defined by morphological differences between themselves and previously

described species, and are referred to as morphospecies. The morphospecies represent the taxonomist's 'first cut' in terms of accuracy of definition. A single morphospecies may, on closer investigation through the comparison of different populations of that morphospecies, turn out to contain several biological species, not separable by morphological differences but with unique characters of behaviour and biology and, if sexually reproducing rather than parthenogenetic, only capable of producing fertile offspring by mating with other members of the same biological species. So, the definition of species at a higher resolution than morphospecies requires the taxonomist to make detailed observations on the life history and biology of live populations. An example of such a study on dust mites is that showing a lack of interbreeding of populations of *Dermatophagoides farinae* and *D. microceras* by Griffiths and Cunnington (1971).

Definitions of taxonomy are numerous and some include taxonomy and systematics as separate but overlapping activities, others do not. Systematics involves the study of the diversity of organisms and their phylogenetic relationships: how they are related

through evolutionary history. Taxonomy supplies the data for studies in systematics and phylogeny. I will try to explain how taxonomy works in practice, as well as to attempt a definition. It is important to state at the outset that taxonomy provides the basis for the identity of species. Its practitioners seek to separate and characterise species, even if they are morphologically very similar. Thus, when operating effectively, taxonomic procedure provides scientists in other disciplines with as much assurance as possible that they are studying a single entity and not a complex of species. Why is this important? Imagine studying the allergens of what had been thought of as a single species of dust mite, but which turned out to be two following a taxonomic investigation. Suppose they have specific allergens and their distribution and biology are different? The result would be that one would draw inaccurate conclusions about the clinical importance of each species; how many people are exposed to it and in which centres of human population, with all the ensuing consequences for the management of allergic reactions caused by those species. This situation has happened, to a limited extent, with

Table 1.1 Classification of the grain mite *Acarus siro* Linnaeus, showing major categories of the taxonomic hierarchy. (Note that not all categories, or taxa, have common names. The ordinal-subordinal classification of the mites is currently unstable: the Astigmata has been proposed to have been derived from within the oribatid sub-order Desmonomata and some of its characters are shared with this group of oribatids (Norton, 1998).)

Category of classification (taxon)	Scientific and common name (in brackets) of taxon, and important defining characters
Kingdom	Animalia (animals, i.e. those multicellular, heterotrophic organisms that develop from a ball of cells – the blastula).
Phylum	Arthropoda (arthropods, i.e. those animals with external skeletons and jointed limbs).
Sub-phylum	Chelicerata (i.e. those arthropods with chelicerate mouthparts and no antennae).
Class	Arachnida (arachnids, i.e. those chelicerates with eight legs and a body divided into two distinct regions).
Sub-class	Acari (mites, i.e. those arachnids with chelicerate mouthparts plus a subcapitulum, with reduced segmentation of the posterior body region, and with a six-legged larva).
Order	Acariformes (i.e. those mites with leg coxae fused to the body, anisotropic setae, a dorso-sejugal furrow and anamorphic postembryonic development).
Infra-order	Sarcoptiformes (i.e. those Acariformes with a toothed rutellum, prodorsal differentiation and no solenidia on tarsus IV).
Sub-order	Astigmata (i.e. those Sarcoptiforms with lateral glands and reduced setation of the opisthosoma).
Superfamily	Acaroidea (i.e. those Astigmata with a clear propodosomal and hysterosomal division).
Family	Acaridae (i.e. those Acaroidea with solenidion ω_1 at the base of the tarsus and usually with a rectangular prodorsal shield).
Genus	<i>Acarus</i> (i.e. those Acaridae with 12 pairs of notogastral setae and solenidion σ_1 on Genu I more than 3 x longer than σ_2).
Species	<i>Acarus siro</i> (i.e. that species of <i>Acarus</i> with dorsal setae d_1 not more than 2 x length of h_1 and with setae d_2 or e_1 no longer than the distance between its base and the base of the seta immediately posterior to it).

at least one pair of dust mite species (*Dermatophagoides farinae* and *D. microceras*), as we will see later, and has caused some confusion.

E.O. Wilson in his autobiography, *Naturalist* (1994), makes clear the importance of identification and taxonomic skills in the armoury of the evolutionary biologist:

If they are also naturalists – and a great many of the best evolutionary biologists are naturalists – they go into the field with open eyes and minds, complete opportunists looking in all directions for the big questions, for the main chance. To go this far the naturalist must know one or two groups of plants or animals well enough to identify specimens to genus or species. These favoured organisms are actors in the theater of his vision. The naturalist lacking such information will find himself lost in a green fog, unable to tell one organism from another, handicapped by his inability to distinguish new phenomena from those already well known. But if well-equipped, he can gather information swiftly while continuously thinking, every working hour, ‘What patterns do the data form? What is the meaning of the patterns? What is the question they answer? What is the story I can tell?’

The message of this chapter is that taxonomy is of relevance equally to ecologists, epidemiologists and biochemists, indeed all life scientists, because they need to know the identity of the animals they are working with as accurately as possible if they are to make any progress with their research. Knowing what something is called unlocks the door to the library of research that has been done on that organism and its relatives. Biologists ignore the taxonomy of the organisms they study at their peril.

1.2 How taxonomy works

1.2.1 Perceptions of taxonomy

Providing the best, most accurate information on the identity of organisms carries with it a big responsibility, especially so if the taxonomist is working with a group that is of economic or medical importance. Taxonomy has gained a reputation as an arcane science; practised in cluttered, dusty rooms in museums by elderly people with no interest beyond the group on which they work. They are uncommunicative (except to other taxonomists), and

unresponsive to the needs of other researchers. They cause confusion by incessant changing of names of organisms, and take perverse delight in so doing, with little thought to the effect their deliberations have on other researchers. They know little or nothing of the biology of the organisms they study, or biology in general, because they only work with dead specimens (Mound, 1983). Some would question whether taxonomy even merits the status of a science, since some of its practitioners treat it more like a craft. This is exemplified by the arbitrary and polarised approach they take to their methodology of defining taxa, classifying themselves as ‘lumpers’ who tend to group variable taxa together, or ‘splitters’ who break existing taxa up into new ones on the basis of the slightest differences (often perceptible only to themselves), according to their propensity to view morphological variation between individuals, populations and species as an asset or a menace.

I would argue that these accusations are largely based on ignorance, outdated notions or are simply untrue. Taxonomy is a science in its own right, based on the phylogenetic species concept and the testing of hypotheses of character distributions, transformations and evolutionary similarity of taxa (Wheeler, 2007). But taxonomists have not been very good at promoting a positive public image. The value of taxonomic research to other scientists is absolute: without it there can be no progress. Yet taxonomists have been slow to capitalise on this fact as well as to recognise the true value of their knowledge and expertise. As an illustration both of the utility of taxonomy and the way in which taxonomists work, let us examine one example: Fain’s (1966a) study of the taxonomy of *Dermatophagoides pteronyssinus*.

When Voorhorst *et al.* (1964) first reported their hypothesis that mites were the cause of allergy to house dust, Spieksma and Spieksma-Boezeman had isolated mites from dust samples taken from houses in Leiden and sent them to Alex Fain in Antwerp for identification. Fain reported back that they included a species belonging to the genus *Dermatophagoides*. As stated here, this sounds like an almost pedestrian event; the day-to-day stuff of research – one scientist seeking advice and information from another. But it conceals a phenomenal amount of detective work on the part of Fain. By the time his provisional identification was reported to Spieksma, he had embarked on a detailed investigation to discover the identity of the mites. First, he had to determine how many species were present in the sample. In fact there were two:

Euroglyphus maynei, described by Cooreman in 1950 from samples of cottonseed collected in Belgium, and another which he identified tentatively as *Dermatophagoides pteronyssinus*, first described by Trouessart in 1897 under the name *Paralges pteronyssoides*. He had seen the species before, having collected it from animal skins in France. But to be sure of his identification Fain had to track down and compare the type specimens (the ones that Trouessart used for his original description) with the Leiden specimens. There is no central register of type specimens, and Fain tried two different museums before he found them in the Berlese Collection in Florence. In order to examine them he had to travel to Italy (the Berlese Collection is too important and valuable to allow for the loan of specimens). Using an unfamiliar microscope and without the convenience of working in his own laboratory, Fain identified which stages in the life cycle were present (there was a larva, 17 nymphs, six males and seven females in the type series). Since Trouessart had described the species before the rules of nomenclature became formalised (see section 1.2.2), no formal type had been designated. Fain chose one of the specimens, an adult female, to serve as the lectotype; the type designated as part of a revisionary work, and he redescribed the species, making a series of some 28 drawings of its external anatomy, including minute details of the positions of the setae on each of the legs and the variation in the shape of the propodosomal shield. Before he visited Florence, Fain had already embarked on a comprehensive examination of the literature on taxonomic acarology. The purpose of this was partly to discover more information about the species but also to find out whether anyone else, not knowing of Trouessart's work, had described *Dermatophagoides pteronyssinus* under a different name. His search uncovered two such examples, *Mealia toxopei*, described by Oudemans in 1928 and *Visceroptes satoi*, described by Sasa in 1950 and a further two, *Dermatophagoides scheremetewskyi* Bogdanov, 1864 and *Pachyllichus crassus* Canestrini, 1894, which may well have been *D. pteronyssinus* but which could not be confirmed as such. This investigation involved further examination of the type specimens of Oudemans, as well as the descriptions and figures by the other authors (types were unavailable for study for various reasons). Finally, Fain searched for previously unidentified specimens in his and other mite collections and made an inventory of them. This provided not only data on the

habitats in which the species was found but also on its geographical distribution.

This sort of investigation is standard work for taxonomists. So what makes it special and important? Apart from the unique blend of scholarship, history, iconography, detective work, linguistics, comparative morphology and morphometrics, the identity of *Dermatophagoides pteronyssinus* was determined and defined. This provided a benchmark for other taxonomists; a basis for comparison with other species of *Dermatophagoides* as they were discovered. Since 1966, nine new species have been described, including several that are of considerable importance in dust mite allergy. Clear definitions of species allowed for the production of identification keys, allowing non-taxonomists to identify specimens and opening up the field of dust mite research to ecologists and physiologists. Differences were found between the distributions of *Dermatophagoides pteronyssinus* and *D. farinae*, which are now known to relate to their different temperature and humidity tolerance and water-balance capabilities. As allergens came to be isolated from *Dermatophagoides* spp., the identity of species in culture could be checked for contamination with other species, and there is now a vast knowledge of the allergen repertoires of different species, and a recognition that each allergen is capable of eliciting a highly specific immune response, which is the basis of studies on dust mite T-cell immunity and immunotherapy, as well as monoclonal antibody production. Allergens from four *Dermatophagoides* species and several other astigmatid mite species have been isolated and purified (discussed further in Chapter 7). The allergen genes have been sequenced, cloned and expressed to produce recombinant allergen products. Patterns of exposure to allergens from different species by different patient populations are being investigated, providing a basis for extending the epidemiology of dust mite allergy. Simply put, without the basic taxonomic research that Fain conducted in the 1960s, none of these other studies would have been possible because confusion would have reigned. As new allergens are sought in previously uninvestigated species, the necessity for sound taxonomic identification remains.

1.2.2 Names and nomenclature

The naming and renaming of species and other taxa is governed by a complex set of rules called the International Code of Zoological Nomenclature,

published in French and English in the same volume. The fourth edition (1999) is the valid edition for current use, and came into effect on 1st January 2000. The Code is administered by a group of commissioners (known as the International Commission for Zoological Nomenclature), who meet to hear appeals and submissions on nomenclatorial matters and publish a journal of their deliberations (*The Bulletin of Zoological Nomenclature*). Similar codes exist for viruses, bacteria, fungi and plants.

To some, nomenclature appears to be an arcane, jurisprudential discipline, having more in common with law than with biological sciences. However, the aim of nomenclature is to achieve stability of scientific names and to minimise taxonomic confusion. Most taxonomists will have listened *ad nauseam* to tea-time discussions in which their non-taxonomist colleagues bemoan some name change to their favourite study group of organisms foisted upon them by the International Commission and the ‘confusion’ that this is going to cause. What is often not apparent to non-taxonomists is that names and species are, in the eyes of taxonomists, two separate and independent entities which are linked together by the concept of the type specimen (explained more fully in 1.2.2.c) and it is vitally important to be clear about which correct, valid name is attached to which organism. For a practical guide to biological nomenclature, see Jeffrey (1989).

a Binomial nomenclature

Every one of the 45 000 described species of mites has a published description and a scientific name, consisting of a genus name, such as *Dermatophagoides*, and a species name, such as *microceras*. This compound name is called a binomial and the idea of binomial names was introduced by Linnaeus (the year of publication of the 10th edition of his *Systema Naturae*, 1758, is the official starting point of animal nomenclature) partly to prevent the confusion of earlier taxonomists, who used multiple, descriptive names. Berenbaum (1995) cites an example of a butterfly known as *Papilio media alis pronis praefertim interioribus maculis oblongis argenteis perbelle depictis*. The binomial has the advantage that it can be descriptive without being too cumbersome: it can be remembered relatively easily. *Dermatophagoides* is derived from the Greek words *dermis* meaning ‘skin’, *phagos* referring to feeding and the suffix *-oides* meaning ‘to look like’ and roughly translates as ‘thing that looks like those that eat skin’. The reason for this name is that Bogdanoff

(1864), the describer of the genus *Dermatophagoides*, thought the mites resembled (though were distinct from) those in the genus *Dermatophagus*, described by Fürstenburg (1861) in his treatise on mites associated with scabietic-type skin diseases. The name *microceras* is derived from the Latin *micro* meaning ‘small’ and *ceres* meaning ‘wax’; *cera* meaning wax image or figure, thus ‘small waxy figure’.

Making the name easy to remember and pronounce is part of the job of taxonomists and there are specific instructions in the International Code of Zoological Nomenclature about the formulation of names. Furthermore, the binomial is rooted into a classification: each species is contained within a genus, each genus within a family, each family within an order and so on (refer to Table 1.1). Most importantly, each binomial name is unique. The binomial is always written in italics, but the family or other group names are not. After the name one often sees a surname and a date (never written in italics). This refers to the person or persons who first described the species and when they did so, such as *Dermatophagoides microceras* Griffiths and Cunnington, 1971. The reason for including this information is so that the description can be looked up in the literature and also to clarify the exact identity of the species being referred to. It cannot be confused with another species, in the same genus, that has been given the same name by somebody else who was unaware that the name had already been used. This occasionally happens, and is called homonymy. It is often brought about by taxonomists using common, simple descriptive names like *spinatus*, *ovatus* or *magna* when spinyness, oval body shape or large size may be common characters within the genus. Thankfully, there are no examples of this as yet in dust mite taxonomy. Where the name of the describer and the date are enclosed in brackets, it means that the identity of the species had been examined by someone other than the person who originally described it and that they decided, for any number of possible good reasons, that it belonged in a different genus. For example *Euroglyphus maynei* (Cooreman, 1950) was originally placed in the genus *Mealia* by Cooreman, but was moved to the genus *Euroglyphus* by Fain in 1965. Although the details of the ‘mover’ are absent in zoological nomenclature (though included in abbreviated form in botanical nomenclature), there is a formal method of citation which gives exact details of who has done what, taxonomically, to the species, when and where. It is called a list of combinations and

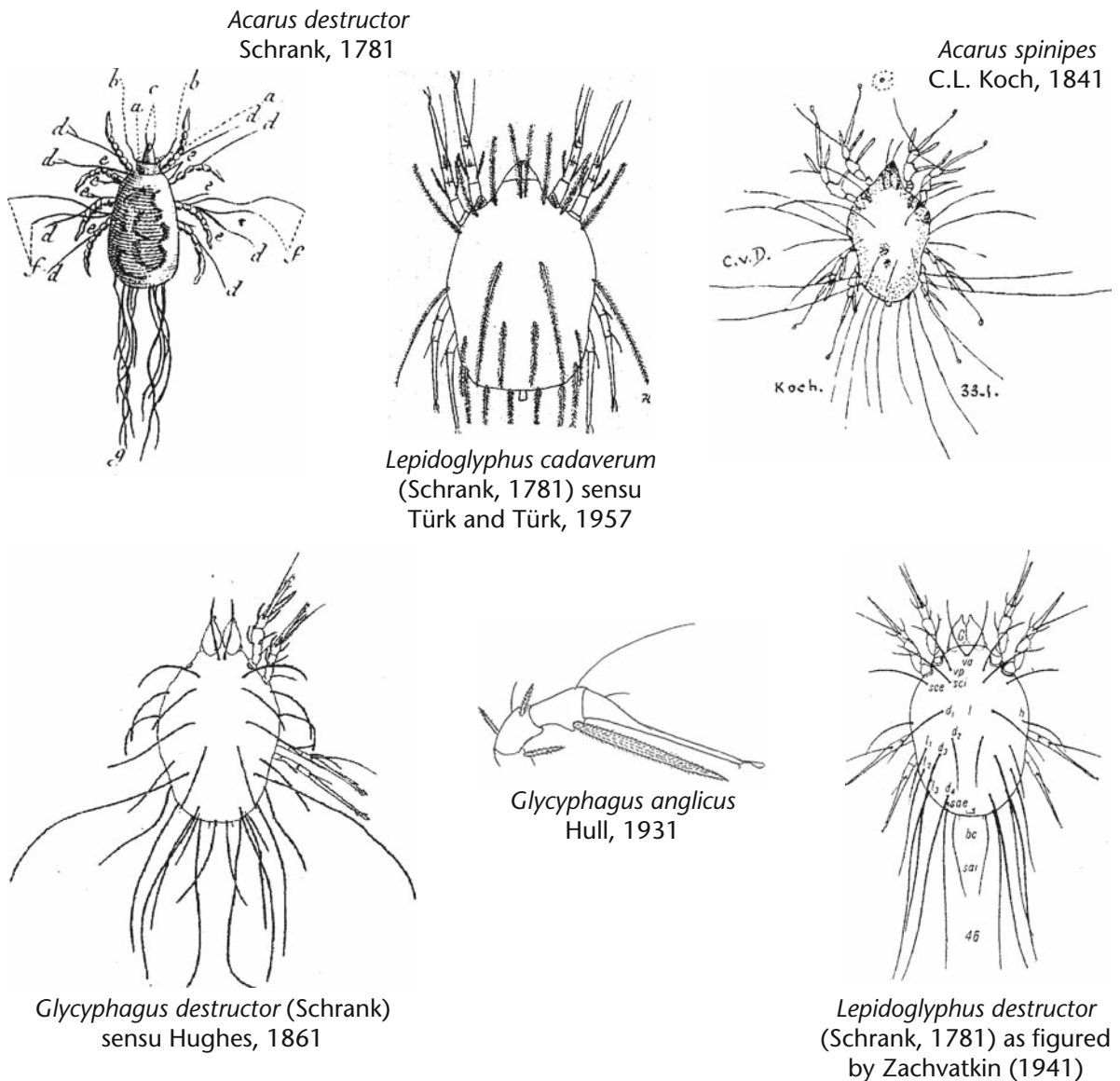


Figure 1.1 Figures and descriptions of *Lepidoglyphus destructor* by various authors (see list of combinations and synonymies in Table 1.2). The differences between them illustrate one of the major problems for taxonomists in determining the identity of classical species. Only the leg of *Glycyphagus anglicus* was ever illustrated.

synonymies (see Table 1.2 below). Some of the illustrations of these various species are provided (Figure 1.1) to show how drawings of the same species can look very different.

b *Synonymy and the oldest name*

When there is more than one name for a taxon, they are called synonyms. The oldest available name has priority, as stated by the International Code of Zoological Nomenclature. Subsequent names are called junior synonyms. There are exceptions to the priority rule, such as when a name is in widespread use and its

replacement by an earlier name, though valid and available, would cause more confusion than it would solve. For example, *Dermatophagoides pteronyssinus*: *pteronyssinus* is not the oldest available name for the species. According to Gaud (1968) and Domrow (1992) it is *pteronyssoides* (see Appendix 1). Furthermore, Oshima (1968) considered the name *Dermatophagoides* as invalid because when the genus was redefined by Fain (1967b) the type species *D. schereemetewskyi* was not redescribed, as required by the International Code, and therefore the next available name, *Mealia*, has priority. *Mealia pteronyssoides* may well be

Table 1.2 A list of combinations and synonymies for the genus *Lepidoglyphus* and the species *Lepidoglyphus destructor* (a frequent inhabitant of damp houses) and how to make sense of it.

<i>Lepidoglyphus</i> Zachvatkin, 1936
<p><i>Lepidoglyphus</i> Zachvatkin, 1936 ← The name, author and year of description of the genus.</p> <p>Type species: <i>Acarus cadaverum</i> Schrank, 1781, 512. ← The number after the date is the page number where the species name was first used.</p> <p>↑</p> <p>The type species of a genus is that species which helps define the genus and is usually the first species to be described.</p> <p><i>Glycyphagus</i> (<i>Lepidoglyphus</i>): Zachvatkin, 1941 ← This is a recombination, or change of status. In 1941 Zachvatkin decided <i>Lepidoglyphus</i> was only a sub-genus of <i>Glycyphagus</i> and did not merit a genus of its own.</p> <p><i>Glycyphagus</i> Hering, 1838 sensu Hughes, 1961 (in part) ← This means part of the genus <i>Glycyphagus</i>, originally described by Hering, used in a restricted sense, as defined by Hughes, is synonymous with <i>Lepidoglyphus</i>.</p>
<i>Lepidoglyphus destructor</i> (Schrank, 1781)
<p><i>Acarus destructor</i> Schrank, 1781 ← This is the name under which Schrank published the original description of the species, in the genus <i>Acarus</i> (in 1781 there was only one genus of mites described).</p> <p><i>Lepidoglyphus cadaverum</i> (Schrank, 1781) sensu Türk and Türk, 1957 ← Schrank's species was redescribed by Türk and Türk. The species they redescribed is the same as <i>Lepidoglyphus destructor</i>. This does not mean that <i>L. cadaverum</i>, as originally described, is a junior synonym of <i>L. destructor</i>, only the species used 'in the sense of Türk and Türk'.</p> <p><i>Acarus spinipes</i> C.L. Koch, 1841 ← A junior synonym.</p> <p><i>Glycyphagus anglicus</i> Hull, 1931 ← Another junior synonym.</p> <p><i>Glycyphagus destructor</i> (Schrank) sensu Hughes, 1961 ← A recombination. Hughes, in her restricted definition of <i>Glycyphagus</i>, recombined <i>L. destructor</i> to the genus <i>Glycyphagus</i>.</p> <p><i>Lepidoglyphus destructor</i> (Schrank) sensu Hughes, 1976 ← In 1976 Hughes changed her mind about <i>Lepidoglyphus</i> and regarded it as a valid genus, as originally conceived by Zachvatkin in 1936. She then re-recombined <i>Glycyphagus destructor</i> back into <i>Lepidoglyphus</i>.</p> <p><i>Glycyphagus cadaverum</i> (Schrank, 1781): Domrow, 1992 ← A recombination, but different from the previous one. Domrow regarded <i>cadaverum</i> as a valid species and not a junior synonym of <i>destructor</i>. Further, by placing it in <i>Glycyphagus</i> he demonstrated that he did not recognise the genus <i>Lepidoglyphus</i> as valid either (like Hughes, 1961). Listing Domrow's combination here, indicates I do not consider <i>G. cadaverum</i> a valid species.</p>

more nomenclatorially correct than *Dermatophagoides pteronyssinus*, but nobody except a few taxonomists would know what it was. One of the consequences would be that all the allergens of *Dermatophagoides pteronyssinus* would all have to be re-named 'Mea p 1, Mea p 2 ...' and so on, according to the rules of allergen nomenclature (see section 7.4.1).

In his essay 'Bully for Brontosaurus' Gould (1991) points out some of the consequences of the legalistic side of taxonomic practice, specifically concerning changes of names of taxa and the Laws of Priority of the International Code of Zoological Nomenclature. He makes the point that taxonomy defines its major activity by the work of the least skilled, and of the Law of Priority he says:

When new species are introduced by respected scientists, in widely read publications, people take notice and the names pass into general use. But when Ignaz Doofus publishes a new name with a crummy drawing and a few lines of telegraphic and muddled description in the Proceedings of the Philomathematical Society of Pfennighal-bpfennig (circulation 533), it passes into well-deserved oblivion. Unfortunately under the Strickland code of strict priority, Herr Doofus's name, if published first, becomes the official moniker of the species – so long as Doofus didn't break any rules in writing his report. The competence and usefulness of his work have no bearing on the decision.

A fair amount of the taxonomist's time is spent sorting out the ambiguities and confusions created by what Gould refers to as 'the veritable army of Doofuses', and requires the sort of bibliographic archaeology illustrated in Table 1.2 below. However, what many critics forget is that taxonomic practice is a consequence of its times. For taxonomists in the 19th century the poor optical quality of microscopes, compared with those of the present day, was a considerable hindrance, especially to acarologists dealing with such small and morphologically complex organisms. The fewer species known at that time and the consequent greater taxonomic 'distance' between them meant that a paragraph of Latin description, with no figures, was all that was necessary for an adequate description of a new species. Thankfully this is no longer so, but taxonomists in 100 years' time will probably be cursing those of us working today, saying, 'they had the technology in the 1990s to be able to produce complete DNA sequences, so why did they stick to those awful, detailed morphological descriptions, with page after page of diagrams and scanning electron micrographs?'

c *Type specimens*

To taxonomists, a name and a species are separate entities. The means of associating a name with a species is to designate type specimens. These are representative individuals of a species that demonstrate the key character states by which that species is defined. They are usually chosen by the taxonomist during his or her description of the species (though taxonomists are able to designate particular kinds of types, under strict guidelines, during the process of revisionary work). Usually they are selected from within the group of specimens that will form the basis of the description of the new species.

1.3 Classification and taxonomy of domestic mites

Classification is not quite the same thing as taxonomy. It represents the next step after species and genera have been described, named and defined. A classification of a group of organisms represents a conceptualisation of the hierarchy of the component taxa. It is formed by identifying particular shared characters and grouping organisms in hierarchies according to whether they possess those characters. If that classification is based on a phylogenetic analysis (see section 1.4 below), then classification and phylogeny are congruent, at least in

theory. In practice, the classification of many groups of organisms may often be artificial and have very little to do with phylogeny, representing little more than a 'pigeon-holing' system based on relatively few characters. Classifications are intended to help make sense of the diversity of living organisms, and serve as working hypotheses of their relatedness. Those classifications that are not based on phylogenetic analyses have very limited predictive value, and their major utility is for identification purposes, reflecting the compulsive human desire to place things into categories, meaningful or otherwise (Crowson, 1970).

The classification of mites found in house dust is a tale of three superfamilies: the Glycyphagoidea, the Acaroidea and the Analgoidea (which contains the family Pyroglyphidae). It is within these three taxa that the vast majority of allergenically important species are found. Furthermore, each of these superfamilies is associated with other animals. Relatively few astigmatid species are not associated with other animals for part or all of their life cycles (see Chapter 5). The Glycyphagoidea are predominantly associated with mammals; the Acaroidea with insects, birds and mammals and the Analgoidea almost entirely with birds. These associations have independently brought members of each superfamily into contact with humans and their dwellings through the activities of their anthropophilic hosts, and from whence habitat shifts have occurred to house dust (see section 1.4.4 below).

1.3.1 Classification of the Astigmata

Figure 1.2a shows the 10 superfamily-group divisions within the Astigmata, based on the phylogenetic analysis by OConnor (1981) (cf. also Norton *et al.*, 1993, their Figure 1.6). This classification was based on an extensive phylogenetic analysis of the non-psoroptidid Astigmata. The Psoroptidia include the feather mite superfamilies Pterolichoidea and Analgoidea (containing the dust mite family Pyroglyphidae) and the superfamily of skin parasites, the Sarcoptoidea. Gaud and Atyeo (1996) include a third superfamily of feather mites, the Freyanoidea. OConnor (1981) gives a comprehensive account of the complex history of the classification of the Astigmata.

1.3.2 Classification of the Glycyphagoidea and Acaroidea

Mites belonging to the superfamilies Acaroidea and Glycyphagoidea have been referred to traditionally as 'storage mites' or 'stored products mites'. More

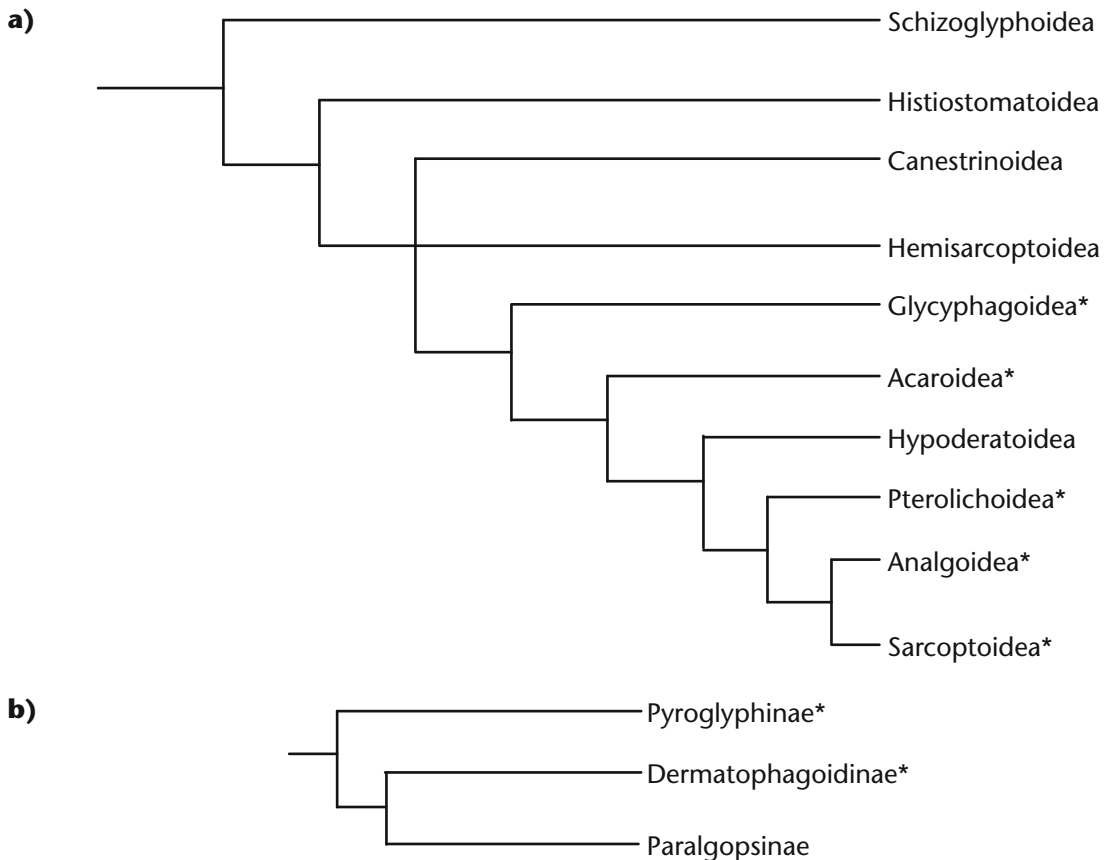


Figure 1.2 a) Phylogenetic relationships of the superfamilies of the Astigmata, modified after OConnor (1981) and Norton *et al.* (1993). Asterisks indicate those superfamilies containing genera and species found in house dust and/or known to produce allergens; **b)** possible phylogenetic relationships within the analgoid family Pyroglyphidae. Subfamily classification based on Gaud and Atyeo (1996).

confusingly, they are also referred to collectively along with all other true house dust-dwelling mites as ‘domestic mites’, reflecting the fact that they are often found associated with stored products and dust within homes as well as within commercial storage premises such as granaries, warehouses and barns.

a The Glycyphagoidea

The Glycyphagoidea contains seven monophyletic families according to the phylogenetic classification of OConnor (1981; 1982a; see Figure 1.3 below). Four families and six genera are found in house dust: Chortoglyphidae (containing the genus *Chortoglyphus*), Echimyopodidae (genus *Blomia*), Glycyphagidae (genera *Gohieria*, *Glycyphagus* and *Lepidoglyphus*) and Aeroglyphidae (genus *Glycycometus* [what used to be called *Austroglycyphagus*]).

The biology and ecology of glycyphagoid mites is the least well known of all the major taxa of domestic mites, yet in recent years they have become recognised

as second only to the Pyroglyphidae as major sources of allergens (see Chapter 8). About 10 species are known to produce allergens of clinical significance.

The genus *Chortoglyphus* has deutonymphs that are endofollicular parasites of rodents in North and Central America, while the adults are presumably nest-dwellers (OConnor, 1981). One species, *C. arcuatus*, is cosmopolitan and associated with stored food and houses (Hughes, 1976) and is of allergenic importance (Puerta *et al.*, 1993). It has been redescribed by Moreira (1978).

The genus *Blomia*, like *Chortoglyphus*, consists predominantly of associates of New World mammals. Again the deutonymphs are endofollicular parasites, while the adults are presumed to be nest-dwellers. Several species have been described from house dust, mostly in the tropics and subtropics. An appreciation of the allergenic importance of *Blomia* has increased greatly in the last 10 years (Arruda and Chapman, 1992; Fernández-Caldas and Lockey, 1995), but unfortunately the taxonomy of the genus is currently badly muddled.

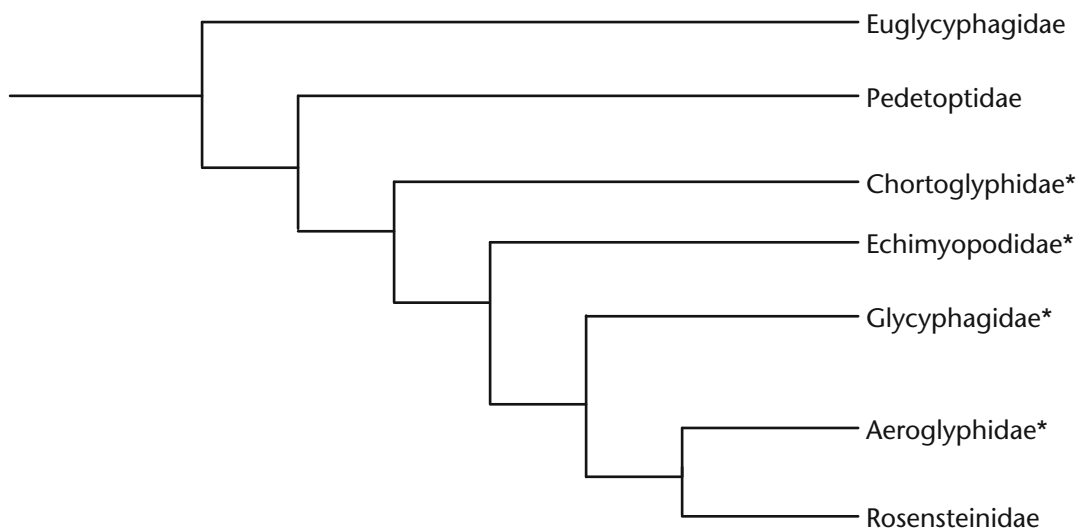


Figure 1.3 Phylogenetic relationships of families of Glycyphagoidea (after OConnor, 1981). Asterisks indicate those families containing genera and species found in house dust and/or known to produce allergens.

Allergens have been isolated from *B. tropicalis* and *B. kulagini*, which are probably the same species (refer to section 1.3.3a below). It would considerably aid an understanding of the epidemiology of *Blomia*-induced allergy if the taxonomic identity and global distribution of its constituent species were delineated clearly. A catalogue of *Blomia* species is given in Appendix 2.

Gohieria species are found in nests of Holarctic rodents and insectivores (OConnor, 1981), and one species, *G. fusca*, is of cosmopolitan distribution, associated with stored products and house dust (Zachvatkin, 1941; Hughes, 1976).

Lepidoglyphus is regarded as a junior synonym of *Glycyphagus* by some authors – for example OConnor (1981) who states that to recognise *Lepidoglyphus* as valid, together with a number of other genera that are cladistically part of *Glycyphagus*, would render *Glycyphagus* paraphyletic. In his opinion, a large number of the undescribed *Glycyphagus* he has examined bridge many of the ‘gaps’ between these other genera. In other words, OConnor tends toward a ‘lumper’ approach (see the earlier section 1.2.1) to *Glycyphagus*. However, until the genus is fully revised and the new species formally described, there are some practical reasons of identification for retaining *Lepidoglyphus* and *Glycyphagus* as separate genera: *Lepidoglyphus* lacks a *crista metopica* on the prodorsal region and has a large, feathery subtarsal-scale, whereas *Glycyphagus* has the *crista* but lacks the scale (Hughes, 1976; see Key 1.12 at the end of this chapter). The two genera contain several species of economic

importance as pests of stored products (Zachvatkin, 1941; Hughes, 1976). The most widespread species found in house dust are *Lepidoglyphus destructor* and *Glycyphagus domesticus*. Both are cosmopolitan, but found predominantly in temperate latitudes in houses, barns and grain storage facilities where they are a major cause of allergies among farmers (Cuthbert *et al.*, 1984; Cuthbert, 1990; van Hage-Hamsten *et al.*, 1985).

The genus *Glycycometus* (= *Austroglycyphagus*) contains species mainly associated with nests of birds and with bat guano (Fain 1976; 1978), but three species have been found in house dust in the tropics: *G. lukoschusi* from Surinam (Fain, 1976), *G. malaysiensis* and *G. kualalumpurensis* from Malaysia (Fain and Nadchatram, 1980). *G. geniculatus* is associated with stored grain and the nests of bees and birds and may be cosmopolitan in distribution (Hughes, 1976). The genus has been pretty much neglected from an allergological standpoint, and although there are sporadic records in the literature on dust mite surveys of the tropics (usually recorded as ‘*Austroglycyphagus* sp.’) it has probably been confused with the better-known genus *Blomia*, and may well be more common and widespread than indicated previously.

b The Acaroidea

The Acaroidea contains four families according to OConnor (1982a, b). Three families and five genera are found in house dust and are known to be allergenic: Lardoglyphidae (containing the genus *Lardoglyphus*), Suidasiidae (genus *Suidasia*) and Acaridae (genera *Acarus*, *Tyrophagus*, *Aleuroglyphus*).

The most important genera of the Acaroidea found in house dust and known to produce allergens are *Acarus* and *Tyrophagus*. They are taxonomically complex, containing species that are morphologically very similar to each other and that are notoriously difficult to identify with any degree of certainty. In this book, I have not attempted to provide keys to *Acarus* and *Tyrophagus* species. In dust mite surveys the most commonly cited species of Acaridae are *Acarus siro* and *Tyrophagus putrescentiae*. Most of these identifications are unreliable for the simple reason that the experience required to reliably and repeatedly differentiate these has always been rare among taxonomic acarologists.

The genus *Acarus* was revised by Griffiths (1964; 1970), the latter paper containing a key to the 10 species then recognised. Hughes (1976) gives a key to eight species. The taxonomy of *Tyrophagus* has been reviewed by Zachvatkin (1941); Türk and Türk (1957); Robertson (1959, 1961); Samsinák (1962); Johnston and Bruce (1965); Griffiths (1984); Lynch (1989) and Fan and Zhang (2007). Griffiths (1984) recognised some 21 species of which 15 were regarded as rare or very rare, restricted to one or two records and limited geographical ranges. The remainder are common, cosmopolitan, economically important pests, some of them found in a very wide variety of habitats including soil, stored products, live plants and dwellings. The most up-to-date keys are those by Fan and Zhang (2007) and Lynch (1987); the latter contains modifications of keys by Johnston and Bruce (1965) and Hughes (1976).

1.3.3 Classification of the Pyroglyphidae

The possible phylogenetic relationships of the three subfamilies of the family Pyroglyphidae recognised by Gaud and Atyeo (1996) are shown in Figure 1.2b (see above). The reason for my having catalogued all the known members of the family Pyroglyphidae (Appendix 1), even though many of them are not inhabitants of domestic dust, may at first seem obscure. The intent is to provide complete documentation of the taxonomic literature of the family, to give an overview of its current classification, and to have a basis from which to discern patterns of evolutionary affinities within the family and with other astigmatid taxa. I am not suggesting that a catalogue of species can alone provide a framework for theories of the evolutionary origins of dust mites, but it is the starting point of the process.

Historically, the classification of the members of the family Pyroglyphidae as it is currently conceived, as with so many other mite taxa, is a litany of uncertainty.

Its species and genera have been shuffled and re-shuffled with each review. The definition and concept of what constitutes Pyroglyphidae have changed considerably since Cunliffe (1958) proposed the family to contain a single species of one genus, *Pyroglyphus*. Members of the genus *Dermatophagoides* were placed in the family Epidermoptidae by Dubinin (1953) and by subsequent authors until Fain's (1965) revision. He recognised the affinities between *Dermatophagoides* and *Pyroglyphus* and transferred *Dermatophagoides* to the Pyroglyphidae. Fain also included in the Pyroglyphidae the genera *Pyroglyphus* (and *Hughesiella* as a subgenus within *Pyroglyphus*), *Bontiella* and *Euroglyphus* (and *Gymnoglyphus* as a subgenus within *Euroglyphus*). Fain (1967b), in a second revision, divided the Pyroglyphidae into two subfamilies, the Dermatophagoidinae (containing *Pyroglyphus*, *Bontiella* and *Euroglyphus*) which he proposed in 1963, previously within the family Psoroptidae, and the Pyroglyphinae (containing *Dermatophagoides* and *Sturnophagoides*). This formed the basis of the classification of the Pyroglyphidae until Fain's (1988b) third revision, where he created three new subfamilies, the Paralgopsinae (containing *Paralgopsis*), the Onychalginae (containing *Kivuicola*, *Onychalges* and *Paramealia*) and the Guatemalichinae (containing *Fainoglyphus*, *Guatemalichus* and *Pottocola*).

O'Connor (1982b) elevated the Pyroglyphidae to superfamily status as a sister group of the Analgoidea, and included within it two other families – the Turbinoptidae which are parasites of the nasal cavities of birds and the feather mite family Ptyssalgidae.

Gaud and Atyeo (1996) used different characters from those of Fain (1988b) to define subfamilies, and do not recognise Fain's subfamilies Onychalginae and Guatemalichinae as valid, synonymising them with Dermatophagoidinae. Neither do they recognise O'Connor's (1982b) superfamily Pyroglyphoidea because of the six characters used by O'Connor to define the Pyroglyphoidea, only one – the dorsoterminal position of placement of solenidion ω_1 on tarsus I (see Figure 1.8) – is not found elsewhere in the Analgoidea. They consider that the Pyroglyphidae has greater affinities with the Analgoidea, and place the Pyroglyphidae within it. Gaud and Atyeo (1996) state:

The Pyroglyphidae occupies a special place amongst the feather mites, but the group is still relatively unknown. This family not only contains a few taxa that are true feather mites,

but a large number of nidicoles and detritivores that are occasionally found in the plumage ... The Pyroglyphidae, with few specialisations, are probably similar to the common ancestors of the Analgoidea and Psoroptoidea. The small number of derived character states makes it difficult to diagnose subfamilies and genera ... The placement of solenidia ω_1 on tarsi I defines, without ambiguity, the Pyroglyphidae among other families of the Analgoidea. This character is not limited to the Pyroglyphidae, it occurs in various Psoroptoidea associated with mammals (Psoroptidae, Cebalgidae, Marsupalidae).

1.3.4 Examples of taxonomic problems with certain dust mites, and some solutions

I make the distinction here between problems of identification and of taxonomy. Examples of identification problems are common with dust mites. One of the most significant involves the commonly experienced difficulty in telling apart the sibling species *Dermatophagoides farinae* and *D. microceras* (see Cunningham *et al.*, 1987). This is despite both species having been clearly and thoroughly described and shown to be reproductively isolated. By contrast, problems of taxonomy arise when there is some doubt over the identity of the species, often due to inadequate descriptions, two or more people having described the same species independently, or the same person having described the same species more than once.

a The identity of *Blomia tropicalis*, *B. kulagini* and *B. gracilipes*

Our current understanding of the taxonomy of *Blomia* is based largely on the work of van Bronswijk *et al.* (1973a, b). In the first of these papers they described *Blomia tropicalis* from house dust in the tropics and subtropics. In the second, they compared the species of *Blomia*, redescribing *B. kulagini* and presenting a key to species. What was intended as a work of clarification has had the opposite effect as a result of not following the standard taxonomic practice of redescribing *B. kulagini* based either on the type material or on specimens collected from the same locality as the type (so-called topotypic material). Fain *et al.* (1977) succinctly summed up the taxonomic confusion within *Blomia*. They found the types of *Chortoglyphus gracilipes* Banks 1917 belonged to the genus

Blomia and recombined the species accordingly. They state:

B. gracilipes belongs to the group which possess a long copulatory tube and has solenidia ω_1 and ω_2 of tarsus I situated at the same distance from the base of the tarsus. These characters are shared by *B. kulagini* Zachvatkin, 1936 and *B. tropicalis* van Bronswijk [et al.], 1973.

B. gracilipes lacks the pair of cuticular projections ('wrats' of van Bronswijk) on the posterior region of the opisthosoma but this character might not be visible owing to the poor condition of the specimens. With this exception it appears to be extremely close to *B. kulagini*. Unfortunately the type of *B. kulagini*, along with the others of Zachvatkin, has been lost so it is impossible to decide if it should fall into synonymy with *B. gracilipes*.

Van Bronswijk [et al.] have chosen what they believe to be specimens representative of *B. kulagini* from Japan but they have noted several differences between the original description [by Zachvatkin] and their material. We think therefore that the identity of the true *kulagini* could be ascertained only after examination of new specimens collected from the typical locality (wheat stored in Moscow granaries).

O'Connor (1981) points out that the various species of *Blomia* associated with stored products and house dust are extremely similar morphologically and suspects that they constitute only a single, synanthropic species. I agree with him. All the *Blomia* specimens I have in my collections (from Burma, Colombia, Brazil, Australia and the Philippines) are very similar and can be referred to as *Blomia tropicalis* van Bronswijk *et al.*, 1973a. If *B. kulagini* were to be redescribed from either topotypic material from Moscow granaries, or from rediscovery of the type material, and found to be synonymous with *B. tropicalis*, then *B. kulagini* would be the valid name because of priority (refer to section 1.2.2b).

The problem of the identity of *Blomia* species highlights a major recurrent problem for taxonomists working on species whose type series were deposited in European institutions before 1939. Many taxonomic collections in major cities were destroyed or lost in World War II, and it seems highly unlikely that the types of *B. kulagini* will be rediscovered.

b The correct name of *Dermatophagoides pteronyssinus*

Baker *et al.* (1956) say it was *Dermatophagoides scheremetewskyi*. Oshima (1968) says *Mealia pteronyssina*. Fain (1966a) says *Dermatophagoides pteronyssinus* and Domrow (1992) says *Dermatophagoides pteronyssoides*. All have a case, but who is right? Gaud (1968) and Domrow (1992) have concluded that *Paralges pteronyssoides* Trouessart, 1886 is the senior synonym of *Dermatophagoides pteronyssinus* (Trouessart, 1897), on the basis of priority (see section 1.2.2b). Gaud's reasoning is based on the list of specimens of *D. pteronyssinus* and their geographical distribution examined by Fain (1966a). Item 7 in the list is of several male and female specimens of *D. pteronyssinus* on a slide from the Trouessart collection at the Muséum national d'Histoire naturelle de Paris, together with a specimen of *Microlichus avus charadricola* Fain and other specimens of a *Thyreophagus* sp. from a species of shrike (*Gallinago nigripennis*) from the Cape of Good Hope, South Africa. This is the host and locality data given by Trouessart (1886) for *Paralges pteronyssoides*. Fain *et al.* (1974) state that since the name *pteronyssoides* was not used for 50 years after its description it should, under Article 23b of the International Code of Zoological Nomenclature, be regarded as a *nomen oblitum* or forgotten name. Article 23b has since been revoked. However, the argument against the use of *pteronyssoides* Trouessart, 1886 as the oldest (and therefore valid) name for the species is the same as that preventing the use of *scheremetewskyi* Bogdanoff, 1864: it would cause too much confusion.

Gaud (1968) goes on to say that *Paralgoides anoplopus* Gaud and Mouchet, 1959 should probably be considered synonymous with *Paralges pteronyssoides* Trouessart, 1887, and there are no differences between the type material and that collected by Trouessart. This is an important point that tells us something about the biology of *Dermatophagoides pteronyssinus*. If, as the evidence suggests, *Paralgoides anoplopus* is synonymous with *Paralges pteronyssoides*, which is in turn synonymous with *D. pteronyssinus*, then this extends the range of avian hosts of *D. pteronyssinus*. *P. anoplopus* has been found on *Cinnyris chloropygius* by Gaud and Mouchet (1959), as well as on *Anthus pratensis*, *Balearica pavonina*, *Eutoxeres aquila*, *Pica pica*, *Sylvia communis* and *Upupa epops* by Gaud (1968). Also, *P. pteronyssoides* has been found on *Aulacorhynchus coeruleicinctus* from South America (Trouessart, 1886), and on *Gallinago nigripennis* from the

Cape of Good Hope. Gaud (1968) reckons that this long list of species, combined with very small numbers of mite specimens found on each bird, indicates that *D. pteronyssinus* is 'accidental' in plumage and not a true feather 'parasite'. This accidental occurrence on feathers may suggest *D. pteronyssinus* is a true nest commensal.

c Races, varieties or sibling species within *Dermatophagoides pteronyssinus*, *D. farinae* and *D. microceras*

Evidence of morphological variation in populations of *D. farinae* and *D. microceras* as identified by Fain (1990), and molecular polymorphisms of *D. pteronyssinus* and *D. farinae* populations recorded by Thomas *et al.* (1992), have led to speculation that each of these three species actually represent a far more complex series of separate, closely related, morphologically very similar, so-called sibling species. For example, I have heard anecdotal evidence of populations of *D. pteronyssinus* from North America and Europe having locality-specific numbers of lobes in the receptaculum seminis of the females (Figure 2.12a). I examined this character in a laboratory population of dust mites from Glasgow. In the first 10 mites the number of lobes varied from eight to 11. In species with a broad global distribution there is a tendency to undergo adaptive radiations and for geographically isolated populations to speciate. However, with synanthropic species there is less likelihood of geographic isolation. More outbreeding could be anticipated because humans are a highly mobile species, moving to new areas and bringing their mites with them.

1.4 Biodiversity, phylogeny and evolution

What are dust mites and where have they come from? Central to the answer is the consideration of evolutionary origins. To get some kind of basic picture we need to construct the phylogenetic relationships of the family Pyroglyphidae and, based on this phylogeny plus inferences from the biology and ecology of dust mites and their relatives, an hypothesis of how dust mites came to live in human dwellings.

1.4.1 Phylogeny and the value of predictive classifications

Phylogeny means, loosely, 'the history of the tribe'. Reconstructing a phylogeny is similar to compiling a genealogical tree in that both indicate, first and foremost, the degree of relatedness between the members of the

‘tribe’. However, a family tree is based on known fact, documentary evidence, whereas a phylogeny is only ever, at best, an hypothesis of the most likely evolutionary history of the taxon, based on fossil evidence (where available), comparative morphology, genomic sequences or other data such as reproductive behaviour.

The value of classifications that are based on phylogeny is that they offer a simple, concise information retrieval system that is predictive in nature. For example, if *Dermatophagoides microceras* is more closely related to *D. farinae* than to *D. pteronyssinus*, one may be able to predict that the allergens of *D. microceras* will have higher sequence homology with those of *D. farinae* than with those of *D. pteronyssinus*, even though there is currently no data available on the sequences of allergens of *D. microceras*. Why is this information of use?

1.4.2 Background – phylogenetic relationships of the sarcoptiform mites

Mites are an order within the Class Arachnida, along with the spiders, scorpions, harvestmen, ricinuleids, whip-scorpions, schizomids, sun-spiders, palpi-grades, false-scorpions and amblypygids. The arachnids are an ancient group, and fossil scorpions of the Silurian were probably among the first terrestrial arthropods. Mites too are an ancient group: the earliest fossils are from Lower Devonian deposits, ca. 400 million years before present (mybp) (reviewed by Bernini, 1991).

The majority of species that have evolved in association with humans and their dwellings belong to the suborder Astigmata, first recorded as fossils in amber some 28 million years ago, though probably much older. The Astigmata are thought to have evolved from within an ancient, soil-dwelling group of mites, the Oribatida, fossils of which have been recovered from 376–379 mybp Devonian mudstones from Gilboa, New York State (Norton *et al.*, 1988). The evidence for the origin of the Astigmata from within the Oribatida is based on an extensive series of shared characters (Norton, 1998).

1.4.3 Biodiversity and phylogenetic relationships within the Pyroglyphidae – out of Africa in the nests of birds?

There has been no phylogenetic analysis of the family Pyroglyphidae and I am not about to attempt one here. However, we can summarise some basic trends in morphology and biology within the

different subfamilies that may give some clues to their evolution, as well as draw on biogeographical and habitat data from the catalogue in Appendix 1. From Appendix 1 and Table 1.3, only members of the subfamilies Pyroglyphinae (three out of eight genera: *Euroglyphus*, *Hughesiella* and *Gymnoglyphus*) and Dermatophagoidinae (all four genera: *Dermatophagoides*, *Hirstia*, *Malayoglyphus* and *Sturnophagoides*) are found in house dust, with 13 species in all. A number of other points emerge:

- the vast bulk of pyroglyphid diversity has been found exclusively on birds or in their nests in the tropics (28 spp.), especially west and central Africa (16 spp.), Latin America and Cuba (9 spp.);
- parrots, swallows and martins, sparrows, waxbills, weavers, woodpeckers and starlings are among the most frequent hosts of pyroglyphid taxa;
- several species, now known to be important inhabitants of dust, were first recorded in atypical habitats (e.g. *Euroglyphus maynei* in mouldy cottonseed cake);
- virtually all bird-associated taxa have been recorded only from the type locality or have restricted distributions;
- only dust-associated species are known to be geographically widespread;
- a large proportion of all the known pyroglyphid species have been described by just two people: Alex Fain and Jean Gaud, accounting for 23 species between them. The systematics of the family, especially subfamilial and generic concepts, is predominantly due to the work of Fain.

Both Fain and Gaud had strong historical research links with Africa and Gaud worked exclusively on feather mites. Is the high diversity of African avian associates a real phenomenon or is it an artefact of the research interests of these two authors? Evidence from research on feather mite taxonomy shows that these mites are often highly host-specific, and that any bird species (of some 8000) may have between two and eight different feather mites associated with it. By way of contrast, house dust is a relatively homogenous microhabitat, so one would expect a higher diversity of bird-associated pyroglyphids than dust-associated pyroglyphids. Furthermore, birds have a far older evolutionary history than humans. The ‘host’ relationships of pyroglyphid species in Table 1.3 are summarised in Figure 1.4 which shows the phylogenetic

Table 1.3 Pyroglyphid mite species known from birds and their geographical distribution.

Birds	Pyroglyphids	Distribution
Psittaciformes		
Psittacidae (true parrots)		
<i>Agapornis pullaria</i>	Dermatophagoidinae	
	<i>Dermatophagoides anisopoda</i>	Central Africa
<i>Ara macao</i>	Paralgopsinae	
	<i>Paralgopsis ctenodontus</i>	South America
<i>Pyrrhura leucotis</i>	Paralgopsinae	
	<i>Paralgopsis paradoxus</i>	South America
Apodiformes		
Apodidae (swifts)		
<i>Tachornis phoenicobia iradii</i>	Dermatophagoidinae	
	<i>Guatemalichus tachornis</i>	Central America
Piciformes		
Picidae (woodpeckers)		
<i>Meiglyptes tristis</i>	Pyroglyphinae	
	<i>Asiopyroglyphus thailandicus</i>	South-East Asia
<i>Phloeoceastes rubricollis</i>	Pyroglyphinae	
	<i>Campephiloptes atyeoi</i>	South America
<i>P. leucepogon</i>	<i>C. paraguayensis</i>	South America
Capitonidae (barbets)		
<i>Pogoniulus scolopaceus</i>	Dermatophagoidinae	
	<i>Pottocola (Capitonocoptes) longipilis</i>	West Africa
	<i>Onychalges spinitarsis</i>	Central Africa
<i>Lybius dubius</i>	Dermatophagoidinae	
	<i>Pottocola (Capitonocoptes) lybius</i>	Central Africa
<i>L. vielloti</i>	<i>P. (C.) lybius</i>	Central Africa
<i>L. torquatus</i>	<i>P. (C.) lybius</i>	Central Africa
<i>L. rubrifacies</i>	<i>P. (C.) lybius</i>	Central Africa
<i>L. bidentatus</i>	<i>P. (C.) ventriscutata</i>	Central Africa
Passeriformes		
Estrildidae (finches and waxbills)		
<i>Lonchura cucullatus</i>	Pyroglyphinae	
	<i>Bontiella bouilloni</i>	Central Africa
<i>Clytospiza monteiri</i>	Dermatophagoidinae	
	<i>Onychalges asaphospathus</i>	West Africa
<i>Euschistospiza dybovskyi</i>	<i>O. asaphospathus</i>	West Africa
<i>Spermestes bicolor</i>	<i>O. asaphospathus</i>	West Africa
<i>Spermophaga haematina</i>	Dermatophagoidinae	
	<i>Onychalges odonturus</i>	West Africa
<i>Estrilda melpoda</i>	Dermatophagoidinae	
	<i>Onychalges pachyspathus</i>	West Africa
<i>E. atricapilla</i>	<i>O. pachyspathus</i>	West Africa
<i>E. nonnula</i>	<i>O. pachyspathus</i>	West Africa

Table 1.3 continued

Table 1.3 Continued

Birds	Pyroglyphids	Distribution
<i>E. astrild</i>	<i>O. pachyspathus</i>	South Africa
<i>Lagonostica rubricata</i>	<i>O. schizurus</i>	West Africa, South Africa
Hirundinidae (swallows and martins)		
<i>Hirundo neoxena</i>	Pyroglyphinae	
	<i>Weelawadjia australis</i>	Australia
<i>Delichon urbica</i>	Dermatophagoidinae	
	<i>Hirstia chelidonis</i>	Europe
<i>Petrochelidon fulva</i>	Dermatophagoidinae	
	<i>Sturnophagoides petrochelidonis</i>	Central America
Ploceidae (sparrows and weavers)		
<i>Passer griseus</i>	Dermatophagoidinae	
	<i>Dermatophagoides aureliani</i>	Central Africa
<i>Passer domesticus</i>	Dermatophagoidinae	
	<i>Dermatophagoides simplex</i>	South America
	<i>Onychalges nidicola</i>	South America
<i>Ploceus nigricollis brachypterus</i>	Dermatophagoidinae	
	<i>Paramealia ovata</i>	West Africa
Sturnidae (starlings and mynahs)		
<i>Buphagus africanus</i>	Dermatophagoidinae	
	<i>Dermatophagoides rwandae</i>	Central Africa
<i>Buphagus erythrorynchus</i>	Dermatophagoidinae	
	<i>Dermatophagoides sclerovestibulatus</i>	South Africa
<i>Sturnus vulgaris</i>	Dermatophagoidinae	
	<i>Sturnophagoides bakeri</i> Fain, 1967	North America
Furnariidae (woodcreepers)		
<i>Certhiaxis erythrops</i>	Dermatophagoidinae	
	<i>Fainoglyphus magnasternus</i>	South America

relationships of the birds. There is no obvious pattern of phylogenetic relatedness between mites and avian 'hosts' as there is with ectoparasitic arthropods such as lice, but then the biological nature of the association of pyroglyphids and birds is not sufficiently defined to be sure of how taxon-specific it really is. The data in Table 1.3 indicate that the two subfamilies of pyroglyphids which contain species found in house dust, the Pyroglyphinae and Dermatophagoidinae, are the most widespread geographically, the most species-rich and are associated with a higher diversity of avian taxa than the subfamily that does not contain species that are found in house dust. This tends to suggest that the Pyroglyphinae and Dermatophagoidinae may represent the more ancestral taxa within the family (see Figure 1.2b).

1.4.4 Evolutionary inferences from the biology and ecology of pyroglyphids and other Astigmata

Probably about 300 species of mites are associated with humans and their homes as parasites, commensals or pests of stored food and other products. The advent of permanent human settlement, agriculture and food storage systems occurred about 10 000 years ago, so the association between astigmatid mites and human habitation has endured for about 0.044% of the duration of the fossil record of the Astigmata; equivalent to 38 seconds in 24 hours. The opportunities afforded to mites by the development of permanent settlement, agriculture and the domestic technologies of food storage and weaving are explored in more detail in Chapter 4.

Bird orders, superfamilies and families	Pyroglyphid subfamilies	Distribution	
Piciformes	Pyroglyphinae	Asia	
Psittaciformes	Dermatophagoidinae	Africa	
	Paralogsinae	C. America	
Apodiformes	Dermatophagoidinae	C. America	
Passeriformes	Furnariidae	S. America	
	Muscicapoidea	America N. America	
	Sylvoidea	Pyroglyphinae	Australia
		Dermatophagoidinae	Africa C. America
	Passerioidea	Pyroglyphinae	Africa
	Dermatophagoidinae	Africa S. America	

Figure 1.4 Summary of phylogenetic relationships of orders of birds and the suborders of pyroglyphid mites found on them. The phylogenetic relationships of the birds follow Sibley and Ahlquist (1990).

a Free-living soil dwellers and the effects of the development of agriculture

The Astigmata consists of species mostly involved in commensal, symbiotic or ectoparasitic relationships with other animals for at least part of their life cycle. Relatively few species are completely free-living, although the Astigmata were probably derived from free-living fungus feeders in rotting logs and vegetation. The most important, the Glycyphagoidea and Acaroidea are free-living as adults and found in diverse habitats including nests of birds and mammals. They differ from the Psoroptidia in that the deutonymph is heteromorphic, non-feeding, resistant to desiccation, and is thus well adapted for dispersal to new habitats via attachment to other animals – a practice known as phoresy. Phoresy is characteristic of species associated with temporary or restricted habitats: to exploit patchy resources successfully the mites need efficient dispersal. Species that are commensal, parasitic or exploit resources in widespread, contiguous habitats have lost the ability to form heteromorphic deutonymphs. This includes all of the Psoroptidia, which have no deutonymphal stage at all, some *Tyrophagus* spp. and all *Aleuroglyphus* spp.

The relatively short time since the inception of agriculture and permanent settlement is inadequate

for the evolution of such a diverse array of morphologies exhibited by the mite taxa that are found in association with human dwellings and stored products. Only rarely are more than one or two species in each genus associated with humans. The rest may be free-living in natural habitats. This suggests that many taxa, from different lineages, have colonised human habitats at different times, rather than a single lineage, on one occasion, followed by an adaptive radiation. This being so, those taxa that have successfully colonised human dwellings and stored products must have been pre-adapted to these habitats, i.e. they lived in ones that provided very similar resources before they made the shift to human dwellings. OConnor (1979) found that of those genera of Astigmata associated with stored products and house dust, six contained species widespread in field habitats, 12 contained mammal nest inhabitants, five were bird-nest dwellers and 12 were found in rare or ephemeral habitats. The trophic specialisations of dust mites and stored products mites in their non-human habitats are mirrored by niches that they have occupied within human dwellings. Thus the pyroglyphids, originally bird-nest dwellers, have encountered similar skin scales in the human nest, the bed, as they have in the feral, avian habitat, together with warmth and