Mites

Mites

Ecological and Evolutionary Analyses of Life-History Patterns

Edited by

Marilyn A. Houck

SPRINGER-SCIENCE+BUSINESS MEDIA, B.V.

Originally published by Chapman & Hall in 1994
Softcover reprint of the hardcover 1st edition 1994

Library of Congress Cataloging in Publication Data

Mites : ecological & evolutionary analyses of life-history patterns / editor, Marilyn A. Houck.
p. cm.
Includes bibliographical references and indexes.
ISBN 978-1-4613-6012-4 ISBN 978-1-4615-2389-5 (eBook)
DOI 10.1007/978-1-4615-2389-5
1. Mites. 2. Mites—Evolution. 3. Mites—Adaptation. I. Houck, Marilyn A.
QL458.M58 1993
595.4'2—dc20 93-18439
CIP

British Library Cataloguing in Publication Data available

DEDICATED
TO
Dr. Edward W. Baker
and
Dr. George W. Wharton

In Recognition of their Creativity and Life-long
Dedication to the Study of Mites

Contents

Foreword

During the past two decades, we have come to realize that the Acari (mites and ticks) rival the insects in their global diversity, abundance, and ubiquity. But what we have yet to realize fully is the potential that this group of metazoans, which are so individually minute, has in providing fresh insights about general biological phenomena and in serving as experimental animals for formulating and testing biological concepts.

The very attribute—small size—that previously impeded research on mites has, with recent technological advances, come to be recognized as advantageous in studying and using them experimentally. The advent of molecular techniques (such as polymerase chain reaction) has overcome the limitation of tiny amounts of substance available for analysis of individual mites. Their smallness also correlates with: short generation time, ease in experimental replication, rapid results, and minimal demands on space. As put so eloquently by Asher Treat in his 1975 book, *Mites of Moths and Butterflies*, modern technology now permits us to share with mites "the strange and beautiful world where a meter amounts to a mile and yesterday was years ago."

Ecological and evolutionary concepts have been based predominantly on studies of vertebrates, vascular plants, a few groups of insects (e.g. *Drosophila*), and selected unicellular organisms. This has led to a somewhat limited and distorted set of generalities on how multicellular organisms adapt and evolve. The Acari are one of a few relatively untapped assemblages (major groups of fungi and crustacea also come to mind) that have almost endless potential as study subjects, to contribute to the overall picture of the complexity and diversity of life now on earth.

This assemblage is remarkable in being very ancient (with extant families represented in the geological record at least as early as the middle Devonian), as well as very disparate. The early presence of acarines enabled them to interact and co-evolve dynamically with subsequent major ecological and evolutionary

radiations of vascular plants, insects, and terrestrial vertebrates, in ways that still continue. Attributes of mites such as the intricacies of their life cycles, the genetic and ecological mechanisms that regulate their abundance and adaptability, and the diversity of their physiological and behavioral adaptations, all provide unique opportunities for exploring fundamental biological processes.

The ancestral Acari was a conservative assemblage of omnivores (predators—fungivores) that stemmed from a predatory class of arthropods, the Arachnida. Through time, however, mite diversification led to habitat and trophic expansion in all manner of niches on land and in fresh and ocean waters, and the assemblage now includes: microorganism filter feeders; fungal and algal grazers; parasites of plants, vertebrates and invertebrates; and parasitoids, commensals and mutualists of invertebrates. What are the attributes that have enabled the Acari, unlike other arachnids, to achieve such unparalleled biological diversity beyond predation? The answers lie among the attributes and patterns that have evolved in their life histories and reproduction.

Based on life history studies of disparate groups of mites living in a variety of habitats, the chapters in this book offer new data synthesized with previous knowledge, which in some cases lead to startling views with broad evolutionary impact. In its breadth and major significance to biological themes, one chapter is salient in challenging a widely held cytogenetic paradigm that does not account for the long-term evolutionary success of major lineages of thelytokous and haplodiploid mites. Among sarcoptiform mites, there is strong evidence for a large, long existent, and diverse group of thelytokous mites. Stranger still, is the evidence for an evolutionary reversal to sexuality in a major lineage derived from this group. Among trombidiform mites, there is much evidence for repeated independent success in highly inbred clades of arrhenotokous mites. This chapter's phylogenetic perspective on the cytogenetic mechanisms which underlie such diversity of life history patterns is elegant in its apparent simplicity not only for mites but for the general lineage of eukaryotic organisms. The prospects highlighted for further research in this area are exciting indeed.

Among other chapters, some consider life history and concomitant reproductive patterns in diverse and speciose lineages of Acari, including the Oribatida and the Astigmata in the suborder Sarcoptiformes, and the Dermanyssoidea and Phytoseiidae in the suborder Parasitiformes. Another is of similar breadth, but deals with symbiotic assemblages of mites co-adapted with a species group of invertebrate hosts, bees in this case. Still other chapters deal in depth with specific examples of hosts, such as fruit flies and carrion beetles, or with particular examples of habitats such as hummingbird-pollinated flowers and water-filled treeholes. The latter are tremendously fascinating because they shed light on phenomena of general biological interest, such as horizontal-transfer vectors of transposable genes between species, and the all-encompassing effects of host-plant morphology and phenology on virtually every aspect of the lives of flower-inhabiting mites.

If readers bear in mind that the included chapters are but tidbits of an almost endless buffet of similarly fascinating associations of mites with other organisms—be they bracket fungi, insectivorous plants, hawk moth-pollinated flowers, subcortical nematodes, intertidal mollusks and crustaceans, sawyer beetles, honeybees, midges, odoriferous glands of coreid bugs, or the bodies and nests of birds and mammals—they will realize that similarly intriguing and biologically significant studies are theirs for the choosing. Ecological and evolutionary analyses of life history patterns, among the many families of protelean parasitic water mites co-adapted with their aquatic invertebrate hosts, await investigators with a bent for freshwater ecosystems. And what on earth do we know of such patterns among the diversity of halacarid mites that have, unlike insects, successfully invaded the sea, including its very depths? Or of the peculiar, vermiform nematalycid mites that somehow do well in soil depths to 10 meters?

The answers to these and similar questions are basic to an eventual understanding of the biodiversity that exists in any of the earth's ecosystems. The Acari offer unique opportunities for investigating other biological phenomena relevant to life history patterns, such as: heterochrony and paedogenesis, demographic polymorphism, adaptations to terrestrial and aquatic ways of life, exploitation of patchy environments, vector and hypervector relationships, specialist versus generalist predators, and resource tracking versus host tracking in coadaptations with fungi, plants, nematodes, insects, and vertebrate animals. Once we have a perspective on the life history patterns of a greater diversity of organisms (including mites), based on ecological and evolutionary analyses superimposed on a phylogenetic background, we will then be in a better position to predict the ways of living and interacting of organisms representing a total array of biodiversity.

There is, moreover, an applied ecological side to these studies. Findings such as the horizontal transfer of genes between species, the effect of prey densities on the evolution of sex mechanisms in predatory mites, and the cytogenetic mechanisms underlying the haplodiploid sex-determining systems characteristic of the most highly adapted groups of phytophagous and predatory mites, have significant implication to the field of integrated control of animal and plant pests. Further, studies of the interaction and coadaptation of mites and ticks with closely associated microorganisms is critical to understanding how they, and other invertebrates, transmit diseases to plants and animals, and how mites in turn may be controlled by microbial pathogens.

As indicated by the diverse backgrounds of the authors of this book, these subjects appeal to the more general students of evolutionary biology as well as to the more specialized (and increasingly few) students of acarology. As well, they appeal to both collaborative, multidisciplinary approaches and individual investigations. And that is precisely the intent of this book: (1) to provide a stimulating source of information and ideas gleaned from the ways of life of mites; (2) to have these ideas pursued further by general ecologists, geneticists, parasitologists, and evolutionary biologists as well as by specialists; and (3) to

link generalists to the increasingly extensive and exciting acarological literature relevant to their areas of interest.

EVERT E. LINDQUIST
Ottawa, Canada
April, 1993

Preface

The work on this dedication volume was begun in December, 1989, when the Acarological Society of America (ASA) chose to publicly recognize **Dr. Edward W. Baker** and **Dr. George W. Wharton** for their life-long contributions to the science of Acarology. A Formal Conference/Acarological Symposium, dedicated to Ed Baker and George Wharton, was held on the afternoon of December 10, 1989, in conjunction with the national Entomological Society of America meeting at the Convention Center, in San Antonio, Texas. The program was entitled *Acari: Life History and Reproductive Patterns*, and the participants included (in order of original presentation): D. E. Johnston, D. L. Wrensch, M. Sabelis, M. J. Kaliszewski (co-moderator), R. A. Norton, B. M. OConnor, N. J. Fashing, R. K. Colwell, G. C. Eickwort, J. M. Brown and D. S. Wilson, and M. A. Houck (organizer and co-moderator).

Coauthors (A. Janssen, J. B. Kethley, S. Naeem) joined the efforts during the process of constructing the volume and F. J. Radovsky graciously agreed to round out the perspective by contributing an additional (and much needed) chapter on mammal associates. Regretfully, due to unforeseen circumstances, two original contributions are not recorded here. The chapter on heterochrony in mites is absent, due to an unresolvable scheduling conflict, and the chapter on the *Evolution of Polymorphism in the Tarsonemina* was not sufficiently developed to bring it to completion at the time of the premature death of M. Kaliszewski on October 14, 1992. We regret that Marek's chapter could not appear in this volume and acknowledge his contribution and influence on modern acarology.

Following the Symposium, a reception dinner was held for the honorees and appropriate comments and goodwill were publically offered by many. Leis were hand-carried by an ASA member, Ms. Sabina Swift, from Hawaii and presented to the two honorees and an exuberant and happy evening was shared by all. Preston Hunter compiled, for a special issue of the ASA Newsletter (published in November 1989), the major accomplishments of E. W. Baker, and Donald

Johnston did the same for G. W. Wharton. The capsular account of the accomplishments of Ed Baker and George Wharton, which follows, is shamelessly parasitized from the recollections of Preston Hunter and Don Johnston published in that issue of the ASA Newsletter.

On December 10th we did not know just how critical the timing of the celebration would turn out to be. George Wharton passed away just four months later (4 April, 1990). In a Memorium statement in a subsequent ASA Newsletter, Don Johnston was quoted as addressing George Wharton as "A Student's Professor," and that is how he is best remembered by those who knew him well.

Edward W. Baker

When Ed Baker, a Ph.D graduate from U.C. Berkeley in 1938, decided to devote his life to an investigation of mites, there was essentially no organized literature available on the identification or biology of the acarines. Preston Hunter described the literature as "scattered and limited" and described the discipline of Acarology as "non-existent." Thus, Ed Baker's degree was actually in entomology and plant pathology but his dissertation focused on the fig mite *Eriophyes ficus*.

Soon after graduation, Ed joined the USDA and was sent to work at the Fruit Fly Lab in Mexico City (1939–1944). His second position was also with the USDA, at the Systematic Entomology Laboratory in Washington, D.C. (Insect Identification and Beneficial Insect Introduction Institute). He held that position for 43 years, earning the highest professional rank possible (ST-16). Ed "retired" in February 1987, but when you want to reach him . . . it is still best to try to locate him in his small, slide- and illustration-filled office at the USDA.

There were so many accomplishments and so many "firsts" in Ed Baker's singular career. He co-authored, with George Wharton, a book entitled *An Introduction to Acarology* (later translated into Russian), a seminal work which birthed and defined a new discipline, Acarology, as Americans know it. But that was just a beginning of an effort to spread the excitement and joy available in the world of the miniature. He expressed enthusiasm for his organism in the most appropriate way possible . . . he described over 700 species, 60 genera and 9 new families of mites, and according to Preston Hunter's account his work totals over 4,200 published pages (over 130 original papers). Each illustration and each interpretation was meticulously crafted by Ed. He did not have benefit of a large support network of artists and technicians. At the same time he was responsible for over 70,000 identifications of mites sent to the USDA from all over the world.

Ed Baker's work has had profound impact on American Acarology. His major books include: *A Revision of the Spider Mite Family Tetranychidae* (Pritchard and Baker, 1955), *Guide to the Families of Mites* (Baker, Camin, Cunliffe, Woolley and Yunker, 1958), *A Manual of Parasitic Mites* (Baker, Evans, Gould,

Hull and Keegan, 1956), *Spider Mites of Southwestern United State and a Revision of the Family Tetranychidae* (Tuttle and Baker, 1968), *An Illustrated Guide to Plant Abnormalities Caused by Eriophyid Mites in North America* (Kiefer, Baker, Kono, Delfinado and Styer, 1982), and *The False Spider Mites of Mexico* (Baker and Tuttle, 1987).

Ed Baker has also studied and lectured in Africa, Central America, Brazil, Egypt, India, Iraq, Pakistan, the Philippines, Thailand and Venezuela. Along the way he helped to establish Acarological programs in many of these locations, as he did in the U.S. where he participated in the creation of the *Institute of Acarology*. Professional accolades have been common in the life of one so singular. He has earned the Distinguished Service Award from the Washington National Academy of Science and was Vice-President and Plenary Speaker at the First International Congress of Acarology (1963), President of the International Congress in 1978, first recipient of the Berlese Award for Outstanding Achievement in Acarology by the *International Journal of Acarology*, recipient of the USDA's Superior Service Award . . . and the list goes on. Ed Baker has been, from the beginning, a giant among his peers, a true "Father" (and obstetrician) of a new discipline which has not been without some growing pains. His insight, intellect, patience, dedication and nurturing of younger proselytes have been unparalleled. My own fond memories of Ed begin with my first visit to his lab where, like a kid in a candy shop, I sorted through boxes of reprints of his publications on his floor shamefully and gleefully carrying out all I could carry. They extend to later remembrances over beer, at the Cattleman's Steakhouse in Tucson, Arizona, when Ed and his lovely wife Mercedes Delfinado-Baker visited to talk about *Varroa*. The science stands as a deserved monument to the scientist in Ed Baker, but our collective memories bear witness to his humanity, generosity, and zest for life around him. His contributions are much more than the sum of his publications.

George W. Wharton

George W. Wharton was born in the same year as Ed Baker (1914), but 11 months earlier. So perhaps his birth-order gives him some seniority in the role of "Father of Acarology" which he shares with Ed Baker. However, while Ed Baker was growing up on the sunny west coast, George Wharton was spending his formative years in Belleville, New Jersey.

George Wharton received his Ph.D from Duke in 1939 and, like Ed Baker, joined government service. He became a Biologist with the Norfolk Naval Shipyard and subsequently joined the Rockefeller group at NAMRU-1 in the Pacific war zone. Following World War II George returned to Duke, and in 1951 he and Ed Baker decided to establish the Summer Teaching Program for acarologists. George assumed the Departmental Headship at the University of Maryland in

1953, and moved the Summer Program to College Park, where it remained until he accepted the Chairmanship of the Department of Zoology and Entomology at Ohio State in 1961. According to Don Johnston, under whose able guidance the Ohio State Acarology Program continues to flourish, it was at Ohio State where the "Acarology Laboratory and the Summer Program have enjoyed their greatest success." The Program trains students from all over the world and remains a singularly valuable resource for material, reprints, and academic training concerning mites.

In 1976 George "retired" as Director of the Acarology Laboratory but continued his teaching and research until diminished eyesight and poor health prevented his active participation. His enthusiasm and influence did not wane with his vision and dexterity, however, and he continued to be a major force in acarology until his untimely death in April, 1990.

Beside his collaborative publications with Ed Baker, mentioned above, George also published *A Manual of the Chiggers* (with H. S. Fuller, 1952) and *A Manual of Mesostigmatid Mites Parasitic on Vertebrates* (with R. W. Strandtmann, 1958). In addition to his life-long interest in mites, George Wharton had a broad interest in biology and published on such topics as the physiology of respiratory pigments in helminths and the ecology of littoral Crustacea. George brought exceptional breadth as well as depth to the arena of Acarology. And, his experiences and exploring curiosity for all of nature would make him most supportive of the spirit of integration and extension which modern Acarology hopes to bring to Biology.

Years of dedication to science have produced approximately 130 publications, and have earned George much professional recognition. George chaired the Tropical Medicine Study Section of the National Institute of Health (NIH), he was President of the Society of Systematic Zoology, and the President of the First International Congress of Acarology (1963). He was a Guggenheim Fellow (1950–1951) and was elected to Honorary Life Membership in the International Congress of Acarology in 1974.

George Wharton had a special dignity among men, was admired as a true teacher, and was a scholar of the highest caliber. His perspective was that acarologists should strive to synergize and respect equally both "basic" and "applied" research for the sake of the wholeness of the discipline. He refused to recognize the perceived dichotomy between them and enjoyed a joint appointment with The Ohio Agricultural Experiment Station (Wooster, OH) during his chairmanship at Ohio State.

George's guidance and his dedication to training quality acarologists has left behind a legacy of equally gifted scholars, the most significant and fitting contribution one can make to one's discipline. He truly deserves the designation, "Father of Acarology". I personally met George Wharton on only a few occasions, which was sufficient for me to understand the influence one dedicated individual can

have on the people that enjoy the dividend of his time. His enthusiasm for the Acari and his generosity with encouragement will stay with me as a remembrance.

Collectively, Ed Baker and George Wharton are a study in contrasts in terms of temperament and personal history. Acarology has benefited greatly from their individuality, perspectives, distinctions and uniqueness. What they shared was a true passion for mites and a keen concern for the future of Acarology. It is this commonality which created a whole far richer than either alone could have contributed to the molding of a discipline. At a time when diminishing funding and attrition in number of contributing acarologists threaten the future health of Acarology, the authors of this volume feel a responsibility to reinforce and continue the traditions established by Drs. Baker and Wharton. The challenge will be to provide equal passion, vigor, and cooperation in order to

> capture the imagination of the public with an understanding of the esthetic values each of us derives from our intimate knowledge of the beauty and symmetry of the form, function, and lifeways of the Acari

and acknowledge that the

> intellectual values to be derived from the study of mites and ticks are yet to be determined. That this is true is evident from the fact that no one yet has any idea of how many kinds of Acari are living at the present time, let alone how and where they live.

[Quotations extracted from the text of Dr. G. W. Wharton's Keynote Address to the First International Congress of Acarology, Fort Collins, CO, 1963.]

As Acarology matures as an autonomous discipline, exciting ecological and evolutionary patterns are emerging and hopefully these patterns will be woven into the fabric of modern biology to give a more balanced interdisciplinary understanding of ecology and evolution.

All of the contributors to this volume, and the 1989 symposium, have direct or indirect gratitude to offer these two gentlemen. The work of all of the contributing authors was possible because of the foundations established by these men. We show them our respect and appreciation by offering to them this compilation of papers on the ecological and evolutionary patterns in mites. In presenting this compilation of papers, the intent is to strengthen an interdisciplinary discussion, awareness, and curiosity about mites among ecologists, evolutionary biologists, parasitologists, population biologists and naturalists. We hope especially to encourage students and researchers to see the excitement and possibilities in the study of mites that we, the contributing authors, have enjoyed in our own work.

I hoped to have assembled a volume with a content and authorship representing the most current and innovative studies focusing exclusively on mites. The authors are individually recognized for the quality, depth, and creativity of their past

work, and each has contributed to this volume with previoulsy unpublished work that will prove to be as well received. The authors have exploited their own past successes, through capsular highlights of completed work, and offered a projection of potential future directions. The authors offer a spectrum of topics that showcase a diversity of acarological taxa, techniques, and perspectives. The intent was not to be inclusive but rather to include innovative studies with the broadest interest.

With absolutely no idea of what was involved in organizing such a volume, I persuasively solicited publishing houses in the Spring of 1989, with the intent of conceding the project to the "highest worthy bidder." Lesson one . . . general enthusiasm for mites needs nurturing. Once Chapman and Hall was selected (from among the two worthy bidders), I petitioned symposium speakers to deliver manuscripts to me for editing at the end of the 1989 symposium session. Lesson two . . . being academicians, acarologists are overcommitted and overworked. I extracted the final included chapter under duress in November, 1992.

While delayed publication became a disappointment, it provided authors with the privilege to update revisions until as late as December 1992. Thus, while the publication was belated, it is by no means outdated. The volume is very current and timely in content—illustration, one diligent author was still updating citations as late as Christmas, 1992.

This volume should prove to be very effective as a supplement for courses in entomology, population biology, and general ecology and evolution, as well as acarology. The level of comprehension is directed toward upper-level undergraduates, graduate students and professional researchers. However, the diversity and clarity of issues is appropriate for all who are interested in broadening their general knowledge of organismal biology.

Modern acarology is beginning to flex its academic muscle, as it exits from a time of maturation to a time of extension and integration. The expectation is that, as mites become better appreciated, they will be relieved of the perception as OTUs or miscellaneous "others" in field samples and become appreciated for their uniqueness, their seductiveness and for the joy they offer to the exploring mind. Mite-watcher's life lists of rare species, mite treks and expeditions led by world-renowned experts, baited mite lures and traps of various sizes and shapes, all are acarological contingency plans for the future.

This editorial experience has been a positive growth step in my learning curve, with many necessary adjustments along the way. It taught me how to nag, how to use an "N" dash, how to sprain sagacious egos without even trying, and most of all how to compromise. With these reflections and facts in place, I wish to thank: Greg Payne of Chapman and Hall for his patience, attention to detail and appreciation of the smaller (acarine) things in life; James Geronimo, production manager, for meticulous and careful handling of the final copy; Rich Strauss (my husband) for fervent encouragement when teaching loads were getting me down; and the dedicated authors who worked so hard to make this volume one that we

could collectively be proud of (oh no, one last dangling participle !*). Special thanks also to Ev Lindquist for taking time from his busy schedule the offer a Foreword. They have been loyal conspirators to the end and deserve much credit and no blame. Any existing errors are mine alone to cherish.

MARILYN A. HOUCK
Texas Tech University, 1993

Contributors

Jonathan M. Brown
Department of Biology
Bucknell University
Lewisburg, PA 17837

Robert K. Colwell
Department of Ecology and Evolutionary Biology
University of Connecticut
Storrs, CT 06269–3042

George C. Eickwort
Department of Entomology
Cornell University
Ithaca, NY 14853

Norman J. Fashing
Department of Biology
College of William and Mary
Williamsburg, VA 23185

Marilyn A. Houck
Department of Biological Sciences
Texas Tech University
Lubbock, TX 79409–3131

Arne Janssen
Department of Pure and Applied Ecology
University of Amsterdam
Kruislaan 302
1098 SM Amsterdam
The Netherlands

John B. Kethley
Center for Evolutionary and Environmental Biology
Field Museum of Natural History
Roosevelt Rd. at Lake Shore Drive
Chicago, IL 60605

Evert E. Lindquist
Bio-Systematics Research Institute
Agriculture Canada
K. W. Neatby Bldg.
OOttawa, Ontario
K1A0C6 Canada

Shahid Naeem
Centre for Population Biology
Imperial College at Silwood Park
Ascot, Berks SL5 7PY
United Kingdom

Roy A. Norton
Faculty of Environmental and Forestry Biology
SUNY College of Environmental Science and Forestry
Syracuse, NY 13210

Barry M. OConnor
Museum of Zoology and Department of Biology
The University of Michigan
Ann Arbor, MI 48109–1079

Frank J. Radovsky
North Carolina Department
of Agriculture
Raleigh, NC 27611

Maurice W. Sabelis
Department of Pure and Applied
Ecology
University of Amsterdam
Kruislaan 302
1098 SM Amsterdam
The Netherlands

David Sloan Wilson
Division of Biological Sciences
SUNY, Binghamton, NY 13901

Dana L. Wrensch
Department of Entomology
The Ohio State University
1735 Neil Ave.
Columbus, OH 43210

1

Poecilochirus carabi: Behavioral and Life-History Adaptations to Different Hosts and the Consequences of Geographical Shifts in Host Communities

Jonathan M. Brown and David Sloan Wilson

CONTENTS

1. Introduction

The concept of trade-offs is central to many aspects of evolutionary biology. Life-history models, for example, routinely assume that some component of fitness, such as fecundity, can only be increased at the expense of another component, such as survival. Models of the evolution of specialization similarly assume that efficiency at one task can be achieved only when an organism is inefficient at others (e.g. Wilson and Turelli 1986). Life-history parameters may themselves be important in the evolution of specialization if, for example, different strategies result in maximum fitness in different habitats or in association with certain hosts.

In its most abstract form, few people would question the basic concept of trade-offs. Nevertheless, the nature of any trade-off is by no means obvious in any

particular ecological setting. Nor is its importance obvious in terms of the evolution of life-history traits and niche specialization. A growing number of empirical studies have either failed to find trade-offs that initially appeared plausible, or found them where they were unexpected (for investigations of longevity in *Drosophila* see Service 1985; Luckinbill et al. 1989; see also Futuyma and Moreno 1988). To proceed beyond abstract generalizations, the study of trade-offs therefore requires a solid foundation in empirical studies.

In this chapter we present an overview of our research on host specialization in a parasitid mite (*Poecilochirus carabi*) that is phoretic upon carrion beetles (Silphidae; *Nicrophorus* [= *Necrophorus*] [Fig. 1.1]). Phoretic mites in general are well suited for the study of specialization because they frequently have access to a number of carrier species (= hosts) that transport them to different environments, each potentially requiring a different set of adaptations for survival and reproduction. Phoretic mites also span the full range from specialists on a single carrier species, to generalists that utilize many carrier species.

P. carabi is particularly well suited to the study of the role of life-history adaptations in the evolution of specialization, as populations vary in relative breadth of host use. By investigating the interaction between mite life-history parameters and their hosts' behavior and ecology, we are documenting the mite's ability to adapt to local host communities. Our research demonstrates that host specialization occurs where strong life-history trade-offs are found across hosts, but also highlights the fact that the presence of trade-offs alone does not guarantee that specialization will be found in any given community. Other factors (e.g. population structure and the ability of organisms to select their hosts) interact with trade-offs to affect the coexistence of specialist mites.

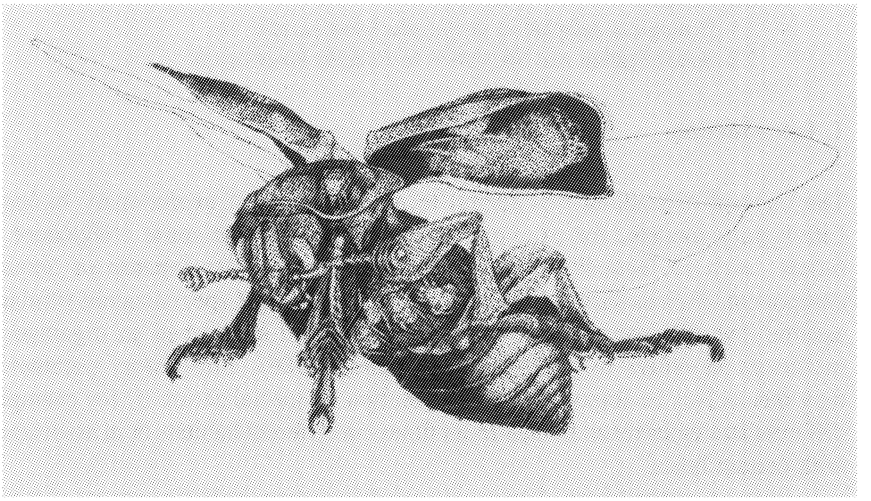


Figure 1.1. *Poecilochirus* species clinging to a flying *Necrophorus* beetle.

One subject of special interest to us is the role of trade-offs and the evolution of specialization in the process of speciation. Is variation in life-history strategies a response to selection for association with different host (carrier) species? In particular, can a single species of mite become polymorphic for adaptations to different carriers, and can the intraspecific morphs ultimately become separate species? Our results, although not yet conclusive, suggest that such a process might operate in *P. carabi*.

2. Natural History

2.1 The Beetles (Nicrophorus)

Most carrion beetles in the family Silphidae reproduce on large animal carcasses. Beetles in the genus *Nicrophorus*, however, sequester small carcasses by burying them underground and then using this resource to raise their brood. Typically a small carcass is discovered by several *Nicrophorus* beetles, but ultimately the carcass is monopolized by a single male and female which remain in the burial chamber throughout most of their brood's development. The social and parental behavior of *Nicrophorus* beetles is an active research area (Bartlett 1987, Müller 1987, Scott and Traniello 1987, Trumbo 1988, Müller and Eggert 1989).

Nicrophorus beetles are found at all geographic latitudes but reach their peak of diversity in the north temperate zone. Some species live primarily in forested habitats, others in grasslands (e.g. *N. marginatus*), and one species in North America is restricted to bogs (*N. vespilloides*; Peck and Kaulbars 1987). Our study focuses on four species that coexist in forested habitats: (1) *N. sayi* is a large nocturnal species that overwinters as an adult and is reproductively active only during the spring. During the early summer and fall *N. sayi* can be collected in pitfall traps but will not subsequently breed in the laboratory, even when provided with a mouse carcass; (2) *N. orbicollis* is also a large nocturnal species that overwinters as an adult, but *N. orbicollis* is reproductively active during the summer; (3) *N. defodiens* is a small crepuscular species that overwinters as an adult and has a reproductive period that coincides with that of *N. orbicollis*; (4) *N. tomentosus* is a medium-sized diurnal species that overwinters as a prepupa, emerging in early summer. It is reproductively active only during the fall, after *N. orbicollis* and *N. defodiens* have entered reproductive diapause.

Interactions among the four beetle species, and the mechanisms that allow them to coexist on a single resource, are fairly well understood (Wilson et al. 1984). While small carcasses are required for reproduction of all four beetle species, adults of *Nicrophorus* also frequent large carcasses to feed and to mate. When co-occurring on large carcasses, the various species mingle nonaggressively. On small carcasses, however, the species interact aggressively with the outcome primarily determined by beetle body size.

The strongest interspecific aggression occurs between the two summer breed-

ers, *N. orbicollis* and *N. defodiens*. A large proportion of carcasses initially found by *N. defodiens* are subsequently discovered and appropriated by *N. orbicollis* during the same or ensuing nights. *N. defodiens* can successfully coexist with *N. orbicollis* primarily by being crepuscular, which allows them to fly during cool periods when nighttime temperatures prohibit nocturnal *N. orbicollis* from searching for carcasses (Wilson et al. 1984). Temperature-dependent competition between *N. defodiens* and *N. orbicollis* probably determines the geographical distribution of *N. defodiens*, which is limited to northern latitudes and higher altitudes (Peck and Kaulbars 1987).

The effect of competition on the reproductive phenology of the four species is only partially understood. Adults of *N. orbicollis* and *N. defodiens* enter reproductive diapause in late summer, after which time any potential offspring would not have sufficient time to develop into their overwintering (adult) stage. *N. tomentosus* overwinters in the prepupal stage and therefore can remain reproductively active longer than *N. orbicollis* and *N. defodiens*. The onset of reproduction in *N. tomentosus* is probably influenced by competition with *N. orbicollis*, although this requires more documentation. It is tempting to think that *N. sayi* breeds only in the spring because of competition with *N. orbicollis*, but pilot experiments (Wilson, unpublished data) have failed to support this hypothesis, and the reason that *N. sayi* foregoes reproduction throughout the summer remains a mystery.

The social behavior and community ecology of *Nicrophorus* beetles is a fascinating subject in its own right. In this paper, however, we are viewing the beetle community primarily as a complex environment inhabited by phoretic mites. From this perspective it is obvious that the choice of a carrier species can have profound consequences for mite fitness, particularly for those species whose reproductive physiology is linked to carcass burial and reproduction by the beetles (see below). A mite that remains attached to *N. sayi* in the summer, for example, will not breed until the following spring. A mite that remains attached to *N. tomentosus* may breed in the fall but its progeny will remain underground until midsummer of the following year. More subtle, but equally important, consequences of carrier choice will be documented below.

2.2 The Mites (Poecilochirus carabi)

Nicrophorus beetles collected from our study sites support an abundant community of mites, comprising at least 14 species from four different families (Histiostomatidae, Macrochelidae, Parasitidae, Uropodidae). Our study focuses on a large (1 mm in body length) parasitid species, *Poecilochirus carabi* (= *P. necrophori* Vitzthum), that feeds on carrion fluids and small organisms associated with carrion such as fly eggs and nematodes. The feeding activities of *P. carabi* tend to have either a neutral or a beneficial effect on the fitness of their beetle carriers (Springett 1968, Wilson 1983, Wilson and Knollenberg 1987).

The most widely accepted definition of phoresy in the Mesostigmata (Farish

and Axtell 1971) requires that the attached animal (the phoretic): (1) actively seek a host; (2) neither feed nor develop while on the host; and (3) attach temporarily and for the purposes of dispersal to an area more suitable for reproduction or development. *P. carabi* satisfies this definition with one minor exception; they sometimes feed while on the host, either on other phoretic associates such as nematodes or on oral secretions of the beetle (Springett 1968). Since this mite is so highly adapted to use *Nicrophorus* beetles as a transport agent and for no other purpose, we describe the relationship as phoretic.

P. carabi is only phoretic in the deutonymphal stage. Unlike many other species of phoretic mites which physically attach to their carrier until their final destination is reached (e.g. members of the family Histiostomatidae), *P. carabi* is extremely mobile and often leaves one carrier temporarily to feed or to permanently switch to another nearby carrier. As outlined above, the natural history of *Nicrophorus* beetles creates frequent opportunities for *P. carabi* to switch carriers on large (and occasionally on small) carcasses.

When a *Nicrophorus* beetle arrives at a carcass that is suitable for its own reproduction, *P. carabi* disembarks and within 24–48 hours molts into the adult stage. The next generation of deutonymphs can potentially: (1) disperse on the parent beetles; (2) accompany the beetle offspring into their pupal chambers; or (3) disperse on other insects that visit the abandoned burial chamber. From the standpoint of the mite's preference, these options can usually be ranked $1 > 2 > 3$. This is presumably because parent beetles will immediately search for new carcasses, whereas their offspring require weeks of development before becoming adults in need of a new resource. In addition, if both the male and the female-beetle parents are present in the burial chamber, deutonymphs of *P. carabi* preferentially embark on the males. Abandoned burial chambers probably are seldom revisited by *Nicrophorus* beetles, since the carcass is usually completely consumed by the brood.

It might seem that *P. carabi* could breed on large carcasses in addition to small carcasses, since the former receive a constant traffic of *Nicrophorus* beetles who visit to feed and to mate. It appears, however, that large carcasses are utilized primarily by another species of *Poecilochirus* (described as *P. silphaphila* in an unpublished Ph.D. thesis; Yoder 1972) that is phoretic both on *Nicrophorus* beetles and other genera of silphids that specialize on large carcasses (Wilson, unpublished data). While the specific cue is unknown, we have found that the only predictable method to induce deutonymphs of *P. carabi* to molt into adults is to place them on *Nicrophorus* pairs burying small carcasses.

The taxonomy of *Poecilochirus* in general, and of *P. carabi* in particular, is unfortunately not helpful in understanding host specialization. The current taxonomic trend is towards lumping previously named species into cosmopolitan, morphologically variable species (for the latest treatments see Hyatt 1980 and Wise et al. 1988). As most recently defined, *P. carabi* has been recorded most often in association with *Nicrophorus* but also with other silphids and other

families of insects (Hyatt 1980). We will argue that, as currently defined, *P. carabi* almost certainly includes several reproductively isolated and morphologically distinct species.

3. The Study

We have studied *Poecilochirus carabi* intensively at two sites in Michigan; the University of Michigan Biological Station (UMBS) at Pellston, MI (latitude = 45° 34′) and Michigan State University's Kellogg Biological Station (KBS) at Hickory Corners, MI (latitude = 42° 34′), 315 km south of UMBS. The general habitat features of the two sites have been described elsewhere (Wilson et al. 1984). For our purposes the main difference concerns the occurrence of *Nicrophorus defodiens*, which (through the mechanism of temperature-dependent competition outlined above) is absent at KBS and abundant at UMBS. Based on our results from KBS and UMBS, we have also taken more limited data from additional sites to test specific hypotheses discussed below. This includes a transect connecting KBS and UMBS, and scattered locations throughout North America.

Our general goal has been to examine carrier-preference by the mite, mite life-history traits, morphology, mating behavior, and natural patterns of association in an integrated fashion. Methods are described in detail elsewhere (Brown 1989, Brown and Wilson 1992) and will be summarized here.

3.1 Carrier Preference of Poecilochirus carabi

The goal of these tests was to mimic situations that occur on or near large carcasses, where mites have an opportunity to choose between different species of beetles. Beetles and mites collected in baited pitfall traps were placed in collection boxes for 24 hours. Individual beetles with their attached mites were then placed individually in small plastic tubs with moist paper towelling. Beetles of a given species (e.g. *N. orbicollis*) were placed under a stream of CO_2. *P. carabi* were dislodged with a fine camel-hair brush and placed in a tub with two beetles of different species (e.g. *N. orbicollis* and *N. tomentosus*) whose *Poecilochirus* mites had been previously removed. The beetles tend to be nonaggressive in this situation, moving independently or resting side by side in the tub as they do on large carcasses. Twenty-four hours later, the numbers of *P. carabi* on each beetle were counted.

These experiments reveal whether mites found on a given beetle species at the start of the experiment, actually prefer that species when given a choice. The experiments do not reveal whether preferences are genetically based or the result of prior experience. Therefore, we have conducted separate experiments in which mites that are found on a given beetle species are forced to breed in association

with another beetle species. Choice experiments are then performed on their offspring (Wilson 1982, Brown 1989).

The choice experiments have one problem that can be illustrated by the following hypothetical example. Suppose that the majority of *P. carabi* in a population are generalists that are indifferent to carrier species but that a small proportion are specialists with strong preferences. The results of a choice experiment would be dominated by the generalists and rare specialists might not be detected. We therefore have conducted two-round choice experiments in which mites originally taken from *N. orbicollis* (for example), that chose *N. orbicollis* during the first round, are given a second choice between *N. orbicollis* and a second species. If *P. carabi* consists of both generalists and specialists, then the proportion of specialists on *N. orbicollis* should increase with each round of the choice experiment, ultimately allowing them to be detected.

The choice experiments can be analyzed statistically in two ways. First, the proportion of mites from beetle species i ($i = 1, 2$) that chose beetle species j ($j = 1, 2$) can be tested against the null hypothesis of no preference. This assumes that each mite choice represents an independent event. It is possible, however, that mites are influenced by the behavior of other mites or that all mites in a given tub are influenced by factors unrelated to beetle species. A more conservative test is, therefore, to score the number of tubs in which more than half of the mites from beetle species i ($i = 1, 2$) chose beetle species j ($j = 1, 2$). This is then tested against the null hypothesis of an equal score for each beetle species (Chi-square test).

3.2 Life-History Traits of Poecilochirus carabi

To measure differences in life-history traits that might correlate with carrier-preference, *P. carabi* were bred in the laboratory with both their preferred and non-preferred carrier species. The standard protocol involved placing beetles, mites, and a dead mouse into soil-filled buckets fitted with lids that allowed the beetles to exit into an emergence trap. In this fashion we recorded the total fecundity of the mites and the distribution of their offspring on the departing male-beetle parent, the departing female-beetle parent, and their emerging beetle offspring. In a separate series of laboratory experiments, the developmental rate of *P. carabi* was measured directly by dismantling burial chambers at periodic intervals and extracting the mites with a sucrose solution.

3.3 Morphological Analysis of Poecilochirus carabi

The analysis of morphological variation in *P. carabi* was performed on both field-caught specimens and on mites from the breeding experiments outlined above. This controls for the effect of carrier-beetle species on mite morphology. Two characters were then measured: (1) body size, measured as the length and width of the sternal shield and/or dorsal shield; and (2) dorsal setal lengths.

A principal components analysis (PCA) was performed on a set of log-transformed lengths of the dorsal podonotal shield setae, using a covariance matrix (SAS Institute Inc. 1985). The number of setae included in the analysis depended on circumstances. Measurements of mites from the laboratory breeding experiments included 19 podonotal shield setal lengths. Because smaller numbers of mites were available from some field collections, and because setae tended to fall off during preparation and mounting of the mites, it was necessary to use fewer setal measurements per individual in these cases, in order to obtain a large enough sample size. At a minimum, we chose to measure four setae (i_3, i_5, z_2 and z_4). Previous studies demonstrated the least overlap in size of these setae between KBS specialists (see below).

4. Results

Results will be presented first for the Kellogg Biological Station (KBS), then for The University of Michigan Biological Station (UMBS), and finally for the other sites for which we have limited data.

4.1 I. Kellogg Biological Station (KBS)

Figure 1.2A (KBS) shows the results of a two-round choice-experiment test performed on August 8, 1981, using *Poecilochirus carabi* collected from *Nicrophorus orbicollis* and *N. tomentosus*. Starting from the left side of the top figure, 86 mites attached to *N. orbicollis* were divided into 11 tubs and provided a choice between *N. orbicollis* (*No*) and *N. tomentosus* (*Nt*). Eighty-six percent chose *N. orbicollis*. Stated more conservatively, the majority of mites chose *N. orbicollis* in 10 out of the 11 tubs.

When these mites were provided a second choice, 95% of those choosing *N. orbicollis* on the first trial, chose *N. orbicollis* on the second trial. When the minority of the mites that chose *N. tomentosus* (*Nt*) during the first round were provided a second choice, 70% again chose *N. tomentosus*. Proceeding to the right side of Figure 1.2A, 92% of 108 mites originally on *N. tomentosus* chose the same carrier during the first round, and 98% of these made the same choice during the second round. Of the 8% that chose *N. orbicollis* during the first round, 88% made the same choice during the second round.

This experiment, which we have repeated several times at KBS, illustrates two important points. First, virtually all *P. carabi* at KBS appear to have a strong preference for one beetle species or the other. Second, having a preference for a carrier species does not guarantee that a mite will be associated with that species. Despite strong preferences, approximately 10% of *P. carabi* taken from beetles in pitfall traps are found on the carrier species that they do not prefer.

It is important to emphasize that *P. carabi* will readily breed in association with its non-preferred carrier species. Wilson (1982) showed that when *P. carabi*

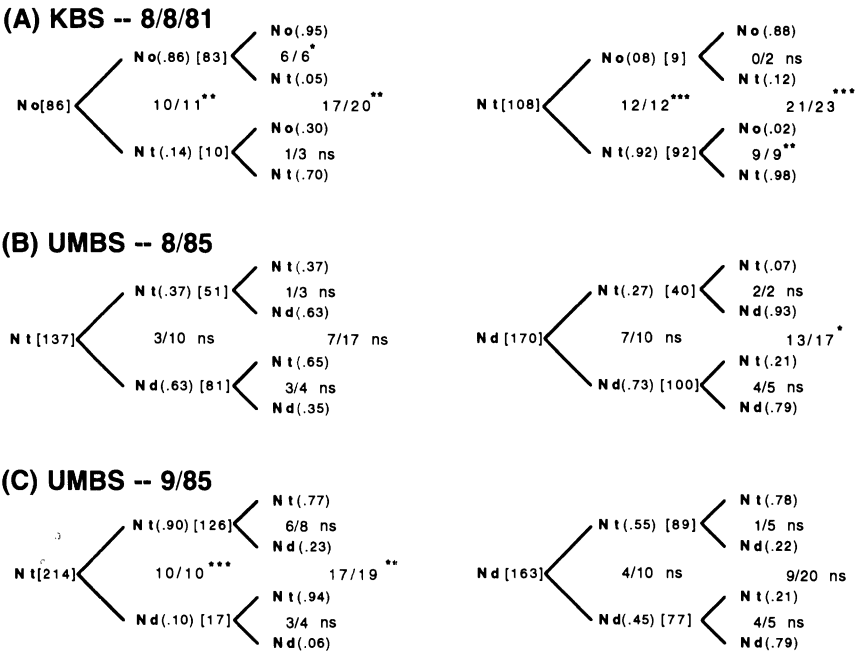


Figure 1.2. Preference tests of *Poecilochirus carabi* for different beetle species. Each pair of branches refers to a set of pairwise tests, with the number of pre-trial mites (found on the beetle species) represented in brackets at each node of the bifurcation. The decimal in parentheses at the end of each bifurcation is the proportion of all mites found on that beetle species in that set of trials. The fraction given, located to the lower right of each bifurcation, is the proportion of all trials "won" by the species at the node. A "win" occurred when one species carried more mites at the end of the trial than the other species (**$p < 0.01$, ***$p < 0.001$, for Chi-square test with the expectation of an equal number of trials won by each species). *Nd, Nt* and *No* refer to the beetle species; *Nicrophorus defodiens, Nicrophorus tomentosus* and *Nicrophorus orbicollis*, respectively (From Brown and Wilson 1992). A) Mites and beetles from KBS, tested on August 8, 1981. B) Mites and beetles from UMBS, tested on August 11, 1985. C) Mites and beetles from UMBS, tested on September 9, 1985.

from *N. orbicollis* are raised in association with *N. tomentosus*, their progeny still prefer *N. orbicollis* (and vice versa), demonstrating that carrier preference is genetically encoded. More recently, Brown and Wilson (1992) demonstrated that the preference types will not interbreed. Finally, the preference types can be discriminated morphologically based on both general body size and setal lengths (Fig. 1.3). There seems to be little doubt that *P. carabi* at KBS consists of at least two good biological species. We shall refer to the KBS mites as the *orbicollis*-specialist and the *tomentosus*-specialist, after their preferred host species.

Why should two closely related species of *Poecilochirus* coexist on *Nicropho-*

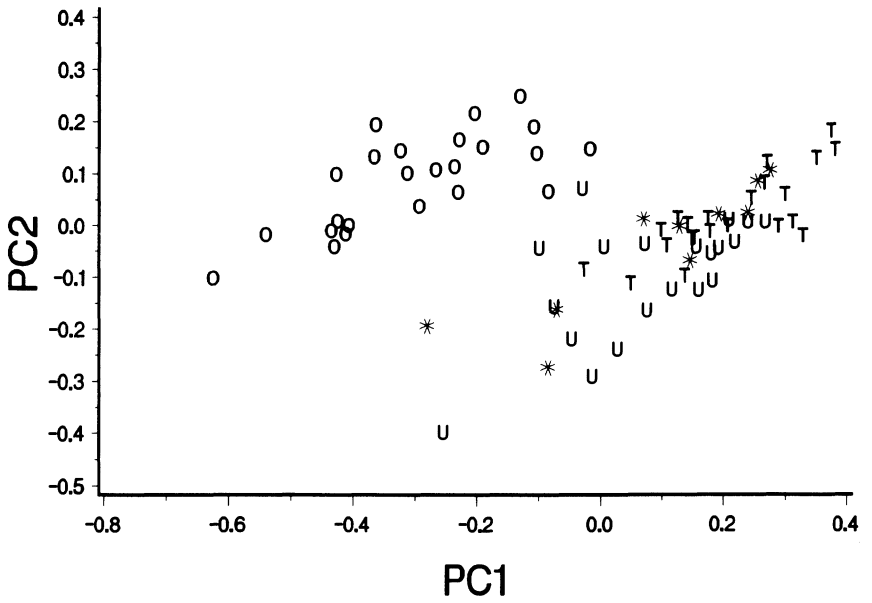


Figure 1.3. Principal components analysis of 19 log-transformed setal lengths of *Poecilochirus carabi* from the Michigan study sites. PC2 is plotted against PC1 for the KBS mites, the *orbicollis*-specialist (*O*) and the *tomentosus*-specialist (*T*), and UMBS mites found on several species (*U*). The few mites that were found on *Nicrophorus orbicollis* beetles at UMBS are plotted with an "*" (From Brown and Wilson 1992).

rus beetles at KBS? Presumably a trade-off exists such that breeding in association with the different carrier species require different adaptations. Our reproductive success experiments tend to confirm this intuition (Table 1.1). The *tomentosus*-specialist produces almost twice as many offspring in association with its preferred carrier (*N. tomentosus*) than with its nonpreferred carrier (*N. orbicollis*). The *orbicollis*-specialist, in contrast, produces equal numbers of offspring in association with either carrier and by this criterion alone should not exhibit a preference.

The pattern of dispersal of the offspring, however, depends greatly on carrier species. In association with *N. orbicollis*, the *orbicollis*-specialist offspring disperse on the male parent, the female parent, and the offspring in roughly equal proportions. In association with *N. tomentosus*, virtually all of the offspring attempt to disperse on the female parent. Since the female parent cannot possibly carry all the *P. carabi* that emerge from the carcass (frequently in excess of 1000 mites), the majority will fall off the beetle when it takes flight. Thus, despite the equal production of offspring on both carriers, the *orbicollis*-specialist more effectively disperses its offspring in association with its preferred carrier. This should result in total fitness differences across the two host species.

Although the differences between the two *P. carabi* species in Table 1.1

Table 1.1. Reproductive success experiments using KBS mites and beetles. Shown are the means for each behavioral specialist raised on both beetle species at KBS. Adapted from Brown and Wilson (1992).

	Orbicollis-specialist Number of Offspring		*Tomentosus*-specialist Number of Offspring	
Beetle species	N	Mean	N	Mean
N. orbicollis				
% on Males		0.21		0.46
% on Females		0.47		0.33
% on Offspring		0.33		0.21
Total (Per Capita)	**15**	**27.10**	**14**	**27.10**
N. tomentosus				
% on Males		0.00		0.06
% on Females		1.00		0.84
% on Offspring		0.00		0.09
Total (Per Capita)	**16**	**27.60**	**17**	**42.40**

probably reflects a number of trade-offs, the one that we have documented most thoroughly originates with the social behavior of the beetles. The male beetle parent leaves the burial chamber slightly before the female in both species, but for *N. orbicollis* the median leaving-times are 9 and 13 days respectively while for *N. tomentosus* they are five and nine days (Fig. 7 in Brown and Wilson 1992). In trials performed in isolation from beetle hosts, *tomentosus*-specialists were shown to complete an entire generation (deutonymph to deutonymph) in six days, while *orbicollis*-specialists took 8.3 days (Wilcoxon $p < 0.001$). The developmental rates of the *orbicollis*-specialist and *tomentosus*-specialist are synchronized with the male leaving-time of their preferred carrier. Since the male represents the earliest dispersal agent to future carcasses, it is obviously important for *P. carabi* to develop fast enough to catch the first ride.

Despite this striking synchrony between generation time and male dispersal, what is the evidence that the differences in behavior between the two host species represent a trade-off for mites? In other words, does lack of synchronization of generation time with male dispersal result in a decrease in fitness? This is clearly the case for *orbicollis*-specialist mites as we have argued above. These mites suffer a loss in fitness when in association with *N. tomentosus* due to their long generation times; lack of synchronization in generation time results in a dispersal pattern that assures lower survivorship during dispersal.

The connection between synchrony and fitness is not as clear for the *tomentosus*-specialist; this specialist produces a lower number of offspring when in association with its non-preferred host (Table 1.1), but this is not obviously directly related to its short generation time. We do know that these mites are ready to disperse after six days, but must then wait several days before dispersing

with *N. orbicollis* males. It is possible that this waiting period results in mortality for mites embarked on a beetle that is still active in the burial chamber.

In summary, these results suggest that the two beetle species represent habitats that differ in their optima for mite generation time. Synchronization of generation time with male dispersal in one beetle species results in a fitness decrease in terms of reproductive success or survivorship during dispersal when reproducing with the other available beetle species (the non-preferred host). These types of trade-offs are necessary if specialization is to evolve within a species, or if multiple specialist species are to coexist in the community.

The reproductive success experiments provide some further information on the behavioral sophistication of these mites. When the *orbicollis*-specialist is raised on its non-preferred host, all offspring attempt to disperse on the female-parent beetle. A slow developmental rate explains why the *orbicollis*-specialist does not disperse on male *N. tomentosus*. But, why does it also fail to disperse on the offspring? The most probable answer is that, by following a *N. tomentosus* larva into its pupal chamber, the *orbicollis*-specialist foregoes any chance of reproduction until mid-summer of the following year. By contrast, if the *orbicollis*-specialist can successfully disperse on the female-parent beetle and transfer to its preferred carrier, then reproduction can commence in mid-spring. Uncertain dispersal and early reproduction may be more adaptive than certain dispersal and delayed reproduction.

Our studies at KBS have focused on *N. orbicollis* and *N. tomentosus*. Our data for *N. sayi* is more limited because this species is relatively uncommon at KBS. *N. sayi* does not appear to have a third *P. carabi* morph, but rather is utilized primarily by the *orbicollis*-specialist, as one would expect from the fact that *N. sayi* parents remain even longer with their brood than do *N. orbicollis* parents (Brown and Wilson 1992).

4.2 II. University of Michigan Biological Station (UMBS)

As previously stated, UMBS differs from KBS primarily in the addition of a fourth *Nicrophorus* species, the competitively subordinate *N. defodiens*. This species is almost identical to *N. tomentosus* in parental dispersal (average leaving-times of the male and female parent are five and nine days for *N. tomentosus* and six and nine days for *N. defodiens*; Fig. 7 in Brown and Wilson 1992), so it is interesting to know if any other trade-offs allow a *P. carabi* "*defodiens*-specialist" to coexist with the *tomentosus*-specialist at UMBS. Figure 1.2B (UMBS –August) shows the results of a two-round choice experiment performed at UMBS on August 11, 1987, using *P. carabi* from *N. tomentosus* and *N. defodiens*.

Starting from the left side of Figure 1.2B, 137 mites attached to *N. tomentosus* were divided into 10 tubs and provided a choice between *N. tomentosus* and *N. defodiens*. Only 37% chose *N. tomentosus*. When these were offered another choice, again only 37% chose *N. tomentosus*. When the remaining 63% of the

mites that chose *N. defodiens* during the first round were tested again, only 35% made the same choice. When analyzed conservatively at the tub level, mites attached to *N. tomentosus* at the beginning of the experiment display little or no preference for the two carrier species.

Proceeding to the right side of Figure 1.2B, 73% of 170 mites originally on *N. defodiens* chose the same carrier during the first round, and 79% of these made the same choice during the second round. Of the 27% that chose *N. tomentosus* during the first round, only 21% made the same choice during the second round. These results suggest that mites attached to *N. defodiens* at the beginning of the experiment display a moderate preference for *N. defodiens* that is significant at the tub level.

Figure 1.2C (UMBS - September) shows that when the same experiment is performed one month later at UMBS, the situation is reversed. Mites initially on *N. tomentosus* exhibit a strong preference while mites initially on *N. defodiens* are either indifferent or perhaps display a mix of preferences that segregate during the second round of the experiment.

A seasonal change in a measure of preference can occur in two ways; individual mites can change their preference, or the relative abundance of mites with fixed preferences can change. Fortunately, these two explanations lead to very different predictions. If individual mites had fixed preferences, we would expect the proportion favoring *N. defodiens* to increase from August to September, since *N. defodiens* breeds during this period while *N. tomentosus* does not. The fact that *P. carabi* favors *N. tomentosus* at the beginning of its breeding period strongly suggests that individual mites can adaptively change their preferences.

In summary, these experiments demonstrate a complex pattern in which overall preference shifts from *N. defodiens* to *N. tomentosus* seasonally, but a spectrum of preferences also exists at any one time. There is no hint of the extreme behavioral types associated with *N. orbicollis* and *N. tomentosus* at KBS, so we provisionally conclude that *N. tomentosus* and *N. defodiens* at UMBS are shared by a single *P. carabi* species.

Although the addition of *N. defodiens* to the *Nicrophorus* community at UMBS has not resulted in a *P. carabi* "*defodiens*-specialist," it is associated with the elimination of the *orbicollis*-specialist from the mite community, despite the fact that *N. orbicollis* remains abundant and competitively dominant at UMBS. Numerous preference experiments show that *N. orbicollis* is always rejected by UMBS mites in favor of *N. tomentosus* and/or *N. defodiens*, regardless of the season (Brown and Wilson 1992).

This result, although mystifying at first, can probably be explained by the asymmetrical nature of competition among the beetles. A very large proportion of the carcasses utilized by *N. orbicollis* at UMBS (up to 70%) have been previously discovered by *N. defodiens*, many of whose mites have already disembarked. Thus, the first *P. carabi* to arrive at a carcass are usually carried by *N. defodiens*, even when *N. orbicollis* is the ultimate beetle victor. From the stand-

point of *P. carabi*, to prefer *N. orbicollis* is usually to be a latecomer. If arriving first at a carcass provides a competitive advantage, it is adaptive for *P. carabi* to prefer *N. defodiens*.

In addition, it can be shown theoretically that a competitively inferior species can actually displace a competitively superior species if its numbers are supplemented by a sufficiently large influx of dispersers from another habitat (MacArthur 1972). Asymmetrical competition among the beetles provides just such an influx of *P. carabi* from the *N. defodiens* into the *N. orbicollis* "habitat." In this fashion the *orbicollis*-specialist could be excluded at UMBS by a morph that is better adapted to *N. defodiens*, even while remaining competitively superior on *N. orbicollis*. The importance of the presence of *N. defodiens* in the presence of the *orbicollis*-specialist mite is indicated by data from sites between UMBS and KBS (see below).

Finally, *N. sayi* at UMBS is avoided by all *P. carabi* throughout the late spring and summer but becomes highly preferred in late fall (Brown and Wilson 1992). This is obviously an appropriate response to a carrier species that is reproductively inactive during the summer but the first to breed in spring, and provides another example of adaptive behavioral flexibility in *P. carabi*.

Morphological analysis in general confirms the results of the behavioral experiments. Figure 1.3 plots the PCA scores of 19 setal lengths for mites raised under lab conditions. The two specialists from KBS segregate into two clouds; the beetle species with which mites were raised has no significant effect on this morphological measure (Brown and Wilson 1992). Mites from UMBS, even those few found *N. orbicollis* at this site (indicated by "*"), are significantly different from both KBS specialists, although they more closely resemble the KBS *tomentosus*-specialist. The *orbicollis*-specialist is not found at this site. To summarize, both behavioral and morphological data suggest that *P. carabi* at UMBS is a single species with complex and seasonally changing patterns of preference for carrier species.

4.3 III. The Region Between KBS and UMBS

To further document the relationship between the appearance of *N. defodiens* and the disappearance of the *orbicollis*-specialist mite, beetles were trapped (on July 7, 1988) at six sites spanning the distance between KBS and UMBS. After determining that site number three was close to the southern limit of *N. defodiens*, beetles were trapped along a second transect spanning the distance between site two and four of the original transect on August 8, 1988. This procedure was repeated at three additional sites between UMBS and KBS in August, 1989. For both transects the *P. carabi* on *N. orbicollis* were subject to morphological analysis. Figure 1.4 shows quite clearly that the disappearance of the *orbicollis*-specialist (here indicated by its larger body size) is not a peculiarity of UMBS, but correlates with the rising abundance of *N. defodiens* along a north/south axis.

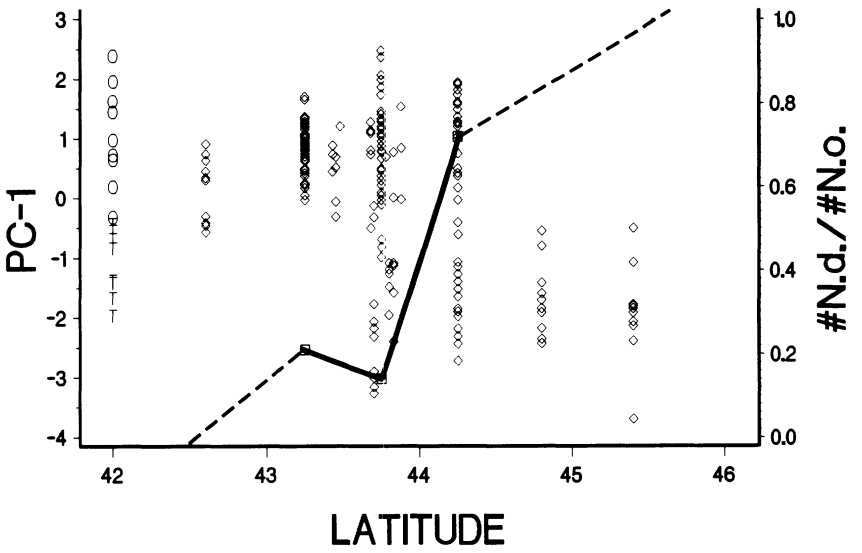


Figure 1.4. Principal components analysis of the size of the sternal shield of mites found on *Nicrophorus orbicollis* beetles across the transect from KBS (South) to UMBS (mites captured in July, 1988 and August, 1989). Plotted at the left are scores for *orbicollis*-(*O*) and *tomentosus*-specialists (*T*) from KBS. Also plotted is the relative density of *Nicrophorus defodiens* (*Nd*) to *Nicrophorus orbicollis* (*No*) individuals in pitfall traps at three sites in the transect in August 1989. The dotted lines connect these relative densities to those reported at KBS and UMBS (Wilson et al. 1984).

5. Discussion

5.1 Ecological Adaptation in Poecilochirus carabi

Poecilochirus carabi is faced with a complex environment in the form of several carrier species that differ in their reproductive phenology, social behavior and competitive interactions. One way that *P. carabi* adapts to this environment is with an impressive degree of behavioral sophistication. Single mites can discriminate between carrier species and can alter their preferences seasonally in ways that enhance their own prospects for reproduction. The KBS *orbicollis*-specialist even appears to distinguish between the immature stages of its carrier species, accepting the pupating larvae of *Nicrophorus orbicollis* but not *N. tomentosus*.

In addition to the behavioral flexibility of individual mites, *P. carabi* also appears to be behaviorally polymorphic, both at KBS and UMBS. In other words, at any one point in time individual mites differ in their preferences for carrier species. At UMBS these differences take the form of some mites preferring a given carrier while other mites remain neutral. At present, we do not know if the behavioral polymorphisms at UMBS have a genetic basis or if carrier preference

correlates with any other traits that adapt mites to their preferred carrier. We only know that the preferences themselves are seasonally labile.

At KBS the behavioral polymorphism takes the form of two specialists with seasonally consistent preferences for *N. orbicollis* and *N. tomentosus*. Furthermore, the specialists are reproductively isolated, morphologically distinct, and have correlated life-history traits that adapt them to their preferred carrier. Here, strong life-history trade-offs across two hosts are associated with the coexistence of two specialists.

Ecologically, the reason that *P. carabi* at KBS and UMBS are so different from each other can be traced to a single beetle species, *N. defodiens*, that appears to alter the complex environment in two ways. First, at UMBS most carcasses found by *N. orbicollis* have been previously buried by *N. defodiens* individuals that carry a large number of *P. carabi*. If they were present, *orbicollis*-specialists at UMBS would have to compete with the large influx of mites that arrive with *N. defodiens*.

Second, mites on *N. orbicollis* have the disadvantage of arriving several hours to several days later than the first arrivals, which might offset the competitive superiority that they otherwise would enjoy. The addition of a beetle species to the community of available hosts has the paradoxical effect of collapsing a two-niche environment into a one-niche environment as far as *P. carabi* is concerned.

This change in the mite community makes an important point about the role of trade-offs in maintaining ecological diversity, namely that trade-offs alone are not sufficient for specialization to evolve or be maintained in the community. Along with natural selection for different trait values in different parts of the environment (i.e. trade-offs), the ability of organisms to select habitats, and the resulting population structure, can have profound influences on the degree of ecological diversity that can evolve or be maintained (Rice 1987, Brown 1989, Diehl and Bush 1989). Figure 1.5 summarizes the aspects of the host community which highly determine these three central factors for these mites.

For example, the constituent beetle species and the local particulars of their parental care behavior will determine whether different values of generation time are selected in association with different hosts, i.e. whether trade-offs in life-history characters across habitats are present. Another example was outlined above in the case of *N. orbicollis* and *N. defodiens* at UMBS. Competitive interactions between beetle species can result in the "involuntary" transfer of mites from one selective environment to another. This weakens the ability of mites to determine their host associations, a condition important in the evolution of host or habitat specialization (Brown 1989). Inability to select habitats also alters the structure of the mite populations, changing the nature of competitive and mating interactions.

In summary, shifts in the host community can profoundly alter the factors that ultimately determine the ecological diversity of the mite community, even to the

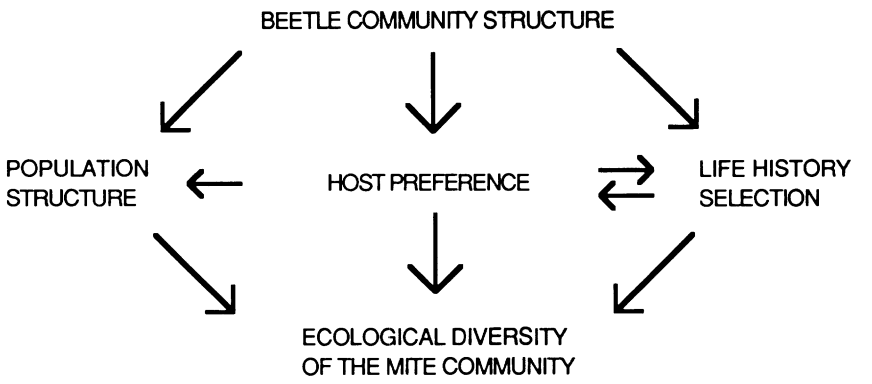


Figure 1.5. Conceptual model of the forces that influence the ecological diversity of a local mite community.

point of eliminating a well-adapted specialist from a community in which its preferred host species is abundant.

5.2 Specialization and Speciation in Poecilochirus carabi

Since *P. carabi* appears to consist of two species at KBS and one species at UMBS, it is interesting to ask how the speciation event occurred. On the one hand, the second species could have arisen allopatrically and then spread into areas that ecologically constitute "two-niche" environments for *P. carabi*. On the other hand, speciation could be the direct outcome of disruptive selection operating within a two-niche environment (Wilson 1982).

We can hardly hope to answer such a complex question with our existing data. Nevertheless, at least two features of *P. carabi* make it interesting from the standpoint of speciation theory. First, some models of sympatric speciation can be described as "microallopatric," in the sense that they require a near-total disruption of gene flow for genetic divergence to occur. The disruption is merely caused by small-scale isolation such as mating on different hosts or breeding at different times of the year (Bush 1975, Rice 1987), rather than by large scale isolation such as a geographical barrier.

The population structure of *P. carabi* clearly does not fit the requirements of these models. Even in their current specialized state, approximately 10% of the specialists at KBS occur on the "wrong" carrier species when taken from pitfall traps (since these traps mimic large carcasses, it is likely that such transfer occurs in nature). Thus, if speciation in *P. carabi* is a local process, it must have occurred in the presence of significant gene flow.

Second, if we expand our scale to include a wider geographical region and more species of *Nicrophorus* beetles, it is possible to envision *P. carabi* as

existing in a mosaic of "one-niche" and "multiple-niche" patches. If species arise allopatrically and then fill the multiple-niche patches of the mosaic by dispersal, we should expect a *P. carabi* species to be more closely related to ecologically similar species from other patches than to coexisting species from the same patch. If speciation is a local process, however, we should find a substantial number of multiple-niche patches in which the coexisting species are most closely related to each other.

To this end, we have initiated a study of *Nicrophorus* beetles and their mites at locations throughout North America and South America. The initial survey indicates a high degree of variation between sites in the local nature of host specialization. Figures 1.6A and 1.7 show one preliminary result from Farmingdale, South Dakota. *N. orbicollis* and *N. tomentosus* were the only species collected and on these grounds alone we might expect to find the two *P. carabi* specialist species, as at KBS.

At the behavioral level, mites on *N. tomentosus* display a moderately strong preference whereas mites on *N. orbicollis* are either indifferent or consist of a mix of specialists (Fig. 1.6A). At the morphological level, mites from *N. orbicollis* that chose *N. orbicollis* are significantly different in setal lengths (though not body size; Brown 1989) from those that chose *N. tomentosus* or those that were originally on *N. tomentosus* (Fig. 1.7; Tables 1.2 and 1.3). Furthermore, this provisional "*orbicollis*-specialist" bears no resemblance morphologically to the *orbicollis*-specialist at KBS, but is similar to the KBS *tomentosus*-specialist (Brown 1989). Although these measurements were performed on field caught individuals with unknown histories, this is a tantalizing suggestion that morpho-

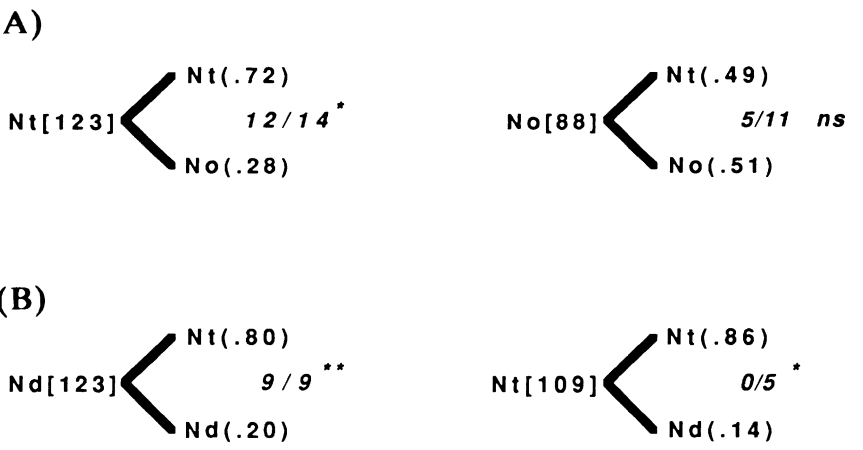


Figure 1.6. Beetle species preference tests using *Poecilochirus carabi* captured in: A) Farmingdale, South Dakota and B) Hill City, South Dakota in July 1988. See Figure 1.2 for an explanation of the symbols.

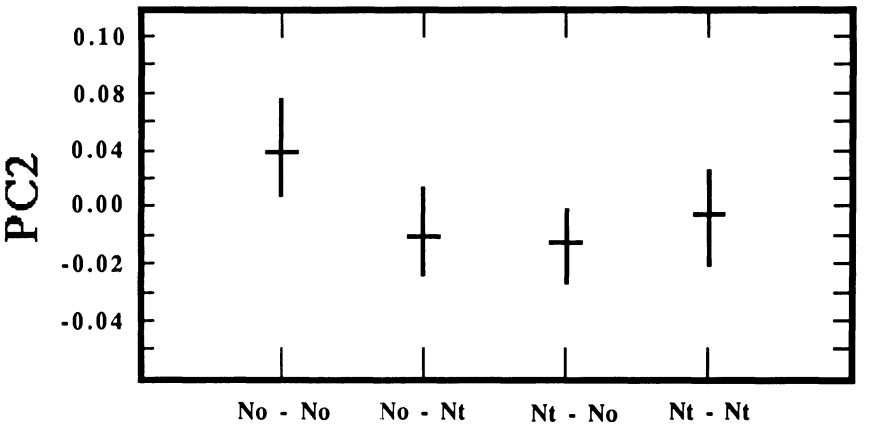


Figure 1.7. A plot of PC2 (from a principal components analysis of dorsal setal lengths of mites from the Farmingdale, South Dakota preference tests) against the results of the choice tests. The mean PC2 ± 1 S.D. is plotted for each behavioral phenotype, defined by the beetle species on which the mite was found (FROM) and the beetle species chosen in the preference trial (CHOSE). *Nt* and *No* refer to *Nicrophorus tomentosus* and *Nicrophorus orbicollis*, respectively.

logical divergence can be a local process and can occur in the presence of substantial gene flow.

Data from other sites outside of Michigan indicate extreme geographical variability in *P. carabi* carrier preference and morphology. In general, our samples from numerous localities show that the *P. carabi* complex does not consist of two morphologically stable species corresponding to the *tomentosus*-specialist and *orbicollis*-specialist at KBS (Brown 1989). For example, at a site near Hill City, South Dakota, members of two beetle species, *N. tomentosus* and *N. defodiens*, were captured in early July. Mites were found on both species, but signifi-

Table 1.2. Correlation of the scores of the first two PCA components (PC1 and PC2) with the eight dorsal podonotal shield setae used in the analyses, and the percent variance explained by the first two components. Analyses are of P. carabi *from Farmingdale, South Dakota.*

	Podonotal Shield Setae								
	*i*3	*i*5	*i*6	*z*2	*z*3	*z*4	*s*3	*s*4	% Variance
PC1	0.82	0.74	0.77	0.84	0.49	0.94	0.85	0.89	0.64
PC2	0.23	−0.40	−0.56	0.34	0.61	−0.04	0.28	0.25	0.16

Table 1.3. Analysis of variance of the scores of the first two principal components, for the eight podonotal shield setae measured on P. carabi *from Farmingdale, South Dakota.* P. carabi *were divided into groups based upon their behavior in choice tests (Fig. 1.6), i.e. the species of* Nicrophorus *upon which they were found (FROM effect) and the species of* Nicrophorus *which they chose in the choice-test (CHOSE effect) (*p < 0.05; **p < 0.01).*

	Source	d.f.	SS	F
PC1	FROM (F)	1	0.007	0.97
	CHOSE (C)	1	0.0004	0.07
	F × C	1	0.004	0.53
	Error	28	0.188	
PC2	FROM (F)	1	0.005	5.55*
	CHOSE (C)	1	0.003	3.59
	F x C	1	0.011	11.50**
	Error	28	0.027	

cantly preferred *N. tomentosus* over *N. defodiens* (Fig. 1.6B). Since these tests were run in early July, presumably when *N. defodiens* are reproducing and *N. tomentosus* are not, one might expect mites to prefer the reproducing beetle species, as they do at UMBS. These results, along with the Farmingdale, South Dakota results, suggest that the nature of mite host association is not predictable based solely on knowledge of the species composition of the host community. The fact that KBS, Michigan and Farmingdale, South Dakota share the same two dominant host species may conceal significant differences in the selective regime associated with each beetle species or the competitive interactions between beetle species.

As outlined above (Fig. 1.5), such aspects of the host community should highly determine the outcome of evolution for specialization in the mites. If beetle traits, such as degree of parental care or reproductive phenology, are themselves geographically variable, the mosaic of "one-niche" and "multiple-niche" localities may not be predictable based on species composition alone. The need for detailed study of both mite and host communities is obvious.

Finally, Müller and Schwarz (1990) have documented a situation for *P. carabi* on *N. vespillo* and *N. vespilloides* in Germany that is remarkably similar to the situation at KBS. *P. carabi* exists as two reproductively isolated forms, with differences in developmental times that match the leaving times of their preferred carriers. In this case, however, the two beetle species are segregated primarily by habitat preferences (forest and meadow, respectively), rather than seasonally. It will be interesting to see if the two *P. carabi* species in Germany conform morphologically to the species at KBS.

If morphological divergence and speciation in *P. carabi* are local processes that depend on the underlying beetle community, we might expect the taxonomic studies based on morphological variation (particularly size-related characters that

may co-vary with life-history variation) of this group to be problematic. This is indeed the case. The more recent taxonomic treatments of the genus (e.g. Hyatt 1980) fault earlier workers for using characters to discriminate species that vary "within samples" (a single "sample" potentially includes mites from several sympatric beetle species). The result is a tendency to subsume many named species in this genus into a single cosmopolitan species, *P. carabi* (Hyatt 1980).

Our studies suggest that "variation within a sample" may in fact reflect the existence of closely related specialist species. However, these two species, along with their typical morphological traits, may not be found everywhere, even when the same host species is used. If divergence is in fact a local process that relies on the conditions set up by the local host community, morphological differentiation may proceed on different characters at different locations, or intraspecific variation at one site might show up as interspecific variation at another. It seems unlikely that any taxonomic treatment will succeed unless it pays close attention to the complex environment in which *P. carabi* resides and the ability of these mites to adapt to these local conditions.

Acknowledgments

The authors wish to thank the members of the KBS Ecology and Evolution group for helpful advice and discussions of this work. D. Johnston and M. L. Moraza first identified morphological variation between specialist mites. Thanks to W. Knollenberg for assistance. This work was supported by NSF BSR #8320457 and a NSF Graduate Fellowship awarded to JMB. This is contribution #704 of the Kellogg Biological Station.

References

Bartlett, J. 1987. Filial cannibalism in burying beetles. *Behav. Ecol. Sociobiol.* 21:179–183.

Brown, J. M. 1989. *Specialization in Poecilochirus carabi, a phoretic mite*. Ph.D. thesis, Michigan State Univ., East Lansing, MI.

Brown, J. M. and D. S. Wilson. 1992. Local specialization of phoretic mites on sympatric carrion beetle hosts. *Ecology* 73:463–478.

Bush, G. L. 1975. Modes of animal speciation. *Ann. Rev. Ecol. Syst.* 6:339–364.

Diehl, S. R. and G. L. Bush. 1989. The role of habitat preference in adaptation and speciation. In: *Speciation and its Consequences* (D. Otte and J. Endler eds.). Sinauer Assoc., Sunderland, MA. Pp. 345–365.

Farish, D. J. and R. C. Axtell. 1971. Phoresy redefined and examined in *Macrocheles muscaedomesticae* (Acarina: Macrochelidae). *Acarologia* 8:16–29.

Futuyma, D. J. and G. Moreno. 1988. The evolution of ecological specialization. *Ann. Rev. Ecol. Syst.* 19:207–33.

Hyatt, K. H. 1980. Mites of the subfamily Parasitinae (Mesostigmata: Parasitidae) in the British Isles. *Bull. Br. Mus. (Nat. Hist.) Zool.* 38:237–378.

Luckinbill, L. S., T. A. Grudzien, S. Rhine, and G. Weisman. 1989. The genetic basis of adaptation to selection for longevity in *Drosophila melanogaster*. *Evol. Ecol.* 3:31–40.

MacArthur, M. L. 1972. *Geographical Ecology*. Harper and Row, NY. 269 pp.

Müller, J. K. 1987. Replacement of a lost clutch: a strategy for optimal resource utilization in *Necrophorus vespilloides* (Coleoptera: Silphidae). *Ethology* 76:74–80.

Müller, J. K. and A-K. Eggert. 1989. Paternity assurance by "helpful" males: adaptations to sperm competition in burying beetles. *Behav. Ecol. Sociobiol.* 24:245–249.

Müller, J. K. and H. H. Shwarz. 1990. Differences in carrier preference and evidence of reproductive isolation between mites of *Poecilochirus carabi* (Acari: Parasitidae) living phoretically on two sympatric *Necrophorus* species (Coleoptera, Silphidae). *Zool. Jahrb. Syst.* 117:23–30.

Peck, S. B. and M. M. Kaulbars. 1987. A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera: Silphidae) of the conterminous United States. *Proc. Entomol. Soc. Ont.* 118:47–81.

Rice, W. R. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evol. Ecol.* 1:301–314.

SAS Institute Inc. 1985. *SAS Users Guide-Statistics*, Version 5. SAS Institute, Cary, NC.

Scott, M. P. and James F. A. Traniello. 1987. Behavioural cues trigger ovarian development in the burying beetle, *Nicrophorus tomentosus*. *J. Insect Physiol.* 33:693–696.

Service, P. M. 1985. Physiological mechanisms of increased stress resistance in *Drosophila melanogaster*. *Physiol. Zool.* 58:380–9.

Springett, B. P. 1968. Aspects of the relationship between burying beetles, *Necrophorus* spp. and the mites, *Poecilochirus necrophori*, Vitz. *J. Anim. Ecol.* 37:417–424.

Trumbo, S. 1988. *The ecology of parental care in burying beetles (Silphidae: Necrophorus)*. Ph.D. thesis, North Carolina State Univ., Raleigh, NC.

Wilson, D. S. 1982. Genetic polymorphism for carrier preference in a phoretic mite. *Ann. Entomol. Soc. Am.* 75:293–296.

Wilson, D. S. 1983. The effect of population structure on the evolution of mutualism: a field test involving burying beetles and their phoretic mites. *Am. Nat.* 121:851–870.

Wilson, D. S. and W. G. Knollenberg. 1987. Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites. *Evol. Ecol.* 1:139–159.

Wilson, D. S., W. G. Knollenberg and J. Fudge. 1984. Species packing and temperature dependent competition among burying beetles. *Ecol. Entomol.* 9:205–216.

Wilson, D. S. and M. Turelli. 1986. Stable underdominance and the evolutionary invasion of empty niches. *Am. Nat.* 127:835–850.

Wise, G. U., M. K. Hennessy and R. C. Axtell. 1988. A new species of manure-inhabiting mite in the genus *Poecilochirus* (Acari: Mesostigmata: Parasitidae) predacious on house fly eggs and larvae. *Ann. Entomol. Soc. Am.* 81:209–224.

Yoder, W. A. 1972. *Acarina (Arthropoda: Arachnida) associated with selected Michigan Silphidae (Coleoptera)*. Ph.D. thesis, Michigan State Univ., East Lansing, MI.

2

Life-History Patterns of Hummingbird Flower Mites in Relation to Host Phenology and Morphology

Robert K. Colwell and Shahid Naeem

CONTENTS

1. Introduction

Hummingbirds and the flowers that they pollinate provide an unambiguous example of mutualism. In many cases the associations present clear evidence of coevolution, in the strictest sense of the term (e.g. Colwell 1989). Certain species of mites (hummingbird flower mites) exploit this bird-plant mutualism, with known examples throughout most of the geographic range of the hummingbirds (Trochilidae), which spans the New World from Alaska to Tierra del Fuego (Colwell 1985). This ecologically-defined group of gamasid mites (all within the Ascidae) encompasses all described species of the genus *Rhinoseius*, which inhabit a zone from northern California to central Chile, plus a diverse tropical

lineage within the genus *Proctolaelaps*. These two ecologically similar lineages have spawned an impressive adaptive radiation of species (Colwell 1979).

To date, only 46 species of hummingbird flower mites have been described (Baker and Yunker 1964; Dusbábek and Černý 1970; Hunter 1972; Fain et al. 1977a, 1977b; Flechtmann and Johnston 1978; Hyland et al. 1978; Colwell and Naeem 1979; Fain and Hyland 1980; Micherdzinski and Lukoschus 1980; Zamudio 1985; OConnor et al. 1991). Additional specimens are currently under study that represent collections from 50 hummingbird species and over 100 plant taxa (17 different families). Moreover, many geographical areas (including most of the Amazon) remain entirely unexplored for hummingbird flower mites.

Hummingbird flower mites feed and mate within the floral corolla, and females lay their eggs on the host plant. The ontogeny begins with a brief egg stage, followed by a six-legged larva, succeeded by an eight-legged protonymph, a deutonymphal stage, and then adult males and females. No diapause is known to occur among these species, and generation time is about a week (Colwell 1973, Dobkin 1984). All stages feed on nectar and later stages include pollen in their diet as well.

Although mites move freely on foot among newly opened flowers within an inflorescence and rest in refuges beneath bracts or bud-clusters of that inflorescence (Dobkin 1984), movement among inflorescences or plants is almost exclusively by hitch-hiking on hummingbirds (Colwell et al. 1974). The mites ride within the nasal cavity of these birds, but they are not parasitic and have no detectable effect on the birds under normal densities (1–15 mites per bird)—a clear case of phoresy (Athias-Binche 1991).

In this chapter, we will explore the role that the host plant plays in the evolution of the life history traits of hummingbird flower mites. We will show that the seasonal timing of flowering profoundly affects patterns of host affiliation, whereas daily flowering patterns affect the evolution of mite behavior. The size of an inflorescence and its phenology play key roles in the population growth and dispersal of these mites. Floral morphology affects mite body size and local breeding-group size, which in turn lead to adaptive differences among species in both the sex ratio of mites within flowers and the sex ratio of dispersers on hummingbirds.

2. Effects of Host-Plant Phenology on Hummingbird Flower Mites

2.1 Adaptations of Mites to Seasonal Flowering

The local species richness of hummingbird flower mites ranges from a single species, at the latitude of California or central Chile, to some 15 sympatric species in lowland tropical forests, such as the Arima Valley of Trinidad (Colwell 1986a). The annual phenology of plants largely determines patterns of host-plant species used by hummingbird flower mites. Each mite species depends upon a clearly

delimited host-plant repertoire of one to several species of hummingbird-pollinated plants. Monophagy is the rule for mites whose host produces flowers all year round—a common flowering pattern in some parts of the wet lowland tropics. In the Arima Valley of Trinidad, for example, 11 of the 15 sympatric hummingbird flower mite species (for which we have adequate data) are monophagous. Each has a single host-plant species that flowers throughout the year (Colwell 1986a), although there are often distinct flowering peaks and lags (Feinsinger et al. 1982). Since hummingbird flower mites have no diapause stage, monophagous species can exist only on such reliable host-plant species.

Where flowering is seasonal (in tropical montane, subtropical, and temperate habitats) hummingbird flower mites are almost exclusively polyphagous and follow an annual cycle of host shifts. As flowering wanes in one host-plant species, they move onto another just coming into bloom. For these "sequential specialists," the annual repertoire of movements is usually tied to hummingbird visitors to these plants, which have the same shifts.

A less common expression of polyphagy in hummingbird flower mites relies on the exploitation of one or two "home base" host-plant species that flower year-round and the additional utilization of one or more secondary hosts that have a brief flowering season. Examples include *Proctolaelaps certator* in Trinidad, and *Rhinoseius colwelli* and *R. richardsoni* at Cerro de la Muerte in the Costa Rican highlands (Colwell 1973, 1983).

Among polyphagous species, host-plant utilization appears to be largely uncorrelated with host-plant phylogeny. *R. chiriquensis* from Monteverde, Costa Rica, for example, occupies five sequential hosts that belong to four different plant orders. *R. epoecus*, which travels on migrant California hummingbirds, expresses a variation on the sequential specialist theme. It has summer host plants in California, and shifts between winter host plants and summer ones, in different plant families, in west-central Mexico (Colwell and Naeem 1979). In the case of monophagous mites, cospeciation in response to the evolutionary divergence of their host plants remains a possibility. An ongoing investigation seeks to explore the phylogenetic relationships of the mites in relation to the phylogenetic relationships of their host plants to evaluate this possibility.

Most host-plant species support only a single species of hummingbird flower mite, but a few cases of "host sharing" by two species are known. In these cases, the role of host phenology is doubly evident. In virtually all known cases of host sharing, the two species involved have identical host repertoires, reflecting independent evolutionary responses to host phenology. We have documented cases of monophagous pairs (e.g. *P. contumex* and *R. uniformis* [Fig. 2.1] share the plant *Cephaelis muscosa* in Trinidad) as well as polyphagous pairs (*P. certator* and *R. klepticos* both share two species of *Heliconia* in Trinidad) (Colwell 1986a).

Like these two examples, all other known cases of regular host sharing also involve a species of the genus *Rhinoseius* and a species of genus *Proctolaelaps*, never two species of the same genus. Host sharing is a key piece of evidence in

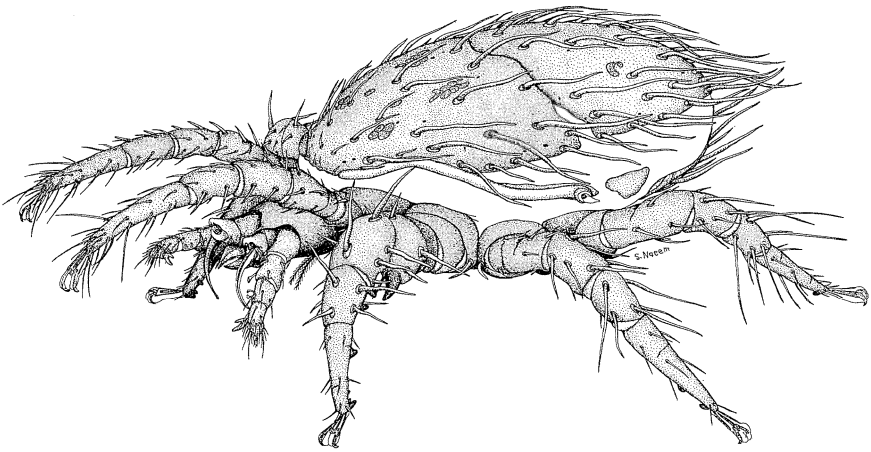


Figure 2.1. Hummingbird flower mite, a male *Rhinoseius uniformis* (Gamasina: Ascidae) from Trinidad, W.I. This species inhabits the flowers of the plant *Cephaelis muscosa* (Rubiaceae) and travels between inflorescences primarily on the hummingbird *Amazilia tobaci*. Drawing and copyright by Shahid Naeem.

support of the hypothesis that the host range is narrowed and that host fidelity is amplified in these mites by selection for mate-finding, using the host plant as a congregation cue (Colwell 1986a, 1986b). The constraint that host sharers must be *non*congeners is explained by the considerable differences observed in courtship behavior and morphology between genera. According to this hypothesis, congeners must use different host plants as mate-finding cues to avoid accidental matings.

In contrast to the strong fidelity that mites have for particular host-plant species, their use of hummingbirds for dispersal appears to be entirely opportunistic. An individual hummingbird, regardless of species, usually carries a sampling of mites from all the host plant species the bird has recently visited. The passenger manifest sometimes includes as many as five mite species. Yet each mite disembarks from the bird only at flowers of the preferred plant species. Behavioral tests show that mites prefer the nectar of their usual host-plant species over nectar of host plants characteristic of sympatric hummingbird flower mite species, or a plain sugar solution (the control) (Heyneman et al. 1991).

2.2 Behavioral Adaptations of Mites to the Phenology of Individual Flowers

Among plant species, individual floral longevity generally tends to increase with both altitude and latitude (Stratton 1989). Flowers utilized by hummingbird flower mites also vary in the period of time they remain in good condition and continue to produce nectar. Depending on plant species, some flowers last less than a day whereas others may persist for more than a week. In the lowland tropics, very few hummingbird-pollinated flowers last more than a single day (Feinsinger et al. 1982, Primack 1985).

Floral longevity profoundly affects the lives of hummingbird flower mites. Behavioral differences among mite species, correlated with longevity, appear to be clearly adaptive. For example, at Cerro de la Muerte in Costa Rica (3100 m), *R. colwelli* completes its entire life cycle within flowers of two species of *Centropogon* (Lobeliaceae). These protandrous flowers produce nectar for more than a week, as they mature from the staminate to the pistillate stage. *R. colwelli* lays its eggs in communal clusters inside the base of the floral tube, where the eggs are bathed in nectar. The eggs require 2–3 days to hatch (Colwell 1973). In lowland Trinidad, the only common plant with flowers that persist for more than a day is another species of *Centropogon*. The reproductive behavior of its resident mite, *P. glaucis*, is identical to that of *R. colwelli*, even though it belongs to a different mite genus.

In contrast with the persistent flowers of *Centropogon*, some hummingbird-pollinated plants in the tropics flower before dawn and by early afternoon not only cease producing nectar, but actually shed their flowers. Mite species affiliated with these plants clearly would not do well to lay their eggs in these flowers—and indeed they do not.

In Trinidad, Dobkin (1984, 1990) has studied *R. trinitatis*, which inhabits the flowers of *Heliconia hirsuta* (Heliconiaceae). In the morning hours the flowers teem with mites, but none can be found in the same flowers later when they fall from the plant, almost synchronously, between 1400 and 1500 h. These mites retreat to cincinnal bracts of *H. hirsuta* to lay their eggs and to await the opening of fresh flowers to feed on the following morning.

The plant *H. psittacorum*, home of *P. phaethornis* in Trinidad, also drops all open flowers each afternoon, but not before the mites abandon the flowers for the safety of the inflorescence bracts. When Dobkin (1984) introduced an "alien" *Proctolaelaps* species (*P. certator*, which had no historical association with *H. psittacorum)* into the flowers of this *Heliconia*, the aliens failed to leave the flower before excision and ultimately perished. The flowers of the four plant species that *P. certator* normally inhabits (Colwell 1986a) all remain on the plant, even beyond pollination and wilting. The behavior of *P. phaethornis* permits it to exploit one-day, deciduous flowers, while the behavior or *P. certator* makes sense in context of the persistent flowers of its own host plant.

In Costa Rica, we have studied in detail the behavior of *P. kirmsei*, which inhabits flowers of *Hamelia patens* (Rubiaceae). In this plant, the tubular flowers begin to open at about 0100 h. Mites that had been waiting in groups in the axils of the cymose inflorescence rush into the slowly enlarging aperture at the tip of the flower as soon as it is wide enough. They immediately begin burrowing into the anthers to feed on pollen grains, while dramatically increasing the level of social interaction. Most matings take place within the flowers before dawn, as nectar begins to flow and hummingbirds begin to visit. By noon, the flowers are easily dislodged from the plant and many fall to the ground, but by then the mites have left the flowers to return to their staging areas in the axils of the inflorescence, or beneath the first pairs of leaves, where they lay their eggs (Colwell 1985).

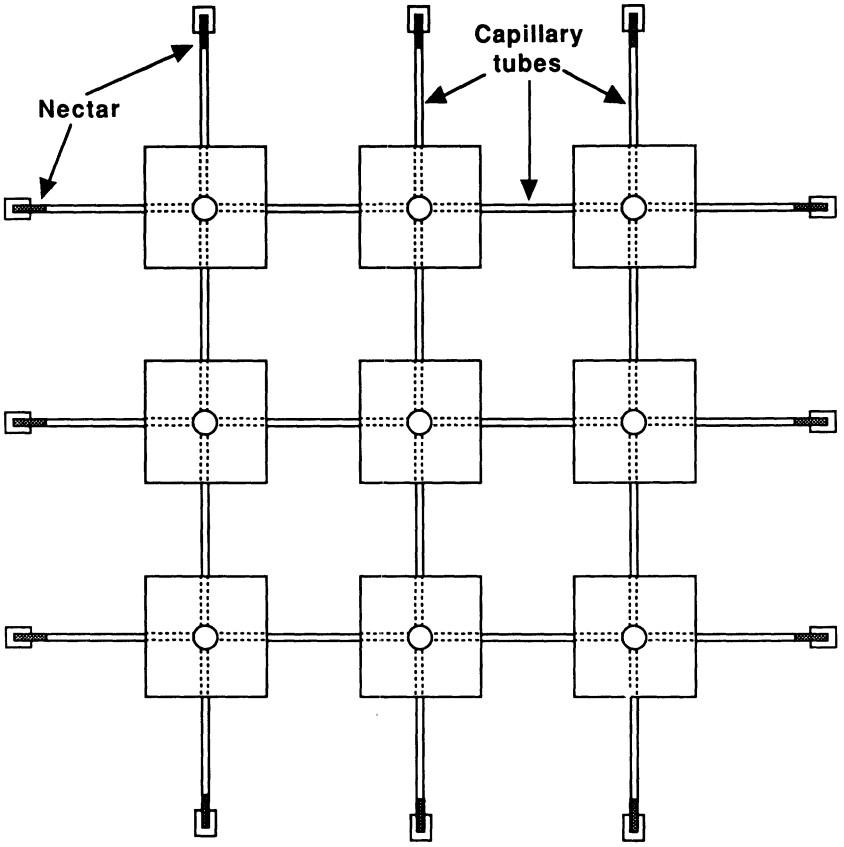
Remarkably, *P. kirmsei* repeated the same temporal pattern of behavior in a completely artificial "habitat" (Fig. 2.2A) in a series of experiments conducted in a screened laboratory at La Selva Biological Station in Costa Rica, under ambient temperature and light conditions. This apparatus was constructed of a lattice of intersecting capillary tubes representing the "inflorescence." Projecting outer tubes represented the "flowers," with fresh, virgin nectar from *H. patens* in their tips; all other tubes were dry. *P. kirmsei*, placed in the outer ("flower") tubes at the beginning of an experiment, initially moved freely throughout the lattice. But mites tended to return to the "flower" tubes at about the same time of night (0100–0700 h) that the flowers of *H. patens* were opening outdoors. Later, in the middle of the day, they moved back out of the "flower" tubes into the lattice as the flowers began to fall from the plants outdoors, even though plenty of nectar remained in the capillary tubes (Fig. 2.2B).

2.3 The Role of Host Phenology in Mite Population Growth and Regulation

The rate at which an inflorescence produces flowers varies greatly among plant species. Most plants pollinated by hummingbirds in the wet tropics produce one or two flowers per inflorescence each day. However, the "lifetime" of any single inflorescence usually spans a few weeks and sometimes much longer. Especially in plants pollinated by circuit-foraging hummingbirds ("trapliners," see Feinsinger and Colwell 1978), an individual plant often produces only one flowering inflorescence at a time. Some inflorescences, such as those of certain *Costus* and *Heliconia* species, may flower for an entire year. In contrast, plants pollinated by territorial hummingbirds tend to have many inflorescences in flower at once, each producing one or a few flowers per day over several weeks.

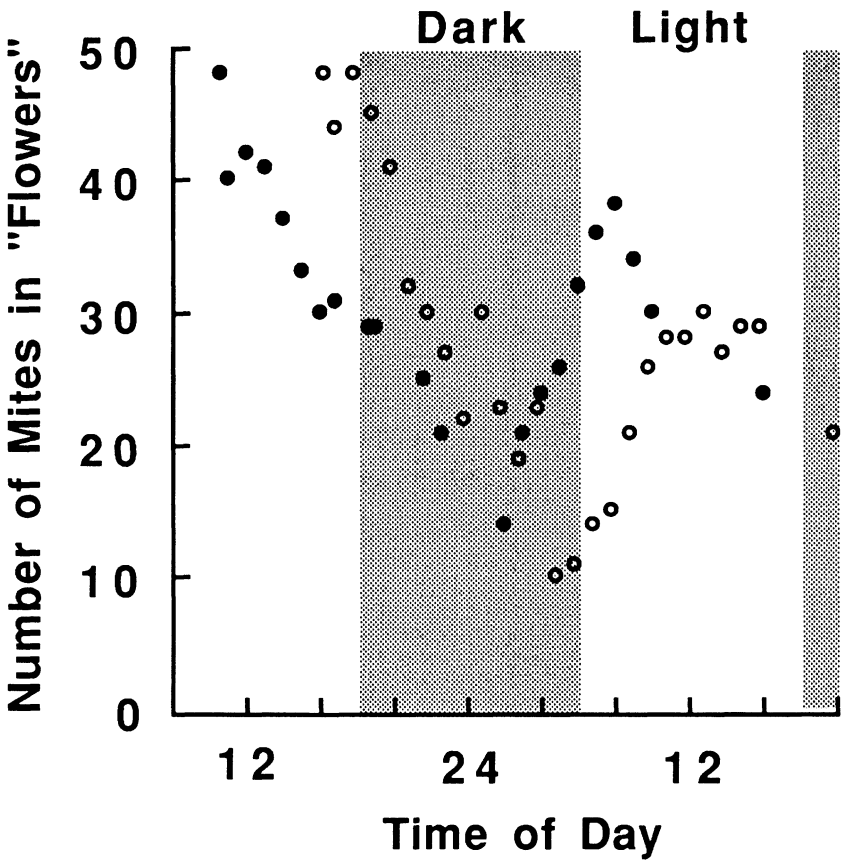
In all cases we have studied, it is clear from observations and experiments that mites move freely (on foot) between successively or simultaneously open flowers of the same inflorescence. Phoresy on hummingbirds is the general rule for movement among inflorescences within a plant, and a necessity for movement among plants. Based on 90 individual hummingbirds representing nine hummingbird species in Trinidad, the number of hummingbird flower mites apparently averages fewer than five per bird (range 0–15). In contrast, the total number of mites collected from all the flowers of an individual hummingbird's exclusive territory or on its foraging circuit would be 2–4 orders of magnitude greater than the mean number of mites the bird carries at any given moment. The inescapable conclusion is that dispersal on birds, however important in the global population structure of these mites, is a relatively rare event in the lives of individuals. Indeed, the great majority of individual hummingbird flower mites very likely never leave their natal inflorescence.

We have carried out a detailed study of the population structure and dynamics of one hummingbird flower mite, *P. kirmsei*, at La Selva Biological Station in Costa Rica. Its host plant, *H. patens*, an understory treelet that can reach 3–4 m



(A)

Figure 2.2. Apparatus and results for an experiment demonstrating adaptive diel movements of hummingbird flower mites in the field laboratory. A) Lattice apparatus. Each of nine Plexiglas blocks (50×50×6 mm) had a central chamber (10 mm ID, 3 mm deep), with four lateral holes drilled to receive standard coagulation capillary tubes (75 mm long, 1 mm ID). Prior to starting an experiment, each central chamber was covered with a circular cover slip (18 mm), secured with clear tape. To represent "flowers," a drop of virgin nectar was placed in the distal tip of each of the outer tubes, which were capped with Critocap PVC tube closures. Mites were introduced by coaxing them into the uncapped end of the lateral tubes before inserting the tubes into the blocks. Mites moved freely throughout the sealed lattice during each experiment. B) Proportion of 48 mites (*Proctolaelaps kirmsei*) found within 3 cm of nectar drops at various hours of the day. Mite movement in the tubes paralleled the pattern of flower use seen in the field. Having started out in the lateral tubes (the "flowers"), the mites tended to move away from them at roughly the time of day when their host flowers cease to be habitable in the field, returning to the lateral tubes during the hours when their host flowers begin to open in nature. Solid and open points represent two replicates typical of a longer series of experiments. Shaded bars represent nighttime hours.



(B)

Figure 2.2. (Continued)

in height, bears from 1–100 simultaneously flowering inflorescences,depending on plant size. The plant flowers all year round, and there is no evidence of synchrony in the initiation of flowering of different inflorescences on the same plant. At the study site, each active inflorescence produces a mean of 1.5 open flowers per day (range: 0–5 open flowers per day). The total number of flowers produced during the life of an inflorescence is quite variable, ranging from about 30 (three weeks of flowering) to more than a 100 (10 weeks of flowering) (Newstrom et al., in press).

One can accurately estimate the number of days since the initiation of flowering of an inflorescence of *Hamelia* (the "age" of the inflorescence) by summing the number the attached fruits and the number of pedicel scars (indicating fruits removed by frugivorous birds or aborted) and dividing by the mean number of flowers per day (1.5 at the study site). Estimating inflorescence age in this manner,

we documented the rate of local population growth in inflorescence breeding groups by censusing the mites in inflorescences of different ages. To census an inflorescence, all open flowers were picked on successive days until no more mites were found. The mites from these flowers were tallied by stage and sex.

Although the great majority of mites were usually collected on the first day, newly-hatched larvae and stragglers of later stages often appeared for up to 3–4 days. After the first day, the inflorescence was covered with a nylon mesh bag and the subtending peduncle (inflorescence stem) was ringed with Tanglefoot to prevent entry or exit of mites, either on foot or by phoresy on hummingbirds.

The results of these censuses show a clear pattern of density-dependent population growth, with no evidence of a "lag phase" (no inflection point) preceding the most rapid phase of population growth (Fig. 2.3). We do not yet know whether a decrease in birth rate, an increase in mortality, emigration, or a combination of these factors accounts for the rapid decline in population growth as the population nears its carrying capacity. Nor do we yet know the potential sources of mortality.

Experimental populations were later initiated by allowing hummingbirds to visit previously censused and cleared inflorescences, followed by rebagging and then censusing at intervals (details to be reported elsewhere). The resulting best-fit population growth curve did not differ significantly from the curve in Figure 2.2. These experiments also produced an estimated immigration rate from birds of only 4–8 mites per day per inflorescence. One day's immigrants from hummingbirds were sufficient to initiate inflorescence populations indistinguishable from those in Figure 2.2B.

What happens to the mites that remain on an inflorescence of *Hamelia* after it finishes flowering? Because buds are formed several days before opening, it is easy to identify an inflorescence that has just one bud left to open before completing its period of flowering. On the morning that the final flower opens, mites gather in a dense aggregation at its tip. A twig touched gently to such a flower is quickly covered with mites rushing to depart. One might presume that a hummingbird's bill receives the same response. In contrast, equally numerous mites inhabiting younger inflorescences can rarely be seen on the flowers at all during the day.

A simple experiment demonstrated the fate of those mites that fail to mount a hummingbird's bill from the final flower in a *Hamelia* inflorescence. Ten such flowers were located. Five were left untouched; the peduncles (inflorescence stems) of the other five were ringed with Tanglefoot to prevent emigration on foot by the mites. No bags were applied in either treatment, leaving all flowers open to visitation by hummingbirds. The final flowers appeared the following day. On the second day, when all flowers had fallen from the inflorescences or had wilted, the inflorescences were examined carefully for mites. In each of the inflorescences that had been ringed with Tanglefoot, we found numerous mites wandering actively on the branches of the inflorescence. In contrast, none of the control inflorescences had any mites at all. Clearly, the mites in these inflores-

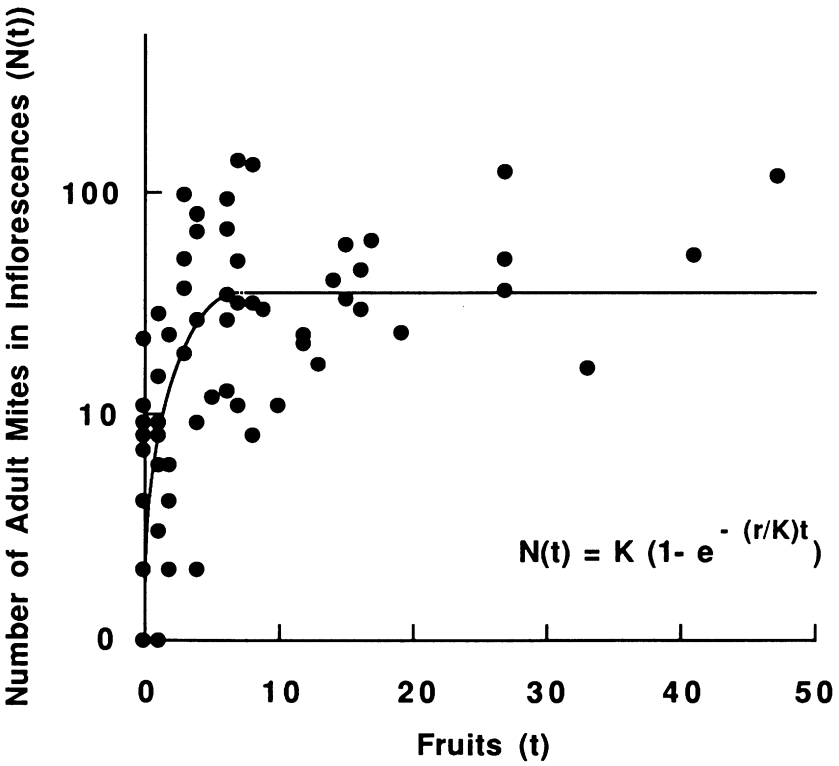


Figure 2.3. Density-dependent population growth for inflorescence breeding groups of the mite *Proctolaelaps kirmsei* on the host plant *Hamelia patens*, inferred from censuses of groups of different ages. "Breeding group," defined here as the total number of adults present (males plus females), is plotted on a logarithmic scale. The flowering age of the inflorescence, and thus the age of its group of inhabiting mites, can be estimated from the number of fruits plus fruit scars on that inflorescence. At the study site (La Selva Biological Station, Costa Rica), the host plant produced an average of 1.5 fruits per day during the study, so that 10 fruits approximate a period of one week. The line was fitted by nonlinear regression ($R^2 = 0.84$) with a least-squares loss function (Wilkinson 1989), with parameters r and K estimated from the data: in arithmetic units, $r = 7.56$ and $K = 33.8$ mites.

cences had left on foot to seek their fortunes elsewhere on the plants. The striking universality of this emigration behavior suggests that it must sometimes pay off.

3. Effects of Host-Plant Morphology on Hummingbird Flower Mites

3.1 Mite Body Size in Relation to Flower Size

The body size of hummingbird flower mites, as measured by the length of the dorsal shield, varies between 0.3 mm–0.7 mm (OConnor et al. 1991). The flowers

that these mites inhabit range from 10 mm to more than 70 mm, as measured by corolla depth. That mite size is positively correlated with flower size (Fig. 2.4) may seem reasonable (an inverse correlation would certainly be more surprising), but no explanation for this pattern can be advanced with certainty. Nectar flow rate (per flower) is generally correlated with flower size in plants (Cruden et al. 1983), and physical space inside the corolla is certainly related to tube depth, on average. But neither nectar flow rate nor total physical space available provides a logical explanation for the relation between mite size and flower size.

Two anomalous cases present informative exceptions. Both the largest mite, *Proctolaelaps contentiosus* (*P. c.* in Fig. 2.4) and the smallest mite, *P. glaucis* (*P. g.* in the figure), inhabit flowers of medium length. The urn-shaped corollas of *Renealmia exaltata* flowers, however, which are inhabited exclusively by *P. contentiosus*, have much greater internal volume than other flowers of medium depth that we studied, perhaps permitting this large mite to prosper. In contrast, the corollas of *Centropogon cornutus* flowers, inhabited exclusively by *P. glaucis*, permit access to the nectaries only through five narrow openings (about 0.4 mm in diameter) between the bases of the filaments (Colwell 1986b). Visiting hummingbirds extract nectar with their tongues through these openings; the unusually small size of *P. glaucis* permits the mite to reach the nectar by walking through them. The body of *P. glaucis* is only slightly smaller than the diameter of the openings.

With these clues in mind, we conjecture that (on average) physical constraints on movement within flowers scale with flower size such that larger mites are at a competitive disadvantage, as compared to smaller mites, in smaller flowers (see Kirk 1991). To complete the explanation, though, we must also propose some advantage to larger size in larger flowers, or else all mites would do just as well to be as small as those in the smallest flowers. Candidate forces include natural selection for greater fecundity, for decreased susceptibility to desiccation (Dobkin 1985) or for faster running, or sexual selection for greater body size through female choice or male-male combat (Colwell 1973).

Selection for faster running might at first seem logical because longer-tubed flowers are necessarily visited by longer-billed hummingbirds (Feinsinger and Colwell 1978). Thus, mites disembarking at such flowers have farther to run to reach a point of contact between bill and corolla, as the bird feeds on the flower. On the other hand, visits to larger flowers last longer because larger flowers have more nectar to be harvested. This issue clearly cannot be resolved by qualitative arguments.

3.2 Mite Breeding-Group Size in Relation to Flower Size

Not surprisingly, the more abundant nectar flow and pollen supply of larger flowers tend to support a greater biomass of hummingbird flower mites than smaller flowers can support. Because mites that live in larger flowers are larger

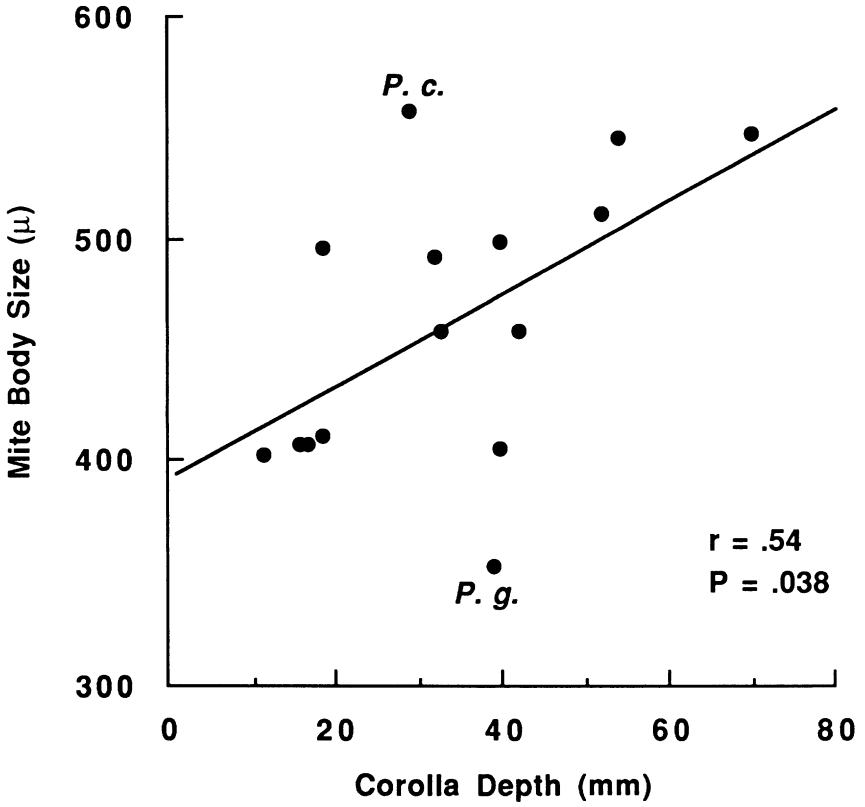


Figure 2.4. Body size of hummingbird flower mites as a function of the depth of the corolla tube of their host plants. Each point on the graph represents a different species of hummingbird flower mite in its characteristic host-plant species. The regression line and significance level indicated were computed for all points, including outliers marked "*P. c.*," which represents *Proctolaelaps contentiosus* in its host plant *Renealmia exaltata*, and "*P. g.*," which represents *P. glaucis* in the flowers of its host plant *Centropogon cornutus* (without these two outliers, $r = 0.776$, $P = 0.002$). These two cases are discussed in the text. Corolla tube depth was measured inside each flower, from the deepest point to the lower "lip" (in zygomorphic flowers) of the corolla. "Mite size" represents the length of the dorsal shield, computed as the intersex mean. The data include all mite species listed in Table 24.1 of Colwell (1986b) for Arima Valley, Trinidad, West Indies, except for those with unknown (*P. mermillion*) or poorly known (*P. phoreticus*) host plants.

in body size (Fig. 2.4), however, larger flowers might nonetheless support the same *number* of mites as smaller flowers. In fact, hummingbird flower mite species that inhabit larger flowers live in larger groups, as measured by the number of adult mites per inflorescence (Fig. 2.5). This pattern would simply be amplified if mites of all species had the same body size.

3.3 Sex Ratio of Hummingbird Flower Mites In Relation to Breeding-Group Size

The life history consequences of mite breeding-group size (and thus, of host-plant morphology) that we have studied, to date, center on issues of variation in

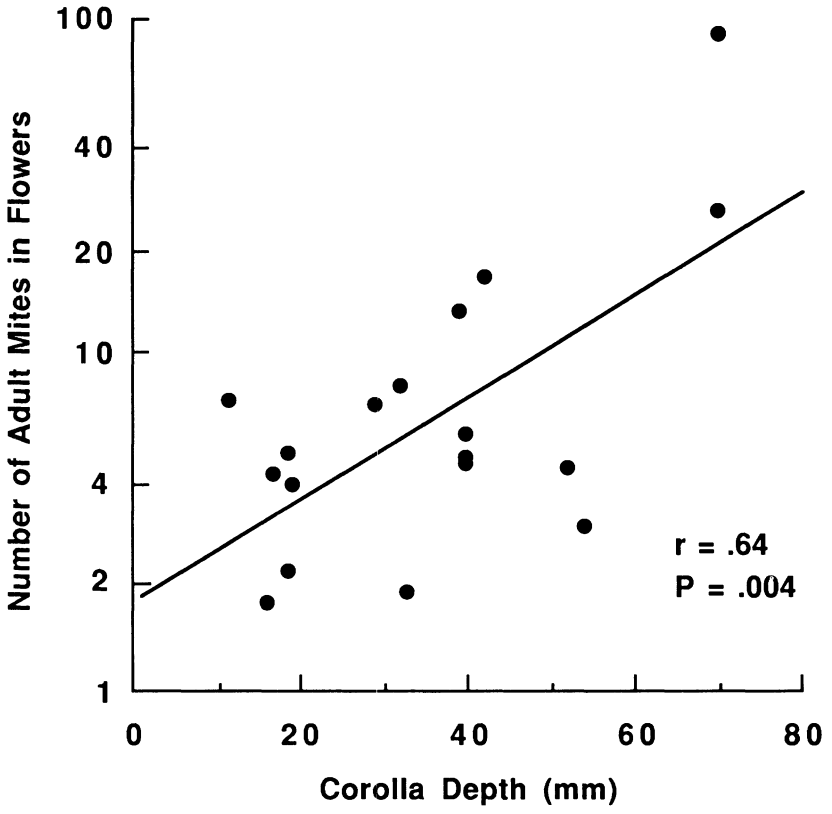


Figure 2.5. Mean numbers of adult hummingbird flower mites in flowers in relation to corolla depth of their host plants. Each point represents a different mite species in a characteristic host-plant species. Data include the same species as in Figure 2.4, with the addition of species listed for Cerro de la Muerte, Costa Rica, in Table 24.1 of Colwell (1986b) and *Proctolaelaps kirmsei* in two secondary hosts in Trinidad. The *Y*-axis is scaled logarithmically; *Y*-values are estimated as the antilog of the mean log number of adults per flower in samples of flowers (n = 4–37, depending upon plant species). Corolla length was measured as described for Figure 2.4.

sex ratio. Like many other species of mites, as well as other arthropods that live in small, relatively isolated breeding groups (Hamilton 1967; Wrensch et al., this volume), hummingbird flower mites have female-biased sex ratios. The degree of bias, however, varies greatly among hummingbird flower mite species and depends upon the typical size of the inflorescence breeding group (Fig. 2.6), defined here as the total number of adults present (males plus females). Mite

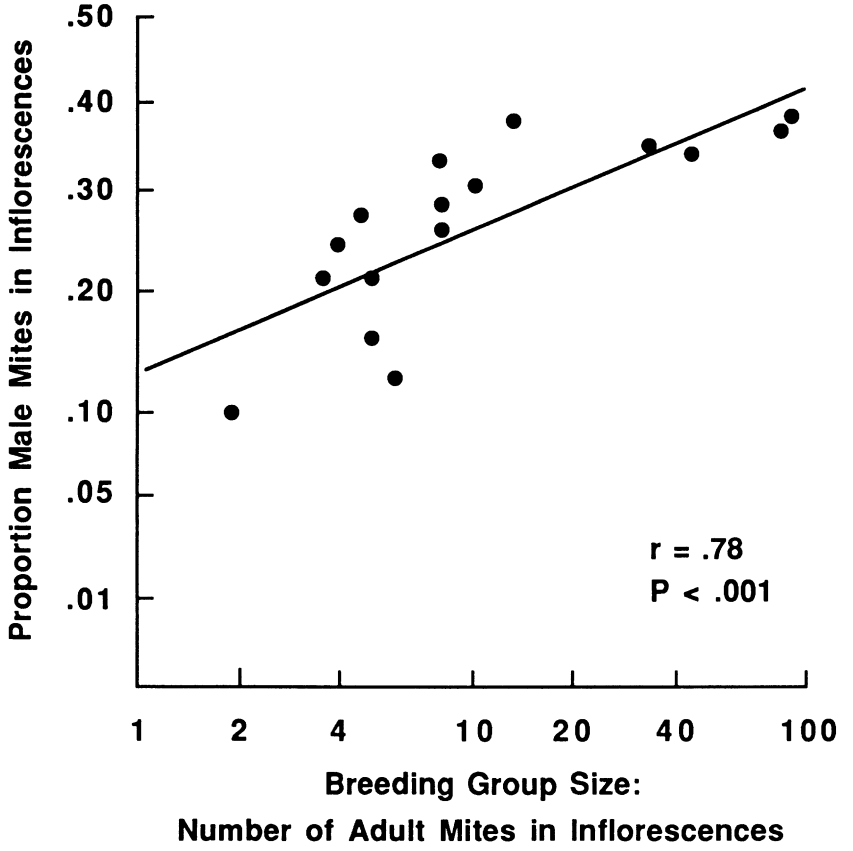


Figure 2.6. Sex ratio of hummingbird flower mites (plotted as proportion males) on their host plants in relation to breeding-group size (number of adults). Species that live in smaller groups have more female-biased sex ratios. The *Y*-axis is an arcsine-square-root scale; *Y*-values of the points plotted represent arithmetic equivalents of the means of arcsine-square-root transformations of the proportion males collected from individual inflorescences (the number of inflorescences ranged from 4–37, depending upon plant species). The *X*-axis is scaled logarithmically; *X*-values of points are estimated as the antilog of the mean log number of adults per inflorescence (for the same samples used for *Y*-values). The points represent the same species as in Figure 2.5, except that the data for *Proctolaelaps kirmsei* on its alternate hosts are not included.

species that breed in small groups (in small flowers) have much more female-biased sex ratios than mites that live in larger groups (in larger flowers). Species with the largest groups of all, such as *Rhinoseius fidelis*, which live in groups of up to 1,000 adults (mean about 100) in the giant flowers of *Costus arabicus* (= *C. niveo-purpurea* of Colwell 1986a) in Trinidad, have nearly equal numbers of male and females.

Unlike certain wasps (e.g. Werren 1980, Herre 1985), hummingbird flower mites show no correlation, *within* species, between breeding-group size and sex ratio. The characteristic sex ratio of each hummingbird flower mite species is apparently a fixed adaptive response to the average conditions the species encounters, rather than the expression of an adaptive capacity for facultative sex-ratio adjustment.

Why should mites living in smaller groups have more female-biased sex ratios? Fisher (1930) showed that, in a random-mating population, a female can maximize her fitness, as measured by copies of her genes among grandprogeny, by producing half daughters and half sons. Colwell (1981) demonstrated that Fisher's conclusions apply with equal force within random-mating, finite groups, however small—even among the progeny of just two females. In a population that is structured into temporarily separate groups, however, those groups with the most female-biased progeny sex ratio produce the most grandprogeny (assuming fecundity is independent of sex ratio). In other words, within-group selection favors unbiased sex ratios, while between-group selection favors the maximum level of female bias possible, consistent with full fertilization.

In the case of hummingbird flower mites and other organisms with temporary breeding groups that persist for several generations, breeding-group size enters into sex-ratio evolution by way of between-group genetic variation. It is this variation that is the grist for the mill of group selection, just as among-individual (in this case, within-group) genetic variation is the raw material of individual selection. For any genetically variable trait, variation in gene frequencies among small groups is greater than that among larger groups, simply due to sampling error. Thus, in a species that tends to form smaller breeding groups, the force of group selection (which favors female progeny) more effectively counters the force of individual selection (which favors equal numbers of sons and daughters) than in a species that forms larger breeding groups. The graded balance between these two opposing levels of selection would be expected to produce just the kind of relationship between group size and sex ratio shown in Fig. 2.6 (Wilson and Colwell 1981).

Alternative models for the evolution of female-biased sex ratios based on genic selection (e.g. Hamilton 1967) are mathematically equivalent to the levels-of-selection approach for the single-generation case (Colwell 1981), but much more difficult to apply in the case of multigenerational groups. Moreover, the verbal exegesis usually given these genic models, which is based on competition for mates (local mate competition; e.g. Alexander and Sherman 1977; Harvey et al.

1985), has little meaning for long-lived groups and may be seriously questioned even for one-generation groups (Colwell 1981, 1982).

To evaluate the potential for significant among-group genetic variation in hummingbird flower mites, a genetic-demographic model is under development that incorporates parameters estimated from the experimental work on *P. kirmsei* discussed above. We will test its predictions through direct molecular assessment of the partitioning of genetic variation within and among groups (Christiansen 1992).

3.4 Sex Ratio Among Mites Dispersing on Hummingbirds

From the analysis of mites collected from hummingbirds, we have discovered that hummingbird flower mite species vary in the sex ratio of dispersing individuals. One might imagine, as a first guess, that the variation would parallel sex-ratio differences among mite species in the flowers of their host plants (Fig. 2.6). Even if females were in general more likely to disperse than males (a common pattern among phoretic mites [Athias-Binche 1991]), a plot of the proportion of migrating males regressed against the size of the inflorescence breeding groups for the same set of species would at least be expected to have a positive slope, although with an intercept below that of Figure 2.6.

In fact, the sex ratio of mites on birds shows precisely the opposite relationship from this naive expectation. Males of mite species that live in smaller groups (which have highly female-biased sex ratios in flowers) are far more likely to disperse on birds than males of mite species that live in larger groups (which have less biased sex ratios), relative to females. The resultant plot of the proportion of males on birds against group size for the same species in flowers (Fig. 2.7) yields a *negative* slope.

The explanation we propose for this pattern depends upon three premises—(1) that there is some cost or risk to dispersal; (2) that the primary reward for dispersal among female mites is the successful founding of a new dynasty in a newly-flowering, unoccupied inflorescence or movement to a less crowded inflorescence; and (3) that the benefit to dispersal among male mites is increased access to unmated females.

There is no reason to expect that the probable dispersal reward to females should vary among species in any regular way with breeding-group size. In contrast, males of species that live in smaller groups often have more to gain from dispersal than males that live in larger groups, because sex ratio ought to vary stochastically more among smaller groups than among larger groups, simply due to binomial sampling error. Dispersal should be a risk worth taking for a male of a species that lives in small groups and who also happens to find himself in a group with a greater proportion males than the average for his species. The next inflorescence the hummingbird visits may well have considerably more females per male. On the other hand, the sex ratio in a species that lives in large

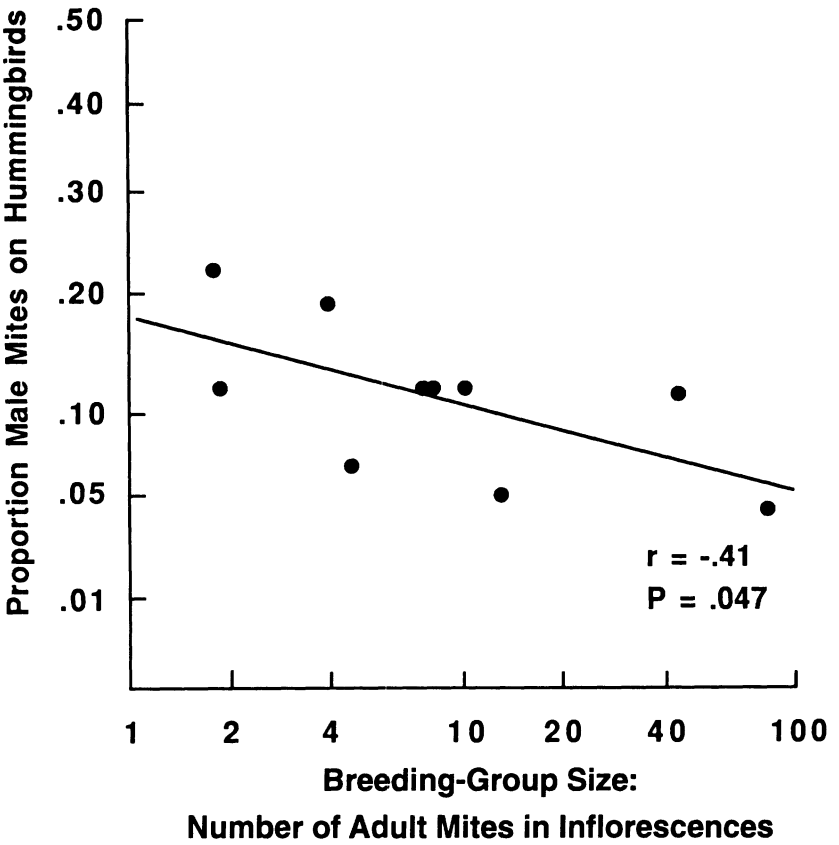


Figure 2.7. Sex ratio of hummingbird flower mites (plotted as proportion males) on their hummingbird carriers in relation to breeding-group size (number of adults) for the same mite species on their host plants. Males of species that live in smaller groups are more likely to disperse on birds than males of species that live in larger groups. Axes are scaled as in Figure 2.6. *Y*-values of the points plotted represent arithmetic equivalents of the arcsine-square-root-transformation of the proportion male mites collected from hummingbirds (pooled data for mites collected from 90 hummingbirds of seven species; sample size for the mite species plotted ranged from 16–153 individuals, depending upon mite species). *X*-values, which correspond to those of Figure 2.6, represent breeding-group size for the characteristic host plant of each mite species. The data plotted are limited to Trinidad and to species for which at least 15 mites were collected from hummingbirds during the study.

groups varies little among inflorescences. In such a species, moving from one inflorescence to another by hummingbird yields little gain for the risk.

As expected from the binomial theorem, variation in sex ratio among inflorescences (estimated by the standard deviations of male proportions, transformed to arcsines of square roots) is negatively correlated with breeding-group size, among mite species ($r = -0.71$, $P = 0.021$ for the same species plotted in Figure 2.6). The positive correlation between sex-ratio variation in flowers and the proportion of male mites on birds, however, is equally significant (Fig. 2.8; $r = 0.71$, $P = 0.022$), concordant with the hypothesis that male mites disperse when variation in sex ratio among groups makes it worthwhile.

We are currently using two experimental approaches to test some of the implications of this hypothesis. First, we have confirmed the ability of male mites to detect local sex ratios and to react behaviorally by seeking groups with more favorable ratios. These experiments were done in experimental "lattices" like the one depicted in Figure 2.2A (data to be reported elsewhere). Second, we have begun to investigate the affects of sex-specific odors in nectar on the behavior of both male and female mites, using apparatus described by Heyneman et al. (1991). We expect these studies to provide a better understanding of the hypothesized relationships among breeding-group size, sex ratio, and migration.

4. Conclusions

The hummingbird flower mites represent an ecologically and phylogenetically coherent group of species. They have enjoyed a highly successful adaptive radiation onto a phylogenetically, phenologically, and morphologically broad spectrum of host-plant lineages, which are united only by their reliance on hummingbirds for pollination. From our explorations of variation in morphology, behavior, and life history among these mites, we conclude that virtually every aspect of their lives is affected by features of host-plant phenology and morphology—including mite body size, daily cycles of behavior, annual shifts in affiliation with host plants, population growth and regulation, breeding-group size, patterns of dispersal, genetic structure of populations, and sex ratio.

Acknowledgments

We gratefully acknowledge the collaboration of David Dobkin and Amy Heyneman in key phases of this work. We also express our thanks, for assistance both technical and intellectual, to Beth Braker, Eugenia Chavarría, Robin Chazdon, Kim Christiansen, David Clark, Deborah Clark, Peter Feinsinger, Marilyn Houck, Marek Kaliszewski, and Barry OConnor. George Hurtt derived the equation fitted in Figure 2.3. This work would not have been possible without the hospitality and facilities of Simla Research Station (Trinidad) and La Selva Biological Station (Costa Rica) or without financial support from the National

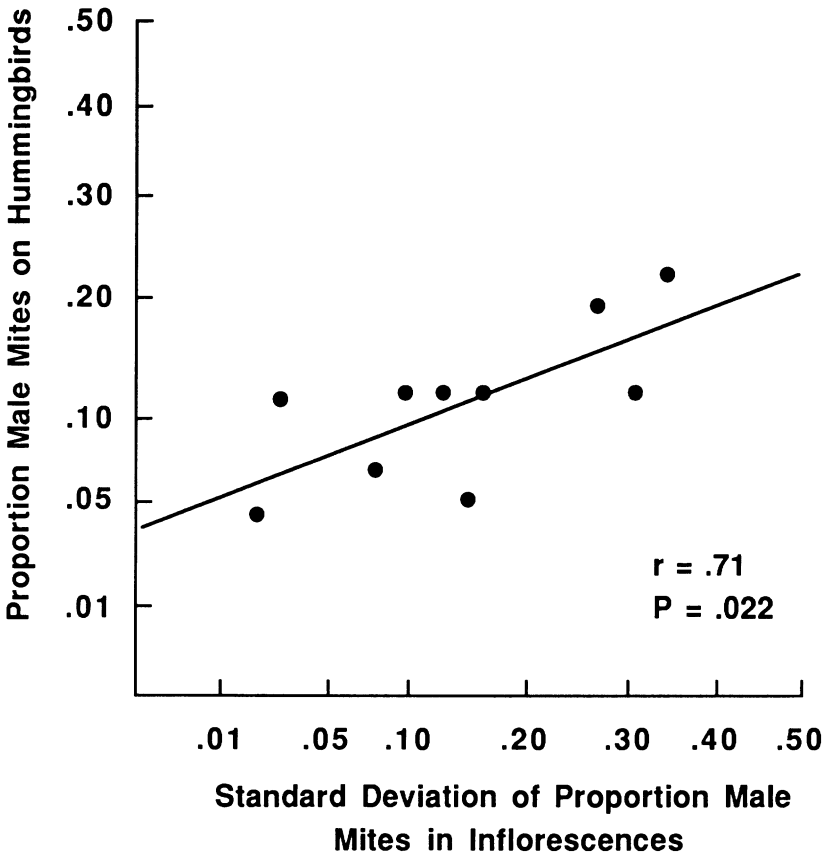


Figure 2.8. Sex ratio of hummingbird flower mites (plotted as proportion males) on their hummingbird carriers in relation to sex-ratio variation for the same mites species on their host plants. Males of species that live in groups that vary more in sex ratio are more likely to disperse on birds than males of species that live in groups that vary less in sex ratio. *Y*-values of the points plotted and the species included are the same as in Figure 2.7. *X*-values of the points, which represent variation in mite sex ratio among inflorescences for the characteristic host plant of each mite species, represent arithmetic equivalents of the standard deviations of arcsine-square-root transformations of the proportion males collected from individual inflorescences (the number of inflorescences ranged from 4–37, depending upon plant species).

Science Foundation (DEB–7812038, BSR 86–04929, BSR–8906228, and BSR–9025024) and from the Universities of California and Connecticut.

References

Alexander, R. D. and P. W. Sherman. 1977. Local mate competition and parental investment in social insects. *Science* 196:494–500.

Athias-Binche, F. 1991. Ecology and evolution of phoresy in mites. In: *Modern Acarology*, Vol. 1 (F. Dusbábek and V. Bukva eds.). Academia, Prague, and SPB Academic Publ., The Hague. Pp. 27–41.

Baker, E. W. and C. E. Yunker. 1964. New blattisociid mites (Acarina: Mesostigmata) recovered from Neotropical flowers and hummingbirds' nares. *Ann. Entomol. Soc. Am.* 57:103–126.

Christiansen, K. M., R. K. Colwell and M. J. Kaliszewski. 1992. Cellulose acetate electrophoretic techniques for the genetic analysis of individual ascid mites (Mesostigmata: Ascidae). *Int. J. Acarol.* 18:97–105.

Colwell, R. K. 1973. Competition and coexistence in a simple tropical community. *Am. Nat.* 107:737–760.

Colwell, R. K. 1979. The geographical ecology of hummingbird flower mites in relation to their host plants and carriers. In: *Recent Advances in Acarology*, Vol. 2 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 461–468.

Colwell, R. K. 1981. Group selection is implicated in the evolution of female-biased sex ratios. *Nature* 290:401–404.

Colwell, R. K. 1982. Female-biased sex ratios. Reply to Charlesworth and Toro, Wildish, and Borgia. *Nature* 298:494–496.

Colwell, R. K. 1983. *Rhinoseius colwelli* (Acaro floral del colibri, totolate floral de colibri, hummingbird flower mite). In: *Costa Rican Natural History* (D. H. Janzen ed.). Univ. Chicago Press, Chicago. P. 619, and pp. 767–768.

Colwell, R. K. 1985. Stowaways on the *Hummingbird Express*. *Nat. Hist.* 7:56–63.

Colwell, R. K. 1986a. Community biology and sexual selection: Lessons from hummingbird flower mites. In: *Ecological Communities* (T. J. Case and J. Diamond eds). Harper and Row, NY. Pp. 406–424.

Colwell, R. K. 1986b. Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. In: *Evolutionary Processes and Theory* (S. Karlin and E. Nevo eds.). Academic Press, NY. Pp. 475–495.

Colwell, R. K. 1989. Hummingbirds of the Juan Fernandez Islands: natural history, evolution and population status. *Ibis* 131:548–566.

Colwell, R. K. and S. Naeem. 1979. The first known species of hummingbird flower mite north of Mexico: *Rhinoseius epoecus* n.sp. (Mesostigmata: Ascidae). *Ann. Entomol. Soc. Am.* 72:485–491.

Colwell, R. K., B. J. Betts, P. Bunnell, F. L. Carpenter and P. Feinsinger. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flower-piercer *Diglossa plumbea*, and its evolutionary implications. *Condor* 76:447–452.

Cruden, R. W., S. M. Hermann and S. Peterson. 1983. Patterns of nectar production and plant-pollinator coevolution. In: *The Biology of Nectaries* (B. Bentley and T. Elias eds.). Columbia Univ. Press, NY. Pp. 80–125.

Dobkin, D. S. 1984. Flowering patterns of long-lived *Heliconia* inflorescences: implications for visiting and resident nectarivores. *Oecologia* 64:245–254.

Dobkin, D. S. 1985. Heterogeneity of tropical floral microclimates and the response of hummingbird flower mites. *Ecology* 66:536–543.

Dobkin, D. S. 1990. Distribution patterns of hummingbird flower mites (Gamasida: Ascidae) in relation to floral availability on *Heliconia* inflorescences. *Behav. Ecol.* 1:131–139.

Dusbábek, F. and V. Černý. 1970. The nasal mites of Cuban birds. I. Ascidae, Ereynetidae, Trombiculidae (Acarina). *Acarologia* 12:269–281.

Fain, A. and K. E. Hyland. 1980. New species of the genus *Rhinoseius* Baker and Yunker, 1964 (Mesostigmata: Ascidae) phoretic on Colombian hummingbirds. *Int. J. Acarol.* 6:15–24.

Fain, A., K. E. Hyland and T. H. G. Aitken. 1977a. Nouveaux acariens Ascidae (Mesostigmates) phorétiques dans les fosses nasales de colibris (Note préliminaire). *Bull. Ann. Soc. R. Belge Entomol.* 113:185–186.

Fain, A., K. E. Hyland and T. H. G. Aitkin. 1977b. Flower mites of the family Ascidae phoretic in nasal cavities of birds (Acarina: Mesostigmata). *Acta Zool. Pathol. Antverp.* 69:99–154.

Feinsinger, P. and R. K. Colwell. 1978. Community organization among neotropical nectar-feeding birds. *Am. Zool.* 18:779–795.

Feinsinger, P., J. A. Wolfe and L. A. Swarm. 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology* 63:494–506.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*, 2nd rev. ed. Dover, NY. 291 pp.

Flechtmann, C. H. W. and D. E. Johnston. 1978. The rediscovery and redescription of *Rhinoseius braziliensis* (Acari: Ascidae). *Rev. Bras. Entomol.* 22:165–166.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.

Harvey, P. H., L. Partridge and L. Nunney. 1985. Group selection and the sex ratio. *Nature* 313:10–11.

Herre, E. A. 1985. Sex ratio adjustment in fig wasps. *Science* 228:896–898.

Heyneman, A. J., R. K. Colwell, S. Naeem, D. Dobkin and B. Hallet. 1991. Host plant discrimination: experiments with hummingbird flower mites. In: *Evolutionary Ecology of Tropical Herbivores* (P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson eds.). Wiley-Interscience, NY. Pp. 455–485.

Hunter, P. E. 1972. New *Rhinoseius* species (Mesostigmata: Ascidae) from Costa Rican hummingbirds. *J. Ga. Entomol. Soc.* 7:27–36.

Hyland, K. E., A. Fain and A. S. Moorhouse. 1978. Ascidae associated with the nasal cavities of Mexican birds (Acarina: Mesostigmata). *J. NY Entomol. Soc.* 86:260–267.

Kirk, W. D. 1991. The size relationship between insects and their hosts. *Ecol. Entomol.* 16:351–359.

Micherdzinski, W. and F. S. Lukoschus. 1980. *Rhinoseius rafinskii*, a new species from Ecuador and Venezuela (Acari, Gamasina, Ascidae). *Zool. Meded.* (Leiden) 55:65–79.

Newstrom, L. E., G. W. Frankie, H. G. Baker and R. K. Colwell. 1993. Diversity of flowering patterns at La Selva. In: *La Selva: Ecology and Natural History of a Lowland Tropical Rain Forest* (L. McDade, K. S. Bawa, G. S. Hartshorn, and H. A. Hespenheide eds.). Univ. Chicago Press, Chicago (in press).

OConnor, B. M., R. K. Colwell and S. Naeem. 1991. Flower mites of Trinidad II. The genus *Proctolaelaps* (Acari: Ascidae). *Great Basin Nat.* 51:348–376.

Primack, R. B. 1985. Longevity of individual flowers. *Annu. Rev. Ecol. Syst.* 16:15–37.

Stratton, D. A. 1989. Longevity of individual flowers in a Costa Rican cloud forest: ecological correlates and phylogenetic constraints. *Biotropica* 21:308–318.

Werren, J. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* 208:1157–1158.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, IL.

Wilson, D. S. and R. K. Colwell. 1981. Evolution of sex ratio in structured demes. *Evolution* 35:882–897.

Zamudio, M. 1985. Acaros foréticos (Mesostigmata: Ascidae) de las cavidades nasales de colibries de Mexico, I. *Folia Entomol. Mex.* 64:81–91.

3

Mites as Potential Horizontal Transfer Vectors of Eukaryotic Mobile Genes: *Proctolaelaps regalis* as a Model

Marilyn A. Houck

CONTENTS

1. Introduction

The chapters in this volume give acarine examples of how ecological and evolutionary events have contributed to the diversification, speciation, adaptation, or coevolution observed within lineages. This chapter focuses on the issue of horizontal transfer of genes between unrelated species, an event that can lead to the rapid alteration of a genome by means of the insertion of foreign DNA. This novel

source of genetic variation is independent of the usual hereditary mechanisms occurring in sexual organisms, and can result in a rapid influence on the phenotype with profound consequences for the lineage of the recipient.

Horizontal gene transfer of transposable (mobile) elements is becoming an increasing important realm of investigation for phylogenetic systematists, and will likely continue to be so for some time. The following is a summary of the role one mesostigmatid mite may play in the horizontal transfer process. However, the Mesostigmata in general offer especially fertile opportunities as the focus of similar studies for many reasons including the large number of species, cosmopolitan occurrence, common ecological interactions with other species (arthropods, nematodes etc.), rapid mobility, and nature of feeding.

1.1 What are Transposable Elements?

Transposable elements are genes that can move freely from site to site within a genome; they are not restricted to a fixed location on a chromosome. They have been called "*jumping genes*" by some authors, and were first described in maize by Barbara McClintock (1948). Transposable elements are not rare but, in fact, have been found in all organisms in which they have been sought.

Transposable elements have been conceptually organized into "families" according to their internal sequence topology, and mechanism of transposition. There are approximately 50 different families of transposable elements, represented by two major classes (Finnegan 1989, 1990): Class I ("viral") elements transpose by a mechanism of reverse transcription of an RNA intermediate (DNA-RNA-DNA), and their action is similar to that of a retrovirus; Class II ("non-viral") elements are believed to transpose directly from DNA to DNA (e.g. *P* elements, detailed below).

The precise mechanism by which Class II elements transpose is not completely understood, but it is known that the elements code for transposases which catalyze their own mobility (O'Hare and Rubin 1983). Because transposable elements have a significant influence on their own biological activity (transposition), they have been called the ultimate "parasitic" or "selfish DNA" by some researchers (Doolittle and Sapienza 1980).

1.2 Horizontal Gene Transfer

There is currently special phylogenetic interest in transposable elements because it is now apparent that not only can transposable elements bolt from one genomic site to another within a genome, but that they also have the potential for mobility leading to interspecific incorporation into unrelated and uninfected species (horizontal gene transfer).

While prokaryotes are well known for the ability to accomplish competent interspecific gene transfer, the possibility of horizontal transfer among eukaryotes

has only been suspected. Specific mechanisms of transfer have not been found. For example, transfer has been suspected to have occurred between: (1) *Drosophila melanogaster* and *D. funebris* (Mizrokhi and Mazo 1990); (2) *Drosophila* and *Zaprionus* (Maruyama and Hartl 1991); (3) *Drosophila* and yeast (Xiong and Eickbush 1988); (4) *D. melanogaster* and *Caenorhabditus elegans* (Harris et al. 1988); and (5) even between *Drosophila* and the plant *Arabidopsis thaliana*, since three retrotransposons of *A. thaliana* had a greater affinity to the *copia* elements of *D. melanogaster* than they had to other *A. thaliana* retrotransposons (Konieczny et al. 1991). Vectors can play an important role in the horizontal transfer of genes, and viruses have been implicated in the transfer of some transposable elements (Miller and Miller 1982).

Most startling was the recent documentation that mouse DNA (homologous to mouse intracisternal A particle and endogenous type C retrovirus) from a particular strain of mice was detected in the DNA of its parasite (*Schistosoma japonicum*) (Iwamura et al. 1991). In this case, host DNA was apparently integrated into the genome of the adult parasites and detectable in their eggs.

Transposable elements hold a lot of promise as candidates for the study of horizontal transfer, as they control their own mobility and usually increase in copy number when inserted into a new genomic site (or new host). Thus, horizontal transfer between eukaryotic species is more likely to be successful with a self-regulating, mobile, multiple-copy gene than with single-copy non-mobile genomic DNA. The increased representation of replicated elements is an important factor, as it reduces the probability of element loss following insertion and enhances the chance of gene representation in future generations, as compared to single-copy genes.

Though, as a rule, genetic mutations resulting from mobile transposable elements are often deleterious, it is clear that transposition could have played an important role in the structuring of eukaryotic genomes (Finnegan 1989). It is an alternate source of genetic variation for diploid species which, under normal circumstances, is influenced mainly by sexual recombination and mutation. No one can yet predict how frequently such events occur, but no one doubts that it can be a powerful evolutionary force.

2. *P* Transposable Elements in *Drosophila*

Between 10%–20% of the genome of *Drosophila melanogaster* consists of transposable elements (Engels 1983, MacKay 1985, Finnegan and Fawcett 1986), occurring as dispersed moderately repetitive sequences which are approximately randomly scattered throughout the genome (Rubin 1983). Approximately half of all spontaneous mutations in *D. melanogaster* are thought to be due to insertions of transposable elements (Finnegan 1990). *P* elements represent one of the most intensively studied groups of transposable elements in *D. melanogaster* (Engels 1988).

2.1 The Structure of P Elements

P elements are mobile genes which code for a transposase required for gene mobility (Rio et al. 1986, Snyder and Doolittle 1988). Elements consist of a single large gene comprised of 2907 base pairs (bp), flanked by short 31 bp inverted repeats (O'Hare and Rubin 1983). *P* elements are not polymorphic in sequence, but can be heterogeneous with respect to size (Daniels et al. 1990).

There are two categorical types of *P* elements which are ranked according to relative size (Kidwell et al. 1988): (1) Autonomous (complete elements) = 2.9 kbp elements and (2) Nonautonomous (defective elements) possessing internal deletions of various numbers of base pairs. Major differences in the complement of autonomous and nonautonomous elements in the genome of *Drosophila* strains have been observed in populations from different geographic origins (Kidwell et al. 1983, Anxolabéhère et al. 1984, 1985b, 1988; Kidwell and Novy 1985, Boussy 1987, Boussy and Kidwell 1987). Defective elements (< 2.9 kbp) are derived from complete P sequences by internal deletions (O'Hare and Rubin 1983). Defective elements can undergo transposition only when in the presence of active autonomous elements (Daniels et al. 1990), probably because they are incapable of accurately coding for their own transposase.

P elements are apparently inserted randomly into a genome (Rubin 1983) or (if defective) inserted adjacent to other intact P elements (Finnegan 1990). They are present in high copy numbers (30–50 copies; Bingham et al. 1982) per haploid genome in individuals of some strains of *D. melanogaster* (called P strains), but functional *P* elements are completely missing in other strains of *D. melanogaster* (called M strains) (Bingham et al. 1982, Todo et al. 1984).

2.2 Transformation Due to P Element Insertion

In the early embryological development of *Drosophila,* the primordial germline cells migrate to the posterior pole of the egg, are enveloped in a membrane, and are expelled from the syncytial mass of the egg. *P* elements can be artificially injected into fertilized eggs of M (P-deficient) strains of *D. melanogaster* and transformed into P strains under controlled laboratory conditions (Rubin and Spradling 1982). Elements inserted in this manner jump into the germline of the receiving M strain, with normal phenotypic expression of the *P* element (Finnegan 1990). Study of the fate of lab-microinjected DNA indicates that injected DNA becomes inserted into the germline of the young embryos (≤ 512 cell stage; 90 min @ 25°C) and that which remains in the cytoplasm slowly degrades (Steller and Pirrotta 1985). Transposition of *P* elements is often premeiotic, identically influencing all resultant progeny (Rubin 1983).

The insertion of *P* elements into an M genome can result in seriously phenotypic consequences which are most commonly restricted to the germplasm (Kidwell et al. 1977, Bregliano et al. 1980, Kidwell 1983, Bregliano and Kidwell 1983).

These consequences include a high frequency of temperature-sensitive gonadal sterility, male recombination, chromosomal aberrations, and an increased number of lethal mutations (Kidwell and Novy 1979).

On the basis of the degree of the dysfunctional properties expressed, the *P* element family includes three kinds of strains (Kidwell 1979, Engels and Preston 1981, Kidwell 1983, Kidwell et al. 1988): (1) P strains which contain functional *P* elements which can potentially lead to sterility in strain hybrids (hybrid dysgenesis); (2) *Q* strains which do not express any potential for sterility, but do express other *P* element characteristics (e.g. chromosomal aberrations); (3) M strains which possess no functional *P* elements and no sterility effects; M′ (pseudo M) strains possess *P* elements but the phenotypic expression of traits varies from low to relatively high.

Recently, *P* element transposition in *Drosophila* has also been utilized as a vehicle to vector foreign DNA into a fertilized eggs of *Drosophila* (Rubin and Spradling 1982, Spradling and Rubin 1982, Cooley et al. 1988). This procedure has tremendous potential for designer engineering of the genome.

2.3 Gene-Cytotype Incompatibility

There are significant gene-cytotype interactions which govern the expression of *P* element hybrid dysgenesis (Engels and Preston 1979). *P* elements are neutral (do not cause dysgenesis) when expressed in a compatible P-cytotype cytoplasm (*inter se* parental crosses). However, a mismatch between genome and cytoplasm can have dire consequences, the magnitude of which depends upon whether the contributing parent was the mother or the father.

Crosses between P-strain males and M-strain females result in gonadal sterility, while interstrain matings between P-strain females and M-strain males result in no symmetrical dysgenic abnormalities. In P-strain crosses, therefore, males can provoke gonadal sterility in the hybrid offspring, while the female cytotype of P strains seems to be able to suppress such a phenotypic disaster (Engels and Preston 1979, Rubin et al. 1982, for review see Engels 1988).

The ability to repress *P* element transposition is a mechanism to moderate (reduce) harmful effects of *P* elements (Snyder and Doolittle 1988). Under these conditions, it would be anticipated that *P* elements would be lost from populations, or that consummated hybrid matings would be selected against. But "selfish" mutants, which were exempt from such repressor action, would be predicted to increase in a population under such circumstances. Such anti-repressor elements could quickly prove fatal to *Drosophila* populations and selection against their propagation would occur at the group level ("the group being the population of *P* elements in a population of flies"; Snyder and Doolittle 1988).

Fitness loss can also be overcome by transposition efficiency (Kidwell et al. 1988). The highly invasive nature of active *P* elements is clearly observed when introduction into susceptible populations is followed over time in lab cultures, or

when accomplished by simulation modeling (Hickey 1982, Kiyasu and Kidwell 1984, Daniels et al. 1987, Good et al. 1989). Such studies indicate that changes in strain status from M to P can occur relatively rapidly in the laboratory (Kidwell et al. 1981). Simulations, using a mathematical population model (Hickey 1982) have shown that selection against heterozygotes carrying a transposable element can be offset by a relatively high rate of transposition. In sexual species, *P* elements can become fixed even when fitness is reduced by 50%. *P* elements, which could exist in low frequencies in populations for long periods of time (Kidwell 1983), could proceed to fixation rather rapidly once a critical threshold is reached.

There are also ecological influences on the phenotypic expression of gonadal sterility in hybrid matings, as well as cytological influences. Where dysgenesis is a potential (hybrid of *P* male X *M* female cross), there is a temperature-dependant expression of the gonadal sterility (Engels and Preston 1979, Schaefer et al. 1979, Kidwell 1983). At high environmental temperatures (27–29°C) there is significant to complete sterility and an obvious reduction in parental Darwinian fitness. Development at lower temperatures are less threatening.

2.4 The Hypothesized Origin of P Elements

Little is known concerning the evolution of mobile elements in general (Daniels et al. 1990). They may have arisen *de novo* by mutation or recombination (Finnegan 1985) or by horizontal transfer from another organism (Hagemann et al. 1990). Homologous P sequences are widespread in the Sophophora radiation of the Drosophilidae (Brookfield et al. 1984, Anxolabéhère et al. 1985a, Daniels and Strausbaugh 1986, Daniels et al. 1990, Montchamp-Moreau et al. 1991), and are also known to occur in *Opomyza germinationis* (Diptera: Opomizydae) and *Trixoscelis frontalis* (Diptera: Trixoscelididae) (Anxolabéhère and Périquet 1987). This indicates that this family of *P* elements may be plesiomorphic and present in the common ancestor of the family Drosophilidae (Hagemann et al. 1990) or may have occurred even earlier in the phylogeny of the Diptera.

Though the *P* element is present in every species group in the subgenus Sophophora, its distribution within species groups is discontinuous (Lansman et al. 1985). *P* elements probably have had a long evolutionary history in the willistoni and saltans lineages (Daniels and Strausbaugh 1986), but it does not occur in other species of the melanogaster subgroup (e.g. *D. simulans*, *D. mauritiana* and *D. sechellis* [Daniels et al. 1990]). *P* elements are unique in that while they are common in *D. melanogaster*, they are not present in all strains of *D. melanogaster*. And, they are completely absent in species most phylogenetically related to *D. melanogaster* (Brookfield et al. 1984, Daniels and Strausbaugh 1986).

There is near-identity of *P* element sequences from *D. melanogaster* and *D. willistoni* with only one base pair difference (Daniels et al. 1990) and high

sequence similarity among *D. melanogaster P* elements from diverse geographic locations (O'Hare and Rubin 1983).

Though *P* elements occur sporadically across the Scaptodrosophila radiation, there is a lack of congruence between *P* element sequence divergence and the divergence time between *Drosophila* species pairs (Hagemann et al. 1990). It is speculated that the genus *Drosophila* originated within the Drosphilidae sometime during the Eocene (40–50 mya; Throckmorton 1975, Beverly and Wilson 1984) and that the Sophophoran radiation produced three modern lineages: (1) melanogaster in the Old World tropics; (2) obscura in the north temperate (Holarctic) zone; and (3) willistoni/saltans in the New World tropics (Patterson and Stone 1952, Throckmorton 1975). Thus, the evolution of the *P* element seems not to have diverged exclusively by classical radiation in the course of speciation (Hagemann et al. 1990).

2.5 Geographic Distribution of P Elements

Natural populations of *D. melanogaster* collected in North America, South America, and Africa are dominated by individuals possessing *P* elements, while most European and Asian populations have defective P homologous sequences (Finnegan 1990). Australia has both *P* element strains and M strains (Boussy 1987). A P-M hybrid dysgenesis cline exists in eastern Australian in *D. melanogaster* with discrete P, Q, and M regions being nearly contiguous (Boussy 1987, Boussy and Kidwell 1987).

P elements are present in contemporary wild populations of *D. melanogaster* and no true M strains have been collected from wild populations of flies since 1974 (Anxolabéhère et al. 1988). By comparison, *P* elements are absent from laboratory strains which were brought into the lab more than 30–40 years ago (Bingham et al. 1982, Kidwell 1983, Bregliano and Kidwell 1983, Kidwell et al. 1983).

2.6 Hypotheses Concerning the Spread of P Elements

Two hypotheses exist which account for the geographic patterns observed in the *P* element distribution in *D. melanogaster* (Kidwell 1983): (1) Recent-loss hypothesis: the loss of *P* elements from laboratory stocks, but with persistence of *P* elements in the wild, has led some to speculate that there has been a stochastic loss of these elements in laboratory populations due to drift (Engels 1981). Evidence supporting this point of view is that there has been an observed change from P to M strains in one laboratory population (Engels and Preston 1980). While this is interesting, there is no evidence that this event could be repeated with the required frequency or magnitude needed to explain the rapid loss of elements hypothesized. The main problem with the Recent Loss Hypothesis is that it requires that individual strains of *Drosophila* must have lost all 30–50

copies of the *P* element in a short period of time, which is unlikely given the invasive biological nature of the element.

A second hypothesis is called the Rapid-invasion hypothesis (Kidwell 1979, 1983) which hypothesizes that *P* elements are recent invaders of *Drosophila* populations. This theory is supported by the fact that until recently *P* elements have been absent in natural populations of *D. melanogaster*, and have only recently been observed to spread in frequency in wild populations. It is hypothesized that prior to 1930 *P* element families were absent (or in low frequency) in all natural populations and that about 30 years ago P strains began a rapid infiltration which lasted until about 1960. After which time, P strains were essentially ubiquitous in the wild.

Interspecific transfer of *P* elements can occur by vertical (mating-dependent = orthologous) transfer or by horizontal (mating-independent = xenologous) transfer (e.g. Montchamp-Moreau et al. 1991). It has been suggested that the rate of global spread of *P* elements could best be explained by mechanisms other than the epidemiological spread through normal sexual contact and interspecific hybridization. Interspecific horizontal gene transfer has been proposed as a potential mechanism for the dissemination of *P* elements worldwide.

The geographic site of origin of the purported recent invasion event was speculated to have been the New World, as evidenced by the fact that the *P* element first appeared there in *D. melanogaster* supposedly in the 1950's (Kidwell 1983). P strains were not found to be present in Europe, Asia, or Australia until about 10 years later. Since 1980, M strains have been determined to occur only in the Iberian peninsula, central Asia, and the southeastern coast of Australia (Anxolabéhère 1985b, Kidwell 1986).

2.7 Evidence for Horizontal Gene Transfer of P Elements

Several corroborating pieces of information endorse the hypothesis of the recent introduction of the *P* transposable element into *D. melanogaster*, from a species of the willistoni group (Daniels and Strausbaugh 1986) by means of horizontal gene transfer: (1) the uneven world-wide pattern of distribution of *P* elements in *D. melanogaster* (Anxolabéhère et al. 1985b, Anxolabéhère et al. 1988); (2) the high sequence fidelity among *D. melanogaster P* elements from incongruous geographic locations (Kiyasu and Kidwell 1984, Daniels et al. 1987, Good et al. 1989); (3) the prevalence of *P* elements in members of the willistoni species group, relative to their rarity in the melanogaster species group (O'Hare and Rubin 1983, Brookfield et al. 1984); (4) the single base pair difference existing between *P* element sequences from *D. melanogaster* and *D. willistoni* (Daniels and Strausbaugh 1986); (5) the lack of correlation between *P* element sequence and topography and the evolutionary divergence time between *Drosophila* species pairs (Daniels et al. 1990); and (6) the recent finding that *P* element sequences of *D. melanogaster* and *D. nebulosa* (willistoni species group) are more similar

to each other than either is to *D. bifasciata* (obscura species group) (Hagemann et al. 1990).

3. The Search for a Potential *P* Element Vector

As outlined above, indirect evidence from several lines of investigation strongly suggest that *P* elements in *Drosophila* are interspecifically transmitted by horizontal gene transfer. There are numerous biological candidates found in association with *Drosophila* which could potentially participate (unilaterally or in combination) in this gene transfer. These include: bacteria, fungi and molds, protozoans, spiroplasms and mycoplasms, viruses, and several kinds of small arthropods (hymenoptera and mites being common associates).

At least 14 different mite species co-occur with *Drosophila* (Ashburner 1989). These include four Astigmatid genera (*Glycyphagus*, *Histiostoma*, *Hormosianoetus*, and *Tyrophagus*), three Prostigmatid genera (*Leptus*, *Trombidium*, and an unidentified Smaridiidae), and seven Mesostigmatid genera (*Androlaelaps*, *Arctoseius*, *Fuscuropoda*, *Gamasides*, *Macrocheles*, *Parasitus*, and *Proctolaelaps*).

Those species previously identified from *Drosophila* laboratory cultures include: *Androlaelaps casalis*, *Glycyphagus domesticus*, *Histostoma feroniarum*, *Histostoma laboratoriun*, *Histostoma sapromyzarium*, *Hormosianoetus aeschlimanni*, *Proctolaelaps hypudaei* (= *P. pygmaeus*), and *Tyrophagus putrescentiae*.

Over time, I have seen several species of mites arrive in fly shipments to individual researchers at several universities. *H. laboratorium* probably is the most common contaminant of *Drosophila* cultures, but it was not a logical candidate for gene transfer because it is primarily a filter-feeder of dissolved and suspended materials in culture media. The deutonymphal instar is phoretic (= passive disperser) on adult flies but has no known trophic interaction with the flies.

A very interesting mite, *Proctolaelaps regalis* (Gamasina: Ascidae) (DeLeon 1963), was discovered in fly cultures at the University of Arizona in 1986. *P. regalis* was intriguing because it seemed to meet the minimum requirements for a potential horizontal transfer candidate (opportunity, motive, and means). (1) *Opportunity*: It is syntopic (on rotting fruit) with members of the suspected donor species-group (willistoni) and with the *P* element recipient, *D. melanogaster*; and it is sympatric with *D. melanogaster* and wild populations of the willistoni species group in the hypothesized site of *P* element radiation (Florida, Central America, and South America [Ehrman and Powell 1982]). (2) *Motive*: it is an omnivore which feeds on *Drosophila*. (3) *Means*: it has a peripatetic feeding behavior, with rapid transit time between potential prey, accomplishing its attack in fruit rot where all fly stages are present.

A realistic hypothesis which could unite accumulating observations, is that *P. regalis* might vector *P* elements if it attacked a member of the willisoni species

group, and then immediately inserted the "bloody" gnathosoma into the posterior pole of a *D. melanogaster* egg (younger than the 512 stage [Steller and Pirrotta 1985]). For these reasons *P. regalis* was the only observed acarine which I chose as appropriate for such detective scrutiny.

4. Proctolaelaps Regalis

Proctolaelaps regalis is a Parasitiform mite of the suborder Gamasida. The Gamasida currently contains about seven superfamilies, most of which are fluid feeders. *P. regalis* is of the superfamily Ascoidea which are known to be widely distributed throughout the tropics and temperate habitats, feeding primarily on nematodes, insects, and fungi (Krantz 1978).

It is a member of the family Ascidae, a large taxonomic group with significant ecological success in terrestrial and subaquatic habits, resulting in a large adaptive radiation (Lindquist 1965). This family exploits habitats on every continent except Antarctica (Lindquist 1965) and is probably one of the most diversified families in North America (Lindquist 1971). Most members of the Ascidae are free-living predators, common on plant foliage in the tropics but seldom in temperate regions, because the Phytoseiidae have competitively dominated that habitat.

P. regalis is in the subfamily Ascinae, one of the "largest and by far the most diverse" subfamilies of the Ascidae (Lindquist 1965). The genus *Proctolaelaps* (erected by Berlese in 1923) is itself cosmopolitan and consists of about 70 species (Lindquist 1965).

P. regalis is a fruit, leaf, bark and litter species (Muma 1975) occurring in the habitat utilized by *Drosophila*. In nature, *P. regalis* is found associated with a "variety of insects in various stages of development" (DeLeon 1963), and E. E. Lindquist (Biosystematics Research Centre, Agriculture Canada) has a "variety of material at hand compared with the type material of this species. It seems to be frequently associated with fallen or rotting fruit" (Biosystematics Research Centre Identification Report 89–0818–01).

4.1 Feeding Morphology

The feeding structures of *P. regalis* are associated with the gnathosoma which is a body region distinctive among mites, having no homologous or analogous tagma in insects or other arachnids. Many traditional "head" structures are not associated with the gnathosoma (e.g. eyes and brain) but are associated with the more caudal idiosoma ("body").

The chelicerae and the pedipalps (Fig. 3.1A) are associated with the gnathosoma. The chelicerae are retractable supraoral structures and in the free-living Mesostigmata are represented by an elongate pistonlike structure, with a musculature that can be used for thrusting penetration of host tissues. It is somewhat progressed toward the form of a piercing stylet, "able with little modification to

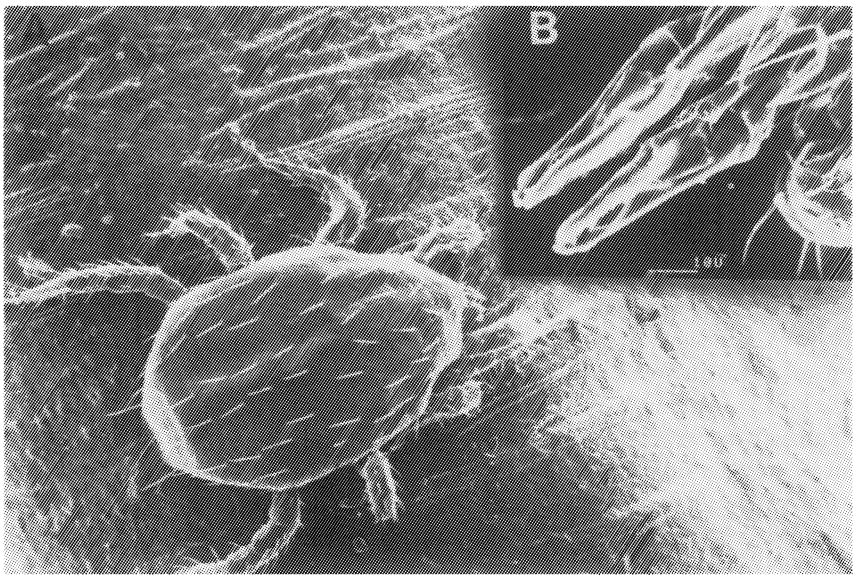


Figure 3.1. The chelicerae and the pedipalps of mites are associated with the gnathosoma. (M. A. Houck, *Science* 1991, 253:1125; Copyright 1991 by the AAAS. A) The feeding posture of an adult female *Proctolaelaps regalis* (body length = ~ 400μm) when attacking a pupa of *Drosophila melanogaster*. Feeding on the pupa requires a significant amount of effort (thrusting and piercing) to penetrate the hard crysalis. B) Omnivores such as *P. regalis* often retain chelate-dentate chelicerae (with a fixed and a movable digit) to handle a broad range of food types. This mite is positioned with the venter-side up.

achieve the same functions as stylets in bloodsucking insects" (Radovsky 1985). The two digits of the chelicerae are approximately the same length in adults.

Cheliceral morphology of ascids correlates with trophic specialization (Evans et al. 1961), with a great deal of diversification. The primitive chelate-dentate state allows for grasping, shearing, and piercing of prey, as opposed to long slender chelicerae with small teeth usually found in mites feeding on other mites or small insects. Obligate parasites may have edentate chelicerae, reduced chelicerae, or a reduced fixed digit.

Omnivores such as *P. regalis* retain chelate-dentate chelicerae (with a fixed and a movable digit) to handle a broad range of food types (Fig. 3.1B), while the over-all morphology of its gnathosoma is (like most other Mesostigmata) well adapted for fluid-feeding (van der Hammen 1964). Even though there are trends in the correlation between cheliceral specialization and the food types eaten in the Mesostigata "some parasites are so subtle that it occasionally may not be possible to tell by morphology alone whether a species is an obligatory parasite" (Radovsky 1985).

This cheliceral morphology is central to the evolutionary success of the Meso-

stigmata and essential in the adaptation to a parasitic life style (see Radovsky this volume). There is a forked structure (tritosternum) located ventrad to the chelicerae. The tritosternum interacts with the deutosternum to recover the overflow of liquid foods during feeding, and move it back to the oral area (Wernz and Krantz 1976).

P. regalis has two large secretory salivary styli (= siphunculi) (Fig. 3.2) positioned laterad and ventrad to the chelicerae. They probably carry the ducts of the salivary glands which are extended in parasitic forms, are partly sclerotized, and are thought to empty into the hypostome where they assist in preoral digestion (Krantz 1978, Woolley 1988).

The spermadactyl (Fig. 3.2) is the male insemination structure used in copulation and is also associated with the chelicerae. Mating is accomplished when the male knocks the female over, and as she recovers her balance he positions himself underneath her with the cheliceral spermadactyl inserted into the sperm induction pores on either side of the mid-ventral epigynal opening (Fig. 3.3, 3.4).

The midgut in the Gamasina (= ventriculus) typically has 2–3 pairs of caecae that consist of cuboidal cells on a basement membrane, and larger vacuolated cells interspersed. As the wall of the gut is extended, the larger cells are pinched

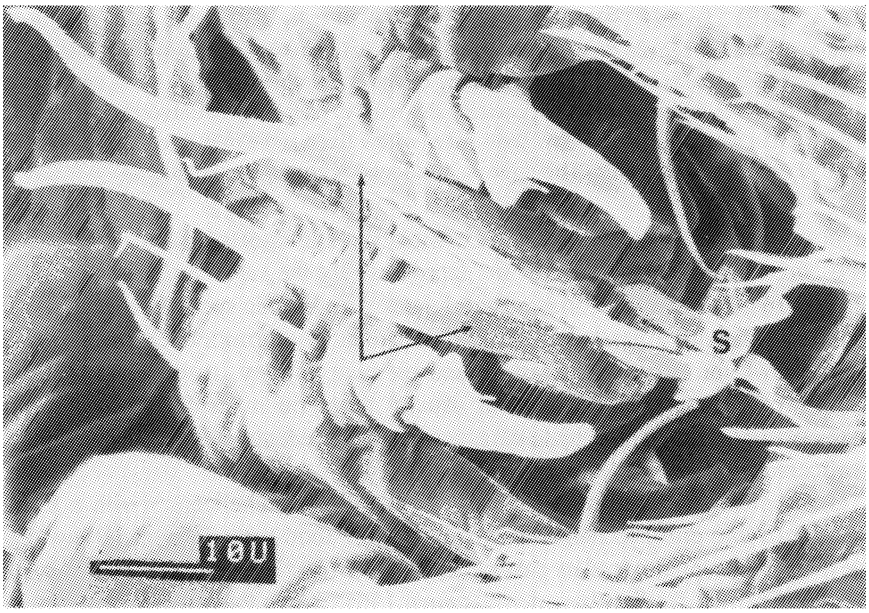


Figure 3.2. *Proctolaelaps regalis* has large secretory salivary styli (= siphunculi) ("s") which are chitinous at the proximal end and fleshy at the distal tip. The spermadactyl (insemination organ) (arrows) of the male is located in the chelicerae and posterioventrad to the salivary styli. The spermadactyl is seen here in its fully extended state (posteriorly recurved).

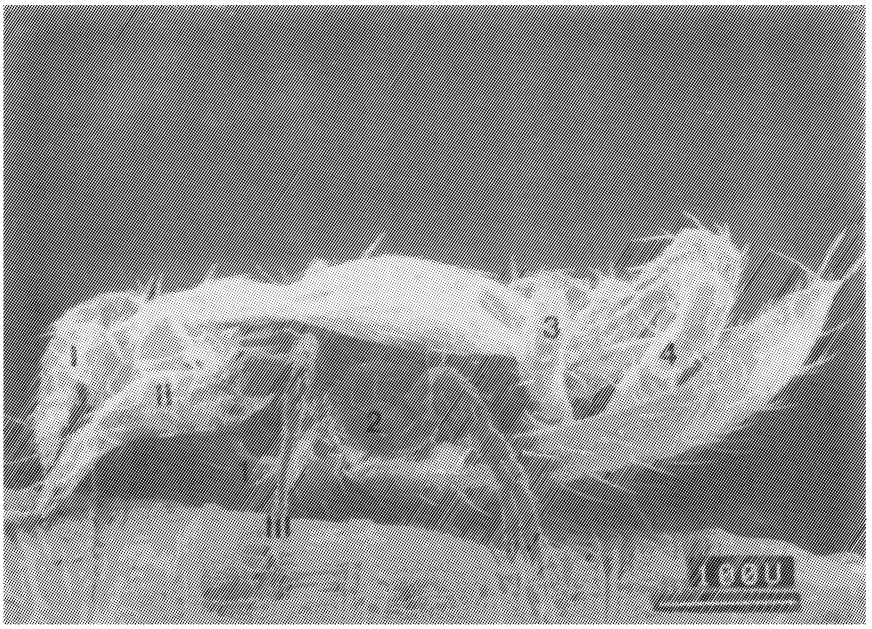


Figure 3.3. The mating position of *Proctolaelaps regalis*. The female is in a normal standing position (Legs I, II, III, IV indicated), with the male positioned below. The male spermadactyl is inserted into the genital aperture, approximately ⅓ the way from the anterior end of the female's body (see Fig. 3.4). Legs III (3) and IV (4) of the male grasp the posterior dorsum of the female. Leg II (2) of the male wraps around leg IV of the female. Leg I (1) of the male steadies the fore part of his body and possibly aids in the positioning of the spermadactyl. Only the dorsal surface of the male has physical contact with the substratum.

off into the lumen of the gut where they form spherical bodies. They are thought to supply digestive juices. Intracellular digestion probably occurs in the ventriculus as evidenced by the presence of vacuolated cells. A peritrophic membrane (envelope) is added to the bolus to protect the gut.

4.2 Feeding Behavior

I would use the term semiparasite (or omnivore) to describe the trophic specialization of *P. regalis*. It is possible that the mite may act either as a predator (kills prey) or as a parasite (does not kill host), depending upon conditions.

In the laboratory I observed that *P. regalis* can survive on fly media alone (feeding perhaps on free nutrients, fungus, and yeast), but *P. regalis* does not appear to reproduce under these conditions. Examination of 18 hours of video tape indicated that *P. regalis* also feeds on all immature stages of *D. melanogaster* by rapid cheliceral thrusting. This action is accomplished swiftly, sending cellular

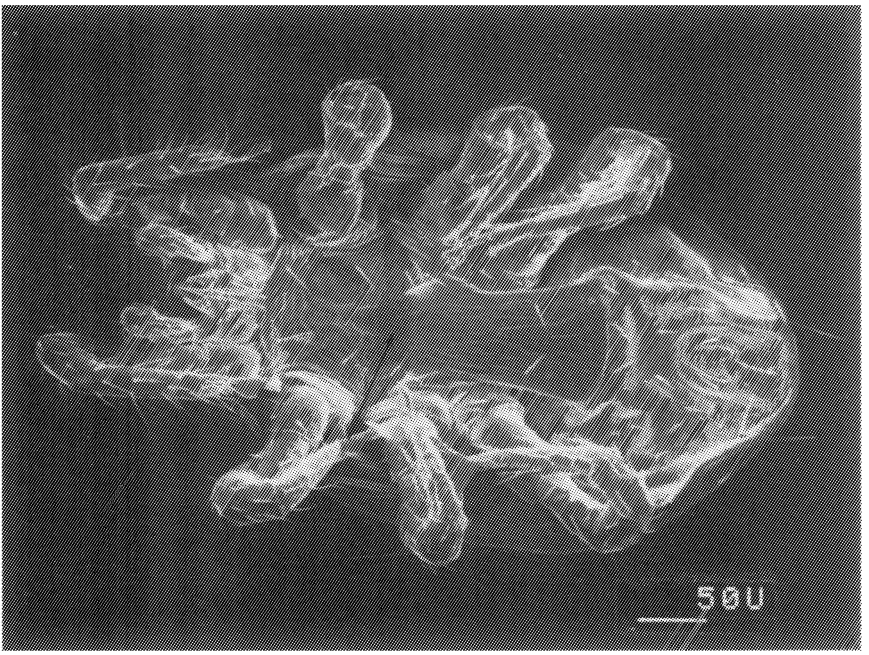


Figure 3.4. Venter of a female of *Proctolaelaps regalis*, with the epigynial plate indicated.

inclusions into the hollow space between the cheliceral shafts (Fig. 3.5). Feeding can last only a few seconds per attack, and immediate feeding on subsequent adjacent hosts is common. In mixed-species fly cultures this behavior provides potential for transfer of cellular inclusions (including DNA) from one individual host to another.

Adult mites also feed on *Drosophila* pupae, where penetration of the puparium requires prolonged thrusting of the chelicerae (continuing for as long a 2 min/attack). Sometimes contamination of fly strains by *P. regalis* ends in population degradation or elimination, possibly as a result of this second (damaging) type of feeding.

All of the various aspects of the biology of this mite, including the semi-parasitism itself, are consistent with *P. regalis* having had a co-evolutionary association with what are now "domesticated" *Drosophila*. This mite may have been co-collected with wild-caught fly stocks in the U.S. originally, but it is equally likely that it secondarily invaded U.S. laboratory stocks because of its natural association with *Drosophila* in the wild. In short, *P. regalis* has the morphological and behavioral capacity, and the ecological and geographical opportunity, to act as a vector for *P* elements.

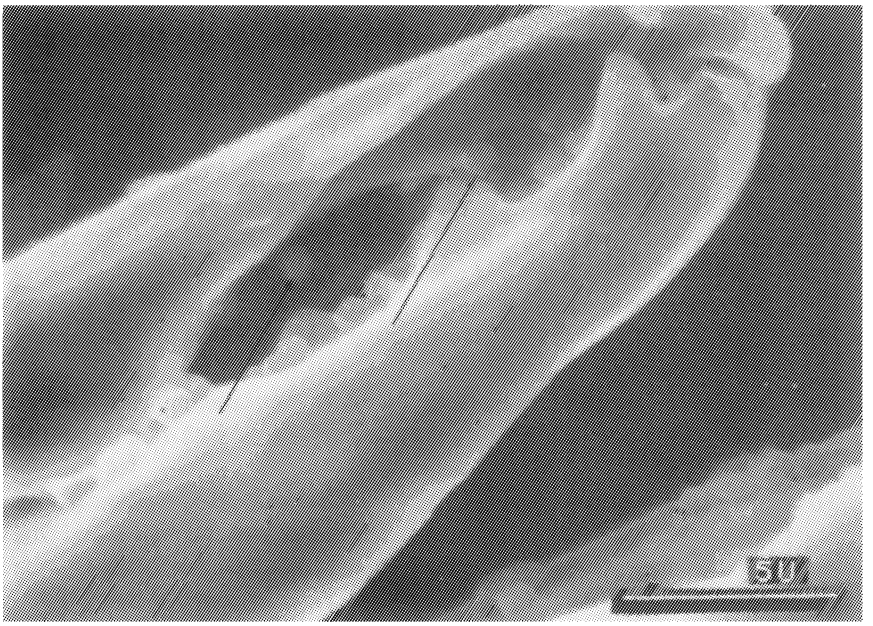


Figure 3.5. Scanning electron photomicrograph of the cheliceral digits of *Proctolaelaps regalis*. Inclusions (spores) are located in the rotund, hollow, cavity formed between the closed cheliceral digits (arrows).

4.3 P Element Experiments

In order to determine if *P. regalis* mites were acquiring *P* element sequences from *D. melanogaster* during feeding, genomic DNA was isolated from mites associated with both P and M strain fly cultures. The first attempt to determine whether *P* elements could be detected in *P. regalis* came in 1986, using Southern blot hybridization, a very laborious task which sometimes resulted in a weak positive signal. This required harvesting 400 mites per sample, using a dissecting scope, and washing each one as collected so as to remove any surface contamination. Once Polymerase Chain Reaction (PCR) technology became generally accessible (Appenzeller 1990), studies such as this became much easier.

Results of Southern blot analyses indicated that hybridization to a *P* element-specific probe occurred only with DNA extracted from the Harwich-w (P) fly strain or with DNA extracted from mites associated with that *P* element strain (for details see Houck et al. 1991). DNA from the Canton-S (M) strain of *D. melanogaster* and from *P. regalis* associated with the Canton-S strain consistently showed no detectable hybridization to the *P* element probe.

Specific PCR primers were synthesized for *D. melanogaster P* elements.

Eight separate samples of template DNA from the Harwich-w strain (P) of *D. melanogaster* and mites associated with that strain were used in PCR with these primers. All consistently yielded a fragment of the correct size. Results from both the Canton-S template and that from mites associated with the Canton-S strain were negative.

To demonstrate that the fragment produced from the mite template DNA was indeed P-specific, the product was isolated and a 250 bp segment was sequenced. The nucleotide sequence in this region was identical to that previously determined (O'Hare and Rubin 1983) for the *D. melanogaster P* element.

The most parsimonious explanation for these results is that *P. regalis* can acquire *Drosophila P* element sequences during feeding. However, two alternative explanations had to be considered. First, that the DNA samples from *P. regalis* (collected from the Harwich-w fly cultures) were contaminated. Second, that the mites themselves carried endogenous sequences with homology to *P* elements.

To address the first question, adult *Histiostoma laboratorium* (ecological correlate) were isolated from the same Harwich-w culture as were *P. regalis* and DNA was prepared in the same manner. No P-specific product was detected when *Histiostoma* DNA was used as a template in PCR, indicating that physical association with the flies was not of itself sufficient to give positive results.

To address the second issue of whether endogenous *P* sequences in Harwich-associated mites might be pleisomorphic or synapomorphic in ascid lineages, we obtained isolates of two species closely related to *P. regalis* (*Lasioseius subterraneus* and a *Proctolaelaps* spp.). Again no P-specific product was detected.

A final important question was whether other gene sequences could also be detected in the mites. The non-mobile small-subunit (18S) rRNA gene was chosen because, like the *P* element, it is present in multiple copies in the *D. melanogaster* genome. Primers, corresponding to highly variable regions within the 18S rRNA gene, were synthesized to be specific for the *D. melanogaster* small subunit rRNA gene.

Because no acarine small-subunit rDNA sequences had been published, we could not rule out that these primers were in fact hybridizing to the endogenous *P. regalis* genes. DNA was isolated from the three mite species sampled previously: *H. laboratorium*, *L. subterraneus*, and the unnamed *Proctolaelaps* species. No PCR product was detected using template DNA from any of these three species, indicating that the *Drosophila* rDNA primers were not hybridizing to endogenous mite sequences.

The amplified DNA fragment from *P. regalis* which was produced with *D. melanogaster*-specific rDNA primers was also isolated and purified. A 300 bp region of the product was sequenced and found to be identical to the corresponding segment of the *D. melanogaster* 18S rDNA. These results suggest that *P. regalis* was acquiring 18S rDNA and *P* element *Drosophila* DNA sequences during its

association with fly cultures, a conclusion consistent with the morphology, ecology, behavior and geography of this mite.

4.4 Has Proctolaelaps regalis Previously Been Observed in Culture?

In light of the controversy surrounding the origin and spread of *P* elements, I wanted to determine how often *P. regalis* had been observed in *Drosophila* cultures by other researchers. From surveying the literature, it became clear that there was no way to estimate this frequency of occurrence. The reasons for uncertainty come from: (1) unfortunate inaccuracies in a chapter on mites in a text heavily consulted and referenced concerning all aspects of the culture of *Drosophila* (Ashburner and Thompson 1978); and (2) neglect of (or disinterest in) the accurate reporting of the mite species encountered by *Drosophila* researchers.

The most comprehensive summary (prior to 1989) concerning mites in *Drosophila* cultures, came from a chapter by Ashburner and Thompson (1978). This reference included a figure (their Fig. 29, p. 75) of a "dangerous egg predator," a mesostigmatid mite. The authors identify this mite as *Proctolaelaps hypudaei* (= *P. pygmaeus*). But it is not clear whether all *Proctolaelaps* individuals thus far found in fly bottles are restricted to the species *hypudaei*.

This is not a trivial issue, as a correct identification of any species provides considerable insight into the ecological role and potential impact of the organism in an ecological community. The genus *Proctolaelaps* can express a wide range of potential diet preferences, depending upon species. *P. hypudaei* is a cosmopolitan omnivore which is known as a predator of mites (Nesbitt 1951) and also consumes fungus (Muma 1961). It is a very versatile mite, being found primarily in: leaf mould and litter, mouldy wheat and barley, rotting wood and plant bulbs, and on leaf surfaces of orchard trees and citrus where they feed on insects, and Tetranychid mites (Nesbitt 1951, Mathys and Tencalla 1959, Ehara 1964, Muma 1975, Hughes 1976). *P. nauphoetae*, however, is solely an ectoparasite of cockroaches (Egan and Hunter 1975); *P. bombophilus* and *P. longisetosus* feed on pollen in bumblebee nests (Krantz 1978), and species of *Proctolaelaps* discussed by Colwell (this volume) feed on nectar as well as pollen. A correct species identification is important to all further assumptions and interpretations concerning the biology of an organism, and can be essential as an intellectual guide or if incorrect can misdirect further studies.

Cantelo and Boswell (1973) reported *P. hypudaei* in their *Drosophila* cultures in 1973. But, the nature of this mite's interaction with *Drosophila* was undocumented, and the focus of the commentary was mite eradication. These authors state:

> When we were confronted by a large infestation of mites in our *Drosophila* colony, we treated the colony with benzyl benzoate, which had been found by others to eliminate mites from their colonies (DIS 20:96, DIS 46:156). However, this treatment was ineffective for us, possibly because we had a different

> mite species. Our colony was infested with *Proctolaelaps hypudaei* (Oudemans) (det. R. L. Smiley) of the family Ascidae, a cosmopolitan mite. It feeds on mites and other small arthropods and probably caused depletion of the *Drosophila* culture by feeding on the *Drosophila* eggs and affecting the *Drosophila* behavior.

The fact that various other insecticides (e.g. binapacryl, dicofol, propargite and methyl benzoate) also did not effectively kill these mites could indicate that some resistance to chemicals had developed over time and that these mites had been more frequent in lab stocks than thought.

The second confirmed report of *Proctolaelaps* occurring in *Drosophila* cultures was from Ashburner and Thompson's own lab. They state that "in Cambridge we suffered at one time from an unidentified species of the same genus." Their cavalier lack of interest in exactly which species points to the second serious issue; the attitude that somehow all species of *Proctolaelaps* are ecologically equivalent. This attitude, by prominent researchers, is regrettable considering that the focus of their mite chapter was to educate the uneducated.

One cannot safely assume that all the *Proctolaelaps* encountered in *Drosophila* cultures have been *P. hypudaei*. From the whole-body drawings of the Mesostigmata, which are quite comparable among species to the untrained eye, *P. regalis* could have been easily missed or mistaken. In any event, the genus *Proctolaelaps* is reported to have had serious effects on lab cultures at least twice previously, and I have had lab strains of *P. regalis* which have ranged from lethal to relatively benign, depending on the fly strain cultured.

If other sightings of *P. regalis* have occurred in cultures, these mites have either not been correctly identified or perhaps the observed high virulence discouraged interest in the mite beyond that of rapid extermination. On my own first encounter with *P. regalis*, I was asked to advise on its eradication. If systematic acarology had not been one of my interests, this mite would probably have been eradicated without eulogy or acknowledgment. I wonder if that has been the fate of other populations. And, what of the potential unknown genetic impact on *Drosophila* cultures prior to local mite extermination?

5. Prospectus: Detecting *P* Element Transmission Events

5.1 Novel Potential for Incorporation of P Elements into the Proctolaelaps regalis Genome

The above findings are particularly intriguing because the feeding behavior of the mite appears to simulate the method of microinjection in the laboratory which has been used by many *Drosophila* researchers for intraspecific and interspecific transfer of genes by *P* element transformation. It is not yet know whether *Proctolaelaps regalis* has the ability to incorporate *P* elements into its own genome, as

was observed in *Schistosoma japonicum* (Iwamura et al. 1991). *P. regalis* may, in fact, act only as a mechanical vector with no consequence to its own genome.

Curiously, a very unusual set of circumstances specific to the Mesostigmata could allow for a remarkable mechanism for integration without necessarily invoking transovarial transmission or other such means of secondary vectoring. Since the spermadactyl (Fig. 3.2) of the male of *P. regalis* is used in copulation and also potentially for feeding, there is the potential mechanism for the integration of *P* elements into the mite genome as a direct result of copulation. What would be required is that the male feed on *Drosophila* containing the *P* element and subsequently insert the "bloody" chelicerae (with spermadactyl) into the sperm induction pores (Krantz 1978) of the female (Fig. 3.4). Because of the powerful mobility and invasive nature of transposable elements, there is a possibility (no matter how remote) of these elements invading awaiting mite eggs. The door is open to the development of testable hypotheses.

What is not yet known is whether males of *P. regalis* can, or do, actively feed. This is an important question about *P. regalis* males that needs to be experimentally explored (see for example discussion by F. Radovsky, this volume).

5.2 Frequency of P Element Transmission

Acquiring *P* elements by mites during feeding may be dependent on stochastic events involving several environmental, behavioral, and demographic factors of both the mites and the flies. The likelihood of heuristically observing a gene-transmission events would be expected to be relatively small; partly because gene transfer itself may be an infrequent event, and partly because of the statistical vagaries involved in assigning responsibility once it has occurred.

The minimum experimental conditions needed for the potential detection of such an event would require that: (1) a *P* element strain of *Drosophila* and an M strain syntopically co-occur (same fruit rot or culture bottle); (2) an egg is laid by an M strain female in proximity to a P strain individual (any immature fly stage) giving *P. regalis* the opportunity to sequentially feed on the P strain and then on the egg of the M strain (mechanical vectoring); (3) the M strain fly eggs be less than 3 hours old (512-cell stage) so that the germline can incorporate the vectored *P* element; (4) the mite, in fact, feeds on the P and M strains sequentially and not interrupt the feedings to graze on fungus or other nutrients and thus potentially purging the gnathosoma of acquired *P* elements; (5) the habitat complexity be conducive to transfer; habitat complexity is a function of culture age and fly density increases as a direct function of habitat complexity, but so does the density of fungal spores. An increase in fungus is correlated with the increased access to fungus which interferes with the relative frequency of mites feeding on flies; (6) any egg receiving the vectored *P* element must survive the act of transfer (feeding) by the mite; (7) any egg receiving the vectored *P* element must be of

the correct cytotype; (8) any adult resulting from that mite-injection event (as a egg) must be under the scrutiny of a researcher, and sampled for *P* element analysis. If each of these events has a low independent probability, the combined probability of detection is multiplicative and extremely low.

In contrast, the factors which act in favor in detecting a successful transfer of *P* elements are: (1) the very invasive and infective nature of the elements themselves; (2) their control over their own excision and transposition; and (3) their mechanism for entering the germline in multiple copies. Even if the initial frequency of infection is low, once incorporated in the germline, *P* elements would persist, perpetuate, and become a potentially significant evolutionary force.

In the future I am going to pursue the question of horizontal transfer by *P. regalis* by uncoupling the above stochastic events, determine a probability estimate for each of the independent events and then stochastically model the interactions. Hopefully this approach will be productive in establishing the first realistic estimate of the frequency of horizontal transfer of *P* transposable elements.

Acknowledgments

The molecular aspects of this work were done in cooperation with K. Peterson (Southern blot analysis) and J. Clark (PCR analysis), in the lab of M. Kidwell, while I was on the faculty of the University of Arizona. I thank S. Daniels, I. Boussey, M. Kidwell, and K. Kymoura for stimulating discussions about *P* element biology. The late M. J. Kaliszewski provided the samples of *Lasioseius subterraneus*, and the unnamed *Proctolaelaps* species.

Special thanks to E. E. Lindquist and G. W. Krantz for clarifying the synonomy of *Proctolaelaps hypudaei* and *P. pygmaeus*, and for directing me to the correct use of the term "induction pore". Also, thanks to E. E. Lindquist and R. E. Strauss for their meticulous reading of the body of the text and for many helpful comments.

References

Anxolabéhère, D., H. Kai, D. Nouaud, G. Périquet and S. Ronsseray. 1984. The geographical distribution of P-M hybrid dysgenesis in *Drosophila melanogaster*. *Genét. Sél. Evol.* 16:15–26.

Anxolabéhère, D., D. Nouaud, G. Périquet. 1985a. Séquences homologues à l'element P chez des espèces de *Drosophila* du groupe *obscura* et chez *Scaptomyza pallida* (Drosophilidae). *Genét. Sél. Evol.* 17:579–584.

Anxolabéhère, D., D. Nouaud, G. Périquet and P. Tchen. 1985b. *P*-element distribution in Eurasian populations of *Drosophila melanogaster*: a genetic and molecular analysis. *Proc. Natl. Acad. Sci.* USA 82:5418–5422.

Anxolabéhère, D. and G. Périquet. 1987. P-homologous sequences in Diptera are not restricted to the Drosophilidae family. *Genét. Ibér* 39:211–222.

Anxolabéhère, D., M. G. Kidwell and G. Périquet. 1988. Molecular characteristics of diverse populations are consistent with the hypothesis of a recent invasion of *Drosophila melanogaster* by mobile *P* elements. *Mol. Biol. Evol.* 5:252–269.

Appenzeller, T. 1990. Democratizing the DNA sequence. *Science* 247:1030–1031.

Ashburner, M. 1989. *Drosophila: A Laboratory Handbook*. Cold Spring Harbor Laboratory Press, NY.

Ashburner, M. and J. N. Thompson, Jr. 1978. The Laboratory Culture of *Drosophila*. In: *The Genetics and Biology of Drosophila*, Vol 2A (M. Ashburner and T. R. F. Wright eds.). Academic Press, NY. Pp. 1–109.

Beverly, S. M. and A. C. Wilson. 1984. Molecular evolution in *Drosophila* and the higher Diptera II. A time scale for fly evolution. *J. Mol. Evol.* 21:1–13.

Bingham, P. M., M. G. Kidwell and G. M. Rubin. 1982. The molecular basis of P-M hybrid dysgenesis: the role of the *P* element, a P strain specific transposon family. *Cell* 29:995–1004.

Boussy, I. A. 1987. A latitudinal cline in P-M gonadal dysgenesis potential in Australian *Drosophila melanogaster* populations. *Genet. Res.* 49:11–18.

Boussy, I. A. and M. G. Kidwell. 1987. The P-M hybrid dysgenesis cline in eastern Australian *Drosophila melanogaster*: discrete P, Q, and M regions are nearly contiguous. *Genetics* 115:730–745.

Bregliano, J. C., G. Picard, A. Bucheton, A. Pelisson, J. M. Lavige and P. L'Heritier. 1980. Hybrid dysgenesis in *Drosophila melanogaster*. *Science* 207:606–611.

Bregliano, J. C. and M. G. Kidwell. 1983. Hybrid dysgenesis determinants. In: *Mobile Genetic Elements* (J. A. Shapiro ed.). Academic Press, NY. Pp. 363–410.

Brookfield, J. F. Y, E. Montgomery and C. H. Langley. 1984. Apparent absence of transposable elements related to the *P* elements of *D. melanogaster* in other species of *Drosophila*. *Nature* 310:330–331.

Cantelo, W. W. and A. L. Boswell. 1973. Mite control with chemicals in a *Drosophila* culture. *Drosophila Inf. Serv.* 50:163.

Cooley, L., R. Kelley and A. Spradling. 1988. Insertional mutagenesis of the *Drosophila* genome with single *P* elements. *Science* 239:1121–1128.

Daniels, S. B. and L. D. Strausbaugh. 1986. The distribution of *P* element sequences in *Drosophila*: the *willistoni* and *saltans* species groups. *J. Mol. Evol.* 23:138–148.

Daniels, S. B., S. H. Clark, M. G. Kidwell and A. Chovnick. 1987. Genetic transformation of *Drosophila melanogaster* with an autonomous *P* element: phenotypic and molecular analyses of long-established transformed lines. *Genetics* 115:711–723.

Daniels, S. B., K. R. Peterson, L. D. Strausbaugh, M. G. Kidwell and A. Chovnick. 1990. Evidence for horizontal transmission of the *P* transposable element between *Drosophila* species. *Genetics* 124:339–355.

DeLeon, D. 1963. A new genus and twelve new species of mites from Mexico and Southeast United States (Acarina: Blattisocidae). *Florida Entomol.* 46:196–198.

Doolittle, W. F. and C. Sapienza. 1980. Selfish genes, the phenotype paradigm and genome evolution. *Nature* 284:601–603.

Ehara, S. 1964. Some mites of the families Phytoseiidae and Blattisocidae from Japan (Acarina: Mesostigmata). *J. Fac. Sci. Hokkaido Univ. Zool.* 15:378–394.

Egan, M. E. and P. Hunter. 1975. Redescription of a cockroach mite, *Protolaelaps nauphoetae*, with notes on its biology. *Ann. Entomol. Soc. Am.* 68:361–364.

Ehrman, L. and J. R. Powell. 1982. The *Drosophila willistoni* species group. In: *The Genetics and Biology of Drosophila* Vol. 3B (M. Ashburner, H. Carson and J. N. Thompson, Jr. eds.). Academic Press, London. Pp. 193–226.

Engels, W. R. 1981. Hybrid dysgenesis in *Drosophila melanogaster* and the stochastic loss hypothesis. *Cold Spring Harbor Symp. Quant. Biol.* 45:561–565.

Engels, W. R. 1983. The *P* family of transposable elements in *Drosophila*. *Annu. Rev. Genet.* 17:315–344.

Engels, W. R. 1988. *P* elements in *Drosophila melanogaster*. In: *Mobile DNA* (D. E. Berg and M. Howe eds.). A. S. M. Publications, Washington DC. Pp. 437–484.

Engels, W. R. and C. R. Preston. 1979. Hybrid dysgenesis in *Drosophila melanogaster*: the biology of female and male sterility. *Genetics* 92:161–174.

Engels, W. R. and C. R. Preston. 1980. Components of hybrid dysgenesis in a wild population of *Drosophila melanogaster*. *Genetics* 95:111–128.

Engels, W. R. and C. R. Preston. 1981. *Drosophila Inf. Serv.* 56:35–37.

Evans, G. O., J. G. Sheals and D. MacFarland. 1961. *The Terrestrial Acari of the British Isles. Volume I. Introduction and Biology*, British Museum (Nat. Hist.), London. 219 pp.

Finnegan, D. J. 1985. Transposable elements in eukaryotes. *Int. Rev. Cytol.* 93:281–326.

Finnegan, D. J. 1989. Eukaryotic transposable elements and genome evolution. *Trends in Genetics* 5:103–107.

Finnegan, D. J. 1990. Transposable elements. *Drosophila Inf. Serv.* 68:371–382.

Finnegan, D. J. and D. H. Fawcett. 1986. Transposable elements in *Drosophila melanogaster*. *Oxford Surveys of Eukaryotic Genes*, Vol. 3 (N. Maclean ed.). Oxford Univ. Press, London. Pp. 1–62.

Good, A. G., H. Brock, T. A. Grigliatti and D. Hickey. 1989. Rapid spread of transposable *P* elements in experimental populations in the genus *Drosophila melanogaster*. *Genetics* 122:387–396.

Hagemann, S., W. J. Miller and W. Pinsker. 1990. P-related sequences in *Drosophila bifasciata*: a molecular clue to the understanding of *P*-element evolution in the genus *Drosophila*. *J. Mol. Evol.* 31:478–484.

Hammen van der, L. 1964. The morphology of *Glyptholaspis confusa* (FOA, 1900) (Acarina, Gamasina). *Zool. Verh.* 71:1–56.

Harris, L. J., D. L. Baillie, and A. M. Rose. 1988. Sequence identity between an inverted repeat family of transposable elements in *Drosophila* and *Caenorhabditus*. *Nucleic Acids Res.* 16:5993–5998.

Hickey, D. A. 1982. Selfish DNA: a sexually transmitted nuclear parasite. *Genetics* 101:519–535.

Houck, M. A., J. B. Clark, K. R. Peterson and M. G. Kidwell. 1991. Possible horizontal transfer of *Drosophila* genes by the mite *Proctolaelaps regalis*. *Science* 253:1125–1129.

Hughes, A. M. 1976. *The Mites of Stored Food and Houses*. Minist. Agric. Fish. Food Tech. Bull. No. 9. H.M.S.O., London. 400 pp.

Iwamura, Y., Y. Irie, R. Kominami, T. Nara and K. Yasuraoka. 1991. Existence of host-related DNA sequences in the schistosome genome. *Parasitology* 102:397–403.

Kidwell, M. G. 1979. Hybrid dysgenesis in *Drosophila melanogaster*: the relationship between the P-M and I-R interaction systems. *Genet. Res.* 33:205–217.

Kidwell, M. G. 1983. Evolution of hybrid dysgenesis determinants in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci.* USA 80:1655–1659.

Kidwell, M. G. 1986. Molecular and phenotypic aspects of the evolution of hybrid dysgenesis systems. In: *Evolutionary Processes and Theory* (S. Karlin and E. Nevo eds). Academic Press, NY. Pp. 169–198.

Kidwell, M. G., J. F. Kidwell and J. A. Sved. 1977. Hybrid dysgenesis in *Drosophila melanogaster*: a syndrome of aberrant traits including mutation, sterility, and male recombination. *Genetics* 86:813–833.

Kidwell, M. G. and J. B. Novy. 1979. Hybrid dysgenesis in *Drosophila melanogaster*: sterility resulting from gonadal dysgenesis in the P-M system. *Genetics* 92:1127–1140.

Kidwell, M. G., J. B. Novy and S. M. Feeley. 1981. Rapid unidirectional change of hybrid dysgenesis potential in *Drosophila*. *J. Hered.* 72:32–38.

Kidwell, M. G., T. Frydryk and J. B. Novy. 1983. The hybrid dysgenesis potential of *Drosophila melanogaster* strains of diverse temporal and geographical origin. *Drosophila Inf. Serv.* 59:63–69.

Kidwell, M. G. and J. B. Novy. 1985. The distribution of hybrid dysgenesis determinants in North American populations of *Drosophila melanogaster*. *Drosophila Inf. Serv.* 61:97–100.

Kidwell, M. G., K. Kimura and D. M. Black. 1988. Evolution of hybrid dysgenesis potential following *P* element contamination in *Drosophila melanogaster*. *Genetics* 119:815–828.

Kiyasu, P. K. and M. G. Kidwell. 1984. Hybrid dysgenesis in *Drosophila melanogaster*: the evolution of mixed P and M populations maintained at high temperature. *Genet. Res.* 44:251–259.

Konieczny, A., D. F. Voytas, M. P. Cummings and F. M. Ausubel. 1991. A superfamily of *Arabidopsis thaliana* retrotransposons. *Genetics* 127:801–809.

Krantz, G. W. 1978. *A Manual of Acarology*, 2nd ed. Oregon State Univ. Book Stores, Corvallis, OR. 509 pp.

Lansman, R. A., S. N. Stacey, T. A. Grigliatti and H. W. Brock. 1985. Sequences homologous to the *P* mobile element of *Drosophila melanogaster* are widely distributed in the subgenus Sophophora. *Nature* 318:561–563.

Lindquist, E. E. 1965. Taxonomic concepts in the Ascidae, with a modified setal nomenclature for the idiosoma of the Gamasina (Acarina: Mesostigmata). *Mem. Entomol. Soc. Can.* 47:1–65.

Lindquist, E. E. 1971. New species of Ascidae (Acarina: Mesostigmata) associated with forest insect pests. *Can. Entomol.* 103:919–942.

MacKay, T. F. 1985. Transposable element-induced response to artificial selection in *Drosophila melanogaster*. *Genetics* 111:351–374.

Maruyama, K. and D. Hartl. 1991. Evidence for interspecific transfer of the transposable element mariner between *Drosophila* and *Zaprionus*. *J. Mol. Evol.* 33:514–524.

Mathys, G. and Y. Tencalla. 1959. Note preliminaire sur la biologie et la valeur predatrice de *Proctolaelaps hypudaei* Oudms. (Acarien, Mesostigmata, Aceosejidae). *Annu. Agric. Suisse* 60:645–654.

McClintock, B. 1948. Mutable loci in maize. *Carnegie Inst. Wash. Yrbk.* 47:155–169.

Miller, D. W. and L. K. Miller. 1982. A virus mutant with an insertion of a *copia*-like transposable element. *Nature* 299:562–564.

Mizrokhi, L. J. and A. M. Mazo. 1990. Evidence for horizontal transmission of the mobile element *jockey* between distant *Drosophila* species. *Proc. Natl. Acad. Sci.* 87:9216–9220.

Montchamp-Moreau, C., G. Périquet and D. Anxolabéhère. 1991. Interspecific transfer of *P* elements by crosses between *Drosophila simulans* and *Drosophila mauritiana*. *J. Evol. Biol.* 4:131–140.

Muma, M. H. 1961. *Mites associated with citrus in Florida*. Bull . Univ. Fla. Agric. Exp. Sta. 640 pp.

Muma, M. H. 1975. *Mites associated with citrus in Florida*. Bull. 640 A, Agric. Exp. Sta. Instit. Food and Agric. Sci. Univ. Florida, Gainsville. 92 pp.

Nesbitt, H. H. J. 1951. A taxonomic study of the Phytoseiinae (family Laelapidae) predaceous upon Tetranychidae of economic importance. *Zool. Verh.* vol.12 (64 pp).

O'Hare, K. and G. M. Rubin. 1983. Structures of *P* transposable elements of *Drosophila melanogaster* and their sites of insertion and excision. *Cell* 34:25–35.

Patterson, J. T. and W. S. Stone. 1952. *Evolution in the genus Drosophila*. Macmillan, NY.

Radovsky, F. J. 1985. Evolution of Mammalian Mesostigmate mites. In: *Coevolution of Parasitic Arthropods and Mammals* (K. C. Kim ed.). Wiley, NY. 800 pp.

Rio, D. C., F. A. Laski and G. M. Rubin. 1986. Identification and immunochemical analysis of biologically active *Drosophila P* element transposase. *Cell* 44:21–32.

Rubin, G. M. 1983. Dispersed repetitive DNAs in *Drosophila*. In: *Mobile Genetic Elements* (J. A. Shapiro ed.). Academic Press, NY. 688 pp.

Rubin, G. M. and A. C. Spradling. 1982. Genetic transformation of *Drosophila* with transposable element vectors. *Science* 218:348–353.

Rubin, G. M., M. G. Kidwell and P. M. Bingham. 1982. *Cell* 29:987–994.

Schaefer, R. E., M. G. Kidwell and A. Fausto-Sterling. 1979. Hybrid dysgenesis in *Drosophila melanogaster*: morphological and cytological studies of ovarian dysgenesis. *Genetics* 92:1141–1152.

Snyder M. and W. F. Doolittle. 1988. *P* elements in *Drosophila*: selection at many levels. *Trends in Genetics* 4:147–149.

Spradling, A. C. and G. M. Rubin. 1982. Transposition of cloned *P* elements into *Drosophila* germline chromosomes. *Science* 218:341–347.

Steller, H. and V. Pirrotta. 1985. Fate of DNA injected into early *Drosophila* embryos. *Dev. Biol.* 109:54.

Throckmorton, L. H. 1975. The phylogeny, ecology and geography of *Drosophila*. In: *Handbook of Genetics*, Vol. 3 (R. C. King ed.). Plenum Press, NY. Pp. 421–469.

Todo, T., Y. Sakoyama, S. I. Chigusa, A. Fukunga, T. Honjo and S. Kondo. 1984. Polymorphism in distribution and structure of *P* elements in natural populations of *Drosophila melanogaster* in and around Japan. *Jpn. J. Genet.* 59:441–451.

Wernz, J. G. and G. W. Krantz. 1976. Studies on the function of the tritosternum in selected Gamasida (Acari). *Can. J. Zool.* 54:202–213.

Woolley, A. 1988. *Acarology: Mites and Human Welfare*. John Wiley and Sons, NY. 484 pp.

Xiong, Y. and Eickbush, T. H. 1988. Similarity of reverse transcriptase-like sequences of viruses, transposable elements and mitochondrial introns. *Mol. Biol. Evol.* 5:675–690.

4

Evolution of Life-History Patterns in the Phytoseiidae

Maurice W. Sabelis and Arne Janssen

CONTENTS

1. Introduction

Among mites that inhabit plants, the Phytoseiidae rank as being well studied with respect to their life-history patterns and capacity for population increase. The number of published papers on the Phytoseiidae (between 1950–1991) is not much less than that for economically important phytophagous mites; there are *c.* 150 papers on Phytoseiidae, compared to *c.* 200 for the Tetranychidae (phytophagous spider mites). The impetus to study life-history patterns in detail comes from the successful use of the Phytoseiidae as predators to control phytophagous mites on agricultural crops (Helle and Sabelis 1985a, 1985b). Fortunate as this abundance of Phytoseiidae literature may seem to anyone interested in studying life-history patterns, there is a danger that the range of species studied is biased towards phytoseiids that are successful predators of economically important plant mites. This would be a serious problem when research hypotheses merely emerge from comparisons among life-history data, but less so when hypotheses stem from more general considerations about the ecological conditions under which life histories may have evolved. Hence, the approach taken here is to formulate hypotheses independent of the actual life-history data. Support by the data does

not mean that the hypotheses hold true, but merely that they are not rejected thus far. The data are only used to falsify hypotheses, and to stimulate thought on more precise hypotheses and more critical tests.

What follows first is a literature review of life-history traits of phytoseiid mites (excluding such aspects as survival, diapause, and dependence on abiotic factors), i.e. rate of development, fecundity and sex ratio. This review relates to the relevant literature published up to mid-1991. As such, it is an updated version of an earlier paper reviewing the literature up to mid-1984 (Sabelis 1985a, 1985b, 1985c, 1985d).

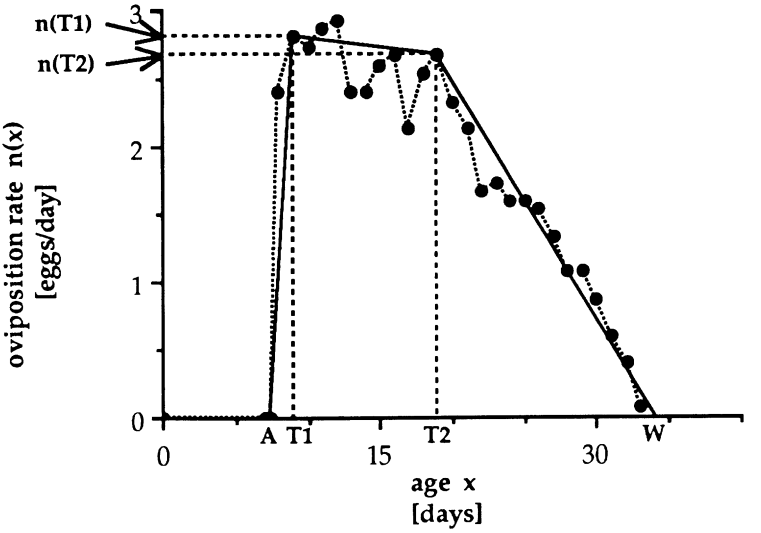
Subsequently, we will argue why local populations of phytoseiid mites are likely to be transient, and then proceed by formulating hypotheses on life-history trends under unconstrained *r*-selection and by testing them using the literature data. Deviations from these hypotheses serve to indicate possible constraints on life-history evolution. Finally, we formulate and discuss a new hypothesis that takes these constraints into account.

2. Criteria for Data Selection

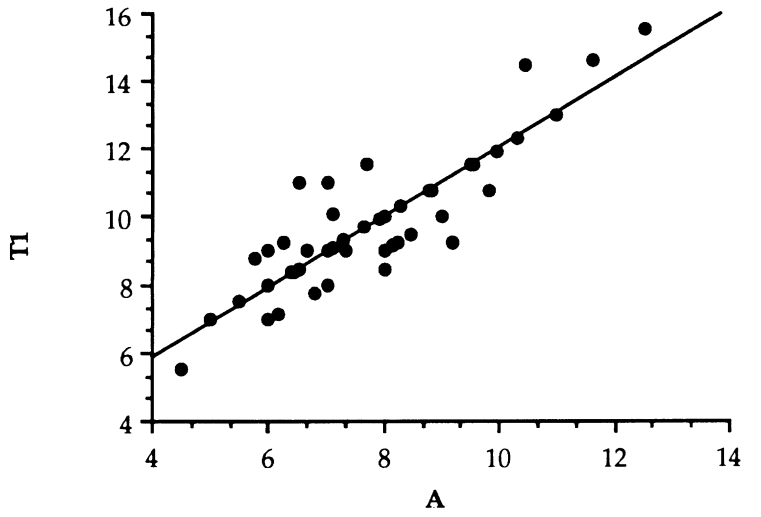
Life-history studies show quite some variation in experimental setup. For example, studies are done at different temperatures, with various food types, and with groups of females or isolated individuals. For these reasons, data were selected according to the following criteria: (1) an ample supply of tetranychids should be offered as prey; (2) temperature should fall within the range of 23°–27°C, and preferably be equal to 25°C; (3) sex ratio should be assessed in the offspring of isolated females; (4) peak and/or mean rates of oviposition should be presented; (5) the intrinsic rate of increase should be calculated from a life table using Lotka's equation (and not from approximating formulas based on simplified reproduction schedules). The data selected are listed in Appendix 4.1 and Appendix 4.2.

3. Review of the Literature

To elucidate what life-history patterns are common among mites and which salient properties pertain to the mite group under consideration, it is useful to compare life-history trends in the Phytoseiidae (Acari: Mesostigmata) with those observed in other mite families. To date, such a comparison can only be made with data from the Tetranychidae (spider mites), as compiled by Sabelis (1991) according to the same selection criteria. This family of phytophagous mites belongs to the order Prostigmata, but, being phytophagous, these mites live in the same microhabitat as phytoseiid mites and have a similar body size. Furthermore, they represent a very important prey item on the menu of phytoseiid mites. Hence, comparison of their life histories goes beyond that of comparing families with

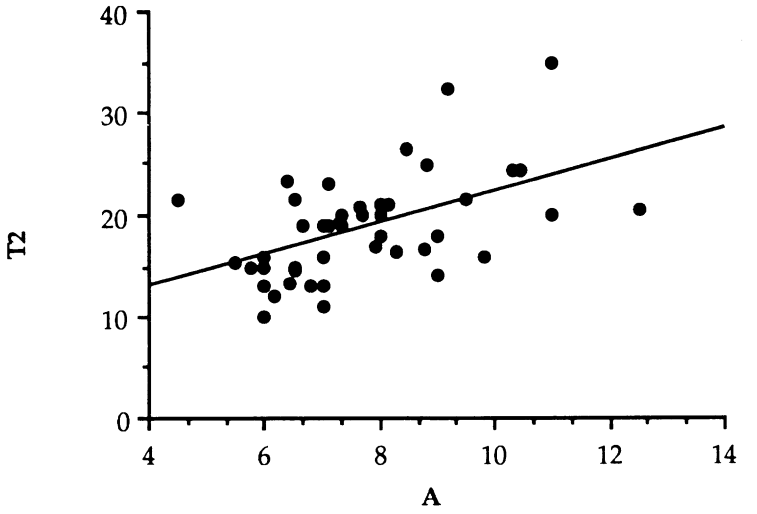


(A)

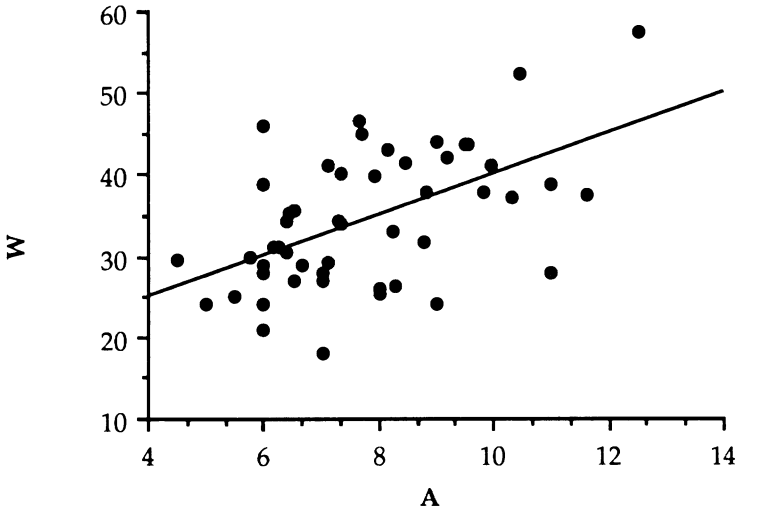


(B)

Figure 4.1. A generalized reproduction schedule of phytoseiid mites. A) An example of a typical reproduction schedule: Data for *Amblyseius idaeus* (Dinh et al. 1988). The *x*-axis gives the age of the female (x). The symbols A, T_1, T_2 and W represent the age at first oviposition, age at the start of peak oviposition, age at the end of the peak oviposition period and age at the end of the oviposition period. The *y*-axis shows the ovipositional rate ($n(x)$). B) Correlation and regression between A and T_1 : $T_1 = 1.73 + 1.03A$ (54 data points; $R^2 = 0.789$). C) Correlation and regression between A and T_2 : $T_2 = 6.76 + 1.56A$ (45 data points; $R^2 = 0.261$). D) Correlation and regression between A and W : $W = 15.2 + 2.47A$ (51 data points; $R^2 = 0.282$).



(C)



(D)

Figure 4.1. (Continued)

widely different phylogenies: it is a comparison of ecological life styles (i.e. predator vs. prey).

Consider the reproduction curves of the species in the families Phytoseiidae and Tetranychidae. Lewontin (1965) suggested that reproduction curves are often triangular. Indeed, the reproduction curves of spider mites generally have such

a form (Sabelis 1991). The rate of oviposition steeply rises to a peak soon after the onset of reproduction, and then decreases gradually. This triangular curve was also observed in phytoseiid mites, but only in less than 20% of the cases. The more general form was a trapezoid, of which an example is shown in Figure 4.1A (following Lewontin's notation as closely as possible). As in spider mites, the ovipositional rate ($\bar{n}(x)$) rapidly increases from the beginning of the reproduction period (A) until it reaches a peak at age T_1, but it then levels off, with a slight increase or decrease towards the end of this plateau phase (T_2). It subsequently decreases until it becomes zero at the end of reproductive life (W). We define peak rate of oviposition as the rate of oviposition at age T_1 (i.e. $n(T_1)$), and the mean rate of oviposition ($\bar{n}(x)$) as the average over the entire reproductive period (from age A to W).

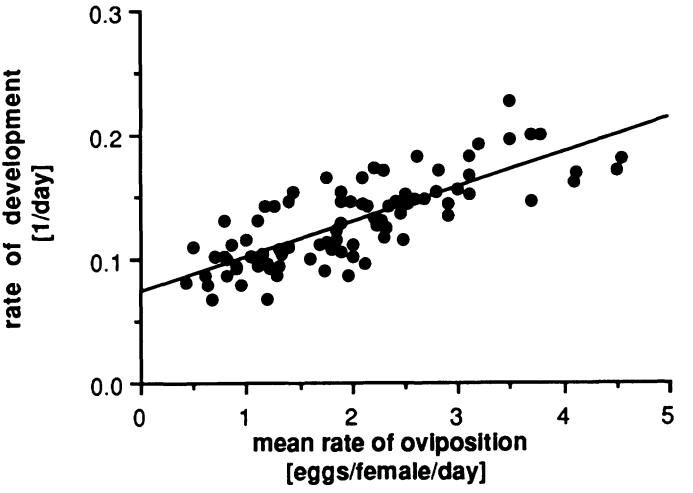
Although the trapezoid qualitatively seems the most common shape of the reproduction curve, its dimensions may vary considerably. Figure 4.1B shows that the age at peak oviposition, T_1, follows within two days after the onset of oviposition at age A and that T_1 is linearly and positively correlated with A; however, as shown in Figure 4.1C and 4.1D, the age at the end of peak oviposition (T_2) and the age at last oviposition (W) are much less associated with A. In conclusion one may consider the reproduction curve to approximate a rectangular trapezoid of rather variable form.

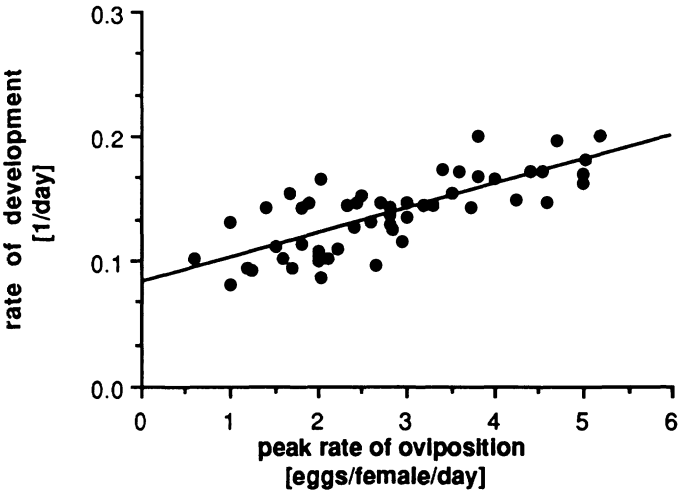
In Figure 4.2A the rate of development is regressed on the (mean or peak) rate of oviposition and in Table 4.1 the reverse regression is given. There is unambiguous evidence for a linear relation. This is in contrast to what has been found for spider mites (Sabelis 1985e, Sabelis 1991). The correlations in the latter taxonomic group is clearly non-linear, indicating that the developmental rates may reach a maximum, whereas oviposition continues to increase.

For phytoseiid mites, the best-fitting regression models are linear, suggesting the absence of a maximum developmental rate. Much the same conclusions can be drawn by considering the relation between fecundity and the rate of development (Table 4.1). For phytoseiid mites this relation is linear, whereas for spider mites it is non-linear. When considering the relation between fecundity and the rate of oviposition for both phytoseiid mites and spider mites (Fig. 4.2B and Table 4.1), the relations do not deviate from linearity. Thus, there is no reason to assume that there is a physiological maximum to either of the two traits.

Figure 4.2C and Table 4.1 show that for phytoseiid mites the proportion of daughters increases starting from 57% up to 91% with the mean and peak rate of oviposition (Sabelis and Nagelkerke 1992). In contrast to earlier reports on logarithmic relations (Sabelis 1985d, Sabelis and Nagelkerke 1988), the extended data set here is described somewhat better by a linear relationship. For spider mites, sex ratios are also always female biased (varying from 55%–91% daughters), but there is no significant correlation with the ovipositional rate (Sabelis 1991 and Table 4.1).

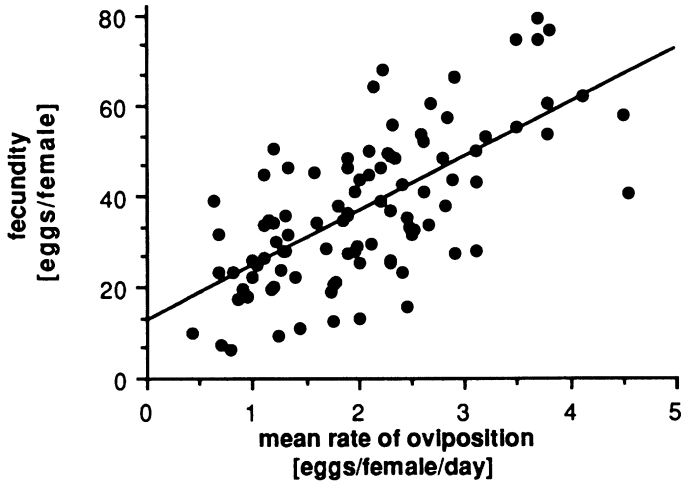
Given that the life-history traits underlying the population growth capacity are

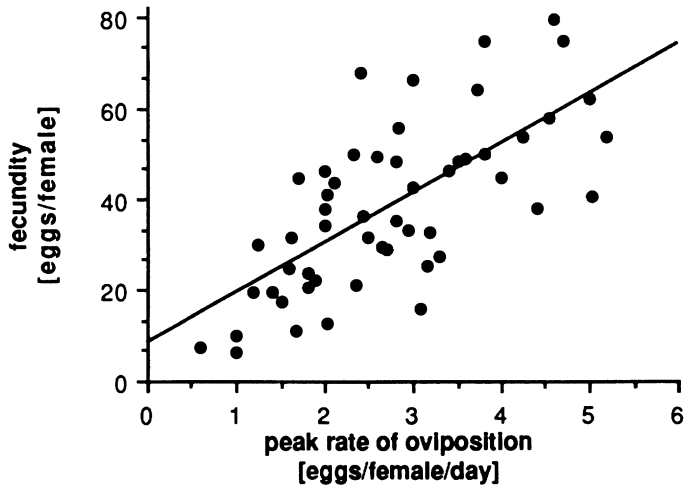




(A)

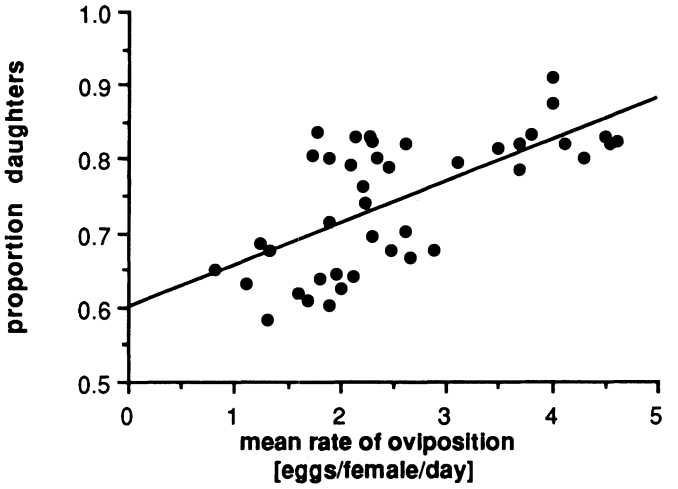
Figure 4.2. Correlations and regressions between various life-history components and either peak or mean rate of oviposition. A) Regression of rate of development on mean (87 data points, $R^2 = 0.619$, $y = 0.0740 + 0.028\,x$) and peak (52 data points, $R^2 = 0.576$, $y = 0.083 + 0.019\,x$) rate of oviposition. B) Regression of fecundity on mean (97 data points, $R^2 = 0.45$, $y = 12.4 + 12.0\,x$) and peak (54 data points, $R^2 = 0.48$, $y = 8.5 + 10.9\,x$) rate of oviposition. C) Regression of proportion daughters in the offspring on mean (42 data points, $R^2 = 0.43$, $y = 0.60 + 0.056\,x$) and peak (28 data points, $R^2 = 0.21$, $y = 0.61 + 0.040\,x$) rate of oviposition. D) Regression of the intrinsic rate of increase on mean (45 data points, $R^2 = 0.76$, $y = 0.07 + 0.075\,x$) and peak (38 data points, $R^2 = 0.83$, $y = 0.05 + 0.069\,x$) rate of oviposition.

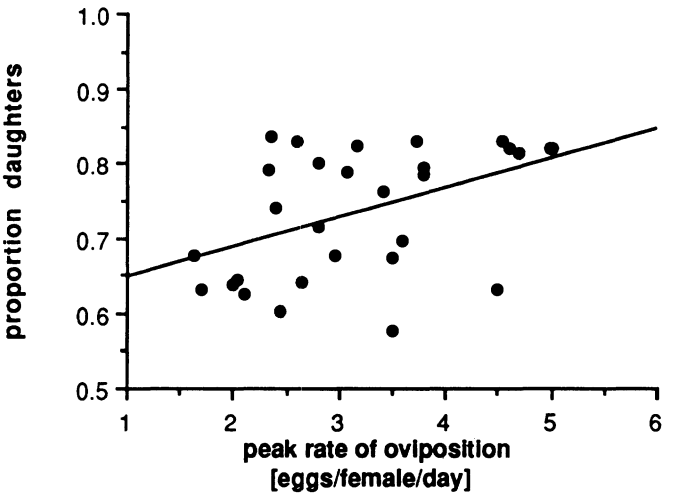




(B)

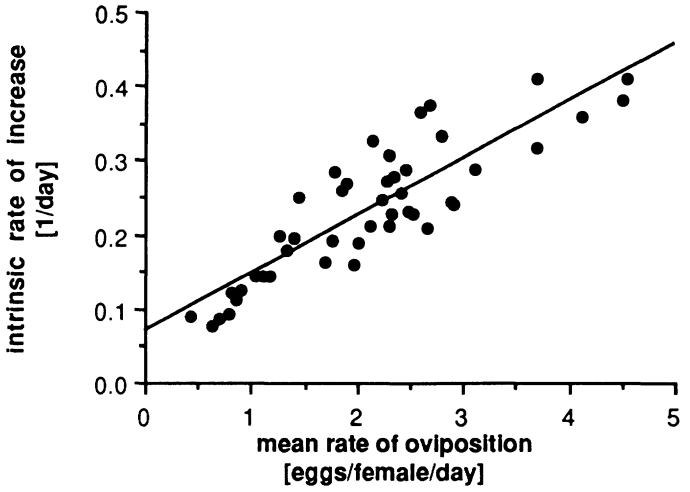
Figure 4.2. (Continued)

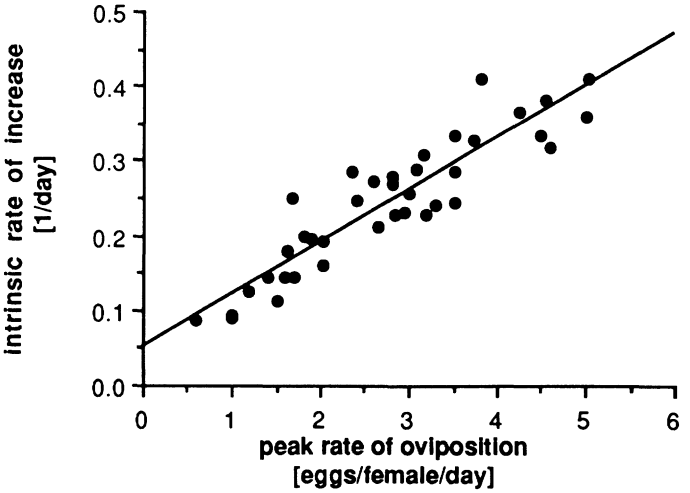




(C)

Figure 4.2. (Continued)





(D)

Figure 4.2. (Continued)

Table 4.1. Regression equations and correlation coefficients between life history traits of phytoseiid mites and tetranychid mites (Janssen and Sabelis 1992, Sabelis 1990). Note that N represents the number of data pairs and R^2 is the square of the correlation coefficient. The regression equations and correlations obtained merely serve descriptive purposes. Error in the x-variables, such as ovipositional rate and developmental rate, is usually quite small, justifying the use of univariate regression.

Variable				
Independent	Dependent	R^2	Regression Equation	N
PHYTOSEIID MITES:				
Rate of Development	Mean Rate of Oviposition	0.619	$y = -0.885 + 22.15\,x$	87
	Peak Rate of Oviposition	0.576	$y = -1.296 + 29.75\,x$	52
	Fecundity	0.232	$y = 9.24 + 219.5\,x$	76
	Sex Ratio	0.434	$y = 0.503 + 1.67\,x$	28
	r_m	0.637	$y = -0.119 + 2.66\,x$	37
Mean Rate of Oviposition	Rate of Development	0.619	$y = 0.074 + 0.028\,x$	87
	Fecundity	0.450	$y = 12.4 + 12.0\,x$	97
	Sex Ratio	0.432	$y = 0.60 + 0.056\,x$	42
	r_m	0.755	$y = 0.07 + 0.075\,x$	45
Peak Rate of Oviposition	Rate of Development	0.576	$y = 0.083 + 0.019\,x$	52
	Fecundity	0.478	$y = 8.5 + 10.9\,x$	54
	Sex Ratio	0.213	$y = 0.61 + 0.04\,x$	28
	r_m	0.834	$y = 0.053 + 0.069\,x$	38
TETRANYCHID MITES:				
Rate of Development	Peak Rate of Oviposition	0.639	$y = 0.7 * 10^{11.82x}$	45
	Fecundity	0.485	$y = 7.85 * 10^{11.51x}$	44
	Sex Ratio	0.063	—	37
	r_m	0.631	$y = -0.007 + 2.67\,x$	40
Mean Rate of Oviposition	Rate of Development	0.235	$y = 0.06 + 0.0041\,x$	27
	Fecundity	0.578	$y = 1.81 + 0.031\,x$	26
	Sex Ratio	0.123	—	18
	r_m	0.646	$y = 0.123 + 0.012\,x$	32
Peak Rate of Oviposition	Rate of Development	0.564	$y = 0.039 + 0.022 \log x$	45
	Fecundity	0.717	$y = 1.425 + 11.5\,x$	37
	Sex Ratio	0.044	—	34
	r_m	0.550	$y = 0.013 + 0.011\,x$	35

linearly interrelated, what would one expect of the relation with r_m (intrinsic rate of increase of a population)? Considering the data presented in Figure 4.2D and Table 4.1, the r_m of phytoseiid mites is linearly related to the rate of development and the (mean or peak) rate of oviposition. The same type of relation was found for spider mites (Sabelis 1991, Janssen and Sabelis 1992). Why this is the case, will be discussed after the next section, in which the data are scrutinized for the effects of overrepresentation of species or genera.

4. Within-Species, Within-Genus and Between-Genus Trends

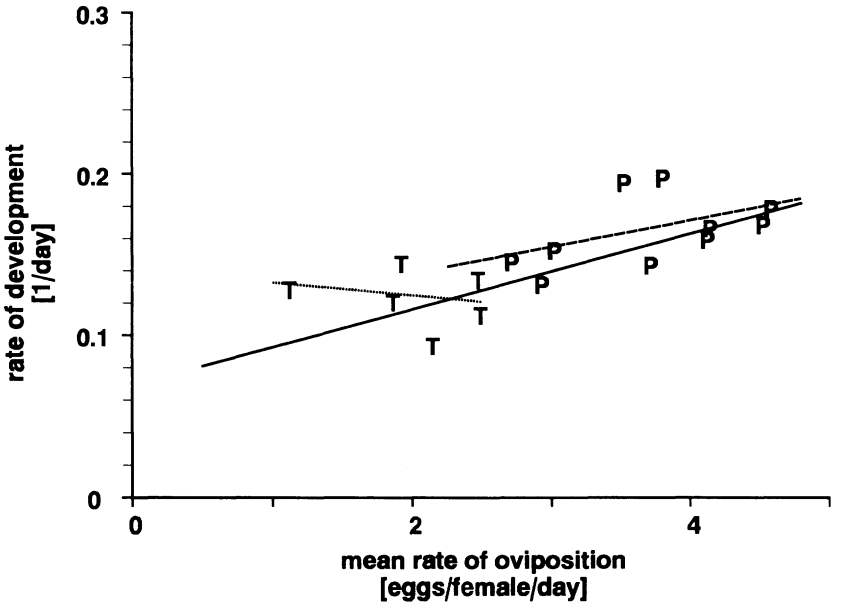
One may wonder to what extent these results are biased by overrepresentation of some species in the data set, especially *Phytoseiulus persimilis* and *Typhlodromus occidentalis* (represented by 10 and 6 data pairs respectively in the data set concerning developmental and ovipositional rates). Figure 4.3A shows that the data of *P. persimilis* alone have a trend of rates of development increasing with mean rates of oviposition in the range of 2.5–5.0 eggs per day. This trend is quite close to the overall regression of the rate of development on the mean rate of oviposition based on averages per species. This suggests that the trends within species conform to those between species, but more rigorous tests are needed. Unfortunately, the few data available for *T. occidentalis* (Fig. 4.3A) vary over a rather small range and are too clustered to negate the hypothesis that within-species trends conform to between-species trends.

Another bias may result from overrepresentation of particular genera. To investigate this effect, Figure 4.3B shows within-genus trends (where means/species are shown and each data set per species is represented by a character indicating the genus). Considering the well represented genera, *Amblyseius* and *Typhlodromus*, the within-genus regression lines conform quite closely to the overall regression lines (albeit that the former is somewhat higher and the latter is systematically lower!). The data of the less represented genera, *Phytoseius* and *Phytoseiulus*, are remarkably close to the overall regression line, which strongly argues for conformity of within-genus trends and within-family trends. In all further analyses we assume that this conformity holds true, making overrepresentation of species or genera less of a problem. However, this assumption needs scrutiny in future investigations.

5. Reproduction Schedules and Their Effect on the Intrinsic Rate of Increase (r_m)

That r_m is linearly related to the rate of oviposition is surprising when considering the following model for the relation between r_m, net reproductive rate (R_0) and the rate of development ($1/A$) for the simple case of big-bang reproduction (a single, large clutch of eggs produced immediately when reaching the reproduction phase):

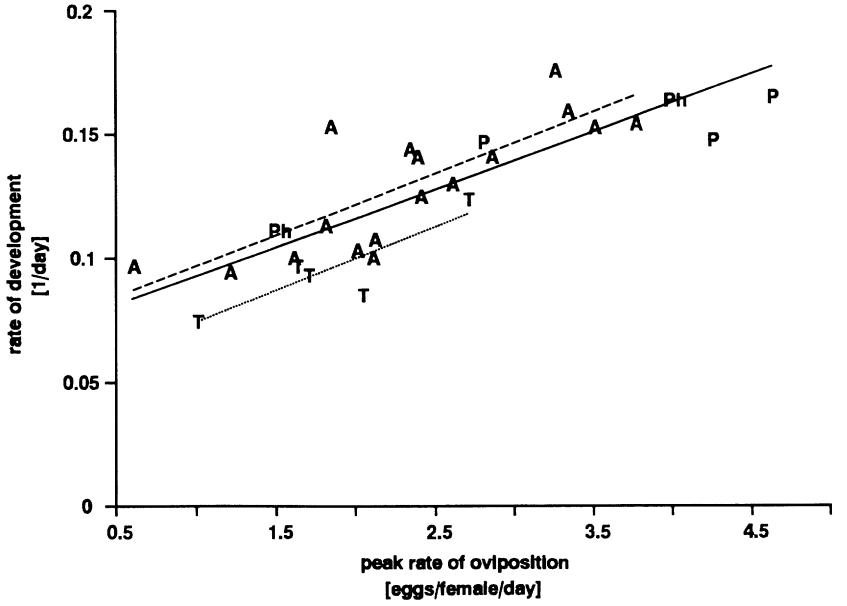
$$r_m = \ln (R_0)/A$$



(A)

Figure 4.3. Examples of within-species and within-genus correlations and regressions. A) Correlations and regressions between mean rate of oviposition and the rate of development for two species of the Phytoseiidae. Shown are the regression lines for *Phytoseiulus persimilis* (dashed line; 10 data points, $R^2 = 0.25$, $y = 0.10 + 0.016\ x$), *Typhlodromus occidentalis* (dotted line; 6 data points, $R^2 = 0.05$, $y = 0.14 - 0.008\ x$) and for all species (drawn line; 48 data points, $R^2 = 0.568$, $y = 0.064 + 0.032\ x$). B) Correlations and regressions between peak rate of oviposition and rate of development for four genera of the Phytoseiidae. Each data point represents the average value per species and is indicated by a character referring to the genus: **A.** = *Amblyseius*, **P.** = *Phytoseiulus*, **Ph.** = *Phytoseius* and **T.** = *Typhlodromus*. Shown are the regression lines for all species (drawn line; 27 data points, $R^2 = 0.67$, $y = 0.069 + 0.024\ x$), for *Amblyseius* (broken line; 17 data points, $R^2 = 0.64$, $y = 0.072 + 0.025\ x$) and for *Typhlodromus* (dotted line; 5 data points, $R^2 = 0.76$, $y = 0.049 + 0.026\ x$).

Clearly, r_m is not linearly, but *logarithmically* related to R_0 (and thus also to the ovipositional rate) and *linearly* to the rate of development ($1/A$) (and thus also to the ovipositional rate via the regression in Figure 4.2A). However, for phytoseiid mites ovipositional and developmental rates covary, which may cause that the effect of one variable on r_m masks the effect of the other. To investigate this effect, a better approximation of r_m is needed than provided by the above formula (which for R_0 taken equal to fecundity times sex ratio grossly overestimates the r_m calculated by the Lotka equation, and for R_0 taken equal to the peak oviposi-



(B)

Figure 4.3. (Continued)

tional rate times the sex ratio grossly underestimates the r_m calculated by the Lotka equation). Such a simple, but better approximator is obtained by taking the reproduction schedule of Figure 4.5a as a starting point, further referred to as the Methuselah version. Here, oviposition reaches its peak immediately upon reaching the reproduction phase and remains so for ever. The formula for calculating r_m is presented in Appendix 4.3. Using this model and taking the linear regressions of the developmental rate and the sex ratio on the peak rate of oviposition (Fig. 4.2A, C) into account (while ignoring age-dependent mortality), the relation between r_m and the peak rate of oviposition becomes *linear* (Fig. 4.4), showing that the changes in the rate of development have a more profound effect on r_m than changes in the rate of oviposition.

Figure 4.4 also demonstrates another important conclusion, which emerges when comparing the Methuselah calculations (where mortality, the increase phase and the decrease phase in the oviposition curve are altogether ignored) and the Lotka calculations based on the full life table (including mortality and age related changes in oviposition). The difference between the two calculations is rather small and will become even less when taking juvenile mortality, the initial increase phase of the oviposition curve, mortality and oviposition later in life into account. Hence, there is little need to discriminate between reproduction schedules such as rectangular, triangular or trapezoid forms (Fig. 4.5b, c, d). The

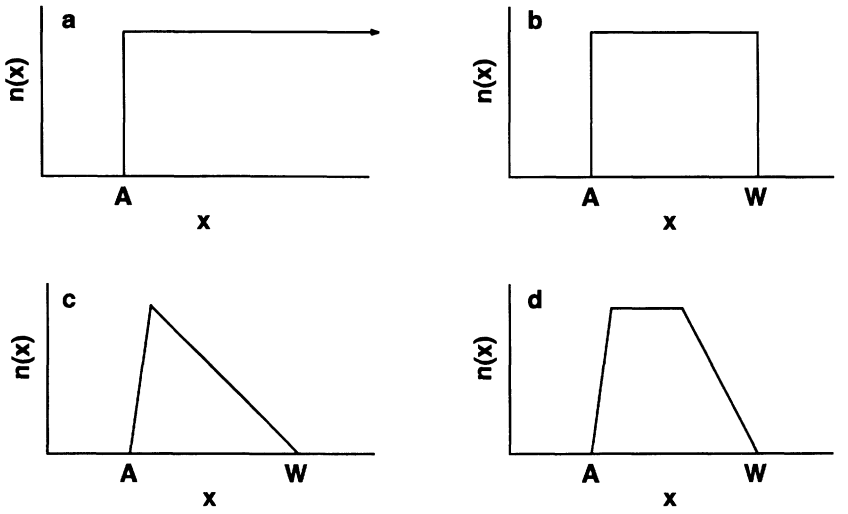


Figure 4.4. Four simplified age-specific reproduction functions (graphs of n(x) against x): (a) the Methuselah schedule; (b) the rectangular schedule; (c) the triangular schedule; (d) the trapezoid schedule.

caricature of Methuselah performs rather well and may therefore be considered to capture the essence of the traits relevant to r-selection. The reason for all this is that reproduction later in life is devalued in terms of its effect on r_m by a factor with a negative exponent including r_m and age x (i.e. exp ($-r_m x$) in the Lotka equation; see Appendix 4.3, Caswell and Hastings 1980, Caswell 1982).

6. Evolution of Life-History Patterns in the Phytoseiidae: an Hypothesis on Constraints

As argued by Sabelis (1991) local populations of spider mites are likely to be transient. Phytoseiid mites are among the causative factors that contribute to extinction of local spider mite populations (Sabelis and Van der Meer 1986, Janssen and Sabelis 1992). Consequently, local populations of phytoseiid mites go through high peaks and troughs, even more so when taking harsh weather conditions (e.g. wind, drought and rain) into account. Under these conditions selection for colonizing ability and for production of dispersers (i.e. r-selection) is likely to prevail. It may well be that fluctuations are less vigorous due to the presence of alternative food or the provision of shelter by host plants (*acarodomatia*). However, for one thing, alternative food is usually of low quality (honeydews, phloem exudates; see Bakker and Klein 1992) or deficient in some nutrients (e.g. pollen, see Dicke et al. 1986) and, for another, plant structures providing shelter can only decrease the impact of weather conditions, but not prevent

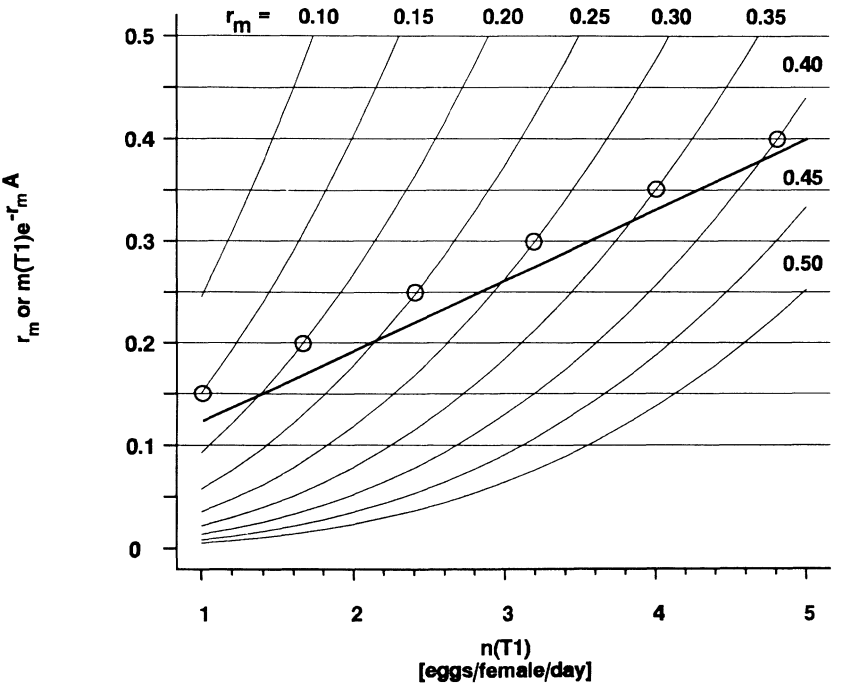


Figure 4.5. Estimation of r_m at various ovipositional rates, assuming that mortality is negligible ($l_x = 1$ for all values of x) and that the rate of oviposition (daughter production) reaches a peak (equal to $m(T_1) = n(T_1)\ s(T_1)$) immediately after the developmental period and remains indefinitely so (i.e. the Methuselah version of the Lotka equation). The estimation procedure is outlined in Appendix 4.3 and is visualized by the intersection (open dots) of the horizontal lines (with r_m on the y-axis) and the curves (with $m(T_1)\ \exp(-r_m A)$ for different values of r_m on the y-axis). The drawn line represents the regression of r_m on $n(T_1)$ (Figure 4.2D). In all calculations the developmental time, A, and the sex ratio $s(T_1)$ are treated as a function of the peak ovipositional rate, $n(T_1)$: $A = [0.084 + 0.019\ n(T_1)]^{-1}$ (see Figure 4.4A) and $s(T_1) = 0.61 + 0.04\ n(T_1)$ (see Figure 4.2C).

them. Moreover, it should be realized that either presence of alternative food or protection will not change the direction of the selective forces.

Returning to the life-history patterns underlying the capacity for population increase, the most salient conclusion is that most life-history traits of phytoseiid mites strongly covary in a positive and linear fashion. This suggests that all life-history traits can change simultaneously so as to increase r_m, and, thus, that there are no trade-offs between the traits involved. Why then, do not all phytoseiid species have a maximum rate of population increase? One possibility is that selection proceeds at a different pace for each species, but, given enough generations, the end product would be that all species ultimately multiply at a maximum

rate. The other possibility is that life-history evolution of the Phytoseiidae is determined primarily by external, rather than internal constraints.

Are there life-history phenomena indicating the presence of (external) constraints? Our review of life-history patterns of the Phytoseiidae did not show an upper asymptote on the rate of development, as was the case for spider mites (Sabelis 1991). Also, non-linearities were absent in all other regressions between life-history components. The only exception is the reproduction schedule, which one would expect to have a single peak early in the reproduction period. This is expected because: (1) shifting reproductive effort to younger ages (i.e. at the expense of reproduction later in life) is most effective in terms of increasing r_m, and because (2) selection on deleterious mutations becomes progressively weaker, the later in life they are expressed (Caswell and Hastings 1980, Caswell 1982). This would lead to evolution of reproduction schedules starting from the Methuselah type to the triangular type. Clearly, phytoseiid mites have a reproduction schedule of a rectangular trapezoid shape, which may be interpreted as 'a truncated triangle.' Moreover, as revealed by our analysis of life-history patterns, the most significant differences between species of phytoseiid mites are found in the timing and magnitude of peak oviposition. We suggest that the truncation of the triangle points to the presence of constraints in the process of egg production.

What determines the rate of egg production? As in most predatory arthropods (Sabelis 1992), this strongly depends on both food acquisition and conversion into egg biomass. Phytoseiid mites allocate a remarkably large fraction of food ingested to egg production. For example, *P. persimilis* converts 70% of the food ingested into eggs and it produces a daily egg biomass equal to its own body weight. In general, oviposition is strongly correlated with predation (Janssen and Sabelis 1992) and both reach an upper asymptote with increasing prey densities, but the level of the asymptotes differs between species. As shown by Sabelis (1986, 1990), the asymptotes are determined by gut capacity and the relative rate of gut emptying. Because egg size and gut volume are roughly in proportion to the size of the adult predator, the trait relevant to explaining the interspecific differences in asymptotes is the relative rate of gut emptying rather than the gut volume. Thus, our original question concerning the rate of egg production can now be rephrased as "What determines interspecific variation in the relative rate of gut emptying?" or "Why should not all predators have a maximal rate of gut emptying?"

We suggest that the relative rate of gut emptying (and conversion into egg biomass) has evolved into an optimum between prey intake rates and the costs associated with food conversion. If the predator would digest and convert slowly, it would save costs involved in food conversion, while loosing opportunity to produce more eggs per time unit. If the predator would be capable of rapid digestion and rapid conversion per unit biomass, it would use energy for food conversion at the expense of egg production. Hence there should be an optimum in the relative rate of food conversion, set by the rate of food intake. For this reason we suppose that the actual constraints are not physiological, but relate to

the densities of the preferred prey. There are good reasons to think that the diets of phytoseiid mites differ, that their prey preferences differ and that various prey types occur in widely different densities (Sabelis and Dicke 1985, Dicke et al. 1988). For example, spider mites do not only differ in the way they defend themselves against their predators, but their densities are partly species-specific and partly host-plant related. This has led to the concept of *characteristic prey densities* (Sabelis 1985e, 1991), which may not only be crucial for understanding life-history evolution of spider mites, but also to understand life-history evolution of phytoseiid mites, their main predators: characteristic prey densities determine the maximum predation rates, the optimal rates of food conversion and thus the (peak) rate of oviposition. In addition to explaining the evolution of the oviposition rate, characteristic prey densities may also be a key factor in explaining the evolution of sex ratios in phytoseiid mites (Sabelis 1985d, Sabelis and Nagelkerke 1988, Sabelis and Nagelkerke 1992).

To conclude, we suggest that the evolution of life-history patterns in the Phytoseiidae is critically dependent on the local distribution patterns of their prey and, as argued earlier (Sabelis 1991), the evolution of local distribution patterns of the prey may at least partly be determined by the impact of predation by phytoseiid mites. The extent to which life-history and distribution patterns are molded by coevolution, is a major question for future research.

Acknowledgments

We thank Andre de Roos for stimulating discussions and Tine Dijkman-Korzilius for moral support and a constant flow of coffee.

References

Bakker, F. M. and M. E. Klein. 1992. Transtrophic interactions in cassava. *Exp. Appl. Acarol.* 14:293–311.

Caswell, H. 1982. Life-history theory and the equilibrium status of populations. *Am. Nat.* 120:317–339.

Caswell, H. and A. Hastings. 1980. Fecundity, developmental time and population growth rate: an analytical solution. *Theor. Popul. Biol.* 17:71–79.

Dicke, M., M. W. Sabelis and A. Groeneveld. 1986. Vitamin A deficiency modifies the response of the predatory mite *Amblyseius potentillae* to a volatile kairomone of the two-spotted spider mite. *J. Chem. Ecol.* 12:1389–1396.

Dicke, M., M. W. Sabelis and M. de Jong. 1988. Analysis of prey preference in phytoseiid mites by using an olfactometer, predation models and electrophoresis. *Exp. Appl. Acarol.* 5:225–241.

Helle, W. and M. W. Sabelis. 1985a. *Spider Mites: Their Biology, Natural Enemies and Control*, Vol. 1 A. Elsevier, Amsterdam. 403 pp.

Helle, W. and M. W. Sabelis. 1985b. *Spider Mites: Their Biology, Natural Enemies and Control*, Vol. 1 B. Elsevier, Amsterdam. 458 pp.

Janssen, A. and M. W. Sabelis. 1992. Phytoseiid life-histories, local predator-prey dynamics, and strategies for control of tetranychid mites. *Exp. Appl. Acarol.* 14:233–250.

Lewontin, R. C. 1965. Selection for colonizing ability. In: *The genetics of colonizing species* (H. G. Baker and G. L. Stabbins eds.). Academic Press, NY. Pp. 79–94.

Sabelis, M. W. 1985a. Capacity for population increase. In: *Spider Mites, their Biology, Natural Enemies and Control*, Vol. 1 B (W. Helle and M. W. Sabelis eds). Elsevier, Amsterdam. Pp. 35–41.

Sabelis, M. W. 1985b. Development. In: *Spider Mites, their Biology, Natural Enemies and Control*, Vol. 1 B (W. Helle and M. W. Sabelis eds.). Elsevier, Amsterdam. Pp.43–53.

Sabelis, M. W. 1985c. Reproduction. In: *Spider Mites, their Biology, Natural Enemies and Control*, Vol. 1 B (W. Helle and M. W. Sabelis eds.). Elsevier, Amsterdam. Pp. 73–82.

Sabelis, M. W. 1985d. Sex Allocation. In: *Spider Mites, their Biology, Natural Enemies and Control*, Vol. 1 B (W. Helle and M. W. Sabelis eds.). Elsevier, Amsterdam. Pp. 83–94.

Sabelis, M. W. 1985e. Reproductive strategies. In: *Spider Mites, their Biology, Natural Enemies and Control*, Vol. 1 A (W. Helle and M. W. Sabelis eds.). Elsevier, Amsterdam. Pp. 265–278.

Sabelis, M. W. 1986. The functional response of predatory mites to the density of two-spotted spider mites. In: *Dynamics of Physiologically Structured Populations, Lecture Notes in Biomathematics 68* (J. A. J. Metz and O. Diekmann eds.). Springer, Berlin. Pp. 298–321.

Sabelis, M. W. 1990. How to analyze prey preference when prey density varies: a new method to discriminate between effects of gut fullness and prey type composition. *Oecologia* (Berl.) 82:289–298.

Sabelis, M. W. 1991. Life-history evolution of spider mites. In: *The Acari, Reproduction, Development and Life-History strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall, London. Pp. 23–49.

Sabelis, M. W. 1992. Predatory arthropods. In: *Natural Enemies: The Population Biology of Predators, Parasites, and Diseases* (M. J. Crawley ed.). Blackwell, Oxford. Pp. 225–264.

Sabelis, M. W. and M. Dicke. 1985. Long range dispersal and searching behaviour. In: *Spider Mites, their Biology, Natural Enemies and Control*, Vol. 1 B (W. Helle and M. W. Sabelis eds.). Elsevier, Amsterdam. Pp.141–160.

Sabelis, M. W. and J. Van der Meer. 1986. Local dynamics of the interaction between spider mites and predatory mites. In: *Dynamics of Physiologically Structured Populations, Lecture Notes in Biomathematics 68* (J. A. J. Metz and O. Diekmann eds.). Springer, Berlin. Pp 322–344.

Sabelis, M. W. and C. J. Nagelkerke. 1988. Evolution of pseudo-arrhenotoky. *Exp. Appl. Acarol.* 4:301–318.

Sabelis, M. W. and C. J. Nagelkerke. 1992. Sex allocation and pseudo-arrhenotoky in phytoseiid mites. In: *The Evolution and Diversity of Sex Ratio in Insects and Mites* (D. Wrensch and M. Ebbert eds.). Chapman and Hall, NY. Pp. 512–541.

Appendix 4.1. Characteristics of the reproductive schedule of phytoseiids. Ages are expressed in days since the start of the egg stage. (A. = Amblyseius, P. = Phytoseiulus, Ph. = Phytoseius, T. = Typhlodromus).

Species	A[a]	T_1	T_2[b]	W[c]	$n(T_1)$	$n(T_2)$[d]	References
A. aberrans	10.3	12.3	24.3	37.3	1.2	1.2	Kropczynska et al. 1988
A. andersoni	10.4	14.4	24.4	52.4	2.0	1.8	Amano & Chant 1977
A. anonymus	7.3	9.0	20.0	40.0	2.6	2.5	Van Dinh et al. 1988
A. bibens	6.5	8.5	21.5	35.5	3.7	3.0	Blommers 1976
A. bibens	6.4	8.4	13.4	35.4	3.8	3.4	Lababidi 1988
A. citrifolius	7.1	10.1	23.1	41.1	2.2	2.3	De Moraes & McMurtry 1981
A. cucumeris	9.5	11.5	.	43.5	2.0	.	Lababidi 1988
A. degenerans	7.7	9.7	20.7	46.7	2.4	2.8	Takafuji & Chant 1976
A. deleoni	6.5	8.5	14.5	.	3.5	2.7	Saito & Mori 1981
A. fallacis	6.3	9.3	.	31.3	3.4	.	Lababidi 1988
A. fallacis	7.1	9.1	19.1	29.1	2.5	2.7	Boyne & Hain 1983
A. fallacis	7.3	9.3	19.3	34.3	2.7	2.8	Boyne & Hain 1983
A. finlandicus	9.8	10.8	15.8	37.8	0.6	0.7	Kropczynska et al. 1988
A. idaeus	7.3	9.0	19.0	34.0	2.8	2.7	Van Dinh et al. 1988
A. idaeus	7.0	8.0	11.0	27.0	2.4	2.8	Janssen & Rook unpubl.
A. idaeus	6.0	7.0	10.0	21.0	3.2	3.6	Janssen & Rook unpubl.
A. idaeus	7.0	8.0	13.0	18.0	3.0	3.0	Janssen & Rook unpubl.
A. largoensis	8.8	10.8	16.8	31.8	1.8	2.0	Tanaka & Kashio 1977
A. longispinosus	6.4	8.4	.	30.4	3.6	.	Lababidi 1988
A. longispinosus	7.7	11.5	20.0	45.0	2.9	3.0	Lo & Ho 1979
A. longispinosus	4.5	5.5	21.5	29.5	3.8	3.4	Mallik & ChanaBassavanna 1983
A. longispinosus	5.5	7.5	15.5	25.0	4.5	2.5	Saito & Mori 1981
A. longispinosus	6.7	9.0	19.0	29.0	1.9	1.5	Shih & Shieh 1979
A. longispinosus	6.2	7.2	12.2	31.2	3.5	4.0	Xin et al. 1984
A. mckenziei	9.9	11.9	.	40.9	2.1	.	Lababidi 1988
A. mesembrinus	6.0	9.0	13.0	39.0	1.8	2.1	Abou-Setta & Childers 1989
A. mesembrinus	6.0	8.0	.	28.0	2.0	.	Abou-Setta & Childers 1989
A. mesembrinus	6.0	9.0	.	46.0	1.7	.	Abou-Setta & Childers 1989

A. ovalis	8.0	8.5	21.0	25.5	1.0	1.6	Shih & Shu unpubl.
A. ovalis	7.0	11.0	16.0	28.0	3.3	3.2	Shih & Shu unpubl.
A. ovalis	8.0	9.0	18.0	26.0	1.4	1.8	Shih & Shu unpubl.
A. ovalis	7.0	9.0	19.0	28.0	3.0	3.2	Shih & Shu unpubl.
A. ovalis	6.5	11.0	15.0	27.0	3.2	3.0	Shih & Shu unpubl.
A. paraki	8.0	10.0	20.0	.	3.5	2.3	Saito & Mori 1981
P. longipes	8.2	9.2	.	33.2	4.3	.	Badii & McMurtry 1984
P. macropilis	6.8	7.8	13.0	.	2.8	2.9	Shih et al. 1979
P. persimilis	8.1	9.1	21.1	43.1	3.0	3.7	Amano & Chant 1977
P. persimilis	5.0	7.0	.	24.0	5.0	.	Janssen & Bol unpubl.
P. persimilis	6.0	7.0	16.0	24.0	4.5	4.8	Janssen & Bol unpubl.
P. persimilis	6.0	7.0	15.0	29.0	5.0	4.2	Janssen & Bol unpubl.
P. persimilis	5.8	8.8	14.8	29.8	4.7	4.7	Lababidi 1988
P. persimilis	6.4	8.4	23.4	34.4	4.6	3.8	Takafuji & Chant 1976
P. soleiger	9.5	11.5	21.5	43.5	1.6	1.3	Kropczynska et al. 1988
Ph. macropilis	8.8	10.8	24.8	37.8	1.5	0.9	Kropczynska et al. 1988
T. exhilaratus	8.4	9.4	26.4	41.4	2.0	2.0	Castagnoli & Liguori 1986a
T. exhilaratus	9.2	9.2	32.2	42.2	1.3	1.0	Castagnoli & Liguori 1986a
T. exhilaratus	9.0	10.0	14.0	44.0	1.6	1.9	Castagnoli et al. 1989
T. floridanus	11.0	13.0	35.0	39.0	2.0	1.7	Tanigoshi & McMurtry 1977
T. occidentalis	8.3	10.3	16.3	26.3	2.8	2.9	Pruszynski & Cone 1973
T. occidentalis	11.0	13.0	20.0	28.0	2.6	2.7	Tanigoshi et al. 1975
T. occidentalis	9.0	10.0	18.0	24.0	3.0	2.7	Tanigoshi et al. 1975
T. occidentalis	7.9	9.9	16.9	39.9	2.4	2.4	Lababidi 1988
T. phialatus	12.5	15.5	20.5	57.5	1.7	2.3	Ferragut et al. 1987
T. pyri	11.6	14.6	.	37.6	1.0	.	Kropczynska et al. 1988

[a] A = Age at first reproduction

[b] T_1 and T_2 = Age at the first and second peak of oviposition

[c] W = Age at the end of the reproductive period

[d] $n(T_1)$ and $n(T_2)$ = Reproductive peaks (eggs/female/day).

Appendix 4.2. A summary of all data used for the review of life history characteristics of phytoseiids.

Species	Oviposition Mean	Oviposition Peak	Fec[a]	Dev[b]	r_m[c]	Sex[d] Ratio	Pred[e]	References
A. aberrans	0.89	1.20	19.4	0.095	0.126	.	.	Kropczynska et al. 1988
A. andersoni	1.32	2.00	46.3	0.104	.	.	.	Amano & Chant 1977
A. anonymus	2.27	2.60	49.2	0.131	0.274	0.830	12.4	Van Dinh et al. 1988
A. bibens	2.84	.	57.1	.	.	.	.	Bloomers & van Arendonk 1979
A. bibens	2.15	3.72	64.1	0.143	0.326	0.830	13.4	Blommers 1976
A. bibens	3.10	3.80	49.8	0.168	.	0.795	16.8	Lababidi 1988
A. bibens	4.62	.	.	.	.	0.823	.	Schulten et al. 1978
A. brazilii	0.50	.	.	0.110	.	.	.	El.Banhawy 1975
A. brazilii	0.60	.	.	0.087	.	.	.	El.Banhawy 1975
A. californicus	2.61	.	41.0	.	.	0.702	10.1	Friese & Gilstrap 1982
A. chilenensis	3.10	.	43.3	0.151	0.287	.	16.2	Ma & Laing 1973
A. citrifolius	2.10	2.33	49.7	0.145	.	0.793	.	De Moraes & McMurtry 1981
A. cucumeris	1.40	2.22	.	0.109	.	.	.	Dosse 1955
A. cucumeris	1.80	2.00	37.8	0.108	.	0.639	11.9	Lababidi 1988
A. degenerans	2.24	2.40	67.8	0.126	0.248	0.740	.	Takafuji & Chant 1976
A. deleoni	.	3.50	.	.	0.286	0.577	.	Saito & Mori 1981
A. fallacis	3.50	.	55.0	0.227	.	.	.	Ball 1980
A. fallacis	1.98	2.70	28.9	0.146	.	.	.	Boyne & Hain 1983
A. fallacis	2.50	2.50	31.4	0.152	.	.	.	Boyne & Hain 1983
A. fallacis	2.20	3.40	46.3	0.173	.	0.764	15.7	Lababidi 1988
A. fallacis	2.82	4.40	37.6	0.172	.	.	.	McClanahan 1968
A. fallacis	3.20	.	53.2	0.192	.	.	10.6	Smith & Newsom 1970a,b
A. finlandicus	0.90	.	.	0.093	.	.	.	Kropczynska 1970
A. finlandicus	0.69	0.60	7.2	0.102	0.087	.	.	Kropczynska et al. 1988
A. finlandicus	1.60	.	.	.	.	0.620	.	Sabelis unpubl.
A. fustis	1.73	.	19.1	0.091	.	0.806	.	Ezulike & Odebiyi 1985
A. gossypi	1.20	.	34.3	0.068	.	.	.	Rasmy & El.Banhawy 1975

A. idaeus	1.79	2.36	20.8	.	0.286	0.836	.	Janssen & Rook unpubl.
A. idaeus	2.30	3.16	25.4	.	0.309	0.824	.	Janssen & Rook unpubl.
A. idaeus	2.47	3.08	16.0	.	0.287	0.790	.	Janssen & Rook unpubl.
A. idaeus	2.35	2.80	48.2	0.142	0.279	0.800	12.8	Van Dinh et al. 1988
A. largoensis	1.75	1.80	20.6	0.114	.	.	.	Tanaka & Kashio 1977
A. limonicus	2.30	.	.	0.118	.	.	.	McMurtry & Scriven 1965
A. longispinosus	2.30	3.60	48.8	0.171	.	0.697	17.6	Lababidi 1988
A. longispinosus	2.33	2.85	55.6	0.125	0.229	.	.	Lo & Ho 1979
A. longispinosus	3.70	3.80	74.6	0.200	0.410	0.785	.	Mallik & ChanaBassavanna 1983
A. longispinosus	.	4.50	.	.	0.333	0.630	.	Saito & Mori 1981
A. longispinosus	1.39	1.90	22.2	0.146	0.194	.	10.7	Shih & Shieh 1979
A. masiaka	1.85	.	.	0.115	.	.	.	Blommers 1974
A. mckenzie	2.00	2.10	43.4	0.101	.	0.625	9.8	Lababidi 1988
A. mesembrinus	1.25	1.80	23.7	0.142	0.199	.	.	Abou–Setta & Childers 1989
A. mesembrinus	1.76	2.02	12.4	0.166	0.191	.	.	Abou–Setta & Childers 1989
A. mesembrinus	1.44	1.68	11.2	0.154	0.250	.	.	Abou–Setta & Childers 1989
A. ovalis	2.42	3.00	42.7	0.146	0.255	.	17.2	Shih & Shu unpubl. data
A. ovalis	0.79	1.00	6.5	0.131	0.094	.	.	Shih & Shu unpubl. data
A. ovalis	2.91	3.30	27.3	0.145	0.240	.	.	Shih & Shu unpubl. data
A. ovalis	1.16	1.40	19.4	0.142	0.145	.	.	Shih & Shu unpubl. data
A. ovalis	2.52	3.20	32.8	0.145	0.227	.	.	Shih & Shu unpubl. data
A. paraki	.	3.50	.	.	0.245	0.672	.	Saito & Mori 1981
A. potentillae	2.00	.	.	0.111	.	.	.	Overmeer 1981
A. potentillae	2.00	.	.	.	0.188	.	.	Sabelis 1985
A. pseudolongispinosus	2.80	3.50	48.5	0.154	0.332	.	.	Xin et al. 1984
A. soleiger	1.04	1.60	24.9	0.101	0.144	.	.	Kropczynska et al. 1988
A. teke	1.90	.	36.0	0.154	.	0.800	.	Ochieng et al. 1987
A. temperellus	1.20	.	50.2	0.096	.	.	.	Ball 1980
A. tetranychivorus	1.57	.	45.3	.	.	.	.	Gupta 1985
A. tetranychivorus	1.15	.	34.5	0.103	.	.	.	Krishnamoorty 1982
A. umbraticus	1.30	.	36.0	0.108	.	0.582	.	Knisley & Swift 1971

Continued

Appendix 4.2. Continued

Species	Oviposition Mean	Oviposition Peak	Fec[a]	Dev[b]	r_m[c]	Sex[d] Ratio	Pred[e]	References
P. longipes	2.59	4.25	53.6	0.149	0.366	.	.	Badii & McMurtry 1984
P. macropilis	2.20	.	38.9	0.133	.	.	.	Ball 1980
P. macropilis	2.62	.	51.8	0.183	.	0.820	6.1	Prasad 1967
P. macropilis	1.90	2.80	48.3	0.128	0.270	0.714	9.5	Shih et al. 1979
P. persimilis	2.91	3.00	66.3	0.134	.	.	.	Amano & Chant 1977
P. persimilis	0.20	.	.	.	.	.	9.0	Ashihara et al. 1978
P. persimilis	0.20	.	.	.	.	.	8.5	Ashihara et al. 1978
P. persimilis	1.90	.	.	.	.	.	28.1	Ashihara et al. 1978
P. persimilis	3.20	.	.	.	.	.	22.1	Ashihara et al. 1978
P. persimilis	3.50	.	.	.	.	.	24.6	Ashihara et al. 1978
P. persimilis	4.50	.	.	.	.	.	28.1	Ashihara et al. 1978
P. persimilis	2.69	.	60.4	0.148	0.374	.	.	Badii & McMurtry 1984
P. persimilis	3.80	.	76.5	.	.	0.834	25.0	Friese & Gilstrap 1982
P. persimilis	3.79	.	60.6	.	.	.	.	Gerlach & Sengonca 1985
P. persimilis	4.10	5.00	.	0.162	.	.	.	Hamamura et al. 1976
P. persimilis	4.56	5.02	40.7	0.181	0.410	0.820	.	Janssen & Bol unpubl.
P. persimilis	4.50	4.53	57.9	0.171	0.380	0.830	.	Janssen & Bol unpubl.
P. persimilis	4.12	4.99	62.2	0.169	0.360	0.820	.	Janssen & Bol unpubl.
P. persimilis	3.50	4.70	74.8	0.197	.	0.813	24.6	Lababidi 1988
P. persimilis	3.78	5.20	53.5	0.200	.	.	.	McClanahan 1968
P. persimilis	4.00	.	.	.	.	0.910	.	Nagelkerke unpubl.
P. persimilis	4.30	.	.	.	.	0.800	.	Sabelis unpubl.
P. persimilis	3.00	.	.	0.155	.	.	.	Sabelis 1981
P. persimilis	4.01	.	.	.	.	0.876	.	Schulten et al. 1978
P. persimilis	3.69	4.60	79.5	0.146	0.317	0.820	.	Takafuji & Chant 1976
P. plumifer	1.00	.	22.3	0.115	.	.	.	Rasmy & El. Banhawy 1975
Ph. hawaiiensis	0.87	.	.	.	.	.	11.9	Sanderson & McMurtry 1984

Ph. hawaiiensis	0.82	.	.	0.086	.	.	.	Sanderson & McMurtry 1984
Ph. hawaiiensis	0.68	.	31.4	0.068	.	.	.	Sanderson & McMurtry 1984
Ph. macropilis	0.85	1.50	17.1	0.112	0.113	.	.	Kropczynska et al. 1988
Ph. plumifer	2.10	4.00	44.8	0.165	.	.	.	Zaher et al. 1969
T. annectens	1.30	.	28.0	0.095	.	.	.	Badii et al. 1990
T. annectens	1.06	.	.	.	.	.	9.5	Badii et al. 1990
T. athiasae	1.10	.	26.4	0.099	.	.	.	Hessein 1977
T. bambusae	1.70	.	28.5	0.112	0.164	0.610	8.4	Saito 1990
T. exhilaratus	1.33	1.63	31.7	.	0.178	0.675	.	Castagnoli et al. 1989
T. exhilaratus	1.21	1.25	30.0	0.093	.	.	.	Castagnoli & Liguori 1986a
T. exhilaratus	1.61	2.00	34.4	0.100	.	.	.	Castagnoli & Liguoir 1986a
T. exhilaratus	0.82	.	22.9	0.100	0.122	0.650	.	Castagnoli & Liguori 1986b
T. floridanus	1.97	2.04	41.2	0.086	0.159	0.643	12.2	Tanigoshi & McMurtry 1977
T. longipilis	3.10	.	28.1	0.182	.	.	.	Ball 1980
T. longipilus	1.90	.	46.0	.	.	.	.	Burrell & McCormick 1964
T. longipilus	1.00	.	26.0	.	.	.	.	Burrell & McCormick 1964
T. longipilus	1.20	.	20.0	.	.	.	.	Burrell & McCormick 1964
T. occidentalis	1.84	.	34.5	0.123	0.260	.	.	Badii & McMurtry 1984
T. occidentalis	1.00	.	.	.	.	.	8.4	Badii et al. 1990
T. occidentalis	2.88	.	43.8	.	0.244	0.677	.	Bruce-Oliver & Hoy 1990
T. occidentalis	2.40	.	.	.	.	.	12.0	Bruce-Oliver & Hoy 1990
T. occidentalis	2.66	.	33.6	.	0.207	0.667	.	Bruce-Oliver & Hoy 1990
T. occidentalis	2.30	.	36.8	.	0.213	.	.	Croft 1972
T. occidentalis	1.23	.	9.4	.	.	0.685	14.4	Friese & Gilstrap 1982
T. occidentalis	2.30	.	25.6	.	.	.	.	Hoy 1984
T. occidentalis	2.40	.	22.9	.	.	.	.	Hoy 1984
T. occidentalis	1.95	.	27.8	.	.	.	.	Hoy 1984
T. occidentalis	2.00	.	25.3	.	.	.	.	Hoy 1984
T. occidentalis	2.00	.	13.4	.	.	.	.	Hoy 1984
T. occidentalis	1.90	2.44	36.3	0.147	.	0.603	15.8	Lababidi 1988
T. occidentalis	2.30	.	.	.	.	.	9.8	Pruszynski & Cone 1973

Continued

Appendix 4.2. Continued

Species	Oviposition Mean	Oviposition Peak	Fec[a]	Dev[b]	r_m[c]	Sex[d] Ratio	Pred[e]	References
T. occidentalis	2.45	2.80	35.2	0.137	.	.	.	Pruszynski & Cone 1973
T. occidentalis	2.13	2.64	29.6	0.096	0.213	0.642	.	Tanigoshi et al. 1975
T. occidentalis	2.47	2.95	33.1	0.115	0.232	0.677	.	Tanigoshi et al. 1975
T. occidentalis	1.10	.	33.7	0.131	.	.	.	Lee & Davis 1968
T. phialatus	1.10	1.70	44.6	0.094	0.144	0.630	.	Ferragut et al. 1987
T. pini	0.95	.	17.7	0.079	.	.	1.9	Charlet & McMurtry 1977
T. porresi	0.59	.	.	.	.	.	7.9	Badii et al. 1990
T. porresi	1.28	.	27.6	0.087	.	.	.	Badii et al. 1990
T. pyri	0.43	1.00	10.2	0.081	0.089	.	.	Kropczynska et al. 1988
T. pyri	0.68	.	23.0	0.067	.	.	.	Herbert 1961
T. pyri	0.63	.	38.7	0.078	0.076	.	.	Overmeer 1981
T. rickeri	1.90	.	27.5	0.106	.	.	.	McMurtry & Scriven 1964
T. sessor	0.79	.	.	0.101	.	.	.	Sciarappa & Swift 1977
T. validus	1.10	.	.	.	.	.	2.8	Charlet & McMurtry 1977

[a] Fecundity

[b] Developmental rate

[c] Intrinsic rate of increase

[d] Proportion of daughters

[e] Predation rate on prey eggs

Appendix 4.3. Derivation of equations:

The classic Lotka or Euler equation for estimating the intrinsic rate of increase, r_m, from life table data is given by:

$$\sum_{x=A}^{W} \exp(-r_m x)\, l_x n_x s_x = 1$$

where x = age, A = age at first oviposition, W = age at last oviposition, l_x = probability of survival from age 0 to age x, n_n = ovipositional rate of a female of age x, and s_x = the proportion of daughters in the offspring of a female of age x. This formula expresses that the age-specific net rate of reproduction ($l_x n_x s_x$) is weighted by a negative exponential (exp ($-r_m$x)) and that r_m should be chosen so as to make the sum of the weighted, age-specific, net rates of reproduction sum to unity.

This formula reduces to more transparent forms for the following simplified reproduction schedules (with T representing the age at peak oviposition), as visualized in Figure 4.5:

(1) $R(T) \exp(-r_m A) r_m^{-1} = 1$
for the Methusalem schedule ($R(x < A) = 0$, $R(A) = R(x > A) = R(T)$),

(2) $R(T)[\exp(-r_m A) - \exp(-r_m W)] r_m^{-1} = 1$
for the rectangular schedule ($R(x < A) = 0$, $R(A) = R(W) = R(T)$),

(3) $(R(T)\{(T-A)^{-1} [\exp(-r_m A) - \exp(r_m T) + (W - T)^{-1} [\exp(-r_m W) - \exp(-r_m T)]\} r_m^{-2} = 1$,
for the triangular schedule ($R(x < A) = R(W) = 0$, $R(T) > 0$, $R(x > W) = 0$; see Lewontin, 1965),

(4) $R(T) \{\{(T_1 - A)^{-1} [\exp(-r_m A) - \exp(-r_m T_1)] + (W - T_2)^{-1} [\exp(-r_m W) - \exp(-r_m T_2)]\}$
$r_m^{-2} + [\exp(-r_m T_1) - \exp(-R_m T_2)]\, r_m^{-1}\} = 1$;
for the trapezoid schedule ($R(x < A) = 0$, $R(T_1) = R_{(2)} > 0$, $R(x > W) = 0$; see Figure 4.1A).

Note that each of the equations can be written in the form:

$$r_m = R(T)\, f(r_m, A, T, \ldots ..)$$

Hence, it is possible to graphically determine the $R(T)$ values for which the r_m horizontal (the left hand side of the equation) intersects the curve of $R(T)\, f(r_m, A, T, \ldots)$ against $R(T)$ (the right hand side of the equation). An example is given in Figure 4.4 for the case of a Methusalem schedule, where $f(f_m, A, \ldots) = \exp(-r_m A)$.

Literature Reviewed in Appendices 4.1 and 4.2

Abou-Setta, M. M. and C. C. Childers. 1989. Biology of *Euseius mesembrinus* (Acari: Phytoseiidae): Life tables and feeding behaviour on tetranychid mites on citrus. *Environ. Entomol.* 18:665–669.

Amano, H. and D. A. Chant. 1977. Life history and reproduction of two species of predaceous mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). *Can. J. Zool.* 55:1978–1983.

Badii, M. H. and J. A. McMurtry. 1984. Life history of and life table parameters for *Phytoseiulus longpipes* with comparative studies on *P. persimilis* and *Typhlodromus occidentalis* (Acari: Phytoseiidae). *Acarologia* 25:111–123.

Badii, M. H. and J. A. McMurtry. 1984. Life history of and life table parameters for *Phytoseiulus longpipes* with comparative studies on *P. persimilis* and *Typhlodromus occidentalis* (Acari: Phytoseiidae). *Acarologia* 25:111–123.

Ball, J. C. 1980. Development, fecundity, and prey consumption of four species of

predaceous mites (Phytoseiidae) at two constant temperatures. *Environ. Entomol.* 9:298–303.

Blommers, L. 1974. Preliminary studies on two predators (Acarina: Phytoseiidae) of the spider mite *Tetranychus neocaledonicus* André (Acarina: Tetranychidae). *Z. Angew. Entomol.* 75:315–321.

Bloomers, L. 1976. Capacities for increase and predation in *Amblyseius bibens* (Acarina: Phytoseiidae). *Z. Angew. Entomol.* 81:225–244.

Bloomers, L. and R. C. M. van Arendonk. 1979. The profit of senescence in phytoseiid mites. *Oecologia* 44:87–90.

Boyne, J. V. and F. P. Hain. 1983. Responses of *Neoseiulus fallacis* (Acarina: Phytoseiidae) to different prey densities of *Oligonychus ununguis* (Acarina: Tetranychidae) and to different relative humidities. *Can. Entomol.* 115:1607–1614.

Bruce-Oliver, S. J. and M. A. Hoy. 1990. Effect of prey stage on life-table attributes of a genetically manipulated strain of *Metaseiulus occidentalis* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 9:201–207.

Burrell, R. W. and W. J. McCormick. 1964. *Typhlodromus* and *Amblyseius* (Acarina: Phytoseiidae) as predators on orchard mites. *Ann. Entomol. Soc. Am.* 57:483–487.

Castagnoli, M. and M. Liguori. 1986a. Tempi di sviluppo e ovideposizione di *Typhlodromus exhilaratus* Ragusa (Acarina: Phytoseiidae) allevato con vari tipi di cibo. *Redia* 69:361–368.

Castagnoli, M. and M. Liguori. 1986b. Laboratory rearing and construction of a life table for *Typhlodromus exhileratus* Ragusa (Acarina: Phytoseiidae). *Redia* 69:591–596.

Castagnoli, M., F. Amato and M. Monagheddu. 1989. Osservazioni e parametri demografici di *Eotetranychus carpini* (Oudemans) (Acarina: Tetranychidae) e del suo predatore *Typhlodromus exhileratus* Ragusa (Acarina: Phytoseiidae) in condizioni di laboratorio. *Redia* 72:545–557.

Charlet, L. D. and J. A. McMurtry. 1977. Systematics and bionomics of predaceous and phytophagous mites associated with pine foliage in California. *Hilgardia* 45:173–236.

Croft. B. A. 1972. Prey stage distribution, a factor affecting the numerical response of *Typhlodromus occidentalis* to *Tetranychus mcdanieli* and *Tetranychus pacificus*. *Great Basin Nat.* 32:61–75.

De Moraes, G. J. and J. A. McMurtry. 1981. Biology of *Amblyseius citrifolius* (Denmark and Muma) (Acarina: Phytoseiidae). *Hilgardia* 49:1–29.

Dosse, G. 1955. Aus der Biologie der Raubmilbe *Typhlodromus cucumeris* Oud. (Acar., *Phytoseiidae*). *Z. Pflanzenkr. Pflanzenschutz* 62:593–598.

El-Banhawy, E. M. 1975. Biology and feeding behaviour of the predatory mite *Amblyseius brazilli* (Mesostigmata: Phytoseiidae). *Entomophaga* 20:353–360.

Ezulike, T. O. and J. A. Odebiyi. 1985. Life history of *Amblyseius fustis* (Pritchard and Baker), an indigenous predator of the cassava red mite, *Oligonychus gossipii* (Zacher) in South Western Nigeria. *Insect Sci. Appl.* 6:193–197.

Ferragut, F., F. Garcia-Mari, J. Costa-Comelles and R. Laborda. 1987. Influence of food

and temperature on development and oviposition of *Euseius stipulatus* and *Typhlodromus phialatus* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 3:317–330.

Friese, D. D. and F. E. Gilstrap. 1982. Influence of prey availability on reproduction and prey consumption of *Phytoseiulus persimilis, Amblyseius californicus* and *Metaseiulus occidentalis* (Acarina: Phytoseiidae). *Int. J. Acarol.* 8:85–89.

Gerlach, S. and Ç. Sengonca. 1985. Comparative studies on the effectiveness of the predatory mite *Phytoseiulus persimilis* Athias-Henriot, and the predatory thrips, *Scolothrips longicornis* Priesner. *Z. Pflanzenkr. Pflanzenschutz* 92:138–146.

Gupta, S. K. 1985. *Handbook Plant Mites of India*. Calcutta: Zoological Survey of India.

Hamamura, T., N. Shinkaji and W. Ashihara. 1976. The relationship between temperature and developmental period, and oviposition of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). *Bull. Fruit Tree Res. Stn.*, Series E 1:117–125.

Herbert, H. J. 1961. Influence of various numbers of prey on rate of development, oviposition, and longevity of *Typhlodromus pyri* Scheuten (Acarina: Phytoseiidae) in the laboratory. *Can. Entomol.* 43:380–384.

Hessein, N. A. 1977. Life history of the predatory mite *Typhlodromus athiasae* Porath and Swirski (Acarina: Phytoseiidae). *Libyan J. Agric.* 6:45–48.

Hoy, M. A. 1984. Genetic improvement of a biological control agent: Multiple pesticide resistance and nondiapause in *Metaseiulus occidentalis* (Nesbitt) (Phytoseiidae). *Acarology* 6:673–679.

Knisley, C. B. and F. C. Swift. 1971. Biological studies of *Amblyseius umbraticus* (Acarina: Phytoseiidae). *Ann. Entomol. Soc. Am.* 64:813–822.

Krishnamoorty, A. 1982. Effect of temperature on the development, survival and fecundity of the predatory mite, *Amblyseius tetranychivorus* (Gupta) (Acarina: Phytoseiidae). *Entomon* 7:447–450.

Kropczynska, D. 1970. Biologia I ekologia drapieznego roztocza *Typhlodromus finlandicus* (Oud.) (Acarina: Phytoseiidae). *Zesz. Probl. Post. Nauk. Roln.* 109:11–42.

Kropczynska, D., M. van de Vrie and A. Tomczyk. 1988. Bionomics of *Eotetranychus tiliarium* and its phytoseiid predators. *Exp. Appl. Acarol.* 5:65–82.

Lababidi, M. S. 1988. Biologische Bekämpfungsmöglichkeiten der Baumwollspinnmilbe *Tetranychus cinnabarinus* (Biosduval) (Acari: Tetranychidae). Ph.D. thesis, Institut für Pflanzenkrankheiten der Rheinischen Friedrich-Wilhelms-Universität Bonn.

Lee, M. S. and D. W. Davis. 1968. Life history and behavior of the predatory mite *Typhlodromus occidentalis* in Utah. *Ann. Entomol. Soc. Am.* 61:251–255.

Lo, K. C. and C. C. Ho. 1979. Influence of temperature on life history, predation and population parameters of *A. longispinosus* (Acarina: Phytoseiidae). *J. Agric. Res. China* 28:237–250.

Ma, W. and J. E. Laing. 1973. Biology, potential for increase and prey consumption of *Amblyseius chilenensis* (Dosse) (Acarina: Phytoseiidae). *Entomophaga* 18:47–60.

Mallik, B. and G. P. ChannaBasavanna. 1983. Life history and life tables of *Tetranychus ludeni* and its predator *Amblyseius longispinosus* (Acari: Tetranychidae: Phytoseiidae). *Indian J. Acarol.* 8:1–12.

McClanahan, R. J. 1968. Influence of temperature of the reproductive potential of two mite predators of the two-spotted spider mite. *Can. Entomol.* 100:549–556.

McMurtry, J. A. and G. T. Scriven. 1964. Biology of the predaceous mite *Typhlodromus rickeri* (Acarina: Phytoseiidae). *Ann. Entomol. Soc. Am.* 57:362–267.

McMurtry, J. A. and G. T. Scriven. 1965. Life-history studies of *Amblyseisu limonicus* with comparative observations on *Amblyseius hibisci* (Acarina: Phytoseiidae). *Ann. Entomol. Soc. Am.* 58:106–111.

Ochieng, R. S.,m G. W. Oloo and E. O. Amboga. 1987. An artificial diet for rearing the phytoseiid mite, *Amblyseius teke* Pritchard and Baker. *Exp. Appl. Acarol.* 3:169–173.

Overmeer, W. P. J. 1981. Notes on breeding phytoseiid mites from orchards (Acarina: Phytoseiidae) in the laboratory. *Med. Fac. Landbouww. Rijksuniv. Genet.* 46:503–509.

Prasad, V. 1967. Biology of the predatory mite *Phytoseiulus macropilis* in Hawaii (Acarina: Phytoseiidae). *Ann. Entomol. Soc. Am.* 60:905–908.

Pruszynski, S. and W. W. Cone. 1973. Biological observations of *Typhlodromus occidentalis* (Acarina: Phytoseiidae) on hops. *Ann. Entomol. Soc. Am.* 66:47–51.

Rasmy, A. H. and E. M. El-Banhawy. 1975. Biology and predatory efficiency of two phytoseiid mites as affected by long-term pollen feeding. *Entomophaga* 20:93–95.

Sabelis, M. W. 1981. *Biological control of two-spotted spider mites using phytoseiid predators*, Part I. Wageningen: Pudoc.

Sabelis, M. W. 1985. Capacity of population increase. In: *Spider Mites, Their Biology, Natural Enemies and Control*, Vol. 1B, edited by W. Helle and M. W. Sabelis, 35–40. Amsterdam: Elsevier.

Saito, Y. 1990. Life-history and feeding habit of *Typhlodromus bambusae*, a specific predator of *Schizotetranychus celarius* (Acari: Phytoseiidae, Tetranychidae). *Exp. Appl. Acarol.* 10:45–51.

Saito, Y. and H. Mori. 1981. Parameters related to potential rate of population increase in three predacious mites in Japan (Acarina: Phytoseiidae). *Appl. Entomol. Zool.* 16:45–47.

Sanderson, J. P. and J. A. McMurtry. 1984. Life-history studies of the predaceous mite *Phytoseius hawaiiensis*. *Entomol. Exp. Appl.* 35:227–234.

Schulten, G. G. M., R. C. M. van Arendonk, V. M. Russell and F. A. Roorda. 1978. Copulation, egg production and sex-ratio in *Phytoseiulus persimilis* and *Amblyseius bibens* (Acarina: Phytoseiidae). *Entomol. Exp. Appl.* 24:145–153.

Sciarappa, W. J. and F. C. Swift. 1977. Biological studies of *Typhlodromus sessor* (Acarina: Phytoseiidae). *Ann. Entomol. Soc. Am.* 70:283–288.

Van Dinh, N., A. Janssen and M. W. Sabelis. 1988. Reproductive success of *Amblyseius idaeus* and *A. anonymus* on a diet of twospotted spider mites. *Exp. Appl. Acarol.* 4:41–51.

Xin, J., L. Liang and L. Ke. 1984. Biology and utilization of *Amblyseius pseudolongispinosus* (Acarina: Phytoseiidae) in China. In: *Acarology VI*, Vol. 2, edited by D. A. Griffiths and C. E. Bowman, 693–698. Chichester: Ellis Horwood Limited.

Zaher, M. A., A. K. Wafa and K. K. Shehata. 1969. Life history of the predatory mite *Phytoseius plumifer* and the effect of nutrition on its biology (Acarina: Phytoseiidae). *Entomol. Exp. Appl.* 12:383–388.

5

Evolutionary Aspects of Oribatid Mite Life Histories and Consequences for the Origin of the Astigmata

Roy A. Norton

CONTENTS

1. Introduction

With densities of several hundred thousand individuals per square meter, oribatid mites are often the most diverse and numerically dominant arthropods in organic

layers of temperate forest soils, where they feed primarily on decomposing higher plant material and on fungi (Harding and Stuttard 1974, Wallwork 1983, Norton 1985). This chapter represents a first attempt at developing a phylogenetic context for the surprisingly large volume of literature that deals with various aspects of oribatid life histories.

A popular approach to life-history studies is to seek an adaptive explanation for any trait that seems important to an organism in its present ecological setting. Sets of such traits are often considered coadapted to form evolutionary "strategies." But claims of life-history adaptation often disregard phylogenetic relationships (Wanntorp et al. 1990), thus ignoring the simpler possibility that a trait is ancestral, and that its prior possession allowed the species to invade its current environment. Much of the literature on oribatid mite life histories seems to suffer from such a one-sided viewpoint, and making this fact more apparent is my primary goal.

Has life-history adaptation played a significant role in oribatid mite diversification? I will address this question simply by seeking patterns in life-history traits. If patterns seem predominantly taxonomic, e.g. if a higher taxon is ecologically diverse but shows constancy in traits, then historical constraints are probably operating. If instead, traits seem correlated with ecological parameters, then hypotheses of life-history adaptation are reasonable. My analysis is incomplete and often unsatisfying, due to our poor knowledge of oribatid mite phylogeny, fragmentary life-history data, and lack of information that would allow us to distinguish heritable variation from phenotypic plasticity. Demographic aspects of life history will be stressed, but aspects of life cycle and reproductive biology are also considered. I do not directly refer to many laboratory studies concerning development time; these can be obtained from cited sources (especially reviews by Lebrun and Luxton). No attempt is made to evaluate the various methods used to investigate oribatid mite demography, though some assumptions are critiqued where relevant. These include life-table analyses (Mitchell 1977a, Schatz 1983, Fernandez and Athias-Binche 1986), deterministic models (Stamou 1987) and other mathematical treatments (Cancela da Fonseca 1980).

Polarization of traits, i.e. their characterization as ancestral (plesiotypic) or derived (apotypic), is necessary in any phylogenetic discussion, and some traits relating to life cycle and reproductive biology can be easily addressed in this manner. For example, fertilization via spermatophores and the oviposition of eggs appear to be plesiotypic within the order Acariformes. But the various demographic traits of individuals and populations are less easily polarized, and the following approach is taken.

Most available data relate to species from temperate forest soils (a habitat which I consider to be ancient and relatively plesiotypic, if not original) and after a general review, the traits of such species will be summarized. Then I examine oribatid mites living in more extreme habitats or in nonsoil microhabitats (situations that can be considered apotypic) and look for apparent adaptations. The

approach can be criticized for overgeneralization and lack of rigor, neither of which can be avoided at present. A secondary objective is to examine the derivation of the Astigmata from a life-history perspective. In general, the traits exhibited by this group differ greatly from those of oribatid mites, and a logical transition is not obvious.

2. Diversity and Phylogeny of Oribatid Mites

The mite suborder Oribatida (= Cryptostigmata, Oribatei) includes about 7,000 nominal species. Oribatid mites have existed at least since the Devonian Period (Norton et al. 1988a), and even some rather derived genera are known from the Jurassic (Krivolutsky and Druk 1986). An impressive morphological diversity exists in some groups (e.g. the Enarthronota, see Norton 1984), and to some extent they utilize non-soil microhabitats (Travé 1963). Yet compared to other major taxa, oribatid mites seem to have been highly conservative in most aspects of their biology. This is often attributed to a paucity of the interspecific relationships with plants and animals that characterize radiations in other mite groups (Krantz and Lindquist 1979, OConnor 1982, Norton 1985).

In part, the conservatism of oribatid mites is illusory in that the Oribatida does not represent a natural, historical group. In its usual sense it is clearly paraphyletic, having given rise to the Astigmata, a diverse group in which interspecific relationships are key (OConnor 1982, 1984). Still, the species richness of oribatid mites is of the same order of magnitude as that of the Astigmata, Prostigmata or Mesostigmata (Parker 1982) and the apparent biological conservatism has made their taxonomic diversity somewhat enigmatic (Anderson 1975a, Norton 1985). Partial explanations for this relate to micro-distribution (Aoki 1967, Hammer 1972, Fujikawa 1974, Anderson 1978a) and feeding specificity (see Harding and Stuttard 1974).

As with any biological attribute, meaningful conclusions about life-history evolution must be rooted in an assessment of phylogeny. A few groups have been analyzed, but there are no published hypotheses relating monophyletic higher taxa of the Oribatida using the rigor of cladistic methodology. Without offering supporting evidence, my view of the relationships of the six commonly recognized but unranked "taxa" of oribatid mites (Grandjean 1969, Marshall et al. 1987) and the Astigmata is shown in Fig. 5.1. This level of resolution is of little value here, but it does provide a framework for discussion. What can be called the "glandulate" oribatid mites (having paired opisthosomal glands) is a monophyletic group, but the relationships of its outgroups, Enarthronota and Palaeosomata, are as yet undefined (see Grandjean 1969). The Parhyposomata seems monophyletic, but the Mixonomata is paraphyletic, having given rise to the Desmonomata (= Nothroidea). The latter is doubly paraphyletic, having produced both the Brachypylina ("higher" oribatid mites, = Circumdehiscentiae) and the Astigmata.

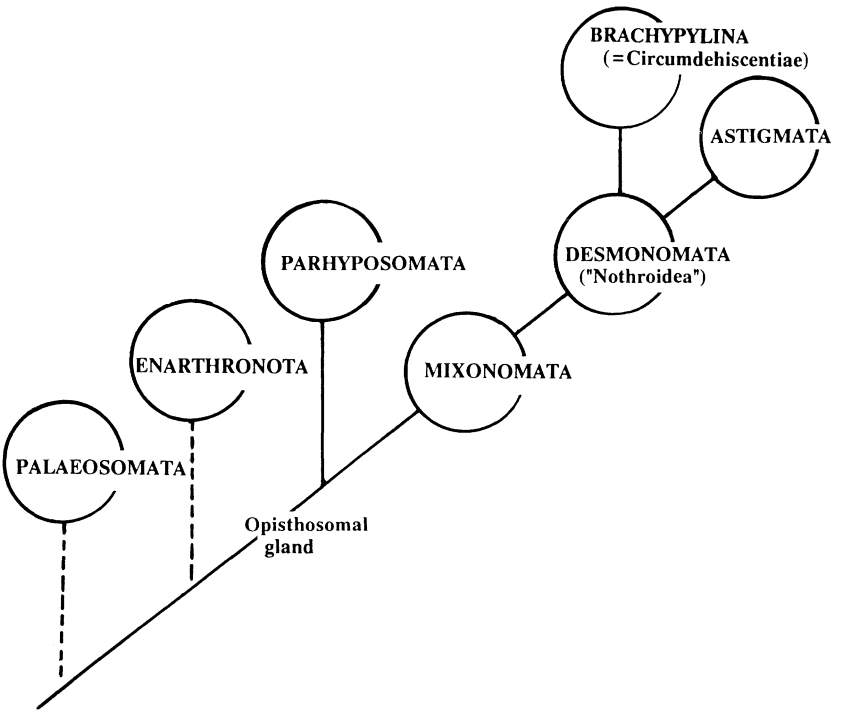


Figure 5.1. Schematic relationships of major oribatid mites groups and the Astigmata (see text for explanation).

3. Review of Oribatid Mite Life-History Traits

3.1 Life Cycle and Parity

Oribatid mites retain the ancestral acariform life cycle of six postembryonic instars (prelarva, larva, protonymph, deutonymph, tritonymph, and adult), though in the aberrant and highly regressive enarthronote family Pediculochelidae the presence of a tritonymph has not been proven. The prelarva is inactive in all known oribatid mites. It is a calyptostase that exhibits various states of regression, and it usually occurs totally or partially within the egg membrane, so that the larva appears to hatch from the egg. Among the remaining instars there are no known cases of calyptostasis; where studied, the larva, nymphs, and adult are active and feed normally.

Oribatid mites vary in the timing of parity relative to offspring development. Most species lay eggs (oviposit) in which case embryos are released at an early developmental stage, but in some species eggs are retained throughout embryogenesis, which ends with the formation of the prelarva. Parity may occur

at this point (prelarviposition), or the female may release progeny only after the larval instar is reached (larviposition). Delayed parity has been called "uterine development" (Lange 1960), but the term "egg retention" will be used here. The taxonomic distribution of egg retention may be underestimated, since eggs can be seen in females with clutches not yet ready for deposition.

Some taxonomic correlates are apparent (Lange 1960, Sitnikova 1960, Grandjean 1962, Lions 1973, Travé 1976), though a paucity of information makes generalization tenuous. Egg retention is especially common in Ptyctima, with prelarviposition evidently fixed in one superfamily, Phthiracaroidea. In the other superfamily, Euphthiracaroidea, all three parity modes are represented, but internal pattern may exist. For example, members of the genus *Oribotritia* (Oribotritiidae) seem to consistently prelarviposit, while oviposition is common in the family Euphthiracaridae. Prelarviposition is common in the Desmonomata, especially within the family Camisiidae. It is also widespread in Ameronothridae (including Podacaridae of authors), and further retention (larviposition) is characteristic of *Ameronothrus*, species of which are found in marine littoral regions and estuaries (Luxton 1964, Schulte and Weigmann 1977). Larviposition seems to be the rule in *Trimalaconothrus* (or at least the subgenus *Tyrphonothrus*), members of which inhabit fresh water. However, egg retention often has a mosaic distribution among taxa. Larviposition is known from two species of *Maerkelotritia* (Walker 1965, pers. observ.), but a third, *M. sellnicki*, lays eggs. Eggs of the latter develop a thick chorion that is absent from those of larvipositing species. Various species of *Nothrus* exhibit all three parity modes, and brachypyline genera such as *Damaeus* and *Liodes* may oviposit or prelarviposit, depending on species.

Many of the higher taxa that exhibit egg retention share other biological attributes. For example, all Ptyctima immatures are endophagous, burrowing in decaying wood or other plant tissues; is there an adaptive rationale? If moisture level is positively correlated with successful substrate penetration by larvae, a female has a better chance of selecting an appropriate substrate if hatching is immediate or only briefly delayed. From another viewpoint, prelarviposition may reduce the time during which eggs are exposed to predators, as Lebrun et. al. (1991) suggested for *Steganacarus magnus*. Yet many burrowing oribatid mites living similar life styles oviposit, such as *Adoristes ovatus* (Lions and Gourbière 1988), *Carabodes willmanni* (Bellido 1979), *Cepheus pegazzanoae* (Bernini and Nannelli 1982), and *Xenillus punctatus* (pers. observ.).

Ameronothrus and *Trimalaconothrus* are aquatic or semiaquatic genera; is their larviposition somehow ecologically adaptive? Luxton (1967) suggested that larviposition by *A. schneideri* precludes eggs being washed away by tidal action. The fact that species of *Trimalaconothrus* are commonly, but not exclusively, found among submerged vegetation in rapidly moving streams and rivers is consistent with Luxton's hypothesis, as is the fact that *Hydrozetes* and *Limnozetes* species (all of which oviposit) are characteristic of stationary waters. In contrast,

Mucronothrus nasalis oviposits yet commonly lives in lotic environments (Norton et al. 1988b), while larviposition is typical of those Astigmata living in water-filled treeholes (Fashing 1977).

While neither aquatic habitation nor flow rate correlate perfectly with larviposition, all oribatid species that consistently larviposit are aquatic, suggesting a need for an adaptive explanation. This pattern extends to the genus *Nothrus*, in which an undescribed species inhabiting wet sphagnum bogs in the northeastern United States is the only known fully larviparous member of the genus (unpublished data). There are conflicting reports concerning *N. palustris*, a species commonly associated with wet meadows. Akimov and Yastrebstov (1987) found fully developed larvae in females from the USSR, while it seems to be prelarviparous in Europe and the United States (Lebrun 1970a, pers. observ.). Grishina (1991) suggested, from field data, that the parity mode of *N. palustris* varies with season in the USSR, with "oviposition" (probably actually prelarvaposition) in spring and "viviparity" (larviposition) in summer, but this remains to be proven.

There is a single reliable record of mixed-parity mode in oribatid mites, and this seems unrelated to the presence of free water. Haq et al. (1991) found *Scheloribates fijiensis* from pasture soil in India to mostly oviposit, but some larvipositing females were noted in both cultures and field samples. Whether its parity mode is environmentally or genetically controlled is unstudied.

A thorough survey of the distribution of egg retention may clarify these trends and elucidate others. For example, allometric scaling may play a role in egg retention. Among arboreal species, those which prelarviposit (*Camisia* spp. and some, but not all *Liodes* species) are generally larger than those for which there are no records of egg retention (e.g. the genus *Scapheremaeus*, the family Oripodidae). Also, prelarviposition is known from the larger-sized species of *Nothrus* (*N. palustris*, Lebrun 1970a) and *Damaeus* (*D. onustus*, Grandjean 1954), but apparently not from smaller species.

A seemingly related phenomenon, in which living larvae are regularly found in the dead and hollow bodies of female oribatid mites of terrestrial species, was considered by some early authors to be a special case of egg retention referred to as "aparity." In effect, it was viewed as a form of semelparity in which progeny feed on the dead mother's body and emerge through a body aperture. In small mites such as *Limnozetes sphagni*, where only one or two eggs are carried at a time, Willmann (1933) suggested that earlier clutches may be laid in the form of eggs, with aparity restricted to the last clutch. Jacot (1933) believed that aparity was necessary if egg diameter was larger than that of the genital aperture. However, Grandjean (1956a) noted that the elasticity of egg membranes allows oviposition to occur even through a small opening, and discounted aparity as a normal reproductive process. Rather, if mature eggs are not deposited prior to the mother's death they may (by default) complete development (i.e. to hatching of the larva) inside her body. Arlian and Woolley's (1970) observation of a dead female *Liacarus cidarus* that contained 12 larvae plus other shriveled eggs is

consistent with this explanation. I have observed larvae in dead adults in a variety of Brachypylina species, but no members of earlier-derivative taxa. The same phenomenon occurs in astigmatic mites (e.g. Fain and Herrin 1978, Rodriguez and Stepien 1973), where such larvae have been noted to die without emerging from the mother's body.

3.2 Fertilization and Thelytoky

With few known or suspected exceptions, fertilization is indirect in oribatid mites. Males produce free-standing spermatophores and have no direct association with females, though local female activity may noticeably increase spermatophore deposition rates (Pauly 1956, Shereef 1972, Haq and Adolph 1981). Only in *Collohmannia* is fertilization clearly direct, though all details of the process are not known. Males of *C. gigantea* have a well-defined courtship behavior during which nuptial food is produced to entice cooperation of a female (Schuster 1962). I observed similar behavior in an undescribed species from West Virginia; spermatophores were not produced, and fertilization may have occurred by direct contact of the long genitalia. Sexual dimorphism or behavioral peculiarities suggest the presence of courtship rituals, or at least close association of mates, in several other groups (e.g. Grandjean 1956b). Male dimorphism can include modified tarsal setae that may have courtship functions, as in *Hydrozetes* and *Montgaillardia* (Grandjean 1948, 1961). Notogastral porose areas are known to be associated with glands (Woodring and Cook 1962a), and the hypertrophied porose areas in males of such taxa as *Mochloribatula* and *Zachvatkinibates maritimus* (Norton 1983, Behan-Pelletier 1988) may be involved in sexual behavior.

Many oribatid mites dispense with fertilization altogether and exhibit thelytoky, the parthenogenetic production of females. Thelytoky is commonly considered adaptive, since the effective reproductive rate of a thelytokous female is theoretically twice that of a sexual counterpart. This may be quite significant in a group with generally low fecundity, such as oribatid mites. The colonization advantage is also much discussed, since any offspring can establish a population, regardless of the ontogenetic stage at which it disperses. Based on field sex-ratio evidence (Grandjean 1941, Luxton 1981a, Norton et al. 1988c, Palmer and Norton 1991) and laboratory proofs (Taberly 1987, Palmer and Norton 1990 and included references), thelytoky is common in oribatid mites. Nearly 10% of known oribatid species may be thelytokous, a figure that is one or two orders of magnitude above the estimates of Bell (1982, 1% of known insects) or White (1978, 0.1% of animals).

As discussed elsewhere (Norton and Palmer 1991), most thelytokous oribatid mites are in families without sexual species. Examples include the moderate to large families Lohmanniidae, Brachychthoniidae, Nanhermanniidae, Camisiidae, Malaconothridae and Trhypochthoniidae, as well as many species-poor families

included in the Parhyposomata and Enarthronota. Clearly thelytoky can be plesiotypic, a reproductive mode of long historical standing, rather than always being a recent adaptation to the current lifestyle of a particular species. For example, it would be incorrect to consider thelytoky in *Mucronothrus nasalis* as an adaptation to life in cold oligotrophic streams and deep lakes, since all species in its family (Trhypochthoniidae) are thelytokous, regardless of their habitat. There is a strong probability that in such groups speciation and radiation occurred in the absence of sexual reproduction, and none of the standard biological correlates of thelytoky seem to obtain (Norton and Palmer 1991).

In contrast, thelytoky may be a recently evolved and adaptive life-history trait when we see it in some members of a genus but not in others, i.e. when its taxonomic distribution conforms to theoretical predictions of a sporadic, but nonrandom, distribution (Bell 1982). Among the early-derivative (non-Brachypylina) groups such a taxonomic distribution is rare. Examples include two genera of the Euphthiracaridae, *Rhysotritia* and *Microtritia*; common Holarctic or Palearctic species are thelytokous, but each genus is represented by sexual species in California (Walker 1965). Also, *Epilohmannia* (Epilohmanniidae) contains both sexual and thelytokous species apparently throughout its range (Wallwork 1962, pers. observ.).

Among the Brachypylina the taxonomic distribution of thelytoky conforms to theoretical predictions by being taxonomically scattered. Wholly thelytokous genera are rare, with exceptions being the aquatic or semiaquatic genus *Limnozetes* (Behan-Pelletier 1989) and the cosmopolitan genus *Tectocepheus*. Norton and Palmer (1991) noted that the ecological distribution of thelytokous Brachypylina agrees with standard interpretations of the adaptive value of thelytoky. For example, they are commonly early colonizers in newly created habitats, such as bulldozed soil (Beckman 1988) and fresh volcanic substrates (Ryabinin and Pan'kov 1987). They also dominate the oribatid fauna of disclimax habitats, such as periodically flooded soil of reservoirs (Tamm et al. 1984), cultivated soils (Norton and Sillman 1985), and other regularly perturbed sites.

The wide geographic and habitat distribution of many thelytokous Brachypylina is consistent with the hypothesis that they have "general purpose genotypes" (e.g. Lynch 1984). The competing "biotic uncertainty" hypothesis, that thelytokous species are relegated to biologically depauperate habitats by their inflexible genomes (Bell 1982), seems incompatible with the observed persistence of these colonizing species in successionally more mature, complex environments.

Other biological traits have also been suggested to correlate with thelytoky, only some of which are supported by patterns observed in oribatid mites (Norton and Palmer 1991). Reduction in egg viability is known in some thelytokous organisms (Bell 1982), but has not been observed in oribatid mites. Nor are generation times shorter in thelytokous species, as was suggested by Gilyarov (1982). Small body size has been suggested to promote thelytoky since there is a lower limit to egg size (Dybas 1966). Presumably, if only one or two eggs are

carried at a time, and egg turnover rate is low, the "two-fold advantage" would be important in keeping fecundity at a viable level. This is consistent with the distribution of thelytoky in some mostly sexual genera of Brachypylina; if thelytokes exist, they are often among the smallest species in the genus. Habitat may also correlate with thelytoky. Only half the known species of *Hydrozetes* are sexual, perhaps reflecting selective forces favoring thelytoky in their aquatic medium. Life in the small pore spaces of deep soil (euedaphic) horizons may promote thelytoky in oribatid mites due to the uncertainty of finding mates. The typically small size of deep soil taxa may contribute to thelytokous tendencies, or may be coincidental to the evolution of this reproductive mode. In some brachypyline genera, no biological or distributional factors seem to apply. For example, the oppiid genus *Quadroppia* includes sexual subspecies among its smallest members (Lions 1982), with no microdistributional pattern evident.

3.3 Fecundity

Lifetime fecundity of oribatid mites is low relative to many other mite groups (usually several dozen eggs per lifetime or fewer), but taxonomic or ecological patterns are not retrievable from the sparse data. Instantaneous clutch sizes are known for some organisms (e.g. Luxton 1981a) but are of little use without corresponding information on turnover rates, which appear to vary with species. The small-bodied species *Oppiella nova* usually carries a single egg but lays about 12 eggs/week in culture (Woodring and Cook 1962b), whereas the large-bodied species *Steganacarus magnus* matures a single clutch of about six eggs (developed to prelarvae) laid individually at lengthy intervals (Webb 1989).

Several factors are known to influence the fecundity of animals raised in culture. A negative effect of crowding on oviposition rate has been demonstrated for *Nothrus palustris* (Lebrun 1970a), *Alaskozetes antarcticus* (Peckham 1967), *Achipteria holomonensis* (Stamou et al. 1981) *Carabodes willmanni* (Bellido 1990), and *Oppia nodosa* (Bhattacharya et al. 1978), but crowding seems irrelevant in *Pergalumna emarginata* (Rockett and Woodring 1966a, = *P. omniphagous*). Stamou and Asikidis (1989) found that in *Scheloribates* cf *latipes* and *Achipteria oudemansi* an optimum density may exist, since very low densities had a negative effect on fecundity. Food quality may also be of prime importance. Shereef (1970) found that species-level differences in fungal food can have a major influence on oviposition rates in *Epidamaeus kamaensis* and *Oppia concolor*. Such nutritional effects have also been shown by Reddy et al. (1978) for *Galumna flabellifera* and by Saichuae et al. (1972) for *Nothrus biciliatus*. Microclimatic influences can also be expected to contribute to variability in fecundity (Bellido 1990), but effects of parameters such as temperature and humidity are rarely partitioned experimentally.

Studies of fecundity conducted by various laboratories are seldom comparable, since we are usually ignorant about where in the spectrum of food quality, ambient

temperature and population density the given culture conditions lie. There is a uniform general picture of low to modest fecundity even under optimal conditions, but future comparative studies will be needed to assess adaptation, especially ones linked to studies of energetics.

Do oribatid mites exhibit the clutch size patterns suggested for insects by Godfray (1987)? For example, is clutch size directly related to female body size, with oviposition sites being readily available and the optimal egg number being more than a mite of given size could produce? Such an argument might be made for *Archegozetes longisetosus*, a mite that fills its hysterosoma with eggs. Or do some groups exhibit optimum clutch sizes, determined by the rates of energy procurement and a limited number of appropriate oviposition sites? *Steganacarus magnus*, a slightly larger mite that may produce fewer than 10 eggs in its lifetime (Webb 1989), might be an example.

3.4 Developmental Rates

Developmental rate is the most investigated life-history trait of oribatid mites (see summaries by Lebrun 1970a, 1971, Luxton 1981a, and Grishina, 1991). Studied mostly between 20°–30° C, the egg-adult developmental period varies from about three weeks in the small *Oppiella nova* to more than one year in *Conoppia palmicincta* (Woodring and Cook 1962b, Michael 1884, respectively). Various developmental studies are often incongruent, even when done at similar temperatures. At room temperature (about 20° C), Haarlov (1960) and Hartenstein (1962) respectively noted development times of 41 days and 119–149 days for *Ceratozetes gracilis*, and of 332 days and 150 days for *Platynothrus peltifer*.

Such major discrepancies can result from a variety of culture effects, though heritable population differences cannot be discounted. For example, temperature conditions cannot fully be described by reporting mean values. The stimulating effect of fluctuating (vs. constant) temperature can be striking, due to high Q_{10} values (Lebrun and Ruymbeke 1971, Lebrun 1977, Stamou 1989, Stamou and Sgardelis 1989, Bellido 1990). Nor can temperature effects be assumed to be constant over the course of ontogeny; they may vary among eggs and instars, as well as among species (Vera and Berthet 1988, Taberly 1989). Other influential factors are food quality (Saichuae et al. 1972, Mitchell and Parkinson 1976, Young and Block 1980, Stefaniak and Seniczak 1981), density (Stamou et al. 1981) and even illumination (Lebrun 1970a).

Few existing laboratory studies have direct field application, if only because cultures are commonly 50–100% warmer than natural conditions. In useful studies, temperature regimes reflect environmental patterns (Weigmann 1975), rearing chambers are placed directly in the field (Lebrun 1971), or mites are studied in near-natural situations where oviposition and emergence can be estimated (Gourbière et al. 1985, Lions and Gourbière 1988). Following changes in age-class distribution is a useful field technique (Mitchell 1977a, Thomas 1979,

Luxton 1981a, 1981b), but only if oviposition is temporally circumscribed and cohorts can be distinguished throughout ontogeny. Often cohort identity is weakened or lost as development proceeds due to increasing length and variability of instar duration, and in such cases populations are rather stable (Lebrun 1970a, Mitchell 1977a, Schatz 1983, 1985).

Gross patterns recognized from the early literature by Lebrun (1970a, 1971) seem to have reasonable applicability. "Higher" oribatid mites (Brachypylina) usually develop more rapidly than most similar-sized early-derivative groups, and within a taxonomic grouping (perhaps at a family or superfamily level) larger species have more lengthy development.

In temperate forest soils the development of most species probably takes from several months to well over a year. Even *Oppiella nova*, which can develop in the laboratory in only three weeks (Woodring and Cook 1962b), appears to have a single annual generation in Denmark (Luxton 1981b). Even under ideal conditions a quarter to a third of development is spent inactive, in preecdysial resting stages (Luxton 1981a), and cold-induced dormancy ("coma" or "quiescence") during winter can significantly extend development. When laboratory studies have included trials at low temperatures, a threshold has been noted below which development is suspended (Weigmann 1975, Bhattacharya et al. 1978, Schatz 1985, Stamou 1989, Taberly 1989, Bellido 1990). Such dormancy has been considered an adaptation by some (e.g. Stamou 1989), but is more simply explained as a manifestation of metabolic constraints at low temperatures (Cannon and Block 1988 and included references).

In discussing the ecological significance of slow developmental rates, Mitchell (1977b) noted that oribatid mites generally are not able to track and exploit short-term changes in resources. However, their low metabolic rates should enable them to survive periods of low food availability.

3.5 Survivorship, Adult Longevity and Sources of Mortality

Reliable laboratory studies suggest that survivorship is optimal at particular culture densities (Stamou and Asikidis 1989), and is inversely related to temperature (e.g. Saichuae et al. 1972, Stamou et al. 1981, Cannon 1987). Moderate to high death rates reported in some studies (e.g. Sengbusch 1954, Woodring 1965) might simply reflect unsatisfactory culture conditions.

Field survivorship studies are few, and most concern species in habitats other than temperate forest soil. Natural mortality seems concentrated in the immature instars, with the rate of loss decreasing during ontogeny. Survivorship to adult in two unrelated species, the alpine *Oromurcia sudetica* and the aquatic *Hydrozetes lemnae*, is similar, about 10% and 8–12% respectively (Schatz 1983, Fernandez and Athias-Binche 1986). Mitchell's (1977a) estimate for the boreal species *Ceratozetes kananaskis* was twice as high (24%), but he assumed one clutch was produced per year. If in fact there are two clutches per year, survivorship would

be similar to the other estimates. Whether the general climate is temperate or cold, little mortality of immatures seems to be associated with winter dormancy (Mitchell 1977a, Schatz 1983, Stamou 1989), probably due to inactivity brought on by chill coma. The ability of adult oribatid mites to withstand freezing temperatures by supercooling is well documented (Cannon and Block 1988).

From laboratory data (summarized by Luxton 1981a) adult longevity of over a half-year is common, and *Damaeus onustus* and *Neoribates gracilis* adults can survive about two years at room temperature. Luxton (1981a) suggested that field longevity should be overestimated by culture data, but the opposite may be true. Low temperatures may considerably extend longevity (e.g. Nannelli 1975), and if winter dormancy is included in rate estimates then 1–2 year longevities may not be uncommon in temperate soils. As a result, iteroparity may be routine (Mitchell 1977b), both within and between years. Multiple clutch production cannot be assumed *a priori*, however; the large-bodied species *Steganacarus magnus* may live longer than three years, yet produce a single small clutch of eggs (Webb 1989).

What are the likely abiotic causes of mortality? In winter, forced quiescence and supercooling ability may keep winter losses low, while summer desiccation may be a principal abiotic mortality factor (Madge 1964). In some dry climates, the need to migrate deeper into soils to encounter moisture may put a premium on small size since mites must traverse pore spaces that generally decrease in size with depth (Athias-Binche 1985, 1989). Biotic mortality sources are varied but little studied. Whereas soft-bodied immatures are vulnerable to a wide array of predaceous arthropods (Luxton 1964, Lebrun 1970b, Wallwork 1980, Walter et al. 1989), the sclerotized adults have fewer known enemies. The latter may include featherwinged beetles (Ptiliidae, Riha 1951), antlike stone beetles (Scydmaenidae, Schmid 1988), short-winged mold beetles (Pselaphidae, Park 1947, but see Walker 1965), ants (E. O. Wilson, pers. comm., 1989), and dragonfly nymphs (V. Behan-Pelletier, pers. comm., 1990). The bdellid mite *Cyta latirostris* (Alberti 1973), and probably a variety of small salamanders (e.g. Norton and MacNamara 1976) are also predators of sclerotized adults. Parasitic nematodes and sporozoans may be significant causes of mortality (Walker 1965, Bäumler 1970, Purrini 1980). Occasionally oribatid mites host ectoparasitic larvae of the mite family Erythraeidae (Norton et al. 1988d).

Evidence of an evolutionary emphasis on adult survival can be seen in a morphology adapted for predator defense. Most adults have a hardened cuticle, while that of immatures is distinctly softer. Hardening usually results from sclerotization, but in some taxa (e.g. Hypochthonioidea, some Ptyctima) it is primarily due to calcification (Norton and Behan-Pelletier 1991). Adult ptychoidy, in which legs are retracted and the prodorsum folds ventrad to cover them, is a defense that has evolved independently at least three times (Norton 1984). Many other taxa have evolved an amazing array of cuticular structures

(tecta) that protect vulnerable articulations and effectively deter most potential predators.

3.6 Voltinism and Generational Synchrony

The number of annual generations in temperate soil species has frequently been overestimated in the literature (Mitchell 1977b, Norton 1985). Perhaps guided by a general belief that mites reproduce rapidly, authors have often simply divided laboratory development time into 365 calendar days to obtain the number of annual generations (see review by Luxton 1981a). This simplistic approach considers neither the unrealistic temperature regime of most studies nor seasonal dormancy enforced by cold weather in nature.

Even if age-distribution studies suggest a one-year ontogeny, it may be incorrect to assume univoltinism. Authors often have ignored the weeks or months necessary for cuticular hardening (teneral period), the procurement of sufficient energy resources, and the development of eggs, as well as the rate-depressing effects of decreasing fall temperatures. It may be common for winter to intervene between the appearance of an adult and its progeny, at least for the later-maturing part of a given cohort. The specific time an egg is laid within the reproductive period can also significantly impact development and therefore generation time (Murphy and Balla 1973, Weigmann 1975, Luxton 1981a). Interpretations vary, but available field studies suggest that the generation time of most oribatid mites is one or two years in temperate soils (e.g. Luxton 1981a, 1981b, Kaneko 1989).

Few patterns in reproductive phenology have been noted in the literature, only two of which are taxonomic; the Phthiracaridae and Liacaridae seem to bear eggs (or prelarvae) continually (Table 2 of Luxton 1981a). Two ecological patterns that have been suggested are somewhat conflicting. Luxton (1981a) found that females of species inhabiting litter layers in a Danish beechwood soil carried eggs throughout the year. However, Mitchell (1977a) found those oribatid mites living in surface layers of a Canadian aspen woodland soil to have circumscribed egg maturation (spring-summer). Those of the deeper (humus) layers contained eggs throughout the year, a pattern also suggested by Smrz (1989). Adaptive explanations for either pattern are easily imagined. One could argue that circumscribed oviposition is beneficial in surface layers that may be more seasonally variable (e.g. in moisture regime, according to Mitchell). One could also argue that the continual presence of eggs in mature females is beneficial in variable surface layers, since eggs could be laid opportunistically when environmental conditions are temporarily favorable.

3.7 Net Reproductive Rates

Net reproductive rate per female (R_0) has been estimated for only a few oribatid species. The relatively stable densities often observed in soil oribatid mites

(Lebrun 1970a, 1970b, Mitchell 1977a) suggest net reproductive rates are near unity, as Mitchell (1977a) calculated for a boreal forest soil species, *Ceratozetes kananaskis*. Various mathematical models utilized by Cancela da Fonseca (1980) for three temperate oribatid mites yielded R_0 values above or below 1.0, depending on the model applied.

As noted above, Mitchell (1977b) thought oribatid mite populations are unable to respond numerically to short-term changes in resource availability. Schenker (1986) depicted reproductive traits of temperate oribatid mites quite differently. High rates for *Platynothrus peltifer*, *Oribatula tibialis* and *Scheloribates pallidulus* (R_0 = 8.82, 9.46 and 6.03, respectively) during what he considered to be periods of changing population density led him to suggest that "new resources (litter etc.) are utilized efficiently." His values are grossly exaggerated, however, since survivorship of adults, rather than survivorship from birth, was used in the calculation of R_0 (see Southwood 1978). Several less critical details of his study are unclear. For example, analyses were based on data from periods of supposed population change, but high variance caused by the aggregated distribution of oribatid mites (described at this site by Schenker 1984) often makes trends difficult to ascertain, and no statistical support for this was offered. The means by which the age-specific number of female offspring (m_x) was determined in this field study were not mentioned; simply counting the number of eggs present for the latter is insufficient since turnover rates were not estimated (see above). The one-month sampling period may approximate the clutch turnover period, but more likely it does not. The author also did not mention whether the fact that *P. peltifer* is thelytokous was considered in fertility calculations. In short, there seems to be no evidence that these three oribatid mites have any unusual ability to track changes in resource availability.

3.8 Dispersal

Dispersal remains one of the least known aspects of oribatid mite biology, but it probably occurs principally in the adult instar. Adults seem better equipped to deal with exposure to predation during dispersal than are immatures. This is clearly true if immatures are strict endophages (e.g. Ptyctima, Carabodidae, Hermanniellidae, many Liacaridae and Xenillidae); they do not emerge from their burrows in decaying wood, leaves, fungi, or lichens before reaching the adult instar. Those few oribatid species known to be phoretic on insects (always insects associated with decaying wood) disperse only as adults (Norton 1980).

Dispersal may usually encompass little more than the seeking of food or favorable oviposition sites by gravid females. Active horizontal movements of soil species may be restricted to a distance of a few centimeters (e.g. Berthet 1964), though vertical migrations into vegetation may be more substantial, both diurnally (e.g. Tarras-Wahlberg 1961) and seasonally (Murphy and Balla 1973). Potentially long dispersal distances may be possible in some *Hydrozetes* species,

in which adults (but not immatures) are made buoyant in water columns by gas bubbles formed in their guts (Newell 1945, Burford 1976).

3.9 Summary of Life Histories in Temperate Soil

The life-history attributes of temperate, soil-dwelling oribatids mites seem typical of organisms considered to be "*K*-selected" or to have "*K* attributes" (MacArthur and Wilson 1967, Pianka 1970). Life-cycles and generation times are usually long relative to other mites, often exceeding one year. Fecundity is low, even though adults are probably long-lived and often iteroparous. Mortality is concentrated in immature instars, and net reproductive rates are such that adult population density fluctuates little from year to year. The ultimate cause of these traits, i.e. whether they are best explained as direct or indirect responses to selective forces, or rather result from internal, historical constraints, will be addressed later.

Assuming this suite of traits to be plesiotypic, do we see apotypic traits in other situations, such as more specialized habitats or regions of environmental severity, that are likely to be adaptive?

4. Life Histories in Apotypic Habitats

4.1 Species in Cold Environments

Oribatid mites of cold environments have attracted considerable attention. Adaptive life-history traits have been suggested, but not clearly demonstrated, and some patterns probably are simply a function of heat budget. For example, a low heat budget seems responsible for the long mean generation time (4.2 years) of *Ceratozetes kananaskis* in boreal Canadian aspen soil (Mitchell 1977b). Heat budget probably also controls the demographics of *Oromurcia sudetica* in alpine Austria, a climatically similar site (Schatz 1983, 1985). For this species extended and variable duration of instars results in overlapping generations, such that development requires 2–4 years with an additional year needed before females lay eggs.

Those studies suggesting life-history adaptation to cold environments are vulnerable to criticism. For three species, West (1982) recognized adaptations to the cold and unpredictable climate of the sub-antarctic island of South Georgia. He considered *Platynothrus skoettsbergi* to have adapted by becoming semelparous. Using field age-class data (but without supportive laboratory studies), he suggested a one-year life cycle, and proposed that population "reserves" were usually present as high numbers of larvae that could rapidly develop into adults in unpredictable periods of favorable conditions. This scenario seems unlikely for several reasons. First, the age-class data (his Fig. 5) could easily be interpreted as showing a development of two years or more; the deutonymph alone seems to take almost one year. Adults of this species (which he called "feeble") are unlikely

to produce the suggested burst of reproduction, even in relatively favorable conditions. Clutch sizes were not mentioned, but Chilean representatives have a maximum clutch size of only 11 eggs per female (pers. observ.), which in the cold South Georgian climate may comprise the annual production. The development of this mite is probably no faster than that of *P. peltifer*, which has a mean generation time of two years in northern Europe (Thomas 1979, Norton 1985). A plesiotypic, iteroparous life history controlled by low heat budget seems much more likely than the demographic adaptations implied by West (1982).

Based on age-class data, West (1982) suggested *Eobrachychthonius oudemansi* had a two-year life cycle, and considered the accumulation of tritonymphs, rather than larvae, to constitute a population "reserve." He also considered it semelparous, but semelparity, definable as a one-time reproductive "burst" (Cole 1954), is hardly feasible in such a small mite, especially when only one or two eggs can develop at a time (Travé 1968). This species is probably thelytokous like other known Brachychthoniidae,[1] but females must average more than one life-time clutch to maintain a population. As noted above, an accumulation of late instars can be induced by low heat budgets, and therefore *E. oudemansi* has no known life-history traits that can be reasonably called adaptations to cold or unpredictable environments.

West (1982) suggested that the life history of *Edwardzetes elongatus* is characterized by an emphasis on adult longevity and iteroparity at the expense of fecundity, and considered this an adaptive strategy in the cold, unpredictable climate. His data are not dissimilar to those of the confamilial (Ceratozetidae) mites studied by Mitchell (1977b) and Schatz (1983, 1985). In fact, as favorable as this combination seems to be, it is typical of oribatid mites in general, and the life history of *E. elongatus* seems to be plesiotypic, rather than adaptive.

Block (1980) argued that *Alaskozetes antarcticus* has an adaptive life-history strategy. He felt that in the cold, rigorous environment of continental Antarctica, selection favored several observed traits: slow development with delayed reproduction; decreased mortality; a longevity of more than one year[2]; and shunting of only a small part of assimilated energy into reproduction. Such traits were suggestive of "*K*-selection," but he noted that others, including small adult body size and absence of a competitive environment, were associated with *r*-strategists. However, this mite is quite large for an oribatid, and *r-K* selection theory stresses relativity. Also, a lack of resource competition and the severe environmental

---

[1]West (1982) assumed that the nongravid, light colored specimens were males, but this is unlikely. Females do not darken or develop eggs until after a teneral period (Travé 1968).

[2]Block (1980, his Fig. 3) proposed a minimum generation time of 14 months, which would require a female to molt from the tritonymph, pass the teneral period, mate, develop eggs, and retain eggs to prelarvae during the same summer. But from a combined energy budget and degree-day analysis, Burn (1986) suggested that the duration of just the deutonymph and tritonymph might together occupy more than three years in a natural temperature regime.

rigor should not force conclusions that something is unusual about the evolution of this particular mite. Instead, it further emphasizes the general utility of the typical oribatid mite life history. Their constrained physiology (rather low feeding and growth rates) does not allow them to adapt in any special way to cold, unpredictable environments, but at the same time their modest requirements and high adult survival give them the quality of perseverance.

In short, *A. antarcticus* seems to exhibit no life-history traits, or combination of them, that clearly constitute adaptation to an Antarctic environment. Survivorship curves are not yet available, but like other known oribatid mites they probably incur most mortality in immature instars (an important determinant of life histories according to Horn 1978) and adults seem to be dispersive (Covarrubias 1968).

Though life history *per se* may not be adaptive in *Alaskozetes antarcticus*, physiological adaptations may somewhat counter low heat budgets. Cold adaptation in this mite seems to consist of a higher temperature-specific metabolic rate than in temperate species, due perhaps to lower activation energies of enzymes (Block 1977, Block and Young 1978, Young 1979). A facet not yet examined is the involvement of gut microbes in digestion (see below). Is observed temperature-dependance of physiological traits in oribatid mites due in any significant way to parameters of microbial physiology? Another physiological trait, the ability to supercool, was first considered a specific adaptation to extreme climates (Block 1980), but now is known also to occur in temperate-zone oribatid mites (Cannon and Block 1988).

The evidence for specific life-history adaptations to cold environments is weak, especially when traits of temperate species are considered, and Danks (1981) expressed similar thoughts about arctic arthropods in general. Oribatid mite species with wide ecological distributions seem to respond to cold climates by elongating the life cycle as a function of heat budget. The cosmopolitan species *Tectocepheus velatus* illustrates this. It seems to be semivoltine in alpine Norway (Solhøy 1975), but bivoltine in more temperate regions of Europe (Thomas 1979, Schenker 1986). Rather than having a rigid diapause control, it exhibits considerable plasticity in being able to overwinter in most, if not all instars. Elongation of the life cycles of arthropods in cold climates may indeed confer a resistance to catastrophic losses of a single age-class (e.g. West 1982, Ring and Tesar 1981). But if elongation is simply due to limited heat resources, it should be considered neither an adaptation nor the principal part of a "strategy" for life in such environments, as some have suggested (e.g. MacLean 1975).

4.2 Species in Hot Deserts

In hot deserts a high heat budget allows relatively rapid life cycles, while reproductive contributions may often be limited by moisture regimes. We have little information on life histories of oribatid mites living in hot, dry climates, but some

adaptive traits have been suggested. As with studies of oribatid mites in cold climates, much of the speculation is unconvincing.

Using a combination of Berlese-funnel and flotation methods, Wallwork (1972) studied *Joshuella striata* and *Haplochthonius variabilis* under *Juniperus* bushes in the Mojave Desert of California. He suggested that reproduction occurred once annually, with full development occurring within weeks in the litter layer, either at the time of winter rainfall (*J. striata*) or in spring (*H. variabilis*). However, immatures were present in all but one sampling period, suggesting that reproduction may not in fact be so highly circumscribed. Also, he took few samples, reported no estimates of variation, and only noted the depth of mineral soil samples (8–14 cm.) in a later paper (Wallwork 1980).

Referring to the ideas of Noy-Meir (1973), Wallwork (1980) considered these as opportunistic, *r*-selected species, tracking a resource (in this case moisture) with pulses of reproduction. But even if we accept the relatively unconvincing data in this study, *r*-selection seems an unreasonable hypothesis. There is no evidence of the multivoltinism, short adult life, and high reproductive potential normally associated with such life histories.

Studies of experimentally watered Chihuahuan desert soil (Wallwork et al. 1984, 1986) suggested that reproduction in *Jornadia larrea* and two species of *Passalozetes* occurs only in summer and cannot be triggered by artificial rainfall. The authors considered this seasonal recruitment an adaptation to the summer rainfall in the region. However, data from Luxton (1981a, his Table 2) indicates that most poronotic oribatid mites (a group including *Passalozetes* and *Jornadia*) produce eggs seasonally, particularly in summer. The observed timing could simply be plesiotypic (i.e. ancestral in poronotic mites), "preadapting" them to the moisture regime of the Chihuahuan Desert.

In contrast, *Joshuella striata* appears able to reproduce throughout the year and does well in the different moisture regimes of both the Mojave and Chihuahuan Deserts (Wallwork et al. 1984, 1986). But the data supporting opportunistic tracking of moisture levels are equivocal, and this mite species may simply have a historical tendency to carry eggs throughout the year. At present we have no data for other members of the family Gymnodamaeidae.

4.3 Freshwater Species

Few oribatid mite lineages have made the transition to freshwater, and while morphological adaptations are known, clear life-history adaptations are not. Thelytoky appears to be derived and probably adaptive in brachypylines, such as Hydrozetidae, but is ancestral and perhaps "preadaptive" in freshwater members of early-derivative groups (e.g. Trhypochthoniidae) (Norton and Palmer 1991).

Fragmentary laboratory and field information (Norton et al. 1988b, Norton and Palmer 1991, unpublished observations) suggests that aquatic Trhypochthoniidae are demographically at least as conservative as soil-dwelling relatives. Living

in cold, oligotrophic waters, *Mucronothrus nasalis* probably has a multiyear generation time and low fecundity.

Adaptive life histories have been suggested for the thelytokous brachypyline species *Hydrozetes lemnae*, associated with duckweed (*Lemna gibba*) in temperate Argentina (Athias-Binche and Fernandez 1986, Fernandez and Athias-Binche 1986). Immatures burrow in the duckweed leaflets and adults disperse. The studied captive population appeared to be bivoltine with nonoverlapping summer and winter generations, and though females of each generation laid about 30 eggs, net reproductive rate per female (R_0) was much lower in winter females than in summer females (0.63, 1.59 respectively).

Fernandez and Athias-Binche (1986) suggested that immatures of the Argentine population are specialized duckweed endophages, and will drown when innundated (due to the absence of a plastron). But if this is true, it is not clear why immatures of European and North American *H. lemnae* may be found dissociated from duckweed (Grandjean 1948, pers. observ.) and are easily reared on fully immersed, decomposing leaves (Burford 1976, Johnson 1983).

Fernandez and Athias-Binche (1986) also suggested that *H. lemnae* tends toward an *r*-selected demography, but they did not specify traits they considered to be so selected. Reproductive rate seems to be no higher than expected for soil species, and they had no laboratory data on development time. Burford (1976) estimated a rather short development time for *H. lemnae* (misidentified as a new species), but considered it univoltine in Colorado. A similar development time was observed by Johnson (1983, mean = 51 days). One could argue that a slightly higher heat budget may be responsible for the proposed bivoltinism of *H. lemnae* in Argentina. If true, such environmental differences reflect heat budgets and not adaptation. Although the analyses of Fernandez and Athias-Binche (1986) are elegant, this experiment was not replicated, and with a single sample taken per time period the significance of the data cannot be judged.

4.4 Tropical Species

Beck (1969, 1972) concluded that the rather depauperate oribatid mite fauna of flooded forests in the Amazon Basin adapted some life-history traits to the seasonal flood rhythm. Only *Rostrozetes foveolatus* seems to survive the extended flooding as adults, though densities are rather low. Females develop eggs while still under water, and Beck considered the thelytoky exhibited by this species a prerequisite for population survival, since low densities and environmental conditions preclude indirect sperm transfer by spermatophores. But since he found *R. foveolatus* also to be thelytokous in non-flooded forests (true also of all North American populations I have examined), this may instead be a "preadapted" trait.

Several other species gradually became abundant after flood waters receded. Beck suggested that their short development time (3–5 months) is synchronized

to flood periodicity, and that flooding was endured by diapausing eggs, since Berlese funnel samples failed to produce specimens. However, laboratory studies will be necessary to confirm the diapause, a phenomenon currently unknown for any oribatid mite species. Also, most species studied were found in nonflooded forests as well (where their life histories were undetermined). This suggests that eurytypic biologies, rather than specific life-history adaptations, may be responsible for their establishment in flood-zone forests.

5. Synthesis of Ideas on Life-History Evolution in Oribatid Mites

5.1 Three Views of "K-attributes"

As noted by Crossley (1977), the general life-history traits of oribatid mites exemplify those of so-called "*K*-selected" species. In this view, life-history traits such as delayed maturity, low reproductive potential, iteroparity and long adult life are adaptations to existence in a competitive environment at stable population densities.

Is competition a significant force in the organic horizons of soil? It may be hard to imagine food as a limiting factor in such environments, but in the spatial mosaic that constitutes this system (Mitchell and Parkinson 1976, Mitchell 1979a) quality food may be quickly utilized. This is supported by observations of seasonal shifts in oribatid mite diets, particularly from fungi to higher plant material as the former becomes less available (Anderson 1975b). Observed redistributions of oribatid mite species in microcosms also seem attributable to competition (Anderson 1978b).

"Bet-hedging" (Stearns 1977) is a second hypothesis consistent with the life-history attributes of most oribatid mites. In such a model, if a variable environment results in variable immature mortality, the above-noted suite of life-history traits could result as a "syndrome." Delayed maturity, smaller and iteroparous reproductive effort, and greater longevity are then viewed as buffers against catastrophic population reductions. If such unpredictable mortality occurs in oribatid mite populations, it seems reasonable that the immatures would bear the brunt of it.

In a recent analysis Lebrun et al. (1991) seem to embrace both ideas, but is it necessary to invoke either model? In a reevaluation of ideas about life-history evolution, Stearns (1980) suggested that individual life-history traits may have strong evolutionary interactions with physiological traits, and constraints in physiology can overwhelm any co-adaptation of life-history traits predicted from theory. Thus, the following third approach to oribatid mite life-history evolution should be considered.

5.2 Constraints in Oribatid Mite Life Histories

Historical constraints, especially those related to digestive physiology, may be the ultimate cause of many life-history traits of oribatid mites. For example,

iteroparity is theoretically one of natural selection's responses to the concentration of mortality in immatures or to the high risk of reproductive failure in any given season (Stearns 1976, 1977, Horn 1978). Yet in small-bodied species that carry only one or two eggs, semelparity is impossible. Even in larger species, slow digestive processes, low metabolic rates (Luxton 1975, Mitchell 1979b, Thomas 1979), and an inability to store significant amounts of energy (Wallwork 1979) may lead to iteroparity.

Can aspects of ancestral feeding biology explain a generally low metabolic rate? Microbial tissues, principally fungal mycelia and spores, were probably the major food of early oribatid mites. Saprophagy (feeding on decaying higher plant structural material) perhaps evolved as a facultative means of getting at non-surface microbial tissue or metabolites when surface mycelia were in short supply (Norton 1985, but see Luxton 1979). Such particulate feeding is very different from that of the fluid-feeding predators that presumably constituted the earliest Acari. Accumulating evidence suggests involvement of gut microbes in the digestive processes of oribatid mites, whether they are fungivorous or saprophagous (Stefaniak and Seniczak 1976, Seniczak and Stefaniak 1978, Stefaniak and Seniczak 1981, Wolf and Rockett 1984, Haq and Konikkara 1988). Yet these intestinal microbes appear to represent a nurtured component of the external microbial community, rather than a specialized obligate flora. The shift from predation to fungivory and saprophagy may have been related to an increased reliance on metabolites or biomass produced by facultative gut microbes. Such reliance may impose upper limits on food utilization, thus constraining metabolic and growth rates.

Based on this idea, Fig. 5.2 suggests possible interrelationships of some life-history traits of oribatid mites. Low metabolic rate is the driving force in this model, resulting in slow development and low time-specific fertility. Due to the latter, population maintenance requires long adult lives. Limited body size plus limited energy storage promote iteroparity. The need for adult longevity provides a selective force for morphological and behavioral adaptations for defense, some of which also enhance dispersal ability. Maintenance requirements during this long adult life and energy costs of dispersal probably further reduce fertility. The rather stable adult population seen by many authors results from extended development, adult longevity and iteroparity.

6. Life-History Aspects of the Origin of the Astigmata

A generalization that life-history evolution did not play a principal role in the radiation of oribatid mites would have one outstanding exception, the Astigmata. These mites exploit protein-rich, high quality foods that are patchy in time and space, and in doing so have evolved important relationships with both plants and animals (OConnor 1982). Such biologies demand life-history traits very different

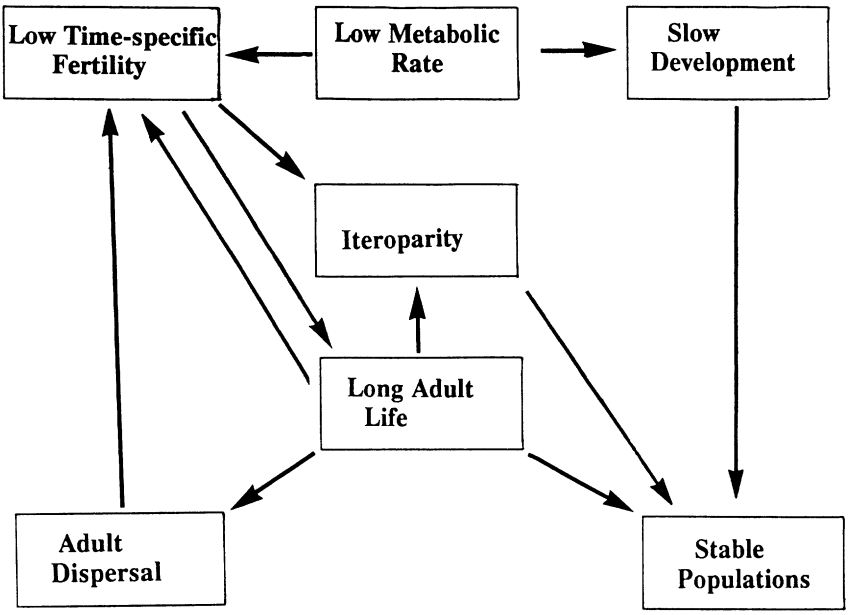


Figure 5.2. Possible relationships of some aspects of oribatid mite life histories, based on low metabolic rate as the dominant influence (see text for explanation).

from those of oribatid mites. The great diversity of free-living and parasitic life styles (see OConnor 1982) and their corresponding life-history adaptations make generalization tenuous, but the Astigmata usually have higher fecundity, much faster development, and thus much higher reproductive rates than do oribatid mites. Adults are relatively short-lived, and egg turnover rates are relatively high (e.g. Gerson et al. 1983). In short, these colonizing mites may exhibit true *r*-selected demographies, unlike any known oribatid mite.

Dispersal ancestrally occurs in the heteromorphic deutonymph ("hypopus"), a nonfeeding instar morphologically and physiologically adapted to phoresy, though in some species the instar may be omitted or included only facultatively. In terms of life-cycle, the loss of one instar in such taxa represents a lowering of age at reproduction, a common trait of exploitative, *r*-selected species. Mating and internal fertilization are ubiquitous in the Astigmata, in contrast to the free-standing spermatophore of oribatid mites.

If the Astigmata originated within an oribatid lineage, two intriguing questions are immediately posed. With such a dichotomy between the basic life histories, how did the transition occur? Since mites are notorious for multiple origins of exploitative life styles, why in the long history of oribatid mites did such a major change in life style occur in only one lineage? The questions may have the same ultimate answer if one aspect of oribatid mite life history was particularly difficult

to change, such that it constituted a barrier (in the sense of Stearns 1980) to "breaking out" of the self-reinforcing system suggested in Fig. 5.2.

Some trait changes are unlikely to have initiated the transition. The abandonment of indirect fertilization by the Astigmata certainly increased mating efficiency, but associative mating seems to have evolved independently several times in oribatid mites (see above) without producing major life-history shifts.

Could a shift to higher quality resources have been the key? Many oribatid mites have been characterized as opportunistic feeders that can utilize protein-rich food. For example, species whose guts normally contain leaf and fungal fragments may feed almost exclusively on pollen at times of peak release by plants (Hammer 1972, Behan-Pelletier and Hill 1983, pers. observ.). Some Brachypylina readily eat living nematodes when they are available (Rockett and Woodring 1966b, Muraoka and Ishibashi 1976, Rockett 1980, Walter and Ikonen 1989). Food quality alone was probably not the key to life-history transition.

A more efficient digestive physiology, allowing higher metabolic and growth rates, probably appeared early in the origin of the Astigmata. Even when environments and food seem similar, the Astigmata are more metabolically active. For example, the acarid *Niadacarus arboricolus* has apparently reverted to an oribatid-like feeding regime by feeding on dead leaves. For an astigmatid mite it is considered "*K*-selected" but its development is shorter and reproductive capacity much higher than that of leaf-feeding oribatid mites (Fashing, this volume). If gradual physiological improvements were the key to the original success of the Astigmata, we might expect intermediate forms of life history in early-derivative groups, but there is no evidence of this.

One clear life-history difference is that oribatid mites disperse as adults while astigmatid mites disperse as immatures, at least ancestrally. The phoretic deutonymph has been a key to the radiation of the Astigmata, but could it have arisen *ad hoc* from an oribatid mite life cycle? An even more basic life-history change, the shifting of dispersal from the adult to one or more immature instars, was probably a necessary precedent (see Houck, Chapter 11, this volume, for discussion of why **deutonymph** is the only immature instar involved in disperal).

Horn (1978) considered age at dispersal to be a major factor in molding life histories. If dispersal as immatures is somehow introduced into a "*K*-style" life history, prior constraints and reinforcements may be profoundly affected. If females are nondispersive, more energy can be invested in egg production. The increased reproductive uncertainty involved with dispersal of immatures places a high priority on maximizing propagules at the expense of adult survival, and such a shift in emphasis characterizes *r*-selected Astigmata.

What could have allowed a change from dispersal as adults to dispersal as immatures in the lineage that produced the Astigmata? Could some functional indifference in the age of dispersal have been involved, such that immatures and adults were equally effective? This hypothesis seems doomed, since a pre-reproductive individual in a sexually reproducing species is less valuable as

dispersive "currency " than is a fertilized female. But if the ancestral lineage was thelytokous there is little difference in the value of adults and immatures as propagules. Immature females are less likely to survive to oviposition, but this is offset by a greater abundance of immatures relative to adults.

Since thelytokous taxa are usually considered long-term evolutionary dead ends, it is necessary to consider the cladistic relationships of the Astigmata to appreciate this possibility (Norton and Palmer 1991). The Astigmata appear to have evolved from within the Desmonomata (Fig. 5.1), but particularly from within the Trhypochthonioidea (including Trhypochthoniidae sensu lato, Malaconothridae; also Mucronothridae, Allonothridae of authors). This group contains no sexual species (Norton et al. 1988c), and appears to have radiated in a thelytokous reproductive mode. Many of these mites are only weakly sclerotized as adults, such that the difference in cuticular hardness between adults and immatures is not great.

If this scenario is correct, the predominance of sexuality in the Astigmata means that a reversion to sexual reproduction occurred early in their evolution (Norton and Palmer 1991), and the added evolutionary plasticity associated with sex may have fueled other changes. Such a proposal goes against the grain of current theory, and for some a reversal to sexuality may be even more difficult to accept than is radiation in a fully thelytokous taxon. Yet, a population of *Oribatula sakamorii* in Japan seems to have incurred such a reversal during gradual habitat improvement (Fujikawa 1987). New cytogenetic perspectives on such reversals are discussed in Chapter 11 of this volume.

Whatever the evolutionary reasons, in giving rise to the Astigmata oribatid mites had a single "fling" at major life-history radiation. The very success of this radiation from an otherwise conservative group has delayed our recognition of its origins.

7. Prospectus for Future Research

In the future it will be important to learn the proximate cause of the relatively low metabolic rates in oribatid mites and the possible contribution of their nonspecific gut flora to digestive processes. Even the hydrolytic enzymes from ingested fungal food may contribute, though there is no strong evidence for this in other studied arthropod detritivores (Martin 1987).

Within this framework, we need to understand the physiological basis for the more rapid temperature-specific development seen in more derived groups. For example, Haq (1978) found the rather primitive species *Lepidacarus ornatissimus* to have a one year generation time even in tropical India, a laboratory development seven times longer than that of similarly sized galumnid mites (Brachypylina).

Such studies will be of general interest in soil ecology. For example, collembolans generally have higher ingestion rates, higher metabolic rates, and shorter

generation times than do oribatid mites (Crossley 1977), while feeding on similar materials. This implies a considerable difference in competitive ability. Though they are of a similar geologic age as oribatid mites, collembolans have a very different evolutionary history and probably did not incur a major shift in food base. Collembolans may also have an advantage from the standpoint of feeding mechanisms. Their mandibulate mouthparts, often with grinding molar plates, seem more efficient for processing fungal and leaf tissue than are the chelicerae of oribatid mites. Chelicerae evolved in association with predation, and probably became useful in particulate feeding only with the origin of the subcapitular rutella; these function with the chelicerae to cut minute individual pieces of substrate.

Further studies of thelytokous parthenogenesis should be especially rewarding, as it appears to be a long-established plesiotypic trait in some groups but a recent apotypic trait in others. Just as importantly, detailed studies of thelytokous species could aid our understanding of phenotypic plasticity. Heritable genetic variation in life-history traits currently cannot be distinguished from phenotypic responsiveness to environmental conditions, making discussions of life-history adaptations rather pointless (Stearns 1980, Sweeney 1984, Scharloo 1989, Stearns 1989). Like collembolans (Amelsvoort and Usher 1989), some members of the Mesostigmata and the Astigmata show phenotypic plasticity (Gerson et al. 1983, Athias-Binche 1987, Knülle 1991), such that development time and fecundity can exhibit *r*- or *K*-attributes, according to quality of food provided.

The multiplicity of clones found in natural populations of thelytokous oribatid mite species (Norton and Palmer 1991, Palmer and Norton 1992) can provide us with fixed genotypes for testing responses to differences in resources and environmental variables. Using thelytokous mites, plasticity can be examined in both colonizing species (e.g. brachypyline species in which thelytoky is probably recently derived) and those characteristic of more stable habitats (e.g. many Desmonomata in which thelytoky is plesiotypic).

Knowledge of clonal composition, which is not difficult to obtain, would have been beneficial in two interesting recent studies. One (Fujikawa 1988) examined long-term changes in a population of the colonizing thelytokous species *Tectocepheus velatus* during gradual site improvement in a field previously farmed with conventional methods. According to the data (her Fig. 4) this population may have changed from univoltine to bivoltine, or at least developed a second oviposition period. Was this due to clonal selection, or the addition of another clone? Or does it reflect phenotypic plasticity in one or more original clones, such that voltinism is related to environmental quality? The latter is not unreasonable, and food-based changes in voltinism have been suggested in insects (Sweeney 1984). Vera and Berthet (1988) found populations of the thelytokous *Platynothrus peltifer* from two forest types to differ in certain developmental parameters. An analysis of clonal structure could have supported their claims of heritable, adaptive differences.

One wholly thelytokous family would be an excellent choice for study. The Trhypochthoniidae contains an interesting array of genera that exhibit a wide range of life styles, including *Archegozetes* (colonizers of disturbed habitats in the tropics, with relatively short life cycles and high clutch sizes), *Trhypochthonius* (mostly temperate, noncolonizing species with moderate life-history parameters), and *Mucronothrus* (long-lived inhabitants of springs and other oligotrophic freshwater) (see Norton and Palmer 1991 and included references). The family is of added interest because of probable close phylogenetic ties with the Astigmata.

Lastly, such studies will not significantly advance our understanding of life-history evolution in the absence of a phylogenetic framework. Carefully constructed hypotheses on phylogenetic relationships of oribatid mites, encompassing at least the common families, will be essential.

8. Conclusions

To suggest that oribatid mites never exhibit adaptive life-history traits would be unreasonable, but most current claims of adaptation are not convincing. Studies initiated with the intent of finding adaptive demographic traits or "strategies" usually fail to address the possibility that beneficial traits are plesiotypic. In the terminology of Gould and Vrba (1982), authors usually do not distinguish between adaptations (apotypic traits developed in response to selective pressures in the environment under study) and exaptations ("preadaptive" plesiotypic traits accrued before the current environmental relationship existed). The general suite of life-history traits exhibited by oribatid mites (slow development, low fecundity, iteroparity and long adult life) seems well suited to life in many different environments, but all may result directly or indirectly from a low metabolic rate.

The Astigmata exhibit the only significant deviations from these traits. As a major radiation from oribatid mites (and hence belonging to the oribatid mites in the cladistic sense), they often have both life cycles and demographic traits that seem adaptive. Compared to their close relatives (the Trhypochthonioidea), life histories seem little constrained by metabolic rate.

Acknowledgments

Research leading to the development of ideas expressed in this paper was supported by a grant from the National Science Foundation (BSR 8415747). I am grateful to several colleagues for their helpful comments on the manuscript: Drs. F. Athias-Binche (Laboratoire Arago, Banyuls sur Mer, France), V. M. Behan-Pelletier (Biosystematics Research Centre, Ottawa), N. Fashing (College of William and Mary, Williamsburg), M. Luxton (Liverpool Polytechnic, Liverpool, England) and M. J. Mitchell (S.U.N.Y.-C.E.S.F., Syracuse).

References

Akimov, I. A. and A. V. Yastrebtsov. 1987. Morphology of certain organ systems of the oribatid mite *Nothrus palustris* (Oribatei, Nothroidae). In: *Soil Fauna and Soil Fertility* (B. R. Strigatova ed.). "Nauka", Moscow. Pp. 534–538.

Alberti, G. 1973. Ernährungsbiologie und Spinnvermögen der Schnabelmilben (Bdellidae, Trombidiformes). *Z. Morphol. Tiere* 76:285–338.

Amelsvoort, P. A. M. van and M. B. Usher. 1989. Egg production related to food quality in *Folsomia candida* (Collembola: Isotomidae): effects on life history strategies. *Pedobiologia* 33:61–66.

Anderson, J. M. 1975a. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *J. Anim. Ecol.* 44:475–95.

Anderson, J. M. 1975b. The enigma of soil animal species diversity. In: *Proc. Vth Int. Colloq. Soil Zool.* (J. Vanek ed.). W. Junk Publ., The Hague. Pp. 51–58.

Anderson, J. M. 1978a. Inter- and intra-habitat relationships between woodland Cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia* 32:341–8.

Anderson, J. M. 1978b. Competition between two unrelated species of soil Cryptostigmata (Acari) in experimental microcosms. *J. Animal Ecol.* 47:787–803.

Aoki, J.-i. 1967. Microhabitats of oribatid mites on a forest floor. *Bull. Nat. Sci. Mus.* (Tokyo) 10:135–138.

Arlian, L. G. and T. A. Woolley. 1970. Observations on the biology of *Liacarus cidarus* (Acari: Cryptostigmata, Liacaridae). *J. Kans. Entomol. Soc.* 43:297–301.

Athias-Binche, F. 1985. Analyse démographique des Uropodides (Arachnides: Anactinotriches) de la hetraie de la Massane, France. *Pedobiologia* 28:225–253.

Athias-Binche, F. 1987. Signification adaptative des différents types de développements postembryonnaires chez les Gamasides (Acariens, Anactinotriches). *Can. J. Zool.* 65:1299–1310.

Athias-Binche, F. 1989. Polymorphismes et hétéromorphies chez les acariens, et la notion de stase selon Grandjean. In: *L'Ontogénèse et le Concept de Stase Chez les Arthropodes* (H. M. André and J.-C. Lions eds.). Agar Publ., Wavre, Belgium. Pp. 41–57.

Athias-Binche, F. and N. A. Fernandez. 1986. Analyse démographique d'une population d'*Hydrozetes lemnae* Coggi, Acarien Oribate inféodé à la lentille d'eau *Lemna gibba* L. en Argentine. 2. Les relations prédateur/proie. *Zool. Jahrb. Syst.* 113:229–249.

Bäumler, W. 1970. Zur Morphologie, Biologie und Ökologie von *Hermannia gibba* (C. L. Koch) (Acarina: Oribatei) unter Berücksichtigung einiger Begleitarten. II. *Z. angew. Entomol.* 66:337–62.

Beck, L. 1969. Zum jahreszeitlichen Massenwechsel zweiger Oribatidenarten (Acari) im neotropischen Überschwemmungswald. *Zool. Anz.* (*Suppl.*) 32:535–40.

Beck, L. 1972. Der Einfluss der jahresperiodische Überflutungen auf den Massenwechsel der Bodenarthropoden im zentral-amazonischen Regenwaldgebiet. *Pedobiologia* 12:133–148.

Beckmann, M. 1988. The development of soil mesofauna in a ruderal ecosystem as influenced by reclamation measures 1. Oribatei (Acari). *Pedobiologia* 31:391–408.

Behan-Pelletier, V. M. 1988. Redefinition of Zachvatkinibates (Acari: Mycobatidae), with description of a new species and immatures of *Z. maritimus* Shaldybina 1973. *Can. Entomol.* 120:797–813.

Behan-Pelletier, V. M. 1989. *Limnozetes* (Acari: Oribatida: Limnozetidae) of Northeastern North America. *Can. Entomol.* 121:453–506.

Behan-Pelletier, V. M. and S. B. Hill. 1983. Feeding habits of 16 species of Oribatei (Acari) from an acid peat bog, Glenamoy, Ireland. *Rev. Écol. Biol. Sol* 20:221–268.

Bell, G. 1982. *The Masterpiece of Nature*. Univ. Calif. Press, Berkeley. Pp. 635.

Bellido, A. 1979. Development postembryonnaire de *Carabodes willmanni* Bernini 1975 (Acari, Oribatei). *Acarologia* 20:419–32.

Bellido, A. 1990. Charactéristiques biodémographiques d'un acarien oribate (*Carabodes willmanni*) des pelouses xérophiles. *Can. J. Zool.* 68:2221–2229.

Bernini, F. and R. Nannelli. 1982. Notulae Oribatologicae XXVI. Contribution to the knowledge of the genus *Cepheus* (Oribatida, Acarida) in Italy. *Redia* 65:155–188.

Berthet, P. 1964. Field study of the mobility of Oribatei (Acari) using radioactive tagging. *J. Anim. Ecol.* 33:443–449.

Bhattacharya, T., V. C. Joyand and S. Joy. 1978. Studies on the effect of temperature on the development of *Oppia nodosa* Hammer (Acari: Cryptostigmata: Oppiidae). *Entomon* 3:149–155.

Block, W. 1977. Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). *J. Exp. Biol.* 68:69–88.

Block, W. 1980. Survival strategies in polar terrestrial arthropods. *Biol. J. Linn. Soc.* 14:29–38.

Block, W. and S. R. Young. 1978. Metabolic adaptations of Antarctic terrestrial microarthropods. *Comp. Biochem. Physiol.* 61 A:363–368.

Burford, D. A., Jr. 1976. Morphology and life history of *Hydrozetes bushnelli* n.sp. (Oribatei, Hydrozetidae). Ph.D. dissertation, Univ. Colorado, Boulder, CO. 127 Pp.

Burn, A. J. 1986. Feeding rates of the Cryptostigmatid mite *Alaskozetes antarcticus*. *Br. Antarct. Surv. Bull.* 71:11–18.

Cancela da Fonseca, J. P. 1980. Quelques approches analytiques en dynamique des populations édaphiques (Acariens Oribates). *Rev. Écol. Biol. Sol* 17:445–447.

Cannon, R. J. C. 1987. Effects of low-temperature acclimation on the survival and cold tolerance of an Antarctic mite. *J. Insect Physiol.* 33:509–521.

Cannon, R. J. C. and W. Block. 1988. Cold tolerance of microarthropods. *Biol. Rev. Camb. Philos. Soc.* 63:23–77.

Cole, L. C. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* 29:103–137.

Covarrubias, R. 1968. Some observations on Antarctic Oribatei (Acarina). *Liochthonius australis* sp.n. and two *Oppia* ssp.n. *Acarologia* 10:313–356.

Crossley, D. A., Jr. 1977. Oribatid mites and nutrient cycling. In: *Biology of Oribatid Mites* (D. L. Dindal ed.). SUNY-CESF, Syracuse. Pp. 71–85.

Danks, H. V. 1981. *Arctic arthropods. A review of Systematics and Ecology with Particular Reference to the North American Fauna*. Entomol. Soc. Canada, Ottawa. 608 pp.

Dybas, H. S. 1966. Evidence for parthenogenesis in the featherwing beetles, with a taxonomic review of a new genus and eight new species (Coleoptera: Ptiliidae). *Fieldiana Zool.* 51:11–12.

Fain, A. and A. Herrin. 1978. La prélarve chez les astigmates (Acari). *Acarologia* 20:566–571.

Fashing, N. J. 1977. The resistant tritonymphal instar and its application in the population dynamics of *Naiadacarus arboricolus* Fashing, a mite restricted to water-filled treeholes (Acarina: Acaridae). *Am. Midl. Nat.* 95:337–346.

Fernandez, N. A. and F. Athias-Binche. 1986. Analyse démographique d'une population *d'Hydrozetes lemnae* Coggi, Acarien Oribate inféodé à la lentille d'eau *Lemna gibba* L. en Argentine. 1. Méthodes et techniques, démographie d'*H. lemnae* comparaisons avec d'autres Oribates. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 113:213–228.

Fujikawa, T. 1974. Comparison among oribatid faunas from different microhabitats in forest floors. *Jap. J. Appl. Entomol. Zool.* 9:105–114.

Fujikawa, T. 1987. Biology of *Oribatula sakamorii* Aoki, a dominant species of the oribatid fauna in nature farming field. In: *Soil Fauna and Soil Fertility-Proc. 9th Int. Congr. Soil Zool.* (B. R. Strigatova ed.). "Nauka," Moscow. Pp. 544–552.

Fujikawa, T. 1988. Biology of *Tectocepheus velatus* (Michael) and *T. cuspidentatus* Knülle. *Acarologia* 29:307–315.

Gerson, U., S. Capua and D. Thorens. 1983. Life history and life tables of *Rhizoglyphus robini* Claparède (Acari: Astigmata: Acaridae). *Acarologia* 24:439–448.

Gilyarov, M. S. 1982. The ecological role of parthenogenesis. *Adv. Mod. Biol.* (Moscow) 93:10–22. (In Russian).

Godfray, H. C. J. 1987. The evolution of clutch size in invertebrates. In: *Oxford Surveys in Evolutionary Biology*, Vol. 4 (P. H. Harvey and L. Partridge eds.). Oxford Univ. Press, NY. Pp. 117–154.

Gould, S. J. and E. S. Vrba. 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15.

Gourbière, F., J.-C. Lions and R. Pepin. 1985. Activité et développement d'*Adoristes ovatus* (C. L. Koch, 1839) (Acarien, Oribate) dans les aiguilles d'*Abies alba* Mill. Relations avec la décomposition et les microflores fongiques. *Rev. Écol. Biol. Sol* 22:57–73.

Grandjean, F. 1941. Statistique sexuelle et parthénogénèse chez les Oribates (Acariens). *C. R. Se*ances *Acad. Sci.* 212:463–467.

Grandjean, F. 1948. Sur les *Hydrozetes* (Acariens) de l'Europe occidentale. *Bull. Mus. nat. Hist. natur.* 20:328–335.

Grandjean, F. 1954. Observations sur les Oribates (31e série). *Bull. Mus. nat. Hist. natur.* 26:582–589.

Grandjean, F. 1956a. Observations sur les Oribates (33e série). *Bull. Mus. nat. Hist. natur.* 28:111–118.

Grandjean, F. 1956b. Observations sur les Galumnidae (1re série). (Acariens, Oribates). *Rev. Fr. Entomol.* 23:137–146.

Grandjean, F. 1961. Les Amerobelbidae (Oribates) (1re série). *Acarologia* 3:303–343.

Grandjean, F. 1962. Prélarves d'Oribates. *Acarologia* 4:423–439.

Grandjean, F. 1969. Considérations sur le classement des Oribates. Leur division en 6 groupes majeurs. *Acarologia* 11:127–153.

Grishina, L. G. 1991. Length of the life cycle of oribatid mites (Sarcoptiformes, Oribatei). *Sib. Biol. Zh.* 3:37–47. (In Russian).

Haarlov, N. 1960. Microarthropods from Danish soils. Ecology, phenology. *Oikos (Suppl)* 3:1–176.

Haq, M. A. 1978. Breeding biology of oribatid mites. In: *Soil Biology and Ecology in India* (C. A. Edwards and G. K. Veeresh eds.). *Univ. Agric. Sci., Techn. Ser. 22*, Bangalore. Pp. 145–151.

Haq, M. A. and C. Adolph. 1981. Spermatophore deposition and transfer in *Pelokylla malabarica* (Acari: Oribatei). *Entomon* 6:135–141.

Haq, M. A. and I. D. Konikkara. 1988. Microbial associations in xylophagous oribatids. In: *Progress in Acarology*, Vol. 1 (G. P. ChannaBassavan and C. A. Viraktamath eds.). Oxford and IBH Publ. Co. Pvt. Ltd., New Delhi. Pp. 469–474.

Haq, M. A., K. Sheela and P. Neena. 1991. Ovoviviparity in oribatid mites. In: *Advances in Management and Conservation of Soil Fauna* (G. K. Veeresh, D. Rajagopal and C. A. Viraktamath eds.). Oxford and IBH Publ. Co. Pvt. Ltd., New Delhi.

Hammer, M. 1972. Microhabitats of oribatid mites on a Danish woodland floor. *Pedobiologia* 12:412–423.

Harding, D. J. L. and R. A. Stuttard. 1974. Microarthropods. In: *Biology of Plant Litter Decomposition* (C. H. Dickinson and G. J. F. Pugh eds.). Academic Press, NY. Pp. 489–532.

Hartenstein, R. 1962. Soil Oribatei. V. Investigations on *Platynothrus peltifer* (Acarina: Camisiidae). *Ann. Entomol. Soc. Am.* 55:709–713.

Horn, H. 1978. Optimal tactics of reproduction and life-history. In: *Behavioural Ecology: an evolutionary Approach* (J. R. Krebs and N. B. Davies eds.). Blackwell Sci. Publ., Boston. Pp. 411–429.

Jacot, A. P. 1933. Aparity among the Oribatidae (Acarina). *Can. Entomol.* 65:263–64.

Johnson, K. 1983. The ontogeny and descriptive anatomy of *Hydrozetes lemnae* (Coggi) (Acari: Oribatei: Hydrozetidae). Thesis, Univ. Kansas, Lawrence, KS. Pp. 57.

Kaneko, N. 1989. Life histories of four oribatid mite species in a mull type soil in a cool temperate forest in Japan. *Pedobiologia* 33:117–126.

Knülle, W. 1991. Life-cycle strategies in unpredictably varying environments: genetic adaptations in a colonizing mite. In: *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall, London. Pp. 51–55.

Krantz, G. W. and E. E. Lindquist. 1979. Evolution of phytophagous mites (Acari). *Annu. Rev. Entomol.* 24:121–158.

Krivolutsky, D. A. and A. Ya. Druk. 1986. Fossil oribatid mites. *Annu. Rev. Entomol.* 31:533–45.

Lange, A. P. 1960. The prelarva of mites of the order Acariformes and its peculiarities in palaeacarids (Palaeacariformes). *Zool. Zh.* 39:1819–1834. (In Russian).

Lebrun, P. 1970a. Écologie et biologie de *Nothrus palustris* (C. L. Koch 1839) 3ème note: Cycle de vie. *Acarologia* 12:193–207.

Lebrun, P. 1970b. Écologie et biologie de *Nothrus palustris* (C. L. Koch 1839). (Acarien, Oribate). IV. Survivance-écondité-action d'un prédateur. *Acarologia* 12:827–848.

Lebrun, P. 1971. Écologie et biocenotique de quelques peuplements d'arthropodes édaphiques. *Inst. R. Sci. Nat. Belg. Mem.* 165:1–203.

Lebrun, P. 1977. Comparaison des effets des températures constantes ou variables sur la durée de développement de *Damaeus onustus* (Acarina: Oribatei). *Acarologia* 19:136–143.

Lebrun, P. and M. van Ruymbeke. 1971. Intérêt écologique de la relation entre la temperature et la durée de développement des Oribates. *Acarologia* 13:176–185.

Lebrun, P., G. Van Impe, D. DeSaint Georges-Gridelet, G. Wauthy and H. M. André. 1991. The life strategies of mites. In: *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall, London. Pp. 3–22.

Lions, J.-C. 1973. Quelques prélarves nouvelles d'oribates. *Acarologia* 15:356–370.

Lions, J.-C. 1982. Statistique sexuelle chez deux formes d'oribates proches de *Quadroppia quadricarinata* (Michael 1885). *Acarologia* 23:373–389.

Lions, J.-C. and F. Gourbière. 1988. Populations adultes et immatures d'*Adoristes ovatus* (Acarien, Oribate) dans les aiguilles de la litière d'*Abies alba*. *Rev. Écol. Biol. Sol* 25:343–352.

Luxton, M. 1964. Some aspects of the biology of salt-marsh Acarina. *Acarologia* (*fasc. h.s.*) 6:172–182.

Luxton, M. 1967. The zonation of salt marsh Acarina. *Pedobiologia* 7:55–66.

Luxton, M. 1975. Studies on the oribatid mites of a Danish beech wood soil . II. Biomass, calorimetry, and respirometry. *Pedobiologia* 15:161–200.

Luxton, M. 1979. Food and energy processing by oribatid mites. *Rev. Écol. Biol. Sol* 16:103–111.

Luxton, M. 1981a. Studies on the oribatid mites of a Danish beech wood soil. IV. Developmental biology. *Pedobiologia* 21:312–340.

Luxton, M. 1981b. Studies on the oribatid mites of a Danish beech wood soil. VI. Seasonal population changes. *Pedobiologia* 21:387–409.

Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. *Q. Rev. Biol.* 59:257–290.

MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, NJ. 203 pp.

MacLean, S. F. 1975. Ecological adaptations of tundra invertebrates. In: *Physiological Adaptation to the Environment* (F. J. Vernberg ed.). Intext Educ. Publ., NY. Pp. 269–300.

Madge, D. S. 1964. The water relations of *Belba geniculosa* Oudms. and other species of oribatid mites. *Acarologia* 6:199–223.

Marshall, V. G., R. M. Reeves and R. A. Norton. 1987. Catalogue of the Oribatida (Acari) of continental United States and Canada. *Mem. Entomol. Soc. Can. No. 139.*

Martin, M. M. 1987. *Invertebrate-Microbial Interactions. Ingested Fungal Enzymes in Arthropod Biology*. Comstock Publ. Assoc., Ithaca, NY. Pp. 148.

Michael, A. D. 1884 (1883). *British Oribatidae, Vol. 1.* R. Soc., London. Pp. 1–336, pl. 1–24.

Mitchell, M. J. 1977a. Population dynamics of oribatid mites (Acari, Cryptostigmata) in an aspen woodland soil. *Pedobiologia* 17:305–319.

Mitchell, M. J. 1977b. Life history strategies of oribatid mites. In: *Biology of Oribatid Mites* (D. L. Dindal ed.). SUNY-CESF, Syracuse. Pp. 65–69.

Mitchell, M. J. 1979a. Effects of physical parameters and food resources on oribatid mites in forest soils. In: *Recent Advances in Acarology*, Vol. 1 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 585–592.

Mitchell, M. J. 1979b. Energetics of oribatid mites in an aspen woodland soil. *Pedobiologia* 17:305–319.

Mitchell, M. J. and D. Parkinson. 1976. Fungal feeding of Oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. *Ecology* 57:302–312.

Muraoka, M. and N. Ishibashi. 1976. Nematode-feeding mites and their feeding behavior. *Appl. Entomol. Zool.* 11:1–7.

Murphy, P. W. and A. N. Balla. 1973. The bionomics of *Humerobates rostrolamellatus* Grandjean (Cryptostigmata-Ceratozetidae) on fruit trees. In: *Proc. 3rd Int. Congr. Acarol.*, Prague, 1971. Pp. 97–104.

Nannelli, R. 1975. Osservazioni sulla biologia di *Oppia concolor* in condizioni sperimentali di allevamento. *Redia* 56: 111–116.

Newell, I. M. 1945. *Hydrozetes* Berlese (Acari, Oribatoidea): The occurrence of the genus in North America, and the phenomenon of levitation. *Trans. Conn. Acad. Arts Sci.* 36:253–68, pls. 1–3.

Norton, R. A. 1980. Observations on phoresy in oribatid mites (Acari: Oribatei). *Int. J. Acarol.* 6:121–130.

Norton, R. A. 1983. Redefinition of *Mochloribatula* (Acari: Mochlozetidae), with new species, recombinations and notes on plant associations. *Acarologia* 24:449–464.

Norton, R. A. 1984. Monophyletic groups in the Enarthronota (Sarcoptiformes). In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood Ltd., Chichester. Pp. 233–240.

Norton, R. A. 1985. Aspects of the biology and systematics of soil arachnids, particularly saprophagous and mycophagous mites. *Quaest. Entomol.* 21:523–541.

Norton, R. A. and M. C. MacNamara. 1976. The common newt (*Notophthalmus viridescens*) as a predator of soil mites in New York. *J. Ga. Entomol. Soc.* 11:89–93.

Norton, R. A. and D. Y. Sillman. 1985. Impact of oily waste application on the mite community of an arable soil. *Exp. Appl. Acarol.* 1:287–305.

Norton, R. A., P. M. Bonamo, J. D. Grierson and W. M. Shear. 1988a. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York State. *J. Paleontol.* 62:259–269.

Norton, R. A., D. D. Williams, I. D. Hogg and S. C. Palmer. 1988b. Biology of the oribatid mite *Mucronothrus nasalis* (Acari: Oribatida: Trhypochthoniidae) from a small coldwater springbrook in eastern Canada. *Can. J. Zool.* 66:622–629.

Norton, R. A., S. C. Palmer and H-f. Wang. 1988c. Parthenogenesis in Nothridae and related groups. In: *Progress in Acarology*, Vol. 1 (G. P. ChannaBassavan and C. A. Viraktamath eds.). Oxford and IBH Publ. Co. Pvt. Ltd., New Delhi. Pp. 255–259.

Norton, R. A., W. C. Welbourn and R. D. Cave. 1988d. First records of Erythraeidae parasitic on oribatid mites (Acari, Prostigmata: Acari, Oribatida). *Proc. Entomol. Soc. Wash.* 90:407–410.

Norton, R. A. and S. C. Palmer. 1991. The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites. In: *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall, London. Pp. 107–136.

Norton, R. A. and V. M. Behan-Pelletier. 1991. Calcium carbonate and calcium oxalate as cuticular hardening agents in oribatid mites (Acari: Oribatida). *Can. J. Zool.* 69:1504–1511.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* 4:25–51.

OConnor, B. M. 1982. Evolutionary ecology of astigmatid mites. *Annu. Rev. Entomol.* 27:385–409.

OConnor, B. M. 1984. Phylogenetic relationships among higher taxa in the Acariformes, with particular reference to the Astigmata. In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood Ltd., Chichester. Pp. 19–27.

Palmer, S. C. and R. A. Norton. 1990. Further experimental proof of thelytokous parthenogenesis in oribatid mites (Acari: Oribatida: Desmonomata). *Exp. Appl. Acarol.* 8:149–159.

Palmer, S. C. and R. A. Norton. 1991. Taxonomic, geographic, and seasonal distribution of thelytokous parthenogenesis in Desmonomata (Acari: Oribatida). *Exp. Appl. Acarol.* 12:67–81.

Palmer, S. C. and R. A. Norton. 1992. Genetic diversity in thelytokous oribatid mites (Acari: Acariformes: Desmonomata). *Biochem. System. Ecol.* 20:219–231.

Park, O. 1947. Observations on *Batrisodes* (Coleoptera: Pselaphidae), with particular reference to the American species east of the Rocky Mountains. *Bull. Chic. Acad. Sci.* 8:45–132, 11 pls.

Parker, S. B. 1982. *Synopsis and Classification of Living Organisms*, Vol. 2. McGraw-Hill, NY.

Pauly, F. 1956. Zur Biologie einige Belbiden und zur Funktion ihrer Pseudostigmatischen Organe. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 84:275–328.

Peckham, V. 1967. Studies of the mite *Alaskozetes antarcticus* (Michael). *Antarct. J. U.S.* 2:196–197.

Pianka, E. R. 1970. On *r*- and *K*-selection. *Am. Nat.* 104:592–597.

Purrini, K. 1980. On the incidence and distribution of parasites of soil fauna of mixed coniferous forests, mixed leaf forests, and pure beech forests of lower Saxony, West Germany. In: *Soil Biology as Related to Land Use Practices* (D. L. Dindal ed.). U.S. Environ. Protection Agency, Washington, DC. Pp. 561–582.

Reddy, A. S., R. Kumar and S. N. Mathur. 1978. Studies on the biology of *Galumna flabellifera* Hammer, 1958 and its role as fungal spore carrier. In: *Soil Biology and Ecology in India.* (C. A. Edwards and G. K. Vereesh eds.). *Univ. Agri. Sci., Tech. Ser. 22.* Hebbal, Bangalore. Pp. 134–143.

Riha, G. 1951. Zur Ökologie der Oribatiden in Kalksteinböden. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 80:407–450.

Ring, R. A. and D. Tesar. 1981. Adaptations to cold in Canadian arctic insects. *Cryobiology* 18:199–211.

Rockett, C. L. 1980. Nematode predation by oribatid mites (Acari: Oribatida). *Int. J. Acarol.* 6:219–224.

Rockett, C. L. and J. P. Woodring. 1966a. Biological investigations on a new *Ceratozetes* and *Pergalumna* (Acarina: Cryptostigmata). *Acarologia* 3:511–520.

Rockett, C. L. and J. P. Woodring. 1966b. Oribatid mites as predators of soil nematodes. *Ann. Entomol. Soc. Am.* 59:669–671.

Rodriguez, J. G. and Z. A. Stepien. 1973. Biology and population dynamics of *Caloglyphus berlesei* (Michael) (Acarina: Acaridae) in xenic diet. *J. Kans. Entomol. Soc.* 46:176–183.

Ryabinin, N. A. and A. N. Pan'kov. 1987. The role of parthenogenesis in the biology of armored mites. *Ekologiya* 1987:62–64. (In Russian).

Saichuae, P., U. Gerson and Y. Henis. 1972. Observations on feeding and life history of the mite *Nothrus biciliatus* (Koch). *Soil Biol. Biochem.* 4:155–164.

Scharloo, W. 1989. Developmental and physiological aspects of reaction norms. *Bioscience* 39:465–471.

Schatz, H. 1983. Über lebensrate von *Oromurcia sudetica* Willmann (Acari, Oribatei) von einer alpinen Wiese Tirols (Obergurgl, Zentralalpen). *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 110:97–109.

Schatz, H. 1985. The life cycle of an alpine oribatid mite, *Oromurcia sudetica* Willmann. *Acarologia* 26:95–100.

Schenker, R. 1984. Spatial and seasonal distribution patterns of oribatid mites (Acari: Oribatei) in a forest soil ecosystem. *Pedobiologia* 27:133–150.

Schenker, R. 1986. Population dynamics of oribatid mites (Acari: Oribatei) in a forest soil ecosystem. *Pedobiologia* 29:239–246.

Schmid, R. 1988. Morphologische Anpassungen in einem Räuber-Beute-System: Amei-

senkäfer (Scydmaenidae, Staphylinoidea) und gepanzerte Milben (Acari). *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 115:207–228.

Schulte, G. and G. Weigmann. 1977. The evolution of the family Ameronothridae (Acari: Oribatei). II. Ecological aspects. *Acarologia* 19:167–173.

Schuster, R. 1962. Nachweis eines Paarungszeremoniells bei den Hornmilben (Oribatei). *Naturwissenschaften* 49:502–503.

Sengbusch, H. G. 1954. Studies on the life history of three oribatid mites with observations on other species. *Ann. Entomol. Soc. Am.* 47:646–67.

Seniczak, S. and O. Stefaniak. 1978. The microflora of the alimentary canal of *Oppia nitens* (Acarina, Oribatei). *Pedobiologia* 18:110–119.

Shereef, G. M. 1970. Observations on the feeding, reproduction and faeces obtained from oribatids fed on different species of *Penicillium* and *Aspergillus*. *IV Colloq. Int. Zool. Sol 1970*. Dijon, France.

Shereef, G. M. 1972. Observations on oribatid mites in Laboratory cultures. *Acarologia* 14:281–291.

Sitnikova, L. G. 1960. Prelarvae of oribatid mites. *Parazitol. Sb.* 19:220–236. (In Russian).

Smrz, J. 1989. Reproductive biology of some soil oribatid and acaridid mites (Acari: Actinedida). In: *Regulation of Insect Reproduction* IV (M. Tonner, T. Soldán and B. Bennettová eds.). Academia Praha, Prague.

Solhøy, T. 1975. Dynamics of Oribatei populations on Hardangervidda. In: *Fennoscandian Tundra Ecosystems. Part 2: Animals and Systems Analysis* (F. Wielgolaski ed.). Springer-Verlag, Berlin. Pp. 111–116.

Southwood, T. R. E. 1978. *Ecological Methods*, 2nd ed. Chapman and Hall, London. Pp. 524.

Stamou, G. P. 1987. A phenological model applied to oribatid mites data. *Rev. Écol. Biol. Sol* 23:453–460.

Stamou, G. P. 1989. Studies on the effect of temperatures on the demographic parameters of *Achipteria holomonensis* (Acari, Oribatida). *Acarologia* 30:171–180.

Stamou, G., M. Kattoulas, J. P. Cancela da Fonseca and N. S. Margaris. 1981. Observations on the biology and ecology of *Achiptera holomonensis* (Acarina, Oribatida). *Pedobiologia* 23:53–58.

Stamou, G. P. and M. D. Asikidis. 1989. The effect of density on the demographic parameters of two oribatid mites. *Rev. Écol. Biol. Sol* 26:321–330.

Stamou, G. P. and S. P. Sgardelis. 1989. Seasonal distribution patterns of oribatid mites (Acari, Cryptostigmata) in a forest ecosystem. *J. Anim. Ecol.* 58:893–904.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3–47.

Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8:145–171.

Stearns, S. C. 1980. A new view of life-history evolution. *Oikos* 35:266–281.

Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* 39:436–471.

Stefaniak, O. and S. Seniczak. 1976. The microflora of the alimentary canal of *Achipteria coleoptrata* (Acarina, Oribatei). *Pedobiologia* 16:185–194.

Stefaniak, O. and S. Seniczak. 1981. The effect of fungal diet on the development of *Oppia nitens* (Acari, Oribatei) and on the microflora of its alimentary tract. *Pedobiologia* 21:202–210.

Sweeney, B. W. 1984. Factors influencing life-history patterns of aquatic insects. In: *The Ecology of Aquatic Insects* (V. H. Resjh and D. M. Rosenberg eds.). Praeger Publ. Co., NY. Pp. 56–100.

Taberly, G. 1987. Recherches sur la parthénogenèse thélytoque de deux espèces d'Acariens Oribates: *Trhypochthonius tectorum* (Berlese) et *Platynothrus peltifer* (Koch). I. *Acarologia* 28:187–198.

Taberly, G. 1989. L'influence de la température sur la dureé des différentes stases immatures des oribates. In: *L'Ontogenese et le Concept de Stase Chez les Arthropodes* (H. André and J.-C. Lions eds.). Agar Publ., Wavre, Belgium. Pp. 117–122.

Tamm, J. C., H.-W. Mittman and S. Woas. 1984. Zur Landmilbenfauna eines jahresperiodisch trockenfallenden Stauseebodens (Edertalsperre, BRD). *Pedobiologia* 27:395–404.

Tarras-Wahlberg, N. 1961. The Oribatei of a central Swedish bog and their environment. *Oikos* (*Suppl.*) 4:1–56.

Thomas, J. O. M. 1979. An energy budget for a woodland population of oribatid mites. *Pedobiologia* 19:346–378.

Travé, J. 1963. Écologie et biologie des Oribates (Acariens) saxicoles et arboricoles. *Vie Milieu* (*Suppl.*) 14:1–267.

Travé, J. 1968. Sur l'existence d'yeux latéraux depigmentés chez *Eobrachychthonius* Jacot (Oribate). *Acarologia* 10:151–158.

Travé, J. 1976. Les prélarves d'Acariens. Mise au point et données récentes. *Rev. Écol. Biol. Sol* 13:161–171.

Vera, H. and P. Berthet. 1988. Fréquence de mue et taux de survie de deux populations de *Platynothrus peltifer* (Acari: Oribatidae). *Acta Oecol./Oecol. Gener.* 9:281–291.

Walker, N. A. 1965 (1964). Euphthiracaroidea of California Sequoia litter: with a Reclassification of the Families and Genera of the World (Acarina: Orib.). *Fort Hays Studies-Science Series*, No. 3. Hays, Kansas. Pp. 154.

Wallwork, J. A. 1962. Sexual dimorphism in the genus *Epilohmannia* Berl. 1916. *Rev. Zool. Bot. Afr.* 65:90–96.

Wallwork, J. A. 1972. Distribution patterns and population dynamics of the microarthropods of a desert soil in southern California. *J. Anim. Ecol.* 41:291–310.

Wallwork, J. A. 1979. Energetics of soil mites: the experimental approach. In: *Proc. 4th Int. Congr. Acarol.* (E. Piffl ed.), Saalfelden, 1974. Akadémiai Kiadó, Budapest.

Wallwork, J. A. 1980. Desert soil microarthropods, an "*r*" selected system. In: *Soil Biology as Related to Land Use Practices* (D. L. Dindal ed.). U.S. Environ. Protection Agency, Washington, DC. Pp. 759–769.

Wallwork, J. A. 1983. Oribatids in forest ecosystems. *Annu. Rev. Entomol.* 28:109–130.

Wallwork, J. A., B. W. Kamill and W. G. Whitford. 1984. Life styles of desert litter-dwelling microarthropods, a reappraisal based on the reproductive behavior of cryptostigmatid mites. *S. Afr. J. Sci.* 80:163–169.

Wallwork, J. A., M. MacQuitty, S. Silva and W. G. Whitford. 1986. Seasonality of some Chihuahuan Desert soil oribatid mites (Acari: Cryptostigmata). *J. Zool.* (Lond.) 208:403–416.

Walter, D. E. and E. K. Ikonen. 1989. Species, guilds, and functional groups: taxonomy and behavior in nematophagous arthropods. *J. Nematol.* 21:315–327.

Walter, D. E., J. C. Moore and S. J. Loring. 1989. *Symphylella* sp. (Symphyla: Scolopendrellidae) predators of arthropods and nematodes in grassland soils. *Pedobiologia* 33:113–116.

Wanntorp, H-E., D. R. Brooks, T. Nilsson, S. Nylin, F. Ronquist, S. C. Stearns and N. Wedell. 1990. Phylogenetic approaches in ecology. *Oikos* 57:119–132.

Webb, N. R. 1989. Observations on the life cycle of *Steganacarus magnus* (Acari: Cryptostigmata). *Pedobiologia* 33:293–299.

Weigmann, G. 1975. Labor-und Freilanduntersuchungen zur Generationsdauer von Oribatiden (Acari:Oribatei). *Pedobiologia* 15:133–148.

West, C. 1982. Life histories of three species of sub-antarctic oribatid mites. *Pedobiologia* 23:59–67.

White, M. J. D. 1978. *Modes of Speciation*. Freeman, San Francisco.

Willmann, C. 1933. Oribatei (Acari) gesammelt von des Deutschen Limnologischen Sunda-Expedition 2. Nachtrag. *Arch. Hydrobiol. Suppl. II, Trop. Binnengewässer* 3:597–603.

Wolf, M. M. and C. L. Rockett. 1984. Habitat changes affecting bacterial composition in the alimentary canal of oribatid mites (Acari: Oribatida). *Int. J. Acarol.* 10:209–215.

Woodring, J. P. 1965. The biology of five new species of oribatids from Louisiana. *Acarologia* 7:564–576.

Woodring, J. P. and E. F. Cook. 1962a. The internal anatomy, reproductive physiology and molting process of *Ceratozetes cisalpinus*. *Ann. Entomol. Soc. Am.* 55:164–181.

Woodring, J. P. and E. F. Cook. 1962b. The biology of *Ceratozetes cisalpinus* Berl., *Scheloribates laevigatus* Koch, and *Oppia neerlandica* Oudemans with a description of all stages. *Acarologia* 4:101–137.

Young, S. R. 1979. Effect of temperature change on the metabolic rate of an Antarctic mite. *J. Comp. Physiol.* 131:341–346.

Young, S. R. and W. Block. 1980. Some factors affecting metabolic rate in an Antarctic mite. *Oikos* 34:178–185.

6

Life-History Modifications in Astigmatid Mites

Barry M. OConnor

CONTENTS

1. Introduction

The Astigmata is a diverse group of acariform mites specialized for exploiting spatially or temporally restricted habitats. This natural lineage is hypothesized to have arisen from within the "glandulate" oribatid mites (OConnor 1984a; Norton, this volume) through paedomorphic modifications of the adult morphology and through extreme morphological and behavioral modification of the deutonymphal instar. This modified deutonymph, termed "hypopus" in older literature, is spe-

cialized for dispersal and resisting adverse environmental conditions (OConnor 1982a). Dispersal is typically accomplished by phoretic association with an insect or other arthropod or with a vertebrate, which carries the deutonymph to another suitable habitat patch. Phoresy in the Astigmata has recently been reviewed by Houck and OConnor (1991).

Along with these morphological and behavioral modifications, the lineage of astigmatid mites has diverged strongly from its closest "oribatid" relatives in a number of life-history parameters. Related groups of "oribatid" mites typically inhabit stable environments, have long generation times and adult life spans, disperse over relatively short distances as adults and accomplish sperm transfer via spermatophores deposited on the substrate (see Norton, this volume). In contrast to these typically "*K*-selected" traits, most astigmatid mites live in ephemeral habitats, have short generation times and adult life spans, disperse over relatively long distances as deutonymphs, and achieve sperm transfer by direct copulation.

Brooks (1985) pioneered a method for analyzing the evolution of ecological associations such as commensalism and parasitism which are exhibited by most species of astigmatid mites. This method entails a phylogenetic analysis of the organisms under study and a subsequent superposition of ecological associations on the resulting phylogenetic tree. Evolutionary shifts in ecology, behavior and life history can be tracked using this method. The discussions presented here are based on phylogenetic analyses of family and subfamily relationships among the non-psoroptidid Astigmata presented in OConnor (1981). The family-level cladograms were transformed into a phyletically sequenced Linnaean classification which was presented in OConnor (1982b) and is followed here.

In this paper I will review the habitat types colonized and exploited by astigmatid mites, discuss some of the life-history parameters exhibited by representative species, and discuss the evolution of these traits and the shift from commensalistic to parasitic associations in the group.

2. Habitat and Host Associations

Astigmatid mites have successfully colonized and specialized on an incredible variety of microhabitat types, most of which are spatially restricted (patchy) and/or temporally restricted (ephemeral). Although I will not attempt to enumerate all habitat types exploited by astigmatid mites, I will provide some overview of the types of habitats used, the diversity and origin of the mites found therein, and the resources used by the mites. Patchy or ephemeral habitats exploited by astigmatid mites typically arise through biotic processes, or through interaction of both physical and biotic processes. Patchy habitats created by purely physical processes such as sand dunes, rock clefts, ponds, lakes and springs rarely harbor astigmatid mites. Suitable habitats are formed when concentrations of organic

materials which can serve either directly as food or substrate for microbial or fungal growth accumulate. Because the ability to disperse directly is limited in mites, most suitable habitats for astigmatid mites must also be attractive to other organisms which serve as hosts to phoretic deutonymphs.

2.1 Habitat Types

It is also useful to distinguish between habitat types that are the result of biotic processes which do not involve modification of the environment by a host (e.g. growth, death, decay) and those resulting from ongoing interaction between the host and the environment (e.g. food provisioning, nest building, etc.). Examples of the first include nonmobile habitats such as flowers, roots, tubers, fungal fruiting bodies, subcortical spaces, treeholes and other plant cavities, sap flows, algal mats, dung and carrion. This category also includes mobile habitats, i.e. the bodies of living animals. The second category includes the nests, burrows, galleries, refuse piles and food stores of solitary, communal and social insects as well as birds and mammals, including humans. Life-history patterns of astigmatid mites which live in these different habitat classes typically differ in the nature, quality, and degree of specificity of the association with the insect or vertebrate on which the mite depends for dispersal and/or permanent habitat.

2.2 Habitats Created by Plants and Fungi

Many astigmatid mites inhabit substrates associated with plants or fungi, however, few occur on such relatively nonpatchy substrates as bark or leaves of living plants. Some astigmatid mites exploit living plant tissue. For example, species of *Rhizoglyphus* (Acaridae) are well known to burrow in and feed on living tissues of bulbs and tubers. A few taxa include species which can feed on living leaf tissue although most species living on leaf surfaces are primarily grazers on fungi growing on the leaves. These taxa include species of *Czenspinskia* and *Oulenzia* (Winterschmidtiidae) and *Neotropacarus* and some *Tyrophagus* (Acaridae). Inflorescences serve as habitat for some *Carpoglyphus* (Carpoglyphidae) and several undescribed genera of Histiostomatidae. Specialized plant parts which hold water (phytotelmata) harbor a diversity of taxa of Histiostomatidae, Algophagidae and Acaridae. Water-filled leaves of two families of pitcher plants are known to harbor specific genera of Histiostomatidae: *Creutzeria*, *Zwickia* and several unnamed genera inhabit the Old World Nepenthaceae, while *Sarraceniopus* inhabits the New World Sarraceniaceae. Leaf axils of the Bromeliaceae are habitat for *Bromeliaglyphus*, *Naiacus* and some species of *Rhizoglyphus* and *Schwiebea* (Acaridae) as well as undescribed species of *Hormosianoetus* (Histiostomatidae). The histiostomatid mites are presumed to be microbial feeders while the feeding habits of the Acaridae in these habitats remain unstudied.

Fruiting bodies of fleshy fungi are exploited by some species of *Histiostoma*

(Histiostomatidae), *Congovidia* (Hemisarcoptidae), *Rhizoglyphus*, *Sancassania* and several other undescribed genera of rhizoglyphine Acaridae. Tougher fruiting bodies of polypore and xylariaceous fungi are inhabited by *Rhizoglyphus* and *Boletacarus* species (Acaridae) and *Nanacaroides* and some species of *Nanacarus* (Hemisarcoptidae). These species tend to specialize either on mycelial tissue or on spores (OConnor 1984b).

Other vegetative substrates occupied by astigmatid mites include holdfasts of marine algae which serve as habitat for species of Hyadesiidae and marine algal mats and halophytic plants or freshwater mosses which harbor species of Algophagidae (*Algophagopsis*, *Algophagus* and *Neohyadesia*). Based upon examination of gut contents, these species appear to be primarily algal feeders.

A much greater diversity of taxa is associated with dead and decaying plants and fungi. Subcortical spaces in decaying tree trunks and logs are inhabited by several genera of rhizoglyphine Acaridae including *Calvoliella*, *Histiogaster*, *Schwiebea* and *Thyreophagus*. Some Histiostomatidae such as *Bonomoia* and many *Histiostoma* species may also be found in decaying wood. Species in these genera typically live in the rotting wood itself and are not restricted to insect galleries as are some other taxa. The Acaridae in these habitats are primarily fungal grazers, while the Histiostomatidae filter microorganisms from wet substrates. Treeholes also provide habitats for a diversity of astigmatid mites. Water filled treeholes contain species of *Naiadacarus* (Acaridae), *Hormosianoetus* (Histiostomatidae) and *Algophagus* and another, undescribed genus of Algophagidae. These taxa have been the subject of exhaustive studies by Fashing (see Fashing, this volume) and will not be discussed further here. Treeholes which are not permanently wet are commonly inhabited by species of *Acotyledon*, *Fagacarus*, *Rhizoglyphus*, *Sancassania*, and *Schwiebea* (Acaridae) and *Histiostoma* (Histiostomatidae). Tree wounds which exude fermenting sap serve as substrates for *Fusohericia* and *Hericia* (Algophagidae) as well as species of *Histiostoma* and *Sellea* (Histiostomatidae). Decaying fungal fruiting bodies are the preferred habitat for *Boletoglyphus* (Acaridae) and *Allocalvolia* and *Saproglyphus* (Winterschmidtiidae). The primary diets of all of these species appear to be fungi, including yeasts.

2.3 Habitats Created by Animals Through Noninteractive Processes

Habitats created by animals through noninteractive processes also harbor a diversity of astigmatid mites. Dung produced by individual vertebrates can contain an extensive community of astigmatid mites including representatives of the families Acaridae (*Sancassania*), Histiostomatidae (*Ameranoetus*, *Aphodanoetus*, *Copronomoia*, *Fibulanoetus*, *Glyphanoetus*, *Histiostoma*, *Myianoetus*, *Rhopalanoetus*, *Syringanoetus*, and probably others), and Winterschmidtiidae (unnamed genus). Guano accumulations produced by colonies of bats or birds contain unique communities composed of species of Rosensteiniidae (many genera), Aeroglyphi-

dae (*Aeroglyphus* and *Glycycometus*), Histiostomatidae (*Glyphanoetus* and *Histiostoma*), Guanolichidae (*Guanolichus* and *Neoguanolichus*), Acaridae (*Acarus* and *Troglocoptes*), and Glycyphagidae (*Glycyphagus*). Frass generated by the activities of wood-inhabiting scarabaeid beetles also serves as habitat for *Acotyledon* and *Sancassania* species (Acaridae). Vertebrate carrion serves as substrate for species of *Acarus* (Acaridae), *Pelzneria* and *Spinanoetus* (Histiostomatidae) in early decay stages, while *Lardoglyphus* (Lardoglyphidae) species inhabit older carcasses. These species are primarily fungivores or microorganismal feeders, but the acarid and lardoglyphid mites may also feed directly on the substrate material.

The bodies of living animals are permanent habitats for a great diversity of astigmatid mites. Over half of all nominal genera of Astigmata comprise the monophyletic group Psoroptidia, most species of which live permanently on or in the bodies of birds or mammals. Psoroptidid mites are microhabitat specialists, with many species often coexisting on a single host. Birds provide an exceptional diversity of microhabitats. The greatest diversity of mite taxa occur on the flight and tail feathers, living along the rachis, between the barbs or in the spaces at the bases of the barbs (families Alloptidae, Avenzoariidae, Caudiferidae, Cheylabididae, Crypturoptidae, Eustathiidae, Falculiferidae, Freyanidae, Gabuciniidae, Kramerellidae, Ochrolichidae, Proctophyllodidae, Pterolichidae, Ptiloxenidae, Rectijanuidae, Thoracosathidae, Vexillariidae, and some Analgidae). Species of the families Analgidae, Psoroptoididae and Xolalgidae typically live on plumaceous barbs of contour feathers or at the bases of flight feathers. The spaces between coverts and flight feathers are the typical habitat for species of Trouessartiidae. The space within the feather quills serves as habitat to species of Dermoglyphidae, Gaudoglyphidae, Oconnoriidae, Ptyssalgidae, Syringobiidae, some Proctophyllodidae and some Pyroglyphidae. Species of Epidermoptidae live in the superficial layers of the skin and in feather follicles, while species of Laminosioptidae inhabit deeper, subcutaneous tissues and the follicles of developing feathers. The respiratory tract of birds is inhabited by species of Turbinoptidae in the nostrils and Cytoditidae deeper in the trachea, lungs and air sacs. These species may feed as actual parasites on host skin, pygidial gland secretions, skin exudates, keratin rich materials from the quills and feather barbs, or rarely, on blood. Mites living on feather surfaces also commonly ingest detritus such as fungal spores and algal cells (Dubinin 1951).

The bodies of mammals provide an equally rich source of exploitable microhabitats. Species of Atopomelidae, Chirodiscidae and Listrophoridae live on the hair shafts of small and medium sized mammals. The Lobalgidae consists of species specialized for the flattened, grooved hairs of Neotropical sloths and spiny rats. The skin surface of many groups of terrestrial mammals is substrate for species of Psoroptidae, some of which also enter the ear openings and inhabit the ear canals. The uniquely modified species of the family Chirorhynchobiidae attach to the wing membrane edges of Neotropical bats, while species of Myocoptidae

anchor themselves to body hairs while feeding from the skin. Species of the Rhyncoptidae (including Audycoptidae) live in hair follicles of primates, carnivores and rodents, while species of Sarcoptidae actually enter the skin and live in the epidermal layers of many mammal groups, most notably bats. As in birds, the respiratory tract is also exploited. Species of Gastronyssidae inhabit the nasal passages of rodents and bats, while Lemurnyssidae occupy similar habitats in primates. The Pneumocoptidae consists of a few species which live in the lungs of rodents. The Gastronyssidae also includes species specialized for living in the orbits of the eyes and in the stomach of their chiropteran hosts. These mites exploit similar resources as do the bird associates although none is known to feed directly on hair proteins. Again, feeding on host blood is rare.

The bodies of birds and mammals are also exploited by other groups of astigmatid mites not belonging to the Psoroptidia. The ears of large mammals harbor populations of the genera *Auricanoetus*, *Loxanoetus*, *Otanoetus* and an undescribed genus (family Histiostomatidae). Some taxa of Rosensteiniidae (*Cheiromelichus*, *Chiroptoglyphus* and some *Nycteriglyphus*) live permanently on the skin of their bat hosts. Feeding habits of these species are unstudied, but the histiostomatids are presumed to be filtering materials from the ear secretions.

Many arthropods are also permanent hosts to astigmatid mites. All species in the families Canestriniidae and Heterocoptidae and the genus *Linobia* (Hemisarcoptidae) live their entire lives on the bodies of many groups of Coleoptera. All species in these taxa parasitize only adult hosts and tend to be specialized for life either on the ventral body surface or in the subelytral space. Most of these mites are presumed to be exudate feeders, but *Linobia coccinellae* pierces the cuticle to feed on host hemolymph. Species in several lineages of Rosensteiniidae have evolved permanent associations with noncoleopterous insects. Species of *Rosensteinia* and one undescribed genus inhabit the bodies of cockroaches (Blattaria) and are superficially similar to the above mentioned Canestriniidae in morphology and presumably feeding habits. Species of *Micronychites* and *Micronychitoides* have been collected from earwigs of the genera *Arexenia* and *Xenaria* (Dermaptera: Arexeniina). Their feeding ecology is unknown. Decapod crustaceans are host to an unusual group of genera in the family Acaridae. Their distinctive morphology has led previous workers to recognize this group as a separate family, Ewingiidae. Species of *Ewingia*, *Hoogstraalacarus* and *Kanakobia* live in the gill chambers of hermit crabs (Coenobitidae) and fresh-water crabs (Potamonidae). Species of *Askinasia* and one undescribed genus live attached to leg or abdominal setae of hermit crabs. The feeding ecology of these mites is unknown.

2.4 Habitats Created by Interaction of Hosts with the Environment

In contrast to the great diversity of habitat types indicated above as harboring astigmatid mites, habitats which are created by the activities of other animals often contain an even greater diversity of these mites.

2.4.1 Habitats Created by Insects

Insects which create habitats exploitable by astigmatid mites include many Coleoptera and Hymenoptera and the Diaspididae (Homoptera). The tunnels of wood-boring beetles of the family Passalidae are home to specialized astigmatid mites such as *Kanoetus* and *Scolianoetus* (Histiostomatidae) and *Passaloglyphus* and some *Schwiebea* species (Acaridae). Galleries constructed by Scolytidae or Bostrichidae harbor species of *Afrocalvolia*, *Winterschmidtia* and related undescribed genera (Winterschmidtiidae), some *Histiogaster* and *Thyreophagus* species (Acaridae), and some *Histiostoma* (Histiostomatidae). Several other genera of Histiostomatidae have been described only as deutonymphs collected from various other groups of beetles which excavate cavities in wood. Associated with Tenebrionidae are *Kaszabanoetus* from *Uloma* species and *Chiloanoetus* from various genera of Pycnocerini. Species of *Curculanoetus* are associated with palm weevils of the genus *Rhynchophorus*. Beetles of the family Scarabaeidae which make excavations in wood (Dynastinae, Rutelinae) or brood cells in soil provisioned with dung or other materials create habitats for species of *Sancassania* (Acaridae). Most of these species are known or presumed to be fungivores (Acaridae) or microorganismal feeders (Histiostomatidae), however *Afrocalvolia nataliae* (= *Calvolia fraxini*) is a predator on eggs and young larvae of its scolytid host (Kielczewski and Seniczak 1972). The other genera of Winterschmidtiinae also share this habitat type and may also be predaceous.

Colonies formed by scale insects of the family Diaspididae are exploited by specialized mites of the genera *Hemisarcoptes* (Hemisarcoptidae) and *Thyreophagus* (Acaridae). Species of *Hemisarcoptes* are predaceous on the scale insects and their eggs, while *Thyreophagus* species are fungivores (Houck and OConnor 1991; Houck, Chapter 10, this volume).

The greatest diversity of astigmatid mites living in habitats created by other arthropods is associated with the nests of solitary and social Hymenoptera. The nests of solitary wasps harbor most species of the subfamily Ensliniellinae (Winterschmidtiidae). Hosts include crabronine Sphecidae (of the mite *Crabrovidia*) and eumenine Vespidae (of the mites *Ensliniella*, *Kennethiella*, *Macroharpa*, *Monobiacarus*, *Vespacarus*, *Zethacarus*, *Zethovidia* and numerous undescribed genera). Species of *Ensliniella*, *Kennethiella* and *Vespacarus* feed on hemolymph of the host larva or on provisioned prey, while *Monobiacarus* feeds only on provisions (Krombein 1967, Klompen et al. 1987). Some Hemisarcoptidae (*Congovidia*) and Acaridae (*Lackerbaueria*) have also been collected from solitary sphecid nests. The latter is apparently a cleptoparasite (Krombein 1967), while the former is likely a fungivore. Solitary bees of the family Megachilidae also harbor enslinielline mites of the genus *Vidia*, species of which feed on fungi in the nest lining (OConnor and Eickwort 1988).

A much greater diversity of solitary bee associates is found in other families of Astigmata. As these associations have been the subject of recent reviews by

Eickwort (1979, Chapter 9, this volume) and OConnor (1988), I will only summarize the associations. All species in the family Chaetodactylidae inhabit the nests of bees: *Chaetodactylus* primarily associated with Megachilidae and Xylocopinae, and *Sennertia* with Xylocopinae. In the family Acaridae, all genera in the subfamily Horstiinae have obligatory associations with bees, the majority of which are solitary. These genera include: *Halictacarus* and *Schulzea* from the Halictidae; *Megachilopus*, *Neohorstia* and *Sennertionyx* from the Megachilidae; *Horstia* from Xylocopinae; *Horstiella* from euglossine Apidae; and an undescribed genus from Anthophorinae. Although not belonging to the Horstiinae, another acarid genus, *Ctenocolletacarus*, is found in the nests of stenotritid bees in Australia. Solitary bee nests may also harbor species of Histiostomatidae (*Anoetus* and some *Histiostoma* from Halictidae; some *Glyphanoetus* from Colletidae and Xylocopinae). Finally, species of *Tortonia* (Suidasiidae) inhabit the nests of both solitary wasps and bees. Feeding ecologies of these taxa range from microorganismal filtration (Histiostomatidae) to provision thieves (*Sennertia*) to true cleptoparasites (*Chaetodactylus*, *Horstia*, some *Tortonia*).

The nests of social Hymenoptera and Isoptera also harbor an extensive fauna of astigmatid mites which has been reviewed by Eickwort (1990). Among the social Vespidae, *Polistes* species harbor species of *Sphexicozela* (Winterschmidtiidae), while the genera *Medeus* (Acaridae) and *Tortonia* (Suidasiidae) occur in *Vespula* nests. Social halictid bee nests are habitat for some species of *Anoetus* (Histiostomatidae), while a diversity of taxa in several families are associated with social Apidae. These include: *Kuzinia* (Acaridae) and *Cerophagus* (Gaudiellidae) associated with *Bombus*, some species of *Carpoglyphus* (Carpoglyphidae) and *Forcellinia* (Acaridae) with *Apis*, and all species of Meliponocoptidae (*Meliponocoptes*, *Meliponoecius* and one undescribed genus) and most Gaudiellidae (*Gaudiella*, *Partamonacoptes*, *Platyglyphus* and unnamed genera) with meliponine stingless bees. Finally, the nests of ants (Formicidae) harbor many genera of mites, primarily from the family Acaridae. A number of these taxa are also shared with the nests of termites (Isoptera). These genera include: *Cosmoglyphus*, *Forcellinia*, *Froriepia*, *Lasioacarus*, *Ocellacarus*, *Rettacarus*, *Sancassania*, *Tyrophagus* and others. Other families represented in the faunas of ant and termite nests include the Suidasiidae (*Lemaniella*) and Histiostomatidae (*Histiostoma*).

2.4.2 Mammal Hosts

The nests of mammals harbor an even greater diversity of astigmatid mites than do the nests of social insects. Some taxa in all major clades are found in these associations although few species have been studied with respect to their ecology and life history. Among the Histiostomatidae, some species of *Myianoetus* and *Psyllanoetus* are associated with mammal nests or nest-inhabiting insects. Species of *Psylloglyphus* (Winterschmidtiidae) have also been described from

phoretic associations with nest-inhabiting insects. Most taxa in the superfamily Glycyphagoidea are known or presumed mammal nest associates. These include the families Chortoglyphidae (*Alabidopus*, *Aplodontopus*, *Chortoglyphus* and two undescribed genera) associated with rodents, insectivores and primates; Echimyopodidae (*Echimyopus*, *Marmosopus*, *Marsupiopus* and *Oryzomyopus*) associated with marsupials and rodents; and Glycyphagidae (many genera) associated with marsupials, edentates, rodents, carnivores and insectivores. Some members of the family Acaridae have been described from mammal nests or nest-inhabiting arthropods. Genera include *Acarus*, *Acotyledon*, *Paraceroglyphus*, *Trichopsyllopus*, and *Viedebanttia*. Finally, some species of Pyroglyphidae (*Pyroglyphus* and occasionally other genera) have been collected from mammal nests.

2.4.3 Bird Hosts

The nests of birds also serve as habitat for specialized taxa of astigmatid mites. *Comyianoetus*, *Hexanoetus* and some *Histiostoma* species (Histiostomatidae) have been collected from the nests of raptors. The monobasic families Euglycyphagidae and Glycacaridae have been collected in nests of raptors and a petrel respectively. Some Glycyphagidae (*Glycyphagus* and *Lophuromyopus*), Aeroglyphidae (*Aeroglyphus* and *Glycycometus*), Acaridae (*Acotyledon* and *Notiopsyllopus*), Lardoglyphidae (*Lardoglyphus*) and Suidasiidae (*Sapracarus*) are also encountered in bird nests. Finally, almost all species of Hypoderatidae and most nonparasitic species of the family Pyroglyphidae (many genera) inhabit bird nests.

The feeding ecologies of vertebrate nidicoles are probably varied, including filter feeding on microorganisms (Histiostomatidae), fungivory (many glycyphagoids), consumption of actual nest materials as well as fungi (Acaridae) and ingestion of prey remains (Lardoglyphidae). Many Glycyphagidae exhibit strong preferences for a restricted number of fungal species as food resources (Sinha 1966), and nidicolous species are notoriously difficult to culture away from natural substrates (Lukoschus et al. 1971, Fain et al. 1972, Lukoschus et al. 1972, Lukoschus et al. 1979).

2.4.4 Habitat Shifts in Nest-inhabiting Astigmatid Mites

An interesting habitat shift has occurred among species representing many genera of vertebrate nest-inhabiting Astigmata and a relatively few taxa from other ecological types. A large number of species has adapted to living in and around human habitations. This diversity of "stored product" and "house dust" mites contains the majority of well-studied species of Astigmata (Hughes 1976). The majority of these taxa belong to the families Acaridae (*Acarus*, *Aleuroglyphus*, *Cosmoglyphus*, *Histiogaster*, *Madaglyphus*, *Rhizoglyphus*, *Sancassania*, *Thyreophagus*, *Tyrolichus* and *Tyrophagus*), and Glycyphagidae (*Ctenoglyphus*, *Diamesoglyphus*, *Glycyphagus*, *Gohieria*, *Lophuromyopus* and *Tropilichus*).

Other families are represented by fewer taxa: Histiostomatidae (*Histiostoma*), Winterschmidtiidae (*Acalvolia* and *Procalvolia*), Hemisarcoptidae (*Nanacarus*), Carpoglyphidae (*Carpoglyphus*), Chortoglyphidae (*Chortoglyphus*), Echimyopodidae (*Blomia*), Aeroglyphidae (*Aeroglyphus* and *Glycycometus*), Suidasiidae (*Suidasia*), Lardoglyphidae (*Lardoglyphus*), and Pyroglyphidae (*Euroglyphus*, *Dermatophagoides*, *Malayoglyphus* and *Pyroglyphus*).

3. Demographics

In contrast to other lineages within the suborder Sarcoptiformes, the Astigmata may be characterized by a series of life-history modifications related to their exploitation of temporary habitats. These so-called "*r*-selected" characteristics include a relatively short generation time, high fecundity, relatively short adult life span, internal fertilization, and dispersal ancestrally as deutonymphs. Although demographic information is available for a number of taxa of astigmatid mites, a word of caution is in order. Studies on these mites have concentrated on species associated with human habitations and food stores or parasites of domestic animals, and the majority of published life-history data deals with these species. Fortunately, there is a diversity of evolutionary lineages represented among these studies, so generalizations may have some validity. On the other hand, many of the ecological categories discussed earlier are completely unrepresented or have few species which have been studied. For example, due to the difficulties of maintaining parasitic astigmatid mites away from their hosts, almost no demographic information is available for this great diversity of taxa.

In examining the available demographic data for astigmatid mites, several general patterns can be observed. The first and most common pattern includes taxa with a generation time in the range of 10–15 days (egg to egg, or deutonymph to deutonymph, in a temperature regime of 22°–27°C), and an average female reproductive period in the range of 15–40 days. Three subgroups may be recognized within this category with respect to the total egg production per female. Some taxa in this group exhibit a moderate fecundity in the range of 100–300 eggs per female. These include soil and litter inhabiting species in the family Acaridae such as *Tyrophagus putrescentiae* (Rivard 1959, 1961; Barker 1967a), *Schwiebea falticis* and *S. rocketti* (Woodring 1969); insect nidicoles such as *Carpoglyphus lactis* (Carpoglyphidae) (Chmielewski 1971) and *Acotyledon formosani* (Acaridae) (Phillipsen and Coppel 1977a); and *Glycyphagus domesticus* (Glycyphagidae) (Barker 1968), a species derived from a vertebrate nidicolous ancestry, but which exhibits a very wide habitat range. A similar length of life cycle and female reproductive period but a lower total fecundity (10–100 eggs/female) is common among vertebrate nidicoles and other stored product mites derived from nidicolous ancestry: *Aleuroglyphus ovatus* (Acaridae) (Hsin and Chen 1964), *Gohieria fusca* (Glycyphagidae) (Boulanova 1937), *Aeroglyphus*

robustus (Aeroglyphidae) (Barker 1967b), and *Dermatophagoides pteronyssinus*, (Pyroglyphidae) (Hart and Fain 1988). Finally, some Acaridae which inhabit concentrated sources of organic matter such as dung, compost, treeholes, bulbs, tubers, fungal fruiting bodies and subcortical spaces exhibit a much higher fecundity (300–1400 eggs/female) within the same temporal parameters. These include *Sancassania berlesei* (Hughes 1976, Timms et al. 1981), *S. anomalus* (Woodring 1969, Pillai and Winston 1969, Barker 1974), *S. rodriguezi* (Rodriguez and Stepien 1973), *Rhizoglyphus robini* (Gerson et al. 1983), *R. echinopus* (Woodring 1969), *Histiogaster arborsignis* and *H. rotundus* (Woodring 1969). High fecundity is also exhibited by *Kuzinia laevis* (Acaridae), an inhabitant of bumblebee nests (Chmielewski 1969).

A second demographic category is exemplified by most species in the family Histiostomatidae for which life-history information is available. These species typically inhabit very ephemeral resources and have shorter generation times, typically in the range of 4–8 days. Female oviposition period and life span are also shorter (5–15 days), with a total egg production between 20–120 eggs/female. Species for which information is available include *Histiostoma heinemanni* (Hill and Deahl 1978), *H. julorum* (Hughes and Jackson 1958) and *H. polypori* (Behura 1957), which typically inhabit decaying vegetation or fungal fruiting bodies; *H. cataglyphi* (Yousef et al. 1979), and *H. formosani* (Phillipsen and Coppel 1977b), from the nests of an ant and a termite respectively; *H. laboratorium* (Perron 1954) from *Drosophila* cultures, and *H. murchei* (Oliver 1962), a predator in annelid egg cocoons. The last mentioned species differs from the others in having a much higher fecundity (up to 500 eggs/female). I have observed undescribed North American species of the carrion inhabiting genera *Spinanoetus* and *Pelzneria* which exhibit the same pattern of very short generation time and female life span, and moderate egg production. In contrast, preliminary observations on undescribed species in the genera *Kanoetus* and *Scolianoetus*, which are associated with the galleries of wood-boring insects, indicate a much longer generation time and adult life span for these taxa.

A third pattern is observed among species which inhabit certain types of insect nests and galleries. Some data is available for the winterschmidtiid genera *Afrocalvolia*, associated with bark beetle galleries, and *Ensliniella*, *Kennethiella* and *Vespacarus*, which inhabit the nests of solitary vespid wasps. In these taxa, the period between original infestation by deutonymphs and the production of the next generation of deutonymphs or tritonymphs is in the range of 20–30 days. In the enslinielline genera mentioned, female oviposition period is short (4–7 days) and egg production is in the range of 25–125 eggs/female, depending on the number of foundresses per cell (Krombein 1967, Cowan 1984, Klompen et al. 1987).

The final category includes species which have more prolonged generation times (30–45 days), longer female reproductive period (40–80 days) and generally low to moderate fecundity. The best studied species, *Naiadacarus arboricola*

(Acaridae), inhabits water-filled treeholes which may persist for yars. The life history of this species has been discussed in detail by Fashing (1975, 1979; this volume) and will not be repeated here. Other examples of this pattern include some species of Pyroglyphidae which inhabit stored products and house dust: *Dermatophagoides farinae*, *Euroglyphus longior* and *E. maynei* (Hart and Fain 1988). The natural habitats of most *Dermatophagoides* species are birds' nests. *Euroglyphus* species have not been collected regularly from natural habitats, but a related species, *Pyroglyphus morlani*, lives in the nests of wood rats (*Neotoma* spp.), many of which are perennial and may be inhabited by a series of hosts for centuries. As pointed out by Fashing (1979) with reference to *Naiadacarus arboricola*, mites exhibiting this type of life-history pattern may be better described as "*K*-selected" although this is only in comparison with other astigmatid mites. When compared with the ancestral and more common life-history pattern in the Sarcoptiformes (i.e. generation times of 1–3 years, female reproductive periods measured in years; see Norton, this volume), these species still show much shorter generation times and life spans.

The few species of astigmatid mites parasitic on vertebrates which have been studied in detail exhibit different demographic parameters. Both *Sarcoptes scabiei* (Sarcoptidae), which lives in the upper epidermal layers of mammalian skin, and species of *Psoroptes* (Psoroptidae), which live on the skin surface, have a generation time similar to the common pattern among free-living Astigmata, i.e. 10–12 days (Mellanby 1972, Meleney 1985, Arlian and Vyszenski-Moher 1988). However, it should be noted that the normal temperature under which these mites develop (i.e. host body temperature) is much higher than that used in laboratory studies of free-living mites. A major difference between these species is evident in the female oviposition period which may extend for 60 days in *Sarcoptes* while only lasting 21 days in *Psoroptes*. Correlated with the female life span, the total fecundity of *Sarcoptes* is reported as 120–180 eggs/female, while in *Psoroptes*, it is only 35–40. A third species, *Chorioptes bovis* (Psoroptidae), which like *Psoroptes* inhabits the skin surface, is quite distinct in having a much longer generation time (21–28 days), shorter female oviposition period (16 days) and much lower fecundity (16 eggs/female) (reviewed in Meleney 1985). Unpublished observations on other sarcoptid taxa suggest other patterns. For example, species of *Nycteridocoptes* which parasitize Megachiroptera probably have a generation time of one year, based upon the observation that adult females are present only during the breeding season of the hosts (J. S. H. Klompen, pers. comm.).

Two serious caveats must be expressed with regard to interpreting the above studies on astigmatid mite demographics. First, with few exceptions, these studies were carried out in laboratory cultures under constant environmental conditions. Many of the studies noted above report variation in life-history parameters under different temperature and humidity regimes, however, most such studies do not duplicate the natural conditions in which the mites actually live. Studies on several species of Acaridae by Boczek and his co-workers indicate that the life

spans of these species may be considerably extended when they are cultured under suboptimal conditions (Boczek 1973, Boczek and Czajkowska 1973, Boczek and Sosnowska 1975). In laboratory culture most taxa exhibit the expected reaction of poikilothermic animals in that developmental time decreases as temperatures increase to the thermal death point. Response to humidity is also predictable in that species whose normal habitat is relatively dry (e.g. *Aeroglyphus robustus* and *Glycyphagus domesticus*) do better under drier conditions than nearer saturation. The reverse is true for Histiostomatidae and other taxa which normally inhabit saturated environments. An appropriate food source is also important in this type of study. More success has been achieved with relative generalists such as the Acaridae and Histiostomatidae than with specialists, a category which apparently includes most Glycyphagoidea and Hemisarcoptoidea. Sinha (1966) has demonstrated that species of Glycyphagidae inhabiting stored food are much more particular about the fungal species upon which they will feed than are species of Acaridae in the same habitats. The difficulties in culturing nidicolous Glycyphagidae (*Baloghella melis* [= *Melesodectes auricularis*], *Lophioglyphus liciosus* [= *Apodemopus apodemi*] and *Marsupialichus marsupialis*) and Echimyopodidae (*Marsupiopus zyzomys*) have been documented by Lukoschus and his co-workers (Lukoschus et al. 1971, Fain et al. 1972, Lukoschus et al. 1972, Lukoschus et al. 1979). Similarly, despite the high level of taxonomic diversity in the family, there are few reports of species of Winterschmidtiidae (= Saproglyphidae) being successfully cultured away from their natural substrates.

A second caveat regards the interpretation of generation time. The life cycle of most astigmatid mites is similar to the ancestral pattern observed in acariform mites (i.e. egg, prelarva, larva, protonymph, deutonymph, tritonymph, adult; see Fashing, Fig. 7.4, this volume) except that in most species, formation of the deutonymphal instar is facultative, or it is not formed at all. In the laboratory cultures which formed the basis for the demographic information reported above, generation time was typically determined for individuals which bypassed the deutonymphal instar. This shortening of the life cycle by the facultative or permanent elimination of an ontogenetic stage has been suggested as a characteristic of "*r*-selected" taxa. On the other hand, it seems reasonable to view as a general pattern the observations that certain astigmatid mites overwinter as deutonymphs. For example, the winterschmidtiid species *Afrocalvolia nataliae* (= *Calvolia fraxini*) undergoes two generations per year in the galleries of its scolytid host, *Leperisinus fraxini*, in Poland (Kielczewski and Seniczak 1972). The summer generation is passed during the month of July and individuals bypass the deutonymphal stage. Offspring of the summer generation, however, all enter the deutonymphal stage in August and overwinter on the adult bark beetle host until the following May, at which time they enter the feeding and reproductive phase of the life cycle. This overwintering generation actually has a generation time of 11 months, while the summer generation time is one month.

A similar situation has been observed among species of the winterschmidtiid

subfamily Ensliniellinae associated with the nests of solitary vespid wasps. Species in three genera have been studied in some detail: *Kennethiella trisetosa* associated with *Ancistrocerus antilope* (Krombein 1967, Cowan 1984), *Vespacarus fulvipes* with *Parancistrocerus fulvipes* (Krombein 1967), and *Ensliniella kostylevi* with *Allodynerus rossi* (Klompen et al. 1987) and *E. parasitica* with *A. delphinalis* (Cooreman 1942). Each of these hosts is bivoltine, with the mite development closely associated with the development of the host larva and pupa. These species differ from *Afrocalvolia nataliae* in that all surviving individuals in each generation pass through the deutonymphal instar. Mites of the winter generation pass the winter as deutonymphs attached to the host prepupa or pupa. Contrasting data is available on other insect nidicoles. Krombein (1967) reported that *Horstia virginica* (Acaridae) and *Chaetodactylus krombeini* (Chaetodactylidae) underwent multiple generations within cells of their solitary bee hosts.

4. Dispersal

4.1 Phoretic Dispersal by Deutonymphs

One major modification in the life cycle of astigmatid mites which has enabled the lineage to undergo such a successful radiation in temporary habitats is the shift from limited dispersal ability restricted to the adult instar to a much greater dispersal potential achieved in a preadult instar, the deutonymph. As noted above, the deutonymphal instar in the Astigmata has a highly modified morphology and behavior which function both in dispersal and typically in resisting adverse conditions. Dispersal in the Astigmata can occur in several modes. The ancestral condition in the group, as evidenced by the morphology of the earliest derivative lineage, the Schizoglyphidae, is dispersal by deutonymphs via phoretic association with an arthropod. The subject of phoresy in the Astigmata has been recently reviewed by Houck and OConnor (1991) and will not be detailed again here. Suffice it to say that phoresy by deutonymphs remains the primary dispersal mode in the non-psoroptidid Astigmata, with phoretic hosts including many groups of arthropods and vertebrates.

4.2 Nonphoretic Dispersal by Deutonymphs

A second dispersal mode known in the Astigmata is nonphoretic dispersal by deutonymphs. This type of dispersal is accomplished via two distinct mechanisms. In the first case, deutonymphs retain the ancestral morphology, including the attachment structures used by phoretic individuals, however, dispersal is typically under the mites own power. Examples of this type of dispersal include species of *Sancassania* (= *Caloglyphus*) (Acaridae) which are associated with certain scarabaeid beetles and their larvae. Feeding stages of the mites occur on dead beetles or larvae; deutonymphs disperse in the soil, encounter beetle larvae

and remain with them until their death (Chmielewski and Lipa 1967). An analogous situation possibly occurs with *Histiostoma murchei* (Histiostomatidae), in which the feeding stages are predaceous in the egg cocoons of earthworms (Oliver 1962). Phoresy is unknown in this species, with deutonymphs presumably dispersing through the litter in search of suitable habitats. Finally, phoresy is poorly documented in the histiostomatid taxa associated with pitcher plants. Robert Naczi (pers. comm.) has observed that species of *Sarraceniopus* only leave the water-filled leaf pitchers as deutonymphs. Deutonymphs wander about the plant and congregate at the tips of unopened leaf pitchers. When the pitchers open, the mites immediately enter. These deutonymphs retain the modifications associated with phoresy and likely use phoresy for long distance dispersal, but most individuals disperse to new pitchers within a single plant or members of a single clone. Few records of phoresy among the Old World *Nepenthes* associates are also known, suggesting a similar dispersal mode.

A more profound modification of the deutonymph, involving highly regressive morphological changes, has led to passive dispersal via air currents in two taxa of Glycyphagidae. Both *Glycyphagus* (*G.*) *domesticus* and *G.* (*Lepidoglyphus*) *destructor* have deutonymphs in which the body setation and legs are strongly regressive or lacking altogether. These deutonymphs typically do not emerge from the protonymphal cuticle which dries around the cyst-like deutonymph (Hora 1934; Knülle 1959, 1987). In contrast with other taxa in which regressive deutonymphs are formed (*Acarus*, *Alabidopus*, *Chaetodactylus* and *Hericia*) but typically do not disperse, deutonymphs of the two *Glycyphagus* species actually do disperse via air currents.

4.3 Loss of the Dispersal (Deutonymphal) Morph

Many taxa of astigmatid mites have lost the ability to form deutonymphs, and in these taxa it is presumed that all dispersal must be accomplished by other instars. These taxa include the family Hyadesiidae, species of which are restricted to marine, intertidal and tidal habitats; arboreal leaf-inhabiting species of the genera *Czenspinskia* and *Oulenzia* (Winterschmidtiidae), and *Neotropacarus* (Acaridae); most species of the genus *Tyrophagus* (Acaridae) which occur in soil, litter and synanthropic habitats; the Aeroglyphidae-Rosensteiniidae lineage which ancestrally occur in bat colonies; and the numerous taxa with nondeutonymphal stages parasitic on arthropods or vertebrates, although a few exceptions to the last occur. Deutonymphs have not been described for a number of other lineages of Astigmata, however, the fragmentary nature of the available data on these species does not permit a definitive statement as yet. Some of these taxa where I suspect deutonymphs are never formed are the subfamily Algophagine (Algophagidae), the genera *Fusacarus*, *Gohieria*, and *Tropilichus* (Glycyphagidae), *Suidasia* (Suidasiidae), and *Aleuroglyphus* (Acaridae).

4.4 Dispersal of Permanent Parasites

Few controlled experimental data are available concerning the details of dispersal by nondeutonymphal stages of astigmatid mites. Dubinin (1951) summarizes a considerable number of observations on the dispersal of astigmatid mites inhabiting bird feathers. He concludes that three basic dispersal modes operate: (1) direct transmission from parent to offspring, in which case the preponderance of dispersers are preadults or teneral adults; (2) direct transfer between adult birds, which accounts for the presence of specific parasites on birds which do not rear their own young; and (3) transfer via the nest. The latter mode, although documented for some individuals of some species (e.g. *Gabucinia delibata* [Gabuciniidae] on crows), was not deemed an important mode of dispersal for any species. Direct contact between hosts seems to be the required mode of dispersal among astigmatid mite parasites of mammals (Meleney 1985), although some species, notably the scabies mite, *Sarcoptes scabiei* (Sarcoptidae), can survive for short periods away from a host (Mellanby 1972).

The life histories of permanently parasitic mites of arthropods (Canestriniidae, Heterocoptidae and some Rosensteiniidae and Hemisarcoptidae) have not been studied. Because these mites parasitize only adult insects, dispersal must take place through direct contact between individuals, presumably during copulation. An interesting potential exception may be found in the genus *Megacanestrinia* (Canestriniidae). This genus, the earliest derivative genus in the family, is the only one of all the permanent parasites of arthropods in which the deutonymph is retained in the life cycle. Feeding stages of the mites occur in the subelytral space on their hosts, African carabid beetles of the genus *Tefflus*, while deutonymphs congregate on the venter of the thorax. In this instance, it seems possible that dispersal to new hosts still involves the deutonymph as this stage is positioned for easier access to another individual during mating.

4.5 Dispersal and Adverse Changes in the Environment

Correlated with the morphological specializations for dispersal in astigmatid mite deutonymphs is the ability to withstand adverse changes in the environment which would be fatal to other ontogenetic stages. In a number of taxa, decline in environmental quality induces individuals to enter the deutonymphal stage (Wallace 1960, Woodring 1963, Griffiths 1966). In taxa in which the ability to form deutonymphs has been lost, the tritonymph typically takes over the function of surviving adverse periods. This phenomenon has been demonstrated for *Czenspinskia transversostriata* (= *lordi*) (Winterschmidtiidae) (Dosse and Schneider 1957), *Tyrophagus longior* (Acaridae) (Sorokin 1948), and populations of *Carpoglyphus lactis* (Carpoglyphidae) which are unable to form deutonymphs (Zyromska-Rudzka 1964). Populations of *Dermatophagoides* (Pyroglyphidae) typically survive adverse conditions in either the protonymphal or tritonymphal instars

(Wharton 1976). Interestingly, *Naiadacarus arboricola* (Acaridae) also survives adverse periods as tritonymphs (Fashing 1976); the deutonymph in this species apparently functioning only in dispersal.

5. Host Associations

An integral aspect of the life history of most astigmatid mites is the quality, duration and specificity of association with another organism. Until recently, it was presumed that the association between astigmatid mite deutonymphs and other arthropods was a case of simple commensalism, with the mite benefiting solely through phoretic dispersal. Recent studies by Houck (Houck and OConnor 1991) which are developed more fully in this volume (Chapter 10) suggest that the association may be more complicated in some taxa, in that deutonymphs may require a period of time spent on a host before developing further. It has long been known that some deutonymphs which are found in mammalian hair follicles and the subcutaneous tissues of birds and mammals are true parasites, acquiring material in an as yet unknown manner from their hosts (Fain and Bafort 1967, Lukoschus et al. 1972).

Specificity of association varies widely among astigmatid mite taxa. Species which live in environments which are only visited by other organisms, and not created by them, tend to show little specificity. For example, Türk and Türk (1957) recorded numerous hosts for species which develop in decaying organic matter and fungal fruiting bodies in Germany. Similarly, OConnor (1990) collected *Histiogaster arborsignis* (Acaridae), a species which inhabits subcortical spaces, from 22 species of insects belonging to three orders. OConnor (1991) noted that this relative nonspecificity was a general pattern among astigmatid mites inhabiting subcortical habitats in Michigan. On the other hand, some species living in other habitats not created by interactive processes exhibit more pronounced specificity. This may relate to a limited pool of potential host species visiting the habitat as in the associations of *Naiadacarus arboricola* with syrphid flies of the genus *Mallota* (Fashing 1975), and *Hemisarcoptes* species with coccinellid beetles of the genus *Chilocorus* (Houck and OConnor 1990). Or it may reflect ecological changes in the habitat itself. For example, different species of Histiostomatidae which develop in cattle dung in the Netherlands use different dung-breeding insects for dispersal (Bongers et al. 1985). These insects typically come to dung piles at different periods during the succession of stages marking the decomposition of the dung, suggesting that the mite species may be exploiting the dung during different time periods as well.

In contrast to these patterns, mites which inhabit host-created environments tend to be specialized for dispersal on those hosts and few others. Specificity among nidicolous mites associated with insects and vertebrates is high. In many such species, life histories of the mites and their hosts are strongly correlated.

This synchronicity of development has been documented for the enslinielline associates of Hymenoptera (Krombein 1967, Cowan 1984, Klompen et al. 1987), some glycyphagid associates of mammals such as *Lophioglyphus liciosus* (Lukoschus et. al. 1972), and hypoderatid associates of birds such as *Hypodectes propus* (Fain and Bafort 1967). Some correlation of life histories between vertebrate hosts and permanently parasitic Astigmata has also been noted. Dubinin (1951) noted the correlation between the size and age structure of feather mite populations with the breeding and molting patterns of the host birds. Similarly, some sarcoptid parasites of bats may time the production of offspring to coincide with the reproduction of their hosts (Klompen, pers. comm.).

6. Evolution of Parasitism

Using the method of Brooks (1985) to hypothesize ecological shifts, the shifts in essential life-history parameters which mark the transition from commensalistic associations to true parasitism may be hypothesized to have occurred in at least 21 different lineages of astigmatid mites (parasitism is here defined in the broadest sense of living permanently on a host or feeding directly from it). Parasitism of arthropods has evolved on 10 separate occasions, seven of which involve permanent parasitism: (1) the family Canestriniidae; (2) the family Heterocoptidae; (3) the genus *Rosensteinia* (Rosensteiniidae); (4) an undescribed genus of Rosensteiniidae also parasitic on roaches which is related to the nonparasitic genus *Nycterilichus*; (5) the genera *Micronychites* and *Micronychitoides* (Rosensteiniidae) which form a monophyletic group; (6) the genus *Linobia* (Hemisarcoptidae); (7) the genera *Askinasia*, *Ewingia*, *Hoogstraalacarus*, *Kanakobia* and two undescribed genera (Acaridae) living on decapod crustaceans. Parasitism of arthropods by species which still retain the deutonymph in the life cycle and disperse in this stage has evolved twice: (1) the clade comprising the genera *Ensliniella*, *Kennethiella* and *Vespacarus* (Winterschmidtiidae), and (2) the genus *Hemisarcoptes* (Hemisarcoptidae) which may act either as a predator or a parasite of diaspidid scale insects depending on the number of mites per host and the stage of the host attacked. Finally, a last lineage of arthropod parasites should be mentioned in which a shift in host and life history has occurred. The family Epidermoptidae comprises species which are normally parasitic on the skin of birds. The genus *Myialges* has undergone a transformation such that the adult females leave the bird host and parasitize lice or hippoboscid flies, the males and nymphs remain on bird hosts, but females lay their eggs on the arthropod host.

A similar analysis of the evolution of parasitism of vertebrates yields a hypothesis of 11 separate instances. Two distinct life-history shifts have occurred, permanent parasitism by feeding stages with the concomitant loss of the deutonymph from the life cycle, and parasitism by deutonymphs only, with the other stages remaining free-living nidicoles. The first pathway has occurred in at least four

lineages: (1) the Psoroptidia forms a monophyletic grouping of approximately 40 families which appears to have originated as parasites of birds, with a secondary radiation onto mammals; (2) the genera *Loxanoetus* and *Otanoetus* (Histiostomatidae) which inhabit the ears of large mammals form a monophyletic group (it is problematical whether these mites are true parasites although it seems likely that at least some of their diet is material of host origin); (3) the genus *Chiroptoglyphus* represents a very early derivative lineage in the family Rosensteiniidae, species of which live permanently in the fur of bats; (4) the rosensteiniid taxa *Cheiromelichus* and *"Nycteriglyphus" asiaticus* probably form a monophyletic lineage, species of which attach to the skin of molossid bats of the genus *Cheiromeles*.

In seven additional lineages species have made the transition to parasitism by a shift from simple phoresy by deutonymphs to a closer association in which the deutonymph actually obtains materials from the host. The exact mechanism of food uptake remains unknown as deutonymphs lack a functional mouth, however, breakdown of host tissue around the mite has been demonstrated in some Glycyphagidae (Lukoschus et al. 1972) and growth of the mite within the deutonymphal stadium can be pronounced. Six of the lineages exhibiting this shift belong to the superfamily Glycyphagoidea, where nondeutonymphal instars are mammalian nidicoles. The lineages include: (1) the monobasic family Pedetopodidae, the single species of which lives as deutonymphs in the hair follicles of the springhare, *Pedetes capensis*; (2) the family Chortoglyphidae which parasitize the hair follicles of rodents and occasionally other mammalian groups; (3) the family Echimyopodidae which occur in hair follicles or subcutaneous tissues of marsupials, edentates and rodents; and three lineages within the family Glycyphagidae; (4) the genus *Baloghella* representing the subfamily Melesodectinae, deutonymphs of which live in the tissues of the ear conchae of European badgers; (5) the subfamily Metalabidophorinae which live in hair follicles of rodents and rarely insectivores; (6) the lineage comprising the subfamilies Lophuromyopodinae and Ctenoglyphinae which live in the hair follicles of rodents, and finally; (7) the nonglycyphagoid family Hypoderatidae, deutonymphs of which occur subcutaneously in birds and rarely in mammals.

7. Summary

The Astigmata is an extremely successful lineage of mites which owes its successful diversification and adaptive radiation to an ancestral switch in life-history parameters which allowed the colonization and exploitation of patchy or ephemeral resources. The ability to quickly colonize such habitats via phoretic associations with arthropods, and to quickly exploit the resources before their disappearance has allowed these mites to diversify in the absence of most other potentially competing groups of mites. Phoretic exploitation of other arthropods, typically insects, which are potential competitors for the same resources, has in numerous

instances led to closer associations with the hosts. As hosts undergo ecological shifts themselves which involve the creation of new habitat types, mites can be carried along, ecologically and evolutionarily speaking. Close phoretic associations may evolve into mutualistic relationships (Eickwort 1979) or parasitic ones. Ultimately, as mites adapt to a completely parasitic existence in a relatively stable "host" environment, the selective pressures which originally favored life-history traits such as fast generation time and good dispersal ability become somewhat reversed and coevolutionary processes begin to dominate. Most parasitic astigmatid mites are relatively innocuous, suggesting a period of coadaptation on the part of both mite and host species.

References

Barker, P. S. 1967a. The effects of high humidity and different temperatures on the biology of *Tyrophagus putrescentiae* (Schrank) (Acarina: Tyrogliphidae). *Can. J. Zool.* 45:91–96.

Barker, P. S. 1967b. Effect of humidity and temperature on the biology of *Aeroglyphus robustus* (Banks) (Acarina: Glycyphagidae). *Can. J. Zool.* 45:479–483.

Barker, P. S. 1968. Bionomics of *Glycyphagus domesticus* (de Geer) (Acarina: Glycyphagidae), a pest of stored grain. *Can. J. Zool.* 46:89–92.

Barker, P. S. 1974. Bionomics of *Caloglyphus anomalus* Nesbitt (Acarina: Acaridae). *Manitoba Entomol.* 8:41–47.

Behura, B. K. 1957. The life-history of *Histiostoma polypori* (Oud.) (Acari: Tyroglyphoidea). *J. NY Entomol. Soc.* 65:51–78.

Boczek, J. 1973. Procesy starzenia sie u owadow i roztoczy. *Kosmos* 6:611–621.

Boczek, J. and B. Czajkowska. 1973. Some aspects of aging in *Acarus siro* (L.) (Acarina: Acaridae). *Ekol. pol.* 21:173–184.

Boczek, J. and B. M. Sosnowska. 1975. Studies on aging in acarid mites, II. *Zesz. Probl. Postepow Nauk. Roln.* 171:169–177.

Bongers, M. G. H., B. M. OConnor and F. S. Lukoschus. 1985. Morphology and ontogeny of histiostomatid mites (Acari: Astigmata) associated with cattle dung in the Netherlands. *Zool. Meded.* (Leiden) 223:1–56.

Boulanova, E. 1937. Notes morphologique et biologique sur *Ferminia fusca* Ouds. *Bull. Soc. Nat. Moscow Biol. N.S.* 46:304–316.

Brooks, D. R. 1985. Historical ecology: a new approach to studying the evolution of ecological associations. *Ann. Mo. Bot. Gard.* 72:660–680.

Chmielewski, W. 1969. Obserwacje nad biologia nowego dla akarofauny polskiej gatunku *Kuzinia laevis* (Dujardin, 1849) (Acarina, Acaridae). *Pol. Pismo Entomol.* 39:603–617.

Chmielewski, W. 1971. Morfologia, biologia i ekologia *Carpoglyphus lactis* (L., 1758) (Glycyphagidae, Acarina). *Pr. Nauk. Inst. Ochr. Rosl.* 13:63–166.

Chmielewski, W. and J. J. Lipa. 1967. Biological and ecological studies on *Caloglyphus* mites (Acarina: Acaridae) associated with Scarabaeidae. *Acta Parasitol. Pol.* 14:179–186.

Cooreman, J. 1942. Notes et observations sur les acariens, II. *Bull. Mus. r. Hist. nat. Belg.* 18:1–10.

Cowan, D. P. 1984. Life history and male dimorphism in the mite *Kennethiella trisetosa* (Acari: Winterschmidtiidae), and its symbiotic relationship with the wasp *Ancistrocerus antilope* (Hymenoptera: Eumenidae). *Ann. Entomol. Soc. Am.* 77:725–732.

Dosse, G. and I. Schneider. 1957. Biologie und Lebensweise von *Czenspinskia lordi* Nesbitt (Acar., Sarcoptiformes). *Z. Angew. Zool.* 44:403–418.

Dubinin, V. B. 1951. Feather mites (Analgesoidea). Part I. Introduction to their study. *Fauna of the USSR, Arachnida*, Vol. 6 (no. 5). (In Russian). 365 pp.

Eickwort, G. C. 1979. Mites associated with sweat bees (Halictidae). In: *Recent Advances in Acarology*, Vol. 1 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 575–581.

Eickwort, G. C. 1990. Associations of mites with social insects. *Annu. Rev. Entomol.* 35:469–488.

Fain, A. and J. Bafort. 1967. Cycle evolutif et morphologie de *Hypodectes* (*Hypodectoides*) *propus* (Nitzsch), acarien nidicole a deutonymphe parasite tissulaire des pigeons. *Bull. Acad. R. Belge Classe Sci.* 53:501–533.

Fain, A., A. W. A. M. de Cock and F. S. Lukoschus. 1972. Parasitic mites of Surinam XVII. Description and life cycle of *Marsupialichus marsupialis* sp. n. from *Didelphis marsupialis* (Glycyphagidae: Sarcoptiformes). *Acarologia* 14:81–93.

Fashing, N. J. 1975. Life history and general biology of *Naiadacarus arboricola* Fashing, a mite inhabiting water-filled treeholes (Acarina: Acaridae). *J. Nat. Hist.* 9:413–424.

Fashing, N. J. 1976. The resistant tritonymphal instar and its implications in the population dynamics of *Naiadacarus arboricola* Fashing (Acarina: Acaridae). *Acarologia* 18:704–714.

Fashing, N. J. 1979. *Naiadacarus arboricola*, a "*K*-selected" acarid mite. In: *Recent Advances in Acarology*, Vol. 1 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 525–529.

Gerson, U., S. Capua and D. Thorens. 1983. Life history and life tables of *Rhizoglyphus robini* Claparede (Acari: Astigmata: Acaridae). *Acarologia* 24:439–448.

Griffiths, D. A. 1966. Nutrition as a factor influencing hypopus formation in the *Acarus siro* species complex (Acarina, Acaridae). *J. Stored Prod. Res.* 1:325–340.

Hart, B. J. and A. Fain. 1988. Morphological and biological studies of medically important houst-dust mites. *Acarologia* 29:285–295.

Hill, A. and K. L. Deahl. 1978. Description and life cycle of a new species of *Histiostoma* (Acari: Histiostomidae) associated with commercial mushroom production. *Proc. Entomol. Soc. Wash.* 80:317–329.

Hora, A. M. 1934. On the biology of the mite, *Glycyphagus domesticus* de Geer (Tyroglyphidae, Acarina). *Ann. Appl. Biol.* 21:483–494.

Houck, M. A. and B. M. OConnor. 1990. Ontogeny and life history of *Hemisarcoptes cooremani* (Acari: Hemisarcoptidae). *Ann. Entomol. Soc. Am.* 83:869–886.

Houck, M. A. and B. M. OConnor. 1991. Ecological and evolutionary significance of phoresy in the Astigmata. *Annu. Rev. Entomol.* 36:611–636.

Hsin, K.-L. and C.-P. Chen. 1964. Studies on the life history of *Aleuroglyphus ovatus* Troupeau (Acarina, Acaridae). *Acta Entomol. Sin.* 13:428–435. (In Chinese).

Hughes, A. M. 1976. The Mites of Stored Food and Houses, 2nd. ed. *Min. Agric. Fisheries, Food, Tech. Bull. 9, H. M. S. O.* London. 400 pp.

Hughes, R. D. and C. G. Jackson. 1958. A review of the Anoetidae (Acari). *Virginia J. Sci.* 9, N.S.(1):5–198.

Kielczewski, B. and S. Seniczak. 1972. Cykl rozwojowy drapieznego roztocza *Calvolia fraxini* E. Türk et F. Türk (Tyroglyphidae, Acarina). *Pr. Z. Zakr. Lesn., Poznan* 34:83–88.

Klompen, J. S. H., F. S. Lukoschus and B. M. OConnor. 1987. Ontogeny, life history and sex ratio evolution in *Ensliniella kostylevi* (Acari: Winterschmidtiidae). *J. Zool.* (Lond.) 213:591–607.

Knülle, W. 1959. Morphologische und entwicklungsgeschichtliche Untersuchungen zum Phylogenetischen System der Acari: Acariformes Zachv. II. Acaridiae: Acaridae. *Mitt. Zool. Mus. Berl.* 35:347–417.

Knülle, W. 1987. Genetic variability and ecological adaptability of hypopus formation in a stored product mite. *Exp. Appl. Acarol.* 3:21–32.

Krombein, K. V. 1967. *Trap Nesting Wasps and Bees: Life Histories, Nests and Associates.* Smithsonian Press, Washington, DC. 496 pp.

Lukoschus, F. S., A. W. A. M. de Cock and A. Fain. 1971. Life cycle of *Melesodectes auricularis* Fain and Lukoschus (Glycyphagidae, Sarcoptiformes). *Tijdschr. Entomol.* 114:173–183.

Lukoschus, F. S., A. Fain and F. M. Driessen. 1972. Life cycle of *Apodemopus apodemi* (Fain 1965) (Glycyphagidae: Sarcoptiformes). *Tijdschr. Entomol.* 115:325–339.

Lukoschus, F. S., G. H. S. Janssen Duijghuijsen and A. Fain. 1979. Parasites of Western Australia IV. Observations on the genus *Marsupiopus* Fain 1968 (Acarina: Astigmata: Glycyphagidae). *Rec. West. Aust. Mus.* 7:37–55.

Meleney, W. P. 1985. Mange mites and other parasitic mites. In: *Parasites, Pests and Predators. World Animal Science B2* (S. M. Gaafar, W. E. Howard and R. E. Marsh eds.). Elsevier, Amsterdam. Pp. 317–346

Mellanby, K. 1972. *Scabies,* 2nd ed. E.W. Classey Ltd., Middlesex, England. 81 pp.

OConnor, B. M. 1981. *A systematic revision of the family group taxa in the nonpsoroptidid Astigmata.* Ph.D. Thesis, Cornell Univ., Ithaca, NY. 594 pp.

OConnor, B. M. 1982a. Evolutionary ecology of astigmatid mites. *Annu. Rev. Entomol.* 27:385–409.

OConnor, B. M. 1982b. Acari: Astigmata. In: *Synopsis and Classification of Living Organisms* II (S. Parker ed.). McGraw-Hill, NY. Pp. 146–169.

OConnor, B. M. 1984a. Phylogenetic relationships among higher taxa in the Acariformes,

with particular reference to the Astigmata. In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood Ltd., Chichester. Pp. 19–27.

OConnor, B. M. 1984b. Acarine-fungal relationships: the evolution of symbiotic associations. In: *Fungus-Insect Relationships: Perspectives in Ecology and Evolution* (Q. Wheeler and M. Blackwell eds.). Columbia Univ. Press, NY. Pp. 354–81.

OConnor, B. M. 1988. Coevolution in Astigmatid mite-bee associations. In: *Africanized Honey Bees and Bee Mites*. (G. R. Needham, R. E. Page, Jr, M. Delfinado-Baker and C. Bowman eds.). Ellis-Horwood, Ltd. Chichester. Pp. 339–346.

OConnor, B. M. 1990. Ecology and host associations of *Histiogaster arborsignis* (Acari: Acaridae) in the Great Lakes region, particularly in the Huron Mountains of Northern Michigan. *Great Lakes Entomol.* 23:205–209.

OConnor, B. M. 1991. A preliminary report on the arthropod-associated astigmatid mites (Acari: Acariformes) of the Huron Mountains of Northern Michigan. *Mich. Acad.* 24:307–320.

OConnor, B. M. and G. C. Eickwort. 1988. Morphology, ontogeny, biology and systematics of the genus *Vidia* (Acari: Winterschmidtiidae). *Acarologia* 29:147–174.

Oliver, J. H., Jr. 1962. A mite parasitic in the cocoons of earthworms. *J. Parasitol.* 48:120–123.

Perron, R. 1954. Untersuchungen über Bau, Entwicklung und Physiologie der Milbe *Histiostoma laboratorium* Hughes. *Acta Zool.* (Stockh.) 35:71–176.

Phillipsen, W. J. and H. C. Coppel. 1977a. *Acotyledon formosani* sp.n. associated with the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Acarina: Acaridae-Isoptera: Rhinotermitidae). *J. Kans. Entomol. Soc.* 50:399–409.

Phillipsen, W. J. and H. C. Coppel. 1977b. *Histiostoma formosana* sp.n. associated with the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Acarina: Acaridae-Isoptera: Rhinotermitidae). *J. Kans. Entomol. Soc.* 50:496–502.

Pillai, P. R. P. and P. W. Winston. 1969. Life history and biology of *Caloglyphus anomalus* Nesbitt (Acarina: Acaridae). *Acarologia* 2:295–303.

Rivard, I. 1959. Influence of humidity on longevity, fecundity, and rate of increase of the grain-infesting mite *Tyrophagus castellani* (Hirst) (Acarina: Acaridae) reared on mould cultures. *Can. Entomol.* 91:31–35.

Rivard, I. 1961. Influence of temperature and humidity on mortality and rate of development of immature stages of the mite *Tyrophagus putrescentiae* (Schrank) (Acarina: Acaridae) reared on mold cultures. *Can. J. Zool.* 39:419–426.

Rodriguez, J. G. and Z. A. Stepien. 1973. Biology and population dynamics of *Caloglyphus berlesei* (Michael) (Acarina: Acaridae) in xenic diet. *J. Kans. Entomol. Soc.* 46:176–183.

Sinha, R. N. 1966. Feeding and reproduction of some stored-product mites on seed-borne fungi. *J. Econ. Entomol.* 59:227–232.

Sorokin, S. 1948. Population of grain mites in hay. *Zool. Zh.* 27:487–491. (In Russian).

Timms, S., D. N. Ferro and R. M. Emberson. 1981. General biology and nomenclature of *Sancassania berlesei* (Michael). *Acarologia* 22:385–390.

Türk, E. and F. Türk. 1957. Systematik und Ökologie der Tyroglyphiden Mitteleuropas. In: *Beiträge zur Systematik und Ökologie Mitteleuropäischer Acarina*, Vol. 1 (H. J. Stammer ed.). Akad. Verlagsges, Leipzig. Pp. 3–231.

Wallace, D. R. J. 1960. Observations on hypopus development in the Acarina. *J. Insect Physiol.* 5:216–229.

Wharton, G. W. 1976. House dust mites. *J. Med. Entomol.* 12:577–621.

Woodring, J. P. 1963. The nutrition and biology of saprophytic Sarcoptiformes. In: *Advances in Acarology* Vol. 1 (J. A. Naegle ed.). Comstock Publ. Assoc., Ithaca, NY. Pp. 89–111.

Woodring, J. P. 1969. Observations on the biology of six species of acarid mites. *Ann. Entomol. Soc. Am.* 62:102–108.

Yousef, A. A., E. A. El-Badry and S. H. Metwally. 1979. Life history of the anoetid mite *Histiostoma cataglyphi* Yousef et Metwally, with a description of the immature stages (Acari, Astigmata, Anoetoidea). *Z. Angew. Entomol.* 87:225–229.

Zyromska-Rudska, A. 1964. Abundance, dynamics and age structure of populations of *Carpoglyphus lactis* (L.) (Acarina, Glycyphagidae) in closed cultures. *Ekol. Pol. Ser. A.* 12:355–367.

7

Life-History Patterns of Astigmatid Inhabitants of Water-Filled Treeholes

Norman J. Fashing

CONTENTS

1. Introduction

It has been known for well over 100 years that certain terrestrial plants hold small bodies of water, and that these bodies of water often contain communities of aquatic arthropods (Fish 1983). Varga (1928) coined the term "*phytotelmata*" (Greek: *phyton* = plant, *telma* = pool) to describe such habitats which include the modified leaves of pitcher plants, inflated leaf axils of such plants as bromeliads and palms, water-collecting flowers such as *Heliconia*, internodal spaces of broken bamboo stems, and the water-collecting depressions on trees (treeholes). In fact, Fish (1983) estimated that habitats suitable for aquatic arthropod development can be found in over 1500 plant species.

In recent years, phytotelmata have received considerable attention as microcosms which can be easily manipulated to investigate fundamental problems in community ecology (see *Phytotelmata: Terrestrial Plants as Hosts for Aquatic*

Insect Communities, 1983, edited by Frank and Lounibos). In this regard, water-filled treeholes have been excellent subjects for the investigation of food-chain length and food-web complexity (Kitching 1971, Kitching and Pimm 1985, Pimm and Kitching 1987, Kitching 1987).

Water-filled treeholes occur in forest ecosystems throughout the world. In areas of frequent rainfall, they contain standing water most of the year and can attain a relatively permanent status. They provide a unique habitat for a number of organisms, many of which are obligate residents. Indeed, it is the exclusive habitat for several acarine species, as well as for the larval instars of certain aquatic dipteran and coleopteran species (Kitching 1971, Fashing 1975a, Kitching and Callaghan 1982, Kitching and Pimm 1985). It is the adaptation of the mite fauna to this unique habitat that forms the focus of this chapter.

I have divided the chapter into five sections. Since habitat is an important factor in shaping the life-history pattern of a species (Edwards 1988), the water-filled treehole habitat is described first, followed by a brief description of the arthropod inhabitants. I then focus on the most common mite inhabitants, the Astigmata, in terms of trophic adaptation. Since the ability to utilize a spatially scattered resource such as water-filled treeholes relies on an ability to disperse, I have devoted a section to dispersal patterns. The fourth section considers general life-history and reproductive patterns common to astigmatid treehole dwellers. Finally, a brief summary concludes the discussion.

2. Characteristics of Water-Filled Treeholes

2.1 The Treehole Habitat

A water-filled treehole (hereafter referred to simply as treehole) is defined as any cavity created by the natural morphology of a tree or any other depression on the surface of a tree which is capable of collecting and retaining water. Treeholes may be classified as "pans," which have an unbroken bark lining and are formed by the natural growth of the plant (e.g. the divergence of limbs or buttress roots), or "rot-holes" which lack a bark lining and have a layer of decomposing wood below. Rot-holes are a result of injury to the tree and may eventually enlarge due to further decomposition of tissue or they may decrease in size due to callus formation (Kitching 1971).

Obligate arthropod inhabitants can exploit only those treeholes which contain some water throughout the year. Free water may evaporate during periods of low rainfall, high temperatures, low humidity, and/or wind, but the treehole debris must remain sufficiently moist to provide a refuge for the organisms until rain replenishes the water (Fashing 1975a). During severe drought, smaller treeholes can dry completely causing most (if not all) of the arthropod inhabitants to perish.

Treehole communities are generally simple in both energy flow and species composition (Fish and Carpenter 1982). In temperate deciduous forests, autumn-

shed leaves landing in the treeholes provide the main allochthonous energy source. Additional nutrients may be derived from dissolved and suspended materials in stem flow (water that runs down the bark during rains) (Carpenter 1982), additional drifting plant matter, and from arthropods which fall into the treehole and die (Fashing 1975a). The treehole community is therefore a detritus based system.

Detrital layering partitions the treehole into microhabitats. The uppermost layer consists of the air-water interface. The second layer is composed of the most recently added leaves in a state of initial decay. Most insects and mites inhabit this second layer. The third layer consists of leaf-mold; leaves which are in more advanced stages of decomposition due to the action of bacteria. If the treehole lacks a bark lining, there is an additional layer of decomposing sapwood (Snow 1958, Kitching 1971).

Microorganisms play a vital role in the treehole community. Through detritus cycling, they increase the available nutrient content of the leaf litter for the macroinvertebrates (Suberkropp and Klug 1976). Microbial activity in the treehole is limited by low temperature in fall and winter. In spring, fungi invade the leaf litter and synthesize extracellular enzymes (pectinases and cellulases) to break down the leaves (Suberkropp and Klug 1976). Fungal hyphae cover the leaves and extend above them, and macroinvertebrates graze on the fungal hyphae. Together the fungi and the macroinvertebrates break the leaves into pieces. This process increases the total surface area of leaves and prepares them for bacterial invasion. As the number of bacteria increases, the fungal count decreases (Suberkropp and Klug 1976). Fungi are therefore important in the initial stages of leaf decomposition and bacteria complete the process of leaf decay.

Leaves from different tree species vary in their concentration of lignins, tannins, etc., which in turn influences the type of microbial growth a leaf can support. Leaf palatability for treehole herbivores depends on the fungal complex that attacks the leaves initially. The available protein of leaves can double depending on the dynamics of fungal growth (Kaushik and Hynes 1971). Therefore the food preferences of detritus feeders are dependent not only on the species of a decaying leaf and the particular stage of decay, but also on the colonizing fungal species.

Since autumn-shed leaves are the primary energy resource for the treehole community, energy input is primarily restricted to one short period during the year. There is a heavy demand on this common resource and it is often exhausted by mid or late summer. This creates a "lean period" for many treehole arthropods, often lasting two months or more (Fashing 1975a). However, this "lean period," like winter, is a cyclical and therefore a predictable stress and one to which treehole organisms must adapt.

2.2 Arthropod Inhabitants of Treeholes

A large diversity of organisms collected from water-filled treeholes are represented in the faunal record (e.g. Lacky 1940, Snow 1949, Rohnert 1950). Many

of these can be considered transient or accidental visitors to this community (the "*Dendrolimnetoxenen*", Rohnert 1950), and others are simply attracted to any moist or semiaquatic habitat (the "*Dendrolimnetophilen*", Rohnert 1950). This chapter concerns the "*Dendrolimnetobionten*" (Rohnert 1950), organisms which are obligate inhabitants of treeholes and seldom, if ever, found elsewhere. These obligate residents are: mid to polysaprophytic, eurythermic, resistant to changes in water chemistry (e.g. solute concentration and pH), able to withstand freezing, and have a high tolerance for dessiccation (Rohnert 1950). To this list I add the requirement that they must also be tolerant of relatively long periods with little food.

In most cases, the obligate insect fauna of treeholes consists of only a small number of species in any given locality. They are present as larvae and include members of the dipteran families Ceratopogonidae, Chironomidae, Culicidae, Psychodidae, and Syrphidae, as well as the coleopteran family Scirtidae (Fig. 7.1). These insect families are present in treeholes throughout the temperate regions of the world, with the exception that the Chironomidae are not represented in North America.

Other than an occasional notation concerning the observation of their presence (e.g. Lackey 1940), the first published literature on mites from treeholes appeared in 1973 (Fashing 1973). Between 1973 and 1980, four species were described

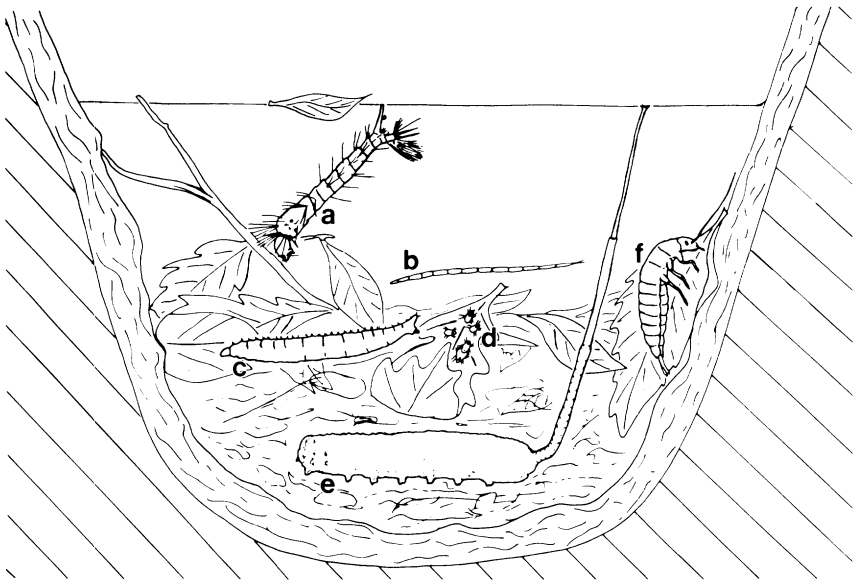


Figure 7.1. Common inhabitants of water-filled treeholes in eastern North America. (Not drawn to scale). a) Culicidae, b) Ceratopogonidae, c) Psychodidae, d) Astigmata, e) Syrphidae, f) Scirtidae.

from North American treeholes (Fashing 1973, 1974; Fashing and Wiseman 1980) and North America remained the only known location for treehole mites until Kitching and Callaghan reported acarine inhabitants from southeast Australia in 1982. To date, eight species of mites representing five families have been reported in the literature (Table 7.1). In addition, R. F. C. Naczi has found four new species of histiostomatids from treeholes in North America (pers. comm.).

3. Behavior of Astigmatid Inhabitants of Treeholes

Life-history studies have been conducted on only three treehole mite species, all of which are astigmatid mites: *Naiadacarus arboricola*, *Algophagus pennsylvanicus*, and *Hormosianoetus mallotae* (Fig. 7.2). In particular, much is known concerning the biology of *N. arboricola*, some concerning *A. pennsylvanicus*, and a smaller amount concerning *H. mallotae*. The remaining portion of this chapter deals primarily with these three species.

N. arboricola is found throughout the midwestern and eastern United States, having been recorded from: Arkansas, Florida, Illinois, Kansas, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, Oklahoma, Pennsylvania, South Carolina, Texas, and Virginia (Fashing 1974, unpublished; OConnor 1989; Naczi, pers. comm.). *H. mallotae* probably shares the same distribution, but has been collected in fewer locations: Kansas, Oklahoma, Arkansas, Illinois, Michigan, Pennsylvania, Virginia and Florida (Fashing 1973; Naczi, pers. comm.; OConnor, pers. comm.). *A. pennsylvanicus* is recorded thus far from

Table 7.1. Acarine Inhabitants of Water-Filled Treeholes.

Taxon	Locality	References
Mesostimata:		
Ascidae		
Cheiroseius sp.	S.E. Australia	Kitching and Callaghan (1982)
Prostigmata:		
Arrenuridae		
Arrenurus kitchingi Smith & Harvey	S.E. Australia	Smith and Harvey (1989)
Astigmata:		
Acaridae		
Naiadacarus arboricola Fashing	Eastern USA	Fashing (1974)
Naiadacarus oregonensis Fashing	Oregon, USA	Fashing (1974)
Algophagidae		
Algophagus pennsylvanicus Fashing & Wiseman	Eastern USA	Fashing and Wiseman (1979)
New Species 1	S.E. Australia	Kitching and Callaghan (1982)
New Species 2	S.E. Australia	Kitching and Callaghan (1982)
Histiostomatidae		
Hormosianoetus mallotae (Fashing)	Eastern USA	Fashing (1973)

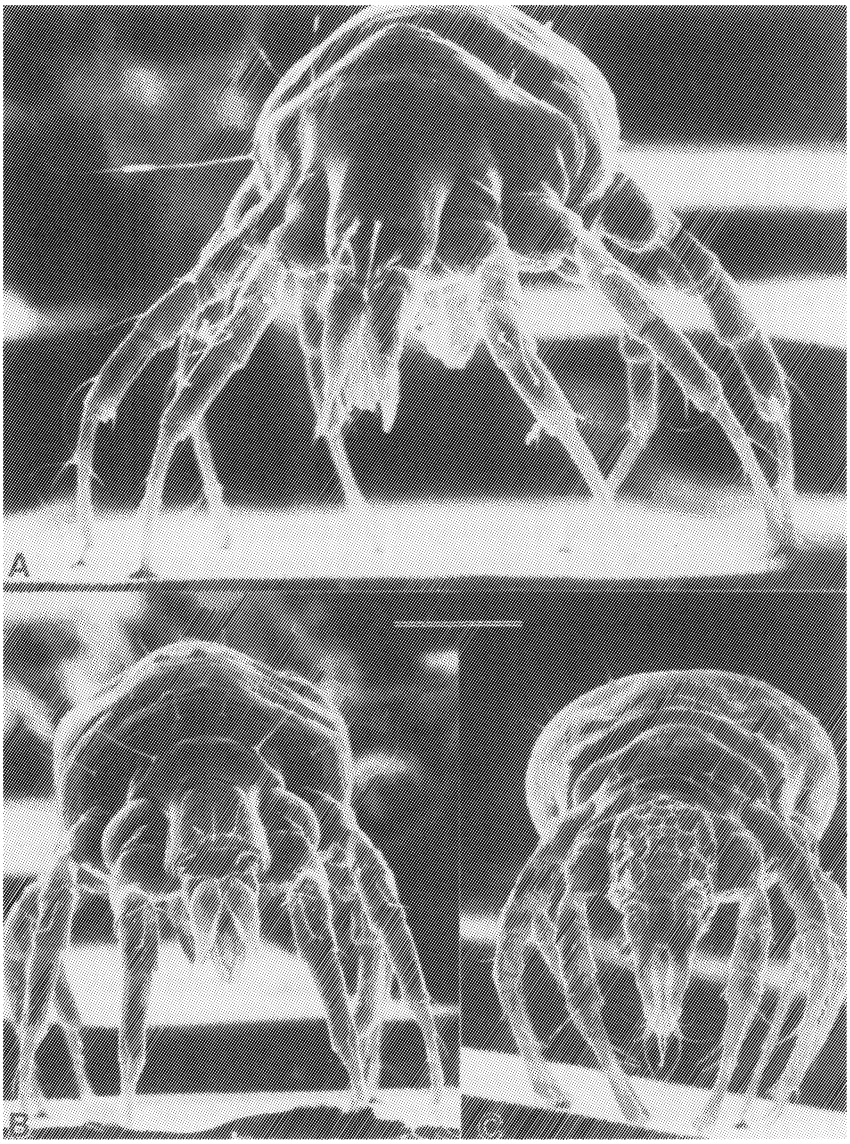


Figure 7.2. Scanning electron photomicrographs of three astigmatid inhabitants of water-filled treeholes in eastern North America. (Scale bar = 100μm). A) *Naiadacarus arboricola*, B) *Algophagus pennsylvanicus*, C) *Hormosianoetus mallotae*.

only four states: Oklahoma, Michigan, Pennsylvania and Virginia (Fashing and Wiseman 1980; Fashing, unpublished; Naczi, pers. comm.; OConnor, pers. comm.).

Of the three species, *N. arboricola* is the most common in terms of occurrence in treeholes as well as numbers within a treehole, and *A. pennsylvanicus* is the second most common. *H. mallotae* is relatively rare, occurring in less than five percent of the treeholes and usually in low numbers (Fashing and Campbell, unpublished). In areas of sympatry, all three species may be found occupying the same treehole, although such instances are rare. The simultaneous occurrence of *N. arboricola* and *A. pennsylvanicus*, however, is quite common.

3.1 Feeding Behavior and Morphology

Since decaying leaves are the energy base for the treehole community, and since food is usually the most limiting resource for an animal species, one would expect vigorous competition for this common resource. Partitioning of resources, therefore, may account for the successful sympatric coexistence of treehole mites.

Examination of the mouthparts of *N. arboricola*, *A. pennsylvanicus*, and *H. mallotae* reveals important morphological differences (Fig. 7.3). *H. mallotae* differs considerably from the other two species by possessing an elongate solenidion as well as a long eupathidial seta on the terminal segment of the pedipalp. In addition, it has chelicerae with no movable digit and the fixed digit is serrated and rakelike, bearing 18–20 small teeth (Fig. 7.3C) (Fashing unpublished). Observations on feeding behavior indicate that *H. mallotae* does not feed on coarse particulate matter, but like most other members of the Histiostomatidae collects fine particulate matter from the fluid medium (Hughes 1953, Krantz 1978, OConnor 1982a, 1984). The whiplike pedipalps are used to move small particles in the fluid medium toward the tip of the rostrum where they are raked into the mouth by the back and forth movement of the chelicerae (Hughes 1953). Members of this species are often observed on leaves near the water surface feeding from the area just below the surface film, an area rich in fine particulate matter as well as microbes (= filtering collector, Cummins and Klug 1979). At other times they feed at the leaf surface, using the pedipalps to stir up fine particulate matter and microbes (= gathering collector, Cummins and Klug 1979) (Fashing unpublished).

N. arboricola and *A. pennsylvanicus* differ considerably from *H. mallotae* in that their mouthparts are the typical sarcoptiform type with chelate chelicerae and short solenidia and setae on the terminal ends of the pedipalps (Figs. 7.3A, 7.3B). However, scanning electron microscopy reveals quite distinct morphological differences between the chelicerae of *N. arboricola* and *A. pennsylvanicus* which in turn are correlated with a difference in mode of feeding (Fashing and Campbell 1992, Fashing unpublished).

The cheliceral bases of *A. pennsylvanicus* are less massive than those of *N.*

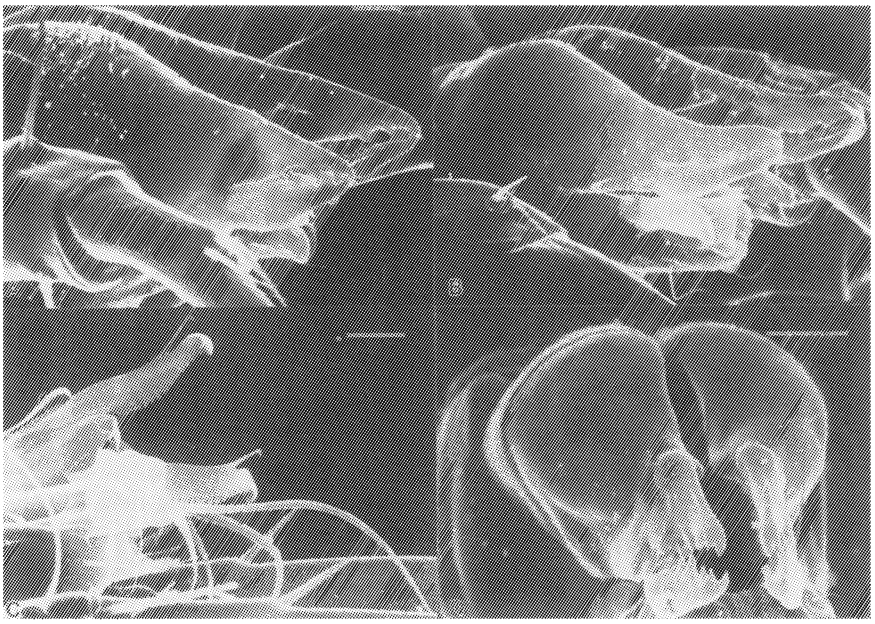


Figure 7.3. Scanning electron photomicrographs of the mouthparts of astigmatid mites from water-filled treeholes. (Scale bar = 10μm). A) *Naiadacarus arboricola*, B) *Algophagus pennsylvanicus*, C) *Hormosianoetus mallotae*, D) Undescribed species of algophagid from S.E. Australia.

arboricola (Figs. 7.3A, B), indicating less musculature to the movable biting digits. In addition, the fixed and movable digits of *A. pennsylvanicus* are not as robust. Further examination indicates that the biting digits of *N. arboricola* have strong teeth over the entire biting surfaces of both digits, and that these teeth interlock when the digits close (Fig. 7.3A). Such chelicerae are adapted for biting and crushing (Fashing unpublished). The biting digits of *A. pennsylvanicus*, on the other hand, have teeth only on the basal portion of the movable digit, the entire biting surface being adapted for cutting and shearing. The biting edges slide past each other in a scissor-like manner when the digits close. Furthermore, the tips of the biting digits curve mesially and are serrate or rakelike (Fig. 7.3B) (Fashing and Campbell 1992).

Behavioral correlates are consistent with the morphological differences observed in *N. arboricola* and *A. pennsylvanicus*. Control leaves left without mites remain intact and become covered with mats of fungal hyphae, whereas leaves on which *N. arboricola* are cultured are skeletonized (Fashing 1975a, unpublished). In contrast, leaves on which *A. pennsylvanicus* are cultured show no evidence of skeletonization, however an examination of the leaf surface reveals only small amounts of fungi (Fashing and Campbell 1992). It is apparent that *N.*

arboricola feeds by biting chunks out of leaves (= shredder, Cummins and Klug 1979), thereby ingesting leaf material along with any associated microbes. *A. pennsylvanicus*, on the other hand, feeds by grazing fungal hyphae from the leaf surface (= scraper, Cummins and Klug 1979). Direct observation of *A. pennsylvanicus* also reveals a possible second mode of feeding behavior. Individuals are often found on leaves or other substrate near the surface film, where they can be seen rapidly extending and retracting their chelicerae through the surface film in an alternating manner. The surface film is rich in microbes and fine particulate matter, and it appears that the serrated distal ends of the chelicerae are used to feed on this resource (= filtering collector, Cummins and Klug 1979) (Fashing and Campbell 1992).

In summary, feeding behavior and diet differ for the three species of treehole mites. *N. arboricola* feeds on coarse particulate organic matter by biting chunks out of leaves. This type of herbivore is typically called a "shredder" and is the most common form in a detritus based system (Barlocher and Kendrick 1973, Cummins and Klug 1979). *A. pennsylvanicus* feeds by shearing fungal hyphae from the leaf surface with specialized chelicerae. It is a "scraper" (= grazer) and represents the second most common type of detritus feeder (Barlocher and Kendrick 1973, Cummins and Klug 1979). In addition, it is possible that *A. pennsylvanicus* filters fine particulate organic matter from the surface film and is therefore a filtering "collector" as well. And finally, *H. mallotae* has mouthparts highly specialized for feeding on fine particulate organic matter and appears to be an extremely efficient filtering and gathering "collector." Little is known concerning the diet of other species of treehole mites, however a cursory examination of one of the two Australian species utilizing SEM suggests it is a shredder (Fig. 7.3D). Studies on resource partitioning by the Australian species will prove quite interesting since they are closely related members of the same family (Algophagidae).

3.2 Dispersal Patterns

In most free-living astigmatid mites, dispersal is effected by a highly specialized and facultative deutonymphal instar (hypopus) (Fig. 7.4). The hypopus, in contrast to other instars, is heavily sclerotized and resistant to desiccation. It has a greatly reduced gnathosoma without a mouth or mouthparts, and bears a ventral sucker plate as well as specialized tarsal setae utilized for phoretic attachment to other organisms (OConnor 1982b, Houck and OConnor 1991).

In most free-living species, the hypopus is present in low numbers or totally absent in a population as long as the habitat is favorable for population growth. However, when environmental conditions become unfavorable, protonymphs molt into hypopi (deutonymphs) rather than directly into tritonymphs. The hypopi then await and attach to organisms that utilize the same habitat, and are then carried by them to a fresh habitat where they leave the host, molt into tritonymphs,

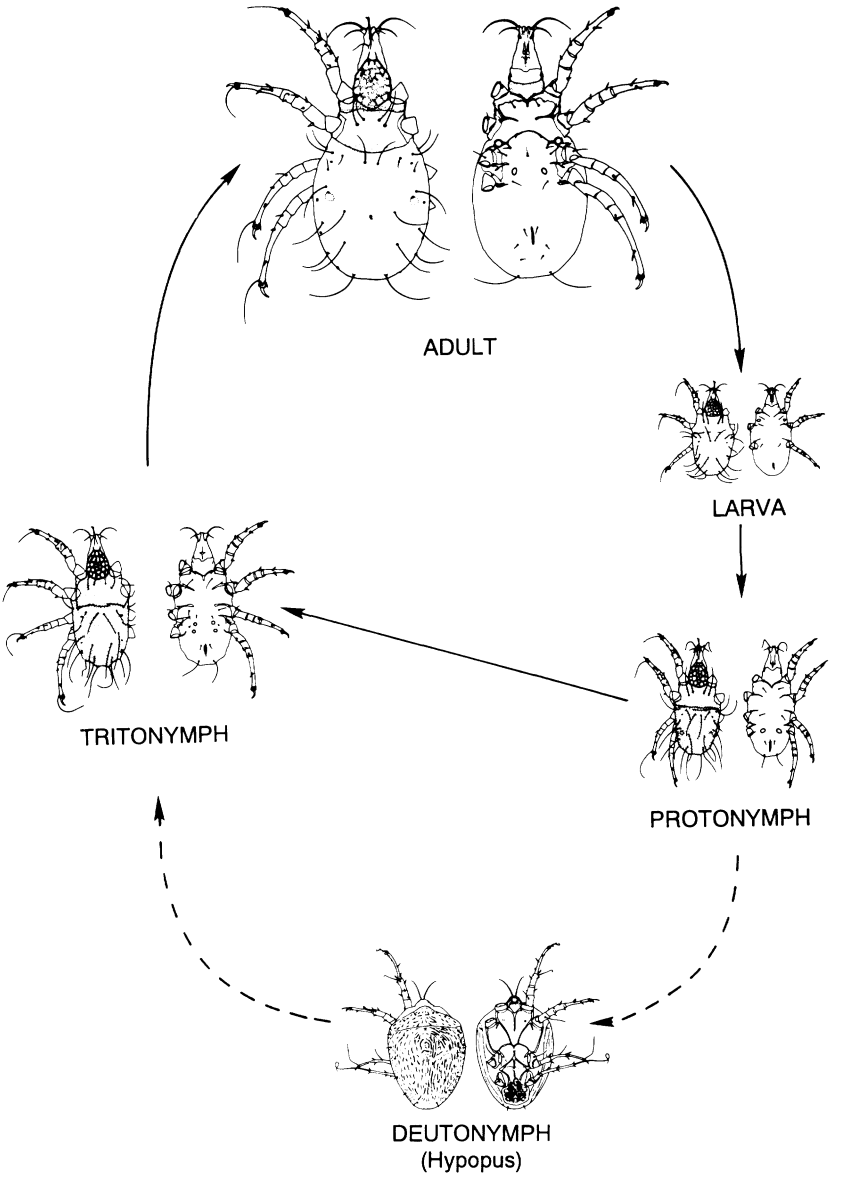


Figure 7.4. Life cycle of *Hormosianoetus mallotae*, typical of the Astigmata except that this species is larviparous. A quiescent period occurs at the end of each immature stadium, after which ecdysis occurs. Note the heteromorphic deutonymphal instar (hypopus), which is phoretic.

and resume their normal life cycle. In this new habitat they may undergo several generations before dispersal, and therefore significant hypopal formation again becomes an important part of their life history.

Both *N. arboricola* and *H. mallotae* conform to the basic astigmatid life cycle containing a facultative hypopus. They do not, however, form hypopi in response to adverse environmental conditions. Rather, hypopi are formed seasonally (only during May and June) when environmental conditions in treeholes appear optimal for population growth (Fashing 1976a). Decomposing leaves (the energy base) are most abundant in spring, and spring rainfall maintains a high water level in treeholes. If adverse conditions stimulated dispersal, hypopi would be found during late summer or early autumn when the food is usually depleted and drying of treeholes more frequent (Fashing 1976a).

In laboratory studies, *N. arboricola* did not form hypopi in response to overcrowding, accumulation of waste products, gradual evaporation of water, and/or lack of food (Fashing 1976a). No hypopal formation resulted among mites reared from larvae on leaves of tree species found to be inadequate for complete development and/or adult reproductive success (Fashing 1975b). In addition, no hypopal formation was observed under thermal stress. Protonymphs maintained at 2°C for four months molted into tritonymphs when transferred to 25°C, bypassing the hypopal stage. Mites reared at 15°C developed into tritonymphs but did not progress beyond this stage (Fashing 1975b). When cultured at 30°C, protonymphs died without completing development (Fashing 1976a).

Studies on *Sancassania boharti* (Cutcher and Woodring 1969), a free-living astigmatid mite, suggest that any adverse condition which retards protonymphal development might induce hypopal development. However, *N. arboricola* reared on seven different resources of varying nutritional values resulted in a wide range of time spent in the protonymphal instar (means of 2.7–7.7 days), but no hypopal formation (Fashing 1975b).

In summary, hypopal formation could not be induced by adverse environmental conditions in the laboratory (Fashing 1976a). Field observations also reveal no direct correlation between adverse conditions and hypopal formation. The relative incidence of hypopi in treeholes in areas of predominantly red oak, the leaves of which are known to be of limited nutritional value for *N. arboricola*, is no higher than in areas where the predominant tree species have leaves of high nutritional value (Fashing 1976a). In the same treehole, one can find some protonymphs transforming into hypopi and others into tritonymphs. This occurs even in treeholes with substantial numbers of hypopi. These treeholes will continue to support mite populations throughout the rest of the year and in subsequent years. It is also interesting that hypopi not encountering a host simply transform to tritonymphs after a period of time even though they are still in the same treehole in which they previously transformed to hypopi (Fashing 1976a).

All evidence, both field and laboratory, therefore indicates that adverse environmental conditions do not induce hypopal formation in *N. arboricola*. Although

H. mallotae has not been studied as extensively, evidence to date indicates that it follows the same pattern as *N. arboricola*. This pattern makes sense when one considers the water-filled treehole habitat in which these species live. Once a treehole is formed, it remains a part of the forest ecosystem for a number of years, both in location and in physical characteristics. Fish (1983) estimated the turnover time for treeholes in an oak woodlot in Indiana to be approximately 10 years. My estimate for both eastern Kansas and eastern Virginia is 15–20 years. In either case, treeholes provide a reasonably permanent and stable habitat for an arthropod.

The stability of habitat might also be indirectly inferred from the relatively large number of obligate inhabitants (Snow 1949). Treehole inhabitants are guaranteed a recurring food supply from the autumn leaf fall, and such resource replenishment occurs simultaneously in all treeholes in a given geographic area. In addition, environmental stress in any locality would probably also be shared equally.

To disperse in response to adverse conditions would not be beneficial since a dispersing mite would almost certainly encounter similar adverse conditions in another proximate treehole (Fashing 1976a). The answer to the question concerning the evolution of dispersal behavior in *N. arboricola* and *H. mallotae* may lie in the degree of permanence of the water-filled treehole habitat. In this environment, selection would favor dispersal when conditions are optimal, thus maximizing the success of the dispersers. It can be hypothesized that the hypopi of these two species have evolved to serve purely as dispersal agents for colonization and outcrossing, not as agents to escape a declining environment (Fashing 1976a). This is probably also true for the insect hosts on which the mites are phoretic; the adults of the eristaline syrphid flies *Mallota posticata* and *M. bautias*. The larvae of these flies are "rat-tailed" maggots which inhabit the lower levels of leaf debris in water-filled treeholes (Fig. 7.1). Adults are present only in May and June, and hypopi utilize female flies for dispersal. Female flies return to treeholes to oviposit, while males seldom reenter treeholes and are therefore ineffective agents for dispersal (Fashing 1976a).

Evidence to date indicates that only females of *H. mallotae* disperse as hypopi. Of 19 hypopi reared to adults, all were female (Fashing, unpublished). In all histiostomatid mites thus far examined, sex is determined by arrhenotoky with fertilized eggs being female and unfertilized eggs male (Norton et al. 1992), and *H. mallotae* is no exception (Fashing, unpublished). If individuals developing from hypopi are arrhenotokous females, it is not necessary for both sexes to disperse since female dispersers can produce male offspring which in turn mate with them. It is of interest that the development to adulthood of *H. mallotae* reared at 25°C is significantly faster for males than for females (males, mean = 14.8 days; females, mean = 19.8 days) (Fashing, unpublished). Since there are usually many dispersers on a fly, it is improbable that a female migrant will mate with her own sons.

In *N. arboricola* sex is determined by diplo-diploidy, thereby necessitating simultaneous dispersal by males and females. Unlike *H. mallotae*, the immature development rate is not significantly different for the two sexes (Fashing 1975b).

Little is known concerning dispersal in *A. pennsylvanicus*. Like other known members of the subfamily Algophaginae, the hypopus (deutonymph) is absent from its life cycle. Which instar(s) is used for dispersal is unknown. Evidence to date indicates, however, that even without a hypopal stage, *A. pennsylvanicus* may be as efficient at dispersal as *N. arboricola* (Fashing unpublished).

4. Life-History and Reproductive Patterns

The life-history patterns of obligate treehole astigmatid mites are probably best introduced by stating that they emulate those of species referred to ecologically as "*K*-selected" (Pianka 1970) or "equilibrium species" (Albert 1983).

There have been a number of critical appraisals of *r*- and *K*-selection theory in recent years (e.g. Stearns 1977, Ito 1980, Boyce 1984, Begon 1985). It is not my intent to provide yet another appraisal concerning the limitations of this theory nor to accept or refute it, but rather to use its well known correlates (Pianka 1970) as a convenient focal point for discussion of treehole astigmatid mites (Table 7.2). A comparison among species or populations is necessary to label an attribute as "*r*-selected" or "*K*-selected" (Force 1975), and such relative statements of selection must involve organisms of similar type (Begon and Mortimer 1986). I will therefore make comparisons whenever possible, and such comparisons will be made with "peer species"; that is, other free-living astigmatid mites. It should be pointed out, however, that detailed life-history studies of astigmatid mites have dealt primarily with pest species and that such species tend to have *r*-type life histories. My comparisons are therefore mainly with so called "*r*-selected species" (Tables 7.3 and 7.4). OConnor (this volume) provides life-history data for several additional species I did not include since only limited data is available concerning their biologies. When more is learned concerning their life histories, it may well turn out that several are "*K*-selected" species.

4.1 Survivorship Curves

K-type species typically demonstrate a Type I survivorship curve (= low mortality until old age) or Type II survivorship curve (= constant mortality rate for all age groups) (Deevey 1947). An *r*-type species, on the other hand, has a characteristic Type III survivorship curve (= high mortality in young age groups) (Deevey 1947).

Survivorship curves have been determined for *Naiadacarus arboricola* and *Algophagus pennsylvanicus*; the former exhibits a Type I curve (Fashing 1975b) and the latter exhibits a curve intermediate between Type I and Type II (Fashing and Campbell, unpublished). As far as I know, however, all investigations on

Table 7.2. Some Correlates of r- *and* K-*Selection as Related to Tree-Hole Astigmatid Mites: Generalities Adapted from Pianka (1970).*

	r-Selection	*K*-Selection
Climate and Habitat:	Variable and/or Unpredictable (Uncertain)	Fairly Constant and/or Predictable (More Certain)
Mortality:	Often Catastrophic, Nondirected Density-independent	More Directed, Density-dependent
Survivorship:	Often Type III (Deevey 1947)*	Usually Type I and II (Deevey 1947)*
Population Size:	Variable in Time Nonequilibrium Usually Well Below Carrying Capacity Of Environment Unsaturated Communities (or portions thereof) Recolonization Each Year Ecological Vacuums	Fairly Constant in Time Equilibrium At or Near Carrying Capacity of Environment Saturated Communities No Recolonization Necessary
Intraspecific and Interspecific Competition:	Variable, Often Lax	Usually Keen
Selection favors:	1) Rapid Development 2) High r_{max} 3) Early Reproduction 4) Small Body Size 5) Single Reproduction	1) Slower Development 2) Lower Resource Thresholds 3) Delayed Reproduction 4) Larger Body Size 5) Repeated Reproduction 6) Parental Care 7) Greater Competitive Ability
Length of life:	Usually Shorter	Usually Longer
Leads to:	High Productivity	High Efficiency

* Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.* 22: 283–314.

mortality of astigmatid mites have been conducted in the laboratory under restricted conditions. Given this fact, it may be unrealistic to use these lab-derived survivorship curves for comparison (also see arguments of Norton, this volume). Under optimal conditions in the laboratory, all species, whether *r*- or *K*-type, would almost certainly demonstrate Type I or II curves. Likewise, given a poor nutritional source for the same species, a Type III and even a Type IV curve (Slobodkin 1964) could be generated (see Fashing 1975b for a discussion of the influence of diet on *N. arboricola*). Survivorship data collected on field populations would clearly be more meaningful, but such data is not available and would be quite difficult (if not impossible) to generate.

Table 7.3. Comparative Life History Data for Various Free-living Astigmatid Mite Species. Data Other than Egg Mortality is Expressed as Means. Time Periods in Days. NG = Not Given; NA = Not Applicable. ▶ = Treehole species.

Taxon (Diet)	°C	Egg→ Larva 1	Larva→ Adult 2	% Egg Mort. 3	Pre-Repro. Period 4	1st Repro. 5	Repro. Period 6	Tot. # Eggs 7	Eggs/ Day 8	Longev. 9	References
ALGOPHAGIDAE											
▶*Algophagus pennsylvanicus* (*Fusarium oxysporum*)	25°	NA	17.9	0.0	6.5	24.4	11.0	18	1.6	44.2	Fashing & Campbell (unpublished)
HISTIOSTOMATIDAE											
Histiostoma polypori (Decomposing insects & plants)	26°	0.9	2.4	NG	1.0	4.3	6.0	74	15.9	14.1	Behura (1957)
▶*Hormosianoetus mallotae* (Microbes on Green Ash leaves)	25°	NA	19.2	0.0	NG	NG	NG	NG	NG	73.0**	Fashing (unpublished)
ACARIDAE											
Acarus siro	20°	4.9	NG	12.5	2.0	NG	23.6	634	26.9	28.1*	Cunnington (1985)
(Wheat germ)	25°	4.2	NG	18.9	1.0	NG	16.9	365	21.9	20.2*	
Histiogaster arborsignus (Brewer's yeast)	23°	4.0	10.1	NG	NG	NG	NG	715	21.9	46.7	Woodring (1969)
H. rotundus (Brewer's yeast)	23°	4.0	8.0	NG	NG	NG	NG	771	29.1	38.5	Woodring (1969)
▶*Naiadacarus arboricola*	20°	NA	30.2	0.0	11.4	41.6	55.5	35	0.6	214.6	Fashing (1975b)
(20°, 25°[1]=Green Ash;	25°[1]	NA	17.0	0.0	8.2	25.2	43.3	62	1.4	82.8	
25°[2]=American Elm;	25°[2]	NA	17.2	0.0	7.3	24.5	57.6	132	2.3	101.7	
25°[3]=Bitternut Hickory leaves)	25°[3]	NA	15.2	0.0	6.8	22.0	97.0	85	0.9	133.1	
Rhizoglyphus echinopus (Dead mealworms)	23°	5.0	11.2	NG	NG	NG	NG	285	13.4	39.5	Woodring (1969)
R. robini (Bot & Meyer's medium)	27°	3.8	7.2	18.6	0.9	11.8	25.6	661	25.8	42.2	Fashing & Hefele (1991)
Sancassania anomalus	15°	6.5	8.3	48.0	3.9	18.7	NG	NG	NG	NG	Pillai & Winston (1969)
(*Escherichia coli*/Bonner's	20°	3.6	6.2	27.8	2.1	12.1	21.4	738	34.5	31–45	
medium)	25°	3.9	5.4	21.8	NG	NG	NG	NG	NG	NG	
	30°	2.4	3.6	50.0	1.3	7.3	NG	NG	NG	NG	

ACARIDAE											
Sancassania anomalus (Dead mealworms)	23°	3.0	6.5	NG	2.0	11.5	NG	930	45.0	32.9	Woodring (1969)
S. rodriguezi (Xenic diet)	25°	2.4	5.6	25.0	1.5	9.6	12.5	588	47.1	23.6	Rodriguez & Stepien (1973)
Schwiebia falticus (Brewer's yeast)	23°	2.0	9.2	NG	NG	NG	NG	155	4.5	46.2	Woodring (1969)
S. rocketti (Brewer's yeast)	23°	2.0	11.2	NG	NG	NG	NG	125	3.9	45.5	Woodring (1969)
Suidasia nesbitti (Wheat germ)	28°	3.2	9.7	4.0	NG	NG	8.3	140	16.9	29.2	Mathur and Dalal (1989)
Tyrophagus putrescentiae	20°	8.0	9.1	26.0	3.1	20.2	29.1	276	9.4	44.2	Rivard (1961a, 1961b)
(Aspergillis)	25°	5.3	7.3	44.5	2.1	14.7	23.2	255	11.0	27.8	
	30°	4.8	6.0	49.5	1.9	12.7	10.8	101	9.4	19.0	
T. putrescentiae (Wheat Flour+Yeast)	27°	4.5	9.5	6.5	2.2	16.2	11.8	118	10.0	NG	Kumud & Mathur (1989)
CARPOGLYPHIDAE											
Carpoglyphus lactus	20°	4.0	8.0	11.0	NG	NG	NG	261	NG	33.0	Chmielewski (1971)
(Brewer's yeast)	25°	3.0	6.0	14.0	2.0	11.0	NG	278	NG	29.0	
	30°	3.0	6.0	15.0	NG	NG	NG	76	NG	20.0	
GLYCYPHAGIDAE											
Glycyphagus destructor (Wheat germ + Baker's yeast)	25°	4.1	12.2	49.0	3.2	19.5	28.8	140	4.9	39.1	Chmielewski (1987)
Glycyphagus domesticus (Wheat germ + Baker's yeast)	25°	4.2	14.7	63.0	3.7	22.6	18.1	51	3.3	35.1	Chmielewski (1988)
PYROGLYPHIDAE											
Dermatophagoides pteronyssinus	23°	8.1	25.6	14.0	~4	38.0	26.2	68	2.8	56.8	Arlian *et al.* (1990)
(Animal Protein + Yeast)	35°	3.9	11.1	13.0	<2	17.0	11.6	48	4.3	26.6	

*Adult longevity,

**Maximum observed.

Table 7.4. Comparative Statistics on the Population Dynamics of Various Astigmatid Mites.

Species (Diet)	°C	r_m (Days)	λ(Days)	λ(Weeks)	References
Acotyledon formosani (Wax moth medium)**	25°	0.46	1.59	25.20	Phillipsen & Coppel (1977)
Carpoglyphus lactus	20°	0.23	1.26	4.93	Chmielewski (1971)
(Baker's yeast)	25°	0.29	1.34	7.61	
	30°	0.23	1.26	4.93	
Glycyphagus destructor (Wheat germ & yeast)	25°	0.13	1.13	2.41	Chmielewski (1987)
Glycyphagus domesticus (Wheat germ & yeast)	25°	0.12	1.12	2.25	Chmielewski (1988)
Rhizoglyphus robini (Garlic)	27°	0.22	1.24	4.60	Gerson et al. (1983)
(Peanuts)	27°	0.29	1.33	7.35	
(Bot & Meyer's medium*)	27°	0.26	1.29	5.98	Fashing & Hefele (1991)
Sancassania berlesi (Artificial diet)	25°	0.38	1.46	13.85	Rodriguez & Stepien (1973)
Tyrolichus casei (Wheat bran & yeast)	30°	0.36	1.43	12.00	Nangia & ChannaBasavanna (1989)
Tyrophagus putrescentiae	28°	0.20	1.22	4.10	Barker (1967)
(Brewer's yeast)	30°	0.27	1.30	6.41	
	32°	0.33	1.39	9.92	
	34°	0.21	1.23	4.24	
Naiadacarus arboricola					
(Green Ash leaves)	25°	0.09	1.09	1.86	Fashing (1975b)
(American Elm leaves)	25°	0.12	1.12	2.25	
(Bitternut Hickory leaves)	25°	0.10	1.10	2.01	
Algophagus pennsylvanicus *(Fusarium oxysporum)*	25°	0.07	1.07	1.60	Campbell & Fashing (unpublished)

* Bot and Meyer 1969.

** Beck 1960.

4.2 Life-History Parameters

Long life, slow immature development, delayed onset of reproduction and low fecundity are attributes of *K*-type species. Table 7.3 compares these demographic statistics, where known, for three treehole species (*N. arboricola*, *A. pennsylvanicus*, and *H. mallotae*) with a number of mostly *r*-type free-living astigmatid species.

N. arboricola demonstrates much greater longevity than other free-living astigmatid mites (Table 7.3, column 9), and *A. pennsylvanicus* and *H. mallotae* are at the high end of the longevity range. All three treehole species demonstrate an exceptionally long development time as immatures (column 2). The time interval from adult molt to first reproduction (prereproductive period; column 4) is considerably longer for both *N. arboricola* and *A. pennsylvanicus*. This coupled with a long immature development extends the period before first reproduction dramatically (column 5), thus constituting a delayed reproduction when compared to the other species. At least part of the delay is due to larviparity, a characteristic shared by all three treehole species (Fashing 1975a). Most astigmatid mites are oviparous, with a comparatively long embryonic development taking place outside the mother's body (column 1). Egg mortality can be high in oviparous species (column 3), but this source of mortality is virtually eliminated in larviparous species. Larviparity might be considered a type of parental care since eggs are retained within the mother until hatching; parental care is yet another characteristic of *K*-type species.

4.3 Fecundity

Relative fecundity is quite low in *N. arboricola* and *A. pennsylvanicus*. For both, the average number of young produced per day (Table 7.3, column 8) and over a lifetime (column 7) fall well below that for the *r*-type species. In fact, the maximum number of young produced by *N. arboricola* over a 24-hour period was nine (Fashing 1979). In contrast, 35 has been recorded for *Sancassania anomalus* (Pillai and Winston 1969), 47 for *S. rodriguezi* (Rodriguez and Stepien 1973), and 52 for *Rhizoglyphus robini* (Gerson et al. 1983).

The above demographic characteristics can be summarized using the intrinsic rate of increase, r_m (Birch 1948). *K*-type species are typified by a low rate of increase and *r*-type by a high rate. The rates of increase for the two treehole inhabiting species (*N. arboricola* and *A. pennsylvanicus*) are quite low in comparison to most other species (Table 7.4). Such information can also be summarized using the finite rate of increase (lambda = factor by which the population increases during a time interval) (Table 7.4). To put this into perspective, in one week under optimal laboratory conditions a population of *R. robini* would increase 7.35 times, *Carpoglyphus lactus* 7.61 times, *Tyrophagus putrescentiae* 9.92

times, *Tyrolichus casei* 12.0 times, and *Sancassania rodriguezi* 13.85 times.[1] In the same time interval, however, a population of *N. arboricola* would increase only 2.25 times and one of *A. pennsylvanicus* only 1.60 times. It is quite apparent that the reproductive pattern of treehole astigmatid mites results in a low reproductive potential relative to most other astigmatid mites.

4.4 Survival during Periods of Starvation

The ability to endure periods with limited food resources is yet another life-history trait of *K*-type species. As discussed above, autumn-shed leaves are the primary energy source for the treehole and this source is often depleted by late summer. In addition, treehole species may be unable to feed during periods when lack of rain has eliminated "free water" in the treehole. *N. arboricola*, the only treehole species studied in this regard, is adapted to withstand long periods without food. In laboratory experiments at 25°C, the average longevity without food for the various instars was found to be: tritonymph 83 days, protonymph 52 days, male 37 days, female 37 days, and larva 10 days (Fashing 1976b). In contrast, instars of *C. lactus* maintained at optimal temperature and humidity (25°C, 85% RH) without food had much lower longevities: tritonymph 15 days, protonymph seven days, adults 29 days, and larva five days (Chmielewski 1971). It is clear that *N. arboricola* is well adapted to cope with these stressful and cyclic levels of food availability.

4.5 Habitat and Niche Breadth

Habitat characteristics of *r*- and *K*-type species also differ. Generally, *r*-type species utilize transient and unpredictable habitats. They also tend to be opportunistic, often feeding on a wide range of substrata and under a wide range of environmental conditions. *T. putrescentiae* may be found almost anywhere that humidity is high and fungus is present. This species has been observed feeding and reproducing on fungi, lichens, algae, grass clippings, and dead or injured mites, as well as on live nematodes (Walter et al. 1986). In addition, it has been reared at temperatures as low as 10°C and as high as 35°C (Cunnington 1969). *Schwiebea rocketti* was observed to feed on decaying root material, decomposer fungi, nematode-destroying fungi, and small soil invertebrates including nematodes and protozoa (Walter and Kaplan 1990). *C. lactus* has been reared at temperatures from 3°C–45°C (Chmielewski 1971), *Acarus siro* from 5°C–30° C (Cunnington 1965, 1985), and *R. robini* from 16°C–35°C (temperatures below

[1] *Acotyledon formosani* has been reported to have extremely high rates of increase (see Table 7.4); e.g. it can increase its population by over 25 times in one week. However, careful examination of the published life-history data (immature mortality 41%, immature development time 9.6 days, oviposition period 14.6 days, oviposition rate 7.8 eggs/day, etc.) suggests an error was probably made in calculating the intrinsic and finite rates of increase.

16°C were not attempted) (Gerson et al. 1983). Such *r*-type species have a wide niche breadth in regard to habitat, range of diet, and temperature tolerance.

Obligate treehole astigmatid mites appear to have a much narrower niche breadth. They inhabit only water-filled treeholes, and their diet range is more restricted. *N. arboricola*, the only species studied in regard to temperature effects, has a very restricted range for immature development. It has been reared successfully only at 20°C and 25°C. At 30°C molting is inhibited and death occurs, and at 15°C development occurs only to the tritonymphal instar (Fashing 1975b). *K*-type species evolve toward specialization in order to more efficiently utilize their habitat. Treehole astigmatid species certainly fit this pattern.

Not all of the potential ecological correlates in Table 7.2 can be addressed in this discussion. Some correlates are not addressed due to lack of basic information. We know little concerning population trends of treehole mites (e.g. equilibrium vs. nonequilibrium), and most sources of natural mortality are unknown. We do know, however, that egg mortality is virtually eliminated due to larviparity, and there are no known predators of mites in North American treeholes (Fashing 1975a). Only one density independent source of mortality is actually known for treehole mite species; the extended period of drought leading to complete drying of a treehole. However, except in treeholes which collect only a small volume of water, this source of mortality is probably rare.

Other correlates yet unstudied include inter- and intra-specific competition. It is thought, through the examination of mouthpart morphology, that there is little (if any) interspecific competition for food among the three species of treehole mites discussed. *H. mallotae* is a collector, *A. pennsylvanicus* is a scraper/collector, and *N. arboricola* is a shredder. Among the treehole inhabitants there are, however, insect larvae in all three of the above functional feeding groups (collectors, shredders, and scrapers) (Merritt and Cummins 1978). Acarine-insect competition and resource partitioning has not yet been studied.

Body size does not seem important when comparing peer species. In fact, in mites a large female body size often indicates the production of a large number of eggs and might thus even be associated with an *r*-rather than a *K*-type species. Since even the longest lived free-living astigmatid species are univoltine and most are multivoltine, the correlate of single vs. repeated reproductions is meaningless.

5. Summary

Due to their small size, it is quite difficult, if not impossible, to gather reliable life-history data from natural populations of most astigmatid species and such data is generally obtained from laboratory populations. Some caution must therefore be taken when interpreting it in light of natural populations. Laboratory data does provide, however, information on the known upper potential of a given species and a comparison of such potentials between species is valid even if they are never realized in nature.

While Pianka's (1970) correlates of *r*- and *K*-selection provide a convenient means for describing the life-history and reproductive pattern of a species, they do not constitute a currently accepted model for life-history evolution.[2] Over the past two decades, a number of theories for life-history evolution have been proposed, but all have their limitations. Each species has its own unique adaptive response to its entire environment and perhaps a single all encompassing model cannot be achieved without making it so simplistic as to be useless. To reiterate Parry (1981), there are many dimensions to a life-history pattern, and life histories can be shaped by constraints imposed by many factors including seasonality, habitat stability, severe climatic stresses, predation, and the need for dispersal. It is my opinion that the relatively permanent (stable) and seasonal but predictable habitat of the water-filled treehole has been extremely influential in shaping the *K*-type life-history pattern observed in the astigmatid inhabitants.

Most astigmatid mites studied thus far exploit habitats which are ephemeral and unpredictable, thus leading to *r*-type life-history patterns. In this regard, many, if not most, of these species are opportunists with a wide niche breadth. In contrast, *N. arboricola*, *A. pennsylvanicus* and *H. mallotae* are specialists with much narrower niche breadths, utilizing only water-filled treeholes as a habitat. The obligate treehole inhabiting astigmatid mites studied thus far are unique in many ways, and it will be interesting to discover whether all treehole mites worldwide exhibit similar patterns once they are studied in detail. In this regard, the two Australian algophagid species are of special interest due to the presence of predators in the treeholes.

Acknowledgments

I thank Barry M. OConnor and Robert F. C. Naczi, University of Michigan, for information concerning the distribution of treehole mites in North America, and Roger Kitching, University of New England, Armidale, N. S. W., Australia, for specimens of Australian treehole mites. Special appreciation goes to Dr. Gisela Fashing, Virginia Department of Health, for critically reading the manuscript, and to Jewel Thomas, College of William and Mary, for her technical assistance. And finally, I thank Marilyn Houck, Texas Tech University, for her critical reading and editing. Some of the research leading to the development of ideas expressed in this paper was supported by grants from the College of William and Mary. The original manuscript was written while the author was on a William and Mary Faculty Semester Research Assignment.

[2]Those that do accept *r*- and *K*-selection as a useful concept restrict its meaning to that originally intended by McArthur and Wilson (1967); the term *r*-selection restricted to selection for high population growth in uncrowded populations and *K*-selection to competitive ability in crowded populations (see Parry 1981 for details).

References

Albert, A. M. 1983. Life cycle of Lithobiidae—with a discussion of the *r*- and *K*-selection theory. *Oecologia* 56:272–279.

Arlian, L. G., C. M. Rapp and S. G. Ahmed. 1990. Development of *Dermatophagoides pteronyssinus* (Acari: Pyroglyphidae). *J. Med. Entomol.* 27:1035–1040.

Barker, P. S. 1967. The effects of high humidity and different temperatures on the biology of *Tyrophagus putrescentiae* (Schrank) (Acarina: Tyroglyphidae). *Can. J. Zool.* 45:91–96.

Barlocher, F. and B. Kendrick. 1973. Fungi in the diets of *Gammarus pseudolimnaeus* (Amphipoda). *Oikos* 24:295–300.

Beck, S. D. 1960. Growth and development of the Greater Wax Moth, *Galleria mellonella* (L.) (Lepidoptera: Galleriidae). *Trans. Wis. Acad. Sci. Arts Lett.* 49:137–148.

Begon, M. 1985. A general theory of life-history variation. In: *Behavioral Ecology* (R. M. Sibley and R. H. Smith eds.). Blackwell Sci. Publ., Boston. Pp. 91–97.

Begon, M. and M. Mortimer. 1986. *Population Ecology, a Unified Study of Animals and Plants*. Blackwell Sci. Publ., Boston. 220 pp.

Behura, B. K. 1957. The life history of *Histiostoma polypori* (Oud.) (Acari: Tyroglyphidae). *J. NY Entomol. Soc.* 65:51–78.

Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.* 17:15–26.

Bot, J. and M. Meyer. 1969. An artificial rearing medium for acarid mites. *J. South Afr. Entomol. Soc.* 29:199.

Boyce, M. S. 1984. Restitution of *r*- and *K*-selection as a model of density-dependent natural selection. *Annu. Rev. Ecol. Syst.* 15:427–447.

Carpenter, S. R. 1982. Stemflow chemistry: effects on population dynamics of detritivorous mosquitoes in tree-hole ecosystems. *Oecologia* 53:1–6.

Chmielewski, W. 1971. Morfologia, biologia i ekologia *Carpoglyphus lactus* (L., 1958) (Glycyphagidae, Acarina). *Pr. Nauk. IOR, Pozan* 13:63–166.

Chmielewski, W. 1987. Parameters of population development of *Glycyphagus destructor* (Schr.) (Acarida, Glycyphagidae)-mite species found in bee-hives. *Pszyr. Zesz. Nauk.* 31:213–221.

Chmielewski, W. 1988. Biological potential of house mite—*Glycyphagus domesticus* (DeGeer) (Acarida, Glycyphagidae)—a pest of pollen and bee bread. *Pszyr. Zesz. Nauk.* 32:169–180.

Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10:147–172.

Cunnington, A. M. 1965. Physical limits for complete development of the grain mite, *Acarus siro* (Acarina, Acaridae), in relation to its world distribution. *J. Appl. Ecol.* 2:295–306.

Cunnington, A. M. 1969. Physical limits for complete development of the copra mite,

Tyrophagus putrescentiae (Schrank) (Acarina, Acaridae). In: *Proc. 2nd Int. Congr. Acarol.* (G. O. Evans ed.). Sutton Vonington, England, 1967. Akadémiai Kaidó, Budapest. Pp. 241–248.

Cunnington, A. M. 1985. Factors affecting oviposition and fecundity in the grain mite *Acarus siro* L. (Acarina: Acaridae), especially temperature and relative humidity. *Exp. Appl. Acarol.* 1:327–344.

Cutcher, J. J. and J. P. Woodring. 1969. Environmental regulation of hypopial apolysis of the mite, *Caloglyphus boharti*. *J. Insect Physiol.* 15:2045–2057.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. *Q. Rev. Biol.* 22:283–314.

Edwards, P. B. 1988. Field ecology of a brood-caring dung beetle *Kheper nigroaeneus*-habitat predictability. *Oecologia* 75:527–534.

Fashing, N. J. 1973. The post-embryonic stages of a new species of *Mauduytia* (Acarina: Anoetidae). *J. Kans. Entomol. Soc.* 46:454–468.

Fashing, N. J. 1974. A new subfamily of Acaridae, the Naiadacarinae, from water-filled treeholes (Acarina: Acaridae). *Acarologia* 14:166–181.

Fashing, N. J. 1975a. Life history and general biology of *Naiadacarus arboricola* Fashing, a mite inhabiting water-filled treeholes (Acarina: Acaridae). *J. Nat. Hist.* 9:413–424.

Fashing, N. J. 1975b. Influence of temperature and food on development and population dynamics of *Naiadacarus arboricola* Fashing (Acarina: Acaridae). *Acarologia* 17:138–152.

Fashing, N. J. 1976a. The evolutionary modification of dispersal in *Naiadacarus arboricola* Fashing, a mite restricted to water-filled treeholes (Acarina: Acaridae). *Am. Midl. Nat.* 95:337–346.

Fashing, N. J. 1976b. The resistant tritonymphal instar and its implications in the population dynamics of *Naiadacarus arboricola* Fashing (Acarina: Acaridae). *Acarologia* 18:704–714.

Fashing, N. J. 1979. *Naiadacarus arboricola*, a "*K*-selected" acarid mite. In: *Recent Advances in Acarology*, Vol. 1 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 525–529.

Fashing, N. J. and L. L. Wiseman. 1980. *Algophagus pennsylvanicus*—a new species of Hyadesidae from water-filled treeholes. *Int. J. Acarol.* 6:79–84.

Fashing, N. J. and D. L. Middleton. 1983. Notes on the biology of *Algophagus pennsylvanicus*, a mite inhabitant of water-filled treeholes. *VA J. Sci.* 34: 128.

Fashing, N. J. and W. J. Hefele. 1991. Biology of *Rhizoglyphus robini* (Astigmata: Acaridae) reared on Bot and Meyer artificial medium. In: *Modern Acarology*, Vol. 2 (F. Dusbábek and V. Bukva eds.). Academia, Prague and SPB Academic Publ., The Hague. Pp. 499–503.

Fashing, N. J. and D. M. Campbell. 1992. Observations on the feeding biology of *Algophagus pennsylvanicus* (Astigmata: Algophagidae), a mite restricted to water-filled treeholes. *Int. J. Acarol.* 18:77–81.

Fish, D. 1983. Phytotelmata: Flora and Fauna. In: *Phytotelmata: Terrestrial Plants as*

Hosts for Aquatic Insect Communities (J. H. Frank and L. P. Lounibos eds.). Plexus Publ., Medford, NJ. Pp.1–27

Fish, D. and S. R. Carpenter. 1982. Leaf litter and larval mosquito dynamics in tree-hole ecosystems. *Ecology* 63:283–288.

Force, D. C. 1975. Succession of *r* and *K* strategists in parasitoids. In: *Evolutionary Strategies of Parasitic Insects and Mites* (P. W. Price ed.). Plenum Press, NY. Pp. 112–129.

Frank, J. H. and L. P. Lounibos. 1983. *Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities*. Plexus Publ., Medford, NJ. 293 pp.

Gerson, U., S. Capua and D. Thorens. 1983. Life history and life tables of *Rhizoglyphus robini* Claparede (Acarai: Astigmata: Acaridae). *Acarologia* 24:439–448.

Houck, M. A. and B. M. OConnor. 1991. Ecology and evolutionary significance of phoresy in the Astigmata. *Annu. Rev. Entomol.* 36:611–636.

Hughes, T. E. 1953. The functional morphology of the mouth parts of the mite *Anoetus sapromyzarum* Dufour, 1839, compared with those of the more typical sarcoptiformes. *Proc. Acad. Sci. Amst.* 56C:278–287.

Ito, Y. 1980. *Comparative Ecology*. Cambridge Univ. Press, NY. 436 pp.

Kamud and R. B. Mather. 1989. Influence of ultraviolet radiation on the survival of the acarid mite, *Tyrophagus putrescentiae* (Astigmata: Acaridae). In: *Progress in Acarology*, Vol. 2 (G. P. ChannaBasavanna and C. A. Viraktamath eds.). Oxford and IBH Publ. Pvt. Ltd., New Delhi. Pp. 249–253.

Kaushik, N. K. and H. B. N. Hynes. 1971. The fate of dead leaves that fall into streams. *Arch. Hydrobiol.* 68:465–515.

Kitching, R. L. 1971. An ecological study of water-filled treeholes and their position in the woodland ecosystem. *J. Anim. Ecol.* 40:281–302.

Kitching, R. L. 1987. Spatial and temporal variation in food webs in water-filled treeholes. *Oikos* 48:280–288.

Kitching, R. L. and C. Callaghan. 1982. The fauna of water-filled tree holes in box forest in south-east Queensland. *Aust. Entomol. Mag.* 8:61–70.

Kitching, R. L. and S. L. Pimm. 1985. The length of food chains: phytotelmata in Australia and elsewhere. *Proc. Ecol. Soc. Aust.* 14:123–140.

Krantz, G. W. 1978. *A Manual of Acarology*, 2nd ed. Oregon State Univ. Book Stores, Corvallis, OR. 509 pp.

Lacky, J. B. 1940. The microscopic flora and fauna of tree holes. *Ohio J. Sci.* 40:186–192.

MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, NJ. 203 pp.

Mathur, S. and M. Dalal. 1989. Influence of food quality on the development and growth of the acarid mite, *Suidasia nesbitti* (Acari: Acaridae). In: *Progress in Acarology*, Vol. 2 (G. P. ChannaBasavanna and C. A. Viraktamath eds.). Oxford and IBH Publ. Pvt. Ltd., New Delhi. Pp. 231–239.

Merritt, R. W. and K. W. Cummins. 1978. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Publ., Dubuque, IA. 441 pp.

Nangia, N. and G. P. ChannaBasavanna. 1989. Influence of temperature and relative humidity on the development of *Tyrolichus casei* (Astigmata: Acaridae). In: *Progress in Acarology*, Vol. 2 (G. P. ChannaBasavanna and C. A. Viraktamath eds.). Oxford and IBH Publ. Pvt. Ltd., New Delhi. Pp. 259–264.

Norton, R., J. B. Kethley, D. E. Johnston and B. M. OConnor. 1992. Phylogenetic perspectives on genetic systems and reproductive modes of mites. In: *Evolution and diversity of sex ratio in insects and mites* (D. Wrensch and M. Ebbert eds.) Chapman and Hall Publ., NY. Pp. 8–99.

OConnor, B. M. 1982a. Acari: Astigmata. In: *Synopsis and Classification of Living Organisms* (S. P. Parker ed.), McGraw-Hill, NY. Pp. 146–169.

OConnor, B. M. 1982b. Evolutionary ecology of astigmatid mites. *Annu. Rev. Entomol.* 27:385–409.

OConnor, B. M. 1984. Acarine-fungal relationships: the evolution of symbiotic associations. In: *Fungus-Insect Relationships: Perspectives in Ecology and Evolution* (G. Wheeler and M. Blackwell eds.). Columbia Univ. Press, NY. Pp. 354–381.

OConnor, B. M. 1989. Systematics, ecology and host associations of *Naiadacarus* (Acari: Acaridae) in the Great Lakes region. *Great Lakes Entomol.* 22:79–94.

Parry, G. D. 1981. The meanings of *r*- and *K*-selection. *Oecologia* 48:260–264.

Phillipsen, W. J. and H. C. Coppel. 1977. *Acotyledon formosani* sp. n. associated with the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Acarina: Acaridae-Isoptera: Rhinotermitidae). *J. Kans. Entomol. Soc.* 50:399–409.

Pianka, E. R. 1970. On *r*- and *K*-selection. *Am. Nat.* 104:592–597.

Pillai, P. R. P. and P. W. Winston. 1969. Life history and biology of *Caloglyphus anomalus* Nesbitt (Acarina: Acaridae). *Acarologia* 11:295–303.

Pimm, S. L. and R. L. Kitching. 1987. The determinants of food chain lengths. *Oikos* 50:302–307.

Rivard, I. 1961a. Influence of temperature and humidity on mortality and rate of development of immature stages of the mite *Tyroglyphus putrescentiae* (Schrank) (Acarina: Acaridae) reared on mold cultures. *Can. J. Zool.* 39:419–426.

Rivard, I. 1961b. Influence of temperature and humidity on longevity, fecundity, and rate of increase on the mite *Tyroglyphus putrescentiae* (Schrank) (Acarina: Acaridae) reared on mold cultures. *Can. J. Zool.* 39:869–976.

Rodriguez, J. G. and Z. A. Stepien. 1973. Biology and population dynamics of *Caloglyphus berlesi* (Michael) (Acarina: Acaridae) in xenic diet. *J. Kans. Entomol. Soc.* 46:176–183.

Rohnert, U. 1950. Wasserfullte Baumhohlen und ihre Besiedlung. Ein Beitrag zur Fauna Dendrolimnetica. *Arch. Hydrobiol.* 44:472–516.

Slobodkin, L. B. 1964. *Growth and Regulation of Animal Populations*. Holt, Rinehart and Winston, NY. 184 pp.

Smith, I. M. and M. S. Harvey. 1989. Description of adult *Arrenurus* (*?Micruracaraus*)

kitchingi sp. nov. (Acarina: Arrenuridae) from water-filled tree holes in Australia. *Can. Entomol.* 121:283–289.

Snow, W. E. 1949. The Arthropoda of Wet Treeholes. Ph.D. dissertation, Univ. Illinois, Urbana, IL. 219 pp.

Snow, W. E. 1958. Stratification of arthropods in a wet stump cavity. *Ecology* 39:83–88.

Stearns, S. C. 1977. The evolution of life-history traits. *Annu. Rev. Ecol. Syst.* 8:145–171.

Suberkropp, K. and M. J. Klug. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* 57:707–719.

Varga, L. 1928. Ein interessanter Biotop der Bioconose von Wasserorganismen. *Biol. Zentralbl.* 48:143–162.

Walter, D. E., R. A. Hudgens and D. W. Freckman. 1986. Consumption of nematodes by fungivorous mites, *Tyrophagus* spp. (Acarina: Astigmata: Acaridae). *Oecologia* 70:357–361.

Walter, D. E. and D. T. Kaplan. 1990. Feeding observations on two astigmatid mites, *Schwiebea rocketti* (Acaridae), and *Histiostoma bakeri* (Histiostomatidae) associated with citrus feeder roots. *Pedobiologia* 34:281–286.

Woodring, J. P. 1969. Observations on the biology of six species of acarid mites. *Ann. Entomol. Soc. Am.* 62:102–108.

8

The Evolution of Parasitism and the Distribution of Some Dermanyssoid Mites (Mesostigmata) on Vertebrate Hosts

Frank J. Radovsky

CONTENTS

1. INTRODUCTION

> Despite the considerable number of species . . . associated with various other animals, there is, however, in only a very limited number of cases any precise knowledge of what the mite does. An urgent need is for an increased knowledge of the biology of the commoner species, for without this it is impossible to arrive at even a relatively true appreciation of the relationships of mites to the general problems of animal ecology.
>
> T. E. Hughes (1959)

> . . . the gaps in knowledge of the bionomics and basic host-parasite relationships are especially glaring. Following a period of considerable interest in the 1950s and early 1960s, there has been a decline in biological studies of the vertebrate-associated Mesostigmata. This important area of research should be revitalized.
>
> F. J. Radovsky (1985)

Whether the subclass Acari is monophyletic or polyphyletic remains unsettled, but the early (pre-Devonian) separation of the orders Parasitiformes and Acariformes is generally accepted (Krantz 1978, Lindquist 1984, Woolley 1988). The suborder Mesostigmata is one of the largest and most ecologically varied of the Acari, and it is the only suborder of Parasitiformes in which there has been significant adaptive radiation into a broad spectrum of general niches. The Mesostigmata associated with vertebrates have notably diverse host relationships, but nearly all are in one superfamily, the Dermanyssoidea.

The importance of using life histories to understand phylogenetic relationships among the dermanyssoid Mesostigmata was first recognized in the 1960s (Bregetova 1964, 1969; Radovsky 1966, 1967, 1969; Evans and Till 1966). Additional information on the life cycles of vertebrate associates in that superfamily is presented here. My principal objective is to clarify the role played by modifications in life-history patterns in inducing taxonomic radiations and new host associations. The correlation between adaptive shifts in life histories and speciation events in this group has previously been discussed, but only cursorily (Radovsky 1985).

After reviewing the plesiomorphic life cycle of dermanyssoids, the vertebrate-host relationships, and the types of life cycles, I treat the origin of parasitism and the history of two related families, Macronyssidae and Rhinonyssidae, to show that taxonomic radiations follow certain adaptive events.

Because most Mesostigmata associated with vertebrates, and nearly all species parasitic on vertebrates, are in the superfamily Dermanyssoidea, this chapter focuses on the evolution of vertebrate parasitism in one of the major acarine suborders. Mesostigmatid associates of invertebrates are also richly represented in the Dermanyssoidea; however, that is not a problem when dealing with the vertebrate associates separately, because the evolutionary lines from free-living dermanyssoids to those associated with invertebrates and vertebrates, respectively, are independent.

Furthermore, that invertebrate/vertebrate separation is reflected in current classification (Table 8.1). It is only in the laelapid subfamily Hypoaspidinae, a stem group from which other dermanyssoids appear to have evolved, that associates of both invertebrates and vertebrates (as well as free-living mites) are classed together. Hypoaspidine associates of vertebrates are basically predatory nidicoles, although some species appear to utilize host-generated food sources opportunistically [e.g. *Hypoaspis sardoa* (Berlese)], and some use nest-building animals for dispersal (Radovsky 1985).

The higher-order classification of the Dermanyssoidea was developed principally by Vitzthum (1940–1943). Subsequent changes resulted, to a large extent, from the recognition of distinctive life cycles as characters appropriate to taxonomic definition at the level of the family group. The classification given here (Table 8.1) agrees in general with Krantz (1978), based primarily on summations by Evans and Till (1966) and Radovsky (1966, 1967, 1969).

The evolutionary sequences of some vertebrate-associated Dermanyssoidea are

Table 8.1. The classification and feeding relationships of the Dermanyssoidea[a].

Taxon	Feeding Relationships
Laelapidae	
Hypoaspidinae	—Free-living; predators in nests of vertebrates or invertebrates; commensals or parasites on invertebrates
Laelapinae	—Facultative or obligatory parasites in nests, principally of mammals
Haemogamasinae	—Facultative or obligatory parasites, nonparasitic predators, or generalists; in nests of mammals
Hirstionyssinae	—Nest parasites of mammals
Myonyssinae	—Nest associates, probably parasitic, of mammals
Mesolaelapinae	—Associated with mammals
Alphalaelapinae	—One species associated with the primitive rodent *Aplodontia rufa*
Melittiphinae	—One species in beehives
Iphiopsinae	—Associated with terrestrial arthropods; includes obligatory parasites
Macronyssidae	
Macronyssinae	—Nest or permanent parasites of mammals, principally bats
Ornithonyssinae	—Nest or permanent parasites of mammals, birds, and reptiles
Rhinonyssidae	—Parasites in the respiratory passages of birds
Halarachnidae	
Halarachninae	—Parasites in the respiratory passages of mammals
Raillietiinae	—Parasites in the external ear of mammals
Ixodorhynchidae	—Parasites of snakes
Omentolaelapidae	—One species parasitic on snakes
Entonyssidae	—Parasites in the respiratory passages of snakes
Dermanyssidae	—Nest parasites of birds (principally) and rodents
Hystrichonyssidae	—One species parasitic on rodents
Spinturnicidae	—Permanent parasites of bats
Dasyponyssidae	—Parasites of armadillos
Manitherionyssidae	—One species parasitic on pangolins
Varroidae	—Nest parasites of honeybees

[a]Subfamilies given for families only where relevant to text.

well suited to host-parasite analysis because of the persistence of intermediate types to modern times. However, it is not necessary to postulate the contemporary existence of ancestral and descendant forms. The extant links are ecological types that have survived because of the continued existence of a suitable general niche. The *general niche* is a functional role in an animal community that can be occupied by various species that are not necessarily taxonomically related (Elton 1966). I postulate, of course, that an intermediate extant form, discussed here to support an evolutionary sequence, is taxonomically related to ancestral forms that occupied the same general niche.

The central thesis of this chapter is that various points of novel adaptation along one extended evolutionary pathway have each been followed by a subsequent major taxonomic radiation. The adaptations relate to (or influence) host-parasite relationships and therefore are more easily discernible than adaptations

to a free-living environment: the parasite and host represent the interaction between only two genotypes, compared to the numerous organisms (hence genotypes) that interact with a free-living animal. That close interaction between host and parasite is the basis for Fahrenholz's Rule, which states that parasites evolve in concert with their hosts so that there is a correspondence in the two evolutionary patterns. Despite many exceptions to the rule, it frequently can provide insight into the history of a parasitic group as well as the history of the host group. For example, a remarkable model of host-parasite coevolution is provided by chewing lice associated with pocket gophers. These interactions have been extensively studied to the benefit of both mammalogists and entomologists (reviewed by Hellenthal and Price 1991). Some parasitologists use the term *host-tracking* for host-parasite interactions that conform to Fahrenholz's Rule and apply the term *resource-tracking* (related to the concept of ecological transfer) for host-parasite patterns that appear to lack consonance (Kethley and Johnston 1975).

2. Life-Cycle Patterns of Dermanyssoids

Dermanyssoid parasitism is permanent (the mite remains on the host throughout its life cycle) or nidicolous (the mite spends part of its life cycle in the nest, roost, or other dwelling but is also found on the host). All endoparasitic mites (e.g. those located in respiratory passages or ear canals) are permanent parasites and leave their internal location only briefly, to transfer between hosts when the hosts are in close contact.

The primitive dermanyssoid life cycle is that of the free-living Mesostigmata: egg, hexapod larva, octopod protonymph, octopod deutonymph, and adult (female and male). Each successive developmental stage shows an increase in the proportion of the idiosomal surface covered by plates (or shields) and an increase in the number of setae on the idiosoma and appendages.

The larva is a nonfeeding stage that has mouthparts too weakly sclerotized to be functional. The protonymph and deutonymph are active feeding stages with sclerotized mouthparts similar to those of the adult female. The most prominent feature of the functional mouthparts is a pair of chelicerae, which are adaptively comparable to the bill of a bird or the teeth of mammals. Each chelicera of free-living females and immatures (other than the larva) has a sturdy shaft tipped by a pair of opposable chelae, one fixed and the other movable. Both chelae are stout and toothed (Fig. 8.1, *Hypoaspis aculeifer*). These chelate-dentate chelicerae are employed in a number of ways, including grasping and penetrating the cuticle of small arthropods during predation. The male chelicera in the free-living type of mite is usually much like that of the female except that the movable chela has an appended spermadactyl, a structure used to transfer sperm packets from the male genital opening to the female (Fig. 8.1) (also see Houck, Chapter 3, this volume).

Table 8.2 shows the range of life cycles occurring in dermanyssoids associated

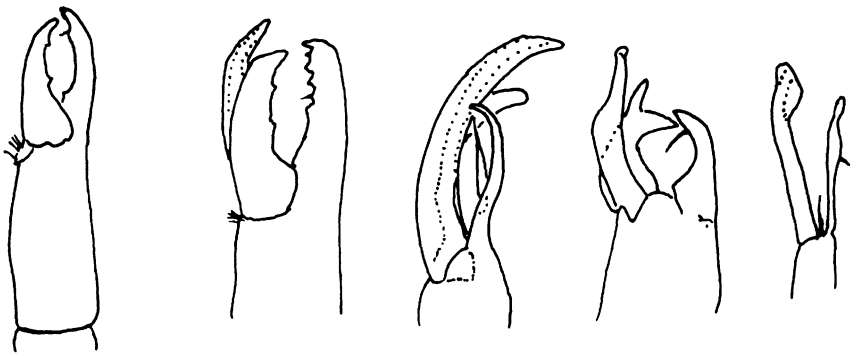


Figure 8.1. Some dermanyssoid chelicerae. Left, *Hypoaspis aculeifer* (Canestrini), female. Other illustrations of male chelae, from left to right: *H. aculeifer, Androlaelaps hirsti* Keegan, *Haemagamasus ambulans* (Thorell), *Haemogamasus liponyssoides* Ewing. Redrawn from various sources.

with vertebrates. These selected examples are in part chosen because of their relevance to the remainder of the chapter. Free-living hypoaspidines and many vertebrate-associated dermanyssoid groups have the primary free-living life cycle as described above, with the larva nonfeeding and all later stages feeding. A majority of the laelapines have this developmental pattern, and so do a number

Table 8.2. Life cycles in Dermanyssoidea associated with vertebrates.

Egg	Larva	Proto-nymph	Deuto-nymph	Adult Female[a]	Examples[b]
HB	NF	FD	FD	FD	Free-living Hypoaspidinae, most Laelapinae, Dermanyssidae
IU	IU	FD	FD	FD	Some Laelapinae, Spinturnicidae
HB	NF	NF	FD	FD	Haemogamasinae (in part)
HB/IU	NF	FD	NF	FD	Macronyssidae, Rhinonyssidae
HB/IU	NF	NF	NF	FD	Halarachnidae

[a]Male excluded because ability to feed, with chelicerae modified for mating, is generally not known.

[b]Not all examples are exclusive but exceptions are rare: e.g. a macronyssid in which the larval stage is entirely intrauterine.

HB = Eggs released into the habitat: in the general environment of free-living mites; nests, roosts, etc. of nidicoles and some parasites; onto the surface of the host or in tissues of some parasites.

IU = Develops in the parental uterus throughout the stage.

NF = Nonfeeding mobile stage.

FD = Feeding and usually requiring food to complete development.

of parasitic dermanyssoid groups. The primary life cycle shows that one sequence of active stages can be correlated with very different biologies, e.g. free-living hypoaspidines and parasitic dermanyssids.

The Dermanyssidae are highly adapted parasites that feed rapidly on the blood of their hosts using long styletiform chelicerae that probably penetrate a venule of the host in a similar fashion to elements of the mosquito fascicle (Radovsky 1969). Nevertheless, mites in this family have retained the same basic life cycle as their free-living ancestors. The dermanyssids may be captives of their specialized mouthparts: the styletiform chelicerae, which have evolved in all feeding stages beginning with the protonymphs, may present a barrier to reversal of a trend and suppression of feeding in any post-larval stage. Although no dermanyssid is known to be a host-restricted parasite or to have suppressed any stage, species such as *Dermanyssus grochovskae* Zemskaya and *D. quintus* Vitzthum tend towards permanent parasitism; they are usually found on birds, attach their eggs to the feathers of their host, have a reduced engorgement capacity, and have strong legs adapted to clinging to volant hosts (Moss 1978). Most dermanyssids are typical blood-sucking nest parasites: (1) they spend most of the time in the nest when not feeding; (2) females represent the dispersal stage and are most often collected on the host; (3) mite eggs are deposited in the host nest (or crevices of roost or under nearby bark); and (4) they have a high engorgement capacity and a very pronounced ability to withstand starvation for months. The last attribute is essential for the survival of nest parasites, particularly those of migrating avian hosts.

Some laelapines illustrate an abbreviation of the general life cycle by the retention of the egg by the female, or by the retention of both the egg and the larva. Thus, they may be larviparous (many facultatively so) presumably depending on nutritional state. Some can deposit either eggs, larvae, or protonymphs, as in the case of *Androlaelaps casalis* (Berlese) (Men 1959).

We should seek a plausible interpretation for the significance of each alteration of the life cycle, in order to understand the evolutionary patterns in these mites. The Dermanyssoidea, in which there is, overall, a rich representation of extant intergradient forms, provide an exceptional opportunity to examine the origins of parasitism and the steps taken from one kind of host-parasite relationship to another. The situation contrasts with fleas, for example, a group for which forms representing intermediates between highly evolved parasites and an ancestral free-living insect have not survived to be observable today.

The adaptive significance of any characteristic is measurable by the degree to which it increases reproductive capacity, decreases mortality, or both. Suppression of the egg or egg and larva by retention in the female protects the developing mite from mortality factors that would otherwise affect those early stages. At the same time, a general consequence of larvipary and nymphipary is the reduction in net reproductive capacity of the mother, because the individual offspring

requires more time *in utero*. However, the nutritional cost to the mother need not be changed by retention of the egg or larva *in utero*, because there is no feeding in those stages.

For those laelapines that are ovoviviparous, there must be a trade off between the elimination of such mortality factors as desiccation and predation directly affecting the delicate and defenseless egg (or egg and larva) and the greater investment per offspring by the female. Most nest mites oviposit, presumably because the reduced reproductive capacity resulting from egg retention counterbalances the protection that that behavior provides.

The highly specialized blood-sucking Spinturnicidae, on the other hand, are uniformly nymphiparous. These mites occur only on bats and usually are restricted to the hairless membranes of the wings and tail, to which they can reliably cling because of specializations in the structure of the body and legs. The spinturnicid ontogeny is fundamentally changed. Evans (1968) studied the development of *Spinturnix myoti* Kolenati and found that the egg was followed by an embryonic prelarva that transformed into a protonymph inside the mother, without forming a larva. By suppressing the egg and larva, the spinturnicid life cycle is restricted to active blood-feeding stages that contribute to maturation or reproduction; the egg and inactive larva that might most easily be lost from the host are eliminated as free stages. However, there are extensive and successful groups of other permanent ectoparasites that retain the inactive stages. For example, both chewing and sucking lice firmly glue their eggs to the host feathers or hair; all nymphal instars as well as adults feed actively and all of them have legs specialized for reliably clinging to the host.

In one large genus, *Haemogamasus*, with more than 40 species, and in some other Haemogamasinae, the protonymph is present in the environment (usually the nest of a rodent or insectivore) but has weakly sclerotized chelicerae and does not feed. *Haemogamasus* is extraordinary in its range of host relations, from polyphagous nest associates to obligatory blood-feeders with chelicerae adapted for puncturing the host's skin.

Only a single species, *Haemogamasus pontiger* (Berlese), has been characterized as facultative in its nest associations, either implicitly by the range of substrates given or explicitly as in Radovsky (1985). However, this species may be adaptively dependent in nature on host and nest associations for its long-term survival. *H. pontiger* is sometimes found on both native rodents and insectivores and on domesticated rodents (*Mus* and *Rattus*). The many other records, which could be thought of as free-living, may be extensions of the nest habitat of domesticated rodents (e.g. barley, rice straw, hay packing, old burlap bagging, and grain spill). The mite may enter these synanthropic habitats from rodent nests or directly from rodents in that environment and survive for some time on such substrates, but the species may be consistently associated with nests and hosts in nature.

For all *Haemogamasus* species then, the rich concentration of food in the nest/host association can account for elimination of feeding in the protonymph. The

female can invest more in each offspring by providing sufficient nutrients in the egg to carry the offspring through to the deutonymphal stage. In those species that have been studied, the nonfeeding stages are brief, typically 1–2 days each for larva and protonymph (Radovsky 1960b). The deutonymph, which may require weeks or months to mature (depending on the status of food in the nest), is more protected than earlier stages by its size, sclerotization, and setation and therefore better able to cope with the hazards of the environment.

Of all the dermanyssoid life cycles, I think the Macronyssidae/Rhinonyssidae specialization is the least likely to have been suspected prior to its discovery. In these two families the protonymph is an active feeding stage and the deutonymph is nonfeeding, relatively inactive, and largely suppressed.[1] Most Macronyssidae are ectoparasites of bats, other mammals, birds, and reptiles. At least in those species that I believe have been adequately studied, the protonymph is a fixed feeder (i.e. it attaches to the host typically for one to several days prior to engorgement). The development that often accompanies such extended feeding is known as neosomy (Audy et al. 1972), which is discussed more fully below, and may lead to unusual levels of engorgement as it does in ixodid ticks. The macronyssid protonymph takes sufficient nutrients so that it can pass through two molts to reach adulthood. The adults of macronyssids apparently are all rapid feeders, engorging in minutes.

The Rhinonyssidae are parasites of respiratory passages of birds, principally the nasal region. They evolved from the Macronyssidae and retain the same life cycle with a feeding protonymph and nonfeeding deutonymph. Internal parasites such as the Rhinonyssidae must have one or more stages that can move between hosts. Adult and protonymphal rhinonyssids are poor transmission stages as they are generally highly specialized as internal parasites and have poorly developed claws and caruncles. The ambulacral apparatus of the deutonymph is reduced in the family as it is most macronyssids. The rhinonyssid larva, however, typically has more robust claws than those of any other stage. Thus, it appears that the larva is the stage that serves for interhost transmission in this family. That is interesting from an evolutionary standpoint, because it is a clear reversal of an adaptive trend. The Ornithonyssinae, from which the Rhinonyssidae arose, all have reduced claws and other ambulacral structures as larvae. However, although

---

[1]Domrow (1987) transferred the genera *Bewsiella* and *Ichoronyssus* from Macronyssidae (Macronyssinae of Domrow) to Laelapinae, giving this rationale: "A deutonymph of *B. fledermaus* (*Hipposideros calcaratus* Dobson, Kukuba Caves, P.N.G, 1.ix 1972, R. L. Vanderwal) shows fully developed functional chelicerae, allowing transfer of this genus (and *Ichoronyssus* on the adult character peritrematal shields setose) from Macronyssinae to Laelapinae." Domrow's proposed action should be deferred pending further study. *Ichoronyssus* is nonfeeding as a deutonymph, based on the nonfunctional chelicerae (Dusbábek 1964), and *Ichoronyssus* and *Bewsiella* have numerous synapomorphies showing that they are closely related. The presence of peritremal plate setae in both of these genera has no bearing on family placement; the Neotropical genus *Parichoronyssus*, which indisputably has a macronyssid life cycle, also has a setose peritremal plate.

reduced, the functional elements of the larval ambulacra have been retained, and apparently they have been readapted for active locomotion in the Rhinonyssidae.

The last family listed (Table 8.2) that exemplifies a distinctive dermanyssoid life cycle is the Halarachnidae. That family now encompasses two groups of endoparasites associated with mammals (Radovsky 1969), a relationship for which there is a clear consensus (Potter and Johnston 1978, Furman 1979, Domrow 1980, Fonseca and Faccini 1985). The Halarachninae occur in the respiratory passages (nares to lungs) of a wide range of mammals. The Raillietiinae are restricted to the ears of bovids.[2] The two subfamilies are similar in life-cycle pattern, with both protonymph and deutonymph being nonfeeding stages and the larva involved in transmission. From a trophic viewpoint, this family is extreme in that all feeding is, or at least can be, concentrated in one stage; sufficient nutrients are stored in the egg to allow complete development with feeding only accomplished by the female.

Of the four species of *Raillietia* occurring in bovids, *R. auris* Leidy in cattle has been sampled extensively. In the first large-scale study of that species, Tsymbal and Litvishko (1955) recovered only larvae (10.2%) and adults (81.8% females and 8.0% males). Fonseca and Faccini (1985) carried out an even larger study and also found only larvae and adults from among 12,726 mites flushed from the ears of cattle. Those authors also reared mites *in vitro*, and they obtained both nymphal stages. Females were larviparous and larvae progressed through the two nymphal stages in about five days. Fonseca and Faccini (1985) observed that "larvae . . . taken from the ears of cattle appear to have fed (large, guts filled with white and opaque material); lab-reared larvae are small and translucent." That larvae do not have to feed is shown by 90% becoming adults *in vitro* with no food present. If feeding by larvae, whether active or passive, does occur in the host, it might actually extend the duration of the larval stage. The significantly large percentage of larvae taken from the host indicates that the stage is not as transitory as would be judged from the *in vitro* studies, and food could cause the mites to remain in the larval stage in order to act in transmission to new host individuals.

The Halarachninae include about 35 species that parasitize primates, terrestrial carnivores, phocid and otariid seals, rodents, hyraxes, and artiodactyls. Information on the biology of these mites has been gathered over several decades by the careful researches on species from several genera by a number of investigators (Hull 1956, Furman and Smith 1973, Furman et al. 1974, Kim et al. 1980; and

[2]*Raillietia australis* Domrow is known from females taken from the ear of the common wombat (*Vombatus ursinus*); it is distinct in a number of morphological features from all other *Raillietia* species, which form a compact group in morphology as well as hosts. Domrow (1980) questioned his earlier placement of the species: "It may be that this morphologically and zoogeographically distinct species . . . should be transferred from *Raillietia* (Halarachninae) to some laelapine genus near *Mesolaelaps* and *Rhodacantha*, whose hosts are also largely Australian marsupials rather than Old World artiodactyls." I believe that Domrow was correct in his assessment and I have not included *R. australis* in the Raillietiinae here.

others). Halarachnines have nonfeeding ephemeral protonymphs and deutonymphs that have very rarely been recovered from a host. Some of the species are larviparous and some oviparous. The larva has well developed ambulacra (Popp 1961) and appears to be the only stage capable of moving between hosts. This reversal of the dermanyssoid trend to reduce the ambulacral size and functional capability in the larva is a convergent feature in the endoparasitic families Halarchnidae and Rhinonyssidae.

The range of life-cycle types in the Dermanyssoidea is extraordinary and is related to the variety of symbiotic relationships in which these mites are involved.

3. Origin and Evolutionary Sequence of a Series of Related Parasites

3.1 Hypoaspidinae to Laelapinae: the Move to Obligatory Nest Association and the Beginnings of Parasitism on Vertebrates

Whether one places the Hypoaspidinae in the Laelapinae (Evans and Till 1966, 1979) or recognizes them as separate subfamilies (Vitzthum 1940–43, Radovsky 1967, 1985) should not obscure the morphological similarity between some genera from each of the two groups combined with a marked biological differentiation between the groups. Laelapinae (*s. str.*) are characterized by male chelicerae strongly modified for sperm transfer. In the majority of Laelapinae, including the largest and typical genera *Androlaelaps* and *Laelaps*, the fixed chela of the male is short and slender and the movable chela has become a weak structure to which is attached an enlarged, often extremely long spermadactyl. It is difficult to see how these chelae can function in feeding (Fig. 8.1). This contrasts with *Hypoaspis* (and related genera) that I include in the Hypoaspidinae, in which the male chelicerae are chelate and usually dentate, typically much like those of the female but with the spermadactyl appended to the dorsal surface of the movable chela (Fig. 8.1). Such chelae appear to be adapted both for feeding and for sperm transfer, representing a balanced compromise in function. This distinction in the male chelicerae is the only morphological separation between some species in the *Hypoaspis* group and *Androlaelaps*.

The *Hypoaspis* group comprises free-living mites, generally found in soil and litter. *Androlaelaps* and *Laelaps* are nest mites, usually associated with small mammals and infrequently with birds. To the extent that these laelapine mites have been studied, they are typically opportunistic feeders, able to use a variety of foods: small nest arthropods, ectoparasites, scabs from or on the host. They sometimes also feed directly from the host by punching a crater in the skin or by imbibing lachrymal fluids or other secretions (see Radovsky 1985, for review).

Androlaelaps and *Laelaps* presumably have been drawn to the host's nest because of the rich food supply and the nest has made male feeding relatively unimportant. One can take this line of reasoning further to suggest that the nest habitat makes male feeding superfluous and thereby allows the specialization of

the chelicerae for fertilization to become a dominant selective influence. The male can easily locate females in the circumscribed sphere of the nest, and a female, once fertilized, retains sperm to last its reproductive life.

At the same time that these mites are functionally bound to the nest, they are also bound to the host. The nest usually represents an ephemeral habitat and even in the more durable dwellings of some hosts (e.g. some *Neotoma* [wood rat] houses, *Aplodontia* [mountain beaver or sewellel] burrow systems) the nest proper may be moved at intervals. The host provides the dispersal capability that compensates for nest-changing and permits nest-inhabiting to be a dependable and successful general niche for small arthropods with limited vagility. Among laelapine nest mites, it is usually the female that is the dispersal stage and the stage that is most often found on the host.

I suspect that most nest laelapines have retained an ability in the male to feed at least opportunistically. These mites feed on liquid food, or food that they liquify, and it is likely that free-flowing blood from host wounds, liquid remains of larger arthropods, and similar substrates will occur in the nest and may be fed on even by males with strongly specialized chelicerae.

Specializations for strict parasitism have occurred because they give access to a more dependable and richer food supply than opportunistic feeding. The use of the host for dispersal may encourage such specializations. The intermittent presence of thin-skinned suckling young incapable of much grooming may encourage them. Some laelapines have become obligatory parasites (see below), and various strictly parasitic laelapid subfamilies, (e.g. Hirstionyssinae) and dermanyssoid families (e.g. Macronyssidae) have branched off the Laelapinae lineage.

As described here, there was a major adaptive shift when the laelapine line, through changes observable in the genus *Androlaelaps*, became bound to the nest (primarily of small mammals) and that event was followed by a taxonomic radiation. Independently but with striking parallels, *Haemogamasus* branched from a hypoaspidine stock, became bound to the nest environment of small mammals, developed male chelicerae extremely adapted for sperm transfer rather than feeding (Fig. 8.1), and radiated taxonomically (Radovsky 1985). *Haemogamasus* is not in the sequence of taxa that is being traced here; however, it is a parallel example that supports my evaluation of laelapine nest adaptation.

3.2 The Laelapinae on Bats and the Line to the Macronyssidae

Bats are ecologically diverse in feeding and in roosting sites and are one of the most successful orders of mammals, second only to the rodents in the number of living species. Among the laelapine mites, only *Neolaelaps* (three species) (Fig. 8.2) and *Notolaelaps* (one species) are known from bats and they are restricted to the suborder Megachiroptera, the Old World fruit and blossom bats.

The rich bat-associated fauna of Macronyssidae occurs only on Microchiroptera and not on Megachiroptera. Macronyssids share some apomorphic features with

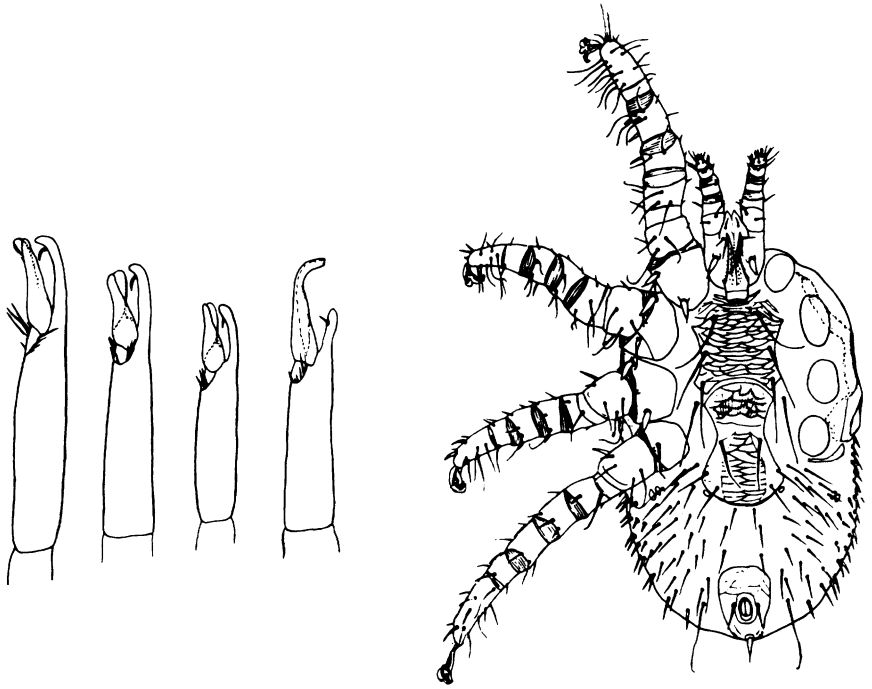


Figure 8.2. *Neolaelaps spinosus* Berlese. Chelicerae, left to right: adult female, deutonymph, protonymph, adult male. Female venter. After Radovsky (1967).

the bat-associated laelapines (see below), which demonstrate their relatedness. The segregation of the bat-associated representatives of these mite families on the two extant chiropteran suborders suggests host-tracking, which is supported by the distribution of other groups of ectoparasites, as in the following examples. In the Spinturnicidae, the two distinctive genera *Ancystropus* and *Meristaspis*, which share conservative features, are on Megachiroptera, and all other spinturnicid genera are on Microchiroptera (Rudnick 1960, Radovsky 1969), producing a situation closely analogous to the Laelapinae-Macronyssidae segregation on the two bat suborders. The bat-fly families Nycteribiidae and Streblidae and the flea family Ischnopsyllidae each have separate genera that parasitize each of the bat suborders without any overlap (see appendix in Kim 1985). The consistency of nonrepresentation of some parasitic groups on the two bat suborders is equally impressive, notably all bats lack both sucking lice (Anoplura) and chewing lice (Mallophaga) (Radovsky 1967, 1969, 1985).

Bats usually have been treated as a monophyletic group, the only mammals to have evolved powered flight and with such consistent features as uniformity in the general structure of the wing. However, there are differences between the two living suborders of bats, and some specialists have concluded that the order

Chiroptera is diphyletic (e.g. Smith and Madkour 1980). The fossil record is of limited use. Microchiroptera representing several Recent families and some assignable to extant genera are known from the Eocene (Table 8.3), but Megachiroptera are known from only two pre-Pleistocene fossils, the earliest in an Oligocene formation (Baker et al. 1991). Interest in a possible diphyletic origin of bats has increased in the past few years, with presentations supporting diphyly (Pettigrew et al. 1989, Pettigrew 1991) or monophyly (Baker et al. 1991, Simmons et al. 1991) of the Megachiroptera and the Microchiroptera. Host-parasite

Table 8.3. Classification and distribution of bats: families (and number of recent species) from Nowak (1991); superfamilies of Microchiroptera from Eisenberg (1981).

Taxon	Distribution
Eochiroptera	
Palaeochiropterygoidea[a]	Laurasia
Megachiroptera	
Pteropodidae (173)	Old World
Microchiroptera	
Emballonuroidea	
Rhinopomatidae (3)	Old World
Emballonuridae (48)	Old World; Neotropical
Craseonycteridae (1)	Thailand
Rhinolophoidea	
Nycteridae (13)	Old World
Megadermatidae (5)	Old World
Rhinolophidae (69)[b,c]	Old World
Hipposideridae (63)[b,c]	Old World
Phyllostomoidea	
Mormoopidae (8)	Neotropical
Noctilionidae (2)	Neotropical
Phyllostomidae (148)	Neotropical
Vespertilionoidea	
Mystacinidae (1)	New Zealand
Natalidae (5)	Neotropical
Furipteridae (2)	Neotropical
Thyropteridae (2)	Neotropical
Myzopodidae (1)	Madagascar
Vespertilionidae (355)[b,d]	Cosmopolitan
Molossidae (86)[b,c]	Cosmopolitan

[a]Extinct; fossils principally Eocene, last in Oligocene (Hand 1984).

[b]Eocene fossils assigned to family (Koopman 1984).

[c]Eocene fossils, from Europe, assigned to Recent genera: Rhinolophidae–*Rhinolophus*, Hipposideridae–*Hipposideros*, Molossidae–*Tadarida* (Hand 1984, Koopman 1984).

[d]*Myotis*, the most speciose Recent vespertilionid genus, appears in the Oligocene of Europe (Hand 1984).

associations were not included in those analyses. (Hall [1984] who refers to the monophyly/diphyly controversy, mentions evidence from insect parasites.)

Parasite associations of other vertebrates have provided convincing evidence concerning the phylogeny of the hosts. For example, the large array of identical or closely related parasites of the ostrich in Africa and the rhea in South America was know before the close relationship of those two ratites had become widely accepted on other grounds.[3] Indeed, one proponent of bat diphyly cited distinctive associations of spinturnicid mites with bats when raising the microchiropteran group Mormoopidae to family level (Smith 1972). Data on Laelapinae-Macronyssidae and other ectoparasites, briefly summarized above, provides evidence of the monophyly of the Chiroptera that is difficult to refute. How else can one explain the shared higher-group associations of so many parasitic taxa? I suggest that mammalogists concerned with bat origins need to accommodate parasitic relationships in their conclusions. Because advanced microchiropterans are known from the Eocene, the separation of the suborders must have occurred by that time, and probably in the earlier Paleocene (65–55 mya) (Hall 1984). Accepting synchronous early evolution of Laelapinae-Macronyssidae with bat hosts, we can conclude that the Macronyssidae first evolved at that early time.

The only clear distinction of *Neolaelaps* and *Notolaelaps* in those features that have generally been used to characterize *Laelaps* and its close relatives (Tipton 1960) is the specialization of the chelae, which are edentate and relatively weak—in fact, the female chelae of *Neolaelaps spinosus* (Berlese) (Fig. 8.2) are intermediate between those of the free-living hypoaspidine type and the skin-penetrating macronyssine type. Nevertheless, these two bat-associated genera are highly specialized parasitic mites that are phylogenetically closer to the Maconyssidae than other laelapines.

Neolaelaps have the pair of spiracular openings (stigmata) enormously enlarged, a feature for which the adaptive significance is obscure (Fig. 8.2). These mites are apparently nymphiparous and feed on blood in both nymphal stages as well as when adults (Fig. 8.2). From our present knowledge, they are probably permanent parasites. They are found on *Pteropus* (the large flying foxes) and on other Pteropodinae of the Australasian and Oriental regions. They have been found on pupiparous bat flies (Nycteribiidae, Streblidae) a number of times; they may use the flies to help them stay on a host, for dispersal among host individuals, or both. The male chelae are suggestive of those in macronyssids (Fig. 8.2). In addition, the sensory field setation of tarsus I is very macronyssid-like (more than in *Notolaelaps*), which confirms a macronyssid relationship (Fig. 8.3).

Notolaelaps novaguinea Womersley was known from only six females on three bats in the mountains of New Guinea, of which two of the hosts were identified as nectar-feeding bats of the genus *Syconycteris* (Macroglossinae) found in Aus-

[3] 1957, Premier Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés. *Inst, Union Biol. Sci., Ser. B*, no. 32, 156–158.

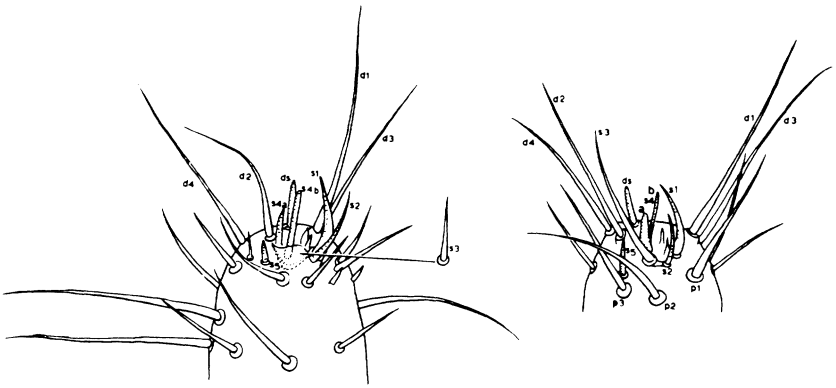


Figure 8.3. Dorsal view of tip of tarsus I showing sensory field, with some setae labelled to show homologies: left, *Neolaelaps spinosus* (Berlese); right *Steatonyssus antrozoi* Radovsky and Furman. After Radovsky (1967).

tralia, New Guinea, and other Australasian islands. In March 1985, I collected six more females plus two males of *N. novaguinea* from three specimens of *Syconycteris* at 1100m near Mount Dayman in eastern Papua (Milne Bay Province, Papua New Guinea; Radovsky, unpublished data). These mites were very difficult to recover by brushing or combing the bat or by washing the surface. Nearly all of them were found by watching the small white mites emerge from the fur and move over the contrasting dark surface of the host. I examined all of these mites alive with a stereoscopic microscope, and none had the appearance of red or dark material in them that could be associated with blood-feeding. I conclude that these mites are probably obligate parasites that feed on some material secreted by the host that does not darken the body, perhaps lachrymal fluids or a mucous secretion from some other body orifice or exocrine gland.

The female chelae of *Notolaelaps* have remained short and relatively stout, as compared to *Neolaelaps*, which supports their not being used to penetrate tissues such as skin. We lack evidence to suggest whether *Notolaelaps novaguinea* is or is not a permanent parasite (as opposed to a roost parasite). Nothing is known about the developmental stages. That the immatures have not been taken from the host may be related to the general difficulty in collecting this mite (and the small size of the nymphs), or the immatures may be in a cryptic location on the host, or they may develop primarily in the roost area.

The male chelicera of *Notolaelaps*, not previously described, is very similar to that of *Neolaelaps*, which is additional evidence that the two genera represent a single lineage and which further supports their close relationship to the Macronyssidae. No other laelapine mite has male chelae that are as close to the macronyssid type as *Notolaelaps*, especially to the chelae of the more conservative

macronyssines. Comparing these structure in *Notolaelaps* to the typical form in *Macronyssus* species, the pilus dentilis on the fixed chela is more developed in *Notolaelaps*, the dorsal arm of the movable chela is straighter and more slender, and the tip of the spermadactyl is more distinctly and sharply curved dorsad.

In my prior writings (Radovsky 1969, 1985) and earlier in this chapter, I have emphasized the sexual dimorphism that has developed in the chelae with adoption of the nest habitat, the apparent reduction of feeding capability in the male, and the sometimes bizarre structures that have evolved in the male chelae to better effect sperm transfer. However, those trends are moderated or even reversed as mites in the same evolutionary lines become obligate parasites. Thus, the male of *Neolaelaps spinosus* has a chelicera (Fig. 8.2) that appears to be used in feeding, certainly more so than in most *Androlaelaps* and *Laelaps* species. Most Macronyssidae, Hirstionyssinae, Myonyssinae, etc. have male chelae that are similar in length to those of the female and that appear to have the capacity of working together as the tip of a tissue-penetrating chelicera, somewhat comparable to those of the female though not as effective. *Haemogamasus* provides an interesting parallel, in that the bizarre male chelae of the polyphagous *Haemogamasus reidi* group can be contrasted with the simple male chelae, quite like those of the female, in the strictly hematophagous *Haemogamasus liponyssoides* group (Radovsky 1960a, 1960b; Williams et al. 1978) (Fig. 8.1).

An explanation of this apparently significant phenomenon may be that the polyphage, taking advantage of the trophic potential of the nest, must use its chelicerae as multi-purpose and adaptable tools. Thus, a female *Laelaps echidninus* Berlese may use its chelicerae to punch a hole in the skin of a rodent, to grasp and puncture a mite or louse, to liquify a scab, to scrape lachrymal material from the corner of a rat's eye, etc. (Furman 1959, Radovsky 1985). Some of those feeding substrates demand chelate-dentate chelicerae, and extreme adaptation of the male for effective insemination is a more practical course for these mites. The obligatory parasite concentrates on one feeding substrate in most cases. Penetration of the skin requires a specialized adaptation; however, that adaptation is to use the chelicerae as a piercing structure for which they are preadapted. The primary requirement in adapting for hematophagy is for the chelae to become slender and more or less pointed, so that they can act together as the tip of a thrusting apparatus. Chelicerae appear to have acquired this form many times in the females of dermanyssoids that have become obligatory parasites (Radovsky 1969). The puncturing capability of these chelicerae apparently is more compatible with sperm transfer than the chelate-dentate structure required for the all-purpose feeding for which chelicerae are used by polyphagous nest mites. The chelicerae of male parasitic dermanyssoid mites are rarely if ever as effective in feeding as those of the female. However, they apparently have an adaptive advantage in feeding that has resulted in a renewed balance between the trophic and reproductive functions of the male chelicerae in these parasitic groups.

Why laelapines have not radiated more widely on the Megachiroptera is not clear. *Neolaelaps* and *Notolaelaps* are both specialized and limited taxa, although *Neolaelaps spinosus* has many pteropodine hosts within its geographic range.

3.3 The Macronyssinae and the First Macronyssid Radiation on Bats

The transition from a laelapine bat-associated ancestor to the Macronyssidae (Radovsky 1966, 1967) was marked by an extraordinary change in the life cycle: the suppression of the deutonymph, which is expressed in the morphological differences between the protonymphal and deutonymphal stages (Fig. 8.4, 8.5). No species of the subfamily Macronyssinae, which encompasses the earlier radiation of mites in this family and is the most diverse, has been reared or observed in the laboratory, so our information about the biology of the Macronyssinae is partly suppositional. However, the protonymph is collected so frequently from the host, relative to other stages, that there can be little question that it is uniformly slow-feeding. In addition, there are direct observations of *Radfordiella* protonymphs embedded in the oral mucosa (see below). We can state with even greater assurance that most and perhaps all species of Ornithonyssinae, a more clearly defined and compact group, are fixed feeders as protonymphs and rapid feeders as adults, which is discussed below. The feeding behaviors of the adult and protonymph have diverged, and the nature of the protonymphal feeding gives the mite the capacity to pass through the deutonymphal stage without additional feeding. The deutonymph has become a resting pupa-like stage. A corollary of that theory is that the protonymph exhibits neosomatic development (Audy et al. 1972), a phenomenon that is also discussed in the following section.

The macronyssid transition to a novel life cycle was accompanied by a major taxonomic radiation, which was almost entirely restricted to bat hosts. There are only three macronyssine species in two genera on rodents, and these are Neotropical forms derived from bat-infesting genera. Of the 12 genera that I assign to the Macronyssinae, eight appear to have originated in the Neotropical Region. The other four are Old World in origin (Table 8.4). *Macronyssus*, the one genus with many species, secondarily entered the New World, radiated moderately in North America, and has a limited presence in the Neotropics (where there are few species and only one endemic). That pattern of distribution raises many questions, at least some of which have plausible answers based on the host associations and the phylogeny of the Chiroptera.

During the Mesozoic Era, the Pangean world continent broke into northern Laurasia (North America, Europe, Asia) and southern Gondwanaland (South America, Africa, India, Australia, Antarctica). Although mammalogists are not in full agreement on the geographic location of early bats, most specialists support a Laurasian origin (Hand 1984). Archonta, a superordinal grouping in which bats are placed with Dermoptera (colugos or gliding lemurs), Scandentia (tree shrews), and Primates by some mammalogists, is considered Laurasian in origin. All the

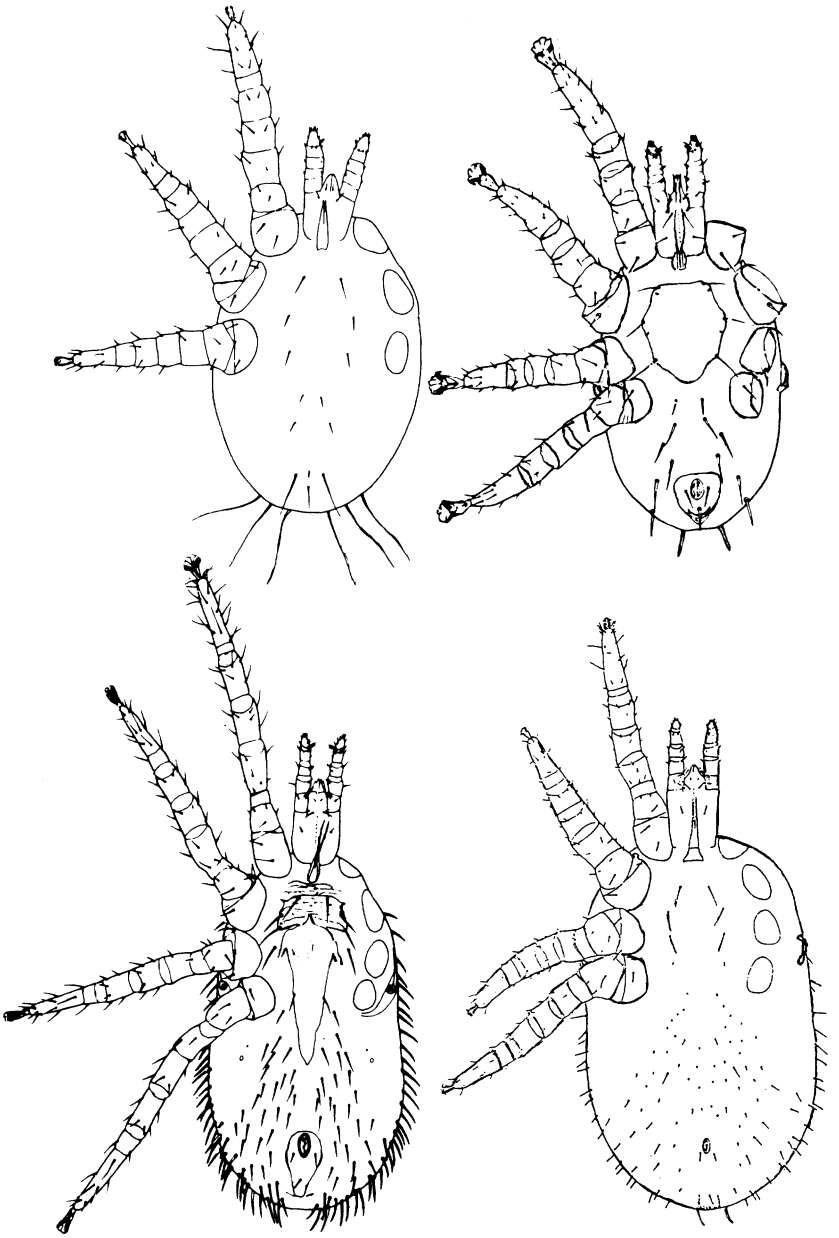


Figure 8.4. Venter of *Steatonyssus* stages, clockwise from upper left: larva, protonymph, deutonymph, adult female. Female is *S. leptus* Radovsky, others are *S. antrozoi* Furman and Radovsky. After Radovsky (1967).

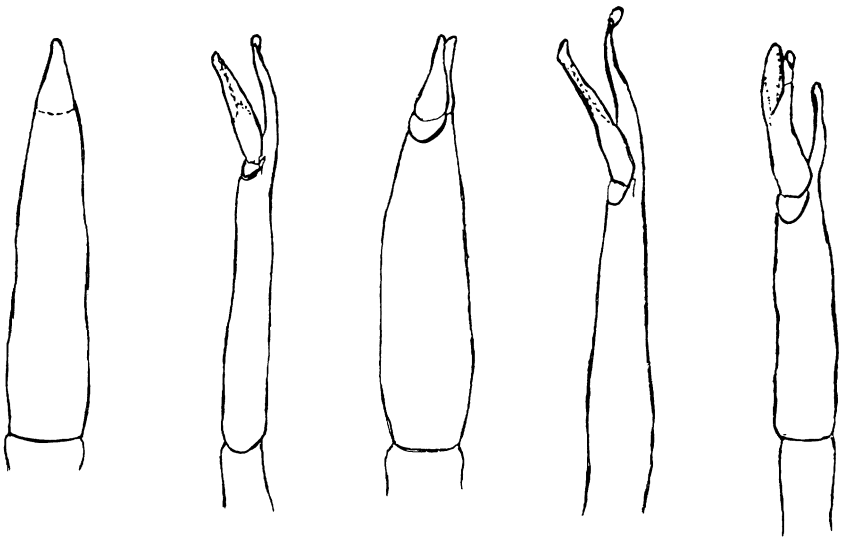


Figure 8.5. Chelicerae of *Steatonyssus antrozoi* Furman and Radovsky, from left: larva, protonymph, deutonymph, adult female, adult male. After Radovsky (1967).

oldest bat fossils (Eocene) and all paleochiropteroid fossils are know only from Laurasia. The present distribution of bats fits most closely with dispersal from Laurasia to the southern continents, which is also true of the distribution of their parasites. One of the microchiropteran superfamilies, Phyllostomoidea (Table 8.3), was long isolated in the Neotropics, radiated there, and is still restricted to that region except for a small number of species that have entered the southern Nearctic in recent geologic time.

The present distribution of Macronyssinae is understandable if we consider that the migrant bat or bats from which the phyllostomoid lineage came was carrying one or more macronyssines when entering South America in the early Tertiary. There is general agreement that the radiation of microchiropteran superfamilies was not later than the Eocene. In the early Eocene, about 55 mya, South America and North America were sufficiently close to have allowed easy dispersal of a flying mammal across the intervening ocean.

There is one more, particularly fascinating piece of evidence that supports such an early dispersal of the phyllostomoid stock into South America. The monotypic bat family Mystacinidae is endemic to New Zealand. It is the only indigenous land mammal there except for another bat that descended from an ancestor that flew from Australia in late geologic time. As summarized by Hand (1984), immunological studies published in 1982 demonstrated that *Mystacina* was closely related to the phyllostomoids and those studies plus reexamination of the morphology unquestionably put *Mystacina* "as an early offshoot of the phyllostomoid lineage" (Table 8.4 follows a conservative interpretation).

Table 8.4. The classification and distribution of genera of the Macronyssidae. The approximate number of valid described species is given in parentheses, where the number exceeds three. Hosts that are apparently accidental are excluded: e.g. a species of Macronyssus *known from only one collection on a rat or* Chiroptonyssus *attacking humans.*

Taxon	Host Range	Geographic Range[a]
Macronyssinae		
Bewsiella	Rhinolophoidea	Old World
Ichoronyssus	Vespertilionidae, Rhinolophoidea	Old World
Macronyssus (40)	Vespertilionidae, Rhinolophoidea	Cosmopolitan
Megistonyssus	Rhinolophidae	Ethiopian
Synasponyssus	Thyropteridae	Neotropical
Parichoronyssus (5)	Phyllostomidae, Emballonuridae	Neotropical
Radfordiella (6)	Phyllostomidae	Neotropical
Macronyssoides	Phyllostomidae	Neotropical
Chirocoetes	Phyllostomidae	Neotropical
Nycteronyssus	Phyllostomidae	Neotropical
Acanthonyssus	Rodents	Neotropical
Argitis	Rodents	Neotropical
Ornithonyssinae		
Trichonyssus (7)	Vespertilionidae primarily, other Microchiroptera	Australian
Mitonyssus	Noctilionidae, Molossidae	Neotropical
Chiroptonyssus (4)	Molossidae	New World
Chelanyssus	Molossidae	Ethiopian
Parasteatonyssus (4)	Molossidae	Old World
Steatonyssus (40)	Microchiroptera (excluding Phyllostomoidea)	Cosmopolitan
Pellonyssus (6)	Birds	Old World, Nearctic
Lepidodorsum	Rodents	Neotropical
Lepronyssoides	Rodents	Neotropical
Ornithonyssus (25)	Rodents and other mammals primarily; birds	New World
Cryptonyssus (20)	Mammals (including Microchiroptera)	Old World, Nearctic
Ophionyssus (8)	Lizards and Snakes	Old World
Draconyssus	Lizards	Neotropical

[a]In a few cases, regions are omitted where they are marginal (e.g. *Radfordiella* on some phyllostomid bats in the southern Nearctic Region) or there apparently were range extensions of mites as the result of dispersal by humans in post-Columbian times (e.g. three species of *Ornithonyssus* widely distributed in the Old World, one species of *Ophionyssus* widely distributed on snakes and lizards in captivity in the New World).

Crossing the ocean gap from the southern tip of South America to Antarctica-Australia and then over another ocean barrier to New Zealand by the mystacinid ancestor would have been most likely not later than the early Oligocene, which "suggests that chiropteran stock ancestral to the phyllostomoids probably entered South America from Laurasia by (at least) the late Eocene" (Hand 1984). The

question will inevitably be asked as to what parasites on *Mystacina tuberculata* may shed light on this relationship; unfortunately that New Zealand bat has lost all of its original parasites. The parasites it now has have evolved on it, probably in New Zealand, or have secondarily transferred to it from another resident host.

Other widespread microchiropteran families apparently entered South America while it was an island continent (Hand 1984). The Molossidae and Emballonuridae may first have arrived there in the Oligocene and Vespertilionidae in the Miocene. The crossover of macronyssids among these groups and between them and phyllostomoids seems to have been limited, which again suggests a high level of host-tracking.

3.4 The Ornithonyssinae and the Higher Macronyssid Radiation

The more derived macronyssids, subfamily Ornithonyssinae (Table 8.4), are a relatively uniform group with: (1) a higher capacity for engorgement by the adult female than in most Macronyssinae; (2) a tendency for reduction of idiosomal plates; (3) a loss of some primary plate setae but often hypertrichy in relation to engorgement; and (4) some characteristic identifying structures, such as the anteriorly directed ventral process on the first free palpal segment (trochanter). Most ornithonyssines probably represent one lineage, but it is plausible that two or more lines came from the macronyssine grade.

The ornithonyssine species that is best understood biologically from laboratory observations and experiments is *Chiroptonyssus robustipes* (Ewing). This is a parasite of the molossid bat *Tadarida brasiliensis* and is relatively easily observed because the protonymph consistently feeds on the glabrous wing membrane and the adults will feed there also. I found that protonymphs require about two days after molting before they are ready to feed and generally need 4–5 days on the host before they are engorged, though some engorged after as little as three days (Radovsky 1964, 1967). With a stereoscopic microscope I observed that protonymphs remain attached in one place unless disturbed. They showed no change in color though they gradually increased in size, yet all mites were bright red when they left the host showing that they had engorged on whole blood.

Lavoipierre and Beck (1967) used a high-power light microscope to examine feeding on the transilluminated bat wing. They injected bats with Evans' blue stain, which showed that protonymphs ingest extra-vasated tissue fluids during their long period of feeding. Then after 3–6 days the protonymphs puncture a venule and engorge rapidly (in about 15–20 minutes) on whole blood before leaving the host. Adult females always feed rapidly by rupturing a vessel and imbibing the blood that pools outside it.

Lees (1952) was the first to demonstrate the ontogenetic basis of major external change of an active arthropod in the absence of a molt, a phenomenon especially widespread among symbionts. He showed that a female ixodid tick, *Ixodes ricinus* (Linnaeus), spends most of its 6–7 days on a host feeding slowly and growing

new cuticle, in order to double the thickness of its soft integument. It engorges on whole blood during its last half-day on the host, stretching the integument back to its original thickness and allowing the tick to enlarge about 125 times. Arthur (1965) reported that *I. ricinus* feeds on tissue fluids and other materials until the rapid engorgement phase. Audy et al. (1972) applied the term *neosomy* to the formation of a new external structure or significant enlargement with the secretion of new cuticle within an active stadium. They noted examples among Acari, fleas, bat flies, parasitic Crustacea, some termite and ant queens, and others.

The protonymph of *Chiroptonyssus robustipes* does not enlarge to anything approaching the scale of a female ixodid tick. However, it does enlarge sufficiently to carry through to the deutonymphal stage without feeding, which is more than dermanyssoid mites usually can take in. I postulate that cuticular growth is taking place during the long period of feeding by the *C. robustipes* protonymph before it engorges, and hence this is an instance of neosomy. Furthermore, I think that fixed feeding and neosomatic growth are characteristic of ornithonyssines, and perhaps of all Macronyssidae.

I also studied *Steatonyssus antrozoi* Radovsky and Furman, a parasite of the vespertilionid *Antrozous pallidus* (Radovsky 1967). This mite stays in the fur of the host and was not directly observed when feeding. Protonymphs left the host in the engorged state after 1.8–4.0 days, usually after 2.5–3.5 days. Some females engorged and left the host in three hours. These results indicate that the protonymph is a fixed slow-feeder and that the adult female is a rapid feeder.

The protonymphs of three species of the macronyssine genus *Radfordiella* are fixed parasites in the oral mucosa (palate) of phyllostomid bats (Phillips et al. 1969, Radovsky et al. 1971). The adults of these mites are not known but presumably are quick-feeding external parasites, as other *Radfordiella* adults appear to be.

Camin (1953) studied the biology of the snake mite, *Ophionyssus natricis* (Gervais), in detail. He observed the protonymph to feed within 24 hours of molting and to remain in one spot, under a scale, until engorged (in 16–21 days at 15°C and in 3–7 days at 25°C). He did not explicitly state the duration of feeding by the adult female. All feeding was on a host and the mite was under a scale. Apparently individual mites were not followed.

Extensive research has been done on three species of *Ornithonyssus* because: (1) two species are pests of poultry; (2) their potential for pathogen transmission; (3) their direct attacks on humans in the absence of a more natural host; and (4) the usefulness of one species as a laboratory model for filarial studies. These are *Ornithonyssus bacoti* (Hirst), the tropical rat mite; *O. sylviarum* (Canestrini and Fanzago), the northern fowl mite; and *O. bursa* (Berlese), the tropical fowl mite. Despite extensive culturing of these species, I am not aware of any study that has demonstrated the nature of protonymphal feeding in which the mites were observed under natural conditions.

Bertram et al. (1946) conducted an impressive set of studies on *O. bacoti* on

a natural host, the cotton rat (*Sigmodon hispidus*), and on the laboratory rat. Mites were given access to the scarified tail of a rat, and the females fed readily, some becoming fully engorged within 10 minutes. However, protonymphs did not feed significantly and the authors concluded that they could obtain fully engorged protonymphs only by giving them free access to a host and recovering them when they dropped off. Skaliy and Hayes (1949) also used the scarified rat tail to feed *O. bacoti*; they believed that protonymphs fed satisfactorily but they noted that mites in that stage required multiple blood meals, and the measurements of "fed" protonymphs suggest that they had fed hardly at all. Sikes and Chamberlain (1954) reported that an individual of *O. bursa* feeding on chickens "usually requires at least two feedings (one or more partial meals and a final complete engorgement) in order to molt." How they were able to conclude that from their experimental design is not clear, but they may have been misled by a study in which they put freshly molted protonymphs (not yet ready to feed) on a chick and recovered mites within six hours that, not surprisingly, had the appearance of having fed only partially, if at all. Similarly, studies on *O. sylviarum*, more recently involving partially developed chicks in eggs or on membranes over blood, have repeatedly been combined with statements that this species needs two or more blood meals in its protonymphal stage (Hogsette et al. 1991).

Research protocols that allow fixed feeding in combination with observability of the process are difficult to design for many ornithonyssine mites that normally feed beneath the feathers or fur. It is not surprising that partial feedings have been obtained by many scientists who preconceived protonymphal feeding based on the adult model and provided artificial feeding systems or hosts. I gave *Chiroptonyssus robustipes* protonymphs access to suckling mice and found that 8/80 (10%) took some blood though they did not engorge (Radovsky 1967). Without the opportunity to study these mites on the wing of a bat, I obviously could have reached some wrong conclusions. Further research is needed before it can be dependably stated that the protonymph of *any* ornithonyssine mite feeds partially and repeatedly or takes blood initially in feeding. Unless such a demonstration is made, I believe we should extrapolate from those species that have been studied and from what is logically adaptive based on our current knowledge, to anticipate that each ornithonyssine protonymph is a fixed feeder taking tissues other than whole blood until it engorges on whole blood just before completing its single meal in that stage. The same supposition about slow feeding by the protonymph can be made for the Macronyssinae, although the evidence is more limited.

The ornithonyssine adaptation is a quantifiable change in feeding capacity in which both the protonymph and the adult female appear capable of greater engorgement than is generally found in the macronyssines; that adaptation led to further radiation on bats and also to radiations on other mammals, birds, and reptiles. About half of the ornithonyssine genera are found on bats (Table 8.4), including *Steatonyssus*, which is cosmopolitan and notably speciose. There are several basically Neotropical genera on rodents, of which *Ornithonyssus* has

radiated significantly. *Pellonyssus* on birds originated in the Old World and is close to *Steatonyssus*. *Ophionyssus* originated on snakes and lizards and is also Old World in origin. *Draconyssus*, known from only two collections of females in Panama, was found in the nares of lizards (Yunker and Radovsky 1966).

Cryptonyssus, on bats and other mammals, originated in the Old World and has only a few species on bats in North America (Radovsky 1967, 1969, 1985). Many of the Old World species assigned to *Ornithonyssus* by authors should be included in *Cryptonyssus*, pending further study, because of their similarities to *Cryptonyssus desultorius* Radovsky 1966, the type species of the genus, and because placement in *Ornithonyssus* is clearly misleading and obscures the systematic and zoogeographic significance of that genus.[4] Furman and Radovsky (1963) redefined *Ornithonyssus*, noting two features that are particularly important in recognizing the genus: the adult female and male and the protonymph all have a number of tapered setae that bear small barbs on one side and the male has a prominent seta-bearing swelling on the palpal femur. Based on those features and the diagnosis as a whole, *Ornithonyssus* originated in the Neotropics and has spread to the Nearctic on such hosts as the opossum and the cotton rat. Some forms have transferred to Nearctic hosts and speciated. The distribution of the genus has been confused by the spread of three species to many parts of the world: *O. bacoti* (includes *O. ondatrae*), *O. sylviarum*, and *O. bursa*. All three species are now relatively nonspecific, which suggests their recent dispersal, and all three species are found primarily in relation to domestic, domiciliated, or generally anthropotopic hosts, which tends to confirm their nearly cosmopolitan spread by human activities in post-Columbian times. An interesting association of *O. bacoti* is its role as the vector and intermediate host of *Litomosoides carinii*, a filarial worm parasitic on *Sigmodon hispidus*, confirming the New World origin of the mite in association with that basically Neotropical rodent.

Ornithonyssus is primarily parasitic on rodents [though *O. wernecki* (Fonseca) is on opossums of the genus *Didelphis*]. However, repeated reference has been made here to two species on birds: *O. sylviarum* and *O. bursa*. These seem to be isolated cases and potentially the starting points for new radiations. Distinctions between these two mites both morphologically and biologically suggest that they were independent transfers to birds. *O. sylviarum* is also interesting as an ornithonyssine that is well on its way to becoming a permanent parasite; most eggs are fastened to feathers and all stages may remain on the host, though vast

[4]Among the host of species lumped into the genus *Ornithonyssus* by Micherdzinski (1980), I believe the following should be retained in or transferred to *Cryptonyssus*: *C. conciliatus* Radovsky, 1967; *C. costai* (Micherdzinski, 1980), new combination; *C. desultorius* Radovsky, 1966; *C. dogieli* (Bregetova, 1953); *C. flexus* Radovsky, 1967; *C. latro* (Domrow, 1963), new combination; *C. nitidulae* (Costa, 1961), new combination; *C. petauri* (Micherdzinski, 1980), new combination; *C. pipistrelli* (Oudemans, 1904); *C. praedo* (Domrow, 1971), new combination. Probably some other Australian species listed in *Ornithonyssus* by Domrow (1987) will eventually be placed in *Cryptonyssus* (and others in *Trichonyssus*). Further analysis of these questions belongs in revisionary works.

numbers of females and protonymphs will leave the host to disperse. Perhaps parasitological or other clues can be found to the original bird hosts of these two species, as has happened with *O. bacoti*, which could shed much light on their evolution and adaptations.

The Nearctic Region appears to have been primarily a corridor and place for secondary speciation events in the Macronyssidae. The two centers for radiations were the Old World and the Neotropics, and the latter was free of the other continents from the Mesozoic until several million years ago. *Macronyssus* in the Macronyssinae and *Steatonyssus* in the Ornithonyssinae are each speciose genera on bats that originated in the Old World. Each came to the Nearctic rather late judging by its more limited radiation there. It appears that each began to enter the Neotropics quite late, perhaps not until the Pliocene-Pleistocene rejoining of the continents. Each genus appears to have produced only a single new species in the Neotropics. While Old World genera have moved into the New World with bat hosts such as vespertilionids, there has not been any significant movement in the other direction. The typically Neotropical taxa in the Macronyssidae have apparently been restricted by the limited spread of their hosts to the north and by the failure of those host groups to colonize the Old World.

3.5 The Rhinonyssidae and the Great Endoparasitic Radiation in Birds

It appears unlikely that the suppression of the deutonymph and the retention of a feeding protonymph should have happened twice, and that is one basis for relating the Rhinonyssidae to the Macronyssidae (Radovsky 1964, 1966, 1969). As far as we know, all rhinonyssids have the macronyssid type of life cycle. Strandtmann (1961) published a landmark paper on the life histories of a major grouping of rhinonyssid genera, in which he said of the protonymph that it is "quite obviously a feeding stage" and of the deutonymph that it is "obviously a nonfeeding stage."

As it happens, we can also demonstrate the relatedness of rhinonyssids to macronyssids and the origin of the former in the latter by a graded series of transitional forms. That series starts with the bat-parasitizing ornithonyssine genus *Steatonyssus*, which includes some species parasitic on bats that roost in treeholes. *Pellonyssus* is derived from *Steatonyssus* but is on birds, and the most primitive *Pellonyssus* is on treehole-nesting African woodpeckers, an obvious opportunity for ecological transfer between hosts. The features differentiating the most conservative rhinonyssids from *Pellonyssus* are slight, though the former consistently have more pronounced plate reduction and hypotrichy (Radovsky 1969).

The Rhinonyssidae are an extraordinarily successful group of parasites. A high proportion of bird species that have been examined are parasitized. Levels of host specificity vary greatly but some rhinonyssids are quite specific. Some acarologists have reported congruence between host and rhinonyssid evolution, have applied rhinonyssid data to problems of avian relationships within host

families, and have suggested host-tracking at higher levels (e.g. Pence and Castro 1976). I am sure that host-tracking has occurred at lower taxonomic levels and I will not attempt to evaluate those cases that have been put forth. At the same time, I question the concept that rhinonyssids tracked the evolutionary radiation of birds at the higher levels such as orders or even families. The more conservative and "ornithonyssine" of the rhinonyssids are now put in the genus *Tinaminyssus* and this group includes mites in a wide range of bird orders, including Passeriformes. One of the most conservative members of the family, separable from *Pellonyssus* only by somewhat more marked reduction of plates and idiosomal setae, was described by Strandtmann and Clifford (1962) from the varied thrush (Passeriformes: Turdidae).

The rhinonyssids apparently derived from a highly specialized ornithonyssine in or near the genus *Pellonyssus*, which is associated with passeriform and piciform hosts. That, in combination with the lack of agreement between relations among parasites and among hosts at higher taxonomic levels, indicates that the rhinonyssids adopted life in the nasal passages after the radiation of the birds into their contemporary orders and most of their present families, no later than the Miocene Epoch, perhaps 15 million years ago. How then did the rhinonyssids spread so quickly and become so ubiquitous in birds compared to the macronyssid radiations on their hosts? I believe there are two factors. First, endoparasites, most particularly in avian nasal passages and feeding on or through the mucosa, are in a relatively constant environment among the greater part of the range of avian hosts; that environmental consistency should encourage resource-tracking and the easy transfer among hosts that come into rather casual contact (see Strandtmann 1958, on the relation of rhinonyssid transfer to gregariousness of hosts). Second, birds surpass all other organisms in their vagility. They are not only preeminent fliers, they also migrate over great distances. The rhinonyssids have gone through several grades of refinement for intranasal parasitism. At each point, there was very likely the relaxation in barriers to changing hosts that we have observed repeatedly with novel parasitic adaptations. At those times, given the relatively uniform substrate and the widespread contact among birds around the globe, it is probable that major resource-tracking radiations took place.

3.6 Sternostoma tracheacolum and a Contemporary Rhinonyssid Radiation

Most species in the genus *Sternostoma* are nasal mites. However, *S. tracheacolum* Lawrence parasitizes the inner respiratory tract, including the lungs and air sacs (Furman 1957, Fain and Hyland 1962, Domrow 1987). This mite species has been found in Columbiformes, Psittaciformes, and many families of Passeriformes (among others) and is known from wild birds on all the continents. The dissemination of this mite may be assisted by human activities, because it is found in such caged birds as canaries. Nevertheless, we see now a mite species with a fresh adaptation that occurs in a great array of hosts, that has an unusual

level of morphological variation, and that causes pathologies indicating recent association with some of its hosts. It appears to be a classic instance of an incipient taxonomic radiation in a parasite that has adopted a new host-parasite relationship, with the emphasis in this case on resource-tracking.

4. Summary

Table 8.5 summarizes the principal sequence of mites in three families that is traced in this chapter, gives some characteristics associated with new host relationships and indicates the nature of the relationships. In nearly every case,

*Table 8.5. Notable taxa, and associated characteristics, listed in a sequence progressing from free-living predators (*Hypoaspis *complex) through various parasitic relationships in three families of dermanyssoid mites.*

Taxon[a]	Morphological Characteristic(s)	Relationship with Hosts
Laelapidae		
Hypoaspis complex	Chelicerae of males similar to females (chelate-dentate), but with appended spermadactyl	Free-living predators (few spp. = nest associates)
Androlaelaps/Laelaps	Chelicerae of males not chelate-dentate, extremely adapted for sperm transfer	Nidicolous; polyphagous opportunists with varying degrees of parasitic feeding
Notolaelaps/Neolaelaps	Tarsus I sensory field chaetotaxy and male chelicerae similar to those of Macronyssidae	Ectoparasites of megachiropteran bats
Macronyssidae		
Macronyssus	Deutonymph nonfeeding	Ectoparasites of microchiropteran bats
Steatonyssus	Increased engorgement in protonymph and female	Ectoparasites of microchiropteran bats
Pellonyssus	Much like *Steatonyssus* but idiosomal plate area reduced	Ectoparasites of birds
Rhinonyssidae		
Tinaminyssus	Further reduction in plates and in setae	Intranasal parasites of birds
Sternostoma, (most spp.)	Extreme reduction in plates and in setae	Intranasal parasites of birds
Sternostoma tracheacolum	Extreme variability in remnant plates and reduced setae	Parasites in the lungs and air sacs of birds

[a]Some genera selected as typifying a grade: e.g. Macronyssus typical of Macronyssinae and *Steatonyssus* of Ornithonyssinae; the latter genus also is close in ancestry to *Pellonyssus*.

the adaptation is accompanied by a taxonomic radiation. The series is unusual in that we can track these changes through study of extant forms and reconstruct the history of the parasites with the help, in some cases, of the host group, including paleontological evidence. The sequence, running through three families of mites and extending from a free-living predatory type to a parasite that lives deep in the respiratory system, is unusual and instructive.

References

Arthur, D. R. 1965. Feeding in ectoparasitic Acari with special reference to ticks. *Adv. Parasitol.* 3:249–298.

Audy, J. R., F. J. Radovsky and P. H. Vercammen-Grandjean. 1972. Neosomy: radical intrastadial metamorphosis associated with arthropod symbioses. *J. Med. Entomol.* 9:487–494.

Baker, R. J., M. J. Novacek and N. B. Simmons. 1991. On the monophyly of bats. *Syst. Zool.* 40:216–231.

Bertram, D. S., K. Unsworth and R. M. Gordon. 1946. The biology and maintenance of *Liponyssus bacoti* Hirst, 1913, and an investigation into its role as vector of *Litomosoides carinii* to cotton rats and white rats, together with some observations on the infection in the white rats. *Ann. Trop. Med. Parasitol.* 40:228–254.

Bregetova, N. G. 1953. Mites of the genus *Bdellonyssus* Fonseca, 1941. *Tr. Inst. Zool. Akad. Nauk UKRSSR* 13:310–319. (In Russian)

Bregetova, N. G. 1964. *Some Problems of Evolution of the Rhinonyssoid Mites.* (Report presented at the 1st Int. Congr. Parasitol.). Leningrad: Nauka. Pp. 1–7.

Bregetova, N. G. 1969. Ontogeny of gamasid mites as a basis of their natural system. *Proc. 2nd. Int. Congr. Acarol.* (G. O. Evans ed.). Sutton Bonington, England, 1967. Akadémiai Kaidó, Budapest. Pp. 289–295.

Camin, J. H. 1953. Observations on the life history and sensory behavior of the snake mite, *Ophionyssus natricis* (Gervais) (Acarina: Macronyssidae). *Chic. Acad. Sci., Spec. Publ.* No. 10. 75pp.

Costa, M. 1961. Mites associated with rodents in Israel. *Bull. Br. Mus. (Nat. Hist.) Zool.* 8:1–70.

Domrow, R. 1963. New records and species of Austomalayan laelapid mites. *Proc. Linn. Soc. N. S. W.* 88:199–220.

Domrow, R. 1971. A new Australian species of *Ornithonyssus* Sambon (Acari: Dermanyssidae). *J. Aust. Entomol. Soc.* 10:109–111.

Domrow, R. 1980. The genus *Raillietia* Trouessart in Australia (Acari: Dermanyssidae). *Proc. Linn. Soc. N.S.W.* 104:183–193.

Domrow, R. 1987. Acari Mesostigmata parasitic on Australian vertebrates: an annotated checklist, keys and bibliography. *Invertebr. Taxon.* 1:817–948.

Dusbàbek, F. 1964. Parasitische Fledermausmilben der Tschechoslowakei. II. Familie Dermanyssidae Kol., 1859 (Acarina: Gamasides). *Cesk. Parasitol.* 11:77–125.

Eisenberg, J. F. 1981. *The Mammalian Radiations*. Univ. Chicago Press, Chicago. Pp. 1–610.

Elton, C. 1966. *Animal Ecology*. University of Washington Press, Seattle (First published in 1927). Pp. 1–237.

Evans, G. O. 1968. The external morphology of the post-embryonic developmental stages of *Spinturnix myoti* Kol. (Acari: Mesostigmata). *Acarologia* 10:589–608.

Evans, G. O. and W. M. Till. 1966. Studies on the British Dermanyssidae (Acari: Mesostigmata). Part 2. Classification. *Bull. Br. Mus. (Nat. Hist.), Zool.* 14:109–370.

Evans, G. O. and W. M. Till. 1979. Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari-Parasitiformes). An introduction to their external morphology and classification. *Trans. Zool. Soc. Lond.* 35:139–270.

Fain, A. and K. Hyland. 1962. The mites parasitic in the lungs of birds. The variability of *Sternostoma tracheacolum* Lawrence, 1948, in domestic and wild birds. *Parasitology* 52:401–424.

Fonseca, A. H. and J. L. H. Faccini. 1985. *In vitro* development of *Raillietia auris* (Leidy) (Acarina: Mesostigmata). *Acarologia* 26:211–214.

Furman, D. P. 1957. Revision of the genus *Sternostoma* Berlese and Trouessart (Acarina: Rhinonyssidae). *Hilgardia* 26:473–495.

Furman, D. P. 1959. Feeding habits of symbiotic mesostigmatid mites of mammals in relation to pathogen-vector potential. *Am. J. Trop. Med. Hyg.* 8:5–12.

Furman, D. P. 1979. Specificity, adaptation and parallel evolution in the endoparasitic Mesostigmata of mammals. In: *Recent Advances in Acarology*, Vol. 2 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 329–337.

Furman, D. P., H. Bonasch, R. Springsteen, D. Stiller and D. F. Rahlmann. 1974. Studies on the biology of the lung mite *Pneumonyssus simicola* Banks (Acarina: Halarachnidae) and diagnosis of infestation in macaques. *Lab. Animal Sci.* 24:622–629.

Furman, D. P. and F. J. Radovsky. 1963. A new species of *Ornithonyssus* from the white-tailed antelope squirrel, with a rediagnosis of the genus *Ornithonyssus* (Acarina: Dermanyssidae). *Pan-Pac. Entomol.* 39:75–79.

Furman, D. P. and S. W. Smith. 1973. *In vitro* development of two species of *Orthohalarachne* (Acarina: Halarachnidae) and adaptations of the life cycle for endoparasitism in mammals. *J. Med. Entomol.* 4:415–416.

Hall, L. 1984. And then there were bats. In: *Vertebrate Zoogeography and Evolution in Australia* (M. Archer and G. Clayton eds.). Hesperian Press, Carlisle (W. Australia). Pp. 837–852.

Hand, S. 1984. Bat beginnings and biogeography: a southern perspective. In: *Vertebrate Zoogeography and Evolution in Australia* (M. Archer and G. Clayton eds.). Hesperian Press, Carlisle (W. Australia). Pp. 853–904.

Hellanthal, R. A. and R. D. Price. 1991. Biosystematics of the chewing lice of pocket gophers. *Annu. Rev. Entomol.* 36:185–203.

Hogsette, J. A., J. F. Butler, W. V. Miller and R. D. Hall. 1991. Annotated bibliography of the northern fowl mite, *Ornithonyssus sylviarum* (Canestrini and Fanzago) (Acari: Macronyssidae). *Entomol. Soc. Am. Misc. Publ.* 76:1–62.

Hughes, T. E. 1959. *Mites or the Acari*. Athlone Press, London. Pp. 1–225.

Hull, W. B. 1956. The nymphal stages of *Pneumonyssus simicola* Banks, 1901 (Acarina: Halarachnidae). *J. Parasitol.* 42:653–656.

Kethley, J. B. and D. E. Johnston. 1975. Resource tracking patterns in bird and mammal ectoparasites. *Misc. Publ. Entomol. Soc. Am.* 9:231–236.

Kim, K. C. (ed.). 1985. *Coevolution of Parasitic Arthropods and Mammals*. Wiley, NY. 800 pp.

Kim, K. C., V. L. Haas and M. C. Keyes. 1980. Populations, microhabitat preference, and effects of infestation of two species of *Orthohalarachne* (Halarachnidae: Acarina) in the northern fur seal. *J. Wildl. Dis.* 16:45–51.

Koopman, K. F. 1984. Bats. In: *Orders and Families of Recent Mammals of the World* (S. Anderson and J. K. Jones, Jr. eds.). Wiley, NY. Pp. 145–186.

Krantz, G. W. 1978. *A Manual of Acarology*, 2nd edition. Oregon State Univ. Book Stores, Corvallis, OR. 509 pp.

Lavoipierre, M. M. J. and A. J. Beck. 1967. Feeding mechanisms of *Chiroptonyssus robustipes* (Acarina: Macronyssidae) as observed on the transilluminated bat wing. *Exp. Parasitol.* 20:312–320.

Lees, A. D. 1952. The role of cuticle growth in the feeding process of ticks. *Proc. Zool. Soc. Lond.* 121:759–772.

Lindquist, E. E. 1984. Current theories on the evolution of major groups of Acari and their relationships with other groups of Arachnida, with consequent implications for their classification. In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood Ltd., Chichester. Pp. 28–46.

Men, Y. T. 1959. Concerning the feeding of the mite *Haemolaelaps casalis* (Gamasoidea, Parasitiformes). *Medskaya Parazitol.* 28:603–609. (In Russian).

Micherdzinski, W. 1980. *Eine Taxonomische Analyse der Familie Macronyssidae Oudemans, 1936. I. Subfamilie Ornithonyssinae Lange, 1958 (Acarina, Mesostigmata).* Panstwowe Wydownictwo Nauk., Warsaw. Pp. 1–264.

Moss, W. W. 1978. The mite genus *Dermanyssus*: a survey, with description of *Dermanyssus trochilinus*, n. sp., and a revised key to the species (Acari: Mesostigmata: Dermanyssidae). *J. Med. Entomol.* 14:627–640.

Nowak, R. M. 1991. Order Chiroptera. In: *Walker's Mammals of the World*, Vol. 1 (5th ed.). Johns Hopkins Univ. Press, Baltimore. Pp. 190–393.

Oudemans, A. C. 1904. Notes on Acari, eleventh series. *Tijdschr. Entomol.* 46:93–104.

Pence, D. B. and S. D. Castro. 1976. Studies on the variation and morphology of the *Ptilonyssus "sairae"* complex (Acarina: Rhinonyssidae) from North American passeriform birds. *J. Med. Entomol.* 13:71–95.

Pettigrew, J. D. 1991. Wings or brain? Convergent evolution in the origins of bats. *Syst. Zool.* 40:199–216.

Pettigrew, J. D., B. G. M. Jamieson, S. K. Robson, L. S. Hall, D. I. McAnally and H. M. Cooper. 1989. Phylogenetic relationships between microbats, megabats and primates

(Mammalia: Chiroptera and Primates). *Phil. Trans. R. Soc. Lond., B, Biol. Sci.* 325:489–559.

Phillips, C. J., J. K. Jones, Jr. and F. J. Radovsky. 1969. Macronyssid mites in the oral mucosa of long-nosed bats: occurrence and associated pathology. *Science* 165:1368–1369.

Popp, E. 1961. Bau und Funktion des Ambulacrums der Larve von *Orthohalarachne laetalis* Popp (Acarina: Halarachnidae). *Zool. Anz.* 167:29–33.

Potter, D. A. and D. E. Johnston. 1978. *Raillietia whartoni* sp. n. (Acari-Mesostigmata) from the Uganda Kob. *J. Parasitol.* 64:139–142.

Radovsky, F. J. 1960a. *Haemogamasus liponyssoides hesperus* n. ssp. with a discussion of the *H. liponyssoides* complex (Acarina: Haemogamasidae). *J. Parasitol.* 46:401–409.

Radovsky, F. J. 1960b. Biological Studies on *Haemogamasus liponyssoides* Ewing (Acarina: Haemogamasidae). *J. Parasitol.* 46:410–417.

Radovsky, F. J. 1964. *The Macronyssidae and Laelapidae (Acarina: Mesostigmata) parasitic on bats*. Ph.D. dissertation, Univ. of California, Berkeley, CA. 600 pp.

Radovsky, F. J. 1966. Revision of the macronyssid and laelapid mites of bats: outline of classification with description of new genera and new type species. *J. Med. Entomol.* 3:93–99.

Radovsky, F. J. 1967. The Macronyssidae and Laelapidae (Acarina: Mesostigmata) parasitic on bats. *Univ. Calif. Publ. Entomol.* 46:1–288.

Radovsky, F. J. 1969. Adaptive radiation in the parasitic Mesostigmata. *Acarologia* 11:450–483.

Radovsky, F. J. 1985. Evolution of mammalian mesostigmate mites. In: *Coevolution of Parasitic Arthropods and Mammals* (K. C. Kim ed.). Wiley, NY. Pp. 441–504.

Radovsky, F. J., J. K. Jones, Jr. and C. J. Phillips. 1971. Three new species of *Radfordiella* (Acarina: Macronyssidae) parasitic in the mouth of phyllostomid bats. *J. Med. Entomol.* 8:737–746.

Rudnick, A. 1960. A revision of the mites of the family Spinturnicidae (Acarina). *Univ. Calif. Publ. Entomol.* 17:157–284.

Sikes, R. K. and R. W. Chamberlain. 1954. Laboratory observations on three species of bird mites. *J. Parasitol.* 40:691–697.

Simmons, N. B., M. J. Novacek and R. J. Baker. 1991. Approaches, methods, and the future of the chiropteran monophyly controversy: a reply to J. D. Pettigrew. *Syst. Zool.* 40:239–243.

Skaliy, P. and W. J. Hayes. 1949. The biology of *Liponyssus bacoti* (Hirst, 1913) (Acarina: Liponyssidae). *Am. J. Trop. Med.* 29:759–772.

Smith, J. D. 1972. Systematics of the chiropteran family Mormoopidae. *Misc. Publ. Mus. Nat. Hist., Univ. Kans.* 56:1–132.

Smith, J. D. and G. Madkour. 1980. Penial morphology and the question of chiropteran monophyly. *Proc. 5th Int. Bat Res. Conf.* (D. E. Wilson and A. L. Gardner eds.). Texas Tech Press, Lubbock, TX. Pp.347–365.

Strandtmann, R. W. 1958. Host specificity of bird nasal mites (Rhinonyssidae) is a function of the gregariousness of the host. *Proc. 10th Int. Congr. Entomol.* 1:909–911.

Strandtmann, R. W. 1961. The immature stages of the *Ptilonyssus* complex (Acari: Mesostigmata: Rhinonyssidae). *Proc. 11th Int. Congr. Entomol.* 1:283–286.

Strandtmann, R. W. and C. M. Clifford. 1962. A new genus and species of nasal mite from the varied thrush *Ixoreus neveus* (Gmelin) (Acarina: Rhinonyssidae). *J. Parasitol.* 48:723–725.

Tipton, V. J. 1960. The genus *Laelaps* with a review of the Laelaptinae and a new subfamily Alphalaelaptinae. *Univ. Calif. Publ. Entomol.* 16:233–356.

Tsymbal, T. G. and N. T. Litvishko. 1955. Acariasis of the ear in cattle. *Zool. Zh.* 34:1229–1241. (In Russian).

Vitzthum, H. G. 1940–43. Acarina. In: *Klassen und Ordnungen des Tierreichs* (H. G. Braun ed.). Leipzig 5(4), Book 5:1–1011.

Williams, G. L., R. L. Smiley and B. C. Redington. 1978. A taxonomic study of the genus *Haemogamasus* in North America, with descriptions of two new species (Acari: Mesostigmata, Laelapidae). *Int. J. Acarol.* 4:235–273.

Woolley, T. A. 1988. *Acarology: Mites and Human Welfare.* Wiley, NY. Pp. 1–484.

Yunker, C. E. and F. J. Radovsky. 1966. The dermanyssid mites of Panama (Acarina: Dermanyssidae). In: *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton eds.). Field Museum of Natural History, Chicago. Pp. 83–103.

9

Evolution and Life-History Patterns of Mites Associated with Bees

George C. Eickwort

CONTENTS

1. Introduction

Bees (superfamily Apoidea, order Hymenoptera) represent one of the major success stories in evolution. With about 20,000 species in 11 families (Michener 1979), they are twice as diverse as birds. All species, except cleptoparasites (cuckoos), construct nests and provision cells with pollen and concentrated nectar (honey), the sole food of both larvae and adults. This niche is otherwise occupied only by a few vespid wasps.

Like other nest-making animals (e.g. birds, rodents, scarab beetles, wasps, ants and termites), bees are hosts to a wide diversity of mites. While recent reviews have dealt with the mites associated with social bees (especially honey bees, stingless bees, and bumble bees) (Delfinado-Baker et al. 1989; Eickwort 1988, 1990 and references therein), there has been no attempt to present an

overview of the mites associated with a much greater diversity of solitary bees. This chapter compares the mites that are associated with each of the major bee lineages and outlines their life-history strategies. The evolutionary patterns of these mites with respect to those of their hosts are also discussed.

I will consider only those mites that are largely or exclusively dependent upon nourishment provided by bees or their nests. As a result, the large number of species that incidentally occur in nests but which also commonly occur in other habitats are excluded. These incidental species may be the most abundant and conspicuous mites in social bee nests, especially the scavenger "stored product mites" that invade the hives of honey bees (Eickwort 1988, 1990). I also exclude generalized parasites which are not host-specific to bees. Although some of these mites can be ecologically important to their hosts, they show no evidence of having evolved specific adaptations for living in bee nests, and their evolutionary patterns have developed independently of apoid evolution.

The distinction between important and incidental associates is not often made in the literature. Most accounts of bee mites involve only descriptions of those stages that are phoretic on the bees. It is not true that every mite that "hitchhikes" on a bee developed in that bee's nest. For example, the conspicuous deutonymphs of Uropodidae are frequently phoretic on solitary bees (e.g. Haeseler 1982), but there is no evidence that any uropodine species develops in solitary bee nests. Moreover, the study of bee mites is in its infancy, and only a few of the vast number of mite species found attached to bees in museum collections have been described.

Given these restrictions, the summary of important bee mites in Tables 9.1–9.3 is mostly preliminary. These tables are based on associations reported in the literature and supplemental associations based on material in the Cornell University Insect Collections. Where one host subfamily predominates among several recorded for a mite genus, that subfamily is marked with an asterisk in the tables.

2. Host Taxa

Traditionally, bees have been divided into two major groupings, the supposedly more primitive "short-tongued bees" (Andrenidae, Colletidae, Ctenoplectridae, Halictidae, Melittidae, Oxaeidae, and Stenotritidae), and the more advanced "long-tongued bees" (Anthophoridae, Apidae, Fideliidae, and Megachilidae) (Michener 1979). Recent studies indicate that most families of short-tongued bees are not of the evolutionary lineage that gave rise to the long-tongued bees, and the relationships among these families are obscure, with considerable plesiomorphy and convergence masking their true phylogeny. My hypothesis of relationships among bee families and subfamilies with known mite associates is given in Figure 9.1.

Most short-tongued bees nest solitarily or communally, with primitively euso-

Table 9.1. Acari associated with short-tongued bees. Numbers in parentheses represent the numbers of described species.

Genus	Host taxon	Distribution[b]	Ecology[c]
ASTIGMATA			
Histiostomatidae			
Anoetus (10)	Halictinae	NE, NT, PA, AU	s
Glyphanoetus[a] (1)	Nomiinae	NE	s
Histiostoma[a]	Diphaglossinae	NE, NT	s
Acaridae			
Sancassania[a] (1)	Halictinae & Nomiinae	NE	c, s
Schulzea[a] (2)	Halictinae & Hylaeinae	NT, PA, OR	s?
Konoglyphus (1)	Halictinae	NT	s?
Halictacarus (1)	Halictinae	ET	s?
Ctenocolletacarus (3)	Stenotritidae	AU	c, s?
Winterschmidtiidae			
New genus[d]	Hylaeinae	AU	s?
PROSTIGMATA			
Trochometridiidae			
Trochometridium[a] (1)	Halictinae, Nomiinae, & Panurginae	NE, NT	s
Pygmephoridae			
Parapygmephorus (Sicilipes) (5)	Halictinae	NE, NT, PA	s
P. (Parapygmephorus)[a] (1)	Nomiinae & Halictinae	ET, OR	s
Scutacaridae			
Imparipes[a] (11)	Halictinae, Nomiinae, Rophitinae, & Andreninae	NE, NT, PA	s
Scutacarus[a] (1)	Halictinae	NE	s
Nasutiscutacarus (2)	Nomiinae	OR	s
MESOSTIGMATAAmeroseiidae			
Neocypholaelaps[a] (1)	Hylaeinae	OR	c
Laelapidae			
Hypoaspis s.l.[a]	Diphaglossinae	NT	pr
Laelaspoides (1)	Halictinae	NE, AU?	c

a = Some species not associated with short-tongued bees.

b = AU = Australian, ET = Ethiopian, NE = Nearctic, NT = Neotropical, OR = Oriental, PA = Palearctic.

c = c = provisions (cleptoparasite); pr = predator; s = scavenger or saprophyte.

d = From OConnor, 1988.

cial colonies occurring only in sweat bees (Halictinae). Most short-tongued bees nest in the soil (a few nest in rotting wood) and line their cells with glandular secretions (Fig. 9.2a). These secretions provide a homeostatic environment for the stored provisions (a semi-solid loaf of dilute honey and pollen) and developing larvae. The adult bees do not tend their brood after they oviposit and close the cells. If a bee larva fails to develop, the provision mass is quickly enveloped by

Table 9.2. Acari associated with long-tongued bees (except Apidae). Numbers in parentheses represent the numbers of described species. Where a host subfamily is predominantly used, among several recorded for a mite genus, that subfamily is marked with an asterisk.

Genus	Host taxon	Distribution[b]	Ecology[c]
ASTIGMATA			
Histiostomatidae			
Histiostoma s.l.[a] (2)	Anthophorinae & Xylocopinae	NE, NT, ET	s
Acaridae			
Sancassania[a]	Megachilinae	NE	c, s
Horstia[a] (14)	**Xylocopinae*** & Megachilinae	NE, NT, PA, ET, OR, AU	c, s?
Neohorstia (1)	Megachilinae	PA	s?
Cerophagopsis[a] (2)	Megachilinae	OR, PA, NE	s?
Megachilopus (1)	Megachilinae	ET	s?
Sennertionyx (1)	Megachilinae	PA, NE	s?
Schulzea[a] (1)	Megachilinae	PA	s?
New genus[d]	Anthophorinae	?	s?
New genus[d]	Anthophorinae	NT	s?
Suidasiidae			
Tortonia[a] (3)	Megachilinae & Xylocopinae	PA, OR, NE, ET	c, s?
Winterschmidtiidae			
Vidia (7)	Megachilinae	PA, NE, OR, ET	s
Chaetodactylidae			
Chaetodactylus (15)	**Megachilinae***, Lithurginae, Xylocopinae, & Anthophorinae	NE, NT, PA, ET	c
Sennertia (59)	**Xylocopinae*** & Megachilinae	NT, AU, PA, NE, OR, ET	c
Roubikia (1)	Anthophorinae	NT	c?
PROSTIGMATA			
Cheyletidae			
Cheletophyes (13)	Xylocopinae	ET, OR, NT	pr
Tarsonemidae			
Tarsonemus[a] (2)	Xylocopinae	NT, OR	s?
Trochometridiidae			
Trochometridium[a] (1)	Anthophorinae	NE	s
MESOSTIGMATA			
Ameroseiidae			
Afrocypholaelaps[a] (2)	Megachilinae & Xylocopinae	ET	c
Neocypholaelaps[a] (6)	Ctenoplectridae, Anthophorinae, Megachilinae, & Xylocopinae	ET	c
Laelapidae			
Hypoaspis s.l.[a] (2)	Xylocopinae & Megachilinae	OR, ET	pr
Dinogamasus (36)	Xylocopinae	PA, ET, OR	s?

a = Some species not associated with long-tongued bees.
b = AU = Australian, ET = Ethiopian, NE = Nearctic, NT = Neotropical, OR = Oriental, PA = Palearctic.
c = c = provisions (cleptoparasite); pr = predator; s = scavenger or saprophyte.
d = From OConnor, 1988.

Table 9.3. Acari associated with apid bees. Numbers in parentheses represent the numbers of described species.

Genus	Host taxon	Distribution[b]	Ecology[c]
ASTIGMATA			
Meliponocoptidae			
Meliponocoptes (3)	Meliponinae	NT	s?
Meliponoecius (1)	Meliponinae	NT	s?
New genus[d]	Meliponinae	NT	?
Acaridae			
Kuzinia (6)	Bombinae	PA, NE, OR	s, c
Cerophagopsis[a] (1)	Meliponinae	AU	s?
Horstiella (2)	Euglossinae	NT	s?
Gaudiellidae			
Cerophagus (2)	Bombinae	PA, NE	s?
Platyglyphus (1)	Meliponinae	OR	s?
Gaudiella (2)	Meliponinae	NT	s?
Partamonacoptes (1)	Meliponinae	NT	s?
Meliponopus (1)	Meliponinae	NT	s?
Carpoglyphidae			
Carpoglyphus[a] (1)	Apinae	NE, PA	c
PROSTIGMATA			
Tydeidae			
Proctotydeus[a] (3)	Meliponinae	NT	s
Melissotydeus (1)	Meliponinae	NT	s?
Scutacaridae			
Imparipes[a] (2)	Apinae & Bombinae	NE, PA	s
Scutacarus[a] (3)	Apinae & Bombinae	PA, NE, NT	s
Parascutacarus (1)	Bombinae	OR	s
Tarsonemidae			
Tarsonemus[a] (1)	Apinae	PA	s?
Pseudacarapis (1)	Apinae	OR	?
Acarapis (3)	Apinae	NT, PA, NE, AU, OR, ET	pa
Podapolipidae			
Locustacarus[a] (1)	Bombinae	NE, AU, PA, OR	pa
MESOSTIGMATA			
Parasitidae			
Parasitellus (18)	Bombinae	PA, NE	pr, c
Family?			
Meliponipachys (1)	Meliponinae	NT	pr?
Macrochelidae			
Macrocheles[a] (1)	Apinae & Bombinae	NE	pr
Trigonholapsis (1)	Meliponinae	NT	pr?
Grafia (3)	Meliponinae	NT	pr?
Ascidae			
Proctolaelaps[a] (2)	Bombinae	PA, NE	c?

Continued

Table 9.3. Continued.

Genus	Host taxon	Distribution[b]	Ecology[c]
Ameroseiidae			
Afrocypholaelaps[a] (1)	Meliponinae & Apinae	ET, AU	c
Neocypholaelaps[a] (7)	Meliponinae & Apinae	AU, OR, ET, PA	c
Edbarellus (1)	Apinae	AU	c
Laelapidae			
Hypoaspis s.l.[a] (3)	Meliponinae	NT	pr
Urozercon[a] (1)	Meliponinae	NT	pr
Pneumolaelaps (18)	Bombinae	PA, NE	pr, c
Neohypoaspis (1)	Meliponinae	NT	pr
Hunteria (1)	Meliponinae	NT	pr?
Stevelus (1)	Meliponinae	NT	pr?
Melittiphisoides (1)	Meliponinae	NT	pr?
Meliponaspis (1)	Meliponinae	ET	pr?
Eumellitiphis (3)	Meliponinae	OR, NT	pr?
Zontia (1)	Meliponinae	NT	pr?
Bisternalis[a] (5)	Meliponinae	NT	pr
Melittiphis (1)	Apinae	AU, PA, NE, OR,	c
Tropilaelaps (2)	Apinae	AU	pa
Varroidae			
Varroa (2)	Apinae	OR, NT, NE, PA, ET, AU	pa
Euvarroa (1)	Apinae	OR	pa
Trachyuropodidae			
Oplitis[a] (1)	Meliponinae	NT	s?
Urodiscella[a] (1)	Meliponinae	NT	s?
Diplogyniidae			
Calaenosthanus (1)	Meliponinae	NT	?
Triplogyniidae			
Triplogynium[a] (1)	Meliponinae	NT	?

a = Some species not associated with apid bees.
b = AU = Australian, ET = Ethiopian, NE = Nearctic, NT = Neotropical, OR = Oriental, PA = Palearctic.
c = c = provisions (cleptoparasite); pr = predator; pa = parasite; s = scavenger or saprophyte.
d = B. M. OConnor, pers. comm.

fungus. If the larva survives, it defecates on the cell wall after it consumes the provision mass, and this fecal mass often becomes fungus-infected. Nematodes and small annelids (Enchytraeidae) also commonly infest provision masses and feces. Mites within nests of solitary bees are most often restricted to individual cells and they typically enter them by being phoretic on the mother bees. Some mites, however, can move through the soil to invade closed cells.

An exception to the above pattern is found in most Colletidae, which line their cells with a cellophane-like secretion and store fluid provisions. The Hylaeinae are renters, reusing natural or insect-made cavities (often in twigs or logs) rather

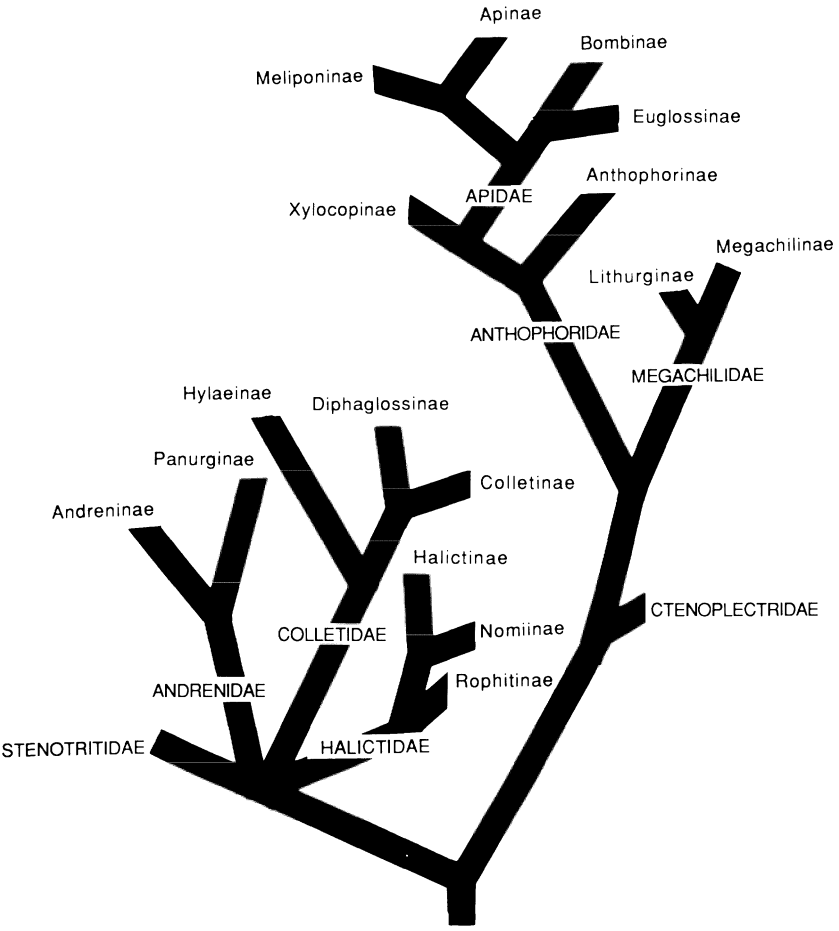
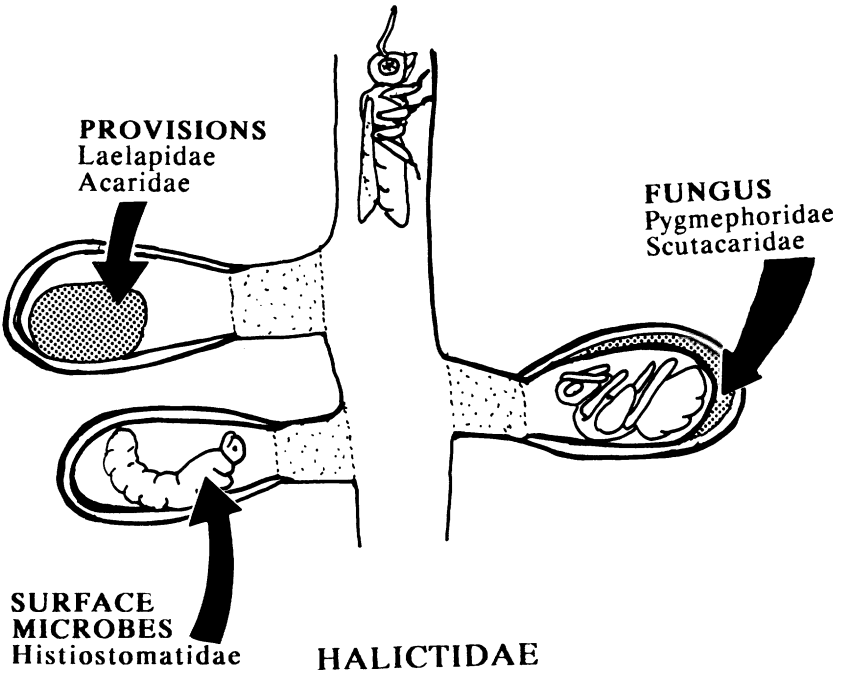


Figure 9.1. Hypothesized phylogenetic relationships of families and subfamilies of bees associated with mites.

than digging burrows themselves. These nests are exposed to mites that inhabit woody vegetation rather than soil.

The long-tongued bees form a monophyletic lineage. Most Megachilidae line their cells with foreign materials (e.g. leaves, plant hairs, or resin) instead of a glandular secretion (Fig. 9.2b). While more primitive Megachilidae excavate nests in soil or occasionally solid wood, many megachilid lineages include renters of preexisting cavities and builders of free-standing masonry nests.

The two subfamilies of noncleptoparasitic Anthophoridae are quite different in their nesting biology. The Anthophorinae are principally solitary or communal soil-nesters, making similar nests to those of the short-tongued bees. The Xylocopinae, or carpenter bees, mostly excavate nests in wood or pithy stems and do



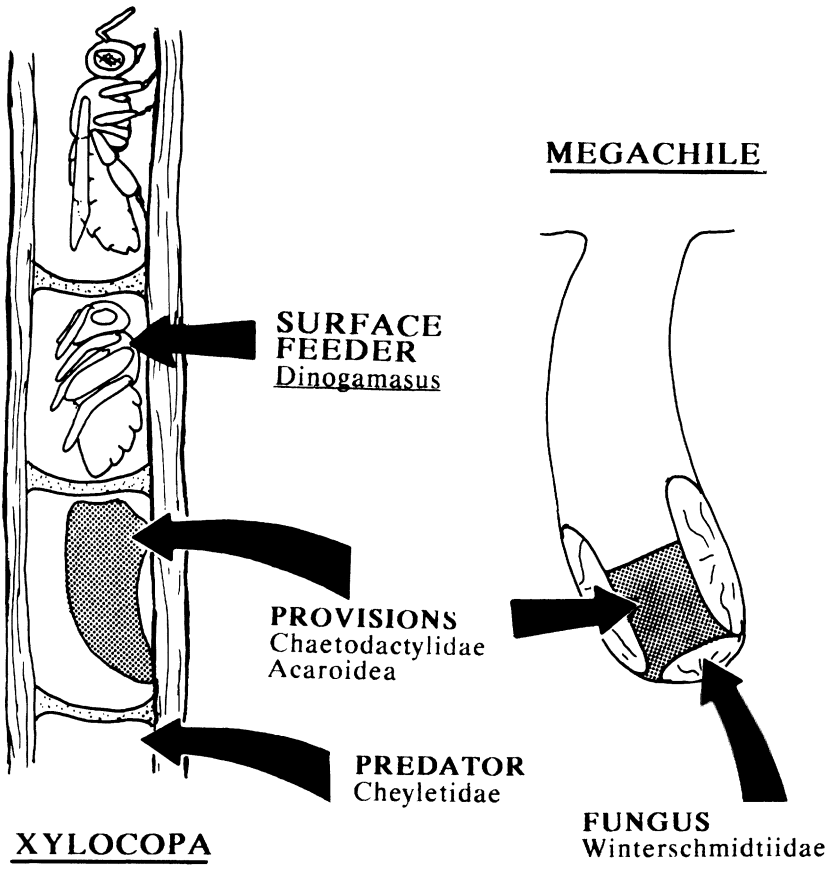
(A)

Figure 9.2. Mite feeding guilds. (A) Feeding guilds of mites within nests of sweat bees (Halictidae). (B) Feeding guilds of mites within nests of large carpenter bees (Anthophoridae: *Xylocopa*) and leafcutter bees (Megachilidae: *Megachile*). (C) Feeding guilds of mites within nests of bumble bees (Apidae: *Bombus*) and honey bees (Apidae: *Apis*).

not secrete a thick cell lining. Adult carpenter bees are comparatively long-lived, most have overlapping generations, and many are semisocial or primitively eusocial.

Bees in the family Apidae (Fig. 9.2c) build free-standing cells of secreted wax and/or foreign materials, especially resins, that are typically clustered in natural cavities. Apid bees are comparatively long-lived and an overlap of generations and reuse of cavities is common. The subfamily Euglossinae are solitary or semisocial neotropical orchid bees, and the remaining apids are all eusocial. Bumble bees (Bombinae) are primitively eusocial and form annual colonies. Their nests are often built in abandoned rodent nests and are consequently exposed to mite residents of those habitats.

The advanced eusocial stingless bees (Meliponinae) and honey bees (Apinae) form perennial colonies that are initiated by swarms of workers accompanying a queen, and they store honey and pollen separate from the developing brood. In contrast to nests of bees in other families, there is extensive waste material



(B)

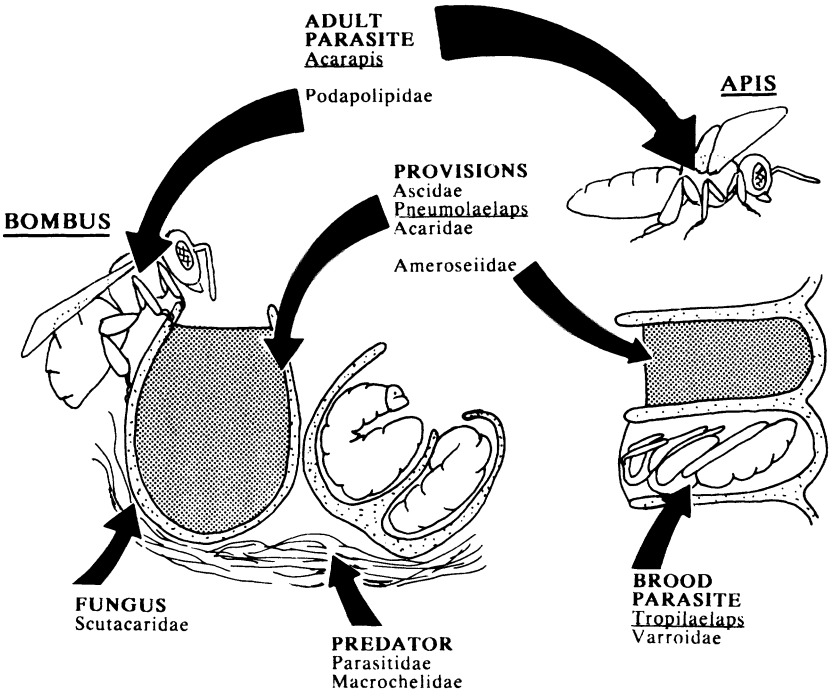
Figure 9.2. (Continued)

produced in apid nests, and this waste provides an ample substrate on which mites can develop outside of the brood cells.

3. Associated Mites

3.1 Astigmata

The Astigmata are typically the most abundant mites in nests of bees, as they are in nests of social insects in general (Eickwort 1990). They are unusual among mites because they are nonpredators that specialize in the exploitation of nutrient-rich, temporary habitats, especially insect and vertebrate nests (OConnor 1982). The development of a specialized phoretic deutonymph is an important aspect of



(C)

Figure 9.2. (Continued)

their adaptation to nest-building insect hosts. The production of deutonymphs is typically synchronized with the emergence of new adult bees within a nest. The phylogeny of insect-associated Astigmata has been the subject of intensive study by OConnor, and his recent review of Astigmata associated with Apoidea (1988) forms the basis of the following summary.

Histiostomatid mites have chelicerae modified for filter feeding and they typically inhabit surfaces with liquid films from which they obtain microorganisms. *Anoetus*, as defined by Mahunka (1974), contains only obligatory associates of halictine (sweat) bees, and they are the most commonly encountered mites in halictine nests worldwide. These mites occur in association with both solitary and social halictine species. Some species of the halictine genus *Lasioglossum* carry deutonymphs of *Anoetus* in a specialized acarinarium on the anterior surface of metasomal tergum I. Deutonymphs remain on their female hosts while the latter hibernate, and they detach from host bees as new cells are constructed in the spring. Tritonymphs and adult females are subsequently found on the provisions where they sweep the surface, presumably feeding on microorganisms. A very small (larva-sized) adult male then becomes apparent, typically when it

climbs on the dorsum of a female. I suspect that these males develop rapidly from the first unfertilized eggs laid by the females, perhaps skipping all nymphal instars, and then mate with females of the parental generation. The inseminated females then lay fertilized eggs, all of which develop into females. Those female eggs are laid on the cell wall and bee larvae, and mite larvae and protonymphs feed on the surfaces of the bee larvae and pupae, apparently consuming microorganisms; they do not harm the bees upon which they feed (Eickwort 1979, and in prep.).

Histiostomatids currently placed in the plesiomorphic catch-all genera *Histiostoma* and *Glyphanoetus* occur on other taxa of bees (Tables 9.1, 9.2). These mites can develop huge populations in cells without killing their hosts, and their development and biology appears similar to that of *Anoetus*.

The Acaridae include numerous mites that occur as scavengers and cleptoparasites in nests of both solitary and social bees, feeding on fungi, honey and pollen. Many of these are stored-product pests that can become the most numerous mites in honey bee hives (Eickwort 1988), although they are not phoretic on bees and are not specialized for associations with them. *Sancassania* (= *Caloglyphus*) contains species with a wide variety of associations with arthropods, including soil-nesting bees (Eickwort 1979; Cross and Bohart 1969, 1991). In cells these mites may occur on feces deposited by bee larvae, but they are especially abundant in cells containing dead bees and moldy provisions. The mites burrow through and tear apart the provision masses, consuming pollen, fungi, and dead brood. There is, however, no evidence that the mites kill the brood; they are presumably scavengers that take special advantage of food resources in cells in which brood fail to develop. Deutonymphs are facultatively produced and are phoretic on bees that develop in other cells; it is probable that these deutonymphs move through the soil to locate their hosts in the nest burrows.

Ctenocolletacarus, an acarid genus closely related to *Sancassania* (OConnor 1988), is restricted to bees of the genus *Ctenocolletes* (Stenotritidae) (Fain 1984a, Fain and Houston 1986). In the nest cells, the deutonymphs molt into tritonymphs and then into adults. Adults are found on the provision masses and cell walls, where females lay eggs. The larval and protonymphal mites occur on developing bee larvae, provisions, and fecal masses. Gut analyses indicate that these mites first consume pollen grains from the provision masses, and then feed on an amorphous substance that may originate from the bee larva's surface or from its feces. Deutonymphs are obligatory and are found in specialized acarinaria on each side of the third and fourth metasomal terga of female bees. Of adult female *Ctenocolletes*, 74%–90% (four species) carry deutonymphs (Houston 1987).

A diverse lineage of the Acaridae, the subfamily Horstiinae (= Tyrophaginae of OConnor, 1982), has evolved in association with bees (OConnor 1988). This includes *Kuzinia* associated with bumble bees; *Horstia* (including *Ceroglyphus*) associated primarily with carpenter bees; *Horstiella* associated with Euglossinae; *Sennertionyx*, *Neohorstia*, *Cerophagopsis*, and *Megachilopus* associated with

Megachilinae and Meliponinae, two unnamed genera associated with Anthophorinae, and *Konoglyphus*, *Halictacarus* and *Schulzea* associated with Halictinae (species of the latter genus also occur on other bees) (OConnor 1988).

Kuzinia is typically the most abundant mite in bumble bee nests, where they feed on pollen, honey, organic refuse, and cocoon substances but do not harm developing bees (Chmielewski 1969, 1971). *Horstia virginica* may produce large populations in cells of the carpenter bee *Xylocopa virginica* after the bee brood die. The mites feed on nectar in the provisions, and it has been hypothesized that the mites frequently kill the bee brood (Krombein 1962a). Infestation rates were very low in Krombein's study; only three nests of "several hundred" contained mites. Although most species of *Horstia* have been described from xylocopine bees, individual deutonymphs have been found on other bees and wasps (Fain 1984b), and one species has even been recovered from house dust (Fain and Chmielewski 1987).

Nothing has been published about the biology of other genera of this lineage, although collection data for three genera indicate that they do not harm the bee brood (OConnor 1988). Also, the females of *Thectochlora alaris* (Halictinae) have a specialized acarinarium on metasomal tergum I in which deutonymphs of an unnamed species of *Schulzea* are phoretic (Eickwort and OConnor, unpubl.).

The Suidasiidae includes *Tortonia*, whose species are all associates of various bees and wasps (OConnor 1988). The biology of *Tortonia* species appears to vary according to host, and host specificity also varies. Some species are apparently obligate associates of Megachilidae, while *T. quadridens* is associated with solitary wasps and the carpenter bee *X. virginica*. *T. quadridens* may kill carpenter bee brood before acting as a cleptoparasite or scavenger (OConnor observed *T. quadridens* killing brood of the sphecid wasp *Trypoxylon*, although Krombein [1962a] observed mites developing in cells containing live larvae of the vespid *Monobia*).

A related lineage of obligatory bee associates has been placed in the family Gaudiellidae by OConnor (1988). It includes *Cerophagus*, associated with bumble bees (OConnor 1992a), and four genera associated with stingless bees. The biology of these mites is unknown.

The superfamily Hemisarcoptoidea is primitively fungivorous and associated with wood-boring insects (OConnor 1982). Representatives of four families have associations with bees. *Vidia* (Winterschmidtiidae) is primarily associated with megachiline bees. These mites occur on the leaf pieces that form the cell linings of leafcutter bees (*Megachile*), where they apparently feed solely on fungi. Deutonymphs are obligatory and attach to the mature bee larva before it spins its cocoon, spending the winter on the diapausing bee larva (OConnor and Eickwort 1988).

An undescribed genus of Winterschmidtiidae occurs in association with Australian Hylaeinae. Feeding stages are attached to the bee larvae (T. Houston, reported in OConnor 1988). The Meliponocoptidae consists of specialized genera

(*Meliponocoptes*, *Meliponoecius*; and an undescribed genus, OConnor, pers. comm.) known from adults in stingless bee nests (Fain and Rosa 1983); nothing is known about their biology.

The family Chaetodactylidae is restricted to associates of bees. *Chaetodactylus* is associated primarily with Megachilidae (Fain 1981b), and *Sennertia* is associated primarily with Xylocopinae (Fain 1981a). *Roubikia* is associated with *Tetrapedia* (Anthophorinae) (Baker et al. 1987, OConnor 1992b). As with *Horstia* and *Tortonia*, *Sennertia* may occur in large numbers on the provision masses in cells of *Xylocopa* that lack developing brood, apparently feeding on pollen (Skaife 1952). Lombert et al. (1987) hypothesized that this mite is a cleptoparasite that may kill the brood. However, *Sennertia* also develops in cells without killing brood (Skaife 1952, Watmough 1974, OConnor 1988). *Chaetodactylus* have been observed to kill eggs or young larvae and then develop as cleptoparasites, feeding on the provisions and undergoing several generations in a cell (Krombein 1962b, Fain 1966, Maeta 1978), although Torchio (pers. comm.) has observed that brood killing is facultative in a species associated with *Osmia lignaria*.

Two types of deutonymphs are produced when the provisions are consumed, an inert deutonymph which is pharate in the protonymphal cuticle and an active deutonymph. The active deutonymphs attach to bees that emerge from other cells and pass through the infested cell, while the inert deutonymphs remain in the cells as a reservoir to infest hosts that reuse a burrow. Infestation rates are low; typically less than 15% of cells in nests of seven species of *Osmia*.

The family Carpoglyphidae is best known as stored product mites, and *Carpoglyphus lactis* occurs in foods with high sugar content that have begun fermentation, including stored pollen and honey in honey bee hives (Eickwort 1988). All nondeutonymphal stages of a species of *Carpoglyphus* have been collected inside flowers and deutonymphs are also phoretic on butterflies and moths (Fain and Rack 1987). It is possible that *Carpoglyphus* (under natural conditions) develops much like *Neocypholaelaps* (Mesostigmata) in flowers, using various flower-visiting insects as phoretic hosts, and is also capable of reproducing on stored provisions in apid colonies.

3.2 Prostigmata

Relatively few taxa of the diverse suborder Prostigmata have evolved important relationships with bees. Among the "red velvet mites" of the Parasitengona, larvae of *Leptus* (Erythraeidae) commonly parasitize bees (e.g. Southcott 1989) but there is no indication that they specialize on them. Fungivorous *Proctotydeus* and *Melissotydeus* (Tydeidae) are abundant in stingless bee colonies and may be mutualistic (Flechtmann and Camargo 1979). Predaceous Prostigmata may facultatively occur in nests (especially of social apids) where they feed predominantly on Astigmata. Species of *Cheletophyes* (Cheyletidae) are restricted to associations with large carpenter bees (Xylocopinae) (Fain et al. 1980, Smiley

and Whitaker 1981, Putatunda and Kapil 1988). All stages occur in nests and adult females are phoretic, often found in the acarinaria of the female bees that house *Dinogamasus* (Mesostigmata). *Cheletophyes apicola* occurs in separate thoracic acarinaria on *Xylocopes latipes* (OConnor 1993). *Cheletophyes* are undoubtedly predators on astigmatid mites in carpenter bee nests, and OConnor (1993) hypothesizes that the increased sclerotization on astigmatids associated with Old World *Xylocopa* may be an evolutionary response to this predator.

The majority of the prostigmatid bee associates are in the Heterostigmata. *Trochometridium tribulatum* (Trochometridiidae) occurs in the nests of diverse soil-dwelling bees and other insects (Cross and Bohart 1979). Adult females, which are phoretic, possess well-developed cavities (sporothecae) in which they place fungal spores (Lindquist 1985). The fungus infests the provision masses in cells in which the bee brood has died, and adult female mites feed on the fungal hyphae. The inactive larvae do not feed before molting into adults. Adult males also do not feed, and they mate with females immediately upon the latter's emergence. Newly mated females disperse from cells to locate bees elsewhere in the nest. Careful observations by Cross and Bohart indicate that these mites do not develop in cells containing living brood; it is not known if the *Trochometridium* actually kill the brood.

Species of the *Pyemotes ventricosus* complex (Pyemotidae) often occur as parasites of bee larvae in nests (Cross and Moser 1975, Eickwort 1988) and *P. ventricosus* itself was described from nests of *Anthophora* (Anthophorinae). However, the mites are not phoretic and there is no indication that any species in the complex is specialized as a bee parasite.

The families Pygmephoridae and Scutacaridae are fungus-feeding heterostigmatids that are among the most frequent and diverse associates of bees, second in abundance only to the Astigmata. *Parapygmephorus* (*Sicilipes*) are restricted to the Halictinae. The life cycle of *P.* (*S.*) *costaricanus* closely follows that of its host, *Agapostemon nasutus* (Rack and Eickwort 1980). Adult female mites are phoretic and detach when the bees prepare cells. They occur on the cell wall (or possibly in the surrounding soil) while the bee larva consumes its provisions. The mites move onto the feces when the mature bee larva defecates. There they lay eggs which hatch into larvae, which feed on the fungus in the feces. The larvae molt into adult males and females, and after mating the females move onto the cell walls. They transfer to the adult bees upon their emergence. The mites do not feed on the surface of either the provisions or the developing bees, and they do not occur in cells in which the brood has died and provisions are moldy.

Many species of *Imparipes* (*Imparipes*) (Scutacaridae) are bee associates, especially of soil-nesting solitary bees. *Imparipes apicola* has been recovered from diverse taxa of bees (Delfinado and Baker 1976), has been studied in association with halictine bees (Eickwort 1979) and is being studied in association with the alkali bee *Nomia melanderi* by Bohart and Cross (pers. comm.). The life cycle is similar to that of *Parapygmephorus costaricanus*. In contrast to *P.*

costaricanus, the adult females appear to readily move through the soil and thus have the potential to invade numerous cells. When the halictine bee brood dies, the mites readily feed on the fungus that infests the decaying brood or provision mass, and several generations and very large populations can develop (although this is not usual in nests of *Nomia*).

Under laboratory conditions, I have observed female mites moving onto bee eggs and becoming physogastric. As halictine eggs nearly always perish under laboratory conditions, this is not evidence that the mites kill the eggs, and Cross has not observed this with *Nomia*. The mites can develop in cells in which living brood occurs, feeding on the fungus that infests the bee feces.

Most *Scutacarus* are not bee associates, but *Scutacarus acarorum* is a cosmopolitan associate of bumble bees. About half of all Danish overwintering bumble bee queens bear phoretic females (Schousboe 1986). Under laboratory conditions, *S. acarorum* fed and developed preferentially on *Histioplasma*, a common fungus in old rodent nests (a preferred nesting site for bumble bees). *S. acarorum* occasionally occurs in honey bee hives, perhaps introduced by bumble bee queens which invaded the hives. Despite the frequent co-occurrence of *S. acarorum* and bumble bees, the species appears not to be restricted to associations with bees, as it is a common inhabitant of meadow soils.

Many Tarsonemidae are also fungivorous, and at least some species phoretic on bees are probably incidental associates (Eickwort 1988). Two *Tarsonemus* species recently described from large carpenter bee nests and in the acarinaria of female bees (Magowski 1986, OConnor 1993) exhibit morphological characters that suggest evolutionary modifications for bee association, as does *Pseudacarapis indoapis* in association with an Asian honey bee (Lindquist 1986). The genus *Acarapis* is restricted to honey bees (Apinae), and its species are parasites of the adult bees. This genus includes the economically important tracheal mite, *A. woodi*, of the European honey bee.

The related family Podapolipidae consists entirely of insect ectoparasites, most of whose hosts are beetles and orthopteroids. The genus *Locustacarus*, predominantly parasites of grasshoppers, contains one species (*L. buchneri*) which is a cosmopolitan ectoparasite of bumble bees (Husband and Sinha 1970). Like *A. woodi*, *L. buchneri* is a tracheal mite; only the inseminated larval female leaves the tracheae to disperse to other bees.

3.3 Mesostigmata

Mesostigmatid mites are primarily large, free-living predators. In comparison to the other suborders, proportionately more mesostigmatid associates occur in nests of long-tongued bees than in nests of short-tongued bees. Predatory mites may, however, incidentally invade the nests of all bees.

Both Macrochelidae and Parasitidae frequently invade the nests of social Apidae, often becoming the most conspicuous mites in them. *Macrocheles* are not

usually phoretic on their bee hosts and are probably not restricted to bee nests. Even *Macrocheles praedafimetorum*, described from bumble bee nests and common as a predator on nematodes and fly maggots in them, depends on beetles as phoretic hosts (Richards and Richards 1977). Cross and Bohart (pers. comm.) found *Macrocheles* feeding on nematodes in an alkali bee (*Nomia melanderi*) nest site, and these mites were phoretic upon the bees. Two genera of Macrochelidae known only as associates of stingless bees (Vitzthum 1930, Krantz 1962) have also been described from nests rather than as phoretic females.

Parasitellus (previously *Parasitus*) (Parasitidae) do appear to be specialized associates of bumble bees, with deutonymphs phoretic on adult bees, including overwintering queens. Under laboratory conditions, the mites feed on provisions and wax as well as being predators on other arthropods (Richards and Richards 1976). *Parasitellus* occur in 96% of bumble bee nests in Canada and on 25%–28% of overwintering potential queens in Denmark (Schousboe 1987).

The subfamily Hypoaspidinae of the Laelapidae contains a diverse assemblage of free-living and insect-associated mites (see Eickwort 1990). The catch-all genus *Hypoaspis sensu lato* contains species found in nests of diverse bees, ranging from ground-nesting colletids, to carpenter bees, to stingless bees. The biology of these mites has not been studied in bee nests.

The closely related genera (or subgenera of *Hypoaspis*) *Pneumolaelaps* and *Laelaspoides* are restricted to bees. The former genus is associated with bumble bees, in whose nests they may be very common. They move rapidly through the nest to explore nectar pots and brood cells. They appear to be especially attracted to bee larvae during provisioning periods. The mites remove honey and surface lipids of pollen from the provisions (Royce and Krantz 1989). They also feed on injured bees and are predators of astigmatid mites (Costa 1966, Hunter and Husband 1973). *Laelaspoides* is associated with halictine bees, in whose nests it also feeds on pollen (Eickwort 1979). The unrelated hypoaspidine genus *Melittiphis* occurs in *Apis* hives (Eickwort 1988), where it has been shown by Gibbins and van Toor (1990) to feed on pollen.

Dinogamasus is restricted to the Old World subgenera of *Xylocopa*, especially *Mesotrichia*, *Koptortosoma*, and *Afroxylocopa*, those large carpenter bees in which females possess a pouch-like acarinarium on the first metasomal tergum (LeVeque 1930; Watmough 1974; OConnor 1993; Newell, pers. comm.). Studies by Skaife (1952) and especially Madel (1975) have elucidated some aspects of the biology of these fascinating symbionts. The acarinarium contains adult female *Dinogamasus* mites (on average, 21 *D. villosior* on the host *X. flavorufa*). The mites disembark gradually as the bees provision cells, so that all cells in a nest receive some mites. The female mites stay on the bee larvae as the latter feed, and each mite lays two to three eggs on the surface of a bee larva or pupa. The developing instars also occur on bee larvae and pupae, and all instars (except the nonfeeding larva) obtain their nourishment from the host's cuticle, probably from surface "exudates" (or contaminants?). They do not appear to harm their hosts

(however, Watmough (1974) considers them to be ectoparasites and claims that there is a weight loss in pupae proportionate to the mite load). Adult female mites transfer to the acarinaria of newly emerged adult female bees; those developing in cells with male bees apparently contact female bees emerging from other cells. Apparently *Dinogamasus* is thelytokous as only females were found in the two studies involving reared material.

Nine hypoaspidine genera are known only from stingless bee nests. Little is known about the biology of these mites; *Neohypoaspis ampliseta* is a predator of astigmatid mites in nests of *Trigona* (Delfinado et al. 1983). Despite the fact that all stages occur in vast numbers in the nests, *N. ampliseta* is not phoretic on the bees, as is also true of other hypoaspidine associates of stingless bees. In contrast, *Tropilaelaps*, *Varroa*, and *Euvarroa* have evolved as ectoparasites of honey bee brood (Eickwort 1988), with the species in the former two genera becoming serious economic pests.

A different association with bees is exhibited by *Neocypholaelaps* and related genera in the Ameroseiidae, as well as by some *Proctolaelaps* (Ascidae). These mites reproduce in flowers and use bees and other insects as phoretic hosts, similar to the hummingbird mites studied by Colwell (see Chapter 2, this volume). The mites feed on nectar and pollen and may invade provisions if they enter bee nests. Most species appear to be nonspecific as to their phoretic hosts, and a wide variety of bees, both solitary and social, are represented among the hosts of *Neocypholaelaps* and *Afrocypholaelaps*. However, *N. phooni* and *N. malayensis* have characteristics that suggest a more intimate association with their Asian stingless bee hosts (Delfinado-Baker et al. 1989).

A number of other mesostigmatid mites have been described from stingless bee nests, although the level of association is unknown. These include the enigmatic gamasine *Meliponapachys*, the trigynaspid *Calaenosthanus*, and uropodines of two genera (*Oplitis* and *Urodiscella*) whose species are otherwise associated with ants or termites and which may be incidental in stingless bee nests.

4. Life-History Strategies

4.1 Nutrition

Saprophagy, especially fungivory, is the predominant nutritional mode among the important mite associates of bees, characterizing 53% of the genera in Tables 9.1–9.3. In solitary bee nests with secreted cell linings, fungal hyphae are not available to mites until the bee larvae finish their provisions and defecate on the cell walls. The feces then commonly become moldy, and saprophagous mites feed, develop, and reproduce on them. If, however, the bee brood dies, the provisions and the brood itself quickly become moldy and many saprophagous

mites are able to take advantage of this opportunity and produce large numbers of offspring. There should be strong selective pressure for such mites to enhance their reproductive potential by killing the bee egg or larva, and this is suspected for *Imparipes*, *Trochometridium*, and *Tortonia*.

There is a contradictory selective pressure for saprophagous mites not to kill the brood in the cells they occupy, because the emerging adult bees will serve as phoretic hosts to take the next generation of mites to new nests. Indeed, in most cases bee brood develops successfully in cells in which saprophagous mites also reproduce. Fungivorous and bacteriophagous mites may even be beneficial to the bees, as discussed in the next section.

The opportunities for fungivorous mites are somewhat different in nests of bees that lack secreted cell linings and in nests of the social apids. The leaves that line the cells of leaf-cutter bees typically become moldy, and this fungus apparently is a nutritional resource for *Vidia*. In the nests of bumble bees, honey bees, and stingless bees, fungal contamination is not limited to the contents of closed brood cells, and saprophagous mites (both obligatory and facultative) may become extremely abundant in moldy debris (Eickwort 1990).

A different type of saprophagy characterizes the bee-associated Histiostomatidae, which appear to be bacteriophages. These mites sweep the surfaces of provision masses and the brood itself, without harming the bees. *Dinogamasus* may also remove surface microbes from carpenter bee brood.

Saprophagous mites in feces and in provision masses may consume pollen and honey as well as fungus and other contaminants. It thus can be difficult to separate cleptoparasitism, the "stealing" of pollen and honey provisions, from saprophagy. *Chaetodactylus*, *Ctenocolletacarus*, *Horstia*, *Kuzinia*, *Sancassania*, *Sennertia* and *Tortonia* are Astigmata (presumably with saprophagous ancestry) that have been recorded as feeding on provisions. As with strict saprophages, there should be a selective advantage for a mite to kill the bee brood in order to have exclusive use of the provisions for its own reproduction. This has been observed facultatively in *Chaetodactylus* and *Horstia*.

The phoretic instars produced in cells in which the brood was killed must locate adult bees which successfully developed in other cells in the nest. These mites thus characteristically attack bees which construct cells in linear series (such as carpenter bees and megachilid bees). Bees emerging from cells basad to infested cells acquire phoretic mites when they pass through those cells. An alternative strategy requires phoretic mites to leave infested cells and move through nest burrows or surrounding soil to actively locate other bees, as occurs with *Sancassania boharti* (Cross and Bohart 1991), *Imparipes* and *Trochometridium*. The strategy of killing brood fails if all cells in a nest are infested, and indeed infestation rates are low.

While one would expect the bees to be under selective pressure to recognize and remove these mites, no such behavior has been observed in solitary bees.

However, halictid bees (including *Nomia*) pack cells containing brood killed by fungus or mites with soil, perhaps isolating them from viable cells in the nest (Cross and Eickwort, unpubl.).

Cleptoparasitism also occurs among mites with different evolutionary backgrounds than saprophagy. Pollen and nectar-feeding mites that develop in flowers frequently use bees as phoretic hosts, and these mites can also act as cleptoparasites if they leave their phoretic hosts in nests instead of on flowers. This is most common in the nests of social apids, in which the provisions are stored separate from the brood, and *Neocypholaelaps* (and related genera) and *Carpoglyphus* in particular can develop huge populations in honey bee and stingless bee nests.

A third route to cleptoparasitism is through predation. Lineages of predatory Mesostigmata have produced genera (*Laelaspoides*, *Melittiphis*, *Parasitellus*, and *Pneumolaelaps*) whose species are at least partially cleptoparasitic. These mites feed on provisions without harming the brood of their bumble bee hosts, and they occur in most nests of bumble bees.

In contrast to the situation with most other social insects, in which cleptoparasitism by mites is uncommon (Eickwort 1990), bee-associated mites commonly practice cleptoparasitism (facultative or obligatory), which occurs in 21% of the genera in Tables 9.1–9.3. This probably occurs because bees store high-quality protein and carbohydrate (pollen and honey) for relatively long periods in nests, in contrast to the progressive provisioning without long-term storage characteristic of ants, termites, and social wasps.

Predators of other associates in bee nests comprise 23% of the mite genera in Tables 9.1–9.3. These mites are disproportionately represented in nests of social apids, where they typically occur outside of the brood cells. The exception is in the nests of large carpenter bees, where *Cheletophyes* are obligate associates. The absence of obligatorily associated predators with other solitary bee taxa is surprising, given the reliable occurrence of Astigmata, Heterostigmata, and nematodes in their nests.

True parasites of adult or immature bees (feeding directly on their hosts) are few among the mites, represented by only 6% of the genera in Tables 9.1–9.3. These are all associates of social apids. Parasitism of larvae, followed by phoresy on other adult bees which develop in the nest, occurs in *Varroa*, *Euvarroa* and *Tropilaelaps*, associated with honey bees. Why this strategy has not evolved among mites associated with stingless bees or the numerous other bee lineages which do not care for their brood after oviposition is difficult to understand.

Parasitism of adult bees occurs in bumble bees (with *Locustacarus*) and honey bees (with *Acarapis*). This strategy requires that adult bees of two generations frequently interact (so mites can transfer from generation to generation), and this excludes most solitary bees as potential hosts. It does not exclude the Xylocopinae, Euglossinae, and Meliponinae, and it is surprising that ectoparasitic mites have not been found on those bees.

There should be strong selective pressure for bees to evolve means of detecting

and eliminating both brood and adult parasites. This, coupled with the major evolutionary steps necessary to transform a saprophagous or predatory mite into a parasite, may account for the rarity of this strategy.

4.2 Mutualism

The majority of mites are commensalistic with their host bees. Their activities in gathering nutrients from nests as saprophages or predators have neither a beneficial nor a harmful effect on the bees, and even those mites that steal pollen and honey may not remove enough nutrients to adversely affect the development of the brood. Consequently, I hypothesize that bees have undergone little or no selection to modify their behavior, physiology, morphology, or development in response to the presence of most mites. In contrast, the mites have undergone considerable selection to modify the timing of their development, the abilities of the various instars to locate appropriate nutrients and phoretic hosts, and to grasp onto (and possibly transfer between) phoretic hosts. One result of this selection is that most lineages of mites are adapted for survival on only one, or a few ecologically similar, lineages of hosts despite the general similarity of nutrients available in most bee nests.

Mutualism, in which the bees benefit from the presence of mites, can be expected to occur when the predatory activities of mites significantly reduce the population levels of other harmful animals in the nests or when their saprophagous activities reduce the level of infestation of fungi or bacteria on provisions or brood. One suspected case of mutualism involving predators concerns *Parasitellus* with *Bombus* (Schousboe 1987); queen bumble bees carrying mites have low levels of parasitic nematodes. The presence of specialized thoracic acarinaria containing *Cheletophyes* in Old World carpenter bees also implies mutualism, as these predatory mites consume astigmatid mites that kill brood of their hosts (OConnor 1993). Mutualism should also be investigated for *Neohypoaspis* and other laelapid genera associated with stingless bees.

In contrast, there is strong circumstantial evidence for mutualism between several lineages of saprophagous mites and their hosts. *Anoetus* have been hypothesized to be mutualistic with halictine bees, removing bacteria from the provisions and brood cuticle (Eickwort 1979). *Ctenocolletacarus* may prevent contamination by microbes that infest feces and uneaten pollen. The mites appear to ingest pollen grains that adhere to bee larvae and to convert the pasty feces to a firmer, drier state (Houston 1987). *Dinogamasus* feed on the surfaces of carpenter bee brood (Madel 1975) and may ingest microbes, while *Proctotydeus therapeutikos* deters fungus infestation in stingless bee nests (Flechtmann and Carmargo 1979).

Despite the appeal of truly mutualistic interactions, there have been no studies that have actually demonstrated a quantifiable benefit (in terms of increased reproduction or decreased mortality) to a bee from a mite's presence. Mutualism implies that the hosts also have undergone selection to encourage the presence of

mites, and the strongest evidence for mutualism is the presence of specialized regions of the female bee's body (acarinaria) for transporting phoretic instars. Acarinaria occur in those *Xylocopa*, *Ctenocolletes*, *Lasioglossum*, and *Thectochlora* which are associated with mites, but they are absent in species of *Xylocopa*, *Ctenocolletes*, and *Lasioglossum* which do not consistently carry mites.

4.3 Phoresy and Developmental Synchronization

As is the case with social insects (Eickwort 1990), phoresy is the principal adaptation required of a mite in order to become an important associate of bees. Bee nests are widely scattered in the environment, and the nutritional resources within them are largely enclosed in cells that are protected by linings from the surrounding substrate. Nests may provide resources for soil-dwelling or arboreal mites that facultatively encounter them, but reliable location of these resources requires that a mite be phoretic on a bee which leaves one nest to initiate another. All obligatory solitary bee associates reproduce within closed cells, and they have specific instars which are adapted to attach onto adult bees that emerge from the same cells, or from other cells in the same nest.

The phoretic instar must possess the sensory capability to identify an adult bee, and the mechanical ability to climb onto and "fly" with the bee while it locates and builds a new nest and forages for provisions. Female bees also possess excellent grooming abilities which the phoretic mites must be able to resist or avoid. Finally the phoretic instar must also possess the sensory capability to identify a newly provisioned cell and be able to disembark and locate the appropriate place where food is or will be available within the cell.

The developments of solitary bees and their obligatory associates are closely synchronized. Mite feeding and reproduction take place in the cell when specific nutrients are available, and a single generation of mites is produced in all cases where the bee brood is not killed. The obligate phoretic instar is produced during the late larval or pupal stadium of the bee, and it remains in the cell until the pupa molts into an adult. In cases in which the host is a univoltine bee, only a single generation of mites is produced in a year, despite the fact that related mites may pass through a generation in a matter of weeks. The phoretic instar is the most resistant stage to adverse environmental conditions and starvation, and is the stage which survives the winter (or other inactive periods).

A variant is seen in those mites that develop as saprophages or cleptoparasites in cells in which the bee brood has died. In such cells the mites typically produce several generations without the interspersing of an obligatorily phoretic instar. The phoretic instar is produced when the food is consumed or otherwise deteriorates, and the timing of this event must coincide with the availability of phoretic hosts that emerge from other cells.

The phoretic instar either firmly grasps host setae with its pretarsal claws or chelicerae (Mesostigmata, Heterostigmata, Chaetodactylidae) or it adheres to the

cuticle with suckers (Astigmata). Phoretic mites are not randomly distributed on the bee. They are highly localized in places that are not groomed, such as ventrally (on the postgenae of the head, between the coxae, on the metasomal sterna), at the junction of the head and thorax (occiput, pronotum), at the junction of the thorax and metasoma (above the leg bases on the propodeum, anterior surface of metasomal tergum I), in the intersegmental spaces between the metasomal sterna and terga, in the genital chamber, on the thorax by the wing bases, and on the surfaces of the wings. Observations of pupal bees indicate that the mites actively seek out these locations, rather than simply being groomed from other sites on the body.

Moreover, different mite species attach to different locations on the same host. On *Xylocopa*, for example, *Sennertia* prefers the head-thorax, thorax-metasoma, and wing base sites, while *Horstia* prefers the metasomal sterna and genital chamber (Abrahamovich and Alzuet 1989). On *Nomia*, *Imparipes* prefers the thorax by the wing bases, *Glyphanoetus* prefers the wing surfaces and (on male hosts) posterior metasomal sterna, and *Sancassania* prefers the intersegmental spaces between the metasomal terga and sterna (Cross and Bohart 1969). In contrast, *Trochometridium*, a nonspecific associate of bees, attaches more or less at random on its phoretic hosts (Cross and Bohart 1969, Eickwort unpubl.).

Male bees do not enter nest cells and are thus less effective vectors of mites to new reproductive sites. All studies that have examined the question of whether phoretic instars avoid cells in which male eggs are laid have determined that the mites do not discriminate between the sexes, and that the mites develop successfully in cells that contain hosts of both sexes. A few studies (Cross and Bohart 1969, Madel 1975, Richards and Richards 1976) have indicated that the phoretic instars either attach less often to the emerging male bees or that they later leave the males in order to seek female bees which emerged from other cells in the nest. For instance, only 20% of recently emerged male *Nomia melanderi* carried phoretic *Imparipes apicola* in contrast to 87% of females, although mites were actually more frequent on overwintering male larvae than on females (Cross and Bohart 1969). However, phoretic instars often do attach to both sexes, and it is typical that the mites attach to the venter (especially the metasomal sterna) or in the genital chamber of the male hosts (Cross and Bohart 1969, OConnor and Eickwort 1988, Eickwort unpubl.). These are the appropriate locations for mites to quickly move to a female bee when copulation occurs. Although such venereal transfer has been documented in *Kennethiella trisetosa* (Winterschmidtiidae) on the solitary vespid wasp *Ancistrocerus antilope* (Cowan 1984), it has not yet been verified in bees. There is no parallel among bee mites for the situation with *K. trisetosa*, which successfully develop only in cells containing male wasp larvae.

Social bees pose a different situation because, by definition, more than one brood of bees develops within a nest. Social sweat bees do not promote any different developmental strategies of their mite associates than occur in nests of solitary sweat bees. Bumble bee nests, although typically annual, have food

available outside of brood cells, and mites such as *Parasitellus* and *Pneumolaelaps* can pass through several generations per year. At the end of the season, it is necessary for phoretic instars to be produced and that they locate the overwintering new queens. This evidently occurs with *Pneumolaelaps*, *Parasitellus* and *Scutacarus*, whose phoretic instars occur in greater numbers on overwintering queens than on workers and males (Hunter and Husband 1973; Richards and Richards 1976; Schousboe 1986, 1987).

The highly social honey bees and stingless bees present an unusual condition for developmental synchronization of mites. On the one hand, these bees have perennial colonies, in which mites can reproduce for many generations without having to intersperse a phoretic instar. On the other hand, these mites require that the phoretic instars attach to the single queen which accompanies a swarm to a new nest site (or to those workers which form the swarm). It is quite striking that the only mites that are commonly phoretic on honey bees are the true parasites; the numerous saprophagous Astigmata in honey bee colonies are facultative and do not invade on the bodies of the bees themselves (Eickwort 1988).

Stingless bee workers are also almost completely free of phoretic mites, despite the very diverse and abundant mite fauna in their colonies. This fauna is largely composed of genera that appear to be obligatory associates and that would be expected to have phoretic instars. How these mites move from nest to nest remains a mystery; however, nest-founding swarms and their accompanying queens have not yet been examined for mites. Stingless bees gradually prepare a new nest and move into it, in contrast to the abrupt swarming that characterizes nest founding in honey bees. Perhaps mites associated with stingless bees are moved to new nests with materials that are carried by the workers.

5. Evolutionary and Phylogenetic Considerations

5.1 Evolutionary Implications of Phoresy

With few exceptions, mites in a solitary bee nest trace their ancestry to the phoretic instars that were carried on the female bee which constructed the nest. By itself, this should lead to extreme inbreeding, as female mites would have only their brothers and first cousins available as mates. Local mate selection should be extreme, and in haplo-diploid lineages (which include most of the bee mites) this should lead to a highly biased female:male sex ratio (Hamilton 1967, Klompen et al. 1987). Unfortunately, sex ratios have never been accurately determined for mites associated with solitary bees, but my informal observations indicate that the sex ratio is indeed female-biased, culminating in the scarce appearance of tiny *Anoetus* males and the complete absence of *Dinogamasus* males. The sex ratio is also highly female-biased in *Kennethiella trisetosa*, associated with a solitary vespid wasp (Cowan 1984; see Klompen et al. 1987).

However, the above model of extreme inbreeding is not completely valid.

Mites have mechanisms which enable host switching, and these same mechanisms permit mites with different parents to meet within individual nest cells. This results in occasional competition among nonrelated male mites for insemination of females (Cowan 1984).

Conspecific mites with different parents will meet when phoretic mites move from a male bee to a female bee when their respective hosts copulate. The same type of transfer may occur if a female bee carrying mites attempts to enter another bee's nest in order to steal provisions or when usurpation is attempted. Similarly, a mite-carrying bee may reuse a vacated nest that contains mites which developed in the previous owner's brood cells.

Mites in cells in which socially parasitic or cleptoparasitic bees or other parasitic insects develop may be phoretic on these insects, as has been observed on *Coelioxys*, *Nomada*, *Oreopasites*, *Psithyrus*, *Sphecodes* bees, and on tiphiid, chrysidid and mutillid wasps (Richards and Richards 1976; Cross and Bohart 1979; Schousboe 1986, 1987; OConnor and Eickwort 1988; Eickwort unpubl.). Such parasites may visit many host nests and serve as potent vectors for the phoretic mites. If mites occasionally leave their phoretic hosts when the latter visit flowers or nest material sites (Roubik 1987), host transfer will occur if the mites then attach to other bees that visit the same locations. For instance, *Parasitellus* deutonymphs have been collected on flowers visited by bumble bees (Richards and Richards 1976).

The same mechanisms can account for transfer of mites to new host species. Bees frequently attempt to usurp nests or reuse vacant nests made by other species. Cavities in wood and stems are particularly valued nest sites for diverse lineages of "renting" bees, and usurpation of such cavities is common, readily allowing transfer of mites among the cavity-dwelling lineages. Bumble bee queens attempting to steal provisions from honey bee colonies have been hypothesized as the source for typical bumble bee mites in *Apis* nests (Schousboe 1987). Social parasites, cleptoparasites and other parasites commonly investigate nests made by several potential host species. Since male bees may pounce on any visual stimulus that vaguely resembles a female, even mistaken copulatory attempts could lead to mite transfer.

It is likely, therefore, that mites are readily transferred among diverse bee lineages. From a mite's viewpoint, it should be adaptive to develop in any nest which it encounters. The fact that most mite lineages are restricted to related bees (see next section) implies that adaptations for coexistence with bees requires some degree of specificity.

5.2 Patterns of Host Specificity

As may be expected among such an evolutionarily diverse group as the bee mites, there are numerous patterns of host specificity. As noted in the introduction, determining the level of host specificity for any taxon of mites is not easy

from the available literature. With this caveat, the following generalizations are apparent concerning the species of mites belonging to the genera listed in Tables 9.1–9.3:

(1) Very few species develop regularly in association with hosts that belong to more than one subfamily. These include *Tortonia quadridens*, *Imparipes apicola*, *Trochometridium tribulatum*, and *Afrocypholaelaps africana*. The latter species is a flower-feeding mite which is primarily phoretic on its various hosts.

(2) Relatively few mite species develop in association with only one host species when other congeneric potential hosts occur in the same habitat. Well-documented examples of monophagous mites primarily involve associates of honey bees: *Varroa underwoodi* and *Pseudacarapis indoapis* on *Apis cerana*, and *Melittiphis alvearius* on *A. mellifera* (Delfinado-Baker et al. 1989). I expect that mites currently restricted to either *A. mellifera* or *A. cerana* will eventually occur on the other species now that these previously allopatric hosts occur in sympatry, as has happened with *Varroa jacobsoni*.

(3) The majority of mite species occur in association with many or most congeneric host species in their ranges, and individual hosts may bear more than one congeneric species of mite. This is especially apparent in the well studied *Scutacarus*, *Parasitellus* and *Pneumolaelaps* mites associated with bumble bees (Hunter and Husband 1973; Richards and Richards 1976; Schousboe 1986, 1987). Even those mites that appear to be the most highly specialized for life with their hosts, as evidenced by the development of host acarinaria, are not entirely host specific. Species of *Ctenocolletacarus*, associated with *Ctenocolletes* (Fain 1984a, Fain and Houston 1986), and *Dinogamasus*, associated with *Xylocopa* (Vitzthum 1930), typically occur on several closely related host species. It is, however, risky to generalize a pattern for any mite genus. For example, some species of *Imparipes* (e.g. *I. apicola*) are not specific in their bee hosts while others (e.g. *I. ithacensis* on *Dialictus rohweri*, *I. vulgaris* on *Lasioglossum titusi*) may be quite host specific (Delfinado and Baker 1976).

Equivalent patterns of host specificity exist at the generic level. About 29% of the genera in Tables 9.1–9.3 contain species that are also known from hosts other than bees. The flower-dwelling mites (*Neocypholaelaps* and *Afrocypholaelaps*, perhaps *Carpoglyphus* and *Proctolaelaps*) are included here because they have developed only loose relationships with their phoretic hosts, including butterflies, beetles, and flies. Also included here are those genera of mites (*Forcellinia*, *Oplitis*, *Triplogynium*, *Urodiscella*, and *Urozercon*) which are most frequently

associated with ants, termites or other insects but also have representative species in nests of stingless bees or honey bees—the extent to which these species are obligate associates of bees is unknown (Eickwort 1990). Similarly, species of *Macrocheles* occur in various social apid nests, but their closer association might be with beetles and other insects that are their true phoretic hosts (Richards and Richards 1987). Many included genera are large, "catch-all" taxa (*Histiostoma*, *Hypoaspis*, *Imparipes*, *Proctotydeus*, *Sancassania*, *Scutacarus*, and *Tarsonemus*), and further phylogenetic analysis might lead to recognition of the bee-associated species as comprising monophyletic subunits (subgenera or species groups). A few well-defined genera, however, are found on diverse host taxa, suggesting that some mites evolved close associations with bees while their congeneric relatives did not. Perhaps the most striking example is *Locustacarus*, which includes species that are tracheal parasites of both grasshoppers and bumble bees (Husband and Sinha 1970).

The remaining 71% of genera listed in Tables 9.1–9.3 contain species that are all obligatorily associated with bees. This association in addition suggests that mites in each genus are predominantly found on a single subfamily (or closely related subfamilies) of bees. Where more than one family of hosts is associated with a mite genus, the hosts are ecologically similar (e.g. species of *Chaetodactylus*, *Horstia*, *Sennertia*, and *Tortonia* are associated with wood-dwelling carpenter bees and megachilid bees). A few apparently incongruous host associations can be similarly explained; for instance, the record of *Vidia undulata* phoretic on *Hylaeus* could easily be due to the fact that *Hylaeus* will make its nests in abandoned megachilid nests (OConnor and Eickwort 1988). I have not included obviously incongruous records in Tables 9.1–9.3 when they are based solely on phoretic instars (e.g. *Sennertia* collected from honey bees; Baker and Delfinado-Baker 1983). Other incongruous records may be clarified in the future by systematic analysis. For instance, "*Pneumolaelaps*" *machadoi*, described from an African megachilid bee (Elsen 1973), lacks some characters of other *Pneumolaelaps*, all of which are associated with bumble bees (Hunter and Husband 1973), and probably represents a separate derivative from a *Hypoaspis*-like ancestry.

What has caused some genera of mites to be speciose (e.g. *Chaetodactylus*, *Dinogamasus*, *Parasitellus*, *Pneumolaelaps*, and *Sennertia*) while others contain just a few, wide-ranging species with numerous hosts (e.g. *Locustacarus*, *Cerophagus*) remains unanswered. What is evident is that each mite genus has generally been found to be associated with its host subfamily throughout the world whenever potential hosts have been adequately sampled (Tables 9.1–9.3). This is especially true of *Vidia* and *Chaetodactylus* (with megachilines), *Horstia* and *Sennertia* (with xylocopines), and *Anoetus* (with halictines), where the ranges of both hosts and mites extend to Australia. I conclude that the mite-bee associations are thus very old, predating the geographic partitioning of the bee lineages and thus originating probably in the Cretaceous.

5.3 Phylogenetic Implications

The evolution of important mite associates of bees can best be summarized as a phenomenon with many independent evolutionary origins, and with subsequent diversification of the mite lineages within major bee lineages. I hypothesize a minimum of 31 separate origins of important bee mites: *Histiostoma*, *Anoetus*, *Sancassania* (+ *Ctenocolletacarus*), Horstiinae, *Tortonia*, Gaudiellidae, *Vidia*, Meliponocoptidae, Chaetodactylidae, *Melissotydeus*, *Cheletophyes*, *Trochometridium*, *Parapygmephorus*, *Imparipes*, *Scutacarus*, *Tarsonemus*, *Pseudacarapis*, *Acarapis*, *Locustacarus*, *Parasitellus*, *Meliponipachys*, *Trigonholapsis* + *Grafia*, *Neocypholaelaps*, *Hypoaspis*, *Pneumolaelaps* + *Laelaspoides*, *Dinogamasus*, *Neohypoaspis* + seven related genera, *Melittiphis*, *Tropilaelaps*, Varroidae, and *Calaenosthanus*. Five of the above may have had multiple separate origins of bee mites within them (*Histiostoma*, *Hypoaspis*, *Imparipes*, *Sancassania*, *Scutacarus*), and I have excluded some genera in which the extent of adaptation for life in social bee nests is uncertain (*Forcellinia*, *Macrocheles*, *Oplitis*, *Proctolaelaps*, *Triplogynium*, *Urozercon*, and *Urodiscella*).

Evolutionary analysis within the mite genera awaits phylogenetic studies of both the bees and the mites, which have not been undertaken for any pair of lineages. The literature suggests that evolutionary patterns in those mite genera that are closely adapted to specific host genera will in part reflect host phylogeny, although strict cospeciation of mites and hosts has not occurred. For example, two closely related species of *Ctenocolletes* share the same two closely related species of *Ctenocolletacarus*, while a third species of *Ctenocolletacarus* occurs on two other host species (Fain 1984a, Fain and Houston 1986). Most subgenera and species groups of *Sennertia* are confined to particular biogeographic regions (Fain 1981a), and separate subgenera of *Horstia* occur in the New and Old Worlds (Fain 1984b). Separate lineages of *Anoetus* and *Vidia* have evolved with different host lineages (OConnor 1988). Different groups of mites are associated with two lineages of *Apis* (Delfinado-Baker et al. 1989).

On a broader scope of bee phylogeny, mite lineages are not well correlated with host lineages above the subfamily level. Mite genera are either broadly spread among bees or they are restricted to only specific subfamilies in a given family of bees. Genera with species that occur in different families of soil-dwelling bees (*Histiostoma*, *Hypoaspis*, *Imparipes*, *Sancassania*, *Schulzea*, and *Scutacarus*) are mostly little modified from their non-bee-associated ancestors and may represent separate invasions in each bee lineage. As an example of subfamily specialization, the mites (*Anoetus* and *Sicilipes*) adapted to Halictinae do not occur on the Rophitinae, the most primitive subfamily in the Halictidae. There is almost no concordance of mite lineages (only *Chaetodactylus*) between the Anthophorinae and Xylocopinae of the Anthophoridae, or among the Apinae, Bombinae, and Meliponinae of the Apidae (only Gaudiellidae and Laelapidae). Similarly, few mites (possibly Horstiinae and Laelapidae) occurring in social

apid nests have a common ancestry with those that occur with solitary bees. Mite lineages thus offer little phylogenetic information concerning the relationships of bee subfamilies and families. The close phylogenetic relationships among the mites that occur with Megachilidae and Xylocopinae reflect similar nesting habits of those two bee taxa, not their phylogenetic relationship.

A summary of mite genera presently known from major bee families and subfamilies is given in Figure 9.3. The Meliponinae are hosts to the greatest diversity of mite genera, which might be explained in large part by their complex perennial nests with abundant and diverse food resources. The Apinae also have complex nests and societies, but the level of diversity of obligate mite associates is only half that of the Meliponinae. This may in large part be explained by many fewer species represented in the Apinae, and until recent times their restriction to the Old World. The facts that only two closely related species (*Apis mellifera* and *A. cerana*) build nests in cavities which provide a habitat for saprophagous mites and their predators, and that differences in swarming and nest-founding make phoresy to new nests more difficult, may also contribute to the relative sparsity of mite associates of Apinae. The Bombinae also exhibit a high diversity of mites, probably due to the diverse and abundant food resources in their nests, as well as their wide distribution.

Solitary bee lineages all present basically the same nutritional resources for mites. One might expect that the lineages have roughly equivalent diversities of mites associated with them, but that is not the pattern exhibited in Figure 9.3.

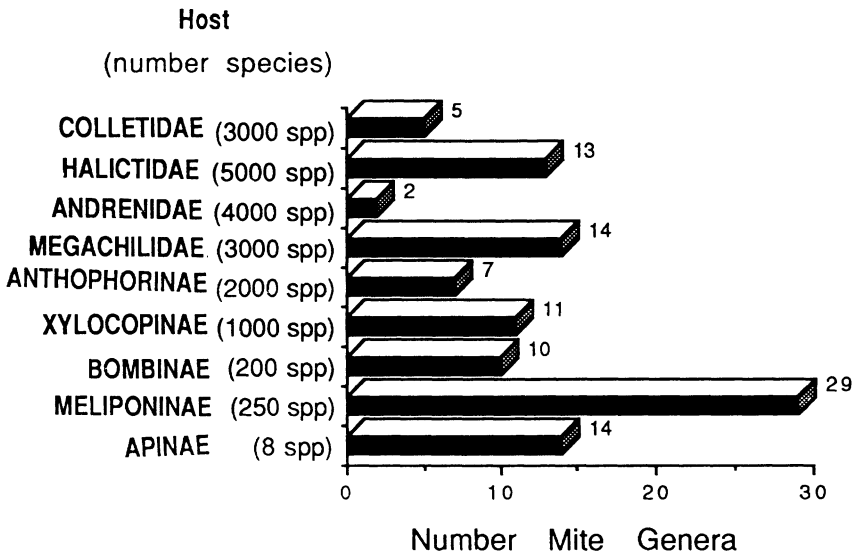


Figure 9.3. Numbers of genera of mites associated with major families and subfamilies of bees. Approximate number of species in each bee taxon indicated in parentheses.

Among the soil-nesting bees, the Halictidae (Halictinae and Nomiinae) exhibit the greatest diversity of mite associates. This may in part be due to my own concentration of studies on these associations, but mites are simply not so apparent on and in nests of other soil-dwelling solitary bees (Cross and Bohart 1969). The fact that many halictines are parasocial or eusocial does not seem to be an adequate explanation, because the mites are not unique to the social species, and parasocial (communal) colonies are also frequent among Andrenidae and Anthophorinae.

The second obvious pattern among solitary bee hosts is the greater diversity of mites associated with the predominantly wood-dwelling and cavity-renting Xylocopinae and Megachilinae as compared with most soil-nesting bees, including the Anthophorinae. Unique taxa of mites have evolved to inhabit the nests of carpenter and leafcutter bees, such as *Chaetodactylus*, *Cheletophyes*, *Dinogamasus*, *Sennertia*, *Vidia*, and six acarid genera (Table 9.2), with only three genera of Astigmata playing an equivalent role with the Anthophorinae. The mites that inhabit nests of Xylocopinae and Megachilidae (with the exception of a few species of the ecologically broad-ranging genera *Sancassania*, *Schulzea*, and *Hypoaspis*) are distinctly separate in their evolutionary origins from those that occur with all other groups of solitary bees.

Ecology may play a major role in explaining these differences. Neither Xylocopinae nor Megachilinae line their cells with impenetrable secreted linings, and the cells are typically constructed in series, facilitating mite transfer. Xylocopine bees are long-lived, facilitating transfer of mites between generations. Both groups typically reuse nest cavities. The frequently arboreal nests are subject to invasion from arboreal lineages such as the Winterschmidtiidae (OConnor 1988), and these mites may share ancestry with those associated with arboreal-nesting solitary wasps. While mites are poorly known from the cavity-renting Hylaeinae, the few records indicate a closer relationship with mites inhabiting megachilid or xylocopine nests than those of other Colletidae.

The patterns of diversity of the mites associated with the major bee subfamilies support the hypothesis that the long-tongued bee families are at least as old phylogenetically as the short-tongued bee families. The mites associated with solitary long-tongued bees (especially the Megachilidae and Xylocopinae) are more morphologically distinctive on the average than are those associated with short-tongued bees, suggesting longer periods of coevolution between bee and mite lineages. The mites associated with stingless bees and honey bees are among the most highly modified of all Astigmata and Gamasina, again suggesting early divergence of these mite lineages from their non-bee-associated ancestors.

6. Conclusions

The majority of mites that have established important relationships with solitary bees are saprophytes or pollen-honey feeders within their nests. Predatory mites

are only important in social bee nests. There are few true parasites of bee brood and adults, and these are limited to the highly social bees.

The most important adaptation for a mite to establish an important relationship with bees is phoresy upon nest-founding female bees. A mite must also modify its developmental cycle to synchronize with that of its host.

Most mites are commensalistic in bee nests, neither harming nor benefitting their hosts. Some species may kill brood in order to feed on the provisions or the microbes that then infest them. Other species may be mutualistic with the bees, principally by deterring microbes. Evidence for diffuse coevolution between mites and bees lies principally in the presence of specialized pouches (acarinaria) on certain female bees for carrying phoretic mites.

Most mite genera are each restricted to one subfamily of bees, or to subfamilies which are ecologically similar. A minority of mite genera are associated with unrelated bee families, or with other insects. Mite evolution has not paralleled bee evolution above the subfamily level. Most mite species are not restricted to just one species of bee, and there is no evidence for bee-mite cospeciation.

The study of bee mites is truly in its early stages. While there is an increasing literature on the few mites that are pathogenic to domestic honey bees, most bee mites are totally neglected biologically. Numerous mite species have been described, but there has been little effort to analyze them phylogenetically. Bee biologists should be encouraged to observe and preserve the mites that occur inside cells, especially those containing developing brood. Many exciting bee-mite associations are awaiting discovery.

Acknowledgments

Dr. Barry OConnor of the University of Michigan has provided many insights on the Astigmata, Dr. Phil Torchio of the USDA Bee Biology and Systematics Lab at Utah State University provided information on *Chaetodactylus*, and Dr. Earle Cross of the University of Alabama provided unpublished information on mites associated with alkali bees. Dr. Mercedes Delfinado of the USDA Beneficial Insects Laboratory at Beltsville, Maryland has generously shared her research on the acarine associates of honey bees and stingless bees. Drs. OConnor, Torchio, Delfinado, and Cross, and Carol Henderson, Kenna MacKenzie, Ulrich Mueller, and Janet Shellman-Reeve of Cornell University provided helpful comments on this manuscript. I thank Dr. Marilyn Houck for the invitation to contribute to this symposium volume, and for her editorial assistance.

References

Abrahamovich, A. H. and A. D. B. de Alzuet. 1989. Relaciones foreticas entre acaros (Acaridae y Chaetodactylidae) e himenopteros (Anthophoridae, Xylocopinae). *Rev. Soc. Entomol. Argent.* 47:115–122.

Baker, E. W. and M. Delfinado-Baker. 1983. New mites (*Sennertia*: Chaetodactylidae) phoretic on honey bees (*Apis mellifera* L.) in Guatemala. *Int. J. Acarol.* 9:117–121.

Baker, E. W., D. W. Roubik and M. Delfinado-Baker. 1987. The developmental stages and dimorphic males of *Chaetodactylus panamensis*, n. sp. (Acari: Chaetodactylidae) associated with solitary bee (Apoidea: Anthophoridae). *Int. J. Acarol.* 13:65–73.

Chmielewski, W. 1969. Obserwacje nad biologia nowego dla akarofauny polskiej gatunku *Kuzinia laevis* (Dujardin, 1849) (Acarina, Acaridae). *Pol. Pismo Entomol.* 39:603–617.

Chmielewski, W. 1971. The mites (Acarina) found on bumble-bees (*Bombus* Latr.) and in their nests. *Ekol. Pol.* 19:57–71.

Costa, M. 1966. The biology and development of *Hypoaspis* (*Pneumolaelaps*) *hyatti* (Acari: Mesostigmata). *J. Zool.* 148:191–200.

Cowan, D. P. 1984. Life history and male dimorphism in the mite *Kennethiella trisetosa* (Acarina: Winterschmidtiidae), and its symbiotic relationship with the wasp *Ancistrocerus antilope* (Hymenoptera: Eumenidae). *Ann. Entomol. Soc. Am.* 77:725–732.

Cross, E. A. and G. E. Bohart. 1969. Phoretic behavior of four species of alkali bee mites as influenced by season and host sex. *J. Kans. Entomol. Soc.* 42:195–219.

Cross, E. A. and G. E. Bohart. 1979. Some observations of the habits and distribution of *Trochometridium* Cross, 1965 (Acarina: Pyemotidae). *Acarologia* 20:286–293.

Cross, E. A. and G. E. Bohart. 1991. Notes on the life history of *Sancassania boharti* (Acari: Acaridae) and its relationship to the alkali bee *Nomia melanderi* (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.* 63:603–610.

Cross, E. A. and J. C. Moser. 1975. A new, dimorphic species of *Pyemotes* and a key to previously-described forms (Acarina: Tarsonemoidea). *Ann. Entomol. Soc. Am.* 68:723–732.

Delfinado, M. D. and E. W. Baker. 1976. New species of Scutacaridae (Acarina) associated with insects. *Acarologia* 18:264–301.

Delfinado-Baker, M., E. W. Baker and A. C. G. Phoon. 1989. Mites (Acari) associated with bees (Apidae) in Asia, with description of a new species. *Am. Bee J.* 129:609–610, and 612–613.

Delfinado-Baker, M., E. W. Baker and D. W. Roubik. 1983. A new genus and species of Hypoaspidinae (Acari: Laelapidae) from nests of stingless bees. *Int. J. Acarol.* 9:195–203.

Eickwort, G. C. 1979. Mites associated with sweat bees (Halictidae). In: *Recent Advances in Acarology*, Vol. 1 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 575–581.

Eickwort, G. C. 1988. The origins of mites associated with honey bees. In: *Africanized Honey Bees and Bee Mites*. (G. R. Needham, R. E. Page, Jr, M. Delfinado-Baker and C. Bowman eds.). Ellis-Horwood, Ltd., Chichester, England. Pp. 327–338.

Eickwort, G. C. 1990. Associations of mites with social insects. *Annu. Rev. Entomol.* 35:469–488.

Elsen, P. 1973. *Pneumolaelaps machadoi* spec. nov. (Acarina: Mesostigmata) et autres acariens mésostigmatiques phorétiques d'Hyménoptères Apidae (Insecta) d'Angola. *Publ. Cult. Cia. Diamantes Angola* 87:179–186.

Fain, A. 1966. Notes sur la biologie des Acariens du genre *Chaetodactylus* et en particulier de *C. osmiae*, parasite des abeilles solitaires *Osmia rufa* et *O. cornuta* en Belgique (Sarcoptiformes: Chaetodactylidae). *Bull. Ann. Soc. R. Belge Entomol.* 102:249–261.

Fain, A. 1981a. A revision of the phoretic deutonymphs (hypopi) of the genus *Sennertia* Oudemans, 1905 (Acari, Astigmata, Chaetodactylidae). *Syst. Parasitol.* 3:145–183.

Fain, A. 1981b. Notes on the hypopi of the genus *Chaetodactylus* Rondani, 1866 (Acari, Chaetodactylidae). *Bull. Inst. R. Sci. Nat. Belg. Entomol.* 53:1–9.

Fain, A. 1984a. A new genus of mite (Acari: Acaridae) phoretic on bees (*Ctenocolletes*) in Australia. *Rec. W. Aust. Mus.* 11:77–86.

Fain, A. 1984b. Notes sur les hypopes du genre *Horstia* Oudemans, 1905 (Acari, Acaridae), phorétiques sur les Hyménoptères. *Acarologia* 25:259–270.

Fain, A. and W. Chmielewski. 1987. *Horstia* (*Horstia*) *longa* spec. nov. (Acari, Acaridae) from house-dust in Poland. *Pol. Pismo Entomol.* 57:367–372.

Fain, A. and T. F. Houston. 1986. Life cycle stages of mites of the genus *Ctenocolletacarus* Fain (Acari: Acaridae) associated with *Ctenocolletes* bees in Australia. *Rec. West. Aust. Mus.* 13:67–77.

Fain, A., F. S. Lukoschus and M. Nadchatram. 1980. Two new species of *Cheletophyes* Oudemans, 1914 (Prostigmata: Cheyletidae) from the nest of a carpenter bee in Malaysia. *Int. J. Acarol.* 6:309–312.

Fain, A. and G. Rack. 1987. Notes on the mites living in the flowers of *Espletia* spp. (Asteraceae) in Colombia. I. *Carpoglyphus sturmi* sp. n. (Acari, Carpoglyphidae). *Entomol. Mitt. Zool. Mus. Hamb.* 9:9–19.

Fain, A. and A. E. Rosa. 1983. Acari domum meliponinarum brasiliensium habitantes. IV. New astigmatic mites from the nest of the bee *Partamona* sp. (Meliponidae). *Bull. Inst. R. Sci. Nat. Belg.* 55:1–13.

Flechtmann, C. H. W. and C. A. de Camargo. 1979. Acari associated with stingless bees (Meliponidae, Hymenoptera) from Brazil. In: *Proc. 4th Int. Congr. Acarol.*, (E. Piffl ed.), Saalfelden, 1974. Akadémiai Kiadó, Budapest. Pp. 315–319.

Gibbins, B. L. and R. F. van Toor. 1990. Investigation of the parasitic status of *Melittiphis alvearius* (Berlese) on honeybees, *Apis mellifera* L., by immunoassay. *J. Apic. Res.* 29:46–52.

Haeseler, V. 1982. Solitäre Wespen und Bienen als Transporteure der Wandernymphen von Uropodiden. *Mikrokosmos* 8:227–229.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.

Houston, T. F. 1987. The symbiosis of acarid mites, genus *Ctenocolletacarus* (Acarina: Acariformes), and stenotritid bees, genus *Ctenocolletes* (Insecta: Hymenoptera). *Aust. J. Zool.* 35:459–468.

Hunter, P. E. and R. W. Husband. 1973. *Pneumolaelaps* (Acarina: Laelapidae) mites from North America and Greenland. *Fla. Entomol.* 56:77–91.

Husband, R. W. and R. N. Sinha. 1970. A revision of the genus *Locustacarus* with a key to genera of the family Podapolipidae (Acarina). *Ann. Entomol. Soc. Am.* 63:1152–1162.

Klompen, J. S. H., F. S. Lukoschus and B. M. OConnor. 1987. Ontogeny, life history and sex ratio evolution in *Ensliniella kostylevi* (Acari: Winterschmidtiidae). *J. Zool.* 213:591–607.

Krantz, G. W. 1962. A review of the genera of the family Macrochelidae Vitzthum 1930 (Acarina: Mesostigmata). *Acarologia* 4:143–173.

Krombein, K. V. 1962a. Biological notes on acarid mites associated with solitary wood-nesting wasps and bees. *Proc. Entomol. Soc. Wash.* 64:11–19.

Krombein, K. V. 1962b. Natural history of Plummers Island, Maryland XVI. Biological notes on *Chaetodactylus krombeini* Baker, a parasitic mite of the megachilid bee, *Osmia (Osmia) lignaria* Say (Acarina: Chaetodactylidae). *Proc. Biol. Soc. Wash.* 75:237–249.

LeVeque, N. 1930. Symbiotic mites used to separate species of a genus of bees. *Science* 71:607–608.

Lindquist, E. E. 1985. Discovery of sporothecae in adult female *Trochometridium* Cross, with notes on analogous structures in *Siteroptes* Amerling (Acari: Heterostigmata). *Exp. Appl. Acarol.* 1:73–85.

Lindquist, E. E. 1986. The world genera of Tarsonemidae (Acari: Heterostigmata): A morphological, phylogenetic, and systematic revision, with a reclassification of family-group taxa in the Heterostigmata. *Mem. Entomol. Soc. Can.* 136:1–517.

Lombert, H. A. P. M., B. M. OConnor, F. S. Lukoschus and J. O. Whitaker, Jr. 1987. Ontogeny, systematics and ecology of *Sennertia (Amsennertia) americana* Delfinado and Baker, 1976 (Acari: Chaetodactylidae) from the nest of the carpenter bee, *Xylocopa virginica* (Hymenoptera: Anthophoridae). *Int. J. Acarol.* 13:113–129.

Madel, G. 1975. Vergesellschaftung der Milbenart *Dinogamasus villosior* mit der ostafrikanischen Holzbiene *Xylocopa flavorufa* (Acarina: Laelaptidae/Hymenoptera: Xylocopidae). *Entomol. Ger.* 1:144–150.

Maeta, Y. 1978. Comparative studies on the biology of the bees of the genus *Osmia* of Japan, with special reference to their managements for pollinations of crops (Hymenoptera: Megachilidae). *Bull. Tohoku Nat. Agric. Exp. Stn.* (Morioka) 57:1–221.

Magowski, W. 1986. Two new species of *Tarsonemus* (Acari: Prostigmata) associated with *Xylocopa* carpenter bees (Hymenoptera: Apoidea). *Entomol. Mitt. Zool. Mus. Hamb.* 8:289–306.

Mahunka, S. 1974. Beiträge zur Kenntnis der an Hymenopteren lebenden Milben (Acari) II. *Folia Entomol. Hung.* 27:99–108.

Michener, C. D. 1979. Biogeography of the bees. *Ann. Mo. Bot. Gard.* 66:277–347.

OConnor, B. M. 1982. Evolutionary ecology of astigmatid mites. *Annu. Rev. Entomol.* 27:385–409.

OConnor, B. M. 1988. Coevolution in astigmatid mite-bee associations. In: *Africanized Honey Bees and Bee Mites*. (G. R. Needham, R. E. Page, Jr, M. Delfinado-Baker and C. Bowman eds.). Ellis-Horwood, Ltd. Chichester, England. Pp. 339–346.

OConnor, B. M. 1992a. Ontogeny and systematics of the genus *Cerophagus,* mites associated with bumblebees (Acari: Gaudiellidae). *Great Lakes Entomol.* 25:173–189.

OConnor, B. M. 1992b. Generic relationships in the Chaetodactylidae (Acari: Astigmata) with description of a new genus (submitted for publication).

OConnor, B. M. 1993. The mite community associated with *Xylocopa latipes* (Hymenoptera: Anthophoridae: Xylocopinae) with description of a new type of acarinarium. *Int. J. Acarol.*, Vol. 19 (in press).

OConnor, B. M. and G. C. Eickwort. 1988. Morphology, ontogeny, biology and systematics of the genus *Vidia* (Acari: Winterschmidtiidae). *Acarologia* 29:147–174.

Putatunda, B. N. and R. P. Kapil. 1988. Seven new species of *Cheletophyes* (Acari: Prostigmata: Cheyletidae) associated with carpenter bees in India. In: *Progress in Acarology*, Volume 1 (G. P. Channabasavanna and C. A. Viraktamath eds.). Oxford and IBH Publ. Co. Pvt. Ltd., New Delhi. Pp. 317–328.

Rack, G. and G. C. Eickwort. 1980. Biology and description of a new pygmephorid mite (Acarina: Tarsonemida) associated with the soil-nesting bee *Agapostemon nasutus* (Hymenoptera: Halictidae). *Acarologia* 21:267–278.

Richards, K. W. and L. A. Richards. 1977. A new species of *Macrocheles* (Acarina: Macrochelidae) found in bumble bee nests (Hymenoptera: Apidae). *Can. Entomol.* 109:711–719.

Richards, L. A. and K. W. Richards. 1976. Parasitid mites associated with bumblebees in Alberta, Canada (Acarina: Parasitidae; Hymenoptera: Apidae). II. Biology. *Univ. Kans. Sci. Bull.* 51:1–18.

Roubik, D. W. 1987. Notes on the biology of anthophorid bee *Tetrapedia* and the mite *Chaetodactylus panamensis* Baker, Roubik and Delfinado-Baker (Acari: Chaetodactylidae). *Int. J. Acarol.* 13:75–76.

Royce, L. A. and G. W. Krantz. 1989. Observations on pollen processing by *Pneumolaelaps longanalis* (Acari: Laelapidae), a mite associate of bumblebees. *Exp. Appl. Acarol.* 7:161–165.

Schousboe, C. 1986. On the biology of *Scutacarus acarorum* Goeze (Acarina: Trombidiformes). *Acarologia* 27:151–158.

Schousboe, C. 1987. Deutonymphs of *Parasitellus* phoretic on Danish bumblebees (Parasitidae, Mesostigmata; Apidae, Hymenoptera). *Acarologia* 28:37–41.

Skaife, S. H. 1952. The yellow-banded carpenter bee, *Mesotrichia caffra* Linn, and its symbiotic mite, *Dinogamasus braunsi* Vitzthum. *J. Entomol. Soc. South. Afr.* 15:63–76.

Smiley, R. L. and J. O. Whitaker, Jr. 1981. Studies on the idiosomal and leg chaetotaxy of the Cheyletidae (Acari) with descriptions of a new genus and four new species. *Int. J. Acarol.* 7:109–127.

Southcott, R. V. 1989. A larval mite (Acarina: Erythraeidae) parasitizing the European honey bee in Guatemala. *Acarologia* 30:123–129.

Vitzthum, H. 1930. Acarologische Beobachtungen (14. Reihe). *Zool. Jahrb. Syst. Oekol. Geogr. Tiere* 59:281–350.

Watmough, R. H. 1974. Biology and behaviour of carpenter bees in southern Africa. *J. Entomol. Soc. South. Afr.* 37:261–281.

10

Adaptation and Transition into Parasitism from Commensalism: A Phoretic Model

Marilyn A. Houck

CONTENTS

1. Introduction

A parasite is "any organism that grows, feeds and is sheltered on or in a different organism while contributing nothing to the survival of its host" (*The American*

Heritage Dictionary of the English Language). The etymology of the word has its origin in the Greek word *parasitos*, "fellow guest." Parasitism is an important ecological and evolutionary role assumed by a variety of animals, and it has been suggested that parasitic insects comprise as many as half of all animals living on earth today (Price 1980). While a comparable projection is not yet available for mites, it is clear that the Acari have been particularly prominent in the exploitation of this mode of existence, both as ectoparasites and (to a lesser extent) as endoparasites (e.g. *Pneumocoptes* = lung parasites of the rodents *Peromyscus*, *Onychomys*, and *Cynomys*; Baker 1951).

Vertebrates (especially birds and mammals, but not fish), are commonly the focus of acarine parasitization. A major exploitation of birds has occurred worldwide in all habitats. Feather mites are obligatory ectoparasites of all major groups of birds except penguins (Peterson 1975) and are thought to have evolved from nidicolous ancestors. Man has not escaped parasitism by mites either and is host to many medically important species of Acari (e.g. chiggers [Trombiculidae] which transmit tsutsugamushi fever [Wharton 1946]; and *Liponyssus bacoti*, the agent of endemic human typhus [Ewing 1933]). *Sarcoptes scabiei* (the sarcoptic mange mite), which infests the skin of domesticated animals (camels, cattle, dogs, goats, horses, rabbits, and sheep) is thought to have originated as an ectoparasite of man (Fain 1968). Husbandry and domestication practices have led to secondary infestation of animals in cohabitation with man; perhaps only the house cat has escaped this common fate (Fain 1968).

Interest in the origin of parasitism, *per se*, is not specific to acarology, but crosses all disciplinary boundaries. The generalities concerning parasitism come from many research areas. The evolution of parasitism is a process which is constrained by four unifying principles: (1) potential hosts protect themselves from exploitation using morphological, physiological, and behavioral defenses, while potential parasites must counterrespond to host defenses in order to successfully continue the relationship (Ehrlich and Raven 1964, Feeny 1976, Berenbaum 1983); (2) subsequent acceleration of attack and counterattack results in parasites and their hosts becoming coevolved (Kim 1985a); (3) the process of attack and counterattack occurs over evolutionary time (Holmes 1973); and (4) commensalism or mutualism may act to initiate the processes leading to parasitism (Price 1980). This last point is significant because it implicitly endorses the concept of a free-living ancestor representing the primitive node in all parasitic clades, with commensalism or mutualism being more advanced states of interaction, and parasitism most highly derived. The feather mites mentioned above are thought to have evolved in such a way, originating from nidicolous free-living ancestors (Peterson 1975).

A number of paradigms have been developed to explain or define host-parasite coevolution (e.g. Ewing 1912, Fain 1969, Fain 1971, Kethley and Johnston 1975, Brooks 1979, Waage 1979, Price 1980, Timm 1983, Kim 1985b, Houck 1992), but experimental evidence regarding the mechanisms and processes in-

volved in the evolution of parasitism from commensalism is difficult to obtain. A deterrent to the understanding of the evolution of parasitism within a particular monophyletic clade is that all grades of interactions (free-living forms, commensals, and parasites) must be available for study. Astigmatid mites (Acari: Astigmata) represent such a monophyletic clade and offer a unique opportunity for the investigation of the evolution of parasitism from a particularly interesting form of commensalism called *phoresy*. This chapter offers some insights and proposed mechanisms into the channels responsible for such a phoretic transition in one astigmatic mite, *Hemisarcoptes corremani* (Hemisarcoptidae).

2. Phoresy in the Astigmata

2.1 What is Phoresy?

Phoresy has been defined, for the Astigmata, as "a phenomenon in which one organism (the phoretic) receives an ecological or evolutionary advantage by migrating from the natal habitat while superficially attached to a selected interspecific host for some portion of the individual phoretic's lifetime. Benefit is not conferred as a nutritional or developmental influence on the phoretic stage" (Houck and OConnor 1991). While the concept of phoresy is susceptible to oversimplification (e.g. "*commensalism* with the implication of *dispersal*"), this definition in its entirety has the advantage of explicitly addressing the consequences of phoresy at two temporal levels: (1) in terms of increased survival and fitness, via ecological interactions (proximate level); and (2) in terms of potential for speciation and major shifts in niche exploitation, across evolutionary time (ultimate level).

Functionally, this definition offers testable criteria to distinguish phoresy as a distinct phenomenon, separate from all other interspecific interactions or dispersal mechanisms: (1) the host is *selected* (not randomly *elected*), with potential ramifications for coevolution to follow; (2) neither the phoretic nor the host receive benefit from the relationship other than passive dispersal; if benefit accrues (e.g. nutrition or enhanced development) then some other form of relationship is suspect (e.g. parasitism or mutualism); (3) it introduces the concept that phoresy may have significant evolutionary benefits, not uncovered by studying ecological interactions alone. The qualifications of nutritional status and developmental participation, first considered by Farish and Axtell (1971), are very important and allow for null and testable hypotheses to become confirmational in defining phoretic associations. If a given interaction contributes to the nutrition or ontogenesis of the phoretic, the relationship is something other than phoresy, and needs further clarification.

2.2 Morphological Adaptations of Phoretic Mites

Phoresy is a prevalent form of commensalism among animals and one of the least understood of the potential ecological interactions. The most spectacular radiation

of phoretic associations occurs in the Acari (mites). The Astigmata, in particular, are masters of phoretic association and have taken the concept to the extreme. There are substantial differences in the effectiveness of phoresy among species of astigmatic mites depending upon variation in: (1) the extent and morphological development of attachment organs; (2) the specificity and predictability of hosts; and (3) the environmental durability of the phoretic stage.

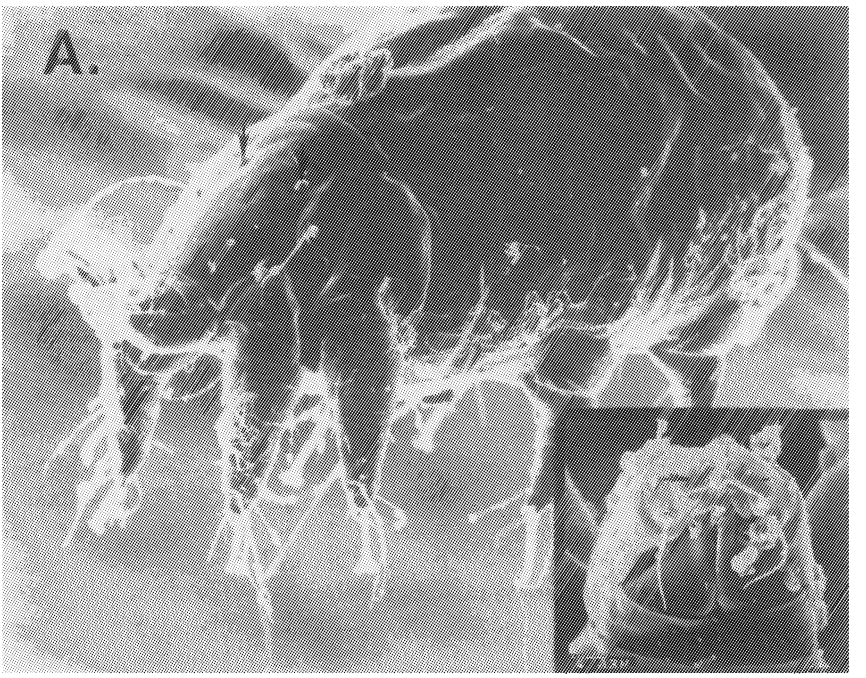
The degree of morphological specialization of the phoretic stage in mites can be classified into three general types: unspecialized homeomorphs, specialized homeomorphs, and heteromorphs (for a review see Houck and OConnor 1991). Heteromorphs are morphologically very different from all other stages of their life cycle. They have been categorized according to their functional morphology and mode of attachment (Zachvatkin 1941, Fain 1968, Fain 1969, Volgin 1971). The most common is the entomophilous ("insect loving") heteromorph, which is very different in morphology from the general body plan of the species (Fig. 10.1A, B, C).

The entomophilous Astigmata are characterized by a dispersal stage which is exemplified by a suite of correlated characters (Stolpe 1938, Hughes and Hughes 1939, Oboussier 1939, Perron 1954, Türk and Türk 1957, Hughes 1959, Wallace 1960, Evans et al. 1961, Kuo and Nesbitt 1971, Woodring and Carter 1974, Hughes 1976, Krantz 1978, Binns 1982, OConnor 1982) including: (1) a rudimentary gnathosoma (Fig. 10.1B); (2) a solid nonfunctional gut; (3) extensive dorsal and ventral sclerotization to withstand long periods of environmental stress while in transit; and (4) an extensive caudoventral sucker plate for attachment to arthropods. An organism with such a heteromorphic suite of morphological characteristics is frequently referred to as a *hypopus*.

While the typical hypopus is as described above, variations on the phoretic theme have occurred in the Astigmata. A modification expressed by some glycyphagids includes passive aerial distribution by an atypical nonphoretic hypopus which is highly regressed from the ancestral hypopal morphology (Knülle 1959, Fain and Philips 1981, Barker 1982, Knülle 1987). This morph is essentially a "mite seed," which lies dormant within a protective modified protonymphal exuvium. It can withstand months of pernicious environmental challenges that are lethal to all other stages. *Lepidoglyphus destructor*, for example, can withstand pesticide fumigation used commercially to control stored-product pests (Barker 1982).

2.3 Ecological and Evolutionary Consequences

Partly because of their small body size, the Astigmata have become champions of phoretic associations. Ecologically, phoresy helps overcome the liability of small size in long-distance migration, the lack of morphological attributes for migration (e.g. wings), the absence of diapause (in most Astigmata), and the threat of predation during migration. It is a means of locating ephemeral resources

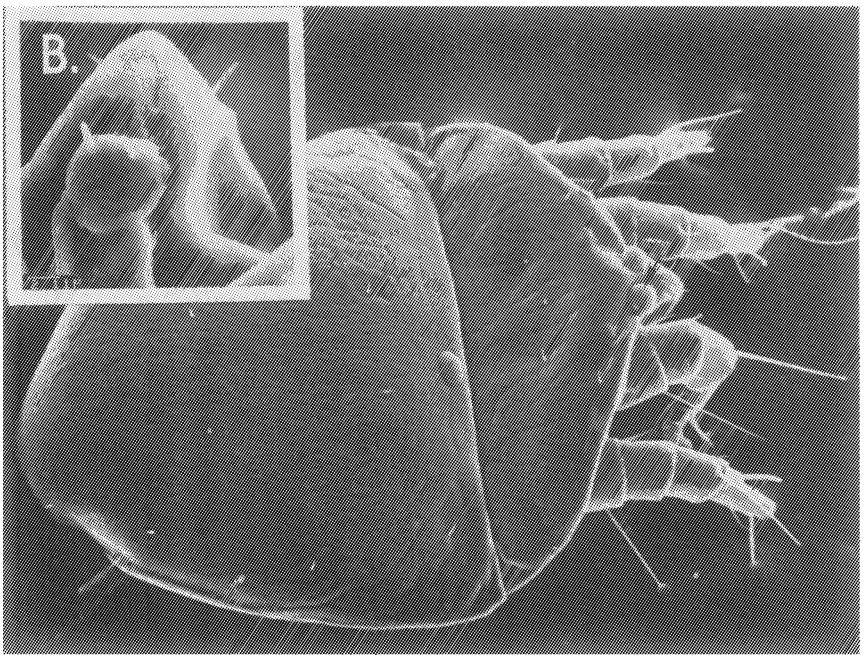


(A)

Figure 10.1. Two stages in the development of *Hemisarcoptes cooremani* which represent the trophic contrasts in the life cycle. Note: The life cycle of *H. cooremani* follows the ancestral acariform pattern diagrammed in Chapter 7 (Fig. 7.4). A) Scanning electron photomicrograph. Lateral view of an adult female (obligate predatory stage), which feeds on Diaspididae. Arrows indicate the position of the dorsal anterior eyes. Insert: an increased magnification of the ventral aspect of the gnathosoma, used for feeding; arrows mark the chelicerae. B) Scanning electron photomicrograph. The entomophilous heteromorph (= hypopus) in dorsal aspect. Arrow indicates the position of the right eye. Note the position of the eyes in this stage, as compared to Figure 10.1A. This landmark emphasizes the morphological reduction of the body, anterior to the eyes. Insert: an increased magnification of the ventral aspect of the degenerate gnathosoma showing the absence of the chelicerae and most other gnathosomal structures (compare to Fig. 10.1A). Arrow indicates the hypothetical position of the absent primordial "mouth." C) The caudal ventral sucker plate, in ventral aspect. This sucker plate is used for subelytral attachment to *Chilocorus*. Insert: an enlargement of the vestigial genital and anal openings.

with some degree of certainty (Moser and Cross 1975) when the host and the phoretic share a common niche.

Phoresy offers a potential for colonization of fresh habitats when the natal habitat degrades. Such transitory habitats may include: carrion, dung, vascular plants of seral communities, nests of arthropods and vertebrates, phytotelmata,



(B)

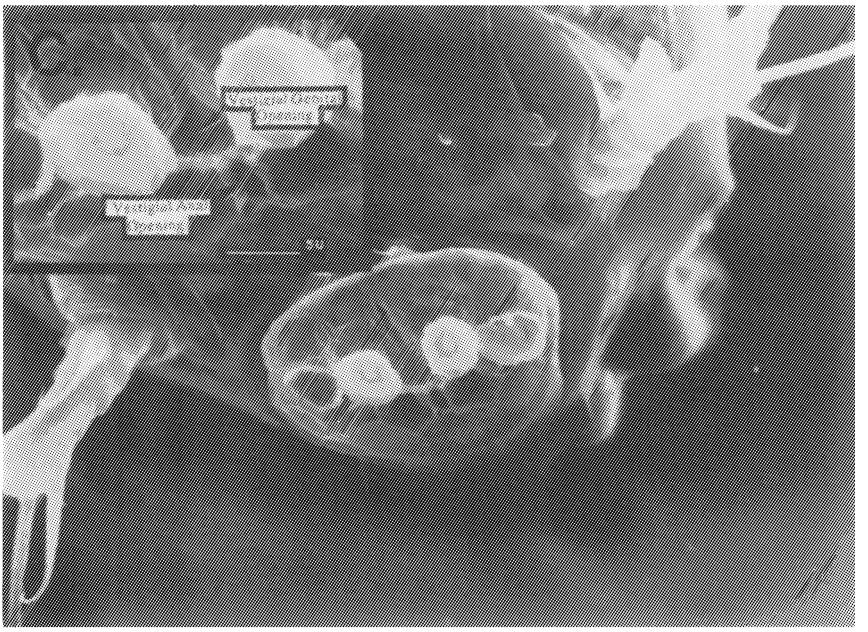
Figure 10.1. (Continued)

and temporary accumulations of decaying materials such as beach wrack. Because of the hypopus, members of the Astigmata have become specialists in exploiting environments in which resources are rich and prevalent, but unpredictably patchy and fleeting.

The hypopus is the only life-cycle stage to have contact with the phoretic host and therefore the only stage to have the potential to construct coevolutionary relationships with the host. Physiological and morphological coevolution is focused on the hypopal stage, while the remainder of the ontogeny remains morphologically conserved and ostensibly unaffected by host-related selection pressures. However, any physiological or chemical adaptations accomplished by the phoretic, which are specific to a host, are accommodations that are secondarily conferred to subsequent nonphoretic developmental stages, because they represent individual units of the same ontogeny.

2.4 Which Developmental Stage is Phoretic?

Where phoresy exists as a dispersal strategy in mites, not all ontogenetic stages in the life cycle have equal capacity for dispersal. In some groups of mites only the adult female is phoretic, while in other groups such as the Astigmata a nymph



(C)

Figure 10.1. (Continued)

(hypopus) is phoretic. The ancestral ontogenetic sequence in astigmatid mites proceeds as follows: egg → prelarva → larva → protonymph → deutonymph (hypopus) → tritonymph → adult (male or female) (refer to Fig. 7.4, this volume). Typically, the deutonymph is the only stage that is phoretic (but see Fashing 1976 for an exception).

If the hypopus is facultative, as it is in many Astigmata, it occurs only in a particular season, under certain environmental stresses, or is expressed only by some genotypes in the population. The absence of that stage at other times prohibits successful phoretic migration and colonization. When colonization attempts are successful, resource exploitation and reproduction by these small creatures immediately follow, and crowding can quickly occur in the rich contingency habitat. Such crowding may provoke serial migration, but any subsequent migration is the responsibility of the next generation of hypopi.

3. Natural Stabilizing Selection of a Particular Demographic Stage for Phoresy

3.1 Differential Benefits of Phoresy Examined by Age Class

What demographic or selective factors determine which stage of the life cycle becomes the disperser? The consequences for natural selection of adult dispersal

are obvious and have been covered in the literature. If dispersers are gravid females or adult parthenogens, each individual is potentially a propagule and colonization of a new habitat is immediate. It is not surprising that in many organisms the sole responsibility for dispersal falls to the reproductive females in the population. A corollary to this is that if phoretics are inseminated females or adult parthenogens, there is little selection pressure for synchronous group migration. If instead, dispersers are sexually mature adults (but not gravid), synchronous migration would provide a selective advantage in the new habitat. Synchronous migration need not imply large numbers of simultaneous dispersers. Mitchell (1970), using a simple probabilistic model, proposed that on average only four individuals are required for both sexes to be represented in the colonizing population, at least 88% of the time.

It is curious that the phoretic dispersal stage in the Astigmata is not an adult, but instead it is a juvenile. In the Astigmata, it is an immature hypopus that arrives at the immigrant habitat. The hypopus must molt into the tritonymphal stage, also sexually immature, before finally molting into a functional adult. This naturally leads to the question of how, and under what conditions, does an intermediate developmental stage become *the* optimal dispersal stage. Again as a corollary, because the hypopus is not a capable propagule, synchronous group dispersal would be expected to correlate with nonadult migration. And, that is often the case in the Astigmata.

The clue to how a juvenile stage takes prominence in the role of dispersal lies, at least in part, in the examination of the relative survivorship and mortality of the various stages in the life cycle.

3.2 Relative Survivorship and Mortality Examined by Age Class

Survivorship and mortality are complementary events in a population and are described in terms of rate functions, particularly in terms of the forms that these functions assume (Deevey 1947). Though survivorship and mortality curves represent a family of continuous curves, they are often partitioned into five basic types: (1) Type I survivorship curves (log scale, Fig. 10.2A) describe populations with high juvenile survivorship (= low juvenile mortality rates), with an exponential increase in mortality rate (Fig. 10.2B) until adulthood is reached (= decline in survivorship). This is known in the amortization literature as Gompertz's law which has been thought to describe human survivorship. (2) Type II survivorship curves describe populations with a nonlinear decrease in survivorship with age and a linear acceleration of mortality rate with age; mortality rate is highest at adulthood. (3) Type III survivorship curves describe populations with relatively equitable survival (and mortality) across all age groups. (4) Type IV survivorship curves describe populations with a nonlinear deceleration of survivorship with age; mortality rate is lowest at adulthood. (5) Type V survivorship curves describe populations with high neonate mortality rate, an exponential deceleration of

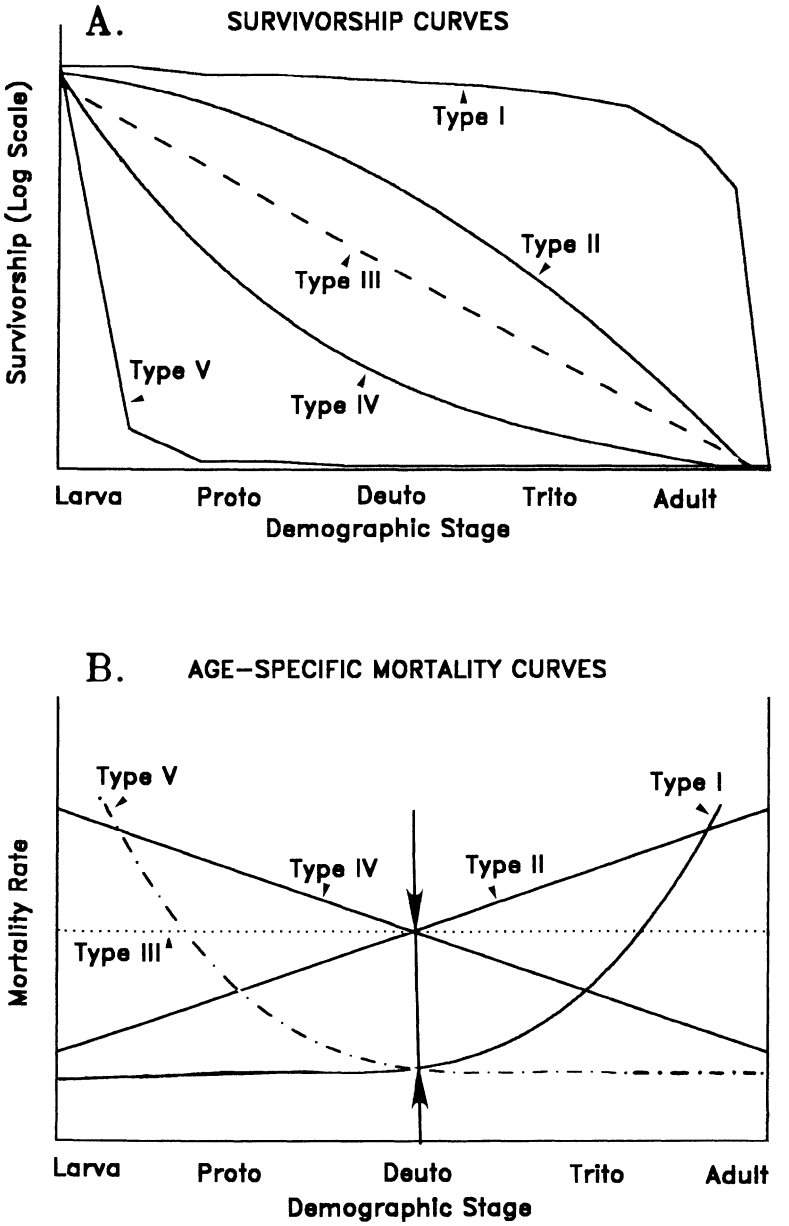


Figure 10.2. Generalized forms of ecological survivorship and mortality curves. Adapted from Ricklefs (1973). A) The five general survivorship curves (logarithmic scale) extracted from the continuum of curves which can describe survivorship in animals. B) Mortality rate curves. Bold arrows indicate the central point, in Euclidean space, about which the potential continuum of curves pivot when there is fluctuation in mortality at either end of the curve.

mortality rate with age, and survivorship becoming relatively asymptotic throughout all postneonate age groups and on into adulthood.

An assumption of the survivorship model is that the environment and other constraints differentially influences organisms within a life cycle. Even under stable environmental conditions, selection pressure may be heavier on some demographic stages due solely to things such as body size or age-related effects. For example, an increase in ambient temperature that is tolerated well by adults may impact nymphs severely in terms of increased evaporative stress due to a higher surface-to-volume ratio in smaller individuals.

The process of molting is also a source of significant risk to mites which influences mortality rate, and the youngest immature stages are the most vulnerable to the vagaries of the ecdysal process. Each successful molt results in a greater probability of survival to adulthood. This risk is additive to the risks of predation and other environmental selective pressures.

Population density may also influence mortality rates at eclosion, as it does in the medfly (*Ceratitis capitata*), the only organism thus far tested in this manner (Carey et al. 1992). Mortality is lowest for medflies maintained in solitary growth chambers, and highest for flies maintained in groups. Since migration in the Astigmata is often correlated with degradation of the natal habitat, resource depletion, and increased population density, high eclosion mortality (Type V survivorship curve) would be experienced in the natal habitat prior to migration, with a potentially lower eclosion mortality in the immigrant habitat (perhaps Type I curve).

The recent studies on *C. capitata* offer a serious caveat to studies of life-history patterns in general and to the Astigmata in particular. Because of the transient life style of the Astigmata, survivorship and mortality rates need to be examined as phenotypic characters of individuals (or populations) relative to the expression of the genotype in various habitats (e.g. natal vs. immigrant). It cannot be assumed that individuals (or populations) have a canalized genetic program for survivorship and mortality expectation. That is to say, there is genotype/habitat interaction (see the excellent work of W. Knülle 1987, 1990, 1991) expressed in the mortality rate, and because habitats vary drastically across the life cycle, one would expect there to be fluctuations in the relative frequency of "survival genotypes" correlated with dispersal history.

All demographic stages except postmolt adults suffer from the potential hazards of molting. However, adults face a unique additional source of mortality. Adult females, in particular, are susceptible to the vulnerabilities and vagaries associated with reproduction; the consequences of unsuccessful parturition or egg laying, injury during mating, and drain of energy allocated to developing progeny. Such risks are in addition to the consequences of molting, and environmental selection, and reproduction-related risks would be expected to increase as habitat quality decreases due to the loss of female vigor.

3.3 Shifting Selection Pressures at Two Ends of the Survivorship Curve

In populations expressing the Type III mortality and survivorship curves, mortality rates and survival are equitable and selection for a "good" demographic stage for dispersal is a moot and irrelevant question. Any stage of the ontogeny would make as good a dispersal agent as any other. Realistically, however, the forces of selection are not constant across time for the Astigmata, but rather vary among the ephemeral habitats they exploit, with preferential impact on various demographic stages in the natal habitat and yet another impact in the immigrant habitats. Because of the inherent differential mortality due to size, age, and habitat shifts, a Type III curve is unrealistic for the Astigmata. Given this, we may ask what stage in the life cycle of the Astigmata has the highest probability of survival across all habitats encountered and across all life-history experiences; or at what stage does the highest mean survivorship occur?

As developed above, under stable environmental conditions Type I and Type V mortality-rate curves are influenced by the relative constraints of the physiological processes of eclosion at one end of the cycle and reproduction at the other end. Mid-life stages (e.g. deutonymphs), on average, experience less impact of mortality due to molting and size constraints than do the larvae, and no mortality due to reproduction. At the populational level, the cumulative effect of fluctuating mortality at the two ends of the Type I and Type V survival curves results in a U-shaped mortality-rate curve, over demographic time.

Such a U-shaped curve can be accentuated by genetic polymorphisms for age-related death rates (e.g. polymorphism for reduced larval mortality or delayed senescence) or by deviations from Gompertzian kinetics (exponential increase in mortality with age) (Carey et al. 1992, Curtsinger et al. 1992). Such deviations can occur because various demes experience different ecological experiences (spatial variation). Deviations can also occur because larvae and adults within a lineage experience different physical habitats and the developmental stages occur in sympatry but are not syntopic. Hence, fluctuating gene frequencies track changes in habitat (temporal shifts).

3.4 The Meaning of a U-shaped Mortality Curve

A U-shaped populational mortality curve is the response to selective mortality (in time and space) between Type I-Type V curves. Pooled across curves, a central point exists in Euclidean space, about which the potential continuum of curves pivots (Fig. 10.2B, arrows). Under varying environmental and stochastic selection pressures, which may be unstable in time, space, or genotype, the point of inflection (most predictable mean survival across time) falls at the middle stage (deutonymph, where there are five life stages). The ecological operative here is *predictable*. It is the point at which, under any given set of vagrant selective forces, the mean mortality rate attains a stable equilibrium value. Because it is

most predictable, and can be tracked through evolutionary time. It is the point at which selection acts to favor survival during dispersal.

3.5 Risks of Dispersal Assessed by Age Class

Dispersal by any demographic stage can be a high risk event which is in addition to mortality losses due to predation and physical stress. If the disperser is successful in subsequent colonization, however, the payback to the entire genetic lineage is enormous. If an ecological void is encountered, the results can be catastrophic.

If we assess the magnitude of the risks associated with a catastrophic loss of any single age class, it is clear that all age classes do not equally impact the survival of the lineage. The loss of dispersers exclusively made up of the youngest age class (larvae) could terminate a lineage if a new habitat is not located before the natal habitat is depleted. Dispersal larvae migrating into this ecological void would drain the lineage of any potential of further phoretic recruitment, and therefore survival from extinction. All subsequent adult reproduction would be wasted, when phoretic larvae are lost.

Adults would also offer a significant potential loss for the lineage if migration were unsuccessful in the quest for a transient habitat. For adults represent not only the loss of a colonizing individual but the loss of an ontogeny (potential larval recruits in the natal habitat which could magnify the colonization probability at some later time).

Migration of an intermediate stage (i.e. deutonymphs) does not disturb the potential for replacement of recruits from the ranks of the larval cohort and eggs produced sometime later by reproductive adults. Migration by a nymph adds two important time lags to the system for further migration attempts: one due to the time delay for dispersal recruitment from the ranks of larvae, and one due to the time delay for dispersal recruitment from the ranks of eggs contributed by parentals. The temporal component (time lag) of a few hours or of a few days between any single migration event and the migration of subsequent recruits is very valuable to the success of new waves of phoretics. Even a small pulse in time delay may be sufficient to allow for significant local environmental change, sufficient to prevent potential future extinction. In the vagaries of vacillating resource quality, in time and space, this hedge could be critical. For example, it may allow for natural periodicity to replenish resources (e.g. beach wack accumulating and dislodging with the tides), unpredictable resources to be replenished (e.g. intermittent rains), or untrackable events to occur (e.g.the death of an organism that will become available carrion).

The least negative influence on the population comes from intermediate stages being invoked for dispersal. Intermediate stages (e.g. deutonymphs), if lost, would be replaced from the ranks of the younger cohort (larvae) and from potential offspring provided at some later time by the parental generation. Again, the time

lag associated with recruitment could provide critical time for enhancement of habitat options.

Thus, I suggest that two influences are critical to the selection of the deutonymph as the dispersal stage for the Astigmata when immigrant habitats are ephemeral and unpredictable: (1) the influence of fluctuating habitat/genotype variation on relative survivorship and mortality; and (2) relative impact of the loss of the developmental stage to the survival of the genotype lineage. I offer this as a hypothesis of how (ultimately) the deutonymph became the prominent dispersal stage characteristic of the Astigmata.

3.6 Further Selection for Dispersal Characteristics in the Hypopus

Assuming that selection for phoretic deutonymphs was initiated as a primitive trait in the Astigmata (OConnor 1982), following the above reasoning, dispersal would be further enhanced by increased modification of this stage over and above that occurring in the rest of the ontogeny. The development of the typical sclerotized hypopal morphology (with caudal ventral suckers etc.) further extends the initial selective process, would enhance longevity while on the host, and allow a greater time component for the selection of a "good" habitat prior to disembarking from the host. The consequences of evolving a hypopus have significantly enhanced the adaptive radiation of the astigmatid lineage.

Ancestrally the Astigmata consisted of free-living fungivores (OConnor 1979), but because of the possession of the hypopus they now exploit a diversity of niches (Fashing 1976, Fashing and Wiseman 1980, Norton 1980; also see Fashing, Norton, and OConnor in this volume) including parasitism. They have become saprophages, nidicoles, synanthropic pests of stored foods, and permanent parasites. Many astigmatid mites are nidicolous (nest) associates of mammals and birds. The nidicolous condition now includes synanthropic "nests" created by the agroeconomic practices of man (e.g. granaries, warehouses, barns, mushroom houses etc.).

Historically, habitat diversification by the Astigmata was also correlated with a wide range of new ecological associations with arthropods. It is the mite-arthropod association which will be the focus of the remainder of the discussion.

4. Evolution and Transition into Parasitism

The discussion thus far has focused on ecological/phenotypic participation in the evolution of a phenomenon called phoresy in the Astigmata. An equally compelling and important theme will now be developed that argues that the *evolutionary* consequence of phoresy in the Astigmata is to rescue astigmatid lineages from the ravages of constant migration, made necessary by chronic ephemeral ecological shifts. Phoresy has provided the necessary and sufficient prerequisites for

mites to enter into a different (and ecologically more stable) evolutionary contract with the host—that of parasitism.

4.1 Hemisarcoptes as an Example of Potential Evolutionary Transition

Hemisarcoptes is the type genus of the family Hemisarcoptidae. Free-living stages of *Hemisarcoptes* (larvae, protonymphs, tritonymphs and adults) (Fig. 10.1A) are generalist predators of diaspidid scale insects, a speciose parasitic family attacking most perennial vascular plants worldwide. Hypopi of *Hemisarcoptes* have established stenoxenic phoretic relationships with beetles of the genus *Chilocorus* (Coleoptera: Coccinellidae) (Gerson and Schneider 1982, Houck 1989, Gerson et al. 1990, Houck and OConnor 1990, Houck and OConnor 1991, Houck and Cohen ms.). Both *Hemisarcoptes* and *Chilocorus* occur in all habitable continents of the world. Both are predators of scale insects (Fig. 10.3).

Hemisarcoptes cooremani (Thomas) is indigenous to southern North America, and is commonly phoretic on *Chilocorus cacti*. Once on the beetle, the mite positions itself subelytrally (Fig. 10.4A, B, C) and is subsequently transported to a new habitat as the beetle forages for scale insects. Since *H. cooremani and C. cacti* both prey on scale insects, post-deutonymphal development of the mite occurs within the habitat of its appropriate prey (Fig. 10.3). Only the phoretic hypopus of *Hemisarcoptes* occurs on the beetle, and all other stages remain under the caps of the scale insects to feed.

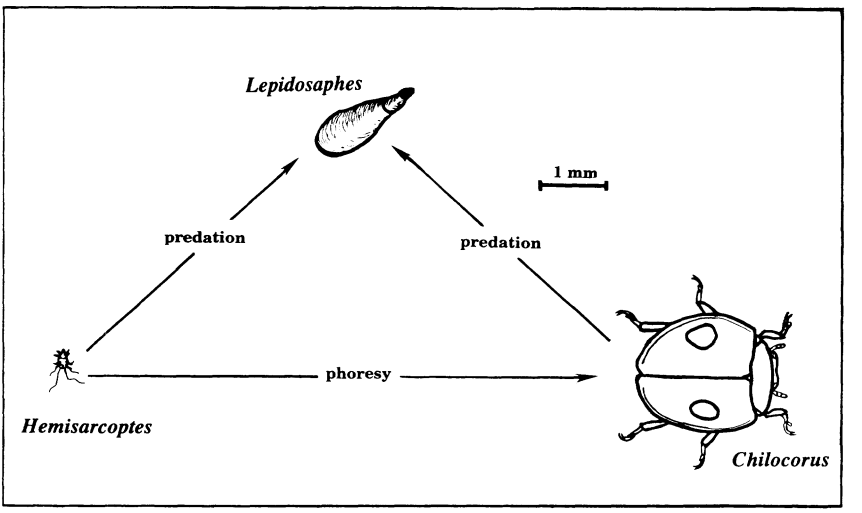


Figure 10.3. Diagram of the tropic and phoretic pathways of interaction among *Hemisarcoptes*, *Chilocorus* and their prey (Diaspididae).

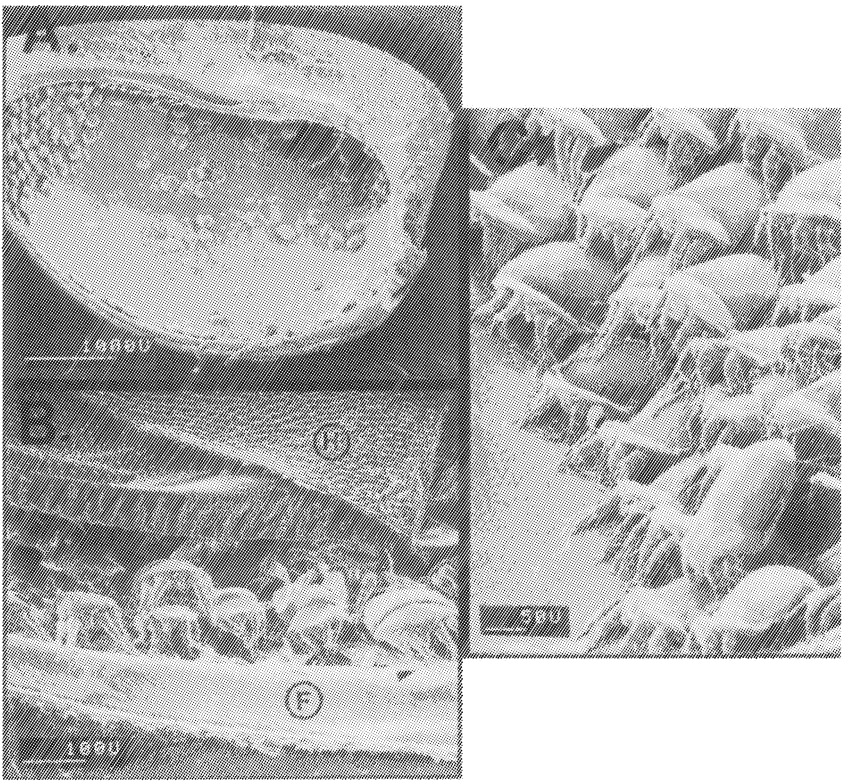


Figure 10.4. Scanning electron photomicrographs of: A) *Hemisarcoptes cooremani* attached to the subelytral surface of *Chilocorus cacti*. Note: the majority of individuals are positioned on the caudoventral tip of the elytron. B) Hypopi positioned on the beetle with their gnathosomal end pointing caudally, in uniform and compact rows. **H** = Hind wing of *Chilocorus*, **F** = outer edge of the Forewing of *Chilocorus*. Mites attach using the caudoventral sucker plate as well as the delicate pretarsi (arrow). C) "Standing room only" on the beetle elytron. As many as 400 hypopi of *H. cooremani* have been collected from one elytron of one individual of *C. cacti*.

4.2 Evidence for "Something Other than Phoresy" in Hemisarcoptes cooremani

4.2.1 Interruption of Ontogenesis

The deutonymph of *H. cooremani* is facultative and represents only 6% of the population (Houck and OConnor 1990). Hypopi of *H. cooremani* that do not encounter a host while waiting to migrate, do not molt to complete ontogenesis; they die. This situation has also been discovered in other astigmatid mites (e.g.

Lardoglyphus; M. Okamoto, pers. comm.). Thus, host contact may not only be employed as an environmental monitor but may also be vital for survival.

This then violates one of the central constructs of the definition of phoresy: "benefit is not conferred as a developmental . . . influence on the phoretic stage." This interruption of ontogenesis, associated with the absence of a host, was one of the earliest clues that something other than phoresy was likely.

4.2.2 Contribution to Mite Nutrition

A second piece of evidence that the *Hemisarcoptes-Chilocorus* interaction should not be considered phoretic is that hypopi maintain a long residency time on *Chilocorus* (5–21 days), which is not completely explained by the need to disperse. Host-attachment may continue even when fresh resources are readily available (pers. observ.). Also, while attached to the host the mites were observed to undergo a visible morphological change (swelling) prior to disembarking from *Chilocorus* (Fig. 10.5).

These observations led to the hypothesis that some "material(s)" essential to hypopal survival and/or development can be acquired in transit. A potential source of available "materials" for hypopi while on the host is reflexed beetle hemolymph. *Chilocorus* defends itself by exuding hemolymph from tibio-femoral joints and from the pronotal-elytral junction. This "reflexive bleeding" is an effective antipredator deterrent, associated with aposematic coloration (Pasteels et al. 1973). Since the hemolymph contains alkaloids (work in progress, with T. Eisner) a serious irritation occurs to the attacker, while the hemolymph oxidizes, coagulates, and cements a potential predator's mouthparts together. Thus the hemolymph acts to chemically and mechanically debilitate the predator.

4.2.3 Hemisarcoptes Has Adapted to Chilocorus Reflexed Hemolymph

Reflexed hemolymph, exuded from the pronotal area, runs down and swaths the subelytral surfaces of *Chilocorus*. It is in this area where *Hemisarcoptes* is attached. Evidence for the adaptation of the mites to this caustic chemical is that it does not appear to cause any mechanical or chemical damage to the mites (Fig. 10.7). They are capable of escaping entrapment and show no signs of ill effects from alkaloids with which they come in contact (pers. observ.).

Active conservation of selected hemolymphal nutrients by the beetle does not appear to occur prior to hemolymphal ejection. Reflexed hemolymph is similar to that in the body cavity, in chemical makeup and concentration, where these have been evaluated (e.g. proline and sucrose, pers. observ.). The mites have direct access to this hemolymph, rich in nitrogen and sugar, whenever the beetle is disturbed. The "disturbance" response can be readily invoked simply by brushing the surface of the beetle with the soft bristles of an artist's brush.

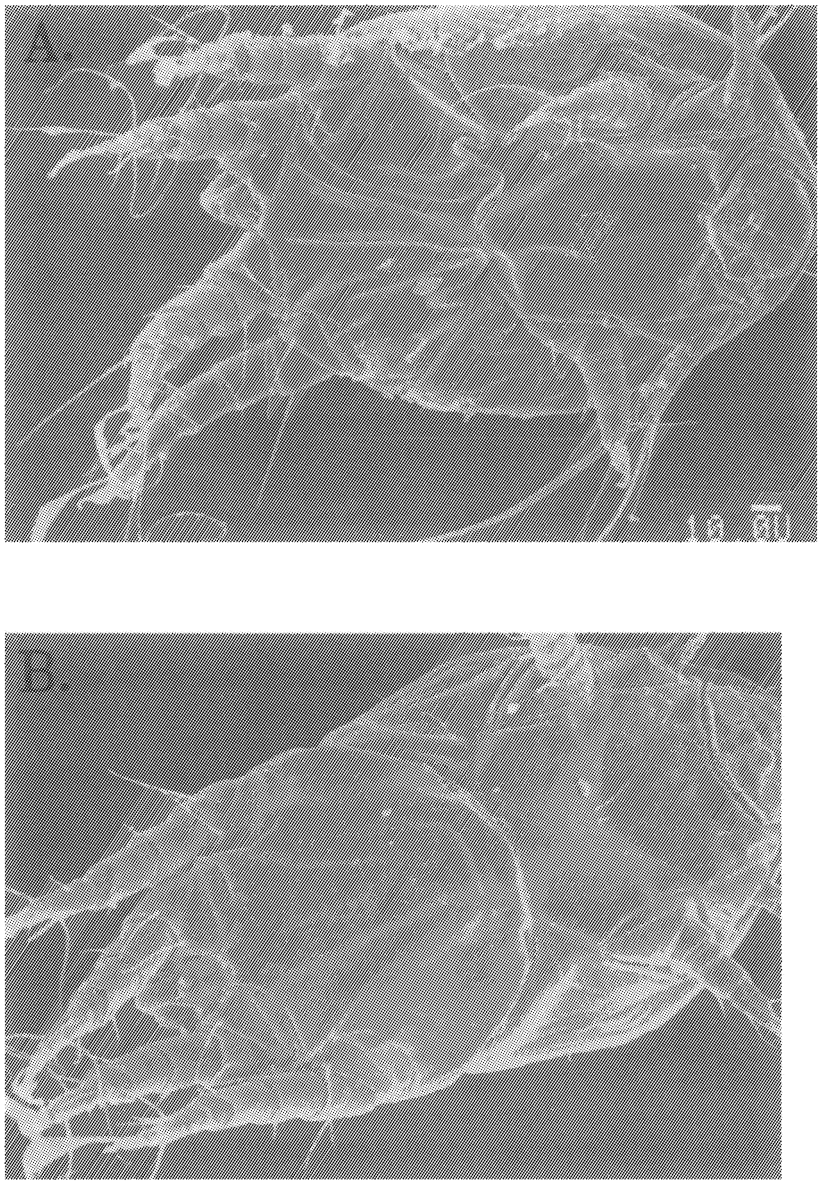


Figure 10.5. Scanning electron photomicrograph (SEM) of two hypopi of *Hemisarcoptes cooremani* (A, B) raised in lab monocultures and extracted from the same lab-reared individual of *Chilocorus cacti*. Both mites were alive, active and appeared to be in good condition when collected. This represents the morphological change that occurs in the mites, when allowed association with the beetles. Scale bar on Figure 10.5A is applicable to both SEMs. [SEM accomplished with the assistance and cooperation of Mr. M. Moratorio and Dr. G. Gordh during a sabbatical at the University of California, Riverside].

4.2.4 Hemisarcoptes Acquires Materials from Chilocorus

From radio-labeling (HTO) studies (Houck and Cohen ms.) it was discovered that hypopi of *Hemisarcoptes* acquire materials (at least water) directly from *Chilocorus*. This acquisition was in addition to atmospheric water taken across the cuticle. This then violates the second tenet of the definition of phoresy: "benefit is not conferred as nutritional . . . influence on the phoretic stage."

There remained the curious question of the mechanism of acquisition of materials in a heavily sclerotized animal without a mouth. While some water enters as water vapor across the tanned cuticle, behavioral and morphological evidence indicated that the suckerplate also might function in acquisition of water in hypopi. The discoidal suckers were observed to pulsate slowly while the hypopus was positioned subelytrally and the anus could be observed to open and close (Hughes 1976, pers. observ.). The modified third and fourth pair of legs, positioned at a 45° angle to the body, acted as lever arms to raise and lower the sucker plate while it is attached to the elytron. This could create a negative pressure on soft elytral tissues sufficient to evacuate small quantities of hemolymph. Hemolymphal drainage would then be accessible to folds of the sucker plate, the vestigial genital opening, and the anal atrium (Fig. 10.1C). Slow acquisition would allow the uptake of provisions, and yet remain nonpernicious to the beetle, so as not to provoke action against the acquisition. This may account for the long (5–21 days) host-association observed in hypopi of *H. cooremani*.

But where would the hemolymph go once extracted from the beetle? Examination of scanning photomicrographs of hypopi revealed vestigial anal and genital openings on the sucker plate (Fig. 10.1C). If the mite was indeed "feeding" through the anus, where did the materials acquired during "feeding" go? How was this proposed "anal feeding" possible if the gut is solid as the literature indicated?

The logical way to examine these question was to section hypopi *in situ*. Such sectioning was unsuccessfully attempted over a three-year period in an effort to determine the physical relationship between the mite and the beetle. Because of the practical and logistical difficulties in obtaining adequate sections, another approach was taken. The hypodermis of the beetle elytron was chemically dehydrated and reflected from the procuticle, exposing the beetle-side of the hypodermis (Fig. 10.8E). One could then look at the beetle tissue and examine its structure for evidence of the effects of hypopal attachment. This procedure revealed small triangular openings in the hypodermis. Looking through these openings, one could observe the medial suckers of the mite sucker plate. While this does not mean that the mites created the openings, they were at the very least associated with them.

The problems associated with preservation and sectioning have recently been resolved (Houck and Lindley 1993). Sectioning of mites attached (*in situ*) to beetle elytra, exposed the presence of a gut in the hypopal stage (Fig. 10.6A, B).

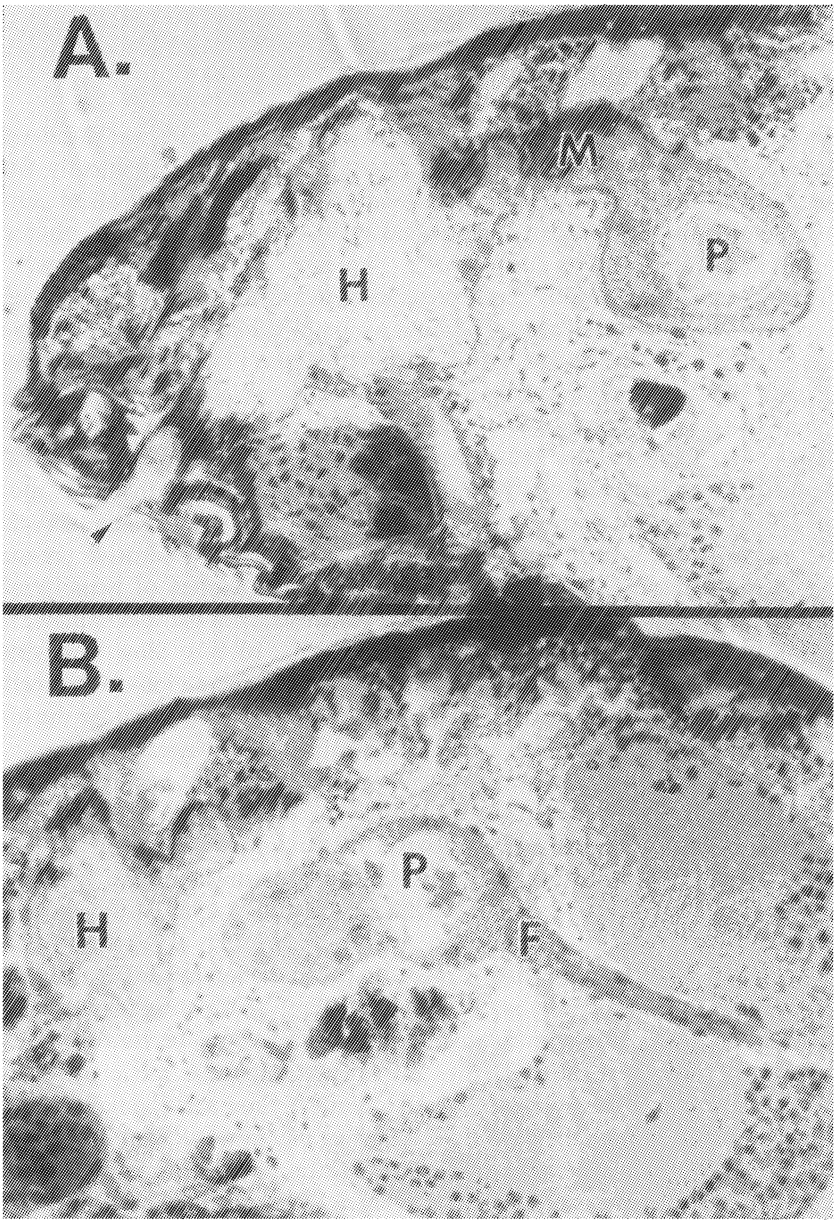


Figure 10.6. Light photomicrographs of longitudinal sections of a hypopus of *Hemisarcoptes cooremani* (400x) attached to the subelytral surface of *Chilocorus cacti*. A) Posterior section; **H** = Hindgut, **M** = Midgut, **P** = Proventriculus. The hindgut opens onto the caudoventral sucker plate (arrow). B) Anterior section; **F** = Fore gut. The fore gut of the hypopus is solid and transverses the sub-esophageal and supra-esophageal ganglia.

This gut has structural integrity which includes a proventriculus, and a midgut which opens onto the sucker plate. The foregut is indeed solid (Fig. 10.6B). The gnathosomal ("head") end is nonfunctional in feeding.

In light of these findings, a reexamination of older literature (Hughes and Hughes 1939, Oboussier 1939, Wallace 1960, Boczek et al. 1969, Woodring and Carter 1974) revealed what appears to be a similar atrium at the vestigial genital and anal openings in other astigmatid mites. The potential significance of this was apparently overlooked by earlier workers. And, the actual distention of the hypopus of *Hypodectes propus* was previously observed by Fain et al. (1980): "parvenu sous la peau, l'hypope augmente considérablement en taille, probablement à la suite de l'absorption de substances nutritives par osmose." The mechanism of this distention has not been explored. Additionally, hosts infested by hypopi of *Echimyopus dasypus* illustrated hyperkeratosis and hypertrophy around embedded mites (Fain and Lukoschus 1977). The mechanism of absorption of lysed tissues is still unexplored.

4.3 Hypothesis for the Evolution of Parasitism from Phoresy

Associations between mites and arthropods are very ancient (Poinar 1985, Poinar and Grimaldi 1990, Norton et al. 1993). The only available fossil (in amber) of an astigmatid mite is *Amphicalvolia hurdi* (Türk and Türk 1957). This specimen dates from the Oligocene or Miocene and can be assigned to a modern lineage, a congener which is associated with subcortical beetles (OConnor, pers. comm.). This, coupled with the fact that hypopi are ancestral in the Astigmata, is evidence for the fact that the Astigmata have had at least 25–38 million years of association with their host (and probably more). Lindquist (1975) suggests that mite-insect associations may be as old as 100 million years old. This is ample time for coevolution to have occurred, for the mites to have gained a strategic advantage in the relationship, and to have begun a sojourn into parasitism.

Interactions of hypopi with their respective hosts have been uniformly labeled as "phoretic" in the Astigmata for over 100 years (Michael 1884, Stolpe 1938, Hughes and Hughes 1939, Oboussier 1939, Perron 1954, Türk and Türk 1957, Hughes 1959, Wallace 1960, Evans et al. 1961, Kuo and Nesbitt 1971, Woodring and Carter 1974, Hughes 1976, Krantz 1978, Binns 1982, OConnor 1982), but this interpretation has been based on morphological criteria alone.

From the accumulating evidence, I propose the following hypothesis of evolutionary events which is compatible with all observed morphological and phylogenetic patterns and the radio-labeling data (Table 10.1): (1) the deutonymph became the demographic focus of differential selection resulting in it becoming the dispersal stage early on the evolution of the Astigmata (as developed in sections 3.1–3.6); (2) dispersal was enhanced by morphological changes (hypopal characteristics) and the association with a carrier organism (e.g. *Chilocorus*); (3) phoresy initially became established with low energetic costs to the host; (4)

Table 10.1. Summary of hypothesized "parasitization" events in the Astigmata, using phoretic interactions of Hemisarcoptes *and* Chilocorus *as a model. See text for support for the hypothesized steps given.*

1.) The deutonymph primitively arose in the Astigmata for dispersal among ephemeral habitats.
2.) Selection for dispersal qualities resulted in the typical astigmatid hypopal morphology (e. g. sucker plate, sclerotizations etc.; Fig. 10.1B, C).
3.) Dispersal was facilitated through host association.
4.) Phoresy was tolerated by hosts because of the relatively small cost.
5.) Extended host contact (over 25–100my) resulted in adaptation by the hypopus to host reflexed hemolymph (toxic alkaloids; Fig. 10.7) which had evolved as an antipredator defense in the host.
6.) *Adaptation* to toxic (and also nutrient rich) reflexed hemolymph led to hemolymphal *utilization* by hypopi (Fig. 10.5).
7.) Reflexed hemolymph was central to host survival from predation. *Utilization* of available reflexed hemolymph (produced at the discretion of the host during predator defense) advanced to hemolymphal extraction by action of the sucker plate and host *exploitation* (Fig. 10.7).
8.) As chemical adaptation proceeded, morphology would offer no clue of the changes in progress.
9.) Hypopal morphology (i.e. sucker plate) was needed to maintain contact with the host and withstand the rigors of the habitat (e.g. sclerotization) and so was conserved during the process of parasitization.
10.) Parasitization required that the hypopus molt on the host, and that subsequent stages also remain as ectoparasites. Subsequent stages were exapted for parasitism (Fig. 10.1A) due to gnathosomal morphology and chemical immunity conferred through hypopal adaptation. This was a change for which there was no rapid correction by the host, once the mutation occurred.
11.) The mutation for molting on the host would be heritable, the mite lineage would become resident on the host, and dispersal would become maladaptive.
12.) The hypopus would drop from the ontogeny once the derived parasitic lineage was fully established.
13.) The benefit of phoresy would be superseded by the greater benefit of not needing to disperse, once the transport vehicle became the resource.

extended contact of the hypopus with the host, and exposure to the toxic hemolymph, resulted in chemical acclimatization to the hemolymph; (5) adaptation to beetle hemolymph accelerated and graded into the utilization of the hemolymph by the mite because of its richness in nitrogenous and energetic nutrients; and (6) the interaction accelerated still further, from *utilization* of reflexed hemolymph (controlled by the host) to removing hemolymph through the caudal ventral sucker (host *exploitation*).

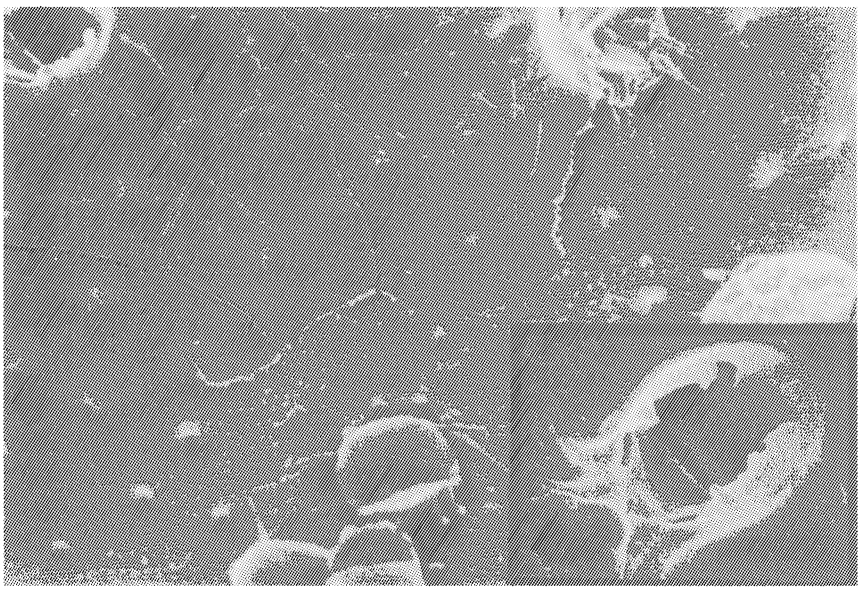


Figure 10.7. Subelytral surface of *Chilocorus cacti*. The arrow in the middle of the field of view indicates a place on the elytron where hemolymph from the pronotal area has run down the subelytral surface, coagulated and subsequently cracked. Arrows in the upper right and left corners show hypopi escaping entrapment by the hemolymph, and the ghost of a previous escapee, respectively. Insert is an enlargement of the image in the upper left.

If the hypopi then remained on the host to molt, only minor morphological adjustments would be required for functional parasitism to occur in post-deutonymphal stages. Chelicerae of mobile stages are adapted to feeding on soft tissues of scale insects and therefore exapted for beetle tissues (Fig. 10.1A). Adaptation by the hypopus to chemicals in the hemolymph is conferred to subsequent feeding stages since these stages represent (genotypically) a single individual. This toxin-resistance hypothesis suggest that the hypopus provides the ultimate potential for transition from the free-living existence in temporary environments, to a more stable parasitic existence.

Phylogenetic patterns of hypopal occurrence among the Astigmata are internally consistent with conclusions derived from my studies. While host-dependence varies considerably among the 69 families and >785 genera in the cohort Astigmata, as defined by OConnor (1982)— from free-living forms (with hypopi) to obligate parasitic forms—the hypopus has not been found to exist as part of the life cycle of any obligate parasite. Hypopi and parasitic life cycles are incompatible. The only possible exception is in the superfamily Canestrinioidea (OConnor, pers. comm.). *Coleoglyphus* and *Megacanestrinia* retain a heteromorphic deutonymph while members of the ontogeny occur as ectoparasites posi-

tioned subelytrally on the thoracic sternites of the host (Samsinák 1971). The hypopus is lost in all more derived parasitic taxa in the superfamily, so this actually argues for the inherent incompatibility of parasitic and hypopal stages in one life cycle.

Hemisarcoptes hypopi are the ultimate "wolf in sheep's clothing." They acquire materials from their host, acting as functional parasites, while retaining the ancestral phoretic morphology. The morphology which was interpreted for so long by researchers as phoretic may actually represents the transitional compromise between obligate parasitism and phoresy. To date this work on *Hemisarcoptes* is the only such attempt to experimentally define such "phoretic" relationships. Experimental studies on the morphological and physiological adaptation of astigmatid mites to their hosts could lead to a greater understanding of coevolution and the mechanisms of the evolution of parasitism. More interest in similar issues, surveyed across the astigmatid clade, would tell us how representative *Hemisarcoptes* is of the grade of potential transitions. The most valuable place to start is in the mites associated with the Coccinellidae and Chrysomellidae because these families of beetles share the character of reflexive bleeding which facilitates and promotes the critical initial process of interaction. It is less likely that semiparasitic transitional grades will be found in associations that offer no readily accessible stimulus or reward, or in situations where the host is provoked to retaliate when the relationship is first established.

Hemisarcoptes may have succeeded in overcoming the defensive volley of counterreaction by *Chilocorus* because it originally established a benign relationship that slowly graded into use of reflexed materials. Initial steps into exploitation required no significant defensive response from the beetle. The main target of the development of reflexed hemolymph was attacking predators, such as ants and other arthropods. Selection for such an important function would be strong. Evolution of exploitation by the mite included chemical adjustment to the host alkaloids, the beetle's major line of self defense.

Once physiologically adapted, the only major change required to bring the transition to closure, was that the mite molt on the host instead of getting off to molt. This has not occurred in *Hemisarcoptes*. This mutational step could be accomplished within one generation, a time frame which could not be countered by the host. Its fate accomplished, the mite would no longer need to move among transient habitats, and the dispersal stage would be selected from the ontogeny. The morphological shift from phoresy to parasitism, if observable, would have had the appearance of a macroevolutionary event when in fact the "phoretic" was slowly adapting physiologically to a parasitic nature while retaining the morphological characters of a phoretic.

Such transition into parasitism also offers potential for the creation of a new lineage within the astigmatid clade if the hypopus is a genetic polymorphism. Females expressing the heteromorph have the potential to step into parasitism, and the step once taken separates them from their nonphoretic sisters which remain tied to the original habitat.

"Vacant niches exist for parasites" (Price 1980), but most potential hosts can defend themselves against exploitation and parasitism by morphological, physiological and behavioral counterreactions. As stated initially, a parasite as "an organism living in or on another living organism, obtaining from it part or all of its organic nutrition, and causing some degree of real damage to its host" (quoted in Price 1980). Using this definition, there is little doubt that *Hemisarcoptes* is more like a parasite than a phoretic but the transformation is not yet complete.

5. Future Work and Prospectus

It seems that all corroborating evidence indicates that *Hemisarcoptes* became associated with *Chilocorus* because of the primitive dispersal relationship of the heteromorphic deutonymph with adult beetles. However, recent studies indicate that the paradigm of phoresy in *Hemisarcoptes* is inconsistent with important observations and that the initially benign relation has graded, over time, into a host-parasite relationship. In order to understand how coevolution has occurred, this research must continue to focus on the mite (*Hemisarcoptes*), but additionally work has begun to elucidate the perspective of the beetle (*Chilocorus*) in the relationship.

If initial studies have given an accurate glimpse of past evolutionary occurrences, there should be some evidence that *Chilocorus* has indeed suffered some differential "degree of damage" which can be correlated to degree of hypopal association. Examination of museum and field specimens indicates that not all Chilocorini are equally likely to transport *Hemisarcoptes* (pers. observ.).

Morphological examination of the subsurface of the elytron of *Chilocorus* has been informative. This is the area of attachment for the mites and represents the "habitat" of the mite while in transit on the beetle. The microsculpturing of the subelytral surface presents obstacles to the attachment of mites to *C. cacti*, in some portions of the elytral surface.

In the zone just caudal to the pronotal area, the elytron projects spines that are less than 10 μm apart (Fig. 10.8A, B). For the mite to attach at this point would require sitting on approximately 4–5 spines, risking damage to the delicate sucker tissues and possibly terminating mite-beetle interaction. Visually scanning the surface caudoventrally along the medial axis, the projections become less dense, smaller and more blunt. Approaching the caudoventral-most tip, the surface looses the armature and the attachment plane contains a fluff of material which is composed of what appears to be anastomosing superficial vessels (presumably the tracheal system) (Fig. 10.8C, D, E, F).

There is a correlation between the morphology of the beetle elytron and the positioning of the mites. Mites which have had time to select an attachment site, do so by anchoring only to the caudal ventral tip (Fig. 10.4A). One hypothesis is that the beetle encourages the mites into a position on the body which provides

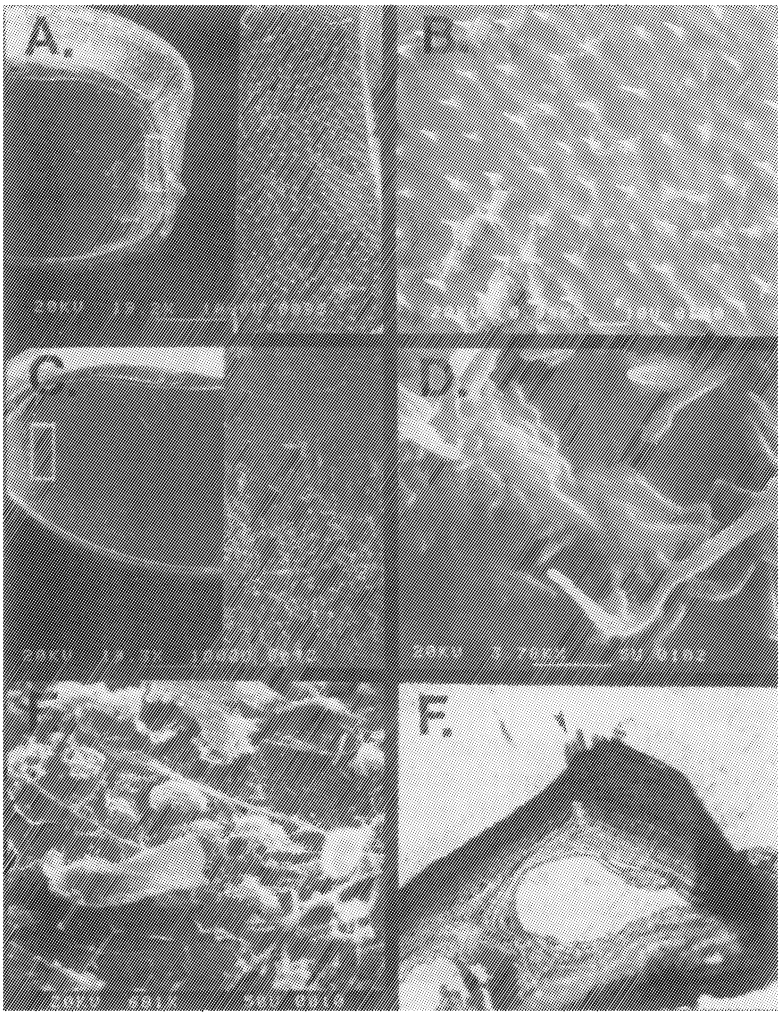


Figure 10.8. Scanning electron photomicrographs (SEM) of the detailed microsculpturing of the subelytral surface of *Chilocorus cacti*. A) Split-screen SEM image of the anterior subelytral area, near the pronotum (Note: elytron removed from the body; the head would have been located to the right of the elytron). Scale bar is with reference to the left portion of the image only. B) An SEM enlargement of the same area as seen in Fig. 10.8A. Spines in this area are less than 10μm apart. Mites are not normally found attached in this area of the elytron (compare with Fig 10.4A). C) Split-screen SEM image of the caudoventral tip of the elytron, where mites most frequently attach. Scale bar is with reference to the left portion of the image only. D) An SEM enlargement of the same area as seen in Fig. 10.8C. Notice that there are no spines in this area. Instead, the tracheal system of the elytron becomes superficial and anastomoses to the surface of the hypodermis. This is the zone of attachment of hypopi. E) Anastomoses of the tracheal system highly magnified using SEM. F) Transmission electron photomicrograph (TEM) of the tracheal elements (arrow), as seen in Fig. 10.8E, showing their orientation with reference to the subelytral surface of the beetle elytron.

the beetle with the greatest mobility or the least energetic drain. Could there be some form of minimal-loss compromise to the occurrence of the mites, on the part of the beetle? Is this some form of counterresponse? Or is it just an aspect of beetle morphology related to some other function? Similar examination of other members of the tribe Chilocorini for microsculpturing would add perspective to this question. Thus far I have examined the two North American species of *Chilocorus* (*C. cacti* and *C. stigma*), a European species (*C. bipustulatus*), and oriental species (*C. kuwanae*), a Mideastern species (*C. nigritus*), and two African species (*C. distigma* and *C. discoideus*).

Sister genera of *Chilocorus* found in North America (Gordon 1985), and also within the tribe Chilocorini include: *Exochromus*, *Brumoides*, *Axion*, *Halmus* (= *Orcus*), and *Arawana*. Thus far representatives of *Exochromus*, *Brumoides*, and *Halmus* have been examined for outgroup comparison of the sculpturing as it relates to morphological changes in the subelytral surface. Such comparison is valuable because *Exochromus*, *Brumoides*, *Axion*, *Halmus* (= *Orcus*), and *Arawana* are not phoretic hosts of *Hemisarcoptes*. A representative of the non-chilocorine coccinellids (*Rhyzobius*, = *Linobius*) is also being examined. The genus *Rhyzobius* was selected because it is also a predator of diaspidid scale insects, is sympatric with *Chilocorus*, and represents an ecological and evolutionary contrast. The full results of these studies will be discussed elsewhere.

Acknowledgments

I would like to acknowledge Uri Gerson (Israel) for introducing me to *Hemisarcoptes* in 1982, and thank Barry M. OConnor (University of Michigan) for an early partnership in the systematic treatment of the Hemisarcoptidae and for encouraging a deep and compelling love of mites. Dr. R. K. Summy assisted in the location of my first field collection of *Hemisarcoptes* in Donna, Texas in 1983. Dr. R. E. Strauss contributed to the clarity of this text. This work was initiated by NSF grant #83-07711 to B. M. O. C. and M. A. H. and continued with funds generated through a Binational Agricultural Research and Development grant #IS-1397–87.

References

Baker, E. W. 1951. *Pneumocoptes*, a new genus of lung-inhabiting mite from rodents (Acarina: Epidermoptidae). *J. Parasitol.* 37:583–586.

Barker, P. S. 1982. Control of a mite *Lepidoglyphus destructor*, including hypopi, in wheat with carbon disulfide. *J. Econ. Entomol.* 75:426–439.

Berenbaum, M. R. 1983. Coumarins and caterpillars: a case of coevolution. *Evolution* 37:163–179.

Binns, E. S. 1982. Phoresy as migration, some functional aspects of phoresy in mites. *Biol. Rev.* 57:571–620.

Boczek, J., C. Jura and A. Krzysztofowicz. 1969. The comparison of the structure of the internal organs of post-embryonic stages of *Acarus farris* (Oud.) with special reference to the hypopus. In: *Proc. 2nd Int. Congr. Acarol.* (G. O. Evans ed.). Sutton Vonington, England, 1967. Akadémiai Kaidó, Budapest. Pp. 241–248.

Brooks, D. R. 1979. Testing the context and extent of host-parasite coevolution. *Syst. Zool.* 28:299–307.

Carey, J. R., P. Liedo, D. Orozco and J. W. Vaupel. 1992. Slowing of mortality rates at older ages in large medfly cohorts. *Science* 258:457–461.

Curtsinger, J. W., H. H. Fukui, D. R. Townsend and J. W. Vaupel. 1992. Demography of genotypes: failure of the limited life-span paradigm in *Drosophila melanogaster*. *Science* 258:461–463.

Cutcher, J. J. and J. P. Woodring. 1969. Environmental regulation of hypopal apolysis of the mite, *Caloglyphus boharti*. *J. Insect Physiol.* 15:2045–2057.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. *Q. Rev. Biol.* 22:283–314.

Ehrlich, P. R. and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608.

Evans, G. O., J. G. Sheals and D. MacFarland. 1961. *The Terrestrial Acari of the British Isles: An Introduction to Their Morphology, Biology and Classification*, Vol. 1. Brit. Mus. (Nat. Hist.), London. 219 pp.

Ewing, H. E. 1912. The origin and significance of parasitism in the Acarina. *Trans. Acad. Sci. St. Louis.* 21:1–70.

Ewing, H. E. 1933. New genera and species of parasitic mites of the superfamily Parasitoidea. *Proc. US Nat. Mus.* 82:1–14.

Fain, A. 1968. Etude de la variabilité de *Sarcoptes scabiei* avec une revision des Sarcoptidae. *Acta Zool. Pathol. Antverp.* 56:73–82.

Fain, A. 1969. Adaptation to parasitism in mites. *Acarologia* 11:429–449.

Fain, A. 1971. Evolution de certains groupes d'hypopes en fonction du parasitisme (Acarina: Sarcoptiformes). *Acarologia* 13:171–175.

Fain, A. and F. S. Lukoschus. 1977. New endofollicular or subcutaneous hypopi from mammals (Acari: Astigmata). *Acarologia* 19:484–493.

Fain, A. and J. R. Philips. 1981. Astigmatic mites from nests of birds of prey in USA. VI. The adult froms of *Echimyopus orphanus* Fain and Philips, 1977 and *Dermacarus pilitarsus* Fain and Philips, 1977. *Int. J. Acarol.* 7:235–237.

Fain, A., D. P. Britt and D. H. Molyneux. 1980. *Myianoetus copromyzae* sp. nov. (Acari, Astigmata, Anoetidae) phoretic on *Copromyza atra* (Meigen 1830) in Scotland. *J. Nat. Hist.* 14:401–403.

Farish, D. J. and Axtell, R. C. 1971. Phoresy redefined and examined in *Macrocheles muscaedomesticae* (Acarina: Macrochelidae). *Acarologia* 13:16–29.

Fashing, N. J. 1976. The resistant tritonymphal instar and its implications in the population

dynamics of *Naiadacarus arboricola* Fashing (Acarina: Acaridae). *Acarologia* 18:704–714.

Fashing, N. J. and L. L. Wiseman. 1980. *Algophagus pennsylvanicus*-a new species of Hyadesidae from water-filled treeholes. *Int. J. Acarol.* 6:79–84.

Feeny, P. P. 1976. Plant apparency and chemical defense. In: *Recent Advances in Phytochemistry: Biochemical interactions Between Plants and Insects*, Vol. 10 (J. Wallace and R. Mansell eds.). Plenum Press, NY. Pp. 1–40.

Gerson, U. 1967. Observations on *Hemisarcoptes coccophagus* Meyer (Astigmata: Hemisarcoptidae), with a new synonym. *Acarologia* 9:623–638.

Gerson, U. and R. Schneider. 1982. The hypopus of *Hemisarcoptes coccophagus* Meyer (Acari: Astigmata: Hemisarcoptidae). *Acarologia* 23:171–76.

Gerson, U., B. M. OConnor and M. A. Houck. 1990. Acari. In: *Armored Scale Insects, Their Biology, Natural Enemies, and Control* (D. Rosen ed.). Elsevier, Amsterdam. Pp. 77–97.

Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *J. NY Entomol. Soc.* 93:1–912.

Holmes, J. C. 1973. Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. *Can. J. Zool.* 51:333–347.

Houck, M. A. 1989. Isozyme analysis of the mite *Hemisarcoptes* and its beetle host. *Entomol. Exp. Appl.* 52:167–172.

Houck, M. A. 1992. Morphological variation in an ectoparasite: partitioning ecological and evolutionary influences. In: *Ordinations in the Study of Morphology, Evolution, and Systematics of Insects: Applications and Quantitative Genetic Rationales* (J. T. Sorensen and R. Foottit eds.). Elsevier, Amsterdam. Pp. 277–308.

Houck, M. A. and A. C Cohen. Ms. Transition from a free-living life form to parasitism via phoresy: experimental evidence from the mite *Hemisarcoptes*.

Houck, M. A. and V. Lindley. 1993. A microwave technique for microscopical studies involving arthropods. *Am. Entomol.* 39:117–119.

Houck, M. A. and B. M. OConnor. 1990. Ontogeny and life history of *Hemisarcoptes cooremani* (Acari: Hemisarcoptidae). *Ann. Entomol. Soc. Am.* 83:161–205.

Houck, M. A. and B. M. OConnor. 1991. Ecological and Evolutionary Significance of Phoresy in the Astigmata. *Annu. Rev. Entomol.* 36:611–636.

Hughes, A. M. 1976. *The Mites of Stored Food and Houses. Min. Agric. Fisheries Food Tech. Bull. 9.* H. M. S. O., London. 400 pp.

Hughes, T. E. 1959. *Mites or the Acari.* Athlone Press, London. 225 pp.

Hughes, T. E. and A. M. Hughes. 1939. The internal anatomy and postembryonic development of *Glycyphagus domesticus. Proc. Zool. Soc.* London 108:715–33.

Kethley, J. B. and D. E. Johnston. 1975. Resource tracking patterns in birds and mammal ectoparasites. *Entomol. Soc. Am. Misc. Publ.* 9:231–236.

Kim, K. C. 1985a. Evolutionary relationships of parasitic arthropods and mammals. In:

Coevolution of Parasitic Arthropods and Mammals (K. C. Kim ed.). Wiley, NY. Pp. 3–82.

Kim, K. C. 1985b. Parasitism and coevolution epilogue. In: *Coevolution of Parasitic Arthropods and Mammals* (K. C. Kim ed.). Wiley, NY. Pp. 3–82.

Knülle, W. 1959. Morphologische und entwicklungsgeschichtliche Untersuchungen zum phylogenetischen System der Acari: Acariformes Zachv. II. Acaridiae: Acaridae. *Mitt. Zool. Mus.* Berlin 35:347–417.

Knülle, W. 1987. Genetic variability and ecological adaptability of hypopus formation in a stored product mite. Exp. Appl. Acarol. 3:21–32.

Knülle, W. 1990. Genetic and environmental determinants of hypopus duration in the store-product mite *Lepidoglyphus destructor*. Exp. Appl. Acarol. 10:231–258.

Knülle, W. 1991. Life-cycle strategies in unpredictably varying environments: genetic adaptations in a colonizing mite. In: *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall, London. Pp. 51–53.

Krantz, G. W. 1978. *A Manual of Acarology, 2nd edition*. Oregon State Univ. Book Stores, Corvallis, OR. 509 pp.

Kuo, J. S. and H. H. J. Nesbitt. 1971. Internal morphology of the hypopus of *Caloglyphus mycophagus*. *Acarologia* 13:156–70.

Lindquist, E. E. 1975. Association between mites and other arthropods in forest floor habitats. *Can. Entomol.* 107:425–437.

Michael, A. D. 1884. The hypopus question, or the life history of certain Acarina. *J. Linn. Soc. London. Zool.* 17:371–394.

Mitchell, R. 1970. An analysis of dispersal in mites. *Am. Nat.* 104:425–431.

Moser, J. C. and E. A. Cross. 1975. Phoretomorph: a new phoretic phase unique to the Pyemotidae (Acarina: Tarsonemoidea). *Ann. Entomol. Soc. Am.* 68:820–22.

Norton, R. A. 1980. Observations on phoresy in oribatid mites (Acari: Oribatei). *Int. J. Acarol.* 6:121–130.

Norton, R.A., J. B. Kethley, D. E. Johnston and B. M. OConnor. 1993. Phylogenetic perspectives on genetic systems and reproductive modes of mites. In: *Evolution and Diversity of Sex Ratio in Insects and Mites* (D. L. Wrensch and M. A. Ebbert eds.) Routledge, Chapman and Hall, NY. Pp. 8–99.

Oboussier, H. 1939. Beiträge zur Biologie und Anatomie der Wohnungsmilben. *Z. Angew. Entomol.* 26:253–96.

OConnor, B. M. 1979. Evolutionary origins of astigmatid mites inhabiting stored products. In: *Recent Advances in Acarology*, Vol. 1 (J. G. Rodriguez ed.). Academic Press, NY. Pp. 273–278.

OConnor, B. M. 1982. Evolutionary ecology of astigmatid mites. *Annu. Rev. Entomol.* 27:385–409.

Pasteels, J. M., C. Deroe, B. Tursch, J. C. Braekman, D. Daloze, and C. Hootele. 1973. Distribution et activités des alcaloides défensifs des Coccinellidae. *J. Insect Physiol.* 19:1771–1784.

Perron, R. 1954. Untersuchungen über Bau, Entwicklung und Physiologie der Milbe *Histiostoma laboratorium* Hughes. *Acta Zool. Stockholm.* 35:71–106.

Peterson, P. C. 1975. An analysis of host-parasite associations among feather mites (Acari: Analgoidea). *Misc. Publ. Entomol. Soc. Am.* 9:237–242.

Poinar, G. O., Jr. 1985. Fossil evidence of insect parasitism by mites. *Int. J. Acarol.* 11:27–38.

Poinar, G. O., Jr. and D. A. Grimaldi. 1990. Fossil and extant macrochelid mites (Acari: Macrochelidae) phoretic on drosophilid flies (Diptera: Drosophilidae). *J. NY Entomol. Soc.* 98:88–92.

Price, P. W. 1980. *Evolutionary Biology of Parasites.* Princeton Univ. Press, Princeton, NJ. 237 pp.

Ricklefs, R. E. 1973. *Ecology.* Chiron Press, Portland, OR. 861pp.

Samsinák, K. 1971. Die aur *Carabus*-Arten (Coleoptera, Adephaga) der palaearktischen Region lebenden Milben der Unterordnung Acariformes (Acari); ihre Taxonomie und Bedeutung fur die Losung zoogeographischer, entwicklungsgeschichtlicher und parasitophyletischer Fragen. *Entomol. Abh. St. Mus. Tierk.* (Dres.) 38:145–234.

Stolpe, S. G. 1938. The life cycle of the tyroglyphid mites infesting cultures of *Drosophila melanogaster. Anat. Rec.* 72 (*Suppl.*):133–34.

Timm, R. M. 1983. Fahrenholz's rule and resource tracking: a study of host-parasite coevolution. In: *Coevolution* (M. H. Nitecki ed.). Univ. Chicago Press, Chicago. Pp. 225–265.

Türk, E. and F. Türk. 1957. Systematik und oekologie der tyroglyphiden mitteleuropas. In: *Beiträge zur Systematik Oekologie Mitteleuropäischer Acarina*, Vol. 1 (H. J. Stammer ed.). Akad., Verlagsges, Leipzig. Pp. 3–231.

Volgin, V. I. 1971. The hypopus and its main types. *Proc. 3rd Int. Congr. Acarol.*, Prague, 1971. Pp. 381–383.

Waage, J. K. 1979. The evolution of insect/vertebrate association. *Biol. J. Linn. Soc.* 12:187–224.

Wallace, D. R. J. 1960. Observations on hypopus development in the Acarina. *J. Insect Physiol.* 5:216–29.

Wharton, G. W. 1946. Observations on *Ascoschongastia indica* (Hirst 1915) (Acarina: Thormiculidae [Trombiculidae]). *Ecol. Monogr.* 16: 152–184.

Woodring, J. P. and S. C. Carter. 1974. Internal and external morphology of the deutonymph of *Caloglyphus boharti* (Arachnida: Acari). *J. Morphol.* 144:275–295.

Zachvatkin, A. A. 1941. *Fauna of U.S.S.R., Arachnoidea.* Transl., A. Ratcliff, A. M. Hughes 1959, American Institute of Biological Sciences, Washington, DC. (In Russian). 573 pp.

11

Cytogenetics of Holokinetic Chromosomes and Inverted Meiosis: Keys to the Evolutionary Success of Mites, with Generalizations on Eukaryotes

Dana L. Wrensch, John B. Kethley and Roy A. Norton

CONTENTS

1. Introduction

1.1 Recombination and Conservation of Genomes: A Preface

The evolution of sexual reproduction has seen a recent and major resurgence as a topic of interest. Many authors (e.g. Ghiselin 1974, Williams 1975, Maynard Smith 1978, Bell 1982, Shields 1982, Bull 1983, Michod and Levin 1988) have refined the now-familiar arguments that generally cast sexual reproduction as the alternative to the asexual production of genetic clones. As theorists have moved further from the usual cytogenetic models (i.e. humans, mice, fruitflies and maize), we have learned that the many strange genetic systems and breeding biologies of plants, animals and protists blur the distinction between "sexual" and "asexual."

Two focal points have now developed, which weigh the evolutionary pros and cons of genetic recombination, particularly that occurring at meiosis. (1) Many authors have focused on the creative role of meiosis, i.e. the provision for genetic flexibility. In this view, recombinant gametes are considered essential to offspring success (various individual-selection arguments) or to the long-term success of lineages (group-selection arguments). (2) Others have considered the conservation of successful genomes as being the more pervasive and ancient effect of meiosis ("what is good for the mother is good for the daughter"). In this view, recombination provides a mechanism for the editing of mutations and the double-strand repair of damaged DNA (Shields 1982, Bernstein and Bernstein 1991). It is the latter view that currently has the most momentum. In the "selfish-gene" paradigm of Dawkins (1976), perhaps the best way to maximize the successful transfer of genes into the next generation is for a female to produce eggs meiotically, while being in control of recombination.

Our goal in this chapter is to redirect thinking about how genetic systems and reproductive modes have influenced the tremendous evolutionary success of mites. We argue that current cytogenetic models leave unresolved questions about the evolutionary success of thelytokous and haplodiploid mites. In proposing

new solutions, we focus on the poorly understood properties of holokinetic chromosomes, and how these properties can influence the control of recombination. We end the discussion with speculations about the cytogenetic systems of eukaryotic organisms in general.

1.2 Overview of Genetic Systems and Reproductive Modes of Mites

The Acari are generally recognized as comprising two rather distinct taxa, the orders Parasitiformes and Acariformes. Each contains taxa of considerable medical, agricultural, and ecological significance. The many fundamental differences between these groups have evoked questions about the monophyly of mites that remain unanswered. In a recent set of papers dealing with the evolution of sex-ratio patterns in insects and mites (Wrensch and Ebbert 1993), Norton et al. (1993) synthesized available information on the genetic systems and reproductive modes of mites (summarized below) and attempted to provide a phylogenetic context for ideas on the evolution of these traits.

Diplodiploidy, without distinct sex chromosomes, appears to be the ancestral system in both mite orders. Diplodiploidy is maintained in the Ixodida (ticks), one of the two major suborders of parasitiform mites, but they have sex chromosomes and have mostly XO or XY males. Middle derivative members of the suborder Mesostigmata (e.g. Parasitidae) retain the ancestral system, but most higher Mesostigmata are haplodiploid. In the Acariformes, the ancestral system is the dominant one in the paraphyletic suborder Oribatida; records of possible haplodiploidy in oribatid mites need confirmation. The Parasitengona (comprising about half the species of the suborder Prostigmata) has the ancestral system, while the higher Prostigmata all seem to be haplodiploid. The Astigmata, a diverse group derived from within the oribatid mites, contains both diplodiploid (with XO or XY males, or rarely without sex chromosomes) and haplodiploid groups.

We use the term haplodiploidy in the general sense of Wrensch and Ebbert (1993, glossary) and Norton et al. (1993). It includes two systems in which males are impaternate: (1) arrhenotoky, in which males develop parthenogenetically from haploid eggs; and (2) parahaploidy (also referred to as paternal genome loss or pseudoarrhenotoky), in which diploid male embryos either undergo expulsion of the paternal genome at some early stage of embryogenesis (e.g. Phytoseiidae) or undergo heterochromatization of the paternal genome and retain it in somatic cells (Otopheidomenidae).

Males of both arrhenotokous and parahaploid species are functionally haploid, and only two functional sperm are produced per spermatagonium; these two sperm carry identical halves of the maternal genome. A unique and important feature of haplodiploidy is that females control the sex ratio of progeny, by regulating the proportion of males, in response to environmental cues (Wrensch 1993; Sabelis and Nagelkerke 1987, 1993). Clearly both arrhenotoky and para-

haploidy have evolved multiple times in mites, but their evolutionary polarity remains unresolved.

Thelytoky—the parthenogenetic development of female offspring—has also evolved multiple times in the Acari, and has been derived from each of the sexual systems noted above. In most higher mite taxa the distribution of thelytoky fits the theoretical prediction of being phylogenetically scattered (Bell 1982). But of particular interest are sizeable genera, families, or even superfamilies of early derivative acariform mites (e.g. certain Endeostigmata) and early to middle derivative oribatid mites that contain no sexual species (Palmer and Norton 1990, 1991; Norton and Palmer 1991; Norton et al. 1993). As discussed next, explanations for this and other aspects of mite reproductive biology have been problematic.

1.3. Mites Do Things They Shouldn't

Success in Thelytokes. Theoretical arguments concerning the evolutionary potential of thelytoky as a reproductive mode usually conclude that thelytoky is a "dead end" strategy. Depending on one's viewpoint, thelytokes fail because of an inability to conserve a successful genome faithfully (Manning 1976, Shields 1982), or because they lack the genetic flexibility necessary to survive competition with sexual species (Ghiselin 1974, Bell 1982) or survive environmental changes (White 1973, Maynard Smith 1986). The last opinion was recently expressed quite strongly by Crow (1992), in an attempt to "put the last nail in the coffin" of thelytoky.

Theoretical considerations derived from evolutionary genetics and cytogenetics (i.e. Suomalainen 1950, Asher 1970, White 1973, Uyenoyama 1987, John 1990) predict disaster, through either increasing homozygosity in the various forms of automictic (meiotic) thelytoky, or increasing mutation load with apomictic (ameiotic) thelytoky (i.e. the infamous Muller's Ratchet).

Even if thelytokes are not short-term dead ends, as some workers have accepted, the often unstated conclusion is that they are *long-term* dead ends—they should not produce significant evolutionary radiations. The existence of rather large groups of acariform mites having no sexual species implies the contrary. These groups are long-lived in evolutionary time and in fact have radiated in a thelytokous reproductive mode. A similarly large and totally thelytokous group, the bdelloid rotifers, has been referred to as an embarrassment to evolutionary theory (Maynard Smith 1986), and the various groups of thelytokous acariform mites add to the embarrassment.

Origin of a Successful Sexual Clade from Thelytokous Ancestors. One of us (RAN; Norton and Palmer 1991, and Chapter 5 of this volume) has suggested that the Astigmata, a predominantly sexual taxon with great taxonomic and biological diversity, arose from within the oribatid mite clade Trhypochthonioidea. Known species of trhypochthonioids are all thelytokous and the group

seems to have radiated in a mode of automictic thelytoky. Thus, not only have these thelytokes been successful in the long term, but an evolutionary reversal to sexuality in Astigmata is implied in the relationship.

Success in Highly Inbred Arrhenotokes. In theory, the reproductive advantages of arrhenotoky are well understood. Relative to diplodiploids, arrhenotokes exhibit extraordinarily rapid adaptive response to changes in environmental selection factors (Griffing 1982), at least in part because deleterious alleles cannot "hide" in the genetically "naked" male (Huxley 1942, Nur 1971). Indeed, in the theory of local mate competition (Hamilton 1967) arrhenotoky plays a central and crucial role. However, evolutionary theory predicts that highly inbred arrhenotoky (HIA) systems should not be very successful, as they are driven to homozygosity and lose genetic flexibility (Futuyma 1986).

This negative perception of HIA contrasts with the widespread existence of such systems in very successful groups of mites. For example, Kethley (1971) found that populations of an arrhenotokous mite inhabiting bird quills are founded by a single mated female whose progeny consist of a single son and 11 daughters. Sib-mating occurs and the second generation in the quill mirrors the first, by a multiple of 11: one son and 11 daughters per mother. At maturity, second generation females mate with their brothers or closer-than-first cousins and then disperse to newly developing quills. Although quill mites represent an extreme example of HIA, the group is quite diverse morphologically and taxonomically (Kethley 1970, Kethley and Johnston 1973). Many Heterostigmata have obligate sib-mating; these have a variety of life styles, and include plant feeders (e.g. *Polyphagotarsonemus latus*, Flechtmann and Flechtmann 1984) and insect parasites (e.g. *Pyemotes ventricosus*, Swan 1934; *Adactylidium* sp., Elbadry and Tawfik 1966). Niche constraints alone tend to ensure sib-mating in the microhabitats of many species. Examples include the heterostigmatid mites that parasitize insect respiratory systems—such as those of honey bees (*Acarapis woodi*, Smith 1990) and ladybird beetles (Podapolipidae, Husband 1972)—or that are commensals in insect nests (e.g. *Sicilipes costaricanus*, Rack and Eickwort 1979). The same is true of the economically important gall mites (Eriophyidae, de Lillo 1991).

All these mites are arrhenotokes with female-biased sex ratios, and all disperse exclusively as inseminated females. Such attributes combine to yield highly inbred populations. In mites, HIAs are not only unexceptional but are, in fact, the norm in parasitic (highly derived) species—another "embarrassment" to evolutionary theory.

1.4. Holokinetic Chromosomes and Cytogenetics

Below we suggest that these "embarrassments," and other interesting aspects of mite biology, are embarrassments not to evolutionary theory, but to the current cytogenetic paradigm. Indeed, they may prove easily explained in light of the

widespread, if not universal, possession of holokinetic chromosomes by mites. The unusual features of holokinetic chromosomes during mitotic and meiotic divisions are well known from extensive research on the Heteroptera (e.g. Hughes-Schrader 1948, Brown and Nur 1964), Lepidoptera (Suomalainen 1953) and plants such as *Luzula* (Nordenskiöld 1962). However, their attributes are not widely known except by specialists in cytogenetics, and the evolutionary consequences of a holokinetic genetic system have been neglected.

In part, this lack of interest may stem from poorly founded generalities. For example, White (1973, 496) proposed that single locus genetics should be the same in monocentric or holokinetic organisms. But he also realized that something significantly different might be occurring in holokinetic systems: "differences between meiotic mechanisms in various groups with holocentric chromosomes and in organisms with monocentric chromosomes may be vitally significant from the standpoint of chromosome evolution." John and Lewis (1965, 142) had also realized previously that certain cytogenetic concepts formulated for monocentric chromosomes were not strictly applicable to holokinetic systems, or would have different implications, but they did not specify what these distinctions might be. In this chapter, we will attempt to do so.

2. Properties of Holokinetic Chromosomes and Their Distribution among Mites

2.1. General Contrast of Holokinetic and Monocentric Chromosomes

2.1.1 Structure and Correlated Features

Holokinetic chromosomes are distinctive because during cell division they behave as if the spindle attachment is not localized. Such chromosomes are also denoted as holocentric or diffusecentric, or are described as having a nonlocalized or diffuse centromere or kinetochore. Ultrastructural studies on the spider mite *Tetranychus urticae* showed spindle microtubules to have points of attachment extending across the entire length of the holokinetic chromosome (Templaar 1980).

Generally, holokinetic chromosomes are small (1–3 μm) and stain uniformly along their whole length. Thus, one of their distinguishing traits is the absence of the differentially staining primary constriction that marks the classic centromere of monocentric chromosomes. Holokinetic chromosomes lack a true kinetochore (i.e. a trilaminar disk, Balczon and Brinkley 1990), although a faint, subterminal constriction is sometimes seen, indicating the site of a nucleolus. We adopt the term "holokinetic" to describe such chromosomes since it is properly descriptive without implying the presence of a centromere, as the alternative and rather oxymoronic term "holocentric" does. Also, "holokinetic" is currently the term

preferred by cytologists (e.g. John 1990) and acarological cytogeneticists (e.g. Helle et al. 1984).

Holokinetic chromosomes may co-occur with unusual cytological features. Cells typically show cask-, barrel-, or cylindrical-shaped spindles (Fig. 11.1) which have been described as anastral (Schrader 1953, White 1973). Anastral spindles are associated with centrosomes lacking a centriole but possessing intranuclear spindles (Kubai 1975). Not all taxa with holokinetic chromosomes lack centrioles, however (e.g. hemipteran spermatogenesis, Hughes-Schrader and Schrader 1961; see Peterson and Berns 1980 for general review).

In holokinetic systems, the nuclear membrane typically does not disintegrate until late telophase in mitosis, or late prometaphase I in meiosis. Instead of kinetochores and localized centromeres that connect by microtubules to centriole-based centrosomes, holokinetic chromosomes use a "primitive" spindle apparatus (Heath 1980). Individually or in groups, holokinetic chromosomes are packaged in membranes called karyomeres; these are functionally distinct from micronuclei, which may or may not contain chromosomes or chromosome fragments.

The absence of a localized centromere featuring a true kinetochore appears to be linked to the absence of a pair of centrioles in a bipolar spindle arrangement. The association of holokinetic chromosomes with persistent nuclear membranes enables them to orient in a fundamentally different pattern than do monocentric chromosomes in kinetochore-centriole spindle systems (see Section 2.1.3).

Another important difference between holokinetic and monocentric chromosomes is their response to irradiation-induced fragmentation. For holokinetic chromosomes, diffuse kinetic activity during mitosis means that fragments are not necessarily lost during cell division, and such chromosomes have "sticky ends" by which breaks can be repaired. Fragments are more numerous in cleavage nuclei than in meiotic figures and can persist for at least four or five consecutive cleavage mitoses (e.g. Cooper 1972). This has been interpreted as greater "healing" capacity during the relatively much longer premeiotic interphase and prophase I than is possible in the rapidly mitotically dividing nuclei and cells of early embryogenesis. The ability of holokinetic chromosomes to fragment and fuse is well known (Hughes-Schrader and Ris 1941, Brown and Nelson-Rees 1961, Chandra 1962, Evans and Pond 1964, LaChance et al. 1970, Jones 1978, Templaar 1979b, Ueshima 1979), and it has both diagnostic value (Section 2.2) and evolutionary significance (Section 4.2).

2.1.2 Behavior of Chromosomes in Mitosis (Figs. 11.1, 11.2)

During mitotic metaphase (Fig. 11.1), only the centromere of monocentric chromosomes—more precisely the kinetochore, if such a structure is present—is strictly on the equator. In contrast, the entire holokinetic chromosome is situated on the equatorial plate and is involved in relative positioning between the poles (Helle et al. 1984). Furthermore, the whole holokinetic chromosome

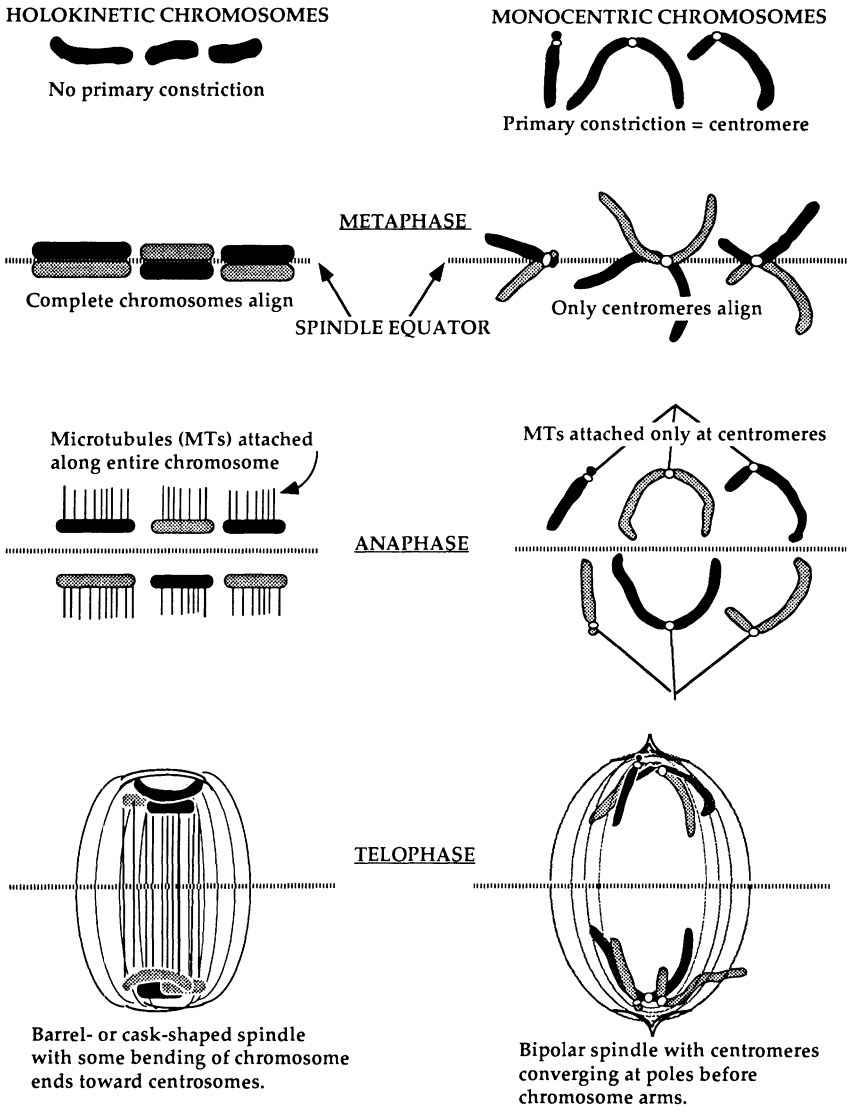


Figure 11.1. Schematic comparison of chromosome behavior for holokinetic and monocentric chromosomes during mitosis.

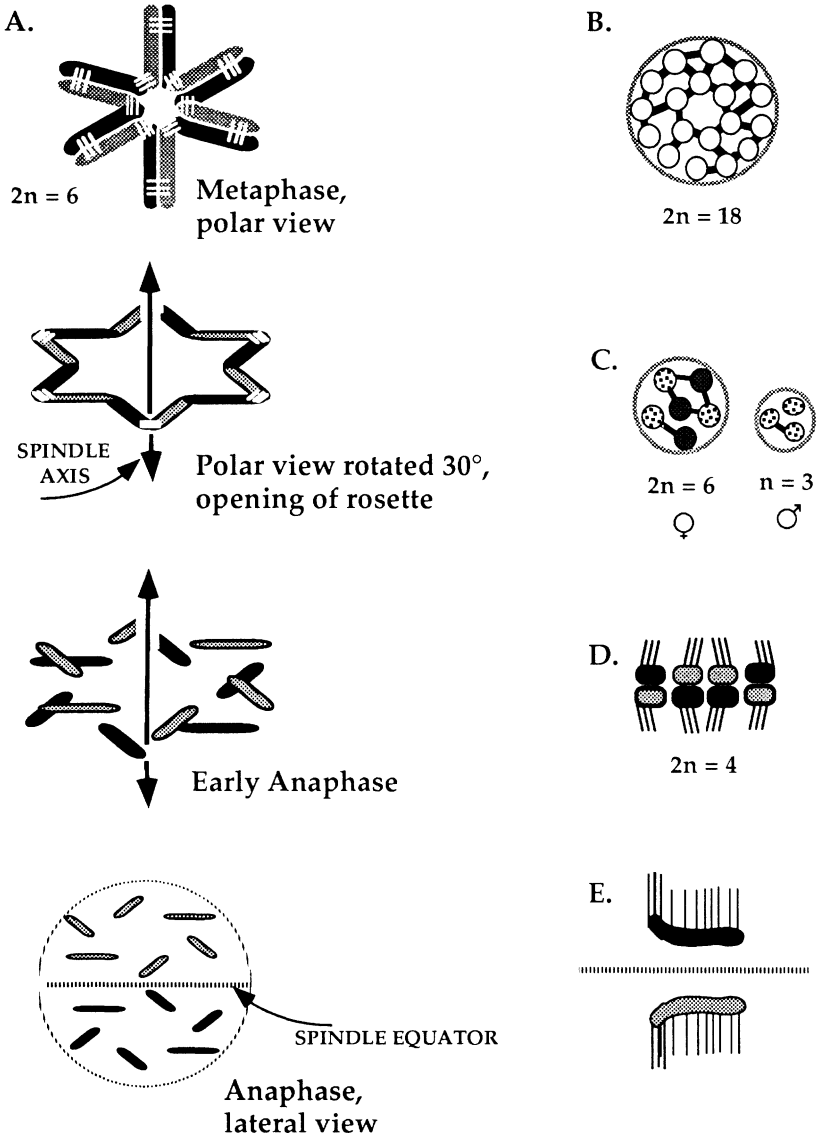


Figure 11.2. Schematic holokinetic chromosome formations during mitosis. A) A "rosette," a distinctive metaphase polar formation seen in parasitiform mites. Our interpretation is presented with white-hatched lines to represent terminal end-to-end associations between nonsister chromosomes. Internal attachments of chromosome ends are interpreted as stickiness caused by the nucleoli adhering together. This orientation is notable in metaphase karyotypes in phytoseiid mites (in Nelson-Rees et al. 1980, *vide* Figs. 8, 9, and 12 and in Wysoki and Swirski 1968, *vide* Figs. 5, 6, 9, 10), in both diploid and

lies within the spindle, whereas chromosome arms of monocentric chromosomes can lie outside in peripheral locations (White 1973, his Figs. 2.3d, c). When limited space is available within the spindle on the metaphase plate, holokinetic chromosomes often become arranged in geometric configurations that are not found in monocentric chromosomes (Fig. 11.2B, 11.C; see also Taberly 1987, Figs. 14–16; Helle et al. 1984, Figs. 1–16). During mitosis (but not necessarily meiosis), holokinetic chromosomes show a pattern of microtubule attachment along the entire poleward surface (Templaar 1985, White 1973) (Fig. 11.1, anaphase).

At anaphase, holokinetic chromosomes separate and remain more or less parallel to the equator, and perpendicular to the spindle axis, as they move *toward* the poles (Fig. 11.1, anaphase). However, relatively long holokinetic chromosomes—or even shorter ones in late anaphase—may bend the pole as they near it, resulting in distinctly bent (V-shaped) or hooked (J-shaped) chromosome figures (Fig. 11.1, telophase, see also Fig. 11.2E). According to Helle et al. (1984) this effect is due to a relaxation of chromosome condensation, i.e. they undergo despiralization.

Such shapes have been misinterpreted by some mite cytogeneticists as evidence for the presence of localized centromeres, since monocentric chromosomes commonly show inverted V-, or J-shaped forms when the arms lag, as chromosomes

---

Figure 11.2 Continued haploid somatic nuclei. Using our interpretation, it is obvious that the rosette readily enables total segregation of one chromosome set from the other. As metaphase proceeds to anaphase (second figure from the top, rotated about 30° into plane of figure), the rosette opens into a star-like chain of alternating homologous sister chromatids. In the third figure down, sister chromatids disjoin in early anaphase, and their alternating sequence in the chain creates complete segregation of the two sets of chromosomes. The bottom figure shows late anaphase with the two sets completely separated. These four sequences present a cytological mechanism through which parahaploid reproduction (paternal genome heterochromatization or elimination) in phytoseiids and other mesostigmatids can thus be understood. This mitotic phenomenon is, we believe, functionally equivalent to meiotic segregation distortion created from ring or chain formations (i.e. segmental interchange complexes, Syren and Luykx 1977; translocation heterozygotes, John 1990). B) Polar view of metaphase featuring an *Oppia* species (schematic drawing of photo in Helle et al. 1984, *vide* Fig. 1). In acariform mites, holokinetic chromosomes do not seem to align in rosette formation, but create regular geometric patterns. Linkages between the ends of uniformly rod-shaped chromosomes create threads forming chains or rings of chromosomes. C) Polar view of metaphase of diploid (left) and haploid (right) tetranychid karyotypes (redrawn from photos in Helle et al. 1981, *vide* Figs. 14 and 18 each having $2n = 6$ as a ring of $4 + 2$, and Figs. 16, 17 and 22 for $n = 3$). D) Lateral view of metaphase of *Eylais setosa* (redrawn from Keyl 1957, *vide* Fig. 4). Metaphase in holokinetic chromosomes features separate spindles for each duplicated chromosome. E) Longer holokinetic chromosomes may exhibit a concentration or restriction of kinetic behavior to one end, so that the chromosomes show telokinetic behavior (Keyl 1957, *vide* Fig. 5).

move poleward at anaphase. Clearly it is not bending alone that is diagnostic, but rather the *direction* of the bend: *away* from the poles in monocentric chromosomes, but *toward* the poles in holokinetic chromosomes. Similar misinterpretations have been associated with "end-on" or "telokinetic" movement of rod-shaped chromosomes in anaphase, as discussed below (Section 2.2.2).

2.1.3 Normal and Inverted Meiosis (Fig. 11.3): *The Importance of Bivalent Orientation at Metaphase I*

An essential difference between meiotic behaviors of holokinetic and monocentric chromosomes lies in their orientation at metaphase I. Whether they are axial or equatorial with reference to spindle coordinates has a profound effect on the sequence of the two meiotic divisions.

In monocentric systems, disjoining half-bivalents are dyads that consist of sister chromatids held together by their centromeres (Fig. 11.3, left column). Centromeres of monocentric bivalents show co-orientation, i.e. the centromeres of the two homologues are in a line parallel to the spindle axis and equidistant from the equator. Co-orientation is thus an *axial* orientation of homologous chromosomes with reference to spindle coordinates. The presence of a kinetochore constrains synaptic monocentric chromosomes to this co-orientation, forcing the duplicated maternal homologue to separate (disjoin) from the duplicated paternal homologue at anaphase I (Fig. 11.3). Thus, the first meiotic division in axially aligned bivalents is *reductional* for loci in noncrossover regions (Rhoades 1961). A schematic representation of what such a "normal" meiosis would look like in a holokinetic system is shown in the central column of Fig. 11.3, but there is little evidence that this occurs naturally (see Section 2.2.3).

Cytogeneticists have realized for some time that an inverted meiotic sequence—an equational division preceding the reductional division—is strictly possible only in organisms with holokinetic chromosomes (Battaglia and Boyes 1955, Rhoades 1961, Brown and Cleveland 1968, Jones 1978). Only holokinetic chromosomes are capable of an *equatorial* orientation of homologues at metaphase I (Fig. 11.3, right column), in which the alignment of homologous chromatids is rotated 90° relative to that of normal meiosis. This orientation causes *equational* segregation of half-bivalents at anaphase I: sister chromatids separate while maternal and paternal homologues remain paired.

As discussed later (Section 4.2) we believe inverted meiosis to be ancestral in holokinetic systems. In such systems, a "normal," reduction-first sequence is unequivocally present only during *spermatogenesis* in some heteropteran insects (but meiosis is inverted in oogenesis); it is associated with the presence of sex chromosomes (Section 2.2.2, see also 3.3.3). A reductional first division of holokinetic chromosomes in *oogenesis* has been claimed but never proven in naturally occurring populations (see Section 2.2.3, and Ueshima 1963 for discus-

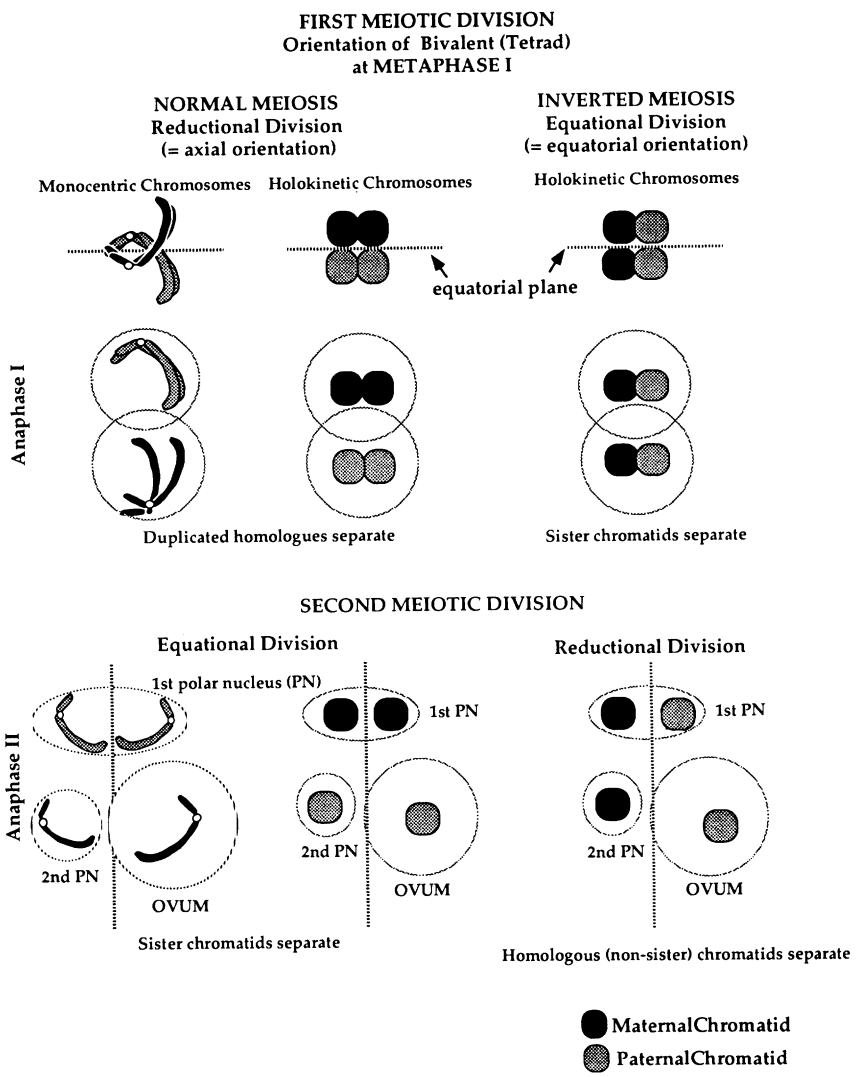


Figure 11.3. Meiosis: oogenesis with monocentric and holokinetic chromosomes.

sion). The only conclusive evidence involves experimentally created hybrids in the hemipteran genus *Cimex* (Ueshima 1963).

The unique attributes of inverted meiosis are summarized next, with comments that are relevant to any oogenesis, whether "sexual" or thelytokous; special attributes of spermatogenesis are discussed later (Sections 3.3, 3.4).

Inverted Meiosis in Holokinetic Systems—Oogenesis in organisms with holoki-

netic chromosomes is usually described cytologically as consistent with key features in monocentric species. One or more chiasmata are seen at diplotene. By prometaphase I these chiasmata are described as terminal. Meiotic distinctions between holokinetic and monocentric systems begin at metaphase I, where holokinetic bivalents are observed to orient with the long axis of the bivalent parallel to the spindle's equator. This cytological orientation reflects the end-to-end association created by telomeric pairing (Fig. 11.4B-C, Jones 1978). However, there may be a subsequent adjustment in orientation, so that the homologues lie side-by-side in a parallel position (Fig. 11.4F, also see Schrader 1940).

Unlike monocentric bivalents, there is no repulsion between holokinetic homologues (Swanson 1957, 341). At diplotene/diakinesis, bivalents with one chiasma have a cross-shape (Fig. 11.4E), while bivalents with two chiasmata form a ring (Fig. 11.5). The cross-shape resolves into the end-to-end association, termed a half-bivalent (Fig. 11.4F). A ring forms when both ends of each homologous pair are attached to the nuclear membrane and both form a telomeric heteroduplex. When the nuclear membrane disintegrates, these chromosome-membrane associations are released and as chromosome condensation intensifies in diakinesis the cytological cross, rod, or ring shapes become visible (e.g. Hughes-Schrader 1955).

Most holokinetic chromosomes show the effects of one terminal chiasma. This feature is the mechanical cause of equational division during the first meiotic division and is not known to occur in monocentric chromosomes, or it occurs only for exceptional chiasmata configurations (White 1973, John 1990). The terminal chiasma in holokinetic chromosomes does not result in the recombination of functional genes.

At anaphase I, equatorially oriented holokinetic bivalents separate as half-bivalents that consist of two nonsister chromatids. These half-bivalents move toward their respective poles with the secondary or interchromatid split (usually the long axis) of each half-bivalent parallel to the equator (Fig. 11.3). Chromatids separating during mitotic anaphase have a similar appearance. The half-bivalents may bend somewhat late in anaphase I, at one or both ends. When both ends curve, as in mitotic anaphase, the curvature is opposite that commonly seen in monocentric chromosomes (Fig. 11.1, telophase).

Restriction or concentration of microtubules at one end of the chromatid in a half-bivalent can cause "telokinetic" behavior (see Section 2.2.2) during anaphase I (Fig. 11.5), but this behavior does not negate equational segregation of the half-bivalents. When, through hybridization, bivalents form between morphologically dissimilar homologues, the end associations are weaker or fail to form at all (Fig. 11.5C). The resulting reductional segregation at anaphase I is a mechanical consequence of half-bivalent instability.

The second meiotic division in inverted meiosis is reductional, so that nonsister chromatids separate to the second polar nucleus and to the egg pronucleus.

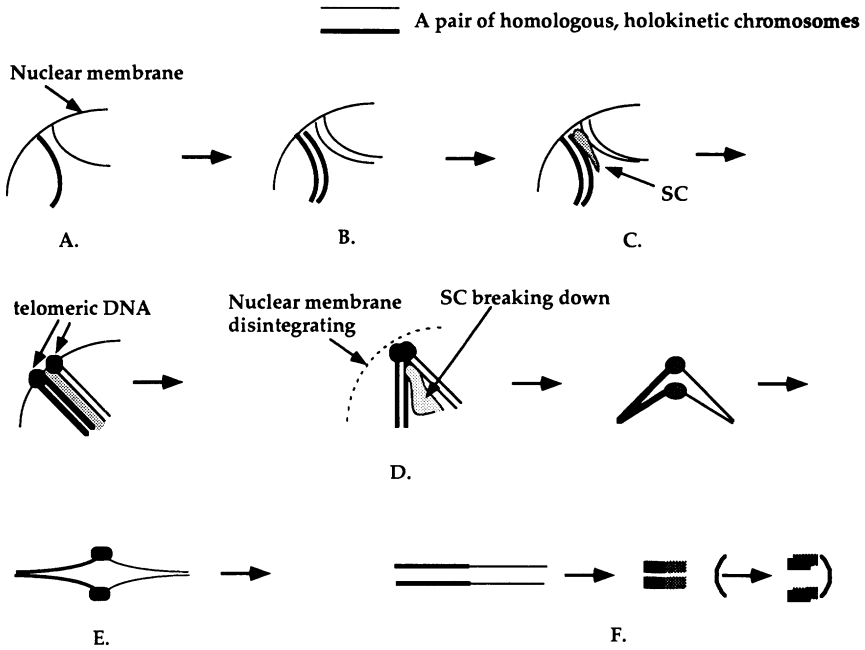


Figure 11.4. Holokinetic chromosome replication (A, B) and formation of bivalents by end-to-end pairing (C-F), the basis for inverted meiosis. A) Chromosome ends imbedded in nuclear membrane (or in karyomere membrane). B) DNA replicates, homologous telomeres adjacent. C) Synaptemal complex (SC) forms. D) Tetrad forms bivalent, telomeric DNA synthesis delayed past pachytene, telomeric DNA heteroduplex links telomeric ends of nonsister chromatids. E) At diakinesis, telomeric synthesis completed, chromatids align so that telomeric ends of paired homologous chromatids are central within each "half-bivalent". F) Chromosome condensation with the "end-to-end" associations that enable an "equitorial" orientation and equational segregation at metaphase I. Each half-bivalent consists of one copy of each of the original homologous chromosomes. Half-bivalents may fold over or shift into parallel alignment, *vide* Ris 1942, Brown 1977. Note: a monocentric chromosome cannot perform this pattern of orientation. The kinetochore is replicated in premeiotic interphase, but its centromeric DNA replication is delayed. Thus in prophase I, sister chromatids are connected at the centromeric DNA region. Their formation at premetaphase is governed then by microtubule (MT) attachments from the centrosome to each chromosome's centromere (kinetochore MTs). Therefore, orientation becomes axial and division is reductional because the forces due to telomeric kinetic activity are overwhelmed by forces of kinetochore MTs.

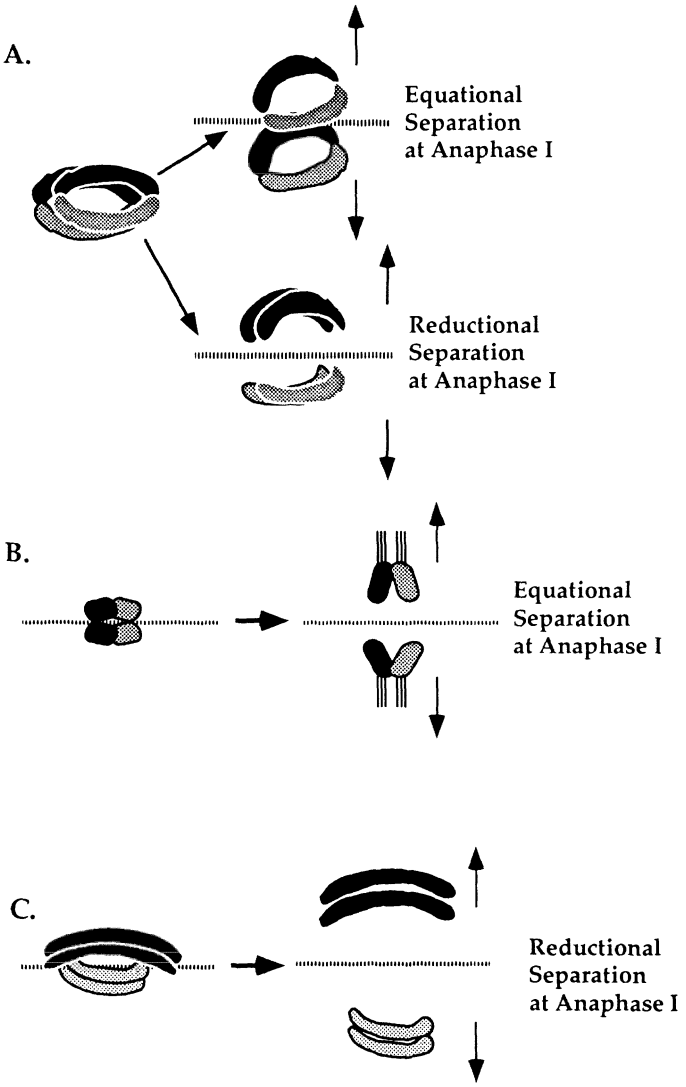


Figure 11.5. Orientation and kinetic behavior of bivalents of holokinetic chromosomes. A) Ring bivalent forms when both ends of each homologous chromatid form attachments to the nuclear membrane. Rings may orient so that segregation is either equational or reductional (*vide* Suomalainen and Halkka 1963). B) Telokinetic behavior at anaphase I of rod-like bivalent of holokinetic chromosomes, as in female spider mites (redrawn from Fig. 4, Schrader 1923). C) Schematic bivalent of heterologous chromosomes in which reductional segregation at metaphase I (*vide* Ueshima 1963) is caused by failure of end-to-end associations to form properly.

2.2 Chromosome Types in Mites: Are They All Holokinetic?

2.2.1 Evidence for Holokinetic Chromosomes in Mites

The most crucial test for a diagnosis of holokinetic chromosomes involves inducing fragmentation of chromosomes by irradiation and studying their behavior during subsequent cell divisions. The persistence of fragments in descendant cell lineages is viewed as the most direct confirmation that a localized kinetochore is not present (Cooper 1972, Hughes-Schrader and Schrader 1961). Such holokinetic behaviors have been confirmed in species of several groups of Prostigmata, including water mites (Keyl 1957), spider mites (Templaar 1979 a, b), and the Heterostigmata (Cooper 1972).

As noted above, there is a correlation between the lack of centrioles and holokinetic chromosomes. Among mites, the absence of centrioles from the spindle apparatus has been noted during cleavage (*Siteroptes* (= *Pediculopsis*) *graminum*, Cooper 1939) and during meiosis (i.e. *Caloglyphus mycophagus*, Heinemann and Hughes 1970; *Histiostoma feroniarum*, Heinemann and Hughes 1969; *Demodex* sperm, Desch 1984; and Eriophyidae sperm, Nuzzaci and Solinas 1984). Unfortunately most authors are silent as to the presence or absence of centrioles, and we have no such information for other major mite groups. Karyomeres, associated with holokinetic chromosomes, have been observed in acariform mites—such as Heterostigmata (Reuter 1909, Pätau 1936, Cooper 1939), Tetranychidae (Templaar and Drenth-Diephuis 1984, Feiertag-Koppen and Pijnacker 1985), Tenuipalpidae (Pijnacker et al. 1981)—and in ticks (i.e. *Ornithodoros papillipes*; Sokolov 1958).

We interpret all literature descriptions of chromosomes in acariform mites as clearly relating to holokinetic chromosomes (Schrader 1923, Pätau 1936, Cooper 1939, Keyl 1957, Moss et al. 1968, Cooper 1972, Helle et al. 1981, Helle et al. 1984, Taberly 1987). The papers by Schrader, Pätau, K. Cooper and Keyl are also exceptional because they assess meiosis in both females and males, and they provide spectacularly clear illustrations. The study of oogenesis is technically difficult (White 1973), and we are fortunate to have excellent papers on oogenesis in tetranychoid (Schrader 1923, Feiertag-Koppen and Pijnacker 1985), tarsonemid (Pätau 1936, Cooper 1939), astigmatid (Heinemann and Hughes 1969, 1970) and oribatid mites (Taberly 1987).

The interpretation of chromosome types in Parasitiformes is more equivocal. Among Mesostigmata, six species of Parasitidae were studied by Sokolov (1934), who concluded that chromosomes seen in spermatogenesis were holokinetic ("diffusecentric"). Oliver (1967) used the terms cephalobrachial or diffusecentric in describing the chromosomes of *Ornithonyssus*, *Ophionyssus* and *Bdellonyssus* spp., noting that no centromeres (i.e. primary constrictions) were seen. Oliver and Bremner (1968) explicitly stated that both holokinetic and monocentric chromosomes were found in *Haemaphysalis* tick species. In other reviews, Oliver

(1967, 1977) has described the autosomes of different tick species as having terminal centromeres, or as being acrocentric or cephalobrachial.

At least in part, reluctance to accept a holokinetic diagnosis for parasitiform mites stems from interpreting the "telokinetic" behavior of chromosomes during meiosis as being evidence of centromeres. As we explain next, holokinetic chromosomes can show the same behavior.

2.2.2 *"Telokinetic" Behavior Is Not Diagnostic of Centromeres*

In monocentric systems, rod-shaped half-bivalents may appear to move "end-on" toward the poles at anaphase I, i.e. to have "telokinetic" behavior (Fig. 11.5B). When the presence of a terminal centromere is assumed, the term "telocentric" is applied, but the eminent animal cytogeneticist M. J. D. White (1973) strongly rebuked the notion of naturally occurring telocentric chromosomes. He insisted that chromosomes exhibiting this behavior be described as acrocentric—having a *nearly* terminal centromere—even if lacking a primary constriction. Most cytogeneticists apparently adopted his preference, and considered any end-on or poleward orientation as *prima facie* evidence for acrocentric chromosomes, whether a subterminal primary constriction was seen or not.

Thus, autosomes are invariably described as cephalobrachial or telocentric in ticks (Oliver 1964) and acrocentric in Phytoseiidae (e.g. Wysoki and Swirski 1968, Nelson-Rees et al. 1980), even though no primary constriction has been observed. In fact most of the terms applied to parasitiform chromosomes—acrocentric, cephalobrachial, subterminal or telocentric—imply the presence of a centromere, though the preeminent student of parasitiform cytogenetics, J. Oliver, has exhibited exceptional caution in this regard. Most such diagnoses were based simply on finding rod-shaped chromosomes that show an end-on orientation.

Ambiguity arises from the fact that holokinetic chromosomes can exhibit a similar behavior during meiosis (Fig. 11.5). In mitosis, holokinetic chromosomes show relatively uniform kinetic activity along their length. However, in the highly condensed condition at meiosis, kinetic activity can be concentrated terminally and an end-on appearance is generated. The elegant work of Hughes-Schrader and Schrader (1961) on Heteroptera demonstrated this ability to have diffuse and restricted kinetic activity in mitosis and meiosis, respectively. Examples of "telokinetic" behavior in holokinetic chromosomes of mites are well known (e.g. Keyl 1957, Heinemann and Hughes 1970, Cooper 1972). Adding to the confusion, chromosomes are almost always characterized during meiotic events (i.e. spermatogenesis), when monocentric chromosomes and holokinetic chromosomes can exhibit similar "telokinetic" behavior.

The lack of a primary constriction in parasitiform mite chromosomes suggests they may be holokinetic. Their "telokinetic" behavior is consistent with such a diagnosis, but there is other evidence. For example, the metaphase arrangements

of examined parasitiform mites differ little from those seen in karyotypes that are unambiguously holokinetic. At mitotic metaphase, phytoseiid (Nelson-Rees et al. 1980) and dermanyssid (Oliver 1965) chromosomes form a rosette in polar view (Fig. 11.2A), with the rod-like chromosomes arrayed like spokes on a wheel around a clear center. This exact formation is typical of mitotic metaphase figures in spiders (Benavente and Wettstein 1980) and Ephemeroptera (Kiauta and Mol 1977) that are clearly holokinetic.

Also supportive of a holokinetic diagnosis in the parasitiform mites are certain parallels that exist with cytogenetically better known insects having holokinetic chromosomes. Males of Hemiptera (Hughes-Schrader and Schrader 1961) and males of some Homoptera (Ris 1942) have normal meiosis (a reductional first division). The end-on configuration of their large holokinetic sex chromosomes is very similar to that seen in tick spermatogenesis, for which chromosomes were diagnosed as cephalobrachial or telocentric (Oliver 1964, 1965). Even more compelling, karyotypes of Hemiptera, like those of ticks, are conspicuously heteromorphic, and have XY or XO males. The X is usually much larger than the autosomes, which show very little size difference.

Parallels also exist between parahaploid phytoseiid mites and parahaploid Homoptera that are known to have holokinetic chromosomes. The photomicrographs in Nelson-Rees et al. (1980) showing chromosome heterochromatization and elimination in a phytoseiid mite, and the detailed drawings of Warren (1940) for *Dermanyssus*, coupled with the sketches of Oliver (1965) which also show elimination, are strikingly similar to the system described for diaspidid scale insects (i.e. Brown and DeLotto 1959, Brown and Nur 1964). Even the formation of sperm—the evagination of the binucleate spermatid's membrane and slender elongation to form two functional sperm—looks amazingly similar, yet is unknown outside these two groups of organisms (compare Figs. 42–53 in Nelson-Rees et al. 1980 with figures in Brown and Nur 1964). Tantalizingly, Treat's (1965) description and photomicrographs of the "comma" in cells in the somatic and spermatogonial nuclei of the moth ear mite (Otopheidomenidae) suggest a system of parahaploidy comparable to the system of holokinetic lecanoid scales (Brown and Nelson-Rees 1961, Brown and Nur 1964).

2.2.3 Evidence of Inverted Meiosis in Mites

Over the last three decades much data has accumulated on karyotypes of mites (mostly spider mites and ticks), but little attention has been paid to meiotic mechanisms. Thus, little evidence exists for determining the order in which meiotic divisions occur in various groups. The lack of evidence for anything unusual has meant that cytogenetic dogma generally has gone unchallenged (Helle et al. 1984).

The order of division in a holokinetic system is often difficult to diagnose from meiotic figures. A cytological diagnosis of normal or inverted meiosis is based

on the orientation of bivalents relative to the spindle at metaphase I, axial or equatorial, respectively (Section 2.1.3, Fig. 11.3). This can be directly observed when chromosomes are rod-shaped, but becomes equivocal as they approach a highly condensed isodiametric form, and as individual chromatids lose their distinctiveness (Ueshima 1963).

With no heteromorphic bivalents, or with all the autosomes appearing similarly small and spherical to rod-shaped, a reductional first division may be mistakenly inferred from the telokinetic behavior. Above, we noted that end-on telokinetic behavior of chromosomes is not diagnostic of the presence of a centromere. As an extension, it is not diagnostic of a reductional first division. In inverted meiosis, holokinetic chromosomes form half-bivalents that are comprised of end-to-end associations of nonsister chromatids. Their contact region can be differentially constricted, and their telokinetic behavior mimics classic reductional division of telocentric chromosomes. Since the genetic consequences of these convergent behaviors are so different, we must be careful in our interpretations of such meiotic figures (e.g. see our discussion of Taberly's work with thelytokous oribatid mites, Section 3.2.2).

When chromosomes are small and spherical, elongated ones may be artificially created during the irradiation procedures used to diagnose holokinetic chromosomes. The chromosomes and fragments produced may fuse, resulting in an artificially elongated morphology that can provide evidence of orientation. In mites, the only such unequivocal evidence of inverted meiosis is from the Tetranychidae (Templaar 1979a, 1979b, 1980, 1985; Templaar and Drenth-Diephuis 1984).

Indirect evidence of inverted meiosis has been observed in another arrhenotoke, the heterostigmatic mite *Siteroptes* (= *Pediculopsis*) *graminum*. In the tetranychids, the tandem arrangement of homologous chromatids undergoes a further modification resulting in their parallel alignment (Fig. 11.4F). Based on Cooper's (1939) original observations, Schrader (1940) noted the same configuration in *S. graminum*.

In the unusual thelytokous tenuipalpid *Brevipalpus obovatus*, inverted meiosis is the only conclusion consistent with four observations of Pijnacker et al. (1981): (1) the karyotype consists of two heterologous chromosomes; (2) the automictic mechanism is by premeiotic doubling; (3) the latter allows the formation of two autobivalents; and 4) after meiosis the heterologous somatic number is restored (Fig. 11.6). The latter configuration could only be achieved by segregation of the homologous chromatids of each member of the heterologous chromosome pair, which in turn could only result from equatorial orientation and equational segregation, the essential features of inverted meiosis (Fig. 11.3). Any other orientation would cause sister chromatids to segregate at anaphase I. The restored karyotype would then consist of two homeomorphic rather than heteromorphic chromosomes, and a dysfunctional aneuploid egg would result.

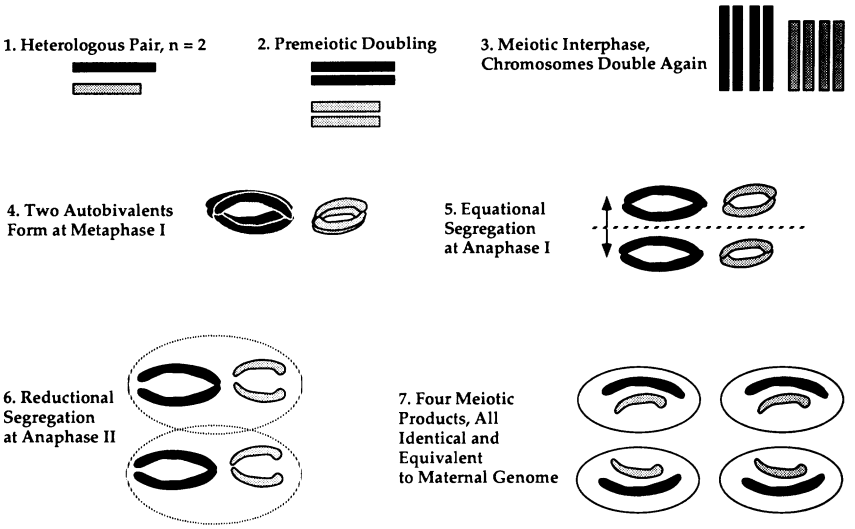


Figure 11.6. Mechanism for genetically faithful thelytokous production of *Brevipalpus* females with n = 2, a heterologous pair of holokinetic chromosomes.

All the above-mentioned taxa are acariform mites; the only claim of inverted meiosis in parasitiform mites was by Oppermann (1935), who suggested an inverted sequence during spermatogenesis in the tick *Argas reflexus*. Oppermann's conclusions were questioned by Goroshchenko (1962), but since we now believe tick chromosomes to be holokinetic the process needs to be reexamined; it appears to us that Oppermann was correct.

3. Genetic Recombination and the Significance of Inverted Meiosis

3.1 Recombination, DNA Repair and Evolutionary Success

The cytology of inverted meiosis has been explored in both plants and animals (Hughes-Schrader 1948, Resende 1953, Chandra 1962, White 1973, John 1990) but the cytogenetic consequences—for thelytokous organisms and haplodiploid organisms in particular—have been completely overlooked.

Any organism's genetic system has itself evolved, and reflects selection for properties that provide it with a balance between: (1) genetic stability that maintains high fitness; and (2) genetic flexibility that provides the variation associated with adaptation. Whether flexibility is "purposeful" or not is contentious. Balance is achieved through a series of trade-offs among the various elements comprising the genetic system (Darlington 1939, Lewis and John 1972). Thoday (1953) understood natural selection to be acting on "units of evolution" where fitness is

"compounded by stability and variability, and increase in fitness becomes a resolution of the antagonism between stability and variability." He further viewed the resolution of this classic conflict as "brought about either by changes of the genetic system that increase the amount of cryptic genetic variation, or by increase of the range of environmental conditions to which the individual is adaptable or adapted, or by adaptation to a stable environment."

Genetic stability is obtained through mechanisms in the genetic system that reduce or eliminate recombination of parental genotypes. As Darlington (1939) stated "Indeed, the history of the evolution of genetic systems may be regarded as the history of the control of recombination."

Components of the genetic system involved in recombination control include chromosome number, mode of reproduction, and breeding system. Mites are conspicuous among all animals for their generally low chromosome numbers (Oliver and Nelson 1967) and they show a diversity of the latter two components. The relationship of mode of reproduction and cytology (chromosome systems, modifications of meiosis) to the control of genetic recombination has not been explored in mites, but in general it is under genetic control (White 1973, Bell 1982, John 1990). The modes of reproduction known in mites span the ends of a continuum from obligate thelytoky to haplodiploidy with obligate sib-mating, the extreme HIA system. But from the perspective of recombination control, obligate thelytoky and HIA are functionally equivalent. The success of HIA systems, and the adoption of thelytokous parthenogenesis by mite lineages that are both ancient and widely distributed (Section 3.2) appears to contradict the traditional notions of which genetic systems permit adaptive stability and phylogenetic divergence.

In the remainder of this section, we summarize types of genetic recombination and then turn to questions of how inverted meiosis affects recombination potential in thelytokous and haplodiploid mites. Note that certain concepts associated with recombination that were formulated in connection with monocentric systems (i.e. prereduction, postreduction), are not strictly applicable to holokinetic ones, or they have a modified meaning (Battaglia and Boyes 1955, John and Lewis 1965). The distinction between crossover and noncrossover segments is ordinarily made relative to a localized centromere. Without a centromere, the idea of crossover segments is meaningful, but that of chromosome arms is not.

Three levels of genetic recombination (GR) within the chromosome-meiotic systems are useful in evaluating cytological and evolutionary consequences.

(1) Intra-chromosomal GR: genetic recombination during pachytene in meiotic prophase. It is observed cytologically as chiasmata at diplotene/diakinesis, and biochemically as a spike of pachyDNA (Stern and Hotta 1987). This is the classic form of GR and arises from crossingover and reciprocal exchange between nonsister chromatids synapsed in bivalents.

Chiasmata are cytological observations of connections between nonsister chromatids. When they occur in the highly repetitive, nontranscribing, telomeric

DNA regions, they are genetically meaningless (John 1990). Thus, these terminal chiasmata that form half-bivalents are not sources of genetic recombination *sensu* generating genetic variation. Observations of one terminal chiasma in bivalents in most holokinetic species cannot be interpreted as evidence for genetic recombination. These so-called terminal chiasmata are therefore mechanical features enabling chromosome segregation (see Section 2.1.3). Older literature refers to "terminalization" of chiasmata implying that real genetic recombination has occurred, and this has been shown to be incorrect (Jones 1978, John 1990).

Recent studies merging cytology and genetics have shown that intrachromosomal GR requires prior chromosome pairing during zygotene, the phase during which the synaptonemal complex (SC) forms between the duplicated homologous chromosomes (Fig. 11.4D). A series of attachment sites have been identified and they are associated with recombination nodules of at least two sorts (Jones 1987).

The earliest event preceding pairing competence is seen in leptotene, where each pair of sister chromatids is joined by the lateral portion of the SC, and one or both ends of each duplicated homologous chromosome are imbedded in the nuclear envelope. A telomeric plate forms in the nuclear membrane at this attachment and pairing site. Such telomeric pairing is sufficient to establish the end-to-end linkages noted earlier (Fig. 11.4) for the formation of half-bivalents, and is required for inverted meiosis as discussed. Telomeric pairing is between nonsister chromatids, but is not the source of genetic recombination.

Synapsis (formation of bivalents) begins in zygotene with recognition between the telomeric regions of homologues, and is associated with a specific form of DNA synthesis (zygDNA, Stern and Hotta 1987). Pairing competence between homologous sister chromatids is then established by the initiation of the central SC at telomere attachment sites. Central SC synthesis is the prerequisite for classic GR when gene conversion occurs.

There is little information about rates of classic GR in holokinetic species. In spider mites, recombination rates have been calculated from crosses using pigment mutants (Helle 1985). Cytologically, Feiertag-Koppen and Pijnacker (1985) reported two to three chiasmata per bivalent, but they make no issue of the genetic consequences stemming from chiasmata location. The terminal associations are the only ones visible at, and after diakinesis.

The failure of the central SC to form causes desynapsis and achiasmate meiosis, even though homologues may remain paired at their ends. Thus achiasmate bivalents, common in spermatogenesis in a variety of taxa, allow normal segregation of equal numbers of chromosome dyads at anaphase I.

The complete failure of synapsis, termed asynaptic meiosis, is relatively rare. Univalents are seen aligning at metaphase I. With asynapsis, either synapsis fails due to the absence of the central SC, or the central SC is not maintained, and bivalents desynapse before diakinesis. These variations in prophase I contribute to chromosome alignment and distribution in subsequent phases of meiosis. They profoundly affect the second level of GR, chromosomal segregation.

(2) Inter-chromosomal GR: recombination due to segregation of homologues in the reductional division, or of crossover regions in the equational division. The recombination of entire chromosome sets is predicted from the expectation of random orientation of bivalents. With haploid numbers of n = 2, 3 or 4, so common in Mesostigmata and Prostigmata, the number of linkage groups capable of segregation is impressively limited. Oliver (1965, 571) interpreted karyotypes of parasitic mites as showing an evolutionary trend toward a reduction in chromosome number. This trend reduces the number of linkage groups, and he speculated that enhanced linkage would lessen genetic flexibility and result in a greater degree of adaptive specialization.

Nonrandom arrangements of bivalents, or bivalents consisting of members that segregate equationally rather than reductionally (in the cytological sense), all further reduce the amount of GR produced during meiosis. Parahaploidy is an extreme example of mitotic segregation distortion, where the entire haploid paternal set is preferentially excluded.

(3) Gametic GR: random inclusion in functional gametes of any meiotic product. Any distortion of gametic equivalence, or of equal probability of meiotic inclusion, will reduce genetic recombination. Gametic selection will result from any modification that produces one, or only a small sample, of the possible array of haploid recombinants. Such an effect is a form of meiotic drive that suppresses the potential overall amount of genetic recombination.

3.2 Inverted Meiosis as an Explanation for Thelytokous Higher Taxa

3.2.1 Types of Thelytoky

As discussed in the Introduction, the persistence and genetic flexibility of thelytokous organisms depends on whether or not oogenesis includes meiosis, and which particular meiotic mechanism is involved. Comprehensive reviews and synopses of this topic are numerous (e.g. White 1973, Bell 1982, Templeton 1982, Cuellar 1987, Lamb and Willey 1987, Suomalainen et al. 1987), but none considers the potential significance of inverted meiosis, and we feel apomixis has been overemphasized, at least among animals.

Apomixis—Apomixis ("ameiotic" thelytoky) is believed to reproduce the mother's genome via an essentially mitotic oogenesis, and eggs produced in this way are considered to be faithful keepers of the clone's genetic bauplan. Such lineages are thought to be prone to a Muller's Ratchet accumulation of mutations, though the central hardship attending apomixis may be the loss of DNA repair at prophase I (Bernstein and Bernstein 1991).

Although apomixis has been proclaimed the predominant thelytokous mechanism in insects (Suomalainen 1950, White 1973, see also Lamb and Willey 1987), many researchers are careful to diagnose it only provisionally, and in such cases reinvestigation is warranted. A truly meiotic division may be mistakenly

considered apomictic if bivalents fall apart before diakinesis, such that the diagnostic zygotene-pachytene stages could not be seen. Even the general absence of genetic segregation is not conclusive evidence of apomixis, since holokinetic systems with inverted meiosis may faithfully conserve the maternal genome (see Section 3.2.2).

Further confusion arises when authors conclude that premeiotic doubling (see below) is a form of apomixis, even though it allows autobivalents to form during prophase I. Such a conclusion (e.g. White 1973) stems from viewing the importance of bivalent formation in a restricted sense: crossing over between genetically identical chromosomes does not provide new genetic variants upon which natural selection could act. But when conservation of genome is considered a benefit, apomixis and premeiotic doubling are not equivalent. The formation of autobivalents in premeiotic doubling affords homologous chromosomes the same opportunity for double-strand DNA repair that is provided by normal bivalents.

Chapman's (1969, 442–3) assignment of apomixis to blattid, aphid, tenthredinid, and curculionid insects followed the tradition of assuming that a single maturation division is equivalent to ameiosis. White (1973) pointed out that apomixis is more common in plants than in animals, but we note that the great majority of animal mechanisms in his survey are automictic, with terminal fusion.

Records of apomixis in mites are rare. Heinemann and Hughes (1969) observed it in a strain of *Histiostoma feroniarum* that was associated with a morphologically indistinguishable arrhenotokous strain. The apomictic strain had only one pseudomaturation division and formed no bivalents (or at least none was found at diplotene, and no cross- or ring-like configurations were observed). This single division produced a single polar body and a functional egg. The egg contained the diploid number of chromosomes and underwent a mitotic division during cleavage; the polar body did not undergo a second division. Apomixis was suggested for the ixodid *Haemaphysalis longicornis* by Takenouchi et al. (1970), a triploid (3n = 33) obligate thelytoke. The closely related bisexual strain has 2n = 22, XX females and 2n = 21, XO males. The case for apomixis is inferential, however, and Oliver et al. (1973) were not persuaded. They noted that an aneuploid parthenogenetic race (2n = 23, 24, 25, 27, 28) was automictic.

Automixis. Automictic (= meiotic) thelytoky enables the advantages and disadvantages arising from crossing over, by permitting the formation of bivalents at prophase I. The difficulties attending automixis stem from the mechanism for the restitution of somatic ploidy. There are at least four major forms of restitution observed in the animal kingdom (Templeton 1982, Lamb and Willey 1987), but only two have been reported in mites.

One involves premeiotic chromosome doubling, and was described for *Brevipalpus obovatus*, in which two bivalents are seen at diplotene (Pijnacker et al. 1981). Females of this obligate thelytoke occasionally produce spanandric males, and males can be induced by irradiation. Both sexes have the same karyotype,

and their 2n = 2 ploidy is exceptional, the lowest known in animals. No cells contain just one chromosome, and the two chromosomes are heterologous. Earlier, we described indirect evidence that the meiotic sequence in this species is inverted. An equational first division permits all four meiotic nuclei to contain both chromosomes, so no restitution of nuclei is required (Fig. 11.6). Thus, premeiotic doubling of the heterologous chromosome pair, which would otherwise have difficulty forming a singleton bivalent (Fig. 11.5C), is accommodated. All Tenuipalpidae have low numbers of chromosomes, and many are thelytokous (Helle et al. 1980), though we do not claim that they constitute a phylogenetic clade within the family. However, the widespread habit of polyphagy and economic importance of these mites attests to the evolutionary vagility of such a superficially "dead end" genetic system, one that works because of inverted meiosis.

The second meiotic mechanism known from mites is *terminal fusion*, the fusion of the egg pronucleus with the second polar nucleus (equivalent to the failure of anaphase II segregation of the secondary oocyte). Terminal fusion has been reported from two species of oribatid mites, *Platynothrus peltifer* and *Trhypochthonius tectorum*, and was suspected in a third, *Nothrus palustris* (Taberly 1958, 1987). The former two species are members of large, totally thelytokous families (Camisiidae and Trhypochthoniidae, respectively), and all known *Nothrus* species are thelytokous (Palmer and Norton 1991).

A third mechanism of restitution is by the fusion of cleavage nuclei (equivalent to endomitosis). This seems to be quite rare, (White 1973), but Regev (1974) thought the prostigmatid mite *Cheyletus malaccensis* restores ploidy in this manner. This conclusion has been reiterated in a number of reviews, but Helle et al. (1984) have doubted a number of Regev's cytological statements, and a reinvestigation is needed.

A fourth mechanism of restitution is *central fusion*, in which the egg pronucleus fuses with a second division product of the first polar nucleus. It is not known in mites, but has some theoretical relevance (see Section 3.3.3).

Related Reproductive Modes. Other modes involving thelytoky, such as pseudogamy or heterogony, can be ameiotic or meiotic. In pseudogamy (= gynogenetic thelytoky), the parthenogenetic development of eggs ensues after penetration by sperm from a closely related species, without inclusion of the sperm's DNA. Heterogony includes a variety of cyclic alterations between thelytokous and bisexual forms. These modes are not known in mites (see discussion in Norton et al. 1993).

3.2.2 Inverted Meiosis and Terminal Fusion Conserve Maternal Genome

According to standard interpretation (White 1973), terminal fusion would occur between sister chromatids, resulting in a zygote homozygous at all loci except those in regions undergoing crossingover at prophase I. Even with some cross-

ingover, homozygotes would rapidly accumulate in the absence of very strong selection for heterozygotes (Asher 1970, Templeton 1982). Central fusion would seem to be much more advantageous, since in this mechanism the maternal genome is conserved *except* in crossover regions, and the degree of crossingover would presumably be under genetic control. If thelytoky serves to conserve and propagate essentially clonal genotypes, terminal fusion should be rare and central fusion should characterize successful automictic thelytokes.

In fact, the opposite is true. Central fusion is quite rare, and seems restricted to insects. Only one naturally occurring species is known to use central fusion in an obligate manner: the fly *Drosophila mangabeirai* (Murdy and Carson 1959). In other insects using this mechanism—the flies *Drosophila parthenogenetica* and *Lonchoptera dubia*, the psychid moth *Solenobia triquetrella*, and the honeybee *Apis mellifera*—thelytoky is sporadic or characterizes races (White 1973, Suomalainen et al. 1987).

In contrast, terminal fusion is quite widespread. Groups in which cytological observations have confirmed terminal fusion in thelytokes include: nematodes (summary in Suomalainen et al. 1987); rotifers[1] (Birky & Gilbert 1971); tardigrades (Suomalainen et al. 1987, *contra* Ammermann 1967 and John 1990); annelids (summary in Suomalainen et al. 1987); crustaceans, such as cladocerans (Bacci et al. 1961, *contra* White 1973, who considered them apomictic), *Artemia* (Wilson 1928), and isopods (Hill 1948); arachnids such as harvestmen (Tsurusaki 1986) and oribatid mites (Taberly 1958, 1987); and insects such as mantids, aphids, thrips, and wasps, as well as occurring racially or sporadically in coccids,[2] flies and acridid orthopterans (White 1973, Suomalainen et al. 1987, John 1990).

Furthermore, another restoration mechanism, the absence of a second division of the secondary oocyte after an equational first division, is equivalent to terminal fusion; it is found in many planarians, grasshoppers and beetles (White 1973).

Classical cytogenetic models predict inevitable complete homozygosity and genetic inflexibility for such systems, so the emphasis on terminal fusion for ploidy restoration in successful groups appears problematic. Palmer and Norton's (1992) recent discovery of a general lack of segregation in populations—and in mother-daughter lineages—of species in the oribatid mite group studied by Taberly (1958, 1987) was similarly incongruous. Apomixis or some central fusion mechanism was hypothetically invoked to explain away the observed conservation of heterozygosity.

---

[1]Bdelloid rotifers, which are exclusively thelytokous, have been described as having two equational divisions: this suggests premeiotic doubling of the 2n = 13 karyotype (Birky and Gilbert 1971). Further observations are necessary, but the presence of an odd-numbered karyotype does suggest why males are hard to produce. Phasmid insects present another case in which both meiotic divisions were described as equational (Hughes-Schrader 1947).

[2]John (1990) notes that the desynapse of bivalents into univalents has been misinterpreted as apomixis.

Such "problems" seem now to be artificial constructs. Models of thelytoky have always assumed a normal, reduction-first meiosis, i.e. they were based on a cytogenetic paradigm developed for organisms with monocentric chromosomes (Fig. 11.3, left). But there can be a very different outcome in groups having holokinetic chromosomes and inverted meiosis. Such a system has an equational first division, so the secondary oocyte segregates two sets of chromatids that are homologues (Fig. 11.3, right). Fusion of these segregants restores the maternal genotype insofar as there is no crossingover. By minimizing chiasmata, such a system would maximize conservation of the maternal genotype while providing the benefits of DNA repair, and seems to represent what from a cytogenetic viewpoint might be considered "ideal thelytoky."

From an ecological viewpoint, the widespread distribution of such a conservative system seems consistent with Lynch's (1984) "general-purpose genotype" theory. He suggested that thelytokes are successful in frequently disturbed environments because they avoid specialized adaptation to local conditions. This is accomplished by producing offspring that are virtual clones; i.e. such organisms have a unit of selection that, in effect, consists of the whole genome. By minimizing crossovers and restoring ploidy by terminal fusion, holokinetic thelytokes having inverted meiosis could possess such large units of selection.

At present, the only unequivocal evidence that meiosis is inverted in holokinetic thelytokes with terminal fusion is that of Hill (1948), who studied the isopod *Nagara modesta*. Taberly (1987) assumed a monocentric system and normal meiosis in his oribatid mites, as we deduce from his discussion of Hill's observations, and from the genetic implications of terminal fusion that Taberly envisioned (his Fig. 17). For example, he referred to prereduction and postreduction segregation, terminology developed for monocentric systems (White 1973) and without meaning in holokinetic systems (Section 2.1.3). Also, Taberly seems to have suggested (399) that the absence of synaptic phenomena prior to the second division in the isopod (the reductional division) is a source of difference between the systems. But such phenomena are not relevant to second divisions in holokinetic systems.

Taberly's cytological observations are in fact quite consistent with the presence of inverted meiosis in these mites. In our interpretation, his Fig. 10 (metaphase I) represents nine bivalents (i.e. nine tetrads, or 36 chromatids) in profile view. This is consistent with an equational separation of homologous chromatids. His Figs. 11 and 12 show metaphase II in polar view; we interpret the symmetrical, coronal distribution of nine dyads ("diplocoque") to reflect holokinetic chromosomes bound to an unstained karyomere membrane, as in other acariform mites (e.g. Cooper 1939). Inverted meiosis is the only interpretation that is congruent with both Taberly's observations and the conservation of maternal genome in this group of mites, as reported by Palmer and Norton (1992).

Superficially, a central fusion restoration with normal meiosis seems equally "ideal" and able to conserve one member of each homologous chromosome pair.

However, the first polar nucleus in anisogametic organisms rarely divides during oogenesis and is unsuitably located in the peripheral cytoplasm of the egg. In *Drosophila,* central fusion is enabled by an unusual 90° rotation of the first division spindle from its normal position perpendicular to the chorion. But this rotation is achieved at a cost, since approximately 40% of eggs are inviable (Templeton 1982).

In summary, the genetic consequences of inverted meiosis with holokinetic chromosomes are profoundly different—completely opposite, in fact—from those predicted by the monocentric model of cytogenetic dogma (Fig. 11.7). Combined with the simple restoration mechanism of terminal fusion, inverted meiosis results in the retention of both original homologous chromosomes. We predict that most successful thelytokes, especially those that have demonstrated some degree of evolutionary success, will prove to have holokinetic chromosomes

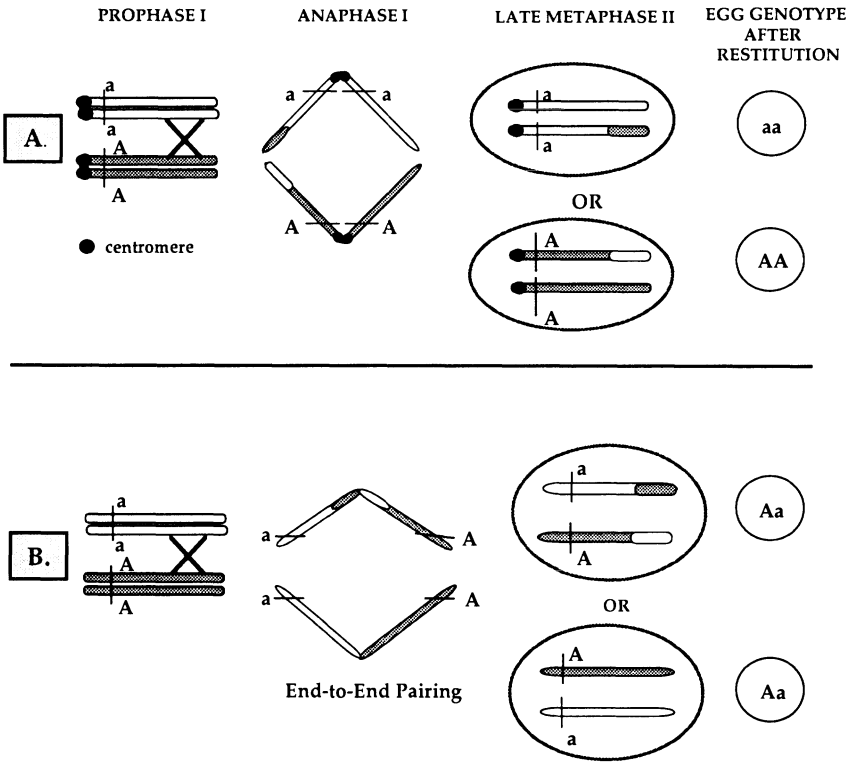


Figure 11.7. Genetic consequences of intrachromosomal genetic recombination assuming terminal chiasmata and one heterozygous locus. Automixis by terminal fusion: egg pronucleus fuses with, or fails to separate from, the second polar nucleus. A) Monocentric chromosomes, normal meiosis. B) Holokinetic chromosomes, inverted meiosis.

and inverted meiosis, and will restore ploidy by terminal fusion or an equivalent process.

3.2.3 Sexuality from Thelytokous Ancestors: the Case of the Astigmata

Recently, Norton et al. (1993) suggested that evolutionary biologists would be challenged to explain the reversal to sexuality that is inferred by a derivation of Astigmata from thelytokous ancestors in the Trhypochthonioidea. When first proposed (Norton and Palmer 1991), this reversal was viewed as a release from the constraints of thelytoky, particularly those previously associated with terminal fusion automixis (i.e. lack of genetic flexibility). But terminal fusion is not necessarily an evolutionary "burden" in groups with holokinetic chromosomes and inverted meiosis.

If we view diversification as an undesirable consequence of less rigid recombination control, then the thelytokous trhypochthonioids were not really "constrained" at all. In fact, they seem to have done very well. The thelytokous family Trhypochthoniidae has existed since the Jurassic period (Krivolutsky and Druk 1986), and one extant species, *Mucronothrus nasalis*, probably predates the breakup of Pangaea (Hammer 1965). But if we view diversification leading to adaptive radiation as evolutionary success, thelytokes are still mightily constrained by the absence of a large gene pool. When sexual reproduction was reestablished in the ancestors of the Astigmata, it resulted in a group of 5000 known (and many more unknown) species with amazing biological diversity. Life-history aspects of this transition are discussed elsewhere in this book (Chapter 5).

The reversal probably represented a reactivation of an ancestral sex determining mechanism, but sex determination in oribatid mites is not yet understood, nor do we have strong hypotheses about the ancestral mechanism in Astigmata. The earliest derivative astigmatid family for which information is available is the Histiostomatidae, an arrhenotokous family. But sex determination seems to be homoplasous in Astigmata, and our current view is that the ancestral Astigmata were diplodiploid (Norton et al. 1993).

It is likely that the common ancestor of Astigmata had one of two karyotypes: (1) similar karyotypes in both sexes (as in oribatid mites, where the sex determination mechanism is unknown)—this currently is known for only one astigmatid mite, the acarid *Rhizoglyphus echinopus* (Sokolov 1945); or (2) an XO/XX system, such as is currently known in Glycyphagidae and some other Acaridae. Within Astigmata, an XY/XX system is known only in the acarid genus *Tyrophagus* (Norton et al. 1993).

Sexuality is regularly restored from thelytokous generations within annual cycles of those (nonmite) taxa exhibiting cyclical parthenogenesis, and we can look to such extant groups for potential mechanisms. Some examples follow, to illustrate that such a switch is not cytogenetically difficult.

As one example, a generational switch from arrhenotoky to thelytoky exists in amphigonic rotifers (Birky and Gilbert 1971) and cynipid gall wasps (Chapman 1969). In these organisms, the sexual generation females produce diploid daughters and haploid sons, by either restitution or nonrestitution (respectively) of meiotically produced haploid eggs. The restitution of diploidy in Cynipidae and other thelytokous Hymenoptera is by terminal fusion (John 1990, 284). Restitution in heterogonic rotifers is similar (Birky and Gilbert 1971, and pers. comm., 1992). A third haplodiploid example is found in a species of the hermaphroditic coccid *Icerya* sp., in which true females arise through suppression of haplodiploidization in gonadal tissue (Hughes-Schrader 1963, John 1990).

Reversions to sexuality in amphigonic thelytokous aphids and hermaphroditic nematodes follow the same mechanisms of nondisjunction of the X chromosome (White 1973, Triantaphyllou 1984, John 1990). These aphids and nematodes—groups with holokinetic chromosomes (see Table 11.1)—are XX, their sexual daughters are XX from one equational meiotic division, and sons are XO. Spermatogenesis in these XO males involves two meiotic divisions, but in both taxa only the X-bearing sperm are viable and thus males are homogametic.

Reversion to sexuality in crustaceans such as *Daphnia* may provide a model for taxa lacking any obvious sex-determining mechanism, e.g. trhypochthonioid mites. *Daphnia* males and both sexual and thelytokous females all share an identical karyotype. Thelytoky is maintained with one equational division, but the sex-determining mechanism is unknown.

The thelytoky option becomes curtailed in the presence of sex chromosomes, in particular when a Y pairs with an X. The XY system in coccids still permits equational first division meiosis because the two heterologues are achiasmate, and orient as univalents. In the Hemiptera, the nearly universal presence of an XY system, with normal spermatogenesis, appears to preclude thelytoky—it is not found in the group (Ueshima 1979).

We have noted the absence of typical cyclical parthenogenesis in mites, but there is one possible example of a reversal to sexuality from a thelytokous population of an extant oribatid mite. During a long-term study of the Japanese soil mite *Oribatula sakamorii*, Fujikawa (1987) found that males were exceedingly rare (suggestive of thelytoky, with spanandric males) in a disturbed cultivated field, but became numerous (suggestive of bisexuality) when land use became less intensive.

3.3 Diplodiploidy and Inverted Meiosis

3.3.1 What is the Role of Sperm in Life Cycles?

Sperm are usually believed to be essential in some way to egg viability and development. White (1973) thought all sperm donated their centrioles, but this cannot by true for either insects (Phillips 1970) or mites (Alberti 1991), groups

in which mature sperm lack centrioles. Many think sperm are necessary for egg activation in bisexual species, but this is obviously not the case for arrhenotokous species, in which virgin females lay eggs that develop into males. In cases of pseudogamous parthenogenesis, sperm serve to activate egg development, but are then expelled. Obviously, sperm play no role at all in the many thelytokous taxa. Sperm, then, do not have a universal role in sexual systems, and their participation in sexual reproduction comes with a cost to females: the loss of control of progeny sex ratio. Females cannot control sex through cytoplasmic or chromosomal sex determination if sperm carry with them some trait essential for offspring viability (Bacci 1965, Brown and DeLotto 1959). This dependence on sperm arises with the evolution of sex chromosomes, as discussed below.

3.3.2 Spermatogenesis and Sex Determination in Diplodiploid Mites (Fig. 11.8)

In diplodiploids, meiosis produces four functional products from one spermatogonium, and we know of no exception in mites. In this case, the orientation

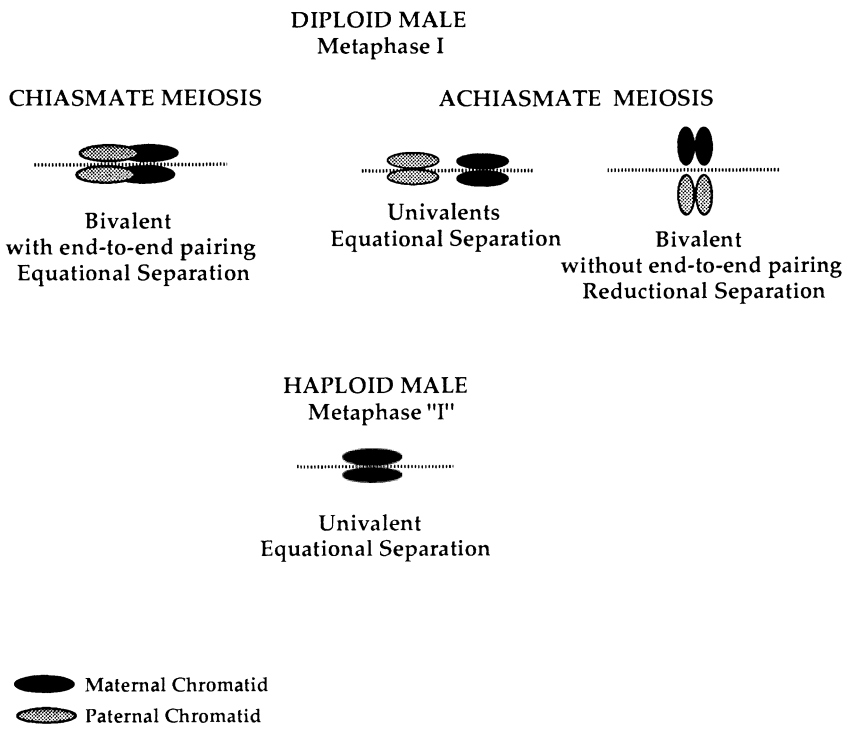


Figure 11.8. Meiosis: spermatogenesis in diploid and haploid males with holokinetic chromosomes. Metaphase I orientations for bivalents and univalents are shown.

of chromosomes at first or second division is of no importance genetically. Recombination can be affected in other ways, such as by mechanisms that reduce crossingover or interfere with random segregation. As noted by Hughes-Schrader (1948), holokinetic chromosomes may predispose diploid males to achiasmate meiosis, a process associated with a reduction in genetic recombination and preservation of linkage groups (White 1973). Achiasmate spermatogenesis is known for two species of water mites (Keyl 1957) and four species of Astigmata (Sokolov 1945). In the water mite *Hydrodroma despiciens* one pair of chromosomes segregates precociously (precluding recombination) at anaphase I (Keyl 1957).

Sex chromosomes usually have aberrant behavior, such that they may lag during congression to the equator at metaphase I, or they may lead precociously or lag at anaphase I, all of which affect recombination. Also, sex chromosomes are often heteropycnotic in males, and thus often lack synapsis and formation of chiasmata.

Males of diplodiploid species exhibit a range of karyotypes and sex determination mechanisms. Sex determination is still a mystery for mite species in which male and female karyotypes contain the same number and kind of chromosomes, such as water mites (Hydrachnellae) and oribatid mites (Sokolov 1954, Taberly 1958). Most acarid mites with diploid males have an XO karyotype, where the X chromosome is smaller than the autosomes. The sex chromosome of ixodid ticks, which have predominantly XO males, can be larger than the autosomes or the same size (Oliver 1977). All known argasid ticks have XY males, with the X being much larger than other chromosomes. Tick spermatogenesis is described as chiasmate, including one terminal association among the XY pair (Oliver 1977). In species with either XO or XY males, sex determination is assumed to be by male digamety and sex ratios are about equal, following Mendelian principles for sex chromosome segregation.

3.3.3 Holokinetic Chromosomes Allow Kinetic Flexibility in Diplodiploids, Necessary for the Evolution of Sex Chromosomes

Previous authors have described a normal order to meiotic divisions in diploid spermatogenesis. Diploid male mites with no morphologically distinct sex chromosomes, such as the water mite *Eylais setosa* (Keyl 1957), and species with XO males, such as the acarid *Caloglyphus mycophagus* (Heinemann and Hughes 1970), have been interpreted as having a reductional first division. Spermatogenesis has also been described as achiasmate in these species. The sex chromosomes of ticks separate reductionally at anaphase I (Oliver 1967), but the behavior of autosomes has not been established.

An unappreciated feature of the holokinetic system is the potential for different meiotic pathways within a species (Fig. 11.3). Inverted meiosis in oogenesis may coexist with normal meiosis in spermatogenesis (White 1973, 492). Such a

mixed system—an equational first division in oogenesis but a reductional one in spermatogenesis—is found in Hemiptera and Homoptera (in higher coccids spermatogenesis is also inverted) (Suomalainen and Halkka 1963, Ueshima 1979). Similarly, the discovery of reduction at metaphase I for sex chromosomes in ticks (i.e. Oliver 1977) does not force the conclusion that meiosis is normal in both sexes.

This flexibility in bivalent orientation, attainable only in holokinetic organisms, appears to be associated with the mechanism for sex determination. With diploidy, spermatogenesis permits reduction, which is antecedent to acquiring an XO or XY system, to male digamety, and eventually to the transfer of control over the sex of offspring from females to males.

The recognition of heteromorphic chromosomes created the view that one karyotype could contain a mixture of holokinetic and monocentric chromosomes (Oliver and Bremner 1968). The hemipteran example described by Hughes-Schrader and Schrader (1961) seems to be equivalent. Interesting parallels exist between ticks (for which we have no information on the order of division in oogenesis) and the mixed hemipteran system described above, in which sexes are typically XX/XY. In ticks, the large sex chromosome gives the appearance of restricted kinetic activity, and the sex chromosome bivalent shows reductional division at anaphase I (Oliver 1967). A similar behavior was experimentally induced in the ends of a long sex chromosome of a hemipteran by fusion of smaller holokinetic chromosomes after radiation (Hughes-Schrader and Schrader 1961). Further, the long X in XO ticks looks and behaves very much like those described in Hemiptera by Schrader (1935).

We believe that great confusion exists concerning the kinetic behaviors of mite chromosomes, and that the actual distribution of inverted meiosis is mostly unknowable because the key karyotypic descriptions—oogenesis in XX/XY and XX/XO species—are generally unavailable. Both tick and hemipteran oogenetic figures are difficult to obtain, but Helenius (1952) and Nokkala and Nokkala (1984) discussed inverted meiosis in the hemipteran families Lygaeidae and Nabidae, respectively.

3.4 Haplodiploidy and Inverted Meiosis

3.4.1 Spermatogenesis and Sex Determination in Haplodiploid Mites

Sex determination, and therefore sex ratio, is progamic (Bacci 1965) and is under maternal control in haplodiploids, organisms in which males are either genetically (arrhenotoky) or phenotypically (parahaploidy) haploid. This control precludes the differentiation of sex chromosomes for haplodiploid males. Regarding a question asked above (Section 3.3.1), the function of sperm in haplodiploids is thus for something other than sex determination.

In arrhenotokous species spermatogenesis is highly modified, with a single

division producing two haploid sperm (Heinemann and Hughes 1969, Pijnacker 1985). This division probably represents an inverted meiosis in which the second (reductional) division is suppressed, as discussed below (Section 3.4.2). There are no bivalents or chiasmata, so that the event is "mitotic" in terms of chromosome behavior and genetic consequences, i.e. the absence of *type A*, *B*, and *C* recombination.

Parahaploid males that start each life cycle as diploids will breed like haploids and transmit no paternal DNA (Brown and Nur 1964). In parahaploidy resulting from the elimination of the paternal genome early in embryogenesis (i.e. Phytoseiidae, Nelson-Rees et al. 1980; and Dermanyssidae such as *D. gallinae*, Warren 1940), the spermatogenetic events are so much like those of arrhenotokous males that Helle et al. (1978) named this parahaploid system "pseudoarrhenotoky." Since no paternal DNA is included in haploid sperm of parahaploids, this is a profound example of nonrandom segregation and preferential gametic inclusion.

Deviations from panmixia also reduce recombination possibilities. Any regular pattern of inbreeding, such as a highly inbred arrhenotoky with obligate brother-sister mating, will reduce the amount of GR arising from amphimixis. Any mode of reproduction that facilitates female control of sex ratio, such as the several forms of haplodiploidy, fosters distortion of the gametic ratio, either through adaptive patterns of sex allocation (species' sex ratio) or by the proportion of progeny allotted to one sex (sex ratio regulation) (see below, and Wrensch 1993 for discussion).

3.4.2 Haplodiploidy Requires Inverted Meiosis

We see the available cytogenetic information on arrhenotoky and parahaploidy as pointing to an important general conclusion: haplodiploid systems can evolve only in lineages having holokinetic chromosomes that exhibit inverted meiosis. In this section we explain that spermatogenesis in haplodiploid systems is in fact meiotic, and then discuss why this type of spermatogenesis cannot succeed in monocentric systems with normal meiosis.

Arrhenotoky—In most known arrhenotokous species, spermatogenesis clearly involves an equational first division with no second division (i.e. Whiting 1945, John 1990). This seems to be the case for rotifers, whiteflies, chalcid wasps, and iceryine scale insects, as well as mites (Whiting 1945). This one division has generally been regarded as "mitotic" in character (i.e. Whiting 1945), due to the absence of bivalents and the separation of univalents into single chromosomes. Writers frequently remark upon the "failure" of an *expected* second division (e.g. White 1973). However, haploid spermatogenesis clearly represents a first meiotic division, rather than simple mitosis, for three reasons (Hughes-Schrader 1948): (1) the duration of prophase "I" is prolonged and features a lengthy diplotene (e.g. "confused" or "diffuse" stage) inferred from the relatively high proportion of nuclei fixed in this part of meiotic prophase I; (2) the enlargement and subsequent

disappearance of nucleoli clearly indicate synthetic activity during meiotic prophase; and (3) the chromosomes at metaphase "I" are more condensed than in somatic metaphases.

Arrhenotoky requires a system with holokinetic chromosomes that form end-to-end associations in the diploid female. These half-bivalents create the physical attachments between nonhomologous chromosomes that lead to inverted meiosis. This segregation pattern is critical to a females' ability to retain control of the genetic content of each egg produced. To understand the significance of this meiotic pathway, we must first consider the results theoretically obtained with normal meiosis.

Assume that a pair of homologous chromosomes replicate and separate without crossingover at metaphase I in normal meiosis. The secondary oocyte would contain an identical pair of chromatids. Their segregation in the second division would produce an egg pronucleus that is haploid for one of the two original homologues. A haploid male arising from such an egg represents one and only one possibility from the maternal genotype; thus, for any primary oocyte, males would always be formed from one or the other homologue. Assuming independent orientation at metaphase I of the bivalent, the pool of haploid eggs from any female undergoing normal meiosis will therefore always consist of 50% one homologue and 50% the other. Consequently, the female has no control of the individual genetic content of her sons.

With inverted meiosis, however, secondary oocytes and polar nuclei are genetically equivalent. Thus, orientation at metaphase I is irrelevant. The secondary oocyte contains one of each homologue, and the segregation of these homologous chromatids at anaphase II generates haploid eggs. Within each egg, there is a 50% probability that a particular homologue is included in the haploid male. Therefore segregation in the secondary oocyte resulting from inverted meiosis permits female control of the genetic complement of haploid males; she controls the genetic content of each egg. With normal meiosis, such control is impossible.

Parahaploidy—The order of meiotic divisions is critical to the genetic consequences of parahaploid spermatogenesis, since it is inverted meiosis that enables the preferential segregation of only the maternal genome into two functional sperm. Males of parahaploid scale insects have inverted meiosis, and whether the system heterochromatizes the paternal set or eliminates it, only two functional sperm are produced. These contain the same half of the maternal genome, i.e. they are genetically identical. The pattern seems the same in parahaploid mites, but their cytogenetics (including that of the confusing system of *Dermanyssus*, J. Oliver, pers. comm., 1992) must be reinvestigated to confirm that meiosis is inverted.

In discussing spermatogenesis in lecanoid coccids, John (1990) considered inverted meiosis to be a "preadaptation" for parahaploidy. In this system two meiotic divisions occur, but the first must be equational for normal sperm to result. After an equational first division, the two haploid nuclei that originate

from the two euchromatic telophase II sets proceed to differentiate into the two functional sperm. This inverted meiosis is considered to be ancestral to the abbreviated type of meiosis in diaspidid coccids, which features just one equational division producing two sperm (Brown 1977).

3.5 Inverted Meiosis Affects Recombination Index

Levels of intrachromosomal genetic recombination (see Section 3.1, *type A*) can be measured in a simple way, if we confine ourselves to relative statements. Intrachromosomal genetic recombination levels directly impinge on the amount of genetic variance available to natural selection. Allelic recombinations sift out homozygotes from heterozygotes that carry cryptic variation (Mather 1953). The integrity of linkage groups is directly affected, and sustained or disrupted by the location and frequency of intrachromosomal, reciprocal exchanges.

To make our case for the effect of holokinetic chromosomes on evolutionary potential, we have to compare how modes of reproduction can directly affect levels of genetic recombination. We have computed the recombination index (RI, Darlington 1939, White 1973) for different modes of reproduction, for each sex, and for an average within the bisexual mode (Fig. 11.9). In addition, we have computed RI for several modes of thelytokous reproduction, where we estimate the values given holokinetic or monocentric karyotypes; a "male" equivalent is based on the type of restitution. To make these comparisons relative, we assume a standard karyotype with $2n = 6$, $n = 3$, one functional crossover per bivalent and progenies with equal proportions of sons and daughters.

A number of insights are gained by this comparison. First, the automictic thelytokes that achieve restitution through terminal fusion have an RI of six, equal to that of a diplodiploid species. Second, holokinetic chromosomes provide consistently higher potential RI than do monocentric systems. Third, diplodiploids have a reduction in their RI directly correlated with departure from normal, complete synapsis in spermatogenesis. Fourth, as expected, all forms of haplodiploidy have the same recombination index, and—given our 1:1 sex ratio assumption—they have the lowest RI of any amphimictic mode.

What is the effect of relaxing the assumption of equal sex ratio in progenies of bisexual modes? The answer that follows reveals how sex ratio variation serves to alter the level of genetic recombination.

3.6 Facultative Recombination Through the Production of Haploid Males

Females of haplodiploid mites, such as the arrhenotokous spider mites (Tetranychidae, Young et al. 1986) and the parahaploid Phytoseiidae (Sabelis and Nagelkerke 1987), produce female-biased progenies. Sex ratio is adjusted in response to cues from the environment (Wrensch 1993), and progeny sex is determined cytoplasmically, through mechanisms yet unknown. In parahaploids, all eggs

	RI-♀ fraction		RI-♂fraction**		RI	
DIPLODIPLOIDY Spermatogenesis chiasmate	6		6(a)		6	
Spermatogenesis chiasmate, autosomes only (males XY, XO)	6		4(b)		5	
Spermatogenesis achiasmate	6		3(c)		4.5	
HAPLODIPLOIDY PARAHAPLOIDY Paternal genome heterochromatic	5		2(d)		3.5	
PG eliminated in early embryo	5		2(d)		3.5	
ARRHENOTOKY	5		2(d)		3.5	
	M	H	M	H	M	H
THELYTOKY AUTOMIXIS A. Restitution by Terminal Fusion: Egg pronucleus + 2nd PN — Chiasmata are: i. proximal	3		3(e)		3	
ii. distal	6	6	6(e)	6(e)	6	6
iii. (i + ii)/2	4.5		4.5(e)		4.5	
B. Restitution by Central Fusion: Two non-sister PNs — i. proximal	6		6(e)		6	
ii. distal	4.5	4.5	4.5(e)	4.5(e)	4.5	4.5
iii. (i + ii)/2	5.25		5.25(e)		5.25	
C. Restitution: Fusion of cleavage nuclei or endomitosis of egg pronucleus	6	6	0(e)	0(e)	3	3
D. Premeiotic Doubling	3	3	3(f)	3(f)	3	3
APOMIXIS	0	0	0(g)	0(g)	0	0

*Recombination Index (for each sex or averaged for both sexes) =
Sum of haploid number (n = No. bivalents) + mean chiasmata/cell
(= average for one meiotic division). For haplodiploids, n' = (female(n) +1)/2.
(from White, 1973)

** a) Diplodiploid sperm = haploid meiotic recombinant set
b) = a. for autosomes, but sex chromosome(s) nonrecombinant
c) = a. but complete haploid set nonrecombinant
d) Haplodiploid sperm = haploid ameiotic nonrecombinant set
e) Automictic thelytokous restitution system = fusion (A,B) or doubling (C) of haploid meiotic recombinants
f) Bivalents are "autobivalents" between sister duplicated homologues, therefore chiasmata do not create GR
g) Apomictic thelytoky = one ameiotic nonrecombinant diploid set

Figure 11.9. Recombination index (RI)* as a function of mode of reproduction. Assume 2n = 6, n = 3, one crossover/bivalent and a progeny sex ratio of 1:1. For monocentric (M) chromosomes, RI related to location of chiasmata (i.e. proximal to centromere or distal, with locus between centromere and chiasma). For holokinetic (H) karyotypes, chiasmata usually form at bivalent ends.**

receive sperm initially, so eggs that produce males must somehow eliminate the sperm's contribution. In arrhenotokes, females produce males by prohibiting sperm entry into a fraction of the eggs.

White (1973, 498) recognized that the lowest RIs in the animal kingdom are those found in mites with haploid males and chromosome counts of n = 2 or n = 3. Wrensch (1993) argued that a conditional increase in the proportion of male progeny represents a facultative increase in the rate of genetic recombination. To illustrate how this effect is achieved, first consider Figure 11.10, which diagrams the effect of haploid males (either arrhenotokous or parahaploid) inseminating virgin females across two generations. The variability due to crossingover and recombination is under female control because only females form bivalents during meiosis. The amount of variability generated is a function of *type A* and *type B* recombination (Section 3.1). The expression of this GR is through haploid males, which act as vectors of either the conserved (without *type A* GR) or recombined (with *type A* and *type B* GR) genome.

Assuming the observed level of crossingover of two per bivalent during spider mite oogenesis (Feiertag-Koppen and Pijnacker 1985), a rough estimate can be computed for both *type A* and *type B* GR effects. The number of different recombinant chromosomes can be gauged from White's presentation (1973, his Fig. 6.6). Since spider mites have 2n = 6 chromosomes, the combinatorial for calculating the different haploid sets of three is straightforward.[3] Figure 11.11 uses these assumptions to provide a simple numerical example of the effects of a shift in sex ratio.

For the same number of eggs, 200, a female that increases the proportion of haploid eggs simultaneously increases the fraction of haploid genetic recombinants that her own genotype meiotically generates. A male develops from an ovum containing an egg pronucleus and maternal cytoplasm. Given the level of recombination observed, each male is likely to be genomically unique (Fig. 11.10).

This helps explain the apparently paradoxical success of highly inbred arrhenotokous (HIA) mites discussed earlier (Section 1.3): why doesn't HIA quickly lead to homozygosity, and hence extinction? For our introductory example of quill mites, there is little recombination potential in the first generation, which contains a single male. However, the progeny of the second generation contains 11 males and, by analogy to the spider mite example above, maximizes the degree of

[3]White's Figure 6.6 (1973, 165) illustrates the types of crossover products that result from two chiasmata per bivalent. Pairs of reciprocal chromatids (p), two kinds of diagonal chromatids (q, r) and complementary chromatids (s) reflect outcomes of 2-strand, 3-strand and 4-strand exchanges, respectively. With the haploid egg n = 3, the combination of types of crossover products is $(p + q + r + s)^3$. By multiplying each combination by its relative frequency and then pooling recombinant sets having the same mean integer of recombinant chromosomes per egg, frequencies of the four categories of eggs in Figure 11.11 are obtained. The relative frequencies of the reciprocal, diagonal and complementary types of crossover products are available in White (1973).

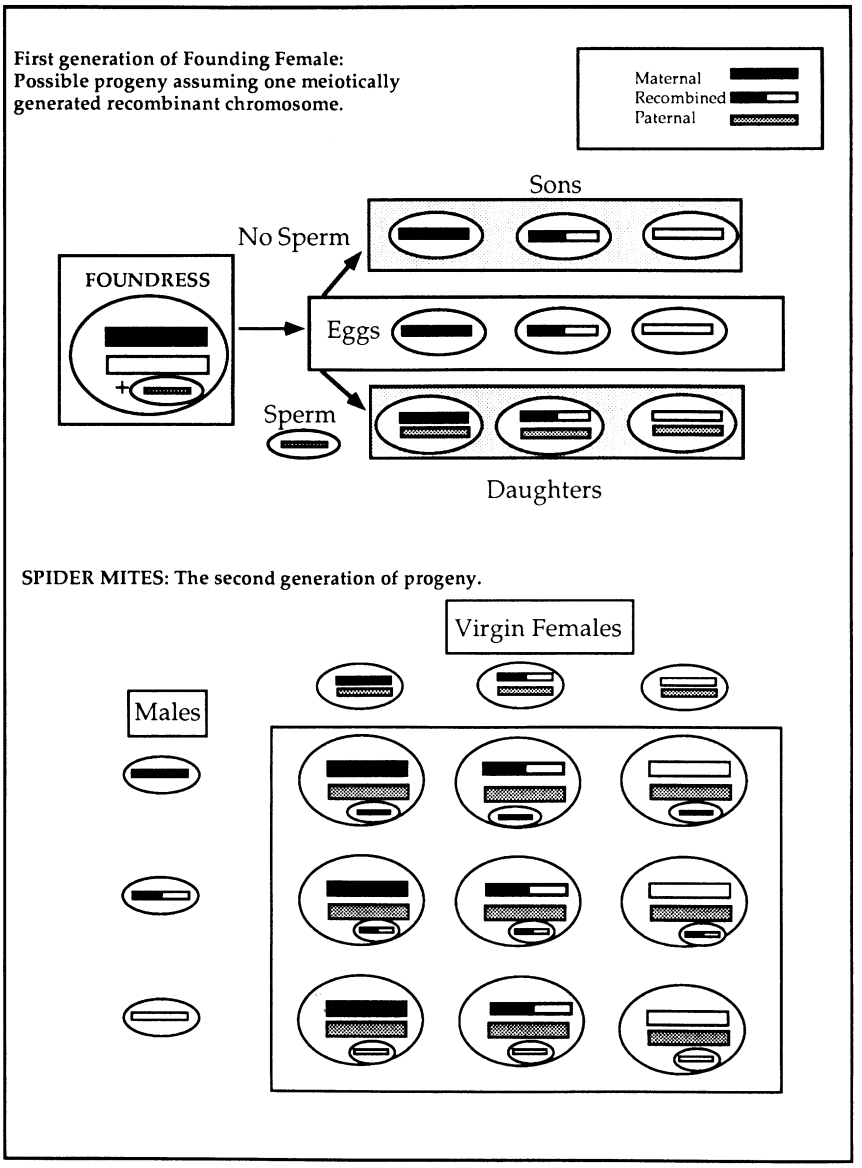
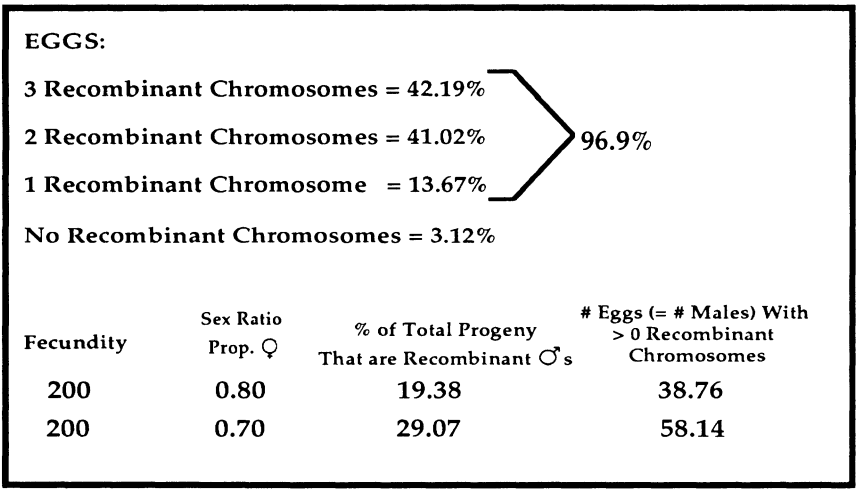


Figure 11.10. Arrhenotokous reproduction in two consecutive generations of spider mites. Only one chromosome is tracked and is diploid in females and haploid in eggs and in males.



Fecundity	Sex Ratio Prop. ♀	% of Total Progeny That are Recombinant ♂s	# Eggs (= # Males) With > 0 Recombinant Chromosomes
200	0.80	19.38	38.76
200	0.70	29.07	58.14

Figure 11.11. Percent of haploid eggs containing 0, 1, 2, or 3 recombinant chromosomes and the effects that varying sex ratio has on the proportion of progeny and the absolute number of offspring that are haploid. Number of cross-overs is assumed to be two per bivalent. See text for details of computations.

recombination with a minimal number of males. As with thelytoky, the paradox is largely an artificial construct resulting from assuming a normal meiosis, rather than the inverted meiosis that arrhenotoky requires.

A highly female-biased sex ratio will reduce RI for any of the bisexual modes listed in Figure 11.9, where a 1:1 ratio was assumed; such a reduction more faithfully conserves the maternal genome in the next generation. On the other hand, a controlled sex ratio shift that increased the proportion of haploid males would increase RI, and therefore raise the potential for genetic variation. From this perspective, the genetic function of males in haplodiploid systems is to make genetic recombination a facultative process.

4. The Big Picture: Holokinetic Systems and the Evolution of Eukaryotes

4.1 Distribution of Holokinetic Chromosomes and Inverted Meiosis in Eukaryotes

> . . . with so little evidence I have no intention of entering this old battlefield of hypotheses.
>
> (Schrader 1936)

Perhaps we should be as cautious as Schrader, but without speculation from spotty evidence, many avenues of biology would be left unexplored. We have suggested that holokinetic chromosomes may be pervasive in Acari, but mites

are probably not unusual in this regard. Major reviewers agree that holokinetic chromosomes are present in numerous animal groups (i.e. Rhoades 1961, White 1973, John 1990), but we believe authors have been conservative. What follows is not intended as a detailed review. Rather, we summarize literature records and suggest groups that may prove holokinetic when more closely examined. Our purpose is to emphasize that chromosomes in numerous groups of protists and fungi, and of both early derivative and higher animals and plants (though botanists traditionally shun the characterization), are holokinetic.

Chromosome characterizations in Table 11.1 were taken either directly from the cytogenetic literature or were made by us after examining primary sources. The monomorphic condition (*) for a listed taxon is provisional. For example, nematodes appear to be exclusively holokinetic to us, and mostly so to Triantaphyllou (1984); but he cautiously did not commit to a global statement because some of the primary literature claimed one species has metacentric (and therefore monocentric) chromosomes. Conversely, while occasional primary literature has assigned a holokinetic karyotype to a beetle (i.e. Blackwelder 1944, Kiauta 1969), Smith and Virkki (1978, 29) regard beetle centromeres as "localized" because "no reliable account exists of a diffuse . . . centromere." Nevertheless, at several places in the latter monograph on beetle cytogenetics, the described chromosome behavior and morphology directly or indirectly suggest that chromosomes are holokinetic (e.g. Smith and Virkki, 95). In particular, Smith and Virkki describe the chromosomes of an arrhenotokous species, *Xyleborus dispar*, as ". . . comparable in size to those of most Lepidoptera" (217). This comparison seems literally correct to us, too, since Lepidoptera have holokinetic chromosomes, and it would be consistent with the argument we have been making concerning holokinetic systems as a precondition for arrhenotoky.

The occurrence of holokinetic chromosomes is even more pervasive in eukaryotic organisms than has been thought. Indeed, they seem to be present in at least some taxa of every major lineage of eukaryotes, with the conspicuous exception of Echinodermata, Chordata. Viewed in a phylogenetic context, the character state of having holokinetic chromosomes is potentially present at every major node of the tree of eukaryotic life. This scattered distribution of holokinetic and monocentric chromosomes among various protist, plant and animal groups poses an obvious question: viewed as character states, is it the absence or the presence of a localized kinetochore that is ancestral? Clearly, with either polarity there must have been multiple derivations; centromeres have evolved many times or have been lost many times.

4.2 Are Holokinetic Chromosomes and Inverted Meiosis Ancestral in Eukaryotes?

It has been suggested that holokinetic chromosomes have given rise to monocentric chromosomes (Vaarama 1954, Halkka 1956, Hughes-Schrader and Schrader

Table 11.1. Organisms known and suggested to have holokinetic chromosomes. Taxa believed to consist exclusively of holokinetic members indicated by "".*

Taxon[1]	Attributes[2]	References[3]
SINGLE-CELLED EUKARYOTES/PROTOCTISTA		
Dinoflagellata		Sarma 1983
Bacillariophyta* (=Diatoms)		Health 1980
Euglenida		Heath 1980
Ciliophora		Heath 1980
Actinopoda (= Radiolaria)		Grell & Ruthmann 1964
Conjugaphyta*		Sharma & Sharma 1984
Desmidaceae		King 1953
Zygnemataceae: *Spirogyra*		Godward 1954, 1961
Chlorophyta		
Coleochaetales: *Coleochaete scutata*		• Margulis et al. 1990
MULTICELLULAR EUKARYOTES		
Fungi		Brown 1972, Vaarama 1954
Plantae		
Bryophyta		Vaarama 1954
Lycophyta		• Jermy et al. 1967
Sphenophyta: *Equisetum*		• Wilson 1928
Pteridophyta		Walker 1984
Cycadophyta		• Khoshoo 1990 and Sharma & Sharma 1984
Ginkgophyta		• Khoshoo 1990
Gnetophyta: Welwitschiaceae		• Khoshoo & Ahuja 1963
Coniferophyta		• Khoshoo 1990
Angiospermae (Anthophyta):		
Monocotyledones		
Commedlinidae		
Commelinaceae		• Morton 1967
Cyperaceae*	IMf	Sharma & Sharma 1984
Gramineae		• Marchant 1967
Juncaceae*	IMf	Sharma & Sharma 1984
Liliidae		• Stebbins 1971

Table 11.1. Continued.

Taxon[1]	Attributes[2]	References[3]
Dicotyledones:		
Magnoliidae and Ranunculidae (=Ranales)		Sybenga 1975
Dilleniidae: Cruciferae: *Brassica*		Swanson 1957
Rosidae		• Stebbins 1971, John 1990
Animalia		
Mesozoa-Rhombozoa: *Dicyema aegira*		Nieuwkoop & Sutasurya 1981
Porifera		• Tuzet 1964
Cnidaria		• Wijsman & Wijsman-Best 1973
Platyhelminthes		Benazzi & Benazzi Lenatati 1976
Nematoda*	A, IMm	Traintaphyllou 1984, John 1990, and John & Lewis 1965
Rotifera*	A	• Birky & Gilbert 1971
Chaetognatha		• Stevens 1910
Mollusca		
Gastropoda		• Bajer et al. 1961, Baccetti & Afzelius 1976 and Nath 1965
Bivalvia		• Wilson 1928
Cephalopoda		• Gao & Natsukari 1990
Annelida	PH, IMf	Christiansen 1980
Tardigrada		• Ammermann 1967, and Bertonlani 1975
Arthropoda:		
Chelicerata		
Acari*	A, PH, IMf	Present Work
Araneae	IMf	Benavente & Wettstein 1980
Opiliones		• Tsurusaki & Cokendolpher 1990
Pseudoscorpionida		• Nath 1965
Scorpionida		Shanahan 1989
Mandibulata		
Crustacea		Chandra 1962, Beerman 1977
Cladocera		• Nath, 1965
Copepoda		Beerman 1977
Decapoda		Stefani & Cadeddu 1967
Isopoda	IMf	Hill 1948
Ostracoda		• Nath 1965
Myriapoda		
Chilopoda	IMm	Ansley 1954, White 1973
Diplopoda		• Nath 1965

Continued

Table 11.1. Continued.

Taxon[1]	Attributes[2]	References[3]
Insecta:		
Collembola		• Nunez 1962
Ephemeroptera		• Kiauta & Mol 1977, Brown 1972
Odonata	IMfm	White 1973, Kiauta & Mol 1977
Blattodea		• John & Lewis 1958, White 1976
Dermaptera*		White 1976
Isoptera*		• John 1983, Syren & Luykx 1977
Orthoptera		White 1973, p. 374; John 1990, p. 24
Anoplura*		Bayreuther 1955
Hemiptera*	IMfm	Ueshima 1979
Homoptera*	A, PH, IMfm	Hughes-Schrader 1948
Mallophaga*		Scholl 1955
Thysanoptera*	A	White 1973
Coleoptera[4]	A, PH, IMf	Smith & Virkki 1978, Piza 1958 and Seiler 1948
Diptera[5]	A, PH	• White 1973, Matuszewski 1961
Hymenoptera[6]	A, PH	• Crozier 1975
Lepidoptera*	IMf	Suomalainen 1953
Megaloptera		• Hughes-Schrader 1980
Strepsiptera		• Rieder & Nowogrodzki 1983
Trichoptera*		Suomalainen 1966

[1]Higher categories follow Margulis et al. (1990) for Protoctista, Friis et al. (1987) for Plantae and Brusca and Brusca (1990) for Animalia. The absence of a particular higher taxon does not imply a monocentric karyotype. For example, we have not yet checked literature for smaller invertebrate phyla or most of the unicellular eukaryotes. Higher vertebrates, or at least their large autosomes, have centromeres. Mammalian autosomes feature a distinctive kinetochore.

[2]Attributes are indicated as: A–arrhenotoky, PH–parahaploidy and IM–inverted meiosis, specifically IMf–oogenesis, IMm–spermatogenesis and IMfm–inverted meiosis in both sexes. Attributes observed in a taxon do not necessarily apply to all members of that taxon.

[3]Authors explicitly describe karyotypes as holokinetic and having attributes listed in Table 1 unless preceded by "•", which denotes reference(s) used by us in suggesting holokinetic chromosomes in taxon.

[4]Smith and Virkki (1978) do not directly diagnose holokinesis or inverted meiosis when interpreting karyotypes, but they effectively grant these conditions in their discussion of beetles in "the Oedionychina mode" on pages 96 and 136 and elsewhere. Many other species appear to be holokinetic by our diagnosis using descriptions and figures in Smith and Virkki (1978), i.e., Elateridae, Lampyridae, Coccinellidae (Fig. 42B, p. 96, p. 135), Chrysomelidae (Fig. 81) and Scolytidae, in particular, i.e., *Xyleborus dispar* (Fig. 102).

[5]For primitive families Sciaridae and Cecidomyiidae, especially their limited or elimination chromosomes.

[6]Holokinetic-looking karyotypes in Crozier (1975) for *Melipona quadrifasicata anthidioides*, Fig. 25, and *Apis cerana indica*, Fig. 3.

1961, Sybenga 1981), based on the argument that holokinetic systems have simpler mechanical constraints, and logically represent greater cellular economy. Jones (1978), and later Holmquist and Dancis (1980), proposed that the telomeric regions of holokinetic chromosomes are the probable ancestors of centromeres. This hypothesis is bolstered by molecular data on monocot plants indicating that zygDNA segments (DNA synthesized during zygotene) do not actually complete synthesis until metaphase I (Stern and Hotta 1987). Molecular data explain the late replicating behavior of end regions and enable the end-to-end pairing that establishes a half-bivalent from a pair of homologous chromatids.

If such a polarity is correct, perhaps the greater plasticity that holokinetic chromosomes seemingly confer on a karyotype was significant in eukaryote evolution. They allow plasticity in two fundamentally different ways, both of which relate to their demonstrated tolerance of fragmentation and fusion (Section 2.1.1). First they permit reduction in chromosome number by fusion (Schrader 1940, Hughes-Schrader and Schrader 1961) or increase by fission (Ueshima 1979), respectively. As a labile system for karyotype evolution, holokinetic chromosomes appear superior to monocentric chromosomes, and this evolutionary lability extends to sex determination. For example, White (1973) discussed the plasticity of sex chromosomes in races of the holokinetic morabine grasshoppers. The fusion (either tandem or centric) of a holokinetic X with an autosome permitted male sex determination to shift from XO to XY within the same population. First division segregation was equational when the fusion was "acrocentric" and was reductional when the fusion was "metacentric." By ignoring the widespread existence of holokinetic chromosomes, we also ignore the explanatory power of their flexibility as features of karyotype evolution and sex determination mechanisms.

Second, holokinetic systems may be fundamentally different from monocentric ones in their constraints or permissiveness during early development, cell differentiation, and gene regulation. For example, the greater repair ability of holokinetic chromosomes should allow injured cells to survive many generations of replication. Thus they could tolerate damage that would be lethal in monocentric systems (Evans and Pond 1964).

We believe further that there is a causal link between the type of chromosome (holokinetic or monocentric) and the type of meiotic division (inverted or normal). As noted earlier, numerous cytogeneticists (e.g. Rhoades 1961, John 1990) have argued that inverted meiosis is possible only in holokinetic chromosomes. The constraint upon monocentric bivalents to co-orient at metaphase I (i.e. have an axial orientation relative to the spindle) appears to result from the dependence of chromosomes upon kinetochores for orientation, and from the necessity in animals for the linkage of kinetochores by microtubules to the centrioles (Peterson and Berns 1980, Balczon and Brinkley 1990).

The phylogenetic consequences of such a causal linkage force a second hypothesis: inverted meiosis could well be ancestral to "normal" meiosis (Halkka 1959,

Suomalainen and Halkka 1963), and therefore normal meiosis may also have evolved independently multiple times. This is not an outrageous idea. The evolutionary path to complexity must start with simplicity, and in this context—from a purely genetic perspective, ignoring the typically cytoplasmic events of maturation and gamete differentiation—the first (equational) division of inverted meiosis mimics mitosis. The second (reductional) division is then seen as the evolutionary innovation, added to the end of an existing process in a parsimonious manner. Intercalation of a reductional division between equational divisions (i.e. the "normal" order of meiosis) is viewed as a further innovation. Since in this case the latter would be the chronologically "inverted" order, we may need to develop new terminology based on the relative position of the reductional division.

4.3 Historical Inertia and the Monocentric Paradigm

If holokinetic chromosomes are so common, why are they so poorly appreciated? Indeed, they virtually have been omitted from the evolutionary cytogenetic synthesis. For example, White (1973) explicitly stated that we can generalize from the karyology described for *Drosophila*, maize and humans to the rest of life, because these organisms share the same key traits, despite their many differences. He argued that not seeing a primary constriction was not proof of its absence, leading most workers to identify any chromosomes with telokinetic behavior as acrocentric. As Peterson and Berns (1980, 103) and Jones (1978, 134) have noted, there has been remarkable tenacity among both animal and plant cytologists to believe almost universally in a nonterminal, localized kinetic organization in chromosomes.

White's three choices to represent life all happen to have a conspicuous centromere that dominates the morphology and behavior of chromosomes in mitosis and meiosis. Furthermore, each provides elegant genetic confirmation of cytological behaviors that conform to the chromosomal theory of inheritance. So, White's inference had added attractiveness: it was a reasonable generalization and it was confirming the predictions of the most significant biological theory of the early twentieth century.

Had the great morphological cytologists E. B. Wilson (e.g. 1928) or Franz Schrader (e.g. 1953) been able to correlate their elegant observations on the exclusively holokinetic Heteroptera with experimental genetic studies, perhaps White would have been more circumspect. Although the chromosomes of the Heteroptera are relatively easy to study, the merging of their cytology and heredity never happened. Why? Bugs, scales, and aphids are not noted in the annals of classical genetics because they are not useful model organisms; they do not generate frequent, conspicuous mutations. Is this just a coincidence, or is there a link between the type of chromosome system and the stability (i.e. immutability) of the phenotype?

Consider this situation from an historical perspective. To study patterns of inheritance, early geneticists had to be able to identify genes with relatively conspicuous and simple phenotypic effects. The necessity of tracking the transmission and expression of distinctive genotypes predisposed workers to select organisms having genetic systems that revealed large, visible and viable mutations. More relevant to our argument, these genetic systems had to expose discrete and unique genetic variants at a relatively high frequency. The organisms selected by geneticists, *Drosophila*, maize, mice or humans, possessed genetic systems that were intrinsically likely to offer the geneticists what they sought. So, it is no surprise that these chosen lifeforms shared a key trait—centromeres—that dominated chromosomal movement during mitosis and meiosis.

With the developing body of knowledge about these organisms, the role of the centromere in chromosome mobility and morphological cytology was seen as central to mechanical orderliness, so much so that the alternative mechanisms associated with holokinetic systems were less compelling. Furthermore, monocentric chromosomes are generally much larger, take up more stain, and occupy cells with larger nuclei or have more nuclei undergoing division. As such, they are simply more amenable to cytological investigation.

The effect of this history is significant. Referring to our earlier theme, there are two central issues in the evolutionary cytogenetics of thelytokous and haplodiploid organisms. One is the ability of a thelytoke's restoration mechanism to generate, maintain, or eliminate heterozygosity (and thus cryptic genetic variability on which selection could act). The other is the ability of males of haplodiploid species (having no paternal DNA) to produce recombinant sperm. All applicable cytogenetic models that could be used for these common reproductive modes are developed for monocentric systems having normal meiosis (i.e. White 1973, Fig. 19.2). Also, White's (1973, 495) assumption that single-locus genetics should be comparable in holokinetic systems has been adopted for nearly all organisms. But his model is backwards for holokinetic organisms with inverted meiosis—the system that most haplodiploids and thelytokes probably have. Thus, evolutionary predictions for the genetic stability or flexibility of such organisms have an erroneous footing—they are "upside-down."

5. Prospectus for Further Research

5.1 Empirical Needs

Clearly our case for holokinetic chromosomes being important in the conservation of mite genomes is based on a paucity of data. The first order of business will be to document the distribution of holokinetic chromosomes in the major lineages of parasitiform mites, and to survey the incidence of inverted meiosis (in both oogenesis and spermatogenesis) in both orders.

Special attention must be paid to basal taxa, those commonly ignored because

they have no direct relevance to man. These include the parasitiform groups Opilioacarida and Holothryida, as well as acariform groups such as the paraphyletic Endeostigmata, and the enarthronote and palaeosomatid Oribatida. Knowledge of early derivative members of anystine and eupodine Prostigmata will also be needed. Studies of sex determination in mites with similar male and female karyotypes are also needed. Such information may help put in perspective the origin of the many wholly thelytokous taxa of Endeostigmata and Oribatida and the reversal to sexuality during the origin of Astigmata.

As is often noted, independently developed hypotheses of phylogenetic relationships among investigated taxa are critical to the analysis of any biological pattern; for mites such hypotheses are developing, but are usually fragmentary (Norton et al. 1993). Especially helpful will be a hypothesis of phylogeny within the mesostigmatid taxon Dermanyssina; they have been a focal group for cytology and reproductive biology, but we have no framework on which to hang the data.

For the big picture we are similarly constrained. Major gaps exist in our knowledge of chromosome type, meiosis, and phylogenetic relationships of eukaryotes. Perhaps our initial attention should be directed toward groups already known to include taxa with both holokinetic and monocentric chromosomes, such as nematodes, annelids, beetles, and the entire group of panorpid insect orders. A synthesis of cytological information and phylogenetic relationships among the heteropteran insects will be illuminating; they exhibit many parallels with mites, in both reproductive mode (e.g. parahaploidy, arrhenotoky, thelytoky) and cytology. In addition, we need basic karyotype data from virtually all of the "minor" taxa of lower eukaryotes.

The availability of several molecular tools makes some of these goals more attainable than in the past. As examples, the CREST antibody, or probes for the par locus of *Escherichia coli*, could be used to identify the presence of kinetochores (Balczon and Brinkley 1990). Not surprising, nothing is yet known about the biochemistry of diffuse kinetochores, which reflects the general bias against holokinetic systems. True sex chromosomes could be identified with the Bkm satellite DNA technique (Jones 1985). Transposable elements such as mariner[4] might be used to track segregation in progeny of thelytokous and sexual mothers in species having no known sex-determining mechanism.

As an aside, we have noted a potentially important, but unexpected ecological correlation of holokinetic chromosomes that should be closely examined. The absence of kinetochores and centrioles, and the use of karyomeres and intranuclear spindles, may be meaningfully related to nutritional regimes. Plants (and fungi) produce antimitotics, such as caffeine and colchicine, as part of their defensive arsenal. Caffeine causes the kinetochores of monocentric higher animal chromo-

[4]"The mariner transposable element is widespread in insects"; H. M. Robertson; Entomological Society of America meeting, Baltimore, December 8, 1992. Note added in proof: see *Nature* 362:241–245.

somes to drop off, leaving the chromosomes lost in a sea of cytoplasm (Balczon and Brinkley 1990). Animals that suck the sap of plants or fungi are "preadapted" to these feeding modes if their genetic systems are unaffected by the antimitotics generated by their meals. They include the many groups of plant-feeding mites and homopteran insects that have holokinetic chromosomes. We suggest that possession of such chromosomes should be an attribute shared by successful sap feeders of any sort; testing this hypothesis may have economic significance.

5.2 Mending The Cytogenetic Synthesis

It has been more than a decade since Bell (1982) called for the emergence of a new discipline, "metagenetics," to integrate theory concerning cytogenetics, population genetics, population ecology and life history. This emergence does not seem to have occurred, perhaps due in part to the fact that the first of these components has been incomplete.

Most cytogenetic theory—i.e. our perceptions of how the dynamic processes of genomic repair and genomic change operate—is based on studies of organisms having one of two major types of systems: (1) prokaryotes with a single circular chromosome; or (2) diploid eukaryotes with monocentric chromosomes and normal meiosis. Clearly, we need to integrate a third type of organism, one having holokinetic chromosomes and inverted meiosis. Also, we must deal with haplodiploid systems and most forms of thelytoky as modifications of the third type, rather than the second.

To be functional, a discipline such as "metagenetics" also requires a fifth component, phylogenetic theory. For example, most models attempting to explain the evolution of reproductive modes employ an ecological perspective to identify selective advantages that drive the system. But the perceptions of the holokinetic system discussed in this chapter have been influenced strongly by combining cytological information with a phylogenetic perspective. Our belief is that these perceptions will hold under the weight of badly-needed additional data; our hope is that they will have heuristic value in unveiling the numerous additional ramifications of holokinetic systems that must exist.

6. Summary

(1) Acari as a group seem to be characterized by a genetic system featuring holokinetic chromosomes.

(2) Only holokinetic systems enable inverted meiosis, with equational segregation of homologous chromatids at anaphase I. This inverted pattern permits double-strand DNA repair while conserving the maternal genotype in secondary oocytes.

(3) The cytogenetic and evolutionary predictions for thelytokes with monocentric systems are not applicable to those with holokinetic

chromosomes and inverted meiosis. When they restore diploidy by the common mechanism of terminal fusion (or an equivalent), organisms with inverted meiosis can both edit mutations and repair adapted genomes, while maintaining the potential for variation. Wholly thelytokous higher taxa can result; apparent examples of which are various groups of endeostigmatid and oribatid mites, and probably bdelloid rotifers.

(4) When functional crossingover is limited, thelytokous species with terminal fusion automixy and inverted meiosis should faithfully conserve maternal genome in progeny, and evidence of this is known for nothroid oribatid mites. Cytogenetically such systems represent "ideal thelytoky," but they also result in the near clonal reproduction that is necessary for the evolution of general purpose genotypes (*sensu* Lynch 1984).

(5) The restoration of sexuality within a thelytokous lineage—such as the trhypochthonioid oribatid mites giving rise to Astigmata—is not a major cytogenetic problem. Parallels are found in various cyclical parthenogens.

(6) Holokinetic chromosomes and inverted meiosis appear to enable arrhenotoky and parahaploidy. Haploid males produce just two sperm per meiotic event and these carry identical halves of the maternal genome.

(7) Haploid males permit facultative change in genetic recombination.

(8) Many other animals and plants appear to have holokinetic chromosomes and thus the potential for inverted meiosis.

(9) Much of the current cytogenetic paradigm is based on monocentric systems (centromeres and normal meiosis), and ignores the real possibility that holokinetic chromosomes and inverted meiosis are ancestral in eukaryotes.

Acknowledgments

We wish to thank D. E. Johnston (The Ohio State University, Columbus; OSU) and W. T. Atyeo and T. W. Kethley, Jr. (University of Georgia, Athens) for facilitating this cooperative effort, and our editor, M. A. Houck, for her patience and support. Constructive comment on the manuscript was provided by R. C. Jackson (Texas Tech University, Lubbock), H. G. Nelson (FMNH, Chicago), S. C. Palmer (Cazenovia College, Cazenovia, NY), and A. T. Peterson (FMNH, Chicago). J. F. Downhower (OSU) provided ideas for Fig. 11.10, and Lavinia Hales (OSU) helped in assembling references.

References

Alberti, G. 1991. Spermatology in the Acari: systematic and functional implications. In: *The Acari: Reproduction, Development and Life-History Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall Ltd., London. Pp. 77–105.

Ammermann, D. 1967. Die Cytologie der Parthenogenese bei dem Tardiagraden *Hypsibius dujardini*. *Chromosoma* (Berl) 23:203–213.

Ansley, H. R. 1954. Alternative pathways of meiosis in *Scutigera*. *Chromosoma* 6:656–695.

Asher, J. H., Jr. 1970. Parthenogenesis and genetic variability II. One-locus models for various diploid popultions. *Genetics* 66:369–391.

Baccetti, B. and B. A. Afzelius. 1976. *The Biology of the Sperm Cell. Monographs in Developmental Biology* 10 (A. Wolsky ed.). S. Karger, NY. 254 pp.

Bacci, G. 1965. *Sex Determination*. Pergamon Press, NY.

Bacci, G., G. Cognetti and G. Vaccari. 1961. Endomeiosis and sex determination in *Daphnia pulex*. *Experientia* (Basel) 17:505–506.

Bajer, A. E. Hansen-Melander, Y. Melander and J. Molè-Bajer. 1961. Meiosis in *Cepea nemoralis* studies by microcinematography. *Chromosoma* (Berl) 12:374–381.

Balczon, R. D. and B. R. Brinkley. 1990. The kinetochore and its roles during cell division. In: *Chromosomes: Eukaryotic, Prokaryotic, and Viral*, Vol. 1 (K. W. Adolph ed.). CRC Press, Boca Raton. Pp. 167–189.

Battaglia, E. and J. W. Boyes. 1955. Post-reductional meiosis: its mechanism and causes. *Carylogia* 8:87–134.

Bayreuther, K. 1955. Holokinetische Chromosomen bei *Hematopinus suis* (Anoplura, Haematopinidae). *Chromosoma* (Berl) 7:260–270.

Beerman, S. 1977. The diminution of heterochromatic chromosomal segments in *Cyclops* (Crustacea, Copepoda). *Chromosoma* (Berl) 60:297–344.

Bell, G. 1982. *The Masterpiece of Nature*. Univ. Calif. Press, Berkeley. 635 pp.

Benavente, R. and R. Wettstein. 1980. Ultrastructural characterization of the sex chromosomes during spermatogenesis of spiders having holocentric chromosomes and a long diffuse stage. *Chromosoma* (Berl) 77:69–81.

Benazzi, M. and G. Benazzi Lenatati. 1976. Platyhelminthes. In: *Animal Cytogenetics*, Vol. 1 (B. John ed.). Gebrüder Borntraeger, Berlin-Stuttgart. 182 pp.

Bernstein, C. and H. Bernstein. 1991. *Aging, Sex and DNA Repair*. Academic Press, Inc., NY. 382 pp.

Bertolani, R. 1975. Citology and systematics in Tardigrada. *Mem. Ist. Ital. Idrobiol.*, 32 (Suppl.):17–35.

Birky, C. W. and J. J. Gilbert. 1971. Parthenogenesis in rotifers; the control of sexual and asexual reproduction. *Am. Zool.* 11:245–266.

Blackwelder, R. F. 1944. Checklist of the coleopterous insects of Mexico, Central America, The West Indies, and South America. *U.S. Nat. Mus. Bull.* 185 (pt. 2):189–341.

Brown, S. W. 1977. Adaptive status and genetic regulation in major evolutionary changes of coccid chromosome systems. *Nucleus* 20: 145–157.

Brown, S. W. and C. Cleveland. 1968. Meiosis in the male of *Puto albicans* (Coccoidea-Homoptera). *Chromosoma* (Berl) 24:210–232.

Brown, S. W. and G. DeLotto. 1959. Cytology and sex ratios of an African species of armored scale insect (Coccoidea-Diaspididae). *Am. Nat.* 93:369–379.

Brown, S. W. and W. A. Nelson-Rees. 1961. Radiation analysis of a lecanoid genetic system. *Genetics* 46:983–1007.

Brown, S. W. and U. Nur. 1964. Heterochromatic chromosomes in the coccids. *Science* 145:130–136.

Brown, W. V. 1972. *Textbook of Cytogenetics*. C. V. Mosby, St. Louis. 346 pp.

Brusca, R. C. and G. J. Brusca. 1990. *Invertebrates*. Sinauer, Sunderland, MA. 922 pp.

Bull, J. J. 1983. *Evolution of Sex Determining Mechanisms*. Benjamin/Cummings Publ., London. 316 pp.

Chandra, H. S. 1962. Inverse meiosis in triploid females of the mealy bug, *Planoccus citri*. *Genetics* 47:1441–1454.

Chapman, R. F. 1969. *The Insects. Structure and Function*. Elsevier, NY. 919 pp.

Christiansen, B. 1980. Annelida. In: *Animal Cytogenetics*, Vol. 2 (B. John ed.). Gebrüder Borntraeger, Berlin-Stuttgart. 81 pp.

Cooper, K. W. 1939. The nuclear cytology of the grass mite, *Pediculopsis graminum* (Reut.), with special reference to karyomerokinesis. *Chromosoma* (Berl) 1:51–103.

Cooper, R. 1972. Experimental demonstration of holokinetic chromosomes, and of differential "radiosensitivity" during oogenesis in the grass mite, *Siteroptes graminum* (Reuter). *J. Exp. Zool.* 182:69–94.

Crow, J. F. 1992. An advantage of sexual reproduction in a rapidly changing environment. *J. Hered.* 83:169–173.

Crozier, R. H. 1975. Hymenoptera. In: *Animal Cytogenetics*, Vol. 3: Insecta 7 (B. John ed.). Gebrüder Borntraeger, Berlin-Stuttgart. 95 pp.

Cuellar, O. 1987. The evolution of parthenogenesis: a historical perspective. In: *Meiosis* (P. B. Moens, ed.). Academic Press, NY.

Darlington, C. D. 1939. *The Evolution of Genetic Systems*, 1st Ed. Cambridge Univ. Press, Cambridge. 149 pp.

Dawkins, R. 1976. *The Selfish Gene*. Oxford Univ. Press, NY. 352 pp.

de Lillo, E. 1991. Preliminary observations of ovoviviparity in the gall-forming mite, *Aceria caulobius* (Nal.) (Eriophyoidea: Eriophyidae). In: *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall Ltd., London. Pp. 223–229.

Desch, C. R., Jr. 1984. The reproductive anatomy of *Demodex folliculorum* (Simon). In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood, Chichester. Pp. 464–469.

Elbadry, E. A. and M. S. F. Tawkik. 1966. Life cycle of the mite *Adactylidium* sp.

(Acarina: Pyemotidae), a predator of thrips eggs in the United Arab Republic. *Ann. Entomol. Soc. Am.* 59:458–461.

Evans, H. J. and V. Pond. 1964. The influence of the centromere on chromosome fragment frequency under chronic irradiation. *Port. Acta Biol.* (Ser. A) 8:125–146.

Feiertag-Koppen, C. C. M. and L. P. Pijnacker. 1985. Oogenesis. In: *Spider Mites, Their Biology, Natural Enemies and Control. World Crop Pests*, Vol. 1A (W. Helle and M. Sabelis eds). Elsevier, NY. Pp. 117–127.

Flechtmann, C. H. W. and C. A. H. Flechtmann. 1984. Reproduction and chromosomes in the Broad Mite, *Polyphagotarsonemus latus* (Banks, 1904) (Acari, Prostigmata, Tarsonemidae). In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood Ltd., Chichester. Pp. 455–456.

Friis, E. M., W. G. Chaloner and P. R. Crane. 1987. *The Origins of Angiosperms and their Biological Consequences*. Cambridge Univ. Press, Cambridge.

Fujikawa, T. 1987. Biology of *Oribatula sakamorii* Aoki, a dominant species of the oribatid fauna in nature farming field. In: *Soil Fauna and Soil Fertility. Proc. 9th Int. Congr. Soil. Zool.* (B. R. Strigatova ed.). "Nauka," Moscow. Pp. 544–552.

Futuyma, D. J. 1986. *Evolutionary Biology*, 2nd ed. Sinauer, Sunderland, MA. 600 pp.

Gao, Y-M., and Y. Natsukari. 1990. Karyological studies on seven cephalopods. *Venus* 49:126–145.

Ghiselin, M. T. 1974. *The Economy of Nature and the Evolution of Sex*. Univ. Calif. Press, Berkeley. 346 pp.

Godward, M. B. E. 1954. The "diffuse" centromere or polycentric chromosomes in *Spirogyra*. *Ann. Bot. N.S.* 18:143–156.

Godward, M. B. E. 1961. Meiosis in *Spirogyra crassa*. *Heredity* 16:53–62.

Goroshchenko, Y. L. 1962. Karyological evidence for the systematic subdivision of the ticks belonging to the genus *Argas* Latr. (Ixodoidea, Argasidae), "*reflexus*" group. *Zool. Zh.* 41:358–363.

Grell, K. G. and A. Ruthman. 1964. Über die Karyologie des Radiolars *Aulacantha scolymantha* und die Feinstruktur seiner Chromosomen. *Chromosoma* (Berl) 15:185–211.

Griffing, B. 1982. A theory of natural selection incorporating interaction among individuals. X. Use of groups consisting of a mating pair together with haploid and diploid caste members. *J. Theor. Biol.* 95:199–223.

Halkka, O. 1956. Studies on mitotic and meiotic cell division in certain Hemiptera under normal and experimental conditions. *Ann. Acad. Sci. Fenn.* (Ser. A IV) 32:1–80.

Halkka, O. 1959. Chromosome studies on the Hemiptera, Homoptera, Auchenorrhyncha. *Ann. Acad. Sci. Fenn.* (Ser. A IV) 43:1–72.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.

Hammer, M. 1965. Are low temperatures a species-preserving factor? Illustrated by the oribatid mite *Mucronothrus nasalis* (Willm.). *Acta Univ. Lund.* (Sect. II) *Med. Math. Sci. Rerum Nat.* 2:1–10.

Heath, B. 1980. Variant mitoses in lower eukaryotes: indicators of the evolution of mitosis? *Int. Rev. Cytol.* 64:1–80.

Heinemann, R. L. and R. D. Hughes. 1969. The cytological basis for reproductive variability in the Anoetidae (Sarcoptiformes: Acari). *Chromosoma* (Berl) 28:346–56.

Heinemann, R. L. and R. D. Hughes. 1970. Reproduction, reproductive organs, and meiosis in the bisexual nonparthenogenetic mite *Caloglyphus mycophagus*, with reference to oocyte degeneration in virgins (Sarcoptiformes: Acaridae). *J. Morphol.* 130:93–102.

Helenius, O. 1952. The mode of bivalent orientation in Hemiptera. *Hereditas* 38:420–434.

Helle, W. 1985. Genetics. In: *Spider Mites, Their Biology, Natural Enemies and Control. World Crop Pests*, Vol. 1A (W. Helle and M. W. Sabelis eds.). Elsevier, NY. Pp. 185–192.

Helle, W., H. R. Bolland and W. R. B. Heitmans. 1980. Chromosomes and types of parthenogenesis in the false spider mites (Acari: Tenuipalpidae). *Genetica* 54:45–50.

Helle, W., H. R. Bolland and W. R. B. Heitmans. 1981. A survey of chromosome complements in the Tetranychidae. *Int. J. Acarol.* 7:147–155.

Helle, W., H. R. Bolland, S. H. M. Jeurissen and G. A. van Seventer. 1984. Chromosome data on the Actinedida, Tarsonemida and Oribatida. In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood, Chichester. Pp. 449–454.

Helle, W., H. R. Bolland, R. van Arendonk, R. De Boer, G. G. M. Schulten and V. M. Russell. 1978. Genetic evidence for biparental males in haplo-diploid predator mites (Acarina: Phytoseiidae). *Genetica* 49:165–171.

Hill, R. 1948. Parthenogenesis bei *Nagara modesta* Dolff (Isopodae). *Chromosoma* (Berl) 3:232–256.

Holmquist, G. and B. M. Dancis. 1980. A general model of karyotype evolution. *Genetica* 52/53:151–163.

Hughes-Schrader, S. 1947. Reversion of XO to XY sex chromosome mechanisms in a phasmid. *Chromosoma* 3:52–65.

Hughes-Schrader, S. 1948. Cytology of coccids (Coccoidea-Homoptera). *Adv. Genet.* 2:127–203.

Hughes-Schrader, S. 1955. The chromosomes of the giant scale *Aspidoproctus maximus* Louns. (Coccoidea-Margarodidae) with special reference to asynapsis and sperm formation. *Chromosoma* 7:420–438.

Hughes-Schrader, S. 1963. Hermaphroditism in an African coccid, with notes on other margarodids (Coccoidea-Homoptera). *J. Morphol.* 113:173–184.

Hughes-Schrader, S. 1980. Segregational mechanisms of sex chromosomes in Megaloptera (Neuropterida). *Chromosoma* 81:307–314.

Hughes-Schrader, S. and H. Ris. 1941. The diffuse spindle attachment of coccids, verified by the mitotic behavior of induced chromosome fragments. *J. Exp. Zool.* 87:429–456.

Hughes-Schrader, S. and F. Schrader. 1961. The kinetochore of the Hemiptera. *Chromosoma* (Berl) 12:327–350.

Husband, R. W. 1972. A new genus and species of mite (Acarina: Podapolipidae) associated with the coccinellid *Cycloneda sanguinea*. *Ann. Entomol. Soc. Am.* 63:1152–1162.

Huxley, J. S. 1942. *Evolution: The Modern Synthesis*. Harper and Brothers, London. 645 pp.

Jermy, A. C., K. Jones and C. Colden. 1967. Cytomorphological variation in *Selaginella*. *J. Linn. Soc.* (Bot.) 60:147.

John, B. 1983. The role of chromosome change in the evolution of orthopteroid insects. In: Chromosomes in Evolution of Eukaryotic Groups, Vol. I (A. K. Sharma and A. Sharma eds.). CRC Press, Boca Raton. Pp. 1–110.

John, B. 1990. *Meiosis*. Cambridge Univ. Press, Cambridge. 396 pp.

John, B. and K. R. Lewis. 1958. Studies on *Periplaneta americana* III. Selection for heterozygosity. *J. Hered.* 112:181–197.

John, B. and K. R. Lewis. 1965. The meiotic system. *Protoplasmatologia* 6:1–335.

Jones, G. H. 1987. Chiasmata. In: *Meiosis* (P. B. Moens ed.). Academic Press, NY. Pp. 213–244.

Jones, K. 1978. Aspects of chromosome evolution in higher plants. *Adv. Bot Res.* 6:119–193.

Jones, K. 1985. Bkm sequences and their conservation. In: *The Origin and Evolution of Sex* (H. O. Halvorson and A. Monroy eds.). Alan R. Liss, Inc., NY. Pp. 213–244.

Kethley, J. 1970. A revision of the family Syringophilidae (Prostigmata: Acarina). *Contrib. Am. Entomol. Inst.* (Ann Arbor) 5:1–76.

Kethley, J. 1971. Population regulation in quill mites (Acarina: Syringophilidae). *Ecology* 52:1113–1118.

Kethley, J. B. and D. E. Johnston. 1973. A numerical phenetic study of the quill mites of the family Syringophilidae (Acari). *J. Parasitol.* 59:520–530.

Keyl, H.-G. 1957. Zur Karyologie der Hydrachnellen (Acarina). *Chromosoma* (Berl) 8:719–729.

Khoshoo, T. N. 1990. The selected works of T. N. Khoshoo on Cytogenetics in Relation to Plant Evolution and Improvement. *Counc. Sci. Industr. Res.*, New Delhi. 728 pp.

Khoshoo, T. N. and M. R. Ahuja. 1963. The chromosomes and relationships of *Welwitschia mirabilis*. *Chromosoma* 14:522–533.

Kiauta, B. 1969. Some remarks on the evolution of the centromere, based upon the distribution of centromere types in insects. *Genen Phaenen* 13:1–6.

Kiauta, B. and A. W. M. Mol. 1977. Behaviour of the spermatocyte chromosomes of the mayfly, *Cloeon dipterum* (Linnaeus, 1761) *s.l.* (Ephemeroptera: Baetidae), with a note on the cytology of the order. *Genen Phaenen* 19:31–39.

King, G. C. 1953. "Diffuse" centromeres, and other cytological observations on two desmids. *Nature* 171:181.

Krivolutsky, D. A. and A. Ya. Druk. 1986. Fossil oribatid mites. *Annu. Rev. Entomol.* 31:533–545.

Kubai, D. F. 1975. Evolution of the mitotic spindle. *Int. Rev. Cytol.* 43:167–227.

LaChance, L. E., M. Degrugillier and A. P. Leverich. 1970. Cytogenetics of inherited partial sterility in three generations of the large milkweed bug as related to holokinetic chromosomes. *Chromosoma* (Berl) 29:20–41.

Lamb, R. Y. and R. B. Willey. 1987. Cytological mechanisms of thelytokous parthenogenesis in insects. *Genome* 29:367–369.

Lewis, K. R. and B. John. 1972. *The Matter of Mendelian Heredity*, 2nd ed. Longman Group Ltd., London. 273 pp.

Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. *Q. Rev. Biol.* 59:257–290.

Manning, J. T. 1976. Is sex maintained to facilitate or minimize mutational advance? *Heredity* 36:351–357.

Marchant, C. J. 1967. Evolution in *Spartina* (Gramineae). II. Chromosomes, basic relationships and problem of S. x. townsendii agg. *J. Linn. Soc.* (Bot.) 60:381–409.

Margulis, L., J. O. Corliss, M. Melkonian and D. J. Chapman. 1990. *Handbook of Protoctista*. Jones and Bartlett, Boston. 914 pp.

Mather, K. 1953. The genetical structure of populations. In: *Symposia of the Society for Experimental Biology*, Number VII. Cambridge Univ. Press, Cambridge. Pp. 66–95.

Matuszewski, B. 1961. Oogenesis in *Mikiola fagi* Hart. (Cecidomyiidae; Diptera). *Chromosoma* (Berl) 12:741–811.

Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge Univ. Press, Cambridge. 222 pp.

Maynard Smith, J. 1986. Contemplating life without sex. *Nature* 324:300–301.

Michod, R. E. and B. R. Levin, eds. 1988. *The Evolution of Sex*. Sinauer, Sunderland, MA. 342 pp.

Morton, J. K. 1967. The Commelinaceae of West Africa: a biosystematic survey. *J. Linn. Soc.* (Bot.). 60:167–221.

Moss, W. W., J. H. Oliver, Jr. and B. C. Nelson. 1968. Karyotypes and developmental stages of *Harpyrhynchus novoplumaris* sp. n. (Acari: Cheyletoidea: Harpyrhynchidae), a parasite of North American birds. *J. Parasitol.* 54:377–392.

Murdy, W. H. and H. L. Carson. 1959. Parthenogenesis in *Drosophila managabeirai* Malog. *Am. Nat.* 93:355–363.

Nath, V. 1965. *Animal Gametes (Male)*. Asia Publ. House, NY. 162 pp.

Nelson-Rees, W. A., M. A. Hoy and R. T. Rousch. 1980. Heterochromatinization, chromatin elimination and haploidization in the parahaploid mite *Metaseiulus occidentalis* (Nesbitt) (Acarina: Phytoseiidae). *Chromosoma* (Berl) 77:263–276.

Nieuwkoop, P. D. and L. A. Sutasurya. 1981. *Primordial Germ Cells in the Invertebrates, From Epigenesis to Preformation*. Cambridge Univ. Press., Cambridge. 258 pp.

Nokkala, S. and C. Nokkala. 1984. Achiasmate mate meiosis in the heteropteran genus *Nabis* (Nabidae, Hemiptera). *Hereditas* 99:131–134.

Nordenskiöld, H. 1962. Studies of meiosis in *Luzula pupurea*. *Hereditas* 48:503–19.

Norton, R. A., J. B. Kethley, D. E. Johnston and B. M. OConnor. 1993. Phylogenetic perspectives on genetic systems and reproductive modes of mites. In: *Evolution and Diversity of Sex Ratio in Insects and Mites* (D. L. Wrensch and M. A. Ebbert eds.). Chapman and Hall, NY. Pp. 8–99.

Norton, R. A. and S. C. Palmer. 1991. The distribution, mechanisms, and evolutionary significance of parthenogenesis in oribatid mites. In: *The Acari: Reproduction, Development and Life-history Strategies* (R. Schuster and P. W. Murphy eds.). Chapman and Hall Ltd., London. Pp. 107–136.

Nunez, O. 1962. Cytology of Collembola. *Nature* 194:946–947.

Nur, U. 1971. Parthenogenesis in coccids (Homoptera). *Am. Zool.* 11:301–308.

Nuzzaci, G. and M. Solinas. 1984. An investigation into sperm formation, transfer, storage, and utilization in Eriophyid mites. In: *Acarology VI*, Vol. 1 (D. A. Griffiths and C. E. Bowman eds.). Ellis Horwood, Chichester. Pp. 491–503.

Oliver, J. H., Jr. 1964. Comments on karyotypes and sex determination in the Acari. *Acarologia* 6:288–293.

Oliver, J. H., Jr. 1965. Karyotypes and sex determination in some dermanyssid mites (Acarina: Mesostigmata). *Ann. Entomol. Soc. Am.* 58:567–573.

Oliver, J. H., Jr. 1967. Cytogenetics of Acarines. In: *Genetics of Insect Vectors of Disease* (S. W. Wright and R. Pal eds.). Elsevier, Amsterdam. Pp. 417–439.

Oliver, J. H., Jr. 1977. Cytogenetics of mites and ticks. *Annu. Rev. Entomol.* 22:407–429.

Oliver, J. H., Jr. and K. C. Bremner. 1968. Cytogenetics of ticks. 3. Chromosomes and sex determination in some Australian hard ticks. *Ann. Entomol. Soc. Am.* 61:837–844.

Oliver, J. H., Jr. and B. C. Nelson. 1967. Mite chromosomes: an exceptionally small number. *Nature* 214:809.

Oliver, J. H., Jr., K. Tanaka and M. Sawada. 1973. Cytogenetics of ticks (Acari: Isodoidea) 12. Chromosome and hybridization studies of bisexual and parthenogenetic *Haemaphysalis longicornis* races from Japan and Korea. *Chromosoma* (Berl) 42:209–288.

Oppermann, E. 1935. Die Entstehung der Riesenspermien von *Argas columbarum* (Shaw) (*reflexus* F.). *Z. Mikrosk.-Anat. Forsch.* (Leipz.) 37:538–560.

Palmer, S. C. and R. A. Norton. 1990. Further experimental proof of thelytokous parthenogenesis in oribatid mites (Acari: Oribatida: Desmonomata). *Exp. Appl. Acarol.* 8:149–159.

Palmer, S. C. and R. A. Norton. 1991. Taxonomic, geographic, and seasonal distribution of thelytokous parthenogenesis in Desmonomata (Acari: Oribatida). *Exp. Appl. Acarol.* 12:67–81.

Palmer, S. C. and R. A. Norton. 1992. Genetic diversity in thelytokous oribatid mites (Acari: Acariformes: Desmonomata). *Biochem. Ecol. Syst.* 20:219–231.

Pätau, K. 1936. Cytologische Untersuchungen an der haploid-parthenogenetischen Milbe *Pediculoides ventricosus* Newpt. *Zool. Jahrb., Abt. Anat. u. Ontog.* (Berl) 56:277–322.

Peterson, S. P. and M. W. Berns. 1980. The centriolar complex. *Int. Rev. Cytol.* 64:81–105.

Phillips, D. M. 1970. Insect sperm: their structure and morphogenesis. *J. Cell Biol.* 44:243–77.

Pijnacker, L. P. 1985. Spermatogenesis. In: *Spider Mites, Their Biology, Natural Enemies and Control. World Crop Pests*, Volume 1A (W. Helle and M. Sabelis eds). Elsevier, NY. Pp. 109–115.

Pijnacker, L. P., M. A. Ferwerda and W. Helle. 1981. Cytological investigations on the female and male reproductive system of the parthenogenetic privet mite, *Brevipalpus obovatus* (Donnadieu) (Phytoptipalpidae, Acari). *Acarologia* 22:157–163.

Piza, S. de T. 1958. Some interesting aspects of male meiosis in an elaterid beetle. *Caryologia* 11:72–78.

Rack, G. and G. C. Eickwort. 1979. Biology and description of a new pygmephorid mite (Acarina: Tarsonemida) associated with the soil-nesting bee *Agapostemon nasutus* (Hymenoptera: Halictidae). *Acarologia* 21:267–278.

Regev, S. 1974. Cytological and radioassay evidence of haploid parthenogenesis in *Cheyletus malaccensis*. *Genetica* 45:125–132.

Resende, F. 1953. Consequiências cito-genéticas do "kinetochoro difuso". *Bol. Soc. Port. Cienc. Nat.* 4:252–264.

Reuter, E. 1909. Merokinesis, ein neuer Kernteilungsmodus. *Acta Soc. Sci. Fenn.* 37:1–56.

Rhoades, M. M. 1961. Meiosis. In: *The Cell. Biochemistry, Physiology, Morphology, Vol. III, Meiosis and Mitosis* (J. Brachet and A. E. Mirsky eds.). Academic Press, NY. Pp. 1–75.

Rieder, C. L. and R. Nowogrodzki. 1983. Intranuclear membranes and the formation of the first meiotic spindle in *Xenos peckii* (*Acroshismus wheeleri*) oocytes. *J. Cell. Biol.* 97:1144–1155.

Ris, H. 1942. A cytological and experimental analysis of the meiotic behavior of the univalent X chromosome in the bearberry aphid *Tamalia* (= *Phyllaphis*) *coweni* (Ckll.). *J. Exp. Zool.* 90:267–330.

Sabelis, M. W. and C. J. Nagelkerke. 1987. Sex allocation strategies of pseudoarrhenotokous phytoseiid mites. *Neth. J. Zool.* 37:117–136.

Sabelis, M. W. and K. Nagelkerke. 1993. Sex allocation and pseudoarrhenotoky in phytoseiid mites. In: *Evolution and Diversity of Sex Ratio in Insects and Mites* (D. L. Wrensch and M. A. Ebbert eds.). Chapman and Hall, NY. Pp. 512–541.

Sarma, Y. S. R. K. 1983. Algal karyology and evolutionary trends. In: *Chromosomes in Evolution of Eukaryotic Groups*, Vol 1 (A. K. Sharma and A. Sharma eds.). CRC Press, Boca Raton. Pp. 177–223.

Scholl, H. 1955. Ein Beitrag zur Kenntnis der Spermatogenese der Mallophagen. *Chromosoma* (Berl) 7:271–274.

Schrader, F. 1923. Haploidie bei einer Spinnmilbe. *Arch. Mikrosk. Anat.* 79:610–622.

Schrader, F. 1935. Notes on the mitotic behavior of long chromosomes. *Cytologia* 6:422–430.

Schrader, F. 1936. The kinetochore or spindle fibre in *Amphiuma tridactylum*. *Biol. Gull.* 70:484–498.

Schrader, F. 1940. The formation of tetrads and the meiotic mitoses in the male *Rhytiodolomia senilis* Say (Hemiptera, Heteroptera). *J. Morphol.* 67:123–142.

Schrader, F. 1953. *Mitosis*, 2nd Ed. Columbia Univ. Press, NY. 170 pp.

Seiler, J. 1948. Die Zytologie eines parthenogenetischen Rüsselkafers, *Otiorrhynchus sulcatus* F. *Chromosoma* (Berl) 3:88–109.

Shanahan, C. 1989. Cytogenetics of Australian scorpions. I. Interchange polymorphism in the family Buthidae. *Genome* 32:882–889.

Sharma, A. K. and A. Sharma. 1984. Trends of chromosome evolution in the plant kingdom. In: *Chromosomes in Evolution of Eukaryotic Groups*, Vol II (A. K. Sharma and A. Sharma eds.). CRC Press, Boca Raton. Pp. 227–239.

Shields, W. M. 1982. *Philopatry, Inbreeding, and the Evolution of Sex*. State Univ. NY Press, Albany. 245 pp.

Smith, A. W. 1990. Population Dynamics and Chemical Ecology of the Honey Bee Tracheal Mite, *Acarapis woodi* (Acari: Tarsonemidae), in Ohio. Ph.D. dissertation, The Ohio State Univ. 130 pp.

Smith, S. G. and N. Virkki. 1978. *Animal Cytogenetics, Vol. 3: Insecta 5. Coleoptera* (B. John ed.). Gebrüder Borntraeger, Berlin-Stuttgart. Pp. 366.

Sokolov, I. I. 1934. Untersuchungen uber die Spermatogenese bei den Arachniden. V. Uber die Spermatogenese der Parasitidae. *Z. Zellforsch.* 21:42–109.

Sokolov, I. I. 1945. Karyological study of some Acari and the problem of sex determination in the group. *Izv. Akad. Nauk*, USSR 6:645–663. (In Russian).

Sokolov, I. I. 1954. The chromosome complex of mites and its importance for systematics and phylogeny. *Tr. O. Estestvoispyt. (Leningrad)* 72:124–159. (In Russian).

Sokolov, I. I. 1958. Cytological studies of the development of the male germ cells in *Ornithodoros papillipes* Bir. (Acari, Ixodoidea). *Rev. Entomol.* USSR 37:260–281.

Stebbins, G. L. 1971. *Chromosomal Evolution in Higher Plants*. Addison-Wesley Publ., Reading, MA. 216 pp.

Stefani, R. and G. Cadeddu. 1967. L'attivita centromerica in *Artemia salina*. *Leach. Rend. Sem. Fac. Sci. Univ. Cagliari* 37:287–291.

Stern, H. and Y. Hotta. 1987. The biochemistry of meiosis. In: *Meiosis* (P. B. Moens ed.). Academic Press, NY. Pp. 303–333.

Suomalainen, E. 1950. Parthenogenesis in animals. *Adv. Genet.* 3:193–253.

Suomalainen, E. 1953. The kinetochore and the bivalent structure in the Lepidoptera. *Hereditas* 39:88–96.

Suomalainen, E. 1966. Achiasmatische Oogenese bei Trichopteran. *Chromosoma* (Berl) 18:201–207.

Suomalainen, E. and O. Halkka. 1963. The mode of meiosis in the Psyllina. *Chromosoma* (Berl) 14:498–510.

Suomalainen, E., A. Saura and J. Lokki. 1987. *Cytology and Evolution in Parthenogenesis*. CRC Press, Boca Raton.

Swan, D. C. 1934. The hay itch mite, *Pediculoides ventricosus* (Newport) (Acarina, Pediculoididae) in South Australia. *J. Agric. (S. Aust.)* 37:1289–1299.

Swanson, C. 1957. *Cytology and Cytogenetics*. Prentice-Hall, Englewood Cliffs, NJ. 596 pp.

Sybenga, J. 1975. *Meiotic Configurations, A Source of Information for Estimating Genetic Parameters. Monographs on Theoretical and Applied Genetics* 1. Springer-Verlag, Berlin. 251 pp.

Sybenga, J. 1981. Specialization in the behaviour of chromosomes on the meiotic spindle. *Genetica* 57:143–151.

Syren, R. M. and P. Luykx. 1977. Permanent segmental interchange complex in the termite *Incisitermes schwarzi*. *Nature* 266:167–168.

Taberly, G. 1958. La cytologie de la parthénogenèse chez *Platynothrus peltifer* (Koch) (Acarien, Oribate). *C. R. Ac. Sc.* 147:1655–1657.

Taberly, G. 1987. Recherches sur la parthénogenèse thélytoque de deux espèces d'acariens oribates: *Trhypochthonius tectorum* (Berlese) et *Platynothrus peltifer* (Koch). III. Etude anatomique, histologique et cytologique des femelles parthénogénétiques. *Acarologia* 28:389–403.

Takenouchi, Y., T. Shiitsu and S. Toshioka. 1970. A chromosome study on two parthenogenetic ticks, *Haemaphysalis bispinosa* Newmann and *H. longicornis* Newmann (Acarina: Ixodidae). *J. Hokkaido Univ. Ed.* (Sec. II B) 20:45–50.

Templaar, M. J. 1979a. Aberrations of holokinetic chromosomes and associated lethality after *X*-irradiation of meiotic stages in *Tetranychus urticae* Koch (Acari, Tetranychidae). *Mutat. Res.* 61:259–274.

Templaar, M. J. 1979b. Fate of fragments and properties of translocations of holokinetic chromosomes after *X*-irradiation of mature sperm of *Tetranychus urticae* Koch (Acari, Tetranychidae). *Mutat. Res.* 63:301–316.

Templaar, M. J. 1980. Radiobiological and structural studies on the chromosomes of the spider mite *Tetranychus urticae Koch*. Thesis, Univ. of Groningen (cited in Helle et al. 1984).

Templaar, M. J. 1985. Fine structure and related properties of the chromosomes. In: *Spider Mites, Their Biology, Natural Enemies and Control. World Crop Pests*, Vol. 1A (W. Helle and M.W. Sabelis eds.). Elsevier, Amsterdam. Pp. 141–148.

Templaar, M. J. and L. J. Drenth-Diephuis. 1984. The nucleolar cycle in karyomeres of *Tetranychus urticae* Koch (Acari, Tetranychidae) in relation to replication of fragments of holokinetic chromosomes. *Protoplasma* 123:78–82.

Templeton, A. R. 1982. The prophecies of parthenogenesis. In: *Evolution and Genetics of Life Histories* (H. Dingle and J. P. Hegmann eds.). Springer-Verlag, NY. Pp. 75–101.

Thoday, J. M. 1953. Components of fitness. In: *Symposia of the Society for Experimental Biology*, VII. Cambridge Univ. Press, Cambridge. Pp. 96–113.

Treat, A. E. 1965. Sex-distinctive chromatin and the frequency of males in the moth ear mite. *J. NY Entomol. Soc.* 73:12–18.

Triantaphyllou, A. C. 1984. Chromosomes in evolution of nematodes. In: *Chromosomes in Evolution of Eukaryotic Groups*, Vol II (A. K. Sharma and A. Sharma eds.). CRC Press, Boca Raton. Pp. 77–101.

Tsurusaki, N. 1986. Parthenogenesis and geographic variation of sex ratio in two species of *Leiobunum* (Arachnida, Opiliones). *Zool. Sci.* 3:517–532.

Tsurusaki, N. and J. C. Cokendolpher. 1990. Chromosomes of sixteen species of harvestmen (Arachnida, Opiliones, Caddidae and Phalangiidae). *J. Arachnol.* 18:151–166.

Tuzet, O. 1964. L'origine de la lignée germinale et la gamétogenèse chez les Spongiaires. In: *L'Origine de la Lignée Germinale chez les Vertébrés et chez Quelquels Groups d'Invertébrés* (E. Wolff ed.). Hermann, Paris. Pp. 79–111.

Ueshima, N. 1963. Chromosome behavior of the *Cimex pilosellus* complex (Cimicidae: Hemiptera). *Chromosoma* 14:511–521.

Ueshima, N. 1979. Hemiptera II: Heteroptera. In: *Animal Cytogenetics, Vol. 3: Insecta 6* (B. John ed.). Gebrüder Borntraeger, Berlin-Stuttgart. 117 pp.

Uyenoyama, M. 1987. Genetic transmission and the evolution of reproduction: the significance of parent-offspring relatedness to the "cost of meiosis." *Evolution* 38:87–102.

Vaarama, A. 1954. Cytological observations of *Pleurozium schreberi*, with special reference to centromere evolution. *Ann. Bot. Soc. Zool. Bot. Fenn. 'Vanamo'* 28:1–59.

Walker, T. G. 1984. Chromosomes and evolution in Pteridophytes. In: *Chromosomes in Evolution of Eukaryotic Groups*, Vol II (A. K. Sharma and A. Sharma eds.). CRC Press, Boca Raton. Pp. 103–141.

Warren, E. 1940. On the genital system of *Dermanyssus gallinae* and several other Gamasidae. *Ann. Natal. Mus.* 9:409–459.

White, M. J. D. 1973. *Animal Cytology and Evolution*, 3rd ed. Cambridge Univ. Press, Cambridge. 961 pp.

White, M. 1976. Blattodea, Mantodea, Isoptera, Grylloblattodea, Phasmatodea, Dermaptera and Embioptera. In: *Animal Cytogenetics*, Vol. 3: Insecta 2 (B. John ed.). Gebrüder Borntraeger, Berlin-Stuttgart. 75 pp.

Whiting, P. W. 1945. The evolution of male haploidy. *Q. Rev. Biol.* 20:231–260.

Wijsman, H. J. and M. Wijsman-Best. 1973. A note on the chromosomes of some madreporian corals from the Mediterranean (Cnidaria, Anthozoa, Scleractinia: Dentrophylliidae, Caryophillidae, Faviidae). *Genen Phaeen* 16:61–64.

Williams, G. C. 1975. *Sex and Evolution*. Princeton Univ. Press, Princeton. 200 pp.

Wilson, E. B. 1928. *Cell in Development and Heredity*, 3rd edition. MacMillan, NY. 1232 pp.

Wrensch, D. L. 1993. Evolutionary flexibility through haploid males, or how chance favors the prepared genome. In: *Evolution and Diversity of Sex Ratio in Insects and Mites* (D. L. Wrensch and M. A. Ebbert eds.). Chapman and Hall, NY. Pp. 118–149.

Wrensch, D. L. and M. A. Ebbert, eds. 1993. *Evolution and Diversity of Sex Ratio in Insects and Mites*. Chapman and Hall, NY. 630 pp.

Wysoki, M. and E. Swirski. 1968. Karyotypes and sex determination of ten species of phytoseiid mites (Acarina: Mesostigmata). *Genetics* 39:220–228.

Young, S. S. Y., D. L. Wrensch and M. Kongchuensin. 1986. Control of sex ratio by female spider mites. *Entomol. Exp. Appl.* 40:53–60.

Index*

* *Page numbers printed in* **boldface** *type refer to tables or figures*