The Acari

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Reproduction, development and life-history strategies

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Preface

During the Inaugural Meeting of the European Association of Acarologists (EURAAC), held in Amsterdam in 1987, it was decided that the holding of a Symposium at regular intervals should be a major objective. With this in view, it was agreed that Professor Reinhart Schuster, the senior editor, be invited to accept the Presidency of the Association and, arising from that Office, to organize the first Symposium in Austria in 1988. There was strong support for a main theme focused on a particular aspect of acarology. From these discussions there emerged the proposal that emphasis be placed on aspects of reproduction, development and life-history strategies of the Acari. These were topics in the forefront of the discipline with exciting developments of interest not only to acarologists but to a wider audience because of the light they cast on fundamental processes in physiology, ecology and evolutionary biology.

The object then was to invite a small number of key workers to present extended papers related to the main theme. There were seven of these all of which appear in the book. The remaining 51 contributions were offered papers a number of which fit within the framework of the Symposium theme.

The Symposium was held at the Karl-Kranzens-Universität in Graz from 9th to 12th August, 1988. Thanks to the generosity of the Rector of the University, excellent facilities were provided at no cost to the organizers. Thanks are also due to the Government of Styria, the Municipal Council of the city of Graz and the scientific instrument manufacturers, Leitz and Olympus, for their very generous financial support. More than 100 acarologists from 15 European countries together with specialists from the USA and Israel attended the Symposium. The staff, technicians and students of the Zoological Institute of the University and, in particular, the Department of Morphology and Ecology, ensured an efficient organization and a well-run meeting. Indeed, participants had nothing but praise for the way in which their needs were catered for. A reception at the invitation of the Governor of the province of Styria – amid the baroque splendour of Schloss Eggenberg,

provided an hospitable and welcome break for participants as did the party at the Town Hall by invitation of the Mayor of Graz. One day was devoted to an excursion through the Styrian countryside, and taking in part of the alpine region of this beautiful province.

The location of a publisher for the Symposium papers was a major headache for the organizers. However, shortly before the commencement of the meeting, Ellis Horwood Ltd. of Chichester offered to publish the book. Some ten months later, the editors were informed that the Publisher was discontinuing publication of their entomological titles. We were informed that they were being taken over by Chapman & Hall of London. The change in Publisher inevitably set back the timetable for publication. There were further complications due to 'house style' differences of the two Publishers, and many of our later difficulties stemmed from this source. Chapman & Hall were very supportive in our predicament; in particular we wish to place on record our appreciation of the scrupulous way they abided by the terms of our original agreement with Ellis Horwood.

Help and assistance in the preparation of the text has come from many quarters. First, our thanks are due in no small measure to the Officers and Executive Committee Members of EURAAC under whose auspices the Symposium was held. Second, we acknowledge with gratitude the co-operation we have received from the 88 authors who contributed to the book. With the short time available for the preparation of the Symposium, it was not possible to provide detailed guidance to contributors before the meeting. In addition, the requirement that the material be published in English has meant considerable work for authors and editors. We are most grateful for the unstinting support we have received.

Space does not permit us to list the many other individuals who have helped in various ways. Nevertheless, the junior editor would ask the reader's indulgence to allow one exception to enable him to acknowledge the assistance provided by his daughter, Jennifer Watters, who helped with typing and index preparation. To all these willing collaborators may we offer our heartfelt thanks.

The last word must rest with the reader. These are exciting times. New techniques and innovative research have resulted in remarkable discoveries with considerable biological, ecological and phylogenetic significance. To mention but two, there is, on the one hand, the intriguing discovery that a pseudo-arrhenotokous mother can determine quite precisely the gender of her offspring. Then there are the elaborate rituals in sperm transfer ranging from complete separation of the sexes to varying degrees of association up to and including intimate contact, and finally the direct transfer of sperm. There are bewildering variations

on this theme often with elaborate behavioural traits. Let us hope that the reader will be stimulated by these and many other equally fascinating insights into the life processes of the Acari provided within the pages of this book.

Reinhart Schuster
Paul W. Murphy

Glossary
Symbols and abbreviations

a	area
ANOVA	analysis of variance
b	breadth
bar	10^5 pascal or 10^6 dyne cm^{-2}
°C	degree centigrade
c	about
cal	calorie
cf.	compare
C_{HL}	haemolymph osmolality
cm, cm^2, cm^3	centimetre, square centimetre, cubic centimetre
cv.	cultivar
d	day
d	diameter
decitonne (dt)	100 kilograms
d.f.	degrees of freedom
et al.	and others
F (test)	the ratio of two independent estimates of the same variance, on which a significance test may be based
g	gram
h	hour
h	height
ha	hectare
k	an estimate of the *K* parameter of the negative binomial distribution
kg	kilogram
kJ	kilojoule

km	kilometre
l	litre
l	length
LD	refers to lengths of light and darkness; thus an LD 16 : 8 regime = 16 hours light and 8 hours darkness
m, m^2, m^3	metre, square metre, cubic metre
mg	milligram
min	minute
ml	millilitre
mm	millimetre
mosm/kg	milliosmol per kilogram
ng	nanogram (10^{-9} g)
nm	nanometre (10^{-9} m)
n.s.	not significant
n. sp.	new species
P	probability
pl	picolitre (10^{-12} l)
r.h.	relative humidity
s.d.	standard deviation
s.e.	standard error
sec	second
SEM	scanning electron microscopy or micrograph
s. lat.	*sensu lato*; in the wide sense
sp.	species (singular)
sp. nov.	new species
spp.	species (plural)
s. str.	*sensu stricto*; in the narrow sense
subsp.	subspecies
t (test)	the ratio of a normal deviate to its estimated standard deviation on which a significance test may be based
TC	thermoperiodic cycle; thus TC 12 : 12 (25° : 15°) is a thermoperiod with a 12-hour thermophase of 25°C and a 12-hour cryophase of 15°C
TEM	transmission electron microscopy or micrograph
V	volume
var.	variety
wt	weight

X	magnification, for example × 1 000 = 1 000 times magnification
*u*g	microgram (10^{-6} g)
*u*l	microlitre (10^{-6} l)
*u*m	micrometre or micron (10^{-6} m)
Σ	sum of
/	solidus; denotes divided by
$\simeq$	approximately equal to
$>$	greater than
$<$	less than
$\geqslant$	equal to or greater than
$\leqslant$	equal to or less than

· PART ONE ·

Life-history Strategies

1

*The life strategies of mites**

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This study tries to discern life strategies developed by mites. The concept of adaptive strategy is defined, and the methodology followed is justified. Six species, considered as models of mites living in contrasting habitats, are compared: *Steganacarus magnus* (Nic.) (Oribatida), *Adoristes ovatus* (Koch) (Oribatida), *Nothrus palustris* Koch (Oribatida), *Dermatophagoides pteronyssinus* (Trt) (Acaridada), *Tetranychus urticae* Koch (Actinedida) and *Hypodectes propus* (Nitzsch) (Acaridida). For each population–environment system, the degree of selectivity of the habitat is estimated in relation to its constraints and perturbations. The main state variables of the mite populations are described (especially density and spatial structure), as well as ontogenetic and demographic features (phenology of immature development and life history). Finally, dispersal and certain behavioural traits are taken into account, in order to complete the study. Comparisons between these models clearly reveal gradients ranging from the saprophagous Oribatida to the parasitic Acaridida. The significance of these gradients is discussed in connection with the environmental characteristics of the mite populations chosen

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* Invited paper.

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INTRODUCTION

Definitions

'Strategy' is the 'art of conducting a group of dispositions, or actions, in order to reach a defined objective'. In terms of population dynamics, the significance and implications of this general concept must be justified within an ecological framework. First, considering a group of dispositions leads one to accept the existence of interactive processes so that no particular disposition may be expressed independently of the others. This, necessarily, finds expression in compromises or, what is better, in a maximization of fitness proceeding from 'solutions' which seem to be imperfect if considered separately but prove logical and well adapted when evaluated using a synthetic approach.

Second, it is clearly apparent that it is, essentially, the population-environment that conditions the vital strategy of a species. Limiting the environment to the habitat constitutes an error which, in fact, has been regularly pointed out in the literature. Let us recall, in this context, the controversy concerning r and K strategies (Cody, 1966; Pianka, 1972; Grime, 1977, 1979, among others). The r profiles would be at an advantage in erratic, that is, unpredictable habitats, in contrast to K profiles which would be advantageous in stable and periodic, that is, predictable biotopes. This conception involved numerous contradictory examples, which became understandable when 'habitat' was extended to 'environment' and, in particular, when genetic structure and variation or predation were taken into account in the systems (Stearns, 1980; Barbault, 1981, among others).

Several authors have demonstrated (cf. Blondel, 1986) that the concept of adaptive strategy is biologically more realistic than the too restrictive notion of demographic strategy. Thus, a causal approach is needed, the aim of which is to relate life-history traits to environmental characteristics. The population-environment concept consequently forms the basis for studies on vital strategies.

This leads us to specify the context of this study. The lack of complete and adequate experimental data has forced us to simplify our approach. Basing our study on the assumption that the environment has conditioned the best-adapted population profiles, we have tried to characterize these profiles. Thus, the habitat has been described, the food supply estimated, competition and predation evaluated, and the demographic and dispersal properties of the species, as revealed in particular conditions, have been studied. The question to be solved can be stated in the following terms: which are the 'risks' encountered by the population in a defined environment, and which are the resources the species can exploit in order to minimize the effects of these risks?

Methodology

Mites live in a remarkable diversity of habitats ranging from within the oceans to mountains, from deserts to ice-fields. In these situations, they usually develop large populations, which is evidence of their fitness to exploit disparate environments. The soil, which is particularly well colonized by mites, represents our starting point. Then, considering several environments in which abiotic conditions induce a decreasing stability, and thus an increasing risk for the maintenance of mite populations, we delineate the following five models:

1. the oribatids, *Steganacarus magnus* (Nicolet) and *Adoristes ovatus* (Koch), and the hemi-edaphic milieu;
2. the oribatid, *Nothrus palustris* Koch, and the edaphic milieu;
3. the acaridid, *Dermatophagoides pteronyssinus* (Trouessart), and the house-dust milieu;
4. the actinedid, *Tetranychus urticae* Koch, and the plant-host milieu;
5. the acaridid, *Hypodectes propus* (Nitzsch), an endoparasitic mite of wood pigeons.

For each of these systems, the degree of selectivity of the habitat has been estimated. Besides characterizing the constraints and perturbations of the biotope, an analysis of the main state variables of the mite populations, especially density and spatial distribution, formed the second step of our study. The objective is not only to estimate these parameters in terms of mean values, but also to estimate their spatial and temporal variations. The ontogenetic and demographic properties of the species, as expressed in their milieu, are then evaluated. Here, the study is concerned with the phenology of immature development, mite survival, age at sexual maturity, reproductive duration and age-specific fecundity, which are the determining parameters of the species' potential for increase and the age structure of their populations. The incidence of the sex ratio has also been estimated. Then, the aptitude of the species for dispersal is considered, particularly in relation to its mechanisms and efficiency. Our analysis concludes with a brief consideration of several behavioural traits such as territoriality, protection of progeny and social structure.

Lorsque les traits d'histoire naturelle d'une population ou, mieux, de plusieurs populations à comparer sont ainsi définis et mesurés et que les caractères et contraintes de l'environnement sont connus et reliés aux premiers, on dispose des ingrédients nécessaires à la définition des stratégies réalisées par ces populations dans ces milieux particuliers (Blondel, 1986).

POPULATION-ENVIRONMENT SYSTEMS

Environment

Habitat and microclimatic environment The oribatids, *A. ovatus* (cf. Gourbiere *et al.*, 1985) and *S. magnus* (cf. Webb, 1977), are two endosaprophagous mites. The juvenile stages live within particular substrata such as coniferous needles (*A. ovatus*), and dead wood (*S. magnus*). These two species are thus bound to dense undergrowth. *Nothrus palustris* (cf. Lebrun, 1970a) is an oribatid mite which colonizes holorganic layers of forests with scattered undergrowth, or even terrain lacking tree cover such as humid grasslands or peat moors. However, this species is the most abundant one in transition woodland, for example, ash plantations, or in replanted forests on alluvial soils, for example, poplar plantations. The *Nothrus*, at all stases, inhabit, in particular, mossy areas underlying fragments of disappearing leaf litter.

Dermatophagoides pteronyssinus is confined to the domestic house-dust environment, particularly to the micro-ecosystems formed by mattresses, carpets and plush toys; these are generally considered to be a substitute for its original habitat, which was probably the nests of birds and small mammals ('natural reservoirs' *sensu* Fain, 1965; Wharton, 1976). The two-spotted spider mite (*T. urticae*) is a well known plant-sucking member of the Actinedida, which colonizes numerous host plants. Lastly, *H. propus* is considered in this study as an example of a vertebrate endoparasite. The great host specificity of these mites, the high intraspecific competition they encounter, and the host defence mechanisms they have to face, are so important that these mites are undoubtedly subjected to severe constraints.

The microclimatic conditions and the seasonal variability of the environment result in highly contrasting situations; these are characterized in Table 1.1. Thus, the two-spotted spider mite lives in rather unfavourable conditions as it has to face wind, precipitation, sun radiation, thermic and hygrometric variations and morphological and physiological modifications of the host plant, etc. However, the relative security of subparasites such as *D. pteronyssinus* or of parasites *sensu stricto*, such as *H. propus*, appears to be conditioned by the spatial and temporal limitations of their habitat. Moreover, the tolerances of these species are rather low compared with the edaphic oribatid mite examples. In this connection, it is worth recalling the high dependence of *T. urticae* on thermic variations (Mori, 1961), of *D. pteronyssinus* on relative humidity or the presence of fungi (van Bronswijk and Sinha, 1973; van de Lustgraaf, 1978a,b; de Saint Georges-Gridelet, 1981, 1987a), and of parasites on the microclimate.

Table 1.1 Characterization of environment of the six mite species, and estimate of level of 'risk' for each species

Species	*Constraint*				*'Risk' level of environment*
	Seasonal variability of environment	*Microclimatic variability*	*Spatial and temporal persistence of habitat and food*	*Predation*	
Adoristes ovatus (Koch) *Steganacarus magnus* (Nic.)	+	+	+ + + + + continuous predictable	+	+
Nothrus palustris Koch	+ +	+ +	+ + + + continuous predictable	+ +	+ +
Dermatophagoides pteronyssinus (Trt)	+ + +	+ to + + +	+ + + discontinuous unpredictable	+ + + ?	+ + +
Tetranychus urticae Koch	+ + +	+ + + +	+ + + discontinuous unpredictable	+ + + + +	+ + + +
Hypodectes propus (Nitzsch)	+ + + +	+	+ to + + + + + discontinuous unpredictable	?	+ + + + +

Food supply and predation As they live in forest litter, the endosaprophagous mites, *A. ovatus* and *S. magnus*, and the saprophagous *N. palustris* profit from a continuous and unlimited food supply. Besides, all saprophage–saprophyte ecosystems have a rich diversity of fungi and bacteria, and these may constitute complementary food sources for edaphic mites. The domestic-dust habitat of *D. pteronyssinus* provides an adequate food supply composed of human and animal squamae. However, food supply is a limiting factor because of its discontinuity. Besides, the dust mite is entirely dependent upon certain fungi (*Aspergillus*), which form an essential component of its diet (de Saint Georges-Gridelet, 1984, 1987b). *Tetranychus urticae* have been recorded on more than 200 host plants (Bovey, 1972) but this apparently unlimited food supply is bound to seasonal cycles. Thus, food appears to be discontinuous, in time as well as space. Finally, *H. propus* encounters no particular alimentary problem, that is, during the endoparasitic part of its life cycle.

As far as predation is concerned, field observations of *A. ovatus* (Gourbiere *et al.*, 1985) reveal a juvenile mortality rate of nearly 20%. This rate can reach nearly 85% for immatures of *N. palustris* (Lebrun, unpublished). Predation is probably a key factor in the population dynamics of *D. pteronyssinus*. Gridelet and Lebrun (1973) showed that there is a simultaneous spatial and temporal co-occurrence, in domestic floor dust, between the abundance of the dust mite and its predator (*Cheyletus* sp.). However, van de Lustgraaf (1978b) and van Bronswijk (1981) pointed out that this co-occurrence could not be confirmed on mattresses. More than 70 predators of *T. urticae* have been reported (Boudreaux, 1963; Putman and Herne, 1966; McMurtry *et al.*, 1970; Rambier and van de Vrie, 1974; Jeppson *et al.*, 1975; McMurtry, 1984). It is clearly apparent that the impact of predation must be considerable as population densities of the two-spotted spider mite under natural conditions, that is, excluding agro-ecosystems, are rather low compared with densities observed in laboratory conditions. Unfortunately, nothing is known about predation of *H. propus*, at least during its endoparasitic life.

State variables of mite populations

Density A summary of the density ranges of the five mite species is given in Table 1.2. The population density of *S. magnus* (adults) in several typical habitats of western Europe ranges from 3800 to 9600 individuals/m^2 (Lebrun, 1965, 1971; Gerard, 1970a,b). Densities of *A. ovatus* (adults) fluctuate between 6800 and 20 000 individuals/m^2

Table 1.2 Maximum and minimum mean densities of six mite species on an annual basis, and season when peak density occurs

Species	*Mean density levels (individuals/m^2 unless otherwise stated)*	*Ratio*	*Phenology*	*Source*
Steganacarus magnus (adults)	3800–9600	1 : 2.5	2 weak seasonal peaks	Lebrun (1965, 1971) Gerard (1970a,b)
Adoristes ovatus (adults)	6800–20 000	1 : 3	1 autumnal peak	Hebrant (1962) de Backer (1963) de Coster (1965)
Nothrus palustris (adults)	1500	~1 : 1	no seasonal peak	
Nothrus palustris (all stages)	4200–17 000	1 : 4	1 aestival maximum sinusoidal pattern	Lebrun (1969, 1984)
Dermatophagoides pteronyssinus (all stages in ground dust)	500–7500 individuals/g	1 : 15	1 aestival peak	Gridelet and Lebrun (1973) de Saint Georges–Gridelet (1981, unpublished)
Hypodectes propus (all stages)	12–42 000 individuals/host	1 : 5000	density related to reproductive cycle of pigeon	André (unpublished data)

Hebrant, 1962; de Backer, 1963; de Coster, 1965). This seasonal oscillation is small when compared with other arthropod populations. The population density of *N. palustris* (all stages) has been studied for three consecutive years by Lebrun (1969, 1984); its course follows a typical sinusoidal pattern. The seasonal range in density is also low (1:4). This sinusoidal evolution is, for the most part, due to the larval density which strictly follows the seasonal thermic changes, unlike the adult stase, which remains numerically stable. Gridelet and Lebrun (1973) and de Saint Georges-Gridelet (1981, unpublished data) found important density variations in *D. pteronyssinus* in the same habitat; in floor dust, for instance, the seasonal range may have a ratio of 1:15. The territory of a young female of *T. urticae* may be no more than a few square millimetres in which its progeny will develop until the adult stage. Density should thus correspond to the fecundity of the female divided by the colonized area. This, in fact, is not the case because of the spatial heterogeneity of the microhabitat due to the silken web spun by the mite (Davis, 1952; McMurtry and Johnson, 1966). Besides, *T. urticae* colonizes its first host plants in spring, and its populations may grow rapidly but, in a second phase, competition – especially with aphids – and predation reduces the density, and may even lead to the extinction of the mite population. This phenomenon can be easily observed, for instance, on nettles (van Impe, unpublished data). Thus, in natural conditions and for a given host plant, there are no real seasonal oscillations of densities in populations of *T. urticae*. Lastly, it is well known that the variability of densities in parasite populations may be considerable. In the case of *H. propus*, André (unpublished data) recorded from 12–42 000 mites per pigeon.

It thus appears from this synthesis that under natural conditions the variability in density levels increases from the edaphic to the parasitic mites, with intermediate levels for the dust mite and the two-spotted spider mite. It is worth noting that this gradient is related to the increasing importance of the volume relationships of the habitat.

The density ranges for each species, reported in Table 1.2, refer to a particular habitat, in order to present comparable situations. The type of habitat or microhabitat is a further major source of variation. For instance, the type of litter clearly influences population densities of saprophagous Oribatida (Wallwork, 1970). As for *D. pteronyssinus*, population densities are usually 10–50 times higher in carpets or plush toys than in floor dust; carpets and plush toys thus represent the main mite reservoir (de Saint Georges-Gridelet, 1981, unpublished data). The density fluctuations become particularly spectacular in the case of populations of *T. urticae* in cultivated host plants. Here, population density may become so high that the plants may succumb to the pest in the absence of control measures.

Table 1.3 Degree of aggregation, expressed as *k* value, of six mite species representing edaphic, phytophagous, dust-inhabiting and animal-parasitic species

Species	*Stage*	k *value*	*Source*
Steganacarus magnus	Adult	4.12	Gerard (1970a,b)
Adoristes ovatus	Adult	2.59	Data from Hebrant (1962)
Nothrus palustris	Adult	2.28	Data from Lebrun (1968, 1984)
	Larva	1.37	
Dermatophagoides pteronyssinus		0.52	Data from Gridelet and Lebrun (1973)
Tetranychus urticae		$\rightarrow 0$	Raworth (1986)
Hypodectes propus	All stages	$\rightarrow 0$ (0.097)	Data from André (unpublished)

Spatial patterns of mite populations Mites are often aggregated, but populations may differ considerably in the degree of their aggregation. Using an index of aggregation defined by Gerard (1970a,b), Cancela da Fonseca (1965) and Berthet and Gerard (1965), namely, the k parameter of the negative binomial distribution (Fisher, 1941; Bliss and Fisher, 1953), we compared our six 'models' (Table 1.3). It is important to remember that k may vary from zero to infinity with low values corresponding to high degrees of aggregation. From Table 1.3 it is apparent that, within the limits of our study, the degrees of aggregation would correspond to risk levels as previously defined. Besides, it is worth noting that clumps of mites are so dense in populations of *T. urticae* that the negative binomial model is, in fact, no longer appropriate (Raworth, 1986). This should be true, *a fortiori*, for *H. propus*.

Adaptative features

Ontogenesis Table 1.4 summarizes the mean developmental durations for all the species except *H. propus* for which data are not available. Clearly, there is a decrease in the length of the development period from the oribatid species to the actinedid mite. Development of the three oribatid species encompasses the six stases of ontogeny typical of the Acari, but in *D. pteronyssinus* and *T. urticae*, immature development is somewhat 'shortened' as one active stase is lacking. Females of *S. magnus* lay prelarvae on the surface of the organic substratum. The females of *A. ovatus* lay eggs near the petioles of dead coniferous needles. In both cases, the larvae actively penetrate into the organic fragments. Prelarvae of *Nothrus palustris* are laid without the selection of particular locations but they develop immediately into larvae. Females of *D. pteronyssinus* lay their eggs directly in the house dust, and those of *T. urticae* on the leaves of the host plant, especially along the leaf veins or on the silken threads of the web.

The ontogenesis in each of the endosaprophagous mites is characterized by a pause affecting a varying proportion of individuals. Gourbiere *et al.* (1985) observed that 46% of the individuals of *A. ovatus* completed development in one year, that 30% of tritonymphs remained in the litter needles for a second year, and that the remaining 24% could even prolong their development to a third year. In the same way, if the average for the 'normal' developmental duration is 392 days for *S. magnus* (Table 1.4), some deutonymphs may remain in their galleries for more than one year (Webb, 1977). Stress conditions, such as low temperatures or overcrowding, may prolong the immature development of *D. pteronyssinus* (Wharton, 1976; de Saint Georges-Gridelet, 1981).

Table 1.4 Mean durations in days for development from egg or prelarva deposition to adult emergence including developmental pauses (in parentheses) for five species of Acari

Species	*Temperature (°C)*	*Stase*							*Source*
		Egg	*Prelarva*	*Larva*	*Protonymph*	*Deutonymph*	*Tritonymph*	*Total duration*	
Adoristes ovatus	—							~365 (~650)	Gourbiere *et al.* (1985)
Steganacarus magnus	20		77	40	50	110	115	392 (~600)	Webb (1977)
Northrus palustris	21		<1	49	57	70	86	262	Lebrun (1970b)
Dermatophagoides pteronyssinus	25	6.7		6.3	4.4		5.3	22.7	Spieksma (1967) de Saint Georges–Gridelet (1981)
Tetranychus urticae	24	3.6		2.0	2.0	2.0		9.6	van Impe (1985 and unpublished)

This prolongation is due to a pause induced in the pre-ecdysial stages of nymphs, especially the protonymph. In *T. urticae*, a diapause *sensu stricto* occurs involving adult overwintering females.

Thus, most of these species are able to avoid abiotic constraints by means of a temporary arrest of their ontogenesis. However, the strategies adopted differ considerably. In the case of the two oribatid species, which have a long immature duration of development, some individuals remain as dormant stages, independently of the others, which follow the normal course of development. This appears as a kind of 'guarantee' for the future of the population against possible hazards. As for *D. pteronyssinus*, it is only in the presence of stress that ontogenesis may be suspended, and in this case all the immatures in the population are affected. Finally, a pause occurs cyclically in *T. urticae*, but only every 15–25 generations. Besides, the only survivors in winter are diapausing females, which are already fecund.

Life history Figure 1.1 is a schematic representation of the life history of a species (cf. Lewontin, 1965). The study may be completed by life tables, which permit a characterization of the structure and rate of increase of populations. The aim of such studies is to evaluate the 'biotic

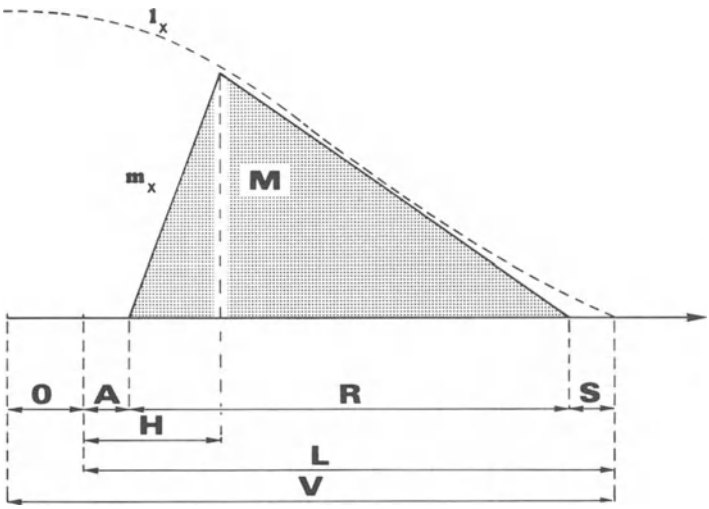

Fig. 1.1 Schematic representation of life history of a mite species (after Lewontin, 1965). A, pre-reproductive period; H, age at maximum egg or prelarra production; L, adult lifespan; l_x, age-specific survival; M, fecundity; m_x, age-specific fecundity; O, ontogenesis; R, reproductive period; S, senescent period; V, total lifespan.

Table 1.5 Duration or age in days of life-history attributes and fecundity of four species of Acari (egg, w; prelarva, PL)

Species	*Total lifespan* (V)	*Ontogenesis* (O)	*Adult longevity* (L)	*Prereproductive period* (A)	*Reproductive period* (R)	*Senescent period* (S)	*Age when 'egg' production at a maximum* (H)	*Fecundity* (M) *progeny/female*	M/R	*Age when 90% of offspring produced*	*Source*
Steganacarus magnus	932	392	540	180	353	7	no max.	6.9 PL	0.02		Webb (1977) Webb (personal communication)
Nothrus palustris	518	262	256	33	200	22	40	16 PL	0.08	100	Lebrun (unpublished)
Dermatophagoides pteronyssinus	92.7	22.7	70	2.5	45	22.5	18	100 w	2.22	37	de Saint Georges–Gridelet (1981) Ho and Nadchatram (1984)
Tetranychus urticae	24.5	9.6	14.9	1.1	8.7	5.1	5	72.5 w	8.33	13	van Impe (unpublished)

potential' *sensu* Chapman (1928, 1931) of a species as expressed by its populations in defined conditions.

Table 1.5 illustrates the main life-history traits of the four species, *S. magnus*, *M. palustris*, *D. pteronyssinus* and *T. urticae*; only fragmentary data are available for *A. ovatus* and *H. propus*. Here again, the listed data, which are mean values, indicate a very clear gradient. The longevity, duration of immature development and adult lifespan, the lengths of the pre-reproductive and reproductive periods, the age when reproduction is at a maximum, and the age at which 90% of the progeny are produced, have values which decrease from the endosaprophagous Oribatida to the phytophagous Actinedida. On the other hand, fecundities and rates of reproduction show a gradient in the reverse order.

Our study of demographic parameters had, unfortunately, to be restricted to two mites, detailed data being lacking for the other species. Table 1.6 summarizes these attributes for *N. palustris* and *T. urticae*, after the observations of Lebrun (unpublished) and van Impe (unpublished), respectively. The units of time correspond to 'days' for *T. urticae* and to '10 days' for *N. palustris*.

The intrinsic rate of natural increase (Table 1.6) r_m, equals 0.083 for the oribatid and 0.265 for the actinedid mite. This reveals greatly differing potentialities, which may be expressed in another way by noting that, under optimal conditions, the population would double in number every 3 months (83.5 days) for *N. palustris*, and in less than 3 days for *Tetranychus urticae* (Table 1.6). Besides, there is a contrast in the two species in their development components as eggs are totally absent in *Nothrus* populations, but represent nearly 70% of the individuals in *Tetranychus* populations. Yet, where there is stable exponential increase, adults form nearly the same proportion in each population.

In fact, this contrast results from their respective life-history traits (Table 1.5). The pre-reproductive period (A) is 33 days for *N. palustris* and 1.1 day for *T. urticae*, a duration corresponding to 13% of the adult lifetime (A/L; Fig. 1.1) for the oribatid, but only 7% of that period for the two-spotted spider mite. On the other hand, *T. urticae* reaches maximum fecundity after 5 days (H), an age which corresponds to 34% of the adult lifetime (H/L). Maximum fecundity for the oribatid mite occurs much later (H = 40 days) but at that age a mere 16% of its adult lifespan has elapsed. In addition, the mean fecundity (M) is very much higher for *Tetranychus* (72.5 eggs/female) than for *Nothrus* (16 prelarvae/female), and this difference is accentuated when rates of egg and prelarva production are compared. Thus, during the phase of demographic increase, the spider mite produces 8.33 eggs/female while the equivalent rate for the oribatid mite is 0.08 prelarvae. A further contrasting feature is that *T. urticae* females have produced 90% of their offspring when 87% of the

Table 1.6 Estimates of life-table parameters for *Nothrus palustris* (after Lebrun, unpublished) and *Tetranychus urticae* (after van Impe, unpublished)

Parameter	*Nothrus palustris*	*Tetranychus urticae*
Intrinsic rate of natural increase (r_m)*	0.083	0.265
Finite rate of increase (λ)*	1.09	1.30
Net reproduction rate (R_o)*	14.6	43.0
Mean generation time (T) (days)	323	14.2
Doubling time (t_2) (days)	83.5	2.6
Stable age distribution (%)		
Eggs	—	68.6
Immatures	92.3	25.8
Adults	7.7	5.6

*Time units for r_m, λ and R_o are 10 days for *N. palustris* and 1 day for *T. urticae*.

adult lifespan has elapsed compared to the production of the same proportion over about two-fifths of the adult duration in the case of *N. palustris*.

The two examples illustrate the two opposing demographic tendencies (Stearns, 1977). On the one hand, *N. palustris* has a long lifespan and a relatively low fecundity resulting in a comparatively low rate of population increase. The objective of such a strategy is to maintain the population in its habitat. *Tetranychus urticae*, on the other hand, has a rather short adult duration together with a precocious and high fecundity, resulting in a large capacity for population increase. The aim here is to compensate for adverse environmental effects by means of an explosive demography.

Sex ratio Nothing is known about the sex ratio of *A. ovatus*. As for the other species, it appears that females predominate but for different reasons. *Nothrus* is thelytokous, and thus a single-sex species reproducing parthenogenetically. With *S. magnus* females represent 60% of the population (Webb and Elmes, 1979). Females of *Dermatophagoides* live twice as long as males. Moreover, the latter are less tolerant to abiotic constraints such as unfavourable humidity conditions (Arlian, 1975), and biotic stress such as overcrowding (de Saint Georges-Gridelet, 1981). In *T. urticae*, which is an arrhenotokous mite, the sex ratio of the offspring is age-specific, namely, the proportion of daughters is max-

imum with young reproducing females, that is precisely when the female makes the maximum contribution to population increase (van Impe, 1985). The ratio in favour of females is further accentuated due to the shorter longevity of males.

Dispersal Little is known about the dispersal capacities of edaphic oribatids such as *S. magnus*, *A. ovatus* and *N. palustris*. It seems that these slow-moving mites have no particular predisposition to disperse. However, their wide distribution (from northern Europe to the Mediterranean, and central Europe), always occurring in the same habitats, clearly indicates that dispersal mechanisms do exist. Phoresy could play an important role, despite the apparent lack of morphological adaptations such as, for instance, the anal pedicel of some Uropodina (cf. Athias-Binche, 1984). It is worth noting that Norton (1980) has reported the occurrence of phoretic dispersal in oribatid mites (Mesoplophoroidea). The morphology of *T. urticae* and *D. pteronyssinus* favours aerial dispersal ('aerial plankton'). This is particularly important for organisms which are capable of high population increase and which, consequently, may easily overcrowd their habitat. The silken web of the two-spotted spider mite seems to be a good adaptation for this purpose (Kennedy and Smitley, 1985). In addition, this mite has a wide range of plant hosts which guarantees the efficiency of its dispersal. Lastly, although dispersal of parasites obviously depends on the complexity of the life cycle, it would appear that contacts between hosts greatly facilitate dispersal of the parasitizing population. Thus, during his study on wood pigeons collected in various locations in Belgium, André (unpublished) found no bird free from *H. propus*.

DISCUSSION

Although this analysis has been intentionally limited to a few types of mites, it is possible to discern some trends in vital strategies in the Acari. An initial conclusion is the relatively sober life-history profile of the edaphic species, which may be related to the high stability of the milieu they inhabit. This leads to some 'fixity' of the population–environment system of the three species.

It seems well established (Ghilarov, 1958; Vannier, 1973) that the conquest of terrestrial habitats by arthropods required a progressive adaptation to the interstitial milieu and, in particular, to the edaphic milieu. In this context, long developmental times, annual or even longer, low but regularly distributed fecundities, stable population densities, high survival and subsequent populations at their carrying capacity, accord with low seasonal variability and the 'predictability' of

the environment. In this connection, it is worth recording that the potential fecundity of *N. palustris* as revealed in the laboratory (16 prelarvae/female) is close to the fecundity observed under natural conditions (nine prelarvae/female), and is sufficient for the renewal of the population (Lebrun, unpublished). On the other hand, thelytokous reproduction surely increases the fitness of *N. palustris*. Palmer and Norton (1988) conclude that parthenogenesis strengthens the stability of well-adapted genotypes in predictable environments. Lastly, the extended lifespan, occurring in only a proportion of the population, accentuates stability in *A. ovatus* and *S. magnus*, in terms of their adaptation to temporary climatic disturbances.

As far as predation is concerned, *S. magnus*, *A. ovatus* and *N. palustris* clearly show adaptive features which tend to limit its impact. Indeed, laying eggs (*Adoristes*) or prelarvae (*Steganacarus*) close to future larval shelters (that is, needles or dead wood) or producing prelarvae which immediately develop into larvae (*Nothrus*), helps to reduce the potential effects of predation. This strengthens the trend in reproductive economy, minimizing mortality of the immobile immature stages, and fits in with the microclimatic stability of the environment.

The buffered and predictably cyclic character of the edaphic milieu undoubtedly favours *K* demographic profiles. A striking example is shown by *Ceratozetes kananaskis*, studied by Mitchell (1977). This oribatid mite lives in Canadian coniferous forests where the climate has a much more regular seasonal rhythm than in western Europe. Its developmental duration lasts nearly 770 days, and the adult may live for 4 years. This mite has an iteroparous mode of reproduction, with a net reproductive rate (R_o) of 1.076, which reveals a remarkable population stability.

We think, therefore, that it should not be concluded that all edaphic Oribatida are *K* strategists. Indeed, it would not be surprising to find, among the numerous microphytophagous species living in the superficial soil layers, mites with demographic features as shown, for instance, by *T. urticae*. In this connection, it should be remembered that *r* strategies have been reported in species such as *Hydrozetes lemnae* and *Halozetes intermedius* (Fernandez and Athias-Binche, 1986; Travé, 1986), which have colonized dulcicolous and sublittoral halophile habitats.

In complete contrast are the adaptive strategies of mites which have broken free from the edaphic milieu. Thus, *D. pteronyssinus* and *T. urticae* are species that show typical colonizing and 'opportunistic' features (*r* profiles). These strategies focus on a precocious mass reproduction, the only aim being to bring forward the next generation. They respond to environmental constraints by having high potentialities for demographic increase; a high wastage is conceded. If the benefit/investment ratio becomes insufficient, particular mechanisms are invoked. For

D. pteronyssinus, the eventual quiescence of eggs and nymphs is a major feature in their strategy to maintain the population in its habitat during unfavourable periods. As for *T. urticae*, its polyphagy, the efficiency of its dispersal, and its ability to enter diapause, constitute adaptative mechanisms permitting it to escape environmental constraints.

Finally, when compared with *D. pteronyssinus* and *T. urticae*, parasites such as *H. propus* reveal demographic traits that are expressed still more intensively. Their strategy corresponds to a considerable investment in a progeny which is subject to high mortality. Moreover, their usual high host specificity has led to spectacular adaptive features such as ontogenetic complications, and the perception of signals to enable them to synchronize with the reproductive cycle of the host. An example of such a signal is the secretion of prolactin by the pigeon as a result of which the reproductive phase of the parasite occurs at the most favourable time for dispersal.

To conclude, we think that new studies on population dynamics in mites should be promoted in order to understand their adaptive strategies. Indeed, these extraordinarily diversified arthropods (500 000 species according to Krantz, 1978) undoubtedly develop a wide range of unknown evolutive strategies. In this context, mites, certainly, are valuable allies on the way to elucidation of the prodigious mysteries of evolution.

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*Life-history evolution of spider mites**

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A literature review of data on life histories of spider mites (Acari: Tetranychidae) under standardized conditions (25 ± 2°C) reveals a large amount of interspecific variation. The intrinsic rate of population increase (r_m) varies from *c.* 0.1/day to 0.3/day. This variation may well be caused by (phylo) genetic factors, host-plant related factors and/or (co-)evolutionary interactions with other organisms (competitors, predators, pathogens). All these may act as constraints to evolutionary change of one or more life-history components. One way to reveal their importance is to assume that constraints are absent, and to test hypotheses on how life-history components evolve under *r* selection. Analysis of available data shows that life-history components (excluding sex ratio among offspring) strongly covary; an increase in r_m arises from a combination of faster development, higher rate of oviposition and higher fecundity. It is when fecundity and oviposition rate enter the range of high values that progress in development rate becomes slower and slower, suggesting that there may be a constraint to speeding up development. Why sex ratio among offspring does not bear a relation to any of the other life-history components, is an open question. In an attempt to provide an explanation, a new hypothesis is discussed stating (1) that spacing and aggregating within a web are two alternative ways of decreasing predation risk; and (2) that these strategies have different consequences for the population mating structure, and hence also for sex-ratio evolution

* Invited paper.

INTRODUCTION

Among the mites that inhabit plants, the Tetranychidae or spider mites stand out as being relatively well studied with respect to life history and capacity for population increase. The impetus to study their life history in such detail comes from their economic importance as pests in agricultural crops (Helle and Sabelis, 1985a,b). Tetranychid mites are phytophagous and may become a pest not so much because of their per capita feeding rate but rather because of their high rate of population increase; the time required to double their population size may be as short as one or two days for some of these pest species. Hence, much effort has been devoted to quantifying life-history components that together determine the capacity for population increase, leading to a wealth of data on life histories of economically important spider mites. In recent years, however, more and more information on non-pest species has become available, especially due to Japanese workers such as Yutaka Saito and Tetsuo Gotoh, but despite their invaluable contributions, our knowledge is no doubt still biased due to a preponderance of data on economically important species.

Should this unbalanced state of our information deter acarologists from testing predictions emerging from theories of life-history evolution? My answer is a firm no! Whatever bias there may be in the data, it remains a justifiable scientific approach to formulate hypotheses based on models of life-history evolution, and to test these hypotheses by use of the available data. Support by data does not mean that a hypothesis holds true but merely that it is not rejected. It should stimulate thought on more precise hypotheses and more critical tests. This is the main objective of this chapter.

What follows is an analysis of life-history trends in spider mites, including development, fecundity and sex ratio but excluding such aspects as survival, diapause and dependence on abiotic factors. I shall first emphasize that local populations of spider mites are likely to become extinct sooner or later, and then proceed by formulating hypotheses on life-history trends to be expected under r selection, and test these using most, if not all the data published up to mid 1989. As such, this chapter is an update of an earlier review of data published up to mid 1984 (Sabelis, 1985a). Finally, some thoughts will be presented on the consequences of differences in population growth among spider-mite species: how do they distribute their offspring? how does that influence their profitability as prey for various predators as well as their investment in defence against predators? what is the influence of spatial distribution on mating structure and sex ratio?

DYNAMICS OF LOCAL POPULATIONS

To understand the selective forces moulding life-history patterns of spider mites, it is important to realize that the spatial distribution of these mites is patchy, and that local populations are not likely to persist for one or more of the following reasons: (1) the host plant is short-lived; (2) the host plant is overexploited by spider mites and becomes exhausted as a food source; (3) the spider mites are outcompeted by other herbivores or plant pathogens; (4) local populations are decimated or even eliminated by natural enemies (predators, parasitic microorganisms); or (5) harsh weather conditions such as wind or rain. The relative importance of these causative factors may differ markedly depending on the species, the location and the time of year. For example, *Tetranychus lintearius* Dufour is frequently observed to overexploit gorse (*Ulex europaeus* L.) a woody leguminous shrub, which is common on the Atlantic seaboard of Europe (Hill and Stone, 1985). Local populations of this spider mite are, therefore, likely to crash due to the limited amount of food available per host plant. Interspecific competition between phytophagous arthropods is another potential cause of population crashes, but the evidence so far obtained comes from experiments under controlled conditions, rather than from field observations. Foott (1963) reported that the European red mite (*Panonychus ulmi* (Koch)) had difficulty in coping with the webs produced by two-spotted spider mites. This and other factors cause European red mites to be competitively inferior (Tanigoshi *et al.*, 1979). Other causes of population crashes have been reported for *Tetranychus evansi* Baker and Pritchard feeding on wild solanaceous weeds in Brazil and Texas. It seems to suffer little from the predators found and tested so far (de Moraes and McMurtry, 1985a,b, 1986), but rather from entomophtoraceous fungi (Humber *et al.*, 1981) which, at times, cause the spider-mite populations to crash. Perhaps the most widely observed cause of population crashes is predation (Helle and Sabelis, 1985a,b; Sabelis *et al.*, 1988). There is much evidence showing that phytoseiid-mite predators are capable of decimating, if not eliminating, local populations of spider mites. Admittedly, most of these observations stem from experiments under agricultural rather than natural conditions, but there is no indication that local populations in the field are more stable. In addition to factors that may cause population crashes, spider-mite populations may suffer considerably from harsh weather conditions. For example, Yaninek *et al.* (1989a) provide evidence that the Cassava green mite (*Mononychellus tanajoa* (Bondar)) in Africa does not become a pest during the wet season due to mortality from heavy rains.

Unfortunately, there is little published information on the local population dynamics of spider mites that experience less rapid successions of colonization, population growth and extinction. The spider mites living on dwarf bamboo in Japan probably experience less violent local dynamics. *Schizotetranychus celarius* (Banks) may be the best example. Each female of *S. celarius* deposits her eggs underneath a shelter-like web, which is generally thought to be helpful in resisting adverse weather conditions, competing herbivores and predators. However, the predatory mite, *Typhlodromus bambusae* Ehara, is among the few predators that has overcome this barrier. Upon invasion by this predator, female and male spider mites leave their nest web initially but return later to defend their offspring from the larvae of the predator hatching from eggs deposited by the intruder. Male spider mites and to a lesser extent the females are capable of killing the predator larvae, thereby increasing the chances of survival of their offspring as otherwise these would suffer from predation by the predators-to-be (Saito, 1986). Thus, in addition to protection by the presence of webbing, there is also a form of biparental defence which seems to be a rather unique phenomenon among the spider mites. This suggests that spider mites in these separate family nests stand a better chance of escape from predation than spider mites living in multifamily webs. Thus, although predation is not completely avoided and still is an important factor in preventing outbreaks of *S. celarius*, their local populations may be relatively more persistent. Moreover, dwarf bamboo plants are long-lived and locally rather abundant so that once this host plant is found and colonized, the probability of finding food will remain quite high. Hence, one may expect that the sequence of colonization, population growth and population crash of this mite is more gradual than is the case with certain other spider mites.

The above examples of *Tetranychus* spp. on the one hand, and *Schizotetranychus* spp. on the other, are extremes of a continuum. I suspect that the build up of local populations of many *Bryobia* spp. (Mathys, 1957; Cox and Lieberman, 1960) are relatively slow, and that populations of *Eotetranychus* spp. (Micinski *et al.*, 1979; Lung-Shu *et al.*, 1984; Gotoh, 1987c; Kropczyńska *et al.*, 1988), *Panonychus* spp. (Keetch, 1971; Rabbinge, 1976; Herbert, 1981a,b; Gotoh, 1987a,b) and *Oligonychus* spp. (Butler and Abid, 1965; Landwehr and Allen, 1982; Congdon and Logan, 1983; Perring *et al.*, 1984) build up faster but often at a lower rate than do populations of most *Tetranychus* spp. (Sabelis, 1985a; but see Gotoh, 1986, for exception). Populations of the latter species are frequently observed in the increasing phase under agricultural and semi-natural conditions. For example, Carey (1982) found that although it may take quite some time for the age distribution to converge to a stable state (Taylor, 1979), there are several published reports providing evidence

for stable-age distributions of *Tetranychus* spp. in the field (66% eggs, 26% immatures and 8% adults). However, there is a lack of information on local dynamics and age distributions under conditions that are more natural than those studied by Carey (1982). Most likely, the increasing phase will be of shorter duration, and the age distribution will be subject to the influence of preferential feeding by predators, but while it is true that spider mites are often scarce under natural conditions, nevertheless local poulation outbreaks and/or extinctions have been observed. Hence, there is reason to assume that many tetranychid mites have a colonizing life style (*sensu* Lewontin, 1965).

HOW LIFE-HISTORY PATTERNS ARE MOULDED BY SELECTION

If spider mites in local populations face a certain death by staying put and death risks vary in space (and time) then selection will tend to promote the ability to find and colonize new resources. Selection may favour genotypes that are better able to survive close to where the resource was depleted when there are good prospects for new resources to arise nearby, but even under these conditions there may be, in addition, selection for 'altruistic' dispersal (Hamilton and May, 1977; Taylor, 1988). In any case, dispersal will be favoured by selection when better food resources are to be found elsewhere, and reproductive prospects more than compensate for risks of death during dispersal.

To find new host plants, spider mites should cover greater distances than is possible by ambulatory means. Being tiny and wingless, spider mites can only disperse by drifting in air currents or by attaching to a larger organism with better dispersal abilities than themselves. While phoretic transport has been reported only occasionally, and the transporters were not organisms specifically searching for food sources that are also favourable to the spider mites, there is much evidence from field experiments with sticky traps, and laboratory observations on take-off behaviour that aerial dispersal is the prevailing mode of long-distance displacement (Kennedy and Smitley, 1985). Thus, dispersal is passive and displacement is random with respect to the position of the host plants. Hence, colonization chances are likely to be very low, and selection will not only favour genes coding for a better ability to find a host plant after an aerial voyage and to discriminate risky sites from less risky, but it will also favour genes coding for a higher capacity of population increase and thus an increased number of dispersers carrying these genes. Note that the evolutionary trend is also expected to occur when dispersal risks are so high that group selection may promote prudent strategies of resource exploitation. This is because despite an

increasing r_m resource exploitation control is still possible through partial dispersal of offspring providing that resource use preceding dispersal is low, as is the case in spider mites and this control strategy may well be selectively superior to resource exploitation control through lowered resource consumption and, therefore, lower r_m. In other words *r* selection is expected to prevail in patchy environments.

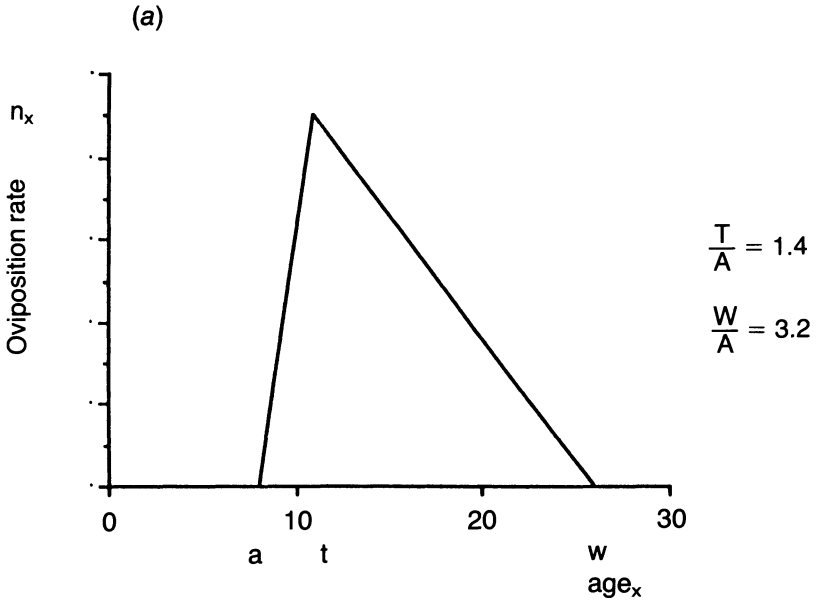
Sabelis (1985a) reviewed the literature on intrinsic rates of increase among the Tetranychidae. To allow intra- and interspecific comparison, a compilation was made of r_m values measured at more or less constant temperature (25 ± 2°C) and, if given a choice, under optimal conditions of humidity and host-plant condition. The results showed that r_m values varied between 0.15 and 0.3 day, and that this range may well be greater given data on the life-history components of other species such as *Tenuipalpoides dorychaeta* Pritchard and Baker (Singer, 1966). Why would the range of r_m values be so large? A reasonable first step to solve this question is to formulate the simplest hypothesis possible. In this paper the hypothesis to be tested is based on the assumption that selection to increase r_m is not considered by physiological possibilities (phylo-) genetic factors or (co-)evolutionary interactions with other organisms (host plant, competitors, pathogens, predators). Under these assumption differences in r_m can only arise from differential rates of natural selection; for a discussion of this term, see Endler (1986) pp. 29–33. Species experiencing frequent local population crashes would be subject to a higher rate of natural selection compared to species whose local populations tend to be more persistent. This may then lead to differences in r_m. Indeed, there are some indications that high r_m values are associated with spider mites feeding on herbs as opposed to spider mites feeding on trees, but a critical test requires much more information on local dynamics of spider mites (Sabelis, 1985a). As these data are lacking, further testing of the above hypothesis is beyond the scope of this paper. Instead the focus is on the underlying assumption that there are no constraints to evolutionary change other than the pace at which beneficial mutations arise in natural populations. The alternative hypothesis is that constraints may arise from various sources, such as constraints resulting from (co-)evolutionary interactions, for example, investment in an arms race with the host plant, with natural enemies and, again, with competitors or resulting from a phylogenetic route in the evolutionary past. The question of biological interest is, therefore, whether there are constraints to increasing the intrinsic rate of increase. Below, an attempt to detect such constraints is made by testing predictions on life-history evolution using models built on the assumption that constraints are absent.

This test is extended by including predictions on how natural selec-

tion would affect each of the life-history components that together determine the value of r_m. Such predictions emerge from the so called Lotka or Euler model. This model helps to elucidate how sensitive r_m is to standardized proportional changes in each of the life-history components. These insights may then be used to predict which of the life-history components is subject to a higher rate of natural selection as a consequence of a larger impact on r_m. In this way, it is possible to predict how life-history components will change relative to each other while promoting progress in r_m. Such a theory has been developed, for example, by Lewontin (1965), Caswell and Hastings (1980), Caswell (1982) and Sibly and Calow (1986) with respect to the relative importance of early reproduction versus reproduction later in life. The rationale stems from the fact that the spread of a particular gene in a population is similar to the increase of capital where compound interest is operating, with the interest being added to the principal at intervals. In a population with overlapping generations, breeding earlier means that the interest is collected more frequently, thus increasing the rate of capital growth and, therefore, r_m also as a measure of fitness. For exactly the same reason, broods when produced later in life, are devalued in terms of their contribution to r_m. In the classic equation of Lotka, this devaluation is expressed as a negative exponential factor ($\exp(-r_m x)$) weighting the contribution of the age-specific net reproductive rate to the summation over all ages but subject to the requirement that the weighted net reproductive rates sum to unity. This may be stated as follows

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

where x = age, A = age at first oviposition, W = age at last oviposition, l_x = probability to survive from age 0 to age x, n_x = oviposition rate of a female of age x and s_x = the proportion of daughters in the offspring of a female of age x. It appears that the reproductive schedule of spider mites can be characterized, and even quite well described by a triangle as given in Fig. 2.1(a) where, between A and W, there is an age T at which the oviposition rate reaches a peak value. Using this model of the reproduction schedule in the Lotka equation (also Lewontin, 1965), it is possible to determine for each life-history component alone, the proportional changes required to obtain a standardized increase in r_m. Components that need relatively little change and, therefore, have a large impact on r_m, are expected to be subject to a higher rate of natural selection. Then, assuming absence of trade offs underlying life-history components as well as the absence of constraints to evolutionary


(a)
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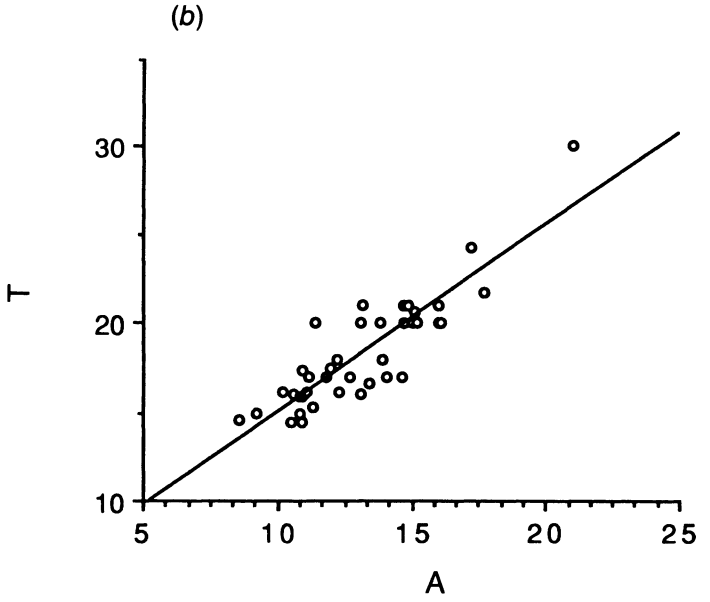
(b)
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change, it follows that all components are expected to change so as to increase r_m, and that those having a larger impact on r_m are expected to undergo larger proportional changes than the others. Essentially, this modelling approach has led to the development of a theory of life-history evolution. Two predictions emerging from models developed by Lewontin (1965) and Caswell and Hastings (1980) are formulated and tested below.

Prediction 1: If fecundity were to be constant, selection to commence oviposition (at age A) and to reach peak oviposition (at age T) earlier in life will be more severe than selection to modify the age when oviposition ends (at age W).

In other words (*prediction 1a*) T is expected to be closer to A than to W, and (*prediction 1b*) A and T are expected to be more closely associated with each other than either A or T is with W.

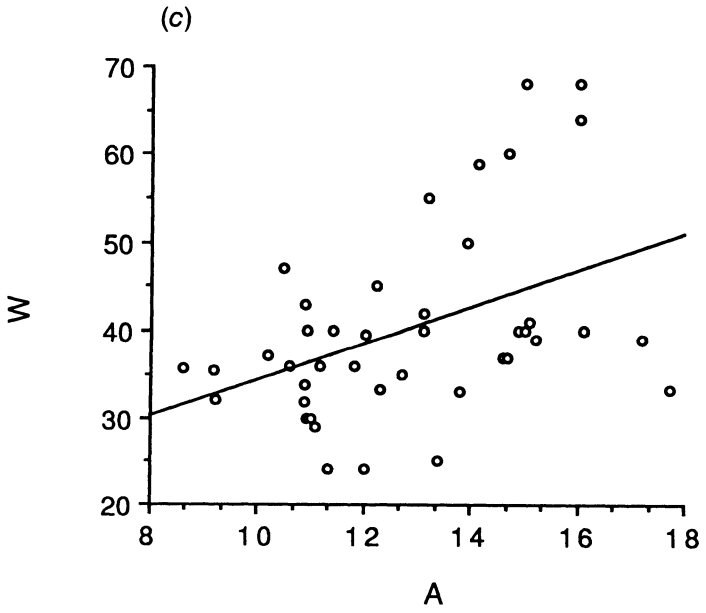

Fig. 2.1 Generalized reproduction schedule (*a*) of spider mite and analysis of relations (*b* and *c*) of mean values of first (A) and last (W) ovipositions and age at which oviposition rate reaches peak (T). Age is expressed in days since birth. Data from Table 2.1. The regression equations for (*b*) and (*c*) are respectively: $T = 4.44 + 1.05 \times A$ (41 data points; $r^2 = 0.776$) and $W = 13.52 + 2.07 \times A$ (42 data points; $r^2 = 0.187$). See footnote, p. 33 for further information on data and their analysis.

These predictions can be tested using the literature data summarized in Table 2.1. Let us assume initially that fecundity is more or less constant, and consider how the age at first oviposition (A) is related to the age at peak oviposition (T; Figure 2.1b), as well as to the age at last oviposition (W; Figure 2.1c). As expected, oviposition peaks soon after the onset of reproduction (T-A = *c.* 4.5 days), and a younger age at first oviposition is strongly correlated with a younger age at peak oviposition (Fig. 2.1b). It is also consistent with the expectations that oviposition reaches its peak very early in the oviposition period (W-A = *c.* 45 ± 20 days), and that there is a very weak correlation between A and W. Yet, there may be some tendency for W to decline with A. If there were to be a trade off underlying reproduction early or late in life or more specifically a gene with pleiotropic effect (Rose and Charlesworth, 1980), then one might expect a stronger correlation. The weakness of the correlation, however, is consistent with an alternative hypothesis related to the mutation–accumulation hypothesis on the evolution of senescence (Rose, 1984). The latter hypothesis applies to the within-species level and is based on the following concept: deleterious genes, exclusively late-acting, will attain higher equilibrium frequencies than mutations that act early because of the relatively minor effects on fitness (r_m) of the former type of mutations, and this results (1) in a lower mean contribution of fitness components acting late in life (in other words to senescence), and (2) in a considerable variation in this contribution, which is especially relevant in the context of variation in W. Hence, when extrapolating this hypothesis from within to across species within a family, one might expect the across-species correlation between A and W in Fig. 2.1(c) to be weak (for example, relative to the across-species correlation between A and T in Fig. 2.1b).

It is also noteworthy that breeding earlier is associated with a decrease in the length of the oviposition period (W-A ≈ 2A). However, as will be shown later, breeding earlier is not associated with lower fecundity but rather the reverse. Likewise, with earlier breeding, the mean rate of oviposition increases rather than decreases. Thus, while there may be a cost in terms of a shorter oviposition period resulting from breeding earlier, there is no reason to assume a cost when age is expressed in physiological units such as the number of eggs produced. This is not to say that there are no trade-off effects underlying the life-history trends under consideration, but only that if they exist, they do not have a large impact on the trends observed.

There is another prediction emerging from Caswell & Hastings (1980) model, again assuming that there are no constraints; a standard proportional increase of the development rate has a larger impact on r_m than an equivalent proportional increase in the oviposition rate early in life,

that is provided that r_m is not too low, a requirement which holds for spider mites in the majority of cases. The same applies to early versus late reproduction. Consequently, evolutionary rates will differ for each of those life-history components. Mutants having a larger impact on r_m will come to prevail in a population within a relatively lower number of generations. Hence, these types of mutants will keep ahead of the mutants with a lesser impact on r_m. This leads to

Prediction 2: Selection to breed earlier will be more severe than selection to increase the oviposition rate early in life. Similarly, selection to increase oviposition early in life will be more severe than selection to increase oviposition late in life or to increase fecundity. These selection differentials will increase as r_m increases.

One way to test this prediction using the available data from the literature is to assess whether standardized proportional changes in development rate are associated with a smaller proportional change in the rate of oviposition or fecundity. If there are no constraints, then selection to increase development rate will be more severe than selection to increase the rate of oviposition (and fecundity). Thus, it is expected that standardized proportional changes in 'egg-to-egg' development rate exceed the associated proportional changes in the rate of oviposition. This prediction, however, is only partially supported by the literature data presented in Table 2.2 and Fig. 2.2*. Consider the relation between the development rate and either the peak oviposition rate or the fecundity (Fig. 2.2a and 2.2b respectively). In both cases, the overall pattern is similar: providing the development rate is sufficiently low, proportional changes in its rate are greater than in peak oviposition rate or fecundity. However, as development rate increases the effects are reversed. In other words, proportional changes in peak oviposition and fecundity are greater than those of the associated rates of development. Thus, while prediction 2 seems to hold when development is slow, it is no longer valid when development is rapid. The reason for this difference is clear: development rate appears to approach a maximum whereas reproduction continues to increase. This suggests that there is a constraint to speeding up development. However, its existence needs

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* Some species and genera are overrepresented (for discussion, see Harvey and Mace, 1982). However, the trends remain virtually the same (even in quantitative terms) if the data are reduced to a single pair of observations for a genus or species. All the data are presented to reflect the full extent of existing variability. The regression equations are for descriptive purposes only, and no causal relationship is intended. It should also be stressed that, as the x variable is subject to error, the regressions suffer accordingly.

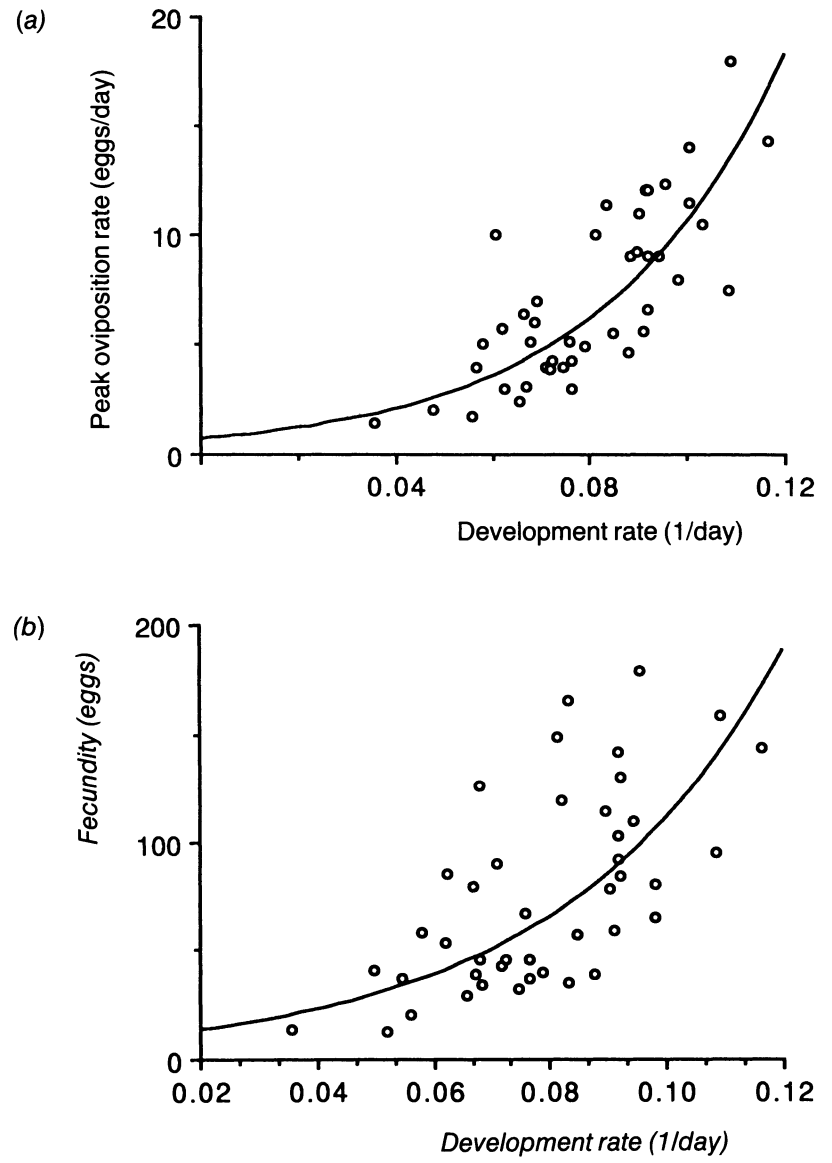
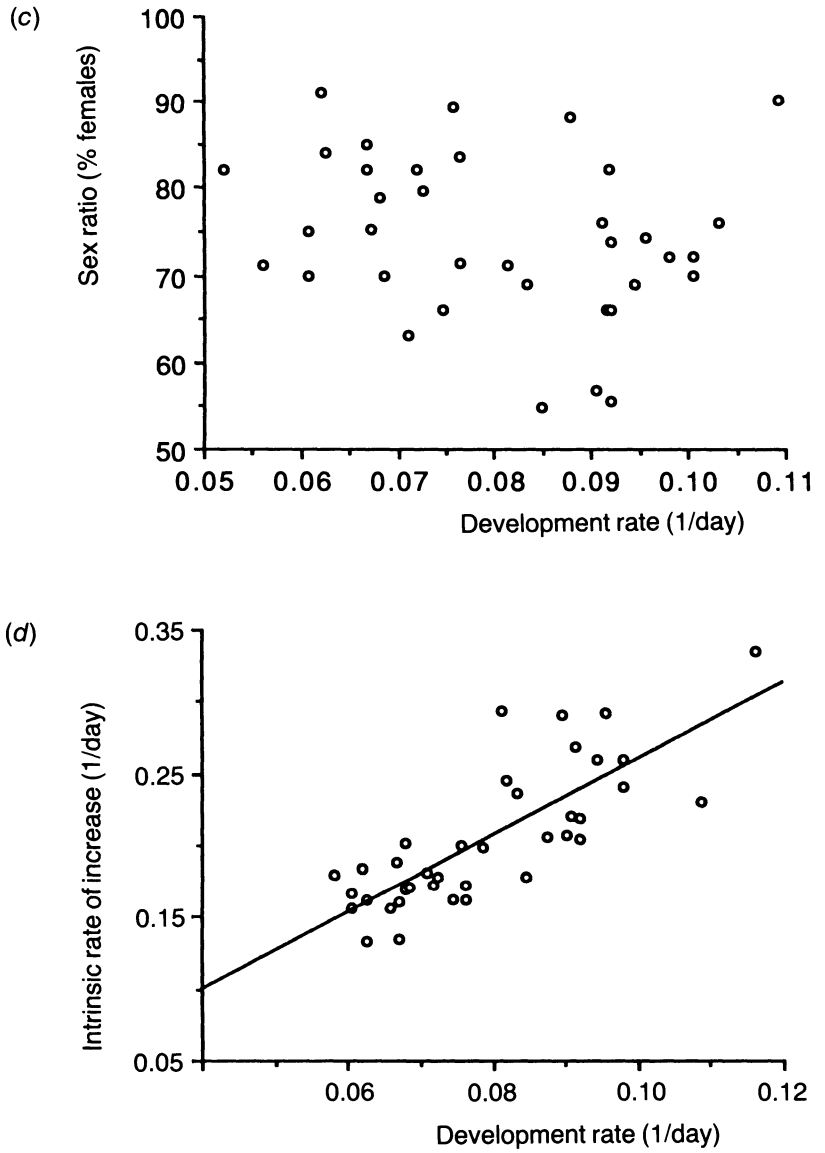


Fig. 2.2 The relation between egg-to-egg development rate (1/day) and life-history attributes among species of the Tetranychidae. Data, which are mean values, are given in Table 2.2. Age at first oviposition = A. See footnote, p. 33 for further information on data and their analysis. (*a*) Development rate versus peak oviposition rate (at age x = T). Regression line: $n(\mathrm{T}) = 0.7 \times \mathbf{10}^{(11.82/\mathrm{A})}$ (45 data points; $r^2 = 0.639$). (*b*) Development rate versus fecundity (F = total eggs). Regression line: $F = 7.85 \times \mathbf{10}^{(11.51/\mathrm{A})}$ (44 data points; $r^2 = 0.485$). (*c*) Develop-



ment rate versus proportion daughters in offspring. Regression equation: $s_x = 87.2 - 156.1/A$ (37 data points; $r^2 = 0.063$). (*d*) Development rate versus intrinsic rate of increase (r_m as female/female/day). Regression line: $r_m = -0.007 + 2.67/A$ (40 data points; $r^2 = 0.631$). Note in addition: (1) $r_m = 0.123 + 0.0122 \times n(T)$ (32 data points; $r^2 = 0.646$; cf. Fig. 2.2d); (2) mean oviposition rate $= 0.51 + 0.59 \times n(T)$ (24 data points; $r^2 = 0.91$).

Table 2.1 Literature survey of mean values for age in days since birth at first and last oviposition, and age at which oviposition reaches peak for species of Tetronychidae

	Species	*First oviposition (days)*	*Peak oviposition (days)*	*Last oviposition (days)*	*Source*
1	*Aponychus corpuzae*	14.100	17.000	59.000	Saito and Ueno (1979)
2	*Bryobia kissophila*	21.000	30.000		Sabelis (unpublished data)
3	*Eotetranychus hicoriae*	11.300	15.300	24.000	Micinski *et al.* (1979)
4	*Eotetranychus tiliarium*	13.800	20.000	33.000	Gotoh (1987c)
5	*Eotetranychus tiliarium*	14.700	21.000	37.000	Gotoh (1987c)
6	*Eotetranychus uncatus*	12.700	17.000	35.000	Gotoh (1987c)
7	*Mononychellus tanajoa*	17.200	24.200	39.200	Yaninek *et al.* (1989b)
8	*Oligonychus platani*	12.000		24.000	Butler and Abid (1965)
9	*Oligonychus pratensis*	9.210	15.000	32.000	Congdon and Logan (1983)
10	*Oligonychus punicae*	10.990	16.000	30.000	Tanigoshi and McMurtry (1977)
11	*Oligonychus ununguis*	11.800	17.000	36.000	Saito (1979)
12	*Oligonychus ununguis*	15.200	20.000	39.000	Boyne and Hain (1983)
13	*Panonychus akitanus*	13.200	21.000	55.000	Gotoh (1987a)
14	*Panonychus akitanus*	16.100	20.000	40.000	Gotoh (1987a)
15	*Panonychus citri*	13.100	16.000	42.000	Saito (1979)
16	*Panonychus citri*	14.600	17.000	37.000	Yasuda (1982)
17	*Panonychus ulmi*	13.400	16.700	25.100	Rabbinge (1976)
18	*Panonychus ulmi*	15.000	20.000	40.000	Gotoh (1987b)
19	*Schizotetranychus celarius*	16.000	20.000	68.000	Saito and Ueno (1979)

20	*Schizotetranychus celarius*	15.000	20.000	68.000	Saito and Takahashi (1982)
21	*Schizotetranychus celarius*	16.000	21.000	64.000	Saito and Takahashi (1982)
22	*Schizotetranychus cercidiphylli*	14.900	21.000	40.000	Gotoh (1983)
23	*Schizotetranychus leguminosus*	13.100	20.000	40.000	Gotoh (1983)
24	*Schizotetranychus schizopus*	11.400	20.000	40.000	Gotoh (1983)
25	*Tetranychus bastosi*	10.900	17.400	29.800	de Moraes *et al.* (1987)
26	*Tetranychus cinnabarinus*	12.000	17.500	39.500	Hazan *et al.* (1973)
27	*Tetranychus desertorum*	11.150	17.000	36.000	Nickel (1960)
28	*Tetranychus evansi*	9.170		35.500	Qureshi *et al.* (1969)
29	*Tetranychus evansi*	15.100	20.600	41.000	de Moraes and McMurtry (1987)
30	*Tetranychus kanzawai*	10.920	14.500	40.000	Kondo and Takafuji (1985)
31	*Tetranychus lintearius*	17.700	21.700	33.200	Stone (1986)
32	*Tetranychus mcdanieli*	14.700	20.000	60.000	Tanigoshi *et al.* (1975)
33	*Tetranychus mcdanieli*	12.200	18.000	45.000	Tanigoshi *et al.* (1975)
34	*Tetranychus neocaledonicus*	10.200	16.200	37.200	Gutierrez (1976)
35	*Tetranychus pacificus*	12.300	16.100	33.400	Takafuji and Chant (1976)
36	*Tetranychus pacificus*	11.070	16.100	28.900	Carey and Bradley (1982)
37	*Tetranychus turkestani*	10.870	15.900	33.700	Carey and Bradley (1982)
38	*Tetranychus urticae*	10.600	16.000	36.000	Saito (1979)
39	*Tetranychus urticae*	10.870	14.900	42.900	Sabelis (1981)
40	*Tetranychus urticae*	10.470	14.500	47.000	Kondo and Takafuji (1985)
41	*Tetranychus urticae*	8.600	14.600	35.600	Shih *et al.* (1976)
42	*Tetranychus urticae*	10.880	15.900	31.800	Carey and Bradley (1982)
43	*Tetranychus viennensis*	13.920	18.000	50.000	Gotoh (1986)

Table 2.2 Literature survey of intrinsic rate of increase and mean estimates of other life-history attributes for species of Tetranychidae

	Species	*Egg-to-egg development time (days)*	*Oviposition rate (eggs/day)*		*Fecundity (eggs)*	*Proportion daughters*	*Intrinsic rate of increase (1/day)*	*Source*
			Peak	*Mean*				
1	*Aponychus corpuzae*	14.100	4.000	2.980	90.700	0.630	0.181	Saito and Ueno (1979)
2	*Bryobia kissophila*	21.000	2.000					Sabelis (unpublished data)
3	*Bryobia rubrioculus*	18.000	1.700					Mathys (1957)
4	*Eotetranychus hicoriae*	11.300	9.000					Micinski *et al.* (1979)
5	*Eotetranychus kankitus*	18.300			36.500			Lung-Shu *et al.* (1984)
6	*Eotetranychus mathyssei*	19.200			12.800	0.820		Reeves (1963)
7	*Eotetranychus tiliarium*	13.800	4.300	3.400	45.800	0.795	0.178	Gotoh (1987c)
8	*Eotetranychus tiliarium*	14.700	5.100	3.400	45.700	0.789	0.169	Gotoh (1987c)
9	*Eotetranychus tiliarium*	16.500	7.000			0.700	0.157	Kropczyńska *et al.* (1988)
10	*Eotetranychus tiliarium*	16.500	10.000			0.750	0.167	Kropczyńska *et al.* (1988)
11	*Eotetranychus uncatus*	12.700	4.940	3.400	39.500	0.836	0.198	Gotoh (1987c)
12	*Eutetranychus orientalis*	8.870		2.000				Rasmy (1977)
13	*Mononychellus tanajoa*	17.200	5.000	2.500	58.000		0.180	Yaninek *et al.* (1989b)
14	*Oligonychus platani*	12.000			35.000			Butler and Abid (1965)
15	*Oligonychus pratensis*	9.210	7.500	5.480	95.500		0.230	Congdon and Logan (1983)
16	*Oligonychus punicae*	10.990	5.600	4.350	59.100	0.760	0.220	Tanigoshi and McMurtry (1977)
17	*Oligonychus ununguis*	11.800	5.500	4.310	57.500	0.549	0.178	Saito (1979)
18	*Oligonychus ununguis*	15.200	2.400	2.310	29.100		0.157	Boyne and Hain (1983)
19	*Panonychus akitanus*	13.200	5.100	3.660	66.900	0.894	0.200	Gotoh (1987a)
20	*Panonychus akitanus*	16.100	5.700	3.020	53.300	0.909	0.184	Gotoh (1987a)
21	*Panonychus citri*	13.100	3.000	1.930	36.900	0.714	0.162	Saito (1979)
22	*Panonychus citri*	14.600	6.000		34.400	0.700	0.171	Yasuda (1982)
23	*Panonychus ulmi*	13.400	4.000	3.070	31.600	0.660	0.162	Rabbinge (1976)
24	*Panonychus ulmi*	15.000	6.400		79.800	0.820	0.189	Gotoh (1987b)
25	*Petrobia latens*	20.100			41.000			Cox and Lieberman (1960)

26	*Schizotetranychus celarius*	16.000	3.000	2.330	85.400	0.840	0.162	Saito and Ueno (1979)
27	*Schizotetranychus celarius*	15.000				0.850	0.135	Saito and Takahashi (1982)
28	*Schizotetranychus celarius*	16.000				0.840	0.133	Saito and Takahashi (1982)
29	*Schizotetranychus cercidiphylli*	14.900	3.080	2.450	39.300	0.753	0.160	Gotoh (1983)
30	*Schizotetranychus leguminosus*	13.100	4.270	3.170	45.200	0.836	0.173	Gotoh (1983)
31	*Schizotetranychus schizopus*	11.400	4.700	3.400	39.300	0.880	0.206	Gotoh (1983)
32	*Tenuipalpoides dorychaeta*	28.000	1.500	0.700	14.000			Singer (1966)
33	*Tetranychus bastosi*	10.900	6.600		91.900	0.820	0.259	de Moraes *et al.* (1987)
34	*Tetranychus cinnabarinus*	9.970	14.000			0.700		Coates (1974)
35	*Tetranychus cinnabarinus*	12.000	11.400		165.100	0.690	0.237	Hazan *et al.* (1973)
36	*Tetranychus desertorum*	11.150	9.200		114.300		0.290	Nickel (1960)
37	*Tetranychus evansi*	9.170	18.000		158.000	0.900		Qureshi *et al.* (1969)
38	*Tetranychus evansi*	15.100	12.500	5.900	243.000	0.580	0.200	de Moraes and McMurtry (1987)
39	*Tetranychus kanzawai*	10.920	12.000		142.200	0.659	0.268	Kondo and Takafuji (1985)
40	*Tetranychus lintearius*	17.700	4.000	2.300	20.000	0.710		Stone (1986)
41	*Tetranychus lombardinii*	9.970	11.500			0.720		Coates (1974)
42	*Tetranychus ludeni*	9.710	10.500			0.760		Coates (1974)
43	*Tetranychus mcdanieli*	14.700		7.500	126.100		0.201	Tanigoshi *et al.* (1975)
44	*Tetranychus mcdanieli*	12.200		8.700	119.300		0.245	Tanigoshi *et al.* (1975)
45	*Tetranychus neocaledonicus*	10.200	8.000		80.300	0.721	0.260	Gutierrez (1976)
46	*Tetranychus pacificus*	12.300	10.000	7.080	148.700	0.710	0.293	Takafuji and Chant (1976)
47	*Tetranychus pacificus*	11.070	11.000		78.900	0.567	0.207	Carey and Bradley (1982)
48	*Tetranychus turkestani*	10.870	9.000		84.600	0.557	0.204	Carey and Bradley (1982)
49	*Tetranychus urticae*	10.200			65.500		0.241	Gutierrez (1976)
50	*Tetranychus urticae*	10.600	9.000	6.620	109.800	0.689	0.259	Saito (1979)
51	*Tetranychus urticae*	10.870	12.000		129.800	0.660		Sabelis (1981)
52	*Tetranychus urticae*	10.470	12.300		178.600	0.743	0.292	Kondo and Takafuji (1985)
53	*Tetranychus urticae*	8.600	14.300	8.000	143.900		0.336	Shih *et al.* (1976)
54	*Tetranychus urticae*	10.880	9.000		103.300		0.219	Carey and Bradley (1982)
55	*Tetranychus viennensis*	13.920	3.900	3.020	43.000		0.172	Gotoh (1986)

scrutiny because there is considerable variation in the range of development rates supposed to be maximal. This variation may be due to differences in experimental conditions and methods used by the various authors. Indeed, if data are considered from authors who compared life histories of two or more species with high development rates, measured under exactly the same conditions (Carey and Bradley, 1982; Gutierrez, 1976; Coates, 1974), then there appears to be very little difference in development rate (just a few hours!) but large differences in fecundity (up to a factor of 2) (Sabelis, 1985a). This is quite strong evidence that selection has driven the rate of development to its physiological maximum. Moreover, it is the most parsimonious explanation, and it has biological appeal as there must be a lower limit to development time. The alternative explanation is that development rate has not reached a maximum, but rather an optimum in that further increases would be to the detriment of other fitness components, thereby causing fitness to shift away from its maximum. One way to distinguish between these two hypotheses is to select for increased development rate using spider-mite species with rates that are supposedly maximal. If selection to shorten development does not succeed whereas selection to prolong development is successful, then the 'physiological maximum' hypothesis may be accepted. If, however, selection drives development rate beyond the supposed maximum, the next step is to test the 'trade-off optimization' hypothesis. The evidence obtained so far supports the 'physiological maximum' hypothesis. A preliminary series of selection experiments in the laboratory showed that development of the 'Koppert' strain of *Tetranychus urticae* Koch cannot be speeded up whereas selection to slow it down can be successful (Sabelis, unpublished data). A more elaborate test has yet to be done where several strains of *T. urticae*, and other tetranychid species with a slow rate of development, are used.

While there are reasons to believe that many tetranychid species face constraints to increasing the rate of development, as yet there is no indication of constraints to increasing the rate of oviposition and fecundity. Species with high rates of development, say, 0.09/day or more, may have fecundities ranging from *c.* 50 to almost 200 eggs. The best-fitting curve describing the relation between fecundity (y axis) and development rate (x axis) appears to be an exponential equation of the form: $y = 7.85 \times 10^{11.5x}$ with $r^2 = 0.485$ and $n = 44$. Very similar conclusions can be drawn with respect to the relation between development rate and the peak oviposition rate. Species with development rates equal to 0.09/day or more may have peak oviposition rates ranging from *c.* 5 eggs/day to almost 20 eggs/day, and again the best fitting curve describing the relation between peak oviposition rate (y axis) and development rate (x axis) is an exponential: $y = 0.7 \times 10^{11.82x}$ with $r^2 =$

0.639 and $n = 45$. Thus, both peak oviposition rate and fecundity tend to increase with development rate in an exponential fashion. Clearly, there is no reason to think that there are intrinsic constraints to increasing fecundity and oviposition rate. Egg production evolves to higher levels whereas development rate seems to approach a maximum. Variability in egg production may be high because (1) its impact on r_m is relatively low and (2), once development rate is near its maximum further progress in r_m may be achieved though slowly by increasing egg production. The closer to maximum development rate, the smaller will be further advances in this rate, while egg production continues to increase. This may have led to the exponential relationship between egg production and development rate.

In contrast to the life-history components discussed so far, sex ratio appears not to bear any relation to the development rate nor to the peak oviposition rate (Fig. 2.2c). In what follows an attempt is made to provide an explanation. Since (1) sex ratio evolution depends on the population mating structure, (2) mating occurs soon after the last moult and (3) juvenile spider mites tend to stay close to where they were born, it is important first to consider how females distribute their offspring and then to discuss the consequences for mating structure and sex-ratio evolution.

HOW WITHIN-PATCH DISTRIBUTIONS OF REPRODUCERS AND THEIR OFFSPRING ARE MOULDED BY SELECTION

It is one thing to understand how selection moulds life-history patterns so as to increase r_m but it is quite another to understand the various ways in which female spider mites distribute their offspring over the host plant. If we consider the mite distribution on leaves within an aggregate of infested leaves (called a patch), there is a remarkable interspecific variability in spatial patterns of oviposition. Females of some species, such as *Bryobia kissophila* van Eyndhoven on ivy, distribute their eggs at distances of several centimetres from each other whereas females of other species, such as *T. urticae* on rose, space their eggs one or two millimetres apart. Wanibuchi and Saito (1983) also reported large differences in resource-utilization patterns, and leaf-to-leaf and plant-to-plant dispersal between *Oligonychus ununguis* (Jacobi) on young chestnut trees and *Panonychus citri* (McGregor) on citrus saplings. Similar differences may also be found at the intraspecific level; for example, the distribution of *T. urticae* on chrysanthemum leaves differs from its distribution on rose leaves in that the latter is more like that of *B. kissophila* on ivy. In all these cases, distribution patterns of spider mites over the host plants are patchy, but they differ in the within-patch density of spider

mites. The important point is that these differences are noticeable in the absence of predators, and that they rely entirely on properties of the spider mites which may or may not have a relation to properties of the host plant.

How would these different types of spaced-out gregariousness be moulded by natural selection? Clearly, spider mites that space out their offspring within a patch represent a less profitable prey for predators than do spider mites that keep their offspring close together. There is much evidence to suggest that it does matter to a predatory mite (Acari: Phytoseiidae) and even more so to larger predators, such as *Stethorus* spp., whether prey are distributed at distances of 1 mm or a few cm. Their rate of predation and egg production is significantly affected by such differences (see Sabelis, 1985b, Chazeau, 1985). Hence, it is reasonable to suppose that spacing out, albeit within aggregations, represents a possible defensive strategy of spider mites provided that the benefits of defence exceed the costs of movement and interruptions in feeding, and that within-patch togetherness, as opposed to spacing out, represents an alternative strategy that has the benefit of less interrupted feeding, but requires other ways of coping with predators.

While all spider mites produce silken threads during ambulatory displacement, they may also use silk to protect themselves and the modes of such use of silk may differ greatly (Gerson, 1985; Saito, 1985). Saito (1983, 1985) provided a classification of various types of silk use, ranging from tools for attachment or roping down (for example, after contact with a predator) to its use for constructing roof-like shelters or labyrinth-like webs. It is tempting to interpret these modes of silk use as part of a defensive strategy and indeed, in some cases there is good evidence for such a function. If so, it is worth recalling that most, if not all, species that produce a web have a relatively high degree of togetherness (eggs spaced out on average at a few mm or even less). However, the relation between togetherness and the intrinsic rate of population increase is not that simple. While virtually all tetranychid species with a high value of r_m (say, 0.25–0.3 female/female/day) produce a web (several species of *Tetranychus* and some *Oligonychus* spp. for example), yet tetranychids with low values of r_m may be either the spaced-out type without webs (for example, *Bryobia, Petrobia, Aponychus, Eutetranychus* and *Panonychus* spp.) or they may show a high degree of togetherness and produce webs (*Schizotetranychus* and *Eotetranychus* spp. are examples). Whether these various modes of silk use entail different costs in terms of the amounts of silk produced, is not really known though quite possible. Togetherness may well impose a cost in terms of extra silk for defence but a quantitative assessment of investment in silk is required. Such an experiment is important for two reasons. One is that it may help

to analyse whether spacing out and togetherness represent two separate peaks in the adaptive landscape or represent part of a continuum of possible adaptations with equal fitness. The other reason is that extra investment in silk involves a cost in terms of amino acids, and may therefore interfere with the production of proteins for other purposes such as egg yolk. Thus, there may be a trade off between investment in silk on the one hand, and the quantity or quality of the eggs on the other. The role of this trade off may become manifest in experiments at the individual level, and maybe also at the (intraspecific) between-individual level, but it is certainly not clear from the interspecific comparisons considered in this chapter: recall that all species with high r_m produce webs. The inevitable conclusion is, therefore, that evolution towards high r_m is associated with the acquisition of a larger quantity of food either through improvement in the ability to digest and detoxify or through increased food supply *per se* or both.

Apart from representing a better or less toxic food source, the host plant may influence the evolution of spacing patterns in various other ways. For example, when host defence is inducible (Karban and Carey, 1984; Karban and English-Loeb, 1988), it may be profitable to the spider mite to avoid plants or plant parts under attack by other herbivores. Dicke (1986) showed that females of the two-spotted spider mite move away from areas where the air is permeated with odour coming from bean plants infested by conspecific mites. This response may be simply to avoid food competition, but it may also be to avoid detection by predators that use the odour to find their prey (Dicke and Sabelis, 1989). Thus, it can be hypothesized that spacing of offspring may be an adaptive strategy evolved in response to induced plant defences or predation pressure or both.

SPACING, MATING STRUCTURE AND SEX-ALLOCATION STRATEGIES

Spacing of progeny over host plants influences population mating structure and thereby also the evolution of sex-allocation strategies. When eggs are deposited at greater distances from each other, broods of different mothers become more and more mixed as mothers do not minimize the circumference–area ratio of their oviposition 'territories'. Population mixing before mating is, therefore, likely to occur, and there will be a tendency towards random mating assuming that 'first met, first mate' is the rule. Under these and some other conditions – equal costs of producing a son or daughter, no costs or interaction between sex ratio and offspring survival and finite population size – selection will favour genes coding for the production of half sons and half daughters (Fisher,

1930). In spider mites one might expect a male bias under random mating because males arise from smaller eggs than females. Such a bias has never been reported, however; all data available point to an excess of daughters in the progeny, albeit in varying degrees. Hamilton (1967), Frank (1985, 1986) and others have shown that there are at least three mechanisms causing the evolution of female-biased sex ratios in structured demes: (1) inbreeding in local groups; (2) local mate competition between brothers; and (3) relatedness between mothers in a local group combined with the possibility of differential proliferation between groups. These mechanisms may operate alone or in combination under sib mating, which is more likely to occur when mothers deposit eggs close to each other, and juveniles stay close to where they were born. One may therefore hypothesize that spider mites with a high degree of togetherness, such as those producing webs (*Tetranychus. Schizotetranychus, Eotetranychus, Oligonychus*), have a higher probability of sib mating than spider mites with a low degree of togetherness (*Panonychus, Aponychus, Eutetranychus, Bryobia, Petrobia*). This is because brothers and sisters are more likely to meet and mate when the circumference–area ratio of an oviposition 'territory' approaches its minimum. Web-producing spider mites are therefore expected to produce sex ratios with a stronger female bias than others. However, this hypothesis does not explain the variability in sex ratios reported in the literature (Table 2.2). For example, sex ratios of web-producing spider mites such as *Tetranychus* spp. range from 0.55 (Carey and Bradley, 1982) to values as extreme as 0.9 (Wrensch and Flechtmann, 1978) and sex ratios of *Panonychus* spp., which do not produce a web and tend to space out more than do *Tetranychus* spp., range form 0.66 (Rabbinge, 1976) to 0.91 (Gotoh, 1987a,b); even *Petrobia* spp. produce sex ratios ranging from 0.57 to 0.80 (Dubitzki and Gerson, 1987). Clearly, the degree of variability is considerable but it is premature to reject the hypothesis on spacing and sex ratio. One reason is that the experimental methods of sex-ratio measurement have frequently been described with insufficient information to know whether mothers were single or in groups when depositing the batch of eggs used to determine the sex ratio. In addition, more careful assessment of the relationship between host plant, spacing of progeny and mating structure is needed. The lack of such data hampers analysis at the interspecific level, but intraspecifically there is more to say. For example, there is good evidence that sex-ratio changes can be associated with changes in probability of random versus sib mating. Females of the two-spotted spider mite, *T. urticae*, produce more daughters than sons when feeding alone on a fresh leaf, but they produce almost half sons, half daughters when feeding in a densely packed group, irrespective of the condition of the leaf (Wrensch and Young, 1978, 1983; Wrensch, 1979; Zaher *et al.*, 1979; Young *et al.*, 1986). This ability to control the sex

ratio in response to the density of the females is well known for arrhenotokous arthropods (Charnov, 1982; Bull, 1983).

Unlike the relationships found in predatory mites (Sabelis and Nagelkerke, 1987), sex ratios in spider mites do not bear a relation with any of the other life-history components. An example is presented in Fig. 2.2c where paired data of sex ratio and development rate are plotted for a number of species. Similar results have been obtained when sex ratio is plotted against oviposition rate, fecundity and r_m. If the absence of a relation is not due to variable female density in measurements of the progeny sex ratio, then the large interspecific variability in sex ratios suggests that the population mating structure is largely independent of life-history traits. Whether this is, in fact, true remains to be elucidated in future experiments.

ARE THERE LIMITS TO ENHANCING r_m?

Selection to increase r_m may be achieved by changing various life-history components, but the rate of natural selection is not equal for each of these components because they have a differential impact on r_m. More rapid development is the trait favoured to the greatest degree by natural selection. However, there are reasons to believe that selection has driven the development rate to a maximal value or, alternatively, to an optimal value. Such a constraint does not seem to apply to egg production, however, and there is no reason to believe that increased egg production is to the detriment of other traits such as development rate or silk production. Nor is there reason to suppose that faster development is achieved at the expense of body size at maturity. To demonstrate this point note that (1) species characterized by rapid development, such as *Tetranychus* spp., are certainly not among the small-sized spider mites and (2), tetranychids that produce small eggs are the ones that have a small body size as an adult, and vice versa; more precisely the ratio between egg size and adult size is rather constant. Thus, faster development is not achieved by maturation at a smaller body size but rather by speeding up the developmental processes themselves which seems possible until a certain maximum is reached. In conclusion, interspecific comparisons of life-history data reported to date do not provide evidence for trade offs between development rate, body size, silk production and egg production. This is not to say that there are no trade offs between development rate, body size, silk production and egg production, but merely that evolutionary progress overrules their effects. Trade offs that may be elucidated at the intraspecific level do not seem to dominate life-history trends at the interspecific level.

When development is the major determinant of r_m but appears to be subject to a constraint, in contrast to many other life-history compo-

nents, then one may wonder how this influences the relation between development rate and r_m. Does r_m continue to increase whereas development rate approaches a maximum with r_m responding to the exponential relationship between fecundity and development rate (Fig. 2.2b)? On the contrary, Fig. 2.2d shows a linear relationship between r_m and development rate; thus there is no indication that r_m increases faster at higher rates of development than it does at low rates of development. Once development approaches its maximum speed, evolutionary progress in components other than the development rate, such as the exponential increase in fecundity, may take over but none of these seems to have a major impact on r_m. This, *a priori*, is certainly not an obvious conclusion. It shows that development remains the most important determinant despite the constraints imposed on its evolutionary change.

The most pressing question left unanswered by this review arises from the interspecific differences in r_m. If it is reasonable to assume that there has been one ancestral type of spider mite with low r_m, then one may ask: do these dissimilarities in r_m reflect different rates of natural selection? If species are like joggers running at different speeds in an endless race, the answer is, probably, yes. However, as shown above, there may well be a finishing line in the evolutionary game, represented by an upper limit to the rate of development. Hence, either some joggers have reached the finish while others are still underway, or each jogger has its own finishing line; for example, think of constraints set by the food quantity and/or quality (including defensive chemistry) of the host plant. In conclusion, interspecific differences in r_m may result either from different constraints or different rates of natural selection. Or, to return to the world of health sports where running is all that matters to gain fitness. Are the joggers' positions determined by their speed or by their self-set finishing line? Which of these race analogies applies to the evolution of life histories in the Tetranychidae, is one of the most important questions for future research.

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3

*Life-cycle strategies in unpredictably varying environments: genetic adaptations in a colonizing mite**

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Many astigmatic mites including *Lepidoglyphus destructor* (Schrank) live in unstable and unpredictably varying habitats; they invade short-lived and newly created habitats as, for example, stored products. Their life cycles are adapted to such conditions by the possession of a facultative and heteromorphic developmental stage, the hypopus, allowing for dispersal and/or dormancy. To understand how their life-cycle patterns are moulded by natural selection, and how evolutionary change can take place, it is crucial to distinguish the genetic and environmental sources of variation for hypopus formation and duration.

Lepidoglyphus destructor faces sudden drought as well as sudden periods conducive to development and reproduction by genetic polymorphism for hypopus formation and duration. The species meets gradual food deterioration by phenotypic plasticity; a short-term switch mechanism, responding to worsened food quality, directs development towards hypopus formation. Phenotypic plasticity of the hypopus response interacting with genetic variability of the trait provides for an extraordinary measure of adaptability to temporally and spatially varying environments and makes *L. destructor* a colonizer and pioneer mite *par excellence*.

* Invited paper.

The excessive amount of additive genetic variance for hypopus formation and duration as seen in artificial-selection experiments, reveals the potential to respond to natural selection, and provides flexibility for shaping adaptive responses at the local level; it permits composite populations to move from one adaptive peak to another. That local populations adapt at the genetic level to changing environmental conditions is displayed, *inter alia*, by laboratory populations kept under consistently favourable conditions. Genetic flexibility based on cumulative gene effects provides a mechanism conducive to evolutionary change. 'Domestic' strains and sibling species with reduced potential for hypopus formation, may have arisen from their feral counterparts along such a route

INTRODUCTION

In conformity with many other astigmatic mites, *Lepidoglyphus destructor* (Schrank) colonizes ephemeral patch habitats with living conditions that fluctuate in unpredictable ways. All obligatory instars of *L. destructor* are highly susceptible to low humidities and die of dehydration below a relative humidity between 70 and 75%, the critical equilibrium humidity in the species (Knülle, 1984). This threshold signifies the lowest humidity value below which the active instars are unable to compensate for water loss by active uptake of atmospheric water vapour to maintain water balance.

The drought-resistant, non-phoretic and wind-dispersed hypopus, a facultative developmental stage homologous to the deutonymph of other Acariformes, not only buffers a population against extinction by low humidities and ensures its persistence in habitats with contrasting humidities but also favours colonization of patchily distributed habitats. This is one main reason why *L. destructor* is such a persistent and widespread stored-product pest.

FACTORS AFFECTING HYPOPUS FORMATION AND DURATION

Formation of the hypopus depends on a genotype–environment interaction and is governed by a 'switch' mechanism. Dietary factors acting on the protonymph affect hypopus formation but the response of individuals to food quality differs greatly according to genotype. Genetic variation is continuous but phenotypic expression of the trait is controlled by a threshold response to nutrient quality of the ingested food. Decreasing diet quality lowers the position of the triggering threshold and thereby increases the proportion of individuals expressing the hypopus trait. Large additive genetic variance in the control of hypopus

formation exists within as well as between populations. Response to selection is rapid and reversible (Knülle, 1987).

The duration of the hypopus stage is highly variable and moulting to the tritonymph is spread out over many months. The length of the stage depends on both the genotype of the individual and the humidity and temperature conditions occurring during dormancy (Knülle, in press).

The traits for hypopus formation and duration vary independently of each other, and each trait is apparently free to adjust without genetic constraints towards an adaptive optimum (Knülle, in press).

The additive effects of the many genes underlying hypopus formation and duration ensure, on the one hand, that some hypopodes are formed in the population under all environmental conditions including those favourable for development and reproduction. Thus hypopodes are always present to provide a safeguard for survival of part of the population should subequilibrium humidities suddenly occur and all other instars succumb to drought. On the other hand, when humidities above the critical equilibrium level return, there are always in the population some hypopodes ready to moult to tritonymphs while others remain as a 'reserve' for periods of favourable humidity interspersed with those in which conditions are deleterious. Both genetic variation for hypopus duration, and asynchrony of individual life cycles, provide the means for the mite to 'test' each potentially favourable humid period for completion of another generation. By these means a proportion of the hypopodes moult to tritonymphs, and the remainder continue dormancy, and thus act as a buffer against 'misinterpretation' in case the length of the humid period is insufficient to complete another generation. This 'strategy' represents a fail-safe device for both survival and reproduction in risky and temporally unpredictable environments.

Both formation and duration traits have substantial adaptive potential as is apparent when directional selection under sustained favourable conditions erodes most of the genetic variation for these two traits. In populations maintained for over 30 years in laboratory cultures under favourable physical and nutritive conditions, hypopus formation no longer occurs with a superior diet although low incidences are still seen when the diet is inferior indicating that some residual genetic variation for the trait is still retained, and is expressed at a lower threshold level (Knülle, 1987). Also, under such conditions a predominance of genotypes with short hypopus duration is clearly evident (Knülle, in press). The obvious selective advantage to individuals with genotypes for hypopus-free development or short hypopus duration, accruing under sustained favourable conditions, underlines the evolutional plasticity of both traits. The short-term process of reversible genetic adaptation to

local conditions as seen for demes of *L. destructor* may, in the long run, lead to an irreversible loss of genetic variation and thereby to evolutionary change as can be inferred from the typical indoor grain mite, *Acarus siro* L. Most populations fail to produce a hypopus even with inferior food; others may form a few but only rarely.

The large reserves of genetic variation for hypopus formation and duration traits in feral populations probably constitute an adaptation to life in acyclic and risky environments with a high level of genetic variation apparently maintained in response to fluctuating selection under opposing environmental conditions. The inferred additive and polygenic character of the genetic system underlying hypopus formation and duration ensures the preservation of adaptive flexibility. It allows for gradual variation between two extremes by reconstitution of a broad spectrum of genotypes in every generation through the process of meiotic segregation and recombination during sexual reproduction.

Temporal programming of life cycles in cyclic and largely predictable environments is based essentially on long-term predictive mechanisms employing token stimuli such as photoperiod, which anticipate a change in environmental conditions (Tauber *et al.*, 1986; Danks, 1987). In contrast, the influences that shape life-cycle patterns and guide evolutionary change in organisms living consistently in acyclic and unpredictable environments are barely recognized. For *L. destructor* and many other astigmatic mites there are no environmental cues that predict sudden, aseasonal and localized drought. The mite meets recurrent and unheralded adversity as well as prosperity by providing each generation with an extensive and continuous spectrum of genotypes, which always include some that are instantaneously fit to meet the respective environmental situation.

Lepidoglyphus destructor possesses a high capacity for population increase (Stratil *et al.*, 1980), and when humidities above the critical level persist for longer periods, this mycophagous mite frequently attains epidemic population levels which can result in overcrowding and food deterioration in patch habitats. Since inferior diet markedly lowers the threshold for hypopus induction in the protonymph, such conditions lead to a substantial increase in the number of hypopodes. This anticipatory mechanism ensures survival and dispersal under conditions of malnutrition.

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4

The evolutionary transformation of osmotic regulation in the life cycle of freshwater mites (Hydrachnidia)

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The characterization of the evolutionary transformation and ontogenetic changes in osmotic regulation of water mites (Hydrachnidia) has been studied by measuring haemolymph osmolality (c_{HL}) of 12 species from six superfamilies, and two species from the terrestrial outgroups, Anystae and Trombidia. As a result of adaptation to a low-concentration medium, freshwater mites regulate c_{HL} hyperosmotically to levels between 233 and 285 mosm/kg, which are significantly less than the c_{HL} levels of the terrestrial examples (366 and 349 mosm/kg). In *Anystis baccarum*, all five motile instars are free-living terrestrial predators. Because of their similar habits, the c_{HL} of larva, deutonymph and adult do not differ greatly (299–349 mosm/kg). In contrast to these plesiomorphic conditions, haemolymph osmolality of the water mites, *Thyas barbigera* and *Limnesia maculata*, undergoes dramatic changes during their life cycles. In the aerial phase – when larvae parasitize nematoceran adults – the larval c_{HL} increases from low 'aquatic' values (260 and 209 mosm/kg respectively) to high 'terrestrial' values (316 and 323 mosm/kg respectively) similar to that of the host. Haemolymph osmolality decreases in the subsequent aquatic phase, to a lesser extent in the more primitive *Thyas* (adult: c_{HL} 285 mosm/kg), and to a greater extent in the more derived *Limnesia maculata* (adult: c_{HL} 250 mosm/kg). The relatively high c_{HL} of *Thyas* seems to be inherited from its terrestrial ancestor, and may be correlated with the amphibious living conditions of *Thyas*

INTRODUCTION

The freshwater mites (Hydrachnidia) are a monophyletic group, which derived from a terrestrial parasitengonic ancestor (Witte and Olomski, unpublished). The change from a terrestrial to an aquatic environment has led to some adaptations in the Hydrachnidia to the new milieu. As in other invertebrates, one of the most important problems in adaptation seemed to be the maintenance of water and salt balance in the low-concentration medium. Therefore, it is of special interest that not all hydrachnidian instars are exposed to water to the same extent. In particular, the parasitic larvae remain essentially terrestrial or are at least aerial for a certain time (Smith and Oliver, 1986).

As part of a more extensive investigation of the phylogenetic adaptation of osmotic and ionic regulation in Hydrachnidia, the following study should answer the questions: what changes in regulation of the haemolymph osmolality will the different environmental conditions cause during the life cycle of Hydrachnidia? Was the evolutionary process in Hydrachnidia paralleled by a transformation in the osmotic regulation specific to the life cycle?

METHODS

To characterize the principal evolutionary changes in osmotic regulation of freshwater mites, the haemolymph osmolality (c_{HL}) of adults of 12 species from six hydrachnid superfamilies, and from two closely related terrestrial Prostigmata, was determined microcryoscopically by the method of Weigmann (1973). The species investigated belong to the Anystoidea: *Anystis baccarum* (L.) = *A. voigtsi* Oud. 1936, non *A. baccarum sensu Oudemans* (1936); Trombidioidea: *Trombidium holosericeum* (L.); Hydrachnoidea: *Hydrachna globosa* (de Geer); Eylaoidea: *Limnochares aquatica* (L.) and *Eylais extendens* (Müll.); Hydryphantoidea: *Hydryphantes ruber* (de Geer), *Thyas barbigera* Viets and *Hydrodroma despiciens* (Müll.); Lebertioidea: *Sperchon setiger* Thor and *Lebertia inaequalis* (Koch); Hygrobatoidea: *Limnesia maculata* (Müll.), *Piona coccinea* (Koch) and *Unionicola crassipes* (Müll.); Arrenuroidea: *Arrenurus sinuator* (Müll.).

To characterize ontogenetic changes in osmotic regulation, measurements were also made of the haemolymph of deutonymphs and larvae of *Anystis*, *Thyas* and *Limnesia*. *Anystis* represents the probable sister group of the Parasitengonae, *Thyas* an early derived Hydrachnidia and, *Limnesia*, a late derived one. The deutonymphs were collected in the wild while they were approaching moulting to the next instar. Haemolymph of hydrachnid larvae was taken, when they had hatched, and again after parasitizing a nematoceran host for a defined time in

culture in the laboratory. The haemolymph osmolality of the hosts – *Aedes annulipes* (Meigen) (Culicidae) for *Thyas*, and *Chironomus* sp. (Chironomidae) for *Limnesia* – was also measured. To obtain a sufficient quantity of haemolymph from the hatched larvae, droplets from three larvae were pooled to form a sample of sufficient size for measurement. The two larval ages of *Anystis* were obtained by collecting individuals in the wild, and rearing from progeny of these which are referred to as 'hatched' and 'fed' larvae in Fig. 4.2. With this species, the droplets of three and two larvae respectively were pooled for each sample.

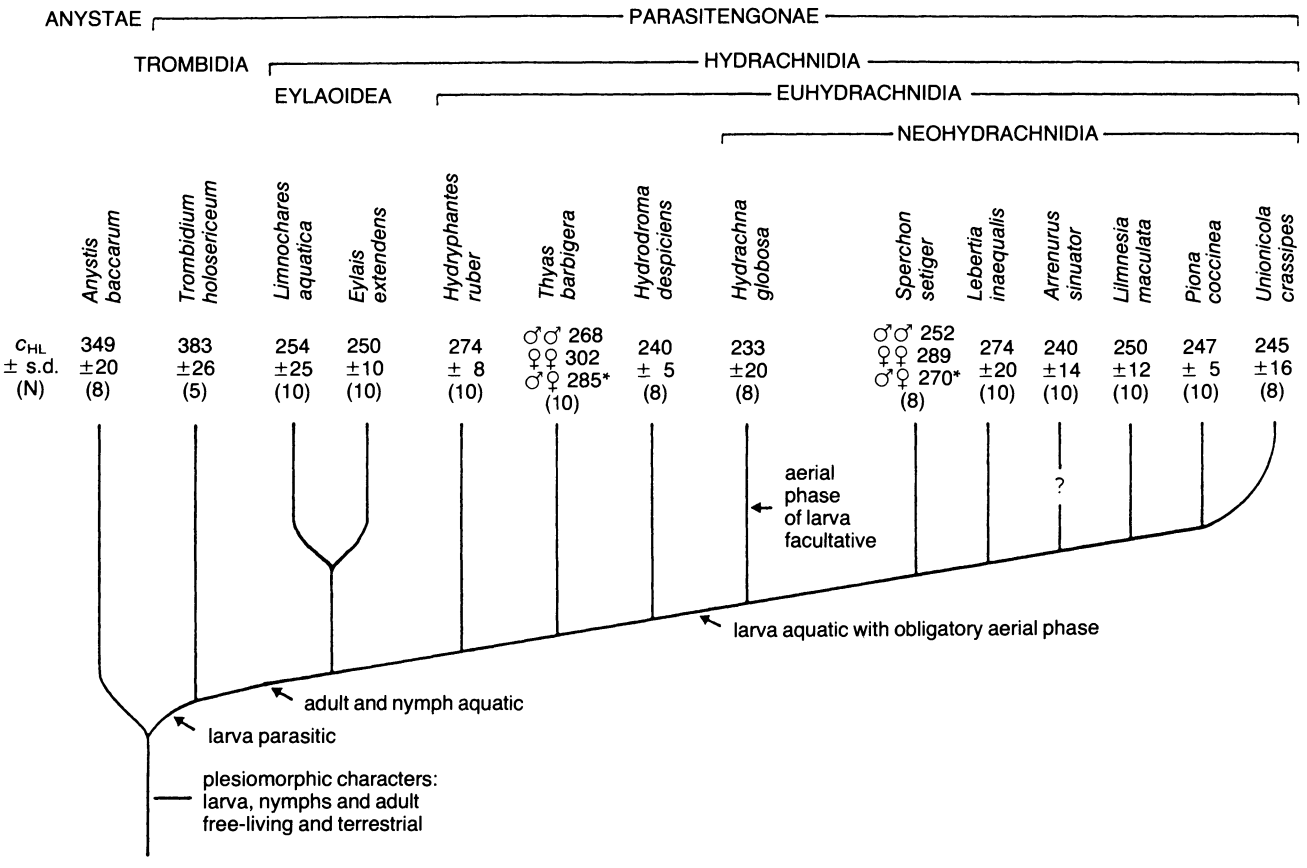
RESULTS

Osmotic regulation in adults

The haemolymph osmolality (c_{HL}) of hydrachnid adults ranged between 233 and 285 milliosmol (mosm)/kg during the reproductive phase (Fig. 4.1). It was, therefore, strongly hyperosmotic to the medium concentration, which was about 10 mosm/kg. Differences in the osmolality between sexes were significant only for *Thyas barbigera* (see below) and *Sperchon setiger*. The osmolality values represent regulatory levels as more detailed investigations of *Limnesia maculata* and *Thyas barbigera* show (Olomski, 1986, and unpublished). As in other limnic invertebrates, adult freshwater mites regulate their haemolymph concentration hyperosmotically to the limnic medium.

In comparison with the closely related terrestrial mites, *Anystis baccarum* (c_{HL} 349 mosm-kg) and *Trombidium holosericeum* (c_{HL} 383 mosm/kg), the regulatory level for the Hydrachnidia was about 17–34% lower. This statistically significant reduction has the potential to save an equivalent amount of energy otherwise required to maintain the haemolymph osmolality at the higher, 'terrestrial' level. Thus, the reduction is regarded as a phylogenetic adaptation of the Hydrachnidia to the limnic environment.

Within the recent Hydrachnidia, the reduction in haemolymph osmolality does not appear gradually in the form of a clear persistent evolutionary transformation lineage (Fig. 4.1). On the other hand, it is obvious that the highest osmolality recorded was that of *Thyas barbigera*, a more primitive species. It lives in temporary pools where it is exposed to terrestrial conditions on a seasonal basis. This habitat is considered to be the possible ancestral habitat from which mites first diverged to an aquatic existence (Wiggins *et al.*, 1980). Thus, it seems possible that the high osmolality of *Thyas* is inherited from its terrestrial ancestor. High osmolality probably helps *Thyas* to endure drought situations in desiccated pools by reducing the evaporation of body water. This suggestion may be supported by the observation of significant seasonal variations


ANYSTAE
PARASITENGONAE
TROMBIDIA
HYDRACHNIDIA
EYLAOIDEA
EUHYDRACHNIDIA
NEOHYDRACHNIDIA
Anystis baccarum
Trombidium holosericeum
Limnochares aquatica
Eylais extendens
Hydryphantes ruber
Thyas barbigera
Hydrodroma despiciens
Hydrachna globosa
Sperchon setiger
Lebertia inaequalis
Arrenurus sinuator
Limnesia maculata
Piona coccinea
Unionicola crassipes
cHL ± s.d. (N)
349 ±20 (8)
383 ±26 (5)
254 ±25 (10)
250 ±10 (10)
274 ± 8 (10)
♂♂ 268 ♂♀♀ 302 ♀♀ 285* (10)
240 ± 5 (8)
233 ±20 (8)
♂♂ 252 ♂♀♀ 289 ♀♀ 270* (8)
274 ±20 (10)
240 ±14 (10)
250 ±12 (10)
247 ± 5 (10)
245 ±16 (8)
aerial phase of larva facultative
?
larva aquatic with obligatory aerial phase
adult and nymph aquatic
larva parasitic
plesiomorphic characters: larva, nymphs and adult free-living and terrestrial

in haemolymph concentration of *Thyas* (Olomski, unpublished). Values below 300 mosm/kg only occurred in the spring, when temporary pools in temperate latitudes are filled with water. From summer until winter, when water can be entirely absent from such pools, the haemolymph osmolality increased to values of 317–353 mosm/kg.

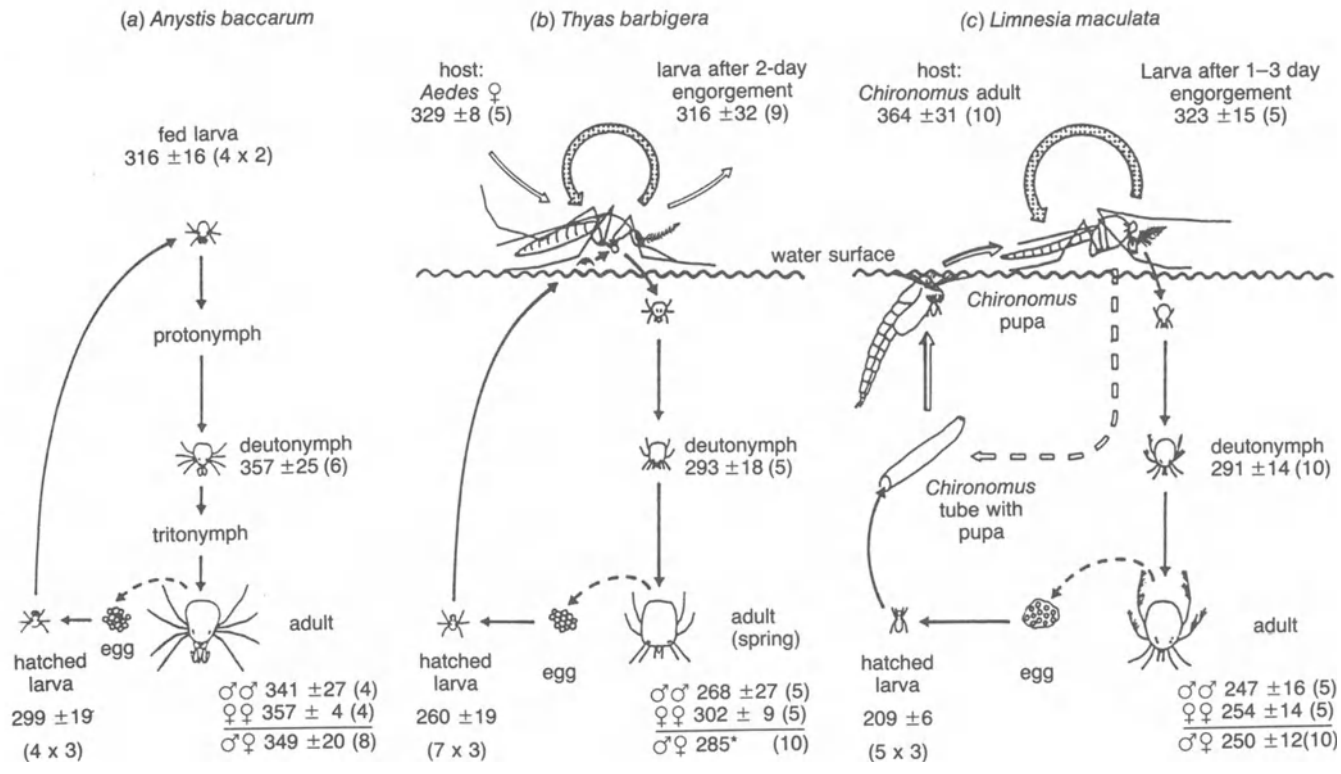
Ontogenetic changes in osmotic regulation

The five motile instars of *Anystis baccarum* (Fig. 4.2a) and all free-living terrestrial predators. Little is known about the life cycle of this species (Oudemans, 1936), and our own investigation has only just begun. The larvae were caught in spring, the three nymphal stages from mid spring until summer, and the adults from late spring until autumn. The overwintering form seems to be the egg or less likely, the larva. Thus, the life cycle of *Anystis baccarum* lasts a maximum of one year but it is possible that there is more than one generation per annum as is the case with *Anystis agilis* (Banks) (Sorenson *et al.*, 1976).

The haemolymph osmolalities of adult (c_{HL} 349 mosm/kg) and deutonymphal *Anystis* (c_{HL} 357 mosm/kg) were nearly equal. The c_{HL} values of the larvae were significantly lower, but still had 'terrestrial' values of 299 mosm/kg for hatched larvae and 316 mosm/kg for fed larvae. In accordance with the rather similar habits of the motile instars of *Anystis*, no major change in osmotic regulation seems to occur in its life cycle. This might have been the situation before Anystae and Parasitengonae separated from each other.

The water mite, *Thyas barbigera* (Fig. 2b), probably has a life cycle of at least two years (Mullen, 1977). Oviposition takes place in spring when temporary pools are filled with water. Larvae appear from late spring to mid summer. The larvae are essentially terrestrial. They come to the surface of the water where they crawl and jump on the surface film, and from which they attach to their hosts. The larva parasitizes ovipositing females, primarily of *Aedes* mosquitoes. After some days of engorgement, it drops off the host into water or into the wet part of a desiccated pool, and moults to deutonymph after an additional 1–3 weeks. The first winter is probably passed as a deutonymph and the second as an adult. Both forms prey on mosquito eggs (Mullen, 1977), and feed on dead nematoceran larvae (personal observation).

Fig. 4.1 Evolutionary changes in haemolymph osmolality (c_{HL}: mosm/kg ± s.d.) of adult males and females (n individuals per sample) of selected species of Hydrachnidia, Trombidia and Anystae tested during reproductive phase, and selected apomorphic characters (arrows). The phylogenetic relations follow Witte and Olomski (unpublished). Asterisk indicates significant difference ($P = 0.05$).


(a) Anystis baccarum
fed larva
316 ±16 (4 x 2)
protonymph
deutonymph
357 ±25 (6)
tritonymph
adult
egg
hatched
larva
299 ±19
(4 x 3)
♂♂ 341 ±27 (4)
♀♀ 357 ± 4 (4)
♂♀ 349 ±20 (8)
(b) Thyas barbigera
host:
Aedes ♀
329 ±8 (5)
larva after 2-day
engorgement
316 ±32 (9)
water surface
deutonymph
293 ±18 (5)
adult
(spring)
egg
hatched
larva
260 ±19
(7 x 3)
♂♂ 268 ±27 (5)
♀♀ 302 ± 9 (5)
♂♀ 285* (10)
(c) Limnesia maculata
host:
Chironomus adult
364 ±31 (10)
Larva after 1–3 day
engorgement
323 ±15 (5)
Chironomus
pupa
deutonymph
291 ±14 (10)
Chironomus
tube with
pupa
adult
egg
hatched
larva
209 ±6
(5 x 3)
♂♂ 247 ±16 (5)
♀♀ 254 ±14 (5)
♂♀ 250 ±12(10)

The hatched larvae of *Thyas* had a low haemolymph osmolality of 260 mosm/kg. After two days engorgement on an *Aedes* host, the haemolymph of the larvae (c_{HL} 316 mosm/kg) had nearly adjusted to the high osmolality of the host (c_{HL} 329 mosm/kg). Overwintered deutonymphs, collected early in the spring, showed a decreased haemolymph osmolality of 293 mosm/kg. In spring adults, a further reduction led to c_{HL} values, which were significantly below that of the engorged larva. The reduction was more marked in males (c_{HL} 268 mosm/kg) than in females (c_{HL} 302 mosm/kg), so that in some years the sexes differed significantly (Olomski, unpublished). Another significant reduction took place during development to the larva. *Thyas* may represent the situation at the base of the hydrachnid lineage when water mites invaded temporary pools, and where there occurred the initial adaptations in osmolality to the limnic environment.

The more derivative water mite, *Limnesia maculata* (Fig. 4.2c), has an annual life cycle (Böttger, 1972). Oviposition takes place from late spring to mid summer, and the larvae appear in the latter season. The larva is aquatic in that it swims and seeks its host under water. The larva loosely attaches to a pupa of Chironominae and commences an aerial phase after transferring to the emerged adult of the host. After 1–4 days' engorgement the larva drops off the host into the water, and moults to deutonymph shortly after. The deutonymph moults to adult before winter, so that only the adult stage hibernates.

As in *Thyas*, the lowest haemolymph osmolality in *Limnesia* occurred in the hatched larvae (c_{HL} 209 mosm/kg). Moreover, it was distinctly lower than the value of *Thyas* larvae. The osmolality increased dramatically when *Limnesia* larvae parasitized the *Chironomus* adults but never reached the higher value of their hosts (larvae: c_{HL} 323 mosm/kg; hosts: c_{HL} 364 mosm/kg. Deutonymphs on the point of moulting to adults, had the significantly lower osmolality of 291 mosm/kg, nevertheless, it was still higher than that of the adults (c_{HL} 250 mosm/kg). Thus, a significant reduction in the regulatory level occurs in three steps: first, from engorged larva to deutonymph, second, from deutonymph to adult and third, in development to the larva of the next generation. Thus in the

Fig. 4.2 Ontogenetic changes in haemolymph osmolality (c_{HL}: mosm/kg ± s.d.) of the anystid mite, *Anystis baccarum* (L.) (*a*) and the water mites, *Thyas barbigera* Viets (*b*) and *Limnesia maculata* (Müll.) (*c*). Filled arrows indicate development path of mite, and unfilled that of host; arrows filled with dots indicate parasitic phase of mite larva. Number in parentheses indicates the number of individuals per sample; where there are two figures, these indicate the number of samples and the number of individuals per sample respectively. Asterisk indicates significant difference ($P = 0.05$).

later derived water mite, *Limnesia*, there was a more pronounced reduction in haemolymph osmolality compared to *Thyas* in all motile instars. A high, 'terrestrial' osmolality is only achieved during the aerial, parasitic phase of the larva. This would appear to be conclusive evidence that in the Hydrachnidia, the transition from a terrestrial to a limnic existence is correlated with a progressive reduction in the regulatory level of haemolymph osmolality in the aquatic stages. As mentioned above, this is considered to be a phylogenetic adaptation to the low concentration in the limnic medium.

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5

Development and life-history strategies in mussel mites (Hydrachnellae: Unionicolidae*)*

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Unionicola intermedia (Koenike) and *U. ypsilophora* (Bonz) are unique in that they spend their life cycle, apart from the larval stage, in freshwater molluscs. *Unionicola aculeata* (Koenike) lays eggs and has its resting stages within *Anodonta anatina* (L.) and *A. cygnea* (L.) but the nymphs and adults are free living. Two of the three species discussed are known to be parasitic on Chironomidae in the larval stage. The eggs and larvae of unionicolids occupy different sites in and on their hosts depending on species. Adult chironomids with attached larval mites can be reared in the laboratory. Attention is paid to the early developmental stages of these mites but overall reproductive strategies are also considered including a review of previous work

INTRODUCTION

Unionicolid mites are known to exist all over the world. A number of species are associated with sponges or bivalve molluscs, and the larvae of some are now known to be carried by and to feed on Chironomidae. Within the mussel-mite group there is a division into resident (= stationary) species which live in mussels as nymphs and adults, and transient (= temporary) species using mussels only for transformation and to lay eggs, the nymphs and adults being free living.

It is now nearly 40 years since Mitchell and Pitchford (1953) described the structure and distribution of the two common water mites resident in British *Anodonta, Unionicola intermedia* (Koenike) *Anodonta anatina* (L.) and *U. ypsilophora* (Bonz) in *A. cygnea* (L.). A third species will also

be considered here – *U. aculeata* (Koenike), a transient unionicolid found in both *A. anatina* and *A. cygnea*.

A large amount of information on the mussel-mite group has been published in the last decade and aspects of this work together with some current work on the larval stage are reviewed here. Life-cycle strategies are also considered.

MATERIALS AND METHODS

Anodonta cygnea was collected from the upper lake at Roundhay Park, Leeds, Yorkshire (national grid reference SE 332384) and *A. anatina* from Wintersett, Yorkshire (reference SE 382150). Both were maintained in aerated tanks in an aquarium at 12°C with a 16-hour light and 8-hour dark regime.

Mite larvae from *A. anatina* were obtained by removing a small area of mantle tissue, *c.* 1 cm^2, and maintaining each piece separately in watch glasses in the dark at 20°C. The water was changed and aerated every few days. Freshly reared mite larvae from *A. anatina* were added, in batches of 20–60 at regular intervals, to mud with no *Anodonta* present. Insects (chironomid adults) emerging from the mud were collected. The temperature was maintained at 24°C with the same light regime. In a second experiment, tanks and trays containing mud and *A. cygnea*, aerated at 12°C, were covered with muslin to trap emerging insects, which were collected using a pooter. Larvae for identification were killed and mounted in 50% lactic acid or preserved in Koenike's fluid. Living specimens were attached to double-sided sellotape on stubs, gold coated, and examined in a Camscan electron microscope.

RESULTS

Larval identification of European species has been made possible by the work of Jones (1978) and Hevers (1980b). Accurate larval identification of American species is not yet possible but Jones and Baker (1984) have described and figured four larval types from New York State.

Larval attachment Soon after the adult insect emerges, *U. ypsilophora* larvae appear to be loosely attached and can easily be displaced from their sites. They become more firmly attached when actively feeding. Initially the body colour is red, believed to indicate haemolymph from the host, changing to grey brown, presumably as the larvae digest their food. The larvae normally lie with their gnathosomas directed towards

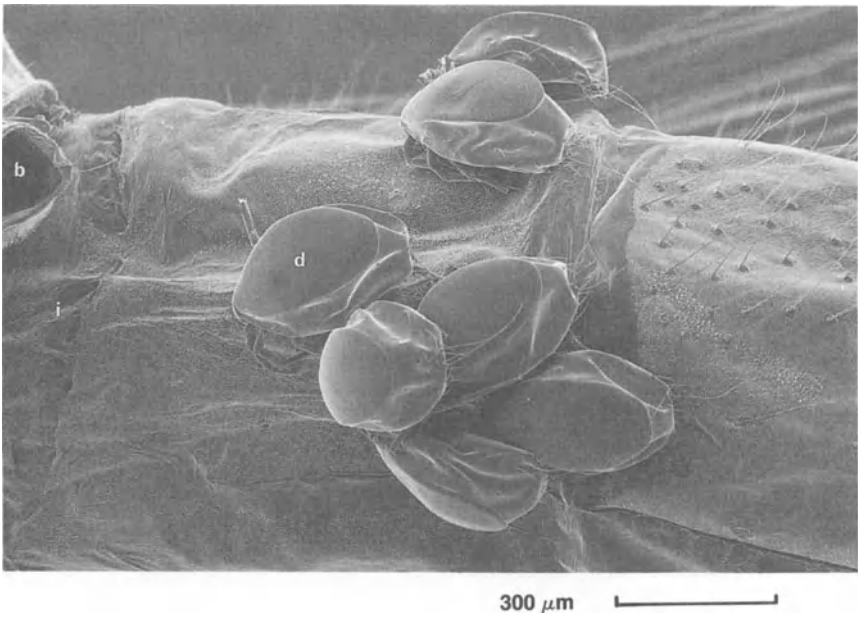

Fig. 5.1 Larvae of *Unionicola* sp. (probably *U. aculeata* (Koenike)) attached to ventral surface of the first abdominal segment of a chironomid adult. b, Base of third leg of insect; d, dorsal plate of larva; i, intersegmental region between thorax and abdomen.

the anterior end of the insect but may be transversely orientated when packed tightly together on the anterior abdominal tergites. The legs of the larva are folded backwards and it lies with the ventral surface of the larva touching the surface of the insect's cuticle. A slow rocking motion of the body has been observed as the pumping action of the pharynx draws in liquid food. Figure 5.1 illustrates larvae attached to the first abdominal segment of a chironomid.

Larvae attach initially to the pupal stage of chironomids. They are dragged through the pupal exuvium and become parasitic on the adult insect (Böttger, 1972; Hevers, 1980a). Details of the gnathosoma of *Unionicola* sp. are illustrated and described in Fig. 5.2. Larvae attach themselves to the host's cuticle by the pedipalps, which appear to be directed backwards below the cuticle of the host. Figure 5.3. illustrates this and the damage caused by the insertion of the pedilalps and chelicerae. The protracted cheliceral digits are blade-like and sharply pointed (Fig. 5.2), and are used for piercing and cutting. Hevers (1978) has described stylostome formation of *U. aculeata* in *Chironomus thummi*

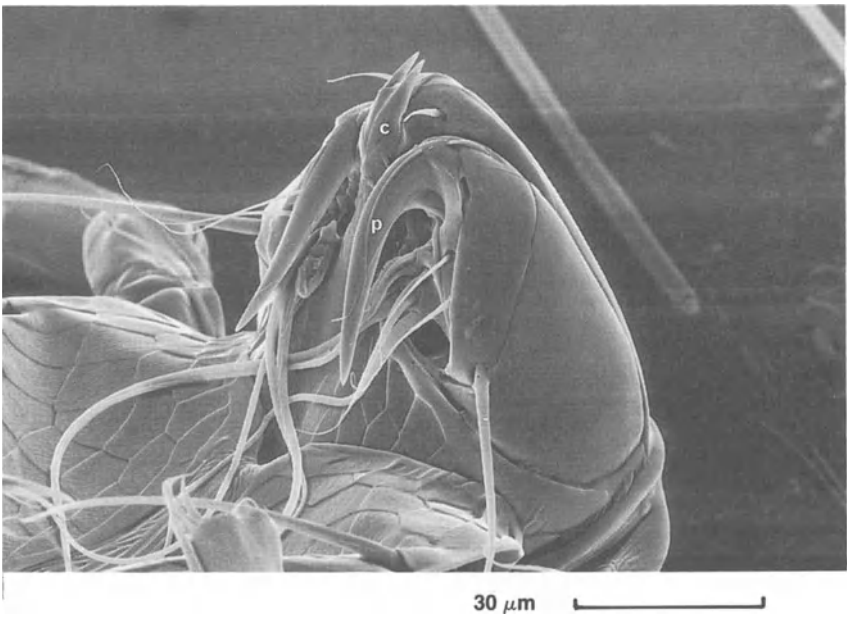

Fig. 5.2 Ventrolateral view of gnathosoma showing the sharply pointed and dorsally directed cheliceral digits (c) protruding through buccal aperture. The digits are used for cutting through the cuticle. The pedipalps are laterally situated, each with a long backwardly directed claw (p), and long slender setae arising from palp.

Kieffer. Jones (1978), by careful measurements, demonstrated considerable growth during this stage and was able to prove that larvae fed on chironomid adults.

Larval distribution on host Hevers (1978) has tabulated the sites selected for the attachment of *U. aculeata* on *C. thummi* in the laboratory, and has shown that the first abdominal segment is the preferred site, whereas in *U. ypsilophora*, the intersegmental region between thorax and abdomen is the site most commonly selected. Böttger (1972) working with *U. crassipes* (Müller) records larvae on the second and third legs and first abdominal segment.

Tables 5.1 and 5.2 summarize preliminary results for the distribution of larvae of *U. ypsilophora* and *U. aculeata* on their hosts. These tables show the proportion of flies parasitized, the average number of larvae per fly and the larval attachment sites on the flies. The proportion of all flies emerging in the laboratory from tanks containing *A. cygnea* infected

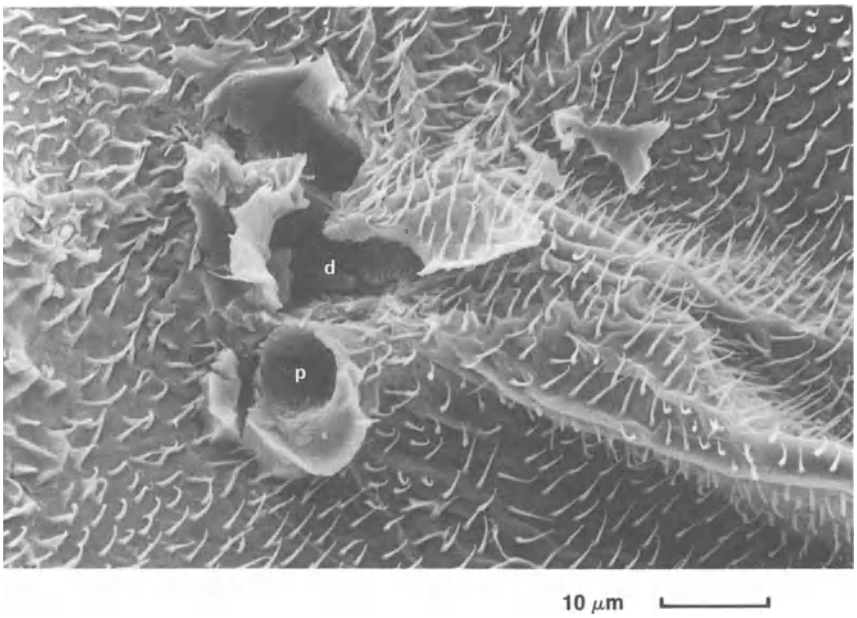

Fig. 5.3 Cuticle of chironomid adult with previously attached larva removed to demonstrate damage caused by insertion of chelicerae and pedipalps. The undulating surface of the cuticle probably indicates positions of pedipalp claws, one of which was inserted through perforation (p). The area damaged (d) by the action of the chelicerae is also shown.

with larvae was 14%, with an average of two mites per infected host (Table 5.1). In this experiment, the majority of larvae selected the intersegmental membrane between the thorax and abdomen as the preferred site for attachment.

Table 5.2 gives the result of the experiment in which larvae consisting of a mixture of *U. aculeata* and *U. intermedia*, hatched from eggs obtained from the mantle tissue of *A. anatina*, were introduced into tanks containing mud but without *Anodonta*. Here an average of three larvae occurred on each host, and roughly half the flies examined were infected. All the attached larvae examined were identified as *U. aculeata*. This confirms the work of Hevers (1980a), and again raises the question as to whether *U. intermedia* can complete its life cycle without an insect host, as discussed by Baker (1989), or on an alternative host to chironomids. Table 5.2 shows that the preferred site of *U. aculeata* is the first abdominal segment. No mites were found in the area between thorax and abdomen.

Table 5.1 Number and location of larvae of *Unionicola ypsilophora* (Bonz) and *U. aculeata* (Koenike) recovered from Chironomidae emerging over 31 days from a tank containing *Anodonta cygnea* (L.), maintained at 12 °C (181 flies examined, 25 of which parasitized)

Location site	*Number*
Intersegmental membrane between thorax and abdomen	21
1st abdominal segment	8
2nd abdominal segment	0
3rd abdominal segment	1
Legs	3
Loose/unattached	17
Total	50

Table 5.2 Number and location of larvae of *Unionicola aculeata* (Koenike) recovered from Chironomidae emerging from tank containing mud but no molluscs maintained at 24 °C (296 larvae of *U. aculeata* and *U. intermedia* (Koenike) added at intervals over 36 days; 30 flies examined, 14 of which parasitized)

Location site	*Number*
Intersegmental membrane between thorax and abdomen	0
1st abdominal segment	33
2nd abdominal segment	8
3rd abdominal segment	1
4th abdominal segment	1
Legs	0
Loose/unattached	1
Total	44

LIFE CYCLES AND STRATEGIES: A REVIEW

The life cycle of several European unionicolid species is known. Each has its preferred host. The life cycle includes egg, prelarva, larva, protonymph (postlarval resting stage I), deutonymph (nymph), tritonymph (postlarval resting stage II) and adult (Böttger, 1972, 1977; Crowell and Davids, 1979; Hevers, 1980a; Davids *et al.*, 1985; Baker, 1987). Dimock (1985) has described the population dynamics and life cycle of *U. formosa* in America and Gordon *et al.* (1979), the same species from Canada. Mitchell (1965) worked on the American species, *U. fossulata* (Koenike).

Hevers (1980a) has demonstrated the eggs of *U. ypsilophora* are laid in the gills and foot of *A. cygnea*, and those of *U. aculeata* in the mantle of

both *A. cygnea* and *A. anatina*. Eggs of *U. intermedia* are also laid in the mantle of *A. anatina*, and Baker (1989) has postulated that the eggs of *U. aculeata* are found more frequently at the siphonal end of the mantle. Although egg production occurs throughout the year, Dimock (1985) believes that oviposition and egg development are seasonal in *U. formosa*. Baker (1987) records ovigerous females throughout the year, forming 94% of all females recovered. Gordon *et al.* (1979) appear to have grouped together the eggs of several species in their analyses. Even a single musselmay contain several species of unionicolid mite (Jones and Baker, 1984), and errors can be made if the eggs are not bred to larvae and identified.

Larval development on chironomids (section Chironomini of the subfamily Chironominae) is now well established (Jones, 1965, 1978; Hevers, 1978, 1980a) for *U. aculeata* and *U. ypsilophora* but not for *U. intermedia*. Paterson and MacLeod (1979) claim to have demonstrated that in the laboratory, the larvae of *U. formosa* can develop to nymphs without an insect, and outside a mussel. Baker (1987) has tentatively suggested that *U. intermedia* may develop directly within mussels under certain conditions. Information on the nymphal stages of unionicolids is conflicting, and that available suggests that seasonal occurrence and incidence varies widely with species. Both Dimock (1985) and Baker (1987) found a winter increase in numbers, some overwintering as nymphs.

Seasonal variations in the abundance of females have been recorded by Dimock (1985) and Baker (1987), both of whom believe that *U. formosa* and *U. ypsilophora* respectively, live for about two years. On the other hand, Gordon *et al.* (1979) suggested a three-year cycle for *U. formosa*, and found no evidence for seasonal variations in females. Nymphs and females overwinter, the largest and oldest females occurring most frequently in the spring. These die off in late spring to early summer as the new generation gradually establishes itself (Baker, 1987).

Female-biased sex ratios are now well documented for unionicolids (Mitchell, 1965; Davids, 1973; Gordon *et al.*, 1979; Hevers 1980a; Dimock, 1983, 1985; Baker, 1987, 1989). They normally have sex ratios of two or more females/male. Dimock (1983) has also described the existence of female-harem or female-defence polygyny where a male gathers several females, establishes a territory consisting of the mantle of a single mussel, and defends up to several dozen females. When two males were maintained together in the laboratory, one killed the other within 72 hours, and frequently within 24 hours (Dimock 1983).

The primary sex ratio is not known. The final ratio of females/males may be determined by the mother, by the aggression of the male or by a combination of these factors. Since arrhenotoky is known to be widespread, and the dominant type of reproduction in the Actinedida (=

Prostigmata) (Oliver, 1983), it is reasonable to assume that unionicolids have unfertilized (haploid) eggs which develop into males, and fertilized (diploid) eggs which develop into females. Thus, the mother may have potential control over the sex ratio by controlling the release of sperm stored in her spermatheca (Sabelis, 1985). The first male larva to arrive in a mussel would mature to an adult, and then guard the territory against other males. Subsequent males would be killed, and females would congregate.

The benefits obtained by a unionicolid living inside a mussel are obvious. They live in a protected, relatively stable environment, competition with other species is avoided, the active stages are provided with an unlimited supply of food (Baker, 1976, 1977), and the eggs and resting stages are protected within the shell. Like other parasites living under similar conditions, unionicolids require appropriate adaptations for the dispersal of the species, and the larval stage is highly specialized to perform this function. In the species under consideration, the eggs are large and numerous. Large eggs are associated with habitats where hosts are abundant (Calow, 1978). Since larval mortality during host finding and feeding is likely to be great, large numbers are required. In entoparasites, eggs are often numerous, large and well provisioned in order to increase larval numbers, the probability of larval survival, and thus the success rate in infecting new hosts (Jennings and Calow 1975). It has been demonstrated that isolated larvae normally survive in the laboratory for an average of two weeks, and some for a month. Since the larval stage does not feed until attached to an insect, the larval lifespan suggests that the eggs are well provisioned. It is likely that *r*-selection strategies apply with a large proportion of resources devoted to reproduction.

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· PART TWO ·

Reproduction

6

*Spermatology in the Acari: systematic and functional implications**

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Sperm ultrastructure in the Acari is reflected against the background of current knowledge on arachnid and xiphosuran sperm cells. Acari possess highly diverse, aflagellate spermatozoa. The division of the Acari into no more than two major groups – Anactinotrichida and Actinotrichida – is supported by spermatological results. Within both groups it is possible to distinguish between plesiomorphic and apomorphic sperm types with taxon-specific characteristics. Spermatozoa are delivered from the male in a transport form, which is specifically altered in the female (capacitation), a process known from the Ixodida, Varroidae, Bdellidae, Tetranychidae, and Acaridida. Since sperm ultrastructure is related to mode of insemination and the fertilization conditions, some functional interpretations are included with special regard to the Anactinotrichida/Gamasida. An hypothesis is outlined which could describe some steps in the evolution of podospermy

INTRODUCTION

Since the discovery of 'animalculi' in the sperm of man by Leeuwenhoek (1676; reference from Taylor, 1963) spermatozoa have fascinated numerous scientists. From the very beginning, the independence of these cells, which behaved like small aquatic animals – Leeuwenhoek compared them to tadpoles – surprised investigators. It was felt that spermatozoa retained some primitive characteristics reminiscent of Protozoa, especially

* Invited paper.

Flagellata (Alexeiff, 1924). Extensive light-microscopy investigations, however, revealed that the sperm cells of Metazoa exhibit a range of interspecific variation unrivalled by any other cell type. Many deviate considerably from the 'Flagellata type'. Comparative studies by Retzius (1904–1921; reference from Baccetti and Afzelius, 1976; Franzén, 1956) laid the foundations for a classification of sperm cells. Another milestone was the detection that sperm-cell morphology was correlated with modes of fertilization (Franzén, 1956). A 'primitive' type of sperm has been defined, which occurs in numerous metazoan phyla and is correlated with external, aquatic fertilization. This type has been altered convergently in numerous taxa with the evolution of internal fertilization (Franzén, 1970; Baccetti and Afzelius, 1976; Baccetti, 1985). It is, thus, possible to discern evolutionary trends when comparing spermatozoa of related taxa, and this renders them suitable for systematic and phylogenetic considerations.

It is important to note that spermatozoa may undergo considerable alterations in the evolution of a particular taxon but remain almost invariably taxon specific. This implies that spermatozoa, often rich in well-defined characteristics, may assist in solving systematic problems. Furthermore, it is a cell type which is very suitable for studying evolution at the cellular level. In this respect, sperm cells differ from muscle cells, for example, which are rather uniform, or intestinal cells, which may exhibit extreme variations depending on their physiological state (Storch, 1979, 1985). Thus spermatozoa have become the cell type most intensively investigated from a comparative aspect. Many more than 1000 species from all major taxa have been studied (Baccetti and Afzelius, 1976; Baccetti, 1985). Wirth (1984) has discussed *in extenso*, aspects concerning the use of spermatological data in phylogenetics.

At present spermatozoa may be classified as follows (cf. Baccetti and Afzelius, 1976):

1. Primitive spermatozoa (aquatic fertilization).
2. Modified (derived) spermatozoa (internal fertilization) with flagellate, biflagellate and aflagellate subtypes.

Transitional forms are also found. The primitive type is characterized by a sperm head comprising a spherical nucleus with tightly packed chromatin, a short middle piece containing, commonly, four mitochondria, a pair of centrioles and a long flagellum ($9 \times 2 + 2$ axoneme) as the sperm tail (Franzén 1956; Baccetti, 1979). A presumably basic characteristic of the metazoan sperm cell is an acrosomal vesicle (vacuole) (Baccetti *et al.*, 1986), which is developed from Golgi vesicles, and is located at the apical part of the sperm head. The acrosomal vesicle is usually accompanied by pre- and subacrosomal material. The latter may contain a

preformed acrosomal filament (perforatorium) as in several Chelicerata (Alberti and Janssen, 1986; Alberti and Weinmann, 1985). The acrosomal region is often referred to as the acrosomal complex (Baccetti, 1979).

The modified flagellate type is still fairly close to the primitive type. The most important alteration is the elongation of the middle portion containing the mitochondria as energy suppliers for the movement of the flagellum. In contrast, aflagellate sperm cells usually deviate considerably from the primitive situation (Fig. 6.1). Each component may be altered and new structures added. This means that the classification just mentioned is only a very rough scheme to describe variations in sperm-cell morphology. Very detailed investigations are needed to detect and interpret the various characteristics, and such studies have only been possible since the introduction of the electron microscope.

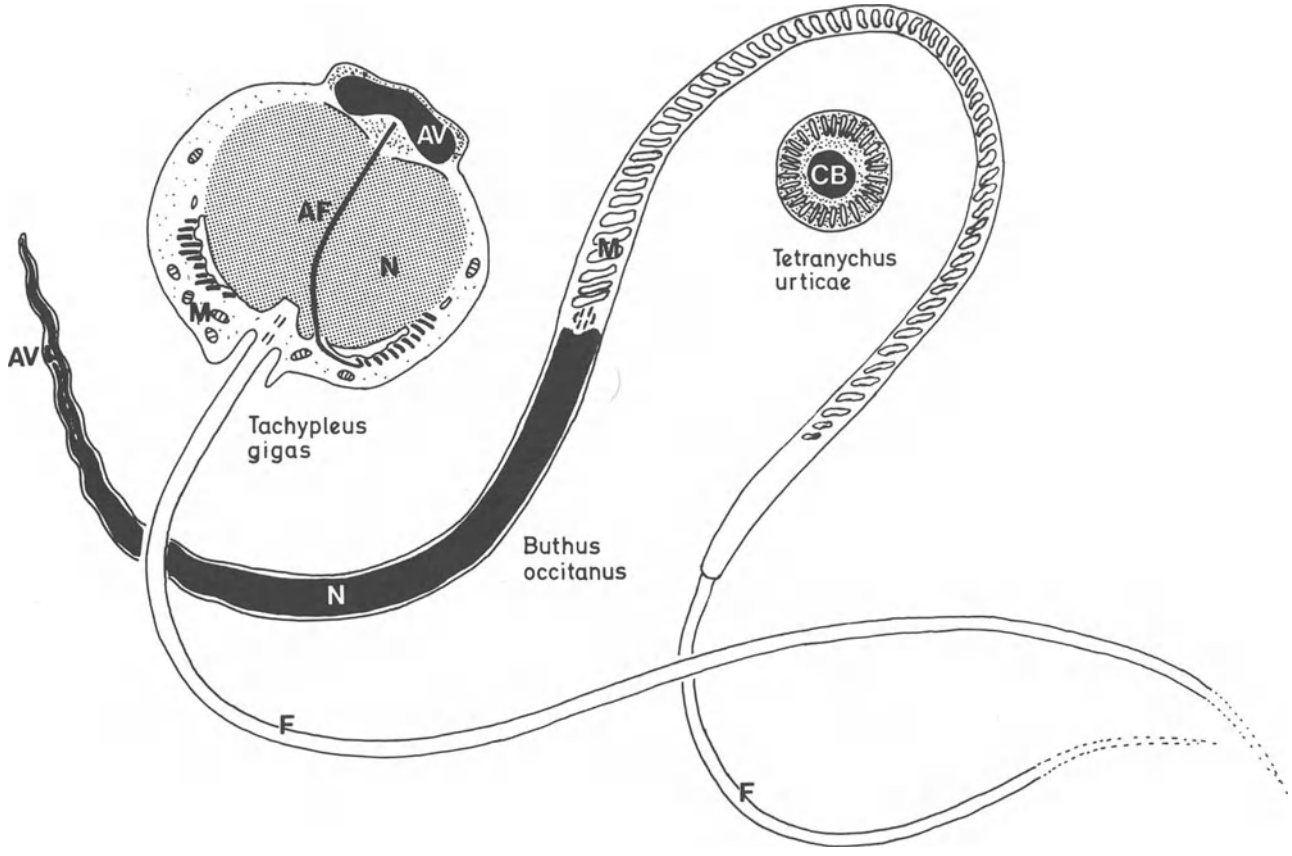
Sperm cells undergo a complex development (spermatogenesis, spermiogenesis) by means of which the cell is transformed from a 'normal' cell – comparable in ultrastructure to a somatic cell – to the highly specialized spermatozoon. Sometimes recapitulations of previous phylogenetic stages are indicated in the course of this transformation. At the completion of spermiogenesis, sperm cells are adapted for transfer into the female (transport form), and this, certainly, is influenced by the mode of insemination.

For several years it has been known that mature sperm cells are often (always?) not able to fertilize female germ cells in the state in which they are delivered by the male but require further alterations influenced by the female. This process, termed capacitation, can be confined to the molecular level as in man (capacitation *sensu stricto*; Baccetti and Afzelius, 1976), or may involve considerable structural reorganization of the spermatozoon (capacitation *sensu lato*; Oliver and Brinton, 1973).

Recently, sociobiological concepts have been introduced into spermatology. It is assumed that the usually very large numbers of spermatozoa compete due to the low probability of success in fertilizing a female germ cell. The concept of sperm competition implies adaptations at the cellular level as well as those of an anatomical or behavioural nature (Smith, 1984).

Although the reasons for the observed diversity of sperm cells are only partly understood (Baccetti and Afzelius, 1976), at least some constraints which may influence sperm morphology can be listed as follows:

1. The spermatozoon is a vehicle for the genetic material of the male. Thus it must contain, at least, DNA (see, for example, *Tetranychus urticae*; Fig. 6.1). However, aberrant (infertile) sperm may be devoid of nucleic acid.


AV
AF
N
M
AV
Tachypleus
gigas
CB
Tetranychus
urticae
M
Buthus
occitanus
N
F
F

2. The sperm cell must be adapted to the mode of insemination ♂ in connection with, for example, aquatic or internal fertilization with various modifications.
3. Where fertilization is internal, spermatozoa have to cope with the physiological environment in the female.
4. Spermatozoa must be capable of introducing the genetic information of the male into the female germ cell. Thus the morphology of the female germ cell is of importance.
5. Sperm cells may compete for an opportunity to fertilize.

These short and rather superficial remarks may suffice to demonstrate the complexity of the problems to be dealt with in investigations of sperm cells. Their description is only a first step in a comprehensive approach to their study.

SPERMATOZOA IN ACARI

The Acari are considered to be rather derived arachnids and this is reflected in their sperm morphology. All major taxa have been investigated including the Holothyrida, knowledge of which has been obtained only recently (Alberti and Mittmann, 1989). It appears certain that the Acari only possess aflagellate sperm. Major acarine sperm types are depicted schematically in Fig. 6.2, which should be regarded as fairly representative as about 80 species representing all the major taxa have been investigated.

This rather simple classification enables one to draw some important conclusions. First, it is shown that the aflagellate sperm cells are represented in an astonishing diversity which can be only partly illustrated here (cf. Figs 6.4 and 6.5). The tick spermatozoon which, because of its large size, was one of the earliest to be studied (for example, Samson, 1909), is not representative of all Acari as is indicated in a number of review articles and textbooks. Furthermore, it is shown that the spermatozoa of the Anactinotrichida (Parasitiformia) and Actinotrichida (Acariformia) are profoundly different; there are no synapomorphies between each (Alberti, 1980*a*,*b*, 1984). Moreover, as a result of the observations on the Holothyrida it is now evident that the very complex and highly

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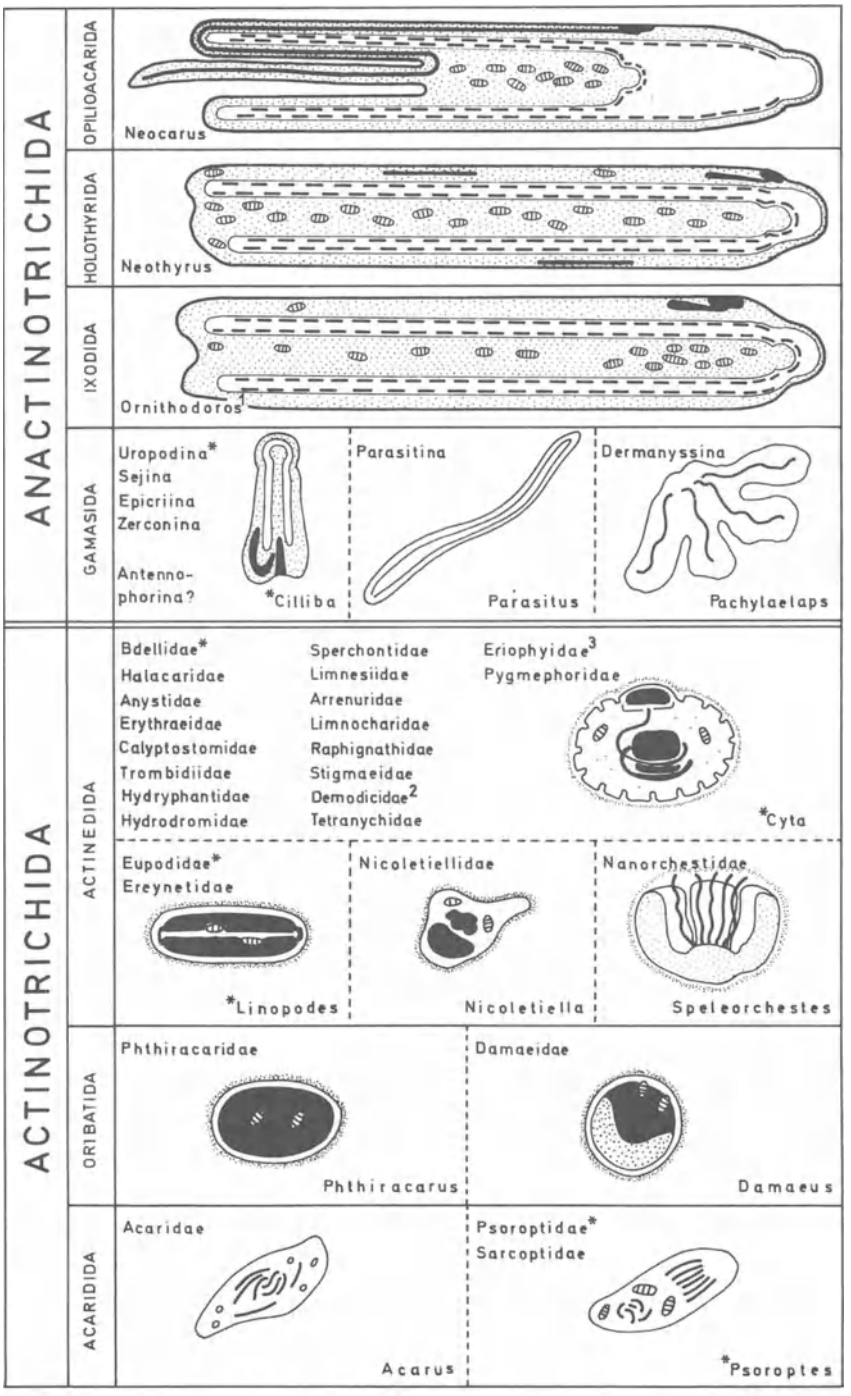
Fig. 6.1 Main types of spermatozoa in Chelicerata. The xiphosuran, *T. gigas*, represents primitive type, the scorpion, *B. occitanus*, modified flagellate, and the actinotrichid mite, *T. urticae*, modified aflagellate type (based on Alberti and Janssen, 1986; Alberti, 1983; Alberti and Storch, 1976*a*). AF, acrosomal filament; AV, acrosomal vacuole; CB, chromatin body; F, flagellum (axonema not shown); M, mitochondria; N, nucleus.

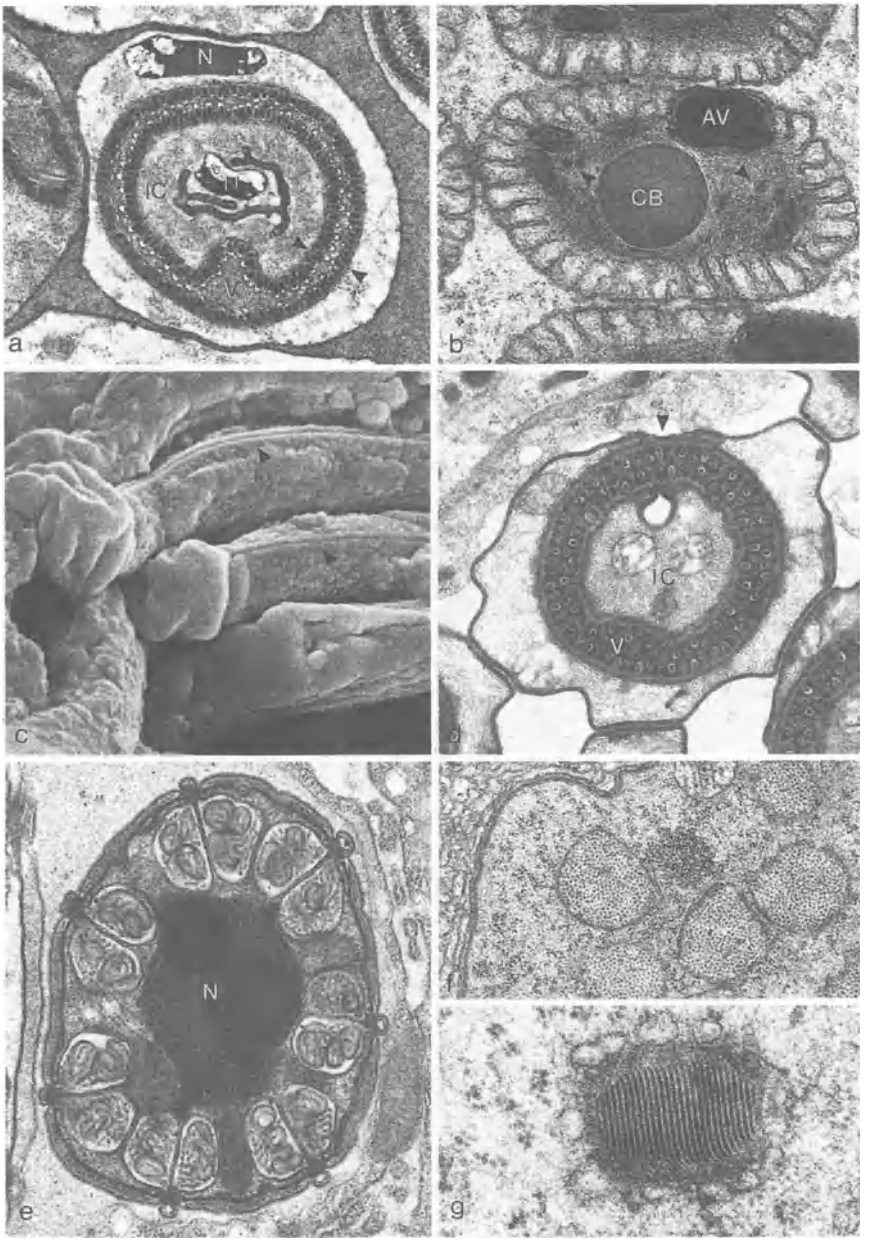

ANACTINOTRICHIDA
OPILIOACARIDA
Neocarus
HOLOTHYRIDA
Neothyrus
IXODIDA
Ornithodoros
GAMASIDA
Uropodina*
Sejina
Epicriina
Zerconina
Antenno-
phorina?
*Cilliba
Parasitina
Parasitus
Dermanyssina
Pachylaelaps
ACTINOTRICHIDA
ACTINEDIDA
Bdellidae*
Halacaridae
Anystidae
Erythraeidae
Calyptostomidae
Trombidiidae
Hydryphantidae
Hydrodromidae
Sperchontidae
Limnesiidae
Arrenuridae
Limnocharidae
Raphignathidae
Stigmaeidae
Demodicidae2
Tetranychidae
Eriophyidae3
Pygmephoridae
*Cyta
Eupodidae*
Ereynetidae
*Linopodes
Nicoletiellidae
Nicoletiella
Nanorchestidae
Speleorchestes
ORIBATIDA
Phthiracaridae
Phthiracarus
Damaeidae
Damaeus
ACARIDIDA
Acaridae
Acarus
Psoroptidae*
Sarcoptidae
*Psoroptes

derived type of sperm known from ticks is found in all major taxa of the Anactinotrichida including the Opilioacarida. This type is certainly a symplesiomorphy of the Anactinotrichida, which is a rather unexpected finding, bearing in mind that the Opilioacarida are regarded as early derived mites and thus, with plausibility, could be expected to possess a more 'primitive' sperm cell. Weygoldt and Paulus (1979a,b), in their comprehensive study of chelicerate morphology and systematics, did not exclude completely the possibility that the Opiolioacarida might have flagellate sperm. The sperm type in question was termed the 'vacuolated type' (Alberti, 1980a, 1984). As a plesiomorphic characteristic it possesses a complete acrosomal complex with acrosomal vacuole and filament (perforatorium). The shape of the acrosomal vacuole, however, is extraordinary and apomorphic. It is a flat cisterna extended below the plasmalemma. Another derived and most conspicuous character is a large vacuole, which is developed in the course of a very complicated spermiogenesis (Breucker and Horstmann, 1972; Alberti, 1980a). The membrane delimiting the vacuole bears numerous microvilli-like protrusions (cellular processes) arranged parallel to the vacuole membrane (Figs 6.3a,d and 6.4).

The 'ribbon' type spermatozoon, in contrast to the vacuolated type, does not possess a large vacuole. Instead, it is characterized by longitudinally arranged bands (stiff bands) of infoldings (Alberti, 1980a, 1984; Witalinski, 1975; 1979) (Figs 6.3e and 6.6c). This type has been found in the Parasitidae, Rhodacaridae, Ologamasidae, Pachylaelapidae, Macrochelidae, Phytoseiidae, and Varroidae (Alberti, 1984; Alberti, 1989; Alberti and Hänel, 1986). There are at least two recognizable subtypes: a regular, highly structured, fusiform type which is found exclusively in the Parasitidae, and an irregular type, which seems to be less structured and occurs in all the remaining groups so far investigated. As a plesiomorphic feature in at least some of these ribbon spermatozoa, flat cisternae are situated under the plasmalemma, and these have been interpreted as homologous with the acrosomal cisternae of vacuolated spermatozoa (Alberti, 1980a). Many structures, for example, inclusion bodies (Fig. 6.3f,g), are new and their function is unknown.

Contrary to the normally very complex and often quite large spermatozoa of the Anactinotrichida – *Ornithodoros tholozani*, for example, is *c.*

Fig. 6.2 Sperm types of Acari. Asterisks indicate taxa illustrated. Note the basic difference between sperm morphology of Anactinotrichida and Actinotrichida (in part after Alberti, 1984; *Ornithodoros* after Feldman-Muhsam and Filshie, 1979; Demodicidae after Desch, 1984; Eriophyidae after Nuzzaci and Solinas, 1984).


N
IC
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1000 μm long in the capacitated state (Feldman-Muhsam and Filshie, 1979) – the sperm cells of the Actinotrichida are small and rather simply structured (Alberti, 1980b, 1984). It is only within the Actinedida (heterostigmatic mites included) that an acrosomal complex has been found as a plesiomorphic character (Figs 6.2, 6.3b and 6.5). Peculiarities include the partial reduction of the nuclear envelope, and an acrosomal filament lying freely in the cytoplasm after penetrating the chromatin body. In many of the Actinedida, the cell periphery is specialized, forming small, regular tubercles (Bdellidae), radial tubules (Tetranychidae), cisternae (Erythraeidae) or chamber-like infoldings (Trombidiidae, Calyptostomidae, some 'Hydrachnidia') (Alberti, 1980b; Alberti and Storch, 1976a,b) (Figs 6.3b and 6.5). However, there are no indications to suggest any homology with the vacuoles or surface structures of sperm cells of anactinotrichids. Very curious are the sperm cells of *Speleorchestes podur-oides*, which is the only endeostigmatic mite investigated so far (Fig. 6.2). These cells look flower-like with loosely dispersed chromatin; there is no acrosomal complex. Microvilli-like processes are located in the centre of the 'flower' (Alberti, 1980b). Certainly, this type of sperm is highly derived. The spermatozoa of Eupodidae, Ereynetidae, Nicoletiellidae, and Tetranychidae, although simple in structure (Fig. 6.2) (Alberti, 1980b, 1984; Alberti and Storch, 1976a; Pijnacker and Drenth-Diephuis, 1973), are also very unusual.

The first investigations of spermatozoa of Oribatida suggested that the morphology of these cells is likewise rather simple (Fig. 6.2). Although this view remains valid in principle, it appears that there are differences between the sperm of *Phthiracaridae* – the only representatives of the 'lower' Oribatida investigated – and several species of 'higher' Oribatida in which 'dense bodies' occur as new (synapomorphic?) structures (Alberti, 1980b; Kümmel, 1982; Kümmel and Dobner, 1986; Witalinski,

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Fig. 6.3 Transmission (a,b,d–g; transverse sections) and scanning (c) electron micrographs of acarine sperm cells. (a) Mature sperm cell of *Neocarus texanus* (× 11 880). Cellular processes are marked by arrows. (b) Pre-mature spermatozoon of *Cyta latirostris* showing acrosomal filament (arrows) (× 23 750). (c) Spermatozoa of *Discourella cordieri* (× 9170). The arrows indicate longitudinal furrow, which corresponds to a cleft within acrosomal vacuole extending below the plasmalemma. (d) Vacuolated sperm cell of *Oodinychus ovalis* showing cleft (arrow) (× 15 830). (e) Ribbon spermatozoon of *Parasitus berlesei* (× 15 830). Note the regularly arranged peripheral chambers which constitute longitudinal ribbons or stiff bands. (f) Early stage of spermiogenesis in *Parasitus berlesei* with granular inclusion bodies (× 15 830). (g) Early stage of spermiogenesis in *Pergamasus crassipes* with inclusion bodies exhibiting striation pattern (striated bodies) (× 46 670). AV, acrosomal vacuole; CB, chromatin body; IC, inner core (cytoplasmic column); N, nucleus; V, vacuole.

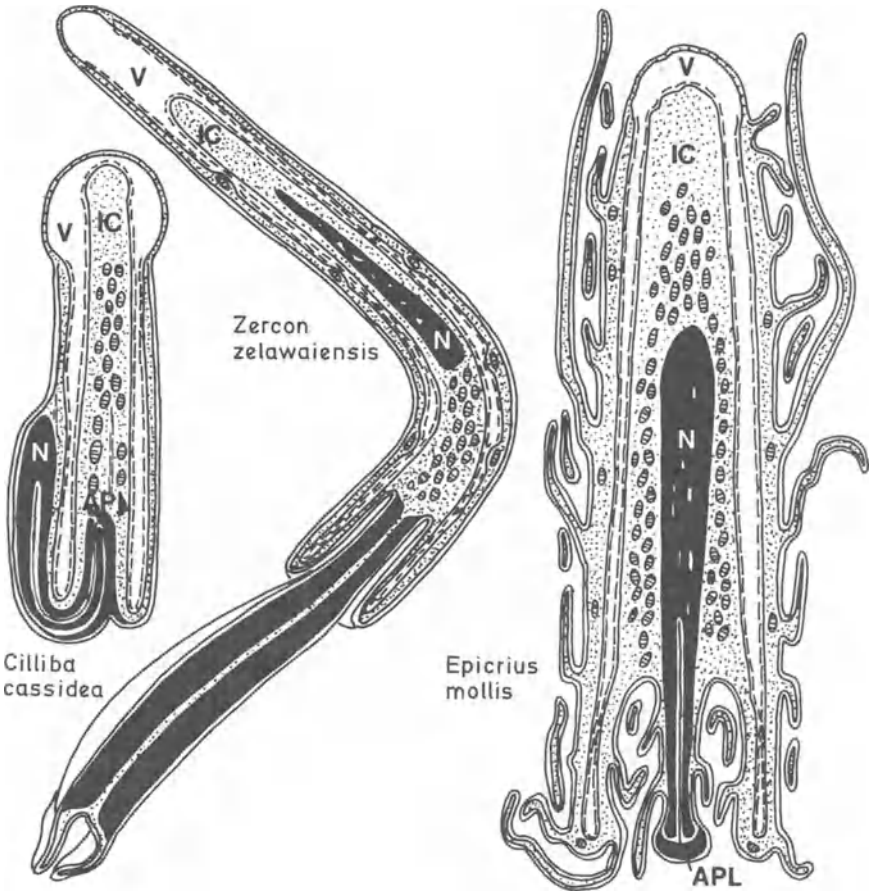

Fig. 6.4 Vacuolated spermatozoa of species belonging to Uropodina (*C. cassidea*), Zerconina (*Z. zelawaiensis*), and Epicriina (*E. mollis*) demonstrating remarkable structural variation (in part after Alberti, 1980a). APL, acrosomal plate; IC, inner core; N, nucleus; V, vacuole.

1982). These authors' and my own unpublished results indicate that the shape of the cell may differ considerably between species, and that further characteristics such as small protrusions also require study.

In contrast to these findings, which reveal more variation in the Oribatida than anticipated, the sperm morphology of Acaridida can still be regarded as rather uniform. Publications are available on Acaridae, Psoroptidae, and Sarcoptidae (Alberti, 1980b, 1984; Witalinski, 1988; Witalinski and Afzelius, 1987; for further references see Witalinski *et al.*, 1986). In all species the chromatin is arranged in fine strands and a

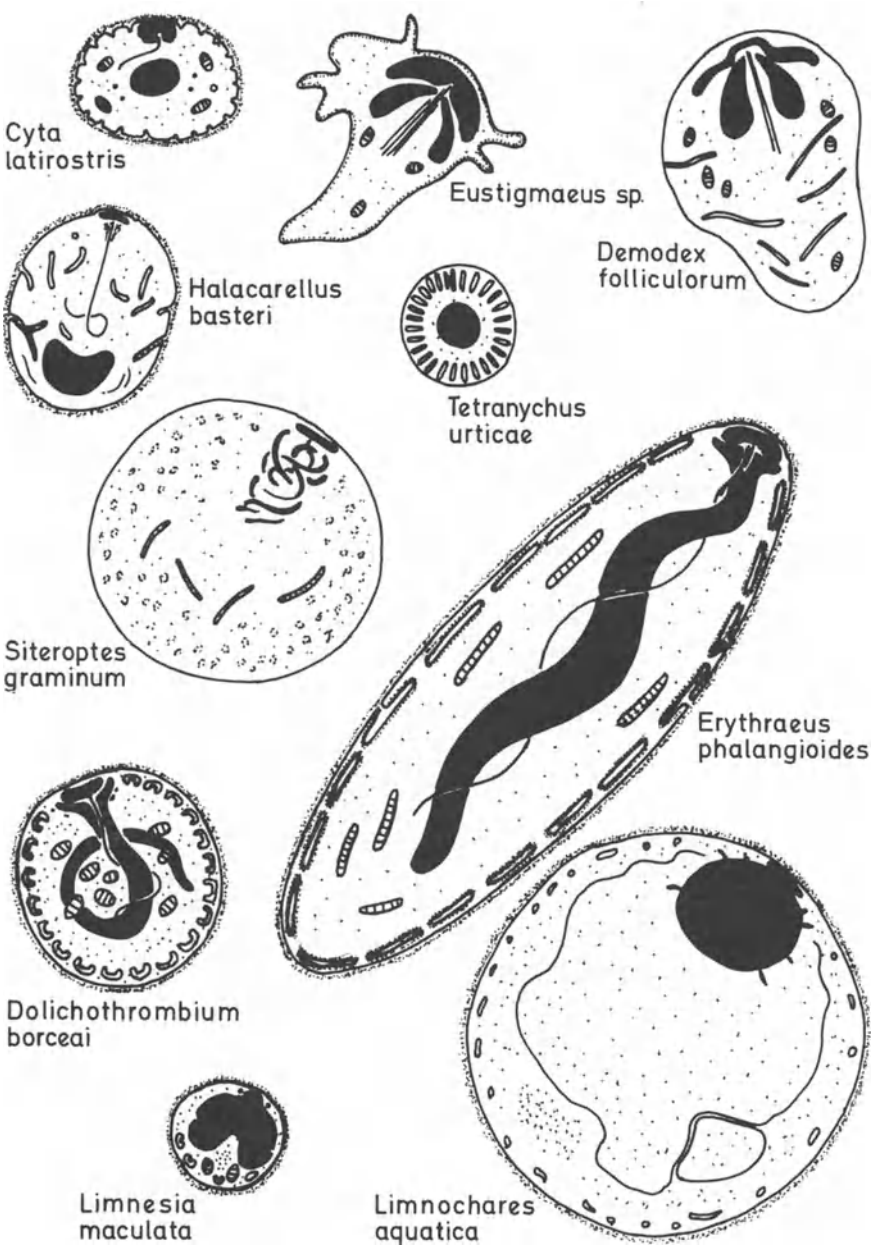

Fig. 6.5 Drawings of 10 spermatozoa depicting variations of the 'bdellid' sperm type in Actinedida: *C. latirostris* (Bdellidae), *H. basteri* (Halacaridae), *Eustigmaeus* sp. (Stigmaeidae), *D. folliculorum* (Demodicidae), *T. urticae* (Tetranychidae), *S. graminum* (Pygmephoridae), *E. phalangioides* (Erythraeidae), *D. borceai* (Trombidiidae), *L. maculata* (Limnesiidae), *L. aquatica* (Limnocharidae) (based on findings of Alberti, 1980b, and Desch, 1984 for *D. folliculorum*).

nuclear envelope is lacking. The cells contain distinct membranes or tubules. In conclusion, a morphology of sperm cells as found in bdellids might be considered plesiomorphic within the Actinotrichida.

ACARINE, OTHER ARACHNID AND XIPHOSURAN SPERM CELLS COMPARED

An outgroup comparison is essential for thorough systematic interpretations. This is possible since at least one species of each of the arachnid orders has been investigated.

It is well known that the Xiphosura are the only Chelicerata having sperm cells still close to the primitive type (Fahrenbach, 1973) though deviations from the classic concept are already recognizable (Afzelius, 1979; Alberti and Janssen, 1986). Scorpions possess modified flagellate sperm of filiform appearance (for further references see Alberti, 1983). In several groups of arachnids, a characteristic reorganization of the flagellate spermatid occurs towards the end of spermiogenesis. The cell is coiled up and the flagellum or axonema, respectively, is withdrawn into the spherical cell body (Pseudoscorpiones, 'Pedipalpi', Araneae and Ricinulei) (Alberti and Palacios-Vargas, 1984, 1987; Alberti and Weinmann, 1985; Alberti *et al.*, 1986; Boissin, 1974; Werner and Bawa, 1988). This process is still recognizable in the cyphophthalm opilionid, *Siro rubens* (Juberthie and Manier, 1978). Mature spermatozoa of opilionids belong to the aflagellate type. Dimorphic sperm cells are produced by *Siro*, which is, without doubt, a derived character. In Palpigradi (Alberti, 1979) and Solifugae (Alberti, 1980c) aflagellate spermatozoa occur but only one species has been studied in each order.

From this short overview it is evident that the spermatozoa of the Acari are among the most derived types. As has already been demonstrated, the vacuolated type is to be regarded as plesiomorphic within the Anactinotrichida, whereas the 'bdellid' type is plesiomorphic within the Actinotrichida. Because of the essential differences between these two types and their lack of synapomorphies, it seems reasonable to compare each with the sperm cells of other arachnids. Unfortunately, it is not possible at present, to determine direct relationships from such comparisons, to support the foundation of sister-group relationships with those taxa most frequently referred to as being most closely related to the Acari, namely, the Opiliones, Ricinulei and Palpigradi (van der Hammen, 1977, 1985; Lindquist, 1984; Weygoldt and Paulus, 1979a,b). Actinedid sperm cells exhibit certain similarities to those of the Solifugae. In the latter, the nuclear envelope is also partly reduced and the chromatin body is penetrated by the acrosomal filament, which is likewise coiled

within the cell. The disc-shaped sperm cell of the Solifugae possesses regular processes at its periphery. The spermatozoa of Solifugae are arranged in regular piles. Sperm bundles have also been observed in bdellids but these are formed within the testicular lumen whereas those of Solifugae are established within the testicular cysts. Moreover, it should be borne in mind that only one species of Solifugae has been investigated, and consequently little is known about spermiogenesis in this order. Nevertheless, it is remarkable that the testes of both the Actinotrichida and Solifugae are composed of a secretory and a germinative part, an arrangement not found to the author's knowledge in any other arachnid order.

Results regarding the Anactinotrichida are similarly disappointing when searching for indications of sister-group relationships. However, from the spermatological point of view, there are, nevertheless, very interesting features. The most conspicuous characteristic of the plesiomorphic sperm of Anactinotrichida is the large vacuole formed, during a very complicated spermatogenesis, by Golgi-derived vesicles arranged at the periphery of the cell. Vacuoles or distinct cisternae, produced early in spermatogenesis by Golgi vesicles, are also found in the Palpigradi and Ricinulei (Alberti, 1979; Alberti and Palacios-Vargas, 1984). In *Prokoenenia wheeleri*, there is a very large vacuole occupying most of the volume of the cell. In contrast, in *Cryptocellus boneti*, two flat cisternae, located beneath the plasmalemma, surround the central cytoplasm like a cyst shell. Small vesicles and cisternae are commonly found also in the Pseudoscorpiones (Boissin, 1974; see also Werner and Bawa, 1988) and 'Pedipalpi' (Alberti and Palacios-Vargas, 1987; Jespersen, 1978). In some Araneae, vacuoles may be quite large (Alberti and Weinmann, 1985). Thus the vacuolation of sperm cells seems to be a rather old phenomenon within the Arachnida, and should be seen in the context of the transport of spermatozoa and their capacitation (see below).

Clearly, the 'vacuole' is not sufficient to indicate a sister-group relationship of the Anactinotrichida with other groups of Arachnida because these vacuoles do not share a specific characteristic (for example, cellular processes) with the vacuoles of anactinotrichid sperm cells. Nevertheless, the assumption of a common phylogenetic basis for this peculiarity appears likely.

A flat acrosomal vacuole, a further very strange structure of the vacuolated type, is also not found in other Arachnida. In the Palpigradi, the acrosomal vacuole is a broad band but again no specific similarities are recognizable. A very interesting aspect is concerned with a probable newly acquired function of the acrosomal vacuole of anactinotrichid sperm. It appears that the expanding flat cisterna is determining the

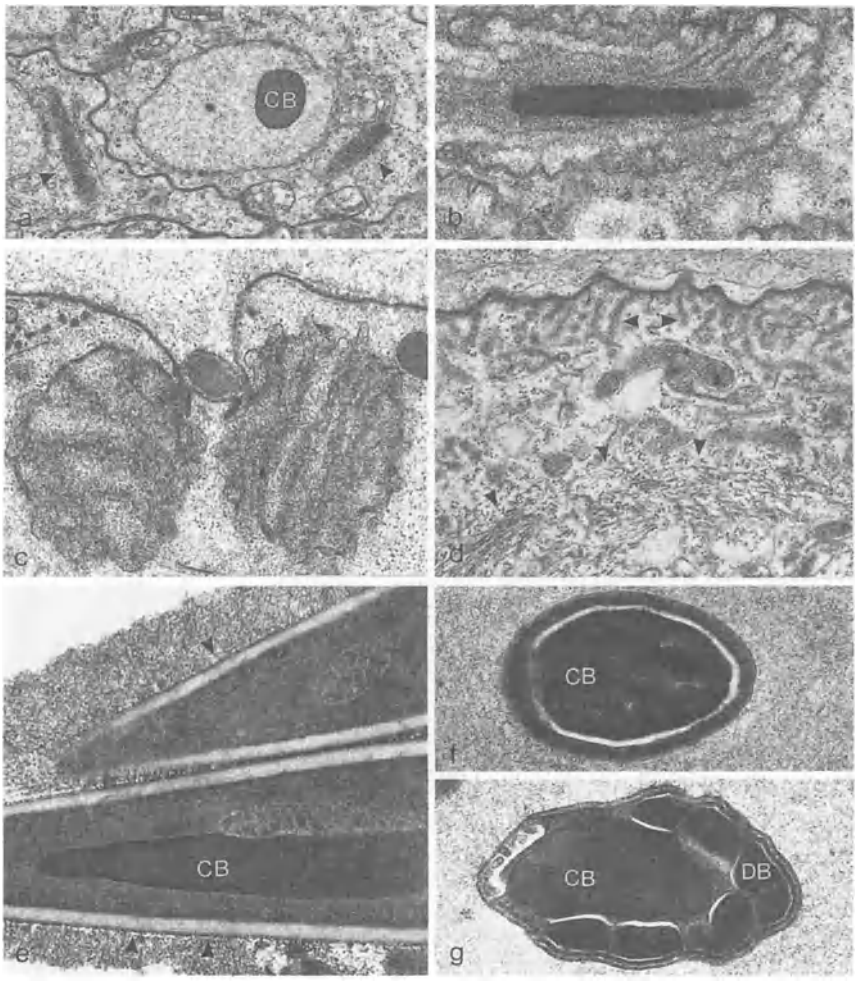

Fig. 6.6 Transmission electron micrographs of sperm cells of Acari at various stages of development (a–e), and two examples of simply structured sperm of Uribalida (f–g). (a) *Cyta latirostris*: early spermatids with intact nuclear envelope and ciliary root-like structure developing from centrioles (arrows) (× 11 880). (b) *Cyta latirostris* with same structure in a late spermatid (× 23 750). (c) *Varroa jacobsoni*: transverse section through ribbon structure in the periphery of pre-capacitated sperm cell (× 15 830). (d) *Varroa jacobsoni*: periphery of capacitated sperm cell. Note smooth surface and different types of filaments (arrows) (× 15 830). (e) *Bdella septentrionalis*: mature sperm cells surrounded by tight secretory sheath (arrows) (× 30 000). (f) *Phthiracarus* sp.: simple spermatozoon with secretory sheath (× 15 830). (g) *Galumna* sp.: spermatozoon with dense bodies and small protrusions (× 15 830). CB, chromatin body; DB, dense body.

shape of the developing sperm cell. In some opilionids, a superficially similar shaping of the spermatid occurs, also starting from the acrosomal region. However, the acrosomal vesicle is not extended, and the shaping of the cell may be the result of a connection between the transforming nucleus and the plasmalemma by a dense (pre-/subacrosomal?) material (Alberti, unpublished). Thus, this similarity is not easily interpreted. Other similarities, such as a superficial resemblance of the shape of the spermatids should not be overstressed.

Though sister-group relationships, based on spermatological characteristics, cannot be established, it is nevertheless noteworthy that the two basic sperm types found in the Acari can be related to sperm cells of other Arachnida with equal or even better justification than to each other. Acari are also derived with respect to their spermatozoa. Although centrioles have been occasionally observed in the early stages of spermiogenesis (Alberti, 1980a,b; Witalinski, 1985a), only in *Cyta latirostris* (Actinedida: Bdellidae) is a structure developed which reminds one of a ciliary root, and which is retained in the mature cell (Fig. 6.6a,b). Furthermore, it is important to remember that the vacuolated type is a very exceptional one, not found in any other arachnid order nor even any other animal taxon. Obviously it is a very strong synapomorphy of the taxa concerned.

SPERMATOZOA WITHIN THE ACARI COMPARED

Whereas the outgroup comparison can be based on a limited but well-selected number of species, much more information is required for interpretations concerning the relations within such a diverse taxon as the Acari. At present, the basis for such an intra-taxon comparison is still rather narrow.

From the spermatological data (see above) it is evident, nevertheless, that the Anactinotrichida and Actinotrichida are widely separated. There are no synapomorphies (Alberti, 1980a,b, 1984) (Fig. 6.2). Furthermore, the Opilioacarida, Holothyrida, Ixodida, and Gamasida are connected by the synapomorphic (outcrop comparison) vacuolated-sperm type, and thus form a monophyletic taxon. From the spermatological point of view, the monophyly of the Anactinotrichida could be doubted only if it were possible to demonstrate that the plesiomorphic actinotrichid sperm had evolved from the vacuolated type. In this case, the Anactinotrichida would be paraphyletic, and monophyly of the Acari as a whole would be the consequence. So far there are no indications which would support such an interpretation. On the contrary, it appears that the vacuolated type has been very stable in evolution, and apparently has only given rise to the ribbon type and its

subtypes. The prevalent modifications, however, are correlated with very specific conditions.

The ribbon type is obviously the derived type within the Anactinotrichida and, most likely, a synapomorphy of the taxa already mentioned. This implies that taxa with vacuolated sperm, the ticks, for example, cannot originate from taxa with ribbon sperm. Uropodina, Sejina, Epicriina, Zerconina and Antennophorina represent early-derived taxa in contrast to those possessing ribbon spermatozoa (Alberti, 1980a; Alberti, 1989; Alberti and Blaszak, unpublished). An extensive analysis should demonstrate sister-group relationships between these taxa possessing vacuolated sperm cells. Figure 6.4 shows that this type is rather variable, and may thus provide enough information for such an analysis; Uropodina, for example, seem to be characterized by a longitudinal cleft in their acrosomal cisterna (Alberti, 1980a, 1984) (Fig. 6.3c,d). The ribbon type also confers much information. Present knowledge suggests that the regular type is only found in the Parasitidae whereas the irregular one is typical of the remaining taxa that have been investigated. Thus the validity of the taxa, Parasitides and Dermanyssides (Evans and Till, 1979) or Parasitina and Dermanyssina (Johnston, 1982) is supported by these findings (Alberti, 1980a, 1984; Alberti and Hänel, 1986; Witalinski, 1975, 1976, 1979). Additional synapomorphies are again detectable at a lower taxonomic level. Within the Parasitidae, specific inclusions, characterized by an intricate striation pattern only occur in *Pergamasus* and *Holoparasitus*; they are not present in *Parasitus* (Fig. 6.3f,g). In the Dermanyssina, the ribbon type seems to differ considerably. These variations still await a detailed analysis which, however, is only possible when more taxa have been studied.

The same situation is found in the Actinotrichida. Spermatozoa are simple but nevertheless very characteristic. The few data available suggest that Acaridida are rather homogeneous. However, Witalinski and Afzelius (1987) have recently demonstrated differences which could indicate, for example, that sarcoptids are more derived than psoroptids. In the Oribatida (Fig. 6.6f,g), it appears again that it will be possible to reach important conclusions after the study of additional taxa. Certain types of sperm may be suitable to unify certain higher-category groupings (Alberti, 1980b; Alberti *et al.*, unpublished; Kümmel, 1982; Kümmel and Dobner, 1986; Witalinski, 1982).

More information about the Actinedida is now available. The spermatozoa of many taxa can be related to the plesiomorphic 'bdellid' type (Fig. 6.5); these include the Halacaridae, Anystidae, Erythraeidae, Trombidiidae, Calyptostomidae, Hydrodromidae, Limnocharidae, Sperchontidae, Limnesiidae, Pionidae, Arrenuridae, Raphignathidae, Stigmaeidae, Demodicidae, Tetranychidae, Eriophyidae and Pygmepho-

ridae (Alberti, 1980b; Alberti and Storch, 1976a,b; Desch, 1984; Nuzzaci and Solinas, 1984; Pijnacker, 1985; Witalinski, 1985a,b; Witte and Storch, 1973). All freshwater mites investigated are rather similar with *Limnochares aquatica* (Limnocharidae; Fig. 6.5), the only exception. The Parasitengona (Erythraeidae, Calyptostomidae, Trombidiidae, 'Hydrachnidia' probably with the exception of *L. aquatica*) are characterized by peripheral cisternae (*Erythraeus*), or chamber-like infoldings (the remaining taxa). The Tetranychidae possess very simple spermatozoa consisting of a chromatin body, some cytoplasm and an elaborate system of radial tubes. This type can be connected to the plesiomorphic type via the sperm of representatives of the related families, Demodicidae, Stigmaeidae and Raphignathidae. The spermatozoa of *Demodex* and *Eustigmaeus* are remarkably alike (Fig. 6.5). The sperm cells of Eriophyidae are less simplified than those of Tetranychidae. This means that the Eriophyidae cannot easily be related to tetranychids as was thought by early acarologists (see also Krantz and Lindquist (1979) for further discussion).

Other genera deviating from the basic 'bdellid' type include *Speleorchestes* (Endeostigmata: Nanorchestidae), *Nicoletiella* (Nicoletiellidae), and *Linopodes* (Eupodidae) as well as *Riccardoella* (Ereynetidae) (Fig. 6.2). Until now it has not been possible to draw up intermediate types to bridge the gap to the plesiomorphic type. The sperm cells of *Linopodes* and *Riccardoella* resemble one another so closely that they could be regarded as a synapomorphy (Alberti, 1984). Curiously enough, the endeostigmatic mite, *Speleorchestes*, has a very strange sperm cell, which bears some characteristics in common with acaridid sperm, and the spermatozoa of *Nicoletiella* resemble those of 'higher' oribatids (Alberti, 1980a). Evidently, more taxa should be investigated, especially from the Endeostigmata and 'lower' oribatid mites. It should be kept in mind that the Acari are of a geological age that equals or even surpasses that of the Insecta (Norton *et al.*, 1988), and thus profound differences between taxa may be the result of a separate evolution over a long period of time.

FUNCTIONAL ASPECTS

There are few publications on functional aspects of acarine spermatozoa and these deal mainly with ticks (Feldman-Muhsam and Filshie 1976, 1979; see Oliver 1982 for further references). As a consequence, most of the following ideas are based on conclusions gained from comparative studies.

Sperm cells have to fulfil well defined tasks (see Introduction) and it is now evident that sperm cells of different species are structured to

differing degrees of complexity for their main purpose: the transport of genetic material (cf. for example, *Neocarus* sperm and *Tetranychus* sperm). The Acari, when adapting to a terrestrial mode of life, had to develop internal fertilization. Several mechanisms have evolved within the order including indirect insemination by means of spermatophores with or without pairing, and with or without gonopodes being involved. Moreover, direct-sperm transfer with a penis has been developed (see Schaller, 1979 for references). The latter occurs in some Actinedida and all. Acaridida. The reproductive biology of the Opilioacarida or Holothyrida is not yet known. All the aflagellate sperm cells of the Acari are, with certainty, passively transferred to the female, and have to find their way to the female germ cell within the female 'environment'.

In species with spermatophores which are deposited on the ground, such as many Actinedida and, presumably, all Oribatida, each sperm cell is surrounded by a more or less elaborate secretory sheath, which might represent an adaptation to protect the sperm cell from abiotic influences (Alberti, 1980b; Kümmel, 1982) (Fig. 6.6e,f,g). This sheath is not observable in the actinedids in which the mode of sperm transfer is direct (Alberti, 1980b) (Fig. 6.2).

In the few taxa which have been investigated in this respect (Ixodida, Varroidae, Bdellidae, Tetranychidae, Acaridida), in every instance, the sperm appear to be delivered by the male in a 'transport form', and are transformed within the female, acquiring only thereafter the capacity to fertilize the female germ cell (capacitation *sensu lato*). This process activates the sperm cell, and enables it to find its way to the female germ cell. In the course of this more-or-less active migration, female somatic tissues have to be penetrated, at least in some of the examples mentioned, and finally the sperm cell has to penetrate the female germ cell. Thus, the spermatozoon has to be adapted to the female 'environment'. Whenever these conditions are changed in the course of evolution, the sperm cell has to cope with the alterations.

The transformations observable in ticks have been known for a long time (Samson 1909), and are so profound that the mature sperm cell delivered by the male has been termed 'prospermium'. The most important event, and most likely occurring in all vacuolated sperm cells, is the opening of the vacuole at a preformed apical portion (cap or operculum). This is followed by the emergence of the inner core (cytoplasmic column). Finally, the whole cell is turned inside out and the membrane, which formerly delimited the vacuole, is now at the surface of the capacitated cell, exposing the cellular processes to the surrounding medium (Breucker and Horstmann, 1968, 1972; Brinton *et al.*, 1974; Feldman-Muhsam and Filshie, 1979; see Oliver, 1982 for further references). Below the cell surface, bundles of filaments have been observed

which, together with the cellular processes, are thought to be responsible for the cell's motility (Feldman-Muhsam and Filshie, 1976, 1979; Wuest *et al.*, 1978). The sperm, in contrast to the 'prospermium', is now capable of several kinds of movement (Oliver, 1982; Feldman-Muhsam, 1986), and migrates, presumably assisted by peristalsis of the oviduct, into the tubular ovary. Here the oocytes, suspended to the ovary by funicle cells, are most likely fertilized after this funicle has been penetrated (Brinton *et al.*, 1974; see also Oliver, 1982). Brinton *et al.* (1974) observed sperm cells within the (somatic) epithelium of the oviduct and ovary, which they had penetrated, apparently, during the 'search' for the female germ cells. These spermatozoa are most likely lost for fertilization.

The ribbon-type sperm cells of *Varroa jacobsoni*, likewise, display fundamental transformations (Akimov and Yastrebtsov, 1984; Alberti and Hänel, 1986). In this species, a specific sperm-access system is developed originating from secondary sperm-induction pores (solenostomes). Spermatozoa are transported to a spermatheca which is close to the ovary, and are completely transformed from the more or less spherical, ribbon-bearing cells to elongate spermatozoa with smooth cell surfaces (Fig. 6.6c,d). In this capacitated state, the sperm cells are, presumably, capable of movement (possessing filaments under the plasmalemma), and may penetrate the ovary, probably assisted by female cells (Alberti and Hänel, 1986).

In contrast, sperm cells of the Parasitidae do not appear to be profoundly transformed within the female. These sperm cells are placed within the female via the primary genital opening. Their course to the ovary, where they are found later (Korn, 1982) is not known. In one female of *Pergamasus* sp., practically unaltered sperm cells have been observed within the haemocoele. They were also seen in the ovary (Alberti, 1989).

Transformations of sperm cells within the female, which probably occur to provide the spermatozoa with organelles required for movement, have been observed in the Bdellidae, Tetranychidae and Acaridida. Within the Tetranychidae, elongated finger-like processes are developed with filaments below the plasmalemma (Alberti and Crooker, 1985; Alberti and Storch 1976a,b; Crooker and Cone, 1979; Mothes and Seitz, 1981). In the Acaridida, the spermatozoon probably becomes fusiform (Witalinski *et al.*, 1986), and likewise possesses filaments below the cell surface (Alberti, 1980b; Witalinski *et al.*, 1986; Witalinski, 1988). In tetranychids, as well as acaridids, a special copulation orifice is present. Whereas the sperm of the Tetranychidae is said to migrate to the ovary through the narrow haemocoele after penetration of the epithelium of the receptacle (Feiertag-Koppen and Pijnacker, 1985;

Mothes and Seitz, 1981; Smith and Boudreaux, 1972), in Acaridida, a sperm-access system is developed leading to the ovary (Griffiths and Boczek, 1977; Prasse, 1968).

It seems likely that fertilization occurs within the ovary in all Acari and probably in all other Arachnida. There are, apparently, no true micropyles in arachnid eggs which would enable fertilization to take place in the distal parts of the genital tract, as, for example, in insects. The micropyles described from ticks (Brinton *et al.*, 1974) refer to a thin region in the vitelline envelope at the attachment site of the oocyte to the funicle (Diehl *et al.*, 1982). This region presumably constitutes the site where the spermatozoon penetrates the oocyte (Brinton *et al.*, 1974). Many structures of acarine spermatozoa are not yet understood functionally, for example the inclusion bodies in ribbon spermatozoa. The functional relevance of the complex transformation described above is most often interpreted from an efficiency viewpoint. Sperm cells in the transport form are considerably smaller (vacuolate sperm cells double in length by capacitation), and thus more sperm can be stored per spermatophore. A further consideration is the obviously inactive state of the precapacitated sperm cell the metabolic rate of which is reduced (Oliver, 1982). Capacitated sperm are capable of penetrating female tissues. It is thus reasonable to assume that, in ticks for example, and also in the ribbon spermatozoa of such mites as *Varroa*, a new cell surface is established by the transformation, which is probably adapted to the function of penetrating tissue. The infoldings in the Actinotrichida (cisternae, chambers, tubules, see above) may similarly serve as plasmalemma stores, which enable rapid transformation, as does the vacuole of the vacuolated type or, presumably, the vesicles and vacuoles in sperm cells of other arachnids referred to earlier.

An interesting analogy can be drawn from observations of the development of ribbon sperm possessed by certain Gamasida and spermatozoa of Acaridida. In both taxa, a secondary plasmalemma is produced after the shedding of peripheral portions of the cytoplasm (Alberti, 1980b; Witalinski and Afzelius, 1987).

The morphology of the female genital system can be expected to have an important influence on the structure of sperm cells. Up till now, vacuolated sperm cells have been observed only in those taxa which possess tubular ovaries or paired oviducts in which the oocytes – suspended from the ovarian tube by funicle cells – develop within pouches of the basal lamina (Opilioacarida, Holothyrida: Vitzthum, 1943; Ixodida: Diehl *et al.*, 1982; Uropodina: Woodring and Galbraith, 1976; Sejina: Michael, 1892). Sperm is transferred, as far as it is known, to the primary genital orifice, which is located medioventrally, an arrangement referred to as tocospermy (Athias-Henriot, 1969). The

males of Ixodida and Uropodina manipulate the spermatophore with parts of the gnathosoma (Faasch, 1967; Oliver, 1982).

Ribbon spermatozoa have only been found in taxa possessing transformed chelicerae: the spermatotreme in the Parasitina, and the spermatodactyl in the remaining taxa (Dermanyssina). In the Parasitina, the spermatophores are placed into the primary genital orifice. In the Dermanyssina, there is the podospermic access system already referred to, and the spermatophores are transferred to the solenostomes close to coxa III or IV (Athias-Henriot, 1969; Evans and Till, 1979; Krantz, 1978).

A review of the literature, and my own studies of females in taxa having ribbon spermatozoa, have shown that in these females, the ovary is differentiated into two parts, one nutrimentary, the other generative. The mature eggs are delivered through an unpaired oviduct (Michael, 1892; Neumann, 1941; Warren, 1941; Pound and Oliver, 1976; Korn, 1982; Akimov and Yastrebtsov, 1984; Alberti and Hänel, 1986; Alberti and Zeck-Kapp, 1986). That is why it seems certain that the development of ribbon sperm is closely correlated with changes in the female genital tract. This observation strongly suggests a phylogenetic interpretation.

A PROBABLE EVOLUTION OF GENITAL SYSTEM WITHIN GAMASIDA

The occurrence of podospermy within the Gamasida is a rather strange phenomenon. As already mentioned, this mode of insemination is characterized by the existence of secondary sperm-induction pores, commonly located near coxae III or IV, the presence of spermatodactyls on the chelicerae of the males and irregular ribbon spermatozoa. Moreover, these spermatozoa are rather complex cells, which have developed from the, equally, very specialized and highly derived (outgroup comparison) vacuolated sperm cells. What are the reasons for this re-organization from one complex cell type to another during the course of evolution? Sperm cells must be adapted to specific insemination/fertilization conditions, and this evidently holds true for the vacuolated sperm cells. How could the translocation of the insemination site from the primary medioventral position to the secondary lateral and paired locations take place without endangering reproductive success? It is very difficult to imagine that this translocation could have happened in one evolutionary step. Instead, it should have evolved slowly with intermediate stages, all of which had to be functional. Furthermore, if there occurred such a complicated and 'dangerous' reorganization of a basic system such as the genital organs/reproductive behaviour, it

should be advantageous to the taxon or, probably, more correctly to the individual or its genes.

It seems reasonable to assume that ribbon spermatozoa are adapted to podospermic conditions. However, they are also found in the Parasitina, which have been described as tocospermic. On closer inspection it appears, however, that the Parasitina occupy a special position which, to a certain degree, is intermediate between podospermy and that type of tocospermy assumed to occur in the Opilioacarida, Holothyrida, Ixodida, Uropodina, Epicriina, Zerconina, Sejina and maybe the Antennophorina. The chelicerae of the Parasitina are modified gonopodes (spermatotremes), and the male genital orifice is in a presternal position as in the podospermic taxa. There are additional similarities in the internal anatomy: the ovary is differentiated into nutrimentary and generative regions and the oviduct is an unpaired structure. These characteristics have also been found in the podospermic taxa including the phytoseiids (Alberti, 1989), in which the sperm-access system (phytoseiid type) deviates from that of the other taxa (laelapid type) (Evans and Till, 1979).

It is probable that the evolution of the genital system and reproductive behaviour in the Gamasida basically followed the course indicated in Fig. 6.7. The spermatological data have thus provided a means to evaluate the direction of this development.

It is evident now that the term 'tocospermy' describes two basically different systems, one plesiomorphic (Opilioacarida, Holothyrida, Ixodida, Uropodina, Epicriina, Zerconina, Sejina and possibly Antennophorina), and one rather derived (Parasitina). The combination of these two systems as 'tocospermy' obscures a very important step in the evolution of the Gamasida. This is the reorganization of the ovaries, which makes possible a nutrimentary development of the oocyte, comparable to that occurring in meroistic/telotrophic insects (Akimov and Yastrebtsov, 1984; Alberti and Zeck-Kapp, 1986). This may accelerate egg development as in insects. As a consequence, the ovaries, instead of being tubular, have become massive structures, and the sperm cell's route to the oocytes is blocked. The reason for the simultaneous appearance of the impaired oviduct is not clear. Could it be due to the development of one large egg at a time or to embryonation of the egg? Further investigation is required to establish cause and effect. Reorganization of the ovary and development of a new oviduct may have been both responsible for the need to establish a new route to the oocytes. It appears that the ribbon sperm cells of Parasitina have already acquired the essential adaptations at the 'tocospermic' level. First results with *Pergamasus* sp. support the assumption that the sperm cells reach the ovary via the haemocoele (Alberti, 1989). In any case, ribbon

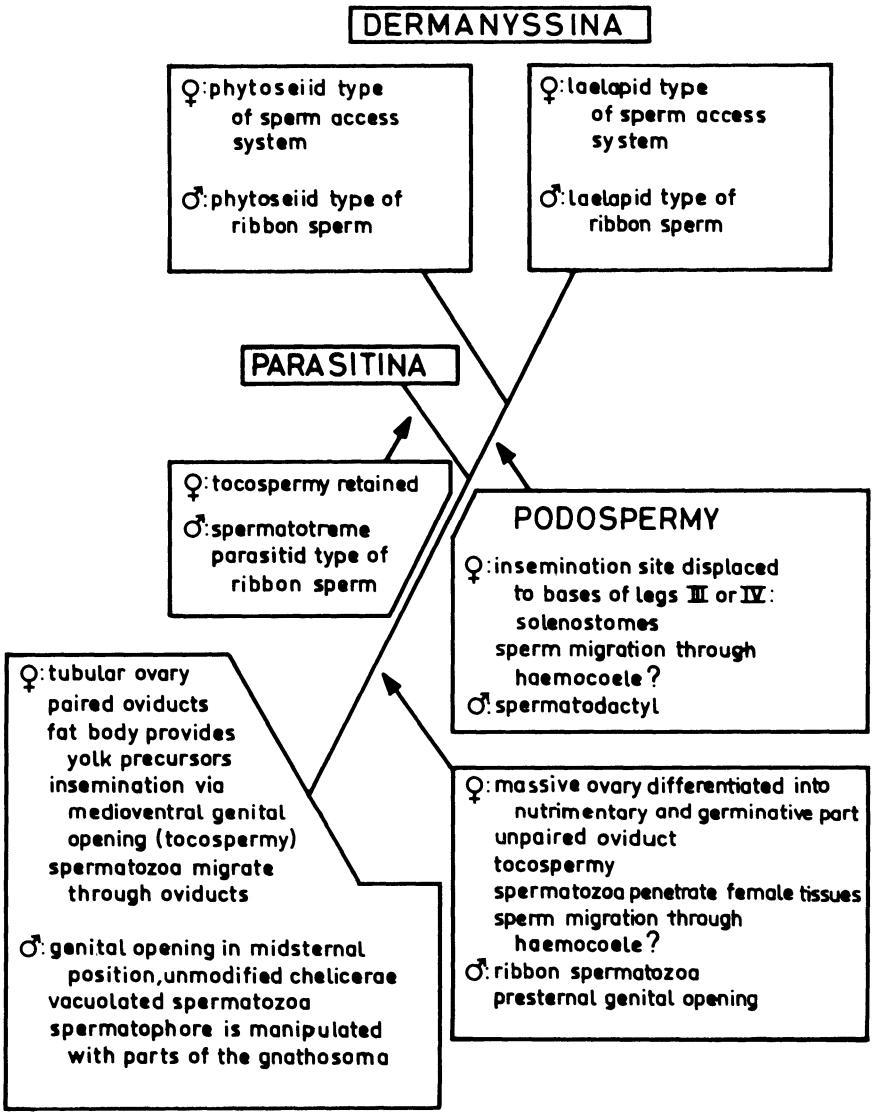

Fig. 6.7 Diagrammatic representation of probable evolutionary changes of genital system and spermatozoa in Gamasida.

spermatozoa penetrate more female tissues than vacuolated sperm cells which only enter the funicle. Sperm cells, which have evolved this greater penetrative capability, could be transferred more readily via secondary copulation sites. In all the Anactinotrichida investigated, a copulatory behaviour has been observed in which the male gnathosoma is involved (see above). This behaviour is further developed within those taxa possessing ribbon spermatozoa (Parasitina, podospermic mites) and which have developed gonopodes, that is, chelicerae with spermatotremes or spermatodactyls, respectively. In the podospermic mites, a sac-like spermatophore is transferred with these gonopodes to the solenostome (Amano and Chant, 1978; Dosse, 1959; Lee, 1974; Pound and Oliver, 1976; Schulten, 1985; Young, 1968). No matter what female structures may have facilitated this translocation of the copulatory site (dermal-gland openings, arthrodial membranes, entapophyses), a penetration of female tissues by the sperm cells was necessary. It is not known whether this stage of development is still present within recent taxa. Some Acari, such as *Liroaspis togatus* (Sejina) and *Celaenopsis badius* (Antennophorina) have the male genital opening in an anterior position, and in the Antennophorina, a marked sexual dimorphism of the chelicerae is obvious. Moreover, *Celaenopsis* has rather peculiar sperm cells which evidently deviate from the 'normal' vacuolated type (Alberti and Błaszak, unpublished). The likely promise of these gamasids in providing 'connecting links' should be a stimulus to investigate not only their anatomy and fine structure but also their copulatory behaviour.

Within the laelapid type, which is the one most thoroughly studied (Michael, 1892; Young, 1968; Pound and Oliver, 1976; de Ruijter and Kaas, 1983; Akimov and Yastrebtsov, 1984; Alberti and Hänel, 1986), a nearly complete access system is developed, and the capacitated sperm cells only have to migrate a short distance to the oocytes, their passage probably being assisted by female cells. Apparently phytoseiids have developed a different system which has become a valuable taxonomic character (Dosse, 1958; Fain, 1963; Athias–Henriot, 1968; Karg, 1983; Evans, 1988). The passage of sperm to the ovary is enigmatic since fine-structure analysis (Alberti, 1989) suggests that the minor duct, often assumed to be a sperm duct, is inappropriate for this purpose. The elucidation of this problem requires serial sectioning, which is currently being carried out.

According to the basic investigations of Athias-Henriot (1968), Fain (1963), Fain *et al.* (1977), Lee (1974) and Michael (1892), the access systems exhibit differing degrees of complexity, and can be rather simple in some taxa, for example Ascidae (Fain *et al.*, 1977). Thus it may be expected that a comparative analysis will provide answers to uncer-

tainties in our understanding of these access systems. The development outlined here may have been favoured by the reorganization of the female genital system with its assumed resultant selective advantages. It may also have been favoured by the translocation of the insemination site, which may have caused an acceleration in reproductive efficiency. As a result the sperm cells may reach the ovary more rapidly, and the possibility of sperm being lost for fertilization (see above) can thereby be reduced. As a result, fewer sperm per copulation are required (Alberti and Hänel, 1986). Furthermore, sperm morphology can be simplified and spermiogenesis shortened. Following the concept of sperm competition, a male developing such strategies could have an advantage compared with those retaining the plesiomorphic state. It is not possible to decide whether the female or the male 'led the way' in the development of podospermy. In any case, only a co-evolutionary change in both sexes could guarantee reproduction during all transitional phases.

These ideas, still somewhat preliminary and speculative, demonstrate that, starting from descriptive morphology, a far-reaching interpretation of the life strategies of different taxa is possible. In principle, the same problems as in the podospermic taxa await elucidation in the actinotrichid Raphignathae and Acaridida in which secondary copulatory pores have been developed. This stage has been realized in all Acaridida, and this is reflected in the apparently very uniform sperm cells.

CONCLUSION

The present study has demonstrated that spermatological investigations can provide substantial results on different levels. At the cellular level, it is shown that the same (homologous) cell type differs considerably in its complexity. A first outline has been presented depicting evolutionary trends of this cell type within the Gamasida. Furthermore, examples are provided of the suitability of spermatological data for systematic purposes. Problems, which cannot be solved with the classic – mainly exomorphological – approaches, can be clarified at least to some extent. The Opilioacarida, which have vacuolated sperm, possess an obvious synapomorphy with the Holothyrida, Ixodida, and Gamasida. Thus, the taxon Anactinotrichida (including Opilioacarida) is very likely monophyletic, as is the taxon Actinotrichida (Evans *et al.*, 1961; van der Hammen, 1968, 1977, 1985; Krantz 1978; Lindquist 1984). Sperm morphology reflects the phylogenetic distance between each group. For both taxa, 'basic types' of sperm can be specified. There are no synapomorphies between them. An outgroup comparison, however, does not indicate with certainty different sister groups for the two taxa. However,

both sperm types can be related to sperm of other Arachnida with equal or even more justification than to each other. A resolution of the question whether Acari are diphyletic or monophyletic – from the spermatological data only these two possibilities remain – has not been possible. Spermatological data are not, at present, capable of bridging the distance between the higher systematic categories.

Within the Anactinotrichida and Actinotrichida respectively, spermatology seems to be a useful tool for systematics (for example, Raphignathae, Parasitengona, Hydrachnidia and probably Oribatida). In the Actinedida the direction of phylogenetic development is recognizable. In the Anactinotrichida, the information provided is very promising; plesiomorphic and apomorphic sperm types can be distinguished, and these can assist in clarifying the division of this suborder into major taxa. Certain families such as the Epicriidae, which were controversially positioned are interpreted with greater confidence. The outstanding phenomenon of 'podospermy' is recognized with certainty as derived, and the interpretation of the characteristics connected with this mode of insemination are brought closer to realization. The phenomenon of 'tocospermy' clearly appears to consist of two basically different types of insemination. Nevertheless, numerous problems still remain unsolved and new questions arise. These may stimulate future research.

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7

*The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites**

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Highly derived oribatid mites (Brachypylina) seem to fit most predictions of evolutionary theory regarding the ecological, geographical and taxonomic distribution of parthenogenesis. Earlier derivative groups generally do not. We suggest that the ancestors of large, completely parthenogenetic families (for example, Brachychthoniidae, Lohmanniidae, Camisiidae, Trhypochthoniidae, Malaconothridae, Nanhermanniidae) were themselves parthenogenetic, and that 'speciation' and radiation occurred in the absence of sexual reproduction. Further, it is speculated that automixy (meiotic thelytoky) was the process involved – even though some extant species may prove to be secondarily apomictic, just as apomicts evolve from sexually reproducing lineages. If mechanisms for maintaining heterozygosity are effective, automixy can provide all the advantages of parthenogenesis, plus the DNA-repair advantage of meiosis. Genotypes can be diversified by the formation of distinct clones, thereby providing the raw material for successful radiation. The disadvantage of such a system would be its slow rate of change due to the absence of an allele-recruitment mechanism. Much of the above remains speculative since available data are meagre. Future work should include surveys of thelytokous mechanisms in oribatid mites, the genetic characterization of populations of a variety of parthenogenetic and sexual species, and the refinement of hypotheses on phylogenetic relationships of parthenogenetic taxa

* Invited paper.

INTRODUCTION: PARTHENOGENESIS AND EVOLUTIONARY THEORY

As Bell (1982) suggested, sex is the queen of problems in evolutionary biology. Why undertake meiosis, mating and syngamy when simple mitosis is much less costly? Why are not all species parthenogenetic? Attempts to understand this 'paradox of sex' without invoking group selection (that is, without claiming that sex is good for the species) have occupied evolutionary biologists for more than a decade (see reviews by Stearns, 1985; Ghiselin, 1988). From another viewpoint, the tremendous cytogenetic problems associated with the transition from sexuality to parthenogenesis cause some to consider parthenogenesis the more paradoxical strategy (Uyenoyama, 1984). Perceived advantages of parthenogenetic reproduction have been discussed many times (for example, Lloyd, 1980; Bell, 1982; Shields, 1982). Most celebrated is the 'twofold advantage' of parthenogens, viewed in the context of resources saved by not producing males (Maynard Smith, 1978) or the relatedness of progeny to their mother (Williams, 1975). Parthenogens also transmit successful genotypes more faithfully to progeny than do outbreeding sexual species. With the most common parthenogenetic mechanism, apomixis (ameiotic thelytoky or the mitotic production of diploid eggs), there are neither segregation loads to lower heterosis effects, nor recombination loads which affect beneficial gene interactions (epistasis), although both could occur with forms of automixy (meiotic thelytoky) (Shields, 1982). In addition, neither costs of mating activity nor costs of failure to mate are assessed to parthenogens.

Disadvantages of parthenogenesis seem mostly to be long term. Parthenogens cannot recruit alleles by shuffling those already existing in a population, that is, lineages are truly linear, not reticulate. Also, the accumulation of deleterious mutations in apomictic populations is ensured by an inability to produce offspring with 'error-free' DNA. The latter is not true of automictic species, a distinction which has important consequences.

The rarity of parthenogenesis is a common theme. Perhaps 1% of known insect species (Bell, 1982) and 0.1% of known members of the animal kingdom (White, 1978) are obligate parthenogens. In this respect, mites of the suborder Oribatida present a striking anomaly; we estimate that more than 600 of the approximately 7000 known species – perhaps 8 or 9% – are parthenogens. This chapter is a preliminary overview in which first evidence of this anomaly is presented and then aspects of the ecology, life-histories, genetics and taxonomic affinities of known or suspected parthenogens are examined. In each case, observed patterns are compared with predictions suggested by current evolution-

ary theory. The comparisons are imperfect and preliminary, in part reflecting the state of both theory and available data. We do not exhaustively review known or suspected examples of parthenogenesis nor do we try to support or discredit theories. Instead, the primary conclusion is that a single theory on the evolution and role of parthenogenesis cannot explain its known distribution in these mites. In reaching this conclusion, we note or imply (by indicating paucity of data) specific areas where further research might be most useful.

EVIDENCE OF PARTHENOGENESIS

The existence and distribution among oribatid mites of arrhenotokous parthenogenesis – in which haploid males are produced parthenogenetically but females are biparental diploids – is poorly documented (see Helle *et al.*, 1984; Taberly, 1987a; Norton *et al.*, 1989). In contrast, thelytokous parthenogenesis – in which unfertilized eggs produce primarily females – is well known in oribatid mites. But as discussed below, the genetic and therefore evolutionary consequences of thelytoky depend greatly on its specific mechanism, our ignorance of which makes application of theory tenuous.

Evidence for parthenogenesis (used as a synonym of thelytoky in the remainder of this chapter) in oribatid mites is both experimental and inferential. To prove it, one simply keeps virgin females from contact with males, and waits for female offspring. However, most oribatid mites have long generation times and culturing can be difficult (Grandjean, 1948b; Taberly, 1987a). Taberly (1987a) listed the few proven instances of thelytoky, a list which has been more than doubled to 26 (Palmer and Norton, 1990). Only one of the proven species is a member of the Brachypylina (*Oppiella nova*); all others represent the Desmonomata (= Holosomata, = Nothroidea *sensu lato*) which reflects both the biased interests of investigators and the frequency of parthenogenesis in this group. Parthenogenesis can also be inferred from field-collected population samples as Grandjean (1941) did in his seminal paper on oribatid-mite sex ratios. When a sample with few or no males is encountered parthenogenesis is inferred to be the reproductive mode but there are two complicating factors which must be addressed.

The first is the possibility that adult males are very short-lived, that is, their occurrence in the population is necessary but ephemeral and easily missed when sampling. The relatively long adult life of oribatid mites (Luxton, 1981a) suggests that this is not true, and although the sexes may not always have equal longevity, males are certainly not ephemeral. Nor do available long-term data show seasonal recruitment of males. Mites, studied from this point of view, include the brachypyline species,

Punctoribates insignis and *Oppiella nova* (Fujikawa, 1987a, 1988) and numerous species of Desmonomata (Palmer and Norton, in press). Luxton (1981a) noted similarly that parthenogenetic species in a Danish beech-forest soil showed no temporal variation in sex ratio. In addition, the absence of spermathecae in the females of any known oribatid species is inconsistent with a very short availability of mature males.

Are there known obligate sexual species whose sex ratio fluctuates greatly, such that they could be mistakenly interpreted as parthenogenetic if sampled when male densities are low? In the Crotoniidae and Hermanniidae, all of which appear to be sexual, and the several species of sexual Nothridae, the minimum proportion of males seems to be about 35% (Norton *et al.*, 1989). In seasonal sampling of the sexual phthiracarid mite *Steganacarus magnus* in Great Britain, Webb and Elmes (1979) found a minimum of about 22% males. In most of the sexual species studies over time by Luxton (1981a) males were present in substantial numbers during all periods. Yet there were several species in which males were occasionally absent from population samples, and Luxton considered these to be 'tending to parthenogenesis'. Since males of these species outnumbered females in other samples from the same site (Luxton, 1981a, Appendix 10.1) this seems unlikely; males may simply be shorter-lived. However, the potential for error when relying on sex-ratio analysis of single samples to indicate parthenogenetic capability is clearly illustrated.

The second complicating factor is the typical rare presence of males in population samples. Although males are unknown in some parthenogens, they may constitute as much as 4–5% of a given sample in others (Grandjean, 1941; Luxton, 1981a; Taberly, 1988; Norton *et al.*, 1989). Are these data possibly being misinterpreted, such that the mites are actually obligate sexuals with a high degree of polygyny, like some Prostigmata? Can such low percentages possibly represent evolutionarily stable sex ratios? Or are these mites facultative parthenogens (see below) in which a small number of females are fertilized and the rest are not? The probable answer to each question is no. What is known of the mating behaviour of sexual oribatid mites suggests that fertilization, and often oviposition, is quite random; strong mate competition among related males, which might promote female bias, seems highly unlikely. Taberly's (1988) work with rare males of *Platynothrus peltifer* and *Trhypochthonius tectorum* strongly suggests that they are not functional. They produce spermatophores but in fewer numbers than do known sexual species, and spermatogenesis is arrested prior to completion, rendering the males sterile. In addition, young females of these mites seem to ignore the few spermatophores produced. It is likely that species in which males consistently comprise 5% or less of a population are indeed

obligate parthenogens, and that Grandjean (1941) was correct in considering rare, parthenogenetically produced males to be atavistic relics of a sexual ancestry. In fact, the production of such rare males, referred to as 'spanandric' (Vandel, 1928), seems widespread among obligate animal parthenogens (Lynch, 1984).

Does facultative parthenogenesis occur?

Ryabinin and Pan'kov (1987), citing Krivolutsky, suggested that parthenogenesis is facultative in several oribatid families but their meaning was unclear; apparently they meant that some species are parthenogenetic, and some are not*. We have no evidence that a given female of any oribatid species has the 'option' of producing offspring by thelytoky if she is not fertilized. In fact, there seem to be no known animal examples where female progeny can be facultatively produced from eggs in such a manner (Maynard Smith, 1986). Indirect support for the absence of facultative parthenogenesis comes from the lack of intermediate sex ratios: males of oribatid mites are either very rare (or absent), or else they are abundant, at least at most times of the year. There is no conclusive evidence that any species are 'tending to parthenogenesis' in the gradual sense used by Luxton (1981a; see above). 'Tendencies' can, however, be seen toward parthenogenesis in the sense of Grandjean (1941), that is, parthenogenesis is clustered in certain genera (see below).

Can populations switch reproductive modes?

Although not framed in evolutionary theory, Fujikawa (1987b) presented an extraordinary study showing that the sex ratio of a population of the oribatulid mite, *Oribatula sakamorii*, exhibited long-term change. An intensively and conventionally farmed Japanese soil was converted to 'nature-farming' by eliminating pesticides and fertilizers, and then studied intensively for nearly a decade. Early in the study the population of *O. sakamorii* had only an occasional spanandric male, clearly indicative of parthenogenesis. This is the only known parthenogen in the Oribatulidae, and is one of the Japanese species least sensitive to perturbation (Aoki and Kuriki, 1980). Two years after conversion to less

* The list of families with 'facultative' parthenogenesis included Lohmanniidae and Nanhermanniidae. The present authors have never encountered a sexual population in either family, despite world-wide surveys of many species. The original paper has not been studied but perhaps Krivolutsky's comments were based on the presence of rare, spanandric males.

intense management, however, the proportion of males increased dramatically and stayed at about 30% for the remaining seven years of the study. As developed below, theory would predict the direction of this apparent switch as the environment became less disturbed with time but the mechanism for regaining sexuality is unknown.

ECOLOGICAL AND GEOGRAPHICAL CORRELATES OF PARTHENOGENESIS

Early theories suggesting that sex is an adaptation for creating genetically diverse progeny in a physically unstable and unpredictable environment have been largely discredited (Bell, 1982). In a more widely accepted theory, it is biotic rather than abiotic unpredictability which is important. The power of genetic innovation should cause sexuality to be favoured over parthenogenesis in communities which are biologically complex and unpredictable; species are envisaged as being engaged in a co-evolutionary battle with sexual parasites, sexual predators and sexual competitors (both intra- and interspecific), such that plastic genomes are a prerequisite to survival of populations (Ghiselin, 1974; Glesener and Tilman, 1978). Inversely, the environments of parthenogens should be biologically depauperate; they are restricted to such situations by a slow evolutionary response rate resulting from inflexible genomes. It is commonly seen that sexuality and parthenogenesis respectively are correlated with abiotically stable and unstable environments because environmental stability favours the development of biological complexity. As geographical correlates of this theory, parthenogenetic species should occur most commonly at high latitudes or high altitudes, in recently glaciated areas or on islands. More locally, ecological correlation should be found with patchy habitats, fresh water, and especially newly formed environments or disclimaxes (sites kept undeveloped by frequent disturbance). Carrying the argument further, the occurrence of parthenogenesis should decrease as successional communities become more complex.

To some extent, such reasoning is challenged by the increasing evidence that parthenogenetic species are not genetically rigid: considerable variation – usually assumed to be clonal variation – exists within populations. Champions of the 'general-purpose' genotype theory (for example, Lynch, 1984) suggest that this variation is subject to selection. Since the whole clonal genotype is the unit of selection, there is more potential for evolving broadly adapted genomes than in sexual species in which selection acts on individual loci or linkage groups. Thus, it is the sexual, not parthenogenetic species which are narrowly adapted; they are at a disadvantage in abiotically unstable habitats because they continuously

track small changes in local environments. The predictions will often be similar to those of the 'biotic-uncertainty' theory outlined above, except that broadly adapted parthenogens might be expected to coexist with sexual species in more stable environments, at least to some degree, and to exhibit wide geographical distributions.

Others see a different reason for broad ecological valence in obligate parthenogens. Hebert *et al.* (1988) believe that the apparent generality results from the existence of multiple clones in a population, each narrowly adapted to particular microenvironments. This belief seems tied to the concept of a separate (polyphyletic) origin for each parthenogenetic clone from sexual ancestors. The general correlates should be the same in either case.

New or disclimax environments

There are many examples of congruence with some of the above predictions. Studying soil-mite succession in newly formed volcanic soil in Kamchatka (USSR), Ryabinin and Pan'kov (1987) found the appearance of two parthenogenetic species, *Liochthonius sellnicki* (Brachychthoniidae) and *Oppiella nova* (Oppiidae), early in soil development, preceded by species of Suctobelbidae, whose mode of reproduction was not characterized*. They noted that the former two species are also dominant in more natural, undisturbed habitats; this is suggestive of broad rather than narrow adaptation. The same authors studied oribatid inhabitants of sulphurous soil and associated microcommunities around two volcanoes on the Soviet island of Kynashir. On barren soil, *O. nova* comprised 50% of the oribatid mites, with most of the remainder belonging to the Suctobelbidae. Luxton (1982a) found the dominant mites in two English coal-shale refuse heaps, another 'newly-created' habitat, to be *O. nova* and *Mixochthonius laticeps* (Brachychthoniidae). Although the reproductive mode of the latter species has not been studied, it is probably parthenogenetic since there seem to be no records of males from the family Brachychthoniidae. As with *O. nova*, *M. laticeps* does not disappear with habitat development; it is common in European forest soil (Niedbala, 1976). Beckmann (1988) found *O. nova* to be a pioneering oribatid species on bulldozed land in West Germany, as was *Tectocepheus sarekensis* (Tectocepheidae), another parthenogen.

* We are unaware of published sex-ratio analyses for the Suctobelbidae. Brief examination of members of the *Allosuctobelba* and *Rhinosuctobelba* shows them to be sexual. Common small *Suctobelbella* species are difficult to sex due to a very short ovipositor but no certain males were seen in samples of several undetermined species.

Parthenogens also dominate in disclimax habitats such as soil subjected to regular flooding. The seven oribatid species represented in the soil of an annually drained reservoir in Germany (Tamm *et al.*, 1984) are all known or suspected parthenogens, and are all widely distributed ecologically. Beck (1969) studied the parthenogenetic species, *Rostrozetes foveolatus* (Haplozetidae), in a Brazilian forest which flooded annually and found it to be the only oribatid mite which survived inundation in significant numbers. Even oviposition could occur under water although this species is normally terrestrial.

Cultivated soil is a highly disturbed environment. Its oribatid fauna is depauperate, and most of the common species are parthenogens. Under experimental conditions, some seem simply to tolerate cultivation, exhibiting densities similar to (*O. nova*) or lower than (*Tectocepheus velatus* and Brachychthoniidae) those in adjacent uncultivated plots (Norton and Sillman, 1985). Others may increase in density as a result of cultivation; *Malaconothrus* spp. are examples (Shaddy and Butcher, 1977), and these are also parthenogenetic.

Other types of human perturbation have been examined, for example the studies of Weigmann (1984 and included references) on urban oribatid communities, or that by Aoki and Kuriki (1978) on the impact of forest clearing, or Ito's (1980) examination of trampling effects. Such studies show that oribatid mites, which flourish under disturbance, are usually parthenogenetic. Some, such as *O. nova*, *Microppia minus*, *T. velatus*, *Rhysotritia ardua*, and many widespread species of Brachychthoniidae among others, seem to be relatively insensitive to even strong perturbation (Aoki, 1979, 1980; Aoki and Kuriki, 1978; Dindal, 1977). That they are also commonly present in more complex, structured habitats supports a concept of broad, rather than narrow adaptation.

Aquatic habitats

Based on relative biological complexity, theory suggests that parthenogenesis should be more common in freshwater than in marine environments (Bell, 1982), and oribatid mites also conform to this prediction. The principal freshwater groups are the brachypyline families, Hydrozetidae and Limnozetidae, and the early-derivative Desmonomata families, Trhypochthoniidae (*Hydronothrus*, *Trhypochthoniellus*, *Mucronothrus*) and Malaconothridae (*Trimalaconothrus*). All members of the latter two families (see below), and all described members of the Limnozetidae (Grandjean, 1951; Behan-Pelletier, 1989) are parthenogens. The Hydrozetidae seem to be about evenly divided between parthenogenetic and sexual species. In contrast, oribatid mites associated with marine environments are sexual (Schuster, 1979).

The very close correlation of parthenogenesis with fresh water caused us to look for a more direct and simple underlying cause than that suggested by theory, which deals with niche exploitation and colonization (Bell, 1982). One possibility is that the normal mating behaviour of terrestrial oribatid mites, in which numerous free-standing spermatophores are deposited by males without direct interaction of the sexes (Taberly, 1988), is for some reason less effective in fresh water. Even those species of *Hydrozetes* which are sexual may have atypical means of mating; they commonly have modified setae on tarsus I (Grandjean, 1948a), which might be associated with direct sexual contact during mating.

Simple explanations, such as osmotic difficulties affecting standing spermatophores in a hypotonic environment or problems with chemical communication between sexes, may be improbable (H. Witte, personal communication). For example, free-standing and unattended spermatophores – a plesiotypic condition – are successfully used in the reproduction of many Hydracarina (freshwater Prostigmata). But in the major lineages of this group there are independent evolutionary tendencies toward closer association of the sexes and more rapid uptake of sperm (I. M. Smith, personal communication, 1988), which suggests that the plesiotypic mode of sperm transfer has some inherent disadvantages in fresh water. Mitchell (1958), for example, found that free-standing spermatophores of *Hydryphantes ruber* had a functional lifespan of only a few minutes.

Detailed comparative studies of sexual and parthenogenetic species of *Hydrozetes*, as well as experimental studies with spermatophores of terrestrial and marine species, are needed. They should help to explain the predominance of parthenogenesis in freshwater oribatid mites, and perhaps indirectly explain the inordinate percentage of presumed parthenogenetic oribatid mites in freshwater bogs (for example, Solhøy, 1979). Many characteristic bog species are members of the Desmonomata (for example, Trhypochthoniidae, Malaconothridae, Nothridae, Nanhermanniidae), which might have been pre-adapted in some way to intermittently wet habitats by the loss of sexual reproduction.

Vertical distribution in soil

Soil presents a contradiction to the common association of environmental stability with biotic complexity; the litter and fermentation horizons are abiotically unpredictable compared to the humus and euedaphic horizons, yet are biologically much more complex. The general-purpose theory would predict that parthenogens tend to occupy the surface layers and sexual species the deeper layers, and this seems to be

true of earthworms (Jaenike and Selander, 1979). In apparent contradiction, oribatid mites present the opposite pattern, but one consistent with the biotic-uncertainty theory. Luxton (1982b), for example, noted that parthenogens are found mostly below the litter in a Danish beech-forest soil. In his original study (Luxton, 1981b), only one of the nine species represented mostly or entirely in litter was parthenogenetic, whereas more than half the species characteristic of the fermentation layer (0–3 cm depth) are known or suspected parthenogens. The two species confined to mineral soil (3–6 cm) are probable parthenogens, as are the three which were evenly distributed between mineral soil and fermentation layer. This pattern seems to have been noticed first by Sitnikova (1962, *vide* Ryabinin and Pan'kov, 1987), and also can be seen in the data of other authors (for example, Lebrun, 1964; Lions, 1978; Märkel, 1964; Poursin and Ponge, 1984). In most cases the common species of humus (*sensu stricto*) and mineral soil were parthenogens representing the Brachychthoniidae, Epilohmanniidae, Euphthiracaridae, and Oppiidae. Small members of Suctobelbidae are also common, and some may be parthenogenetic as noted earlier.

Although the abiotically stable soil layers beneath the litter cannot be considered disclimax or novel environments, they do exhibit some of the same characteristics such as lower biotic diversity and resource availability. A burrowing earthworm can easily move through regions with differing characteristics, but a small oribatid mite with limited mobility may need to be either very specialized or very generalized to live there. Some of the humus and mineral-soil species (for example, those in the Oppiidae and Euphthiracaridae) seem to be generalists; they have a high ecological valence, and are tolerant of disturbance. Euedaphic and humicolous species such as *Elliptochthonius profundus*, *Gehypochthonius rhadamanthus*, and *Eulohmannia ribagai* seem to be specialized (Norton, 1975; Lebrun and Wauthy, 1981), and the latter at least is highly susceptible to disturbance (Aoki and Kuriki, 1978). Parthenogens may dominate the oribatid fauna of the lower soil horizons but all examples cannot be explained with the same evolutionary rationale.

Species which do not fit theories of broad ecological adaptation

The last example points to a common conflict. For each reference to a parthenogenetic oribatid mite which is broadly adapted, one could be cited which has a relatively narrow ecological distribution, or is found only in biologically well-developed habitats. *Mucronothrus nasalis*, for example, has little ecological valence, being restricted to permanently wet mosses or fully aquatic, oligotrophic habitats (Hammer, 1965; Nor-

ton *et al.*, 1988b); it is a proven parthenogen (Palmer and Norton, 1990). All species of *Camisia* are parthenogenetic, and most seem to be specifically arboreal, feeding on lichens or fungi (Grandjean, 1950; André and Voegtlin, 1982). Species of *Nothrus*, *Platynothrus*, *Heminothrus*, *Nanhermannia*, and other parthenogenetic Desmonomata typically are found in biologically diverse leaf-litter or fermentation-layer communities in forest soils; some may become established before forest succession is complete but only a few species occur in the early stages. It can be concluded that many parthenogenetic species, in particular members of early-derivative taxa, have ecological distributions indistinguishable from those of sexual oribatid mites.

Untenable ecological correlates

Some other ecological predictions seem to fail almost entirely. Ryabinin and Pan'kov (1987, citing work by Ananyeva *et al.*) mentioned the predominance of Brachychthoniidae in mossy arctic tundra but a clear correlation of high latitude with parthenogenesis does not seem to exist. Certainly parthenogenetic species occur in abundance at high latitudes but sexual species are also common, and in proportions that seem no different from those in temperate soils. The paucity of data on the reproductive mode of most species is a problem in such analyses. However, there is no reason to believe, for example, that parthenogens dominate the long lists of oribatid mites from high northern (for example Hammer, 1952; Dalenius, 1963; Cadwalladr, 1969) or southern (for example Dalenius 1965; Wallwork, 1973; Travé, 1976) regions of the globe. Similarly, no clear relationship exists with altitude; sexual species seem to be common at all elevations (for example, Dalenius, 1962; Itoh and Aoki, 1981). Nor is there a paucity of presumed sexual oribatid species in xeric habitats (for example, Wallwork *et al.*, 1984, 1986). It is not simply general rigour or periodic environmental stress which correlates with the dominance of parthenogenetic oribatid mites over sexual species.

Other than disclimax habitats, which are usually discontinuous on a scale which is large to a mite, there seem to be no clear examples of parthenogens being more associated with patchy environments than are their sexual relatives. Microhabitats such as mosses and lichens are well known for their oribatid faunas (for example, Travé, 1963; Seyd and Seaward, 1984) but these are not biased toward parthenogens. The same is true of decaying wood, and the few known oribatid mites which colonize such microhabitats by phoresy on insects (Norton, 1980) are apparently sexual.

Geographical distribution

An in-depth analysis of geographical distributions is not the present intent, but species which are characteristic of disturbed environments are widely distributed, as expected or organisms with great ecological valence. *Oppiella nova*, for example, may be the earth's most widespread and abundant terrestrial arthropod. Most disclimax species mentioned earlier have Holarctic distributions. *Rostrozetes foveolatus* is pantropical but what appears to be the same species is common in forest soils in the Appalachian region of eastern North America and sphagnum bogs in the north-eastern USA (Norton, unpublished) and south-eastern Canada (Behan-Pelletier, personal communication). *Archegozetes longisetosus*, another disclimax species, appears to be pantropical. The same can be said, however, of some parthenogenetic species inhabiting more stable environments. *Malacoangelia remigera* is pantropical but is commonly a forest species. A comparison of Balogh and Mahunka (1983) and Marshall *et al.* (1987) shows many of the forest and aquatic species of Desmonomata to be Holarctic. *Mucronothrus nasalis* has a clearly relictual distribution on all continents except Africa and Antarctica (Hammer, 1965; Norton *et al.*, 1988b). Again there is more than one rationale for a correlate of parthenogenesis in oribatid mites. Broad distributions of early-derivative parthenogens seem to be relictual (cf. Hammer and Wallwork, 1979) but the common disclimax Brachypylina species may have dispersed widely.

Parthenogens would seem to be more likely to inhabit islands (Cuellar, 1977) due to their colonization potential, and perhaps a third of the taxa recorded from South Pacific islands are known or suspected parthenogens (data from Hammer, 1982). Most of these belong to the Desmonomata or Lohmanniidae. Also found are the nearly ubiquitous parthenogens, *Rhysotritia ardua*, *Fosseremus laciniatus*, *Tectocepheus velatus* and *Oppiella nova*. Many other species represented on these islands belong to the Oppioidea – a group in which both sexual and parthenogenetic species are common – but there is no information about reproduction in individual species. In contrast, data from Dalenius and Wilson (1958), Wallwork (1973) and Travé (1976) suggest that sexual species dominate the oribatid fauna on subantarctic islands. This pattern is consistent with Wallwork's (1973) hypothesis that species distributions in this region represent relictual effects more than colonization.

Except for the zone bordering retreating glaciers, there is no clear evidence of intraspecific, glaciation-related patterns as in some other arthropods where sexuality is distributed relictually, and parthenogenetic populations occupy glaciated areas (Suomalainen, 1950). Geographi-

cal variation in sex ratio has rarely even been suggested, and in each case the data are meagre. Grandjean (1941), for example, reported different sex ratios (suggesting different local reproductive strategies) in several French and Moroccan populations of *Scutovertex minutus*. Sitnikova (cited by Ryabinin and Pan'kov, 1987) apparently found female-biased sex ratios in a Russian population of *Ceratozetes gracilis* but it is sexual in North America (Mitchell, 1977; Behan-Pelletier, 1984) and Denmark (Luxton, 1981a). Norton *et al.* (1988b) reported an Australian population of *Mucronothrus nasalis*, widely known as a parthenogen, in which males may be unusually common, but the sample size was too small (eight individuals) to be conclusive. No species represented in a study of world-wide populations of Desmonomata (Norton *et al.*, 1989; Palmer and Norton, in press) shows geographical variation in sex ratio. ratio.

LIFE-HISTORY AND POPULATION CORRELATES

Egg and body size

The size of egg in arthropods has a theoretical lower limit, and if body size is reduced to the point where only one or a few eggs can mature at one time, parthenogenesis might be favoured due to the disadvantage of producing males when fecundity is low (Dybas, 1966). Based on few data, the correlation does not have general application but some individual cases of seemingly adaptive parthenogenesis may be interpreted in this way. In the Brachypylina, single eggs are commonly developed by small parthenogenetic species of Oppiidae such as *Oppiella nova* and *Microppia minus*, and in small Suctobelbidae such as *Suctobelbella* spp., which may also be parthenogenetic; larger Oppiidae and Suctobelbidae seem to be sexual. In the Damaeidae, the single known parthenogen is perhaps the smallest species known (*Damaeobelba minutissima*; Grandjean, 1955). Among the many *Ceratozetes* species represented in North America, only the smallest, *C. parvulus*, lacks males (Behan-Pelletier, 1985). There is, however, no notable size difference between parthenogenetic and sexual subspecies of the small oppiid, *Quadroppia quadricarinata*, or the various sexual and parthenogenetic species of *Hydrozetes*. In the 'lower' oribatid mites, correlation seems to exist in the Epilohmanniidae where the known parthenogens are small species such as *Epilohmannia pallida*, *E. cylindrica* and *Epilohmannoides terrae*. Yet parthenogenetic and sexual species of *Rhysotritia* are not greatly dissimilar in size, nor are those of *Microtritia*. Most Lohmanniidae are relatively large mites and all are parthenogenetic. Among the parthenogenetic Desmonomata, both large and small species are common, with egg numbers

ranging from one or two in the Malaconothridae to dozens in *Archegozetes*.

Fecundity and egg viability

Compared with close sexual relatives, the fecundity of parthenogenetic insects is sometimes reduced (Bell, 1982). One explanation is lower viability, at least during transitions from sexuality (Templeton, 1982). There are few comparative data for oribatid mites but no such pattern is apparent; there is considerable overlap in the egg production of sexual and parthenogenetic species (Luxton, 1981a). There seems to be no fecundity difference between the parthenogenetic *Rostrozetes foveolatus* and the apparently sexual *R. flavus**, although available data are incomplete (Beck, 1969; Woodring, 1965). *Archegozetes longisetosus*, a pantropical parthenogen, is the only oribatid mite known to us with a clear tendency toward an *r*-selected life history. The combination of rapid development (6–8 weeks at room temperature) and unusually high fecundity (several dozen eggs per batch and multiple batches per female; personal observations), causes cultures rapidly to overflow with mites. There is no indication that viability of the eggs produced is at all related to reproductive mode. In observing many cultures of parthenogenetic species (Palmer and Norton, 1990), there have rarely been any eggs that failed to hatch.

Generation time

Ghilarov (1982) and Ryabinin and Pan'kov (1987) suggested, without theoretical framework, that generation times of parthenogens are shorter. This might be predicted in apomictic parthenogens since rapid development shortens the time during which mutations (most of which are deleterious) can appear in an individual (Shields, 1982).

Although mites in general are viewed as having relatively rapid life cycles, oribatid mites usually do not (Lebrun, 1970). For most species studied, parthenogenetic or sexual, the literature (compiled by Luxton, 1981a) suggests one or two generations per year in nature. Considering that few studies distinguish cohorts in different reproductive phases from recruitment of successive generations, Norton (1985) suggested

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* *Rostrozetes flavus* is inferred to be sexual from Woodring's (1965) discussion of the spermatophore (his only mention of males), and this assumption is made throughout this chapter. Non-functional spermatophores may also be produced by spanandric males of thelytokous species (Taberly, 1988), so there is doubt about the validity of comparisons. In addition, *R. flavus* and *R. foveolatus* may be synonyms (Marshall *et al.*, 1987).

instead that one or two years per generation may be typical of temperate forest species. In warmer climates, multiple generations per year may be more common but differences are often tied to taxonomic relationships rather than reproductive mode. In the laboratory, members of the Brachypylina generally develop faster than those of early-derivative taxa (Lebrun, 1970) whether sexual or not. Even in tropical India, the parthenogenetic lohmanniid mite, *Lepidacarus ornatissimus*, seems to have a one-year generation time in nature, and a laboratory development seven times longer than that of sexual galumnid mites of comparable size (Haq, 1978). Two sets of laboratory data allow comparisons between brachypyline species. At 25 °C, the sexual *Oppia concolor* develops slightly faster than the smaller and parthenogenetic *Oppiella nova* (Woodring and Cook, 1962; Nannelli, 1975). Beck (1969) reported a development time of 6 weeks for the parthenogenetic *Rostrozetes foveolatus* reared at 30 °C, which is within the range of 35–45 days reported for the sexual species, *R. flavus*, by Woodring (1965), even though the latter was reared at 23 °C. Available data indicate no relationship between generation time and mode of reproduction.

Population size

Maynard Smith (1984) has noted that in populations with an effective size of under one million individuals, even apomictic parthenogens can successfully combine two independent favourable alleles, arguing that the first would be fixed in the population before the second appears. In small populations sex would, therefore, lose its advantage of genetic innovation relative to parthenogenesis. In contrast, the deleterious effect of accumulating mutations in apomictic species might discourage small, discrete populations where the best (least mutationally loaded) clones can be lost simply by chance catastrophe (Leslie and Vrijenhoek, 1980; Shields, 1988). These predictions cannot be tested since neither absolute nor effective population size seems to have been estimated for any oribatid mite.

TYPES OF PARTHENOGENESIS AND GENETIC CORRELATES

Before examining some genetic predictions of evolutionary theory, the types of thelytokous parthenogenesis, and their very different consequences for the genotypes of offspring, must be distinguished. This has been reviewed many times (for example, Asher, 1970; White, 1973, 1978; Suomalainen *et al.*, 1976; Bell, 1982; Templeton, 1982). With apomixis – the mitotic production of diploid eggs – progeny are genetically identical

to the mother, barring new mutation. Theoretically, such a mechanism ensures high levels of heterozygosity since without a means of producing newly homozygous progeny, maternal heterozygosity is maintained and new mutations accumulate. In contrast, there are several types of automixy, that is, meiotic thelytoky, which differ in the way diploidy is restored, and consequently in their genetic implications. The most common type, intrameiotic restoration by fusion of haploid meiotic products, theoretically enforces homozygosity in a population of stable size since there is no possibility of regaining a heterozygote individual in a lineage which becomes homozygous by recombination.

In a simplistic view, the long-term results of apomixy and most forms of automixy are complete heterozygosity and complete homozygosity, respectively. In apomicts, any beneficial effects of heterozygosity will be decreased gradually by the accumulation of non-functional alleles. This is often relieved temporarily by the acquisition of polyploidy, which serves as a buffer by 'absorbing' non-functional alleles while maintaining functional heterozygosity (Suomalainen *et al.*, 1976; Lokki and Saura, 1980; Shields, 1982; Lynch, 1984). In the long term, however, even polyploidy cannot absorb all unfavourable mutations. As noted by Asher (1970) and Lynch (1984), it is because of such seemingly predictable results that parthenogenesis – either apomictic or automictic – has long been considered an evolutionary 'dead-end' strategy.

Empirical data have not supported predictions of genetic poverty in parthenogens. There is considerable genetic diversity in both apomictic and automictic populations (for example, Suomalainen *et al.*, 1976; Nevo *et al.*, 1984; Lynch, 1984; Hebert, 1987). How is this diversity accumulated and maintained? Continued mutation, and various non-meiotic mechanisms (Lynch, 1984), can cause change to accrue differently among lineages, and we might expect the resulting genetic structure of a population to be more diverse if the organism is automictic than if it is apomictic. Theoretically, the various types of automixy would lead heterozygous loci to homozygosity at different rates, depending on the method of restoring diploidy and the amount of crossing-over which occurs. Asher (1970) demonstrated that a certain amount of heterozygosity can be indefinitely maintained in automicts, just as in inbreeding sexual populations, by selection against homozygotes and by various mechanisms which affect the amount of recombination. In order that heterozygosity be maintained, selection pressures against homozygotes need be less intense with central fusion (fusion of second division non-sister pronuclei) than with terminal fusion (fusion of second-division sister pronuclei). This is because with central fusion a mother, heterozygous at a given locus, produces homozygous progeny only if cross-over occurs whereas with terminal fusion, progeny are homozygous in the absence of cross-over.

Although apomixy is the most common form of parthenogenesis, it seems that the transition from sexuality is usually accomplished through automixy (Lokki and Saura, 1980; Templeton, 1982). Since central fusion is the mechanism least different from sexual reproduction – it entails fewer genetic difficulties than terminal fusion, and can maintain heterozygosity with only modest selection against homozygotes – it should be the most common form of automixy (Asher, 1970; Templeton, 1982).

For present purposes some predictions from these patterns and theories might be as follows: (1) most parthenogens should be apomictic with populations exhibiting some degree of genotypic variability depending on the number of successful clones; (2) high heterozygosity and polyploidy should be common; (3) if a species is automictic, it should restore diploidy by central fusion rather than terminal fusion, and should not exhibit as much heterozygosity as apomicts.

Parthenogenetic mechanisms and genetic diversity

Information relevant to an understanding of parthenogenetic mechanisms is not easy to obtain, and cytological studies of oogenesis are particularly difficult and time-consuming (Maynard Smith, 1978). For parthenogenetic oribatid mites, oogenesis has been described only in the excellent works of Taberly (1958, 1960, 1987b). He found that in *Platynothrus peltifer* and *Trhypochthonius tectorum* (representing the Desmonomata families Camisiidae and Trhypochthoniidae, respectively) diploidy is restored by a joining of the anaphase plates of the second meiotic division, a form of terminal fusion. Such a mechanism should strongly promote homozygosity, and therefore contrasts with theoretical predictions. Taberly (1987b) also discussed data (unfortunately incomplete) concerning an apparent recessive albino allele in *Trhypochthonius tectorum*, which seemed to support his histological evidence. He suggested that the same restoration process seems to occur in a third species, *Nothrus palustris* (Nothridae), but his information was not conclusive.

Allozyme electrophoresis can provide insight into genetic diversity and the presence or absence of recombination, but with common starch-gel techniques, the small size of most oribatid mites precludes the necessary multiple-enzyme assays of single individuals. Vera-Ziegler and Wauthy (1983) briefly outlined a study of *Platynothrus peltifer* in which putative esterase genotypes of tritonymphs were variable in one population (larch plantation) but almost all the same in another (beech forest). Although this was not discussed, in doing so they demonstrated genetic variation in a thelytokous species known to restore diploidy by terminal fusion. Adult esterase variation was also apparently found (Wauthy *et al.*, 1986). Wauthy *et al.* (1986) studied esterase in what were

considered two subspecies of the brachypyline mite, *Quadroppia quadricarinata*; the subspecies, *virginalis*, is parthenogenetic whereas *maritalis* is sexual. The need to pool specimens restricted their conclusions, but the latter subspecies was variable for esterase whereas the former was not.

Cellulose acetate electrophoresis (Easteal and Boussy, 1987) has significantly higher sensitivity, allowing the assay of as many as six enzyme systems per individual mite, and therefore recognition of multi-locus genotypes. The presence or absence of recombination can be detected if parthenogenetically produced offspring of a single mother can be reared and assayed, providing the mother is heterozygous at an interpretable locus. Negative evidence is not conclusive: uniformly heterozygous progeny could result from either apomixy (or its equivalent) or from fixed heterozygosity in an automictic organism. In either case, a minimum estimate of the number of clones can be obtained by sampling field populations for different multi-locus genotypes.

We have used cellulose acetate electrophoresis to study genetic diversity in the Desmonomata and certain other taxa. For populations of five 'parthogenetic' species, Table 7.1 presents preliminary data on the percentage of loci exhibiting allelic polymorphism and mean observed heterozygosity; see Hughes and Hughes (1988) for discussion of the calculation of mean observed heterozygosity in asexual organisms. It should be stressed that parthenogenesis is implied from the absence of males in all populations except *Archegozetes longisetosus* in which it has been proven for both populations (Palmer and Norton, 1990). An important result, even considering the relatively low number of systems which were consistently interpretable, is that most populations show genotypic variation at one or more loci. A comparison of observed heterozygosity data with the compilation of Nevo *et al.* (1984) suggests two interesting points. First, heterozygosity in the Puerto Rican population of *A. longisetosus* is higher than the average for invertebrate parthenogens (0.18) and parthenogens in general (0.21). This is consistent with apomictic reproduction since most data used in the Nevo *et al.* compilation come from species which are probably apomictic and thus, presumably, represent the upper end of the heterozygosity spectrum. Preliminary electrophoretic data from reared sisters (not presented here) are consistent with apomixy since there is no recombination at loci which are heterozygous in mothers. The observed variability in the Puerto Rican population seems to derive from at least four genetically distinct clones. In contrast, the Tahitian population appears to be a single clone; it exhibits fixed heterozygosity at one locus but constant homozygosity at all other interpretable loci. Tahiti is smaller than Puerto Rico, and much further from a mainland, suggesting a founder-effect.

Table 7.1 Percentage of loci exhibiting allelic polymorphism, and mean observed heterozygosity, in populations of parthenogenetic oribatid species determined by cellulose acetate electrophoresis (loci numbers refer to those clearly interpretable from ⩾15 enzyme systems examined for each population)

Species	*Provenance*	*Loci examined* (number)	*Polymorphic loci* (percentage)	*Loci examined* (number)	*Mean heterozygosity*
Lohmanniidae					
Meristacarus sp.	Puerto Rico	10	20	10	0.05
Nanhermanniidae					
Nanhermannia 'nana' (*sensu* Willmann, 1931)*	New York, USA	11	18	10	0.07
Nothridae	New York, USA	5	60	5	0.07
Nothrus n. sp.					
Trhypochthoniidae					
Archegozetes longisetosus	Tahiti	11	9	11	0.09
	Puerto Rico	9	44	9	0.25
Camisiidae					
Platynothrus peltifer	West Virginia, USA	5	50	4	0.12

*This species is being named elsewhere.

The second point is that the other four taxa, all with significant genotypic variation, exhibit considerably lower heterozygosity than most parthenogens. The observed range (0.05–0.12) is similar to that of sexual spiders, for example (0.03–0.11; Nevo *et al.*, 1984). Unlike the Puerto Rican population of *A. longisetosus*, the accumulation of heterozygosity, which is characteristic of apomixy, is not apparent, nor is there strong homozygosity as one might expect if automixy were to lead inexorably in that direction. In the only comparable study of sexual oribatid mites, Bernini *et al.* (1988) found little genetic variation among eight Italian populations of the large phthiracarid, *Steganacarus magnus*, with a heterozygosity of about 0.02–0.07. We speculate that for a genotypically variable parthenogenetic population, a level of heterozygosity similar to that of sexual species may be indicative of automixis.

If the terminal-fusion mechanism discovered by Taberly proves to be more general in distribution, we would expect most of the heterozygosity observed in *Nothrus*, *Platynothrus*, *Nanhermannia*, and *Meristacarus* to be fixed in some way, and for variation within populations to reflect clonal structure. If not fixed, heterozygosity would be quickly lost in the absence of strong selection against homozygotes as theory and Taberly's work with the albino *P. peltifer* suggest. How such fixation might occur is unclear. One such mechanism requires a position close to the centromere (Asher, 1970) but oribatid-mite chromosomes do not seem to have a localized centromere (Helle *et al.*, 1984).

At present there is no electrophoretic evidence of polyploidy in the species listed in Table 7.1, nor in several other taxa under investigation. Sokolov (1954) examined cells of *Nothrus silvestris*, which appeared to be tetraploid, but he concluded that they were probably somatic cells, and not those involved in spermiogenesis.

In summary, the predictions referred to earlier do not seem to be generally supported by parthenogenetic oribatid mites although the data are meagre. Apomixy or its equivalent may exist but preliminary data suggest that it is not dominant. Automixy with terminal fusion, a type considered extremely rare (Lynch, 1984), is the thelytokous mechanism in the only two species studied cytologically. In four genotypically variable parthenogens, automixy is inferred from levels of heterozygosity similar to those of sexual species. There is neither cytological nor electrophoretic evidence for polyploidy.

TAXONOMIC CORRELATES OF PARTHENOGENESIS

Although many have attacked the 'dead-end' hypothesis for a variety of reasons (for example, Ghilarov, 1982; Templeton, 1982; Lynch, 1984), the genetic variance in parthenogens is usually viewed as temporary, to

be eventually sorted out by clonal selection or driven to homozygosity by automixis. While rejecting short-term 'dead-ends', it seems that most still believe in longer-term dead ends. For those who consider most parthenogens to be narrowly adapted, the limiting factor would be the period of existence of the specialized niche. If the parthenogen is broadly adapted, the accumulation of deleterious alleles and non-functional heterozygosity may limit its persistence, assuming it is apomictic.

Using taxonomic patterns to look back on evolution, the obvious predictions have been outlined a number of times. Maynard Smith (1984) suggested the following correlates, which he considered borne out by the evidence: (1) most existing parthenogens should be similar to sexual species or, on a larger scale, there should be no isolated parthenogens unrelated to a sexual taxon; (2) we would not expect to find large taxa, for example families or orders, consisting wholly of parthenogens. In Bell's (1982) terms, parthenogenesis is expected to be sporadic but not random; clustering of parthenogens in primarily sexual higher taxa might be expected if shared life-history traits, mating systems or other biological attributes predispose a particular group to parthenogenesis.

Oribatid mites that conform

Present knowledge of the Brachypylina (for lists see Grandjean, 1941; Luxton, 1981a; Taberly, 1987a), that is, the more highly derived oribatid mites, generally supports the predictions. Sporadic distribution is confirmed by the fact that the 25 known parthenogenetic species represent 10 (9%) of the approximately 110 families. Only one member of the large family Damaeidae is a suspected parthenogen (*Damaeobelba minutissima*). Again some genera with a moderate to large number of nominal species, such as *Rostrozetes*, *Oribatula* and *Ceratozetes*, contain a single suspected parthenogen. The clustering effect is seen in *Oppia* and related genera, which contain both sexual and parthenogenetic species; the same is true of *Hydrozetes*. The monogeneric family, Limnozetidae, has no known sexual species (see above), nor does the diverse and common genus, *Tectocepheus*, although only three species seem to have been investigated.

Do parthenogens seem to have close relatives which are sexual? In *Hydrozetes*, the presence of specialized hairs (see above) on spanandric males of the parthenogenetic *H. lacustris* and *H. lemnae* (Grandjean, 1948a) supports a hypothesis that each parthenogenetic species arose from a sexual ancestor. Beck (1969) noted that the parthenogenetic haplozetid *Rostrozetes foveolatus* was a close relative of *R. rimachensis*, a sexual species. Woodring's (1965) *R. flavus* seems morphologically indis-

tinguishable from *foveolatus* and the two have even been synonymized (Marshall *et al.*, 1987). Certain of the parthenogenetic and sexual oppiids (for example, *Oppia nitens* and *O. concolor*, respectively) seem to be closely related. Lions (1982) described two subspecies of the common *Quadroppia quadricarinata*, one of which is sexual (*maritalis*) and the other is parthenogenetic (*virginalis*). These two entities are distinguishable both morphologically and enzymatically (Wauthy *et al.*, 1986) but their close relationship is certain. The predicted correlates also hold in some early-derivative oribatid-mite taxa. Both *Rhysotritia* and *Microtritia*, whose common European species are parthenogenetic, have sexual species in California: *R. scotti* and *M. paeneminima* (Walker, 1965). Clustering of parthenogens occurs in the Epilohmanniidae: no males are known in *Epilohmannoides* (Norton *et al.*, 1978) and *Epilohmannia* has both sexual and parthenogenetic species (Wallwork, 1962)*.

Oribatid mites that do not conform

The above patterns contrast strongly with what is seen in most early-derivative taxa (Norton *et al.*, 1989) where parthenogens are found in more than half of the approximately 40 families. Using Grandjean's (1969) classification of major groups, there are a number of phylogenetically isolated, apparently relictual taxa (each monotypic or with few species) in which no males are known. These include: all three families of Parhyposomata (Parhypochthoniidae, Gehypochthoniidae, Elliptochthoniidae), the Mixonomata families, Nehypochthoniidae and Eulohmanniidae, the Enarthronota families, Phyllochthoniidae, Atopochthoniidae, and Pterochthoniidae, as well as the isolated genus, *Gozmanyina* (misplaced in the Cosmochthoniidae) and the Palaeosomata family, Palaeacaridae.

Most of the species-rich families of early-derivative groups also seem to be entirely parthenogenetic. No males are known in the most diverse enarthronote family (about 100 nominal species), the Brachychthoniidae. The Lohmanniidae is a supposedly isolated family containing about 140 species (Balogh and Balogh, 1987) in which parthenogenesis seems to be ubiquitous. The dominance of parthenogenesis in the Desmonomata (= 'Nothroidea' *sensu lato* of Grandjean, 1969), which collectively contains well over 300 nominal species, has been discussed by Norton *et al.* (1989). Sexual species are unknown in the Camisiidae, Malaconothridae, Trhypochthoniidae (*sensu lato*; including Mucro-

* *Epilohmannia styriaca* can be added to the list of sexual species (R. Schuster, personal communication).

nothridae, Trhypochthoniellidae and Allonothridae of various authors) and in Nanhermanniidae. Members of the large family Nothridae are parthenogenetic except for the small genera, *Novonothrus* and *Trichonothrus* (comprising a total of three species), which have restricted, 'gondwanan' distributions (Palmer and Norton, in press).

SYNTHESIS

From the viewpoints of ecology, life history, genetics and taxonomy, parthenogenetic oribatid mites may either conform or be distinctly at odds with current theory. The Brachypylina, generally considered the most highly derived and by far the most species-rich major oribatid group, follow some theoretical predictions closely. In these mites, parthenogenesis is relatively rare; it occurs sporadically but not randomly, and parthenogens predominate in new and disclimax environments. The latter is also true of species in some early-derivative genera (for example, *Rhysotritia*, *Microtritia*) which contain sexual relatives. Most of these parthenogens seem to be generalists, and although nothing is known about their cytogenetics, it is predicted that they are apomictic, since broad ecological valence is most easily developed by apomixy and clonal evolution (Lynch, 1984). In contrast to the taxa mentioned above, most early-derivative oribatid mites conform poorly to theoretical expectations. Does this result from faulty theory, or are we simply guilty of overgeneralization about the evolution of parthenogenesis? The following discussion pertains mostly to these 'lower' oribatid mites, and suggests that by recognizing the evolutionary potential of some forms of parthenogenesis, the apparent anomalies may be explainable.

Speciation and radiation in parthenogenetic lineages?

Theory suggests that the distribution of parthenogenesis should not conform to taxonomic (implying phylogenetic) patterns, that is, its distribution should not have a strong historical basis. In early-derivative oribatid mites, the reverse is more often true, and the generalization of Oliver (1971) and White (1978) that whole genera and families of mites are never thelytokous is clearly wrong. Grandjean (1941) and Taberly (1987a) noted that parthenogenesis had 'captured' whole families but the evolutionary significance of this has been realized only recently (Norton *et al.*, 1989). Diverse taxa such as Brachychthoniidae, Lohmanniidae, and most families of the Desmonomata show that not only short-term genetic change, but true long-term evolution, speciation and radiation can occur in parthenogenetic lineages. Like the often men-

tioned bdelloid rotifers (White, 1978; Maynard Smith, 1984), these mites are somewhat of an embarrassment to evolutionary theory.

What is the alternative to an explanation that these taxa radiated under a thelytokous reproductive strategy? To assume that each of the hundreds of known (and hundreds of unknown) species in these families developed parthenogenesis independently is unreasonable. But given that assumption, we must also explain the extinction of an equal number of sexual species when it is the parthenogenetic species which are supposed to be short-lived in evolutionary time. Such non-parsimonious reasoning is illogical as Mayr (1963) and White (1978) suggested with regard to the bdelloid rotifers.

If parthenogenetic radiation was indeed the cause of these patterns, we might expect to find in early-derivative oribatid mites a different thelytokous process from that characterizing the majority of animal parthenogens, which have not so radiated. In particular apomixy, with its relative genetic inflexibility, should not be the rule. With automixy, mechanisms exist for maintaining limited heterozygosity while still retaining DNA-repair capabilities (see above; Asher, 1970). Automixy has been proven in the Desmonomata but the only mechanism currently known is terminal fusion. If this, rather than central fusion, is widespread, the retention of observed heterozygosity is more likely to result from fixation than from selection against homozygotes. In any event, there seems to be no unassailable rationale precluding the divergence of automictic populations under selection, and the eventual emergence of populations recognizable to systematists as distinct 'species'.

Whether sexual reproduction speeds or slows evolution is debatable (Michod and Levin, 1988), but it can be assumed that speciation under automixy would be slow without recruitment of alleles from other lineages. This is apparent in the restriction of parthenogenetic radiation, assuming it is real, to early-derivative families with little morphological diversity. It is almost certain that the genera and families seen in the large parthenogenetic groups are very old. Oribatid mites constitute an ancient lineage, which dates back at least 370 million years (Norton *et al.*, 1988a). The family, Trhypochthoniidae, is known from the Jurassic period as fossils (Krivolutsky and Druk, 1986), and biogeographical evidence suggests that even the species, *Mucronothrus nasalis*, is extremely old, predating the breakup of Pangea some 200 million years ago (Hammer, 1965). Travé (1973) found that the only changes, accumulated among the disjunct global populations of the latter parthenogen, seem to be minor statistical differences in leg setation, and suggested that parthenogenesis was responsible for the species' persistence. Many of the earlier-derivative 'living fossils' (that is, Parhyposomata, Nehypochthoniidae, Eulohmanniidae and some Enarthronota), which at least at the family level must have existed in the Jurassic, are parthenogenetic.

Parthenogenesis as a historical constraint

If the present view is correct, the many discrepancies between theory and observed patterns should be explainable, given sufficient ecological, cytogenetic, and phylogenetic information. Also, certain other patterns may now come into focus. For example, when apparent revolutions in morphology or rates of radiation have occurred in groups which are mostly parthenogenetic, a reversion to sexuality may have been involved. Among the Enarthronota, most of which are parthenogenetic, the two families, Mesoplophoridae and Protoplophoridae, which evolved, independently, a ptychoid body form, are sexual (Norton, 1984; Norton *et al.*, 1983, 1989). More interesting is the probability that the morphologically diverse, species-rich, and overwhelmingly sexual Brachypylina evolved from within the Desmonomata. An even more striking example exists: there is considerable evidence that the extremely diverse and predominantly sexual mite 'suborder', Astigmata, also originated within the Desmonomata (Norton, unpublished).

In this light, the slow evolutionary change associated with parthenogenesis is viewed as a constraint, from which the Astigmata, the enarthronote taxa and perhaps the Brachypylina, were released by reverting to sexuality. The pattern suggests that such reversion was not easily accomplished. For example, it is unlikely that a single gene can suppress meiosis as Hebert (1987) suggested is true in cladocerans. Although highly speculative to begin with, reversion seems conceivable only if the ancestral parthenogens were automictic. Much might be learned by studying what appears to be facultative reversion to sexual reproduction in *Oribatula sakamorii* (see above).

Parthenogenesis and adaptation

If parthenogenesis can be either an ancestral or a derived character-state, depending on the taxon, adaptive value should not always be expected. If it is recently derived from a sexual ancestor as is usually considered to be the case in parthenogenetic species, an adaptive value might be clear. If it has been maintained as a constraining ancestral character-state, it may have no observable value although some might consider faithful preservation of a successful genome to be advantageous in any species (for example, Shields, 1982). Further, ancestral parthenogenesis may have pre-adapted the species to some environment (i.e., water) or life style (i.e. colonizer) which is atypical of oribatid mites, so that parthenogenesis is incorrectly seen as an adaptation.

This can be illustrated in a tentative way by two unrelated aquatic species. The brachypyline mite, *Hydrozetes lemnae*, lives in warm lentic

water where highly specialized immatures feed only inside floating duckweed (*Lemna*) (Fernandez and Athias-Binche, 1986). The unpredictable nature of their habitat and food supply suggests the importance of colonization potential. In addition, unlike most oribatid mites, their life history is *r*-selected with two generations per year and marked seasonal fluctuations. In contrast, *Mucronothrus nasalis* inhabits cold, oligotrophic water, either stable, spring-fed lotic habitats or deep lakes. It is an unspecialized feeder with low fecundity, and probably a multi-year generation time (Norton *et al.*, 1988b). Parthenogenesis is clearly derived in *H. lemnae* (it has close sexual relatives, as discussed earlier), and seems adaptive for its colonization advantage, and perhaps also from the standpoint of possible mating inefficiencies associated with fresh water (see above). Parthenogenesis is ancestral in *M. nasalis* (there are no confamilial sexual species), yet may be pre-adaptive both in preserving a well adapted genome in an extremely stable, biotically simple environment, and in avoiding possible mating difficulties in fresh water.

Taxonomic as well as ecological comparisons will be valuable as the database grows. For example, the biologies of *M. nasalis* and two other members of the Trhypochthoniidae show interesting contrasts. Parthenogenesis in *Archegozetes longisetosus* is seemingly adaptive; the mite is a good colonizer, and lives in disclimax habitats. It also has a relatively *r*-selected life history with high fecundity and short generation time (see above). Theory would predict apomixy and high heterozygosity in this species, both of which appear to be true. *Trhypochthonius tectorum* seems to acquire no obvious advantage from parthenogenesis. It is found commonly in mosses (Taberly, 1987c), and its biology is generally similar to that of sexual oribatid mites in the same habitat. Fecundity and generation time (Taberly, 1984, 1987c) seem to be intermediate between those of *M. nasalis* and *A. longisetosus*. Automixy with terminal fusion is known in *T. tectorum*, as discussed above, but no genetic data are available for either this species or *M. nasalis*. What should we expect in a parthenogen like *M. nasalis*, which is both extremely old and restricted to rather unchanging abiotic conditions? One rationale is that DNA repair would have been important over such time-spans, and a combination of automixy, habitat specialization, and long persistence may have produced a genome which is resistant to change.

Unusual species like *M. nasalis* and *A. longisetosus* are interesting and theoretically important. Yet, it is parthenogens such as *T. tectorum* or others, sharing environments with many biologically similar sexual species, which may prove to best exemplify the cytogenetic systems characteristic of large, slowly evolving parthenogenetic groups.

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8

*Indirect sperm transfer in prostigmatic mites from a phylogenetic viewpoint**

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The mechanisms of indirect sperm transfer of prostigmatic mites are reviewed from a phylogenetic point of view. The significance of indirect sperm-transfer characters to phylogenetic systematics is elaborated using the Hydrachnidia as an example, and the phylogenetic tree of this group is presented. The evolutionary transformation of spermatophores and strategies for their deposition, signalling methods and partner-behaviour modes in the Anystidae and Parasitengonae is reconstructed on the basis of the phylogenetic system together with a synthesis of the reproduction mechanisms of the stem species of the Parasitengonae. The adaptation of indirect sperm-transfer mechanisms to various environmental conditions is discussed with regard to aquatic and terrestrial mites. Key elements are the adaptation of spermatophores to low and changing humidities by passive water uptake from the atmosphere; osmotic protection of the sperm cells; spermatophore viability; the types of signals used to guide individuals to spermatophores or to a partner, and the relationship of these to the spatial structure of the habitat and the mode of locomotion of the mite; and finally the conditions which, in evolution, have favoured the deployment of spermatophores in the absence of the female, and those favouring partner contacts and pairing

INTRODUCTION

Indirect sperm transfer by means of spermatophores is common in terrestrial arthropods. Apparently it had already evolved in the stem

* Invited paper.

lineages of the Antennata and the Arachnida (Schaller, 1971; Ax, 1984; Weygoldt and Paulus, 1979). Although indirect sperm transfer has been discussed from a phylogenetic point of view by several authors (for example, Alexander, 1964; Schaller, 1971, 1979; Weygoldt, 1975; Mann, 1984), a number of important issues are still controversial or have not been fully resolved. These include:

1. The possible contribution of indirect sperm-transfer characters to phylogenetic systematics.
2. The course of phylogenetic transformation of indirect sperm-transfer mechanisms within most groups of the arthropods. Here it would be useful to follow Weygoldt's (1966) exemplary investigation of this process in the pseudoscorpions.
3. The environmental adaptation of spermatophores, signalling mechanisms and partner behaviour.

It is the aim of this chapter to elaborate these points using as an example the prostigmatic mites. Within this group I shall focus on the Parasitengonae and on the Anystae, which are the probable sister group of the Parasitengonae (Lindquist, 1976). Original investigations have been carried out on the following species: Trombidioidea: *Allothrombium fuliginosum, Trombidium holosericeum, Camerothrombidium rasum, Johnstoniana errans* and *J. ventripilosa*; Calyptostomatoidea: *Calyptostoma velutinus*; Erythraeoidea: *Erythraeus phalangioides, E. regalis, Urrbrites* sp., *Abrolophus rubipes, A. quisquiliarum, A. passerinii, Charletonia cardinalis* (= *Sphaerolophus cardinalis*), *Leptus trimaculatus* and *L.* cf. *rupestris*; Hydrachnidia: *Eylais extendens, E. infundibulifera, Limnochares aquatica, Hydryphantes ruber, Thyas barbigera, Euthyas truncata, Hydrachna cruenta, Sperchon setiger, Lebertia inaequalis, Limnesia maculata* and *Hygrobates nigromaculatus*; Anystidae: *Anystis baccarum* and *A. rosae*.

Where only the generic name is given in the text, the species stated above is referred to. A detailed account of the original results will be published elsewhere.

RECONSTRUCTION OF PHYLOGENETIC RELATIONSHIPS

In order to reconstruct phylogenetic relationships, morphological and behavioural characters of the reproductive mechanisms can be used in the same way as other phenotypic characters, where the homology and synapomorphy in sister groups can be substantiated (Hennig, 1966; Ax, 1984). The main difficulty in the applicability of these characters is that several structures and behavioural modes of indirect sperm transfer are highly adaptive, and apparently have evolved several times convergently. In what follows it is shown that the sheath which covers the

sperm droplet, obligatory pairing behavioural modes initiating spermatophore deposition and direct sperm transfer, among other characters, have each evolved several times convergently within the Parasitengonae. Therefore, characters used in phylogenetic systematics should be complex in structure, and should occur continuously within the postulated sister groups.

Such characters of indirect sperm-transfer mechanisms may be demonstrated in the Hydrachnidia (Witte and Olomski, unpublished), in which they evolved mainly near the base of the group, and in Hygrobatoidea and Arrenuroidea as can be seen in Fig. 8.1. On the basis of these, and additional synapomorphic characters, presented in Table 8.1, it can be demonstrated that within the water mites, the superfamilies, Hydryphantoidea, Lebertioidea and Hygrobatoidea are each paraphyletic groups, and that the Hydrachnoidea did not deviate from the base of the Hydrachnidia (Smith and Oliver, 1976), but must be placed within the late-derivative water mites, which Witte and Olomski (unpublished) term 'Neohydrachnidia' (Fig. 8.1).

PHYLOGENETIC TRANSFORMATION AND ENVIRONMENTAL ADAPTATION

Methods

The course of phylogenetic transformation and phylogenetic adaptation of species and their characters can be reconstructed on the basis of the phylogenetic system in the following steps:

1. Reconstruction of characters of the stem species: the characters of the stem species are reconstructed to establish the original character pattern from which transformations ensued in the course of the adaptive radiation of a monophyletic group. Stem-species characters may be reconstructed by means of commonly derived characters of the group itself, and on the basis of symplesiomorphic characters which species of the group share with one or several outgroups.
2. Reconstruction of the course of phylogenetic transformation of characters: which character states are derived, and when in the sequence of branching events they have evolved, can be inferred from their distribution within the phylogenetic system.
3. Reconstruction of phylogenetic adaptation: phylogenetic adaptation can be defined as 'phylogenetic transformation of species and their characters under the control of environmental selection'. In other definitions, such as those given by Stern (1970), Curio (1973), de Jong (1980) and Sluys (1988) among others, 'selection' is not re-

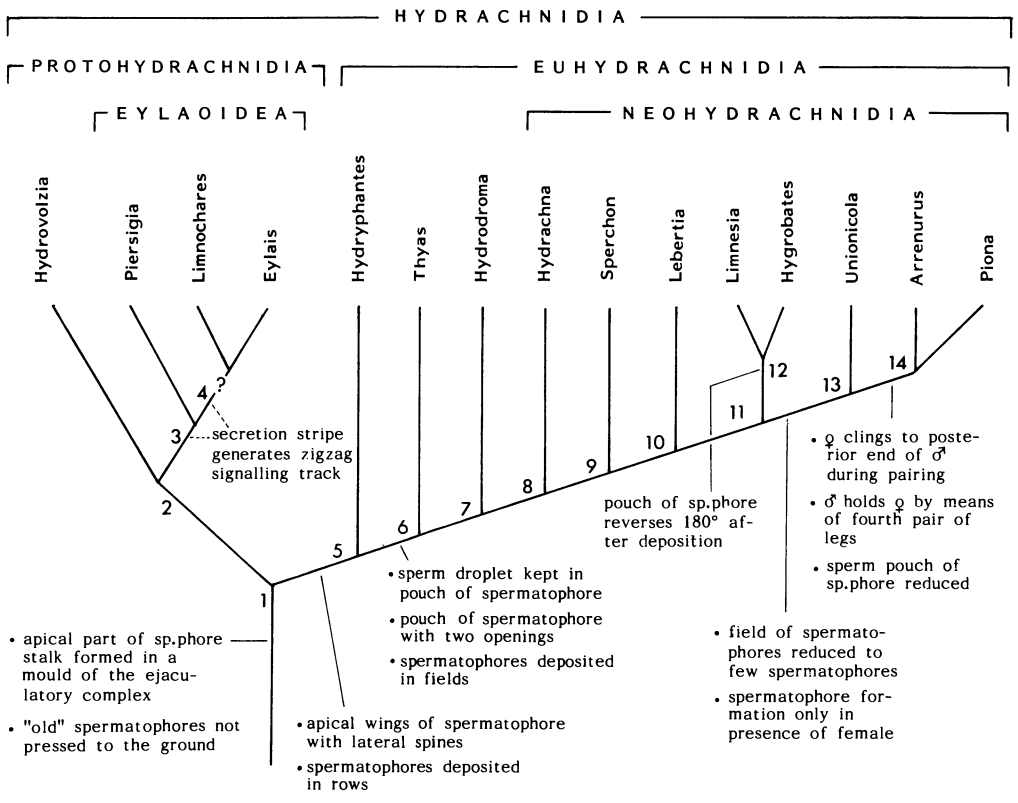


Fig. 8.1 Phylogenetic relationships within the Hydrachnidia (Witte and Olomski, unpublished) with characters relating to indirect sperm-transfer mechanisms. For key to further synapomorphic characters (1–14), see Table 8.1.

Table 8.1 Synapomorphic characters of the Hydrachnidia. Numbers refer to those given in phylogenetic tree in Fig. 8.1

1. Anal sclerite in larva with one pair of setae; anal pore in larva and adult surrounded by single sclerite; median eye dorsal; glandularia; acrosome filament of sperm cell reduced; posterior rami of proximal-arm sclerite of ejaculatory complex form distally an apex projecting into atrium.
2. Last pair of idiosomal dorsoventral muscles arranged in median position; distal-sclerite arms and apical setae of ejaculatory complex reduced; lateral eyes without muscles.
3. Trichobothrium on telofemur of each leg in larva; mouth opening surrounded by membraneous ring; orbitae fused with dorsal shield; anterior part of chelicerae fused by membrane.
4. Membraneous ring of mouth opening closed dorsally; acetabular fields without surrounding sclerite; seta-bearing platelet of glandularia prolonged internally to form a tube.
5. Post-anal median muscle (anal 4) reduced; posterior-keel sclerite of ejaculatory complex forms plate-shaped carina; capitulum retractor muscle 3 reduced (plesiomorphically, the muscle originates at the endosternite); unpaired anterior accessory gland of male genital tract reduced; antero-median rami of proximal-arm sclerite, which project into mid section of ejaculatory complex, provide mould for spines of apical wings and pouch of spermatophore; distal-arm sclerite of ejaculatory complex provided with prominent arms.
6. Anal sclerite of larva with two pairs of setae; larva parasitizes Nematocera.
7. Median eye of larva reduced; anterior anal muscle (anal 2) reduced; one pair of accessory eyes beneath prodorsal cuticle; swimming by means of legs I–IV.
8. Legs of swimming larva with five segments; empodial claw of larva with two lateral spurs; larva finds host under water; seta-bearing sclerite of glandularia fused with ring sclerite of gland pore to form single sclerite.
9. Tibial claw of larva simple; grasping palps with tibia opposing femur; eggs enclosed in common protective envelope; glandularia 6c reduced but setae still present antero-lateral to anal aperture.
10. Prominent urstigmal blade in larva; pharynx flexor muscles reduced except most posterior one; lenses of lateral eyes attached to internal surface of cuticle by peduncle; internal cuticular basket of glandularia reduced; both lobes of glandularia broadly fused; coxal plates II and III of larva fused.
11. Genital acetabula located on acetabular plates flanking gonopore; orbita of lateral eyes reduced; apodeme cone of eye muscles attached to anterior lens; each pair of lateral eye lenses connected by internal chitinous bridge.
12. Coxal plates I–III of larva fused; pouch of spermatophore rotates through angle of 180° after deposition.
13. Unifollicular testis; spermatophore fields reduced in size to few spermatophores; formation of spermatophores only in presence of females (a few exceptions evolved secondarily).
14. Female clings to posterior end of male during pairing, and male holds female using legs IV; sperm pouch of spermatophore reduced.

stricted to 'environmental selection'; it would include courtship-mode selection, a characteristic not necessarily offering a selective advantage with respect to the environment, but one that increases fitness. In order to reconstruct phylogenetic adaptation in the sense defined above, it must be shown that the phylogenetic transformation of characters was controlled by distinct selection agents. Such a control may be assumed, if – on the basis of the phylogenetic tree – the transformation of a character in the sequence of branching events can be correlated with a change in environmental conditions. This method is included in the criterion of correlation, proposed by Curio (1973). More direct evidence of adaptation, for example, proof of an increased fitness, cannot be obtained from species long extinct, and where the niche of each of the recent successor species has probably altered.

In terms of methods, the Parasitengonae are, for a number of reasons, well suited to investigations on the evolution of reproduction mechanisms:

1. The phylogenetic system of the group is largely known and, as a result, one is able to reconstruct the course of transformation of the reproductive mechanisms. The former is clear from the reconstruction of the phylogenetic relationships of the Hydrachnidia (Fig. 8.1) already discussed. In addition, the phylogenetic system of the Trombidia has been presented in outline by Witte (1984).
2. The reproductive mechanisms of the stem species can be reconstructed by means of an outgroup comparison with the closely related Anystidae in which quite similar mechanisms are found.
3. The Parasitengonae have adapted to a wide variety of xeric, hygric and aquatic habitats, and a remarkable diversity of spermatophore types, signalling mechanisms and partner-related behavioural patterns has evolved within the group.

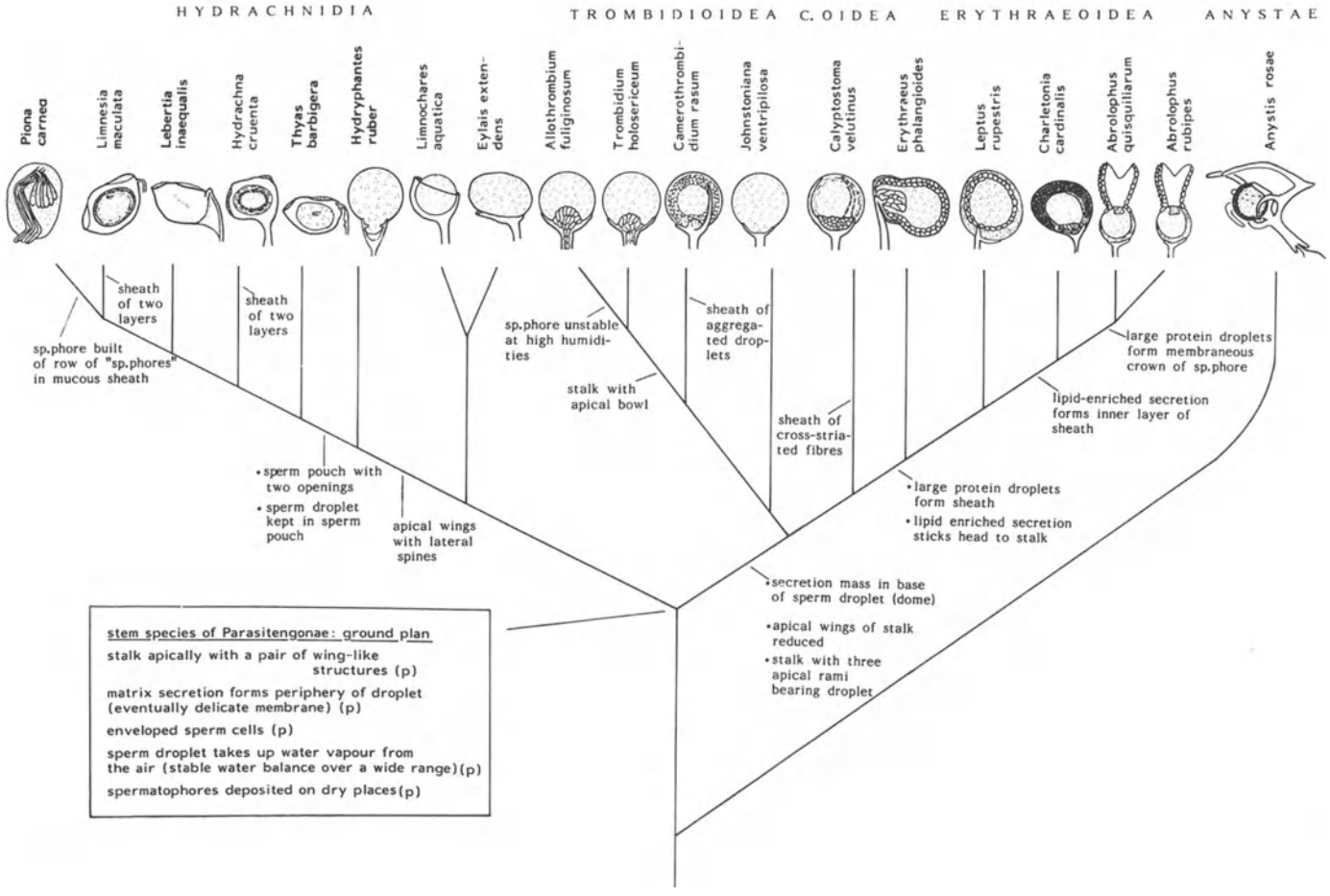
Characters of stem species in Parasitengonae

The probable characters of indirect sperm transfer in the stem species of the Parasitengonae are briefly described here, and an assessment of the likely habitat conditions under which these spermatophores were deposited, is presented.

Plesiomorphic (*p*) reproductive characters of the stem species are reconstructed by means of characters which the Parasitengonae share with the outgroup Anystidae (*Anystis rosae* and *A. baccarum*). Apomor-

phic (*a*) characters of the stem species are reconstructed by means of synapomorphic characters of the sister groups, Hydrachnidia and Trombidia (Trombidioidea, Erythraeoidea and Calyptostomatoidea), the two groups emerging from the first splitting of the stem species. The distribution of the characters within the Parasitengonae is shown in Figs 8.2 and 8.8. In the stem species, the stalk of the spermatophore had a pair of apical wings, probably to protect the sperm droplet against accidental shearing off (*p*). The periphery of the sperm droplet consisted of a matrix secretion of the sperm, and a peripheral sheath was lacking (*a*). The sperm droplet was, apparently, able to maintain a stable water balance by means of a mechanism allowing it to take up water vapour from the atmosphere over a wide range of humidities (*p*). The sperm cells were provided with a secretion sheath (Alberti, 1980). It is likely that this protected them from the highly hygroscopic matrix secretion of the sperm fluid (*p*). The spermatophores were deposited on dry substrates where surface water was not present (*p*). Several spermatophores were deposited on each deposition site and, frequently, spermatophores previously deposited were knocked on to the ground (*p*), and the semi-fluid droplets from these were not picked up by the females. The deposition site was marked by signalling threads. These were laid down as the male followed a circular course (*p*) which changed to a zigzag configuration as he approached the site where deposition was to take place (*a*). It is believed that the mating behaviour of the partners consisted of an encircling dance. Spontaneous deposition occurred facultatively but the presence of spermatophores previously deployed by the male itself or by other males also stimulated spermatophore deposition (*p*). Males neither defended the site of mating nor that of spermatophore deposition against other males – as is the case with the Allothrombiinae – but fighting between members of the species did occur, for example, where a prey is captured by a male which, in turn, is attacked by another male in order to seize the captured prey (*p*).

Habitat requirements of stem species An outgroup comparison of the Parasitengonae with the Anystae shows that most of the terrestrial species live in xeric habitats or those with fluctuating humidities. This can be regarded as an indication that the stem species was adapted to xeric conditions. The ability of the spermatophore to function at low humidities as well as the deposition of spermatophores on dry substrates by most terrestrial Parasitengonae and by the Anystidae strengthen this hypothesis, and indicate that spermatophores were deposited on dry surfaces.


HYDRACHNIDIA
TROMBIDIOIDEA
C. OIDEA
ERYTHRAEOIDEA
ANYSTAE
Piona carnea
Limnesia maculata
Lebertia inaequalis
Hydrachna cruenta
Thyas barbigera
Hydryphantes ruber
Limnochares aquatica
Eylais extendens
Allothrombium fuliginosum
Trombidium holosericeum
Camerothrombidium rasum
Johnstoniana ventripilosa
Calyptostoma velutinus
Erythraeus phalangioides
Leptus rupestris
Charletonia cardinalis
Abrolophus quisquiliarum
Abrolophus rubipes
Anystis rosae
sheath of two layers
sp.phore built of row of "sp.phores" in mucous sheath
sheath of two layers
• sperm pouch with two openings
• sperm droplet kept in sperm pouch
apical wings with lateral spines
sp.phore unstable at high humidities
stalk with apical bowl
sheath of aggregated droplets
sheath of cross-striated fibres
large protein droplets form membraneous crown of sp.phore
lipid-enriched secretion forms inner layer of sheath
• large protein droplets form sheath
• lipid enriched secretion sticks head to stalk
• secretion mass in base of sperm droplet (dome)
• apical wings of stalk reduced
• stalk with three apical rami bearing droplet
stem species of Parasitengonae: ground plan
stalk apically with a pair of wing-like structures (p)
matrix secretion forms periphery of droplet (eventually delicate membrane) (p)
enveloped sperm cells (p)
sperm droplet takes up water vapour from the air (stable water balance over a wide range)(p)
spermatophores deposited on dry places(p)

Transformation of spermatophoral structures

Apical structures and sperm pouches Apical structures of the stalk, found in the Anystidae and other early-derivative Prostigmata (Fig. 8.16), are preserved relatively unchanged only in the hydrachnid members of the Parasitengonae. Within this group, the spermatophore of *Hydryphantes* still bears two membraneous apical leaves within which the base of the sperm droplet rests (Fig. 8.3*a*). The leaves are provided with a pair of lateral spines, which project medially and hold the droplet in position.

In the later-deviated Hydrachnidia commencing with *Thyas*, the apical leaves form a pouch which holds the sperm droplet (Fig. 8.3*b–f*). The leaves join medially, leaving anterior and apical apertures. In the spermatophores of most species the lateral spines are retained. In *Hydrachna cruenta* (Fig. 8.3*c*) the spines have become quite small but in *Lebertia inaequalis* (Fig. 8.3*e*) and *Hygrobates nigromaculatus* (not shown), they are no longer present. The firm dorsal union of the lateral membranes of the pouch is also lost secondarily in some species, such as *Hydrodroma despiciens* (Meyer, 1985), *Hygrobates nigromaculatus*, *Sperchon setiger*, *Unionicola intermedia* and *U. tricuspis* (Hevers, 1978). In *Arrenurus*, the spermatophore consists of just a simple droplet without a pouch (Böttger, 1962). The evolution of sperm pouches in the water mites was correlated with the evolution of the practice of depositing numerous spermatophores in one field (see below). With such behaviour, the sperm pouches apparently provide protection against damage due to bodily contact by mites, which frequently occurs when males deposit row after row of spermatophores close together in one field. It is interesting to note that in the Halacaridae, in which numerous spermatophores are also deposited in fields, similar sperm pouches have evolved convergently (A. Pahnke, 1974; Kirchner, 1967, 1969).

It is difficult to decide whether the apical rami of the spermatophores of the Trombiculidae (Lipovsky *et al.*, 1957; Wen, 1958). *Calyptostoma velutinus* (Vistorin-Theis, 1975), *Camerothrombidium*, *Erythraeus* and *Leptus*, are also homologous with the original wing-shaped structures. In any case, they have a supporting function and do not provide protection against mechanical shock.

Sheaths and matrix secretion of sperm droplet In most of the early-derivative Parasitengonae, *Limnochares*, *Eylais*, *Hydryphantes*, *Thyas*, *John-*

Fig. 8.2 Spermatophores in the Parasitengonae: original state listing apo- (*a*) and plesio-morphic (*p*) characters of stem species and phylogenetic transformation. C. OIDEA, Calyptostomatoidea.

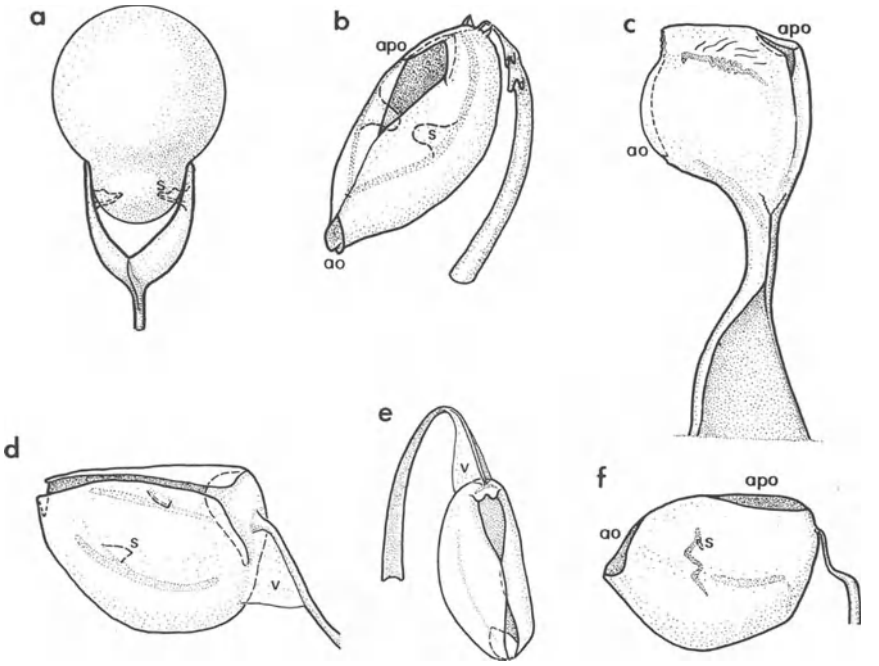


Fig. 8.3 Spermatophores and sperm pouches of Hydrachnidia. (*a*) *Hydryphantes ruber*; (*b*) *Thyas barbigera*; (*c*) *Hydrachna cruenta*; (*d*) *Sperchon setiger*; (*e*) *Lebertia inaequalis*; (*f*) *Limnesia maculata*. ao, anterior opening; apo, apical opening; s, lateral spine; v, velum.

stoniana, *Trombidium*, *Allothrombium*, the sperm droplet lacks a sheath. In *Calyptostoma*, there is only a loose sheath of cross-striated fibres around the sperm mass (Fig. 8.5*e*). The sheath is permeable to the matrix secretion of the sperm which, at high atmospheric humidities, can also occur outside the sheath. It is probable that the lack of a sheath is a synapomorphic character state of the Parasitengonae, since in the outgroup Anystidae, a filamentous to granulated sheath is found (Fig. 2 in Witte, 1984). Within the late-derivative Parasitengonae, sheaths, formed from quite different secretions, evolved several times convergently (Fig. 8.2). Thus the sheath of *Hydrachna* has an inner layer consisting of small protein droplets, and an outer one of small secretion filaments (Fig. 8.4). *Limnesia* also has an inner layer of small protein droplets, and a delicate outer layer showing radial striation (Fig. 8.4). In *Camerothrombidium*, the sheath consists of a broad layer of aggregated droplets covered by a thin layer of a granulated secretion (Fig. 8.5*f*). In the Erythraeidae, the sperm droplet was originally covered by a sheath

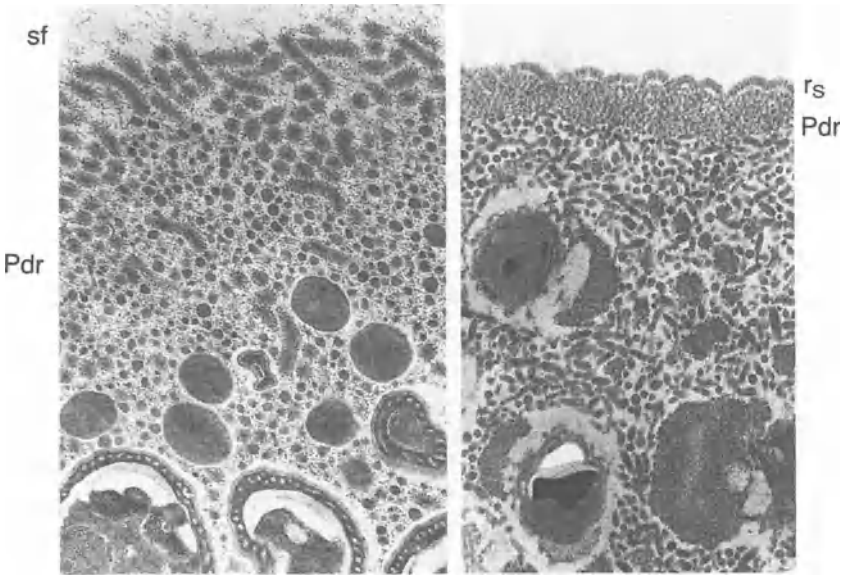
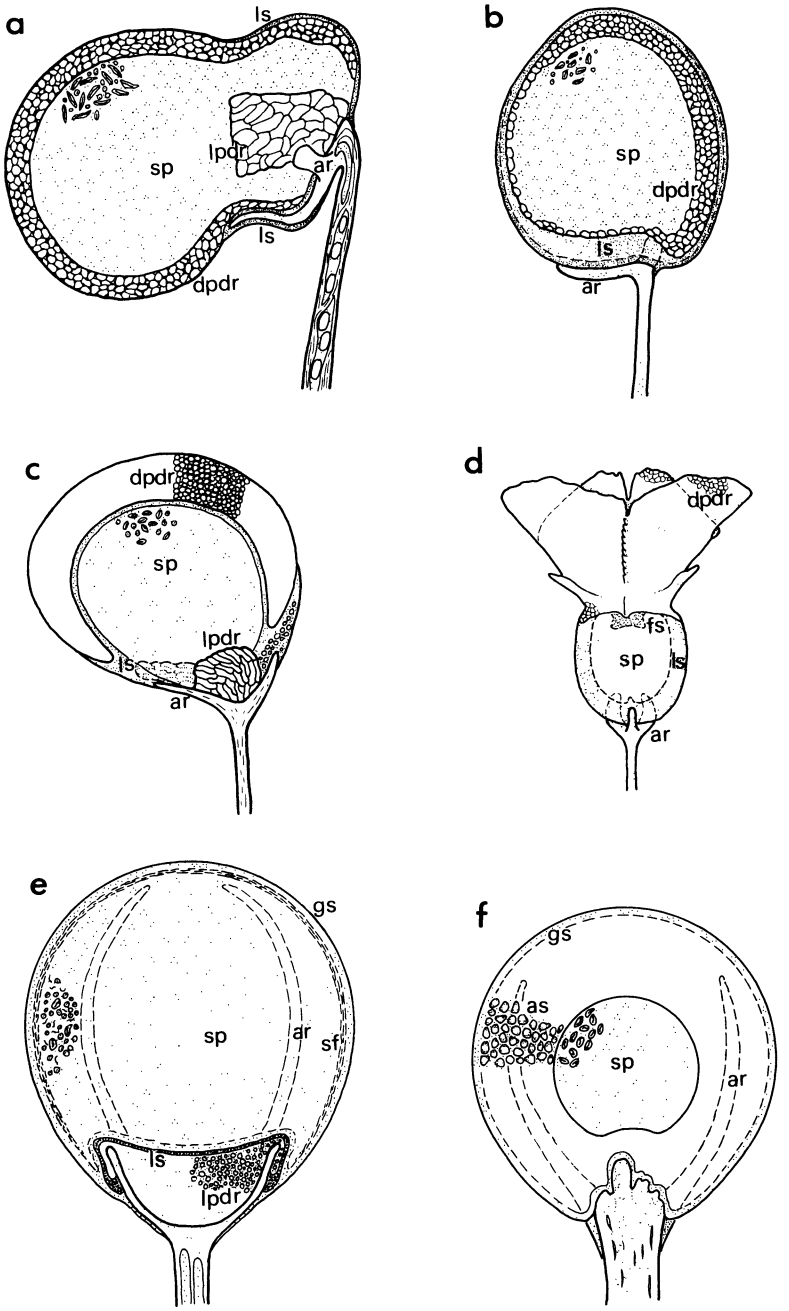


Fig. 8.4 Transmission electron micrographs of sheaths of sperm droplet of the water mites, *Hydrachna cruenta* (× 19 500) (left) and *Limnesia maculata* (× 24 000). pdr, proteinaceous secretion droplets; rs, radially striated secretion sheath; sf, secretion filaments.

made of relatively large electron-dense proteinaceous droplets (Fig. 8.5*a*,*b*). These droplets are secreted by the glandular part of the testis (secretion type III, Witte, 1975). The whole sperm droplet is glued to the stalk by means of a lipid-enriched secretion produced by the lateral accessory glands (Witte, 1975). This plesiomorphic state is found in the Erythraeinae (*Erythraeus phalangioides*, *E. regalis* and *Urrbrites* sp.) and, similarly, in the Leptinae (*Leptus trimaculatus* and *L.* cf *rupestris*). In the latter group, the lipid-enriched secretion expands over the whole droplet, and forms two slightly different layers corresponding to the division of the lateral accessory glands into two pairs in the Leptinae. In *Charletonia* and *Abrolophus* spp. the lipid-enriched secretion is translocated and forms a layer, which immediately covers the sperm (Fig. 8.5*c*,*d*). In *Charletonia*, however, the original sheath of electron-dense protein droplets is maintained as an outer layer of the sheath whereas in *Abrolophus*, these droplets form a membraneous crown, above the sperm, which contains a mucous secretion in its basal part (not shown in Fig. 8.5*d*).

The function of the sheath seems to differ in the various groups. In most terrestrial Parasitengonae, the sheath is quite sticky, for example, in *Abrolophus*, *Leptus* and *Camerothrombidium* and, as a result, the sperm


a
ls
sp
lpdr
ar
ls
dpdr
b
sp
dpdr
ls
ar
c
dpdr
sp
lpdr
ls
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dpdr
fs
sp
ls
ar
e
gs
sp
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ls
lpdr
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droplet can be captured more easily by the female. In the spermatophore of *Hydryphantes ruber*, which does not have a sheath, secretion filaments project out of the matrix secretion, and these enable the sperm droplet to stick to an animal even if the contact is only transitory. In the Hydrachnidia, the sheath probably protects the sperm mass against disintegration. It has often been assumed that in terrestrial arthropods the spermatophore sheath forms a protection against desiccation. However, in the Anystidae and Parasitengonae, no evidence has been found to support this assumption.

Water balance In the Anystidae and Parasitengonae, a mechanism has evolved to enable the spermatophore to take up water vapour from unsaturated air. By this means, a stable water balance can be maintained at low and fluctuating humidities. This mechanism has been investigated by Döring and Witte (1985), and Witte (unpublished observations) in humidity gradients of 33–100% r.h. When the humidity is altered, an equilibrium state of transpiration and water-vapour uptake of the sperm droplet is reached within a short time, and this causes a change in volume (Fig. 8.6). The sperm droplet maintains a stable water balance down to 33% r.h. in most species, for example, *Anystis rosae, Camerothrombidium, Trombidium, Allothrombium, Erythraeus phalangioides, Abrolophus rubipes* and *A. quisquiliarum*. At high humidities, some spermatophores become unstable. In *Allothrombium*, for example, the stalk softens at 76% r.h. within 12–15 min due to uptake of water. This occurs in *Anystis* at 100% r.h. In *Abrolophus rubipes* and *A. quisquiliarum*, the droplet absorbs water at 100% r.h. until the crown becomes unstable and coalesces with the droplet. Finally, the sperm droplet reaches the ground and is lost. Only the spermatophores of the hygric species, *Johnstoniana errans* and *J. ventripilosa*, desiccate between 76 and 93.5% r.h.

The mechanism of water uptake by the droplet is independent of an outer sheath because the effectiveness of the mechanism is quite similar in spermatophores provided with a peripheral sheath, for example, *Abrolophus, Camerothrombidium* (Fig. 8.6) and *Anystis*, and in spermato-

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Fig. 8.5 Spermatophores of terrestrial Parasitengonae illustrating sheath structures and location of secretory materials. Structures and secretions having the same labels are probably homologous. (*a*) *Erythraeus phalangioides*; (*b*) *Leptus* cf. *rupestris*; (*c*) *Charletonia cardinalis* (Witte and Wendt, unpublished); (*d*) *Abrolophus rubipes*; (*e*) *Calyptostoma velutinus*; (*f*) *Camerothrombidium rasum*. ar, apical rami; as, aggregated secretion droplets; dpdr, electron-dense proteinaceous droplets; fs, fibrillar secretion; gs, granulated secretion; lpdr, electron-light proteinaceous droplets; ls, lipid-enriched secretion; sf, secretion filaments; sp, sperm.

phores without a sheath, as in *Allothrombium* and *Trombidium* (Fig. 8.6). The mechanism is almost certainly passive and depends on the hygroscopic properties of the matrix secretion of the sperm. This can be concluded from the fact that old spermatophores, in which the sperm cells are dead, have an equilibrium curve in a humidity gradient quite similar to that of fresh spermatophores. This has been investigated in 7-day-old spermatophores of *Abrolophus rubipes* and *Camerothrombidium*

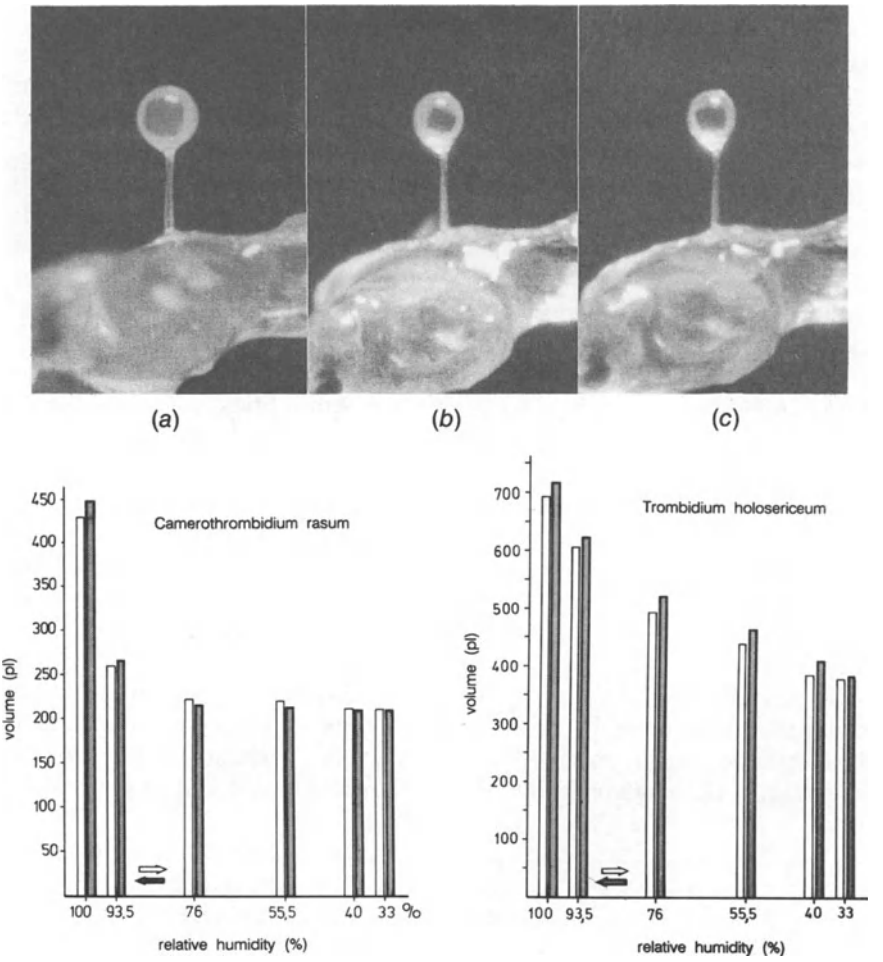


Fig. 8.6 Volumes (1 pl = 10^3 μm^3) of spermatophore droplets of *Camerothrombidium rasum* (below) and *Trombidium holosericeum* (below) in descending (unfilled columns) and ascending (filled columns) humidity gradients. Above are illustrations of droplets of *C. rasum* at (*a*) 100, (*b*) 76 and (c) 33% r.h.

rasum, and in 2-month-old spermatophores of *Johnstoniana ventripilosa*. Even the droplets of the signalling stalks of *Johnstoniana ventripilosa*, which consist mainly of the matrix secretion of the sperm, but are devoid of sperm cells, show similar humidity reactions. One may conjecture that the passive uptake of water vapour is effected by means of a mucopolysaccharide or a polysaccharide. The alternative – that an osmotic mechanism could be responsible for the water uptake – is impossible at relative humidities of 33 or 40% r.h., degrees of dryness at which spermatophores are deposited by several species.

In most terrestrial Parasitengonae the spermatophores are deposited in situations with a degree of dryness corresponding to their physiological aridity adaptation (Wendt, 1986; Wendt and Witte, 1985). In the examples shown in Fig. 8.7, *Erythraeus phalangioides* (and *Abrolophus rubipes*, not shown) prefers extremely low humidities. *Allothrombium fuligi nosum* at least avoids the highest humidities whereas *Charletonia* shows no particular preference in the five humidity sectors between 33 and 100% r.h. Only a few species deposit spermatophores on wet ground: *Johnstoniana errans*, *J. ventripilosa*, *Calyptosoma velutinus* and *Camerothrombidium rasum*. In all these species, the plesiomorphic behaviour of marking an area by means of signalling threads is lost. This seems to be due not only to a loss of stability and elasticity of the threads of terrestrial Parasitengonae when in contact with water but also, it can be assumed, due to a loss of their pheromonic properties.

Transformation of signalling mechanisms

Within the Parasitengonae, the most important signals by means of which the animals are guided to spermatophores are fields of threads, zigzag tracks, and chemical 'long-distance' signals, namely pheromones, which are to be found mainly in the Hydrachnidia.

Signalling threads The deposition of signalling threads is a plesiomorphic behavioural character within the Parasitengonae. During the deposition of the thread, which is elastic in the terrestrial species, the genital opening touches the ground at intervals, and in the process the thread is drawn out to the next point of attachment. The thread usually runs just above the ground (Fig. 8.9). It seems to consist of the same secretion as the stalk of the spermatophore (secretion type II, produced in the glandular part of the testis; Witte, 1975). Such threads are found in *Anystis baccarum* and *A. rosae*, the Erythraeidae, *Allothrombium*, *Trombidium* and most Hydrachnidia (Fig. 8.8). Within the terrestrial Parasitengonae, these threads are reduced only in the hygric Johnstonianidae, in *Calyptostoma* and in *Camerothrombidium*. The threads produced by non-

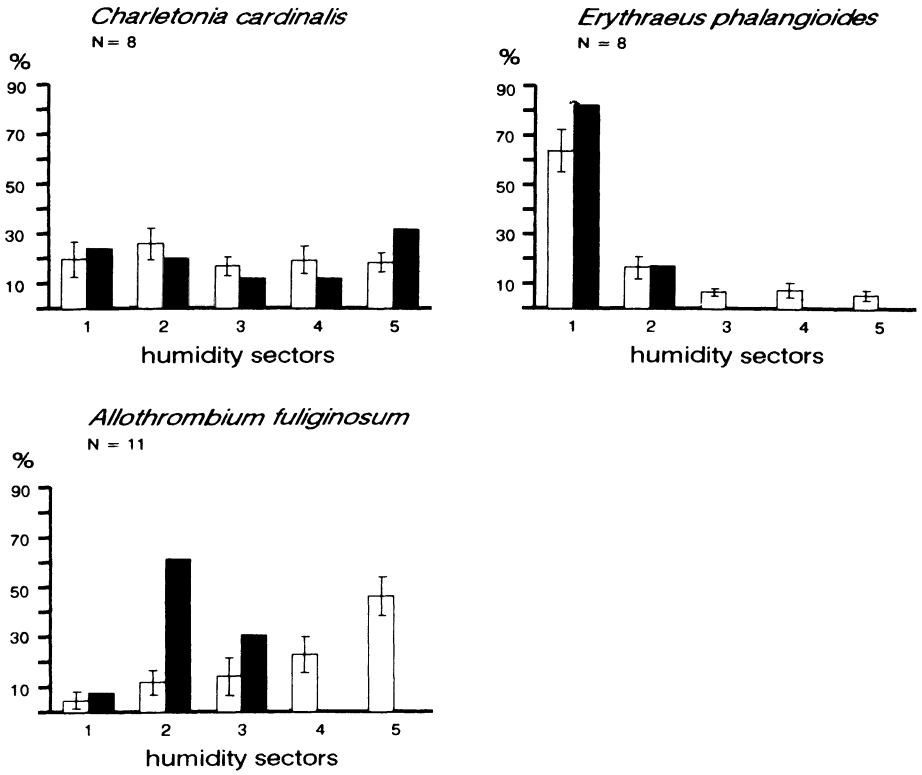


Fig. 8.7 General activity (unfilled columns) and spermatophore production (filled columns) of three species of terrestrial Parasitengonae in a humidity gradient, expressed as mean percentages (with s.d. for former) of totals for the five sectors obtained from a number of tests (N), each with 9–16 individuals. The results for *A. fuliginosum* are expressed as fields of spermatophores. Relative humidity sectors are: 1, 33%; 2, 55.5%; 3, 76%; 4, 93.5%; 5, 100% (after Wendt, unpublished).

hygric ancestors of these groups were probably unstable upon contact with water, as they still are in those recent terrestrial Parasitengonae investigated in this chapter. This seems to have been the reason for reduced usage of this signalling mechanism in the course of adaptation to hygric habitats.

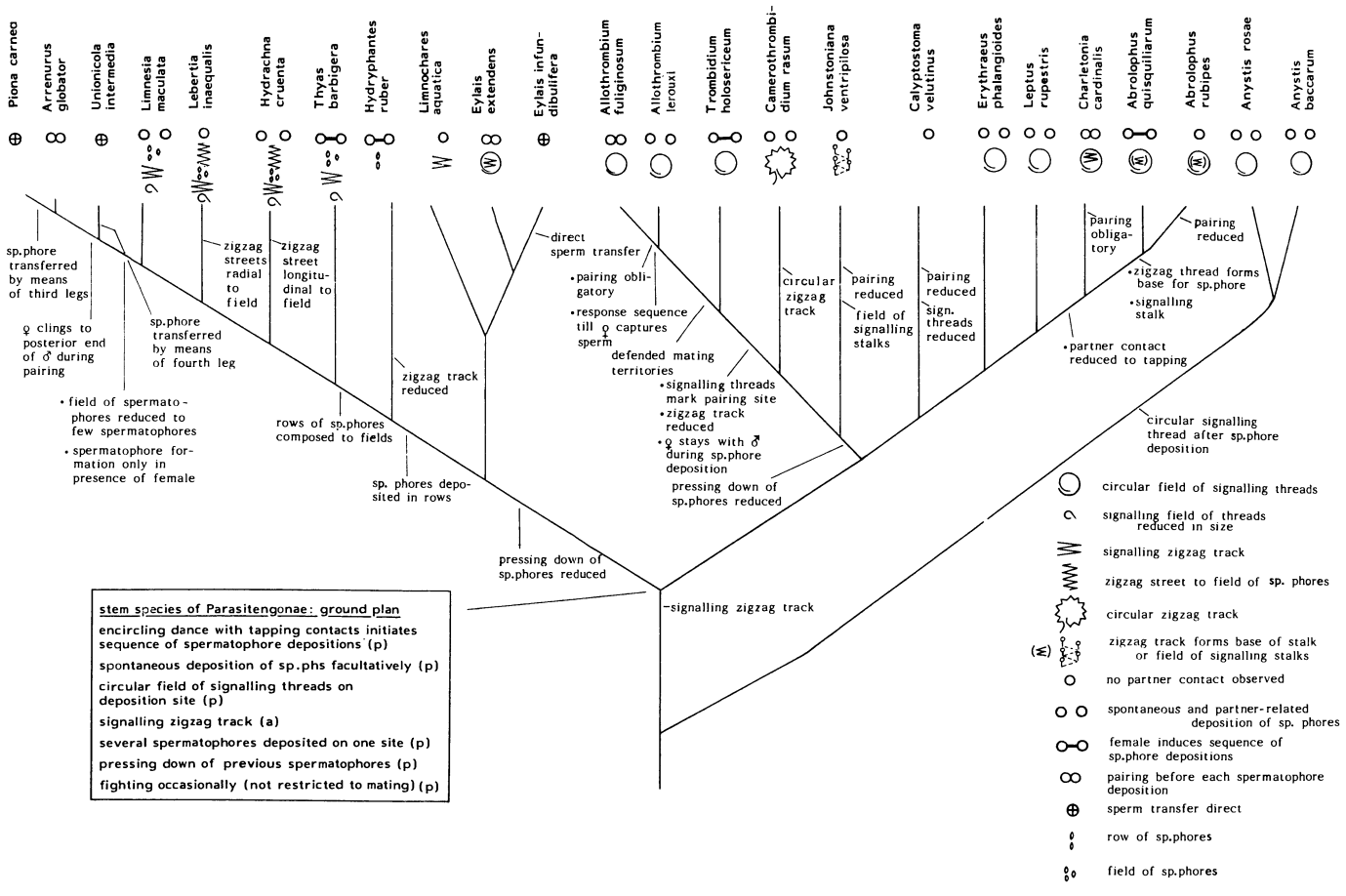
Within the Hydrachnidia, *Eylais extendens* is the only one with signalling fields fairly similar to the terrestrial Parasitengonae (see below). However, in those Hydrachnidia that deposit spermatophores in fields (Fig. 8.8), signalling threads have lost much of their importance as the area marked is not much greater than that occupied by the spermatophores (*Hydrachna, Lebertia, Limnesia*). In *Thyas barbigera*, however, the

threads (length *c.* 5–8 mm) immediately harden as they issue from the genital opening, and are placed on the surface of the ground in a random fashion even if no spermatophores are deposited subsequently. No signalling threads have been found in *Hydryphantes* and *Limnochares*.

There are at least three situations in which signalling threads are used by males when transferring sperm by an indirect means:

1. Pairing-dance signalling threads: these threads are produced during a facultative or obligatory encircling dance by the partners. This behaviour usually leads to the deposition of a spermatophore, which can be placed on the pairing site while the partners remain in contact (*Allothrombium fuliginosum*, *Trombidium holosericeum* and *Eylais extendens*). Alternatively, the male deposits the spermatophore a short distance from the pairing site without further contact with the female. In this event, the male marks this final site with threads laid down in a circular pattern before depositing a spermatophore (*Anystis*, *Erythraeus*, *Leptus*, *Charletonia* and occasionally, *Trombidium*).
2. Deposition-site signalling threads: the males of several species also use threads to mark the location of spermatophores in the absence of females. With this procedure, the male lays down threads in a circular pattern, usually over a small area, followed by the deposition of one or several spermatophores. Examples of mites with this behaviour include *Erythraeus*, *Leptus*, *Abrolophus rubipes* and *Anystis*, the latter only occasionally. It is usual to deposit a sequence of 4–12 spermatophores over a time interval of 20–60 min, either at one or several deposition sites. The area covered by the threads is usually small, for example with *Erythraeus*, it has a diameter of 1.5–2.5 cm, and with *Abrolophus*, 0.5–1.0 cm.

   Allothrombium fuliginosum and *Trombidium holosericeum*, in the absence of females, also deposit signalling threads in a circular area, *d* 3–4 cm, to form a primary signalling field. During the laying of these threads, which takes 1–2 h, the male may pause at intervals or may move into the surrounding area during the course of which further threads are deposited but rather sparsely to form a subsidiary signalling field. The process of creating primary and subsidiary signalling fields may be repeated at daily intervals, a new site being chosen each time. Spermatophore deposition does not take place in the primary field until a female enters the territory, and a pairing dance takes place (see 1. above). Both sexes only recognize the marked area on the day the threads are laid; the next day the male usually marks a new area. Several males of *Trombidium* may deposit threads on one site but in the case of *Allothrombium fuliginosum*, only


HYDRACHNIDIA
TROMBIDIOIDEA
C. OIDEA
ERYTHRAEOIDEA
ANYSTAE
Piona carnea
Arrenurus globator
Unionicola intermedia
Limnesia maculata
Lebertia inaequalis
Hydrachna cruenta
Thyas barbigera
Hydryphantes ruber
Limnochares aquatica
Eylais extendens
Eylais infundibulifera
Allothrombium fuliginosum
Allothrombium lerouxi
Trombidium holosericeum
Camerothrombidium rasum
Johnstoniana ventripilosa
Calyptostoma velutinus
Erythraeus phalangioides
Leptus rupestris
Charletonia cardinalis
Abrolophus quisquiliarum
Abrolophus rubipes
Anystis rosae
Anystis baccarum
sp.phore transferred by means of third legs
♀ clings to posterior end of ♂ during pairing
sp.phore transferred by means of fourth leg
• field of spermatophores reduced to few spermatophores
• spermatophore formation only in presence of female
zigzag streets radial to field
zigzag street longitudinal to field
zigzag track reduced
rows of sp.phores composed to fields
sp. phores deposited in rows
pressing down of sp.phores reduced
direct sperm transfer
• pairing obligatory
• response sequence till ♀ captures sperm
defended mating territories
• signalling threads mark pairing site
• zigzag track reduced
• ♀ stays with ♂ during sp.phore deposition
pressing down of sp.phores reduced
circular zigzag track
pairing reduced
field of signalling stalks
pairing reduced
sign. threads reduced
pairing obligatory
pairing reduced
• zigzag thread forms base for sp.phore
• signalling stalk
• partner contact reduced to tapping
circular signalling thread after sp.phore deposition
signalling zigzag track
stem species of Parasitengonae: ground plan
encircling dance with tapping contacts initiates sequence of spermatophore depositions (p)
spontaneous deposition of sp.phs facultatively (p)
circular field of signalling threads on deposition site (p)
signalling zigzag track (a)
several spermatophores deposited on one site (p)
pressing down of previous spermatophores (p)
fighting occasionally (not restricted to mating) (p)
circular field of signalling threads
signalling field of threads reduced in size
signalling zigzag track
zigzag street to field of sp. phores
circular zigzag track
zigzag track forms base of stalk or field of signalling stalks
no partner contact observed
spontaneous and partner-related deposition of sp. phores
female induces sequence of sp.phore depositions
pairing before each spermatophore deposition
sperm transfer direct
row of sp.phores
field of sp.phores

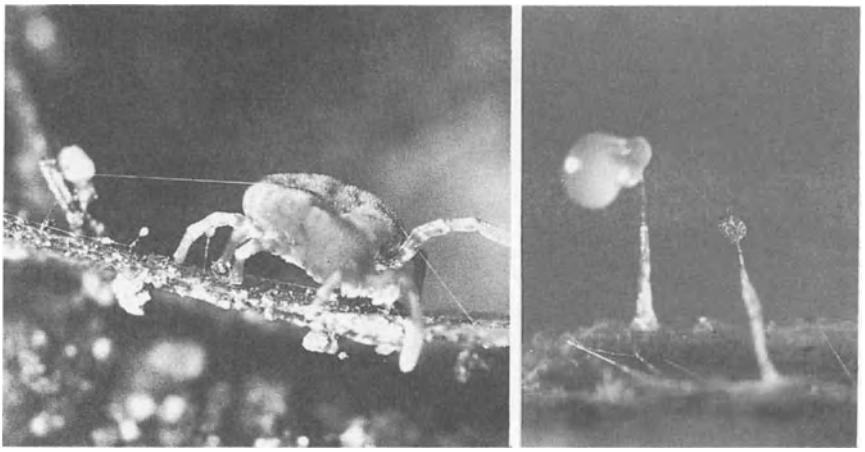


Fig. 8.9 Spermatophores and signalling threads of *Trombidium holosericeum* (left; × 13 and *Erythraeus phalangioides* (× 20). The *Trombidium* male, with a thread lying over it produced by another male, is in the process of depositing a spermatophore. Another thread runs towards a spermatophore. Signalling threads, resting on the substrate, surround a spermatophore of *Erythraeus*.

one male is involved. With this species, if another male enters the marked area, it is attacked by the occupant male, and fighting takes place until finally one of the combatants flees. A subsidiary signalling field is not defended.

3. Subsidiary signalling threads: the practice of marking with a sparse covering of threads, a relatively large area surrounding the primary site where the threads are much more concentrated is also used by the Anystidae, Erythraeidae (except *Charletonia*) and *Eylais extendens*. Spermatophores are only deposited in the primary site but it is likely that the subsidiary threads aid the females in their search for spermatophores. With members of the Anystidae, Erythraeidae and usually *Trombidium*, subsidiary threads are deployed after the deposition of each spermatophore; in the case of *Eylais extendens* and sometimes *Trombidium*, this takes place after the placement of several spermatophores by an individual. In either case, the male makes

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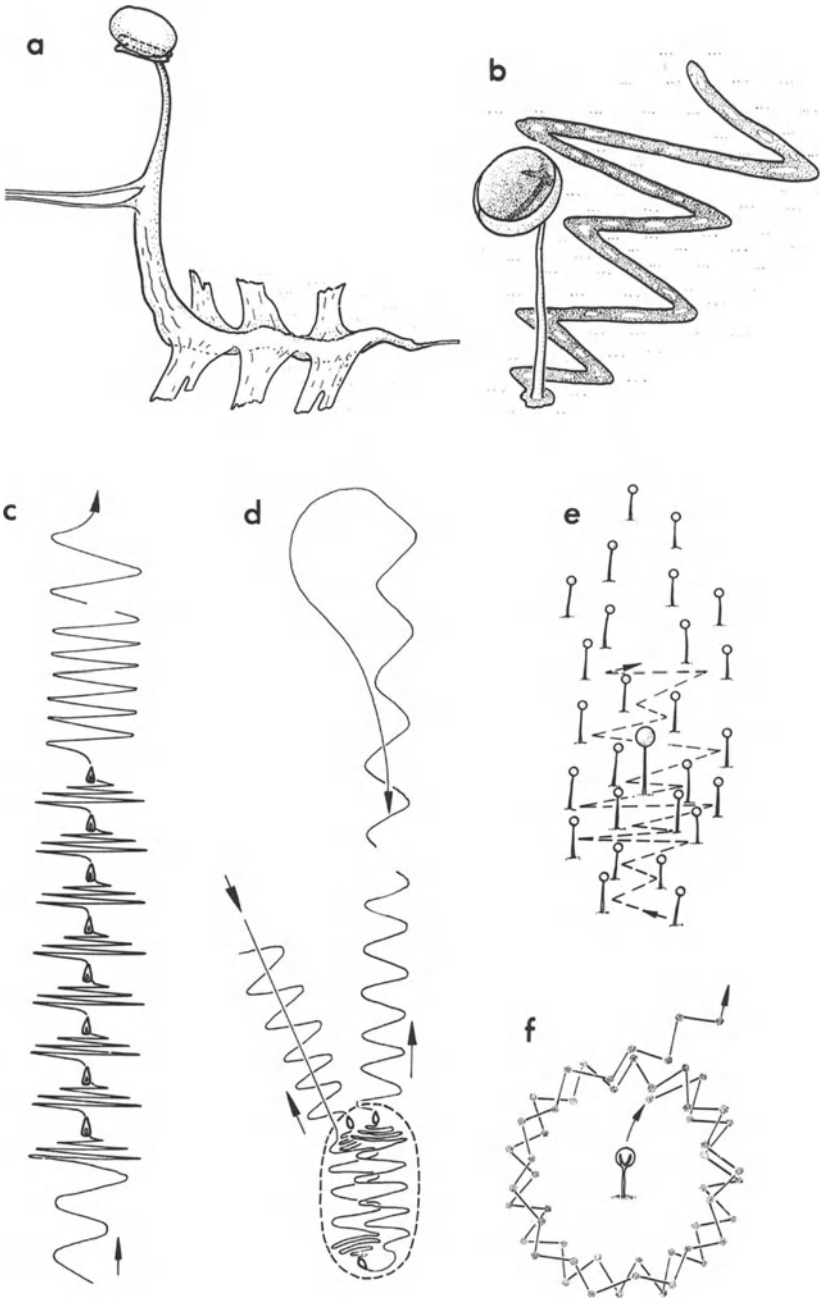
Fig. 8.8 Original state and phylogenetic transformation of signalling mechanisms and mating behaviour in the Parasitengonae with apo- (*a*) and plesio-morphic (*p*) characters of stem species. *A. globator* (after Böttger, 1962); *A. lerouxi* (after Moss, 1960); *T. barbigera* (in part after R. Rutkis, personal communication); *U. intermedia* (after Hevers, 1978); C. OIDEA, Calyptostomatoidea.


a
b
c
d
e
f

a hasty retreat after spermatophore deposition in the course of which he may travel a considerable distance before returning to the original deposition site. Alternatively he may establish a new primary site at another location. Whichever course is adopted, he lays down fresh threads on the site before spermatophore deposition.

Observations under natural conditions indicate that males of *Abrolophus rubipes, Anystis baccarum, A. rosae, T. holosericeum* and *A. fuliginosum* may return to a deposition or pairing site several times. *Erythraeus phalangioides*, however, which frequently deposits spermatophores in groups when in rearing cages, in nature, rarely returns to a deposition site, probably because it is unusual for a male of this species to cross a thread.

Zigzag tracks The use of zigzag markings leading to spermatophores and signalling their presence, probably evolved as a special form of guiding device in the stem lineage of the Parasitengonae. These types of markings have been termed 'zigzag tracks' (Witte, 1984). They have been retained in present-day Hydrachnidia as well as in some Trombidioidea and Erythraeoidea (Figs 8.8 and 8.10). In most Hydrachnidia and in the terrestrial genus, *Abrolophus*, the marking consists of a secreted thread. This is probably the original material for these guiding devices. It would appear that its initial function was to indicate the direction from which the female should approach the spermatophore in order to pick up the sperm. This was only possible from one side due to the presence of apical wings (a stem-species character; see Fig. 8.2). In addition to short zigzag tracks which, in the Hydrachnidia, are deposited in front of each spermatophore, in some genera of the group, for example, *Hydrachna* (Fig. 8.10*c*) and *Lebertia* (Fig. 8.10*d*), zigzag markings extend a long way beyond the area containing the spermatophores. The male of *H. cruenta* deposits spermatophores one after the other in a rapid sequence to form a row with a zigzag track in front of each spermatophore (Fig. 8.10*c*). There may be several rows in close proximity. With *L. inaequalis*, however, the spermatophores are placed in series of 1–3,

Fig. 8.10 Examples of zigzag signalling devices of the Parasitengonae leading to spermatophores. *Eylais extendens* (*a*) and *Limnochares aquatica* (*b*) form tracks consisting of secretory stripes. *Hydrachna cruenta* (*c*) and *Lebertia inaequalis* (*d*) lay down a delicate thread to form long zigzag streets leading to a spermatophore field with a short zigzag track in front of each spermatophore. *Johnstoniana errans* (*e*) follows a zigzag course marking each turning point by a slender signalling stalk with droplet at its tip. *Camerothrombidium rasum* (*f*) encircles the spermatophore following a zigzag path, and touches the ground at intervals with its genital aperture.

several of these series being concentrated in a small area (Fig. 8.10*d*). After each deposition, he moves away in a direction radially orientated to the deposition zone, following a zigzag course for a distance of 15–20 mm. He, then, immediately returns to the field of spermatophores and deposits a further series in the same manner as before (Fig. 8.10*d*). *Limnochares aquatica* (Fig. 8.10*b*) and *Eylais extendens* (Fig. 8.10*a*) secrete markings in the form of zigzag bands while in *Hydryphantes ruber*, this particular signalling device (not shown) is no longer present.

Within the terrestrial Parasitengonae, zigzag markings, when they do occur, are considerably altered, and most of these species do not behave in this way. This is probably connected with the reduction of the apical wings of the spermatophore, and hence the ability of the female to acquire sperm from either side of that structure. Thus the male of *Camerothrombidium rasum* (Microthrombidiinae), immediately after depositing the spermatophore, moves in a zigzag fashion and encircles the spermatophore one or twice (Fig. 8.10*f*). During this perambulation, he touches the ground at intervals with his genital aperture. A hyaline secretion can be seen in the genital aperture but a thread is not deposited. The male of *Microthrombidium* sp. walks around the spermatophore 4–5 times in a similar zigzag conformation (Wendt, personal communication). Thus, it may be that the circular track made up of zigzag elements is a synapomorphic character of the Microthrombidiinae.

The males of *Johnstoniana ventripilosa* and *J. errans* also move in a zigzag fashion but the overall direction is in a straight line (Fig. 8.10*e*). Each turning point is marked by a slender signalling stalk with a droplet at its tip (Fig. 8.10*e*). The droplet consists of the matrix secretion of the sperm in which fibres of the stalk secretion are to be found. The droplet is usually devoid of sperm cells. In *Abrolophus rubipes* and *A. quisquiliarum*, there is again, a zigzag track but with a quite different function, and it probably does not act as signalling device. Here, the delicate threads, laid in a zigzag pattern, form a base on which the stalk of the spermatophore rests. *Charletonia cardinalis*, however, produces a small but distinct zigzag track consisting of a delicate secretion band (Witte and Wendt, unpublished).

Chemical signals operating at a distance Chemical signals or pheromones, which emanate from spermatophores, appear to occur in terrestrial and aquatic Parasitengonae. Within the terrestrial members of the group, such signals can be conjectured when, for example, males of *Abrolophus rubipes* return to a deposition site in order to depress a previously deposited spermatophore. If this spermatophore is picked up with a needle before the male has come into contact with it, he is directly

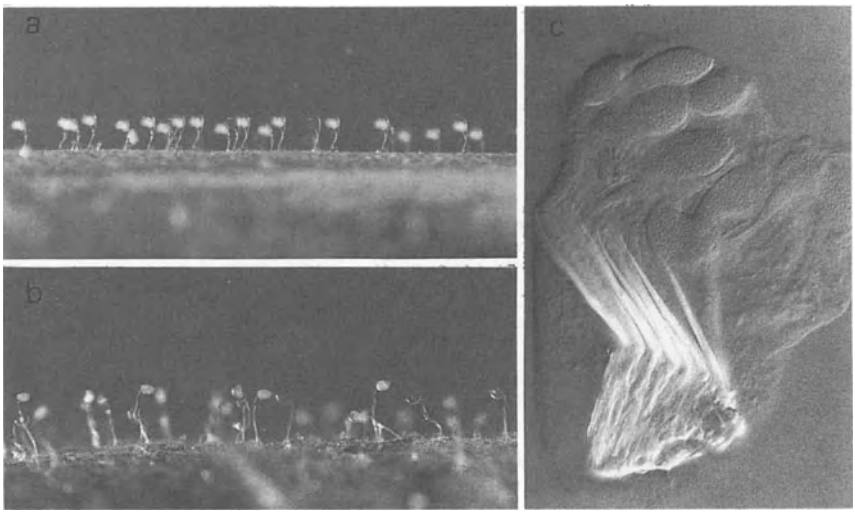


Fig. 8.11 Fields of spermatophores of the water mites, *Hydrachna cruenta* (*a*), *Limnesia maculata* (*b*), and an aggregated 'spermatophore' of *Piona carnea* (*c*), courtesy of J. Leimann.

attracted to it, and will quickly follow the spermatophore if it is moved, presumably in order to press it to the ground.

It would appear that in the Hydrachnidia, chemical 'long-distance' signals have become an important mode of signalling associated with the evolution of fields of spermatophores. Originally, the water mites as well as the terrestrial Parasitengonae deposited spermatophores in small groups. This plesiomorphic condition is still to be found in *Limnochares* and *Eylais extendens*. *Hydryphantes*, however, shows a derived deposition behaviour in that it deposits spermatophores in single rows of about 4–12 spermatophores – two or three rows may occur together but only rarely. In the later-derived Hydrachnidia (Fig. 8.8), beginning with *Thyas*, several rows of spermatophores are arranged close together in fields, often deposited by several males, and may comprise hundreds of spermatophores (Fig. 8.11). A number of the swimming Euhydrachnidia perceive these fields at a distance. Swimming individuals of *Hydrachna cruenta*, for example, change direction within about 12–20 mm of the field, and move directly towards it irrespective of whether the field is positioned horizontally or vertically. Meyer (1985) observed similar behaviour in *Hydrodroma*.

The selective advantage arising from a large number of spermatophores grouped together in close proximity is likely to result from the

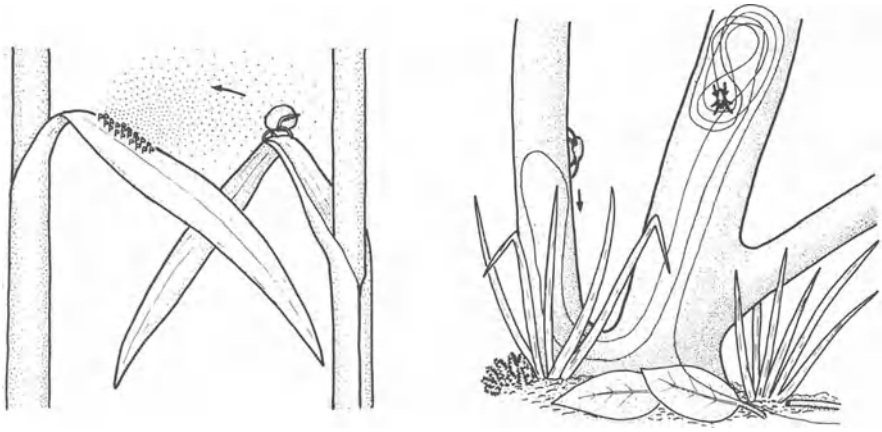


Fig. 8.12 A schematic comparison of spermatophore locatory mechanisms in swimming water mites and their terrestrial relatives. On the left are submerged plants on one of which there is a field with a large number of spermatophores producing a pheromone which attracts female *Hydrachna cruenta* located on a nearby plant. On right, the terrestrial *Allothrombium fuliginosum* female is guided to pairing site by signalling theads (not to scale).

production of a distinct pheromone gradient; with the plesiomorphic scattering of spermatophores, one would expect a diffuse distribution of the attractant. Compared to other locatory methods such as threads applied to the substrate, the emission of a pheromone from a concentration of spermatophores and, in particular, the formation of a pheromone plume, may increase the range over which the chemical operates. This type of signalling device is particularly advantageous for swimming water mites as they are capable of following a pheromone gradient in a three-dimensional space to a spermatophore field located, for example, on a submerged plant (Fig. 8.12). A crawling mite, in an analogous situation would, of necessity, have to take a circuitous route to reach the spermatophores (Fig. 8.12), and this requires a different signalling mechanism. It is worth noting that in the Arrenuridae, Unionicolidae and Pionidae, in which the presence of a female is obligatory to induce spermatophore formation, only one or a few spermatophores are deposited.

Spermatophore deposition strategies and partner behaviour

Sperm transfer in the Parasitengonae and Anystidae is ensured by different strategies. The process can be *partner-related*, that is, where spermatophore deposition is initiated by stimulation of the male by the

female, usually by bodily contact. Or the male may distribute spermatophores either singly or in discrete groups throughout its habitat without the need for contact with the female. This, is referred to as habitat-related deposition. Here deposition may be spontaneous but often sites are chosen with preferred abiotic conditions. Alternatively, deposition may be induced by the presence of previously deposited spermatophores or signals, usually resulting in the deposition of discrete groups of spermatophores. Since partner-related as well as habitat-related deposition of spermatophores occur in single species of the Parasitengonae (for example, *Erythraeus*, *Leptus*, *Abrolophus quisquiliarum*, *Camerothrombidium* and *Limnesia*) and in the Anystidae (*Anystis baccarum* and *A. rosae*), they are surely plesiomorphic within the Parasitengonae and a behavioural trait of the stem species (Fig. 8.8). In those species utilizing both deposition modes, the presence of a female usually increases the rate of spermatophore deposition considerably, as can be seen in the examples of *Erythraeus phalangioides*, *Camerothrombidium rasum*, and *Anystis baccarum* in Fig. 8.13, which shows the rate of deposition in the presence and absence of females.

At present it is largely unknown whether a preference for a particular deposition strategy is influenced by seasonal abiotic habitat conditions. The only example is that described by Rutkis (1987), who compared spermatophore deposition by *Limnesia maculata* using single individuals, five males and the latter number together with five females, at temperatures of 4–20 °C over five days (Fig. 8.14). She found that at 8 °C, the highest number were deposited by males in the presence of females; the number for grouped males was less, and none was deposited by single males. However, at 16 ° and 20 °C, single males deposited more than grouped males, and males and females had the least spermatophores.

The original pairing behaviour in the Parasitengonae as well as in the Anystidae is an encircling dance with the partners making tapping contacts (Fig. 8.15). During the dance, in some species of *Anystis* (Fig. 8.15) and in *Trombidium holosericeum*, the male is the more mobile partner. It runs in circles and loops around the female, which is more or less stationary. The female of *Allothrombium fuliginosum* walks slowly in loops or circles keeping contact with the male which likewise traverses looped or circular orbits within the ambit of the female (Fig. 8.15) (see also Robaux, 1974). In *Eylais extendens*, *Erythraeus phalangioides*, *Leptus* cf. *rupestris* and *Camerothrombidium rasum*, both partners move at the same pace while encircling each other. In some species the encircling dance is reduced to simple tapping contacts. Examples of the latter behaviour include *Anystis baccarum*, *Abrolophus quisquiliarum*, *Charletonia cardinalis*, *Hydryphantes ruber*, *Hydrachna cruenta* and *Limnesia maculata*. In some species a form of contact occasionally observed, mainly by the male,

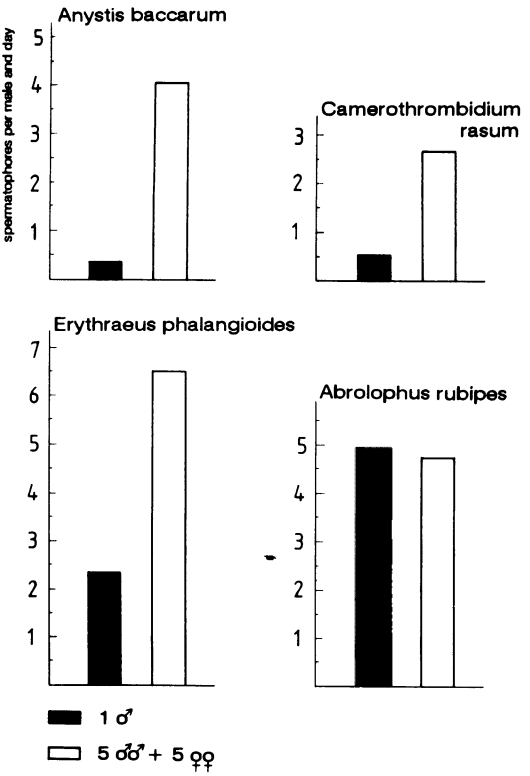


Fig. 8.13 A comparison of number of spermatophores deposited in one day for 4 species of Parasitengonae, produced by single males (filled columns) and 5 males in presence of 5 females (unfilled columns).

consists of a gentle stroking of the dorsal surface of the partner using the inner surface of the anterior part of leg I.

Partner contacts seem to be absent in several Parasitengonae, for example *Abrolophus rubipes* (Fig. 8.13), *Johnstoniana errans* and *J. ventripilosa*, in which there is no difference in the rates of spermatophore deposition in the presence or absence of females. Also with *Calyptostoma velutinus* and *Limnochares aquatica*, it has been found that spermatophores were deposited in the absence of females and no partner behaviour has been observed (Theis and Schuster, 1974; J. Pahnke, 1974). I have had similar results with *Lebertia inaequalis*.

On the other hand, spermatophore deposition only occurs in the presence of a female in a number of species. In some species the deposition of a whole sequence of spermatophores on one site is initiated by a single partner contact or a signal from the female. This applies to the

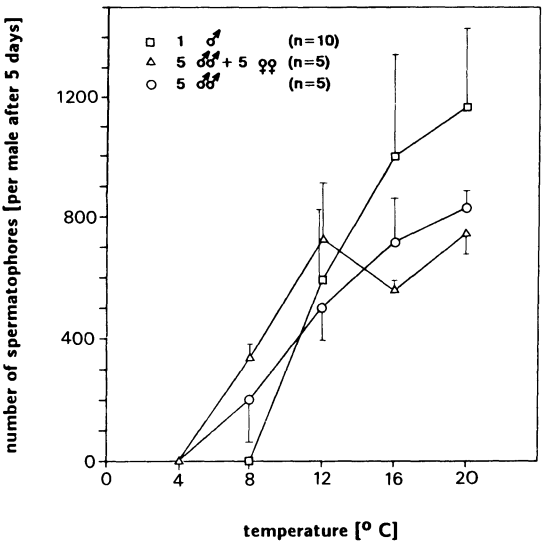


Fig. 8.14 The effect of temperature on mean spermatophore deposition per male (n tests) of *Limnesia maculata* over 5 days by single individuals (□), groups of 5 males (○) and 5 males in presence of 5 females (△). (After Rutkis, 1987.)

Anystidae where partner contacts are the most frequent mode to induce spermatophore deposition. In *Anystis rosae*, usually the first or one of the first few tapping contacts leads to a pairing dance, and the deposition of a spermatophore. The same applies to *Anystis baccarum* but here no pairing dance occurs. A brief tapping of the female by a male is usually followed immediately by the deposition of a circular field of signalling threads and a spermatophore. In both species, further spermatophores are deposited preferably after renewed contact of the partners; however, virgin females were seen to acquire only one sperm droplet. Quite often – in *A. rosae* more often than in *A. baccarum* – spermatophores are deposited after contact with a previously deposited spermatophore, the latter being usually knocked to the ground. In the absence of females, however, spermatophore deposition is uncommon. Thus, in 50 tests with single males of *A. baccarum*, only seven produced spermatophores over a period of 4 h (cf. Fig. 8.13), and only 4 out of 50 males of *Anystis rosae* did so in the same time period. In *Hydryphantes ruber* from Europe tapping contacts by the partners is usually necessary to induce the deposition of a row of spermatophores. Böttger (1966) never observed spermatophore deposition of single males maintained in isolation and I have observed it on only one occasion. However, in American *H. ruber*, Mitchell (1958) frequently observed spontaneous deposition. Tapping

contacts by the partners is also an obligatory behavioural trait prior to the deposition of a sequence of spermatophores in *Thyas barbigera* (Rutkis, personal communication).

A variant of partner-induced deposition on an obligate basis as already described is illustrated by *Trombidium holosericeum* and *Abrolophus quisquiliarum*. With these two species, contact of the male with a

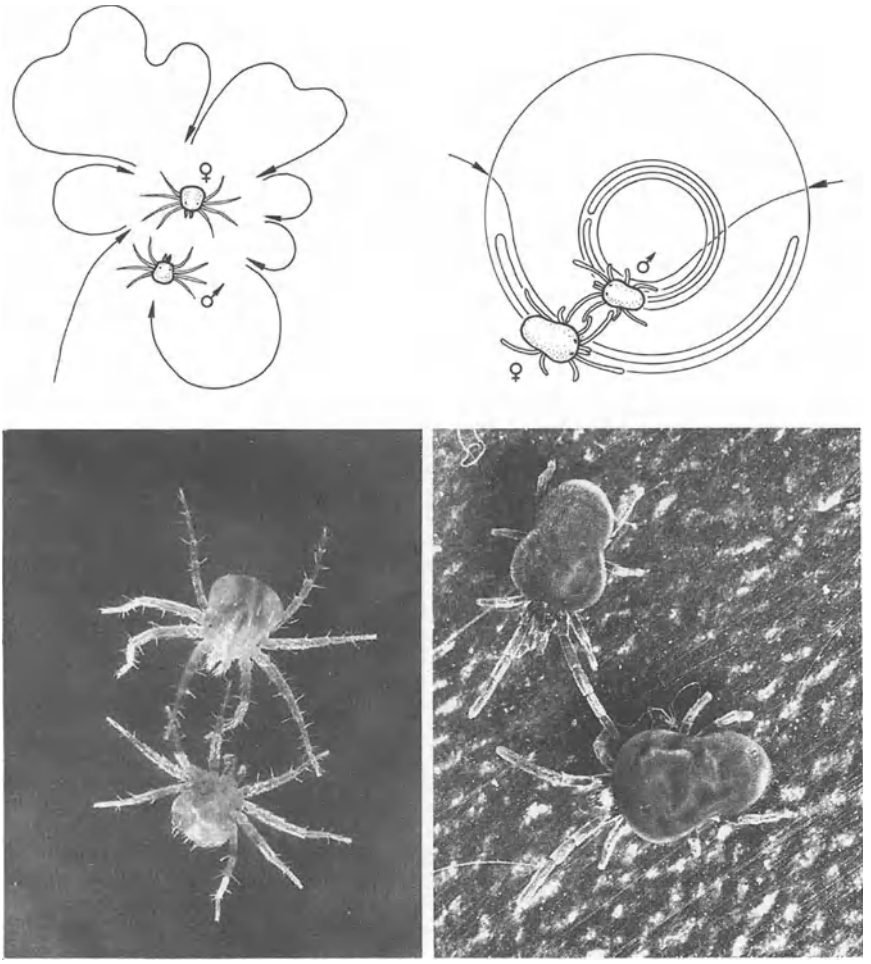


Fig. 8.15 Photographic and diagrammatic illustrations of pairing dance of *Anystis* sp. (left) and *Allothrombium fuliginosum*. For *Anystis*, the lines indicate the male's movements around his rather immobile partner, and arrows indicate the points at which they make contact. For *Allothrombium*, the lines represent the route traversed by the partners, each of which makes tapping contacts during the whole dance.

female initiates not only the deposition of several spermatophores by the male, but can also result in deposition on the same site by another male, which has not had previous contact with a female (spermatophore-induced deposition). Single reared males of *A. quisquiliarum*, cultured in isolation, have never been observed to deposit spermatophores, and of 12 males of *T. holosericeum*, cultured individually, only one produced three spermatophores, all on one day, over a period of 10 days. In some Unionicolidae, the mere presence of a female can induce the deposition of spermatophores, probably as the result of a pheromone, whereas individually cultured males do not deposit spermatophores (Hevers, 1978).

Obligatory partner contact previous to the deposition of each spermatophore occurs in the terrestrial Parasitengonae; *Charletonia* and *Allothrombium* are examples. In *Charletonia cardinalis*, however, Witte and Wendt (unpublished) observed in one instance that contact between two males resulted in the deposition of a spermatophore. In *Callidosoma metzi*, which is closely related to *Charletonia*, the presence of a female also seems to be obligatory (Sharma *et al.*, 1983). Within the Trombidiidae, real mating territories, which in *Allothrombium fuliginosum* and *A. lerouxi* (Moss, 1960) are furiously defended against male invaders, would appear to have evolved in the stem lineage of the Allothrombiinae. Whereas *A. lerouxi* deposits spermatophores in the absence of females, in *A. fuliginosum* there is an obligate pairing dance of the partners prior to the deposition of each spermatophore. In a sequence of responses the partners stay in tapping contact with each other until the spermatophore is finally deposited, and is immediately acquired by the female.

Within the Hydrachnidia, in which the original encircling dance of the partners only occurs in some Eylaidae, for example, *Eylais extendens* and several other species of *Eylais* (Lanciani, 1972), intimate pairing behaviour has evolved in some groups convergently. This is the case in several eylaid mites where sperm is transferred directly from genital opening to genital opening (Böttger, 1962; Lanciani, 1972). Within the Hygrobatoidea, it is likely that the presence of females to induce the formation of spermatophores became obligatory in the common stem lineage of the Pionidae, Unionicolidae and Arrenuridae *sensu lato*. Within the Hygrobatoidea, the Arrenuroidea is almost certainly the sister group of the Pionidae and, therefore, should be given family status (Witte and Olomski, unpublished). It is probable that at the common base of these three families, simple tapping contacts of partners or the mere presence of a female induced the deposition of spermatophores (Figs 8.1 and 8.8). Such behaviour modes still exist in most Unionicolidae (Hevers, 1978).

In some Unionicolidae, however, pairing behaviour has become more intimate. For example, in *Unionicola tricuspis*, each time the male deposits two spermatophores side by side. Then, he lowers his body to the ground, and holds the spermatophores by legs IV in a position to enable the female to acquire a sperm droplet easily. The male of *Unionicola intermedia*, however, transfers the spermatophore directly by means of a fourth leg on which the spermatophore has been already positioned. Exceptionally, a spermatophore can also be produced in the absence of a female (Hevers, 1978).

In the common stem lineage of the Arrenuridae *sensu lato*, and the Pionidae, a pairing behaviour with intimate bodily contact evolved. This can be characterized with some certainty by the following synapomorphic characters (Witte and Olomski, unpublished): (1) in the course of pairing the female clings to the posterior end of the male; (2) the male holds the female in position by means of his fourth pair of legs, at least at the beginning of the pairing ceremony. One may speculate that even the modification of the fourth article of leg IV, by means of which the male clings to the female, is a synapomorphy. This, however, remains doubtful since this character differs considerably in various genera. The fourth article in the Arrenuridae *sensu lato* possesses a distal process in *Arrenurus* (Lundblad, 1929b), whereas it is distally only somewhat enlarged and provided with modified setae in *Aturus* (Viets, 1936). Within the Pionidae, the fourth article has a deep indentation in the Pioninae (Viets, 1936; Böttger, 1962) whereas in *Typhis* (Typhisinae), it is plate-shaped, and in *Pionaceropsis*, it is provided with a distal process. In other genera of the Typhisinae, however, the fourth article is unspecialized (Viets, 1936). In *Brachypoda*, the phylogenetic position of which is controversial, there is, again, a distal process (Viets, 1936). In consequence, the only additional synapomorphic character of both families referred to here is the reduction of the sperm pouch of the spermatophores.

In addition to these common characters, different modifications of pairing behaviour evolved in both families. In all Pioninae, the male transfers the spermatophore directly to the female by means of the third pair of legs (Mitchell, 1957; Böttger, 1962; Schwoerbel, 1962; Leimann, 1989). Since *Brachypoda* transfers the spermatophore in a quite similar way (Halik, 1955), one may be quite sure that it belongs to the Pionidae, but that placing it near *Aturus* in the phylogenetic system is incorrect. Whereas in most Pionidae, the spermatophore is produced in the presence of a female (Mitchell, 1957; Viets, 1914), *Piona nodata* and *P. carnea* form the spermatophore in the absence of a female, and store it in the genital atrium until they meet a partner (Viets, 1914; Böttger, 1962; Leimann, 1989).

In most Arrenuridae *sensu lato*, the spermatophores are still deposited on the substrate. During pairing, the male of *Arrenurus globator* initially holds the female towards the posterior end of his dorsal surface by means of his fourth pair of legs but, after a short time, the female is fastened to him by an adhesive substance. In this position, the male helps the female to acquire the sperm in that he guides the genital opening of the female directly to the spermatophore (Lundblad, 1928b; Böttger, 1962). In *Aturus*, the female clings to the male in a quite similar position, and is held there by means of his fourth pair of legs (Lundblad, 1929a). Because of this character and indeed, for morphological reasons, *Aturus* is placed within the Arrenuridae *sensu lato*, and not in the Pionidae (Witte and Olomski, unpublished). Likewise in *Midea*, direct sperm transfer has evolved convergently. Here, the sperm mass is transferred from one genital aperture to the other. The male, however, holds the female not by legs IV, but by the modified third pair of legs (Lundblad, 1929a).

Derived mechanisms of direct transfer of spermatophores often embody the integration of phylogenetically old structures and behavioural modes, two examples of which are referred to here. The 'spermatophore' of the Pionidae (Fig. 8.11*c*) which has been described by Viets (1914), Böttger (1962) and Leimann (1989), is in reality, homologous with a whole row of spermatophores, the most common mode of deposition among the water mites (Fig. 8.11*a*). Leimann (1989) found that in *Piona carnea*, during the formation of such an aggregate, several single spermatophores, which lack a sperm pouch, are formed in rapid succession in the ejaculatory complex. By means of the tarsi of the third pair of legs they are retained in the genital atrium where they are finally provided with a common sheath consisting of a mucous secretion. The second example concerns the behaviour of male Pionidae and several Eylaidae to seek and grasp a female before pairing. Apparently this was originally an element of predatory behaviour. Males grasp swimming or crawling animals rather unselectively, and it is only after bodily contact that they appear to distinguish between a prey and a member of their own species. Moreover, if a male of *Eylais infundibulifera* or *Piona nodata* accidently loses contact with its partner during pairing, he swims in small circles seeking the female (Böttger, 1962). This again is a characteristic behavioural response when a prey is lost (Böttger, 1962).

STEM-SPECIES CHARACTERS OF THE PROSTIGMATA

It is beyond the scope of this chapter to elaborate on the phylogenetic transformations of indirect sperm-transfer mechanisms in the Prostigmata as a whole. However, a brief reconstruction of the original repro-

ductive mechanisms of the Prostigmata is useful for two reasons: First, to understand more clearly the origin of the reproduction mechanisms of the Anystidae and Parasitengonae; and second, to have a base for future investigations on the adaptive transformations of indirect sperm transfer in the whole group of the Prostigmata.

At present there are two main difficulties to reconstructing the reproductive characters of the stem species in detail. In the first place – apart from the Parasitengonae – some mechanisms are poorly investigated, for example, physiological properties of the spermatophores, signalling mechanisms and facultative partner contacts; and second, the phylogenetic system for the Prostigmata is still uncertain. As a phylogenetic basis for this reconstruction, I refer to the cladogram of the Prostigmata proposed by Krantz (1978), which is based mainly on Lindquist (1976). Following this dendrogram, I regard as apomorphic those characters of the stem species, which the Eleutherengonina – in particular the Anystae, Parasitengonae and Eriophyoidea – share only with species of their probable sister group the Labidostommatina + Eupodina (Bdelloidea, Halacaroidea, Tydeoidea and Eupodoidea). Those characters which the Prostigmata share with their endeostigmatic outgroups – in particular the Nanorchestidae (Pachygnathina) and Saxidromidae (Adamystina) – I regard as plesiomorphic characters of the stem species. In what follows the only literature cited refers to the Endeostigmata and Prostigmata, but excluding the Parasitengonae and Anystidae, which have already been discussed.

Spermatophores

It would appear that the stem species of the Prostigmata produced a spermatophore with a stalked droplet, and provided with a pair of wing-shaped apical structures (Fig. 8.16). Such spermatophores are to be found in the Anystidae (Fig. 8.16*c*) as well as in several Labidostommidae (Fig. 8.16*a*) (Schuster and Schuster, 1969; Vistorin, 1978), Halacaridae (Fig. 8.16*b*) (Kirchner, 1967, 1969; A. Pahnke, 1974), and they are transformed only slightly in the early-derived Bdellidae (Cytinae, Spinibdellinae) according to Alberti (1974, 1975), and in the Eriophyoidea (Oldfield *et al.*, 1970; Sternlicht and Griffiths, 1974).

It is likely that spermatophores were deposited originally in small groups, and 'old' spermatophores were pressed to the ground before new ones were added. This behaviour is maintained within several taxa including Tydeidae (Schuster and Schuster, 1970), Bdellidae (Alberti, 1974), Anystidae (Schuster and Schuster, 1966) and Parasitengonae. Among the Endeostigmata there is a quite similar arrangement in the Nanorchestidae (Schuster and Schuster, 1977).

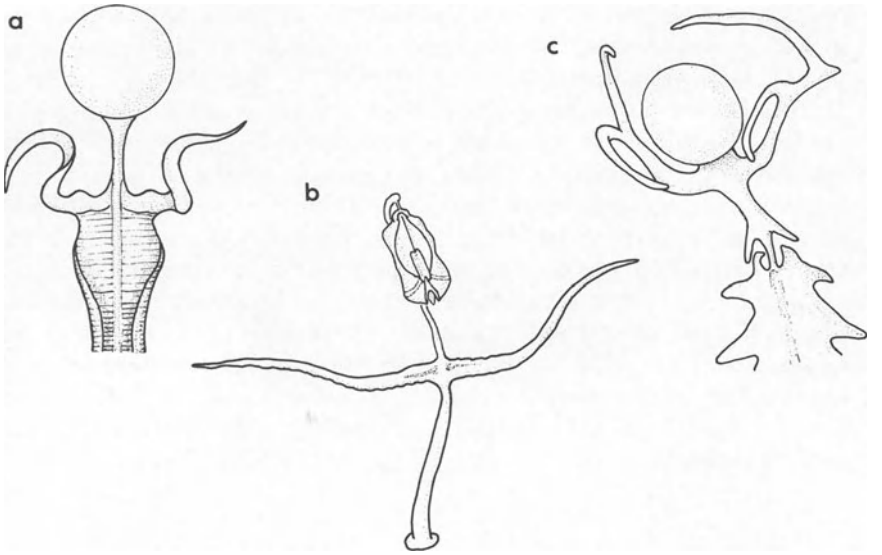


Fig. 8.16 Spermatophores of Prostigmata showing wing-shaped apical structures. (*a*) *Nicoletiella jaquemarti* (Labidostommidae) (redrawn after Vistorin, 1978); (*b*) *Halacarellus subterraneus* (Halacaridae) (redrawn after A. Pahnke, 1974); (*c*) *Anystis rosae* (Anystidae).

Signalling mechanisms

Signalling threads, similar to those produced by the Anystidae and Parasitengonae, probably already existed in the stem species of the Prostigmata. Although such signals have not been described for the Labidostommatina and Eupodina, their behaviour suggests that they occur in these taxa. Thus, a circular course, similar to that followed by the Anystidae and Parasitengonae during the deposition of signalling threads, has been observed in *Nicoletiella cornuta* (Labidostommidae) by Schuster and Schuster (1969) and Vistorin (1978), and in the Tydeidae (Schuster and Schuster, 1970). In the Rhagidiidae (Eupodoidea), unstalked spermatophores are deposited on threads released from the genital opening (Ehrnsberger, 1977). These threads are reminiscent of signalling threads but now have a different function or at least an additional one.

Partner behaviour

In respect to partner behaviour, it has been reported that, for most groups apart from the Eleutherengonina, the presence of a female is not

necessary in order to induce the deposition of spermatophores by the males. However, this does not necessarily mean that the species completely lack a pairing behaviour. It may be that this behaviour is facultative, similar to that of the Anystidae and several Parasitengonae, and that such behaviour had already existed in the stem species of the Prostigmata. For example, among the endeostigmatic outgroups there exists a close-pairing behaviour in the Saxidromidae (Coineau, 1976), and in the Nanorchestidae, the presence of females at least increases the rate of spermatophore deposition (Schuster and Schuster, 1977). Again *Nicoletiella denticulata* (Labidostommidae) only produces spermatophores if a female is present (Vistorin, 1978). Kirchner (1969) described similar behaviour in *Halacarus basteri* (Halacaridae) but A. Pahnke (1974) observed spermatophore deposition in this species in the absence of females. In several other Labidostommidae and Halacaridae the presence of a female is not necessary (Vistorin, 1978; A. Pahnke, 1974).

ENVIRONMENTAL ADAPTATION

Spermatophores

The modification of spermatophores in terrestrial arthropods in relation to environmental conditions is poorly described in the literature, and there is little known about their adaptation to various types of habitats. In my view the most important adaptations concern, first, the mechanisms to ensure that they can function in xeric, hygric or secondarily colonized aquatic environments (mainly water balance, osmotic and ionic balance), and second, mechanisms to enable sperm cells to maintain viability for a sufficient length of time.

Water and ionic relationships The ability of a spermatophore to maintain a stable water balance under a wide range of atmospheric humidities by taking up water vapour passively from the air, is an adaptation, which transforms the spermatophore into what might be termed an aerial structure. This mechanism differs fundamentally from the adaptations of indirect sperm transfer to xeric habitats already described. In these, the loss of water from the spermatophores is either reduced, for example, by the presence of sheaths, or the spermatophore is located more rapidly as a result of mechanisms that increase the chances of females finding a spermatophore while it is still viable, for example, signals and partner contacts.

The mechanism of passive water uptake is not restricted to the spermatophores of prostigmatic mites. An analogous mechanism has also evolved in the Collembola (Döring and Witte, 1985; Döring, 1986).

The spermatophores of the epedaphic *Orchesella cincta* maintain a stable water balance down to 76% r.h., whereas the spermatophores of the hemi-edaphic *Isotoma viridis* do not survive at 93.5% r.h.

With the evolution of hygroscopic properties in spermatophores of the Prostigmata, other adaptive transformations became possible, opening the way for further modifications. Thus, the development of a strong hygroscopicity in the sperm droplet made necessary the development of a barrier in the form of a secretion to prevent desiccation of the sperm cells. Again, the spermatophores could be reduced in size, since the efficacy of passive water uptake does not depend on the size of the protective peripheral sheaths but on hygroscopic properties of the matrix secretion of the sperm. Even the spermatophores of micro-arthropods have been able to adapt to low or fluctuating ambient humidities. A further example is the evolution of a multi-layered sheath enclosing a single sperm cell which, apparently, protects the water and osmotic balance of the sperm cell against the strongly hygroscopic matrix secretion. In the course of adaptation of the Hydrachnidia to an aquatic existence, this osmotic protection would appear to be an important pre-adaptation to enable sperm cells to tolerate the strongly hypo-osmotic limnic milieu. It is curious that such an adaptation to a xeric environment was, apparently, an important prerequisite to the colonization of aquatic habitats. The strong hygroscopic properties of the matrix secretion of terrestrial spermatophores imply that the spermatophores are stable only under aerial conditions, whereas in several species the periphery of the droplet, at least, disintegrates rapidly after contact with water (*Anystis baccarum, A. rosae, Johnstoniana, Allothrombium, Trombidium* and *Abrolophus*). Therefore, in terrestrial arthropods, one can regard the stalks or threads, on which the sperm droplets are usually deposited, as adaptations by means of which the contact of the sperm mass with free water of the substrate is prevented.

Viability Although there is no direct evidence about the viability of spermatophores in mites, it can be estimated from the ultrastructure of the sperm cells. In 4-day-old spermatophores of *Abrolophus rubipes*, exposed to a relative humidity of 40%, there were still groups of cells showing a more or less intact ultrastructure whereas others showed massive degeneration (Fig. 8.17). In *Camerothrombidium*, the sperm cells seem to remain intact for at least 48 hours.

Direct evidence concerning the viability of spermatophores has been obtained by Döring (1986) from the springtail, *Orchesella cincta*. In 45-hour-old spermatophores, Döring was able to activate the sperm cells by dipping the spermatophores in a chloride solution. In 60 hour-old spermatophores, the sperm could not be activated (Döring, personal

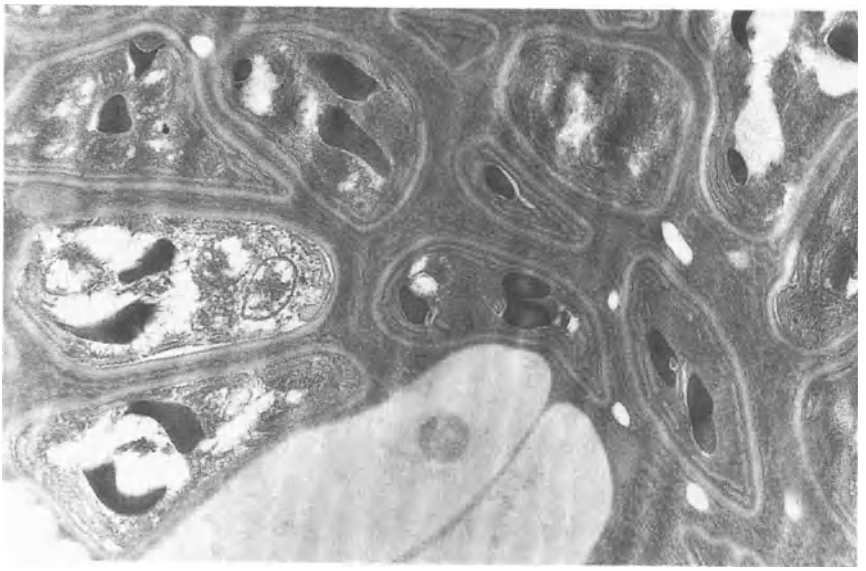


Fig. 8.17 Transmission electron micrograph of sperm cells in 4 day-old spermatophores of *Abrolophus rubipes* showing intact (right) and degenerate cells (× 20 300).

communication). In the Parasitengonae as in Collembola, the sperm cells in the spermatophores are in a state of rest. In the latter, the filiform spermatozoa are coiled and encysted until activated (Döring, 1986). Capacitation of the sperm cells in the Prostigmata takes place only after transfer to the female. Alberti and Storch (1976) observed this in the Bdellidae, and I have found it in *Fessonia callitricha* (Smarididae).

Partner relationships

The example of sperm-transfer behaviour in the Parasitengonae demonstrates that, on the one hand, obligatory pairing previous to indirect sperm transfer as well as direct sperm transfer have each evolved several times, and that, on the other hand, partner contacts have been reduced in several species convergently. With such diversity one may ask what conditions favoured the evolution of the different modes. It would appear that their evolution has been canalized by two types of factors: (1) environmental conditions acting as selection agents, for example, ambient humidity and spatial structure of the habitat; (2) characters of the individuals and population properties which, having once evolved, influence further transformation in that they can constrain the evolu-

tionary possibilities. In respect to partner behaviour, such features include modes of locomotion and signalling, spermatophore viability, rate of deposition of spermatophores, and energy consumption and resources of the population during the reproductive season. Bock and Wahlert (1965) have termed the syndrome of organismal features and environmental agents, which together influence evolutionary transformation, a synerg.

Habitat-related spermatophore deposition The main selection advantage of habitat-related deposition of spermatophores is likely to be that a male can multiply his sexual presence by the production of a number of spermatophores. The basic requirements are that the viability of the spermatophores and the deposition rate are sufficiently high, as is the case with mites and springtails (see above). Habitat-related deposition of spermatophores, apparently, was favoured mainly by arthropods living in habitats with an intricate spatial structure such as soil, litter and vegetation, and where movement is dependent on traversing solid surfaces. Under such circumstances, direct signals from partner to partner, which usually favour pairing, have rarely evolved (for example, vibration signals in some Diplopoda (Haacker, 1974)). It is likely that their absence in soil and litter habitats is due to the interstitial structure which greatly limits the range of such signals. Likewise in plant habitats with an intricate spatial structure where the means for movement usually prohibits the direct tracking of chemical, acoustic or visual signals.

In contrast to this, in such habitats, persistent signals placed on the ground, are well suited to guide a female to a spermatophore or to a male. This type of signal has evolved several times convergently, for example, in the Prostigmata, Diplopoda-Pselaphognatha (Schömann, 1956), probably in Pseudoscorpiones of the family Cheliferidae (Weygoldt, 1966), and as aggregation pheromones in the Collembola (Verhoef *et al.*, 1977). Since substrate signals mark relatively small areas but stay functional for a relatively long time, they are likely to favour the evolution of long-lasting spermatophores and their deposition on a number of sites in the absence of females, thus multiplying the sexual presence of a male. Such signals, however, do not, in principle, preclude the evolution of obligatory pairing as the examples of the Cheliferidae (Weygoldt, 1966) and *Allothrombium fuliginosum* show.

Pairing The main factor in favour of pairing is surely the saving of energy. Pairing, of course, increases the probability of spermatophore acquisition by a female. As a result, fewer spermatophores are required with a consequent reduction in the amount of energy used in their

production. This has probably been a major selection factor in the convergent evolution of close-pairing modes in the Hydrachnidia in which spermatophores originally were deposited in large groups or fields. However, energy shortage may be an important selection factor in favour of pairing only if it occurs in the season of sperm transfer. If, on the other hand, the size of a population is limited in other seasons, either because of energy shortage or for other reasons, lack of hosts of the larvae, for example, then spermatophore 'wastage' will cause no selection pressure towards pairing. This could explain why the facultative ability to deposit spermatophores in the absence of females is retained in several species of prostigmatic mites and Collembola (Döring, 1986, 1988) in which a well-developed pairing behaviour is also present.

Spermatophores that are poorly adapted to the normal habitat conditions of a species may also favour the evolution of pairing. This was probably the case with *Allothrombium fuliginosum*, for example, in which the spermatophores become unstable at the commonly occurring ambient humidities of 76–100% r.h. A third factor, usually correlated with pairing, is a low population density (Schaller, 1971), which reduces the probability that a female finds a viable spermatophore in time without the assistance of the male.

SOME CONCLUSIONS

Spermatophores, signalling mechanisms and pairing-behaviour modes in indirect sperm transfer are, in the Acari and Collembola, at least, highly adaptive. The spermatophores of terrestrial species, and probably of all terrestrial arthropods, are adapted to aerial conditions. They are freed from the need for an aqueous environment although not always from the need for a humid atmosphere. The deposition of spermatophores in the absence of females (habitat-related deposition) is not primitive; it has evolved several times convergently within the terrestrial arthropods and has developed from ancestors in which the sexes paired. The distribution of pairing in the early-derivative taxa of the Arachnida (Scorpiones, Uropygi, Amblypygi and Araneae) as well as in the Antennata (Chilopoda, Diplopoda-Chilognatha, Archaeognatha and Zygentoma) suggests that pairing was already part of the original indirect sperm-transfer behaviour in both groups of terrestrial arthropods (for literature see Weygoldt, 1975; Weygoldt and Paulus, 1979; Schaller, 1971, 1979). Habitat-related deposition of spermatophores increases the sexual presence of males. It has evolved particularly in groups, which live in habitats with small spaces having an intricate spatial structure, and in which the animals depend on the

substrate for locomotion. In these groups persistent substrate signals have evolved several times. It would appear that the particular selection advantages in favour of pairing in euedaphic, hemi-edaphic and epedaphic arthropods are the saving of energy and the advantage it provides where densities are low.

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9

Spermatophore deposition in relation to atmospheric humidity among terrestrial Parasitengonae (Prostigmata)

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For a long time, indirect sperm transfer by means of spermatophores has been considered to be poorly adapted to habitats with low atmospheric humidity. In certain mites, however, this is obviously not the case. It can be shown that spermatophores are deposited even under extremely dry humidity conditions.

Locomotory activities and deposition rates of spermatophores were investigated at the following five levels in a humidity-gradient apparatus: 33, 55.5, 76, 93.5 and 100% relative humidity. Locomotory activities were measured as the actual distribution of the animals in the respective humidities at intervals of 10 min over a period of 4 h. The deposition rates of spermatophores in the respective humidities were recorded during the experiment, and finally checked with a stereomicroscope.

PREFERRED HUMIDITIES FOR SPERMATOPHORE DEPOSITION

No preference The erythraeid, *Charletonia cardinalis* (Koch), shows no preference for a particular humidity, that is, the deposition rate of spermatophores as well as the locomotory activity are not correlated with relative humidity.

Medium humidity *Trombidium holosericeum* (L.) (Trombidiidae) prefers 76% r.h. for the deposition of spermatophores and, in this respect, it is significant that it avoids the highest humidity. Locomotory activity is the same in all the humidities tested.

Low humidity In contrast to the other species, males of *Allothrombium fuliginosum* (Herrmann) (Trombidiidae) establish thread-marked reproduction territories in the absence of females before depositing spermatophores in a close partner contact. They do this, preferably, at 55.5% r.h., avoiding higher humidities, although the maximum locomotory activity of other individuals occurs in the more humid sectors. Thus, the preferred humidity for mating location is lower than that preferred for locomotory activities.

Very low humidity *Erythraeus phalangioides* (de Geer) (Erythraeidae) prefers 33% r.h. for the deposition of spermatophores as does the littoral erythraeid, *Abrolophus rubipes* (Trouessart). Signalling threads (*A. rubipes*) are deposited on the ground by males most abundantly in the region of preferred locomotory activity (both species: 33% r.h.), and around the spermatophores (both species). It is thus possible that the juxtaposition of preferred humidities for locomotory activity and spermatophore deposition is an important element in ensuring a massed deposition of spermatophores. Partner contacts in *E. phalangioides* might also operate in the same manner.

CONCLUSIONS

The choice of different humidities for spermatophore deposition and maximum locomotory activity by *A. fuliginosum* may represent a phylogenetic 'relic' and is therefore of special interest. The preference for low humidities in indirect sperm transfer is, possibly, a primitive (plesiomorphic) character within the Parasitengonae. The mechanism of indirect sperm transfer in this group exhibits, in eco-ethological respects, an astonishing adaptation to low terrestrial atmospheric humidities. The generalized view that this mode of sperm transfer is not fully emancipated from humid habitats can no longer be supported. The original results with full details will be published shortly.

10

The role of Adlerocystis sp. *in the reproduction of argasid ticks*

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In the Ixodoidae, there are two methods of supplying viable sperm to ensure fertilization: in the Ixodidae, insemination only occurs when the female is ready to oviposit whereas in *Ornithodoros*, the vitality of the sperm is maintained until the female is ready to oviposit. In almost all Ixodidae, the female copulates only in the middle of her feed, unlike the Argasidae where copulation may take place before the female has had a blood meal. In such cases, the sperm must be kept alive until the female finds a suitable host. It is assumed that the adlerocysts (*Adlerocystis* sp.) the symbiotes of the sperm cells, contribute to the preservation of the viability of the sperm until the female has taken a blood meal

Reproduction in the Acari has been studied by a number of workers in various groups of this order (Diehl *et al.*, 1982; Oliver, 1986; Pappas and Oliver, 1972; Pound and Oliver, 1979). Nevertheless, there are still many gaps in our knowledge of the nature of the sperm cell (Reger, 1961) and its movement (Rothschild, 1961; Feldman-Muhsam and Filshie, 1976), the site of fertilization and its mechanism (Robinson, 1942; Wagner-Jevseenko 1958; Guglielmone and Moorhouse, 1983). The best-documented fact is that there are wide differences with regard to a number of aspects between different groups of the order and even within families and genera (Feldman-Muhsam, 1973, 1986).

This chapter discusses one such difference which relates to the biological strategy adopted by a species – males and females in co-ordination – to ensure that, when the ova have matured and are ready for fertilization, viable sperm cells are available. This is achieved, at least in ticks,

in two different ways, one of which consists in an appropriate timing of copulation, and the other in maintaining the viability of the sperm cells. The former is characteristic for the Ixodidae and the latter for Argasidae.

REPRODUCTIVE STRATEGIES IN IXODIDAE AND ARGASIDAE

Most Ixodid females do not copulate unless they have fed for 2–3 days. In general, each female is attached to the host together with a male, in a venter-to-venter position. After copulation, the female feeds to repletion without changing her point of attachment. The fully engorged and fertilized female descends from the host, and proceeds to a suitable place for oviposition. Thus, copulation takes place only under circumstances where immediate maturation of the ova and subsequent oviposition are ensured.

Argasid ticks copulate off the host, and the male may copulate with an unfed, sexually mature, pheromone-producing female. Such an impregnated female cannot oviposit until she has found a host and taken a blood meal. As a consequence, the interval between copulation and oviposition may be very long – in some instances it may be several years.

The existence, in Ixodidae, of a well timed, obligatory sequence of feeding, copulation and oviposition, which ensures a short interval between mating and egg laying, raises the question of how, in the Argasidae where such a relation does not exist, the vitality of sperm cells is maintained, if necessary, for a long time. The hypothesis is presented here that the adlerocysts play a major role in this prolongation of the vitality and fertilizing power of sperm.

THE SPERM SYMBIOTE, *ADLEROCYSTIS* SP.

Adlerocystis sp., referred to in what follows as adlerocyst, has been described as a symbiote of the sperm cells of several species of *Ornithodoros* (Feldman-Muhsam and Havivi, 1962, 1964). In these species, *O. tholozani* (Lab. & Meg.) for example, the adlerocyst develops and multiplies in a pair of accessory lobes of the male genital system (Feldman-Muhsam and Havivi, 1963). It is transferred to the female during copulation within the spermatophore, together with the sperm and other components of the spermatophore (Feldman-Muhsam, 1967, 1974). It should be mentioned here that, whereas, under certain circumstances such as in very young, very old, or sexually exhausted males, the sperm may be missing from a spermatophore (Feldman-Muhsam and Havivi, 1967), we never found a spermatophore without adlerocysts, except for one example out of several thousands examined; this exception is

referred to later. This seems to indicate that, at least in those species in which adlerocysts are attached to the sperm cells, they play an essential role in reproduction.

In both argasid and ixodid ticks, the spermatophore is formed on the external side of the male gonopore (Feldman-Muhsam, 1967). First, a droplet of secretion is ejected from the male gonopore. Then, sperm, adlerocysts and other components are injected into this droplet, which thereby becomes a bulb for which the term, ectospermatophore has been coined (Feldman-Muhsam, 1967). Finally, a droplet of another secretion is injected into the ectospermatophore. This secretion serves first as a stopper for the ectospermatophore, and later evaginates from the ectospermatophore, and invaginates into the female genital tract to serve as a container for the sperm cells, adlerocysts and other elements; this is the endospermatophore. In the ectospermatophore, sperm cells and adlerocysts remain separated from one another (Feldman-Muhsam, 1964). They only intermingle when the endospermatophore reaches the female genital tract, and the contents of the ectospermatophore are pushed into the endospermatophore (Feldman-Muhsam *et al.*, 1973).

ATTACHMENT OF ADLEROCYSTS

In *O. tholozani*, adlerocysts start to attach to a specific locus of the sperm cell after about 4 hours, and about two days later, the attachment locus of every sperm cell is fully covered with adlerocysts (Fig. 10.1) (Feldman-Muhsam and Havivi, 1963). They remain attached to the sperm cell until the latter leaves the endospermatophore to proceed to the oviducts for fertilization. When the sperm cells leave the endospermatophore, they shed the adlerocysts (Fig. 10.2) which remain in the endospermatophore.

During the last stages of spermateleosis, that is, the transformation of the prospermium (the immature sperm cell) into the spermiophore (the mature sperm cell) (Feldman-Muhsam and Filshie, 1979), some adlerocysts are enveloped by the outer sheath of the prospermium and carried with it into the newly formed spermiophore (Fig. 5 in Feldman-Muhsam, 1974). In the spermiophore, the invaginated outer sheath of the prospermium constitutes the acrosomal canal, where the adlerocysts presumably remain, close to the nucleus of the spermiophore until fertilization takes place (Fig. 16 in Feldman-Muhsam, 1974). It may be conjectured that these adlerocysts enter the ovum together with the nucleus of the sperm cell and, thus, ensure transovarial transmission of the adlerocysts.

Two species of Ixodidae namely, *Hyalomma excavatum* Koch and *Rhipicephalus sanguineus* (Latr.), were found to harbour very similar adlero-

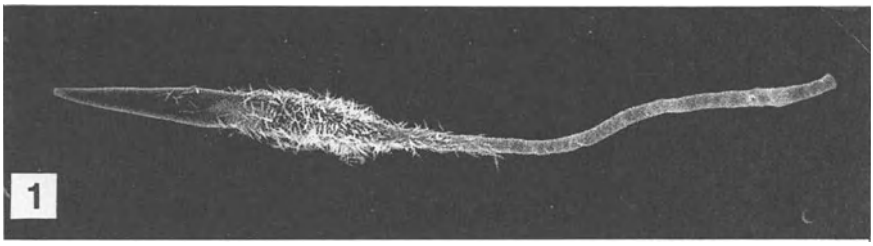

Fig. 10.1 Scanning electron micrograph of sperm cell from an endospermatophore of *Ornithodoros tholozani* (Lab. & Meg.) covered with adlerocysts at the specific locus of attachment (× 206).

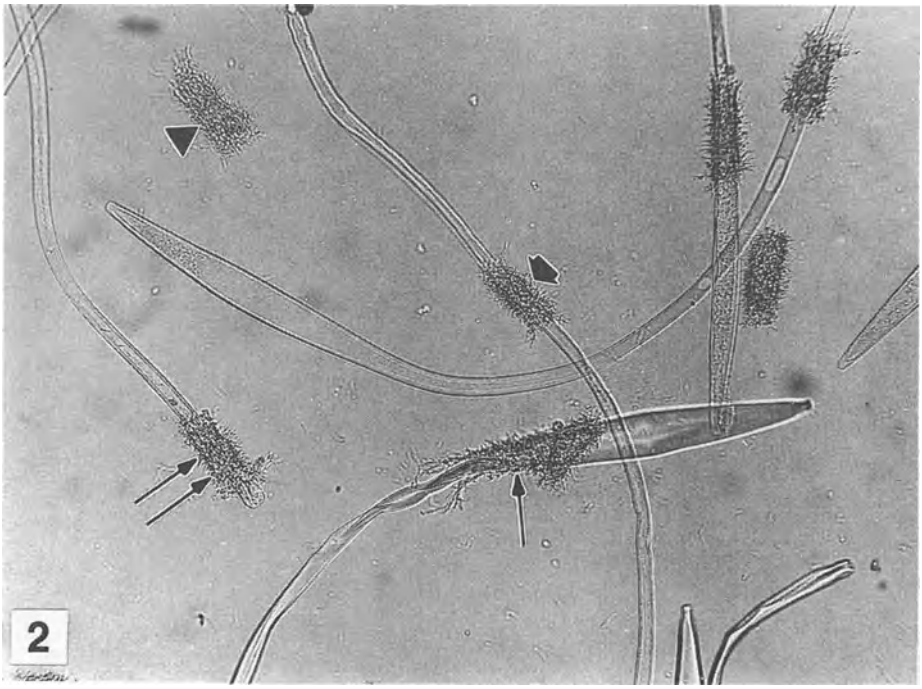

Fig. 10.2 Micrograph of unstained sperm cells, in saline, of *Ornithodoros tholozani* showing various stages in the shedding of adlerocyst aggregates. Adlerocyst muff, originally located on specific locus of attachment (single long arrow), moves along to narrow posterior portion of cell (short arrow) and then to tip double long arrow as sperm cell slides out of its sheath of adlerocysts, which is finally shed (▲) (× 195).

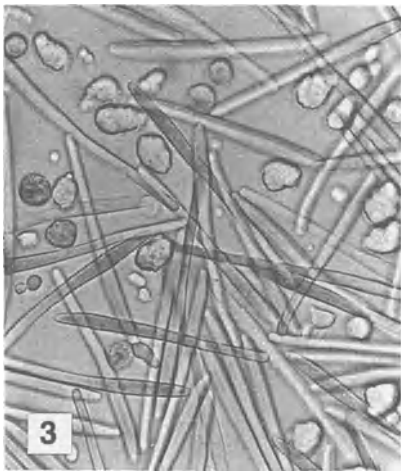

Fig. 10.3 Micrograph of prospermia of *Hyalomma* with clusters of adlerocysts from an endospermatophore immediately after copulation (× 150).

cysts. As in *Ornithodoros*, the adlerocysts develop in the posterior accessory lobes of the male genital system, and are found there in the form of conglomerates of morulae, each of which is composed of several spherule-shaped adlerocysts enclosed in a membrane (Figs 2 and 3 in Feldman-Muhsam, 1974). At subsequent stages, the development of the adlerocysts in Ixodidae differs from that in *Ornithodoros*: in the latter, individual adlerocysts emerge from the morulae during copulation, and are injected into the ectospermatophore as separate, highly refractive spherules; in the Ixodidae, they reach the ectospermatophore in the morula stage, and have never been observed to attach to the sperm cells nor to become spindle-shaped (Fig. 10.3).

It appears from the above description that, at least in the species in which the relationship between adlerocysts and sperm cells was studied, there is a correlation between the pattern of feeding–copulating–ovipositing behaviour of a given species and the attachment of its adlerocysts to sperm cells: in species in which oviposition follows closely after copulation, adlerocysts do not attach to sperm cells, whereas where there may be a long interval between copulation and oviposition, adlerocysts do attach. This correlation seems to be significant evidence in support of the hypothesis that in the species in which females are able to oviposit a long time after copulation, the adlerocysts contribute to the preservation of the viability and the fertilizing power of the sperm. They

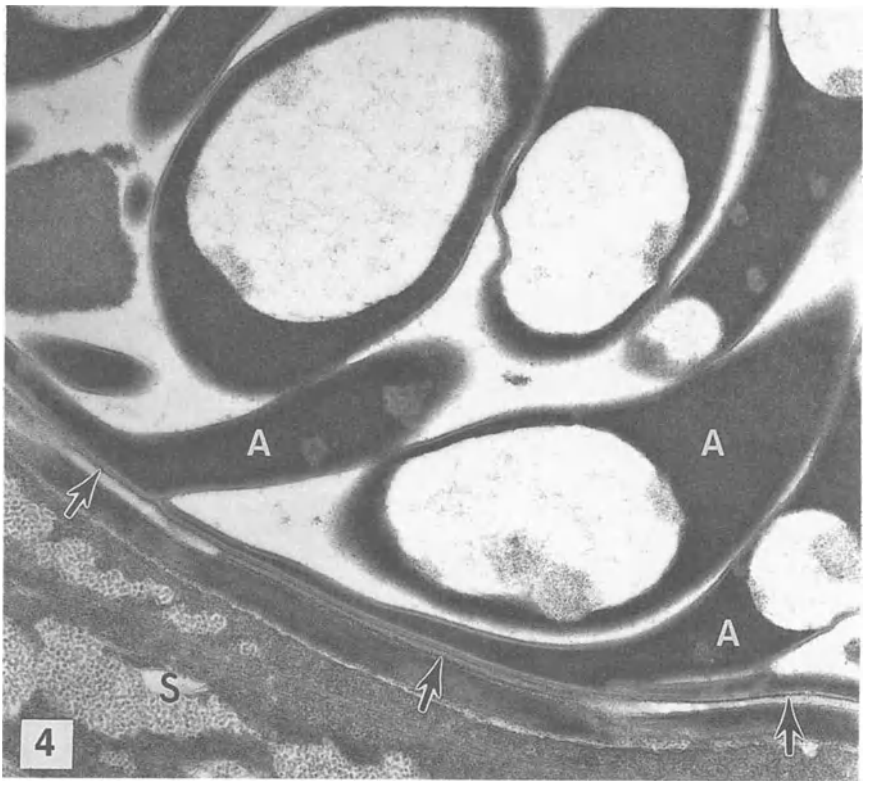

Fig. 10.4 Transmission electron micrograph of longitudinal section of sperm cell of *Ornithodoros tholozani* to illustrate intimate contact (arrows) between sperm cell (S) and the elongated ends of spindle-shaped adlerocyst (A) (× 35 600).

presumably make this contribution while attached to the sperm cells but the nature of this contribution has still to be elucidated.

It has been observed in electron micrographs that the adlerocysts establish very close contact with the sperm cell to which they are attached (Fig. 10.4). The adlerocyst adapts its shape to the surface of the sperm cell (Figs 10.4 and 10.5) to maximize the area of contact, and its membrane forms very thin projections which infiltrate between the cellular processes of the sperm cell (Fig. 10.6). At the same time these processes change their position and their size as if attracted by the adlerocysts (Fig. 10.5). It should be stressed, however, that the adlerocysts have never been observed to penetrate through the cell membrane of the sperm.

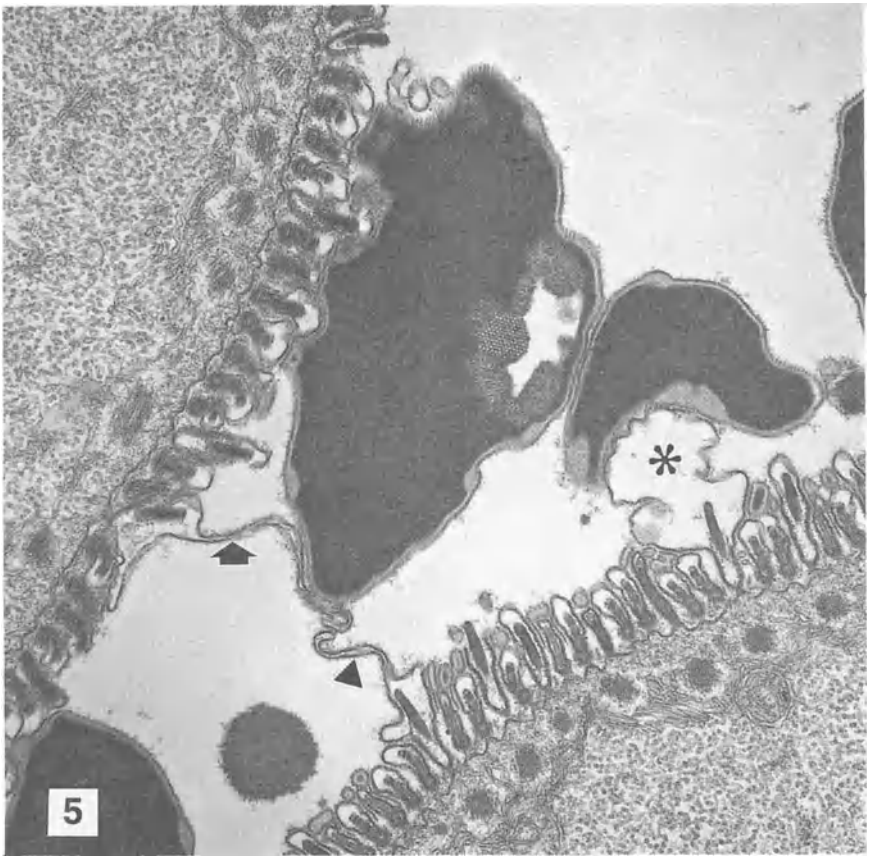

Fig. 10.5 Transmission electron micrograph illustrating intimate contact between adlerocysts and cellular processes of two sperm cells of *Ornithodoros tholozani*. Note thin extensions of cellular processes (▲ and arrow) of two sperm cells making contact with adlerocyst, and expanded cellular process (*) adapting its size and shape to establish maximum contact with a second adlerocyst (× 20 900).

SUPPORTING OBSERVATIONS

The hypothesis outlined here regarding the function of the adlerocysts is also supported by the fact that the sperm cells seem to require the support of the adlerocysts while they wait in the endospermatophore for the ova to become ready for fertilization. At that moment, the sperm cells shed the adlerocysts and proceed to the ova. All the adlerocysts attached to a sperm cell are shed in one piece. At this stage, they are

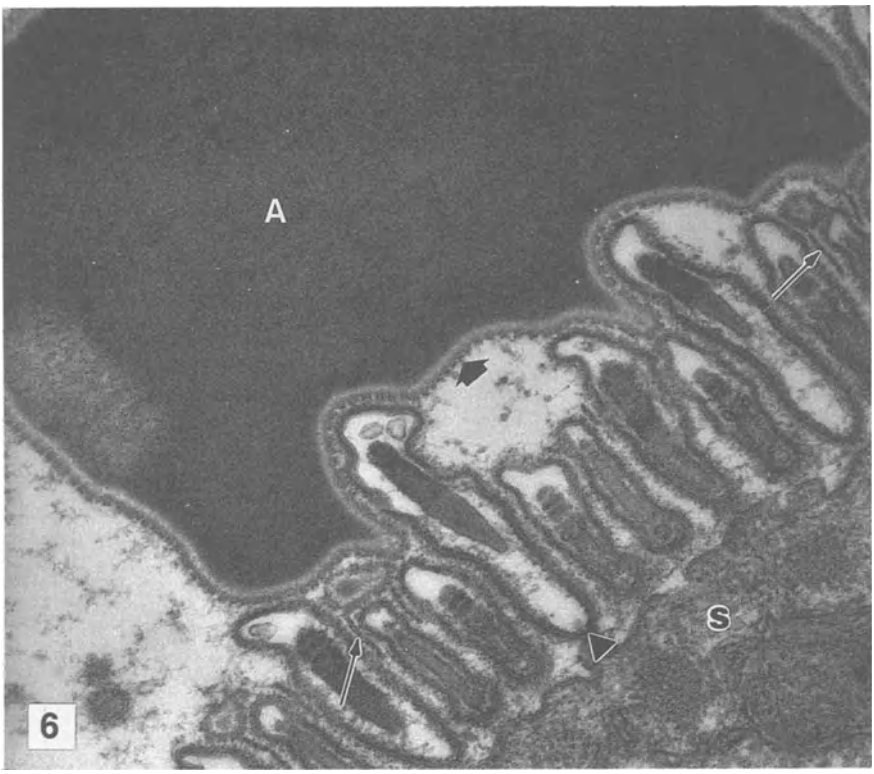

Fig. 10.6 Transmission electron micrograph of transverse section of adlerocyst (A) in close contact with cellular processes (▲) of a sperm cell (S) of *Ornithodoros gurneyi* Warb. Note thin projections of adlerocyst (long arrows) infiltrating between cellular processes, and peculiar outer membrane of adlerocyst (short arrow)(× 66700).

stuck together and form a muff, around the area of attachment. When the sperm cell is about to leave the endospermatophore, it quickly slides out of its muff and leaves it behind (Fig. 10.2). Sperm cells with unshed muff-like aggregates consisting of deformed adlerocysts, which are stuck together (Fig. 10.7) may be found in endospermatophores when either the female or the male has been subjected to unfavourable conditions such as prolonged starvation or high temperature. It is likely that these adlerocysts, have degenerated after having contributed all that they could to the sperm or because of senescence or desiccation.

Further evidence in support of this hypothesis is provided by the observation of the fate of adlerocysts which remain attached to sperm

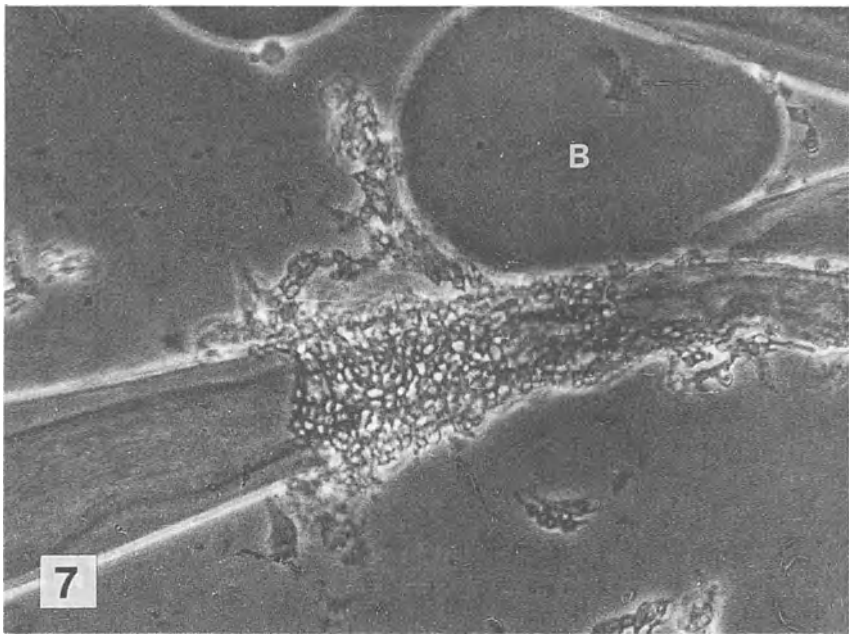

Fig. 10.7 Deformed adlerocysts stuck together and attached to a spermiophore of *Ornithodoros tholozani*, in saline, from an endospermatophore of a tick subjected to prolonged unfavourable conditions. B is an air bubble (× 660).

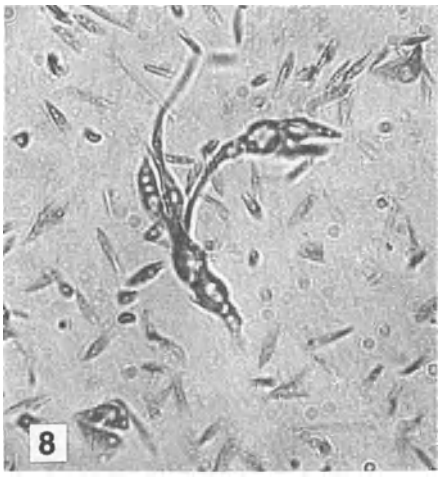

Fig. 10.8 Micrograph of a giant hypertrophied adlerocyst among small, normal spindle-shaped ones in saline (× 233).

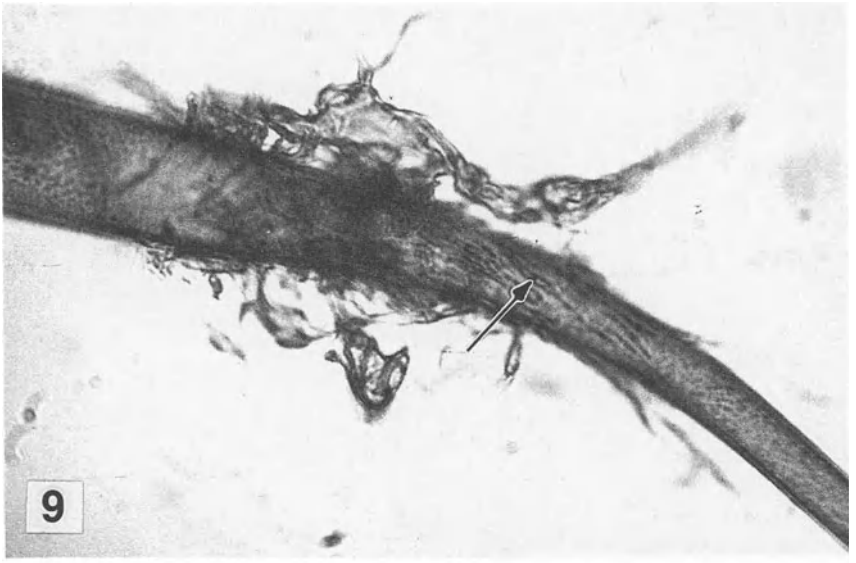

Fig. 10.9 Micrograph of giant adlerocysts together with normal spindle-shaped ones (arrow) attached to a sperm cell of *Ornithodoros tholozani* (× 660).

cells for a long period. This situation can be studied in the laboratory when females are permitted to copulate, and are then kept under conditions such as low temperature or starvation which prevent them from ovipositing. Such females can be dissected at various times after copulation, and the state of sperm and adlerocysts determined. At 9–10 months after copulation, the sperm cells of starved females of *Ornithodoros tholozani* and *O. savignyi* (Aud.) were alive and the adlerocysts attached to them at the specific locus. The adlerocysts, however, were much thinner and paler than normal, and it is considered that they had degenerated. When two years have elapsed after copulation, the sperm cells have also deteriorated.

Another type of degeneration of the adlerocysts has been observed in fed females of *O. savignyi*, *O. tholozani* and *O. gurneyi* Warb. About 8 months after copulation, sperm in the endospermatophore was still alive and active with many adlerocysts still attached, but these are degenerate, and many of them have become hypertrophied (Figs 10.8 and 10.9). They become greatly enlarged and much distorted. In some cases, there is little evidence of the original spindle-shaped conformation; such adlerocysts show irregularly shaped outgrowths with numerous vacuoles and many invaginations. Electron micrographs of these giant adlerocysts reveal intricate evaginations and invaginations of the

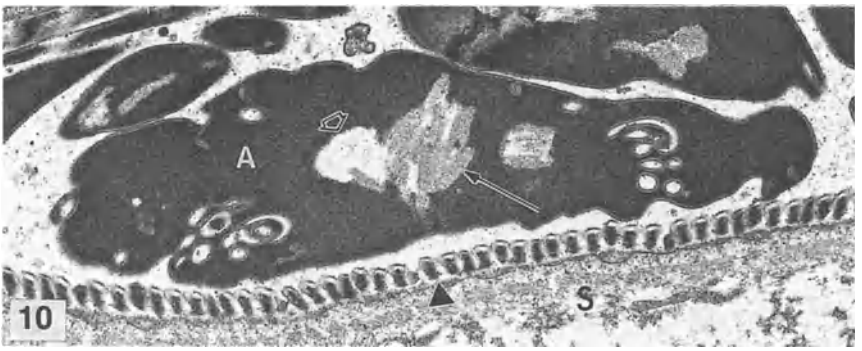

Fig. 10.10 Transmission electron micrograph of a giant adlerocyst from an endospermatophore of *Ornithodoros tholozani* illustrating the no longer recognizable form of the adlerocyst (A) with vacuole (short arrow), crystals (long arrow) lying adjacent to a sperm cell (S), cellular processes (▲) of a sperm cell (× 14 900).

external membrane, and these changes including the irregular outgrowths render the adlerocysts unrecognizable. In these sections, only the ultrastructural characteristics of the membrane, the vacuoles and the presence of crystals establish their identity as adlerocysts (Fig. 10.10). Such giant forms are also found under other circumstances of adlerocyst degeneration. For instance, old males which have taken only one blood meal, and continued to copulate for a long time after that meal, often produce similar adlerocysts.

A final and most interesting case, which could also be cited in support of the present hypothesis regarding the function of adlerocysts, namely, that of maintaining the fertilizing power of sperm, is provided by the unique observation of a spermatophore lacking adlerocysts. Such a spermatophore was found in a female of *O. tholozani* which had copulated with two males. One of them had produced a perfectly normal spermatophore and the other, one without adlerocysts. All sperm cells in the latter spermatophore were dead while those of the former were alive and normal.

CONCLUSIONS

There is no doubt that much further research is needed to elucidate the relationship between adlerocysts and sperm cells. In view of the peculiarity of this unique, presumably symbiotic association between the sperm cell and this micro-organism, such research can be expected to yield interesting results with the likelihood of economically important

consequences. If at any stage of their development, the symbiotes could be eliminated and aposymbiotic ticks obtained, the reproductive cycle of the tick could be interrupted. This might become an important contribution in the struggle against argasid ticks transmitting diseases to man and livestock.

ACKNOWLEDGEMENT

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11

A scanning electron-microscopy study of spermatogenesis in Pergamasus barbarus *Berl. (Gamasida)*

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Electron microscopy of sectioned material is a valuable tool in the study of spermatogenesis in mites, but provides only fragmentary information on the spatial aspect of developmental changes. Scanning electron-microscopical (SEM) technique is more suitable for such purposes, especially in groups like the Gamasida, where the male gonad does not have a compact structure, and germ cells can easily be isolated. In the family Pergamasidae, as in most mites, the architecture of the testis is unknown. The maturation of germ cells occurs in cysts, which only weakly adhere to each other and, after isolation, can be processed for SEM observation.

Males of *Pergamasus barbarus* Berlese were used for the study. Testes were dissected in isotonic sucrose solution, transferred to a droplet of the same solution on a coverslip, and teased apart with needles to release the cysts which then adhere to the glass. A droplet of a fixative containing 3% glutaraldehyde was then added in order to obtain simultaneous fixation of the cell structure and to ensure that the material did not become detached from the glass surface. After a gentle wash, the material was postfixed in 1.4% osmium tetroxide, subsequently dehydrated in ethanol and isopropanol, air dried, coated with carbon and gold, and examined in a JEOL JSM 35 scanning electron microscope.

Spermatogenesis in *P. barbarus* occurs in cysts. The germ-cell surface could not be observed directly due to the presence of a thin layer of cyst cells covering it. The spatial distribution of spermatids is, however,

retained. Moreover, artifactual shrinkage of the cells results in a relief reflecting the real sculpture of the germ-cell surface.

At the commencement of spermatogenesis, four spermatocytes are packed in a tetrahedral arrangement in each cyst. After meiosis, the resulting 16 early spermatids are located radially, and ridges appear on their surface. When the elongation of the spermatids begins, a concavity is formed at the protruding end of each spermatid, but later a peg-like elevation appears at this site. As elongation proceeds, the radial arrangement of the spermatids becomes clearer, and superficial ridges, representing the so-called longitudinal bands, located in the peripheral cytoplasm of each spermatid, are more pronounced due to alterations in the longitudinal band structure and, possibly, to an increase in their density. The number of superficial ridges (and longitudinal bands) can vary in one cyst. In cysts containing nearly mature spermatids, the portion of each spermatid devoid of a nucleus protrudes radially, whereas the portion with a nucleus is directed towards the centre of the cyst, and these parts of the cells adhere to each other in this region. Observations using SEM also suggest a regular arrangement of superficial structures such as the longitudinal bands which, in neighbouring spermatids, exactly oppose each other.

12

Precise sex-ratio control in the pseudo-arrhenotokous phytoseiid mite Typhlodromus occidentalis *Nesbitt*

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Pseudo-arrhenotoky implies that males develop from fertilized eggs but transmit only the maternal genome. They become, effectively, haploid after elimination of the paternal chromosome set. This is in contrast to arrhenotoky where males are also haploid but arise from unfertilized eggs. It is shown that females are the pseudo-arrhenotokous phytoseiid mite, *Typhlodromus occidentalis* Nesbitt, produce highly underdispersed non-binomial sex ratios. In addition, they adjust their sex ratio to the density of conspecific females, broadly in agreement with the theory of Local Mate Competition. It is concluded that phytoseiid females not only have the ability to regulate their sex ratio but that they can also determine the sex of each individual egg with high precision. The control seems as flexible as in arrhenotokous arthropods, suggesting that pseudo-arrhenotoky is not at a disadvantage compared to arrhenotoky with respect to maternal control of the sex of the offspring. Precise sex ratios could confer on phytoseiids a fitness advantage compared to a binomial sex ratio because of their often subdivided population structure, characterized by mating in small groups. However, the existence of precision does not need to depend solely on this advantage. It could be an integral property of the mechanism of sex-ratio control

INTRODUCTION

Several systems of sex determination exist where males are uniparental. The most important are arrhenotoky and pseudo-arrhenotoky. They share the property that males are, effectively haploid, and transmit the

maternal genome only. In arrhenotoky, males normally arise from unfertilized eggs, whereas in pseudo-arrhenotoky, they arise from fertilized eggs but become haploid after inactivation and/or elimination of the paternal chromosome set. Arrhenotoky is a fairly widespread system, mainly among the Arthropoda. It has probably not more than about twelve independent origins (Bull, 1983) but occurs in a large number of species as, for example, among the sexual Hymenoptera. Pseudo-arrhenotoky is rated a much less common system. It has three known origins, all among the arthropods, and has radiated less extensively. It is, however, much more difficult to detect than arrhenotoky, and has not been investigated in a systematic way. Consequently, it could be much more common than current evidence suggests. Pseudo-arrhenotoky is known to occur in the phytoseiid mites (Schulten, 1985), and it is probably ubiquitous among the sexual species of that family of predatory mites. This can be inferred from the fact that in every species so far investigated, the males are haploid (Wysoki, 1985) while unmated females never produce males as is the case with arrhenotoky.

The evolution and distribution of the different sex-determining systems are still areas of ignorance and active interest (Bull, 1983). It is, therefore, important to gain an insight into their relative advantages and disadvantages. From the viewpoint of the female, both systems with uniparental males have the selective advantage that her genes have a twofold representation in the gametes of her sons, compared to the gametes of diploid sons of biparental origin. This results in a greater genetic identity with her grandchildren. An advantage of arrhenotoky compared to diploidy is that a female can determine the sex of her offspring by influencing the fertilization of each egg. This permits the mother to adjust the sex ratio (proportion of daughters) of the offspring to the environment in an adaptive way. Bull (1983) assumed that with pseudo-arrhenotoky, maternal control of the sex of the offspring is not possible, and that this confers a disadvantage compared to arrhenotoky. This is, however, a questionable assertion; the fact that it is the paternal genome which is eliminated points to the possibility that the elimination process is controlled by the mother, and, thus, that she may also be able to control the sex of her eggs.

One situation wherein it is advantageous to control the sex ratio is a spatially structured population where mating occurs mainly or exclusively between the progeny of a few females, and generally results in a high probability of sib mating. This selects for a female-biased sex ratio, depending on the number of ovipositing females in a group; the lower that number, the higher the sex ratio (Hamilton, 1967; Charnov, 1982). This situation is generally referred to as Local Mate Competition (LMC) although Local Parental Control (LPC) seems a better term (Nunney,

1985), because competition between brothers for mates is not necessary for a female-biased sex ratio in a structured population. The concept of LPC refers to the amount of influence which the sex ratio of the progeny of a mother has on the sex ratio of the mating group that contains her offspring. Because the term LPC has not come into general usage, LMC will be used here. The predictions of the theory on LMC about the influence of the size of the local mating group on the sex ratio have been successfully tested in the case of parasitic wasps (Werren, 1983; Waage, 1986; Charnov, 1982).

Phytophagous spider mites, the dominant prey of many phytoseiid species, often have a strong tendency to form patchy infestations. As a consequence, phytoseiids generally have a subdivided population structure (Sabelis, 1985). Each prey patch is probably invaded by only a few females, and a high, local prey density results in the clumping of eggs of individual females and in little dispersal of the offspring until mating. This leads to the assumption that mating groups will probably be small, their size depending upon prey and predator density. For many phytoseiid species it will be advantageous, therefore, to produce a female-biased sex ratio, and to be able to adjust that sex ratio to the local conditions which influence the probability of sib mating.

Sabelis and Nagelkerke (1987) have published evidence that phytoseiid females indeed have control over the sex ratio of their offspring. They gave two lines of evidence: (1) when species are compared, there is a negative correlation between the sex ratio and the expected size of the mating group inferred from life-history data; and (2) in experiments, individual females change the proportion of daughters they produce in response to the density of females of the same species. A higher density results in a lower sex ratio, as predicted by theory, assuming that a higher density results in a larger size of the mating groups. They concluded that pseudo-arrhenotoky does not exclude sex-ratio control.

This chapter presents additional evidence concerning the ability of phytoseiids to control the sex of their progeny. The aim is to investigate the precision of the control mechanism. Do females only regulate the probability of producing a daughter, or can they more or less precisely manipulate the sex of each individual egg? The first possibility, given a constant probability, results in a binomial distribution of daughters over different clutches. In the second, they are able to produce non-binomial distributions, which can have a different variance compared to the binomial. Sex ratios are referred to as *precise* when the variance in the number of daughters in clutches of a given size is lower than the variance expected in a binomial distribution with the same mean sex ratio.

In infinite mating groups, individuals do not gain selective advantage

by producing precise sex ratios (Kolman, 1960; Charnov, 1982). In finite groups this is different (Verner, 1965). Taylor and Sauer (1980) have modelled the effect of a non-binomial distribution in finite mating groups for the case of a 1 to 1 overall sex ratio. They concluded that females which produce precise sex ratios have a selective advantage compared to binomial females. Green *et al.* (1982) have investigated models of the extreme LMC situation where all the mating takes place between the offspring of one female. The mother then has to produce only enough males to inseminate all her daughters. They also reported that females which produce a precise number of sons have a greater reproductive success. Females with binomial broods run the risk that due to statistical variation some clutches contain no males. Hartl (1971) has pointed out that this results in a lower optimal sex ratio than that predicted by Hamilton's model (1967) which does not take variance into account. The intermediate case of LMC with a group size larger than one has not, to our knowledge, been investigated. The assumption is, however, that it is generally true that in finite mating groups, precise sex ratios have an evolutionary advantage over binomial ones. This implies that, in a structured population, it will be adaptive for females not only to be able to control the mean of the proportion of females in their broods, but also to keep the variance as low as possible.

Most animals have an XY-like chromosomal sex-determining mechanism (Bull, 1983), which puts constraints on the possibilities of producing precise sex ratios (Williams, 1979). Their sex-ratio distributions are normally close to the binomial. Arrhenotokous organisms such as parasitic wasps, however, are provided with a mechanism which is ideally suited to the production of a precise sex ratio. Precision can be achieved by controlling the fertilization of each egg. In many cases they also have the structured population that will make it profitable to do so. Precise sex ratios have indeed been found in a number of parasitic wasps (Green *et al.*, 1982; Waage, 1982 and others, as reviewed by Waage, 1986).

Phytoseiids also have a population structure that would make precise sex-ratio control an adaptive trait. Its existence will, of course, depend on the capability of the pseudo-arrhenotokous mechanism to provide the necessary degree of fine tuning. The absence of that capacity would make the reproductive mode disadvantageous compared to arrhenotoky.

This chapter reports an investigation of the precision of sex-ratio control in a phytoseiid species. It does so by testing for the occurrence of a non-binomial distribution of the sexes in the offspring of individual females and females in groups. The experiment presented here also allows for testing of the sex-ratio response to female density using a

much greater number of replicates than in the experiments described by Sabelis and Nagelkerke (1987).

MATERIALS AND METHODS

The species studied was *Typhlodromus occidentalis* Nesbitt, a phytoseiid known to be pseudo-arrhenotokous (Hoy, 1979; Nelson-Rees *et al.*, 1980). It was obtained from laboratory cultures grown on leaves of the Lima bean (*Phaseolus lunatus* L.) infested with the spider mite, *Tetranychus urticae* Koch. During the experiment the mites were kept on Lima bean leaf discs with a diameter of 25 mm (*a* 5 cm^2), placed lower surface upwards on wet cotton wool in Petri dishes. Two different densities of predator females were used; a high density with ten females on each disc and a low one with a single female. The leaf discs were supplied with prey eggs of *T. urticae*. The high-density discs were provided with 200 prey eggs to begin with and the low density ones, 75 eggs. This is an ample supply of prey for maximum oviposition (Sabelis, 1981). The initial supply of eggs was provided by allowing a number of spider-mite females to oviposit on the discs during one day before the commencement of the experiment, removing them and bringing the number of eggs to the required level by addition or removal. During the experiment, hatched spider-mite larvae were removed daily and the eggs replenished. A predator female consumes about 10 eggs per day under these circumstances (Sabelis, 1981) so there was always sufficient prey. Young inseminated females were put on the discs just before the start of egg laying. To ensure a sufficient level of fertilization there were, in addition, one or two males on each disc throughout the experiment. The experiment lasted 7 days. Every 12 hours the eggs laid by the phytoseiids were collected, counted and sexed 8–12 h later. A number of females strayed into the cotton wool or disappeared, especially in the high-density treatment, and the few low density replicates where this occurred were discarded. In the high-density treatment, these females were replaced by others from a parallel series of discs kept under exactly the same conditions of prey and predator density. The environmental conditions were: 25 °C, 70% r.h. and continuous light. To keep the amount of work manageable, replicates were partly done sequentially rather than simultaneously.

The sex of the progeny was determined from chromosome counts in egg squashes stained with orceine, made when the eggs were between 8 and 24 hours old. Male eggs of *T. occidentalis* have three, and female eggs, six chromosomes. Replicates where the success rate of sexing was less than 95% were discarded. Eventually the high-density treatment

was successfully completed in six, and the low density in 60 replications, implying that in both cases a total of 60 mites was used. Taking all losses into account, sexing in the replicates used for analysis was about 97% successful.

For determination of the nature of the distribution of the sexes, the daily clutches of the 60 females kept individually and the six groups of 10 were analysed. In the latter case, the 'clutches' consisted of the combined daily production of all 10 females because the eggs of each individual mother cannot be distinguished. Incompletely sexed clutches were excluded from the analysis. Only the data of days 2–7 inclusive were used because by day 2, the sex ratio appeared to have reached a stable level (Fig. 12.1). This was done because the mixing of distributions with different means gives an aggregate distribution with a variance higher than the variances of the compounding distributions. This may mask the existence of underdispersion in the original distributions. The distribution was tested by comparing the variance in the number of males in clutches of a particular size with the variance expected under a binomial distribution. For the high-density clutches use was made of the regression method described by Green *et al.* (1982), which treats the binomial distribution as approximately normal. For the low-density data with a mean clutch size of about 3.0, this approximation is not appropriate. The low-density data were therefore analysed with a dispersion test, devised by E. Meelis, tailored to the analysis of

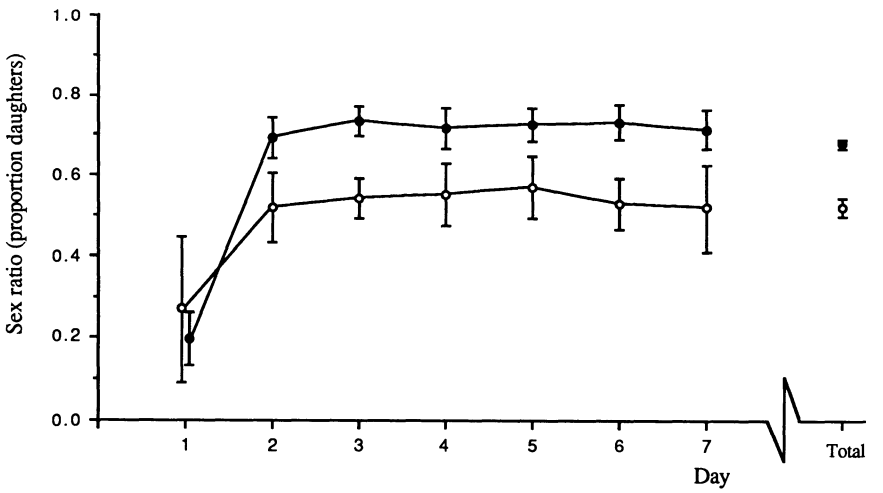

Fig. 12.1 Means and 95% confidence intervals of daily and total proportions of daughters of females of *Typhlodromus occidentalis* Nesbitt kept on leaf discs either singly (filled circles) or in groups of 10 (unfilled circles).

data from a large number of small clutches. A derivation of this test is given in the Appendix.

RESULTS

The daily mean sex ratios at the two densities are given in Table 12.1 and plotted in Fig. 12.1. The mean proportion of daughters (the total sex ratio) in the offspring of single females (0.678) is higher than for the females kept at high density (0.517). A Mann–Whitney test on the overall sex ratios of the discs of the two densities showed that the means are significantly different ($Z = 4.02$, $P < 0.001$). In each group there is a conspicuous difference between the sex ratio produced on the first day and those on the other 6 days. On the first day the ratio is male-biased whereas it shows a rather constant female bias on the subsequent days (Fig. 12.1). Kruskall–Wallis tests showed for both densities that the difference between the first day and the other days is significant ($P < 0.05$), and that the last six days are homogeneous. Of the single females, there were 28 which produced only one egg during the first day and all these eggs were male. This points to a sons-first pattern as is well known in phytoseiids (Sabelis, 1985). A similar pattern is found in some parasitic wasps where the first egg laid in a clutch often develops into a male (Waage, 1986). A difference is that in phytoseiids the pattern refers to lifetime production and not to individual clutches. The sons-first

Table 12.1 Daily means of sex ratio and oviposition rate of *Typhlodromus occidentalis* Nesbitt at two density levels, kept on leaf discs for 7 days with abundant prey (total with standard deviation is mean of overall value of discs)

	1 female/disc (60 replicates)		*10 females/disc (6 replicates)*		
Day	*Proportion daughters*	*Eggs/female/day*	*Proportion daughters*	*Eggs/female/day*	*Females replaced (total)*
1	0.20	1.6	0.27	0.98	4
2	0.69	2.6	0.52	1.5	6
3	0.73	3.2	0.54	1.9	4
4	0.72	3.1	0.55	1.7	6
5	0.73	3.2	0.57	1.6	8
6	0.73	3.2	0.53	1.7	6
7	0.71	3.2	0.52	1.6	3
Total	0.678	2.90	0.571	1.57	
s.d.	0.045	0.3	0.020	0.13	

Table 12.2 Joint distribution of clutch size (daily egg production) and number of male eggs in clutches of each of 60 females of *Typhlodromus occidentalis* kept singly on leaf discs for 7 days with abundant prey. The analysis compares the observed variances of number of males for the different clutch sizes with those expected assuming a binomial distribution (data from completely sexed clutches of days 2–7 inclusive)

Number of males in a clutch	*Clutch size*					*Total*
	1	*2*	*3*	*4*	*5*	
0	3	33	33	3	·	72
1	2	30	142	61	·	235
2	·	·	2	25	8	35
Total	5	63	177	89	8	342
Proportion daughters	0.6	0.762	0.725	0.688	0.600	0.717
Variance of the number of males	0.3	0.253	0.168	0.256	0.00	0.205
Expected binomial variance	0.24	0.363	0.598	0.858	1.20	0.632
Variance ratio	1.25	0.699	0.281	0.299	0.00	0.324
U*	·	−2.42	−8.27	−5.38	−2.07	−9.07***

***$P < 0.001$.
*Negative value indicates underdispersion. See text and Appendix for analytical details.

Table 12.3 Joint distribution of the number of eggs ('clutch' size) and number of male eggs produced per day by six groups of 10 females of *Typhlodromus occidentalis* kept on leaf discs for 7 days with abundant prey (data from completely sexed clutches of days 2–7 inclusive)

Number of male eggs	*Number of eggs*																*Total*
	9	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	
3	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1
4	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
5	·	·	1	·	2	·	·	·	·	·	·	·	·	·	·	·	3
6	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	2
7	·	·	·	·	2	1	2	1	1	2	·	1	·	·	·	·	10
8	·	·	·	·	·	·	1	2	·	1	1	·	·	·	·	·	5
9	·	·	·	·	·	·	·	1	3	1	1	·	1	·	·	·	7
10	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	1	2
11	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	1
Total	1	·	1	·	4	1	5	4	4	4	2	2	2	·	·	1	31

pattern could be a strategy of the female to ensure that her daughters have a high probability of being inseminated immediately on becoming adult, and/or to give her sons a head start in the competition with other males. Among the 24 females that had produced two eggs on the first day, 19 had one son and one daughter, and five had two sons, indicating that the second egg is likely to be female but not exclusively so.

The high-density females have a significantly lower oviposition rate than the single females, 1.57 eggs per female per day compared to 2.90 (Mann–Whitney: $Z = 4.07$, $P < 0.001$).

Table 12.2 shows the distribution of the number of sons in the clutches of single females over days 2–7 inclusive. The total observed variance (0.205) in the number of males is estimated by the mean squared error within clutch sizes. The expected variances for the different clutch sizes, assuming a binomial distribution, were calculated as pqN where N = clutch size, p = mean proportion of males in clutches of size N and $q = 1 - p$. The expected total binomial variance is the mean of pqN over the clutches, giving a value of 0.632, much higher than the observed variance. The ratio between the two variances is 0.324. Applying the test for non-binomiality discussed in the Appendix, and combining the results for the different clutch sizes, showed that this underdispersion is significant ($U = -9.07$, $P < 0.001$). From this it follows that females produce precise sex ratios.

The results for the females kept at high density are shown in Table 12.3. The regression equation (Table 12.4) of the number of sons (M) on clutch size (N) is: $M = 0.44N + 0.327$; $r^2 = 0.66$. For a given clutch size N, the expected binomial variance can be calculated again as pqN, but with

Table 12.4 Analysis of variance with linear regression of number of sons (M) as a function of total number of eggs produced ('clutch' size: N) per day by 6 groups of 10 females (data from Table 12.3). The regression equation is $M = 0.44\,N + 0.327$ with $r^2 = 0.66$

Source of variation	*Degrees of freedom*	*Sum of squares*	*Mean square*	*Variance ratio*
Between clutch sizes	11	66.127	6.012	
Linear regression	1	57.561	57.561	67.244***
Deviations from regression	10	8.566	0.856	0.755 n.s.
Within clutch sizes	19	21.550	1.134	
Total	30	87.677		

***$P < 0.001$.

p obtained from the regression equation, $p = (0.44N + 0.327)/N$. Taking the mean of pqN over clutches gives a total expected variance of 4.078. The observed variance, estimated by the mean squared error within clutch sizes, is 1.134. The ratio between observed and binomial variances is 0.278, that is, somewhat lower than that of females kept at low density. The resulting test statistic (Green *et al.*, 1982) treating the binomial distribution as approximately normal, is $\chi^2 = (29)(0.278) = 8.06$; $P < 0.001$, implying a significant underdispersion. Thus, the high-density females produce precise sex ratios too.

DISCUSSION

The low and high predator densities reveal a difference in sex ratio and oviposition rate (Table 12.1), both of which are lower in the high-density treatment. The reason for the difference in oviposition rate between the two treatments is unclear. Why should a female produce fewer eggs when the density of conspecifics is high, and there is sufficient prey? This positive relationship between oviposition rate and sex ratio is frequently found in phytoseiids. Circumstances which cause a low oviposition rate, such as low temperature or low prey density, generally also result in low sex ratio (Sabelis and Nagelkerke, 1987). The adaptive importance of this has yet to be elucidated.

A lower sex ratio at high density confirms the results published in Sabelis (1985) and Sabelis and Nagelkerke (1987) for *T. occidentalis* and *Phytoseiulus persimilis* A.-H., and shows that phytoseiid females can control the proportion of daughters in their offspring in response to density. The difference in sex ratio is qualitatively in agreement with the theory on LMC but a quantitative test is, however, more complicated. The mean sex ratio of the high-density females after the first day is 0.539. The value predicted by Hamilton (1979) for haplo-diploids with maternal control and a group size of 10 females is 0.562, but before making an exact comparison some potential confounding factors have to be considered. The first is differential mortality between the sexes. Here, the procedure of sexing in the early egg stage and its high success rate ensures that this can be neglected. A further factor is that sex-allocation theory basically refers not to numbers but to the relative investment in the sexes in terms of resources. In *P. persimilis*, eggs destined to be female weigh about 15% more than eggs developing into males (Nagelkerke, Hofker and Sabelis, unpublished). If weight is a good indicator of investment, and ratios of egg weights of the sexes are similar throughout the Phytoseiidae, the expectation of the numerical sex ratio changes to 0.527. In a one-sample t test, this value is statistically indistinguishable from the one observed ($t_s = 1.231$, d.f. = 5, $P = 0.273$ (two tailed)).

The sex ratios show a considerable degree of precision. Taking the ratio between the observed variance and the expected binomial variance as a measure of precision, the observed ratios of the predatory mites can be compared with the values reported for parasitic wasps: 0.48 (*Goniozus emigratus* (Rohwer), Green *et al.* (1982)), 0.08 (*Goniozus legneri* Gordh, calculated from Gordh *et al.* (1983)), 0.25 (*Nesolynx albiclavus* (Kerrich), Putters and van den Assem (1985)), 0.41 (*Gryon atriscapus* Gahan, calculated from Waage (1982)) and 0.39 (*Trichogramma kalkae* Schulten and Feijen, calculated from Feijen and Schulten (1981)). A low ratio implies high precision. Thus, the two values of about 0.3 measured here for *T. occidentalis* indicate a degree of precision comparable to the highest reported for parasitic wasps.

As discussed in the introduction, precise sex ratios have a selective advantage over binomial sex ratios when mating takes place in finite groups. This advantage increases with decreasing group size and with increasing survival of the offspring until mating (Taylor and Sauer, 1980; Green *et al.*, 1982). Survival owes its influence to the supposed random nature of mortality, which diminishes existing precision. The effect of decreasing group size is due to the larger impact that variance in the number of males has in smaller groups. Group size here refers not only to the number of participating females but also to the absolute number of offspring each contributes.

Considering these factors of group size and survival, and given the observed precision, one may ask what is the magnitude of the fitness effect on the mites? As long as prey is sufficiently abundant, which is probably the case during the first stage of exploitation of a prey patch, survival of immature phytoseiids is high (± 90%; Sabelis, 1981). At least in this phase therefore, mortality will not reduce the importance of precision very much. Assessing the size of the mating group, and the number of offspring contributed by each participating female, is difficult. The models of the effect of precision assume that all matings take place within groups which are mutually completely separate. This situation is thought to exist in many parasitic wasps for the offspring arising from the eggs laid in one host or a clumped group of hosts (Waage, 1986). In phytoseiids the situation is more complicated; there, the partitioning between groups is probably rather diffuse, depending more on low mobility than on the 'hard' borders assumed in the described patch models.

Two important factors determining the size of the mating group are the way in which individual females distribute their eggs in relation to each other, and the movement of the progeny before mating. Female phytoseiids tend to avoid places with a high density of conspecific females, and places recently visited by other females (Sabelis, 1981 and

unpublished results). At high prey density, the dispersal of phytoseiids before first mating is very low (Nagelkerke, unpublished results), generally less than 1 cm. Thus it is probable that the size of the mating group is often small but not well defined. When considering the number of offspring contributed by each female, it should be realized that in the experiment described here the 'clutches' are designated according to the largely arbitrary interval of one day. So 'clutch size' is a rather artificial concept in this experiment and does not necessarily correspond to the size of the contribution of one female to a mating group. This contribution will depend on, among other things, the distance between the eggs of one female and also on the dispersal of the juveniles. The inter-egg distance under natural conditions is unknown. In the experiment, the females were confined to leaf discs of 5 cm^2, and were not allowed to distribute their eggs over a wider area. Due to these uncertainties, it is difficult to quantify the effect on fitness of the observed precision without further research on mating structure. However, the described subdivided population structure makes it a reasonable assumption that precision will often be advantageous; the degree will depend on conditions such as prey and predator density.

As explained above, the selective advantage of a given amount of precision is dependent on the size of the mating group. Assuming that the variance ratio is a good measure of the amount of precision, the high-density females had sex ratios which were at least as precise as those for the single females. This means that the degree of precision is not dependent on the supposed size of its selective advantage. Thus, the production of precise sex ratios probably will not have large costs associated with it. Precision could be an integral property of the mechanism of sex-ratio control. For example, if a female produces alternately one son and a fixed number of daughters, she is not only assured of precision (Waage, 1986) but obviously also, of a certain proportion of daughters. Hence a more or less deterministic sequence of son–daughter production may be an easy way of maintaining given sex ratio, with the resulting precision as an added consequence, beneficial under some circumstances and not harmful under others.

As yet nothing is known about the mechanism of paternal genome loss in the eggs. It requires the ability to recognize and eliminate the chromosomes of the father. Interestingly, the elimination only takes place after several mitotic cycles, and in many cells at the same time (Nelson-Rees *et al.*, 1980). The unravelling of the mechanism would be a fascinating endeavour.

It is concluded that phytoseiid females not only have the ability to regulate their sex ratio, but can also determine the sex of each individual egg with high precision. This is an additional argument in favour of

maternal control of sex determination, the existence of which can now be considered to be firmly established. The control seems as flexible as in arrhenotokous organisms. Thus, there is now good evidence that pseudo-arrhenotoky is not at a disadvantage compared to arrhenotoky with respect to the capacities for sex control that it gives to the mother.

APPENDIX

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Statistical Test for non-binomality in data with a large number of small clutches.

The dispersion test applied for testing homogeneity of k independent binomial distributed random variables $X_1, \ldots\ldots, X_k$ with common parameters n and p, where the probability p of a male is unknown, can be derived as follows:

As is well known the total number of males

$$s = \sum_{i=1}^{k} X_i$$

is a sufficient statistic. Hence, a test which is, essentially, a comparison of the estimated variance under the assumption of a binomial distribution, can be based on

$$\sum_{i=1}^{k} X_i^2 \text{ on the condition that } \sum_{i=1}^{k} X_i = s.$$

The conditional mean M and variance V of

$$\sum_{i=1}^{k} X_i^2$$

can be derived by using the joint conditional distribution of the X_i's, which is equal to

$$\left\{ \prod_{i=1}^{k} \binom{n}{X_i} \right\} \binom{kn}{s}^{-1} \tag{1}$$

We denote the ith conditional factorial moment

$$EX^{(i)} = E\{X(X-1) \ldots\ldots (X-i+1)\} \text{ by } \mu_{(i)}.$$

It follows from Equation (1) that

$$\mu_{(i)} = \frac{s^{(i)} \cdot n^{(i)}}{(kn)^{(i)}} \tag{2}$$

For the conditional expectation $\mu_{(i,j)}$ defined by $\mu_{(i,j)} = E\{X_u{}^{(i)} \cdot X_v{}^{(j)}\}$ $(u \neq v)$ it follows that

$$\mu_{(i,j)} = \frac{s^{(i+j)} \cdot n^{(i)}}{(kn)^{(i+j)}} \cdot n^{(j)} \tag{3}$$

where $a^{(i)} = a\ (a-1) \ldots\ldots (a-i+1)$.

By application of the fact that the conditional mean M of

$$\sum_{i=1}^{k} X_i^2$$

is equal to $\{k(\mu_{(2)} + \mu_{(1)})\}$ it is easy to show that

$$M = \frac{s\{s(n-1) + n(k-1)\}}{kn-1}. \tag{4}$$

Straightforward but tedious calculations show that the conditional variance V equals

$$k\{\mu_{(4)} + 6\mu_{(3)} + 7\mu_{(2)} + \mu_{(1)} + (k-1)\mu_{(2,2)} + 2(k-1)\mu_{(1,2)} + (k-1)\mu_{(1,1)} - k\,(\mu_{(2)} + \mu_{(1)})^2\} \tag{5}$$

Substitution of Equations (2) and (3) in Equation (5) results in

$$V = \frac{s^{(4)}(n-1)\{kn(n-1) - (4n-6)\}}{(kn-1)^{(3)}} + \frac{4s^{(3)}(n-1)^{(2)}}{(kn-1)^{(2)}} + \frac{2s^{(2)}(n-1)}{kn-1} - \frac{s^2(s-1)^2(n-1)^2}{(kn-1)^2} \tag{6}$$

The test statistic U defined by

$$U = \frac{\left(\sum_{i=1}^{k} X_i^2 - M\right)}{\sqrt{V}} \tag{7}$$

follows under the null hypothesis of homogeneity approximately a standard normal distribution provided that k is large enough and, unless k is large, n is not very small. This test is locally most powerful against

alternatives of under- or overdispersion. Large negative values indicate underdispersion, large positive values, overdispersion.

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13

Sex ratio, fitness and capacity for population increase in Pyemotes tritici *(L.-F. & M.) (Pyemotidae)*

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Laboratory studies were designed to assess the reproductive capacity of *Pyemotes tritici* (L.-F. & M.) reared on pupae of the Cigarette beetle, *Lasioderme serricorne* (F.). Data were obtained on sex ratio, daily rates of offspring emergence, male mating ability, fertility of females as a function of the order of mating and time interval between matings, and the effects of crowding during feeding. Females produced, on average, 254 offspring of which about 8% were males. In individual progenies, male emergence was 2 days earlier than that of females. Individual males mated with up to 57 females over a 3-day period, and the full complement of 25 males sired over 8500 daughters in their lifetimes. However, males were only fully potent for the first 15 matings after which the proportion of male offspring increased rapidly, and progeny number declined. Thus the sex ratio is strongly dependent on male mating history, and fecundity is enhanced by insemination. The very low proportion of males in average progenies was, nevertheless, sufficient to inseminate all female offspring. An increase in the length of time between matings enabled males to recover, to some degree, their ability to inseminate. The mean progeny numbers of crowded and uncrowded females did not differ but the variances and shapes of the frequency distributions were dissimilar. Using data from these studies the

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intrinsic rate of increase was found to be 0.63 with a population-doubling time of 1.1 days. The high rate of population growth suggests that *P. tritici*, in a favourable environment, is capable of exceeding the growth rate of any potential arthropod host. Additionally, mass-rearing conditions lead to mite populations with consistently high numbers of inseminated host-seeking females

INTRODUCTION

The straw itch mite, *Pyemotes tritici* (Lagrèze-Fossat and Montané 1851), has great potential as a biological-control agent because it is a cosmopolitan parasite of arthropods, causing immediate paralysis with its venom, and eventual death of the host (Bruce and LeCato, 1979, 1980). Its venom has been the focus of toxicological analysis (Tomalski *et al.*, 1988) and is currently the cynosure of genetic-engineering studies.

Pyemotes tritici is ovoviviparous with adult females and males emerging from a birth canal opening on the opisthosoma. Copulation occurs just outside the opening of the birth canal, and females are mated almost immediately. Females that escape mating neither disperse nor attach normally and cannot copulate later (Bruce, unpublished observation; Krczal 1959 for two other *Pyemotes* species). In addition, males assist in the birth of females, and greatly accelerate the rate at which births take place (unpublished observations; Moser *et al.*, 1971, for *P. parviscolyti* Cross and Moser). Reproduction is haplo-diploid and the sex ratio can be extremely female-biased, with 5% or fewer males in progenies. Bruce (1989), however, points out that the sex ratio for this species is more variable than the literature would suggest (for example, Stryker, 1966; Moser, 1975). Because information on male mating ability and the proportion of male progeny is currently very limited, the present study emphasizes sex ratio and factors that cause variation in the relative proportion of sons and daughters. Furthermore, mass-rearing projects related to either biological control or biotechnology must focus on the production of maximum numbers of inseminated host-seeking females. Only females disperse, parasitize and produce the extremely toxic venom. Thus, fundamental knowledge of the reproductive and population biology of these females under laboratory-rearing conditions is essential.

MATERIALS AND METHODS

Two studies were undertaken to characterize progeny emergence rates and male mating potential.

Study 1: progeny emergence

Stock cultures of *P. tritici* were maintained as in previous studies (Bruce and LeCato, 1980; Bruce, 1984). Gravid females were removed from these cultures one day before the emergence of the offspring, and placed on square arenas cut from black construction paper. An inner square-shaped arena was made with double-sided sticky tape to prevent the escape of the newly emerged offspring. The squares were kept in desiccators over a saturated-salt solution at 85% r.h. and 26 ± 1 °C. Mites that emerged were counted, sexed, and removed daily until all offspring had emerged or until each gravid female died.

Study 2: male mating potential

Gravid females were placed on filter-paper discs for observation of emergence. Emerging daughters were removed until the first son was born, after which all subsequent males were removed. This first male was allowed to mate with his sisters or was provided with newly emerged females from other gravid females as long as copulation appeared to have been completed (the male had disengaged). The mated females were removed, placed singly in glass tubes, and provided with a cigarette-beetle pupa (CBP) (*Lasioderma serricorne* (F.)) as a source of food. At the end of each day, all the surviving males and gravid females were placed individually in a glass tube (without CBP). All tubes were kept in desiccators at 26 ± 1 °C and 85% r.h. On the following day, each male was returned to the opisthosoma of the female it occupied the previous day to continue mating. Males which had emerged during the night were removed. This procedure was continued until the male ceased to copulate. On a number of occasions the newly emerged female would seemingly not tolerate the male and appeared to attack him. Such males were observed to die shortly thereafter.

The number of times a male copulated, and the time interval between copulations, were scored. Offspring which had emerged from the mated females were counted and their sex recorded. The sex ratio, expressed as proportion of males, was arcsin square-root transformed for statistical analysis.

RESULTS AND DISCUSSION

Study 1: progeny number, sex ratio and daily progeny emergence rates

The mean total offspring and proportion males produced by 126 gravid females are summarized in Table 13.1. Females produced, on average,

Table 13.1 Means and standard errors (in parentheses) of total offspring and proportion males in study 1 and 2. Study 2 data are presented as total study, and two subsets of total study (study 1, 126 females in stock cultures; study 2, 25 males; 447 females cultured singly)

	Study 1 *(average crowding)*	***Study 2*** *(no crowding)*		
		Total study	*Matings 1–3*	*Progenies with no daughters*
Number of matings	126	447	62	14
Total offspring	254.2[a] (4.3)	254.6[a] (4.2)	285. 0[b]) (11.5)	123.0[c] (23.8)
Proportion males	0.087[a] (0.01)	0.199[c] (0.01)	0.036[b] (0.03)	1.00[d] (0)

Superscripts with same letter are not significantly different in t tests at $P < 0.05$.

254 offspring of which about 9% were male. Thus, these parental females utilized about 232 sperm during their lifetime egg production. The mean duration of the period during which progeny emerged was 15.3 days (s.d. ± 0.5), with a maximum of 35 days. However, over half the daughters and 75% of sons were born by day 6 of the emergence period, and over 99% of the progeny had emerged by day 19 (Fig. 13.1). The rates of production of sons and daughters differed. Figure 13.1 shows the mean numbers of sons and daughters emerging per female per day expressed as percentages of the mean of total offspring per female for each sex. Males emerged proportionately much earlier, and with greater relative abundance than female offspring.

To compute the point in time of maximum emergence in the daily birth pattern for sons and daughters, a mode-day analysis was performed. A mode day represents the time of the most frequently occurring maximum number of sons or daughters, and is an average for the 126 progenies. The mode day for sons was 3.4 whereas emergence of daughters peaked 2 days later, with their mode at 5.4 days. In each of the 126 progenies, male mode day preceded female mode day. Furthermore, a disproportionately high number of first births were sons; of 124 progenies for which the precise early birth sequence was observed, 35.5% (44) of the first offspring were male while 64.5% (80) were female.

Figure 13.2 illustrates the proportion of offspring emerging daily over 19 days expressed as in Fig. 13.1. In addition it shows the number of males emerging each day expressed as a percentage of the mean total of males and females emerging on that day. As revealed by the mode-day

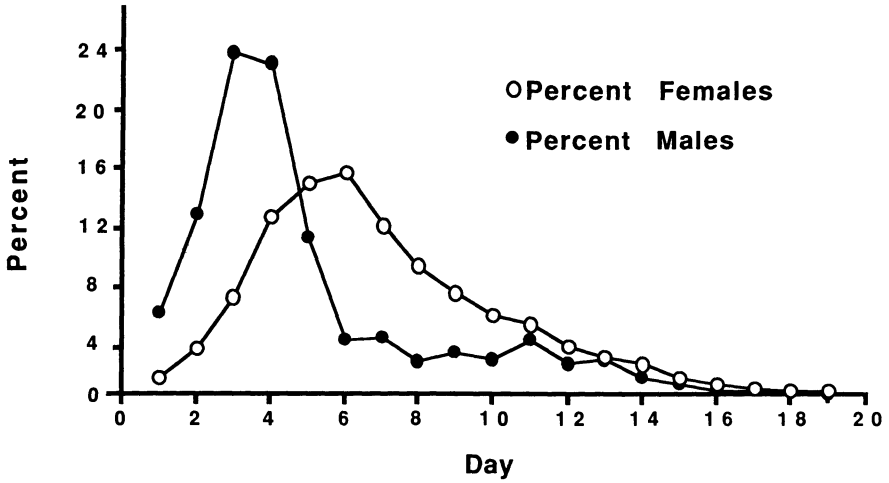

Fig. 13.1 Daily emergence of sons and daughters from 126 progenies in study 1 expressed as percentages of totals for each sex. Mean daily numbers are divided by mean total numbers of each sex and multiplied by 100. Although progeny emerged for up to 35 days, the figure is truncated at day 19 by which time 99.46% of all offspring had emerged.

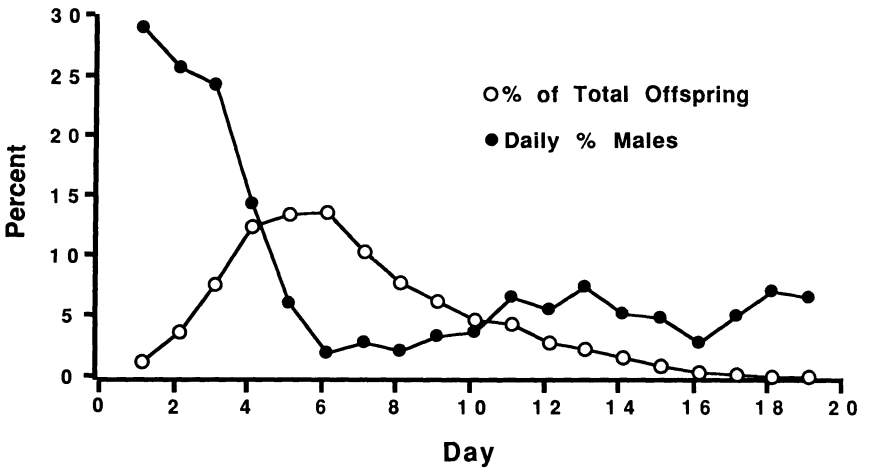

Fig. 13.2 Daily percentage males (mean number of males divided by mean number of offspring for each day, multiplied by 100) from 126 progenies in study 1, and percentage total offspring.

analysis and birth-sequence data, sons are relatively more common during the first four days of emergence than later on. During days of high offspring emergence (days 5–10), males are a small fraction of the daily total. As emergence continues past day 10, the proportion of offspring contributing to lifetime progeny numbers declines below 5% per day, while the proportion of males increases slightly.

Study 2: male mating ability

Twenty-five males mated a total of 559 females over a period of 3 days. Figure 13.3 shows the frequency distribution (consecutive order of mating) of these matings (filled columns). The unfilled columns show the same distribution for the 447 matings that were able to be scored for progeny number and sex ratio (results of 112 matings were lost due to technical difficulty). The range of matings per individual was five to a maximum of 57 times, with an average of 22.4 matings/male. The 25 males averaged 18.2 matings on day 1; a subset of six of these males averaged 16.0 matings on day 2, and one male survived to day 3 and mated seven times on that day.

The 447 matings, scored for progeny number and sex ratio, represented a mean of 16.4 matings per sire. The average mating produced 254.6 offspring of which 19.9% were sons (Table 13.1). Progeny number

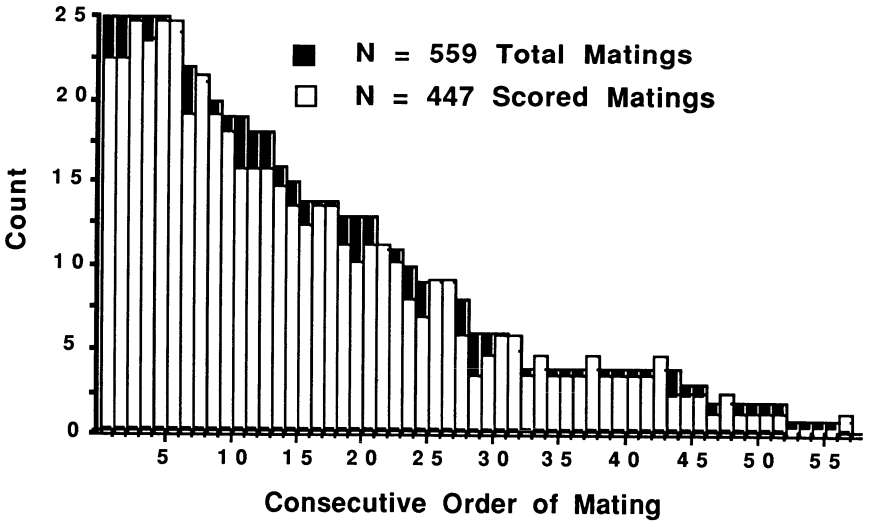

Fig. 13.3 Frequency distributions of number of matings in the lifetimes of 25 males in study 2. A total of 559 matings was observed (filled columns) of which 447 (unfilled columns) were able to be scored for numbers of sons and daughters.

was significantly higher on day 1 ($N = 374$ matings) than on day 2 ($N = 73$ matings) with means of 260.0 versus 227.4 offspring respectively (t test, $P < 0.01$). The proportion of males was significantly lower on day 1 than day 2 (0.141 versus 0.494, $P < 0.001$). Only the progeny (141 offspring, all male) of one mating was scored for the male that mated seven times on day 3, and this was not used in the comparisons.

The decline in progeny number and increase in sex ratio can be better analysed by linear regressions on mating order (the consecutive order of matings), which evaluate effects due to sequential mating. Figures 13.4 and 13.5 show, respectively, the regressions of proportion of males and total offspring on mating order. The proportion of males increases significantly with mating order ($N = 447$, $b = 0.016$, $P < 0.0001$, $r^2 = 0.46$). At the same time, total offspring decreases significantly with mating order ($N = 447$, $b = -1.29$, $P < 0.001$, $r^2 = 0.031$). The increase of sex ratio with mating order suggests that males become reproductively depleted and effectively 'run out of sperm'. The decrease of progeny number as the order of mating sequence increases, although statistically weaker, indicates that the order of mating *per se* affects fecundity.

The combined relationship between total offspring and sex ratio is illustrated in Fig. 13.6. Total offspring is set as the dependent variable, with proportion of males representing not only the measured sex ratio, but also as an indication of the quality of the insemination. The linear regression of this relationship is significant ($N = 447$, $b = -32.9$, $P <$

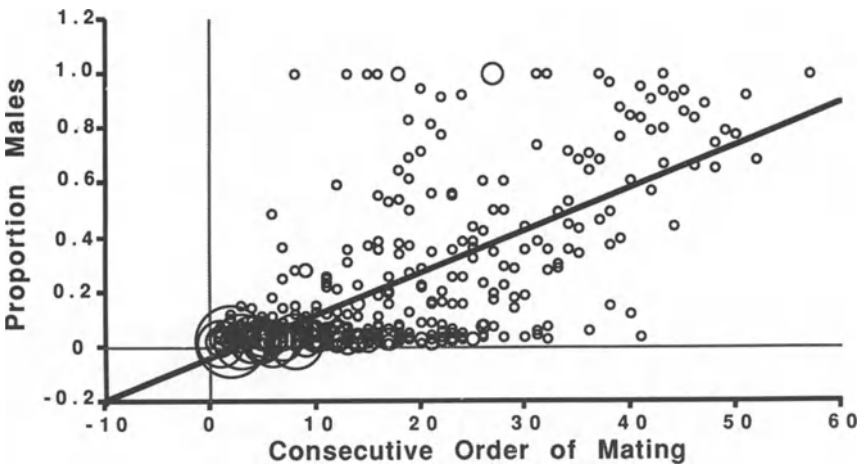

Fig. 13.4 Linear regression of proportion of male offspring in 447 progenies as a function of order of mating, that is, 1 . . . . n matings for each of the 25 males in study 2. Larger circles represent exactly overlapping data.

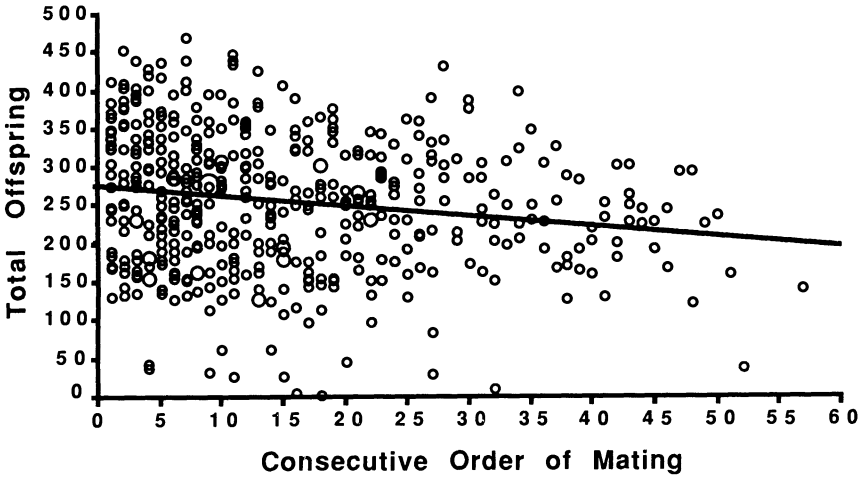

Fig. 13.5 Linear regression of total offspring in 447 progenies as a function of order of mating, that is, 1 . . . . *n* matings for each of 25 males in study 2. Larger circles represent exactly overlapping data.

0.03, $r^2 = 0.011$). Thus males becoming reproductively depleted sire progenies with fewer daughters, and their mates have reduced fecundity. Or, conversely, insemination enhances fecundity. Whether or not this statistical significance is paralleled by biological significance requires further study. Much of the unexplained variability in these linear analyses, as reflected in the low r^2, stems from males being rested overnight. There is also very large among-male variability. However, data presented by Boudreaux (1969), and by Wrensch and Young (1975), for two tetranychid species, show significantly lower fecundity in unmated females. A similar phenomenon has been observed with *Hypoaspis aculeifer* (G. & R. Can.) (P. Murphy, personal communication). Unlike *P. tritici*, female spider mites can mate later in life if they are initially uninseminated. After late insemination, a dramatic increase in fecundity is associated with the production of female offspring (Wrensch, unpublished observations; Boudreaux, 1969). These data were not interpreted as enhancement by these authors but the situation may be analogous to that reported here.

One particular objective of the present studies was to determine whether the characteristically small proportion of males observed in *P. tritici* progenies is sufficient fully to inseminate the relatively greater proportion of females. From the regression of proportion of males on mating number (Fig. 13.4) in study 2, it was found that, for the first 14 consecutive matings, males appear to be able to mate and inseminate

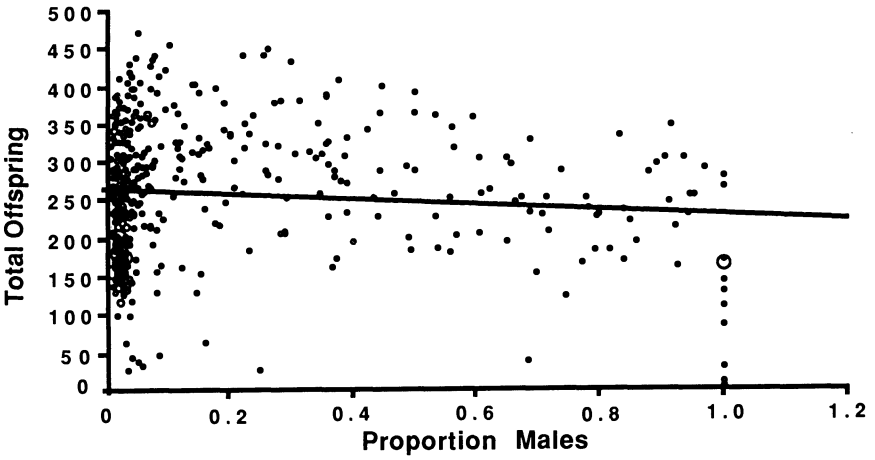

Fig. 13.6 Linear regression of total offspring as a function of proportion males in each of 447 progenies in study 2. Larger circles represent exactly overlapping data.

normally. The mean proportion of males is 0.059 and progeny number, with an average of 268.5, does not significantly decline over the mating sequence. These first 14 matings are, therefore, superior to those occurring in study 1. The mean number of males produced per female under mass-rearing conditions is 22 (study 1). If these 22 males mate 14 times, on average, then they should be able adequately to inseminate a total of 308 females. Since the average number of female progeny is 233 (study 1), then males in progenies with sex ratios averaging approximately 9% sons are more than competent to produce fully inseminated host-seeking females.

Effect of time interval between matings

The time intervals between 526 matings (overnight intervals excluded) averaged 15.0 minutes, but were very variable (s.d. 18.3) and non-normally distributed. Individual males had mean mating intervals ranging from 3.7 min (a male that mated seven times) to 23 min (a male that mated 10 times). This time interval (log-transformed) was positively correlated with sex ratio ($N = 421$, $r = 0.129$, $P < 0.01$) and significantly negatively correlated with progeny number ($r = -0.117$, $P < 0.05$). Thus, males – at least to some extent – have a tendency to recover their potency with rest. We expect that some of the unexplained variation here stems from occasional cases of technical difficulties in supplying

the males with newly emerged females, and thus artificially extending the time between matings. There was, however, no systematic error, and the relationships observed are probably valid.

Effects of mite crowding

The data in study 1 were obtained from females mated and fed to repletion under normal mass-rearing conditions. Numerous females attached to each beetle pupa. They were removed 6 days after attachment and isolated for progeny assessment. Females in study 2 fed to repletion in isolation with one female per pupa. Thus, the progeny-number and sex-ratio records from studies 1 and 2 are pseudo-replicates, with host crowding of feeding females a major contrasting variable.

Table 13.1 contains the results of statistical comparisons of the mean total offspring and sex ratios between studies 1 and 2. Mean total offspring of the 126 gravid females in study 1 is 254.2, and is not significantly different from that of the 447 females in Study 2, which averaged 254.6 offspring. The sex ratio was significantly higher in the total progenies in study 2 compared to study 1. However, if the first three matings of the study 2 sires are considered, the sex ratio of their progeny is significantly lower (0.036 male) compared to the mean of 0.087 in study 1. Thus fresh males, whose mates feed in isolation on a host, produce relatively more daughters than those in mass-rearing conditions. In addition, the progeny numbers of the females mated by these fresh males were significantly higher (285.0) than those of the mass-reared and crowded females in study 1. Furthermore, mean progeny number of the 14 matings from study 2 that produced no daughters is significantly lower. These are further indications that the quality of the mating enhances fecundity.

Although the means of total offspring in studies 1 and 2 do not differ significantly, the distributions are very different. Study 1 progenies exhibit a significantly leptokurtotic distribution compared to what is, essentially, a normal distribution in study 2. For mass-rearing purposes, as in study 1, progeny number is stabilized, the sex ratio is generally low, and thus optimal conditions for the production of large numbers of host-seeking females. The normal distribution of progeny numbers in study 2 reflects the incorporation of two extremes absent in study 1: females with small numbers of offspring deriving from inadequate inseminations by exhausted males, and those with unusually large progenies as a result of insemination by fresh males.

The relatively greater variance in progeny size of males that had mated repeatedly suggests that there may be a limit to the reduction in

sex ratio. Some matings in study 2 produced fewer than 2% males in progenies exceeding 350 offspring. These males, if otherwise normally potent, could be expected to mate with up to 14 sisters consecutively before becoming depleted. Clearly, some sisters will receive incomplete inseminations and produce relatively more sons. Some sisters will escape mating, and thus be unlikely to seek hosts, attach and reproduce. Both consequences would tend to slow the rate of colonization. If a founding female should produce such a low proportion of sons, then her colonizing episode might be less competitive than that of a female who initiated a colonizing episode with a less biased ratio. On the other hand, very low sex ratios would be less risky in established colonies, where many females were reproducing. The likelihood of brother–sister matings would decrease as males travelled about the virtually contiguous opisthosomal sacs seeking emerging females.

The optimal sex ratio must be a balance between the necessity to produce sufficient males to fully inseminate females – females do not disperse, host-seek, or feed as well unless mated – while simultaneously producing the highest proportion of daughters to disperse and found new colonies. *Pyemotes* species have the most consistently extreme sex-ratio bias and concomitant high fecundity observed in haplo-diploid organisms (Hamilton 1967), and thus have resolved the balancing problem uniquely. Perhaps accelerated development is a key to the extreme sex ratio, since females are usually assisted in the birth process by males, and males are immediately available for mating. This increased probability of mating may reduce selection for numbers of males, and permit the proportion of daughters to increase.

Factors influencing variation in sex ratio

Factors which caused variability in the sex ratio are important from the perspective of maximizing numbers of host-seeking females for biological-control purposes or supplying genetic-engineering experiments. These studies identify three features which contribute to sex-ratio variability: (1) crowding of female mites on hosts; (2) male mating history; and (3) time interval between matings. The sex ratio is correlated with fecundity, a relation we interpret as causal. It reflects the quality of insemination that females receive during mating, with fresher males transmitting more (or better) seminal fluid and sperm, and thus enhancing fecundity. Clearly, fecundity alone is not an adequate measure of colony fitness. These factors influencing sex ratio and fecundity, identified empirically, are probably of general importance to haplo-diploid animals.

Intrinsic rate of increase

The instantaneous rate of population increase can be estimated from the data obtained in study 1, and information on rate of development from Bruce (1984). Using the method of Lewontin (1965) as applied to haplo-diploid mites (Wrensch and Young, 1975), $r_m = 0.63$ (time in days) with a doubling time of 1.10 days. This is an extraordinarily high r_m, and, to our knowledge, exceeds that measured for any spanandrous micro-arthropod (for example, Hamilton, 1967; Sabelis, 1985) including that of *Pediculaster flechtmanni* (Wicht), (Cross and Kaliszewski, 1988). The latter authors used Birch's (1948) method of estimation to compute an r_m of 0.84; using their method – which we believe is inappropriate – we obtain from our data an r_m of 1.36. Our high value stems particularly from the rapid rate of development (4 days, adult to adult), the high fecundity and high proportion of daughters. *Pyemotes tritici* has a much higher rate of increase than any host for which it might be considered a biological-control agent.

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14

Preliminary observations of ovoviviparity in the gall-forming mite, Aceria caulobius *(Nal.) (Eriophyoidea: Eriophyidae)*

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A study has been conducted on the ovoviviparous behaviour of females of *Aceria caulobius* (Nal.), a gall-forming eriophyid mite living on the stems of *Suaeda fruticosa* Forsk. Galls were collected at 2-week intervals from September, 1987 to May, 1988, and dissected to obtain a sample of live mites for microscopic examination. Live migrating mites from the shoots were also examined. Ovoviviparity was observed in females recovered from the galls and, in some instances, nymphs or chorion residues within their bodies. It is possible that in the case of individuals containing chorion remnants, the nymph may have emerged through the mother's genital opening without harming her. The occurrence of females containing eggs in the cleavage phase indicates that embryonic development can commence within the female's body. No eggs were found in migrant females. No relationship has been established between ovoviviparity in *A. caulobius* and the density of the gall population, the growth of the galls or the migration of the eriophyids

INTRODUCTION

Eriophyid mites are usually oviparous: the females lay eggs in which embryonic development is still not discernible. Sometimes, however, the eggs may start to cleave, and an embryo may develop into a nymph which hatches inside the female's body. This particular reproductive behaviour has been reported in a number of species such as *Phytoptus*

avellanae Nal. (Nalepa, 1889), *Aculus uleae* Boczek and *Rhyncaphytoptus ulmivagrans* K. (Boczek, 1961), *Eriophyes laevis* (Nal.) (Shevtshenko, 1961), *Vasates quadripedes* Shimer and *Phyllocoptruta oleivora* (Ashmead) (Hall, 1967), *Eriophyes chondriphora* (K.) (Briones and McDaniel, 1976), *Aceria caulobius* (Nal.) (Nuzzaci, 1976) and *Aceria stefanii* (Nal.) (de Lillo, 1986). On the basis of these observations, eriophyids are considered to be, occasionally, ovoviviparous (Shevtshenko, 1961; Hall, 1967; Jeppson *et al.*, 1975) and occasionally viviparous (Boczek, 1972).

Several hypotheses have been proposed to explain this behaviour (Jeppson *et al.*, 1975) as follows: (1) the eggs do not move far enough towards the genital opening; (2) it may be a haphazard occurrence; and (3) the old females are unable to extrude the eggs. Unfortunately, the information at present available on embryonic development does not suffice to explain these mechanisms. In fact, no research with periodic observations of this reproductive behaviour on live eriophyid females has as yet been carried out. Up till now there have been few reports on this aspect, and there is a complete lack of field observations. In the present study, therefore, a gall-forming eriophyid species was examined at regular intervals for this reproductive behaviour in the field. The purposes of these observations were to establish the frequency of ovoviviparity, and to verify the possible relationship between ovoviviparity, the mite's life cycle and the host's phenology.

MATERIALS AND METHODS

The observations were carried out on *Aceria caulobius* (Nal.) (Eriophyidae: subfamily Eriophyinae), a species that induces marked gall formation on the shoots of *Suaeda fruticosa* Forsk. (Chenopodiaceae), which grows along the salt pan in the vicinity of Margherita di Savoia in southern Italy.

At two-week intervals, the galls were collected at random from September, 1987, when the small galls contained an adequate number of individuals (*c.* 100–200), to May, 1988, when the old galls had become completely lignified, and the eriophyids had completed their migration towards the apexes of the young shoots. Twelve galls were dissected at each sampling. Then, using a stereomicroscope, about 50 live specimens

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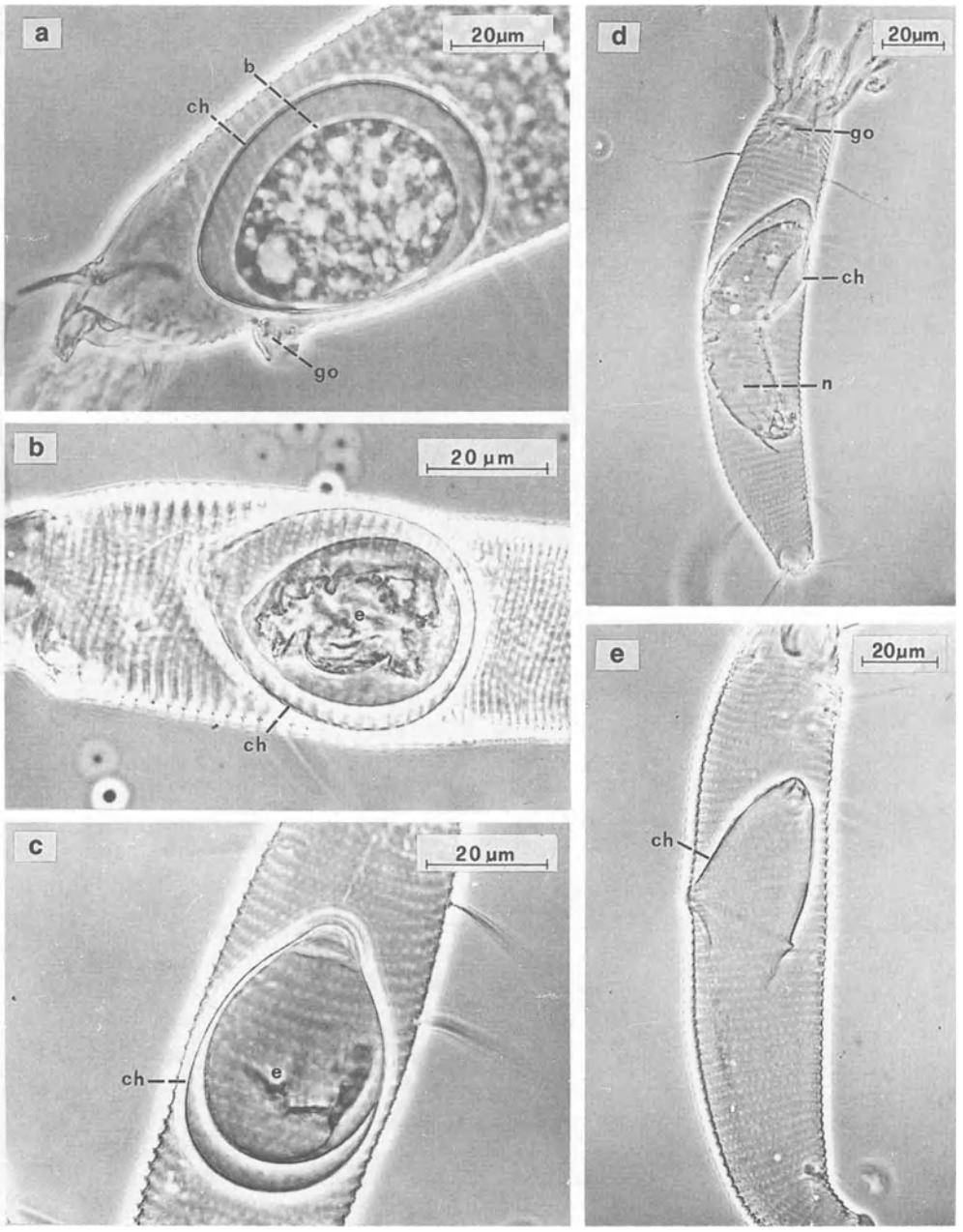
Fig. 14.1 Phase-contrast micrographs of reproducing females of the eriophyid mite, *Aceria caulobius* (Nal.). (*a*) Egg within body of mother with embryo in cleavage phase. (*b, c*) Embryo in later stages of development. (*d*) Hatching nymph ready to emerge from mother. (*e*) Ruptured and empty chorion within body of female. b, Blastoderm; ch, chorion; e, embryo; go, genital opening; n, nymph.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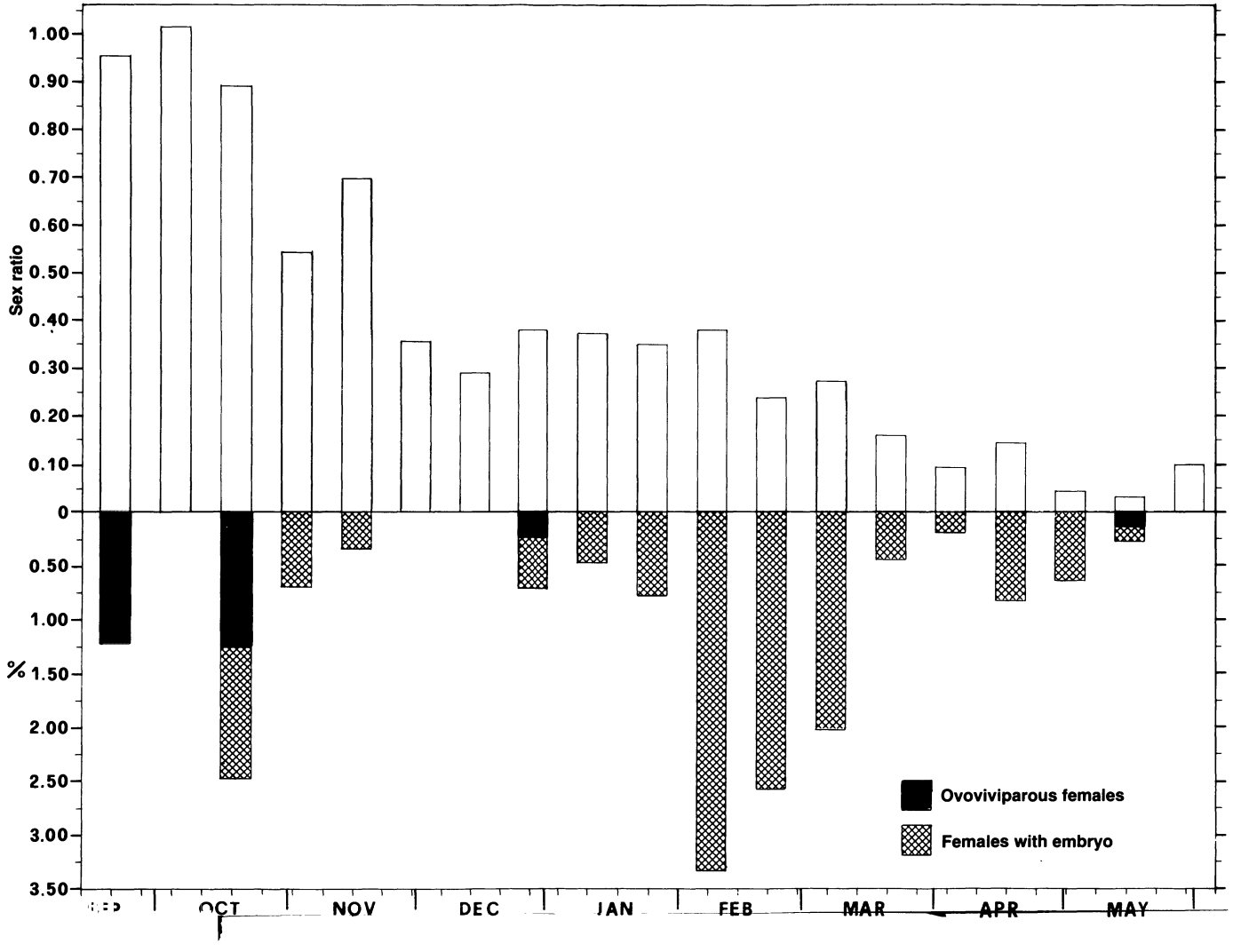
Sex ratio
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0.80
0.70
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0.50
0.40
0.30
0.20
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0
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1.00
1.50
2.00
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%
OCT
NOV
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MAY
Ovoviviparous females
Females with embryo

per gall were collected and mounted on slides using the usual technique. In addition, samples of live migrant mites were collected and mounted in the same way. The mounted eriophyids were studied under an optical phase-contrast microscope to count the males, pre-ovigerous, ovigerous and ovoviviparous females.

RESULTS

Inside the bodies of the live females within the galls, the following were found to occur in separate individuals: (1) eggs without an evident embryo; (2) eggs containing an embryo in the 'blastula' or subsequent phases; (3) a nymph and residues of its chorion; (4) the residues of the chorion.

The egg in cleavage activity (Fig. 14.1*a*) is characterized by an outer transparent zone and a very thin membrane surrounding the embryo, which appears to be a blastoderm or other embryonic envelope. The egg is enclosed in an evident chorion (Fig. 14.1*a*). The transparent portion, the size of which varies depending on the degree of embryonic development, first becomes visible on the anterior pole of the egg and, eventually, it encloses the whole embryo (Fig. 14.1*b*,*c*). There were only 0.76% females in this stage with respect to the total number of females, reaching a maximum during the initial phase of the female's migration. Migration usually reaches a maximum in early summer. Sometimes the chorion ruptures at the posterior pole of the egg, and a nymph hatches inside the female's body (Fig. 14.1*d*). This nymph is directed towards the mother's anal lobes, and the chorion residues envelop the nymph's anal region as described in previous reports. When only the residues of the chorion were found inside the female's body (Fig. 14.1*e*), this was taken as an indication of nymphal hatching.

The course of ovoviviparous behaviour was irregular (Fig. 14.2). In fact, it was observed that very few females (0.09% of the total number of females) contained hatched nymphs or chorion residues inside their bodies. The migrant females (99.4% of the migrant mites, the rest being males) did not have eggs, nymphs or chorion residues inside their bodies. During the investigation it was observed that there was: (1) a constant decrease in the sex ratio (number of males divided by number of females) of the mite population living in the galls (Fig. 14.2); (2) a constant growth and lignification of the galls; (3) the presence of migrants outside the galls from February to May, 1988; and (4) the appearance of new, small soft galls in May, 1988.

Fig. 14.2 Percentage of females of *Aceria caulobius* from galls on *Suaeda fruticosa* reproducing ovoviviparously and those having eggs with embryos. The sex ratio is number of males divided by number of females.

DISCUSSION AND CONCLUSIONS

During the growth of the galls, which occurs actively from November to April, ovoviviparity was irregular and rare in females living within the galls (Fig. 14.2). The empty broken chorion present within a few entire females, suggests that the females might bring forth some nymphs as do those of *Proctolaelaps nauphoetae* (Womersley) (Mesostigmata: Ascidae). In the latter species, the caudal end of the larva emerges first from the mother's genital opening (Egan and Hunter, 1975). The eriophyid nymph might emerge in a similar manner without harming the mother.

Some females were found to contain eggs in the cleavage phase, which indicates that embryonic development may also commence within the female's body. This phenomenon reached its maximum during the initial phase of the female's migration. This might indicate that a decrease in the duration of embryonic development may hasten population increase and facilitate migration. Migrant females, on the contrary, are not ovigerous, and it is thus impossible to observe ovoviviparity in them; in fact, young pre-ovigerous females are the most active stage for dispersal.

It was not possible to establish any relationship between ovoviviparity and environmental or biological factors. As a matter of fact, the variable density of the mite population living in the galls, the growth and constant lignification of the galls, and the migration of the eriophyids do not seem to influence the reproductive behaviour in nature. However, a constant decrease in the sex ratio was observed in relation to gall growth and lignification, and to the female's migration. Ovoviviparity should be tested in the laboratory, as has been done with the macrochelid mites (Filipponi and Mosna, 1969) where feeding appears to be the factor with the greatest influence. In fact, fasting appears to increase the incidence of ovoviviparity. With such an approach it should be possible to obtain a better understanding of the factors involved. However, at present there are many technical difficulties in rearing most species of Eriophyidae in the laboratory.

ACKNOWLEDGEMENT

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Laboratory observations on duration of copulation and egg production of three Phytoseiid species fed on pollen

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The influence of the duration of copulation on egg production was studied in three phytoseiid mites, *Typhlodromus exhilaratus* Ragusa, *Amblyseius californicus* (McGregor) and *A. cucumeris* (Oud.), cultured in the laboratory at 25 ± 1°C, 70 ± 10% r.h. and an LD 16 : 8 hour photoperiod, using *Carpobrotus* sp. pollen as food. The average durations for the first copulation were 243, 351 and 380 min for *T. exhilaratus*, *A. californicus* and *A. cucumeris* respectively. In all three species, artificial curtailment of copulation to half or quarter the average duration resulted in reductions in the percentage of reproducing females, fecundity, oviposition duration and the proportion of females in the progeny. The degree of these effects differed in the three species being greatest for *A. cucumeris* in which copulation took the longest time. The number and size of the endospermatophores do not appear to be correlatable with the total number of eggs produced or the commencement of oviposition

INTRODUCTION

The importance of the Phytoseiidae as natural enemies of various phytophagous mites is now universally recognized (Huffaker *et al.*, 1969; McMurtry *et al.*, 1970; McMurtry, 1982). However, in spite of the increase in knowledge of these predators, many of their biological features still remain to be clarified. Among these is that related to reproductive strategies, an aspect of considerable importance for the

ecological success of these species. Although data on mating behaviour are available for a number of species (Herbert, 1956; Dosse, 1959; El-Badry and Zaher, 1961; Elbadry and Elbenhawy, 1968; Zaher and Shehata, 1971), direct investigations of the influence on oviposition of the quantity of sperm transferred have been made only for *Phytoseiulus persimilis* Athias-Henriot, *Amblyseius bibens* Blommers, *Amblyseius andersoni* (Chant), *Amblyseius potentillae* (Garman), *Typhlodromus pyri* Scheuten (Amano and Chant, 1978; Schulten *et al.*, 1978; Overmeer *et al.*, 1982).

At present, part of our research is concerned with the reproductive behaviour of some of the most common phytoseiids in the Italian agricultural environment (Castagnoli and Liguori, 1986a; Ragusa and Paoletti, 1985). In the context of this research, some of the preliminary data are presented regarding *Typhlodromus exhilaratus* Ragusa, *Amblyseius californicus* (McGregor) and *A. cucumeris* (Oud.).

MATERIALS AND METHODS

Research has been carried out on individuals fed on *Carpobrotus* sp. pollen, in culture units consisting of an aluminium disc surrounded by a film of water, and placed in a thermostatically controlled incubator at 25 ± 1 °C, 70 ± 10% r.h. and an L : D regime of 16 : 8 hours. A full description of the experimental procedure is given in Castagnoli and Liguori (1986*b*,*c*).

For the experiment, we used individuals from strains which have been cultured in our laboratory for 2–3 years on a mixed diet of various pollens and *Tetranychus urticae* (Koch). The original sources of *Typhlodromus exhilaratus* were Chianti vineyards (Castelnuovo Berardenga, Siena); *Amblyseius californicus* and *A. cucumeris* were obtained from greenhouse crops of beans, *Phaseolus vulgaris* (L.), near Florence.

Eggs of each species were isolated from the stock cultures to obtain males and females that had been fed only on *Carpobrotus* sp. When adult, a male was transferred to each of the cultures containing a single female in order that copulation could take place. They were left together for the time necessary for complete copulation, or separated artificially at shorter time intervals (about a half and a quarter of the average duration for copulation). Copulation was considered to commence when the two sexes were in a venter-to-venter position, and the average duration to complete copulation was determined in preliminary tests (Table 15.1). In the main experiment, there were three treatments: removal of the male when copulation was completed referred to as 'normal' copulation, and curtailed copulation where the male was removed after the elapse of quarter or half the average time for normal copulation. Some females

Table 15.1 Mean duration in minutes of a single copulation in three species of Phytoseiidae

	Typhlodromus exhilaratus	*Amblyseius californicus*	*Amblyseius cucumeris*
Mean	243	351	380
Range	221–300	280–408	280–540

were killed and mounted in Hoyer's medium for microscopic observation of the spermathecae and the endospermatophores. The diameters of the vesicle of the spermathecae and of the globular part of the endospermatophore were measured. Each of the remaining females was separated from its male and fed on *Carpobrotus* sp. pollen. They were examined daily during the whole of the oviposition period. The eggs produced were then, in their turn, isolated and the progeny of each female closely followed to determine the sex. The sex ratio, expressed as the ratio of males to females, was calculated from the individuals which reached the adult stage.

RESULTS

In the three species studied, the male was observed to be strongly attracted to the moulting female deuteronymph. When the male is transferred to the arena of a young female, it explores the new territory methodically with circular movements, starting at the edge, and the actual meeting of the two sexes appears to be casual. This may occur immediately or after some hours. The mating behaviour follows the same pattern as that described for other *Typhlodromus* and *Amblyseius* species (Amano and Chant, 1978; Schulten *et al.*, 1978; Overmeer *et al.*, 1982). The initial contact, when the male approaches the female with the palps and the first pair of legs, can occur indifferently from the front, the side or from the rear. The other preliminary phases are rapid and constant: the male climbs on to the female's dorsum, initially with the gnathosoma in the same direction as that of the female, then he turns through an angle of 180° to place himself in the venter-to-venter copulating position. In all three species, the male tends to fill first one spermatheca, showing no preference for left or right, and then the other. Table 15.1 gives the mean and range for copulation duration in the three species. Table 15.2 gives the number and size of the endospermatophores for normal and curtailed copulation for each species.

Table 15.2 Number and mean diameter (± s.d.) of endospermatophores in relation tc normal and curtailed copulation in three species of Phytoseiidae (No pairs of means differ significantly (*t* test, $P > 0.05$))

Species	*Copulation duration*	*Endospermatophores*			
		Females examined	*Number per spermatheca*	*Endosper. examined*	*Mean diameter (μm)*
Typhlodromus exhilaratus	Normal	6	1 + 1	12	16.80 ± 1.56
	1/2 normal	2	1 + 1	9	15.02 ± 3.21
		5	1 + 0		
	1/4 normal	7	1 + 0	7	15.42 ± 0.76
Amblyseius californicus	Normal	6	1 + 1	10	22.80 ± 4.20
		3	1 + 0		
	1/2 normal	5	1 + 0	7	23.89 ± 3.80
		1	1 + 1		
	1/4 normal	5	1 + 0	5	22.08 ± 4.50
Amblyseius cucumeris	Normal	8	1 + 1	15	24.09 ± 2.76
	1/2 normal	3	1 + 0	6	23.90 ± 2.29
		2	1 + 1		
	1/4 normal	4	1 + 0	3	23.00 ± 0.86
	♂ ♀ contact 24 h	6	1 + 2	10	22.30 ± 2.00
		1	1 + 3		

Typhlodromus exhilaratus

With this species in the conditions described, copulation lasts about 4 h. The females, examined microscopically (Table 15.2), showed two inflated spermathecae, with a vesicle diameter of *c.* 29.53 μm, and in each, an endospermatophore of *d* 16–19 μm. Apart from two instances where 3 and 6 eggs were laid in 3 and 8 days respectively, the total number of eggs per female ranged from 21 to 30, and the number of days for oviposition from 13 to 19. Thus, during this period, each female produced an average of 1.53 eggs per day, and the male/female ratio was 1 : 1.97 (Table 15.3).

When the copulation duration was artificially reduced by half, in five of the seven females examined, only one spermatheca had an endospermatophore while the other was hardly ever even inflated. In the remaining two individuals, however, both spermathecae were inseminated just as in females with normal copulation. The endospermatophores appeared slightly smaller (mean *d* 15.02 μm). Only 72.7% of these females oviposited and they produced about half the number of eggs in comparison with normal copulation, in an oviposition duration which

Table 15.3 The effect of normal and curtailed copulation on oviposition duration, fecundity, rate of egg production and sex ratio of progeny for three species of Phytoseiidae cultured at 25 °C with *Carpobrotus* pollen as food

Species	*Copulation duration*	*Females*		*Oviposition data (means ± s.d.)*			
		Total	*Ovipositing (number)*	*Duration (days)*	*Eggs/female*	*Eggs/female/day*	*Sex ratio progeny (♂ : ♀)*
Typhlodromus exhilaratus	Normal	12	12	13.41 ± 4.64	21.16 ± 8.07	1.53 ± 0.20	1 : 1.97
	1/2 normal	11	8	8.75 ± 2.12	11.87 ± 3.52	1.34 ± 0.12	1 : 1.33
	1/4 normal	12	5	3.42 ± 2.51	3.20 ± 2.28	1.04 ± 0.08	1 : 1.16
Amblyseius californicus	Normal	11	8	19.25 ± 9.11	23.62 ± 10.44	1.26 ± 0.39	1 : 1.95
	1/2 normal	11	4	14.00 ± 1.41	21.25 ± 2.06	1.51 ± 0.06	1 : 1.44
	1/4 normal	6	2	5.50 ± 0.70	10.50 ± 3.53	1.85 ± 0.35	1 : 1.00
Amblyseius cucumeris	Normal	8	7	16.85 ± 5.39	21.00 ± 7.43	1.22 ± 0.31	1 : 1.84
	1/2 normal	7	1	5	3	0.6	1 : 0.50
	1/4 normal	7	—	—	—	—	—
	♂ ♀ contact 24 h	6	5	25.00 ± 12.10	32.00 ± 11.26	1.34 ± 0.39	1 : 1.91

never exceeded 10 d. The average number of eggs per day per female fell to 1.34, and the sex ratio of the progeny was 1 : 1.33 (Table 15.3). With a 60-min copulation duration, that is, a quarter of normal, only one endospermatophore was present in the seven females examined. However, the percentage of those producing eggs fell to 41.66%, and the fecundity was very low (1–6 per female) over an oviposition period of not more than 6 days. On the other hand, neither the rate of egg production (1.04 eggs/female/day) nor the sex ratio (1 : 1.16) differed from the other curtailed copulation treatment. The sizes of the endospermatophores did not differ significantly in the three treatments. Postembryonic mortality was about 15%.

Amblyseius californicus

For this species the average duration of copulation is *c.* 6 h, with a range of 280–408 min. With normal copulation each spermatheca contained an endospermatophore in six of the nine females examined while the other three females had only one, and with these, the second spermatheca did not even appear to be inflated. The diameter of the vesicle of the spermatheca was 27–35 μm, and that of the endospermatophores, 16–27 μm. Just under three-quarters of the females oviposited, and the total number of eggs per female varied considerably having a range of 7–36 with oviposition durations of 6–32 days. The egg-production rate was 1.26 eggs/female/day, and the sex ratio, 1 : 1.95 (Table 15.3).

With a halved copulation time, only 36% of the females oviposited, despite the presence of an endospermatophore in one of the two spermathecae in five of the six females examined, and the sixth female had an endospermatophore in each spermatheca. The fecundity of the few females which oviposited was slightly lower than with normal copulation, and the duration of oviposition was shorter; the ratio between the sexes was 1 : 1.44.

With a 90-minute copulation time (one quarter of normal), the proportion of females producing eggs is practically the same, while the total number of eggs is further reduced, as is the oviposition period, and the progeny sex ratio is 1 : 1. In the five females examined there was only one endospermatophore present in one of the two spermathecae. Postembryonic mortality in the three treatments was about 30%.

Amblyseius cucumeris

The duration of the first copulation in this species was very variable but on average lasted a little more than 6 h (Table 15.1). In the eight females examined, one endospermatophore of *d* 20–27 μm was present in each

spermatheca, and the diameter of the vesicle was *c.* 37 μm. In this test, 87.5% of the females produced 5–26 eggs in 7–25 days, with an average daily egg production of 1.22 eggs per female. The progeny sex ratio was 1 : 1.84 (Table 15.3).

With a three-hour copulation period (half normal copulation), only one of seven females oviposited producing three eggs in 5 days. In two of the five females examined, both spermathecae had an endospermatophore and, in the other three individuals, at least one spermatheca appeared to be inseminated. When copulation was reduced to *c.* 1.5 h, no eggs were produced despite the fact that the four females examined microscopically had a reasonable-sized endospermatophore (*c.* 23 μm) in one spermatheca. In further tests, no oviposition was recorded when the 3-hour copulation duration was reduced by 30 min.

During the experiment, it was observed that *A. cucumeris* – unlike the other two species – after an interval of a few minutes, frequently copulated for a second time. This second copulation lasted for a shorter time (2–4 h). In the majority of the females left with the male for 24 hours, and consequently presumably with at least two copulations, a second endospermatophore was present in one of the two spermathecae and more rarely a third (Table 15.1). However, not even in this situation did all the females produce eggs. The total number of eggs ranged between 15 and 43, and the oviposition period lasted 15–46 days. The rate of oviposition appears slightly higher (1.34 eggs/female/day), and the sex ratio favoured the females (Table 15.3). The post-embryonic mortality recorded for this species during the experiment was *c.* 30%.

DISCUSSION

All three species have average copulation times (Table 15.1) comparable to those recorded for other phytoseiids. The duration recorded for *A. cucumeris* is the longest and the most variable, and exceeds that recorded for this species when fed on *Tetranychus cinnabarinus* (Boisd.) (El-Badry and Zaher, 1961). In spite of this, it tends to mate again immediately after the first copulation, thus further increasing egg production.

As has already been shown for other phytoseiids (Schulten, 1985), and also for *T. exhilaratus*, *A. californicus* and *A. cucumeris*, artificial curtailment of copulation results in reductions in the percentage of females producing eggs, fecundity, and the number of female progeny. This is particularly evident with *T. exhilaratus* where reduced copulation durations appear almost proportional to total egg production and the duration of oviposition. In the other two species, the extreme variability of the data obtained, and the higher mortality in postembryonic stages may be accounted for not only by the reduced copulation time, but also

perhaps by an additional adverse effect due to the food used. In fact, females of *A. californicus* and *A. cucumeris* which, with curtailed copulation, had not produced eggs for over a month, unexpectedly began to oviposit after a few days when fed on *T. urticae*.

The number and size of the endospermatophores observed in the microscopically examined females can hardly ever be directly correlated with the data obtained on oviposition. Under the conditions of the experiment, although the presence of an endospermatophore, the size of which did not differ significantly from those observed in the case of normal insemination (Table 15.2), did not always ensure the beginning of oviposition. Thus the physiological mechanism which induces egg production appears to be rather complex, and further experiments are needed to clarify the relationship between the duration of copulation, the quantity of sperm transferred, and the quality and quantity of food to be used. A comparison of these data and those of a further experiment at present in progress, using *T. urticae* which is a more suitable food source for all three species, may provide a more useful evaluation of these relationships.

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Precopulatory mate guarding in the spider mite, Tetranychus cinnabarinus *(Boisd.) (Tetranychidae)*

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ABSTRACT

In spider mites, males compete for access to females. Fertilization is restricted to a brief period after the eclosion of the female. The first male to copulate is usually the most successful (Helle, 1967). To enhance their probability of mating, males commence guarding females before they eclose, that is, female deutonymphs. At 27 °C the deutonymphal stage lasts on average 40 h. Precopulatory mate guarding starts, at the earliest, 20 h before a female's eclosion. To maximize reproductive success, a male should only guard large females as fecundity is positively correlated with female size (Mitchell, 1973). Given that large males are more likely than small ones to succeed in contests over females (Potter *et al.*, 1976), these males should monopolize large females, and force small males to guard small females. Under these conditions, one would expect to observe size-assortative mating. Alternatively, a male should minimize the time investment per female. Spider-mite males can distinguish the lengths of time individual females will take to reach maturation (Everson and Addicott, 1982). If a male selects the more mature female to guard, he will save guarding time and thereby maximize the number of females he inseminates during his reproductive lifespan.

Data were collected from a field population of *Tetranychus cinnabarinus* (Boisd.) on violets (*Viola odorata* L.) at Montpellier in the south of France, in 1986 and 1987. The analysis provided evidence that (1) assortative

mating for size does not hold for these spider mites; and (2) time minimization is practised by spider-mite males.

In contrast to Everson and Addicott (1982), not only the density of deutonymphs but also the operational sex ratio, that is, the number of males to the number of males and females, and male body size, are important factors influencing the duration of precopulatory mate guarding by male spider mites.

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· PART THREE ·

Diapause, Development and Trophic Relations

17

*Physiological aspects of diapause in plant-inhabiting mites**

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The spider mite, *Tetranychus urticae* Koch and the phytoseiid predatory mite, *Amblyseius potentillae* (Garman), both exhibit a facultative reproductive diapause, which is expressed in females only. Profound similarities of a qualitative nature were found in the responses to photoperiod of these two species, which might indicate the presence of a common physiological basis for the photoperiodic induction of diapause.

Dietary studies showed that vitamin A is essential for photoperiodic induction in both species of mite. The exact function of vitamin A has not yet been established; it is not inconceivable, however, that vitamin A or a derivative of vitamin A, serves as photoreceptor pigment for the photoperiodic clock. Although light is important for photoperiodic induction since no diapause is found in constant darkness, it could be shown that it is essentially the night length which is being measured by the photoperiodic clock in both species. The sensitivity to short light interruptions of the dark phase also revealed characteristic similarities; two points of light sensitivity were found, one in the beginning and one towards the end of the night, in both the spider mite and the predatory mite. So-called resonance experiments demonstrated a circadian influence on the photoperiodic response in each mite, albeit much more pronounced in the spider mite. A further similarity was encountered in the way in which photoperiodic information, contained in a sequence of long-night cycles, is accumulated by the photoperiodic 'counter' mechanism.

However, apart from these similarities, certain differences were found, the most important of which concerns the reaction of the two species to temperature. Whereas daily fluctuating temperatures (thermoperiods) in-

* Invited paper.

duced diapause in *A. potentillae* in the complete absence of light, no such thermoperiodic response could be detected in *T. urticae*.

Some striking similarities could be demonstrated between the photoperiodic and thermoperiodic response mechanisms. The thermoperiodic-response curve determined for *A. potentillae* appeared to be closely similar to the photoperiodic-response curve. The summation of thermoperiodic cycles occurred in a similar fashion as demonstrated earlier for photoperiodic cycles. Another similarity between the thermoperiodic and photoperiodic mechanism was found in the fact that vitamin A is also essential for the thermoperiodic response. The possibility of the existence of a common basic mechanism for photoperiodic induction in arthropods is discussed

INTRODUCTION

Most work on diapause in terrestrial arthropods, with respect to both its ecological and physiological aspects, has been done with insects, and many of the current concepts of photoperiodism have been developed with insects as the main test objects. Nevertheless, the study of the same phenomena in mites has contributed much to our general understanding of diapause and its photoperiodic and temperature control mechanisms. In this respect the pioneering work of Lees (1950, 1953a, b), Bondarenko (1950, 1958), Geispitz (1960, 1968) and Cranham (1972) should be mentioned. Certain aspects which may have general significance for photoperiodism in arthropods, such as the need for vitamin A, have even been discovered in mites first, and only later have they been shown to be valid also for insects (Veerman *et al.*, 1983, 1985).

This chapter gives a short review of present knowledge of photoperiodic induction of diapause in two species of plant-inhabiting mites, the spider mite, *Tetranychus urticae* Koch and the phytoseiid predatory mites, *Amblyseius potentillae* (Garman). Both species exhibit a facultative reproductive diapause in the females only, induced by short-day photoperiods experienced during the pre-imaginal stages (Veerman, 1977; van Zon *et al.*, 1981). Emphasis will be laid on the similarities as well as the differences in response to photoperiod and temperature between both species, and comparisons are made with the responses of insects in similar experiments.

MATERIALS AND METHODS

The experiments were done with Dutch strains of the spider mite, *T. urticae* and the predatory mite, *A. potentillae*. The spider-mite strain has been kept in the laboratory since 1961. The mites were reared on bean plants (*Phaseolus vulgaris* L.) under long-day illumination (17 h light : 7 h darkness, (LD 17 : 7)). For the experiments, the mites were kept on

detached-leaf cultures of beans. Criteria for diapause in *T. urticae* have been described by Veerman (1977, 1985).

The strain of *A. potentillae* has been maintained in the laboratory since 1977 on plastic rearing units under long-day illumination (LD 16 : 8) as described by Overmeer and van Zon (1983). The mites were fed on pollen of either the broad bean, *Vicia faba* L., or the ice plant, *Dorotheanthus bellidiformis*, each of which were equivalent to live prey as regards development and reproduction of the predaceous mites. For experiments on diapause, the *Vicia* pollen was enriched with 5 mg of β-carotene (Merck, synthetic, crystalline) per 100 g of pollen (cf. Overmeer and van Zon, 1983). The diapause characteristics of *A. potentillae* have been described by van Houten *et al.* (1988).

Experiments with both mite species were done in photoperiod- and thermoperiod-controlled incubators. Temperatures were maintained within ± 0.5 °C. Light : dark regimes were set by electronic timers. For experimental details see Veerman and Vaz Nunes (1987) and van Houten *et al.* (1988). The term photoperiod is used to denote the complete cycle of light and dark, the constituent phases of light and darkness being referred to as photophase and scotophase, respectively. Similarly, thermoperiod means a temperature cycle consisting of warm (thermophase) and cool (cryophase) phases.

RESULTS AND DISCUSSION

Functional involvement of carotenoids and vitamin A

Photoperiodic induction is a light-dependent process, which presupposes the presence of a photoreceptor pigment absorbing the appropriate wavelengths of visible light. The first indications that carotenoids might be functionally involved in photoperiodic induction of diapause came from genetic studies with several pigment mutants of the spider mite, *T. urticae*. It was shown that the lowered diapause incidence found in the albino mutant was caused by lack of β-carotene (Veerman and Helle, 1978; Veerman, 1980).

More direct evidence for the involvement of carotenoids in the photoperiodic response came from feeding experiments with the predatory mite, *A. potentillae*. When these mites were reared for two generations solely on eggs of the albino strain of *T. urticae*, short days failed to induce diapause whereas predators fed on eggs of the wild-type strain of the spider mite entered diapause normally in response to the short-day regime (van Zon *et al.*, 1981). When *A. potentillae* was reared for two or more generations on broad-bean pollen as its sole source of food, the short-day response was also found to be absent. But, as shown in Table

Table 17.1 Diapause incidence (%) in *Amblyseius potentillae* (Garman) females using diets with and without carotenoids or vitamin A (data from Veerman *et al.*, 1983)

Pigment supplement	*LD, light:dark cycle (hours)*			
	LD 8:16		*LD 16:8*	
	%	*Total tested*	%	*Total tested*
None	0	48	0	33
β-Carotene	98	147	0	127
3-Hydroxyechinenone (rac)	100	103	2	60
Astaxanthin (rac)	0	44	0	33
Vitamin A acetate	100	167	1	137
Vitamin A acid	4	131	1	140

17.1, addition of either β-carotene, 3-hydroxyechinenone or vitamin A to the pollen diet led to the induction of full diapause under the short-day regime whereas the addition of astaxanthin or vitamin A acid was without effect (Veerman *et al.*, 1983). The results show that vitamin A or carotenoids, which may serve as precursors of vitamin A, are essential for the induction of diapause, and suggest that vitamin A or a derivative of vitamin A may function as photoreceptor for the photoperiodic response in these mites.

Similar results have since been obtained in feeding experiments with two insect species, the parasitoid wasp, *Apanteles glomeratus* (L.) (Veerman *et al.*, 1985), and the silkworm, *Bombyx mori* L. (Hasegawa and Shimizu, 1988), which might indicate a general need for vitamin A in the photoperiodic mechanism of mites and insects. In feeding experiments with the spider mite, *T. urticae*, using a semisynthetic liquid diet (van der Geest *et al.*, 1983), it has been shown that the addition of vitamin A to the diet also restored the photoperiodic response in the albino strain of the spider mite (Bosse and Veerman, unpublished results).

Absence of diapause incidence in mites fed on a diet of *Vicia* pollen, and restoration of the photoperiodic response after addition of β-carotene, could also be demonstrated for another phytoseiid predator, *Amblyseius cucumeris* (Oud.) (Table 17.2). There was a quite different result when pollen of the ice plant was the food source. Here there was 97–100% diapause incidence with *A. potentillae* and *A. cucumeris*. This finding might be explained on the basis that the two pollen species differed in their carotenoid content. This was confirmed by comparative chemical analysis of pollen of the broad bean and the ice plant, which showed that the amount of β-carotene in the latter pollen was about 30 times greater than that found in broad-bean pollen (Table 17.3).

Table 17.2 Influence of pollen diets on incidence of diapause in three species of predatory phytoseiid mites under short (LD 8 : 16) and long days (LD 16 : 8) at 18 °C (data from Overmeer *et al.*, 1989)

Pollen diet	*Diapause*			
	LD 8 : 16		*LD 16 : 8*	
	%	*Total tested*	%	*Total tested*
Amblyseius potentillae (Garman)				
Vicia	3	449	0	> 150
Dorotheanthus	97	251	0	> 150
Amblyseius cucumeris (Oud.)				
Vicia	3	67	0	> 150
Vicia pollen + β-carotene	100	51	0	> 150
Dorotheanthus	100	252	0	> 150
Typhlodromus pyri Scheuten				
Vicia	100	526	0	> 150
Dorotheanthus	100	288	0	> 150

The effect of the above diets on the photoperiodic reaction of a third species of predatory mite, *Typhlodromus pyri* Scheuten (Table 17.2), was unexpected. It appeared that the photoperiodic response of this species was unaffected by the diets used, full diapause being found under short-day photoperiods in mites fed on pollen of either plant species. This might indicate that the photoperiodic response in *T. pyri* is not dependent on carotenoid but other explanations are possible. For instance, the broad-bean pollen is not completely devoid of carotenoids (Table 17.3), and it is not inconceivable that *T. pyri* is able to utilize the minute amounts of β-carotene present (Overmeer *et al.*, 1989). Although the need for carotenoids has now been demonstrated in mites as well as insects, it may be too early yet for generalizations to be made concerning their indispensability, especially since nothing is known about the

Table 17.3 Carotenoid content of pollen (μg/mg dry weight) of two plant species used as food for *Amblyseius potentillae* (data from Overmeer *et al.*, 1989)

	β-carotene	*Lutein-esters*
Vicia faba	0.26	absent
Dorotheanthus bellidiformis	8.5	large amounts present

Table 17.4 Thermoperiodic induction of diapause in *Amblyseius potentillae* reared on diets with and without β-carotene or vitamin A (data from van Houten *et al.*, 1987)

Diet supplement	*Temperature regime*							
	15 °C constant		*27 °C constant*		*16 h (15 °C) : 8 h (27 °C)*		*16 h (27 °C) : 8 h (15 °C)*	
					Diapause incidence			
	%	*Total tested*	%	*Total tested*	%	*Total tested*	%	*Total tested*
None	0	70	0	67	5	226	0	109
β-Carotene	16	113	0	88	100	139	0	70
Vitamin A acetate	20	105	0	124	99	130	14	117
Test generation none, maternal generation vitamin A acetate	1	98	1	115	99	87	4	106

physiological function of carotenoids or retinoids in the photoperiodic mechanism.

Another finding is that carotenoids or vitamin A are also necessary for thermoperiodic induction of diapause in *A. potentillae*, by which is meant the induction of diapause by daily fluctuating temperatures in the complete absence of light (van Houten *et al.*, 1987). This thermoperiodic response is discussed in more detail in a later section. Table 17.4 shows that a daily temperature cycle consisting of a 16-h cold phase (15 °C) and 8-h warm phase (27 °C) (a 'short-day' thermoperiodic regime) is capable of inducing full diapause in *A. potentillae*, but only in mites reared on a diet of *Vicia* pollen supplemented with either β-carotene or vitamin A. The same response was found when only the maternal generation received vitamin A, which indicates that minute amounts of vitamin A present in the eggs are sufficient to elicit the thermoperiodic response later in life. No response or only a low incidence of diapause was found under a 'long-day' thermoperiodic regime or under constant temperatures (Table 17.4).

The fact that vitamin A appears to be necessary for both photoperiodic and thermoperiodic induction of diapause in *A. potentillae* could mean that the vitamin functions in both a photoreceptor and a thermoreceptor involved in diapause induction in these mites, or in a photoreceptor which functions equally well as a thermoreceptor. However, it is also conceivable that vitamin A (or a derivative of vitamin A) is not operative in the receptor *sensu stricto* but is involved in a more central part of the induction mechanism. Experiments have shown that the presence of vitamin A is required during the sensitive stages, and not just at the time of expression of the photoperiodic or thermoperiodic response, which indicates that vitamin A is indeed involved in the induction process itself (van Houten and Veerman, 1990). However, at present the question of the exact function of vitamin A in the photoperiodic mechanism is still unanswered.

Effect of photoperiod

One of the most intriguing questions in the field of photoperiodism concerns the way in which organisms are able to discern a 'long' day from a 'short' day or, in other words, the way in which photoperiodic time measurement is accomplished. In most insects and mites that have been investigated, long days lead to uninterrupted development and/or reproduction, and short days to the incidence of diapause. The effect of different day lengths on diapause induction in *T. urticae* – expressed as a photoperiodic response curve – is shown in Fig. 17.1. It is a typical long-day response, with full diapause induced over a range of short day

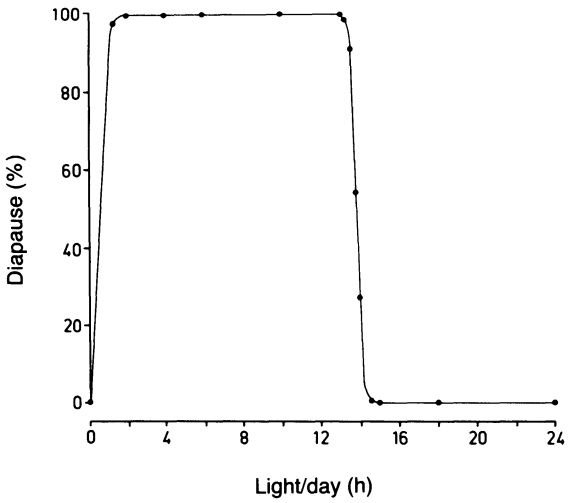

Fig. 17.1 Effect of photoperiod on incidence of diapause in *Tetranychus urticae* Koch (data from Veerman, 1977).

lengths, no diapause under long daylengths, and a sharp transition in between, the so-called critical daylength. Quite characteristic, not only for the spider mite but also for many insects, is the sharp drop in diapause incidence which occurs at the left-hand extreme of the curve (cf. Veerman, 1977). An almost identical response curve was obtained for the predatory mite, *A. potentillae* (solid line, Fig. 17.8), which shows that photoperiodic time measurement occurs with about equal accuracy in both mite species.

The above response curves do not present information about the way the photoperiodic clock works. A first indication of the operation of the clock is gained from the experiment shown in Table 17.5, which presents the effect of all four combinations of a long (16 h) and a short (8 h) photophase with a long (16 h) and a short (8 h) scotophase. The results show that it is essentially the night length that is being measured by the photoperiodic clock in both species of mites. Nevertheless, light plays an important role in the photoperiodic induction of diapause since no diapause is observed in mites reared in continuous darkness (Figs 17.1 and 17.8). In view of these results the terms, short-night and long-night regime, and critical night length, seem more appropriate than the commonly used terms, long-day and short-day regime and critical day length (cf. Veerman and Vaz Nunes, 1987).

Various techniques have been developed to analyse the kinetics of the

Table 17.5 Effect of various combinations of 'long' and 'short' photophases and scotophases on diapause induction in *Tetranychus urticae* and *Amblyseius potentillae* (Garman)

Light : dark regime (h)	*Tetranychus urticae* *Diapause (%)*	*Amblyseius potentillae* *Diapause (%)*
16 : 8	0	0
8 : 16	100	93
16 : 16	100	97
8 : 8	0	5

photoperiodic clock, one of the most frequently used being the light-break technique in which the scotophase of a long-night regime is systematically probed with short interruptions of light. Figure 17.2 shows the response curve obtained with 1-h light interruptions 'scanning' the night of an LD 10:14 cycle in *T. urticae*. Two zones of sensitivity to the light-breaks were observed, one in the beginning of the night and one towards the end. These peaks of light sensitivity, called the

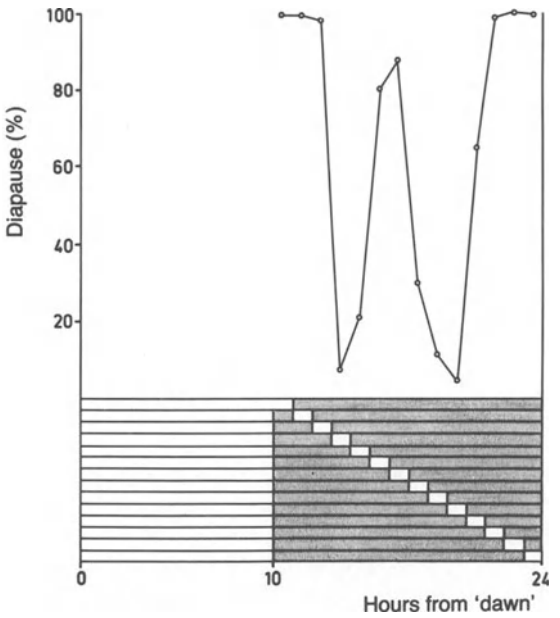

Fig. 17.2 Effect on diapause incidence in *Tetranychus urticae* of 1-hour light interruptions 'scanning' the night of light-dark (h) (LD 10:14) regime (data from Veerman, 1977).

A-peak and B-peak, respectively (Saunders, 1982) have also been observed in a number of insect species. A similar response curve has recently been obtained for the predatory mite, *A. potentillae* (van Houten, unpublished results). Notwithstanding these striking similarities in light-break experiments with mites and insects, different explanations have been offered, either based on the concept that the photoperiodic clock is a circadian oscillator (Pittendrigh, 1966; Saunders, 1982) or on the concept that the clock is a non-repetitive timer or hour-glass clock (Lees, 1973; Vaz Nunes and Veerman, 1982, 1984). Clearly, these results in themselves are not sufficient proof of the rhythmic or non-rhythmic nature of the photoperiodic clock (cf. Pittendrigh, 1981; Saunders, 1982; Veerman and Vaz Nunes, 1984a).

The experimental technique which is used most frequently to investigate whether the circadian system is involved in a photoperiodic response is the so-called T experiment or resonance experiment. Resonance experiments consist of light–dark cycles with a constant photophase of, for instance, 12 h, and a scotophase which is varied from about 4 to about 70 h, in a number of repetitions of the experiment. Total cycle lengths, therefore, may differ considerably from 24 h. Figure 17.3 shows the results of a resonance experiment with a constant light phase of 8 h with the spider mite, *T. urticae*. The results clearly show that the incidence of diapause is a rhythmic function of the duration of darkness. Peaks of high diapause incidence recur with total cycle lengths (L + D) of about 24, 44, 64 and 84 h. The conclusion of this experiment, therefore, is that circadian rhythmicity is involved in the photoperiodic determination of diapause in the spider mite. The circadian rhythm involved appears to have a rather short free-run period of about 20 h (Veerman and Vaz Nunes, 1980).

The responses of *T. urticae* were next determined in a large series of resonance experiments with constant photophases of 1, 2, 4, 8, 12, 16, 20 and 24 h. The response curves obtained revealed four to five maxima and minima of diapause incidence, with peak-to-peak intervals of about 20 h (Vaz Nunes and Veerman, 1986a). The results of these separate resonance experiments were then redrawn in the form of an 'extended circadian surface' (Fig. 17.4), showing diapause 'mountains' in the form of long 'ridges' running parallel to lights-off. The form and position of these ridges of high diapause appear to be largely independent of the duration of the light phase; instead they are determined entirely by the duration of the dark phase, appearing at mutual distances of about 20 h in the night. The conclusion from these experiments, therefore, is that photoperiodic induction of diapause in *T. urticae* is influenced by a 'dusk' oscillator, that is, a circadian oscillator which starts running at the transition from light to dark.

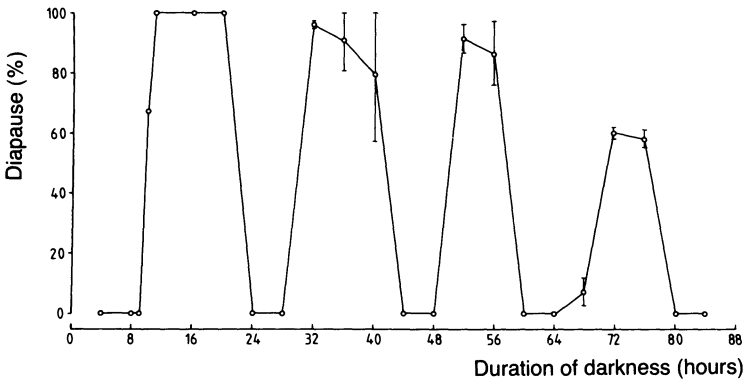

Fig. 17.3 Diapause incidence in *Tetranychus urticae* in cycles of 8 hours of light and (abscissa) different durations of darkness. Vertical lines represent ±1 s.e. of mean (data from Veerman and Vaz Nunes, 1980).

A resonance experiment carried out with *A. potentillae*, with a constant photophase of 12 h, showed a weak rhythmic response with two diapause maxima and minima (van Houten, unpublished results). Although the rhythmic effects are not as clear-cut as in *T. urticae*, the outcome of these experiments shows that the circadian system is somehow involved in the photoperiodic response of both mite species. Similar results have been found with some, though not with all, insects tested (for a review see Vaz Nunes and Veerman, 1986a).

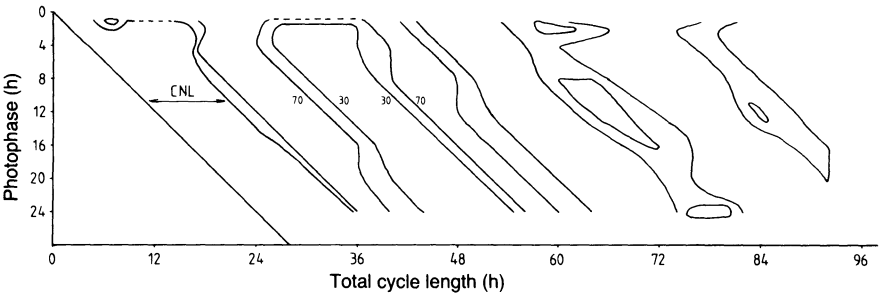

Fig. 17.4 'Extended circadian surface' for diapause induction in *Tetranychus urticae*, constructed from data of eight resonance experiments with constant photophases of respectively 1, 2, 4, 8, 12, 16, 20 and 24 hours. Points of equal diapause induction have been joined to form 'iso-induction contours', only two of which have been drawn: one on 70% diapause level and one on 30% level. Length of photophase is shown to left as a 'light-wedge'. CNL, critical night length. (Data form Vaz Nunes and Veerman, 1986a.)

The finding of rhythmic responses in resonance experiments has generally been interpreted as evidence for the circadian nature of the photoperiodic clock itself (for example, Pittendrigh, 1981; Saunders, 1982). However, an alternative interpretation of the data has been given by Vaz Nunes and Veerman (1982, 1986a) who hypothesized that the clock might be a non-rhythmic or hour-glass timer measuring night length, the rhythmic responses found being caused by a more or less strong modulating influence exerted by the circadian system on the expression of the photoperiodic response in certain unnatural light–dark regimes. Thus the high incidence of diapause observed in resonance experiments when the period of the light–dark cycle is close to 24, 48 or 72 h is the result of unimpaired long-night accumulation in cycles where the circadian system can entrain to the natural solar day or multiples thereof, whereas the low incidence of diapause in cycles close to 36, 60 or 84 h reflects severe disruption of entrainment (Vaz Nunes and Veerman, 1982; Veerman and Vaz Nunes, 1984a,b).

According to the oscillator-clock hypothesis, the photoperiodic clock is a circadian oscillator, which resets itself in periods of prolonged darkness. The successive peaks of high diapause incidence found in certain resonance experiments (cf. Fig. 17.3) would, according to this hypothesis, represent subsequent acts of time measurement by the oscillator clock. The question about the repetitive or non-repetitive character of the photoperiodic clock could be investigated further by making use of the way in which repeated acts of time measurement are processed by the photoperiodic mechanism.

It has been known for a long time that diapause induction in mites and insects requires a number of long-night cycles, the exact number being dependent on the species or population. This has led to the concept of a photoperiodic 'counter' (for review see Saunders, 1982), a mechanism which adds up and integrates the output of the photoperiodic clock over a sequence of light : dark cycles. Figure 17.5 shows some aspects of this phenomenon of cycle summation in the spider mite, *T. urticae*. When sequences of 1–7 long-night cycles were given while the mites were kept in constant darkness during the remainder of their developmental period, diapause incidence was found to rise in proportion to the number of long-night cycles experienced by the mites. A minimal number of three cycles around day 4 of the sensitive period (during the protonymphal stage) was sufficient to induce diapause in half the population of mites; more than 90% diapause was attained with seven long-night cycles. The increase in percentage diapause with the number of long nights experienced implies an underlying distribution of diapause thresholds among individuals of the population (Veerman and Vaz Nunes, 1987).

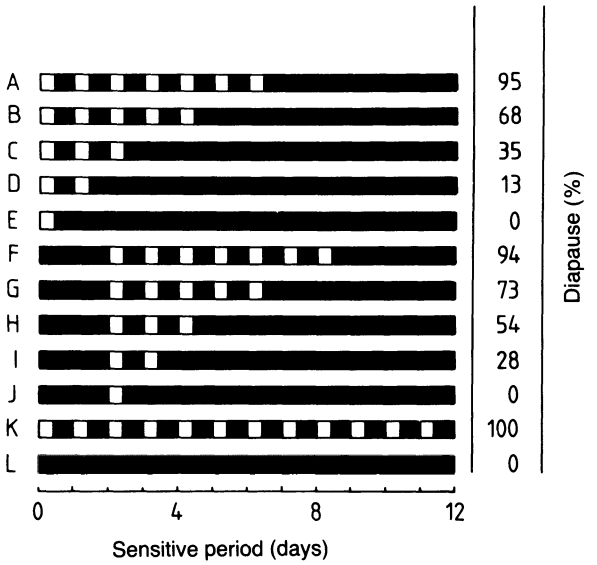

Fig. 17.5 Diapause incidence in *Tetranychus urticae* in response to 1–12 (A–L) long-night cycles (LD 10:14); the mites were kept in continuous darkness during remainder of their development (data from Veerman and Vaz Nunes, 1987).

Based on this principle of the additive effect of long-night cycles, a test was devised which discriminates between single and repeated night length measurements, and thus between clocks operating according to hour-glass or oscillator kinetics (Veerman and Vaz Nunes, 1987). The essential difference between both clock types is that an hour-glass executes a single act of time measurement, even in experimentally extended nights, and requires a period of light to prepare the mechanism for another act of time measurement, whereas an oscillator clock resets itself in extended dark phases and repeats itself with circadian periodicity. An hour-glass clock would, therefore, 'read' nights of 12 and 36 h long as just one long night. An oscillator clock, on the other hand, would be expected to reset itself within the longer night, and perform two acts of time measurement during the 36-h night, against only one during the 12-h night. Thus, sequences of equal numbers of 12-h and 36-h nights (in the regimes, LD 12:12 and LD 12:36, respectively) would be expected to have about equal inductive 'strength' in the case of non-repetitive or hour-glass time measurement, whereas a series of 36-h nights would be expected to be about twice as inductive as the same number of 12-h nights, if the clock were a self-sustained oscillator. Differences in the kinetics of night-length measurement between an

hour-glass and an oscillator clock in constant darkness (DD) and in cycles of LD 12 : 12 and LD 12 : 36 are shown schematically in Fig. 17.6.

The outcome of experiments to test this model with *T. urticae* is presented in Fig. 17.7. The inductive effect of four, six and eight LD 12 : 12 cycles (C, F, K, N and P) was compared with that of, respectively, two, three and four cycles of LD 12 : 36 (B, E, J, M and O). In each pair of experiments the light : dark sequences were applied during the same

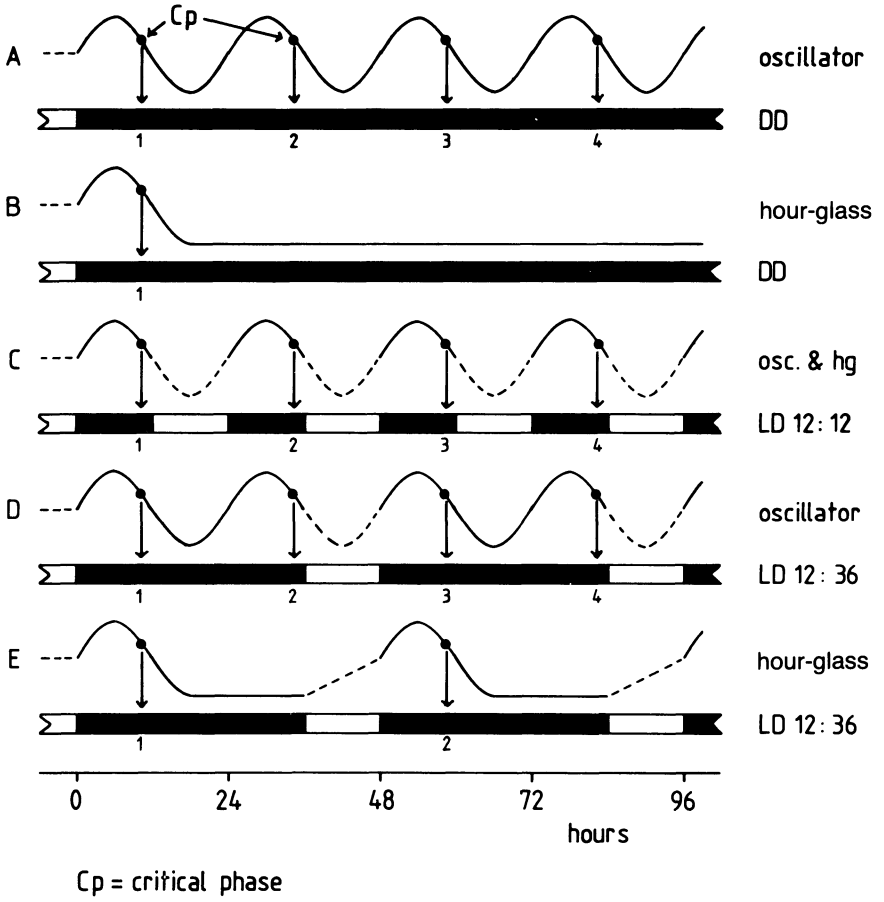

Fig. 17.6 Model presentation showing the difference in kinetics between a photoperiodic clock based on oscillator concept and one based on hour-glass concept. Clocks based on oscillator principle would perform two acts of time measurement in nights, 36 h long, against only one measurement by hour-glass clock. Consequently, an oscillator clock would count twice as many 'inductive events' during the same number of LD 12:36 cycles, as hour-glass clock (data from Veerman and Vaz Nunes, 1987).

section of the sensitive period; for the remainder of their development the mites were kept in darkness. The controls (experiments Q and R) show that both regimes (LD 12 : 12 and LD 12 : 36) result in 100% diapause when applied throughout the sensitive period.

The results (Fig. 17.7) show that, with the exception of the experimental pair O and P, for each pair, diapause incidence in the LD 12 : 36 regime is only half or even less than half the diapause incidence in the LD 12 : 12 regime. The regimes for O and P, however, are nearly saturated, which may explain the deviating results. The results show that nights, 36 h long, are not measured twice by the photoperiodic clock in *T. urticae*. This means that the spider mite's clock is not a self-sustained circadian oscillator, and probably not even a damped oscillator. To be recognizable as an oscillator, it should have performed at least two consecutive acts of time measurement in prolonged darkness; it is more probably a non-repetitive or hour-glass timer (Veerman and Vaz Nunes, 1987).

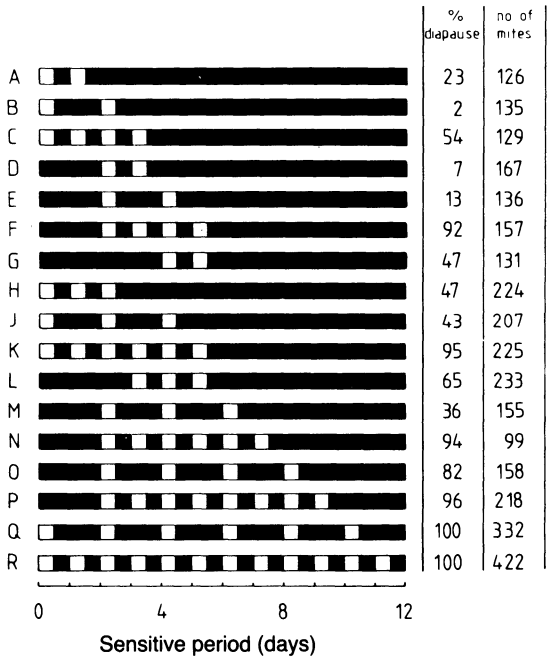

Fig. 17.7 Experimental test of model presented in Fig. 17.6 to compare effect on diapause incidence in *Tetranychus urticae* of various sequences of LD 12:12 and LD 12:36 (A–R) applied during corresponding days of sensitive period (data from Veerman and Vaz Nunes, 1987).

These experiments have not yet been done with the predatory mite, *A. potentillae*, but results similar to those reported here for the spider mite have been obtained recently for some species of insects (Saunders and Lewis, 1988; Veerman *et al.*, 1988). The outcome of the experiments shows that the photoperiodic clock in the insect and mite species studied is not a self-sustained oscillator, which means that the subsequent diapause peaks found in resonance experiments with these species are not the expression of repeated acts of time measurement by an oscillator clock. These results, however, are in accordance with the alternative hypothesis, based on the concept of 'resonance', proposed by Vaz Nunes and Veerman (1982, 1986a) and briefly discussed above.

Effect of temperature

Induction of diapause in mites and insects is not only controlled by photoperiod but also by temperature. Although in most cases the effect of photoperiod is predominant, the effect of temperature is important and complex. A common temperature effect in long-day species is the suppression of diapause induction at higher temperatures. This was observed in both *T. urticae* (Table 17.6) and *A. potentillae* (Table 17.7). This effect of a gradual lowering of diapause incidence at progressively higher temperatures might be caused either by a general temperature sensitivity of the photoperiodic mechanism (a direct effect of temperature), or by a decrease in the number of inductive cycles experienced by the mites during their sensitive period, which becomes progressively shorter with increasing temperature (an indirect effect of temperature). This question was solved by exposing the mites to an LD 12 : 12 photoperiod in combination with a thermoperiod consisting of a 12 h warm phase and a 12 h cool phase (experiments nos 4 and 5, Tables 17.6 and 17.7). In both mite species, full diapause was found when the cool phase coincided with the dark phase, but no diapause occurred under the reversed conditions. These results show that scotophase temperature is of much greater importance for diapause induction than photophase temperature, and that the suppression of diapause induction by higher temperatures is a direct effect of temperature on the photoperiodic mechanism.

Another important question is whether temperature is of significance in these mites as a signal factor on its own, capable of inducing diapause independent of photoperiod. This effect of temperature, that is, the induction of diapause by daily fluctuating temperatures in the complete absence of light, has been observed in only a few insect species (for review see van Houten *et al.*, 1988). When these experiments were done with the spider mite, *T. urticae*, using a thermoperiod with a 12 h warm

Table 17.6 Effect on diapause induction in *Tetranychus urticae* of a thermoperiod (°C) in combination with a photoperiod or in continuous darkness (data from Veerman, 1977)

Experiment no.	*Regime*	*Diapause %*	*Total tested*
1	LD 12 : 12, 15°	100	199
2	LD 12 : 12, 20°	95	316
3	LD 12 : 12, 25°	0	548
4	LD 12 : 12, TC 12 : 12 (25° : 15°)	98	524
5	LD 12 : 12, TC 12 : 12 (15° : 25°)	1	529
6	DD, 20°	0	425
7	DD, TC 12 : 12 (25° : 15°)	2	302

LD, light-dark cycle; DD, constant dark; TC, thermoperiodic cycle, *e.g.* TC 12 : 12 (25° : 15°) is a thermoperiod with 12-hour thermophase of 25 °C and 12-hour cryophase of 15 °C.

phase of 25 °C and a 12-h cold phase of 15 °C, no trace of a thermoperiodic response was found (experiment no. 7, Table 17.6). However, a strong thermoperiodic response was obtained when the experiment was repeated with the predatory mite, *A. potentillae* (experiment no. 7, Table 17.7), with only low percentages of diapause found in the controls (different constant temperatures of 15–27 °C in continuous darkness) (experiment nos 8–11, Table 17.7). These results show that a thermoperiod can act as an inductive factor in its own right for diapause induction in *A. potentillae*, but not in *T. urticae*.

Table 17.7 Incidence of diapause in *Amblyseius potentillae* exposed to various thermophotoperiods (°C) (data from van Houten *et al.*, 1988)

Experiment no.	*Regime*	*Diapause %*	*Total tested*
1	LD 12 : 12, 15°	100	146
2	LD 12 : 12, 21°	99	432
3	LD 12 : 12, 27°	2	337
4	LD 12 : 12, TC 12 : 12 (27° : 15°)	100	331
5	LD 12 : 12, TC 12 : 12 (15° : 27°)	0	552
6	LL, TC 12 : 12 (27° : 15°)	0	138
7	DD, TC 12 : 12 (27° : 15°)	73	214
8	DD, 15°	29	212
9	DD, 19°	11	356
10	DD, 21°	1	219
11	DD, 27°	0	118

LD, light-dark cycle; DD, constant dark; LL, constant light, TC, thermoperiodic cycle, *e.g.* TC 12 : 12 (27° : 15°) is a thermoperiod with 12-hour thermophase of 27 °C and 12-hour cryophase of 15 °C.

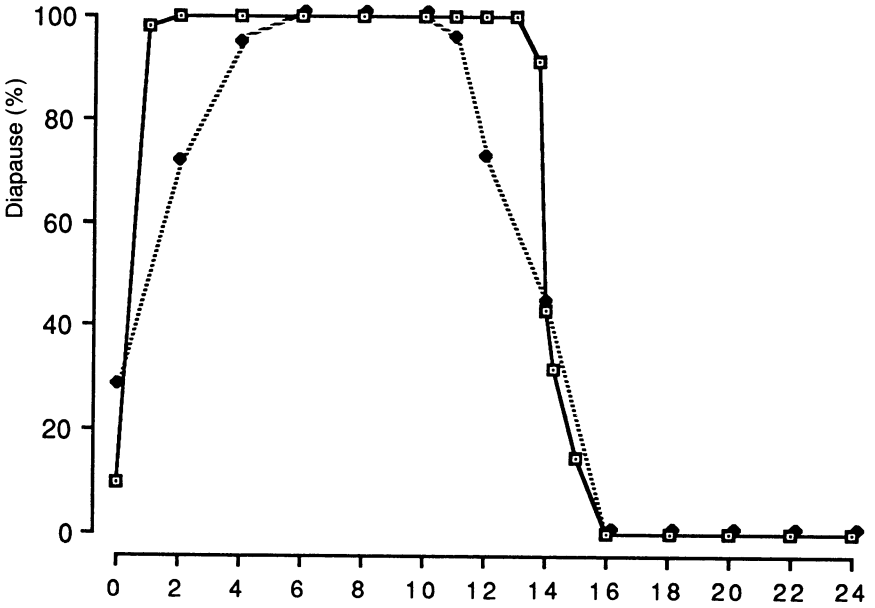

Fig. 17.8 Effects of photoperiod (solid line) and thermoperiod (broken line) on induction of diapause in *Amblyseius potentillae*. Horizontal axis represents hours light per day for photoperiod (temperature, 19°C), and for thermoperiod (27°C: 15°C/DD), hours per day at 27°C (data from van Houten *et al.*, 1988).

The effect of the lengths of the warm and cool phases of a thermoperiod was investigated next. A thermoperiodic response curve was obtained by plotting the observed incidences of diapause against the phase durations of the thermoperiod. Figure 17.8 presents the thermoperiodic response curve (broken line) for *A. potentillae*, based on a 27 °C : 15 °C thermoperiod in continuous darkness, as well as the photoperiodic response curve (solid line) determined at a constant temperature of 19 °C. The thermoperiodic response curve shows that thermoperiods with cryophases of 14–18 h result in 100% diapause while diapause induction is completely prevented with cryophases of 8 h or less. A close conformity is seen between the photoperiodic and thermoperiodic response curves, not only in their overall shape (both are of the 'long-day' type) but also in the critical scoto- and cryophase, which are both about 10 h in duration. An interesting similarity is also to be seen in the sharp decline in diapause incidence at ultra-short photo- and thermophases, resulting in a low incidence of diapause in continuous darkness at constant low temperatures. Such a close similarity between a photo-

periodic and thermoperiodic response curve has been demonstrated only once before – for the large white butterfly, *Pieris brassicae* L. (Dumortier and Brunnarius, 1977).

The next question concerned the effect of the amplitude of the thermoperiod used. Judging from the thermoperiodic-response curve, a maximal response with a 6 °C amplitude (27 °C : 15 °C) could be obtained with a thermoperiod consisting of a 16-h cryophase and an 8-h thermophase. This regime was therefore chosen to test the effect of different thermoperiod amplitudes, with both the lower and upper temperature levels varied over a wide range (Table 17.8). The results show that the incidence of diapause is clearly dependent on the amplitude of the thermoperiod employed. With the exception of treatments with high temperatures for both phases (experiments C and G, Table 17.8), diapause incidence increased with increasing amplitude of the thermoperiod. A fair amount of induction was obtained only with an amplitude of only 2 °C, but full induction was obtained only with an amplitude of 4 °C and above. Although diapause induction did occur with a cyrophase temperature of 23 °C, diapause incidence was low, and in this case appeared to decrease with increasing amplitude. This reversal might result from an indirect effect of temperature on the induction of diapause. It is quite possible that, as a consequence of the increased rate of development of the mites at higher temperatures, the sensitive period has

Table 17.8 Effect of temperature levels and thermoperiod amplitude on diapause incidence in *Amblyseius potentillae* reared in continuous darkness (data from van Houten *et al.*, 1988)

Experiment	*Regime*	*Amplitude of thermoperiod (°C)*	*Diapause (%)*	*Total Tested*
A	TC 8 : 16 (19° : 15°)	2	59	174
B	TC 8 : 16 (23° : 19°)	2	31	150
C	TC 8 : 16 (27° : 23°)	2	6	223
D	TC 8 : 16 (19° : 13°)	3	73	240
E	TC 8 : 16 (21° : 15°)	3	89	233
F	TC 8 : 16 (25° : 19°)	3	73	259
G	TC 8 : 16 (29° : 23°)	3	2	226
H	TC 8 : 16 (21° : 13°)	4	95	131
I	TC 8 : 16 (23° : 15°)	4	98	224
J	TC 8 : 16 (27° : 19°)	4	58	71
K	TC 8 : 16 (27° : 15°)	6	100	379

TC 8 : 16, thermoperiodic cycle with 8-hour warm phase T (thermophase) and 16-hour cold phase C (cryophase).

become too short for the mites to perceive the minimal number of cycles required for diapause induction (van Houten *et al.*, 1988). The results indicate that temperature levels are probably of minor importance for diapause determination in *A. potentillae;* phase durations of the thermoperiod as well as thermoperiodic amplitude seem to be the determining factors for thermoperiodic induction of diapause in this mite.

CONCLUSIONS

Photoperiodic and temperature control of diapause in the plant-inhabiting mites, *T. urticae* and *A. potentillae,* shows, besides fundamental similarities, also some notable differences, the most important of which is the presence or absence of a response to thermoperiod. Similarities and differences of the same kind have been found in insects, and sometimes the differences between these two mite species seem greater than between either of them and certain species of insects (cf. Vaz Nunes and Veerman, 1986b, 1987). Another point of interest is the fact that many similarities have been found between photoperiodic and thermoperiodic induction of diapause in *A. potentillae,* not only in the shape of the response curves, but also in the way photoperiodic and thermoperiodic cycles are accumulated (van Houten and Veerman, 1990). Another intriguing similarity is the need for vitamin A in both the photoperiodic and thermoperiodic mechanism, which might be seen as an indication of unity in the physiological mechanism concerned with photoperiodic and thermoperiodic induction of diapause in mites and insects.

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18

Repeated induction and termination of diapause in the predacious mite, Amblyseius potentillae *(Garman) (Phytoseiidae)*

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Egg-laying adult females of *Amblyseius potentillae* (Garman) appeared to enter diapause in response to short-day photoperiods. Under a continuous short-day regime, diapause development occurred slowly. No change in conditions was required for diapause termination. Diapause development could be accelerated by long-day photoperiods. After diapause termination, egg-laying females entered diapause for a second time when transferred to short-day photoperiods

INTRODUCTION

The phytoseiid mite, *Amblyseius potentillae* (Garman), is a natural enemy of various phytophagous mites, and is used as a biological-control agent of spider mites in orchards and vineyards in Europe. In the temperate zones of Europe, the males of *A. potentillae* die before or during winter but the females demonstrate a facultative reproductive diapause to survive the winter period.

Diapause is the physiological state through which many insects and mites may synchronize their life cycle with the seasons. This enables them to overcome less favourable conditions. In general the onset, development and termination of diapause are controlled by environmental factors, the most important of which is photoperiod.

In females of *A. potentillae,* diapause is induced in autumn by short-day photoperiods. Most species of mites are sensitive to diapause-inducing stimuli only during restricted stages of their development. Some species of phytoseiid mites, however, are known to be more or less sensitive in the adult stage as well, namely, *Typhlodromus caudiglans* Schuster (Putman, 1962), *T. occidentalis* Nesbitt (Hoy, 1975) and *Amblyseius fallacis* (Garman) (Swift, 1987). For *A. potentillae* it has been demonstrated that the immature stages are sensitive to diapause-inducing photoperiods (McMurtry *et al.*, 1976). The sensitivity of the adult stage is examined in this chapter.

Once insects and mites have entered diapause they cannot leave this state instantly in reaction to more favourable conditions. First, a dynamic physiological process called 'diapause development' has to be completed. The rate of diapause development often appears to be under photoperiodic control (Tauber and Tauber, 1976). For a number of phytoseiid mites it has been demonstrated that diapause development can be completed under continuous diapause-inducing conditions (*T. occidentalis* (Hoy and Flaherty, 1970), *A. fallacis* (Rock *et al.*, 1971) and *Amblyseius longispinosus* (Evans) (Hamamura, 1982)). Furthermore, it has been shown that diapause development can be accelerated by transferring the animals to long-day photoperiods. Whether these findings also hold for *A. potentillae* is discussed in this chapter.

A further question concerns the photoperiodic sensitivity of post-diapause egg-laying females. From a few studies in insects it is known that such egg-laying females are able to enter diapause again (cf. Tauber *et al.*, 1986). Here we report the same phenomenon for the first time in a mite.

MATERIALS AND METHODS

Mites

The strain of *A. potentillae* used originates from an apple orchard in the Province of Zeeland, The Netherlands (McMurtry *et al.*, 1976). This strain has been maintained in the laboratory since 1977 on plastic rearing units or 'arenas' as described by Overmeer *et al.* (1982). Until 1981, the strain was kept using the spider mite, *Tetranychus urticae* Koch, as prey. Thereafter it was fed on pollen of the broad bean, *Vicia faba* L., a diet equivalent to live prey as regards development and reproduction of the predacious mites, but more economical to use. For experiments on diapause, however, the diet needs to be supplemented with β-carotene since predacious mites fed on broad-bean pollen alone do not respond to photoperiod (Overmeer and van Zon, 1983) or thermoperiod (van

Houten *et al.*, 1987). Complete restoration of the ability to enter diapause occurs when the diet is enriched with 5 mg of β-carotene (Merck, synthetic, crystalline) per 100 mg of pollen. For the present experiments the mites were reared on this β-carotene-supplemented pollen diet.

Criterion for diapause and its induction

The most conspicuous characteristic of diapausing females of *A. potentillae* is that they do not produce eggs. In the experiments it was made certain that enough males were present to inseminate all females and absence of egg production was taken as the criterion for diapause. Egg production by individual females could easily be determined by feeding them for one or two days on the purple pollen of the ice plant, *Dorotheanthus bellidiformis* (Burman). Mites that eat the pollen become purple in colour; diapausing mites do not eat and remain pale. In the non-diapausing female the large white egg stands out clearly against the surrounding purple-coloured intestine. It has been shown that ice-plant pollen is an adequate food source for reproduction in *A. potentillae* (cf. Overmeer and van Zon, 1983).

Laboratory experiments have established that the so-called 'critical daylength' for *A. potentillae* is 14 hours at 19 °C (van Houten *et al.*, 1988). This means that diapause is induced by photoperiods of 1–14 h whereas no diapause is found with photoperiods of more than 14 h. In the experiments described in this chapter, a photoperiod of 8 h light and 16 h darkness (LD 8:16) was used to induce diapause.

Experiments

The experiments commenced by placing a cohort of eggs, ranging from 0 to 24-h old, on an arena. Consequently the hatched females to be used in the experiments were of about the same age. For the duration of the experiments the arenas were kept in temperature and photoperiod controlled incubators (Heraeus). Temperature was maintained constant within $\pm$ 0.5 °C. For illumination two daylight fluorescent tubes, each of 15 W, were used. At the level of the mites, illumination varied from 1000 to 1200 lux. Ample amounts of food were always present.

Sensitivity of adult females to short-day photoperiods Eggs were incubated in a long-day regime (LD 16 : 8, 26 °C). On day 8 the hatched females started egg laying. One day later, two groups of 75 females were transferred to long-day conditions (LD 16 : 8), at 19 °C. On day 11 the mean oviposition rates were determined. On day 12 one group of females was transferred to short-day conditions (LD 8 : 16, 19 °C). Three

and a half weeks later, the mean oviposition rate in both groups was again determined.

Diapause termination under different photoperiods Eggs were incubated in a diapause-inducing regime (LD 8 : 16, 19 °C). Diapause development and termination were examined during the following six months, the proportion of females that had terminated diapause being determined after 4, 12, 20 and 26 weeks. On each occasion, a group of 100 non-ovipositing females was transferred to a long-day regime (LD 16 : 8, 22 °C) and diapause termination determined under these conditions.

Re-induction of diapause by short-day photoperiods Eggs were incubated in a diapause-inducing regime (LD 8 : 16, 19 °C). Three weeks later, all females were transferred to continuous light at the same temperature to accelerate diapause termination. On day 42 some females started to oviposit. On day 49 a group of 170 egg-laying females was transferred to a long-day regime (LD 16 : 8, 19 °C), and a group of 175 egg-laying females was transferred back to the short-day regime. Thereafter, the mean oviposition rate for both groups of females was recorded every two days for a period of 65 days.

RESULTS

Sensitivity of adult females to short-day photoperiods

The effect of short-day photoperiods on non-diapausing females is shown in Table 18.1. On day 11 the mean oviposition rate for both groups of females (LD 16 : 8, 19 °C) was approximately equal, that is, 0.8 and 0.9 egg/female/day. On day 35 the group of females that had remained under long-day conditions still produced 0.8 egg/female/day on average. The oviposition rate in the group of females transferred on day 11 to a short-day photoperiod (LD 8 : 16) decreased from 0.9 to 0.01 egg/female/day on day 35. Egg production was resumed within a few weeks after transferring this group back to long-day conditions (LD 16 : 8) (not shown in the table). The results of this experiment indicate that short-day photoperiods induce reproductive diapause in adult females of *A. potentillae*.

Diapause termination under different photoperiods

Table 18.2 shows the results of diapause termination under short-day photoperiods (LD 8 : 16, 19 °C). After 4 weeks at short days all mites were still in diapause. After 12, 20 and 26 weeks at short days, 1, 15 and

Table 18.1 Egg production on days 11 and 35 of *Amblyseius potentillae* (Garman) exposed to long-day (group 1) or short-day (group 2) photoperiods during adult life

	Light–dark (LD) and temperature regimes			*Eggs/female/day*			
	Days 0–8 (egg → adult)	*Days 9–11*	*Days 12–35*	*Day 11*	*Number females*	*Day 35*	*Number females*
Group 1	LD 16 : 8, 26°C	LD 16 : 8, 19°C	LD 16 : 8, 19°C	0.8	61	0.8	36
Group 2			LD 8 : 16, 19°C	0.9	68	0.01	31

Table 18.2 Termination of diapause in 4 groups of females of *Amblyseius potentillae* exposed to short-day photoperiod (LD 8 : 16, 19 °C) for 4–26 weeks from egg stage onwards

Weeks spent in short days	*Diapause termination (%)*
4	0
12	1
20	15
26	51

51% of the females, respectively, had terminated their diapause. These results indicate that diapause termination in *A. potentillae* takes place under prolonged diapause-inducing conditions.

After 4, 12, 20 and 26 weeks at short day conditions, groups of diapausing females were transferred to long-day photoperiods (LD 16 : 8, 22 °C). The effect of this long-day regime on diapause termination can be seen in Fig. 18.1. It appears that the longer a group of mites has experienced the short-day regime, the shorter it has to be under the long-day regime for complete diapause termination. Moreover, it may be concluded that long-day conditions accelerate diapause development: four weeks under short days plus five weeks under long days results in 100% diapause termination whereas nine weeks under short days leads to virtually no termination of diapause at all (Table 18.2).

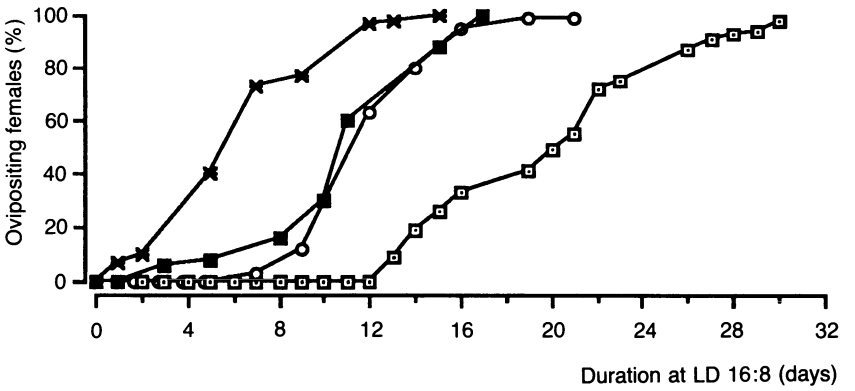

Fig. 18.1 Effect of long-day photoperiod (LD 16:8, 22°C) on diapause termination in 4 groups of *Amblyseius potentillae* (Garman) females which had been kept in short-day photoperiod (LD 8:16, 19°C) for 4–26 weeks from egg stage onwards. Total period spent in short days: 4 weeks (⊡), 12 weeks (○), 20 weeks (■), 26 weeks (x) (see also Table 18.2).

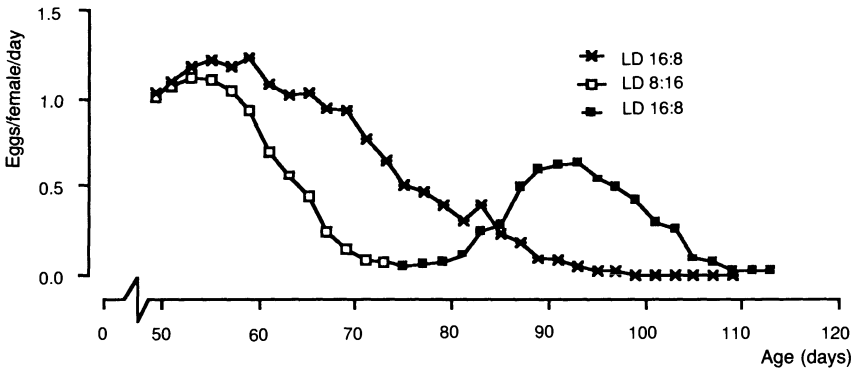

Fig. 18.2 Daily oviposition rates of *Amblyseius potentillae* females under long-day and short-day photoperiods. The mites were reared and maintained under short days for first three weeks of their lives, and then transferred to constant light on day 21 to accelerate diapause termination. Short and long-day photoperiods in the figure commenced on day 49.

Re-induction of diapause by short-day photoperiods

Figure 18.2 shows the influence of day length on the mean oviposition rate of post-diapause females. By day 49 the females had produced 3 ± 2 eggs each. In the group of females transferred to a long-day regime (LD 16 : 8) the mean oviposition rate increased from 1 egg/female/day on day 49 to 1.2 eggs/female/day on day 59. Thereafter, the oviposition rate decreased slowly. From day 99 onwards no more eggs were laid by any of the 36 surviving females.

In the group of females transferred to a short-day regime (LD 8 : 16) the mean oviposition rate increased to 1 egg/female/day on day 56, and then rapidly decreased to 0.07 egg/female/day by day 75. This indicates that virtually all females had re-entered diapause. On day 75 this group of females was transferred back to long-day conditions (LD 16 : 8). In response to these conditions the mean oviposition rate increased to a maximum of 0.6 egg/female/day on day 95. After day 110, no more eggs were laid by the 39 remaining females.

The result of this experiment indicates that diapause can be re-induced in adult females of *A. potentillae* that have experienced a previous diapause, induced in their immature stages.

DISCUSSION

The results of this study can be summarized as follows: egg-laying adult females of *A. potentillae* appear to enter diapause in response to short-

day photoperiods. Under a continuous short-day regime, diapause development occurs slowly. No change in conditions is required for diapause termination. Diapause development is accelerated by long-day photoperiods. After diapause termination, egg-laying females can enter diapause for a second time when transferred to a short-day photoperiod.

Only a few species of insects are known in which a second diapause can be induced after a post-diapause ovipositional period (for reviews see Tauber *et al.*, 1986; Zaslavski, 1988). Except for the grasshopper, *Oedipoda miniata* (Pall.) (Pener and Broza, 1971), all these species live for more than one year. The return of photoperiodic sensitivity seems to be a prerequisite for diapause induction to take place in successive years. *Amblyseius potentillae* is the first example of a mite in which reproductive diapause can be re-induced in post-diapause females.

It is tempting to consider possible ecological implications of the results of this study. In autumn all stages of *A. potentillae* are present. It has already been shown that the immature stages are sensitive to diapause-inducing short-day photoperiods (McMurtry *et al.*, 1976). Now it is shown that egg-laying female adults are also sensitive to diapause-inducing photoperiods. This could mean that these females are able to postpone a part of their oviposition to the following spring when conditions will probably be more favourable for their offspring. Whether this actually takes place remains to be investigated; as yet no field experiments have been carried out.

Whether it is fruitful or not – in terms of egg production – for an adult female to enter diapause will depend, among other things, on the costs – in terms of egg production – of diapause. Preliminary experiments have shown that the total number of eggs laid in a female's lifetime is highest when she does not enter diapause and lowest when she enters diapause twice. This means that diapause implies a cost in terms of decreased fecundity. Diapausing females require very little food. The difference between the egg productions of starved and un-starved females, appeared to be negligible. So the cost of diapause seems to be higher than can be explained by mere starvation. More data need to be collected but so far results are promising.

The ecological significance of the ability to enter diapause for a second time remains to be demonstrated. The sequence of photoperiods used in this study to re-induce diapause (namely, short day, long day, short day) in nature never occurs within a mite's lifetime. The re-induction might therefore concern no more than a property of the physiological mechanism, elicited under laboratory conditions. A factor that does fluctuate within a mite's lifespan, and hence could be ecologically more important in the light of the double induction of diapause, is tempera-

ture or thermoperiod. It has been shown that diapause can be induced in *A. potentillae* by thermoperiods (van Houten *et al.*, 1988). Further experiments will show if diapause can also be re-induced by thermoperiods.

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Inheritance of photoperiodic responses controlling diapause in the two-spotted spider mite, Tetranychus urticae *Koch*

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The two-spotted spider mites (*Tetranychus urticae* Koch) were collected in 1961 from a number of bushes of the common elder (*Sambucus nigra* L.) in the dunes of Voorne in The Netherlands, and a 'Sambucus' strain was established in the laboratory. Since then, this strain has been cultivated on beans (*Phaseolus vulgaris* L.) in strict isolation under controlled conditions. The population size never fell below approximately 2000 individuals (Helle, 1968).

From the Sambucus culture the strains, ND_1 and ND_2, were selected for absence of diapause under a short-day regime (LD 10 : 14, 18 °C). A number of tests suggested that these non-diapausing strains reacted with a low percentage of diapause (range 1–4%) to a regime for which there was a strong diapause response by the original Sambucus mites (Ignatowicz, 1985).

The genetic basis for the suppression of diapause in ND_1 and ND_2 stocks was analysed by means of Mendelian crosses and backcrosses, using the photoperiodic cycle, LD 10 : 14, as the diagnostic to distinguish diapausing and non-diapausing phenotypes. Suppression of diapause is inherited as a recessive trait. From backcross analysis, it was concluded that the suppression of diapause in the ND_1 and ND_2 strains is under monogenic control. The major genes for diapause suppression in ND_1 and ND_2 are alleles at a locus designated as *d*. A mutation for albinism of the locus *a-p* is pleiotropic for suppression of diapause. From

crosses between ND_1 and the albino strain it was shown that *d* and *a-p* are distinct loci (Ignatowicz and Helle, 1986).

The non-diapausing strains, ND_1 and ND_2, were crossed with the 'Leningrad' strain, an allopatric strain responding with *c.* 100% diapause incidence under short-day conditions. The diapause responses were observed in the F_1 and backcross progeny. The results obtained show: (1) the 'diapause' trait of the Leningrad strain exhibited incomplete dominance over the 'non-diapause' trait; (2) maternal effects were present in crosses of females of both non-diapausing strains with the Leningrad males; and (3) the expression of maternal effects was different in the ND_1 and ND_2 strains when crossed with the Leningrad strain (Ignatowicz, 1986).

A strain of *T. urticae* collected from the castor bean, *Ricinus communis* (L.), in Egypt – the E strain – does not enter diapause; under the prevailing conditions, a photoperiodic response is absent in these mites. Determinants for the 'diapause' trait of the Leningrad and Sambucus strains are expressed as dominant after hybridization with the E strain. When mated to E males, females of the albino strain produce hybrid daughters with the wild pigmentation and normal capability to diapause. The effect of overdominance appears in the hybrids of crossings between different non-diapausing strains, for example, ND_1 or ND_2 with E (Ignatowicz, 1987).

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Some observations on diapause in winter eggs of Panonychus ulmi *(Koch) (Tetranychidae)*

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Some observations are presented on factors influencing winter-egg laying density in autumn, and environmental requirements to break diapause of winter eggs in the European red mite, *Panonychus ulmi* (Koch), on apple. In our field trial, the presence of phytoseiid mites in the autumn had a decisive influence on the winter-egg density. Deltamethrin treatments eliminated the predatory mite, *Amblyseius andersoni* (Chant), and as a consequence the number of winter eggs increased. In untreated trees, phytoseiids reduced the winter-egg density in the same period. Chilling requirements to break diapause differ in eggs collected from two localities. In Valencia, the warmer region, only 70 days at 1 °C were needed to break diapause whereas in Lerida it took 90–100 days. The mean incubation time to hatch eggs decreased steadily with time after the cold requirements had been fulfilled. In our trial, the reduction in post-chilling incubation time seems to be independent of mite provenance or temperature (provided that the development threshold of 7 °C is not reached). The longer time required to incubate eggs immediately after the completion of the cold treatment seems to be a final phase in the diapause development of this species

INTRODUCTION

The European red mite, *Panonychus ulmi* (Koch), is one of the most serious pests of apples, being widely distributed in apple-producing regions. It overwinters as a diapausing egg stage. Females begin to lay winter eggs at the end of the summer, and these eggs hatch in the

following spring. Marked differences in mite attacks have been observed from year to year in Spanish apple orchards, related in part to environmental factors affecting winter-egg laying, survival, and time of hatching in spring. The time of hatching is monitored to decide on the chemical treatments to be used against the pest in spring. Lees (1953) found that winter eggs of *P. ulmi* needed a cold period to break diapause. The chilling requirements seem to vary in different localities as differences in regional climatic conditions have resulted in selection for those genotypes appropriate for such conditions (Cranham, 1973).

This chapter presents some observations on the influence of pesticides applied in summer on winter eggs laid in autumn, and also on the requirements to break diapause of winter eggs. The effect of insecticides on winter egg-laying density was evaluated in a field trial. Investigations were carried out using shoots with eggs brought to the laboratory, and kept under constant low temperatures to determine the factors that influence diapause development and to establish differences between two different climatic areas, the provinces of Lerida and Valencia. In Lerida, situated in north-east Spain, the winters are cold, whereas Valencia, located in the east of the country, has mild winters.

MATERIAL AND METHODS

The field trial was carried out in an apple plot in Albesa (Lerida) containing *P. ulmi* and the phytoseiid mite, *Amblyseius andersoni* (Chant). Some trees were treated on 25 July 1987 with deltamethrin at 0.03% of a formulation containing 7.5 mg of active ingredient per litre to reduce the numbers of *A. andersoni*, and others at the same rate on 20 August 1987. Untreated trees were sampled as controls. Each of the three treatments had five replicates of two trees each. The phytoseiid mite population was monitored by sampling 20 randomly selected leaves, and counting all the mites present with a hand lens. To evaluate winter-egg density, each replicate consisted of five portions of shoot, 10–15 cm long, which were brought to the laboratory, and the eggs counted using a stereomicroscope. Egg density is expressed as number leaf scar (that is, the small scars or 'creases' (wrinkles), remaining on a stem after the abscission of the bud scales). This sampling unit was chosen due to the direct relation established between the number of bud scars and number of eggs on each shoot fragment.

The experiments on diapause requirements were carried out using eggs collected in November from an orchard in Lerida and one in Valencia, located in different climatic regions. The trials were repeated over two years: the winters of 1986–87 and 1987–88. In the results these are referred to as 1987 and 1988 respectively. Eggs were kept at constant

temperatures of 1° or 4 °C to determine the length of the cold treatment required to break diapause.

In 1988, a further experiment was carried out in which batches of eggs were withdrawn from 1° or 4 °C at intervals of 10–50 days, and placed at 24 °C to determine the proportion of eggs hatching and incubation period in relation to duration of exposure to low temperature after completion of the initial cold treatment (70–90 days) to break diapause.

RESULTS AND DISCUSSION

Females began to lay winter eggs in the field by the middle of August. The fecundity of winter-egg laying females seems to be lower than that of normal females. Winter-egg laying females collected from the field on 30 August and taken to the laboratory laid only 65% of the eggs of normal females ($P < 0.01$).

Photoperiod is usually considered the main factor causing the onset of diapause in *P. ulmi* but two other factors, temperature and nutrition, can also modify the onset to a certain degree (Veerman, 1985). In our field trial a delay in winter-egg laying was observed in the mites from trees treated with deltamethrin (Fig. 20.1). As this effect did not appear to be related to nutrition, it is possible that certain pesticides could also affect the onset of diapause through a change in the behaviour of the mites.

Our field trial suggests that the presence of phytoseiid mites in Autumn has a decisive effect on winter-egg density. Deltamethrin treatments eliminate the predatory mites and, as a consequence, the number of winter eggs per scar rises steadily from 4–5 to 15–17 between August and November (Fig. 20.1). In untreated trees, phytoseiids reduce the winter-egg density from 6 to 1 eggs in the same period. Apparently, *A. andersoni* feeds actively on winter eggs in September and October, thus reducing the probability of mite outbreaks in the following year.

Chilling requirements to break diapause differ in eggs collected from the two localities (Fig. 20.2). In the warmer conditions occurring in Valencia, only 70 days at 1 °C are needed to break diapause whereas in Lerida, this duration is 90–100 days. The lengths of the cold periods for Spanish populations are much shorter than those reported by other authors. Lees (1953) reported that the maximum percentage of hatched eggs was reached after 150–200 days at low temperature while Granham (1972) quoted 200–230 days. When the 1988 results at 1° and 4 °C are compared, it is found that the diapause ends about 10 days earlier at the lower temperature (Fig. 20.3).

The mean egg incubation period decreases steadily with time once the cold requirements have been fulfilled (Fig. 20.4). Shortly after chilling

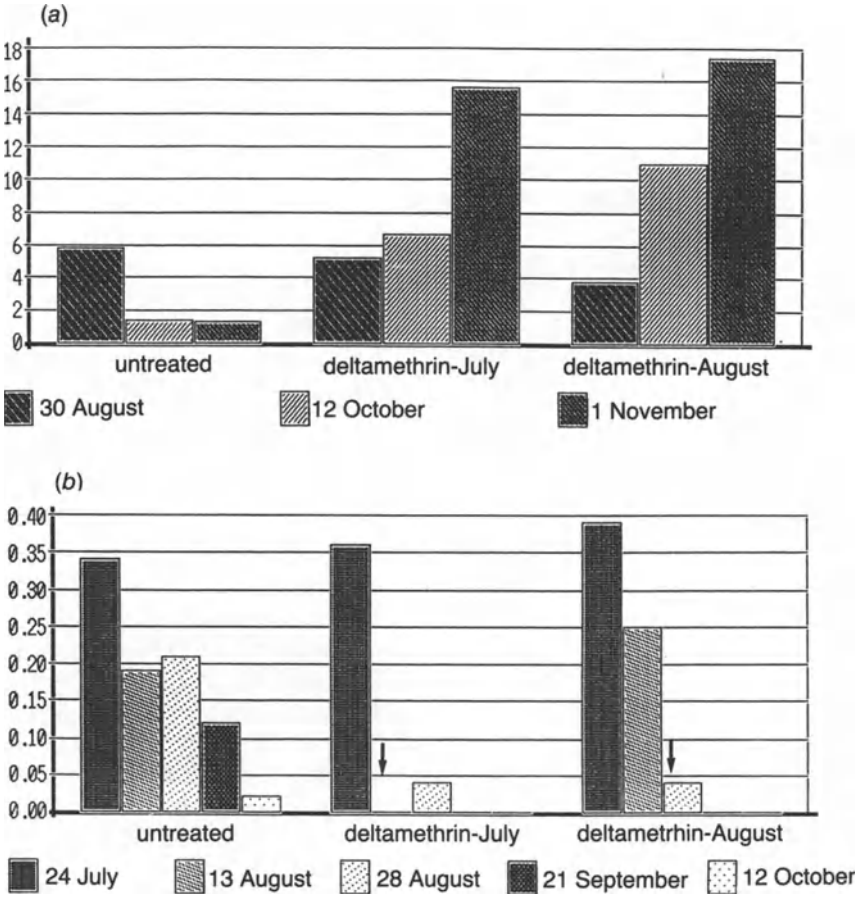

Fig. 20.1 Influence of deltamethrin, applied on 25 July and 20 August (arrows), on (*a*) winter eggs of *Panonychus ulmi* (Koch) on shoots (mean number bud-scale scar) and (*b*) mean number per leaf of active stages of *Amblyseius andersoni* (Chant) in a Lerida apple orchard.

completion, the eggs of *P. ulmi* need 18–20 days to hatch at 24 °C. This period decreases to 10–12 days if the cold period is prolonged to 50 days. In our trial, the reduction in post-chilling incubation time seems to be independent of mite provenance or temperature – provided that the development threshold of 7 °C is not reached – as 1° and 4 °C give similar results (Fig. 20.4). Thus, after the cold requirements have been fulfilled if the temperature is higher than 7 °C, the mean incubation time decreases owing to the operation of heat summation. If, however, the

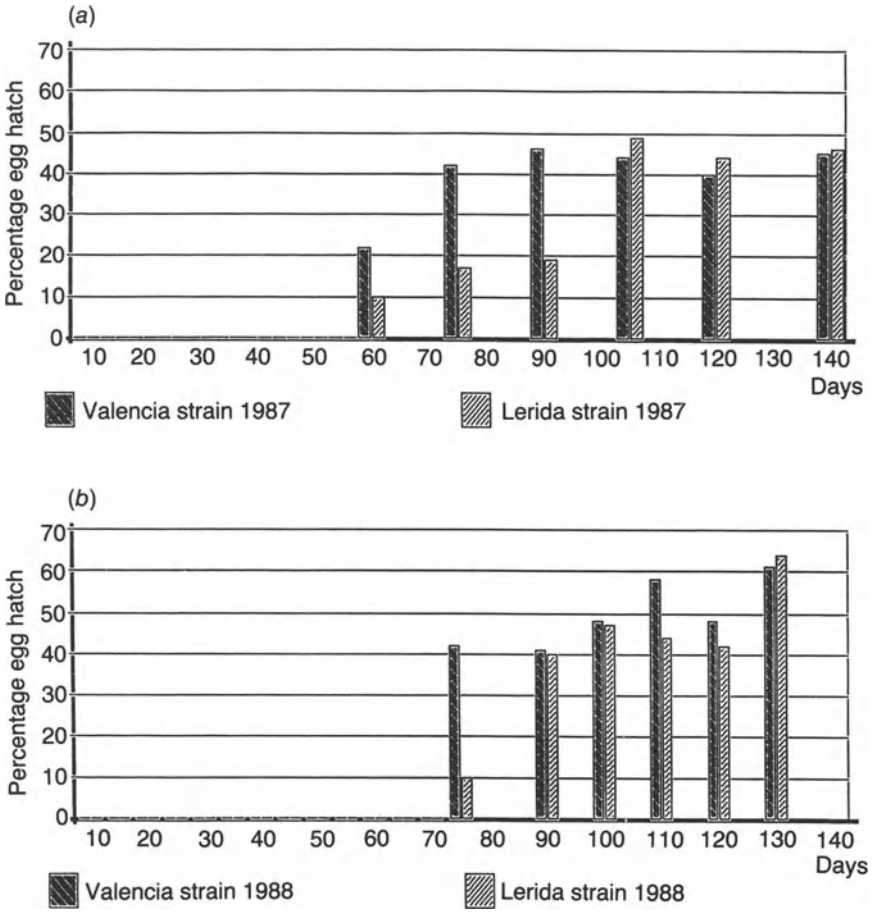

Fig. 20.2 The proportion of winter eggs, which hatched, of two populations of *Panonychus ulmi* from Lerida and Valencia, Spain, respectively, in (*a*) 1987 and (*b*) 1988. The eggs were collected in November and maintained for *c.* 60–*c.* 140 days at 1°C to break diapause, and then transferred to incubate at 24°C.

temperature falls below 7 °C, the period required for egg incubation seems to decrease with time without being influenced by temperature. The longer duration for egg incubation required immediately after the completion of cold treatment at 1–4 °C seems to be a final process in the development of diapause in this species. Our results support Cranham's (1972) findings that the late stages of diapause development are completed slowly at low temperatures, but that these later stages can be accelerated if the temperature is higher.

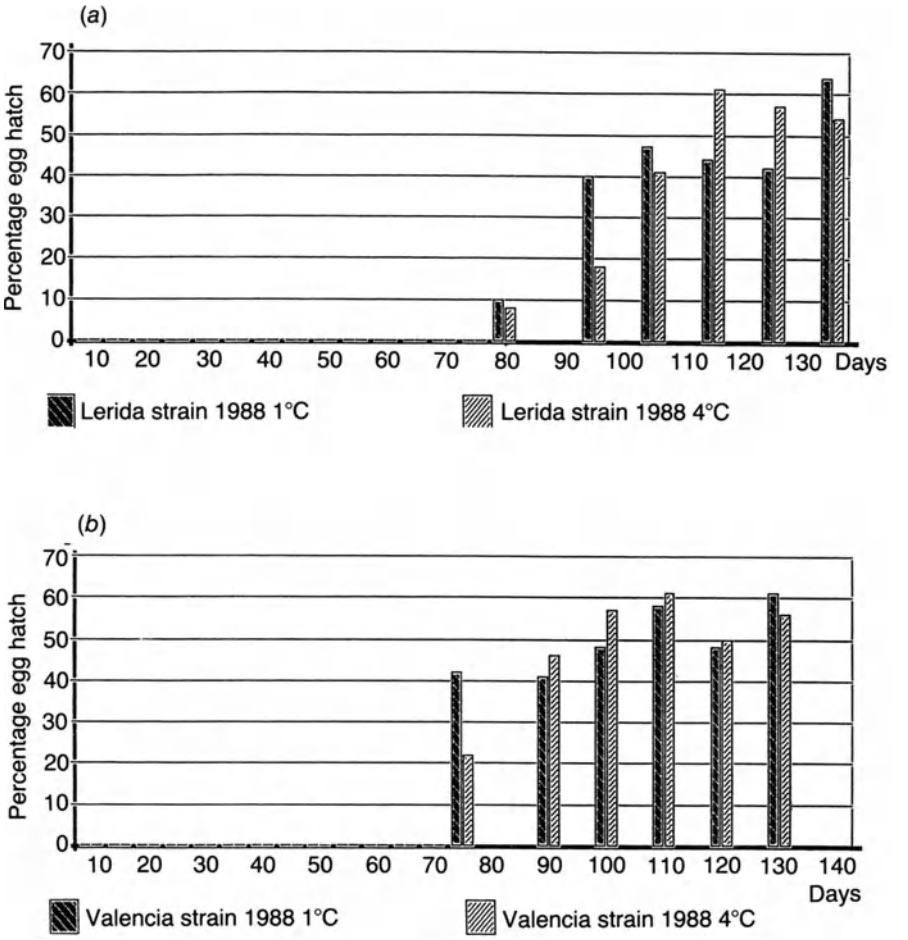

Fig. 20.3 A comparison of the percentage of winter eggs, which hatched, of populations of *Panonychus ulmi* from (*a*) Lerida and (*b*) Valencia, collected in November 1988 and maintained for *c.* 80–*c.* 135 days at 1°C and 4°C to break diapause, and then transferred to incubate at 24°C.

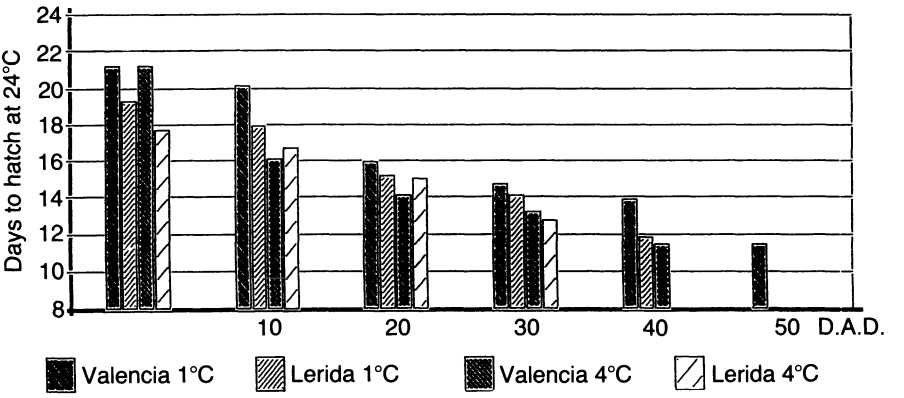

Fig. 20.4 Effect on incubation duration (days at 24°C) for winter eggs of two populations (Lerida and Valencia) of *Panonychus ulmi* in relation to continued storage at constant low temperature for 0–50 days (D.A.D.) after completion of cold treatment at 1° or 4°C to break diapause.

ACKNOWLEDGEMENT

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21

Reproduction, embryonic and postembryonic development of Trichouropoda obscurasimilis *Hirschmann & Zirngiebl-Nicol 1961 (Anactinotrichida: Uropidina)*

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The reproductive behaviour of the litter-inhabiting uropodid mite, *Trichouropoda obscurasimilis* Hirschmann and Zirngiebl-Nicol, is quite similar to that reported for other uropodid species. It is mycetophagous, and the adult, and all juvenile stages including the larva, feed readily on the hyphae of the fungus, *Sphaeronema* sp. Embryonic development occurs after oviposition with the same five phases as described for gamasid mites. In the laboratory, at room temperature, embryongenesis takes about 11 days during the cold period of the year. The duration of postembryonic development of the pre-adult stages was determined at room temperature at monthly intervals from July to April inclusive. The overall mean duration (egg eclosion to adult emergence) was 80.8 days for males and 81.5 days for females

INTRODUCTION

There have been few studies of the biology of uropodid mites. Successful rearing experiments related to this group of mites have revealed some aspects of their reproductive behaviour (Radinovsky, 1965b; Faasch, 1967; Compton and Krantz, 1978; Athias-Binche, 1981), as well as their postembryonic development (Krasinskaya, 1961; Radinovsky,

1965a; Faasch, 1967; Athias-Binche, 1981). In total, there are observations on ten uropodid species, which is much less than the existing references on gamasid mites.

Huţu (1979) carried out an experiment in an attempt to determine the feeding habits of the nine commonest forest species of uropodid mites in Romania. Among these, the embryonic and postembryonic development of the leaf-litter mite, *Trichouropoda obscurasimilis* was studied, and information was obtained on its feeding habits and some aspects of its reproductive behaviour. The data on embryonic development are original for uropodid mites. Thus, it is only possible to compare the embryonic development of this uropodid species with that referring to the gamasid mites (Zukowski, 1964, 1966; Ignatowicz, 1974).

MATERIALS AND METHODS

Trichouropoda obscurasimilis was described by Hirschmann and Zirngiebl-Nicol (1961) in Hungary but they did not give a biotope specification. Later, it was found in Czechoslovakia (Pecina, 1971) and in Poland (Błoszyk, personal communication), in litter and decayed trunks in beech forests. In Romania this species was collected from many localities (Huţu, 1979). from the same biotopes, which demonstrates its clear preference for the environmental conditions of such forests.

Adults of both sexes of *T. obscurasimilis*, were extracted from litter collected in a mixed forest of beech and hornbeam (*Carpino-Fagetum*) surrounding Jassy using Balogh's modification of the Tullgren-funnel apparatus. The animals, caught in plastic cells with water, were examined daily, under a stereomicroscope, to recover the individuals required for the study.

The mites were cultured in weighing bottles, using the method described by Ignatowicz (1974). The cultures were maintained in the laboratory at room temperature. The ambient temperature fluctuated daily and seasonally during the experiment although the laboratory was heated by a stove. The humidity in the culture vessels was maintained at an almost constant level by the addition of drops of distilled water whenever necessary. The embryonic development was studied from December 1976 to March 1977, and the postembryonic stages from July 1976 to May 1977. All observations on embryonic development were made once daily under a binocular microscope, on eggs placed in drops of distilled water on microscope slides with depressions. Observations on mating and other reproductive behaviour were made more frequently, sometimes hourly, under a stereomicroscope. The mean durations in days of the development stages and of the whole lifespan of *T. obscurasimilis* were determined.

FEEDING HABITS

It is known that the species of the genus *Trichouropoda* are, usually, mycetophagous. For this reason, three fungal species, cultured on agar, were chosen for the feeding tests: *Penicillium* sp., *Spicaria* sp. and *Sphaeronema* sp. The mite showed a clear preference for the hyphal material of *Sphaeronema* sp., a fungus obtained from a soil extract from the same forest from which the mites had been obtained. This preference was strikingly demonstrated when all three fungus species were offered simultaneously as food for the mite. The mites ignored the agar pieces with *Penicillium* and *Spicaria* but rapidly colonized the agar with *Sphaeronema* on which they fed.

REPRODUCTIVE BEHAVIOUR

Copulation

Detailed descriptions of the mating behaviour of some uropodid species have been given (Radinovsky, 1965b; Faasch, 1967; Athias-Binche, 1981). These studies emphasized that uropodid mites are characterized by an elaborate reproductive behaviour pattern similar to that of gamasid mites. My observations on the copulation of *T. obscurasimilis* are in agreement with those referred to above for other uropodid species, and suggest that there are only small interspecific differences in mating behaviour. These differences concern some minor aspects such as the duration of the mating phases, the position of the male on the female, the method used to maintain contact with the female during copulation, and the post-mating behaviour of the male. The mating duration of *c.* 30 minutes for the present species – when sperm transfer occurs – is shorter than that reported for other uropodid species (45 min to 8 h). The shortest mating phase is the premating one (1–2 min) and the longest, the post-mating phase (15–20 min) when sperm transport within the female's genital tract occurs.

The investigations on mating procedure provided a better understanding of the way in which the male chelicerae participate in the transfer of the sperm package from his genital opening to that of his partner. Contrary to other authors (Radinovsky, 1965b; Athias-Binche, 1981), in *T. obscurasimilis*, the sperm package is transferred by the male chelicera only, without the assistance of other mouthparts or the legs. After the formation of the sperm package, the male suddenly bends one of his chelicerae in a posteriour direction until it lies parallel to his body; the sperm package is then grasped and transferred to the female's genital orifice.

It is worth noting that males were twice observed displaying a premating behaviour with female deutonymphs just before they moulted to become adults. Similar instances are well known in gamasid mites but this is the first time such behaviour has been observed with uropodid mites.

Oviposition

In the hysterosoma of the fertilized female of *T. obscurasimilis* only 1–2 eggs are observed at any one time. The mature egg fills almost the whole of the opisthosomal part of the female's body. I was unable to observe a female laying an egg during this study. Once a female was observed covering a newly laid egg with filter-paper fibres from the culture cell. The eggs occur singly and are usually inserted in the substrate. In culture, the preferred place for egg laying is the space between the filter-paper and the glass wall of the culture cell. The eggs were always found hidden and covered by substrate debris, suggesting that during oviposition, the female of this species practised a degree of parental care. Similar behaviour has been reported for other uropodid species (Radinovsky, 1965b; Faasch, 1967; Athias-Binche, 1981).

LIFE HISTORY

The eggs of *T. obscurasimilis* have an ellipsoid shape and are milky white in colour. The newly laid egg is 200–220 μm long, its size being relatively large compared to that of the female (700–720 × 500–530 μm). During embryonic development the egg increases in size reaching a length of 270–290 μm.

No published information has been found on the structure and formation of the egg coverings in uropodid mites. It is possible that these develop in a similar fashion to those in the gamasid mites. In these latter mites, the formation of the egg coverings was closely studied by Bielozierov (quoted by Žukowski, 1964). As in gamasid mites, the egg of *T. obscurasimilis* has three coverings: a thin and translucent vitelline membrane enclosing the yolk, only clearly visible in the first stage of embryonic development; a smooth and whitish cuticle; and a sticky capsule to which particles of debris such as filter-paper fibres adhere, and forming an easily detachable protective layer.

Embryonic development

The main phases of embryonic development are presented in Fig. 21.1. It is necessary to stress that the data on the duration of the different

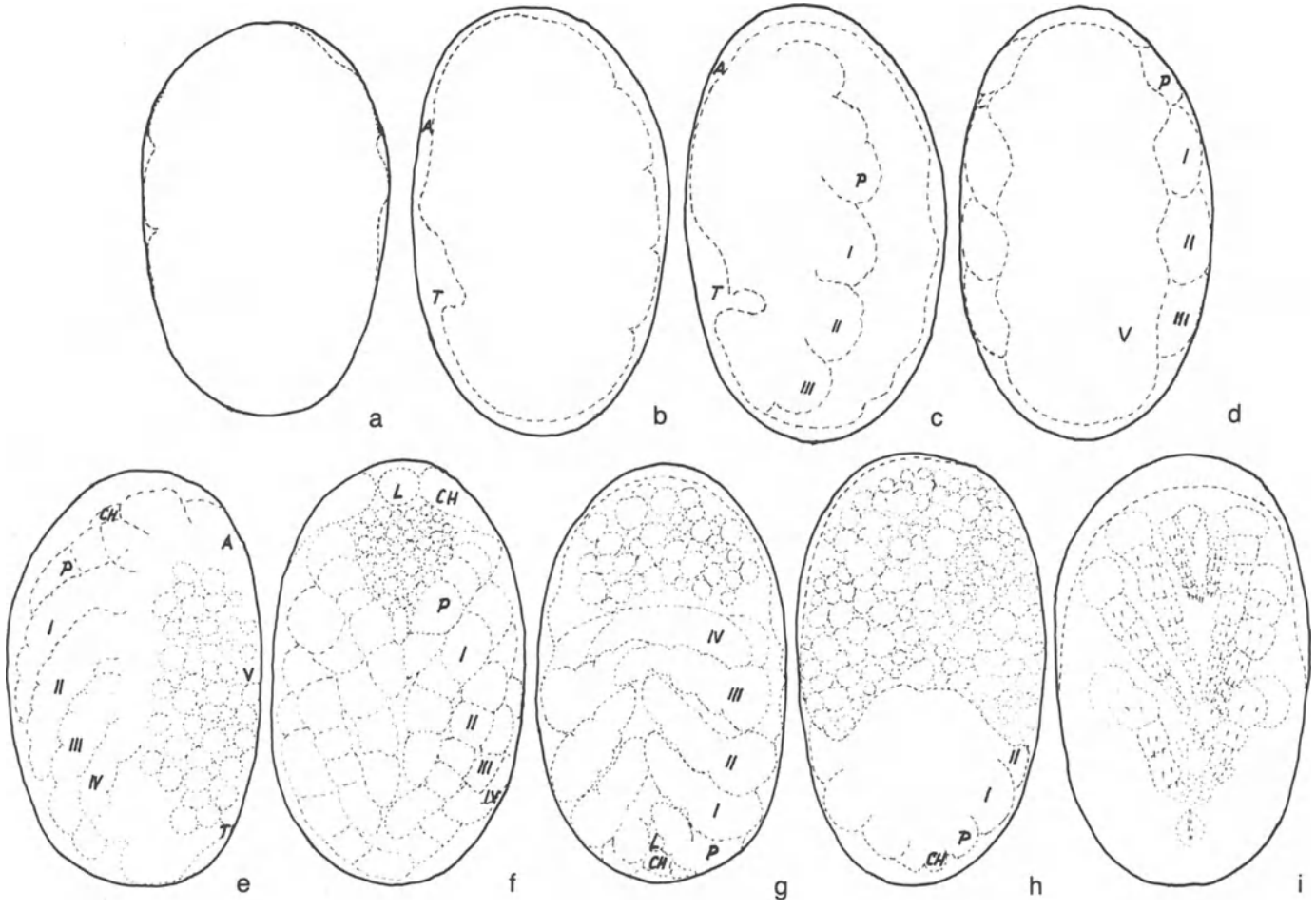
phases are approximate because of quite frequent interruptions in development, especially in the later stages, due to removal of eggs for examination. For the same reason it was not possible to determine the progress of all the developmental stages in the same egg.

These observations establish that in the newly laid egg the embryo is not yet formed. At this stage, the entire egg is filled with yolk. The first surface cleavages only appear after about 24 hours as a result of the formation of the shallow blastoderm layer (Fig. 21.1*a*). After a further 24 h, three regions can be clearly distinguished in the germ band: the cephalic lobe (acron) and the anal lobe (telson), both situated on the dorsal surface of the embryo and, ventrally the median part of the germ band exhibiting five protuberances separated by four depressions (Fig. 21.1*b*).

In the next phase the depressions of the lateral wall of the germ band become deeper, and the protruberances appear as the buds of the first three pairs of legs and the pedipalps; these buds are separated by a broad band of yolk (Fig. 21.1*c* in lateral and Fig. 21.1*d* in frontal view). This is followed by the formation of the fourth pair of legs and the cheliceral buds (Fig. 21.1*e*). As the legs grow in length, the yolk bands between them become narrower and each pair of legs gradually approaches the median line.

Simultaneously with these transformations, there is germ-band shortening, which seems to be characteristic for the embryonic development of all mites (Zukowski, 1964; Ignatowicz, 1974). This contraction proceeds by a gradual migration of the cephalic lobe from a dorsal to a ventral position, the anal lobe remaining in its initial position. In the first stage of the contraction process, the cephalic lobe reaches the level of the chelicerae, and the remains of the yolk can be seen lying between the pedipalps (Fig. 21.1*f*). As the germ band becomes shorter, the embryo undergoes a rotary movement through 180° around its short axis so that the whole embryo appears to be compressed in the narrower end of the egg, the remaining portion being filled with yolk (Fig. 21.1*g* in ventral and Fig. 21.1*h* in dorsal view). When the embryo reaches this stage the contraction process is completed.

Concomitant with this process is the formation of the mouthparts and their arrangement in their final position. During germ-band contraction, the labrum appears in the central part of the cephalic lobe and, beneath it, the stomodaeum is formed as a result of the invagination of the cephalic endoderm. At the same time, the rest of the yolk between the pedipalps disappears, and the labrum migrates beneath the chelicerae (Fig. 21.1*g*). In the region of the anal lobe, the proctodaeum and anus form, and the yolk lying between the fourth pair of legs and the anal lobe disappears (Fig. 21.1*i*).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The next step in embryonic development is the retrogressive movement of the embryo (Zukowski, 1964). Although this movement has not been observed in *T. obscurasimilis*, there is evidence that it occurs in uropodid mites. About 72 h before the larva hatched, the embryo was seen to make strong contracting movements of its body, which probably lead to the retrogressive rotation. The striking proof that the embryo undergoes this movement is its position in the next phases of development when it appears reorientated with its anterior part lying in the broader pole of the egg.

About 48 h before the mite leaves the egg coverings, its legs become elongate, and bend in a posterior direction, to become almost parallel with the longitudinal axis of the body. The pedipalps, and especially the chelicerae, also move to take up the same orientation as the legs. Legs IV regress slowly under the hypoderm, until they are only visible through the integument.

In the next 24 h, the movements of the embryo are very sluggish. During this period one can observe the formation of the body and leg setae as well as the claws and associated structures. About 24 h before eclosion, the egg changes in colour becoming pinkish. Under the microscope the embryo appears well formed, and from time to time it moves its mouthparts and legs. Legs IV are no longer visible; the other legs are directed posteriorly, and the third pair almost reach the anal opening (Fig. 21.1*i*). At this point embryonic development is complete.

The embryo of this species is not equipped with a special organ for cleaving the egg coverings. During eclosion, the egg cuticle is split along its median line, probably by an increase in the internal pressure within the egg due to muscular contractions of the embryo. Just before hatching, the embryo moves vigorously, often making rhythmic contractions, which finally result in the rupture of the egg cuticle. The larva leaves the cuticle either through its anteriour portion or posteriorly.

It is remarkable that in *T. obscurasimilis*, normally the eggs are laid at a stage when the embryo has not yet formed. However, there are probably exceptions to this. As a result, all phases of embryonic development

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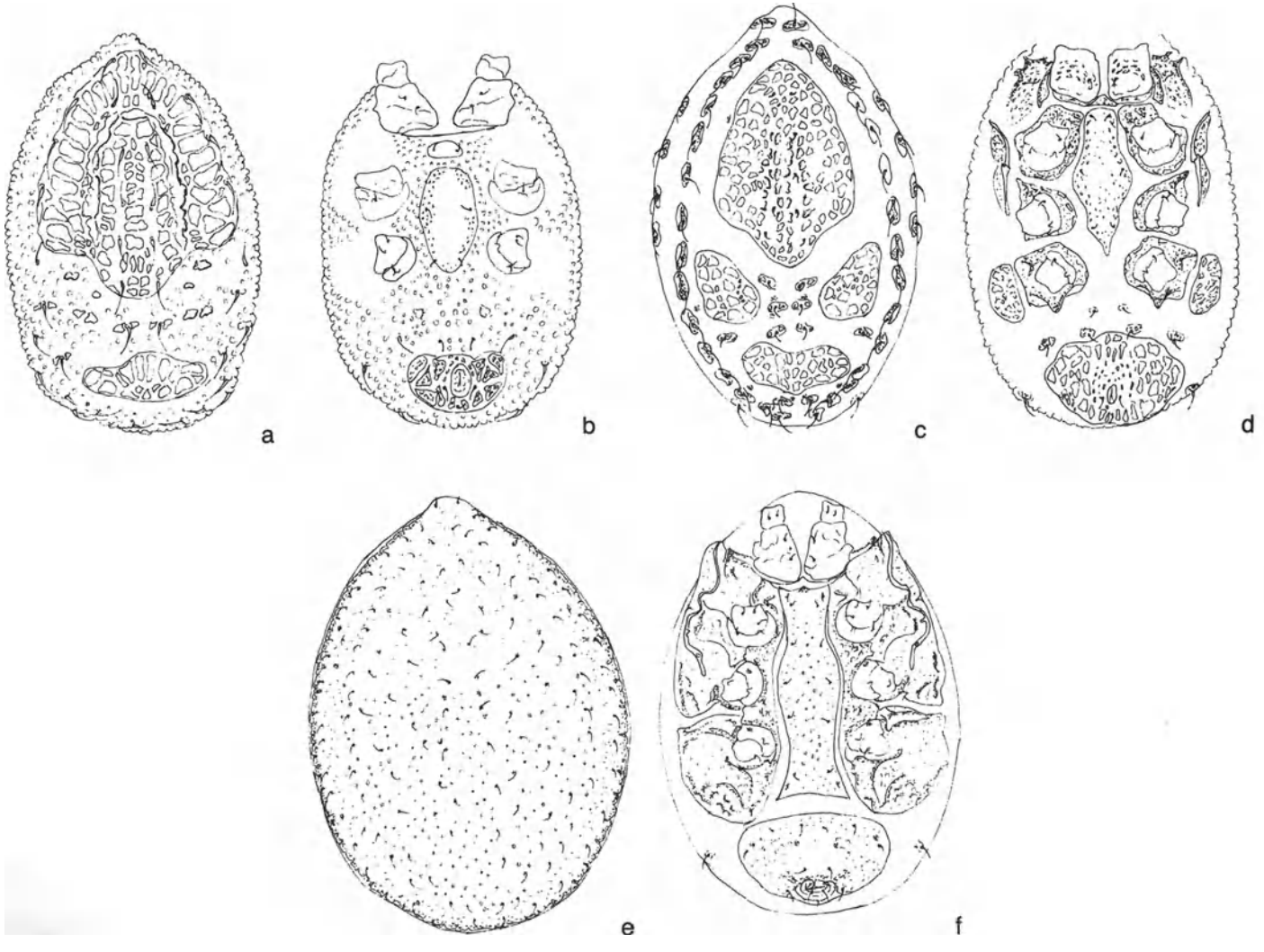
Fig. 21.1 The main phases in embryonic development of *Trichouropoda obscurasimilis* Hirschmann & Zirngiebl-Nicol. (*a*) Blastoderm formation during the first 24 h of embryonic development. (*b*) Blastoderm differentiation. (*c*) and (*d*) Segmentation of germ band in lateral (*c*) and frontal (*d*) aspect. (*e*) and (*f*) Commencement of shortening of germ band in lateral (*e*) and frontal (*f*) aspect. (*g*) and (*h*) Final stage of shortening of germ band in ventral (*g*) and dorsal (*h*) aspect. (*i*) Embryo just before hatching with retrogressive rotation completed. A, acron (cephalic lobe); CH, cheliceral buds; L, labrum; P, pedipalps; T, telson (anal lobe); V, vitellus (yolk); I–IV, legs I–IV.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occur outside the body of the female, hence its relatively long duration. It usually takes 10–12 days from the moment of egg laying to the hatching of the larva; the mean duration of the development of 15 eggs in the cold period of the year, is 11.1 days. The data given by Krasinskaya (1961) for six species of uropodid mites indicate incubation durations of 6–19 days depending on species. In the species investigated by Radinowsky (1965a), the average duration of embryonic development varied greatly depending on the temperature conditions (ranging from 26.1 days at 10 °C to 2.5 days at 30 °C).

Although Radinowsky did not study embryonic development, he affirmed that, in an egg examined under the microscope 24–48 h after laying, he saw an embryo with well-developed legs. This showed that in the newly laid egg of *Leiodinychus krameri* (Can.), there was already a formed embryo as is usual with the gamasid mites. In *T. obscurasimilis*, a single case was observed in which the embryo developed very quickly in an egg laid by a female soon after emergence to the adult stage. In this female, copulation took place 4 days after emergence. After another 4 days she laid an egg, and the larva hatched after a further 4 days. This egg developed in 4 days compared to the usual duration of 10–12 days for other eggs incubated at the same time, thus excluding the influence of temperature. One might assume, therefore, that the embryo was already formed when the egg was laid or, if not, embryo development was more rapid than normal. It is thus possible that the age of the female may be a factor influencing the duration of embryonic development in uropodid mites.

Postembryonic development

The pre-adult stages of *T. obscurasimilis* have not yet been described. I shall concentrate in what follows, on such aspects as the duration and behaviour of these stages. Dorsal and ventral views of the postembryonic stages are illustrated in Fig. 21.2*a–f*.

All stages, including the adults, emerge similarly, after a pre-ecdysial resting period during which they do not feed, and remain immobile in hiding places, usually at the edge or under the filter-paper in the culture vessel, and only leave these places if disturbed. In this phase, in each stage, a complete reconstruction of internal structures takes place. Its duration differs from stage to stage, and increases in length as develop-

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Fig. 21.2 The larva (*a*, *b*) protonymph (*c*, *d*) and deutonymph (*e*, *f*) of *Trichouropoda obscurasimilis* Hirschmann and Zirngiebl-Nicol in dorsal (*a*, *c*, *e*) and ventral (*b*, *d*, *f*) aspects.

ment proceeds. Thus, this quiescence in the larva lasts 1–3 days, in the protonymph 4–5 days while in the deutonymph, it sometimes takes 5–8 days. Completion of pre-ecdysial quiescence is indicated by a change in colour. The larva, initially a whitish colour, changes to a pinkish-yellow. The protonymph changes from pinkish-yellow to a brownish colour and the deutonymph, which is usually brownish, becomes darker.

Before moulting begins, the integument of the previous stage slips anteriorly but remains unseparated posteriorly. The moulting individual first extricates its mouthparts and forelegs, than the posterior ones and finally leaves the exuvia. The process of emergence lasts 30–120 min depending on the stage. In all stages, the newly emerged individual is soft and fragile. It hides and remains motionless until its legs strengthen. Then, it becomes very active exploring its surroundings with its pedipalps and first pair of legs, looking for food. All postembryonic immature stages, including the larvae, feed intensively on the same food as the adults. After feeding they grow rapidly, usually doubling in size before ecdysis to the next stage.

Under the present experimental conditions the duration of each pre-adult stage differs seasonally depending on the external temperature to which the duration is inversely related – the higher the external temperature, the shorter the duration. The data on the duration of post-embryonic development obtained in the present experiment for each of the months, July 1976 to April 1977 inclusive, are given as mean values in Table 21.1. Analysing these data, it can be seen that the larval stage is the shortest one and the deutonymphal stage, the longest one. Thus, the larval stage lasts 11.5–18.7 days, depending on the time of year development took place, with an overall mean of 13.9 days for the 91 larvae reared (Table 21.1). The equivalent mean durations for the protonymphs were 17.0–33.0 days, and an overall mean of 20.0 days (54 individuals). Likewise, the means for deutonymphs were 25.0–42.8 days, and an overall mean of 37.0 days (25 individuals). The total duration for postembryonic pre-adult development is, on average, 58.0 days in July–August, and 85.3 days in September–November (Table 21.2). The development of the male is, usually, a little more rapid (1–2 days) than that of the female, but not in all months (Table 21.1). This has also been observed in gamasid mites (Ignatowicz, 1974). Of those reaching the adult stage, 58.3% were females.

The present data on the duration of each stage as well as of the complete cycle from egg to adult are roughly similar to those obtained by Krasinskaya (1961) for *Urodinychus janeti* Berl. (= *T. spatulifera*) and by Radinowsky (1965a) for *Leiodinychus krameri* (= *T. orbicularis*) at a temperature of 20 °C. This suggests that the duration of development among *Trichouropoda* species may be similar. The duration of embryonic and

Table 21.1 Mean duration of postembryonic development (egg eclosion to adult emergence) of *Trichouropoda obscurasimilis* Hirschmann & Zirngiebl-Nicol at room temperature in relation to month of emergence of larva

	Development duration (days)								
Month	*No.*	*Larva*	*No.*	*Protonymph*	*No.*	*Deutonymph*	*Adult (sex)*	*No.*	*Total*
July, 1976	4	11.5	2	17.0	1	25.0	F	—	—
							M	1	58.0
August	5	12.5	2	25.5	—	—	—	—	—
September	8	13.4	8	28.8	8	39.9	F	5	80.2
							M	3	81.6
October	3	13.6	—	—	—	—	—	—	—
November	7	15.6	5	27.5	5	42.8	F	2	84.5
							M	3	94.3
December	8	14.4	4	33.0	2	36.0	F	1	90.0
							M	1	79.0
January, 1977	10	18.7	8	27.1	4	28.5	F	2	77.5
							M	2	71.5
February	7	14.6	2	27.0	2	40.5	F	2	85.0
March	15	14.6	15	25.2	3	33.3	F	2	78.0
April	24	13.1	8	21.5	—	—	—	—	—
Overall mean	91	13.9	54	20.0	25	37.0	F	14	81.5
							M	10	80.8

Table 21.2 Averaged durations of development from egg eclosion to adult emergence of *Trichouropoda obscurasimilis* at room temperature on a seasonal basis (see Table 21.1 for monthly data)

	Development duration (days)			
Months	*Larva*	*Protonymph*	*Deutonymph*	*Total*
July–August	11.9	21.2	25.0	58.0
September–October	14.3	28.1	41.0	85.3
November–February	16.1	28.8	33.0	79.6
March–April	13.6	23.9	33.0	78.0

postembryonic development of an individual of *T. obscurasimilis* to the adult stage varies between 91.9–92.6 days. It is, thus, possible that with this species, there may be as many as four generations a year under experimental conditions. These data are quite similar to those obtained for a field population of this species (Huţu, 1979).

The mortality rate, within each stage, under laboratory conditions, was 40.7% for the larval, 53.7% for the protonymphal, and 4% for the deutonymphal stage. These data confirm previous observations, which indicated that the deutonymphal stage is the most resistant one in uropodid mites (Athias-Binche, 1981). The high mortality in the first two postembryonic stages may be due, on the one hand to the greater vulnerability of these stages because of their soft integument and, on the other, to their relatively long duration (especially the protonymph), thus increasing their chances of being exposed to adverse environmental conditions. Under natural conditions, the mortality of these stages may be much greater because of natural enemies and, sometimes, lack of food.

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22

Resource allocation and utilization contrasts in Hypoaspis aculeifer *(Can.) and* Alliphis halleri *(G. & R. Can.) (Mesostigmata) with emphasis on food source*

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Feeding experiments with *Hypoaspis aculeifer* (Can.) indicated that when *Onychiurus* Collembola, *Rhabditis* nematodes and *Tribolium* eggs were used as prey, the durations from egg deposition to adult emergence were 31–34 days at *c.* 15 °C but fecundities were low. Collembola were the least suitable prey. Females with access to males for 1, 3 and 6 days, and fed on *Tyrophagus putrescentiae* (Schrank), produced on average, 95 eggs/female over 88 days. The female : male sex ratio of the progeny was 1.1 : 1.0. With females in the absence of males, oviposition commenced earlier and continued for a longer time than with those reproducing sexually. Egg production was 51 eggs/female.

Three nematodes were used as prey for the 2-sex cultures of *Alliphis halleri* (G. &. R. Can.). The pre-adult life cycle lasted 9.0–17.1 days at *c.* 15 °C. The pre-oviposition period was very short in all treatments. The fecundities with *Pelodera* (*P.*) *strongyloides* (Schneider) and *Nematospiroides dubius* Baylis prey were 96 and 110 eggs respectively oviposited over 34 and 69 days. In almost all comparisons the third nematode, *Globodera rostochiensis* (Woll.), proved the least suitable prey. The estimated fresh weights of nematodes captured

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by the adult female were 786 μg of *Pelodera* and 752 μg of *N. dubius*. The equivalent weights for males were 372 and 213 μg. The pre-adult means for these two nematodes were 30 and 15 μg respectively. For adults and pre-adults the amounts for *Globodera* were very much less. The chapter concludes with a brief discussion of the contrasting lifestyles of the two predators

INTRODUCTION

In recent years there has been considerable interest in the role of predatory soil mites in reducing populations of pest species inhabiting this milieu. The experiments described here refer to laboratory studies of two gamasine mites, *Hypoaspis aculeifer* (Can.) and *Alliphis halleri* (G. & R. Can.), which commonly occur in soil among other habitats. They were carried out in 1976–78, and form part of a field and laboratory research project of the Mesostigmata of grassland soil (Sardar, 1980). One of the objectives was to determine the effect of arthropod and nematode food sources on durations of the pre-adult and adult stages, juvenile mortality, fecundity, the lengths of the pre-oviposition, oviposition, and post-oviposition periods, and egg viability of the progeny.

MATERIALS AND METHODS

The mites were cultured in circular containers (*d* 5–6 cm) with floors of a plaster of Paris–charcoal mixture and sealed with cling film. The cultures were maintained in an illuminated incubator with heating and cooling facilities to provide a temperature of *c.* 15 °C (15.0–16.5 °C). This temperature was chosen because of its use as a reference point in population-dynamics studies of soil arthropods. In most instances the mites were cultured in replicated groups of between two and five individuals. The stage–day method as described by Usher and Stoneman (1977) was used to estimate durations. Because of the death of individuals during an experiment, the analysis of variance used had an unbalanced-block design with replicates as blocks, and food sources, etc. as treatments. With the exception of the first experiment with *H. aculeifer*, the eggs and other individuals used were those of females reared from birth on the same diet as that chosen for the experimental test. Most of the prey provided were laboratory-reared, an abundance of live prey being added at 1–4 day intervals after the removal of uneaten prey items. Where nematodes were the food source, Ito's (1971) method was used, the prey – in an aqueous suspension – being placed in a circular depression (*d* 1.4 cm and *c.* 0.2 cm deep) in the plaster floor of the culture vessel. There was no evidence of cannibalism with either species (for *H. aculeifer* cf. Usher and Davis, 1983). In two experiments

adults were measured after death. Four dimensions were determined: idiosomal length, greatest breadth, and lengths of the tibia and tarsus of leg I.

RESULTS

Hypoaspis aculeifer

Hypoaspis aculeifer, with a female idiosomal length of *c.* 700 μm, is a medium-sized laelapid mite. It is somewhat stockily built with a length : breadth ratio of 1.9 : 1.0, and with its relatively long, powerful legs and large chelicerae, gives the impression of considerable strength. It is said to be a voracious predator (Ignatowicz, 1974) and has been characterized as polyphagous (Karg, 1961). The larva is sluggish in its movements and does not feed. According to Ignatowicz it utilizes the yolk remaining from the embryonic stage.

In the first experiment reported here a comparison was made of *Onychiurus armatus* group, *Rhabditis* nematodes, and eggs of *Tribolium* spp. as prey for *H. aculeifer*. Between 10 and 15 Collembola, 20–25 *Tribolium* eggs, and *c.* 0.5 ml of a concentrated suspension of nematodes were given daily to each of six replicates per prey with five mites per replicate. The pre-adult durations (egg deposition to adult emergence) were 30.8–33.7 days (mean of 31.0 days for *Rhabditis* and *Tribolium*), and differed little among treatments. Fecundity was low with means of 11–14 eggs/female for the *Onychiurus* and *Rhabditis* prey, and 27 for the *Tribolium* eggs. In a number of respects, including immature mortality and size of adult, *Onychiurus* proved the least suitable prey. In both sexes these individuals had at least one dimension that was smaller than that of those reared on *Tribolium* eggs. The progenies from each treatment had egg viabilities >90%.

In a second experiment the predator was fed on *Tyrophagus putrescentiae* (Schrank), the prey consisting of all postembryonic stages including adults. The experiment was designed primarily to test the effect on females of access to males for 24 hours, 3 days, and 6 days, and because of its nature had to be limited to a total of six females. The discussion here centres mainly on fecundity, longevity, and other durations (Table 22.1). We have no data for the pre-adult lifespan using *T. putrescentiae* as prey. Lobbes and Schotten (1980), in a series of experiments with this food source, determined this duration in the dark at a range of temperatures and found that it lasted 35.8 days at 15 °C.

There were no significant differences among replicates or treatments for adult longevity, pre-oviposition, oviposition, and post-oviposition periods. The overall mean adult lifespan was 185 ± 5.8 days, and the

oviposition period, 87.5 ± 8.4 days. The pre-oviposition and post-oviposition durations were very variable, the former lasting about one-quarter to one-third the adult longevity in most instances. The mean egg productions/female for the three treatments were 94.0–96.5 (overall mean 95.3 ± 4.9), which is much higher than in the first experiment. Barker (1969), using the same prey, recorded a mean fecundity of 55.4 eggs for cultures at 24 °C. In cultures maintained at 18.5 °C Lobbes and Schotten obtained a mean fecundity of 88.9 eggs/female. They found that total egg production increased with decreasing temperature, which would support the conclusion that their finding and ours are in close agreement. These results would suggest that *T. putrescentiae* is a suitable food source for this species.

A total of 572 eggs were recovered, and these were placed in culture to determine their sex at the adult stage. With the exception of one mother, non-viable eggs were < 9% of the total. Mortality in the postembryonic juvenile stages was close to 10%. The sex ratios of the progenies were very slightly greater than unity in the three treatments, the overall female : male ratio being 1.1 : 1.0. This was a somewhat surprising result but it is worth noting that it is close to the ratio of 1.06 : 1.00 given by Lobbes and Schotten where females had access to males throughout their adult life. Irrespective of duration of access to males there was a quite striking pattern in the sexes of the progeny in relation to time of production of eggs in the oviposition period. In the early part of this period a high proportion of the progeny was female, whereas eggs produced toward the end of oviposition were almost all males.

It has now been established that *H. aculeifer* is an arrhenotokous species (de Jong *et al.*, 1981). However, at the time these experiments were carried out the literature suggested that this species reproduced

Table 22.1 Mean durations (days) and fecundities of adult females of *Hypoaspis aculeifer* (Can.) having access to males for 1, 3, and 6 days (2 replicates/treatment; 1 female/replicate)

	Access to male (days)			
Adult stage	*One*	*Three*	*Six*	*F-ratio (treatments)*
Longevity	197.5	175.0	183.0	3.87
Eggs/female	96.5	95.5	94.0	0.07
Pre-oviposition period	53.5	47.0	61.0	0.08
Oviposition period	77.5	84.0	101.0	2.11
Post-oviposition period	66.5	44.0	21.0	0.67

only sexually. In an earlier experiment we had evidence of parthenogenetic reproduction, and because of this it was decided to obtain information on the fecundities of individuals reproducing in the absence of males, using the same culture conditions as in the previous experiment. Three populations were compared: two laboratory cultures, one of which had been maintained as a stock culture for about 17 months, and the third, the F_2 generation of a field population.

The results for the three populations are given in Table 22.2. There are few significant differences when the populations are compared. The overall mean pre-oviposition period was 5.7 ± 0.6 days, and oviposition lasted 153.1 ± 7.5 days. The mean fecundities of the three populations were 43–58 with an overall mean of 51 ± 6.6 eggs/female. These fecundities are much lower than that obtained by Lobbes and Schotten (1980) who reported 89.8 eggs/virgin female in cultures maintained at 24.5 °C using *T. putrescentiae* as prey. This fecundity was appreciably higher than that of two-sex cultures at this temperature. The populations differed markedly in the rate of egg production. In the two laboratory cultures 49–81% of the eggs were oviposited in the first four weeks of oviposition. The situation in the field population was quite different. Here egg production in the first eight weeks was low, and did not reach a peak until weeks 13–16 after oviposition commenced. This would suggest that for some reason there was a selection in the laboratory stocks for females that produced a large proportion of their eggs at an early stage in the reproductive phase.

There are some striking differences in the dynamics of reproduction when the two-sex and single-sex experiments are compared (Table 22.3). Thus the pre-oviposition duration is much shorter and oviposition longer in the one-sex cultures, whilst egg production is just over half

Table 22.2 Mean durations (days) and fecundities of 3 populations of adult females of *Hypoaspis aculeifer* (Can.) reproducing parthenogenetically (3 replicates of 5 individuals for each population)

Observation	*Population*			*F-ratio (populations)*
	Laboratory	*Laboratory (stock culture)*	*Field*	
Longevity	212.4	192.5	214.9	3.41
Eggs/female	51.7	42.8	58.1	1.34
Pre-oviposition period	5.4	5.0	6.8	2.16
Oviposition period	154.3	156.3	148.7	0.28
Post-oviposition period	52.7	31.2	59.4	3.64

Table 22.3 Overall mean and standard error of adult durations in days and fecundity of *Hypoaspis aculeifer* (Can.) in one-sex and two-sex cultures (one-sex: 3 replicates/treatment, 5 females/replicate, 3 treatments; two-sex: 2 replicates/treatment, 1 female/replicate, 3 treatments)

Observation	*One-sex culture*	*Two-sex culture*
Adult longevity	206.6 ± 6.6	185.2 ± 5.8
Eggs/female	50.8 ± 6.6	95.3 ± 4.9
Pre-oviposition period	5.7 ± 0.6	53.8 ± 25.2
Oviposition period	153.1 ± 7.5	87.5 ± 8.4
Post-oviposition period	47.8 ± 7.7	43.8 ± 27.8

that of those where both sexes are present. The major differences between the field and laboratory populations is the more rapid production of eggs by the laboratory females.

Recent theories concerning sex allocation have a bearing on how this property should be regarded in ecological terms. With a reproductive mode such as arrhenotoky, sex – from certain points of view – might be regarded as a resource which can be manipulated depending on circumstances. In this context an arrhenotokous species may have more than one string to its bow: first, the parthenogenetic production of males is an obvious advantage if this sex is scarce or absent; and second, the possibility that the sex ratio can be modified when reproduction is biparental, although in theory daughters would be expected in these circumstances.

Alliphis halleri

The second predator, *A. halleri*, belongs to the family Eviphididae. The female has an idiosomal length of about 460 μm with a length : breadth ratio of 1.5 : 1.0, and is much smaller than *H. aculeifer*. The chelicerae have short digits, and the legs are somewhat stumpy, all being shorter than the idiosma. Both nymphs and adults move very rapidly in culture. So far as is known it is monophagous (Sardar and Murphy, 1987), feeding on nematodes. Unlike *H. aculeifer* the larva is an active, feeding stage, and deuteronymphs and adults can have a phoretic association with insects such as Coleoptera and Diptera.

It was cultured in the same way as *H. aculeifer* with food added at 2-day intervals, using three nematodes as prey: third-stage infective larvae of *Nematospiroides dubius* Baylis, a strongylid parasite of rodents; larvae of *Pelodera* (*P.*) *strongyloides* (Schneider), a bacterial-feeding species, and second-stage larvae of the Potato cyst nematode, *Globodera rostochiensis*

Table 22.4 Mean durations (days) of pre-adult and adult stages of *Alliphis halleri* (G. & R. Can.) in relation to food source (4–5 replicates/prey)

Stage	*Nematospiroides dubius*	*Pelodera strongyloides*	*Globodera rostochiensis*	*F-ratio (prey)*
Pre-adult durations (4–5 mites/replicate)				
Egg	2.0	2.0	2.2	1.00
Larva	2.2	2.0	2.7	6.44*
Protonymph	2.3	2.0	4.5	21.49***
Deuteronymph	2.9	3.0	7.7	93.24***
Total	9.4	9.0	17.1	
Adult longevity (2 ♂ ♂ + 2 ♀ ♀/replicate)				
Male	86.4	52.3	41.5	7.94*
Female	87.9	55.8	47.7	3.42
Pre-oviposition period	3.2	3.4	9.2	
Oviposition period	69.3	33.6	31.8	8.18*
Post-oviposition period	18.2	22.2	13.2	0.57

*$P < 0.05$; ***$P < 0.001$.

(Woll.). For the most part, stocks of live nematodes were maintained in water in a refrigerator at a temperature of about 4 °C.

The pre-adult life cycle had means per treatment of 9.0–17.1 days (Table 22.4) and mortalities of 12–28%. The sex ratio of the adults was 0.97 : 1.00. Mean adult longevities were 41.5–86.4 days for males, and 47.7–87.9 days for females. Pre-oviposition periods were short, with means of 3.2–9.2 days; oviposition lasted 31.8–69.3 days, and post-oviposition, 13.2–22.2 days (Table 22.4). Mean fecundities were 10–110/female, and the egg viability of the progeny, 68–91%. In the *N. dubius* and *Pelodera* treatments most of the non-viable eggs were laid toward the end of the oviposition period. The duration of each pre-adult stage except the egg was longer when *G. rostochiensis* was the food source (Table 22.4); immature mortality was greater, the adults were smaller, pre-oviposition longer, and fecundity and egg viability very much lower than in the other two treatments. In most respects there were no significant differences for the other two prey. The major exception was the oviposition period which lasted 34 days with *Pelodera* compared to 69 days with *N. dubius*. The question arises as to why egg production should take so much longer when *N. dubius* was used as prey. It is likely that the nutrient composition of the two nematodes differs, and the rates of egg production might be a reflection of this. The infective third-stage larva of *N. dubius* is not unlike a diapausing insect, and contains

Table 22.5 Mean number and biomass (μg) of nematodes captured by immature and adult stages of *Alliphis halleri* (G. & R. Can.) (5 replicates/prey; 5 individuals and 4 adults/replicate)

	Nematospiroides dubius		*Pelodera strongyloides*	
Stage	*Number*	*Biomass*	*Number*	*Biomass*
Pre-adult	94	14.8	109	30.0
Adult				
'Individual'*	3037	482.5	2124	579.0
Male	1331	212.9	1499	371.7
Female	4743	752.1	2749	786.3

*Mean/individual of 2 males and 2 females.

considerable food reserves in the form of lipids (Bryant, 1973). The *Pelodera* larvae were from cultures consisting of individuals which were developing to the adult stage, and there was no evidence of an arrest of growth in this species. It is possible that with *Pelodera*, nutrients were present in a more readily assimilable form, and this may account for the more rapid rate of egg production with this diet.

The fresh weights of nematodes captured were estimated, using a measuring technique devised by Andrássy (1956). Table 22.5 gives the numbers and biomass for *N. dubius* and *Pelodera*. The mean predation by the 'adult' (male + female) was 81 μg per individual for *Globodera*, 483 μg for *N. dubius*, and 579 μg for *Pelodera*. All combinations had very highly significant differences. The equivalent means for the immatures were respectively 17, 3, and 5% of the total lifetime predation (juvenile + 'adult') with predation of the latter two species 15 and 30 μg respectively. It should be stressed that the amounts ingested will be less as the predator discards the outer integument of the nematode. As these data referred to replicates containing two males and two females, a separate test was carried out to determine adult male predation of *Pelodera* and *N. dubius*, and these results were used to derive a mean biomass per adult female for each treatment (Table 22.5). The means for the latter were 752 μg for *N. dubius* and 786 μg for *Pelodera*; the values for males were 213 and 372 μg respectively.

DISCUSSION

It is clear from existing information that *H. aculeifer* and *A. halleri*, although found in the same habitat, have contrasting lifestyles, and the

Table 22.6 A comparison of the biological and population-dynamics attributes of sexually reproducing *Hypoaspis aculeifer* (Can.) and *Alliphis halleri* (G. & R. Can.) when cultured at 15 °C

Attribute	*Hypoaspis aculeifer*	*Alliphis halleri*
Idiosomal length (♀)	*c.* 700 μm	*c.* 450 μm
Prey specificity	Polyphagous	Nematophagous
Reproduction	Arrhenotokous	? Obligate sexual
Phoresy	? No	Yes
Non-feeding larva	Yes	No
Pre-adult life cycle	*c.* 31 days	*c.* 9 days
Female longevity (adult)	*c.* 180–200 days	*c.* 55–90 days
Pre-oviposition period	*c.* 50 days (variable)	*c.* 3 days
Oviposition period	*c.* 90 days	*c.* 30–70 days
Eggs per female	*c.* 95 days	*c.* 100 days

results reported here reinforce this viewpoint. Thus when the two species are compared (Table 22.6), *H. aculeifer* has a relatively long pre-adult life cycle at 15 °C, a non-feeding larva, and all feeding stages accept a wide spectrum of prey. The adult female has a long lifespan, and reproduction is arrhenotokous. When reproduction is sexual the pre-oviposition period is variable and can be extremely long. *Alliphis halleri* is a smaller mite, a phoretic species, and resource utilization is geared to rapid development. It has an active, feeding larva, and a very short pre-adult duration. All stages are probably monophagous and feed on nematodes. The results of the experiments suggest that the adult female has a longevity approximately half that of *H. aculeifer*, and a short pre-oviposition period. Neither the oviposition period nor the fecundity differed greatly in the two species.

Alliphis halleri is an early but possibly transient colonizer of agricultural habitats especially where soil micro-arthropods have been reduced in number by chemical or other means (see, for example, Buahin, 1965). It could be regarded as an opportunistic species capable of rapidly exploiting such a situation. *Hypoaspis aculeifer*, also widely distributed, is a permanent inhabitant of grassland and arable soils but does not appear to be very abundant in these situations. The biological attributes of *A. halleri* would appear to be of the type that tends to maximize its rate of population increase. This would suggest that it is an *r*-strategist, capable of rapidly exploiting resources when conditions are appropriate. *Hypoaspis*, in contrast, would appear to have some of the attributes of a *K*-strategist, and present knowledge of the dynamics of field populations of this species would support this view.

CONCLUSION

All the evidence suggests that *H. aculeifer* is a particularly good subject for population-dynamics studies in the laboratory. It is readily available and easy to culture. It has a non-feeding larva, a stage easily damaged in handling procedures, and it is not subject to cannibalism except perhaps under extreme conditions. With this species it is possible that access to the male over a short period is sufficient to ensure a full complement of eggs. This could be an important advantage in energetics studies as, for example, in the *A. halleri* experiment where it was only possible to obtain indirectly an estimate of the food consumption of the female.

Finally, there are some practical implications arising from certain of the results reported here. The first, though by no means a new finding, concerns the hazards resulting from experimentation using a population maintained over a long period in laboratory culture. There is always the danger, as exemplified in the third experiment with *Hypoaspis*, that changes may occur resulting in the population being no longer representative of that occurring in the field. The second relates to the use of rate of egg production as a yardstick when comparing treatments such as diets or other factors. There are obvious dangers when such a measure has been determined over a short period, and often without reference to the part of the oviposition period chosen for the comparison. Further, although fecundities may be similar with different food sources, the durations of the oviposition period may differ as, for example, *A. halleri* provided with *Pelodera* and *N. dubius* prey. There is a further example with the field and laboratory populations of *H. aculeifer*. In such circumstances the use of egg-production rates over a limited period could be very misleading. With arrhenotokous species there is the possibility of an additional complication in that egg production may differ in one-sex and two-sex cultures.

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23

The influence of different host plants on the reproductive potential of Tyrophagus putrescentiae *(Schrank) and* Tyrophagus neiswanderi *Johnston and Bruce (Acaridae)*

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The importance of acarid mites of the genus *Tyrophagus* as pests of ornamental plants was shown by Wilkin *et al.* (1976), Ciampolini *et al.* (1985) and Czajkowska *et al.* (1988). Preliminary results of investigations on the bionomics and damage caused by these mites were published by Czajkowska *et al.* (1988). In this report, the results of further observations on the bionomics of *Tyrophagus putrescentiae* (Schrank) and *T. neiswanderi* Johnston and Bruce are presented.

The effect of four different host plants (freesia and crocus corms, tulip and hyacinth bulbs) on the duration of development (egg deposition to adult emergence), mortality, fecundity and longevity of the mites was studied. All rearings were carried out in sterilized rearing cages placed in desiccators at constant humidity (85% r.h.) and a temperature of 25 °C. The data were calculated in the form of demographic parameters. The unit of time for the latter is a week.

As shown in Table 23.1 and Fig. 23.1, the nature of the food had a marked effect on the development and fecundity of the mites. For both species, corms proved a more favourable food than either tulip or hyacinth bulbs. In most instances, *T. neiswanderi* had a lower rate of

Table 23.1 Mean duration from egg deposition to adult emergence and mortality of *Tyrophagus putrescentiae* (Schrank) and *T. neiswanderi* Johnston and Bruce in relation to host plant at 25 °C

Host plant	*T. putrescentiae*			*T. neiswanderi*		
	Duration (days)		*Mortality*	*Duration (days)*		*Mortality*
	Mean	*Range*	*(%)*	*Mean*	*Range*	*(%)*
Freesia corms	12.5	11–16	16^{bc}	13.4	12–15	29^{c}
Crocus corms	13.0	11–17	8^{c}	17.0	12–20	29^{c}
Tulip bulbs	17.5	12–22	56^{a}	18.0	10–23	55^{b}
Hyacinth bulbs	21.0	12–26	28^{b}	22.0	19–22	50^{b}

[a,b,c] Duncan test: percentages with the same superscript do not differ significantly at $P \leq 0.05$.

Table 23.2 Estimates of demographic parameters for populations of *Tyrophagus putrescentiae* and *T. neiswanderi* on 4 host plants

Tyrophagus species	*Host plant*	*Parameters*				
		Intrinsic rate of increase (r_m)	*Net reproduction rate (R_0)*	*Mean generation time (T)*	*Finite rate of increase (λ)*	*Gross rate of reproduction*
T. putrescentiae	Freesia corms	0.908	82.104	4.856	2.476	118.600
	Crocus corms	1.441	68.935	4.225	2.938	84.100
	Tulip bulbs	0.588	13.376	4.408	1.801	34.000
	Hyacinth bulbs	0.478	24.001	6.648	1.613	39.900
T. neiswanderi	Freesia corms	0.999	32.200	3.510	2.714	52.000
	Crocus corms	0.779	18.650	3.754	2.180	26.800
	Tulip bulbs	0.456	7.868	4.523	1.578	21.200
	Hyacinth bulbs	0.241	5.529	7.104	1.272	13.500

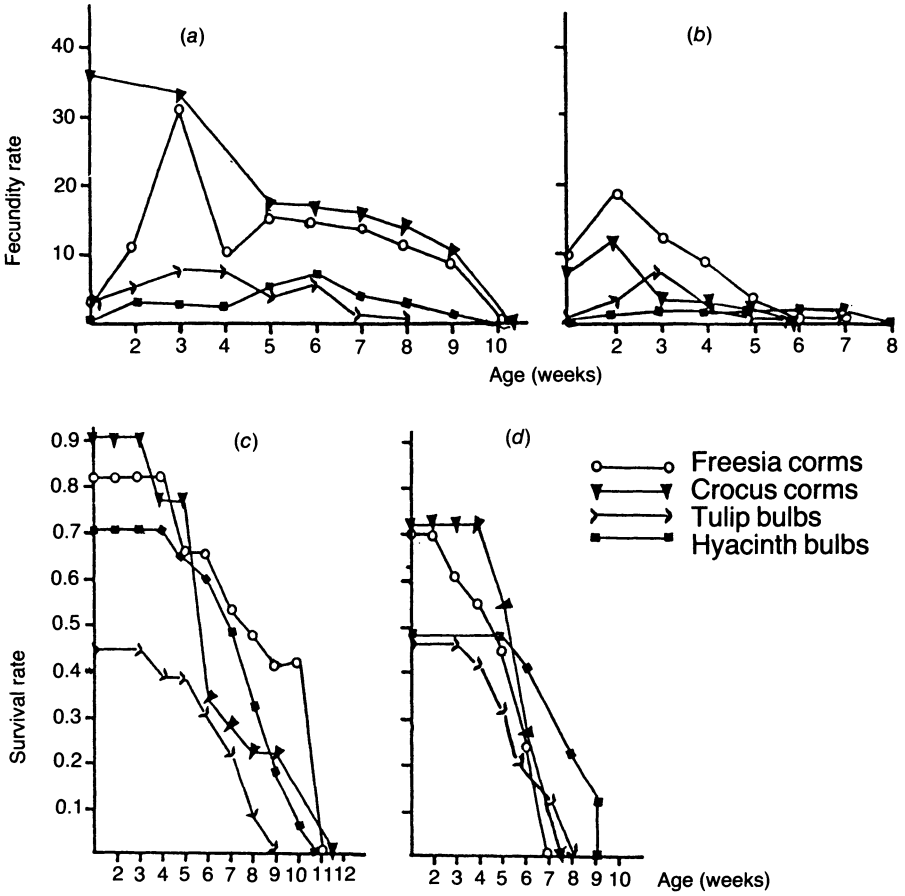

Fig. 23.1 Agespecific egg production (m_x) and survival rates (l_x) of *Tyrophagus putrescentiae* (Shrank) (*a, c*) and *T. nieswanderi* Johnston and Bruce (*b, d*) in relation to host plant at 25°C.

population increase than *T. putrescentiae*. High intrinsic rates of increase (r_m) were obtained when mites were fed on crocus and freesia corms in the case of *T. putrescentiae*, and on the latter in the case of *T. neiswanderi* (Table 23.2). The population of *T. putrescentiae* had the most rapid rate with an 82-fold increase during the generation development period (R_o = 82.104) on freesia corms; on the same host plant *T. neiswanderi* increased only 32 times. For both species, the lowest value of R_o occurred on bulbs. The relatively high demographic parameters obtained with the chosen plants explains the frequent occurrence of these species as pests of ornamental plants under greenhouse conditions.

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24

The relationship between house-dust mites and fungi

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Two xerophilic fungi, *Aspergillus penicilloides* Spegazzini and *Wallemia sebi* von Arx, were isolated from the alimentary tract of laboratory cultures of pyroglyphid dust mites. Between 60 and 84% of adult female mites bore fungi. In *Dermatophagoides microceras* Griffiths and Cunnington, *Euroglyphus longior* (Trouessart) and one culture of *D. pteronyssinus* (Trouessart), *A. penicilloides* was the dominant fungus and *W. sebi* was isolated from 10% or fewer mites. In *E. maynei* (Cooreman), *D. farinae* Hughes and a second culture of *D. pteronyssinus*, the incidence of fungi was reversed, with *W. sebi* in 56–73% of mites and *A. penicilloides* in only 8–10% of mites. Acetone-washed beard shavings, a dietary component of laboratory cultures of dust mites, contain a variety of xerophilic fungi including *A. penicilloides* and *W. sebi*. It is concluded that mites select *A. penicilloides* and *W. sebi*, and other fungi are not ingested or are killed by the digestive processes of the mites. Possible reasons for the variation in fungi associated with different cultures of mites are discussed

INTRODUCTION

Xerophilic fungi of the genus *Aspergillus* have been isolated from laboratory cultures of pyroglyphid house-dust mites (van de Lustgraaf, 1978a). They have also been reported free-living in house dust (van de Lustgraaf, 1978b; van Bronswijk, 1981), and may be particularly abundant in dust infested with mites (Sinha *et al.*, 1970).

Although very few experimental studies have been conducted on the relationship between dust mites and these fungi, there is a general consensus in the literature that the fungi may be of nutritional significance to the mites. Van Bronswijk and Sinha (1973) reported a sixfold population increase of *Dermatophagoides pteronyssinus* (Trouessart), over

two generations on a diet of defatted dander and yeast, but a 35-fold increase if the diet was pre-incubated with *A. amstelodami* Thom and Church. Douglas and Hart (1989) demonstrated an increased developmental rate of *D. pteronyssinus* when the diet of yeast and wheat germ was supplemented with *Aspergillus penicilloides* Spegazzini. It has been proposed that the fungi contribute to the sterol and vitamin requirements of the dust mites (van Bronswijk and Sinha, 1973; de Saint Georges-Gridelet, 1987).

Apart from these few investigations on possible nutritional interactions in *D. pteronyssinus*, virtually nothing is known about the relationship between dust mites and fungi. This is so despite the well documented involvement of these mites in the allergenicity of house dust (reviewed by Fain *et al.*, 1988), and the suggested role of fungi in that allergenicity (Sinha *et al.*, 1970; van Bronswijk, 1981). The study reported here concerns the taxonomic identity of fungi in laboratory cultures of dust mites.

MATERIALS AND METHODS

Mite cultures were maintained in continuous darkness at 25 °C and 75% relative humidity, on a 5 : 1 (w/w) mixture of Yestamin dried yeast (English Grains Ltd, UK) and acetone-washed beard shavings, unless stated otherwise. Micro-organisms within individual surface-sterilized mites were isolated as described in Douglas and Hart (1989), and incubated at 25 °C for 2–4 weeks on malt-extract agar containing 3% malt extract (Oxoid L39, Oxoid Ltd, UK) and 0.5% (w/v) mycological peptone (Oxoid L40), solidified with 1.5% (w/v) technical agar No. 1 (Oxoid L11) and supplemented with 40% (w/v) sucrose. This medium was also used to isolate micro-organisms from the dietary components of the mite cultures.

RESULTS

Fungi in laboratory cultures of pyroglyphid dust mites

In the first experiments, the fungi in surface-sterilized *D. pteronyssinus* culture Holl/CAB were investigated. The sole isolate was the xerophilic fungus, *A. penicilloides* (a member of the *A. glaucus* group), which was recovered from 75–80% of adult females and 25–30% of adult males and tritonymphs. *Aspergillus penicilloides* has previously been isolated from *D. pteronyssinus* cultures by van de Lustgraaf (1978a).

Subsequent studies on the fungi associated with different species of pyroglyphid dust mites were conducted exclusively on adult females.

Table 24.1 The incidence of fungi isolated from surface-sterilized adult females of five species of pyroglyphid dust mites (means ± s.e. of 5 replicates (10 mites/replicate)

Mite species	*Mites containing fungi**		*Fungus-free mites*
	Aspergillus penicilloides	*Wallemia sebi*	
Dermatophagoides			
farinae Hughes	0.8 ± 0.5	6.4 ± 0.6	3.2 ± 0.6
microceras Griffiths & Cunnington	6.0 ± 0.5	0.4 ± 0.2	4.0 ± 0.5
pteronyssinus (Trouessart)	8.0 ± 0.5	0	2.0 ± 0.5
Euroglyphus			
maynei (Cooneman)	0.8 ± 0.5	5.6 ± 0.5	3.6 ± 0.5
longior (Trouessart)	6.6 ± 0.6	1.0 ± 0.4	1.6 ± 0.4
ANOVA	$F_{4,21} = 21.96$ $P < 0.01$	$F_{4,21} = 55.90$ $P < 0.01$	$F_{4,21} = 3.90$ $0.05 > P > 0.01$

*Some mites contained both *A. penicilloides* and *W. sebi*.

These investigations, summarized in Table 24.1, revealed, first, a further xerophilic fungus, *Wallemia sebi* von Arx, and second, considerable variation in the incidence of these fungi among the different mite species. Application of analysis of variance and Scheffe's multiple range test to the data in Table 24.1 demonstrated significant differences in the number of fungus-free mites between species, and the mean value for *D. microceras* Griffiths and Cunnington was greater than that for *Euroglyphus longior* (Trouessart) ($0.01 < P < 0.05$). At least 60% of adult females of all species contained fungi, and a distinct pattern in the number and identity of fungi in the different species was apparent. In *D. pteronyssinus*, *D. microceras* and *E. longior*, *A. penicilloides* was dominant (in 60–80% of mites), and *W. sebi* was present in 10% or fewer mites, but in *D. farinae* Hughes and *E. maynei* (Cooreman), *W. sebi* was dominant (in 55–65% of mites) and only 8% of individuals contained *A. penicilloides*. Individual mites containing either *A. penicilloides*, or *W. sebi* or both fungi were recorded in all species except *D. pteronyssinus* in which *W. sebi* was never observed.

As a first approach to investigate the basis for the occurrence of different fungal dominances in the mite species, use was made of the *D. pteronyssinus* culture, Holl/D53, that had been separated from the culture Holl/CAB of this species 18 months earlier, and maintained at room temperature (18–21 °C). In contrast to the mites in culture Holl/CAB, which bore *A. penicilloides* exclusively, 29 (73%) of 40 adult females in the culture Holl/D53 contained *W. sebi* and only four individuals (10%) had *A. penicilloides*; seven mites (17%) were fungus-free. These data indicate that the differences in the incidence of *A. penicilloides* and *W. sebi* between mite species is not inter-specific but an inter-cultural variation.

Location of *A. penicilloides* in *D. pteronyssinus*

Light- and electron-microscopical studies indicate that the fungi associated with *D. pteronyssinus* are located exclusively in the alimentary canal (Douglas and Hart, 1989). These observations suggest that *A. penicilloides* and *W. sebi* are ingested by the mites and, therefore, the fungi associated with the dietary components, dried yeast and acetone-washed beard shavings, were investigated. Acetone-washed beard shavings, but not the dried yeast, bore mycelial fungi of the genera *Penicillium*, *Aspergillus*, *Wallemia* and *Cladosporium*. Both *A. penicilloides* and *W. sebi* were present, but other fungi, especially members of the *A. glaucus* and *A. niger* groups, were more abundant.

DISCUSSION

The observation that *A. penicilloides* and *W. sebi*, recovered from dust mites, are not the most common fungi in the diet of mites suggests that these two species are selected by the mites and other fungi are discriminated against. Perhaps the mites do not ingest most species of fungi in their diet or, alternatively, *A. penicilloides* and *W. sebi* may survive the digestive processes of the mites.

The pattern of incidence of the fungi in the five species of mites is intriguing. No relationship between the identity of the 'dominant' fungus, that is, a fungus present in at least 60% of individuals, and mite genus (*Dermatophagoides/Euroglyphus*) was evident, and the dominant fungus even differed between the two cultures of a single stock of *D. pteronyssinus*. Furthermore, the incidence of fungi in *D. pteronyssinus* (the only species studied over a period of months) was stable for at least eight generations in the culture Holl/CAB, and at least three generations in the culture Holl/D53 (Hart and Douglas, unpublished results). These results raise two questions: why is one fungus dominant and why does the identity of the dominant fungus differ between cultures?

The possibility that the fungi in mites reflect those in the diet is unlikely because all the cultures of mites were maintained on an identical diet that contained both *A. penicilloides* and *W. sebi*. There remain differences in the feeding behaviour and/or digestive physiology between mite cultures as the major determinant(s) of the identity of the dominant fungus. We suggest that such differences may arise even within one stock of mites because the mite cultures pass through 'bottlenecks', that is, the population is reduced to a few individuals which do not include the full range of variants in the original population and which, by chance, may be atypical of that population. These 'bottlenecks' are a routine part of laboratory maintenance because a few individuals, usually mating couples, are occasionally isolated from a culture to generate a fresh culture.

In conclusion, the implications of these data on the relationship between mites and fungi are twofold. First, only a few fungi (including *A. penicilloides* and *W. sebi*) persist in the alimentary canal of pyroglyphid dust mites, and different individual mites are predisposed to different taxa among these 'acceptable' fungi. Second, laboratory practice may have an appreciable effect on the characteristics of mites in culture, in this case with respect to their relationship with fungi. This issue has previously been raised by Colloff (1987), who found differences in the temperature and humidity requirements of laboratory and 'wild' *D. pteronyssinus* populations.

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25

How plants maintain body-guards: plant exudate as a food source for phytoseiid mites

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Typhlodromalus limonicus (Garman and McGregor) is the most abundant species of the Phytoseiidae in South American cassava (*Manihot esculenta* Crantz). It persists in the crop in the absence of arthropod prey. This study established that this persistence is due, at least in part, to a resource provided by the plant. Cassava exudes, mainly from the petioles, a cyanide-free sugary solution. When confined on leaf discs with this exudate, the mites survive longer than those provided with water (control) and, in addition, they can develop from egg to adult. Moreover, we have been able to demonstrate that the exudate elicits an olfactory response in predators after a food-deprivation period of 24 hours. Two-choice disc experiments showed that it also had a strong arresting effect on larvae but less so on adult females. However, a diet of exudate alone does not result in oviposition.

Because these predatory mites cannot rely on the exudate for egg production, it is expected that other food sources are suitable for this purpose. *Typhlodromalus limonicus* produces eggs when fed with plant pathogens such as the mildew fungus, *Oidium manihotis*, and phytophagous arthropods such as spider mites and thrips larvae. Thus, plants may profit from predatory mites, and they may gain a selective advantage by providing exudate as food, thereby maintaining a population of body-guards.

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· PART FOUR ·

Systematics, Morphology, Physiology and Behaviour

26

Distribution of characters and phylogenetic age – systematic problems in the higher taxa of the Oribatida

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The great phylogenetic age of oribatid mites may be responsible for a considerable number of characters being distributed in a mosaic pattern, especially in their older taxa. Therefore, simple combinations of characters are certainly not sufficient to create monophyletic groups within the Oribatida, groups which are urgently needed for ecological investigations. Most of the higher taxic categories, therefore, may be more or less artificial, and their phylogenetic status remains to be established

INTRODUCTION

The species, *Protochthonius gilboa* and *Devonacarus sellnicki*, (Norton *et al.*, 1988) from the Devonian period, and the species, *Jureremus foveolatus*, *Cultroribula jurassica* and *Achipteria* (?) *obscura* (Krivolutsky and Druk, 1986) from the Jurassic period, signal the considerable phylogenetic age of oribatid mites. Therefore, while the lower oribatid mites have lived on this planet for more than 350 million years, the higher oribatid taxa, certainly, can be traced back to the Triassic or even the Permian period. Such old organisms – surviving as they have done from the Palaeozoic and Mesozoic eras to the present day – may have retained the morphological features of their radiation phase.

As is known, this is the case with *Ornithorhynchus anatinus* (Monotremata) the interclavicula of which as well as the organization of the urogenital system, the shape of the spermatozoids and the mode of

reproduction, show reptilian features while the remaining structures are highly specialized or typical of modern mammals. The predecessor of *Ornithorhynchus*, which has been named *Obdurodon*, was already present 100 million years ago in the Cretaceous period. The mosaic distribution pattern of characters is even greater in the extinct group of Therapsida. If, therefore, therapsid genera such as *Probainognathus* and *Diarthgrognathus* would have survived to the present day, the definition of higher taxa within mammalian or mammal-like vertebrates would become a very difficult process.

ANALYSIS OF CHARACTERS

Among the higher Oribatida the number of genera surviving from the Mesozoic era, and still extant, seems to be fairly large. As one of the higher oribatid mites surviving from the Jurassic period is of the poronotic type, characters appearing in different taxa of the Poronota may provide an inkling of the radiation of these mites which occurred in the past. For the adult stages of the pterogasterine type, this is not the case as these species, when compared to the Oppiidae, are very well defined by the carina circumpedalis, and the blade-like trochanters and femora of the hind legs.

Apopheredermy during the ontogeny of the Oribatellidae, and the plicated or wrinkled nymphs of the Pelopidae and Achipteriidae, are characters of a mosaic distribution pattern. Plicated nymphs are common to the Scapheremaeidae, Cymbaeremaeidae and the Micreremidae, all of which belong to the Apheredermata in the sense of Grandjean (1954). Indeed, the apopheredermy of the Oribatellidae seems to be a special case of eupheredermy, which also characterizes the ontogeny of the Liodidae, Damaeidae, Belbidae, Cymbaeremaeidae, etc. This will explain why the Microzetidae are eupherederm mites with pteromorphae, a combination which is not common in the Oribatida, and which is only known from a few species such as *Polypterozetes cherubin* (Berl.) (Grandjean, 1959). In fact the morphological characters of the Microzetidae seem to indicate their nearer relationship to the Oribatellidae.

A mosaic distribution pattern of characters is also shown by the species, *Hermannia gibba*. The similar shape of genu and tibia of the legs – common in lower oribatid mites – the structure of the infracapitulum, and the method of moulting (as in the Nothroidea) are characters of the lower oribatid mites. Otherwise, the formation of a definitive notogaster and a totally fused ventral plate (prodorsum, epimera and anogenital region form a fused ventral covering) are characters of the higher oribatid mites. As the Hermanniidae are not parthenogenetic, one might

say that these characters remind one more of the higher than the lower oribatid mites. Perhaps the Hermanniidae, therefore, are foreshadowing the characters of higher Oribatida.

Another very interesting species is *Scapheremaeus argentinensis* Travé and Fernandez 1986. According to Travé and Fernandez (1986), the notogaster of this genus possesses a laterally located desclerotized band. This resembles, to some degree, a similar condition in the genus *Ameronothrus*, where many species have an incompletely desclerotized band in the lateral region of the notogaster. As in some species of *Ameronothrus* and in the species, *Aquanothrus montanus* Engelbrecht 1975 (Engelbrecht, 1975), many of the tarsal setae of the legs of *S. argentinensis* have a hook-shaped distal end, a form of seta which does not occur in *S. corniger* or in *S. rustenburgensis* Engelbrecht 1975. The greyish colour of the cuticle of *S. argentinesis* is reminiscent of the colour of the pellicule of the Ameronothridae.

Consequently, it may not be so surprising that the male genital organ resembles to some extent that of *Podacarus auberti*, a selenoribatid mite which, certainly, is related to *Ameronothrus*. In addition, in *S. argentinesis* the iteral setae on the tarsi of the legs are absent as in the Hermanniellidae, Plasmobatidae and some of the Zetorchestidae. In the latter family, the tarsus has a pulvillus unlike the Cymbaeremaeidae where only the nymphs possess such a structure with a lobe on each side of the claw. The Cymbaeremaeidae, like the Ameronothridae and the Liodidae, are furnished with brachytracheae. Though there is a difference between the aphererderm nymphs of *Carabodes coriaceus* and the plicated ones of the Scapheremaeidae, the similarity of their lateral notogastric aspects is striking. Otherwise, the shape of the notogaster of the Passalozetidae differs greatly from that of the Scapheremaeidae despite the fact that both have plicated nymphs and a lenticulus.

Passalozetes, too, provides a good example of the distribution of characters in a mosaic pattern. This genus has a lenticulus in common with *Aquanothrus*, *Hydrozetes*, *Scapheremaeus*, *Scutovertex*, *Licneremaeus* and *Eupelops*. As in all these genera, it has plicated nymphs but such nymphs are also to be found in the genus *Achipteria*, which has no definite lenticulus. Otherwise, *Passalozetes* has legs furnished with sockets and a large horn on tibia I. This can be seen in some of the Scapheremaeidae as well as the Gymnodamaeidae. The latter family is characterized by eupherederm nymphs and, in some cases, the adults are also eupherederm. At least *Passalozetes* is poronotic, a feature which this genus has in common with most of the 'Pterogasterina'. *Oribatella*, however, which is also a pterogasterine oribatid mite has apopherederm nymphs, and to a degree they resemble the opsio- eupherederm nymphs of the genus *Eremaeus*, the Hermanniellidae, the Plasmobatidae, the

Zetorchestidae, the Liodidae, the Gymnodamaeidae, the Damaeidae/Belbidae and the Amerobelbidae.

PHYLOGENETIC CONSIDERATIONS

All the characters referred to here are certainly homologous. If they were convergent, relatively complex structures such as the nature of the articulation of the legs, the shape of the nymphs, the brachytracheae and the lenticulus would have been acquired independently by many different species. According to the criteria of comparative morphology, structures of high complexity are more likely to be homologues rather than the result of convergent evolution. It should be pointed out, however, that in comparative morphology there is no method available to prove the status of homology or convergence. Thus, if the porus on the posterior end of the notogaster of *Porobelba spinosa* is an area porosa, the Poronota *sensu* Grandjean from this as well as from an ontogenetic point of view, is not a clearly defined group. If most of the different morphological structures in higher oribatid mites should be homologues and not convergencies, the relationship between the different species should be very much closer than the present classification system would suggest. Moreover, in such old groups as the oribatid mites, one must take account of two types of relationship: on the one hand, stem-groups, and on the other, groups which have evolved over a longer geological period. In old groups, both types of relationship are intermingled, and no decision can be made as to which relationship is the dominant one.

CONCLUSION

Therefore, in oribatid mites, a simple 'ensemble des caractères' in the sense of Grandjean (1954) will not be sufficient to define the higher taxa. To obtain well-reasoned differential diagnoses, the weighting of characters should be done according to the criteria of comparative morphology. In such an analysis, one character is, *ad hoc*, no more important than any other, whether they are adult or ontogenetic characters. The systematic importance of characters for the definition of higher taxa has to be proved by comparative analysis. Otherwise, one ends up with totally artificial higher taxa which are useless for comparative ecological investigations.

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27

A new approach to the systematics of the genus Steganacarus (Oribatida)

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One of the most serious problems in oribatid systematics is our complete ignorance of the genetic bases of the phenotype. The study of enzyme polymorphisms by biochemical methods is a new approach to this basic question. The relationships between the genus *Steganacarus*, and *Tropacarus*, a taxon of uncertain and questionable validity, were analysed using these biochemical procedures. The morphological and, in particular, the genetic study of some steganacarid species reveal the presence of two distinct phyletic lines, namely, *Steganacarus (S.) magnus* and *S. (Tropacarus) carinatus*, separated by a very large genetic distance. Moreover, the genetic distance of an easily recognizable subgenus, *Rhacaplacarus*, with respect to *Steganacarus (s. str.)* demonstrates the rank of *Tropacarus* to be that of subgenus

INTRODUCTION

The greatest problem in systematics has always been the selection and evaluation of the most suitable characters for revealing the relationships between the different taxa in order to construct their phylogenetic tree. This operation is much more difficult when one is dealing with a taxonomic group as homogeneous as the Phthiracaroidea in which the possible diagnostic phenotypic characters are uniform and relatively few, particularly when one takes into account the large number of described taxa (Niedbala, 1986a,b). The most appropriate phenotypic

diagnostic characters are the pattern of the genital and ano-adanal setae, the presence of the dorsal seta accompanying the genual solenidion on leg IV, and the body microsculpture. Phenetic analysis of 128 characters of 53 euptyctimous species demonstrated that the differences at generic level do not exceed 10% (Sheals, 1969). As a result of this, the nomenclature has become cluttered with many 'nomina' given to taxa often described only on the basis of artificial characters (Niedbala, 1986a). The taxonomic confusion in this group is further increased by the absence of a recent redescription of the classical species. The latest taxonomic procedures should help to solve these problems.

A preliminary attempt to clarify the taxonomic problems of the Phthiracaroidea using cladistic procedures has been undertaken recently (Niedbala, 1986a) but without precise identification and delineation of the different features utilized to establish similarities and dissimilarities between taxa. Some details such as the notogastral keel and/or the body microsculpture have not been precisely defined, and other elements have not been exactly interpreted and/or studied in sufficiently large populations. Character identification is not without practical and theoretical difficulties. In such small animals, it is only with the use of the most sophisticated techniques, for example, scanning electron microscopy (SEM), that minute morphological details can be observed. For instance, it has been suggested recently that the families Phthiracaridae and Steganacaridae may be distinguished on the basis of setal morphology (Niedbala, 1986a). The Phthiracaridae should have slender, glabrous notogastral setae whereas those of the Steganacaridae are generally ciliate, stick-like, etc. Analysis using SEM reveals that this character is not meristic in the family. There are ciliate setae in the Phthiracaridae, and glabrous setae in the Steganacaridae (Bernini and Avanzati, unpublished). It is thus clear that setal morphology cannot be regarded as a diagnostic tool at family level.

The most serious theoretical difficulty in the determination of character states is our complete ignorance of the genetic control of the phenotype. There is no information about the genetic bases of phenotypic characters. Evident phenotypic characters, which are apparently very suitable for distinguishing one taxon from another, sometimes lose all taxonomic weighting when carefully analysed. Thus, the presence of an anterior notogastral tectum, a character traditionally used to distinguish *Steganacarus (Steganacarus) anomalus* (Berl.) and *Steganacarus (Tropacarus) pulcherrimus* (Berl.) from *S. (S.) magnus* (Nic.) and *S. (T.) carinatus* (Koch), respectively, is not sufficient to justify separate specific status for the first two species (Bernini and Avanzati, 1988a,b). The analysis of numerous populations from western and southern Europe and North Africa has demonstrated the existence of individuals with intermediate

tectal sizes, and probably dependent on different ecological conditions, thus revealing the taxonomic inconsistency of these two separate entities.

ENZYME POLYMORPHISM AS A TAXONOMIC TOOL

One of the most recent approaches (for Acarida, of course!) to the basic question of the relationships between genotype and phenotype, is the study of enzyme polymorphisms by gel electrophoresis. This is a simple procedure which has been used extensively for taxonomic purposes in many animal and plant groups during the last two decades (Ayala, 1983; Nevo *et al.*, 1984). This method provides a further series of good meristic taxonomic characters, that is, enzymes, the genetic bases of which can be directly studied. According to Ayala (1983), enzymes can be readily considered as taxonomic characters of particular diagnostic value because they are not subject to significant phenotypic modification, for example, age and environment, are generally independent of each other, and all have the same taxonomic weighting.

The first application of these new taxonomic procedures to oribatid mites confirmed that *Steganacarus (S.) anomalus* and *S. (S.) magnus* (Bernini *et al.*, 1988a) are identical and, likewise, *Steganacarus (Tropacarus) pulcherrimus* and *S. (T.) carinatus* (Bernini and Avanzati, 1988b). This had previously been suspected on the basis of morphological data (Bernini and Avanzati, 1988a,b).

STATUS OF *S.* (*STEGANACARUS*) AND *S.* (*TROPACARUS*)

Recently attention has been directed to the relationships between the genus *Steganacarus*, and *Tropacarus*, a taxon of uncertain rank (Bernini, 1971; Bernini *et al.*, 1988b) and questionable validity (Balogh and Mahunka, 1983; Niedbala, 1986a,b). Traditionally the only distinction between the two is the median notogastral ridge, but according to Niedbala, this character is variable and not suitable for diagnostic purposes because in some species (for example, *Steganacarus (T.) brevipilus* (Berl.)), it is only present on the posterior portion of the notogaster. This ought to justify the inclusion of the *Tropacarus* species in *Steganacarus*. The results of a morphological, biogeographical and, in particular, a genetic study of *Steganacarus (T.) brevipilus* (Bernini and Avanzati, 1989) were compared with those available for *S. (S.) magnus* and *S. (T.) carinatus* with the aim of determining as objectively as possible the taxonomic status of *Tropacarus* with respect to *Steganacarus*.

From the morphological point of view, the study of many populations of *S. (T.) brevipilus* from southern Europe, including the previously

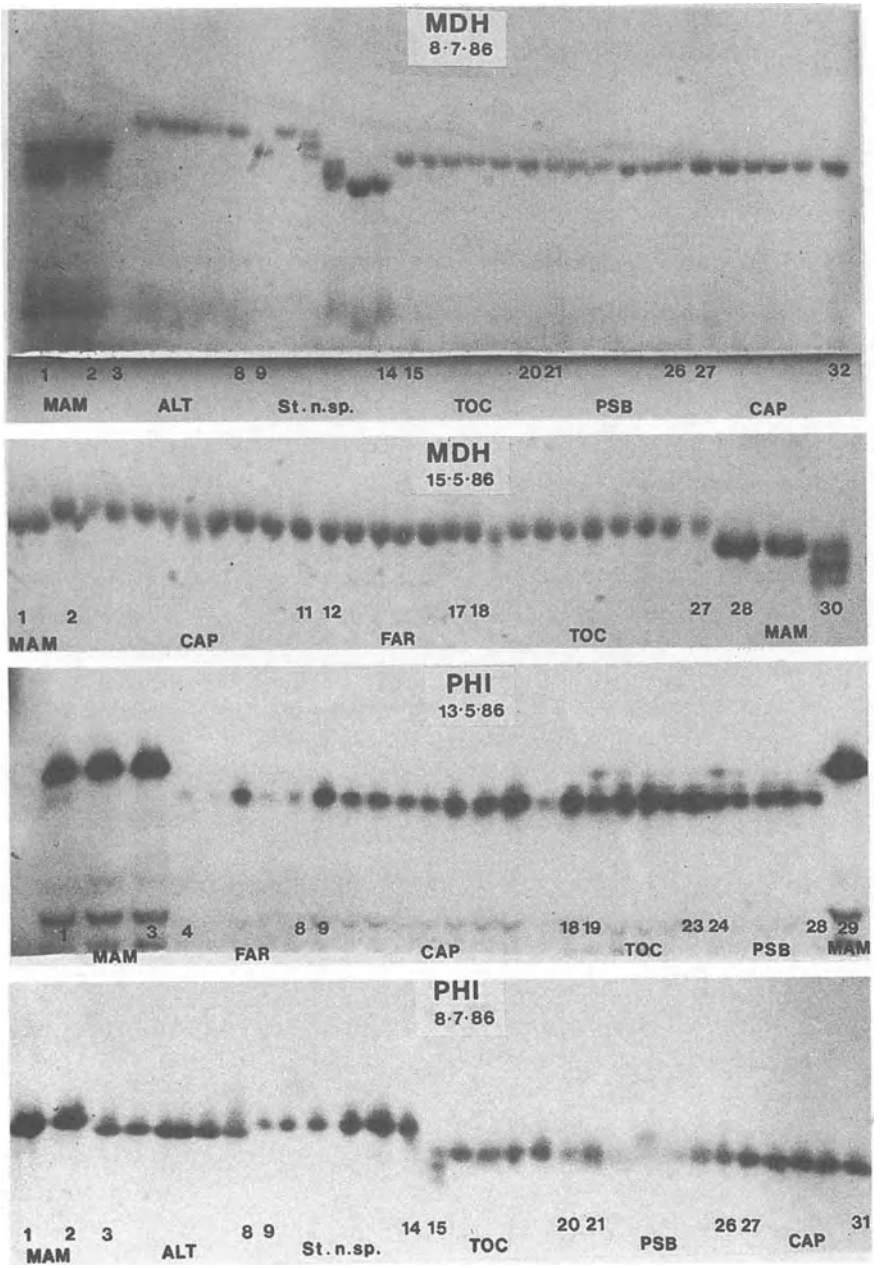

Fig. 27.1 Gene enzyme systems (gene loci MDH-1 and PHI-1), determined by starch-gel electrophoresis, in *Steganacarus (Steganacarus) magnus* (Nic.) (MAM), *S. (Tropacarus) brevipilus* (Berl.) (CAP, FAR), *S. (T) carinatus* (Koch) (PSB, TOC) and *S. (Rhacaplacarus) ortizi* Pérez-Iñigo (ALT). The designations MAM, etc. refer to collection sites.

described variety, *perfecta* (Sell.) (Sellnick, 1931), has revealed in this species, considerable variation in the main diagnostic character used to distinguish tropacarid species. Moreover, some populations consisted of individuals with either complete or reduced median notogastral ridges together with others showing all the intermediate dimensions of this keel. Although this character is not meristic for *S. (T.) brevipilus*, it can, again, be considered wholly valid from the taxonomic point of view for distinguishing *Steganacarus (s. str.)* and *Tropacarus*. The value of a certain character state does not in fact influence its diagnostic standing.

Table 27.1 Allele frequencies at 12 gene loci (indicated by their international symbols) codifying for enzymes of 6 steganacarid populations (data in part from Bernini *et al.*, 1988a and Bernini and Avanzati, 1989)

		S. (S.) magnus		*S. (T.) carinatus*		*S. (T.) brevipilus*	
Locus	*Alleles*	*MAM**	*AST*	*TOC*	*PSB*	*FAR*	*CAP*
PHI-1	100	1.00	1.00	—	0.018	—	—
	95	—	—	0.982	0.982	1.00	1.00
	90	—	—	0.018	—	—	—
PHI-2	100	1.00	1.00	—	—	—	—
	97	—	—	1.00	1.00	1.00	1.00
MDH-1	103	—	—	1.00	1.00	1.00	1.00
	100	0.882	0.978	—	—	—	—
	95	0.118	0.022	—	—	—	—
MDH-2	102	—	—	1.00	1.00	1.00	1.00
	100	1.00	1.00	—	—	—	—
GOT	100	0.953	0.915	—	—	—	—
	96	—	—	—	—	1.00	1.00
	95	0.047	0.085	—	—	—	—
	93	—	—	1.00	1.00	—	—
G-6PDH	100	1.00	1.00	—	—	1.00	1.00
	92	—	—	1.00	1.00	—	—
PGM	100	1.00	1.00	—	—	—	—
	90	—	—	1.00	1.00	1.00	1.00
MPI	100	1.00	1.00	1.00	1.00	1.00	1.00
ADK	100	1.00	1.00	—	—	—	—
	92	—	—	1.00	1.00	1.00	1.00
HK	100	1.00	1.00	—	—	—	—
	92	—	—	1.00	1.00	1.00	1.00
CK	100	1.00	1.00	—	—	—	—
	92	—	—	1.00	1.00	1.00	1.00
6-PGDH	100	1.00	1.00	—	—	—	—
	64	—	—	1.00	1.00	—	—
	50	—	—	—	—	1.00	1.00

*MAM, etc. refer to collection sites.

Table 27.2 Matrix giving number of genetic loci with common (upper triangle) and alternative alleles (lower triangle) among the 4 steganacarid species examined

	magnus	*carinatus*	*brevipilus*	*ortizi*
magnus	—	1	2	1
carinatus	11	—	9	1
brevipilus	10	3	—	1
ortizi	11	11	11	—

The taxonomic position of *brevipilus* appears to be closer to the *Tropacarus* species also by virtue of other morphological characters (Bernini and Avanzati, 1989). Nevertheless, apart from the notogastral ridge – the traditional character – morphological, biogeographical and ecological analyses do not enable a clear decision to be made about the validity of the *Tropacarus* taxon.

Genetic analysis of the three species referred to above (Figs 27.1 and Table 27.1) has revealed two phyletic lines: those of *S. (S.) magnus* and *S. (T.) carinatus* which are, genetically, very widely separated, and the close affinity of *brevipilus* to *carinatus* (Bernini and Avanzati, 1989). *Magnus* and *carinatus* are differentiated by at least 10 alternative genetic loci out of the 12 examined. The *brevipilus* and *carinatus* lines are separated by a small genetic distance (0.289) and only three alternative loci (Table 27.2).

The indications from phenotypic analysis, in themselves inconclusive, are thus confirmed and reinforced by the biochemical data. The separation of *Tropacarus* and *Steganacarus* is justified by the traditional morphological character plus 10 other good diagnostic taxonomic characters (10 alternative loci codifying for enzymes) (Ayala, 1983).

Now that the separation between the two taxa has been established, it remains to decide their taxonomic rank. Is *Tropacarus* a genus or a subgenus? To verify and evaluate the taxonomic rank of the *magnus* and *carinatus* lines, we also carried out a genetic study of *Steganacarus (Rhacaplacarus) ortizi* Pérez-Iñigo, a taxon recently included in another *Steganacarus* subgenus (Niedbala, 1986a,b). The results of this study indicate that this line is even further separated from the other two by virtue of 11 alternative genetic loci (Table 27.2). The test of the genetic distance of this morphologically distinguishable representative of the *Rhacaplacarus* subgenus gave comparable results (2.477 and 2.489), and provides good evidence that the *Tropacarus* entities can also be consid-

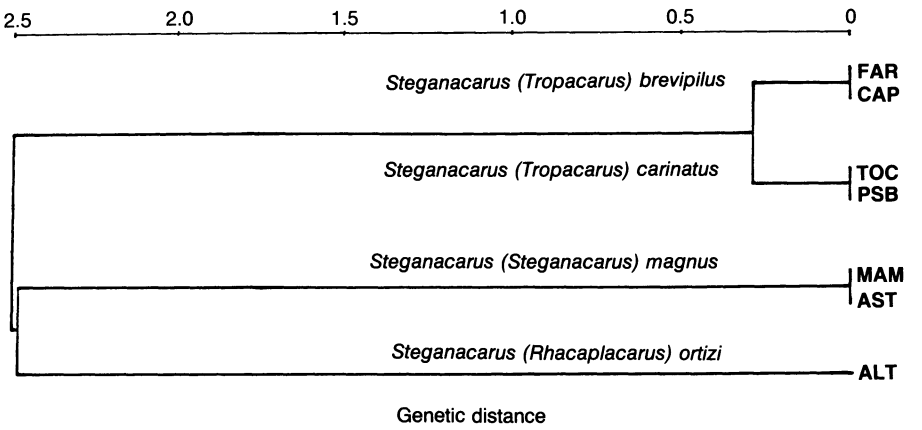

Fig. 27.2 Cladogram based on unweighted pair-group arithmetic average (UPGMA) clustering of the genetic-distance data showing genetic relationships between populations (FAR, CAP, etc.) of the four steganacarid species examined (redrawn from Bernini and Avanzati, 1989).

ered to belong to a genetically well-differentiated *Steganacarus* sub-genus (Fig. 27.2) (Bernini and Avanzati, 1989).

CONCLUSIONS

The use of these new taxonomic techniques has, therefore, enabled some old 'nomina' to be deleted from the oribatological literature, and has clarified the relationships of *S. (T.) brevipilus* and *Tropacarus* with respect to *Steganacarus (s. str.)*. It is necessary to stress, however, that this technique gives additional taxonomic characters and not 'the' determinant characters. Indeed, phenotypic characters when accurately studied and selected, are often sufficient to determine the real systematics of different taxa, but the genetic characters can reinforce or, alternatively, reveal the feeble and incomplete nature of the former.

Biochemical systematics has an increasingly important role to play because of the means it provides to study directly the genetic processes in these animals. The knowledge of certain parameters such as the expected mean heterozygosity per locus, the observed mean heterozygosity, the percentage of polymorphic loci and the mean number of alleles per locus, as well as the use of F statistics and multivariate analysis, can reveal patterns of the speciation processes in this animal group (Bernini *et al.*, 1988a, Bernini *et al.* unpublished). The wider and more detailed study of oribatid species with these genetic procedures,

therefore, promises to elucidate many unsolved general biological problems.

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The morphology of the immature stages of Phthiracaroidea (Oribatida)

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Details are given of the morphological characters which distinguish the immature stages of the Phthiracaroidea (Oribatida). These are the shape and nature of the body cover, the chaetotaxy of the prodorsum, notogaster, epimera, legs, and genito-aggenital and ano-adanal plates, and the number of lyrifissures. An analysis of these morphological features indicates that there are three which may be regarded as plesiomorphic characters in the adults. The first of these is the shape of the prodorsal and notogastric setae, which are smooth and taper to an elongated point in all immature stages. The second is the arrangement of the anal and adanal setae in the tritonymph, and the third, seta d on tibia IV, which is always separated from the solendion

The developmental stages of Phthiracaroidea have been examined by various authors on numerous occasions but their description is still incomplete. The author has not examined the prelarva as it has already been adequately described (Grandjean, 1940, 1950; Lions, 1968, Travé, 1976).

LARVAE AND NYMPHS

The egg with prelarva is deposited by the female in a small hemispherical cavity hollowed out by the female with her mandibles in the wall of the gallery in dead wood. The flat ventral surface is placed next to the

wall of the gallery. After hatching, the larva burrows in the wood to form its own gallery, and moves away from the egg site. The larva and nymphs are well adapted to their living conditions. They are virtually incapable of movement except within their galleries (Grandjean, 1934).

In general appearance, the larva and nymphs differ completely from the adult. They are not ptychoid, and are whitish in colour with a smooth, shiny integument. The cuticle is completely colourless apart from the tips of the strong mandibles and rutella, which are coloured. The body is soft, sac-like, without carinae or concavities. The prodorsum is triangular in shape, with normally developed chelicerae. The chelicerae always bear two setae, cha and chb. The bothridium and sensillus are absent in the larva, but appear in subsequent stages in vestigial form. They are not needed by these stages as they live within decayed wood, which they do not leave until they become adults. These organs appear for the first time in their normal form in the adult.

CHAETOTAXY AND POROTAXY

The rostral, lamellar and interlamellar setae are present in all stages; they are smooth, and taper to an elongated point, The exobothridial setae are absent in the larva, protonymph and deutonymph but appear in the tritonymph (Table 28.1, Fig. 28.1). The notogaster bears two fissures, r_2 and r_3, which divide into three parts. These two fissures are clearly discernible only in the dorsal region. The anterior portion of the notogaster bears five pairs of setae: c_1, c_2, c_3, cp and d_1. Between the two fissures there are three pairs of setae, d_2, e_1 and e_2. All these setae occur in all stages (Table 28.1). In the larva, the notogaster has 10 pairs of setae; the absent setae are h_3, ps_1–ps_4. The protonymph bears 14 pairs of setae, that is, all except seta ps_4. In the deutonymph, 14 or 15 pairs of setae develop, with seta ps_4 sometimes absent. The tritonymph has the full gastronotic setal complement of 15 pairs of setae (Fig. 28.1*b*). The vestigial setae f_1 and f_2 are already clearly discernible in the larva. Thus, if all the setae are counted, the larva is unideficient, that is, the gastronotic number is less than 15; and the protonymph is holotrichous with a gastronotic number of 16. From the deutonymphal stage onwards there is hypertrichy, that is, the number of setae exceeds 16 pairs. The larva bears lyrifissures, ia, im, ip and ih. In the protonymph and deutonymph, all lyrifissures are present except iad. All lyrifissures are present in the tritonymph as follows: ia, im, ip, ips, ih and iad.

In all stages, the infracapitulum is normally developed with all setae present. On the pedipalp of all immature stages, the seta V'' on the basal segment is absent (Figs 28.2*a*,*c*). This seta is only present in the adult. The chaetotaxy of the epimera in all stages except the larva is 1-0-1-1

Table 28.1 Chaetotaxy and porotaxy of immature stages of Phthiracaroidea indicating presence (+) or absence (−) of setae and lyrifissures

Stage	*Setae*											
	Prodorsum				*Notogaster*		*Lyrifissures*					
	ro	*le*	*in*	*ex*	*Pairs present*	*Absent*	*ia*	*im*	*ip*	*ips*	*ih*	*iad*
Larva												
Iran	+	+	+	−	10	h_3, ps_1–ps_4	+	+	+	−	+	−
Protonymph												
Grandjean (1934, 1950)					14	ps_4	+	+	+	+	+	−
Deutonymph												
Iran	+	+	+	−	15,16	−	+	+	+	+	+	−
Uganda	+	+	+	−	15	−	+	+	+	+	+	−
Turkey	+	+	+	−	14	ps_4	+	+	+	+	+	−
Tritonymph												
Turkey	+	+	+	+	15	−	+	+	+	+	+	+
Syria	+	+	+	+	15	−	+	+	+	+	+	+
Iran	+	+	+	+	15	−	+	+	+	+	+	+
Papua	+	+	+	+	15	−	+	+	+	+	+	+
Uganda	+	+	+	+	15	−	+	+	+	+	+	+

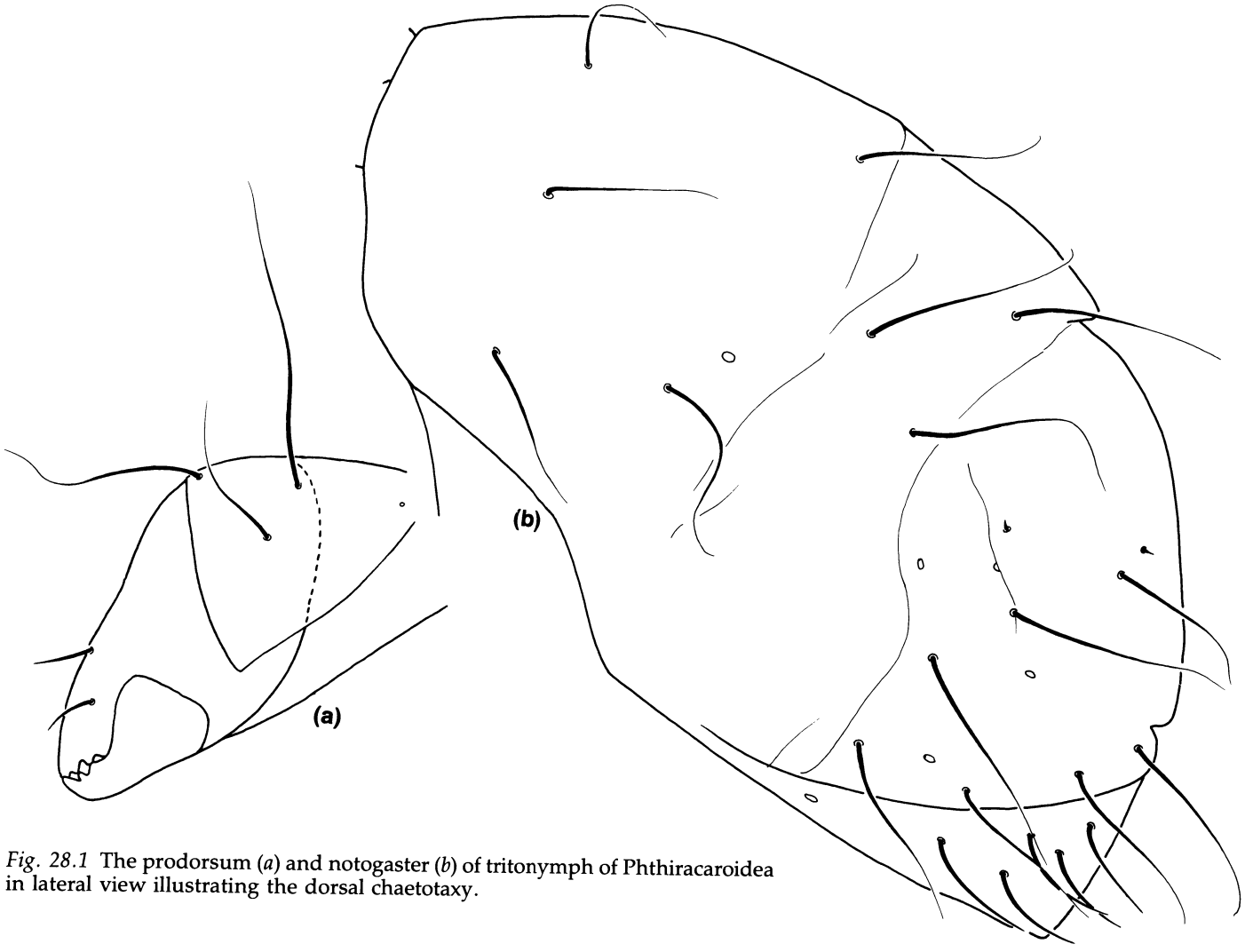

Fig. 28.1 The prodorsum (*a*) and notogaster (*b*) of tritonymph of Phthiracaroidea in lateral view illustrating the dorsal chaetotaxy.

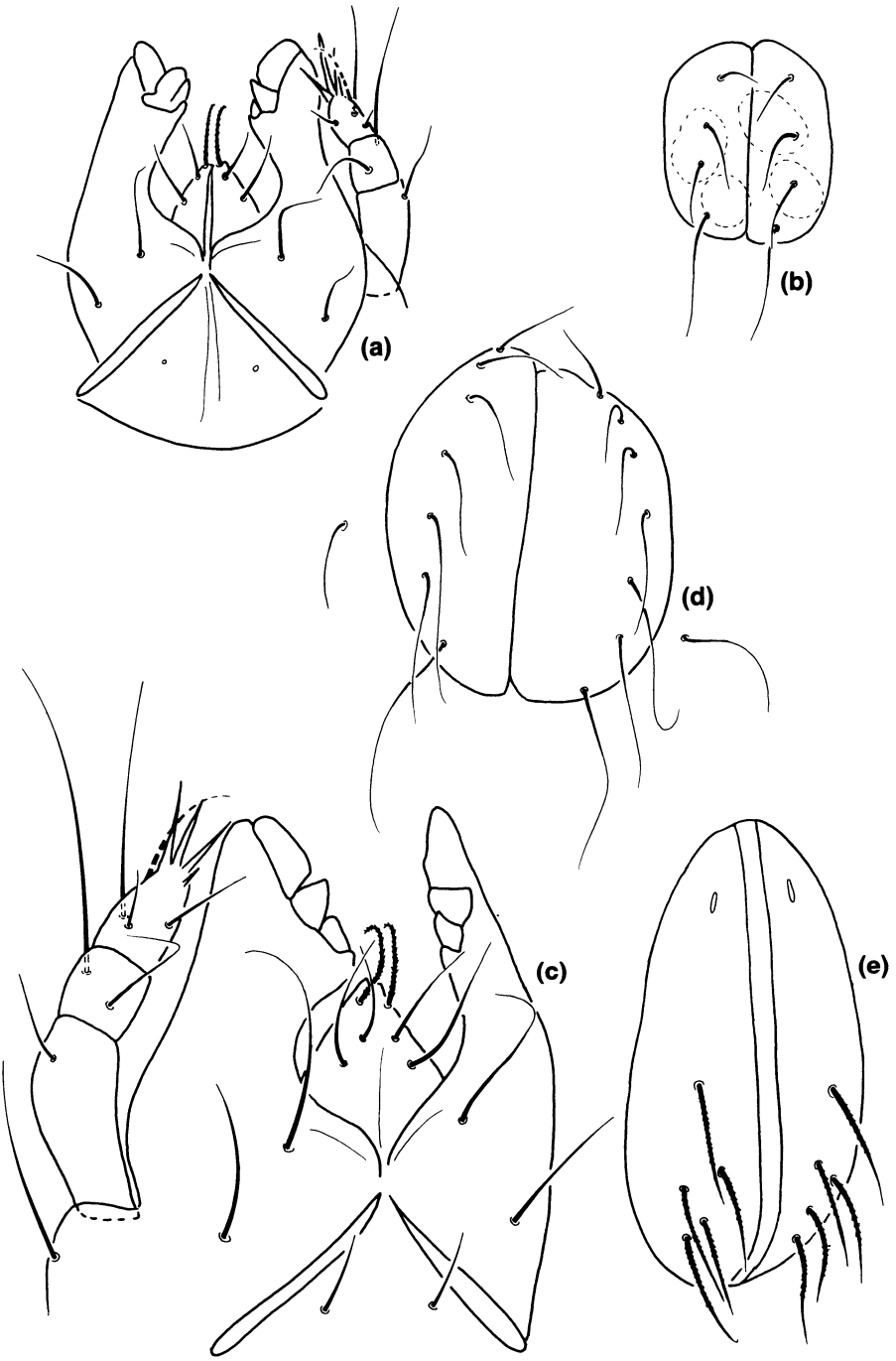

Fig. 28.2 Structures of venter of deutonymph (*a*, *b*) and tritonymph (*c–e*) of Phthiracaroidea. Infracapitulum with palps (*a*), and genital plate (*b*) of deutonymph; infracapitulum with palps (*c*), and genital (*d*) and anal (*e*) plates of tritonymph.

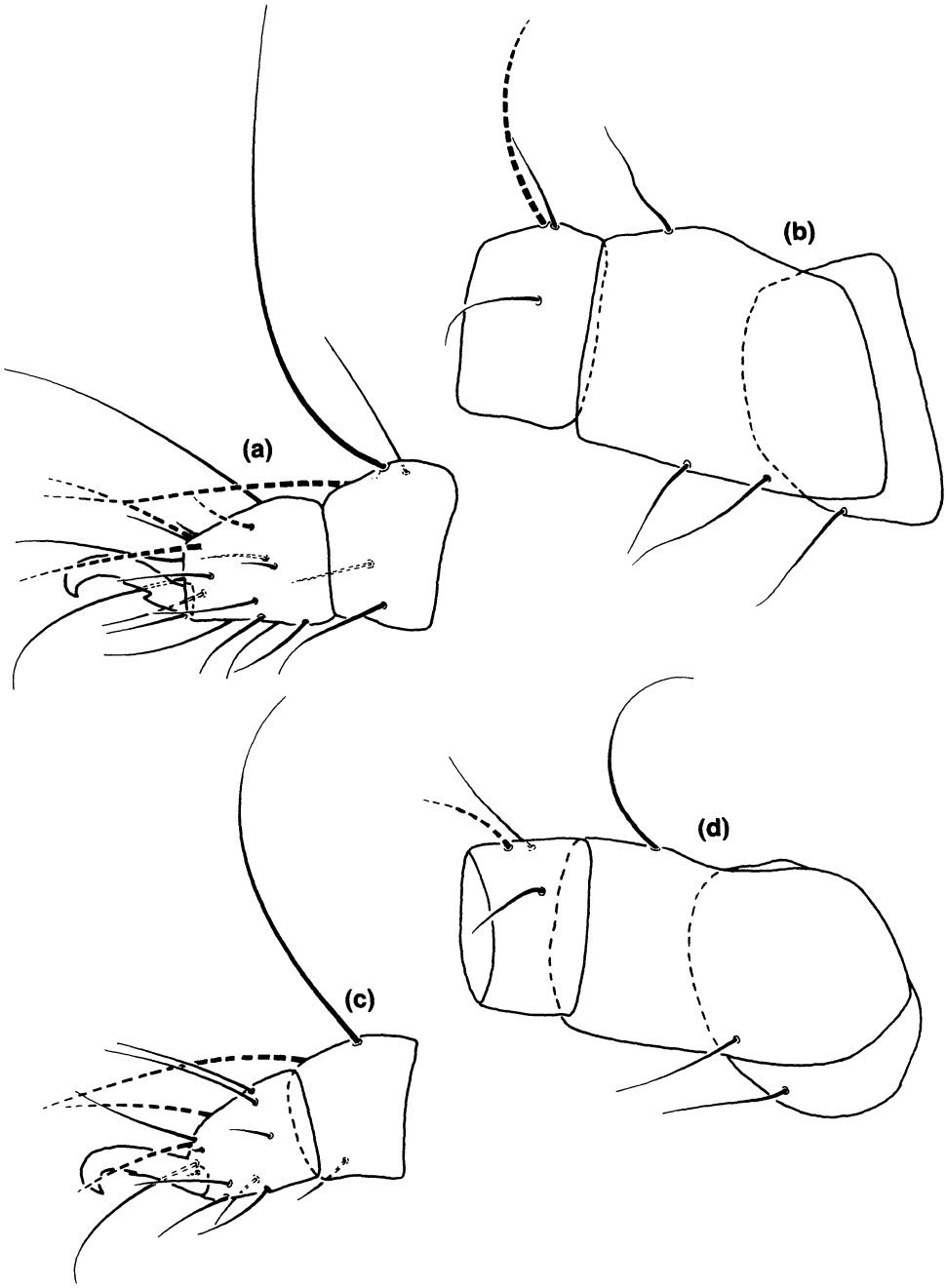

Fig. 28.3 Parts of legs I (*a*, *b*) and II (*c*, *d*) of tritonymph of Phthiracaroidea illustrating leg chaetotaxy. (*a*) Tibia, tarsus and (*b*) trochanter, femur and genu of leg I. (*c*) Tibia, tarsus and (*d*) trochanter, femur and genu of leg II.

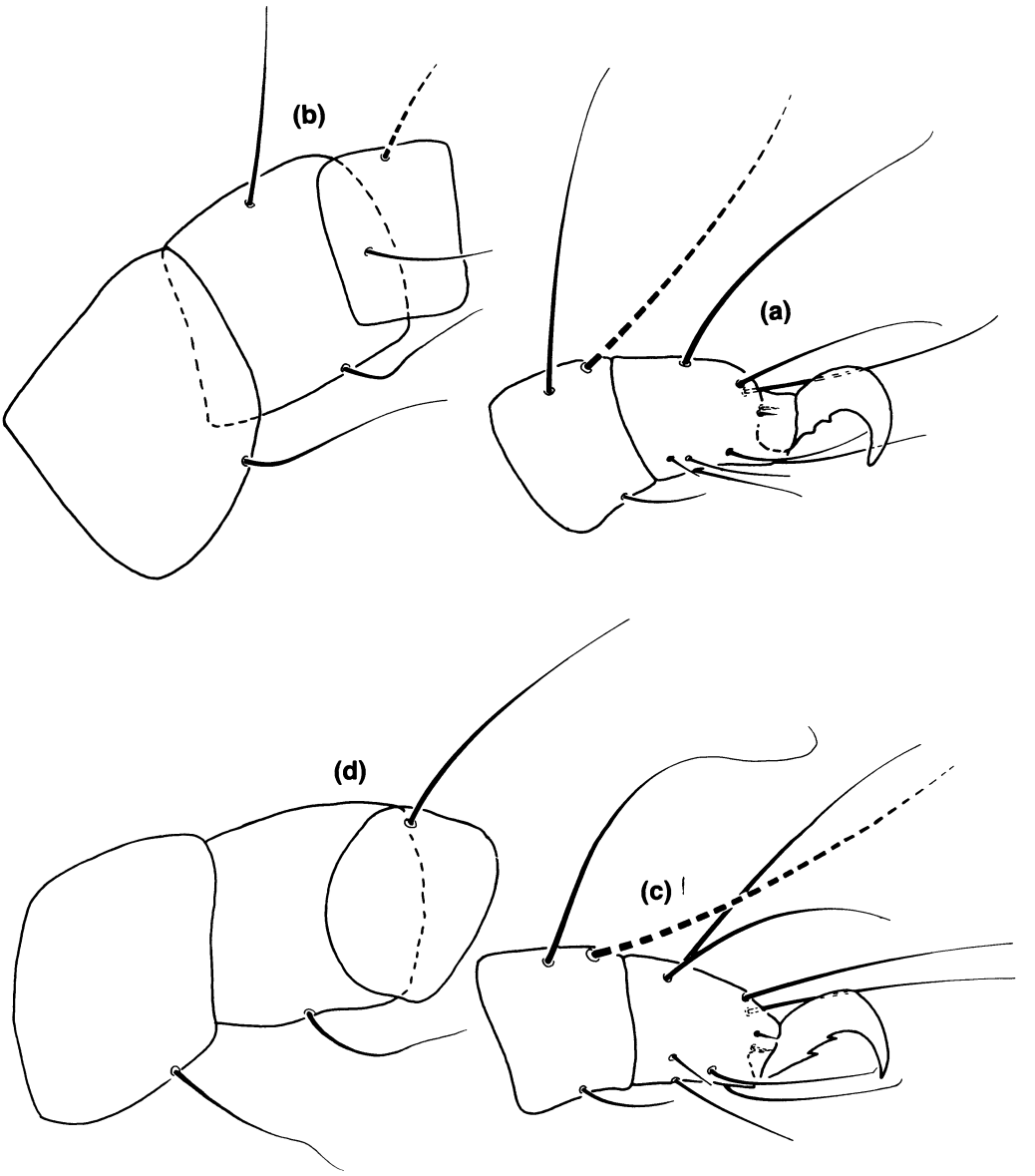

Fig. 28.4 Parts of legs III (*a*, *b*) and IV (*c*, *d*) of tritonymph of Phthiracaroidea illustrating leg chaetotaxy. (*a*) Tibia, tarsus and (*b*) trochanter, femur and genu of leg III. (*c*) Tibia, tarsus and (*d*) trochanter, femur and genu of leg IV.

Table 28.2 Setal formulae of the epimera, genital and anal regions and legs of immature stages of the Phthiracaroidea

	Setal formulae			*Solenidia and Setae of legs*			
	Epimeral	*Genital*	*Anal and adanal*	*Leg I*	*Leg II*	*Leg III*	*Leg IV*
Larva				2-1-	1-1-	1-1-	
Iran	1-0-1			0-2-2-4-?	0-2-2-2-?	0-1-1-2-?	
Protonymph							
Grandjean (1934, 1950)		1 : 0					0-0-0-0-5
Deutonymph				1-1-	1-1-	1-1-	1
Iran	1-0-1-1	4 : 0	0 : 3	1-2-2-4-?	1-2-2-2-?	1-1-1-2-?	1-0-1-1-10
				1-1-	1-1-	1-1-	1
Uganda	1-0-1-1	4 : 0	0 : 3	0-2-2-4-?	1-2-2-2-?	0-2-1-2-?	1-0-0-1-?
				1-1-	1-1-	1-1-	1
Turkey	1-0-1-1	4 : 0	0 : 3	0-2-2-2-?	0-2-2-2-?	1-1-1-2-?	1-0-0-1-?
Tritonymph				1-1-3?	1-1-2	1-1-0	0-1-0
Turkey	1-0-1-1	7 : 1	2 : 3	1-3-2-4-15	1-2-2-2-11	1-2-1-2-10	1-1-1-2-10
				2-1-	1-1-	1-1-	0-1-0
Syria	1-0-1-1	7 : 1	2 : 3	1-2-2-4-?	1-2-2-2-?	1-2-1-2-?	1-1-1-2-?
				2-1-	1-1-	1-1-	0-1-0
Iran	1-0-1-1	7 : 1	2 : 3	1-2-2-4-?	1-2-2-2-?	1-2-1-2-?	1-1-1-2-?
				2-1-	1-1-	1-1-	0-1-0
Papua	1-0-1-1	7 : 1	2 : 3	1-2-2-4-?	1-2-2-2-?	1-2-1-2-?	1-1-1-2-?
				1-1-	1-1-	1-1-	1
Uganda	1-0-1-1	7 : 1	2 : 3	1-2-2-4-?	1-2-2-2-?	1-2-1-2-?	1-1-1-2-?

(Table 28.2). The genito-aggenital plates bear one pair of genital setae in the protonymph, four pairs in the deutonymph (Fig. 28.2*b*) and seven pairs in the tritonymph (Fig. 28.2*d*). The aggenital seta appears in the tritonymph. The anal opening is always bordered on each side by a well-sclerotized but colourless ano-adanal plate, triangular in shape, and laterally separated from the notogaster. The ano-adanal plates are glabrous in the larva and protonymph. The deutonymph has three pairs of adanal setae (Table 28.2) but no anal setae. In the tritonymph all setae are present, namely, three pairs of adanals and two pairs of anals. The adanal setae are always some distance from the proximal margin of the plate (Fig. 28.2*e*). The legs are short (Figs 28.3 and 28.4). The chaetotaxy (Table 28.2) is poorly understood, for example, the arrangement of the setae in the protonymph has not been described, and requires further study. It should be noted that seta d on tibia IV is always separated from the solenidion.

CONCLUSION

In many cases it is possible to estimate the plesio- and apomorphic state of an adult character by referring – with caution however – to its state in the different ontogenetic stages. Analysis of the morphological characters of the immature stages has enabled three of them to be regarded as plesiomorphic in the adults. The first is the form of the prodorsal and notogastral setae, all of which are smooth and taper to an elongated point in all the immature stages. The second is the arrangement of the anal and adanal setae in the tritonymph. The two anal setae are located near the paraxial margin of the ano-adanal plate, and the three adanal setae are always some distance from the paraxial margin of the plate. The third character is seta d on tibia IV, which is long and always separated from the solenidion. The estimation of the plesio- or apomorphic character state of the morphological features referred to above, proved useful for the construction of the system of the Phthiracaroidea following the principles of cladistic procedure (Niedbała, 1986).

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A new interpretation of the epimeral theory of Grandjean

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ABSTRACT

Latreille (1825) subdivided the legs of Insecta *sensu* Linnaeus into four parts, the first of which should be a ball and socket joint. This feature caused Latreille to rename the Insecta, calling them Condylopes. Burmeister (1832) changed the terminology: the 'rotule' was termed an acetabulum, and the 'trochanter', a coxa. Siebold (1848) referred to the parts of the leg as podomeres. He discarded the name Condylopes, and its analogy with the Vertebrata, and created the Arthropoda, but retained the old terminology for the parts of the leg. Like Burmeister, he called the first free podomere, a coxa. Michael (1884) described the ball-and-socket joint of the leg in oribatid mites, and sought a coxa *sensu* Siebold but did not refer to the trochanter. Grandjean (1952, 1968, 1970) referred to the structure of the oribatid ball-and-socket joint stating that it consisted of a *paroi cotyloide* and a trochanter but described its function as a rotation joint.

In fact the coxa as a free podomere, *sensu* Siebold, does not occur in the Oribatida. All that is present is a sclerotized region of the epimeron, which is incorporated into the ventral wall of the podosoma. Grandjean applied the term coxa to this sclerotized region. In reality the so-called glenoid cavity of a 'rotule' or acetabulum corresponds to the *facies auricularis* of the *os sacrum*, and by analogy the acetabulum must be part of the *os coxae*. The difficulty is that so far an acetabulum has not been observed.

In the case of the Oribatida one must compare the pleuron with the *facies auricularis*. Grandjean (1970) shows the internal border of the pleuron as an internal contour of the *paroi cotyloide*, labelled *ci*; this is

labelled *bi* in his 1968 paper. In fact *ci* (or *bi*) is an articulation comparable to the *articulatio sacroiliaca*, and is the basal joint of the leg. In oribatid adults one finds a kind of gomphosis, that is, an articulation between the pleuron and the coxa where a fold of the pleuron is seated in a groove of the coxa close to the capitular angle.

Grandjean (1970) figures the dorsal part of the coxa but does not name it. In earlier papers he referred only to the free border of a circumtrochanteral opening. In his 1970 paper he also illustrates a surface between contour *ci* and the free border *b*. In the adults of the higher Oribatida this area is much larger, and its internal surface resembles the acetabulum of a hip joint. The anterior condyle is located here and not on the concave surface of the *paroi cotyloide sensu* Grandjean. Grandjean (1970) correctly figures the supracoxal spine which lies between *ci* and *b*.

The podocephalic canal and stigma 1 are structures of the pleuron (*paroi cotyloide*). The propodosomal condyle *K* is an extension of the paraxially directed fold of the pleuron. The external surface of this fold is adjacent to the external surface of the infracapitulum. The pleural fold extends over the *tectum rostrale*, and the condyle articulation does not lie within the body of the mite. The principal error was the declaration that the dorsal basal opening of the coxa was stated to be the distal border. The lines *bi* and *be* of Grandjean (1968) are not contiguous but are separated as shown in the figures. The *'fossette supracoxal'* of Grandjean (1937) corresponds to the *'sclerit coxal'* of Grandjean (1970). The term, epimeron, should only be used in the sense of Michael (1884), that is, the ventral part of the coxa (*hanche*) *sensu* Dugès (1834).

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A comparison of the sclerotized parts of the reproductive organs of house-dust mites of the genus Dermatophagoides *using scanning electron microscopy*

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The sclerotized parts of the male and female reproductive organs of *Dermatophagoides farinae* Hughes and *D. pteronyssinus* (Trt) have been investigated using electron microscopic techniques of whole and dissected specimens, and their functions are described. The structures used for sperm transfer and storage differ in the two species. It can be assumed that the movement of the penis is entirely responsible for the transport of the non-motile spermatozoa into the receptaculum seminis of the female

INTRODUCTION

House-dust mites and their medical importance have been the subject of many investigations, and their anatomical as well as histological structures have been studied using both light-microscopic and electron-microscopic techniques. *Dermatophagoides* is certainly one of the most thoroughly investigated genera of mites (van Bronswijk and Sinha, 1971; van Bronswijk, 1981). The arrangement of the reproductive organs is the same as in other Astigmata so that the individual parts can be homologized (Knülle, 1959). Differences exist, however, in the appearance of those structures used in the direct transfer of sperm (Walzl, 1978). This led Nalepa to suspect, as early as 1884, that the copulatory organs might be used to differentiate species.

Dermatophagoides pteronyssinus (Trt) and *Dermatophagoides farinae* Hughes, described in detail by Fain (1966, 1967), Griffiths and Cunnington (1971) and Hughes (1961), belong to the Pyroglyphidae, the species of which adopt a retroconjugate mating orientation, which means that the posterior ends of male and female face in opposite directions, with the smaller male (*c.* 350 μm long) being carried about by the larger female (c. 590 μm). Several distinct auxiliary copulatory organs are employed in this mating arrangement. The two species investigated have proved to be favourable subjects for demonstrating the complexity and distinctiveness of their reproductive organs by means of electron-microscopic techniques.

MATERIALS AND METHODS

Males and females of *D. farinae* and *D. pteronyssinus* were taken from stock cultures that had been maintained at a temperature of 25 °C and 75% r.h. for the former and 80% r.h. for the latter species. They were prepared for scanning electron microscopy according to the method of Walzl and Waitzbauer (1980). For observation of sclerotized structures occurring within the body, mites were dissected with the aid of slender pointed needles after maceration in lactic acid, and then treated for critical-point drying. The dried objects were fastened to stubs by means of double adhesive tape or with 'Tempfix' thermoplastic adhesive and, after sputtering with gold, they were examined under a Cambridge Stereoscan Mark A2 microscope. In order to obtain a better understanding of structures hidden within the body and muscle attachments, dissected individuals were also examined.

FEMALE OVIPOSITOR AND ASSOCIATED STRUCTURES

When not in use for egg laying, the female genital opening, situated between the third and fourth pairs of legs, is a V-shaped slit with the narrow end of the V pointing anteriorly (Fig. 30.1*a*). According to Knülle (1959), it represents the transverse binary type which can be deduced from the basic ternary type. This type is the only one that has developed an epigynal lip. The V-shaped slit is framed by the epigynum, a crescentic sclerite, which serves as a strengthening structure for the ovipository organ. During oviposition, the epigynal lip drops outwards like a trap door, due to the pressure of haemolymph and eggs (Fig. 30.1*b*). Now the grooved and wrinkled membraneous outer border of the vulva and its orifice, and also the genital plates become visible, the latter being previously hidden in the vestibulum. From the orifice, the wide thinly sclerotized duct of the ovipositor leads to the interior. Seen

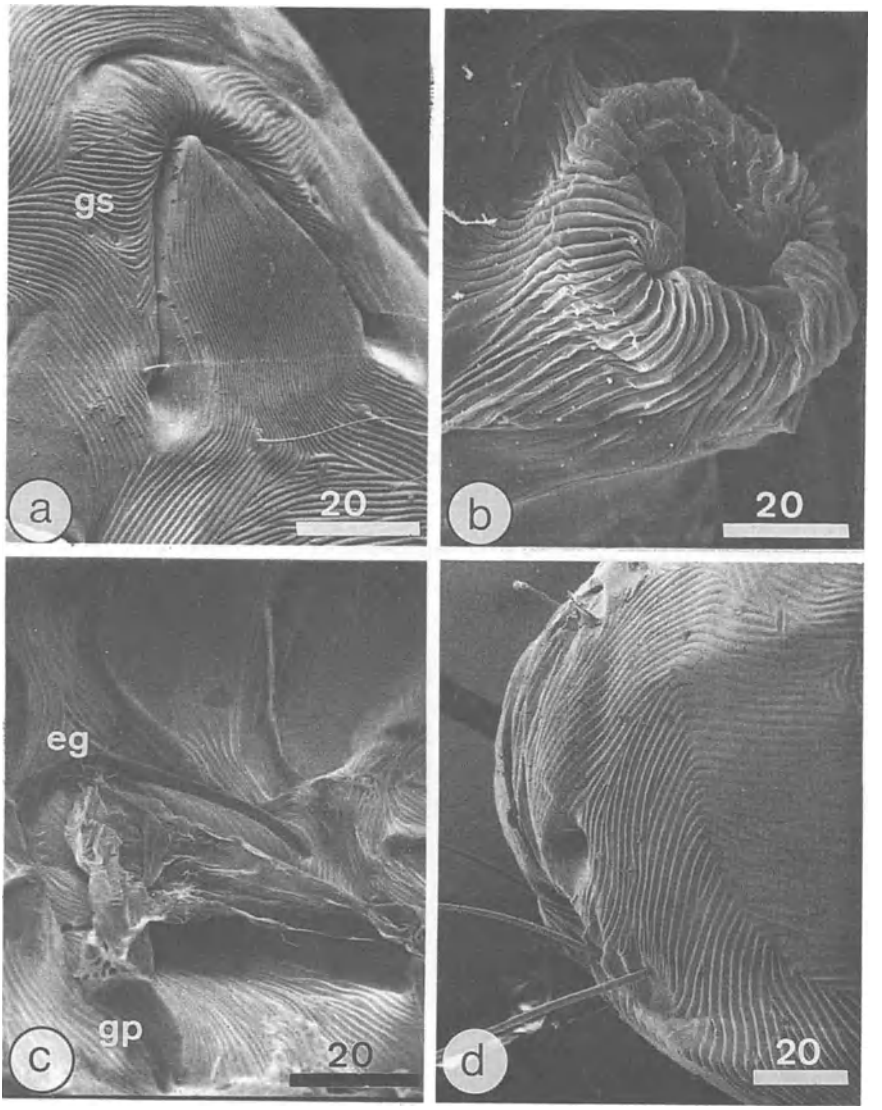

Fig. 30.1 Scanning electron micrographs of ovipository organ (*a–c*) and bursa copulatrix opening (*d*) of females of *Dermatophagoides farinae* Hughes. Scale bar in μm. (*a*) Ovipositor in inoperative position (ventral view). (*b*) Ventral view of ovipositor ready for oviposition. (*c*) Ovipositor of dissected specimen, seen from inside. (*d*) Lateral view of anal region showing opening of bursa copulatrix. eg, epigynum; gp, genital plate. gs, genital sucker.

from the inside (Fig. 30.1*c*), the dorsal border of the ovipositor is expanded outwards in order to receive a mature egg so that the trap door does not open before egg laying. The reinforced epigynum (eg) and genital plates (gp) are clearly visible.

The so-called genital suckers (gs; Fig. 30.1*a*) are situated outside the vestibulum, and represent two pairs of pits in the cuticula where muscles are attached. There is no indication that they have a sensory function. One pair of ovipositor, that is, vaginal muscles, and one pair of genital-plate muscles, serve to retract the vulva and to close the genital opening. The ovipository organs do not differ in appearance in the two species.

MALE COPULATORY STRUCTURES

As is common in mites with a retroconjugate mating orientation, auxiliary copulatory organs in the form of suckers have developed in the males. Two suckers (ts; Fig. 30.2*a*) are present at the distal ends of the tarsi of the fourth pair of legs. They are bell-shaped setae, *d* 2 μm, where muscles are probably inserted. During mating, they are attached to the female in the region of her oil-gland opening, and serve to precisely regulate the mating position. However, the two large paranal suckers (Fig. 30.2*c*) are primarily responsible for the final adjustment of the mating position. These are located within circular sclerites adjacent to the anal slit, and are retracted into the body when not in use. For attachment to the female, they are protruded by haemolymphatic pressure. Each disc and the surrounding ring are sclerotized plates. The disc is retracted by groups of anal-sucker muscles (that is, dorso-ventral muscles). A partial vacuum is formed between the sucker plate and the surface of the female due to the action of the muscles, as a result of which the ring adheres to the dorsum of the female. The tendons of the anal-sucker muscle groups insert on the inner surface of the disc.

The male copulatory organ, usually hidden within the body, is covered by the paragynal lips. When retracted, the extremity of the penis (or aedeagus) is directed anteriorly, and is enveloped in a smooth deflated copulatory sac. As in the female, the genital plates and genital suckers of the male have tendons attached. For mating, the penis is protruded due to haemolymphatic pressure. The copulatory organ unfolds, and the genital plates (gp) become visible (Fig. 30.2*b*). When ready for mating, the penis turns backwards at 90° and the copulatory sac (cs) is protruded (Fig. 30.2*a*). Only the tip of the penis is visible; most of this structure remains hidden in the channel formed by two lateral sclerites, the transmission sclerites (tsc) according to Knülle (1959). The two lateral

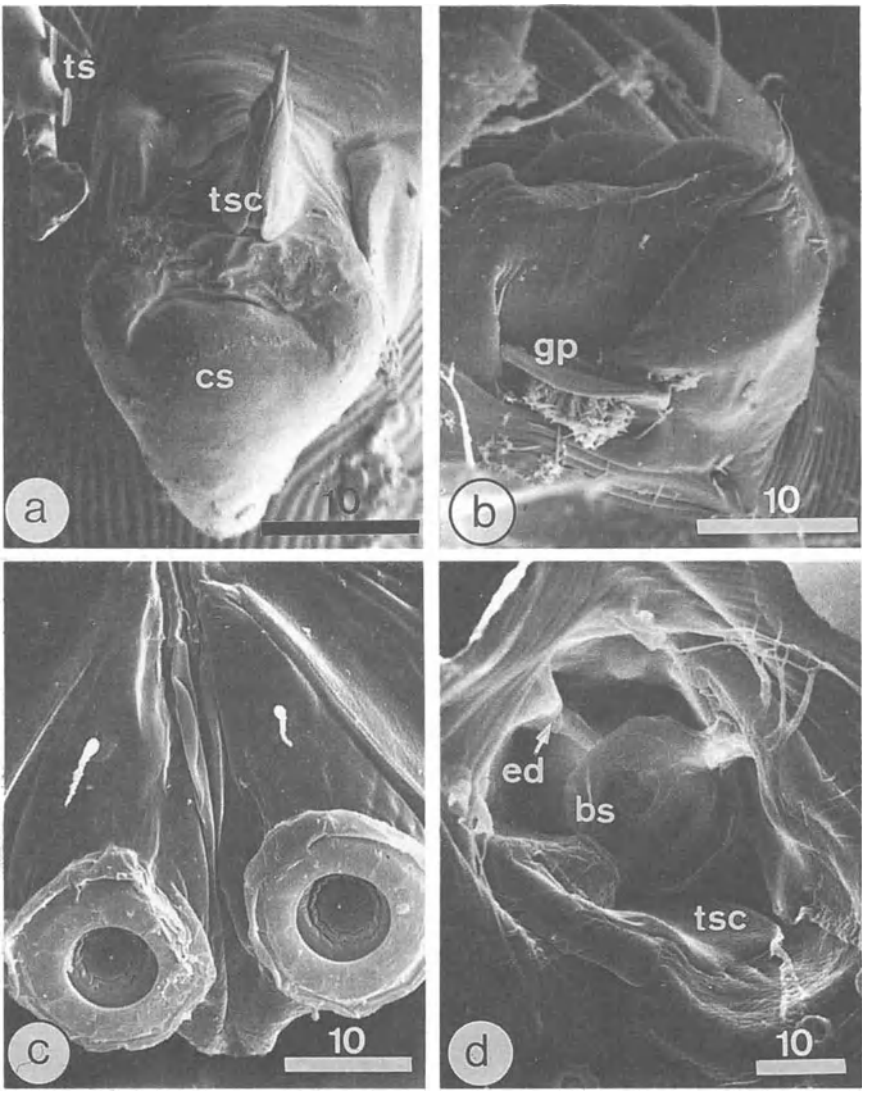

Fig. 30.2 Scanning electron micrograph of males of *Dermatophagoides*. Scale bar in μm. (*a*) Ventral view of protruded copulatory organ of *D. pteronyssinus* (Trt). (*b*) Lateral view of partly protruded copulatory organ of D. farinae. (*c*) Anal region of *D. farinae* showing protruded anal suckers. (*d*) Copulatory organ of *D. pteronyssinus* seen from inside. bs, basal sclerite; cs, copulatory sac; ed, ejaculatory duct; gp, genital plate; ts, tarsal suckers; tsc, transmission sclerite.

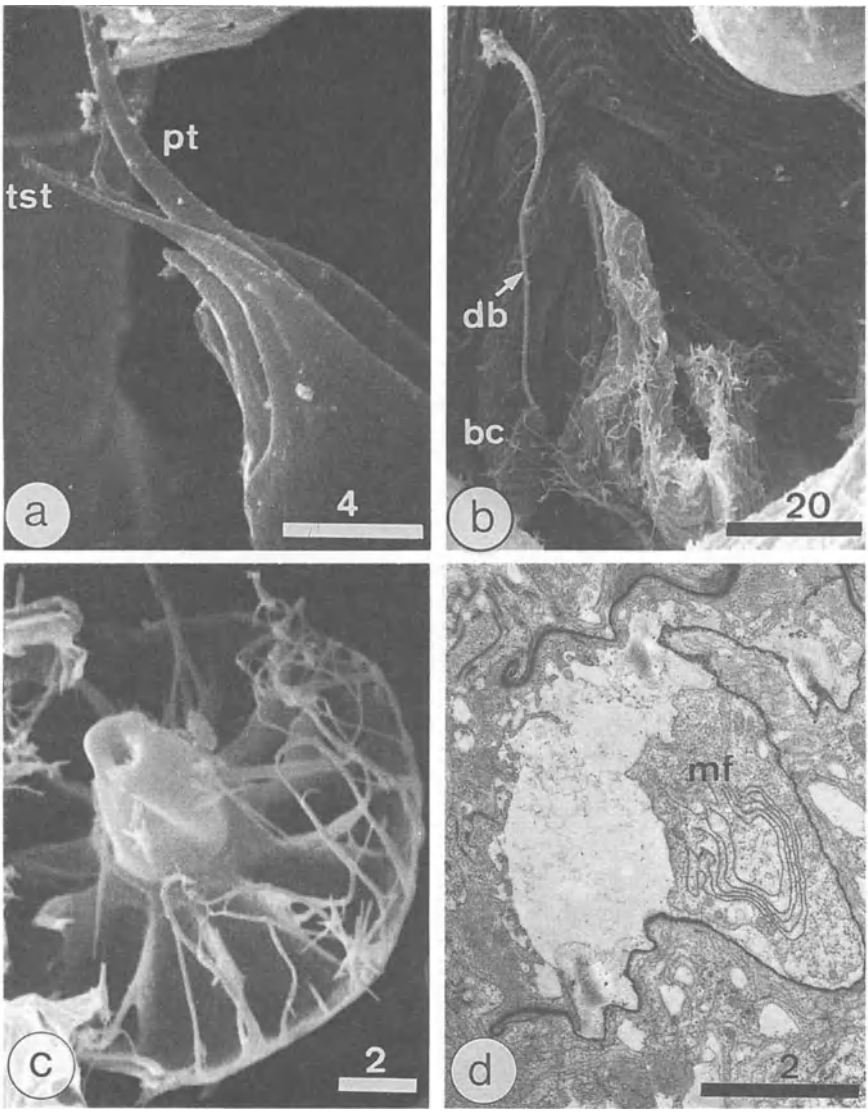

Fig. 30.3 Scanning (*a–c*) and transmission (*d*) electron micrographs of reproductive structures of *Dermatophagoides*. Scale bar in μm. (*a*) Lateral view of penis tip (pt) and tip of transmission sclerite (tst) of *D. farinae*. (*b*) Interior view of anal region of dissected female of *D. farinae* showing bursa copulatrix (bc) and ductus bursae (db). (*c*) Ductus bursae opening into receptaculum seminis of dissected female of *D. pteronyssinus*. (*d*) Sperm in the lumen of ejaculatory duct of *D. pteronyssinus* illustrating the membraneous folds (mf).

sclerites of *D. farinae* terminate in long backwardly pointing tips (tst) as does the penis (Fig. 30.3*a*).

If the inside of the protuded copulatory organ is examined (Fig. 30.2*d*), it can be seen that the transmission sclerites (tsc) and the penis are joined to a median basal sclerite (bs). The ejaculatory duct (ed) terminates here. The muscle tendons insert on the basal sclerite, on the two transmission sclerites and on the four genital suckers. In addition, there are openings in the basal sclerite that lead to a cavity between the two transmission sclerites, through which nerves pass. There may be sensory organs in the tips of the two transmission sclerites. The copulatory apparatus is folded by the muscles which insert on the basal sclerite, the transmission sclerites, and on the genital plates.

In general, the copulatory apparatus of *D. pteronyssinus* consists of the same structures as those of *D. farinae*. There is, however, a difference in the shape of the distal end of the penis; in *D. pteronyssinus*, it is shorter and tapered (Fig. 30.2*a*), and the transmission sclerites do not end in extended tips. During mating, this short extremity of the penis of *D. pteronyssinus* is inserted in the opening of the female's bursa copulatrix, which is located in a terminal position near the anus. In a population of females of *D. farinae*, observed over an extended period, 55% had the external bursa opening to the left, and 45% to the right of the anal slit (Fig. 30.1*d*). In *D. farinae*, the long thin distal end of the penis (pt; Fig. 30.3*a*) and, possibly, the distal ends of the transmission sclerites are also inserted in the jug-shaped orifice of the bursa copulatrix (bc; Fig. 30.3*b*) during copulation.

BURSA COPULATRIX AND ASSOCIATED STRUCTURES

The ductus bursae (db; Fig. 30.3*b*) leads from the bursa copulatrix to the receptaculum seminis and, in *D. farinae*, the opening into the receptaculum is a small cone. In *D. pteronyssinus*, however, it consists of a large cone with the receptaculum having a chambered sclerotized base (Fig. 30.3*c*). The ductus bursae is a heavily sclerotized and, certainly, a non-extensible duct with a lumen of 1 μm. Consequently the movement of the penis must be responsible for forcing the non-motile spermatozoa into the bursa copulatrix, directly through the winding duct (50 μm long) and into the receptaculum. The membraneous folds (mf; Fig. 30.3*d*) in the sperm are typical of astigmatic mites (Alberti, 1980; Witalinski *et al.*, 1986), and probably have a protective function during sperm transfer and transport. The sperm is stored in the lumen of the receptaculum, the epithelium of which has a brush and a ring of cuboid cells at the border of short thin microvilli, opening to the receptaculum probably closes this opening if the haemolymphatic pressure increases thus

preventing a backflow of spermatozoa through the ductus bursae. If haemolymphatic pressure is exerted on the receptaculum seminis, the sperm is transported to the ovaries via the two receptacular ducts. Detailed electron-microscopic investigations of representatives of this family together with those of other families of the Astigmata may help to clarify the phylogenetic relationship between proconjugate and retroconjugate mating within and between the individual families.

ACKNOWLEDGEMENT

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31

Reproductive systems in Acaridida – some peculiar features

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ABSTRACT

Semithin serial epon sections and electron microscopy were used to reconstruct the male and female genital systems in representatives of the Acaridae and Sarcoptidae. The female genital system, which possesses two apertures – a copulatory opening and an oviporus – is composed of an inseminatory canal, receptaculum seminis, ovaries, oviducts, uterus, pre-oviporal canal and paired accessory glands. In the male, there can be seen two testes, vasa deferentia, and an ejaculatory duct ending at the apex of the aedeagus as well as a single accessory gland. Special attention has been paid to the structure and function of the receptaculum seminis, as well as the structure of an unusual central cell occurring in the testis. The origin and function of this cell is discussed. Some of the results of this study have been published elsewhere (Witalinski *et al.*, 1990).

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32

A respiratory apparatus in eggs of certain mites

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The respiratory apparatus was first described by Dittrich (1971) in eggs of *Tetranychus urticae* Koch. Dittrich also found it in eggs of *Panonychus ulmi* (Koch), *Panonychus citri* (McGregor) and *Eotetranychus tiliarium* (Hermann), and he concluded that it is a common feature in the family Tetranychidae.

The present author examined eggs of 31 mite species belonging to different families and suborders, and he discovered a similar respiratory apparatus in all the investigated species of the following families: Bryobiidae (two species), Stigmaeidae (one species), Tenuipalpidae (five species) and Tetranychidae (six species). However, no such apparatus was found in six species belonging to the superfamily Eriophyoidea. Also this apparatus was not found in species from outside the subcohort Raphignathae, that is, Acaridae (four species), Phytoseiidae (one species), Tarsonemidae (four species) and Tydeidae (two species).

The apparatus, essentially, is similar to that described by Dittrich in all the species of Bryobiidae and Tetranychidae investigated, and also in *Brevipalpus* sp. and *Tenuipalpus* sp. However, it shows considerable modification in *Dolichotetranychus* sp. and in *Zetzellia mali* (Ewing) (Suski, 1988).

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33

Fine structure and functions of the mouthparts involved in the feeding mechanisms in Cenopalpus pulcher *(Canestrini and Fanzago) (Tetranychoidea: Tenuipalpidae)*

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The mouthparts of *Cenopalpus pulcher* (Can. and Fan.) have been studied using scanning and transmission electron microscopy. The fine morphology of the labrum, pre-oral groove, inferior oral commissure, 'salivary pump' and chelicerae are described for the first time. On the basis of the morphology of these structures, two different channels are described: on the one hand, 'the food channel', which is composed of a labrum interlocked with the stalked lateral margins of the pre-oral groove; and on the other, 'the salivary channel' formed by the cheliceral stylets which interlock when protracted. The fine structure of the ductule connecting the inferior oral commissure to the pharyngeal pump suggests that its relationship with the function of the pharyngeal pump is similar to that of a vacuum valve. Examination of the distal portion of the median salivary duct indicates the presence of a 'salivary pump' and explains its function

INTRODUCTION

At present our knowledge of the feeding mechanisms of the Tetranychoidea is incomplete. Few anatomical studies have been conducted to elucidate the morphology and functioning of the gnathosoma, and these investigations have been concerned with the main species only such as

Tetranychus urticae Koch (Blauvelt, 1945; André and Remacle, 1984; Akimov and Jastrebtsov, 1981; Alberti and Crooker, 1985). *Tetranychus atlanticus* McGregor (Baker and Connell, 1963), *Bryobra praetiosa* Koch and *Panonychus ulmi* (Koch) (Alberti and Crooker, 1985) and *Bryobra rubrioculus* (Sch.) (Summers *et al.*, 1973). Moreover, there are few published scanning electron microscopy (SEM) studies of tetranychid and tenuipalpid mouthparts (Hislop and Jeppson, 1976; Akimov and Barabanova, 1977; André and Remacle, 1984).

These authors have interpreted the mode of feeding in various ways:

1. The protracted cheliceral stylets fit together for piercing, and form a tube to inject the saliva into plant tissues, whereas the retracted stylets make possible the suction of the plant fluid.
2. The protracted and interlocked cheliceral stylets are used alternately as a structure for piercing and sucking.

No anatomical observations are available on the mouthparts of the Tenuipalpidae, the false spider mites. The only observations on their external morphology were made by Hislop and Jeppson (1976) using SEM but they are less than adequate.

The purpose of the present study was twofold:

1. To make a detailed description by SEM and transmission electron microscopy (TEM) of the mouthparts of the tenuipalpid mite, *Cenopalpus pulcher* (Can. and Fan.), in order to deduce the piercing and ingesting mechanisms.
2. To compare the morphology of the tenuipalpid mouthparts with those described for the tetranychids.

MATERIALS AND METHODS

The overwintering females of *Cenopalpus pulcher* collected from branches of *Prunus domestica* L. in southern Italy were examined. Material for TEM was prepared by dissecting specimens with a microbistury and prefixing in 4% glutaraldehyde in phosphate buffer at pH 7.2. The dissected specimens were then washed in buffer, and post-fixed for 3 hours in 1% osmium tetroxide in the same buffer. The selected portions were dehydrated through a graded series of ethanol solutions and embedded in Araldite 502, which was then polymerized at 70 °C. The blocks were sectioned with an ultramicrotome LKB III using a diamond knife, and stained with 0.5% uranyl acetate and lead citrate. Sections were made from the region where the adoral sensilla arise to that of the infracapitular setae, and observed and photomicrographed using a Zeiss EM 109 transmission electron microscope. The heterogeneity of the blocks made

it difficult to obtain a complete serial sequence of sections. It was only possible to obtain these by removing single sections from the knife edge and collecting each on a separate grid. For examination and illustration of external features by SEM, freshly killed specimens were observed using a Cambridge S100 instrument.

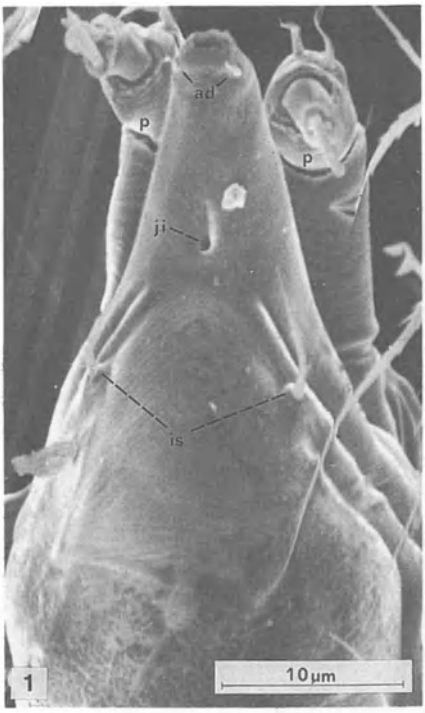
THE MOUTHPARTS

The conically shaped infracapitulum or 'rostrum' contains a pharynx, an oral opening, an inferior oral commissure, and houses the cheliceral grooves. The rounded rostral apex is softer than the rest of the rostrum and bears two pairs of conical sensilla, the adoral setae (or adoral sensilla); the dorsal pair is slightly anterior to the ventral pair (Fig. 33.1).

The inferior oral commissure (the 'rostral fossette' of Summers *et al.*, 1973) and the pre-oral groove (Paran, 1982) (Fig. 33.2*a*,*b*) are the vestiges of the fusion of the lateral lips (van der Hammen, 1968). The inferior oral commissure opens anterior to the infracapitular setae on the ventral surface of the infracapitulum, and communicates with the pharynx through a constricted chitinous tube. The walls of the tube, tricuspid-shaped in cross section (Fig. 33.2*c*), form a valve system that closes during the decompression of the pharyngeal pump and opens during its compression to permit the regular flow of plant fluid during ingestion.

The pre-oral groove and the labrum are described together as they are both involved in the sucking function. They are deeply recessed in the rostral gutter (Fig. 33.2*b*). The pre-oral groove is a sclerotized trough bordered by two prominent dorsolateral margins (Fig 33.2*a–d*). Proximally, the pre-oral groove is connected to the pharyngeal chamber and, dorsally, it is covered by the labrum within which nerve fibres are embedded (Fig. 33.3*b*). In this region, the labrum is dorsally enlarged and the ventral portion is laminar and soft, the two parts being connected by a thin vertical plate (Fig. 33.2*d*). The margins of the pre-oral groove are sclerotized and shaped in such a way that the ventral part of the labrum fits into them exactly (Figs 33.2*d* and 33.3*b*).

The labrum (Figs 33.2*a–c*), anterior to the portion already described, is dorsally and ventrally enlarged and sclerotized. In this way the labrum, juxtaposed to the sclerotized margins of the pre-oral groove, constitutes a double valve (Figs 33.2*a*,*c*). The adjacent distal portion of the labrum is also sclerotized, and the margins of the pre-oral groove are inserted on thin, elastic bases. As a result, the stalked margins of the pre-oral groove act like an elastic packing to form a hermetic seal for the food channel (Fig. 33.3*a*). Towards its distal end, the labrum is reduced, almost triangular in cross section (Fig. 33.3*c*), and covers the distal part of the pre-oral groove. Here are located the bases of the adoral sensilla (Fig.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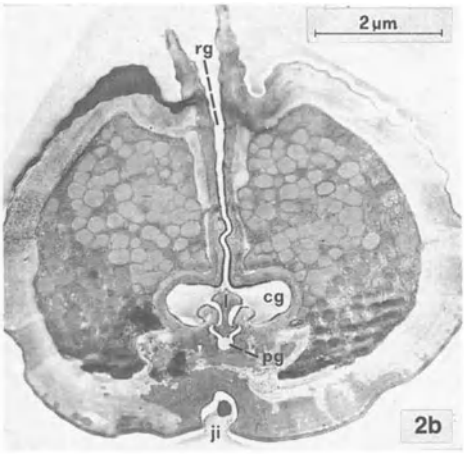
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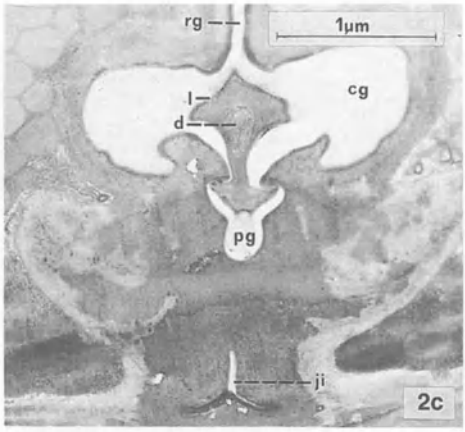
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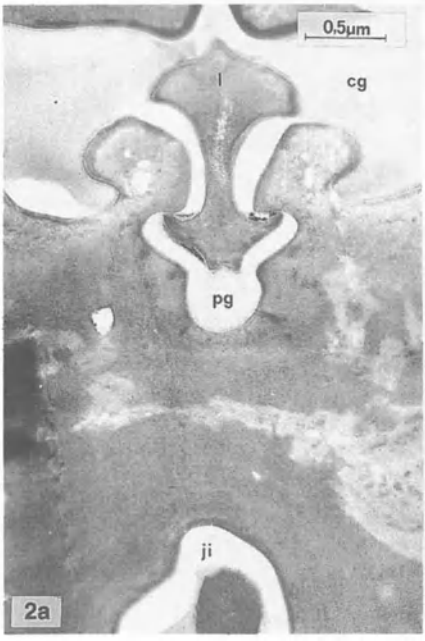
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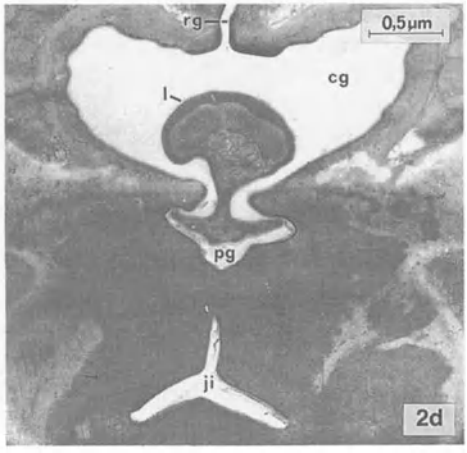
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33.3*d*), and the cheliceral grooves are surrounded by an annular sclerotized reinforcement with soft flaps.

The terminal portion of the salivary duct, the 'median taenidium' of André and Remacle (1984), shows the existence and explains the action of the 'salivary pump'. At J (Fig. 33.5), the median salivary duct is embedded in the strong cervical apodeme (Fig. 33.3*e*), and does not appear to communicate with the cheliceral stylets. Distally (H-I, Fig. 33.5), the duct opens into a vestibulum that is delimited anteriorly by the dorsal ridge of the labrum, and laterally by two flexible salivary plates (sp; Fig. 33.4*a*). Two narrow canaliculi lie on each side of the dorsal ridge of the labrum, and connect the vestibulum to the 'salivary channel' of the stylets (Fig. 33.3*f*).

Mesally, the cheliceral stylets have three tongues and two grooves (Fig. 33.4*b*) which fit together during their protraction, and there are nerve fibres running lengthwise. The retracted stylets lie separately inside the cheliceral grooves (Fig. 33.3*e*). The protracted stylets, on the other hand, are interlocked forming a single tube (Fig. 33.4*c*). The digiti fixi have a dorsal and vertical laminar part sliding in the rostral gutter and ventrally, a horizontal plate sliding in the cheliceral grooves (Fig. 33.3*b*). There are two accessory sclerites beneath the digiti fixi, and between the digiti mobili, where they are joined to the stylophore (Figs 33.3*b* and 33.4*b*).

DISCUSSION AND CONCLUSIONS

For the first time, a detailed description has been given of the morphology of the labrum, its relationship with the pre-oral groove, and the relationship between the inferior oral commissure and the pharyngeal pump. The salivary pump and its connection with the stylar salivary channel was also observed. With a knowledge of these structures, it is possible to explain the feeding mechanisms in a phytophagous mite such as *Cenopalpus pulcher* (Fig. 33.5).

Fig. 33.1 Scanning electron micrograph of gnathosoma of *Cenopalpus pulcher* (Can. and Fan.) in ventral view.

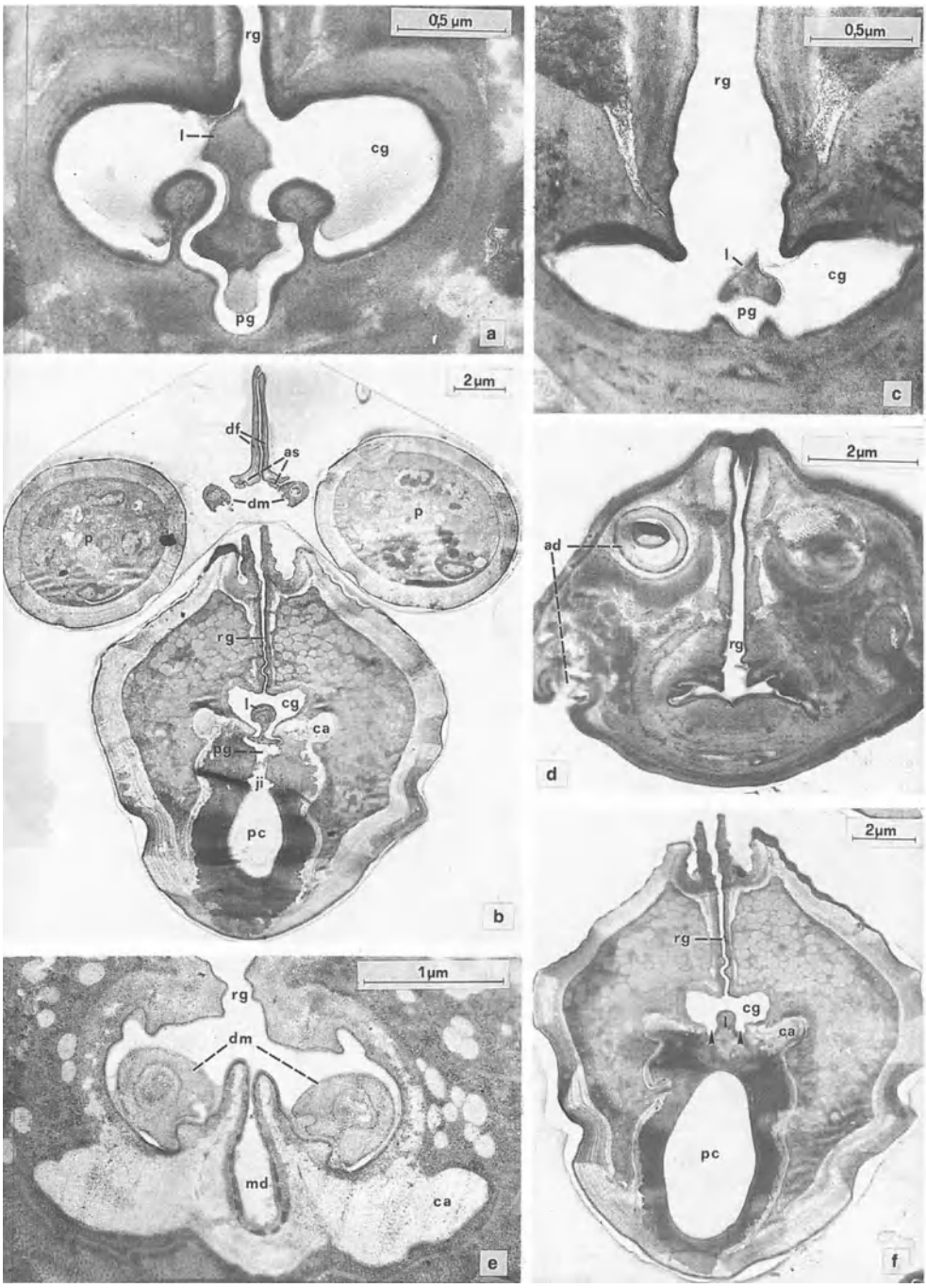
Fig. 33.2 Transmission electron micrographs of cross sections of gnathosoma. The letters D–F refer to section locations as shown in Fig. 33.5. (*a*) Detail of labrum, pre-oral groove and inferior oral commissure (D). (*b*) General view at level of distal end of inferior oral commissure (D). (*c*) Labrum and pre-oral groove at a level about half-way along length of inferior oral commissure (E). (*d*) Section towards proximal end of inferior oral commissure (F). ad, Adoral setae; cg, cheliceral grooves; d, dendrites; is, infracapitular setae; ji, inferior oral commissure; l, labrum; p, palps; pg, pre-oral groove; rg, rostral gutter.

Our observations demonstrate the presence of two independent channels: (1) a salivary channel within the interlocked cheliceral stylets; and (2) a food channel composed of the pre-oral groove and the labrum. The interlocked stylets (Hislop and Jeppson, 1976) have the function of piercing the tissues during feeding in the same manner as in *T. urticae* (André and Remacle, 1984; Alberti and Crooker, 1985) and *B. rubrioculus* (Summers *et al.*, 1973). During protraction of the stylets, the accessory sclerites, interposed between the digiti mobiles and the stylophore (Figs 33.3*b* and 33.4*b*), exert a pressure on the flexible salivary plates (Fig. 33.4*a*), causing a flow of saliva from the median salivary duct into the salivary channel. The retraction of the stylets causes the stream of plant fluid to reach the surface of the plant; the turgor pressure of the cells could facilitate this flow of plant juices.

The rostral apex, which is softer than the proximal part and possesses very specialized mechanoreceptors, is pressed on to the plant surface. The food channel, which is directly connected to the pharyngeal chamber, is hermetically sealed by the soft subapical flaps of the annular sclerotized reinforcement surrounding the pre-oral groove (Fig. 33.3*d*). The morphology of the inferior oral commissure and the sealing of the food channel during suction ensure the continuity of fluid flow through the food channel towards the pharyngeal pump. Any air bubbles can be eliminated through the inferior oral commissure without interrupting the capillary flow in the food channel. The double-valve arrangement provided by the labrum has an active role in closing the food channel during the operation of the pharyngeal pump both in the compression and decompression phases. This demonstrates that the interlocked stylets are used for piercing and injecting saliva into the plant tissues, and that the pre-oral groove and the labrum are used for sucking plant fluids.

A comparison with other phytophagous mite groups such as the Tetranychidae, is possible only with reference to the median salivary duct, which is similar to that in *Tetranychus* and *Bryobra*, and the shape

Fig. 33.3 Transmission electron micrographs of cross sections of gnathosoma at A–C, G, H, J (Fig. 33.5). (*a*) Detail of labrum and pre-oral groove towards distal end (C). (*b*) General view at level of proximal end of inferior oral commissure (G). (*c*) Detail of distal part of labrum and pre-oral groove (B). (*d*) General view of rostral apex at level of bases of adoral setae (A). (*e*) Detail at level of cervical apodeme (J) showing median salivary duct. (*f*) General view at level of pharyngeal chamber (H). Arrows indicate canaliculi connecting to 'salivary channel' of stylets. ad, Adoral setae; as, accessory sclerites; ca, cervical apodeme; cg, cheliceral grooves; df, digitus fixus; dm, digitus mobilis; ji, inferior oral commissure; l, labrum; md, median salivary duct; p, palps; pc, pharyngeal chamber; pg, pre-oral groove; rg, rostral gutter.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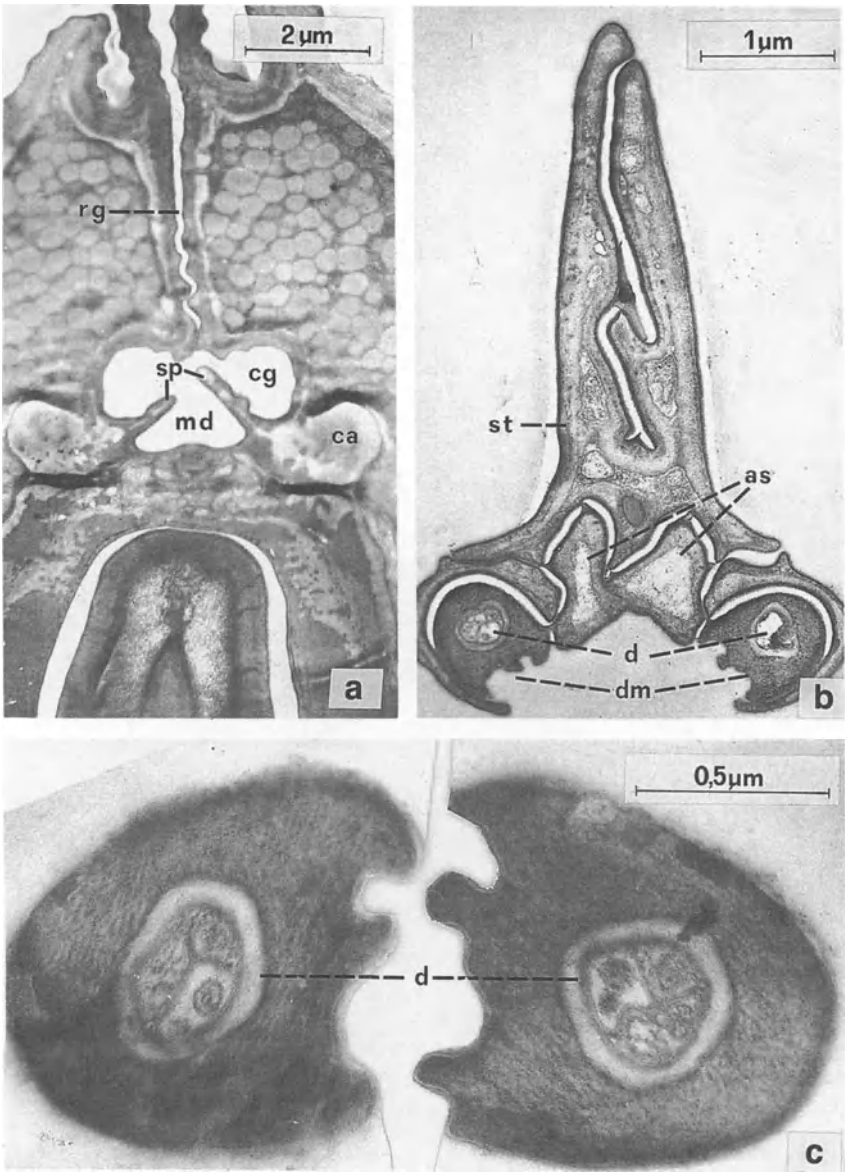

Fig. 33.4 Transmission electron micrographs of cross sections of gnathosoma. I refers to Fig. 33.5. (*a*) Detail of distal portion of median salivary duct showing 'salivary pump' (I). (*b*) Detail of cheliceral complex at level of 'salivary pump' (I). (*c*) Detail of digiti mobiles showing tongues and grooves. as, Accessory sclerites; ca, cervical apodeme; cg, cheliceral grooves; d, dendrite; dm, digitus mobilis; md, median salivary duct; rg, rostral gutter; sp, salivary plates; st, stylophore.

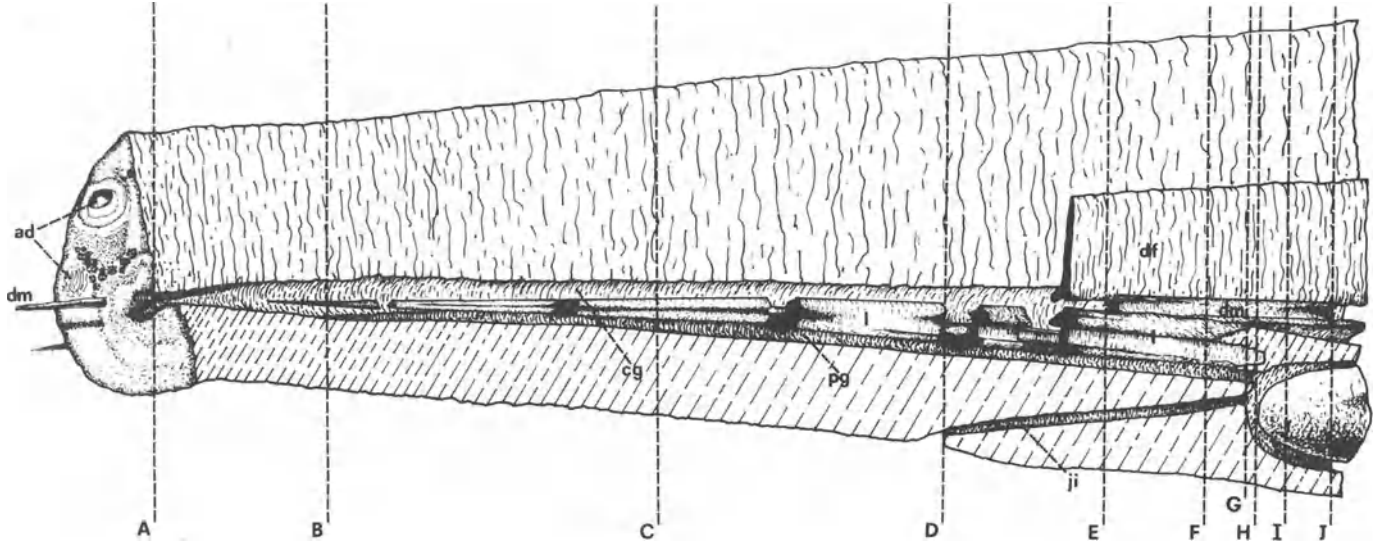

Fig. 33.5 Semischematic drawing of the mouthparts of *Cenopalpus pulcher* and showing locations (A–J) of TEM sections illustrated in Figs 33.2–33.4. ad, adoral setae; cg, cheliceral grooves; df, digitus fixus; dm, digitus mobilis; ji, inferior oral commissure; l, labrum; pg, pre-oral groove.

of the stylets which have a stronger interlocking mechanism in *Tetranychus* and *Bryobra* than in *Cenopalpus pulcher*. In order to extend our interpretations to other phytophagous groups related to the Tenuipalpidae, further in-depth studies of the apical part of the rostrum are required.

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34

The alveolar salivary glands of the active phases of trombiculid mites (Trombiculidae)

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The results are given of a detailed study of the histological and ultrastructural organization of the alveolar salivary glands in free-living phases of the life cycle in trombiculid mites. A study was made of unfed larvae of *Hirsutiella zachvatkini* and *Euschoengastia rotundata*; of larvae of *H. zachvatkini* and *Neotrombicula pomeranzevi* feeding on their natural hosts; and unfed deutonymphs of *H. zachvatkini* together with individuals which had fed many times, and adults of the same species obtained from culture.

Heteromorphic parasitic larvae, active free-living deutonymphs and adult mites, have four distinct pairs of simple alveolar salivary glands. Each gland is formed by one type of acinary cell situated around the intra-alveolar lumen, and has its own salivary duct. The alveoles contain neither cambial nor interstitial cells except those that take part in the formation of the lumen and the duct. The organization of the wall of the duct, formed by two layers of the cuticle, provides for expansion of its lumen and for its contraction leading to complete closure.

The course of the ducts and other characteristics reveal a single mode of organization of the salivary-gland complex although homologous pairs of glands in larvae and the subsequent phases occupy different relative positions, and have their own historically related names. Also, they differ greatly in the structure of the cytoplasm and the secretion granules, and are characterized by a specific, asynchronous and mainly not obvious secretory dynamics. The mode of organization of the cells, and the simple oval secretion granules of variable electron density,

shows that the secretion of each of the glands is mainly of a serous nature.

In larvae, for some time after hatching, there occurs transformation and final formation of the secretion granules, and also differentiation of the glandular cells, which determines their postlarval development. In nymphs and adult mites, the salivary glands contain mature secretion granules already formed, and thus enabling them to feed on insect eggs immediately after eclosion. Secondary parasitism of larvae underlying the redistribution of functions among homologous pairs of glands, and also specificity of their ultrastructural organization, did not affect the anatomical structure of the salivary-gland complex on the basis of which different adaptive mechanisms are developed for various phases of their life cycle. A comparison with other closely related groups has shown that the trombidiform mites appear to have, initially, a single mode of organization of the salivary glands.

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Pigmentation in water mites of the general Limnochares *Latr. and* Hydrodoma *Koch (Hydrachnidia)*

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The body pigmentation of the red-coloured *Limnochares aquatica* (L.) and *Hydrodroma despiciens pilosa* Bess., and the yellowish-brown *Hydrodroma danuviensis* Schw. were studied. Absorption spectroscopy indicated the presence of carotenoids in all three species. Using high-pressure liquid chromatography (HPLC), co-chromatography of reference pigments and absorption spectroscopy of collected HPLC fractions, the following main carotenoids were identified: zeaxanthin and/or lutein, cryptoxanthin, canthaxanthin, astaxanthin (in *H.d. pilosa*) and possibly β-carotene. In addition in *H. danuviensis*, a polar water-soluble pigment was detected which could not be identified further and which, in combination with the carotenoids, may be responsible for the typical colour of this species. Male and female *L. aquatica* and *H.d. pilosa* have a similar pigment composition, but with higher concentrations in male *H.d. pilosa* and lower concentrations in male *L. aquatica* compared to their female counterparts. Pigment concentration per unit dry mass is about 8–10 times greater in *L. aquatica* than in the *Hydrodroma* spp.

INTRODUCTION

Water mites (Hydrachnidia) exhibit a broad spectrum of body pigmentation, and the occurrence of very bright colours is a striking feature of the group. It is especially noticeable that many of the more primitive genera or species are bright red in colour (Viets, 1936) and, in addition, are often large in size and soft-bodied. The pigmentation of three species

have been studied: the bright red-coloured mites, *Limnochares aquatica* (L.) (Eylaoidea; Cook, 1974) and *Hydrodroma despiciens pilosa* Bess., and the yellowish-brown *Hydrodroma danuviensis* Schw. (Hydryphantoidea; Cook, 1974). The main objective of the study was, to determine the biochemical nature of the pigments. Interesting results were expected in the closely related *Hydrodroma* species, whose exact systematic relationship is still uncertain (Meyer, 1988). Another point of interest is the different colour intensities of the sexes of *L. aquatica* and *H.d. pilosa*. According to our observations, male *H.d. pilosa* appear to be darker, and male *L. aquatica* lighter in colour than their respective females. No corresponding observations were found in the literature on this kind of sexual dimorphism in the above species or indeed in other species. According to Green (1964), Czezuga and Czerpak (1968a,b,c), and Czezuga (1972, 1986), the red colour in water mites is due to the presence of carotenoids. Brown colours, on the other hand, could be caused either by other pigments, pigment combination (Fox and Vevers, 1960), or carotenoproteins (Cheesman *et al.*, 1967). Again the presence of both carotenoproteins and free carotenoids may also result in red coloration as observed in the water mites, *Eylais extendens* (Müll.), *E. hamata* Koenike, and *Hydryphantes dispar* (Schaub) (Green, 1964; Czezuga, 1986).

MATERIAL AND METHODS

Hydrodroma despiciens pilosa was collected from Lake Mindelsee in south-west Germany, and *Limnochares aquatica* in the outlet stream of the same lake. *Hydrodroma danuviensis* was found in the River Danube near Beuron, also in south-west Germany. Live individuals of *L. aquatica* and *H.d. pilosa* were sexed according to the arrangement of their genital setae (Bader, 1975; Meyer, 1983). Subsequently all specimens were placed in a deep freeze. Those mites required for chromatography were freeze-dried and weighed on a micro-balance in portions of 6–15 mg for each extract.

Extraction

Prior to extraction the water mites were pulverized. Extraction for the absorption spectra was carried out in acetone, methanol or hexane. Additionally with *H. danuviensis*, an extract with distilled water was used to test the solubility of pigments other than carotenoids. For pigment analysis by reversed-phase high-pressure liquid chromatography (HPLC), extraction was carried out either in 100% acetone or directly in the eluent, which consisted of 85% acetone, 15% ultrafiltrated distilled water, and 1 g/l TEAA (tetraethylammonium-acetate-

tetrahydrate). This extraction procedure also releases carotenoids from carotenoproteins (Czezuga, 1986). The extraction vials were enveloped in aluminium foil to protect the light-sensitive carotenoids. Freeze-dried specimens were moistened a little to facilitate the extraction procedure. During extraction, ultrasound disintegration with a microtip was used to achieve a more effective pigment extraction. All procedures were carried out at room temperature.

Absorption spectroscopy

The extracts were cleaned by filtering them on a polytetrafluoroethylene filter (PTFE) with a pore width of 0.45 μm. The spectra were measured in a double-beam photometer against the extraction medium as reference substance, and were charted directly on a recorder. Absorption was measured in the range of the visible light spectrum (350–700 nm) and, in addition, in some cases, in the ultraviolet range of 210–350 nm.

Reversed-phase high-pressure liquid chromatography

About 100 μl of the extract was injected through a 20-μl sampling loop, and was eluted at a rate of 1 ml/min corresponding to about 82.7 bar. The chromatograms were plotted by an integrator which also calculated the area under the respective peaks. For the evaluation of pigment levels in male and female water mites, the ratios of these areas were compared rather than the absolute values. Reference pigments for identification were: zeaxanthin, lutein, canthaxanthin, cryptoxanthin, astaxanthin and β-carotene. These carotenoids were chosen because they are known to be present in other water-mite species (Green, 1964; Czezuga and Czerpak, 1968a,b,c; Czezuga, 1972, 1986). For more detailed pigment identification in *L. aquatica* and *H.d. pilosa*, absorption spectra of collected fractions eluted from the column (corresponding to 150 μl, and a 9-s sampling frequency) were measured. In this procedure methanol was used as extraction medium and solvent.

RESULTS

Biochemical nature of pigments

The absorption maxima of acetone extracts (Fig. 35.1*a*) from *L. aquatica* at 467–468 nm, and *H.d. pilosa* at 455 nm, indicate the presence of carotenoids in both species. The same is the case for *L. aquatica* where the maximum at 398 nm only became apparent in methanol extracts. The characteristic red colour of the extracts themselves is also typical for

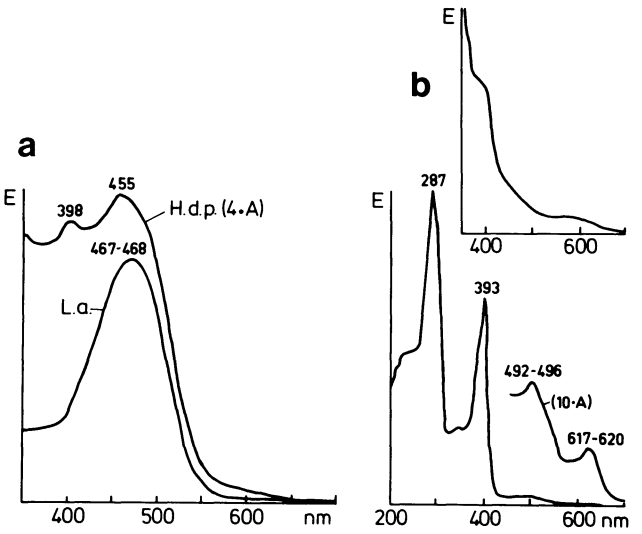

Fig. 35.1 Absorption spectra using a double-beam photometer to determine pigments in three species of water mites. (*a*) Acetone extracts of *Limnochares aquatica* (L.) (L.a.) and *Hydrodroma despiciens pilosa* Bess. (H.d.p.), the latter recorded at 4 times higher amplification. (*b*) Acetone (upper) and methanol (lower) extracts of *Hydrodroma danuviensis* Schw. To right, upper range of methanol extract with 10 times higher magnification.

carotenoids (Fox, 1979). Unlike the other two species, the acetone extract of *H. danuviensis* is greenish-yellow. At a low amplification, only a steep increase from 450 nm towards the ultraviolet range of the spectrum was found (Fig. 35.1*b*). In a methanol extract, however, at a higher amplification, small absorption maxima occurred at 617–620 nm and 492–496 nm. At low amplification (Fig. 35.1*b*), a peak is visible at 393 nm after which absorption decreases until a wavelength of 320 nm, which is followed by a further maximum at about 287 nm. A phase separation between hexane and methanol, which separates xanthophylls and carotenes (Fox, 1979), yielded the complete spectrum in the methanol phase whereas, in hexane, there was hardly any measurable absorption. This suggests the presence at most of very low amounts of carotenes in *H. danuviensis*. In distilled water, the extract showed, basically, the same increase towards the ultraviolet range of the spectrum but this was weaker than in acetone. In the water extract unlike that in acetone absorption below 350 nm could also be measured and here a maximum was recorded at 333 nm.

Chromatograms of the acetone extracts for the three species are shown in Figs 35.2 and 35.3. In *H. danuviensis*, within 0.9 min of injection high absorbtion maxima appear at wavelengths of 350 and

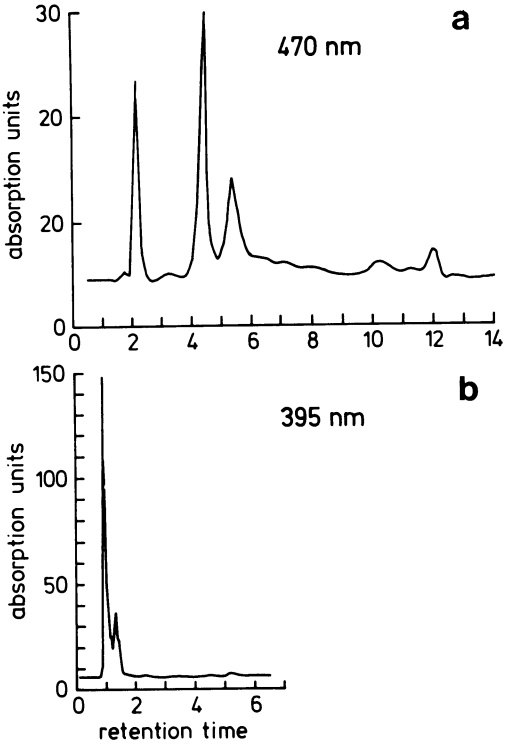

Fig. 35.2 Chromatograms of acetone extracts of *Hydrodroma danuviensis* at 470 nm (*a*) and 395 nm (*b*). Retention time is in minutes after injection.

395 nm, which could not be detected at 470 nm (Fig. 35.2*a*, *b*). Judging by its early elution, this pigment must be very polar; also characteristic is a weak fluorescence. Figure 3.52(*a*) shows that at 470 nm, the remaining pigments show smaller absorption maxima with retention times of 2–12 min after injection. This is typical for carotenoids. Indeed, most of the latter have retention times of 2 to 5 min as do the xanthophylls, while only smaller absorption peaks can be detected on the chromatograms at the retention times of carotenes (for example, β-carotene *c.* 12 min). Thus, the absorption of carotenoids may be the cause of the absorption maxima of *H. danuviensis* extracts at 492–496 nm. At least one other pigment was present with absorption maxima at 333 nm in distilled water, and at 287, 393 and 617–620 nm in methanol. It could not be identified further despite comparison of its properties with the data in the literature (for example, Vuillaume, 1969; Needham, 1974; Fox, 1979).

The retention times of the pigments from *L. aquatica* and *H.d. pilosa* range from about 2 to 15–16 min (Fig. 35.4*a*,*b*). The reference pigments

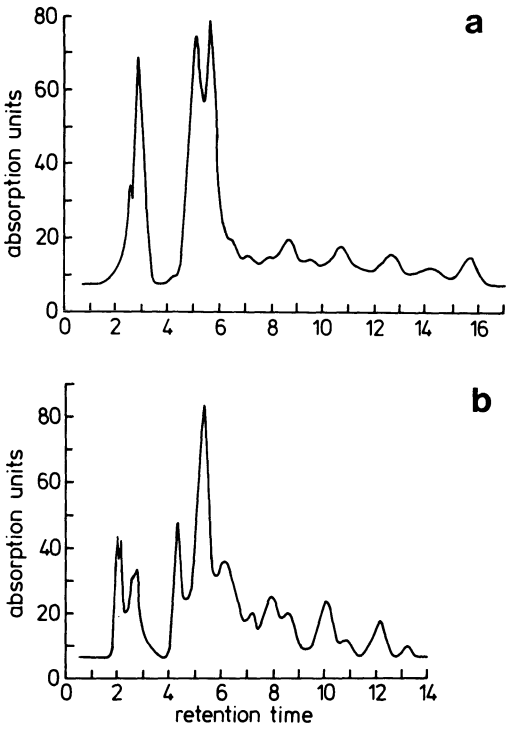

Fig. 35.3 Chromatograms of acetone extracts of *Limnochares aquatica* (*a*) and *Hydrodroma despiciens pilosa* (*b*) at 470 nm. Retention time is in minutes after injection.

were also eluted in the same time period. This indicates that the red colour in both species is caused by the presence of carotenoids. A comparison of the co-chromatography of the extracts of the three species with reference pigments, yielded the following results. There is a correspondence in the retention time of β-carotene (*c.* 12 min) as well as with that of zeaxanthin and lutein (2.1 min). These xanthophylls leave the column at the same time and thus cannot be distinguished on the chromatograms. The same retention time as with canthaxanthin (*c.* 2.7 min) was found in both *L. aquatica* and *H.d. pilosa*. A pigment with the retention time of astaxanthin (*c.* 2.5 min) only appeared on the chromatogram of *H.d. pilosa* extracts. If astaxanthin is present in the other species, its concentration must be so low that it cannot be detected even by the sensitive HPLC method. The chromatograms (Fig. 35.3*a*,*b*) show that, apart from these pigments, all three species have common pigments with absorption maxima after *c.* 5.3 and 10 min.

Table 35.1 Absorption spectographic analysis to determine pigments of *Limnochares aquatica* (L.) from collected fractions leaving high-pressure liquid chromatography column together with comparison of data from the literature (reference pigments only available for lutein and canthaxanthin)

Pigment	*Present study*			*Literature data*		
	Retention time (min)		*Absorption maxima in methanol (nm)*	*Absorption maxima (nm)*	*Solvent*	*Reference*
	Acetone	*Methanol*				
Violaxanthin		2.0	439,468	415, 440, 469	Methanol	Karrer and Jucker (1950)
or neoxanthin				415, 438, 467	Ethanol	Mallams *et al.* (1967)
Lutein	2.1	2.9	422, 446, 475	418, 444, 474	Methanol	Karrer and Jucker (1950)
Canthaxanthin	2.8	1.7?	474	474	Ethanol	Hager and Stransky (1970)
Neochrome		3.5	402, 425, 452	401, 424, 451	Ethanol	Cholnoky *et al.* (1969)
Echinenon		3.9	460–462	461	Ethanol	Hager and Stransky (1970)
				460	Acetone	Francis and Halfen (1972)
Cryptoxanthin-5,6, 5′6′-diepoxide		8.2	423, 440.5, 470	423, 442, 472	Ethanol	Stransky and Hager (1970)
β-Carotene		11.1	418, 440.5, 464	417, 440, 470	Ethanol	Chapman and Haxo (1963)

In summary, *L. aquatica* has at least 16 different carotenoids (that is, 16 absorption maxima appear on the chromatograms), *H.d. pilosa* has at least 13, and *H. danuviensis* at least six. In *L. aquatica* (Fig. 35.3*a*), two pigments appeared after the retention time for β-carotene had elapsed, that is, after 13.2 and 15 min, respectively, indicating their unpolar nature. Integration of the areas under the absorption peaks suggests an 8–10 fold greater pigment concentration per unit dry mass in *L. aquatica* than in the *Hydrodroma* species.

The results of the HPLC fraction analyses are given in Tables 35.1 and 35.2, where the identified carotenoids for *L. aquatica* and *H.d. pilosa* are listed. Carotenoids of other fractions could not be clearly identified because they either had no unequivocal properties as compared to literature data or they left the column in concentrations too low for further absorption spectroscopy.

Pigment concentrations in males and females

Total pigment ratios, and ratios of individual pigments according to their retention times in the HPLC column, are shown for male and female *L. aquatica* and *H.d. pilosa* in Fig. 35.4*a*,*b*. In *L. aquatica*, the female has, on average, pigment concentrations 1.6 times greater than their male counterpart, and with single pigments up to 5.4 times greater (retention time 2.5 min). Identified pigments occurring in greater concentrations in females of *L. aquatica*, are lutein (retention time 2.2 min, ratio 2.8:1) and canthaxanthin (retention time 2.8 min, ratio 4.9:1). There were three pigments that occurred in computable concentrations only in females (Fig. 35.4*a*, last dotted column). In *H.d. pilosa*, on the other hand, for all pigments, the males have greater concentrations than the females (Fig. 35.4*b*).

DISCUSSION

According to the results of the present study, carotenoids, and possibly carotenoproteins, are responsible for the red body colour in *Limnochares aquatica* and *Hydrodroma despiciens pilosa*. Those pigments or substances, respectively, have also been identified in the red water mites, *Eylais hamata* (Czezuga and Czerpak, 1968c; Czezuga, 1972), *E. extendens* (Green, 1964), *Hydryphantes dispar* (Czezuga and Czerpak, 1968a; Czezuga, 1986), *Hydrachna geographica* (Müll.) and *Piona nodata* (Müll.) (Czezuga and Czerpak, 1968b). While these authors found between 5 and 10 different carotenoids, we detected a minimum of 16 and 13 different carotenoids, respectively, in *L. aquatica* and *H.d. pilosa*. However, it is important to point out that with the HPLC method carotenoid amounts

Table 35.2 Absorption spectrographic analysis to determine pigments of *Hydrodroma despiciens pilosa* Bess. from collected fractions leaving high-pressure liquid chromatography column together with comparison of data from the literature (reference pigments only available for zeaxanthin, lutein and β-cryptoxanthin)

Pigment	*Present study*			*Literature data*		
	Retention time (min)		*Absorption maxima in methanol (nm)*	*Absorption maxima (nm)*	*Solvent*	*Reference*
	Acetone	*Methanol*				
Zeaxanthin	2.1	2.5	449, 478	421.5, 449.5, 480.5	Methanol	Karrer and Jucker (1950)
Lutein	2.1	2.7?	422, 446.5, 475	418, 444, 474	Methanol	Karrer and Jucker (1950)
Violaxanthin or neoxanthin		2.7	415, 437, 470	415, 440, 469	Methanol	Karrer and Jucker (1950)
				415, 438, 467	Ethanol	Mallams *et al.* (1967)
Echinenon		4	460	461	Ethanol	Hager and Stransky (1970)
				460	Acetone	Francis and Halfen (1972)
β-Cryptoxanthin	4.4	4.6	425*, 450, 474	428*, 449, 473	Ethanol	Hager and Stransky (1970)
Torulen		8.2	455, 487, 516	456, 486, 520	Ethanol	Karrer and Jucker (1950)

*Shoulder in absorption spectrum.

of 0.5 ng are detectable (Braumann and Grimme, 1981), whereas the other quoted studies were carried out using the less sensitive thin-layer chromatography with which pigments are only traceable in amounts >0.15–1.0 μg or more (Jeffrey, 1981).

The carotenoids found in water mites by the above-mentioned authors, for example, β-carotene, astaxanthin, canthaxanthin, zeaxanthin and/or lutein, seem to be the main pigments in this group, and for the most part are also present in *H.d. pilosa*, *H. danuviensis* and *L. aquatica* as well. Yet the pigment composition and their relative levels may differ between the species. Take, for example, astaxanthin which in *H. danuviensis* and *L. aquatica* is either absent or, at most, present in very small amounts; in *Eylais extendens* and *E. hamata*, it is the dominant carotenoid together with its esters, and forms up to 70% of the total pigment

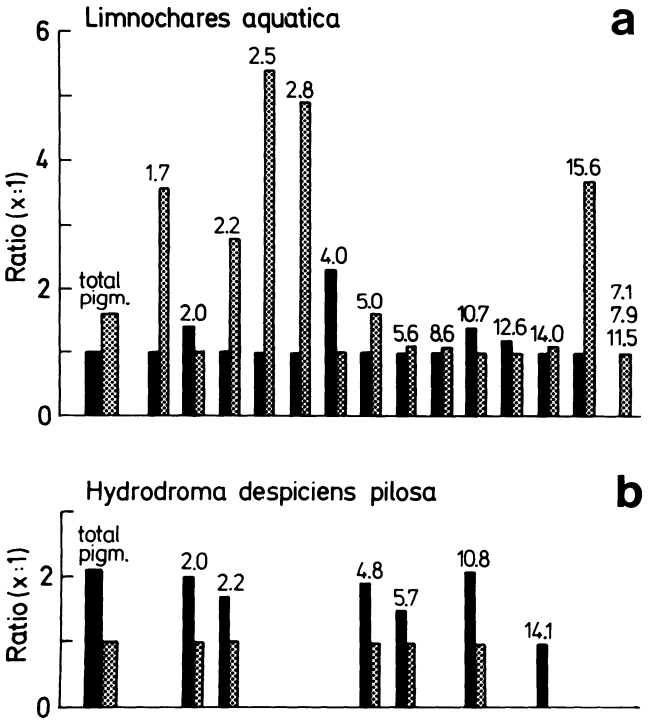

Fig. 35.4 Total pigmentation and individual pigment ratios of males (black columns) and females (dotted columns) of *Limnochares aquatica* (*a*) and *Hydrodroma despiciens pilosa* (*b*) expressed as ratios where sex with lower concentration is given value of unity. Number above column is retention time of pigment in minutes.

content (Green, 1964; Czezuga, 1972). The carotenoid, β-carotene, occurred in all the water-mite species studied by Green (1964), Czezuga and Czerpak (1968a,b,c) and Czezuga (1972) and, according to the co-chromatography results is, apparently, also present in *H.d. pilosa*, *H. danuviensis* and *L. aquatica*. The presence of cryptoxanthin has not yet been established with certainty in other water-mite species but there are indications that it occurs in *Piona nodata* and *Hydrachna geographica* (Czezuga and Czerpak, 1968b). Obviously, the yellowish-brown colour of *H. danuviensis* is caused by a mixture of carotenoids and other water-soluble pigments with absorption maxima at 287, 393 and 617–620 nm in methanol. According to Fox and Vevers (1960), brown colours in *Metridium senile* L. are also caused by a combination of melanine and carotenoids. However, there was no evidence for the presence of melanine (Fox, 1979) in *H. danuviensis*.

The significance of the bright-red colours has been discussed repeatedly. The universal occurrence of β-carotene might be related to its physiological importance as a precursor of vitamin A, and thus to light perception (for example, Needham, 1974). Bright colours in water mites may serve as warning signals as observed in the interaction between water mites and fish (Kerfoot, 1982) with dark-coloured individuals being preyed on to a greater extent than light ones. Red colours might also serve as protection against ultraviolet light as in zooplankton (Hairston, 1980; Luecke and O'Brien, 1983) where it has been reported that carotenoid concentrations can even vary according to previous light treatment (Hairston, 1979a) or according to season (Berthon, 1980). Yet both *Hydrodroma* species are well protected from direct sunlight; populations of *H.d. pilosa* remain between the floating-leaved plants and, in autumn, move to deeper zones in the lake (Meyer, 1985) while *H. danuviensis* lives in the sedimented mud on the banks of the River Danube (Meyer, 1988). *Limnochares aquatica*, on the other hand, is found at the bottom of the slow-flowing outlet stream of the lake, and there may be exposed to a higher light intensity than the other two species.

Our results suggest that the differences in colour intensity of the sexes is due to the carotenoid concentration levels, and that the pigments present are basically the same in the male and female. What then is the biological significance of this difference? In male *H.d. pilosa*, carotenoids could serve as 'fertilization hormones' as has been shown for *Salmo gairdneri* Richardson (Hartmann *et al.*, 1947). Just as in *H.d. pilosa*, fertilization obviously occurs a long time after spermatophore transfer or spermatophore storage in the receptacula seminis (Meyer, 1985). In some diaptomids, the occurrence of higher carotenoid concentrations in females is explained as follows: eggs and offspring, which are found close to the water surface, and thus are exposed to more radiation, have

been provided with more carotenoids by the mothers (Hairston, 1979b). In *L. aquatica*, our analysed specimens had a high proportion of ovigerous females, and it is possible that this species, likewise, accumulates carotenoids in the eggs. As the hatched larvae are not aquatic because they parasitize pond skaters (Heteroptera: Gerridae), the presence of carotenoids would ensure greater protection from sunlight. The larvae of *H.d. pilosa*, however, also pass through an aerial phase during parasitization (Meyer, 1985), and consequently these females should also accumulate carotenoids in their eggs. Nevertheless, ovigerous females of this species have lower carotenoid concentrations than the males. The present results and reflections on the significance of body coloration indicate the importance of further research on water-mite pigmentation.

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36

Biomass studies of water mites of the genera Limnochares *Latreille and* Hydrodroma *Koch (Hydrachnidia)*

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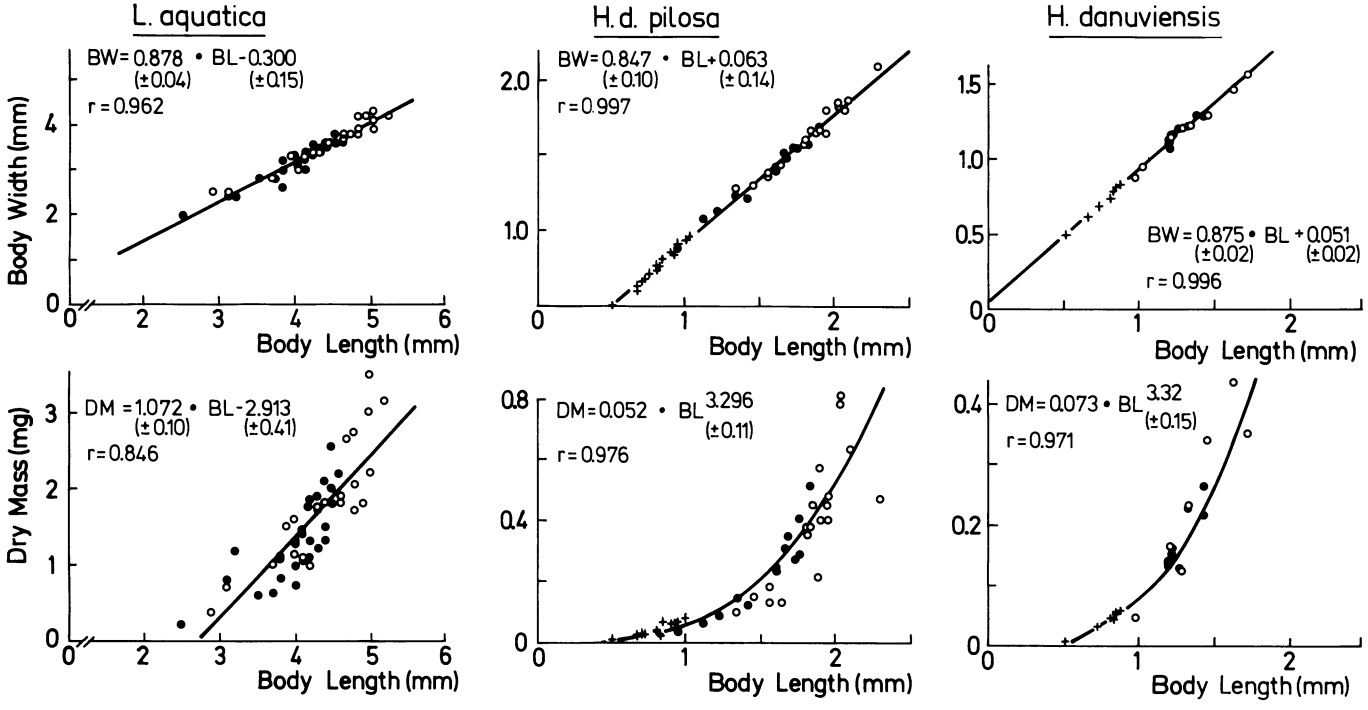
The species studied were *Hydrodroma descpiciens pilosa* Bess. from Lake Mindelsee, south-west Germany, *Limnochares aquatica* (L.) from the outlet of the lake and *Hydrodroma danuviensis* Schw. from the River Danube near Beuron, also in south-west Germany. For all three species, size, fresh and dry mass relationships and water content were investigated. In addition, the relative levels of protein, lipid, carbohydrate and chitin of *L. aquatica* and *H. despiciens pilosa* were determined.

The data are given in Table 36.1. Length–width and length–fresh mass relationships can be described by a linear regression model whereas length–dry mass relationships – except in *L. aquatica* – follow a power function (Fig. 36.1). *Hydrodroma despiciens pilosa* and *L. aquatica* have mean water contents of about 75 and 79%, respectively (Table 36.1), whereas in *H. danuviensis*, the mean water content is 69% of the total fresh mass. Water content is inversely correlated with dry mass with a steeper slope for nymphs (Fig. 36.1). We hypothesize that this is due to the accumulation of excretory cells in the midgut during growth. There were no significant differences between the sexes.

The major biochemical body compounds revealed high interspecific variations. Mean levels of protein, lipid, carbohydrate, chitin and ash in *L. aquatica* accounted for 38.8, 12.1, 17.7, 5.5 and 3.1% of the total dry mass. In *H.d. pilosa* the corresponding values were 50.4, 6.8, 9.0, 4.8 and 3.8%.


L. aquatica
BW= 0.878 • BL-0.300
(±0.04) (±0.15)
r = 0.962
Body Width (mm)
Body Length (mm)
DM = 1.072 • BL-2.913
(±0.10) (±0.41)
r=0.846
Dry Mass (mg)
Body Length (mm)
H.d. pilosa
BW= 0.847 • BL+0.063
(±0.10) (±0.14)
r=0.997
Body Length (mm)
DM=0.052 • BL 3.296
(±0.11)
r=0.976
Body Length (mm)
H. danuviensis
BW = 0.875 • BL + 0.051
(±0.02) (±0.02)
r = 0.996
Body Length (mm)
DM=0.073 • BL 3.32
(±0.15)
r=0.971
Body Length (mm)

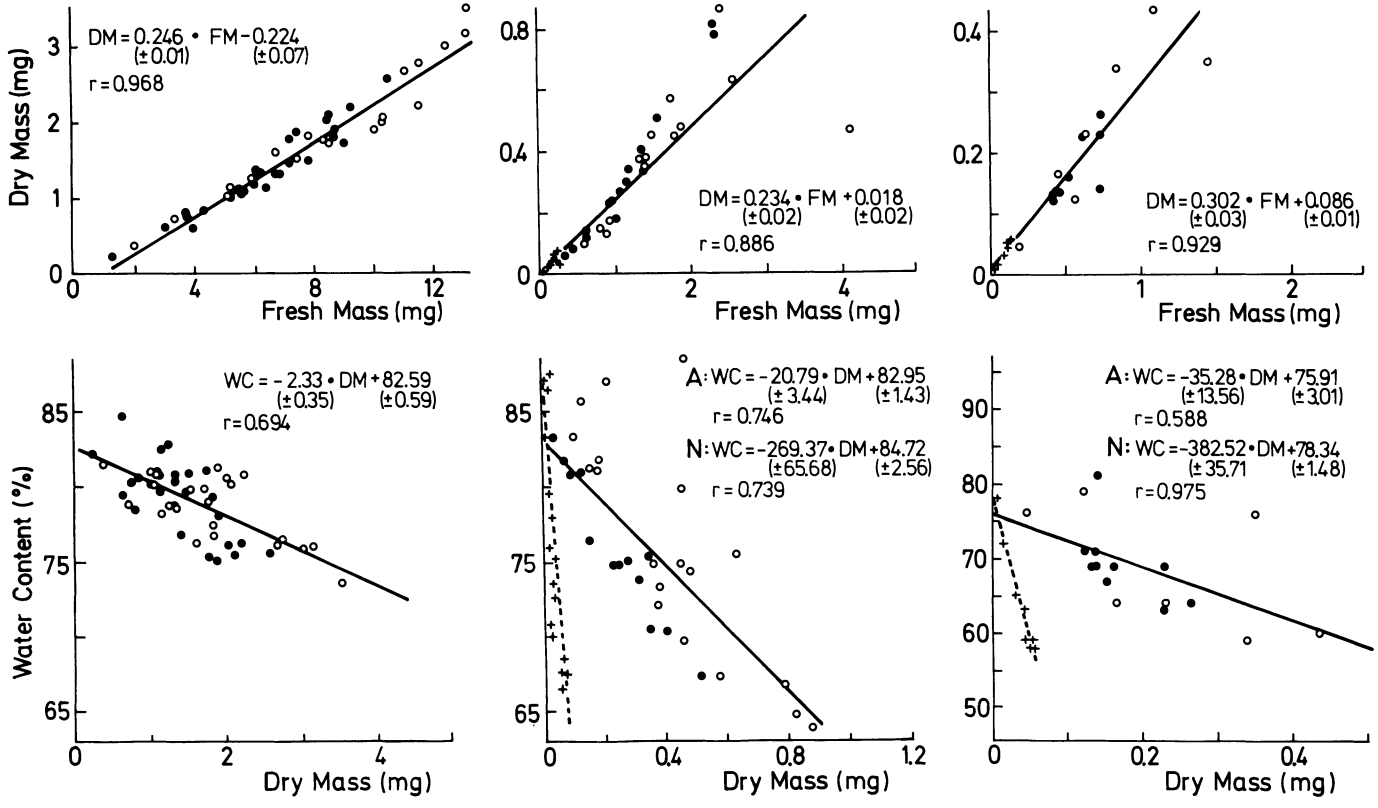


Fig. 36.1 Body width–length, dry mass–fresh mass and water-content relationships of adult males (•) and females (○) of *Limnochares aquatica* (L.), *Hydrodroma despiciens pilosa* Bess. and *H. danuviensis* Schw., and nymphs (+) of the latter two species with regression equations and standard errors of the variables.

Table 36.1 Mean dimensions and fresh and dry weights of male and female adults of the water mites, *Limnochares aquatica* (L.), *Hydrodroma despiciens pilosa* Bess. and *Hydrodroma danuviensis* Schw., and nymphs of the latter two species. N is number of individuals in sample

	H. despiciens pilosa				*H. danuviensis*				*L. aquatica*			
	N	*Mean*	*s.d.*	*Range*	*N*	*Mean*	*s.d.*	*Range*	*N*	*Mean*	*s.d.*	*Range*
Male	14				10				29			
Length (mm)		1.5	0.3	1.0 – 1.9		1.3	0.1	1.2 – 1.4		4.0	0.5	2.5 – 4.6
Width (mm)		1.3	0.2	0.9 – 1.6		1.2	0.1	1.1 – 1.3		3.2	0.4	2.0 – 3.8
Fresh mass (mg)		0.9	0.4	0.2 – 1.6		0.6	0.1	0.4 – 1.7		6.4	2.1	1.3 – 10.5
Dry mass (mg)		0.2	0.1	0.03 – 0.5		0.2	0.1	0.1 – 0.3		1.4	0.5	0.2 – 2.6
Water content (%)		76.2	4.8	67.5 – 83.3		69.3	4.9	63.0 – 81.0		79.3	2.5	75.0 – 84.7
Female	18				8				21			
Length (mm)		1.9	0.2	1.3 – 2.3		1.3	0.3	1.0 – 1.7		4.4	0.6	2.9 – 5.2
Width (mm)		1.6	0.2	1.3 – 2.1		1.2	0.2	0.9 – 1.6		3.6	0.6	2.5 – 4.3
Fresh mass (mg)		1.8	0.8	0.6 – 4.1		0.7	0.4	0.2 – 1.4		8.9	3.2	2.0 – 10.2
Dry mass (mg)		0.5	0.2	0.1 – 0.9		0.2	0.1	0.1 – 0.4		2.8	0.3	0.4 – 3.5
Water content (%)		75.2	7.3	64.0 – 88.6		68.3	8.4	59.0 – 79.0		78.6	2.2	73.5 – 82.5
Nymph	18				8							
Length (mm)		0.8	0.1	0.5 – 1.0		0.8	0.1	0.5 – 0.9				
Width (mm)		0.8	0.1	0.5 – 1.0		0.7	0.1	0.5 – 0.8				
Fresh mass (mg)		0.1	0.06	0.03 – 0.3		0.1	0.04	0.03 – 0.1				
Dry mass (mg)		0.03	0.02	0.004 – 0.1		0.04	0.02	0.01 – 0.1				
Water content (%)		75.6	7.3	66.5 – 87.5		64.0	7.4	58.0 – 78.0				

37

The saltatory capacity of an oribatid mite

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Since the first description of the oribatid genus, *Zetorchestes* (Berlese, 1883), it has been known that its members are able to jump. Hitherto, however, the jumping ability of these mites with a length of about 0.5 mm has not been investigated. The present chapter refers to laboratory experiments using *Z. falzonii* (Coggi, 1898), a common litter-inhabiting species in deciduous woodland in Styria.

A white-painted panel with concentric circles, 0.5 cm apart, and with the centre of the panel as starting point, served as the test area for determining the distances jumped. The panel was coated with paste to immobilize the mites when they landed. In this way it was possible to measure the horizontal distance of each jump. To determine jumping height, use was made of a wooden frame in which a glass sheet with its undersurface coated with paste could be inserted at vertical intervals of 1 cm to cover the test area. The mite was stimulated to jump by applying a hairbrush bristle to the anterior part of the body. All tests were carried out at room temperature.

Undamaged animals can jump in any direction. The greatest distance covered was 14.6 cm, which is 280 times the body length. Most jumps had lengths of 1–7 cm. Tests were made to determine the effect on jumping ability of surfaces with different degrees of roughness. With take-off surfaces of wax or paper the lengths jumped showed no significant differences when surfaces were compared. The maximum jump height was 11 cm, which is 220 times the body length. This height was rare but 62% were at least 4 cm high.

An important structure in the jumping process is leg IV. It is longer and more robust than the other legs, and has a peculiarly formed process on the trochanter, hence its characterization in the literature (for

example, Berlese, 1888; Willmann, 1931; Grandjean, 1951) as modified for jumping. Mites without legs IV only jump backwards; with these individuals the force for forward motion appears to be lacking, and jumps in this direction have not been observed. Such specimens can jump distances of up to 3.5 cm with a maximum height of 3 cm. Investigations of the functional anatomy, and an analysis of the jumping process with a high-speed camera, will be published shortly.

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38

Thanatosis or feigning death in mites of the family Scutacaridae

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First indications of thanatosis or feigning-death reaction in species of the terrestrial Scutacaridae were seen in the course of breeding experiments with different species of the genera *Scutacarus*, *Pygmodispus* and *Lamnacarus*. Seven of the 19 species studied reacted to foreign touch stimuli by retracting their legs and remaining immobile for a maximum of 6 min 20 s (Fig 38.1*a*, *b*). In all species in which larvae and males were also available, it was found that only females displayed this behaviour. The larvae and males, which differ from females in their morphological structure, moved away rapidly when touch stimuli were applied.

Females of the genus *Pygmodispus* as well as *Lamnacarus ornatus* Balogh and Mahunka possess morphological adaptations related to thanatosis. The anterior sternal plate (Fig. 38.1*b*, *astpl*) and gnathosoma (*gn*) are tilted upwards, causing a dorsal shift in the joints of legs I and II (Fig. 38.1*a*). This makes possible the withdrawal of these legs into the deep recess between the sternal plate/gnathosoma, and the clypeus (Fig. 38.1*b*, *cl*) which covers them. They also possess a very enlarged posterior sternal plate (Fig. 38.1*b*, *pstpl*) together with 'lateral plates' (*lpl*) which turn downwards from the lateral edges of the body, thus creating deep recesses into which legs III and IV (Fig. 38.1*c*) can be withdrawn and hidden (Fig. 38.1*d*). Trochanter IV has, on its inner edge, a plate (Fig. 38.1*c*, *tr*) that has developed to cover and protect the other segments of the leg when retracted (Fig. 38.1*d*). In the genus *Pygmodispus*, the increasing development of these adaptations is seen as a morphological series involving the transformation of leg IV. In species of the subgenus *Pygmodispus* there is a pre-adaptive structure on the inner edge of the trochanter in the form of a spine of varying size. It is not known whether these species display thanatosis. Passing through the intermediate sta-

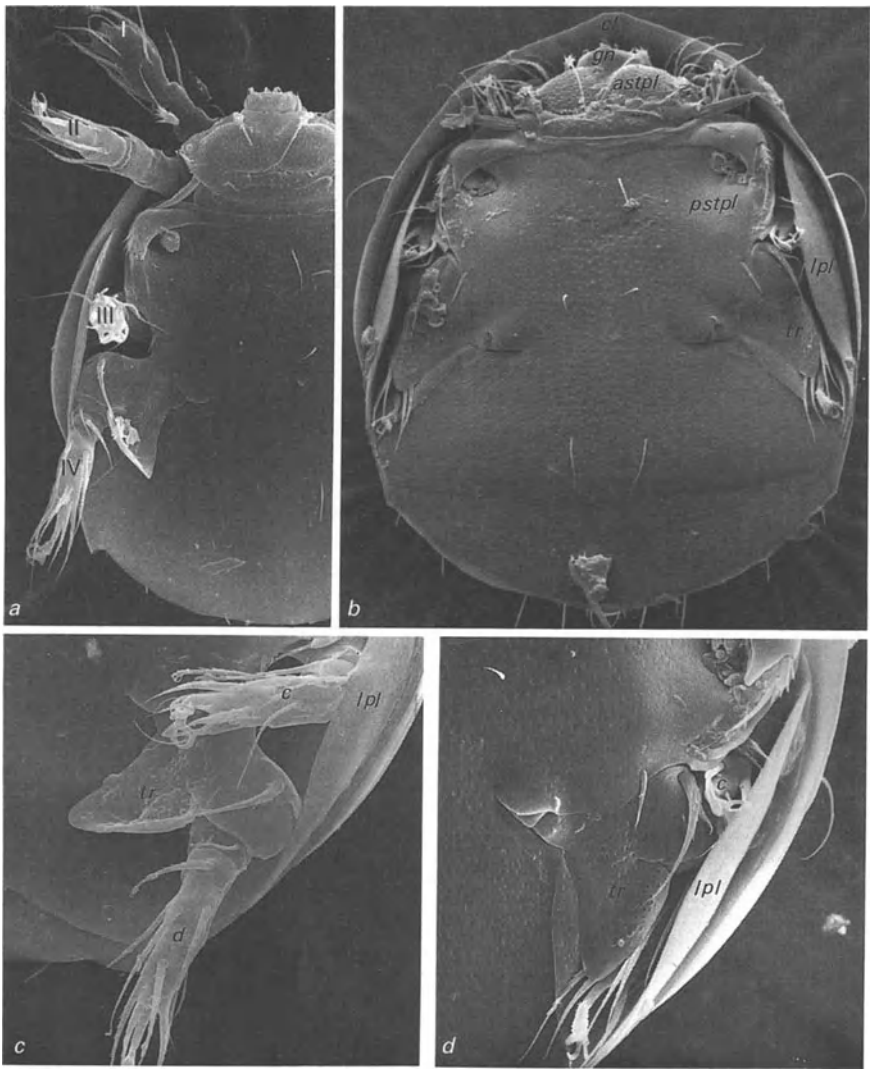

Fig. 38.1 Scanning electron micrographs of females of *Pygmodispus (Allodispus)* sp. in ventral view, illustrating method of concealment of legs in thanatosis. Specimen in (*a*) has body length of 140 μm and, in (*b*), 150 μm. (*a*) Active female. (*b*) Legs concealed. (*c*) Legs III and IV in active individual. (*d*) Legs II–IV concealed. I–IV, Legs I–IV; *astpl*, anterior sternal plate; *cl*, clypeus; *gn*, gnathosoma; *lpl*, 'lateral plate'; *pstpl*, posterior sternal plate; *tr*, modified trochanter of leg IV.

ges of the series, the trochanter spine is most dramatic in the form of a plate-like structure in the subgenus *Allodispus* and, more specifically, in *Pygmodispus* (*A.*) *mancus* Mahunka, *P.* (*A.*) *latisternus* Paoli and *Pygmodispus* (*A.*) n. sp. Thanatosis has been observed in the latter two species.

Thanatosis, a plesiomorphic behavioural trait, is thus present in different genera of the Scutacaridae. Moreover, morphological adaptations connected with this behaviour are found in astonishingly similar form in *Pygmodispus* and *Lamnacarus*, genera which are only distantly related. Clearly species with these adaptations have, as a result, an improved passive defence mechanism against predators in that they can conceal their legs. Comparative studies on the protective effects of thanatosis against predators in morphologically adapted and non-adapted scutacarid species are now in progress.

· PART FIVE ·

Field Studies and Applied Aspects

39

The effects of spider-mite feeding on plant performance in relation to biological control

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Integrated plant management is aimed at keeping the abundance of pest organisms below economic threshold levels. Knowledge of the effects of low spider-mite populations on host-plant performance is essential in establishing economic threshold levels. Studies on the influence of low spider-mite populations showed that photosynthetic intensity increased in cucumber and chrysanthemum. The rate of plant growth was also increased when spider-mite infestation was low and, as a result, plant productivity was greater. The predacious mite, *Phytoseiulus persimilis* (A.-H.), kept *Tetranychus urticae* Koch at non-damaging levels during the entire growing period in year-round chrysanthemum production in the greenhouse

INTRODUCTION

Rational spider-mite control requires knowledge of the relationship between the abundance of phytophagous mites and their economic importance. Establishing economic threshold levels is complicated because many variables are involved including host-plant species, mite species, climate and market value of the crop among several others. The aim of integrated mite management, and especially biological control of spider mites, is not the total elimination of the pest but to restrict their abundance to a level below the economic threshold (Hussey and Scopes, 1985). This requires knowledge of the effects of low spider-mite popula-

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tions or short periods of mite feeding on host-plant performance, for instance the effects on flower and fruit formation or growth of the host plants. Basically, there is a need of knowledge about the influence of mite feeding on host-plant physiology, especially in the first stages of infestation.

The results of our experiments demonstrate that plants injured by low spider-mite populations can have defence reactions which should be taken into consideration in the timing of mite control (Tomczyk *et al.*, 1989). Studying the physiological processes in the host may provide information on the limits of plant tolerance to and, defence against, mite activity.

MATERIALS AND METHODS

Studies were conducted on the cucumber cultivars Atos, Replika and Wilanowski and on chrysanthemum cv. Belcome Yellow, Bronze Bornholm, Crimson Robe, Super White and Penny Lane. Plants were infested with the two-spotted spider mite, *Tetranychus urticae* Koch. Intensity of photosynthesis, rate of growth and cropping of plants were studied either after a short period of mite feeding or after feeding by a low mite population.

Photosynthesis measurement Carbon dioxide assimilation by chrysanthemum and cucumber plants was measured 4, 7 and 35 days after infestation using a CO_2 infra-red analyser, 'Infralyt IV', in a closed system.

Growth measurements The growth of young cucumber and chrysanthemum plants was determined after 10 days of mite feeding. The heights of the cucumber and chrysanthemum plants were measured, and in the case of cucumber, the number of leaves and number of lateral shoots were counted.

Cropping The fruit production of Atos and Replika cucumber plants, infested with spider mites at densities of less than 0.5 mites/cm^2 leaf surface and <1.6 mites/cm^2 leaf surface was determined. The number and weight of fruit produced by infested and non-infested plants were compared.

Control of spider mites on chrysanthemum with Phytoseiulus persimilis *(A.-H.)* An experiment was conducted on chrysanthemum cv. Penny Lane infested with *T. urticae*. The average spider-mite density when predators were introduced was four mites/leaf. Predatory mites, at a density of one per plant, were introduced when the plants had formed a

closed canopy. The development of the spider-mite population was monitored over a period of 16 weeks.

RESULTS

Effects of feeding when mite densities are low

The photosynthetic intensity of infested plants increased between the third and ninth days of mite feeding. This was observed when the mite population on cucumber and chrysanthemum was not greater than 0.5 mites/cm^2 of leaf. With the chrysanthemum cultivars, Belcome Yellow and Crimson Robe, photosynthesis increased even after 5 weeks of spider-mite feeding while the mite population density remained at a level of 0.5 mites/cm^2 of leaf (Table 39.1). With both cucumber and chrysanthemum, the growth rate of infested plants increased during the first period of mite feeding by approximately 10–15% (Table 39.2).

As a consequence of photosynthesis and growth-rate stimulation, the cucumber plants produced more flowers and came into fruit earlier; an increase in yield was also observed (Table 39.3). With the variety, Replika, which is sensitive to mites, a yield increase occurred when the average mite density was <0.5 mites/cm^2. In the case of Atos, a more tolerant variety, an average density of 0.8–1.6 mites/cm^2 did not adversely affect fruit production.

Phytoseiulus persimilis as control agent on chrysanthemum

The results of the experiment are presented in Table 39.4. It was observed that one release of *P. persimilis* at a density of one predator

Table 39.1 Photosynthesis in chrysanthemum and cucumber expressed as a percentage of that of the control plants after feeding by spider mites at low population density (0.5 mites/cm^2 leaf surface)

Cultivar	*Feeding period (days)*	*Photosynthesis (%)*
Chrysanthemum		
Super White	4	112
Belcome Yellow	35	150
Crimson Robe	35	114
Cucumber		
Wilanowski	7	145

Table 39.2 Growth of cucumber and chrysanthemum plants after 10 days infestation by spide mites at low population density

Cultivar	*Treatment*	*Mites/cm²*	*Plant height (cm)*	*Leaves (number)*	*Lateral shoots (number)*
Cucumber					
Atos	Control	—	134.8	8.0	12.5
	Infested	0.02	148.8**	8.1	10.6*
Replika	Control	—	112.8	9.0	7.6
	Infested	0.02	124.3**	9.3	5.1**
Chrysanthemum					
Bronze Bornholm	Control	—	24.0		
	Infested	0.3	29.5*		

*$P < 0.05$; **$P < 0.02$.

Table 39.3 Yield of cucumber plants after feeding by spider mites at low densities

Cultivar	*Treatment*	*Mites/cm²*	*Fruit per plant*	
			Number	*Weight (g)*
Atos	Control	—	18.0	4817
	Infested	0.3–0.5	17.6	4937
	Control	—	11.0	2777
	Infested	0.8–1.6	10.7	2858
Replika	Control	—	14.8	4166
	Infested	0.3–0.5	17.1*	4895*
	Control	—	7.7	2119
	Infested	0.8–1.6	7.1	1777*

*$P < 0.05$.

per plant was sufficient for good control of the mites when the initial density was four spider mites/leaf. By the fourth week after introduction of predators, the mite population had decreased and, after 16 weeks, mites were eliminated from the chrysanthemum leaves.

DISCUSSION

Hussey and Scopes (1985) discuss the criteria which determine successful biological control of spider mites on cucumber, pointing out that it is essential not to eliminate spider mites from the host plants because disturbing the balance between prey and predator results, ultimately, in

Table 39.4 Mean number of individuals and eggs per leaf of *Tetranychus urticae* Koch on chrysanthemum cultivar Penny Lane over a 16-week period after introduction of *Phytoseiulus persimilis* (A.-H.)

Treatment	*1 week*		*4 weeks*		*8 weeks*		*12 weeks*		*16 weeks*	
	Mites	*Eggs*	*Mites*	*Eggs*	*Mites*	*Eggs*	*Mites*	*Eggs*	*Mites*	*Eggs*
T. urticae	4	8	12	31	15	28	16	50	21	48
T. urticae + *P. persimilis*	2	8	3	12	2	12	3	14	0	12

the extermination of the predator. Their advice is that the predator should not be introduced until the mean leaf-damage index reaches 0.4. Successful control of spider mites on cucumber can be achieved within 6 weeks. Scopes and Biggerstaff (1973) and Cross *et al.* (1983) found that biological control of *T. urticae* on chrysanthemum can be achieved within 4 weeks after releasing the predatory mites.

From the above discussion, it can be concluded that the timing of predator releases is very important to get optimal results with biological-control methods, both from the economic and ecological viewpoint. During the initial period of spider-mite feeding, stimulation of some physiological processes in the host plant were observed, and these were manifested in an increase in the rate of growth, and in the flowering and cropping of the infested plants. At the same time, biochemical changes occurred in the leaves of infested plants which appeared to have an adverse effect on the development of spider-mite populations (Kolodziej-Tomczyk, 1976; Tomczyk and Kropczyńska 1985). In the light of these results we may expect that early release of *P. persimilis* could cause a rapid decrease in the pest population resulting, ultimately, in extermination of the predator. Further, there has not been sufficient time for the development of the plant's stimulative processes. Releases of predators after a spider-mite feeding period of approximately six weeks during which time the mite population may have increased to an average density of 0.5 mites/cm^2 leaf surface, may even be advantageous. On some varieties, *P. persimilis* can be released at a later stage of mite population development without risk of economic loss. Stimulative effects during the first period of spider-mite feeding have also been observed with chrysanthemums as long as the population does not increase above a level of 0.5 mites/cm^2 of leaf. No control measures were necessary while mite populations remained below this density. On some chrysanthemum varieties, for instance Belcome Yellow and Crimson Robe, populations never reached high densities, and stimulative processes occurred during the long period of plant development.

In summary, the following procedures should be considered for the management of spider-mite populations using predators:

1. The introduction of *P. persimilis* as soon as defence reactions of the plants to spider mites are likely to occur.
2. The introduction of predatory mites at a low density so that control will not take place until 6–9 weeks later.
3. The introduction of predatory-mite species which act more slowly, thus keeping the spider-mite population at a low density over a long period, for example, *Metaseiulus occidentalis* (Nesbitt).

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Dispersion indices and constant precision sampling programmes for Panonychus ulmi *(Koch) and* Amblyseius andersoni *(Chant) in Spanish apple orchards*

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All active stages of *Panonychus ulmi* (Koch) and *Amyblyseius andersoni* (Chant) were counted on leaves from two apple orchards in Lleida and València, Spain, to develop and evaluate a sampling programme. Samples were taken from May to September, each sample consisting of 20 leaves from one tree. A total of 264 samples were examined.

Dispersion parameters, and the relationship between proportion of leaves with mites and the mean number of mites per leaf, were calculated and compared in the two orchards, and at different times of the year. Based on the results obtained, binomial sampling programmes were developed for *P. ulmi* and *A. andersoni*, and the optimal number of leaves to be sampled at various constant precision levels was determined as a function of mite density

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Herbicides and the reproduction of Tetranychus urticae *Koch*

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The herbicides, 3-amino-1,2,4-triazole (AT) and pure and commercial dinoseb-acetate were tested in the laboratory and on a semi-field scale in a bean plant–spider mite system (*Phaseolus vulgaris* L. and *Tetranychus urticae* Koch) using concentrations at and below the recommended rate. Changes in the composition of the spider-mite populations, the number per leaf unit, and the histology of mite organs were determined following foliar and soil applications.

Application of AT at one-fifth and one-tenth the recommended rate resulted in structural alterations of the protein-synthesizing apparatus of the midgut and salivary-gland cells irrespective of its mode of application. There was, in addition, a decrease in mite numbers. With prolonged incubation times, cytological defects became more intense and spread to further cells and tissues. The resultant effects on yolk and egg formation were expressed as an inhibition of egg deposition that led to a decrease in the reproduction rate of *T. urticae*. The effects of AT are discussed with respect to the formation of an alanine conjugate in beans.

Soil application of pure dinoseb-acetate in a laboratory system resulted in severe abnormalities in mitochondrial ultrastructure of midgut and coxal-organ cells followed by total lysis of tissues 14 days after treatment. Dinoseb-acetate, commercial Aretit and Aretit diluted 10-fold, showed heterogeneous effects on spider-mite populations under semi-field conditions. With the pure herbicide, there was little difference in the densities of treated and control populations whereas Aretit, Aretit (1:10), and a soil sample from arable land treated with Aretit, resulted in a significant reduction in numbers 6 days after treatment. Cytological changes occurred mainly in the midgut mitochondria, and these

changes were not dependent on the nature of the formulation. The reproductive organs were less affected although there were obvious reductions in the number of eggs deposited. Mite numbers in the dinoseb-acetate and Aretit treatments were still depressed 21 days after treatment whereas with dilute Aretit, the density had increased. Preliminary histopathological results demonstrate heterogeneous changes in addition to defects in the midgut mitochondria, possibly due to a secondary effect following mitochondrial destruction. The results are discussed with regard to the action of dinoseb-acetate on oxidative phosphorylation and its accumulation in animals.

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Phytoseiid mites associated with vines in Sicilian vineyards

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A survey was carried out in Sicilian vineyards to ascertain the phytoseiid mites associated with this crop. So far 19 species have been collected, the two dominant ones being *Phytoseius finitimus* Ribaga and *Typhlodromus exhilaratus* Ragusa. A study of population fluctuations of phytoseiidae in a vineyard was also undertaken from April 1987 to February 1988. The population's trend was irregular with a peak in January. This was most probably due to the particularly favourable weather conditions during the sampling period

INTRODUCTION

Viticulture is considered of great economic importance in Sicily where vines are grown to produce both wine and table grapes. According to Stellwaag (1928), there are several hundred vine pests among the most important of which is the moth, *Lobesia botrana* (Den. and Schiff.) and, among the mites, the European red mite, *Panonychus ulmi* (Koch).

To control pests, farmers generally use chemical methods. However, in those areas where only moderate use is made of these, which is usual in the western part of Sicily, phytophagous mites are not a serious problem. On the other hand, where intensive chemical-control methods are applied, especially in those areas where table grapes are grown, problems have arisen in recent years and, as a consequence, it is difficult to find predacious mites in these vineyards. However, as is already

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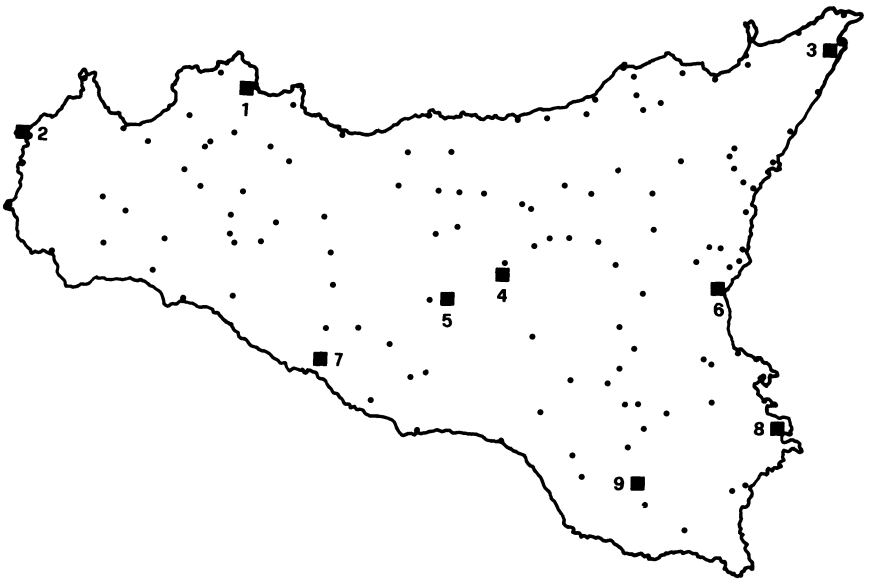

Fig. 42.1 Location of collection sites (■) used in survey of phytoseiid mites in Sicilian vineyards. (1) Palermo, (2) Trapani, (3) Messina, (4) Enna, (5) Caltanissetta, (6) Catania, (7) Agrigento, (8) Siracusa, (9) Ragusa.

known, predacious mites – mainly phytoseiids – are important from a practical point of view. Therefore, every effort should be made to preserve them and increase their presence in vineyards. With this aim, we commenced a survey of the phytoseiid mites associated with vines, collecting them from 135 vineyards in the different Sicilian provinces (Fig. 42.1). In addition, we have begun a study of the population fluctuations of these mites in a vineyard in Alcamo, Trapani.

MATERIALS AND METHODS

Mites were collected by shaking vine branchelets. The specimens were put in 70% alcohol, cleared with Nesbitt's solution, mounted in Hoyer's medium, and observed under a differential interference-contrast microscope for identification.

For the study of population density we chose a vineyard located in Alcamo where the only chemical used was sulphur. Phytoseiids were collected from 15 randomly selected plants by shaking 20 branchelets per plant (20 branches in winter), and counting the mites which had fallen on to a black plastic tray. Sampling was carried out at weekly

intervals. Maximum and minimum air temperaturs and rainfall were also recorded in the field.

RESULTS AND DISCUSSION

Survey of vineyards

The locations of the 135 collection sites are shown in Fig. 42.1, and the phytoseiid species found are given in Table 42.1. The 19 phytoseiid species collected can be divided into five groups. The first group includes the two dominant species, *Phytoseius finitimus* Ribaga followed by *Typhlodromus exhilaratus* Ragusa. The second group consists of three species: *Amblyseius stipulatus* Athias-Henriot, *Kampimodromus aberrans* (Oud.) and *Iphiseius degenerans* (Berlese). These were not as widely distributed and numbers were less than those of the first group. The third group includes five species: *Typhlodromus athenas* Swirski and Ragusa, *Typhlodromus cryptus* Athias-Henriot, *Amblyseius rubini* (Swirski and Amitai), *Typhlodromus rhenanoides* Athias-Henriot and *Amblyseius finlandicus* (Oudemans), collected in small numbers in some vineyards. Finally the last two groups have two and seven species respectively, collected sporadically and occasionally, only one specimen being recorded for most of them.

Phytoseius finitimus is not a common species in vineyards. It was reported as common by Vacante and Grazia (1987) in the eastern part of Sicily, and was recorded as *Phytoseius plumifer* (Can. and Fan.) in

Table 42.1 Check list of phytoseiid mite species collected from vines in 135 vineyards in Sicily

Group 1	Group 4
Phytoseius finitimus Ribaga	*Seiulus amaliae* Ragusa & Swirski
Typhlodromus exhilaratus Ragusa	*Amblyseius potentillae* (Garman)
Group 2	Group 5
Amblyseius stipulatus Athias-Henriot	*Amblyseius cucumeris* (Oudemans)
Kampimodromus aberrans (Oudemans)	*Amblyseius rademacheri* Dosse
Iphiseius degenerans (Berlese)	*Neoseiulus barkeri* Hughes
Group 3	
Typhlodromus athenas Swirski & Ragusa	*Typhlodromus pyri* Scheuten
Typhlodromus cryptus Athias-Henriot	*Phytoseiulus persimilis* Athias-Henriot
Amblyseius rubini (Swirski & Amitai)	*Amblyseius messor* (Wainstein)
Typhlodromus rhenanoides Athias-Henriot	*Amblyseius italicus* (Chant)
Amblyseius finlandicus (Oudemans)	

Tuscany (Liguori, 1980), and in lower Egypt and its coastal areas (Yousef, 1970). This species can be reared successfully on both prey and pollen (Elbanhawy, 1974; Zaher *et al.*, 1969). Being a dominant species, it would be worthwhile studying its relationship with phytophagous mites of vines and its population fluctuations, especially if it is to be considered as a candidate for use in an integrated-control programme.

Typhlodromus exhilaratus was the second dominant species collected. It was first found in Sicily (Ragusa, 1977), and is a common species on citrus trees being associated with other phytoseiids, especially *A. stipulatus*. Its population fluctuations have been studied on this crop. These results indicate that the abundance of this species on citrus is limited by the presence of *A. stipulatus*; *Typhlodromus exhilaratus* only increases if the population of *A. stipulatus* is reduced due to the occurrence of particular weather conditions. For this reason it would be interesting to determine if the same phenomenon occurs when *P. finitimus* is the dominant species. *Typhlodromus exhilaratus* was also found in vineyards in Tuscany (Castagnoli and Liguori, 1987) where its population fluctuations have been studied in vineyards in the province of Siena. These results indicate that this species increases when phytophagous mites are abundant. However, when other phytoseiids are present the numbers of *T. exhilaratus* decrease. In fact, in other Tuscanian vineyards where *K. aberrans* was the dominant species, the populations of *T. exhilaratus* and *P. finitimus* had the same trend but always at a lower level than *K. aberrans* (Castagnoli and Liguori, 1985). *Typhlodromus exhilaratus* has been bred in the laboratory on pollen of *Carpobrotus edulis* (L.) for more than three years, and its behaviour and food preferences have also been studied under laboratory conditions (Castagnoli and Liguori, 1986a, b; Ragusa, 1979).

As far as *A. stipulatus* is concerned, this species is dominant in citrus orchards (Ragusa, 1986) and its food preferences have been investigated in laboratory experiments (McMurtry, 1977). Another common species is *K. aberrans*. It has been recorded in Switzerland (Baillod and Venturi, 1980) and France (Rambier, 1958). It is considered a major species in vineyards in northern Italy, mainly in Veneto (Benciolini, 1982; Duso and Liguori, 1984; Ivancich-Gambaro, 1984), in Lombardia (Lozzia *et al.*, 1984), in Tuscany (Liguori, 1980; Castagnoli and Liguori, 1987), although in the latter region (Castagnoli and Liguori, 1987) it has been less frequent in recent times, being replaced by species such as *T. exhilaratus* (Castagnoli and Liguori, 1986c), which are more resistant to pesticides. On the other hand, it should be mentioned that in some regions such as Piedmont where organo-phosphorus compounds such as parathion are abundantly used, resistant strains of this species are common (Corino *et al.*, 1986).

Kampimodromus aberrans is considered a good biological-control agent in Veneto. For this reason, it was re-introduced into vineyards where the density was low (Girolami, 1985). In other vineyards where fungicides such as zineb were replaced by Bordeaux mixture, this species reappeared (Ivancich-Gambaro, 1972).

According to Ivancich-Gambaro (1982), fungicides such as those for combating mildew, are largely responsible for eliminating phytoseiid

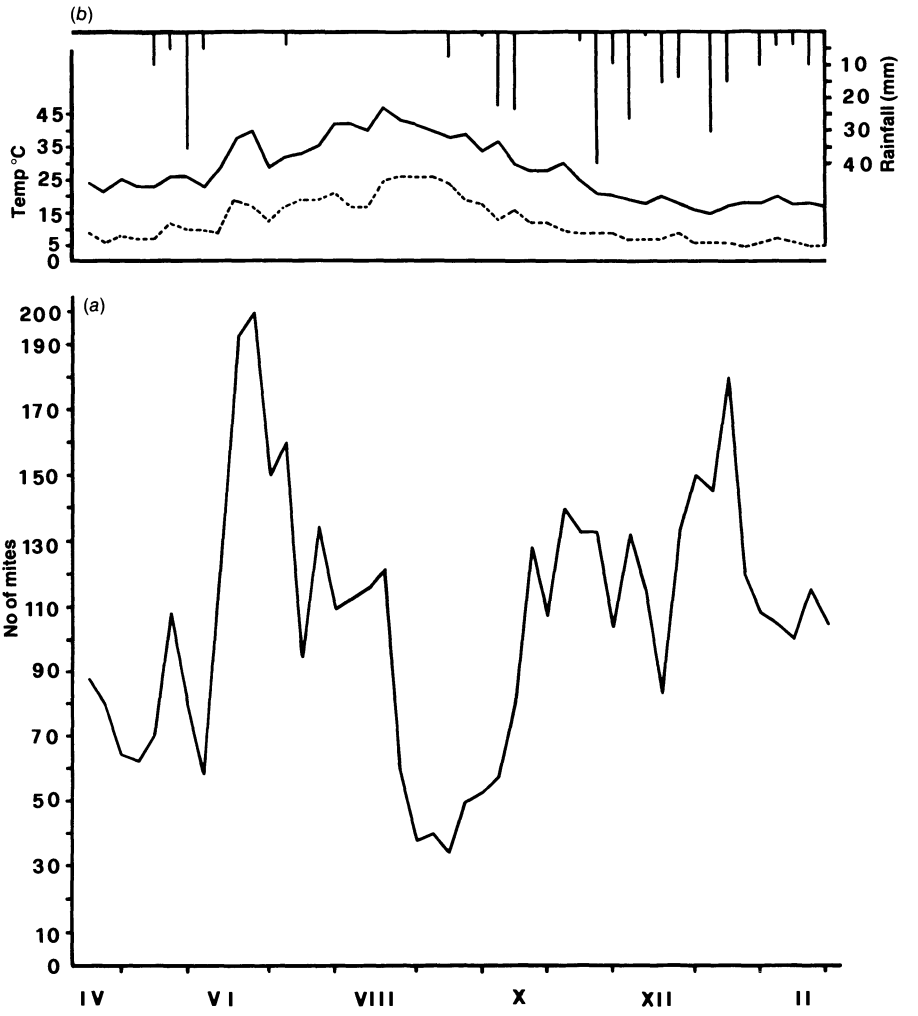

Fig. 42.2 (a) Total number of Phytoseiidae in a Sicilian vineyard from 15 plants (20 branchlets or branches (winter) per plant) at weekly intervals from April 1987 to February 1988. (*b*) Maximum and minimum air temperatures and rainfall.

mites. In relation to what has been stated above, we should husband this species, using laboratory breeding and field release to increase its presence in vineyards. Daftari (1979) and Ivancich-Gambaro (1972) give information on the biology and role of this predator.

Density fluctuations

The results of the sampling of phytoseiid mites in a vineyard in Alcamo, Trapani, are given in Fig. 42.2, which also gives the trends of maximum and minimum air temperatures and rainfall data. The figure shows that during the 46 weeks of sampling, the population trend was somewhat irregular with two peaks, the first at the end of June and the second at the end of January. It also appears that there was a generally high population density during the whole period including the winter months. This was most probably due to the particularly favourable weather conditions. Only sulphur was used in the vineyards in this area. As is well known, this product does not harm phytoseiid mites (Duso *et al.*, 1983). The lowest densities were recorded in September when the highest maximum temperature (47°C) was registered. As already shown for phytoseiids living on citrus, temperatures of 40°C have an adverse effect on these predactious mites (Ragusa, 1986). Weather conditions were exceptional during the sampling period. For this reason, further investigations are necessary before definite conclusions can be drawn.

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Studies on mites associated with lucerne in Greece

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Some results are given of a qualitative and quantitative study of arthropods associated with an old and a newly established lucerne plantation in the Kopais region, Co. Boiotia in central Greece, which commenced in April 1984. The species composition of mites in both plantations was found to be almost identical, and comprised approximately 30 species belonging to 21 families. The evaluation of taxa found using the criteria of dominance and frequency, showed that the most characteristic taxa in both plantations were: *Tydeus cochii* Baker, *Zygoribatula* spp., *Lasioseius* sp. and Tarsonemidae. During the first year of sampling, population densities of most taxa were much higher in the old than the new crop. Seasonal trends, however, were similar at both sites. During the second year of the study, there was a substantial increase in the densities of most mite taxa in the newly established crop

Knowledge of the arthropods associated with lucerne (*Medicago sativa* L.) in Greece is very limited. Lucerne is, however, a most valuable fodder plant because of the need to develop the inadequate stock-breeding industry in Greece, and research on various aspects of the arthropod fauna associated with it is certainly needed. A study from this standpoint was carried out in the Kopais region, Co. Boiotia in central Greece commencing in April 1984. The present chapter concerns the acarine fauna associated with the aerial part of a lucerne stand during the first two years of its establishment. A comparison is also made between this newly established plantation and one, three years old.

METHODS

The sampling area consisted of two plots approximately 1500 m apart, each 1000 m^2 in area and located on the Agricultural College farm in the Kopais region, Co. Boiotia. The soil in this region is rich in organic matter with a pH of 7.5. Plot I was sown with lucerne on 30 March 1984 whereas plot II had been sown two years previously. Both plots received the usual cultural treatments, that is, phosphate fertilizer in February, and the aerial parts of the plants were cut on the following dates: 14 June, 21 July, 5 September, 3 October in 1984, and 4 May, 5 June, 2 July, 6 August, 13 September, 20 October in 1985 and 25 April 1986 for plot I; and plot II on 3 July, 7 August, 7 September, 4 October in 1984, and 16 May, 10 June, 9 July, 6 August, 16 September and 24 October in 1985. No herbicide was used. The crop was irrigated on two occasions: 24 May and 4 June, 1984.

In both years the meteorological data (temperatures, rainfall, relative humidity) for the area during the period April 1984 to May 1986 are comparable, and reflect the dry, warm weather prevailing in the summer (Emmanouel and Papadoulis, 1987).

Plots I and II were sampled on 14 and 16 occasions respectively in the first year (April 1984 to March 1985) while the corresponding numbers for the second year (April 1985 to April 1986) were 18 and 19 occasions. On each sampling date, twelve samples of the aerial parts of the plants were taken at random. Each sample comprised 6–10 stems. These were brought to the laboratory with the minimum delay and disturbance, and placed in a Berlese-Tullgren apparatus for the extraction of the arthropod fauna. All the arthropods recovered were counted but the results reported here refer to the acarine fraction.

RESULTS

Species richness

Over half the species found belonged to the Prostigmata with Mesostigmata ranking second and Cryptostigmata third. The Astigmata had the smallest representation (Table 43.1). In the Prostigmata, there were 11 families as follows: Tarsonemidae, Tydeidae, Tetranychidae, Tenuipalpidae, Pyemotidae, Eupodidae, Bdellidae, Eriophyidae, Anystidae, Cunaxidae and Erythraeidae. The families of the Mesostigmata were: Ameroseiidae, Ascidae, Eviphididae, Phytoseiidae, Rhodacaridae and Parasitidae.

There were two families from the Cryptostigmata (Oribatulidae and Brachychthoniidae), and two from the Astigmata: Acaridae and Anoeti-

Table 43.1 Total number of species of Acari and mean number of individuals per sample from the aerial parts of newly established and old lucerne in central Greece sampled from April 1984 to April 1986

Order	*New (plot 1)*				*Old (plot II)*			
	1984–85		*1985–86*		*1984–85*		*1985–86*	
	Species	*Individuals*	*Species*	*Individuals*	*Species*	*Individuals*	*Species*	*Individuals*
Prostigmata	19	128.2	14	394.1	21	330.3	19	439.7
Mesostigmata	6	69.4	6	58.2	9	48.3	9	58.1
Cryptostigmata	3	37.7	3	191.2	3	94.8	3	567.4
Astigmata	1	5.6	1	3.6	1	4.5	1	9.1
Total	29	240.9	24	647.1	34	447.9	32	1073.3

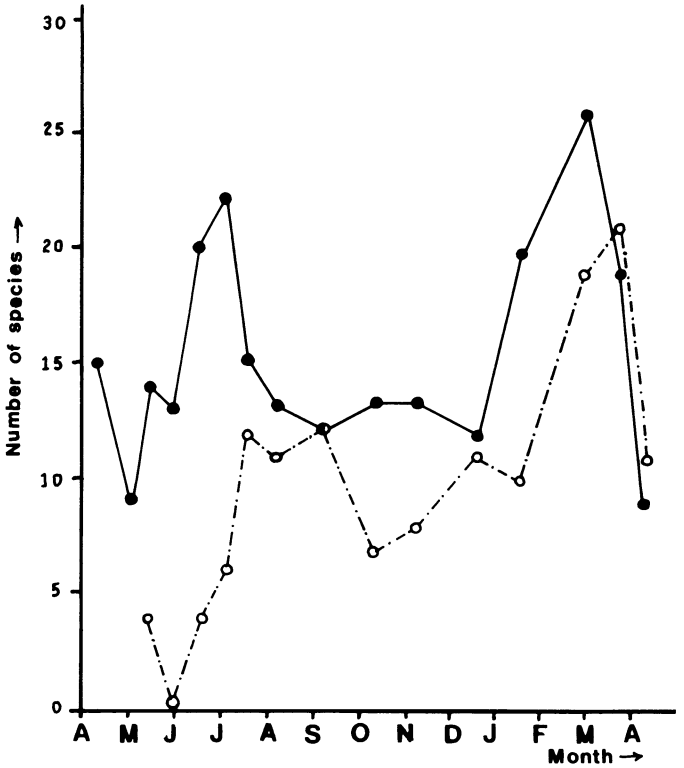

Fig. 43.1 Number of species of Acari per sampling occasion (1984–85) extracted from herbage of newly established (○) and 3-year-old (●) lucerne plots in the Kopais region in central Greece.

dae. The newly established plantation (plot I) had fewer species than the old one (plot II) in both years. The families, Cunaxidae, Pyemotidae, Erythraeidae, Rhodacaridae, Parasitidae and Anoetidae only occurred in plot II.

During 1984–85 the number of species recorded in plot I was very low at first but increased rapidly to a level comparable with the species numbers in plot II, and reached a peak in the following spring (Fig. 43.1).

Population densities

Table 43.1 gives the mean number of individuals per plot for each year. The Prostigmata had the highest density except in plot II in 1985–86, and the Astigmata were the least abundant. The Cryptostigmata were more

abundant than the Mesostigmata except in plot I during the first year. Differences in numbers of Prostigmata and Cryptostigmata were particularly marked within the same plot in different years. These were largely due to *Tarsonemus lucifer* Schaar. and *Zygoribatula* spp. which had much higher densities during the second year of the study. The population densities of the twelve species, each of which constituted more than 1% of the total arthropod fauna recorded from either plot in either year, and the number of samples in which they occurred, are given in Table 43.2.

All these species were present in both plots but *Neotarsonemoides* sp. was only found in 1985–86, and only three – *Tydeus cochii* Baker, *Lasioseius* sp. and *Zygoribatula* spp. – contributed more than 1% of the total arthropod individuals in each plot in each year. Table 43.3 lists the species which were most characteristic of the plots for each year based on the criteria of dominance and frequency used by Weis-Fogh (1948).

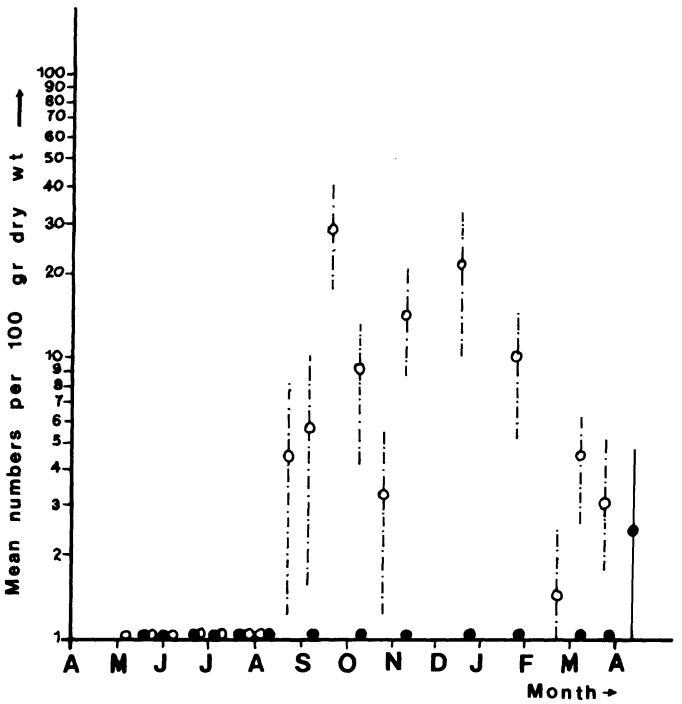

Fig. 43.2 Seasonal fluctuations in mean number of *Eriophyes medicaginis* Keifer per 100 g dry wt (±s.e.) of herbage from newly established lucerne plot in the Kopais region in central Greece from April 1984 to March 1985 (●) and April 1985 to April 1986 (○).

Table 43.2 Mean population densities per 100 g dry weight herbage of the more abundant species in new (plot I) and old (plot II) lucerne crop and number of samples in which they occurred

Species	*1984–85*				*1985–86*			
	Plot I		*Plot II*		*Plot I*		*Plot II*	
	Mean number	*Number samples*	*Mean number*	*Number samples*	*Mean number*	*Number samples*	*Mean number*	*Number samples*
Prostigmata								
Tarsonemidae								
Tarsonemus confusus Ewing	*	48	5	108	14	22	*	24
T. lucifer Schaar.	*	48	10	168	188	103	86	168
T. smithi Ewing	7	96	17	168	9	28	2	96
T. waitei Banks	9	108	16	180	26	62	12	216
Neotarsonemoides sp.					13	36	15	108
Xenotarsonemus belemnitoides (Weis-Fogh)	2	72	*	12	5	23	17	132
Tydeidae								
Tydeus cochii Baker	103	156	254	192	117	127	254	216
Tetranychidae								
Tetranychus urticae Koch	2	60	6	84	15	52	18	168
Mesostigmata								
Ameroseiidae								
Ameroseius sp.	5	48	10	120	29	55	2	96
Kleemannia sp.	3	84	9	120	2	18	*	48
Ascidae								
Lasioseius sp.	57	96	19	132	23	50	35	144
Cryptostigmata								
Zygoribatula spp.	38	156	92	192	191	151	555	228
Total number of samples		168		192		216		228

*< 1 per 100 g dry weight herbage.

Table 43.3 The most abundant and frequently occurring mite species in the aerial parts of a new (plot I) and old (plot II) lucerne crop

	1984–85		*1985–86*	
Species	*Plot I*	*Plot II*	*Plot I*	*Plot II*
Tarsonemus lucifer			DA	DC
T. waitei			IA	
T. smithi		IC		
Tydeus cochii	DC	DC	DC	DC
Ameroseius sp.			IA	
Lasioseius sp.	DC	IC		IC
Zygoribatula spp.	DC	DC	DC	DC

D, dominant: ⩾ 5% of total individuals; I, influent: 2–5% of total individuals; C, constant: in ⩾50% of samples; A, accessory: in 25–50% of samples.

Four species (*Tarsonemus lucifer, Tydeus cochii, Lasioseius* sp. and *Zygoribatula* spp.) were dominant and constant in at least one plot and/or year but only two, *T. cochii* and *Zygoribatula* spp., reached this status in each plot each year.

Although the population densities for all these species except *Lasioseius* sp. are greater in the second year, the seasonal trend of each for the first two years of the newly established lucerne plantation (plot I) seems to be similar. *Tetranychus urticae* Koch (Fig. 43.3) increases to high densities during the summer whereas *Zygoribatula* spp. (Fig. 43.5), *T. lucifer, Xenotarsonemus belemnitoides* (Weis-Fogh), *T. cochii* (Fig. 43.4), *Eriophyes medicaginis* Keifer (Fig. 43.2) and *Lasioseius* sp. each of which shows a decline. The same trends are also evident in plots I and II for the year 1984–85.

DISCUSSION

Investigations on acarine species associated with lucerne in Greece is part of a study in progress on the whole arthropod fauna in that habitat. The large number of mite species found is not uncommon as in most studies involving micro-arthropod extraction from herbage using the Berlese-Tullgren method, the mites constitute a large or the largest component both qualitatively and quantitatively (Curry, 1976; Curry and Tuohy, 1978; Purvis and Curry, 1980; Emmanuel *et al.*, 1985a). Apart from the extraction method, this is undoubtedly related to the feeding habits of the mite species found on the herbage which often are not strictly phytophagous. In the literature, many phytophagous mites are recorded in lucerne. In the present study, three of these (*T. urticae, E.*

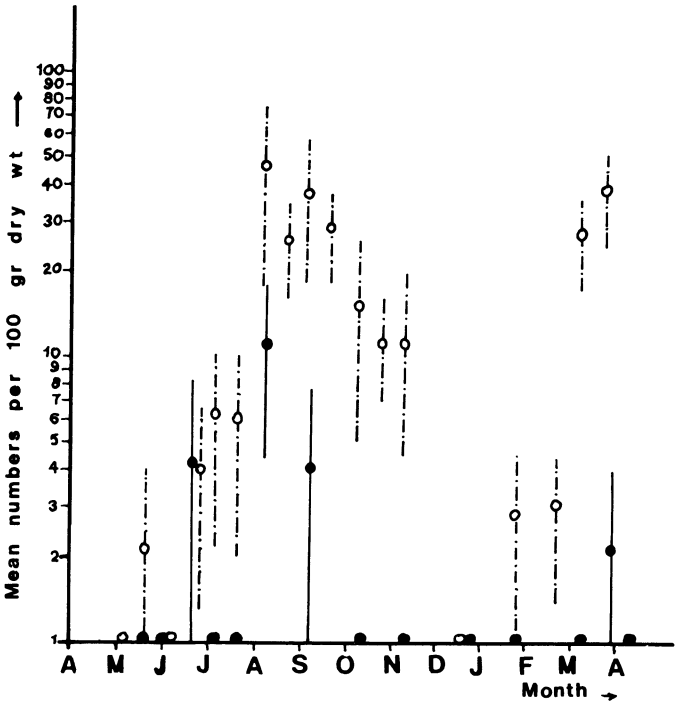

Fig. 43.3 Seasonal fluctuations in mean number of *Tetranychus urticae* Koch per 100 g dry wt (±s.e.) of herbage from newly established lucerne plot in the Kopais region in central Greece from April 1984 to March 1985 (●) and April 1985 to April 1986 (○).

medicaginis and *Bryobia* sp.) were found. *Eriophyes medicaginis*, a specialized phytophagous species, although commonly found in the old crop, only occurred in the new crop in the second year of its establishment (Fig. 43.2), and then only in small numbers. *Tetranychus urticae*, on the other hand, being more widely distributed on various plants, was present much earlier (Fig. 43.3). This was also true for almost all the other recorded species, which sooner or later colonized the young lucerne plants. Among these species, those found to be more abundant and frequent such as *T. cochii* and *Zygoribatula* spp., were already present on young plants from the first sampling date, that is, one and a half months after sowing. Tarsonemid mites, which are known to be widely distributed in vegetation and soil, were among the most frequent and abundant taxa in both plots in the two years. High population densities occurred mainly during the more humid months. This was especially the case with such species as *X. belemnitoides* and *T. lucifer*,

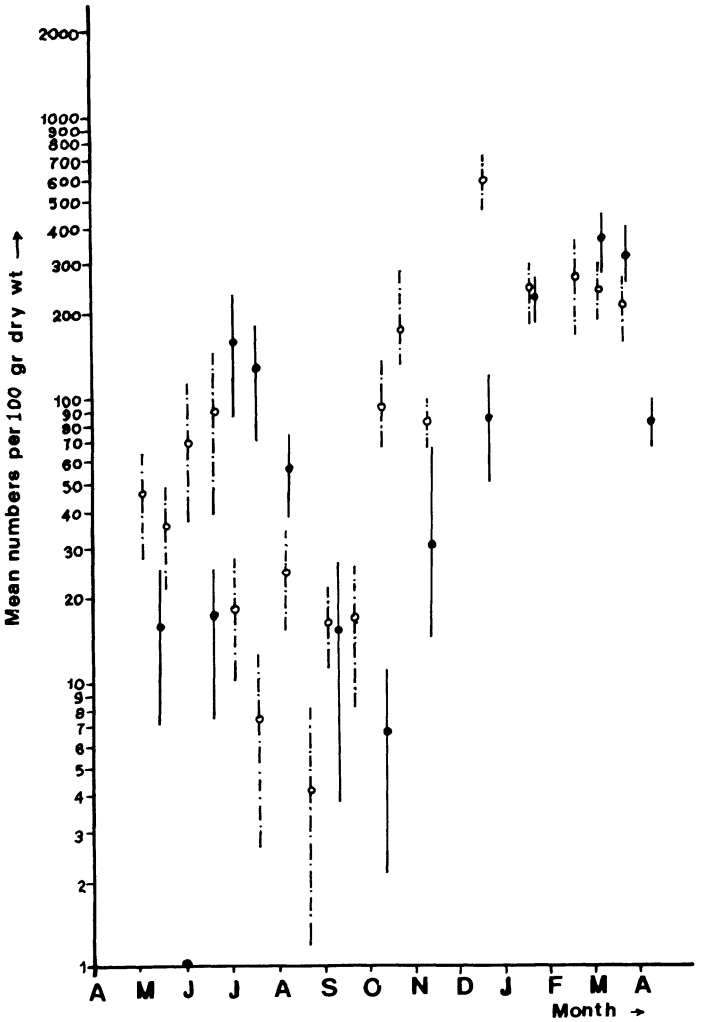

Fig. 43.4 Seasonal fluctuations in mean number of *Tydeus* sp. per 100 g dry wt (±s.e.) of herbage from newly established lucerne plot in the Kopais region in central Greece from April 1984 to March 1985 (●) and April 1985 to April 1986 (○).

which are known to be mainly soil species. The same also applies to *Zygoribatula* spp. and *T. cochii*, which reached very high densities mainly during the winter. Species of Tarsonemidae, *Zygoribatula* spp. and *T. cochii* were found to be very common in lucerne residues on the soil surface (Emmanuel *et al.*, unpublished), and this is, apparently, the source of lucerne colonization as was found with barley in an earlier study (Emmanuel *et al.*, 1985b).

Although the species richness of plot I in the second year seems to be less than in the first year, this is due to the absence of *Steneotarsonemus* species on lucerne in the second year. The presence of *Steneotarsonemus* species in samples in the first year may be due to the fact that the previous crop on plot I was a cereal, a well-known host of *Steneotarsonemus* species.

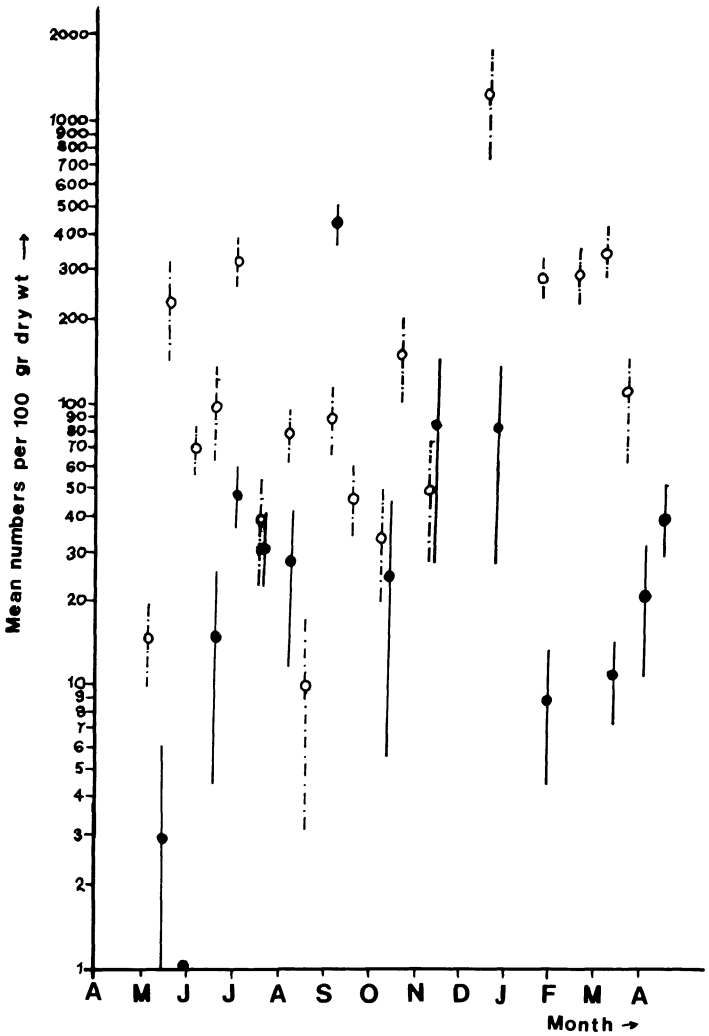

Fig. 43.5 Seasonal fluctuations in mean number of *Zygoribatula* spp. per 100 g dry wt (±s.e.) of herbage from a newly established lucerne plot in the Kopais region in central Greece from April 1984 to March 1985 (•) and April 1985 to April 1986 (○).

While comparison of the two plots within or between years is complicated by differences in sampling and in particular, harvesting dates, it can be said that the qualitative composition of the mite fauna is almost identical within each plot in both years. The species richness of the old plantation appears to be greater than that of the new one. However, if the most frequent and dominant species are considered, there is a qualitative similarity in both plots and years. Although in the absence of detailed information on the factors influencing the population dynamics of the main species, no definite conclusion can be made, it is apparent that the seasonal decline in densities of many of the species is due to their preferences for more humid and cooler conditions. The effect, however, of frequent cutting of the crop must not be ignored. It is probable that species such as *T. cochii, Tarsonemus waitei* Banks and *E. medicaginis* are affected to a greater extent by frequent cutting than other species such as *Zygoribatula* spp., *T. lucifer, T. urticae* and *Lasioseius* the densities of which are affected mainly by the climatic conditions. Astigmatic mites also belong to the latter category, and it is interesting to note that the low densities of these mites in the present study contrast with the high number found on herbage in the more humid climates of northern Europe. *Tyrophagus palmarum* (Oud.), the only species of Astigmata found with relatively high densities, occurred mainly in winter and spring.

Considering that major differences were not apparent in climatic conditions in the two years of the study, the observed marked differences in densities between the two years in both plots should not be attributed to climatic factors but to the maturity of the plantation as such. A further effect influencing population numbers could have been the tendency to sample the plants closer to the ground in the second year, and thus include more of the abundant leaf residues resting on the soil surface. This residue as indicated before has large numbers of *Zygoribatula* spp. and tarsonemid mites, especially *T. lucifer*, and these species had a marked increase in their densities in the second year.

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44

Vertical distribution and life stages of oribatid communities on beech trees

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In an acid-humus beech wood near Ettlingen in the northern Black Forest, two beech trees were cut down, the first in October 1987 and the second in February 1988. Immediately after felling, samples of trunk bark were taken up to a height of 32 m. In the laboratory, the samples were brushed and washed with 70% ethanol to remove the corticolous fauna. After brushing, the surface area of each piece of bark was determined. The bark-brushing method is very efficient for recovering corticolous oribatid mites including immatures (André and Lebrun, 1979).

The oribatid community on beech bark shows a characteristic vertical distribution pattern. Each of the six species typical for the smooth beech bark colonize a particular part of the trunk. In the lower region up to a height of 8 m, *Carabodes labyrinthicus* (Mich.) occurs in high density (maximum 44 adults/100 cm^2). This species together with *Dometorina plantivaga* (Berl.) inhabits the lichens growing on the bark; immatures of both species develop in lichen thalli (André, 1975). In the upper trunk region, 8–20 m high, *Cymbaeremaeus cymba* (Nic.) is found at high frequency but low density (maximum 5 adults/100 cm^2). *Ommatocepheus ocellatus* (Mich.), *Micreremus brevipes* (Mich.) and *Liebstadia humerata* (Sell.) are rarely found on trunk bark but occur in considerable numbers in the canopy at a height of 20–32 m. The latter species mainly inhabits dead wood still attached to the tree including knot holes and small crevices in the bark layer (Christensen, 1980) where high population densities were recorded (maximum 95 adults/100 cm^2).

Table 44.1 The sex ratio, adult to immature and female to egg ratios of 6 species of oribatid mites collected from the bark of 2 beech trees, one felled in October 1987, and the second in February 1988

Oribatid species	*Male : female*		*Adult : immature*		*Female : egg*	
	Oct. 87	*Feb. 88*	*Oct. 87*	*Feb. 88*	*Oct. 87*	*Feb. 88*
Carabodes labyrinthicus	1 : 1 · 1	1 : 1 · 2	1 : 3 · 1	1 : 4 · 3	1 : 0 · 9	1 : 1 · 9
Dometorina plantivaga	1 : 1	—	1 : 1 · 4	1 : 1 · 5	1 : 0 · 1	1 : 2
Cymbaeremaeus cymba	1 : 1	1 : 1 · 1	1 : 2 · 2	1 : 2 · 1	1 : 1 · 2	1 : 1 · 1
Liebstadia humerata	1 : 1	1 : 0 · 5	1 : 0 · 7	1 : 1 · 3	no eggs	no eggs
Micreremus brevipes	1 : 1 · 1	1 : 0 · 8	1 : 0 · 9	1 : 1 · 1	no eggs	no eggs
Ornmatocepheus ocellatus	1 : 0 · 3	1 : 1 · 3	1 : 4 · 4	1 : 3	1 : 1	1 : 1 · 2

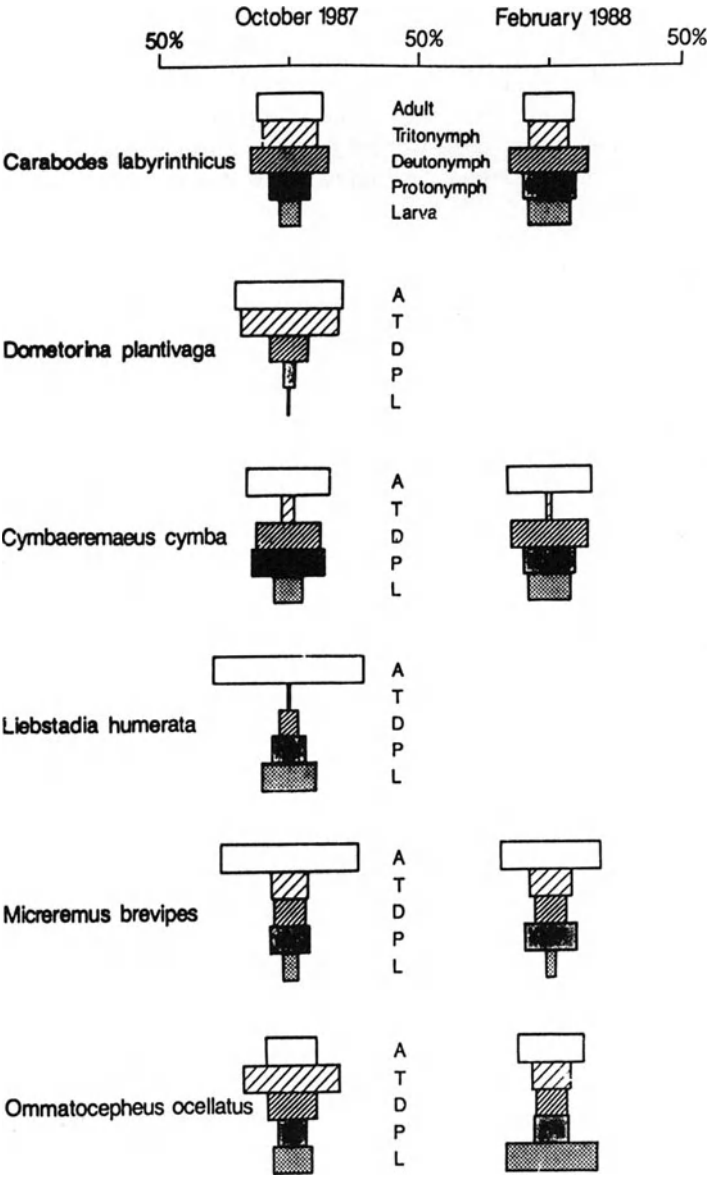

Fig. 44.1 Life-stage pyramids illustrating the percentages of larvae, protonymphs, deutonymphs, tritonymphs and adults of 6 species of oribatid mites recovered from the bark of 2 beech trees, one felled in October 1987, and the second in February 1988.

The sex ratios, adult : immature and female : egg ratios of the six species are given in Table 44.1. Determination of the immature stages has made it possible to indicate the age structure of the mite populations (Fig. 44.1), and to suggest possible seasonal fluctuations. The reproduction rate of *C. labyrinthicus* seems to be higher in late winter than in autumn. In February, the number of larvae, and the number of eggs present in females, is twice as high as four months earlier. In October 1987, a third of the *O. ocellatus* population consisted of tritonymphs. These tritonymphs presumably develop into the February adults. The high number of larvae present in this month may represent the commencement of a new generation of this species.

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45

Histiostoma murchiei *Hughes and Jackson (Anoetidae) as a parasite in the cocoons of some Danish earthworms*

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The mite, *Histiostoma murchiei* Hughes and Jackson (Acaridida: Anoetidae), has been found to parasitize about 20% of the cocoons of the earthworm, *Aporrectodea caliginosa* (Sav.) from the Strødam nature reserve in Denmark. About 7% of the cocoons of *Lumbricus terrestris* L. were also infested. Until now this species has only been known from Michigan in the USA, and it is believed that this is the first time it has been recorded in Europe

INTRODUCTION

Mites of the genus *Histiostoma* (Acaridida: Anoetidae) are common inhabitants of wet microhabitats of a surprising variety, and most are free living, occurring in decaying organic matter. However, parasitic members are also known. Thus, Fain and Lambrechts (1987) recorded *Histiostoma ocellatum* sp. nov. from Discus fish (*Symphysodon* spp.), and Fain and Belpaire (1985) reported *H. anguillarum* sp. nov. from the gills of young eels. Another species, *H. berghi* Jensen, feeds on leeches (Hughes and Jackson, 1958).

In terrestrial environments, *H. laboratorium* Hughes is known to feed on eggs and larvae in *Drosophila* cultures, but Hughes and Jackson (1958) first reported parasitic *Histiostoma* mites from the cocoons of the earthworm species, *Allolobophora chlorotica* (Sav.), *Eisenia rosea* (now *Aporrect-*

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odea rosea (Sav.)) and possibly *Allolobophora caliginosa* (now *Aporrectodea caliginosa* (Sav.)) from areas near Carp River, Michigan, USA. Oliver (1962) investigated the life cycle and host–parasite relationship of *H. murchiei* (Hughes and Jackson, 1958) in *A. chlorotica* and *Eiseniella tetraedra* (Sav.) at Carp River, an area heavily forested and subject to spring floods. Earthworms do not hatch from mite-infested cocoons. No recent papers on *H. murchiei* have been found.

MATERIAL AND METHODS

The field site is in the Strødam nature reserve, about 35 km north-west of Copenhagen. The samples were collected from a fenced part of a permanent pasture (Bøgemose) surrounded by woodland and grazed by calves and heifers. The soil is dark, poorly drained, with a pH of about 6.0, and loss on ignition of *c.* 35% (Holter and Hendriksen, 1988).

In an investigation of the mineralization of the dung of heifers and calves in the pasture, it was found that earthworms aggregated in the topsoil beneath the dung pats, and were important in the incorporation of dung in the soil. In addition, the cocoons of different earthworm species seem to be aggregated close to the pats (Hendriksen, unpublished observation).

Soil samples were washed through a sieve with a mesh size of 1 mm, and the cocoons were separated from the remaining material by flotation in a saturated magnesium sulphate solution. When it was recognized that some cocoons were parasitized by mites, all cocoons of the different earthworm species were dissected, and the mites identified. The sampling was carried out between 28 August 1984 and 15 September 1987.

RESULTS AND DISCUSSION

Table 45.1 shows the incidence of infestation of the earthworm species found. Only cocoons of *Aporrectodea caliginosa* and *Lumbricus terrestris* L. were infested with mites (*c.* 20 and 7% respectively); all the mites were identified as *Histiostoma murchiei*. Oliver (1962) also found that *H. murchiei* had a host preference but not host specificity.

Table 45.2 shows the number of cocoons of *A. caliginosa* parasitized in relation to sampling date. This varies markedly and seems to be greater in 1984 than in 1985. On average, about 20% of the cocoons were infested with mites. The weather conditions in 1984 and 1985 did not appear to differ.

Very few adult males and females were observed in the cocoons. Thus, there was only one cocoon with three females, 16 cocoons with two females, in one of which there were 10 males, and 47 cocoons were

Table 45.1 The number of mite-infested cocoons in relation to earthworm species in 407 samples collected from a permanent pasture in Strødam nature reserve in Denmark

Earthworm species	*Cocoons*		
	(number)	*infested (number)*	*infested (%)*
Aporrectodea caliginosa (Sav.)	818	121	19.9
A. rosea (Sav.)	11	0	
Lumbricus terrestris L.	29	2	6.8
L. castaneus (Sav.)	224	0	
L. festivus (Sav.)/*rubellus* Hoffm.	589	0	

found with only one female present often together with between two and five males. Many cocoons contained no males or females but large numbers of hypopi (Hendriksen).

Oliver (1962) found about three males per female in the cocoons he examined. When the adult female stage is reached, she reproduces parthenogenetically depositing 2–9 eggs, which become adults in 3–4 days, all being males. They copulate even with their mother, and each female produces up to 500 fertilized eggs. These eggs develop to the hypopal stage, and become dormant until the cocoons disintegrate. The hypopi then seem to infest new cocoons. It is, thus, possible that reproduction is of the haplo–diploid type as Hughes and Jackson (1958) have demonstrated in a few other anoetid species.

Oliver (1962) found that the life cycle of the mite is rather complex with two types of developmental cycle. The female passes through egg,

Table 45.2 Incidence of mite-infested cocoons of *Aporrectodea caliginosa* (Sav.) in samples from a permanent pasture in Strødam nature reserve between August 1984 and September 1987

Sampling date	*Samples (number)*	*Cocoons*		
		(number)	*Infested (number)*	*Infested (%)*
28 August 1984	24	35	15	42.9
18 October 1984	63	101	24	23.8
2 May 1985	8	9	3	33.3
4 June 1985	61	168	38	22.6
21 June 1985	130	299	46	15.4
22 June 1985	65	125	25	20.0
12 July 1985	46	53	9	16.0
15 September 1987	10	28	3	10.7

protonymph, hypopal, second nymphal, tritonymphal and adult stages in two different cocoons. The male, in contrast, has no hypopal stage, and passes through all its immature stages at a greatly accelerated rate in one cocoon.

The number of cocoons infested is dependent on the time of year with the greatest number of infested cocoons occurring in the summer. Apparently in the spring, new cocoons are infested by hypopi which have overwintered in old cocoons. It is still a mystery how the hypopi invade the cocoons. It has been suggested that they adhere to the anterior segments of the earthworms, and are enclosed in the cocoons when they are formed. However, hypopi have never been found within earthworms. It, therefore, seems more likely that the mites crawl into a duct of the worm, the spermatheca for example, and then enter the cocoon as it is being formed.

CONCLUSIONS

The parasitic mite, *Histiostoma murchiei*, first reported from the cocoons of earthworms in the USA (Hughes and Jackson, 1958), seems to be common in at least one Danish pasture area, parasitizing about 20% of the cocoons of *A. caliginosa* and about 7% of the cocoons of *L. terrestris*. Although the degree of infestation is less than that of the cocoons of *A. chlorotica* in the USA where *c.* 45% were infested, the dynamics of some earthworm populations may be influenced by the mite.

Hughes and Jackson (1958) and Oliver (1962) concluded that since *A. chlorotica* has a wide geographical distribution, it would seem probable that this mite is also quite widely distributed. In fact, *A. chlorotica* and other lumbricid species seem to have reached the United States from Europe (Gates, 1970; Reynolds, 1977; Edwards and Lofty, 1972). Thus *H. murchiei* may also have originated from the latter continent.

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46

Rearing deutonymphs of Iphidosoma fimetarium *(J. Müller), a mesostigmatic mite associated with carabid beetles*

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Four species of mesostigmatic mites are reported from carabid beetles in Sweden. Of these, *Antennoseius masoviae* Sellnick and *Iphidosoma fimetarium* (J. Müller) occurred on more than one species. Deutonymphs of *I. fimetarium* have been found on all six *Carabus* spp. studied, on two *Pterosticus* spp. and on one *Nebria* sp. The host species are relatively large, their lengths ranging from 1–4 cm. Most of the deutonymphs were found under the elytra of the beetles. The number of deutonymphal *I. fimetarium* on the beetles increased from August to October. By that time the beetles start to hibernate in southern Sweden, and it became difficult to catch them in Barber traps. To follow the developmental cycle of *I. fimetarium*, beetles of the genus *Carabus* infested with deutonymphs were collected alive and kept in perspex containers in a regime to simulate natural winter conditions (4 to −2°C, 100% r.h.). The deutonymphs were active and mobile even at temperatures below freezing. At the end of January, the temperature was slowly increased to *c.* 8°C. In mid February, they showed signs of becoming distended. They were often seen on the prosternum and around the coxae of the beetles. At the end of February, the first deutonymph moulted to an adult. The adults are referable to the genus *Stylochirus* G. and R. Canestrini

INTRODUCTION

Among the Actinotrichida at least two families have been reported as associated with carabid beetles in Europe, namely, the astigmatic Canestriniidae (Samšiňák, 1971) and the prostigmatic Podapolipidae (Regenfuss, 1968). However, apart from the Parasatidae, only a few studies

Table 46.1 Mesostigmatic mite species found in southern Sweden in association with carabid beetles

Mite species	*Carabid species (number)*
Eviphididae Berlese	
Iphidosoma fimetarium (J. Müller)	9
Parasitidae Oudemans	
Vulgarogamasus kraepelini (Berlese)	1
Poecilochirus necrophori Vitzthum	1
Ascidae Voigts and Oudemans	
Antennoseius masoviae Sellnick	3

have been carried out on mesostigmatic mites associated with carabid beetles (cf. Johnston and Wrensch, 1981).

A large collection of carabid beetles revealed four species of Mesostigmata on the bodies of the beetles (Table 46.1). One species, *Antennoseius masoviae* Sellnick 1943, was found in small numbers but on more than two host species. Another species, *Iphidosoma fimetarium* (J. Müller 1859), was found in such large numbers that the presence of this mite on the body of carabid beetles cannot be merely accidental. Kethley (1983) discussed, in detail, the systematic position of the genus *Iphidosoma* in which the second nymph is the only known stage. The genus was placed in the family Eviphididae by Karg (1965) and Ghilarov and Bregetova (1977) but this is open to question due to the shape of the tectum, the palpal apotele and leg chaetotaxy of the deutonymphs. Neither is the genus easily placed in the family Rhodacaridae *sensu* Lee (1970) because of the holonotal dorsal sclerite; this sclerite is normally divided in the Rhodacaroidea. Kethley, therefore, erected a new subfamily, the Epiphidinae in the family Rhodacaridae, in which he placed the genera *Epiphis* Berlese 1916, *Iphidosoma* Berlese 1892, and *Stylochirus* G. and R. Canestrini 1882. *Iphidosoma fimetarium* is the type species of the genus and hence it is of interest to determine its systematic status. This was one reason for the rearing experiments described in this chapter.

COLLECTING AND REARING METHODS

Carabid beetles were collected at Stensoffa, the ecological field station of Lund University, situated 16 km east of Lund, southern Sweden (N 55°42′, E 13°42′). Ten Barber traps, that is, glass jars, *d* 55 mm, used as pitfall traps, and one-third filled with ethylene glycol, were operated

from 10 May to 7 October 1980. The traps were emptied at irregular intervals, usually 2–4 weeks. Carabid beetles more than 5 mm long were determined to species, and 576 individuals of this size range were collected. A total of 1983 deutonymphs of *Iphidosoma fimetarium* were found on the bodies of these beetles.

Live specimens of the genus *Carabus* were collected in pitfall traps consisting of rectangular perspex containers (26 × 42 cm), each with a layer of dry leaves. The beetles were kept in a cool store-room (15°C) in the laboratory and fed on lumbricid worms, commercially available 'maggots' and larvae of *Tenebrio molitor* L. In mid November the temperature was gradually lowered to between *c.* 4° and −2°C.

In one set of rearing experiments the beetles were kept in the large perspex containers in which they were caught. They had plenty of dry leaves to hide under, and the boxes were sprayed with water every week, and kept in a store room at 4 to 0°C. The temperature was raised to about 13°C on 23 January. Fully engorged nymphs which had left the beetles, were removed from the culture vessels and placed in small perspex Petri dishes, having a layer of plaster of Paris mixed with charcoal with one individual per dish, and were observed daily.

In a second set of rearing experiments, the beetles were kept in containers (9 × 9 cm) with a basal layer of a mixture of plaster of Paris and charcoal. Three beetles were kept in each container. The cultures were stored at 0 to −2°C from the beginning of December until mid February, when the temperature was raised to 4°C. In mid March the temperature was increased to 8°C. In the beginning of April, the cultures were moved to a cool store-room (15°C).

RESULTS

Host selection

Beetles, more than 5 mm long, of the three families, Carabidae, Staphylinidae and Scarabaeidae (genus *Geotrupes*), were found on a regular basis in the pitfall traps. Deutonymphs of *I. fimetarium* were found only on the carabid beetles. In southern Sweden, deutonymphs have been found (Lundqvist, unpublished data) on all investigated *Carabus* species namely, *C. granulatus* L. (16–23 mm), *C. nemoralis* Müll. (22–26 mm), *C. hortensis* L. (22–28 mm), *C. glabratus* Payk. (22–30 mm), *C. violaceus* L. (20–30 mm), and *C. coriaceus* L. (32–40 mm), on two *Pterosticus* species (*P. niger* Schall. (15–20.5 mm) and *P. melanarius* Ill. (12–18 mm)), and on *Nebria brevicollis* (Fabr.) (10–14 mm) (size ranges from Lindroth 1985, 1986). The size of the host seems to be an important factor for host selection by deutonymphal *I. fimetarium* but it is not the ultimate

criterion; the species, *Cychrus caraboides* (L.) (14–19 mm), was regularly encountered in the pitfall traps but very rarely hosted any *I. fimetarium*.

Seasonal occurrence

Deutonymphs of *I. fimetarium* were present on carabid beetles throughout the sampling period from the beginning of May to October. *Carabus hortensis* was one of the few beetle species found in the spring as well as in the autumn, and was therefore chosen as a suitable host for studying the seasonal occurrence of *I. fimetarium* (Fig. 46.1). Infestation was low during spring with about one deutonymph per 10 beetles. In late August the density of deutonymphs began to increase, reaching a maximum of 4.7 deutonymphs/beetle in September when all the beetles examined had nymphs. In addition, the variance:mean ratio increased from August to September (Fig. 46.1), suggesting a more clumped distribution of *I. fimetarium* on *C. hortensis* at the end of the season.

Rearing to adult stage

Deutonymphs of *I. fimetarium* were reared on beetles of the genus *Carabus*. Late in the autumn, the deutonymphs were usually found

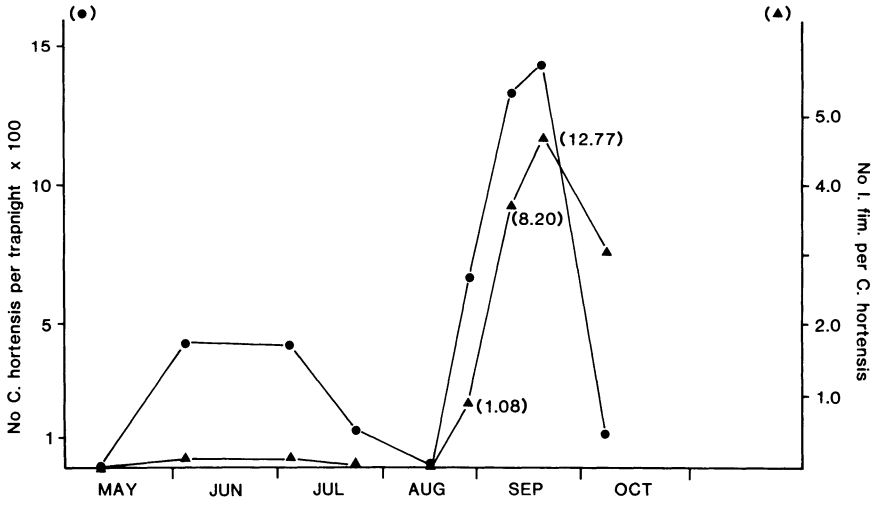

Fig. 46.1 Seasonal occurrence of deutonymphs (▲) of *Iphidosoma fimetarium* (J. Müller) found on *Carabus hortensis* L., and number of latter (●) collected in pitfall traps in southern Sweden from May to October 1980. The 3 values in parentheses are variance:mean ratios.

under the elytra of the beetles; they were never observed off the beetles. The insects together with their deutonymphal mites were kept under 'winter conditions' (4 to −2°C, 100% r.h.) in the laboratory. The beetles started to hibernate when the temperature was lowered, and were practically immobilized when the temperature went below 5°C. The mites, however, were still active even at temperatures below 0°C.

In late December when the temperature was 4° to 0°C, the deutonymphs showed the first signs of swelling. At this time, the deutonymphs were often seen on the prosternum and around the coxae of the beetles. In early February when the temperature was 15°C, several large nymphs were observed, and on 17 February the first deutonymphs were found on the floor of the culture vessel. Fully distended deutonymphs are almost spherical. After a few days the deutonymphs usually became quiescent for 1–2 days. In this state, the first pair of legs could move in a questing fashion but legs II–IV where firmly fastened to the substrate.

In the second rearing experiment when the temperature was lower (0° to −2°C), the deutonymphs showed no signs of swelling. In the middle of March, the temperature was increased to 8°C, and the first signs of enlargement were observed. At the beginning of April, the temperature was 15°C, and the deutonymphs began to swell more frequently. The first adult mites were observed in mid April.

DISCUSSION

The number of deutonymphs of *I. fimetarium* on the bodies of large carabid beetles in southern Sweden increased from late August till early October, after which the beetles could no longer be caught in Barber traps. In the spring few, if any, were found on the beetles. I believe that the deutonymphs of this species accumulate on the beetles in order to overwinter in close association with the insects. In the middle of the winter they begin to feed for *c.* 2 months after which they leave the host and moult to adults in March–April. This is the time when fully engorged deutonymphs and adults can be found in litter samples in southern Sweden (personal observation).

SYSTEMATICS

The adult mites are almost globular and heavily sclerotized. The holonotal sclerite is continuous posteriorly with the ventri-anal region, and anterolaterally with the peritrematic sclerites. The peritreme is short, reaching the middle of coxa II. In the female, there is one pair of well-developed presternal sclerites. Sternal setae 4 seem to be situated on

sternal sclerites. The tectum is relatively short and blunt. The male spermatodactyls are greatly elongated, styliform and about half the body length. Near the apex of tarsus I there is a conspicuous bulbous sensillum. The above description falls within the definition of the genus *Stylochirus* G. and R. Canestrini 1882, *sensu* Ghilarov and Bregetova (1977) as well as *Epiphis* Berelese 1916, as defined by Kethley (1983). Further studies will be necessary to separate the different genera in the subfamily Epiphidinae.

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Mites of the house mouse, Mus musculus *L., in the north-eastern part of the Iberian Peninsula in Spain*

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Studies carried out in Spain on the mites of the house mouse, *Mus musculus* L., and of small mammals in general, have been limited to taxonomic and faunistic aspects. In order to extend these to include biological attributes, a study has been made of the annual cycle of the mite parasites of *M. musculus* from the 'Delta del Ebro' situated in the north-eastern part of the Iberian Peninsula in Spain. Monthly collections were made from February 1985 to January 1986 in nine sites in this area. From these, 397 specimens of *M. musculus* were captured, 357 of which were obtained from a salty lagoon surrounded by reeds.

In all, 15 mite species have been recorded including *Dermacarus* hypudaei (Koch) (4.5%), *Xenoryctes krameri* (Mich.) (9.3%), *Afrolistrophorus apodemi* Fain (43.6%), *Myocoptes* (*M.*) *musculinus* (Koch) (6.8%), *Trichoecius romboutsi* (van Eyndhoven) (3.0%), *Crocidurobia* (*C.*) *michaeli* (Poppe) (0.7%), *Myobia* (*M.*) *musculi* (Schrank) (49.9%), *Eulaelaps stabularis* (Koch) (3.5%), *Haemogamasus horridus* (Mich.) (4.0%), *Echinonyssus butantanensis* Fonseca (9.8%), *Laelaps algericus* (Hirst) (29.5%), *Myonyssus decumani* Tiraboschi (3.5%), and *Ornithonyssus bacoti* (Hirst) (0.7%).

The qualitative analysis indicates a low frequency for the Glycyphagidae (*D. hypudaei, X. krameri*) in an environment in which, due to the high relative humidity, one would expect it to be suitable for their development. The salinity of the area may have played an important role in restricting the occurrence of these species. On the other hand, from the

data we have, *X. krameri* has not been recorded as a parasite of *M. musculus*, and thus this small mammal constitutes a new host for this mite species while *H. horridus* is a new Spanish record. The presence of *C.* (*C.*) *michaeli* on *M. musculus* should be regarded as an accidental contaminant due to the transfer of this mite from its usual host, *Crocidura russula* (Herm.), which is very widespread in the area. This is easily explained by the close cohabitation of the two hosts in the Delta del Ebro.

The results of this study of the annual cycle of the mite population of *M. musculus* indicate that the largest number of species occurred in December when *O. bacoti* was the only one not recorded. If *M.* (*M.*) *musculinus and T. romboutsi* are excluded, the rest of the permanently parasitic species were present during practically the whole year. Neither the sex nor the age of the host appears to influence their frequency. Climatic conditions, however, would appear to have a role in determining the frequency of the host-nest dwelling species, *D. hypudaei*, *X. krameri*, *E. stabularis*, *H horridus* and *E. butantanensis*.

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Records of Ixodoidea from the Trentino-Alto Adige region in northern Italy

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There is little information available on the tick fauna (Ixodoidea) from Trentino-Alto Adige (Canestrini, 1890; Reimoser, 1934; Conci, 1951; Starkoff, 1958; Starkoff and Cagnolati, 1962; Petrelli, 1976; Manilla and Sobrero, 1982; Manilla, 1985). No data are available from the province of Bolzano apart from reference in the media to the invasive presence of *Argas reflexus* (Fab.), which occurred in 1987 in dwellings of the city of Bolzano. In the two provinces of Trentino-Alto Adige Trento (TN) and Bolzano (BZ), the following species have already been recorded: *A. reflexus* (BZ), *Dermacentor marginatus* (Sulzer) (TN), *Haemaphysalis punctata* Can. & Fan. (TN), *Hyalomma marginatum* Koch (TN), *Ixodes hexagonus* Leach (TN), *I. ricinus* (L.) (TN), *I vespertilionis* Koch (TN), *Rhipicephalus bursa* Can. & Fan. (TN), *R. sanguineus* (Latr.) (TN).

This chapter is a contribution to the knowledge of the tick fauna in these provinces and reports data of research carried out from 1983 to 1988. Ticks from nine heavily infested sheep flocks, one human dwelling and from the small collection of K. Hellrigl (Bressanone) were examined. In all 172 ticks were identified. The following species, arranged in order of abundance, were recorded: *D. marginatus* (124 specimens), *H. punctata* (39), *I. hexagonus* (3), *I. ricinus* (3) and *R. sanguineus* (3). Details of hosts, localities and sexes are given in Table 48.1. The species, *D. marginatus*, *H. punctata*, *I. hexagonus*, *I. ricinus* and *R. sanguineus* were reported for the first time from the province of Bolzano.

Table 48.1 Records of species of Ixodoidea from the Bolzano area in the Trentino–Alto Adige region in northern Italy

Species	*Number of individuals*	*Source*	*Date collected*	*Locality*	*Male*	*Female*
Dermacentor marginatus	124	Sheep	23/3/1983	Laces	+ +	+ +
		Sheep	2/5/1984	S. Martino Laces	+ +	+ +
		Sheep	8/6/1984	Laces	+ +	+ +
		Sheep	15/6/1984	Laces	+ +	+ +
		Sheep	10/5/1987	Silandro	+	+
Haemaphysalis punctata	39	Sheep	23/3/1983	Laces		+ +
		Sheep	2/5/1984	S. Martino Laces		+ +
		Sheep	8/6/1984	Laces	+ +	+ +
		Sheep	15/6/1984	Martello	+ +	+ +
Ixodes hexagonus	3	Burrows of *Talpa* sp.	11/11/1960	Bressanone	+	
		Rodent burrows	27/2/1962	Seeburg Bressanone	+	+
Ixodes ricinus	3	Soil	30/3/1961	Bressanone		+
		Homo sapiens	7/5/1983	Mitterberg Caldaro		+ (nymph)
		Homo sapiens	1/6/1983	Caldaro		+ (nymph)
Rhipicephalus sanguineus	3	Human dwelling	17/3/1988	Bolzano		+ +

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Seasonal and spatial variation in food intake by the oribatid mites of beech woodland soil

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Approximately 50% of the oribatids sampled during the year in a Danish beech woodland contained food boluses. Macrophytophages may be the most active feeders with 79% of the adults containing food during the year. These are followed by the panphytophages (58% of the adults) and the microphytophages (41% of the adults). The lower percentage for microphytophages may reflect the ingestion of liquid food not amenable to microscopic investigation. Some seasonal variation in food intake was noted, the peak month for ingestion for all trophic groups being December. This coincided with peak litter fall, which was one month later than the maximum rainfall recorded. When expressed as a percentage of total individuals with gut content, the microphytophages had the highest proportion with food boluses/m^2. Most adult macrophytophages (59%) and microphytophages (53%) with food content are to be found in the 0–3 cm layer of the soil but most fed adult panphytophages (54%) occur in the litter. Individual species or life stages within these general trophic groups may display their own idiosyncratic distribution patterns of feeding in space and time. The measurement of food intake from gut-content observations reveals different seasonal patterns from those predicted on the basis of laboratory extrapolation. It is emphasized that many factors interact to determine quantitative seasonal patterns of ingestion but that oribatids seem to be able to respond readily to periodic renewal of acceptable food resources

INTRODUCTION

Oribatid mites display a wide range of food choice and feeding habit (Luxton, 1972). The macrophytophagous species consume material originating from vascular plants which is usually (as noted by Krantz and

Lindquist, 1979), but by no means always, dead or dying. Microphytophagous species, on the other hand, consume microflora exclusively – perhaps ingesting both dead and living material. Panphytophagous species, which are the majority, have the combined feeding attributes of the microphytophagous and macrophytophagous groups. According to Luxton (1981c) each of these feeding groups in beech woodland soil account for about one-third of the total energy consumed annually by the oribatid community of this habitat.

Within these general feeding groups, considerable selectivity of food items may take place between species. Even developmental stages of the same species may elect to consume quite different food elements. This selectivity might, in turn, determine mite distribution in space and time according to the relative distribution of food. However, as Wallwork (1958) pointed out, a number of other factors may be involved in limiting or permitting food choice including the moisture content of the food material itself, and the importance of such factors may also vary with species or life stage.

Much of the work on oribatid feeding biology has been restricted to the laboratory, and there may be dangers in extrapolating these results to the field (Luxton, 1972, 1984; Haq and Prabhoo, 1977; Mitchell and Parkinson, 1976). A few studies have attempted to bridge the gap by identifying food contained within the guts of animals caught in the field (Schuster, 1956; Murphy and Jalil, 1964; Anderson, 1975; Mitchell and Parkinson, 1976; Hågvar and Kjøndal, 1981; Luxton, 1984), and this chapter continues the theme introduced in Luxton (1984). The same techniques are used as described in that paper, and the mites are from the same site at Hestehave in Denmark. This time, however, a general overview of the entire oribatid community is presented.

RESULTS

Approximately 50% of the oribatids sampled during the year contained food boluses, a figure which applies to all life stages (Table 49.1). The macrophytophagous oribatids appear to be the most active feeders with 79% of the adults containing food during the year. These are followed by the panphytophages (58% of the adults) and the microphytophages (41% of the adults). However, this undoubtedly reflects the nature and relative digestibility of the food, with the remains of higher-plant detritus being more easily seen in gut-content scanning. Many of the smaller microphytophages are recorded as possessing little solid matter in the gut during the year. The Suctobelbidae, in particular, with 11% containing boluses, are almost certainly liquid feeders ingesting material which is not detectable by microscopic examination. The design of the needle-like mouthparts of these mites lends support to this conclusion. The

mouthparts of *Gustavia microcephala* are also highly modified with sickle-like scraping organs. The diet of *Gustavia* is almost certainly bacterial (Luxton, 1972), another food material, possibly in a fine state of suspension and rapidly digested, which might not be readily observed in gut-content scanning. The low percentage of the *Gustavia* population recorded as containing food (35%) lends weight to this conclusion. *Hypochthonius rufulus* is also thought to be a bacterial-feeding specialist (Luxton, 1972) and is also, accordingly, recorded as containing few food boluses (48%). In addition, brachychthoniids may be partly bacterial or liquid feeders as evidenced by the low counts (32%) of food boluses in the annual population. *Tectocepheus velatus* may also be added to this category for the same reason, the figures given in Table 49.1 (20–38%) matching quite well those already quoted by Murphy and Jalil (1964) of

Table 49.1 Percentages of adult and juvenile oribatid mites with food boluses over one year in a Danish beech woodland soil (expressed as percentage of total number/m^2/year of feeding category or taxon)

	Total	*Adult*	*Nymphs*	*Larva*
Macrophytophage	—	79	—	—
Steganacarus spinosus (Sell.)	—	85	—	—
Phthiracarus spp.	—	64	—	—
Steganacarus magnus (Nic.)	—	57	—	—
Panphytophage	59	58	59	60
Xenillus tegeocranus (Herm.)	83	85	78	83
Nothrus silvestris (Nic.)	68	84	67	66
Adoristes ovatus (C. L. Koch)	—	74	—	—
Ceratozetes gracilis (Mich.)	56	63	50	59
Nothrus palustris C. L. Koch	65	62	74	59
Chamobates cuspidatus (Mich.)	71	57	79	80
Galumna lanceata Oud.	64	57	71	70
Hemileius initialis (Berl.)	50	54	46	52
Achipteria coleoptrata (L.)	53	40	61	49
Microphytophage	43	41	46	45
Oppiidae	64	66	50	53
Damaeus clavipes (Herm.)	74	65	76	86
Belba corynopus (Herm.)	57	63	54	57
Oribella paolii (Oud.)	64	57	74	54
Hypochthonius rufulus C. L. Koch	48	50	55	42
Brachychthoniidae	32	32	33	31
Gustavia microcephala (Nic.)	35	29	47	16
Tectocepheus velatus (Mich.)	30	20	32	38
Suctobelbidae	11	11	6	0
Total	51	51	52	52

17–30%. In terms of proportions recorded with food inclusions, the juveniles of feeding groups or of individual species seem to differ little from each other or from their adults. At most the difference is between 10 and 20%, with no regular pattern evident.

Some seasonal variation in food intake was noted by Luxton (1984) for one species of macrophytophage (*Steganacarus magnus*). This mite appeared to be reacting adversely to the low water content of the litter in July, and positively to the peak litter input in December. Similar patterns may be deduced for all three feeding groups of oribatids (Fig. 49.1). Thus, all stages of all groups registered a peak in the number of food boluses present in their populations/m^2 in December at the time of peak litter fall, and one month subsequent to peak rainfall. This reinforces the previously stated view (Luxton, 1982) that soil oribatids react quickly to the seasonal renewal of resources. Only the macrophytophages responded immediately to the next highest rainfall peak registered in May although delayed responses were recorded in June for panphytophage adults and microphytophage nymphs. All larvae monitored displayed an increased food-bolus incidence during the summer and early autumn months. During this period, the total food intake was less for most adults and nymphs in all feeding groups although microphytophage nymphs and panphytophage adults responded positively to the temporary rise in litter water content in August.

Many of the microphytophagous mites may feed virtually continuously when food is in an available or acceptable form. The oppiids, for example, frequently display continuous strands of amorphous food material within the upper part of their guts before this is eventually formed into a globular bolus. As a group, the microphytophages register the largest number of food boluses/m^2 overall (*c.* 50% of the boluses/m^2 of the total adult community) (Table 49.2). Not infrequently, the nymphal and larval stages of species are recorded as bearing proportionally the largest number of food boluses/m^2 suggesting that, per individual, these stages are the most active feeders. In the case of the Oppiidae, however, the reverse is evidently the case. It may be that, as with the Suctobelbidae and other small species, boluses are not being registered in juvenile oppiids simply because, at this stage in their development, they are liquid or suspension feeders.

At any given depth in the soil profile, most of the adult macrophytophages (*c.* 80%) have food in their guts during the year (Table 49.3). However, most (59%) of the fed individuals are to be found in the 0–3 cm layer of the soil. This result is not surprising in view of the fact that the bulk of the macrophytophagous community is located at this depth. Among the adults of the panphytophagous feeding category at each depth, the equivalent figure for those with food in their guts is similar

Table 49.2 Food boluses/m^2 over one year for adult and juvenile oribatid mites in a Danish beech woodland soil (expressed as percentage of total boluses/m^2/year of each life stage)

	Total	*Adult*	*Nymphs*	*Larva*
Macrophytophage	(20)	33	—	—
Steganacarus spinosus	—	27	—	—
Phthiracarus spp.	—	4	—	—
Steganacarus magnus	—	2	—	—
Panphytophage	32	19	51	51
Xenillus tegeocranus	2	2	1	2
Nothrus silvestris	5	1	7	13
Adoristes ovatus	—	3	—	—
Ceratozetes gracilis	6	4	9	7
Nothrus palustris	2	<1	3	4
Chamobates cuspidatus	4	2	9	4
Galumna lanceata	1	1	<1	5
Hemileius initialis	5	3	7	10
Achipteria coleoptrata	6	2	15	6
Microphytophage	48	48	49	49
Oppiidae	19	29	5	4
Damaeus clavipes	3	2	6	6
Belba corynopus	6	3	12	10
Oribella paolii	3	2	5	2
Hypochthonius rufulus	7	2	9	19
Brachychthoniidae	6	7	5	2
Gustavia microcephala	<1	<1	1	<1
Tectocepheus velatus	3	1	6	6
Suctobelbidae	1	2	<1	0

(*c.* 60%), but a majority of the individuals with gut content (54%) are located in the litter. Again, this results from the location of most panphytophages at this depth. Among the adults of the microphytophage group, the greatest percentage containing food (57%) are to be found in the litter but most of the fed individuals (53%) are in the top 3 cm of the soil. Approximately the same proportion of juvenile panphytophages as adults have food in their guts in each of the three depth layers, and the distribution of fed individuals is also much the same. By the same token, the distribution of microphytophage larvae is similar to that of their adults although the percentages of total larvae with boluses are fractionally more evenly spread through the vertical levels monitored. These general results suggest that, although the trophic groups may feed adequately at any depth, the most active feeding on the part of each category may occur in particular horizons. Thus, of the macrophyto-

phage and microphytophage oribatids, those inhabiting the 0–3 cm soil layer feed most actively, whereas amongst the panphytophage adults, the litter fraction is the most active. It is also possible, however – as suggested by Luxton (1981b) – that some species populations may feed most actively in one horizon before migrating elsewhere to lay eggs.

Individual species within these general trophic groups may display their own unique distribution patterns in relation to recorded bolus inclusions (Table 49.3). The population of *Steganacarus magnus*, for example, does not follow the general trend for macrophytophages, with most of its food boluses/m^2 being found in the litter instead of the 0–3 cm soil layer. Among the panphytophages, the populations of *Nothrus silvestris* and *Ceratozetes gracilis* differ from the general trend, and have most food boluses/m^2 in the 0–3 cm fraction of their populations. Among the microphytophages, the populations of *Damaeus clavipes* and *Belba corynopus* appear to feed most actively in the litter rather than in the 0–3 cm soil layer, which is the norm for their trophic group. However, the juveniles of *Belba corynopus* (as predicted in Luxton (1972)) feed most actively in the 0–3 cm depth. Substantial fractions of the populations of *Nothrus silvestris*, *Ceratozetes gracilis*, *Galumna lanceata*, Oppiidae, *Oribella paolii*, *Hypochthonius rufulus*, Brachychthoniidae, *Tectocepheus velatus* and Suctobelbidae feed at the 3–6 cm soil level but the bulk of oribatid feeding activity appears to occur at depths above 3 cm.

DISCUSSION

The oribatid community sampled for one year revealed that only half its numbers had food in their guts (Table 49.1). This compares with annual percentages for Collembola of 31–53% (Bödvarsson, 1970) and 47–63% (Anderson and Healey, 1972). The low percentages for Collembola were attributed to the influence of the moulting cycle but the same reasoning cannot be applied so readily to oribatids. The percentage of individuals which had fed, however, varies according to trophic group (Table 49.1) with the macrophytophages appearing to contain the greatest proportion of these individuals, the microphytophages the least, and the panphytophages having an intermediate position. As indicated earlier, this might well be a 'false' result arising from the ingestion of liquid food, bacteria or food in suspension by many of the smaller microphytophages. Indeed Walter (1987) has reported 'opportunistic polyphagy' as a common feeding behaviour in soil micro-arthropod populations (including some oribatids) in which animals such as nematodes present in the micro-arthropod feeding environment, are as readily ingested as the more conventional food. As Walter indicates, such animal remains in the gut are not visible and therefore not reported.

Table 49.3 The vertical distribution of adults, nymphs and larvae of oribatid taxa with food boluses in a Danish beech woodland soil (data expressed, respectively, as percentage of total of all individuals in taxon for each depth (columns 2–4), and percentage of total in taxon for the 3 depths but excluding those without boluses (columns 5–7))

	Litter	*0–3 cm*	*3–6 cm*	*Litter*	*0–3 cm*	*3–6 cm*
Adult						
Macrophytophage	79	80	73	35	59	6
Steganacarus spinosus	91	84	78	31	63	6
Phthiracarus spp.	57	69	73	41	49	10
Steganacarus magnus	60	55	20	61	38	1
Panphytophage	62	57	61	54	38	8
Xenillus tegeocranus	84	88	76	70	25	5
Nothrus silvestris	67	89	73	5	76	19
Adoristes ovatus	73	73	34	89	10	1
Ceratozetes gracilis	62	63	62	5	78	17
Nothrus palustris	70	50	100	54	38	8
Chamobates cuspidatus	64	43	40	74	21	5
Galumna lanceata	64	40	80	60	27	13
Hemileius initialis	62	38	38	76	21	3
Achipteria coleoptrata	37	40	75	60	32	8
Microphytophage	57	38	37	28	53	19
Oppiidae	79	65	59	25	50	25
Damaeus clavipes	83	20	0	93	7	0
Belba corynopus	83	49	60	55	42	3
Oribella paolii	72	52	70	9	64	27
Hypochthonius rufulus	69	48	43	21	60	19
Brachychthoniidae	41	29	30	36	50	14
Gustavia microcephala	31	29	0	36	64	0
Tectocepheus velatus	5	44	24	1	88	11
Suctobelbidae	22	12	5	22	67	11

Table 49.3 (continued)

	Litter	*0–3 cm*	*3–6 cm*	*Litter*	*0–3 cm*	*3–6 cm*
Nymphs						
Panphytophage	58	60	59	28	56	16
Xenillus tegeocranus	83	0	0	100	0	0
Nothrus silvestris	75	68	64	3	61	36
Ceratozetes gracilis	90	49	49	5	63	32
Nothrus palustris	80	73	67	8	88	4
Chamobates cuspidatus	86	76	75	36	51	13
Galumna lanceata	67	0	100	80	0	20
Hemileius initialis	46	48	40	89	9	2
Achipteria coleoptrata	64	58	76	15	76	9
Microphytophage	48	45	41	21	60	19
Oppiidae	57	51	46	17	43	40
Damaeus clavipes	83	68	81	57	36	7
Belba corynopus	73	48	38	33	63	4
Oribella paolii	100	71	80	6	71	23
Hypochthonius rufulus	53	59	45	15	65	20
Brachychthoniidae	18	35	31	17	54	29
Gustavia microcephala	80	40	25	35	61	4
Tectocepheus velatus	22	32	44	12	70	18
Suctobelbidae	0	7	4	0	67	33

Larva						
Panphytophage	61	59	59	34	51	15
Xenillus tegeocranus	86	50	100	86	7	7
Nothrus silvestris	100	66	61	5	68	27
Ceratozetes gracilis	100	58	58	1	69	30
Nothrus palustris	100	57	43	12	81	7
Chamobates cuspidatus	88	62	0	86	14	0
Galumna lanceata	90	67	61	23	56	21
Hemileius initialis	51	48	75	86	11	3
Achipteria coleoptrata	48	49	67	28	68	4
Microphytophage	55	45	36	17	64	19
Oppiidae	70	64	35	24	48	28
Damaeus clavipes	86	83	0	83	17	0
Belba corynopus	71	56	42	19	74	7
Oribella paolii	0	56	50	0	67	33
Hypochthonius rufulus	44	44	37	7	69	24
Brachychthoniidae	39	24	33	39	35	26
Gustavia microcephala	33	8	0	66	34	0
Tectocepheus velatus	23	42	33	6	75	19
Suctobelbidae	0	0	0	0	0	0

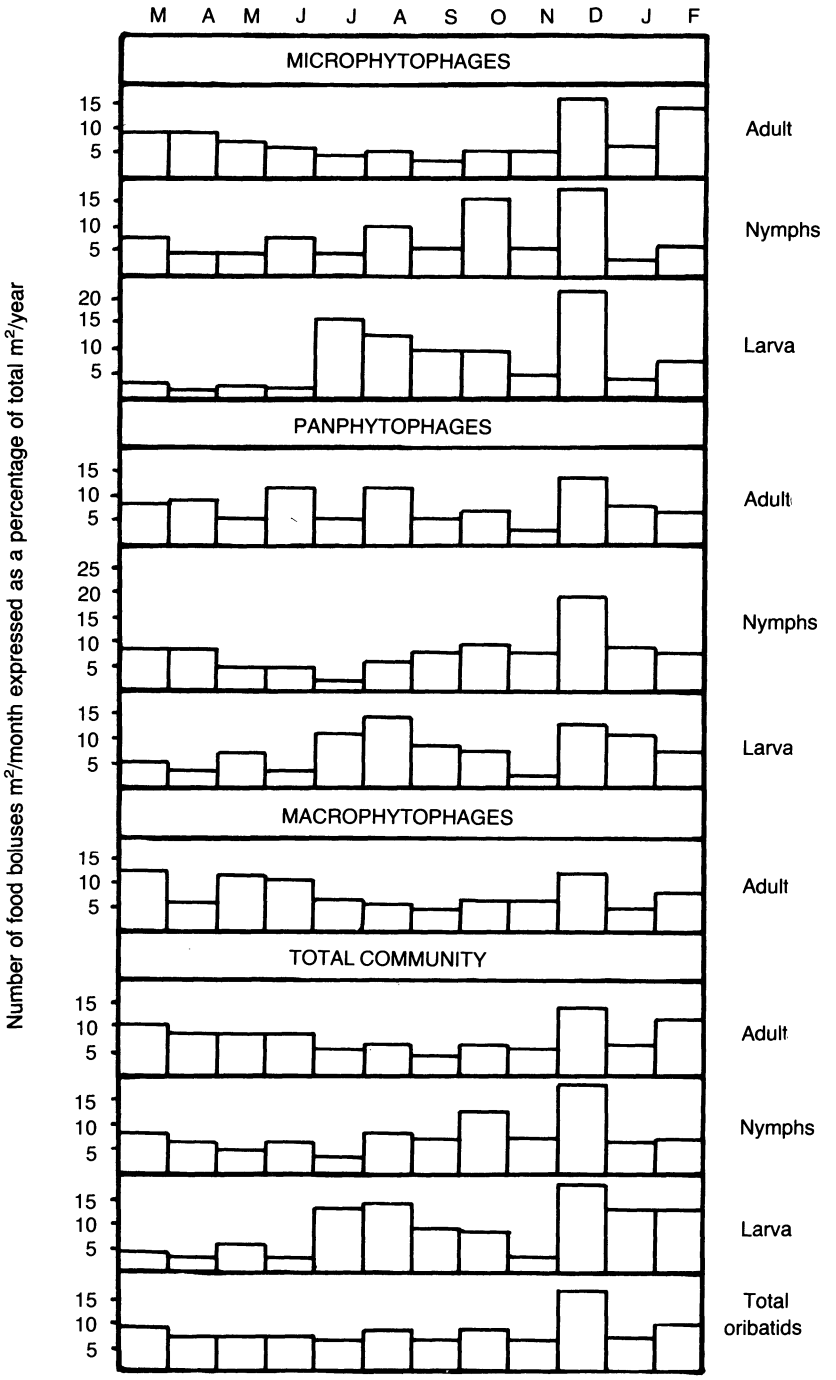

Fig. 49.1 Monthly numbers of food boluses for oribatid life stages, and also grouped according to trophic category in a Danish beech woodland soil, expressed as percentage of total number of food boluses/m^2/year in each category.

There were some seasonal changes in the number of food boluses recorded per m^2. This, by and large, followed population-density trends but could also be associated with changes in the feeding environment. Thus, the greatest monthly bolus density recorded occurred in December (Fig. 49.1), at the time of the greatest litter input, and one month after the highest recorded rainfall. These two events undoubtedly improved resource availability for all feeding groups. The literature is unclear about seasonal patterns of food ingestion by mites. Some authorities (Anderson, 1975; Schatz, 1979) could find no clear seasonal trends whereas others (Witkamp, 1960; Murphy and Jalil, 1964; Mitchell and Parkinson, 1976; Luxton 1984) have reported them. Any patterns detected may vary among taxa and developmental stages. Figure 49.1 clearly shows that the contribution made by larval feeding increased in the summer months, a trend reported for *Tectocepheus* spp. by Murphy and Jalil (1964). In the beech woodland, larval densities were high at this time (Luxton, 1981a), and the larvae may have hatched or may have been stimulated to feed by the unseasonally elevated rainfall in that month.

A large majority of the fed individuals among the microphytophages is to be found in the 0–3 cm soil layer (Table 49.3). This correlates with the known depth distribution of the microbial flora of this woodland, most of which is located in the soil (Holm and Jensen, 1972, 1980). Among the panphytophages, most of the fed adults are to be found in the litter, whereas most of the juveniles in this category are in the 0–3 cm depth. This suggests not only that panphytophages begin life mainly as microbivores, and include more plant litter in their diets when adult, but also that they change the feeding location in the profile during development. Only the adults of macrophytophages were monitored during sampling, and most of the fed individuals were found in the 0–3 cm soil depth.

Individual species amongst all these trophic groups, however, may display idiosyncratic depth-distribution patterns with respect to food intake. For example, among the macrophytophages, *Steganacarus magnus* has most of its fed population in the litter. Among the panphytophage adults, *Nothrus silvestris* and *Ceratozetes gracilis* have most of their fed populations in the 0–3 cm soil layer suggesting that, unlike most of the panphytophagous species recorded, they remain principally microbivorous throughout life. Among the microphytophages, *Damaeus clavipes* and *Belba corynopus* adults feed principally in the litter, possibly, as is the case with *Steganacarus magnus*, a partial consequence of their large size. Although most feeding by all life stages in the *Damaeus clavipes* population takes place in the litter, the majority of the juvenile *Belba corynopus* population feeds in the 0–3 cm layer. Thus, not only can there be different patterns of feeding behaviour between individual

species according to depth, there may also be differences between life stages of the same species. This may arise from the acknowledged fact that juveniles of some species feed on different food materials to their adults (Sengbusch, 1954; Wallwork, 1958; Woodring and Cook, 1962; Woodring, 1963; Luxton, 1966), which in turn effectively reduces intraspecific competition for energy and space resources (Luxton, 1972).

It is generally agreed that for most oribatids the immatures are the most important feeding stages (Riha, 1951; Woodring, 1963; Murphy and Jalil, 1964). Taking into account the relative sizes of the food boluses of adults and of juveniles (nymphal bolus sizes being estimated as half and larval, one-quarter, of those of adults), it can be deduced from Table 49.2 that during the year adult and juvenile (nymphs plus larvae) microphytophages ingest approximately equivalent amounts, although this might be misleading in view of the greater possibility of juveniles ingesting non-visible food. Panphytophagous juveniles, on the other hand, ingest twice as much as their adults. These calculations are quoted in absolute terms whereas the rate of turnover is probably of most importance. Thus, Luxton (1981c) states that immatures in this woodland are responsible for only 28% of the energy consumption of the entire oribatid community. In the same paper, the quantities of food consumed by the oribatid community of the beech woodland were calculated on a seasonal basis. It was demonstrated that: (1) consumption by adults followed a symmetrical curve with its peak in August; (2) consumption by nymphs also peaked in August but the annual curve was shifted somewhat towards the autumn; and (3) larvae consumed most during the summer with the curve slightly displaced towards the earlier part of that season. It should be emphasized that these results were derived from a laboratory-calculated expression linking consumption with temperature, and that the pitfalls inherent in extrapolating to the field were discussed. Direct measurement of food intake from field-caught specimens (Fig. 49.1) reveals some differences from above conclusions. Thus, adult consumption diminishes in the summer months, and is elevated in the late spring and late autumn. Nymphal consumption begins to rise in mid summer and peaks during the autumn. The annual consumption by larvae shows two peaks, one in the summer and one in late autumn. In all cases, the peak month for consumption is December, coinciding with the major input of tree litter, and one month later than the highest monthly rainfall recorded. It is clear that many other aspects of the oribatid environment are as important as, or more important than, temperature as a determinant of feeding. Undoubtedly changing ambient temperature plays a critical role in initiating and controlling life-cycle progress but feeding also depends on the availability, quantity and palatability of the food, all of which may change –

sometimes erratically – during the year. Oribatids seem to be able to respond readily to seasonal renewal of acceptable food resources. Indeed, some species may co-ordinate their life cycles with seasonal food availability, and others may respond by moving up and down the soil profile (Luxton, 1982).

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The effects of ploughing and rotary cultivation on soil mites with particular reference to the Mesostigmata

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The influence of ploughing and rotary cultivation on soil mites was investigated over a period of two years. Prostigmata, Astigmata, Cryptostigmata and species of Mesostigmata are compared. The density of total Acari is, in general, higher with rotary cultivation than in the ploughed field. The difference for the Mesostigmata is significant at the 1% level. Food requirements and the special habitat needs of some genera and species are considered. Thus, mites which prefer decomposition with putrefaction, predominate in the rotary-cultivated plot, for example, *Alliphis siculus* (Oud.), *Dendrolaelaps* sp. and *Parasitus hyalinus* (Willm). Only one mite, *Arctoseius cetratus* (Sell.) occurs somewhat more frequently in the ploughed plot. This species prefers advanced decomposition without putrefaction. To compare the diversity of Mesostigmata in the two treatments, the 'Shannon-Wiener index' is used. An 'evenness' calculation measures the degree to which individual densities have an equal distribution. The two soil-cultivation methods cause changes in the species composition

The effect of ploughing and rotary cultivation on crop yield, soil structure, incorporation of organic residues and weed occurrence have been investigated by Siebeneicher (1985). Krüger (1952), Wilcke (1963) and El Titi (1984) examined the influence of different soil-cultivation methods on soil animals involved directly or indirectly in soil fertility. In 1986 and 1987, we investigated the influence on soil mites of two soil-cultivation methods – ploughing and rotary cultivation, which have been used since 1985. Mites are of particular interest to us because some species

differ in their ecological requirements (Karg, 1982). Bacterial-feeding and fungus-feeding mites, for example, have a close relationship with the activity of soil microflora (Karg, 1968). Mesostigmata feed on nematodes, other mites, springtails, enchytraeids and small insect larvae. Variation within the prey spectrum can cause changes in the occurrence of Mesostigmata (Karg, 1968, 1982). Thus, we used Mesostigmata as an indicator group for changing soil conditions (Höller, 1962; Alleinikova and Utrobina, 1975; Karg, 1968, 1982, 1986).

MATERIALS AND METHODS

The fields investigated are in the northern outskirts of Oldenburg, Lower Saxony. They have a humus sandy soil of the 'podzol brown earth' type. In 1986, the fields were cropped with maize, and in 1987 with barley. One field was ploughed to a depth of 30 cm, and another was rotary cultivated 15 cm deep. The same amounts of manure, fertilizer, herbicides and fungicides were applied to both fields.

Ten soil samples (250 cm^3/sample) per field were taken on three occasions in 1986 and four in 1987. In the first year, we used a spade to take the samples. Later a special soil sampler was constructed (after Bieri *et al.*, 1978). The mites were extracted using the 'Berlese method' and preserved in 70% ethanol. For identification the mites were macerated in lactic acid and observed on microscope slides.

POPULATION STUDIES

The results for total Acari, the major orders and selected species are shown in Fig. 50.1. Generally the mite density was greater in the rotary-cultivation treatment than in the ploughed field, and the difference is significant at the 1% level. After rotary cultivation, the mite population increased in June 1986, April 1987 and again in November 1987, even though no manure was applied in the rotary cultivation in October 1987 shortly before the latter sampling. After ploughing, the mite population increased once (June 1986) and decreased twice (April 1987 and November 1987). After the barley harvest (August 1987), the mite population decreased (September 1987) presumably because of the lack of vegetative cover thus exposing the mites to large temperature and humidity variations. After the maize harvest (October 1986), the mite population in the ploughed field increased. Whether or not the crop had a decisive role cannot be determined at present. Moreover, there is a long gap between the date of harvest and the date of sampling, and thus it is not possible to draw a firm conclusion.

In the maize crop more mites were found within than between rows.

The root zone has greater pore volume, more organic material and the microclimate is more favourable for mites. Moreover, fertilizer placement within rows plays a crucial role.

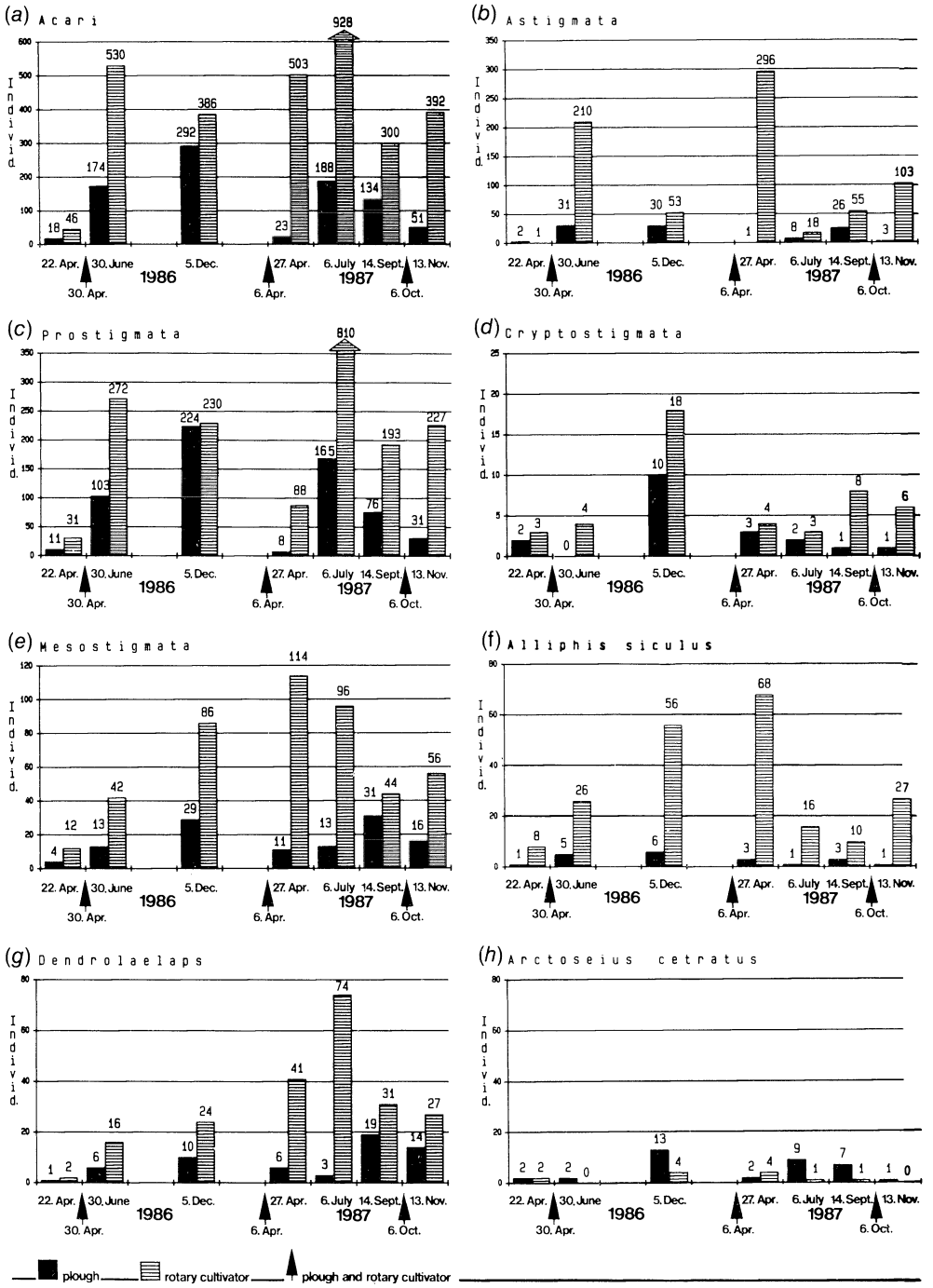
For statistical analysis, we chose the *U* test of Wilcoxon, Mann and Whitney (Sachs, 1974) for comparing two independent samples. Taking the Astigmata (Fig. 50.1b) first, the number of individuals in the rotary-cultivated plot is greater than in the ploughed one at the 5% level. In the former treatment, there are conspicuous fluctuations in the densities of this order within each year. The large increases are positively correlated with the occurrence of the Acaridae, which are indicative of putrefaction processes (Höller-Land, 1958; Karg, 1967). Acaridae often occur in cultivated soils (Hermosilla *et al.*, 1978). With rotary cultivation we also found more individuals of Anoetidae than in the ploughed field. These mites ingest putrifying liquids which contain numerous micro-organisms (Scheucher, 1957 in Karg, 1963).

The Prostigmata populations (Fig. 50.1c) are dominated by the families Tarsonemidae and Pygmephoridae. The number of tarsonemid individuals is significantly greater at the 10% level in rotary cultivation compared with ploughing. Tarsonemidae feed on plant liquids (Höller-Land, 1958), and seem to prefer anaerobic environments (Hermosilla, *et al.*, 1978). Together with the Acaridae and Anoetidae, they are indicative of putrefaction processes. The Pygmephoridae show no significant differences. In general, light, warm soils have more Prostigmata than heavy, moist and cold soils (Tischler, 1980); this sandy soil belongs to the former group.

The numbers of Cryptostigmata (Fig. 50.1d) in the two treatments do not differ greatly but the difference is, nevertheless, statistically significant at the 2.5% level. These were, for the most part, small species such as *Oppiella nova* (Oud.) and species of the family Brachychthoniidae.

The difference in abundance of the Mesostigmata in the two treatments is significant at the 1% level. The generally greater number of individuals with rotary cultivation (Fig. 50.1e) can be attributed to the greater prey spectrum for these predatory mites. Soil tilling without inversion as in ploughing is less disturbing for soil organisms (El Titi, 1984). El Titi compared rotary cultivation and ploughing – both to the same depth – and found that the Mesostigmata differed significantly with greater densities in the rotary-cultivated treatment. Some Mesostigmata genera and species are rather specific in their food requirements while some occur mainly in particular habitats.

Alliphis siculus (Oud.) (Fig. 50.1f) was present in both treatments. More individuals occurred in the rotary-cultivated plot, and the difference was significant at the 0.1% level. The highest number of individuals was recorded in the sampling on 27 April 1987. Shortly before


(a) Acari
(b) Astigmata
(c) Prostigmata
(d) Cryptostigmata
(e) Mesostigmata
(f) Alliphis siculus
(g) Dendrolaelaps
(h) Arctoseius cetratus
Individ.
22. Apr.
30. Apr.
30. June
1986
5. Dec.
27. Apr.
6. Apr.
6. July
14. Sept.
1987
13. Nov.
6. Oct.
plough
rotary cultivator
plough and rotary cultivator

this date, the field had been rotary cultivated and manured. *Alliphis siculus* seems to react positively to both. This predatory mite feeds exclusively on nematodes (Karg, 1962, 1965, 1971, 1983), and occurs mainly in habitats where decomposition with putrefaction predominates. Species of the genera, *Parasitus and Cheiroseius*, prefer the same substrate and the same prey (Karg, 1982, 1983). In this case also, more *Parasitus* individuals occurred in the rotary-cultivated plot. We only found two individuals, for example, *P. hyalinus* (Willm.) among others of this genus, of *Cheiroseius*, and these occurred in the rotary-cultivated plot. Mrs Arens, who also investigated these fields, writes in her 'Diplomarbeit' that there were more nematodes with rotary cultivation but there were many more parasitic nematodes in the ploughed site. It seems that the increase of *A. siculus* is correlated with an increase of nematodes in the rotary-cultivated field.

In the rotary-cultivated plot, the genus *Dendrolaelaps* (Fig. 50.1*g*) had a peak density in July, 1987. Perhaps it successfully competed with *A. siculus* as its increase coincided with a decrease in the latter species. The densities of *Dendrolaelaps* differed in the two fields, and this difference is statistically significant at the 2.5% level.

Very few *Arctoseius cetratus* (Sell.) (Fig. 50.1*h*) were found in the rotary-cultivated plot. In the ploughed treatment, this species occurred a little more frequently in the winter of 1986 and again in the summer of 1987. The *U* test gives an error probability of 5%. It feeds on nematodes, dipterous larvae (Karg, 1983) and young cryptostigmatic mites (Karg, 1965). The genera, *Arctoseius* and *Dendrolaelaps*, indicate advanced decomposition without putrefaction. They also prefer sandy soil. *Dendrolaelaps* feeds on nematodes (Karg, 1983) and springtails (Karg, 1963). However, according to Karg (1982), there may be a degree of indifference to the type of decomposition with the result that some species of this genus also live in habitats where decomposition with putrefaction predominates. When the soil samples from the two treatments were compared, two-thirds of those from the rotary-cultivated field contained more *Dendrolaelaps* individuals. Species of *Amblyseius* were rarely found in the soil of the maize crop, and then only in the rotary-cultivated treatment. One individual each of *Macrocheles* sp. and *Pergamasus runcatellus* Berl. was found in the final sampling of the rotary-cultivated field. One species of Uropodina occurred in this treatment in September 1987.

Among the Mesostigmata, there are 3–4 genera indicative of a habitat where decomposition with putrefaction predominates. These mites

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Fig. 50.1 Comparison of mean number of individuals/1000 cm^3 of Acari (*a*) and acarine taxa (*b–h*) to a depth of 15 cm in ploughed and rotary-cultivated arable soil cropped with maize (1986) and summer barley (1987).

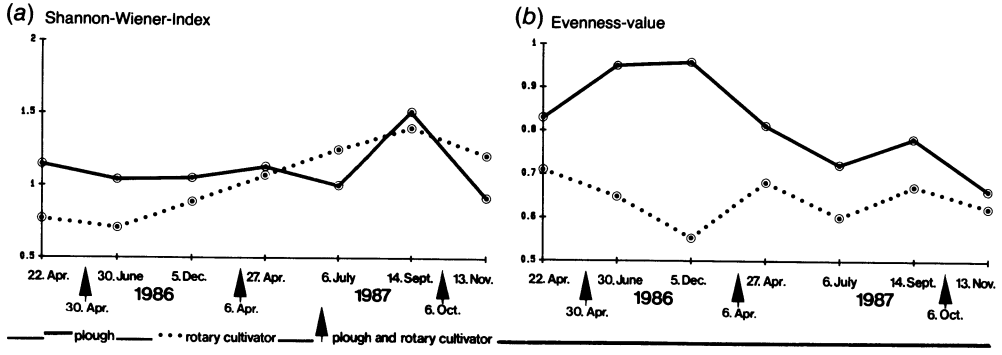

Fig. 50.2 Comparison of Shannon-Wiener index (*a*) and eveness value (*b*) for soil Acari in ploughed and rotary-cultivated soil to a depth of 15 cm cropped with maize (1986) and summer barley (1987).

occur more frequently with rotary cultivation. It is possible that there was local oxygen deficiency due to greater metabolism by micro-organisms, and there was only partial decomposition as a result. Poor soil aeration is unlikely because of the nature of the soil. Bacterial-feeding nematodes and dipterous larvae, likewise, are characteristic of putrefaction processes, and these are the prey of some Mesostigmata. In 1986, we found more dipterous larvae in the ploughed plot but the difference was not significant whereas in 1987 the situation was reversed with a decrease in the ploughed land and an increase with rotary cultivation. Karg (1962) found that in arable soils, anaerobic and aerobic conditions appeared to alternate. It is possible that with rotary cultivation the superficial mixing of manure, fertilizer and crop residues yield more favourable living conditions in the uppermost 15 cm of this plot. As a result, soil animals and micro-organisms increased, and this could have led to local oxygen deficiency.

The distribution of soil organisms at a depth of 15–30 cm has still to be studied because during ploughing the soil is inverted and, as a result, some soil organisms are buried and others are killed. In addition, the soil is also fragmented, and it is possible that there may be suitable living conditions for mites in the 15–30 cm layer. Krüger (1952) reported that important edaphic fauna occurred, as a rule, in large numbers at a depth of 12–23 cm. Edwards and Lofty (1969) reported that the greatest number of micro-arthropods were obtained within six months of ploughing. Höller (1962) writes that regular ploughing results in a deeper and more uniform distribution of soil animals, although some animals are destroyed by the inversion of the soil. Regular ploughing can also cause the formation of a hard pan or compaction zone which soil animals avoid.

DIVERSITY AND EVENNESS MEASUREMENTS

Using the 'Shannon-Wiener index' (Schaefer and Tischler, 1983) (or Shannon-Weaver index), we can describe the diversity of the Mesostigmata communities (Fig. 50.2a). With this index, the relationship between the number of species and number of individuals per species can be delineated. A high index value indicates a large number of species and, at the same time, an equal distribution of individual densities. The Shannon-Wiener index was calculated for each plot on each sampling occasion. Between April 1986 and April 1987, the index for the ploughed plot is generally higher than that for rotary cultivation. The index values for the latter, however, rise steadily, and in July and November 1987 they even exceed the values for the ploughed field.

In both situations, the number of species is small, and thus for the Shannon-Wiener index, the equal distribution of individual densities

plays a decisive role. An 'evenness' calculation gives a higher value for the ploughed field on every sampling occasion (Fig. 50.2b) but the difference between treatments decreases with time. The ploughed plot had fewer species but the density fluctuations within species are less. That is the reason why the index is frequently greater in the ploughed plot. In the course of time, the index for the rotary-cultivated plot should rise, and we think that a slow stabilization of the Mesostigmata will involve an equalizing of individual densities.

Finally, we can say that the rotary-cultivated plot had more soil animals than the ploughed one. Reduced physical working of the soil had a beneficial effect on the Mesostigmata. It is also likely that the prey spectrum is greater. This study shows that rotary cultivation favours those mite groups indicative of decomposition with putrefaction. Only one species, *A. cetratus*, indicates advanced decomposition without putrefaction. We think that the soil organisms of the rotary-cultivated plot are still in the establishment stage, because the introduction of this method of cultivation only took place three years ago. The previous tillage method can still show effects three years later (Höller, 1962; Naglitsch and Steinbrenner, 1963 in Butcher *et al.*, 1971).

CONCLUSION

The crop results show that in 1986, the maize yield was greater with ploughing than with rotary cultivation whereas in the year before, the result was the other way round. In 1987, the summer barley yields showed no significant difference. These results do not establish definite differences in crop yield dependent on cultivation method. It is probable that still more time is needed for changes in soil organisms to be established, and consequently it is necessary to continue sampling for a further period to determine the nature of such changes.

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The influence of soil cultivation methods on the edaphic fauna, and especially the Gamasina (Mesostigmata), in two southern German vineyards with different cultural treatments

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The edaphic fauna was investigated in two adjoining, 12-year-old vineyards to compare the effects of two different cultural methods. The site, a parabrown soil on loess, is situated in south-west Germany in the area of the 'Kaiserstuhl' at 315 m above sea level. The cultural treatments differed in each vineyard with conventional cultural practices (Kon) in one and, in the second, an alternative method (Alt). The first involved the use of mineral fertilizers and the application of synthetic organic fungicides, insecticides and herbicides applied within the rows. The alternative method consisted of the use of composted manure as soil fertilizer, and the application of copper and plant extracts as fungicides and *Bacillus thuringiensis* as the insecticide. No herbicide was applied to the soil within the vine rows. With both methods, the vegetation, consisting of a diverse flora, was allowed to grow in the inter-row areas and a green mulch was applied.

As a result of low rainfall in the summer of 1985, every second inter-row area of the two vineyards was mechanically cultivated on one occasion using a milled cutter in the Kon treatment, and a grubber in the Alt treatment. To determine the effect of soil cultivation on the Collembola, Actinedida, Oribatida and Gamasina, soil samples were taken at

monthly intervals from adjacent tilled and untilled inter-row areas of the Kon and Alt plots. Five soil cores (*d* 5.8 cm and 30 cm deep) were taken from each plot from August to October, and commencing three weeks after the cultivation had been carried out. The cores were subdivided into 5-cm layers, and the fauna thermodynamically extracted in Berlese-Tullgren funnels.

Soil tillage had a marked effect on all soil-faunal groups. In contrast to the Collembola, the Actinedida and Oribatida were more abundant in the cultivated soil in both vineyards. This was especially the case with the Alt treatment in which the increase of the latter two groups was maintained throughout the sampling period. In the Kon plot, the initial increase was followed by a marked decrease in the October sampling.

The Gamasina increased in abundance throughout the sampling period in the Alt treatment with cultivation but there was no increase in the Kon plot. The reactions of the Gamasina to soil tillage could be explained on the basis of zoocoenological properties especially species composition and species densities, which were about 54 and 55% higher in the Alt vineyard. Factors such as different pesticide applications, mineral or organic fertilizers and soil-cultivation methods can cause a marked differentiation in coenosis between homogeneous experimental sites. The species present, and their autecological properties, determine the reaction of the coenosis of the soil fauna. This has been shown for the gamasine species, *Rhodacarellus silesiacus* Willmann occurring in both treatments, and *Dendrolaelaps strenzkei* Hirschmann which was only present in the Alt vineyard.

In this way, soil tillage can result in contradictory reactions of a whole group of the soil fauna. This can only be understood by studying the structure and dynamics of the populations at species level. A better knowledge of the autecology and synecology of the species of the euedaphon, the predatory mites, for example, which are representatives of the ends of different food chains, should make it possible to obtain meaningful results about the anthropogenic impacts on the soil ecosystem.

ACKNOWLEDGEMENT

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The density of Tarsonemida in cropped arable soil in relation to fertilizer and crop-protection treatments

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There have been only a few detailed publications dealing with the Tarsonemida of Germany (Karafiat, 1959; Krczal, 1959; Rack, 1964a,b, 1967, 1972, 1974, among others). There has been no detailed investigation of this group in arable soil at generic and specific level. In the present investigation, each of three crops consisting of winter wheat, winter barley and sugar beet with four application levels (10, 11, 12, 13) of fertilizer, herbicide, fungicide, insecticide and growth regulators (Table 52.1) were sampled on six occasions (*c.* 4-week intervals) from 1 April to 1 September 1987. On each occasion, 14 sampling units of soil were taken to a depth of 10 cm from each treatment, and extracted in a high-gradient apparatus.

There was a considerable range of densities (<100–27 000 individuals/m^2) among the species of Scutacaridae, Pygmephoridae, Pyemotidae and Tarsonemidae recorded from the experimental plots. There were six species of Scutacaridae present (Fig. 52.1a). Winter wheat had the fewest species of this family, and densities were very low. Species numbers and their densities were greater in winter barley, and there was a further increase in sugar beet (Fig. 52.1a). *Scutacarus acarorum* (Goeze) had the highest density with an overall mean number of *c.* 1000 individuals/m^2 in treatments 11 and 12. With all crops, very few scutacarids were found in treatment 13, which represented the highest levels of fertilizer, herbicide and pesticide applications.

The overall mean numbers of four other species are shown in Fig. 52.1b. Of the three crops, winter barley tended to have the highest densities. Both *Bakerdania blumentritti* (Krczal) and *B. quadrata* (Ewing) were most numerous in barley with 20 000 and 10 000 individuals/m^2 respectively. In wheat and barley, the density of *B. blumentritti* increased with level of fertilizer, herbicide and pesticide application (Fig. 52.1), the highest means occurring in treatment 13. *Tarsonemus* sp. was most

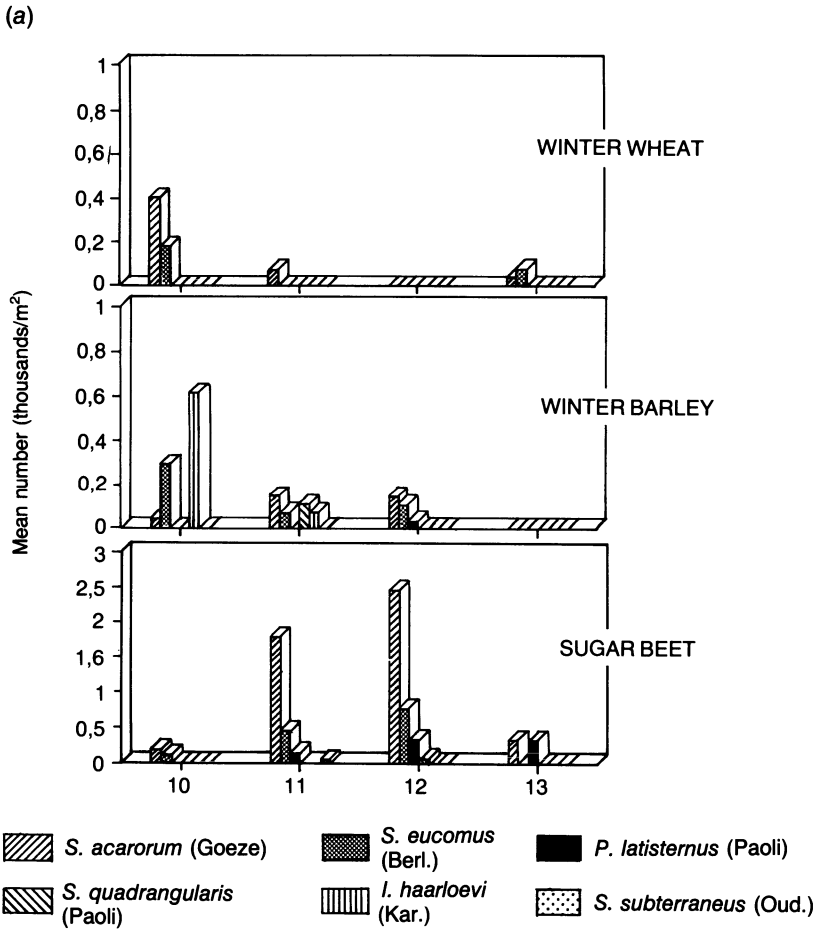

Fig. 52.1 Overall mean number (thousands/m^2) of (*a*) six species of Scutacaridae and (*b*) 4 other species of Tarsonemida from soil (0–10 cm deep) of wheat, barley and sugar-beet plots with 4 levels of fertilizer and crop-protection treatments (10–13). The experimental plots were sampled on six occasions (April to September 1987).

(*b*)

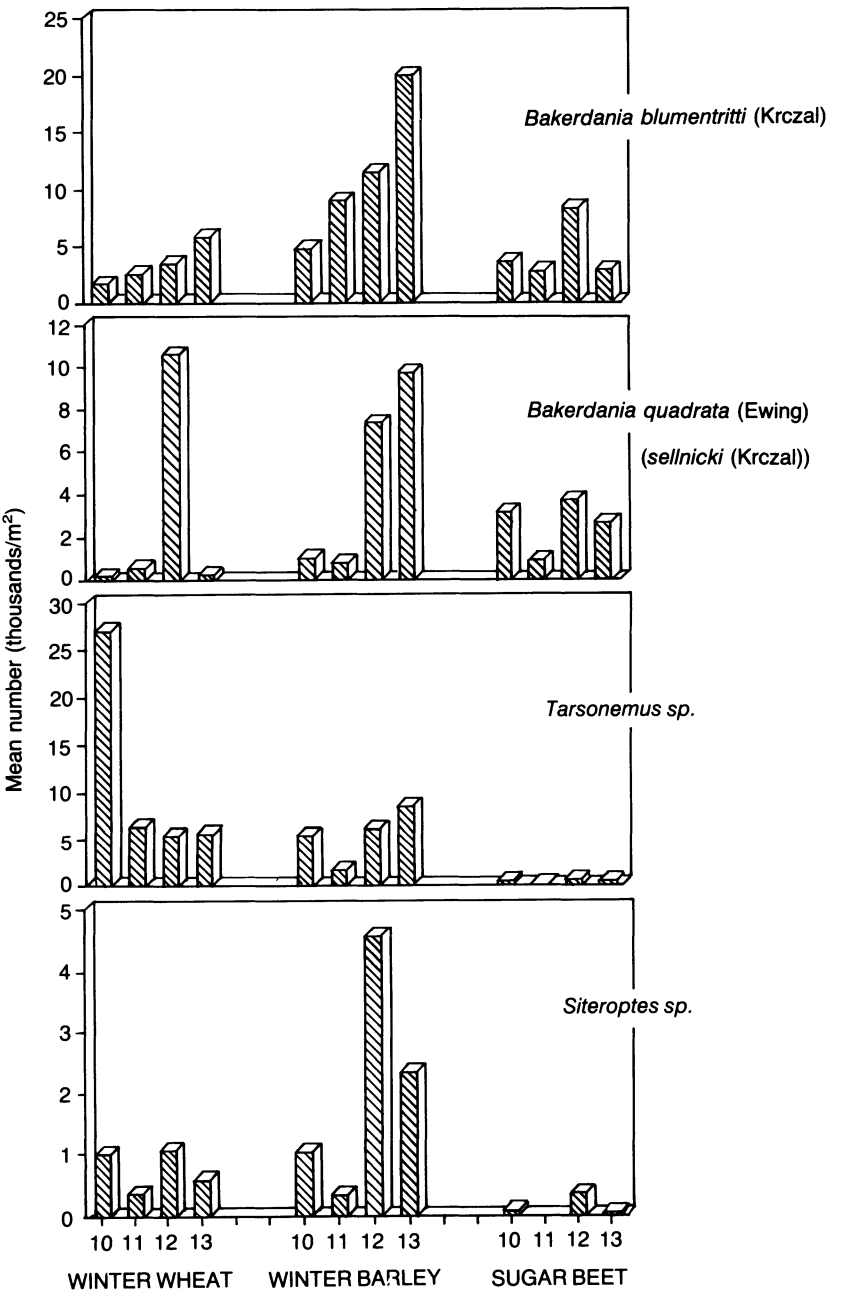
Mean number (thousands/m²)
Bakerdania blumentritti (Krczal)
Bakerdania quadrata (Ewing)
(sellnicki (Krczal))
Tarsonemus sp.
Siteroptes sp.
10 11 12 13
10 11 12 13
10 11 12 13
WINTER WHEAT
WINTER BARLEY
SUGAR BEET

Table 52.1 Fertilizer (urea, calcium ammonium nitrate), herbicide, pesticide and growth regulator treatments (10–13) applied to plots of winter wheat, winter barley and sugar beet sampled for soil Tarsonemida

	Winter wheat				*Winter barley*				*Sugar beet*			
Treatment	*10*	*11*	*12*	*13*	*10*	*11*	*12*	*13*	*10*	*11*	*12*	*13*
Nitrogen fertilizing (kg/ha)	41.0	178.5	227.0	254.5	41.0	128.5	169.0	197.5	115.0	155.0	165.0	175.0
Herbicides (kg or l/ha)	—	4.0	4.0	8.5	—	4.0	6.0	9.0	—	9.5	9.5	15.5
Fungicides (kg or l/ha)	—	2.8	6.1	8.3	—	—	0.5	2.5	—	—	—	—
Insecticides (kg or l/ha)	—	—	—	0.2	—	—	—	—	—	0.5	0.5	1.0
Growth regulators (l/ha)	—	1.0	2.0	2.5	—	—	1.3	2.0	—	—	—	—

numerous in winter wheat especially in treatment 10, and *Siteroptes* sp. in barley. Unlike *B. blumentritti*, the density of the latter species fluctuated in treatments 10–13.

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Soil mites and acidification: a comparative study of four forest stands near Heidelberg

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Forests near Heidelberg suffer considerably from acid-rain precipitation since they are growing on soils (based on red sandstone) with low buffer capacity, and acidities of around pH 3 are commonly encountered. For several years artificial liming has been carried out by the local forest administration at regular intervals as a means to lower acidification rates in these soils. The method used is to blow the lime into the forest at a rate of 28 decitonne lime/ha. This would appear to be a rather sudden and severe interference with the soil subsystem, which has probably become adapted to increasing acidity over many years. For this reason, the present field study was initiated to investigate whether the soil-mite fauna is influenced by the liming treatment.

Four forest stands were compared over one year (1985–1986). Three stands (nos 1–3) were located on red sandstone two of which were treated with lime – no. 1 in 1984 and no. 2 in 1985. A fourth stand (no. 4; on loess/shell-lime) served as a second control site. A total of 800 samples each 250 cm^3 were obtained in 25 samplings at fortnightly intervals. On each occasion eight samples were collected from each stand: four beneath a spruce tree (F; *Picea abies* Karst.) and four beneath a beech tree (B; *Fagus sylvatica* L.) making a total of 32 samples per

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occasion. The Gamasida and Oribatida were extracted using Berlese–Tullgren funnels. So far all the samples have been examined for Gamasida but for the Oribatida, only 52 samples over 13 occasions (monthly intervals) – all from spruce – have been enumerated.

The preliminary results suggest the following conclusions:

1. With respect to number of species and abundance of individuals (Fig. 53.1), the limed stands (1 and 2) – when compared with the control stands (3 and 4) – are within the normal range. With respect to dominance patterns, sites F3 and B3 resemble the situation prevalent in extreme habitats, that is, the presence of a few very abundant species. On the other hand, in sites F4 and B4 there was a greater diversity with population densities less extreme.
2. In general, there is no adverse influence visible in respect of the gamasid and oribatid fauna due to liming. Indeed, the dominance patterns even suggest a 'positive' effect towards a greater homogeneity. This has resulted from a decline in species which are markedly dominant in the control plots, F3 and B3.
3. It appears that the tree-species/litter composition exerts an influence. Often the spruce sites exhibit the more extreme values.
4. It would appear that there are species which react positively and others which react negatively to the addition of lime. Among the first

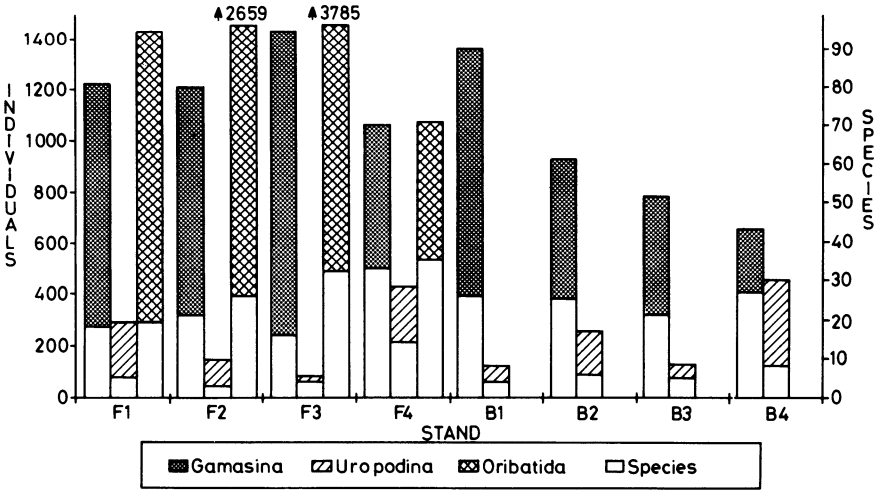

Fig. 53.1 Total number of species and individuals obtained from the soil of limed (1 and 2) and unlimed (3 and 4) stands containing spruce (F) and beech (B) near Heidelberg, Germany, sampled over 12 months (1985–86). Oribatida (from spruce only) sampled at monthly and other taxa at fortnightly intervals.

group are the leaf-litter inhabiting gamasine mites, *Veigaia nemorensis* (C.L. Koch) and *Pergamasus lapponicus* Trägårdh, whereas the density of the deep soil inhabitant, *Rhodacarus haarlovi* Shcherbak, was reduced. Further, it is probable that the Uropodina were favoured by the treatment in contrast to the Oribatida which seemed to decline slowly. Gamasina increased in species numbers. Thus a qualitative alteration in the composition of the soil-mite fauna induced by liming is recognizable.

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Reactions of mite populations to the influence of environmental chemicals in a beech-wood floor

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The acarine community, other than the Oribatida, of a modern beech-wood soil on the northern foothills of the Black Forest was investigated over a 5-year period from 1977 to 1982 by means of square samples. In addition, the succession of these mites during leaf-litter decomposition was studied from 1981 using litter bags. In 1981 and 1982, some sample plots were treated with pentachlorphenol (PCP) and 2,4,5-trichlorphenoxyacetic acid (2,4,5-T) at 1 and 5 g/m^2 at 2-month intervals to determine the impact of these chemicals on the forest-floor ecosystem.

The mean monthly densities of Mesostigmata, Trombidiformes and Astigmata were, respectively, 13202, 10549 and 10739 individuals/m^2. Numbers peaked in the spring and again in the late autumn during leaf-litter fall. The mean monthly biomass of Acari ws 731 mg fresh weight/m^2, and the energy release in metabolism was calculated to amount to 43.8 kJ/m^2/year. Knowledge of the feeding habits of the 103 species present, and their ecophysiological parameters led to the calculation of a tentative energy budget for the whole community. This suggests that the sapro-mycophagous mites respire only 0.2% of the energy represented by the annual litter input to the soil, and it is concluded that their ecological role is quantitatively small, and probably entails mediation of the activities of the soil microbes.

The results indicated that acarine populations, especially of the Uropodina *s. lat.* and the Acaridiae, are only slightly affected by the application of PCP and 2,4,5-T in contrast to those of the Enchytraeidae and

most nematode species. No direct effects of these chemicals have been found, and parallel measurements of soil microfloral activity showed extreme reduction for only short periods of time. Increases of up to more than 200% of the densities in the control plots, occurring after the end of herbicide treatment, clearly demonstrate the reproductive potential especially of the Acaridiae.

In general, the population sizes of the gamasid and prostigmatic species, most of which are carnivorous, are strongly correlated with those of the nematodes, enchytraeids and dipteran larvae. These latter groups are rapidly reduced to less than 10% by PCP and 2,4,5-T applications, and such reductions are related to the concentration level of the herbicide application (PCP (5) > PCP(1) = 2,4,5-T (5) > 2,4,5-T (1)). They recover rapidly when the chemical concentration is reduced after the end of herbicide treatment. Only a few species such as *Leioseius bicolor* are able to tolerate high PCP concentrations. This is likely to be due to the high dominance of the nematode, *Filenchus resistens* Zell, which is the only species resistant to PCP, and is assumed to be the preferred prey of *L. bicolor*.

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Population studies on the house-dust mite, Euroglyphus maynei *(Cooreman 1950) (Pyroglyphidae)*

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The house-dust mite, *Euroglyphus maynei* (Coor.), produces potent allergens but is little studied because it is difficult to grow *in vitro*. In the absence of viable cultures, information for this study was gained exclusively from analysis of dust samples, and comparison with *Dematophagoides pteronyssinus* (Trt). Distribution, frequency and abundance of *E. maynei* in mattresses, pillows and bedroom carpets in homes in Glasgow, UK were determined. Homes were assessed visually for signs of dampness and graded 'damp' or 'dry'. The focus of infestation for *E. maynei* was the bed, especially in damp homes; it was rarely found in carpets. It was found that *E. maynei* was rarely present in large numbers without comparable numbers of *D. pteronyssinus*. In dry homes, *D. pteronyssinus* was often the only species present in samples. These data suggest that *E. maynei* has a higher critical equilibrium activity than *D. pteronyssinus* and is confined to damper habitats.

The ratio of adult female body volume to egg volume of *E. maynei* was far lower than for *D. pteronyssinus*, which may indicate that egg production, and hence population increase of *E. maynei*, is lower compared with *D. pteronyssinus*. A low rate of increase combined with a need for high humidity, conducive to growth of fungal contaminants, helps explain the difficulty of establishing stable, productive, *in vitro* cultures of *E. maynei*

INTRODUCTION

Almost all studies on the biology of house-dust mites and their allergens have been conducted on species of the genus *Dermatophagoides*, in particular *D. pteronyssinus* (Trt) and *D. farinae* Hughes. Yet another species, *Euroglyphus maynei* (Coor.) is a common inhabitant of house dust, especially in temperate latitudes, and has been shown to be highly allergenic (Voorhorst *et al.*, 1969; Mumcouglu, 1976; Nannelli *et al.*, 1983). In dwellings where it is present in large numbers, *E. maynei* may make a considerable contribution to the mite-derived allergen pool.

Very little is known of the immunological and physico-chemical properties of the allergens of *E. maynei*. To date, studies on cross-reactivity with those of *Dermatophagoides* spp. have been carried out using crude extracts only, and it is not known whether *E. maynei* possesses any unique allergens. The consequences of this are important. Existing commercial preparations for immunotherapy and diagnostics are based on well-characterized major allergens harvested from *D. pteronyssinus* or *D. farinae*. There is potential for considerable mis-diagnosis and/or inappropriate immunotherapy for house-dust mite-allergic patients who may be sensitized to species-specific allergens of *E. maynei*, if such allergens exist.

The lack of information on the allergens and biology of *E. maynei* is due to the considerable difficulties of maintaining productive cultures *in vitro* on a long-term basis. In the absence of cultures, data on the biology of the species used in this study were derived solely from analysis of house-dust samples. The aim was to compare distribution, abundance and frequency of occurrence of *E. maynei* with *D. pteronyssinus* as well as allometry of eggs and gravid females in order to help explain why *E. maynei* is so difficult to maintain in culture.

METHODS

House-dust samples were taken from three locations in bedrooms in the homes of patients with atopic asthma or dermatitis, and those of normal volunteers, in Greater Glasgow. Mattresses (n = 233), pillows (n = 64) and carpets (n = 109) were sampled between January and April, 1984 and December, 1984 and April, 1985. There were no significant differences in mite-species diversity or numbers between the two sampling periods in ten reference homes used for long-term monitoring (data not shown), hence the data from samples from 1984 and 1984–1985 were not analysed separately.

Homes were assessed visually for signs of damp and graded 'damp' or

'dry'. These signs included mould growth, peeling or water-stained wallpaper, heavy condensation on bedroom windows, moist plasterwork and other surfaces, and signs of direct water penetration. Methods of dust sampling and mite extraction have been described previously (Colloff, 1987). In brief, dust was collected by means of a portable vacuum pump using a zigzag sweeping pattern, covering an area of 0.25 m^2 in 1 min. Mites were extracted manually following the suspension and clearing of dust in warm lactic acid and lignin pink. Clearing time and temperature were kept to a minimum, and swelling of the mites was found to be negligible. The mites were washed in distilled water and mounted in gum chloral on microscope slides using a mass-transfer technique (Colloff, 1989). Coverslips were raised to prevent excessive distortion of the specimens. The mites were identified and classified as 'damaged' or 'intact' to provide an indication of the numbers of live and dead mites at the time of sampling.

Forty intact gravid females of *E. maynei* and 40 *D. pteronyssinus*, each containing a single intact egg, were selected, and the lengths and maximum breadths of females and eggs were measured. A crude estimate of volume was calculated using the formula $(d^3/6) + \pi r^2 h$ (where d is the diameter, r, the radius and h, the height) which assumes both egg and adult approximate in shape to cylinders with hemispherical ends. The ratio of gravid-female volume to egg volume was also calculated.

Chi-square tests were used to compare frequency of occurrence between the two species in different habitats. Unpaired t tests were used to compare raw data of gravid female to egg volume ratio and square-root transformed data of relative abundance.

RESULTS

Distribution and abundance

Percentage frequency of intact *E. maynei* was nearly equal in mattresses and pillows, and lowest in carpets (Table 55.1), *Euroglyphus maynei* was numerically dominant to *D. pteronyssinus* in only 8% of beds, 6% of pillows and 1% of carpets. It was not found in any samples without some intact *D. pteronyssinus* also being present. Indeed, in 60% of the samples where ten or more *E. maynei* were present, equal or greater numbers of *D. pteronyssinus* were also present.

Intact *D. pteronyssinus* were almost equally as frequent in mattresses, pillows and carpets and had a significantly higher frequency than *E. maynei* ($P < 0.001$ in each case). *D. pteronyssinus* was present without *E. maynei* in over 70% of the samples.

Table 55.1 Distribution, frequency and numerical dominance of *Euroglyphus maynei* and *Dermatophagoides pteronyssinus* in dust from homes in Glasgow, UK (sample nos: mattresses, 233, pillows, 64, carpets, 109 of which 167, 48 and 62, respectively, had intact mites)

	Samples					
	With mites		*with intact mites*		*Numerical dominance* (intact mites)*	
	No.	%	*No.*	%	*No.*	%
Mattresses						
E. maynei	89	38.2	58	24.9	18	7.7
D. pteronyssinus	233	100.0	169	72.5	147	63.1
Pillows						
E. maynei	25	39.1	16	25.0	4	6.3
D. pteronyssinus	63	98.4	46	71.9	41	65.6
Carpets						
E. maynei	20	18.4	5	4.6	1	0.9
D. pteronyssinus	109	100.0	63	57.8	62	56.9

**E. maynei* and *D. pteronyssinus* numerically co-dominant in 4 samples from mattresses (1.7%) and 1 sample from pillows (1.4%).

Table 55.2 Distribution and frequency of intact *Euroglyphus maynei* and *Dermatophagoides pteronyssinus* in dust from damp and dry homes in Glasgow, UK (sample nos: mattresses, 123, pillows, 41, carpets, 55 from damp homes and 110, 23 and 54, respectively, from dry homes)

	Samples			
	Damp homes		*Dry homes*	
	No.	%	*No.*	%
Mattresses				
E. maynei	54	43.9	4	3.6
D. pteronyssinus	109	88.6	60	54.6
Pillows				
E. maynei	16	39.0	—	—
D. pteronyssinus	28	68.3	18	78.3
Carpets				
E. maynei	5	9.1	—	—
D. pteronyssinus	47	85.5	16	29.6

Table 55.3 The abundance (mites/0.25 m^2/min expressed as geometric mean numbers (± 95% confidence intervals) of intact mites of *Euroglyphus maynei* and *Dermatophagoides pteronyssinus* in samples of dust from damp and dry homes in Glasgow, UK (for sample numbers see Table 55.2)

	Damp homes	*Dry homes*	*All homes*
Mattresses			
E. maynei	9.4 + 128.3 − 8.7	2.5 + 8.5 − 1.9	8.6 + 118.9 − 8.0
D. pteronyssinus	10.03 + 104.8 − 9.1	7.0 + 214.3 − 6.8	8.9 + 143.6 − 8.3
Pillows			
E. maynei	5.2 + 41.1 − 4.6	−	5.2 + 41.1 − 4.6
D. pteronyssinus	5.2 + 24.6 − 4.3	4.0 + 32.6 − 3.5	4.6 + 28.5 − 4.0
Carpets			
E. maynei	1.4 + 5.6 − 0.6	−	1.4 + 5.6 − 0.6
D. pteronyssinus	5.4 + 59.8 − 4.9	3.4 + 29.7 − 3.0	4.8 + 55.9 − 4.4

Table 55.2 shows that intact *E. maynei* occurred far more frequently in samples from homes graded as damp than those graded as dry (34% and 2% respectively). In dry homes it was absent from pillows and carpets. The frequency of *D. pteronyssinus* was lower in mattresses and carpets but slightly higher in pillows in dry homes than damp ones. In all comparisons of the two categories of homes, *D. pteronyssinus* had a significantly higher frequency than *E. maynei* except for pillows in damp homes where there was no significant difference.

The abundance, expressed as geometric mean number of intact mites/ 0.25 m^2 min, is shown in Table 55.3. *Euroglyphus maynei* was most abundant in mattresses (8.6 mites) then pillows (5.2 mites) and least abundant in carpets (1.4 mites). *Dermatophagoides pteronyssinus* was also most abundant in mattresses (8.9 mites). In pillows and carpets it was almost equally abundant (4.6 and 4.8 mites respectively). There were no statistically significant differences in abundance between or within the two species in different homes or habitats.

Allometry of eggs and gravid females

The dimensions of females and the eggs they contained are shown in Fig. 55.1. Arithmetic mean lengths and breadths (in μm) of gravid

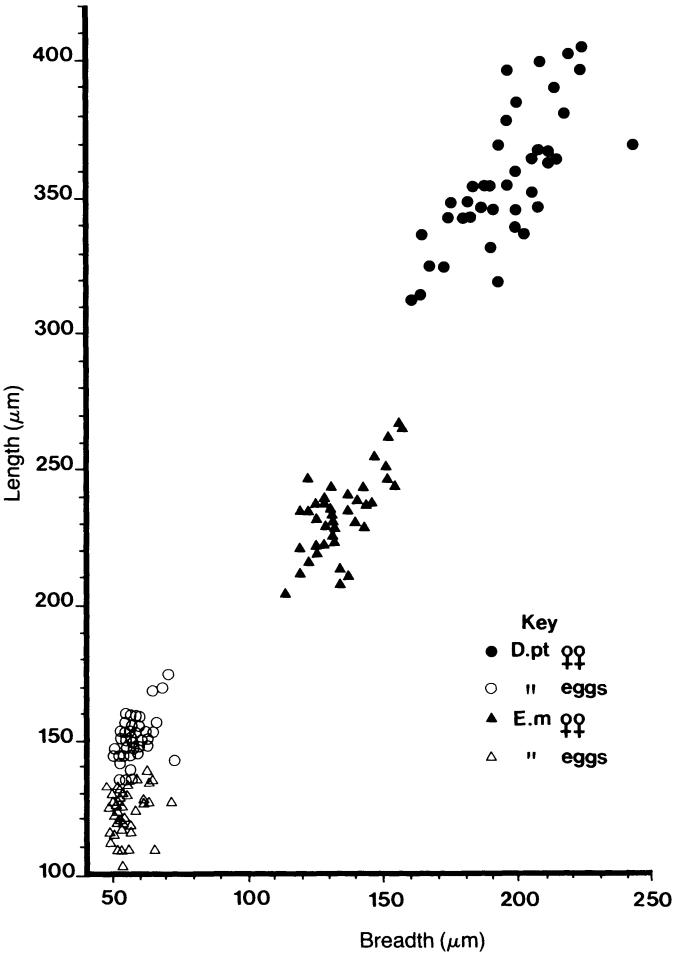

Fig. 55.1 Lengths and breadths of gravid females and eggs of *Euroglyphus maynei* (E. m) and *Dermatophagoides pteronyssinus* (D. pt).

E. maynei and *D. pteronyssinus* (± standard deviation) were: 233 ±15 × 136 ±12 and 356 ±25 × 198 ±18 respectively. Arithmetic mean lengths and breadths (± s.d.) of eggs of *E. maynei* and *D. pteronyssinus* were 122 ±9 × 55 ±6 and 151 ±9 × 59 ±5 respectively.

The arithemetic means (± s.d.) of estimated volumes of gravid females of *E. maynei* and *D. pteronyssinus* were (units are $\mu m^3/10^6$) 2.75 ± 0.61 and 9.12 ± 2.14 respectively and differed significantly ($P < 0.001$). The egg volumes of the two species were 0.25 ± 0.06 and 0.35 ± 0.08 respectively, and also differed significantly ($P < 0.01$). The arithmetic

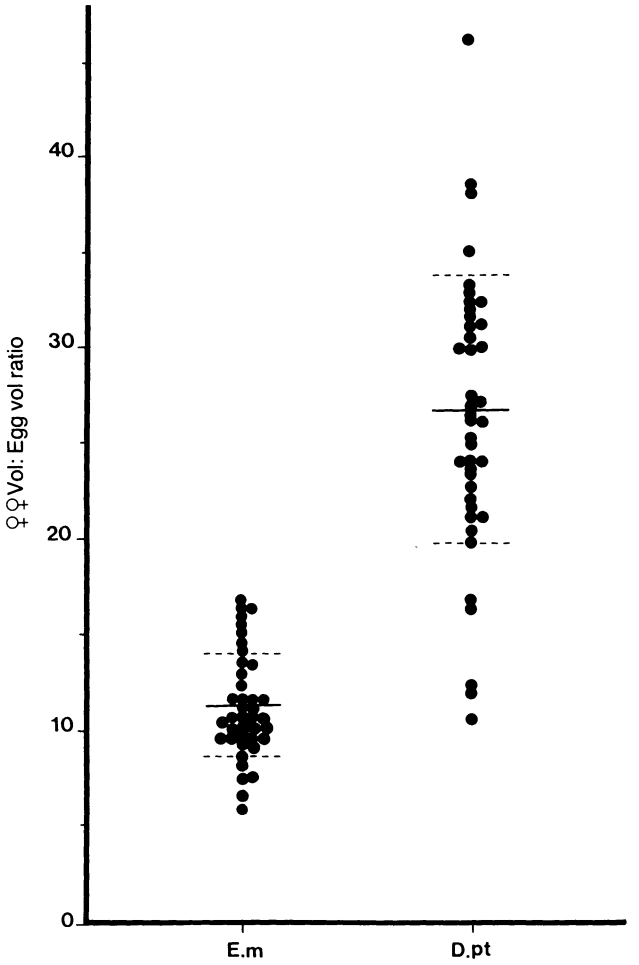

Fig. 55.2 The distributions of ratios of volume of gravid female to egg volume for 40 individuals of *Euroglyphus maynei* (E. m) and 40 *Dermatophagoides pteronyssinus* (D. pt) with arithmetic mean (solid line) ± one standard deviation (broken line).

mean of the gravid female to egg volume ratio was 11.4:1 ± 2.8 for *E. maynei* and 26.8:1 ± 7.1 for *D. pteronyssinus*, and the difference was very highly significant ($P < 0.001$) (Fig. 55.2).

DISCUSSION

The nature of the data, derived as they are solely from dust-sample analysis, only allow for predictions rather than conclusions on the

biology of *E. maynei*. These predictions need to be tested experimentally once productive *in vitro* cultures can be maintained. They are as follows:

1. *Euroglyphus maynei* has a higher critical equilibrium activity (CEA) than *D. pteronyssinus* and is, therefore, more susceptible to dehydration.
2. Female *E. maynei* produce fewer eggs than *D. pteronyssinus* and therefore its rate of population increase is lower than that of *D. pteronyssinus* (see below).

The prediction that *E. maynei* has a higher CEA than *D. pteronyssinus* comes from two sources: first, its small size, and second its higher frequency and abundance in damp homes and habitats than in dry ones. The small size of *E. maynei* compared with *D. pteronyssinus* indicates a higher surface area to volume ratio, and hence greater potential susceptibility to water loss. Surface area to volume ratios were not calculated because the model for calculating volume is a crude one.

The greater frequency of *E. maynei* in damp habitats confirms the findings of Blythe *et al.* (1974), Charlet *et al.* (1978) and Walshaw & Evans (1987) that *E. maynei* is far more restricted to the mattress habitat than *D. pteronyssinus*. Mattresses retain more moisture for longer periods than pillows and carpets, and evaporation of water derived from nocturnal sweating is impeded by coverings of bedclothes (Colloff, 1988). Burr *et al.* (1980) found *E. maynei* present in large numbers in mattresses of enuretic children and attributed this to dampness. Walshaw and Evans (1987) found a positive correlation between sodium levels in beds – used as a measure of sweat input – and abundance of *E. maynei*, although they suggested that this was due to unknown factors such as 'high sodium load' and not high humidity. This explanation follows from their assumption that *E. maynei* has a *lower* CEA than *D. pteronyssinus*, and they quote Wharton (1976) as the source of this statement. In fact Wharton (1976) does not mention the CEA of *E. maynei* at all. In any event, for a mattress containing high levels of solutes from sweat, namely, sodium chloride and potassium chloride, water will be absorbed if the water vapour activity (a_v) of the air above the mattress is greater than the water activity (a_w) of a saturated solution of the solutes. For a saturated NaCl + KCl solution at 20°C, a_w is 0.7 (70% r.h.) (Winston and Bates, 1960). In parts of the mattress this microclimate may prevail for at least 4–5 h/day (Coloff, 1988).

The prediction that *E. maynei* produces fewer eggs than *D. pteronyssinus* is based on the gravid-female to egg volume ratio. Eggs of species with a low female to egg volume ratio receive greater bestowal of energy per egg than those with a high ratio and, as a consequence, fewer eggs are produced per female. At 25°C and 75% r.h., Taylor (1975) found the

maximum daily oviposition rate of *E. maynei* was 1.3 eggs over 25 days with a mean of 1.1 over 15 days. In the same microclimate, Gamal-Eddin *et al.* (1983) found *D. pteronyssinus* produced a mean of 2.7 eggs/day over 46 days and Spieksma (1967) recorded a maximum rate of 2.9 eggs/day over 27 days.

Euroglyphus maynei cannot afford to produce eggs in large numbers. As Wharton (1985) pointed out, when large eggs or large batches of eggs are produced the water loss can be a significant part of body weight. Based on gravid-female to egg volume ratios, this would amount to a body-water loss of about 9% per egg for *E. maynei* compared with about 4% for *D. pteronyssinus*.

The combination of high CEA, low fecundity and low population increase are probably the major factors contributing to the difficulty of maintaining productive cultures of *E. maynei*. Most attempts to do so have used the microclimatic conditions which are optimal for *D. pteronyssinus*, namely, 75% r.h. and 25°C. This humidity may be below the CEA of *E. maynei*. At higher humidities heavy fungal growth appears in cultures with resulting detrimental effects on the mites (Mumcouglu, 1977). It is doubtful whether *E. maynei* has any highly specific dietary requirements. Hart and Le Merdy (1988) reported moderately good growth (700 mites in 8 weeks) on a mixture of dried milk, wheat-germ, flour, dried liver and dried yeast. Indeed, the problem is not so much one of establishing cultures, but of maintaining them on a long-term basis. One solution may be the use of meridic diets as used for culturing *D. farinae* (Rodriguez and Blake, 1978).

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Management of mite development in the home

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Household contamination with allergen-producing mites, mainly members of the family Pyroglyphidae, is of extensive medical and public-health importance. Effective management may led to clinical improvement of patients. It starts with an inventory of the nature and scale of the problem and its underlying causes. Where a medically relevant problem already exists, the inventory phase should be followed by chemical extermination of the mites, and subsequent removal of their allergenic products. Preventive measures such as reducing moisture and house-dust levels are essential to anticipate the recurrence of the problem. In the case of projected new dwellings, the preventive measures should be incorporated into the design and construction of the building as well as its furnishings and use, to achieve an effective management of this world-wide problem of mite allergy. Unfortunately European as well as American acarologists still take too little interest in these applied aspects of their discipline

INTRODUCTION

Mites occur in a great variety of habitats. They are not only present in desert, tundra, mountain and arctic regions but also in soil, caves, hot springs and oceans. In addition, they exploit a number of favourable niches in domestic dwellings (Krantz, 1978). Here, they may be found in the house-dust habitat covering the surface of floors, furniture, furnishings, textile toys and clothing (van Bronswijk, 1981; Wharton, 1976). In European and American dwellings, the family Pyroglyphidae (house-dust mites) takes first place both in abundance and medical relevance although other groups or sources such as stored-product mites, fungi and pet emanations, may be significant in certain homes (Bessot and

Pauli, 1986). The best-known illness associated with pyroglyphid mites appears to be the atopy syndrome, with asthma, rhinitis and atopic dermatitis as resulting inflictions after sensitization to allergens resulting from the presence of the mites (van Bronswijk, 1981; van Bronswijk and Pauli, 1988). The purpose of this study is to promulgate effective mite management for dwellings with due regard to our knowledge of the mite protagonists.

SCALE OF PROBLEM

Exposure of atopic patients to house-dust mite allergen(s) is so extensive – both locally and on a geographical scale – that mite allergy is considered a world-wide problem urgently requiring more research (de Weck and Todt, 1988). If about half of inhalant allergies are attributed to mites (45–85% of all asthmatics are mite-sensitive according to Platts-Mills and de Weck, 1988), and 5% of the world population are considered atopic and sensitized (asthma prevalence varies from < 1–30% in different regions according to Charpin, 1986), more than 100 million of the 5 billion inhabitants of our planet are affected today by house-dust mites. Such data give the acaralogical investigation of homes, a public-health dimension. Management of mite densities and contamination with mite products in dwellings, play a key role in reducing the public-health threat due to Acari colonizing domestic buildings.

MANAGEMENT CONCEPTS

In nature, members of the family Pyroglyphidae are normal saprophagous inhabitants of nests of birds as well as some mammals (van Bronswijk, 1981). Their presence in dwellings – especially in beds – should not amaze a biologist, and they should not be considered harmful to our health unless proven otherwise. In fact, only atopic individuals may experience ill effects. Therefore, a proven mite allergy is the starting point of any mite-control effort.

The purpose of avoidance measures or home sanitation – in fact acarological management – as recommended by physicians, is a reduction in exposure to mites to harmless levels. Recently these have been set provisionally at 100 mites/g house dust or less (Platts-Mills and de Weck, 1988) for the majority of patients. Home-sanitation studies attaining that aim or the equivalents of 0.6 mg guanine/g house dust and 2 μg Der p^1 antigen/g house dust (van Bronswijk, 1988a) resulted in clinical improvement such as a decrease in the need for medicaments, an increase in expiratory volume, and a diminution of asthma symptoms (Bischoff *et al.*, 1986, 1987; Platts-Mills *et al.*, 1982).

Effective management of Acari in dwellings is only possible when the problem at hand as well as its technical solutions are both well known and clear-cut. Within the home of a proven patient an inventory of the acarological situation should be the prelude to any further action. At the present time, such an inventory is usually based on house dust collected by a vacuum cleaner. The dust may be analysed according to three different techniques: investigation of the mite content by a trained acarologist, quantification of mite-derived allergens by an immunologist or assessment of the guanine content by patient or chemist (Platts-Mills and de Weck, 1988). In routine mite management, guanine quantification is the recommended method. It has been commercialized in a handy test set for the layman, and the result can be obtained in a few minutes. The laboratory methods are useful for assessing specific exposure or studying the ecosystem present in homes.

The known technical solutions resulting in reduced mite numbers and their products can be separated into three categories: prevention, extermination and cleaning (Table 56.1). Since all these procedures must be evaluated for their effectiveness, safety, practicability and possible environmental damage, the result is first and second choices. Moreover, many of the techniques need further acarological study.

It is clear that for individual problem dwellings, knowing the cause of dampness and dustiness, the two main contributing factors to mite development, is paramount for successful management of the mite fauna. In this phase, the acarologist in charge of mite management will need advice from trained building technicians to distinguish among rising damp, penetrating damp, cold bridges and condensation, and to recognize the underlying constructional causes. In tropical and subtropical regions, this may be irrelevant since even the humidity out-of-doors supports extensive mite growth.

EXTERMINATION AND REMOVAL

In the case of heavily infested homes of proven mite-allergy patients, the noxious mites need to be eliminated and their allergenic products removed. A number of household procedures as well as chemicals have been tested for this purpose (Bischoff and van Bronswijk, 1986; Colloff, 1986; Korsgaard, 1983; Mitchell *et al.*, 1985; Schober, 1986, Schober *et al.*, 1987; Wassenaar, 1988a,b), but up till now only a few have succeeded in lowering mite and allergen concentrations in dwellings (Table 56.2) below the hygienic thresholds. Effective measures usually combine acaricidal with cleaning treatments since it is not the mites themselves but their faecal products which contain the source of allergenicity (Voorhorst *et al.*, 1969). Recently, the chemical products marketed in

Table 56.1 Programme for prevention or reduction of allergenic mite contamination in dwellings to acceptable levels (after van Bronswijk, 1988c)

Phase 1: Prevention of infestation	*Phase 2: Extermination of noxious creatures*
First choice: REDUCING MOISTURE LEVELS • rising damp • penetrating damp • cold bridges • condensation • ventilation • heating IMPROVING CONSTRUCTION • cleansability	First choice: CHILLING • furniture • mobile furnishings BIOCIDAL SURFACE TREATMENT • floors • walls • ceilings • carpets • furniture • furnishings MACHINE WASHING ≥ 60 °C • clothing • mobile home textiles
Second choice: IMPREGNATION • home textiles DECORATION CHANGES • materials • positioning	Second choice: FUMIGATION • older mattresses • antique furniture

Phase 3: Cleaning to remove allergenic products
First choice: MECHANICAL • sweeping • beating • vacuum cleaning • wiping • waxing CHEMICAL SURFACE TREATMENT • detergent solution • shampoo • foam • powder • extraction washing machine (carpets) MACHINE WASHING • textiles
Second choice: DRY CLEANING • textiles

Table 56.2 Treatments which have proved effective in the households to reduce mite and/or allergen levels below hygienic thresholds (after van Bronswijk, 1988b)

Mite habitat	*Treatment*
Bedding	Encasing and cleaning
	Acarosan
	Paragerm
Padded furniture	Acarosan
Carpets and remaining home textiles	Acarosan
	Pirimiphos-methyl

western Europe were compared for effectiveness as well as safety and practicability (de Saint-Georges Gridelet *et al.*, 1988), thus providing physician and acarologist with the necessary information to select the best procedure to suit individual circumstances.

PREVENTION

It could be argued that if prevention is taken seriously, mite extermination and the removal of mite products by cleaning is superfluous. In fact, dampness is a key factor that could be regulated. However, in existing problem situations, a rapid improvement is in the interest of the patient, consequently extermination and cleaning should be the first control measures undertaken. Even then, only preventive measures may anticipate a recurrence of the problem.

It is a well-established fact that damp homes contain more mites and more mite allergen than dry ones (Leupen and Varekamp, 1966; Burr *et al.*, 1980; Korsgaard, 1982, 1983). In temperate climates, humidity appears to be the main limiting factor for mite development in the home (Schober, 1988). The ambient relative humidity (r.h.) indoors, and moisture content of the building and furnishing materials, together govern the microclimate in the relevant niches where house-dust mites occur. From the allergologist's point of view, the minimal value for relevant development of pyroglyphid mites is about 50% r.h. Maximum population development and allergen production (antigen P1) of mites occur at 70–90% r.h. (Fig. 56.1). At higher humidities, mite allergens are replaced by those of fungi as the major source. It appears possible to reduce allergen producers in the home by lowering indoor humidity. When humidities of 50% r.h. (Schober, 1988) or 7 g water/m^3 air (Korsgaard, 1982; Platts-Mills and de Weck, 1988) are present for a considerable length of time, no burdening of the patient is expected by the

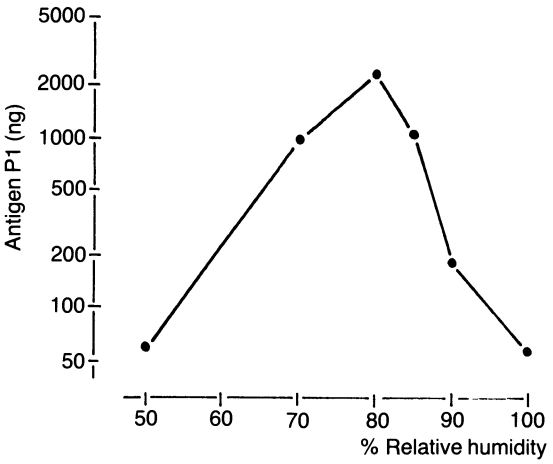

Fig. 56.1 Relative humidity in relation to estimated production of antigen P1 by *Dermatophagoides pteronyssinus* (Trt) after 28 days in culture at 25°C. It is assumed that no deterioration of antigen P1 occurred during culture period (after Schober, 1988).

allergen-producing organisms. In this respect, it is surprising that so far no data have been published on the acarological and clinical effects of drying out an infested building despite the availability of technology to achieve a dry dwelling such as the use of vapour-checking or vapour-proof layers or injecting the walls with hydrophobic chemical substances (Adan *et al.*, 1988). There is here a wide field for further interdisciplinary research.

BUILDING, FURNISHING AND USE OF NEW DWELLINGS

With new dwellings, it is only in those suitably designed, constructed, furnished and used, that mite management can easily be 100% successful, at least in a temperate climate. As far as prevention (Table 56.1) is concerned, rising and penetrating dampness, cold bridges and condensation can be prevented, and ventilation plus surface cleanliness brought to an acceptable level. Furnishings and non-textile floor covering that support fewer mites (Wassenaar, 1987) should be chosen. Mite-contamination levels should be checked at regular intervals during the full-time occupation of the dwelling (Kniest, 1988). If hygienic thresholds are about to be exceeded, mite extermination and allergen removal can be carried out.

Low-risk buildings have been constructed and used in Denmark with appreciable success both acarologically and clinically (Korsgaard, 1988) but from the economic point of view are not suited for large-scale use.

Further research should show whether adherence to the management scheme outlined here will have the same positive result at more realistic cost levels.

CONVENTIONAL VERSUS MODERN MITE MANAGEMENT

The management of mite development in the home is not of recent origin, but has occupied the allergist's mind for at least half a century (Dekker, 1928; Kremer, 1932). The numbers of mites and fungi present in those early days in soft furnishings such as mattresses, were enormous. Mites could be found comparatively readily, and exterminated by removal of the offensive material. Clinical results were oustanding. Probably due to the exclusive use of natural products in the home, most mites occurring abundantly belonged to the families Acaridae and Glycyphagidae. Pyroglyphid mites were uncommon or present only in low numbers (van Bronswijk, 1981). Through the decades, the number of mites per home appeared to decrease – at least in western Europe – and the composition changed. However, the sanitation advice of the doctors remained the same: removal or washing of home textiles and regular vacuum cleaning to lower mite and dust levels. Nowadays, there exists an endless list of different pamphlets telling the patient how to improve his or her home according to the procedures just referred to. Every pharmaceutical company working in the allergy field, and most hospitals, have their own versions. All these guide-lines have two points in common implicitly or explicitly: (1) if the patient has a mite allergy, there must be mites in the home; and (2) if there are mites, they can be exterminated by removal of home textiles, washing and vacuum cleaning. These two starting points are even employed in some clinical trials (for example Burr *et al.*, 1976; Korsgaard, 1983; Murray and Ferguson, 1983). From the acarological point of view, this is, more or less, a 'blind' endeavour since the actual mite situation is not determined at any point in the process. We regard this concept as 'conventional' mite sanitation or management.

Removal of infested furniture or furnishings is undoubtedly effective in reducing exposure to mite-derived allergen. But in conventional mite management there are no tests to determine whether the objects in the home to be treated, are infested to dangerous levels; rather, they are all removed. Moreover, as may be concluded from data collected by numerous investigators in the last ten years, vacuum cleaning is inconsistent and not really effective in achieving a significant lowering of mite or allergen levels (Bischoff and van Bronswijk, 1986; van Bronswijk, 1985; Carswell *et al.*, 1982; Colloff, 1987; Massey and Massey, 1984; Wassenaar, 1988a,b).

Table 56.3 Comparison of 'conventional' and 'modern' mite sanitation of homes

Sanitation	*Sanitation type* *Conventional*	*Modern*
Effective	No or possibly	Yes
Practicable	No or possibly	Yes
Safe	Yes	Possibly
Minimum environmental hazard	Yes	Possibly

'Modern' mite management – as is advocated by us – starts from the viewpoint that significant mite contamination should be proven before treatment is commenced (see Management Concepts section), whereas the effect of anti-mite and anti-allergen treatment should be measured in house dust, preferably by the patient or another member of the household. Since removal of all textiles is not always feasible from the viewpoint of comfort, and since normal vacuum cleaning of rooms may not be considered effective in reducing exposure to mite allergen, chemical formulations should not be excluded (Bischoff *et al.*, 1986; Bischoff and van Bronswijk, 1986; Dorward *et al.*, 1988; Elixmann *et al.*, 1988). Unless the mattress is the only significant focus of contamination in which case enclosing it in plastic is effective (Walshaw and Evans, 1986), the required use of chemicals could be considered a drawback in our environment-sensitive society, even when only low-toxicity products are used. However, in the damper regions of our planet, such as The Netherlands, this appears to be the only possibility for effective anti-mite strategies in an appreciable number of homes.

In summary (Table 56.3), it may be said that conventional mite sanitation, which is still commonly employed, is safer and with fewer environmental hazards, but is hardly practical and not consistently effective. Modern sanitation, on the other hand, is highly effective and practical, but we should remain aware of its safety and environmental aspects.

ACAROLOGIST'S ROLE IN MITE MANAGEMENT

Over the last 20 years, some 90% or more of published reports concerning pyroglyphid mites have dealt with clinical and immunological aspects. Acarologists feature comparatively little among the authors of house-dust mite articles originating from North America and from Europe. Most participants at the World Conference on Mite Allergy in Bad Kreuznach, Germany in 1987 had a medical background. This is even more surprising since many of the unsolved problems in house-

dust allergy management are of a biological rather than a clinical or immunochemical nature. These include identification of the species involved, ecological interrelationships in the house-dust ecosystem, water relations between mites and their natural substrates, allergen production in relation to nutrition, and physical and chemical extermination under home conditions, etc.

It appears that even in the daily routine of home sanitation, the applied acarologist neglects his/her rightful advisory role. Allergists and other physicians treating mite-allergy patients, should seek the advice of trained acarologists when unsolved mite problems arise in the patient's home. However, recent history has taught us that the medical profession is unlikely to take the initiative to consult entomologists such as acarologists, partly because they doubt their clinical insight, and partly because in the past, the advice of scientists was not of a sufficiently practical nature. Here lies a case for professional organizations, such as EURAAC or SALF, to provide advanced training as well as an upgrading of our professional outlook.

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An indirect effect of cleaning on house-dust mites (Dermatophagoides *spp.*) *in carpets*

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The control of house-dust mite (HDM) populations in dwellings is important for people suffering from HDM allergy. The direct effects of cleaning on the numbers of dead and living mites (*Dermatophagoides pteronyssinus* (Trt), *D. farinae* Hughes and *D. microceras* Griffiths and Cunnington), and the quantities of HDM allergens, has received much attention in the literature. In contrast, the indirect effect of cleaning, through the removal of food for example, is poorly documented. An attempt to investigate the suitability of cleaned and uncleaned rugs as habitats for HDM was undertaken. In order to do this, 80 individuals from a culture of *D. farinae* were placed on each of a large number of pieces of cleaned and uncleaned carpet. These were stored at 25°C and 75% r.h. At weekly intervals of 3–7 weeks inclusive from the experiment's inception, the number of live mites was ascertained by the 'heat escape method'. In this method, the mites are driven to a piece of adhesive tape by applying heat to one edge of the carpet.

There were three cleaning treatments: (1) vacuum cleaning in which both surfaces were vacuumed for an equal length of time; (2) 'wet cleaning' where the carpet was cleaned with rotating brushes after adding a soap solution, and then thoroughly rinsed using lots of water; and (3) autoclaving in which the material was heated in an autoclave to 110°C for 20 minutes.

Autoclaving was the most effective treatment. Apart from killing the

mites, the allergens (P1 and DpX) were destroyed, and the development of a new mite population was severely retarded, possibly due to the destruction of vitamins. The other two methods were less effective. The mites were neither killed nor removed in substantial numbers by either method, and approximately half or more of the allergens were still present after cleaning. However, the development of a mite population after wet cleaning was markedly affected (Wilcoxon signed-rank test, $P < 0.001$, one-tail test), probably as a result of the removal of food. The effect of vacuum cleaning on population development was also appreciable for some of the rugs and, on the whole, statistically significant (Wilcoxon signed-rank test, $P < 0.001$, one-tail test).

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Astigmatic and prostigmatic mites of grain stores, mills and sawmills in Finland

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Allergic reactions caused by dust in the working environment in Finland are most common in the various phases of handling grain and grain products, and also in sawmills. Therefore, these environments were selected for this study financed by The Finnish Work Environmental Fund.

In Finland, the presence of a clear, seasonal variation in mite populations is correlated with our cold winters. In grain-handling locations, layers of old fine dust and debris were found to be one of the main sources of dense mite populations. The species composition in Finnish grain stores and mills is similar to those of other countries of the northern temperate zone. The most important differences are:

1. The mesostigmatic 'meal mite', *Leiodinychus orbicularis* (Koch) is not found in these habitats in Finland.
2. *Tyrophagus putrescentiae* (Schrank) was not found in grain stores, and seems to be a casual occupant in all situations with a low winter temperature. It is both common and abundant in Finland in continuously warm work conditions.
3. The minute tarsonemid mite, *Tarsonemus granarius* Lindquist, is abundant in Finland but may have been overlooked elsewhere.

The abundant astigmatic species of grain-handling locations are *Acarus siro* L. *s. lat.* and *Lepidoglyphus destructor* (Schrank). These and many other common species have been clinically tested elsewhere, and

[†]Unfortunately the author Dr I. Oksala died in October, 1989.

found to be certain allergenic sources. *Cheyletus* spp. are the most abundant prostigmatic species, and recently have been found to contain allergens. Tarsonemids for many years have been referred to as 'itch mites' by mill workers although clinical tests have not been carried out with these mites. Mites are not the main cause of allergic reactions arising from sawdust, and it is unusual to find large populations in sawmills. Astigmatic species are most numerous in sawmills at the beginning of the handling procedure. Species most commonly found are *Acarus tyrophagoides* (Zachvatkin) and *Calvolia romanovae* Zachvatkin.

Several taxonomic problems have still to be solved. The *A. siro* complex has been treated as a single species as the present material does not warrant subdivision. This research programme has led to numerous proposals for minimizing risks but the details are outside the scope of this brief chapter.

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