Temperature and host effects on key morphological characters of *Hemisarcoptes cooremani* and *Hemisarcoptes malus* (Acari: Hemisarcoptidae)

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(Received 12 June 1996; accepted 1 October 1996)

ABSTRACT

We investigated the influence of temperature and resources on six morphological characters thought to distinguish two North American species of *Hemisarcoptes* (*H. malus* and *H. cooremani*). We raised mites at three temperatures (15, 24 or 30°C) and on two different scale insect prey (*Aspidiotus nerii* or *Aonidiella aurantii*) which were cultured on two different substrates (potato tubers and lemon fruit). In general, the temperature had more of an influence on the character variation than did the host and the highest temperature resulted in the smallest mean body size. The two species did not respond to changes in the temperature or host in a symmetrical fashion. The temperature significantly influenced the lengths of the external scapular setae (*sce*) of *H. malus* and the *sce* and first coxal setae (*1a*) of *H. cooremani*. The relative lengths of the setae *sce* and *1a* of *H. cooremani* were significantly influenced by the temperature, while the host type significantly influenced the paraproctal setae (ps_2). Major-axis regressions indicated that *H. cooremani* had an absolutely longer mean setal length for *1a* and for ps_2, than *H. malus*, but a relatively shorter *sce*. An ANOVA of the size-adjusted shield characters of *H. malus* resulted in non-significant effects of the temperature or host on either the prodorsal shield area or circumference. The temperature, but not the host, statistically influenced the shield circumference and area in *H. cooremani*. Regressions of the shield area (size) on body length, resulted in two clear groupings by species. *Hemisarcoptes cooremani* had an absolutely larger shield area and increased circumference (complexity), as compared to *H. malus*. A plot of the shield circumference in relation to the shield area, however, resulted in a single trajectory, indicating that shield complexity is an allometric consequence of an increase in body size in both species. Though characters can be influenced significantly by environmental parameters, the species-specific patterns of some characters of North American *Hemisarcoptes* are distinctive enough to allow diagnosis and identification.

Key words: Acari, character variance, ecophenotypic plasticity, mites.

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INTRODUCTION

Mites of the genus *Hemisarcoptes* (Acari: Acariformes) are obligate parasites of armoured scale insects (Coccoidea: Diaspididae) (Houck and OConnor, 1990). The genus is widely distributed throughout the northern hemisphere, Africa, the Oriental region and Australia. Across its geographic range, the genus is morphologically conservative with few distinguishing characters expressed between species. As part of a systematic revision of the genus, we have looked for key morphological characters in the five nominal species and a number of undescribed species.

Two nominal species of *Hemisarcoptes* occur in North America: *Hemisarcoptes malus* (Shimer, 1868) and *Hemisarcoptes cooremani* (Thomas, 1961). *Hemisarcoptes malus* is distributed throughout most of the northern and central United States and southern Canada. *Hemisarcoptes cooremani* occurs from the southern United States to northern South America and the Caribbean region. *Hemisarcoptes malus* and *H. cooremani* are central to the work reported here because they are currently being used by American and Israeli workers in a biocontrol programme and an accurate discrimination of species is required for this purpose.

This paper investigates the morphological stability of six characters, previously determined to potentially have diagnostic qualities in distinguishing the two North American species. The characters examined in this study include the total body length, the area and circumference of the prodorsal shield and the mean lengths of the external scapular setae (*sce*), the first coxal setae (*1a*) and the paraproctal setae (ps_2). The nomenclature for the idiosomal setae follows Griffiths *et al.* (1990). The prodorsal shield represents the only rigid sclerotized structure present on the dorsum of these mites (Fig. 1A). The shield area is used here as an estimator of the overall shield size and the circumference (standardized with respect to area) is a proxy for the shield complexity. The shield of *H. malus* is qualitatively different from that of *H. cooremani* (Fig. 2). In *H. malus*, the anterior portion of the shield is somewhat triangular, the subocular area somewhat heart shaped and the shield does not abut the ocelli. The anterior portion of the shield of *H. cooremani* is square-shaped, the subocular area is expanded posteriorly and the shield is inclined to adjoin the ocelli. Clearly there appear to be qualitative differences in the shields of the two species and we wanted to test whether the shield would be consistently diagnostic across the range of environmental parameters.

The three other characters which distinguished the two species in a previous study were the lengths of three setae: the external scapular setae (*sce*) of the prodorsal region, the first pair of coxal setae (*1a*), and the paraproctal setae (ps_2) (Fig. 1A and B).

In a parallel multivariate study of the nominal species of *Hemisarcoptes* (Houck and OConnor, ms.), we examined the morphological variation and static

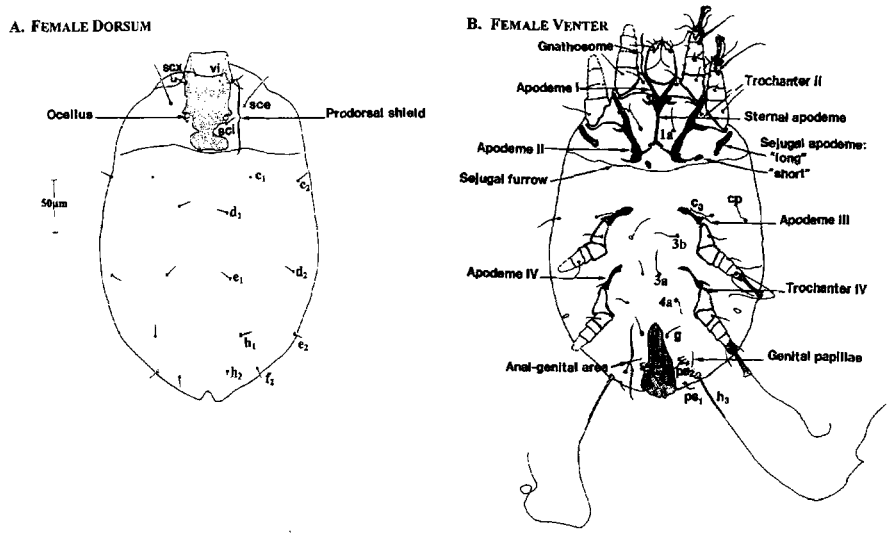

Fig. 1. Anatomical morphology of *Hemisarcoptes*. (A) Dorsum of *H. cooremani*. (B) Venter of *H. malus*.

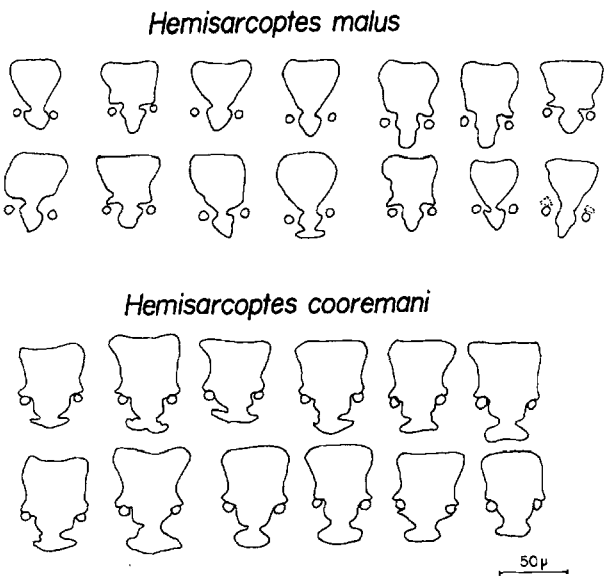

Fig. 2. Camera-lucida tracings of the prodorsal shield of randomly selected representatives of *H. malus* and *H. cooremani*.

allometric aspects of the adult morphology. In relation to the present work, four findings were derived from that study: (1) the males and females were completely dimorphic in body size, (2) although all four taxa examined were discriminated via a size-independent discriminant function analysis, the character variation expressed among males was much less than that for females, (3) males lacked interspecific diagnostic characters and (4) there were significant static allometric differences in females, which were also correlated with the differences in the total body size. Because the male morphology was relatively uninformative, the present work concentrates on the character variation among females, using the previously determined diagnostic characters as a focus. In particular, we address the following questions.

(1) How are the female body length, prodorsal shield circumference and area and the lengths of three potentially diagnostic setae influenced by temperature and resources within an ontogeny?

(2) Are the setal lengths of females sufficiently stable across temperature and resources to be reliable discriminatory characters under a range of experimental conditions?

(3) What general statements of character variance and habitat variability may extend from this study?

MATERIALS AND METHODS

Stock cultures

Stocks of *Hemisarcoptes* were field collected from diaspidid hosts as follows: *H. malus* from *Lepidosaphes ulmi* on apple bark in the vicinity of Ithaca, New York and *H. cooremani* from *Lepidosaphes beckii* on citrus near Donna, Texas. The mites were transported to the laboratory where axenic cultures were expanded on the diaspidid *Aspidiotus nerii* (oleander scale) grown on potatoes. The stock cultures were maintained in 16 ft^3 incubators at 24°C. Open trays of water were placed beneath the cultures and fans within the units provided air circulation. The humidity was not controlled, but remained relatively consistent at 100% saturation.

Monoculture stocks of adult mites were incubated under these conditions until they produced first-generation eggs. This protocol provided both species of mites with a common conditioning experience, but did not allow sufficient time for significant genetic selection effects to have occurred in the culture prior to treatment.

Experimental treatment

Laboratory studies were designed to simulate the potential range of environmental factors encountered by the mites and test the degree of character variation correlated with environmentally realistic regimes. We tested the

temperature at three experimental levels (15, 24 and 30°C) and the resource base at two levels (*A. nerii* grown on potatoes and *Aonidiella aurantii* cultured on lemons). The 15 and 30°C temperatures represent the lower and upper limits of tolerance for scale insect survival. The two diaspidids represent important contrasts in both morphology and plant-host type. *Aspidiotus nerii* has a convex cap and no velum. *Aonidiella aurantii* is flat in profile and has a ventral velum. Another obvious difference was that the plant substrate upon which the scales were grown offers contrasts. *Aspidiotus nerii* was presented to the mites on starch-laden plant tubers, while *A. aurantii* was incubated on acidic citrus fruits (lemons). No distinction was made in this study between the influence of scale host species and scale host resource (potato or lemon) in defining the resource base for the mite.

Using a dissecting microscope, first-generation eggs of mites were collected from the host (*A. nerii*) by lifting the scale cap and locating the eggs. Eggs were collected from monocultures of *H. malus* and *H. cooremani* and placed under the scale cap of one of the two treatment scale species. Ten replicates from each resource treatment group were maintained at each of the three experimental temperatures. The combinations of species : temperature : resource represent a $2 \times 3 \times 2$ statistical block design. The first-generation eggs of *Hemisarcoptes* were cultured at the chosen temperature–resource combination until reaching adulthood.

Data collection

The first-generation adult female mites were collected, cleared in lactophenol and mounted on microscope slides using Hoyer's medium. Camera-lucida drawings were produced using a Wild M-20 phase-contrast microscope. From these drawings a series of points along the length of each seta and along the perimeter of the prodorsal shield was electronically converted to Cartesian coordinates using a digitizing pad (Houston Instrument Hipad DT-114) and an IBM PC microcomputer. The setal lengths and shield circumference were determined by summing the Euclidean distances between consecutive points. The shield area was computed using the method of Harvey (1981). All the measurements were scaled in micrometres.

The total body length was measured within and between treatments. Because the body size may be responsible for (or contribute to) character differences between the experimental groups, the size effects were partitioned from the data by regressing the logarithm of each character on the logarithm of the body length and using the residuals in subsequent statistical comparisons. This allowed biological patterns to be interpreted as size-free contrasts, independent of the allometric consequences of the mean size differences between the groups. Analyses of variance were carried out on pooled regression residuals using the general linear model. Statistical differences ($p = 0.05$) were determined using Tukey's studentized range test (SAS Institute, 1982).

RESULTS

Effect of temperature on body length

The mean body length data for *H. malus* and *H. cooremani* are given in Table 1. In general, the highest culture temperature (30°C) resulted in the smallest mean body size for females of both species. However, in only one case (i.e. 30°C for *H. malus*) was the difference statistically significant ($p = 0.008$), as determined by MANOVA.

When the body lengths for *H. malus* and *H. cooremani* were pooled across the temperature and resources, they were significantly different from one another ($p = 0.004$, two-tailed test) with *H. cooremani* (mean = 329 μm) being larger than *H. malus* (mean = 300 μm). The analysis of variance procedure indicated that the species and temperature significantly influenced the body length ($p < 0.0001$ in both instances), but resources did not ($p = 0.831$). The interaction terms indicated that there was not a significant temperature–resource interaction ($F_{2,190} = 0.24$, $p = 0.785$), a significant interaction between the species and resources ($F_{1,190} = 2.72$, $p = 0.100$) or an interaction between the species, temperature and resources ($F_{2,190} = 1.81$, $p = 0.166$).

Occasionally, extreme teratogenic effects were observed in the mites cultured at 30°C, primarily the degeneration of legs IV. It is not clear whether this reflects a sudden shift in the developmental temperature of as little as 6°C (from 24 to 30°C) which can provoke serious morphological consequences or whether higher temperatures themselves represent a significant ontogenetic stress.

Temperature and resource effect on setal lengths

The temperature significantly influenced the length of seta *sce* for *H. malus* (Fig. 3; analysis of variance given in Table 2) with the *sce* being shortest at 30°C. The

TABLE 1

Summary of mean total body length measurements for *H. malus* and *H. cooremani* at the three treatment temperatures and on alternate hosts

Host	15°C	24°C	30°C
H. malus			
A. aurantii (lemon)	299 ± 29	302 ± 19	281 ± 24[a]
A. nerii (potato)	300 ± 18	295 ± 23	278 ± 23[a]
H. cooremani			
A. aurantii (lemon)	325 ± 22	326 ± 11	322 ± 23
A. nerii (potato)	344 ± 34	334 ± 32	330 ± 22

[a] Statistically significant difference ($p = 0.05$), Tukey's studentized range test.

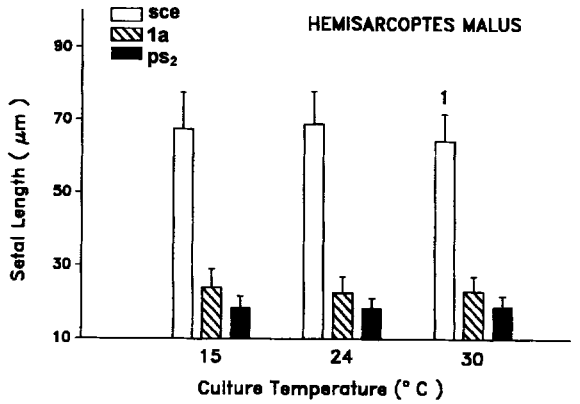

Fig. 3. Relationship between the setal length and temperature for *H. malus*. The bars represent mean values (±SD). The number 1 above the bar at 30°C represents the only pairwise contrast which is significantly different. *sce*, external scapular setae of the prodorsal region; *1a*, the first pair of coxal setae; ps_2, paraproctal setae.

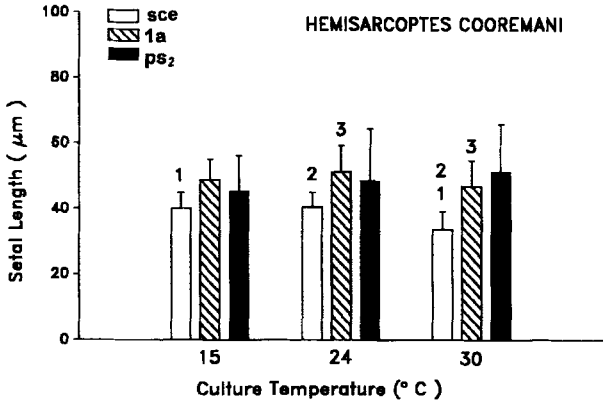

Fig. 4. Relationship between the setal length and temperature for *H. cooremani*. The bars represent mean values (±SD). The numbers above the bars represent those pairwise contrasts which are significantly different from one another. *sce*, external scapular setae of the prodorsal region; *1a*, the first pair of coxal setae; ps_2, paraproctal setae.

temperature significantly influenced the length of setae *sce* and *1a* for *H. cooremani* (Fig. 4; analysis of variance given in Table 2). The *sce* was significantly longer at culture temperatures of 15 and 24°C as compared to 30°C and *1a* was significantly longer at 24°C as compared to mites cultured at 30°C. The lengths of the paraproctal setae (ps_2) of *H. malus* and *H. cooremani* were not significantly influenced by the temperature.

TABLE 2

Summary of the analysis of variance of setal lengths (unadjusted for size) for *H. malus* and *H. cooremani*

	H. malus ($n=120$)			*H. cooremani* ($n=96$)		
	sce	*1a*	ps_2	*sce*	*1a*	ps_2
Temperature	$F=3.88$	$F=0.98$	$F=0.17$	$F=21.25$	$F=3.24$	$F=1.17$
	$p=0.02$[a]	$p=0.38$	$p=0.84$	$p=0.0001$[a]	$p=0.04$[a]	$p=0.31$
Host	$F=0.80$	$F=0.02$	$F=2.54$	$F=1.31$	$F=3.36$	$F=18.59$
	$p=0.37$	$p=0.89$	$p=0.11$	$p=0.26$	$p=0.07$	$p=0.0001$[a]

[a] Statistically significant difference ($p=0.05$), Tukey's studentized range test.
sce, external scapular setae of the prodorsal region; *1a*, the first pair of coxal setae; ps_2, paraproctal setae.

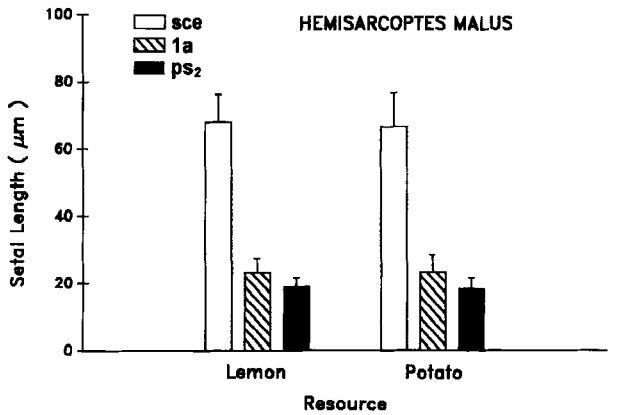

Fig. 5. Relationship between the setal length and host for *H. malus*. The bars represent mean values (± SD). *sce*, external scapular setae of the prodorsal region; *1a*, the first pair of coxal setae; ps_2, paraproctal setae.

The temperature and resources had no effect on the setal lengths of *H. malus* (Fig. 5 and Table 2) and only a limited influence on *H. cooremani* (i.e. ps_2; Fig. 6 and Table 2). The lengths of the paraproctal setae of *H. cooremani* grown on *A. aurantii* (on lemons) were shorter than those grown on *A. nerii* (on potatoes).

A MANOVA analysis of the significant interaction terms for the treatment variables indicated that the species *per se* had an effect on the setal lengths ($p \geqslant 0.001$) and that the temperature had a significant effect ($p \geqslant 0.0001$), but resources did not ($p=0.831$). The interaction of species and resources was not significant ($p=0.101$) nor was the interaction term for the temperature and resources ($p=0.785$). Because the resources and temperature were not confounded it is justifiable to discuss the data by resources and temperature separately.

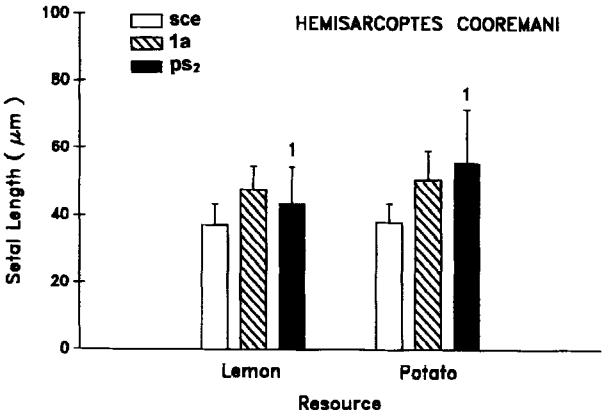

Fig. 6. Relationship between the setal length and host for *H. cooremani*. The bars represent mean values (±SD). The numbers above the bars represent those pairwise contrasts which are significantly different from one another. *sce*, external scapular setae of the prodorsal region; *1a*, the first pair of coxal setae; ps_2, paraproctal setae.

TABLE 3

Summary of the analysis of variance of size-adjusted setal lengths for *H. malus* and *H. cooremani*

	H. malus			*H. cooremani*		
	sce	*1a*	ps_2	*sce*	*1a*	ps_2
Temperature	$F=2.25$	$F=0.67$	$F=1.86$	$F=26.53$	$F=4.82$	$F=0.66$
	$p=0.11$	$p=0.52$	$p=0.16$	$p=0.0001$[a]	$p=0.01$[a]	$p=0.52$
Host	$F=0.63$	$F=0.04$	$F=2.48$	$F=1.47$	$F=3.02$	$F=18.66$
	$p=0.63$	$p=0.84$	$p=0.12$	$p=0.23$	$p=0.08$	$p=0.0001$[a]

[a] Statistically significant difference ($p=0.05$), Tukey's studentized range test.
sce, external scapular setae of the prodorsal region; *1a*, the first pair of coxal setae; ps_2, paraproctal setae.

Allometric comparisons of setal lengths

For *H. malus*, the size-adjusted setal lengths were not statistically different at any of the experimental temperatures or resources (Table 3). The relative lengths of two setae of *H. cooremani* (*sce* and *1a*) were significantly influenced by the temperature, while the resource type significantly influenced only the paraproctal setal length. These results are in line with those for the setal lengths when not corrected for body size, but indicate that the setal lengths measured on *H. malus* tend to be isometric while the patterns for *H. cooremani* deviate from those predicted on body size alone (allometric).

Major axis regressions of setal lengths, pooled across the resources and temperature, indicated an increase in the setal length relative to an increase in

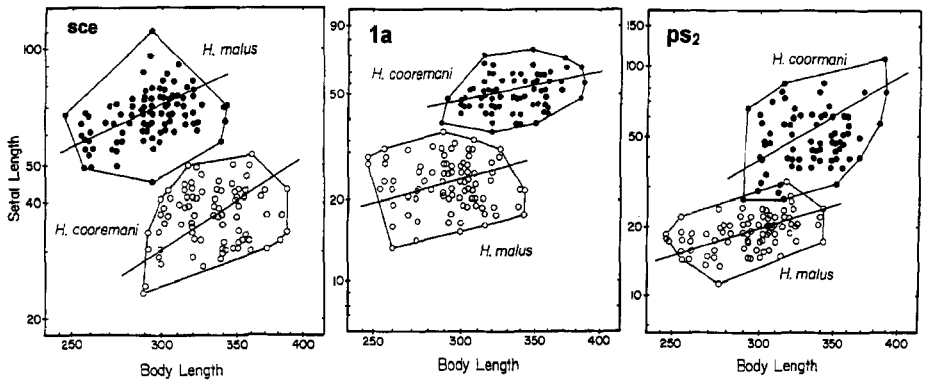

Fig. 7. The regression of the setal length against the body length for *H. malus* and *H. cooremani*. The lines of best fit were calculated using major-axis regression.

the body size for *H. malus* and *H. cooremani* for all three setae measured (Fig. 7). *Hemisarcoptes cooremani* had an absolutely longer mean setal length for *1a* and ps_2, but a relatively shorter mean setal length for *sce* as compared to *H. malus*. These differences were statistically significant. In addition, there was a greater increase in the relative paraproctal setal lengths with increasing body size (i.e. a greater allometric coefficient) in *H. cooremani* than in *H. malus*.

Allometric comparisons of prodorsal shields

Camera-lucida tracings of the prodorsal shield of *H. malus* and *H. cooremani* demonstrated apparent qualitative interspecific differences and an intraspecific variation in size and complexity (Fig. 2). Regressions of the shield area ('size') in relation to the body length, pooled across the temperature and resources, resulted in two clear groupings by species (Fig. 8). *Hemisarcoptes cooremani* had an absolutely larger shield size (mean = 2394 μm^2, N = 48) and little overlap with that of H. *malus* (mean = 1343 μm^2, N = 60) even where the absolute body lengths were within equivalent ranges (e.g. at 290–340 μm).

A comparison of the prodorsal shield circumference ('complexity') with the body length (Fig. 9) indicated that the shield of *H. cooremani* was more complex (mean = 232 μm, N = 48) than that of *H. malus* (mean = 173 μm, N = 60), with a minimal overlap in the ranges even where the body lengths were similar (e.g. at 310 μm). Both the shield area and circumference were weakly correlated with the total body length.

Though *H. malus* and *H. cooremani* clearly differed in the shield area and circumference, a plot of the shield circumference in relation to the shield area (Fig. 10) indicated a single size-complexity trajectory for the two species. No *ad hoc* explanation need be invoked concerning the evolution or function of the

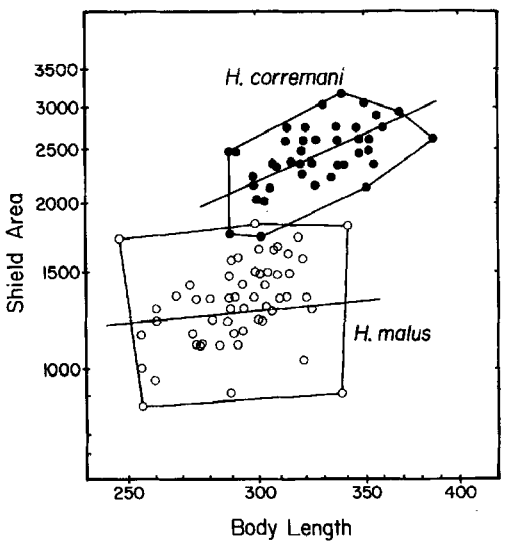

Fig. 8. The regression of the prodorsal shield area against the body length of *H. malus* and *H. cooremani*. The lines of best fit were calculated using major-axis regression.

increased prodorsal shield complexity in *H. cooremani*, as it represents an allometric extrapolation due to an increase in the shield area (positive allometry). An increase in the body length contributes naturally to the increased complexity of the shield, resulting in a continuous allometric transformation series by size.

An ANOVA of the size-adjusted shield characters resulted in non-significant effects of the temperature and resources on the prodorsal shield circumference ($R^2 = 0.07$) and area ($R^2 = 0.03$) for *H. malus* (Table 4). The temperature but not the resource type statistically influenced the shield circumference and area in *H. cooremani*. This effect is correlated with the weak influence of temperature on size, but indicates that the temperature has a relatively greater influence on the prodorsal shield than it does on the body length.

The temperature had an influence on the prodorsal shield of *H. malus* (Table 5). Pair-wise comparisons of the temperature effects indicated that the shield circumference in *H. cooremani* is significantly less for mites grown at 15°C as compared with those at 24°C and 30°C (Table 5). No statistically significant differences were found for mites cultured at 24°C as compared with those at 30°C. This pattern is consistent with that for the shield area. Lower temperatures, which result in a larger body size, produce relatively smaller prodorsal shields with a relatively reduced area. The resources had no influence on the prodorsal shield characters for either species of mite.

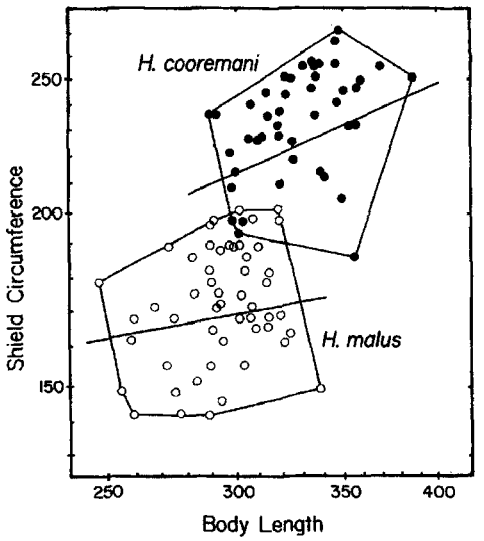

Fig. 9. The regression of the prodorsal shield circumference against the body length for *H. malus* and *H. cooremani*. The line of best fit was calculated using major-axis regression.

TABLE 4

Summary of the analysis of variance of size-adjusted shield characters for *H. malus* and *H. cooremani*

	H. malus		*H. cooremani*	
	Circumference	Area$^{\frac{1}{2}}$	Circumference	Area$^{\frac{1}{2}}$
Temperature	$F=1.72$	$F=0.79$	$F=11.76$	$F=3.29$
	$p=0.19$	$p=0.46$	$p=$ 0.0001[a]	$p=0.05$[a]
Host	$F=0.58$	$F=0.00$	$F=$ 1.65	$F=0.10$
	$p=0.45$	$p=0.97$	$p=$ 0.21	$p=0.75$

[a] Statistically significant difference ($p=0.05$), Tukey's studentized range test.

DISCUSSION

In only a few studies of character variation in astigmatid mites has the role of allometry or environmental influence been investigated. OConnor and Reisen (1978) showed that simple allometry accounted for the extreme male polymorphism in *Chiroptoglyphus americanus* (Rosensteiniidae). Griffiths (1970) noted that individuals of *Acarus siro* (Acaridae) reared on a 'rich diet' had longer idiosomal setae than those reared on a 'poor diet'. Gerson and Capua

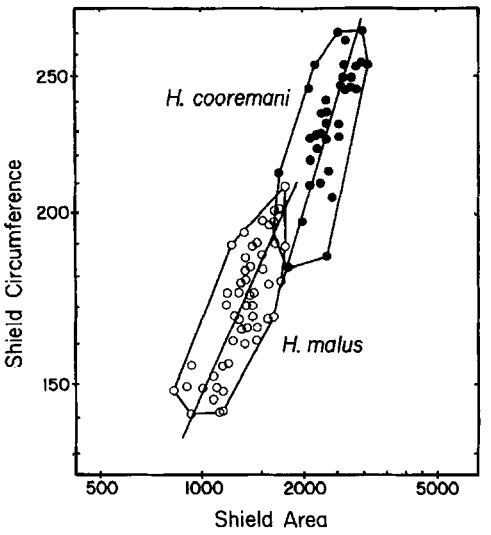

Fig. 10. The regression of shield circumference vs shield area for *H. malus* and *H. cooremani*. The line of best fit was calculated using major-axis regression.

(1982) reared the bulb mite, *Rhizoglyphus robini* (Acaridae) on three diets of decreasing nutritive value (peanuts, peanut extract and filter paper). They showed that the morphological structures and setal lengths used in taxonomic diagnoses can vary with diet.

From the present study, it is clear that culture temperature and resource can have important allometric influences both on the structural body components such as the prodorsal shield and on sensory components such as the tactile setae in *Hemisarcoptes*. The ecophenotypic effects on particular structures cannot be determined *a priori*, as evidenced by the differential responses of closely related species in our experiments. Even very closely related species may differ in their patterns of response both in kind and in magnitude.

Hemisarcoptes cooremani naturally ranges from the far southern United States to northern South America and throughout the Antilles. *Hemisarcoptes malus* is allopatrically distributed to the north, ranging from southern Canada to northern Louisiana, westward to the Rocky Mountains. In our experiments, *H. cooremani* expressed a greater range of character variance in relation to the experimental conditions than did *H. malus*. This correlates with the fact that *H. cooremani* normally experiences a relatively moderate and stable diurnal and seasonal regime (tropical and subtropical), whereas *H. malus* survives seasonal temperature fluctuations of 50°C or greater in the northern part of its range and

TABLE 5

Means (±SD) for the shield circumference and area for females of *H. malus* and *H. cooremani* at three temperatures and on two hosts

Temperature/host	*n*	Circumference (μm)	Area (μm^2)
H. malus			
15°C	40	171 ± 10^a	1339 ± 243^a
24°C	40	179 ± 14^a	1400 ± 185^a
30°C	40	168 ± 17^a	1291 ± 211^a
A. aurantii (lemon)	60	174 ± 16^a	1347 ± 188^a
A. nerii (potato)	60	170 ± 17^a	1339 ± 205^a
H. coormemani			
15°C	16	207 ± 27^a	2177 ± 483^a
24°C	40	241 ± 18^b	2445 ± 256^b
30°C	40	232 ± 21^b	2431 ± 378^b
A. aurantii (lemon)	52	252 ± 22^a	1337 ± 378^a
A. nerii (potato)	44	239 ± 17^a	2461 ± 301^a

Significance: $p = 0.05$, Tukey's studentized range test.
Means followed by the same letter are not significantly different from one another.

diurnal fluctuations of as much as 15°C are not uncommon. It would appear that *H. malus* has developed a more stable expression of character variance across a broader range of environmental influences, perhaps due to stabilizing selection pressures.

Higher environmental temperatures resulted in a smaller mean body size for both species. If the growth rate is inversely correlated with the length of time required to complete a developmental increment, the trend for a smaller body size in *Hemisarcoptes* may be correlated with a relatively faster growth rate at higher seasonal temperatures.

The observation that a shift in food resources (host species) has minimal effects on both *H. malus* and *H. cooremani* is consistent with the fact that, although *Hemisarcoptes* species are obligate specialist predators of diaspidid scale insects, within that family (Diaspididae) they are generalists in their diet. This particular family of scale insects is large and exhibits considerable morphological (and presumably physiological and chemical) variation. An estimate of the number of genera included is approximately 340, including an estimated 1700 species, but possibly only half of the extant species have been described (Borchsenius, 1966). *Hemisarcoptes* has been found in association with many of these species (Gerson *et al.*, 1990) and readily transfers from host to host (M. A. Houck, personal observation).

In conclusion, our experiments have demonstrated that plasticity in morphological character development correlates with environmental variables

in the characters that we studied. However, even considering that the characters evaluated in this study are allometrically constrained by the experimental parameters, taken together the species-specific patterns of shield complexity, shield size and setal lengths are sufficiently distinctive to allow the diagnosis and identification of these two North American species. Caution is warranted, however, when considering the complexity of the prodorsal shield as a key character, as it appears to be a continuous character (not discrete) dictated by the body size. Larger *H. malus* could be mistaken for small *H. cooremani* and vice versa in a geographic range where the body size is similarly affected by the temperature. Perhaps the most useful character for diagnosis would be the *sce* setal pair because it is so distinctive. It is relatively shorter in the larger of the two species, *H. cooremani*, which is counter to the general pattern of an increase in character size with an increase in general body size. The degree to which the two species exhibit variation in their morphology under different environmental regimes appears to be inversely correlated with the environmental variation the two species encounter across their natural ranges.

ACKNOWLEDGEMENTS

We would like to thank Rod Summy (US Department of Agriculture) and Victor French (Texas A & M Citrus Center) for assisting in the location of the collection sites and for generously providing working space in Weslaco, Texas. Robert F. Luck provided the California red scales. Richard E. Strauss added useful comments on the manuscript. This work was partially supported by the National Science Foundation (BSR no. 83-07711 to B.M.O. and M.A.H.) and BARD (no. IS-1397-87 no. US-2359-93C to M.A.H.).

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