

MORPHOLOGICAL ADAPTATIONS ASSOCIATED WITH MATE-GUARDING BEHAVIOUR IN THE GENUS *HERICIA* (ACARI: ALGOPHAGIDAE)

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Abstract

Males of an undescribed astigmatic species of the algophagid genus *Hericia* demonstrate precopulatory contact mate-guarding behaviour. Adults are sexually dimorphic, and most of the morphological differences found in males are associated with guarding behaviour. In this regard, coxae IV of the male are located ventrally and mesiad of coxae III, thereby resulting in legs IV taking a position directly below legs III. Legs IV are also bowed ventrally and can be rotated forward to form a 'basket' under the idiosoma. Males use their baskets for 'scooping' up quiescent tritonymphal females and holding them securely under their idiosomas. Males thereby guard immature females until they ecdyse to adults, at which time mating takes place. Some males were observed guarding adult females for extended periods of time, presumably after copulation. It is therefore possible that this species also exhibits post-insemination mate-guarding behaviour, however details concerning this behavior are poorly known.

INTRODUCTION

The principal measure of a male's success is the production of offspring, and, as Parker (1970) pointed out in his classic paper on sperm competition, an individual male's reproductive success can be advanced by (1) inseminating the partners of other males and (2) preventing his own sexual partners from being inseminated by rival males. The latter is often accomplished by means of mate guarding (Alcock 1994; Choe and Crespi 1997). While post-insemination mate guarding appears to be the most commonly used method in arthropods (see Alcock 1994), precopulatory mate guarding (= precopula) is often reported, especially among crustaceans (Manning 1975; Grafen and Ridley 1983; Jivoff and Hines 1998), and is not uncommon among the Arachnida (for examples see Benton 1992 for Scorpiones, Watson 1990 for Araneae; and Potter *et al.* 1976; Yasui 1988; Evans 1992; Witalinski *et al.* 1992 for Acari). The following account describes precopulatory mate-guarding behaviour in an undescribed mite species of the algophagid genus *Hericia*, an inhabitant of sap flux on trees.

MATERIALS AND METHODS

Bark and wood from sap-flux regions on oak trees (*Quercus* sp.) containing *Hericia* were collected near Williamsburg, Virginia, U.S.A. during the month of June. A stereomicroscope was used to make behavioural observations of mites on their natural substrate. Mensural data were collected on idiosomal length (micrometres) and leg relative lengths (percentage of idiosomal length) for tritonymphs, males, and non egg-bearing females. Analyses of variance and post hoc Tukey HSD tests were used to determine statistically significant differences. To examine the morphological adaptations of males associated with mating, both phase contrast microscopy and scanning electron microscopy (SEM) were used. For SEM preparation, living mites were briefly submerged in water near the boiling point in order to force protrusion of the legs. Specimens were then dehydrated in ethyl alcohol, dried using the critical point procedure, affixed to stubs using double-sided sticky tape, and coated with gold paladium in a sputter coater. For SEM preparation of males in amplexus with quiescent

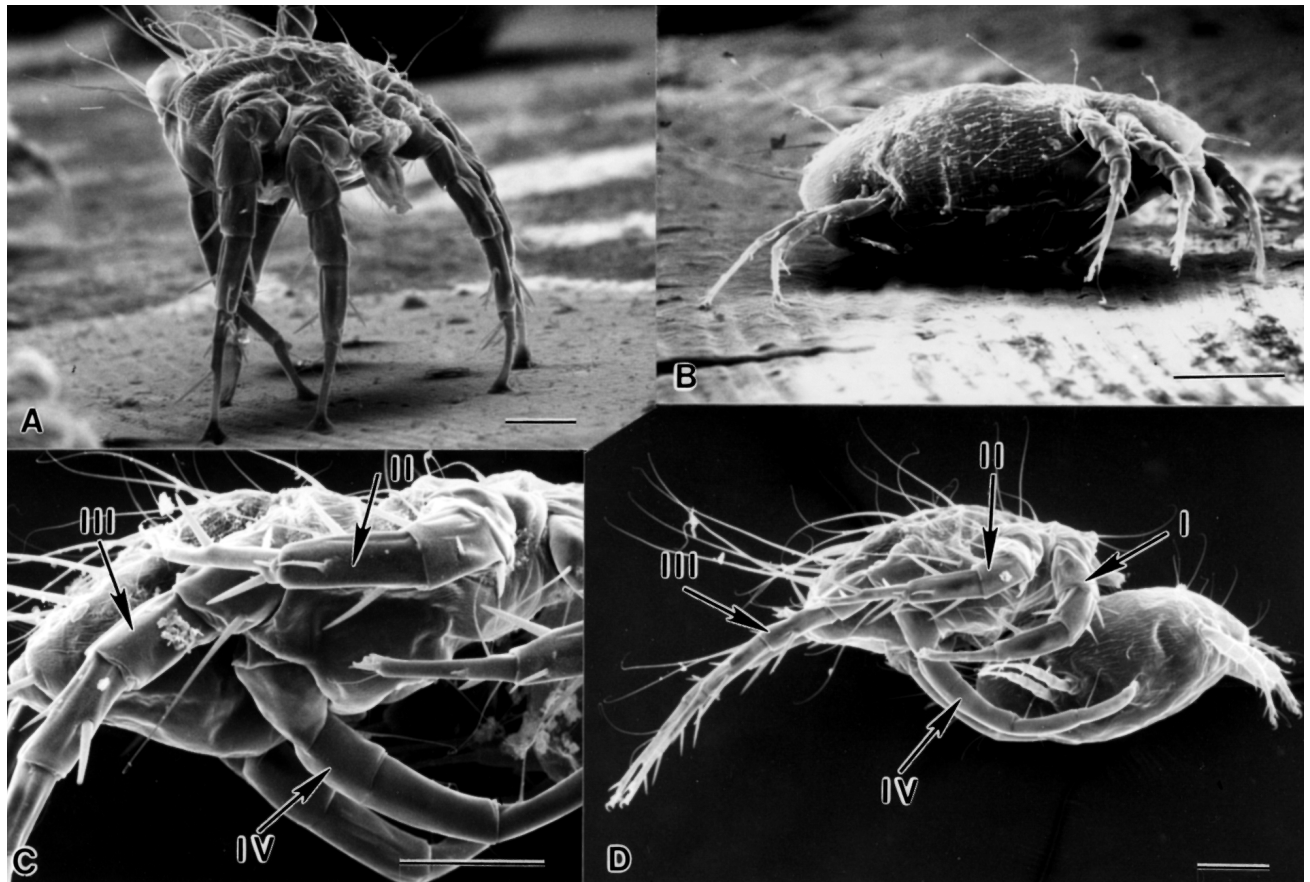


Figure 1 *Hericia* sp. Scale bar = 100 micrometres. A. Anterior/lateral view of male illustrating long legs; B. Lateral view of female illustrating relatively short legs; C. Lateral view of male illustrating ventral articulation of legs IV below legs III; D. Lateral view of male in amplexus with tritonymph. I = leg I, II = leg II, III = leg III, and IV = leg IV.

tritonymphs, the same protocol was used except that pairs in pre-copula were immersed in liquid nitrogen rather than hot water. SEM microscopy was performed on an AMR-1810.

RESULTS AND DISCUSSION

Hericia inhabits the sap fluxing regions of trees, and accomplishes movement primarily by pulling itself through the sap flux using legs I and II; legs III and IV are generally dragged along behind. The dorsolateral origins of legs I and II (Figs 1A, 1B) aid in this process.

Measurements on idiosomal length and relative leg lengths are given in Table 1. Results from analysis of variance tests followed

by Tukey HSD multiple comparisons tests indicate that males and females do not differ significantly in idiosomal length ($p = 0.948$), but tritonymphs are significantly smaller than both males ($p = 0.01$) and females ($p = 0.039$). For legs I through III, males have significantly longer legs than females ($p < 0.0005$ for all comparisons) and tritonymphs ($p < 0.0005$ for all comparisons), and females have significantly longer legs than tritonymphs ($p < 0.0005$ for all comparisons). The lengths of legs IV do not differ significantly between males and females ($p = 0.997$), but those of tritonymphs are significantly shorter than males ($p < 0.0005$) and females ($p < 0.0005$). Although legs I–IV of females are somewhat longer than those of tritonymphs, legs I–III of males are considerably longer than those of both females and tritonymphs

Table 1 Measurements of males, females and tritonymphs. Means and their standard errors for idiosomal lengths expressed in micrometers, and for lengths of leg I–IV expressed as a percentage of idiosomal length. Sample size equals 10 for males and tritonymphs and 7 for females.

	Idiosomal Length μm	Leg I Length %	Leg II Length %	Leg III Length %	Leg IV Length %
MALE	368 ± 14.0	89.3 ± 1.20	100.4 ± 1.29	112.5 ± 1.78	85.4 ± 1.22
FEMALE	363 ± 11.8	65.9 ± 5.05	74.3 ± 2.06	82.8 ± 2.21	85.2 ± 2.94
TRITONYMPH	320 ± 5.9	48.4 ± 1.68	54.2 ± 2.04	54.8 ± 2.36	54.3 ± 2.07

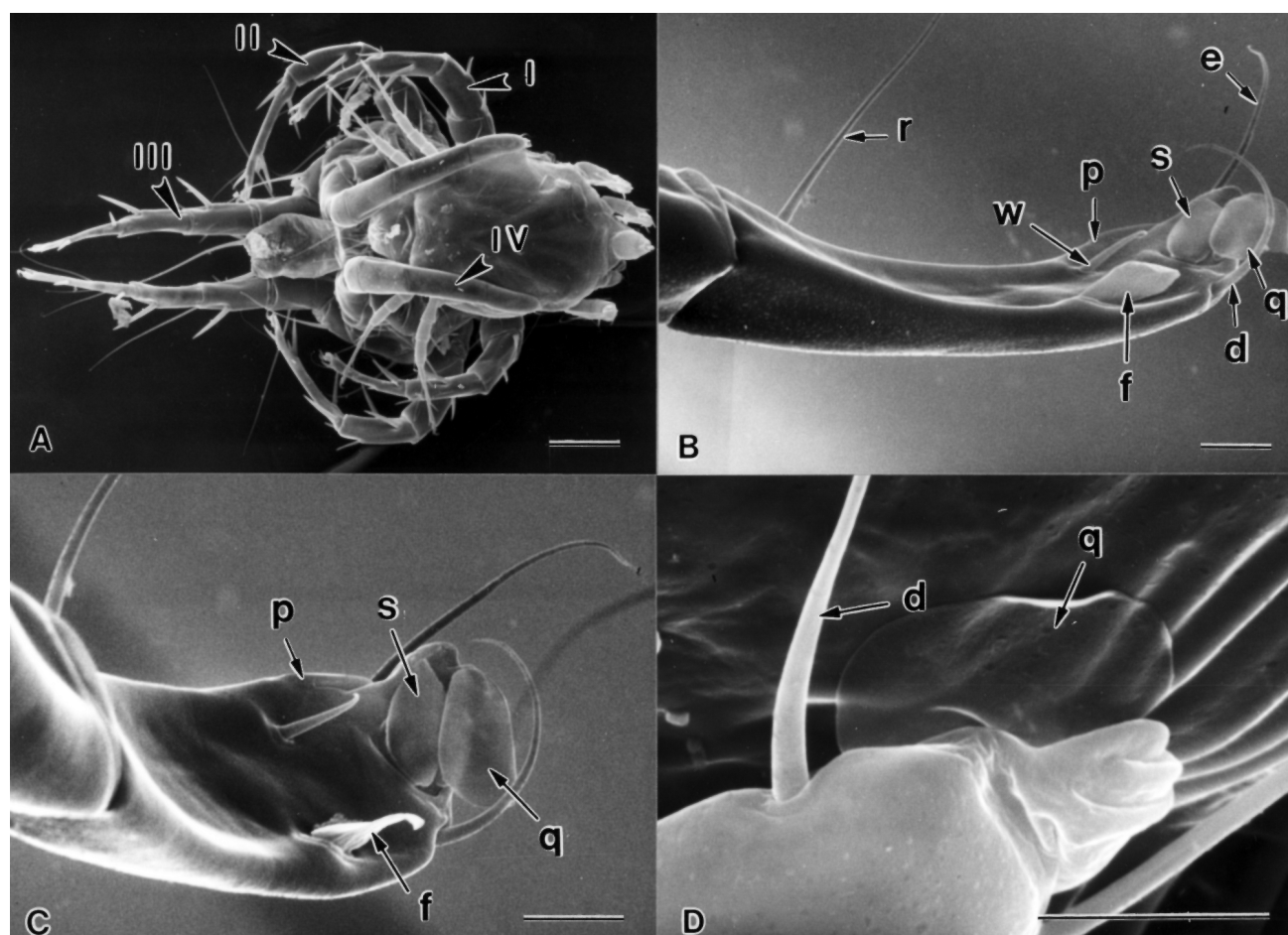


Figure 2 *Hericia* sp. Scale bar of A = 100 micrometres; scale bar of B, C, D = 10 micrometres. A. Ventral view of male in amplexus with tritonymph; B. Lateral view of tarsus IV; C. Ventrolateral view of tarsus IV; Dorsolateral view of apical region of tarsus IV illustrating attachment of seta q to tritonymphal integument. I = leg I, II = leg II, III = leg III, and IV = leg IV.

(Table 1). Males therefore have a 'spider-like' appearance (Fig. 1A), when compared with females (Fig. 1B) and especially to tritonymphs (Fig. 1D), and their long legs allow their idiosomas to be carried high off the substrate while moving about.

The legs of males also differ in many other attributes from those of females and immatures. Legs I–III are much more robust, and many setae take the form of long, stout spines. Legs III also originate dorsolaterally, and coxae IV are located ventral to and mesiad of coxae III (Fig. 1C), with the result that legs IV are positioned directly below legs III. The articulation of the coxae is such that legs IV can be rotated and thereby directed anteriorly (Fig. 1C). Legs IV are also bowed ventrally, and when rotated forward form a basket under the idiosoma (Fig. 1C). Legs IV of the male are also highly modified when compared to his other legs. In addition to being concave ventrally, both the tibiae and tarsae of legs IV are broader and flatter (Figs 1C, 2A–C). The ambulatorium forms a fleshy pad (Fig. 2D), and the claw is absent (rarely vestigial). And finally, ventral apical setae f, q and s are broadly expanded and thin, forming membrane-like flaps (Figs 2B–C).

All of the sexually dimorphic attributes of the male discussed above are associated with mate-guarding behaviour. When a male

encounters a quiescent tritonymphal female, he approaches from the rear, rotates legs IV so that they are directed forward, and uses them to 'scoop' her up and position her in the basket formed under his idiosoma (Figs 1D, 2A). The flattened, concave nature of the tibiae and tarsi aid in clasping the tritonymph, and the enlarged, flattened, membrane-like apical setae conform to the contour of the cuticle of the tritonymph (Fig. 2D) and secure her in place by surface tension. Long legs I–III allow the male to carry the tritonymph above the substrate while moving about, tenaciously holding her in place; males seldom release quiescent tritonymphs even when pushed about with a small probe. Males guard quiescent tritonymphal females until they ecdyse to adults, at which time mating takes place.

On occasion males were observed to remain with adult females for extended periods of time, carrying them about in the same 'fork-lift-like' manner. Since ample time lapsed for copulation to take place, it is assumed that the females were inseminated. It is therefore possible that post-insemination guarding behaviour also occurs in this species, however confirmation of this behaviour awaits further study. Both precopulatory and postcopulatory mate-guarding behaviour have been observed in a species of

isopod, *Thermosphaeroma thermophilum* (Cole & Bane) (Jormalainen and Shuster 1999).

It is obvious that as long as a male guards the tritonymphal or adult female by holding her in amplexus, no other male has access to her for copulation. Such behaviour helps insure the guarding male's paternity of the resultant offspring, but it is not without cost. It is advantageous for a male to mate with as many females as possible, and time spent guarding is time lost in acquiring additional mates (Alcock 1994). In *Hericia*, the benefits must far outweigh the costs as evidenced by the selective pressures that have led to the extreme morphological modifications associated with mate guarding in the male.

Many questions remain unanswered concerning mating behaviour in *Hericia*. Precopulatory mate guarding is expected to occur in species where receptive females are in short supply (Dickinson 1997). This can be due to a short period of female sexual receptivity, usually occurring immediately after the molt. It is therefore advantageous for a male to guard a quiescent female so he will be present to mate when she molts. Although high densities of both males and females were observed in populations during this study, it is not known when and for how long *Hericia* females are receptive. Post-insemination guarding behaviour is observed in species where females mate more than once (Alcock 1994), and a male therefore remains with a female to guard his sperm investment. In some species, the last sperm in takes precedence in fertilisation as is the case with the acarid mite *Sancassania* (= *Caloglyphus*) *berlesei* (Michael) (Radwan 1991). In others, there is no sperm precedence but the male remains with the female until his sperm has fertilised at least some of the eggs as is the case with the acarid mite *Rhizoglyphus robini* Claparede (Radwan and Siva-Jothy 1996). Both the frequency of mating by female *Hericia* and the nature of sperm precedence are unknown. In addition, it is unknown if larger males have a higher reproductive fitness. Since males must carry tritonymphs while guarding, it would seem likely that smaller males would be limited to guarding only small tritonymphs whereas large males could guard any size. In some arthropod species, rival males attempt to dislodge the guarding male and take possession of the female; in these cases, larger males have a definite advantage in female 'take-over'. I did not observe such behaviour in the case of *Hericia*, however the bright light necessary to observe mite behaviour under the stereomicroscope may have inhibited these interactions. In some acarine species, e.g. spider mites (Cone *et al.* 1971) and *Macrocheles muscaedomesticae* (Scopoli) (Yasui 1992), the quiescent nymph produces a pheromone that attracts males. It is not known how males of *Hericia* detect quiescent tritonymphs. Finally, it is unknown if females have a choice in mate selection. Although observations on mate guarding were made on only one species of the genus *Hericia*, it is quite likely that others have the same behaviour. Illustrations of *H. fermentationis* Vitzthum (Vitzthum 1931, Samsinak 1972) and *H. georgei* Michael (Samsinak 1972) reveal that males possess the morphological adaptations for mate guarding discussed above.

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