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Review

Phoresy by *Hemisarcoptes* (Acari: Hemisarcoptidae) on *Chilocorus* (Coleoptera: Coccinellidae): influence of subelytral ultrastructure

M.A. Houck*
Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409–3131, USA
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ABSTRACT

The non-phoretic stages of mites of the genus *Hemisarcoptes* are predators of the family Diaspididae. The heteromorphic deutonymph (hypopus) maintains a stenoxenic relationship with beetles of the genus *Chilocorus*. The mites attach to the subelytral surface of the beetle elytron during transport. There is variation in mite density among species of *Chilocorus*. Both *Hemisarcoptes* and *Chilocorus* have been applied to biological control programmes around the world. The objective of this study was to determine whether subelytral ultrastructure (spine density) plays a role in the evolution of symbiosis between the mite and the beetle. The subelytral surfaces of 19 species of *Chilocorus* and 16 species of *Exochomus* were examined. Spine density was determined for five subelytral zones: the anterior pronotal margin, medial central region, caudoventral tip, lateral distal margin and epipleural region. Spine density on the subelytral surface of *Chilocorus* and *Exochomus* was inversely correlated with the size of the elytron for all zones except the caudoventral tip. This suggests that an increase in body size resulted in a redistribution of spines and not an addition of spines. The pattern of spine density in *Exochomus* and *Chilocorus* follows a single size–density trajectory. The pattern of subelytral ultrastructure is not strictly consistent with either beetle phylogeny or beetle allometry. The absence of spines is not correlated with either beetle genus or size and species of either *Chilocorus* or *Exochomus* may be devoid of spines in any zone, irrespective of body size. A general difference between species of *Chilocorus* and *Exochomus* is the fact that while spine density in *Chilocorus* is clinal relative to the size gradient, *Exochomus* is dichotomous and likely to have either many spines or no spines in a particular zone. No species of *Chilocorus* was completely devoid of spines. Five species of *Exochomus* had no spines at all, thus making it difficult to interpret the primary function of the subelytral spines in a general way. Within the genus *Chilocorus*, spine density may play a synergistic role in host association. Based on morphological evidence alone, these findings lead to the hypothesis that the species of *Chilocorus* that would be most conducive to biological control application in conjunction with *Hemisarcoptes* would be *Chilocorus cacti, Chilocorus*

* To whom correspondence should be addressed at: Tel: 1 806 742 2715; Fax: 1 806 742 2963; e-mail: y1mah@ttacs.ttu.edu

distigma, Chilocorus fraternus, Chilocorus orbus, Chilocorus tristis and, to a lesser extent, *Chilocorus bipustulatus*.
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Key words: *Chilocorus*, Coccinellidae, *Exochomus*, *Hemisarcoptes*, ultrastructure, phoresy, biological control, parasitism.

INTRODUCTION

Phoresy: role in the evolution of parasitism

Phoresy is a symbiotic process by which an organism – the phoretic – passively hitchhikes on the exterior of a host organism, disembarking as the host traverses a replenished or suitable environment. The phoretic relationship represents a continuum, from apparent casual serendipity, for example *Histiogaster arborsignis* with over 40 acceptable hosts representing three insect orders, to stenoxenic, for example members of the genus *Hemisarcoptes* (Houck and OConnor, 1991). As the phoretic becomes more committed to one particular host species, that host becomes an important selective force in the evolution of traits affecting symbiosis in the phoretic.

Astigmatid mites are small, soft-bodied acarines which are specialists of temporally and spatially patchy habitats (e.g. carrion, dung, phytotelmata, beach wrack, etc.) and which use phoresy to traverse the long distances between ephemeral or degrading environments (Houck and OConnor, 1991). It has been suggested that phoresy is a possible transitional step into the most extreme form of symbiosis, that of parasitism (e.g. Fain, 1971). Parasitism may originate from free-living members of a cohesive community by a series of steps involving phoresy (Fig. 1). The conceptual model is that the formation of symbiotic relationships within this community is a logical and necessary step prior to parasitism. Stenoxenic relationships are likely to be candidates for the gradation into parasitism and interspecific associations which are not tangled in multiple channels of community interactions offer the simplest and most successful pursuit for the study of the evolution of parasitism.

The above scenario is problematic in that it is a *post hoc* explanation. Once parasitism is accomplished in a taxon, phoresy (dispersal) would become maladaptive and traces of the phoretic activity would be removed from the life cycle (e.g. *Linobia*). The opportunity to examine intermediate symbiotic relationships, which have a potential to extend into parasitism, is uncommon in nature. Phoresy in the Astigmata offers such a window into the process of transition.

One apparent phoretic relationship appears to be in the process of grading into parasitism from phoresy (Houck and OConnor, 1990, 1991; Houck and Lindley, 1993; Houck and Cohen, 1995). This association exists between beetles of the

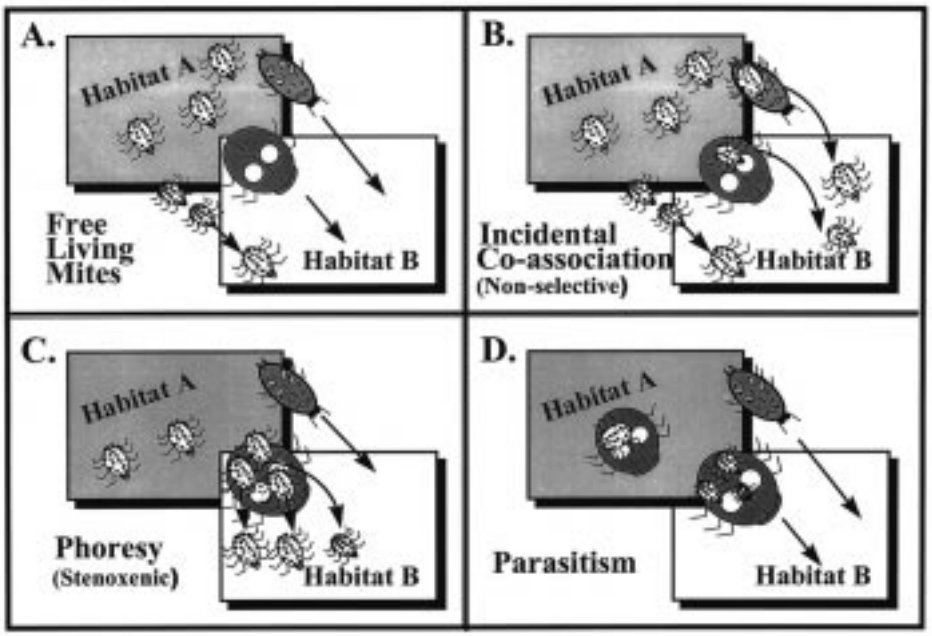

Fig. 1. Parasitism is an evolutionary response to long-term ecological interactions among organisms within a community. Parasitism is thought to have arisen in free-living organisms (A) from an initial non-selective symbiotic relationship such as incidental phoresy (B) which progressed into a stenoxenic (restrictive) relationship (C). Parasitism (D) emerged as an evolutionary phenomenon when the phoretic extended its dependence on the host from simple habitat dispersal to nutritional dependency.

genus *Chilocorus* (Coleoptera: Coccinellidae) and phoretic mites of the genus *Hemisarcoptes* (Acari: Acariformes: Hemisarcoptidae).

The phoretic mite

Hemisarcoptes malus was one of the first mites described from North America (Shimer, 1868) and one of the first mites applied to biological control in the US (e.g. Shimer, 1868; Riley, 1873; Ewing and Webster, 1912; Tothill, 1918). The genus *Hemisarcoptes* occurs throughout the northern hemisphere, Africa, the Oriental region and Australia. Currently, five species of *Hemisarcoptes* are known from the literature, but a worldwide revision is in preparation (OConnor and Houck, 1989a,b; Houck and OConnor, 1996, 1998; B.M. OConnor and M.A. Houck, ms.in preparation). The genus is clearly more diverse than previously considered.

The nominal species and their type locations, as reported from the literature, are *Hemisarcoptes coccisugus* Lignières (Lignières, 1893), Paris, France, (2) *H. malus* (Shimer) (Shimer, 1868), Mt Carroll, Illinois, USA, (3) *Hemisarcoptes cooremani* (Thomas) (Thomas, 1961), Weslaco, Texas, USA, (4) *Hemisarcoptes coccophagus*

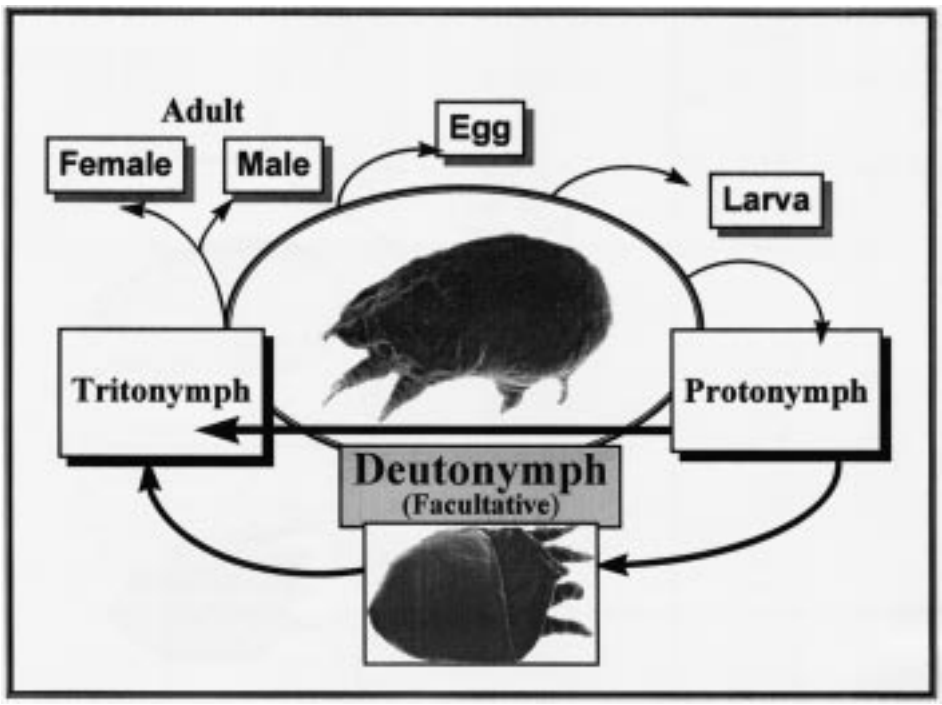

Fig. 2. The life cycle of *Hemisarcoptes*. Most stages of the mite (i.e. larva, protonymph, tritonymph and adult) are predators of scale insects of the family Diaspididae. The heteromorphic deutonymph (hypopus) is facultative and phoretic on beetles of the genus *Chilocorus*. In *H. cooremani*, the deutonymph is a low-level polymorphism (only represented in ~6% of the ontogenies within natural populations) and is not required to complete the life cycle (Houck and OConnor, 1990).

Meyer (Meyer, 1962), Letaba, Transvaal, South Africa and (5) *Hemisarcoptes dzhashii* Dzhibladze (Dzhibladze, 1969), Zelenyy Cape, Georgian SSR, USSR.

All of the non-phoretic stages of *Hemisarcoptes* (larva, protonymph, tritonymph and adult; Fig. 2) are predators of armoured scale insects of the family Diaspididae (Gerson *et al*., 1990; Houck and OConnor, 1990). All non-phoretic stages occur under the scale cap with their chelicerae imbedded into the host tissues. The deutonymphal stage, however, is a heteromorph (hypopus) which maintains a symbiotic relationship with beetles of the genus *Chilocorus* (Houck and OConnor, 1991; Houck and Lindley, 1993; Houck, 1994; McCormick *et al*., 1994; Houck and Cohen, 1995; Xiongwei *et al*. 1995). *Hemisarcoptes* has not been found to occur on any other genus of beetle under natural conditions and is considered stenoxenic.

Hemisarcoptes is interesting not only from the point of view of its phoretic characteristics, but it is also an economically interesting mite in terms of biological control (Houck and OConnor, 1990, 1991; Hill *et al*., 1993; Houck, 1994; Charles

TABLE 1

Occurrence and distribution of genera of the tribe Chilocorini (Drea, 1952; Chapin, 1965; Gordon, 1985)

Taxa examined	Number of species in the genus	Regions of distribution
Anisorcus Crotch (1)	3	Australia and the Orient
Arawana Leng (1)	3	North America, Central America and Cuba
Axion Muls. (2)	2	North America
Brumoides Chaplin (2)	9	Worldwide
Brumus Muls. (1)	1	Palearctic and the Orient
Chilocorus Leach (19)	70	Worldwide
Cladis Muls. (1)	1	Mexico and West Indies
Corystes Muls.	2	South America
Curinus Muls. (3)	3	Central and South America
Egius Muls. (1)	1	Cuba
Elpis Muls. (1)	2	Africa
Endochilus Weise (1)	8	West Africa
Exochomus Redtenbacher (16)	30	Worldwide
Halmus (= *Orcus*) Muls. (3)	3	Australia and the Orient
Harpasus Muls. (1)	1	South America
Parapriasus Chaplin (1)	2	Australia
Phaenochilus Weise (1)	3	Philippines
Priasus Muls. (1)	1	Australia
Trichorcus Blackburn (1)	2	Australia
Zagreus Muls. (1)	9	Jamaica

et al., 1995a,b; Houck and Cohen, 1995; Izraylevich and Gerson, 1995a,b,c). Currently, *H. cooremani* and *H. coccophagus* are used in agricultural programmes to control diaspidids.

The beetle host

The Chilocorini Costa, 1849, is a cosmopolitan tribe of beetles within the family Coccinellidae, subfamily Chilocorinae. All species are small, oval and moderately to strongly convex, with an upper glabrous or pubescent surface (Chapin, 1965). The tribe radiated in the tropics (Gordon, 1985) and is particularly diverse in Africa. *Chilocorus* and *Exochomus* are the most widely distributed of the species (Table 1). Korschefsky (1931–1932), in his *Coleopterorum Catalogus*, recognized 24 generic or subgeneric divisions within the Chilocorini, but four of these taxa (*Clanis, Notolipernes, Cortystes* and *Elpis*) were not supported in a later revision by Chapin (1965). Chapin (1965) synonymized *Notolipernes* with *Telsimia* and moved it out of the tribe Chilocorini. *Cortystes* was listed by Korschefsky (1931–1932) as within the Chilochorini but was placed in the Hyperaspini by Chapin (1965). A third genus (*Elpis*) was transferred by Chapin (1965) to the Coccinellini, near *Menochilus*. Currently, 20 taxa are considered to comprise the Chilocorini. The

TABLE 2

The biological control application of species of the Chilocorini used to control scale insect pests

Species of beetle applied to biological control	Year of application (if given)	Beetles exported from	Beetles imported into	Imported to control (Note: scientific name sometimes not given)
Axion pilatei Muls.	1901	California	South Africa	Diaspididae *Aonidiella aurantii* (Mask.)
Brumus suturalis (F.)	1937	South India	Kenya	Pseudococcidae *Planococcus kenyae* (LePelley)
Curinus caeruleus Muls.	1951	Trinidad	Bermuda	Asterolecaniidae
	1965	West Indies	Sao Tome	*Asterolecanium* spp. Diaspididae *Aspidiotus destructor* Sign.
Chilocorus angolensis Crotch	1932	Kenya	Indigenous	Pseudococcidae
	1946	South Africa	liberation	mealybugs
	1949	South Africa, Zanzibar	Ghana	Diaspididae
	1966	Kenya	Israel	*Aonidiella aurantii* (Mask.)
C. bijugus Muls.	1960	India	Bermuda	Diaspididae
	1961	India	Switzerland	*Quadraspidiotus perniciosus* (Comstock)
C. bipustulatus (L.)	1924	Italy	Bermuda	Diaspididae
	1947	France	Bermuda	*Parlataria blanchardii* (Targ.)
	1950	Portugal	Bermuda	*Pseudaulacaspis pentagona* (Targ.)
	1951	Cuba, ex. P.R., ex Trinidad	Bermuda	*Aspidiotus destructor* Sign.
	1963	India	West Transvaal, Zebedeila	
	1963	Pakistan	South Africa	
	1968	Iran	Mauritania	
C. cacti (L.)	1947	Puerto Rico	Bermuda	Diaspididae
	1951	Jamaica	Bermuda	*Aonidiella aurantii* (Mask.)
	1965	USA	Sao Tome	Margarodidae
	1966	USA	West Transvaal, Zebedeila	*Icerya purchasi* Mask.
	1966–1968	USA	Pretoria	Asterolecaniidae
	1969	Caribbean	Peru	*Asterolecanium* spp.
	1977	Caribbean	Columbia	Diaspididae *Aspidiotus destructor* sign. *Parlagena bennetti* Williams *Selenaspidus articulatus* (Morg.)

C. circumdatus (Gyll.)	1898	Ceylon	South Africa	Pseudococcidae
	1902	Hong Kong	West Australia	mealybugs
	1959	India via Trinidad	Bermuda	Diaspididae
	1960	India	USA	*Aonidiella aurantii* (Mask.)
	1965	India	West Transvaal, Zebedeila	*Aspidiotus* sp.
	1965	India	South Africa	
	1968	India	Cyprus	
C. discoideus Muls.		Uganda	Mauritius	Diaspididae
C. distigma (Klug)	1936	East Africa	Seychelles	Diaspididae
	1946	Zanzibar, Kenya	Mauritania	*Parlatoria blanchardii* (Targ.)
	1947	South Africa	Bermuda	
	1968	Senegal	Mauritania	
C. dohrni Muls.	1920s	Indigenous liberation?	Sierra Leone	Diaspididae
				Aspidiotus destructor Sign.
C. hauseri Weise	1960	India	Bermuda	Diaspididae
	1960	India	USA	*Pseudaulacaspis pentagona* (Targ.)
	1968	India	Cyprus	
C. kuwanae Silv.	1924	Far East	Bermuda	Diaspididae
	1958	China	Bermuda	*Aonidiella aurantii* (Mask.)
	1961	Japan	Switzerland	*Pseudaulacaspis pentagona* (Targ.)
	1961	Japan	India	*Quadraspidiotus perniciosus*
	1961	Japan	Pakistan	(Comstock)
	1965	Japan	Zebedeila	
	1965	Japan	South Africa	
C. nigritis (F.)	1936	India	Seychelles	Diaspididae
	1939	Ceylon	Mauritius	*Carulaspis minima* (Targ.)
	1947	Sri Lanka	Bermuda	*Aspidiotus destructor* Sign.
	1955	Mauritius	Agelega Islands	
	1956	Mauritius	Chagos Archipelago	
	1959	Ceylon	Hawaii	
C. politus Muls.	1928	Java	Indonesia	Diaspididae
	1937	Java	Mauritius	*Asipidoitus destructor* Sign.
	1937	Figi	Mauritius	
C. schioedtei Muls.	1920s	Indigenous liberation?	Sierra Leone	Diaspididae
				Asipidiotus destructor Sign.

TABLE 2 (*continued*)

Species of beetle applied to biological control	Year of application (if given)	Beetles exported from	Beetles imported into	Imported to control (Note: scientific name sometimes not given)
C. stigma Say (= *bivulnarus* Muls.)	1900	USA	South Africa	Diaspididae
	1907	USA	West Australia	*Parlatoria blanchardii* (Targ.)
	1908	USA	Italy	*Aonidiella aurantii* (Mask.)
	1927	USA	New South Wales	*Quadraspidiotus perniciosus*
	1947	USA	Bermuda	(Comstock)
	1951	USA	Bermuda	*Asipidiotus destructor* Sign.
	1968	USA	Mauritania	
C. wahlbergi Muls.	1936	East Africa	Seychelles	
	1946	Zanzibar, Kenya	California	
Egius platycephalus Muls.	1947	USA	Bermuda	Diaspididae
	1948	Cuba	Bermuda	*Aspidiotus destructor* Sign.
E. platycephalus Muls.	1952	Caribbean	Hawaii	Asterolecaniidae
				bamboo scales
Exochomus bisbinotatus Gohr.	1947	USA	Bermuda	Diaspididae
	1951	Trinidad	Bermuda	*Aspidiotus destructor* Sign.
E. quadripustulatus (L.)	1947	USA	Bermuda	Diaspididae
	1950	Portugal	Bermuda	*Aspidiotus destructor* Sign.
E. jamaicensis Sic.	1951	Jamaica	Bermuda	Diaspididae
				Asipidiotus destructor Sign.
E. flavipes (Thunb.)			Ghana	Pseudococcidae
	1918–1925	South Africa	California	mealybugs
				Diaspididae
				Aonidiella aurantii (Mask.)
Orcus chalybeus (Boisd.)	1947	Australia	Bermuda	Diaspididae
				Aspidiotus destructor Sign.
O. chalybeus	1900	New South Wales	Tasmania	Scale insects
	1902	New South Wales	West Australia	
O. bilunulatus (Boisd.)	1901	Tasmania	West Australia	Scale insects
O. lafertei Muls.	1902	New South Wales	West Australia	Scale insects
				Aphids
O. sp.	1907–1910	Queensland	Victoria	Diaspididae
				Aonidiella aurantii (Mask.)

Summarized mainly from Bennett and Hughes (1959), Wilson (1960), Greathead (1976), Cock (1982) and Rao *et al*. (1971).

members of this tribe are, for the most part, beneficial insects which prey on soft scales (Coccidae), oystershell scales (Diaspididae) and aphids (Aphididae) (Drea, 1952; Gordon, 1985; Drea and Gordon, 1990).

Chilocorus is a particularly interesting member of the Chilocorini because of its prominence in the application of biological control of scale insects of the family Diaspididae. It is a generalist predator of diaspidid scales and many species have been imported into various countries in an effort to control scale pests (Table 2).

Chilocorus is also the most diverse genus within the Chilocorini. The genus probably originated in the Ethiopian region and spread into the Palearctic and later into the New World, the Orient and Australia. The genus is represented throughout the world, with the greatest diversity in the Ethiopian region followed by (in descending sequence) Palearctic, Indo-Malayan, Nearctic and Australian and Neotropical regions. Extensive collecting and museum work (M.A. Houck, personal observation) have yielded no native species in South America. However, I have made one collection in the Atlantic coastal area of Brazil (probably *Chilocorus nigritus* imported from India via South Africa).

The elytral patterns within the genus *Chilocorus* are very variable both in colour and surface texture. The most common colour pattern is a red dot on a smooth black or brown elytral background and a dark pronotum (e.g. *Chilocorus bipustulatus*, *Chilocorus cacti*, *Chilocorus distigma*, *Chilocorus fraternus*, *Chilocorus hexacyclus*, *Chilocorus kuwanae*, *Chilocorus orbus*, *Chilocorus renipustulatus*, *Chilocorus sexguttatus*, *Chilocorus similis*, *Chilocorus stigma*, *Chilocorus tricyclus* and *Chilocorus tumidus*). However, the single dot may elongate into a stripe (e.g. *Chilocorus wallacei*), the dots may be missing completely (e.g. *Chilocorus calvis*, *Chilocorus cerberus*, *Chilocorus insularis*, *Chilocorus nigritus* and *Chilocorus reinecki*) or the dots may envelop the whole of the elytra such that the entire dorsal surface becomes a solid brownish red (*Chilocorus adustus*, *Chilocorus circumdatus*, *Chilocorus hauseri*, *Chilocorus melanophthalmus*, *Chilocorus politus* and *Chilocorus rubidustibialis*). *Chilocorus pilosus* is unusual in that the dorsal surface is pilose instead of smooth. Several species have a reddish pronotum (e.g. *Chilocorus cruentus*, *Chilocorus dohrni* and *Chilocorus silvestri*) and/or a reddish caudal dorsal tip (*Chilocorus malasiae* and *C. dohrni*).

Several species of *Chilocorus* have been exported by the Commonwealth Institute of Biological Control (CIBC) from India, Pakistan and the US to Africa for the control of red scale (*Aonidiella aurantii*). However, only *C. cacti* from the US showed signs of permanent establishment of the predatory beetles or the ability to control low densities of scale insects (Greathead, 1971). In one case, *C. cacti* was able to outcompete the native species of *Chilocorus* (i.e. *C. distigma*) (Greathead, 1971). *Chilocorus cacti* was able to bring concentrated infestations of red scales under control in Africa during the vulnerable period of transition from the use of parathion to integrated scale control and was found to be a good control agent of red scale under conditions of local and sporadic population expansion (Greathead, 1971).

Phoretic association

Exploitation of the phoretic association between *Hemisarcoptes* and *Chilocorus* offers a novel approach to biological control programmes of diaspidids because both the phoretic and the host consume diaspidid scale insects, but *Chilocorus* and *Hemisarcoptes* have very different patterns of feeding on scales. The beetle is a predator which exploits patches of scale incompletely and then disperses without effectively depleting local populations. The mite, however, gradually reduces scale fecundity and depletes the resource slowly, but with a high fidelity to a local area because the non-phoretic stages cannot effectively disperse long distances from the natal patch. Thus, a joint-implementation strategy of inundation by hypopus-laden beetles and chronic control by the dispersed mites could more efficiently bring scales under control and be more effective than either would be alone. Because of this, it is most important to understand the biological and behavioural characteristics of both the mite and the beetle and the interactions between them (Houck, 1989).

A large number of *Hemisarcoptes* have been collected both from museum specimens and from field samples of *Chilocorus* beetles. There is significant variation in mite density among individual beetles and among species of *Chilocorus* (M.A. Houck, personal observation). It also appears that mites from a particular geographical area are not adapted exclusively to indigenous species of *Chilocorus*. For example, under laboratory conditions, mites (*H. cooremani*) from Texas, US, removed from *C. cacti* readily recognized and attached to *C. nigritus* imported from India (M.A. Houck, personal observation). In addition, under certain laboratory conditions, this mite may make a weak phoretic association outside of the genus *Chilocorus*, with the beetles *Scymnus fagus* and *Halmus chalybeus* (Hill *et al*., 1993). However, more work needs to be done to validate these anecdotal observations.

The lack of host specificity by the mite presents an advantage, from a biological control perspective, because it allows the mixing and matching of different beetle and mite species to accommodate specific management goals. For example, a species of mite could be selected for application because of its enhanced voracity for scales and matched with a beetle with greater dispersal ability. Species could be selected because of specific environmental demands (e.g. high or low humidity tolerance).

Chilocorus cacti seems to have special promise for biological control. Individuals of *C. cacti* have been found to carry large numbers of *H. cooremani*, sometimes as many as 400 per elytron (Houck, 1994). *Hemisarcoptes cooremani* do not attach at random locations on the subelytral surface of *C. cacti* (Houck, 1994), but rather concentrate along the epipleural margin and the caudal ventral tip of the elytron (Fig. 3). Scanning electron photomicrographs (Houck, 1994) have indicated that all other elytral areas of *C. cacti* contain sharp spines in concentrations which could significantly damage the soft caudoventral sucker plate of mites attempting attachment (Fig. 4).

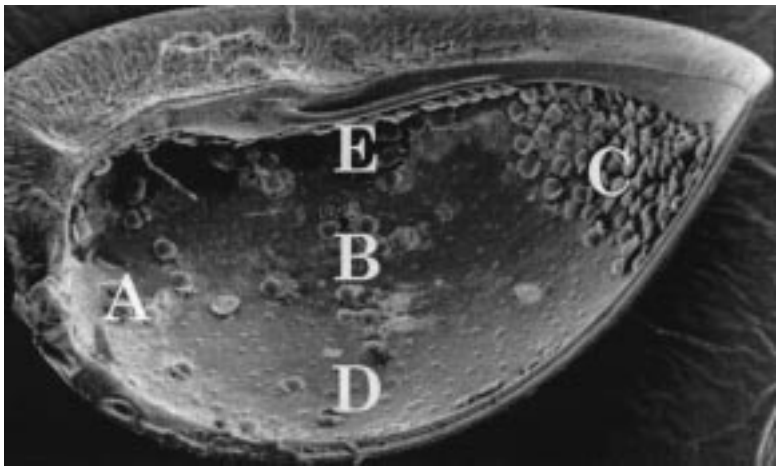

Fig. 3. An example of the subelytral surface of *Chilocorus*: *C. cacti* (containing *H. cooremani*). The subelytral surface of the various species of *Chilocorus* and *Exochomus* was divided into five major zones, to assess relative spine density. Notice the prevalence of *H. cooremani* in zones C and E. The five zones examined were (A) anterior pronotal margin, (B) medial central zone, (C) caudoventral tip, (D) lateral distal margin, and (E) epipleural harbour.

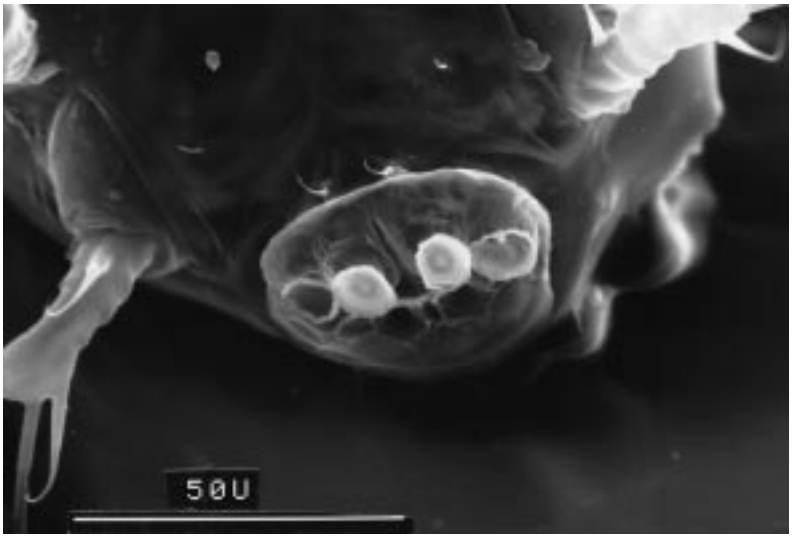

Fig. 4. Caudoventral view of *H. cooremani* showing the caudoventral sucker plate. During attachment to the subelytral surface of *Chilocorus*, this sucker plate can become damaged by spines at the point of attachment. In areas of dense spination, the sucker plate would be impacted by many of these spines. See Fig. 6 for comparison.

Why hypopodes attach specifically to some subelytral sites and not others (Fig. 3) is an interesting question and may eventually help us to understand why some species of *Chilocorus* are more conducive to mite transport than others. One hypothesis is related to the differences observed in the microsculpturing on the subelytral surface of the beetle elytron. Specifically, the hypothesis tested here is that the species of *Chilocorus* that are more conducive to the attachment of *Hemisarcoptes* would be those with reduced spination or with spination consistently restricted to localized zones. While some work has been done on the ultrastructure of integumentary glands of adult coccinellids (e.g. Barbier *et al*., 1992), very little attention has been given to the subelytral microsculpturing of beetles. My purpose is to examine the extent and prevalence of subelytral microsculpturing (1) within several families of the order Coleoptera, (2) within the coleopteran tribe Chilocorini and (3) within the genus *Chilocorus*. A preliminary survey of beetles representing 17 families within the order Coleoptera was conducted to gain an understanding of general elytral variation in the broadest taxonomic sense. I examined members of the following beetle families: Bruchidae, Buprestidae, Cantharidae, Carabidae, Cerambicidae, Chrysomelidae, Cicindelidae, Cleridae, Coccinellidae, Curculionidae, Dermestidae, Gyrinidae, Histeridae, Hydrophylidae, Meloidae, Scarabaedae and Silphidae. Of the families examined, only the Cleridae had no subelytral spines, indicating that spines are a prevalent (but not universal) feature of coleopteran elytral morphology. The details of this study will be reported elsewhere.

Learning that spines were a common feature of beetles, I examined the variation in spine configuration within the Chilocorini. I examined 17 of the 19 known genera of the tribe Chilocorini, representing 56 different species (Table 1). The results of this portion of the full study indicated that subelytral spines were also a consistent feature throughout the Chilocorini. The details of this study will be reported elsewhere.

I report here the variation and implications of the subelytral microsculpturing of 19 species of the genus *Chilocorus* and contrast this with the next most diversified genus within the tribe, *Exochomus*, for which 16 species were obtained. The comparison of *Chilocorus* and *Exochomus* was done (1) in order to determine whether there was any indication that spine density might be phylogenetically or allometrically constrained and (2) as a phoretic contrast at the genus level, since some species of *Chilocorus* carry large numbers of *Hemisarcoptes* while *Exochomus* have none. The implications of my findings are discussed in light of biological control programmes wishing to employ a combined *Hemisarcoptes*–*Chilocorus* management protocol.

MATERIALS AND METHODS

The subelytral surfaces of adults of 19 species of *Chilocorus* and 16 species of *Exochomus* were examined (Tables 3 and 4 and Fig. 3). Dried museum specimens were placed in a 100% humidity chamber for 48 h until the elytra became pliable.

TABLE 3

Subelytral spine density, tallied by zone (see Fig. 3), for 19 species of *Chilocorus*

	Anterior pronotal margin	Medial central zone	Caudoventral tip	Lateral distal margin	Epipleural harbour
C. australasiae	59.7 (11.4)	34.0 (4.5)	69.0 (5.0)	35.7 (3.1)	9.7 (5.5)
C. bilineatus	44.3 (5.5)	24.3 (4.9)	42.0 (11.5)	11.7 (1.5)	0.00
C. bipustulatus ($n = 3$)	23.6 (20.3)	12.9 (2.7)	11.6 (2.3)	10.3 (2.9)	0.00
C. cacti ($n = 10$)	46.3 (10.3)	42.7 (7.8)	1.3 (1.2)	0.00	0.00
C. cerberus	31.0 (9.2)	10.0 (8.2)	27.0 (8.7)	31.7 (4.5)	9.7 (2.1)
C. circumdatus	66.7 (2.1)	0.67 (1.2)	73.0 (11.3)	1.0 (1.0)	0.00
C. dorhni	46.7 (6.4)	1.7 (2.1)	21.0 (4.4)	26.3 (3.1)	0.33 (0.58)
C. distigma	53.7 (8.6)	10.0 (4.6)	1.7 (2.1)	3.0 (3.5)	0.00
C. fraternus	50.3 (2.1)	13.3 (0.58)	2.0 (0.0)	0.67	0.00
C. infernalis	57.3 (9.9)	44.0 (2.6)	36.0 (1.7)	51.0 (3.5)	8.6 (1.5)
C. kuwanae ($n = 2$)	41.0 (18.4)	38.8 (2.2)	46.7 (11.0)	54.9 (5.1)	13.4 (6.0)
C. melanopthalamus	53.0 (10.5)	0.33 (0.58)	57.3 (8.5)	1.3 (1.2)	6.7 (0.58)
C. nigritus ($n = 2$)	67.5 (15.2)	5.3 (4.1)	11.4 (7.2)	23.0 (2.5)	0.00
C. orbus	49.7 (9.9)	5.6 (4.0)	1.0 (1.0)	0.00	0.33 (0.58)
C. renipustulatus	39.7 (21.1)	27.0 (10.6)	45.0 (3.6)	13.3 (7.1)	21.7 (4.9)
C. rubidus	28.3 (26.3)	13.3 (11.0)	15.6 (14.6)	6.0 (4.0)	0.00
C. schioedtei ($n = 2$)	37.0 (7.4)	23.5 (3.5)	20.5 (13.5)	9.7 (9.1)	0.00
C. stigma ($n = 2$)	44.5 (8.2)	25.9 (2.4)	49.0 (3.9)	22.3 (4.7)	11.2 (3.3)
C. tristis	32.7 (2.1)	9.0 (4.0)	1.0 (1.7)	0.00	0.33 (0.58)
Mean across species (range)	46.0 (24–68)	18.0 (0–44)	28.0 (1–73)	19.0 (0–55)	8.0 (0–22)
Range of non-zero variables	44.0	44.0	72.0	55.0	22.0
Number of species with no spines	0.0	0.0	0.0	3/19 = 16%	9/19 = 47%
Number of species with ≤ 15 spines	0.0	11/19 = 58%	7/19 = 37%	12/19 = 63%	18/19 = 95%

Numbers listed by zone are the mean spine densities (±SD). A '0.00' indicates zones which had no spines present per 100 μm^2. Means calculated across species are for non-zero data. *n*, number of individuals examined ($n = 1$ when not mentioned)

The elytra were removed carefully with forceps and mounted on a metal stub using carbon-impregnated tape, with the subelytral surface exposed. Elytra were grounded to the stub using silver paint in colloidal suspension and sputter-coated with gold–palladium in a Technic's Hummer V Sputter Coater. Scanning electron microscopy (SEM) was conducted using a Hitachi S-570 microscope.

To determine spine density across the subelytral surface, the surface was divided into five zones: the anterior pronotal margin (Fig. 3A), medial central zone (Fig. 3B), caudoventral tip (Fig. 3C), lateral distal margin (Fig. 3D), and epipleural harbor (Fig. 3E). At each of the five zones, spine density was estimated by averaging the number of spines in three contiguous sectors of a zone (sector = 100 μm^2). Spines were counted directly from the viewing screen of the SEM.

TABLE 4

Subelytral spine density, tallied by zone (see Fig. 3), for 16 species of *Exochomus* examined

Exochomus	Zone A	Zone B	Zone C	Zone D	Zone E
E. aethiops	55 (4.0)	46 (2.6)	0.00	41 (15.9)	26 (7.5)
E. apustulatus	0.00	0.00	0.00	0.00	0.00
E. bimaculosus	0.00	0.00	0.00	0.00	0.00
E. californicus	0.00	0.00	0.00	0.00	0.00
E. childreni	86 (2.5)	0.00	0.00	0.00	50 (1.7)
E. constristatus	93 (6.9)	0.00	2 (4.0)	9 (4.2)	0.00
E. fasciatus	0.00	94 (0)	0.00	111 (11.4)	70 (4.5)
E. flavipes	115 (2.3)	95 (3.5)	2 (3.2)	115 (9.5)	66 (1.5)
E. jamaicensis	75 (10.3)	60 (3.0)	0.00	68 (2.1)	42 (3.1)
E. marginipennis	0.00	0.00	0.00	0.00	0.00
E. metallicus	73 (8.2)	49 (3.2)	0.00	78 (7.6)	47 (5.3)
E. nixidus	58 (13.0)	54 (0.6)	69.00 (3.8)	72 (5.0)	27 (5.0)
E. negripennis	83 (2.5)	60 (3.8)	0.00	84 (4.5)	45 (2.6)
E. orbiculus	0.00	0.00	0.00	0.00	0.00
E. subrotundus	71 (0.6)	0.00	0.00	53 (12.3)	0.00
E. uropygialis	88 (5.7)	61 (3.6)	0.00	3 (12.7)	47 (1.5)
Mean across species (range)	79.7	64.9	23	63.4	46.7
Magnitude of the range	60	49	67	112	44
Number of species with 0 spines	6/16 = 38%	8/16 = 50%	13/16 = 81%	6/16 = 38%	7/16 = 44%
Number of species with ≤ 15 spines	6/16 = 38%	8/16 = 50%	15/16 = 94%	8/16 = 50%	7/16 = 44%

Numbers listed per zone are the mean spine densities (±SD) (see text for explanation). A '0.00' indicates zones which had no spines present per 100 μm^2. Means calculated across species are for non-zero data.

Five univariate size measurements were recorded from each elytron: (1) the straight-line distance from the medial pronotal edge of the elytron to the distal tip of the elytron, (2) the straight-line distance from the proximal pronotal edge of the elytron to the distal tip of the elytron, (3) the circumference of the elytron, (4) the area of the elytron and (5) the length of the inside margin of the epipleural region to the tip of the elytron. One elytron from each beetle was examined using an Olympus BHS stereomicroscope attached to an image analysis system with Image-Pro software. One to three specimens per species were examined, depending on availability. The exception to this was the intraspecific comparison of ten specimens of *C. cacti*, a species of particular biological control interest, to assess the intraspecific variation within one species.

Since adults vary considerably in body size (both within and between species), a multivariate estimate of general size (Bookstein, 1989) of the subelytral surface was calculated for the various species. A principal component analysis (PCA) was done on the log transformed data, with the first PCA representing a general size axis. This was done to determine allometric relationships between spine density and elytron size.

RESULTS AND DISCUSSION

Spine density in the five zones of the subelytral surface of *Chilocorus* and *Exochomus* was inversely correlated (among species) with PC1 (general size) for all zones except the caudoventral tip (Fig. 5). This suggests that (except for the caudoventral tip), variation in body size is associated with a redistribution of spines across the subelytral surface, rather than an addition or deletion of spines. It also may reflect the fact that the tip of the elytron (the caudoventral tip) is less influenced by variation in general body size and is more geometrically constrained as size increases.

In general, the pattern of spine density is similar in *Exochomus* and *Chilocorus* and follows a single size–density trajectory. On average, *Chilocorus* has a larger general body size than *Exochomus*, which allometrically leads to fewer spines per unit area, perhaps making it a better *a priori* candidate for phoresy by *Hemisarcoptes* on allometric grounds alone. *Chilocorus cacti*, being one of the largest of the *Chilocorus* species, extends this general pattern. The exception to this pattern is in the caudoventral tip, in which all but one of the *Exochomus* are devoid of spines. *Chilocorus cacti* is unusual in that it is more similar to *Exochomus* in this zone than it is to many other species of *Chilocorus*. In general, the absence of spines in a zone appears to be independent either of beetle genus or size: species of either genus (*Chilocorus* or *Exochomus*) may be devoid of spines in any particular zone irrespective of body size.

A general difference between species of *Chilocorus* and *Exochomus* is the fact that, while *Chilocorus* has a cline of spine density relative to the size gradient, *Exochomus* seems to respond more in a binary fashion (Tables 3 and 4). It is likely to have either many spines or none in a particular zone (Table 4). In addition, several species of *Exochomus* were examined which had no spines in the anterior pronotal margin, but no species of *Chilocorus* were found to be devoid of spines in this zone.

No species of *Chilocorus* was found to be completely devoid of spines on the subelytral surface, while five species of *Exochomus* were completely devoid. Eight species of *Chilocorus* had spines in all five zones (*Chilocorus australasiae*, *C. cerberus*, *C. dohrni*, *C. infernalis*, *C. kuwanae*, *C. melanopthalmus*, *C. renipustulatus* and *C. stigma*). The lateral distal margin and epipleural harbour were the only zones which had no spines (Table 3). *Chilocorus bilineatus*, *C. bipustulatus*, *C. circumdatus*, *C. distigma*, *C. fraternus*, *C. nigritus*, *Chilocorus rubidus* and *Chilocorus schioedtei* had no spines in the epipleural harbour, *C. orbus* and *Chilocorus tristis* had no spines in the lateral distal margin and *C. cacti* had no spines in either.

If spine density is considered in terms of relative density (≤ 15 spines 100 μm^2) instead of absolute presence/absence, the anterior pronotal margin is still the most spinose across species of *Chilocorus* (Table 3). The hierarchy of spine density across species (≥ 15 spines 100 μm^2) for *Chilocorus* was anterior pronotal margin

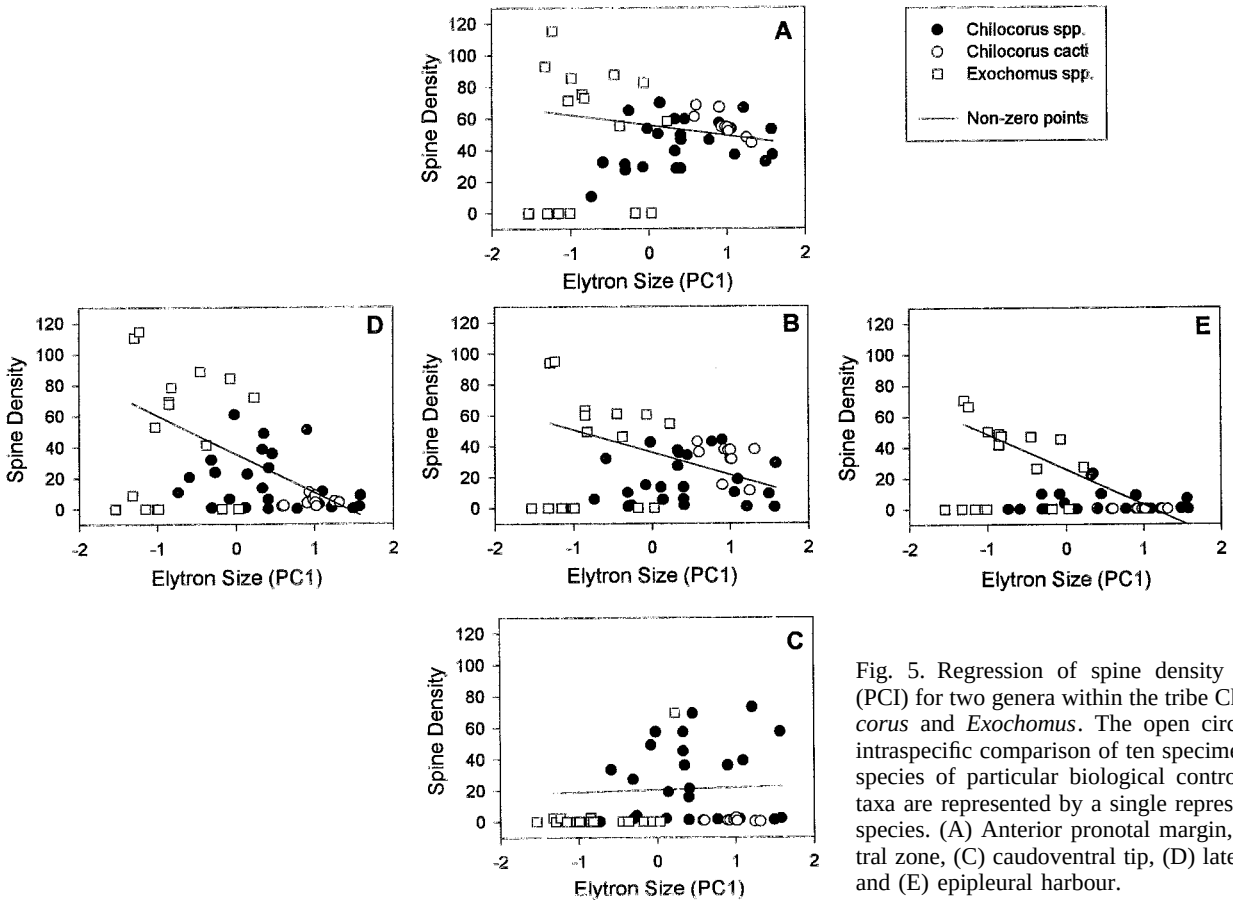

Fig. 5. Regression of spine density on general size (PCI) for two genera within the tribe Chilocorini, *Chilocorus* and *Exochomus*. The open circles represent an intraspecific comparison of ten specimens of *C. cacti*, a species of particular biological control interest. Other taxa are represented by a single representative for their species. (A) Anterior pronotal margin, (B) medial central zone, (C) caudoventral tip, (D) lateral distal margin and (E) epipleural harbour.

(100%) > caudoventral tip (63%) > medial central zone (42%) > lateral distal margin (37%) > epipleural habour (5%). The epipleural harbour had the fewest spines per unit area. The pattern for *C. cacti* was anterior pronotal margin (46 spines 100 μm^2) > medial central zone (43 spines 100 μm^2) > caudoventral tip (1.3 spines 100 μm^2) > lateral distal margin and epipleural harbour (0 spines 100 μm^2). This partially correlates with the pattern of attachment preference for the caudoventral tip and epipleural harbour seen in *H. cooremani* for the phoretic host *C. cacti*, indicating that spines may influence the positional attachment of the mites (Fig. 3). The characteristic of having low spine number in the caudoventral tip is not unusual for *Chilocorus*, but *C. cacti, C. distigma, C. orbus* and *C. tristis* have the lowest caudoventral tip densities.

In *Exochomus*, the hierarchy of spinal density among species ($\geq$ 15 spines 100 μm^2) was anterior pronotal margin (62%) > epipleural harbour (56%) > medial central zone and lateral distal margin (50%) > caudoventral tip (6%). *Chilocorus* was found to have fewer elytral zones devoid of spines than the related genus *Exochomus* and all other members of the Chilocorini.

Within the genus *Chilocorus*, spine density may play a synergistic role in host association. Additional factors (i.e. genus-level chemical cues) may also play a role, but are as yet unexamined. Since there is a generalized recognition and attraction to beetles within the one genus (*Chilocorus*), it is likely that long-distance chemical cues are important in the recognition and localization of appropriate individual hosts. And, once a host is located in this manner, successful phoresy is related to the ability to attach properly to the host without inflicting injury to the soft caudoventral sucker plate. Thus, the pattern and density of subelytral spines could prevent or facilitate attachment by the mites once a host is located.

If mites represented a significant mechanical or physiological cost to beetles of one species, evolutionary responses would act to dissuade phoretic attachment. If the beetle benefited from the association, the spine density should decrease. In addition, differential spine densities across the subelytral surface could influence zones where mites would successfully attach and zones where they would not within a single beetle species. Thus, beetles could indirectly maintain some governance over the pattern of distribution of the mites.

Is there evidence to suggest that this may be the case? First, the beetles are reflexive bleeders which expel haemolymph from weak sutures for anti-predator defence. Radiolabelling studies with *H. cooremani* and *C. cacti* (Houck and Cohen, 1995) indicated that *H. cooremani* can extract haemolymph from the beetles by perforating the hypodermis of the elytron by the negative pressure exerted by the powerful caudoventral suckers. The beetle haemolymph contains toxic heptacylic and spirocyclic alkaloids (McCormick *et al*., 1994; Xiongwei *et al*., 1995), which appear not to be an impairment to hypopodes of *Hemisarcoptes* (Houck 1994). The abrasion by the suckers provides an open chemical conduit from the haemolymph of the beetle to the vestigial anal and genital openings of the sucker plate (Houck, 1994). Sectioning of attached mites shows a non-functional foregut in attached mites, a proventriculus in the mid-gut and a large hind gut which opens onto the

sucker plate (Houck and Lindley, 1993), indicating that mites feed through the anus.

With an incomplete tubular gut (i.e. the foregut is solid with no oral opening) any metabolic wastes created by the mite would be retained or expelled into the opening created in the beetle hypodermis. Thus, potential bidirectional flow of materials between the beetle and the mite is possible. Large molecules (e.g. hormones and enzymes), as well as amino acids and sugars excreted as metabolic wastes, could pass from mites to the host and vice versa without selective constraints of transmembrane transmission. With a compliment of 400–800 mites per beetle, a realistic number, this could be significant to the beetles. Such benefit or liability could influence setal density or pattern.

CONCLUSIONS

Clearly the pattern of subelytral ultrastructure is not strictly consistent along phylogenetic or allometric lines. This suggests a complex set of selective forces influencing the subelytral architecture and does not negate the possibility that one potential selective force may be the interaction with phoretic mites.

Five species representing *Exochomus* had no spines at all, which makes it very difficult to interpret the primary function of the subelytral spines in a general way. Clearly, spines are not necessary for wing folding or flight dynamics, since there is no evidence that any member of the Chilocorini lacks the ability to fly. The primary function of these spines remains unclear.

Assuming that low spine densities are more conducive to mite attachment than high densities, there is a hierarchy of morphological suitability among *Chilocorus* for attachment by *Hemisarcoptes*. Based on the morphological evidence alone, these findings lead to the prediction that the species of *Chilocorus* that are least conducive to biological control application in conjunction with *Hemisarcoptes* hypopodes (Table 5) would be *C. australasiae*, *C. infernalis*, *C. kuwanae*, *C. stigma*, *C. renipustulatus* and *C. circumdatus*. Among the species of *Chilocorus* that would be the most conducive to biological control application in conjunction

TABLE 5

Chilocorus species which were least morphologically compatible with *Hemisarcoptes*, as defined by the number of spines/zone per 100 μm^2

Zone	A	B	C	D	E	Total number of spines
C. australasiae	60	34	69	36	10	209
C. infernalis	57	44	36	51	9	197
C. kuwanae	41	39	47	55	13	195
C. stigma	45	26	49	22	11	153
C. renipustulatus	40	27	45	13	22	147
C. circumdatus	67	0	73	1	0	141

TABLE 6

Chilocorus species which were most morphologically compatible with *Hemisarcoptes*, as defined by the number of spines/zone

Zone	A	B	C	D	E	Total number of spines
C. tristis	33	9	1	0	0	43
C. orbus	50	6	1	0	0	57
C. bipustulatus	24	13	12	10	0	58
C. fraternus	50	13	2	0	0	65
C. distigma	54	10	2	0	0	66
C. cacti	46	43	1	0	0	90

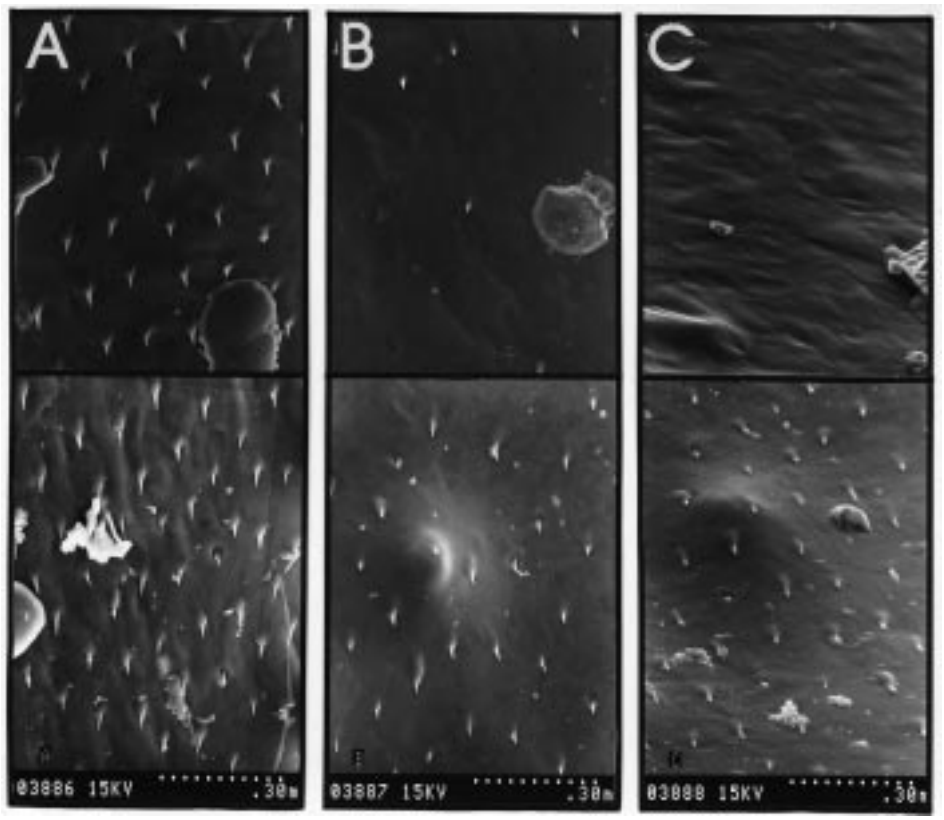

Fig. 6. Example of the contrast of the subelytral microsculpturing of *C. orbus* (top three panels) and *C. renipustulatus* (bottom three panels) for the anterior pronotal margin, medial central zone and caudoventral tip. *Chilocorus orbus* has very few spines in the medial central zone and no spines in the caudoventral tip. *Chilocorus renipustulatus* has spines in all three zones, making attachment of the mites in these areas problematic.

with *Hemisarcoptes* (Table 6) would be *C. orbus*, *C. tristis*, *C. cacti*, *C. distigma*, *C. fraternus* and, to a lesser extent, *C. bipustulatus* (Fig. 6). This conclusion is based on two criteria: (1) absolute spine density and (2) the distribution of spines. Those species with overall low spine density and also with more zones with no spines (or just a few spines) would provide maximum area for mite attachment.

The pattern of spine distribution clearly differs in *Chilocorus* as compared to other members of the Chilocorini. It is still not clear whether *Hemisarcoptes* hypopodes have exploited these patterns of elytral spine distribution for purposes of attachment or whether they may have influenced it by their presence over evolutionary time.

Future work needs to focus on four areas: (1) whether materials actually move from the mites to the beetles during phoretic association, (2) whether beetles with mites are advantaged in terms of life-history characters (i.e. longevity, fecundity etc.) during their association, (3) whether chemical cues contribute to long-distance host location and (4) whether examination of the extensive museum records on *Chilocorus–Hemisarcoptes* associations validate the predictions proposed in this work.

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