DEVELOPMENT AND BIONOMICS OF *CHRYSOMELOBIA LABIDOMERAE* (ACARI: TARSONEMINA; PODAPOLIPIDAE), A PARASITE OF THE MILKWEED LEAF BEETLE (COLEOPTERA: CHRYSOMELIDAE)

THOMAS C. BAKER[1] and GEORGE C. EICKWORT
Entomology Department, Cornell University, Ithaca, New York

Abstract

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Adult females of *Chrysomelobia labidomerae* Eickwort lay eggs on the upper surfaces of the hind wings of *Labidomera clivicollis* (Kirby). The eggs hatch in approximately 7 days and male and female larvae feed at the base of the wings and in the meso–metathoracic crevice and swell to about twice their original length. For about the second half of the approximately 7-day larval stadium, the larvae are inactive (pharate adults) and are usually cemented to the undersurfaces of the elytra. Inactive female larvae are accompanied by adult males that apparently copulate with the newly emerged adult females. The pharate adult is enclosed in a cuticular sac that may represent a calyptostatic nymphal instar. Adult females feed on the beetle's abdominal terga and sometimes also occur on its venter where they do not feed. Females disperse from host to host when the beetles copulate. The species is arrhenotokous. Mites overwinter on the diapausing adult beetles and do not infest the immature stages of their host. Even at high population levels, the mites do not noticeably affect the longevity or fecundity of their hosts.

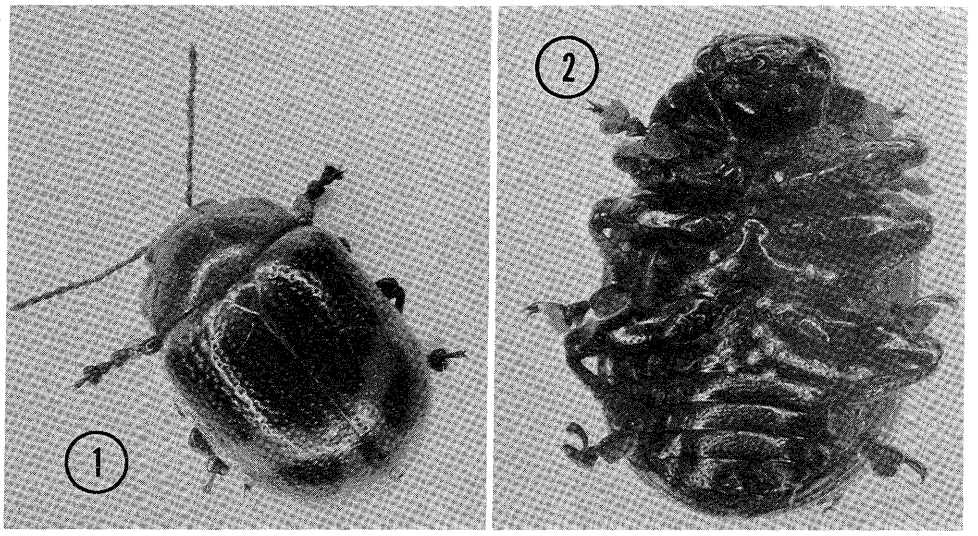
Introduction

Chrysomelobia labidomerae Eickwort is a common subelytral ectoparasite of adult milkweed leaf beetles, *Labidomera clivicollis* (Kirby) (Fig. 1), in North America. *Chrysomelobia* exhibits many characteristics that are primitive for the Podapolipidae (Regenfuss 1968, 1973; Eickwort 1975) and knowledge of the biology of its species should aid in understanding the evolution of this family of highly specialized insect parasites. There are no previous published observations on living *Chrysomelobia* and prior to Eickwort (1975) the genus was known only from one museum specimen of its type-species, *C. mahunkai* Regenfuss, that was found under the elytra of a European leaf beetle, *Chrysomela graminis* Linnaeus (Regenfuss 1968).

The majority of Podapolipidae, including all the more primitive genera, have been found under the elytra of beetles, especially Carabidae. Specialized podapolipids also occur on roaches, grasshoppers, and bumblebees, including a few species endoparasitic in the body cavity (Regenfuss 1968, p. 239), genital system (Stannard and Vaishampayan 1971), and tracheal system (Husband and Sinha 1970). For an excellent summary of host relations and an evolutionary analysis, see Regenfuss (1973). Detailed observations on living podapolipids have only been conducted on the primitive genera *Eutarsopolipus* and *Dorsipes*, subelytral ectoparasites of carabid beetles (Regenfuss 1968, 1972, 1973), and on *Locustacarus buchneri* (Stammer), a tracheal system parasite of bumblebees (Husband and Sinha 1970). All podapolipids apparently obtain nourishment by puncturing the cuticle of their hosts with their styliform chelicerae and sucking hemolymph (Regenfuss 1973). Like nearly all members of the Tarsonemina, Podapolipidae have at most three developmental stages — egg, larva, and adult. The nymphal instars characteristic of more generalized acariform mites are usually lacking.

We describe in this paper the development of *C. labidomerae*, its dispersal from host to host, its seasonal cycle, and aspects of its population biology and effect upon its host as determined from field-caught beetles and from laboratory rearings. All instars of this new species are described in a companion paper (Eickwort 1975).

[1]Present address: Entomology Department, New York State Agricultural Experiment Station, Geneva, N.Y. 14456.



FIGS. 1–2. *Labidomera clivicollis*. 1, dorsal view; 2, ventral view showing phoretic female *Chrysomelobia labidomerae*.

Methods

Our study of *Chrysomelobia labidomerae* extended from July 1969 to November 1972. Mites were reared on milkweed leaf beetles, *Labidomera clivicollis*, that were obtained from the laboratory population maintained by Dr. Kathleen Eickwort for her study on the beetle's ecology (Eickwort 1971). Studies were initiated at the E. N. Huyck Preserve in the summer of 1969 by G.C.E. on beetles and mites obtained from Albany, N.Y. and were continued at Cornell University by T.C.B. with additional beetles and mites from the Cayuga Lake region of New York. Approximately 100 mite-infested beetles yielded data in the laboratory.

Beetles were reared following the techniques of Eickwort (1971). They were maintained in 12-cm-diameter, clear plastic, covered petri dishes. Filter paper lined the bottom of each dish. The beetles were fed milkweed (*Asclepias syriaca* L.) leaf halves at 2- to 3-day intervals, at which times deionized water was squirted onto the filter paper. In the winter, frozen milkweed was used. Since frozen milkweed quickly became infested with fungus, a fungicidal agent, Tegosept M, was dissolved in the water to help retard a mold growth. Eggs laid by the beetles were placed on leaves in separate petri dishes where eclosion of larvae and development to the final instar occurred. These fully developed larvae were then placed in dirt-filled dishes where they burrowed, pupated, and emerged as adults.

To examine the mites, the elytra and hind wings of the host beetle were raised and impaled to a cork with number 0 insect pins to expose the abdominal terga (Fig. 3). Observations were made under a stereo microscope with a water-filter placed between the lamp and beetle to minimize desiccation. When a beetle was examined more than once, pinning holes in the elytra were reused so that injury to the beetle was minimized.

Mites were transferred from one beetle to another with a damp camel's-hair brush or a curved minuten-nadel probe. On some beetles the mites formed large stock cultures of from 10 to 50 adults per beetle. Beetles bearing stock cultures or awaiting infestation were usually kept in groups of two to seven beetles per dish; those beetles used

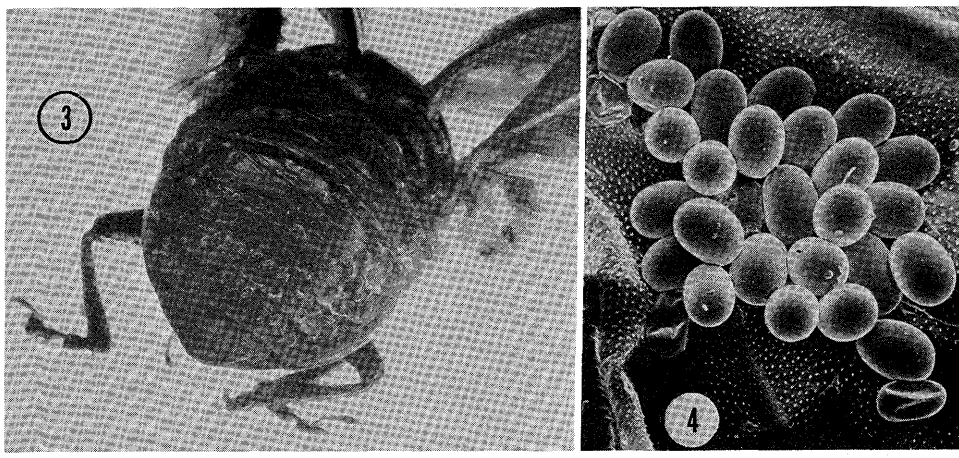
experimentally were maintained individually or in pairs. A 16:8 light:dark photoperiod was maintained during the winter to retard ovarian diapause in the beetles, allowing reproduction throughout the year, although at a lower rate in winter. The beetles were reared at room temperature.

Length of stadia and oviposition rate were determined by transferring single adult female mites onto previously uninfested beetles and recording mite eggs at 1- to 3-day intervals. These females were removed before their first eggs hatched, and the subsequent eclosion (noted by the disappearance of intact eggs) and development of larvae recorded. Observations were terminated when all mites had emerged as adults or when the beetles were damaged or killed by the observational procedure. The effects of heavy infestations upon the beetles and maximum population levels of mite colonies were investigated by infesting beetles with one or two adult female mites and foregoing observations until the colonies were at least 25 days old. To determine dispersal, an infested male or female beetle was paired with an uninfested beetle of the same or opposite sex in a petri dish, and the uninfested beetle was examined at 1- to 3-day intervals. The longevity and fecundity of a single female mite was determined by placing her alone on a beetle and removing and counting her eggs until the mite died. Parthenogenetic development was investigated by transferring young larvae to the meso–metathoracic crevices of beetles and allowing the mites to develop into adult females. The sex of the mites developing from eggs laid by these females was recorded.

Pinned specimens of *L. clivicollis* in the Cornell University insect collection were relaxed and examined for mites to obtain distributional data and infestation rates. Mites were mounted on slides following the techniques of Eickwort (1975). Alcohol-preserved specimens and slide-mounted representatives of all instars are deposited in the Cornell University insect collection.

Life Cycle of Host

The following account of the life cycle of *Labidomera clivicollis* (Fig. 1) in central New York is summarized from Eickwort (1971). Adult beetles are first encountered as early as 15 May, when the first sprouts of their food plant, milkweed (*Asclepias*), are appearing. Eggs are laid on the undersides of milkweed leaves. While the beetles



FIGS. 3–4. *Chrysomelobia labidomerae* on *Labidomera clivicollis*. 3, beetle with wings raised to expose adult female mites on abdominal terga and eggs on hind wing; 4, scanning electron micrograph of eggs on hind wing.

develop equally well in the laboratory on the five species of milkweed tested by Eickwort (1971), they prefer to oviposit on swamp milkweed (*A. incarnata* L.), their most common host in nature. The eggs hatch in 5 to 9 days and the larvae commence feeding on the milkweed leaves after consuming their chorions. The fourth instar larvae leave the food plants and burrow 3 to 5 cm into the soil, where they become inactive prepupae for about a week. The prepupae then ecdyse to expose the pupae, whose stadium lasts about 2 weeks more. The emerging adults leave the soil and feed on milkweed for a week or more before ovipositing. Adults live several months and the generations overlap. Second (and possibly third) generation adults enter diapause in the soil or other protected locations in the fall; the latest collection date for active adults is 9 October.

Life History of Mite

The life cycle of *Chrysomelobia labidomerae* consists of an egg stage, active and inactive larval stages, and adult. Eggs are first laid by the adult female in a single layer on the upper surface of the hind wings of the beetle between the cubitus and second anal vein (Fig. 5). After this area is filled, eggs are also deposited between the radius and cubitus as well as between the second and third anal veins and on the underside of the wings. The pale yellow eggs (length, $\bar{x} = 218\ \mu$; width, $\bar{x} = 154\ \mu$; $n = 10$) are about two-thirds the length and width of the adult female and are affixed to the wings with a viscous cement (Fig. 4). A female usually deposits two to six eggs on one wing and then she begins to lay on the other wing. Individuals were observed to lay up to three eggs per day, although most laid one or two ($\bar{x} = 1.4$, S.D. $= 0.5$, $n = 54$). The maximum number of eggs laid by a female was 49 in 26 days; she was still ovipositing when observations were terminated. The egg stadium lasts a mean of 6.8 days (S.D. $= 0.8$, $n = 47$).

After eclosion, larvae crawl to the base of the hind wing or to the crevice between the meso- and metathoracic terga (Fig. 5) where they begin to feed. Both areas have relatively soft, thin cuticle. Seventy per cent of the feeding larvae ($n = 72$) prefer the thoracic crevice. Newly hatched larvae are clear but become orange as they feed. Full engorgement requires 2½ to 3½ days. Fully engorged larvae attach themselves with a viscous substance to the sides of the thoracic crevice, the bases of the hind wings, or to the undersurfaces of the elytra near their bases, and become inactive. The elytral undersurfaces have the greatest number of inactive larvae of these three areas (Fig. 6). The period of inactivity represents half of the larval stadium of 5.5 to 7.5 days ($\bar{x} = 6.5$, S.D. $= 1.0$, $n = 15$). Development from deposition of egg to emergence of adult takes 10 to 15 days ($\bar{x} = 12.5$, $n = 21$), with no observed difference between sexes.

The engorged, inactive larva is about twice the length of the newly hatched larva. The entire hysterosoma is swollen after feeding and the previously contiguous dorsal plates are widely separated by membranes (see figs. 8 and 10 of Eickwort 1975). Within 1 day after the onset of inactivity, the pharate adult is visible within the larval cuticle in cleared specimens.

The pharate adult (Figs. 7, 8) lies completely within the larval idiosoma. The anterior two pairs of legs extend anteriorly, with the first pair lying parallel to the lateral margins of the propodosoma and just covered by the body dorsally, and tarsi I extending to the level of the gnathosomal base. The second pair of legs lies parallel to and in contact with the first pair medially. The third and fourth pairs of legs in the pharate female extend posteriorly, with the third pair lying parallel to the lateral margins of the opisthosoma and just covered by the body dorsally, and the fourth pair lying parallel to and in contact with the third pair medially. The tarsi of legs IV cross near the posterior tip of the body and their terminal setae are directed anteriorly along the venter. The third

pair of legs in the pharate male (Fig. 7) are oriented like those of the female but the fourth pair are extended medially across the dorsum with the tarsi crossing just anterior to the posterior tip of the body.

Inactive larvae represent the first stage in which the sexes can be distinguished. This requires observation of the pharate adult in cleared specimens. No external morphological differences between the male and female larvae could be detected.

In cleared inactive larvae of both sexes, a thin cuticular sac enveloping the pharate adult is visible just beneath the larval cuticle. By carefully applying pressure to a specimen in lactophenol, the sac can be extruded and freed from the larval cuticle without losing the enclosed pharate adult. Two sclerotized bars on the sac are positioned ventrally under the pharate adult and are easily visible in extruded sacs, especially those in which the adult cuticle is just beginning to form (Fig. 8). A similar sac was observed in *Coreitarsonemus* (Tarsonemidae) by Fain (1970).

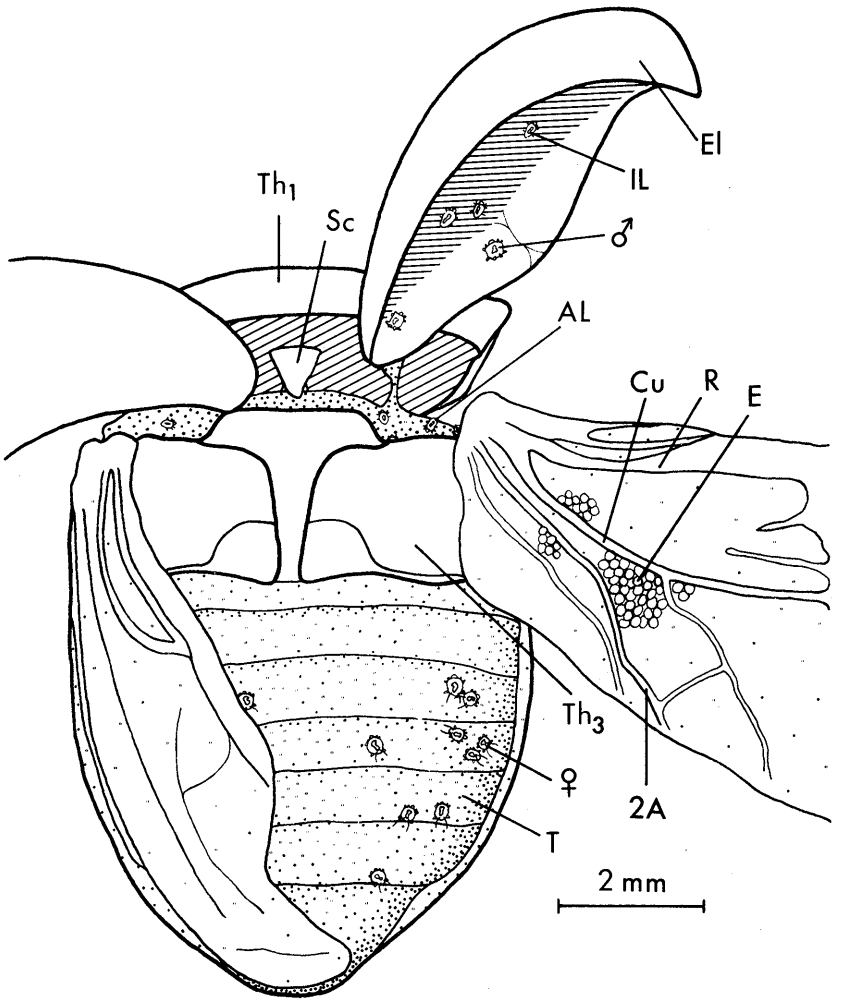


FIG. 5. *Labidomera clivicollis* with wings raised to expose *Chrysomelobia labidomerae*. 2A, 2nd anal vein; AL, active larva; Cu, cubitus; E, egg; El, elytron; IL, inactive larva; R, radius; Sc, scutellum; T, abdominal tergum; Th_1, prothorax; Th_3, metathorax; ♀, adult female; ♂, adult male.

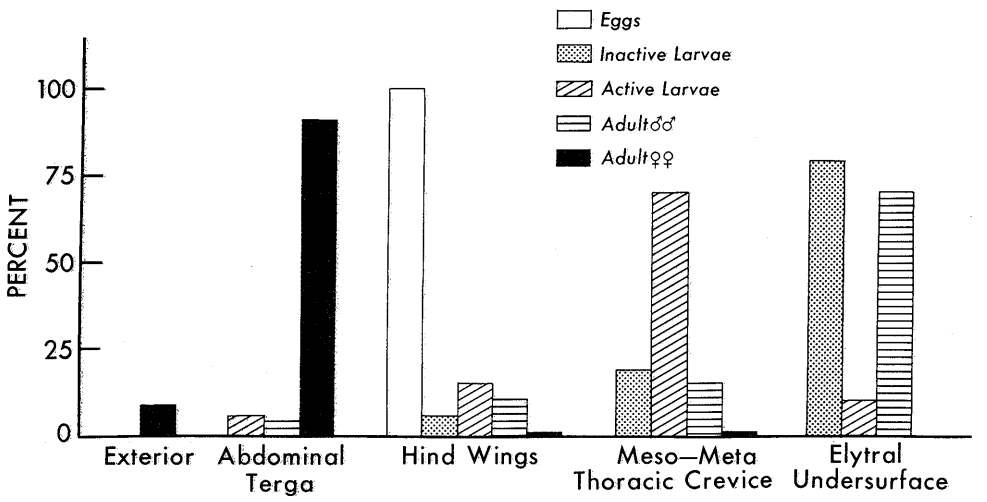
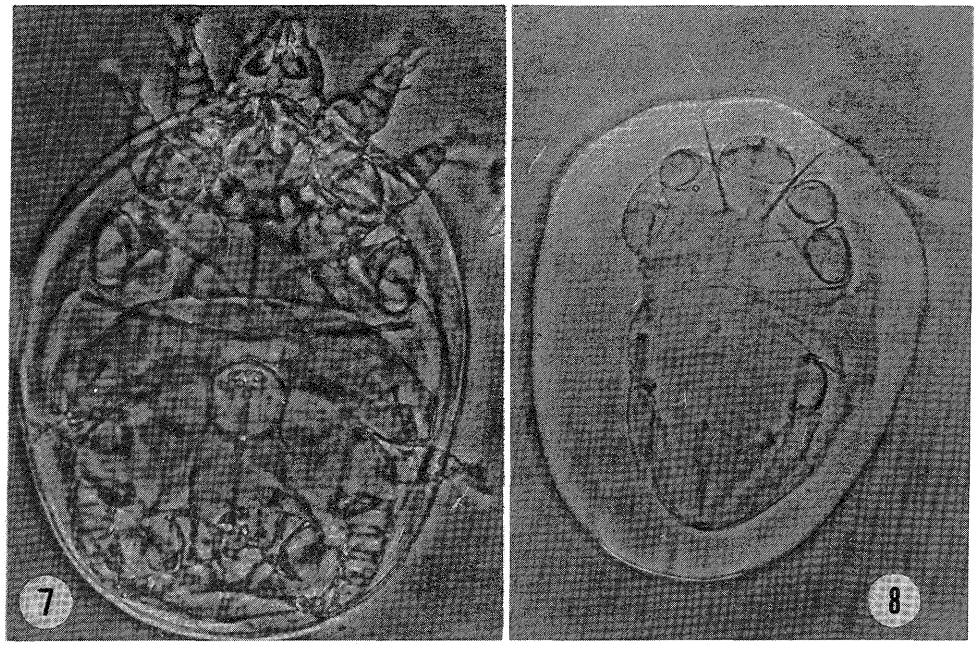


FIG. 6. Location of the developmental stages of *Chrysomelobia labidomerae* on *Labidomera clivicollis*.

Adult female mites occur principally on the abdominal terga (Figs. 3, 5), but also in the crevice between the meso- and metathoracic terga (Fig. 6). Feeding is presumably accomplished in these areas, although the actual puncturing of the host's cuticle with the chelicerae was never observed. Adult females do not become physogastric. Older females are only slightly longer than newly emerged ones and their opisthosomal terga remain partially overlapping. They become less flattened and their color deepens from a light orange to orange-red. In both larvae and adults a white streak, probably of guanine, is visible middorsally through the cuticle and contrasts strikingly with the orange body.

Adult males occur wherever inactive larvae are located, and are thus most prevalent on the undersurfaces of the elytra (Figs. 5, 6). Groups of up to seven adult males often wait near an inactive female larva and approach and touch her with their front legs from time to time. Copulation probably takes place upon the emergence of the adult female, although this was never observed. One adult male was observed beneath an inactive female larva with his dorsum against her venter. The copulatory apparatus of the male is dorsally located (see fig. 6 of Eickwort 1975) and copulation with the pharate adult female cannot be ruled out. Adult males do not increase in size with age, although they do vary slightly in degree of depression, and they remain light orange in color. The feeding apparatus of the adult male is well developed (see fig. 5 of Eickwort 1975) and some feeding in this stage seems probable.

Typically only 5 to 15% (median = 7.5%) of the adults in a thriving colony of *C. labidomerae* are males. To test if this species is arrhenotokous, young larvae were placed singly on isolated beetles. Only three successfully developed into adult females. All three laid eggs from which only adult males developed, giving strong evidence for arrhenotoky. The oviposition rate of these uninseminated females was much lower ($\bar{x}$ = 0.5 eggs/day) than that of inseminated females. Ten other laboratory colonies initiated by single females consisted of up to 90% males and were markedly slower in reaching high population levels than were identically initiated colonies which produced mostly females (Fig. 9). We hypothesize that these 10 colonies were initiated by uninseminated females, and that these females produced only haploid male eggs until their first offspring matured into adults. These males apparently then mated with their mothers, which then laid diploid female eggs.



FIGS. 7–8. Pharate adults of *Chrysomelobia labidomerae*: 7, male within larval cuticle; 8, female in cuticular sac, removed from larval cuticle.

Dispersal

Only adult females of *Chrysomelobia labidomerae* have the ability to move from one beetle host to another. Dispersal of the mites normally occurs when the beetles copulate or when male beetles undergo "homosexual courtship." In lab pairings of beetles left together for at least 24 h, movements of female mites from male to female, female to male, and male to male beetles readily occurred from infested to uninfested beetles (Table I). Movement of mites from female to female beetles occurred more rarely and at a lower rate (Table I),[2] probably because female beetles do not undergo homosexual courtship. In mating, the male beetle mounts the female so his venter is in contact with her elytra and both are facing in the same direction. His long aedeagus is extended caudally around the apices of the female's elytra and inserted into her vulva. Copulation is prolonged and both sexes mate repeatedly throughout their adult lives. Males mount other males in similar positions when undergoing homosexual courtship.

Healthy laboratory beetles of both sexes carrying 30 or more adult female mites usually have some of these female mites (median = 4.9%) riding exposed on their venters, usually in the vicinity of the coxae (Fig. 2). These mites are flattened and pale orange and apparently do not feed in this position. Mites may also move back under the elytra from this ventral location, as shown by occasional decreases in exterior mites that exactly matched increases in subelytral mites on isolated, daily observed laboratory beetles. While high population density under the elytra may be a factor promoting migration, it is not the only one: some beetles with 40 to 60 subelytral females had more exterior mites than did hosts with over 150 subelytral females. Old, moribund beetles within a few days of death in the laboratory carry a higher percentage (median =

[2]After the female–female pairings cited in Table I, all donor beetles were immediately paired with male beetles and donated mites to them 1 or 2 days after pairing.

32.4%) of their female mites ventrally, even at low mite densities. While these exterior mites are in a particularly advantageous position to disperse to another host when beetles copulate, beetles carrying only subelytral mites are also effective donors (Table I). Larvae and adult males were never observed on the exterior of their hosts.

Chrysomelobia labidomerae did not parasitize eggs or larvae of *L. clivicollis* which were reared in the same dishes as infested adults, nor were any mites found on these stages in the field. In the laboratory, some female mites abandoned their hosts when the beetles died and moved for a short distance on the filter paper before dying themselves.

Seasonal Cycle, Population Parameters, and Effect upon Host

The mites apparently overwinter under the elytra of the diapausing adult beetles. Although no beetles could be located in winter to confirm this hypothesis, beetles captured on 30 April in Indiana and 19 May in Ohio (Eickwort 1975), very soon after their probable emergence from hibernation, bore adult female mites and eggs. Males and larvae were also present on the 19 May beetle. The first generation of adult beetles in 1970 was captured on 7 July at Albany when overwintered beetles were still present, and both generations bore mites. Since the generations of the beetles overlap and the beetles copulate throughout their adult lives, the mites can infest new adult beetles as the latter emerge and mate throughout the summer and early autumn. Both female and male *C. labidomerae* were collected on beetles as late as 27 September 1973 in Ithaca.

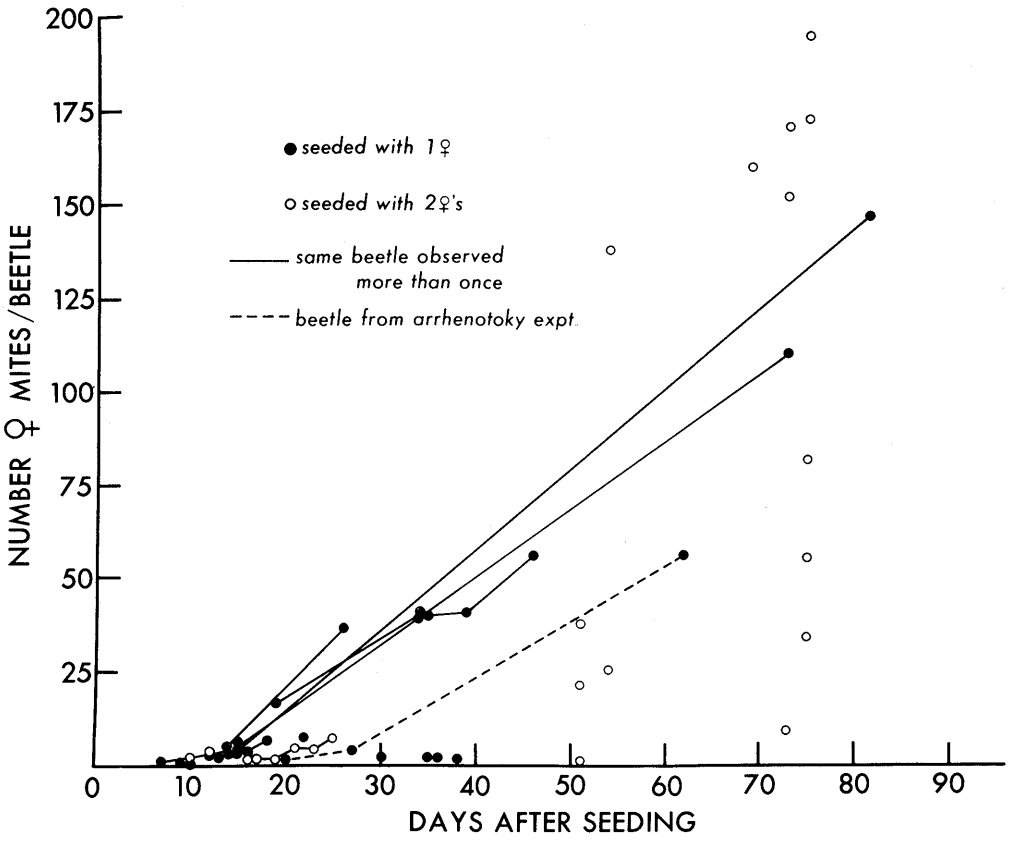


FIG. 9. Number of adult female *Chrysomelobia labidomerae* per laboratory host, plotted as a function of the age of the mite colony. Colonies were initiated with 1 or 2 adult female mites and the beetles were maintained in isolation.

Table I. Dispersal of *Chrysomelobia labidomerae* from infested donor host to previously uninfested recipient host (*Labidomera clivicollis*) in the laboratory

Donor beetle	Recipient beetle	No. ♀ mites on donor*		Total no. ♀ mites on recipient				
		Exterior	Subelytral	Day†:	1	2	3	5
♀	♂	0	24		2		5	
♀	♂	1	23		2		3	
♀	♂	2	7			3		
♀	♂	6	Many			28		
♀	♂	6	Many			4		
♀	♂	0	13			1		
♀	♂	4	?				0	2
♂	♀	12	Many				9	
♂	♀	4	7			1		
♂	♀	4	7			2		
♂	♂	9	0		0		1	
♂	♂	24	6				3	
♂	♂	7	7		1			3
♀	♀	2	Many		0		1	1
♀	♀	0	9		0		0	0
♀	♀‡	6	7				0	0

*Prior to caging with recipient beetle.
†Days 1, 2, 3, 5 indicate first, second, third, and fifth days after donor and recipient beetles were first caged together.
‡On day 10, recipient had 0 mites.

The relative rarity of *L. clivicollis* (Eickwort 1971) caused difficulty in estimating the proportion of infested beetles in a population. Two collections of *L. clivicollis* made for this study yielded 0 mites from over 20 beetles collected at Bridgeport, N.Y., on 16 September 1973, but 83% of 35 beetles collected in the Montezuma National Wildlife Refuge, New York, on 13 July 1972 bore mites. Of 163 museum specimens of *L. clivicollis* collected on various dates and localities, 16.6% bore mites. Of these 163 beetles, 56 were from the Ithaca, N.Y., vicinity and 14.3% of the latter bore mites.

Examination of museum specimens of *L. clivicollis* suggests that the range of *C. labidomerae* coincides with that of its host species, including the subspecies *clivicollis* and *rogersii* (Eickwort 1975). The mite has not been found on any other chrysomelid beetle. However, a laboratory population of *C. labidomerae* was maintained on the related Colorado potato beetle, *Leptinotarsa decemlineata* (Say), for one complete generation of the mite before the experiment was terminated.

The maximum number of adult females collected on any one beetle in central New York State was 49 ($\bar{x}$ = 10.9, S.D. = 11.4, n = 47 infested beetles). In the laboratory, initial infestations of one or two adult female mites per isolated beetle yielded populations up to 194 adult female and 17 adult male mites at the end of 75 days (Fig. 9). Population estimates in Fig. 9 are based only on adult female mites because mite eggs on older beetles are difficult to count (due to incrustation of old chorions) and larval and male mites are difficult to find without damaging the beetles or dehydrating the mites by overlong exposure to the lamp. The number of mites did not increase geometrically on isolated beetles; instead, the rate of population increase decreased greatly in older colonies.[3] This decrease was caused by decreased egg production by female mites — we do not know if each female mite produced fewer eggs or if a smaller proportion of the mites laid eggs.

[3]The number of observations conducted on any one beetle was limited due to the damage or loss of elytra caused by repeated pinnings, making direct measurement of the rate of population increase on individual beetles difficult.

Chrysomelobia labidomerae does not appear to harm its host even at very high densities. Infested beetles appear to be as fecund as uninfested ones and live as long in laboratory populations. Large populations of female mites cause a gummy, whitish exudate that hardens into plaques that appear on the host's abdominal terga. The source of this exudate is unknown.

Discussion

Chrysomelobia exhibits several developmental characteristics that are unique in the Podapolipidae, as summarized in Table II. All of these characteristics, except possibly physogastry of the larvae, are primitive and form the base from which the typical life cycle of more advanced podapolipids evolved. Moreover, these characteristics are also typical of the most closely related family to the Podapolipidae, the Tarsonemidae (see Beer 1954).

Regenfuss (1973) has proposed an evolutionary sequence within the Tarsonemina progressing through three phases as follows: (1) The adult female copulates end-to-end (retroconjugate) with the male (characteristic of some Pyemotidae s.l.). (2) The male grasps the inactive female larva (actually the pharate adult) with his specially modified fourth pair of legs and carries her in precopula until she moults, when retroconjugate copulation occurs (characteristic of the Tarsonemidae). (3) The male copulates with the larval female, with the male slipping under the female from behind in the proconjugate position, anterior of male against posterior of female (characteristic of the Podapolipidae). *Chrysomelobia labidomerae* is in some ways intermediate between the second and third phases. Adult males locate inactive larval females (pharate adults) and wait by them, but they do not actually hold the larger larvae in precopula with their modified hind legs. Presumably copulation occurs as soon as the adult female emerges (it was never observed).

The unusual cuticular sac that encloses the pharate adult can be interpreted as a highly degenerate nymphal cuticle, as did Fain (1970) for *Coreitarsonemus*. If so the nymph is a pharate, calyptostatic instar in the sense of Johnston and Wacker (1967). The presence of even a calyptostatic nymphal instar is a very primitive feature, since this instar is otherwise known in the Tarsonemina only as active nymphs in the Pygmephoroidea — in *Siteroptes* (Reuter 1900, questioned by Cross 1965) and in *Pediculaster* and *Pseudopygmephorus* (Gurney and Hussey 1967; Wicht and Snetsinger 1971). The significance of sclerotized bars on the cuticular sac of *C. labidomerae* is not clear.

The subelytral space of carabid beetles has been subdivided by Regenfuss (1972) into seven interconnecting microspaces that are differently used as habitats by different species of *Eutarsopolipus* and *Dorsipes* (Podapolipidae). When more than one species of mite occurs on the same host species, each uses a different microspace, thus avoiding

Table II. Unique features of development of *Chrysomelobia labidomerae*

Chrysomelobia	Other Podapolipidae
1. Male eggs hatch into larvae	1. Male eggs hatch directly into adults*
2. Larvae become physogastric	2. Larvae do not become physogastric
3. Pharate adult enclosed in cuticular sac	3. Pharate adult not reported to be enclosed in sac
4. Adult females swell slightly	4. Adult females become physogastric
5. Adult female dispersal stage	5. Larval female dispersal stage
6. Males copulate with adult females	6. Males copulate with larval females

*Husband and Sinha (1970) believe that in *Locustacarus* most males are larvae that mate and do not moult into adults.

direct competition. A comparable resource partitioning is apparent among the different stages of *C. labidomerae*. Adult females feed on the abdominal terga (space A of Regenfuss 1972) and, like the carabid-parasitizing species in this microspace, are large and flat. The feeding larvae are located at the bases of the wings (spaces B and C of Regenfuss) and in the crevice between the meso- and metathoracic terga (space G of Regenfuss) and are swollen similar to the spherical body shape of the carabid-parasitizing species in those microspaces. Moreover, the two nonfeeding stages of *C. labidomerae* occupy spaces that on carabids are used as microhabitats by a few other species: the eggs are laid on hind wing upper surfaces (space D of Regenfuss) and the inactive larvae and their accompanying adult males are frequently on the undersurfaces of the elytra (space E of Regenfuss).

The subdivision of the subelytral space into different microhabitats for the different stages of *C. labidomerae* is not the only indication of the high degree of adaptation of this mite for its host. The inseminated female is adapted to respond to (chemical?) cues of the beetles' copulation and to move from host to host at this time. The hibernation and long life of adult milkweed beetles which lead to overlapping generations allow their parasitic mites to exist solely on adult hosts, never leaving them to parasitize other stages of the host species or even to touch the substrate. Even in the artificially dense populations induced in the laboratory, the mites were remarkably non-pathogenic to their hosts. Despite its primitive morphology and development, *Chrysomelobia labidomerae* is as well adapted a parasite as are those in the specialized genera of Podapolipidae.

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*Not seen in original