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PARASITOIDS ACQUIRED BY *COLEOPHORA PARTHENICA* [*LEPIDOPTERA : COLEOPHORIDAE*] TEN YEARS AFTER ITS INTRODUCTION INTO SOUTHERN CALIFORNIA FOR THE BIOLOGICAL CONTROL OF RUSSIAN THISTLE

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Parasitism of the stem and branch-boring moth *Coleophora parthenica* Meyrick [*Lepidoptera : Coleophoridae*], introduced into California for the biological control of Russian thistle, *Salsola australis* R. Brown [*Chenopodiaceae*] was studied in the Coachella Valley of southern California during 1985-1986.

Eight parasitoid species were reared from overwintering larvae of *C. parthenica*, but none from the F_1 larvae, and just 2 individuals of one species from the F_2 summer generation. The level of parasitism of overwintering larvae was positively correlated with branch diameter, and ranged from 2 % in the primary (main) branches to 45 % in the tertiary branches in the spring 1985 sample, and from 2 % to 19 % in the spring 1986 sample, respectively. Rates of parasitism > 20 % were only found at sites with higher plant cover and chenopod diversity, but no other plant source or alternate hosts of the parasitoids of *C. parthenica* were found. The 2 dominant species, the solitary, hymenopterous ectoparasitoids, *Norbanus perplexus* (Ashmead) [*Pteromalidae*] and *Eurytoma strigosa* Bugbee [*Eurytomidae*], are both congeners of native parasitoids of *C. parthenica* in Pakistan. The 2 other species of parasitoids of *C. parthenica* in southern California for which other hosts are known are polyphagous and external on the larvae. No specialized endoparasitoid Braconidae, like those which dominate the native parasitoid complex in Pakistan and the U.S.S.R., have transferred to *C. parthenica* during its first 10 years in southern California.

KEY-WORDS : *Coleophora, Eurytoma, Norbanus, Salsola*, biological weed control, parasitoids.

Coleophora parthenica Meyrick [*Lepidoptera : Coleophoridae*] is a stem and branch-boring moth introduced into southern California from Egypt, Pakistan, and Turkey in 1973 and 1974 for the biological control of Russian thistle, *Salsola australis* R. Brown [*Chenopodiaceae*] (**Hawkes** *et al.*, 1975). The colonization, establishment, and impact of *C. parthenica* on this accidentally introduced annual weed was studied in California by **Hawkes & Mayfield** (1978) ; **Goeden** *et al.* (1978) ; **Goeden & Ricker** (1979) and **Pemberton** (1986). Up to 3 generations per year were reported from southern California, with larvae of the last generation overwintering within the stems and branches and emerging from the dead plants the following spring.

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The impact of spider and rodent predation on *C. parthenica* was studied by **Nuessly & Goeden** (1983, 1984). The external prasitoid of *C. parthenica* larvae, *Norbanus perplexus* (Ashmead) [*Hymenoptera : Pteromalidae*] was reported by **Goeden** *et al.* (1978). Newly acquired parasitoids may transfer from native phytophagous hosts related at least at the family level, or more commonly are polyphagous ectoparasitoids with broad ecological niches (**Zwölfer & Pschorn-Walcher**, 1968 ; **Goeden & Louda**, 1976 ; **Crawley**, 1987). This report describes a field study of the parasitoids that have colonized *C. parthenica* 10 years after its intentional introduction into southern California. Special emphasis was given to the seasonal variation, plant-part relations, and habitat specificity of the parasitoids. The parasitoid complex in southern California is compared with parasitoids known from the host's native areas in Pakistan, Turkey, and the U.S.S.R.

MATERIALS AND METHODS

Study area

The study was conducted during 1985 and 1986 near Indio, within 2 km of the 1974 release site for *C. parthenica* in the Coachella valley of southern California [**Goeden** *et al.*, 1978]. Annual rainfall at this low-elevation, northern Colorado Desert location is 5 to 8 cm, most of which occurs between December-March. Temperatures vary widely, reaching medium summer highs of 48-50 °C and winter lows of 0-5 °C. The 10 study sites were located within a 10 × 10-km area of undeveloped industrial and residential tracts located between Indio and Coachella. The most common plant species at these sites on wind-blown alluvial soils were the *Chenopodiaceae,* namely Russian thistle, *Atriplex canescens* (Pursch) Nutall, *A. polycarpa* (Torrey) Watson, *A. lentiformis* (Torrey) Watson, *Chenopodium album* L., and *Bassia hysopifolia* (Pallas) Kuntze. Other regarded plants were *Haplopappus acradenius* (Greene) Blake [*Asteraceae*], *Tamarix ramosissima* Ledebaur [*Tamaricaceae*], *Hordeum glaucum* Stendal [*Gramineae*] and *Cynodon dactylon* (L.) Persoon [*Gramineae*].

Egg samples

Eggs of *C. parthenica* were collected on 50 plants at each of 7 sites on 2 occasions during the first summer generation (9 IV-16 V), and on 40 VI and 22 VIII 1985, respectively, for the 2 following generations. The number of eggs sampled varied between 40 and 100 eggs per site. Eggs were left attached to pieces of Russian thistle, mainly apical leaves, and held individually in gelatine capsules for 20 days or until the larvae hatched.

Larval and pupal samples

From 10 larger to 25 smaller, randomly selected plants were collected at each of 10 sites on 8-III and 4-VII-1985 to obtain overwintering F_3 host larvae, and at each of 7 sites on 7-VI and 23-VII-1985 to obtain F_1 and F_2 larvae, respectively. In addition, the overwintering generation of 1985/86 was sampled at 3 localities on 17-IX, 28-X, and 9-XIII-1985 and on 30-I and 1-IV-1986.

Branch dissections and rearings

Branches were classified as main or primary (1°) branches, secondary (2°) branches, and tertiary (3°) branches (generally > 1.3 cm in diameter and without flowers). Primary branches arose from the first main stem ; secondary branches, from these, and so on. Ten-m aggregate lengths of 1° branches and 25 m each of 2° and 3° branches were included in each sample, which approximated the proportions of these branch types comprising a plant. Immediately after collection, 20 % of each branch sample was dissected under a microscope using a single-edged razor blade to slit each branch lengthwise. The *C. parthenica* and parasitoid larvae and pupae were removed and placed individually in gelatine capsules for adult emergence. The remaining 8 m of 1° branches and 20 m each of 2° and 3° branches were placed in separate emergence cages in an air-conditioned greenhouse at the University of California, Riverside, where temperatures approximated those at the sample sites.

RESULTS

Emergence and larval densities for generations and branch type

The total number of moths and parasitoids that emerged during 4 host-generations, together with larval densities within each branch type (including parasitized larvae) are recorded in fig. 1. Herbivore pressure, expressed as the number of larvae per m of branch, varied widely among branch types and generations, but was distinctly higher after seed set, i.e., for the overwintering generations. A larger proportion of the larvae was found in the 2° and 3° branches during the summer than in the winter. The bright yellow eggs are laid near the actively growing tips of the mostly short, 2° and 3° branches during the vegetative period of Russian thistle. Thus, larval distribution reflects the oviposition sites of the 2 summer generations (F_1 and F_2) ; however, when the nutrients in these branches are depleted later in the year, the majority of the overwintering larvae move into the 1° branches (**Nuessly & Goeden,** 1984 ; **Pemberton,** 1986).

Egg and adult parasitism

Neither eggs nor adults (N + 1,500 field-collected moths) were parasitized. Less than 1 % of the eggs were unfertile, and the larvae generally hatched within 10 days. The 1st instar larvae bore through the bottom of the eggs and enter the leaves directly without being exposed (**Hafez** *et al.*, 1978 ; **Hawkes & Mayfield,** 1978).

Parasitism of the 2 summer generations

The emergence periods of the 2 summer generations studied lasted from 14-VI to 16-VIII-1985 and from 2-VIII to 20-IX-1986, respectively. Branch samples from 7 sites yielded a total of 446 and 366 moths from the 2 summer generations, respectively. Two female parasitoids of *Eurytoma strigosa* Bugbee [*Eurytomidae*] emerged, one each on 14-VI and 6-VII-1985 (table 2).

Parasitism of the overwintering generation 1984-85

The samples collected on 8-III-1985 containing overwintering larvae yielded average parasitization rates by the 2 chalcidoid species, *N. perplexus* and *E. strigosa*, of 6.9 % and 3.3 %, respectively (fig. 2). Two specimens each of *Microdontomerus anthonoi* Crawford [*Torymidae*] and *Eupelmus* cf. *limneriae* Howard [*Eupelmidae*], and one specimen of *Euderus* sp. [*Eulophidae*] were also reared from these overwintering larvae and pupae (table 1), in addition to 486 moths.

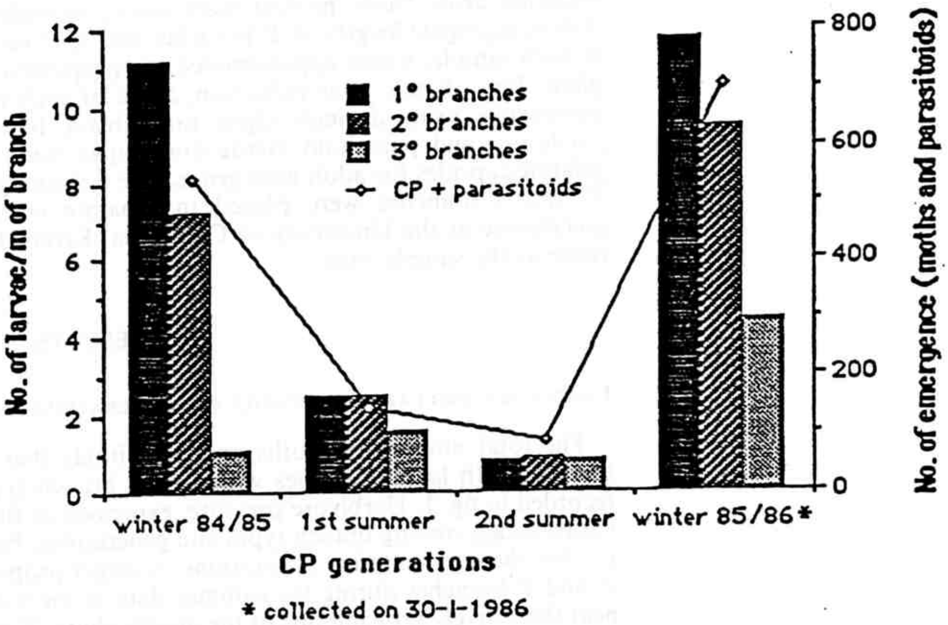

Fig. 1. Branch-type-specific larval densities (based on branch dissections) and moth and parasitoid emergence during 4 generations of *C. parthenica* (CP) (data from 3 field sites).

Parasitization ranged from 2 % in the 1° branches to 45 % in the 3° branches (fig. 2). The central diameter of each of 20 randomly selected 20-cm sections of each branch type was measured at 8 sites. A highly significant correlation was found between the branch diameter (log transformed) and the parasitization rate ($r = 0.66$, $p < 0.001$) (fig. 3).

Emergences of the moths and parasitoids are recorded in fig. 4. Emergence of *N. perplexus* peaked in early April, and again about 1 month later, reflecting 2 successive generations. *Eurytoma strigosa* emerged *ca.* 2 weeks later than *N. perplexus*, but only 1 individual from a possible 2nd generation was reared. The fact that these 2 chalcidoid species emerged before the hosts suggests that the sample collected on 8-III-1985 did not yet contain the last parasitoid generation that developed on the overwintering larvae.

To test the hypothesis that the parasitoids transferred from related native phytophagous hosts, which were assumed to be more common at sites with other *Chenopodiaceae* and a higher plant cover, the flora was identified at all the 10 sites sampled in spring, 1985. Each site was classified as having either more than 1 chenopod species present and plant cover above 25 %, or $\leqslant$ 1 chenopod species and plant cover below 25 %. No clear relation could be observed, but higher rates of parasitism (> 20 %) were only found at sites with higher plant cover (table 2). In order to identify alternate native hosts of the parasitoids, more than 100 lepidopterous and dipterous larvae were collected from surrounding plants (see Study area), but none of the parasitoid species reared from *C. parthenica* was recovered.

PARASITISM OF THE OVERWINTERING GENERATION 1985-1986

Approximately half of the *C. parthenica* moths recovered from the 1st sample collected on 23-IX-1985 emerged before 18-X-1985, indicating the possibility of a partial 4th

TABLE 1

Parasitoids reared from Coleophora parthenica *(CP) sampled in 1985-86 in the Coachella Valley of Southern California*

	Parasitoids ([a])		
	reared from generations of CP		Reported from other hosts
	winter	summer	
ICHNEUMONIDAE			
Calliephialtes notandus (Cresson)	+		
EULOPHIDAE			
Euderus sp.	+		
EUPELMIDAE			
Eupelmus cf. *limneriae* Howard	+		Lepidoptera, Braconidae ([b])
TORYMIDAE			
Microdontomerus anthonomi Crawford	+		Lepidoptera ([c]), Coleoptera, Braconidae ([b])
PTEROMALIDAE			
Norbanus perplexus (Ashmead)	+ +		reared from *Artemisia*
Neocatolaccus sp.	+		
EURYTOMIDAE			
Eurytoma strigosa Bugbee	+ +	+	*Xanthium strumarium* L.

([a]) From each of two winter (84/85, 85/86) and summer (1985) generations. + : 5 individuals ; + + : > 40 individuals reared.
([b]) Possible hyperparasitoid.
([c]) *Coleophora malivorella* Riley.

TABLE 2

Levels of parasitism of C. parthenica *(CP) in relation to site-specific plant diversity*

Site no.	Additional *Chenopodiaceae* spp. present	% Plant cover	No. of CP emerged	Rates of parasitization: Total	*Norbanus perplexus*	*Eurytoma strigosa*
Site with higher plant cover and chenopod diversity						
8	2	50	3	100.0	33.3	66.6
10	2	60	103	35.7	20.4	15.3
9	2	30	35	22.8	17.1	5.7
4	3	50	229	11.7	7.6	4.0
5	4	30	235	10.8	9.5	1.3
3	5	60	44	9.3	2.3	7.0
2	2	30	272	6.8	4.7	2.1
x̄		44.3	131.6	8.16	13.56	14.47
Site with lower plant cover and chenopod diversity						
6	1	10	134	6.1	4.5	1.5
7	1	10	315	5.4	2.2	3.1
1	1	5	10	0.0	0.0	0.0
x̄		8.3*	153 n.s.	3.83*	2.23*	1.53*

n.s. not significantly different, * $p < 0.05$ (Mann-Whitney-U-Test between site diversity types).

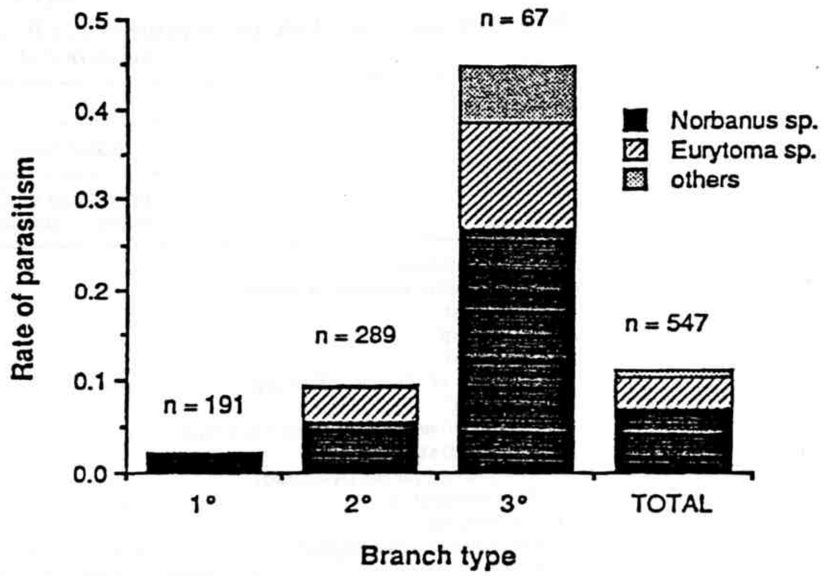

Fig. 2. Branch-type-specific levels of parasitism of overwintering *C. parthenica* collected in March, 1985 (results from 8 m of 1° branches and 20 m each of 2° and 3° branches from each of 3 localities).

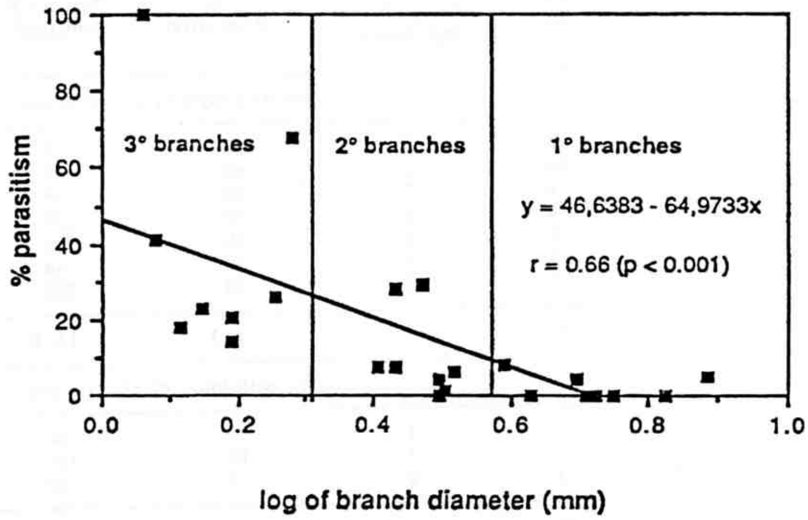

Fig. 3. Correlation between branch diameter and level of parasitism of overwintering *C. parthenica*, collected in March 1985.

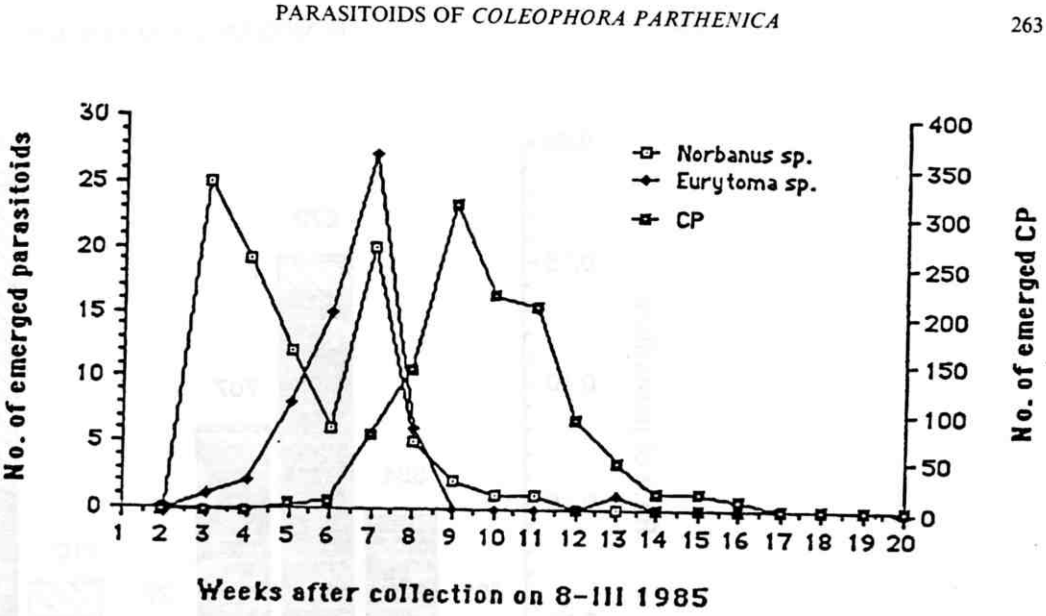

Fig. 4. Emergence of overwintering *C. parthenica* (CP) and parasitoids from branches collected on 8-III-1985 (results from 8 m of 1° branches and 20 m each of 2° and 3° branches from each of 10 localities).

generation. All other moths emerged in 1986. Data on moth emergende showed that the earlier a sample was collected, the later the moths emerged. In addition, only 3 % of the moths collected in IX-1985, compared to 82 % of the moths collected on 1-IV-1986, had emerged by August, 1986 (table 3).

Dissections further revealed that, although some of the remaining larvae had died by August, 1986, the majority were still alive and moths continued to emerge for more than a year. Some of the individuals in the April, 1986, sample had already emerged in the field, which explains the reduced number of larvae found during dissection (table 3).

TABLE 3

Emergence of overwintering C. parthenica *in relation to larval sampling date (pooled results from 3 sites) in the Coachella Valley of Southern California*

Site no. ([a])	Collection date	No. of moths ([b]) emerged from branches (obs.)	No. of larvae found in dissections (exp.)	Emergence rate (observed/expected)
A	25-IX-1985	6	182	0.03
B	29-X-1985	46	365	0.13
C	30-XII-1985	80	262	0.30
D	30-I-1986	162	26	0.61
E	1-IV-1986	94	114	0.82

([a]) Corresponding to fig. 5.
([b]) Total of moths emerged by August, 1986, calculated for 36 m of branches to correspond with the results of the dissections.

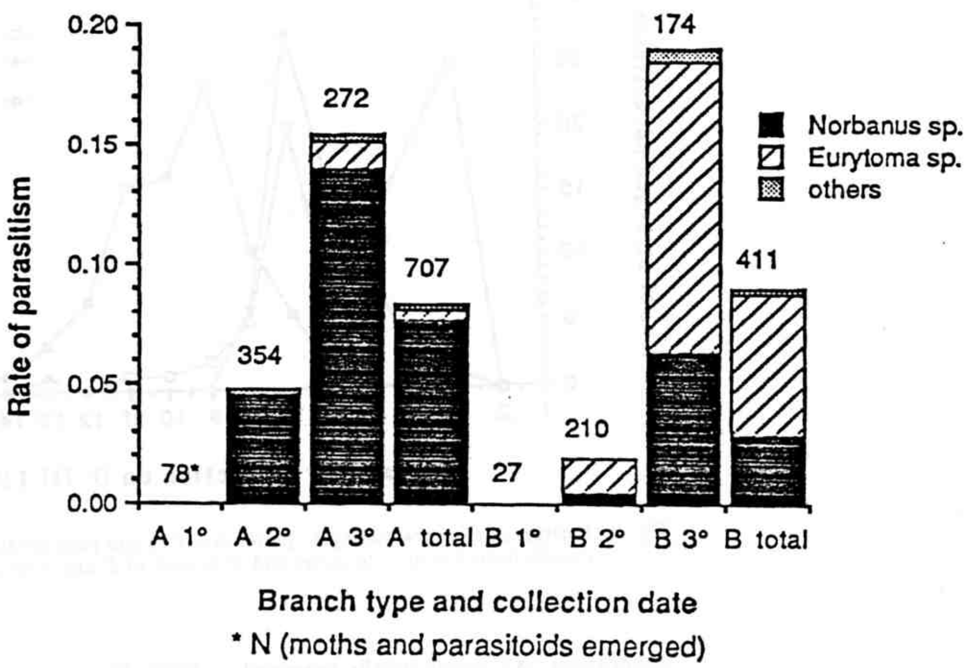

Fig. 5. Branch-type-specific levels of parasitism of overwintering *C. parthenica* (CP) larvae from samples collected on 30-I (A) and 1-IV-1986 (B) (results of 8 m of 1° branches and 20 m each of 2° and 3° branches from each of 3 localities).

A total of 73 *N. perplexus*, 31 *E. strigosa*, 3 *Neocatolaccus* sp., and 1 *Calliephialtes notundus* (Cresson) emerged from these overwintering larvae (table 1). Parasitism in the first 3 samples collected in 1985 was well below 1 %, and reached 5.5 and 8.8 % for the 30-I and 1-IV-1986 samples, respectively. However, as only 61 % and 82 % of the larvae emerged from the 1986 samples (table 3), actual parasitism was even lower. The highest rate of parasitism was 19 %, reached in 3° branches of the 30-IV-1986 sample (fig. 5). *Norbanus perplexus* predominated in the January sample, and *E. strigosa* in the April sample, probably because the former parasitoid had already emerged from these branches in the field (fig. 4).

Parasitism of *C. parthenica* in its native areas

Parasitoids of *C. parthenica* known from its native areas are listed in table 4. **Baloch & Mustaque** (1973) mentioned unidentified ectoparasitoids reared from larvae and pupae in *H. glomeratus*, and that ants apparently damaged pupae inside stem tunnels. **Baloch & Khan** (1978) reported 70 % parasitism of *C. parthenica* larvae by *Apanteles* sp. [*Braconidae*] and *Eurytoma* sp. No parasites were reported from Egypt, with the exception of the polyphagous mite, *Pyemotes herfsi* Oudemans, which was found on a few occasions attacking overwintering larvae (**Hafez** *et al.*, 1978). Shipments of *C. parthenica* from the U.S.S.R., Turkey and Pakistan for direct release in southern California were received in quarantine at the University of California, Riverside. Quarantine reports for 2 shipments

TABLE 4

Parasitoids of C. parthenica *known from its native areas : field records (F) and quarantine rearings (Q)*

	Origin of *C. parthenica*		
	Pakistan	Russia	Turkey
BRACONIDAE			Q
Apanteles sp.	F	Q	
Apanteles sp. nr. *firmus*	Q		
Microchelonus sp.		Q	
Rhaconotus sp. nr. *scirpophage*	Q		
PTEROMALIDAE		Q	
Norbanus sp. (not *N. perplexus*)	Q		
EURYTOMIDAE			
Eurytoma sp.	Q, F		

F : **Baloch & Khan** (1978).
Q : Reared from *C. parthenica* shipments for field release in southern California ; received in quarantine at the University of California, Riverside, during 1973 to 1975.

collected on 27-30-III-1975 at Kopet-Dag, Ashkhabad, Turkmenia, U.S.S.R., recorded 72 % and 78 % total parasitism by an unidentified species of *Pteromalidae, Microchelonus* sp., *Apanteles* sp., and another unidentified species of Hymenoptera. *Braconidae* parasitized 5 % of the larvae collected from material in January, 1974, near Antalya, Turkey, and received at Riverside. Overwintering larvae from Warsak, Pakistan, collected between 10-XII-1973 and 22-I-1974, were sent in 3 shipments to Riverside. Twenty-seven to 30 % parasitism was recorded in these shipments, but not all of the specimens reared from this material could be located during this study. However, 3 series of different parasitoid species from this Pakistan material, each containing > 20 individuals, were identified as *Norbanus* sp. (not *N. perplexus*, **E. E. Grissell**, pers. communication), and the braconids *Rhaconotus* sp. nr. *scirpophagae* Wilkinson and *Apanteles* sp. nr. *firmus* Telenga as well as a single specimen of *Eurytoma* sp. **Hawkes & Mayfield** (1978) reported that unidentified Hymenoptera and the predaceous mite, *Pyemotes ventricosus* (Newport), were reared in quarantine at Albany, California, from overwintering larvae collected in Egypt and Pakistan.

DISCUSSION

Larvae were present and abundant all through the year at the study sites, with 3 complete and a possible 4th partial, generation annually. Some overwintering larvae spent more than one year in dead branches before emerging the following spring ; hence, they represented a reliable and common resource for parasitoid exploitation. Mining in the central part of the plant, i.e., in the 1° branches, was shown to reduce the risk of parasitization (figs. 2, 5). The thin layer of plant tissues surrounding the larvae in the 3° branches as well as their peripheral position and, hence, easier access to parasitoids helps to explain this niche-specific parasitization pattern. The effects of larval position and branch diameter on the rates of parasitism could not be separated by field observations, as these 2 factors are highly interrelated ($r^2 = 0.9$, $p < 0.001$).

Niche-specific occurrence of *C. parthenica* larvae does not seem to be mainly determined by branch-specific parasitism, but rather by plant structure and nutritive value. Larvae can only enter the plant at the soft succulent growing tips of the plant branches, which is the preferred oviposition site, from where they tunnel downward into the 1° branches. The fact that an average 62.9 % of the pitch of 2° branches was already mined in December (**Goeden & Ricker**, 1979) explains the observed predominance of larvae in the 1° branches during the winter (figs. 2, 5). Since maximum rates of parasitism, even in 3° branches, only reached 32 %, within-plant distribution did not seem to play a major role in limiting the levels of parasitism. The absence or extremely low occurrence of parasitoids during the summer and early winter, despite the presence of numerous larvae, suggested the use of alternate hosts, but this could not be confirmed.

Hawkins & Lawton (1987) recently found herbivore feeding-niche and plant architecture to be the most important factors determining parasitoid richness. Few parasitoid species, especially of Lepidoptera, would be predicted for both of these factors in the system with which this paper is concerned (**Hawkins**, 1988). As stem borers benefit from both low visibility and high physical protection, they are relatively parasitoid species-poor as hosts. In addition, lowest parasitoid numbers are associated with phytophagous host on herbs. Compared to literature records analyzed by **Hawkins** (1988), the observed total of 8 parasitoid species is relatively high.

At least 2 of the ectoparasitoids listed in table 1, *E.* cf. *limneriae* Howard and *M. anthonomi* Crawford, are known to exploit hosts in different orders, and are probably also facultative hyperparasitoids. The latter species is also reported from other coleophorid moths (table 1). The 2 dominant ectoparasitoids, *N. perplexus* and *E. strigosa*, were thought to be phytophagous on *Asteraceae* (**Grissell**, pers. communication), but they most certainly emerged from stem borers within these plants.

The level of parasitism was generally greater in the native areas of *C. parthenica*, reaching up to 70 % in Pakistan and Russia (**Baloch & Mustaque**, 1973). Interestingly, the 2 dominant species exploiting *C. parthenica* in California are congeners of members of its native parasitoid complex. However, the endoparasitoid braconids represented in the native parasitoid guild are not present in California. **Zwölfer** (1963) studied the parasitoid complex of 3 *Coleophora* species, *C. deauratella* Zeller, *C. alcyonipennella* Koll. and *C. spissicornis* Haworth, in their native Europe. He also found well-synchronized, specialized, endoparasitoid braconids to dominate their parasitoid guilds, otherwise composed of polyphagous and less synchronized species, usually dependant on alternate hosts. Hence, the number and composition of the parasitoid complex acquired by *C. parthenica* during its 10 years in California agreed with the findings of **Zwölfer & Pschorn-Walcher** (1968). Where authochthonous and allochthonous parasitoid faunas still show some similarities, e.g., between the Nearctic and Palearctic, congeners in the native parasitoid fauna assumed to be physiologically preadapted, as well as polyphagous parasitoids with a wide range ecological niches, generally are the first to adopt introduced phytophagous hosts (see **Goeden & Ricker**, 1986, for similar findings on phytophage species acquisition by colonizing asteraceous thistles).

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RÉSUMÉ

Parasitoïdes obtenus de *Coleophora parthenica* [*Lepidoptera : Coleophoridae*], dix ans après son introduction en Californie du Sud pour la lutte biologique contre le chardon de Russie.

Le parasitisme de la mineuse des tiges et des branches, *Coleophora parthenica* Meyrick [*Lepidoptera : Coleophoridae*], introduite en Californie dans le cadre de la lutte biologique contre le chardon de Russie, *Salsola australis* R. Brown [*Chenopodiaceae*], a été étudié dans la vallée de Coachella au sud de la Californie entre 1985 et 1986.

Huit espèces de parasitoïdes ont été obtenues à partir des chenilles en hibernation. Aucun parasitoïde n'est issu des chenilles de la 1[re] génération, et seulement 2 individus d'une même espèce ont été obtenus des chenilles de la 2[e] génération estivale. Le niveau du parasitisme des chenilles hibernantes est en corrélation avec le diamètre des branches attaquées. Ce taux de parasitisme a varié, entre 2 % sur les branches primaires et 45 % sur les branches tertiaires au printemps 1985, et respectivement entre 2 % et 19 % au printemps 1986. Les localités avec une diversité végétale élevée ont présenté des taux de parasitisme significativement supérieurs par rapport aux localités moins riches. Aucun hôte alternatif des parasitoïdes de *C. parthenica* n'a été trouvé. Les 2 espèces dominantes, *Norbanus perplexus* (Ashmead) [*Pteromalidae*] et *Eurytoma strigosa* Bugbee [*Eurytomidae*], sont des hyménoptères ectophages solitaires apparentés aux parasitoïdes indigènes attaquant *C. parthenica* au Pakistan. Les 2 autres espèces de parasitoïdes ayant d'autres hôtes connus et attaquant *C. parthenica* en Californie du Sud sont des ectophages polyphages. Aucune espèce de braconide endophage et spécialisé, similaire à celles qui dominent dans le complexe parasitaire des zones d'origine du Pakistan et d'URSS, ne s'est établie sur *C. parthenica* au cours des 10 années suivants son introduction en Californie du Sud.

MOTS CLÉS : *Coleophora, Eurytoma, Norbanus, Salsola,* lutte biologique contre les mauvaises herbes, parasitoïdes.

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