

## ***Rhyzobius ventralis* (Erichson) and *R. forestieri* (Mulsant) (Coleoptera: Coccinellidae), their biology and value for scale insect control**

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### **Abstract**

Life-cycles and voltinism are described for *Rhyzobius ventralis* (Erichs.) and *R. forestieri* (Muls.) living in the region of Sydney, Australia, and also the role each plays in its particular biocoenosis. Colour variation and wax production are described for the larvae, prepupae, pupae and adults of both species, also the defensive and feeding behaviour. New and known host records are listed for both species. Reasons are suggested for the success, partial failure or failure of the species as biological control agents in various parts of the world.

### **Introduction**

Requests for identifications during the course of biological and ecological studies of various Australian Coccinellidae led to the discovery (Pope, 1981) that *Rhyzobius ventralis* (Erichson), used as a scale insect control agent in various parts of the world between the 1890s and the 1920s, consisted of two quite separate species, which are readily separable as larvae, pupae and adults, and quite distinct in their biology. Despite the importance of the control experiments undertaken in the past, there seems to have been little or no attempt to study the biology of the "species" before introductions were tried. Had such investigations been carried out in time, the success of *R. ventralis* might have been greater and at least some of the failures could have been avoided. Almost certainly, the confusion of identity would not have occurred. The purpose of the present paper is to describe the biology and ecology of the two species formerly called *Rhyzobius ventralis*, and to examine, in the light of the information obtained and by means of other available bionomic data, the reasons for their success and failure as scale insect controls. The present study complements the taxonomic treatment and historical discussion by Pope (1981), and it is hoped that it will provide some basis for prediction in any future use of the species as introduced predators.

### **Biology**

During 1978, breeding populations of *R. ventralis* and *R. forestieri* (Mulsant) associated with several different coccid species were studied in the Sydney area of Australia. Regular weekly samplings of the populations allowed a comparison to be made of the relationships between the various predators and parasites of the coccids and their influence on the biology of the two coccinellids. Supplementary information was obtained during the spring of 1979.

The main population of *R. ventralis* studied was at Randwick, but subsidiary

colonies were also studied at Kensington, Rosebery and Cowan. The principal prey of *R. ventralis* is the gum tree scale, *Eriococcus coriaceus* Maskell, which is common on several eucalypt species around Sydney. Minor hosts are the mealybugs *Nipaecoccus aurilanatus* (Maskell) on the hoop pine (*Araucaria cunninghamii*) and *Pseudococcus longispinus* (Targioni Tozzetti) on *Eucalyptus viminalis*; a margarodid, *Icerya* sp., on *Grevillea pumicea*; and the diaspidid *Phenacaspis grandilobis* (Maskell) on *Banksia* sp.

### Biocoenoses

At Randwick, between August and November 1978, heavy infestations of *Er. coriaceus* attacked leaves and young branches of *Eu. robusta*. In mid-August, larvae of *R. ventralis* were first observed feeding on *Er. coriaceus*, and throughout September adults and larvae of all instars were present in large numbers. During the first half of September, a large chamaemyiid, *Pseudoleucopis benefica* Malloch, another major predator of this coccid, appeared in the colony. A hymenopterous parasite, *Metaphycus* sp. (Encyrtidae), and a lepidopteran predator, *Stathmopoda melanochra* Meyrick (Tinaegeriidae (Stathmopodidae)), were also common, as well as an unidentified syrphid species. The competition for food which followed led to a dramatic decrease in numbers of *R. ventralis* larvae and also to a noticeable decrease in the size of adult beetles emerging during October. Between them, predators and parasites caused the almost total destruction of the *Eriococcus* colony. Minor predators, a green lacewing, *Chrysopa ramburi* Schneider, and larvae of four other coccinellid species, were also associated with the eriococcid. Of the coccinellids, *R. umbratus* Blackburn was present in the second half of September, a large species of *Diomus* and the larva of a species belonging to an unidentified genus towards the middle of October, and *Cryptolaemus montrouzieri* Mulsant in mid-November. All were apparently unable to become established successfully because of the decline in numbers of *Er. coriaceus*. A similar pattern was observed in 1979.

In early October 1978, adults and larvae of *R. ventralis* were found with *Er. coriaceus* on *Eu. bridgesiana* at Rosebery, and adults appeared for the first time amongst *Er. coriaceus* on *Eu. robusta* at Kensington. Later in the month, larvae were discovered at Kensington together with larvae of *P. benefica*, but both species had disappeared by early November after almost completely destroying the coccid colony. Two minor predators, larvae of the large species of *Diomus* and the same unidentified coccinellid species as at Randwick, were present in late October, but could not compete with the major predators and soon disappeared. In October, an ant, *Iridomyrmex* sp., was common attending the eriococcid.

Six weeks later, in the latter half of December, several fourth-instar larvae and a pupa of *R. ventralis* were found at Kensington under loose bark of *Eu. viminalis* in association with larvae and adults of the coccinellid *Midus pygmaeus* Blackburn. They preyed on small populations of *Er. coriaceus* and *Pseudococcus longispinus*. Adults of *R. ventralis* reared from this population were much smaller than those reared on *Er. coriaceus* earlier in the season. In the first half of December 1979, fourth-instar larvae, prepupae and pupae of *R. ventralis* were again found aggregating under loose bark of the same *Eu. viminalis*. Unlike 1978, adults reared from this population were of average size.

From late October to early December 1979, a heavy infestation of *Er. coriaceus* attacked a young unidentified eucalyptus tree at Cowan. During this period, major predators on the coccid included adults and larvae of *R. ventralis*, *Pseudoleucopis benefica*, *S. melanochra* and an unidentified syrphid. A single larva of a small species of *Diomus* was also present.

At Kensington between October and December 1978, large infestations of *N. aurilanatus* were preyed on by *C. montrouzieri* and a syrphid, *Melangyna viridiceps* (Macquart), together with a minor predator, a small species of *Diomus*. In early

December, several fourth-instar *R. ventralis* larvae were observed in the association, but no adults. Failure to become established was probably due to the reduced numbers of *N. aurilanus* and the intense competition for food. The *R. ventralis* population in October 1978 was very small, and no other predators or parasites were found associated with it on *Icerya* sp. on *Grevillea buxifolia* at Cowan. Similarly at Cowan in November 1979, a single specimen of *R. ventralis* was the only predator associated with *Phenacaspis grandilobis* on *Banksia* sp.

During 1978, only one breeding population of *R. forestieri* was studied. At Hornsby Heights, from early April to the end of May, larvae of *R. forestieri* were observed feeding on nymphs and adults of the eriococcids *Gossyparia casuarinae* Maskell and *Rhizococcus casuarinae* Maskell. They also occasionally fed on nymphs of the margarodids, *Monophlebulus* sp. and *Icerya purchasi* Maskell. The population of *R. forestieri* was quite small and confined to *Casuarina* trees from which the main coccinellid predator (*Telsimia subviridis* (Blackburn)) on the coccids was absent. Larvae of another cocciduline coccinellid were also present in small numbers. No dipterous larvae were observed, but an unidentified moth and an unidentified hymenopterous parasite of *G. casuarinae* were present. *R. forestieri* did not occur on *Casuarina* in spring, summer or winter.

From late September to late November 1979, a small breeding population of *R. forestieri* was associated with a very heavy infestation of pink wax scale, *Ceroplastes rubens* Maskell, on the leaves of several umbrella trees, *Schefflera actinophylla*, at Kensington. A population of *Cryptolaemus montrouzieri* was also present on the trees throughout this period, but the two species rarely occurred on the same leaf. It is perhaps significant that in the laboratory, even although coccid food was plentiful, *C. montrouzieri* larvae preyed on larvae of *R. forestieri*. No other predators of the scale were observed.

Two fourth-instar larvae of *R. ventralis* taken from under bark of *Eu. viminalis* at Kensington in late November 1979 proved to be parasitised. One produced four adults and the other two adults of an encyrtid, *Anagyrus australiensis* (Howard). No evidence of parasitism was found in *R. forestieri*.

### Life-cycle and voltinism

Oviposition has not been observed in *R. ventralis*, and the total number of eggs produced by any female is not known, nor the length of period over which they are laid. The ovipositor is very long, narrow and heavily sclerotised, so that it can be inserted inside female *Er. coriaceus* sacs. The eggs are laid singly, either against female coccids or amongst wax produced by large numbers of developing coccid nymphs, thus ensuring an adequate food supply for the young larva. Each egg is usually placed horizontally. It is pale yellow, oval and 0.7 mm in length by 0.3 mm in width. The empty chorion is not eaten.

From mid-August to the end of October 1978, 22 specimens were reared from eggs to adults at room temperature on *Er. coriaceus*. In addition, many more were collected in the field at various larval instars, and a total of 118 adults was successfully reared. Sizes of individuals within each instar varied, as did the duration of time spent in each instar (Table I), being influenced by food supply, temperature and photoperiod. The mean total time from first-instar larva to adult was 33 days (range 29–36 days) in September and 25 days (range 22–30 days) in October. Maximum and minimum mean room temperatures were 21.6 and 17.7°C for September and 23.3 and 20.0°C for October, respectively. The number of hours of daylight between sunrise and sunset was 11.58 (range 11.27–12.09) in September and 12.56 (range 12.25–13.07) in October. Adults were kept alive in the laboratory for up to three months. Provided plentiful supplies of *Er. coriaceus* were available, the larval and pupal mortality rates were very low at 3.6%. A further 79 adults were reared in 1979 and again fed on *Er. coriaceus*.

The ovipositor of *R. forestieri* is not as long or as heavily sclerotised as that of *R.*

TABLE I. *The size and duration of preadult instars in R. ventralis*

Instar	Length (mm)	n	Duration of each instar (days)		
			Range	Mean	Standard deviation
1	1.4	22	3-5	4.1	0.75
2	2.5	22	3-7	4.9	1.08
3	3.7	22	4-6	4.9	0.81
4	6.4	22	2-7	4.8	1.46
Prepupa	5.1	22	2-4	3.1	0.61
Pupa	4.3	22	6-10	8.0	1.04
Total larval instars		22	12-24	18.7	3.56
Total larval and pupal instars		22	22-36	29.8	4.66

*ventralis*. Eggs are laid singly on, under or against *Gossyparia casuarinae*, *Rhizococcus casuarinae* and *Ceroplastes rubens*, there being no sac as in *Er. coriaceus*. They are usually placed horizontally. The egg is pale yellow, oval and 0.6 mm in length by 0.25 mm in width.

In 1978, five out of seven specimens were reared through to the adult stage at room temperature from second- and third-instar larvae collected in the field. They were fed on *G. casuarinae*. As with *Rhizobius ventralis*, the size of individuals within each instar varied, and the duration of time spent in each instar (Table II) was influenced

TABLE II. *The size and duration of preadult instars in R. forestieri*

Instar	Length (mm)	n	Duration of each instar (days)							
					Range		Mean		Standard deviation	
			Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn
1	1.2	3	—	3-4	—	3.3	—	0.47	—	
2	2.2	3	5	3-4	—	3.7	—	0.47	—	
3	3.4	3	7	4-5	11-16	4.7	13.2	0.47	1.92	
4	6.0	3	7	5-6	5-10	5.7	6.8	0.47	2.16	
Prepupa	4.7	3	5	3	4-6	3.0	5.4	0.00	0.74	
Pupa	4.0	3	5	6-7	7-8	6.3	7.4	0.47	0.54	
Total larval instars		3	—	17-18	—	17.3	—	0.47	—	
Total larval and pupal instars		3	—	26-27	—	26.7	—	0.47	—	

by food supply, temperature and photoperiod. The total time from third-instar larva to adult was 30 days in April in both specimens reared and 35 days (range 29-39 days) in May. Maximum and minimum mean room temperatures were 24.2 and 22.0°C for April and 21.6 and 19.4°C for May, respectively. The number of hours of daylight between sunrise and sunset was 11.06 (range 10.47-11.41) in April and 10.20 (range 10.07-10.35) in May. The mortality rate of 29.4% was much higher than in *R. ventralis*.

Between late September and late October 1979, a further three individuals of *R. forestieri* were reared through to the adult stage at room temperature, being fed on *C. rubens* (Table II). The mean total time from first-instar larva to adult was 27 days (range 26-27 days). Maximum and minimum room temperatures were 21.7 and 18.6°C for September and 22.6 and 19.9°C for October, respectively. The number of hours of daylight was as for 1978. These adults and others were kept alive in the laboratory for over two months.

The rate of development was more rapid in spring than in autumn (Table II). While it is unlikely that the small variations in temperature between the two seasons

were significant, differences in daylength and food may both have been important. The spring generation was exposed to an extra two hours of daylight, with daylength gradually increasing. In addition, *C. rubens* may have been preferred to *G. casuarinae* as an essential food. The rate of development in spring is similar to that of *R. ventralis* at the same time of year when fed on *Er. coriaceus* (Table I).

In the Sydney area, *R. ventralis* appears to be univoltine. It is essentially a spring species, emerging from diapause early in the season. It is common during September and October, but few larvae survive into November or December, lack of essential food being a limiting factor. It is possible that some adults maturing in late September or early October may give rise to a partial second generation overlapping with the protracted first generation. In November 1979, a second generation was reared through to fourth-instar larvae before *Er. coriaceus* disappeared. The inability of *R. ventralis* to compete with the very voracious *Cryptolaemus montrouzieri* may be a major factor inhibiting an autumn generation, for although *Er. coriaceus* is again abundant in late summer and early autumn, *C. montrouzieri* is its major predator and no *R. ventralis* larvae or adults were observed.

In contrast, *R. forestieri* may be bivoltine, although this has yet to be demonstrated. In 1978, it was reared only in the autumn. Larvae first appeared in late March and were present throughout April and May, with a few surviving into early June. The absence of a spring generation at Hornsby Heights may be related to the species' inability to compete with *Telsimia subviridis*. There is a spring generation when *R. forestieri* is associated with other coccids. At Kensington in 1979, larvae and adults were present in small numbers during October, with a few larvae surviving into the second half of November.

Larvae of *R. forestieri* were also reared from citrus mealybugs, *Planococcus citri* (Risso), at Waikerie, South Australia, in late October and early November 1971; from green scale, *Coccus viridis* (Green), on citrus at Brisbane in late October and November 1973; from *Eriococcus* sp. near Maleny in south-east Queensland in early November 1975; from *Ceroplastes rubens* on citrus and *Schefflera actinophylla* in Brisbane in October 1974; and from *Parthenolecanium persicae* (F.) on an unknown host at Guyra, New South Wales, in mid-November 1931.

### Behaviour

Both larvae and adults of *R. ventralis* feed mostly on *Er. coriaceus*. The female coccid appears especially vulnerable to predation because of a large opening at the posterior end of its sac through which the tip of its abdomen protrudes and crawlers escape. However, although it may attack through this opening, the *R. ventralis* larva usually makes a hole in the lower part of a sac, curls itself around the sac and remains there feeding until it is empty. First-, second- or third-instar larvae may occasionally share a single sac. They sometimes moult there. When disturbed, first-instar larvae may take refuge inside empty sacs, and first- and second-instar larvae sometimes occupy the shallow shapes of empty open sacs. When feeding, some larvae keep their abdomens outside their respective sacs. If these larvae are touched, the projecting abdomen is raised and lowered several times in quick succession. A similar reaction is elicited from pupae. This is often an effective deterrent to any intending predator. Larvae of all instars live in close proximity on leaves and branches, and up to 10 have been observed on a single leaf. Cannibalism has not been observed in the field.

*R. forestieri* larvae and adults are polyphagous, and their feeding behaviour varies. If feeding on infestations of *C. rubens*, their behaviour is similar to that of *R. ventralis* on *Er. coriaceus*. A hole is made through the waxy covering, and the larva curls itself around or over the scale, remaining there until it has been eaten. If feeding on *G. casuarinae*, *Rhizococcus casuarinae* and *Monophlebulus* sp., which do not aggregate, then much time is spent searching for food. When feeding, the larva rests partly on the coccid, which is not enclosed in a sac or covered with wax. Unlike *Rhyzobius ventralis*, it is rare to find more than two or three larvae in close proximity.

On being lightly touched, larvae and prepupae of *R. ventralis* may produce large droplets of orange-brown or tomato-red fluid from the intersegmental membranes between the abdominal tergites. These droplets rapidly coagulate and may adhere to the cuticle. At ecdysis, the droplets sometimes remain attached to the exuvium. Larvae of *R. forestieri* produce yellow droplets. When irritated, reflex bleeding as a means of defence occurs in adults of both species. Blood is produced from the femoro-tibial articular membranes of all six legs, but especially from the forelegs. It is more readily exuded in teneral than in more mature adults. Up to three drops may be produced at any one time from a single leg under repeated stimulation, the second drop being the largest. As in the larva, the droplets rapidly coagulate. *R. forestieri* adults produce yellow droplets, but the colour varies in *R. ventralis*, tomato red, orange-brown and yellow having been recorded, and in all cases the beetles were feeding exclusively on *Er. coriaceus*.

### Colour variation and wax production

The normal colour of *R. ventralis* larvae is brownish-orange (Table III). In early instars this is overlaid by a grey bloom, and it is later more or less obscured by production of melanic pigment. In the fourth instar and prepupa it is even further obscured by greyish cuticular pigmentation. In all larvae, the head is black, the pygidium dark grey and the sternites brownish-orange to tomato red, as is the haemolymph. Initially, the pupa is light brown with head, prothorax and wing buds orange, but occasionally it is totally orange. The colour gradually changes to a uniform dark brown. The teneral adult has a black head, pronotum and legs, testaceous abdominal sternites, and elytra varying from tomato red through orange to gamboge. Over a period of 24 h, the elytra change through light brown to darker brown to black.

TABLE III. *Inter- and intraspecific colour variation*

Instar	<i>R. forestieri</i>	<i>R. ventralis</i>		
		Normal colour range	Red morph	
Larva	1	Greenish-yellow strongly overlaid by melanic pigment	Brownish-orange to mid-brown with grey bloom	Orange-red
	2	Greenish-yellow strongly overlaid by melanic pigment	Brownish-orange to mid-brown with grey bloom	Tomato red
	3	Greenish-yellow strongly overlaid by melanic pigment	Deep brownish-orange to mid-brown overlaid by melanic pigment	Tomato red with traces of melanic pigment
	4	Greenish-yellow strongly overlaid by melanic pigment	Deep brownish-orange to mid-brown strongly overlaid by melanic pigment	Tomato red very thinly overlaid by melanic pigment
Prepupa	Olive-brown	Deep brownish-orange to mid-brown strongly overlaid by melanic pigment	Tomato-red very thinly overlaid by melanic pigment	
Pupa	Teneral	Cream	Orange to light brown	
	Mature	Deep olive brown	Dark brown	As normal morph
Adult	Teneral	Brown head and pronotum elytra fawn	Black head and pronotum elytra orange to light brown	
	Mature	Black above except anterior pronotal angles	Black above except anterior pronotal angles	

During September 1978, a red larval morph was present amongst a population feeding on *Er. coriaceus* on *Eu. robusta*. It was not common, but eight larvae were reared through to the adult stage. Three were reared from eggs laid on a leaf collected in early September. A week later, the remaining five were taken as second-instar larvae from a twig on the same tree. Both groups could have come from eggs laid by the same female. The red morph was more elongate than the normal form, but the pupae and adults were identical. The general colour was orange-red, sometimes over-

laid by very vaguely indicated darker areas, probably stemming from a very much reduced production of melanic pigment (Table III). The morph was most readily distinguished during the second instar, when it generally had no visible deposits of pigment and appeared a bright tomato red.

Colour differences were also noticed between populations of otherwise normal *R. ventralis* larvae. Larvae feeding on *Er. coriaceus* on *Eu. viminalis* were mid-brown overlaid with melanic pigment, whereas larvae feeding on *Er. coriaceus* on *Eu. robusta* were brownish-orange to red, partly obscured by melanic pigment. Third- and fourth-instar larvae feeding on *Icerya* sp. were closer in colour to *R. forestieri* larvae (see below) than to those of *R. ventralis* feeding on *Er. coriaceus*, and were more heavily pigmented. However, unlike *R. forestieri*, the pupa was initially a uniform golden tan, gradually changing to the dark brown of *R. ventralis*.

The general colour of *R. forestieri* larvae is a greenish-yellow heavily obscured by production of melanic pigment (Table III). The head is black, the ventral sternites yellowish-grey and the haemolymph yellow. Initially, the pupa is a uniform cream colour with black spiracular spots. After 24 h, it changes to pale olive-brown with darker markings on the pro- and mesonota, and eventually darkens to uniform deep olive-brown. The mature adult is the same colour as *R. ventralis*, but the teneral has a brown head and pronotum, pale fawn elytra with an olive brown tinge, a fawn abdomen with pale reddish-brown tip and black legs. Over a period of 24 h, the head and pronotum turn black, the elytra change to light brown, to darker brown to black, while the abdomen becomes reddish-brown.

Normal wax production in larval instars is similar in both species. The description and illustrations given by Flanders (1930) are actually of *R. forestieri* but could apply equally well to *R. ventralis*. No wax has been observed in first- and second-instar larvae, but in the third instar the six circles on each abdominal tergite and the meso- and metanota become very pronounced and raised as tubercles. Wax is produced in small amounts (Pope, 1979) as fine threads around each tubercle and over the large, dark rugose markings on the pronotum. In the fourth instar, more wax is produced over the entire pronotum and pygidium, most of the meso- and metanota and on the abdominal tergites from areas surrounding the tubercles. However, the threads are quite short, and the body surface between the tubercles remains clearly visible. Later in the instar, the amount of wax gradually increases, but the actual quantity produced varies between different individuals. Throughout the prepupal stage, large quantities are produced and the threads may be very long. Initially, the greatest amounts are produced from the thoracic nota, the pronotum in particular so that the head is completely covered, and from the lateral abdominal tubercles. The terga may still remain visible, or the whole body of the larva may be completely covered with wax. The amount produced increases over a period of three to four days. It is a very good camouflage, helping the prepupa to merge into the background of *Eriococcus* sacs on *Casuarina* bark. In the red morph of *R. ventralis*, wax production is very low; the wax circles are absent, their position being marked by short, dark setae. The pupa produces no wax but may be partly covered by traces of prepupal wax. Small quantities of wax may be present amongst the dorsal setae of the adult.

Stereoscan electron microscope examination of both dried and de-waxed examples of *R. ventralis* and *R. forestieri* has shown that the tentative suggestion as to the origin of the wax given by Pope (1979) was wrong. It is now clear (Pope, pers. comm.) that the two species extrude fine threads of wax, some 1.0–1.5  $\mu\text{m}$  in diameter, from modified socketed setae set around and upon the six setiferous tubercles on each abdominal segment and scattered over the thoracic nota. The red morph of *R. ventralis* possesses the same type of secretory setae as those in the normal, wax-producing form.

#### Host records

Examination and identification of material from museums and Departments of

Agriculture throughout Australia have revealed a number of host records additional to those above, mainly associated with *R. forestieri* (Table IV). In three cases, on *Saissetia oleae* (Olivier), *Eriococcus ironsidei* Williams and *Ceroplastes rubens*, *R. forestieri* was misidentified as *R. ventralis* (Wilson, 1960; Ironside, 1978). The association with *Aonidiella aurantii* (Maskell) is probably accidental; *R. debilis* Blackburn, *R. lophanthæ* (Blaisdell) and *Orcus* spp. are its major predators, while *R. forestieri* normally preys on other pests of citrus. This appears to be the first record of *Rhyzobius* preying on the widely distributed tropical species *Coccus viridis* (Bartlett, 1978).

TABLE IV. *Host records for Rhyzobius forestieri in Australia*

Coccid hosts	Host-plants	Adult beetle	Adult beetle and larvae	State	Locality
<i>Gossyparia casuarinae</i>	<i>Casuarina</i> sp.	Yes	Yes	N.S.W.	Hornsby Heights
<i>Rhizococcus casuarinae</i>	<i>Casuarina</i> sp.	Yes	Yes	N.S.W.	Hornsby Heights
<i>Monophlebulus</i> sp.	<i>Casuarina</i> sp.	Yes	Yes	N.S.W.	Hornsby Heights
<i>Icerya purchasi</i>	<i>Casuarina</i> sp.	Yes	Yes	N.S.W.	Hornsby Heights
<i>Parthenolecanium persicae</i>	Unknown	Yes	Yes	N.S.W.	Punchbowl Gosford Guyra
<i>Paralecanium frenchii</i> (Maskell)	Unknown	Yes	No	N.S.W.	Sydney
<i>Saissetia oleae</i> (Black scale)	Citrus	Yes	No	N.S.W.	Narara Baulkam Hills Kenthurst Sydney
<i>Aonidiella aurantii</i> (Red scale)	Citrus	Yes	No	N.S.W.	Kenthurst Penrith
<i>Eriococcus ironsidei</i> ( <i>Macadamia felted</i> coccid)	<i>Macadamia integrifolia</i>	Yes	Yes	Q'ld	Lagoon Pocket Nambour Beerwah
<i>Coccus longulus</i> (Douglas)	Citrus	Yes	No	Q'ld	Brisbane
<i>Coccus viridis</i> (Green scale)	Citrus	Yes	Yes	Q'ld	Brisbane
<i>Cryptes baccatus</i> (Maskell)	<i>Acacia</i> sp.	Yes	No	Q'ld	Brisbane
<i>Ceroplastes rubens</i> (Pink wax scale)	Citrus	Yes	Yes	Q'ld	Brisbane
<i>Planococcus citri</i> (Citrus mealybug)	<i>Schefflera actinophylla</i>	Yes	Yes	N.S.W.	Kensington
	Citrus	Yes	Yes	S.A.	Waikerie

There is only one new host for *R. ventralis*: adult beetles and larvae feeding on *Rhizococcus viridis* Green on *Acacia* sp. at Brisbane.

## Discussion

Over the years, a number of Australian coccinellids have been exported around the world for use in experiments on biological control of insect pests. In the 1890s, when many of them were first introduced into other countries, no attempts were made to study their biology before they were released. Until now the only information available on *Rhyzobius ventralis* concerned its role as a biological control agent in New Zealand (Kirk & Cockayne, 1909; Clark, 1938). The accounts given by Essig (1910) and Quayle (1911) almost certainly refer to *R. forestieri*.

Defensive behaviour is characteristic of many coccinellids. Reflex bleeding as a deterrent to potential predators has been known for a long time in adult coccinellids. It has also been recorded in fourth-instar larvae of *Hyperaspis binotata* (Say) (Böving, 1917), larvae and pupae of *Cryptognatha nodiceps* Marshall (Taylor, 1935), larvae of *Scymnodes lividigaster* (Mulsant) (Richards, 1980) and now in *R. ventralis* and *R. forestieri* larvae. Essig (1910) referred to a sticky yellow fluid being emitted by larvae

of "*R. ventralis*". Unfortunately he did not say whether it came from the mouth or intersegmental membranes. The quantity of fluid produced depends on the degree of irritation. In some species it may be resorbed (Taylor, 1935), but this has not been observed in *R. ventralis* or *R. forestieri*, for in these species it coagulates very rapidly. The fluid, which is a secretion from hypodermal glands (McIndoo, 1916), is brightly coloured as well as unpleasant to taste. The present observations of tomato-red fluid in *R. ventralis* appear to be the first record in coccinellids of a red instead of a yellow fluid, but, as shown above, the colour of the fluid produced by adults of this species may be variable, even within one population.

Many coccinellid larvae produce wax as a deterrent against predators (Pope, 1979). As the smaller instars of *R. ventralis* often shelter inside coccids, this perhaps explains why there is no visible wax until the third instar. In both *R. forestieri* and *R. ventralis*, it is produced in greatest quantities during the immobile and vulnerable prepupal stage. Contrary to Pope's (1979), hypothesis recent observations have shown that it may act as a very efficient camouflage by merging with the background.

Coccinellid pupae permanently attached to a leaf or stem are very vulnerable to predation or cannibalism. Bright colours and reflex bleeding may be aposematic in pupae of some species, while the more drably coloured ones have developed other means of protection. The rapid up and down jerky movements of irritated *R. ventralis* and *R. forestieri* pupae is a phenomenon common to many coccinellids. Taylor (1935) has recorded it in *Cryptognatha nodiceps*, and here the rapid tapping of several pupae moving in unison must be an even more effective deterrent. Many coccinellid pupae, including those of *Rhyzobius*, are covered by an armature of long, stout setae. The waxy covering left behind by certain larvae at pupation often acts as a shelter for their pupae. In both species of *Rhyzobius*, the amount of wax tangled amongst the long pupal setae varies, some pupae being completely naked.

It was originally thought that differences in larval coloration between the two species of *Rhyzobius* might be explained by *R. forestieri* feeding on coccids with yellow body fluids, such as *Gossyparia casuarinae* and *Rhizococcus casuarinae*, while the normal prey of *Rhyzobius ventralis*, *Er. coriaceus*, had red body fluid. The fact that *R. ventralis* when feeding on *Icerya*, which has brownish body fluid, developed a body colour closer to that of *R. forestieri*, supports this hypothesis. However, the discovery that populations of *R. ventralis* feeding on *Er. coriaceus* on *Eu. viminalis* were brown, while those feeding on *Er. coriaceus* on *Eu. robusta* were brownish-orange to red makes this interpretation less credible. Nevertheless, recent observations have shown that in coccinellids intraspecific coloration of larvae and pupae can be induced to vary when immature stages of the life-cycle are completed on different prey, each associated with a different host-plant. *S. lividigaster* changed from brown when fed on *Aphis eugeniae* van der Goot on *Glochidion ferdinandi* to yellow when fed on *Myzus persicae* (Sulzer) on *Solanum tuberosum*. Variation in coloration between different instars depends on how much of the body fluids are visible through the insect cuticle, the degree of tanning of the exocuticle and the amount of melanic pigment produced.

There are few records of parasitism in the genus *Rhyzobius*. Koebele (1893) records 21 larvae of *R. ventralis*, collected at Melbourne from under bark of *Eucalyptus* infested with *Eriococcus*, as being parasitised by 84 larvae of an encyrtid, *Homalotylus*. Evidently, due to secondary parasitism, only 15 of these parasites emerged. Riley (1893) refers to two species of *Homalotylus* reared from coccinellid larvae sent by Koebele from Australia. One of these was from *R. ventralis* and was presumably the species reported by Koebele. He also records another encyrtid from a new genus near *Aphycus* as parasitising *R. debilis*. Howard (1898) identified four specimens of this latter parasite as *Heterarthrellus australiensis* Howard. He listed two records, one from larvae of *R. debilis* collected from Adelaide, South Australia, and the other from pupae of *Diomus pumilio* (Weise) (cited as *Scymnus flavifrons* Blackburn) from Parramatta, New South Wales. The specimens reared from two *R. ventralis* larvae at Kensington, New South Wales, belong to the same species, now known as *Anagyrus*

*australiensis*. It is not closely related to *Homalotylus* (J. S. Noyes, pers. comm.). There are no records of parasitism in *R. forestieri*.

Very little is known about the biocoenoses to which *R. ventralis* and *R. forestieri* belong in Australia. In our experience, *R. ventralis* has a relatively limited host range, its principal prey being the very common and widely distributed multivoltine gum tree scale, *Er. coriaceus*, which attacks many species of *Eucalyptus* (Froggatt, 1900, 1921; Patel, 1971). This coccid is heavily parasitised and attacked by predators. Patel (1971) has listed a number of its natural enemies, and the author has added to the count, in particular increasing the number of coccinellids from one to six species. However, *R. ventralis* remains the main coccinellid predator and plays an important role in controlling the coccid. The rearing of *R. ventralis* on *Icerya* sp. in 1978 has shown it to be an essential but less favoured food of this species. The present observations and identifications appear to be the first records of *R. ventralis* associated with *Nipaecoccus aurilatus* on *Araucaria cunninghamii*, *Rhizococcus viridis* on *Acacia* sp. and *Phenacaspis grandilobis* on *Banksia* sp. However, in all biocoenoses with which it is associated, except that based on *Er. coriaceus*, *Rhyzobius ventralis* appears to play a minor role.

During his travels in Australia, Koebele (1890, 1893) recorded *R. ventralis* as associated with various species of *Eriococcus* and with *Icerya* sp. In South Australia, Tasmania and Victoria, it was very common under bark of eucalypts infested with what was stated to be *Er. eucalypti*, and in South Australia it was occasionally found on *Icerya* sp. The rearing of *R. ventralis* on *Icerya* sp. in 1978 has shown it to be an essential but less favoured food of this species. The present observations and identifications appear to be the first records of *R. ventralis* associated with *Nipaecoccus aurilatus* on *Araucaria cunninghamii*, *Rhizococcus viridis* on *Acacia* sp. and *Phenacaspis grandilobis* on *Banksia* sp. However, in all biocoenoses with which it is associated, except that based on *Er. coriaceus*, *Rhyzobius ventralis* appears to play a minor role.

Many of the food preferences attributed to "*R. ventralis*" are very probably those of the polyphagous *R. forestieri*. Specimens collected by Koebele at Cairns, northern Queensland from *Casuarina kuanda* and now in the B. P. Bishop Museum, Honolulu, have proved to be *R. forestieri*, as have specimens taken from *C. glauca* at Brisbane in 1917 and now in the Department of Primary Industries Collection, Brisbane. In New South Wales, Koebele (1893) recorded "*R. ventralis*" feeding on *Er. leptospermi* Maskell on *Leptospermum laevigatum* at Mt Victoria and on *Er. araucariae* Maskell on *Araucaria heterophylla* at Sydney. The present records show that *R. forestieri* is associated with *Er. leptospermi* on *L. laevigatum* at Sydney, and on *A. bidwillii* and *A. cunninghamii* at Mt Nebo and Brisbane, Queensland; but that *R. ventralis* occurs on *A. cunninghamii* at Sydney. Beetles taken by Koebele at Whitton, New South Wales, feeding on *Gossyparia* or *Rhizococcus* were also probably *Rhyzobius forestieri*. Pope's (1981) identifications have confirmed that *R. forestieri* is a predator of citrus pests in Australia, supporting my view that it was almost certainly this species that Koebele observed feeding on "*Lecanium*" on citrus and other trees in New South Wales.

The apparent acceptance by *R. forestieri* of a number of exotic coccids as essential food has led to its being used with mixed success in biological control experiments in various parts of the world, including Australia, on a number of pests, particularly those associated with citrus and other fruit trees. Black scale, *Saissetia oleae*; soft brown scale, *Coccus hesperidum* L.; white wax scale, *Ceroplastes destructor* Newstead; pink wax scale, *C. rubens*; and several mealybugs: *Planococcus citri*, *Dysmicoccus brevipes* (Cockerell), *Nipaecoccus filamentosus* (Cockerell) and *N. nipae* (Maskell) (Wilson, 1960; Clark, 1938; Thompson & Simmonds, 1965; Leeper, 1976; Zimmerman, 1948) have been confirmed as hosts. References to "*R. ventralis*" feeding on nigra scale, *Parasaissetia nigra* (Nietner); San José scale, *Quadrapsidiotus perniciosus* (Comstock); the mealybug *Pseudococcus calceolariae* (Maskell) (cited as *P. gahani* Green) and the citrus aphid *Toxoptera citricida* (Kirkaldy) (Thompson & Simmonds, 1965) cannot be verified; neither can the Californian record of it as predaceous on *Pulvinaria innumerabilis* (Rathvon) on apple (Marlatt, 1904).

The control of *Er. coriaceus* by *R. ventralis* in New Zealand is one of the success stories of biological control, but it has not been repeated elsewhere with this species.

Reasons for the success, partial failure or failure of *R. ventralis* and *R. forestieri* as biological control agents may be related to the following factors:

1. *Voltinism*.—Climatic and seasonal changes influence voltinism in coccinellids. In Australia, few coccinellids are found in arid or semi-arid areas, most preferring the humid coastal regions. Yet, even here, the summer heat may be too severe for the survival of coccinellid larvae and their prey. As a result, some Australian coccinellids produce spring and autumn generations and enter reproductive diapause during summer and winter (Anderson & Richards, 1977). In Sydney, *R. ventralis* appears to be univoltine. Although *R. forestieri* may be bivoltine, records from other parts of Australia suggest that, like *R. ventralis*, it prefers to breed in spring. However, both species possess facultative voltinism if there is a plentiful food supply and temperature and photoperiod are favourable. This type of voltinism has also been recorded in North America for several species of *Hippodamia* (Hagen, 1974). In New Zealand, where *Er. coriaceus* can build up to pest proportions, *R. ventralis* is at least bivoltine (Clark, 1938), and its active presence over a greater period of the year has helped control the eriococcid. There is no information available on voltinism for *R. forestieri* in New Zealand, but adults taken on citrus near Auckland in October 1938 and December 1956 suggest there is a spring generation. In California, *R. ventralis* failed to become established. *R. forestieri* (then called *R. ventralis*) also failed to become established in the hot arid counties of California but was more successful in coastal areas, adult beetles having been collected there over 60 years after the original date of release. Essig (1910) recorded that in coastal Ventura County, although larvae of *R. forestieri* were present throughout the year, they were in significant numbers only from October to December and were very scarce in June and July. This allowed *S. oleae*, with both summer (June) and late autumn (November) generations, to reassert itself during the summer months. Biological control of *S. oleae* was inadequate probably because of lack of synchronisation between predator and prey, the two species having different phenology and temperature thresholds for feeding and reproduction. Normally, for successful control the predator should have more generations per year than its prey.

2. *Natural enemies and competitors*.—Parasitism and predation of the two coccinellids appear to be of minor importance in limiting their effectiveness in biological control. In Australia, two parasites of *R. ventralis* have been recorded, *Homalotylus* sp. (Koebele, 1893; Riley, 1893) and *Anagyrus australiensis* referred to earlier in this paper. In neither case did they appear to pose a serious threat to the coccinellid population. There are no records of parasitism in *R. forestieri*. In California, Essig (1910) considered the green lacewing, *Chrysopa* sp., to be the only enemy of *R. forestieri*.

Both species have difficulty competing with other predators. In New Zealand, the remarkable success of *R. ventralis* in controlling *Er. coriaceus* was strongly influenced by the absence of other parasites and predators of the coccid. Although introduced into California to control black scale, "*R. ventralis*" showed a preference for mealybugs (Essig, 1910). As *Cryptolaemus montrouzieri* is a very voracious predator of mealybugs and was imported into California at about the same time as "*R. ventralis*", this may have led to competition between the two species, although it has not been recorded. The same situation could have arisen in Hawaii, where both species were also introduced (Swezey, 1915). In Australia, there is supporting evidence that neither *R. ventralis* nor *R. forestieri* can compete with *C. montrouzieri* and that both eat mealybugs.

3. *Voracity and specificity*.—*R. ventralis* is very voracious on *Er. coriaceus*, both as a larva and an adult. It feeds almost continuously throughout the day, remaining in one area until most coccids in its immediate vicinity have been eaten. It appears to have marked prey specificity, which is very important in biological control. *R. forestieri* is a more general predator and therefore less effective. Neither species has shown great searching ability, but the high reproductive rate of the coccids with which they are usually associated has perhaps reduced the need for this.

4. *Length of adult life*.—Length of adult life in both species is not known but must be relatively long, for both have been kept alive in the laboratory for between two and three months. Adults often live for a period exceeding the complete life-cycle of the species. Both Koebele (1890, 1893) and Froggatt (1902) refer to large aggregations of adult *R. ventralis* hiding under bark of eucalypts. If their essential food disappears or is severely reduced, adult coccinellids have the ability to consume alternative food and enter reproductive diapause, in which they may remain for considerable periods (Anderson & Richards, 1977). The level of reduction in size of a coccid population when the coccinellids enter diapause influences its ability to increase to pest proportions during their absence and hence the effectiveness of the coccinellid species as a control agent. This is well illustrated with "*R. ventralis*" and *S. oleae* in California.

5.—*Fecundity*.—The total egg-laying capacity per female is not known, but the New Zealand results with *R. ventralis* (Kirk & Cockayne, 1909) suggest it is adequate to keep pace with the reproductive output of its prey.

6. *Dispersal*.—The natural distribution of *R. ventralis* and *R. forestieri* extends throughout south-eastern and eastern Australia, respectively (Pope, 1981, Fig. 11), and records from DSIR, Auckland, show that *R. forestieri* has spread naturally throughout New Zealand. Nevertheless, both species have demonstrated poor powers of dispersal, which is a major limiting factor in their usefulness as biological control agents. When *R. ventralis* was released on to *Er. coriaceus* in New Zealand, it became established rapidly, but artificial re-distribution was necessary to cope with fresh outbreaks of the coccid (Clark, 1938; Bartlett, 1978). Records from DSIR indicate that the distribution of *R. ventralis* is still centred around the areas of original release of the species. In California, although *R. forestieri* extends along the western coast, it also appears commonest in areas where it was originally released, suggesting that it too does not disperse readily. In contrast with *R. ventralis* in New Zealand, attempts at re-distribution have proved of little benefit against *S. oleae* (Bartlett, 1978). Examination of the wings of numerous specimens of *R. ventralis* and *R. forestieri* has shown no evidence of brachyptery, although this has been recorded in other species belonging to the genus (Pope, 1977). The author's records show that in Australia only 15 out of 574 specimens of *R. ventralis* have been taken in light-traps, and no specimens of *R. forestieri*. There are two records of *R. forestieri* taken at light outside Australia. One is from Taupo, New Zealand, and the other from Barber's Point, Oahu, Hawaii.

Thus in New Zealand, the success of *R. ventralis* over *Er. coriaceus* is probably due to its ability to meet most of the requirements for biological control, with the important exception of satisfactory dispersal.

In conclusion, reasons for the failure or partial failure of *R. ventralis* and *R. forestieri* as biological control agents in other parts of the world may be summarised as follows:

1. Voracity on pest species confined to very limited areas and linked with inability to disperse.
2. Inability to adjust to new habitats.
3. Lack of specificity in food preferences by *R. forestieri*, and rejection of pest species by *R. ventralis*.
4. Inability to produce more generations than their prey.
5. Lack of synchronisation between predator and prey of temperature thresholds for feeding and reproduction.
6. Lack of phenological synchronisation between predator and prey.

#### Acknowledgements

I should like to express my special thanks to Dr D. J. Williams (Commonwealth Institute of Entomology) for many helpful discussions during the construction of this paper, for the loan of important reference works and for the identification of Coccidae.

I also thank Miss F. Wheelhouse for technical assistance with the field work. I am grateful to the following for the identification of other non-coleopterous material: Dr J. S. Noyes (Hymenoptera) (British Museum, Natural History (BMNH)), Mr B. H. Cogan (Diptera) (BMNH), Dr D. K. McAlpine (Diptera) (Australian Museum, Sydney), Dr R. H. Crozier (Hymenoptera) (University of New South Wales), Dr I. F. B. Common (Lepidoptera) (CSIRO, Canberra). I am also grateful to Mr R. D. Pope (BMNH) for allowing me to examine all the *Rhyzobius* loaned to him for his own study, coccinellid identifications, information concerning wax production and his general help with the manuscript. Finally, I wish to thank Dr P. Freeman (BMNH) for permission to work in his department and for generous facilities granted during the writing of this paper.

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(Received 18 April 1980)

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