

**Defensive adaptations and behaviour in *Scymnodes lividigaster*  
(Coleoptera: Coccinellidae)**

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The Australian coccinellid *Scymnodes lividigaster* (Mulsant) makes use of elaborate and distinctive defensive adaptations and behaviour to protect itself from predators. These include a well developed larval and pupal armature, cryptic colouration, production of wax by larvae and pupae, production of a protective waxy smear surrounding the pupa, aggregation of larvae before pupation, and reflex bleeding. It is the only known coccinellid species in which the pupa has an armature of parascoli and strumae, produces large quantities of wax on dorsal and ventral surfaces, and is surrounded by a protective smear.

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**Introduction**

*Scymnodes lividigaster* (Mulsant) is one of a very small number of Australian Coccinellidae which are aphidophagous. It occurs in eastern Australia, where it is a major predator on *Aphis eugeniae* van der Goot, but it also feeds on *A. gossypii* Glover and *Myzus persicae* (Sulzer), and is an important predator of the citrus aphids *Toxoptera aurantii* (Boyer de Fonscolombe) and *T. citricidus* (Kirkaldy). On one of his visits to Australia in search of insects suitable for use in biological control experiments, Koebele (1893: 28) observed *S. lividigaster* feeding on citrus aphids at Harwood, New South Wales. In 1894, when he returned to Australia, he collected and sent specimens of this species to Hawaii to help control aphids affecting the sugarcane and citrus industries (Leeper, 1976: 300; Clausen, 1978: 37). It became established there (Illingworth, 1929: 249), but although well distributed throughout the islands, remained rather uncommon (Williams, 1931: 183). In 1902, it was taken to Western Australia to help control *T. aurantii*, but did not establish (Wilson, 1960: 7). More recently, in 1938, it was introduced into Puerto Rico

from Hawaii to attack the yellow sugarcane aphid, *Sipha flava* (Forbes), but once again failed to establish. Today it extends across the Pacific from Australia to New Caledonia, New Zealand, Cook Islands, Tahiti and Hawaii.

The adult beetle is black, with a black pronotum bearing a large yellow area on either side. The head is black in the female, but the frons is yellow in the male. Both larvae and pupa are very distinctive in appearance. Koebele (1893: 28) referred to "this peculiar larva with a double row of lateral long, fleshy spines". Williams (1931: 184) figured both larva and pupa, but did not describe them. It was not until recently that the biology of *S. lividigaster* was studied. During 1977 and 1978, its strange defensive behaviour was observed, and this has proved to be as distinctive as the insect's appearance. Many coccinellids produce wax (Pope, 1979), but none use it for their own protection more effectively than this species.

At Cremorne Point, a suburb of Sydney, *S. lividigaster* forms part of a biocoenosis centred upon *Aphis eugeniae* on the cheese tree, *Glochidion ferdinandi* (Euphorbiaceae) (Plate I(a)). It is one of three coccinellids which are major predators of this aphid, the others being *Coelophora inaequalis* (Fab.) and *Harmonia conformis* (Boisd.). Other predators of *A. eugeniae* include the syrphid *Melangyna (Austrosyrphus) viridiceps* Macquart and the hemerobiid *Micromus tasmaniae* Walker. *A. eugeniae* is attended and milked by several species of ants, including *Myrmecia* sp., *Crematogaster* sp. and *Paratrechina* sp. The latter is extremely common, and at times may completely cover the aphids. *Crematogaster* is very aggressive to all the aphid's predators.

In the spring, adults of *S. lividigaster* appear on *Glochidion* trees in the first half of September when small colonies of *A. eugeniae* are becoming established, and oviposition occurs when the aphid colonies are about three weeks old. A week later, first instar larvae appear. By the middle of October, large numbers of larvae, including fourth instars, are present in the population. *C. inaequalis* and *H. conformis* larvae do not become numerous until two to three weeks after *S. lividigaster*, when many *S. lividigaster* larvae have already reached the prepupal and pupal stages. Syrphid and neuropteran larvae are also numerous about this time. By late October, competition for food becomes increasingly intense as the aphid population is on the wane, and by early November all aphids have disappeared. *S. lividigaster*, as the smallest of the three coccinellid species, may be attacked by the other two, as well as by ants, hymenopterous parasites and syrphid and neuropteran larvae. Cannibalism may also occur. Consequently there is a need to establish in large numbers before other predators appear. A similar pattern is repeated in the autumn. As a means of protection, larval, prepupal and pupal stages of *S. lividigaster* have developed elaborate defensive adaptations and behaviour, making use of armature, cryptic and aposematic patterns, protective wax smears, reflex bleeding and aggregation. They are described in this paper.

#### Armature

Both larvae and pupae of *S. lividigaster* have a very distinctive and well developed armature for protection against predators.

#### Larval armature

Numerous senti, very long, thin, horn-shaped projections from the body wall with very short branches which bear setae (Gage, 1920: 252), are present in all four larval

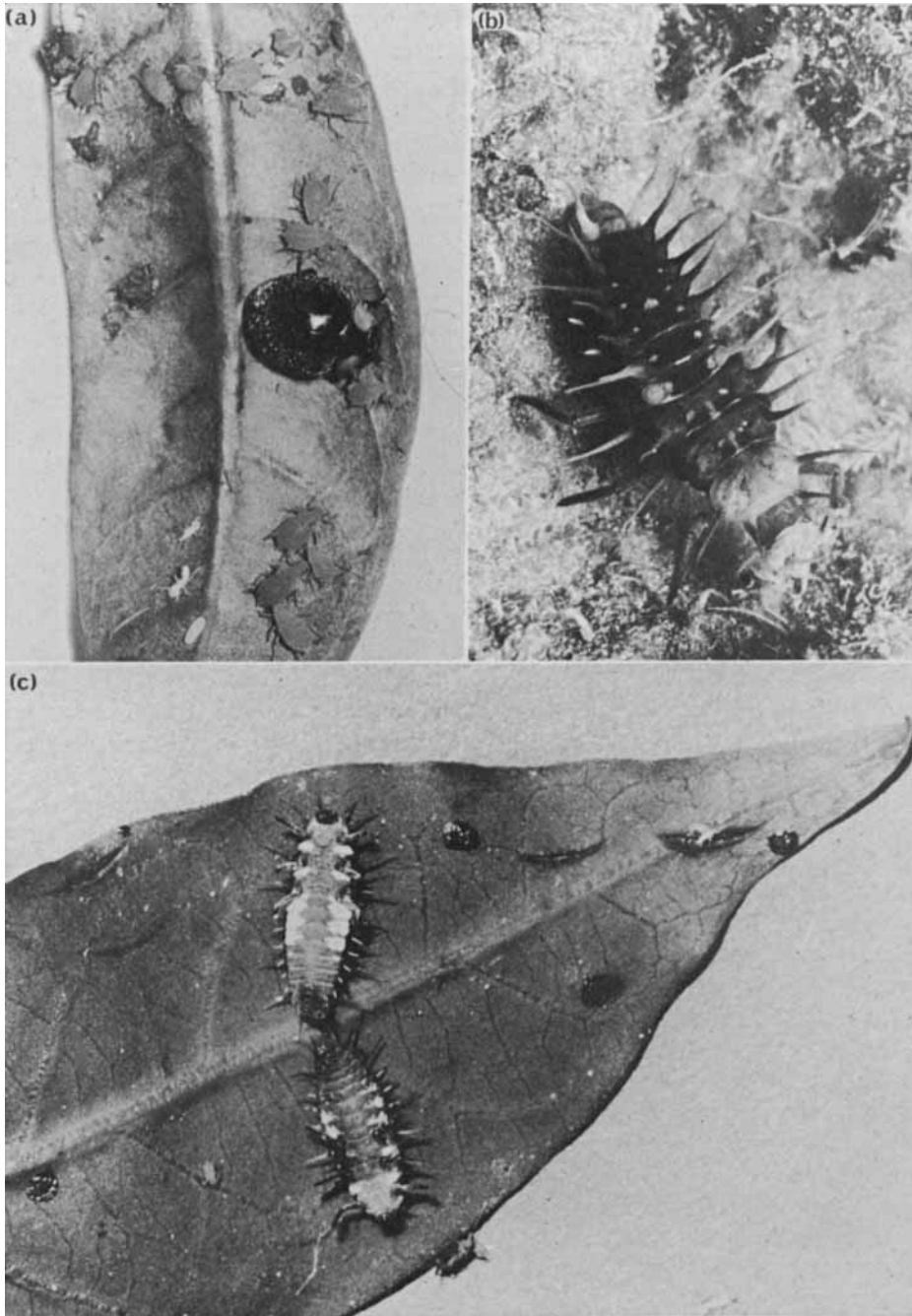


PLATE I. (a) *Scymnodes lividigaster* female with *Aphis eugeniae* on a *Glochidion ferdinandi* leaf ( $\times 5.6$  linear). (b) Third instar *Scymnodes lividigaster* larva feeding on *Aphis gossypii* in culture ( $\times 11.2$  linear). (c) Ventral view *Scymnodes lividigaster* fourth instar larva with wax, and prepupa with very little wax. Both on a *Glochidion ferdinandi* leaf ( $\times 4.9$  linear). (Photos: A. M. Richards.)

instars, and increase in length up to and including the third instar (Plate I(b)). They range from 0.08 to 0.2 as wide as long, and form two rows, one dorsal and one ventral, along each side of the body. The dorsal row occurs on the dorso-lateral region of all thoracic nota and abdominal tergites 1 to 8. The pronotum has an additional pair on the antero-lateral margin which project anteriorly. Those on abdominal tergites 1 and 6 project dorsally, those on tergite 8 project posteriorly, and all others project dorso-laterally. They vary in size and colour, and may be bent or broken during the life of a larval instar. Those on abdominal tergites 1, 2 and 8 are light brown, all others are black. The ventral row occurs on the ventro-lateral region of the meso- and metathoracic sternites and abdominal sternites 1 to 8. They all project laterally. The ventral abdominal senti are light brown and much smaller than the dorsal ones, that on sternite 1 having almost disappeared. The meso- and metathoracic ones are similar in length to the dorsal ones, and are dark and light brown respectively. In the second and fourth instars, the length of the longest senti is approximately 0.5 the width of the body, but in the third instar they are equal to the width of the body. In all three instars they are equal to approximately 0.25 its length.

Any prospective predator approaching a larva from the anterior, posterior, dorsal, dorso-lateral or lateral aspects is met by long, projecting senti armed with setae. It is necessary to penetrate this hedge to reach the larva's body, and the length of the senti alone may act as a deterrent. The dorso-lateral senti may be raised dorsally if the larva detects an unusual vibration from above. Touching the senti usually elicits an immediate response. The larva may withdraw rapidly, or give an aggressive display. It may anchor itself to the substrate by its tarsi, while the abdomen is rapidly raised and lowered for about 30 seconds, or it may attach itself to the substrate by its anal sucker allowing the whole larva to rear up and down.

#### *Pupal armature*

The projections from the body wall are similar to those in larvae, so as there is no pupal terminology, the larval terminology of Gage (1920) is followed. Dorso-lateral parascoli, not more than 0.5 to 0.33 wider than long, replace the larval senti on abdominal tergites 1 to 6. They are shorter and stouter than senti, and bear chalazae, stout setae each mounted on a base. The two largest are on tergites 1 and 2, while those on tergite 6 are much smaller than the others. The parascoli on tergites 1 and 2 are thickly coated with wax, while those on tergites 5 and 6 are thinly coated. In all cases the chalazae protrude through the wax. Parascoli on tergites 2 and 4 are naked. Postero-medially the mesothorax bears a struma, a much shortened parascolus with chalazae. In addition, each developing elytron bears two strumae, one adjacent to its junction with the mesonotum, and the other adjacent to its junction with the metanotum. The strumae bear very little or no wax.

Both parascoli and strumae form an important part of the elaborate defence mechanism of the *S. lividigaster* pupa. Any predator which has successfully penetrated the protective wax smear (see p. 163) must encounter them when avoiding the thick coating of wax which covers most of the pupa.

#### **Colour pattern**

The different colour patterns in the various instars of *S. lividigaster* play an important role in protecting it from predation. Larval colouration varies from instar to instar, and

each is distinctive. The first instar is greeny-fawn, with two dark grey markings on pro-, meso- and metanota. The second instar is dark grey, with head and pygidium light brown. In the third instar, the first eight abdominal tergites are black; the meso- and metanota are brownish-grey with antero-median areas black; the head, pygidium, abdominal tergite 8 and anterior portion of the pronotum are light brown, with the posterior part of the pronotum and legs brownish-grey. The fourth instar is basically brown; the meso- and metanota have lateral dark brown areas; the head, pygidium, abdominal tergite 8 and anterior half of the pronotum are light brown, and the legs grey. Sternites in all instars are light brown, as is the haemolymph. Initially the pupa is an orange-red; the mesonotum and developing elytra are a deeper orange which gradually darken through brown to brownish-black, with two small black spots on the mesonotum; three large spots, one median and two dorso-lateral, on each of abdominal tergites 3, 4, 5 and 6 gradually darken from brown to dark brown to black.

The basic colour of *S. lividigaster* is brown, and the variations in larval and pupal instars are influenced by how much of the body fluids are visible through the cuticle, the degree of tanning of the exocuticle, and the amount of melanic pigment produced. Overlying this is the secretion of varying quantities of white wax over selected areas of the cuticle depending on the instar. The whiteness of the wax is accentuated by the dark colour of the cuticle.

No wax occurs in first and second instar larvae. In the third instar, it is present on both dorsal and ventral surfaces. Very small amounts are secreted from a groove across the central area of the mesonotum, and from intersegmental membranes between the meso- and metanota, and the metanotum and abdominal tergite 1. Dorso-laterally on either side a row of small white spots of equal size are formed, a pair on the metanotum and on each of abdominal tergites 1 to 5. Much smaller spots are formed on tergites 6 and 7. The antero-median portion of tergite 4 produces a half circle of wax. On the ventral surface, large quantities of wax are produced ventro-laterally near the base of the legs and the two thoracic and first four abdominal spiracles.

In the fourth instar the pattern is similar, although more strongly developed. Wax on the antero-median area of abdominal tergite 1 becomes confluent with the two dorso-lateral spots. Similar much smaller areas of wax may appear antero-medianly on tergites 5, 6 and 7. Ventrally much larger quantities of wax are produced near the base of the legs and the first six spiracles, and extend dorso-laterally along the intersegmental membranes to the wax spots (Plate I(c)). A thin coating of wax completely covers the legs. At the prepupal stage, wax production increases on the intersegmental membranes between the pro-, meso- and metanota and abdominal tergite 1. It extends onto tergites 1 to 7, and the spots increase in size. Wax is also present on the legs (Plate II(a)). A heavy coating of wax develops on both dorsal and ventral surfaces of the pupa. It forms first on the head, pro-, meso- and metanota, and on abdominal tergites 1 and 2, then develops over the elytra and leg buds and over parts of the other abdominal tergites (Plate II(b)).

The variations in colour pattern and quantities and distribution of wax are concerned with defence.

#### *Cryptic colouration*

All four instars of *S. lividigaster* are cryptically coloured and merge into their respective backgrounds. The colouration of first instar larvae is similar to that of *Aphis eugeniae*

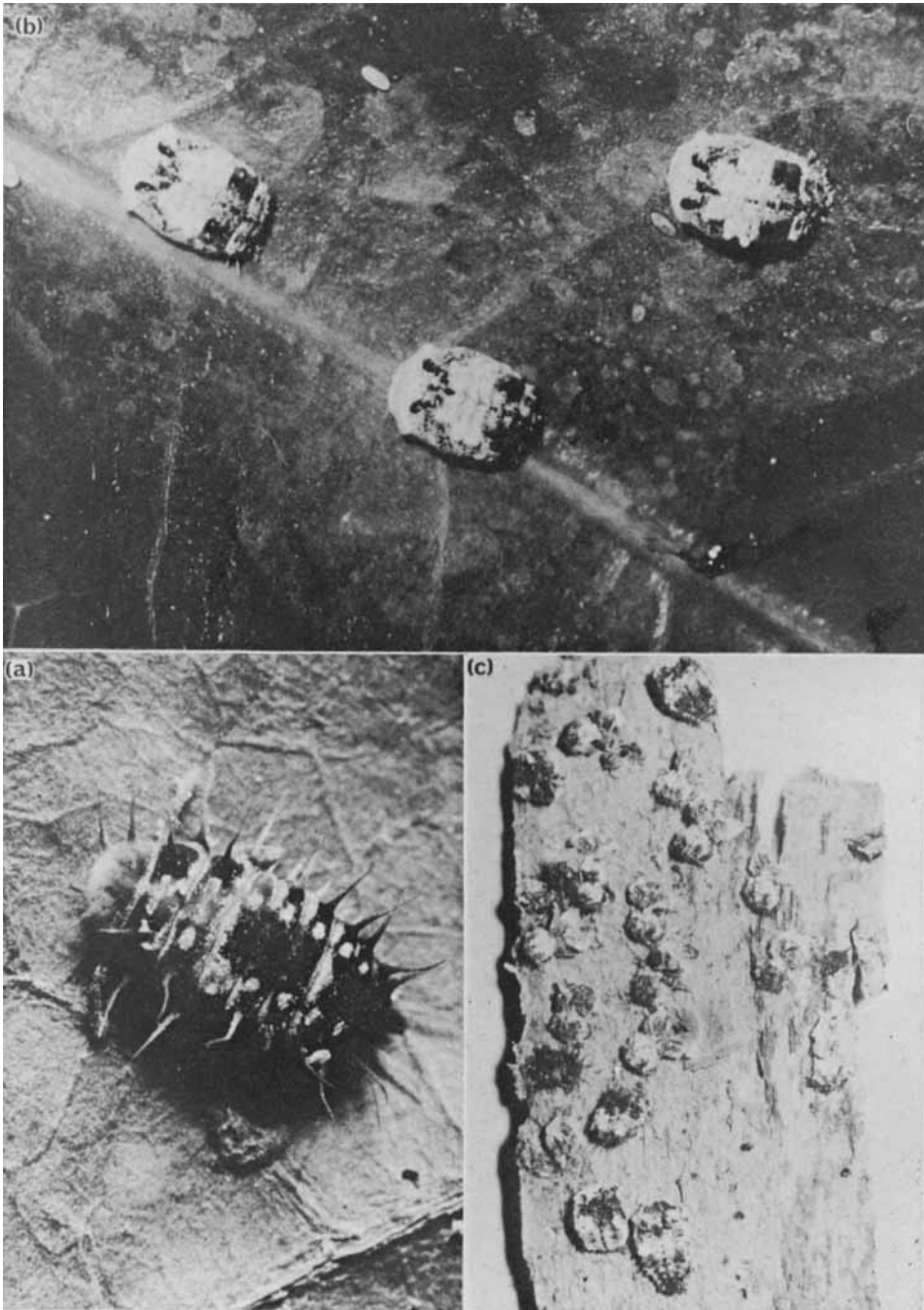


PLATE II. (a) Dorsal view *Scymnodes lividigaster* prepupa on a dead *Glochidion ferdinandi* leaf. Smear not very distinct ( $\times 9.1$  linear.) (b) *Scymnodes lividigaster* pupae with smears on a *Glochidion ferdinandi* leaf ( $\times 6.3$  linear). (c) *Scymnodes lividigaster* pupae on *Glochidion ferdinandi* bark, Cremorne Point, Sydney ( $\times 3.2$  linear.) (Photos: A. M. Richards.)

and the *Glochidion* leaves on which they both live, making the larvae very difficult to detect. Similarly the mottled brown patterns of older larvae blend into the variegated browns of the *Glochidion* bark and dead leaves over which they crawl in search of food. Even on green leaves they are not obvious, resembling small brown marks. The small amount of wax on the dorsal surface of third and fourth instar larvae increases the deception.

#### *Aposematic behaviour*

The large quantities of white wax produced by larvae, prepupae and pupae are used very effectively by *S. lividigaster* when defending a territory. While larvae often share their territory and its food with other members of their own species, they become irritated by intruders. Third and fourth instar larvae and prepupa may rear up and down several times in quick succession exposing large areas of thick wax on the ventral surface. They then rest before repeating the sequence. Pupae are also easily disturbed, the display being similar to that of the larva. The startle effect produced by the rapid movement and the flashes of white is usually an effective deterrent to any potential predator. Although feeding on aphids on the same tree at the same time, it is very rare to find larvae, prepupae or pupae of *Coelophora inaequalis* on the same leaves as *S. lividigaster*. Smaller instars of *Harmonia conformis* may also be intimidated by the display, but fourth instar larvae often prey on *S. lividigaster* larvae and pupae, even when aphids are plentiful. Neuropteran and syrphid larvae may also attack and eat smaller instars, but do not normally attack fourth instar larvae, prepupae or pupae.

#### **White smear**

Just before prepupation, fourth instar larvae apply a coating of wax to the substrate as a thin white smear of rather uneven texture. It may be kidney-shaped or oval, but is most often almost circular, its diameter being approximately three times the length of the prepupa (Plate II(b)). During the latter part of the fourth instar there is a marked increase in wax production from the papillae on the ventral surface. To produce the smear, the larva rears itself up and rubs its legs against these areas of thick wax until they are thickly coated along their whole length. Then it stretches itself to its fullest extent, spreads out its legs and rubs the wax onto the leaf. The process is continuously repeated as the larva rotates around its point of attachment. Wax may be spread several times over the same area, accounting for the uneven texture of many smears. The smear may be laid down quite rapidly. The prepupa usually sits in the centre of the smear, having cemented itself to the substrate by its anal organ. If the smear is kidney-shaped, the prepupa is attached near the base of the indentation leaving its posterior region unprotected. Prepupae which are removed from a smear appear unable to make a second one, as wax production is greatly reduced in the prepupal stage.

*S. lividigaster* may apply its smear to various substrates. It is very obvious on green leaves where the prepupa or pupa is most exposed, and may be applied to either side of a leaf. It has been observed on leaves of *Glochidion ferdinandi*, various varieties of *Citrus* including *Eromocitrus glauca*, *Eucalyptus* sp., *Rumex brownii*, *Plantago lanceolata* and *Helianthus* sp. Many larvae pupate on grass, but here the blades are too narrow for smears to be produced. On red or brown *Glochidion* leaves or dried *Eucalyptus* leaves,

the smear is not as obvious. On bark it is often very difficult to recognize as it blends into the background. Photographs taken of pupae and smears using a light source rich in ultraviolet and with a narrow-band ultraviolet filter between the subject and the camera (Pope & Hinton, 1977), clearly demonstrate the wax to be highly ultraviolet reflective. The whiteness is an "insect white"; that is it scatter-reflects light in the ultraviolet region as well as throughout the entire visible spectrum. Certain smears, faded and indistinct to the human eye, stand out clearly in an ultraviolet photograph, demonstrating they are still visible to insects.

The smear is no deterrent to other *S. lividigaster* larvae, and may even be an attractant. It does not effect aphids, and does not always stop voracious fourth instar larvae of *Harmonia conformis*; but syrphid larvae, neuropteran larvae and ants have not been observed to cross it.

### Aggregation

When selecting an area to pupate, *S. lividigaster* larvae become attracted to one another. Groups of three often occur on a single leaf, and up to 10 have been recorded. They may be arranged in a straight row or in a triangle, or they may be randomly scattered over a leaf (Plate II(b)). On tree trunks they seek out indentations and form small groups, but the largest aggregations are formed under strips of loose bark where it is not uncommon to find 23 pupae in an area of 4.5 cm<sup>2</sup> (Plate II(c)). The largest group observed consisted of 57 pupae on 12.5 cm<sup>2</sup> of bark. Although very close together, it is unusual for pupae to touch. However, through larval aggregation white smears often overlap resulting in increased density of wax and increased area over which it is spread. As both pupal wax and smears are ultraviolet reflectant, they may still be visible to an intruder in reduced light intensity.

### Reflex bleeding

On being lightly touched, third and fourth instar larvae may produce large droplets of light brown fluid from their intersegmental membranes. These droplets rapidly coagulate, and often adhere to the cuticle. No fluid has been observed associated with the femoro-tibial articulations of the adult beetle. Irritation of the larva may cause it to emit a light brown fluid from its mouth.

### Discussion

Most fourth instar coccinellid larvae have a well developed and distinctive body armature for use in defence. In some larvae it is simplified or reduced in size, and replaced by a covering of wax, or by repugnatorial glands along the sides of the abdomen. The degree of development of the armature and the amount of wax secreted are very variable throughout the family. Some tribes may have only one of these three types of defensive adaptations, suggesting they may have developed in the course of evolution of the family (Hodek, 1973: 38). In *S. lividigaster*, larvae have a very well developed armature and also produce wax, but although they exhibit reflex bleeding, they lack repugnatorial glands.

According to Hodek (1973: 38), a distinctive type of larval armature is characteristic of each coccinellid tribe. However, Gage (1920: 252) described senti from *Chilocorus bivulnerus* Mulsant (Chilocorini), and also from *Anatis 15-punctata* Oliv. (Coccinellini).



Recently they have been recorded from *S. lividigaster* (Coccidulini) (Pope, 1979: 185). This suggests that *senti* at least may be more widely distributed within the Coccinellidae than was supposed by Hodek.

Production of wax by many predaceous coccinellid larvae often leads to their developing a resemblance to their prey, scale insects and mealybugs, many of which have thick coverings of wax. *S. lividigaster* is an exception to this as it feeds on green aphids and is the only member of its biocoenosis which produces wax. Very little wax is visible on the dorsal surface of the larva, but it becomes more obvious in the prepupal stage. However, *S. lividigaster* appears to differ from other known coccinellid larvae in producing large quantities of white wax from its ventral surface. Wax producing structures from both surfaces resemble the cylinders and papillae present in several coccidiphagous species of *Hyperaspis* Dejean (Pope, 1979: 185), and suggest relationships between the two genera.

Ants may attack and kill aphid and coccid predators, including both adult and larval coccinellids. Smith & Armitage (1931: 55) refer to ants killing adult *Cryptolaemus montrouzieri* Mulsant, and Pope (1979: 191) has suggested that production of wax by some coccinellid larvae is to protect them from molestation by ants attending coccids. This may not always be successful, as Cochereau (1969: 76,80) records *Pheidole javana* Mayr., *P. megacephala* F. and *Paratrechina longicornis* Lat. feeding on the wax producing larvae of *Cryptognatha nodiceps* Mshl., *Azya trinitatis* Mshl. and *Scymnus aeneipennis* Sic. Although wax on its own may not always give adequate protection against ants, the combination of wax and white smear in *S. lividigaster* appears to be an effective deterrent against *Crematogaster* sp. and *Paratrechina* sp. The smear's effectiveness may be due to its whiteness, its texture may be unpleasant to touch, or it may contain a chemical substance which is an attractant to other members of the same species, while acting as a repellent to intruders. So far as is known, this type of wax smear is unique amongst the Coccinellidae. The ultraviolet reflectiveness of coccinellid wax already demonstrated by Pope (1979: 191) is of major importance in its defensive behaviour.

Coccinellids are usually solitary insects, but at certain times in their life they may become attracted to one another and aggregate. The large aggregations of adult beetles during winter months are well known in Europe and North America (Hodek, 1973: 166), and have also been recorded from Australia (Anderson & Richards, 1977: 14). Certain coccinellid larvae have a tendency to aggregate shortly before pupation. In Australia, they may form very conspicuous displays as in *Cryptolaemus montrouzieri* where the brilliant white wax from large clusters of prepupae and pupae is clearly visible from a distance against the dark trunk of the Hoop Pine, *Araucaria cunninghamii*; or in *Coelophora inaequalis* where up to nine brightly coloured larvae may aggregate and pupate on a single green leaf. The overlapping white smears of aggregating *S. lividigaster* pupae on green leaves is yet another example. On exposed trunks or on leaves, the bright colours of the coccinellids may act as visual releasers attracting other larvae to a particular area.

Larvae may also aggregate in areas that are sheltered from harmful effects of the environment, such as under loose bark, irrespective of whether they are cryptically coloured like *S. lividigaster*, or aposematic as in *C. inaequalis* and *Harmonia conformis*. Here it is likely an aggregation pheromone is involved. The pheromone may be in the form of a terrestrial trail laid down on bark by larvae moving towards an aggregation site, but is more likely to be secreted by a larva once it has found a suitable site (Shorey, 1973: 356).

Gradually, as more larvae are attracted, large aggregations are built up as in the case of *S. lividigaster*. Very little is known about coccinellid larval pheromones, although a trail laying pheromone linked with gregarious behaviour has been demonstrated by Fomenko (1975: 1004) in larvae of *Chilocorus bipustulatus* L.

Until recently, very little information has been available about coccinellid pupae. Taylor (1935) illustrated pupae belonging to the Cryptognathini, Azyiini and Scymnini. Binaghi (1941) and Savoiskaya (1962) described pupae belonging to the Chilacorini. Hodek (1973) illustrated a few of the commoner European species belonging to the Coccinellini, Hippodamiini, Chilacorini and Psylloborini. The widest coverage so far has been by Phuoc & Stehr (1974). They described pupae belonging to 32 genera and 49 species from 11 tribes, mostly from North America. These included Serangiini, Sticholotidini and Scymnillini, representatives of which have not been seen by the author. Coccinellid pupae permanently anchored to the substrate are very vulnerable to predation or cannibalism. Study of pupae in 71 species, belonging to 44 genera in 16 of the 28 known tribes in five of the six subfamilies, has shown that a number of protective devices have developed amongst the different tribes. Bright colours are common in many pupae, particularly those belonging to the Coccinellini and Psylloborini, and may act aposematically or cryptically. More drably coloured pupae have developed other means of protection. The waxy covering left behind by many larvae at pupation may act as a shelter for pupae in the Coccidulini, Telsimiini, Hyperaspini, Ortaliini, Scymnini and Azyiini, while many of the Chilacorini, Hyperaspini and Noviini remain inside the partly split larval exuvium. Some pupae in the Coccidulini and Epilachnini are covered by an armature of long, stout setae, and others in the Coccidulini, Scymnini, Stethorini and Cryptognathini are thickly covered with short glandular setae which secrete a colourless, possibly repellent fluid. Most pupae have a single protective device, but a number have combined long, stout setae or short glandular setae with shelter under larval wax. The Cryptognathini have combined short glandular setae with repugnatorial glands.

Although a dorsal armature of long, stout setae is present in some coccinellid pupae, nothing has been found comparable to the parascoli and strumae of *S. lividigaster*. Further, *S. lividigaster* is the only known coccinellid with a pupa which secretes wax. The mechanism for wax production is strongly developed, and large quantities are produced on both dorsal and ventral surfaces. Thirdly, the protective white waxy smear which surrounds each pupa appears to be unique. Each of these characteristics on its own is highly distinctive, but together they place *S. lividigaster* in a group apart on pupal characters alone.

Currently *S. lividigaster* is placed in the Coccidulini, but Pope (1979: 185) considers that as the eyes and antennae of the adult beetle are closer to the Scymnini, and its methods of larval wax production are related to the Hyperaspini, it should probably be placed in a new tribe within the Scymninae. The elaborate protective devices of both larva and pupa support this.

*S. lividigaster* is a highly specialized and distinctive species which has characteristics found in both aphidophagous and coccidiphagous coccinellids. Although a successful green aphid eater, it has the coccid eater's drab colouration and ability to produce wax. As production of wax often leads to coccinellid larvae resembling the scale insects and mealybugs on which they feed, secretion of large quantities of wax from the dorsal surface of a green aphid eater would be of no advantage, and may explain why very little is

produced. However, wax is an important defence mechanism against predators, and this may have led to the development of wax producing papillae on the ventral surface of the thorax and abdomen where they can be kept hidden, but are ready for use whenever required. By making use of wax to startle intruders and to produce a large white smear, *S. lividigaster* has devised very effective methods, totally unrelated to those in coccidiphagous species, for protecting itself against predators in the aphid biocoenosis. *S. lividigaster* also has a well developed defensive armature more characteristic of aphid eaters. Its long, thin senti resemble those in certain species of *Chilocorus* Leach, a group of coccinellids which feed on both aphids and coccids, but are non wax producing (Pope, 1979: 190).

As a result of its elaborate defensive adaptations and behaviour, *S. lividigaster* is a very successful species. Its major limiting factor is related to the seasonal fluctuations in aphid populations.

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