

size and depressed body form. The separation of *R. major* and *R. boucardi* is more difficult, but the orange elytral pubescence of *R. major* is a useful character contrasting strongly with the pale golden pubescence of *R. boucardi*. All *Rodatus* males have a pair of large foveae on the fifth abdominal sternite. The genitalia of all three species are distinct.

On one of his visits to Australia in search of insects suitable for biological control experiments, Koebele (1893) found two specimens of *R. boucardi* under the bark of a eucalypt near Sydney. As cocoons of the coccidophagous moth *Thalcoephares cocciphaga* Meyr. were present on the tree, he assumed it to be infested with a gum tree scale, *Eriococcus* sp., and that *R. boucardi* was also a scale feeder. This single observation appears to be the only biological information published so far concerning the genus *Rodatus*.

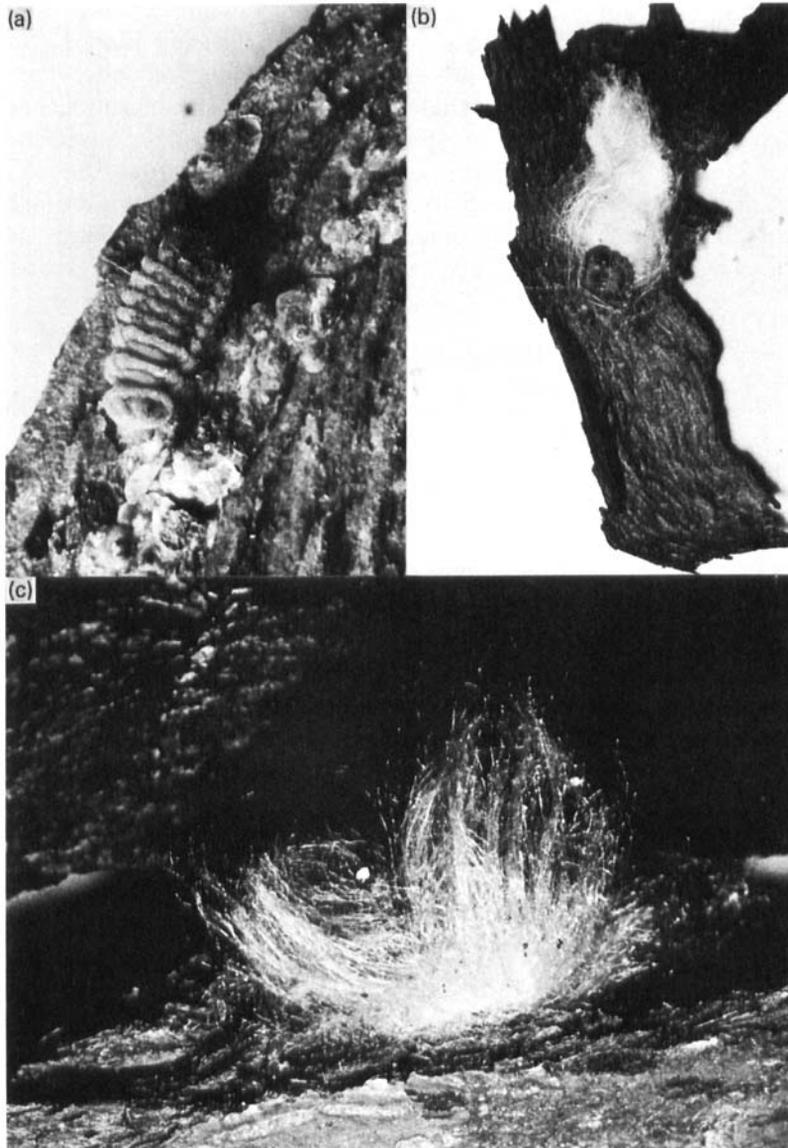
During spring and early summer, beetles of all three species occur singly under bark. *Rodatus boucardi* has been taken from the brush box, *Lophostemon conferta* at Rose Bay, from *Angophora costata* at Cowan, and both it and *R. australis* from *A. costata* at Hornsby Heights. *Rodatus major* has been taken from *L. conferta* at Hornsby. *Rodatus boucardi* and *R. major* have always been associated with the hemipteran *Monophlebulus pilosior* (Maskell) (Margarodidae), while *R. australis* has been observed feeding on eggs of the mealybug *Pseudococcus longispinus* (Targ.), and has also been associated with a margarodid genus near *Nodulicoccus* Morrison. The larvae of *R. boucardi* and *R. australis* are unknown to the author, but larvae of *R. major* have been observed feeding on *M. pilosior* eggs, and have been successfully reared to adults on a diet of these eggs, demonstrating that *M. pilosior* is an essential food of *R. major*.

Apart from the cottony cushion scale, *Icerya purchasi* Maskell, almost nothing is known about Australian monophlebines Margarodidae. *Monophlebulus* Cockerell is widely distributed throughout Australia on native Myrtaceae (Froggatt, 1906), but, as its five species are not regarded as pests, their biology had not been studied until very recently (Richards, 1981). The biology and specialized relationship between *R. major* and *M. pilosior* are described in this paper.

Biology of *Monophlebulus pilosior*

The mottled brick-red and purple aposematic coloration of both adults and immatures of *M. pilosior* makes them very obvious when crawling over the trunk or branches of trees. Females retain their facilities for movement until formation of the ovisac, when they crawl under loose bark and remain there for the rest of their lives. The mature female is flattened, broadly oval, and very variable in size. The body may be sparsely dusted with wax. The ovisac, a dense mat of white wax, is secreted from the abdominal sternites. Production of wax is slow and the sac may take up to 14 or more days to complete, but before this, eggs are being produced. The sac varies in length, but averages twice the length of the female (Plate I(b)), and is not fluted. Sacs may be stretched by the weight of eggs and crawlers, and pressure from continuous egg production often leads to loss of eggs from the lower part of the sac. The eggs are reddish, oval and 0.8 mm in length by 0.3 mm in width, the total number produced by a female over a two to three months period being close to one thousand. Females kept in the laboratory without food for up to two months still produced eggs continuously, demonstrating their remarkable ability to tolerate starvation for long periods of time. Throughout the year, egg-producing females are available for predators seeking food and protection inside the ovisac. Mortality rates are unknown. In the Sydney area there are three or four generations a year.

Two endoparasites, a hymenopteran, *Aphycopsis* sp. (Encyrtidae), and a dipteran, *Cryptochetum monophlebi* (Skuse) (Cryptochetidae), have been reared from *M. pilosior*. Both emerged



[Photos: A. M. Richards]

PLATE I. (a) Third instar larva *Rodatus major* associated with *Hemiberlesia lataniae* on *Lophostemon conferta* bark ($\times 8.3$ linear). (b) *Monophlebus pilosior* adult female with ovisac on *L. conferta* bark ($\times 2.1$ linear). (c) Prepupa *R. major* with its shroud on *L. conferta* bark ($\times 4.1$ linear).

from the adult female, but it is not known which stage of the margarodid's life cycle is initially attacked. A single *Aphycopsis* sp. emerges from its host, while up to 20 flies of *C. monophebi* may develop inside a female *M. pilosior*, their emergence holes forming a series of horizontal parallel lines across the host's body.

Five egg predators are associated with *M. pilosior*. The hymenopteran *Ophelosia* sp. (Pteromalidae) is the commonest, large numbers of larvae, pupae and adults having been taken from ovisacs. An occasional larva, pupa or adult of *Telsimia subviridis* (Blackburn), *Rhyzobius satelles* Blackburn and *Diomus* sp. (Coccinellidae) may occur either inside or outside ovisacs, and may even share one. All three species are polyphagous and other food sources are known. Larvae of a fourth much larger coccinellid, *R. major*, never share an ovisac with other species.

Potential predators of *M. pilosior* include the coccinellids *R. boucardi* and *Harmonia conformis* (Boisd.), an occasional neuropteran larva, numerous species of spiders and birds. *Monophlebulus pilosior* is attended by the ant *Iridomyrmex* sp. which is aggressive to the margarodid's predators.

Biology of *Rodatus major*

During November and December 1979, second and third instar larvae of *R. major* were discovered on *L. conferta* feeding on *M. pilosior* eggs, but none survived beyond the fourth instar. From July to September, in both 1980 and 1981, a small breeding population of *R. major* was associated with *M. pilosior* on the same tree as in 1979, but it failed to reappear in late spring and was also absent throughout 1982. There was no evidence of an autumn generation. Thus in Sydney, *R. major* is a spring species emerging from diapause very early in the season. Development is slow, with larvae hatching in early to mid July and not becoming adult until mid September or later. Despite extensive searching throughout the Sydney area over a three-year period, no other breeding sites of *R. major* have been discovered, although *M. pilosior* is widely distributed on *L. conferta*.

Colour pattern and wax production

Larval coloration in *R. major* is similar in all instars. The larva appears reddish due to body fluids visible through the pigmentless cuticle. The head is fawn. The pupa is a mixture of red, cream and dark brown due to body fat and haemolymph visible through the cuticle, except in the thoracic region where they are partly obscured by melanic pigment. The pronotum and mesonotum are dark brown, the metanotum and abdominal tergites are a mixture of red and cream, while the wing buds, abdominal pleurites, sternites and intersegmental membranes are cream. The teneral imago is initially cream, gradually changing over a 24-hour period to yellow, light orange, light red and finally brick-red. About 72 hours after emergence, the elytra commence to darken, and over a further 24 hours gradually change to mid to dark brown. The rest of the beetle remains brick-red.

In all larval instars, the thoracic nota and abdominal tergites are completely covered with a thick white wax encrustation, while a much thinner layer over the sternites and legs only partly obscures the reddish body colour. The intersegmental membranes between the tergites are free from wax. Wax production is thickest in the fourth instar, when the head is also covered. Wax is secreted from modified socketed setae thickly scattered over the pronotum. Six circles present across each of the abdominal tergites, as well as across the meso- and metanota, become raised as tubercles, but they are not very pronounced, and the two dorsal tubercles are very shallow. The socketed setae around and upon these tubercles produce wax, and wax is also produced from other setae scattered over the whole body surface. Throughout the prepupal stage, very large quantities of wax are produced over the dorsal surface of the body. The pupa is thickly clothed with short setae, but lacks both wax-producing and glandular setae.

Cryptic coloration

All four larval instars of *R. major* are cryptically coloured and merge into their respective backgrounds. Inside the ovisac, the wax-covered larva is almost impossible to detect, and when it moves the flashes of reddish colour from its intersegmental membranes resemble *M. pilosior* eggs seen through the ovisac. During the 24 hours required for secretion of its new wax covering, the newly moulted larva merges into the reddish background of *L. conferta* timber. The cream and reddish coloured pupa glimpsed through the thick covering of prepupal wax threads also resembles *M. pilosior* eggs seen through the ovisac.

The shroud

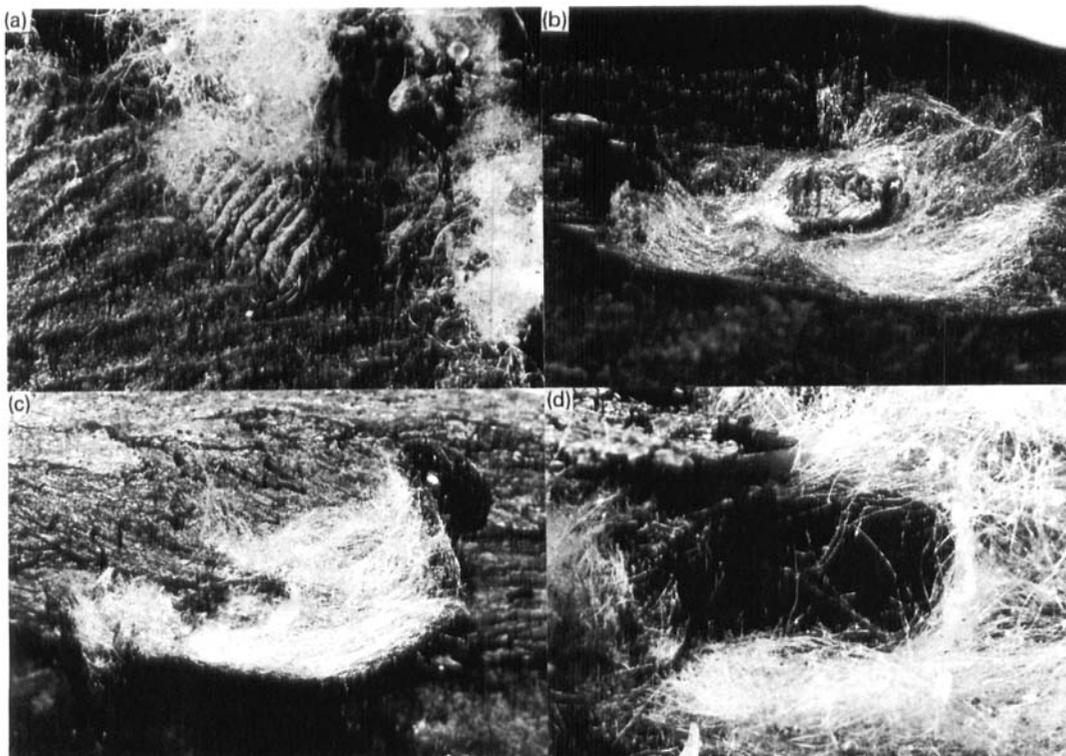
Just before prepupation, the fourth instar larva leaves its ovisac, and either inserts itself into a crack in the bark, or conceals itself under a covering of loose bark, before cementing itself to the substratum by its anal organ. The encrusting type of wax produced by the larva is now replaced by wax of a different texture, similar in appearance to that used by margarodids to construct their ovisacs. Large quantities are produced over the dorsal surface of the body. The threads secreted project stiffly around the prepupa, and over a seven-day period gradually increase in length to form a thick protective covering completely concealing the prepupa. This covering differs from a cocoon—'a covering composed partly or wholly of silk or other viscid fluid, spun or constructed by many larvae as a protection to the pupa' (Torre-Bueno, 1962), and more closely resembles a shroud which clothes, covers, or conceals an object so as to protect or screen it from injury or attack (Onions, 1973). It is oval in shape, with a height approximately half its length which is at least four times the length of the prepupa (Plate I(c)). It resembles a margarodid ovisac and is an effective deterrent against potential predators.

At the pupal ecdysis, many of the wax threads attached to the prepupal tergites are broken, creating a small air space around the pupa (Plate II(b) and (d)). After emergence, the teneral adult can move about in a limited way inside this space without becoming covered with wax or disturbing the camouflage, and it may remain inside the shroud for two or three days while its cuticle hardens and its colour changes to that of the mature beetle (Plate II(c)).

Behaviour

Both larvae and adults of *R. major* are very voracious and appear to be monophagous, feeding only on the eggs of *M. pilosior*. Although they may crawl over large infestations of the diaspid scale *Hemiberlesia lataniae* (Signoret) (Plate I(a)) on *L. conferta* bark, they have not been observed to eat it. Several early instar larvae of *R. major* may share an *M. pilosior* ovisac without cannibalism occurring, but a single fourth instar larva (10 by 4 mm) may fill an ovisac completely. It feeds almost continuously throughout the day, lying with its mouth close to the margarodid's genital opening so that it can eat the eggs as they are produced. One fourth instar larva can consume the entire egg production of at least two *M. pilosior* females, leaving the ovisac only to search for more food or to pupate.

Apart from the heavily chitinized pronotum, there is no special larval armature. Instead, the wax produced by *R. major* larvae is used for defence. If irritated by an intruder when outside a margarodid ovisac, a third or fourth instar larva may arch its body into a half circle, prominently displaying its white tergites, and may hold this posture for several minutes. During wax production following ecdysis, each larva remains beside its exuvium, which has been left fully



[Photos: A. M. Richards]

PLATE II. (a) Third instar larva *Rodatus major* beside *Monophlebulus pilosior* ovisac ($\times 9.1$ linear). (b) Shroud partly displaced to expose pupa *R. major* and air space ($\times 4.1$ linear). (c) Air space and pupal exuvium of *R. major* inside remains of shroud, with newly emerged adult beetle beside it ($\times 5.2$ linear). (d) Close up of air space and pupal exuvium inside prepupal shroud of *R. major* ($\times 12.3$ linear).

extended so that its alternate transparent and thick wax bands are very prominent. These bands may produce a startle effect and so act as a deterrent to potential predators such as the ant *Iridomyrmex* sp., neuropteran larvae and spiders. No parasites have been recorded from *R. major*.

When irritated, *R. major* adults may feign death, and reflex bleeding as a means of defence may also occur, especially in teneral. Large droplets of reddish fluid are produced from the femoro-tibial articular membranes of the second and third pair of legs, but especially from the second pair, and they rapidly coagulate. Their colour resembles that of *M. pilosior* eggs. No reflex bleeding has been observed in larvae.

Discussion

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 and often large ovisacs. Wax is also used by coccinellids as a deterrent against predators, and it is produced in greatest quantities during the immobile and vulnerable prepupal stage (Richards, 1981). *Rodatus major*, by developing a very specialized relationship with its margarodid prey, fits

into both categories. The production of its shroud appears to be unique amongst coccinellids, both in the very large quantities of wax secreted, and in its type of construction. It has the same dimensions in proportion to size of the prepupa as does the white smear produced by *Scymnodes lividigaster* (Mulsant) (Richards, 1980). This may be significant, as both smear and shroud have proved to be very effective deterrents against ants. The prepupal wax's effectiveness may be due to its whiteness, its ultraviolet reflectiveness (Pope, 1979; Richards, 1981), its strength, or its texture, but probably its density is most important.

Taxonomically, *Rodatus* is related to *Rhyzobius*, so it is to be expected that wax production might be similar in both genera. Unlike *Rhyzobius* (Pope, 1979), no scanning electron microscope studies have been made on the cuticle of *Rodatus*. However, comparison of light microscope studies on *R. major* with similar studies on *Rhyzobius ventralis* (Er.) (Pope, 1979; Richards, 1981) and *Rhyzobius forestieri* (Mulsant) (Richards, 1981) has revealed certain differences in the morphology of the setiferous tubercles. Wax production is on a much larger scale in *Rodatus* and, unlike *Rhyzobius*, where the same type of tightly curled wax threads are produced in varying quantities during larval and prepupal instars, two different types of wax are secreted. The very long, straight threads of the shroud would be unsuitable for a larva living inside the ovisac of its prey, while the thick encrusting layers of powdery wax covering the larval tergites would not offer adequate protection outside the ovisac. The differences between the two genera have probably developed because of differences in prey selection and feeding behaviour. Unfortunately, very little is known about the biology and wax production in other Coccidulini for further comparison. *Scymnodes lividigaster* is currently placed in the Coccidulini, but Pope (1979) considers it should be removed from that tribe, and the elaborate protective devices of both larva and pupa support this (Richards, 1980).

All stages of *R. major* have been found under bark, and both larvae and adults exhibit negative phototaxis. Adults of *R. boucardi* and *R. australis* behave similarly. *Rodatus boucardi* hibernates in large aggregations under loose bark of eucalypts. These have been found near Canberra (B. P. Moore, pers. comm.) and on Mt. Wilson in the Blue Mountains of New South Wales. Specimens from a Mt. Wilson aggregation are in the British Museum (Natural History) in London. Nothing is known about this behaviour in other species of *Rodatus*.

Five species of *Monophlebulus* are known from Australia. Three were described by Maskell (1889), with Froggatt (1906) supplying additional information; two further species were described by Morrison & Morrison (1923). With the exception of *Icerya purchasi*, Maskell (1889) considered the Australian monophlebinae Margarodidae to be harmless. He reported that individual female *Monophlebulus* were parasitized by large numbers of small dipterous flies, later described by Skuse (1889) as *Lestophonus monophlebi*, and closely related to *L. iceryae* Williston which parasitizes *I. purchasi*. Both species are now placed in *Cryptochetum* Rondani (Colless & McAlpine, 1970). Between 1888-1892, Koebele collected and sent back to the United States large numbers of *Monophlebulus* spp. and *I. purchasi* in order to introduce their natural enemies. The two species of *Cryptochetum* which emerged from these margarodids were successful in controlling *I. purchasi* in California, but *C. monophlebi* failed to survive (Thorpe, 1930). Introduction of *C. monophlebi* into Mauritius also led to successful control of *I. seychellarum* (Westwood) (Bartlett, 1978). Undoubtedly, both species of *Cryptochetum* play a major rôle in controlling margarodids throughout Australia. The stage of *M. pilosior* attacked by *C. monophlebi* is not known, but *C. iceryae* prefers second instar *I. purchasi* females, although larger females, or even males, may be attacked (Bartlett, 1978). Up to 17 individuals of *C. iceryae* may occupy a single host (Bartlett, 1978), which is similar to the author's observations for *C. monophlebi*, but very different from Koebele's (1890) record of 62.

The present observations of *Monophlebulus* being attacked by Pteromalidae appears to be a first record. Valentine (1967) records *Ophelosia* spp. as 'predatory' on eggs of *Pseudococcus longispinus* (Targ.) (Pseudococcidae), *Pulvinaria* sp. (Coccidae) and *I. purchasi*. He also refers to *Ophelosia* sp. as being hyperparasitic on coccids attacked by encyrtids, but there is no evidence of this with *Monophlebulus*. The parasitizing of female *M. pilosior* by the encyrtid *Aphycopsis* sp. also appears to be a first record.

In Australia, the biological relationships between coccinellids and margarodids has received little attention, although the successful control of *I. purchasi* by *Rodolia cardinalis* (Mulsant) (Noviini) is well documented overseas (Bartlett, 1978). Recently, *Rhyzobius forestieri* and *Rh. ventralis* have been recorded preying on *I. purchasi* and *Monophlebulus* spp. near Sydney (Richards, 1981), and in 1981 large numbers of *Rd. cardinalis* were observed by the author attacking a large infestation of *Auloicerya australis* (Maskell), a new host record for this species. It has been established here that *R. major*, *Rhyzobius satelles*, *Telsimia subviridis* (Telsimiini) and *Diomus* sp. (Scymnini) all prey on *M. pilosior*. Larvae and adults in all seven species are margarodid predators, *R. major* attacking eggs; *Rh. satelles*, *T. subviridis*, and *Diomus* sp. eggs and immature stages; *Rh. forestieri* and *Rh. ventralis* immature stages; and *Rd. cardinalis* all stages. Perhaps due to greater prey specificity, only *Rd. cardinalis* and *R. major* resemble their prey during the vulnerable pupal stage. This deception is possibly to confuse their predators, especially ants.

As a result of this study, it is possible to speculate on the potential of *R. major* as a biological control agent of margarodids. In the Sydney area, it appears to be univoltine and is essentially a spring species, allowing the polyvoltine *M. pilosior* to increase in numbers during summer and autumn. Difficulty in competing with other predators and parasites of *M. pilosior*, particularly the very successful *C. monophlebi* and *Ophelosia* sp., may be a major factor in limiting the size of the *R. major* population. It may also influence the slow rate of development of its immature stages, and may be responsible for the absence of an autumn generation. The total egg-laying capacity per female is not known. There is no record of parasitism or predation at any stage of the life cycle. *Rodatus major* has marked prey specificity, important in biological control, with both larvae and adult very voracious on *M. pilosior*, but the high reproductive rate of the prey has perhaps reduced the need to develop a high level of searching ability, and must be at least partly responsible for its specialized feeding behaviour. The total number of eggs produced by an *M. pilosior* female is similar to that recorded for a female *I. purchasi* (Bartlett, 1978), and the number of eggs consumed by *R. major* appears to be similar to those consumed by *Rd. cardinalis*, except that the latter also eats all other stages of the margarodid, including the adult female. Length of adult life is not known, but, as *R. major* is closely related to *R. boucardi*, which hibernates as adults under bark of eucalypts, *R. major* may behave in a similar manner. The natural distribution of *R. major* extends throughout eastern Australia, but locality records are very disjunct, suggesting poor powers of dispersal, a limiting factor in a potential biological control agent, especially as *Monophlebulus* is widely distributed throughout Australia.

While *R. major*'s great voracity and prey specificity support its use as a biological control agent, they are countered by its inability to produce more generations than its prey, its inability to compete successfully with other predators and parasites, and possibly its poor powers of dispersal, these factors applying under natural Australian conditions. On its own under different environmental conditions, the situation could change, as was the case in New Zealand where *Rh. ventralis* was very successful in controlling the gum tree scale *Eriococcus coriaceus* Maskell in the absence of parasites and predators of the coccid (Richards, 1981).

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