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'*Rhyzobius ventralis*' (Coleoptera: Coccinellidae), its constituent species, and their taxonomy and historical roles in biological control

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Abstract

The *Rhyzobius* (or *Lindorus*) *ventralis* frequently referred to in the literature of biological control is shown to be a mixture of two distinct, though similar, species. The origin of the confusion is traced to the nineteenth century searches in Australia for insects to control scale insect infestations on citrus and other crops in California. Adults of the two species are defined and illustrated, and a key is provided for their separation. Lectotypes are designated for *R. ventralis* (Erichs.), its synonym *Scymnus restitutor* Sharp and for *S. halli* Broun, newly synonymised with *R. ventralis*. A lectotype is designated for *Platyomus forestieri* Muls., the second species of the complex, here transferred to *Rhyzobius*, and for *S. circularis* Sharp, newly synonymised with *R. forestieri*. Distribution data for both species, based on actual specimens examined, are listed, and their Australian distribution is summarised in a map. Past usages of '*R. ventralis*' as a biological control agent are reviewed in the light of the revised taxonomy. The taxonomy and nomenclature of *Rhyzobius* Stephens is discussed in order to establish the correct generic placement of and binomina for *R. ventralis* and *R. forestieri*.

Introduction

Rhyzobius ventralis (Erichson) (more usually referred to as *Rhizobius ventralis* or, occasionally (e.g. by Timberlake, 1927), *Lindorus ventralis*) is a well-known name in the history of biological control. The present taxonomic, historical and biological studies have uncovered considerable confusion. Two fairly closely related species of the genus *Rhyzobius* Stephens have, up till now, been identified as "*ventralis* (Er.)". In addition, both of them have been described independently as new species in another genus, indeed in another subfamily of the Coccinellidae. The true identity of each species has been discovered and, by examination of the relevant type series, it has been possible to confirm one synonymy and establish two others. The two species are sufficiently different as adults, larvae and pupae, as well as in their biology, to ensure that any future study or possible use as a biological control agent is soundly based on one or other of them.

Historical resumé

Erichson (1842) described *Scymnus ventralis* from amongst material collected by Oberintendant Schayer at Cape Grimm ('Woolnorth') in the north-west corner of

Tasmania. Mulsant (1850) transferred Erichson's species to *Rhyzobius* (as *Rhizobius*), basing his interpretation on Erichson's original material and other specimens from Tasmania in the Paris Museum. Crotch (1874) added Queensland, Victoria (Melbourne) and South Australia to the recorded distribution of the species. Blackburn (1889) identified material from near Port Lincoln and near Adelaide, South Australia, as *R. ventralis*, commenting that his specimens agreed with Erichson's description in all but the oblong shape, but that they disagreed with the measurements given by Mulsant.

During the course of early attempts to control scale insect infestations in the Californian citrus-growing areas, Albert Koebele, one of the Californian Agents of the Entomology Division, U.S. Department of Agriculture, made a lengthy trip to Australia and New Zealand (August 1888–March 1889) in search of natural predators and parasites for use against the "fluted scale" (*Icerya purchasi* Maskell). Samples of the coccinellids collected by him and shipped to California were sent for identification to Sharp in England, who described one of them as a new species, *Scymnus restitutor* (Sharp, 1889). However, he quickly changed his mind, for Koebele (1890: 14 [footnote]) reported a letter from Sharp synonymising *S. restitutor* with *R. ventralis* and commenting that the species seemed much more like a *Scymnus* than a *Rhyzobius*. In the same paper, Koebele referred to *ventralis* as having been sent by him in large numbers to California and as being "only occasionally found with *Icerya*, yet very abundant on various Eucalyptus scales, especially on *Eriococcus eucalypti*".

Two years later, Koebele was sent on a second trip to Australia and New Zealand, this time to look for parasitic and predaceous insects for the control of red scale (*Aonidiella aurantii* (Maskell)), the pernicious scale (*Quadraspidiotus perniciosus* (Comstock)) and "various black scales (*Lecanium*)". Many species of scale-feeding coccinellid were collected and sent to California, identifications being made on this occasion in Australia, either by Blackburn or by Koebele himself. In a subsequent report on the expedition, he recalled (Koebele, 1892) that, in New South Wales, he found *Rhyzobius* in large numbers on orange trees infested by black scales. In a later and more detailed account (Koebele, 1893) he summarised his experience of *R. ventralis* in Australia, noting it as "one of the most numerous of all the Coccinellidae in South Australia and Victoria, becoming more rare toward Queensland". He also commented that he "did not recognise the insect at first on this last trip at Sydney, where they were found on various *Lecanium*, on citrus, and on other trees; in fact the larvae feeding upon these are much lighter in color than those feeding on *Eriococcus*". Koebele said that he "saw in this the most effective enemy for all our *Lecanium*" and sent large numbers of adults to California "by every steamer".

The fate in California of the 1888–89 consignment of *R. ventralis* was referred to by Riley (1892) who reported it (under the name *Scymnus restitutor*) as having been "set at liberty in the vicinity of Los Angeles" but subsequently "lost sight of". In contrast, the shipments sent during Koebele's 1891–92 trip evidently prospered, for Koebele (Coquillett & Koebele, 1893) recorded *R. ventralis* at Santa Barbara "by the millions" feeding on "*L[ecanium] oleae*". The immense initial success of the second series of *R. ventralis* shipments led to the beetle's being deployed as a black scale control in many Californian counties and when, late in 1893, Koebele left California to work in Hawaii, he arranged for American material of the species to be imported into the islands. That it established successfully is evident from the reports by Swezey (1912), Fullaway (1920) and Illingworth (1929) recording it as a predator of various mealybugs on cotton, citrus and coffee. It continues to thrive and has been taken in the islands at various times during the last ten years.

The early success of Koebele's efforts awakened a wide interest in the use of Australian coccinellids as agents for biological control. Material accepted as *R. ventralis* was sent from Queensland and New South Wales to Western Australia in 1898 and 1902 (Wilson, 1960), from New South Wales to New Zealand in 1899 and to Tasmania at around the same time (Froggatt, 1902) and to India and Ceylon in 1900

(Clarke, 1900; Froggatt, 1902). The shipments to Western Australia, India and Ceylon were for the control of black scale, but the importations to New Zealand were to be used against the araucaria scale (*Eriococcus araucariae* Maskell) on Norfolk Island pine (*Araucaria heterophylla*) in northern Auckland. The purpose for which the species was sent to Tasmania seems to be unrecorded. During 1900, Californian material of *R. ventralis* was sent to South Africa as a possible control for black scale (Lounsbury, 1901), and in 1903 the same experiment was tried in Chile (Bartlett, 1978). A few years later, in 1907, the importation from New South Wales to New Zealand was repeated, this time for the control of an outbreak of blue gum scale (*E. coriaceus* Maskell) on various eucalypts near Timaru on the east coast of the South Island. At about the same time, Silvestri (1908) imported *R. ventralis* from California or Hawaii to Italy and later (Martelli, 1913) to Sicily, in both cases for the control of dictyospermum scale (*Chrysomphalus dictyospermi* (Morgan)) (Malenotti, 1918). The most recent introduction appears to have been from Hawaii to Java, when *R. ventralis* was imported in the hope of controlling various, unspecified scale insects (van der Goot, 1920).

The post-1894 biological control experiments using *R. ventralis* achieved only a mixed success. The transfers to Western Australia seem to have been effective, although doubt was cast by A. M. Lea, who declared, according to Wilson (1960), that the species was already present in the area before the imports arrived. The exports to India and Ceylon appear to have been failures (Froggatt, 1902), as does the Chilean introduction (Duran & Cortes, reported by Bartlett, 1978), but the result of the South African experiment in 1900 is uncertain. Both of the New Zealand importations seem to have been successful (Kirk, 1908), but although Silvestri's introductions seem to have established themselves (Malenotti, 1918, and reported by Bartlett, 1978) they were apparently of little use in controlling the scale. The importation from Hawaii to Java seems also to have ended in failure, judging by the comment in Schilder & Schilder (1928).

From these accounts and from the earlier reports, the effectiveness of *R. ventralis* as a biological control agent seems to have depended not only on the intended prey but also upon the country from which the *ventralis* was exported. Such a situation could well be explained if more than one species had been passing under the name '*ventralis*'. In fact the evidence would seem to support a suggestion that Koebele should not have reconciled his doubts about the identity of the "Sydney *ventralis*" and that the specimens he sent to America during the course of his second Australian trip were of another species, similar as an adult to Sharp's interpretation of *R. ventralis* but more readily distinguishable as a larva and having different food preferences.

Examination of the type specimens of *R. ventralis* and *Scymnus restitutor* has confirmed the synonymy reported by Koebele and so proved that the true *R. ventralis* was certainly sent from Australia to California in 1888–89. However, a study of over 1400 specimens considered to be *R. ventralis*, some 390 of them collected in California and Hawaii between 1897 and 1976, revealed only two twentieth-century examples of the true *R. ventralis* from the United States, both of them from California. Almost all the other specimens from America and the Hawaiian Islands, including many from Santa Barbara, proved to belong to a second species, sufficiently similar to *R. ventralis* to be mistaken for it in the field, but usually smaller in size and slightly more rounded in outline. This species, recorded as feeding on five different species of coccid in Hawaii (Leeper, 1976), on three in California (Bartlett, 1978) and many more in Australia, is without doubt the "*ventralis*" that Koebele found at Sydney feeding on "*Lecanium*" and shipped in large quantities to California during his second collecting trip.

This second species, to which a majority of the published accounts of "*Rhyzobius ventralis*" refer, is *Scymnodes* (= *Platyomus*) *forestieri* (Mulsant), described from Australia in 1853. Fortunately, the name has had no currency in the literature, apart from inclusion in a key to the species of *Platyomus* by Blackburn (1895), since its first

appearance, and so its introduction will cause less confusion than might well have been the case.

Taxonomy

Rhyzobius Stephens

Rhyzobius Stephens, 1829: 239; 1832: 396. Type-species: *Nitidula litura* Fabricius, 1787, by monotypy.

Rhizobius Stephens, 1832: 373. [Lapsus.]

Rhizobius Agassiz, 1846: 325, 327. [Unjustified emendation.]

Lindorus Casey, 1899: 161. Type-species: *Scymnus lophanthae* Blaisdell, 1892, by monotypy. **Syn. n.**

Rhizobiellus Oke, 1951: 21. [Unnecessary new name for *Rhizobius* Agassiz, 1847 nec Burmeister, 1835.]

The genus *Rhyzobius* currently includes 85 species. A majority (58) are from Australia, but 8 have been described from South America, 10 from Africa, 3 from New Guinea, 1 from South-east Asia and 5 from the Palaearctic Region. They are a relatively primitive group of small to medium-sized (1–5 mm long) coccinellids having the following characters in common: eyes coarsely facetted; antennae 11-segmented and distinctly longer than width of head between eyes; head, pronotum and elytra obviously pubescent, the pubescence often consisting of a mixture of upstanding and subrecumbent setae; tarsi cryptotetramerous; tarsal claws often sexually dimorphic; abdomen with six visible sternites in both sexes.

Very little is known about the life-histories of a majority of the species, but such records as exist indicate that coccids will prove to be the preferred food of most. Exceptions are the European species *R. litura* (F.) and *R. chrysomeloides* (Herbst), which are reported to feed on aphids.

Rhyzobius Stephens, 1829 is a correct original spelling and available under Articles 12 and 16 of the International Code of Zoological Nomenclature. It is the oldest name for the genus as defined by Stephens and is not a junior homonym. It is therefore the valid name of the group. *Rhizobius* Agassiz, an etymological 'correction' followed by many authors even today, is an unjustified emendation, a junior homonym of *Rhizobius* Burmeister, 1835 (Hemiptera) and a junior objective synonym of *Rhyzobius* Stephens. *Rhizobiellus*, coined by Oke as a replacement name for *Rhizobius* Agassiz nec Burmeister, is therefore also a junior objective synonym of *Rhyzobius* Stephens.

In 1899, Casey erected the genus *Lindorus* to include *Scymnus lophanthae* Blaisdell. He included *Lindorus* in his tribal grouping Rhyzobiini, contrasting it with a definition of *Rhyzobius* based on his new species *Rhyzobius trimeni* from Wellington, South Africa. *R. trimeni* is a very unusual member of Stephens' genus and at once the status of *Lindorus* is called into question. Examination of 55 species currently assigned to *Rhyzobius*, most of them from Australia, has led to the conclusion that, although the genus may well prove composite following a thorough taxonomic revision, Casey's *Lindorus* is unlikely to represent a valid grouping, even at subgeneric level. The name is therefore here included in the synonymy of *Rhyzobius* Stephens.

The following abbreviations are used in the text for depositories containing specimens:

BMNH British Museum (Natural History), London;
MNHB Museum für Naturkunde der Humboldt-Universität, Berlin;
MNHN Muséum Nationale d'Histoire Naturelle, Paris.

Rhyzobius ventralis (Erichson)

Scymnus ventralis Erichson, 1842: 239. **Lectotype** ♀, TASMANIA (MNHB), here designated [examined]. [Transferred to *Rhyzobius* (*Rhizobius*) Stephens by Mulsant, 1850: 1005.]

Rhizobius ventralis (Erichson): Crotch, 1874: 297.
Rhizobius ventralis (Erichson): Blackburn, 1889: 203, 204; 1892: 259.
Scymnus restitutor Sharp, 1889: 364. **Lectotype** ♀, AUSTRALIA (BMNH), here designated [examined]. [Synonymised by Koebele, 1890: 14.]
Scymnus halli Broun, 1914: 265. **Lectotype** ♀, NEW ZEALAND (BMNH), here designated [examined]. **Syn. n.**

Diagnosis. Length 3·26–4·85 mm. Breadth 2·45–3·80 mm. Average (22 examples) 3·96 × 2·95 mm.

Male. Outline similar to that shown in Plate I but usually slightly more elongate. Upper surfaces black except for membranous anterior clypeal border, narrow pale,

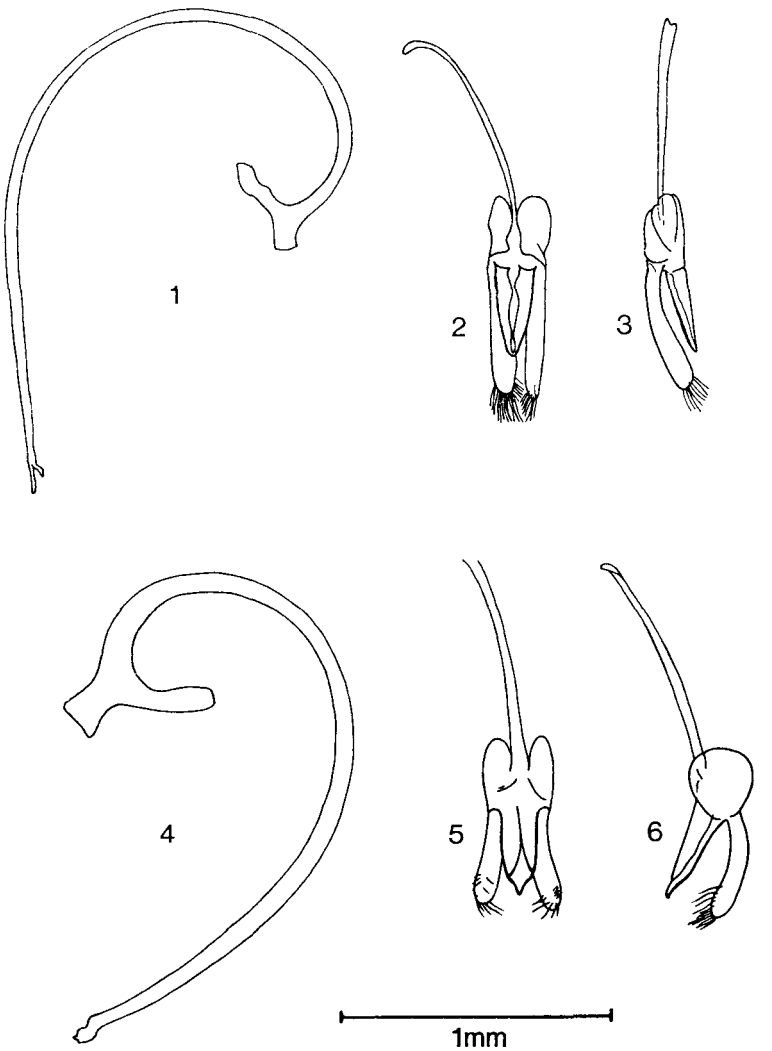

Fig. 1–6.—Male genitalia. 1–3, *Rhyzobius ventralis*; 1, sipho; 2, median lobe, parameres, etc., dorsal view; 3, same, lateral view. 4–6, *R. forestieri*; 4, sipho; 5, median lobe, parameres, etc., dorsal view; 6, same, lateral view.

translucent areas along anterior and lateral pronotal margins on either side of anterior angles. Antennae, mouthparts and tarsi castaneous to fuscous. Legs and underside of thorax usually black to fuscous, occasionally lighter; abdomen testaceous to pale castaneous. Head with eyes rather shallowly emarginate behind antennal insertions; clypeus with anterior margin emarginate within membranous anterior area; frons more closely punctured toward eyes than on disc, lateral punctures a little smaller than eye

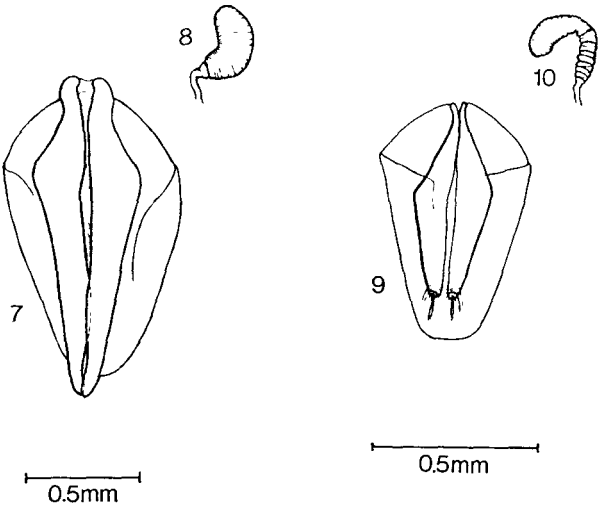

Fig. 7–10.—Female genitalia. 7–8, *Rhyzobius ventralis*; 7, coxites and ninth segment; 8, spermatheca; 9–10, *R. forestieri*; 9, coxites and ninth segment; 10, spermatheca.

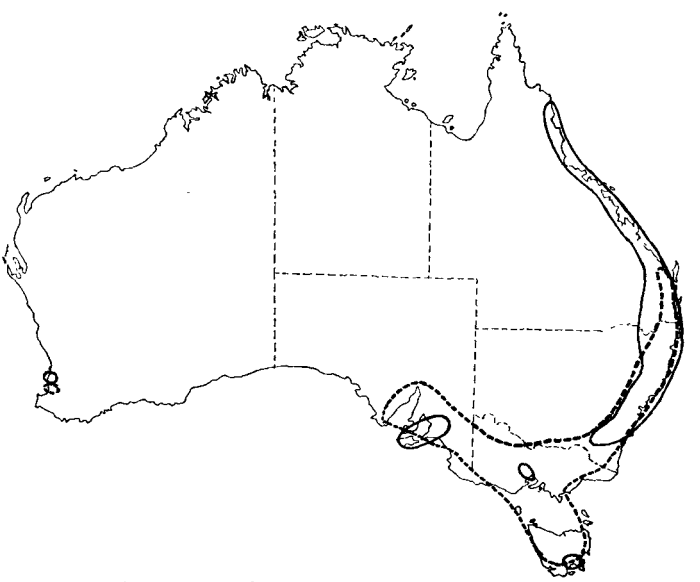

Fig. 11.—Distribution of *Rhyzobius ventralis* (broken outline) and *R. forestieri* (solid outline) in Australia.

facets, sometimes separated by no more than one diameter, intervals between punctures smooth, shining. Pronotum a little more than twice as broad as median length, broadest at hind-angles; anterior border shallowly emarginate to rounded anterior angles; lateral margins each with an entire, narrowly raised border, borders more strongly convergent over anterior half than from sharply formed hind-angles to middle; hind-margin without a raised hind-border, shallowly arcuate in front of scutellum, oblique and almost without emargination to posterior angles; disc of pronotum evenly convex longitudinally and transversely, with at most only slight extra convexities near anterior angles (Plate I*a*); punctures of disc generally smaller than eye facets, usually separated by considerably more than one diameter, punctures distinctly larger toward lateral borders; intervals between punctures smooth, shining; pubescence fine, greyish white, subdepressed, mostly directed more or less anteriorly or antero-laterally. Scutellum small, more or less triangular. Elytra about 1·15 × as long as their greatest combined breadth, broadest at about anterior fourth, narrowed anteriorly to become a little broader at base than hind-border of pronotum; lateral and apical margins with an entire, narrowly reflexed border; punctures of disc and margins a little larger than those of pronotal disc, more deeply impressed; intervals between punctures smooth, shining; pubescence double, consisting mostly of subdepressed, almost white setae, similar to those of pronotum but variably directed to form a swirling, symmetrical pattern (Plate I*e*); scattered amongst the pattern hairs are more upstanding, golden setae, usually more readily visible toward elytral margins. Prosternum with intercoxal carinae convergent anteriorly but meeting anterior border separately. Postcoxal plates of first abdominal segment as in Plate I*c*; apex of fifth abdominal segment more or less evenly arcuate. Legs with anterior and middle tarsal claws bifid, tarsal claws of hind-legs appendiculate.

Genitalia (Fig. 1–3). Sipho very long, with an asymmetrically bifid apex. Parameres long, parallel-sided, flat. Median lobe distinctly shorter than parameres, symmetrical, triangular.

Female. Very similar to male, but with tarsal claws of all legs appendiculate.

Genitalia (Fig. 7 & 8). Coxites very long, narrow, heavily sclerotised, without apical styli. Spermatheca as illustrated.

Distribution. Australia (Fig. 11) (Queensland, New South Wales, ACT, Victoria, South Australia, Tasmania, Western Australia); New Zealand; USA.

Type material examined. Scymnus ventralis Erichson, lectotype ♀, 4735/Van Diemensland, Schayer/Typus [red printed label]/ventralis Er. *Scymnus halli* Broun, lectotype ♀, Mt. Hutt Feby 1912/Broun Coll. Brit. Mus. 1922: 482/3676/Scymnus halli. *Scymnus restitutor* Sharp, lectotype ♀, Scymnus restitutor Type D.S. Australia. Riley [on mounting card]/4391[01] Australia/4/.

Other material examined from: AUSTRALIA: Queensland: Bundaberg; Brisbane (Corinda, Oxley Research Station); Mt. Tambourine. New South Wales: Dorrigo; 10 km S. of Ebor; Armidale; Weston; Orange; Narrara; Gosford; Blue Mts.; Blackheath; Cowan; Hornsby; Waitara; Sydney (Cabramatta, Rosebery, Randwick, Kensington, Liverpool, Waterfall); 9 km W. of Marulan; Goulbourn; Yarra River, Kew; Duran Dura; N. of Braidwood; 8 km N. of Batlow; 2–6 km N.W. of Bungendore; Michelago; Cooma District; Jindabyne; Eucumbene. ACT: Canberra; Black Mountain; Tharwa Road; Gibraltar Falls; Cooma Road; Pearce; "4 m E. of Piccadilly Circus". Victoria: Lake Hattah; Birchip; Porepunkah; Wellington River, 17 km N. of Licola; "Victorian Alps"; Grampians; Merrijig; Timbertop [Gippsland]; Fleatje, Creswick; Korweinguboora; Marysville; Connor Plains; Ballarat; Kangaroo Ground [Yarra Glen]; Healesville; Fitzroy River; Warrandyte; Melbourne (including Nunawading & Montmorency); Warburton district; Elaine; Heathmount; Meredith; Ferntree Gully; Macclesfield; Oakleigh; Dandenong Ranges; Mt. Elelyn; Woori, Yallock; Mordialloc; Seaford; Ballan; Bacchus Marsh; Anglsea; 3 km N. of Kawarren, Otway Ranges. South

Australia: Mt. Remarkable; Port Lincoln; Adelaide (including Cheltenham); Long Gully; Mt. Lofty Ranges; Myponga; 2 m N.W. of Woods Wells, Coorong National Park; Lucindale. Western Australia: 17 km E. of Wilga. Tasmania: King Island; Latrobe River survey; Beaconsfield; Launceston; Karoola; Blackrock; Cradle Mt.; Tyenna; Lauderdale; New Norfolk; Hobart (including Mt. Wellington); "Swamp near Olga River, 19 km above Gordon River junction"; Lake Pedder; Huon River. NEW ZEALAND: North Island: Auckland (including Papatoetoe, Mt. Albert); Clevedon; Mt. Te Aroha; New Plymouth; Wellington (Mt. Hutt). South Island: Nelson; Blenheim; Christchurch. UNITED STATES OF AMERICA: California: Santa Barbara, Dec. 1918 (*H. M. Armitage*) 1ex; ditto, but Dec. 1919 1ex. (UCR Entomological Teaching and Research Collection, University of California, Riverside).

Total number of specimens examined: 598 (Australia 581; New Zealand 15; USA 2).

Rhyzobius forestieri (Mulsant) **Comb. n.**

Platyomus forestieri Mulsant, 1853: 286. **Lectotype** ♂, AUSTRALIA (MNHN), here designated [examined].
Scymnodes forestieri (Mulsant): Korschefsky, 1931: 85.
Scymnus circularis Sharp, 1889: 365. **Lectotype** ♂, NEW ZEALAND (BMNH), here designated [examined]. **Syn. n.**
Rhizobius ventralis sensu auct. partim not (Erichson, 1842).
Lindorus ventralis (Erichson): Timberlake, 1927: 532.

Diagnosis. Length 2·66–3·70 mm. Breadth 1·90–2·30 mm. Average (22 examples) 3·20 × 2·28 mm.

Very similar to *R. ventralis* except as indicated in the key to species below and in the following points: the typical body outline (Plate I*e*) is slightly less elongate. The species exhibits two other secondary sexual characters apart from the tarsal claw dimorphism that it shares with *R. ventralis*. In the *male*, the postcoxal plates of the first abdominal segment are somewhat flattened apically (Plate I*d*) and the apical border of the fifth abdominal segment is more or less broadly truncate medially. In the *female*, the postcoxal plates are almost identical with those of *R. ventralis* (Plate I*c*) and the apical border of the fifth abdominal segment is evenly arcuate medially.

Male genitalia (Fig. 4–6). Sipho very long, cranked near apex and with a minute apical tooth. Median lobe as long as parameres, produced apically into a short, slightly recurved spike. Parameres less flattened than in *R. ventralis*, more strongly curved in profile.

Female genitalia (Fig. 9 & 10). Coxites much shorter, wider and more weakly sclerotised than in *R. ventralis*, with vestigial apical styli bearing a few, long setae. Spermatheca distinctly different from that of *R. ventralis*, the proximal half taking the form of a compressed, spiral tube.

Distribution. Australia (Fig. 11) (Queensland, New South Wales, ACT, Victoria, South Australia, Tasmania, Western Australia); New Zealand; New Caledonia; Fiji; USA.

Type material examined. Platyomus forestieri Mulsant, lectotype ♂, platyomus forestieri [handwritten by Mulsant]/1140 platyomus forestieri n. g. n. sp. Mulsant, Woodlark [handwriting typical of Perroud collection, except for "Woodlark" which is clearly a later, erroneous, addition]/type [handwritten, writing different from both previous labels]/[small red disc] (MNHN). *Scymnus circularis* Sharp, lectotype ♂, Scymnus circularis. Types D.S. Picton N.Z$^{d.}$ Helms 1884 [on mounting card]/Picton, New Zealand Helms. Paralectotypes 1♂, 3♀. 1♂ mounted on same card as lectotype. 1♀, Picton, N.Z$^{d.}$ Helms [on mounting card]/Picton New Zealand, Helms. 1♀, Picton, New Zealand, Helms. 1♀, Picton, Helms [on mounting card]/Picton, New Zealand, Helms. (All BMNH).

Other material examined from: AUSTRALIA: Queensland: Kuranda; Mt. Nebo; Bundaberg; Childers; Blackall Ranges; Lagoon Pocket; Nambour; Buderim; Nananga; Cairncross Park, near Maleny; Beerwah; Maroochydore; North Pine River; Brisbane (including Wellington Point & Oxley Research Station); Toowoomba; Redland Bay; Tambourine Mts.; Nerang. New South Wales: 18 miles N. of Boonoo; Gyra; Dorrigo; Armidale; Wollomombi; Upper Williams River; Narrara; Gosford; Kenthurst; Penrith; Hornsby; Waitara; Wiseman's Ferry; Sydney (including Cabramatta, Baulkham Hills, Punchbowl, Vaucluse, Newport, Canley Vale, Sans Souci, Neilson Park, Fairfield, Chinaman's Beach); Cape Banks; Illawarra; 1 km N. of Geary's Gap; Federal Highway near Lake George; 8 km N. of Batlow. ACT: Gibraltar Falls. Victoria: Bullarook Forest; Melbourne (including East Kew). South Australia: Darling—Waikerie; Mt. Lofty; Adelaide; Point Reynolds, W. of Pennington Bay; Kangaroo Island. Western Australia: Fremantle; Swan River. Tasmania: Hobart; Great Forester River, 15 km N.W. of Forester. NEW ZEALAND: North Island: Spirits Bay; Cape Reinga; Paihia, Bay of Islands; Whangarei; Hen Island; Copper Mine Island, Chicken Islands; "Bayles Beach"; Windy Ridge, Wellsford; Great Barrier Island (Okiwi, Kaiarara Valley, Whangaparara); Little Barrier Island (Te Titoki Flat, Awaroa Point); Auckland (including Rangitoto Island, St. Heliers, Henderson, Mt. Eden, Grafton Gully, Karamatura Valley, Huia, Mt. Mangere, Owairaka); Tauranga; Puhi Puhi Reserve; Taupo; Ketetahi Springs; Waipuna Stream; Devil's Elbow, Tatarere Stream, Napier; Wanganui (region behind Waverley); Feilding; Featherston; Orongorongo Valley. South Island: Collingwood; Totaranui Beach; French Pass; Kapowai, D'Urville Island; Riwaka Valley; Rosedale, Nelson; Picton; Maitai Valley; Port Underwood; W. end of Rabbit Island; Motuipiko; Spooner Range; Redhill, mineral belt 750′ N. of Whangamoa; Wairau, Top Valley, Staircase Ridge; Mt. Altimarlock, Blackbirch Range; West port; Rika Valley, Clarence River; Mt. Snowflake; Mt. Oxford; Kaituna; Speargrass Valley, near Coronet Peak; Pisa Range, north end; Cromwell Flats; The Doone, inland road; Kawarau Gorge; Waimatua. NEW CALEDONIA: No detailed localities, "xi. 04 (Compère) California Academy of Sciences, San Francisco). FIJI: No detailed localities, "(Compère)" (UCR Entomological Teaching and Research Collection, University of California, Riverside). UNITED STATES OF AMERICA: California: Carson Pass; Guerneville; Fort Braggs; Martinez; Mill Valley; El Cerrito; Berkeley; Corte Madera; Sausalito; Hills back of Oakland; Palo Alto; Alameda; Piedmont; Hayward; Felton; San Francisco; Lagunitas; Millbrae; Muir Woods; Stevens Creek, Santa Clara; Jose State College; La Honda; Santa Cruz; Monterey; Carmel; Atascadero; Saticoy; Ventura; Santa Barbara; Carpinteria; Monte Cito; Santa Paula; Fillmore; Santa Monica; Passadena; Duarte; Alhambra; Los Angeles; San Marino; Anaheim; Santa Ana Canyon; Whittier; Norwalk; Long Beach; Laguna Beach; Avalon; Fall Brook; San Diego. Hawaiian Islands: Oahu (Koko Head region, Honolulu, Barbers Point, Wahiawa, Mt. Kaala, Kunia, Mauna Lahilahi, Kainulai, Wailupe, Pauoa, Mt. Olympus, Mt. Tantalus, Ewa Coral Plain, Kolekole Pass, Waialua, Puu Palika, Puu Hapapa, Koolau Range, "Olea Forest Reserve"); Hawaii (Humuula, Holualoa, Kiluaea, Kilohana, Hilo); Molokai (Kaunakakai, Kainalu, Kamiloloa Gulch); Maui (Kipahulu, Makawao, Lanai, Olinda, Halehaku, Waikamoi stream, Nahiku, Lao Valley, Kailua, Wailuanui); Kaui (Nualolo, Eleele, Alakai Swamp).

Total number of specimens examined: 809 (Australia 284; New Zealand 151; New Caledonia 12; Fiji 1; USA: California 304, Hawaiian Islands 57).

KEY TO SPECIES

1 Pronotum swollen toward anterior angles and then abruptly impressed to form a well-marked groove immediately inside raised lateral borders (Plate I*b*); pronotal punctures usually much larger and closer toward anterior angles than elsewhere; male genitalia Fig. 4–6; female genitalia Fig. 9 & 10 ..... *forestieri* (Mulsant)

— Pronotum (Plate I*a*) sometimes slightly swollen near anterior angles, but never

with a groove immediately inside raised lateral borders; pronotal punctures smaller, except very close to lateral borders; male genitalia Fig. 1–3; female genitalia Fig. 7 & 8 ..... *ventralis* (Erichson)

The size, outline and overall black colour cause both species to stand somewhat isolated in the genus *Rhyzobius*. It is possible that very small examples of *R. forestieri* might be taken for *R. satelles* Blackburn, or vice versa, but in *R. satelles*, the long, upstanding setae of the pronotum and elytra are a medium to dark brown, contrasting strongly with the whorled, subdepressed setae which are clearly white. The male genitalia of *R. satelles* have long, narrow parameres, distinctly longer than the median lobe, similar to those of the otherwise very different *R. ventralis*. Also, the postcoxal plates of the first abdominal segment are more or less evenly arcuate, again more like those of *R. ventralis* than *R. forestieri*. However, if certain tribal and generic characters are overlooked, or misinterpreted, the species could well be confused with those of *Scymnodes* Blackburn or *Bucolus* Mulsant, both of which have finely faceted eyes and short antennae and belong to the Scymnini, or with *Erithionyx* Blackburn, which, although belonging to the Coccidulini and so closely related to *Rhyzobius*, has totally upstanding pubescence, all of which is yellow and none of which forms a swirling pattern.

The use of "*R. ventralis*" in biological control

The factors governing the success or failure of a predator as a biological control agent are complex and often interdependent. A detailed knowledge of the biology of both predator and prey in the environment where an encounter is to take place is a prerequisite for the reliable prediction of its outcome. Much the same is necessary for the evaluation of past results. The biology of both species of the *R. ventralis* complex has been studied in Australia by Dr A. M. Richards of the University of New South Wales who, in the following paper (Richards, 1981), examines the reasons for their effectiveness, or lack of it.

In the meantime, it is possible to make one or two observations based solely on the literature and on data attached to identified specimens. Amongst other desirable characteristics, a predator should be well-suited to the environment of its introduction, be capable of sustaining its population on a fairly low prey density, have its own main feeding and growth periods coincident with the times of maximum prey reproduction, be efficient in dispersion and relatively restricted as to the number of prey species upon which it can live and reproduce.

The natural distribution of both species in Australia, plus what might well be the result of early translocations within the continent (Fig. 11), shows a wide thermal tolerance and, as far as *R. forestieri* is concerned, some ability to withstand arid conditions. Climatic races may well exist within each species. Had this possibility been realised in the early days, the efficacy of *R. ventralis* in South Island, New Zealand, and of *R. forestieri* in California might well have been improved by selecting native stock from appropriate regions.

The original export of the true *R. ventralis* to California was almost certainly doomed to failure, even if it had been properly looked after on arrival. As Koebele (1890) noted and as identified material has corroborated, its principal food is species of *Eriococcus*, usually on eucalypts, but occasionally on other trees, such as wattle. To date, no records of it have been found feeding on *Icerya* species on citrus. The attempt to control '*Lecanium*' (*Saissetia*) species in India and Ceylon seems to have failed for the same reason. Froggatt, the originator of the consignments, referred to *R. ventralis* as "the Eriococcus ladybird" (Froggatt, 1902); that it fed also on '*Lecanium*' was known to him only via reports from California. There is little doubt that he sent his colleagues shipments of the true *R. ventralis*, and it is hardly surprising that the experiments did not succeed. The New Zealand introductions were, with hindsight, as assured of success as the American and Asiatic ones were of failure.

Froggatt was again involved and the control agent was *R. ventralis*, but on both of these occasions the intended prey was an *Eriococcus* species, one of them being *E. coriaceus*, the coccinellid's commonest food. Effective control continued for many years (Clark, 1938), *R. ventralis* proving more cold-hardy and so better able to survive the relatively rigorous winters of South Island than the other *Eriococcus* predators introduced at the same time.

All other introductions, including that to Hawaii in 1893, were of *R. forestieri*. Its spectacular initial success in California had largely failed by the mid-1920s (Essig, 1931), although the species is still present today over a large part of the state from Carson Pass to San Diego. It also lives on in Hawaii, feeding on at least six different hosts (Leeper, 1976). The Italian import ignored the intended prey but apparently established itself none the less. Java and South Africa seem to have been outright failures. Such bionomic data as is attached to the 809 specimens so far examined record the species as associated with twelve different coccids on ten kinds of tree or shrub. These, together with the non-overlapping part of Leeper's list and the host records established by Richards (1981) carry the total to over 20 species. Doubtless some of these are 'casuals' or, at best, non-essential, alternative foods, but one thing seems clear: *R. forestieri* is a successful, adaptable species. However, this may also mean that it is too catholic in its choice of food to be a lasting success as a biological control agent in areas where other scale insects live alongside an important pest species.

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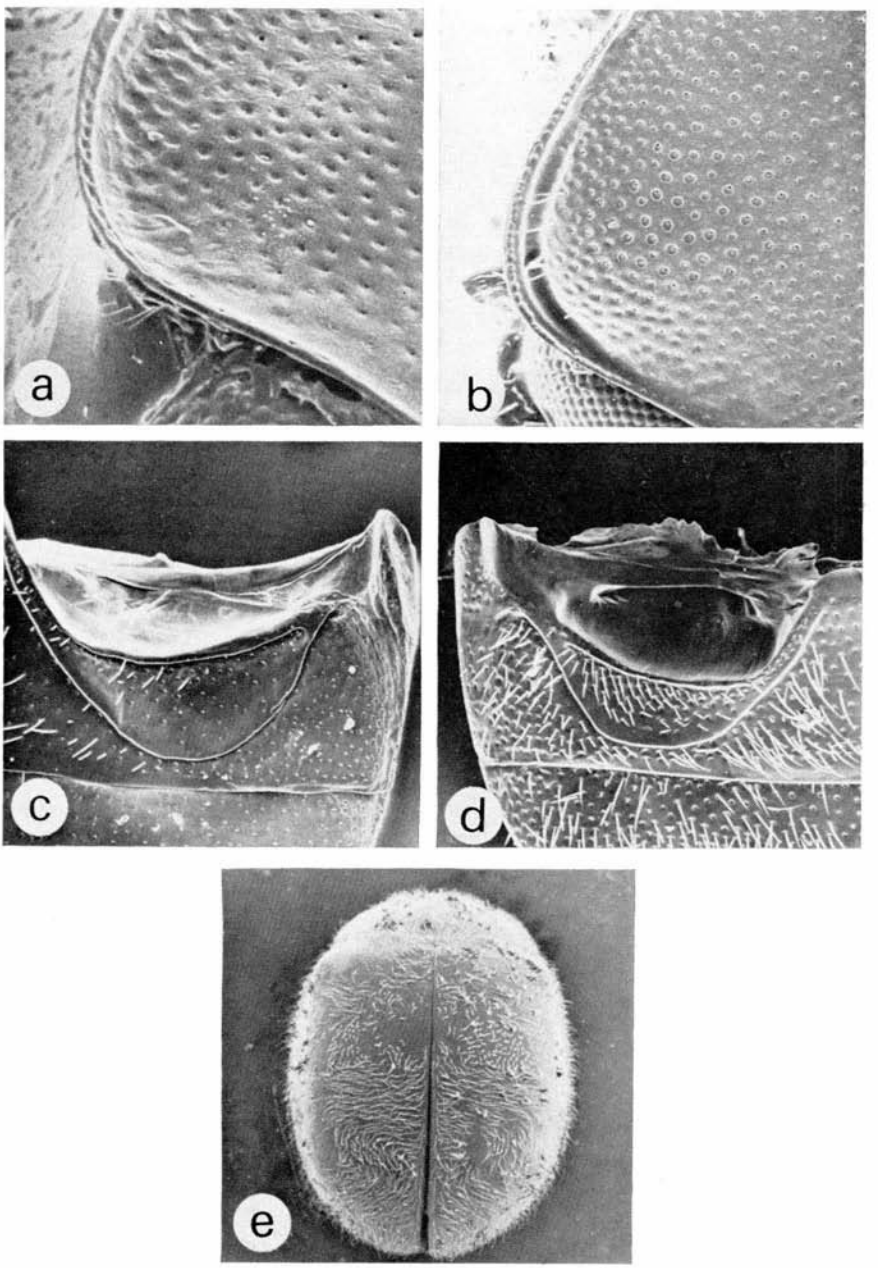

Rhyzobius species. *a–b*, anterior angles of pronotum; *a*, *R. ventralis*; *b*, *R. forestieri*; *c–d*, postcoxal plate of first abdominal segment; *c*, *R. ventralis*; *d*, *R. forestieri* ♂; *e*, *R. forestieri*, adult, showing outline and whorled setal pattern on elytra.