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Descriptions of the larva and pupa of *Mecynodera balyi* Clark, 1864, with notes on its life history (Coleoptera: Chrysomelidae: Sagrinae)

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Abstract

The larva and pupa of the sagrine chrysomelid *Mecynodera balyi* Clark, 1864 are described and life history notes provided for this species. The larva of *Mecynodera balyi* is spermophagous and feeds inside seed pods of *Pandorea*, a vine in the Bignoniaceae. This is the first record of larval spermophagy in any chrysomelid other than Bruchinae, the sister subfamily to Sagrinae. Several morphological features of the immature stages are newly recorded for the Sagrinae. The implications of these new data for systematic placement of Sagrinae are discussed.

Key words: Sagrinae, morphology, immature, spermophagy, Australia, Bignoniaceae

Introduction

The hyperdiverse leaf beetle family Chrysomelidae includes 11 subfamilies, of which Sagrinae is one of the least speciose (Reid 2017), with approximately 64 described species in 13 genera (Monrós 1960; Sekerka 2007, 2010; Sekerka & Voisin 2013). Little is known of the biology of Sagrinae or the morphology of their immature stages.

Some information on life history and immature stages is available for two sagrine genera. *Sagra* Fabricius, 1792, is widespread in the old world tropics and includes more than a third of all Sagrinae species. *Sagra* species are large, often brightly coloured, and at least one is an occasional crop pest, so their biology is reasonably well understood, if little documented (Maulik 1941; Kalshoven 1951; Tandon *et al*. 1975; Tayade 1978; Jolivet & Hawkeswood 1995; Li *et al*. 2004; Katsuki *et al*. 2014; Lee 2015; O'Brien *et al*. 2017). The larvae of *Sagra* form large stem galls, in a wide variety of hosts, and pupate within the galls, with the adults chewing their way out of the host. Larvae and pupae of this genus have been illustrated, but only incompletely described. The larva of the South American genus, *Atalasis* Lacordaire, 1845, has been described (Monrós 1955). This also forms a larval stem gall, in Malvaceae, but it is not known if pupation is internal. The larval biology of the remaining genera of Sagrinae is unknown. The stem-mining behaviour of *Sagra* and *Atalasis* is in stark contrast to the larval behaviour of Bruchinae, the sister taxon of Sagrinae (Reid 1995, 2000, 2014; Haddad & McKenna 2016). Bruchinae larvae are seed pod inhabitants, where they are spermophagous (Kingsolver & Pfaffenberger 1980; Morse 2014). This biology has been observed in almost all Bruchinae, including *Rhaebus*, considered the most basal or plesiomorphic species (Morse 2014). The single known exception, a larva mining in stems of Apiaceae, is a species in a relatively derived taxon, *Bruchidius* Schilsky, 1905, whose other species are spermophagous (Morse 2014). Stem mining in Bruchinae is evidently derived from spermophagy (Kergoat *et al*. 2008; Morse 2014). Spermophagy has not been recorded in any other member of the Chrysomelidae and therefore has been considered a trait unique to the Bruchinae (Jolivet & Hawkeswood 1995; Leschen & Beutel 2014, particularly chapters 2.7.1–2.7.12; Reid 2017).

The greatest morphological diversity of Sagrinae is in Australia (Monrós 1960; Lawrence & Reid 2014), but so far very little is known of the biology of the Australian taxa. A first instar larva of an unknown genus and species of Australian sagrine was illustrated from larvae that hatched in an earth covered egg mass attached to a myrtaceous shrub in central Western Australia (Reid 1995). Only adults of *Megamerus* McLeay, 1826 have been collected in the same area (Terry Houston, *pers. com*., December 2016), so this larva may possibly belong to *Megamerus*, although it seems unlikely that such a small larva belongs to such a large beetle. Larvae from such egg masses might be either

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stem or root mining. Pupae of species of *Mecynodera* Hope, 1840 and *Polyoptilus* Germar, 1848 have been discovered in cells in soil (Lawrence & Reid 2014), but larvae of these genera are hitherto unknown.

The limited available information on behaviour of adults of Australian Sagrinae (except *Sagra*) provides little clue to the hostplants of the larvae. Adults are most commonly collected at light and few specimens in collections have any biological data. Label data indicate adults are associated with flowers and may feed on pollen. Some species may be restricted to flowers of certain plant genera or families but others are certainly polyphagous. The senior author has observed about 20 *Diaphanops westermannii* Boheman, 1845 in southwest Western Australia feeding only on *Melaleuca* flowers, family Myrtaceae, at a coastal dry heathland locality (Sugarloaf Rock). However, no other host records are available for this relatively common species in Western Australia. *Carpophagus banksiae* Macleay, 1826, has been collected on *Angophora* flowers (label data in Australian Museum) and by the senior author on *Leptospermum* flowers, both in the family Myrtaceae. *Carpophagus banksiae* was so named because it was "said to be found on *Banksia*" (Macleay 1826: 447), family Proteaceae. There are no additional records for this plant host (despite considerable searching by the senior author) and this seems to have been an accidental association. Very few Australian chrysomelids feed on Proteaceae (Reid *et al*. 2009; Reid 2017). The single occurence of *C. banksiae* on fronds of a cycad (*Macrozamia*) "in some numbers" (Walker 1906: 23) is also the only record of this association and it does not record feeding. Walker's report has provided much wishful thinking about 'primitive' hostplant associations (Crowson 1981). From the above slight evidence, adults of *Carpophagus banksiae* may preferentially feed on flowers of Myrtaceae but the larval host remains unknown. In contrast, adults of *Mecynodera coxalgica* (Boisduval, 1835) have been observed at, or collected on, several unrelated flowers, including *Acacia* (Fabaceae), *Lomatia* (Proteaceae), *Xanthorrhoea* (Asphodelaceae), unidentified Elaeocarpaceae, Myrtaceae and exotic weeds, such as *Asclepias* (Asclepiadaceae) and *Coreopsis* (Asteraceae) (Jefferies 2010; Lawrence & Reid 2014; Richter 2017). Nothing is known of the biology of the remaining sagrine genera in Australia.

The report presented here is based on the discovery of an Australian sagrine genus breeding in a garden near Sydney.

Observations

The senior author has developed a small 'native' garden in Helensburgh, NSW (34º10'S 150º 59'E), on the southern edge of Royal National Park and within 300 m of a rainforest gully in that park. Several commercially sourced *Pandorea* vines (family Bignoniaceae) were planted in the garden in 2004, including both *P. jasminoides* and *P. pandorea* (the latter including cultivars 'ruby belle' and 'snow bells'). There is some confusion about the status of these two *Pandorea* species in the Helensburgh area. Online websites (Atlas of Living Australia 2019; Australian Virtual Herbarium 2019) indicate that both species occur near Helensburgh, but regional botanical treatises are uniform in excluding *P. jasminoides* from the native flora of this area (Hnatiuk 1990; Carolin & Tindale 1993; Mills & Jakeman 1995; Howell & Benson 2000; Robinson 2003; Harden *et al*. 2007), placing its native range north of 31º30'S (about 300km north of Helensburgh). Therefore only *P. pandorana* is native to the area. The garden *Pandorea* plants have produced abundant seedlings, particularly of *P. pandorana*, which is now well-established throughout the garden. *Pandorea* is typical of tribe Bignoniae, family Bignoniaceae, with deep bell-like flowers and large seed pods densely packed with flat winged seeds, in two valves either side of a stiff seminiferous column (Casoti *et al.* 2016; Stevens 2017).

Plants in the garden are intermittently inspected, beaten or swept for Chrysomelidae. In late December 2014 and early January 2015, eight adults of *Mecynodera balyi* Clark, 1864, were collected by beating one patch of *Pandorea pandorana* vines, dominated by the 'snowbells' cultivar (Fig. 1). At this time only foliage was present, the flowers and seed pods having dehisced. Four beetles were kept alive for 2 weeks on cut stems and foliage of *Pandorea*, but failed to eat anything, or lay eggs. It was assumed that the larval habitat of these sagrines would be in stems, similar to *Sagra* and *Atalasis* (Monrós 1955; Jolivet & Hawkeswood 1995), therefore the stems of all plants in the vicinity of these beetles were regularly checked for possible gall development and for egg masses. Nearby mature plants included the vine *Hibbertia scandens* (Dilleniaceae), and 2–3 metre high bushes or small trees of *Callitris* (Cupressaceae), *Leptospermum* (Myrtaceae), *Melaleuca* (Myrtaceae), *Syzygium* (Myrtaceae), *Tristaniopsis* (Myrtaceae) and *Cupaniopsis* (Sapindaceae). All of these plants are native to the area within 10 km radius of the garden. No stem galls were seen.

FIGURE 1. Male *Mecynodera balyi* Clark, 1864 on *Pandorea pandorana* leaf, Helensburgh, NSW, October 2018.

In the Helensburgh area, *M. balyi* is otherwise only known from a single specimen beaten from rainforest vegetation at Red Cedar picnic area (34° 11’S 151° 01’E), Royal National Park, 2.5km from the Helensburgh garden (in Australian Museum, Sydney). *Mecynodera balyi* is a relatively rarely collected species and seems restricted to rainforest localities, from the Nowra area north to the Bunya Mountains, Queensland. Another species of *Mecynodera*, *M. coxalgica* is more frequently collected in the area. There are several specimens of *M. coxalgica* in the Australian Museum from Helensburgh (34° 11’S 151° 01’E) and also nearby Darkes Forest (34° 13’S 150° 54’E), Mount Westmacott (34° 08’S 150° 58’E), Woronora Dam catchment (34° 12’S 150° 54’E), Waterfall (34° 08’S 150° 59’E) and Royal National Park. Dumel (cited by Clark 1864) claimed that both species were collected together, but they do not appear to have been collected together since then. The only other sagrine in the area, *C. banksiae*, is a rarely collected species on flowering Myrtaceae in the dry heathland or woodland of Royal National Park, with the nearest collection site more than 5km from the garden.

In November 2015 and November 2016, a few mature seedpods of *Pandorea pandorana* were observed to have circular exit holes, just before they dehisced and dropped. No insects were found in association with these holes and they were not investigated further as they were thought to be caused by a lepidopteran or weevil.

In September 2017 there was prolific flowering of *Pandorea pandorana* in the garden. Flowers and foliage were beaten for insects generally but no *Mecynodera* were seen. In November 2017 it was obvious that many seedpods of *P. pandorana* had exit holes, more than in previous years (Fig. 2). The pods with exit holes were filled with frass from destroyed seeds and the seminiferous column, but shed larval insect cuticle was absent (Figs 3–4). The identity of the culprit was not obvious from examination of the empty pods. Therefore 131 mature and externally complete seedpods were collected from 11 to 23 November 2017 and split open to determine the causative agent (Table 1). 31% of the seedpods contained a single sagrine larva (Figs 5–6), which, by association with the adults in the garden, was considered to be that of *Mecynodera balyi*. The larva was identified as sagrine by its C-shape, well-developed legs, and deeply inserted and parallel-sided head capsule (Figs 7–9).

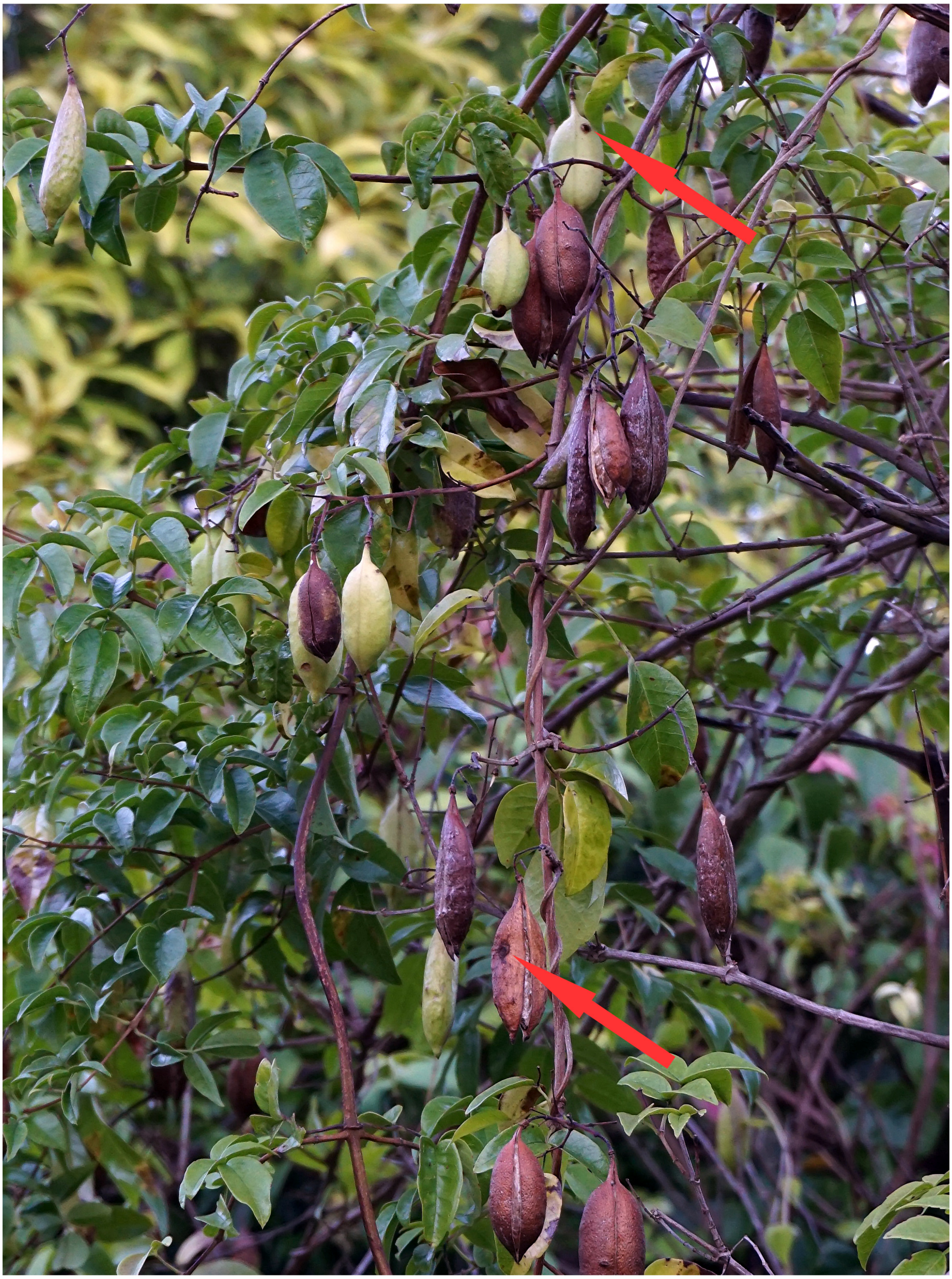

FIGURE 2. Mature and maturing *Pandorea pandorana* pods, Helensburgh, NSW, xi.2017. Arrows show exit holes.

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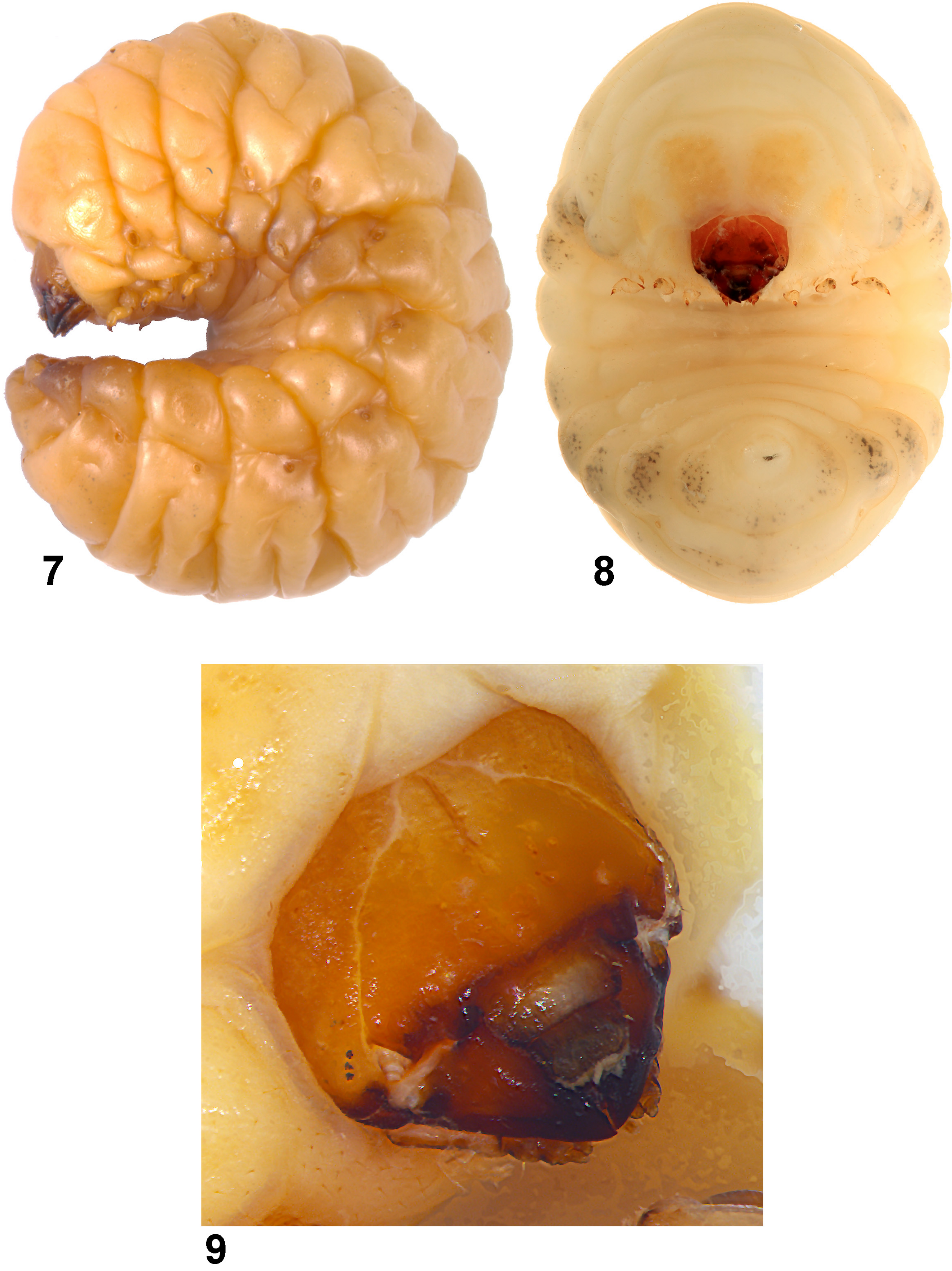
FIGURES 3–6. *Pandorea pandorana* pods: 3, unopened, with exit holes; 4, opened, with chewed contents, Helensburgh, NSW, xi.2017. 5–6, Pandorea *pandorana* pods opened, with small early instar larvae of *Mecynodera balyi* Clark, 1864, Helensburgh, NSW, xi.2017.



FIGURES 7–9. Late instar larva of *Mecynodera balyi* Clark, 1864. 7, lateral; 8, ventral; 9, oblique view of head capsule.

10 of the sagrine larvae collected on 11 November 2017 were kept alive, in their pods. The pods had been split open to confirm presence of a larva, then the two halves were bound together with elastic bands. They were placed in the bottom of a large polythene box packed with the contents of pods from which larvae had been extracted (seed masses, larval frass and the woody walls of the pods). The box was kept in a dark cupboard and its contents were sprayed with water weekly, to prevent dessication (the ambient temperature reached 36ºC during the first 4 weeks). The larvae were checked weekly at first. They emerged from the decaying pods and wandered around the bottom of the box, making tunnels in the decomposing debris. None produced pupal cells. All were still alive but quiescent on 23 December 2017. Some larvae returned to the inside of their pods via the exit hole they had created. By 14 January 2018, two had died, possibly from fungal infection or dessication. There were still eight living larvae, all apparently quiescent. Two were still inside rotting pods, although by this date all pods had split and fallen off the *Pandorea* plants in the garden. The pod shells provided a moister environment than the loose debris in the box, so two of the loose larvae were placed inside pods, with debris added to fill them if necessary, and the halves held together with elastic bands. Three larvae were preserved at this time because they were moribund and appeared unlikely to live. Two of the remaining five larvae were dead and mouldy on 20 January. By 29 January, 11 weeks after original collection, three larvae were still alive, still quiescent, but not pre-pupal. One was shrivelled and appeared to be dying so was removed for preservation. Six weeks later, on 11 March 2018, the two larvae were re-examined. One had pupated, without a cocoon or surrounding case, but in a slightly deformed state (one antennal theca not fully formed, one pterotheca not fully expanded) and with two different fungal spots, one of which had apparently penetrated the abdomen and killed the pupa. The other larva was dead and had become hard and opaquely white.

There was also a small larval weevil (family Curculionidae) in nine of the 131 sampled seedpods, initially identified as a species of Molytinae by comparison with larval descriptions (May 1996). Three of these larvae were kept alive in their pods, surrounded by a mulch of *Pandorea* seeds and sagrine larval frass. Between 29 January and 11 March 2018 one of the larvae had developed into a pupa and one into an adult. This adult was determined as an undescribed species of *Storeus* (subfamily Curculioninae), henceforth referred to as *Storeus* sp A, by our colleague Rolf Oberprieler. Three of the sampled seedpods contained both a sagrine larva and a curculionid larva (Table 1).

In contrast to *P. pandorana*, *P. jasminoides* did not exhibit a discrete flowering period in the garden but instead produced scattered single or small clusters of flowers from November to May. It was not observed to produce pods. No *Mecynodera* adults were found on this species.

In the following season, the first open flowers of *Pandorea pandorana* were observed on 30 August 2018 and during 5–25 September there was prolific flowering of the two cultivars, with either white ("Snow Bells") or orange-red ("Ruby Belle") flowers, and their hybrids. No *Mecynodera balyi* adults were found by beating or searching from 5 to 17 September. Diurnal flower visitation (pollination) by Hymenoptera was largely by the native stingless bee *Tetragonula carbonaria* (Smith, 1854) and to a lesser extent the exotic honey bee, *Apis mellifera* Linnaeus, 1758. The bees generally only visited flowers in sunshine. There were also numerous specimens of two *Epuraea* species (Nitidulidae). Flowers of *P. pandorana* were present until 23 November, three months after first flowering.

An adult male *M. balyi* was found on *Pandorea pandorana* foliage, on 18 September 2018. It was retained alive but died on 26 September. The beetle was offered leaves and flowers of *P. pandorana* but only fed on the petals, eating through the base and ends of the flower tube, not the apices of the petals. It may possibly have fed on pollen, as four anthers are attached to the inside of the tube, but the flowers also contain numerous glandular scales and hairs (Hyland *et al*. 2010). An adult female *M. balyi* was beaten off foliage on 23 September and placed with the male, but copulation was not observed. The female also only fed on flowers, not leaves. It was still alive on 2 October, when it was sacrificed. Its dissected gut appeared to be empty and its ovarioles were undeveloped. Beating and searching on foliage day and night from 18 September to 7 October did not produce any other adult *M. balyi*.

By 6 October some flowers had dehisced on the *P. pandorea* and small immature pods, 8–20 mm long, had developed. Five were dissected on 6 October 2018 to look for eggs or first instar larvae of *M. balyi*. Two had small holes and local internal necrosis but no sign of eggs or larvae. On 8 October a female *Storeus* sp. A, was collected feeding and/or drilling a hole at the base of a 12 mm pod at night. On the 8 October the ratio of empty (dehisced) flower stalks to pods showed that about 90% of flowers had not been fertilised. A coreid bug, genus *Amorbus*, was collected on 12 October, attacking a pod at night, and on 16 October a pentatomid bug, *Nezara viridula* (L., 1758), was collected feeding on a pod in daylight. 10 immature pods, 3–5 cm long, were harvested on 12 October and dissected. Three had small holes and a tiny area of internal necrosis, possibly from probing by one of the hemipterans. One pod had a tiny hole and an oval white egg inside, shaped like an inverted pear or light-bulb, with narrow base attached to the base of the seed wall. No larvae of any kind were found. A female *Storeus* sp A was seen on a pod during the day, on 13 October, and collected. 10 immature pods, 5–7cm long, were harvested on 14 October and dissected. Although eight had external spot-like scars, suggesting disturbance of the plant tissue, only four had an inserted light-bulb egg (like the above) and no larvae were present. By 18 October all four eggs had hatched and all were weevil larvae. On 5 November 11 maturing pods were dissected; four contained a single weevil larva, seven lacked larvae.

From 12–14 November 2018, 100 intact pods were sampled (Table 1) and an additional 15 shrivelled and rotted pods noted (seven with bird damage, rotting contents and chloropid fly maggots; eight black and shrivelled). Of the 100 pods, 65 lacked larvae, 24 included one weevil larva, nine included two weevil larvae and two included three weevil larvae. From 12 November onwards, pods were maturing, splitting and dehiscing. From 23–25 November 42 intact pods were sampled: 29 were empty, 11 included one weevil larva and two included one sagrine larva. During 28–30 November a further 47 intact pods were sampled: 30 were empty, seven included one weevil larva, three included two weevil larvae, seven included one sagrine larva. Two sagrine larvae were kept for rearing but died within three weeks. Two weevil larvae were kept for rearing and by February 2019 produced adult *Storeus* sp. A.

The larva and pupa of *Mecynodera balyi* are described below.

TABLE 1. Survey of contents of *Pandorea pandorana* seedpods in garden, Helensburgh, NSW, 11–19 November 2017 and 5–30 November 2018. NB in 2017 three pods had both a *Mecynodera* and a *Storeus* larva.

Contents of seedpod	number of seedpods		percentage of seedpods	
	2017	2018	2017	2018
intact seed mass	88	131	63.5	65.5
Mecynodera larva	37	9	31.25	4.5
Storeus larva	9	60	7.5	30
Total pods examined	131	200	100	100

Methods

Terminology: the naming of larval segment folds is based on the pattern of sclerites in Chrysomelinae larvae, as elucidated by Kimoto (1962)**;** larval mouthparts from comparison with Cerambycidae (Ślipiński & Escalona 2013; Svacha & Lawrence 2014), and general coleopteran morphology (Lawrence & Ślipiński 2013).

Descriptions of the larva and pupa of *Mecynodera balyi*

Larva. The following description is based on all preserved material (28 specimens). To determine the number of instars present the relatively rigid head capsule was measured at greatest width of the frons (above the antennae), using an eye-piece graticule. This produced two broad clusters, suggesting that only two instars were present in this sample (Table 2). The shed larval head capsule of the male pupa described below had a frontal width of 1.36 mm, suggesting that the 18 specimens in the upper size category (1.26–1.55 mm) were final larval instars. Whether these are third or fourth instars is not clear.

TABLE 2. Width of frons in a sample of 28 *Mecynodera balyi* larvae collected from *Pandorea pandorana* pods, Helensburgh.

Width of frons (mm)	Number of larvae
0.86–0.95	2
0.96–1.05	5
1.06–1.15	1
1.16–1.25	2
1.26–1.35	4
1.36–1.45	13
1.46–1.55	1

General appearance of living larva (compare with preserved larva, Figs 7–9): white, with reddish-brown head capsule, two or four yellowish-brown relatively strongly sclerotised patches on prothoracic dorsum and yellowish-brown legs, without pigmented sclerites; body C-shaped or at least strongly convex in lateral view but capable of straightening out and crawling on flat surfaces, elongate-ovate in dorsal view; head capsule deeply retracted in prothorax, with a membranous attachment between capsule and prothorax at about half length, just posterior to base of ecdysial lines, but head usually buried deeper than this; spiracles annular.

FIGURE 10. *Mecynodera balyi* Clark, 1864: dissected head capsule late instar larva, dorsal and ventral view, with thoracic integument and labiomaxillary complex removed.

Head (Figs 10—16): width 0.89–1.47mm across frons (widest point of head usually buried in prothorax, therefore maximum head width not measurable (Fig. 10). Whole capsule prognathous, elongate ovate with almost truncate anterior margin of frons and attenuated posterior terminating in pair of slightly separated lobes; frontal arms V-shaped, diverging from about middle of capsule, slightly sinuate, reaching antennal foramen; median endocarina reaching half length of frons, its terminus marked by a circular depression on frons; surface not strongly microsculptured; six small weakly differentiated stemmata present on each side, inner three closely clustered at edge of antennal foramen, and outer three widely spaced posterior to this; posterior half of capsule without setae; anterior of vertex with four pairs of setae around outer stemmata; frons with three pairs of median setae and one pair of anterior setae; anterior edge of frons almost flat, with pair of prominent truncate condyles articulating with mandibles; antennae small and inconspicuous, three segmented, first two segments broadly transverse, apical segment minute, size similar to apical basiconic sensillum; clypeus produced between frontal condyles and well-defined at base by frontoclypeal suture, basal half strongly pigmented with two pairs of discal setae and one pair of lateral setae, anterior half lightly pigmented and glabrous; labrum strongly sclerotised and slightly transverse, with four pairs of pre-apical setae, apical margin slightly concave; epipharynx apical margin with row of short seta-like sensilla or spicules, slightly longer at sides, central field with densely microspiculate triangular area, without obvious setae; tormae present, but fused into surface of epipharynx, from slot at junction of labrum and clypeus to base of epipharynx; mandibles symmetrical, triangularly pyramidal, base with deep acetabulum for frontal condyle on anterior edge and globular condyle on posterior edge, articulating with deep acetabulum on gena, with one seta at middle of base and one seta at middle of outer edge, scissorial edge with three slightly apically directed teeth, partly demarkated by an apicodorsal ridge; maxilla with prominent cardo and stipes, large transverse palpifer, and three segmented palp, first segment large with convex outer margin, second segment short and transverse and continuous with second, third narrow and elongate-cylindrical; mala elongate-conical, prominent, almost reaching apex of maxillary palp; labium with two distinct segments, articulated on transverse unpigmented base (gula or gulamentum) which is apicolaterally lobed on either side of labium, submentum with well-defined sutures at base and apex and narrow strip of basal pigmentation, mentum defined basally by V-shaped pigmented strip and fused apically to unpigmented prementum, with well-developed two-segmented labial palpi; chaetotaxy of labiomaxillary complex: cardo (1 lateral), stipes (2 lateral), palpifer (2 apical), gula/gulamentum (2 discal), submentum (2 discal), mentum plus prementum (2 median, 2 apical); hypopharynx with pair of long straight hypopharyngeal rods.

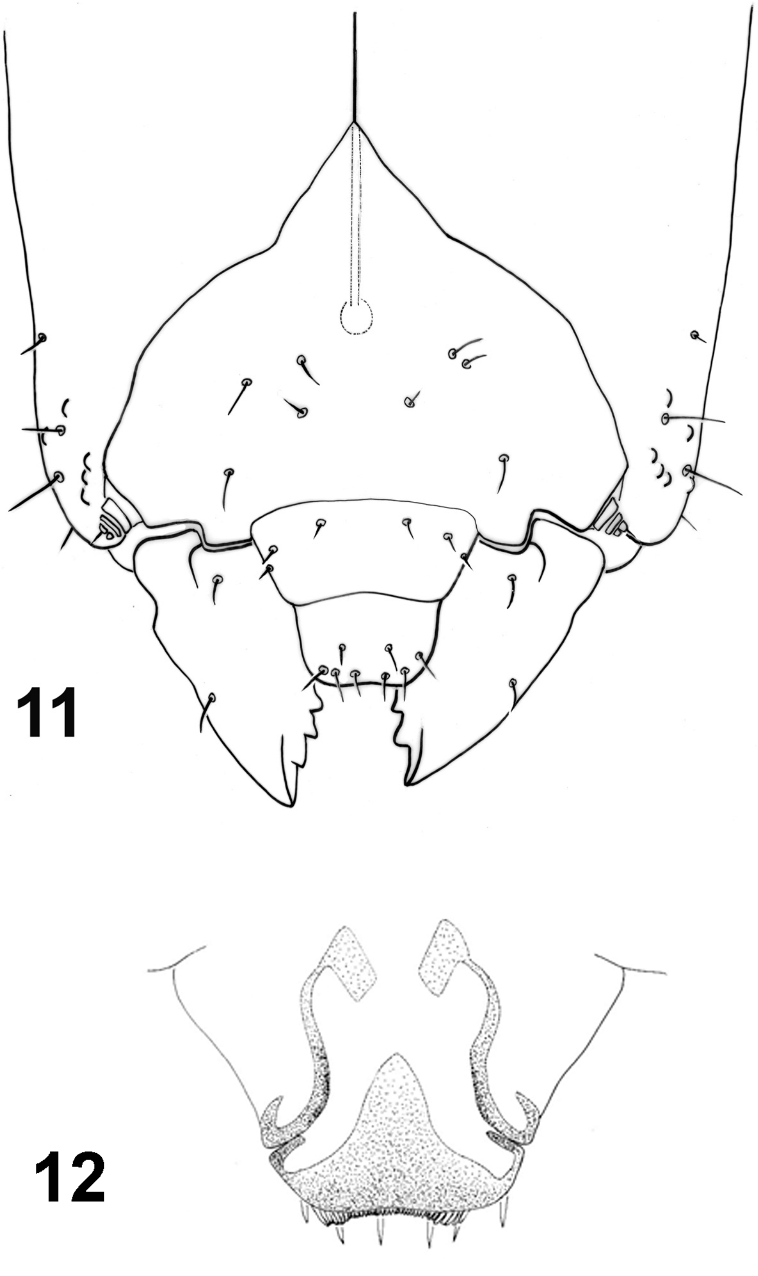
Thorax: segments with scattered erect setae on dorsal and lateral surfaces; prothorax with large undivided protergum slightly darkened and rugose on either side anterodorsally, separated laterally from legs by prominent epipleural swelling; mesothorax with a transverse dorsolateral groove isolating a convex anterior fold from the flat posterior fold, the latter laterally separated into dorsolateral, spiracular and epipleural folds by oblique longitudinal grooves; mesothoracic spiracle placed at anterior edge of segment and at lower edge of spiracular fold; metathorax as mesothorax but without spiracle, with a transverse dorsolateral groove isolating a convex anterior fold from the flatter posterior fold, this laterally divided by longitudinally oblique grooves into dorsolateral, spiracular and epipleural folds above legs, grooves often shallow or partly obliterated; legs with five well-defined segments, elongate pretarsus, tibiotarsus, femur, trochanter and coxa (Fig. 17).

Abdomen: spiracles present on segments I–VIII; segments I–V: each segment with a single dorsal median groove which splits into two grooves laterally, both joining a shallow oblique groove above the spiracular lobe, thus the area above the spiracular fold with anterodorsal fold, dorsolateral fold and large posterodorsal fold; spiracular fold large and reniform, dorsal to a narrower but laterally prominent epipleural fold, which is dorsal to a small pleural fold; VI–VII spiracular fold not clearly distinguished from dorsal folds, pleural fold ventral, obscured laterally by epipleural fold; VIII with a single transverse dorsal groove extending laterally to spiracular fold, oblique or longitudinal grooves absent, pleural folds not visible laterally; IX with single shallow transverse dorsal groove, reaching epipleural fold; X usually telescoped into IX but may be everted and dorsally visible, with apical transverse anus (Fig. 18).

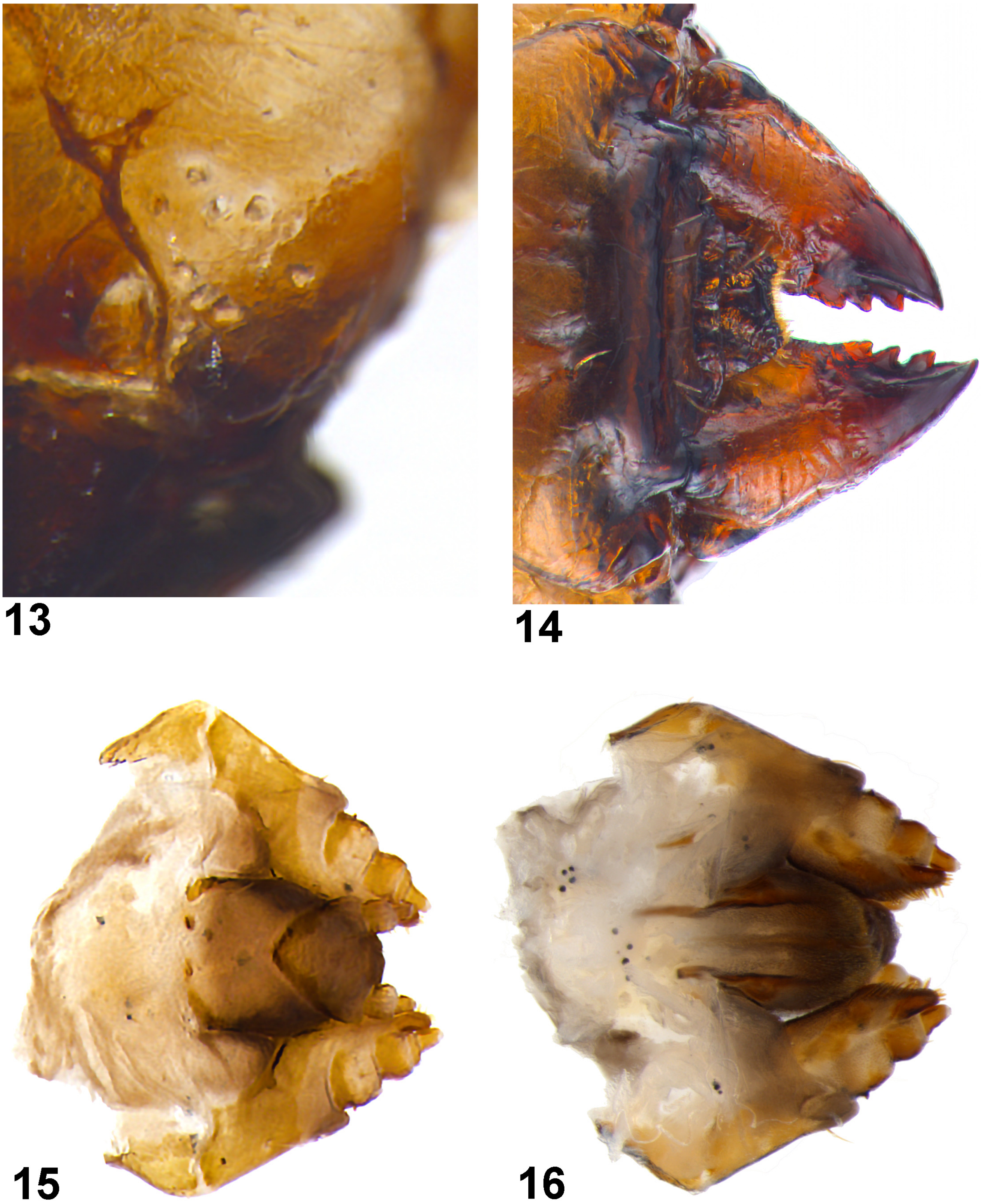
Pupa (Figs 19–25). This description is based on a single deformed specimen which is asymmetric, the right (dorsal) side largely undeformed, except apical abdominal segments. The pupa is male as it has a densely setose patch visible through the transparent pupal surface on the first abdominal ventrite (only present on adult male). The larval head capsule associated with this pupa has been retained.

Body length 10.6 mm; head width 1.9 mm; pronotal width 2.6 mm. Cuticle exarate and creamy white; head hypognathous; setae present on head, most dorsal body segments, and apices of femora; antennal theca curved around anterior and middle legs; apices of antennal segments with small tubercles (Fig. 24); abdomen with eight distinct tergites and six distinct undivided ventrites (sternites III–VIII); small clavate urogomphi placed laterally on segment nine (Fig. 25); male sternite VIII broadly rectangular, sternite IX shorter and narrower, protogenitalic sclerites present as a pair of hemispherical lobes either side of a narrow projection (Fig. 25); spiracles conspicuous and presumably functional, but decreasing in size, on abdominal segments I–VI.

Chaetotaxy. Head (Fig. 23): setae not on tubercles, three pairs in a transverse row between eyes; mandibular thecae rounded, without apical spine or seta. Thorax (Figs 21–22): pronotum: discal setae on tubercles, one transverse row of 10 (five each side) across anterior half, and one transverse row of eight (three and five each side), with each lateral seta placed anteriorly to the rest; three setae not on tubercles at each posterior pronotal angle and slightly anterior to this; mesonotum: setae on tubercles in a single transverse row of nine (six and three each side); metanotum: setae on tubercles in a pair of oblique rows, one side with 13 setae, the other nine setae, plus two setae placed poster to the middle of each row; apex of each femur with three setae on small tubercles (Fig. 24). Abdomen (Fig. 22): tergites I–V with minute setae, not placed on tubercles, approximately in a single transverse row on each tergite, I & II with four each side, III with four one side and six the other, IV with two on one side and three the other, V with one on one side. Tergites VI–IX of this specimen are deformed with strong cuticular wrinkling, obscuring setae, if present.



FIGURES 11–12. Late instar larva of *Mecynodera balyi* Clark, 1864. 11, chaetotaxy of head; 12, epipharynx.



FIGURES 13–16. *Mecynodera balyi* Clark, 1864. 13, shed cuticle of last instar larval head capsule, showing stemmata; 14, dried head capsule late instar larva, apicodorsal; 15—16, late instar larva, labiomaxillary complex, external and internal views.

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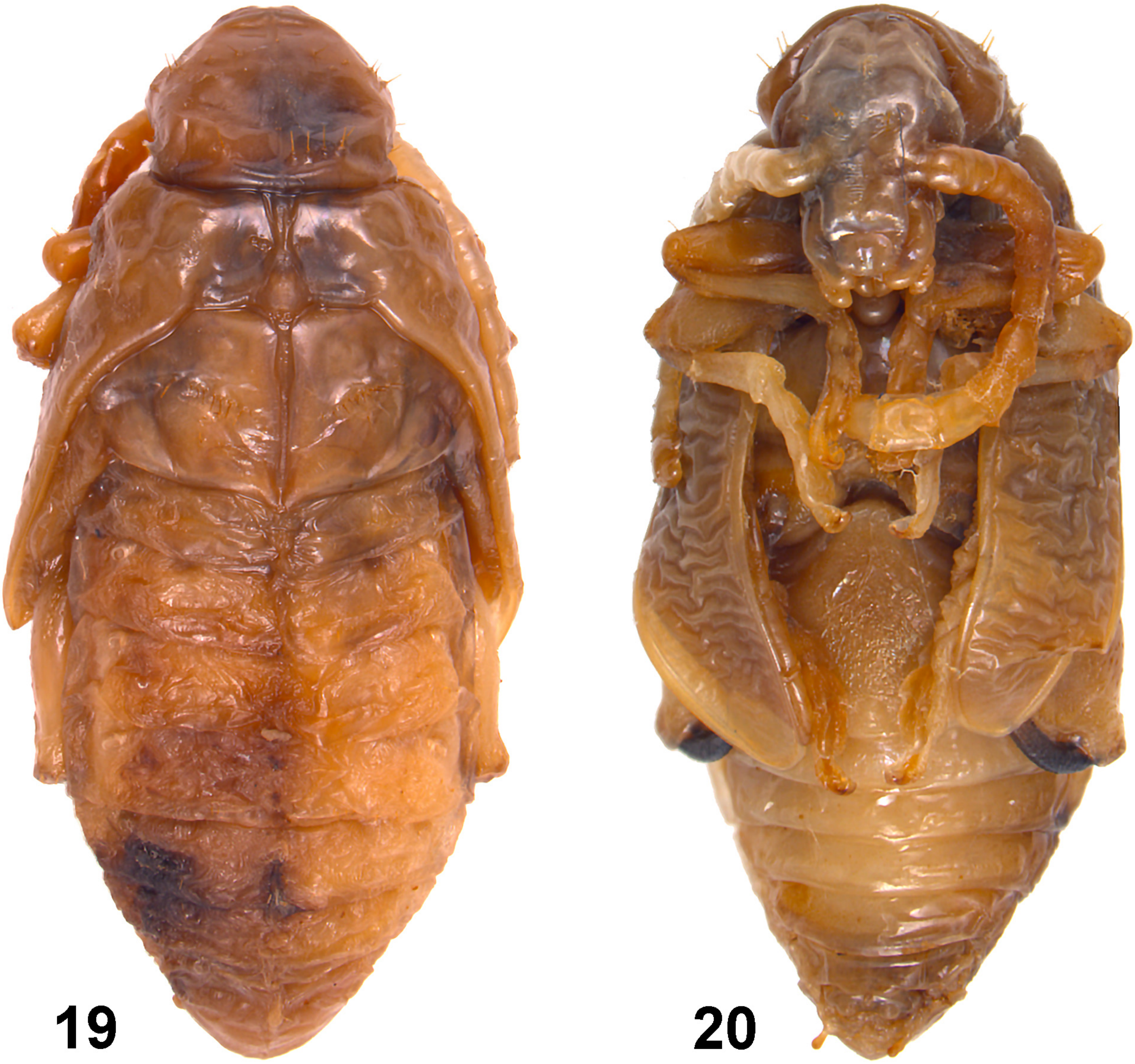
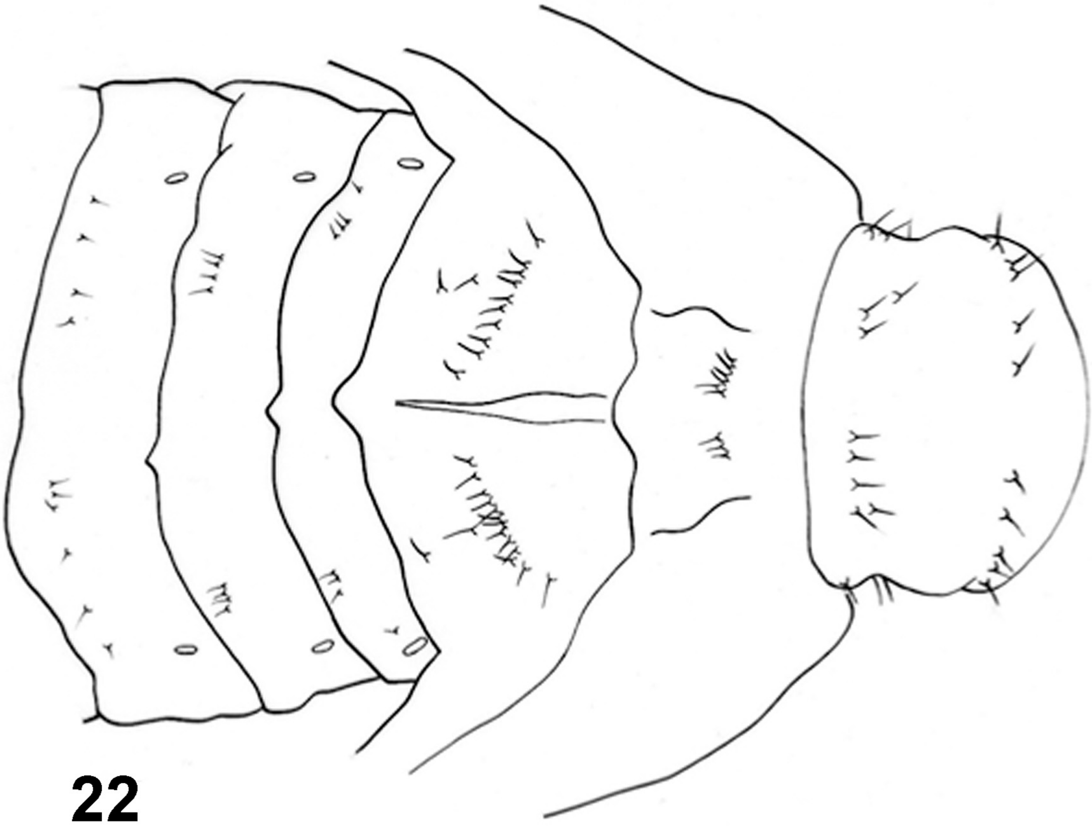
FIGURES 17–18. Late instar larva of *Mecynodera balyi* Clark, 1864. 17, prothoracic leg; 18, abdominal segments IX & X in apical view, showing anus.



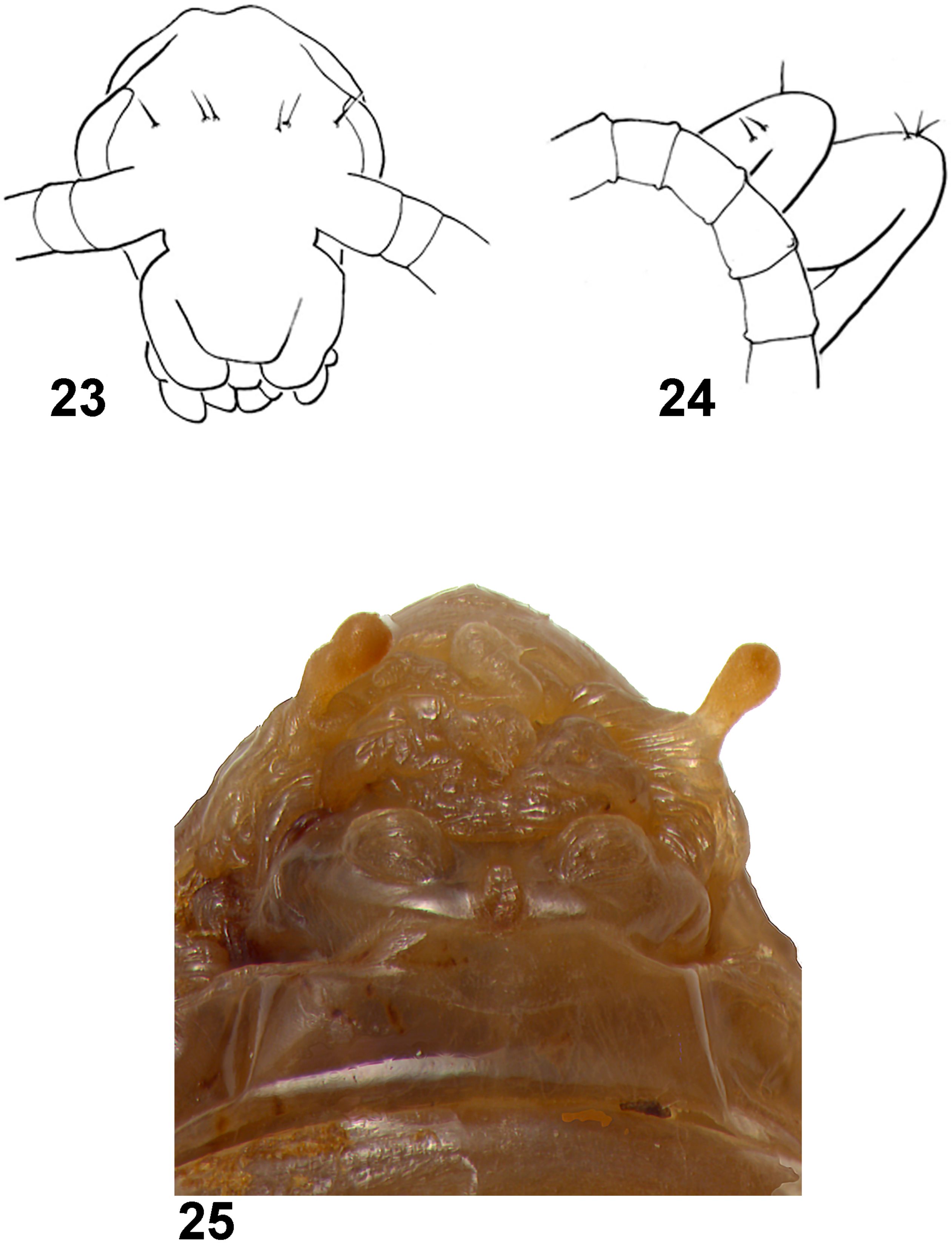
FIGURES 19–20. *Mecynodera balyi* Clark, 1864: male pupa, dorsal and ventral.

Discussion

The following features of *Mecynodera balyi* are new for the Sagrinae: 6 pairs of larval stemmata; scissorial teeth on the larval mandibles; epipharynx without setae but with distinct labral tormae; 3–segmented larval maxillary palp; pupal setae; pupal urogomphi; spermophagy within a pod; host in Bignoniaceae. The stemmata, maxillary palpi, tormae, pupal setae and pupal urogomphi are all plesiomorphic for Chrysomelidae (Cox 1996; Reid 2000) and Phytophaga as a whole (Leschen & Beutel 2014). The structure of the larval scissorial teeth is apparently unique to *Mecynodera* within Chrysomelidae, and differs markedly from the single apical tooth in previously described sagrine taxa (Mauilk 1941; Monrós 1955; Reid 1995) and in Bruchinae (Morse 2014). The epipharynx lacks median setae unlike Bruchinae, except *Pachymerus* Thunberg, 1805 (Prevett 1971; Kingsolver & Pfaffenberger 1980; Costa *et al*. 1988; Pfaffenberger 1990). Spermophagy within a pod was hitherto only known in Bruchinae in the Chrysomelidae (chapters 2.7.1 to 2.7.12 in Leschen & Beutel 2014).



FIGURES 21–22. Male pupa of *Mecynodera balyi* Clark, 1864. 21, dorsal, detail of thoracic segments; 22, chaetotaxy of thoracic dorsum.



FIGURES 23–25. Male pupa of *Mecynodera balyi* Clark, 1864. 23, chaetotaxy of head; 24, oblique lateral view of left antenna and anterior and middle leg thecae, showing chaetotaxy; 25, ventral, detail of abdominal apex.

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The life history of *Mecynodera balyi* and morphology of both larva and pupa are further evidence, if any was needed, of the close relationship between Sagrinae and Bruchinae (Reid 2014; Haddad & McKenna 2016). The data also strengthen the evidence for a single clade including these and the Criocerinae and Donaciinae, named the sagrine clade (Reid 2014). Re-analysis of the morphology matrix for subfamilies of Chrysomelidae (Reid 2000), using the new data for larval Sagrinae and Spilopyrinae (Reid & Beatson 2011), with Orsodacnidae as outgroup, results in three minimum length trees each with the clade ((Criocerinae + Donaciinae) + (Sagrinae + Bruchinae)). This arrangement has also been recovered in one of the few molecular analyses that have included Sagrinae (Bocak *et al*. 2014), although the relationships of the other chrysomelid subfamilies in that study are not supported by morphology. The tree variation in re-analysis with the new data is in the position of Spilopyrinae, which resolve as either sister to (Synetinae + Eumolpinae), or (Cassidinae), or (Cassidinae + (Galerucinae + Chrysomelinae)).

The variation of life history and morphological characters in known Sagrinae, *Atalasis*, *Mecynodera* and *Sagra*, compared with Bruchinae, intriguingly raises the issue of paraphyly of Sagrinae, implied or suggested by earlier workers (Crowson 1953; Medvedev 1971; Jolivet 1988). The Sagrinae retain almost all the plesiomorphic character states by comparison with Bruchinae and spermophagy is no longer a uniquely bruchine trait. Further work on the Sagrinae would help resolve this issue.

This is only the second record of a chrysomelid feeding on Bignoniaceae in Australia and the first for Sagrinae worldwide. The largely tropical family Bignoniaceae, with 110 genera and 790 species, is most diverse in South America (Stevens 2017) and only includes 5 genera and 13 species in Australia (Australian Plant Census 2019). In the Americas, several species of Cassidinae, Eumolpinae and Galerucinae are recorded feeding on the leaves of Bignoniaceae (Jolivet & Hawkeswood 1995), which is typical adult feeding behaviour for these subfamilies (Reid 2017). In Australia, only the chrysomeline *Johannica gemellata* (Westwood, 1849) is known to feed on Bignoniaceae (Reid 1991). Bruchinae are not known to breed in the seedpods characteristic of this plant family (Morse 2014). Bignoniaceae is one of many families in the Lamiales (Stevens 2017) and unrelated to the Malvaceae, hosts of the South American sagrine *Atalasis* (Monrós 1955), or the plant families listed for the polyphagous Palaeotropical genus *Sagra* (Jolivet & Hawkeswood 1995).

The discovery of the first known life history of an Australian sagrine breeding in a suburban garden near Sydney, exposes how little is known of the biology of Australian Chrysomelidae (Reid 2017). As a result of this discovery the senior author searched for seedpods of *Pandorea pandorea* at Red Cedar Picnic Ground, Royal National Park, where *Mecynodera balyi* had been collected, in November 2017 and 2018. The host plant is common there, but no seedpods were seen, in fact no reproductive structures of any kind, and most of the foliage was observed to be higher than 10 m above ground, on the tops of the host trees. This may explain why the biology of *Mecynodera* has not been observed previously; in the wild, *Pandorea* seedpods are often inaccessible in the forest canopy. There are three other species of *Mecynodera* (Monrós 1960) and they also occur where *Pandorea pandorana* is present, including New Guinea. The original collector of *M. balyi* noted that "it was taken (with many examples of *coxalgica*) from the twigs not the flowers of shrubs" (Damel, cited in Clark 1864: 248). This surprising observation suggests that both species have the same host. A seed pod of *Pandorea pandorana* with identical damage to that caused by *M. balyi* has been photographed near Cairns (van Raders 2002), where the only *Mecynodera* species known is *M. wickhami* Waterhouse, 1885. *Pandorea pandorana* may therefore be the host of the three *Mecynodera* species in Australia.

The vine genus *Pandorea* is widespread in Australia, in woodland and forest, and could also be the host of other sagrine genera.

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