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Biology of *Aproida balyi* Pascoe, 1863 (Coleoptera: Chrysomelidae: Cassidinae: Aproidini) on its host plant, *Eustrephus latifolius* R. Br. ex Ker-Gawl (Asparagaceae) in Australia

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Abstract. Within the leaf-beetle subfamily Cassidinae (Coleoptera: Chrysomelidae), *Aproida* Pascoe, 1863 (Aproidini) from Australia has been considered a transitional genus between mining cassidines ("hispines") and exophagous cassidines ("tortoise beetles"). To illuminate this transition, a detailed study was conducted over one year of the biology of *Aproida balyi* Pascoe, 1863 on the host plant, *Eustrephus latifolius* R. Br. ex Ker-Gawl (Asparagaceae). Distribution maps of the host plant and three *Aproida* species are provided. The life cycle of *A. balyi* comprises single eggs in a foamy ootheca, three larval instars that feed openly, a pupa suspended from the larva III exuvia, and sexually dimorphic adults. The larva's green color resembling the host and the narrow body fitted to the narrowed leaf blade allow them to camouflage. They possess a single long caudal process, unlike the paired processes of most other tortoise beetles. Fecal pellets are observed sometimes on this process, but accumulation is rare and lacks the permanent structure of exuvio-fecal shields that distinguishes the ten tribes of tortoise beetles. The larvae exhibit adhesive lobes on the abdominal sternites that appear to help their locomotion, a novel feature in Cassidinae. The pupa is suspended from the larva III exuviae and together they resemble the host's pendant flower buds, suggesting mimicry. Males have the profemora and protibiae toothed. Both sexes can fly, unlike flightless *Aproida cribrata* Lea, 1929. These many morphological and behavioral findings contribute potential novel characters that underscore the aberrant nature of Aproidini within Cassidinae and point to another Australian evolutionary oddity.

Key words. Morphology, biology, behavior, defenses, mimicry, Eulophidae.

ZooBank registration. urn:lsid:zoobank.org:pub:025EBD5A-4914-47FE-A33C-1A668B2F440C

Introduction

The immature stages of insects are poorly known despite their vast diversity as a driver of success of Insects, Earth's largest group of animals. Research on immature insects has focused on problematic pests or biocontrol species and so these stages remain underrepresented in museum collections and poorly studied. Chrysomelidae

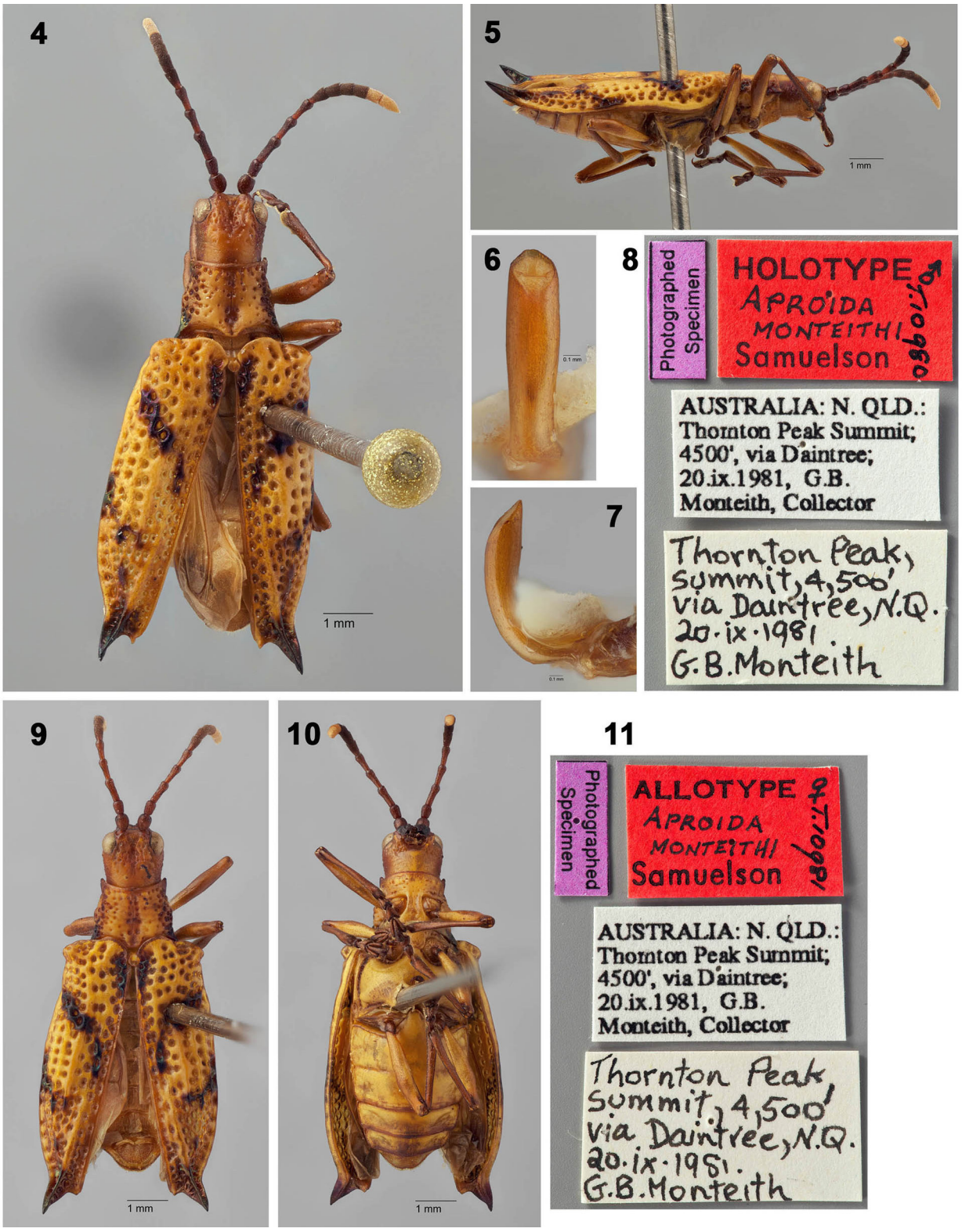
(leaf beetles) is a top megadiverse clade with over 40,000 described species (Leschen and Beutel 2014). They are primarily herbivores and specialize on diverse plant families. Many species attack food crops, garden ornamentals, and weeds and are of economic interest. Studying the ecology, behavior, and morphology of chrysomelid juveniles is crucial for comprehending Chrysomelidae megadiversity and evolution, and for developing effective management strategies against leaf beetle pests.

This paper focuses on the chrysomelid subfamily Cassidinae, commonly called leaf mining beetles (= formerly Hispinae, 'hispines') and tortoise beetles (= ten tribes; Chaboo 2007). Today, we recognize 6,321 species in 37 tribes (Borowiec and Świętojańska 2012–2023; Staines 2015). Chaboo (2007) identified major evolutionary shifts linked to ecological and morphological changes: 1) between different habitats and feeding (mining; cryptic axils; cryptic leaf shelters; cryptic phytotelmata; open exophagy), 2) between monocotyledon and eudicotyledon host plants, 3) morphology correlated with these shifts, and 4) the shield of feces and exuviae constructed by larvae. This shield, constructed with a telescopic anus and supported by caudal processes, provides protection, camouflage, and defense to the exposed cassidine larvae against abiotic (e.g., sun) and biotic (predators and parasites) threats (see Chaboo et al. 2023 and citations therein). The shield and related structures form a morpho-behavioral landmark that defines the tortoise beetle clades (10 tribes, 2,669 species) in the Cassidinae tree of life (Chaboo 2007).

Studying life cycles, especially of taxa at major evolutionary transitions, is vital for understanding evolution in any taxon. Cassidinae life cycles are not well-known overall; Świętojańska (2009) and Staines (2015) summarize documented records. We aim here to report the life cycle and biology of *Aproida balyi* Pascoe, 1863 (Tribe Aproidini) that can further illuminate the transition zone between basal 'hispines' and the derived tortoise beetle clade.

The Australian tribe Aproidini Weise, 1911 comprises one genus with three species (Fig. 1–11). Adults are diagnosed by a boat-shaped elongate body (Samuelson 1989 used "navicular") with the head and elytral apices inflected upwards (seen in lateral views, Fig. 2, 5) The elytral apices extend into posteriad projections that explain

Figures 1–3. Type specimen of *Aproida cribrata* Lea, 1929 (QM; Photos: Geoff Thompson). **1)** Dorsal view. **2)** Lateral view. **3)** Type labels. Scale bar = 1 mm. Note the left elytron appears to have been removed and glued back in position; the protibial apex has shallow notch and a small process.



Figures 4–11. Types of *Aproida monteithi* Samuelson, 1989 (QM; Photos: Geoff Thompson). **4)** Holotype, dorsal view. **5)** Lateral view. **6)** Aedeagus, dorsal view. **7)** Lateral view. **8)** Type labels. **9)** Allotype (QM), dorsal view. **10)** Ventral view. **11)** Type labels. Note fully developed wings and profemur and protibia unmodified.

the common names, 'two-tailed beetle' and 'two-tailed leaf beetle' (Chew 2012). These species exhibit sexual dimorphism with males having the tibiae slightly to strongly bowed and the femora and tibiae with slight to well-developed teeth (Pascoe 1863: 33, fig. 8; Würmli 1975: 13, fig. 15).

Pascoe (1863) erected *Aproida* Pascoe, 1863 with the type species, *Aproida balyi* Pascoe, 1863 from Australia; unfortunately, the type specimen is lost though figured in his paper. The other two species are *Aproida cribrata* Lea 1929: 239 (Fig. 1, type ♂, QMBA; Fig. 12) and *Aproida monteithi* Samuelson 1989: 603 (Fig. 4–11, QMBA) [QMBA=Queensland Museum, Brisbane, Australia]. Samuelson (1989) illustrates and keys the three species based on adult body sizes, color patterns, elytral and antennal differences and expands descriptions of the adults of *A. balyi* (based on 79 specimens), the flightless *A. cribrata* (based on the single specimen, the holotype), and the first description of *A. monteithi* (based on two specimens). Kasap (1978) included *A. balyi* in a comparative study of chrysomelid alimentary tracts. Staines (2012) presents diagnostic features and Staines' (2015) hispine catalog includes one photograph of an adult of *A. balyi.*

Aproida is considered unique within Cassidinae. Pascoe (1863: 33) commented that "This is probably the most remarkable genus of the Hispidae, wholly distinct in habit from other known species, although most nearly related to *Eurispa*." Samuelson (1989) reviewed the adult morphology and the hypotheses of possible phylogenetic relationships of Aproidini with Anisoderini Chapuis, 1875, Exothispini Weise, 1911 and Eurispini Chapuis, 1875 (Weise 1911; Würmli 1975). Chaboo's (2007) phylogenetic study recovered a relationship as (*Eurispa* + (*Aproida* + *Exothispa*)) among mid-basal Cassidinae ("hispines").

Monteith (1970) gave the first natural history notes on *A. balyi,* indicating the host plant, *Eustrephus latifolius* R. Br. Ex Ker-Gawl (Asparagaceae), the foamy ootheca, caterpillar-like exophagous larvae, and the suspended pupa resembling the plant's flower buds. Later, Hawkeswood (1987) reported *Dryomophila* [sic] (=*Drymophila* R.Br., Alstroemeriaceae) as a host of *A. balyi*, then *Alocasia macrorrhiza* (L.) G. Don. (Araceae) and *Convallaria* sp. (Convallariaceae) (Hawkeswood 2007) as additional hosts. However, Conran (1985) discarded *Drymophila* as a host based on feeding trials. Samuelson (1989) examined specimens in several museums and reported five specimens with data indicating feeding, *in copula*, and laying on *Eustrephus* leaves. Monteith (1991) determined only *Eustrephus* as the true host after years of field observations failed to confirm Hawkeswood's (1987) report of *Alocasia* or *Convallaria* as *Aproida* foodplants. Staines (2015) does not catalog *Alocasia*, *Convallaria* or *Drymophila* as hosts; we assume these plants are resting records.

Our primary objective here is to report the biology of *A. balyi* and expand on Monteith (1970). Targeting the one certain host plant, *Eustrephus*, was key to our study. Through a one-year field study and rearing program, we observed and collected all life cycle stages. We aim to examine the camouflage and mimicry conditions and the unique pupation of *A. balyi* and discuss phylogenetic and evolutionary implications.

Materials and Methods

Specimen collection was authorized under permit WIF418701617 issued by Queensland Department of Environment and Science to the Entomological Society of Queensland (Principal Investigator: C. Lambkin), Australia.

Conducted over one year spanning 2018–2019, the study involved fieldwork with collections of live wild beetles, rearing all life stages in outdoor and indoor conditions over a nine-month period, and the examining and vouchering of museum specimens. The research yielded many specimens of all life stages and significant photo-documentation including short movies of unique behaviors. Author initials used below indicate specific research contributions.

Field study. Authors VS and GM conducted the field study and rearing in AUSTRALIA: Queensland, Brisbane, Mount Coot-tha Reserve, focusing on the host, *E. latifolius*. Most observations occurred near the gold mine picnic area along the Ghost Hole Track, -27.474°S, 152.945°E, elev. 235m, where beetles are easily found. Fieldwork and collections took place on multiple dates in 2018–2019: 11 Sep. 2018, 19 Sep. 2018, 4 Oct. 2018, 11 Nov. 2018, 20 Nov. 2018, 2 Dec. 2018, 6 Dec. 2018, 9 Apr. 2019, 11 Apr. 2019, 24 Apr. 2019, mid-Sept 2022, March 2024 with additional casual visits over 2022–2023 to confirm the beetle-plant presence and activity.

Study site of *Aproida balyi* (Fig. 18–23). The Ghost Hole Track picnic area is situated in a former gold mine turned reserve with visitor facilities. The Mt. Coot-tha reserve is 7 km W of central Brisbane and spans over 1,600 hectares, featuring open eucalypt forest (= sclerophyll forest), rainforest gullies, and creek lines on shallow gravelly soil.

Taxonomic identifications. *Aproida balyi* in this habitat and host plant was previously identified by Monteith (1970). Samuelson's (1989) key separates adults of the three *Aproida* species. The identification of *E. latifolius* (Fig. 19–23) was validated using field guides (Queensland Parks and Wildlife Service 2015; Leiper et al. 2017); author MC synthesized its biology through a literature survey.

Beetle rearing (Fig. 24–27). Field caught adults were maintained on existing plants in the authors' Brisbane gardens and trained into the 3 observation cages (Fig. 24). In Monteith's garden, two plants transplanted long ago had grown large; vines were trained through holes of the cage and wild beetles were introduced into the cages for observation. Mating and oviposition behaviors of 17 wild-caught adults released in the cages were observed for a month (19 Sept–20 Oct 2018). The 29 oothecae laid in these cages were numbered (Fig. 25) as laid and subsequent hatching and larval development was observed.

Additional oothecae and larvae were collected at Mt Coot-tha during 2021–2022 and transported on cut twigs of host plant, which were maintained indoors in individual water containers (Fig. 26–27). VS tracked development of 150 individuals (Fig. 28–86) in this way with daily observations.

Egg parasites. Author GM and his hymenopterist colleague at Queensland Museum, Chris Burwell, reared parasites from the oothecae and dissected eggs to observe and collect parasitic larvae.

Determining the number and duration of larval instars. Instar number was determined firstly by direct observation assisted by the fact that shed exuvia remain attached to the leaf after molt, and by plotting head capsule width of 72 larvae (Fig. 48) using the Brooks-Dyar method (Brooks 1886; Dyar 1890). Late-stage eggs were dissected to ensure that the pre-hatching neonate larvae expanded to the same size as observed first instars.
Film documentation. Author VS used a Canon EOS 6D full-frame CMOS digital single-lens reflex camera with a Canon EF 100 mm macro lens to capture numerous photographs and films and document all aspects of the natural history (mating and oviposition, larval instars, pre-pupation, pupation, and adult emergence). Our study involved 150 live specimens from field work and rearing on transplanted plants and potted stems. Films were produced, ranging from 20 seconds to several minutes; some are available on YouTube as our supplementary data. We use a mini measuring tool for scale. In our descriptions under RESULTS below, we indicate times (T) from the start to end of a process (e.g., pupal emergence).

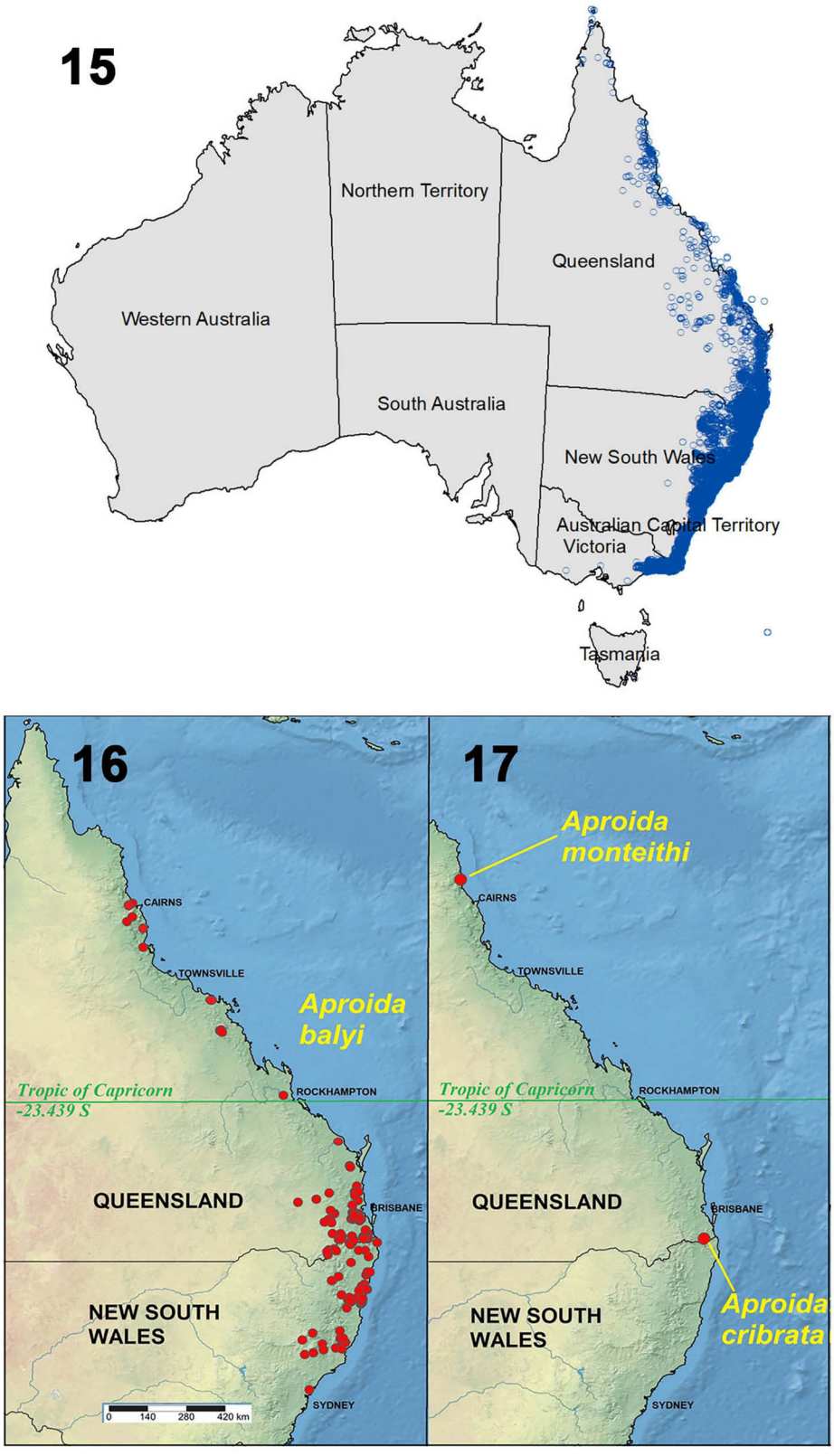
Taxonomic names. Plant names follow the Australian Plant Census (2006). Cassidinae names follow Borowiec and Świętojańska (2012–2024) and Staines (2015).

Specimens studied. Vouchers from our reared beetle study were preserved in various ways to support different analyses (70% and 95% ethanol, methanol, and Pampel's fluid). For better dissections, juveniles were dropped into hot water for a few seconds, then transferred to Pampel's fluid for fixation and storage. For cryogenic specimens, both larvae and adults were collected into 95% ethanol (DNA-grade). These vouchers are deposited at the Queensland Museum (QM), Brisbane, Queensland : QLD: 27.475°S x 152.945°E, Mt Coot-tha, 240m, Oct 2022, euc. Forest, reared ex eggs *Aproida balyi*, G. Monteith, 40438 [10 ♀ and 4 ♂ (2 ♀, 1 ♂ pinned; rest in ethanol)]; 2 ♀, 1 ♂ (in ethanol at present). The reared parasite wasps (ethanolic and pinned) are deposited also in QM. A voucher subset of *A. balyi* is at the University of Nebraska State Museum, Lincoln, Nebraska, USA (UNSM) under export permit to Registered Institution US066 according to Australian regulations for the export of biological material. Additionally, pinned adults of *A. balyi* were examined in the following museums (Codens follow Evenhuis 2023):

Australian National Insect Collection, Canberra (ANIC; 15), Adam Ślipiński
Australian Museum, Sydney (AM; 30), Chris Reid and Natalie Tees
Bernice P. Bishop Museum (BPBM; 6), Neil Evenhuis
British Museum of Natural History (BMNH; 15), Michael Geiser
National Museum of Victoria (MV; 3), Ken Walker
New South Wales Department of Agriculture (NDAA; 2)

Figure 12. Dorsal habitus of *Aproida cribrata* Lea, 1929, collected by pyrethrin spray of forest canopy at Green Mountains, Australia (Photo: Geoff Thompson and Natalie Tees, Australian Museum).

Figures 13–14. Type localities of *Aproida* species (Photos: G. Thompson). **13)** Lamington National Park. **14)** Thornton Peak from ocean view.



Figures 15–17. Distribution maps of beetle and host plant based on Atlas of Living Australia (ALA) records, museum collections and *i*Naturalist records (see Methods). **15)** *Eustrephus latifolius* R. Br. Ex Ker-Gawl (Asparagaceae) (prepared by M. Campos). **16)** *Aproida balyi*, **17)** *Aproida cribrata* and *A. monteithi* (prepared by G. Monteith).

South Australian Museum (SAM; 6), Ben Parslow
University of Queensland Insect Collection (housed now at QM; 16)
Queensland Museum (QM; 50 reared in 1999)
Queensland Dept of Agriculture and Fisheries Collection (QDPC = DAF; 21), Justin Bartlett
U.S. National Museum (USNM; 6), Floyd Shockley

Photographic records of *Aproida* specimens registered in the Atlas of Living Australia (ALA, 2024) and *i*Naturalist (2024) were checked and confirmed by GM.

Maps (Fig. 15–17). The distribution map of *Eustrephus* (Fig. 15) was generated by MC based on data from ALA (2024) which were digitized and uploaded by individual Australia collections. To map the distribution of the three *Aproida* species (Fig. 16–17), GM combined examined specimen locality records with published literature records and a subset of 'citizen science' records (ALA 2024; *i*Naturalist 2022) and used the free online map-making software, SimplMappr (Shorthouse 2010)

Parasitoid wasp attacking eggs of *A. balyi*. During the current study, GM reared or dissected egg parasitoids: Mt Coot-tha, Qld, 25.ix.2022, G.B. Monteith, dissected ex one egg of *Aproida balyi,* 13 parasitoid larvae (in ethanol): Mt Coot-tha, 17.ix.2022, ex *Aproida balyi* eggs [QM].

Morphological study. Specimens were preserved throughout the field study to understand development; for example, we preserved a newly formed pupa in ethanol to examine the attachment and suspension for the larval III exuvia. *Other body measurements.* VS observed, collected, and measured ~106 individuals over a 3-month period and monitored 44 larvae through pre-pupation, pupation, and metamorphosis in our cages. CC examined ethanolic specimens of all life stages.

Special terminology in Cassidinae. Urogomphi is an umbrella term for diverse caudal projections in unrelated larvae so cassidine researchers use "caudal process" to convey homology of tergite IX projections (Chaboo 2007). Chaboo et al. (2023) discussed "exuvia" (singular) and "exuviae" (plural) for the exoskeletons ("skins") after Snodgrass (1935) and Chapman (1982). The term "pharate" is noted here due to the retention of exuviae by tortoise beetles and to the unique pupation in *Aproida*, however it does not apply to *Aproida* whose pupa is suspended outside the larva III exuvia. *"Pupa adheraena"* is a term that applies to hanging or suspended pupa (e.g., Erotylidae: *Cypherotylus californicus* Lacordaire, 1842; Graves 1965; Hydrophilidae: *Amphiops mater* Sharp, 1873; Hu 2022).

Results

Biology of *Eustrephus* R.Br. 1809 (Asparagaceae) (Fig. 19–23)

Asparagaceae comprises 114 genera with about 2900 species. *Eustrephus* R.Br. 1809 is a monotypic genus with the species, *Eustrephus latifolius* R.Br. This is native to Australia, New Caledonia, and Papua New Guinea (GBIF Secretariat 2023), and is extensively distributed through the eastern coast of Australia (Australasian Virtual Herbarium (AVH) 2021) where it occurs in dry and wet forests and heaths in Queensland, New South Wales, and Victoria, growing well in semi-shade (ANPSA 2021). Its altitudinal range is from near sea level to 900 m (Australian National Botanic Gardens 2024). It has been recorded as a non-native species in New Zealand, continental USA, and Hawai'i (GBIF Secretariat 2023).

Eustrephus latifolius typically thrives in shaded positions, either as small perennial climbers or as scrambling ground cover (Fig. 18–23). It is an evergreen climbing vine (reflected in the genus' etymology) with lance-like narrow leaves that have prominent longitudinal veins (Fig. 21, 23–24, 47) (ANPSA 2021). It is hardy in various soils and climates and withstands extended periods of dryness once established; the species is not excessively vigorous and unlikely to smother other plants (ANPSA 2021). In Australia, it is sold as a native groundcover and potted garden plant (e.g., Growing Illawara Natives 2024) and is commonly called wombat berry or orangevine (Australian Native Plants Society 2024).

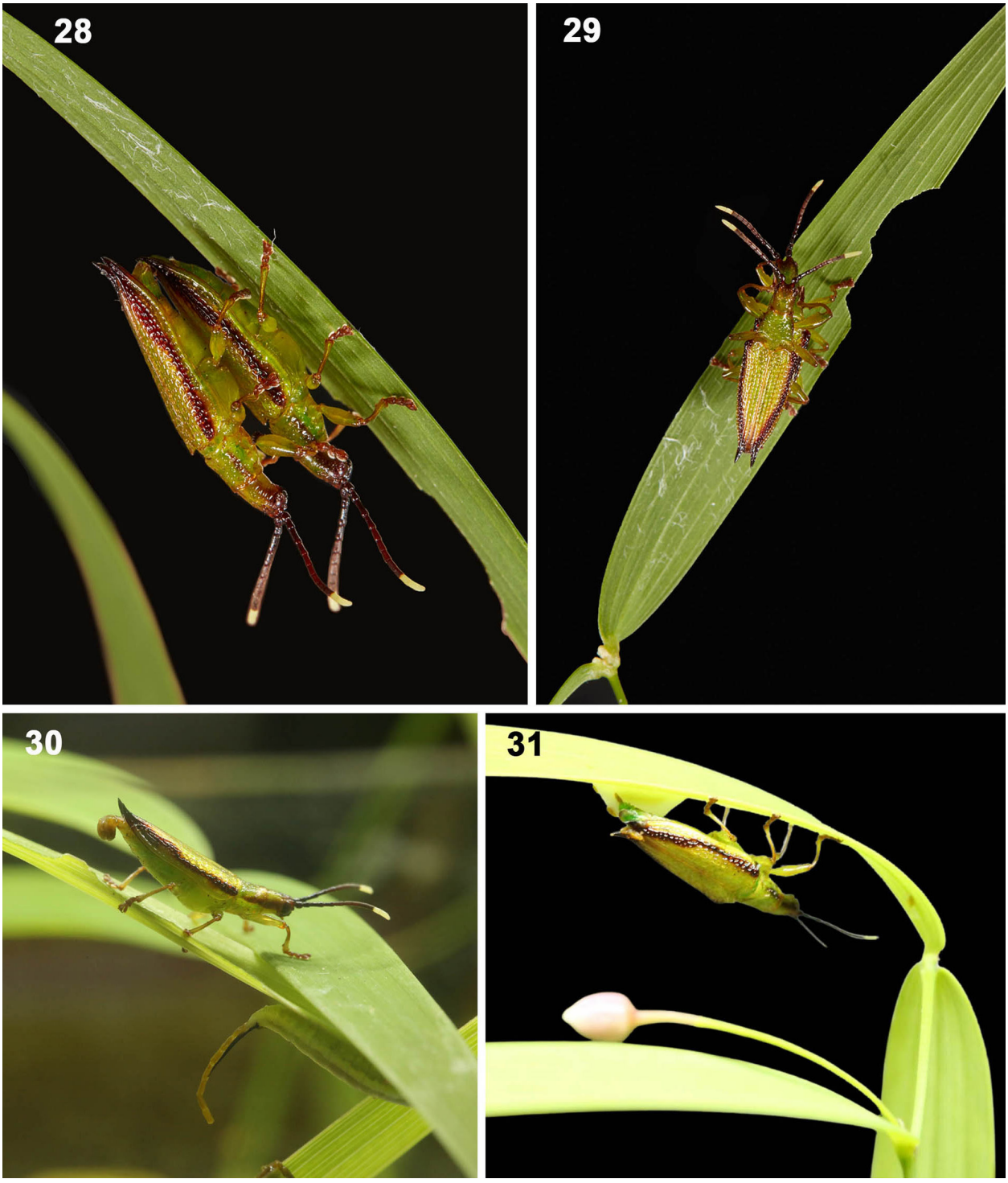
The small flowers (Fig. 22–23; 10–18 mm diameter; PlantNET 2023) appear in clusters of a few flowers from September to November (Native Plants Queensland 2023). These are fly-pollinated (Diptera: Drosophilidae, Mycetophilidae, Sciaridae; Vislobokov 2017), like other genera in this family. The fruit (Fig. 23) is about

Figures 18–23. Habitat and host plant of *Aproida balyi* Pascoe, 1863 (Photos: V. Sandoval, except where noted). **18)** Mt Coot-tha Forest Reserve, Queensland, Australia, open *Eucalyptus*forest. **19)** *Eustrephus latifolius* R. Br. Ex Ker-Gawl (Asparagaceae), vining around small stems. **20)** Vine on forest floor. **21)** Intact leaf and beetle larva-chewed leaf. **22)** Pinkish white flowers appear in spring to summer (see inset). **23)** Vine with flowers (mostly unopened) and fruits (orange color, black seed) (Photo: M. Marathon, Etna Caves National Park, via Wikimedia Commons).

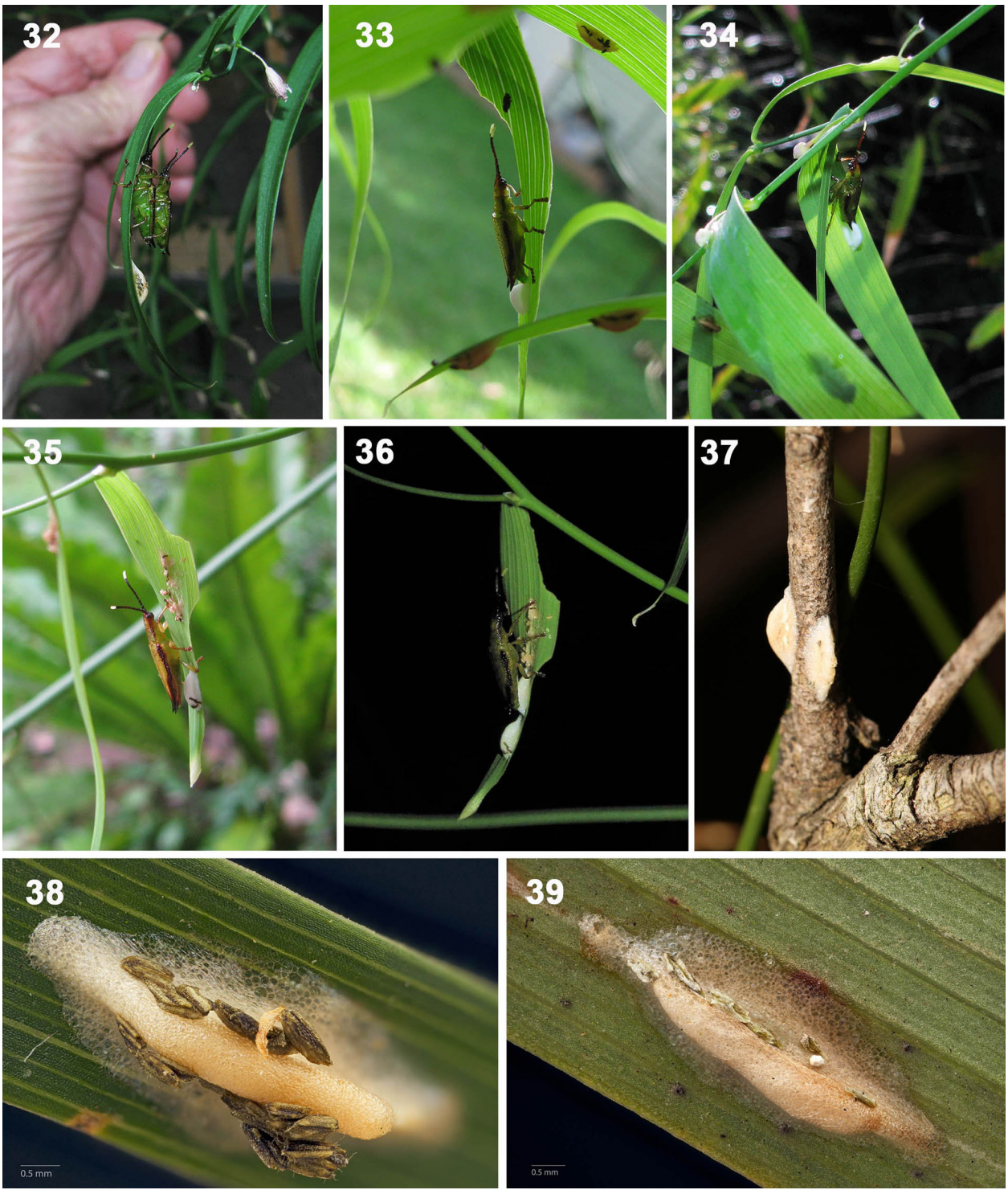
Figures 24–27. Rearing *Aproida balyi* on *Eustrephus latifolius*, October 2018, Brisbane, Australia (Photos: V. Sandoval). **24)** Cages constructed for outdoor observations. **25)** Close up of plant vine in cage with eggs laid by the adults collected at Mt. Coot-tha and released into cages in St Lucia, QLD. **26)** Cut vine sections with eggs and immatures collected at Mt Coot-tha and maintained indoors to document beetle development. **27)** Larva with measuring scale.

10–20 mm diameter in size and has a green color that turns to an attractive orange as it ripens (Fig. 23). Fruits have white arils around the black seeds and are dispersed by birds. The tubers are eaten by wombats, giving this plant its popular name, 'wombat berry'; tubers are also eaten raw or baked by indigenous Aboriginal Australians (Maiden 1889; Simpson 2018). Several Lepidoptera caterpillars feed on the plant (Simpson 2018).

Laferrière's (1995) review of nomenclature found *Eustrephus* mentioned in very few articles. French (1977) included it under the synonym *Luzuriaga latifolia* in a comparison of vine growth relationships. Crous et al. (2019) indicated *Phyllosticta longicauda* (Fungi) as an endophyte from healthy *Eustrephus latifolius* leaves, while Shivas and Alcorn (1996) listed *Asterina* spp. as microfungi on the leaves. Sun and Liddle (1993) compared trampling and untrampled effects. Benson and Picone (2009) documented an increase in this species, as well as other vines, in a 30-year vegetation monitoring study of a Sydney bushland area. Kim et al. (2016) presented the complete plastid genome of *E. latifolius* to enable the study of chloroplast genome evolution in Asparagales for which only Orchidaceae was mapped.



Figures 28–31. Adult of *Aproida balyi*. **28)** Mating pair, lateral view. **29)** Dorsal view. (Photos: G. Thompson). **30)** Female preparing to oviposit (larva on venter of leaf). **31)** Female ovipositing (Photos: V. Sandoval).



Figures 32–39. Oviposition in *Aproida balyi* (Photos: V. Sandoval, except where noted). **32)** Females can begin ovipositing while still attended by male. **33)** Female covering egg with soft oothecal foam; she moves forward and back over the egg in the process of depositing the foam. **34)** Female uses elytral spines to shape oothecal foam into narrow dorsal ridge (Photo: Geoff Monteith). **35)** Female depositing a new egg capsule immediately after consuming an older egg capsule on the leaf in front of her. **36)** Female deposits a second new egg capsule on same leaf (Photos: G. Monteith). **37)** Oothecae on old dead stem. **38)** Ootheca decorated with fecal pellets. **39)** Older ootheca with dried, shrunken fecal pellets (Photos: G. Thompson).

In earlier studies of *Aproida*, its *Eustrephus* food plant has been attributed to the plant families Liliaceae (e.g., Monteith 1970; Conran 1985) or Philesiacae (e.g., Hawkeswood 2007). Modern botanical taxonomy places it in Asparagaceae.

Natural history of *Aproida balyi* Pascoe, 1863

This life cycle is somewhat typical of exophagous Cassidinae since all stages live openly on the plant. Adults emerge in the Australian spring to feed on young foliage and mate. Single eggs are deposited mainly on the underside of the leaves and are enclosed within a protective ootheca. Unlike typical tortoise beetles with five instars (Chaboo 2007), these larvae pass through three instars. Our observations of the caged population during the Australian spring–summer season revealed three generations.

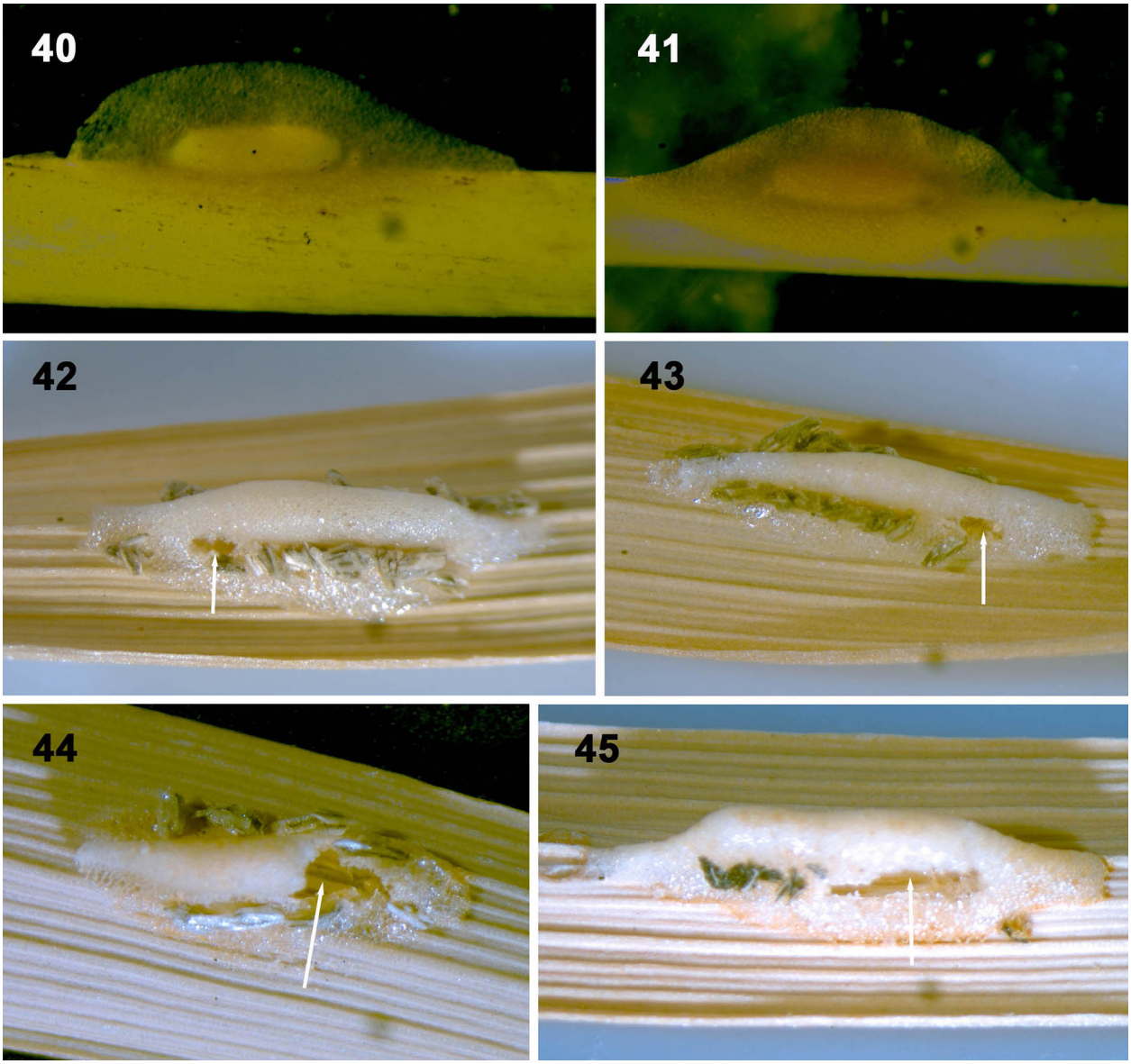
Author VS followed 44 larvae from oviposition to adult emergence during 19.IX.2019–1.XII.2019. A typical life cycle, from oviposition to adult is about 24–35 days. Eggs last 8–9 days before hatching. We obtained all larval instars, pupae and adults from caged rearing and determined the larval duration of 20–24 days: instar I lasts 5–6 days; instar II lasts 4–5 days; instar III lasts 6–10 days. The pre-pupa phase is 2–3 days. Pupation occurs about 1 month (30 days maximum observed) after egg hatching. Pupation lasts ~5–9 days before the teneral adults emerge. Below we report behavioral and morphological observations for each stage.

Female ovipositional behavior (n = many; Fig. 28–29, 32; Supp. Film 1). The female typically grasps both edges of the narrow leaf and then oviposits a single egg directly to the leaf surface. The leaf is not prepared (e.g., no gnawing to create a depression). As the egg is being extruded, the mother almost simultaneously secretes a foam to cover it. The egg is never fully exposed and is soon entirely enclosed in the frothy foam (Fig. 30–31). The male may sit atop the female (Fig. 32) while she is ovipositing. Females take over an hour per oviposition (egg laying and oothecal secretion). She walks backwards and forwards several times, producing foam and builds it up into a low mound over the egg. Her ovipositor valves appear to squeeze and shape the foam gently during secretion (Fig. 33). She moves her abdomen round to the sides to deposit more foam. Once the foam is in place, completely covering the egg and sealing the base to the substrate, but is still wet, the female uses her elytral spines, going back and forth, to shape it into a narrow upright keel (Fig. 34). After foam is deposited the female remains with her posterior over the foam mound and methodically deposits about 6–10 elongate blackish fecal pellets (each of which is a 'bite' of fibrous, partly digested leaf material) on the sides of the foam mound (Fig. 37). She walks back and forth slightly during this process and swings the tip of her abdomen down on each side of the mound to place them methodically in position. Numbers of pellets per egg vary from 2–3 to up to about 10 per egg. The ootheca-deposition substrate is usually the abaxial surface of the leaf lamina, but some are also attached to the stem of the vine or even to old dead stems on old growth (Fig. 37); these latter two are curved surfaces compared to the flattened leaf lamina. Late in the breeding season when adult numbers are high, eggs may be laid in large numbers. In one of our caged plants, we counted 41 oothecae from multiple females on a branch; oothecae were found on the leaf blade (up to four per leaf) and both leaf surfaces and the stems. Some oothecae were almost touching (Fig. 37) or proximate but on opposite sides of the same stem (Fig. 37).

Ootheca (Fig. 38–45; *n*=300+ observed; *n*=10 measured, dried: 4–7mm L, 1–2mm W). The shape is distinct (Fig. 38–39), narrow, elongate, and ovoid in dorsal aspect; in lateral aspect, it has as an elongate ridge with pinched-in sides (Fig. 40–41). Most frequently there are ~6–10 elongate fecal pellets attached on both sides (Fig. 42–45); pellets are separated, or touching (of 10 dried intact specimens, only one lacked fecal pellets). The oothecal foam has distinct bubbles (Figs 38, 39) when deposited and these remain when the foam dries.

The female's investment in oothecal production likely protects the eggs from abiotic and biotic dangers. After hatching, the remnant ootheca (Fig. 44–45) can last a long time on the plant; torn pieces of 'foam' are still apparent season after season. We observed females eating other oothecae before ovipositing on that leaf (Fig. 36–37), suggesting female-female competition despite the high density of ootheca observed on leaves and on the plant.

Egg (*n* = >300 observed; Fig. 40–41). We observed only one egg being deposited per ootheca, the original observations by Monteith (1970). GM dissected over 70 oothecae and never found more than a single egg; CSC found only one egg in seven dissected oothecae; in ethanolic specimens, the single egg is plain to see through the oothecal cover (Fig. 40–41). It is elongate, oriented lengthwise within the ootheca. In dried dissected oothecae,



Figures 40–45. Ootheca of *Aproida balyi* (Photos: C.S. Chaboo), (arrows indicate exit hole). **40–41)** Single eggs. **42–43)** The exit hole is small, towards one end. **44–45)** Enlarged exit holes in old oothecae still on plant.

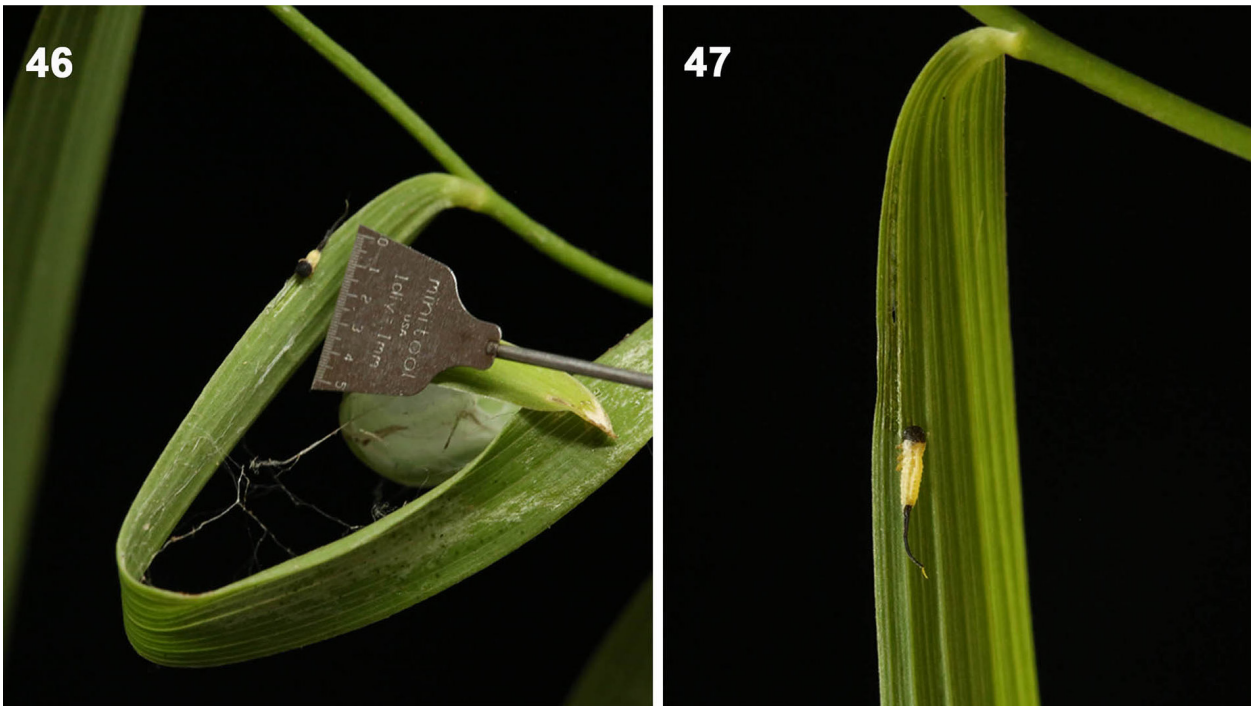
the hatched egg membrane is thin, transparent, and smooth. The egg phase lasts 8–9 days. The egg hatches by the neonate larva chewing its way slightly obliquely forward so it emerges through a cylindrical hole to the left or right of the lower apex of the egg, just above leaf level. The neonate larva does not seem to eat any of the foam cover apart from that necessary to make the exit hole. After hatching (n = 29), the exit hole in the ootheca is variable, often on one side of the oothecal base, either as a clean round hole (~ 0.5 mm diameter, Fig. 42) or a rough tear (Fig. 43). The ootheca lasts a long time on the plant; over time, the hole enlarges and tears (Fig. 44–45).

Egg parasites. In 1999, Chris Burwell, QM, reared specimens from *A. balyi* eggs and he identified all the specimens as Hymenoptera: Eulophidae: Entedoninae. In the current study, GM also dissected many eggs in 2022–23 with the same parasite larvae. When parasitized, each egg usually has multiple parasites (usually 2–3, but occasionally as many as four per egg). One dissected egg had three emerged adult wasps inside, still inside their own pupal skins, but alive and wriggling; some were reared and have been determined so far to Eulophidae by Chris

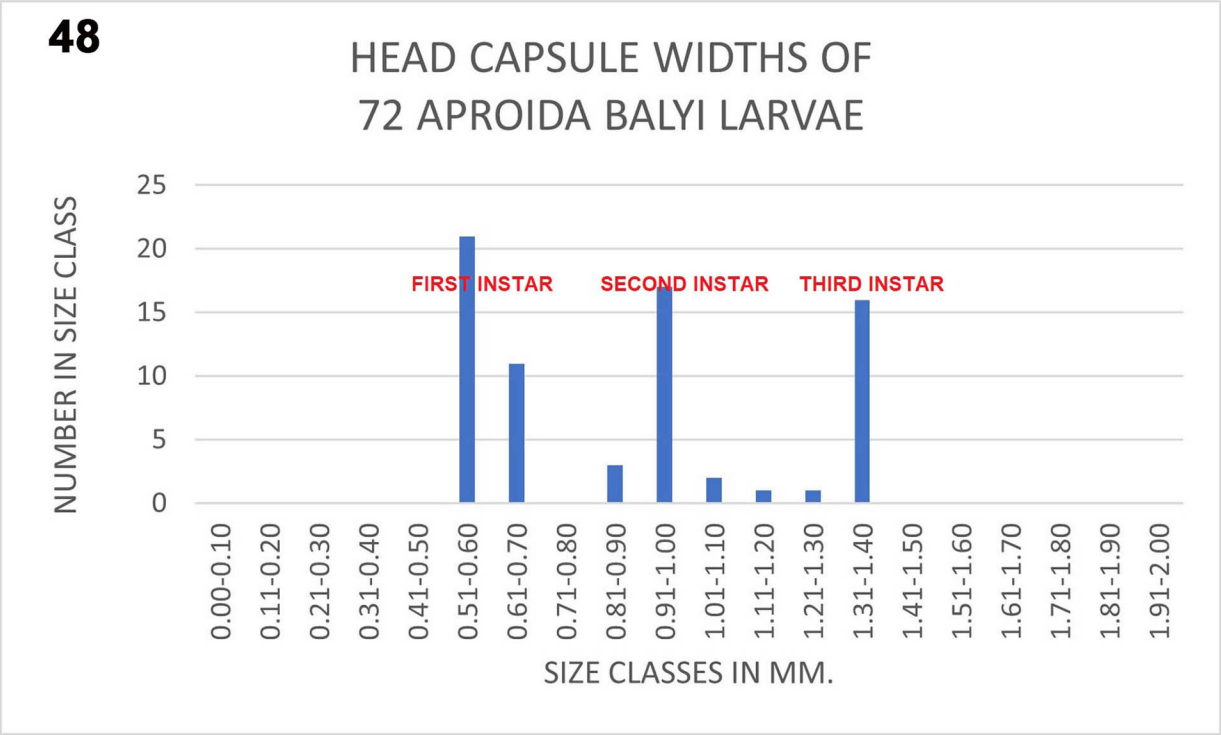
Burwell/QM. Placing these into one of the recognized genera has been difficult. It appears close to *Chrysocharis* Förster, 1856, but further study is needed to assign generic placement. Generally, three adult wasps emerged per *A. balyi* egg, usually through a single chewed exit hole on one side of the egg. In most cases two females and one male of the parasitoid emerged per egg but in one case a single female and two males emerged.

Larva I (*n* = >50 hatched, L = 5–9 mm; Fig. 25, 27, 46–47, 53). Prehatching eggs were dissected to examine the neonate larva. These rested in the egg with the caudal process flexed ventrally beneath the body. Head capsule width was the same as post-hatching Instar 1 larvae thus precluding possibility of an earlier neonate instar. *Color.* Live color contrasting; body cream with narrow dorsal yellow stripes from thorax to posterior abdominal segment; bands correspond to trachea and internal fat body; head and single caudal process brown-black; apex of caudal process cream. *Body* color in ethanol-preserved specimens with head dark brown, body and legs cream, claws brown. Body in dorsal aspect tear-drop shaped, widest across the head, tapered posteriad to narrowed elongate single caudal process. In lateral aspect, body dorso-ventrally flattened; caudal process at hatching ~1.5 times longer than rest of body, becoming relatively shorter as larva feeds and expands. *Head* in dorsal aspect fully exposed, rectangular; stemmata on antero-lateral corner, six stemmata arranged as pairs in two diagonal rows. *Mouthparts* hypognathous; antenna near mandible base. In lateral profile, head frontal area flattened. Clypeolabrum frontal shape triangular, apical margin with medial indentation; mandible frontal shape triangular, apical margin tri-dentate. *Thorax* in dorsal aspect with segment margins simple, without lateral extension. *Legs* at ventro-lateral margins; legs short with single claw; claw curved, margins simple. *Abdomen* segment margins simple, without lateral extension. *Caudal process* single, simple, not branched, tapered to apex, stout but not rigid, capable of movement; longer than rest of body. In cross-section, dorsum of process curved; venter concave, grooved from base to apex. *Anus* posterior, at base of caudal process, flat, not telescopic. *Shield* absent.

Comments: Feces are not retained as a shield. *Molting* (Fig. 48–51). The larva stretches out to full length on a leaf surface then becomes immobile while a sticky secretion is emitted from the anus which sets hard and glues the anal area, not the caudal process, to the leaf. Once the instar I head capsule and thorax have split, the instar II crawls forward, leaving the old skin stretched straight behind it and attached to the leaf. The new instar then rests



Figures 46–47. Larva instar I of *Aproida balyi* (Photos: V. Sandoval). **46)** Early instar I with single caudal process ~2 x longer than rest of body. **47)** Mature instar I feeds in grooves between veins of leaf, leaving long scraped marks with a few tiny holes.



Figures 48. Plot of head capsule width frequency of larvae indicate three instars (*n*=72).

for some time just in front of its cast exuvia before starting to move around and feed. The latter remains attached to the substrate (Fig. 48), becoming abraded over time in the loose body section while the caudal section remains attached for a long time (Fig. 51).

Larva, instar II (*n* = >50; Fig. 54–55). Measurement of body: L = 6–12 mm (anterior margin of head to posterior margin of last abdominal segment (excluding caudal process). Color of live specimens: head yellow, body yellowish with longitudinal white stripes from internal organs; legs developed, yellowish; caudal process black. Body shape more elongate than instar I, not dorso-ventrally flattened; in dorsal aspect elongate, somewhat even width from thorax through abdominal segments; segments transversely shaped; widest in mesothorax; posterior slightly tapered. *Caudal process* present, generally as in Larva I but length is reduced relative to body, ~1/4 body length. *Anus* as in larva I; feces may cluster at apex of process.

Comments. Larvae feed solitarily (Fig. 50–52). Fecal pellets are somewhat sticky; in a few larvae, pellets adhere to the caudal process.

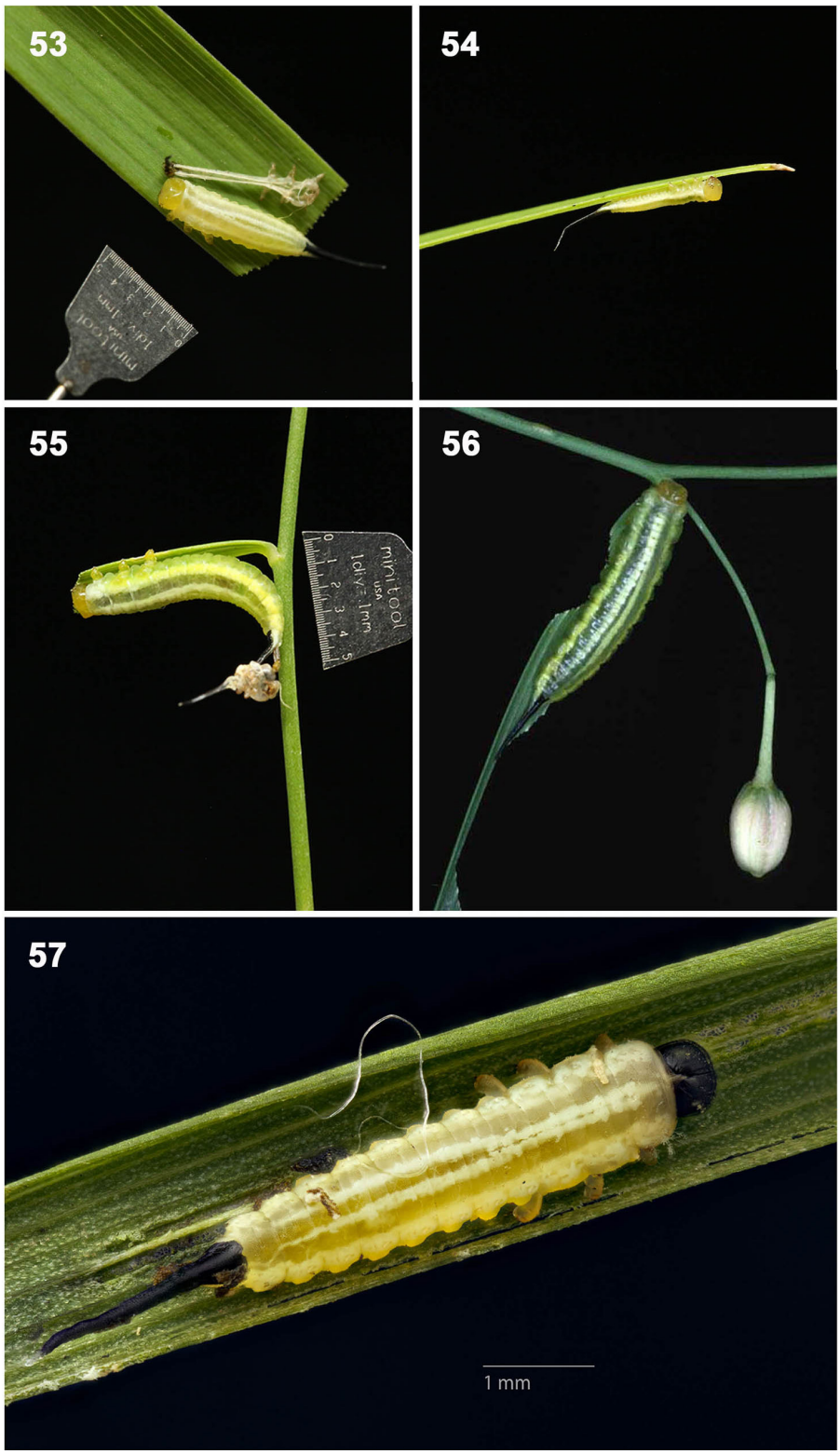
Larva, instar III (*n* = >50; Length: 10–18.5 mm; Fig. 55–57). Body color in life creamy yellow, dorsal appearance with white-colored longitudinal stripes from pronotum to abdomen due to internal nervous and tracheal systems. Head and caudal process yellow; legs golden. Color of dead ethanolic specimens is white, except for dark dorsum of caudal process. Body form and external morphology generally as in larva I–II; caudal process shorter than body, representing ~1/3 total body length. Thoracic segments similar sizes, pronotum only slightly overlapping dorso-posterior margin of head. Abdominal segments I–VIII are similar lengths but very gradually narrowed posteriad, so segment VIII is half the width of segment I. Segment IX is modified with the caudal process. *Legs* and *anus* as in instar I. *Comments.* Larvae feed solitarily. In rare cases, fecal pellets may adhere to the single caudal process (Fig. 62–67), clustering at the apex; a few pellets may fall and stick to body.

Behavior of larvae (Fig. 25, 27, 46–58, 62–71). Our observations of >200 larvae in the field and in rearing revealed many unusual behaviors. *Camouflage and mimicry.* In general, they are difficult to see on plants. These larvae live solitarily and do not contact other larvae even when they are on the same leaf. The difficulty to see these larvae at first glance is due to their color and body form that make them well-camouflaged on the narrow lance-shaped

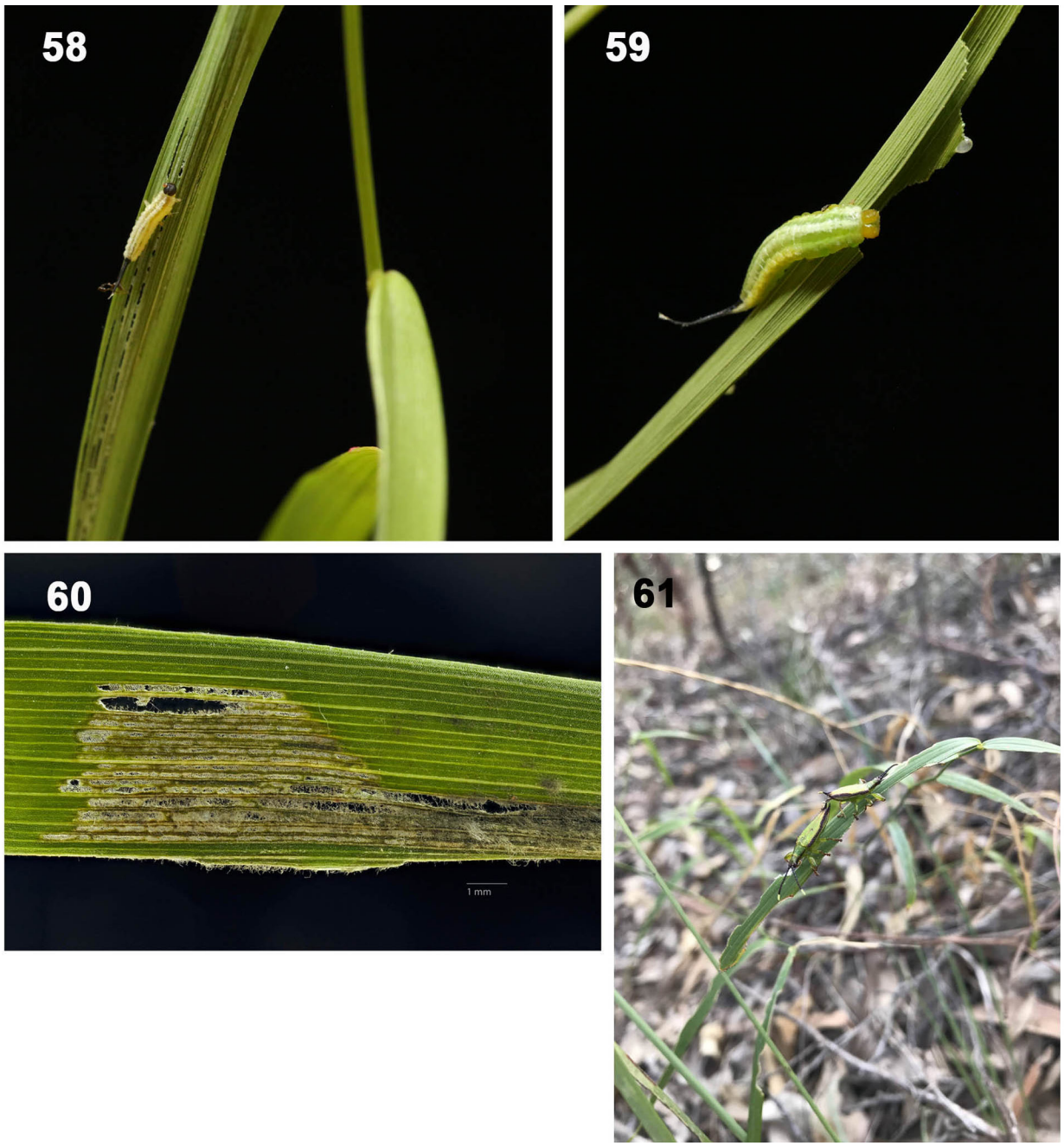
Figures 49–52. Larva of *Aproida balyi* (Photos: V. Sandoval). **49)** Instar II walks out and away from exuvia I. **50)** Exuvia I remains attached to the plant. **51)** Exuvia I, dorsal aspect, showing attachment only at posterior sternites. **52)** Exuvia I caudal process left embedded and glued onto leaf surface.

leaves with longitudinal veins (Fig. 23, 25). Larvae tend to stay on the venter of the leaf. However, as they get older, the interior structures (alimentary and tracheal systems, fat bodies) appear as paired continuous striped bands extending from prothorax to the abdominal segment IX. The outer pair of bands are yellow, and the medial pair are whiteish. These alternate with the dark green "stripes" of the body and so the larva blends with the leaf's color and protuberant veins.

Feeding (Fig. 58–61; Suppl. Film 2). Instar I feed only on the surface of leaves (Fig. 27, 47) resulting in patches of proximate linear grooves where the larva has bitten into the soft tissue between the hard parallel leaf veins. Some



Figures 53–57. Larva of *Aproida balyi* (Photos: V. Sandoval). **53)** Instar I with black head; note how the larva fits along the narrow leaf-blade and its stripes line up with the leaf lines (Photo: G. Monteith). **54)** Instar II next to Instar I exuvia. **55)** Instar II, lateral aspect. **56)** Instar III emerging from Instar II exoskeleton. **57)** Mature instar III has striped appearance with dark green (like the plant) and yellow-cream bands.



Figures 58–61. *Aproida balyi* feeding damage on *Eustrephus latifolius* (Photos: V. Sandoval, except where noted). **58)** Younger larva scrapes leaf and leaves elongate holes. **59)** Older larvae feed on full depth of leaf margins. **60)** Close-up with larval scraping damage (Photo: G. Thompson). **61)** Adults also feed on full depth of leaf margins.

feeding tracks have small windows where the larval feeding penetrates to the other side (Fig. 58); instar I scraping and scarring can leave large sections damaged (Fig. 60). Instar II–III feed on the edges of leaves with the body usually resting on the underside of leaves. Their feeding leaves large cut-outs on leaf edge and apex (Fig. 59). One can distinguish hungry larvae from larvae with full gut. Adult beetles also feed on leaf edges (Fig. 61) leaving similar embayments in the leaf margin.

Locomotion. Larvae of *A. balyi* are not sedentary, walking all over the plant, but they drop off the plant easily when disturbed. Our films show a surprising motion of protuberant areas of the abdominal sternites that appear to aid locomotion. We describe three cases with associated films:

Case 1, instar I (Suppl. Film 3). This larva climbs upwards along the edge of the leaf blade with legs contacting each side of the leaf edge. As it ambulates forwards, medial protuberances of each abdominal sternite attach and detach.

Case 2, instar II (Suppl. Film 4). The abdominal sternal protuberances are apparent and function as in instar I. In this closer view, areas around the legs appear swollen and small protuberances anterior to the meso and meta-legs appear to also be attaching also to the plant. The caudal process does not participate in locomotion.

Case 3, instar III (Suppl. Film 5). For a faster movement (e.g., to change direction), the larva completely lifts the abdomen into the air, and uses just the legs. Once it is going in the desired direction, the abdomen is re-positioned horizontal to the substrate. The abdominal protuberances contact the surface as the larva moves forward.

The abdominal protuberances appear in all three instars and are used in a consistent way, to attach and detach as the legs walk forwards. In the pre-pupa (described below) they are protuberant and those on the two posterior sternites (VII–IX) glue to the substrate.

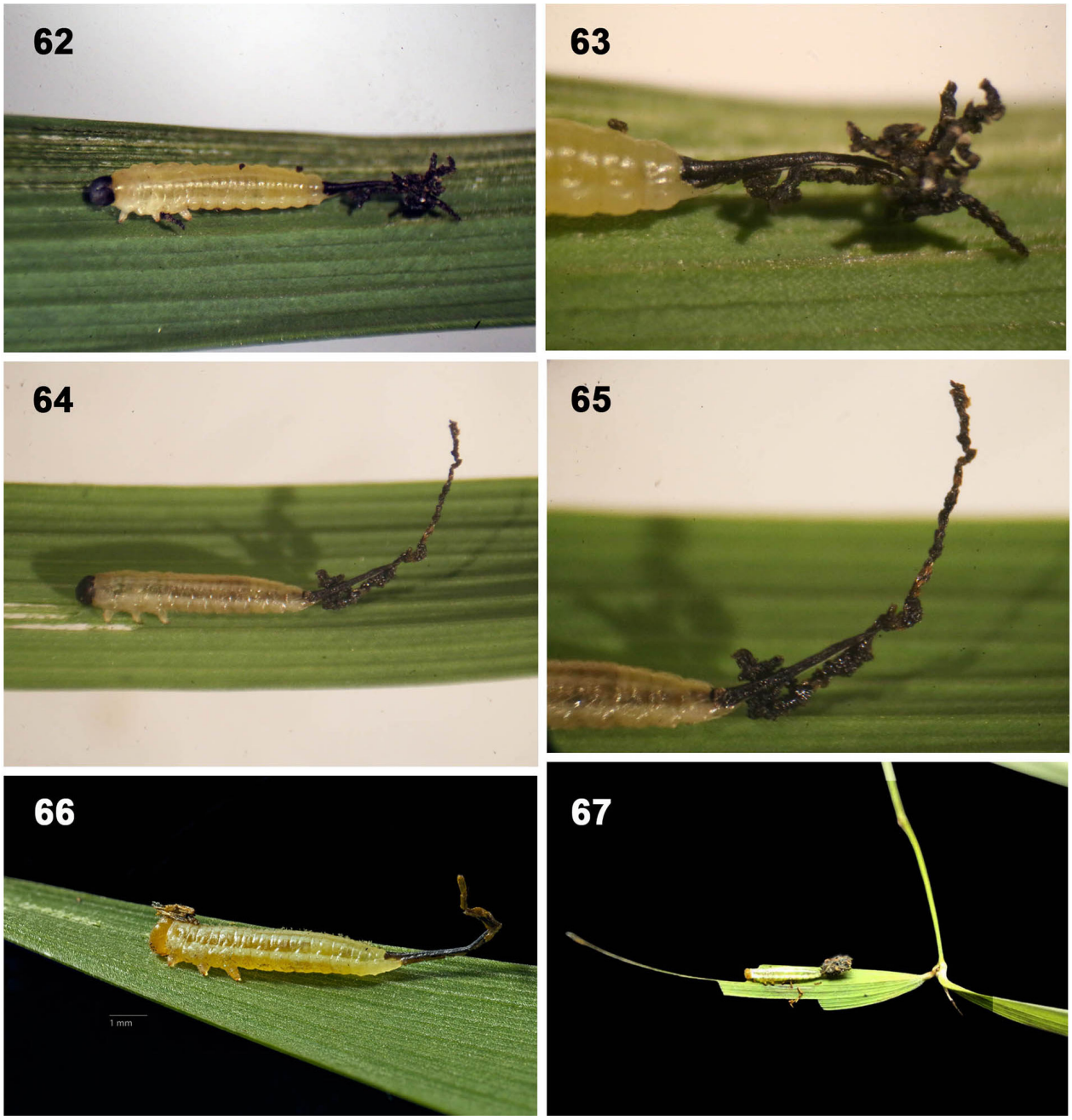
Fecal accumulation (Fig. 62–67; Suppl. Film 6). In all instars, emerging fecal pellets are elongate and are channeled along the concave ventral groove of the process. We observed occasional larvae with temporary clusters of sticky fecal pellets on their single caudal process. The pellets accumulate as strings or small clusters, when the larva is stationary (Fig. 62–67), but easily drop when it becomes active in search of food. One rare observation was one larva with a "ball" of frass with fungal growth attached to its caudal process (Fig. 67). Any occasional fecal accumulation on the caudal process is shed at molting.

Pre-pupa (*n*= >20; Fig. 68–70; Suppl. Film 7). When ready to pupate, the mature instar III takes up a quiescent position on the underside or edge of a leaf (or, sometimes on the stem, and once on another pupa). A few minutes before pupal dehiscence, the larva produces glue from its anus which firmly attaches the medial section of sternites VII–IX to the leaf apex (Fig. 69), leaf venter (Fig. 71–73, 75), or to the stem (Fig. 74). The body color matches the host leaf, appearing pale green and with the yellow or chartreuse-colored alimentary tract visible through the integument. The body is positioned longitudinally on the long narrow leaf blade which helps it to blend with the leaf. The body is usually clean, but when it voids the stomach, some fecal pellets may remain on the caudal process (Fig. 70). During this period, the pre-pupa is somewhat quiescent with occasional trembling and slight shaking movements.

Pupation (*n*= >20; Fig. 71–77; Suppl. Film 7). After some time, the pre-pupa's legs release the substrate and it hangs downwards from its hind end for several hours. If touched at this stage, it jerks from side to side violently while held firmly by its glue. Eventually the instar III head and thorax split open, and the pupa slips steadily down out of the larval skin. The pupa is unusual in having a long attenuate tapering hind end. At the time that the pupa is released to start to fall (or perhaps just before), the anal area (adhesive glands, perhaps) emits glue which coats the anal tip of the pupa as it slips downwards. The pupa does not fall freely but descends slowly, being slowed as the larval trachea are pulled out of its spiracles. The pupa's fall comes to a halt when its hind end is level with the thoracic part of the larval exuvia, corresponding with the tracheae being almost completely pulled out of the body and still attached at the spiracle openings. The pupa then hangs quietly without movement and the shed larval skin contracts closely around the elongate, tapering glue-covered posterior of the pupa. Soon the glue dries and hardens, and the pupa is then firmly attached to the skin. The attenuate pupal caudal region may provide an extended area for glue contact with the larval exuvia. The shed tracheal tubes can be seen inside the length of the shed exuvia and appear to add to its suspension strength. Once the pupa is hardened and the glue dried, the pupa then sways and can thrash violently when touched, but it stays very firmly attached to the exuvia III.

In these descriptions below, the timing corresponds to our films of three observed pupa emergence events.

Case 1 (Suppl. Film 7). When preparing to pupate, the attached pre-pupa (larva III) flips backwards, suspended vertically and upside down from the stem (Fig. 69–71). About 24 hours after the instar III glued the abdomen to the substrate, the pre-pupa gradually stiffens. After about 3 mins**,** the exuvia III head capsule splits along the ecdysial line, and the pupa slowly drops downwards and out of exuvia III. The pupal thorax appears



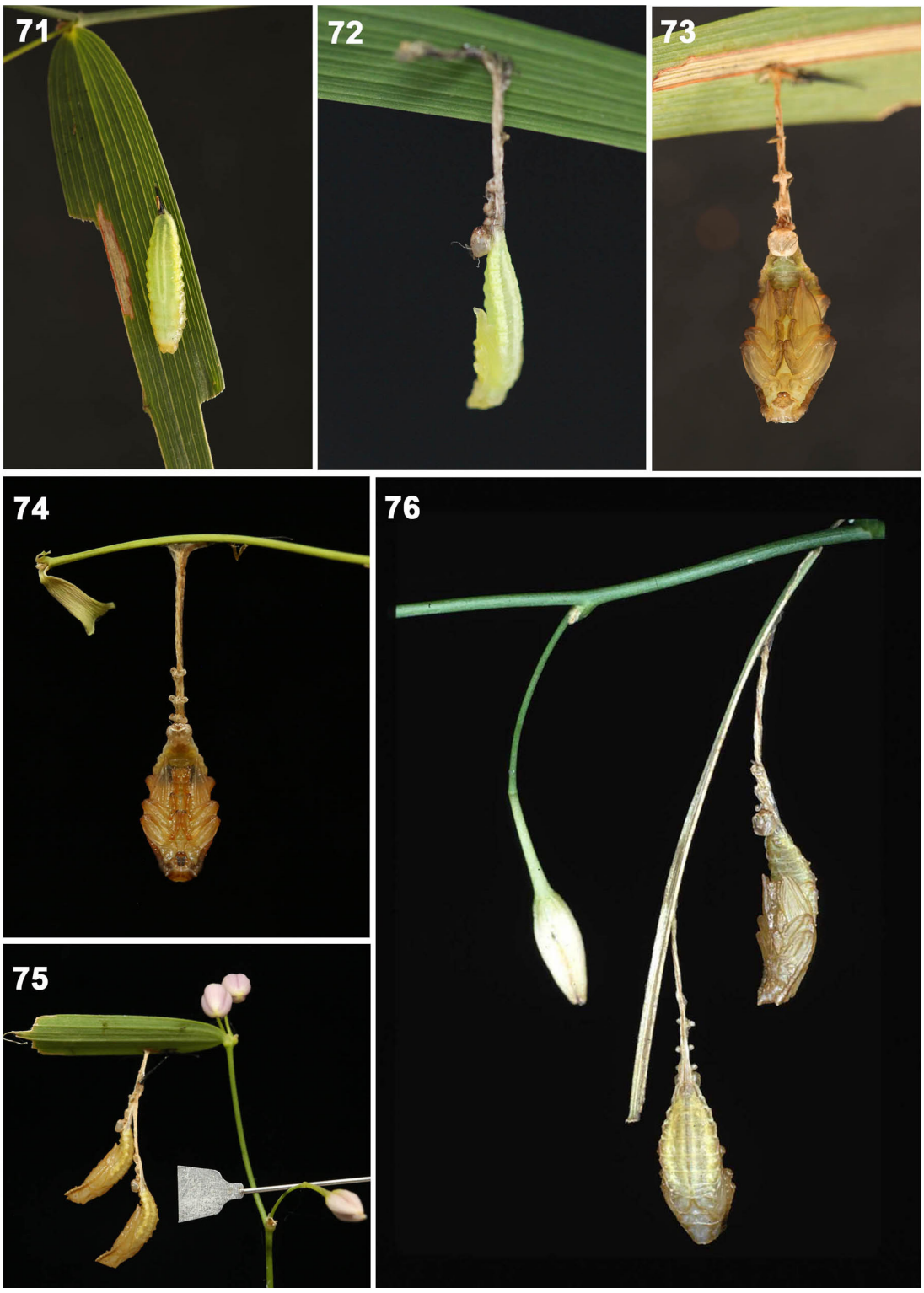
Figures 62–67. Temporary fecal retention in larva of *Aproida balyi* (Photos: V. Sandoval, except where noted). **62)** Larva instar III with temporary loose mass of fecal pellets on single caudal process. **63)** Close-up view of fecal mass. **64)** Larva instar III with long thread of fecal pellets on single caudal process. **65)** Close-up view of fecal mass. **66)** Larva instar III with small fecal pellets (photo: G. Thompson). **67)** Larva instar III with mass of fecal pellets and fungal filaments.

slightly inflated, with some separation. After small movements and air inspiration, the pupa appears swollen, including the legs. The larval exuvia III stretches and its legs are stretched apart; it elongates as the teneral pupa slides and falls out, using gravity, until the pupa stops at the point of the exuviae III head capsule. This dropping process takes about 5 mins. Once the pupal thorax is free of the exuvia III (about 4 min 49 secs on the film), then the rest of the pupa exits faster with dorso-ventral wriggling. The pupae remain green (Fig. 72) for 1–2 days after pupation, then turn light brown (Fig. 73), eventually darkening to resemble the buds of this host plant (Fig. 76).

Figures 68–70. Pre-pupation in *Aproida balyi* (Photos: V. Sandoval). **68)** Posterior abdominal sternites glued to leaf blade. **69)** Glued to leaf apex. **70)** Ready to pupate, glued to leaf blade, alimentary tract voided and feces on caudal process.

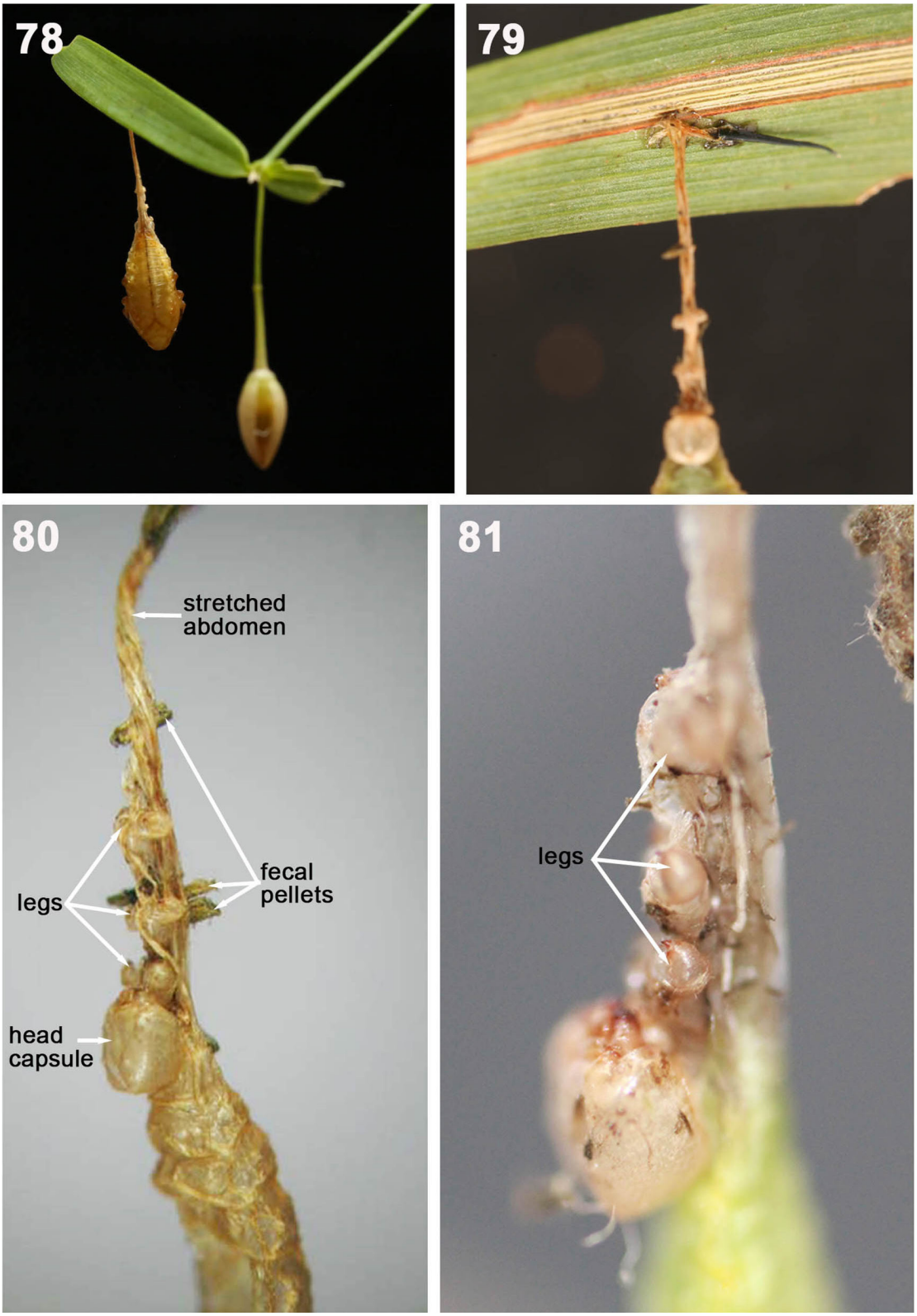
Case 2. At T 3 mins 15 secs, the larval head capsule splits along the ecdysial line and, shortly afterwards, the pupal head emerges. At T 3 mins 42 secs, the pupal stemmata are visible. At T 4 mins 32 secs, the antennae are freed of the larval exuvia III. The exuvia is stretched further, with the pupa acting as ballast, relying on gravity to fall, slide down, and exit the larval exuvia. At this point, the pupa's body has exited the larval abdomen but is still held within the larval thorax (the larval legs serve as markers in our film). The larva's abdomen becomes a narrowed cord (Fig. 79–81), stretched from its attachment to the leaf blade.

Case 3. At T 4 mins 02 secs, the larval exuvia III thorax splits open and the pupa wriggles and expands, gradually falling out of the exuvia. Between T 6 mins 5 secs – 6 mins 45 secs, the pupa is largely free of the larval exuvia. It stops falling when the pupa's posterior end reaches the same level as the now-distended larval head capsule. The thorax of the larval exuvia is so stretched that the legs appear as three rounded bumps at the caudal end of the pupa (Fig. 79).



Figures 71–76. Pupa of *Aproida balyi* (Photos: V. Sandoval except where noted). **71)** Prepupa, yellowish color of younger stage, caudal process black. **72)** Yellowish pupa suspended from extended larva III exuvia, lateral view. **73)** Mature pupa, suspended from leaf, frontal view. **74)** Mature pupa, suspended from stem, frontal view. **75)** Two mature pupae (darker color, lateral view) with unopened flower buds of *Eustrephus latifolius* to show similarity. **76)** Two mature pupae (darker color, posterior view) with unopened flower buds (Photo: Jeff Wright).

Figure 77. Pupa of *Aproida balyi*, ventral view (Photo: Geoff Thompson).



Figures 78–81. Pupal attachment of *Aproida balyi* (Photos: V. Sandoval). **78)** Mature pupa, posterior view, adjacent to unopened flower bud of host. **79)** Exuvia III attached at its abdominal apex to leaf; its black caudal process is free. **80)** Extended instar III exuvia. **81)** Legs of extended instar III exuvia.

Pupa, early stage (*n*= >20; Fig. 72–77). Teneral pupa yellow (Fig. 72), with alimentary and tracheal systems appearing as longitudinal white stripes. After some mins, the pupa appears pale brown in color (Fig. 73). Later, the antenna, mouthparts and margins of legs become darker brown. Pupa dorso-ventrally flattened, oval shape, with posterior abdominal segments sharply narrow, seemingly continuous with enclosing exuvia III.

Pupa, late stage (*n* = >20; Fig. 73–81). Color, living specimens cream-brown. Dorsal color (dead specimens in alcohol) unevenly yellow-cream with scattered small brownish patches on pronotal anterior margin, small circular spots on each segment; abdominal scoli I–II dark brown, scoli III–IV brownish, scoli V–VI yellow cream. Ventral color (Fig. 77) golden brown, with darker brown on antennal scape, anterior scoli, and frontal margin of pronotal shield. *Body* dorso-ventrally flattened, oval in dorsal and ventral aspects, broadest across abdominal segment I. Posterior shape rounded, apex hidden by instar III exuvia; apex and exuviae form attachment to host plant substrate. Removing exuvia III reveals elongate single caudal process of pupa (Fig. 77).

Comments. Pupation is generally solitary, but in high-density situations, pupae can closely associate, appearing gregarious (Fig. 75), but this state is not to be mistaken for the true gregarious pupation in some tortoise beetles. The pupal appearance mimics the unopened plant buds— the stretched exuvia is as narrow and long as the bud's petiole; the pupa has a similar shape, size, and color to the flower buds (Fig. 75–76).

Based on our observations, it seems that the larval tracheal tubes prevent the pupa from completely falling out of the larval exuvia. When touched, mature pupae thrash violently, swinging on each side right up to the leaf they are suspended from. They never come loose from their attachment to the larval skin. Pulling a mature pupa from the larval skin results in the pupa breaking at its caudal region. Careful dissection of the hind area of newly formed pupae shows that the thoracic area of the larval skin has not only tightly contracted around the tapering caudal process of the pupa but is glued to it by a hard clear secretion. We can only assume that this glue has the same glandular origin as the anal glue which has also glued the anal area of the prior larval and prepupal stages of the same individual to the substrate prior to earlier molts. The pupa's elongate caudal process (Fig. 77) presumably gives a greater surface for the glue to act on.

Adult eclosion (*n* = >40; Fig. 82–87, Suppl. Film 8). After the pupal head capsule and the thorax along the dorsal ecdysial sutures split, the teneral adult emerges, and is very active, moving its white-tipped antennae constantly. It uses its legs to extract its body out of the pupal exoskeleton, like pulling down a stocking. This adult often clings to the hanging pupal exuvia while it hardens, and the wings expand.

Adult behavior (Suppl. Film 9). Adults move the antennae a lot, often in circles, like a wasp. When disturbed they readily drop from the plants. Adults are solitary, only coming together for mating. Males spend more time than females moving about the foliage. We observed many mated pairs (Fig. 28–29) in the wild and in caged populations and determined copulations to last ~15 mins to prolonged (several hours). Often, the male remains on the female's back (Fig. 32) for periods before and after actual connection begins or ceases. Some mate guarding may be occurring since other males have been seen to actively try to grapple with and dislodge other males riding on a female's back. The mating position is typical of Cassidinae, with the male mounting the female from the rear, then atop her and holding her sides with all the legs.

Seasonality. Adults overwinter away from the plants, presumably down in the leaflitter, and first appear on the plants in early spring. Eggs, larvae, and pupae do not overwinter.

Predation. The large assassin bug, *Pristhesancus plagipennis* Walker, 1865 (Hemiptera: Reduviidae) is common in the Brisbane area and both adults and nymphs were often seen to predate on both larvae and adults (Fig. 91). Ants were sometimes seen to chew open the oothecae and feed on the egg, and sometimes to kill very young larvae (Fig. 92).

Distribution of *Aproida* species (Fig. 16–17)

Aproida shows a familiar altitudinal pattern exhibited by many ancient taxa of plants and animals in Australia in that it occurs down to lowlands in the southern half of the continent but is restricted to high cool mountains in tropical regions. This does not seem so from the map which has localities for *A. balyi* at Bowen (sealevel), Cairns (sealevel), Kuranda (350m) and Johnstone River (sea-level). But all modern, authenticated records of *Aproida* in the tropics are from above 750m and those lowland ones are all based on specimens more than 100 years old

Figures 82–87. Adult eclosion in *Aproida balyi* (Photos: V. Sandoval). **82)** Frontal view. **83)** Lateral view. **84)** Dorsal view. **85)** Teneral adult actively exits pupal exoskeleton. **86)** Once out, the adult pauses to harden up. **87)** Teneral adult sits nearby to further harden.

which date from a time when locality names were often just attributed to a nearby population centre. The lowland areas of North Queensland have been subjected to intense field work in the last 50 years but the only places north of the Tropic of Capricorn where *A. balyi* has been genuinely detected are on the Eungella Range, Mt. Macalister, and the Atherton Tableland, all above 750m. The other tropical species, *A. monteithi*, is known only from the even higher Thornton Peak at 1400m.

The original Pascoe (1863) description of *A. balyi* is from material from 'Moreton Bay', the original name for the first convict settlement in Queensland in 1824; later changed to Brisbane when it became a free settlement. This type locality for *A. balyi* is thus essentially synonymous with the broader Brisbane area, as depicted on our distribution map (Fig. 16). Many *A. balyi* specimens have accumulated in museums, particularly from the northern part of its range and the distribution range is from the latitude of Cairns to a little north of Sydney. This species exhibits uniform morphology throughout its range.

Both *A. cribrata* (Fig. 1–3) and *A. monteithi* (Fig. 4–11) are distinct and well-defined species although both are known from just the type specimen and one additional specimen. We report only one new locality below.

Figures 88–92. Other arthropods on *Eustrephus latifolius,* Mount Coot-tha Reserve, Australia (Photos: V. Sandoval except where noted). **88)** Spider 1 (Araneae). **89)** Spider 2, Oxypodidae. **90)** Homoptera: Flatidae. **91)** Assassin bug, *Pristhescancus plagipennis* Walker, 1865 (Hemiptera: Reduviidae) eating adult *A. balyi* (photo: G. Monteith). **92)** Ants (Hymenoptera: Formicidae) eating ootheca of *A. balyi*.

Notes on *Aproida cribrata* Lea, 1929 (Fig. 1–3)

For 100 years, only the holotype (Fig. 1–3) has been known with data label: National Pk, Q., H. Hacker, Dec., 1921 [QM]. As also suggested by Samuelson (1989) we assume that the type locality is Lamington National Park, one of the earliest National Parks in Queensland. Further, it is known from Queensland Museum records that the collector, Henry Hacker, then insect curator at the Queensland Museum, often visited Lamington via O'Reilly's Guest House which was the only easy access point at that time (by horseback) to the Park. For this reason, it is assumed that the type locality is near the Guest House from which a second specimen has been recorded in recent times (see below).

Lea (1929: 239) reported *A. cribrata* as flightless without details or illustrations, but Samuelson (1989: 602–602) figured the species and determined that flightlessness is due to brachyptery with the wing length reduced and simplified and the metasternum very short and distorted.

Chris Reid, Australian Museum, Sydney, identified a second specimen of *A. cribrata* (Fig. 12), among chrysomelids received from Roger Kitching's pyrethrin canopy fogging for insect diversity studies in 1989–1990

(Kitching et al. 1993). This specimen was found at: 'Green Mountains', an alternative name for the area around O'Reillys' Guesthouse (28°13′S; 153°07′E) where the type was taken. The specimen label says: "pyrethrin fogging host 'H-16-7', O'Reillys, Jan–Feb 1991, R. Kitching". Kitching et al. (1993) describe the vegetation as notophyll rainforest. Kitching (pers. comm.) advises that his pyrethrin-spray protocol used two sprays at each place, a low (L) spray below the main canopy and a high (H) one in the main canopy as indicated on the labels. Thus, this *A. cribrata* specimen was from the main canopy, ~20–30 m high at that location. Although details about the host tree or epiphytes are lacking, the site was on the Wishing Tree Track close to O'Reillys' Guesthouse. It is likely that Henry Hacker obtained the holotype from the same general area. If *A. cribrata* is a regular canopy dweller, its host may be some epiphytic monocot.

Notes on *Aproida monteithi* Samuelson, 1989 (Fig. 4–11, 17)

Known from only the male holotype (Fig. 4–8) and female paratype (Fig. 9–11), in QMBA, collected together and with data as on pictured labels. The type and only known locality (Fig. 14, 17) is Thornton Peak which is the highest point of the Thornton Uplands sector of the Wet Tropics Biogeographic Region of Australia (Bryant and Krosch 2016; Yeates and Monteith 2008), The Thornton Uplands is bordered by the Bloomfield River valley to the north and the Daintree River valley to the south. Thornton Peak has many other insect endemics and a summary of them and history of collecting there, with additional photographs, are given by Theischinger (2019).

Samuelson (1989) described mouthparts and genitalia (Fig. 6–7) from the dissected holotype. The male does not have modifications of the protibia and profemora as seen in *A. cribrata* and *A. balyi*. The female allotype was not dissected but he inferred it was female based on differences in the abdominal apex. The antennae have two apical antennomeres cream, contrasting with the dark brown basal articles.

Discussion

Our study fills a gap in knowledge about the life cycle and biology of *Aproida* within Cassidinae and is another contribution in our ongoing study of Australian Cassidinae—*Notosacantha* (Monteith et al. 2021), *Austropsecadia* and *Meroscalsis* (C. Deane, pers. comm.). The Australian fauna of Cassidinae comprises 65 species in 24 genera in nine tribes (ALA 2024). We build on Monteith's (1970) brief illustrated description of the life cycle with an ootheca, three larval instars with single caudal process, and the unique suspended pupa (also with single caudal process). Below, we discuss aspects that can aid analyzing its systematic position between basal 'hispines' and derived tortoise beetles.

Choice of host plants. Cassidinae are documented on many families of host plants (Jolivet and Hawkeswood 1995; Borowiec and Świętojańska 2012–2024; Staines 2015). *Eustrephus* in the Asparagaceae is the recorded foodplant for *Aproida balyi*. No foodplant is known for the other two species. Asparagaceae is not reported for any other Cassidinae species. A few Criocerinae and Cryptocephalinae have been reported on this family (Clark et al. 2004). Some of these are pests of cultivated Asparagus (e.g., Morrison and Szendrei 2014). *Aproida balyi* is openly exophagous, highlighting the unappreciated trophic diversity of basal Cassidinae (the classical "hispines") with many miners, sheath-feeders (Mariau 2004; Staines 2004), Zingiberales specialists (Staines 2004), bamboo and grass specialists (Chaboo, unpubl. data), and palm feeders (e.g., Chaboo and Nguyen 2004; Prathapan and Shameem 2017).

Eustrephus does not have sheathing leaf bases, which is unusual for monocots, and this may be a driving force for adoption of exophagous feeding in *Aproida*. Being able to feed on the full depth of the leaf margin in instars II and III, unlike most non-mining cassidines which are surface feeders, probably gives it a feeding advantage also.

Life cycle. *Ootheca.* In Cassidinae, a range of egg-laying techniques have been reported, including site preparation (e.g., chewing a groove or slit and covering with plant material), eggs that are solitary, loosely or tightly aggregated, ootheca, glues, and some with maternal care. Mothers coat eggs with anal glandular and excremental applications, often mixed with buccal secretions, and may further cover eggs with chewed plant debris, oothecal membranes, and/or feces (Muir and Sharp 1904; Fiebrig 1910; Hinton 1981; Jolivet and Verma 2002; Müller

and Hilker 2004). Anal applications for maternal microbiome transmission are likely. The single egg within an ootheca contrasts with some other cassidine oothecae that contain multiple eggs (e.g., Becker and Frieiro-Costa 1988; Adam et al. 2022). In *A. balyi* the foamy oothecal cover is a barrier, and the few fecal pellets may offer some offense or even physical protection against ovipositing egg parasites. Verma and Kalaichelvan (2004: Fig. 6) hypothesized features in the elaboration of the cassidine oothecae—strengthening ridges (furrows, creases, keel), lamella layers, and fecal deposit (perhaps with offensive chemicals).

Larva. The stages differ in the body shape and the relative proportions of the caudal process to the rest of the body; otherwise, most features are similar, but scanning electron microscopy will uncover other differences such as the macro- and micro setation and cuticular processes.

One unusual feature of *Aproida* larvae is that they have a soft pliable abdomen, not tough leathery or sclerotised terga and sterna, and pronounced abdominal segmentation, as do many exophagous Cassidinae larvae. This enables the larva to take in more food and expand its abdomen in size much more within one instar, than happens in other cassidines. This may have enabled *Aproida* to have only three instars rather than the common five instars in Cassidinae. This gives *Aproida* the great advantage of having two less molts during larval development and accelerates the speed and efficiency of metamorphosis. Because its abdomen is long, soft, and flexible compared to the more strengthened and box-like abdomen of other tortoise beetles, it may have become necessary to develop the abdominal ampulla system which aids adhesion and forward progression of that long soft abdomen.

The single caudal process in *Aproida* larvae and pupae is another remarkable feature. It is naked most of the time, however, we observed a few instances of fecal pellets on the process. These two aspects, the process with fecal retention, are a significant landmark in the Cassidinae tree of life (Chaboo 2007). The crown-clade of 12 tribes in Cassidinae is supported by this complex feature, the exuvio-fecal shield supported on paired caudal processes (Chaboo 2007; Adam et al. 2022; Chaboo et al. 2023). Caudal processes appear within Cassidinae, not over all Chrysomelidae (thus, not homologous with 'urogomphi'). Tortoise beetles typically have paired processes, but exceptions include a single process in *Discomorpha* Chevrolat, 1838 (Omocerini) (Flowers and Chaboo 2015) and *Hybosa* Duponchel, 1842 (Cassidini), and no process in *Eurypepla* Boheman, 1854 (Ischyrosonychini) (Chaboo 2004). In Hemisphaerotini, lateral scoli may be co-opted with the paired caudal processes to support that unique basket-like shield in a less mobile way (Chaboo and Nguyen 2004). Among plesiomorphic Cassidinae ('hispines'), many larvae have a heavily sclerotized urogomphal plate, like a broad paddle or shovel (see Chaboo 2007). However, single processes occur in juveniles of exophagous *Leptispa*, Baly, 1858 (Leptispini) (Prathapan et al. 2009).

Do *Aproida* larvae retain an exuvio-fecal shield? In *A. balyi* larvae, fecal pellets are elongate and sticky and may sometimes accumulate as a chain along the caudal process (Fig. 62–66) or they may be clumped on the caudal process (Fig. 55, 63; Suppl. Film 6). In some pupae, fecal pellets voided by the larva III may stick to the larva III exuviae (Fig. 70, 79). These clusters of fecal pellets in *A. balyi* juveniles are temporary and fall off when the larva is active, walking around, and are shed at molt. We conclude that their fecal deposits are not fecal shields as in tortoise beetles. However, we gain some insights into how the fecal shield may have originated with the way pellets may stick together into clumps. The offensive/defensive properties of tortoise beetle shields suggest that feces in *A. balyi* may function similarly. The caudal process of *A. balyi* certainly provides clues as to how the shield, caudal process and telescopic anus assembled at the root of the tortoise beetle branch. The presence of the single caudal process in Aproidini and Leptispini suggests that the caudal process originated before the other two features.

Larval locomotion. In our supplementary films 4–5, we can see medial areas of the abdominal sternites protruding, contacting, adhering, retracting, and detaching from the substrate. These lobes appear to help the larva move forward and provide adhesion. Their motion brings to mind some Staphylinidae beetle larvae that have high-friction pads with small teeth that allow larvae to push against the substrate or, less likely, have "sticky" eversible membranous lobes with fine teeth (A. Newton and M. Thayer, pers. comm.). Some Staphylinidae larvae do use the pygopodium (segment X), with or without hooks on the eversible membrane, as a "sucker-foot" to push the body forward. These structures in *A. balyi* larvae resemble the locomotory abdominal ampullae in some chrysomelid Chrysomelinae (Gustafson and Chaboo 2009, Film: https://www.youtube.com/watch?v=QOQaHaSiaMs).

The inflation or swelling of ventro-lateral areas of the thoracic sterna is another feature to note. These bulges also appear to be contacting the substrate but there does not seem to be exertion and force so they may

not function in locomotion. It is unclear what is their function. Detailed morphological analyses of the surface and underlying musculature of these lobes and swollen structures on larval thorax and abdomen of *A. balyi* are needed.

Ambulatory ampullae in Chrysomelidae larvae have been discussed (Peterson 1953; Lee 1993; Reid 1995, 2000). The 'ambulatory' ampullae in the larvae of *A. balyi* is a first record for Cassidinae.

Molting ($n = 44$ in cages; Fig. 69). This gluing down of larvae was known until now only for Cassidinae pre-pupation when the final larva attached to the substrate before pupation. In tortoise beetles, the exuvia is compressed onto the caudal process and not glued down and discarded. It is novel and unique for Cassidinae (so far) that all larval instars of *A. balyi* glue down first before molting, which enables the new larva to walk out of the old skin.

It is interesting that the *A. balyi* pupa retains the larva III exuvia with its own caudal process nested within the old skin. This resembles the inter-nesting of caudal processes that holds the exuviae together within the exuvio-fecal shields of tortoise beetles (Chaboo et al. 2023). In *Calyptocephala attenuata* Spaeth, 1919 (Spilophorini), the adult remains partly enclosed by the pupal exuvia while it hardens (see Chaboo et al. 2023: Fig. 58). The situations present clues to how exuvial retention could have originated, after the origin of the caudal process which perhaps made exiting the old exoskeleton more difficult or provided some extra armor while the new stage hardened up.

Anal adhesive. A secretion is apparent in the *Aproida* larval attachment to the plant and in attachment of the pupa to the larval exuvia. It is used to (1) anchor the larva to the leaf, prior to molting, (2) anchor the final instar to the leaf underside (or, sometimes to the stem) prior to the pupal molt, and (3) anchor the anal end of the pupa to the head capsule end of the larval skin after pupation occurs. This adhesive may be produced by an anal gland and possibly may also make the fecal pellets sticky.

Pupation. Pupae of *A. balyi* occur as singletons, not gregariously as in some derived Cassidinae. *Aproida* is a new example of *pupa adhereana* among beetles and is unique among Cassidinae and Chrysomelidae. Within Coleoptera, some Erotylidae exhibit pupae suspended from the final larval exuvia from the underside of logs (e.g., *Erotylus* Fabricius, 1775, *Cypherotylus* Crotch, 1873, *Prepopharus* Erichson, 1847; J. McHugh, pers. obs.). The glued attachment in all larval stages before molting allows the new teneral instar to exit the old skin by wriggling out. The *Aproida* pupa falls most of the way, but not completely, out of the exuvia but its abdominal hind segments, specially VII–IX, remain inside the larva III exuvia and the caudal process extends a long way into the exuvia, thus the pupa's caudal process acts as a locking mechanism to promote attachment to the old exuvia which was glued to the substrate. Additional "attachment ropes" that maintain pupal suspension could be links with the thread-like lines of the respiratory system and the gut lining, as suggested by Frania (2011) in other cases of *pupa adhereana*. Thus, *Aproid*a pupal suspension is maintained in several ways: the strong anal glue that affixes the larval exuvia to the host, the exuvia itself, the inter-nesting of the pupal caudal process within the larval exuvia, and gut and respiratory "ropes".

Graves (1965: 122) wrote about one erotylid "The last larval exuvium continues to cover the posterior half of the abdomen, so it is doubtful that the posterior abdominal spiracles, even if functional, would be of much use." This may be the case in *Aproida* too.

Adult morphology. Samuelson (1989) provides solid morphological descriptions of the adults of the three species. In life, we found the adults do not show reversible color changes as in some Cassidinae. The intra-generic variations in sexual dimorphism, in the toothed femora of some males, and morphology of flighted-flightless species suggest character state variations for phylogeny reconstruction.

The function of the male's toothed femora in mating is unclear. The male sits atop the female while the female holds the stem or leaf with her legs (Fig. 28–29) and the position of and contact with the female of his legs varies. In photographs of many courting pairs, we observed that all his three pairs can be on top of the female's elytra and the tarsomeres are in contact. In some couples, we observed the male's meso- and meta-legs may be extended with tarsomeres in contact with the female's thorax and/or abdomen. In some films, the pre-apical femoral notch appears to be coincident with the edges of the female's elytra but it is not actually hooked to her margins.

Adult *A. balyi* have fully developed hind wings and were seen to fly in the field and in captivity. *Aproida monteithi* has fully developed hind wings and presumed flight ability but *A. cribrata* is clearly functionally flightless.

A few other Cassidinae are flightless—Cassidini: *Cassida* (*Mionycha* Weise, 1891), *Fornicassis* (Spaeth, 1917), *Pilemostoma* Desbrochers, 1891 (Jolivet and Hawkeswood 1995) and Mesomphaliini: *Elytrogona* Chevrolat, 1836 and *Stoiba* Spaeth, 1909 (Chaboo 2000). These flightless cassidine adults can exhibit distortions (convex dorsum, metasternum), reduced flight musculature, reduced pteronotal sclerotization, and possible elytral fusion.

Mimicry and camouflage in *A. balyi*. All life stages display remarkable mimicry that enhance their camouflage on the host plant. The larva's narrowed form and muted colors with a striped appearance blends in with this host's lanceolate leaf blades with raised veins. These larvae are difficult to discern on the plants. Hawkeswood (2003) suggested that these larvae resemble sawfly larvae, but none occur on this plant. We independently assessed a large volume of data (reared specimens, photographs, films, and measurements) that supports the mimicry hypothesis. The pupa resembles the flower buds of this host (Fig. 74) due to its color, ovoid shape, the exuvia stretched like a pedicel, and the way it is suspended (Fig. 76–77), another layer of mimicry as first noted by Monteith (1970)

An enemy-rich habitat probably promoted aspects of mimicry in *Aproida*. We found spiders and ants attacking the beetle ootheca and larvae (Fig. 88–92). Tillyard (1926) wrote that adults appear to mimic coreid bugs. Hawkeswood (2007) described coloration of live adults of *A. balyi* and drew comparisons to pentatomid body and antennal color. To us, the adults appear like little grasshoppers, active on the plants and constantly moving their white-tipped antennae (Suppl. Film 9), resembling brachypterous acridid genera (Orthoptera), e.g., *Methiolopsis* Rehn, 1957 and *Praxibulus* Bolivar, 1906 (Rentz 2004), which sit around and waggle their antennae in these habitats.

Systematic status of *Aproida* and Aproidini. The monophyly of Aproidini is not controversial, well-supported by multiple features of the adults. The tribe has been considered as related to Anisoderini, Exothispini, and Eurispini (Pascoe 1863; Weise 1911; Würmli 1975; Samuelson 1989; Chaboo 2007). These positions place Aproidini among derived 'hispines'. Our findings support this position, that Aproidini is a clade of exophagous feeders that pre-date the origin of the crown-clade of tortoise beetles. Importantly, the larval caudal process indicates that the latter originated well before the telescopic anus and permanent fecal shield. We gain some insights into the steps towards the origin of tortoise beetles. Many aspects of the morphology of all stages of *A. balyi* suggest numerous unexplored phylogenetic characters. The ootheca, larvae with a single caudal process and abdominal ambulatory structures, the unique pupation, the flight capability, and sexual dimorphism of adults are the tip of the iceberg for further examination. Secretory glands for adhesive may exist in all the larval instars and in the pupa. Ambulatory ampullae have been used as phylogenetic characters at the level of the family Chrysomelidae (Lee 1993; Reid 1995, 2000).

Within the genus *Aproida*, *A. balyi* and *A. monteithi* appear to be phylogenetic sister species with respect to the flightless *A. cribrata*. Both *A. balyi* and *A. monteithi* occur at high altitude in the same Wet Tropics Biogeographic Region (WT). A major biogeographic barrier zone, known as the Black Mountain Barrier (BMB), divides the mountains of the northern half of the WT region (where *A. monteithi* occurs) from the mountains of the southern half of the region (where *A. balyi* occurs). As for many other sister-species pairs in the Wet Tropics region the BMB can be assumed to be the driving force behind their phylogenetic split (Yeates and Monteith 2008; Bryant and Krosch 2016).

Conclusions. Natural history information provides a wealth of characters that can improve recognition and resolution of evolutionary patterns. Our detailed study of *A. balyi* contributes novel characters and states that can further support the monophyly of Aproidini when these are tested to assess the phylogenetic status of Aproidini. Our study contributes to better understanding some major evolutionary transitions—endophagy to axillary feeding and exophagy, and the shield complex—in Cassidinae.

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Supplementary Materials

Supplementary film 1. Oviposition behavior in the beetle, *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Film: Vivian Sandoval, 1 min 5 secs.

Youtube link: https://youtu.be/YDaqXzUCga8
Video: 1H9A82987

Supplementary film 2. Feeding by larva, *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Note the caudal process with some fecal pellets. Film: Vivian Sandoval, 2 mins 44 secs.

Youtube link: https://youtu.be/MMuL2pS6oEg
Video: 1H9A3276

Supplementary film 3. Retractable abdominal suckers used in locomotion in the beetle larva, *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from (Australia). This is instar I; note the caudal process with some fecal pellets. Film: Vivian Sandoval, 22 seconds.

Youtube link: https://youtu.be/iZMUWGKYX0E

Video: 1H9A3549

Supplementary film 4. Retractable abdominal suckers (segments 1–VIII) used in locomotion in the beetle larva, *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. This is instar II; note the thoracic lobes at base of legs. Film: Vivian Sandoval, 1 min 56 secs.

Youtube link: https://youtu.be/eyw9xC24El0

Video: 1H9A3235

Supplementary film 5. Major movements, turning, and ambulation in the beetle larva (instar III), *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Film: Vivian Sandoval, 1 min 55 secs.

Youtube link: https://youtu.be/-_KervTVCPc

Video: 1H9A3213

Supplementary film 6. Temporary retention of fecal pellets in the beetle larva (instar I), *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Film: Vivian Sandoval, 1 min 40 secs.

Youtube link: https://youtu.be/qBiSWFoLGkw

Video: 1H9B3327

Supplementary film 7. Beetle larva (instar III) pupates, *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Film: Vivian Sandoval, 9 mins 39 secs.

Youtube link: https://youtu.be/0o7Pd75QfuQ

Video: 1H9A3100

Supplementary film 8. Beetle adult eclosion in *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Film: Vivian Sandoval, 1min 26 secs.

Youtube link: https://youtu.be/To2QFHSWk_c

Video: H9A3517

Supplementary film 9. Antennal movements of adult beetles, *Aproida balyi* (Chrysomelidae: Cassidinae: Aproidini) from Australia. Film: Vivian Sandoval, 2 mins 25 secs.

Youtube link: https://youtu.be/O9bbslm4hlg

Video: 1H9A3264