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Natural history of *Cassida sphaerula* Boheman, 1854
(Coleoptera: Chrysomelidae: Cassidinae: Cassidini)
on *Arctotheca prostrata* (Salisb.) Britten
(Asteraceae: Arctotidinae) in South Africa, with a checklist
of South African Cassidinae (leaf-mining and tortoise beetles)

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Natural history of *Cassida sphaerula* Boheman, 1854
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Abstract. The tortoise beetle, *Cassida sphaerula* Boheman, 1854 (Coleoptera: Chrysomelidae: Cassidinae: Cassidini) is endemic to South Africa. Its endemic host, *Arctotheca prostrata* (Salisb.) Britten (Asteraceae) has been introduced in other countries where it is becoming invasive. *Cassida sphaerula* could provide a potential biocontrol of *Arctotheca* weeds as it spends the entire life cycle on this host. An intensive field study, with rearing, photography, and short films of *C. sphaerula* was conducted in its native habitat to document the life cycle. A checklist of Cassidinae genera in South Africa, along with 19 new host records for Cassidini species in South Africa are presented. Oothecae are simple, with few laminate membranes enclosing fewer than five eggs. There are five larval instars. Larvae and adults feed by making a series of cuts in the ventral cuticle, forming an arc, and they consume the mesophyll as the cuticle is rolled to one side. This creates many ventral craters, thickened on one margin with the rolled cuticle; these ventral craters correspond to ‘windows’ in the dorsal leaf surface where the dorsal cuticle is left intact. This unusual feeding pattern is known in three *Cassida* species, all in South Africa. Like many tortoise beetles, instar I initiates a feces-only shield on its paired caudal processes (= urogomphi); this construction is retained, along with exuviae, by subsequent instars. The shield construction was studied by film and dissections. This revealed that the columnar or pyramidal shield in this species has an exterior of dry or moist feces that obscures the central nested stack of exuviae,

each exuviae compressed onto the caudal processes. Pupae may retain the entire larval shield of exuviae and feces or only the 5th instar exuviae; this behavioral flexibility in pupal shield retention is novel for tortoise beetles. Behaviors of *C. sphaerula* are discussed in the context of phylogenetic characters that can give evolutionary insights into the genus, tribe, and subfamily.

Key words. Invasive species, pest, weed, larva, herbivore.

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Introduction

Cassida Linnaeus, 1758 is the type of the genus of the chrysomelid subfamily Cassidinae (Gyllenhal 1813) and of the tribe Cassidini Chapuis, 1875. As currently defined, Cassidinae comprises 37 tribes, the former ‘Hispiinae’ and the tortoise beetles (Chen 1940; Staines 2002; Chaboo 2007). The tortoise beetle tribes of Cassidinae are distinguished from plesiomorphic “hispiines” and other cryptic-feeding tribes by the exophagous larvae possessing paired caudal processes (= urogomphi) on the 9th abdominal tergite. Furthermore, these tortoise beetle larvae exhibit a unique behavior—they build and carry a shield, held on the caudal processes, and composed of materials of their cast exuviae only or cast exuviae + feces (Olmstead 1994; Müller and Hilker 2003). The shields have different architectures depending on the texture, quantity, and form of the feces that are stacked unto the exuviae; the feces on these shields may be semi-liquid or dry, and loose, lumpy, or filamentous (see Świętojańska 2009 and citations therein). In many tribes, the pupae can also have paired caudal processes and retain the shield from the 5th instar (Steinhausen 1950). These complex ecological, morphological, and behavioral features subtend the crown clade of Cassidinae comprising eight tribes (Chaboo 2007): Basiprionotini, Cassidini, Eugenyssini, Hemisphaerotini, Ischyrosonychini, Mesomphaliini, Omocerini, and Spilophorini.

The online catalog of Borowiec and Świętojańska (2002–2022) treat Aspidimorphini as a tribe, but it has been synonymized in Cassidini (López-Pérez et al. 2018). Their catalog includes the tribes Delocraniini, Imatiidiini, and Notosacanthini; larvae in these tribes do not carry shields (Bondar 1940; García-Robledo et al. 2010; Sekerka et al. 2013; Monteith et al. 2021) and are plesiomorphic to the crown-clade Cassidinae (Chaboo 2007).

The tribe Cassidini has both Old World and New World species but all other cassidine tribes have either Old World or New World distributions (Weise 1911; Spaeth 1914). Cassidini contains 87 genera; *Cassida* is the most speciose with 459 recognized species distributed in both Old World and New World (Borowiec and Świętojańska 2002–2022). López-Pérez et al.’s (2018) morphology-based phylogenetic analyses of Cassidini did not recover a monophyletic Cassidini (unless it includes Ischyrosonychini) nor a monophyletic *Cassida*. There are many synonyms in the long history of *Cassida* reflecting the poor definition of the genus; still, more refining of species concepts is needed to achieve a rigorous monophyletic genus concept.

Documented host plants of *Cassida* are from about 16 plant families (Jolivet and Hawkeswood 1995; Borowiec 1995; Borowiec and Świętojańska 2002–2022); *Cassida* species can be mono- or oligophagous (Bordy and Doguet 1987). Goedært (1662) is the earliest report on juvenile stages in Cassidinae, for *Cassida vibex* Linnaeus, 1767 and *Cassida viridis* Linnaeus, 1758. Today, data on juveniles are available for 136 species of Cassidini (Świętojańska 2009) and for about 61 species of *Cassida*, however, most morphological descriptions are not detailed. *Cassida* larval shields have diverse architectures; the pupae retain the shield from the 5th instar (Heron 2008; Świętojańska 2009).

The fundamental problem in the systematics of *Cassida*, indeed in all Cassidinae, is the gap in knowledge about life history and ecology of species and limited specimen collections of all life stages for detailed comparisons. These would generate novel characters and states to better resolve more natural monophyletic groups and relationships.

This paper addresses that gap by reporting the first natural history account of *Cassida sphaerula* Boheman, 1854, a South African endemic. The Cassidinae of South Africa comprises 10 tribes, 32 genera, and ~205 species (Table 1; Staines 2015; Borowiec and Świętojańska 2002–2022). *Cassida* has 36 species documented in South Africa; six new species are being described (Borowiec and Świętojańska 2022). For those South African Cassidinae species using Asteraceae, host plants are listed in Table 2; we provide 20 new host records. *Cassida sphaerula* ranges from the Cape region to the Transvaal and KwaZulu-Natal (Borowiec and Świętojańska 2002–2022). Based on label data of specimens reared in Australia, this species was reported to use the host plant, *Arctotheca*

Table 1. Checklist of tribes and genera of Cassidinae in South Africa (Chrysomelidae). ‘Hispinæ’ = 6 tribes; 16 genera; 103 species (see Staines 2015 for species). Tortoise beetles = 4 tribes, 16 genera; ~101 species (see Borowiec and Świętojańska 2002–2022 for species).* = 6 species newly described by Borowiec and Świętojańska (2022).

Tribe Basiprionotini Hincks, 1952

Metrioepepla Fairmaire, 1882: 1 sp.

Tribe Callispini Chapuis, 1875

Callispa Baly, 1858: 8 spp.

Tribe Cassidini Gyllenhal, 1813

Aspidimorpha Hope, 1840: 19 spp.

Cassida Linnaeus, 1758: 41 spp.*

Chiridopsis Spaeth, 1922: 9 spp.

Conchyloctenia Spaeth, 1902: 8 spp.

Fornicocassis Spaeth, 1917: 1 sp.

Hybosinota Spaeth, 1909: 1 sp.

Ischiocassis Spaeth, 1917: 4 spp.

Laccoptera Boheman, 1855: 11 spp.

Limnocassis Spaeth, 1952: 3 spp.

Orobiocassis Spaeth, 1934: 3 spp.

Oxylepus Desbrochers, 1884: 6 spp.

Psolidoma Spaeth, 1899: 1 sp.: questionable record)

Rhytidocassis Spaeth, 1941: 3 spp.

Smeringaspis Spaeth, 1934: 1 sp.

Trichaspis Spaeth, 1911: 3 spp.

Tribe Cryptonychini Chapuis, 1875

Cryptonychus Gyllenhal, 1817: 2 spp.

Tribe Gonophorini Chapuis, 1875

Agonita Strand, 1942: 4 spp.

Tribe Hispini Gyllenhal, 1813

Callanisa Uhmman, 1959: 1 spp.

Chrysispa Weise, 1897: 1 spp.

Dactylispa Weise, 1897: 30 spp.

Di cladispa Gestro, 1897: 36 spp.

Dor cathispa Weise, 1900: 3 spp.

Hispellinus Weise, 1897: 1 spp.

Platypria Guérin-Méneville, 1840: 3 spp.

Polyconia Weise, 1905: 1 spp.

Pseudispella Kraatz, 1895: 1 spp.

Thoracispa Chapuis, 1875: 3 spp.

Trichispa Chapuis, 1875: 1 spp.

Tribe Leptispini Fairmaire, 1868

Leptispa Baly, 1858: 6 spp.

Tribe Notosacanthini Hincks, 1952

Herminella Spaeth, 1913: 4 spp.

Notosacantha Chevrolat, 1837: 11 spp.

Tribe Oncocephalini Chapuis, 1875

Oncocephala Agassiz, 1846: 2 spp.

calendula (L.) Levyns (Asteraceae: Arctotidinae; Heron and Borowiec 1997) which is native to South Africa but has become an introduced invasive in Australia (Groves et al. 2003) and California (Brossard et al. 2000). Taylor (1965) reported *Combretum* Loefl. (Combretaceae) as a host plant, but this is possibly erroneous as Combretaceae is not considered a host of tortoise beetles (Borowiec and Świętojańska 2002–2022) and it is a host for a few other chrysomelids (Jolivet and Hawkeswood 1995). Little else is known about *C. sphaerula* in its native habitat in South Africa.

Here we document the second native host, *Arctotheca prostrata* (Salisb.) Britten. Access to a good-sized population of *C. sphaerula* is allowing ongoing study and specimen collection of *C. sphaerula*. We note its potential as a biocontrol agent for *A. prostrata* outside of the native range, where the plant poses a weed risk.

Arctotheca prostrata (Fig. 1–5) is endemic to South Africa where it has several common names, including prostrate Cape weed and Cape dandelion. It can be regarded as a weed in South African gardens—hundreds of plants are dug and removed every year from author SA’s garden. However, seed packets and garden plants are sold in local nurseries. The genus *Arctotheca* Vaill. comprises five species (McKenzie et al. 2005): *Arctotheca calendula* (Fig. 6), *Arctotheca forbesiana* K. Lewin, *Arctotheca populifolia* (P.K. Bergius) Norl., *Arctotheca prostrata* (Fig. 1–5), and *Arctotheca marginata* Beyers (Beyers 2000). These are perennial or, occasionally, annual, trailing, or erect herbs (Ghafoor and Bean 2015). *Arctotheca calendula* and *A. prostrata* have been recognized as weeds in multiple countries (Hinojosa-Espinosa and Villaseñor 2015; Atlas of Living Australia 2021; California Invasive Plant Council 2021; GBIF 2021a, b, c; Jepson eFlora 2021) and *A. populifolia* is a weed in Australia. These three species became weeds after escaping from cultivation (Mahoney and McKenzie 2008; Hinojosa-Espinosa and Villaseñor 2015; Lucid Central Weeds of Australia 2021) or due to being contaminants of stock fodder and packing straw (Wood 1994).

One UK-based gardening website (Candide 2021) lists all three weedy *Arctotheca* species with photos and promotes two of them: *A. populifolia* as a garden species that attracts bees and acts as weed suppressors and dune stabilizer; and *A. calendula* as a bee and butterfly attractant that can be planted as a showy ground cover or bedding plant for spring and early summer display (Candide 2021). These plants can cover large landscapes and have

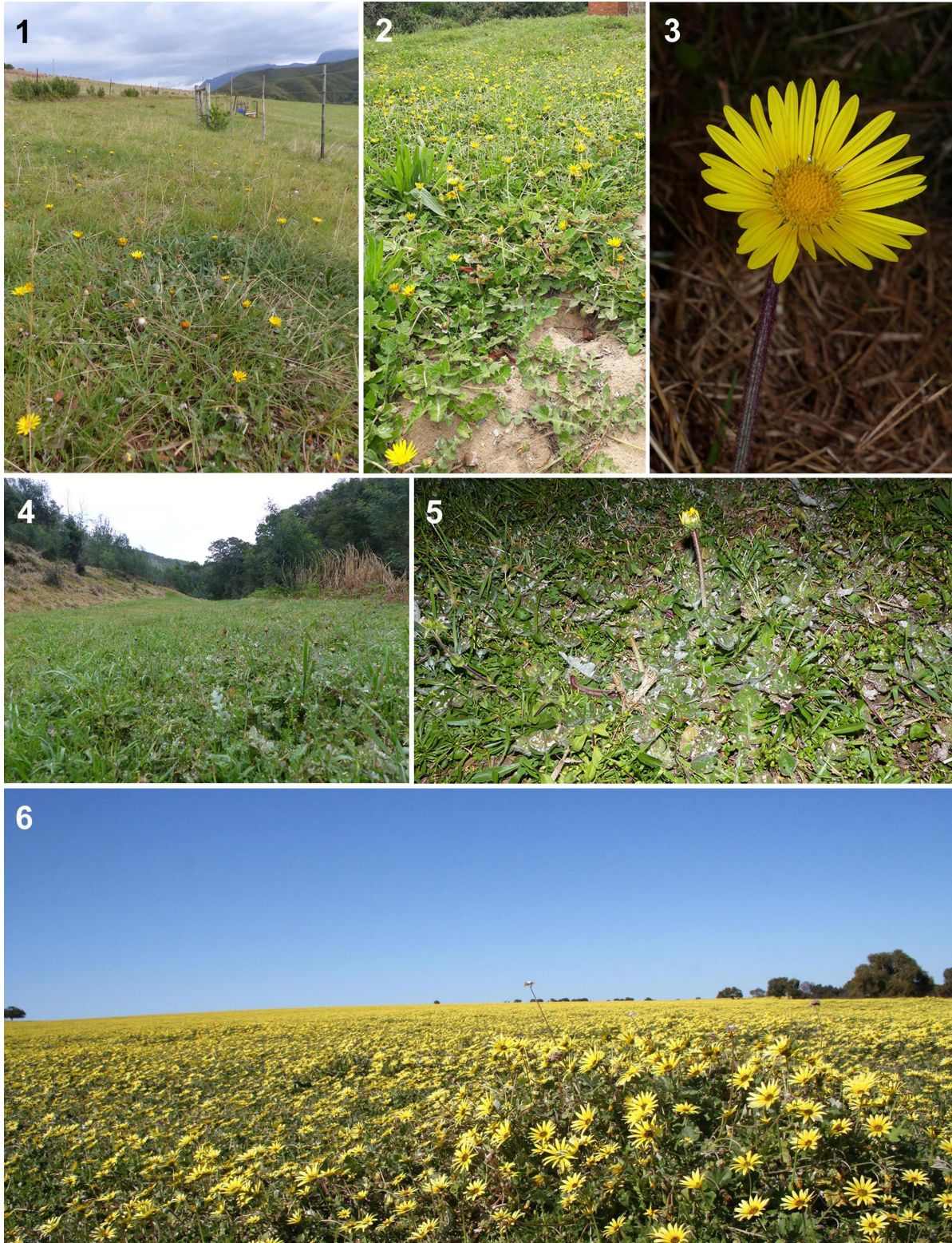
Table 2. Asteraceae host plants used by Cassidinae in South Africa.

Host plant	<i>Cassida</i> species	Comments and references
<i>Arctotheca calendula</i> L.	<i>Cassida sphaerula</i> Boheman, 1854	Heron and Borowiec 1997
<i>Arctotheca prostrata</i> (Salisbury) Britten	<i>Cassida sphaerula</i> Boheman, 1854	new record of S. Adam www.inaturalist.org; confirmed breeding
<i>Berkheya bipinnatifida</i> (Harvey) Roessl	<i>Cassida guttipennis</i> Boheman, 1862	Heron and Borowiec 1997; Heron 2003, 2011; confirmed breeding
<i>Berkheya heterophylla</i> (Thunberg) O.Hoffmann	<i>Cassida guttipennis</i> Boheman, 1862	Label inf., SANC, PPRI
<i>Berkheya maritima</i> J.M. Wood & M.S. Evans	<i>Cassida quatuordecimsignata</i> Spaeth, 1899	new record ; confirmed feeding
<i>Berkheya onopordifolia</i> (DC) O. Hoffmann ex Burt Davy.	<i>Cassida quatuordecimsignata</i> Spaeth, 1899	new record ; nomad; confirmed feeding
<i>Berkheya pinnatifida</i> (Thunberg) Thellung	<i>Cassida quatuordecimsignata</i> Spaeth, 1899	new record ; confirmed breeding
<i>Berkheya rhapontica</i> (DC) Hutchinson & Burt Davy	<i>Cassida guttipennis</i> Boheman, 1862	new record ; confirmed breeding
<i>Berkheya seminivea</i> Harvey	<i>Cassida guttipennis</i> Boheman, 1862	new record ; confirmed breeding; Label inf., SANC, PPRI
<i>Berkheya speciosa</i> (De Candolle) O. Hoffmann	<i>Cassida guttipennis</i> Boheman, 1862	Heron and Borowiec 1997; Heron 2003; confirmed breeding
	<i>Cassida vespertilio</i> Boheman, 1862	at Howick, Natal; confirmed breeding
	<i>Cassida</i> sp. nov. 2 (Borowiec and Świętojańska 2022)	at Umzinto; confirmed breeding
<i>Berkheya</i> sp. #1	<i>Cassida vespertilio</i> Boheman, 1862	new record ; observed at Ingeli; confirmed breeding
<i>Berkheya</i> sp. #2	<i>Cassida quatuordecimsignata</i> Spaeth, 1899	new record ; Howick, Natal; confirmed breeding
<i>Berkheya</i> sp. #3	<i>Cassida quatuordecimsignata</i> Spaeth, 1899	new record ; Voorkeur Siding, Natal; confirmed breeding
<i>Berkheya</i> sp. #4	<i>Cassida guttipennis</i> Boheman, 1862	new record ; confirmed breeding.
<i>Brachylaena discolor</i> De Candolle	<i>Basipta stolidi</i> Boheman, 1854	Borowiec 2002; Heron and Borowiec 1997; Heron 2003; Muir and Sharp 1904; species erroneously given as <i>Basipta</i> <i>glauca</i> , Identification corrected in Borowiec 1999; confirmed breeding
	<i>Cassida granulicollis</i> Spaeth, 1905	Heron and Borowiec 1997; confirmed breeding
	<i>Cassida unimaculata</i> Boheman, 1854	Heron and Borowiec 1997; Heron 2003; Muir and Sharp 1904; confirmed breeding
<i>Brachylaena elliptica</i> (Thunberg) De Candolle	<i>Basipta stolidi</i> Boheman, 1854	new record ; confirmed breeding
	<i>Cassida unimaculata</i> Boheman, 1854	new record ; confirmed breeding
<i>Brachylaena huillensis</i> O.Hoffmann	<i>Cassida granulicollis</i> Spaeth, 1905	new record ; Label inf. SANC, PPRI (shaken from tree)
<i>Brachylaena rotundata</i> S. Moore	<i>Cassida granulicollis</i> Spaeth, 1905	new record ; Label inf. SANC, PPRI

Host plant	<i>Cassida</i> species	Comments and references
<i>Brachylaena uniflora</i> Harvey	<i>Basipta stolidata</i> Boheman, 1854	new record ; Label inf. SANC, PPRI (identified as “ <i>Brachylaena</i> sp. cf. <i>uniflora</i> ”); Heron 2018; confirmed breeding
	<i>Cassida unimaculata</i> Boheman, 1854	Heron 2018; confirmed breeding
<i>Chrysanthemoides incana</i> (Burman f.) Norlindh	<i>Cassida foveolatipennis</i> Borowiec and Świętojańska, 2001	Borowiec and Świętojańska 2001; confirmed breeding
<i>Chrysanthemoides monilifera</i> (L.) Norlindh subsp. <i>monilifera</i> (L.) Norlindh. (= <i>Chrysanthemoides monilifera</i> (L.) Norlindh)	<i>Cassida chrysanthemoides</i> Borowiec and Świętojańska, 2001	Borowiec and Świętojańska 2001; confirmed breeding
<i>Chrysanthemoides monilifera</i> (L.) Norlindh subsp. <i>pisifera</i> (L.) Norlindh	<i>Cassida foveolatipennis</i> Borowiec and Świętojańska, 2001	Borowiec and Świętojańska 2001; confirmed breeding
	<i>Cassida chrysanthemoides</i> Borowiec and Świętojańska, 2001	Borowiec and Świętojańska 2001; confirmed breeding
<i>Chrysanthemoides monilifera</i> (L.) Norlindh. subsp. <i>rotundata</i> (De Candolle) Norlindh	<i>Cassida diversipunctata</i> Borowiec and Świętojańska, 2001	Borowiec and Świętojańska 2001; confirmed breeding
<i>Chrysanthemoides monilifera</i> (L.) Norlindh. subsp. <i>subcanescens</i> (De Candolle) Norlindh	<i>Cassida spatiosiformis</i> Borowiec and Świętojańska, 2001	Borowiec and Świętojańska 2001; beetle erroneously given as <i>Cassida spatiosa</i> in Heron and Borowiec 1997; confirmed breeding
<i>Othonna quinqueidentata</i> Thunberg	<i>Cassida pudens</i> Boheman, 1854	Borowiec and Świętojańska 2001; Heron and Borowiec 1997 (under <i>Cassida subplana</i> Spaeth, 1928)
<i>Sonchus asper</i> (L.) Hill var. <i>asper</i> (Kuntze) O. Hoffmann	<i>Cassida sulphurago</i> Boheman, 1854	new record ; label inf., SANC, PPRI
<i>Tarchonanthus littoralis</i> P. Herman	<i>Basipta luteocincta</i> Boheman, 1854	new record ; Label inf., SANC, PPRI, under <i>T. camphoratus</i> L.; confirmed breeding; <i>T. camphoratus</i> group revised by Herman 2002
<i>Tarchonanthus obovatus</i> De Candolle	<i>Cassida sulphurago</i> Boheman, 1854	new record ; H. de Klerk photo inf. under <i>T. camphoratus</i> L.; <i>T. camphoratus</i> group revised by Herman 2002; confirmed feeding
<i>Tarchonanthus trilobus</i> De Candolle	<i>Basipta stolidata</i> Boheman, 1854	new record ; confirmed breeding
	<i>Cassida unimaculata</i> Boheman, 1854	new record ; suspected feeding

attractive yellow flowers (Fig. 6). *Arctotheca calendula* is promoted on a USA-based website (Gardenia.net 2021) as a tough and easy-to-grow perennial that blooms most of the year. Such information is likely to appeal to some gardeners and encourage its propagation.

Arctotheca prostrata has recently been recorded in new countries. The first herbarium record of this species in Australia dates to 1946 (Australasian Virtual Herbarium 2021), whereas the first records in Mexico are from 2015 (Hinojosa-Espinosa and Villaseñor 2015) and in Italy from 2018 (Galasso et al. 2019). In Italy it is hypothesized to have been introduced via stolons transported in soil (Galasso et al. 2019). In the U.S.A., the species was introduced as ground cover (Veit 2014, date unspecified) and records of its occurrence begin in 2002 (EDDMapS 2021). Records of *A. prostrata* have in the past been amalgamated with *A. calendula*, despite being two distinct species (Mahoney and McKenzie 2008). The Calflora website (Calflora 2021) lists *A. prostrata* as: “the infertile form. The fertile form is *Arctotheca calendula*”. However, Veit (2014) found that Californian *A. prostrata* is fertile and able to produce achenes/seeds that germinate; if the populations become more numerous and closer together, cross-pollination may allow for fertile seeds to be produced. *Arctotheca prostrata* is a sterile perennial that spreads aggressively by prostrate stems; invasions favor roadsides and other disturbed sites (Mahoney and McKenzie



Figures 1–6. *Arctotheca prostrata* (Salisb.) Britten (Asteraceae) in its native habitat, South Africa (photos: S. Adam, September 2021). **1–4** Various sites on the farm Laaiplaats, Mossel Bay. **5**) Leaves appear spotted due to beetle feeding damage, farm Laaiplaats. **6**) *Arctotheca calendula* in Australia, showing how successfully these plants overtake bare soil (photo: Stephen D. Hopper).

2008). In California, this plant is listed as having an overall risk score of “Moderate” (Brusati 2004). Due to the invasive and weedy nature of *A. prostrata*, natural history of its native herbivores is important to document as they can lead to the development of biological control agents (Harley and Forno 1992).

This detailed record of feeding habits of *C. sphaerula* on *A. prostrata* raises the possibility of its development and use as a biocontrol agent. Good biocontrol agents should exhibit three fundamental qualities: (1) specificity to the host species and host genotype, (2) damage (the more damage it causes the better as a biocontrol agent); and (3) potential for establishment in the introduced range (Knutson and Coulston 1997; van Klinken and Raghu 2006; Müller-Schärer and Schaffner 2008). *Cassida sphaerula* has been documented as a natural enemy of *A. calendula* (Scott and Way 1990) and possibly without enough species-specificity. Species specificity, however, is more important in the designation of a biological control agent than in its natural range. If no other non-invasive plant species are recorded as plant hosts, the use of *C. sphaerula* could still be supported as a biological control agent where it is wanted.

Materials and Methods

Author SA studied, reared, collected, photographed, and filmed many individuals of *C. sphaerula* on multiple plants of *A. prostrata* scattered in several locations (Fig. 1–5), including her own garden: SOUTH AFRICA: Province Western Cape, Mossel Bay, Laaiplaats 59, –33.966030 22.089960, 188m elev., farm habitat, 18.VIII.2021–31.I.2022, coll. S. Adam. Another site within the same farm was at –33.967890 22.094130, 95m elev., 18.VIII.2021–31.I.2022, coll. S. Adam; Mossel Bay, farm ‘Bosrug’, –33.961200 22.093260, 91m elev., 18.VIII.2021–3.XI.2021, coll. S. Adam; Moordkuil River, –33.967890 22.094130, 95m elev., 18.VIII.2021–3.XI.2021, coll. S. Adam; Bosman River, –33.966030 22.089960, 188m elev., 18.VIII.2021–3.XI.2021, coll. S. Adam; Blommekloof, grassy field, –33.94271805, 22.0601465875, 280m elev., 3.VI.2022 and 10.VI.2022, coll. S. Adam

At Goukamma Reserve (near Knysna), –34.06556 22.94379, 21.X.2021, on the coast about an hour from Mossel Bay, the “lawn” area around the picnic site (Fig. 8–9) and amenities was very disturbed by the activity of Cape dune mole-rat (*Bathyergus suillus* (Schreber, 1782): Bathyergidae, Bathyerginae)) and the *Arctotheca* plants were extensive and abundant. The Cape Mole-rat, *Georychus capensis* (Pallas, 1778) (Bathyergidae, Georychinae) also occurs in the same area. However, inspection did not turn up any *C. sphaerula*, only snails eating the plants. On 30.X.2021, one 50 Km reconnaissance trip was conducted by SA and a coastal trip, –34.0765, 22.1655 to –33.8732, 22.0307, was done by Wendy Wiles and Sandra Falanga, searching for additional locations of plants and beetles. These trips found plants with beetle-feeding damage and beetles in multiple areas along the routes, but not above 750 m ASL elev.

Throughout spring to autumn 2021, the beetles were always present at the farm habitat (Laaiplaats 59), with teneral (straw-colored) and mature (green) adults. Brief examinations found seven larvae (three young, four mature) on 3.XI.2021; five larvae, no pupae, two green adults, one yellow-green adult, on 4.XI.2021; and one pre-pupa and a few adult teneral adults on 14.XI.2021. The last *Cassida* individual was seen on 23.XII.2021; no individuals have been found on the plants in mid-summer. Beetle activity resumed in autumn (early May 2022) and was observed in several sites (maximum temperature of 82.4°F (28°C) and minimum temperature of 35.6°F (2°C)).

Habitat ecology. Mossel Bay is on the south coast of South Africa. The climate is classified as semi-arid (Koppen climate classification, Kottek et al. 2006) and is moderated by proximity to the ocean. The area has short dry summers (late November to late March) and long, cool, windy winters. Temperatures range from 52–75°F; precipitation (~420 mm/yr) is somewhat even throughout the year, as rain or snow (WeatherSpark 2021).

Identifications. Photos were uploaded to the online repository, iNaturalist (2021) and the beetle species was identified initially by RW. Vouchers of juveniles and adults of the beetle were collected, deposited at South Africa National Insects Collection, South African National Biodiversity Institute (SANBI), and loaned to CSC. The beetle species was confirmed after studying collected specimens by CSC and by Elizabeth Grobbelaar, ARC Identification Services, Pretoria. The type is housed in Museum für Naturkunde de Humboldt-Universität (ZMHU), Berlin, which is currently relocating their insect collection so access to types is not possible. Vouchers of the



Figures 7–8. Coastal area with extensive growth of *Arctotheca prostrata*, Goukamma Reserve, South Africa. Plants intact but soil disturbed by the activity of Cape dune mole-rat (Bathyergidae: Bathyerginae: *Bathyergus suillus* (Schreber, 1782)).

host plant are deposited with and identified by Robert McKenzie, Dept. of Botany, Rhodes University and Nicola Bergh, Compton Herbarium, SANBI.

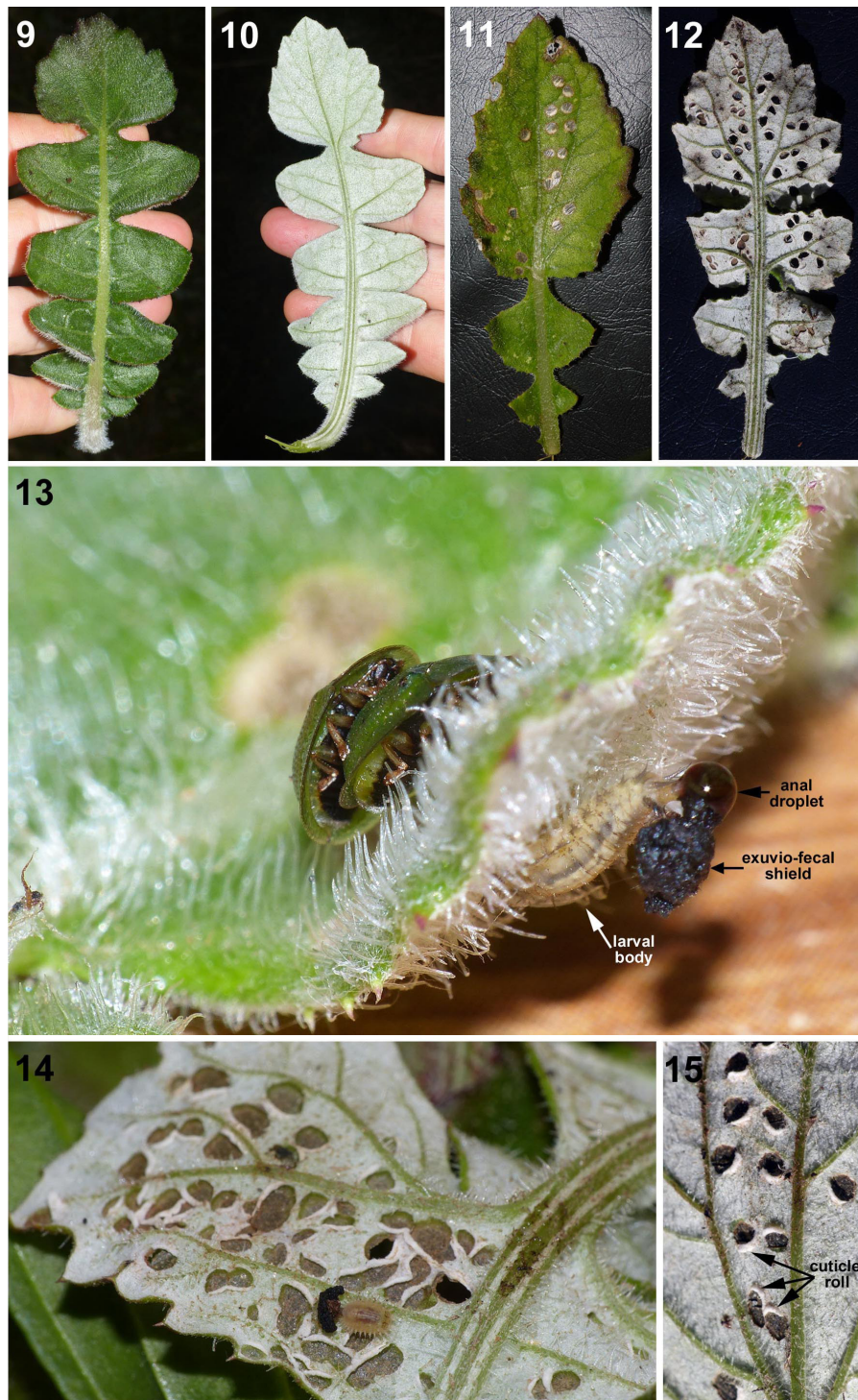
Imaging. Photos were taken with a Panasonic® DMC-FZ200 camera with a Raynox® macroscopic lens M-150. Specimens were studied with a Zeiss® stereoscopic microscope with a Dino-Lite® eyepiece digital microscope/camera. Photo editing was done in Paint.net or Photoshop®.

Specimen study. Only specimens from field collections and rearing are studied here. These are deposited at the South Africa National Insect Collection, Pretoria, and the University of Nebraska-Lincoln. Specimens of *C. sphaerula* are in South African institutions (mainly, South Africa National Insect Collection, Iziko Museums, Dipsong Museum, and National Museum of Bloemfontein) but we are unable to travel at present, to study and confirm identifications and add more locality information in the present study.

Observations. Author SA checked the *C. sphaerula* population on their host daily from August 2021 to June 2022. She brought eggs, larvae of different ages, pupae, and adults indoors for observation and rearing. She successfully followed eggs to hatching, and three of these hatchlings were followed through all instars, pre-pupation, pupation, and then the emergence of teneral adults.

Feeding behavior. Multiple adults and larvae were maintained in small plastic containers (at ambient temperature, humidity, and light) to determine the feeding pattern. Intact leaves were presented for feeding and the larva (different ages) or adult was removed at different times to view their cuts into the leaf (the expanded pronotum obscures feeding in both larvae and adults of this species). Both larval and adult feeding were observed and filmed (Video 1–4); larvae were discovered cutting and eating trichomes (Video 2).

Exuvio-fecal shield architecture and construction. In several subfamilies of Chrysomelidae, larvae retain their feces directly on the body (Criocerinae, certain Galerucinae) or use it as a construction material in cases they live in (Camptosomata) or carry as an umbrella over the body (Cassidinae: tortoise beetles) (Chaboo 2007, 2011; Chaboo et al. 2007, 2008). In tortoise beetles, the larvae retain the shield on the caudal processes, holding it over the body like an umbrella, or moving it in different angles, even bringing it flat against the dorsum. The caudal processes in Cassidinae have been called “apical furci”, “supra-anal processes”, and “spines” in the cassidine literature (see Chaboo 2007: 68–74); “urogomphi” is used in the insect literature but these structures are not all homologous. Other materials may be added or become established in the fecal medium of the shield, e.g., exuviae, gut microbes, trichomes, fungi, other chemicals. Author SA followed multiple larvae of various instars in plastic dishes at ambient conditions and took photos at 2-hour time intervals to capture the initiation,



Figures 9–15. *Arctotheca prostrata* with feeding damage by beetle, *Cassida sphaerula* Boheman, 1853 (photos: S. Adam, September 2021). **9)** Intact leaf, dorsal view. **10)** Intact leaf, ventral view. **11)** Leaf, dorsal view, with window-pane pattern where beetles leave dorsal cuticle intact. **12)** Leaf, ventral view, with craters left by beetle feeding damage. **13)** Leaf with paired green adults (dorsal) and cream-colored larva showing blackish exuvio-fecal shield (held on caudal processes) and wet anal droplet to apply to shield. Note hirsute dorsal and ventral surfaces of host leaf. **14)** Leaf with many feeding craters and single larva with exuvio-fecal shield; note feeding is only between veins. **15)** Feeding craters, each with marginal cuticle roll.

expansion, and maintenance of the exuvio-fecal shield. Shields were removed, by gently prying them off the living caudal processes, and abraded with a forceps to remove small fecal pieces. This allowed determination of the shield architecture. We describe the construction process based on many days of observations, many dissections of exuvial-fecal shields, and a large archive of imagery (stills and films).

Results

Beetles and plants are found in several areas within our main study site, the 97-ha farm, and in many populations along the Moordkuil and Bosman rivers in the area. Some *A. prostrata* plant patches can be heavily infested and show considerable damage with leaves appearing spotted (Fig. 5). No nearby plants of other species were found to host *C. sphaerula*. During winter, *A. prostrata* plants show some die-back/browning of the leaves, especially in areas subject to frost; in more temperate areas, they continue to grow. From early summer (27.XII.2021) until autumn (mid-May 2022), the *Arctotheca* plants are quite patchy, and get burned to a crisp in sunny spots but do better in shaded areas. Other animals on the plants are rare during this hot period, with only the occasional slug found on *Arctotheca*. At the Goukamma Reserve on the coast, we observed the “lawn” around the picnic site and amenities (Fig. 7–8) to be very disturbed by Cape dune mole-rat activity. The *A. prostrata* growth is excellent, but no *C. sphaerula* were found eating these plants, only snails.

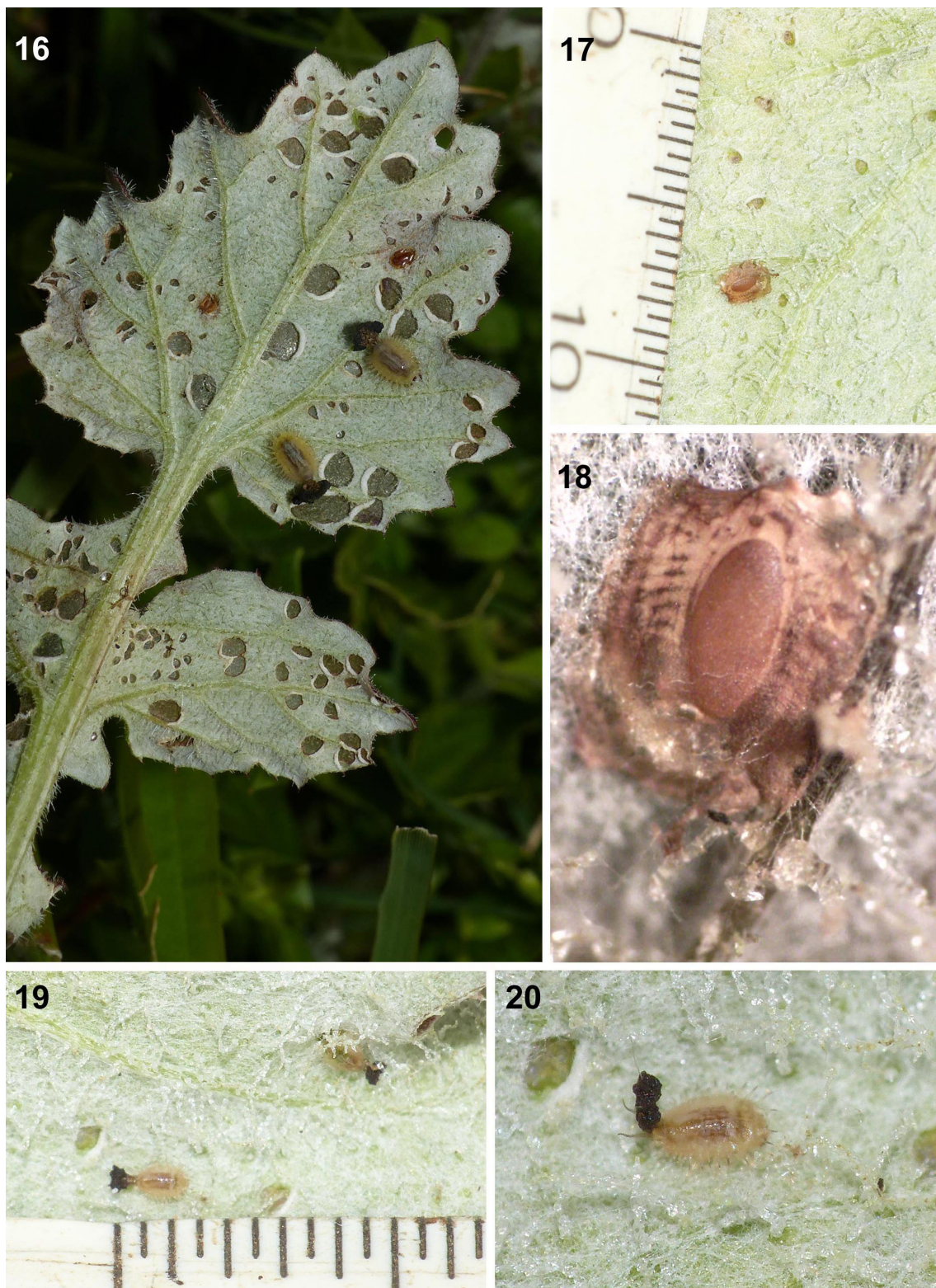
Natural history of *Cassida sphaerula* Boheman, 1854

Field observations over almost one year revealed the beetle’s cycle of activity. Our observations began at the end of one breeding season. From early summer (27.XII.2021) till early autumn (mid-May 2022) no adults or larvae were seen. Then the new breeding season began in late autumn. The first sign of beetle activity is the small ‘windows’ chewed on the plant leaves in autumn (late May); then the larvae can be seen on the underside. Egg-laying begins in May, with much larval activity by mid-June, when minimum temperatures are around 35.6°F (2°C). Up to 8 egg cases have been found on a single leaf. Thus, we believe this species is an autumn/winter breeder.

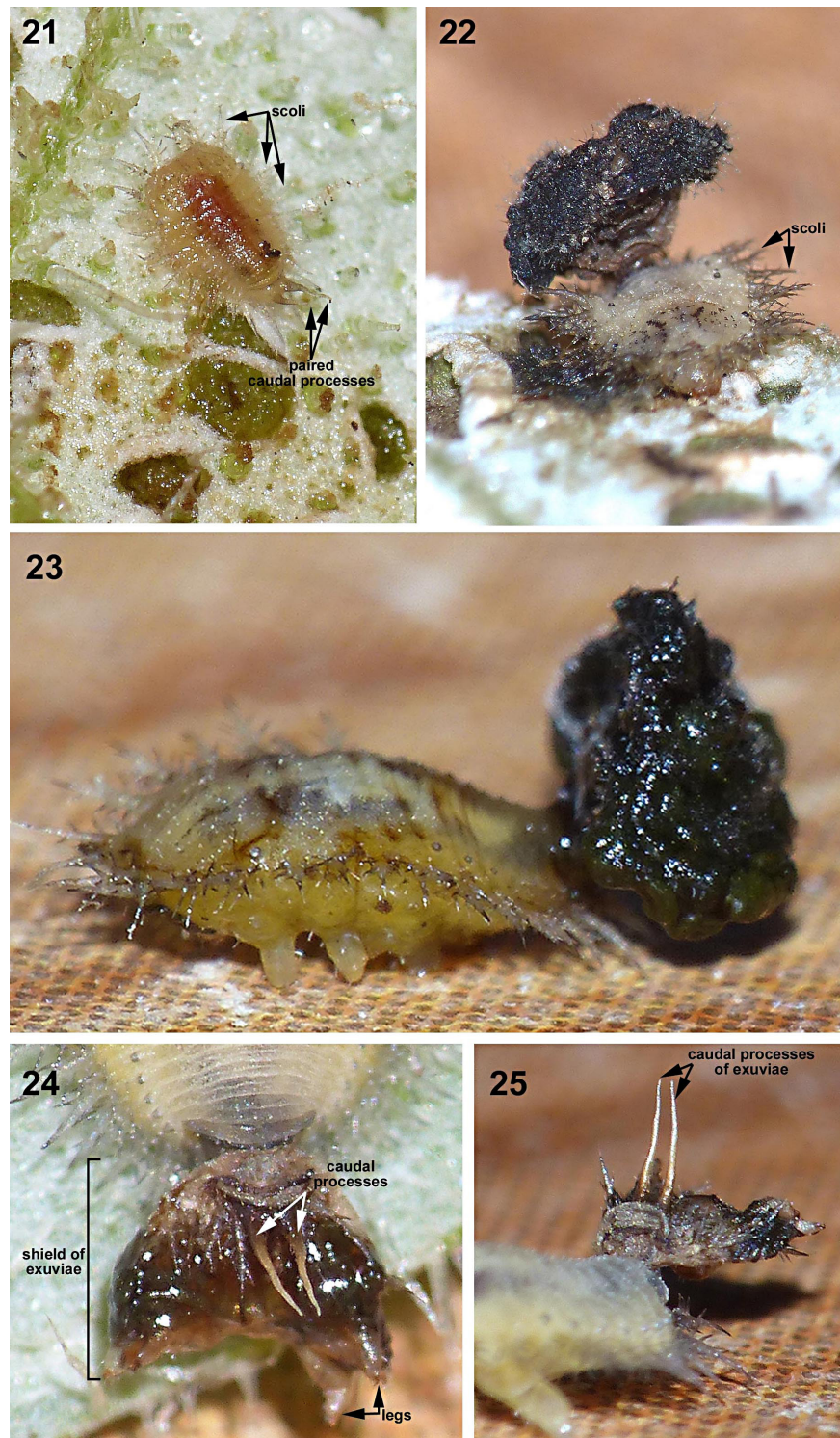
Egg cases (n=4) (Fig. 16–18). Oothecae are deposited on the venter of the leaf (Fig. 16) in apparently random areas between veins. We observed a maximum of eight oothecae per leaf. The ootheca lies flattened on the long axis, shallowly tucked into the leaf surface as there is a slight depression under each one; it is not stalked, suspended or protuberant from the leaf surface, as in some other Cassidinae. *Oviposition* was not observed so it is unclear how the female may prepare a site before depositing her eggs (see Müller and Rosenberger (2006) for possible oviposition sequences in Chrysomelidae). The ootheca, secreted by colleterial glands (Hinton 1981; Gillet 2002), comprises a thin opaque outer laminate membrane that appears shiny and dark brown (Fig. 17–18). The few enclosed eggs (less than 5) are cream-colored (Fig. 17–18), dorsoventrally compressed (lying flattened on leaf), and elongate-oval shaped. The ootheca lacks any additional coverings, no fecal or chewed plant material. *Egg hatch.* One ootheca was collected on 11.X.2021 and three larvae hatched on 18.X.2021, confirming that more than one egg is oviposited at a time. We did not observe how the larvae exited the egg case, but we found the ootheca roughly torn at one end and left behind, therefore not eaten by the neonate.

Larva (n=20; Fig. 13–14, 16, 19–25). The larvae are solitary, not apparently gregarious, but may be found mixed with others of different stages in a dense situation, even feeding side by side with scoli (lateral projections) in contact. They do not respond to disturbance by moving into groups or with coordinated cycloalectic (ring) defense where larvae move into a tight, somewhat circular, group and all flex the shield in unison (see Jolivet et al. 1990).

Larvae are found mostly on the venter of the leaves. Instar I (n=3; Fig. 19–20) are tear-dropped shaped, about 2 mm long X 1 mm at maximum width (across pronotum). The body is tan-colored. The paired caudal processes (Fig. 21, 24–25; = supra-anal processes, urogomphi) are almost half as long as the body. Older larvae (Fig. 23) are creamy yellow and with a dark brown central area; their cuticle is almost transparent, and the internal organs are somewhat visible (internal movements are easily seen). The scoli pattern (Fig. 21–22) and caudal processes are similar between instars and fit with Świątojańska’s (2009: 74) generalized *Cassida* larvae having an ovoid dorso-ventrally flattened body with 16 pairs of lateral scoli.



Figures 16–18. Ootheca and young larvae of *Cassida sphaerula* (photos: S. Adam, September 2021). **16)** Venter of host leaf with two oothecae (arrows) and two instar III with their black exuvio-fecal shields. **17)** Ootheca (~2 mm long). **18)** Ootheca with oval-shaped egg. **19)** Two young instar I (~2 mm long) with tiny black shield composed entirely of its own feces. **20)** Mature instar I with larger shield (reared from Fig. 19).



Figures 21–25. Larva of *Cassida sphaerula* (photos: S. Adam, September 2021). **21)** Young instar with lateral projections called scoli; shield removed to expose paired caudal processes. **22)** Older instar (frontal view) with exuvio-fecal shield attached to caudal processes; feces appear dry. **23)** Older instar with moist exuvio-fecal shield. **24)** Older instar, dorsal view, with feces removed; legs and caudal processes of exuviae of previous instar apparent. **25)** Hind end of older larva with dry exuvio-fecal shield. Paired caudal processes of previous instar are exposed, projecting dorsad. The caudal processes of this larva is hidden, stacked within the observable caudal processes.

Exuvio-fecal shield. The larval shield is initiated in Instar 1 (Fig. 19) shortly after it initiates feeding. This shield is comprised only of larval feces that is applied to the caudal processes by the muscular telescoped anus. The shield grows into an elongate mass on the larva's paired caudal processes (Fig. 20). The shield can appear dry (Fig. 22) or wet (Fig. 23) and the telescoped anus periodically applies a dark wet droplet (see Fig. 13) to the shield. Dissections of shields reveal a fan (Fig. 22) or pyramidal shape (Fig. 23) with a central scaffold of stacked, nested exuviae and all entirely covered in dry or moist feces. The exuviae are not easily discerned in intact shields (e.g., Fig. 23). In dissected shields (Fig. 24–25), the feces are abraded to reveal the stack of exuviae; each exuviae can be individually teased off to show the caudal processes of older instars. The larvae continue to build, applying fresh feces and wet droplets (note wet appearance in Fig. 24).

Pupa ($n=10$; Fig. 26–27). The pre-pupal stage is typically when the mature larvae ceases feeding, become sedentary and fixes its abdomen to the substrate. Five young larvae were followed (three from egg hatch) to adulthood; three pupated; pupation lasted nine days, 15 days, and 20 days. Six mixed-age pupae/pre-pupae were placed in a container on 28.VIII.2021 and the first adult appeared on 7.X.2021 (9 days); two of these pupae failed and four adults were reared. Thus, pupation ($n=7$) ranges from 9–20 days. No parasitoids emerged from these laboratory pupae.

Pupae (Fig. 26–27) are ~9 mm long, solitary, affixed by their abdomen to the leaf venter, never on the upper part. There is seldom more than one pupa per leaf. The pupa is tan-colored, and the body is ovoid and dorso-ventrally flattened. Only the abdominal segments have lateral scoli.

The pupa of *C. sphaerula* shows two types of shields. It may retain the final exuviae (Fig. 26) and the former larval shield may be found discarded nearby or the pupa may retain the entire shield structure of the 5th instar larva (exuviae I–IV and their fecal matter) (Fig. 27). As far as we know, this is the first observation of such flexibility in shield retention in cassidine pupal shields. After the adults have emerged, the pupal exuviae remains attached to the plant for a long time, with or without the fecal shield. A few adults seem to have some difficulty eclosing, taking longer and struggling to exit the exuviae, but these adults eventually became hardened and moved away.

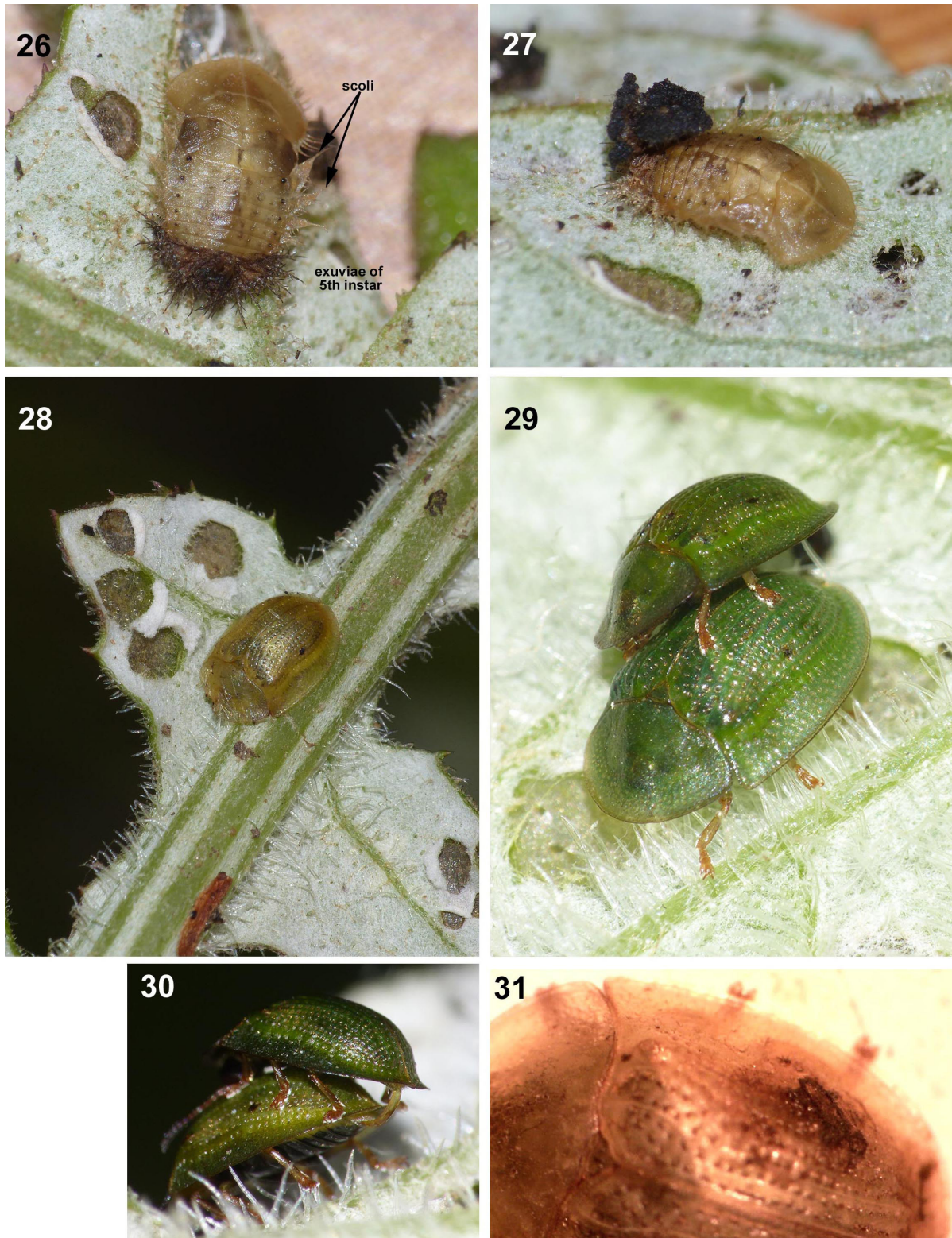
Adult ($n=30$; Fig. 28–30). These are ~9 mm long (along midline, head to posterior margin) by 4–5mm at their maximum width (across pronotum). The dorsum is generally pale green in color but can vary from translucent straw to a deep green. They were observed as early as 30 August (reared) and 23 September (wild) and are generally solitary. During the observation period, the habitat experienced a frost (late August) and the beetles remained sluggish but resumed activity as temperatures rose.

Color/pattern variations. Newly eclosed or teneral adults are straw (pale-brown) colored and the mature hardened adults are green. We only observed mating pairs of green individuals. As adults age, some acquire permanent circular blackish marks in different locations of the elytra (Fig. 30), but we did not detect marked color polymorphism as in some Cassidini (Simon Thomas 1964; Verma and Kalaichelvan 2004).

Courtship and mating (Fig. 13, 29). Mating pairs were first observed on 24.VIII.2021, as the frost season ended, and the region transitioned to spring. Courtship was not observed by the many mating pairs found, but pairs in copula were noted. Mature green adults exhibited no rapid (a few seconds) color changes (with temporary black spots or to golden or straw colors) as documented for some Cassidinae during mating or when disturbed (Barrows 1979).

Dormancy. Beetle activity ceased as the summer peaked and it is unclear where they hide. The host plants do not lose leaves in winter, suggesting that the beetles can have a steady food supply, further supporting them as a good biocontrol agent. We continue observations in 2022 but have not determined if beetles pass the winter hidden under stones or in dead vegetable matter, as they tend to do in the Natal area (Heron, pers. obs.).

Feeding patterns (Fig. 11–12, 14–16, 28) of *C. sphaerula*. Larvae and adults feed in similar ways, which creates a distinct pattern of craters on the venter of the leaf, each crater with the cuticle rolled to one side (Fig. 15). The craters of instar 1 are small (Fig. 19–20); older larvae and adults make craters up to 4 mm long. The craters are hollowed out by feeding and are irregularly shaped (hemispherical, ovoid, rounded). They have a deep basin, with the rolled ventral cuticle forming a thickened margin on one side. The dorsal cuticle of the leaf remains intact (Fig. 11), with a window-pane pattern. The mid-rib and secondary veins are not eaten but the leaves are intact dorsally and do not have a skeletonized appearance.



Figures 26–31. Pupa and adult of *Cassida sphaerula* (photos: S. Adam, September 2021). **26)** Pupa, attached by venter of leaf, with shield comprising only exuviae of 5th instar. **27)** Pupa with shield of exuviae I–V and feces. **28)** Teneral adult is straw colored. **29–30)** Mature adults are green, in copula. **31)** Older adult with black spots on elytra.

Larvae start feeding shortly after hatching. Their feeding exhibits a stereotyped repertoire. The site is prepared by eating most of the trichomes (Video 1). The first cut of the ventral cuticle (including the leaf's epicuticular wax layer) is made by a series of bites that create an arc-shaped cut, about the same size of the pronotum. The larva starts feeding on spongy mesophyll, and its head action pushes the cuticle layer, rolling it over and ventrad. As the larvae feed on the exposed mesophyll, a crater forms, deepens, and enlarges ventrad underneath the larvae. The rolled cuticle is pushed further ventrad, underneath the larva. When the larva finishes feeding in that crater, it moves to a different spot on the same leaf.

A single larva can spend many days feeding on the same leaf. We observed and filmed the larvae of *C. sphaerula* cutting and eating trichomes (Video 1). Plants in the tribe Arctotidinae have mostly non-glandular trichomes, although some glandular hairs can be present in certain organs (Karis et al. 2009). Glandular trichomes would be more deterrent to herbivory. Trichome-eating has not been observed for any Cassidinae. No trichome fragments appear in the shields we dissected ($n = 4$) so we assume trichomes are digested.

In *C. sphaerula*, adult feeding resembles larval eating. The adult also makes multiple cuts in the cuticle, in an arc-shape; as it feeds deeper into the trough, the head movements push the cuticle ventrad, under the beetle, towards the posterior margin of that feeding depression (Video 4). The depression deepens and widens, and the cuticle becomes a ridge at the margin of this feeding crater. We did not observe the adults consuming trichomes. The pattern resulting from adult feeding resembles the larval pattern, but the craters are larger. Both stages leave the dorsal cuticle intact, forming windows.

Natural enemies of *C. sphaerula*. SA observed other animals on the host plant: snails, slugs, spiders, velvet mites, springtails, insects (wasps, aphids, stink bugs, lace bugs, other beetles including one chrysomelid (to be determined), Lepidoptera caterpillars), but noted few interactions that might clarify which are competitors, predators, and parasites of *C. sphaerula*. We observed and filmed one *C. sphaerula* larva walking over a leaf and a smaller-sized aphid moved out of its way (Video 3). In another instance, a smaller mite moved out of the way of an approaching *C. sphaerula* larva.

Observations of interactions in the field were almost impossible as the host leaves lie flat, pressed against one another and it is necessary to grasp each leaf and gently pull it up to see the underside. This tends to dislodge or scare off many of the other individuals on the plant. The *C. sphaerula* larvae raise their shields whenever they are disturbed, including by others of the same species. They seem to spend a great deal of time sitting still, but adults are alert—they freeze when there is any movement of the leaf. Then they scuttle to the underside of the leaf, out of the light and view. Like many cassidines, adults show a definite tendency to tumble off the leaf to the ground and then scuttle to the plant stems where they are better protected.

Discussion

The behaviors and life cycle of *C. sphaerula* was studied in detail and over many months (early spring-late autumn). We confirmed the choice of host plant, *A. prostrata*, in the indigenous habitat in South Africa; *C. sphaerula* is now known on two *Arctotheca* species (Heron and Borowiec 1997). In South Africa, hosts documented for Cassidini are in the Amaranthaceae, Asteraceae and more infrequent hosts are in Aizoaceae, Fabaceae, Polygonaceae, Salvadoraceae, Solanaceae, and Zygophyllaceae (Borowiec and Świętojańska 2002–2022). This is the second publication to record the feeding habit of *C. sphaerula* on an *Arctotheca* species; a comprehensive survey of agents against *A. calendula* was carried out in South Africa 1986, 1987 and 1988, where *C. sphaerula* was noted as a potential agent although possibly not sufficiently specific (Scott and Way 1990). Our study shows a strong association of *C. sphaerula* with *A. prostrata*. Further observations and testing of the specificity of *C. sphaerula* would be necessary to determine whether it could be considered a potential agent for biological control.

Chrysomelid females provide several lines of physical and chemical protection of their eggs, including oothecal and excremental coverings (Hilker 1994). Eggs have been documented for 13 *Cassida* species in South Africa and females deposit their eggs singly or in small groups to the undersides of their host leaves (often alongside a vein) in simple oothecae that lacks a stalk. The ootheca of *C. sphaerula* has a single layer enclosing the eggs, in contrast to the large complex multi-membrane oothecae with many eggs in *Conchylotenia* (Heron 1999) and *Aspidomorpha* (Muir and Sharp 1904). In *C. sphaerula*, ootheca have no fecal cover. Within the genus *Cassida*, *C.*

coagulata Boheman, 1854 is a notable exception with a larger more elaborate oothecae generally attached to their host plant stem (Amaranthaceae hosts in this case, not Asteraceae; H. Heron, pers. observ.). Female oviposition behaviors, including site preparation and coverings of the ootheca, the oothecal structure, and qualities of the egg mass appear to vary within the genus *Cassida* and suggest novel phylogenetic characters.

We observed the distinct feeding pattern that pushes the epidermis to one side and leaves craters on the dorsal surface of the leaf. Comparison with images and data for other species suggests this is a distinct pattern, now known for at least three South African *Cassida* species. Author Heron photographed similar patterns for *Cassida guttipennis* Boheman, 1862 on the host, *Berkheya bipinnatifida* (Harvey) Roessl (Asteraceae), and *Cassida quatuordecimsignata* Spaeth, 1899 on the host, *Berkheya maritima* J.M. Wood and M.S. Evans (Asteraceae) (see Heron and Borowiec 1997: 643, Fig. 19; Heron 2011: 137, Fig. 9; Heron 2003: 43, Fig. XXV) without discussing how the pattern arose. These three species are the only ones where such a pattern is reported; the midrib and secondary veins are not eaten, and the craters are found in areas between veins. Bieńkowski (2010) described the more typical chewing pattern in two other *Cassida* species. These patterns suggest intrinsic intra-generic variations within *Cassida*. As more feeding patterns are recognized, novel hypotheses about their significance are emerging; for example, a masquerade strategy in some leaf beetles (Konstantinov et al. 2018).

The careful observation and filming of feeding in *C. sphaerula* allow us to determine how the windowpane feeding pattern arises. It is unclear if the rolling over of the epidermis is related to the sheer density of trichomes (see Fig. 13)—pushing trichomatous cuticle out of the way avoids energy and time costs to cut trichomes and clear a feeding path. We observed *C. sphaerula* larvae consuming trichomes, which has not been reported for any Chrysomelidae before. In Chrysomelinae chrysomelids, larvae of some *Platyphora* species were observed to cut and throw trichomes backwards unto their fecal shields (Bernardi and Scivittaro 1991; Flinte et al. 2017: 15). In Campostomate chrysomelids, larvae trim and store trichomes into a section (“attic”) of the fecal case (Brown and Funk 2005) or incorporate trichomes and feces to make the case wall (Chaboo et al. 2008). Trichome-consumption may not be a regular part of the diet and the nutritive value is unclear. The feeding process may be flexible when trichomes are less dense. Trichome density impacts movements of cassidine larval (larvae use the tarsungulus to insert into the epidermis and “tiptoe” to move) (Medeiros et al. 2004; Medeiros and Moreira 2005). Author Heron’s observations of *C. guttipennis* feeding revealed that more typical circular feeding scars without rolled cuticle margin is left on those plants with less dense pubescence, e.g., *Berkheya speciosa* (DC.) O. Hoffm. (Asteraceae).

In *C. sphaerula*, all five larval instars and the pupa retain an exuvio-fecal shield. Instar I has a feces-only shield (Fig. 19–20); instars II–V retain previous exuviae in a stack, with feces applied. The pupae exhibit variability, retaining either the instar V exuviae only (Fig. 26) or the entire structure of the larval stages (Fig. 27). It is unclear what the different benefits are of each shield form. Within the genus *Cassida*, shields vary in architecture, some with exuviae only, or with exuviae covered with fecal or with fecal filaments (Świętojańska 2009).

Life history data can provide a great deal of comparative information to support species concepts and evolutionary relationships. Some of our findings are relevant to character hypotheses presented in two phylogenetic analyses of Cassidinae, Borowiec (1995), particularly his characters 15–19, and Chaboo (2007; 16 larval characters). Our findings also suggests new characters and new states to expand López-Pérez et al.’s (2018) dataset for the phylogeny of Cassidini. The similarity of feeding pattern in *C. guttipennis*, *C. quatuordecimsignata*, and *C. sphaerula* may be clues to shared behavior and morphology, possibly defining a sub-group within *Cassida*. The production and relative simplicity of the ootheca in *C. sphaerula* compared to the more complex one in *C. coagulata* indicate intra-generic variations and other potential characters, for example ootheca present or absent, size (e.g., number and arrangement of eggs), structure (membranes, additional layers of chewed plant material or feces). The preparation of the oviposition site and the post-ovipositional behaviors of the female await comparative study and evolutionary analysis.

The exuvio-fecal shield that diagnoses the eight derived tribes of Cassidinae is a unique morpho-behavioral complex (Chaboo 2007), an example of an extended phenotype, like a bird’s nest (Dawkins 1989). This is a significant macroevolutionary event in the evolution of Cassidinae, however, our current picture of its origin is murky. At the base of the tortoise beetle clade, Delocraniini larvae were described as “pouco encobertas pelos excrementos” (=barely covered by excrement) so *not* carrying a shield (Bondar 1940: 1 02), Hemisphaerotini larvae have caudal processes and a unique “bird-nest” shield architecture (Chaboo and Nguyen 2004), and Spilophorini larvae have caudal processes and an exuviae-only shield (Nishida et al. 2020). In contrast, the mining larvae of

Notosacanthini lack caudal processes and lack shields (Monteith et al. 2021). Also, remarkable is the independent origin of shield retention in the distantly related ‘hispine’, *Oediopalpa* Baly, 1858 (Bruch 1906).

The tortoise beetle shield has been considered as a protection and a defense. Réaumur (1737) hypothesized that it protected against sun and flies. Weise (1893) hypothesized its function as defense against desiccation. More observations led to the hypothesis that shields are a defense against enemies and used cheaply-available defecation products and exuviae and perhaps even chemicals in exocrine glands of those exuviae (Olmstead 1994). Mechanical defense against predators has been tested experimentally, with support by several researchers (Eisner et al. 1967; Olmstead and Denno 1993; Eisner and Eisner 2000) but contradicted by others (Müller and Hilker 1999; Nogueira-de-Sá and Trigo 2002). Further studies with *Cassida* larvae point to more selective shield defense to certain enemies: Schenk and Bacher (2002) showed shields were effective against vespid predators only, while Bacher and Luder (2005) showed they were effective against parasitoids only and offer some protection against desiccation and wind, but not so against abiotic factors of UV-radiation. Müller (2002) also found variable effectiveness of shields to deter different predators. Chemical defense via enteric discharges in shields was proposed by Pasteels et al. (1988). Chemicals sequestered from host plants or by de novo synthesis can enhance shield defenses (Gómez et al. 1999; Vencl et al. 1999, 2005, 2009, 2011; Nogueira-de-Sá and Trigo 2002, 2005), however, chemicals were also found to have no impact on larval survival (Bottcher et al. 2009). This succession of ideas and continuing testing are crucial to illuminating the origin, function (i.e., cost benefit analyses), and diversity of fecal architectures.

Phylogenetic studies in Cassidinae have relied largely on adult characters. In the past, a few characters and states of juvenile stages have been proposed: Borowiec (1995) tested four characters of larvae for his phylogeny of Cassidinae, Chaboo’s (2007) study included 20 from juveniles, López-Pérez et al. (2018) tested one larval character. Going forward, we anticipate more studies like López-Pérez et al. (2021) that hypothesized nine novel characters with their possible states for pupae (their shield present/absent is equal to Chaboo 2007: char. 19). Juvenile stages, behavior, and ecology offer a wealth of new characters that could strengthen systematics of Cassidinae (indeed, all insects), from species concepts to tribal relations. Juvenile stages of most insects are extremely underrepresented in museum collections. The research challenge is detailed field studies and collections and descriptions of specimens.

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Supplementary Materials

Video 1. *Cassida sphaerula* larva feeding, site preparation, trichome-eating, first cut. The beetle larva clears the site by chewing trichomes, then making an arc-shaped cut in the epicuticle that is rolled underneath the body. The larva then feeds on the spongy mesophyll. Filmed by Sally Adam, Cape Town, South Africa (2021). Link: https://youtu.be/rlyAl_jj3VA (1.5 minutes).

Video 2. Larva of *Cassida sphaerula* (Chrysomelidae) eating trichomes. Trichomes are considered an anti-predatory innovation of plants yet here is a beetle larva cutting and consuming trichomes of its host plant, of *Arctotheca prostrata* (Asteraceae). The black structure at the hind end of the larvae is made of its own feces. Filmed by Sally Adam, Cape Town, South Africa (2021). Link: <https://youtu.be/Ea-kbpM2qU4> (1.4 minutes).

Video 3. *Cassida sphaerula* larva walking over a leaf with aphid. The larva ignores the aphid on the host, *Arctotheca prostrata* (Asteraceae). Filmed by Sally Adam, Cape Town South Africa (2021). Link: <https://youtu.be/yoJzpn9FtXg> (20 seconds).

Video 4. *Cassida sphaerula* beetle adult feeding. The adult beetle feeds by cutting and rolling the epicuticle out of the way as it consumes the spongy mesophyll of its host, *Arctotheca prostrata* (Asteraceae) in South Africa. Filmed by Sally Adam, Cape Town, South Africa (2021). Link: <https://youtu.be/8RZ3VWtkTRk> (3 minutes).

