METAMORPHOSIS

LEPIDOPTERISTS' SOCIETY OF AFRICA

Volume 27: 82–89

ISSN 1018–6490 (PRINT)
ISSN 2307–5031 (ONLINE)

# Life history observations of the myrmecophilous lycaenid butterfly *Argyraspodes argyraspis* (Trimen, 1873) (Lepidoptera: Lycaenidae: Aphnaeinae), with notes on ant behaviours and interactions and comparisons with allied species

Published online: 21 December 2016
DOI: https://dx.doi.org/10.4314/met.v27i1.17

Alan Heath[1*] and C.W. Stewart Fisher[2]

[1] Iziko South African Museum, Cape Town, South Africa. Email: alanheath3@gmail.com
[2] Wicken, Northamptonshire, United Kingdom. Email: fisherepitola@gmail.com
*Corresponding author

Copyright © Lepidopterists' Society of Africa

**Abstract**: Life history observations of this herbivorous and myrmecophilous butterfly are described and illustrated here, together with notes on its mutualistic ant symbionts *Crematogaster melanogaster* Emery and host-plant *Hermannia* (Malvaceae) species. It was noted that the female oviposited on dead plant material or on the sandy substrate some distance from its host-plant. A tentative explanation given for this is that the eggs might otherwise suffer predation by ants nesting beneath the host-plant. A structural and colour similarity exists between the larvae of *Argyraspodes* Tite & Dickson and larvae of *Trimenia* Tite & Dickson, *Aloeides* Hübner and *Erikssonia* Trimen. This corresponds well with the monophyletic clade of *Argyraspodes, Aloeides, Erikssonia* and *Trimenia* as presented by Boyle *et al.* (2014).

**Key words**: *Crematogaster melanogaster*, *Hermannia*, *Trimenia*, *Aloeides*, *Microloma*, herbivorous, mutualistic, aphytophagous, monophyletic, DNO (Dorsal Nectary Organ), honeydew, instar, brood, satellite ant nest, clade, common ancestor.

**Citation**: Heath, A. & Fisher, C.W.S. (2016). Life history observations of the myrmecophilous lycaenid butterfly *Argyraspodes argyraspis* (Trimen, 1873) (Lepidoptera: Lycaenidae: Aphnaeinae) with notes on ant behaviours and interactions and comparisons with allied species. *Metamorphosis* **27**: 82–89.

## INTRODUCTION

The 'Warrior Silver-spotted Copper' *Argyraspodes argyraspis* (Trimen, 1873) is a distinctive and robust butterfly in the lycaenid subfamily Aphnaeinae. It is the single representative of its genus and is closely related to species in the genus *Trimenia* Tite & Dickson, 1973 (Heath, 1997; Boyle, *et al*., 2014). It is widely distributed in the western, arid parts of southern Africa (see also Mercenero *et al*., 2013).

A partial life history account of the butterfly was published by Heath & Zielske (2015). In that account the egg and first instar larva were described and illustrated in detail; also the ovipositing behaviour of the adult female was described. Several hypotheses concerning behaviour in the pre-adult stages were also given. In September and October 2016 a visit was made by the present authors to the same area as in the earlier study in order to complete our knowledge of this interesting butterfly.

## MATERIALS AND METHODS

*Received: 3 December 2016*
*Accepted: 21 December 2016*

Copyright: This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License. To view a copy of this license, send a letter to Creative Commons, Second Street, Suite 300, San Francisco, California, 94105, USA, or visit: http://creative commons.org/licenses/by-nc-nd/3.0/

Study sites: Two sites were visited between September 13 and October 3 2016. Site 1: About 4 km north of Kotzesrus, Northern Cape Province (coordinates: 30°56.19′S; 17°51.47′E, elevation 213 m). Site 2: About 7 km north of Kotzesrus (coordinates: 30°54.98′S; 17°52.65′E, elevation 163 m). Both sites are in the southern half of the Namaqualand Coastal Plain or Sandveld, (red sand) (Cowling, *et al.* 1999; Desmet, 2007).

Symbionts: Unless otherwise stated, all references to ants in this study refer to *Crematogaster melanogaster* Emery, 1895 (subfamily Myrmicinae). A nest of ants is here termed a satellite nest when no brood is present, irrespective of how many individuals inhabit the nest. The commonly encountered ant *Crematogaster peringueyi* is now to be known as *Crematogaster capensis* Mayr, 1862 (=*C. peringueyi* Emery, 1895) (B. Blaimer and H. Robertson respectively, pers. comm.)

An undescribed species of *Hermannia* (Malvaceae), (D. Gwynne-Evans *pers.comm.* 20 October edge2016) with dark red flowers is abundant in both areas studied and will be referred to below as the 'host-plant'.

In captivity: Larvae and ants together with some sprigs of host-plant were kept in polythene containers of varying sizes; the sides of which had been coated with Fluon (a synthetic fluoropolymer) to inhibit escape by the ants. Moist tissue paper was occasionally added to the containers to provide adequate humidity as well as a source of water for the ants. The containers were kept at moderate temperatures (±15–24°C); closed with a sealed or partly-sealed lid, when the contents were not being studied. Larvae and ants were shielded from bright light, except on a few occasions, to study their response.

Inducing oviposition: An open plastic container 13 x 9 x 5cm deep was covered by netting. Several dry twigs and a small piece of host-plant together with three ants were placed inside; a female butterfly was then added. The container was placed beneath an angle-poise lamp and adjusted until the butterfly started walking about without fluttering. A piece of tissue paper soaked in water-diluted honey was placed on the netting; this provided daily sustenance for the butterfly and the ants.

Photography. Camera kit: Olympus OM-D E-M5 camera and an Olympus M.Zuiko Digital ED 60mm F2.8 macro lens and an OM-System Zuiko Auto-macro 20mm 1:2 lens, Auto-macro 50mm lens and bellows were used. A Metz 15MS-1 digital flash unit with a home-made diffuser was also used. Stacking: The stacking software used was Zerene Stacker (http://zerenesystems.com/).

Caveat: The results and following discussion herein apply to the areas studied (Sites 1 & 2), since the host-plant and some behavioural aspects may not necessarily apply to other biomes where this butterfly occurs. Similarly, some of the observations made whilst the subjects were in captivity might not always reflect their behaviour in nature.

## RESULTS

13 September 2016
Site 1. A freshly emerged adult female *Argyraspodes argyraspis* (Fig. 1) was seen to emerge from the sand beneath a species of *Hermannia* that had *C. melanogaster* ants in the sand beneath.

**Figure 1** – Female *A. argyraspis* (right: dorso, left: verso).

Site 2. A female was followed, as she was in a fluttering mode and clearly ready to oviposit. She appeared to oviposit on the sandy substrate. She did this three times at different spots within about 40 cm from one *Hermannia* plant. The plant was then dug out and in the pile of removed sand a late instar larva was discovered on a crumbling lump of sand, accompanied by at least four or five ants. The *Hermannia* plant was examined; there was no sign of scale or aphid on the stem or roots. A problem with the vehicle necessitated a hasty return to Pinelands for a period of 17 days. The larva was taken back to Pinelands where it was kept together with a few ants but without the *Hermannia* plant. At the end of the 17 days without food it appeared to have suffered no ill-effects but resumed feeding as soon as further plant material was available.

30 September–4 October 2016
Site 2. A wide variety of plant species were examined for the presence of ants or *Argyraspodes* larvae during the four days; among these over a hundred *Hermannia* host-plants were examined. Where ants were found, one or more *Argyraspodes* larvae were usually found too. No ants or larvae were found beneath any of the other plant species examined.

No live pupae were found during the four days of searching, although one parasitized pupa was found c. 4 cm below ground with a large hole on one side; by the look of the undamaged side it appears to have died just prior to eclosion with the finished wings clearly visible through the pupal casing.

The host-plants with ants present had a space (±3mm) surrounding the stem that permitted egress for ant and larvae. All larvae encountered were found below ground at a depth of 3–6 cm. It appears that they create alcoves in the sand connected to access holes, where it seems, they rest during the day accompanied by a few ants.

On two occasions, an access hole in the sand was discovered almost a metre from the nearest host plant; within the hole were some ants and one or more larvae. One such 'nest hole in the sand' was carefully removed and taken to Pinelands for close observation. It was later found that the hole contained two *Argyraspodes* larvae as well as a small number of ants. Only one of the many ant nests examined was found to contain brood but its contents were hastily moved elsewhere by the ants before its collection or further study was possible. All the other nests of ants encountered were devoid of brood and appeared to exist solely for the purpose of tending *Argyraspodes* larvae.

The undescribed *Hermannia* sp. host-plant (Fig. 2), has dark red flowers and was very common in the areas studied; it was the only plant seen to be associated with *Argyraspodes* larvae or *C. melanogaster* ants. Note that the only ants found together with *Argyraspodes* larvae or the host-plants were *C. melanogaster*.

Other *Hermannia* species were also present at both sites, one having pink flowers being *H. heterophylla* (Cav.) Thunb., but these were far less common and no larvae or *Crematogaster* ants were found with them, although many were infested with white scale insects. Adult females were observed to remain within small isolated territories for long periods, sometimes a whole day, or longer. Each territory (100–150 sq. m. in size) was circumscribed by the presence of both ants and host-plant. The localities studied had several such female territories; Site 1 having only one but Site 2 had at least four and on the roadside between the two sites there were others. The terrain at each of these territories was flat and lacking in features or prominences (Fig. 3). It was noted that males seldom invaded these female territories and were presumed to favour more prominent localities.

**Figure 2** – *Hermannia* undescribed sp. host-plant.

**Figure 3** – Namaqualand Coastal Plain near Kotzesrus, N.Cape.

Over a period of four days, ovipositing females were followed and seen to lay single eggs on various dried twigs and stems and also on the sandy substrate away from the host-plant; sometimes over a metre from the nearest host-plant. They nectared on flowers of several annual plants and were occasionally observed taking nectar from a red host-plant flower but were never seen to oviposit on the plant. Among many eggs seen laid, a total of five were collected and taken for later study. An adult female was also collected and taken for oviposition purposes; later, after ovipositing 9 eggs the butterfly was released near Clanwilliam (within the normal range of the species). Several *Argyraspodes* larvae of varying sizes were collected, together with ants and samples of host-plant; they were taken to Pinelands, for closer study.

**In captivity** (Pinelands: 4 October–26 November 2016)

Egg and first instar larvae

The egg is 1.28 mm diameter and 0.85 mm high (Fig. 4). It takes 14 days to eclose and the resulting first instar larva was measured to be 2.9 mm long. In order to simulate natural conditions a first instar larva was placed on the sand away from the nest hole. It found its way to a sprig of host-plant left near the hole. Ants followed it about as it walked up and down the stem but they did not pick it up or make any physical contact, other than to wave their antennae over the larva. (Fig. 5). The larva appeared to seek solitude and two days later it was found walking about (unaccompanied) looking for fresh host-plant. It was then kept separate and provided with sprigs of host-plant in order to rear it to its second instar.

**Figure 4** – Egg of *Argyraspodes argyraspis.*

**Figure 5** – First instar larva being followed by *C. melanogaster* ants

As a first instar larva it did not adopt a definitive colouring until it had started to feed; it then took 24 days to reach a length of 4.75 mm before ecdysis (Fig. 6). Three more eggs hatched and the emerging larvae were placed on the sand some 30 cm away from both the nest hole and sprigs of host-plant. The next day one of these (at least) had found the host-plant. Wandering ants were often seen walking close to a first instar larva and pausing only to wave their antennae above the larva, but they always moved on without lifting or touching the larva. A further two eggs eclosed and the emerging larvae were placed in a small container with a piece of an alternative plant species - *Hermannia pinnata* L. as this species was more easily obtained locally at Kirstenbosch. The larvae readily accepted the *H. pinnata* plant and one was successfully reared through to second instar.

**Figure 6** – Late first instar larva (4.75 mm), just prior to ecdysis.

Ants and later instar larvae

The ants kept with the larvae were provided with water-diluted honey and insect carrion but they showed no interest in either, yet many survived for up to 21 days. On one occasion, whilst adding fresh stems of host-plant it was noticed that the ants were very attracted to the stems and leaves. Several ants began sucking phloem at a leaf or stem and remained motionless in that position for minutes at a time (Fig. 7).

**Figure 7** – *C. melanogaster* ants imbibing host plant phloem.

The larvae fed on the leaves of the *Hermannia* host-plant mostly at dusk and periodically during the night. The smaller, younger larvae sometimes fed during the day if conditions suited them (presumably low light intensity). They all seemed to prefer the smaller narrow leaves of the long flowering stems of the host-plant. During the day, larvae remained sheltering beneath anything able to provide cover and were clearly agitated when exposed to any light; this was particularly true for the final instar larvae that were very light-sensitive. When deliberately exposed to daylight and deprived of shelter, larvae burrowed into the sand. The ants avidly accessed the DNO for honeydew (Fig. 8) from what was estimated to be 4$^{th}$ instar larvae during dusk, but in the final instar, taking honeydew was not seen quite so often. The final instar larvae were noticeably very lethargic and over the study period their growth rate was perceived to be very slow indeed.

**Figure 8** – *C. melanogaster* ant imbibing honeydew from the DNO of an *A. argyraspis* larva while another awaits its share.

When a larva was feeding, one to three ants would position themselves on the closest parts of the host-plant to the DNO. It was noted that only one particular ant did the drinking of honeydew from the DNO but then regurgitated (trophallaxis) to other ants when they approached; thereby sharing with her nest-mates. The larval feeding activity appeared to be partly ant-stimulated, hence as the ants gradually reduced in numbers due to natural mortality, the feeding activity of the larvae also reduced. Three larvae died with their three posterior segments having turned black; believed to be an infection due to untapped honeydew. During this study a fresh supply of ants was obtained and introduced to the larvae because the earlier batch began to die-off. This unfortunately resulted in fights between the few existing ants and newcomers, and it may even have caused aggression towards the larvae, as some larvae developed black bruises (or bite marks) on the sides of some middle segments.

Description of *A. argyraspis* final instar larva (Figs. 9 & 10)

23mm long at rest; 29mm fully extended. Overall appearance maroon with yellow and white markings. Pair of TOs (tentacular organs) on eighth abdominal segment, each clad with a dull pinkish, tapering, tubular casing with rim armed with spines of unequal length. DNO (dorsal nectary organ) medially on seventh abdominal segment, usually concealed in fold between abdominal segments 7 and 8. Integument of larva densely adorned with short, erect bristles, each with three to five fine shorter spikes splayed from its

**Figure 9** – *Argyraspodes argyraspis* final instar larva.

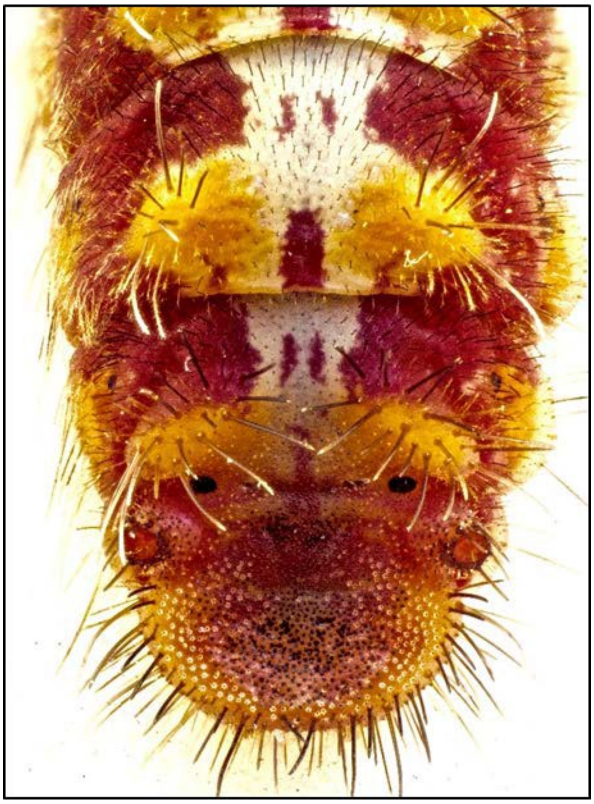

**Figure 10** – Posterior of *A. argyraspis* final instar larva.

tip. Broad dorsal longtitudinal whitish stripe (sometimes with faint blue suffusion) with maroon-coloured patch located posteriorly on each segment.and pair of smaller maroon markings anteriorly. Flanks mostly reddish-maroon, intruding into dorsal white stripe anterior of each segment. Each segment with two prominent yellow mounds on each side; one placed dorso-laterally within white stripe posterior of segment; the other much larger mound located laterally, low down, just above the legs; each armed with several sharp white-tipped black spines of varying lengths. Dorso-lateral yellow mounds on seventh segment slightly elongate, resembling spiky "eyebrows". Viewed dorsally final segment half-moon shape, its flattened and pitted top surface adorned with many tiny black and translucent mushroom-shaped setae; its central surface pinkish-brown with pale yellow margin fringed with many sharp spines of varying lengths. Head carapace dull pinkish-brown colour, anteriorly rimmed yellow and densely adorned with black spines and a few longer white setae.

Further observations: Apart from their size, the appearance of the larvae remained remarkably similar throughout all instars in structure, colour and markings, although the head and tail carapaces varied slightly between instars in both size and shape (Figs 6 & 9). In view of this overall similarity we were unable to determine the exact number of instars, although we suspect it may be as many as six.

The process of pupation took several days and during this time the larvae gradually faded to translucent yellowy-green. At first the pupae were bright yellow, soon changing to vivid orange-red and finally to yellowish-brown. Although equipped with cremastral hooks the pupae were not securely attached to anything. Prior to eclosure the wing colour and markings gradually became visible (Fig. 11). The first *Argyraspodes* larvae to pupate took 18 days to eclose and it emerged as a male; a further male and two females each took 19 days.

**Figure 11** – Pupa of *A. argyraspis* three days prior to eclosion.

## DISCUSSION

It was a surprise to both authors to discover that *A. argyraspis* larvae are herbivorous. The fact that the female butterfly is reluctant to oviposit on or close to its host-plant had suggested aphytophagy (see Heath & Zielske, 2015) but this is now shown to be incorrect; nevertheless it remains a curious trait and we are unable to offer a convincing explanation for it, other than perhaps the eggs might suffer greater predation by the ants if laid on the host-plant. There would be little risk to an ovipositing female since the daytime presence of ants on the host-plant was seen to be minimal. Several species of *Aloeides* and one of *Erikssonia* are known to oviposit on or in sand beneath their host-plant (see Heath & Claassens, 2003: 11; Henning & Henning, Feb. 1984: 3) but only in *Argyraspodes* (this study) and *Aloeides barklyi* (Trimen, 1874) was oviposition recorded some distance from its potential host-plant (see Heath *et al.,* 2008: 130). It is also curious that this behaviour has never been recorded with any *Chrysoritis* species (A. Heath *pers. observ.*).

The longevity of the ants was also surprising; three weeks in captivity without food; their only intake appeared to be water, *Hermannia* phloem and honeydew from the larvae. It is unlikely they would obtain much nutrition from phloem or the honeydew; however, their relative longevity and reluctance to feed is not unusual for workers, although their behaviour may have changed if brood had been present (Blaimer *pers.comm.*).

The secretions of Hemiptera species are avidly sought by *C. capensis* ants (A. Heath *pers. observ.*) and *C. melanogaster* ants may behave similarly, but there was no sign of Hemiptera on any of the many host-plants examined, above or below ground. However, they may have occurred on other nearby plants such as were found on *H. heterophylla*. Note that none of the satellite ant nests examined had brood – this suggests that the ants' presence may have been due solely to the presence of the larvae and their DNO. It is probable that behaviour and interactions could vary according to time of year and locality – for example the larvae might seek shelter much further down in the sand during the hottest and driest months; also periods of high brood creation may invoke different interactions between ants and larvae.

The very slow perceived growth rate of the larvae in this study is yet another question that we have been unable to answer satisfactorily but may be related to the ability to survive without food for long periods. This would surely be a desirable trait in order to cope with the unique climatic conditions that are a feature of the habitats frequented by this butterfly (see also Cowling *et al.,* 1999; Desmet, 2007). Possibly a more prolonged diapause may also take place during drought periods.

In Boyd, *et al.* (2014: 12) it was predicted that the common ancestor of the Aphnaeinae was associated with a *Crematogaster* species of ant. This study has now revealed that a *Crematogaster* species of ant is associated with *A. argyraspis*, the only member of the *Argyraspodes–Aloeides–Erikssonia–Trimenia* clade known to do so. Despite this, one might question whether the common ancestor of the clade was also associated with a species of *Crematogaster*.

In view of the chloroplasts reportedly found in the gut of a larva of *Trimenia argyroplaga*, further study is planned on that butterfly.

**Comparisons with closely related Aphnaeine genera**

The larva of *A. argyraspis* (Fig. 9) has a very similar structure and colour to that of *Trimenia argyroplaga* Dickson, 1967 (Fig. 12), except that the proportion of maroon colouring is much greater. The adult butterflies also share a similarity of wing shape, pattern and colouring.

The male genitalia of *A. argyraspis* are illustrated in Heath (1997), where they can be compared with those of *Trimenia* species. The uncus and aedeagus are similar but the valves, although spatulate are quite different. Female *Trimenia* species have an anal tuft, the scales of which are deciduous and adhere to eggs when laid. *Argyraspodes argyraspis* females do not possess this structure.

**Figure 12** – Final instar larva of *Trimenia argyroplaga.*

**Figure 13** – Final instar larva of *Aloeides apicalis* Tite & Dickson.

The larvae of *Aloeides* Hübner (Fig. 13) and *Erikssonia* Trimen species also have a similar structure and colouring to those of *A. argyraspis* and *T. argyroplaga*. Note that *Argyraspodes, Aloeides, Erikssonia* and *Trimenia* are presented as a monophyletic clade by Boyle *et al.* (2014). The genera of ant-associates of *Aloeides* species are varied and to date are known to include *Lepisiota* (Formicinae); *Monomorium* and *Pheidole* (Myrmecinae) [Heath, *et al*., 2008]. With *Erikssonia edgei* Gardiner & Terblanche the ant genus is *Lepisiota* (=*Acantholepis*) [Henning & Henning, 1984, as *E. acraeina*] and with *Trimenia* it is *Anoplolepis* (Formicinae) [Heath & Claassens, 2003]. Thus the ant-associate (*Crematogaster* species) of *Argyraspodes argyraspis* is different from those currently known for the other genera in the clade.

It should be noted that, although the larvae of *Trimenia* species are thought to be aphytophagous (see Cottrell, 1978: 53; 1984: 13; Heath, 1997: 21; Heath & Fisher, 2010: 115), dissection of the gut recently taken from a final instar of *T. argyroplaga* by Melissa Whitaker, Harvard University, apparently revealed the presence of chloroplasts.

There are at least two other aphnaeine species commonly occurring at each of the sites studied:

1. *Chrysoritis thysbe bamptoni* (Dickson), whose ant-associate is *Crematogaster capensis* Mayr and its locally common host-plant being *Roepera teretifolia* (Schltr.) Beier & Thulin (Zygophyllaceae) (A. Heath *pers. observ.*).

2. *Phasis clavum clavum* Murray, whose ant-associate is also *Crematogaster capensis* and its host-plant locally is *Searsia* (=*Rhus*) species (A. Heath *pers. observ.*).

The nearest known *Trimenia argyroplaga* population occurs about 10km south-west of Site 1 but *Argyraspodes* has not been recorded there; likewise *Trimenia* species have not been recorded at either of the two study sites.

## CONCLUSIONS

From a review of the life history detailed in both the previous study (Heath & Zielske, 2015) and this one, the salient points known to date are as follows:

*Argyraspodes argyraspis* is herbivorous and myrmecophilous. It has a mutualistic association with the ant *Crematogaster melanogaster* Emery (subfamily Myrmicinae). In the area studied it has a predilection for ovipositing near an undescribed species of *Hermannia* (Malvaceae) with *C. melanogaster* ants present, but only oviposits on the nearby sand substrate or dead plant material away from its host-plant. In captivity the first instar larvae emerge after two weeks and find their own way to the host-plant unaided. In captivity the newly emerged larva will readily feed on more than one species of *Hermannia*; they do not directly associate with the host ant and no physical contact takes place. Later instars however, are keenly attended by the host ant and the DNO is actively exploited. The structure and colour markings of the larvae appear to be uniform throughout all the different instars. Both the larval structure and colours are also similar to species of *Trimenia, Aloeides* and *Erikssonia*.

Adults of *A. argyraspis* have a strong preference for nectaring on 'Bokhoring' *Microloma saggitatum* (L.) R.Br. (Apocynaceae) when these flowers are in season. They force their proboscis into the closed flower. Note that this flower does not open and is normally fertilized by sunbirds (Pauw, 1998). No other butterfly species was seen at these flowers.

In captivity many of the ants were still alive and active three weeks after collection and they showed only a mild interest in honey-water and none for insect carrion; however, they were seen to take honeydew from the DNO and were once seen to nibble or drink phloem from both leaves and stem of fresh sprigs of *Hermannia*. Some deaths of larvae in this study seem to have been caused by ant-aggression towards larvae previously tended by ants from a different colony. Other mortalities may have been caused by surplus of honeydew resulting in blockage or infection when there were insufficient ants to remove it. The parasitised pupa that was found indicates that in nature they do pupate in the sand well-below ground level.

## ACKNOWLEDGEMENTS

We thank the farm owners Carel Louw and Dirk du Toit for permission to conduct research on their respective properties. We wish to acknowledge Jan Vlok for botanical advice and David Gwynne-Evans, CasaBio for providing IDs of the *Hermannia* species. Special thanks go to Jürgen Zielske for processing the stacking photographs and for other photographic advice. Thanks also to Rod Eastwood, ETHZ, Zürich also John (Jack) Boyle and Melissa Whitaker, Harvard University for their valuable inputs. We would like to thank Bonnie, B. Blaimer, Smithsonian Institute, Washington DC and Hamish Robertson, Iziko South African Museum, Cape Town respectively for their help and insight on the ants. Finally we wish to acknowledge the Northern Cape Department of Environment and Nature Conservation for permission to collect and remove material from the Province.

## LITERATURE CITED

BOYLE, J.H., KALISZEWSKA, Z.A., ESPELAND, M., SUDERMAN, T.R., FLEMING, J., HEATH, A. & PIERCE, N.E. 2014. Phylogeny of the Aphnaeinae: myrmecophilous African butterflies with carnivorous and herbivorous life histories**.** *Systematic Entomology* 40: 169–182.

COTTRELL, C.B. 1978 Aspects of the biogeography of Southern African butterflies. *Zambezi Journal of the University of Rhodesia* (Supplement), i–viii, 100 pp.

COTTRELL, C.B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zoological Journal of the Linnaean Society* **79**: 1–57.

COWLING, R., ESLER, K. & RUNDEL, P. 1999. Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology* **142**: 3–21.

DESMET, P.G. 2007. Namaqualand – A brief overview of the physical and floristic environment. *Journal of Arid Environments* **70** (4): 570–587.

HEATH, A. & CLAASSENS A.J.M. 2003. Ant-association among southern African Lycaenidae. *Journal of the Lepidopterists' Society* **57**: 1–16.

HEATH, A & FISHER, C.W.S. 2010**.** Notes on the life histories of *Chrysoritis* Butler, *Aloeides* Hübner and *Trimenia* Tite & Dickson (Lepidoptera: Lycaenidae: Aphnaeini). *Metamorphosis* **21**: 110–119.

HEATH, A. & ZIELSKE, J.F. 2015. Preliminary observations on the life history and behaviour of the enigmatic lycaenid 'Warrior Silver-spotted Copper' *Argyraspodes argyraspis* (Trimen, 1873), including detailed descriptions and illustrations of the egg and first instar larva. *Metamorphosis* **26**: 97–101.

HEATH, A., MCLEOD, L., KALISZEWSKA, Z.A., FISHER, C.W.S. & CORNWALL, M. 2008. Field notes including a summary of trophic and ant-associations for the butterfly genera *Chrysoritis* Butler, *Aloeides* Hübner and *Thestor* Hübner (Lepidoptera: Lycaenidae) from South Africa. *Metamorphosis*. **19**: 127–148.

HEATH, A. 1997. A review of African genera of the tribe Aphnaeini (Lepidoptera: Lycaenidae). *Metamorphosis Occasional Supplement* No. 2: 60 pp.

HENNING, S. & HENNING, G. 1984. Life history and behaviour of *Erikssonia acraeina* Trimen (Lepidoptera: Lycaenidae). *Metamorphosis* No. 5 - February 1984: 1–4.

MECENERO, S., BALL, J.B., EDGE, D.A., HAMER, M.L., HENNING, G.A., KRÜGER, M., PRINGLE, E.L., TERBLANCHE, R.F. & WILLIAMS, M.C. (eds). 2013. *Conservation assessment of butterflies of South Africa, Lesotho and Swaziland: Red List and Atlas.* pp. 13–33. Saftronics (Pty) Ltd., Johannesburg & Animal Demography Unit, Cape Town. 676 pp.

PAUW, A. 1998. Pollen transfer on bird's tongues. *Nature* **394**: 731–732.