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Chrysoritis Butler (Papilionoidea: Lycaenidae: Aphnaeinae) – Part II: Natural history: morphology, ecology, and behaviour, with accounts of larval ecology and insights into the aphytophagous *C. dicksoni* (Gabriel)

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Alan Heath [1 *] Email: alan.heath333@icloud.com; Ernest L. Pringle [2] Email: epringle@eastcape.net; Swee-Peck Quek [3] Email: queksp@gmail.com.
[1] Iziko South African Museum, Cape Town, South Africa.
[2] Huntly Glen, Bedford, Eastern Cape 5780, South Africa.
[3] Integrative Biology Department, University of California, Berkeley, CA, USA.

Abstract: The natural history, morphology, ecology, and behaviour of adults and juveniles of *Chrysoritis*, and their larval associations with host ants, are described in detail, including insights into the aphytophagous species *C. dicksoni*.

Key words: wing scales, iridescence, structural colour, aphytophagy, trophallaxis, myrmecophily, male patrolling terrain, *Crematogaster*.

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INTRODUCTION

In this second of three papers on *Chrysoritis*, we provide an account of adult and juvenile morphology, and we describe the natural history, ecology and behaviour of *Chrysoritis*, including larval associations with host ants. A description of the ecology and behaviour of the aphytophagous *C. dicksoni* and its association with ants is also presented. The three papers (QEA22, the present one, and Heath *et al.*, 2023, in press) are best read as a single unit due to extensive cross-referencing of each to the others. To maintain consistency across the three papers, all *Chrysoritis* names used herein follow the taxonomic revision of Heath *et al.*, 2023), thus some names used here are technically not yet valid until published. The affected names are: *C.* aridimontis (currently *C. adonis aridimontis*), *C.* amatola (currently *C. turneri amatola*), and *C.* wykehami (currently *C. turneri wykehami*). To recognize their provisional status, the species epithets are not italicised in the text of this publication.

MATERIALS AND METHODS

This account of *Chrysoritis* is based on opportunistic field observations of adult and juvenile stages made across >90 person years by E.L. Pringle and A. Heath combined. These observations were coupled with the rearing of juvenile stages in captivity, dissections and studies of genitalia, and the preparation of wing venation slides. All photographs and line drawings presented are by A. Heath except where otherwise stated. The equipment used for image capture includes an Olympus E-M5 micro 4/3 camera, 60mm Macro lens, 20mm Macro lens and Olympus Bellows. Editing, including focus-merging, was done using Affinity Photo. Images of wing scales taken at the Iziko Museum Entomology Department by S. van Noort were taken with a Leica LAS 4.9 imaging system, comprising a Leica® Z16 microscope (using either a 2X or 5X objective) with a Leica DFC450 Camera and 0.63x video objective attached. The imaging process, using an automated Z-stepper, was managed using the Leica Application Suite V 4.9 software installed on a desktop computer. Diffused lighting was achieved using a Leica LED5000 HDI dome.

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Abbreviations

QEA22: Quek *et al.* (2022)
COI: Cytochrome c oxidase subunit I (partial gene fragment)
DNO: Dorsal nectary organ
TO: Tentacular organ

Adult morphology

Chrysoritis are small to medium-sized robust lycaenids; their upper wing surfaces are bronze, red or ochre with black markings. Some taxa also have silvery-blue scaling extending from the base of the wings, with the males having an additional iridescent sheen over the discal area of both wings. Undersides are varied, patterned or plain, but usually pale ochre to very dark red and even black, and many with small silvery spots or markings, especially beneath the forewing, a typical feature of the Aphnaeinae. The number of forewing veins is 12, except *C. chrysantas*, *C. zeuxo* and *C. zonarius* that have 11 or 10. Males have forelegs terminating in a single claw with the segments of the tarsus fused which is typical of all Aphnaeinae except *Aphnaeus* Hübner where the male foreleg ends in a stump. Female forelegs have a double claw and tarsal segments that are fully functional. For other structural features see Stempffer (1967: 176–179, as *Poecilmitis* and *Chrysoritis*).

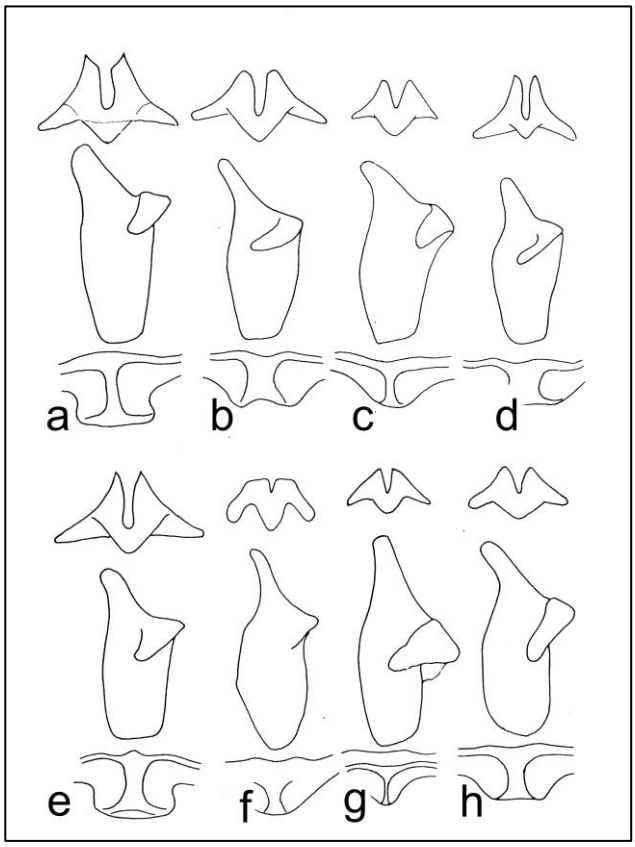

Figure 1 – Flattened components of male genitalia of eight *Chrysoritis* species. From top to bottom: juxta (furca), valve, and saccus. (a) *C. thysbe*, (b) *C. p. pyroeis*, (c) *C. oreas*, (d) *C. zonarius*, (e) *C. f. felthami*, (f) *C. l. lycegenes*, (g) *C. dicksoni*, and (h) *C. phosphor*. Reproduced from Heath (1997: 60). See also Fig. 2 in Heath *et al*., 2023.

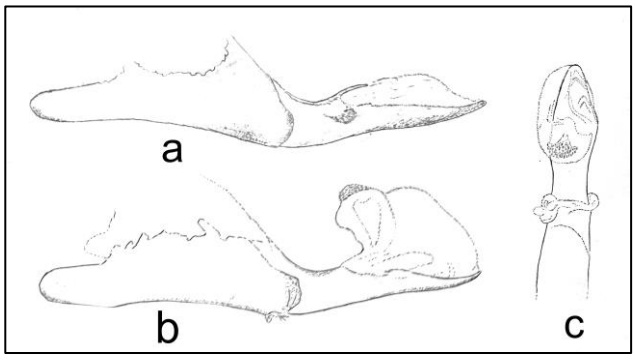

Figure 2 – *C. t. thysbe* aedeagus: (a) lateral view, (b) with vesica everted, (c) dorsal view.

Male genitalia are remarkably similar throughout the genus as shown in illustrations of eight representative species (Fig. 1), even between two species with such divergent facies as *C. phosphor* and *C. oreas* (Figs 1c and 1h respectively; Figs 2A and 2B respectively in Heath *et al*., 2023). Within the *thysbe* clade, genitalia are exceptionally uniform. Among the characteristics of the genus is the presence of a semi-membranous transtilla (valvae joined dorsally); the vinculum is distinct from the tegumen (joined but not merged laterally); dorsal elements substantial; uncus rectangular and laterally rounded, also slightly concave on the distal margin; valvae oblong with a finger-like apex (Fig. 1); simple notched juxta (lower fultura) always present; aedeagus simple and rather slender, tapering towards the apex. In some species, a vesica containing a tiny cluster of cornuti is present, such as a fan-shaped cluster ~60µ wide in all the *thysbe* clade species (a typical *C. thysbe* aedeagus is depicted in Fig. 2, see also Heath, 1997a: pl. 4).

Wing scales

The following description of scales are generalisations for the wing's upper surface; the scales along the forewing costa, veins and cilia may vary considerably from the norm in their length, shape and colour.

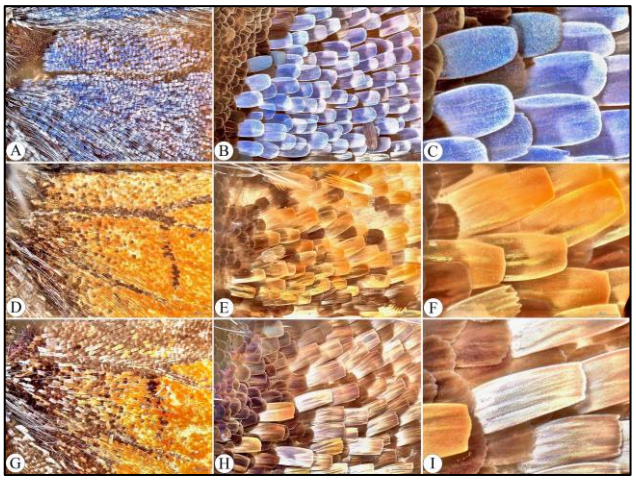

Figure 3 – Micrographs of basal hind wing scales at three magnifications, under dorso-lateral lighting intending to invoke iridescence if any. Images show the base of the wing. A–C: *C. violescens* (Komsberg Pass, sample SAM-LEP-A041390). D–F: *C. aridus* (Studer's Pass, SAM-LEP-A041391). G–I: *C.* amatola **stat. nov**. (Groot Winterberg, SAM-LEP-A041392). Images by S. van Noort.

Wing scales are connected proximally to the wing membrane by a short petiole and overlap as in roof tiles. All *Chrysoritis* have two types of scales – tulip-shaped scales and common scales which overlie the tulip-shaped scales. Iridescent males additionally have cover scales which overlie common scales. Tulip-shaped scales are mostly dark brown and patchily distributed. They underlie common scales and impart a deeper colour to them, but where the wing joins the thorax, they are more numerous and are not covered by other types of scales (Figs 3 B & H). Tulip-shaped scales are ~75µ wide and ~110µ long and smaller than common scales.

Common scales are opaque and mostly pigmented in brown, orange and/or yellow. They are ~62µ wide by 200–225µ long and are longitudinally ribbed (Figs 4D–F). The apex terminates in 5–6 apical teeth or prongs that appear to be extensions of the ribbing. Common scales extend over most of the wings but close to the base of the wing they tend to differ in shape by lacking apical teeth and the shape of the apex is square. Where the wing joins the thorax, common scales are absent.

Males that appear iridescent in lateral light have an additional layer of translucent wing scales that overlie the common scales. They are known as cover scales and impart a silvery-blue structural colour as well as iridescence. They occur from the basal area of the wings extending outwards towards the wing margins, varying in extent depending on the species but also sometimes varying among populations

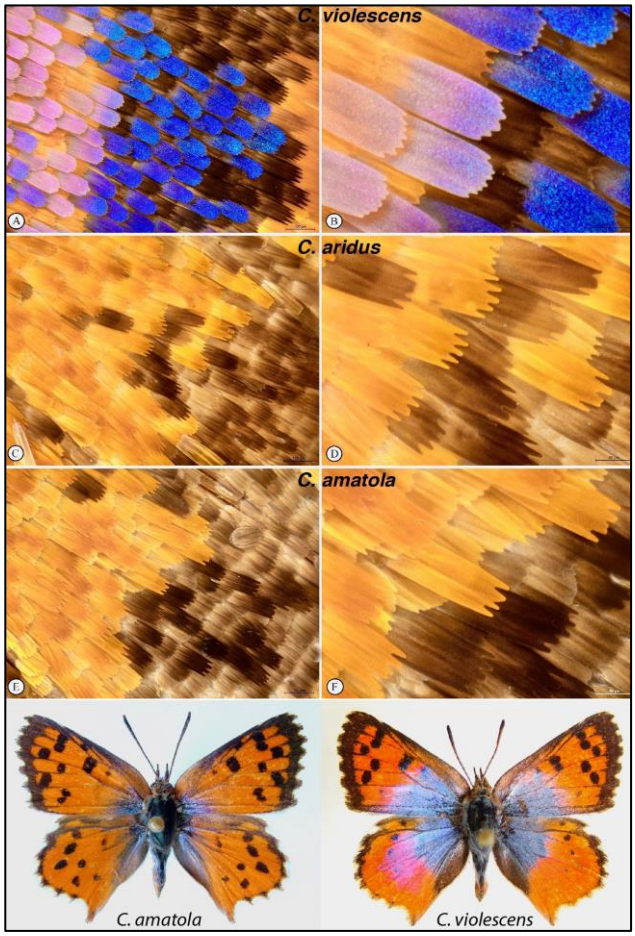

Figure 4 – Micrographs of wing scales taken at two magnifications under dorso-lateral lighting, intending to invoke iridescence if any. Images show the centre of the right hind wing (between veins Rs and M1). (A) & (B): *C. violescens*, an iridescent species. (C) & (D): *C. aridus*, a non iridescent species. (E) & (F): *C.* amatola **stat. nov**. a non iridescent species . Sample and location information as in previous figure. Bottom images show adult males of *C.* amatola & *C. violescens.* Images A–F by S. van Noort.

(Figs 4A–B) and even among individuals within populations (e.g., of *perseus*, *thysbe*, *lyndseyae*, and *pan*; see Table 1 also). The cover scales are of similar size to the common scales, very finely ridged and generally have a rounded apex that is either entire or serrated (Figs. 4B and 3B–C). They reflect ultra-violet (UV) light whereas the pigmented common scales absorb it (Heath, 2011: 99). The cover scales differ in appearance depending on lighting conditions and on the colour of the scales beneath them: 1) under most *normal* lighting, the cover scales appear pale silvery-blue but when under-lain by dark scales the colour produced is a cobalt blue (notably in the basal area of the hind wing), referred to in some older *Chrysoritis* literature as "solid blue"; 2) under certain *lateral* lighting conditions, the cover scales iridesce and display a rich royal blue colour when above dark scaling but pink when above yellow or orange scales (Fig. 4A–B). Structural colouring occurs in *C. pyroeis* and in all species in the *thysbe* clade except *palmus*, *blencathrae*, amatola, *aridus*, *turneri*, and wykehami. These species that lack structural colouring are scattered throughout the *thysbe* clade in the COI tree (Fig. 1 in QEA22) and none of them is another's closest relative, suggesting repeated independent losses of structural colour.

Microscopic examination of the wing scales of the non-iridescent taxa in the *thysbe* clade (and also of *C. chrysantas* and *C. f. felthami*) reveal that they may possess iridescent scales, possibly vestigial, mostly in the discal or basal area of the hind wing, and in highly reduced numbers and sparsely scattered (see *C. aridus* and *C.* amatola scales in Fig. 5); these scattered iridescent scales differ from those of iridescent taxa – they are of a shape and texture that is intermediate between the cover scales of iridescent species and the underlying common scales, *e.g.*, the apical teeth may be shorter than those of the common scales (see Fig. 5).

Female counterparts of the iridescent males also possess

Table 1 – Within-species variability in extent of melanism and structural colouring in wings, qualitatively assessed. Values range from 0 (invariant) to 4 (highly variable); ? = insufficient data; NA = not applicable (structural colour absent).

taxon	melanistic scaling	structural colour	taxon	melanistic scaling	structural colour	taxon	melanistic scaling	structural colour
adonis	1	0	*felthami*	1	NA	*pyramus*	4	2
aethon	1	NA	*irene*	1	2	*pyroeis*	2	1
amatola	1	NA	*lyncurium*	?	NA	*stepheni*	2	1
aridimontis	3	1	*lyndseyae*	3	4	*swanepoeli*	4	2
aridus	0	NA	*lysander*	?	?	*t. bamptoni*	4	3
aureus	1	NA	*mithras*	3	1	*t. psyche*	4	3
azurius	4	3	*natalensis*	1	NA	*t. schloszae*	4	2
beaufortia	4	1	*nigricans*	1	1	*t. thysbe*	4	2
beaulah	2	1	*oreas*	4	NA	*trimeni*	0	1
blencathrae	3	NA	*orientalis*	1	1	*turneri*	1	NA
braueri	3	1	*palmus*	2	NA	*uranus*	3	0
brooksi	1	2	*pan*	1	3	*violescens*	1	0
chrysantas	0	NA	*pelion*	1	1	*williami*	1	1
chrysaor	1	NA	*penningtoni*	1	1	wykehami	3	NA
daphne	3	1	*perseus*	3	3	*zeuxo*	0	NA
dicksoni	1	NA	*phosphor*	?	NA	*zwartbergae*	3	1
endymion	4	2	*plutus*	1	1			

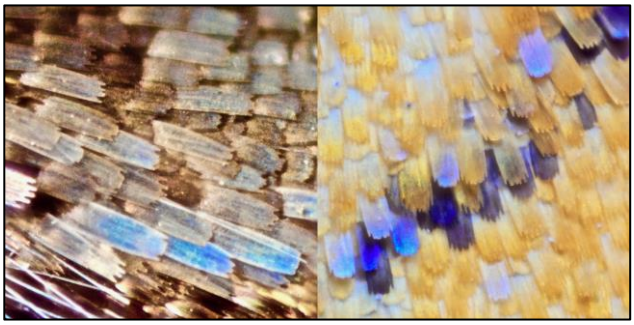

Figure 5 – Obscure iridescent scales of *C.* amatola **stat. nov**. (left) and *C. aridus* (right).

Figure 6 – A common posture of *C. thysbe psyche* male (Kotzesrus).

silvery blue translucent scaling at their wing basal area, but this is less extensive than in the males, and iridescence is very weak or absent. Furthermore, these scales in females are unlike the silvery-blue cover-scales of the male, being mostly shaped as common scales with the apex terminating in 5–6 prongs (as opposed to the rounded or serrated apex of male cover scales). This sexual dimorphism in *Chrysoritis* indicates an important role for structural colour, particularly iridescence, in mate recognition. The presence, absence, or extent of such structural colouring, including UV reflection, may serve as a barrier to mating between interspecific taxa in sympatry via female choice of mates. The silvery-blue colouring might additionally enhance the butterfly's control over body temperature when it is at rest with the wings held partly open (as in Fig. 6).

Melanistic versus pallid scales

The presence of melanistic wing scaling (*e.g.*, *C. pyramus*, *C.* aridimontis, *C. swanepoeli* and *C. blencathrae*) appears scattered throughout the COI phylogeny of *Chrysoritis* (Fig. 1 in QEA22). Melanism may be affected by a range of environmental factors, including temperature (Goulson, 1994; Hazel, 2002; Solensky & Larkin, 2003), ground cover (Cheng *et al*., 2018), and humidity (Goulson, 1994). High elevation habitats are generally colder and often result in melanism in a butterfly population (Gautam & Kunte, 2020), but high elevation does not always produce melanistic populations, even in the same species, *e.g*., *C. swanepoeli* and *C. pyramus balli*. The cause of this discordance is likely due to environmental differences between micro-habitats, even at similar elevations (Heath & Pringle, 2007: 36). Thus, a significant presence of melanism in a population may be treated here either as an intraspecific form, or sometimes as a subspecies if supported by molecular divergence and representative of a population. Table 1 shows the variability in melanistic covering across species. We regard pallid wing facies to be environmentally induced, such as by arid conditions, and treated in the same way as melanistic forms, *e.g*., *C. t. thysbe*; *C. azurius*, etc. The extent of wing melanism or paleness can vary among individuals of the same species and subspecies (Fig. 3 in QEA22)

Morphology of *Chrysoritis* juvenile stages

In the superb work of Clark and Dickson (1971), life history details of 122 South African lycaenid species are described and illustrated in detail. Only 13 *Chrysoritis* species are included (as *Poecilmitis*), of which eight are from the *thysbe* clade. Unfortunately, scant reference is made to the species of host ants or their relationship with the larvae. Twenty-two photographs of typical *Chrysoritis* eggs and larvae of various instars are depicted in Heath & Pringle (2007, pl. 3 & 4). For natural history accounts of *C. lycegenes* see Henning, S.F. (1983: 71).

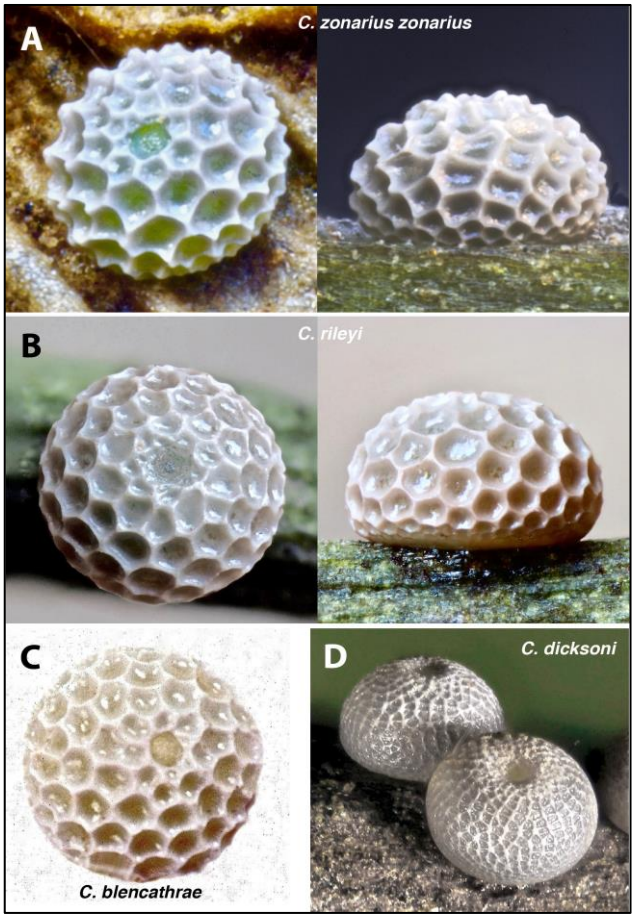

Figure 7 - Eggs of four *Chrysoritis* species (not to scale). A. *C. z. zonarius* (Churchhaven). B. *C. rileyi* (Brand Vlei). C. *C. blencathrae* (Waaihoek Mt.). D. *C. dicksoni* (Witsand; photo: S.E. Woodhall).

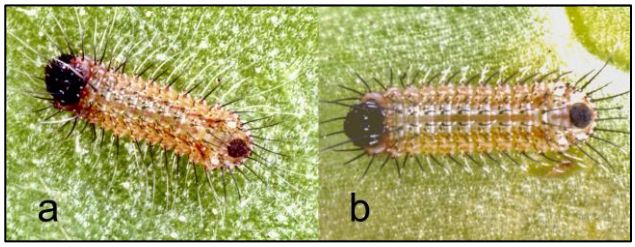

Figure 8 – Lateral setae of 1st instars. (a) *C. blencathrae* (Waaihoek), (b) *C. plutus* (Kango, Oudtshoorn).

There is some variation in egg morphology across *Chrysoritis* (Fig. 7), but among the *thysbe* clade species, eggs are bun shaped and fairly uniform (Figs 7B & C), varying slightly in the density of dimples. Eggs are pale green or white when laid, and later, whitish in colour but individual eggs are sometimes stained dark brown or black. First instar larvae are somewhat flat in cross-section, varying mostly in the length and colour of the lateral setae (see below and Fig. 8); they are pale straw-coloured at first but this generally changes once the larvae have begun to feed as their colour is affected by the host plant ingested. A pair of rudimentary tentacle organs (TOs) occurs on the eighth abdominal segment, initially without tubercle casings in the first instar; in second and subsequent instars, the TOs are encased in protective tubercle casings (see below and Fig. 9); when everted they are angled toward the

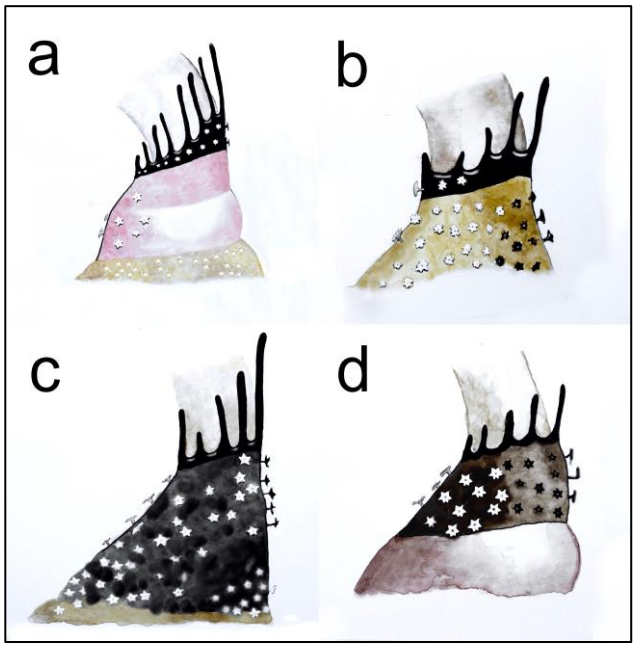

Figure 9 – Four tubercles (excluding tentacular organ) re-drawn from Clark & Dickson (1971). (a) *C. nigricans*, (b) *C. pan*, (c) *C. p. palmus*, (d) *C. u. uranus*.

dorsal nectary organ (DNO). A DNO appears in the second instar and subsequent instars, a feature shared with *Crudaria* Wallengren; in other aphnaeines it appears in the third instar. It occurs as a median transverse slit at the distal end of the seventh abdominal segment. Late instar larval colouring varies not only between taxa, but also among siblings, ranging from dull red, brown, grey to bright green. (see *Metamorphosis*, 2007 vol. 18, issue 1, rear cover). In reality, the patterns of the three posterior segments are not as consistent or well defined as those depicted in Clark & Dickson (1971).

Table 2 – Lengths of the upper row of lateral setae of first instar larvae of 19 *Chrysoritis* taxa. Setae lengths are expressed as a proportion of the larva's width. Measurements were made from images taken by A. Heath. Larvae were photographed in their natural state (unflattened). As shown in the table, there is a considerable range of lengths and they do not correlate with the COI phylogeny. Illustrations in Clark & Dickson (1971) appear to be in accord with these measurements that suggest relative uniformity within species.

Taxon	Setae length	*thysbe* mt clade
C. plutus	0.41	3
C. turneri	0.42	1
C. pan	0.43	1
C. brooksi	0.47	3
C. thysbe schloszae	0.47	2
C. thysbe psyche	0.47	2
C. perseus	0.5	1
C. pyramus pyramus	0.5	3
C. pyramus whitei	0.51	3
C. beaufortia sutherlandensis	0.52	4
C. beaufortia charlesi	0.53	4
C. endymion rileyi	0.55	3
C. palmus palmus	0.56	3
C. daphne	0.66	3
C. swanepoeli	0.88	3
C. uranus uranus	0.95	1
C. zwartbergae rubrescens	1.15	3
C. blencathrae	1.4	3
C. nigricans	1.4	3

In early first instar larvae of species in the *thysbe* clade, the lateral setae in the upper row are black with a white tip and show a ~three-fold variation in length from one species to another (from 0.4 to 1.4 times the larval width; see Fig. 8 to compare extremes between the upper row of lateral setae in *plutus* with that of *blencathrae*; see also Table 2 comparing 19 taxa examined). In particular, the first instars of *C. blencathrae* and *C. nigricans* have atypically long lateral (and other) setae, in comparison to those of other species in the *thysbe* clade. The length of the lateral setae does not seem to correlate with phylogeny, but does appear to be constant within species, suggesting it may be a taxonomically informative trait.

The length and shape of the tubercles housing the tentacular organs appear to differ significantly among *Chrysoritis* species (see Fig. 9 for four examples of final instar tubercles in the *thysbe* clade). These variations (also seen in 7 of the 8 *thysbe* clade illustrations in Clark & Dickson (1971), species nos. 84–91) are postulated here to be an interspecific characteristic. However, the nature of this variation within or across species has not been studied, thus its taxonomic utility is presently unclear.

Pore Cupola Organs are specialised setae positioned around the spiracles and DNO of larvae (see Cottrell, 1984:

29 and Fiedler, 1991: 13 for a full account of these myrmecophilous organs). These have not been studied here as the magnification requirements are beyond the scope of this study.

The juvenile morphology traits discussed above are severely data deficient and hence have played little part in our taxonomic revision (Heath *et al*., 2023, this volume). However, expanded sampling of species and of individuals within species will shed light on their potential in this respect.

Late instar larvae are densely clad with short mushroom-like setae with star-shaped heads, visible only under a microscope (Fig. 10). Examinations of macro-photos reveal that the number of points on the setae heads can, to a limited extent, vary on a single larva, hence these setae are of limited value in species circumscription.

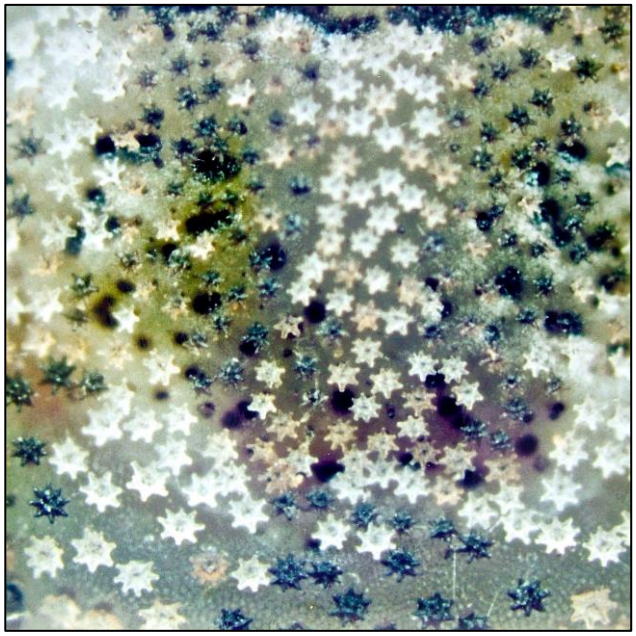

Figure 10 – *C. t. thysbe* larval epidermis setae.

Ecology and behaviour of *Chrysoritis*

Chrysoritis are mostly associated with open veld, montane and coastal fynbos with the striking exception of *C. phosphor* (Trimen), which is arboreal. Following emergence from pupae, adult females of the *thysbe* clade migrate to a particular geographical feature where males of their species or population patrol, awaiting the arrival of virgin females. Depending on the species or population, this male patrolling terrain (MPT) can be a hilltop, a gully, a slope, flat ground or a depressed area, etc. This aggregation of males at particular types of terrain may be a form of lekking. Males of the *thysbe* clade are territorial and are often seen rapidly circling one another in a fight for a small territory. After meeting and mating, the female will seek localities suitable for ovipositing. In species outside the *thysbe* clade, males and females tend to remain in the vicinity of their host plants and male aggregation sites have never been observed by the authors (but see Natural History of *Chrysoritis dicksoni*, below). MPT, where known, is listed for each of the *thysbe* clade species in Heath *et al.*, 2023.

Chrysoritis are obligately associated with specific host ants, mostly *Crematogaster* (Myrmicinae) but two species are associated with *Myrmicaria* (Myrmicinae). Other than the aphytophagous *C. dicksoni*, they are all phytophagous. Using olfactory cues, the adult female seeks out a plant or an ant trail frequented by a particular species of ant to oviposit one or more eggs (see also Cottrell, 1984: 40–41). A female typically lays her eggs on multiple plants.

Figure 11 – *C. t. thysbe* 5th instar plus two *Crematogaster peringueyi* ants engaged in mutual trophallaxis, sharing honeydew that was taken from the larva's DNO (Blaauwberg N. Res.)

On emergence, the first instar larva will feed on the leaf surface of its host plant. *Crematogaster liengmei* ants have been recorded carrying a newly hatched larva of *C. lyncurium lycegenes* to a suitable host plant (S.F. Henning, 1983a), presumably because the larva was found away from its host plant. The second and subsequent instars (usually six) have a DNO that the ants frequently palpate with their antennae for honeydew that the larvae secrete. In nature, the larva is always attended by one or two ants; observations indicate that it is generally the same individual ant that harvests the honeydew but this is then passed on to their nestmates by trophallaxis (Fig. 11). When a larva no longer has honeydew to secrete (or perhaps withholds it) but the ant persists in palpating the DNO, the larva everts its TO toward the DNO, presumably in an attempt to deter the ant's behaviour; the TO also everts when a larva is prodded or handled by researchers (A. Heath, pers. obs.), thus TO eversion appears to be a response to irritation; it may also be used to recruit ant chaperones (see below). As the larva feeds and grows it is better able to exude honeydew from the DNO. This fluid is quickly imbibed by a host ant and subsequently shared via trophallaxis with one or more of its nestmates, as in Fig. 11.

If a larva is taken from its natural habitat and reared in captivity on its food plant without host ants, honeydew builds up on the surface of the DNO, resulting in mildew and death. However, in captivity, larvae can be reared successfully to pupation if the eggs are hatched in the absence of ants, reared without ever being exposed to ants, and their DNO never stimulated (provided spiders and other predators are kept away). In this way, honeydew is never secreted (suggesting honeydew production may be ant-mediated). This method of rearing butterflies presumably allowed Gowan Clark, one of the authors of *Life Histories of the South African Lycaenid Butterflies* (Clark & Dickson, 1971) to depict microscopic details of larval morphology throughout all instars with scant

reference to ants. However, their natural behaviour, biology and ecology can only be studied properly in the presence of their host ants. This is possible for late final instar larvae collected together with sufficient ants but impractical for earlier stages. Butterflies reared in the absence of ants throughout all larval stages are often smaller, sometimes even miniature in size (Heath & Kaliszewska, 2013: 19), and their ability to produce viable offspring in the wild would likely be compromised.

In addition to their relationship with *Chrysoritis* larvae, the ants have a mutualistic relationship with Hemiptera, usually scale insects (but possibly also root aphids) which are always present on the larval host plant. The Hemiptera exude honeydew that is imbibed by the ants that protect them.

Figure 12 – Silken refuge of *C. perseus* larva.

During the day, and after feeding on foliage at dusk and night, the larva shelters in leaf litter or in a similar dry refuge on or below the host plant while still attended by one or two host ants. This refuge is usually strengthened or lined by strands of silk spun by the larva (Fig. 12) and sometimes further protected by grains of sand or other material placed by the host ants. A refuge can also be a dried and curled leaf, with its petiole secured by strands of silk. The larva usually returns to the same refuge after feeding. At dusk, as the larva moves from its refuge to feed, it everts its TOs frequently. We assume that this behaviour is intended to recruit nearby host ants to accompany and protect the larva during its vulnerable moments of exposure. The ants become aggressive if the larva is disturbed and may defend their source of honeydew from predator, parasitoid and researcher alike.

Larvae go through six and occasionally seven instars, then pupate within their refuge on or below their host plant, still tended by one or two host ants. Clark & Dickson (1971) recorded that *C. lyncurium lycegenes* pupate within their host plant larval refuge, although S.F. Henning (1983a: 72) recorded that at Karkloof, KZN, he found several pupae of this same taxon inside a nest of *Crematogaster liengmei*. It seems likely that these pupae had also used the ant nest as their larval refuge; this behaviour would be dependent on the close proximity of their larval host plant to the ant nest. We suspect that *Chrysoritis* species associated with the larger *Crematogaster peringueyi* ants could also find refuge in their ants' carton nest if it is in close proximity. In over 40 years studying lycaenid life histories, all late instar larvae and pupae encountered (several dozen) were found in their refuges close to or on the host plant (A. Heath, pers. obs.). However, investigating the contents of *Crematogaster peringueyi* nests by a researcher would seldom be attempted, due to the ants' highly aggressive nature. Although refuge within a *Crematogaster peringueyi* carton nest was once confirmed for a herbivorous larva of *Phasis thero* Linn. (A. Heath, pers. obs.), it may occur more widely in *Chrysoritis* than the available evidence suggests.

Pupae are secured loosely within their refuge by cremastral hooks attached to the silk inner lining. On eclosion the adult butterfly hurriedly escapes upwards to avoid being killed and eaten by the same host ants that previously protected it. It then proceeds to a safe vantage point to expand and dry its wings.

Figure 13 - *C. zonarius* 1st instar, in captivity, feeding on *Osteospermum moniliferum* (Silwerstroomstrand, Cape Town) in a manner described for *C. zeuxo* by Clark & Dickson (1971:168). The usual host plant for *C. zonarius* in nature is *O. incanum*.

The species of host ant is generally specific to populations of the butterfly but not necessarily constant throughout the entire distribution of the species (*e.g.*, *C. pan*, *C. perseus* and *C. azurius*). Larvae in the *thysbe* clade are associated with a wide variety of host plants, indicating that they are all polyphagous (Table S1 in Heath *et al.*, 2023). For *Chrysoritis* in general, larvae that appear to be monophagous may also feed on alternative plants in captivity (*e.g.*, Fig. 13). The localised choice of host plant on which the female oviposits appears to depend on the presence of ants; that in turn is maintained by the presence of hemipterans which are tended by the ants and whose secretions the ants imbibe. Very little is known about the taxonomy of the hemipterans involved in this chain of interactions. Based on field observations, they appear to comprise mostly various morphological forms of scale insects but root aphids are possibly also involved. It is unclear to what extent the ants specialise on hemipteran taxa or the hemipterans to plant taxa; this is a topic worthy

of further research, together with the use of *Thesium* as host plants (see below).

Many species of *Thesium* are used as host plants within the *thysbe* clade but only two species outside that clade are known to feed on *Thesium* – *C. oreas* and *C. pyroeis*. Interestingly they are also the only two species whose host ant is *Myrmicaria*. Utilisation of *Thesium* as host plants may have enabled the prolific diversification of the *thysbe* clade in the Greater Cape Floristic Region (see QEA22).

Herbivorous larvae are always accompanied by attendant ants on or beneath the host plant. In 1998, a final instar of *C. thysbe thysbe* was recorded making low-pitched grunting sounds, and some very high-pitched sounds (Heath, 1998); these were slightly different from the sounds noted below for *C. dicksoni*. A possible explanation for this difference may lie in the different acoustic properties of their larval environment (leaf litter for *C. t. thysbe* vs. ant carton nest for *C. dicksoni*). "Squeaking" sounds were also heard from pupae of both *C. nigricans* and *C. b. brooksi* by M. Schlosz (1991: 19); see also Cottrell (1984: 38). The functions that these different sounds might fulfil have yet to be determined, but other lycaenid larvae are known to communicate with ants via substrate-borne vibrations, and even employ acoustic mimicry of ant queens (Travassos & Pierce, 2000; Barbero *et al.*, 2009).

Natural history of *Chrysoritis dicksoni*

The natural history of the critically endangered *C. dicksoni*, the largest of the *Chrysoritis* species, has been summarised by Heath (2014). Here, we provide a brief reassessment of this cuckoo species together with additional insights into its ecology, particularly its relationship with its host ant and mechanisms for eliciting tending and feeding behaviours from the ant.

Within *Chrysoritis*, *C. dicksoni* larvae are the only ones known to be aphytophagous; however, plant feeding appears to have been lost multiple times within the Aphnaeinae, typically by individual species within otherwise phytophagous genera (Boyle *et al.*, 2014: 13). The female oviposits on any one of a variety of plants frequented by *Crematogaster peringueyi* ants and infested by scale insects. In captivity but under semi-natural conditions outdoors, about ten first instar larvae were experimentally placed beside mature, live scale insects where they remained for over two weeks. Each larva remained where it was placed but raised its front portion when visited by a host ant and was briefly fed by the ant via trophallaxis (mouth to mouth regurgitation). Some of these larvae eventually disappeared, perhaps taken into the ant carton nest or taken by spiders. Some 1st instar larvae were separately reared, each with two host ants, within a petri-dish; here too, under magnification, trophallaxis was observed. Additionally, the ants were seen to behave unusually when close to the larva – cringing, staggering about in a jerky manner, and waving their antennae.

The possibility that *C. dicksoni* larvae feed on ant brood was suggested in Clark & Dickson (1971) but ant brood as food is discounted on two counts here: 1) three final instar larvae in captivity were each presented with ant larvae (eggs were not available) taken from the ant carton nest on two separate occasions, but they showed no interest (Heath, 1998: 162). 2) Additionally, these larvae were strictly sedentary, which is incompatible with a predatory lifestyle. In a separate experiment, final instar larvae were placed in exposed locations with their host ants nearby but the larvae remained *in situ*, never moving away; their host ants would find them and trophallaxis would resume, even in exposed locations. Hence, the available evidence indicates that *C. dicksoni* larvae subsists solely on food provided by the worker ants. It is conceivable however, that larval diet, especially for late instar larvae, is supplemented by trophic eggs (unfertilised ant eggs) delivered by worker ants (Heath, 2014: 9). A number of ant taxa, including *Crematogaster* species, are known to feed trophic eggs to their own young, so it is quite plausible that highly integrated myrmecophiles, like nest-inquiline *Chrysoritis*, may have evolved the ability to solicit such food items from ants (K. Fiedler, pers. comm.). Heath & Claassens (2000: 8; 2003: 11) noted that a final instar larva of *Aloeides pallida grandis* Tite & Dickson kept in an ant nest chamber of a formicarium chose to feed only on ant eggs whilst plenty of other stages of ant brood were available (see also Pierce & Dankowicz, 2022). Thus trophic eggs provided by *Crematogaster* ants may prove to be a supplementary or major food for the sedentary *C. dicksoni* larvae.

After the larvae entered their 2nd instar, the ants continued to behave strangely. They were reluctant to leave their charge – they stood motionless over the moist DNO and appeared intoxicated, jerky and unable to walk normally, and they continually cleaned themselves (Heath & Brinkman, 1995).

Figure 14 – *C. dicksoni* final instar with *Crematogaster peringueyi* ant attending the DNO. Eggs of *C. dicksoni* are shown in Fig. 7D.

These observations are consistent with the finding that lycaenid larval secretions can manipulate ant behaviour by altering levels of biogenic amines in the attending ant brain (Hojo *et al.*, 2015; see also Henning, 1983b). These behavioural observations around the 2nd instar were repeated with the larva's final instar (Heath, 1998). The DNO of the final instar was active and produced honeydew droplets that the attending ant imbibed (Fig. 14), but this occurred infrequently. The final instar also had a small specialised seta located on some segments that frequently attracted the host ant who seemed to nibble at it. The seta appeared as a curved structure resembling a bottle-brush, and is illustrated by Heath (1998: 169). The 3rd–5th instars

have yet to be observed, but it is likely that the ant interactions would be similar to those of the final instar.

It is possible that the main function of the DNO of *C. dicksoni* is to secrete an olfactory agent, rather than for the provision of nutritional honeydew which is produced only infrequently. This olfactory substance is possibly an allomone that facilitates the larva's subterfuge, allowing this cuckoo species to not only reside in the carton nest unchallenged by the ants, but also elicit feeding and tending behaviours. However, the relative importance of one function over the other (allomone vs. nutrition) is unknown. Cottrell (1984: 43) posited an inability of aphytophagous butterfly species to obtain the necessary plant-derived sugars in sufficient quantities to produce honeydew. Also, it appears that a major portion of the ants' diet comes from hemipteran honeydew, which is then regurgitated to feed the butterfly larva (A. Heath, pers. obs.). Hence any honeydew that the larva secretes would be derived indirectly from the ants in the first place, and thus be of doubtful nutritional quality. For comparison, the final instars of *Aloeides pallida grandis* Tite & Dickson, which are non-herbivorous and feed solely on ant eggs, lack a DNO, but earlier instars which are herbivorous have one Heath & Claassens (2000: 8; 2003: 11). It is possible that honeydew as a nutritional product has a diminished mediatory role for *C. dicksoni* and its host ant, as in the final instar of *Aloeides pallida grandis*.

Compared to other species, the tubercles of *C. dicksoni* are reduced in size (Fig. 14); this may be an adaptation to accommodate the larva in the confined spaces within the carton nest.

In 1998 a captive final instar larva of *C. dicksoni* was heard making tapping sounds by jerking its front portion. We suspect that these sounds mimic those made by the queen ant (Heath, 1998: 161; 2014: 1) as such queen-ant-mimicking behaviour has been demonstrated in other lycaenid species (Barbero *et al*., 2009). This may further explain provisioning behaviour by worker ants.

Like other *Chrysoritis* species, eclosion is a hurried affair, escaping out of the carton nest with deciduous fine hairs adhering to its soft abdomen, thereby impeding any attack by the ants. It then proceeds to a high vantage point to expand and dry its wings. Meeting and mating (observed once in nature by A. Heath) was a functional affair that lacked a nuptial flight or any form of courtship (see also Giliomee & Edge 2015: 40). Within a given population, males of *C. dicksoni* are gregarious and tend to congregate in small sub-colonies or leks, described by Cottrell (1978b) as appetitive sexual assembly areas. *Chrysoritis dicksoni* is the only species outside the *thysbe* clade known to show male aggregation behaviour, but unlike *thysbe* clade species, no consistent topographical feature serving as a focus for male aggregation has been identified (A. Heath and E. Pringle, pers. obs.); the focus of male aggregation could be olfactory, e.g., driven by the presence of ants and/or Hemiptera). Cottrell also noted that females did not show the same attachment to a localised area as do the males (see also Edge & Terblanche, 2010).

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