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Chrysoritis Butler (Papilionoidea: Lycaenidae: Aphnaeinae) – Part III: An integrative taxonomic revision

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Abstract: A taxonomic revision of *Chrysoritis* butterflies based on morphological, ecological and distributional data cross validated with molecular phylogenetic analyses by Quek *et al*. (2022) is presented. The number of *Chrysoritis* species is raised from 43 to 49, of which 37 (previously 28) are in the *thysbe* clade. The taxonomic changes are summarised as follows: Synonymised and reduced to subspecific status: *C. chrysaor natalensis* **stat. nov.** (van Son); *C. lyncurium lycegenes* **stat. nov.** (Trimen 1874) and *C. chrysaor midas* **stat. nov.** (Pennington). Reassigned subspecies: *C. zwartbergae rubrescens* **stat. nov.** Heath & Pringle. Elevated to specific status: *C. whitei* **stat. rev. (**Dickson); *C. wykehami* **stat. rev.** (Dickson); *C. mithras* **stat. rev.** (Pringle); *C. aridimontis* **stat. nov.** Heath & Pringle; *C. amatola* **stat. nov.** (Dickson & McMaster), *C. stepheni* **stat. rev.** (Dickson); *C. williami* **stat. rev.** Heath and *C. lysander* **stat. rev.** (Pennington) from the Kamiesberg area; *C. zwartbergae* **stat. nov** (Dickson). The former *C. thysbe* subspecies *osbecki* reverts to form, f. osbecki **stat. rev.** The binomial name *pan lysander* is no longer in use, being superseded by the above changes. An updated list of larval host plants and host ants for *Chrysoritis* is provided, as well as the conservation status of each species.

Key words: sympatry, Cytochrome C Oxidase I, introgression, iridescence, hilltopping, male patrolling terrain, *Crematogaster*.
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INTRODUCTION

In this final of three papers on *Chrysoritis* Butler, the analyses of Quek *et al*. (2022, hereafter abbreviated to QEA22) are integrated with morphological, ecological and distributional data to provide a taxonomic revision of *Chrysoritis*. The three papers (QEA22, Heath *et al*., 2023, abbreviated to HEA23, and the present one) are best read as a single unit due to extensive cross-referencing of each to the others.

In preparing taxonomic revisions for species in the young *thysbe* clade, the authors were faced with a dearth of morphological characters, limited sampling in many taxa, and poor resolution in nuclear loci. Under these constraints and the non-discrete nature of young species evolving in dynamic environments, the taxonomic hypotheses proposed herein for the *thysbe* clade have been achieved with difficulty and substantial deliberation. The *thysbe* clade is an example of what happens when taxonomists "try... to stuff complex, evolving, sexually reproducing organisms into 'species boxes'" (Williams, 2004). In reality, recently diverged species such as these are more akin to probability density clouds that morph and intersperse over time and over physical and biological space (morphospace, ecospace, *etc*.), and attempts to fit them into discrete bins can leave much to be desired. Nonetheless, names have value so with taxonomic hypotheses informed by morphology, ecology and distribution, and cross validated by molecular data, we present this revision of the taxonomy of *Chrysoritis*.

The presence of a significant number of species and phenotypes in the *thysbe* clade that are polyphyletic at COI clearly indicates that a lot more is going on in the *thysbe* clade than COI and phenotypes can reveal. In particular, species with multiple COI lineages that are phylogenetically and (seemingly) geographically disjunct with inconclusive support from nuclear data (*C. beulah* and *C. wykehami*) or no support from nuclear data (*C. perseus*) point to the need for deeper investigation. Several taxonomic issues also remain to be resolved: 1) *Chrysoritis swanepoeli hyperion* as well as the three morphs within *C. pan* (*pan*, *henningi* and *atlantica*) may turn out to better fit the description of forms rather than subspecies as designated herein; 2) within each of the following pairs, the latter may turn out to be subspecies of the former, instead of full species as designated herein: i) *C. zeuxo* + *C. zonarius*, ii) *C. aethon* + *C. aureus*, iii) *C. endymion* + *C. rileyi*; a single subspecies designation may be a better fit for *C. thysbe psyche* + *C. t. bamptoni*. Shedding light on these issues will likely require the application of molecular techniques that sample variability throughout the entire genome, or even whole genome sequencing. Regardless of the nature of the data used, for the *thysbe* clade at least, dense sampling of species and subspecies covering the span of each taxon's distribution will be imperative if we are to be more confident of taxonomic circumscriptions. Complementing the genetic data, future morphological studies should include microscopic examinations of the larval stages, particularly the final instars, the length of the upper row of lateral setae in early first instar larvae and the

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length and shape of the tubercles housing the tentacular organs (see QEA22 and HEA23).

Abbreviations and terminology

CAD: Carbamoyl-phosphate synthetase 2/aspartate transcarbamylase/dihydroorotase (partial gene fragment); tree is shown in Fig. S3A of QEA22
COI: Cytochrome c oxidase subunit I (partial gene fragment); tree is shown in Figs. 1 & S1 of QEA22.
Crem.: *Crematogaster*
EC: Eastern Cape Province
EF: Elongation factor 1-alpha (partial gene fragment); tree is shown in Fig. S3B of QEA22
H3: Histone 3 (partial gene fragment); tree is shown in Fig. S3C of QEA22.
HEA23: Heath *et al.* (2023)
ILS: incomplete lineage sorting, explained in Note S2.
Introgression: Explained in Note S2.
mtDNA: mitochondrial DNA
MY(A): Million years (ago)
MPT: Male patrolling terrain
NC: Northern Cape Province
NM: National Museum
NHM: Natural History Museum
KZN: KwaZulu-Natal
QEA22: Quek *et al.* (2022)
TEA20: Talavera *et al.* (2020)
WC: Western Cape Province

IUCN Conservation Status
CR: Critically Endangered
EN: Endangered
LC: Least Concern
VU: Vulnerable

MATERIALS AND METHODS

A description of taxon identifications and morphological and ecological traits (host plants, host ants and MPT) can be found in the Materials and Methods section of QEA22. All photos shown have been taken by A. Heath unless otherwise indicated. The conservation status of species and subspecies is based on Mecenero *et al.* (2013) if still valid or Mecenero *et al.* (2020) if revised there [= (2020)].

Concepts and definitions: species, subspecies, and forms

Taxonomic determinations in this article are guided by the biological species concept (BSC) of Mayr (1942). According to the BSC, "species are groups of actual or potentially interbreeding populations that are reproductively isolated from other such groups." Establishing whether or not a *Chrysoritis* population interbreeds with another is not usually feasible. Thus if two populations have overlapping or contiguous distributions but maintain distinctive traits in the areas where they can potentially interbreed, then we assume they are reproductively isolated. For this reason, sympatry is an important aspect in circumscribing species, especially in the *thysbe* clade.

The working definition of subspecies used here follows Braby *et al.* (2012), where subspecies are "partially isolated lineages of a species that are allopatric, phenotypically distinct, [and] have at least one fixed diagnosable character state; … [and furthermore,] these character differences are (or are assumed to be) correlated with evolutionary independence according to population genetic structure." Hence a subspecies can be viewed as a diagnosable incipient species.

"Form" (f.) is used in the classification of organisms based solely on morphology, with no underlying assumptions about genetic relatedness. Under the *International Code of Zoological Nomenclature*, "form" is not a recognised taxonomic rank or category. However, the term is sometimes useful in describing an altitudinal or geographic cline in morphology.

RESULTS OF TAXONOMIC REVIEW

All mention of trees/ phylogenies/topologies and the COI network refer to that presented in QEA22 as follows: COI: Fig. 1 (only species names shown) and Fig. S1 (all samples shown). CAD: Fig. S3A. EF: Fig. S3B. H3: Fig. S3C. COI network: Fig. 2B. Total dataset: Fig. S2.

Recorded distributions of butterfly taxa in South Africa, Lesotho and Swaziland can be found in Pringle *et al.* (1994), Williams (2021) and Mecenero *et al.* (2013). Host plant and host ant records and their sources are listed in Table S1; these are based on past and recently recorded ant and plant hosts, and may not reflect the entire range of hosts. Supplementary Table S1 and supplementary notes (Notes S1–3) can be viewed and downloaded at https://doi.org/10.6084/m9.figshare.21936108
All supplementary figures (Figs. S1–3) can be downloaded at https://doi.org/10.6084/m9.figshare.21936234

Chrysoritis Butler

Chrysoritis Butler (1897), type species *Zeritis oreas* Trimen 1891, by original designation. *Chrysoritis* are commonly known as Opals and Coppers.
= *Nais* Swainson (1833), type species *Nais splendens* Swainson, by monotypy; junior homonym of *Nais* Müller 1771.
= *Poecilmitis* Butler, 1899e, type species *Zeritis lycegenes* Trimen 1874, by original designation. Synonymised with *Chrysoritis* by Heath (1997: 17).
= *Bowkeria* Quickelberg 1972, type species *Zeritis phosphor* Trimen 1864, by monotypy. Synonymised with *Chrysoritis* by Heath 1997: 17.
= *Oxychaeta* Tite & Dickson, 1973, type species *Phasis dicksoni* Gabriel 1947, by original designation. Synonymised with *Chrysoritis* by Heath (1997: 17).

Recent analyses by Kawahara *et al.* (2023) suggest *Chrysoritis* diverged from its sister group 22.9 MYA (95% highest posterior density interval 21.9–25.0 MYA [D. J. Lohman, pers. comm.]). The genus comprises two major clades – the Eastern Lineage, with an ancestral distribution and origin in the east, and the Western Lineage in the west (QEA22, see also Terblanche & Hamburg 2003).

Eastern Lineage

Seven species: *oreas, phosphor, dicksoni, chrysaor, aethon, aureus, lyncurium*. All seven lack iridescence or structural colouring. The Eastern Lineage is found in the

COI, EF, CAD and Total Dataset trees (98%, 95%, 84%, and 92% respectively); in the H3 tree, it is paraphyletic but this is most likely due to misplaced rooting in the analysis. All trees are shown in QEA22.

Chrysoritis oreas (Trimen, 1891), type species of *Chrysoritis*. *Zeritis oreas* Trimen, 1891: 176. Holotype: Iziko Museum. Type locality: "Near summit of Niginya" in Natal. (Coll. J.M. Hutchinson).

Characters: Upper side ground colour yellowish orange, marked with black spots and broad black margins, especially the forewing. Underside with a submarginal series of sagittate markings on both wings; hind wing with dense pattern of browns and orange. Outer margin of forewings noticeably convex in both sexes; hind wing without tail or tornal development in either sex. Forewing with eleven or twelve veins (depicted in Stempffer 1967: 295). Male genitalia shown in Figs 2b & 2c; apophysis on subunci vestigial or absent; aedeagus lacks cornuti. Juvenile stages are illustrated in Fig. 1. *Chrysoritis oreas* is one of two *Chrysoritis* species to associate with the 'droptail' *Myrmicaria* (Myrmicinae) ants, the other being *C. pyroeis* (Trimen). Conservation status: LC – Rare (2020).

Figure 1 – *C. oreas* (Bushman's Nek). 1st instar (top) and ~4th instar (bottom). Not to scale.

Chrysoritis phosphor (Trimen 1864). *Zeritis phosphor* Trimen 1864: 178. Holotype: Iziko Museum. Type locality: "Bashee River, Kaffraria" (Eastern Cape Province). This is the only *Chrysoritis* species with arboreal habits, occasionally descending to nectar. Juvenile stages unknown. Host ant: unrecorded. This is a phenotypically well defined species. CAD and EF data are not available for this taxon.

Characters: Upper side red with dark markings. Male with acute forewing apices and large dark apical patch. Underside hind wing with obscure dark markings on a plain orange-brown background. Forewing with twelve veins. Male aedeagus lacks prominent cornuti; apophysis on subunci elongated. This species superficially resembles a species of *Lipaphnaeus* Aurivillius in many respects but the male genitalia are typical of *Chrysoritis* (see Fig. 2A here and Fig. 1h in HEA23) and quite different from that of *Lipaphnaeus* (Heath 1997a: 46–53). The COI and H3 trees place it unequivocally within *Chrysoritis*.

C. phosphor phosphor (Trimen 1864). Holotype: Iziko Museum. Type locality: "Bashee River, Kaffraria" (Eastern Cape Province). Conservation status: LC.

C. phosphor borealis (Quickelberge 1972). *Bowkeria phosphor borealis* Quickelberge (1972: 90). Type locality: "Yellowwoods, Natal" (KwaZulu-Natal). Conservation status: EN (2020).

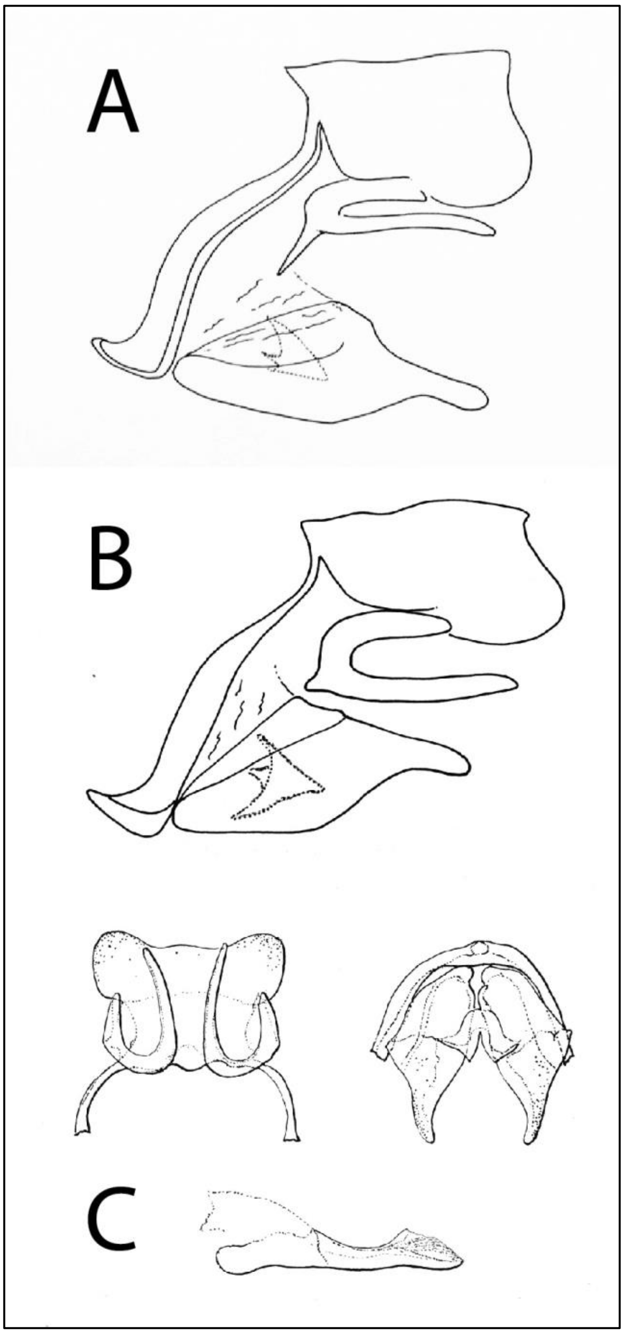

Figure 2 – Male genitalia. (A) *C. phosphor* lateral view with aedeagus removed (illustration by A. Heath); see also Fig. 1h in HEA23. (B) *C. oreas* lateral view with aedeagus removed. (C) *C. oreas* genitalic components; see also Fig. 1c in HEA23. Parts (B) and (C) reproduced from Stempffer (1967) by courtesy of The Natural History Museum, London. Not to scale.

Chrysoritis dicksoni (Gabriel 1947). *Phasis dicksoni* Gabriel 1947: 60. Placed in *Oxychaeta* by Tite & Dickson (1973) and later in *Chrysoritis* by Heath (1997) based mainly on its genitalia. Molecular support for this treatment was later provided by Rand *et al*. (2000) and TEA20/QEA22. Holotype: NHM, London. Type locality: "Nr. Melkbosch Strand".

Characters: Upper side copper-red, densely marked with black spots and broad black margins, especially on the forewing. Underside with a submarginal series of sagittate markings on both wings; hind wing with a dense pattern of browns and orange. Outer margin of forewings noticeably convex in both sexes; hind wing without tail or tornal development in either sex. Male genitalia: aedeagus lacks cornuti; apophysis on subunci vestigial or absent. Venation: forewing with twelve veins.

This is a subcoastal species that appears to be extinct at its previously known localities near Cape Town but currently thrives near Witsand on the South coast, albeit strictly monitored.

A partial account of the natural history of this insect was published by Clark & Dickson (1971), Heath & Brinkman (1995), and Heath (1998) and a more comprehensive one was summarised by Heath (2014); further natural history is discussed in QEA22 and HEA23. Host ant: *Crem. peringueyi*. This is the largest and the only species of *Chrysoritis* known to be aphytophagous. Larval and pupal stages develop within the ants' carton nest and food is provided by host ants at least partly by trophallaxis. The larvae are strictly sedentary. We propose here that trophic eggs are supplied by worker ants. (see HEA23). The DNO is present and active in the 2nd and subsequent instars. The morphology of juvenile stages is illustrated in Clark & Dickson (1971: 210); Heath & Brinkman (1995); Heath (1998, 2014), and in Figs. 7D & 14 in HEA23. Male genitalia are illustrated in Fig. 1g in HEA23. The natural history of *C. dicksoni* is described in detail in HEA23. Conservation status: CR.

Chrysoritis chrysaor (Trimen 1864). *Zeritis chrysaor* Trimen 1864: 177. Holotype: NHM, London. Type locality: Cape Colony, British Kaffraria & Kaffraria. Note: "Cape Town. Wynberg" is written on the holotype label. *C. chrysaor* is monophyletic and well supported in all trees, and is sister to the clade containing *C. aethon, C. aureus* and *C. lyncurium* in the COI, CAD and EF trees. The natural history of *C. chrysaor* is described and illustrated in great detail by C.G.C. Dickson (1943). Host ants: see below.

<u>*C. chrysaor chrysaor*</u>

Characters: Upper side glossy yellowish-orange to copper-red with narrow dark margins. Underside of hind wing yellow to reddish-brown and often with a greenish tinge among females, sometimes spots showing through obscurely from upper side. Male: aedeagus lacks cornuti. Forewing with twelve veins. Hind wing vein 1 margin is produced to a varying extent and usually with a short filiform tail extending from it. Wing profile, size of black markings and tail length may vary between populations and individuals. Conservation status: LC.

<u>Eastern populations</u>: Known from inland, along the mountain ranges of southern Mpumalanga through Lesotho and the eastern Free State to the mountains of the Eastern Cape, and thence westwards. The filiform tail is often longer and broader in the eastern populations than those in the west (see also Williams 2021).

Host ants for low elevations: *Crem. gallicola* and *Crem. liengmei* (see *C. chrysaor midas* below). High elevation populations of *C. c. chrysaor* (Lootsberg Pass; Great Winterberg, EC) share the exact same ecology as *C. c. midas* (below) but they may not have such dark scaling. Host ants for high elevations: *Crem. peringueyi.*

<u>Western populations</u>: Often having a yellowish tint (f. lycia Riley); filiform tail vestigial or absent. Host ant: *Crem. gallicola* and *Crem. liengmei*, although the host ant and host plant are not yet known for the high elevation populations on the Hottentot-Holland Mountains. The range of host plants recorded is more diverse than those of the eastern populations (Table S1).

Taxonomy: There is no consistent morphological or ecological trait to support a split between eastern and west coast populations of *C. chrysaor chrysaor*, hence no taxonomic distinction is accorded.

The *chrysaor* holotype specimen from Wynberg is part of the west coast population. A small coastal population of *C. chrysaor* overlooking the sea near Sarrisam Farm, 37km SE of Hondeklip Bay, NC, is placed as sister to the other west coast populations of *C. chrysaor* in the COI tree. However, it does not differ in its range of facies, nor in its observed ecology.

<u>*C. chrysaor midas*</u> (Pennington 1962) **stat. nov.** *Poecilmitis midas* Pennington 1962: 272. Holotype: Ditsong NM. Type locality: Oukloof Poort, Nieuwveld Mts. It occurs only at the higher elevations (> 1650m).

Taxonomy: The clade of *C. chrysaor midas s.s.* (n = 5) is monophyletic and nested within *C. chrysaor* in the COI tree. We consider this to be *bona fide C. c. midas*. The single sequences of *C. c. midas* in the EF, CAD and H3 trees are all also nested within *C. chrysaor*. Identifications of most extant published records of *C. c. midas* have been based solely on wing facies (blackish hind wing verso); these identifications were usually backed up by their ecology (montane distribution, host ant and host plant). *C. chrysaor midas s.s.* can occur in the same neighbourhood as *C. c. chrysaor*, but avoiding sympatry on account of their different elevations. In these areas of parapatry, *C. chrysaor midas s.s.* differs from its lower altitude kin in host ants (*Crem. peringueyi*) and host plants (*Diospyros austro-africana* De Winter). Being ecologically and genetically differentiated, *C. chrysaor midas s.s.* may have the makings of an incipient species, but morphologically it differs from the nominate *chrysaor* only in the greater degree of melanistic scaling in the hind wing verso; furthermore, samples of nominate *chrysaor* closely resembling *C. c. midas* are also found scattered among samples of *C. c. chrysaor* in the COI tree (eg., C004, C398, C399 and C005, treated here as *C. c. chrysaor*), and are considered to be a part of *C. c. chrysaor*. *Chrysoritis midas* is here synonymised as *Chrysoritis chrysaor midas* **stat. nov.** Conservation status: LC.

<u>*C. chrysaor natalensis*</u> (van Son 1966) **stat nov**. *Poecilmitis natalensis* van Son 1966: 84. Holotype: Ditsong NM. Type locality: Howick, Natal. Subspecies *natalensis* is geographically separated from nominate *chrysaor*, having a coastal or near coastal distribution along the Wild Coast from Morgans Bay near East London through the Transkei (Bashee River and Port St Johns) to the KZN south coast, and thence inland to the Karkloof and

Ngoye Forest areas. Juvenile stages as for nominate *chrysaor.* Host ant: *Crem. liengmei*. Host plant of *natalensis*: larvae commonly utilise *Osteospermum moniliferum*; however, adults of both sexes have been recorded frequenting *Vachellia karoo* at Ongoye, KZN (S. E. Woodhall pers. comm.). This could be for nectaring purposes. *Vachellia* has never been confirmed as a host for *natalensis* larvae, although inland it is a widespread host plant of nominate *chrysaor* eastern population.

Compared to the facies of nominate *chrysaor* the typical characteristics of *natalensis* consist mainly of: 1) a more prominent tornal lobe and tail; 2) the presence of a dorsal hind wing cell marking and 3) usually, a more caudal-elongated hind wing in the male; 4) underside hind wing markings more conspicuous; 5) the diffuse postdiscal brown patch in spaces 3–4 of the hind wing verso (present in many *chrysaor*) is more extensive, forming a dark brown band extending to space 2 in both sexes. However, *C. c. natalensis* wing facies can be variable, *e.g.*, sample T745 from Port Shepstone has a more rounded outer margin to its hind wings, whereas sample T727 from Umtamvuna N.Res has its outer margin straighter and elongated as in the *natalensis* holotype. Variations in the size of dorsal black markings may be attributed to environmental differences in micro habitat (*e.g.*, warmer/wetter vs. cooler/drier, S. E. Woodhall, pers. comm.). The identification of most extant records of *natalensis* are based solely on wing facies; these identifications are usually in agreement with the geography and local associated vegetation.

Taxonomy: *C. chrysaor natalensis* appears to be allopatric in relation to the nominate subspecies; it has 96% support and is sister to the remainder of *C. chrysaor* samples in the COI tree. The *natalensis* facies differ from nominate *chrysaor* in the characteristics described above, but partial overlap with *C. chrysaor* may occur in one or more of these characters. As a result, some *C. c. chrysaor* might be misidentified as *natalensis* and vice versa. Thus, *C. natalensis* is here synonymised as *Chrysoritis chrysaor natalensis* **stat. nov**. Conservation status: LC.

Chrysoritis aethon (Trimen 1887). *Zeritis aethon* Trimen 1887: 176. Holotype: Iziko Museum. Type locality: Lydenburg District. This species is sister to *C. aureus.* Host ant: *Crem. liengmei*. Host plant: *Searsia zeyheri* Sond. (Anacardiaceae); *Crassula* species (Crassulaceae). Conservation status: LC.

Chrysoritis aureus (van Son 1966) *Poecilmitis aureus* van Son 1966: 82. Holotype: Ditsong NM. Type locality: Heidelberg. Host ant: *Crem. liengmei* (same as *C. aethon*). Host plants recorded: *Clutia pulchella* (Euphorbiaceae); *Diospyros lycioides* (Ebenaceae). Final instar larva shown in Fig. 3.

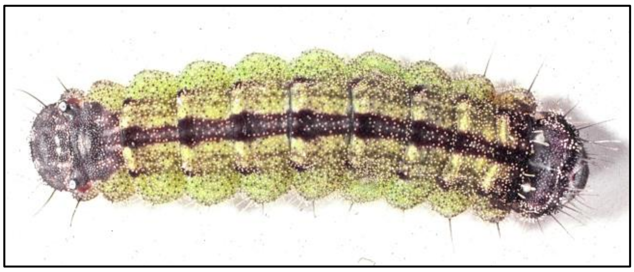

Figure 3 – *C. aureus* final instar (Heidelberg).

Taxonomy: *C. aureus* is sister to *C. aethon* in the COI tree (100% support) and CAD tree (98%); facies differ in its pallid wing scaling. Synonymy with *C. aethon* was considered but further research with more samples is needed. Conservation status: EN.

Chrysoritis lyncurium (Trimen 1868) *Zeritis lyncurium* Trimen 1868. Holotype: NHM, London. Type locality: “Nr. Tsomo River.” The nominate subspecies is known from a few widely separated localities, from Mbulu near Tsomo in the Eastern Cape, to Kokstad and Bushmans Nek in the southern KZN Drakensberg. Host ant: *Crem. liengmei*.

Taxonomy: This species is sister to *C. aethon* + *C. aureus*. Conservation status of *C. l. lyncurium*: VU.

C. lyncurium lycegenes **stat. nov.** (Trimen 1874: 337) *Zeritis lycegenes* Trimen 1874. Holotype: NHM, London. Type locality: “Natal”. Juvenile stages illustrated in Clark & Dickson (1971: 186). Known from localities scattered over KZN and southern Mpumalanga, from Wakkerstroom to the lower ridges of the Drakensberg as far south as Loteni, and to the grassy hills of the KZN Midlands.

Taxonomy: Similar facies and possibly a cline between populations of ssp. *lyncurium* in the west and ssp. *lycegenes* in the east as proposed by Owen-Johnston (1991). Formerly given species status, this subspecies (n = 3) groups with C. *lyncurium* (n = 2) in the COI tree (100%), EF tree (98%) and CAD tree (77%). It has a very similar appearance to *C. lyncurium*, having no consistent differences apart from the extent of black scaling. It is here synonymised as *Chrysoritis lyncurium lycegenes* **stat. nov.** Conservation status of *C. lyncurium lycegenes*: LC.

Western Lineage: non *thysbe* clade

Five species: *zeuxo*, *zonarius*, *pyroeis*, *felthami*, *chrysantas*. *C. pyroeis* has iridescence and structural colouring which the other four species lack. The Western lineage is found in the COI, Total Dataset and all nuclear gene trees (>92% bootstrap support in all trees). *C. chrysantas* is the only one in this grouping represented by a single specimen in this study; the others are each supported by 100% bootstrap values in the COI and Total Dataset Trees and >93% in the CAD, H3 and EF trees.

Chrysoritis zeuxo (Linnaeus 1764). *Papilio zeuxo* Linnaeus 1764: 331. Lectotype: Swedish NHM. Type locality: *Cap. Bonae Spei.* (Cape Peninsula). Characters: Upper side orange with broad dark margins and dark quadrate post-discal spots and sub-marginal markings. Hindwing verso, greyish-brown to orange with a weak pattern of spots outlined in a darker shade that correspond with the spots of the upper surface. Male aedeagus contains a tiny cluster of cornuti attached to the vesica. Forewings with ten or eleven veins. *Chrysoritis zeuxo* is derived from *C. zonarius* in the COI and EF trees; *C. zeuxo* renders *C. zonarius* paraphyletic, possibly as a consequence of ILS. Univoltine. Host ant *Crem. liengmei* host plant *Osteospermum moniliferum.* Juvenile stages illustrated in Clark & Dickson, 1971: 190. See *C. zonarius* (below) for taxonomic notes. Conservation status of *C. zeuxo zeuxo*: LC.

C. zeuxo cottrelli (Dickson 1975), *Poecilmitis* (*Chrysoritis*) *cottrelli* Dickson 1975: 225. Holotype:

NHM, London. Type locality: Buffelsnek Forestry, N. of Knysna. Conservation status: LC.

Chrysoritis zonarius (Riley 1938) *Phasis zeuxo zonarius* Riley 1938: 239. Holotype: NHM, London. Type locality: Nr. Melkbos Strand. Similar to but smaller than *C. zeuxo*, its putative daughter species. Univoltine. Host ant *Crem. peringueyi* and host plant *Osteospermum incanum*.

Figure 4 – *C. zonarius* 2nd (top) and 4th (middle) instars (Churchhaven) and 6th/final instar (bottom; Platrug Farm). Not to scale. An egg of *C. zonarius* is shown in Fig. 7A in HEA23.

Juvenile stages Figs. 13 & 7A in HEA23, and Fig. 4 here. Conservation status of *C. z. zonarius*: LC.
Taxonomy: *Chrysoritis zeuxo* renders *C. zonarius* paraphyletic in the COI and EF trees (in the CAD and H3 trees, their phyletic relationship is unclear). Although there are no recent confirmed records of *C. zeuxo* and *C. zonarius* occurring sympatrically, there are accounts of them being sympatric in recent history (Cottrell, 1978: 55) but these accounts are ambiguous and difficult to verify, so it is unclear whether their distributions currently overlap, or did so in the recent past. Here, we regard them as potentially sympatric currently or in the recent past. The two taxa have maintained differences in facies and behaviour (Woodhall, 2020: 234; *C. zonarius* preferring to stay very close to its host plant) as well as ecology (different host ants and host plants) while being sympatric. It is, however, possible that the smaller size of *C. zonarius* may be due to developmental plasticity resulting from poorer nutritional quality of its host plant (A. Heath, pers. obs). The two taxa likely diverged recently and a subspecies designation for each might also be a reasonable call. However, we believe that their multifaceted differences maintained in sympatry point more to full than to partial reproductive isolation (see Species and Subspecies Concepts in Materials and Methods). Thus they each remain as separate species, *C. zeuxo* and *C. zonarius*. Conservation status of *C. zonarius zonarius*: LC.
C. zonarius coetzeri Dickson & Wykeham 1994. Holotype: NHM, London. Type locality: Nieuwoudtville. Specimens with similar wing facies also occur along the Namaqualand coast. Conservation status of *C. zonarius coetzeri*: LC.

Chrysoritis pyroeis (Trimen 1864). *Zeritis pyroeis* Trimen 1864: 178. Holotype: NHM, London. Type locality: Cape Province.
C. pyroeis pyroeis
Host ant: *Myrmicaria nigra* (Mayr 1862)**.** Host plants: *Roepera flexuosa; R. sessilifolia; R. morgsana* (Zygophyllaceae); *Thesium* species. Cottrell (1984) hypothesised that the structural colouring and iridescence in *C. pyroeis* may have evolved independently from that seen in the *thysbe* clade. Forewing with twelve veins. Larvae have unusually long tubercle casings to their TOs. Juvenile stages illustrated in Clark & Dickson (1971: 191). Conservation status: LC.
C. pyroeis hersaleki (Dickson 1970). *Poecilmitis pyroeis hersaleki* Dickson 1970: 157. Holotype: NHM, London. Type locality: Lady's Slipper, Witteklip Mts. Host ants unknown. Host plants: *Roepera flexuosa; R. sessilifolia* (Zygophyllaceae). This subspecies was not included in the molecular studies. Conservation status: LC (2020).

Chrysoritis felthami (Trimen 1904). *Zeritis felthami* Trimen 1904: 233. Holotype: NHM, London. Type locality: Muizenberg Vlei. Forewing with twelve veins. Larvae have unusually long tubercle casings to their TOs; a characteristic shared with *C. pyroeis*. Host ants *Crem. gallicola* and *Crem. peringueyi* and host plants *Roepera* species (Zygophyllaceae).
C. felthami felthami Juvenile stages illustrated in Clark & Dickson (1971: 187). Conservation status: LC.
C. felthami dukei (Dickson 1967). *Poecilmitis felthami dukei* Dickson 1967: 65. Holotype: NHM, London. Type locality: Roodeberg nr. Vink, Robertson Karoo. Conservation status: LC.

Chrysoritis chrysantas (Trimen 1868). *Zeritis chrysantas* Trimen 1868: 85. Holotype: NHM, London. Type locality: Murraysburg. Sister species to the *thysbe* clade. Host plant *Salsola tuberculata* (Chenopodiaceae) and host ant *Crem. melanogaster*. Conservation status: LC.
Characters: Upper side orange-red with narrow black margins and prominent white interneural cilia. Underside hind wing mottled light and dark grey. Male aedeagus lacks cornuti. Forewing with eleven veins. Juvenile stages shown in Fig. 5 (p. 17). This species is placed as sister to the *thysbe* clade in the COI tree, but not in the nuclear gene trees.

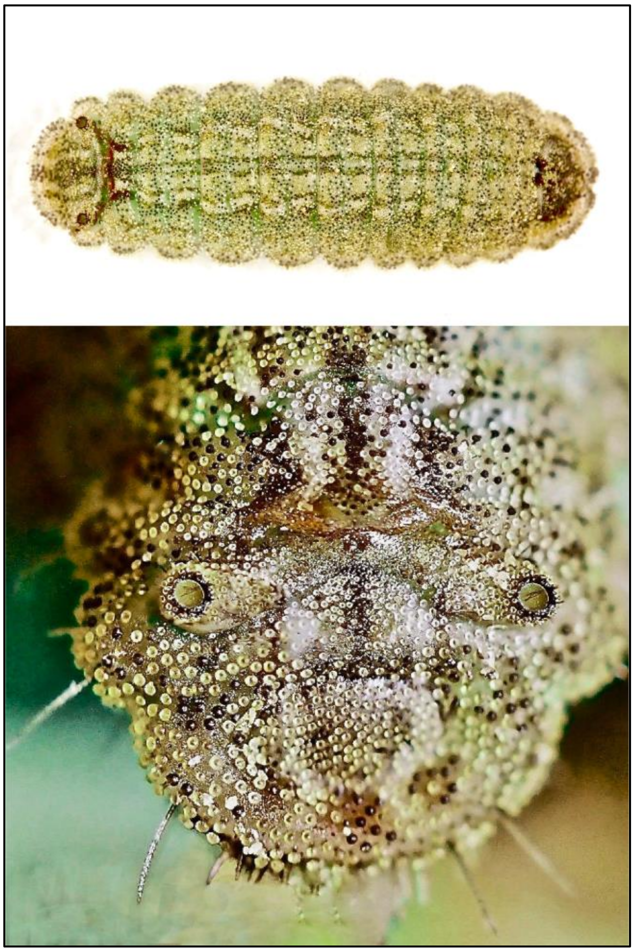

Figure 5 – *C. chrysantas* (Garies). Final instar (top), *C. chrysantas* distal four larval segments (bottom). Not to scale.

Western Lineage: *thysbe* clade

TEA20 estimated the age of the *thysbe* clade to be 2–3.6 MY(95% confidence interval), but given that Kawahara *et al.* (2023) inferred a much younger maximum age for the split between *Chrysoritis* and its sister group than TEA20 (25 vs. 41 MYA), by extrapolation, this older limit of 3.6 MY is likely to be a significant overestimate. The origin of the *thysbe* clade likely coincided with the start of the Pleistocene ~2.6 MYA.

There are 37 named species in the *thysbe* clade. All but six (marked with asterisks) have some structural colour and iridescence. The *thysbe* clade species are:
pelion, *amatola**, *violescens.*
mt Clade 1: *williami*, *pan*, *aridus**, *turneri**, *lysander azurius*, *trimeni*, *wykehami**, *lyndseyae*, *perseus*, *uranus*, *aridimontis* (also in mt Clade 3).
mt Clade 2: *thysbe.*
mt Clade 3: *pyramus, whitei, endymion, rileyi, mithras, daphne, plutus, blencathrae*, palmus*, brooksi, swanepoeli, irene, nigricans, zwartbergae, adonis, beulah* (also in mt Clade 4), *aridimontis* (also in mt Clade 1).
mt Clade 4: *beaufortia, stepheni, beulah* (also in mt Clade 3), *braueri, penningtoni, orientalis.*

Reassignment of taxa: The COI data indicate that a few subspecies might have historically been assigned to the wrong species; those subspecies are treated as separate entities or re-assigned in this review. Characters: Upper side yellowish red with dark borders, discal and apical spots. In most taxa both sexes have some silvery-blue structural colouring in the basal part of the wing while males also have iridescence, however, in males of five species, both structural colouring and iridescence are absent to the naked eye. Hind wing verso with distinctive pattern of light ochre and brown or reddish-brown striae. This pattern varies in contrast and definition between and within species and in some specimens or populations it can be obscure, *e.g*., *C. pan pan* and *C. p. henningi*. The hind wing in both sexes has the tornus markedly produced. Forewing with twelve veins; vein 5 (M2) may be extended to varying degrees in some taxa, causing the outer margin to appear concave. Also, outer margin of both wings may be serrated in some species but this is variable. Male genitalia: aedeagus vesica with a ±60µ wide fan-shaped cluster of very fine cornuti (see Heath, 1997 pl. 4). All taxa in the *thysbe* clade are herbivorous and have an obligate relationship with a species of *Crem.* ants. The *thysbe* clade comprises six main mitochondrial lineages: *C.pelion*, *C. amatola* + *C. violescens*, and mt clades 1 – 4.

Chrysoritis pelion (Pennington, 1953) *Poecilmitis pelion* Pennington, 1953: 106. Holotype: Ditsong NM. MPT: upper montane; "hollows in rocky outcrops" (Woodhall, 2020). For notes on juvenile stages see Heath & Kaliszewska (2012: 17). Host ant: *Crem. amabilis*. Host plant: *Thesium* sp.. Conservation status: LC.

***Chrysoritis amatola* stat. nov**. (Dickson & McMaster, 1967). *Poecilmitis turneri amatola* Dickson & McMaster, 1967: 209. Holotype: NHM, London. Type locality: Mt. Kubusie, Eastern Cape. Lacks iridescence or structural colouring. MPT: montane slopes. Host ant unconfirmed but *Crem. peringueyi* is common in the close vicinity (Great Winterberg).
Taxonomy: Previously treated as a subspecies of *C. turneri*. The COI tree places *C. amatola* as separated from *C. turneri*; it groups with *C. violescens* instead. However, *C. violescens* is nested within *C. amatola* **stat. nov.** rendering the latter paraphyletic, possibly due to ILS. *C. amatolas* and *C. violescens* are recognised as separate species due to the structural colouring and iridescence (Figs. 11–13) on the wings of *C. violescens* that are perceived to be absent in *C. amatola.* Geographically, these two taxa are about 500km apart. *Chrysoritis amatola* **stat. nov.** is here raised to species status. Conservation status: LC.

Chrysoritis violescens (Dickson, 1971) *Poecilmitis violescens* Dickson, 1971: 1. Holotype: NHM, London. Type locality: Komsberg Pass, nr Sutherland. MPT: suitable high slopes but shuns the tops of prominences where males of *C. beaufortia* may occur; *C. violescens* shares host plant with *C. beaufortia*. Host ant: *Crem. peringueyi.*
Taxonomy: In the COI tree, *C. violescens* is monophyletic (n = 3, all haplotypes identical or nearly identical [see Total Dataset tree]) and derived from *C. amatola*, rendering the latter paraphyletic. See also *C. amatola* **stat. nov.**, above. Conservation status: LC.

thysbe mt Clade 1

Chrysoritis williami (Heath 1997) **stat. rev.** *Poecilmitis dicksoni* W.H. Henning (1977). Holotype: Ditsong NM. Type locality: "18km E. of Hondeklip Bay." MPT: ridge tops and the upper slopes of hills and dunes; this is unlike all known populations of *pan*, where males patrol gullies. Host ant: *Crem. liengmei*. Juvenile stages as for *C. pan.* A slightly smaller insect than *pan*; the male forewing silvery-blue generally extends to about halfway across the cell spot. Distribution: within the broad area ~40 km S. of Hondeklip Bay northwards to Port Nolloth and eastwards to Killians Pass. The hind wing verso on coastal populations is often dark, similar to *C. trimeni*, whilst in *C. williami* from the more arid terrain inland to Killian's Pass, the verso is pallid.

Taxonomy: Formerly treated as *C. pan lysander* (Heath 1997) but revived here as *Chrysoritis williami* owing to its consistent MPT and discrete distribution differing from that of *C. pan,* its sister species in the COI tree. Samples of *C. williami* are monophyletic with 100% bootstrap support in the COI tree. The cluster of *C. williami* is four mutational steps removed from *C. pan* in the COI network, and sister to *C. pan* + *C. aridus* in the COI tree. In the CAD tree, all samples of *C. williami* (n = 2) form a well supported clade (98% bootstrap). *C. williami* is sympatric with *C. aridus* at Killians Pass but clearly distinguishable on the basis of iridescence, and their males patrol different terrains. See also the relationship with other closely related taxa under *C. turneri* (below). With sufficient support for its separate status, it is reinstated as *Chrysoritis williami* **stat. rev.** Conservation status: LC.

Chrysoritis pan (Pennington 1962) *Poecilmitis pan* Pennington 1962: 273. Holotype: Ditsong NM. Type locality: Platrug Farm, Malmesbury Distr. The most widespread species in the *thysbe* clade; the name *pan* formerly included *C. williami* and *C. lysander* (both as *C. pan lysander*) and *C. pan henningi.* Juvenile stages Fig. 6 and (misidentified as *Poecilmitis lysander*) in Clark & Dickson, 1971:198.

Figure 6 – *C. pan* final instar (Lamberts Bay).

MPT: low to moderate elevation gullies and similar terrain. Host ant: *Crem. peringueyi*, in coastal regions from Leipoldtville northwards as far as the provincial border but for southern and inland populations the host ant is recorded as *Crem. liengmei* (*e.g.,* Malmesbury Distr.; Vanrhyn's Pass; Huis River Pass; Gamka Mountain N.R.). Both ant species have been recorded as hosts at Leipoldtville. In the COI tree, *C. pan* is rendered paraphyletic by *C. aridus*, possibly due to ILS; the clade of samples from both species has 75% bootstrap support and forms the sister to *C. williami*. Conservation status: LC.

Taxonomy:

Chrysoritis pan pan Cape Town to Leipoldtville and intervening non-arid coastal region. The forewing cell spot is prominent and always discrete; the forewing borders and cilia are black; the hind wing verso is plain or weakly marked. Host ant: *Crem. liengmei.* Our mtDNA dataset for specimens resembling *C. pan pan* includes samples from Yzerfontein (56 km from Platrug Farm [type locality]), Leipoldtville and Lamberts Bay. *Chrysoritis pan pan* is sympatric with *C. pan atlantica* in the area from Leipoldtville to Lambert's Bay. In this and surrounding areas, they intermingle and merge, resulting in intermediate forms.

C. pan henningi (Bampton 1981). *Poecilmitis henningi* Bampton 1981: 189. Holotype: Ditsong NM. Type locality: "Huis Riv. Pass, nr. Calitzdorp". Occurring in arid areas within the Little Karoo, *C. pan henningi* closely resembles *C. pan pan* but in the former, the dorsal surface of forewing blue rarely covers the cell spot completely (whereas in *C. pan pan* the blue seldom reaches the cell spot); like *C. pan pan*, the hindwing verso is weakly marked or plain, but that of *henningi* is generally paler, possibly as a consequence of its arid environment; *C. pan henningi* host ant: *Crem. liengmei* (same as *C. pan pan*). Our mtDNA dataset for specimens resembling *C. pan henningi* includes samples from Huisrivier Pass and Nieuwoudtville, indicating a geographically disjunct taxon separated by ~330 km between its two locations (see Fig. S1A for other recorded locations). The specimen from Nieuwoudtville appears intermediate in wing facies between *C. pan henningi* and *C. pan atlantica* but is much closer to *C. pan henningi*.

C. pan atlantica (Dickson 1966). *Poecilmitis atlantica* Dickson 1966: 181. Holotype: NHM, London. Type locality: "Lange Valley, S.E of Lambert's Bay". Widespread, occurring in non-arid areas from Leipoldtville northwards to the W. Province boundary and eastwards to Leeu-Gamka. Host ant: *Crem. peringueyi.* Hindwing verso well marked, in contrast to that of *C. pan pan* and *C. pan henningi*. *Chrysoritis pan atlantica* occupies most of the range taken up by the former *C. pan lysander*, a now obsolete name. Specimens formerly answering to *C. pan lysander* (from Garies northwards) are here reassigned as *C. lysander* and *C. williami*; thus specimens south of the Kamiesberg and south of latitude ~30.6° S no longer carry the nomen *lysander*, but are reclassified as *C. pan atlantica*. Our mtDNA dataset for specimens resembling *C. pan atlantica* includes samples from Leipoldtville, Lamberts Bay, Ruitersvlei.se.mond, Calvinia, Fraserburg, and Leeu-Gamka. *Chrysoritis pan atlantica* is sympatric with *C. pan pan* in the area from Leipoldtville to Lambert's Bay. In this and surrounding areas, they intermingle and merge, resulting in intermediate forms.

Are the different morphs of *C. pan* subspecies or forms?

The three morphs of *C. pan* (hereafter referred to as *pan*, *atlantica* and *henningi*) appear to follow the classic pattern of "geographic replacement forms," a term that has been synonymous with subspecies, particularly in the era preceding molecular data. Their respective specificity to ant hosts (*Crem. liengmei* or *Crem. peringueyi*) suggests an additional dimension of divergence consistent with subspecies. Braby et al. (2012) states that subspecies are "partially isolated lineages of a species that are [1] allopatric, [2] phenotypically distinct, …[3] have at least one fixed diagnosable character state…and…[4] these character differences are (or are assumed to be) correlated with evolutionary independence according to population genetic structure." To varying degrees, the *C. pan* morphs conform to the first three of these requirements but not the fourth.

[1]. They are largely allopatric, but at Leipoldtville and nearby Lamberts Bay, *pan pan* and *pan atlantica* have been observed to fly a mere 100 m apart thus they are sympatric at these locations.

[2]. The three morphs are generally distinct (type specimens are shown in Fig. S2): *pan* has a hindwing verso that varies from plain to weakly marked and associates with *Crem. liengmei*; *henningi* is very similar to *pan*, but hindwing verso is generally paler, also varying from plain to weakly marked, and it also associates with *Crem. liengmei*; *atlantica* has a hindwing verso that is patterned/marked, and it associates with *Crem. peringueyi*.

[3]. Fixed diagnosable character state: character states among the three morphs are generally diagnosable (as described in [2]) but they are not fixed since variations and overlaps exist, *e.g.*, at Leipoldtville and Lamberts Bay, where two morphs and their intermediates have been observed. A specimen from Nieuwoudtville also presents wing facies that are intermediate between *henningi* and *atlantica* but closer to *henningi*; more such specimens with *henningi* facies have been observed at other arid areas in the region between Vanrhyns Pass and Vanrhynsdorp.

[4]. Population genetic structure. In this aspect, the *C. pan* morphs fail to conform to subspecies as defined here. From a mtDNA perspective, they are genetically indistinguishable from one another (explained in the next paragraph). No population genetic structure that can be ascribed to wing facies is apparent in the COI data; the absence of mtDNA differentiation among the morphs of *C. pan*, however, requires confirmation by wider DNA sampling in the Little Karoo as well as other arid areas north of the Swartberg, particularly the region between Nieuwoudtville and Vanrhynsdorp where *henningi*-like morphs have been collected by A. Heath and A. J. Coetzer. On the other hand, the distribution of the three morphs appear correlated with aridity levels: *pan* is associated with west-coastal non arid habitats, *henningi* with arid areas in the Little Karoo region, and *atlantica* with non-arid areas from the West Coast to the Great Karoo. At the same time, the morphs with plain hindwing undersides (*pan* and *henningi*) are hosted by *Crem. liengmei* while *atlantica* with its well marked hindwing verso is hosted by *Crem. peringueyi*. It is possible that aridity, substrate colour, species of ant, or all three, may affect wing facies during larval development. If so, the three *C. pan* morphs would be better described as forms rather than subspecies. Then again, it is possible that these morphs are the result of adaptation, and future investigation utilising a higher resolution marker set and greater sampling could reveal genetic differentiation which has accrued too recently to be captured by mtDNA. Hindwing verso patterning in lycaenids is often driven by the substrate on which they settle, with strong selection for crypsis (M. Braby, pers. comm. 2022); with enough time, such selection may eventually translate into genetic differentiation recognizable as subspecific. However, based on the available data and following the subspecies concept of Braby *et al*. (2012), the answer remains ambiguous.

In the haplotype network (Fig. S1B), 19 samples of *C. pan* sorted into 10 haplotypes (possibly nine, explained in Note S1). Two of the haplotypes are associated with multiple morphs: one includes *pan* and *henningi* (bicoloured haplotype in Fig. S1B) while the other includes all three morphs (tricoloured haplotype). All haplotypes but one are associated with *atlantica*, placing it as the ancestral morph, with the other two morphs being derived from it. Apart from encompassing all morphs, the tricoloured haplotype is geographically highly dispersed, with a span of ~300 km. Among our DNA samples, no other haplotype in the entire genus is even half as widespread (however there may be other more widespread haplotypes in species that have been poorly sampled in our study, e.g., the widespread *C. chrysantas*). Furthermore, genetic variation within *C. pan* is low (a maximum of 7 mutation steps between the most distant haplotypes in the network) in comparison to other well sampled species. This combination of low genetic variation and a well dispersed haplotype suggests a species that has undergone rapid and recent geographic expansion, possibly as a result of release from a biological or ecological constraint enabling a high population growth rate, consistent with the observation that *C. pan* is relatively common where it occurs. Such a release would also allow the species to explore morpho- and ecospace, resulting in the varied morphs, host ant species, and environments occupied.

Chrysoritis aridus (Pennington 1953). *Poecilmitis aridus* Pennington 1953: 104. Holotype: Ditsong NM. Type locality: Kamiesberg Mts., Namaqualand. Lacks iridescence or structural colouring. MPT: low to medium elevation slopes, gullies and depressed areas. Host ant: *Crem. peringueyi*. Juvenile stages illustrated in Clark & Dickson 1971: 207.

Taxonomy: Matrilineally, *C. aridus* is monophyletic and derived from *C. pan* (it is nested within *C. pan* in the COI tree); it is also closely related to *C. williami* and *C. turneri*, resembling the latter in lacking iridescence. See also *C. turneri* (below). Conservation status: LC.

Chrysoritis turneri (Riley 1938: 241). *Poecilmitis turneri* Riley 1938: 241. Holotype: NHM, London. Type locality: Matjiesfontein. Recorded from Komsberg Pass, southwards to the Swartberge and Little Karoo. Like *C. aridus*, this species lacks any iridescence or structural colouring. Host ant: Unrecorded. MPT: submontane slopes and prominences.

Taxonomy: *C. turneri* is monophyletic and well supported in the COI tree (99%), where it is sister to the group comprising *C. aridus*, *C. pan* and *C. williami*; it is sympatric with *C. pan* at Huis River Pass but both these species are clearly distinguishable on the basis of the presence/absence of iridescence and no intermediates have been observed at this locality across 40+ years of observation. Conservation status: LC.

Chrysoritis lysander (Pennington 1962) **stat. rev.** *Poecilmitis lysander* Pennington 1962. Holotype: Ditsong NM. Type locality: Kamieskroon, Namaqualand Distr. MPT: low, mid and submontane gullies. Host ant: unrecorded. Material from this study is from Kamiesberg and its foothills.

Taxonomy: Monophyletic in the COI tree (100% bootstrap). Sample specimens from Kamieskroon, formerly treated as *C. pan lysander*, are morphologically similar to *C. azurius*. However its closest taxon in the COI tree is not *C. azurius* but a *C. aridimontis* (sample AH07C166 in mt clade 1), 12 mutational steps away in the network. Despite resembling *C. azurius*, the two species are well separated phylogenetically and geographically. Material from the Kamiesberg region, formerly treated as *C. pan lysander*, is returned to species status as *Chrysoritis lysander* **stat. rev**. Also, material taken from 2 km north of Eksteenfontein, Richtersveld and recently from near Oranjemund, southern Namibia (S. Braine) may also be this species. Conservation status: LC.

Chrysoritis azurius (Swanepoel 1975). *Poecilmitis azurius* Swanepoel 1975. Holotype: Ditsong NM. Type locality: Roggeveld Mts. MPT: submontane gullies. Host ant: *Crem. peringueyi* and *Crem. melanogaster*. Populations occurring in the Sutherland district, Middelpos, Nieuwoudtville, and Keiskie Road (20 km S of Calvinia) are deemed *C. azurius*. Material originally described as *lysander hantamsbergae* (Dickson) from near the summit of the Hantamsberg, Calvinia (not included in the study) may also answer to this taxon.

Taxonomy: This species is monophyletic in the COI tree (96%). Wing facies of *C. lysander* (n = 2) matches that of *C. azurius* (n = 9) but the network and COI phylogeny shows them to be distinct. Conservation status: LC.

Chrysoritis trimeni (Riley 1938). *Poecilmitis thysbe trimeni* Riley 1938: 240. Holotype: NHM, London. Type locality: Port Nolloth. MPT: flat sheltered coastal areas. Host ant: *Crem. peringueyi*. Final instar larva can be seen in Heath et al. (2008 pl. 7). Restricted to the NW coastal area, Port Nolloth and Kleinsee.

Taxonomy: This taxon is polyphyletic in the COI tree due to a lineage comprising five *trimeni* samples (C042, C069, C070, M601, M602 from Kleinsee intermingling with members of the main lineage) being nested within *C. lyndseyae*. These specimens resemble both *C. trimeni s.s.* and *C. williami* with which they occur sympatrically, intermingling on flat ground behind coastal dunes at Kleinsee. However, the two samples of *C. trimeni* in the CAD tree (representing both COI lineages of *C. trimeni*) are monophyletic (99%). The polyphyly of *C. trimeni* in the COI tree can be explained by historical introgression, specifically, past capture of *C. lyndseyae* mtDNA by *C. trimeni* (explained in Results of QEA22, under *C. trimeni*). Conservation status: VU.

Chrysoritis wykehami (Dickson 1980) **stat. rev**., *Poecilmitis wykehami* Dickson 1980: 40. Holotype: NHM, London. Type locality: Hantamsberg, Calvinia. Wing facies closely resembles *C. turneri*. Lacks iridescence and structural colouring. MPT: montane slopes. Host ant: *Crem. liengmei.*

Taxonomy: Formerly considered to be *C. turneri wykehami*, this taxon is returned to species status as *Chrysoritis wykehami* **stat. rev.** Both *C. wykehami* and *C. turneri* lack iridescence but they do not group together in the COI tree. *Chrysoritis wykehami* is polyphyletic in the COI tree on account of two samples, Z040 and Z041, taken near Sutherland, more than 130 km SE of the type locality (Calvinia) for *wykehami*. In the CAD data/tree, the two samples of *C. wykehami*, representing both lineages in the COI tree, are identical where their CAD sequences overlap (570/745 bp). However, two other samples also share that sequence in regions of DNA overlap. The Sutherland specimens are here treated as part of *C. wykehami s.l.* The COI-polyphyly of *C. wykehami* may be the result of historical introgression (explained in Note S2) but our data are insufficient to identify the original vs. the “captured” mtDNA lineage; As the two COI lineages are separated both phylogenetically and geographically (unlike other polyphyletic taxa such as *C. aridimontis, C. trimeni* and *C. perseus* where both COI lineages co-mingle) and support from nuclear data is not definitive, further investigation is needed. Conservation status: LC – Rare.

Chrysoritis lyndseyae (Henning 1979). *Poecilmitis lyndseyae,* Henning S.F 1977. Holotype: Ditsong NM. Type locality: 10km N. of Wallekraal. Also recorded from Hondeklip Bay and Sarrisam Farm, 37 km S.E. of Hondeklip Bay (ID confirmed by mtDNA sequencing). Further records from Kotzesrus and 12 km N.E. of Groenriviersmond. Invariably occurs in close sympatry with *C. t. bamptoni*. Some material may be difficult to ID in the field due to an overlap of appearance with some specimens of *C. perseus* or *C. thysbe bamptoni* (see Fig. 3 in QEA22). MPT: low to medium elevation flat ground. Host ant: *Crem. peringueyi*. Final instar larva illustrated here (Fig. 7; see also Heath (2011, pl. 4).

Figure 7 – *C. lyndseyae* late instar with *Crematogaster peringueyi* host ants (Wallekraal).

Taxonomy: This species occurs in a clade containing *trimeni, wykehami* and *perseus,* all of which are polyphyletic. It frequently flies sympatrically with *C. thysbe bamptoni* with which it can be easily mistaken (see Heath 2011, pl. 1–3). The two taxa share the same space, host plants and host ants but are genetically and phylogenetically distant from each other. *Chrysoritis lyndseyae* is rendered paraphyletic in the COI tree by a group of *C. trimeni* samples (likely a result of past capture of *lyndseyae* mtDNA by *C. trimeni*, explained in QEA22). This clade of *C. lyndseyae* + *C. trimeni* has 99% bootstrap support in the COI tree. Conservation status: LC – Rare.

Chrysoritis perseus (Henning 1977). *Poecilmitis perseus,* Henning 1977: 27. Holotype: Ditsong NM. Type locality: 18 km E. of Hondeklip Bay, MPT: flat and sloping ground, avoiding prominences. Final instar larva illustrated here in Fig. 8. Host ant: *Crem. castanea* at the type locality and *Crem. peringueyi* and *Crem. castanea* at Groenriviersmond.

Taxonomy: *Chrysoritis perseus* is polyphyletic in the COI tree with the “main” larger lineage divided into two west

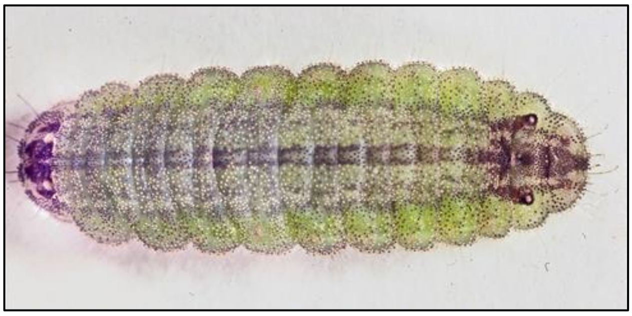

Figure 8 – *C. perseus* final instar (Groenriviersmond).

coastal allopatric populations (labelled “North” and “South" respectively in the COI tree). Hind wing "solid blue" invariably reaches the post-discal spots especially in the north population. Some specimens from the northern population are easily confused with *C. lyndseyae* due to a greater extent of silvery-blue scaling. The coastal population ranging from 7km south of Lambert’s Bay (now fenced off) northwards to Doring Bay is treated here as the southern population of *C. perseus* with only *Crem. peringueyi* recorded as its host ant. Wing facies of this southern population are variable but often differs from nominate *C. perseus* by having a weaker (transparent) silvery-blue scaling on the forewing; the hind wing having a smaller "solid blue" basal patch that fails to reach the post-discal spots. The undersides are even more variable in the density of markings, some specimens being quite weakly marked and others are distinct.

The southern population has highly variable wing facies but no consistent differences from the north population, other than the extent of "solid blue" on hind wing more often being reduced.

The six outlier samples (C163, C329, C369, C378, U292, M674 in the COI tree) which render *C. perseus* polyphyletic mingle with the southern population of *C. perseus* at Lambert’s Bay, sharing the same host ants and larval host plants; they constitute over a third of all 16 *C. perseus* sampled there. There are no consistent differences in appearance or behaviour, hence there is no way to identify these six outliers from the main clade of *C. perseus* except by molecular means. It is possibly a product of past mitochondrial capture (historical introgression of mtDNA) by *C. perseus*, (explained for *C. trimeni*, above) but unlike the scenario for *C. trimeni*, the mitochondrial “donor” taxon (which, in the case of *C. trimeni*, was *C. lyndseyae*) is extinct (or possibly yet to be sampled) but its mitochondrial lineage has survived to the present in these specimens, similar to Neanderthal and Denisovan DNA found in present day humans. Also unlike the case for *C. trimeni*, whose samples form a well supported clade in the CAD tree, the four CAD sequences of *C. perseus* are scattered widely therein. This species requires further investigation. Conservation status: LC.

Chrysoritis uranus (Pennington 1963). *Poecilmitis uranus* Pennington 1963: 277. Holotype: Ditsong National Museum. Type locality: Gydo Mt., Ceres. MPT: mid to upper montane prominences.

<u>*C. uranus uranus*</u>. Host ant *Crem. gallicola*. Juvenile stages illustrated in Clark & Dickson (1971: 202) and here in Fig. 9. This is a morphologically well defined species. Conservation status: LC.

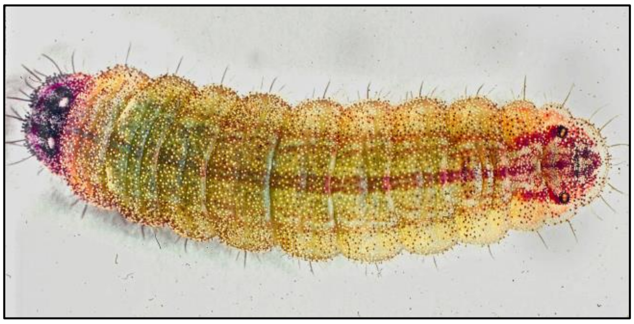

Figure 9 – *C. u. uranus* final instar (du Toits Kloof Pass).

<u>*C. uranus schoemani*</u> (Heath 1994). *Poecilmitis uranus schoemani* Heath, 1994: 225. Holotype: Ditsong NM. Type locality: Gifberg Mt., Vanrhynsdorp. Host ant: unrecorded. Conservation status: LC – Rare.

Chrysoritis aridimontis is found in *thysbe* mt Clades 1 and 3. See *thysbe* mt Clade 3 for description.

<u>*thysbe* mt Clade 2</u>

Chrysoritis thysbe (Linnaeus 1764). *Papilio thysbe* (Linnaeus 1764: 330). Lectotype: Swedish NHM. Type locality: Cap. Bonae Spei (Cape Peninsula). Host ants *Crem. peringueyi*. MPT: hilltops and/or prominences.
Taxonomy: Monophyletic in the COI tree (100% support, 93% in Total Dataset tree). Juvenile stages illustrated here in Fig. 10; see also HEA23: Figs. 1A & 2 (genitalia), and Figs. 10 & 11 (larval epidermal setae and larvae with ants, respectively).

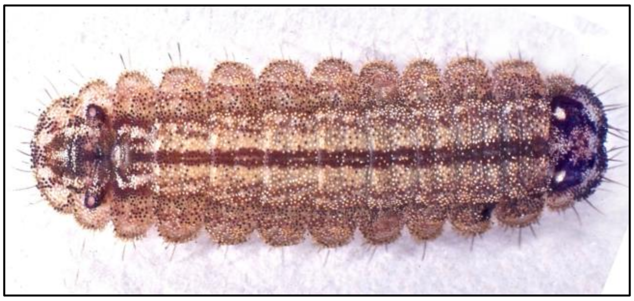

Figure 10 – *C. t. thysbe* final instar (11km NW of Clanwilliam).

This species is divided into two main mt lineages comprising 1) *C. t. thysbe*, and 2) *C. t. psyche* + *C. t. bamptoni* + *C. t. schloszae*. Each of the subspecies is highly variable and there is limited phenotypic overlap among them but most specimens can be readily identified, with locality only sometimes required to confirm identification of these subspecies. Distributions of the subspecies are shown in Fig. S3.

<u>*C. thysbe thysbe*</u>: The populations from Pearly Beach to the Cape Peninsula and northwards to the Lambert’s Bay area (and ~50km inland) are effectively uninterrupted, with frequent gene-flow being unavoidable. The diversity of wing facies is considerable within this region and despite them being variable geographically and seasonally, there are numerous intergrades. MPT: hilltops (including tops of dunes and mounds) and prominences at low elevation (but see ecological note below). Our sampled locations include Redhill, Simonstown, ~20 km from the type locality. Conservation status: LC.

Taxonomy: Within the area stated, the different facies (e.g. Fig. 3 in QEA22) cannot be treated as subspecies but rather as forms of *C. thysbe thysbe*. The same is true for *C. thysbe osbecki* (Aurivillius 1882), originally described as a full species (*Phasis osbecki*). Pennington (1962: 273) considered osbecki to be an autumn form of *thysbe*; Clark and Dickson (1971: 172) treated it as a form having many intergrades with other forms of *thysbe*. Thus, osbecki is synonymised as a form *i.e., C. thysbe thysbe* f. osbecki **stat. rev**.

An ecological and MPT note for *C. t. thysbe*: Males of this taxon are known to frequent low elevation hilltops and prominences but there are some localities for *C. t. thysbe* where this is not the case. Eleven km NW of Clanwilliam beside the N7, males were observed to patrol gullies; also at Graafwater and other localities beside the R364 road leading to Lambert's Bay the males frequent flat or depressed areas. In these localities the underside of both sexes are distinctively marked and yellowish or orange-brown in colour during springtime; the upper side is sometimes heavily marked in black scaling. There also seems to be some seasonal fluctuation in the definition of the hind wing verso in these populations, summer specimens being pallid and less distinctive.

C. thysbe psyche (Pennington 1967) *Poecilmitis psyche* Pennington 1967: 121. Holotype: Ditsong NM. Type locality: Bitterfontein. *C. thysbe* material from Klaver to Bitterfontein and to Kotzesrus is treated here as belonging to this subspecies. Conservation status: LC.

C. thysbe bamptoni (Dickson 1976) *Poecilmitis bamptoni* Dickson 1976. Holotype: NHM, London. Type locality: Hondeklip Bay. A coastal and subcoastal insect. Ranges from Kleinsee south to Strandfonteinpunt. Conservation status: LC.

C. thysbe schloszae (Dickson 1994) *Poecilmitis thysbe schloszae* Dickson 1994: 214. Holotype: NHM, London. Type locality: Nr. Moorreesburg. MPT: medium to high elevation prominences. A specimen labelled under *C. thysbe osbecki* in the Natural History Museum (London) collection, captured by Dixon in October 1956 on the Piketberg was identified as *schloszae* (A. Heath); this led to a successful search for it on the Piketberg by L. McLeod. Two specimens were also collected from ~17km north of Het Kruis in September 1988 (A. Heath). Conservation status: CR.

thysbe mt Clade 3

The subspecies *C. thysbe mithras* and *C. thysbe whitei* were found to be phylogenetically unaffiliated with *C. thysbe* and are here reassigned as *C. mithras* and *C. whitei* respectively.

Chrysoritis pyramus (Pennington 1953). *Poecilmitis pyramus* Pennington 1953: 105. Holotype: Ditsong NM. Type locality: Zwartberg Pass. Host ant: *Crem. peringueyi* for both subspecies. MPT: upper montane slopes and prominences.

Taxonomy: All subspecies combined form a monophyletic group, with 100% bootstrap support in the COI tree.

C. pyramus pyramus: This nominate subspecies is probably a localised melanistic form of the insect. Late instar illustrated in Fig. 11. Conservation status: LC – Rare.

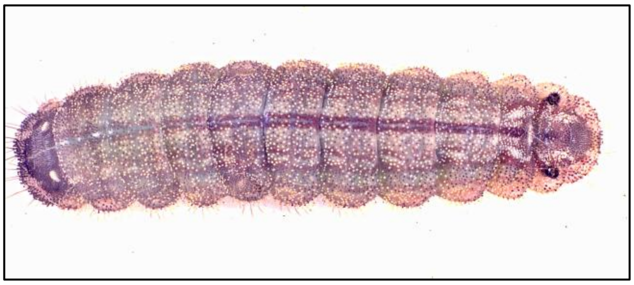

Figure 11 – *C. p. pyramus* final instar larva (Swartberg Pass).

C. pyramus balli (Dickson & Henning 1980). *Poecilmitis balli* Dickson & Henning 1980: 294. Holotype: Ditsong NM. Type locality: Kammanassie Mts., Uniondale. Conservation status: LC.

Chrysoritis whitei (Dickson 1994), **stat. rev.** *Poecilmitis whitei* Dickson 1994: 215. Holotype: NHM, London. Type locality: Nr. Port Elizabeth. MPT: slopes and even flat ground in coastal dune terrain; only slightly above sea level, see Heath & Fisher (2010). Host ant: *Crem. peringueyi*. Juvenile stages illustrated (as *Poecilmitis thysbe*) in Clark & Dickson (1971: 194).

Taxonomy: Previously assigned as *C. thysbe whitei* (n = 3), it groups clearly with *C. pyramus* (n = 4) in the COI tree (100% support) and not with *C. thysbe.* In the CAD tree, it also occurs in a well supported clade (72%) with the same group of species it clusters with in the COI tree (*C. endymion*, *C. rileyi* and *C. pyramus*). Given its similarity to *C. thysbe* in facies and habitat, the phylogenetic placement of *C. whitei* as sister to *C. pyramus* was surprising, furthermore because *C. pyramus* occurs in the alpine zones on mountain summits 250 km inland from the locations known for *C. whitei*, two mountain ranges away, and there are no records of *C. whitei* for any of the mountain ranges close to Port Elizabeth. Assignment as a subspecies of *C. pyramus* was considered but *C. whitei* occurs in an entirely different habitat from the former. *C. whitei's* six known localities occur just above sea level in sandy duneveld, where it specifically inhabits the dunes about 1 km inland of the coast, avoiding the coastal dunes. *Chrysoritis thysbe whitei* is here reassigned as *C. whitei* **stat. rev.**

A melanistic aberration assumed to be this taxon but resembling *C. zwartbergae* was taken by S. Collins (Fig. 12) from the *C. whitei* locality in November 2019. Its

Figure 12 – *C. whitei* aberration (photo: S. Collins).

identification awaits molecular confirmation; a second similar specimen has since been seen and photographed. Conservation status: EN.

Chrysoritis endymion (Pennington 1962). *Poecilmitis endymion* Pennington 1962: 274. Holotype: Ditsong NM. Type locality: Du Toit's Kop, Franschhoek. MPT: high elevation montane slopes. Host ant: *Crem. peringueyi*. For taxonomy, see *C. rileyi*, below. Conservation status: LC – Rare.

Chrysoritis rileyi (Dickson 1966). *Poecilmitis rileyi* Dickson 1966: 241. Holotype: NHM, London. Type locality: Brandvlei Dam area (Worcester); now also known from a locality 45 km eastwards near Robertson (A. Morton pers. com.). Host ant: *Crem. peringueyi*. MPT: low elevation, in flat and gently sloping terrain. It flies in sympatry with *C. brooksi brooksi*. Juvenile stages illustrated here in Fig. 13. The CAD tree additionally groups a putative *brooksi-rileyi* hybrid with this taxon, whereas in the COI tree it groups with *brooksi*, thus confirming its hybrid status.

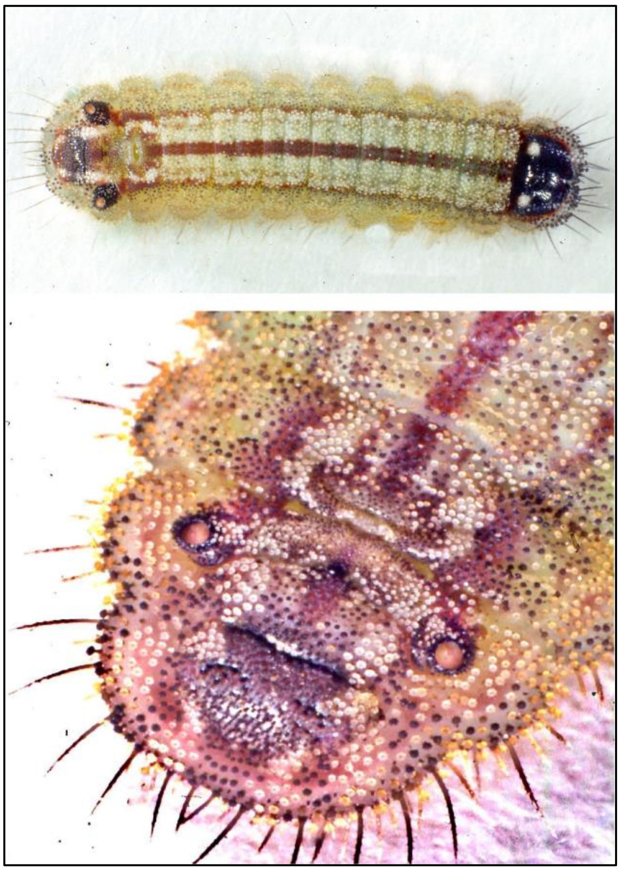

Figure 13 – *C. rileyi* (Brand Vlei) 4th instar (top) and final instar (bottom). Not to scale. An egg of *C. rileyi* is shown in Fig. 7B in HEA23.

Taxonomy: This species (n = 2) groups with *C. endymion* (n = 1) in the COI tree (98%). In the COI tree, a sample of *C. rileyi* (C010) groups with the single *C. endymion* sample in 84% of bootstrap trees, thus *C. endymion* appears to render *C. rileyi* paraphyletic but more samples are needed to confirm this. In the COI network, *C. rileyi* sample C010 is closer to *C. endymion* than to its conspecific (only a single nucleotide change between the two taxa). However, these two taxa differ in several ways: *C. endymion* is a high elevation species whilst *C. rileyi* is at low elevations in the same geographic region. Compared to *C. endymion*, *C. rileyi* has more extensive structural colouring that also has a more greenish tinge to the blue iridescence under lateral lighting; finally, *C. rileyi* wing veins are more extensively blackened than in *C. endymion*. Further investigation is needed to confirm species status in these two taxa, given that only a single COI point mutation separates them. Conservation status: EN (2020).

Chrysoritis mithras (Pringle 1995), **stat. rev.** *Poecilmitis mithras* Pringle 1995: 107. Holotype: NHM, London. Type locality: Brenton-on-Sea, Nr. Knysna. Paratypes from near Still Bay. MPT: hilltops and prominences in coastal terrain. Host ant: *Crem. peringueyi.*

Taxonomy: This is the only taxon in the *thysbe* clade supported by EF (95% support for the two samples) in addition to COI (95%). The two CAD sequences of *C. mithras* are identical but also shared with two other samples. The two sister clades of C. mithras in the COI tree (explained below) are represented in the EF and CAD trees. The population from the type locality at Brenton, formerly treated as *C. thysbe mithras*, is here revised back to *C. mithras* **stat. rev.** Conservation status: CR.

The western population from Mossel Bay to Cape Agulhas, (n = 5) formerly *C. thysbe thysbe,* is provisionally treated here as an undescribed subspecies of *C. mithras* but more thorough investigation is needed; its conservation status has not been assessed. This western population of *C. mithras* is morphologically and ecologically similar to *C. thysbe thysbe*. It is separated from the Brenton 'type' population (n = 2) by 12 mutational steps in the network and their wing facies differ minimally. The COI tree places samples from Mossel Bay, Gourits River Mouth, Still Bay, Witsand and Cape Agulhas, previously assigned to *C. thysbe thysbe*, as sister to the Brenton population and not associated with *C. thysbe* phylogenetically. Material from Pearly Beach westwards to the Cape Peninsula remains *C. t. thysbe*. The distance from Cape Agulhas to Pearly Beach (~50 km) has not yet been adequately searched to assess the allopatric gap between *C. t. thysbe* and *C. mithras*.

Chrysoritis daphne (Dickson 1975), *Poecilmitis* (*Poecilmitis*) *daphne* Dickson 1975: 227. Holotype: NHM, London. Type locality: Kammanassie Mts. and only known from this one locality. MPT: gullies, ledges and depressions on montane slopes. Host ant: *Crem. amabilis*. This species is sister to *C. plutus* in the COI tree Conservation status: LC – Rare.

Chrysoritis plutus (Pennington 1967). *Poecilmitis plutus* Pennington 1967: 4. Holotype: Ditsong NM. Type locality: Sevenweekspoort, Zwartberg Mts. MPT: hilltops. Host ant: *Crem. peringueyi*. Juvenile stages: illustrated in Heath & Pringle (2007: Pl. 3); *C. plutus* (n = 2) is sister to *C. daphne* in the COI tree. Conservation status: LC.

Chrysoritis palmus [Stoll 1781]. *Papilio palmus* Stoll 178]: 100. Lectotype: Swedish NHM. Type locality: Kaap de Goede Hoop Cape Peninsula.

<u>*C. palmus palmus*</u> Lacks iridescence and structural colouring. Low and medium elevation insect; sexes may occur together near streams. MPT: medium elevation near streams. Host ant: *Crem. gallicola.* Juvenile stages illustrated in Clark & Dickson, 1971: 206. This is a

phenotypically and morphologically well defined species. Conservation status: LC.

C. palmus margueritae (Dickson 1982). *Poecilmitis palmus margueritae* Dickson 1982: 43. Holotype: NHM, London. Type locality: 6 miles E. of Knysna. This subspecies was not included in this study or TEA20. MPT unknown. Host ant: Unrecorded. Conservation status: LC.

Chrysoritis blencathrae (Heath & Ball 1992) *Poecilmitis blencathrae* Heath & Ball 1992: 86. Holotype: NHM, London. Type locality: Waaihoek Mt., Ceres and only known from this one locality. A well defined montane species very similar in appearance to *C. e. endymion* but lacking iridescence and structural colouring. Both sexes fly together. MPT upper montane slopes. Host ant: *Crem. amabilis*. Juvenile stages: Fig. 7C in HEA23 & Fig. 14 here. Conservation status: LC – Rare.

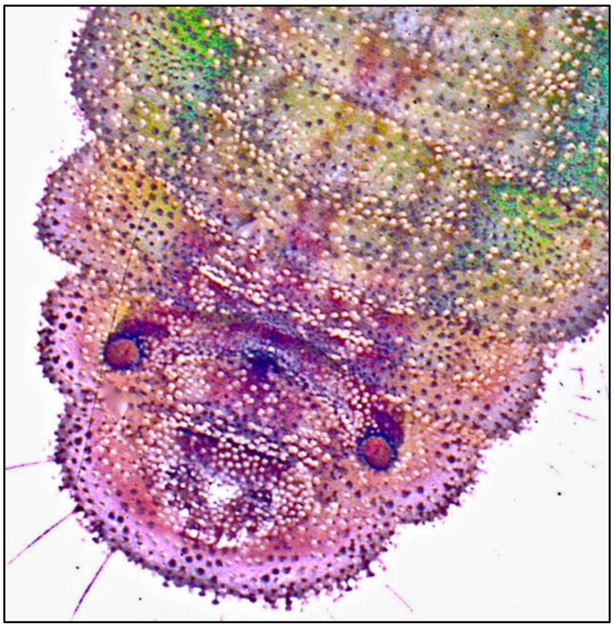

Figure 14 – *C. blencathrae* final instar (Waaihoek Mt.). An egg of *C. blencathrae* is shown in Fig. 7C in HEA23.

Chrysoritis brooksi (Riley 1938). *Poecilmitis thysbe brooksi* Riley 1938: 241. Holotype: NHM, London. Type locality: Nr. Philadelphia, Cape Prov. A mid and low elevation insect. MPT: low elevation slopes and flat ground. Host ant: *Crem. peringueyi*. Juvenile stage: Fig. 15.

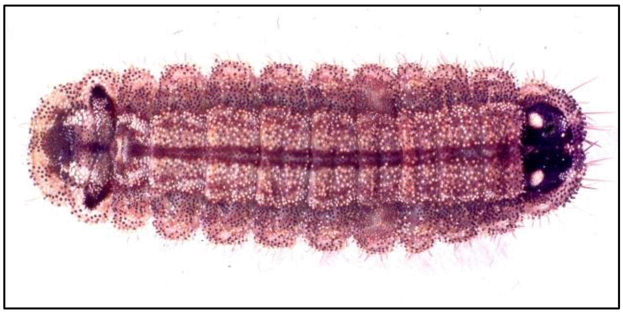

Figure 15 – *C. b. brooksi* final instar (Pella, Mamre).

Taxonomy: Supported by CAD and COI data. Monophyletic in the COI tree (100%) with the inclusion of a *brooksi-endymion* hybrid. In the CAD tree, all *C. brooksi* samples (n = 2 but not the hybrid sample) are clustered and have identical sequences for 659/745 bp. Conservation status of *C. b. brooksi*: LC.

C. brooksi tearei (Dickson 1966). *Poecilmitis brooksi tearei* Dickson 1966. Holotype: NHM, London. Type locality: East of Riversdale. Low elevation insect. MPT: flat ground. Host ant: *Crem. peringueyi*. Conservation status of this subspecies: EN.

C. brooksi-rileyi hybrid (sample AH12C011, Fig. 16). This specimen was taken on flat ground at Brand Vlei Worcester from a concentrated population of *C. rileyi* and where *C. b. brooksi* occurs sparsely. Its wing facies are wholly typical of *C. rileyi* but it is placed among the *C. brooksi* in the COI tree. Sample C011 is treated here as a *brooksi-rileyi* hybrid. This hypothesis is supported by the CAD tree, where the hybrid clusters with both *C. rileyi* and *C. endymion* samples (726/745 bp overlap).

Figure 16 – *C. brooksi-rileyi* hybrid (Brandvlei Dam).

Chrysoritis swanepoeli (Dickson 1965). *Poecilmitis swanepoeli* Dickson 1965: 160. Holotype: NHM, London. Type locality: “Prince Albert”. MPT: low, medium and high elevation gullies. Host ants: *Crem. castanea* and *Crem. alulai.* Host plants: *Thesium* species (Santalaceae); also *Tylecodon paniculatus* (L.f.) Toelken (Crassulaceae) oviposition observed only. Final instar larva is shown in Fig. 17. Conservation status of *C. s. swanepoeli*: LC.

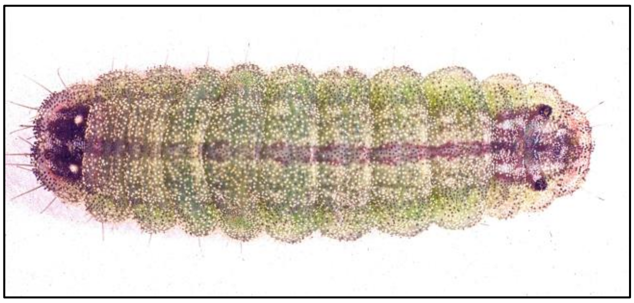

Figure 17 – *C. swanepoeli* final instar (Schoemanspoort).

Taxonomy: In our sampling, *C. swanepoeli s.s.* (n = 2) consists of two haplotypes, one of which is shared with the single *C. s. hyperion* sample (larger blue circle, COI haplotype network; see also Table S1 in QEA22). Thus, *swanepoeli* and *hyperion* are indistinguishable in their COI sequences. From all collection material examined, together with limited DNA data, it is evident that *hyperion* is no more than a variable melanistic form of *C. swanepoeli*. However, further sampling is required to confirm this view; hence *hyperion* provisionally remains as a subspecies of *C. swanepoeli*. Conservation status of *C. s. hyperion*: LC – Rare.

Chrysoritis irene (Pennington 1968). *Poecilmitis irene* Pennington 1968: 7. Holotype: Ditsong NM. Type locality: Du Toit's Kloof Pass. *C. irene* also occurs at Greyton (M. Schlosz, pers comm.); so far recorded on mid to high elevation slopes. MPT: below kranzes (cliffs) at the type locality, see Heath & Kaliszewska (2013: 18). Host ant: *Crem. gallicola* or *Crem. amabilis*. Host plant record: *Dimorphotheca chrysanthemifolia* (Vent.) DC. (Asteraceae) at its type locality although reared on Zygophyllaceae species in captivity (by A. Heath and M. Schlosz, [pers. com.]). Taxonomy: This taxon is sister to *C. swanepoeli* in the COI tree (100%). In the CAD tree, the three *C. swanepoeli* samples are found in one weakly supported clade (61% bootstrap support, but intermixed with three other species, and further out, 97% bootstrap and mixed with 6 other samples), while the single *C. irene* sample is well separated from that clade and on a long branch on its own; this arrangement is consistent with morphological differences between the two species. There is a marginal overlap between *C. irene* and *C. swanepoeli* in the upperside wing facies but *C. irene* differs notably in having a plain hind wing verso. The two species are separated by 180 km based on known records. This taxon remains as *C. irene*. Conservation status: LC – Rare.

Chrysoritis nigricans (Aurivillius 1924). *Phasis thysbe* var. *nigricans* Aurivillius 1924: 430. Holotype: Iziko Museum. Type locality: Muizen Mts. (the three samples here were collected at low elevation at Pella Mission, Mamre). Host ant: *Crem. alulai.* MPT: sloping ground, mostly montane but low elevation at Pella, Mamre, including samples in this study. Juvenile stages of *C. nigricans* are illustrated in Clark & Dickson 1971: 199 and here in Fig. 18.

Figure 18 – *C. nigricans* (Pella, Mamre).1st instar (top); final instar (bottom). Not to scale.

Note that the pupae are a pale yellowish; this colour is also seen in *C. zwartbergae* and some (but not all) *C. uranus* pupae (A. Heath, pers. obs.); all others in the *thysbe* clade have been brown to olive-brown. Morphologically similar to *C. zwartbergae* but consistent differences are apparent (description in *C. zwartbergae*).

Taxonomy: In the COI tree, this species is monophyletic and appears as sister to *C. adonis*, another montane species. Conservation status: LC.

***Chrysoritis zwartbergae* stat. nov**. (Dickson 1982) *Poecilmitis nigricans zwartbergae* Dickson 1982: 41. Holotype: NHM, London. Type locality: Zwartberg Mts. MPT: montane slopes but also at lower elevations. Host ant: *Crem. liengmei*.

Taxonomy: Polyphyletic in the COI tree but monophyletic in the CAD tree (90% support, all COI lineages represented in the CAD tree). One of its two COI lineages occurs in the Swartberge, Ladismith, and Kamanassieberge; the other is scattered among three south coast localities; the five samples of this taxon span ~185 km from Shaws Pass to Ladismith, WC. This taxon was previously treated as a subspecies of *C. nigricans* with which it shares similar facies. Although similar, its wing facies differs minimally but consistently in the margin of blue structural scaling. Hence it is raised to species status, *C. zwartbergae* **stat. nov.** This decision was made prior to analysis of the CAD data, and despite it appearing polyphyletic in the COI tree. The three populations from the south coast are here placed as undescribed subspecies of *C. zwartbergae* subject to a more in-depth molecular study and more extensive sampling. Conservation status of *C. z. zwartbergae*: LC.

C. zwartbergae rubrescens **stat. nov.** Heath & Pringle 2007. Holotype: Ditsong NM. Type locality: Gamkaberg N.R; 30km WSW of Oudshoorn. MPT: montane slopes. Host ant: unrecorded. Taxonomy: Samples of this taxon are reassigned from *C. nigricans* as *C. zwartbergae rubrescens* **stat. nov.** Conservation status: LC – Ex Rare.

C. zwartbergae ssp. (undescribed, from south coast): Samples taken from Vermaaklikheid, De Hoop (low elevation) and Shaw's Pass are placed as *C. zwartbergae* subject to wider sampling. MPT: sloping ground. Host ant only recorded for Vermaaklikheid: *Crem. gallicola*.

Chrysoritis adonis (Pennington 1963). *Poecilmitis adonis* Pennington 1963: 277. Holotype: Ditsong NM. Type locality: Gydo Mt., Ceres. Montane. Host ants: *Crem. alulai*. Host Plants: *Roepera* species (Zygophyllaceae); *Thesium* species (Santalaceae). MPT: medium elevation montane gullies. Juvenile stages of *C. adonis* illustrated in Clark & Dickson (1971: 203). Conservation status: CR.

Chrysoritis aridimontis Heath & Pringle 2007. **stat. nov.** Holotype: Ditsong NM. Type locality: Elandsberg (WC). This species is only known from the type locality. Host plants unrecorded. MPT: montane prominences on north-west facing slopes. Host ant: *Crem. gallicola*.

Taxonomy: Formerly *C. adonis aridimontis*, it is similar in appearance to *C. adonis*; the geographic distance between the two discrete populations is 190 km and their different ecologies indicate separate species. *C. aridimontis* is polyphyletic in the COI tree where the two lineages occur in separate clades (*thysbe* mt Clades 1 and 3) but are sympatric. The sample AH07C166 in Clade 1 has facies similar to *C. aridimontis;* it was collected with other similar specimens in 2008 (A. Heath and H. Selb) at Elandsberg, WC, the exact and only locality known for *C. aridimontis*. The MPT for these individuals collected in 2008 were noted to be montane slopes and prominences, very similar to *C. aridimontis s.s.* which was not seen at the time these were collected. This specimen was deemed to be *C. aridimontis* by E. Pringle, and A. Heath reckoned it looked very similar to *C. aridimontis* but with minor differences. As *C. plutus* also occurs at that location, it was earlier postulated to be an *aridimontis* – *plutus* hybrid. However, the COI tree groups it with neither *C. plutus* nor the other *C. aridimontis* specimens (and nuclear data are absent), thus it is not a hybrid. The COI-polyphyly of *C. aridimontis* is possibly a product of past capture (historical introgression) of a mitochondrial lineage from a taxon now extinct. However, it is not possible to infer which of the mtDNA lineages was present during speciation and which was later "captured" through hybridization. *Chrysoritis adonis aridimontis* is here raised to *Chrysoritis aridimontis* **stat. nov.** Conservation status: LC – Ex Rare.

Chrysoritis beulah is found in *thysbe* mt Clades 3 & 4. See *thysbe* mt Clade 4 for species description.

thysbe mt Clade 4

Mt clade 4 comprises long-established species – each has a long subtending branch in the COI tree; only one species, *C. beulah* occurs at low elevations, the rest occurring at mid to high elevations. *Chrysoritis penningtoni*, *C. orientalis*, *C. braueri* and *C. beulah* all occur outside the GCFR. The former three are montane; *C. beulah* occurs with *C. braueri* on the Somerset East mountains but at a lower elevation. The mt clade 4 matriline appears to have originated in the Eastern Cape (the first two branches of the clade lead to Eastern Cape species, *C. penningtoni* and *C. braueri*; see Fig. 1A in QEA22) and then spread progressively westward, first to the Great Karoo region (where *C. beaufortia* and *C. stepheni* occur), then on to Namaqualand (where another population of *C. stepheni* occurs). The lineage leading to *C. orientalis* also spread from the Eastern Cape, heading northeast to the Kwazulu-Natal & Lesotho area.

Chrysoritis beaufortia (Dickson 1966). *Poecilmitis beaufortia* Dickson 1966: 109. Holotype: NHM, London. Type locality: Nieuwveld Mts. MPT: montane prominences. Host ant: *Crem. peringueyi*; larval host plant *Dimorphotheca cuneata* Thunb.

Taxonomy: Monophyletic and well supported in the COI tree (100%). In the CAD tree, three of the four *C. beaufortia* samples form a well supported (99%) clade. Morphologically similar to *C. stepheni* (see below), and there is also overlap among all three subspecies.

C. beaufortia beaufortia. Appearance remarkably uniform, with prominent white interneural flecks at the margin of both wings. Although it is only known from the Nieuwveld Mountains near Beaufort West, a single worn specimen answering to this taxon was once taken from the Compassberg area in the Eastern Cape (E. Pringle). Conservation status: LC.

C. beaufortia sutherlandensis Heath & Pringle 2007. Type locality: Swaarweerberg, Sutherland. This subspecies occurs from the Komsberg to the Swaarweerberg, Sutherland district and has the black markings reduced to a variable extent. Host ant and plant as in nominate subspecies. Conservation status: LC.

C. beaufortia charlesi (Dickson 1970), *Poecilmitis beaufortia charlesi* Dickson, 1970: 93. Holotype: NHM, London. Type locality: "Quagga Fontein, 25 miles N.W of Sutherland". Although variable, this is a much darker subspecies, often with an almost black forewing. It occurs on upper montane slopes from its type locality on the Roggeveldberge close to the NC Province and Tankwa Karoo boundary and northward to Kieske Mt. (within 17 km of Hantamsberg, Calvinia). Host ant and host plant as in nominate subspecies. Conservation status: LC – Rare.

Chrysoritis stepheni (Dickson 1978) **stat. rev.** *Poecilmitis stepheni* Dickson 1978: 294. Holotype: NHM, London. Type locality: Hantamsberg, Calvinia. See also Heath & Pringle (2007: 24). MPT: montane slopes and prominences. Host ant: *Crem. peringueyi.* Larval host plants: *Dimorphotheca cuneata* Thunb., at Calvinia and *Osteospermum amplectens* (Harvey) T.Norl., at Garies; both Asteraceae and of very similar structure. In captivity late instar larvae readily transferred from one of these host plants to the other with no change observed in feeding behaviour (A. Heath).

Taxonomy: *Chrysoritis stepheni* has 100% bootstrap support in the COI tree and is sister to *C. beaufortia*. Thus far *C. stepheni* has been treated as a subspecies of *C. beaufortia* due to its morphological similarity with the subspecies *C. b. beaufortia* and its shared ecology with all of *C. beaufortia* (same MPT, elevation, and host ant species). *Chrysoritis stepheni* is separated from the similar looking *C. b. beaufortia* by 270 km, but from the darker *C. b. charlesi*, it is separated by only 17 km. The long subtending branches between *C. beaufortia* and *C. stepheni* in the COI tree indicate deep divergences and warranted a look at their pairwise fixation index (Φ_{ST} see Note S2 in QEA22) from the AMOVA analyses. The Φ_{ST} value for *C. beaufortia* (n = 6) vs. *C. stepheni* (n = 4) is 0.725 ($p < 0.05$; see Note S3 here). Thus, despite only a 17 km (minimum) separation, an overwhelming proportion (72%) of the total genetic variation among all individuals occurs *between* the two taxa (versus 28% *within* taxa). This is much higher than a typical range for subspecies (explained in Note S3). Thus, *C. beaufortia stepheni* is raised to *C. stepheni* **stat. rev**.

Chrysoritis stepheni itself consists of two discrete populations known to the authors, one on the Hamtamsberg, Calvinia (n = 2) and the other 195 km NW on the Kamiesberge (n = 2), Despite their geographic distance, they are ecologically comparable and morphologically identical – two populations yet to meet the requirements for subspecies (Braby *et al.*, 2012). Conservation status: LC – Rare.

Chrysoritis beulah (Quickelberge 1966). *Poecilmitis beulah* Quickelberge 1966: 4. Type locality: Nr. Steytlerville, Eastern Cape Province. MPT: low to medium elevation gullies. Host ant: *Crem. castanea* (unconfirmed); host plant: no data.

Taxonomy: Polyphyletic in the COI tree due to a specimen (C374) from Smithskraal 20 km NE of Willowmore occurring in *thysbe* mt Clade 3. This locality was discovered by D. A. Edge (pers. comm.) and specimens from there were identified as *C. beulah,* having indistinguishable facies from type locality specimens. In the CAD tree the two *C. beulah* samples (representing both COI lineages) are identical. However, their haplotype is also shared with a *C. violescens* sample; these three samples form a weakly supported clade with 56% bootstrap support. COI-polyphyly could be a consequence of historical introgression involving a now extinct donor taxon but the available data are insufficient to identify the original vs. the "captured" mtDNA lineage. With support suggested by the CAD data, the Smithskraal specimen is treated as *C. beulah* here. As the two COI lineages are separated both phylogenetically and geographically (unlike other polyphyletic taxa such as *C. aridimontis*, *C. trimeni* and *C. perseus* where both COI lineages co-mingle) and support from nuclear data is not definitive, further investigation is needed. Conservation status: LC.

Chrysoritis penningtoni (Riley 1938). *Poecilmitis penningtoni* Riley 1938: 239. Holotype: NHM, London. Type locality: "Gaika's Kop". Host plant: *Thesium* sp. Host ant: no data. MPT: upper montane slopes; "hollows in rocky outcrops" (Woodhall, 2020). This species (n = 2) is sister to all other species in mt clade 4 in the COI tree. Conservation status: VU.

Chrysoritis braueri (Pennington, 1967) *Poecilmitis braueri* Pennington, 1967: 122. Holotype: Ditsong NM. Type locality: Madeira Hill, Queenstown Dist. MPT: montane gullies. Host ants: *Crem. gallicola*. For notes on juvenile stages see Heath *et al.* (2008: 132). A final instar larva is illustrated in Fig. 19; egg and 1st instar illustrated in Clark & Dickson (1971: 195). Conservation status: LC.

Figure 19 – *C. braueri* final instar (Bedford, E. C.).

Chrysoritis orientalis (Swanepoel, 1976), *Poecilmitis orientalis* Swanepoel, 1976: 119. Holotype: Ditsong NM. Type locality: Boesmansnek, Nr. Underberg. MPT: upper montane, ledges in rocky outcrops (Woodhall, 2020). Host ant: *Crem. castanea*.

Taxonomy: Despite having vaguely similar facies, *C. orientalis* (n = 2) and *C. pelion* (n = 1) are not matrilineally closely related. Conservation status: LC – Rare.

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