

The application of life history information to the conservation management of *Chrysores* butterflies (Lepidoptera: Lycaenidae) in South Africa

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Due to their intricate life histories and the unique wing patterns and colouring the butterflies of the genus *Chrysores* are of significant conservation and aesthetic value. This overview probes into practical examples of butterfly life history research applicable to environmental management of this relatively well-known invertebrate group in South Africa. Despite the pioneer work on life histories of *Chrysores* in the past, more should be done to understand the life history of the butterflies in the wild, especially their natural host plants and the behaviour of adults and larvae. A system of voucher specimens of host plants should be introduced in South Africa. Although various host plant species in nature are used by the members of *Chrysores*, including the *Chrysores chrysaor* group, the choice of these in nature by each species is significant for conservation management and in the case of *Chrysores aureus* perhaps even as a specific characteristic. A revision of the ant genus *Crematogaster* will benefit the conservation management of *Chrysores* species since some of these ant species may consist of a number of species with much more restricted distributions than previously thought. Rigorous quantified studies of population dynamics of *Chrysores* butterflies are absent and the introduction of such studies will benefit conservation management of these localised butterflies extensively.

Key words: *Chrysores*, myrmecophilous, endemic, conservation, life histories, management, taxonomy, ecology, synecology.

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Introduction

Williams (1996) reported a lack of information on the life histories of South African butterflies despite the most valuable efforts of the past. Pioneer lepidopterists (including Clark, Claassens, Dickson, Cottrell, G.A. Henning, S.F. Henning and Heath) provided a rich source of life history information in the past, useful for environmental management. Further research priorities are identified here. This paper reviews the life history information on the *Chrysores* genus to date, and discusses how applicable this information is for conservation management.

World-wide, the symbioses of butterflies and ants are found only among members of the Riodinidae and Lycaenidae (De Vries 1997) and at present the Riodinidae is often regarded as a subfamily Riodininae within the Lycaenidae (Eliot 1973; Eliot 1990; Pierce *et al.* 2002). Although the Riodininae is poorly represented in Africa, the rest of the Lycaenidae is well-represented in most habitat types on the continent. Judging by the number of species, the majority of South African butterflies belong to the family Lycaenidae. From our list of 674 butterfly species, i.e. superfamilies Hesperioidea: 'skipper butterflies' and Papilionoidea: 'true

butterflies' in South Africa, 49 % of the species belong to the family Lycaenidae. The majority of these Lycaenidae species are associated with ants. A diversity of strategies has developed into ant associations among the Lycaenidae. Extremes, from aphytophagy (Cottrell 1984) to facultative ant associations, have been recorded. The term entomophagous is used by Pierce *et al.* (2002) instead of aphytophagy, which alter the normal use of entomophagous as 'insect-eating' to 'eating insect-derived food sources'. Apart from the term entomophagous, all the other definitions to describe lycaenid-ant associations as defined by Pierce *et al.* are followed here. Note that Pierce *et al.* (2002) use the terms obligate and facultative ant associations in terms of survival under field conditions, which is strictly followed here.

Given the nature and complexity of larvae ant symbioses, there is much to be learnt from their studies that will be relevant to all branches of biology (De Vries 1997). The various types of associations with ants (Henning 1983a; Cottrell 1984; Pierce *et al.* 2002) by Lycaenidae butterflies, should be appreciated in that different conservation strategies should probably be applied to conserve these, often localised, butterflies.

Discussion

Detailed life history descriptions that entail most stages and some illustrations have only been published for 35.7 % of all the *Chrysoritis* species in South Africa (Table 1). It should be added that ecophysiological studies of interactions between butterfly larvae and host plants as well as attendant ants are absent, not only for *Chrysoritis* but for almost all the butterflies of South Africa. At least one host plant and one attendant ant are known, respectively, for 83.3 % and 88.1 % of the *Chrysoritis* species. These relatively high numbers are due to the contribution of Heath (1997a) (Table 1). Dickson (1940, 1943, 1944, 1945a, 1945b, 1946, 1947, 1948, 1953, 1959 and 1965) gave either detailed and well-illustrated (by Clark)

descriptions of the life histories of some *Chrysoritis* species or information on the host plants and attendant ants. The first major work on the life histories of Lycaenidae butterflies of South Africa was that of Clark & Dickson (1971) that contains a number of detailed life history descriptions. A summary of recent observations of ant associations and life history adaptations of Lycaenidae butterflies in South Africa is given by Heath & Claassens (2000). Heath (1997) for the first time reported the extensive use of *Thesium* plants (Santalaceae) as host plants by *Chrysoritis* species. The importance of the presence of the correct ant as an oviposition stimulus for most *Chrysoritis* species, at least in captivity, is reported (Heath & Claassens 2000). Clark & Dickson (1971) concluded that *Chrysoritis dicksoni* is aphytophagous, since larvae refused to feed on any plant that females had laid on. The mature larvae and pupa were found in *Crematogaster* ant nests (Cottrell 1984). Heath & Brinkman (1995), Heath (1998) and Heath & Claassens (2000) demonstrated that at least in some larval stages, the larvae of *Chrysoritis dicksoni* are sustained by trophallaxis. Among the *Chrysoritis* genus trophallaxis (ants feeding caterpillars by regurgitation) has thus been reported only for *Chrysoritis dicksoni* by Heath (1998). The majority of the *Chrysoritis* species, with the possible exception of *Chrysoritis dicksoni*, seems to be phytophagous accompanied by an obligate ant association (Tables 1- 4).

No voucher material of host plants has been cited in all the above cases. Although the genera and even some of the plant species identified leave little doubt about its identification, the lack of voucher specimens may be a limitation to future research efforts. Cottrell (1984) highlighted the problems associated with the fragmented observations of life histories of aphytophagous butterflies. These are also applicable to the ant-dependent phytophagous *Chrysoritis* species. Thomas *et al.* (1989) summarised the difficulties with the accuracy of interpretations of captive observations, the misinterpretation of field data, as well as the misidentification

of ant species concerning research on *Maculinea* butterflies and their ant associations in Europe.

The question is whether quantitative laboratory-controlled observations and careful observations in the field concerning the life histories of *Chrysochiton* species are available or not. Most *Chrysochiton* species were bred in captivity (where behaviour and requirements are abnormal). Therefore little information exists under controlled conditions or in the field. We discuss the present knowledge of the host plant association and attendant ant association separately for simplicity.

The host plant association

A summary of the host plant genera, host plant families, and attendant ant genera associated with the species groups of *Chrysochiton* is given in Table 2. *Chrysochiton* species have adapted to use a variety of host plants from different genera and families as larval food (Table 2). Different species groups share some genera and families. The ability of some species to use succulents of the family Crassulaceae as host plants gives rise to the hypothesis that such host plants may have been important for the survival of these butterflies especially during dry spells. The full significance of the use of host plants will only become apparent if more research on their use in specific ecosystems were conducted. Another research priority is that some host plants for the *Chrysochiton* species need confirmation. *Chrysochiton chrysaor* was observed to oviposit on *Acacia karroo* (Heath 1997), but it is not clear whether the larvae use these trees as a host plant. During research on *Chrysochiton aureus* from 1998 to 2002, it was found that the females often oviposit on rocks close to the host plant and in fact close to the attendant ant trails (Roos & Henning 2000). The proof for the use of a specific host plant remains the larvae eating the host plant in its habitat. The type of observation (egg laying, larva at base of host plant) about the host plant should be stated clearly in publications. The significance of the host plants on a taxonomic and ecologi-

cal level is discussed by using *Chrysochiton aureus* as an example.

Heath (2001) demonstrated that the choice of larval host plant is not a major issue within a species group of *Chrysochiton* and should not be regarded as a specific characteristic. The variety of host plants used by *Chrysochiton*, even in the same species group such as the *Chrysochiton chrysaor* species group seems to support this hypothesis. Pierce (1984) proposed two ways by which ant association could have enhanced diversification of the Lycaenidae, once it evolved. The first is by inducing a higher incidence of host plant switching and the second is by modifying the butterfly population structure. An example in *Chrysochiton* is the observation that *Chrysochiton aethon* larva used a *Crassula* species as host plant, and not only the known host plant *Rhus zeyheri* (Anacardiaceae), that was reported by Owen-Johnston (1991). This phenomenon should be further investigated since it might be ecologically significant. Heath (2001) states that *Chrysochiton aureus* has been successfully bred in captivity on another plant, *Diospyros lycioides*, an important observation in the context of the *Chrysochiton chrysaor* species group to which *Chrysochiton aureus* belongs. Up to date, *Clutia pulchella* individuals were observed as host plants of *Chrysochiton aureus* larvae in the field. Only once (17 March 2004) was *Diospyros lycioides* observed to be a host plant, despite its presence at many of our research sample plots. *Clutia pulchella* has a wide distribution in the northern provinces of South Africa (Retief & Herman 1997) as well as South Africa (Arnold & De Wet 1993) but is not used by any *Chrysochiton* species other than *Chrysochiton aureus*. The only Euphorbiaceae plant known to be utilised by any *Chrysochiton* species is *Clutia pulchella*. It is utilised by larvae of *Chrysochiton aureus* (Tables 2 and 3). The unidentified Morgenzon *Chrysochiton* entity, as well as *Chrysochiton lyncurium* (closely related to *Chrysochiton aureus* within the *Chrysochiton chrysaor* species group), is also thought to use *Diospyros* as a host plant (Owen-Johnston 1991). This has been assumed from the adult behaviour and has

Table 1

A summary of the life-history studies published on *Chrysoritis*. The types of descriptions (A,B,C) include: A - a description of all or some of the stages (from egg to adult), B - the host plant has been reported, C - the attendant ant has been reported. The literature sources are those that reported previously unknown aspects of the life-histories. The literature sources used were, Dickson (1940, 1943, 1944, 1945a, 1945b, 1946, 1947, 1948, 1953, 1959, 1965), Clark and Dickson (1971), Dickson and Kroon (1978), S.F. Henning (1983a), Owen-Johnston (1991), Heath and Brinkman (1995), Heath (1997a), Heath (1998), Claassens (2000) and Heath (2001)

Chrysoritis Species	Description			Literature
	A	B	C	
Chrysaor Species Group				
<i>Chrysoritis aethon</i> (Trimen & Bowker, 1887)	1	1		Owen-Johnston (1991)
<i>Chrysoritis aureus</i> (Van Son, 1966)	1	1	1	Henning (1983a)
<i>Chrysoritis chrysaor</i> (Trimen, 1864)	1	1	1	Dickson (1943), Dickson (1944), Heath(1997a), Claassens (2000)
<i>Chrysoritis lycogenes</i> (Trimen, 1874)	1	1	1	Clark & Dickson (1971), Henning (1983a)
<i>Chrysoritis lyncurium</i> (Trimen, 1868)			1	Heath (1997a)
<i>Chrysoritis midas</i> (Pennington, 1962)		1	1	Heath (1997a)
<i>Chrysoritis natalensis</i> (Van Son, 1966)		1		Dickson & Kroon (1978)
<i>Chrysoritis phosphor</i> (Trimen, 1866)	—	—	—	
Chrysantas Species Group				
<i>Chrysoritis chrysantas</i> (Trimen, 1868)	—	—	—	
Oreas Species Group				
<i>Chrysoritis dicksoni</i> (Gabriel, 1946)	1		1	Dickson (1953), Dickson (1965), Clark & Dickson (1971), Heath & Brinkman (1995), Heath (1997a), Heath (1998)
<i>Chrysoritis oreas</i> (Trimen, 1891)		1	1	
Zeuxo Species Group				
<i>Chrysoritis zeuxo</i> (Linnaeus, 1764)	1	1	1	Dickson (1953), Dickson (1975), Clark & Dickson (1971), Heath (1997a)
<i>Chrysoritis zonarius</i> (Riley, 1938)	1	1	1	Heath (1997a), Claassens (2000)
Pyroeis Species Group				
<i>Chrysoritis felthami</i> (Trimen, 1904)	1	1	1	Dickson (1940), Clark & Dickson (1971), Heath (1997a), Claassens (2000)
<i>Chrysoritis pyroeis</i> (Trimen, 1864)	1	1	1	*Dickson (1948), Clark & Dickson (1971), Heath (1997a), Claassens (2000)
Thysbe Species Group				
<i>Chrysoritis adonis</i> (Pennington, 1962)	1	1	1	Dickson (1965), Clark & Dickson (1971), Heath (1997a)
<i>Chrysoritis aridus</i> (Pennington, 1953)	1	1		Dickson (1965), Clark & Dickson (1971)
<i>Chrysoritis azurius</i> (Swanepoel, 1975)	—	—	—	
<i>Chrysoritis beaufortius</i> (Dickson, 1966)	—	1	1	Heath (1997a)
<i>Chrysoritis beulah</i> (Quickelberge, 1966)	—	—	—	
<i>Chrysoritis blencathrae</i> (Heath and Ball, 1992)	—	1	1	Heath (1997a)
<i>Chrysoritis braueri</i> (Pennington, 1967)	1	1	1	Clark & Dickson (1971), Heath (1997a)
<i>Chrysoritis brooksi</i> (Riley, 1938)		1	1	Dickson (1959), Clark & Dickson (1971), Heath (1997a)
<i>Chrysoritis daphne</i> (Dickson, 1975)		1	1	Heath (1997a)
<i>Chrysoritis endymion</i> (Pennington, 1962)		1	1	Heath (1997a)
<i>Chrysoritis irene</i> (Pennington, 1968)	—	—	—	
<i>Chrysoritis nigricans</i> (Aurivillius, 1924)	1	1	1	Dickson (1944), Dickson (1947), Clark & Dickson (1971), Heath (1997a), Claassens (2000)
<i>Chrysoritis orientalis</i> (Swanepoel, 1976)		1	1	Heath (1997a)
<i>Chrysoritis palmus</i> (Stoll, 1781)	1	1	1	Dickson (1945a,1945b), Dickson (1953), Dickson (1965), Clark & Dickson (1971), Claassens (2000)
<i>Chrysoritis pan</i> (Pennington, 1962)	1	1	1	**Dickson (1965), **Clark & Dickson (1971), Heath (1997a)
<i>Chrysoritis pelion</i> (Pennington, 1953)	—	—	—	
<i>Chrysoritis penningtoni</i> (Riley, 1938)	—	—	1	Heath (1997a)
<i>Chrysoritis perseus</i> (Henning, 1977)		1	1	Heath (1997a)

Table 1 (continued)

Chrysothrips Species	Description			Literature
	A	B	C	
<i>Chrysothrips plutus</i> (Pennington, 1976)	1	1		Heath (1997a)
<i>Chrysothrips pyramus</i> (Pennington, 1953)	1	1		Heath (1997a)
<i>Chrysothrips rileyi</i> (Dickson, 1966)	1	1		Heath (1997a)
<i>Chrysothrips swanepoeli</i> (Dickson, 1965)	1	1		Heath (1997a)
<i>Chrysothrips thysbe</i> (Linnaeus, 1764)	1	1	1	Dickson (1947), Dickson (1965), Clark & Dickson (1971), Heath (1997a), Claassens (2000)
<i>Chrysothrips trimeni</i> (Riley, 1938)	1	1		Heath (1997a)
<i>Chrysothrips turneri</i> (Riley, 1938)	1	1		Dickson (1953); Heath (1997a)
<i>Chrysothrips uranus</i> (Pennington, 1962)	1	1	1	Dickson (1965), Clark & Dickson (1971), Heath (1997a)
<i>Chrysothrips violescens</i> (Dickson, 1971)	1	1	1	Heath (1997a)
TOTAL	15	35	37	
Percentage Of Total Species	35.7	83.3	88.1	

* See Heath (1997a) that the *Camponotus* associate that Dickson reported was never repeated

** Note this was observed for *Chrysothrips lysander* (now regarded as synonym of *Chrysothrips pan* by Heath (2001).

not been verified. An alternative explanation is that *Diospyros lycioides* is an ancestral host plant for *Chrysothrips lyncurium*, *Chrysothrips lycegenes*, the Morgenzon *Chrysothrips* entity, as well as *Chrysothrips aureus* and *Chrysothrips aethon*—all belonging to the *Chrysothrips chrysaor* species group. In general, it is common practice for lepidopterists to use substitute host plants for breeding butterflies, plants that may not necessarily be used in the wild. Although various host plant species are used by the members of *Chrysothrips*, including the *Chrysothrips chrysaor* group, the choice of these, in nature, by each species is significant for conservation management, in the case of *Chrysothrips aureus* perhaps even as a specific characteristic. The proper management of *Clutia pulchella* at the habitats of *Chrysothrips aureus* would be very important for the survival of the butterfly in its increasingly urbanised distribution. In the light of the above it is furthermore significant that *Chrysothrips aureus* is the only *Chrysothrips* species apart from the ubiquitous *Chrysothrips chrysaor* that extended its distribution into the Rocky Highveld Grassland via *Clutia pulchella* and its attendant ant (Bredenkamp & Van Rooyen 1996).

The ant association

For a number of *Chrysothrips* species, the attendant ant is perhaps of more importance than the host plant as a signal for the female to lay eggs (Heath 1997, 2001). Various adaptations and strategies exist among the rich myrmecophilous lycaenid fauna of Africa, of which various are described by S.F. Henning (1983a) and Cottrell (1984). During the day, *Chrysothrips* larvae shelter for protection and only venture forth at night to feed on their host plants (Henning 1987a). Although the morphological and physiological adaptations among the myrmecophilous larvae have been described, the role of these has been more difficult to demonstrate. There are a number of accessory structures that are associated with larvae that adopted a myrmecophilous life style. Most lycaenid larvae have a median dorsal organ (honey gland) (Henning 1983a), which is referred to as a dorsal nectary organ (DNO) by Cottrell (1984). These are present in all the *Chrysothrips* larvae studied up to date. A pair of dorso-lateral eversible organs is also found on many lycaenid larvae (Henning 1983a). These are referred to as tubercle organs (TOs) by Cottrell (1984) and are also found on all the larvae of *Chrysothrips* studied to

Table 2

Summary of the host plant genera, host plant families and attendant ant genera associated with the different species groups of *Chrysoritis*. The literature sources: Dickson (1940, 1943, 1944, 1945a, 1945b, 1946, 1947, 1948, 1953, 1959, 1965), Clark & Dickson (1971), Dickson & Kroon (1978), S.F. Henning (1983a), Owen-Johnston (1991), Heath & Brinkman (1995), Heath (1997a), Heath (1998), Claassens (2000) and Heath (2001). Plant genera and families are in alphabetic order

	No. of species: Heath (2001)	Known host plant genera	Known host plant families	Host ant Genera
<i>C. chrysaor</i> sp. group	8	<i>Acacia</i> <i>Clutia</i> <i>Chrysanthemoides</i> <i>Cotyledon</i> <i>Diospyros</i> <i>Myrsine</i> <i>Rhus</i> <i>Tylecodon</i> <i>Zygophyllum</i>	<i>Anacardiaceae</i> <i>Asteraceae</i> <i>Crassulaceae</i> <i>Ebenaceae</i> <i>Euphorbiaceae</i> <i>Fabaceae</i> <i>Myrsinaceae</i> <i>Zygophyllaceae</i>	<i>Crematogaster</i>
<i>C. chrysantas</i> sp. group	1	Unknown	Unknown	Unknown
<i>C. oreas</i> sp. group	2	<i>Thesium</i> ¹	<i>Santalaceae</i> ¹	<i>Crematogaster</i> <i>Myrmecaria</i>
<i>C. zeuxo</i> sp. group	2	<i>Chrysanthemoides</i>	<i>Asteraceae</i>	<i>Crematogaster</i>
<i>C. pyroeis</i> sp. group	2	<i>Zygophyllum</i> <i>Thesium</i>	<i>Zygophyllaceae</i> <i>Santalaceae</i>	<i>Crematogaster</i> <i>Myrmecaria</i>
<i>C. thysbe</i> sp. group	27	<i>Aspalathus</i> <i>Berzelia</i> <i>Centella</i> <i>Chrysanthemoides</i> <i>Dimorphotheca</i> <i>Lebeckia</i> <i>Osteospermum</i> <i>Thesium</i> <i>Tylecodon</i> <i>Zygophyllum</i>	<i>Apiaceae</i> <i>Asteraceae</i> <i>Bruniaceae</i> <i>Crassulaceae</i> <i>Fabaceae</i> <i>Myrsinaceae</i> <i>Santalaceae</i> <i>Zygophyllaceae</i>	<i>Crematogaster</i>

(¹Perhaps no plant utilised in the case of *Chrysoritis dicksoni*)

date. These organs tend to be important with regard to the ant associations as defined by Pierce *et al.* (2002). In the case of *Chrysoritis aureus*, the anterior part of the head of the *Crematogaster liengmei* ant sometimes disappears into the DNO in search of the nectar produced by the larvae. Furthermore, the inner part of the tubercles is often everted in the presence of the ants or to 'attract the attention of the ants'. The above studies emphasise the extent to which these butterfly larvae are adapted for ant associations. In the case of *Aloeides dentatis* Henning (1983b) found that epidermal glands (pore copula organs) have a secretion that mimics the

brood pheromone of the attendant ant. Such detailed studies have not yet been published on any of the *Chrysoritis*.

Audible squeaking sounds, produced by pupae of *Chrysoritis brooksi* (Schlosz & Schlosz 1990) and *Chrysoritis irene* (Schlosz 1991), might be of ecological significance and should be studied further. Drumming sounds from the larvae of *Chrysoritis dicksoni* and *Chrysoritis thysbe* were recorded by Heath (1998). De Vries (1990, 1992) has provided detailed descriptions and research techniques that detected audible rituals and other accessories that enhance symbiotic

Table 3
 Summary of the host plants used by species belonging to the *C. chrysaor* species group in the genus *Chryсоритis* and the literature source where the host plant was first reported.

^a Larvae were bred on the plant in captivity or in the laboratory.

^{aa} Only oviposition on the plant observed (Heath 1997).

^{aaa} Larvae or pupae were observed on or at the base of the host plant in the field

Species	Plant Species with indication of type of observation	Plant Family	Literature Source	Information About Voucher Specimens
<i>Chryсоритis aethon</i> (Trimen & Bowker, 1887)	<i>Rhus zeyheri</i> ^{aaa}	Anacardiaceae	Owen-Johnston (1991)	No voucher material sited
	<i>Crassula</i> sp. ^{aaa}	Crassulaceae	Heath (2001)	
<i>Chryсоритis aureus</i> (Van Son, 1966)	<i>Clutia pulchella</i> ^{aaa}	Euphorbiaceae	Henning (1983)	No voucher material sited
	<i>Diospyros lycioides</i> ^a	Ebenaceae	Heath (2001)	
<i>Chryсоритis chrysaor</i> (Trimen, 1864)	<i>Cotyledon orbiculata</i> L. ^{aaa}	Crassulaceae	Dickson (1943)	No voucher material sited
	<i>Rhus</i> sp. ^{aaa}	Anacardiaceae	Dickson (1943)	
	<i>Acacia karroo</i> ^{aa}	Fabaceae	Heath (1997a)	
	<i>Zygophyllum retrofractum</i> ^{aa}	Zygophyllaceae	Heath (1997a)	
	<i>Tylecodon paniculata</i> ^{aa}	Crassulaceae.	Heath (1997a) [#]	
<i>Chryсоритis lycegenes</i> (Trimen, 1874)	<i>Royena hirsuta</i> ^{aaa}	Ebenaceae	Clark & Dickson 1971	No voucher material sited
	<i>Myrsine africana</i> ^{aaa}	Myrsinaceae	Clark & Dickson (1971)	
	<i>Diospyros lycioides</i> ^{aaa}	Ebenaceae	Henning (1983a)	
	<i>Diospyros austro-africana</i> ^{aaa}	Ebenaceae	Henning (1983a)	
<i>Chryсоритis lyncurium</i> (Trimen, 1868)	<i>Rhus</i> sp. ^{aaa}	Anacardiaceae	Henning (1983a)	
	not confirmed	not confirmed		
<i>Chryсоритis midas</i> (Pennington, 1962)	<i>Diospyros austro-africana</i>	Ebenaceae	Heath (1997a)	No voucher material sited
<i>Chryсоритis natalensis</i> (Van Son, 1966)	<i>Chrysanthemoides monilifera</i>	Asteraceae	Dickson & Kroon (1978)	No voucher material sited
	<i>Cotyledon orbiculata</i> (No reference to observations)	Crassulaceae	Dickson & Kroon (1978)	
<i>Chryсоритis phosphor</i> (Trimen, 1866)	Unknown	Unknown		

[#]Note this information is for the entity *Chryсоритis lycia* (Riley, 1938), which is now regarded as a synonym of *Chryсоритis chrysaor* by Heath (2001).

associations between Riordininae larvae and ants. At present, no such detailed research exists for any of the African Lycaenidae.

A number of instances have been reported where *Chryсоритis* species have been bred in captivity in the absence of ants. Nevertheless, in the field the association seems to be

vital. The latter confirms the importance of observations in the field—associations that may not be essential for survival in the laboratory might be obligatory in the field. Most of the *Chryсоритis* species fall into the category of phytophagous, but with a myrmecophily, where the butterfly is dependent on ants (see Henning 1983a).

The reasons for the evolution of ant associations are discussed by Cottrell (1984), especially whether these associations are for protection from parasites and predators (Thomann 1901) or to avoid ant aggression (Lenz 1917). Quantitative and controlled observations in this regard are also rare. Cottrell (1984) suggests that both factors had differing and probably complementary parts to play in different taxonomic groups within the Lycaenidae. Evidence that the presence of ants associated with myrmecophilous butterflies reduces the risk of attack from predators and parasites are provided by Pierce & Mead (1981) and Pierce *et al.* (1987). Pierce *et al.* (2002) provides an overview of costs and benefits of lycaenid-ant interactions. Specific detailed experiments of the South African fauna seem to be absent, and seems to be important for conservation since the importance of ant protection seems to vary among species (see Pierce *et al.* 2002).

Despite the variety of host plants used by the *Chrysoritis* species (Tables 2 & 3), only ants of the subfamily Myrmicinae are used as attendant ants (Table 4). The larvae of *Chrysoritis aureus* are constantly attended by *Crematogaster* ants (Henning 1983a). The ant genus *Crematogaster* is a large genus of small, monomorphic, blackish or brownish-yellow ants of which at least 50 species have been described from southern Africa. They occur from the Cape to Ethiopia (Prins 1978). It is interesting to note that the *Chrysoritis* genus is confined to the south-western and south-eastern parts of South Africa, despite the ability to use various host plants and being associated with *Crematogaster* ants, of which numerous species are widely distributed in Africa. Perhaps the various other Aphnaeini (Lycaenidae: Theclinae) butterflies that are also associated with *Crematogaster* ants might be better adapted to savanna and forest ecosystems than *Chrysoritis* species.

Heath (2001) noted the importance of ant associates in the systematics of the genus *Chrysoritis* as well as the possibility that the ant species are themselves composed of species groups that should not be over-

looked. The importance of *Crematogaster liengmei* and *Crematogaster peringueyi* as attendant ants can be appreciated for the *Chrysoritis chrysaor* species group (Table 4). Both these ant species are also attendant ants for *Chrysoritis* species that belong to other species groups (see Heath 2001). Therefore, the correct *Crematogaster* species in each case, that seems to be essential for the survival of these butterflies may be less widespread than is currently understood. The implication of Heath's observation is that a revision of the *Crematogaster* ant species will benefit the conservation management of *Chrysoritis* species.

In the absence of ants, a fungal infection occurs in the dorsal nectary organ and the larva usually dies after a few days (Henning 1987; Roos & Henning 2000; Terblanche *et al.* 2003). All the larval instars of *Chrysoritis aureus*, as well as the pupae in the ant nest were observed to be accompanied by at least two but often more *Crematogaster liengmei* individuals. This was found every time that larvae or pupae were observed during the field work done in the wet seasons of 2000–2004 by R.F. Terblanche in the Heidelberg district of South Africa. When an ant nest underneath a rock contained pupae, it was carefully turned over (Fig. 1), the *Crematogaster liengmei* individuals were observed to lift their gasters and some would position themselves on the dorsal part of the pupae. In these cases the ants that rarely bite when disturbed, now did so fiercely. The pupae, and not only larvae, seem to be protected, but the mechanisms of the pupa to enhance protection seem to be poorly studied. The presence of larvae and especially pupae in the ant nests could be a response to a variety of unfavourable factors, such as mammalian grazing and trampling pressures, frost and fire (Cottrell 1984). Although these factors make sense considering for example the field observations on *Chrysoritis aureus*, Cottrell (1984) noted that such explanations should be based on much more detailed quantitative studies of individual lycaenid biology.

Brussard (1991) and New (1997) verified the importance of detailed auto-ecological information. New (1997) noted the importance of studying butterfly population dynamics at least for a number of seasons, but also mentioned that the duration of the studies or urgency sometimes permits for one flight season only, or sometimes even less. Heath & Brinkman (1995) have described aspects of the population dynamics of *Chrysoritis dicksoni* based on collections and observations in the field. No published literature could, however, be found where the size or the abundance of the colonies of *Chrysoritis* had been measured or quantified with the aid of sample plots, transects or any well-described mark-and-recapture procedure. In fact, few population studies have been published for any of the myrmecophilous Lycaenidae of Southern Africa. An unpublished report by De Wet (1992) on the butterfly *Eriksonia acraeina* contains numbers and sex ratios.

Conclusions

Pioneer lepidopterists (including Clark, Claassens, Dickson, Cottrell, G.A. Henning, S.F. Henning and Heath) provided a rich source of life history information in the past which in the end is a source of information for environmental management. This paper indicates that much more should be done to understand the life history of the butterflies in the wild, especially their natural host plants and the behaviour of adults and larvae. The circumstances and types of associations with host plants and



Fig. 1. Wall of ant nest with pupae and attendant *Crematogaster liengmei* ants.

attendant ants should be more precisely described so that traceability and repeatability could be enhanced. Experiments of microclimate on the morphology of *Chrysoritis* species should be described in detail, as well as the results, if one were to prove the relevant hypotheses. No system of voucher specimens of host plants exists in South Africa. Such a system would enhance the traceability of host plant information, especially if taxonomic changes regarding the plants have taken place. Fish (1999) gives clear guidelines on the preparation of herbarium specimens that are recommended to study the life histories of butterflies.

The physiological interactions during the life cycle of myrmecophilous butterflies with their attendant ants and host plants in South Africa are unknown for *Chrysoritis* species (and also for all the Lycaenidae in Southern Africa). The research will therefore most probably be rewarding.

Much remains to be done to quantify the population dynamics of *Chrysoritis* species and in fact all the localised butterflies in Africa. Although it would prove to be very difficult, efforts should also be made to quantify predation and competition, or at least make an effort to do so. The use of alternatives for mark-and-recapture methods, such as transecting methods, is a research field worth exploring in Africa. A better idea of dispersal behaviour of *Chrysoritis* butterflies would enhance the

understanding of distribution, population dynamics and especially metapopulations.

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