JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 57 2003 Number 1

Journal of the Lepidopterists' Society
57(1), 2003, 1–16

ANT-ASSOCIATION AMONG SOUTHERN AFRICAN LYCAENIDAE

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ABSTRACT. Known life history data, ant-associations and larval feeding habits for southern African lycaenids are summarized and discussed with a focus on recently acquired knowledge. Of the 392 lycaenid species represented in southern Africa, over three quarters are ant-associated, two thirds of which are obligate. The Poritiinae is represented by two tribes of algae/lichen feeders that are not ant-associated. Of the Miletinae, three quarters are obligately ant-associated, and all are believed to prey on Homoptera or their secretions during their larval stage. Within the Lycaeninae, the tribe Theclini are all believed to be facultative. The tribe Aphnaeini constitutes one third of all lycaenids, almost all obligately ant-associated. The tribe Polyommatini accounts for a third of all lycaenids and is 95% ant-associated, containing similar proportions of facultative and obligate associations. The presence, absence and function of myrmecophilous organs at various larval stages is discussed. Ovipositing below the soil or on sand surface is recorded for the first time. The various trophic strategies of larvae are discussed. *Crematogaster* (Myrmicinae) and *Anoplolepis* (Formicinae) ants together account for almost 80% of obligate relationships. It is suggested that many synonymies exist among obligately ant-associated taxa.

Additional key words: evolution, myrmecophily, trophallaxis, aphytophagy, entomophagy, detritus, acoustics, South Africa.

Of 3607 Afrotropical butterfly species, 42% are in the family Lycaenidae (Ackery et al. 1995), a similar figure (47%) is given for southern Africa[2] by Pringle et al. (1994). Of the 397 Australian butterflies, 36% are in the family Lycaenidae (Braby 2000). These figures imply that a higher level of diversification has occurred in the Lycaenidae than in other families, and Pierce (1984) suggested that this may have been caused by ant-association (myrmecophily). Many species of lycaenids are ant-associated in the early stages (Fiedler 1991), ants being among the leading predators of insects (Hölldobler & Wilson 1990). Lycaenid larvae are vulnerable to predatory ant species, hence various strategies have evolved to prevent or reduce attack. Dense and long hair serves as one effective strategy, endophagy (feeding inside plant material) is another. Other lycaenids possess an extra-thick cuticle with the head protected beneath a tough carapace. Many such larvae have organs that serve specific functions in their association with ants. A dorsal nectary organ (DNO), present on the seventh abdominal segment of some larvae provides honeydew for ants to imbibe. A pair of tentacle organs (TOs) located on the eighth abdominal segment and several minute perforated cupola organs (PCOs) are present on the larva's cuticle which all secrete substances that can influence ant behavior (Cottrell 1984). Note that ant-organs found in ant-associated Riodininae differ from those in other lycaenids; see DeVries (1991, 1997) for a comparison. By using these organs, free-living mutualistic caterpillars provide nutritious secretions and emit chemical signals (Henning 1983b) that can manipulate ant behavior to reduce aggression and obtain protection from predators and parasitoids (Lenz 1917, Hinton 1951, Pierce & Mead 1981, Pierce 1984, Pierce et al. 1987, DeVries 1988, 1991, Fiedler 1991). In some cases this manipulation is extended to inducing regurgitations from adult ants (trophallaxis) or enabling the larva to prey directly on the ant brood (parasitism) (Henning 1983b,

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[2] Southern Africa: Countries south of Angola, Zambia and the Zambezi River in Mozambique. The region includes Namibia, Botswana, Zimbabwe, South Africa, Swaziland, Lesotho and southern Mozambique.

Pierce 1995, Heath 1998, Elmes et al. 1991, Thomas 1983, Thomas & Wardlaw 1992).

The DNO was first described by Guenée (1867), subsequently more knowledge was gathered about the myrmecophilous organs (Newcomer 1912, Ehrhardt 1914, Hinton 1951, Clark & Dickson 1956). Their structure and function was studied in greater detail by Malicky (1969, 1970). More recently, secretions from these organs were chemically analyzed (Maschwitz et al. 1975, Pierce 1983, DeVries & Baker 1989). Many, but not all ant-associated lycaenids possess these organs, whose presence and possibly function can vary throughout the larval stage (Cottrell 1984). Some lycaenid tribes and genera are known to be more strongly ant-associated than others, but even within a single genus, the type of association can be quite varied (Pierce 1989).

Ant-associated lycaenid larvae are known to produce a substrate borne call to recruit ants (DeVries 1988, 1990, 1991, Travassos & Pierce 2000). Southern African aphnaeine larvae also produce sounds (Heath 1998), as do pupae (Schlosz 1991, Claassens 1991).

Numerous field and laboratory studies have contributed to our knowledge of African ant-lycaenid associations. One of the earliest accounts detailing ant-association in African lycaenids was Lamborn (1914) who recorded observations on early stages of 27 species (14 genera) from southern Nigeria. Nine of these genera are also represented in southern Africa. Observations in Kenya and Uganda by Jackson (1937) described obligate ant-associations in seven species and discussed 25 facultative associations. The first major study on South African lycaenid early stages was by Clark and Dickson (1971), who described and illustrated 125 species at different stages of their development, including myrmecophilous organs. Behavioral studies under laboratory conditions were done subsequently by Claassens (1972, 1976) and Claassens and Dickson (1977). On a global scale, lycaenid-ant associations have been reviewed by Cottrell (1984), Fiedler (1991) and Pierce et al. (2002).

This paper summarizes and discusses our understanding of myrmecophilous lycaenids in southern Africa during the past ten years. Recent accounts include: Schlosz and Brinkman (1991), Williams and Joannou (1996), Heath and Brinkman (1995a, b), Heath (1997a, b, 1998), Claassens and Heath (1997), Edge and Pringle (1996), Heath and Claassens (2000), Lu and Samways (2001). The number of species for each genus follows Pringle et al. (1994), Ackery et al. (1995), Williams (1999) and Heath (2001). A comprehensive list of food plants and ant-associates for southern African Lepidoptera is found in Kroon (1999).

Our classification here follows Scott (1985), Eliot (in Corbet et al. 1992), Ackery et al. (1999) and Pierce et al. (2002), who treat Riodininae[3] as a subfamily within Lycaenidae, along with Poritiinae (including Pentilini and Liptenini), Miletinae (Miletini, Liphyrini and Spalgini) and Lycaeninae (Theclini, Aphnaeini, Lycaenini and Polyommatini). Examples of adult lycaenids from the region are illustrated (Figs. 1–20).

METHODS USED FOR STUDYING LYCAENIDS IN THE FIELD AND LABORATORY

Inducing oviposition. Inducing oviposition facilitates life history studies in the laboratory. The method for inducing oviposition among *Chrysoritis* Butler is to place not more than three known or 'suspected' host ants together with some stems preferably of a known larval foodplant, inside an open plastic container about 130 × 100 mm and 70 mm deep covered tightly with fine netting (e.g., ladies' stockings) and kept warm, but not hot, or in the sun. A female *Chrysoritis* is added once the ants have settled down. More than three ants often results in an escape hole chewed in the netting. The female butterfly is fed daily with a small lump of tissue paper soaked in weak sugar water placed on the netting. Eggs are often laid on the netting. Attempts to induce oviposition among *Aloeides* Hübner in this manner have been unsuccessful, but oviposition among captive *Thestor* Hübner occurred on almost any surface without either ants or vegetation present (Heath & Claassens 2000).

Obtaining early stages in the field. Methods for finding early stages in the field vary with life history characteristics. Many myrmecophilous species spend part or all of their juvenile phases in or close to subterranean ant nests which makes them difficult to discover and study. Others are found under rocks and associated with a particular plant or ant nest. The method used to find *Chrysoritis* larvae is to search the debris beneath potential food plants where ants are present. On occasions, the larvae are found in small fibrous shelters built on the plant stems by the ants, presumably intended for Homoptera. For *Aloeides* we search in the soil beneath potential food plants or beneath nearby rocks. In *Trimenia* Tite & Dickson, the early stages are sought by digging in the gravel or by prizing open cracks in bedrock where nests of the host ants occur (Heath & Brinkman 1995b). For *Phasis* Hübner, hollowed out stems of the foodplants are examined where ants are present. For *Thestor* and *Tylopaedia* Tite & Dickson, we search beneath large boulders covering ant nests in areas where the adults

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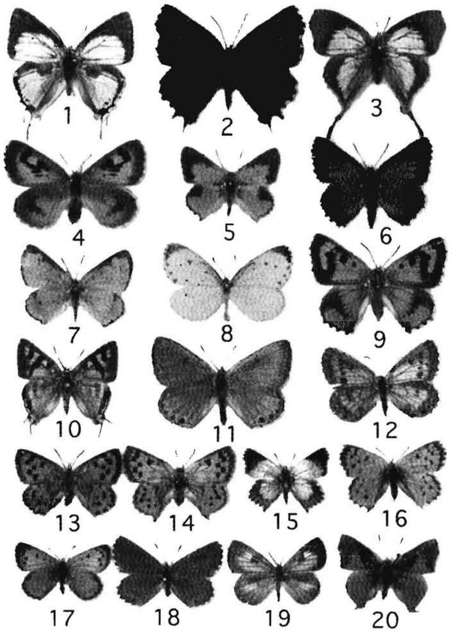
[3] Riodininae is not represented in southern Africa.



FIGS. 1–20. Lycaenidae from southern Africa. **1,** *Iolaus (Iolaphilous) trimeni* Wallengren. **2,** *Phasis thero thero* (Linnaeus) female. **3,** *Myrina silanus ficedula* Trimen male. **4,** *Thestor protumnus protumnus* (Linnaeus) female. **5,** *Aloeides aranda* (Wallengren) male. **6,** *Aloeides pallida grandis* Tite & Dickson male. **7,** *Erikssonia acraeina* Trimen male. **8,** *Pentila tropicalis tropicalis* (De Boisduval) male. **9,** *Tylopaedia sardonyx sardonyx* (Trimen) female. **10,** *Cigaritis natalensis* (Westwood) male. **11,** *Lepidochrysops trimeni* (Bethune-Baker) male. **12,** *Lepidochrysops oreas oreas* Tite female. **13,** *Chrysoritis brooksi brooksi* (Riley) female. **14,** *Chrysoritis thysbe thysbe* (Linnaeus) female. **15,** *Chrysoritis nigricans nigricans* (Aurivillius) male. **16,** *Chrysoritis palmus palmus* (Stoll) female. **17,** *Lycaena orus* Stoll male. **18,** *Lepidochrysops robertsoni* Cottrell male. **19,** *Lachnocnema bibulus* (Fabricius) female. **20,** *Axiocerces amanga* (Westwood) male.

are known to fly. Rocks under which juvenile *Thestor* species are found, are often turned over by baboons looking for *Thestor* larvae and pupae, and scorpions.

Study of behavior in captivity. Due to the subterranean habits of many juveniles, close study of the interactions between ants and larvae in nature is not feasible. Hence, for taxa like *Aloeides*, *Thestor*, *Lepidochrysops*, *Orachrysops* and *Trimenia*, where a formicarium similar to that described by Claassens (1972, 1974) is required, a nest of host ants with brood and queen is installed within the formicarium. Before being introduced into the nest section of the formicarium, larvae are left among the ant brood for about two hours. This is to acquire the scent of the ant colony and avoid subsequent attack by ants, but also to see what interaction takes place between larvae and brood. Pieces of suspected food plant are kept in water within the arena, as described by Claassens and Dickson (1977). *Chrysoritis* species do not generally enter ant nests but are constantly attended while feeding on the foodplant and resting in the debris beneath it; their early stages can be studied in the natural environment. It is nevertheless possible to rear these in captivity with or without the host ant.

CATEGORIES OF ANT-ASSOCIATION AND FEEDING STRATEGIES

There have been many attempts to categorize feeding strategies and relationships between lycaenids and ants; e.g., Fiedler (1991), DeVries (1991), Pierce (1995), Eastwood and Fraser (1999), Heath and Claassens (2000) and Pierce et al. (2002). The following three broad categories of ant-association are used here: (1) 'Not ant-associated' (direct and close interaction with ants is absent or rare, even if ants are present). (2) 'Facultative' (intermittently attended by ants but not wholly dependent on them for survival under field conditions). (3) 'Obligate' (dependent on one species of ant for survival under field conditions).

Three categories of larval feeding strategy used here are 'algae/lichen-feeding', 'herbivorous' and 'entomophagous'. The latter term being re-defined by Pierce et al. (2002) to mean dependant upon any insect-derived resource, and may include homopteran secretions, ant regurgitations and/or the insects themselves (carnivory). More than one of these categories may be employed during the larval phase.

GENERA, LIFE HISTORY AND ANT-ASSOCIATIONS

For completeness, all 64 lycaenid genera occurring in southern Africa are included here, whatever their ant-association. More specific details are shown in Table 1 and summarized in Table 2.

PORITIINAE: Larvae of Pentilini and Liptenini (together including 13 genera) are clothed with long hairs and not directly ant-associated; they possess no DNO or TOs. Larval food is mostly algae or lichen (Bampton 1995), but *Deloneura* were recorded taking honeydew from Homoptera in the company of ants (Pringle et al. 1994), although ants ignore the larvae (Jackson 1937).

Pentilini (three genera): *Alaena* De Boisduval, 1847; *Pentila* Westwood, 1852; *Ornipholidotos* Bethune-Baker, 1914.

Liptenini (ten genera): *Durbania* Trimen, 1862; *Durbaniella* van Son, 1959; *Durbaniopsis* van Son, 1959; *Cooksonia* H. H. Druce, 1905; *Mimacraea* Butler, 1872; *Euthecta* Bennett, 1954; *Teriomima* Kirby, 1887; *Baliochila* Stempffer & Bennett, 1953; *Cnodontes* Stempffer & Bennett, 1953; *Deloneura* Trimen, 1868.

MILETINAE: Larval food can be regurgitations from ants but is mostly Homoptera or their secretions. Homoptera are almost always attended by ants but di-

TABLE 1. Life history details for all known Southern African lycaenids, showing presence of DNO or TOs, larval feeding category[a] and ant-association. Abbreviations: * = probable but unconfirmed. DNO, TOs: + = yes; – = no; Feeding category: A = Algae or Lichen feeder; H = Herbivorous; E = Entomophagous. Ant-association: N = none; F = facultative; O = obligate; ? = unknown. Principal sources: 1 = Clark and Dickson (1971); 2 = Pringle et al. (1994); 3 = Jackson (1937); 4 = Heath and Claassens (2000); 5 = Heath (1997); 6 = Bampton and Congdon (pers. com.); 7 = Stempffer (1967); 8 = Henning (1983a, b); 9 = Claassens (1976); 10 = Edge and Pringle (1996); 11 = Schlosz and Brinkmann (1991); 12 = Heath (pers. obs.); 13 = Kroon (1999); 14 = Lamborn (1914); 15 = Heath and Brinkmann (1995b); 16 = Williams and Joannou (1996); 17 = Lu and Samways (2001); 18 = Larsen (1991); 19 = Pennington (1956); 20 = Atsatt (1981); 21 = Braby and Woodger (1994); 22 = Henning and Henning (1982); 23 = Henning (1984a); 24 = Ackery and Rajan (1990); 25 = van Someren (1974); 26 = Claassens and Dickson (1977); 27 = Claassens and Dickson (1980); 28 = Fiedler and Hagemann (1992); 29 Clark and Dickson (1956); 30 = Congdon and Bampton (1995); 31 = Edge (1990).

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
PORITIINAE							
Pentilini (8)							
Alaena	*amazoula*	–	–	A	N		1, 29
	brainei	–	–	A	N		2, 6
	nyassa	–	–	A	N		2, 6
	margaritacea	–	–	A	N		2, 6
Pentila	*pauli*	–	–	A	N		12
	swynnertoni	–	–	A	N		2, 6
	tropicalis	–	–	A	N		2, 6
Ornipholidotos	*peucetia*	–	–	A	N		2, 12, 18
Liptenini (22)							
Durbania	*amakosa*	–	–	A	N		1, 12, 29
	limbata	–	–	A	N		2, 12
Durbaniella	*clarki*	–	–	A	N		2, 12
Durbaniopsis	*saga*	–	–	A	N		2, 12
Cooksonia	*neavei*	–	–	A	N		2
Mimacraea	*marshalli*	–	–	A	N		2
	neokoton	–	–	A	N		2
Euthecta	*cooksoni*	?	?	A*	N*		2
Teriomima	*puellaris*	?	?	A	N		2
	puella	?	?	A	N		2
	zuluana	?	?	A	N		2
Baliochila	*aslanga*	?	?	A	N		2
	barnesi	?	?	A	N		2
	neavei	?	?	A	N		2
	lipara	?	?	A	N		2
	singlaris	?	?	A	N		2
Cnodontes	3 species	?	?	A*	N*		19
Deloneura	*sheppardi*	–	–	A	N		1
	millari	–	–	A	N		2, 3, 19
	subfusca	–	–	A	N		2, 3, 6, 19
MILETINAE							
Spalgini (1)							
Spalgis	*lemolea*	?	?	E	N		3, 8, 14
Lachnocnemini (32)							
Lachnocnema	*bibulus*	–	–	E	N		1, 8, 14, 29
	durbani	–	–	E	N		1, 2, 29
	brimo	–*	–*	E	N*		2
Thestor	*basutus*	–	–	E	O	*A. custodiens*	1, 4, 16, 29
	brachycerus	–	–	E	O	*A. custodiens*	12
	pictus	–	–	E	O	*A. custodiens*	12
	protumnus	–	–	E	O	*A. custodiens*	1, 12
	rileyi	–	–	E	O	*A. custodiens*	12
	rossouwi	–	–	E	O	*A. custodiens*	12
	strutti	–	–	E	O	*A. custodiens*	4
	yildizae	–	–	E	O	*A. custodiens*	4
	dicksoni	–	–	E	O	*A. custodiens*	1, 2, 29
	+20 species	–*	–*	E*	O*	*A. custodiens**	2
Liphyrini (3)							
Aslauga	3 species	–*	+*	E*	N*		3, 6, 7, 14
LYCAENINAE							
Aphnaeini (131)							
Aphnaeus	*erikssoni*	+*	+*	H*	O	*Crematogaster* sp.	2
	hutchinsonii	+	+	H	O	*Crematogaster* sp.	1, 3, 29, 31
	marshalli	+*	+*	H*	O*	*Crematogaster* sp.*	2
Cigaritis	*natalensis*	+	+	H	O	*C. castanea*	1, 2, 6, 29
	ella	+	+	H	O	*C. castanea*	1, 2, 6, 18
	namaqua	+	+	H	O	*Crematogaster* sp.	8, 6
	phanes	+	+	H	O	*C. castanea*	8, 6
	apelles	+*	+*	H	O	*Crematogaster* sp.	2, 6
	+5 species	+*	+*	H*	O*	*Crematogaster* sp.*	2, 6
Lipaphnaeus	*aderna*	+*	+*	H	O*	*Crematogaster* sp.*	6, 30
Chloroselas	*pseudozeritis*	+	+	H	O	*C. gerstaeckeri*	2, 6, 3
	argentea	+*	+*	H	O	*Crematogaster* sp.	2, 6
	mazoensis	+*	+*	H	O	*Crematogaster* sp.	2, 6, 19

TABLE 1. Continued.

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
Zeritis	*sorhagenii*	?	?	H	?		2
Axiocerses	*tjoane*	+	+	H	F		1, 6, 29[b]
	amanga	+	+	H	F[c]		3, 6
	punicea	+*	+*	H	F		2, 6
Phasis	*braueri*	+*	+	H	O	*C. peringueyi*	1, 4
	clavum	+*	+*	H	O*	*Crematogaster* sp.*	2
	pringlei	+	+	H	O	*C. peringueyi*	12, 13
	thero	+[d]	+	H	O	*C. peringueyi*	1, 4, 12, 29
Tylopaedia	*sardonyx*	+	+	H	O	*C. melanogaster*	11, 29
Argyraspodes	*argyraspis*	?	?	H	?	?	5
Trimenia	*argyroplaga*	?	+	H	O	*A. custodiens*	12
	malagrida	?	+	?	O	*A. custodiens*	15
	+3 species	?	+	?	O*	*A. custodiens**	2
Aloeides	*apicalis*	+[e]	+	H	O	*Monomorium fridae*	4
	aranda	+[f]	+	H	O	*Pheidole capensis*	1, 4, 29
	clarki	+	+	H	O*	Unidentified sp.*	1, 2
	damarensis	+	+	H	O*	Unidentified sp.*	1, 2
	dentatis	?[g]	+	H	O	*L. capensis*	2, 4, 8
	depicta	+	+	H	O*	Unidentified sp.*	1, 2
	gowani	+	+	H	O*	Unidentified sp.*	1
	pallida	+	+	H, E[h]	O	*L. capensis*	4
	pierus	+	+	H	O	*L. capensis*	4, 29
	thyra	+	+	H	O	*L. capensis*	2, 4, 26
	trimeni	+	+	H	O	*L. capensis*	1, 2
	rossouwi	+*	+*	H	O	*Lepisiota* sp.	22
	taikosama	+	+*	H	O*	Unidentified sp.*	2, 29
	almeida	+	+*	H	O*	Unidentified sp.*	2, 29
	+39 species	+*	+*	H	O*	Unidentified sp.*	2
Erikssonia	*acraeina*	+	+	H	O	*Lepisiota* sp.	2, 23
Chrysoritis	*adonis*	+	+	H	O	*C. liengmei*	5
	aethon	+	+	H	O	*C. liengmei*	5
	aridus	+	+	H	O	*Crematogaster* sp.	5
	aureus	+	+	H	O	*C. liengmei*	5
	azurius	+	+	H	O	*C. liengmei*	5
	beaufortia	+	+	H	O	*C. peringueyi*	5
	beulah	+	+	H	O	*Crematogaster* sp.	5
	blencathra	+	+	H	O	*Crematogaster* sp.	5
	braueri	+	+	H	O	*C. liengmei*	5
	brooksi	+	+	H	O	*C. peringueyi*	5
	chrysantas	+	+	H	O	*C. melanogaster*	5
	chrysaor	+	+	H	O	*C. liengmei*	5, 29
	daphne	+	+	H	O	*C. liengmei*	5
	dicksoni	+	+	E	O	*C. peringuey*	5
	endymion	+	+	H	O	*C. peringuey*	5
	felthami	+	+	H	O	*C. peringuey*	5, 29
	irene	+	+	H	O	*Crematogaster* sp.	5
	lycegenes	+	+	H	O	*C. liengmei*	5
	lyncurium	+	+	H	O	*C. liengmei*	5
	midas	+	+	H	O	*C. peringueyi*	5
	natalensis	+	+	H	O*	*Crematogaster* sp.*	5
	nigricans	+	+	H	O	*Crematogaster* sp.	5
	oreas	+	+	H	O	*Myrmicaria nigra*	5
	orientalis	+	+	H	O	*C. liengmei*	5
	palmus	+	+	H	O	*C. liengmei*	5, 29
	pan	+	+	H	O	*C. liengmei*	5
	pelion	+	+	H	O*	*Crematogaster* sp.*	5
	penningtoni	+	+	H	O	*Crematogaster* sp.	5
	perseus	+	+	H	O	*C. melanogaster*	5
	phosphor	+*	+*	H*	O*	*Crematogaster* sp.*	5
	plutus	+	+	H	O	*C. peringueyi*	5
	pyramus	+	+	H	O	*C. peringueyi*	5
	pyroeis	+	+	H	O	*Myrmicaria nigra*	5, 29
	rileyi	+	+	H	O	*C. peringueyi*	5
	swanepoeli	+	+	H	O	*C. liengmei*	5
	thysbe	+	+	H	O	*C. peringueyi*	5, 29
	trimeni	+	+	H	O	*C. peringueyi*	5
	turneri	+	+	H	O	*C. liengmei*	5
	uranus	+	+	H	O	*C. liengmei*	5
	violescens	+	+	H	O	*C. peringueyi*	5
	zeuxo	+	+	H	O	*C. liengmei*	5
	zonarius	+	+	H	O	*C. peringueyi*	5
Crudaria	*leroma*	+	+	H	O	*A. custodiens*	1, 5, 12, 29
	wykehami	+	+	H	O	*A. custodiens*	12
	capensis	+*	+*	H*	O*	*A. custodiens**	12
Lycaenini (2)							
Lycaena	*clarki*	–	–	H	N		1, 12
	orus	–	–	H	N		1, 12

TABLE 1. Continued.

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
Theclini (47)							
Amblypodiiti [2]							
Myrina	*silenus*	+	+	H	F		1, 3,14, 29
	dermaptera	+	+	H	F		1, 29
Iolaiti [21]							
Iolaus	*aemulus*	+	+	H	F*		1, 2, 29
	alienus	+	+	H	F		1, 2, 29
	aphnaeoides	+*	+*	H	F*		2
	australis	+*	+*	H	F*		2
	bakeri	+*	+*	H	F*		2
	bowkeri	+	+	H	F		1, 2, 12, 29
	diametra	+*	+*	H	F*		2
	lalos	+*	+*	H	F*		2
	lulua	+*	+*	H	F*		2
	mimosae	+	+	H	F		1, 2, 12, 29
	nasisii	+*	+*	H	F*		2, 12
	obscurus	+*	+*	H	F*		2
	pallene	+*	+*	H	F*		2, 12
	penningtoni	+*	+*	H	F*		2
	poultoni	+*	+*	H	F*		2
	sidus	+	+	H	F*		1, 2, 12, 29
	silarus	+	+	H	F		2, 12
	silas	+	+	H	F		1, 2, 12, 29
	subinfuscata	+*	+*	H	F		2, 12
	trimeni	+*	+*	H	F*		2, 8, 12
	violacea	+*	+*	H	F*		2, 12
Hypolycaeniti (9)							
Hypolycaena	*philippus*	+	–	H	F		1, 3, 14, 29
	lochmophila	+*	–*	H	F*		2
	caeculus	?	?	H	F		2, 6
	+2 species	+*	–*	H*	F*		2
Leptomyrina	*hirundo*	+	–	H	F		1, 2
	lara	+	–	H	F		1, 2, 27, 29
	gorgias	+	–	H	F		1, 2
	henningi	+*	–*	H	F*		2
Deudorigiti [15]	15						
Deudorix	*antalus*	+	–	H	F		1, 2, 29
	dariaves	+*	–*	H	F*		2
	dinochares	+	–	H	F		1, 2, 24
	dinomenes	+*	–*	H	F*		2
	diocles	+	–	H	F		1, 2, 29
	lorisona	+*	–*	H	F*		2
	magda	+*	–*	H	F*		2
	penningtoni	+*	–*	H	F*		2
	vansoni	+*	–*	H	F*		2
	caerulea	+*	–*	H*	F*		2
	zeloides	+*	–*	H*	F*		2
Capys	*alphaeus*	+	–	H	F		1, 27, 29
	penningtoni	+	–	H	F		2, 12
	disjunctus	+	–	H	F		1, 2, 12
	connexivus	+	–	H	F		2, 12
Polyommatini (146)							
Lycaenesthiti [26]							
Anthene	*amarah*	+	+	H	F		1, 3, 29
	butleri	+	+	H	F*		1, 29
	contrastata	+*	+*	H	F*		2
	crawshayi	+	+	H	F*		3
	definita	+	+	H	F		1, 27, 29
	kersteni	+	+	H	F		1[i]
	lemnos	+	+	H	F*		1, 29
	liodes	+	+	H	F*		2, 14
	lunulata	+	+	H	F		3
	wilsoni	–	–	?	O	Unidentified sp.	3
	otacilia	+	+	H	F		1, 6, 25, 29
	talboti	+	+	H	F*		1
	nigeriae	+	+	H	O	Unidentified sp.	3
	+13 species	?	?	H*	F*		2
Polyommatiti [120]							
Cupidopsis	*cissus*	+	+	H	F*		1, 3
	jobates	+	+	H	F*		1
Pseudonacaduba	*sichela*	?	?	H	?		2
Lampides	*boeticus*	+	+	H	F		1, 3, 27, 29
Uranothauma	*antinorii*	–*	–*	H	N*		2
	poggei	*	–*	H	N		2, 6

TABLE 1. Continued.

Genus	Species	DNO	TOs	Feeding category[a]	Ant-association	Ant	Principal sources
	nubifer	–	–	H	N		2, 3
	vansomereni	–*	–*	H	N*		2
Cacyreus	*dicksoni*	–	–	H	N		1, 2, 27
	lingeus	+	–	H	N		1, 3, 27, 29
	marshalli	–	–	H	N		1, 2, 27, 29
	tespis	–	–	H	N		1, 2, 27, 29[j]
	virilis	+	–	H	N		1, 2, 27
Harpendyreus	*notoba*	+	–	H	F*		1
	tsomo	+*	–*	H	F*		2
	noquasa	+*	–*	H	F*		2
Leptotes	*pirithous*	+	+	H	F*		1, 3, 27, 29[k]
	brevidentatus	+	+	H	F*		1
	jeanneli	+	+	H	F*		2, 29
	babaulti	+*	+*	H	F*		2
	pulcher	+*	+*	H	F*		2
Tuxentius	*calice*	+	+	H	F*		1, 2
	melaena	+	+	H	F*		1, 2, 29[l]
	hesperis	+*	+*	H	F*		2
Tarucus	*sybaris*	+	+	H	F*		1
	thespis	+	+	H	F		2, 27, 29
	bowkeri	+	+	H	F*		1, 29
Zintha	*hintza*	+	+	H	F		1, 2, 3
Zizina	*antanossa*	+	+	H	F*		1
Zizeeria	*knysna*	+	+	H	F		1, 12, 28, 29
Actizera	*lucida*	+	+	H	F*		1, 29
	stellata	+	+	H	F*		1, 29
Zizula	*hylax*	+	+	H	F*		1, 21
Brephidium	*metophis*	+	+	H	F*		1, 20
Oraidium	*barberae*	?	?	H	F*		1, 2
Azanus	*ubaldus*	+	+	H	F*		1, 29
	jesous	+	+	H	F*		1, 3, 29
	natalensis	+	+	H	F		1, 3
	moriqua	+	+	H	F*		1, 29
	mirza	+*	+*	H	F*		2
Eicochrysops	*messapus*	+	+	H	F*		1, 29
	eicotrochilus	+*	+*	H	F*		2
	hippocrates	+	+	H	F*		1
Euchrysops	*osiris*	+	+	H	F		1, 3
	barkeri	+	+	H	F		1
	malathana	+	+	H	F		1, 3, 14
	dolorosa	+	+	H	F		1, 2, 29
	subpallida	+*	+*	H	F*		2
Lepidochrysops	*asteris*	+	–	H, E*[m]	O*	*Camponotus* sp.*	1, 2, 29[n]
	bacchus	+	–	H, E*	O*	*Camponotus* sp.*	1, 2, 29
	ignota	+	–	H, E	O	*C. niveosetus*	2, 8
	ketsi	+	–	H, E*	O*	*Camponotus* sp.*	1, 2
	methymna	+	–	H, E	O	*C. maculatus*	1, 2, 29
	oreas	+	–	H, E	O	*C. maculatus*	1, 2
	patricia	+	–	H, E	O	*C. maculatus*	1, 2, 29
	puncticilia	+	–	H, E*	O*	*Camponotus* sp.*	1, 2
	trimeni	+	–	H, E	O	*C. niveosetus*	1, 2
	variablis	+	–	H, E	O	*C. niveosetus*	1, 2
	+49 species	+*	–*	H, E*	O*	*Camponotus* sp.*	2
Orachrysops	*lacrimosa*	+	+	H*	F*		1, 2, 29
	niobe	+	+	H*	F*[o]		10, 2
	ariadne	+	+	H*	O	*C. natalensis*	17, 2
	+7 species	+*	+*	H*	F*		2
Oberonia	*bueronica*	?	?	H	F		2
Chilades	*trochylus*	+	+	H	F*		1
Thermoniphas	*micylus*	?	?	H	N		2, 6

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[a] For Feeding category, and Ant-association, see section "Categories of ant-association and feeding strategies" above.
[b] As *A. bambana* (misidentified).
[c] *A. amanga* is attended only by *Pheidole* species but often found unattended (Bampton pers. com.).
[d] *P. thero* has DNO but not in final instar.
[e] Has DNO but absent in final instar (also *A. depicta, A. pallida* and *A. thyra*).
[f] DNO present in final instar (also *A. pierus*).
[g] DNO absent in final inmstar (Henning 1983) but earlier instars unknown.
[h] Herbivorous but in final instar, feeds solely on ant eggs.
[i] As *A. larydas* (misidentified).
[j] As *C. palemon* (misidentified).
[k] As *Syntarucus telicanus* (misidentified).
[l] As *Castalius melaena* (misidentified).
[m] *Lepidochrysops* are herbivorous for first two instars, thereafter mainly carnivorous on ant brood, supplemented by trophallaxis.
[n] As *Lepidochrysops caffrariae* (misidentified).
[o] Currently regarded as facultative—it can be reared without ants.

TABLE 2. Summary of ant-association: Conf. = based on published and confirmed observations. Predict. = confirmed + predicted but unconfirmed associations.

		Obligate		Facultative		None		Unknown	
Taxon	Total species	Conf.	Predic.	Conf.	Predic.	Conf.	Predic.	Conf.	Predic.
PORITIINAE	30								
Pentilini	8	0	0	0	0	8	8	0	0
Liptenini	22	0	0	0	0	18	22	4	0
MILETINAE	36								
Spalgini	1	0	0	0	0	1	1	0	0
Lachnocnemini	32	9	29	0	0	2	3	21	0
Liphyrini	3	0	0	0	0	0	3	3	0
LYCAENINAE	326								
Aphnaeini	131	66	126	3	3	0	0	62	2
Lycaenini	2	0	0	0	0	2	2	0	0
Theclini	47	0	0	20	47	0	0	27	0
Polyommatini	146	9	62	15	73	8	10	114	1
TOTALS	392	84	217	38	123	39	49	231	4

rect interaction between ant and larva may not necessarily occur.

Liphyrini (one genus): *Aslauga* Kirby, 1890 (14 Afrotropical species, three in southern Africa). Scarce, arboreal butterflies with a distinctive wingshape. Virtually nothing is known of the early stages of southern African *Aslauga* species but suspected to be the same as those observed by Jackson (1937) and Lamborn (1914). Larval skin is leathery, the carapace being extraordinarily heavy; head small and carried on an extendable neck which can be retracted under a carapace; TOs present, but DNO absent. Although the presence of TOs is unique in this subfamily, they are small and do not evert. Larvae feed on Coccidae (Homoptera) tended by *Crematogaster* ants that do not interact directly with the larvae.

Spalgini (one genus): *Spalgis* Moore, 1879 (four Afrotropical species, one in southern Africa). Larvae feed on Coccidae (Homoptera), do not associate with the ants directly, but ants are always present tending Homoptera. Larvae cover themselves with a waxy secretion produced by the Homoptera and lack both DNO and TOs (see Lamborn 1914, Jackson 1937).

Lachnocnemini (two genera): In these genera, larvae lack DNO and TOs. *Lachnocnema* Trimen & Bowker, 1887 (38 Afrotropical species, 3 in southern Africa). Feeding habits of *L. bibulus* Fab. have been described by South African authors, but by a different account of *Lachnocnema* from Kenya (Cripps & Jackson 1940), larvae were carried by ants down to their nest, and trophallaxis occured. The genus was revised by Libert (1996a–c) who described 25 new species, hence the life history accounts from Kenya most probably apply to what are now considered different species. Accounts are given by Clark and Dickson (1971) of *L. bibulus* and *L. durbani* Trimen from South Africa. Early instar larvae of *Lachnocnema bibulus* feed on young psyllids (Homoptera) and their droppings. Mature larvae creep up behind adult psyllids, seize their wings, and devour them. Larvae do not associate with ants directly but ants are always present tending the Homoptera.

Thestor Hübner, 1819 (29 species, all endemic to southern Africa). Medium-size, moth-like, with stout bodies, and either blackish or yellow and brown; they always settle on the ground or rocks. Adults possess a vestigial proboscis and do not nectar. Most *Thestor* species are univoltine. All species appear to associate with *Anoplolepis* (Formicinae) ants (Claassens & Dickson 1980, Cottrell 1984, Claassens & Heath 1997). During the first three instars of *T. protumnus aridus* Van Son and *T. basutus* (Wallengren), larvae feed on Homoptera (Clark & Dickson 1960, 1971, Williams & Joannou 1996). In *T. yildizae* Koçak, *T. pictus* Van Son and *T. basutus* food of the final two instars is regurgitated food from ants (Fig. 21). We suspect that all *Thestor* are entomophagous but only in *T. basutus* is the life history fully known. The remarkable *Thestor* larva (Fig. 22) lacks both DNO and TOs, and possesses an extremely small head with an extendable fleshy "neck". Larval antennae are elongate and project forward; each with a long terminal seta. In *T. yildizae* these antennae remain in contact with the ant's mandibles during exchange of food. It is possible these antennae simulate the ant's mandibles, facilitating the larva's acceptance as a nestmate and/or to stimulate the ant to regurgitate.

Williams and Joannou (1996) observed females of *Thestor basutus capeneri* (Dickson) ovipositing on blades of grass infested by grass-feeding coccids *Pulvinaria iceryi* (Signoret) (Homoptera: Coccidae) which in turn were tended by *Anoplolepis custodiens* Smith

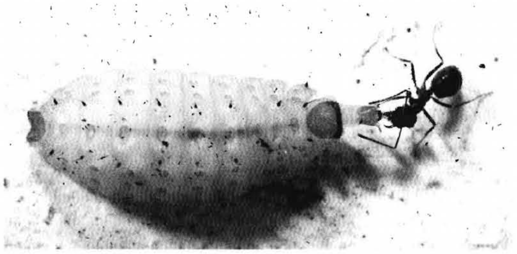

FIG. 21. Final instar larva of *Thestor yildizae* Koçak being fed regurgitations from a "Pugnacious ant" *Anoplolepis custodiens* F. Smith.

ants. They were observed to oviposit on a wide variety of vegetation, often without ants or Homoptera being present. In the wild and in captivity the first three instars were predaceous on coccids, the ants taking no interest in the larvae. After moulting, fourth instar larvae in captivity refused to feed on coccids and were left in the formicary where they entered the artificial ant nest. While in the ant nest, they were ignored by the ants but subsequently died, presumably of starvation (Williams & Joannou 1996). Similar observations were recorded by Clark and Dickson (1960, 1972) for *T. basutus basutus*.

In November 2002 four final instar larva of *T. basutus basutus* (Wallengren) were taken from an *Anoplolepis custodiens* ant nest in KwaZulu-Natal and studied in captivity together with *Anoplolepis* ants from a nearby locality (AH, AJMC, S. P. Quek). A larva was often seen to approach two ants engaged in trophallaxis and insert its head between theirs. It proceeded to imbibe regurgitations passed between them and continued to accept regurgitations from the donor ant after the other ant had departed. The larva was occasionally seen to 'pull' on ant eggs and larvae and drag them beneath its carapace; it is assumed these were eaten. The larva also appeared to scavenge for detritus on the nest substrate. Although *T. basutus* appears to utilize four food sources in its larval stage, during the week it was studied (prior to pupation) the major food was obtained by trophallaxis. An earlier study in captivity of *T. basutus* larvae from KwaZulu-Natal with an ant species from Cape Town resulted in the larva feeding on detritus only and then dying after almost four weeks without any trophallaxis having been observed (Heath & Claassens 2000). This would indicate larvae are highly specific to certain *Anoplolepis* ants.

The larva occasionally 'groomed' an ant, the latter remaining motionless while the former may have derived some form of detritus from the process (AH, AJMC unpublished obs.). This grooming behavior was also recorded in the case of *Lepidochrysops* larvae (Polyommatini) and its ant-associate *Camponotus maculatus* Fab. (Formicidae) (Claassens 1976).

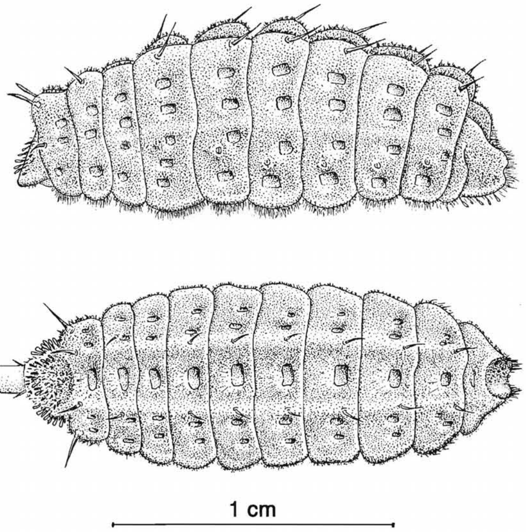

FIG. 22. Final instar larva of *Thestor yildizae*, lateral view (upper), dorsal view with head extended (lower). Scale bar = 1 cm.

The behavior of *T. basutus* differed from the observed behavior of *T. yildizae* and *T. pictus* larvae which solicited regurgitations from individual passing ants. The ant species associated with *Thestor* have so far been recorded as *A. custodiens* but this is currently believed to constitute a species complex. A preliminary molecular study of *A. custodiens* at Harvard University suggests that at least three distinct clades exist (S.P. Quek unpublished).

LYCAENINAE: Some ant-association occurs in all tribes except Lycaenini. Almost all species have a DNO and most have TOs.

Theclini (six genera): The number of larval instars is normally four and the DNO first appears in the second or third instar, the TOs appearing in the second instar except in endophytic feeders, where they are absent in all instars.

Myrina Fabricius, 1807 (five Afrotropical species, two in southern Africa); *Iolaus* Hübner, [1819] (116 Afrotropical species, 21 in southern Africa); *Hypolycaena* Felder, 1862 (extralimital[4]: 28 Afrotropical species, five in southern Africa); *Leptomyrina* Butler, 1898 (nine Afrotropical species, four in southern Africa); *Capys* Hewitson, 1965 (14 Afrotropical species, four in southern Africa); *Deudorix* Hewitson, 1863 (extralimital: 89 Afrotropical species, nine in southern Africa). All six genera are regarded as having a facultative association with ants. Ants (often *Crematogaster* species) may be present but do not attend the larvae permanently, and larvae do not depend on any species of ant for survival. Larvae of the first three genera possess DNO and TOs but those of *Leptomy-*

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[4] Extralimital: Genus also represented outside Africa.

rina, Capys and *Deudorix* are endophytic and lack TOs (Clark & Dickson 1971). *Leptomyrina* larvae feed inside the fleshy leaves of Crassuleaceae (Jackson, 1937). *Capys* larvae feed inside *Protea* flower buds (Proteaceae) (Murray 1935, Clark & Dickson 1971); the hollowed out buds are later often occupied by *Crematogaster* ants (AH pers. obs.). *Deudorix* larvae feed inside pods and immature fruit of a variety of trees (Pinhey 1965, Clark & Dickson 1971).

Aphnaeini (14 genera): All known life histories of the Aphnaeini indicate an obligate ant-association. The number of larval instars is normally six, the DNO first appearing in second or third instars, but TOs occur in all instars.

Chrysoritis Butler, 1898 (42 species, all endemic to southern Africa). A revision and molecular phylogeny of *Chrysoritis* can be found in Heath (2001) and Rand et al. (2000). The genus comprises small to medium-sized robust butterflies, associated with open veld, coastal and montane fynbos[5]. Most *Chrysoritis* are multivoltine, except in montane areas, but *C. dicksoni* (Gabriel) which flies in non-montane localities, is entomophagous and univoltine. With this one exception, *Chrysoritis* are all herbivorous feeding on a wide variety of plants (see Heath 1997a) and can be reared in captivity without ants. They are nevertheless considered obligate, as larvae are continuously attended by ants and oviposition only occurs in the presence of the correct ant species (Heath 1997a). *Crematogaster* ants are the most common associates for *Chrysoritis*, but one species of *Myrmicaria* (Myrmicinae) is known to associate in two species of this genus (Heath 1997a). Excepting *C. dicksoni*, larvae in nature rest in a corral (or byre) beneath the food plant and are tended by three or more ants. Larvae were often found singly or in pairs but as many as five or six of varying sizes could be found together within a corral (Heath 1997a).

In *Chrysoritis* the DNO appears in the second instar, a feature shared only with *Crudaria* Wallengren. The larva's DNO is frequently visited and stimulated by the ant's antennae and the secretion is eagerly taken by the ant. The TOs are active, everted quickly and as quickly withrawn; this happens whenever the larva is disturbed. When ants are over-eager to access honeydew, the larva will evert its TOs causing them to jump in alarm. Among this large and otherwise herbivorous genus, *C. dicksoni* larvae are entomophagous and were observed in the field and laboratory by Heath (1998). The first two instars fed on ant regurgitations but stayed on the plant close to scale insects, also tended by the host ant. The DNO was present in the second instar, but secreted no honeydew, however, when everted it attracted, but stupified nearby ants. When offered a red Homopteran juvenile, the second instar larva ate it and half a second one, but died the following day. The final instar also fed on ant regurgitations living and pupating within the carton nest of the host ant *Crematogaster peringueyi* Emery. It is assumed that the intervening three instars had the same feeding behavior as first and last instars. In areas where *C. dicksoni* flies, armored scale insects (Homoptera) are always nearby and may somehow be necessary for the survival of the larva (Heath 1998). The DNO was still present in the sixth (final) instar, although it was infrequently visited by ants. The final instar also had specialized setae on each segment that frequently attracted the host ant who seemed to nibble at them. These setae appeared as a curved structure resembling a bottle-brush, and are illustrated by Heath (1998). Heath and Brinkman (1997b) inferred that in the wild, females are only stimulated to oviposit by ants attending this unidentified species of scale insect. Colonies of *C. dicksoni* adults occupy small areas, seldom larger than a tennis court, and where females oviposit on a wide variety of plants near the host ant nest.

Aloeides Butler, 1819 (58 Afrotropical species, 53 in southern Africa). A large genus of small to medium-size brown or orange butterflies obligately associated with ants. All species are found in open or grassland habitat. The genus is in need of taxonomic revision, as we believe it contains many taxa of dubious status. Until recently, the only ant genus known to be associated with *Aloeides* larvae was *Lepisiota* (=*Acantholepis*) (Formicinae). However, two additional ant hosts have recently been discovered (Heath & Claassens 2000)—*Monomorium fridae* Forel (Myrmicinae) and *Pheidole capensis* Mayr (Myrmicinae). Larval food plants are species of *Aspalathus* (Fabaceae), *Hermannia* (Sterculiaceae), *Sida* (Malvaceae) (Kroon 1999), and *Gnidia* (Thymelaeaceae) (A. Gardiner pers. com.). *Aloeides* larvae have TOs in all instars but the DNO first appears in the third. In some species, e.g., *A. apicalis* Tite & Dickson, *A. pallida grandis* Tite & Dickson, *A. thyra* (Linnaeus) and *A. dentatis* (Swierstra), the DNO is absent in the final instar (Heath & Claassens 2000, Henning 1983a, b). However, in at least four species, *A. pierus* (Cramer) *A. gowani* Tite & Dickson, *A. trimeni southeyae* Tite & Dickson and *A. aranda* (Wallengren), larvae retain their DNO until pupation (Clark & Dickson 1971, Heath & Claassens 2000).

Early instar larvae of *A. pallida grandis* are assumed to feed on species of *Aspalathus* always found close to where the larvae are found. Heath and Claassens (2000)

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[5] Fynbos: Characteristic treeless shrubland vegetation of the southern and south-western Cape of South Africa.

observed that, in captivity final instar larvae remained inside the nest of *Lepisiota capensis* Mayr for four months, and grew without foraging outside. Despite ample ant brood of all stages present in the nest, the larvae fed only on ant eggs.

Despite the DNO of *A. thyra* being absent in its final instar, it is herbivorous on *Aspalathus* species and rests in an *L. capensis* ant nest (Claassens & Dickson 1977) but it is not known if trophallaxis or ant eggs form a supplementary part of its diet. In contrast, *A. apicalis* and *A. aranda* which associate with *Monomorium* and *Pheidole* ants respectively, were not inside the ant nest but were generally tended by four or five ants in a corral just below the soil surface close to the food plant, often two or three meters from the ant nest (AH, AJMC unpublished). Ovipositing females of *A. molomo coalescens* Tite & Dickson were observed inserting their abdomens deep into the sand beneath a species of *Gnidia* (Thymelaeaceae) (A. Gardiner pers. com.). Eggs of *A. aranda* (Wallengren) were found buried ca. 1 cm in the sand beneath its food plant *Aspalathus* sp. (C. Penz, P. De Vries, AH pers. obs.).

Erikssonia Trimen, 1891 (three Afrotropical species, one in southern Africa). *E. acraeina* Trimen is scarce and local, its larval food plant is *Gnidia kraussiana* Meisner and it has an obligate ant association with *Lepisiota* sp. (Henning 1984a). The final instar have both DNO and TOs. This orange-red butterfly apparently mimics unpalatable species of *Acraea* Fabricius (Nymphalidae). *Erikssonia* is closely related to *Aloeides* and could be synonymized with *Aloeides* based upon genitalia (Heath 1997a), but other small differences occur in the adult (Henning & Henning 2001). Eggs are laid among soil particles beneath the foodplant (Pringle et al. 1994).

Phasis Hübner, 1819 (four species, all endemic to southern Africa). Large brown lycaenids restricted to the southern and south-western Cape; their larval food plants include *Rhus* (Anacardiaceae) and *Melianthus* (Melianthaceae) and they have an obligate ant association with *Crematogaster peringueyi*. The DNO on *Phasis thero* (Linnnaeus) larvae appears on third and subsequent instars (Clark & Dickson 1971) but is absent in the final instar (Heath & Claassens 2000). TOs are present in all instars (Clark & Dickson 1971). Larvae and pupae are found inside hollow stems and although associated with their host ants, interaction has not been studied closely.

Trimenia Tite & Dickson, 1973 (five species, all endemic to southern Africa). Medium-to-large orange and brown butterflies with silvery spots on the ventral surface of all wings. The genitalia are all very similar. They are restricted to arid habitats in the southern and south-western region of South Africa; they are univoltine and all are presumed to be aphytophagous (Heath 1997a). A final instar larva and pupa of *Trimenia malagrida maryae* (Dickson) were found in small fissures about 5 cm deep inside the bedrock tended by *Anoplolepis custodiens* ants (Heath & Brinkman 1995b). In captivity it could not be determined what the larval food was since the larva shunned any light. When disturbed, it was tended by many ants, with a concentration around the head of the larva (AH pers. obs.). There was no vegetation within a meter of the site where the larva was found, but after collection it survived among ants without vegetation for two weeks before pupating, supporting the notion that it is aphytophagous, at least in the final instar. We suspect it was feeding on ant eggs or ant regurgitations. Despite the presence of TOs, the final instar larva had no DNO and was very similar to that of *Trimenia argyroplaga* (Pringle in Pringle et al. 1994). A *T. argyroplaga* larva in its penultimate instar (presumed) had an active DNO, but in the final instar it was absent. The larva was seen to accept ant regurgitations, presumably its sole diet as it did not feed on ant brood or eggs. The larva often sought a dark place between the nest and arena to rest, and sometimes at night, it would go into the arena but the ants would manoever it back to the nest entrance again (Heath & Claassens 2000).

Argyraspodes Tite & Dickson, 1973 (one species, endemic to southern Africa); *Zeritis* De Boisduval, 1836 (extralimital; six Afrotropical species, one in southern Africa). Life histories of these two genera are unknown, although the former is closely related to *Trimenia* and may also be aphytophagous.

Tylopaedia Tite & Dickson, 1973 (one species, endemic to southern Africa). This large, robust lycaenid is orange and black and univoltine. *Tylopaedia sardonyx peringueyi* (Aurivillius) is recorded as using a species of *Aspalathus* for its larval food plant (Schlosz & Brinkman 1991). The same authors observed the ant-associate to be *Crematogaster melanogaster* (Emery) and noted that the female would not oviposit without the presence of ants.

Lipaphnaeus Aurivillius, 1916 (four Afrotropical species, one in southern Africa); *Chloroselas* Butler, 1885 (=*Desmolycaena*, Trimen) (13 Afrotropical species, three in southern Africa); *Crudaria* Wallengren, 1875 (three Afrotropical species, all in southern Africa); *Aphnaeus* Hübner, 1819 (20 Afrotropical species, three in southern Africa); *Axiocerses* Hübner, 1819 (25 Afrotropical species, five in southern Africa); *Cigaritis* Donzel, 1847 (=*Spindasis* Wallengren; *Apharitis* Riley) (extralimital; 37 Afrotropical species, ten in southern Africa). The life history of these six genera have not been studied in recent years. Their larvae all possess DNO and TOs (Clark & Dickson 1971, Edge 1990), and are all believed to be herbivorous and obligately ant-associated, excepting *Axiocerses*, which are facultative. TOs occur in all instars, the DNO first appears in the third instar, excepting *Crudaria* where it appears in the second. Clark and Dickson (1971) described additional saucer-like glands referred to as "dewpatches" on the dorsum of the A2–A4 segments of *Cigaritis* and *Crudaria* final instar larvae. These glands secrete a fluid the ants consume. These six genera are mostly associated with *Crematogaster* ants, except for *Crudaria* which associate with *Anoplolepis custodiens* (Heath 1997a). Larvae and pupae of *Crudaria wykehami* Dickson taken from an ant nest beneath a large flat stone were heavily parasitized (ca. 80%) by wasps and a tachinid fly (AH unpublished obs.)

Lycaenini (one genus): *Lycaena* Fabricius, 1807 (extralimital; three Afrotropical species, two in southern Africa). Small coppery-red butterflies. Larvae naked, lacking DNO and TOs, and not ant-associated.

Polyommatini (25 genera): Normally having four larval instars, the DNO appears in the second or third instar, the presence of TOs variable.

Euchrysops Butler, 1900 (five in southern Africa). Medium-sized blue or brown lycaenids. The phytophagous larvae possess DNO and TOs, the former appearing in the second instar, the latter in the third and have a facultative ant-association (Clark & Dickson 1971). The genitalia are of the same type as *Lepidochrysops* from which *Euchrysops* are not easily separated on morphological grounds (see Gardiner 1998).

Lepidochrysops Hedicke, 1923 (127 Afrotropical species, 59 in southern Africa). Medium to large, blue or brown with spotted undersides frequenting open and sparsely wooded grassland. Morphologically similar to *Euchrysops* with remarkably uniform genitalia. All are assumed to be phytopredacious (herbivorous in early instars, later becoming predacious on other insects), associated with *Camponotus* ants, and in many respects, similar in appearance and behavior to the palaearctic *Maculinea* (see Frohawk 1916, Elmes et al. 1991, Thomas 1983, 1995). The larva feeds on flower buds for the first two instars, then it is carried by a species of *Camponotus* ant to its brood chamber in the third instar where it is predacious on ant brood. Despite the large size of this genus, few life histories have been studied in any depth. Our current knowledge is based upon the life history of eleven species by Clark and Dickson (1971), Claassens (1972, 1974, 1976), Henning (1983a, b) and Williams (1990), some being incomplete. However, Claassens (1972, 1974, 1976) studied the interaction between larvae and ants in the laboratory, and observed that larvae of *L. trimeni* (Bethune-Baker) and *L. methymna* (Trimen) did not possess TOs at any stage, but the DNO appeared in the second instar and remained until pupation. Claassens also observed that trophallaxis supplemented the diet of ant brood, also that the larva sometimes groomed an ant. Henning (1983b) studied *L. ignota* (Trimen & Bowker), and made similar feeding observations. Henning (1983b) demonstrated that larvae of *L. ignota* and *Aloeides dentatis* chemically mimic the brood of their attending ants *Camponotus niveosetosus* and *Lepisiota capensis*. Corn grits were soaked in epidermal extracts of ant brood or larvae and then offered to the appropriate species of ant. Treated grits were carried by ants to their brood chamber, untreated grits were ignored. Gas chromatograms of epidermal extracts confirmed that chemicals found on the larva were similar to those on the ant brood. In captivity, a fourth instar larva of *L. p. plebeia* (Butler) was observed feeding on ant eggs as soon as they were laid, when ant brood supply was exhausted (Williams 1990).

Orachrysops Vári, 1986 (11 species, all endemic to southern Africa). Formerly included in *Lepidochrysops*, these medium-sized dull blue and gray lycaenids are superficially similar to *Lepidochrysops*, but their genitalia differ. Little is known about ant-association in their early stages. Formerly thought to be phytopredacious, as in *Lepidochrysops* (Henning & Henning 1994) but recent work suggests otherwise (Edge & Pringle 1996). The larvae of *O. niobe* (Trimen) feed on *Indigofera* (Fabaceae), and in captivity, were bred to adult without ant presence. However it is unknown if ant-association is obligate or facultative under natural conditions and whether other sources supplement its diet. The DNO and TOs appear in the second and subsequent instars, the TOs are not well developed. The ant suspected of being an associate is *Camponotus niveosetosus* (Mayr) (Edge & Pringle 1996), recorded among the roots of the food plant where the larvae shelter. Recently, Lu and Samways (2001) showed that *O. ariadne* (Butler) has an obligate ant-association. Larvae were found in soil beneath the foodplant at depths up to 10 cm, always attended by *C. natalensis* (Smith).

Anthene Doubleday (25 species in southern Africa), *Zintha* Eliot (one species in southern Africa), *Tuxentius* Larsen (three species in southern Africa), *Leptotes* Scudder (five species in southern Africa), *Lampides* Hübner (one species in southern Africa), *Tarucus* Moore (three species in southern Africa), *Harpendyreus* Heron (three species in southern Africa), *Pseudonacaduba* Stempffer (one species in southern Africa), *Eicochrysops* Bethune-

Baker (three species in southern Africa), *Cupidopsis* Karsch (two species in southern Africa), *Thermoniphas* Karsch (one species in southern Africa), *Oboronia* Karsch (one species in southern Africa), *Actizera* Chapman (two species in southern Africa), *Zizeeria* Chapman (one species in southern Africa), *Zizina* Chapman (one species in southern Africa), *Brephidium* Scudder (one species in southern Africa), *Oraidium* Bethune-Baker (one species endemic to southern Africa), *Azanus* Moore (five species in southern Africa), *Chilades* Moore (one species in southern Africa), *Zizula* Chapman (one species in southern Africa). All 20 of these genera (71 species) are facultatively ant-associated, most having DNO and TOs but often without attendant ants (see Clark & Dickson 1971).

Uranothauma Butler (four species in southern Africa), *Cacyreus* Butler (five species in southern Africa). Not ant-associated, TOs and DNO are absent, except for two species of *Cacyreus* which have a DNO.

Vibrational communication. Using a cardboard poster tube with a paper membrane at one end, final instars of *Chrysoritis thysbe* (Linnaeus), *C. dicksoni*, *Aloeides pierus* and *A. pallida grandis* were heard to produce ticking or drumming sounds, but *C. thysbe* also made an intermittent high-pitched buzzing sound (Heath 1998). Sounds have also been noted in the pupae of *Chrysoritis brooksi* Riley and *P. irene* Pennington (Schlosz 1991). These sounds likely play an additional role in communication with ants (De Vries 1990, 1991).

Ant-associations and feeding strategies. More than three quarters of the 392 southern African lycaenids are ant-associated, over two thirds of these have obligate relationships. The Poritiinae constituting 8% of lycaenids (30 species) have no direct ant-association[6] and the Miletinae (36 species) representing 9%, three quarters of which are obligately ant-associated although the remainder feed in the presence of ants. The subfamily Lycaeninae (326 species) accounts for 83% of species, of which the Aphnaeini (131 species) contains a third of all southern African lycaenids, almost all being obligate. Theclini (47 species) and Polyommatini (146 species) account for 12% and 37% respectively; the former being facultative, and latter split between facultative and obligate. The Lycaenini has only two species, neither ant-associated.

TABLE 3. Lycaenids obligately associated with ant genera.

		Number of obligately ant-associated lycaenids (%)	
	Ant genus	Confirmed only	Confirmed and predicted
Myrmicinae			
	Pheidole	1 (1)	1 (0.5)
	Monomorium	1 (1)	1 (0.5)
	Crematogaster	51 (61)	62 (28)
	Myrmicaria	2 (2)	2 (1)
Formicinae			
	Anoplolepis	13 (15)	37 (17)
	Lepisiota	7 (9)	7 (3)
	Camponotus	7 (9)	60 (28)
Unidentified		2 (2)	47 (22)
Totals		84	217

It can be seen from Table 1 that algae or lichen feeders are unique to the two tribes of Poritiinae. The Miletinae feed mostly on Homoptera but also on homopteran secretions, ant regurgitations and possibly detritus and ant early stages at times. Among the Lycaeninae, almost all the entomophagous records are from the Polyommatiti, with only two confirmed cases from the Afrotropical Aphnaeini, although there may well be more still undiscovered[7].

Symbiont ant genera. The two main ant genera confirmed in obligate association with lycaenids are *Crematogaster* (Myrmicinae) and *Anoploplepis* (Formicinae), together 76%, whereas *Camponotus* and *Lepisiota* (Formicinae), represent 9% each (Table 3). Three accounts of ant distribution (Samways 1983, Donnelly & Giliomee 1985, H. Robertson pers. com.) indicate the two dominant ant genera in Southern Africa are *Pheidole* (Myrmicinae) and *Anoplolepis*, the latter more so in open habitats. *Crematogaster* species are also numerous in denser vegetation while *Lepisiota* and *Camponotus* although not always numerous, are to be found in most habitat types in southern Africa (H. Robertson pers. com.). Despite the comparative dominance of *Pheidole* ants, only one species has been identified as an obligate symbiont (to a widespread species of *Aloeides*).

DISCUSSION

Reliability of data. Considerable disparity exists in the Polyommatini between confirmed and predicted ant-association (Table 2) mainly because *Lepidochrysops* (Polyommatiti) life histories are widely believed to be uniform, but few have been confirmed.

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[6] In *Deloneura* and certain other Liptenini further north in Africa e.g., *Epitola*, larvae are found in the company of ants but no interaction has been observed. It is possible that ant-derived detritus supplements the algae on which the larvae feed, or it may enrich the algae, making it more attractive, but these hypotheses have yet to be confirmed.

[7] Cottrell (1984), Elmes et al. (2001) list *Cigaritis takanonis* Matsumura from Japan as accepting ant regurgitations. Jackson (1937) infers insect feces as additional food for *Chloroselas pseudozeritis* (Trimen). Fiedler (1991) infers possible ant regurgitations for several Aphnaeini.

Obligately ant-associated Afrotropical lycaenid species show little morphological differences among closely related species (Heath 1997b), and recently Heath (2001) synonymized many *Chrysoritis* taxa, reducing the species by 28%, inferring that similar synonymies probably exist in *Aloeides,* and we believe this is the case for *Lepidochrysops*. We suspect that southern Africa has an oversplit taxonomy among the ant-associated lycaenids, particularly those with an obligate relationship.

Changes in feeding strategy. Although most lepidopterous larvae are herbivores, some lycaenid species are known to switch from one trophic strategy to another midway through their larval phase; e.g., the *Maculinea* (Thomas 1983, 1995). In southern Africa this occurs in *Lepidochrysops, Thestor,* and at least one *Aloeides* species (Cottrell 1984, Heath & Claassens 2000). More than one food source can also be exploited at the same time e.g., trophallaxis and carnivory in *Cigaritis* (Sanetra & Fiedler 1996), and in some *Maculinea* (Thomas & Wardlaw 1992), and in *Lepidochrysops* (Claassens 1976, Henning 1983) and *Thestor* (AH, AJMC) in southern Africa.

Dorsal nectary organ and tentacle organs. The DNO and TOs are completely absent in the Poritiinae and Miletinae except in *Aslauga* (Liphyrini) but one or both are usually present among the Lycaeninae. In some Aphnaeini (*Phasis*, some *Aloeides*) the DNO is present in earlier instars but absent in the final instar. Second instar *Chrysoritis dicksoni* had a DNO that did not secrete honeydew but rather it gave off a pheromone, causing the ants to remain close and stupified (Heath & Brinkmann 1995a). Although the TOs are absent in all instars of *Lepidochrysops*, the DNO appears in the second instar (Clark & Dickson 1971) and is retained until pupation, as in Palaearctic *Maculinea*. Fiedler (1998) suggested DNO secretions supplement the adoption procedure. However, Henning's (1983b) experiments using corn cob grits do not support this for *Lepidochrysops*.

Fiedler (1998) attributed the lack of TOs in *Maculinea* to the endophytic life-habit of the early larval instars rather than its life-habit within the ant nest, but in Afrotropical Polyommatini (including *Euchrysops*) the TOs generally appear in the third or fourth instar (Clark & Dickson 1971). *Lepidochrysops* larvae cease to be herbivorous after the second instar, and hence the TOs would not have been present during any early instar. An alternative hypothesis for *Lepidochrysops* is that within the nest, the TOs became redundant as a means of recruiting ants and may also have been a hinderance within the confined space.

ACKNOWLEDGMENTS

We thank Adrian Armstrong and the Natal Parks Board (South Africa) and the Chief Executive Officer of the Western Cape Nature Conservation Board for permission to study and collect material in areas under their control. Hamish Robertson, South African Museum, Cape Town is acknowledged for identifying ant species provided by the authors and for giving related input on this paper. Ivan Bampton and Colin Congdon are acknowledged for some recent life history data. Simon Joubert and Swee Peck Quek are thanked for helping to locate the *T. basutus* larvae and ant associates in KwaZulu-Natal. Phil DeVries is especially thanked for his many helpful comments on the manuscript.

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Received for publication 4 February 2002; revised and accepted 5 August 2002.