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A REVIEW OF AFRICAN GENERA OF THE TRIBE
APHNAEINI (LEPIDOPTERA: LYCAENIDAE)

By ALAN HEATH
Editorial
This, the second issue of the irregular series *Metamorphosis Occasional Supplement*, comprises the long awaited comprehensive revision of the African genera belonging to the tribe Aphnaeini by Alan Heath. The author is a well-known council member of The Lepidopterists' Society of Africa as well as a fellow of The Royal Entomological Society. He spend many years studying the butterflies of Zambia and Zimbabwe. He later moved to Cape Town, South Africa, where he concentrated his studies on the lycaenids, in particular the theclinines, a discipline he now pursues full time.
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Hermann Staude

Cover
Front: *Axiocerses amanga* (Photo: J. Joannou)
Back: *Spindasis ella* (Photo: J. Joannou)
A REVIEW OF AFRICAN GENERA OF THE TRIBE APHNAEINI  
(LEPIDOPTERA: LYCAENIDAE) 

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ABSTRACT: The following genera are synonymised: *Argyrocupha* Tite & Dickson, 1973 and *Trimenia* Tite & Dickson, 1973; *Desmolycaena* Trimen, 1898 and *Chloroselas* Butler, 1866; *Apharitis* Riley, 1925 and *Spindasis* Wallengren, 1857. *Desmolycaena rogersi* Riley, 1932 is assigned to a new genus, *Vansomerenia* gen. n. and *Spindasis waggae* Sharpe, 1898 is assigned to a new genus, *Jacksonia* gen. n. The genera *Poecilmitis* Butler, 1899, *Bowkeria* Quickelberge, 1972 and *Oxychaeta* Tite & Dickson, 1973 are all treated as synonyms of *Chrysoritis* Butler, 1898. *Chrysoritis williami* nom. n. replaces the junior homonym *Poecilmitis dicksoni* W. H. Henning, 1977. Morphological information of all Aphnaeini genera is given, including illustrations of male genitalia. Information is given on larval host-plants and associated ants, including many which were previously unpublished.

Key Words: Lepidoptera, Lycaenidae, Lycaeninae, Theclinae, Aphnaeini, *Chrysoritis*, systematic revision, taxonomic arrangement, life histories, host-plants, myrmecophily, genitalia, Afrotropical region.
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INTRODUCTION

The naturalists of the nineteenth century and shortly thereafter classified taxa without the techniques, equipment and information now available to us, such as genitalia dissection, macrophotography, scanning electron microscopy, DNA and chromosome analysis, etc. Similarly, we now have the advantage of accessing considerably more material and biological information on which to base our classifications. In the past, the erection of genus and species names was based upon the scant knowledge then available to those pioneers of natural history; unavoidably, some of their work is now seen to be erroneous. In the past few decades, however, a further flood of taxonomic work has emerged; some of this has also been based upon superficial characters, without the support of any detailed morphological studies. It is to address the former anomalies applicable to the tribe Aphnaeini Distant, 1884 that this contribution is aimed, but its purpose is also to draw attention to the latter in principle and to seek a way to eliminate unnecessary names.

This paper redefines, discusses and illustrates the characteristics of all genera of the tribe Aphnaeini, emphasising the similarities and differences which are apparent between them and that these suggest some natural groupings, as reflected in a new arrangement of genera. Apart from regrouping the genera, no phylogenetic analysis is attempted. However, this new arrangement may serve as a reference point for the cytogenetic studies currently being carried out by Professor Naomi Pierce at Harvard University and as a preliminary scheme for subsequent studies on the phylogeny of this group. Special focus is placed upon the species included in the genera *Chrysoritis* Butler, *Poecilmitis* Butler, *Bowkeria* Quickelberge and *Oxychaeta* Tite & Dickson; these genera are referred to as the *Chrysoritis* complex.

The definition and composition of the Aphnaeini has been controversial. Distant (1884) proposed a grouping of 21 lycaenid genera based upon venational characters under the collective name Aphnaria; genera from different parts of the world were included, among them the African genera *Spindasis*, *Hypolycaena* and *Deudorix*. Distant's grouping remained unchanged until Stempffer's (1967) massive work *The Genera of African Lycaenidae*, which proposed a subfamily Aphnaeinae, distinct from the Theclinae, for the following genera: *Aphnaeus* Hübner, 1819; *Paraphnaeus* Thierry-Mieg, 1904; *Apharitis* Riley, 1925; *Cigaritis* Denzel, 1847; *Spindasis* Wallengren, 1857; *Lipaphnaeus* Aurivillianus, 1916; *Chloroselas* Butler, 1866; *Zeritis* Boisduval, 1836; *Desmolycaena* Trimen, 1898; *Axioerces* Hübner, 1819; *Phasis* Hübner, 1819; *Aloeides* Hübner, 1819; *Poecilmitis* Butler, 1899; *Chrysoritis* Butler, 1898; *Crudaria* Wallengren, 1875; *Erikssonia* Trimen, 1891, *Pseudaletis* Druce, 1888. Eliot (1973) relegated Stempffer's Aphnaeinae to tribal level within Theclinae, containing all the genera listed by Stempffer (1967). Scott (1985) regarded Theclini as a tribe, separate from Aphnaeini, placing both in subfamily Lycaeninae. This arrangement was retained during subsequent classification changes by Scott & Wright (1990), Eliot (1990), Fiedler (1991) and Eliot in (Corbet et al., 1992) and is followed here, however, Ackery *et al.* (1995) chose to retain Eliot's (1973) classification.

A further genus *Bowkeria* in this group was erected by Quickelberge
(1972) for *Zeritis phosphor* Trimen, in distinction from *Poecilimitis*. Tite & Dickson (1973) reviewed *Aloeides* and the various species attributed at that stage to *Phasis*. From their studies, five new genera, previously included under *Phasis*, were described: *Tylopaedia*, *Oxychaeta*, *Argyraspodes*, *Trimenia* and *Argyrocupha*. GA Henning, (1993) presented a tentative phylogeny of *Aloeides*, and Henning & Henning (1996) reviewed *Axiocerses*, adding nine new species and three subspecies.

The early stages of several aphnaeine species, including their biology and host-plants, were described and figured by Clark & Dickson (1971). Biological studies, mainly on life histories, were carried out by Henning & Henning (1984) and Henning (1985) on *Erikssonia acraeina* Trimen. Henning (1983) described the life histories of several myrmecophilous lycaenids. Schlosz & Brinkman (1991) described the life history of *Tylopaedia sardonyx peringueyi* (Aurivillius), and Schlosz (1996) listed the host-plant of the nominate race of *T. sardonyx* (Trimen).

In his work on myrmecophily within the Lycaenidae, Fiedler (1991) listed hostplants and ant associations among the Aphnaeini. Pringle et al. (1994) listed hostplants and life history information on many of the aphnaeine genera. The life histories of all known predatory and parasitic lycaenid larvae were summarised by Pierce (1995). Heath & Brinkman (1995a,b) discussed the life history of *Oxychaeta*, *Trimenia* and *Argyrocupha* species. During the past eight years the life histories of many of the western Cape species of *Poecilimitis* and *Chrysoritis* have been studied, the results of which have not previously been published. Ivan Bampton and Steve Collins, both from Nairobi, listed (pers. comm.) many new host-plants and ant associations of Aphnaeini; with their kind permission these are incorporated into this document.

**MATERIAL AND METHODS**

Almost 100 species of Aphnaeini were studied, including the type species of all genera as currently listed in this tribe. The morphological investigation covered wing pattern, genitalia, venation, legs, palpi and the female abdominal hair tufts. In most cases, three or more dissections were made of the genitalia of each species to ensure reliability and to make provision for individual variation. Photographic slides were taken of the dissected genitalia on which the drawings (figs. 9-177) were based. Each of the components are figured separately to facilitate comparison between related genera, however the figures are not necessarily drawn to the same scale. In most cases, a dorsal and a lateral view of the whole armature is given, the former showing the aedeagus tip to the same scale. A lateral view of the aedeagus is shown and the uncus is depicted in a flattened state. For comparisons within genera, certain components such as the valves, juxta and saccus are sometimes also figured in a flattened state; in such cases this is clearly indicated. The aedeagus was examined of all type species of Aphnaeini and of all species within the *Chrysoritis* complex, to determine the presence of cornuti and their type. Of the 43 *Chrysoritis* species with cornuti attached to the vesica, six were further dissected and scanning electron microscope photographs prepared; these are depicted in Plate 4. Details of the early stages, where these are known, have been listed and taken into account; this includes ant
association and larval food. Westwood (1857) and Trimen (1887) referred to the presence of a spur at the lower extremity of tibiae in some lycaenids. Tite & Dickson (1973) also mentioned such a process in their generic key, however the structure they refer to does not appear to be what is currently understood as a tibial spur (Scoble, 1995). Eliot (1973) referred to this as a short chitinous projection. It is here called a **spicule** and defined as a minute, pointed, chitinous process, integral to and at the distal end of the tibia. Both the spicule and the spur are well developed in *Aloeides pierus* Hübner, as illustrated in figs 1-3.

In the descriptions, the terms of certain characters are abbreviated as follows f/w - forewing; h/w- hindwing. The following terms used by Cottrell (1984: 29-34) have been adopted here: ONO - dorsal nectary organ (also referred to as a honey gland or Newcomer's gland) located on the dorsum of the seventh abdominal segment; TOs - a pair of eversible tentacle organs or tubercles, located on the dorsum of the eighth abdominal segment; PCOs - perforated cupola organs or lenticles, which are minute epidermal glands present on both larvae and pupae and capable of secreting substances which may be attractive to certain ant species; DOs - dish organs or dew patches, which are circular depressions on certain segments of larvae which secrete a fluid attractive to ants. These DOs are currently known only from the later instars of *Spindasis* and *Crudaria* (Clark & Dickson, 1971; Cottrell, 1984).

Some characteristics of Aphnaeini taxa are listed in Table 1, as follows number of species; type of spicule on male tibiae; presence of a tuft of specialised scales at the distal end of the female abdomen; number of veins on f/w and, where variability exists, the alternative is shown in parenthesis; presence of cornuti on vesica of male genitalia. The male foretarsal claw is depicted of *Aloeides pierus* Hübner (fig. 4a), *Spindasis natalensis* Westwood (fig. 4b), *Aphnaeus* areas Drury (fig. 4c) and *Pseudaletis agrippina* Druce (fig. 4d).

In the account of the life histories, the host-plants were identified by Jan Vlok, Cape Nature Conservation, and the ants were identified by Dr. H.G. Robertson, South African Museum, Cape Town. Some of this ant material has been accessioned in the South African Museum collection under accession numbers such as SAM-HYM-C006744. To record these life histories, an adult female was usually induced to oviposit by introducing up to three associated ants to a small container (140 x 90 x 60mm), in which the female and small pieces of the hostplant had been placed. A piece of nylon gauze covered one side of the container to provide ventilation and light and to permit observation. When the eggs hatched, the young larvae were placed on a potted host-plant covered in nylon gauze to exclude predation by spiders and were bred through to adults on the potted hostplant, usually without the presence of ants. Where possible, larvae were also observed in their natural environment and the host-plant and attending ants identified. In most cases, photographic slides were taken of eggs and larvae.
TAXONOMIC CHARACTERS

Study of the structures outlined above, yielded the following results.

Genitalia

The *Chrysoritis* complex is identifiable as a group by a specific type of genitalia (figs 19-31, 62-73, 103-106, 135-138, 170-177) that also exhibits small differences between the species, except for the group hitherto known as the "thysbe group". In this group, no significant differences between the constituent species are detectable under normal magnification (x40), and even the S.E.M. photographs of the cornuti show that *C. thysbe* (Linnaeus), *C. nigricans* (Aurivillius), *C. zonarius* (Riley) and *C. felthami* (Trimen) all have cornuti of a similar type. The profile of juxta apices in *Chrysoritis* was found to vary considerably, being pointed (fig. 174), rounded (fig. 171), partly truncated (fig. 170) or truncated (fig. 175); such variation was often observed within species. The juxta was observed to be the most variable genital component in Aphnaeini genera and unsuitable as a generic character. The genitalia of the male (figs 50, 91, 123, 164) and female of both subspecies of *Tylopaedia sardonyx* (Trimen) do not show any constant structural differences that would suggest a specific distinction between these two taxa. The genitalia of all four species of *Phasis* show only small differences in their juxta, saccus and valve apex (figs. 166-169).

The genitalia of *Jacksonia waggae* (Sharpe) are not typical of *Spindasis*, in which genus it had originally been placed, but much closer to *Crudaria*. The ground colour of *J. waggae* on both the upperside and underside of the wings is also similar to *Crudaria* species.

Specialised scales

The female of *J waggae* possesses a thick tuft of scales at the end of the abdomen, similar to those present in *Pseudaletis, Lipaphnaeus, Chloroselas, Crudaria* and *Trimenia* (Table 1). This character is not evident in any of the *Spindasis* species.

Spicule

The foretibial spicule exists in some genera such as *Aloeides* but is absent in others, e.g. *Aphnaeus*. Where it occurs, it varies between species from a very small pointed peak to a long sharp structure; the fore-, mid- and hind-legs usually possess different sized spicules but their size and arrangement, although sometimes variable within genera, are constant at species level. The different types of spicule (labelled a-f) are illustrated in fig. 5, and the presence and type of this structure is mentioned under each genus; a formula is given to indicate the arrangement of spicule type on fore-, mid- and hind-leg, e.g. d-d-f.

Labial palpi

The scales covering the palpi are extremely variable in width, some being very slender as in *Phasis* but others less so, but often this is a matter of degree only and in some cases the palpi possess scales of different widths mixed together. The scales are all ribbon-like in structure, including those on *C dicksoni* (Gabriel) which are exceptionally narrow and pointed.
BIOLOGY

Ant associations

The available knowledge of the ant association and host-plant of species within the Chrysoritis complex is summarised in Table 4. The species of ant encountered are Crematogaster peringueyi Emery, C. liengmei Forel, C. melanogaster Emery and Myrmicaria nigra Mayr. Small but constant differences are evident between samples collected, especially of C. peringueyi and C. liengmei; some of these possibly represent new species, however it requires an extensive revision of the whole genus Crematogaster to determine their true identity and status (Robertson, pers. comm.).

In investigating the early stages of the Chrysoritis complex, it became evident that in many cases the only satisfactory stimulant for oviposition by the female is the presence of the correct ant species. In captivity, the presence of host-plant alone seldom stimulated the female to oviposit, whereas females were usually prepared to oviposit on almost any surface when the correct ant species was present. A similar situation exists in some of the Aloeides species (Henning, 1983). In the Chrysoritis complex, no females could be stimulated to oviposit by more than one species of ant. In some instances seemingly conspecific ants had very different stimulatory effects upon the female butterflies, noted also by Heath & Brinkman (1995a: 121). The presence of ants was found to be unnecessary for survival of larvae when rearing Chrysoritis species in captivity, providing parasites and predators were excluded; secretions from the ONO did not cause mould to develop, however, mould was observed on the ONO on some larvae taken from the wild and subsequently kept without ants. The reared larvae rested on a leaf or stem during the first two instars but later instars preferred more sheltered places in crevices on the plant or in leaf litter beneath the host-plant and generally fed after sunset, after which they returned directly to their resting place, without any searching behaviour. In this study, larvae found in their natural environment were always attended by two or more ants, and in the only instance where first instar larvae were found in the field, those of C. lycenes (Trimen), ants were in constant attendance. Larvae were found on the host-plant, in leaf litter beneath the host-plant or in a type of kraal or nursery at the base of the host-plant. In the latter cases, up to six larvae in various stages of development were attended by a sub-colony of ants and afforded protection by fibrous shelters constructed by the ants. The larvae partially lined their resting places with silken fibres. Only very rarely were larvae found under stones and never inside an ant's nest, i.e. with queen and brood, except for C. dicksoni. Of the Chrysoritis species bred in captivity from egg to adult without the presence of ants, the first to pupate provided the largest adults, although seldom as large as any captured in the field. The predominant colours of the later-instar larvae were green and/or brown but this was highly variable, even between larvae from the same parent, and colour inter-grades were common. Although not yet confirmed statistically, it appears that the sex ratio of bred adults is biased towards females, possibly as much as a 3:2 ratio.
Host plants
Very occasionally the presence of Thesium plants (Santalaceae) alone acted as a stimulatory cue for females to oviposit. This was particularly evident in Chrysoritis brooksi brooksi (Riley) at Mamre near Cape Town, where two females were observed ovipositing exclusively on short, dead and dry stems of Thesium plants growing in the grass, close to bushes of Aspalathus spinosa L. (Fabaceae), the roots of both of which are parasitised by Thesium. A larva of C. brooksi was later found on one of these Thesium plants and reared through to adult. There were many small Crematogaster peringueyi ant shelters on the stems of the A. spinosa bushes similar to those described by Dickson (1959), however no early stages of C. brooksi were found within these shelters, despite an extensive search. In captivity, with three C. peringueyi ants present, the same females refused to oviposit on Aspalathus but did so readily on Thesium. Also, the resulting first instar larvae refused to feed on Aspalathus but did so readily on Thesium. These experiments were repeated once with the same results.

Subsequent to this first observation, Thesium was found to be widely used among the Chrysoritis complex of butterflies as a larval host-plant (see Table 4). The smaller Thesium plants become very inconspicuous where vegetation is dense and are, as a result, easily overlooked. Often several species of Thesium occur in each habitat where this plant is utilised as food, and the butterflies do not appear to be specific to only one species of this plant. A wide variety of alternative host-plants were acceptable to larvae of the Chrysoritis complex in captivity, but the growth rate varied according to the plant used. Larvae feeding on Chrysanthemoides incana (Burm. f.) Nori. (Asteraceae) took 8 to 11 months to develop but only 3 to 8 months when feeding on Thesium. The most problematic predators experienced whilst rearing larvae in captivity were spiders.

Biological species limits
Some of the taxa bred and studied lack sufficient differences from each other to justify separate specific status. For example, the behaviour, associated ant, hostplant, eggs, larvae, pupae, adult wing venation and genitalia of Chrysoritis coetzeri Dickson are identical to those of Chrysoritis zonarius (Riley), and no other specific characteristics could be found to distinguish these two taxa. A similar case exists between C. kaplani (Henning) and C. stepheni (Dickson) and many more similar affinities are evident between other species in the Chrysoritis complex. In contrast to these cases, examples exist of similar genitalia, eggs, larvae, pupae and host-plants, yet with mutually exclusive ant associations, as in C. bamptoni (Dickson), C. perseus (Henning) and C. williami, three sympatric species in Namaqualand whose respective females refused to oviposit in the presence of any of the others' host ant species.

Specialised scales
The existence of a dense tuft of specialised scales at the distal end of the female abdomen has been noted in certain genera among the Hesperiidae and Lycaenidae (Evans, 1937; Eliot, 1973). After ovipositing, a female will repeatedly press the tip of its abdomen against a freshly laid egg leaving
ribbon-like scales adhering to the egg. This has been observed in *Trimenia malagrida* (Wallengren), *Crudaria leroma* (Wallengren) and the hesperiid *Tagiades flesus* (Fabricius) (Heath unpubl.). Newly emerged larvae of *Cupidesthes* sp. have been observed to feed upon these scales (Bampton & Collins, pers. comm.).

**SYSTEMATICS**

**Characteristics of Aphnaeini**

Stempffer (1954, 1967) characterised the Aphnaeini (treated as a subfamily) by the feature of the sheathing of the aedeagus by the valves. He noted the existence of a median, fragile and translucent connecting band joining the upper surfaces of the valves above the aedeagus. Eliot (1973) confirmed this characteristic. The present study has also shown this band to always be present, sometimes entirely sclerotized but sometimes reduced to a translucent membrane.

Other characteristics of the tribe are: eyes naked (except some *Aphnaeus*); palpi variable; thorax robust; f/w with 10, 11 or 12 veins; h/w often produced or with a tail at 1A+2A and sometimes at CuA₂; some metallic, silvery or nacreous markings on the wing undersides (except the *Pseudaletis* section, where the whitish markings lack metallic reflection); in some genera females have a tuft of specialised scales at the distal end of their abdomen; in many genera, e.g. *Aloeides*, *Trimenia*, *Chrysoritis*, *Chloroselas* the males when at rest, rub their h/w together (Heath, unpubl.), also noted in *Axiocerses* and *Spindasis* (Migdoll, 1988); male genitalia symmetrical except in *Zeritis*; aedeagus asymmetrical in some genera, juxta often kite- or shield-shaped but very variable within a genus; male fore-tarsus fused into a single tapered segment that is curved and sharply pointed distally (figs. 1 & 4) but rounded in *Aphnaeus* (fig. 4c); tibiae sometimes with a spicule but no secondary sexual characteristics in the males; always some form of symbiotic relationship with ants during the early stages, in most cases these myrmecophilous relationships obligatory and specific (Fiedler, 1991) and *Crematogaster* is the dominant ant genus involved (see Table 2 for exceptions); larvae longish, of fairly uniform width, the last two segments somewhat flattened, head capsule not fully retractable; TOs present in all instars housed in short raised cylinders and equipped with protective spines (Eliot in Corbet et al, 1992); DNO present after the first or second instar (apparently absent in the later instars of *Trimenia* and some *Aloeides*); DOs recorded in two genera; pupae not usually girdled but secured by cremaster in some form of shelter.

Larvae are predominantly phytophagous, subsisting on a wide variety of plants included in the following 21 families: Loranthaceae, Santalaceae, Olacaceae, Crassulaceae, Bruniaceae, Fabaceae, Zygophyllaceae, Euphorbiaceae, Anacardiaceae, Sapindaceae, Melianthaceae, Rhamnaceae, Malvaceae, Sterculiaceae, Thymelaeaceae, Myrsinaceae, Ebenaceae, Oleaceae, Verbenaceae, Rubiaceae and Asteraceae (see Table 3). Some species have been recorded accepting ant regurgitations, whilst a few are believed to be completely aphytophagous (Cottrell, 1984).

The Aphnaeini species are basically confined to the Ethiopian region, with only a dozen *Spindasis* species occurring in the Oriental region and a further dozen (*Apharitis* and *Cigaritis*) occurring in desert regions ranging from
North Africa to Central Asia (Fiedler, 1991). The remaining 233 species are almost exclusively confined to the Afro-tropical region. This constitutes a significant component (16%) of the African lycaenid fauna (Fiedler, 1991).

A new arrangement is proposed here for the tribe Aphnaeini based upon the structure of genitalia and other characteristics.

**Generic Characteristics**

Based upon detailed examination of over 500 Aphnaeini, the male genitalic structure is a very constant characteristic with very few unstable features. The following discussion is based on the principle that genitalic features should serve as the primary basis for separating species and that other characteristics must be considered supplementary, as the latter tend to be much more adaptive to the environment of the species and will consequently evolve faster and more erratically than internal genital characters, which form part of a complex reproduction regime helping to maintain the identity of the species.

Wing venation within the tribe Aphnaeini is rather unreliable. Tite & Dickson (1973) considered the venation to be a constant characteristic and of generic value, as did Trimen (1898) and others. While it can at most be a good indicator, it is not a reliable feature unless the characteristics selected are significant enough and that sufficient examples are studied to assess variability and to ensure uniformity of characters. Stempffer (1967: 113) noted that the h/w venation of *Pseudaletis* was not entirely uniform throughout the genus, veins CuA₁ and M₂ being sometimes stalked and the origin of vein R₅ varied. Stempffer (1967: 160) also demonstrated that *Lipaphnaeus* sometimes has 12 and sometimes 11 veins in the f/w, vein R₄ sometimes being absent, and that *Chloroselas* has 10 or 11 veins, vein R₁ sometimes being absent, veins M₁ and R₅ sometimes stalked, individual variations of a similar kind are not infrequent. He observed similar venational variations in *Desmolycaena* and *Chrysoritis*, as did Riley (1932). This instability of venation in *Pseudaletis, Lipaphnaeus, Chloroselas, Desmolycaena* and *Chrysoritis* indicates that such venational characters are unsuitable for the definition and distinction of closely related taxa.

The presence of one or more h/w tails is sometimes used as a supporting generic characteristic, but the following example illustrates that it is invalid as a characteristic for separating genera: *Aphnaeus areas* (Drury) and *Spindasis natalensis* (Westwood) both have two long filiform tails at vein 1A+2A and at CuA₂, but in *A. jacksoni* Stempffer and also *S. namaqua* Trimen the tail at CuA₂ is reduced to a mere stub, while in *A. erikssonii* Trimen and *S. modesta* Trimen the tail at CuA₂ is absent altogether.

Eliot (1973) presumed that the scales forming the tuft at the end of the female abdomen (where present) serve as an effective 'chevaux-de-fris' against predators and presumed that these scales diffuse scent to attract males or to repel predators. He concluded that it was not possible to use such an uncommon character in higher classification and that its occurrence in widely separated genera must be due to convergence. Due to its patchy occurrence across genera and even between families, this characteristic should indeed be regarded with caution; nevertheless, its presence in several genera of
Aphnaeini is noteworthy and warrants a closer study, including the possibility that it may be useful in defining certain genera or higher taxa.

Genera

**PSEUDALETIS** DRUCE (Plate 1)

*Pseudaletis* Druce, 1888.

Type species *Pseudaletis agrippina* Druce, 1888, by original designation.

**Diagnosis:** Fairly large, believed to mimic day-flying moths (Ackery *et al.*, 1995). F/w usually slightly larger than h/w, venation consisting of 11 veins (fig. 4), variable, CuA₁ and M₃ sometimes stalked, origin of vein R₅ varying (Stempffer 1967). H/w produced to form an enlarged lobe at tornus extending to CuA₂; a filiform tail present at veins 1A+2A and CuA₂. Male tibial spicules absent on all legs, formula 0-0-0; foretarsal claw accompanied by numerous terminal spines (fig. 4d). Thorax robust. Palpi exceptionally small, almost microscopic. Female with a dense tuft of specialised scales at the distal end of abdomen. Underside without any metallic silvery markings. Genitalia (figs. 9, 52, 93, 125): uncus with four prominent finger-like projections but no subunci, in the natural state the outer projections lying in a similar position to where subunci would normally be (possibly performing a similar function); aedeagus swollen at base, external portion tubular, bearing a dorsal tooth, vesica with numerous fine cornuti; valves oval, tapering to a finger-like apex curved inwards; juxta composed of two weakly joined triangular portions attached to the ventral edge of a valve; vinculum wide, narrowly sclerotized with a broad rounded saccus.

**Larval host-plants:** S. Collins (pers. comm.) surmises the larvae to feed on algae.

**Associated ant** According to S Collins (pers. comm.), T. Bouyer found pupae inside a *Crematogaster* nest.

**Distribution:** Forests from Zaire and Uganda to West Africa.

**Generic affiliations:** With its atypical uncus, distinctive wingshape and minute palpi, *Pseudaletis* is unlike any other genus within the Aphnaeini, but might be considered closer to *Lipaphnaeus* than to any other genus in the tribe. This is based upon the facts that the uncus of *Pseudaletis* is deeply divided medially, which is also true for *Lipaphnaeus*; the valves of both genera are broad at their base and finger-like at their apices; both have h/w tails at veins 1A+2A and CuA₂; the venation is variable within both *Pseudaletis* and *Lipaphnaeus* (Stempffer, 1967); and the females of *Pseudaletis* have a tuft of specialised setae at the distal end of the abdomen, as is the case with *Lipaphnaeus*. All these features may be coincidental, but at this stage there appears to be no other closer affiliation.

**Comments:** During the past three years more material has been obtained of this group of hitherto rare butterflies. This has largely been due to the collecting work done by S. Collins who confirmed (pers. comm.) that some of the specimens he obtained show silvery white markings but not quite the metallic silver seen on other Aphnaeini. There are currently 17 species known.
**LIPAPHNAEUS AURIVILLIUS** (Plates 2 & 3, fig.1)

*Aphnaeus (Lipaphnaeus)* Aurivillius, 1916.

Type species *Aphnaeus spindasoides* Aurivillius, 1916 (now a ssp. of *L. aderna* Plotz, 1880), by original designation. At the end of his original description, Aurivillius having placed *spindasoides* in *Aphnaeus*, erected a subgenus *Lipaphnaeus* for it, but later (in Seitz, 1923) he raised *Lipaphnaeus* to generic level.

**Diagnosis:** Medium-sized, resembling *Axiocerses*, especially the females. F/w with 12 or 11 veins. H/w with filiform tail at veins 1A+2A and CuA₂. Palpi fairly long. Thorax robust. Male tibial spicules absent on all legs, formula 0-0-0. Female abdomen distally bearing a dense tuft of specialised scales. Genitalia (figs. 10-11, 53-54, 94-95, 126-127): uncus narrow and bifid, forming two tapering points, subunci long and slender; valves broad at base narrowly finger-like at apex.

**Larval host-plants:** Known only for *L. aderna*, which feeds on *Maesa lanceolata* Forsk. (Myrsinaceae) (Bampton & Congdon, pers. comm.).

**Associated ant:** *Crematogaster* sp. (Bampton & Congdon, pers. comm.).

**Distribution:** Forests and forest clearings throughout Africa.

**Generic affinities:** Initially thought to be associated with both *Aphnaeus* and *Spindasis*, subsequent examinations of the genitalia, especially by Stempffer (1966, 1967), have shown that *Lipaphnaeus* is very close to *Chloroselas* Butler.

**Comments:** Stempffer (1967: 160) illustrated the variability of f/w venation in this genus, some having 12 veins and others 11. *Lipaphnaeus* is now recognised to be a valid genus and contains four species: *L. aderna* (Plotz), *L. eustorgia* (Hulstaert), *L. leonina* (Sharpe) and *L. loxura* (Rebel).

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**CHLOROSELAS BUTLER** (Plates 2 & 3, figs. 2 & 3)

*Chloroselas* Butler, 1886

Type species *Chloroselas esmeralda* Butler, 1886, by original designation. = *Desmolycaena* Trimen, 1898, type species *Desmolycaena mazoensis* Trimen, 1898, by original designation. **syn. n.**

**Diagnosis:** Very small, fast flying, upperside usually with some blue reflective scaling; underside brownish with small silvery spots. F/w has 10 or 11 veins, with R₁ and S₂ being either separate, touching or anastomosed. H/w with a filiform tail at vein 1A+2A and sometimes also at vein CuA₂. Palpi long. Male tibial spicules absent on all legs, formula 0-0-0. Male fore-tibia slightly shorter than femur, tarsal claw slightly angled. Female abdomen distally bearing a dense tuft of hair-like scales. DNO present on larvae (Fiedler, 1991) Genitalia (figs. 12-15, 55-58, 128-131): uncus fairly narrow with a median notch or depression, slender subunci; valves similar to *Lipaphnaeus*, broad and fused for basal third , distal third being finger-like; aedeagus slender distally but considerably swollen basally.

**Larval host-plants:** *C. pseudozeritis tytleri* Riley recorded feeding on *Acacia drepanolobium* Harms ex Sjostedt (Fabaceae) (Collins & Bampton, pers. comm.), *C. p. pseudozeritis* (Trimen) on *Julbernardia globiflora* (Benth.) Troupin, and *C. argentea* Riley on *Brachystegia spiciformis* Benth. and *Acacia* sp. (Fabaceae) (Pringle et. al. 1994). *C. pseudozeritis umbrosa* Jackson has been recorded accepting ant regurgitations (Pierce, 1995).
Associated ant: *Crematogaster* species (Pringle et al., 1994)

**Distribution:** *Acacia* and *Brachystegia* woodland in the eastern half of Africa from South Africa to Ethiopia, Sudan and Saudi Arabia.

**Generic affinities:** Very closely related to *Lipaphnaeus*, differing slightly in its uncus and in its f/w venation.

**Comments:** *Chloroselas* and *Desmolycaena* have been treated hitherto as separate entities. Stempffer (1967: 165) noted that the genitalia of *C. mazoensis* are very similar to those of *C. esmeralda* Butler; he examined the genitalia of five species of *Chloroselas* and of all three known *Desmolycaena* species and noted that by the structure of their genitalia as well as their facies, *Desmolycaena* is closely allied to *Chloroselas*. *Desmolycaena* was based upon the f/w venation, but this has been shown to be an unstable characteristic in *Lipaphnaeus* (Stempffer, 1967: 160); *Chloroselas* (Stempffer, 1967: 162) and *Desmolycaena* (Riley, 1932: 150) and must be considered an invalid character for separating these genera. The genitalia of *C. mazoensis* comb. n. (figs. 15, 58, 99, 131) are of exactly the same type as those of *C. esmeralda* (figs. 14, 57, 97, 129), having the same shape of aedeagus, valves and uncus. Consequently *Desmolycaena* is here treated as a synonym of *Chloroselas*, and the following species are transferred to *Chloroselas* as new combinations: *C. mazoensis* (Trimen) comb. n. and *C. arabica* (Riley) comb. n. The other species included in *Chloroselas* are *C. argentea* Riley, *C. azurea* Butler, *C. esmeralda* Butler, *C. minima* Jackson, *C. ogadenensis* Jackson, *C. overlaeti* Stempffer, *C. pseudozeritis* (Trimen), *C. tamaniba* (Walker), *C. taposana* Riley, *C. vansomereni* Jackson and *C. trembathi* Collins & Larsen.

**VANSOMERENIA** gen. n.

**Type species:** *Desmolycaena rogersi* Riley, 1932, by present designation.

**Description** (Illustrated in D’Abrera, 1980: 484) Similar to *Chloroselas* particularly in size and upperside colouration but with chequered cilia. Underside different from *Chloroselas*, with much larger markings, a distinctive white patch near the costa and chequered cilia. F/w with 10 or 11 veins, R₁ and S₃ being variable from separate to touching to anastomose. H/w with a short tail at vein 1A+2A. Palpi long. Eyes smooth. Male tibial spicules absent on all legs, formula 0-0-0. Female abdomen distally bearing a dense tuft of specialised scales. Mature larvae differing from *Chloroselas* in having a very prominent black head-shield and tending to be more cigar-shaped (Collins & Bampton, pers. comm.). Genitalia (figs. 16, 59, 100) uncus (fig. 16) almost rectangular with a weak median depression; subunci rudimentary; aedeagus (fig. 59) as in *Chloroselas* (figs. 55-58), swollen internally but very slender distally; valves (fig. 100) also as in *Chloroselas* (figs. 96-99), oval basally but finger-like at apex.

**Larval host-plants:** *V. rogersi* recorded on *Acacia drepanolobium* Harms ex Sjostedt (Fabaceae), often together on the same plant with *C. p. tytleri* Riley (Collins & Bampton, pers. comm.).

**Associated ant** *Crematogaster* sp. (Collins & Bampton, pers. comm.).

**Distribution:** Dry *Acacia* woodland from north eastern Tanzania to northern Kenya (Collins, pers. comm.).
**Etymology:** This genus is named for V.G.L. Van Someren, who worked with A. Rogers on East African butterflies in the 1920's and 30's.

**Generic affinities:** Closely related to *Chloroselas* as evidenced by its valves and aedeagus but distinguished by its unusual uncus which perhaps, is rather closer to that of *Crudaria*.

**Comments:** When describing *Desmolycaena rogersi*, Riley (1932) was at first uncertain whether to place it in *Chloroselas* because in one pair of specimens R₁ and S₂ anastomosed and in several others they were touching, however in the majority of specimens he examined they were free, as in *Desmolycaena*. Although the valves and aedeagus are of a similar type to *Chloroselas*, the uncus (fig. 16) is very different. The underside markings, cilia and larvae are unlike those of *Chloroselas* (Bampton & Collins, pers. comm.). A new genus *Vansomerenia* is therefore proposed here, resulting in the new combination *V. rogersi* (Riley). No other species referable to this genus are currently known.

**Jacksonia** gen. n. (Plates 2 & 3, fig. 5)

**Jacksonia** gen. n.

**Type species:** *Spindasis waggae* Sharpe, 1898, by present designation.

**Description:** Facies somewhat similar to both *Crudaria* and *Chloroselas*, upperside lacking the blue reflective scaling of the latter and with larger underside spots. Dull grey-brown upperside with outer margins finely edged in black, cilia white; underside light brown with many elongate silvery spots. Venation (fig. 7), f/w with 11 veins, h/w with a filiform tail at 1A+2A and a shorter one at CuA₂, a small lobe is present at the anal angle. Male tibial spicules absent on all legs, formula 0-0-0. Tibia and femur of equal length on male fore-leg, tarsal claw curved. Eyes smooth. Female abdomen distally bearing a dense tuft of specialised scales. Genitalia (figs. 17, 60, 101): uncus composed of two prominent rounded lobes with a median depression, intermediate between those of *Chloroselas* and *Crudaria*, but closer to the former; subunci small but not as small as in *Crudaria* nor as slender as in *Chloroselas*; aedeagus (fig. 60) as in *Crudaria* (fig. 61) but with numerous minute comuti attached to vesica; valves (fig. 101) oval but finger-like at apex, also as in *Crudaria* (fig. 102) and *Chloroselas* (figs. 96-99) but more blunted.

**Larval host-plants** and **Associated ant:** Unknown.

**Distribution** Somalia and possibly eastern Ethiopia (D’ Abrera, 1980).

**Etymology:** This genus is named for T.H.E. Jackson, who contributed so much to our knowledge of the lycaenid butterflies of Africa.

**Generic affinities:** As evident from the genitalia (figs. 12-18, 55-61, 96-102 & 128-134) and the habitus (Plates 2 & 3, figs. 2-5), *Jacksonia* has an affinity to both *Crudaria* and *Chloroselas* in the structure of its genitalia, especially the valves and aedeagi, as well as in the underside wing markings and h/w tail at 1A+2A.

**Comments:** When figuring the genitalia of *J. waggae*, Stempffer (1967) noted that they differ from those of typical species of *Spindasis* (figs. 35-38, 77-80, 110-113) on account of their genital characters. *J. waggae* (figs. 17, 60, 101) is
clearly much closer to Crudaria and Chloroselas than to Spindasis, but it does not belong in either genera, as its genitalia and facies are somewhat intermediate between Crudaria and Chloroselas. A new genus Jacksonia is therefore proposed here, resulting in the new combination J. waggae (Sharpe). No other species referable to this monotypic genus are currently known.

**CRUDARIA** WALLENGREN (Plates 2 & 3, fig. 4)

**Crudaria** Wallengren, 1875.

**Type species:** Arhopala leroma Wallengren, 1857, by monotypy.

**Diagnosis:** Medium to small but very variable in size; dull brown upperside without any blue scaling; underside very variable, usually a creamy brown or grey, sometimes with some silvery flecks. F/w with 11 veins. H/w with a filiform tail at 1A+2A, of very variable length, a small lobe is present at the anal angle. Head broad, palp i long and thorax fairly robust. Male tibial spicules absent on all legs, formula 0-0-0. Tibia and femur of equal length on fore-leg, tarsal claw curved. Female abdomen distally bearing a dense tuft of specialised scales. DNO present in second and subsequent larval instars (Clark & Dickson, 1971); DOs present in third and subsequent instars. Genitalia (figs. 18, 61, 102, 134): not a useful characteristic in distinguishing species; uncus consisting of two large rounded lobes with a depression between; subunci short; saccus very large and rounded; valves broad basally, the distal third being finger-like; aedeagus rather swollen proximally and obliquely truncated distally; vesica bearing indistinct cornuti; juxta v-shaped.

**Larval host-plants:** C. leroma recorded on Acacia karroo Hayne, A. sieberiana DC. [Zimbabwe] and other Acacia species (Fabaceae) (Pringle et al., 1994). C. capensis Van Son probably feeds on Zygophyllum retrofractum Thunb. (Zygophyllaceae) (Heath, unpubl.).

**Associated ant:** Anoplolepis sp.

**Distribution:** Arid Acacia woodland, often near dry river beds, from the Western Cape Province, S.A., to Tanzania.

**Generic affinities:** Trimen (1898) noted similarity of the undersides of Chloroselas mazoensis (Trimen) and C. leroma (Wallengren). Crudaria is quite closely related to both Jacksonia and Chloroselas as evidenced by their genitalia and other characters. There also seems to be a weak affinity between the genera Pseudoletis, Lipaphnaeus, Chloroselas, Vansomerenia, Jacksonia and Crudaria, their genitalia all having similar valves and aedeagi. All these genera also have a tuft of scales at the distal end of the female’s abdomen, although the value of this characteristic in higher classification is still uncertain.

**Comments:** There are three species, C. leroma (Wallengren), C. capensis van Son and C. wykehami Dickson. The type species, C. leroma, is widespread and very variable; the northern specimens from Tanzania have longer tails and are generally darker than their southern-Cape counterparts, although some individuals at hand from the Eastern Cape Province and southern KwaZulu-Natal are also very dark but have shorter tails. Despite these facial differences, the genitalia of C. leroma do not show any significant differences between the widely separated and different populations, and it may require a study of the life
history to provide solid evidence of speciation. Nevertheless, it is possible that more than one species are represented by this taxon. *C. capensis* Van Son is less widespread, being recorded from the Cape provinces only, and is distinctive in its underside markings and exceptionally convex outer f/w margin. *C. wykehami* Dickson has not been recorded from its type locality (south of Fraserburg) since it was first discovered, although *C. leroma* is very common there. Male specimens from populations at Willowmore and at Bedford closely match the facies of the type specimen of *C. wykehami* in the Natural History Museum, London, and may possibly represent this species; however, if true, the female paratype in the Natural History Museum may have been misidentified and could possibly be *C. capensis*.

**CHRYSORITIS** BUTLER (Plates 2 & 3, fig. 21)

*Chrysoritis* Butler, 1897.

**Type species:** *Zeritis oreas* Tri men, 1891, by original designation.

= *Poecilmitis* Butler 1899e, type species *Zeritis lycegenes* Trimen, 1874, by original designation. **syn. n.**

= *Bowkeria* Quickelberge, 1972, type species *Zeritis phosphor* Trimen, 1864, by monotypy. **syn. n.**

= *Oxychaeta* Tite & Dickson, 1973, type species *Phasis dicksoni* Gabriel, 1947, by original designation. **syn. n.**

**Diagnosis:** Mostly small to medium-sized; uppersides predominantly orange-red with dark brown markings, some species glossy, others with some pale blue scaling and with a blue reflective sheen in males; underside mostly brown or grey. F/w with 12 or 11 veins but sometimes only 10. H/w produced at 1A+1B in many species and some with a short tail. Palpi long, eyes smooth, thorax robust. Male tibial spicule very variable (see Table 1). Female without tuft of scales at end of abdomen. Genitalia (figs. 19-31, 62-73, 103-106, 170-177) very uniform, not very useful for distinguishing species; uncus as in *Trimenia*, subrectangular with broadly rounded lateral angles and distal margin with a rounded median depression; subunci robust, usually with an apophysis varying in size between species, large in *C. felthami*, small and difficult to detect in *C. oreas* and *C. lycegenes* but absent altogether in *C. dicksoni*; valves oblong with a finger-like apex; juxta smallish, shield-shaped with a median notch; aedeagus tubular, slender, internal portion slightly swollen; vesica with a minute group of cornuti in some species (Table 1, Plate 4) but absent in others, Table 1 indicating those having cornuti. DNO present in the second and subsequent instars (Clark & Dickson, 1971; Heath & Brinkman, 1995a); the number of larval instars may vary from five as in *C. pyroeis* comb. n. to seven as in *C. palmus* comb. n. (Clark & Dickson, 1971).

**Larval host-plants:** (Tables 3 & 4) *Osteospermum, Dimorphotheca, Chrysanthemoides* (Asteraceae); *Berzelia* (Bruniaceae); *Diospyros* (Ebenaceae); *Aspalathus, Lebeckia* (Fabaceae); *Rhus* (Anacardiaceae); *Zygophyllum* (Zygophyllaceae); *Cotyledon, Tylecodon* (Crassulaceae); *Myrsine* (Myrsinaceae); *Clutia* (Euphorbiaceae); *Thesium* (Santalaceae) (see Table 4 for references).

**Associated ant:** (Tables 2 & 4). All species associated with *Crematogaster*
except for two which are associated with *Myrmicaria* (Heath, unpubl.).

**Distribution:** Endemic to South Africa with a concentration in the southern and western part of the country, habitat type generally fairly short vegetation such as strandveld, mesic and wet mountain fynbos, limestone fynbos, mountain rhenosterveld, karroid vegetation, grassveld, etc. There are two notable exceptions: *C. palmus*, which frequents dense shrubby vegetation near streams in the Western Cape Province, and *C. phosphor*, which frequents forests in the Eastern Cape Province and KwaZulu-Natal.

**Generic affinities:** The valves of *Chrysoritis* are similar to those of *Chloroselas* but not the uncus, which indicates slightly closer affinity to *Jacksonia*, nor the aedeagus, which shows affinities to *Lipaphnaeus, Chloroselas* as well as *Jacksonia*. A relationship may thus exist between *Chrysoritis* and the above group of genera.

**Comments:** Tite & Dickson (1973: 232) observed that larvae of *Poecilmitis, Chrysoritis, and Oxychaeta* showed an affinity to one another. Heath & Brinkman (1995) confirmed that the structure of the first two larval in stars of *C. dicksoni* (Gabriel) is typical of that of known species within the *Chrysoritis* complex. In their description of *Oxychaeta*, Tite & Dickson (1973: 232) used the sharpness of setae on the labial palpi and the existence of a spicule on the male foretibia as generic characters. However, the setae on the palpi of *C. dicksoni* comb. n. are ribbon-like and differ from those of other taxa only in width, which is not a valid generic character. Tite & Dickson (1973: 228) also considered the presence of a foretibial spicule in males divide the genera they reviewed into two groups but it appears that they examined the type species only and failed to notice the presence of the spicule in other species. The present study shows that this spicule varies considerably in size between species of the *Chrysoritis* complex and other genera, and that it also varies between the fore-, mid- and hind- legs (Table 1). It is clear that neither of the two features discussed above represents a generic characteristic, whilst the genitalia and facies of *Oxychaeta* clearly show a close affinity to *Chrysoritis*. When Quickelberge (1972) erected *Bowkeria* and removed *C. phosphor* from *Poecilmitis*, he made comparisons with the type species of the latter, *C. lycegenes*, but the present study shows that, when compared with all the species in the *Chrysoritis* complex, the structural differences of *C. phosphor* are insufficient to merit generic status; its most notable feature being its forest canopy habitat, which is unique in this complex but not a generic characteristic. Stempffer (1967 179) considered that *Chrysoritis* and *Poecilmitis* could well be united, and Tite & Dickson (1973) and Cottrell (1978, 1985) also noted the close relationship between these two genera. Their genitalia are very uniform in structure (figs. 19-31, 62-73, 103-106), especially when the valves are depicted in a flattened state (figs 170-177). Also, where cornuti are present in the *Chrysoritis* complex, they are of exactly the same type. There can thus be little doubt that only one genus is represented here, and accordingly *Poecilmitis, Oxychaeta* and *Bowkeria* are placed as synonyms of *Chrysoritis*. As a result of these synonymies and the resulting placement of *C. dicksoni* (Gabriel, 1947) in *Chrysoritis*, the name *dicksoni* W.H. Henning, 1977 becomes a junior secondary homonym of the older *dicksoni* Gabriel. *Chrysoritis dicksoni* (Henning) is therefore renamed *C. williami* nom. n. for its original author William H. Henning.
Chrysoritis species groups
The synonymies proposed above result in a large number of new combinations as listed below in the natural groupings apparent within Chrysoritis, namely C. chrysaor species group, C. dicksoni species group, C. oresas species group and C. thysbe species group. The constituent species of these three groups are as follows:

C. chrysaor species group: C. phosphor (Trimen) comb. n.; C. chrysaor (Trimen) comb. n.; C. lycia (Riley) comb. n.; C. midas (Pennington) comb. n.; C. natalensis (Van Son) comb. n.; C. aethon (Trimen) comb. n.; C. aureus (Van Son) comb. n.; C. lyncurium (Trimen) comb. n.; C. lycegenes (Trimen) comb. n. This is a homogenous group with orange or red, often glossy upperside, and the h/w underside is plain with some indistinct spots, some species having short h/w tails at 1A+2A. Very small genitalic differences can be detected between some species, and cornuti are always absent. All species possess tibial spicules (Table 1) and 12 f/w veins. Associated ant (where known, see Table 4): Crematogaster species. C. phosphor is the only species in this group to frequent forest canopy.

C. dicksoni species group: C. dicksoni (Gabriel) comb. n. This is a monotypic species group with an upperside wing pattern similar to that of C. zeuxo but with a different underside and usually much larger in size; f/w also with 12 veins, and h/w not produced at 1A+2A. The tibial spicule is present. Probably aphytophagous, its associated ant being Crematogaster peringueyi Emery.

C. oresas species group: C. oresas Trimen; C. chrysantas (Trimen); C. zeuxo (Linnaeus); C. cottrelli (Dickson); C. zonarius (Riley); C. coetzeri Dickson; C. felthami (Trimen) comb. n.; C. pyroeis (Trimen) comb. n. This group is the least homogenous and could possibly be further subdivided. F/w with 12, 11 and sometimes only 10 veins (Table 1); all share a similar underside pattern except C. oresas. H/w is produced at 1A+2A in C. cottrelli, C. zeuxo, C. zonarius, C. coetzeri, and C. felthami, but not in the others. Tibial spicules are always absent.

Associated ant: Crematogaster, except C. pyroeis and C. oresas which associate with Myrmicaria (Table 4). C. pyroeis is the only species in this group with blue reflective scales.

C. thysbe species group: C. thysbe (Linnaeus) comb. n.; C. adonis (Pennington); C. aridus (Pennington); C. atlantica (Dickson); C. azurius (Swanepeol); C. balli (Dickson & Henning); C. bamptoni (Dickson); C. beaurotta (Dickson); C. beulah (Quickelberge); C. blencathra (Heath & Ball); C. braueri (Pennington); C. brooksi (Riley); C. daphne (Dickson); C. endymion (Pennington); C. henni (Bampton); C. hyperion (Dickson); C. irene (Pennington); C. kaplani (Henning); C. lyncslae (Henning); C. lysander (Pennington); C. mithras (Pringle); C. nigricans (Aurivillius); C. orientalis (Swanepeol); C. palmus (Stoll); C. pan (Pennington); C. pelion (Pennington); C. penningtoni (Riley); C. perseus (Henning); C. pluto (Pennington); C. psyche (Pennington); C. pyramus (Pennington); C. rileyi (Dickson); C. stepheni (Dickson); C. swanepeoli (Dickson); C. trimeni (Riley); C. turneri (Riley); C. uranus (Pennington); C. violescens (Dickson); C. whitei (Dickson); C. william; C. wykehami (Dickson). This is an extremely homogenous group with a uniform h/w underside pattern, although its colour contrast varies considerably, even within species. Genitalia almost identical and cornuti always
present. Male tibial spicules always absent. F/w with 12 veins, the h/w produced at 1A+2A. Associated ant (where known, see Table 4): *Crematogaster* species. The majority of species possess blue reflective scales in males.

Clark & Dickson (1971) described and illustrated the life history of *C. lycene*, *C. felthami*, *C. zeuxo*, *C. pyroeis*, *C. thysbe*, *C. lysiander*, *C. nigricans*, *C. uranu*, *C. adonis*, *C. palmu*, *C. aridu* and *C. braueri*. Aspects of the life history of *C. dicksoni* were described by Clark & Dickson (1971) and Heath & Brinkman (1995a).

**TRIMENIA** TITE & DICKSON (Plates 2 & 3, figs. 16 & 17)


**Type species:** *Zeritis wallengrenii* Trimen, 1887, by original designation.

= *Argyrocurha* Tite & Dickson, 1973, type species *Cigaritis malagrica* Wallengren 1857, by original designation. **syn. n.**

**Diagnosis:** Brown and orange upperside; underside with numerous silver lines and spots. F/w with 12 veins. Palpi long. Male tibial spicule formula f-f-0 with foretarsal claw curved gradually to a sharp point. Female abdomen distally with a tuft of specialised scales. TOs present but ONO absent in final instar (Clark & Dickson, 1971). Genitalia (figs. 32-33, 74-75, 107-108): uncus subrectangular with broadly rounded lateral angles and distal margin with a rounded median depression; subunci robust, without apophysis; valves oblong with their apices spatulate when viewed from the rear, being curved sharply inwards distally, upper surfaces connected by a broad median band passing above the aedeagus, the distal margin of this band normally convex and well sclerotized but the proximal edge weakly defined, giving way to a membranous band; juxta a simple shield shaped structure, usually with a V-shaped median depression; aedeagus robust and fairly long, with numerous minute teeth on one or both sides, distal portion open dorsally, the sides forming a U-shape in cross section, these side flaps subtriangular, but often curling up like a dried leaf to form a pointed apex, with its left side overlaying the right, sometimes one or both sides remaining upright or upper margin of these sides folding into the median depression, the distal end of the aedeagus obliquely truncated and often weakly sclerotized; lateral profile varying considerably because of variable features as above.

**Larval host-plant:** Possibly aphytophagous (Cottrell, 1984); probably also accepting ant regurgitations (Heath, unpubl.).

**Associated ant:** Probably *Anoplolepis* sp. (Heath & Brinkman, 1995b).

**Distribution:** Endemic to South Africa, open and arid ground in the south and west of the country.

**Generic affinities:** *Trimenia* has a similar uncus to that of *Chrysoritis* but also to that of *Jacksonia*; however, its aedeagus and valves differ from both these genera. *Trimenia* and *Jacksonia* both have a tuft of specialised setae at the end of the female abdomen, but their facies differ considerably. Thus, a relationship appears to exist between these three genera but it is not very close.

**Comments:** When Tite & Dickson (1973: 233, 234) erected *Trimenia* and *Argyrocurha*, the distinctions drawn were based on minor differences in venation, and due to the highly variable and unstable nature of these differences
their validity as generic characters is doubtful and rejected in this study. Clark & Dickson (1971) illustrated the egg and the first-instar larva of *T. argyroplaga* and *T. malagrida* showing that their eggs and larvae are almost identical, and Heath & Brinkman (1995b) noted the remarkable similarity between their final-instar larvae. The genitalia of both *Trimenia* and *Argyrocupha* are also identical in structure (figs. 32-33, 74-75, 107-108, 141-148), and the females of both taxa bear a tuft of scales at the end of the abdomen. The only significant difference between these two taxa exists in the male wing profile, which in *Trimenia* is rather elongate and angular but more rounded in *Argyrocupha*. The females, however, share a very similar wing profile, particularly the h/w concave feature between 1A+2A and CuA2. There appears to be no valid distinction between *Trimenia* and *Argyrocupha*, consequently *Argyrocupha* is here placed as a synonym of *Trimenia*, resulting in the new combination *T. malagrida* (Wallengren). The species now included in *Trimenia* are: *T. wallengrenii* (Trimen), *T. argyroplaga* (Dickson), *T. wykehami* (Dickson), *T. macmasteri* (Dickson) and *T. malagrida* (Wallengren).

**Trimenia** species

The following are identifying characteristics of the constituent species:

*T. wallengrenii* (Trimen) (Plates 2 & 3, fig. 17): Genitalia (figs. 32, 74, 107, 141) with aedeagus finely toothed on the left side only of its external portion; distal profile of the band joining the valves, convex but with the median third flattened; saccus usually subrectangular.

**Distribution**: Confined to localised areas in the Western Cape Province in two subspecies, *T. w. wallengrenii* and *T. w. gonnemoi* Ball, 1994.

*T. argyroplaga* (Dickson): Very similar to *wallengrenii* in most respects. Genitalia (fig. 143) with external portion of aedeagus finely toothed on left side but larger teeth (larger than in *T. wallengrenii*) lower down; distal profile of the band joining the valves usually very slightly concave in its median third; saccus much broader and more rounded than in *T. wallengrenii*. The structural and facial differences of this species from *T. wallengrenii* are extremely small, hence its true status is uncertain, but life history and DNA studies may clarify this in time.

**Distribution**: Confined to the Western Cape Province but just allopatric with *T. wallengrenii*, the separation distance being as short as 30km and its range extending over a far greater distance to the east into the Eastern Province and north into Namaqualand. There are two subspecies, *T. a. argyroplaga* and *T. a. cardouwae* Dickson & Wykeham (in Pringle, et al., 1994).

*T. wykehami* (Dickson): Genitalia (fig. 144) with external portion of aedeagus well toothed on both sides (a unique feature in this genus); distal profile of the band joining the valves, evenly convex; saccus fairly deep and rounded.

**Distribution**: Roggeveld escarpment in the south-west Karoo.

*T. macmasteri* (Dickson): A smaller species. Genitalia (fig. 145) with aedeagus toothed on left side but far fewer than in other species; valves slightly shorter in relation to the aedeagus than in other species; distal profile of the band joining the valves convex but very shallow, with a small convex bump in its median third; saccus rounded but smaller than in other species; v-shaped median
depression evident in the juxta of the other species, is shallower and often absent. **Distribution:** Namaqualand, Northern Cape Province, and as far as the Little Karoo, Western Cape Province where it flies together with *T. argyroplaga*. There are two subspecies, *T. m. macmasteri* and *T. m. mijburghi* Dickson. 

*T. malagridge* (Wallengren) (Plates 2 & 3, fig. 16) Smaller than the other species except for *T. malagridge maryae*; males lacking the sharply angled wings of the other species. Genitalia (figs. 33, 75, 108, 142) with external portion of the aedeagus exceptionally finely toothed on left side as in *T. macmasteri*; distal profile of the band joining the valves slightly convex, having a small peak in the centre, but varying slightly between subspecies. Very small genitalic differences exist between the four subspecies (figs. 142, 146-148). The distal end of the aedeagus in *T. malagridge paarlensis* is sometimes poorly sclerotized, preventing the tip of the aedeagus from scrolling, and making it appear blunted from a lateral perspective. The other noticeable difference is in the distal profile of the median band joining the valves when viewed dorsally. This is due to the way the sclerotized band is curled-down at its edges, rather than to any real structural differences. In view of this, it is appropriate that their current status as subspecies be retained. 

*T. malagridge malagridge* (Wallengren), *T. malagridge paarlensis* (Dickson), *T. malagridge cedrusmontana* (Dickson & Stephen) and *T. malagridge maryae* (Dickson & Henning).

**Distribution:** Very small localised populations in the Western Cape Province not recorded flying with the other species.

**ARGYRASPODES** TITE & DICKSON (Plates 2 & 3, fig. 20)

*Argyraspodes* Tite & Dickson, 1973.

**Type species:** *Zeritis argyraspis* Trimen, 1873, by original designation.

**Diagnosis:** Very similar to *Trimenia*, particularly the underside silvery markings. F/w with 12 veins, h/w with a very short tail at veins A+2A and at CuA2. Palpi long. Male tibial spicule formula d-e-a; male foretarsal claw curved gradually to a slender point. Female without abdominal tuft of scales (present in *Trimenia*). Genitalia (figs. 34, 76, 109, 139): uncus subrectangular with a shallow flat median depression on distal margin and with rounded lateral angles; valves with well-defined but very small spatulate apices, not curved inwards, their upper surface consisting of a pair of semi-oval projections weakly attached medially; juxta shield-shaped; aedeagus massive, banana-shaped, curving downward distally towards its tip, with lateral flaps enfolding vesica; a few very fine, needle-like cornuti attached to the vesica; saccus large and rounded.

**Larval host-plant and Associated ant:** Unknown, possibly aphytophagous (Cottrell, 1984).

**Distribution:** Endemic to southern Africa, arid slopes in the west and south west of South Africa, including Botswana and Namibia.

**Generic affinities:** The genus *Argyraspodes* seems to have a very close relationship with *Trimenia* because of the similarity of its aedeagus, uncus and spatulate valves; the facies are also extremely similar (Plates 2 & 3, figs. 16, 17 & 20). The dissimilarities lie in the unusual juxta (fig. 139) and the absence of a tuft of specialised scales on the female abdomen of *Argyraspodes*. 
Comments: The genus contains one species, *A. argyraspis* (Trimen). Despite its closeness to *Trimenia*, particularly in its facies, its status as a separate genus is here retained until life history or DNA studies are able to provide more comparative information.

**SPINDASIS** WALLENGREN (Plates 2 & 3, figs. 7 & 8)

*Spindasis* Wallengren, 1857.

**Type species:** *Spindasis masilikazi* Wallengren, 1857 (syn. of *Aphnaeus natalensis* Westwood, 1851), by monotypy.

= *Apharitis* Riley, 1925. Type species *Polyommatus epargyros* Eversmann, 1854, by original designation. **syn. n.**

**Diagnosis:** Attractive fast-flying insects often with some reflective blue scales on upperside; underside with yellowish basal colour marked with dark-edged continuous or broken bars. F/w with 11 veins, h/w with a filiform tail at 1A+2A and another at CuA2 which is stunted in some cases and totally absent in *S. modesta* (Trimen). Palpi fairly long, thorax robust. Male tibial spicules absent, formula 0-0-0. Foretarsal claw angled acutely to a point (fig. 4d) in many species but in a few such as *S. phanes* (Trimen) more evenly curved. Female abdomen without dense tuft of scales. DNO present in the third and subsequent instars, and DOs present in the fifth and final instars (Clark & Dickson, 1971). Adult often settling on twigs with its head lowered whilst rubbing its h/wings together (Migdoll, 1988). Genitalia (figs. 35-38, 77-80, 110-113, 149-152): uncus very distinctive, composed of two oblong or rectangular lobes lying obliquely and deeply divided medially, very broad when flattened; subunci very robust and sharply curved in middle; aedeagus short and broad, internal portion having a dorsal projection, external portion adorned with many minute teeth; vesica has numerous small cornuti; valves oblong, narrowly tapering to their apices; juxta shield-shaped with a deep median v-shaped depression; juxta large and very sharply pointed in *S. natalensis* but smaller in many other species; saccus fairly large.

**Larval host-plants:** Wide variety of host-plants within the Afrotropical region, include *Ximenia* (Olacaceae), *Tapinanthus* (Loranthaceae), *Brachystegia, Entada, Acacia* and *Julbernardia* (Fabaceae), *Zygophyllum* (Zygophyllaceae), *Canthium* (Rubiaceae), *Clerodendrum* (Verbenaceae) (Pringle et al., 1994). Note that *S. nyassae* (Butler), *S. acamas* (Klug) and the Japanese species *S. takanonis* Matsumura have been recorded as also accepting ant regurgitations (Pierce, 1995).

**Associated ant:** *Crematogaster* sp. (Clark & Dickson, 1971) and *Pheidole* sp. (Fiedler, 1991)

**Distribution:** Throughout Africa, extending to India and Japan.

**Generic affinities:** *Spindasis* shares its wingshape with *Aphnaeus* and also the way the vesica attachment is adorned with minute spines is similar. However, the robust uncus of *Spindasis* is unlike that of any other genus in the tribe except for *Cigaritis*.

**Comments:** Heath (1983) figured the genitalia of *Spindasis modesta heathi* D’Abrera and noted the similarity in facies between *S. modesta* and *S. buchanani* (Rothschild, 1921) whilst observing that the *S. modesta* genitalia
were typical of *Spindasis*. When Riley (1925) erected the genus *Apharitis*, he argued that the species concerned were structurally near to *Spindasis* (in venation and in other characters), but differed only in colouration. Examination of the genitalia of the type species of *Apharitis*, *A. epargyros* (Eversmann), and of *A. nilus* (Hewitson) (figs. 37–38), as well as of the genitalia figured by Riley (1925) and Stempffer (1967) provided no feature or characteristic to distinguish *Apharitis* from *Spindasis*. The venation, wing shape and markings are also of the same type, although often a little paler in *Aphalitis*, a common phenomenon among butterflies of arid areas. There therefore is no sound basis for the retention of *Apharitis*, and it is here treated as a synonym of *Spindasis*, resulting in the new combinations *S. acamas* (Klug); *S. buchanani* (Rothschild); *S. gilletti* (Riley); *S. myrmecophila* (Dumont); *S. nilus* (Hewitson); *S. ciissa* (Lederer); *S. epargyros* (Eversmann) and *S. lilacinus* (Moore), the last three being extralimital to this review. *Spindasis* currently contains 35 species in Africa including those transferred from *Apharitis*.

**CIGARITIS DONZEL** (Plates 2 & 3, fig. 6)

*Cigaritis* Donzel, 1847.

**Type species:** *Cigaritis zohra* Donzel, 1847, by subsequent designation (Scudder, 1875).

**Diagnosis:** Similar to *Spindasis*, underside with whitish basal colour marked with dark-edged broken bars. Wings not as angular as in *Spindasis*. F/w with 11 veins, h/w with a short tail at CuA₂ and 1A+2A Palpi fairly long, thorax robust Male foretibial spicule absent, formula 0-0-0. Female abdomen without dense tuft of specialised scales. Genitalia (figs. 39, 81, 114, 140) as in *Spindasis*; uncus composed of two narrow strips lying obliquely and very deeply divided medially, pointed at their lateral angles, very broad when flattened; subunci fairly robust; aedeagus with internal portion stout with a slight dorsal projection, external portion stout with some minute teeth on ventral surface; vesica has numerous small cornuti; valves oblong, narrowly tapering to their apices with a small projection in their dorsal surface; juxta lozenge-shaped with a very deep median v-shaped depression; saccus large.

**Larval host-plant:** Fabaceae (Fiedler, 1991)

**Associated ant:** *Crematogaster* sp. (Fiedler, 1991)

**Distribution:** None in the Afrotropical region.

**Generic affinities:** The genitalia indicate a close relationship to *Spindasis*.

**Comments:** A palaearctic genus closely allied to *Spindasis*.

**ZERITIS** BOISDUVAL (Plates 2 & 3, fig. 9)

*Zeritis* Boisduval, 1836.

**Type species:** *Zeritis neriene* Boisduval 1836, by monotypy.

**Diagnosis:** Fairly small, rather inactive butterflies with numerous small colourful metallic spots on undersides; closely allied to *Axiocerses* (Stempffer, 1967). F/w with 10 veins, h/w with a filiform tail at CuA₂ and at 1A+2A. Palpi fairly short. Male tibial spicules present on first and second pair of legs only, formula d-d-0. Female abdomen without dense tuft of scales. Genitalia (figs. 40-41, 82-83, 115-116, 153-154): (asymmetrical); uncus composed of two
triangular lobes; subunci fairly robust basally and very sharply curved, each one bearing an apophysis but not positioned symmetrically, in *Z. fonteinei* Stempffer with at least two smaller apophyses; valves oblong, tapering to in-curving points; juxta an asymmetrical v-shaped structure with the right arm of the vee narrow and ending in a rounded apex, the left arm in the form of a truncated strip with a serrated apex; in *Z. fonteinei* the arms of the juxta each taper to a sharp point, the right side longer with the apex curved into a small hook; median portion of tegumen extending proximally towards eighth abdominal segment; saccus triangular; aedeagus long and slender, the external portion with a large tooth projecting laterally on the right, the distal end of the aedeagus truncated very obliquely, with some large cornuti present.

**Larval host-plant and Associated ant:** Unknown.

**Distribution:** Very localised throughout Africa, north of the Zambezi.

**Generic affinities:** Very closely related to *Axiocerses* as evidenced by the similarity of their genitalia, the distinction lying in the asymmetrical nature of the *Zeritis* genitalia and to a lesser extent in their facies.

**Comments:** An old and originally large genus, but most of its original species have since been attributed to other genera. There are currently six species remaining in it: *Z. fonteinei* Stempffer, *Z. krystyna* D'Abrera, *Z. neriene* Boisduval, *Z. pulcherrima* Aurivillius, *Z. aurivillii* Schultz and *Z. sorhagenii* (Dewitz).

**AXIOCERSES HÜBNER (Plates 2 & 3, fig. 10)**

*Axiocerses* Hübner, [1819] in Hübner [1816-[1826]].

**Type species** *Papilio perion* Stoll, 1781 (*Papilio harpax* Fabricius, 1775), by monotypy.

**Diagnosis:** Mostly reddish-orange and dark brown butterflies with some small nacreous or silvery markings on undersides. F/w with 10 veins, h/w with a filiform tail at 2A+1A. Palpi fairly short, thorax robust. Tibial spicules present but barely evident on front legs, formula a-c-0. Femur and tibia very robust and densely clothed with hair. Female abdomen without dense tuft of scales. DNO present in third and subsequent instars (Clark & Dickson, 1971). The adult often settling on twigs whilst rubbing its h/wings together (Migdoll, 1988). Genitalia (figs. 42-43, 84-85, 117-118, 155-156) uncus composed of two subrectangular lobes folded over obliquely near the lateral angle to appear oval, (flattened out in figure); subunci very robust basally and very sharply angled with an apophysis forming a produced elbow at the angle (this apophysis is absent in *A. jacksoni* Stempffer); median portion of the tegumen extending proximally towards the eighth abdominal segment; saccus subtriangular; valves subrectangular for basal two-thirds, distally tapering sharply to a slightly helical and rounded apex with a slight ventral apical curve; juxta consisting of a pair of narrow tapering processes with rounded apices equipped with many small spines (in *A. amanga* (Westwood) the juxta is longer, whilst in *A. bambana* Smith it is very short and rounded); aedeagus very long, slender and slightly curved up, the external portion with a tooth projecting laterad on the right and some fine spines laterad, the distal end of the aedeagus open dorsally with many cornuti attached to the vesica; saccus broad.

**Larval host-plants:** *Acacia* (Fabaceae) (Clark & Dickson, 1971), *Ximenia*
(Olacaceae), *Peltophorum* (Fabaceae) (Pringle *et al.*, 1994), *Tapinanthes* (Loranthaceae), *Brachystegia, Burkea, Julbernardia* (Fabaceae) (Bampton, pers. comm.). *A. harpax* (Fabricius) has been recorded as accepting ant regurgitations (Pierce, 1995).

**Associated ant:** *Crematogaster* sp. and *Pheidole* sp. (Fiedler, 1991). Bampton (pers. comm.) stated that *A. amanga* seldom associates with ants but when it does, they are *Pheidole* sp. and not *Camponotus* as stated by Jackson (1937).

**Distribution:** Woodland and forests throughout Africa.

**Generic affinities:** *Axiocerses* is very closely related to *Zeritis* as evidenced by their genitalia.

**Comments:** The genus was recently revised by Henning & Henning (1996), who divided the genus into two groups, the *A. harpax* super-group and the *A. amanga* super-group. There are sixteen species included in it at present.

**ALOEIDES** HÜBNER (Plates 2 & 3, fig. 11)

*Aloeides* Hübner, [1819] in Hübner [1816-[1826]]

**Type species:** *Papilio pierus* Cramer, by subsequent designation (Scudder, 1875).

**Diagnosis:** A large genus of mostly bright orange-and-brown or brown butterflies; underside h/w sometimes brightly coloured but very variable within species. F/w with 12 veins, no tail on h/w. Palpi long, thorax robust. Spicules on male tibia present, formula f-f-a, slightly variable between species; male foretarsal claw sharp (fig. 4a). Mesofemur at least twice the length of tibia. Female abdomen without dense tuft of specialised scales. DNO sometimes present in third and subsequent instars (Clark & Dickson, 1971), but late instars of some species, e.g. *A. thyra*, without DNO (Claassens & Dickson, 1977, 1980). Adults invariably settling on the ground and frequently rubbing their h/w wings together (Heath, unpubl.). Genitalia (figs. 44-46, 86, 119, 157-159): not very useful for distinguishing closely related species; uncus in the form of a narrow strip overlaying the large tegumen, distal edge very slightly convex in the flattened state; subunci fairly short but swollen at their bases; tegumen extending proximally towards eighth abdominal segment; aedeagus short, slightly swollen in middle (dorsally) and very slightly curved down, some fine spines laterally on external portion; valves oblong with very broad rounded finger-like apices; juxta triangular with a shallow medial notch; saccus small and rounded.

**Larval host-plants:** *Aspalathus* (Fabaceae) (Claassens & Dickson, 1974), *Zygophyllum* (Zygophyllaceae) Heath (unpubl.), *Hermannia* (Sterculiaceae) (Tite & Dickson, 1973); *Sida* (Malvaceae) (Pringle *et al.*, 1994).

**Associated ant:** *Lepisiota* sp. (= *Acantholepis*) (Claassens & Dickson, 1974).

**Distribution:** Most species are endemic to southern Africa, particularly to the Cape provinces but one species extends as far north as Kenya.

**Generic affinities:** Probably related to *Aphnaeus* as evidenced by the type of uncus and valves.

**Comments:** The genus *Aloeides* was revised by Tite & Dickson (1973) and later by Henning (1993), who divided the genus into three "super-groups", the *A. pierus*, *A. thyra* and *A. aranda* groups, and determined their relationship according to wingshape, upperside markings and h/w underside markings of
the males. The genus currently includes over 50 described species, some of which are of doubtful status.

**ERIKSSON/A TRIMEN (Plates 2 & 3, fig. 12)**

*Erikssonia* Trimen, 1891.

**Type species:** *Erikssonia acraeina* Trimen, 1891, by monotypy.

**Diagnosis:** Brightly coloured orange and red, structurally similar to *Aloeides* but showing a superficial resemblance to *Acraea*. F/w with 12 veins. Head small but with long palpi. Spicules on male tibia present, formula e-e-a. Male foretarsal claw very sharp, unaccompanied by spines. DNO present in the larval stages (Henning & Henning, 1984). Genitalia (figs. 47, 87, 120, 160): as for *Aloeides* but aedeagus longer than in *Aloeides piersus*.

**Larval host-plant:** Life history of *E. cooksoni* Neave, is not known; host-plant of *E. acraeina Gnidia kraussiana* Meisner (Thymelaceae) (Henning & Henning, 1984).

**Associated ant:** *Lepisiota* sp. (= *Acantholepis*) (Henning & Henning, 1984).

**Distribution:** *E. cooksoni* is known from southern Zaire and may possibly occur in Zambia. *E. acraeina* has been recorded from Northern Namibia (Owamboland), eastern Zambia and the northern part of South Africa (Transvaal).

**Generic affinities:** *Erikssonia* shares exactly the same type of genitalia with *Aloeides*, thereby demonstrating an exceptionally close relationship between these genera.

**Comments:** The structure of their genitalia, their facies and their association with *Lepisiota* ants suggests that *Erikssonia* and *Aloeides* are congeneric; however, the head of *Erikssonia* is rather smaller. Differences in their life histories are not necessarily generic characteristics and the life histories of very few *Aloeides* species are known at this stage, hence the precise status of *Erikssonia* is not certain. DNA studies may provide more comparative information. The genus currently comprises only two species, *E. acraeina* and *E. cooksoni*.

**APHNAEUS HÜBNER (Plates 2 & 3, figs. 14 & 15)**

*Aphnaeus* Hübner, [1819] in Hübner [1816-[1826]]

**Type species** *Papilio orcas* Drury, 1782, by subsequent designation (Scudder, 1875). = *Paraphnaeus* Thierry-Mieg, 1904. Type species *Aphnaeus hutchinsonii* Trimen, 1887 (syn. Stempffer, 1954: 516)

**Diagnosis:** Fast-flying, fairly large lycaenids, in size and wingshape similar to *Spindasis* species. F/IN with 12 veins, h/w with a filiform tail at CuA₂ & 1A+2A, the tail at CuA₂ stunted in some species and absent altogether in others. Eyes clothed in fine short hairs in *A. orcas* but less densely so in other species. Palpi fairly long, thorax robust. Male tibial spicules absent, formula 0-0-0, foretarsus rounded at its tip and armed with a clump of spines (fig. 4c) not ending in a sharp claw (figs. 4a & 4b) as in other Aphnaeini; tibia and femur of the male foreleg about the same length but tarsus considerably shorter. Female abdomen without dense tuft of scales. DNO present in third and subsequent larval instars (Clark & Dickson, 1971). Genitalia (figs. 48-49, 88-90, 121-122, 161-163): uncus in the form of a narrow strip similar to *Aloeides* but subunci
slightly longer and not swollen at their bases; valves bifid for distal third, upper portion narrow and lower portion much broader with a rounded apex and folded under upper portion; juxta as in *Aloeides* but variable between species; aedeagus curved slightly down, with a dorsal swelling on internal portion, its external portion with some small spines on lateral surface; vesica with numerous cornuti and several small spines where it attaches to aedeagus.

**Larval host-plants:** *Acacia*, *Julbernardia*, *Burkea*, *Entada*, (Fabaceae), *Loranthus* (Loranthaceae) (Pringle *et al.*, 1994); *Rhus* (Anacardiaceae), *Paulina*, *Blighia* (Sapindaceae), *Alchornea* (Euphorbiaceae), *Olea* (Oleaceae) (Bampton, pers. comm.). *A. adamsi* Stempffer has been recorded as accepting ant regurgitations (Pierce, 1995).

**Associated ant:** *Crematogaster* sp. (Pringle *et al.*, 1994)

**Distribution:** Woodland and forest throughout Africa, from South Africa to western Africa and Sudan.

**Generic affinities:** Probably related to *Aloeides* as evidenced by the shape of the uncus and the valves.

**Comments:** *Aphnaeus hutchinsonii* Trimen, 1887 was placed in that genus by its author, but Thierry-Mieg (1904) later erected a genus *Paraphnaeus* for this species based on the rounded shape of the underside spots. Stempffer (1954) first expressed the opinion that it should fall under *Aphnaeus* but subsequently (Stempffer, 1967) treated *Paraphnaeus* as a distinct genus, stating as reason, differences in the juxta and aedeagus of *A. hutchinsonii*. The shape of the underside spots is certainly not a generic character, nor is it unique to *A. hutchinsonii*. From the description of *A. adamsi* Stempffer, 1954 it is evident that its juxta is almost identical to that of *A. hutchinsonii*, a similarity that Stempffer (1967) clearly overlooked. Also, the aedeagus of *A. hutchinsonii* (fig. 163) is similar to those of both *A. affinis* Riley (fig. 162) and *A. orcas* Drury (fig. 161) and quite typical of *Aphnaeus*. No characteristics were found that justify retaining *Paraphnaeus* as a distinct genus or even subgenus, it is therefore here treated as a synonym of *Aphnaeus*, as Stempffer (1954) did initially. There are 20 species.

**TYLOPAEDIA TITE & DICKSON (Plates 2 & 3, fig. 13)**


**Type species** *Zeritis sardonyx* Trimen, 1868, by original designation.

**Diagnosis:** F/w with 12 veins, h/w with a very short tail at vein 1A+2A. Palpi long. Spicule on male foretibia barely evident, formula a-c-b; male foreleg femur and tarsus of similar length but tibia much shorter, mesotarsus and metatarsus very long. Female abdomen without dense tuft of scales. DNO present in the larval instars (Schlosz & Brinkman, 1991). Genitalia (figs. 50, 91, 123, 164) uncus oval, distal margin slightly convex and with a median point; valves broadly bifid at their distal extremities, apices broad and rounded, the upper portion longer and lower portion curled under upper portion, valve upper surfaces linked by a very narrow v-shaped band, weakly sclerotized medially; aedeagus massive, particularly the internal portion which possesses a large unsclerotized dorsal swelling (also present in *Aphnaeus*), external portion sculptured above in a wave-like formation, internal cornuti very prominent,
composed of a scrolled mat of small spikes; juxta exceptional in being equipped
with a pair of long rod-like processes extending distally, a little beyond the lower
valve apices; saccus rounded.

**Larval host-plants:** *Euclea undulata* Thunb. (Ebenaceae) recorded for *T. s.
sardonyx* (Schlosz, 1996), *Aspalathus spinosa* L. (Fabaceae) (Schlosz &
Brinkman, 1991) and *Phylica oleaeifolia* Vent. (Rhamnaceae), (Heath, unpubl.)
for *T. s. peringueyi* (Aurivillius). Previously thought to be aphytophagous by

**Associated ant:** *Crematogaster* sp. nr. *melanogaster* Emery (Schlosz &

**Distribution:** Endemic to South Africa. The nominate subspecies flies in the
Karoo and Namaqualand as well as the southern and eastern Cape, whilst
*T. s. peringueyi* is confined to the Western Cape Province from Piketberg
northwards almost as far as Vanrhynsdorp; both subspecies fly on exposed
rocky hillsides.

**Generic affinities:** The closest genus appears to be *Aphnaeus*, whose
wingshape, uncus, valves, aedeagus and facies are similar, but the sharp
foretarsal claw, foretibial spicule, much longer tarsi and unusual juxta (fig. 164)
in *Tylopaedia* justify retaining separate generic status.

**Comments:** A monotypic genus with two subspecies: *T. s. sardonyx* and
*T. s. peringueyi.*

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**PHASIS HUBNER (Plates 2 & 3, fig. 19)**

*Phasis* Hübner, [1819) in Hübner [1816-(1826))

**Type species:** *Papilio salmoneus* Cramer, 1781 (*Papilio thero* L., 1764) by
subsequent designation (Scudder, 1875).

**Diagnosis:** Large brown lycaenids with some orange upperside markings and
silvery-grey markings on the underside. F/w with 12 veins, h/w with a short tail
at 1A+2A and another at CuA2 which is stunted or absent in some species.
Head broad, palpi long, thorax robust Spicules present on second and third legs
only, formula 0-c-b. Male foretarsal claw sharp, unaccompanied by spines.
Female abdomen without distal tuft of scales. DNO thought to be present in the
third and subsequent larval instars (Clark & Dickson, 1971), however such an
organ not detected by Malicky (Clark & Dickson, 1971: 200), possibly becoming
redundant in final instar. Genitalia (figs. 51, 92, 124, 165): uncus subrectangular
with rounded lateral angles; tegumen oval; subunci strongly curved and swollen
at bases; valves with serrated spatulate apices, curved slightly inwards, their
upper sclerotized surfaces touching but not joined except by a membrane; juxta
composed of a v-shaped strap beneath the aedeagus and equipped with a pair
of pointed processes extending for a short distance distally; aedeagus very
short and stout with its internal portion swollen, constricted in the middle, apex
truncated obliquely to create a large opening; very prominent internal cornuti
composed of numerous fine spikes; saccus prominent and triangular with a
rounded apex.

**Larval host-plants:** *Rhus* (Anacardiaceae) (Dickson, 1965, 1968) and
*Melianthus* (Melianthaceae) (Clark & Dickson, 1971).

**Associated ant:** *Crematogaster peringueyi* Emery apparently associated with
all four known species.
**Distribution:** Endemic to South Africa, in the southern and western regions.

**Generic affinities:** In its spatulate valves (figs. 165-169) *Phasis* is similar to *Argyraspodes* (fig. 34), and to *Tylopaedia* in its uncus (fig. 51), however, its short broad aedeagus (fig. 92), together with its facies, make *Phasis* unlike any other genus of the tribe.

**Comments:** There are four known species in this genus, *P. thero*, *P. braueri* Dickson, *P. clavum* Swanepoel and *P. pringlei* Dickson.

**DISCUSSION AND CONCLUSIONS**

The life histories of many of our lycaenids were described by Clark & Dickson (1971), who, with their excellent detailed illustrations and many other publications, formed a suitable foundation for Cottrell's (1978, 1984) studies of lycaenid larval feeding behaviour. Clark & Dickson (1971) used *Zygophyllum* and *Aspalathus* extensively as host-plants when rearing larvae, although these were not always determined as the host-plants in nature. Cottrell (1978) noted that other authors have since, assumed these to be natural host-plants. The current knowledge of larval host-plants and associated ants of *Chrysoritis* species is summarised in Table 4 with annotations of whether the associations are assumed, based upon oviposition (either natural or captive) or proven (found tending the larvae). From Table 4 it is evident that *Theesium* is a very widely exploited natural larval hostplant, a fact that had not been recognised when Cottrell (1978, 1984) investigated larval feeding behaviour. *Theesium* may prove to be a host-plant of many more *Chrysoritis* species than recorded thus far. This study shows that most, if not all, *Chrysoritis* species are species-specific to their host-ant as far as female oviposition is concerned, although nothing is known about the behaviour towards these larvae by other ant species. One exception may occur in *C. pyroeis* the larvae of which have been observed many times being tended only by *Myrmicaria nigra* (Mayr) ants. Dickson (1948) recorded both *M. nigra* and *Camponotus dicksoni* Arnold ants "milking" a larva but did not indicate which of the two ‘tended’ the larvae. It is probable that the presence of *Camponotus dicksoni* was a facultative event and that oviposition is obligate and specific only regarding *M. nigra*.

The accurate identification of ants is not only a pre-requisite in the study of ant-butterfly relationships but it is also a key to the taxonomy and possibly the phylogeny of lycaenid butterflies. It has been shown (Table 4) that *Chrysoritis* are essentially ant-species specific, and mostly associated with *Crematogaster* species, however, the provisional nature of the ant identification at present is not satisfactory and needs to be investigated, particularly for *C. peringueyi* Emery, *C. liengmei* Forel and *C. melanogaster* Emery.

The development of a DNO varies among those species of *Aloeides* whose life history is known, being present in the third and subsequent instars of *A. pierus* (Cramer), *A. gowani* Tite & Dickson and *A. aranda* (Wallengren) (Clark & Dickson, 1971) but absent in *A. dentatis* Swierstra (Henning, 1983), *A. thyra* L. and *A. depicta* Tite & Dickson (Clark & Dickson, 1971; Claassens & Dickson, 1980). The presence of a DNO is a significant characteristic and needs further investigation in the *Aloeides*, where its presence can vary between larval
stages and between species. *Aloeides* species are known to have myrmecophilous relationships with *Lepisiota* sp. (= *Acantholepis*) (Claassens & Dickson, 1974; Henning & Henning, 1982; Henning, 1983), but this is a generalisation based on the published information of only a few species and yet there are over 40 described species in this genus whose associated ants and host-plants are still unknown. There is a dire need to address this huge gap in our knowledge. In an introductory note on *Aloeides*, D'Abrera (1980) stated "This is a most contentious group. I am not convinced of the validity of many of the taxa proposed, particularly in recent years". Currently 110 species are recognised in *Chrysoritis* and *Aloeides* together, most of whose specific status is based on facial characteristics alone, and hence their taxonomic status is questionable. There are two possible reasons for this.

**Evolutionary spurt**

The remarkable uniformity of the genitalia of *Chrysoritis* is also apparent to some degree in all genera of Aphnaeini, all of which are ant-associated and many, like *Chrysoritis*, have an obligate and host-specific relationship with ants (Fiedler, 1991). This uniformity of genitalia is also evident in strongly ant-associated lycaenid genera outside the Aphnaeini, such as *Thestor* Hübner and *Lepidochrysops* Hediecke (Stempffer, 1967: 183, 228; Fiedler, 1991: 160, 192). This phenomenon contrasts greatly with the genital variation in genera such as *Iolaus* Hubner, *Leptotes* Scudder and *Tarucus* Moore, etc. which are not obligately associated with ants (Fiedler, 1991: 170-188) and whose genitalia exhibit wide variations between superficially identical species (Stempffer, 1967: 122, 216, 220; Heath, 1983: 150-161). The assumption that ant-association correlates with genitalic uniformity is admittedly subjective and certainly untested for other regions of the world, but it appears to have validity for the Afrotropical region. It seems plausible to conclude from this that speciation of myrmecophilous taxa is a much faster process than the usual evolutionary differentiation of specific genitalic characters. Such a hypothesis suggests that taxa with ant-specific associations and similar genitalia are very modern in evolutionary terms and that perhaps myrmecophily itself is a fairly recent development.

Further study is required into the relationships between the different aphnaeine taxa to determine the true phylogeny of those that are apparently in the process of speciation, particularly *Chrysoritis* whose ant relationships are an important key to our understanding of this process.

**Unscientific naming**

The naming of many South African butterfly taxa in recent years has seldom been supported by any substantial evidence based on differences in the structure of the egg, larval stages or adult, nor in their specific ant associations. As a result, it is probable that a large number of our described 'species' are, in reality, no more than local forms. The assumption that genitalia do not differ significantly between closely related taxa has encouraged authors to confidently describe and name taxa based on superficial and often very minor characters. It is advocated that these inappropriately named taxa be recognised as such and their correct status be determined, of course a much more difficult task than it was to quickly name them in the first place.
Plate 1, Figs. 1-2. *Pseudaletis agrippina*: 1, upperside; 2, underside
Plate 2. Figs. 1-24. Aphnaeini uppersides: 1, Lipaphnaeus aderna; 2, Chloroselas esmeralda; 3, C. mazoensis; 4, Crudaria leroma; 5, Jacksonia waggae; 6, Cigaritis zohra; 7, Spindasis epargyros; 8, S. natalensis; 9, Zeritis neriene; 10, Axiocerses harpax; 11, Aloeides pierus; 12, Erikssonia acraeina; 13, Tylopaedia sardonyx; 14, Aphnaeus areas; 15, A. hutchinsonii; 16, Trimenia m. malagrida; 17, T. wallengrenii; 18, Chrysoritis dicksoni; 19, Phasis c. clavum; 20, Argyraspodes argyraspis; 21, Chrysoritis areas; 22, C. lycegenes; 23, C. phosphor; 24, C. thysbe.
Plate 3. Figs. 1-24. Aphnaeini undersides: 1, Lipaphnaeus aderna; 2, Chloroselas esmeralda; 3, C. mazoensis; 4, Crudaria leroma; 5, Jacksonia waggae; 6, Cigaritis zohra; 7, Spindasis epargyros; 8, S. natalensis; 9, Zeritis neriene; 10, Axiocerses harpax; 11, Aloeides pierus; 12, Erikssonia acraeina; 13, Tylopaedia sardonyx; 14, Aphnaeus areas; 15, A. hutchinsonii; 16, Trimenia m. malagrida; 17, T. wallengrenii; 18, Chrysoritis dicksoni; 19, Phasis c. clavum; 20, Argyraspodes argyraspis; 21, Chrysoritis oreas; 22, C. lycegenes; 23, C. phosphor; 24, C. thysbe.
Plate 4, Figs. 1-4. SEM photographs of cornuti in Chrysoritis species: 1, C. thysbe; 2, C. nigricans; 3, C. felthami; 4, C. zonarius.
them in the first place. It is hoped that a more scientific approach is adopted in future, and to this end it is urged that stricter criteria be applied by journal publishers in accepting descriptions of new taxa.

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| 233 |

* Afrotropical region only.
# Only first & final instar known to date; these were without DNO.
## May lack a DNO in final instar.
$ DOs also present in late instars
$$ All those observed had a DNO
### Table 2

**Associated Ant Genera**

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(*= Acanthopis, Camponius, Myrmecia, *Crematogaster*, *Philidole*).
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* Possibly Algae (Collins, pers. com.)
** Suspected of being aphytophagous (Cotterell, 1984; Heath & Brinkman, 1995b).
# C. dicksoni (Gabriel) is most probably aphytophagous; first and second instar larvae solicit ant regurgitations; also a possible association exists with armoured scale (Heath & Brinkman, 1995a).
### Some species of Chloroselas, Spindasis, Axioceres and Aphnaeus also recorded as accepting ant regurgitations (Pierce, 1995)
HOST-PLANT AND ANTS ASSOCIATED WITH CHRYSORITIS

The following references to Crematogaster sp. nr liengmei Forel and Crematogaster sp. nr. peringueyi Emery represent their current status. However they may each represent species groups, hence where Robertson examined the relevant Crematogaster material he provisionally categorised each taxon as "sp.1", "sp.2", etc. Each of these ant taxa is shown below with the South African Museum "SAM-HYM" accession numbers.

The following references attributable to an author in respect of ant associations or host-plant are as follows:

[L/P]: Ants observed tending the larvae or pupae. - Larvae or pupae found on or beneath the plant.
[Ov]: Ants in the butterfly's habitat provided stimulation for oviposition. - Oviposition on the plant was observed.
[Vi]: Ants found in the butterfly's habitat but stimulation of female not confirmed. - Probable host-plant; found in vicinity.
[U]: Unspecified reference to the ant. - Unspecified reference to a host-plant.

### C. CHRYSAOR SPECIES GROUP

**C. chrysaor** (Trimen, 1864) - Coastal material  
Host-plant: *Cotyledon orbiculata* L. (Crassulaceae) [L/P] and *Rhus* sp. (Anacardiaceae) [Ov] (Dickson, 1943)  
Ant: Crematogaster *liengmei weilzaeckeri* Emery, det. G. Arnold [L/P] (Dickson, 1943). Crematogaster sp.4 (C009862) det. Robertson, [Vi] (Heath, unpubl.)

**C. chrysaor** (Trimen, 1864) - Inland, montane material  
Host-plant: *Acacia karoo* Hayne (Fabaceae); *Zygophyllum retrofractum* Thunb. (Zygophyllaceae) [Ov] (Heath, unpubl.)  
Ant: Crematogaster sp. nr. *liengmei* For. [Ov] (Heath, unpubl.)

**C. lycia** (Riley, 1938)  
Host-plant: *Tylecodon paniculata* (L.f.) Tŏlken (Crassulaceae) [Ov] (Heath, unpubl.)  
Ant: Crematogaster sp. nr. *liengmei* For. [Ov] (Heath, unpubl.)

**C. midas** (Pennington, 1963)  
Host-plant: *Diospyros austro-africana* De Winter var. *microphylla* (Ebenaceae); [L/P] (Heath, unpubl.)  
Ant: Crematogaster sp. nr. *liengmei* For. [U] (Dickson et al., 1978)

**C. natalensis** (Van Son, 1966)  
Host-plant: *Chrysanthemoides monilifera* (L.) Nori. (Asteraceae); *Cotyledon orbiculata* L. (Crassulaceae) [U] (Dickson et al., 1978)  
Ant: Unknown, probably Crematogaster sp. [U] (Heath, unpubl.)

**C. phosphor** (Trimen, 1868)  
Host-plant: Unknown  
Ant: Unknown but suspected to be arboreal Crematogaster sp. [U] (Heath, unpubl.)

**C. aethon** (Trimen, 1887)  
Host-plant: *Rhus zeyheri* Sond. (Anacardiaceae) [L/P] (Owen-Johnson, 1991)  
Ant: Crematogaster sp. [L/P] (Owen-Johnson, 1991)

**C. aureus** (Van Son, 1966)  
Host-plant: *Clutia galpinii* (= *C. pulchella*) (Euphorbiaceae) [L/P] (Henning, 1983)  
Ant: Crematogaster sp. [L/P] (Henning, 1983)

**C. lyncurium** (Trimen, 1868)  
Host-plant: *Diospyros* sp. (Ebenaceae) [U] (Owen-Johnson, 1991)  
Ant: Crematogaster sp.1 (C009251) det. Robertson, [Vi] (Heath, unpubl.)

**C. lycegenes** (Trimen, 1874)  
Host-plant: *Myrsine africana* L. (Myrsinaceae); *Diospyros lycioides* Desf.; *D. austro-africana* De Winter (Ebenaceae); *Rhus* sp. (Anacardiaceae). [L/P] (Henning, 1983)  
Ant: Crematogaster sp. nr. *liengmei* Forel [L/P] (Henning, 1983). Crematogaster sp.1 (C009860) det. Robertson, [L/P] (Heath, unpubl.)
C. DICKSONI SPECIES GROUP

C. dicksoni (Gabriel, 1847)

Larval food: Believed to be aphytophagous (Clark & Dickson, 1971). Trophallaxis confirmed (Heath & Brinkman, 1995a) Ant: Crematogaster peringueyi Emery [L/P] (Clark & Dickson, 1971) also [L/P] (Heath & Brinkman, 1965a)

C. oreas (Trimen, 1891)
Host-plant: Thesium sp. (Santalaceae) [Ov] (Heath, unpubl.)
Ant: Myrmicaria sp. nr. nigra det. Robertson, [Ov] (Heath, unpubl.)

C. zeuxo (Linnaeus, 1764)
Host-plant: Chrysanthemoides monilifera (L.) Norl. (Asteraceae) [Ov] (Dickson, 1952)
Ant: Crematogaster sp. 1 (C009864) det. Robertson, [Ov] (Heath, unpubl.)

C. cottrelli (Dickson, 1975)
Host-plant: Chrysanthemoides monilifera (L.) Norl. (Asteraceae) [Vi] (Dickson, 1975)
Ant: Crematogaster sp. 7 (C007956) det. Robertson, [Vi] (Heath, unpubl.)

C. zonarius (Riley, 1938)
Host-plant: Chrysanthemoides incana (Burm. f.) Norl. (Asteraceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster peringueyi Emery [L/P] (Heath, unpubl.)

C. coetzeri Dickson, 1994
Host-plant: Unknown. Ant: Unknown

C. chrysantas (Trimen, 1868)
Host-plant: Unknown. Ant: Unknown

C. felthami (Trimen, 1904)
Host-plant: Zygophyllum sessilifolium; Z. flexuosum Eckl. & Zeyh. (Zygophyllaceae) [L/P] (Dickson, 1940)
Ant: Crematogaster peringueyi Emery [L/P] (Heath, unpubl.)

C. pyroeis (Trimen, 1864)
Host-plant: Zygophyllum spp. including Z. flexuosum Eckl. & Zeyh. (Zygophyllaceae) [L/P] (Dickson, 1948), Thesium sp. (Santalaceae) [L/P] (Heath, unpubl.)
Ant: Myrmicaria nigra (Mayr, 1862) [L/P] (Dickson, 1948) also det. Robertson, (C006744) [L/P] (Heath, unpubl.) Camponotus dicksoni Arnold (as Camponotus sp.) was also observed at DNO (Dickson, 1948).
Note: M. nigra ants have been observed sheltering and closely tending C. pyroeis larvae on over ten separate occasions but Dickson’s observation of Camponotus has not been repeated (Heath, unpubl.). Further confirmation may be required of Camponotus dicksoni being associated.

C. THYSBE SPECIES GROUP

C. aridus (Pennington, 1954)
Host-plant: Chrysanthemoides incana (Burm. f.) Norl. (Asteraceae) [Ov] (Dickson, 1965)
Ant: Unknown but suspected to be Crematogaster sp. [U] (Heath, unpubl.)

C. turneri (Riley, 1938)
Host-plant: Zygophyllum. (Zygophyllaceae) [Ov] (Dickson, 1953)
Ant: Unknown but suspected to be Crematogaster sp. nr. liengmei For. [U] (Heath, unpubl.)

C. wykehami (Dickson, 1980)
Host-plant: Dimorphotheca cuneata (Thunb.) Less. (Asteraceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp. nr. liengmei For. [L/P] (Heath, unpubl.)

C. blencathra (Heath & Ball, 1992)
Host-plant: Dimorphotheca venusta (T. Norl.) T. Norl. (Asteraceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp. 6 (C006753) det. Robertson, [Ov] (Heath, unpubl.)
C. palmus (Cramer, 1781)
Host-plant: Aspalathus sarcantha Vog. (Fabaceae) [Ov] (Dickson, 1953); Chrysanthenoides monilifera (L.) Norl. (Asteraceae) [Ov] (Dickson, 1965); Berzelia intermedia Schidl.; B. lanuginosa Brongn., B. abrotanoides Brongn., (Bruniaceae) [Ov] (Dickson, 1944)
Ant: Crematogaster peringueyi Emery var. angustior Arn. [L/P] (Clark & Dickson, 1971)

C. brooksi brooksi (Riley, 1938)
Host-plant: Thesium sp. (Santalaceae) [L/P] (Heath, unpubl.) Zygophyllum sp. (Zygophyllaceae) [L/P] (Schlosz, pers. comm.); Aspalathus spinosa L. (Fabaceae) [L/P] (Dickson, 1959) NB. For this record, see under Biology above.
Ant: Crematogaster peringueyi Emery [L/P] (Dickson, 1959)

C. brooksi tearei (Dickson, 1967)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp.3 (C006746) det. Robertson: [L/P] (Heath, unpubl.)

C. trimeni (Riley, 1938)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp. [L/P] (Heath, unpubl.)

C. pan (Pennington, 1963)
Host-plant: Chrysanthemoides incana (Burm. f.) Norl. (Asteraceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp.1 (C009861) det. Robertson, [L/P] (Heath, unpubl.)

C. atlantica (Dickson, 1967)
Host-plant: Chrysanthemoides incana (Burm. f.) Norl. (Asteraceae) [Ov] (Heath, unpubl.)
Ant: Crematogaster sp. nr. liengmei For. [Ov] (Heath, unpubl.)

C. williami nom. n. (formerly Poecilmitis dicksoni Henning, 1977)
Host-plant: Osteospermum sp. (Asteraceae) and Zygophyllum sp. (Zygophyllaceae) [Ov] (Heath, unpubl.)
Ant: Crematogaster sp.1 (C006745) det. Robertson, [Ov] (Heath, unpubl.)

C. perseus (Henning, 1977)
Host-plant: Zygophyllum sp. (Zygophyllaceae) also Thesium sp. (Santalaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp. nr. melanogaster Emery det. Robertson, [UP] (Heath, unpubl.)

C. rileyi (Dickson, 1967)
Host-plant: Thesium sp. (Santalaceae) and Aspalathus sp. (Fabaceae) [Ov] (Schlosz, pers. comm.)
Ant: Crematogaster peringueyi Emery [Ov] (Heath, unpubl.)

C. henningi (Bampton, 1981)
Host-plant: Zygophyllum retrofractum Thunb. (Zygophyllaceae) [Ov] (Heath, unpubl.)
Ant: Crematogaster sp. 1 (C006747) det. Robertson, [Ov] (Heath, unpubl.)

C. lysander (Pennington, 1963)
Host-plant: Zygophyllum (Zygophyllaceae) [Ov] (Dickson, 1965)
Ant: Unknown

C. azurius (Swanepoel, 1975)
Host-plant: Unknown
Ant: Unknown but suspected to be Crematogaster sp. [VI] (Heath, unpubl.)

C. psyche (Pennington, 1967)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster peringueyi Emery [L/P] (Heath, unpubl.)

C. lyndseyae (Henning, 1979)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster peringueyi Emery [L/P] (Heath, unpubl.)
C. bamptoni (Dickson, 1976)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [L/P] (Dickson, 1976); Lebeckia plukenetiana E. May. (Fabaceae) [U] (Pringle et al., 1994)
Ant: Crematogaster sp. 3 (C006755) det. Robertson, [L/P] (Heath, unpubl.)

C. thysbe (Linnaeus, 1764)
Host-plant Lebeckia plukenetiana E. May. (Fabaceae) [L/P] (Clark & Dickson, 1971); Zygophyllum sp. (Zygophyllaceae); Chrysanthemoides incana (Burm. f.) Norl. (Asteraceae) [Ov] (Dickson, 1952); Thesium sp. (Santalaceae), Aspalathus sp. (Fabaceae), Osteospermum polygaloides L. (Asteraceae) and Zygophyllum sp. (Zygophyllaceae) [all L/P] (Heath, unpubl.)
Ant: Crematogaster peringueyi Emery [L/P] (Heath, unpubl.)

C. mithras (Pringle, 1995)
Host-plant: Unknown
Ant: Unknown but suspected to be Crematogaster peringueyi [U] (Heath, unpubl.)

C. whitei (Dickson, 1994)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [U] (Pringle et al., 1994); Chrysanthemoides monilifera (L.) Norl. (Asteraceae) [Ov] (Heath, unpubl.).
Ant: Crematogaster peringueyi Emery [Ov] (Heath, unpubl.)

C. pyramus (Pennington, 1954)
Host-plant: Osteospermum asperulum (D.C.) T. Norl. (Asteraceae) [L/P], Thesium sp. (Santalaceae) [Vi] (Heath, unpubl.)
Ant: Crematogaster sp. 3 (C006752) det. Robertson, [L/P] (Heath, unpubl.)

C. balli (Dickson, 1980)
Host-plant: Dimorphotheca montana T. Norl. (Asteraceae) and Thesium sp. (Santalaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster sp. 3 (C009480) det. Robertson, [L/P] (Heath, unpubl.)

C. daphne (Dickson, 1975)
Host-plant: Thesium sp. (Santalaceae) [Ov] (Heath, unpubl.)
Ant: Crematogaster sp. 8 (C009481) det. Robertson, [Ov] (Heath, unpubl.)

C. pluitus (Pennington, 1967)
Host-plant: Thesium sp. (Santalaceae) [L/P] (Heath, unpubl.)
Ant: Crematogaster peringueyi Emery [L/P] (Heath, unpubl.)

C. braueri (Pennington, 1967)
Host-plant: Zygophyllum sp. (Zygophyllaceae) [U] (Clark & Dickson, 1971); Myrsine africana (Myrsinaceae) [Vi] (Heath, unpubl.).
Ant: Crematogaster sp.4 (C007958) det. Robertson, [Vi] (Heath, unpubl.).

C. beulah (Quickelberge, 1966)
Host-plant: Unknown
Ant: Unknown

C. irene (Pennington, 1968)
Host-plant: Unknown
Ant: Unknown

C. penningtoni (Riley, 1938)
Host-plant: Unknown
Ant: Crematogaster sp.8 (C009253) or sp.1 (C009250) det. Robertson, [Vi] (Heath, unpubl.)

C. pelion (Pennington, 1954)
Host-plant: Unknown
Ant: Unknown

C. orientalis (Swanepoel, 1976)
Host-plant: Thesium sp. (Santalaceae) [L/P] (Heath & Joubert, unpubl.)
Ant: Crematogaster sp. 7 (C009252) det. Robertson, [L/P] (Heath, unpubl.)
C. swanepoeli (Dickson, 1965)
Host-plant: *Thesium* sp. (Santalaceae) *Tylecodon paniculata* (L.f.) Tölken (Crassulaceae) [L/P] (Heath, unpubl.)
Ant: *Crematogaster* sp. nr. *liengmei* For. [L/P] (Heath, unpubl.)

C. hyperion (Dickson, 1975)
Host-plant: Unknown but suspected to be *Thesium* sp. (Santalaceae) [VI] (Heath, unpubl.)
Ant: Unknown but suspected to be *Crematogaster* sp. [VI] (Heath, unpubl.)

C. endymion (Pennington, 1963)
Host-plant: *Thesium* sp. (Santalaceae) [Ov] and *Thesidium* sp. (Santalaceae) [VI]. (Bampton, pers. comm.)
Ant: *Crematogaster* peringueyi Emery [Ov] (Heath, unpubl.)

C. violescens (Dickson, 1971)
Host-plant: *Dimorphotheca cuneata* (Thunb.) Less. (Asteraceae) [Ov] (Heath, unpubl.)
Ant: *Crematogaster* peringueyi Emery [Ov] (Heath, unpubl.)

C. beaufortia (Dickson, 1966)
Host-plant: *Dimorphotheca cuneata* (Thunb.) Less. (Asteraceae) [Ov] (Heath, unpubl.)
Ant: *Crematogaster* peringueyi Emery [Ov] (Heath, unpubl.)

C. stepheni (Dickson, 1979)
Host-plant: *Dimorphotheca cuneata* (Thunb.) Less. (Asteraceae) [Ov] (Heath, unpubl.)
Ant: *Crematogaster* peringueyi Emery [Ov] (Heath, unpubl.)

C. kaplani (Henning, 1979)
Host-plant: *Osteospermum amplectens* (Harvey) T. Norl. (Asteraceae) (very similar to *Dimorphotheca cuneata* with which it was previously confused) [Ov] (Heath, unpubl.)
Ant: *Crematogaster* peringueyi Emery [L/P] (Heath, unpubl.)

C. nigricans (Aurivillius, 1924)
Host-plant: *Thesium* sp. (Santalaceae) [L/P] (Heath, unpubl.); *Osteospermum polygaloides* L. (Asteraceae). [Ov] (Dickson, 1947) and *Zygophyllum* sp. (Zygophyllaceae) [L/P] (Heath, unpubl.)
Ant: *Crematogaster* sp.7 (C005631 & C006768), sp.4 (C006749), sp.1 (C006751) det. Robertson, [L/P] (Heath, unpubl.) Note: The ants sampled were each taken from widely separate populations of this butterfly.

C. uranus (Pennington, 1963)
Host-plant: *Centella* sp. (Apiaceae) [L/P] Heath (unpubl.); *Aspalathus* sp. (Fabaceae), *Zygophyllum* sp. (Zygophyllaceae) [U] (Clark & Dickson, 1971)
Ant: *Crematogaster* sp. 5 (C006750) det. Robertson, [L/P] (Heath, unpubl.)

C. adonis (Pennington, 1963)
Host-plant: *Zygophyllum* sp. (Zygophyllaceae) [U] (Clark & Dickson, 1971); *Thesium* sp. (Santalaceae) [L/P] (Heath, unpubl.)
Ant: *Crematogaster* sp.1 (C007954) det. Robertson, [L/P] (Heath, unpubl.)
Figs. 1-4. Legs of male *Aloeides pierus* 1, foreleg; 2, midleg; 3, hindleg
Figs. 5-8. Types of spicule: 5a - f.
Venation of male 6, *Pseudaletis agrippina*; 7, *Jacksonia waggae*; 8, *Chrysoritis thysbe*
Figs. 57-73. Aedeagus: 57, Trimenia wallengrenii; 58, T. malagrida malagrida; 59, Argyraspodes argyraspis; 60, Spindasis natalensis; 61, S. ella; 62, S. epargyros; 63, S. nilus; 64, Cigaritis zohra; 65, Zeritis neriene; 66, Z. fonteinei; 67, Axiocerses amanga; 68, Axiocerses harpax; 69, Aloeides pierus; 70, Erikssonia acraeina; 71, Aphnaeus orcas; 72, A. affinis; 73, A. hutchinsonii.
Figs. 74-90. Aedeagus: 74, Chloroselas esmeralda; 75, C. mazoensis; 76, Vansomerenia rogersi; 77, Jacksonia wagga; 78, Crudaria leroma; 79, Chrysoritis thysbe; 80, C. pyroeis; 81, C. felthami; 82, C. chrysantas; 83, C. zonarius; 84, C. dicksoni; 85, C. oreas; 86, C. lycegenes; 87, C. chrysaor; 88, C. aethon; 89, C. aureus; 90, C. phosphor.
Figs. 91-102. Aedeagus: 91, Tylopaedia sardonyx; 92, Phasis thero. Lateral view of uncus and left valve: 93, Pseudaletis agrippina; 94, Lipaphnaeus leonina bitje; 95, Lipaphnaeus aderna; 96, Chloroselas overlaeti; 97, C. esmeralda; 98, C. pseudozeritis; 99, C. mazoensis; 100, Vansomerenia rogersi; 101, Jacksonia waggae; 102, Crudaria leroma.
Figs. 115-124. Lateral view of uncus and left valve: 115, Zeritis fonteinei; 116, Z. neriene; 117, Axiocerses amanga; 118, Axiocerses harpax; 119, Aloeides pierus; 120, Erikssonia acraeina; 121, Aphnaeus orcas; 122, A. hutchinsonii; 123, Tylopaedia sardonyx; 124, Phasis thero.
Figs. 133-140. Dorsal view with uncus removed: 133, Jacksonia waggae; 134, Crudaria leroma; 135, Chrysoritis thysbe; 136, C. oreas; 137, C. dicksoni; 138, C. phosphor, 139, Argyraspodes argyraspis; 140, Cigaritis zohra.
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