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Anoplolepis steingroeveri (Forel, 1894) (Hymenoptera: Formicidae), a new associated ant species record for myrmecophilous butterflies in Africa and new host-plant records for *Crudaria* (Wallengren, 1875) (Lepidoptera: Lycaenidae: Aphnaeinae)

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Abstract: *Anoplolepis steingroeveri* is reported for the first time as an associated ant species for a myrmecophilous butterfly species in Africa. Two new host-plant species records for the genus *Crudaria* are noted; the geoxylic suffrutex *Elephantorrhiza elephantina* and the thorn tree *Vachellia hebeclada* subsp. *hebeclada*. The habitat of an apparently unique *Crudaria* population at Tswalu Kalahari Reserve is closest in profile to a sand ramp and contains both associated ant species *A. steingroeveri* and host-plant *E. elephantina*. A geoxylic suffrutex such as *E. elephantina* is an important alternative host-plant type in the harsh climate of the southern Kalahari but its use by *Crudaria* could be restricted by other factors such as depth of sandy soils and presence of appropriate associated ant species. Different kinds of sand dune ecosystems and plains adjacent to the Korannaberg Mountains and their use by different butterfly populations are indications of underestimated habitat diversity for butterflies in the southern Kalahari.

Key words: *Crudaria*, life history, host-plant species, *Elephantorrhiza*, *Vachellia*, geoxylic suffrutex, associated ant species, *Anoplolepis custodiens*, *Anoplolepis steingroeveri*, Kalahari sands

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INTRODUCTION

The discovery of a unique population of the genus *Crudaria* (Wallengren 1875) in October 2014 by the author at Tswalu Kalahari Reserve, Northern Cape, South Africa led to further ecological studies of this taxon, provisionally referred to as morpho-species *Crudaria* sp. TAS 6. The butterfly genus *Crudaria* belongs to the largely Afrotropical subfamily Aphnaeinae, which shows an unusual diversity of diets and types of symbiotic relationship (Boyle *et al*., 2014). The common ancestor of aphnaeines is likely to have been associated with myrmicine ants in the genus *Crematogaster* and plants of the order Fabales (Boyle *et al*., 2014). Only *Crudaria* and one other genus (*Trimenia*) in the Aphnaeinae are known to be associated with formicine ants in the genus *Anoplolepis* (Heath & Brinkman 1995, Heath 1997, Boyle *et al*., 2014). The three species currently recognized in genus *Crudaria* i.e. *Crudaria leroma* (Wallengren, 1857), *Crudaria capensis* (van Son, 1956) and *Crudaria wykehami* (Dickson, 1983) are restricted to southern and eastern Africa (Heath 1997; Boyle *et al*., 2014). The only ant species known to be associated with *Crudaria* is the large Pugnacious Ant *Anoplolepis custodiens* (Pringle *et al*., 1994).

The consensus among Lepidopterists is that the genus *Crudaria* deserves taxonomic work because there are likely to be undescribed taxa contained in the genus (Kielland, 1990; Pringle *et al*., 1994). Similar to other myrmecophilous genera in Africa, such as *Aloeides*, *Chrysoritis*, *Thestor* and *Lepidochrysops*, species of *Crudaria* could be difficult to distinguish on wing patterns and colouration alone. Compared to other myrmecophilous aphnaeine genera, such as *Aloeides* and *Chrysoritis*, the genus *Crudaria* appears to be neglected both in terms of taxonomy and ecology. Detailed studies of life histories, host-plants, associated ants and behavioural ecology could inform taxonomy, ecology and phylogeny of the genus.

This study is part of the Tswalu Kalahari Butterfly Project which is supported by the Tswalu Foundation and focuses on butterfly diversity and ecology in the field. New records of host-plants and attendant ants will hopefully stimulate further contributions of myrmecophilous butterfly life cycles to an encouraging initiative of the Lepidopterists' Society of Africa, the Caterpillar Rearing Group (Staude *et al*., 2016).

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STUDY AREA

Tswalu Kalahari Reserve (110, 000 ha) is located approximately 50 km west of Hotazel, Northern Cape Province, South Africa (Fig. 1). The landscape consists of the rugged Korannaberg Mountains, which are embedded in sandy plains and dune landscapes. Altitudes at Tswalu Kalahari Reserve range from 1000 to 1570 m.a.s.l. The Savanna Biome is represented by five vegetation types in the Tswalu Kalahari Reserve, of which four represent the Eastern Kalahari Bushveld Bioregion and one represents the Kalahari Duneveld Bioregion. The Eastern Kalahari Bushveld Bioregion experiences more than twice as much frost as the Central Bushveld Bioregion (Mucina & Rutherford 2006). Mean annual precipitation of vegetation types in the Tswalu Kalahari Reserve range from 180 to 380 mm (Mucina & Rutherford 2006). Tswalu Kalahari Reserve is therefore part of a semi-arid savanna with mean annual precipitation of less than 400 mm. Climatic conditions of the Eastern Kalahari Bushveld Bioregion and Kalahari Duneveld Bioregion are therefore harsh for butterflies compared to the Central Bushveld Bioregion and Lowveld Bioregion.

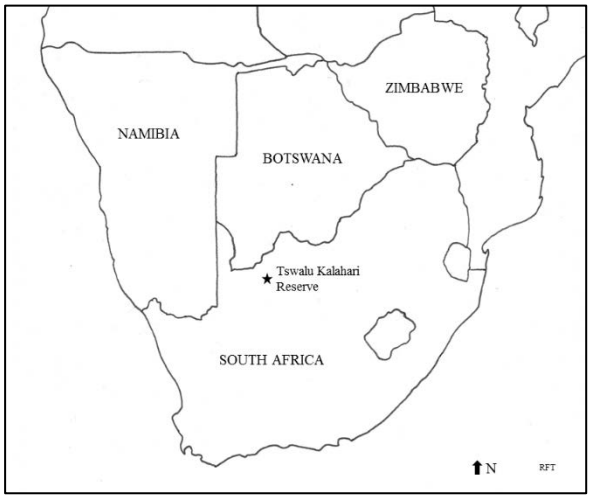

Figure 1 – Location of Tswalu Kalahari Reserve in southern Africa.

MATERIALS AND METHODS

Observations on the behaviour and ecology of *Crudaria* adults and larvae were made as part of the Tswalu Kalahari Butterfly Project, which commenced in July, 2013. A few *Crudaria* larvae that were found under the soil at the base of host-plants in the field were collected and raised to adults. In the field there is often more than one ant species at bases of the host-plants of myrmecophilous butterfly species so that much care has been taken to identify the correct associated ant species. Finding correct associated ant species was facilitated by 1) Careful digging around the base of the host-plant, 2) Repeated observations of larvae being sheltered and being among the associated ant species, and 3) Observing appropriate ant responses to parts of larvae that are specialised for myrmecophilous associations, such as when ants repeatedly feed from the dorsal nectary organ (DNO). Replications of observations and excavations were done selectively and with great care so that impacts on the ecosystem were minimized. Once enough information in the field had been obtained excavations immediately ceased. Larvae were raised indoors in clear plastic honey jars and fed with fresh leaves, or cut stems with leaves, of the host-plant species. A few ants were placed in these jars. Lids of jars were loosened during later instars to promote aeration and maintain a stable environment. Herbarium specimens of host-plants were collected by R.F. Terblanche according to Victor *et al*. (2004). Herbarium specimens were deposited in the A.P. Goossens Herbarium (Potchefstroom, North West Province) and McGregor Museum (Kimberley, Northern Cape Province).

Ant specimens were collected selectively in the field and preserved in > 90% ethanol; some of these specimens were kept in ethanol for future genetic work. Ant specimens for reference collections were then mounted singly on paper triangles following standard procedures as described by Lattke (2000). At least three major workers and minor workers of *Anoplolepis custodiens* and *Anoplolepis steingroeveri* of the colonies associated with *Crudaria*, were deposited in the AfriBUGS collection and the R.F. Terblanche collection (RT; Ant division). During August 2017, a collaboration between the author and AfriBUGS collection had been initiated. The AfriBUGS collection is a well-referenced collection which has an invertebrate reference collection, mainly of ant specimens, with the collection code AFRC (see The Insect and Spider Collections of the World) and which has links with AntWeb. Important sources used for characters and basic external morphology to identify the ants to subfamily and generic levels are Hölldobler & Wilson (1990) and Bolton (1994). Identification of *Anoplolepis* ant species by the author relied in particular on the latest revision of the genus by Prins (1982). Notes on ant identifications from discussions (including courses) with Peter Hawkes (AfriBUGS, South Africa), Hamish Robertson (Iziko South African Museum, South Africa) and Alan Andersen (CSIRO, Australia) were taken into account. Characters of ant taxa compiled for a preliminary annotated list of Gauteng ant species were consulted as well (Terblanche, 2003). Characters and ant species listed by Slingsby (2017) were also used as a helpful source.

RESULTS

Finding of *Crudaria* sp. TAS 6, new host-plant species records and associated ant species

A population of a small *Crudaria* of lighter colouration than *Crudaria leroma* was discovered by the author on 11 October 2014 on aeolian sands, 3 km east of Dedeben in the Tswalu Kalahari Reserve, at bottomlands of the Korranaberg Mountains (Figs 2–4). This finding is regarded as significant because this sandy habitat was only 3 km east of a flat area where the widespread, larger “normal” Silver-spotted Grey,

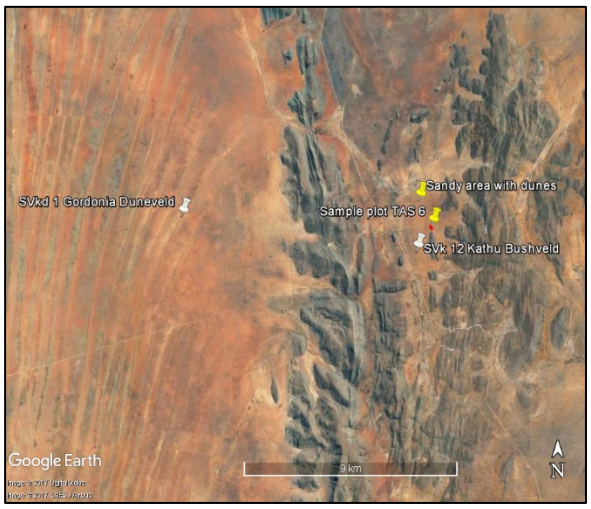

Figure 2 – Map of study area at Tswalu Kalahari Reserve indicating sand dunes west of Korannaberg in the Gordonia Duneveld vegetation type; sample plot TAS 6; and sandy area with dunes in the Kathu Bushveld vegetation type. Map information analysed and depicted on Google images with the aid of Google Earth Pro (US Dept. of State Geographer, MapLink/ Tele Atlas, Google, 2017).

Figure 3 – Map of study area at Tswalu Kalahari Reserve indicating Dedeben where "normal" *Crudaria leroma* was found in the Olifantshoek Plains Thornveld vegetation type, as well as sample plot TAS 6 in Kathu Bushveld where *Crudaria* sp. TAS 6 was found, 3 km east of Dedeben.

C. leroma occurs at Dedeben (Fig. 3). The taxon inhabiting the sands east of Dedeben was at once recognized as different (lighter colouring of upperside of wings; smaller size). This taxon is provisionally named *Crudaria* sp. TAS 6 and is the subject of further taxonomic and ecological studies. The code of the morpho-species refers to the ecosystem at sample plot TAS 6 where detailed vegetation and butterfly surveys take place as part of a larger butterfly project (Figs 2–4).

On 16 November 2014 oviposition behaviours of *Crudaria* sp. TAS 6 females were suspected when these females were observed flying between individual *Elephantorrhiza elephantina* plants in the area. It was,

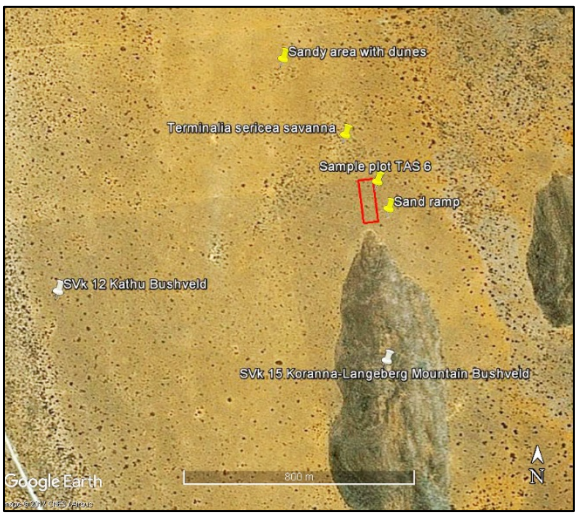

Figure 4 – Map of study area at Tswalu Kalahari Reserve indicating vegetation types, sample plot TAS 6, sand ramp, and an area where a patch of *Terminalia sericea* trees is found locally.

however, difficult to observe actual egg-laying. When selectively digging at the bases of a few *E. elephantina* plants, where ant activity was high, an early instar *Crudaria* larva was found in sandy soil around the rootstock of *E. elephantina* at sample plot TAS 6. This early instar larva was attended by the Small Pugnacious Ant, *Anoplolepis steingroeveri*. A similar observation was made on 29 October 2016. This larva fed on the leaves of *E. elephantina* in captivity. Final confirmation of the host-plant and associated ant species for *Crudaria* sp. TAS 6 was provided on 8 May 2017 when a number of final instar and earlier instar larvae were found together with *A. steingroeveri* below the surface of sandy soil, at and near rootstocks of *E. elephantina*. (Figs 5 & 6).

Figure 5 – Final instar larva of *Crudaria* sp. TAS 6 and an *Anoplolepis steingroeveri* minor worker on the host-plant *Elephantorrhiza elephantina*. Note that dark minors of *A. steingroeveri* could be mistaken for *Lepisiota* in the field.

A few of these larvae were collected and bred through to adults. These larvae fed on the leaves of *E. elephantina* and left characteristic patterns of missing pinnules at the rhachis of the bipinnately compound leaves. In the field, and in captivity, *A. steingroeveri* ants were repeatedly observed to feed at the dorsal nectary organs (DNO) of larvae (Fig. 7).

Figure 6 – Final instar larvae of *Crudaria* sp. TAS 6 with head and anterior part in the air ('searching for host-plant substrate'), and lateral view of *Anoplolepis steingroeveri* on dorsal part of larva.

Figure 7 – *Anoplolepis steingroeveri* ant feeding at dorsal nectary organ (DNO) of final instar larva of *Crudaria* sp. TAS 6.

Apart from visits to the DNO, ants also appeared to show interest in other dorsal areas of the larvae but the exact nature of this attention was not clear.

At Dedeben 'typical' *C. leroma* individuals were noted on flat areas on 11 October 2014. Females were seen to oviposit on twigs of *Vachellia hebeclada* subsp. *hebeclada* with *A. custodiens* ants nearby. One small larva of *C. leroma* at Dedeben was observed, on 30 October 2016, to feed on *V. hebeclada* subsp. *hebeclada* at night and was attended by *A. custodiens*. This larva was bred through to the adult. *A. custodiens* is noticeably common on flat areas north of Dedeben. Larvae of *Crudaria* sp. TAS 6 appear to differ morphologically from those of *C. leroma* at Tswalu Kalahari Reserve as well as from those depicted in Clark (1951) and Clark & Dickson (1971) but further details fall beyond the scope of this paper.

Outline of some vegetation and landscape attributes of the habitat of *Crudaria* sp. TAS 6

The sand dune area east of Dedeben, where *Crudaria* sp. TAS 6 is present, is partially enclosed by mountains (Figs 2-4). On the micro-habitat scale the dune landscape east of Dedeben ends, at least in profile, in sand ramps where sand slopes up against rocky hills (Fig. 4). *Crudaria* sp. TAS 6, its host-plant, and the ant *A. steingroeveri* all occur at such a sand ramp, of which the gradual slope and relatively large size enhance suitability of sustainable habitat.

Compared to the habitat where 'normal' *C. leroma* is found, the habitat of *Crudaria* sp. TAS 6 population is conspicuously different (Fig. 3). The vegetation type at the flat areas of Dedeben is SVk 13 Olifantshoek Plains Thornveld (Mucina & Rutherford 2006). Here *C. leroma* is found among a number of *V. hebeclada* subsp. *hebeclada* (Candlepod Thorn), *Vachellia erioloba* (Camel Thorn) and *Boscia albitrunca* (Shepherd's Tree). In contrast, *Crudaria* sp. TAS 6 is confined to a sand ramp with less dense tree cover, but which includes another thorn tree species, *Vachellia haematoxylon* (Grey Camel Thorn).

Lower down, on the sandy area north of the *Crudaria* sp. TAS 6 habitat, a patch of *Terminalia sericea* (Silver Clusterleaf) exists (Fig. 4). Towards the south suitable habitat for *Crudaria* sp. TAS 6 ends abruptly on the lower slopes of a rocky hill with vegetation in which *Croton gratissimus* (Lavender Feverberry) is abundant (Fig. 4). The vegetation on this rocky hill is part of the SVk 15 Koranna-Langeberg Mountain Bushveld vegetation type (Mucina & Rutherford 2006).

DISCUSSION

Host-plant use in the genus *Crudaria*

A summary of the host-plant species used by *Crudaria* species is given in Table 1. The host-plant species used by *C. capensis* is not known. Host-plant species recorded for *C. leroma* are *Vachellia karroo* (Clark & Dickson, 1971), *Vachellia sieberiana* for material from Zimbabwe (Pringle *et. al.*, 1994) and *Elephantorrhiza burkei* for material from South Africa (Woodhall, 2005). Kielland (1990) noted *Crudaria* larvae feeding on young shoots and thorns for *C. leroma* from Tanzania but did not refer to a specific host-plant species. In this study *V. hebeclada* subsp. *hebeclada* is reported as another host-plant species of *C. leroma*. *E. elephantina* (Eland's Bean) is recorded as a new host-plant species record for *Crudaria*. *E. elephantina* occurs through much of South Africa but is not endemic to South Africa (Williams, 2008; Raimondo *et al.*, 2009).

The above results confirm the importance of the host-plant genera *Vachellia* and *Elephantorrhiza* for *Crudaria*. Both *Vachellia* and *Elephantorrhiza* belong to the mimosoid group of the family Fabaceae. Overall, the above findings emphasize the importance of the plant order Fabales as host-plants for the

Table 1 – Summary of host-plant use in the genus *Crudaria*.

***Crudaria* species**	**Host-plant species**	**Reference for recording of host-plant**	**Plant family and subfamily accepted at present for the species**	**Locality/ Region/ Country**
C. capensis	Not confirmed. Possibly *Tetraena retrofracta*.	Heath, 1997 (noted as probably *Zygophyllum retrofractum*)	Not confirmed. ZYGOPHYLLACEAE could be a host-plant family.	South Africa. Locality not specified.
C. leroma	*Elephantorrhiza burkei.*	Woodhall, 2005.	FABACEAE: Mimosoideae	South Africa.
	Vachellia karroo.	Clark & Dickson, 1971.	FABACEAE: Mimosoideae	E. Cape, South Africa.
	Vachellia sieberiana.	Pringle *et. al.*, 1994.	FABACEAE: Mimosoideae	Zimbabwe.
	Vachellia hebeclada. subsp. *hebeclada.*	Terblanche (this paper).	FABACEAE: Mimosoideae	Tswalu Kalahari Reserve, N. Cape, South Africa.
C. sp. TAS 6	*Elephantorrhiza elephantina*	Terblanche (this paper)	FABACEAE: Mimosoideae	Tswalu Kalahari Reserve, N. Cape, South Africa.
C. wykehami	No published data.	No published data.	No published data.	No published data.

Table 2 – Summary of ant associations in the genus *Crudaria*.

***Crudaria* species**	**Associated ant species**	**Reference for host ant species record**	**Locality/ Region/ Country**
Crudaria capensis	Not confirmed or published.	No published data.	No published data
Crudaria leroma	*Anoplolepis custodiens.*	Pringle *et al.*, 1994.	South Africa, Baviaans River (Pringle *et.al.* 1994 noted that this is for Baviaans River material, which appears to be different to East London material depicted by Clark & Dickson, 1971 (Further investigation is needed to confirm the identity of the butterfly for which this association is listed)
		Terblanche (this paper).	Dedeben, Tswalu Kalahari Reserve, Northern Cape, South Africa
Crudaria sp. TAS 6	*Anoplolepis steingroeveri*	Terblanche (this paper)	3km east of Dedeben, Tswalu Kalahari Reserve, Northern Cape, South Africa
Crudaria wykehami	Not confirmed or published	No published data	No published data

subfamily Aphnaeinae. The genera *Vachellia* and *Senegalia* were previously included in the polyphyletic genus *Acacia* (Kyalangalilwa *et al.*, 2013). Within *Acacia* (*sensu lato*) it would be of interest to investigate why *Crudaria* species do not utilize any *Senegalia* species as host-plants. While specific host-plant species usage might be regarded as less important in shaping the diversification of myrmecophilous butterfly species, there are nevertheless discernable patterns of host-plant use by myrmecophilous butterfly species. The choice of certain plant species and groups as host-plants thus remains vital in the conservation management of myrmecophilous butterfly species.

In contrast to the shrub, or even small tree, *E. burkei*, which has been reported as a host-plant species for *Crudaria* by Woodhall (2005), *E. elephantina*, noted here as a host-plant species for *Crudaria* in the Eastern Kalahari Bushveld Bioregion, is a geoxylic suffrutex. A geoxylic suffrutex or geoxyle refers to a plant that functions as an herbaceous plant above ground (often annually) but which has woody subterranean xylopodia (a lignified complex of perennial root and shoot tissue with a high capacity to resprout) (White, 1979; Low & Rebelo, 1998; Simon & Pennington, 2012; Appezzato-da-Glória *et al.*, 2008; Maurin *et al.*, 2014). *E. elephantina* is such an "underground tree" with a considerable woody rootstock under the soil surface. While the growth form represented by a geoxylic suffrutex may be an important adaptation to fire, its value in surviving frost and dry periods should also be considered. Ecologically, *E. elephantina* could be an important alternative host-plant type for *Crudaria* in a more arid savanna with substantial occurrence of frost, such as in the southern Kalahari. However, a lack of sandy soils and suitable associated ant species would prohibit use of *E. elephantina* in many other areas where this geoxylic suffrutex is present.

Ant species associated with the genus *Crudaria*

The ant species associated with *C. leroma* is the Large Pugnacious Ant, *A. custodiens* (Table 2). Associated

ant species for both *C. capensis* and *C. wykehami* are unknown. *A. steingroeveri*, the Small Pugnacious Ant, is associated with the morpho-species *Crudaria* sp. TAS 6. While *Anoplolepis* is confirmed as the associated ant genus for *Crudaria*, the addition of *A. steingroeveri* signifies a possible role of different lineages of *Anoplolepis* in *Crudaria* evolution and ecology.

At Tswalu Kalahari Reserve *A. steingroeveri* workers (majors and minors) appear decidedly more compact, darker and smaller than *A. custodiens*, the latter with lighter colouration and steel-grey gasters (Terblanche, pers. obs.) The checkered pattern on the gaster of *A. custodiens* is caused by reflection of light on hairs which are arranged in two different directions on each side compared to the rows of pubescent hairs that are only arranged in one direction in *A. steingroeveri* (Prins, 1982). In *A. steingroeveri* the gaster of minors often have less hairs and may be shiny so that at a glance confusion with workers of the black sugar-ant *Lepisiota* [*Acantholepis*] *capensis* is possible (Fig. 5). *A. steingroeveri* appears to be more common in the drier parts of South Africa than *A. custodiens*, whereas in the north-eastern parts of South Africa *A. custodiens* appears to be the commoner of the two species (Prins, 1982). *A. custodiens* and *A. steingroeveri* are therefore identifiable and distinct species with fairly large distributions. Even if each of these two species contains a number of undescribed taxa, the 'species groups/complexes' are still discernable and of considerable taxonomic, ecological and phylogenetic importance.

Pierce *et al.*, 2002 note the high level of obligate ant association that is observed in African Lycaenidae as well as the possibility that ant associations could have both promoted and constrained diversification of Lycaenidae. Boyle *et al.* (2014) highlight the importance of discovering more about life histories of Aphnaeinae to better understand the phylogeny of Aphnaeinae, which in turn provides a framework for exploring how ant associations and loss of phytophagy have affected subsequent diversification in Lycaenidae.

Associations of myrmecophilous lycaenid butterflies in Africa with *Anoplolepis custodiens* and *Anoplolepis steingroeveri*

A. custodiens has been, apart from in the genera *Crudaria* and *Trimenia* (Aphnaeinae) (Pringle *et al.*, 1994; Heath, 1997; Boyle *et al.*, 2014), also recorded as the associated ant for butterfly species and subspecies in the genus *Thestor* (Miletinae) (Clark & Dickson, 1971; Claassens & Dickson, 1980; Williams & Joannou, 1996; Claassens & Heath, 1997). No *Anoplolepis* species have been recorded for the large myrmecophilous genus *Lepidochrysops* (Polyommatinae), which is mostly (for the known life histories) associated with another formicine genus, *Camponotus* (Claassens, 1972; Claassens, 1976; Henning, 1983; Williams, 2016). No mention of *A. steingroeveri* as associated ant species for myrmecophilous butterfly species in Africa could be found in literature, so it is assumed that *A. steingroeveri* is reported here for the first time as a lycaenid associated ant species.

Landscape ecology and the use of sand ramps as habitat by a butterfly population

Habitat where a unique population *Crudaria* sp. TAS 6 has been found at Tswalu Kalahari Reserve is described as a sand ramp. Sand ramps are dune-scale sedimentary accumulations found at mountain fronts and consist of a combination of aeolian sands (from multiple or single sources) and deposits of other geomorphological processes associated with hillslope and/or fluvial activity (Bateman *et al.*, 2012). Different types of sand dune systems exist on Earth and also, for example, on Mars. Sediment and airflow interactions with topographies on various scales in mountainous regions significantly affect dune location, size, shape, and orientation (Pye & Tsoar 1990; Chojnacki *et al.*, 2010). Sand ramps are different from climbing and falling dunes but are linked to sand dune systems. Climbing dunes are formed when migrating dunes encounter and ascend a substantial slope or cliff, where there is no major wind blockage (Pye & Tsaor, 1990). Falling dunes, found on the downwind side of large topographic highs, are formed by unidirectional down-slope winds and gravity in certain environments, such as desert valleys (Chojnacki *et al*., 2010; Al-Enezi *et al*., 2008). While a number of sand ramps have been observed by the author in the Eastern Kalahari Bioregion and Tswalu Kalahari Reserve, the steep slope and/or small size of some of these ramps could be limiting in sustaining a specific colony-forming myrmecophilous butterfly species. Different sand dune types and sand ramps found in this study suggest that detailed studies of such types of sandy areas could be a fascinating field in the study of butterfly habitats.

The sandy area containing the habitat where *Crudaria* sp. TAS 6 was found at Tswalu Kalahari Reserve also differs from the sand dune landscape west of the Korannaberg Mountains, where numerous parallel linear dunes and alternating inter-dune troughs stretch for considerable distance westwards across the Kalahari landscape (Figure 2). These linear sand dunes west of the Korannaberg are part of the Gordonia Duneveld (SVkd 1) vegetation type (Mucina & Rutherford). Sandy area with dunes east of Dedeben (where *Crudaria* sp. TAS 6 is found) is a different type of sand dune area, which is part of the vegetation type Kathu Bushveld (SVk 12) of the Eastern Kalahari Bushveld Bioregion (Mucina & Rutherford, 2006). Sands and dunes east of Dedeben, where *Crudaria* sp. TAS 6 is present, are partially enclosed by mountains, which alter the formation of the sand dune landscape.

CONCLUSIONS

The widespread 'underground tree', *E. elephantina* (Fabaceae: Mimosoideae) as well as *V. hebeclada hebeclada* (Fabaceae: Mimosoideae) are added as host-plant species for the genus *Crudaria.* The Small

Pugnacious Ant, *A. steingroeveri* is reported as associated ant species of myrmecophilous butterflies in Africa for the first time. *A. custodiens*, the associated ant species of *C. leroma* (Pringle *et. al.*, 1994) is also confirmed to be an associated ant species of *C. leroma* in the Eastern Kalahari Bushveld Bioregion of South Africa (in general terms part of the southern Kalahari). All host-plant species of *Crudaria* are woody shrubs or trees, apart from the host-plant *E. elephantina*, which is a geoxylic suffrutex. Geoxylic suffrutex's, such as *E. elephantina*, may be an important alternative host-plant type in the harsh climate of the southern Kalahari. However, use of *E. elephantina* by *Crudaria* larvae in the wild will also depend on restrictive conditions, such as depth of the sand and resources such as appropriate associated ant species.

It is remarkable that the smaller *A. steingroeveri* is associated with a *Crudaria* population that appears to be morphologically smaller, of light colouration (also in the larvae) compared to other *Crudaria* species. It is also noteworthy that it is associated with a unique ecosystem, which is in profile is a sand ramp, with relatively few trees. This study also draws attention to different kinds of sand dune landscapes and sand ramps, which enhance the diversity of suitable habitats for butterfly species. These findings emphasize that from a biodiversity perspective 'not all Kalahari sandy areas are the same' and that more detailed studies on butterfly fauna and sand dune habitats are desirable.

The importance of *Anoplolepis* ants for the myrmecophilous butterfly genus *Crudaria*, and the plant order Fabales as host-plant group for Aphnaeinae, are underscored by the results reported above. More field observations and life-history studies in Lycaenidae will benefit phylogenetic studies and an understanding of the role that ant-associations have in constraining or diversifing lineages of lycaenid taxa (Pierce *et al.*, 2002; Boyle *et al.*, 2014).

It is hoped that two main distinct species/species groups of *Anoplolepis* in southern Africa, the *A. custodiens* species/ species group and *A. steingroeveri* species/ species group will receive more specific attention in the study of myrmecophilous butterflies in Africa. Tswalu Kalahari Reserve provides an ideal opportunity for comparative life history analyses of *Crudaria* populations in the Kalahari landscape. Analyses of quantitative data of butterfly assemblages, vegetation and ants are currently continuing and should enhance the understanding of landscape ecology of *Crudaria* in the southern Kalahari. A revision of the genus *Crudaria* will be conducted in phases; the possible new entity at Tswalu Kalahari Reserve will receive priority. *Crudaria* is a neglected genus of the myrmecophilous butterfly fauna of southern Africa and this fascinating taxon deserves more research.

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LITERATURE CITED

AL-ENEZI, A., K. PYE, R. MISAK, and S. AL-HAJRA. 2008. Morphologic characteristics and development of falling dunes, northeast Kuwait, *Journal of Arid Environments* **72**: 423–439.

APPEZZATO-DA-GLÓRIA, B., CURY, G., KASUE MISAKI SOARES, M., ROCHA, R. & HISSAE HAYASHI, A. 2008. Underground systems of Asteraceae species from Brazilian Cerrado 1. *The Journal of the Torrey Botanical Society* **135**: 103–113.

ANTWEB: https://www.antweb.org.

BATEMAN, M.D., BRYANT, R.G., FOSTER, I.D.L., LIVINGSTONE, I. & PARSONS, A.J. 2012. On the formation of sand ramps: A case study from the Mojave Desert. *Geomorphology* **161**: 93–109.

BOLTON, B. 1994. *Identification guide to the ant genera of the world.* Harvard, Cambridge, USA.

BOYLE, J.H., KALISZEWSKA, Z.A., ESPELAND, M., SUDERMAN, T.M., FLEMING, J., HEATH, A. & PIERCE, N.E. 2014. Phylogeny of the Aphnaeinae: myrmecophilous African butterflies with carnivorous and herbivorous life histories. *Systematic Entomology* **40**: 169–182.

CHOJNACKI, M., MOERSCH, J.E. & BURR, D.M. 2010. Climbing and falling dunes in Valles Marineris, Mars. *Geophysical Research Letters* **37**: 1–7.

CLAASSENS, A.J.M. 1972. *Lepidochrysops trimeni* (Bethune-Baker) (Lepidoptera: Lycaenidae) reared from larva found in the nest of *Camponotus maculatus* Fab. (Hymenoptera: Formicidae). *Journal of the Entomological Society of Southern Africa* **35**: 359–360.

CLAASSENS, A.J.M. 1976. Observations on the myrmecophilous relationships and parasites of *Lepidochrysops methymna methymna* (Trimen) and *Lepidochrysops trimeni* (Bethune-Baker) (Lepidoptera: Lycaenidae). *Journal of the Entomological Society of Southern Africa* **39**: 279–289.

CLAASSENS, A.J.M. & DICKSON, C.G.C. 1980. *Butterflies of the Table Mountain Range*. Struik, Cape Town.

CLAASSENS, A.J.M. & HEATH, A. 1997. Notes on the myrmecophilous early stages of two species of *Thestor* Hübner (Lepidoptera: Lycaenidae) from South Africa. *Metamorphosis* **8**: 56–60.

CLARK, G.C. 1951. The life history of *Crudaria leroma*. *Journal of the Entomological Society of Southern Africa* 14 (2): 127–132.

CLARK, G.C. & DICKSON, C.G.C. 1971. *Life Histories of the South African Lycaenid Butterflies*. Purnell, Cape Town.

HEATH, A. 1997. A review of African genera of the tribe Aphnaeini (Lepidoptera: Lycaenidae). *Metamorphosis*, Occasional Supplement Number **2**: 1–60.

HEATH, A. & BRINKMAN, A.K. 1995. Notes on the early stages of *Argyrocupha malagrida maryae* (Wallengren) (Lepidoptera: Lycaenidae) *Metamorphosis* **6**: 167–173.

HENNING, S.F. 1983. Biological groups within the Lycaenidae (Lepidoptera). *Journal of the Entomological Society of Southern Africa* **46**: 65–85.

HÖLLDOBLER, B. & WILSON, E.O. 1990. *The ants.* Harvard, Cambridge, USA.

KIELLAND, J. 1990. *Butterflies of Tanzania*. Hill House, Melbourne and London.

KYALANGALILWA, B., BOATWRIGHT, J.S., DARU, B.H., MAURIN, O. & VAN DER BANK, M. 2013. Phylogenetic position and revised classification of *Acacia* s.l. (Fabaceae: Mimosoideae) in Africa, including new combinations in *Vachellia* and *Senegalia*. *Botanical Journal of the Linnean Society* **172**: 500–523.

LATTKE, J.E. 2000. Specimen processing: Building and curating an ant collection. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds). *Ants: Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, p. 155–171.

LOW, A.B. & REBELO, A.G. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Pretoria: Department of Environmental Affairs and Tourism.

MAURIN, O., DAVIES, T.J., BURROWS, J.E., DARU, B.H., YESSOUFOU, K., MUASYA, A.M., VAN DER BANK, M. & BOND, W.J. 2014. Savanna fire and the origins of "underground forests" of Africa. *New Phytologist* **204**: 201-214.

MUCINA, L. & RUTHERFORD, M.C. (Eds). 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* **19**. South African National Biodiversity Institute, Pretoria.

PIERCE, N.E., BRABY, M.F., HEATH, A., LOHMAN, D.J., MATHEW, J., RAND, D.B. & TRAVASSOS, M.A. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annual Reviews of Entomology* **47**: 733–771.

PRINGLE, E.E.L., HENNING, G.A. & BALL, J.B. (Eds.) 1994. *Pennington's Butterflies of Southern Africa*. 2nd ed. Struik Winchester, Cape Town.

PRINS, A.J. 1982. Review of *Anoplolepis* with reference to male genitalia, and notes on *Acropyga* (Hymenoptera, Formicidae). *Annals of the South African Museum* **89**: 215–247.

PYE, K. & TSOAR, H. 1990. *Aeolian Sand and Sand Dunes.* Unwin Hyman, London.

RAIMONDO, D., VON STADEN, L., FODEN, W., VICTOR, J.E., HELME, N.A., TURNER, R.C., KAMUNDI, D.A. & MANYAMA, P.A. (Eds). 2009. Red list of South African Plants 2009. *Strelitzia* **25**. South African National Biodiversity Institute, Pretoria.

SIMON, M.F. & PENNINGTON, T. 2012. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* **173**: 711–723.

SLINGSBY, P. 2017. *Ants of southern Africa: The ant book for all.* Slingsby Maps, Muizenburg.

STAUDE, H.S., MECENERO, S., OBERPRIELER, R., SHARP, A., SHARP, I. WILLIAMS, M.C. & MACLEAN, M. 2016. An illustrated report on the larvae and adults of 962 African Lepidoptera species. Results of the Caterpillar Rearing Group: a novel, collaborative method of rearing and recording lepidopteran life-histories.

TERBLANCHE, R.F. 2003. *Gauteng Ant Atlas (with preliminary annotated species list of ant species of Gauteng).* Unpublished Report for the Gauteng Directorate of Agriculture and Rural Development (GDARD).

THE INSECT AND SPIDER COLLECTIONS OF THE WORLD. hbs.bishopmuseum.org/codens/codens-r-us.html.

VICTOR, J.E., KOEKEMOER, M., FISH, L., SMITHIES, S.J., & MÖSSMER, M. 2004. Herbarium essentials: the southern African herbarium user manual. *Southern African Botanical Diversity Network Report No.* **25**. SABONET, Pretoria.

WHITE, F. 1979. The Guineo-Congolian Region and its relationship to other phytochoria. *Bulletin Jardin Botanique National de Belgique* **49**: 11-55.

WILLIAMS, M.C. 2016. *Afrotropical Butterflies and Skippers*. www.metamorphosis.org.za.

WILLIAMS, M.C. & JOANNOU, J.G. 1996. Observations on the oviposition behaviour and larvae of *Thestor basutus capeneri* Dickson (Lepidoptera: Lycaenidae: Miletinae) in South Africa. *Metamorphosis* **7**: 12–16.

WILLIAMS, V.L. 2008. *Elephantorrhiza elephantina* (Burch.) Skeels. *National Assessment: Red List of South African Plants version 2017.1*. Accessed on 2017/08/14.

WOODHALL, S.E. 2005. *Field Guide to the Butterflies of South Africa*. Struik, Cape Town.