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Acraea trimeni Aurivillius, [1899], *Acraea stenobea* Wallengren, 1860 and *Acraea neobule* Doubleday, [1847] on host-plant *Adenia repanda* (Burch.) Engl. at Tswalu Kalahari Reserve, South Africa

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Abstract: The climber *Adenia repanda* (Passifloraceae) is a new host-plant species record for *Acraea trimeni*, *Acraea stenobea* and *Acraea neobule*. Final instar larvae and pupae of *A. trimeni* and *A. stenobea* are described for the first time. Keys are provided with alignment of terminology to studies of Heliconiinae from the Neotropical Region. The final instar larvae of *A. trimeni* differ from others in the *zetes*-group. Use of host-plant *A. repanda* on the plains of semi-arid Eastern Kalahari Bushveld Bioregion with periodic droughts, is significant for *A. trimeni* which belongs to a tropical centred *zetes*-group. *A. repanda* is favoured by stock and often grows from under the canopies of *Boscia albitrunca* and *Senegalia mellifera* subsp. *detinens* trees. It is hypothesised that low stocking rates and the presence of large predators such as lions (*Panthera leo*) could favour abundance of *A. repanda*. *A. repanda* is an ant-associated plant species whose stems and leaves (with extrafloral nectaries) are constantly patrolled by ants of genera *Anoplolepis* and *Crematogaster*. *Anoplolepis custodiens* attack the larvae of *A.neobule* on *A. repanda* rather than forming symbiotic relationships which it has with many myrmecophilous lycaenid larvae.

Key words: *Adenia repanda*, *Acraea trimeni*, *Acraea stenobea*, *Acraea neobule*, larvae, pupae, *Boscia albitrunca*, *Senegalia mellifera*, stocking rates, lions, ants, *Anoplolepis*, *Crematogaster*, Eastern Kalahari Bushveld Bioregion, Griqualand West Centre of Plant Endemism.

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INTRODUCTION

Life history studies *in the wild* are fundamental to address landscape ecology and conservation of Lepidoptera. Findings presented in this paper stem from a butterfly landscape study by the author initiated in July 2013 by the Tswalu Foundation. Description of life histories and host-plant usage is also a contribution to an encouraging initiative of the Lepidopterists' Society of Africa, the Caterpillar Rearing Group (Staude *et al.* 2016). The study area, Tswalu Kalahari Reserve (TKR) is part of the Eastern Kalahari Bushveld Bioregion, one of six bioregions of the Savanna Biome of South Africa (Mucina & Rutherford 2006, Mucina *et al.* 2014). There is a particular interest in *Acraea* species from the Eastern Kalahari Bushveld Bioregion because this Bioregion is located at the southwestern extremities of *Acraea* species distributions, a genus whose core range is in the tropical savannas and forests of Africa. No data on the life histories of *Acraea* from the Eastern Kalahari Bioregion have hitherto been published.

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MATERIALS AND METHODS

Study sites

The 110 000 ha TKR is located approximately 50 km west of Hotazel, Northern Cape Province, South Africa (Fig. 1). The landscape consists of the rugged Korannaberg mountains, embedded in sandy plains, at altitudes ranging from 1000 m to 1570 m. There are five Savanna vegetation types at TKR – four representing the Eastern Kalahari Bushveld Bioregion [Kathu Bushveld (SVk 12), Olifantshoek Plains Thornveld (SVk 13), Koranna-Langeberg Mountain Bushveld (SVk 15), Gordonia Plains Shrubland (SVk 16)] and one representing the Kalahari Duneveld Bioregion [Gordonia Duneveld (SVkd 1)]. Conspicuous indigenous trees in the study area include the Black Thorn *Senegalia mellifera* (Vahl) Seigler & Ebinger subsp. *detinens* (Burch.) Kyal. & Boatwr. and the Shepherd's Tree *Boscia albitrunca* (Burch.) Gilg & Gilg-Ben. The Eastern Kalahari Bushveld Bioregion has more than twice as much frost as the Central Bushveld Bioregion (Mucina & Rutherford, 2006).

The mean annual precipitation of the vegetation types occuring in TKR ranges from 180–380 mm (Mucina & Rutherford, 2006). TKR is therefore a savanna with mean annual precipitation < 400 mm (Note: the terms arid-savanna and desert are *not* normally applicable to the Kalahari).

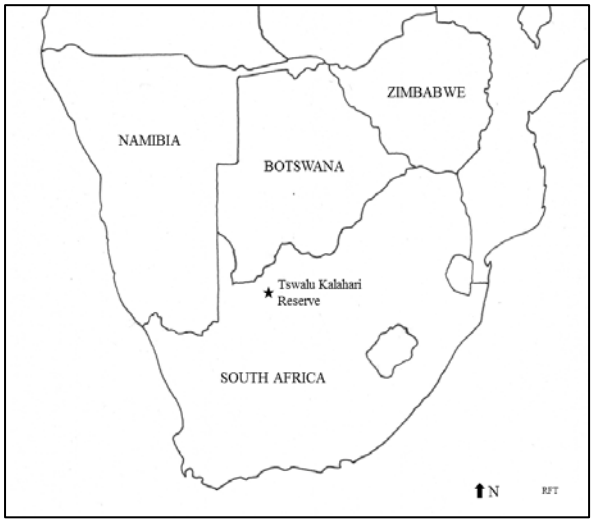

Figure 1 – The location of TKR in the Northern Cape Province of South Africa.

Rearing of larvae

Eggs and larvae of *Acraea trimeni* Aurivillius, [1899], *Acraea stenobea* Wallengren, 1860 and *Acraea neobule* Doubleday, [1847] found on host-plant *Adenia repanda* (Burch.) Engl. in the field were collected and carefully raised to adults from April 2016 to June 2016. Larvae were raised indoors in clear plastic honey jars and fed with fresh leaves or cut stems with leaves of *A. repanda* only. Lids of jars were loosened during later instars to promote aeration and maintain a stable environment. Herbarium specimens of host-plants were collected by the author according to Victor *et al.* (2004). Herbarium specimens are deposited in the A.P. Goossens Herbarium (Potchefstroom, North West Province) and McGregor Museum (Kimberley, Northern Cape Province). Plant material of *A. repanda* has been reported to be "deadly poisonous to man" (de Wilde 1976) and the necessary precautions were taken.

Terminology

The terminology used to describe *Acraea* larvae and pupae has been aligned and standardised for better comparisons of Heliconiinae larvae across the Afrotropical and Neotropical Regions. Fig. 2 gives an outline of the basic body plan and terminology for setose scoli. It should be noted that "spines with barbs" (van Someren & Rogers, 1925), "hairy processes", "setose processes", "setose spines" (van Son 1963) all have a similar meaning to setose scoli used here. These setose scoli are for much of the *Acraea* larval body, longitudinally arranged in three rows; dorsal scoli, supraspiracular scoli and subspiracular scoli (Fig. 2). At this stage a more complete chaetotaxy such as for *Heliconius sara apseudes* and *Dione glycera* (Barão *et al.* 2015, Vargas *et al.* 2014) are beyond the scope of this paper and verrucae are only noted briefly for *A. trimeni*. Such detailed descriptions of chaetotaxy of larvae of Heliconiinae of Neotropical Region are certainly a methodology to consider for future life history descriptions of *Acraea* from the Afrotropical Region. Terminology used here for descriptions of head of final instar larvae is given in Fig. 3 and for descriptions of pupae in Fig. 4 (p. 94).

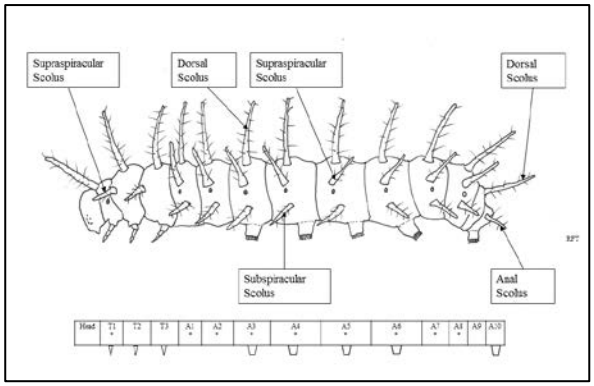

Figure 2 – Drawing to illustrate basic body plan applicable to final instar larvae of *Acraea* described in this paper. Terms which are used to refer to rows of setose scoli in descriptions of final instar larvae, are given. Inserted bar gives a diagrammatic outline of head and segments (thoracic T1-T3), abdominal segments (A1-A10), spiracles (asterisk), true legs symbol: triangles) and prolegs (symbol: quadrilaterals) for easier reference.

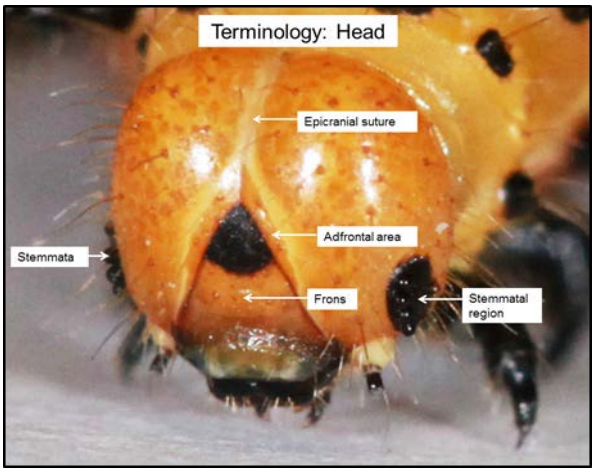

Figure 3 – Terminology used in descriptions of characters of head of final instar larvae of *Acraea* (example *A. trimeni*).

RESULTS

Finding of *A. repanda* and larvae of three *Acraea* species that feed on *A. repanda*

On 31 March 2016 the author found the climber *A. repanda* growing over a small *Senegalia mellifera* subsp. *detinens* tree north-northeast (NNE) of Dedeben at TKR in an area where *A. stenobea* females were searching for host-plants (Fig. 5). Subsequently a number of *A. repanda* individuals were found north-northeast of Dedeben during detailed vegetation surveys for butterfly landscape studies in April 2016. Unique *A. repanda* was identified at once and listed as new addition to the checklist of plant species of TKR. *A. repanda* individuals were often found growing from under canopies of *Boscia albitrunca* and also *Senegalia mellifera* subsp. *detinens* at TKR. A few smaller individuals of *A. repanda* were sometimes found next to grasses or low shrubs.

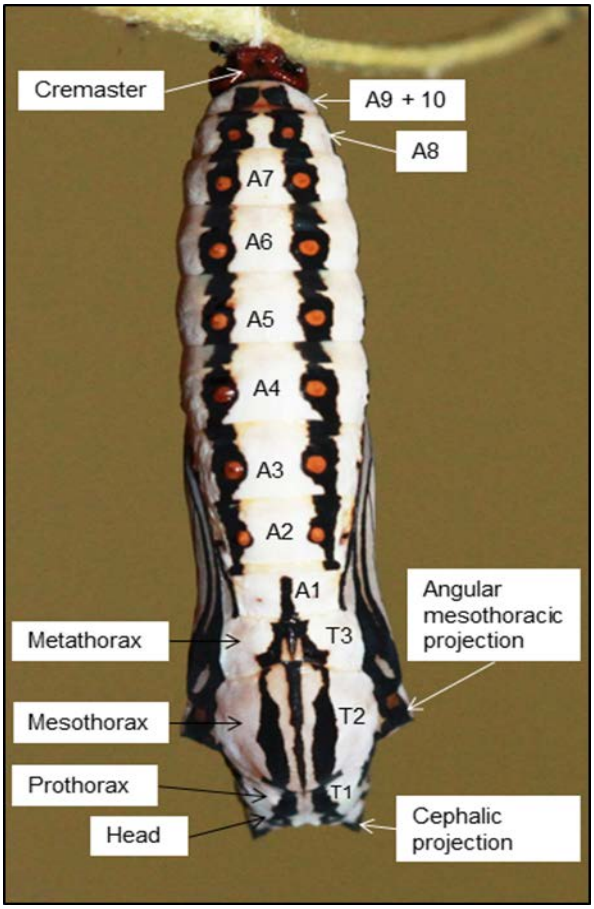

Figure 4 – Terminology used in description of characters of pupae of *Acraea* (example *A. trimeni*).

Figure 5 – *A. repanda* on canopy of shrub-height *S. mellifera* subsp. *detinens* at TKR.

D. Smith (DS), Wildlife Manager of TKR, indicated that similar plants are found at the Legabe section further north at TKR where prides of lions are present. A survey by DS and the author (RFT) on 2 April 2016 at Legabe resulted in finding a spot particularly rich in *A. repanda* individuals. During this survey at Legabe single *A. neobule* larvae (DS & RFT) and a batch of eggs of *Acraea trimeni* (RFT) were found on *A. repanda*. Nearly a month later on 1 May 2016, early instar larvae of a third *Acraea* species that uses *A. repanda* as a host-plant, *A. stenobea*, were found by the author north-northeast of Dedeben. Discovery of host-plant and early stages of *Acraea* in autumn 2016 followed on a very dry, hot summer and late but substantial autumn rains (> 100 mm) at TKR.

Larvae of *A. trimeni*, *A. stenobea* and *A. neobule* were successfully reared through to adult stage in captivity on *A. repanda* only. All larvae fed on leaves of *A. repanda*, though occasionally larvae of *A. trimeni* fed on periderm (with cork cambium) of stems of *A. repanda*.

Observations on ants that patrol *A. repanda* and attack *A. neobule* larvae

From 31 March 2016 to June 2016 ants of genera *Anoplolepis* and *Crematogaster* were noted to constantly patrol along the stems and leaves of *A. repanda* individuals at TKR. Ants regularly visited conspicuous leaf blade glands (extrafloral nectaries) (Fig. 6). A few attacks by *Anoplolepis custodiens* ants on early instar *A. neobule* larvae were observed on 2 April 2016 (RFT & DS) (Fig. 7). *Anoplolepis* ants bit into bodies of larvae and exhibited typical stance of spraying formic acid on larvae. Loss of body fluids from the larvae were observed on and next to the larvae following these attacks. A number of *A. neobule* larvae were found on grass or twigs next to *A. repanda* (Fig. 8). Some attacks by *Anoplolepis* ants at a short distance from an *A. repanda* plant continued in one instance, even though the larva was already on a grass blade next to the *A. repanda*.

Figure 6 – Leaves and flower of *A. repanda* from TKR.

Figure 7 – *Acraea neobule* larva on blade of grass next to *A. repanda* being attacked by *Anoplolepis custodians* ant.

Figure 8 – Larva of *A. neobule* and ant *A. custodiens* on a leaf blade of grass next to *A. repanda* at TKR.

Description of final instar larvae of *A. trimeni, A. stenobea* and *A. neobule* from TKR

A. trimeni (Fig. 9)

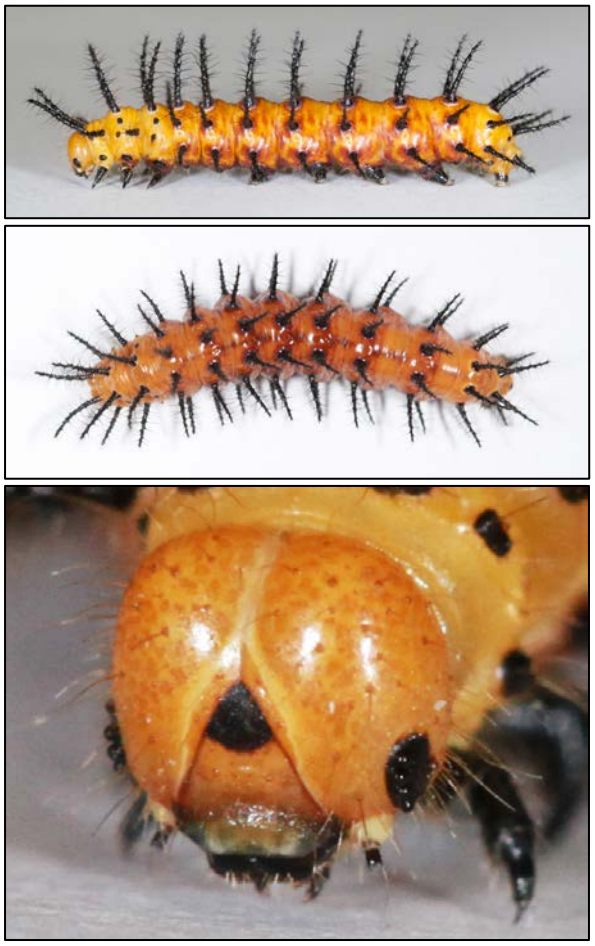

Figure 9 – Final instar larva of *A. trimeni* found during April–June 2016 at TKR. Top: lateral view; middle: dorsal view; bottom: anterior view of head from slight angle.

General: Background colour of body ochre with some reddish-purple suffusions. Reddish-purple suffusions concentrated at A1–A7. Head, thorax and posterior three abdominal segments decidedly lighter than middle section of body. Head: Ground colour of epicranium ochre with pale narrow lining at epicranial suture and vicinity of adfrontal areas. Head rounded and smooth. Clear extensive semi-triangular black marking at upper angle of frons; bottom edge of triangular black marking convex. Entire stemmatal region a discrete uniform black. Body behind head: Ochre background colour with very slight traces of transverse reddish-purple bands along bases of dorsal and supraspiracular scoli of some abdominal segments. Elevated areas around bases of the setose scoli purple. Two black dots (black verrucae) beneath dorsal scoli at second (T2) and third (T3) thoracic segments. One pair of spiracles, with ochre lining, laterally at each of segments T1 and A1–A8; in total 9 pairs of spiracles. True legs black. Four pairs of ventral prolegs and one pair of anal prolegs black with silvery-white crochets. Setose scoli: Conspicuously long setose scoli black with dark purple bases. In total 31 pairs (altogether 62) prominent black setose scoli. Three pairs of dorsal thoracic scoli (one pair at each segment). Two pairs of anterior supraspiracular scoli very close to intersections of thoracic segments T1, T2 and T2, T3. Three pairs of setose scoli at each of abdominal segments A1–A8. One pair of dorsal scoli at abdominal segment A9 and one pair of anal scoli at anal segment A10.

A. stenobea (Fig. 10)

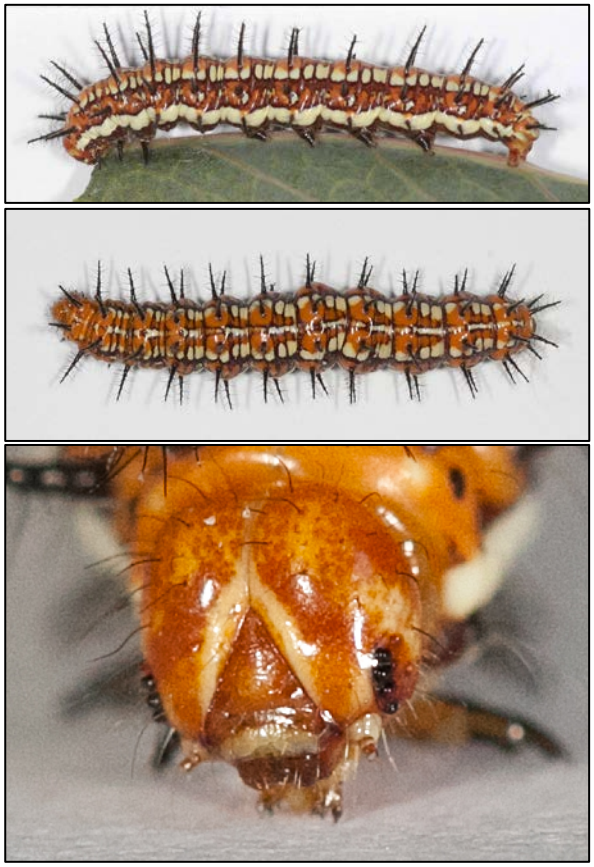

Figure 10 – Final instar larva of *A. stenobea* found during April–June 2016 at TKR. Top: lateral view; middle: dorsal view; bottom: anterior view of head from slight angle.

General: Intricate patterns of cream-white stripes, irregular dorsal orange stripe with thicker and thinner areas, dark brown lines as well as orange areas near bases of supraspiracular setose scoli. Head: Background colour of epicranium burnt orange. Broad white lining present along bottom part of epicranial suture and vicinity of adfrontal areas. Entire frons burnt orange. Conspicuous white areas around stemmatal

region. Stemmatal region bicoloured; anterior part black and posterior part burnt orange. Body behind head: Thin cream-white stripe with dark brown lining dorsally at central axis along length of body with only faint orange or transverse brown lines. Irregular orange stripes with thicker and thinner areas along rows of dorsal setose scoli. Dorso-lateral cream-white stripes with alternating expanded and contracted areas (and transverse dark brown lines at regular intervals) between rows of dorsal scoli and supraspiracular scoli. Lateral brown stripe with orange areas around bases of supraspiracular setose scoli. A continuous white stripe from behind head and all along series of subspiracular scoli. Thin dark brown ventro-lateral line at bottom of lateral side. One pair of spiracles at each of segments T1 and A1–A8; in total 9 pairs of spiracles. Spiracles with dark brown lining. White areas extend around posterior sides of spiracles. True legs at thorax black and ventral prolegs at A3–A6 also black. Anal prolegs burnt orange. Setose scoli: In total 31 pairs (altogether 62) prominent black setose scoli. Three pairs of dorsal thoracic scoli (one pair each segment). Two pairs of supraspiracular scoli anteriorly and very close to intersections of T1, T2 and T2, T3. Three pairs of setose scoli at each of abdominal segments A1–A8. One pair of dorsal scoli at abdominal segment A9 and one pair of anal scoli at segment A 10. Elevated areas around bases of all dorsal setose scoli and supraspiracular scoli an orange colour; only with some white at spiracles. Orange tinges at dorsal side of black subspiracular scoli.

A. neobule (Fig. 11)

General: Intricate patterns of irregular cream-white and dark brown stripes along length of body, with orange areas around bases of setose scoli. Series of transverse orange areas and white areas, the latter with thin brown transverse lines, dorsally. Head: Background colour of epicranium burnt orange with paler thin lining at epicranial suture and vicinity of adfrontal areas. A triangular blackish marking at upper angle of frons; bottom edge of blackish triangular mark slightly concave, almost straight. Stemmatal region bicoloured; anterior part of stemmatal region black and posterior part burnt orange. Body behind head: Dorsal transverse orange areas associated with bases of dorsal setose scoli, large cream-white areas with thin transverse dark brown lines. Lateral dark brown stripe with orange areas around bases of supraspiracular setose scoli. White stripe along subspiracular scoli with orange areas at bases of subspiracular scoli. Irregular dark brown line along length of body below subspiracular scoli. Ventral part of body cream-white. Three pairs of true legs burnt orange with dorsal congruent dark brown lines. Four pairs of ventral prolegs beige. One pair of anal prolegs orange. One pair of spiracles, with blackish lining at each of segments T1 and A1 – A8; in total 9 pairs of spiracles. Narrow cream white areas around dark linings of spiracles. Setose scoli: In total 31 pairs (altogether 62) prominent black and brown setose scoli. Three pairs of dorsal thoracic scoli (one pair at each thoracic segment). Two pairs of supraspiracular scoli anteriorly and very close to intersections of T1, T2 and T2, T3. Three pairs of setose scoli at each of abdominal segments A1–A8. One pair of dorsal scoli at abdominal segment A9 and pair of anal scoli at anal segment A10. Swollen orange areas around bases of all setose scoli.

Figure 11 – Final instar larva of *A. neobule* found during April–June 2016 at TKR. Top: lateral view; middle: dorsal view; bottom: anterior view of head from slight angle.

Key to characters of thorax and abdomen (body) of final instar larvae of *A. trimeni*, *A. stenobea* and *A. neobule*

1. Background colour of body ochre with reddish-purple suffusions and very faint reddish-purple bands at bases of setose scoli. Both anterior and posterior parts a lighter shade of ochre. Conspicuously long setose scoli black with purple around bases. Two black dots (verrucae) beneath dorsal scoli at second (T2) and third (T3) thoracic segments. Spiracles with ochre lining similar to background colour of body. Anal prolegs black with silvery white crochets ……..*A. trimeni*
   - Intricate patterns of cream-white and dark brown stripes along length. Orange areas at bases of setose scoli. Lateral dark brown stripe with orange areas around bases of supraspiracular scoli. Absence of prominent black dots beneath dorsal scoli of second and third thoracic segments. Spiracles with dark brown lining. Anal prolegs orange or burnt orange 2
2. Thin cream-white stripe dorsally at central axis along length of body with faint orange and brown markings. Orange stripes along dorsal setose scoli and white stripes next to dorsal setose scoli, both these stripes with distinct thicker and thinner

areas. Continuous white stripe on lateral side from behind head all along row of subspiracular scoli. True legs at thorax and ventral prolegs at A3–A6 all black ……..…….… *A. stenobea*

- Dorsal transverse orange areas associated with bases of dorsal setose scoli and adjacent transverse cream-white areas with thin transverse dark brown lines each. True legs burnt orange with congruent dark brown lining. Ventral prolegs at A3–A6 beige .....… *A.neobule*

Key to characters of head of final instar larvae of *A. trimeni, A. stenobea* and *A. neobule*

1. Background colour of epicranium ochre. Upper angle of frons with clear extensive semi-triangular black marking; bottom edge of clear semi-triangular marking distinctly convex. Entire stemmatal region discrete uniform black …..…… *A. trimeni*
   - Background colour of epicranium burnt orange. Stemmatal region bicoloured: anterior part of stemmatal region black and posterior part burnt orange. …….……..… 2
2. Broad white lining along bottom part of epicranial suture and vicinity of adfrontal areas. Absence of black markings at upper angle of frons. Conspicuous white areas around stemmatal region …….....……..…… *A. stenobea*
   - Pale narrow lining along epicranial suture and vicinity of adfrontal areas. Black marking at upper angle of frons with straight or slightly concave bottom edge. Stemmatal region not surrounded by conspicuous white areas. ……. *A. neobule*

Description of pupae of *A. trimeni, A. stenobea* and *A. neobule* from TKR

A. trimeni (Fig. 12)

General: Ivory background colour, two dorsal black stripes and two lateral black stripes with orange spots; intricate tower-shaped black pattern at dorsum of thorax and first abdominal segment (A1). Black lining of veins at wing cases. Head: Ivory coloured with black markings. Eye case ivory coloured with black linings and diagonal black mark. Body behind the head: Intricate dorsal black and tower-shaped patterns at thorax and first abdominal segment with blade-like black bars and spoon-like ivory markings, one on each side of central dorsal axis of mesothorax (T2). Most of veins of wing cases with thin black lining. Black lining of wing veins bolder at posterior margin of cell, at median veins, at bottom half of costa and very thick at inner margins of wing cases. Angular projection of mesothorax at base of each wing case ivory with black lining and orange spot dorsally. Two dorsal black stripes (from A3 to posterior end of abdomen) and lateral black stripes (A5 to posterior end) with white incisions into black areas. Orange spot in dorsal and lateral black stripes at each segment (dorsal stripes with orange spots at A3–A9; lateral stripes with orange spots at A5–A9). Well-developed cremaster reddish brown.

A. stenobea (Fig. 13)

Figure 12 – Pupa of *A. trimeni* found during April–June 2016 at TKR. Left: dorsal view; right: lateral view.

Figure 13 – Pupa of *A. stenobea* found during April–June 2016 at TKR. Left: dorsal view; right: lateral view.

General: Background colour seashell white with pink-brown undertones. Two diffused dorsal black stripes and two lateral black stripes with off-centre orange spots. Narrow delicate black tower-shaped pattern on dorsum of thorax and first abdominal segment. Veins of wing cases with thin, subtle black linings. Head: White with delicate black linings. Eye case white, with black lining and central diagonal black mark. Body behind head: Intricate delicate black tower-shaped pattern on dorsal area of thorax and first abdominal segment. Two fine in-and-outward curving black lines and two widely-spaced black dots on mesothorax. Veins of wing cases with thin and often faint black lining. Angular projection of mesothorax at base of each wing white with small square black pattern and enclosed white dot. Two faint or very faint broken greyish-black dorsal stripes with off-centred orange dots from A3 to posterior end. Two continuous black stripes, one each lateral side of pupa from A5 to posterior end, with off-centre orange spots. Orange dots of faint broken dorsal black stripe only at each of segments A4–A9 and for lateral black stripe only at A5–A8.

A. neobule (Fig. 14)

Figure 14 – Pupa of *A. neobule* found during April–June 2016 at TKR. Left: dorsal view; right: lateral view.

General: Two dorsal black stripes with orange dots and two lateral black stripes with orange dots on an ivory background. Background colour of wing cases, seashell white with strong pinkish-brown undertone; most veins of wing cases not blackened; bold blackening of veins along central axis of wings and at inner margin. Tower-shaped black pattern on dorsum of thorax with bold black lining and yellowish-orange central areas. Head: Ivory with black markings. Eye case is ivory, lined with black ventrally; diagonal black mark at centre of eye-case. Body behind head: Tower-shaped black pattern at dorsum of thorax and first abdominal segment with two bold angulated black lines and enclosed yellowish-orange central areas at mesothorax (T2) and metathorax (T3). Black triangle of tower-shaped pattern at A1. Most veins of wing cases immaculate with contrasting bold black lining at posterior margin of cell, at one or two median veins and at basal two thirds of inner margins. Angular projection of mesothorax at base of each wing case black with white suffusion. Two dorsal black stripes (A3 to posterior end) and two lateral black stripes (one on each side from A5 to posterior end) along length of abdomen with orange dots and number of white incisions into black areas.

Keys to characters of pupae

1. Two diffuse and broken dorsal black stripes (from A3 to posterior end of abdomen) and two black lateral stripes (one on each side from A5 to posterior end of abdomen) with off-centre orange spots on a seashell-white background. Thin and subtle black lining of veins of wing cases. Two widely spaced black dots at mesothorax. Two in-out-curving thin dorsal black lines, one on each side of central black line of mesothorax. Narrow, delicate, tower-shaped dorsal black pattern from thorax to abdominal segment A1. ..…… *A. stenobea*
   - Two prominent dorsal black stripes (from A3 to posterior end of abdomen) with centred orange spots and two lateral black stripes (one on each lateral side from A5 to posterior end of abdomen) with centred orange spots on ivory white or orange tinged white background. Bold black lining of some veins at posterior margin of cell, at some median veins and at inner margins of the wing cases. Tower-shaped dorsal black patterning at thorax and abdominal segment A1 wider and with well-spaced bold black markings on either side of central axis of mesothorax. …..……. 2
2. Veins of wing cases with thin black lining and only bolder black lining posterior margin of the cell, median veins and inner margins. Intricate dorsal black and ivory tower-shaped patterns at thorax and first abdominal segment with blade-like black bars and spoon-like ivory markings of mesothorax (T2). Angular projection of mesothorax at base of each wing case ivory with black lining and an orange spot dorsally. ..... *A. trimeni*
   - Most veins of wing cases immaculate with contrasting bold black lining at posterior margin of cell, at one or two median veins and at basal two thirds of inner margins. Bold angulated black lining of tower-shaped pattern with enclosed yellowish-orange central areas at mesothorax (T2) and metathorax (T3). Black triangle of tower-shaped pattern at dorsum of A1. Angular projection of mesothorax at base of each wing case black with white suffusion. ……..…. *A. neobule*

DISCUSSION

Significance of *Adenia repanda* as the host-plant of *Acraea trimeni* in the Eastern Kalahari Bioregion

A. repanda is currently the only known host-plant species of *A. trimeni*. *A. repanda* has often been regarded as "rare" or "uncommon" and grows in open or partly shaded places in woodland, among rocks, on sandy soils, red sand and granite (de Wilde, 1976). Though *A. repanda* was only added to the plant species list of TKR during this study on 31 March 2016 it was soon realised that once one of these *A. repanda* was found, more were seen. It was surprising how easily this climber could have been overlooked before the first one was seen, a situation often encountered by the naturalist. *A. repanda* may therefore be less rare than experienced by other workers.

A. repanda belongs to a genus of plants containing c. 100 species throughout the Old World Tropics whose habitat use and growth form diversity are exceptional (Hearn, 2006; 2009). The external appearance of *A. repanda* epitomises this growth form diversity, with leaves much elongated, shallowly lobed with repand leaf margins, and quite different in appearance to any other South African *Adenia* species, the latter with their more rounded but often deeply lobed leaves. *A. repanda* represents a monotypic section *Paschanthus* of the genus *Adenia* (Wilde, 1976) and its distribution is the southwesternmost of all *Adenia* species in Africa. *A. repanda* is the only known *Adenia* species in the Eastern Kalahari Bushveld Bioregion – an area with a mean annual precipitation of < 400 mm

and about twice as much frost as the Central Kalahari Bushveld Bioregion (Mucina & Rutherford, 2006).

A. repanda, an available host-plant in a very dry area with significant frost in winter is the key to the distribution of *A. trimeni*, a butterfly species that belongs to the *zetes*-group with its tropical affinities (Henning & Williams, 2010). *A. trimeni* has been recorded from Steinkopf in the west to Kimberley in the east in South Africa and also in Namibia and Botswana (Mecenero *et al.*, 2013). *A. trimeni* is an inhabitant of semi-arid savanna and upper regions of the Karoo Biome. *A. trimeni* is conspicuously less abundant than other *Acraea* species in the Kalahari and it seems likely that *A. trimeni* is monophagous where only *A. repanda* is available. No indigenous *Passiflora* species is present in the Kalahari bushveld, so that host-plant species options in Passifloraceae is very limited for *A. trimeni.*

It was anticipated that any host-plant of *A. trimeni* in the Kalahari would be growing on rocky slopes or in kloofs (steep cuttings or valleys in mountains) where some kind of protection from the harsh conditions would be available. It was therefore surprising that at TKR *A. repanda* has so far only been found on flatter ground in the Olifantshoek Plains Thornveld (SVk 13) and Kathu Bushveld (SVk 12) vegetation types.

A. repanda obtains some protection from frost and herbivores on these plains by often growing in the undergrowth beneath canopies of *Boscia albitrunca* (Shepherd's Tree) or among foliage of *Senegalia mellifera* (Black Thorn) subsp. *detinens* with its density of branches and thorns. At the Legabe section of the TKR, where two prides of lions (*Panthera leo*) and some males in coalition groups roam, *A. repanda* is conspicuously tall and abundant in some of these areas. This is at odds with the observation by Bryant (who collected specimens) that *A. repanda* was "greedily eaten by stock" (de Wilde 1976). One could however hypothesise that the presence of large predators such as lions would promote larger populations of *A. repanda* by preventing megaherbivores settling down to feed and thus limiting grazing beneath the *Boscia albitrunca* canopies.

Host plant use by *A. stenobea* and *A. neobule* in the Kalahari

Both *A. stenobea* and *A. neobule* are migrants and are much more widespread and common than *A. trimeni*. *A. stenobea* is in turn conspicuously less abundant than *A. neobule*, based on experience and field observations (quantitative counts are currently being undertaken to confirm abundances of the two species). The only known host plant for *A. stenobea* is *A. repanda* (reported here) and the descriptions of its larvae given here could lead to more observations and knowledge of *A. stenobea* in the wild.

A. neobule is known to be polyphagous throughout its substantial distribution, flying in the Gambia and Senegal to Nigeria and then through virtually all of tropical Africa (Larsen, 2005). The species can be quite a serious pest on tossa jute (*Corchorus olitorius*) in the Kumasi area of Ghana and has also been reported as a pest on sweet potato, tobacco, and various *Hibiscus* used as vegetables in Ashanti villages (Lawson & Duodu, 1990; Larsen, 2005). *Hybanthus enneaspermu*s (Violaceae) has been recorded from Côte d'Ivoire (Pierre & Vuattoux, 1978) and from Bénin by D. Bernaud (*pers. comm.*) *vide* Larsen (2005). *Corchorus* (Tiliaceae), *Hibiscus* (Malvaceae), *Ipomoea* (Convolvulaceae), *Barteria, Tryphostemma* and *Adenia* (Passifloraceae) are others (Larsen, 2005).

Table 1 lists the known host-plant species of *A. neobule*, which now includes *A. repanda*, which are from the plant families Passifloraceae, Malvaceae, Violacaeae, Convolvulaceae and Solanaceae. It seems unlikely that a localised and often rare plant species, such as *A. repanda*, could sustain large numbers of *A. neobule* in the southern Kalahari. It is therefore surmised that *A. neobule* is also polyphagous in the Kalahari, and must use other suitable plants on occasion.

Table 1 – Host plant species recorded for *A. neobule*

Host plant species	Family	Recorded by
Adenia gummifera (Harv.) Harms	Passifloraceae	van Son (1963)
Adenia repanda (Burch.) Engl.	Passifloraceae	Terblanche (2016)
Barteria fistulosa Mast.	Passifloraceae	Kielland (1990)
Basananthe zanzibarica (Mast.) W.J.de Wilde	Passifloraceae	van Someren (1974)
Passiflora edulis Sims.	Passifloraceae	Platt (1921)
Passiflora incarnata Linn.	Passifloraceae	Platt (1921)
Turnera angustifolia	Turneraceae	Legrand (1965)
Corchorus olitorius L.	Malvaceae	Ewete (1990)
Hibiscus species	Malvaceae	Larsen (2005)
Hybanthus enneaspermus (L.) F.Muell.	Violaceae	Pierre & Vuattoux (1978)
Ipomoea species	Convolvulaceae	Larsen (2005)
Nicotiana species	Solanaceae	Larsen (2005)

Patterns of host-plant use in the tribe Acraeini are: *Pardopsis* feeding on herbaceous plants of family *Violaceae*, *Acraea* and *Bematistes* feeding preferentially on Passifloraceae, ''Old World Actinote" feeding mainly on Urticaceae, and Neotropical species of which life-histories are known feeding on Asteraceae only (van Son 1963, Pierre 1987, Francini 1992, Larsen 2005, Silva-Brandão *et al.* 2008). The ancestor of all Acraeini (*sensu stricta*) appears to have used Passifloraceae as its larval host plant, and this family may also be considered ancestral for all the Heliconiinae clade (Silva-Brandão *et al.* 2008). The continuation of the use of Passifloraceae in southwestern semi-arid extremes of distribution of *Acraea* in the Afrotropical Region, reported here, highlights the fidelity of *Acraea* to Passifloraceae.

Systematic outlines of species-groups in *Acraea* Fabricius, 1807, were given in Pierre (1987), Henning (1992, 1993) and Henning & Williams (2010), and all

concur that *A. neobule*, *A. stenobea* and *A.trimeni* belong to different species groups. *A. neobule* is part of the *neobule*-group; *A. stenobea* is part of the *caecilia*-group (also noted as *natalica*-group in some literature); and *A. trimeni* is part of the *zetes*-group. Moreover *A. neobule* and *A. trimeni* are both listed under the subgenus *Acraea* while *A. stenobea* is a representative of subgenus *Stephenia* Henning, 1992. It is remarkable that these three *Acraea* species, belonging to three different species-groups and two subgenera in the genus *Acraea* are feeding on one host-plant species *A. repanda*. Characters of larvae and pupae described here for the first time correlate well with distinctiveness of species-groups within *Acraea*. For example, final instar larva and pupa of *A. stenobea* show similarities with final instar larva and pupa of *A. oncaea* that also belongs to the *caecilia*-group. Ecological resource partitioning of *A. repanda* by the three *Acraea* species from three species groups and two subgenera could reveal valuable ecological-evolutionary insights to *Acraea*.

Ant-associated *A. repanda* and attacks by ants on *A. neobule* larvae

Some kind of association exists between *Anoplolepis* and *Crematogaster* ants and *A. repanda*, as described above in the results section. Ant attacks of *A. custodiens* on *A. neobule* could explain the behaviour of *A. neobule* larvae that move onto grasses or stems of other plants in close proximity to *A. repanda*.

Ants appear to protect *A. repanda* from defoliating insects such as larvae of *A. neobule*. Defoliating insects have in their evolutionary paths often developed ways of resisting chemical defences of plants but rarely acquired successful counter adaptations against ants (Coley & Kursar, 1996, Dejean *et al.*, 2008). In Cameroon Dejean *et al.* (2008) found that small *Acraea zetes* L., 1748 caterpillars were stung and then discarded by single workers of the ant *Tetraponera aethiops* F. Smith, 1877, when these ants were protecting their host myrmecophyte *Barteria fistulosa* Mast. (Passifloraceae). *A. custodiens*, that patrols and protects *A. repanda* is an opportunistic ant with a wide distribution across South Africa. By no means is the association of *A. custodiens* with *A. repanda* an exclusive mutualism on a species level, but for individual *A. repanda* plants ant-association with either *Anoplolepis* or *Crematogaster* could be vital for enhanced survival. Another scenario that should be researched is whether the extrafloral nectaries of *A. repanda* are visited by a number of ant species or only a single ant species per plant. At Costa Rica in the Neotropical Region Smiley (1986) noted that up to 29 ant species visit extrafloral nectaries of *Passiflora vitifolia* and *P. quadrangularis* which are used as host-plants by *Heliconius ismenius*. Nature of ant-protection of *Adenia* and survival of *Acraea* species in Savanna Biome of southern Africa is a fascinating research field that could stem from these observations. These hostile interactions of ants with butterfly larvae are in sharp contrast to symbiotic relationships between ants and larvae of many myrmecophilous Lycaenidae in South Africa.

Interspecific differences between larvae of *A. trimeni* and those of other members in the *zetes*-group

A. trimeni final instar larvae described above differ from images and descriptions of other members of the *zetes*-group. Final instar larvae of *A. trimeni* lack the distinct and prominent dark purplish black bands that are present in final instar larvae of other members of the *zetes*-group. These differences are further confirmation that *A. trimeni* is a unique species of which the distribution largely overlaps with Griqualand West Centre of Plant Endemism (van Wyk & Smith, 2001).

Intraspecific variation in *A. neobule* larvae and importance of regional studies of life histories of widespread species

A. neobule final instar larvae described here are in some aspects different to those of life history descriptions from other regions for the same species. Striking features of final instar larvae of *A. neobule* from Tswalu Kalahari Reserve are much bolder markings, prominence of white areas with transverse brown lines dorsally and presence of extensive orange areas (almost forming bands), unlike final instar larvae of *A. neobule* illustrated by Clarke in van Son (1963). The importance of studying life-histories not only from the wild, but in different kinds of wild, such as the Kalahari region, is highlighted by these results. These findings highlight importance of repeated life-history studies by people from different regions that contribute to the Caterpillar Rearing Group.

CONCLUSIONS

The rare and unusual climbing plant *A. repanda* (Burch.) Engl., is recorded as a host-plant species of *Acraea* for the first time (*A. trimeni* and *A. stenobea* have no other known host-plant, whereas *A. neobule* is broadly polyphagous).

Fidelity of the African genus *Acraea* to Passifloraceae is underscored by representatives of three species-groups and two subgenera all using the same *Adenia* species as host-plant in an area with a rainfall < 400 mm and sporadic droughts. Resource partitioning of the host-plant *A. repanda* between *A. trimeni*, *A. stenobea* and *A. neobule* could shed light on some ecological aspects of diversification of species groups within *Acraea*.

A. repanda has so far only been found on the plains of Olifantshoek Plains Thornveld (SVk 13) and Kathu Bushveld (SVk 12) at TKR. *A. repanda* climbs amongst substantial undergrowth beneath the canopies of *Boscia albitrunca* or the dense thorny branches of *Senegalia mellifera* subsp. *detinens* This may offer it protection against the harsh climate and megaherbivore browsing, although it is reportably favoured by stock when it is accessible. Conspicuously tall and healthy populations of *A. repanda* are found in the Legabe section of TKR where lions (*Panthera leo*) roam. It appears that low stocking rates and the presence of large predators such as lions favour abundance of

A. repanda. *A. repanda* is an ant-associated plant species at TKR. Individual plants are constantly patrolled by *Anoplolepis* or *Crematogaster* ant species that often visit leaf blade glands (extrafloral nectaries). Attacks by *Anoplolepis custodiens* ants on *A. neobule* larvae could explain the frequent habit of *A. neobule* larvae to rest on grass (if *A. repanda* is still small) or twigs (where *A. repanda* climbed in trees) alongside *A. repanda* stems and leaves. These host-plant-ant-butterfly interactions at *A. repanda* are in contrast to symbiotic relationships between many South African myrmecophilous Lycaenidae and ants. While it appears the ants protect *A. repanda* defoliation by herbivores, the exact nature of this association could make a fascinating research subject.

Interspecific differences such as the lack of clear dark purplish black bands on the final instar larvae of *A. trimeni* in contrast to other members of the *zetes*-group, support the unique position of *A. trimeni* in this group. *A. trimeni* is regarded here as a near-endemic of the Griqualand West Centre of Plant Endemism (van Wyk & Smith, 2001). Survival of *A. trimeni* in areas with lower rainfall and more frost than in savannas where other relatives of the *zetes*-group are found, could be of evolutionary significance.

Intraspecific variation seen in the larvae of *A. neobule* from the Kalahari highlights importance of studying life histories not only from the wild, but regionally in different kinds of wild. Repeated life history studies of common and widespread species by people from different regions could be another valuable contribution of the Caterpillar Rearing Group.

This study reconfirms the importance of observing use of host plant species *in the wild* to effectively address conservation management of Lepidoptera in natural landscapes.

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