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## Polymorphism in four tortoise beetles from Queensburgh, South Africa (Chrysomelidae: Cassidinae)

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ABSTRACT. Four tortoise beetles belonging to four different genera and exhibiting balanced polymorphism were studied by means of an informal census over periods ranging from six to eighteen years at Queensburgh, a few kilometres inland of Durban, in coastal Natal, South Africa. *Cassida guttipennis* Boheman was trimorphous (normal maculate orange-brown form, and forms *romula* and *fenestralis*), and the remaining three species were dimorphous: *Chiridopsis nigrosecta* (FAIRMAIRE) (normal and form *vernica*), *Lacoptera cicatricosa* (BOHEMAN) (brown and black forms) and *Conchyloctenia punctata* (FABRICIUS) (variably maculate form *parummaculata* and black form *luteicollis*). Results revealed that in *C. guttipennis*, form *romula* : normal : *fenestralis* :: ~5 : 4 : 1, in *Ch. nigrosecta*, form *vernica* : normal :: 7 : 3, in *L. cicatricosa* the brown form was only marginally dominant over the black form (ratio ~13 : 12) and in *Con. punctata*, *parummaculata* : *luteicollis* :: 49 : 2. It is suggested that crypsis confers an advantage to the *romula* and *fenestralis* forms of *C. guttipennis*, and both the light and dark forms of *L. cicatricosa* may benefit almost equally, hence the almost 1 : 1 ratio of the two forms. The normal form of *C. guttipennis* could be a mimic of an *Epilachna* ladybird on the same host plant and both *Ch. nigrosecta* forms are postulated to be part of wide mimetic ring complexes involving Coccinellids, Chrysomelids (including other Cassidines), Hemipterans and spiders. There appears to be an increase in the percentage of *vernica* in *Chiridopsis nigrosecta* populations from north to south through Africa, with the form being absent in Ethiopia and increasing to become dominant in the study area in South Africa. The study also reveals that a great deal of unsuspected movement takes place over fair distances: Cassidines as a group are generally considered to be reluctant fliers.

Key words: entomology, biology, polymorphism, Coleoptera, Chrysomelidae, Cassidinae, South Africa.

## INTRODUCTION

Relatively few observations have been published on the subject of polymorphism in Cassidine beetles and many of these have been passing mention or implied comments in papers dealing with other facets of their biology (CHABOO 2007 and references therein). South Africa is home to approximately 119 tortoise beetle species (BOROWIEC 1999, 2005), about 48 of them (~40%) endemic, but almost no observations have been specifically made about their polymorphism and colour/pattern variations. Observations on these beetles at Escombe, Northdene and Malvern in the Borough of Queensburgh, Natal (~29°52-53'S, 30°52-55'E), revealed that four species (one endemic) exhibit definite colour/pattern polymorphism.

## POLYMORPHISM DEFINED

The classic definition of genetic polymorphism was given by FORD (1940) as follows: "... *the occurrence together in the same locality, at the same time, of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation.*"

This definition excludes geographical races, seasonal variations, environmental variants and mutational variants. The different forms must also be present at a reasonable frequency: taken at an arbitrary 1% by FORD.

A more flexible definition was given in ABERCROMBIE *et al* (1961): "*Having different forms ... distinct kinds of individuals belonging to one species, occurring in fairly constant proportions within a freely inbreeding population.*"

In Queensburgh, a few kilometres inland of Durban, four species' populations were monitored for a number of years and found to exhibit balanced polymorphism, viz. *Cassida guttipennis* BOHEMAN, *Chiridopsis nigrosepta* (FAIRMAIRE), *Lacoptera cicatricosa* (BOHEMAN) and *Conchyloctenia punctata* (FABRICIUS).

## MATERIALS AND METHODS

The Cassidine observations reported in this study were from populations in the Borough of Queensburgh, about 20km inland of Durban, in coastal Natal, South Africa. The area is bounded in the north and south by the Umbilo River and Umhlatuzana River, respectively: an area of warm (~24°-32°C) wet and humid summers with rainfall (approximately 1000mm p.a.) from *circa* October to April, and mild (~16°-22°C) dry winters from ~May to September. The study areas included the margins of semi-closed canopy riverine scrub forest and patches of open bushy coastal grassland and thicket in the North Park Nature Reserve at Northdene (29°52'S, 30°52'E) (HERON 2003), as well as areas of disturbed and degraded suburban vegetation (railway track, roadsides, gardens): principally at Escombe.

Personnel at the Natal Herbarium, Durban, identified the host plants from dried flowering specimens, and the beetle identifications were based upon specimens submitted to Professor Lech BOROWIEC at Wrocław University, Poland, and in specimens present in both the National Collection of Insects (Pretoria) and the small collection of the Durban Natural Science Museum.

Statistical record keeping was done informally and did not employ a structured census method such as marking and releasing. As often as possible, counts were made and the totals of individual Cassidine species and forms observed were recorded. In most cases, the counts were of a general nature since the host plants and beetles were dispersed over a wide area in an open population. Two of the polymorphic species thus studied were *Conchyloctenia punctata* (low level polymorphism) and *Laccoptera cicatricosa* (significant level of polymorphism). In both of these cases the records were erratic, far from complete, and only very general conclusions could be drawn from them. Closer census studies, employing the same informal method, were made of two discrete colonies viz. *Cassida guttipennis* and *Chiridopsis nigrosepta*. These populations, whilst not closed, were nevertheless more isolated since the host plants were found in a limited area and not widely distributed. Both species exhibited marked polymorphism at significant levels. Although the imprecise census methodology employed may compromise the value of the statistics to a degree, it represented a first attempt at quantifying the proportions of the forms present and is considered more accurate than form assessments based upon randomly collected specimens preserved in collections.

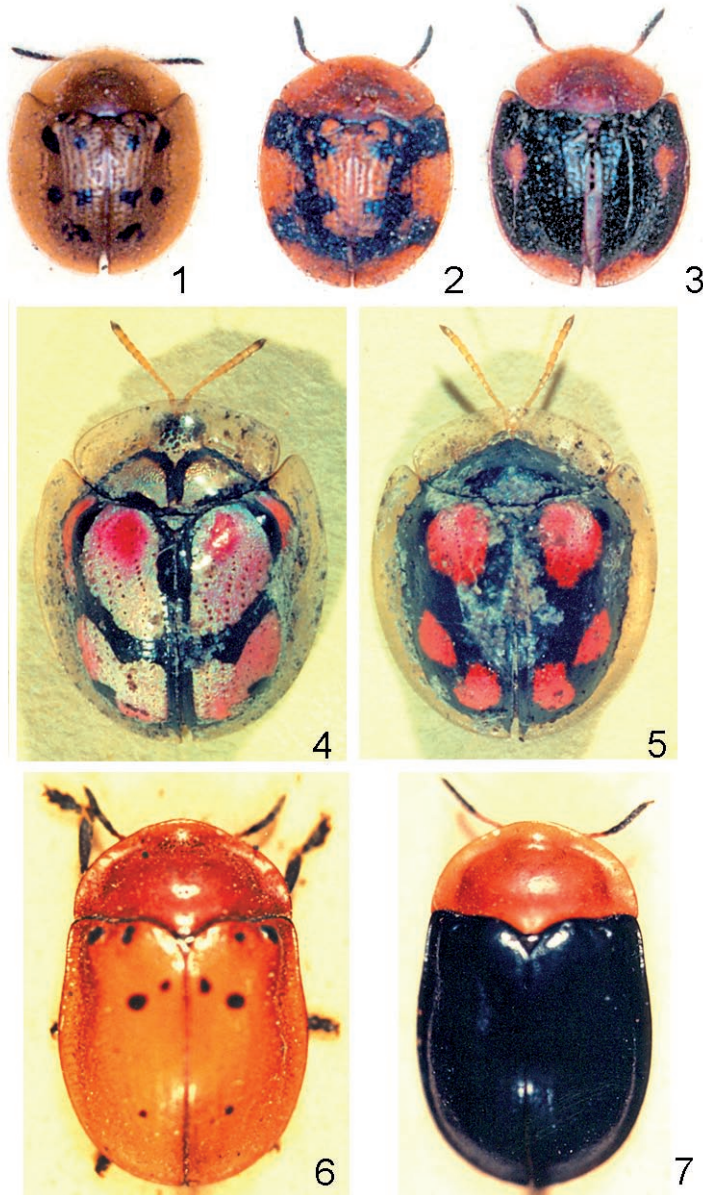
The two semi-closed polymorphic populations studied were as follows:

1. *Cassida guttipennis* BOHEMAN, 1862. This small natural colony was monitored in a south-west-facing area of disturbed partly shaded grassy vegetation on land formerly occupied by Stella Road and a portion of the Escombe Primary School playing grounds prior to elimination of the railway level crossing in 1973/74. The host plant was *Berkheya bipinnatifida* (HARV.) ROESSL. (Asteraceae), and the beetle's presence was readily betrayed by circular scrapings, produced from the ventral leaf surface, that usually did not penetrate the dorsal epidermal cuticle (HERON 1997, 2003). The colony was periodically badly disturbed when the vegetation was cut and cleared by the local Municipality. The population was studied from September 1987 to May 2004. The small (~5 x 4mm), rounded and flattened beetles were active for about eight months of the year, appearing in mid-August and vanishing during mid to late April. Although secretive and spending much of their time on the ventral leaf surfaces, they were active amongst the host plant leaves, and moved from one plant to another, in the colony.

Three colour forms of the beetle were present in the Escombe colony, viz. typical, ab. *romula* SPAETH 1911 and ab. *fenestralis* SPAETH 1933. Pattern variation only affected the elytra. The typical and *fenestralis* forms are illustrated in BOROWIEC & ŚWIĘTOJAŃSKA (2011).

a) The normal form (Fig. 1) was orange-brown with an immaculate pronotal disc. The elytral disc had ten small black maculae.

b) Form *romula* (Fig 2) had black to blackish-brown markings on a yellowish/



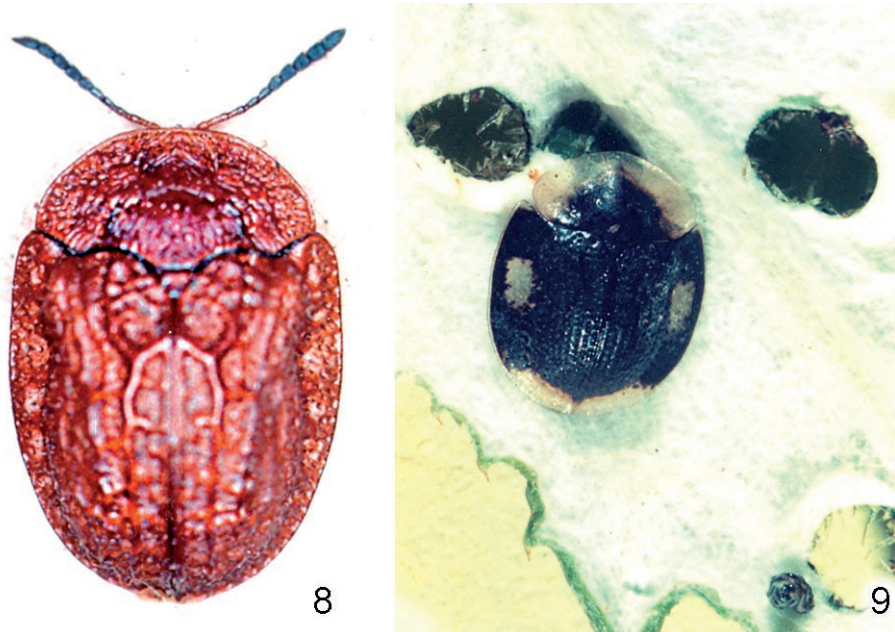
1-3. *Cassida guttipennis*: 1 – typical form; size: 5.0 x 4.0mm. Collected November 1898 from Malvern, Queensburgh; 2 – *Cassida guttipennis* var. *romula*; size 5.0 x 4.0mm. No date or locality; 3 – *Cassida guttipennis* var. *fenestralis*; size 5.0 x 4.0mm. No locality or date. all collection of the Durban Natural Science Museum. 4, 5. *Chiridopsis nigrosepta* ♂: 4 – typical form; Living specimens from the study colony at Escombe, Queensburgh; 5 – *Chiridopsis nigrosepta* var. *vernicata* ♂: living specimens from the study colony at Escombe, Queensburgh. 6, 7. *Conchyloctenia punctata*: 6 – var. *parummaculata*: Lightly maculate form. Malvern, Queensburgh; 7 – var. *luteicollis*: Malvern, Queensburgh. Both collection of the Durban Natural Science Museum

whitish to brownish background. The dark variable pattern consisted of humeral and postero-lateral patches with a broad variable irregular marginal band. Four dark maculae, fused with the marginal band and of variable size, were present on the elytral disc. The explanate margin between the postero-lateral angle and the sutural angle was yellowish/whitish to brownish. Uncommonly, the maculae were reduced and the ground colour orange-brown: the beetle was an intermediate between the normal and *romula* forms.

c) Form *fenestralis* (Fig. 3). The whitish ground-colour of the elytral disc was reduced to a narrow elongated window midway along the lateral discal edge. In some specimens the window was almost absent. The yellowish/whitish explanate margin between the postero-lateral angle and the sutural angle was identical to *romula*. Form *romula* graded into *fenestralis* but the latter was persistent and there is no difficulty in distinguishing between them.

The species is endemic to north-eastern and eastern South Africa (BOROWIEC 1999): Mpumalanga, Natal and the Eastern Cape Provinces.

2. *Chiridopsis nigrosepta* (FAIRMAIRE, 1891) was monitored on a small patch of its exotic host plant, *Ipomoea carnea* JACQ. subsp. *fistulosa* (MART. ex CHOISY) D.F. AUSTIN (Convolvulaceae), established by the writer in his garden. The beetles arrived



8. *Laccoptera cicatricosa*. Brown form. Size: 8.2 x 6.0mm. Malvern, Natal. Specimen: collection of the Durban Natural Science Museum. 9. *Cassida guttipennis* var. *fenestralis* on pubescent ventral surface of *Berkheya bipinnatifida* leaf. The beetle is relatively inconspicuous amongst the semi-circular feeding scrapings. The lunular pubescence pushed to one side of the scrapings resembles the whitish apical portion of the elytral epipleura

naturally and unexpectedly in October 1996 and the colony existed until April 2004. The species varied in size from 6.5 to 7.5mm x 5.3-6.xmm and stood 2.2-2.5mm high. Two colour forms, both with colourless elytral and pronotal epipleura, were present in the population of this domed, Coccinellid-like species, *viz.* typical and *ab. vernicata* FAIRMAIRE. Intermediate forms were only very rarely observed.

a) The typical form (Fig 4) had black linear markings on a ground colour varying from pinkish white through pale to deep orange. The pronotal margin was outlined with black and a black band, thickest near the head, extended to the black scutellum. The elytral disc edge was outlined in black, as also was an elongated ground-colour macula extending from the humeral area to central elytral disc edge. The elytral suture was outlined in black and the central disc divided into four large oval to angular ground-colour patches. The size and shape of the ground-colour patches varied, as also did the width and completeness of the black band linking the elytral suture band with the elytral marginal band.

b) Form *vernicata* (Fig. 5) was essentially black with, on each elytron, the ground colour reduced to a large rounded reddish to orange patch towards the elytral base, and two smaller rounded and similarly coloured patches in the postero-lateral and basal portions of the elytron. Populations from other parts of the species' range exhibited considerable variation and inter-gradation of colour and pattern (see BOROWIEC & ŚWIĘTOJAŃSKA 2011).

The two polymorphic species from open, scattered, populations were as follows:

3. *Laccoptera cicatricosa* (BOHEMAN, 1855). A species relatively seldom encountered because of its crepuscular behaviour (HERON 2004) and disruptions caused by vegetation clearance. There was a widely dispersed open population on the indigenous host plants *Convolvulus farinosus* L., *Hewittia malabarica* (L.) SURESH, *Ipomoea cairica*, *Ipomoea ficifolia* LINDL., and *Ipomoea wightii* (WALL.) CHOISY. The exotic species *Ipomoea alba* L., *Ipomoea batatas* (L.) LAMK. and *Ipomoea congesta* R.BR. were also used (HERON & BOROWIEC 1997). All plants belonged to the Convolvulaceae. Two colour forms were present: a variable moderate to dark leaf-brown (Fig. 6), and a dark blackish form with two translucent pale yellowish-white maculae on the anterior margin of the pronotum. No brown forms were observed with the pale maculae. Full descriptions of this species appeared in BOROWIEC (1994) and HERON (2004), and both forms are illustrated in BOROWIEC & ŚWIĘTOJAŃSKA (2011). Records noting polymorphic forms were maintained from January 2001 to October 2007.

4. *Conchyloctenia punctata* (FABRICIUS, 1787). A highly variable species noted for the cycloalexical behaviour of its larvae (HERON 1999). The population was open and its host plants were the indigenous *Convolvulus farinosus*, *Hewittia malabarica* and *Ipomoea cairica* (L.) Sweet, and exotic *Ipomoea batatas* (all Convolvulaceae). Two forms of the beetle were present in Queensburgh: the sparse to moderately maculate *parummaculata* (BOHEMAN, 1854) (Fig. 7) and the black *luteicollis* (WEISE, 1899) (Fig 8). In the study area, a range of intermediate forms, between lightly maculate and heavily

maculate *parummaculata* were present (*maculipennis* was absent), but there were no intermediate forms leading to *luteicollis*. Full descriptions of this species appeared in BOROWIEC (1994) and HERON (1999), and are illustrated in BOROWIEC & ŚWIĘTOJAŃSKA (2005). Census records were maintained from January 1987 to November 2003 (those for 2004 to 2009 were considered too erratic to be meaningful).

## RESULTS OF THE CENSUS STUDIES

1. *Cassida guttipennis*. Table 1 gives the statistics for the colony compiled over 18 seasons (2945 surveys) and reveals that form *romula* was consistently dominant at 53.74% (range 44.95% to 77.87%), followed by the normal form at 35.96% (range 10.37% to 46.50%) and *fenestralis* at 10.28% (range 1.58% to 23.3%): an average approximate ratio of 5 : 4 : 1. The normal form was, with two exceptions (the seasons 1991/92 and 2000/01) dominant over form *fenestralis* but the figure for the latter

Table 1. Rough field statistics for colony of <i>Cassida guttipennis</i> BOHEMAN on <i>Berkheya bipinnatifida</i> (HARV.) ROESSL. (Asteraceae) (Escombe, Queensburgh)								
Season	Total numbers of individuals				Sum	Percentage		
	Normal	<i>romula</i>	<i>fenestralis</i>			Normal	<i>romula</i>	<i>fenestralis</i>
1987	97	155	25	277		35.01	55.95	9.02
1987/88	11133	11682	1123	23938		46.50	48.10	4.49
1988/89	1292	1461	497	3250		39.75	44.95	15.29
1989/90	893	1447	561	2901		30.78	49.89	1.93
1990/91	1458	2706	1289	5453		26.73	49.62	23.63
1991/92	198	717	469	1384		14.30	51.80	33.88
1992/93	176	494	100	770		22.85	64.15	12.98
1993/94	358	1070	148	1576		22.71	67.89	9.39
1994/95	529	1078	73	1680		31.48	64.16	4.34
1995/96	91	345	7	443		20.54	77.87	1.58
1996/97	249	1485	190	1924		12.95	77.18	9.87
1997/98	422	1595	174	2191		19.26	72.79	7.94
1998/99	192	322	155	669		28.69	48.13	23.16
1999/00	39	274	63	376		10.37	72.87	16.75
2000/01	55	220	56	331		16.61	66.46	16.91
2001/02	147	303	32	482		30.49	62.86	6.63
2002/03	232	741	70	1043		22.24	71.04	6.71
2003/04	156	381	36	573		27.22	66.49	6.28
<b>SUM</b>	<b>17717</b>	<b>26476</b>	<b>5068</b>	<b>49261</b>				
<b>MEAN</b>	<b>984.27</b>	<b>1470.88</b>	<b>281.55</b>	<b>2736.72</b>		<b>35.96</b>	<b>53.74</b>	<b>10.28</b>

season was close and may have been skewed by the imprecise census methodology employed.

In the North Park Nature Reserve at Northdene, *Cassida guttipennis* was present on scattered *Berkheya bipinnatifida* plants along the north bank of the Umhlatuzana River and intermittent examinations of the beetles (48 surveys) from 2003/04 to November 2007 revealed that form *romula* was again dominant (74.00%: n = 117) followed by the normal form (14.55%: n = 595) and form *fenestralis* (11.44%: n = 92).

A third, small, locality in Northdene, visited on 43 occasions since the close of 2001 (total of 145 beetles) had *romula* : *fenestralis* : normal = 83.44% (n = 17): 11.72% (n = 121): 4.82% (n = 7)..

Questionable though the census method may have been, it is confidently asserted that Queensburgh *Cassida guttipennis* populations have form *romula* dominant over the normal form, and the normal form dominant over form *fenestralis*.

2. *Chiridopsis nigroseta*. Table 2a gives the data from the colony established in the writer's garden (2598 surveys). With the exception of the 1996/97 and 2003/04 seasons, the form *vernica* was consistently dominant at 68.26% (range 42.23% to 89.57%), The normal form was present at 31.73% (range 10.42% to 57.76%): an average approximate ratio of 7 : 3. For much of the study period a census was done morning and evening and the figures are considered relatively accurate.

Two exotic *Ipomoea arborescens* (HUMB. & BONPL.) DON. trees along a roadside less than a kilometre west of the writer's colony were also noted to host this beetle in 2004 and intermittent records were kept of it using the same method (177 surveys). The results (Table 2b) also indicate that *vernica* was dominant over the normal form (ratio approximately 5: 4). Since these trees were fairly tall, the beetles could only be counted on the lower branches and the results must be considered incomplete.

Table 2a. Rough field statistics for colony of <i>Chiridopsis nigroseta</i> (FAIRMAIRE) on <i>Ipomoea carnea</i> JACQ. subsp. <i>fistulosa</i> (MART. ex CHOISY) D.F. AUSTIN (Convolvulaceae) (Escombe, Queensburgh)						
	Total numbers of individuals				Percentage	
	Form				Form	
Season	Normal form	<i>vernica</i>	sum		Normal form	<i>vernica</i>
1996/97	842	1778	2620	⊗	32.13	67.86
1997/98	3859	2910	6769	⊗	57.00	42.99
1998/99	2190	3900	6090	⊗	35.96	64.03
1999/00	935	8030	8965	⊗	10.42	89.57
2000/01	1444	5028	6472	⊗	22.31	77.68
2001/02	891	1452	2343	⊗	38.02	61.97
2002/03	797	888	1685	⊗	47.29	52.70
2003/04	294	215	509	⊗	57.76	42.23
<b>SUM</b>	<b>11252</b>	<b>24201</b>	<b>35453</b>	⊗		
<b>MEAN</b>	<b>1406.50</b>	<b>3025.12</b>	<b>4431.62</b>	⊗	<b>31.73</b>	<b>68.26</b>



Table 2b. Rough field statistics for colony of <i>Chiridopsis nigrosetpa</i> (FAIRMAIRE) on <i>Ipomoea arborescens</i> (HUMB. & BONPL.) Don. (Convolvulaceae) (Escombe, Queensburgh)						
	Total numbers of individuals				Percentage	
	Form				Form	
Season	Normal form	<i>vernicata</i>	sum		Normal form	<i>vernicata</i>
2004/05	3	9	12	⊗	25.00	75.00
2005/06	52	65	112	⊗	44.44	55.55
2006/07	72	85	157	⊗	45.85	54.14
<b>SUM</b>	<b>127</b>	<b>150</b>	<b>277</b>	⊗		
<b>MEAN</b>	<b>42.33</b>	<b>50.00</b>	<b>92.33</b>	⊗	<b>45.84</b>	<b>54.15</b>

Two polymorphic species from open, widely scattered, populations were also studied but the statistical gathering was hampered by the writer's long working hours and by disturbance of vegetation (roadsides through cutting and clearing, and railway trackside by the use of herbicides). The populations were thus severely disrupted and figures gathered serve only a very general purpose.

3. *Laccoptera cicatricosa*. Combined census figures for several areas in Queensburgh, including the North Park Nature Reserve, are presented in Table 3 (362 surveys). The common brown form was dominant at 51.91% (range 81.25% to 30.23%) over the black form at 48.08% (range 69.76% to 18.75%): an approximate ratio of nearly 1 : 1. The dominance of the black form during the first (2001) season was curious. The census figures do not accurately reflect the presence of the adult beetle in Queensburgh (larvae are not uncommon at times), principally because the census method did not accommodate the species' crepuscular to partially nocturnal habits. Nevertheless, it

Table 3. Rough field statistics for open population of <i>Laccoptera cicatricosa</i> (BOHEMAN) on members of the Convolvulaceae (Queensburgh)						
	Total numbers of individuals				Percentage	
	Form				Form	
Season	Brown form	Black form	sum		Brown form	Black form
2001	26	60	86	⊗	30.23	69.76
2001/02	15	15	30	⊗	50.00	50.00
2002/03	26	6	32	⊗	81.25	18.75
2003/04	13	3	16	⊗	81.25	18.75
2004/05	2	1	3	⊗	66.66	33.33
2005/06	6	2	8	⊗	75.00	25.00
2006/07	7	1	8	⊗	51.91	48.08
<b>SUM</b>	<b>95</b>	<b>88</b>	<b>183</b>	⊗		
<b>MEAN</b>	<b>15.83</b>	<b>14.66</b>	<b>30.50</b>	⊗	<b>51.91</b>	<b>48.08</b>

would appear that the normal and dark forms are almost equally represented in Queensburgh.

4. *Conchyloctenia punctata*. Census figures, representing combined results for several areas in Malvern, Escombe and Northdene (including the North Park Nature Reserve) in Queensburgh, are presented in Table 4 (2789 surveys). The common *parummaculata* form, usually sparsely maculate, was dominant at 98.20% (range 100% to 71.79%) over the *luteicollis* form at 1.7% (range 28.20% to 0%). The unexpectedly high figures for *luteicollis* in the 1997/98 and 2002/03 seasons came from two roadside groups on *Hewittia malabarica* at Escombe. The 1997/98 group had a *luteicollis* population of up to 36% (HERON 1999). The form *luteicollis* was distinct: there were no intermediates with *parummaculata*: the suggestion in VERMA & KALAIICHELVAN (2004) appears invalid.

Season	Total numbers of individuals				Percentage	
	Form		sum		Form	
	<i>parummaculata</i>	<i>luteicollis</i>			<i>parummaculata</i>	<i>luteicollis</i>
1987	145	2	146	X	98.63	1.36
1987/88	476	2	478	X	99.58	0.42
1988/89	129	0	129	X	100.00	0.00
1989/90	144	0	144	X	100.00	0.00
1990/91	235	5	240	X	97.91	2.03
1991/92	602	1	603	X	99.83	0.17
1992/93	666	2	668	X	99.70	0.30
1993/94	379	0	379	X	100.00	0.00
1994/95	384	4	388	X	98.96	1.03
1995/96	184	0	184	X	100.00	0.00
1996/97	12	0	12	X	100.00	0.00
1997/98	271	40	311	X	87.13	12.86
1998/99	185	0	185	X	100.00	0.00
1999/00	91	1	92	X	98.91	1.08
2000/01	80	2	82	X	97.56	2.43
2001/02	42	0	42	X	100.00	0.00
2002/03	56	22	78	X	71.79	28.20
<b>SUM</b>	<b>4081</b>	<b>61</b>	<b>4142</b>	X		
<b>MEAN</b>	<b>240.05</b>	<b>3.58</b>	<b>24.36</b>	X	<b>98.2</b>	<b>1.7</b>

## DISCUSSION

For the majority of the Cassidines in Queensburgh, monomorphism, with only relatively minor continuous variations in patterns/colours, is the norm. The four species selected in this study differ in that their populations contain discrete colour/pattern forms at a reasonable frequency (ranging from 1.7% for the *luteicollis* form of *Conchyloctenia punctata* to 48.08% for the dark form of *Lacoptera cicatricosa*). Field monitoring of the four species over time periods ranging from six years (*Lacoptera cicatricosa*) to eighteen years (*Cassida guttipennis*) has revealed that, although there may be proportional differences in form frequency in some years (e.g. the normal form of *Chiridopsis nigrosepta* was dominant over the *vernicata* form on *Ipomoea carnea* subsp. *fistulosa* for the seasons 1997/8 and 2003/04, and *Cassida guttipennis* var. *fenestralis* was slightly dominant over the normal form in the 2000/01 season), the individual forms do not appear to be increasing or decreasing relative to one another. Thus we appear to be dealing with balanced rather than transient polymorphism. Polymorphism is considered to be the product of selective factors and/or forces that maintains the various forms in the population. The factors/forces involved are, as yet, unknown for South African Cassidines. For the discrete forms to survive as balanced polymorphism, they must confer some advantage to the species that is lacking in intermediate forms. The challenge is to determine the nature of the advantage. Three defensive possibilities arise: crypsis, aposematism and pseudo-aposematism (mimicry).

1. **Crypsis:** Many Queensburgh Cassidines exhibit cryptic colours and patterns, e.g. the rounded green *Cassida viridipennis* BOHEMAN and *Aspidimorpha confinis* (KLUG) are suggestive of water drops on green leaves, and some metallic species may suggest water drops in sunlight (JOLIVET 1994, HERON 2008).

It has been suggested that the black form of *Lacoptera cicatricosa* resembles the frass voided by large caterpillars of some lepidoptera but, equally, the brown forms superficially resemble shrivelled leaf sections or faecal material (HERON 2004). The possibility that both brown and black forms are equally advantageous for the species may be the reason for their being present in the Queensburgh population in an almost 50:50 percent ratio. It would be interesting to learn whether this is just a local phenomenon (or an artefact of poor census methods) or whether it holds true for *Lacoptera cicatricosa* populations elsewhere in its range (south of the Sahara, principally eastern and southern regions: BOROWIEC 1994).

In *Cassida guttipennis*, the beetle's size, shape and low profile is reminiscent of the near circular scrapings produced in the ventral leaf surfaces (leaving the transparent dorsal epidermal cuticle intact: Heron, 2003) and this, coupled with the propensity of the species to remain on the ventral leaf surface, may constitute a form of crypsis (Fig. 9). But why are there three different forms? On *Berkheya bipinnatifida*, both the dark forms (*romula* and *fenestralis*) appear conspicuous against the whitish pubescence of the ventral leaf surface, but so also are the feeding trenches/scrapings as viewed from below. Further, the mottled pattern of *romula* may be taken as suggestive of partially developed feeding scrapings. Although they look almost circular from the dorsal sur-

face, most of the scrapings appear less so from below: the beetles feed by pushing back the ventral epidermal pubescence and many scrapings appear gibbous to sub-circular. It is suggested that forms *romula* and *fenestralis*, although somewhat larger than their feeding traces, may derive cryptic protection from their resemblance to them, as viewed from the ventral leaf surface. The same appears to be true for their *fenestralis*-like pupae and for the larvae bearing dark faecal-exuvial shields. The pale brownish orange maculate normal form (see BOROWIEC & ŚWIĘTOJAŃSKA 2011) appears to be a mimic of a Coccinellid (see below). *En passant*: a very pale whitish normal form with maculae greatly reduced to almost absent is commonly found on the white pubescent ventral leaf surfaces of *Berkheya speciosa* (DC) O. HOFFM. on the farm “Bethel” at Paddock in southern Natal (30°44’S 30°12’E). This form has not yet been closely studied.

*Conchyloctenia punctata* is more difficult. At this stage, it is not known what advantage the *luteicollis* form confers upon the species. Maculation may serve to break up the outlines of the *parummaculata* form but more work is needed.

2. Aposematism: Toxic, distasteful, and similarly defended insects are rendered conspicuous to, in particular, higher predators with colour vision such as lizards and birds, by their bold patterning and contrasting colours: usually varying combinations of spots and bands involving black, yellow red and white. Lower predators such as spiders appear not to recognise or be deterred by aposematic species (HERON 1988). Amongst the Coleoptera, members of the Coccinellidae (ladybirds) provide, perhaps, the most familiar examples of aposematism. At this stage, it is not known whether any African Cassidines are aposematic or whether they sequester toxins from their host plants. The larval colours and behaviour of *Chiridopsis nigrosepta* and *Aethiopocassis vigintimaculata* (THUNBERG, 1789) are suggestive of aposematism (yellowish colouring and dwelling in the open on the dorsal leaf surface) but the larvae of both species also have large faecal-exuvial shields beneath which they hide and their colouring is not always readily apparent in later instars.

3. Mimicry: True mimicry, as distinguished from crypsis, has been defined as “*protective similarity in appearance of one species ... to another*” (ABERCROMBIE et al. 1961). It is not clear whether Batesian mimicry (similarity to unpalatable or toxic models) or Müllerian mimicry (aposematic species sharing similar warning colours/patterns) is involved as far as South African tortoise beetles are concerned.

The normal maculate brownish orange form of *Cassida guttipennis* appears to be a mimic of a dull orange-brown to greyish variably spotted herbivorous ladybird, possibly *Epilachna* sp. (Coccinellidae, Epilachninae), commonly found sharing its host plants. The resemblance is not very close but passable: the Coccinellid measures ~5.0 x 4.1mm but has a higher profile (2.1mm), and spends much of its time on the dark green dorsal leaf surface where it produces irregular whitish to brown patches of zigzag scrapings.

The shape, size, colour and patterning of many Cassidines belonging to the Afro-Oriental genus *Chiridopsis* closely resembles that of ladybirds (Coccinellidae) (BOROWIEC & ŚWIĘTOJAŃSKA 2011). *Chiridopsis suffriani* (BOHEMAN, 1854) from the

North Park Nature Reserve (HERON 2003) is, for example, a very passable mimic of the widespread and locally common ladybird *Cheilomenes lunata* (FABRICIUS), despite the fact that the Cassidine is smaller, less rounded, and spends much of its time secreted beneath its host plant leaves. *Chiridopsis nigrosepta* also seems to be a Coccinellid mimic. The normal form has, as a reasonable model, some forms the variable ladybird *Harmonia vigintiduomaculata* FABRICIUS (V. WHITEHEAD, pers. comm.) and, on one occasion, an unidentified Coccinellid species that evaded capture was observed to be a close model for form *vernicata* at Escombe. Intermediate forms in *C. nigrosepta* were rare in the Queensburgh populations.

Several papers have appeared dealing with Chrysomelids, including Cassidines, involved in postulated mimetic ring complexes with other Chrysomelids, beetles of other families, as well as bugs (e.g. HESPENHEIDE 1991, and MAWDSLEY 1992: cited in CHABOO 2007). A number of African Cassidines share the patterning and colour found on the normal form of *Chiridopsis nigrosepta* and this raises the question: is the species part of a defensive mimetic complex? Too little is known of the biology of African Cassidines at present to attempt an answer but several African species have very similar elytral patterning and colours (four large yellow to orange maculae on a black background). These include *Aspidimorpha areata* (KLUG), *A. bimaculata* (FABRICIUS), *Chiridopsis congoana* (SPAETH), *C. opposita* (BOHEMAN), *C. quadriguttata* (BOHEMAN) and *Cassida circumflexa* SPAETH. If one were to include variants such as *Aspidimorpha areata* where the black transverse elytral band is greatly reduced or missing, then several additional Cassidines could be drawn into the complex including *A. pseudoareata* BOROWIEC, several members of the *A. biguttata* and *A. bimaculata* groups, *Chiridopsis boutareli* (SPAETH), *C. laetifica* (BOHEMAN), and *Cassida ancorifera* BOHEMAN. To be so widespread, the presence of this colour/pattern combination must confer some advantage upon the species involved: the challenge is to determine the nature of that advantage. As noted by STAINES (1999), demonstration of selective advantages for a species in the field, as also experimental design, is difficult. Some boldly patterned Araneid spiders may also be involved in defensive complexes (e.g. LEROY 2004: 36). In another complex, the bug *Steganocerus multipunctatus* THUNBERG (Scutelleridae) may be involved with the *Chiridopsis suffriani* mentioned above. Further, longitudinally striped ladybirds such as *Cheilomenes propinqua* (MULSANT) and *Micraspis striata* FABRICIUS may be involved in another complex with Cassidines north of South Africa, such as *Chiridopsis aubei* (BOHEMAN), *C. circe* (WEISE), *C. quadriguttata* (BOHEMAN) and *C. aequinoctialis* (OLIVIER). Some small Araneid spiders of the genus *Singa* C.L. KOCH may also be included.

How widespread and constant are the different forms for the four species of this study?

*Cassida guttipennis*, and its different forms, appears to be widespread in Natal in association with its known host plants. Incomplete records are available for 14 localities, as follows:

On *Berkheya bipinnatifida*: Oribi Gorge Nature Reserve (2 visits, 10 beetles: 8 normal, 1 *romula*, 1 *fenestralis*), Shallcross in Pinetown (2 visits: 2 normal, 2 *romula*, 3 *fenestralis*), New Germany Nature Reserve, Pinetown (2 visits: 1 *romula*, 1 *fenestralis*),

Padfield Park, Pinetown (1 visit: 1 normal, 6 *romula*), Kranzkloof Nature Reserve at Kloof (5 visits, 11 normal, 2 *romula*, 1 *fenestralis*), Glenholme Nature Reserve, near Hillcrest (1 visit: 1 normal, 1 *romula*), Bothas Hill (2 visits: 3 normal, 1 *romula*, 1 *fenestralis*), Delvillewood station, near Shongweni (2 visits, a single *romula* form), Kranskop, Tugela valley (2 visits, 2 normal, 10 *romula*) and Dlinza Forest, Eshowe (1 visit: 1 normal form).

On *Berkheya speciosa* DC: Bothas Hill (9 visits: 15 normal, 1 *fenestralis*), Inchanga (1 visit, 5 normal form), Springside Nature Reserve at Hillcrest (2 visits: 8 normal, 3 *romula*) and Tugela Gorge in the Royal Natal National Park, near Bergville (1 visit, 3 normal form).

*En passant*, on two occasions *romula* forms of the beetle exhibited a peculiar bronzy sub-iridescence (1 at Northdene, 2 at Springside Nature Reserve). Could these be the result of be a recessive gene?

*Chiridopsis nigroseta* has only been personally observed at Queensburgh (this study) and at Bothas Hill. At the latter locality it was observed only once: on *Ipomoea wightii* (3 beetles, 1 normal, 2 *vernicata*). The dominance of the *vernicata* form is curious. In correspondence, Dr Lech BOROWIEC commented that *vernicata* becomes more abundant as one moves south in the species' range. He reported that, in the material he had studied, only the normal form was present in Ethiopia but *vernicata* was present at not more than 20% in Kenya, Tanzania and Democratic Republic of Congo, rising to 30% in Zambia. Once possible Coccinellid models are identified for the two forms, it would be interesting to chart their presence over the Cassidine's range.

No statistics are currently available for the dark form of *Lacoptera cicatricosa* or for the *luteicollis* form of *Conchyloctenia punctata* from other regions.

An interesting sidelight revealed by this study concerned Cassidine movement. It is generally considered that most tortoise beetles are reluctant to fly (CHABOO 2007) but this perception may not be entirely accurate. When disturbed, almost all the Queensburgh species dropped to the undergrowth and feigned death rather than attempting to escape by flight, but the searching for different species during the compiling of census records revealed that they regularly appeared and disappeared from their localities, some of which were several kilometres away from where other host plants were present. Clearly there was movement, sometimes over considerable distances, but it was only rarely that individuals are observed in sustained flight. Greater attention needs to be given to this aspect of their behaviour.

#### CONCLUSION

Census figures compiled for four tortoise beetles from four different genera present in Queensburgh, near Durban, in Natal, South Africa, suggests that they exhibited balanced polymorphism. Two species were present in discrete colonies, viz. *Cassida guttipennis* (three forms: normal, *romula* and *fenestralis* in the ratio 4 : 5 : 1) and *Chiridopsis nigroseta* (two forms: normal and *vernicata* in the ratio 3 : 7), and two were in open populations over larger areas where sampling was less precise, viz. *Lacoptera cicatricosa* (a brown & a black form in the ratio of approximately 13

: 12, and *Conchyloctenia punctata* (forms *parummaculata* and *luteicollis* in the ratio 49 : 2. Hypotheses are presented to account for the advantages conferred through polymorphism. Crypsis may be the key to the success of *Cassida guttipennis* forms *romula* and *fenestralis* (resembling the rounded feeding patterns as viewed from beneath the leaf), and *Lacoptera cicatricosa* (pale form resembling dead vegetable matter or faecal material, and dark form resembling frass). Mimicry, possibly of members of the Coccinellidae, is suggested to account for the success of the normal form of *Cassida guttipennis*, and both the normal and *vernicata* forms of *Chiridopsis nigrosepta*. Although the informal census method employed may have had its drawbacks, the results are considered more meaningful than form estimations based upon randomly collected dried specimens in collections.

#### FUTURE RESEARCH

Careful captive breeding would bring greater precision to the ratios of the different forms for the species exhibiting polymorphism and genetic research would provide valuable insights. The possibility of the existence of several African mimetic ring complexes, involving not just Cassidines and other Chrysomelids, but also other Coleopteran families, Hemipterans and arachnids, opens an interesting field of study. Determining whether or not any African Cassidines are aposematic or make any use of toxins from their host plants would be of interest. Questions regarding the constancy of the ratios between the various forms in other portions of the species' ranges need to be addressed and reasons for differences, *e.g.* the proportional increase of *Chiridopsis nigrosepta* var. *vernicata* over the normal form from north to south through Africa, also need consideration. This is the first study to specifically deal with polymorphism in African tortoise beetles and, since very little work has been done on the African fauna apart from taxonomy, it is hoped it will provide a platform, albeit a small one, upon which more detailed future investigations can be built.

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