



METAMORPHOSIS

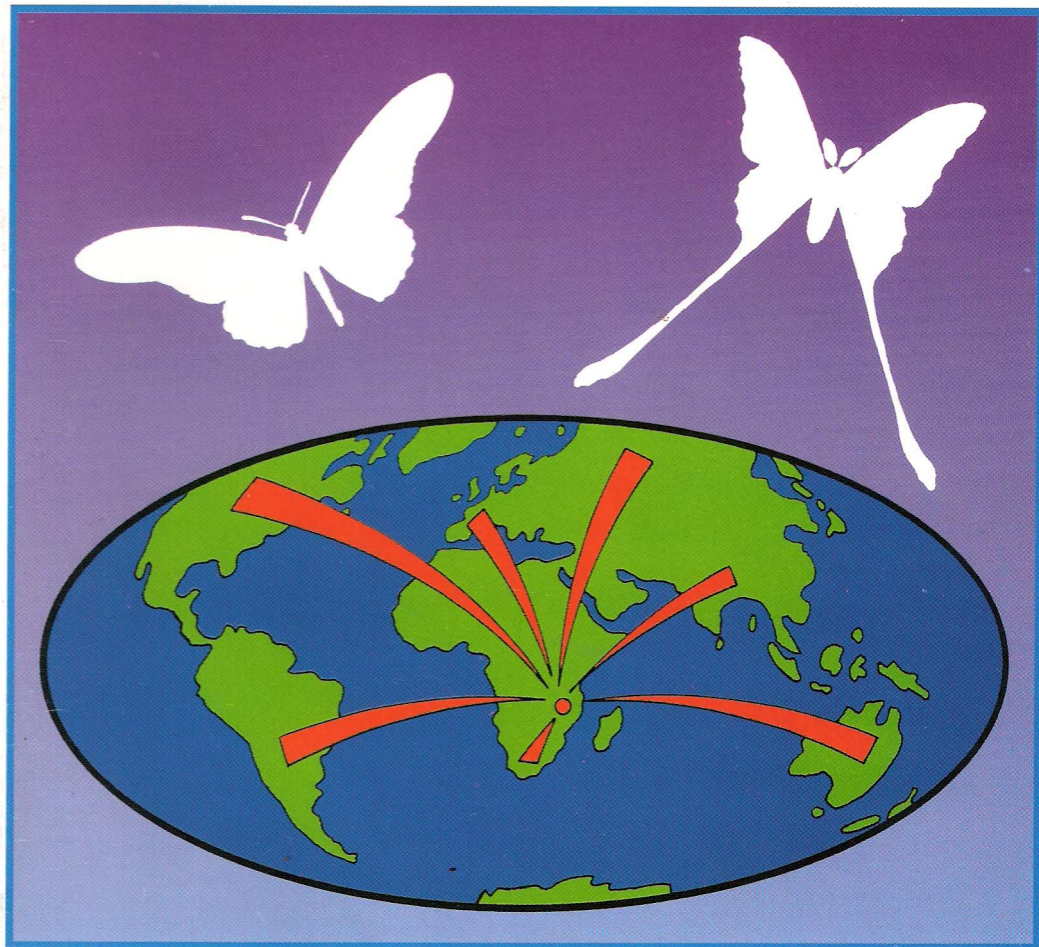
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MYRMECOPHILY AND THE MALE GENITALIA OF AFRICAN LYCAENIDAE: A PRELIMINARY DISCUSSION

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Abstract: An analysis of 25 African lycaenid genera shows that variation between species in the morphology of male genitalia is greater in non-ant-associated genera than in ant-associated genera. This phenomenon is presented and discussed as a preliminary note to a more thorough investigation.

Key Words: Lepidoptera, Lycaenidae, myrmecophily, genitalia, speciation, sexual selection, evolution.

Introduction

The extraordinary uniformity of genitalia noted in African ant-associated lycaenid genera generally, and Cape genera in particular prompted a closer examination of the phenomenon. In one group of 40 obligately myrmecophilous species in *Chrysoritis* Butler, there are no observable differences in the genitalia between species of either sex. A somewhat similar phenomenon occurs among *Aloeides* Hübner (50 species), *Lepidochrysops* Hedicke (120 species) and *Thestor* Hübner (22 species). This is in striking contrast to genera which are not strongly ant-associated, such as *Iolaus* Hübner (115 species), where genitalia differ significantly, even between species whose adult fascies are similar (Heath, 1997b:30). In this paper, the level of genitalic uniformity and the degree of ant-association in African lycaenid genera are compared and discussed. This is not intended to be an exhaustive account, but serves as a pilot study which is to be continued in greater depth.

Several authors, including Hinton (1951), Malicky (1969) and Eliot (1973), suggested that ant-association, or myrmecophily, is an ancestral trait in the Lycaenidae. More recently, Fiedler (1991) rejected this idea, although he argued that secondary reduction of larval structures had probably taken place in some instances. DeVries (1991, 1997) also argued against ancestral myrmecophily in the group, favouring the hypothesis that (1) lycaenids and riodinids represent separate monophyletic families, and (2) ant-association arose independently in these two groups. He based this argument on the observation that dorsal nectary organs (DNO's), which secrete a sugary reward for attendant ants, are found on the seventh abdominal segment in lycaenids, but the eighth in riodinids, and are thus unlikely to be homologous. Pierce (1984) proposed two ways by which ant-association, once it had evolved, could have enhanced diversification of the Lycaenidae, firstly by inducing a higher incidence of host-plant switching, and secondly by modifying the butterfly population structure.

Material & methods

Selection of taxa. Twenty-five African genera were selected whose male genitalia have been well illustrated and whose life history characteristics have been independently documented, as listed in Fiedler (1991: table 17). These included: *Baliochila* Stempffer & Bennett, *Iolaus* Hübner, *Pentila* Westwood, *Uranotauma* Butler, *Leptotes* Scudder, *Teriomima* Kirby, *Tuxentius* Larsen, *Cacyreus* Butler, *Azanus* Moore, *Tarucus* Moore, *Leptomyrina* Butler, *Anthene* Doubleday, *Mimacraea* Butler, *Chloroselas* Butler, *Deudorix* Hewitson, *Euchrysops* Butler, *Axiocerses* Hübner, *Spindasis* Wallengren, *Aphnaeus* Hübner, *Aloeides* Hübner, *Lepidochrysops* Hedicke, *Thestor* Hübner, *Chrysoritis* Butler and *Phasis* Hübner. Only genera containing two or more species were included in the analysis.

Scoring of genitalia.

The male genitalia of these genera were studied by referencing relevant works, including Bethune Baker (1910, 1923); Cottrell (1965, 1985); Stempffer (1954, 1956, 1961, 1967); Stempffer & Bennett (1953, 1958, 1959); Swanepoel & Vári (1983); Heath (1983, 1985, 1997); Henning & Henning (1993, 1996); Kielland (1990); Murray (1956, 1958); Pennington (1962); Pringle *et al.* (1994) and Van Son (1941, 1951). The 25 genera were each rated on a subjective scale ranging from 0 to 100 for degree of uniformity of male genitalia, with 100 representing totally uniform genitalia and 0 representing highly varied genitalic characters for a genus.

Degree of ant-association.

The degree of ant-association was determined by reference to Fiedler (1991: 157), who tabulated published lycaenid life history information and apportioned a number from 0 to 4 for each species, indicating degrees of ant-association so far recorded, with 4 representing obligate dependency on ants and 0 representing the absence of ant-association. Two assessments were taken. First, the values assigned by Fiedler were averaged for each genus and calculated as a percentage of the maximum value (4) so that they could be expressed on a scale of 1 to 100. Second, the percentage of species within each genus designated by Fiedler to have an obligate relationship with ants was also calculated.

Tabulated data.

The genitalia uniformity, average ant-association and the proportion of obligate ant-association for each genus are listed in Table 1. This follows the classification and order adopted by Fiedler (1991) who in turn followed the classification of Corbet *et al.* (1978).

Statistical tests.

The Spearman rank correlation coefficient (Sokal and Rohlf, 1969) was calculated and tested for significance using the statistical package Statview.

Subfamily	Tribe	Genus	Genitalia uniformity	Average ant- association	Proportion obligate ant- association	*Sample size
Poritiinae			%	%	%	
	Liptenini					
		<i>Pentila</i>	5	0	0	4
		<i>Mimacraea</i>	80	0	0	4
		<i>Teriomima</i>	25	0	0	4
		<i>Baliochila</i>	5	0	0	6
Miletinae						
	Miletini					
		<i>Thestor</i>	90	100	100	8
Lycaeninae						
	Aphnaeini					
		<i>Aphnaeus</i>	80	100	100	4
		<i>Spindasis</i>	80	95	100	16
		<i>Axiocerces</i>	70	90	60	5
		<i>Chloroselas</i>	75	88	50	2
		<i>Phasis</i>	95	100	100	4
		<i>Aloeides</i>	85	97	92	13
		<i>Chrysoritis</i>	95	97	89	27
	Eumaeini					
		<i>Iolaus</i>	5	11	0	20
		<i>Leptomyrina</i>	65	63	0	4
		<i>Deudorix</i>	80	58	0	14
	Polyommagini					
		<i>Anthene</i>	65	71	24	33
		<i>Uranothauma</i>	25	0	0	4
		<i>Cacyreus</i>	30	0	0	8
		<i>Leptotes</i>	25	54	0	9
		<i>Tuxentius</i>	30	50	0	5
		<i>Tarucus</i>	55	70	23	13
		<i>Azanus</i>	50	75	0	7
		<i>Eicochrysops</i>	80	75	0	3
		<i>Euchrysops</i>	80	64	0	8
		<i>Lepidochrysops</i>	85	99	100	35

*Sample size represents the number of species listed by Fiedler (1991)

Results

The degree of ant-association within a genus is significantly positively correlated with levels of morphological variation in male genitalia among species within that genus (Spearman rank correlation = .801, $N = 25$, $p < 0.001$) (Figure 1). A notable exception to this relationship are the species of *Mimacraea*, whose male genitalia are very similar, despite a lack of ant-association.

Similarly, the proportion of each genus believed to have an obligate ant-association is positively correlated with the uniformity of male genitalia (Spearman rank correlation = .702, $N = 25$, $p < 0.001$) (Figure 2). Apart from *Mimacraea*, species of *Leptomyrina*, *Deudorix*, *Euchrysops* and *Eicochrysops* also have relatively similar genitalia whilst lacking any obligate ant-association.

Discussion

The data presented here rely in part on subjective evaluations, both in the degrees of ant-association as listed by Fiedler (1991), being his own interpretation from field observations and a variety of different literature sources, and also in my own assessment of overall morphological similarity among species' male genitalia. The sample also consists entirely of genera occurring in Africa. Although the phylogenetic relationships of these taxa have not been taken into account explicitly in making this comparative analysis (cf Harvey & Pagel 1991), they include representatives from three subfamilies of Lycaenidae and five tribes (cf Fiedler, 1991). A more quantitative analysis taking into account evolutionary history, will be possible once more specific information has been obtained regarding the phylogenies of the groups in question.

Despite the above limitations of the data set and analysis, a strong correlation appears to exist between patterns of morphological diversification in genitalia and the degree of larval ant-association, leading to the following tentative conclusions: (1) Where there is strong ant-association, the male genitalia tend to be fairly uniform, and (2) Where there is little or no ant-association, the male genitalia are fairly diverse. At least four hypotheses, some of which may be compatible, could account for this phenomenon:

(1) Ant-associated taxa may be of relatively recent origin compared with their non ant-associated relatives. Provided that morphological divergence is correlated with genetic divergence, ant-associated lycaenids may have simply had less time than non ant-associated lycaenids to evolve distinctively different genitalic characters. This explanation would also imply that the development of genitalic characters is a relatively lengthy process in evolutionary terms. It is compatible with the hypothesis put forward by Pierce (1984) that obligate ant-association can facilitate rapid rates of speciation.

(2) Strong ant-association may slow down the differentiation of specific genitalic characters, perhaps by replacing the genitalia as a "lock and key" mechanism for preserving species integrity. Males of lycaenids with species-specific, obligate ant associates may be able to rely on ants as cues in finding mates, thereby relaxing selection for species-specific genitalic morphologies to ensure appropriate pairings. However, there is little evidence to indicate whether genitalia have any significant influence over mate selection (Eberhard 1985).

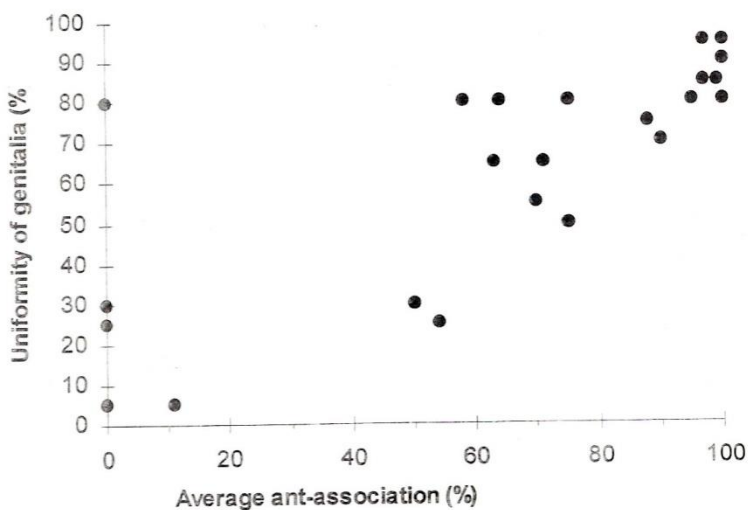


Figure 1.

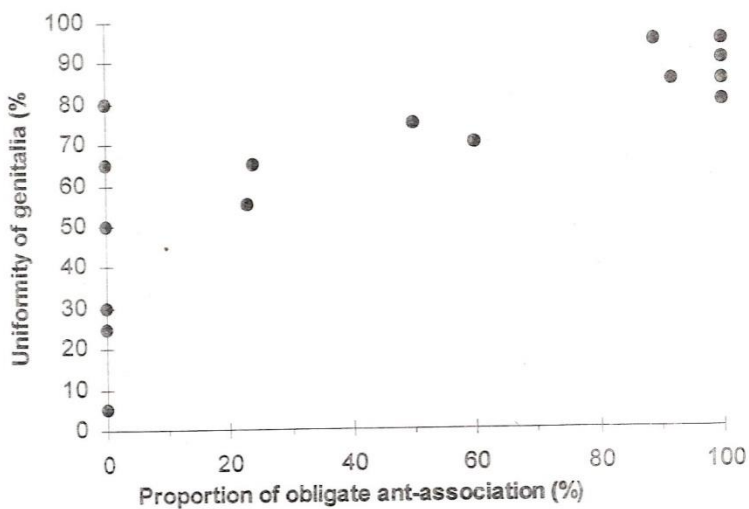


Figure 2.

(3) Genitalic characters may evolve through sexual selection via female choice (Eberhard 1985). In the case of ant-associated lycaenids, males may use attendant ants as cues in discovering the locations of prospective female mates, thus reducing the possibility of female choice (and the sexual selection associated with it). For example, this effect has been demonstrated experimentally in an Australian lycaenid butterfly *Jalmenus evagoras* Donovan, with obligate ant-association (Elgar & Pierce 1988). Males of this species trap-line trees containing conspecific pupae, and females are often mated before they have even expanded their wings. This has the effect of preventing female choice during mating, thereby also reducing the possible strength of sexual selection. As a consequence, ant-associated taxa may have more uniform genitalia than non-ant-associated taxa.

(4) Finally, it is possible that genes coding for morphological adaptations necessary for ant-association (such as the formation of the DNO of the larvae) are linked in some way with genes coding for the formation of the genitalia. This could conceivably constrain the evolution of variability in genitalic characters. Why this might be the case is unclear, and again, although it cannot be discounted, there is little evidence to support this hypothesis.

One genus that appears to contrast strikingly with the findings is *Mimacraea*, whose larvae lack ant-association but whose adults have highly uniform genitalia (Stempffer, 1967: 30). Perhaps the tendency to mimic other species has acted in a similar manner to that of ant-association. One of the two ways by which evolution could be influenced, as suggested by Pierce (1984), is by modifying the butterfly population structure. She suggested that the distribution and size of lycaenid populations may have been restricted directly by the localised presence of ants. This may have enhanced rate of divergence of isolated butterfly populations and hence their rate of speciation. It is conceivable that the localised presence of the mimic's model, coupled with the limited availability of its larval diet of lichen/ algae, had a similar effect on population structure.

The Torre-Bueno (1989) definitions of a genus include "an assemblage of species agreeing in some or other character or series of characters" and "a set of similar species of relatively recent common ancestry". It seems reasonable to lump together species whose genitalia are of a similar type; however, it has also been the practice to erect genera to accommodate species with varying genitalia, despite other characters being extremely similar. For example, the Liptenine genus *Teriomima* Kirby was split into three separate genera by Stempffer & Bennett (1953), thereby creating two additional genera, *Baliochila* and *Cnodontes*. This was based on male genitalic differences, despite the species showing an extraordinary uniformity of all other characters. In the genera *Brephidium* Scudder and *Oraidium* Bethune Baker, a similar splitting appears to have taken place, as well as in *Zizeeria* Chapman, *Zizina* Chapman and *Zizula* Chapman, their species having many characters in common. In both groups, species occur in both Africa and South America. There is probably some relationship between these two archaic groups which originated before the breaking up of Gondwanaland (cf. Stempffer, 1967: 276).

The examples above are taxa whose genitalia showed sufficient diversity to justify division into the smaller genera accepted today, whilst showing homogeneity in all other respects. The species in these groups of genera are not known to be ant-

associated and would further strengthen the results of this study if the term genus was used in a broader sense. (Note that they are not included in this analysis because in each case, a "genus" was reduced to a small number or single species.)

It is not the intention here to question the wisdom of erecting or retaining these genera, but rather to illustrate the diversity of genitalia among related taxa which might otherwise be considered congeneric, and which are not ant-associated. Thus because of the way in which a genus is delimited, the sample shown in Table 1 may actually represent an underestimation of the association between myrmecophily and genitalic uniformity. Additional examples where generic or subgeneric names have, at some time been created because of small venational or other characters of secondary importance include *Deudorix* (*sensu* Aurivillius), *Iolaus*, *Chloroselas*, *Chrysoritis*, and *Spindasis* (Stempffer, 1967: 108,122; Heath, 1997b: 13,17,23).

To summarise this topic with the limited data available, the strong association between myrmecophily and uniformity in the male genitalia of African Lycaenidae raises questions regarding the influence of ant-association on the evolution of the group. At least four hypotheses, some of which are not mutually exclusive, might account for this association. Further research is necessary to test the different possible mechanisms which might account for the observed pattern.

Acknowledgments

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MOTHS COLLECTED IN THE KAKAMEGA FOREST(EASTERN KENYA), AND A POSSIBLE USE OF MOTHS TO CHARACTERISE TROPICAL FORESTS

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Summary

During four nights, samples of moths were taken with different types of light traps in the Kakamega Forest (Eastern Kenya). On a total of 255 species, 129 were identified to the species level, 65 to the genus level, and 61 to the family level. A proposal is made to publish tables of numbers of species or corresponding percentages per family, even if all specimens are not fully identified. Such tables, or the graphics produced from them, could possibly be used to characterise tropical forests. A note is added on the Tervuren collection as systematic tool.

Introduction

After the Inaugural Conference on African Lepidoptera, organised by the African Butterfly Research Institute in Nairobi from May 1st to 3rd 1997, a field trip was organised to the Kakamega Forest. This forest is situated at about 50 km to the south-east of Eldoret.

During this field trip from May 4th to 8th, moths were collected in and near a centre called Rondo Retreat, a few km to the East of the village of Kapsabet. This centre is situated inside the forest and the level there is about 1.650 m a.s.l. For the moth collecting, the light traps were placed in the centre itself, in a place called the quarry (open spot in the forest), close to a nearby river and also between these different sites.

The light traps

Two different types of light traps were used. The first consisted of a 160 watt mercury vapour lamp attached at about 10 cm from the upper edge of a vertically suspended blanket of ca. 2 x 2 m and will be called the 'Maes Trap'. A second type is the one described in 'A practical Guide to Butterflies and Moths in Southern Africa'. It is composed of a vertically suspended 15 watt wood lamp connected to a car battery underneath an umbrella about 2 m high and 1.5 m in diameter. Around the umbrella, a transparent gauze tissue is suspended, which is an ideal material on which the moths can rest. This trap will be called the 'South African Trap'. Each night there were one 'Maes Trap' and 8 'South African Traps' running. These traps were entrusted to the different participants of the trip.

Working method

The moths listed here were those collected with the 'Maes Trap' and a few 'South African Traps'. The small specimens were killed in vials with ethyl acetate, the large specimens were injected with ammonia. All moths were taken but the Pyralidae (collected by Koen Maes) will be published in a separate paper. The Eupterotidae,

Saturniidae, Bombycidae and Sphingidae were collected by Thierry BOUYER who kindly passed on to the author the identifications of the moths belonging to these families.

Family/ subfamily	Species level	Genus level	Family level	Total	%
Cossidae	1	0	0	1	0.4
Limacodidae	7	0	1	8	3.1
Chrysopolomidae	2	0	0	2	0.8
Geometridae	21	26	22	69	27.1
Lasiocampidae	10	1	1	12	4.7
Eupterotidae ⁰	2	2	0	4	1.6
Saturniidae ³	14	0	0	14	5.5
Bombycidae ³	1	1	0	2	0.8
Sphingidae ³	12	1	0	13	5.1
Notodontidae	7	3	2	12	4.7
Lymantriidae	9	4	1	14	5.5
Ctenuchinae	5	2	0	7	2.7
Arctiinae (-Cten)	13	6	6	25	9.8
Noctuidae (-Ag)	24	19	28	71	27.8
Agaristinae	1	0	0	1	0.4
TOTAL	129	65	61	255	100.0

Fig. 1. Families / subfamilies found in the Kakamega forest, with indication of the number of species identified at the species level, at the genus level, only at the family level, the total number of species per family and the respective percentages.

The specimens collected by the author were set and labelled | Kenya : Kakamega | Forest/Rondo Retreat | ca. 1700 m.5-8/05/1997 | Réc. U. Dall'Asta | and are deposited in the Royal Museum for Central Africa, Tervuren, Belgium.

Identifications of the specimens collected by the author were carried out by comparing them with the collections of the same museum. Not all species captured were present in this collection, therefore some specimens could only be identified to the genus or to the family level. The latter level could always be found using the family identification key in Holloway et al (1987). A few specimens could also be identified by comparing them with the plates of the volumes 14-16 of Seitz (1930-).

Characterising Tropical Forests

Recently, the author had the possibility to collect moths in West Africa : in south-west Cameroon (Mount Cameroon and Korup National Park) and in Eastern Ivory Coast (Forêt classée de la Bossematié and Forêt de Mabi). Due to the vast amount of material collected, complete data for these sites are not yet available, but partial data

already give some interesting indications. The samples of the Bossematié Forest for example are surprisingly poor in Geometridae compared to those of Korup and Kakamega, but they hold a lot of Metarbelinae specimens, not present in the Kakamega sample. Possibly there will also be some relevant differences in other families. Therefore it could be interesting to make tables when light trap samples of moths are taken in tropical rainforests. It's always possible to identify all specimens to the family level, and it is also possible to sort specimens into species to a certain extent. Even if the specimens are not fully identified and there are sorting problems with difficult genera or groups, a table could be edited in which the number or percentage of species are listed alongside the name of the family to which they belong (first and two last columns of fig.1). Maybe this could become a kind of 'moth fingerprint' (fig.2) of the forest in question.

The first 'moth fingerprint' of the Kakamega Forest

To produce the first 'moth fingerprint' of the Kakamega forest, the data from fig. 1 were used. Only the 10 families were chosen in which the number of species was the highest. The results are seen in fig.2.

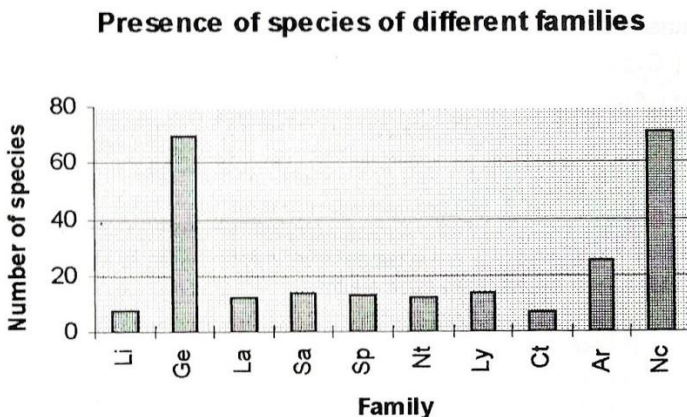


Fig. 2. First 'moth fingerprint' of the Kakamega Forest. Number of different species in the different families. Li : Limacodidae, Ge : Geometridae, La : Lasiocampidae, Sa : Saturniidae, Sp : Sphingidae, Nt : Notodontidae, Ly : Lymantriidae, Ct : Ctenuchinae, Ar : Arctiidae (excluded Ctenuchinae) and Nc : Noctuidae

What strikes most is the nearly equal number of species of Noctuidae and Geometridae. Arctiidae (Ctenuchinae excluded), come third, and it can be considered that the remainder of the 7 families possess more or less one fifth of the number of species of the two biggest ones. It would be interesting to compare the results of samples of the other participants to see if the general trend of the graph is the same.

The Afrotropical Lepidoptera collection of the Royal Museum for Central Africa

As mentioned earlier in the chapter 'Working method', the collections of the Tervuren Museum were used for identifying the specimens. This method is well known by lepidopterists analysing moth samples: the only African moth species that can possibly be identified with the literature are those belonging to the families Sphingidae and to some extent the Saturniidae. For all other families, the literature is scattered over numerous publications and comprehensive works, if available, and most of the time have no keys nor colour pictures. The only way to identify these moths is to compare the specimens with the correctly identified specimens in the collection. But research on biosystematics of African moths is continuously progressing and this results not only in the description of new taxa, but often also in changes in names of the existing ones. All this information must be incorporated in the collections (called curation), and this is continuously done in the Lepidoptera laboratory. In this way the collections of the Tervuren Museum can be used as a biosystematic tool: the names available on the labels of the boxes are in principle the most recent ones.

Decades of curation work in the moth collections of the Tervuren Museum showed that from 25 to 30% of the Afrotropical moth species are present. Great gaps are the Isles (Madagascar amongst other) and South Africa. Now the table mentioned as fig.1 gives some more information. In the Kakamega sample, 255 different species are present. Amongst these, 61 could only be identified to the family level and are thus not present among the identified specimens of the collection (it still holds quite a lot of unidentified specimens). Amongst the species identified to the genus level are the famous difficult groups: the genera *Zamarada*, *Cleora*, *Colocleora* (Geometridae) and *Eilema* (Arctiidae). Amongst the latter, it can be considered that roughly half of them are represented in the collection. The missing species in the Tervuren collection would then amount to a total of about 90. If this figure is compared to the total of 255, it can be considered that the collection holds a little less than $\frac{2}{3}$ of the Kakamega species. This shows that, even for East Africa, the Tervuren collection is a fairly good biosystematic tool for identifying moths.

Species list

B 1: 31

Family COSSIDAE

Azygophleps grisea Hampson

Family LIMACODIDAE

Cosuma rugosa Walker

Ctenocompa hilda Druce

Ctenolita anacompa Karsch

Sporetolepis mincki Strand

Latoia karschi Dyar

Delorhachis viridiplaga Karsch

Stroter capillatus Karsch

Family level: 1 species

Family CHRYSOPOLOMIDAE

Chrysopoloma venata Aurivillius

Chrysopoloma albibasalis Hampson

Family GEOMETRIDAE

Derambila sp.

Pingasa hypoxantha Prout

Anthermostes sp.

Prasinocyma *Thalassodes* sp. 6 species

Disclisoprocta natalata Walker

Epigynopteryx curvimargo Hampson

Epigynopteryx sp.

Xenimpia erosa Warren

Megadrepana sp.

Plegapteryx mabira Carcasson

Entomopteryx contenta Prout

Hyposidra mixtilinea Warren

Miantochora griseata Carcasson

Semiothisa warreni Prout

Semiothisa fulvimargo Warren

Semiothisa fulvisparsa Warren

Buzura abruptaria Walker

Buzura subocularia Mabille

Buzura sp. 2 species

Cleora sp. 5 species

Colocleora spuria Prout

Colocleora leucostephana Prout

Colocleora probola Prout

Colocleora sp. 4 species

Xylopteryx gibbosa Herbulot

Aphilopota symphronima Prout

Zamarada sp. 4 species

Rhodophthitus microstictus Prout

Melinoessa midas Prout

Melinoessa amplissimata Walker

Family level: 22 species

Family LASIOCAMPIDAE

Lechriolepis conjuncta Grünb.

Philotherma sordida Aurivillius

Olyra reducta Walker

Bombycopsis indecora Walker

Taragama vesta Druce

Odontogama nigricans Aurivillius

Leipoxais rufobrunnea Strand

Leipoxais sp.

Mimopacha gerstaeckeri Dewotz

Gonometa nysa Druce

Pachymeta contraria Walker

Family level: 1 species

Family EUPTEROTIDAE

(Identifications by Th. BOUYER)

Jana preciosa Aurivillius

Janomima nigricans Gaede

Phiala sp. (near *alba* Aurivillius)

Phiala sp. (near *flavina* Gaede)

Family SATURNIIDAE

(Identifications by Th. BOUYER)

Ludia orinoptera Karsch

Pselaphelia gemmifera Butler

Tagoropsis rougeoti Darge

Nudaurelia anthina Karsch

Nudaurelia dione Fabricius

Nudaurelia alopia Westwood

Imbrasia obscura Butler

Imbrasia epimethea Drury

Aurivillius triramis Rothschild

Pseudobunaea cleopatra orientalis

Pseudobunaea tyrrhena Westwood

Lobobunaea phaedusa Drury ?

or *L. christyi* Sharpe ?

Epiphora ploetzi Plötz
Epiphora rectifascia watulegei

Family BOMBYCIDAE
 (Identifications by Th. BOUYER)
Ocinara signicosta Strand
Ocinara sp.

Family SPHINGIDAE
 (Identifications by Th. BOUYER)
Agrius convolvuli Linnaeus
Coelonia fulvinotata Butler
Poliana buchholzi Plötz ?
Poliana witgensi Strand
Macropoliana ferax Rothschild
Dovania poecila Rothschild & Jordan
Chloroclanis virescens Butler
Pseudoclanis sp.
Acanthosphinx ruessfeldii Dewitz
Nephela aequivalens Walker
Temnora albilinea Rothschild
Temnora spiritus Holland
Temnora crenulata Holland
Euchloron megaera Linnaeus

Family NOTODONTIDAE
Stenostaura impedita Walker
Eurystauridia triangularis Gaede
Pseudoscrancia africana Holland
Chlorochadisra sp.
Drapetides angulata Gaede
Elaphrodes nephrocrossa Bethune-Bak.
Epidonta variegata Aurivillius
Desmeocraera sp. 2 species
Antheua simplex Gaede
 Family level: 2 species

Family LYMANTRIIDAE
Hyaloperina nudiuscula Aurivillius
Euproctis putris Hering
Euproctis rubroguttata Aurivillius
Naroma signifera Walker
Thamnocera aeschra Hampson
Laelia rocana Swinhoe
Laelia incerta Hering

Oecura stegmanni Grünb.
Rhyopteryx psoloconiana Collenette
Porthesaroa sp.
 Family level : 1 species

Family ARCTIIDAE excl. Ctenuchinae
Asura obliterata Walker
Chionaema ugandana Strand
Chionaema rubrigris Holland
Phryganopsis sp.
Eilema fuscifasciata Butler
Eilema obliterata Walker
Eilema melanosticta Bethune-Baker
Eilema sp. 5 species
Spilosoma bifurca Walker
Disparctia vittata Druce
Kiriakoffalia costimacula Joicey & Talbot
Amerila luteibarba Hampson
Soloella guttivaga Walker
Aganais speciosa Druce
Phaegorista leucomelas Herrich-Schäffer
 Family level : 6 species

Subfamily CTENUCHINAE
Rhipidarctia invaria Walker
Rhipidarctia sp. 2 species
Rhipidarctia sp.
Balacra rubrostriata Aurivillius
Balacra pulchra Aurivillius
Metarctia rubripuncta Hampson
Metarctia pallida Hampson
Anace perpusilla Walker
Anace sp.

Family NOCTUIDAE excl. Agaristinae
Euxootera chrysophaes Fletcher
Nyodes sp. 2 species
Perigea capensis Guenée
Neostichtis nigricostata Hampson
Callopietria maillardi Guenée
Callopietria sp.
Cetola pulchra Bethune-Baker
Lophotarsia ochropuncta Hampson
Aletis leuconephra Hampson
Aletis sp. 2 species
Sciomesa sp.

Callyna trisagittata Berio

Callyna sp.

Ozarba sp.

Amyna punctum Fabricius

Acontia chrysoproctis Hampson

Characoma sp.

Maurilia sp. 2 species

Plusiocalpe sp.

Leocyma camilla Druce

Trichoplusia orichalcea Fabricius

Agrapha limbirena Guenée

Audea sp.

Cyligramma sp.

Achaea catocaloides Guenée

Dysgonia sp.

Colbusa euclidica Walker

Taviodes excisa Hampson

Crionica cervicornis Fawcett

Ericeia inangulata Guenée

Serrodus trispila Mabille

Trisulana senex Bethune-Baker

Marcipa xanthomochla Fletcher

Marcipa sp. 2 species

Hypocala deflorata Fabricius

Anomis sabulifera Guenée

Mesogenea sp.

Plusiodonta sp.

Avitta atripuncta Hampson

Family level : 28 species

Subfamily AGARISTINAE

Tuerta chrysochlora Walker

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INTRODUCTION TO AFRICAN AND SOUTHERN AFRICAN SATYRINAE

By Graham Henning,
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Abstract: The Satyrinae of Africa and Southern Africa are discussed with regard to their taxonomy, evolution and survival strategies in Southern Africa.

The Satyrinae are distributed throughout most parts of the world where there are grasses, from sea level to the highest peaks, deserts and tropical rain forests. Throughout this vast range they retain their distinctive characteristics and flight. The higher classification is based on Miller, 1968.

SATYRINAE

Characteristics: Adults with cells of fore and hind wings closed by tubular veins, forewing veins swollen at the base, larvae feed on monocotyledons.

Tribes in Africa: 3 Tribes; Melanitini, Elymniini, Satyrini

MELANITINI

Characteristics of Melanitini; forewing cell long (60% of forewing), hindwing veins M3 & Cu1 well separated, claws bifid, male foreleg not greatly reduced, female foretarsus not strongly clubbed.

Melanitini - no subtribes, 2 genera; *Melanitis*, *Gnophodes*

ELYMNIINI

Characteristics of Elymniini; forewing cell not long (much less than 50%), hindwing veins M3 & Cu1 not well separated, claws single, male foreleg not greatly reduced, female foretarsus not strongly clubbed.

Elymniini - 3 subtribes; Elymniina, Lethina, Mycalesina

Elymniina - 1 genus; *Elymnias*

Mycalesina - 2 genus groups; *Bicyclus*, *Henotesia*

Bicyclus group - 2 genera; *Bicyclus*, *Hallelesis*

Henotesia group - 5 genera; *Henotesia*, *Houlbertia*, *Masoura*, *Admiratio*, *Heteropsis*.

Lethina - 2 genus groups; *Aeropetes*, *Lethe*

Aeropetes group - 2 genera; *Aeropetes*, *Paralethe*

Lethe group - 2 genera; *Aphysoneura*, *Lasiommata*

SATYRINI

Characteristic of Satyrini; forewing cell not long, hindwing veins M3 & Cu1 not well separated, claws single, male foreleg greatly reduced, female foretarsus strongly clubbed often with fewer than five subsegments.

Satyrini - 3 subtribes; Satyrina, Ypthimina, Dirina

Satyrina - 1 genus; *Hipparchia*

Ypthimina - 4 genus groups; *Ypthima*, *Physcaeneura*, *Neita*, *Melampias*.

Ypthima - 3 genera; *Ypthima*, *Ypthimomorpha*, *Mashuna*.

Physcaeneura - 4 genera; *Neocoenyra*, *Coenyropsis*, *Coenyra*, *Physcaeneura*.

Neita - 1 genus; *Neita*.

Melampias - 6 genera; *Melampias*, *Strabena*, *Cassionympha*, *Pseudonympha*, *Paternympha*, *Stygionympha*.

Dirina - 1 genus group, 5 genera; *Dira*, *Tarsocera*, *Dingana*, *Serradinga*, *Torynesis*.

A total of 34 African genera.

REGIONAL ENDEMISM IN AFRICAN SATYRINAE

Subtribes and genus-groups.

1 subtribe endemic to southern Africa - Dirina

1 genus group of Lethina endemic to southern Africa - *Aeropetes*

SOUTHERN AFRICA - 13 genera endemic to southern Africa; 2 Lethina, 5 Dirina, 6 Ypthimina

LETHINA; *Aeropetes*, *Paralethe*.

DIRINA; *Dira*, *Tarsocera*, *Dingana*, *Serradinga*, *Torynesis*.

YPTHIMINA; *Coenyra*, *Melampias*, *Cassionympha*, *Paternympha*, *Pseudonympha*, *Stygionympha*.

MADAGASCAR - 5 genera endemic to Madagascar; 4 Mycalesina, 1 Ypthimina

MYCALESINA; *Houlbertia*, *Masoura*, *Admiratio*, *Heteropsis*.

YPTHIMINA; *Strabena*.

WEST AFRICA - 1 genus endemic to West Africa; Mycalesina

MYCALESINA; *Hellelesis*

EAST AFRICA - 1 genus endemic to East Africa; Ypthimina.

YPTHIMINA; *Neocoenyra*

COMPARATIVE ENDEMISM IN SOUTHERN AFRICA SATYRINAE

1 endemic subtribe - Dirina.

1 endemic genus group of Lethina- *Aeropetes*.

23 genera; 13 endemic - 56%.

92 species; 65 endemic - 71%.

No other family has nearly as many endemic genera.

In the Papilionidae, Pieridae & other Nymphalidae there are no endemic genera.

In the Hesperidae there are only 2, *Alenia*, *Moltena*.

In the Lycaenidae of 67 genera there are 15 endemic - 22%, less than half that of the Satyrids.

THE SATYRINAE IN AFRICA

The Satyrinae probably dispersed through Africa over the past 100 million years in waves of temperate and tropical climates. The western tropical/subtropical habitats mixed and matched with the tropical Indian fauna. The temperate genera spread through Africa during the cooler climates along the dry eastern side of the rift valley. These temperate populations could have originated from ancient relict populations in southern Africa moving northwards or from Indian populations moving west and southwards.

1. The most ancient groups appear to be the temperate Elymniini and Satyrini which could have stretched from the Indian plate through Madagascar and eastern and southern Africa to South America.

The Elymniini are currently represented by the *Aeropetes* group of the Lethina (now 2 genera restricted to southern Africa) and the primitive (hairy eyed) Mycalesina which could have evolved on Madagascar or on the Indian plate, and later invaded mainland Africa. There are currently 5 genera of Mycalesina on Madagascar (hairy eyed).

The Satyrini are represented by the endemic South African subtribe Dirina (now 5 genera) and the temperate Ypthimina (Melampias group, now 5 genera in South Africa). On Madagascar there is one genus of Ypthimina of the *Melampias* group, *Strabena*.

2. The Melanitini evolved in the tropical habitats to the north and were spread by periods of wet warm weather where the forests spread and the temperate conditions were restricted. The Melanitini could have spread back and forth with the Indian tropics thereby resulting in so few genera.

The Elymniini evolved into the tropical Mycalesina with naked eyes (restricted to 2 genera) and the *Physcaeneura* and *Neita* groups of Satyrini (now 5 genera).

3. The intermittent temperate periods possibly connected the habitats in Africa with the Indian/Asian zone and brought with it the Lethe group of the Lethina, now genus *Aphysoneura*. Similarly the next tropical/subtropical period brought in the Elymniina and the *Ypthima* group of the Ypthimina from the Indian/Asian tropics.

4. A recent temperate invasion possibly brought in the Satyrina genus *Hipparchia* and the Lethina genus *Lasiommata* into the northern limits of the Afrotropical region from the Palaearctic region.

Temperature as a factor in satyrinae distribution

As the foodplants are grasses this should have enabled the genera to have a wider distribution than other butterflies, in fact the opposite is the case. Therefore other factors must determine the distribution of the Satyrinae.

Temperature may be a primary factor in determining generic and specific distribution.

The Satyrinae can therefore firstly be divided into two groups apparently based on their origins. The first group have originated in tropical or subtropical climates and are adapted to warmer temperatures, the second group has originated in temperate climates and are very temperature sensitive.

The effect of temperature is evident in that many species show an inordinately high level of precision in emergence times. Even flight periods during the day indicate temperature sensitivity, some species flying only in the cool of the morning (Curle & Henning, 1996). Altitude also determines temperature as does humidity of habitat; marsh, forest, hillside etc.

Tropical/subtropical genera have a fairly wide distribution through the lowveld and extend down from the warmer climates through the montane forest belt. Temperate species are restricted to montane forest, high altitude grassveld and the Capensis region.

One measurement of temperature affecting temperate Satyrinae distribution that could be used is the Effective Temperature (Bailey, 1960; Stuckenberg, 1960) (TEMPERATURE (T) and the MEAN ANNUAL RANGE OF TEMPERATURES (AR) (the difference between the means of the warmest and coldest months).

$$\text{EFFECTIVE TEMPERATURE} = 8T + 14AR/AR + 8.$$

The effective temperature appears to be one of the most significant factors in the distribution of temperate Satyrinae. How the EFFECTIVE TEMPERATURE achieves its ends must still be determined for most temperate species. Quickelberge, 1993 gives evidence of the efficacy of the effective temperature in determining the distribution of the South African genus *Paralethe*.

An analysis of the southern African Satyrinae

MELANITINI - tropical/subtropical genera - 2 genera

Both genera widely Afrotropical, marginal genera in southern Africa.

Melanitis; 2 species - *leda*, *libya*

Gnophodes; 1 species - *betsimena*

Primitive characters; bifid claws, large size, crepuscular
Derived characters; forewing eye spots, cryptic underside
(Primitive and derived characters based on Miller, 1968)

ELYMNINI

Mycalesina - tropical/subtropical genera - 2 genus groups

Both genus groups widely Afrotropical, marginal genera in southern Africa
Bicyclus; 7 species - SA, *ena*, *safitsa*, *anyana* ZIM, *angulosus*, *campinus*, *condamini*, *cottrelli* (*condamini* endemic to ZIM)
Henotesia; 2 species - *perspicua*, *simonsii* (on Madagascar and other indian ocean islands almost 50 species, predominant satyrid plus 4 related endemic genera, total mainland 10 species)

Primitive characters; hairy eyes (*Henotesia*)
Derived characters; naked eyes (*Bicyclus*), androconial patches, bases of 3 forewing veins strongly swollen.

Lethina - temperate genera - 2 genus groups - *Lethe*, *Aeropetes*

Lethe - 1 genus

Afro-montane forest, marginal genus

Aphysoneura; 1 species - *pigmentaria vumba* (mimetic - bamboo)

Aeropetes - 2 genera ENDEMIC

Aeropetes; 1 species - *tulbaghia* (mimetic)

Paralethe; 2 species - *dendrophilus*, *indosa* (mimetic)

Primitive characters; Large size (*Aeropetes*, *Paralethe*), eyes hairy, upper median and subcostal veins joined by a cross vein at the base of the hindwing (*Paralethe*), only subcostal vein swollen slightly (*Aeropetes*), lack of androconial patches, midtibia very spiny (*Aeropetes*, *Paralethe*), eggs scattered (*Aeropetes*, *Paralethe*), male aedeagus produced distally into large dentate process (*Aeropetes*, *Paralethe*).
Derived characters; Long antennae (*Aeropetes*), tarsi single jointed in both sexes (*Aeropetes*), mimetic pattern.

SATYRINI

Dirina - temperate genera - ENDEMIC - 5 genera

Dira; 4 species - *clytus*, *oxylus*, *jansei*, *swanepoeli* (largely allopatric except for possible narrow overlap at East London)

Tarsocera; 7 species - *cassina*, *cassus*, *fulvina*, *southeyae*, *imitator*, *dicksoni*, *namaquensis*

Dingana; 5 species - *dingana*, *alaedeus*, *jerinae*, *angusta*, *alticola* (allopatric) (*Dira* and *Dingana* allopatric).

Serradinga; 2 species - *bowkeri*, *clarki* (allopatric) (*Dira* and *Serradinga* allopatric).

Torynesis; 5 species - *mintha*, *hawequas*, *magna*, *pringlei*, *orangica* (allopatric) (*Dira* and *Torynesis* allopatric)

Primitive characters; Large size, eyes hairy, only subcostal vein swollen slightly, mid-tibia very spiny, eggs scattered, male aedeagus produced distally into large dentate process in some genera.

Derived characters; flash colouration on upperside, cryptic underside.

Ypthimina - tropical/subtropical genera - 4 genus groups

Physcaeneura - 4 genera, 1 Endemic (E) - tropical/subtropical genera

Coenyra (Endemic); 3 species - *aurantiaca*, *rufiplaga*, *hebe* (allopatric)

Physcaeneura; 2 species - *panda*, *pione*

Coenyropsis; 2 species - *natalii*, *bera*

Neita - 1 genus, 0 Endemic - subtropical

Neita; 4 species - *neita*, *extensa*, *durbani*, *lotenia* (allopatric)

Melampias - 5 genus groups, 5 Endemic - temperate genera

Pseudonympha (Endemic); 15 species - 5 species groups

1. *magus*, *magoides*, *cyclops* (allopatric)

2. *varii*, *swanepoeli*, *arnoldi* (allopatric)

3. *trimenii*, *poetula*, *gaika*, *paragaika* (largely allopatric)

4. *hippia*, *paludis*, *penningtoni*, *machacha*

5. *southeyi*

Cassionympha (Endemic); 3 species - *cassius*, *detecta*, *camdeboo*

Melampias (Endemic); 2 species - *huebneri*, *steniptera* (allopatric)

Paternympha (Endemic); 2 species - *narycia*, *loxopthalma* (allopatric)

Stygionympha (Endemic); 10 species - 3 species groups

1. *vigilans*, *scotina*, *coetzeri* (allopatric)

2. *wichgrafi*, *vansoni*, *robertsoni*, *curlei* (largely allopatric)

3. *irrorata*, *dicksoni*, *geraldi* (allopatric)

Ypthima - 3 genera - tropical & subtropical

Ypthima; 7 species - *asterope*, *impura*, *antennata*, *granulosa*, *pupillaris*, *condamini*, *rhodesiana*

Ypthimomorpha; 1 species - *itonia*

Mashuna; 1 species - *mashuna*

Primitive characters; falces of male genitalia absent (*Ypthima*)

Derived characters; small size, flash colouration on undersides, large eye spots on forewings, very reduced forelegs.

Biological factors in African Satyrinae

MELANITINI; no subtribes, 2 genera; *Melanitis*, *Gnophodes*

Melanitis - Forest & bushveld, multivoltine, fermentation feeders, tropical.

Gnophodes - Forest, multivoltine, fermentation feeders, tropical.

ELYMNIINI; 3 subtribes; Elymniina, Lethina, Mycalesina

Elymniina - 1 genus; *Elymnias*

Elymnias - Forest, multivoltine, fermentation feeders, tropical.

Mycalesina - 2 genus groups; *Bicyclus*, *Henotesia*

Bicyclus - Forest, multivoltine, fermentation feeders, tropical.

Henotesia - Bushveld, multivoltine, fermentation feeders, tropical

Lethina - 2 genus groups; *Aeropetes*, *Lethe*

Aeropetes group - 2 genera; *Aeropetes*, *Paralethe*

Aeropetes - Montane grassveld, multivoltine, flower feeders, temperate.

Paralethe - Forest, univoltine, fermentation feeders, temperate.

Lethe group - 2 genera; *Aphysoneura*, *Lasiommata*

Aphysoneura - Forest, multivoltine, fermentation feeders, temperate.

Lasiommata - Palearctic species.

SATYRINI

Satyrini - 3 subtribes; Satyrina, Ypthimina & Dirina

Satyrina - 1 genus; *Hipparchia*

Hipparchia - Palearctic species

Ypthimina - 3 genus groups; *Ypthima*, *Physcaeneura*, *Melampias*

Ypthima - 3 genera; *Ypthima*, *Ypthimomorpha*, *Mashuna*

Ypthima group - Bushveld, multivoltine, flower feeders, tropical.

Physcaeneura - 4 genera; *Neocoenyra*, *Coenyropsis*, *Coenyra*, *Physcaeneura*.

Physcaeneura group - Bushveld, multivoltine, flower feeders, tropical.

Neita group - 1 genus; *Neita*.

Neita group - Montane grassveld and bushveld, univoltine, flower feeders, tropical.

Melampias - 6 genera; *Melampias*, *Strabena*, *Cassionympha*, *Pseudonympha*, *Paternympha*, *Stygionympha*.

Melampias group - Montane grassveld, univoltine, flower feeders, temperate.

Dirina - 1 genus group, 5 genera; *Dira*, *Tarsocera*, *Dingana*, *Serradinga*, *Torynesis*.

Dira group - Montane grassveld, univoltine, flower feeders, temperate.

Survival factors in the Satyrinae of southern Africa

Flight

The method of flight has also been a subject for some conjecture. The bobbing flight is possibly a protection against bird predators, such as swifts and swallows (Pringle, 1983). If specimens are disturbed they can also drop into the grass and effectively disappear. Their sombre colouring sometimes makes way for startling finery, such as the silvery undersides of the *Pseudonympha*'s. This apparently is a flash adaptation where, as the butterfly flies, it flashes its underside with each upbeat of the wings. The silvery flash is what the predator "homes in" on for attack, but because it is flashing and moving it is very difficult to follow, coupled of course with the up and down bobbing of the target. What the prey presents to the predator is a target moving horizontally as well as vertically and flashing! A difficult task for any predator. The browns can make it even more difficult by presenting hundreds of moving, bobbing, flashing targets on a single hillside. The characteristic eye-spot near the apex of the forewing is apparently used as a scare tactic. If disturbed while at rest the butterfly will flick its wings open and the attacker would believe it is staring into the eyes of some larger animal and may hesitate long enough for the butterfly to escape.

Temperature

Some species apparently shun the heat of the day and shelter under rocks while others appear to revel in the heat. Many fly almost exclusively in the shade only flitting from tree to tree when necessary. Some species are crepuscular, such as the large Melanitini.

There are not many forest browns in southern Africa and these are usually at the extent of their range and are fairly widespread throughout the Afrotropical forests. One endemic species, *Cassionympha cassius*, has found its way into the forest biome and is the commonest butterfly in all the forests from the Cape Peninsula around the east to as far north as the Zoutpansberg in the Northern Province. This common brown does not occur outside of South Africa. Why this is so has not as yet been ascertained although the amount of competition from the *Bicyclus* increases from Zimbabwe northwards. The forests inhabited by *C. cassius* could be classified as cool montane forests so perhaps the temperature precludes it occurring outside the borders of South Africa.

Similarly the endemic genus *Paralethe* has evolved to inhabit forests and apparently mimics the unpalatable danaid *Danaus chrysippus*.

Feeding and size

Browns feed on flowers or suck at damp sand or suck up the juices from fermenting matter. These can be classified into two groups, nectar feeders and fermentation feeders.

The most spectacular is *Aeropetes tulbaghia* which feeds on red flowers. Almost any Red-Hot Poker (*Kniphofia*) growing on the mountain hillsides will, within a short time, have a *A. tulbaghia* delving into its depths. The famous Red Disa Orchid (*Disa uniflora*) of the Cape mountains is exclusively pollinated by this large brown as are 15 other fynbos plants. All of these plants have large red flowers and bloom only from

December to May, the flight period of the butterfly. Some of these species are; *Narine sarniensis*, *Gladiolus cardinalis*, *Cyrtanthus purpureus*, the rare *Cyrtanthus guthrei* and *Disa ferruginea* which produces no nectar and relies solely on its red flowers to attract the butterfly.

The ability to pollinate a flower is apparently proportionate to the size of the flower. Small butterflies feed on small flowers, large butterflies on large flowers. There are both structural and behavioural factors which determine which butterflies visit which flowers. It could be energetically disadvantageous for a large butterfly to visit and feed on a small flower, considering the rewards. It could then be postulated that for the *Disa*, and the other large red mountain flowers, *A. tulbaghia* has evolved in size along with them.

Adult size

The sizes of many adult populations of browns are incredibly uniform in comparison with other butterflies. A hillside of many hundreds of specimens can be found to vary in size by only a relatively small degree. This does assist in the confusion to predators as the search pattern of avian predators cannot then differentiate on size. This consistency in size is possibly due to the length of time it takes for the larva to develop and process the grass it needs to attain adulthood. If it is subject to a bad spell of weather or other catastrophe it can wait (diapause) and recover its lost growth when conditions improve and still attain the required size.

Mimicry

The Lethina appear to be genetically malleable enough to adapt their appearance for mimicry. *Paraetha* apparently mimiother butterfly its size in those high mountains, the common Citrus Swallowtail - *Papilio demodocus*. The benefit gained by this could be that the size of *P. demodocus* is a deterrent to the smaller hillside predators, and an effective model should also be more common than the mimic. Both these factors could have determined the apparent mimicry by *A. tulbaghia* of *P. demodocus*. Of course the most important factor in mimicry is that the mimic has the genetic ability to match the model, in other words it becomes a mimic because it can, genetically, develop the physical characteristics of the model! The pattern of both the species in the *Aerpetes* group are considered primitive. But, as in many Lethina around the world, a mimetic ability is apparent and is utilized.

Protective resemblance

Browns are masters at protective resemblance, which is the ability to mimic inanimate objects, the dead-leaf underside of the large *Melanitis* and *Gnophodes* is a match for any species in the world. The variations are endless for these large slow-flying species. It is apparent that in the browns, which are relatively slow flying, the larger the size the more adaptations must be made to survive! For example *Paraetha* mimics *D. chrysippus*; *Aerpetes* mimics *P. demodocus* and *Melanitis* and *Gnophodes* mimics dead leaves and fly at dusk; these being the four largest species in southern Africa and their adaptations are apparently the most complex. The Dirini usually fly in the morning and shun the warmer parts of the day by secreting themselves under rocks or bushes.

Most browns have cryptic undersides, the forest and woodland genera of *Bicyclus* and *Henotesia* have the prominent leaf-like mid-rib, the grassveld and scrub genera have rock-like undersides; the bushveld species who live in grass under the shade of trees have striped undersides etc.

Predators

Satyrids have been recorded as prey for swifts and swallows in mountain conditions (Pringle, 1983) of the genus *Pseudonympha*. Other records for swifts or swallows in South Africa are for the lycaenid genera *Thestor* (H. C. Ficq *pers. comm.*) and *Lepidochrysops* (I. A. Coetzer *pers. comm.*). These instances were also in grassy mountain terrain and in all instances the butterflies predated upon were flying plentifully. Previous authors on bird predation apparently agree that for a butterfly to be included in the search image of a predatory bird it should be numerous enough to be exploitable (Dempster, 1984). Below a certain density of prey the search image could be more profitably used on some other organism.

Satyrids who spend time under rocks or bushes can be predated upon by lizards, geckos and frogs. Their best defence against these predators is a cryptic underside, but if found they can flash their eye spots or escape because the predator attacks the distractive colouration at the edges of the wings.

Defensive behaviour

The Browns have a somewhat erratic flight and when disturbed they closed their wings and dropped straight down for about a metre before flying off swiftly, this has also been recorded by Pringle, 1983, who concluded that this action appeared to be a defensive strategy against air-borne predators.

Defensive colouration

The browns have ocellate spots and red or yellow markings around the margin of the wings, these are apparently instrumental in attracting predatory attack away from the body.

Early stages

The life histories of the Satyrinae in South Africa revolve around grasses (Poaceae) but they may also feed on related plants such as restios (Restionaceae). Some species lay their eggs singly on blades of grass (Ypthimina) while others scatter them amongst the clumps of grass (Dirina). This adaptation may be due to the size of the species or may be primitive; the Ypthimina are smaller and more capable of depositing eggs on a single grass stalk while the larger, more ungainly, Dirina may have resorted to the more unconventional method of scattering.

The eggs are usually rounded and smooth with a finely etched surface, while some species have a more prominent scalloped surface with longitudinal ridges. As the larvae are grass feeders the head shields are fairly large to accomodate the strong mouth parts. The larvae are long and narrow and longitudinally striped to cryptically blend in with the food plants. The head shields may also be dorsally extended into a forward projecting pair of horns. If the larva is disturbed it may thrash its head and deter the attacker. The larvae feed at night and shelter during the day at the base of the clumps of grass. If disturbed they will often drop down into the grass.

The duration of the early stages are largely spent as a larva, either feeding or hibernating when food is scarce. The egg and pupal stages last about three weeks each, as does the adult, and during the other ten months of the year the butterfly is in the larval stage. The number of larval moults also appears to be fairly variable and appears to be dependent on climatic conditions, the larvae goes through a minimum of four instars to a maximum of seven. The instars increase in duration as the weather warms and the final instar is the longest often lastr really goes into complete diapause but may feed at any time during this period.

The pupa is secreted in the debris at the base of the grass and is brown to brownish yellow or even green in colour and generally rounded in shape. They are usually attached by the cremaster but may be found lying free (van Son, 1955).

Conclusion

The Satyrinae of southern Africa occupy a unique place in the scheme of African Lepidopterology. They have managed to survive and adapt into the genera and species seen today that allow us to speculate from where they originated and how they have evolved.

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ON PREPARATION OF THE BUTTERFLIES OF THE WORLD SERIES

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Butterflies have always been a part of my life. From my earliest memories at the age of 3, flood back images, particularly one of a blue butterfly on the roof of my baby cot. Memories of sailing butterflies in sun-drenched fields with me in hot pursuit, with nothing but a small uprooted daisy bush in my hand to bring them down. When at last I struck an enormous yellow butterfly and picked up its mangled body, I found to my horror that its beautiful buttry scales came too easily off its broken wings onto my little pink fingers, and I burst into tears at the sight of its squashed abdomen. Sympathetic parents then initiated me into the mysteries of 'the net'. Years later I would make my own - but I would always let my captives go. The early years were more concerned with finding caterpillars of butterflies and moths (in the case of certain hairy ones of the latter, with disastrous consequences for my skin), watching them pupate and then counting the days excitedly until I could hear scratching noises inside my shoe boxes, which noises would reveal that a little creature within wanted to escape into the large world without. My greatest joy was to permit the butterflies to walk onto my fingers and watch them coil and un-coil their filamentous tongues, trying to ingest the moisture (sometimes chocolate-flavoured) that covers the fingers of small boys. Then to watch them flap their wings and soar into the air, swooping and gliding with the unspeakable freedom, that only the birds (and the angels) of living creatures, share with them. How I too longed to be a butterfly - or perhaps one day, an angel!

Now, in decidedly non-angelic, gravity-bound middle age, I still dream occasionally of being able to gently float off into the blue at about the height of a low tree, and travel effortlessly over enormous distances, with arms outstretched in lieu of wings, in search of new places and new sights and new friends. In the first decade after the war, my father having left England, took up duties as Government Pathologist at the Kandy General Hospital in Ceylon. The years 1952 to 1956 were the most glorious years of my serious butterfly life. That was when I began collecting butterflies in earnest, together with my elder brother, and some of our local friends. The rivalry was intense and the adventures hair-raising. We scaled mountains, crossed raging torrents (I recently visited one such raging torrent at Halloluwa in Kandy, and cannot believe how outrageous the folly of that boyhood deed. Ignorance and innocence are truly bliss). My father would depart for his daily rounds, leaving us ostensibly at our desks, under orders to get on with our studies. My dear mother (God rest her soul), noticing as mothers do, what joys really possess the souls of their sons, would wait until my father was safely out of sight, slip us her little Rolex watch, give us a small packet of sandwiches, and say with a twinkle in her eye "make sure you're at your desks by the time your father gets home at 4.00 o'clock". She covered for us, every day of the vacations, and what fruit her foresight has now born. From Ceylon we went on to Malaya, where my father took up another post with the University of Malaya in Singapore, and after a little delay my brother and I resumed our butterflying in that country. Thence to Australia, where we were to finally settle

down, with correspondence with collectors all over the world now well established - principal among these being Major Neville Vissian of Rusape (in what was Rhodesia), A.E.G. Best of Assam, and various German and Swiss collectors. In 1965, tragedy struck our family with the unexpected death of my brother at a motor racing meeting in Tasmania. I was at university at the time, and should have gone on to finish Medicine, and perhaps another degree, but instead lost the stomach for further study - took a degree in History and Philosophy of Science, and ran away to Europe. In 1967 I married my wife Lucilla and in that year also began planning *The Butterflies of the Australian Region*. It was the beginning of a fruitful partnership, not only in terms of our children, but also for the books we have produced. I remember a brief rivalry with Charles McCubbin the artist/naturalist, who at the same time as my first book, produced a very beautiful *Butterflies of Australia* for Collins - one sagacious critic (it was Baron de Worms, of whom more later) said of Charles "and what is he going to do for an encore? You my boy have the world as your oyster" - and so it all began.

Of course the blame for all of this (if blame be attributed to anyone) should be placed fairly on the shoulders of one R.I. Vane-Wright who then in 1969, was Head of the Butterfly Department at the B.M.(N.H.), and who made the grievous mistake of giving me permission to work on the Greatest Collection in the World. One of Dick's nicknames in those days (I think Bob Smiles coined it), was appropriately 'The Dick Veined-White', and when four year later I approached this eponymously-named gentleman (now a good friend), and announced to him that I was now about to undertake *Butterflies of the Whole Planet Earth* - he gasped, threw his head back in laughter, and immediately lost fifty percent of his hair in anticipation of having to put up with the d'Aberreras for another five years. That, I said optimistically and heroically, is how long I will take to do the job. That was in 1976. Well, I have now completed *Butterflies of the World* - but it has taken me 26 years to do it, and I have scars to prove it. In 1979 Dick V-W (also known as 'Stain-Bright') rose to the challenge, and informed me that it was his "wish" that I should put aside my own plans for the Oriental Region, and commence a book on the Ethiopian Region, on the basis of Carcasson's unpublished Catalogue. It was not altogether successful experience for me, not least because of a clash of personalities between myself and the Late Bob Carcasson. But the revision of that work in 1997 surely has begun to exorcise the little incubuses that have plagued me ever since. Incidentally I was perhaps the first to use the term 'Afrotropical' in a major faunal monograph, to replace the far less accurate 'Ethiopian', to describe this region.

Along the way I met many joyful and not-so-joyful characters. The greatest influences on my life were the late M.W.F. Tweedie, T.G. Howarth, and the Late Col. Charles Cowan, who taught me the basics of entomology and taxonomy respectively. The Late N.D. Riley also imbued me with the secrets of the craft of taxonomy. Other great influences in my life have been Col. J.N. Eliot, Dr. Arthur Rydon, D.G. Sevastopoulo, Richard Carver, G.E. Tite, and of the younger generation, R.I. Vane-Wright, Phil Ackery, Steve Collins, and Phil de Vries in the U.S. I have greatly admired the enormous knowledge and common sense of Dr. Gerardo Lamas and come to respect the vast output of Jacques Hecq and the Late Drs. Guilleaumin and Jacques Plantrou.

Some of my funnier experiences have involved such luminaries as the famous Baron Charles de Worms, whose culinary appetite was legendary if not notorious.

The great Wicky Fleming once swore that when Charles de Worms visited him in Malaya, he observed the good Baron devour at one sitting an entree, two roast chickens with sundry vegetables and garnishing, 5 pints of beer, 3 servings of dessert (in addition to the servings of some of the other guests, who sacrificed theirs in amazement), a whole pineapple followed by several cups of coffee, an entire bottle of brandy, and then another two rounds of coffee, followed by Schnapps, at which point he let out a very loud burp and said in that growling laconic voice "What ho! And what do you have in mind for breakfast tomorrow?" At one B.M.(N.H.) Christmas party, the good Baron arrived first amongst the guests, and proceeded like a vacuum cleaner down the assembled trestle tables groaning with goodies, where at the end of the semi-circle Kathy Smiles had placed a plate of coloured polystyrene foam extrusions of different shapes - which were devoured nonchalantly by the good Baron, who then proceeded to let out his customary burp, and begin all over again. On the occasion in which Charles de Worms inspired me to write the World series, he came laboriously up to my desk, leaned heavily against one of the cabinets, flipped his food-stained tie out of his equally stained waistcoat, burped loudly, and said sonorously "What ho young d'Abrera, what ho - knocked McCubbin into a cocked hat eh - what's he going to do for an encore? As for you young fellow, the world is your oyster" and then he waddled off. Bob Smiles once opined that if you could boil down Baron de Worms' tie, you could make enough soup to keep all the Oxfam shops happy for years.

Of the African cognoscenti, I never met Charlie Dickson, but I would love to have done so. We stared off in enmity and ended up dear friends. He too taught me a great deal about South African butterflies, and made me aware of a great deal of the rich culture and traditions of the South African butterfly world. Through him I learned to appreciate the names of Pennington, Gowan Clark, Pinhey, Vári and Swanepoel, Bill Henning and his sons and others.

One of the most comical experiences of my career involved being bogged with the young Andrew Neild (it was all his fault) in mud, up the Amazon somewhere in Ecuador. We were travelling in one of those pathetic Japanese soap-boxes masquerading as a 4-wheel drive, and there was no way we were going to extract the inadequate little vehicle from the quagmire. Requests for help from the local 'campesinos' brought looks of disdain and contempt. Now, when I am in the jungle I always wear a shirt and tie - this is for protection against mosquitoes and leaches as much as for the principle that 'a gentleman should always appear to be a gentleman wherever possible'. Mind you I also take pains to wear underwear, trousers and socks and shoes, but in this case the tie was the point of the story. It was in fact a black tie, decorated with my university crest bearing the red cross of St. George - the emblem of New South Wales. That, plus a naturally academic visage heightened by half-frames positioned delicately on bridge of nose, were sufficient to convince one of the 'campesinos' of Andrew Neild's outrageous story that I was a Catholic priest in need of assistance. For eight hours I had to keep up appearances, pulling out my rosary beads to emphasis the point, and even blessing little children with it in response to their request. Fortunately I had on my person two religious medals given to me by the good bishop of Baños for my own children when I should return to Australia. These I presented to the respectful 'campesino's' even more respectful children as a token of my pastoral concern. Finally, just as the sun began to set over the Amazonian rainforest, a very large Caterpillar bulldozer arrived from Puyo on the back of a trailer,

and proceeded to pull our bogged pseudo-Land Rover back onto the main road. The most embarrassing moment of this entire episode was when I had to give the by-now-gathered throng of several dozen people, an ostentatious pastoral blessing. Fortunately my altar boy's memory of traditional Latin liturgy is intact, and served me well. I pray God forgives me for this involuntary but highly necessary masquerade. What must have really puzzled them all was why this 'priest' who had come all the way from 'la tierra de los Kanguros', was lying on his belly in the mud photographing butterflies close up, in the company of a lunatic red-head (El Pele Rojo), armed with a butterfly net. In this case I can advise all my friends that there are times when it pays to be a Catholic - even if at heart they really believe in fairy tales such as Evolution.

BUTTERFLY CONSERVATION IN SOUTH AFRICA

By G.A. Henning,
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The following sequence of events resulted in conservation awareness for the plight of butterfly species in South Africa:

1953 - David Swanepoel whose book *Butterflies of South Africa - Where, When and How they fly* gave details of rarity and localities.

1976 - Charles Dickson had a list of 16 of his special butterflies added to Schedule 2 of protected wild animals in the Cape Province:

Lycaenidae: *Aloeides egerides* and *lutescens* (D), *Argyrocupha malagrida malagrida*, *Trimenia wallengrenii*, *Oxychaeta dicksoni*, *Lepidochrysops bacchus*, *Poecilmitis endymion*, *lyncurium*, *nigricans* and *rileyi* (D), *Thestor dicksoni* and *kaplani* (D) (D = Dickson as describer).

Nymphalidae: *Charaxes xipharex occidentalis*, *Stygionympha dicksoni*

Hesperiidae: *Metisella syrinx*, *Tsitana disksoni*

1983 - Ordinance 12 of the Transvaal list of protected wild animals in 1983 included in Schedule 7; *Poecilmitis aureus* and all species of the genus *Charaxes*.

1985 - Proclamation of the Ruimsig Entomological Reserve in Roodepoort initiated by the Hennings with the Lepidopterists' Society of Southern Africa and the Wildlife Society of South Africa.

1985 - South African Natural Heritage Programme. Controlled by Department of Environmental Affairs. Natural Heritage Sites in private or public ownership (100th site registered in 1989) are given a conservation status.

Butterfly sites:

Chrysoritis aureus

Erikssonia acraeina

Orachrysops ariadne

1987 - First Lepidoptera Conservation Symposium held at Roodepoort on 8th August 1987. (Chairman organising committee G.A.Henning).

1989 - *South African Red Data Book - Butterflies* by S.F. & G.A. Henning, published by CSIR.

1990 - Transvaal Nature Conservation Division appoint full time conservator to investigate Red Data Butterflies.

1990 - IUCN Red List of Threatened Animals ex RDB.

1992 - Conservation of Lepidoptera in Southern Africa by G.A. & S.F. Henning. In, *A practical guide to butterflies and moths in Southern Africa*, published by Lepidopterists' Society of Southern Africa. Red Data list updated and other Southern African lists.

1993 - *Conservation Biology of Lycaenidae (Butterflies)*, Occasional Paper of the IUCN Species Survival Commission.

- South Africa by S.F. Henning, G.A. Henning & M.J. Samways.
- Threatened Lycaenidae of South Africa by M.J. Samways.

1995 - Updating the status of South African Red Data butterfly species by G.A. & S.F. Henning. *Metamorphosis* 6(2). Updating lists in view of revised *Penningtons' Butterflies of Southern Africa*, 1994.

1995 - Brenton Blue Project, Lepidopterists' Society of Southern Africa. Initiated by G.A. Henning who became coordinator of the project.

1996 - Brenton Blue Trust, Lepidopterists Society of Southern Africa with Endangered Wildlife Trust and other conservation bodies.

Conservation projects undertaken in South Africa - surveys of reserves

Ruimsig Entomological Reserve - Gauteng
Blyderivierspoort Nature Reserve - Mpumalanga
Suikerbosrand Nature Reserve - Gauteng
Lapalala Wilderness - Northern Province
Golden Gates Highlands National Park - Free State
Pilanesberg National Park - North West Province
Lagalametse Nature Reserve - Northern Province

Management projects

Erikssonia acraeina - Northern Province
Alaena margaritacea - Northern Province
Orachrysops ariadne - KwaZulu-Natal

Conservation projects

Brenton Blue Project

Regional representatives

Western Cape
southern Cape
Eastern Cape
KwaZulu-Natal
Free State
Zimbabwe
Mpumalanga

South African Constitution

Representations made by Lepidopterists' Society of Southern Africa and other conservation bodies and individuals.

ACT 108 of 1996

Bill of Rights:

Environment

24. Everyone has the right -

- a. to an environment that is not harmful to their health or well being and
- b. to have the environment protected, for the benefit of present and future generations, through reasonable legislative and other measures that -
 - i. prevent pollution and ecological degradation;
 - ii. promote conservation; and
 - iii. secure ecologically sustainable development and use of natural resources while promoting justifiable economic and social development.

South African Red Data Book - Butterflies

In the South African Red Data Book-Butterflies, 1989, issued by the Council for Scientific and Industrial Research, S.F. & G.A. Henning have listed 141 species and subspecies of butterfly from South Africa for which some degree of threat has been established or is suspected. There are about 650 species of butterfly in South Africa with about 16% having some level of threat. Significant is the fact that 96% of threatened species are endemic. Of these about 75% are lycaenids, most of which are ant associated in some way. The richest area for these species is the Cape Fold Mountains which offer some measure of protection as water catchment areas. A scant 23% of the threatened lycaenids occur in nature reserves and wilderness areas, which can be compared with over 90% for each of the vertebrate groups and 74% for vascular plants (Samways, 1993).

Red data classification (as revised):

EXTINCT -

Deloneura immaculata Bowker in 1863, 3 females.

Lepidochrysops hypopolia Morant in 1870 and Ayres in 1879, 3 males.

ENDANGERED -

Lepidochrysops methymna dicksoni Habitat destroyed mid 1950's

Orachrysops niobe - 1995 Brenton Blue Project

Trimenia malagrida malagrida Originally Vulnerable

Chrysoritis dicksoni Originally Vulnerable

(*Chrysoritis cottrelli* was included in the original but is now rare)

VULNERABLE -

Alaena margaritacea Transvaal Nature Conservation Project

Erikssonia acraeina Transvaal Nature Conservation Project

Lepidochrysops lotana Transvaal Nature Conservation Project

Orachrysops ariadne Natural Heritage Site, was rare.

(*Trimenia malagrida maryae* was included in the original but is now rare)

Butterfly conservation

i. Population dynamics are not the issue.

a. The butterfly and other insect populations are largely determined by a predator/prey ratio in which the major predators are parasitic and predatory insects.

b. Insect communities may have an entire population turnover of a matter of weeks, compared to plant communities which have trees and seed resources which can have a turnover of many decades or even centuries. (eg *Calvaria major* and the Dodo on Mauritius)

ii. Habitat conservation is the only solution.

a. National Parks and state nature reserves certainly do their part in preserving the species which fall within their boundaries, but the great majority of threatened species are either on private land or on land controlled by the Department of Environmental Affairs.

b. Natural heritage sites

Action plans

1. Education.

Direct education.

a. Education of conservation and governmental bodies.

b. Education of children and public to enforce influence on government in future.

Education through media and directly.

a. High profile media education to the masses. Articles in widely read magazines and newspapers. Continued pressure vital.

b. Articles in magazines aimed at conservation and outdoor enthusiasts.

c. Direct promotions to children by means of lectures and demonstrations at schools and public places.

d. Direct promotions to conservation bodies and outdoor enthusiasts through lectures and outdoor demonstrations.

e. Butterfly houses, 2 in SA, Butterfly World & Oudthoorn.

f. Publication of books, pamphlets and regional brochures.

2. Habitat destruction

Habitat destruction can only be prevented through education of conservationists, government, NGO's and public.

3. Economic implications

In a largely third world country like South Africa job opportunities are essential to promote conservation. Education costs money and the amount of conservation education is proportionate to the money available.

4. Motivation and Justification in South Africa

Large scale self-sustaining employment opportunities in conservation and tourism is essential to promote butterfly conservation as a viable proposition in South Africa. Capital inflow is needed to promote butterflies into conservation and tourism.

Aspects of butterfly interest must be promoted and be seen to aid in the development of the disadvantaged masses in South Africa while providing a scientific service.

Projects:

- a. butterfly watching
- b. butterfly houses
- c. butterfly gardening
- d. butterfly reserves
- e. responsible recreational collecting

Risk elements for butterflies - direct habitat destruction

1. Housing & Development

These are primary requirements of developing South Africa but are also a primary source of Habitat Destruction.

2. Agriculture

Agriculture is Habitat Destruction. Vast tracts of land are under monocultures in South Africa. In third world rural areas incorrect agricultural methods are applied which result in massive soil erosion and subsequent Habitat Destruction.

3. Draining of Wetlands & Riparian habitats

Water is of prime concern throughout much of rural South Africa. Dams are constructed to provide communities. Marshes are considered to harbour disease such as Malaria and are drained.

Indicator species and biodiversity

Butterflies in other parts of the world are considered good indicator species for well-being of habitats. They are also good indicators of biodiversity as they are the most well researched group of invertebrates. These factors are not utilised in South Africa.

If local butterfly species are in residence at a particular locality but not elsewhere it has been shown that the particular habitat harbours many other scientifically valuable organisms. This has been the case at the Ruimsig Entomological Reserve in Roodepoort, Gauteng and in other parts of the world (New, 1992).

As butterflies are chemically bound to react with other living organisms such as plants, ants, parasites, parasitoids, invertebrate and vertebrate predators etc. Adverse conditions affecting any of the its co-habitants will manifest itself in their population.

The distribution and taxonomy of butterflies are not entirely dependant on professional, government financed, manpower but has its origins in individual privately financed members of the Lepidopterists' Society of Africa.

The monitoring and assessment of risk elements using indicator species and biodiversity is again dependent on finances available.

Habitat destruction cannot always be avoided as it is necessary to satisfy the insatiable demands for housing, food, transport, industry and so many more facets of human activities which involve space. Cities are often situated in locations favourable to commerce or agriculture, sites at the confluences of major rivers, near major embayments, or along coastlines are favoured. In South Africa, urbanization and agriculture conversion on the sandveld, to the north of Cape Town, has brought the endemic *Oxychaeta dicksoni* to the verge of extinction. Along the south coast of KwaZulu-Natal urbanization has destroyed much of the natural habitat and at Durban itself several good localities have been destroyed. The KwaZulu-Natal midlands has also been affected by forestry and agriculture which has affected the populations of *Orachrysops ariadne*. The Garden Route, a major tourist attraction, has become so developed that the last known colony of the *Orachrysops niobe* (Brenton Blue) is threatened by a housing development. The Brenton Blue Project is currently in progress in an endeavour to save this species from extinction.

The draining of wetlands or the lowering of water tables has destroyed, or threatens to destroy, many habitats of marsh-adapted insect communities. On the Witwatersrand in Gauteng Province the draining of marshes and vleis has resulted in the loss of many colonies of *Metisella meninx*. Conversion of natural habitats for agricultural purposes, particularly for planted food and fibre crops, is one of the most extensive land uses and has resulted in the greatest loss of native insect populations.

Threats by invasive species

Not only is man directly involved in habitat destruction but also indirectly by introducing alien fauna and flora:

Pieris brassicae - negative impact in terms of destruction potential.

Argentine Ant

Another harmful alien which is active in habitats of many butterflies is the introduced Argentine Ant (*Iridomyrmex humilis*) regarded as the most pernicious ant in the world.

This little species was first discovered in this country in Cape Town in the early years of this century. It is believed that it was introduced during the Anglo-Boer war. It has since spread far inland and in northerly and easterly directions.

It appears to have been first recorded in Johannesburg in the 1970's. However little is known about the true distribution of this destructive creature in South Africa, but people are well aware of its harmful activities wherever it establishes itself. Apart from doing harm in many other respects, it drives away our indigenous ants by harassing them, killing them and taking over their nests and food supplies. Sugar ants such as the Spotted Sugar Ant (*Camponotus maculatus*) and the Black Marsh Ant (*Camponotus niveosetosus*). The small Black Sugar Ant (*Acantholepis capensis*) are absolutely defenceless against this intruder. These and other ants play an important role in the life-cycles of various lycaenid butterflies and hence they are necessary components of the ecosystems in which these butterflies occur.

By killing and replacing indigenous ants, the Argentine Ants adversely affect the butterfly fauna and that of other insects and the organisms depending on them in yet another way.

Many ants, including the species which act as hosts to lycaenid butterfly larvae, are agents in dispersal of elaiosome-bearing seeds. These seeds have fleshy, oily structures attached to them which contain powerful ant attractants. The ants laboriously collect these seeds and take them to their underground nests, in the safety of which they eat off and consume the elaiosomes. The seeds without the elaiosomes, but still viable, are either left lying in the ants' nests or they are carried to them. In both situations the seeds are more likely to germinate. The seeds are thus widely dispersed and those left behind in the ants' nests are protected against seed-eating birds, rats and mice. When their seeds are not dispersed by ants, the plants depending on this method of seed dispersal become rarer and rarer and eventually disappear completely. The Argentine Ants play no part in seed dispersal because, although they eat elaiosomes, they do not collect and transport seeds. Instead they leave them lying about under the parent plants, where they are easily found and eaten by birds and small mammals (Slingsby, 1982). The disappearance from an area of certain plants adversely affects the associated insects, including butterflies, whose larvae feed on these plants. The Argentine Ant thus not only causes the disappearance of ants associated with butterflies but also of those larval food-plants of which the seeds are dependent on ant dispersal.

Invasive plant species

Alien vegetation has invaded and even destroyed large tracts of natural flora, a process which is extremely difficult to reverse and very expensive to control on a large scale.

Alien vegetation usually is unsuitable as food for indigenous fauna, including our butterflies and moths. The establishment of plant invaders in existing plant communities upsets the delicate balances which operate between competitive plant communities. This usually results in the dominance of the invader species over the indigenous, usually multispecies, plant communities. The success of plant invaders can be seen all around us and is due to a great extent to the absence of natural enemies of these species. In South Africa the introduction of exotic plants, especially

from Australia, has had a serious effect on butterfly populations over the past 40 to 50 years.

The coastal, or near coastal, belt to the north of Cape Town is a prime example. Endemic lycaenid butterflies such as *Poecilmitis brooksi* and *P. pan* have largely disappeared once relatively abundant.

Even in remote areas like the Eastern Cape, north of the Kei River, invasive plants are threatening the last colony of *Poecilmitis lyncurium*.

When an ecosystem has changed, either due to habitat destruction or by invasive vegetation, it is usually no longer suitable for the fauna associated with the original plant communities and even ants, certain species of which are host to butterfly larvae and pupae.

Protected habitats

Some positive aspects of butterfly conservation in South Africa are the areas stringently protected from destruction:

Rainfall catchment areas;

National parks & nature reserves:

1 Ruimsig entomological reserve.

First insect reserve in southern hemisphere which was proclaimed in 1985 after a prolonged media battle. It has proved that small reserves are a viable option for some, particularly ant associated, butterflies.

It has shown that African butterflies are good indicators of biodiversity as the area of the reserve has been found to contain a large number of valuable plant species. The other invertebrates have not been adequately researched at this stage. The reserve has been utilized as a monitoring project to develop mark/recapture procedures in African butterflies.

2 Brenton blue project, reserve to be proclaimed.

Commenced early in 1995. The Lepidopterists' Society of Africa decided to become involved in the project at a council meeting on 10th May 1995. The action plan included:

Display cases at Brenton Hotel and Information centre;

Promotional material to the residents of Brenton-on-Sea;

Sale of sets of prints;

Magazine and newspaper articles;

Meetings with Cape Nature Conservation and government;

Scientific research into life history, ants, foodplants, habitat;

Television campaign;

Collecting funds through professional fund raising organisation.

Brenton Blue Trust

Trust formed in 1996, administered by Endangered Wildlife Trust who have the infrastructure and contacts to approach large commercial enterprises to provide funds

and sufficient influence on government to stop further development.

In 1997 the South African Government committed itself to proclaiming the locality a nature reserve.

Plans for Butterfly Conservation in SA

Central & regional government attitudes

NGO attitudes

African and Worldwide Butterfly Conservation

Government attitudes

NGO attitudes

Role for Lepidopterists' Society of Africa in Butterfly Conservation

Advisory role with regard to legislation.

Use of butterfly farms and commercial breeding to increase awareness and education.

Conclusion

The Lepidopterists' Society of Africa is committed to conservation throughout the continent. Activities aimed at Education and promoting general interest in Butterflies and Moths are encouraged, and we hope that the Lepidopterists' Society of Africa will be a force in African Butterfly Conservation.

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THE POTENTIAL USE OF BUTTERFLIES & DUNG BEETLES IN ENVIRONMENTAL IMPACT STUDIES: AN EXAMPLE FROM ZIMBABWE

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Abstract: A system for monitoring the health of terrestrial environments is required. In Africa most environmental studies are involved with large mammals while the invertebrates have been neglected. Of the Invertebrates butterflies and dung beetles in particular are two possible candidates. For environmental monitoring the advantages and disadvantages of using these groups are discussed. Results from a recent study, suggest butterflies as a good possibility. It is recommended that systems are produced that:

- 1) help local people monitor their area;
- 2) identify areas of high diversity and interest and;
- 3) make use of "sacred" patches for conservation.

Introduction

Worldwide there is a growing awareness of the impact of man on the environment. Sub-Saharan Africa has lagged behind the more developed countries in formulating procedures to identify and measure the major effects of human activities on our particular conditions. However, concerned scientists, in many countries, are presently trying to produce a set of standardised procedures for tackling environmental impacts (for instance: R. Reid in Kenya, S. Kiema in Burkina Faso and K. Esler in South Africa).

Unfortunately, in Africa, there has been such an obsession with the rich and highly visible large mammal fauna, that smaller, less eye-catching or stirring animals have been neglected. Many invertebrate groups may prove more suitable for measuring environmental change than mammals. Invertebrate studies may also be less costly and yield results faster than parallel mammalian investigations.

This paper examines the possibility of using butterflies and dung beetles to monitor environmental change in Sub-Saharan Africa. Both groups have been relatively well studied and are easily visible, making it possible to produce identification guides for local people.

A recent (1996) study evaluating the impacts of tsetse control induced land-use changes on the number of species and abundance of selected animal groups.

In Zimbabwe the objective of a study just completed by the author (under the auspices of the International Livestock Research Institute & Regional Tsetse and Trypanomiasis Control Programme) was to evaluate the impacts of tsetse control induced land-use changes on environmental processes and variables. I use some results from this study to illustrate certain points. The study took place at two sites in North-western Zimbabwe. The first, in the Busi Valley, compared a system where

crop production and livestock are in use (Simchembu), to one where indigenous megaherbivores use the land (in Chizarira National Park). The second, in the Western portion of Kanyati, Makande, compared a large area that has been set aside as a wildlife area, to a neighbouring area that is extensively cultivated. I have in some cases added information from other studies in Western (Hwange & Matopos), and Central Zimbabwe (Wedza).

Methods

The methods describing dung beetle capture and analysis are given in Gardiner (1995). The method used for obtaining butterfly abundance per hectare is outlined below. Transects measuring 20m by 500m were marked out using white wash and coloured plastic tape. An observer, a recorder and a collector were used to collect the data. On the first visit to Busi, data was collected from each transect on at least four separate occasions. Within a fixed swath (depending on butterfly density, but not more than 20m), the butterflies seen were identified and their numbers recorded. The collector caught any specimens the observer could not immediately identify. Unclassified species were kept and identified later. The patches were visited at least once during the two time periods 0900-1100hrs and 1100-1600hrs. The time taken to walk the transect varied from 10 to 20 minutes. On the other sampling occasions the number of visits to a transect depended on the abundance of butterflies. If very few butterflies were encountered the transect was visited twice. With high butterfly activity up to eight visits were made to a transect. Other species seen in the transect, after the abundance measurements, were recorded. For each visit to an area an estimate of the average number of butterflies per hectare was calculated for each transect (this is illustrated for 20 species in Table 1). In addition two trapnets were hung in the transects, approximately 160 meters from either end of the transect. The trapnets provided information, for the Nymphalidae, on the average number of specimens per trap for each species and each trap position.

Results

One group of organisms may or may not correlate with changes in the environment and may not be a good indicator for other groups. For instance different patterns can be obtained using dung beetles compared to birds and butterflies. In the case of birds and to a lesser extent butterflies there appears to be a higher number of species in the areas where domestic livestock is used compared to wildlife areas (Table 2). When dung beetles are used, in most cases there is a higher number of species in the wildlife areas (Table 2). The results suggest that various groups should be studied, and the abundance of the component species or selected groups investigated.

Advantages & disadvantages of using butterflies and dungbeetles for environmental studies

These points may also apply to other groups such as birds. Some of them have been discussed by Samwais (1995).

Advantages

- 1) They are sensitive to changes in the environment.
- 2) Large numbers may be present, so that time spent in the field quickly yields a substantial data-bank.
- 3) Groups that are relatively easy to identify can be selected. For some regions detailed taxonomic information is available, for instance Penningtons Butterflies of Southern Africa (1978), Butterflies of Kenya (1991) and a Key to the Dung Beetles of Zimbabwe (Gardiner 1995).
- 4) They can be collected in a quantitative and qualitative manner.

Disadvantages

- 1) There can be large changes in their abundance due to natural conditions. For instance they can change from year to year (Table 3). Although these changes are present, degradation of the environment may be an overriding influence.
- 2) The abundance of the component species change through the year (in Zimbabwe very different population levels are recorded in October compared to May). For a particular area should sampling takes place at the time when most species are present?
- 3) There is a lack of taxonomic expertise.
- 4) There is very little data on the movement of individual specimens of the various butterfly species. This could influence the interpretation of collected data, as insects collected in a degraded area could have moved in from another neighbouring area. Some results from this and other studies suggest movement may be of more importance than previously thought (Shreeve 1995). More "mark and recapture" experiments are required.
- 5) There is a negative attitude in certain scientific circles to the use of what are perceived as 'glamorous' insects.

Future directions

There is a need for terrestrial monitoring systems which can be easily and accurately implemented. Indicator species that are unmistakable would be of great value. Such species must be carefully chosen for their sensitivity to change and their usefulness in measuring environmental integrity. A certain genus of dung beetle, *Onitis*, may be a useful indicator of certain environmental changes (Table 4). It would be relatively simple to set up a monitoring system where this group is used as an indicator. A similar system could be used for certain butterfly genera such as the *Charaxes*.

The study should also take in to account 'special' species or patches of high diversity and attention focussed on these parts of the environment. For instance certain transects showed both a high number of species and butterfly abundance (transects with bold numbers in Tables 3 & 5). These patches may need more protection or special conservation measures. It may be possible to give them the status of a sacred patch. An example of a sacred patch that contained a rare and endangered species is found in Dondo Forest, Mozambique. A sacred patch in this forest was one of the flying areas for the rare *Euthecta cooksoni* (pers. obs.).

An additional reason for trying to set up a terrestrial monitoring system is not only to keep a healthy environment but also to highlight the aesthetic value of preserving species.

Unfortunately we still do not know at what stage of environmental change we lose species. Two important factors to take in to account when considering human induced changes on ecosystems are: firstly, what does it take to cause a species to become exceedingly low in numbers or locally extinct? If this does happen, is it important to record? Secondly, does a change in the abundance of the component species indicate that there is a change in the quality of the environment? A lot of work needs to be done to get a terrestrial monitoring system into operation. Butterflies are an ideal candidate as it is the group we have the most information for.

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MODE AND TEMPO IN THE EVOLUTION OF MIMICRY IN AFRICAN BUTTERFLIES – A RESEARCH PROGRAMME

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Abstract: The genus *Amauris* is a driving force in the evolution of mimicry within African butterflies. Amongst the many mimics of *Amauris*, *Papilio dardanus* is a celebrated and much-studied species, but controversy continues regarding the sequence of evolutionary events that have produced this remarkable insect. Even less well understood is the possible relationship between mimicry and the evolution of new species. A research programme using molecular biology to explore these issues is outlined. Ways in which African-based lepidopterists might contribute to this work are briefly noted.

Introduction

An unanswered question concerns whether or not, and to what extent, the evolution of mimicry is linked to species formation and the generation of new taxic diversity (Vane-Wright, 1978). One of the goals of our group¹ is to investigate the co-evolution of *Amauris* and some of its primary mimics, notably butterflies of the genera *Hypolimnys* and *Papilio*, using molecular biology techniques. Such a research programme, which would attempt to match and calibrate absolute rates of evolution in both model and multiple mimetic lineages, has not been undertaken before.

Amongst the more than 3600 species of butterflies known from Africa and the Malagasy region, species of *Amauris* are some of the most important models, being mimicked by a variety of unrelated butterfly species, and even some day-flying moths (Eltringham, 1910; Vane-Wright & Boppré, 1993). If it were possible to assess the age of the various *Amauris* species, then we would have some idea of the upper time limit for the evolution of a whole series of mimics. At present we have very little idea about how long particular model patterns have existed, or how long it has taken for individual species, or sets of species, to respond to the evolutionary opportunities offered by new models once they have been formed.

In this context, one particular member of the group, *Amauris comorana*, is of great interest. Only known from the Indian Ocean island of Grande Comore, some 300 km off the coast of northern Mozambique, *A. comorana* appears to be one of the oldest lineages within the genus, yet Grande Comore itself, an island produced from an ocean floor 'hot spot', is considered by geologists to be no more than 112,000 years old (Emeric & Duncan, 1982). Is it possible that the species of *Amauris*, and the many mimics that have been affected by them, have all evolved within less than a million years? Or does the restriction of *A. comorana* to Grande Comore have some other, completely different explanation, and has the genus and its attendant flock of mimics taken much longer to develop?

The polymorphism and mimicry of *Hypolimnas* and *Papilio* species

Mimics of *Amauris* occur in a number of papilionid and nymphalid genera in Africa, including *Graphium*, *Aterica*, *Acraea*, *Pseudacraea* and *Euxanthe*. The two genera with the largest number of convincing *Amauris* mimics, however, are *Hypolimnas* and *Papilio*. Within *Hypolimnas* these include *H. anthedon* (= *dubius* in older literature), *H. monteironis*, *H. mechowii*, *H. bartelloti*, *H. dinarcha*, *H. deceptor*, and *H. usambara*. Within *Papilio*, mimicry of *Amauris* is always limited to the female sex, as seen in *P. arnoldiana*, *P. echerioides*, *P. plagiatus*, *P. jacksoni*, *P. fuelleborni*, and the most celebrated mimetic butterfly of all, *P. dardanus*.

In a series of papers (e.g. Vane-Wright, 1978, 1981, 1984; Vane-Wright & Smith, 1991) I have suggested that the tailed, yellow, male-like females *Papilio dardanus* found in Ethiopia, Somalia, Grande Comore and Madagascar are, contrary to most previous views, among the most recently evolved of *dardanus* female forms, and not the most primitive. According to this more recent perspective, the most primitive female forms of *P. dardanus* are the morphs that mimic *Amauris niavius* (Turner, 1963, suggested that these forms represent the oldest living *mimetic* form of the species, but still adhered to the traditional view that the tailed male-like females are even older). Taking into account a related hypothesis, now well-supported by molecular data and hybridization studies in addition to morphological evidence (Vane-Wright & Smith, 1991; Clarke *et al.*, 1991; Vane-Wright *et al.*, submitted), that the closest living relative of *dardanus* is *Papilio phorcas* (the only other African swallowtail with female-limited polymorphism that includes a distinct male-like form), it seems worth considering the possibility that *Papilio dardanus* came into existence as a result of the evolution of mimicry (Vane-Wright, 1978).

Thus another aim of our research programme is to investigate the polymorphism of *Papilio dardanus* in depth, in an attempt to locate the multi-allelic gene (the *H*-locus) demonstrated by Clarke & Sheppard (e.g. 1960; see review in Nijhout, 1991) to be responsible for controlling the colour pattern shifts of the different female morphs, and endeavour to sequence it. We will also try to do this for *P. phorcas*, if it proves to have an homologous locus. If successful, this should make it possible to make a good estimate of the time of separation of *dardanus* from *phorcas*, including the distinctive *P. d. humbloti* from Grande Comore. We also hope to discover evidence critical to reconstructing the sequence whereby the various morphs of female *dardanus* arose, and even understand the structure and evolution of the gene itself, and its mode of action during development. To do this will involve re-creating some of the classic Clarke & Sheppard inter-racial hybrids, notably using *P. d. antinorii* from Ethiopia and *P. d. tibullus* from the African east coast region.

The species, patterns, age and origin of *Amauris*

Ackery & Vane-Wright (1984) proposed a cladistic classification for the 15 species of *Amauris* recognised by Talbot (1940), the last person to revise the entire group. Recently, d'Abrera (1997) has increased this number to 16 by asserting that the nominal taxon *Amauris hyalites* Butler is separate from the parapatric *A. damocles*².

Following Pinhey (1977), two basic *Amauris* patterns stand out: black and white with a large white area on the hind wings and white spots or areas on the fore wings (*niavius* pattern), and black and yellow, with a large yellow area on the hind wing and scattered, generally smaller whitish spots on the fore wings (*echeria* pattern). The 15 or 16 *Amauris* species can be grouped³ as follows:

black and white (*niavius* pattern):

niavius, *tartarea*, *ochlea*, *nossima*, *dannfelti*, *damocles/hyalites*, *hecate*, *inferna*, *vashti*

black and yellow (*echeria* pattern):

echeria, *albimaculata*, *crawshayi*, *elliotti*, *comorana*, *phoedon*

A pressing need is to investigate *Amauris* itself, to see if we can calibrate the basic model system and get a defensible estimate for the age of the whole genus, and of the divergence times of its component species. Previous work on morphology (Ackery & Vane-Wright, 1984) and pheromone-gland chemicals of *Amauris* (Vane-Wright *et al.*, 1992; Schulz *et al.*, 1993) has revealed an apparently robust cladistic framework, in which *Amauris* as a whole is most closely related to the Asian genera *Ideopsis* and *Parantica*. Internally, *Amauris* is divisible into two unequal lineages, subgenus *Amaura* (13 or 14 species) and subgenus *Amauris* (2 species). The two members of subgenus *Amauris* (*niavius* and *tartarea*) only exhibit the black and white patterns, while the black and yellow patterns appear to be primitive in the evolution of subgenus *Amaura*: the first three sub-clades are the three all-yellow and black species³; the fourth sub-clade is *A. echeria* itself; and, with the exception of the curious *A. vashti* (currently regarded as the fifth branch of *Amaura*), the several black and white members of subgenus *Amaura* all belong to a terminal clade (within which another yellow species, *A. albimaculata*, also occurs).

The age of origin of the genus would thus give an upper bound for one or other of the two basic *Amauris* colour patterns, and the age of separation of the two subgeneric lineages would give an upper bound for the second of the two colour patterns. Within subgenus *Amaura*, *A. comorana*, the species only known from the young island of Grande Comore, apparently evolved as a very early off-shoot, while another early-diverging *Amaura* species, *A. phoedon*, is restricted to the far older island of Mauritius. At the other end of the scale, the black and white *A. ochlea* appears to be one of the two most recent *Amauris* species to have evolved, and may be an example of secondary pattern convergence within the genus (Müllerian mimicry).

For a preliminary investigation we will need samples of both lineages of subgenus *Amauris*, together with as many species and subspecies as possible of the subgenus *Amaura* (and some species belonging to the Indo-Malayan outgroups *Parantica* and *Ideopsis*). The data obtained from DNA sequencing will be used, first to check and refine the current cladistic classification, and then to make a preliminary estimate of the age of *Amauris*, of the subgenera *Amaura* and *Amauris*, and of key species within *Amaura* (e.g. *A. comorana* and *A. ochlea*). Once we have developed

the baseline techniques needed, we hope to obtain funds for a full scale investigation into *Amauris* and its attendant mimics, in our attempt to understand the tempo and mode of speciation within this group of African insects.

Currently we have funds to pursue some of the preliminary work on *Papilio dardanus*, and are seeking other funds to support baseline studies on *Hypolimnias* and the critical *Amauris*. We would be very grateful to any African lepidopterists able help us in this endeavour by collecting small samples for us of species and subspecies of *Amauris*, *Hypolimnias* and *Papilio*, according to the methods recently described in this journal for DNA sampling (Carter *et al.*, 1997). We will also need to make pedigree crosses of various *dardanus* (and eventually *phorcas*) races, for investigation of the *H*-locus. Help from anyone likely to be able to obtain suitable livestock and make it available for the rearing work, to be carried out in Kenya or the UK, would be most welcome.

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Notes

1 The extended research group includes Michael Boppré, Ali Cieslak, Sir Cyril Clarke, Steve Collins, David Heckel, Fred Nijhout, Campbell Smith and Alfred Vogler, in addition to the author.

2 Bernard d'Abrera (1997) separates *A. hyalites* from *damocles* on the grounds that Ackery & Vane-Wright (1984), who treated them as a single species, employed "indifferent philosophy" (i.e., cladistic methods), and that "the traditional view of species and taxonomy" should prevail. *A. d. damocles* (West Africa, to Nigeria) and *A. d. hyalites* (Cameroun to Angola and central Africa) differ slightly in colour pattern, and replace each other geographically. They were first united as a single species (under the invalid name *A. egialea* Cramer, [1777]) by Talbot (1940), a traditional view ignored by later workers such as Peters (1952) and d'Abrera (1980), but accepted by Ackery & Vane-Wright (1984) even though they found no (cladistic) evidence for or against Talbot's position. According to Ackery & Vane-Wright (1984), and taking into account the more recent results of Vane-Wright *et al.* (1992), *A. damocles* sensu Talbot (including *d. makuyensis* Carcasson, 1964, from western Tanzania) forms a clade with two other species (*A. nossima* and *A. ochlea*), but the various nominal taxa included within *damocles* s. l. can only be grouped by default (i.e. they lack the distinguishing characters of the other two species in the clade, but have no currently recognised synapomorphy or special character of their own). My friend Bernard d'Abrera offers no new data in support of his assertion. As, in my view, empiricism has primacy over philosophy (indifferent or divine), we will have to await new comparative data if this is to be settled. Molecular data could provide an

excellent insight (indeed, Schulz *et al.*, 1993, list pheromone components so far only known from *A. d. damocles*, but the pheromone bouquets of *A. d. hyalites* have yet to be examined).

3 While this simple classification is used in the discussion below, reality is more complex (at least to the human observer). *A. inferna*, *A. hecate* and some forms of *A. tartarea* have very restricted white areas on the hindwings, while *A. vashti* has none. With regard to the white areas of the forewings, only some forms of *A. tartarea* and *A. ochlea* match *A. niavius* in extent; the forewing white of *A. nossima* (Madagascar and Mayotte) exceeds *niavius*, while the other 'black and white' species have forewing spots that are, generally, barely more extensive than those species that mainly conform to the *echeria* pattern. With regard to colour, the hindwings of such 'black and white' species as *A. dannfelti* have a chestnut cast, and this warmer tone is exceeded in *A. damocles/hyalites* by a distinctly yellowy-tan tint. Amongst the yellow and black group, the yellow hindwing areas of some *A. crawshayi* *crawshayi* are very pale, while three species (the upland *A. ellioti*, and two island isolates, *A. comorana* from Grande Comore and *A. phoedon* from Mauritius) have yellow forewing spots, the same colour as the hindwing markings. Many of these variations, that also seem to be matched more or less faithfully by some mimics, are potentially explicable by the notion of generalization (see e.g. Turner, 1983; Ackery & Vane-Wright, 1984: 104), whereby some predators distinguish patterns very precisely, while others generalize across a wider spectrum of patterns, allowing intermediates to persist or even proliferate.

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BUTTERFLY MONITORING IN ARABUKO-SOKOKE FOREST, KENYA

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The butterfly monitoring exercise was carried out in 1993 to collect baseline data for the Kipepeo Project prior to the start of its activities in butterfly farming 1994. This database was useful in the planning of the project's breeding activities. Systematic collecting and trapping was carried out to determine the butterfly diversity and seasonal fluctuations in Arabuko-Sokoke Forest.

The monitoring was carried out by counting the numbers of 60 butterfly species along set transects on a weekly basis. From the systematic collecting and trapping a total of 134 species of butterflies were caught, which were representative of 5 families, 14 subfamilies and 58 genera. The monthly butterfly abundance correlated positively with change in rainfall.

Most of the transects had statistically significant Shannon diversity indices. These differences were present even amongst transects in the same vegetation zone. Currently, I am repeating the surveys to determine if wild populations have suffered any adverse impact after three years of intensive butterfly farming around the forest.

BUTTERFLY FARMING AND FOREST CONSERVATION: A CASE STUDY FROM THE NORTH COAST OF KENYA

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This paper describes the Kipepeo Project which aims to win the support of local communities for the conservation of Arabuko Sokoke Forest (ASF) through the sustainable utilisation of its butterflies for their benefit. This forest is famous for its avifauna which includes six rare and endangered species (Sokoke Scops Owl, East Coast Akalat, Spotted Ground Thrush, Sokoke Pipit, Amani Sunbird and Clarke's Weaver) in addition to a further 17 species which are coastal endemics. It is also home to four rare or threatened mammals (Elephant, Ader's Duiker, Golden-Rumped Elephant Shrew, and Sokoke Bushy-Tailed Mongoose). Situated on the north coast of Kenya, over 400Km² in area and containing no human settlements, Arabuko-Sokoke is the largest remaining piece of the coastal forest mosaic which once stretched from Southern Somalia to northern Mozambique. During long periods of isolation from other forests this coastal mosaic evolved a distinctive fauna and flora of its own which is now seriously eroded. The protection of ASF is the last best hope of retaining a viable fragment of this once extensive ecosystem. For its birds alone, it has been ranked as the second most important forest in Africa. Its conservation is therefore of global significance.

All of this however means little to the people around the forest. Their numbers are growing rapidly and they are hungry for land, short of cash incomes and jobs, impoverished and harassed by forest wildlife, misled by local politicians, and hostile to the forest. Independent surveys estimated their *per capita* cash incomes at less than US\$50 per year, and showed that over 90% are unhappy with the forest's presence with over 50% wanting the entire forest cleared for settlement. Wildlife crop-raids by elephants and baboons cause much anguish and economic hardship, and are a major cause for resentment. The population surrounding the forest cultivates to its edges and erodes its interior through subsistence demands for fuelwood, poles, game-meat, wild honey, fruits and medicinal plants. The forest has been invaded no less than six times in the last three years, each time with the aim of cutting plotting in anticipation of de-gazettement, and each time led or encouraged by people with official positions in the administration. In March 1995, the Kilifi District Development Committee supported a call for the excision of 1,200 ha in its south-eastern portion for settlement.

It is obvious that Arabuko-Sokoke cannot survive without the long-term support of the local people and their leaders, but there is little prospect of this unless it is seen to be of benefit to them. The Kipepeo Project is one of several efforts (including, most notably, assistance for schools and water supplies from the Kenya Wildlife Service and the incoming Birdlife International Project funded by the EU) to build such support. It is situated near the forest at the National Museums of Kenya site at Gede Ruins 18 km south of Malindi and is administered by the East Africa Natural History Society in Nairobi. Set up in June 1993 with an initial grant of US\$ 50,000 from the Global Environmental Facility Small Grants Programme administered by UNDP, it has introduced butterfly farming to the forest-adjacent community as a means of earning

cash income from the forest. More recently, with the arrival of a British volunteer [VSO], Transy Bliss, it has also become a vehicle for environmental education with an active schools programme centred on ASF in collaboration with the Wildlife Club of Kenya. By showing that the forest can provide unexpected sources income to the local community, and by teaching local children about extraordinary biodiversity and conservation importance, the Kipepeo Project aims to help to secure its future.

CLASSIFICATION OF THE AFRICAN SATURNIIDAE (LEPIDOPTERA) - THE QUEST FOR NATURAL GROUPS AND RELATIONSHIPS

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Abstract: The development of the higher classification of the African Saturniidae is reviewed, concluding that the current system, which dates back to Bouvier (1936), is typologically orientated and largely obscures the indicated natural, phylogenetic relationships of this fauna. The five major groups of these moths, viz. Micragonini, Urotini, Bunaeini, Saturniini and Attacini, are briefly discussed, rectifying several nomenclatural errors (such as the homonymy and synonymy of Ludiini and Pseudapheliini *auctt.*), giving some diagnostic characters of possible phylogenetic significance and commenting on the composition of these groups. It is concluded that a natural classification of the African Saturniidae is only possible by conducting a careful and thorough phylogenetic analysis of all features, especially of preimaginal characters, which were largely ignored in the past, and also of genetic and molecular aspects.

Introduction

It has been recognized for some time that the Afrotropical fauna of saturniid moths contains some special and unique elements, and the various classification schemes of the family have generally attempted to reflect this. However, the precise characters of the typically African elements of saturniids have not been adequately identified, and the relationships of these groups to each other and to extra-African groups are equally poorly studied. In particular, the methodology of phylogenetic systematics (cladistics), which yields testifiable hypotheses about genealogical relations between taxa, has not been applied comprehensively to these insects at all, and the current classification system and its groups are orientated along typological concepts only. In addition, the nomenclature of the family group names is confused and in places in violation of the International Code of Zoological Nomenclature.

A full and proper cladistic analysis of such an enormous and taxonomically perplexing group as the African Saturniidae is no easy, small and quick endeavour, and this paper does not claim to present the results of such. However, the character data gathered on these moths over the last few decades (in particular on their immature stages) indicate beyond any doubt that the current classification system is a highly artificial one that obscures the real relationships between groups to a considerable extent. Despite the lack of a rigorous cladistic analysis of these moths to date, this Inaugural Conference on African Lepidoptera offers a unique opportunity to present a critical review of the higher classification of the African Saturniidae and, at the same time, offer some stimuli for further investigation of the pertinent problems in this context.

The aims of this review are therefore the following:

- * to briefly list the major historical contributions to the higher classification of the African Saturniidae;
- * to clarify the nomenclature of the family-group names;
- * to introduce a few salient preimaginal characters of apparent phylogenetic significance;
- * to outline the major natural groupings as evident at this stage; and
- * to highlight the main and most urgent problems still to be addressed.

Historical review

The African fauna of Saturniidae began to become scientifically explored in the late 18th and the 19th century, but its uniqueness on higher level (above the generic) was not recognized until the beginning of this, the 20th, century. Within a few years of each other, in 1902 and 1904 respectively, Alphaeus Spring Packard in the U.S.A. and Per Olof Christopher Aurivillius in Sweden proposed the first family-group names for the African fauna, although certainly Packard's (1902, 1914) concept and general knowledge of the African fauna seems poor and confused to us now. Aurivillius (1904) evidently had a much clearer understanding of these moths and was also the first author to publish comprehensively about their larvae, as they were known at that stage.

In 1922 Karl Jordan of the Tring Museum in London produced a very comprehensive monographic treatise of the subfamily Ludiinae, which is endemic to Africa. This work is remarkable not only for its consideration of genital and other, then less obvious and traditional, morphological features, but also for the author's recognition that different characters have different significance in establishing relationships between taxa and a classification system in general. He wrote: "*Community of certain features is not necessarily evidence of close relationship. The evidence requires to be corroborated and to be weighed.*" (p. 252) and "*It is, of course, much simpler to seize upon any structure and divide up a family according to the presence or absence of this or that morphological detail regardless of true affinity*" (p. 251). Having been written half a century before the advent of the method of phylogenetic systematics, these words sound surprisingly familiar to us today, who operate with the more clearly defined concepts of synapomorphy, symplesiomorphy and homoplasy. Jordan was also honest enough to admit that his system of the Ludiinae had its shortcomings and was not perfect but based on the data available then, and in the entire literature on the African Saturniidae this monograph remains the most thorough comprehensive taxonomic treatment to this day.

In the 1920's, E.-L. Bouvier in France began studying Saturniidae world-wide with particular emphasis on the African fauna, and between 1927 and 1936 he produced a classification system for these that is largely the one still in use today (Table 1). He operated with several levels of categories - though not very consistently -, but only some bear official names, while others do not. The two major problems with his system are the following:

Table 1. Classification of the African Saturniidae after Bouvier (1936)**Sous-famille I. - LUDIINAE**1^{re} Tribu. **Ludiidae** Jordan*Ludia, Vegetia, Pseudoludia, Holocera*2^e Tribu. **Goodiidae** Jordan*Orthogonioptilum, Carnegia, Goodia***Sous-famille II. - SATURNIINAE** Jordan**Section I. - SATURNITAE** Bouvier1^{re} Tribu. **Micragoniidae** Bouvier*Micragone*2^e Tribu. **Decachordiidae** Bouvier*Decachorda*3^e Tribu. **Pseudapheliidae** Bouvier

I. - Pseudaphéliicés anoures

Pselaphelia, Pseudaphelia, Eosia, Parusta, Tagoropsis, Pseudantheraea

II. - Pseudaphéliicés macroures

Eustera, Antistathmoptera

III. - Pseudaphéliicés armés

*Usta, Urota*4^e Tribu. **Bunaeidae** Bouvier1^o Groupe mélanocérien*Heniocha, Leucopteryx, Melanocera, Rohaniella*2^o Groupe des Bunéens inermes*Aurivillius, Bunaeopsis, Parabunaeopsis, Lobobunaea, Bunaea, Nudaurelia, Imbrasia, Eochroa*3^o Groupe des Bunéens armés*Gonimbrasia, Ubaena, Pseudobunaea, Cinabra, Cirina, Athletes, Gynanisa*5^e Tribu. **Saturniidae** Bouvier, nec Schüssler1^o Groupe anthéréen*Antherina, Ceranchia, [Antheraea, etc.]*2^o Groupe actien*Argema, [Actias etc.]***Section II. - ATTACITAE** BouvierTribu I. **Rhodiidae** Bouvier*[Rhodinia etc.]*Tribu II. **Attaciidae** Bouvier*Epiphora, Drepanoptera, [Attacus etc.]*

Firstly, he did not generally credit existing family-group names to their original authors, but mostly attributed them to himself (evidently in the meaning of "*sensu* Bouvier", although this is never so stated). In particular, earlier names coined by Packard are not reflected as such; and

Secondly, Bouvier's groups are mostly based on single and very superficial characters only, such as the presence of hindwing tails or the colour of the antennae, and genera not readily fitting into bigger groups are often simply placed into tribes of their own. Thus, *Decachorda*, which he had originally (Bouvier 1928) placed in the Pseudapheliini because of its bipectinate male antenna, he later (Bouvier 1934) moved into a tribe of its own largely because of its simple female antenna.

This Bouvierian system was adopted rather commentless in the second half of this century by his countryman Pierre-Claude Rougeot in many papers and two larger publications (1955, 1962), the latter of which represents his most comprehensive contribution to the study of the African Saturniidae. Rougeot did modernize Bouvier's tribal endings and abandoned several of the informal categories, but he did not improve on it essentially.

Elliot Pinhey of the National Museum in Bulawayo, Zimbabwe, in turn, followed Rougeot rather closely in his book on the emperor moths of South and South Central Africa (Pinhey 1972), which popularized these giant moths of Africa like no other work but unfortunately also had a major share in perpetuating several old and often serious nomenclatural and taxonomic mistakes.

Charles Michener, whose impressive study of the Saturniidae of the Western Hemisphere (Michener 1952) remains the most comprehensive morphological-taxonomic work ever undertaken of saturniids, only dealt with the African fauna in passing and merely gave a diagnosis for the subfamily "Ludiinae", in comparison with the other six subfamilies he recognized. Since this study had a strong phylogenetic approach, however, he did also comment on the relative primitiveness of the "Ludiinae" and on their evident close relationships to the Saturniinae.

More recently, similar but independent changes were made to the concept of the Ludiinae/i by Minet (1994), Oberprieler & Nässig (1994) and Bouyer (1995), mainly by inclusion of the genus *Micragone* in this group, but the nomenclatural implications of this action were left unattended in these papers.

In essence thus the African Saturniidae are currently still classified as Bouvier proposed 70 years ago. Over the last two decades the study of this fauna has picked up considerable momentum, both in Africa and in Europe and on the taxonomic as well as on the ecological and applied fronts. However, the higher classification has received no attention in this and has fallen behind modern principles and theories of classification. Does the Bouvierian scheme live up to the modern expectations of a classification system? Does it possess the powers of information storage and predictiveness required from a modern scheme such as we need now not only to reconstruct the past (the phylogeny, evolution and biogeography of the family), but also to predict the future (e.g. decline to possible extinction of specialist or relict species due to loss of habitats; expansion of generalists due to modified environments, such as shifts onto introduced plants)? The answer is an emphatic NO!

THE MAJOR GROUPS OF AFRICAN SATURNIIDAE

1. Micragonini

Evidently the least-derived but also the best-defined group of African Saturniidae are the Micragonini. This is the group referred to as Ludiinae or Ludiini since Aurivillius coined such a name in 1904. However, Ludiinae is not a valid name in the Saturniidae because it is a junior homonym of the older Ludiinae Candèze, 1891 based on the click-beetle genus *Ludius* Berthold, 1827. This means that any group in the Saturniidae bearing this name must be renamed, either by a possible oldest synonym or by a new, or replacement, name. Since the concept of the Ludiinae in Jordan's (1922) sense was widened by the inclusion of the genus *Micragone* (Darge 1990, Minet 1994, Oberprieler & Nässig 1994, Bouyer 1995), the oldest available synonym for this group is Micragoninae Cockerell, 1914. An even older family-group name is available in Cyrtogoninae Packard, 1902, but this name is not valid, as Cockerell (in Packard 1914) proposed Micragoninae as a replacement name for Cyrtogoninae because *Cyrtogone* was synonymized with *Micragone* (Packard 1914) and as Micragoninae has won general acceptance since (Art. 40 (b) of the ICZN 1985). The inclusion of *Decachorda* into this group (Oberprieler & Nässig 1994) does not affect its name, as Decachordini Bouvier is a younger name. The full synonymic list of this group is as follows, the individual synonymies automatically dating to the inclusion of the relevant type genera in the group:

Micragonini Cockerell

Micragoninae Cockerell in Packard, 1914 (1902)

= Cyrtogoniinae [*sic*] Packard, 1902 (replaced by Micragoninae because of synonymy of their type genera before 1961 and being accepted as such, Art. 40 (b) of the ICZN 1985)

= Ludiinae Aurivillius, 1904 (*nec* Candèze, 1891 for *Ludius* Berthold, 1827 (Elateridae))

= Micragoninae Cockerell in Packard, 1914 (as replacement name for Cyrtogoninae)

= Holocerinae Packard, 1914 (unavailable because of homonymy of its type genus *Holocera* Felder, 1874 (see Fletcher & Nye 1982 and Art. 39 of the ICZN 1985), but no replacement name currently necessary)

= Goodiicae Jordan, 1922

= Decachordiicae Bouvier, 1934

How are the Micragonini in this sense defined? Common characters were listed by Minet (1994) and further discussed by Oberprieler & Nässig (1994), although only few of these are as yet proved to be synapomorphies for the group. The most obvious character commonality of the group is the larval scoli. All micragonine larvae have a characteristic type of low scoli with sharp bristles that administer a histamine-type of irritant. This scoli type was termed "Stechborstenscoli" ("stinging-bristle-scoli") by Nässig (1989) and, although somewhat similar (and probably related) to the "Sekretborstenscoli" of the Saturniini, the bristles of which secrete liquid irritants, it

is typical of the Micragonini and occurs in a comparable form only in a few Saturniini. This similarity needs further investigation, and the exact character polarity (i.e. apomorphic or plesiomorphic) of this scolus type is also not quite clear yet. However, in Africa it serves to characterize the Micragonini rather well, and it is largely on account of this structure that *Micragone* and *Decachorda* were included in the group by Oberprieler & Nässig (1994). Other similarities in larval characters include the plumose hairs, which are most evident in *Ludia*, *Vegetia* and *Decachorda* and do not occur in other African Saturniidae.

The pupal stage, too, is characteristic of all the genera here included in the Micragonini. Pupation always occurs in a parchment-like cocoon with a brittle front-end spun among plant debris at the base of the foodplant (or on the bark as in *Holocerina*), and the pupa always has a granular surface. Again however, the character polarity of this type of pupa and cocoon is not clear yet.

In the imaginal stage, all Micragonini are characterized by a flatly quadripectinate male antenna with flattened lateral rami. This is evidently a plesiomorphic antennal type in the Saturniidae, as more derived types occur in other groups. Also, its configuration in the Micragonini is not uniform and consistent, and modifications in several directions are indicated to have occurred within the group. In *Goodia* the anterior rami are more dorsolateral in position and not so closely approximated to the posterior ones of the preceding segment. In *Eosia* the anterior pair of rami has evidently been reduced, as stumps of these are still present in some specimens (which is i.a. why this genus is here included in the Micragonini, in absence of knowledge of its immature stages), while a full reduction to an entirely bipectinate state antenna has seemingly occurred in *Decachorda*. Such reductions are known to have occurred several times independently in the Saturniidae (Michener 1952, Oberprieler & Nässig 1994).

In the male genitalia, finally, a clearly apomorphic development has transformed the apex of the 8th tergite into an uncus-like structure (a "superuncus"), not known in this form in other emperor moths. However, this character is absent in some genera (*Ludia*, *Vegetia*), and its phylogenetic significance requires further study.

Eosia insignis Le Cerf is here tentatively moved back to the Micragonini, in which it was described originally because of its wing venation - Fawcett (1915) even described its synonym *crenulata* under *Ludia*. Bouvier later placed *Eosia* in his Pseudapheliidae because of its allegedly bipectinate antenna; however, this antenna is in some specimens (females, male antenna not investigated) clearly quadripectinate with the front rami reduced but still visible. Its natural place therefore appears to be in the Micragonini, and in anticipation of discovering that its larva is also hairy with a micragonine-type of scoli and that it spins a cocoon, *Eosia* is here placed back in the Micragonini.

While the Micragonini are thus clearly characterized by a number of common features in all stages, the synapomorphy of all of these still needs to be demonstrated beyond doubt. Though apparent, the monophyly of the group is not yet proven. Even less certain are the relationships among its genera, where conflicting characters make it extremely difficult to derive at natural lower groups. This had already been

realised by Jordan (1922), who wrote on p. 252 "*We have ... here combined in one subfamily some characters which in other Saturnians distinguish whole subfamilies from one another*". Had he included *Micragone*, *Decachorda* and *Eosia* in his concept, the situation would have been even more complex, and it is not yet resolved. At least in this group, however, the immature stages of all genera except *Eosia* are known, and the material to study the relationships of these genera in detail is thus available.

2. Urotini

This taxon essentially comprises the group known as "Pseudapheliini" since Bouvier and usually attributed to him, although both the names "Urotinae" and "Pseudapheliinae" were actually coined by Packard, the former in 1902 and the latter in 1914. Any family-group containing both *Urota* and *Pseudaphelia* must therefore be known as Urotinae/-ini/-ina. This name does not have priority over Eudaemoniini, being established in the same work, but it is here given preference (Principle of the First Reviser, Art. 24 of the ICZN 1985), because the relationship of *Urota* to *Pseudaphelia* and the majority of the other genera hitherto combined in Pseudapheliini is less doubtful than that of *Eudaemonia*. The full synonymy of this group is as follows:

Urotini Packard

Urotinae Packard, 1902

= Eudaemoniinae Packard, 1902

= Pseudapheliinae Packard, 1914

= Eusterini Testout, 1941

Packard (1902, 1914) gave no unequivocal diagnosis of his "Urotinae", and Bouvier was the first author to clearly list the constituent genera of this group and to provide a proper definition for it. This definition, however, is a very flimsy one and rests in essence solely on the possession of bipectinate antennae, in contrast to nearly all other African Saturniidae, which possess quadripectinate ones in at least the male sex. While, at face value, this antennal type appears to constitute a suitable character to delimit such a grouping, the detailed morphological study of Michener (1952) has shown that the quadripectinate saturniid antenna has become reduced to a bipectinate state in several different lineages in the New-World groups, the gradation clearly traceable in certain genera. In Africa, too, such a reduction is evident in several genera, e.g. *Goodia* and *Eosia*, and in phylogenetic terms such a parallel reduction is a clear homoplasy and can never identify a natural group (see also Oberprieler & Nässig 1994). Bouvier himself seems to have realized this, as he originally included *Decachorda* in his "Pseudapheliicae" because of its bipectinate male antenna (Bouvier 1928) but later placed it in a separate tribe of its own because of its simple female antenna (Bouvier 1934).

Is there then a natural group called Urotini? A core group of the genera of the "Pseudapheliini" in Bouvier's sense does indeed seem to form a monophylum, but this suspected monophyly still needs to be demonstrated convincingly by means of proper synapomorphic characters. What evidence is there so far for a natural group Urotini?

In the adult stage, the genera *Pseudantheraea*, *Maltagorea*, *Tagoropsis*, *Pseudaphelia*, *Pselaphelia* and the Asian *Sinobirma* share a very similar wing pattern and, particularly the first two of these and *Sinobirma*, also a strong similarity in the structure of the male genitalia (see Nässig & Oberprieler 1994 for details). In the egg stage there occurs a peculiar and evidently apomorphic type of cluster in *Tagoropsis* and *Pseudaphelia* (see plate 10b in Oberprieler 1995), possibly in some other genera as well but not in *Pselaphelia*, in which it may have been modified secondarily to accord with the solitary and cryptic life style of the larvae of this genus. The larvae of *Pselaphelia* and *Pseudaphelia* are characterized by the anal tergite being drawn out into a spine, and similar but shorter attenuations also occur in *Tagoropsis* and *Urota*. The larva of *Urota* is also similar to that of *Tagoropsis* in other respects and generally appears to represent a derived type of the latter. In the pupal stage finally, a similar long caudal spine is present in *Pselaphelia* and *Pseudaphelia*, whose pupae are highly derived also on other features and formed under leaf litter on the ground. A much smaller but comparable caudal elongation is also present in the pupae of *Tagoropsis* and *Urota*, which are formed shallowly subterraneously and are very similar to each other. The pupa of *Pseudantheraea* is formed in a loose cocoon hanging from vegetation (Aurivillius 1904, Rougeot 1955, 1962), presumably a relict though specialized way of pupation with corresponding structures in the pupa (cremastral hooks, various strong spines), but similar smaller spinosities also occur on the pupae of *Tagoropsis*, *Pselaphelia* and *Pseudaphelia* and suggest a relationship between these genera too. The immature stages of *Maltagorea* are unfortunately very poorly known, but its pupa also appears to display several similarities to thoinobirma.

On the balance of all these features, it does therefore appear that the above six genera may indeed form a monophyletic group, but further studies of these and other characters are still needed to corroborate this.

More problematic in this context is the genus pair of *Parusta* and *Usta*. These two genera share a similar wing pattern and genitalia, except that *Parusta* possesses a strongly sclerotized and bispinose eighth sternite (cf. *Maltagorea* and *Sinobirma* in Nässig & Oberprieler 1994), but apart from this feature and some general similarity of their genitalia to those of *Maltagorea*, a close relationship to the above core group of Urotini is not clearly indicated. In larval features, *Usta* displays no evident relationships to any Urotini at all, but the scoli of its caterpillar rather resemble those of the more primitive Bunaeini such as *Melanocera*. Its pupa, too, is more similar to that of Bunaeini but displays a unique cremastral configuration. The immature stages of *Parusta* are unfortunately as yet unknown, but could form an important link in tracing the relationships of this generic pair.

The long-tailed *Eudaemonia* and *Antistathmoptera*, finally, which also form part of Bouvier's Pseudapheliini on account of their bipectinate antennae, share no obvious character (genital or otherwise) with any of the above genera, nor with each other, and their classificatory position has to remain obscure until more information on their immature stages becomes available.

Discounting the bipectinate male antenna, the only character indicated at this

stage to be of possible significance in delimiting the Urotini is the bispinose condition of the eighth abdominal sternite, which occurs prominently in *Maltagorea* (not all species), *Sinobirma*, *Pselaphelia*, *Pseudaphelia* (here in its most extreme form) and *Parusta*, with traces of it also visible in *Tagoropsis* and *Usta* but not in *Pseudantheraea* or *Urota* nor in *Antistathmoptera* and *Eudaemonia*. However, this same condition is also present in *Eochroa* (doubtfully of Bunaeini, see below), and for the Urotini in the wide sense (*Pseudapheliini sensu* Bouvier) it can therefore only be regarded as a symplesiomorphy that was reduced or lost several times subsequently. Extraordinary as this feature undoubtedly is, its precise phylogenetic significance needs further investigation. The phylogenetic relationships of the Urotini are thus still highly obscure, both within the group and also with other tribes. On several tentative similarities in the imaginal, larval and pupal stages they appear most closely related to the Bunaeini (see also below), but striking resemblances between the larva and pupa of *Pselaphelia* and of the Asian *Salassa* (see Nässig 1994) suggest that a relationship to this relict genus is also possible.

3. Bunaeini

This group comprises the bulk of the African genera and generally represents the most derived members of the entire subfamily Saturniinae. The nomenclature of this group is less confused than that of the preceding ones, except that the name originates from Packard (1902) and not Bouvier. The synonymy is as follows:

Bunaeini Packard

Bunaeinae Packard, 1902

= Melanocerini Rougeot, 1955

The monophyly of the Bunaeini, however, is far from certain. Bouvier (1928, 1936) characterized his tribe "Bunaeicae" by the possession of completely ringed eyespots (compared to the divided, asymmetrical ones of the Saturniini), by the larval scoli being transformed into strong spines, and by their habit of pupating in the soil.

Typical Saturniini and typical Bunaeini can well be differentiated by means of their eyespots, but the distinction between symmetrical and asymmetrical (excentric) ones is not always clear. Henke's (1936) detailed study of saturniid wing patterns demonstrated that asymmetrical eyespots can originate in different ways and are often highly complex in nature and apparently also in development. In some bunaeine genera, such as *Aurivillius* and *Heniocha*, a partial asymmetry of the eyespot is also present, but this is probably an independent development of that occurring in most Saturniini. It nonetheless appears that the symmetrical eyespot is a plesiomorphic trait (and thus unsuitable for defining the Bunaeini in any case) and that the asymmetrical one may have evolved several times and in different ways in the Saturniidae. Its phylogenetic significance remains to be demonstrated.

The strong spine-like scoli (Nässig's (1989) "Stechdornscolus") of the Bunaeini are indeed a feature not known outside this group, but this character occurs only in the mature larva (the fifth instar) and only in the "higher" genera. The early instars and

the less derived genera have multi-spined scoli not easily distinguished from those of the Urotini and of some Saturniini and Attacini. In these scoli, *Eochroa* and *Melanocera* agree to a considerable degree with each other but also with *Usta*, even in the final instar, but differ from all other Bunaeini. If the Bunaeini can be defined on their larval scoli, some more precise and unique characteristic needs to be found.

The monophyly of the Bunaeini is also in question on account of some other features. For example, the pupae of the higher Bunaeini carry dorsally on their caudal segment two large cavities that form hollow globules on the inside, while in less derived genera such as *Melanocera* these cavities are only shallow grooves connected to the apical margin of the segment. Similar cavities or their equivalent grooves are also present in all examined Urotini, in the micragonine *Goodia* and *Micragone*, and in the saturniine *Antherina* and *Salassa*. They are not, however, evident at all in *Eochroa*, which still spins a rudimentary cocoon among debris on the ground and has cremastral hooks in the pupa to attach to this cocoon. On account of this character, therefore, *Eochroa* does not appear to belong in the Bunaeini. Its male antenna, too, is flat with lateral rami and decidedly less derived than those of all other Bunaeini, being most similar to that of the Asian *Salassa* instead.

The "higher" Bunaeini certainly do appear to represent a natural group, sharing several derived features in all stages (i.a. antennal and genital structures in the adult, scoli and coloured integumental platelets in the larva, caudal cavities in the pupa), but the relationships of the more primitive genera *Eochroa*, *Melanocera* and possibly *Bunaeopsis* to these are less clear. On features of the larva and pupa, it seems quite possible that the Urotini as above may have diverged from a bunaeine ancestor not in common with *Eochroa*, possibly also not with *M* its present sense. Only a careful analysis of all relevant characters can clarify this issue.

4. Saturniini

Africa has only two groups of true Saturniini, one represented by the genus *Argema*, and the other by the Madagascan endemics *Antherina* and *Ceranchia*. The nomenclature of this tribe is clear (see Fletcher & Nye 1982), and the only family-group name within the tribe relevant to the African fauna is that of Actiadini (Testout 1941, as "Actiini"). This synonymy is as follows:

Saturniini Boisduval

Saturnides Boisduval, [1837] 1834

= Actiadini (emend.) Testout, 1941

The monophyly of the Saturniini is beyond the scope of this paper, and only the affinities of its African members require comments here.

Argema currently comprises three continental species and one Madagascan one, *A. mittrei* (Guérin-Ménéville), which is more primitive on several imaginal and preimaginal features and less close to the continental species than these to each other. A separate generic name, *Cometesia* Bouvier 1928, is available for this species. It may represent the ancestral form of the continental species (in which case

Argema in its present constitution is a monophylum), but some similarities between *A. mittrei* and the (South-East Asian) *maenas* group of the mainly northern-hemisphere *Actias* (especially in the larva) suggest that this group of species may also have a direct relationship with *A. mittrei* (in which case both *Argema* and *Actias* are paraphyletic). The precise relationships among all "Actiadini" remain to be resolved.

Antherina and *Ceranchia* are evidently saturniine in nature on account of their asymmetrical eyespots and cocoon-spinning larvae, but their affinities to other Saturniini are obscure. No close relationships with the Eurasian nor with the Australian saturniines are apparent. Instead, some of their preimaginal features suggest as affinity with the African Bunaeini and Urotini. The larval scoli of *Ceranchia apollina* are not of the typical 'Sternwarzen'-type of the Saturniini but show a remarkable semblance to those of the more primitive Bunaeini, such as *Melanocera*, and the pupa of *Antherina* also has shallow dorsal caudal grooves like *Melanocera* and as seem to have developed into the deep cavities of the higher Bunaeini (see above). It would appear from this that *Antherina* and *Ceranchia* may be survivors of an old saturniine lineage that gave rise to the Bunaeini/Urotini on the African continent but subsequently disappeared there, with possible remnants surviving only in the form of *Eochroa*. Such putative relationships need to be corroborated by definite characters and a full phylogenetic analysis, though.

5. Attacini

Only a single representative of this tribe occurs in Africa, the genus *Epiphora*. Originally split into two genera, *Epiphora* and *Drepanoptera*, based on wing venation characters, this separation proved impossible to uphold and was later abandoned, and *Epiphora* has since intrinsically been regarded as a monophyletic group. Rather than a division existing between *Epiphora* (type species *E. mythimnia*) and *Drepanoptera* (type species *E. albida*), the basic dichotomy in this genus lies between the eastern *E. antinorii* group and all other species, as based on wing markings as well as on genital and larval features. Though apparent, the monophyly of *Epiphora* needs to be demonstrated by means of proper synapomorphies, and the relationships between its various species groups also require investigation.

Equally uncertain are its relationships to other attacine genera, the latest (but tentative) study being that of Peigler (1989). Recently, more information has become available on the larvae of both *Epiphora* and *Attacus*, allowing a much better comparison of these two genera. In *Epiphora*, the known larvae (unfortunately those of the *E. antinorii* group are still undescribed) can be roughly divided into two types, o-tipped scoli (the *Epiphora* type) (see fig. 13 in Oberprieler & Nässig 1994), the other containing yellow larvae with blue to blackish scoli (the *Drepanoptera* type) (see fig. 23 in Oberprieler & Nässig 1994) and possessing an olfactory defence system in producing a secretion with a strong citrus smell from their scoli. Very similar larval types occur in the Asian genus *Attacus*. The plesiomorphic species such as *A. aurantiacus* have the very same *Epiphora*-type of larva with waxy coating and blue-

tipped scoli (see figs 2-3 in Nässig & Taschner 1996), while those of more derived species again secrete a citrus-smelling substance from their scoli or even, in the most highly developed forms, can squirt this from scoli reduced to cupolas (Nässig 1983, 1989, Nässig & Taschner 1996).

On the basis of the larva, thus, *Epiphora* seems more closely related to *Attacus* than to any other attacine genus. However, the fact that the same larval types occur in both these genera places some doubt on their surmised monophyly. More extensive knowledge and studies of the larvae of *Attacus* and particularly of *Epiphora* are required to assess this possibility. Nonetheless, the apparent affinity of *Epiphora* to the Asian *Attacus* (and possibly to the other Asian Attacini) is an interesting parallel to that of *Argema* to *Actias* and may have a similar evolutionary history. The occurrence of *Sinobirima* and probably also of *Salassa* in Asia further strengthens this apparent evolutionary-biogeographical connection between Africa and South-East Asia, and the proper understanding of this link may indeed turn out to be the key to the phylogeny and classification of the African Saturniidae.

Conclusion

Apart from clarifying the higher-level nomenclature of the African Saturniidae, this review highlights the major problems pertaining to resolving the phylogeny and classification of this fauna. In particular, it intends to stress the critical need to study features of the immature stages and to include these in proper phylogenetic analyses of characters and taxa. Such studies are also needed below the tribal level, as many genera are in dire need of proper delimitation, too. The huge and confused conglomerate called *Imbrasia* and its satellite taxa *Nudaurelia*, *Gonimbrasia*, *Bunaea*, *Cirina* and probably *Pseudimbrasia* spring to mind here foremost, and it seems likely that the taxonomy of this complex can only be resolved by means of preimaginal features and a careful analysis of many characters, including molecular ones.

This Inaugural Conference on African Lepidoptera provides a suitable forum for sketching these problems to the lepidopterological community of Africa, and it is sincerely hoped that all lepidopterists active in Africa can and will help to solve them. What is needed most of all is for lepidopterists to collect, rear and - most importantly - preserve saturniid larvae and pupae and make them available for scientific study. And those who actively study the African Saturniidae are likewise urged to concentrate on the immature stages by breeding these moths and gathering biological data on them, rather than merely engaging in descriptions of more and more new (and often very ill-defined) species.

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A CLASSIFICATION OF VISUAL-SIGNALS EMANATING FROM THE WINGS OF AFROTROPICAL LEPIDOPTERA

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Abstract: Adult Lepidoptera use four types of strategies as defense against predators: visual (morphological) signals, behavioral signals, acoustic signals and olfactory signals. This paper deals with the first of these, i.e. visual signals. A classification of similar visual signals emanating from adult Afrotropical Lepidoptera is presented. The classification is based on the perceived predator response to those signals. Visual signals are classified under three main categories: Those that trigger (1) an avoidance response, (2) a confusion response or (3) a distraction response in predators. This paper deals in detail with signals that trigger a predator avoidance response. The avoidance response can either be a response avoiding perceived danger or one avoiding perceived inedibility. The inedibility response can either be one of perceived physical inedibility or one of perceived chemical inedibility. Five major signals of chemical inedibility emanating from Afrotropical Lepidoptera are presented. The value of classifying these signals based on predator response is shown. It is shown that there probably is a predator-spectrum impacting on a species resulting in more than one signal emanating from one species. It is therefore vitally important to classify the signals and not the taxa that the signals emanate from.

Key words: Afrotropical Lepidoptera, Survival strategies, visual signals, mimicry, aposematic, Insectivorous Birds, crypsis, Predator distraction.

Introduction

All forms of life have, through natural selection, developed defense mechanisms that contribute to their survival. These mechanisms are commonly referred to as **survival strategies**.

The survival strategies of **adult Lepidoptera** that are in operation against **potential predators**, can be classified into four major categories:

- A. Survival strategies using visual (morphological) signals.
- B. Survival strategies through behaviour.
- C. Survival strategies using acoustic signals (see Dunning & Kruger, 1995).
- D. Survival strategies using olfactory signals.

(Many Lepidoptera are chemically unpalatable to predators but such chemical defenses can only work in conjunction with one of the above and can therefore not be included as a fifth category.)

This paper deals with the first of these categories i.e. morphological visual signals used by Lepidoptera against potential predators.

The phenomenon in which **unrelated** taxa are **morphologically similar** is widespread and well known.

The authors assume this phenomenon to be an indication that the common visual signal (the similarity) is a successful signal against predators and can thus be classified as a survival strategy. These signals are often dealt with in the literature under the concepts of mimicry, crypsis and aposematism. The authors reviewed a number of papers dealing with the above concepts: (Endler, 1981; Vane Wright, 1976, 1981; Turner, 1984; De Vries, 1987; Punnet, 1915; Rothschild, 1981; Nijhout, 1994; Scoble, 1992; Larsen, 1991; Sbordoni V. & Forestiera S., 1984; Nijhout & Wray, 1990; Millar, 1996; Pasteur, 1982; Wickler, 1965, 1968) and found contradicting definitions. Not one of the concepts was found to cover the whole spectrum of visual signals. It was found that in most of the literature reviewed the important role of the predator was neglected. In the absence of established paradigms, the authors decided it would be unwise to use any of these concepts as a basis for classifying visual signals, and thus embarked on a system based on predator response.

Although much has been written about "butterfly mimicry" (Wickler, 1968 cites 1500 papers written), very little has been done on the classification of the actual types of patterns (signals), especially for the Afrotropical region. Many examples of "mimicry complexes" have been illustrated in various publications (Punnet R. G., 1915; De Vries, 1987; Rutland D. B., 1991; Larsen, T. B., 1991; Sbordoni V. & Forestiera S., 1984; Dickson C.G.C. & Kroon D. M., 1978; Henning, 1993 etc.). The above papers, however do not attempt to classify similar signals but rather only show some examples of similar taxa. Henning, 1993, proposed a group of "mimicry rings" to classify similarities in Acraeinae (Nymphalidae) the Acraeinae of the Afrotropical region. In the majority of cases the above examples are restricted to the superfamily Papilionoidea, neglecting members of the illustrated "mimicry-complex" that belong to other Lepidoptera superfamilies and taxa belonging to other orders. One exception is Punnet R. G., 1915 who also shows Lepidoptera other than Papilionoidea.

In this paper the authors include signals emanating from all Lepidoptera but have not included those emanating from non Lepidoptera taxa. The second restriction in this paper is that only signals emanating from Lepidoptera occurring in the Afrotropical region are used in the classification. The authors accept that these restrictions are less than ideal and aim to lift these in the ongoing study.

Many species of Lepidoptera clearly display more than one signal. A common example is an aposematic signal on the upperside of the wings and a cryptic signal on the underside. The reason for this is probably because the potential predators, when the individual is in flight, differ from the potential predators, when it is at rest. The authors call this the predator-spectrum impacting on a species.

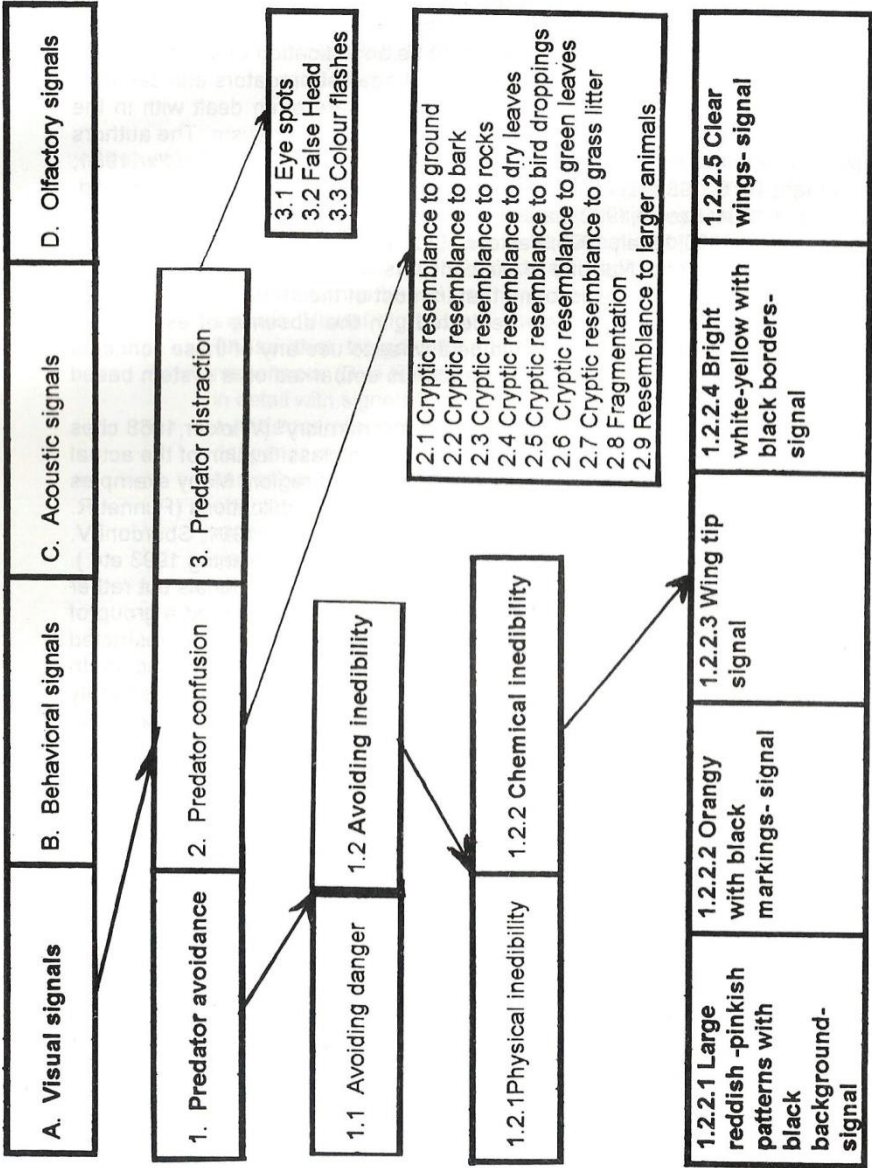


Fig. 1 An overview of a classification of visual signals emanating from Afrotropical Lepidoptera.

These different predators probably respond to different signals. It is therefore vital to classify the actual signals rather than the species that display these signals (see fig.2).

What follows is an attempt to create a suitable classification system that will seek to classify similar visual signals emanating from adult Lepidoptera, using the perceived predator response to those signals as a basis for the classification.

RESULTS

A classification of visual signals emanating from Afrotropical Lepidoptera

Fig. 1 gives an overview of the classification and should be referred to throughout the results section. The group names that are bolded in figure 1 show those signals that the authors dealt with in more detail, in this paper, and does not signify importance.

Three main types of visual signals are identified:

1. Signals that trigger **predator avoidance**;
2. Signals that trigger **predator confusion**;
3. Signals that trigger **predator distraction**.

1. **Predator avoidance**

Signals classified here are those signals that trigger an avoidance response in predators that have already recognized the lepidopteran emitting the signal as potential prey. The concepts of “butterfly mimicry” and “aposematism” were formed as a result of the existence of these signals and the resulting predator prey interaction.

Signals classified here are unique in that they can only trigger the required response in predators that have the ability of discretion (either learned or innate). In this group species that emit the signal are identified as potential prey by the predator but are not taken because the signal triggers an avoidance response in the predator. Evidence suggests that Reptiles, Amphibians and Arthropods do not have this ability of discretion (Punnet, 1915; Evens and Schmidt, 1990; De Vries, 1987; Larsen, 1992a; Staude, unpublished) but that Avians and Mammals do (Punnet, 1915; De Vries, 1987; Rutland, 1991; Larsen, 1991). If this proves to be the case then the number of potential predators that entrench these signals is limited to these two classes.

Predator avoidance is broken into two main sections of which the second is the largest and probably the most written about in Butterfly publications:

- 1.1 Predator avoiding a signal of danger;
- 1.2 Predator avoiding a signal of inedibility.

1.1 **Predator avoiding a signal of danger.**

Signals classified here are those that warn the predator of imminent danger. Examples are many Ctenuchidae and Sessidae that resemble stinging Hymenoptera. There are no true signals emanating from Lepidoptera here, only false signals (mimics). This has been well documented in the literature (Pinhey, 1975; Sbordoni & Forestiera, 1984)

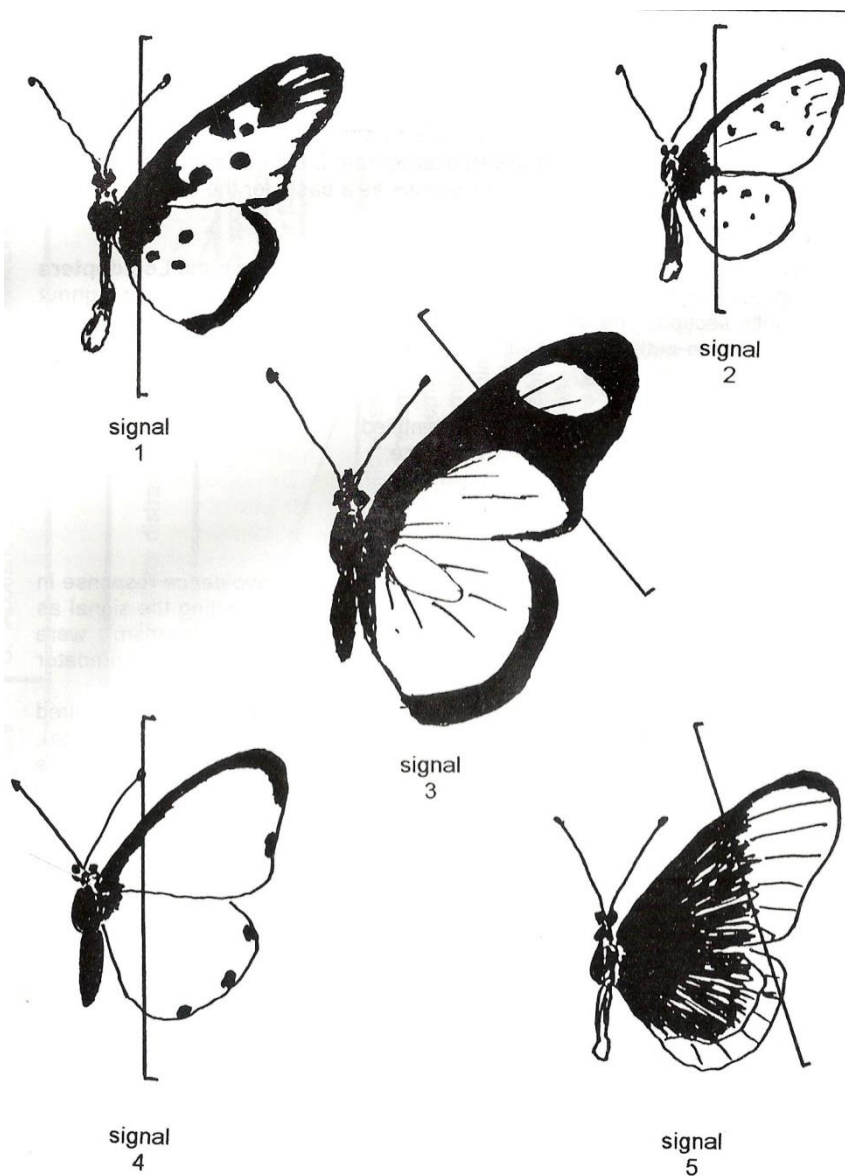


Fig. 2. Five main chemical avoidance signals emanating from Afrotropical Lepidoptera.

1.2 Predator avoiding a signal of inedibility

Signals classified here are again broken up into two main groups:

- 1.2.1 signals of physical inedibility;
- 1.2.2 signals of chemical inedibility.

1.2.1 Signals of physical inedibility

These signals trigger an avoidance response because the predator regards the signal to mean that the potential prey is too physically daunting to eat. Here the signal may also be used by mimics. Henning, S. F., 1989 identified some smaller(edible) *Charaxes* sp. closely resembling larger robust (inedible) species.

1.2.2 Signals of chemical inedibility

This, is the largest group for classification, includes the theories of Batesian, Mullerian and Automimicry as Lepidopterists know them. Five main groups of signals, identified on the wings of Afrotropical Lepidoptera, are classified here (fig.2):

- 1.2.2.1 Large reddish or pinkish patterns on black background;
- 1.2.2.2 Orangy with black markings;
- 1.2.2.3 Light spots or band towards the apex of the forewing on a dark background;
- 1.2.2.4 Bright white or bright yellow background with black borders (solid or dotted);
- 1.2.2.3 Clear wings.

1.2.2.1 Large reddish or pinkish patterns on black background

These signals are confined to Lepidoptera occurring in mainly forest or thick bush localities and in south western desert areas. It is well represented in the Central African Forest Block but there are examples North and South in suitable areas. Three distinct signals can be identified here:

- reddish signals;
- pinkish signals;
- reddish to orangy signals.

reddish signals (fig.3)

The many large red *Acraea* sp. are emitting this signal in this group. Within this group, one also finds *Papilio antimacus*, *Graphium ridleyanus* and *Pseudacrea boisduvali*. These signals are emitted by Lepidoptera occurring in forest areas. There are probably a number of subgroups, which further research will clarify.

pinkish signals (fig.4)

Here one finds the unusual group which one might define as “the desert group” . Lepidoptera that emit this signal occur widely in the arid south western areas of the continent. The question here, is why they are all pinkish and black and why they are

of similar medium to large in size. The authors suggest that while they don't fly together in the concept of older mimicry theories, they do fly within one biome or clearly identifiable veld type. The suggestion here is that far ranging predators will associate the aposematic colours and size with unpalatable species. Another point of significance is that there are few apparent, if any, mimics within the group.

reddish to orangy signals (fig5)

This signal is found in areas that are well wooded but that are not wet tropical forests. The pattern is the same as in the above signals but the colour has changed to become more orangy. Perhaps this signal is changing to conform with the next signal group as the habitat is becoming drier and more seasonal.

1.2.2.2 Orangy with black markings (fig.6)

Species emitting this signal are normally associated with grasslands, high mountain meadows, wetlands, savanna and partially wooded areas. The question that confronted the authors was what was the connecting link between all these different species ranging in these specific biomes across the Afrotropical region and beyond. Clearly not all the species within this wide group fly together, yet they all emit the same aposematic signal. The authors concluded that there must be a common predator or predator spectrum, which ranges over the same areas, that responds to this signal.

The first connecting link that the authors propose lies in the biomes in which the species that emit this signal occur. The one thing that African grasslands, high mountain meadows, savanna and dry woodland areas all have in common is that they experience distinct seasons associated with high or low densities of insects. If one would examine the abundance of resident insectivorous predators in these areas it is logical to accept that their sustainable numbers are restricted to the available food supply at its lowest level. It follows that in times of seasonal abundance there would be far more food supply than what the resident predators could consume. It is this phenomenon that is probably the main reason for the occurrence of migratory insectivorous predators. These migrants exploit this seasonal abundance of free available food. The authors suspect that these predators are responsible for the entrenchment of this signal.

The migratory routes of Afrotropical birds was investigated (Elpich, 1985, Newman, 1996, Turpie, 1996, Turpie, *pers. comm.*).

It was found that the distributions of many intercontinental birds correlate with the biomes of seasonal abundance and thus with the distribution of the Lepidoptera that emit this "orange with black markings" aposematic signal. The next step would be to investigate what specifically birds feeding on nocturnal Lepidoptera have been observed by the authors and others (Duke, N. J., *pers. comm.*, Joannou, J., *pers. comm.*) very few instances of diurnal Lepidoptera being taken are known to the authors in spite lengthy searches (only Larsen, 1992b, Henning, G. A., *pers. comm.*, Joannou, *pers. comm.*).

During several days of observing these birds in the alpine grasslands (above

3000m) of Lesotho in January 1997, H. S. Staude could not observe a single instance of any of the birds present taking diurnal Lepidoptera, in spite of an abundance of both birds and Lepidoptera present. The birds were taking mostly clear-winged Odonata. Clearly there is much more research to be done on this subject. The authors conclude that the fact that this signal occurs so widely in areas of seasonal abundance and is virtually absent in the stable forest biome is probably due to the impact of migratory predators that range over the same areas and regard this signal as one of unpalatability.

Although the 'orangy with black markings signal' is striking, the colour tone and the extent of the black markings varies considerably between species emitting this signal. Not only over the vast range of occurrence but also between species that occur together. This is usually not the case in signals emitted by Lepidoptera that occur in stable forest biomes where there is very little variance within signals. The authors suspect that the reason for this is that migratory predators are in an area for only a short while at a time of seasonal abundance. As a result of the abundant food supply they have no need to take risks and will therefore respond to even the weakest aposematic signal. On the other hand the local resident predators in a stable biome need to maximize their food supply because of maximum competition and have more time to adjust to their environment. These predators are constantly attempting to remove false signals (the Batesian mimics) resulting in little variance in signals.

From the above one could assume that these areas of seasonal abundance would be ideal for the development of Batesian mimics. There is some evidence that this is the case. Many Lycaenid butterflies (*Aloeides*, *Chrysoritis*, *Axiocerses* etc.) as well as nymphaline butterflies (*Junonia*, *Precis* etc.) and others that are normally regarded as being palatable display this signal, often on the forewings with a cryptic signal on the hindwings. The authors suspect that these are Batesian mimics that are successful against migratory predators. Some *Precis* spp. (*P. octavia*, *P. archesia*) emit this signal from their summer not from their winter forms when the predators have gone. Another possible example is the European Map butterfly, which emits this signal in its early season brood when the African migrants are there but lacks the signal in its late season brood when the African migrants have gone.

In the Lesotho Alpine biome a geometrid moth occurs that seems to be in the process of becoming diurnal. The moth (*Biclavigera uloprora*), which flies freely by day as well as at night, clearly emits this signal on its very common form (A very rare brown form that does not emit the signal still exists). All the other known species of *Biclavigera* are cryptic and are only nocturnal (fig.7). One would assume that the moth is unpalatable and that it is therefore developing the aposematic signal. Observation by M. Kruger (unpublished) however contradicts this assumption. He fed large numbers of dead *B. uloprora* together with other cryptically marked moths to domestic chickens at Oxbow Lodge, Lesotho. The chickens consumed all the moths including the *B. uloprora* without suffering any ill effects. The host plant of the larva of *B. uloprora* is unknown. In this alpine biome there is no model signal for any possible resident predator to learn from, in order to entrench the signal in *B. uloprora*. We have

here a case of a seemingly palatable diurnal lepidopteran that emits a wide ranging aposematic signal, which does not occur otherwise within its range. The only conclusion that the authors could make is that, as above, this signal is developing in *B. uloprora* as a result of an avoidance response by migratory birds.

In the dry Karroo areas of South Africa we have exactly the same thing happening as in the case of *B. uloprora*. Here the geometrid *Isturgia focalaria* became diurnal, and it emits the same aposematic signal of this group in the absence of a model. Yet its close relative *Isturgia inconspicua* is cryptic and nocturnal. M. Kruger (*pers. comm.*) regards these species as closely related in his as yet unpublished revision of the tribe (see fig. 7).

1.2.2.3 The wing-tip signal (figs. 8-18)

Light spots or a band are found towards the apex of the forewing on a dark background.

This is perhaps the largest group and very diverse linked by one common denominator. Generally, the background colour of this group is dark to black. The "apex" spots or band range in colour from white to yellow to orange to red to brown.

It is not yet clear if this colour spectrum is of significance except to say that the spots or bands are "flashed" to the world at the end of each clap or fling process of flight. Even in species that tend to glide the outer wing extremities tend to "flick" at intervals. This exposes a predator to a "neon" light effect. The colour spectrum is of interest and this requires significantly more study from the predator view point. (It is known that birds have a far more detailed spectrum of colour visibility than do humans. See Finger & Birkhart, 1993) Although the authors have no idea which predators respond to this signal, its occurrence on the wing tips of so many unrelated aposematic Lepidoptera indicates that it is a significant aposematic signal. This is particularly evident when diurnal moths are examined: In many diurnal geometrids that occur in tropical rain forests (*Pithecia* spp., *Mimaletis* spp., *Cartaletis* spp., *Geodina* spp. etc.), this wing tip signal is present always in conjunction with the local aposematic signal of the area in which the species occurs. Yet this pattern is entirely absent from geometrids that have remained cryptic and nocturnal. This same signal also developed in noctuids, agaristids, arctiids etc., whenever members of these families became diurnal. A number of local groups that carry this signal can be identified. The existence of these local groups, with each their own signal in addition to the main signal, is probably as a result of the impact of the local component of the predator spectrum. Figures 8-10 show examples of species emitting a strong wing-tip signal. Figures 11-18 show examples of species that emit local signals in addition to the wing-tip signal. There seems to be numerous local signals here and only the more spectacular signals are given in this paper:

The *Danaus chrysippus* signal (fig. 8) Some of the species shown are probably more closely related than others. The Danaidae and the Acraeinae in the group would

claim to be models. The Nymphalinae and Papilionidae have been described as mimics.

Perhaps a more detailed study of Afrotropical plants is required. Class I and Class II chemicals have an important influence on the palatability spectrum (see Turner, 1984). This is not the time or the place to pursue these aspects in depth and, further, much more information needs to be gathered before significant conclusions can be made. However, certain facts have come to light. Plants belonging to the family Asteraceae, are known to contain unpalatable chemicals. Ivan Bampton (*pers. comm.*) confirms that *Hypolimnys missipus* larvae, apart from other plants, can feed on *Ageratum haustonianum* - (Asteraceae). Does this mean that *H. missipus* is an aposematic species in its own right?

The black and white *Amauris* signal (fig. 9) The Danaidae, *Bematistes* and Agaristidae are probably the models while the other Nymphalidae and the Papilionidae have been described as Batesian mimics.

Plants belonging to the Sapotaceae are commonly known as the "Milk berry" plants and a number of them, specifically those used by *Pseudacraea* sp., have a milky latex in their leaves. It would be of considerable interest to see if these plants carry unpalatable chemicals.

The black/yellow *Amauris* signal (fig. 10). The Danaidae, *Bematistes* and Agaristidae are the models while the other Nymphalidae and Papilionidae are the supposed mimics.

The signal is found in more tropical than sub-tropical areas and a number of local signals have developed within the main signal. Some of the more interesting local signals are discussed here:

The *Charaxes lydiae* signal (fig. 11). This signal has captured the attention of one of the authors. The lymantriid moth - *Otroede plavax* and the agaristid moth - *Heraclia terminalis* presumably act as the models with *Cymothoe becheri* and *Charaxes lydiae* the supposed mimics. In South Africa, *Cymothoe alcimeda* feeds on *Kiggelaria africana* (Flacourtiaceae) the same plant as the unpalatable *Acraea horta*. Other *Cymothoe* species from Central Africa tend to send aposematic signals and the reason for this is not clear. The other *Cymothoe* spp. in South Africa - *Cymothoe coranus* feeds on *Rawsonia lucida* (Flacourtiaceae) along with the species *Hyalites cerasa* - a model for other species.

There are other *Cymothoe* spp. further north. Red males, as in the Kenyan *C. hoberti hoberti*. Is this signal sexual or aposematic? Females of some *Cymothoe* have the aposematic colours of black, red and yellow. Perhaps the colours are in reverse when compared to the *Agaristids*.

The *Euphraedra zaddachi* signal (fig. 12). Theoretically, species belonging to the families Agaristidae and Hypsididae are the models while the *Euphraedra* spp. - *Euphraedra zaddachi* and *Euphraedra eusemoides imitans* are the mimics. Can it be assumed that the food plant here is not poisonous?

The *Charaxes fournierae* signal (fig. 13). Here, the agaristids and the *Bematistes* spp. act as the models while the *Charaxes*, *Euphraedra* and the satyrines are the mimics. We had some difficulty in interpreting the signal until it was pointed out by S. C. Collins (*pers. comm.*) that these particular species of *Euphraedra* tend to fly higher above the ground than most. It was also discovered that at least some species of agaristids feed, as larva, on *Cissus* spp. (Wild grape). As Wild grape is a climber, there appears to be a link between species flying lower and higher in the forest.

The *Aletis* signal (fig. 14). Species belonging to Arctiidae, Agaristidae, Geometridae and Lymantriidae would seem to be the models. The *Euphraedra ruspina* (Nymphalidae) would seem to be a mimic.

The *Neptis* signal (fig. 15). Species belonging to Arctiidae, Agaristidae, and Geometridae would seem to be the models. The nymphalids may be mimics. However, *Neptis* sp. are of interest in that they use plants belonging to the Euphorbiaceae and Sapindaceae as larval food plants.

The white, black and blue signal (fig. 16). This signal is unique in that no butterfly emits it. It roughly follows the previous group yet the blue colouring is unusual in Afrotropical species. The *Pitthea* spp. emitting this signal are the only Afrotropical Geometridae that have a metallic blue colour on the wings. *Cyanocratis grandis* (Xyloryctidae), which flies with the *Pitthea* spp. and emits the same signal is not only the only member of the family to have a metallic blue colour on the wings but it is also a unique giant of the family. It is more than double the size of any other member of the family (in order to be of similar size to the *Pitthea* and agaristid species emitting the same signal). It is also the only diurnal member of the family. The diurnal agaristids in the area also emit the same metallic blue signal. This is a truly remarkable signal restricted to the central African forest block. It is unlikely that there are false signals (mimics) amongst this group.

The *Bematistes* signals (fig. 17). Several signals can be identified. Some species emit only the main wing-tip signal, but others also emit a local signal in addition to the main signal and are classified here:

One signal is emitted by *Bematistes poggei*, the model, with *Pseudacrea* spp., some Papilionidae and *Mimicacraea* spp. as the mimics;

Another *Bematistes* signal has the colour pattern more uniformly black and brown like *B. tellus*.

More work needs to be done here and a number of signals will still be classified here.

The *Pseudaleatis/Carteletis* signal (fig.18). A number of small species belonging to Geometridae and Lycaenidae, which seem to be restricted to high up in the tree canopy of tropical African forests, emit this signal.

1.2.2.4 **Bright white or bright yellow background with black borders (solid or dotted)**

This signal has a background of white or yellow. This signal emanates from many species belonging to the family Pieridae although a number of other species also emit this signal. Again a number of local signals can be identified.

The *Mylothris* signal (fig. 19). It has been suggested by Larsen, 1991, that the Pierids include “striking examples of mimicry in Kenyan butterflies.” The extent of palatability versus unpalatability amongst Pieridae has yet to be ascertained.

The *Catopsilia* signal (fig.20). This signal is similar to the last. At first glance, perhaps they are all palatable? Is there another protective function in force - i.e. large confusing numbers?

The forest whites signal (fig. 21). A small group of lepidoptera, which fly conspicuously around forests, emit this signal.

The forest yellows signal (fig 22). Another small group of lepidoptera, which fly conspicuously around forests closer to the ground, emit this signal.

1.2.2.5 **Clear wings (fig. 23)**

This is one of the groups proposed by Henning, 1993. The signal occurs widely in several species of clear wing moths. These *Lepidoptera* are found largely in forests, riverine bush or areas of thick bush. The significance of clear wings is not apparent. One assumes that *Acraea* sp. are chemically unpalatable and that the group therefore displays the Aposematic colours of unpalatability.

Clear wings are said to be used elsewhere in the world by *Lepidoptera* [in the Neotropics, the *Danaidae* *Ituna ilione* and *Ithomiidae*, *Methona confusa* (De Vries, 1987)] as an aposematic signal. Why clear wings are only partially clear in Afrotropical species and are blended with other Aposematic colours may represent a multi-functional approach to warnings. The colours warn certain species while the clear outer wings resemble certain species of Hymenoptera. (This was demonstrated for the author A I Curle at Eshowe where *Hyalites cerasa* were flying amongst a large number of orange/brown wasps.) This would infer a signal of physical inedibility and would place this group under that heading.

Finally, some of the clear wings through transparency or reflection (much like glass) may act as a distraction to predators. Further, transparency may act to “display” through the wings other general forest colours such as green and brown. (This may not be true for all predators as in grassland areas, author H. Staude has observed clearwinged Odonata (Dragonflies and Damselflies) being taken by birds

without hesitation.) This would support the suggestion that predators will behave differently in different environments. Also different predators may be present in different environments. In conclusion the authors are not sure if this signal belongs here at all as far as Afrotropical Lepidoptera are concerned, but provisionally place it here because it is regarded as an aposematic signal in the literature.

Some avoidance signals that need further study (fig. 24)

Danaus chrysippus, form with the white hindwing - In West Africa this form becomes prevalent. One wonders why. Perhaps the white and black signal is very strong in this area and that this signal has developed in addition to the wing-tip signal.

Egybolis vaillantina. The authors are not aware that this is unpalatable, yet this diurnal moth belongs to a predominantly nocturnal family (Noctuidae) and does not emit a signal that is similar to any known aposematic signal in the biome in which it flies. It seems similar to some stinging *Hymenoptera* and the signal may well be a signal of danger.

Eligma laetipocita. Pinhey, 1975, wrote that it is a "diurnal forest flier like *Agaristid* moths". Yet it belongs to the Noctuidae. The question arises as to why it should it turn brightly coloured and diurnal but emit a signal that does not match any of the known aposematic signals?

Amauris nossima. This butterfly is almost white. It seems to be losing most of the typical black pattern that typifies the *Amauris* signal. The species occurs on an island where the typical *Amauris* signal is absent. Perhaps its signal is being changed by Island predators to become more like the bright white pierid signal, which the predators may be more familiar with?

In the predator avoidance group, there are a number of spectacular examples, where virtually the same signal is emitted by many unrelated lepidoptera that live within the range of common predators. One possible reason for this is that there is a mutualistic predator/prey relationship in place. The prey benefits from the avoidance response because it is not eaten and the predator benefits because it does not have an unpleasant experience. The problem for the predator is that false signals limit its potential food supply. The resultant 'abundance of food supply versus unpleasant experience interaction' probably is the cause of the observed closer similarity of signals in areas of scarce food supply than the similarity of signals in areas of abundant food supply.



Papilio antimachus Drury



Graphium ridelyanus White



Acraea oscar Rothschild



Acraea egea Cramer



Psudacraea clarkii Butler & Rothschild
Fig. 3. Red with black dots. (Forest block)



Psudacraea dolmena Hewitson



Acraea acara acara Hewitson
Fig. 4. red and Orange with Black Dots. (Savanah)



Psudacraea boisduvalii trimeni Butler



Acraea acara melanophanes Le Cerf *Acraea hypoleuca* Trimen *Eochroa trimeni* Felder
Fig. 5. Orange and/or Pink with Black Dots/Marks. (Desert)



Alena amazoula amazoula Boisduval *Hyalites rahira rahira* Boisduval
Petovia dichroaria Herrick - Schaffer



Hyalites anacreon Trimen

Acraea nohara Boisduval

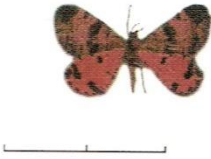


Acraea violarum Boisduval

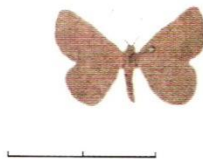
Veniliodes inflammata Warren



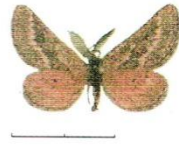
Zerenopsis leopardina Felder *Pardopsis punctatissima* Boisduval *Paidia pulchra* Trimen
Fig. 6. Yellow/Orange to Pink Black Markings. (Small)



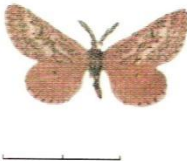
Isurgaria focularia



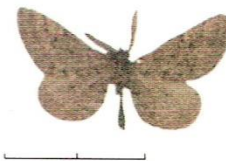
Isurgaria inconspicua



Biclavigera uloprora (common form)



Biclavigera uloprora (rare form)
Fig. 7. Day/Night Moths.



Biclavigera fontis



Biclavigera praeanaria



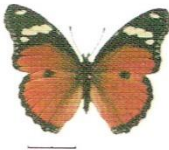
Danaus chrysippus aegyptus Schreber



Hyalites encendon encendon Linnaeus



Hypolimnas misippus Linnaeus



Pseudacraea poggei Dewitz

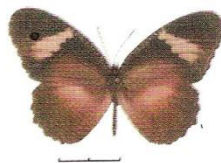


Euphaedra eleus Drury



Papilio dardanus cenea ♀ f. *aikenii* van Son

Fig. 8. *Danaus Chrysippus* signal

*Bematistes macaria hemileuca* Jordan*Amauris niavius dominicanus* Trimen*Pseudacraea eurytus imitator* Trimen*Hypolimnias anthedon wahlbergi* Wallengren*Papilio dardanus cenea* ♀ f. *hippococonides* Haase*Heraclia hornimani* ♀ DruceFig. 9. *Amauris* signal - Black and White.*Amauris echeria echeria* Stoll*Hypolimnias anthedon wahlbergi* f. *mima* Trimen
Bematistes aganice aganice Hewitson*Heraclia nandi* Kiriakolf*Papilio dardanus cenea* f. *cenea* Stoll*Elymnias bammakoo* WestwoodFig. 10. *Amauris* signal - Black and Yellow



Charaxes lydiae Holland



Otroede plavax Holland



Cymothoe beckeri Herrick - Schaeffer
Fig. 11. *Charaxes Lydiae* signal.



Heraclia medeba Druce



Euphaedra zaddachii Dewitz



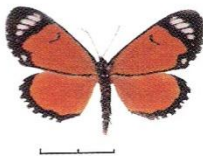
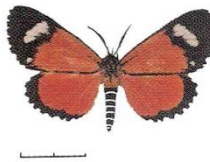
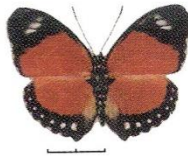
Euphaedra eusenoides Grose-Smith & Kirby



Heraclia superba Butler
Fig. 12. *Euphaedra zaddachii* signal.



Phaegorista formosa Butler

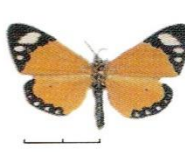
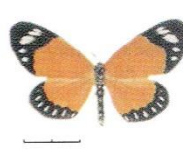
*Charaxes fournierae kigeziensis* Howarth*Euphaedra adonina* Hewitson*Hyalites alciope* Hewitson*Bernatistes tellus tellus* Aurivillius*Elymnias bammakoo* Westwood*Heraclia karschi* HollandFig. 13 *Charaxes fournierae* signal*Aletis helsita* Prout*Heraclia poggei* Dewitz*Phaegorista similis* Walker*Eohemera fulleri* Druce*Oetroeda* app. (similar to *O. papilionaris* Ford)*Euphaedra ruspina* hewitsonFig. 14. *Aletis* signal

*Neptis laeta* Overlaet*Neptidopsis ophione ophione* Cramer*Pseudathyma neptidina neptidina* Karsch*Pitthea fumula* Drury*Nyctemera leuconoë* Hopffer*Hespagarista caudata eburnea* Jordan

Fig. 15. *Neptis* signal (smaller black and white).

*Cyanocratis grandis* Druce*Massaga maritona* Butler*Pitthea* Species (unidentified).*Syringura pulchra* Butler

Fig. 16. Black White and Blue signal

*Bematistes poggei* Dewitz*Pseudacraea kuenowii* Dewitz*Bematistes consangiunea* AürivilliusFig. 17. *Bematistes* signal.*Pseudacraea kuenowii* Dewitz*Pseudaletis agrippina* Druce*Telipna hollandi* Joicey & Talbot*Mimaletis paucialbata* Prout*Carteletis forbeci* DruceFig. 18. *Pseudaletis* signal.*Mylothris agathina* Cramer*Belenois thyrsa* Hopffer*Appias sabina* Felder & FelderFig. 19. *Mylothris* signal.*Pseudaphelia apollinaris* Boisduval



Catopsilia florella Fabricius *Belenois rubrosignata* Weymer *Charaxes subornatus* Schultze
Fig. 20. *Catopsilia* signal



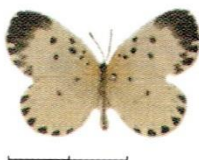
Larinopoda tera Hewitson

Leptosia alcesta Stoll



Marblepsis melanocraspis Hampson
Fig. 21. Forest Whites.

Dissoprumna plenifascia Rbl.



Pentila abraxas maculata Kirby
Fig. 22. Forest Pale Yellows.

Northecusa tenuiorata f. *lutei* Prout



Acraea satis Ward ♂



Acraea satis Ward ♀



Acraea igati Boisduval



Acraea leucographa Ribber
Fig. 23. Clear Wings.



Hyalitis semivitrea Aurivillius



Hyalitis igola Trimen



Danaus chrysippus aegyptius Schreber



Amauris nossima Ward



Egybolis vaillantina Stoll
Fig. 24. Special cases.



Eligma laetipicta Oberthür

2 Predator confusion

Signals classified here are those that confuse a potential predator's search image for prey. The predator therefore does not identify the individual displaying the signal as potential prey. Most of these signals are commonly known as crypsis. Many species of Lepidoptera from most superfamilies display this signal on those wing surfaces that are exposed when the individuals are at rest. Many species that display aposematic signals when in flight display these signals when at rest (e.g. Papilionoidea- *Chrysoritis* sp., *Aloeides* sp., many Pieridae & Nymphalidae; Noctuoidea- *Othreis* sp., *Hypocala* sp., *Paratuerta* sp., Notodontoidea- *Catochria* sp., Sphingidae- *Hippotion* sp. etc.). The authors believe that the reason for this double signal is that the predators, which the species are exposed to when in flight, are higher animals that have the ability to respond positively to aposematic signals (e.g. birds), whereas many of the predators, which the species are exposed to when at rest, are lower animals that have not developed the ability to respond positively to aposematic signals (e.g. lizards, frogs, mantis etc.). [Larsen, 1992, found that a chameleon only temporarily learned to avoid an aposematic signal. H. S. Staude observed geckoes and frogs repeatedly taking and then discarding aposematic Arctiidae.]

Eight groups are identified in Afrotropical Lepidoptera (space constraints allow that only the lesser known signals are described):

2.1 Cryptic resemblance to ground

2.2 Cryptic resemblance to bark

2.3 Cryptic resemblance to rocks

2.4 Cryptic resemblance to dry leaves

2.5 Cryptic resemblance to "bird droppings"

Many moths (eg. *Somatina* spp., *Scopula* spp., Geometridae; *Cradiosace* spp., Noctuidae, etc.) resemble bird droppings and are often found on the upper leaf-surface of plants when at rest.

2.6 Cryptic resemblance to green leaves

2.7 Cryptic resemblance to grass litter

2.8 Fragmentation- break up of outline in confusing patterns

Signals belonging here are signals that do not resemble any specific object or form. The patterns break up the outline of the individual thus confusing the predators search image and the individual displaying the signal escapes detection.

2.9 Resemblance to larger inedible animals

Signals belonging here are signals that are commonly found in Geometridae

and Noctuidae. Species that emit this signal usually have enlarged discal cell spots, they rest with their wings flat on the surface, the pattern on the wing surfaces that are thus exposed are arranged in such a way that the whole signal is that of the head of a much larger animal that is deemed to be inedible to the predator receiving the signal.

3. Predator distraction

Signals classified here are those that sufficiently distract the predator to facilitate escape for the individual displaying the signal. In other words, predators identify their potential prey but are sufficiently distracted by these signals that they fail to capture their prey. For the most part these signals are well known and often reported in the literature. It is interesting to note that, here too, unrelated species emit similar signals. The possibility of common predators would be worth investigating. Three groups are identified in Afrotropical Lepidoptera:

3.1 Eyespots

Many species have eyespots towards the apex of their wings (e.g. Satyrinae and Nymphalinae) that distract the predator away from the body. These signals often result in the predator only taking a part of the wing allowing the individual to escape relatively unharmed.

3.2 False Head

Converging lines on the wings to a false head with the tails acting as antennae, emit a signal that distracts the predator away from the actual body. The wings move to draw attention to the false head causing the predator to attack the wrong "head". This signal again results in the predator only taking a part of the wing allowing the individual to escape relatively unharmed. This signal is emitted by many Lycaenidae.

3.3 Colour flashes

In most cases a brightly coloured area, on that part of the wings which is concealed when the species is at rest, is the signal. The signal is suddenly revealed when the lepidopteran is approached by a potential predator, thus distracting the predator and allowing it to escape. This signal is used by many Saturniidae and Noctuidae as well as some Lycaenidae.

Conclusion

The study, so far, has made it clear to the authors that a classification system of visual survival signals, which is not phylogenetically restricted and is predator based, is an essential prerequisite for the understanding of these strategies. It is believed that the system proposed here fulfills this need.

The study of survival strategies really is a study of predator/ prey interaction. Very little empirical evidence is available on this interaction and field observations between adult Lepidoptera and their predators is dearly needed. In the absence of such observations we are left with the assumption that morphological similarities

observed in unrelated taxa is evidence that these similarities are survival signals. In this paper we aimed to separate the signals from the taxa that emit them and to classify these signals based on the perceived predator response to those signals. The next step is to study the distribution of the signals and compare these distributions with the distributions of possible predators. One can narrow down the field of potential predators where these distributions match. This would then help to focus a study of predator/prey interaction. It is such an exercise that has led the authors to believe that migratory birds are responsible for the wide ranging orangy/black aposematic signal of seasonal habitats.

This study is far from complete, only a small start has been made, but the authors believe that this paper lays the foundation for the study of survival strategies. As we accumulate more knowledge on the subject the groupings proposed here will be challenged and changed and in the standing the intricate predator/prey interactions at play here.

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AN OVERVIEW OF THE DISTRIBUTION PATTERNS OF AFROTROPICAL RAINFOREST BUTTERFLIES (LEPIDOPTERA: RHOPALOCERA)

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Introduction

The present distribution of Afrotropical rainforest butterflies represents a snapshot of a long, complex, dynamic evolutionary process. At various times during the Miocene, Pliocene, and Pleistocene the rainforest contracted dramatically, usually to the same refuge areas on each occasion. One of the strongest such contractions was as recently as the late Pleistocene (15,000 - 20,000 years ago).

It has been suggested that much of Afrotropical speciation took place during these contractions, and that is doubtless correct. For long periods the rainforest was divided into discrete blocks. However, suggestions that much of the speciation is very recent (late Pleistocene) seem unlikely - there has not been time enough, and differences between various areas of the rainforest zone would have been larger than they actually are (there is, for instance, very little endemism at genus level, and that not in typical forest butterflies).

Table 1 summarizes the main regions of the rainforest, the major refuges within each region, and some of the sub-refuges (mainly mountainous regions, though not necessarily montane). The numbers in brackets refer to the number of species present, including open habitat species that colonize the forest zone. In the limited space allowed, I shall try to summarize the special characteristics of the main refuges, and list some of the special faunal elements.

Western West Africa Region

The forest zone of western West Africa stretches from the level of Guinea to Ghana, and is now separated from the rest of the forest zone by the Dahomey Gap, a wedge of savannah through Togo and Benin, taking in also the Accra Plains in Ghana. The forests in the mountains straddling the border between Ghana and Togo are somewhat species-poor, and will be discussed later. Small patches of impoverished forest are found as far west as the Basse Casamance in Senegal. Of the 950 species present, some 120 are endemic to the Region; of these, about half are found in both Sub-regions, while about 30 are endemic to each Sub-region.

At various points in time, the forests of western West Africa have been isolated into two main refuges - the Liberian Sub-Region and the Ghana Sub-region, each currently containing about 850 forest butterflies.

The genus *Cymothoe* shows these differences well. Thus *C. adela* Staudinger, 1889 is found in Sierra Leone (and almost certainly Liberia), while *C. aubergeri* Plantrou, 1977 replaces it in western Côte d'Ivoire and Ghana. *C. hartigi* Belcastro, 1990 from Liberia and Sierra Leone is closely related to the equatorial *C. anitorgis* Hewitson, 1874, but this group has no representative in the Ghana sub-Region. The otherwise widespread *C. coccinata* Hewitson, 1874 is only found in the Ghana Sub-region, while the very similar endemic West African *C. mabillei* Overlaet, 1944 is found in both Sub-regions.

There are two sub-refuges in the Liberia Sub-region. The Loma mountains in central Sierra Leone rise to more than 2,000 metres and have a belt of isolated forest. *Euriphene lomaensis* Belcastro, 1986 is an amazing endemic of this mountain, pertaining to a species-group that is not represented elsewhere in the Region. A detailed investigation of this mountain is the most urgent research need in West Africa.

The Nimba Mountains on the border between Liberia, Guinea, and Côte d'Ivoire have also had some independent evolutionary history. The population of *Vanessula milca angustifascia* Joicey & Talbot, 1928 is remarkably different from that of *Vanessula milca milca* Hewitson, 1873 which is found sporadically throughout the Region. Here is also the only population of *Melanitis ansorgei* Rothschild, 1904, which only recurs in Cameroun.

There is a single sub-refuge in the Ghana sub-region. This is the Atewa Range near Kibi, a mountain ridge that rises to 850 metres. The very distinctive *Mylothris atewa* Berger, 1974 is endemic to the area and it holds the only West African population of *Acraea kraka* Aurivillius, 1893 (ssp. *kibi* Usher, 1986 is hardly distinct from the nominate subspecies which recurs in Cameroun. Almost 600 species have been collected on the Atewa Range.

The Nigerian mix-zone

The area between the Volta River in Ghana and eastern Nigeria appears to have been subjected to a significant amount of climatic buffeting. What is now the Dahomey Gap must at times have covered almost the entire area, while at other times having allowed the unimpeded passage of forest species. However, two sub-refuges for the forest fauna are identifiable.

The Volta Mountains lie as a forested island in the Dahomey Gap and have a surprising degree of endemism. Among such endemics are *Papilio nobicea* Suffert, 1904 (= *maesseni* Berger), *Telipna maesseni* Stempffer, 1970, *Iolaus kyabobo** Larsen, 1996, and *Junonia hadrope** Doubleday, 1847 (* very distinct from any other species). Also present in the area are isolated populations of species found in Nigeria, but which do not cross the Volta River into the Western West Africa Region proper (e.g. *Larinopoda aspidos* Druce, 1890 and *Euphaedra ruspina* Hewitson, 1865; the common *Bebearia cocalia* Fabricius, 1793 occurs in the very different Nigerian subspecies with no intergradation whatever).

There must also have been a sub-refuge in the Niger Delta area. There are isolated populations of certain species in the area that only recur to the east in Calabar (e. g. *Graphium tynderaeus* Fabricius, 1793 and *G. latreilleanus theorini* Aurivillius, 1881). There are quite distinctive subspecies of at least three butterflies that only recur in Calabar (*Bebearia flaminia leventisi* Hecq & Larsen, 1997, *Cymothoe hypatha okomu* Hecq & Larsen, 1997) or even deep into Cameroun (*Cymothoe hesiodotus nigeriensis* Overlaet, 1952). Finally, there are a number of species of evident West African origin which do not cross the Niger Delta (e.g. *Euriphene coerulea* Boisduval, 1847).

The Cameroun/Congo/Gabon Region

Afrotropical butterfly diversity is highest in the Cameroun/Congo/Gabon region, with more than 1,400 forest species. This is hardly surprising. In addition to containing

major centres of speciation during forest contractions, the region was able to recruit species from both east and west, when the forest refuges expanded to the point where they again became contiguous.

The single area of highest diversity in Africa is the Oban Hills and Korup National Park, which are contiguous and straddle the Nigeria/Cameroun border. The butterfly fauna of this area is no less than 1,100 species (on a conservative estimate), more than a quarter of the entire Afrotropical fauna, a third of the fauna of the continental fauna of sub-Saharan Africa, and two-thirds of the combined fauna of Nigeria and Cameroun. There is significant endemism as well, and the area is one of the most important conservation areas in Africa. Nowhere in the Oriental Region contains such levels of diversity in a single site (the Malayan Peninsula has 1,000 species in all, including a submontane element). Only in the Neotropics is diversity higher, with favoured single sites on the upper Amazon having as many as 2,000 species.

The Region has a Northern Sub-Region and a Southern Sub-Region, centered on the Cross River Loop and the Gabon area respectively, each of which has a certain level of endemism. The Northern Sub-Region takes in most of the Central African Republic, including northwestern Zaïre. The Southern Sub-region includes the Mayumbé Province of Zaïre, which probably adds a hundred species or so to the fauna of that country. The main frontier between the two Sub-Regions is the Sanaga River.

The outstanding sub-refuge of the Northern Sub-Region is the Cameroun/Nigeria mountains with their limited, but very distinctive, sub-montane fauna, closely related to that of eastern Zaïre and East Africa.

The highlands of Angola, inland from Luanda, may be considered a sub-refuge of the Southern Sub-Region, with many of the same characteristics of the Cameroun/Nigeria mountains.

The Eastern Zaïre (Ituri) Region

The next major Region is centered on eastern Zaïre, as typified by the Ituri Forest. Though the rainforests of central Zaïre appear to be the very epitome of rainforest, looking from the air like broccoli gone wild, most of it is very recent, having been part of the Kalahari desert during the Pleistocene.

There are probably some 1,000 forest species in the Region, and another 200 in the highlands of Ruwenzori, Kivu, and Shaba, which may be considered a sub-refuge of the Ituri.

Between Shaba and Zambia/Malawi, the true forest region is replaced by Miombo woodland, the fauna of which partly consists of forest butterflies that have evolved to the special ecological conditions of this area. Some very interesting butterflies are endemic to the area.

The Uganda/Kenya forest Region

The fourth main forest region has much commonality with the Ituri Region and covers parts of Uganda and western Kenya, a few of the species extending to central Kenya. The area has not recently been wholly covered in forest, and remains a mosaic of savannah and forest. There are more than 1,200 butterfly species in Uganda, of which about 950 are lowland forest species. One forest, Minziro near Bukoba, in northwestern Tanzania has produced no less than 800 species, though some of these

are savannah species. The numbers drop sharply in western Kenya to about half the Ugandan number.

The remaining forests of northern Kenya, southern Sudan, and Ethiopia may be considered sub-refuges of Uganda/Kenya forest Region. The Kenyan forests are found on the various tall mountains that tower above the dry savannahs and sub-deserts of the north (Maralal, Marsabit, Mt. Nyiro, etc). It is very regrettable that no full lists have been published for these areas. However, in terms of lowland forest species, the species numbers are quite low - mostly less than a hundred. The lowland forest fauna of southern Sudan and Ethiopia is somewhat richer and with higher levels of endemism, but still somewhat marginal in terms of the forest fauna as a whole.

The East African coastal forest Region

The final forest region consists of a narrow band of forest, often interrupted by open country that stretches along the East African coast from Somalia to Mozambique, just reaching Natal in South Africa. These forests stretch inland to the Usambara and other mountains in Kenya and Tanzania.

The coastal forests have for long been almost disjunct from the main forest zones, with only the upland forests of Malawi as a tenuous connection. The forest butterflies of the Region are not many (200 or so) but there is a significant degree of endemism at both species and subspecies level, and the genera *Eresinopsides*, *Euthecta*, and *Teriomima* are endemic.

The eastern arc mountains

From southern Kenya through Tanzania to Malawi and parts of northern Zambia there is an arc of mountains, most of which have small areas of submontane forest. Though technically not within the scope of this paper, they deserve mention. Mostly the forest fauna is relatively limited (150 species or so), but each and every mountain has a few endemic species or subspecies, and some surprising differences in faunal composition.

The eastern arc mountains are - literally - a laboratory of evolution and speciation, the secrets of which are now more accessible due to the technology of DNA analysis.

Unfortunately the forests of these mountains are the most endangered habitats on the African continent - only surpassed in threatened status by the islands of Sao Tome and Principe.

Conclusion

Space constraints have not allowed as thorough documentation of distribution patterns as would have liked, but it should be clear that the five main forest regions are well characterized by endemic species. Nonetheless, they also present a great degree of homogeneity at the level of genera. Thus West Africa has a single endemic genus in the HesperIIDae (*Pyrrhiades*). The Nymphalid genus *Euryphaedra* is endemic to the Cameroun/Congo/Gabon Region and the Nymphalid genus *Kumothales* is endemic to the highland refuge areas surrounding the Ituri.

The bulk of forest butterfly genera are shared between at least two Regions, and usually more than that. Because of the limited fauna of the East African Coastal Forest Region, the number of genera sharing all five Regions is relatively small. The

number of genera sharing four of the Regions, however, is higher than those sharing only two or three.

This homogeneity at genus level, the high levels of diversity compared with the Oriental Region, and the firm - but not overwhelming - levels of Regional diversity may be testimony to a slow and orderly contraction and expansion of the forest (and its fauna), not forcing most species to adapt to catastrophic changes.

In his paper to the ABRI Conference, Lee Miller gave his reasons for assuming that butterflies might be much older than is often thought. I agree. I have a strong suspicion that if I were given the opportunity of visiting an African rainforest 20 million years ago, I would get few dramatic surprises.

Following the ABRI Conference, my fondest wish is that ABRI can mobilize all the knowledge of their members to create a database of Afrotropical butterflies that would become one of the most detailed of its kind, allowing us - and future generations of lepidopterists - to let butterflies talk of the past, the present, and - hope springs eternal - the future.

Table 1 Refuges of the rainforest during periods of maximum contraction (numbers give the approximate number of present rainforest butterflies - i.e. excluding savannah species).

REGIONS	Sub-regions	Sub-refuges
WESTERN WEST AFRICA* (950)	Liberia (850)	Loma Mountains Nimba Mountains area
	Ghana (850)	Atewa Range
	Nigerian mix-zone (750)	Volta/Togo mountains Niger Delta
CAMEROUN/ GABON/CONGO (1400)	Oban/Korup (1100) (Dorsale Camerounaise)	Montane elements
	S. Cameroun/Gabon (1200)	Central Angola
EASTERN ZAIRE (1000)		Montane elements Shaba/Malawi mosaic
UGANDA/KENYA MOSAIC (900)		Montane elements S. Ethiopia/S. Sudan Maralal/Marsabit/etc.
COASTAL EAST AFRICA (200)		Montane offshoots

* also known as Upper Guinea or Guineo-Congolese

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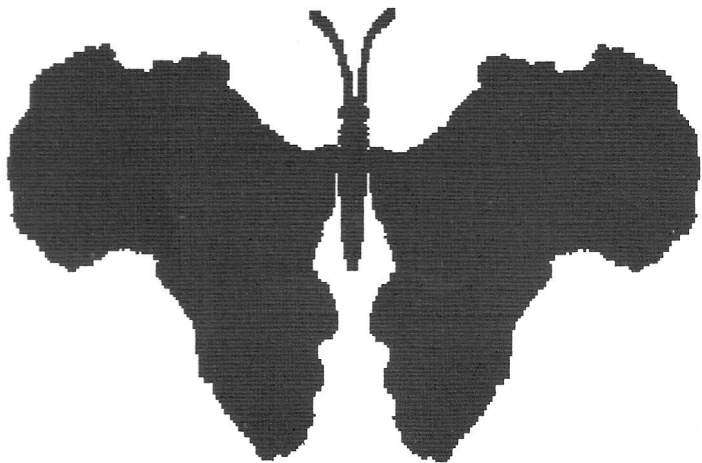
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