Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
Photo: M Mills

Editors:

John M Mendelsohn
Brian J Huntley
Pedro Vaz Pinto

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CONTENTS

Huntley BJ, Mendelsohn JM & Vaz Pinto P Preface to endemism on the highlands and escarpments of Angola and Namibia ..... i–iii

Huntley BJ, Mendelsohn JM & Vaz Pinto P The biological importance of the highlands of Angola and Namibia: Synopsis and conclusions ..... v–xiii

Geography of the highlands and escarpments

Jarvis AM The highlands and escarpments of Angola and Namibia: orientation maps 1–6

Mendelsohn JM & Huntley BJ Introducing the highlands and escarpments of Angola and Namibia 7–22

Miller RM Geology and landscape evolution of the highlands and escarpments of western Angola and Namibia 23–28

Huntley BJ Biomes and ecoregions of the highlands and escarpments of Angola and Namibia 29–41

Mendelsohn JM & Gomes AL The human environment in the highlands and escarpments of Angola and Namibia 43–51

Vaz Pinto P, Russo V & Veríssimo L The highlands in Angolan conservation areas 53–62

Diversity and endemism

Craven P & Kolberg H An overview of plant endemism on the highlands of Namibia 63–76

Goyder DJ, Gomes AL, Gonçalves FMP, Luís JC & Darbyshire I A botanical assessment of Mt Namba, Cuanza-Sul, Angola: an isolated mountain towards the northwestern limits of the Great Escarpment of southern Africa..... 77–92

Meller P, Lages F, Finckh M, Gomes A & Goyder D Diversity and endemism of geoxylic plants on the Angolan Planalto..... 93–109

Bruyns PV, Hanáček P & Klak C Diversity and endemism in the species-rich Ceropegieae (Apocynaceae) and *Euphorbia* in the highlands and escarpments of Angola and Namibia 111–134

Dexter KG, Swanepoel W, Loiseau O, Darbyshire I, Nanyeni L, Gonçalves FM, Chase F & Manzitto-Tripp EA High endemism of the genus *Petalidium* (Acanthaceae) in the highlands and escarpments of Angola and Namibia 135–147

Weeks A & Swanepoel W *Commiphora* of the highlands and escarpments of Angola and Namibia 149–159

Lautenschläger T, Aime MC, Clausnitzer V, Langer L, Meller P, Müller F, Nuss M, Teutloff N & Ernst R Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem..... 161–172

Kipping J, Clausnitzer V & Dijkstra K-DB The highlands and escarpment of Angola as an endemism hotspot for African dragonflies and damselflies (Insecta: Odonata)..... 173–186

Gunter F, Jürgens N & Henschel JR Observations on the diversity of termites in Angola and Namibia..... 187–192

Mansell MW The Neuroptera of the highlands and escarpments of Angola and Namibia 193–196

Gomez K, Hawkes PG & Fisher BL Ant endemicity in the highlands and escarpments of Angola and Namibia (Hymenoptera, Formicidae) 197–203

Gardiner AJ & Williams MC The endemic butterflies of Angola and Namibia and their evolutionary implications..... 205–230

Prendini L & Bird TL Endemism of Arachnida (Amblypygi, Scorpiones and Solifugae) in the highlands and escarpments of Angola and Namibia: current knowledge and future directions..... 231–244

Becker FS, Baptista NL, Vaz Pinto P, Ernst R & Conradie W The amphibians of the highlands and escarpments of Angola and Namibia..... 245–257

Bauer AM, Ceríaco LMP, Marques MP & Becker FS Highland reptiles of Angola and Namibia 259–276

Conradie W, Lobón-Rovira J, Becker FS, Schmitz A & Vaz Pinto P Flat gecko (*Afroedura*) diversity, endemism and speciation in the highlands and escarpments of Angola and Namibia 277–281

Skelton PH Fishes of the highlands and escarpments of Angola and Namibia..... 283–292

Mills MSL & Melo M Birds of the highlands and escarpments of Angola and Namibia: ornithological significance, avifaunal patterns and questions requiring further study 293–309

Palmeirim AF, Monadjem A, Vaz Pinto P, Taylor P, Svensson MS & Beja P Mammal endemism in the highlands and escarpments of Angola and Namibia..... 311–322

De Matos D, Zastrow J, Val A & Mendelsohn JM Caves and their fauna in the highlands and escarpments of Angola and Namibia 323–330

The endemic butterflies of Angola and Namibia and their evolutionary implications

AJ Gardiner[1], MC Williams[†]

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[1] Southern African Wildlife College, University of Stellenbosch, South Africa; agardiner@sawc.org.za
[†] Deceased: 10 September 2023

ABSTRACT
The currently described endemic butterfly species and subspecies to Angola and Namibia are presented together with their known distributions. This butterfly fauna has been placed into the biogeographic units of Carcasson (1964) and Burgess *et al*. (2004). Aspects of the evolution and biogeography of the fauna, such as their association with other mountainous areas of Africa and their linkage to dry areas of East Africa, are discussed. The information suggests large gaps in our knowledge of the Angolan highland fauna. The importance of utilising such fauna for identifying conservation priorities in these two countries is highlighted.

Keywords: Angola, biogeography, butterfly, endemism, escarpments, evolution, highlands, Lepidoptera, Namibia

INTRODUCTION

Angola and Namibia form a geographical region of great biodiversity interest (e.g., Huntley *et al*. 2019). The unique and interesting biodiversity of Angola has been demonstrated for plants (Goyder & Gonçalves 2019) and a few animal groups, mostly the large and charismatic vertebrates: fish (Skelton 2019), amphibians (Baptista *et al*. 2019), reptiles (Branch *et al*. 2019), birds (Dean *et al*. 2019) and mammals (Beja *et al*. 2019). While the above authors all consider their group to be understudied in Angola, this is even more pronounced for the group with the most species described globally: the invertebrates.

Butterflies belong to the insect order Lepidoptera, or scale-winged insects. The butterflies have been traditionally grouped under the term Rhopalocera which is allied to the more recent superfamily name Papilionoidea. The Papilionoidea includes the following butterfly families: Hesperiidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae and Nymphalidae. It should also include the moth-like butterflies – the Hedylidae – which do not occur in Africa and are not dealt with here.

The recording of butterfly species from Angola effectively began in the 1860s (Mendes *et al*. 2019) with a noticeable increase in records during the first ten years and then a constant increase over the next 70–80 years. During the period of political unrest, from about the 1960s to the 1990s, the number of species recorded decreased but then picked up once the country had stabilised (Mendes *et al*. 2019). Recording butterfly species in Namibia also began in the mid-19th century and from about this time the area was documented as part of southern Africa, for instance any species known from Namibia was documented by Ronald Trimen in his "Rhopalocera Africae Australis; a catalogue of South African butterflies" (Trimen 1862–1866). This trend continued up until the 1990s with the publication of "Pennington's butterflies of southern Africa" (Pringle *et al*. 1994). The level of invertebrate sampling in Angola remains low compared to most other African countries (e.g., Ferreira 1971, Serrano & Capela 2015) probably largely due to the fear of land mines, which are still being cleared, and poor infrastructure especially in rural areas.

In Huntley *et al.*'s (2019) "Biodiversity of Angola" the Odonata – dragonflies and damselflies – (Kipping *et al*. 2019) and the Papilionoidea – all butterflies except Hedyloidea – (Mendes *et al*. 2019) are presented as indicator groups for the invertebrates. Kipping *et al*. (2019) provided a revised checklist for the Odonata comprising 260 species and discussed the history of research and the biogeography of the fauna, indicating the rate of endemism (7%) and the potential for further discoveries. The national total for Angola has now risen to 288 species, of which 12% are endemic (Huntley *et al*. 2023), which makes Angola one of the richest countries for Odonata in Africa. The evolution and biogeography of the invertebrates, particularly the butterflies, is dealt with in less detail than the vertebrates but useful checklists with endemism were provided. Mendes *et al*. (2013a, 2013b) have provided some taxonomic and ecological information on the Angolan butterflies.

In this paper, we document the present knowledge on the geographical distribution of the endemic butterflies (Papilionoidea) of Angola and Namibia. We also provide some insights into possible factors influencing the evolution of the butterfly fauna in this region.

NUMBER OF SPECIES AND ENDEMISM

There are currently about 4,500 described species of butterflies in the Afrotropical Region (Williams 2022). Of these, 800 species (ca. 18% of the Afrotropical fauna) have been recorded from Angola (Mendes *et al*. 2019, Williams 2022) and nearly 220 species (ca. 5%) from Namibia (Table 1; Figure 1).

Fifty-seven species have been recorded from Namibia but not from Angola, giving a total of 857 species for Angola and Namibia combined. Of these, 76 species are endemic or near-endemic resulting in 6.5% endemism for the two countries (Table 1). Presently Angola has an endemism rate of 5.3% (Figures 2–4, also see Mendes *et al*. 2019 for further data on endemism in Angola) and Namibia 3.6% (Table 1).

Table 1: *The number of butterfly species and endemics for Angola, Namibia and selected African countries. Numbers in brackets indicate that the number is for the combination of species and subspecies. Also provided is endemism for a few other Angolan invertebrate taxa: Cicindelinae, Paussini and Odonata.*

Taxon	Country	Number of species	Number of endemic species	% of endemic species	Source
Rhopalocera (butterflies)	Angola	800	42 (64)	5.3 (8)	Mendes *et al*. 2019
	Namibia	220	8 (14)	3.6 (6.4)	Williams 2022
	Angola & Namibia	857	76	6.5	Williams 2022
	Kenya	900	63	7	Williams 2022
	Zimbabwe	527	22	4.2	African Butterfly Database 2023
	Zambia	940	28	3	Williams 2022
	Tanzania	1,583	135	8.5	Williams 2022
	South Africa	668	167	25	Woodhall 2020
Cicindelinae (tiger beetles)	Angola	(89)*	(31)	(33.3)	Serrano & Capela 2013
Paussini (ant nest beetles)	Angola	46	11	22	Serrano & Capela 2015
Odonata (dragonflies)	Angola	260	18	7	Kipping *et al*. 2019

*74 species and 15 subspecies

Figure 1: *A selection of butterflies endemic to Angola: a)* Brakefieldia ochracea, *a central highland endemic found in the grassland–woodland mosaic; b)* Mashunoides carneiromendesi, *a monobasic endemic genus occurring in wetland areas on the eastern parts of the central highland watershed; c)* Acraea bellona, *a widespread endemic from the central highlands of Angola to the eastern watershed, with one doubtful record from western Zambia; d)* Zeritis krystna, *a small, strikingly marked, widespread endemic on and east of the Angolan highlands. Photos: Alan Gardiner, except* Acraea bellona: *Jonathan Francis.*

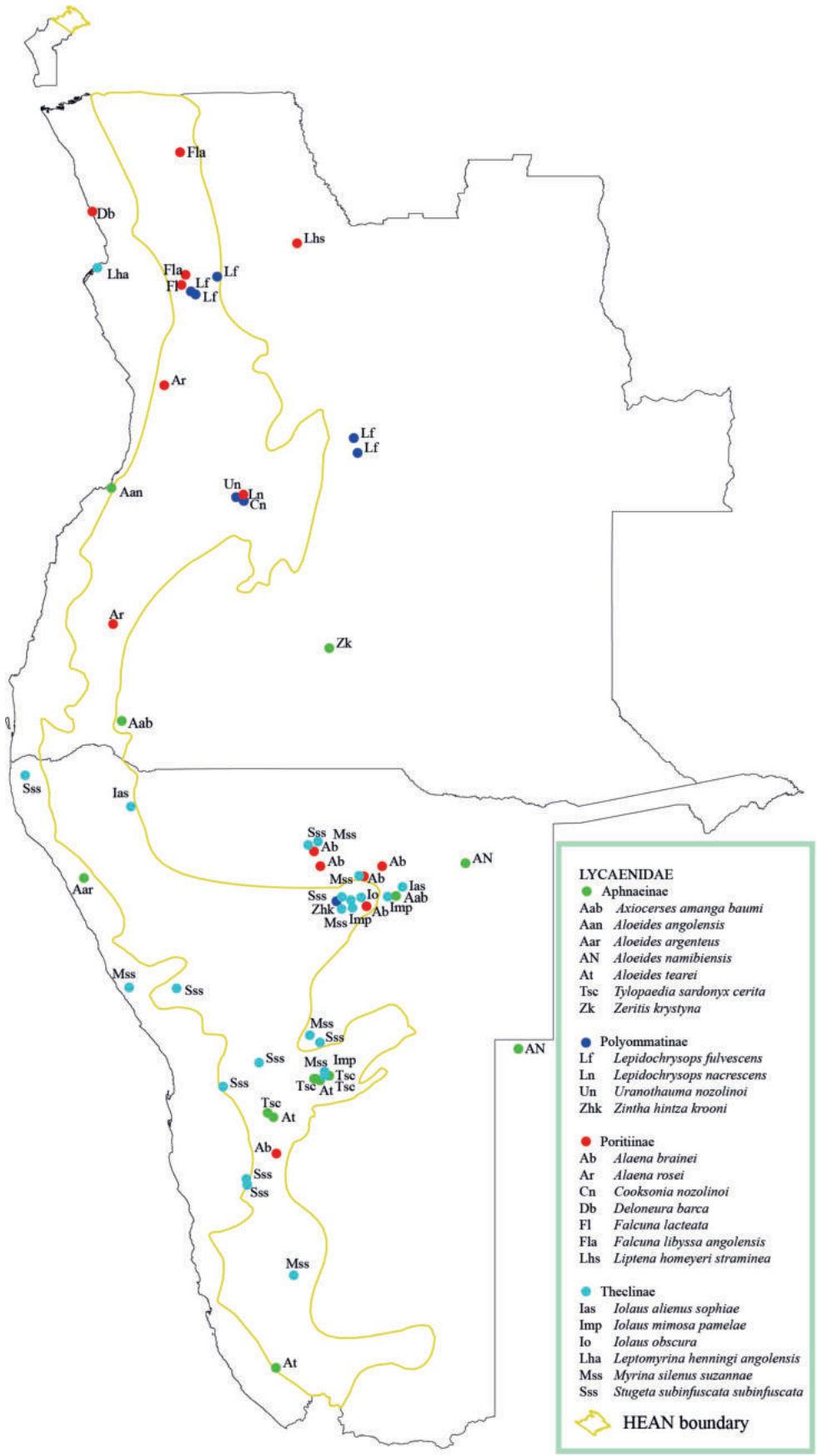

Figure 2: *Locations of endemic butterflies of the family Lycaenidae recorded in Angola and Namibia: subfamilies Aphnaeinae, Polyommatinae, Poritiinae and Theclinae. Due to the low level of sampling there is some uncertainty as to which of the endemic species are associated with highlands. There is more butterfly information for Namibia than Angola, although Namibia remains less surveyed than South Africa, Botswana and Zimbabwe. (HEAN = highlands and escarpments of Angola and Namibia.)*

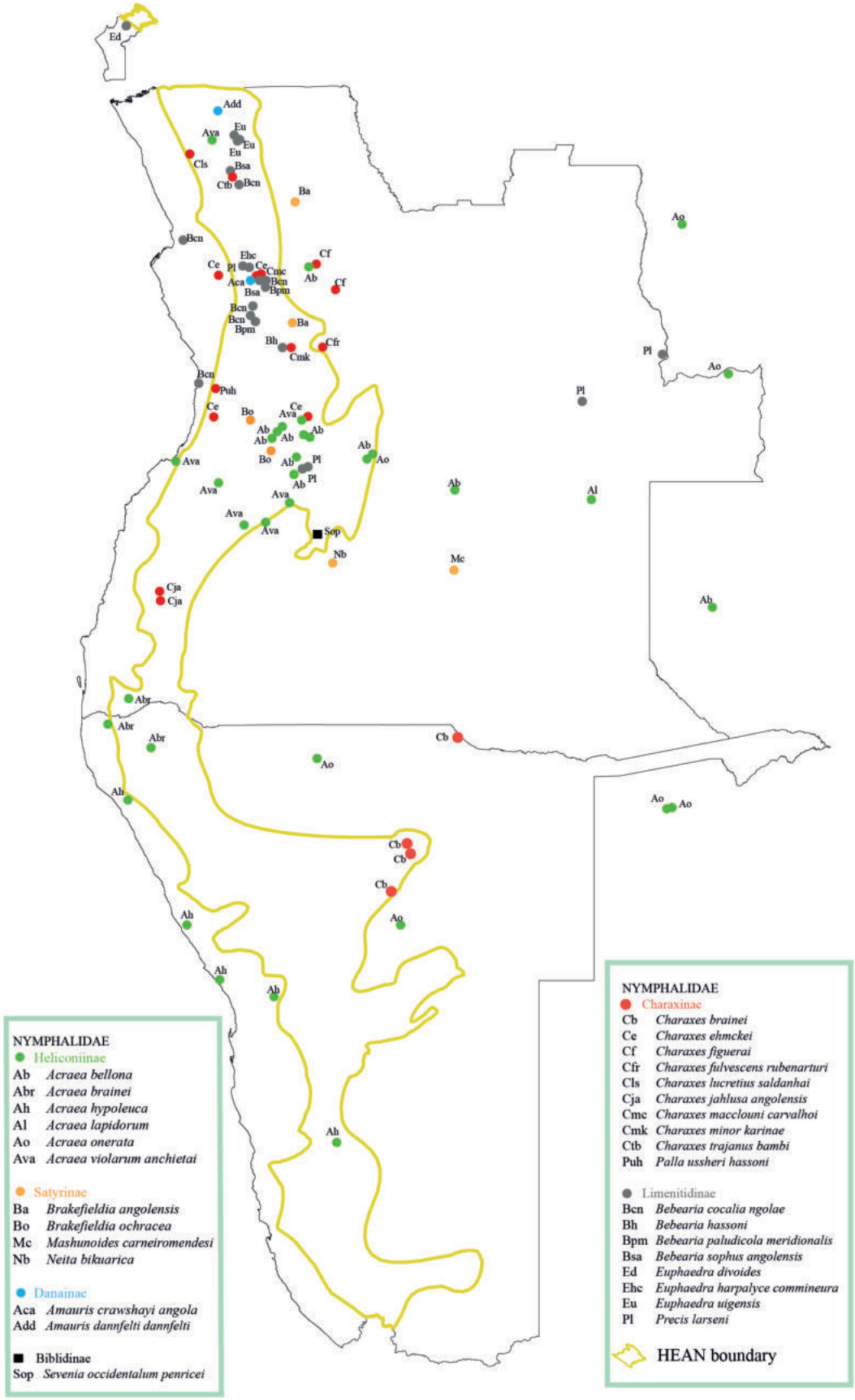

Figure 3: *Locations of endemic butterflies of the family Nymphalidae recorded in Angola and Namibia: subfamilies Heliconiinae, Satyrinae, Danainae, Biblidinae, Charaxinae and Limenitidinae. Due to the low level of sampling there is some uncertainty as to which of the endemic species are associated with highlands. There is more butterfly information for Namibia than Angola, although Namibia remains less surveyed than South Africa, Botswana and Zimbabwe. (HEAN = highlands and escarpments of Angola and Namibia.)*

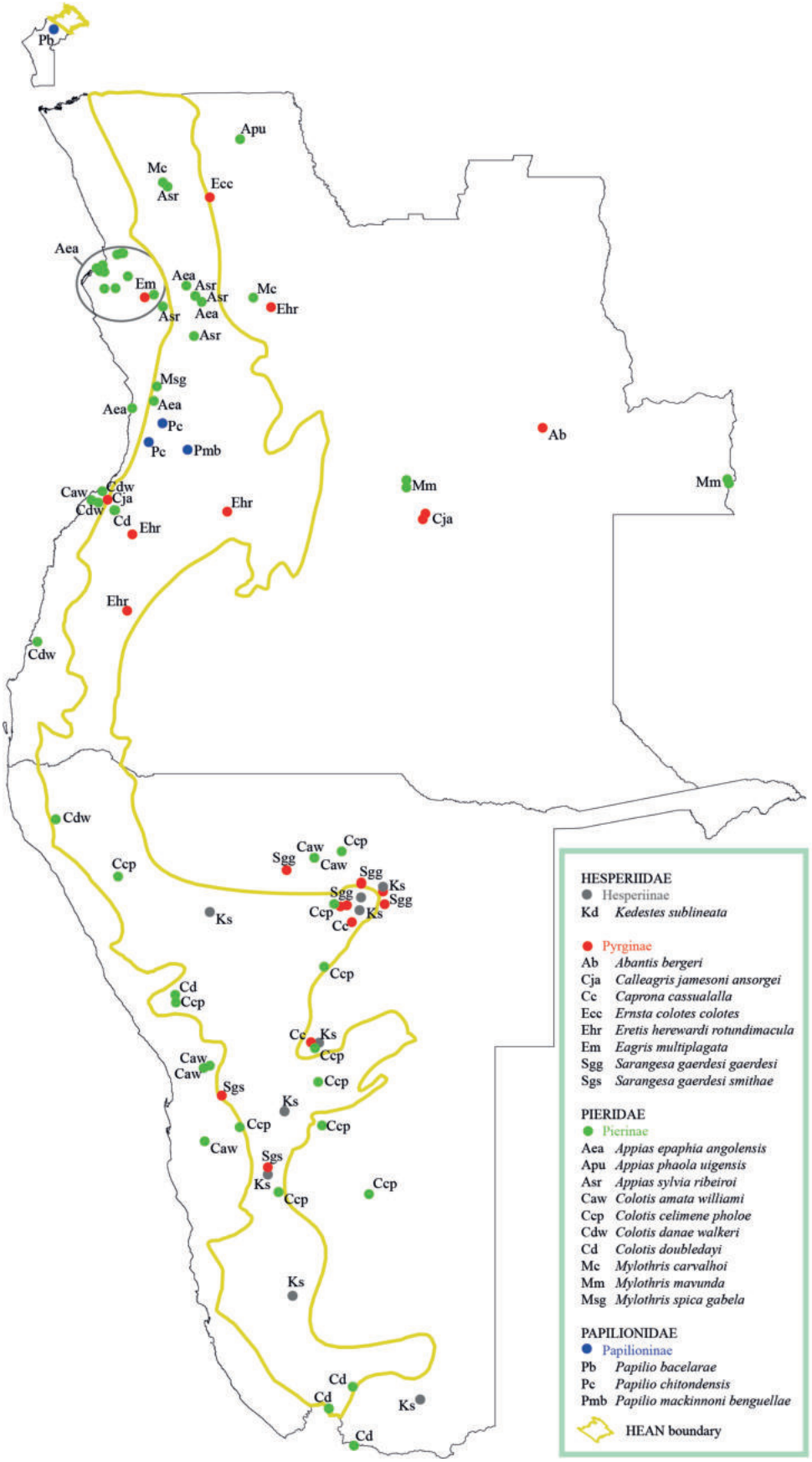

Figure 4: *Locations of endemic butterflies of the families Hesperiidae, Pieridae and Papilionidae recorded in Angola and Namibia: subfamilies Hesperiinae and Pyrginae (family Hesperiidae); subfamily Pierinae (family Pieridae); and subfamily Papilioninae (family Papilionidae). Due to the low level of sampling there is some uncertainty as to which of the endemic species are associated with highlands. There is more butterfly information for Namibia than Angola, although Namibia remains less surveyed than South Africa, Botswana and Zimbabwe. (HEAN = highlands and escarpments of Angola and Namibia.)*

High levels of endemism are typically an indication of the presence of unique habitats. Compared to the butterfly endemism of some other African countries, Angola has an endemism slightly higher than Zimbabwe (ca. 4.2%) and Namibia slightly higher than Zambia (ca. 3%). Tanzania, with its eastern arc of mountains, has an endemism of ca. 8.5% while Kenya, with a similar number of species to Angola, has an endemism of ca. 7%. South Africa has an extremely high level of endemism – about 25% – mostly due to the Western Cape's Mediterranean climate, the Cape Fold Mountains and the Drakensberg. Comparing the endemism of a few other invertebrate groups from Angola (Table 1), both the Cicindelinae (33.3%; Serrano & Capela 2013) and Paussini (22%) have very high levels of endemism while the Odonata have 12% endemism (Kipping *et al*. 2023). The lower level for the Odonata is expected, as many species are widespread and have good flying and dispersal capabilities. However, butterfly endemism is lower than might be expected from the topography, climatic conditions and vegetation types, suggesting the area is undersampled.

SUB-SAHARAN BUTTERFLY BIOGEOGRAPHY

Before we discuss the biogeography of the Angolan and Namibian butterflies we need to put it into the context of Africa. Carcasson (1964) was the first person to undertake a detailed analysis of the distribution of Africa's sub-Saharan butterfly fauna (Afrotropical Region). Carcasson dealt with 2,674 species in his publication. Even though the number of described species in sub-Saharan Africa is now about 1.7 times higher, his study remains the benchmark for the biogeography of Africa's butterfly fauna (Larsen 2005). Carcasson (1964) suggested the butterfly faunas were associated with the various vegetation types (habitats) and using the 1959 vegetation map of Africa (Aubréville *et al*. 1959) he produced his faunistic regions (Figure 5). Carcasson's divisions are briefly described below; many of the main divisions are represented in Angola and Namibia.

Carcasson's divisions

The geographic divisions of the sub-Saharan African butterflies (modified from Carcasson 1964) are shown in Figure 5.

I) Sylvan Subregion

This subregion comprises all evergreen forests on the continent and is divided into two divisions, lowland and highland forest. Angola has both Lowland and Highland Forest.

A. Lowland Forest
The separation of the Lowland and Highland Forest is around 1,500 masl at the equator, however the

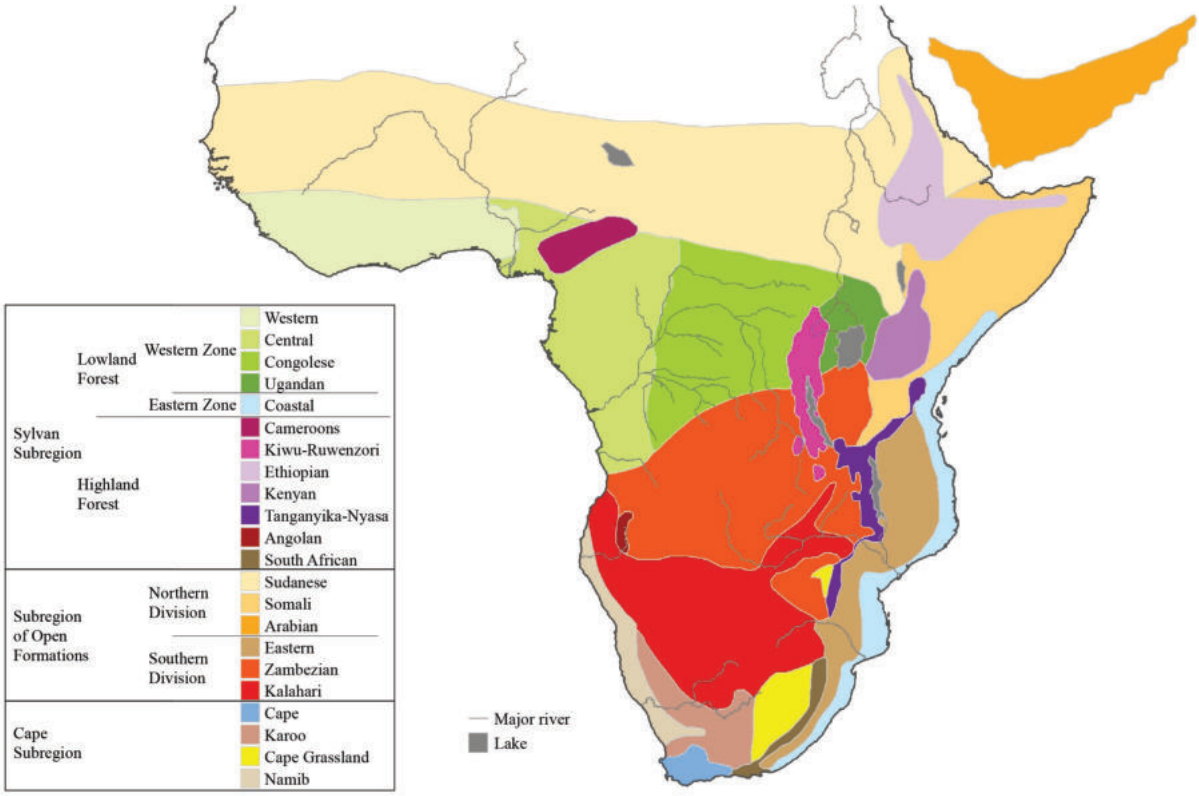

Figure 5: *Geographic divisions of the sub-Saharan African butterflies (modified from Carcasson 1964).*

Highland Forest progressively descends to sea level at 33°S (the Knysna forests of the Eastern Cape, South Africa). There is some vertical overlap of the two divisions. The greatest density of both butterfly species and individuals occurs in the Lowland Forest. The Lowland Forest was subdivided into Western and Eastern zones. The Eastern or Coastal Zone comprises all the Lowland Forest east of the African eastern highlands, from Kenya to KwaZulu-Natal. The Eastern Zone is comparatively species-poor compared to the Western Lowland Forests. The Western and Eastern Lowland Forests have a number of genera in common such as *Euphaedra*, *Cymothoe*, *Bebearia*, *Pentila* and *Ornipholidotos*, indicating a link between the two; at one or more times they were probably linked from the Democratic Republic of the Congo (DRC) and Angola through northern Zambia, Tanzania, northern Malawi and the neighbouring areas of Mozambique.

The Western Lowland Forest comprises the entire Central and West African lowland forest block from Sierra Leone (9°N) in the west to Kakamega Forest in western Kenya. This division is the most species-rich. It has four zones: i) Western, ii) Central, which includes part of Northern Angola, iii) Congolese (DRC) and iv) Ugandan (Figure 5).

B. Highland Forest

Many of the highland forest species are related to lowland species and the various patches of highland forest species have strong affinities with one another. This suggests that, at one or more times, they were more continuous with one another than they are today. Isolation periods provide ideal conditions for speciation (as is seen for other groups e.g., Roy 1997). For the East African highland forests it has also been suggested that dispersal of a species from one forest to another has resulted in minor radiations (de Jong & Congdon 1993). Both means of speciation are possible. Carcasson divided the Highland Forest into seven zones: i) Cameroons Zone; ii) Kiwu–Ruwenzori Zone; iii) Ethiopian Zone; iv) Kenyan Zone; v) Tanganyika–Nyasa (Tanzania–Malawi–Zimbabwe) Zone; vi) Angolan Zone; and vii) the South African Zone. It is worth noting that even at this time Carcasson realised the uniqueness of the Angolan highlands.

II) Subregion of Open Formations

"This subregion includes a great variety of vegetation types, in fact all formations other than closed canopy evergreen forest, montane grassland and moorland, from about 20°N to about 25°S" (Carcasson 1964). This was divided by Carcasson into a Northern and a Southern division. The Northern division contained three zones: i) Sudanese; ii) Somali; and iii) Arabian. The Southern also had three zones: iv) Eastern; v) Zambezian; and vi) Kalahari. Angola has large areas of Zambezian but also some Kalahari (Figure 5), while Namibia has some Zambezian and a significant amount of Kalahari.

The Zambezian Zone is the largest southern area of open formations and, for an open formation, the richest in species. It is mostly high plateau of an elevation between 1,100–1,500 masl. It stretches from southwest Tanzania through Zambia, Shaba Province of DRC, most of the Highveld of Zimbabwe to Angola in the west. Soils are mainly sandy and acidic, and much of the vegetation is deciduous woodland of varying density. The predominant vegetation is Miombo with dominant trees being the numerous species of *Brachystegia* and *Julbernardia*, together with *Uapaca*, *Monotes*, *Parinari* and with *Cryptosepalum pseudotaxus*, *Guibourtia coleosperma* and *Marquesia*. Annual average rainfall is up to 1,500 mm in the north, but there is a long dry season.

The Kalahari Zone is much drier than the Zambezian Zone. It stretches from the northern provinces of South Africa, southwestern Zimbabwe, Botswana, Namibia and parts of southern Angola. Most of the zone consists of Subdesert Steppe, with *Vachellia* [previously *Acacia*] spp. predominant and other genera such as *Euclea*, *Commiphora*, *Combretum*, *Terminalia*, *Boscia* and *Cadaba* being common.

III) Cape Subregion

This subregion was subdivided into four zones: i) the Namib Zone, which is the extremely arid coastal belt of western South Africa, Namibia and southern Angola; ii) the Karoo Zone, a vast area covered by low-growing, mostly succulent vegetation (Aizoaceae) which penetrates Namibia in the south; iii) the Cape Zone, the winter rainfall areas of the Western Cape Province which are home to a very characteristic vegetation, the Fynbos or Cape Maquis and which have a Mediterranean appearance; and iv) Cape Grassland Zone, the high-level grasslands which occupy much of the plateau of the Orange Free State, KwaZulu-Natal, Mpumalanga, Limpopo, as well as mountains in Lesotho and the Cape (Eastern and Western Cape provinces). The fauna of this subregion has a high level of endemism in butterflies especially in the Lycaenidae and Satyrinae (see Cottrell 1978, 1985).

BIOGEOGRAPHY OF THE ENDEMIC ANGOLAN AND NAMIBIAN BUTTERFLY FAUNA

Carcasson's butterfly ecogeographic divisions or zones, although less detailed, tie in with the ecoregions produced by Burgess *et al*. (2004); the two are compared for Angola and Namibia in Table 2. We have used the faunistic zones (ecoregions) of Burgess *et al*. (2004) in Table 2 and

Figure 6 to describe and form a guide to the biogeography of the Angolan and Namibian butterfly fauna. Ecoregion 43 Western Congolian Forest-Savanna Mosaic and ecoregion 42 Southern Congolian Forest-Savanna Mosaic penetrate, in a mixed form, into northern Angola (Figure 6; 42 & 43), this area is characterised by lowland forest species such as: *Coeliades chalybe*, *Pyrrhochalcia iphis desjongi*, *Papilio zalmoxis*, *Papilio antimachus*, *Papilio mechowi mechowi*, *Graphium tynderaeus*,

Table 2: *Biogeographic units of Burgess* et al. *(2004) and Carcasson (1964) with the known associated endemic butterfly taxa in Angola and Namibia.*

Burgess Ecoregion	**Carcasson**	**Endemic taxa**
32 Zambezian *Cryptosepalum* Dry Forests	Zambezian	**Species**: *Mylothris mavunda*
42 Southern Congolian Forest-Savanna Mosaic 43 Western Congolian Forest-Savanna Mosaic	Congolese Lowland Forest Central Lowland Forest	**Species**: *Bebearia hassoni*, *Euphaedra divoides*, *E. uigensis, Falcuna lacteata*, *Mylothris carvalhoi*, *M. gabela* **Subspecies**: *Amauris crawshayi angola*, *Appias phaola uigensis*, *A. sylvia ribeiroi*, *Bebearia cocalia ngolae*, *B. paludicola meridionalis*, *B. sophus angolensis, Charaxes fulvescens rubenarturi*, *C. lucretius saldanhai, C. macclouni carvalhoi*, *C. minor karinae*, *C. trajanus bambi*, *Euphaedra harpalyce commineura*, *Falcuna libyssa angolensis*, *Palla ussheri hassoni*, *Sevenia occidentalium penricei*
49 Angolan Miombo Woodlands	Zambezian	**Species**: *Abantis bergeri*, *Acraea bellona*, *A. lapidorum*, *Cooksonia nozolinoi*, *Deloneura barca*, *Lepidochrysops fulvescens*, *L. nacrescens, Zeritis krystyna* **Subspecies**: *Axiocerses amanga baumi*, *Calleagrius jamesoni ansorgei*, *Charaxes jahlusa angolensis*, *Cigaritis modestus modestus*, *Liptena homeyeri straminea*
43 Western Congolian Forest-Savanna Mosaic 49 Angolan Miombo Woodlands 81 Angolan Scarp Savanna and Woodlands	Central Lowland Forest Zambezian	**Species**: *Brakefieldia angolensis*, *Charaxes ehmckei*, *C. figueirai, Neita bikuarica*, *Precis larseni* **Subspecies**: *Appias sylvia ribeiroi*
82 Angolan Montane Forest-Grassland Mosaic	Angolan Highland Forest	**Species**: *Eagris multiplagata, Uranothauma nozolinoi* **Subspecies**: *Eretis herewardi rotundimacula*
58 Kalahari *Acacia-Baikiaea* Woodlands 105 Kalahari Xeric Savanna 106 Kaokoveld Desert 109 Namibian Savanna Woodlands	Kalahari Namib Karoo	**Species**: *Acraea hypoleuca* (109), *A. brainei* (109), *Alaena brainei* (58, 105), *Aloeides angolensis* (106, 109), *A. argenteus* (107, 109), *Aloeides namibiensis* (105, 109), *Aloeides tearei* (105, 109), *Caprona cassuallala* (58, 105, 106, 109), *Charaxes brainei* (58, 105), *Colotis doubledayi* (106, 108, 109), *Eretis gaerdesi* with two subspecies *E. gaerdesi gaerdesi* (105, 109) and *E. gaerdesi smithae* (106), *Iolaus obscura* (105), *Kedestes sublineata* (58, 105) **Subspecies**: *Colotis amata williami* (106, 109), *C. annae walkeri* (106, 109), *C. celimene pholoe* (58, 105), *Iolaus alienus sophiae* (58, 105, 109), *I. mimosa pamelae* (58, 105, 109), *Myrina silenus suzannae* (105, 109), *Stugeta subinfuscata subinfuscata* (105, 109), *Tylopaedia sardonyx cerita* (105), *Zintha hintza krooni* (58, 105)

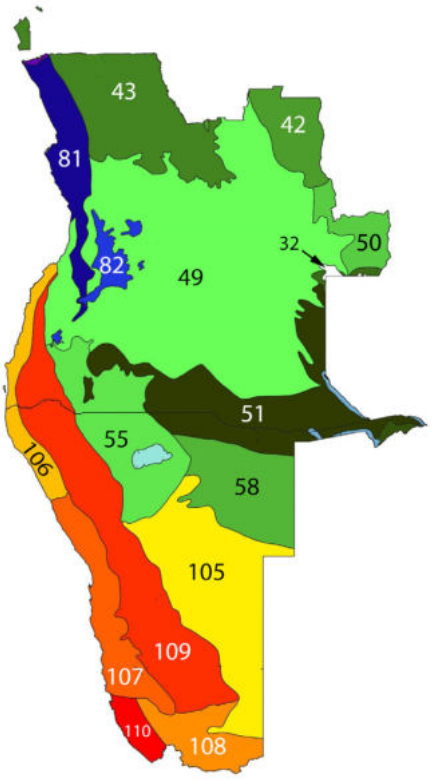

Figure 6: *The faunistic zones of Angola and Namibia (modified from Burgess* et al. *2004).*

Liptena fatima fatima, *Afriodinia tantalus*, *Charaxes zingha*, *Palla violinitens coniger*, *Cymothoe excelsa deltoides, Cymothoe beckeri beckeri*, *Cymothoe coccinata coccinata* and *Euphaedra coprates*. There are six endemic Angolan species and 15 endemic subspecies belonging to these two ecoregions (Table 2).

Little is known about the fauna of the Angolan Highland Forests (contained within ecoregion 82). Two of the recorded species are likely to be montane forest endemics: *Uranothauma nozolinoi* and *Eagris multiplagata* (Table 2). There is also one endemic subspecies *Eretis herewardi rotundimacula*. Endemics which have been recorded on, or close to, the highlands or escarpments of Angola and Namibia are mapped in Figures 2–4, but with our present knowledge it is difficult to know how strongly the species are related to these formations. There are at least two butterfly examples to suggest the former existence of a south equatorial arc: *Acraea oreas* and *Papilio mackinnoni*, both of which occur in the highlands of East Africa through higher elevations to the highland forests of Angola. It is likely this arc ran from the high plateau southwest of Lake Tanganyika (Marungu Highlands, DRC) through the Kundelungu and Mitumba mountains in Shaba (DRC) and the highlands north of Lake Nzilo (Lualaba Province, DRC) to the Angolan Highlands.

One endemic butterfly – *Mylothris mavunda* – is known from the faunistic zone Zambezian *Cryptosepalum* Dry Forest (32) and is also found just across the border in northwest Zambia. The Angolan Miombo Woodlands (49) has eight endemic species and five endemic subspecies (Table 2), however the taxonomic status of some of these needs to be examined. In addition, there are five endemic species and one subspecies associated with the following three faunistic zones: Angolan Miombo Woodlands (49), Angolan Scarp Savanna and Woodlands (81) and Western Congolian Forest-Savanna Mosaic (43) (Table 2). The Angolan and northern Namibian endemic *Acraea onerata* occurs in a number of faunistic zones: Angolan Miombo Woodlands (49), Zambezian *Baikiaea* woodlands (51) and the Angolan Mopane Woodlands (55). As a whole these wet woodlands have 21 endemic or near-endemic taxa, a surprisingly high number, and six endemic subspecies.

The drier habitats also have a surprisingly high number of endemics. There are 23 endemic or near-endemic taxa, thirteen species and 9 subspecies, associated with the following four ecoregions: Kalahari *Acacia-Baikiaea* Woodlands (58), Kalahari Xeric Savanna (105), Kaokoveld Desert (106) and Namibian Savanna and Woodlands (109). There are also two dryland endemic subspecies which are associated with the Angolan Scarp Savanna and Woodlands (81) but one, *Appias epaphia angolensis* seems to also be associated with the Namibian Savanna Woodlands (109).

SPECIAL HABITATS

In addition to ecoregions, Carcasson (1964) also associated some butterfly species with particular habitats, namely: Montane Grassland, which forms part of the Angolan Montane Forest-Grassland Mosaic (82) of Burgess *et al*. (2004); Highland Swamp Habitat and Lowland Swamp Habitat, which can be a subunit within a number of Burgess *et al*.'s (2004) ecoregions Angolan Miombo Woodlands (49), Central Zambezian Miombo Woodlands (50) and Zambezian Baikiaea woodlands (51); and Littoral Sand Dunes which similarly could be a subunit within a number of Burgess *et al*.'s coastal ecoregions. With our present knowledge, we can only briefly discuss Montane Grassland and Swamp habitats and even for these there is a lack of information.

It can be difficult to differentiate some highland species in terms of Montane Grassland, especially as grassland areas are often present within Miombo, and Miombo in a stunted form can occur at high elevations. Species such as *Zeretis* spp. occur in the Grassland Miombo ecotone and it is likely the Angolan endemic *Brakefieldia ochracea* is also

present in this ecotone; it has recently been observed in grassy highland areas (Hines pers. comm.) and in Miombo woodland (Gardiner pers. obs.), and older records suggest it may also be present at lower elevations down to about 1,200 masl. There is only one endemic species which could be referred to as a Montane Grassland species; an undescribed *Erikssonia* species from Tundavala (14.82S, 13.38E) near Lubango found by S. Braine (pers. comm.).

Mashunoides carneiromendesi is not only an endemic species but the genus is monobasic and is a wetland specialist; the type specimen was caught near Longa (ca. 14.60S, 18.48E, 1,380 masl) in southeastern Angola (an area with Miombo woodland) and recently the lead author has seen it near Tempué (13.43S, 18.87E, 1,400 masl). *Mashunoides carneiromendesi* is related to the genus *Mashuna* which is also a wetland genus with two species: *Mashuna mashuna,* an endemic to wetland areas in the Highveld of Zimbabwe, and *Mashuna upemba* which has been recorded in Angola (Ackery *et al*. 1995, but exact localities are not known), DRC (Shaba Province) and southwestern Tanzania.

AN EVOLUTIONARY PERSPECTIVE ON THE BIOGEOGRAPHY OF THE BUTTERFLY FAUNA OF ANGOLA AND NAMIBIA

Geological processes, in combination with climatic factors such as temperature and rainfall, are probably the most important drivers of biological change (also implied by Lorenzen *et al*. 2012). Landscape changes promote the evolution of the flora and fauna. These have been referred to as first order controls (Turner 1989). The various factors involved are also likely to be interconnected and may take place at different times and intensities across Africa (see Knight & Grab 2016). Hence, each landscape needs to be considered in as much detail as possible in order to postulate feasible hypotheses for the origin(s) and development of the present fauna. Unfortunately, detailed geological and climatic studies are lacking for many parts of Africa including Angola and Namibia, although more information is becoming available (see references in Knight & Grab 2016 and Huntley *et al*. 2019). Here, we try to put together a brief evolutionary account for one relatively small invertebrate group, the butterflies (Papilionoidea).

African continental-scale warping took place about 85 to 42 mya which resulted in the formation of a composite, low-lying surface of continental extent that is termed the African Surface (Burke & Gunnell 2008). Analysis of only a few African genera has been completed but we know that certain African genera were formed during these turbulent times, such as the *Charaxes* about 45 mya in central Africa (Aduse-Poku *et al*. 2009). During this period, at about 60 mya, along the Okavango–Kalahari–Zimbabwe Axis (which covers part of Angola, Zambia, Namibia, Zimbabwe and Botswana) crustal flexing was occurring (Moore & Larkin 2001) and these movements must have affected the biogeography of the Angola–Namibia area. There then seems to be a period of relative geographical calm until uplifting and tilting through tectonics resulted in a change in the topography of Africa about 19 to 15 mya. Up until this time, it appears there was more connectedness amongst the fauna and it may have been a period of relative stasis. These movements resulted in the Post African I Surface (Knight & Grab 2016); this must have again disrupted the distribution patterns of many butterflies and forced a number of biological changes to take place. This is about the time when a number of African genera were established, such as *Mylothris* (17 mya), *Junonia* (20 mya), *Lepidochrysops* (22 mya), *Euchrysops* (22 mya) and *Cassionympha* (25 to 15 mya) (Monteiro & Pierce 2001, Kodandaramaiah & Wahlberg 2007, Espeland *et al*. 2023). Subsequent events or combinations of them may have resulted in the formation of other genera. For instance, the Middle Miocene climatic transition (16 to 14.8 mya) produced a drier period, and at about the same time the origin of the genus *Cymothoe* (15 mya) and major diversification within the genus *Charaxes* (Kodandaramaiah & Wahlberg 2007) occurred. Further aridification during the Miocene–Pliocene climatic transition (8 to 3 mya) may have been important for the origin of more southerly centred genera such as *Aloeides* and *Thestor* around 9.5 to 5.5 mya (Boyle *et al*. 2015). With many geological and climatic changes having taken place and the systems, working on the fauna independently or in any number of combinations, at any one period, these factors would have interacted in a complex way to form the African genera, their associated species and their present distributions.

The low level of highland endemism in Angola is likely to be due to our lack of knowledge of the Angolan highland fauna. This lack of information is also illustrated by the recent discovery of a new *Erikssonia* species near Lubango (Tundavala; Braine pers. comm.). The species of the highlands of Namibia are relatively well known, but are related, in most cases, to the dry fauna further south. The rainfall conditions and elevation, which are interconnected, have probably worked together to produce the highland endemics of Namibia. A large number of endemics are associated with the relatively dry vegetation types of this region, with many of these species having a Cape origin, or secondary Cape origin, such as the various *Aloeides* spp., while others are likely to have a dry woodland origin such as *Abantis* (*Caprona*) *cassuallala*. Some species indicate the presence of a link between the dry areas of southwestern Africa and the dry areas of East Africa. *Colotis doubledayi* in southwest Africa (Namibia–Angola) has its probable counterpart species *Colotis*

aurigineus and possibly *C. chrysonome* in East Africa (Kenya and Tanzania). Another interesting species is *Acraea hypoleuca* which is found in dry gullies of the Namibian escarpment where its food-plant *Adenia pechuelii* is found; it has as its counterpart *Acraea chilo* which frequents riverbeds in dry savanna areas of Kenya and Tanzania. *Acraea chilo* feeds on *Adenia globosa* which, like *A. pechuelii,* is well adapted to dry conditions. These major biogeographic distribution patterns have also been shown for other taxa, for instance: i) intraspecific differences for ostrich (Miller *et al*. 2011), impala, hartebeest, wildebeest and roan (Lorenzen *et al*. 2012 and references within), and ii) interspecific connections for the Beisa oryx and gemsbok (Lorenzen *et al*. 2012) as well as connections between the various giraffe taxa (Lorenzen *et al*. 2012). This evidence suggests that populations of arid-adapted species have been isolated due to the expansion of moist conditions, stretching from the central block to the east of the continent leaving isolated populations in the southwest and northeast of Africa. This scenario is likely to have occurred on a number of occasions; for example the Pleistocene had at least five full pluvial cycles (Szabo *et al*. 1995).

This information supports the idea that on a number of occasions an arid corridor stretched from the arid parts of Kenya via the Luangwa and Zambezi valleys to southwestern Angola and western Namibia over certain periods of time. The arid parts of northern Namibia and southern Angola may have some species that have an East African origin (e.g., *Colotis doubledayi*, but DNA data is required to provide evidence for the direction of movement) while others are more likely to have a southern origin, e.g., members of the genus *Aloeides* (although *Aloeides* may have their initial origin in East Africa and then massive speciation in South Africa which resulted in their movement up the west coast from South Africa). These movements and isolating factors have resulted in the arid areas of this region being important for endemism.

From an evolutionary perspective, although not an endemic, *Metisella meninx* (marsh sylph) is of interest. This small, but striking and distinctive butterfly is restricted to the highlands of central-western Angola and to highland areas of South Africa, centred on Gauteng (Johannesburg area) but extending into the neighbouring provinces. Evans (1937) recorded three Angolan specimens but these were largely considered as some sort of error and the species began to be considered endemic to South Africa. There are now about 15 Angolan specimens in the Natural History Museum (NHM), London, with five different printed locality labels, by three different collectors (Larsen unpub. manuscript). The Angolan records are all from the central Angola mountains and plateau, except one from Zambezi (Moxico).

Metisella meninx inhabits marshy ground, usually with clean water, between 1,600 m and 1,700 m in elevation and hence is a habitat specialist. In South Africa it only oviposits on *Leersia hexandra* (Poaceae) (Henning & Roos 2001), an aquatic or semi-aquatic pantropical to subtropical grass, which often grows in fairly large, pure stands. The butterfly is considered vulnerable in South Africa (Henning *et al*. 2009), and this is likely to be the same in Angola.

The Angolan and South African populations of *Metisella meninx* appear to be disjunct by about 1,500 km and do not seem to have formed subspecies. This suggests either a connection in the comparatively recent past and/or that its habitat has remained stable in the two areas. For the similarly disjunct populations of *Erikssonia – E. edgei* in the Highveld of South Africa and *E. acraeina* in Angola and western Zambia – Gardiner and Terblanche (2010) suggested the following hypothesis. The crustal flexing along the Okavango–Kalahari–Zimbabwe Axis (Moore & Larkin 2001) is likely to have occurred too early to explain the disjunct distribution of *Erikssonia* from the Upper Zambezi to the Limpopo systems. However, subsequent to this flexing, a major endorheic system formed that drained into the Kalahari Basin (Moore & Larkin 2001). Erosion upstream of the Mid-Zambezi led to the capture of the Upper Zambezi in the Lower Pleistocene. This link was severed in the mid- to late Pleistocene (0.5 mya) by displacement along the Linyanti and Chobe faults, diverting the flow of the Cuando and the Zambezi headwaters into the Palaeo-Makgadikgadi, which filled to around the 945-m level (Moore & Larkin 2001). *Erikssonia* appears to be associated with rainfall of at least 600 mm per annum. It is possible that before the capture of the Upper Zambezi, the wet environment allowed a widespread distribution of *Erikssonia* from the highlands of Angola to the Waterberg in Limpopo Province, South Africa. *Erikssonia* in the north would then have been connected to the southern population via eastern Botswana and western Zimbabwe. The movement or previous widespread occurrence of *Erikssonia* may also have been influenced by cyclical climatic changes during the last 2.6 million years (Zachos *et al*. 2001, deMenocal 2004, Brown *et al*. 2007). The wetter and warmer interglacial periods are likely to have provided a more suitable and widespread habitat. It is possible that the isolation of *Erikssonia edgei* and *Metisella meninx* in South Africa is the result of more recent environmental barriers and not past climatic isolation. Without genetic studies on these species, it is impossible to tell when and if separation occurred and on how many occasions.

The monobasic and endemic *Mashunoides carneiromendesi* is of interest because it is the only butterfly species which is endemic at the genus level. This species may be associated with the headwaters and catchment area of the Lungué-Bungo [Lungwebungu], Cuando, Cuanavale and Cuito rivers. These headwaters have permanent water bodies which is unusual as they are associated with the Kalahari sand system.

It seems Miombo woodland has a relatively recent origin (4 to 3 mya) (Boom *et al*. 2021), and it has certain butterfly taxa associated with it. The origin of Miombo appears to be towards the east of Africa (oldest clade), followed by a more recent clade in southern Central Africa and the youngest in southwest Africa (Angola). The increasing aridity with periods of climatic instability and expansion of C4 savanna, due to C4 plants having a carbon fixation advantage under conditions of drought, high temperatures, and nitrogen or CO_2 limitation, experienced by the fragments of Miombo over the last million years or so would have been ideal for speciation events. Not only is the Angolan Miombo influenced by this east-to-west pattern of Miombo movement but it is also influenced by changes due to the retraction, or expansion, of forest from the north. In this regard, Angola and northwestern Zambia form a zone of "double influence". This may be the reason for the present high butterfly endemism of the Angolan Miombo and the high number of species in the Miombo–Forest intergrade. This part of Angola encompasses the following ecoregions of Burgess *et al*. (2004): Angolan Miombo Woodlands (49), Southern Congolian Forest-Savanna Mosaic (42) and the Western Congolian Forest-Savanna Mosaic (43).

GAPS IN KNOWLEDGE, AND RESEARCH AND CONSERVATION PRORITIES

It is apparent that our knowledge of the butterfly species of the Angolan highlands and Angola in general is lacking. This is also the case for many other invertebrate groups; for instance, Serrano and Capela (2013) found that some species of tiger beetles (Cicindelinae) are only represented by the holotype specimen (some without a locality), and some records are based on a single specimen or the type series. In their article, records were given for six species of Cicindelinae previously unknown from Angola which included two undescribed species, *Foveodromica* sp. n. 1 and *Foveodromica* sp. n. 2. This situation is similar for other invertebrate groups such as the longhorn beetles (Cerambycidae; Ferreira 1971), the ant nest beetles (Paussini; Serrano & Capela 2015) and the dragonflies (Odonata; Kipping *et al*. 2019), although dragonfly collecting has recently increased (Kipping *et al*. 2019).

Although butterflies can be considered charismatic, as far as invertebrates go, they receive comparatively little attention from professional taxonomists, ecologists and biologists on the African continent. We therefore rely on amateur butterfly enthusiasts to obtain knowledge on this group. The activity of amateur enthusiasts and citizen science projects means that butterflies are now our best known invertebrate taxonomic group in Africa, both in terms of identification and distribution.

It has been shown for South Africa that areas of butterfly endemism do not overlap with those of vertebrate endemism (Mecenero *et al*. 2013, Edge & Mecenero 2015) and this is likely to be the case for other invertebrates. As a result of the "Conservation Assessment of Butterflies of South Africa, Lesotho and Swaziland: Red List and Atlas" (Mecenero *et al*. 2013) it has been shown that although there is some overlap with areas of vertebrate biodiversity, most areas of butterfly interest and endemism have no form of protection (Edge & Mecenero 2015). This is undoubtedly the same for Angola and Namibia. Our present limited knowledge indicates that the Miombo woodlands and drier habitats have a high level of butterfly endemism, but it is important to locate other areas of invertebrate endemism in Angola. The Lepidoptera, in particular the butterflies, are an ideal candidate for invertebrate studies. They are more visual and charismatic than most invertebrate groups, for Africa they are relatively well known (Gardiner 1997), and they can be included in citizen science projects. Such taxonomic and ecological work is required not only in the Angolan highlands but also in the rest of Angola and parts of Namibia. We still do not know how well the ecoregions of these two countries are represented for invertebrate conservation. We also need to keep in mind that invertebrates have the highest number of species of any animal group and, although their role in driving ecosystems is not well understood, it is undoubtedly important for the health and functioning of systems (Wheeler 1990). The butterflies provide a unique opportunity to study, in more detail, biological areas of interest for Angola. They can have very short life cycles (from three months to a year), can have a very limited population distribution (sometimes only tens of metres squared), and have a wide variety of life history strategies, ranging from herbivory to predation.

For both the linkage from the dry southwest of Angola to Kenya (with *Colotis doubledayi* and *Acraea hypoleuca* in the southwest and *C. aurigineus* and *A. chilo* in the northeast) and the link between the Angola highlands and the South African Highveld (*Erikssonia* spp. and *Metisella meninx*) we do not know the origin and hence original direction of species movement. Genetic studies providing divergence times between the populations are required in order

to provide evidence for the cause of the present distributions. These species provide ideal material for genetic studies and for elucidating relationships between geological events and climatic conditions with speciation and biogeography. Targeted phylogenetic studies need to be undertaken. DNA sampling would help reveal the relatedness of these species both in relation to isolated sister species as well as to other members of the group. For instance, how is *Acraea hypoleuco* related to *A. chilo*, as well as to the much more widely distributed savanna species such as *Acraea acara*? Lepidopterists need to work closely with geologists in an attempt to further unravel periods of significant evolutionary events.

In this paper, we have focused on the endemic species and a few species of interest, but a detailed analysis of the complete Angolan and Namibian butterfly fauna would be worthwhile. This would provide more information on the biogeography and origins of species as well as illustrating areas of high diversity and endemism.

It is very likely, as in most parts of Africa (Burgess *et al*. 2006), that human-induced changes are a threat to many invertebrate species in Angola. These threats are well documented (IUCN 2023) and the impacts of human activities on our systems are now obvious. These impacts are currently mainly due to land use changes and increased population pressures, especially in the highland areas, but the significance of broad climatic changes is likely to increase over the next decades (e.g., Hussain *et al*. 2020). Focusing efforts on maintaining biodiversity and minimising human impact on – and protecting – the few remaining healthy systems should be a priority. An in-depth and thorough butterfly analysis could help to inform these actions. The consideration of invertebrates in conservation planning is likely to result in improved functioning of systems.

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Appendix 1: *List of endemic and near-endemic butterfly taxa of Angola and Namibia*

NYMPHALIDAE

Charaxinae

1. *Charaxes brainei* van Son, 1966 – sp. near-endemic to Namibia and Angola
Type locality: [Namibia]: "Kombat, S.W. Africa". Holotype (male) in the Transvaal Museum, Pretoria, South Africa. **Diagnosis**: The female differs from that of *Charaxes vansoni* in the marked suffusion of blue into the postdiscal spots of the forewing upperside and the discal band of the hindwing, and the slight violaceous shade on the hindwing underside (Pringle *et al*. 1994). **Distribution**: Angola (south), Botswana (northwest), Namibia (northeast). **Specific localities**: Botswana – Western Okavango (Larsen 1991l). Namibia – Kombat (TL; J Braine); between Otavifontein and Grootfontein (Pennington); western Caprivi (S Braine); Waterberg Plateau Park (Swart 2004). **Habitat**: Dry savanna. **Habits**: Similar to those of *Charaxes vansoni* but seems to be more readily attracted to fermenting fruit than *C. vansoni* (Pringle *et al*. 1994). **Flight period**: October to June; commonest in March and April (Pringle *et al*. 1994). **Early stages**: Henning (1989: 348). **Larval food**: *Peltophorum africanum* Sond. (Fabaceae) [Henning 1989: 348].

2. *Charaxes ehmckei* Homeyer & Dewitz, 1882 – sp. endemic to Angola
Type locality: Angola: "Pungo Andongo". Female first described by Bivar de Sousa 1992 (*Boletim da Sociedade Portuguesa de Entomologia* Supplement No. 3: 531 (523-541).). **Distribution**: Angola. **Specific localities**: Angola – Pungo Andongo (TL); Canhoca (Jordan 1908). **Habitat:** Evergreen, moist forest. **Habits:** Typical of the group, often flying rapidly along roads stopping to feed. **Larval food**: Probably *Senegalia schweinfurthii*.

3. *Charaxes figueirai* Bivar de Sousa & Mendes, 2014 – sp. endemic to Angola
Type locality: Type material: "MA: Duque de Bragança (today Kalandula), 5/1971, 1 holotype ♂ (BS-13287) 3 paratype ♂♂ (BS-13288/13290); 20/3/1973, 1 paratype ♂ (AF-NYM14952). Malanje, 19/3/1973, 1 paratype ♂ (AFNYM14951)". **Relevant literature**: Bivar de Sousa & Mendes (2014) on Angolan *Charaxes*.

4. *Charaxes fulvescens rubenarturi* Bivar de Sousa & Mendes, 2017 – ssp. endemic to Angola
Type locality: Angola: "Kwanza Sul: Mussende, XII-2015, AS + RC, 1 1 (BS-34880)". Place of deposition of holotype not given. **Distribution**: Angola. **Specific localities**: Angola – Mussende (TL); Quiminha (Mendes *et al*. 2017); Golungo Alto (Mendes *et al*. 2017); Salazar (Mendes *et al*. 2017); Calulo (Mendes *et al*. 2017); Inga (Mendes *et al*. 2017).

5. *Charaxes jahlusa angolensis* Mendes & Bivar de Sousa, 2017 – ssp. endemic to Angola
Type locality: Angola: Namibe: Bruco, 8-IX-1974, 1 1, PC (BS-12669). Place of deposition of holotype not given. **Distribution**: Angola. **Specific localities**: Angola – Bruco (TL).

6. *Charaxes lucretius saldanhai* Bivar de Sousa, 1983 – ssp. endemic to Angola
Type locality: Angola: "Bessa Monteiro". Type specimen in the collection of Bivar de Sousa. **Distribution**: Angola (northwest). **Specific localities**: Angola – Bessa Monteiro (TL).

7. *Charaxes macclouni carvalhoi* Bivar de Sousa, 1983 – ssp. endemic to Angola
Type locality: Angola: "Kwanza Norte: Dalatando (Salazar) 1 1 (BS-1918)". Type specimen in the collection of Bivar de Sousa. **Distribution**: Angola (northwest). **Specific localities**: Angola – Dalatando (TL); Calulo (Mendes *et al*. 2017).

8. *Charaxes minor karinae* Bouyer, 1999 – ssp. endemic to Angola
Type locality: Angola: "Cuanza Sul, I/II-1999 (T. Bouyer & M. Hasson)". Holotype (male) and allotype (female) in the Royal Museum for Central Africa (MRAC). **Distribution**: Angola. **Specific localities**: Angola – Cuanza-Sul (TL). **Larval food**: *Albizia gummifera* (J.F.Gmel.) C.A.Sm. (Fabaceae) [Bouyer 1999].

9. *Charaxes trajanus bambi* Bivar de Sousa & Mendes, 2006 – ssp. endemic to Angola
Type locality: Angola: "Uíge: Rio Bambi banks, 15-X-1964, (Bivar de Sousa – 13605)". **Diagnosis**: Differs from the nominate subspecies in the yellowish-green colour of the dorsal discal area of the hindwing (greyish-white and smaller in the nominate subspecies); much rounder shape; the clearly more individualised postdiscal white spots (dorsal and ventral surface) of the forewing; marginal brown area of hindwing in female much narrower; in the male the included white dots are much smaller and the Uíge specimens are larger (Bivar de Sousa & Mendes 2006). **Distribution**: Angola. **Specific localities**: Angola – Bambi River, Uíge Province (07°26'S, 14°27'E; 600 m) (TL). **Habits**: A scarce to rare butterfly, usually found as single specimens scattered in the forest. It keeps to

deep shade (Larsen 2005). The flight is slow and buzzing, somewhat resembling day-flying moths (Larsen 2005).

10. *Palla ussheri hassoni* Turlin & Vingerhoedt, 2013 – ssp. endemic to Angola
Type locality: Angola: Cuanza-Sul, Dinguir, 458 m, 11°19'S, 14°10'E, 13/17-III-2005. Holotype (male) in the MRAC, Tervuren, Belgium. **Distribution**: Angola. **Specific localities**: Angola – Dinguir (TL); Cassoco [11°25'S, 14°01'E] (Turlin 2013).

Danainae

11. *Amauris crawshayi angola* Bethune-Baker, 1914 – ssp. endemic to Angola
Type locality: Angola: "N'Dalla Tando, N. Angola". **Distribution**: Angola.

12. *Amauris dannfelti dannfelti* Aurivillius, 1891 – ssp. endemic to Angola
Type locality: [Angola]: "Congo-Gebiete". Holotype in the Swedish Natural History Museum (images available at www2.nrm.se/en/lep_nrm/d). **Distribution**: Angola.

Heliconiinae

13. *Acraea bellona* Weymer, 1908 – sp. endemic to Angola
Type locality: Angola: "Benguella". [Benguela, Benguela Province]. **Distribution**: Angola. **Specific localities**: Angola – Benguella (TL).

14. *Acraea brainei* Henning, 1986 – sp. endemic to Namibia and Angola
Type locality: [Namibia]: "Hartmanns Valley, 44 km S. of Cunene River". **Diagnosis**: Bears some resemblance to *Acraea nohara* but the genitalia show that it is more closely related to *Acraea neobule*. It can be distinguished from *Acraea nohara* by the following: the shape and distribution of the black spotting; the absence of heavy black spotting along the margin and outer part of the veins of the forewing; a row of spots on the marginal black border of the hindwing (Pringle *et al*. 1994). **Distribution**: Angola, Namibia (northwest). **Specific localities**: Angola – Iona Peak, Iona National Park [16°55'02.8"S, 12°36'10.6"E] (Willis 2009). Namibia – Hartmann's Valley in Kaokoland, in an area extending from about 30 km south of the Kunene River to the Engo River (TL; Pringle *et al*. 1994); Etanga, 100 km west of Opuwo (Swart 2004). **Habitat**: Dry savanna. Granite outcrops on hills and ridges (Pringle *et al*. 1994). **Habits**: Both sexes feed from the flowers of the larval host-plant (Pringle *et al*. 1994). **Flight period**: February to April (Pringle *et al*. 1994). **Early stages**: Henning (1986). **Larval food**: *Turnera oculata* Story (Turneraceae) [Braine, in Henning (1986)?]. **Relevant literature**: Schutte (2021) on evolution and host-plant relationship.

15. *Acraea hypoleuca* Trimen, 1898 – sp. endemic to Namibia
Type locality: None given in the original description (the unique holotype label data stated only 'Coll. Watson, 1871'). **General remarks**: "The first specimen of *Acraea hypoleuca* was a male collected in 1871 but with no recorded locality. Trimen did his description in 1898 from this specimen. The origin of that specimen was a point of contention for many years; Eltringham came to the conclusion that it could be from South West Africa [Namibia]. The closest relative of *Acraea hypoleuca* is *Acraea chilo* Godman, which occurs from East Africa to Arabia. The second specimen was taken by Dr Brown at Maltahöhe in South West Africa; it was a female and was described by Dr Pinhey in 1972. This specimen is illustrated in *Pennington's butterflies of southern Africa* (1978) as No. 120. In 1979 I [Stephen Braine] collected a female at Rössing and in 1982 I found a male at the Ugab River. In January 1983 I collected six males at the Ogam Hills and another male at the Ugab River. All these localities are in South West Africa [Namibia]. This butterfly is not as rare as it was originally thought to be. It has been found at several other localities by myself. … I have recorded this butterfly from the Swakop River northwards to the Sechomib River in the central section of Kaokoland." (Braine & Henning 1984). **Distribution**: Namibia. **Specific localities**: Namibia – Farm Mooirivier in the Maltahöhe district, on the edge of the Zaris mountains (H Brown); Rössing (S Braine); Ugab River (S Braine); Ogams Fountain, in Kaokoland (S Braine); Khumib Konkol (Ficq); Khan River Valley near Arandis (J Dobson, pers. comm.). **Habitat**: Arid savanna. Flies in gullies and on granite outcrops where its larval host-plant grows (Braine & Henning 1984). **Habits**: Adults fly from 10h00 to 18h00. It has been found to feed on the flowers of two *Psilocaulon* species, with a marked preference for the flowers of *Calicorema capitata* (Braine & Henning 1984). **Flight period**: December to June, with peak emergence in January and February (Braine & Henning 1984). **Early stages**: Braine & Henning (1984: 6). **Larval food**: *Adenia pechuelii* (Engl.) Harms (Passifloraceae) [Braine & Henning (1984: 6)]. **Relevant literature**: Schutte 2021 [evolution and host-plant relationship; African Butterfly News 2021 no. 2: 9].

16. *Acraea lapidorum* Pierre, 1988 – sp. endemic to Angola
Type locality: Angola: "Upper Lungwe-Bungo River, S.E. Angola". **Distribution**: Angola (southeast). Known only from the holotype. **Specific localities**: Angola – Upper Lungwe-Bungo River (TL).

17. *Acraea onerata* Trimen, 1891 – sp. endemic to Angola
Type locality: [Angola]: "Okavango River". **Diagnosis**: Similar to *A. nohara* but the hindwing upperside marginal band in *onerata* is clearly spotted with the ground-colour of the wings (Pringle *et al*. 1994). **Distribution**: Angola. **Specific localities**: Angola – Okavango River (TL); Bihe (Eltringham 1911). **Flight period**: December appears to be the only recorded month (Pringle *et al*. 1994).

18. *Acraea violarum anchietai* Mendes & Bivar de Sousa, 2017 – ssp. endemic to Angola
Type locality: Angola: "HUAMBO, Cuíma, XII-2015, 1 1, (BS-34931", Holotype (male) in the MUHNAC, Portugal. **Diagnosis**: Differs from the nominate subspecies in the triangular rather than round white markings on the margin of the hindwing underside (Bivar de Sousa *et al*. 2017). **Distribution**: Angola. **Specific localities**: Angola – Cuima (TL); Bihé (Eltringham 1912); Calweha (Eltringham 1912); Caconda (Eltringham 1912); Cubal R. (Eltringham 1912); Cambo (Eltringham 1912); Caquenje (Eltringham 1912); Benguella (Eltringham 1912); Baillundo [Bailundo] (le Doux 1922); Kalukembé (Monard 1956); Sangevé (Monard 1956); Tiytunda (Monard 1956); Bimbi (Monard 1956); Chimporo (Monard 1956); Chianga (Bivar de Sousa *et al*. 2017); Nova Lisboa (Bivar de Sousa *et al*. 2017); Sacaala, Nova Lisboa (Bivar de Sousa *et al*. 2017).

Limenitidinae

19. *Bebearia cocalia ngolae* Mendes, Bivar de Sousa & Lopes, 2021 – ssp. endemic to
Type locality: "Holotype, ANGOLA, Cuanza Sul, Calulo, Fazenda Klein, 1-XII-2015 (BS-35041). Paratypes: Bengo: Tentativa, 1 1, 13-III-1972 (NY6650489). Cuanza Norte, Salazar (Dalatando), 2 00, 25-V-1972 (PC-nn); Ibid, 1 1, 25-VI-1972 (PC-1000), det. as B. mardania; Ibid, 11, 25-VII-1972 (PC-nn); Ibid, 1 1, 21-XI-1972 (PC-1001); Ibid, 1 0, 31-I-1973 (PC-19824); Ibid, 1 0, 18-II-1973 (BS-14606); Ibid, 1 1, 12-VIII-1974 (PC-140); Ibid, 1 1, 18-VIII-1974 (PC-157); Ibid, 11, 23-I-1975 (PC-nn). Cuanza Sul, Cabuta, 1 1, 29-XI-2015 (n. 49) (BS-35040). Calulo, Aldeia Catembo, 1 1, 5-XI-2014 (BS-33505). Calulo, Alto Ventura, Fazenda Monte Café, (n. 49), 2 11, 1-XII-2017 (BS-36692, 36693). Calulo, Fazenda Klein, 1 1, 1 0, 1-XII-2015 (BS-35042, 35043); Ibid, 10, 8-XII-2017 (n. 44) (BS-36694) plus 1 1, 1 0 (BS-36690, 36691). Novo Redondo (Sumbe), 4 11, I-1963 (BS-15735, 15737, 15740, 15742). Uíge, Fazenda S. José, Nova Caipemba, 1 1, XII-1975 (BS-15741)." **Distribution**: Angola.

20. *Bebearia hassoni* Hecq, 1998 – sp. endemic to Angola
Type locality: Angola: Cuanza-Sul. **Distribution**: Angola. **Specific localities**: Angola – Cuanza-Sul (TL).

21. *Bebearia paludicola meridionalis* Mendes, Bivar de Sousa & Lopes, 2021 – ssp. endemic to Angola
Type locality: "Holotype, ANGOLA, Cuanza Norte: Salazar (Dalatando), 10-IV-1972 (BS-14605). Paratypes: Cuanza Norte: Salazar (Dalatando), 1 1, 14-III-1975 (PC-nn). Cuanza Sul, Calulo, Alto Ventura, Fazenda Monte Café, (n. 44), 1 0, 8-XII-2017 (BS-36695)."

22. *Bebearia sophus angolensis* Mendes, Bivar de Sousa & Lopes, 2021 – ssp. endemic to Angola
Type locality: "Holotype, ANGOLA, Cuanza Norte, Salazar, 6-I-1975 (PC-nn). Paratypes: ANGOLA, Cuanza Norte, Salazar, 1 1, III-1973 (AF-NY681001, in the NHMUP). Uíge, Inga, 1 0, IX- 1964 (BS-15791)."

23. *Euphaedra divoides* Bivar de Sousa & Mendes, 2019 – sp. endemic to Angola
Type locality: "Angola: Holotype (female): Buco Zau, Cabinda, 18-V-1952"; in the Natural History and Science National Museum, Lisbon, Portugal. **Distribution**: Angola (Cabinda). **Specific localities**: Angola – Buco Zau (TL). **Habitat**: Forest. **Habits**: Typical *Euphaedra* flies rapidly gliding above the ground, settling in patches of semi-light or to feed on the ground, often with wings open. **Note**: *Euphaedra divoides* Bivar de Sousa & Mendes (2019) is probably a synonym of *E. permixtum diva* Hecq, 1982.

24. *Euphaedra harpalyce commineura* Hecq, 1999 – ssp. endemic to Angola
Type locality: Nothing published. **Distribution**: Angola. **Specific localities**: Nothing published.

25. *Euphaedra uigensis* Bivar de Sousa & Mendes, 2017 – sp. endemic to Angola
Type locality: Angola: "Uíge, Inga, near the Vale do Loge colonial settlement, October 1964, 1 1 (BS-16154", holotype (male) in the Museu Nacional de História Natural e da Ciência (MUHNAC), Portugal. **Distribution**: Angola. **Specific localities**: Angola – Inga, near the Vale do Loge colonial settlement (TL). **Habitat**: Gallery forest on the Loge River (Bivar de Sousa *et al*. 2017). **Flight period**: October, November, December (Bivar de Sousa *et al*. 2017).

Nymphalinae

26. *Precis larseni* Mendes, Bivar de Sousa, Vasconcelos & Lopes, 2018 – sp. endemic to Angola
Type locality: "Holotype: Moxico: Lumeje, IV-1965, 1 1 DSF (BS-17687). Paratypes: Huambo: Chianga, V-1972, 1 1 DSF (PC); VII-1975, 11 DSF (PC). Cuanza-Norte: Golungo Alto, ?-1962, MM, 2 11, 1 0 DSF (MUHNAC-17324, 17328, 17330). Moxico: As for the holotype, 1 1, 1 0 DSF (BS-17688-17689), 1 1 WSF (BS-17690); V-1965, 1 1 DSF (BS-17691); VIII-1965, 1 1 DSF (BS-17692). Teixeira de Sousa, II-1965, 1 1 WSF (BS-17693). All the types in the MUHNAC. Non-type material: Huambo: Nova Lisboa, IV-1964, 1 1, 4 00 (NA); V-1964, 1 1 (NA); VI-1964, 1 1, 1 0 (NA); VI-1965, 1 1, 1 0 (NA-); V-1970, 1 0 (NA)". **Habitat**: The studied representatives of the species were all obtained above 1,000 masl in areas with "Miombo" – mixed savanna with trees, *Brachystegia,* and open forest margin (Wild & Grandvaux-Barbosa 1967, Grandvaux-Barbosa 1970). **Habits**: The African leaf commodore, eared commodore or African leaf butterfly, *Precis tugela*, was reported by Larsen (1996) in Kenya in forest clearings and along roads but also in more open areas including agricultural fields and Kielland (1990) stressed it is common in Tanzania in forests and forest margins and that it may fly from 350–2,500 masl. (*P. tugela aurorina*) or from 800–2,000 masl. (*P. tugela piryformis*). Willis & Woodhall (2010, sub *Junonia*) reports the nominate *Precis tugela* to occur in the Afromontane forests of the South African eastern escarpment.

Biblidinae

27. *Sevenia occidentalium penricei* (Rothschild & Jordan, 1903) – ssp. endemic to Angola
Type locality: Angola: "Calweha River, Angola". **Distribution**: Angola.

Satyrinae

28. *Brakefieldia angolensis* (Kielland, 1994) – sp. endemic to Angola
Type locality: Angola: "Bango, Dr Ansorge (no date)." Holotype in NHM, London. **Distribution**: Angola.

29. *Brakefieldia ochracea* (Lathy, 1906). Aduse-Poku *et al*. 2016 comb. n.
Type locality: Angola: "Bihé District, Angola". **Distribution**: Angola (central plateau). **Specific localities**: Angola – Benguella (Weymer, 1908); Upper Cubango-Cunene Watershed (Talbot 1932). Serra de Namba; Mount Mocco.

30. *Mashunoides carneiromendesi* Mendes & Bivar de Sousa, 2009 – sp. and genus endemic to Angola
Type locality: Angola. "Cuando Cubango Province". **Distribution**: Angola (southeast – Cuando Cubango Province, Mendes & Bivar de Sousa 2009d). **Habitat**: Wetlands.

31. *Neita bikuarica* Mendes & Bivar de Sousa, 2006 – sp. endemic to Angola
Type locality: Angola: "Huila Province: Capelongo, ?/XI/1957, EAU (CZ-2964)". Described from a single male captured by the "Estudos Apicolas do Ultramar" mission (EAU) near Capelongo (14°53'S; 15°05'E, ca. 1,200 m). Holotype (male) in the Instituto de Investigação Cientifica Tropical entomological collection (CZ), Lisbon, Portugal. **Diagnosis**: Closest to *Neita victoriae*, from which it differs in the more acute forewing apex, narrower orange ring surrounding the ventral hindwing ocelli, greater width of the area delimited by the brown line enclosing the hindwing ocelli, and the presence on the posterior ventral wing of a well-defined oblique brown line that crosses the cell. On the upperside of the forewing the orange halo that surrounds the ocellus enters space two, while in *Neita victoriae* it does not pass the first cubital (Mendes & Bivar de Sousa 2006). Also resembles *Neita extensa*, which has a larger forewing ocellus but with a deep invagination on the peri-ocellar line on the hindwing underside. *Neita orbipalus* is also similar but has better developed orange/yellow in the ocelli and lacks (as do the other species in the genus), an oblique dark line across the cell on the hindwing underside (Mendes & Bivar de Sousa 2006). **Etymology**: Named for its geographical origin, close to the northern border of the Bicuar National Park. **Distribution**: Angola. **Specific localities**: Angola – Capelongo, Huíla Province (TL). Known only from the type locality (Mendes & Bivar de Sousa 2006). **Habitat**: *Brachystegia* woodland (Mendes & Bivar de Sousa 2006).

LYCAENIDAE

Poritiine

32. *Alaena brainei* Vári, 1976 – sp. endemic to Namibia
Type locality: [Nambia]: "South West Africa: Tiger Valley, Kombat". **Diagnosis**: Differs from the similar *Alaena amazoula* in that it has smaller, sharply edged ochreous-yellow spots (especially on the hindwing of males), and broader, sharply edged fuscous brown wing borders in females (Vári 1976). **Distribution**: Namibia (north-central). **Specific localities**: Namibia – Tiger Valley, Kombat (TL; Kroon); Grootfontein (J. Braine); Abachaub (Pringle *et al*. 1994); Otjiwarongo district (Pringle *et*

al. 1994); Namutoni (Pringle *et al*. 1994); Tsumeb (Pringle *et al*. 1994); Maroelaboom (Pringle *et al*. 1994); Otavi (Pringle *et al*. 1994). **Habitat**: Rocky grassland. **Habits**: Nothing published. **Flight period**: November to early May (Pringle *et al*. 1994). **Larval food**: Algae (Cyanophyta) on rocks [Pringle *et al*. 1994: 127].

33. *Alaena rosei* Vane-Wright, 1980 – sp. endemic to Angola
Type locality: Angola: "10 miles east of Gabela". **Distribution**: Angola. **Specific localities**: Angola – 16 km east of Gabela (TL); vicinity of Sadabandeira (Ackery *et al*. 1995).

34. *Cooksonia nozolinoi* Mendes & Bivar de Sousa, 2007 – sp. endemic to Angola
Type locality: Angola: "Huambo Province: Nova Lisboa [= Huambo], 12/9/1975, (NA, no number) (CZ-5265)". Holotype (female) in the CZ, Lisbon, Portugal. Known only from a single female found in the collection of the late Armando Nozolino de Azevedo, taken at Huambo (12°46'S, 15°44'E; 1,650 m). **Diagnosis**: Closest to *Cooksonia neavei* but differs from it in that the dark dot of the forewing (dorsal and ventral cell apex) is completely isolated from the costal area, the hindwing marginal area is narrower and shows small white punctuations, and the hindwing irregular blackish spots of the underside are less numerous and less extended (Mendes & Bivar de Sousa 2007). **Distribution**: Angola (Angolan Planalto). **Specific localities**: Angola – Huambo (TL). **Habitat**: Miombo woodland.

35. *Deloneura barca* (Grose-Smith, [1901]) – sp. endemic to Angola
Type locality: Angola: "Kinsombo". **Distribution**: Angola.

36. *Falcuna lacteata* Stempffer & Bennett, 1963 – sp. endemic to Angola
Type locality: Angola: "Angola". **Distribution**: Angola. **Habitat**: Primary forest.

37. *Falcuna libyssa angolensis* Stempffer & Bennett, 1963 – ssp. endemic to Angola
Type locality: Angola: "Angola". **Distribution**: Angola (north – "Uíge and Cuanza-Norte Provinces" (L Mendes pers. comm. 2018). **Habitat**: Primary and secondary forest with a canopy (Larsen 2005). **Habits**: Widely and evenly spread in forest. Males perch on the ends of twigs along forest roads and in clearings, defending their territories with vigour and a rapid flight for a poriitine. They return to their perch where they alight on the very tip with great skill. Males engage only with relatively fast-flighted congenerics, ignoring other more weakly flying poriitines (Larsen 2005). Both sexes feed at extrafloral nectaries of Marantaceae and other creepers, often in the company of other poriitines. Males of *libyssa* are aggressive at such feeding sites, pushing other individuals away with sharp flicks of their wings (Larsen 2005).

38. *Liptena homeyeri straminea* Stempffer, Bennett & May, 1974 – ssp. endemic to Angola
Type locality: Angola: "Bange Ngola". **Distribution**: Angola (except southeast). **Specific localities**: Angola – Bange Ngola (TL).

Aphnaeinae

39. *Aloeides angolensis* Tite & Dickson, 1973 – sp. endemic to Angola
Type locality: Angola: "Benguella". Holotype (male): Benguella, 26.ix.1904 (Dr Ansorge), B.M. Type No. Rh. 17228. Allotype (female); data as holotype. B.M. Type No. Rh. 17229). **Diagnosis**: Most similar to *A. damarensis*. **Distribution**: Angola. **Specific localities**: Angola – Benguella (TL). Benguela is a town and province in southwest Angola.

40. *Aloeides argenteus* Henning & Henning, 1994 – sp. endemic to Namibia
Type locality: Namibia: "riverbed near Sima Hill, Kaokoland, 30 Mar. 1986, H.C. Ficq." Holotype in Transvaal Museum, Pretoria. **Diagnosis:** Characterised by the pale orange ground-colour on the upperside of the wings, and the very pale ochreous underside with large silvery markings (Pringle *et al*. 1994). **Distribution**: Namibia. Known only from the type locality. **Specific localities**: Namibia – Ganias River, near Sima Hill, 19°15'S, 13°00'E (TL; Braine and Ficq). **Habitat**: Very arid area just inland of the coastal dunes. The type locality is in a dry riverbed (Pringle *et al*. 1994). **Habits**: Specimens settle on rocks and pebbles, many of which are white quartzitic) (Pringle *et al*. 1994). **Flight period**: March (Henning & Henning 1994).

41. *Aloeides namibiensis* Henning & Henning, 1994 – sp. near-endemic to Namibia
Type locality: Namibia: "Omatako Omuramba, 30 Dec. 49." Holotype in Windhoek Museum, Namibia. **Diagnosis**: Most closely related to *Aloeides trimeni*, from which it can be separated by the ochreous greyish brown of the upperside basal area (brown to orange in *trimeni*) and broad postdiscal markings (narrow in *trimeni*) (Pringle *et al*. 1994). **Distribution**: Botswana, Namibia. Known only from two pairs from the type locality and specimens from a single locality in Botswana. **Specific localities**: Botswana – According to G Henning (pers. comm.), I Coetzer caught this species near the tarred road between Windhoek and Ghanzi (Tsootsha) in January 1999 (Larsen 1991). Namibia – Omatako Omuramba, approximately

19°00'S, 19°30'E (TL). **Habitat**: Arid savanna. **Flight period**: The type series was collected on 30 December (Pringle *et al*. 1994).

42. *Aloeides tearei* Henning & Henning, 1982 – sp. endemic to Namibia
Type locality: [Namibia]: "13 km north of Aus". **Diagnosis**: Differs from *Aloeides simplex* in the following respects: smaller; on the upperside of the wings the dark margins are wider. The markings on the upperside of the wings strongly resemble those of *Aloeides bamptoni*, while the hindwing underside markings are similar to those of *Aloeides nollothi*. Differs from these two taxa in the darker brown hindwing underside ground-colour and better developed submarginal lunules (Pringle *et al*. 1994). **Distribution**: Namibia (south). **Specific localities**: Namibia – 13 km north of Aus (TL; Littlewood); Kupferberg Pass, 30 km southwest of Windhoek (Stephen); Gamsberg in southwest Namibia (Swart 2004). **Habitat**: Semi-desert. **Habits**: Has the usual habits of the genus, flying rapidly for a short distance before settling abruptly, with closed wings, on rocks or on the ground. It is particularly fast-flighted and elusive for an *Aloeides* (Pringle *et al*. 1994). **Flight period**: August to October, February and May are the months so far recorded (Pringle *et al*. 1994).

43. *Tylopaedia sardonyx cerita* Henning & Henning, 1998 – ssp. endemic to Namibia
Type locality: Namibia: "Namibia: Regenstein, 4.xi.1995, F. Swart." Described from a large series from the type locality and a single male from Kupferberg Pass, west of Windhoek. **Distribution**: Namibia (central). **Specific localities**: Namibia – Regenstein, 30 km southwest of Windhoek (TL; Swart); Kupferberg Pass, 30 km southwest of Windhoek (Stephen); Gross Herzog peak, Auas Mountains, just south of Windhoek (Swart 2004); Gamsberg in southwest Namibia (Swart 2004).

44. *Axiocerses amanga baumi* Weymer, 1901 – ssp. endemic to Namibia and Angola
Type locality: Angola: "Palmfontain und Vogelfontain". **Distribution**: Angola, Namibia. **Specific localities**: Angola – Palmfontein and Vogelfontein (TL). **Habitat**: dry woodland (savanna).

45. *Zeritis krystna* d'Abrera, 1980 – sp. endemic to Angola
Type locality: Angola: "Muene Indala, Angola". **Distribution**: Angola (central). **Specific localities**: Angola – Muene Indala (TL). **Habitat**: Open Miombo woodland and dambos.

Theclinae

46. *Iolaus alienus sophiae* Henning & Henning, 1991 – ssp. endemic to Namibia
Type locality: Namibia: "26 km N. of Grootfontein". **Diagnosis**: Differs from the nominate subspecies in its more rounded wing shape, different shade of blue, restricted blue area on the forewing upperside, and more extensive white areas on the upperside of the wings in the female (Pringle *et al*. 1994). **Distribution**: Namibia (Grootfontein area). **Specific localities**: Namibia – 26 km north of Grootfontein (TL; Ficq); Opuwo in Kaokoland (Swart 2004).

47. *Iolaus mimosae pamelae* (Dickson, 1976) – ssp. endemic to Namibia and Angola
Type locality: [Namibia]: "South West Africa: Kombat". **Diagnosis**: The blue on the upperside of the wings is much paler than in the nominate subspecies and the underside is very pale, uniform grey. In addition, the lines on the underside are much thinner and more regular. Compared to subspecies *I. m. rhodosensae* the hindwing is more elongated towards the anal angle in the male; the blue on the upperside is of a purer tone; the discal and postdiscal lines on the underside are less widely separated; and the more regular discal line (Pringle *et al*. 1994). **Distribution**: Namibia (north). **Specific localities**: Namibia – Kombat (TL Braine); Otavifontein (Pennington); Grootfontein (Pennington).

48. *Iolaus obscura* – sp. endemic to Namibia and Angola
Type locality: [Namibia]: "Windhuk in the Damaraland". Holotype in the Swedish Natural History Museum (images available at www2.nrm.se/en/lep_nrm/o). **Diagnosis**: Similar to *Iolaus mimosae* but the underside of the wings is much darker; on the upperside forewing the blackish marking extends further basad; on the upperside of the hindwing the dark marking near the anal angle is much reduced, with only a single, well-defined, small spot in area 1B (Pringle *et al*. 1994). **Distribution**: Namibia (north), Angola (Mendes *et al*. 2018). **Specific localities**: Namibia – Windhoek (TL; two specimens); Kombat, 137 km north of Windhoek (Bampton & Braine pers. comm.; two bred specimens); eastern suburbs of Windhoek (Swart 2004). **Habitat**: Dry savanna. **Habits**: Nothing published. Despite much searching this species remained known from only four specimens (Pringle *et al*. 1994). More recently F Swart (2004) collected and bred numbers from the eastern suburbs of Windhoek. **Flight period**: December is the only month recorded (Pringle *et al*. 1994). **Early stages**: Nothing published. **Larval food**: *Plicosepalus kalachariensis* (Schinz) Danser (Loranthaceae), parasitic on *Senegalia mellifera* (Vahl) Seigler & Ebinger (Fabaceae) [Pringle *et al.* 1994: 156].

49. *Leptomyrina henningi angolensis* Dickson, 1976 – ssp. endemic to Angola
Type locality: Angola: "Luanda [08°50'S, 13°15'E". **Distribution**: Angola. **Specific localities**: Angola – Luanda (Mendes & Bivar de Sousa 2009b).

50. *Myrina silenus suzannae* Larsen & Plowes, 1991 – ssp. endemic to Namibia
Type locality: Namibia. **Diagnosis**: Characterised by the very reduced basal blue area on the upperside of the wings (Pringle *et al*. 1994). **Distribution**: Namibia (north). **Specific localities**: Namibia – Okahandja (Gaerdes); Otavifontein (Pringle *et al*. 1994); Tsumeb (Pringle *et al*. 1994); Namutoni (Pringle *et al*. 1994); Tiras Mountains (Pringle *et al*. 1994); Brandberg (Pringle *et al*. 1994).

51. *Stugeta subinfuscata subinfuscata* Grünberg, 1910 – ssp. endemic to Namibia
Type locality: [Namibia]: "Windhuk". **Diagnosis**: The main difference between *Iolaus subinfuscata* and *I. bowkeri* is the more extensive dark markings on the underside of the wings in the former (Pringle *et al*. 1994). **Distribution**: Namibia. **Specific localities**: Namibia – Windhoek (TL); Sesriem (Pringle *et al*. 1994); Namib Desert (Pringle *et al*. 1994); Namutoni (Pringle *et al*. 1994); Otavi (Pringle *et al*. 1994); Kombat (Pringle *et al*. 1994); Kaokoveld (Swart 2004); Brandberg (Swart 2004); Tsaobis Leopard Farm, Karibib district (Swart 2004); Bloedkoppie (Swart 2004). **Habitat**: Arid savanna and river courses in the Nama Karoo. **Habits**: Often flies in proximity to its larval foodplant, frequently resting on the sides of bushes (Pringle *et al*. 1994). **Flight period**: Throughout the summer months, being particularly plentiful in September and October. The nominate subspecies is possibly on the wing throughout the year (Pringle *et al*. 1994). **Early stages**: Clark & Dickson (1971: 144) [as *Stugeta bowkeri subinfuscata*; Little Namaqualand, Northern Cape Province]. Early stages unrecorded (but referred to in a comparison made with *Iolaus bowkeri* by Clark & Dickson (1971: 144)) – "The early stages have given no indication of *Stugeta bowkeri bowkeri* (Trimen) (from the eastern Cape) and *Stugeta bowkeri subinfuscata* Grünberg (from Little Namaqualand) being other than conspecific. The latter is, nevertheless, a well defined race and where it has been found by us, in Little Namaqualand, always breeds true to type." **Larval food**: *Loranthus* species (*sensu lato*) (Loranthaceae) [Pringle *et al.* 1994: 153]. *Tapinanthus oleifolius* (J.C.Wendl.) Danser (Loranthaceae) [Bampton, *vide* Pringle *et al.* 1994: 153].

Polyommatinae

52. *Lepidochrysops fulvescens* Tite, 1961 – sp. endemic to Angola
Type locality: Angola: "Samba Acenda". Holotype (male): 16.x.1903, Ansorge, B.M. Type No. Rh. 16495. Allotype (female): Cambo Caquenje, Bihe, Angola, 3.xi.1904, Ansorge, B.M. Type No. Rh. 16496. **Distribution**: Angola (highlands). **Specific localities**: Angola – Samba Acenda (TL; Ansorge); Cambo Caquenje, Bihe (Ansorge); Menjori River, Bihe (Ansorge); Ndalla Ango [Ndalatando; 9.300S, 14.910E] (Ansorge); Pedreira, Bihe (Ansorge). **Habitat**: Miombo woodland primary or degraded. **Flight period**: The type series was recorded from mid-October to the first week of November (Tite 1961).

53. *Lepidochrysops nacrescens* Tite, 1961 – sp. endemic to Angola
Type locality: Angola: "Nova Lisboa". [now Huambo -12.774°S; 15.734°E]. Holotype (male): ix.1957, J.C.[G.] Williams, B.M. Type No. Rh. 16494. **Distribution**: Angola. Known from the male holotype only. **Specific localities**: Angola – Nova Lisboa (TL). **Flight period**: The unique holotype was captured in September (Tite 1961).

54. *Uranothauma nozolinoi* Bivar de Sousa & Mendes, 2007 – sp. endemic to Angola
Type locality: Angola: "Huambo Province: Nova Lisboa, 18/IV/1965, NA, male holotype (CZ-5266)". **Diagnosis**: Most similar to *Uranothauma nubifer*. The wings are lighter but the ventral pattern is not substantially different to that of *Uranothauma nubifer*. However, the brown elements of the hindwing pattern are less distinctly individualised. The androconial patch is smaller and the shape of the valves and the development of the apical teeth of the valves are distinct from those of *Uranothauma nubifer* (Bivar de Sousa & Mendes 2007). **Distribution**: Angola. Known only from the male holotype (Bivar de Sousa & Mendes 2007). **Specific localities**: Angola – Nova Lisboa, Huambo Province (TL).

55. *Zintha hintza krooni* (Dickson, 1973) – ssp. endemic to Namibia
Type locality: [Namibia]: "Otavi". **Diagnosis**: Differs from the nominate subspecies in that it usually has more pronounced white markings on the upperside of the wings (Pringle *et al*. 1994). **Distribution**: Namibia. **Specific localities**: Namibia – Otavi (TL).

PIERIDAE

Pierinae

56. *Appias epaphia angolensis* Mendes & Bivar de Sousa, 2006 – ssp. endemic to Angola
Type locality: Angola: "Luanda: Luanda town". **Distribution**: Angola (Luanda, Bengo, Malanje, Cuanza-Norte and Cuanza-Sul Provinces). **Specific**

localities: Angola – Luanda [08°50'S, 13°15'E] (TL); Aeroporto e Estrada de Grafanil [08°50'S, 13°15'E] (Mendes & Bivar de Sousa 2006); Estrada de Catete [08°50'S, 13°15'E] (Mendes & Bivar de Sousa 2006); Caxito [08°35'S, 13°40'E] (Mendes & Bivar de Sousa 2006); Estrada da Muxima [08°50'S, 13°15'E] (Mendes & Bivar de Sousa 2006); Grafanil [08°53'S, 13°18'E (Mendes & Bivar de Sousa 2006); Quicolo [08°48'S, 13°20'E] (Mendes & Bivar de Sousa 2006); Viana [08°54'S, 13°23'E] (Mendes & Bivar de Sousa 2006); Lucala [09°24'S, 15°02'E] (Mendes & Bivar de Sousa 2006); Bom Jesus [09°10'S, 13°34'E] (Mendes & Bivar de Sousa 2006); Cacuaco [08°47'S, 13°21'E] (Mendes & Bivar de Sousa 2006); Catete [08°35'S, 13°42'E] (Mendes & Bivar de Sousa 2006); Quicama [09°11'S, 13°23'E] (Mendes & Bivar de Sousa 2006); Quiminha [08°58'S, 13°47'E] (Mendes & Bivar de Sousa 2006); Tentativa [08°36'S, 13°36'E] (Mendes & Bivar de Sousa 2006); Cassoalala [09°29'S, 14°22'E] (Mendes & Bivar de Sousa 2006); Golunga Alto [09°08'S, 14°46'E] (Mendes & Bivar de Sousa 2006); Salazar [09°18'S, 14°55'E] (Mendes & Bivar de Sousa 2006); Zenza do Itombe [09°17'S, 14°13'E] (Mendes & Bivar de Sousa 2006); Novo Redondo [11°12'S, 13°51'E] (Mendes & Bivar de Sousa 2006); Roca Rio Bimbe [11°05'S, 14°13'E] (Mendes & Bivar de Sousa 2006).

57. *Appias phaola uigensis* Mendes & Bivar de Sousa, 2006 – ssp. endemic to Angola
Type locality: Angola: "Uíge: Inga". **Distribution**: Angola. **Specific localities**: Angola – Inga, Uíge Province [07°27'S, 14°27'E] (TL).

58. *Appias sylvia ribeiroi* Mendes & Bivar de Sousa, 2006 – ssp. endemic to Angola
Type locality: Angola: "Calulo, Kuanza Sul". **Distribution**: Angola (Cuanza-Sul, Cuanza-Norte and Uíge Provinces). **Specific localities**: Angola – Calulo, Cuanza-Sul Province [09°59'S, 14°54'E] (TL); Cassoalala [09°29'S, 14°22'E] (Mendes & Bivar de Sousa 2006); Dalatando [09°18'S, 14°55'E] (Mendes & Bivar de Sousa 2006); Salazar [09°18'S, 14°55'E] (Mendes & Bivar de Sousa 2006); Inga [07°27'S, 14°27'E] (Mendes & Bivar de Sousa 2006).

59. *Colotis amata williami* Henning & Henning, 1994 – ssp. endemic to Namibia and Angola
Type locality: [Namibia]: "Namib, 7 Mar. 1976, L. Heinrich." Holotype in the Transvaal Museum, Pretoria. **Distribution**: Angola, Namibia (central and north). **Specific localities**: Angola – 10 km NNW of Namibe (Namibe) [30 m] (Willis 2009); granite inselberg 36 km NE of Namibe (Namibe) [390 m] (Willis 2009); giant *Welwitschia* site 56 km ESE of Tombua (Namibe) [177 m] (Willis 2009); floodplain of Curoca River (Namibe) (Willis 2009); Espinheira, Iona National Park [440 m] (Namibe) (Willis 2009). Namibia – Namib (TL); Brandberg [870 m] (Pringle *et al*. 1994); Etosha [1,100 m] (Pringle *et al*. 1994); Namutoni [1,098 m] (Pringle *et al*. 1994); Tsaobis Leopard Farm, Karibib district [1,006 m] (Swart 2004); Epupa Falls [614 m]; Bloedkoppie [729 m].

60. *Colotis celimene pholoe* (Wallengren, 1860)– ssp. near-endemic to Namibia and Angola
Type locality: [Botswana]: "Ad lacum N'Gami Africae". Holotype in the Swedish Natural History Museum (images available at www2.nrm.se/en /lep_nrm/p). **Distribution**: Angola, Botswana (west), Namibia, South Africa (Northern Cape Province). **Specific localities**: Botswana – Lake Ngami (TL). Namibia – Brandberg (Pringle *et al*. 1994); Kuiseb Canyon (Pringle *et al*. 1994); Okahandja (Pringle *et al*. 1994); Okosongomingo, east of Otjiwarongo (Pringle *et al*. 1994); Otavi (Pringle *et al*. 1994); Owamboland (Pringle *et al*. 1994); Rehoboth (Pringle *et al*. 1994); Sesfontein (Pringle *et al*. 1994); Windhoek (Pennington). Northern Cape Province – Tswalu Game Reserve (G. Henning and P. Roos); Richtersveld (G. Henning).

61. *Colotis danae walkeri* (Butler, 1884) – ssp. endemic to Namibia and Angola
Type locality: Angola: "Elephant Bay, south-west coast of Africa". **Distribution**: Angola (southwest), Namibia (northwest). **Specific localities**: Angola – Elephant Bay (TL). Namibia – Damaraland (Braine, Ficq & Collins); Kaokoland (Braine, Ficq & Collins); Orupembe [874 m] in Kaokoland (Brown).

62. *Colotis doubledayi* (Hopffer, 1862) – sp. near-endemic to Namibia and Angola
Type locality: [Angola]: "Congo". **Distribution**: Angola (coast), Namibia (west), South Africa (Northern Cape Province – extreme northwest). **Specific localities**: Angola – Lobito Bay (Talbot 1929); Belas Rd., 10 km S of Luanda; Luanda. Namibia – Naiam Hills, 20 miles west of Keetmanshoop (van Son 1949); Keetmanshoop (van Son 1949); Ai Ais (Pringle *et al*. 1994); Blutkuppe (Pringle *et al*. 1994); Brandberg (Pringle *et al*. 1994); Damaraland (Pringle *et al*. 1994); Fish River Canyon (Pringle *et al*. 1994); Kaokoland (Swart 2004); Kuiseb Canyon (Swart 2004); Namib Desert (Swart 2004); Orupembe (35 km east of), Spitzkoppe (Swart 2004); north of Okangwati (Swart 2004). Northern Cape Province – Vioolsdrif (Pringle *et al*. 1994); Hellskloof (Williams & Garvie pers. comm.). **Habitat**: Very arid, semi-desert. Often in dry, stony streambeds in valleys (Pringle *et al*. 1994). **Larval food**: *Maerua schinzii* Pax (Capparaceae) [Cottrell, *in* Dickson & Kroon 1978; Vioolsdrif, Northern Cape Province].

63. *Mylothris carvalhoi* Mendes & Bivar de Sousa, 2009 – sp. near-endemic to Angola
Type locality: [Angola]: "Uíge Province: Inga, Vale do Loge, ?/IX/1964, coll. A. Bivar de Sousa". The types are in the Instituto de Investigação Científica Tropical, in Lisbon. **Distribution**: Democratic Republic of Congo, Angola (Uíge Province, Mendes & Bivar de Sousa 2009a). **Specific localities**: Democratic Republic of Congo – Lukolela [1.07S, 17.16E] (Warren-Gash 2020); Kinshasa area (Warren-Gash 2020); mouth of the Congo River (Warren-Gash 2020). Angola – Inga, Loge River valley [07°23'S, 14°22'E] (TL); Ndalla Tando [Ndalatando] (Warren-Gash 2020). **Habitat**: Gallery forest.

64. *Mylothris mavunda* Hancock & Heath, 1985 – sp. near-endemic to Angola
Type locality: Zambia: "80 km south of Mwinilunga". Holotype (male) in NHM, London (Warren-Gash 2020). **Distribution**: Zambia (northwest), Angola (Mendes *et al*. 2018). **Specific localities**: Zambia – 80–100 km south of Mwinilunga, Chiwoma area (TL) (Heath *et al*. 2002). **Habitat**: *Cryptosepalum* forest. **Habits**: Nothing published. **Flight period**: Recorded in March, April, May, November and December.

65. *Mylothris spica gabela* Berger, 1979 – sp. endemic to Angola
Type locality: Angola: "7 mls W. de Gabela". Holotype (male) in the NHM, London (Warren-Gash 2020). Paratype in the MRAC, Tervuren, Belgium. **Distribution**: Angola (central). Known only from the type series. **Specific localities**: Angola – seven miles west of Gabela (TL).

PAPILIONIDAE

Papilioninae

66. *Papilio bacelarae* Bivar de Sousa & Mendes, 2009 – sp. endemic to Angola
Type locality: Holotype 1: "Cabinda: Buco Zau, dia, 27-VII-1952 (CZ-5639)". Paratype 1: No labels (Cabinda series) (CZ-5640). The female is unknown. **Distribution**: so far only in Cabinda, Angola. **Habitat**: Low altitude primary rainforest.

67. *Papilio chitondensis* Bivar de Sousa & Fernandes, 1966 – sp. endemic to Angola
Type locality: Angola: "Roça Chitonde-Jungo-Novo Redondo. Fevereiro de 1963". Holotype (male) in Museu Bocage. Female described by Bouyer (2005). **Distribution**: Angola. **Specific localities**: Angola – Roça Chitonde-Jungo-Novo Redondo, Cuanza-Sul Province (TL). **Early stages**: Nothing published. **Larval food**: Nothing published. **Habitat**: The species seems localised around 1,000 masl down to sea level on the western part of the Angolan Planalto. Seles in Cuanza-Sul. **Relevant literature**: Bouyer (2005) [notes and description of female].

68. *Papilio mackinnoni benguellae* Jordan, 1908 – ssp. endemic to Angola
Type locality: Angola: "Cuval River, Benguella". **Distribution**: Angola (central highlands). **Specific localities**: Angola – Cuval River (TL); Benguela Province; Huambo Province; Cuanza-Sul Province (Mendes *et al*. 2013a, 2013b). **Habitat**: Montane forest.

HESPERIIDAE

Hesperiinae

69. *Kedestes sublineata* Pennington, 1953 – sp. endemic to Namibia
Type locality: [Namibia]: "Okahandja, S.W.A.". **Diagnosis**: Distinguished from other members of the *Kedestes lepenula* group by the black scaling of the veins and the absence of black spotting on the underside of the wings (Pringle *et al*. 1994). **Distribution**: Namibia. **Specific localities**: Namibia – Okahandja [1,354 m] (TL; Gaerdes); Otjitambi [1,189 m] (Pringle *et al*. 1994); Farm Portsmut, Windhoek district [1,500 m] (Strydom and Jones, *vide* Pringle *et al*. 1994); Karasberg [1,011 m] (Pringle *et al*. 1994); Tiras Mountains [1,700 m] (Pringle *et al*. 1994); Naukluftberge [1,850 m] (Pringle *et al*. 1994); Kombat [1,609 m] (Pringle *et al*. 1994); Tsumeb [1,335 m] (Pringle *et al*. 1994); Grootfontein [1,444 m] (Pringle *et al*. 1994). **Habitat**: Dry savanna. **Flight period**: All months of the year except the winter months (Pringle *et al*. 1994).

Pyrginae

70. *Abantis bergeri* Mendes & Bivar de Sousa, 2009 – sp. endemic to Angola
Type locality: Angola: "Moxico Province, Lumeje, 20-IV-1965, (BS-14091), det. L. Berger as *Abantis b. bismarcki* (CZ-5372)". Holotype (male) in the entomological collection of the Instituto de Investigação Científica Tropical / Jardim Botânico Tropical. Described from a single male; female unknown (Mendes & Bivar de Sousa 2009c). **Diagnosis**: Similar to *A. bamptoni*. **Distribution**: Angola. **Specific localities**: Angola – Lumeje, Moxico Province [-11.561 20.782] [1,138 m] (TL). **Habitat**: Woodland (Mendes & Bivar de Sousa 2009c). **Larval food**: *Uapaca kirkiana*.

71. *Calleagris jamesoni ansorgei* Evans, 1951 – ssp. endemic to Angola
Type locality: Angola: "Elandswater, Benguella". **Distribution**: Angola. **Specific localities**: Angola – Elandswater, Benguella (TL); Benguela Province;

Bié Province; Cuando Cubango Province; Cuanza-Sul Province; Huambo Province; Lunda-Sul Province (Mendes *et al*. 2013b).

72. *Caprona cassuallala* Bethune-Baker, 1911 – sp. endemic to Namibia and Angola
Type locality: Angola: "Cassualalla, N. Angola". Type in the NHM, London. **Distribution**: Angola, Namibia (north). The distribution of this species and that of *Caprona pillaana* is discussed by Vári (1976). Recorded, erroneously, from Nigeria (Larsen 2005). **Specific localities**: Angola – Cassualalla (TL) [800 m]; Cuanza-Norte Province (Mendes *et al*. 2013b). **Habitat**: Very dry savanna. **Habits**: Similar to those of other species of the genus. Both sexes feed from the flowers of trees in spring (Pringle *et al*. 1994). **Flight period**: September to June (Pringle *et al*. 1994). Ficq, *vide* Pringle *et al*. (1994) has recorded seasonal forms of this species. **Larval food**: *Grewia* species (Tiliaceae) [G. Hobohm, in Dickson & Kroon (1978: 186)].

73. *Eagris multiplagata* Bivar de Sousa & Mendes, 2007. – sp. endemic to Angola
Type locality: Angola: "Kuanza Norte, Zenza do Itombe, 29-V-1971 (Bivar de Sousa – 14312)". **Diagnosis**: Most similar to *Eagris nottoana* but has more hyaline spots, a lighter underside, and there are genitalic differences. **Distribution**: Angola. **Specific localities**: Angola – Zenza do Itombe, Cuanza-Norte Province (09°17'S, 14°13'E; ca [82 m]) (TL). **Habitat**: Forest and dense savanna mosaic (Bivar de Sousa & Mendes 2007). **Habits**: Found flying along a forest road (Bivar de Sousa & Mendes 2007).

74. *Eretis herewardi rotundimacula* Evans, 1937 – ssp. endemic to Angola
Type locality: Angola. **Distribution**: Angola. Recorded, in error for the nominate subspecies, from Mozambique by Congdon *et al*. (2010). **Specific localities**: Angola – Benguela Province; Huambo Province; Huíla Province; Malanje Province (Mendes *et al*. 2013b).

75. *Ernsta colotes colotes* (Druce, 1875) – ssp. endemic to Angola
Type locality: Angola. **Distribution**: Angola. **Specific localities**: Angola – Loanga (Plötz 1884) [58 m]; Bengo Province; Cabinda Province; Luanda Province; Namibe Province (Mendes *et al*. 2013b).

Diagnosis: Median band of hindwing underside composed of separate spots; forewings pointed (Pringle *et al*. 1994). **Habitat**: Dry and moist savanna (bushveld). Also in forest clearings (Cock 2016).

76. *Sarangesa gaerdesi gaerdesi* Evans, 1949 – sp. endemic to Namibia
Type locality: [Namibia]: between Abenab [1,303 m] and Grootfontein [1,445 m] (TL; Gaerdes); Otavi [1,400 m] (Gaerdes); Gaub Valley [1,542 m] (Kroon); near Tsumeb [1,335 m] (G. Henning); Halali in the Etosha National Park [1,114 m] (Ficq). **Habitat**: Dry savanna. Specimens are always found in the close vicinity of their larval host-plants. The wing coloration of each of the two subspecies is a remarkable match for the colour of the leaves of their respective host-plants. **Habits**: They fly rapidly and erratically around stands of the host-plant, usually settling on the leaves with opened wings. Both sexes feed from the small flowers of the host-plant (Pringle *et al*. 1994). **Flight period**: Possibly all year for the nominate subspecies but commonest in the midsummer months following rains (Pringle *et al*. 1994). Subspecies *smithae* has been recorded from August to October (Pringle *et al*. 1994) and in late February (Swart 2004). **Early stages**: Dickson & Kroon (1978: 185) [as *Sarangesa gaerdesi smithae*; Swakop River, Namibia]. Pringle *et al.* (1994: 314) [both subspecies]. The larva attaches several leaves together with silk to form a shelter. These shelters are normally found on the outer edge of the bush. The larva is brownish grey and pupates within the shelter. **Larval food**: *Petalidium englerianum* (Schinz) C.B.Clarke (Acanthaceae) [Dickson & Kroon (1978: 185); as *Petalidium latifolium* (Schinz.) C.B. Cl.; for the nominate subspecies].

77. *Sarangesa gaerdesi smithae* Vári, 1976. – ssp. endemic to Namibia
Type locality: [Namibia]: "South West Africa: Bloedkoppie, [about] 40 km east of Swakopmund, Namib Desert National Park". **Diagnosis**: Differs from the nominate subspecies in its ochreous coloration and the presence of a central hyaline spot on the hindwing (Pringle *et al*. 1994). **Distribution**: Namibia (south-central). **Specific localities**: Namibia – Bloedkoppie, 40 km east of Swakopmund [729 m] (TL; Bampton and Smith); Remhoogte Pass [1,600 m]. **Larval food**: *Petalidium variabile* (Engl.) C.B.Clarke (Acanthaceae) [Dickson & Kroon 1978: 185; for subspecies *smithae*].