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

Published with support and funding from:

Ongava Research Centre (ORC)
Namibian Chamber of Environment (NCE)
Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO)
B2Gold Namibia
TotalEnergies

Language editor: Carole Roberts
Design and layout: Alice Jarvis

NJE Namibian Journal of Environment

2023: Volume 8 www.nje.org.na

ISSN: 2026-8327 (online)

» DOWNLOAD THE MONOGRAPH

CONTENTS

Geography of the highlands and escarpments

Diversity and endemism

The highlands and escarpments of Angola as an endemism hotspot for African dragonflies and damselflies (Insects: Odonata)

J Kipping[1], V Clausnitzer[2], K-DB Dijkstra[3]

URL: https://www.nje.org.na/index.php/nje/article/view/volume8-kipping
Published online: 15th December 2023

[1] BioCart Ökologische Gutachten, Leipzig, Germany; biocartkipping@web.de
[2] Senckenberg Museum für Naturkunde Görlitz, Görlitz, Germany
[3] Naturalis Biodiversity Center, Leiden, The Netherlands

ABSTRACT
The plateaus and escarpments of Angola are a major centre of Odonata endemism in Africa, rivalling and possibly surpassing the highlands of Ethiopia and South Africa. We discuss 34 likely endemic species and 8 near-endemics found in Angola's highland area. Remarkably, 20 of these endemics and near-endemics do not occur either along the western escarpment or on the high central plateau, but on the lower sandy plateaus farther east. Despite the western scarp having traditionally received much scientific attention, the first odonatological discoveries were made there only recently. Of the 42 species of interest discussed here, the taxonomy of 21 of them has yet to be fully resolved. Furthermore, many regions, particularly in northeastern Angola, are still to be explored.

Keywords: Angola, endemism hotspot, escarpments, highlands, Namibia, Odonata

INTRODUCTION

Dragonflies and damselflies (Odonata) are restricted as larvae to freshwater habitats, with range-restricted species largely confined to permanent water (Dijkstra *et al.* 2011, Clausnitzer *et al.* 2012). Odonate endemism in the highlands and escarpments of southwestern Africa is therefore limited to Angola, generally in areas with an average annual rainfall above 700 mm. While the Namibian fauna has been well studied, with 130 species recorded (Suhling & Martens 2014), serious research in Angola has only been undertaken in the last decade or so. Kipping *et al.* (2019) listed 260 species, 24 more than in the first checklist published only two years earlier (Kipping *et al.* 2017). The national fauna is predicted to include well over 300 species, making Angola one of the richest countries for Odonata in Africa. Up to the end of 2022, another 28 species were indeed added, the majority of which are new to science, and likely to be regionally endemic. While the taxonomic work is still in progress, here we discuss the ecology and distribution of all Angola's endemic and near-endemic Odonata known so far.

MATERIALS AND METHODS

The Odonata Database of Africa (ODA; see Kipping *et al.* 2009), currently holds about 142,000 records from the African continent and associated islands, with 8,700 records from Namibia and 6,840 records from Angola. Details on research history and the origin of the records are provided by Suhling and Martens (2007, 2014) for Namibia and by Kipping *et al.* (2017, 2019) for Angola. Point locality data for the plateaus, inselbergs and escarpments as delineated for this project (Mendelsohn & Huntley 2023) were selected spatially using geographic information system (GIS) software (ESRI ArcMap 10.0) and the shapefiles provided, applying a buffer of 5 km. We also consider other species known only from Angola but with localities lying outside the focal area, separating them from the western highland endemics in the tables and discussion where possible. The altitude for each point locality was inferred in GIS using an open-source global elevation model.

ENDEMIC ODONATA OF THE WESTERN HIGHLANDS

Table 1 summarises the known diversity and endemism of Odonata in Angola, Namibia and their western highlands. No endemic species are known to occur in Namibia despite potentially suitable regions such as the Erongo and Naukluft mountains and the Khomas Hochland which are all relatively well studied (Suhling & Martens 2007, 2014). Angola, on the other hand, is rich in endemic species which are clearly concentrated in the western and central plateaus, escarpments and inselbergs where average annual rainfall is higher than 700 mm.

While the proportion of endemics in Angola (12%, Table 2) is similar to that in the Ethiopian Highlands (12 endemic species; 11%) and lower than that in South Africa (30 endemics; 18%), overall species diversity is much greater in the highlands and escarpments of Angola. This ranks the region as one of Africa's foremost centres of Odonata endemism, rivalling the highlands of Cameroon (13 endemics),

Table 1: *Numbers of known and endemic Odonata species in Angola and Namibia.*

Country list of Odonata	Total number of species	Number of endemic (and near-endemic) species	Percentage (%) of endemic species
Angola: Kipping *et al*. (2019) and recent additions	288	34 (8)	11.8
Namibia: Suhling & Martens (2014)	130	0	0

Table 2: *Numbers of known and endemic Odonata species of the strictly delineated highlands and escarpments of Angola and Namibia (HEAN).*

Region	Total number of species	Number of endemic species	Percentage (%) of endemic species
HEAN	168	18	10.7
Angolan Planalto	158	18	11.4
Namibia's highlands, escarpments and plateaus	51	0	0
Escarpments	91	12	13.2
Inselbergs	142	15	10.5
Plateaus	121	11	9.1

the Albertine Rift, the Eastern Arc, and Katanga in southern Democratic Republic of the Congo (DRC).

Different levels of endemism

Table 3 lists 34 endemic species that are only known from Angola and 8 near-endemic species that extend just slightly beyond its political borders. The range and habitat, as well as the taxonomic status and relationships, of each endemic and near-endemic are briefly discussed, showing the complexity of their occurrence, ecology and affinities.

Twelve of these range-restricted species occur on Angola's western escarpment (Table 2). Three are among the longest known (Longfield 1959, Pinhey 1975, Tarboton 2009) and widest ranging endemics: *Platycypha angolensis* (Figure 1a), *Pseudagrion angolense* (Figure 1b) and *Pseudagrion estesi* (Figure 1c). Found roughly between 250 and 2,200 masl, these species range up from the escarpment to the highest parts of the central plateau (see Figure 5a). All favour streams and small rivers, usually with some forest and often with rocks (Figure 1d), and barely extend farther east onto the sandy plateaus.

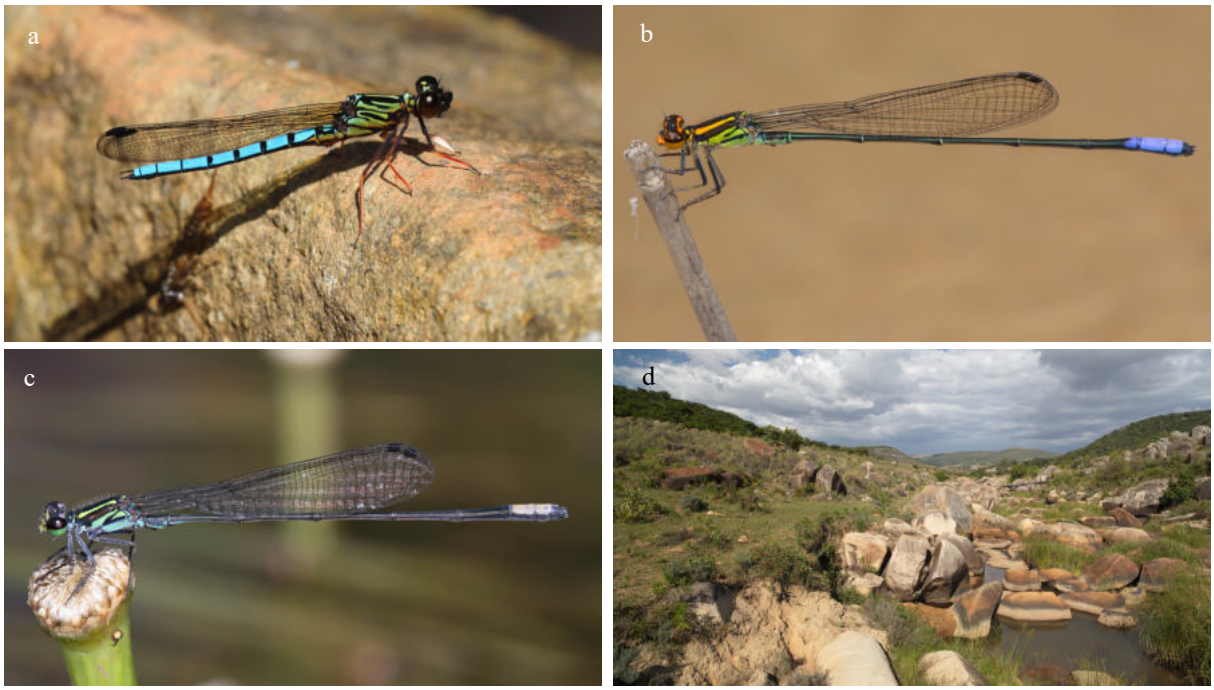

Figure 1: *a) Angola dancing jewel,* Platycypha angolensis*, male (photo by J Kipping, 13 January 2019, Ebanga, Benguela); b) Angola sprite,* Pseudagrion angolense*, male (photo by J Kipping, 2 December 2017, stream at Preciosa Mineral Water source, Lubango, Huíla); c) Estes' sprite,* Pseudagrion estesi*, male (photo by J Kipping, 15 May 2012, Cubango River source near Huambo); and d) Neve stream near Humpata, habitat of* Platycypha angolensis*,* Pseudagrion angolense*,* Pseudagrion estesi *and other endemics (photo by J Kipping, 3 December 2017, Huíla).*

Table 3: *Endemic and near-endemic Odonata species of the Angolan Planalto and surroundings.*

Species	Elevation (masl)			Occurrence and habitat	Taxonomy and biogeography
	Min.	Max.	Mean		
Calopterygidae					
Sapho sp. 'Nhime' broadwing – undescribed species	413	963	792 n = 23	Low-altitude endemic of rocky streams and small rivers in western scarp forest	Near *S. gloriosa* McLachlan, 1873 and *S. orichalcea* McLachlan, 1869 from Cabinda to Congo and Nigeria; genetics and morphology differ more from these two than they do from each other
Umma femina Longfield, 1947 Angola sparklewing (Figure 6b)	(1,345)	2,154	2,055 n = 72	High-altitude endemic of open and often rocky streams; all sites except for inaccurate (lower elevation) record "north of Cuché" (Pinhey 1975) on central plateau	Distinct, may be nearest to sympatric *U. electa* Longfield, 1933 although this has not been tested genetically
Chlorocyphidae					
Platycypha angolensis Longfield, 1959 Angola dancing jewel (Figure 1a)	261	2,127	1,189 n = 132	Wide-ranging endemic of open but often sheltered and sometimes rocky streams and small rivers; mostly along western escarpment and on Angolan Planalto	Morphologically most distinct member of Angolan radiation of genus; also genetically well defined
Platycypha bamptoni (Pinhey, 1975) highland blue jewel (Figure 7c)	1,612	2,104	1,993 n = 22	High-elevation endemic of open and often rocky streams and small rivers; largely confined to western edge of Angolan Planalto	Member of Angolan radiation of genus, but taxonomy unresolved
Platycypha sp. 'white tibiae' jewel – undescribed species	1,249	2,127	1,750 n = 33	High- and mid-elevation endemic of open streams and rivers on both Angolan Planalto and eastern plateaus	Member of Angolan radiation of genus, but taxonomy unresolved, hard to separate from *P. bamptoni* by white-coloured tibiae and abdominal pattern
Platycypha crocea (Longfield, 1947) Angola blue jewel	1,220	1,982	1,581 n = 44	High-elevation endemic largely confined to the Angolan Planalto, inhabiting smaller and softer-bottomed (e.g., muddy) streamlets than *P. bamptoni*	Fairly distinct member of Angolan radiation of genus, but taxonomy not entirely resolved
Platycypha rubriventris (Pinhey, 1975) red-bellied blue jewel	1,098	1,098	1,098 n = 1	Only type series known; two males collected in 1965 at Teixeira de Sousa, interpreted as Luau on DRC border in Lunda-Sul	Presumably also belongs to Angolan radiation of genus (Dijkstra 2007b)
Platycnemididae					
Elattoneura flavifacies (Pinhey, 1981) yellow-faced threadtail	829	1,428	1,263 n = 18	Mid-altitude near-endemic, widespread at boggy streamlets on eastern plateau, just extending into adjacent DRC and NW Zambia	Genetically and morphologically rather distinct member of genus
Elattoneura tarbotonorum Dijkstra, 2015 stout threadtail (Figure 6c)	1,238	2,215	1,788 n = 52	High- and mid-elevation endemic found at open streams and smaller rivers (often, but not always, rocky and fast flowing) around Lubango and Mt Namba on Angolan Planalto, but also lower down on eastern plateau	Distinct, probably sister species of Western Cape endemic *E. frenulata* (Hagen in Selys, 1860) (Dijkstra *et al.* 2015)

Species	Elevation (masl)			Occurrence and habitat	Taxonomy and biogeography
	Min.	Max.	Mean		
Elattoneura sp. threadtail – undescribed species (Figure 4)	111	1,695	1,091 n = 84	Possible mid- and low-elevation near-endemic widespread at open streams and rivers across Angola and northwards at least to western DRC, but mostly absent on Angolan Planalto	Morphologically nearest *E. glauca* (Selys, 1860) from southern and eastern Africa, but separated geographically and genetically
Coenagrionidae					
Aciagrion rarum (Longfield, 1947) tiny slim	1,171	1,171	1,171 n = 1	Only type series known, collected near Dala on Tyihumbwe River (tributary of the Kasai) in NE Angola in 1932	Distinctive, but affinities unclear
Aciagrion zambiense Pinhey, 1972 Zambia slim	1,184	1,476	1,281 n = 4	Mid-elevation near-endemic known from two sites in E Angola and one in nearby NW Zambia; habitat probably open temporary pools	Close to *A. africanum* Martin, 1908 that is widespread in West and Central Africa
Africallagma sp. 'Hama' bluet – undescribed species (Figure 9d)	1,421	1,421	1,421 n = 7	Mid-elevation endemic found only at reedy marsh near Alto Hama, on Angolan Planalto	Morphology distinct from other members of genus; genetic testing underway
Agriocnemis angolensis Longfield, 1947 Angola wisp	958	2,223	1,408 n = 67	Wide-ranging near-endemic found at open and often rocky streams and small rivers from high on Angolan Planalto down to rocky sections of the Okavango River in NE Namibia and NW Botswana	Genetically nearest sympatric *A.bumhilli* Kipping *et al*., 2012; former subspecies *spatulae* Pinhey, 1974; see *A. spatulae* below
Agriocnemis bumhilli Kipping *et al*., 2012 Bumhill wisp	973	1,375	1,225 n = 28	Mid-elevation near-endemic of boggy and marshy streams and rivers from eastern plateau to NE Namibia	Genetically nearest sympatric *A.angolensis* Longfield, 1947
Agriocnemis canuango Dijkstra, 2015 bog wisp (Figure 9b)	1,224	1,614	1,508 n = 28	Mid-elevation endemic of oligotrophic bogs west and east of (but not on) Angolan Planalto	Genetically and morphologically rather distinct member of genus (Dijkstra *et al*. 2015)
Agriocnemis spatulae Pinhey, 1974 finger-tipped wisp	1,349	1,445	1,438 n = 4	Mid-elevation near-endemic found at boggy and well-vegetated pools on the sandy plateaus in eastern Angola and adjacent NW Zambia	Described as a subspecies of *A. angolensis* Longfield, 1947 but morphologically and genetically distinct and probably a good species
Agriocnemis toto Dijkstra, 2015 Toto's wisp (Figure 9c)	1,210	1,421	1,261 n = 4	Mid-elevation endemic preferring dense vegetation of reeds west of (but not east of or on) Angolan Planalto	Genetically and morphologically well-defined member of genus with unclear nearest relatives (Dijkstra *et al*. 2015)
Ceriagrion sp. 'Cassongo' citril – undescribed species	1,343	1,358	1,354 n = 7	Mid-elevation endemic found at temporary pools in boggy regions on sandy eastern plateau	One of many similar members of genus, but genetics and morphology distinctive; possibly sister species of widespread and sympatric *C. whellani* Longfield, 1952
Pseudagrion angolense Selys, 1876 Angola sprite (Figure 1b)	261	2,106	1,549 n = 97	Wide-ranging endemic of often rocky and (partly) forested streams and small rivers, mostly along western escarpment and on Angolan Planalto	Sister species of *P. grilloti* Legrand, 1987 from Gabon and western Congo (expected to occur in Cabinda)

Species	Elevation (masl)			Occurrence and habitat	Taxonomy and biogeography
	Min.	Max.	Mean		
Pseudagrion dundoense Longfield, 1959 Dundo sprite	660	660	660 n = 1	Only holotype known, male presumably collected near Dundo in Lunda-Norte on border with DRC in 1949	Status and affinities entirely unclear (Longfield 1959)
Pseudagrion estesi Pinhey, 1971 Estes' sprite (Figure 1c)	750	2,215	1,497 n = 88	Wide-ranging endemic of often rocky and mostly open streams and small rivers, mostly along western escarpment and on Angolan Planalto; scarce further east, e.g., isolated type locality at Quimbango, Malanje Province	Probably closest to *P. kibalense* Longfield, 1959 that is widespread in forests of Central Africa
Pseudagrion sarepi Kipping & Dijkstra, 2015 Sarep sprite	1,078	1,375	1,295 n = 40	Mid-elevation endemic found on all open sandy streams and rivers on eastern plateau almost up to border of Zambia, where likely to occur	Very close to *P. greeni* Pinhey, 1961 found higher up in Angola, northern Zambia and southern Katanga (DRC), and especially to *P. fisheri* Pinhey, 1961 from N Zambia, NE Angola, and (questionable) old records from N Botswana as *P. fisheri* in Pinhey (1976)
Gomphidae					
Notogomphus kimpavita Dijkstra & Clausnitzer, 2015 Angola longleg (Figure 3a)	612	1,777	962 n = 17	Mostly low-elevation endemic of often (partly) forested streams and small rivers along western escarpment, but extends quite high onto Angolan Planalto at Mt Namba	Genetically and morphologically well separated from sister species *N. praetorius* (Selys, 1878) from Angolan Planalto to Katanga (DRC) and South Africa
Onychogomphus rossii Pinhey, 1966 Angola claspertail (Figure 6d)	1,381	2,132	1,852 n = 7	High- and possibly mid-elevation endemic known only from rocky streams and small rivers on Angolan Planalto	Probably nearest to *O. kitchingmani* Pinhey, 1961 from NW Zambia (Dijkstra 2007a)
Paragomphus sp. 'Cuemba' hooktail – undescribed species (Figure 11c)	1,423	1,423	1,423 n = 1	Mid-elevation endemic known from single male at sandy stream near Cuemba on sandy eastern plateau (Sara Fernandes Elizalde pers. comm.)	Morphology unlike any member; no genetic data available
Paragomphus sp. 'Gabela' hooktail – undescribed species (Figure 3d)	581	953	870 n = 11	Low-elevation endemic of rather open (often disturbed) streams and small rivers with rocks or gravel along forested western escarpment	One of several superficially similar members of genus, but morphology distinct; genetic testing underway
Libellulidae					
Aethriamanta sp. 'Micongo' basker – undescribed species (Figure 23)	1,240	1,358	1,318 n = 11	Possible mid-elevation near-endemic of oligotrophic bog pools on sandy eastern plateau and in NW Zambia	Genetics and morphology rather distinct from *A. rezia* Kirby, 1889 that is widespread in Angola, tropical Africa and Madagascar
Atoconeura sp. 'Namba' highlander – undescribed species	1,705	1,705	1,705 n = 1	Possible high-elevation endemic, known only from single female from Mt Namba	Morphology inconclusive, but isolated population of mostly high-elevation genus may well be distinct (see Dijkstra 2006); genetic testing underway

Species	Elevation (masl)			Occurrence and habitat	Taxonomy and biogeography
	Min.	Max.	Mean		
Eleuthemis eogaster Dijkstra, 2015 sunrise firebelly (Figure 3c)	616	1,214	848 n = 12	Low- and mid-elevation endemic known only from several large streams and rivers near Uíge (western scarp) bordered by forest	Nearest relative is unnamed species near *E. buettikoferi* Ris, 1910 from NW Zambia to W Tanzania (Dijkstra *et al*. 2015)
Eleuthemis libera Dijkstra & Kipping, 2015 free firebelly (Figure 14)	1,120	1,435	1,276 n = 24	Mid-elevation near-endemic, widespread at (mostly open) streams and rivers on eastern plateau, extending to NW Angola (near Negage) and NW Zambia	Most distinctive member of genus (Dijkstra *et al.* 2015)
Micromacromia flava (Longfield, 1947) Angola micmac (Figure 7a)	1,148	1,849	1,543 n = 25	High-elevation endemic of small boggy streams and seeps on Angolan Planalto as well as near Negage	Distinct member of genus with two species in forests of West and Central Africa and another restricted to Usambara Mountains, E Tanzania (see Longfield 1947, Dijkstra & Vick 2006)
Nesciothemis sp. blacktail – undescribed species	405	2,127	1,174 n = 67	Possible wide-ranging near-endemic found at most open streams and rivers in Angola and into N Namibia and N Botswana	Genetically most distinct within complex including widespread *N. farinosa* (Förster, 1898) and *N. pujoli* Pinhey, 1971; morphology also fairly distinct
Orthetrum sp. 'Cuanavale' skimmer – undescribed species	1,275	1,390	1,369 n = 7	Mid-elevation endemic known from two bogs on sandy eastern plateau	Nearest to widespread African *O. abbotti* Calvert, 1892, but genetics and morphology distinct
Porpax sp. 'Tempue' pricklyleg – undescribed species	1,343	1,390	1,353 n = 2	Mid-elevation endemic of boggy source areas on eastern plateau	Genetics and morphology unlike any other member of genus; Africa's smallest true dragonfly
Rhyothemis sp. 'Cuito' flutterer – undescribed species	1,238	1,446	1,318 n = 11	Mid-elevation endemic that is common and widespread at open waters on eastern plateau	Genetics and morphology unlike any other member of genus
Tetrathemis sp. 'Cambondo' elf – undescribed species	412	798	666 n = 2	Low-elevation endemic found near shaded streams and rivers (probably breeds in associated pools) near Uíge and in Cambondo Forest on western escarpment	Close to *T. fraseri* Legrand, 1977 from Gabon, but genetics and morphology fairly distinct
Trithemis sp. 'Cuanavale' dropwing – undescribed species	1,209	1,358	1,261 n = 3	Mid-elevation endemic found in boggy areas along sandy rivers at three sites on eastern plateau	Only female specimens available, but these unlike any other member of genus both in genetics and morphology
Trithemis sp. 'Cumbira' scarp dropwing	831	879	855 n = 1	Possible low-elevation endemic, single males found at shaded streams on forested western scarp near Uíge and at Cumbira Forest	Near *T. integra* Dijkstra, 2007 from Albertine Rift but geographically isolated and morphology somewhat distinct; genetic comparison so far unavailable
Trithemis sp. 'Namba' dropwing – undescribed species (Figure 7b)	1,774	2,048	1,920 n = 4	High-elevation endemic found only away from water at Mt Namba; may breed in bog streams	Morphologically unlike any other species of genus; genetic testing underway
Zygonyx sp. 'Cunde' cascader – undescribed species	1,249	1,296	1,272 n = 2	Mid-elevation endemic collected only at Cunde Falls on eastern plateau	One of at least six species in complex near *Z. flavicosta* (Sjöstedt, 1900), but genetics and morphology unlike any other member

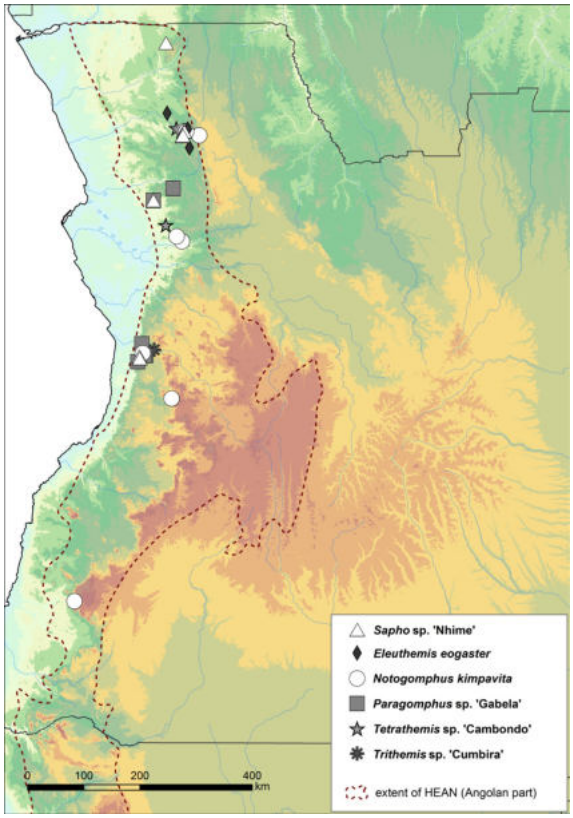

Figure 2: *Point locality data of selected endemic species of the western scarp forests of the highlands and escarpments of Angola (HEAN):* Sapho *sp. 'Nhime',* Eleuthemis eogaster, Notogomphus kimpavita, Paragomphus *sp. 'Gabela',* Tetrathemis *sp. 'Cambondo' and* Trithemis *sp. 'Cumbira'.*

As far as known, six of the twelve species are completely restricted to flowing waters (or associated pools) on the forested Angolan escarpment (Figure 2). They have a comparatively low and narrow elevation range, found mostly between 400 and 1,000 masl, although *Notogomphus kimpavita* (Figure 3a) almost reaches 1,800 masl at a stream in Mt Namba's gallery forests (Figure 3b). Remarkably, the existence of these endemics has only just come to light: *Eleuthemis eogaster* (Figure 3c) and *N. kimpavita* were described in 2015, while new species in the genera *Paragomphus* (Figure 3d), *Sapho* and *Tetrathemis*, and possibly one in *Trithemis* remain to be described.

The final three of the twelve species appear widespread but have been confused with species found commonly elsewhere in Africa, so their exact ranges are imperfectly known. It is likely that new species of *Elattoneura* (Figure 4) and *Mesocnemis* are found at open running waters below 1,700 masl.

While being largely absent from the high plateau, they occur close to sea level, and at least the *Elattoneura* species extends into adjacent DRC. A distinct taxon of *Nesciothemis* is probably the widest ranging (near-)endemic in Angola, occurring at almost any open stream or river, while extending into northern Namibia and northern Botswana as well.

Figure 3: *a) Angola longleg,* Notogomphus kimpavita*, male (photo by J Kipping, 5 December 2017, Bruco Pass, Tundavala, Huíla); b) stream at Mt Namba, habitat of* Notogomphus kimpavita *and* Atoconeura *sp. 'Namba' (photo by J Kipping, 20 January 2019, Cuanza-Sul); c) sunrise firebelly,* Eleuthemis eogaster*, male (photo by K-DB Dijkstra, 3 October 2013, Lumanie River, Uíge); and d)* Paragomphus *sp. 'Gabela', male (photo by J Kipping, 16 January 2019, Uiri River near Conda, Cuanza-Sul).*

Figure 4: Elattoneura *sp. near* glauca*, male (photo by J Kipping, 16 January 2019, Uiri River near Conda, Cuanza-Sul).*

Another ten species which rarely occur below 1,200 masl and frequently up to 2,200 masl are largely confined to the Angolan Planalto, although some were found in suitable habitat farther north and east (Figures 5a and 5b). All inhabit streams and rivers, generally in open grassland (Figure 6a). *Umma femina* (Figure 6b), *Elattoneura tarbotonorum* (Figure 6c), *Onychogomphus rossii* (Figure 6d) and a possible new *Atoconeura* species appear to favour faster flowing and often rocky waters. *Micromacromia flava* (Figure 7a) was found at boggy seeps and streamlets, which may also be the habitat of a new *Trithemis* species from Mt Namba with spectacularly marked wings (Figure 7b).

Aside from *Platycypha angolensis*, the endemic radiation of blue *Platycypha* species here includes the localised *P. crocea* on soft-bottomed, and the more widespread *P. bamptoni* (Figure 7c) on hard-bottomed, streams. The latter, however, has a form that is also widespread on sandy rivers farther east, and whose status as a possibly separate species is unresolved (Figure 8). Near-endemic *Agriocnemis angolensis* (Figure 7d) is unusual for the genus in being common at rocky streams on Angola's highest plateaus, as well as at fast-flowing and rocky sections of the lower Okavango in Namibia's 'Caprivi Strip'. Another taxon so far named as its subspecies *Agriocnemis angolensis spatulae* Pinhey 1974, is known from eastern Angola and northwestern Zambia. Recent collections revealed that it is most likely a distinct species favouring soft-bottomed and boggy stagnant habitats.

Notably, about half of Angola's (potential) endemics and near-endemics occur neither along the western escarpment nor on the high central Angolan Planalto. These twenty species are restricted to oligotrophic habitats on sandy soils, such as bogs and clear rivers

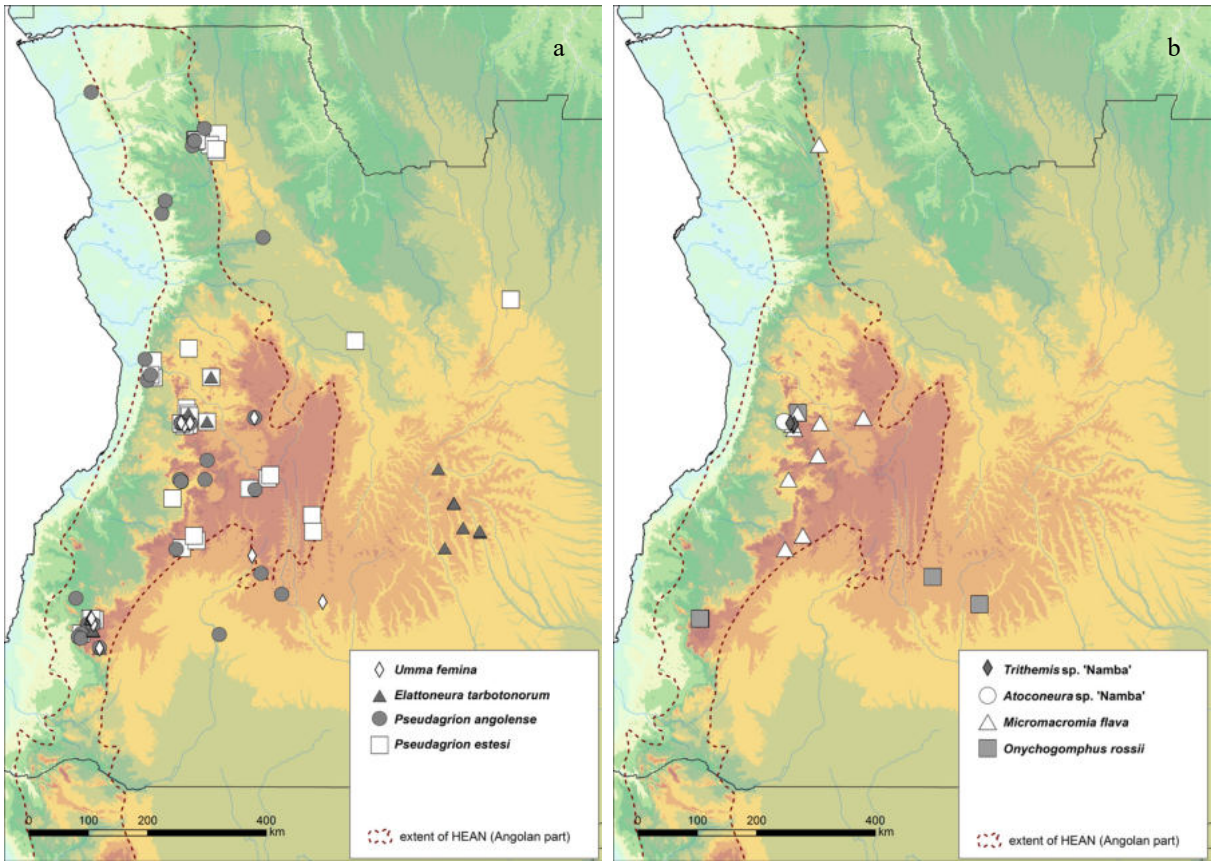

Figure 5: *Point locality data of selected endemics: a) Zygoptera species of the high Angolan Planalto* Umma femina*,* Elattoneura tarbotonorum*,* Pseudagrion angolense *and* Pseudagrion estesi*; and b)* Anisoptera species *of the Angolan Planalto* Trithemis *sp. 'Namba',* Atoconeura *sp. 'Namba',* Micromacromia flava *and* Onychogomphus rossii*. (HEAN = the highlands and escarpments of Angola and Namibia.)*

Figure 6: *a) Tchiamena stream near Tundavala, Lubango, habitat of* Elattoneura tarbotonorum*,* Onychogomphus rossii*,* Platycypha bamptoni *and* Umma femina *(photo by J Kipping, 6 December 2017, Huíla); b) Angola sparklewing,* Umma femina*, male (photo by J Kipping, 26 January 2019, Tchiamena stream near Lubango, Huíla); c) stout threadtail,* Elattoneura tarbotonorum*, male (photo by J Kipping, 6 December 2017, Tchiamena stream near Lubango, Huíla); and d) Angola claspertail,* Onychogomphus rossii*, male (photo by J Kipping, 6 December 2017, Tchiamena stream near Lubango, Huíla).*

Figure 7: *a) Angola micmac,* Micromacromia flava*, male (photo by R Ferreira, 18 November 2022, Cassongue, Cuanza-Sul); b)* Trithemis *sp. 'Namba', male (photo by R Ferreira, 29 April 2013, Mt Namba, Cuanza-Sul); c) highland blue jewel,* Platycypha bamptoni*, male (photo by J Kipping, 13 January 2019, Ebanga, Benguela); and d) Angola wisp,* Agriocnemis angolensis*, male (photo by J Kipping, 12 May 2012, Cacuchi River north of Menongue, Bié).*

(Figure 9a), mostly between 1,000 and 1,500 masl. The two endemic *Agriocnemis canuango* (Figure 9b) and *A. toto* (Figure 9c) and a recently discovered species of *Africallagma* (Figure 9d) have been found at mid-elevations north of the Angolan Planalto (Figure 10); the remainder have only been recorded on the lower sandy plateau that dominates Angola's eastern half (see Figures 12a and 12b).

Three species have not been reported for half a century or more, being known only from their type specimens and localities in northeastern Angola: *Aciagrion rarum*, *Platycypha rubriventris* and *Pseudagrion dundoense*. We owe most of the remainder of our knowledge of this sand fauna to the Okavango Wilderness Project (OWP), which focuses on the eastern plateau's importance as Angola's water tower, with sources and headwaters of many major rivers (e.g., Congo, Kasai, Cuanza, Cubango, Cunene and Zambezi) lying close to each other in the area.

Six species that were described from the eastern plateau's periphery and that (probably) just extend beyond Angola's eastern border were found to have their main occurrence here during OWP fieldwork (NGOWP 2018): *Aciagrion zambiense*, *Agriocnemis bumhilli*, *Agriocnemis spatulae* (often considered a subspecies of *Agriocnemis angolensis*; see above), *Elattoneura flavifacies*, *Eleuthemis libera* and *Pseudagrion sarepi* (Figure 11a). Moreover, distinctive new species of *Aethriamanta* (Figure 11b),

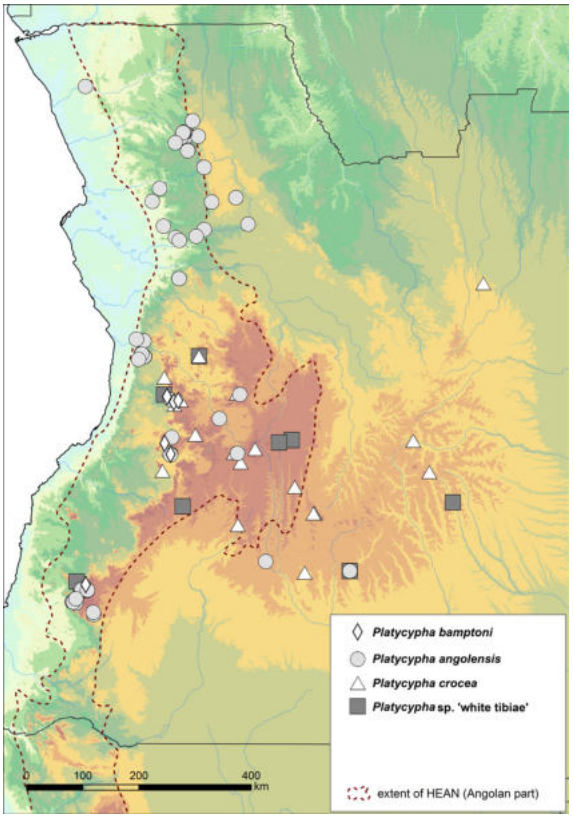

Figure 8: *Point locality data of endemic members of the blue* Platycypha *complex in Angola:* Platycypha angolensis, Platycypha bamptoni, Platycypha *sp. 'white tibiae' and* Platycypha crocea. *(HEAN = the highlands and escarpments of Angola and Namibia.)*

Figure 9: *a) The sandy Longa River, type locality of* Pseudagrion sarepi *(photo by J Kipping, 20 May 2012, Cuando-Cubango); b) bog wisp,* Agriocnemis canuango, *male (photo by J Kipping, 24 January 2019, Cassongue, Cuanza-Sul); c) Toto's wisp,* Agriocnemis toto, *male (photo by J Kipping, 24 January 2019, Cela, Cuanza-Sul); and d)* Africallagma *sp. 'Hama', male (photo by J Kipping, 1 February 2019, Hama River north of Alto Hama, Huambo).*

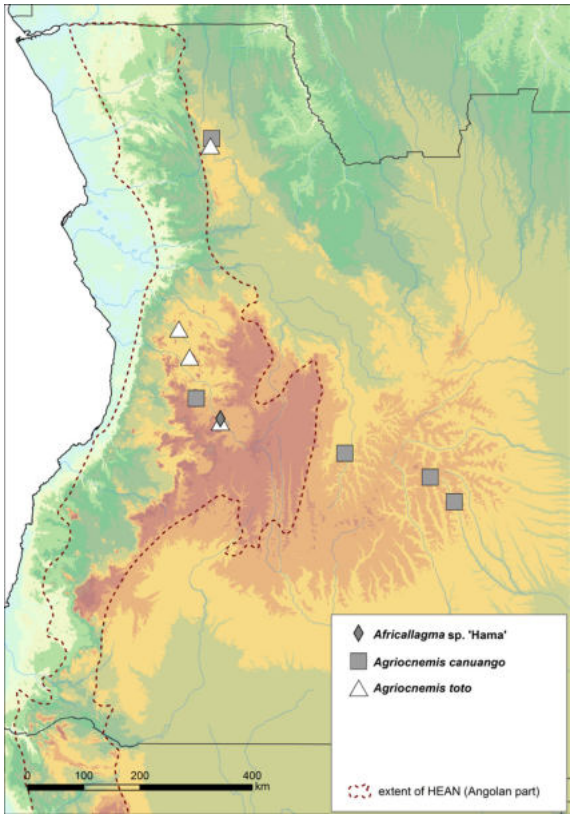

Figure 10: *Point locality data of selected endemic Zygoptera species of the lower Angolan Planalto:* Africallagma *sp. 'Hama',* Agriocnemis canuango *and* Agriocnemis toto. *(HEAN = the highlands and escarpments of Angola and Namibia.)*

Ceriagrion, *Orthetrum*, *Paragomphus* (Figure 11c), *Porpax*, *Rhyothemis*, *Trithemis* and *Zygonyx* were discovered (Figures 12a, 12b and 13).

The eastern plateau is unusual because highly seasonal rainfall is held and released by very nutrient-poor sandy soils: water flows abundantly year-round, but in a largely unforested landscape. The region owes its nutrient-poor conditions to a thick layer of loose aeolian sand, deposited during episodes of Plio-Pleistocene aridity (Moore *et al*. 2009). Subsequently, aquatic habitats that are rare elsewhere in Africa dominate here. These include grassy bogs with small streams and pools, open sandy rivers with associated peaty lakes and oxbows, and extensive seasonally flooded pans.

Not only are many specialised species present, but species that are common in open habitats throughout the rest of Africa are virtually absent because of the exceptional oligotrophic and partly acidic water conditions. Population densities and the average size of individuals of most species, meanwhile, appear exceptionally low. The new *Porpax* species, for example, is the smallest true dragonfly (i.e., excluding damselflies) in Africa by far and among the smallest in the world, while the new *Aethriamanta*, *Rhyothemis* and *Trithemis* species are (among) the smallest species in their genera.

Figure 11: *a) Sarep sprite,* Pseudagrion sarepi*, male (photo by J Kipping, 20 May 2012, Longa River, Cuando-Cubango); b)* Aethriamanta *sp. 'Micongo', male (photo by J Kipping, 13 December 2022, Ikelenge, Zambia); and c)* Paragomphus *sp. 'Cuemba', male (photo by D Elizalde, 19 October 2018, Cuemba, Bié).*

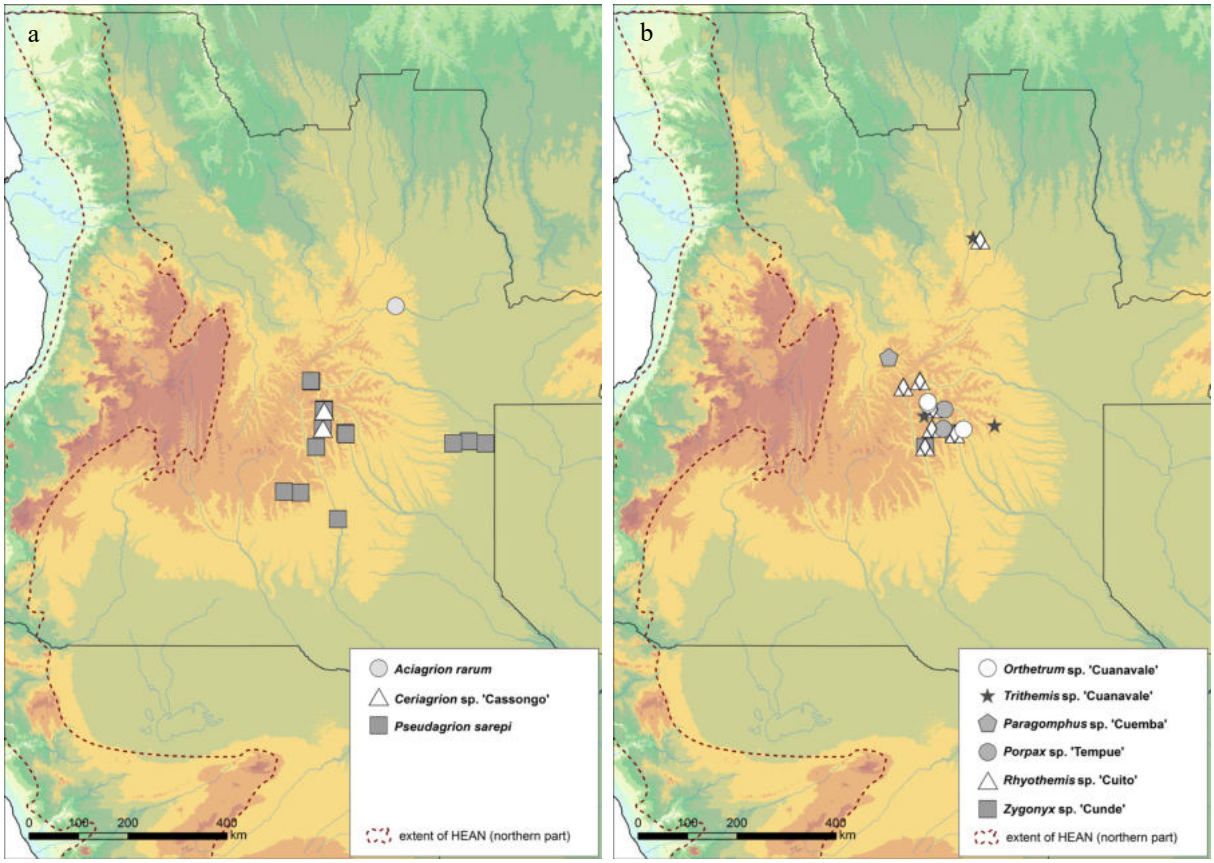

Figure 12: *Point locality data of selected endemics: a) Zygoptera species of the eastern lower plateau* Aciagrion rarum*,* Ceriagrion *sp. 'Cassongo' and* Pseudagrion sarepi*; and b) Anisoptera species of the eastern lower plateau* Orthetrum *sp. 'Cuanavale',* Trithemis *sp. 'Cuanavale',* Paragomphus *sp. 'Cuemba',* Porpax *sp. 'Tempue',* Rhyothemis *sp. 'Cuito' and* Zygonyx *sp. 'Cunde'. (HEAN = the highlands and escarpments of Angola and Namibia.)*

This, as well as our observation that more widespread species are present at sites in the region that are eutrophicated by organic pollution, indicates that the endemism is linked to the eastern plateau's exceptional ecology rather than to its relative isolation.

Origins

While some familiar patterns are apparent in the biogeographic affinities of Angola's (near-)endemic odonate species, many of them seem to be remarkably distinct phylogenetically, making their origins less clear (see Table 3).

Pseudagrion angolense, *P. estesi* and the four probably new species on the escarpment (in the genera *Paragomphus*, *Sapho*, *Tetrathemis* and *Trithemis*) have sister taxa in similar forest-stream habitats in Central Africa, with the *Trithemis* confined to the Albertine Rift. This pattern is common in escarpment birds too. Similarly, the nearest relatives of some endemics of generally more open and higher-elevation streams and rivers (*Eleuthemis eogaster*, *Notogomphus kimpavita*, *Onychogomphus rossii*, *Pseudagrion sarepi*, *Umma femina* and probably the possibly new *Atoconeura* species) are in similar habitats directly east. *Elattoneura tarbotonorum* is an exception, with the nearest relative being confined to the mountains of the Western Cape in South Africa.

The sister taxa of a majority of the (near-)endemics, however, are either very widespread in Africa, not especially obvious or are also restricted to Angola. Those with widespread relatives are *Aciagrion zambiense* and the (possible) new *Aethriamanta*, *Ceriagrion*, *Elattoneura*, *Mesocnemis*, *Nesciothemis*, and *Orthetrum* species, while those with Angolan sister taxa (but unclear affinities beyond that) are *Agriocnemis angolensis*, *A. bumhilli* and *A. spatulae*, and the four or five species of the endemic *Platycypha* radiation. *Agriocnemis canuango*, *A. toto*, *Elattoneura flavifacies*, *Eleuthemis libera* (Figure 14), *Micromacromia flava* and the new *Porpax*, *Rhyothemis* and two *Trithemis* species are among the most distinctive species in their genera, sometimes being the sister taxon to all others in the genus. We know little about the affinities of *Aciagrion rarum*, *Pseudagrion dundoense*, the new *Africallagma* species, and the new *Paragomphus* and *Zygonyx* from the eastern plateau, although each appears taxonomically unique too.

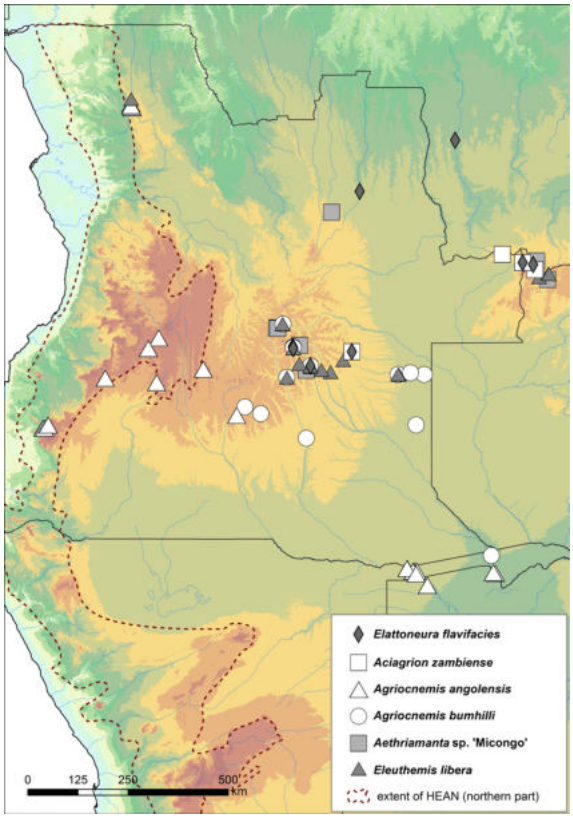

Figure 13: *Point locality data of selected near-endemic species of the Angolan plateaus and adjacent regions:* Elattoneura flavifacies, Aciagrion zambiense, Agriocnemis angolensis, Agriocnemis bumhilli, Aethriamanta *sp. 'Micongo' and* Eleuthemis libera. *(HEAN = the highlands and escarpments of Angola and Namibia.)*

These affinities suggest that, while the isolation of Angola's highlands and escarpments contributed to the evolution and survival of its (near-)endemic species, the unusual ecological conditions there may have contributed even more to localised speciation. This confirms the inferences drawn above from the species' distributions.

Figure 14: Free firebelly, *Eleuthemis libera*, male (photo by J Kipping, 3 March 2023, Mwinilunga, Zambia).

GAPS IN KNOWLEDGE AND RESEARCH PRIORITIES

Large parts of Angola have not, or only poorly, been surveyed for Odonata. One focus of this review, the western highlands, is fortunately among the better-studied regions. Many records are available from the Serra da Chela, for example, notably from around Lubango and Humpata, often over a longer period (e.g., Ris 1931, Pinhey 1975, Tarboton 2009). The recency of much of the knowledge presented for the western escarpment, however, implies that systematic surveys of the remaining forest habitats there will lead to further discoveries. So far, even well-known sites like Cumbira Forest have been visited only briefly and Serra da Neve has never been studied for Odonata yet.

However, most priorities for further research in Angola lie in the northern half of the country. Lunda-Norte Province should yield the greatest number of unrecorded species. Survey priorities for endemic species are the remaining forests north of Dondo and N'dalatando (e.g., in mountain ranges like Serra Canda and Serra Cananga), the higher-lying areas around the Cuanza Basin (notably the northern edge of the central plateau and above the escarpment between the Cuanza and Congo catchments), and the northern part of the eastern plateau (e.g., between Luena and Saurimo). Photographs taken near Saurimo, for example, show possibly unnamed species of Chlorocyphidae and Coenagrionidae (Russell Tate, pers. comm.).

In Namibia there are some mostly unexplored and hardly accessible mountain ranges in the northwest with streams flowing off to the Cunene River. Namely the Baynes and Otjihipa mountains and Ehomba Hills might hold populations of some of the highland endemics so far only known from farther north on the Angolan Planalto (F Suhling, pers. comm.).

ACKNOWLEDGEMENTS

We thank Alvaro Bruno Toto Nienguesso, the driving force behind biodiversity research in Uíge Province (Angola), and Prof. Dr Neinhuis and Dr Thea Lautenschlaeger from Technische Universität Dresden for inviting us to the field survey in Uíge Province. Part of the fieldwork in Angola was supported by a travel fund from the German Academic Exchange Service (DAAD). The published results were obtained in collaboration with the Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC) of the Ministry of Environment of Angola who also provided all necessary permits. We are grateful to Dr Paula C Francisco Coelho for making the 2012 Southern African Regional Environmental Programme (SAREP) survey in southern Angola possible, and to Dr Chris Brooks of SAREP for the preparation and organisation of this survey. We are also very grateful to Sara and David Fernandes Elizalde (Lubango) for providing their own data and expertise and for their generous support on various expeditions within

Angola. Chris Hines (now South Africa) helped with collected specimens and, together with Katy Sharpe (Windhoek), provided logistical support and company on a collecting trip. Dr André Günther (Freiberg, Germany) helped to collect specimens and provided valuable knowledge to the taxonomy of Chlorocyphidae. Further data and photographic records of Odonata were provided by Dr Manfred Haacks, Dr John Mendelsohn, Riquita Sampaio, Dr Warwick Tarboton, Russell Tate, Carel van der Merwe, Dr Pedro Vaz Pinto, and others. Prof. Dr Michael Samways of Stellenbosch University and Prof. Dr Frank Suhling (Technische Universität Braunschweig) gave valuable comments to the manuscript. This paper is dedicated to the late Rogério Ferreira (Luanda), who helped on various expeditions and provided many photographic records. He also donated some of his excellent photographs for this paper.

REFERENCES

Clausnitzer V, Dijkstra K-DB, Koch R, Boudot J-P, Darwall WR, Kipping J *et al.* (2012) Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern. *Frontiers in Ecology and the Environment* 10(3): 129–134. https://doi.org/10.1890/110247.

Dijkstra KDB (2006) The *Atoconeura* problem revisited: taxonomy, phylogeny and biogeography of a dragonfly genus in the highlands of Africa (Odonata, Libellulidae). *Tijdschrift voor Entomologie* 149(2): 121–144. https://doi.org/10.1163/22119434-900000193.

Dijkstra K-DB (2007a) The name-bearing types of Odonata held in the Natural History Museum of Zimbabwe, with systematic notes on Afrotropical taxa. Part 1: Introduction and Anisoptera. *International Journal of Odonatology* 10(1): 1–29. https://doi.org/10.1080/13887890.2007.9748285.

Dijkstra K-DB (2007b) The name-bearing types of Odonata held in the Natural History Museum of Zimbabwe, with systematic notes on Afrotropical taxa. Part 2: Zygoptera and descriptions of new species. *International Journal of Odonatology* 10(2): 137–170. https://doi.org/10.1080/13887890.2007.9748296.

Dijkstra K-DB, Boudot J-P, Clausnitzer V (2011) Chapter 5. Dragonflies and damselflies of Africa (Odonata): history, diversity, distribution and conservation. In: Darwall WR, Smith K, Allen D, Holland R, Wright E, Harrison I (eds) *The diversity of life in African freshwaters: underwater, under threat. An analysis of the status and distribution of freshwater species throughout mainland Africa*. 126–177. IUCN, Gland and Cambridge.

Dijkstra K-DB, Kipping J, Mézière N (2015) Sixty new dragonfly and damselfly species from Africa (Odonata). *Odonatologica* 44(4): 447–678. https://zenodo.org/record/35388.

Dijkstra K-DB, Vick GS (2006) Inflation by venation and the bankruptcy of traditional genera: the case of *Neodythemis* and *Micromacromia*, with keys to the continental African species and the description of two new *Neodythemis* species from the Albertine Rift (Odonata: Libellulidae). *International Journal of Odonatology* 9(1): 51–70. https://doi.org/10.1080/13887890.2006.9748263.

Kipping J, Clausnitzer V, Elizalde SRF, Dijkstra K-DB (2017) The dragonflies and damselflies (Odonata) of Angola. *African Invertebrates* 58(1): 65–91. https://doi.org/10.3897/AfrInvertebr.58.11382.

Kipping J, Dijkstra K, Clausnitzer V, Suhling F, Schütte K (2009) Odonata database of Africa (ODA). *Agrion* 13: 20–23.

Kipping J, Clausnitzer V, Fernandes Elizalde SRF, Dijkstra K-DB (2019) Chapter 9. The dragonflies and damselflies of Angola: an updated synthesis. In: Huntley JH, Russo V, Lages F, Ferrand N (ed.) *Biodiversity of Angola, science & conservation: a modern synthesis.* 141–165. Springer International Publishing: Cham.

Longfield C (1947) The Odonata of South Angola: results of the Mission Scientifiques Suisses 1928–29, 1932–33. *Arquivos do Museu Bocage* 16: 1–31.

Longfield C (1959) The Odonata of North Angola, Part 2. *Publicações Culturais, Companhia de Diamantes de Angola* 45: 16–42.

Mendelsohn JM, Huntley BJ (2023) Introducing the highlands and escarpments of Angola and Namibia. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment* 8: 7–22.

Moore A, Blenkinsop T, Cotterill F (2009) Southern African topography and erosion history: plumes or plate tectonics? *Terra Nova* 21(4): 310–315. https://doi.org/10.1111/j.1365-3121.2009.00887.x.

NGOWP (National Geographic Okavango Wilderness Project) (2018) *Initial findings from exploration of the upper catchments of the Cuito, Cuanavale and Cuando rivers in central and south-eastern Angola (May 2015 to December 2016)*. Unpublished report: NGOWP. pp. 352.

Pinhey E (1975) A collection of Odonata from Angola. *Arnoldia Rhodesia* 7(23): 1–16.

Pinhey E (1976)). Dragonflies (Odonata) of Botswana, with ecological notes. *Occasional Papers of the National Museum of Southern Rhodesia* B5: 524–601.

Ris F (1931) Odonata aus Süd-Angola. *Revue Suisse Zoologie* 38(7): 97–112.

Suhling F, Martens A (2007) *Dragonflies and damselflies of Namibia*. Gamsberg Macmillan, Windhoek.

Suhling F, Martens A (2014) Distribution maps and checklist of Namibian Odonata. *Libellula Supplement* 13: 107–175.

Tarboton W (2009) A dragonfly survey of the Humpata District. In: Huntley B (ed) *Projecto de estudo da biodiversidade de Angola. (Biodiversity rapid assessment – Huíla/Namibe.) Report on pilot project*. SANBI, Cape Town.