Demise and rise : the biogeography and taxonomy of the Odonata of tropical Africa

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Demise and rise

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Klaas-Douwe B. Dijkstra

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Demise and rise: the biogeography and taxonomy of the Odonata of tropical Africa
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Back cover photo: the author in Ankasa, Ghana, by Eric F. Thomassen
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Demise and rise
the biogeography and taxonomy of the Odonata of tropical Africa

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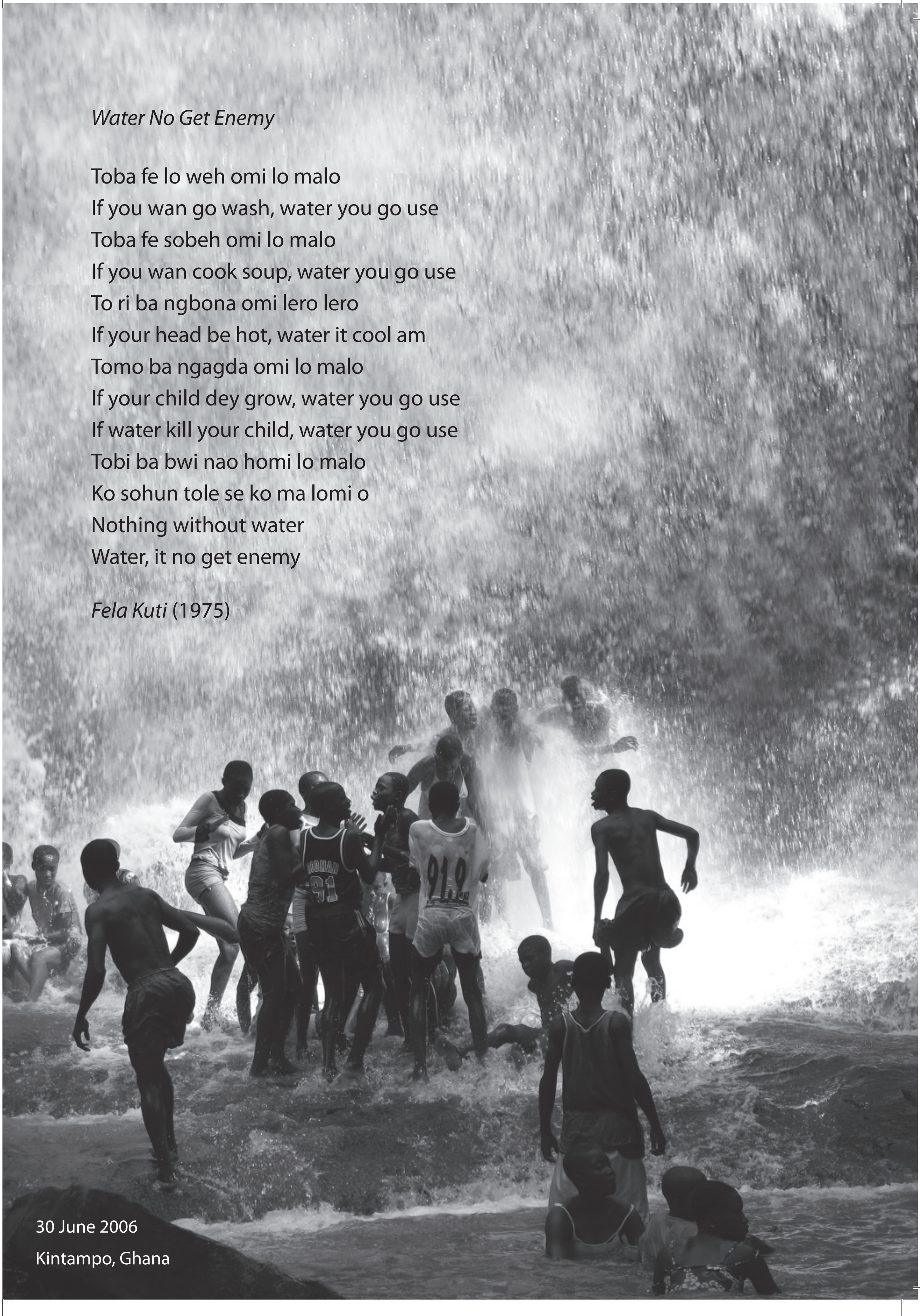

Water No Get Enemy

Toba fe lo weh omi lo malo
If you wan go wash, water you go use
Toba fe sobeh omi lo malo
If you wan cook soup, water you go use
To ri ba ngbona omi lero lero
If your head be hot, water it cool am
Tomo ba ngagda omi lo malo
If your child dey grow, water you go use
If water kill your child, water you go use
Tobi ba bwi nao homi lo malo
Ko sohun tole se ko ma lomi o
Nothing without water
Water, it no get enemy

Fela Kuti (1975)

30 June 2006

Kintampo, Ghana

for beauty

CONTENTS

chapter 1

A review of the taxonomy of African Odonata: finding ways to better identification and biogeographic insight

Cimbebasia 18: 191–206, 2003

Klaas-Douwe B. Dijkstra

A review of the taxonomy of African Odonata - finding ways to better identification and biogeographic insight

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The taxonomy of the approximately 850 species of sub-Saharan African Odonata is relatively well-known, probably due to the impoverished nature of the fauna as compared to that of other tropical regions. The need for revisions, study of higher classification, comprehension of (often clinal, environmentally induced) variability and knowledge of larvae, phylogeny and biogeography are stressed. Taxonomic priorities are discussed for each family. Supportive activities include the production of identification manuals for a broader public, the accumulation of supplementary material and the conservation of existing collections. A list of genera with estimated numbers of species, taxonomic status and references is provided, as well as a list of important regional works.

INTRODUCTION

Although not as well studied as the Holarctic and Australasian Region's faunas, knowledge of the taxonomy of African Odonata is well ahead of those of the Oriental and Neotropic Regions. The main reason is that the African fauna is relatively impoverished, harbouring only about 60% of the number of species found in each of the two other tropical regions. The writer here defines the African fauna as that occurring south of the Sahara, with the inclusion of the Indian Ocean islands (Comoros, Madagascar, Mascarenes and Seychelles). It numbers around 850 species, placed in 125 genera. The former figure is about 15% of the World total. Around 95% of species are not found beyond the region. Despite the fact that the African Odonata are relatively well-known, numerous taxonomic issues remain uncertain, or at least unsettlingly hazy. Elucidating the relationships between species, and finding ways to distinguish them, is perhaps the primary challenge of African odonatology. This knowledge is required as a fundament for future research, particularly for the almost untouched field of African odonate biogeography. The first priority for the taxonomy of African Odonata is, therefore, revisions.

REVISIONS & REVIEWS

It is hardly an exaggeration to say that all genera require at least some study. Elliot Pinhey tackled many problems, as can be seen from the numerous referrals to his work in the Appendix. Due to their size, large genera generally have the greatest problems. *Pseudagrion* is by far the largest genus with almost a hundred species. *Phyllomacromia* and *Trithemis* both number around forty species, *Chlorocypha*, *Paragomphus* and *Orthetrum* nearly thirty, and *Ceriagrion*, *Platycnemis*, *Gynacantha*, *Notogomphus* and *Phyllogomphus* about twenty. Other larger genera are *Lestes*, *Nesolestes*, *Agriocnemis*, *Elattoneura* and *Zygonyx*. Subtraction of the well-studied genera from the largest genera creates an idea of revision priority (*vide* Appendix). Besides full-scale revisions, many smaller issues of suspected synonyms, nomenclature, mix-ups, identification problems and species limits require attention. Some of the larger genera that appear fairly well sorted could be reviewed to straighten out the identification of the

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species. The problems are reviewed for each family below.

HIGHER CLASSIFICATION

Next to taxonomic work with a species-group (most often genus) approach, there are numerous problems in higher classification that require to be addressed. These are often relative to the fauna of the Oriental Region, with which the African fauna has most in common. It is a lucky coincidence that when Elliot Pinhey's 'trailblazer' Frederic Fraser began studying the African fauna intensively in the 1940s, he had about twenty years of experience of the oriental fauna. Many of the higher level problems are worldwide issues, and the knowledge of the African fauna shall profit from research in this field. The phylogeny of the Odonata is still much debated (e.g. Bechly 1995; Lohmann 1996; Trueman 1996). Especially the use of molecular techniques, which are used increasingly to study Odonata, holds the promise of new phylogenetic insights.

THE PROBLEM OF VARIABILITY

One of the greatest practical problems in African Odonata taxonomy is that of variability, particularly in size and melanisation (intensity of black pigmentation). Much of this variation is related to environmental conditions. The African Continent forms a vast, rather continuous landmass, and many of the species are wide-ranging. Numerous gradients in humidity and temperature lie across the continent, with the seasons adding another dimension of environmental variation. Specimens have been collected only fragmentarily along these clines in space and time, which may result in the false perception of discreteness in forms. The status of countless subspecies, as well as species, may be re-assessed with these recurrent variation trends in mind. Particularly sensitive to this problem are genera in which structural characters are of little taxonomic value (*Chlorocypha*) and groups that are difficult to collect (Gomphidae). In cases where discrete forms exist, one must ask why these are not worthy of species status, and if they are forms, what the ecological or behavioural backgrounds of them might be. Examples are the forms of *Palpopleura lucia* (Drury, 1773) (e.g. O'Neill & Paulson 2001) and *Eleuthemis buettikoferi* Ris, 1910 (Lempert 1988) and the subspecies of *Atoconeura biordinata* (Karsch, 1899) (Longfield 1953).

LARVAE

Most of what has been published on African Odonata (and most of what is written in this review) is about adults, but perhaps the greatest taxonomic frontier lies in the field of the larval stages. Although their study has (logically) lapsed behind, the larvae or exuviae of many genera have been described. Numerous genera and species are still awaiting such descriptions. The study of larvae shall offer a whole new set of characters for phylogenetic study. Many species are much easier to collect as larva than as adult (e.g. corduliids and gomphids) and, therefore, larvae also hold promise for biogeographic and ecological research. The rearing of larvae to adults must be especially stimulated, as it is the most reliable means to establish their specific identity.

PHYLOGENY & BIOGEOGRAPHY

Taxonomic research can be taken beyond the level of nomenclature and identification. With the aid of phylogenetic analysis and molecular techniques, hypotheses of the evolutionary history of African Odonata may be created. Combined with distribution data, this may serve to understand more about the climatology and geography of Africa and the origins and dispersive capacity of its dragonflies. Odonata have a number of biological advantages in this regard. Their strong relation with freshwater and different types of vegetation (particularly the forest-savanna contrast) make dragonflies sensitive to the environmental vicissitudes which characterise the continent's history. The species range from extremely good to very poor dispersers, which offer insight in different degrees of vicariance and dispersal. The Odonata are also a relatively ancient group, giving it a deep grasp in time. It of course remains to be seen (from the biogeographic and phylogenetic analyses advocated) if the present-day representatives are descendants of such ancient faunas. This combination of advantages is distinct from that of other well-studied groups, such as vertebrates, butterflies and plants. Therefore, what may be learnt from Odonata about African biogeography may be not only of affirmative, but even of supplementary value.

REVIEWS OF THE FAMILIES

The Appendix lists genera of African Odonata. For each genus the number of species, and the need for revision and biogeographic valuation, are estimated. An attempt is also made to provide the most recent, comprehensive or relevant references, i.e. those treating all species known (at the time of writing), a large proportion thereof, or that provide a good overall impression of the genus. In the following paragraphs the taxonomic status of each family is briefly outlined. These reviews are not exhaustive, but do stipulate the most urgent cases.

AMPHIPTERYGIDAE & CALOPTERYGIDAE

Due to the small numbers of species in these families and their conspicuous nature, they are well-known. The generic distinction between *Sapho* and *Umma* requires some attention, especially in relation to the species *puella* Sjöstedt, 1917, that is variably placed in either genus (G.S. Vick pers. comm.).

CHLOROCYPHIDAE

This family was treated in its totality by Pinhey (1967a). Nevertheless, the taxonomy is still unsound as a result of the lack of structural characters in this group (Figure 1). As a result, the morphological basis of the genera is rather slim. Problems are greatest in the red-bodied *Chlorocypha* species, particularly the *dispar*- and *rubida*-groups. These range throughout Africa's equatorial forests and demonstrate strong variation in markings (related to age and environment), which is at the same time the sole foundation of the many species and subspecies that are currently recognised. A possible source of new characters, though not easily quantified, are the agonistic and courtship displays of males (e.g. Robertson 1982).

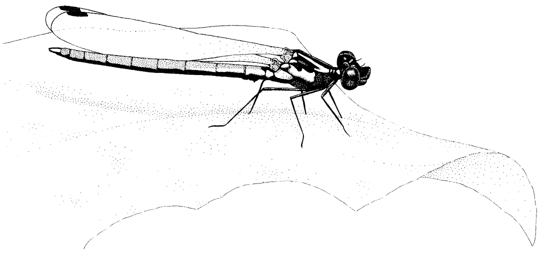

Figure **1**. Male of *Chlorocypha tenuis* Longfield. "*It has been realized for many years that some of the confusion is due to maturation changes in colour and markings*" writes Pinhey (1967a) in his revision of the African Chlorocyphidae. This variability still cripples the taxonomy of the group, which is poor in morphological characters, today.

LESTIDAE, PERILESTIDAE & SYNLESTIDAE

These families are small and taxonomically well-known. *Lestes* has been split into several (sub-) genera, six of which are recognised in Africa (Pinhey 1980b). The value of these can only be assessed after a complete phylogenetic treatment of this cosmopolitan group. Most of the African synlestids have limited ranges and knowledge of their phylogeny would yield insight into the biogeography of the Cape Region.

MEGAPODAGRIONIDAE

Coryphagrion grandis exhibits a strong ecological and morphological resemblance to the neotropical giant damselflies (Pseudostigmatidae). Thorough investigations should reveal whether these are mere analogies, or if the two are actually related (Clausnitzer & Lindeboom 2002). In the latter case it would provide a neotropical link at the 'wrong' side of Africa. The other genera seem more typically megapodagrionid, and their geographically isolated positions warrant biogeographic investigation relative to neotropical, oriental and australasian genera. The limits between *Allolestes*, *Nesolestes* and *Neurolestes* may require re-evaluation. Reviews of the three Malagasy genera also seem timely.

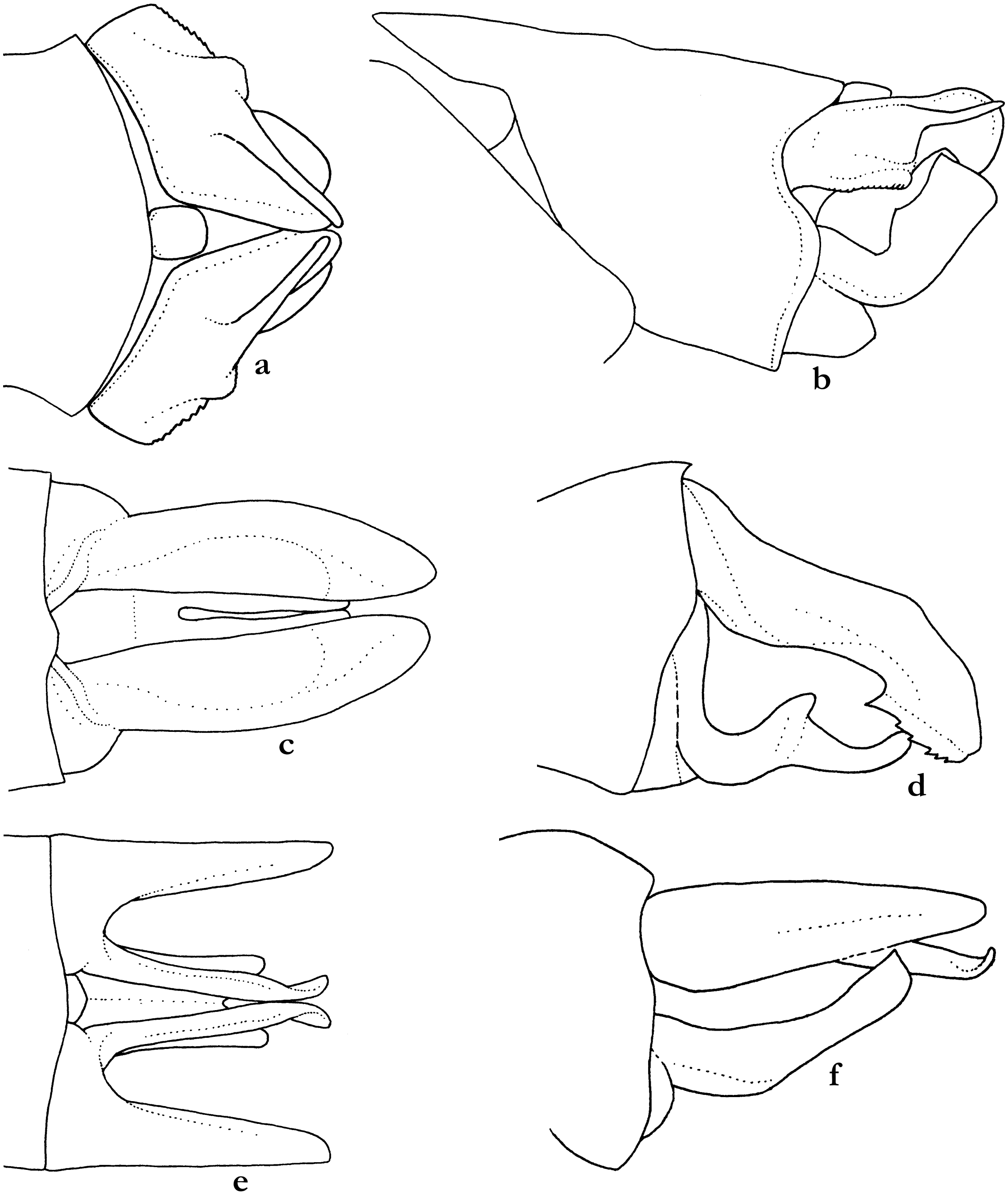

Figure **2**. Male appendages of African Gomphidae. **a**, *Ceratogomphus pictus* Hagen (dorsal aspect); **b**, *Ceratogomphus pictus* Hagen (lateral aspect); **c**, *Crenigomphus renei* Fraser (dorsal aspect); **d**, *Crenigomphus renei* Fraser (lateral aspect); **e**, *Microgomphus camerunensis* Longfield (dorsal aspect); **f**, *Microgomphus camerunensis* Longfield (lateral aspect). "*The main emphasis is on the Gomphidae since their appendages are far more diverse than other anisopterous families*" writes Pinhey (1969c) in what is still the most thorough investigation of odonate tandem linkage. Despite the morphological richness, no family requires more taxonomic attention than this one.

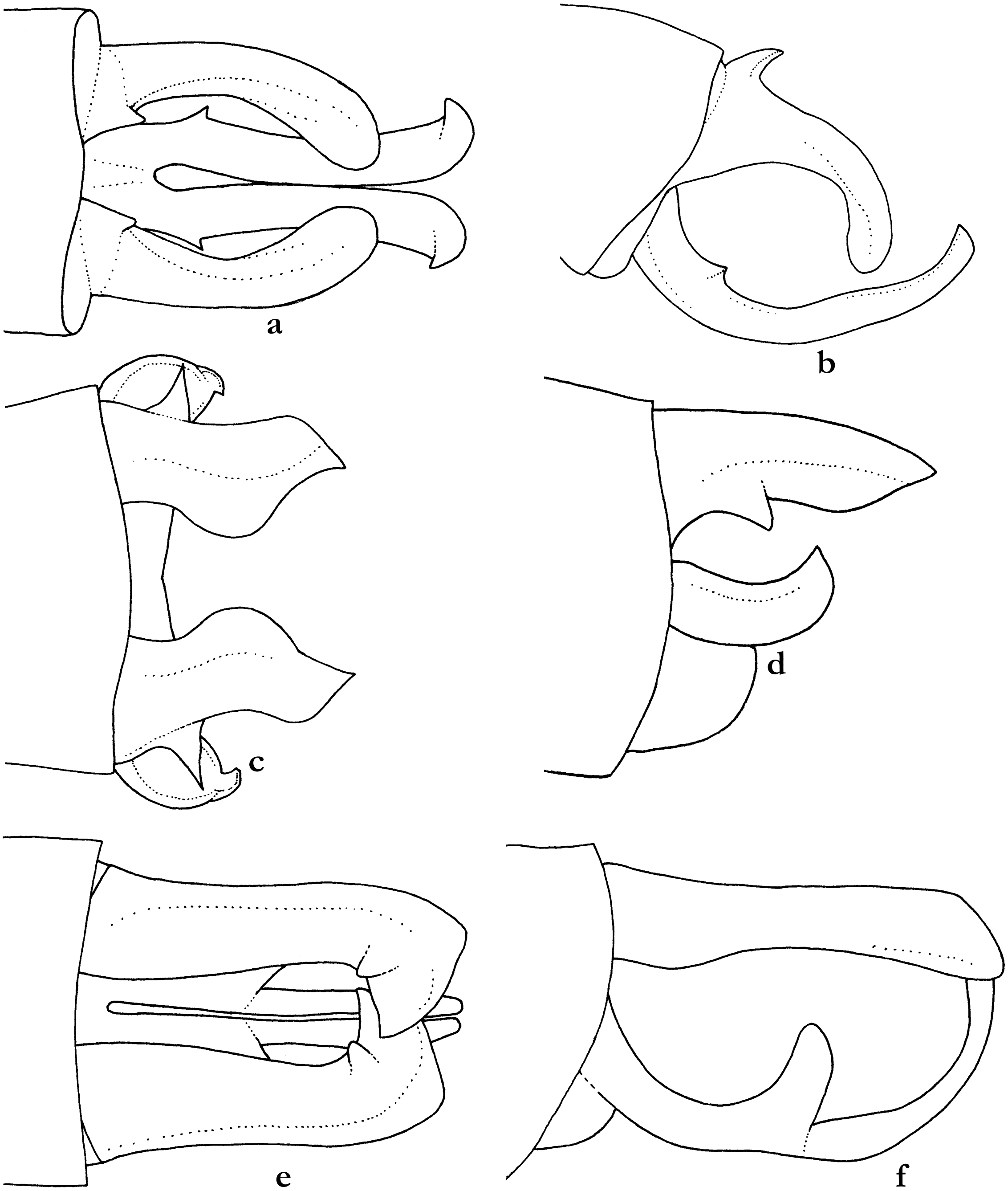

Figure **3**. Male appendages of African Gomphidae. **a**, *Nepogomphoides stuhlmanni* (Karsch) (dorsal aspect); **b**, *Nepogomphoides stuhlmanni* (Karsch) (lateral aspect); **c**, *Notogomphus lecythus* Campion (dorsal aspect); **d**, *Notogomphus lecythus* Campion (lateral aspect); **e**, *Onychogomphus styx* Pinhey (dorsal aspect); **f**, *Onychogomphus styx* Pinhey (lateral aspect). "*The main emphasis is on the Gomphidae since their appendages are far more diverse than other anisopterous families*" writes Pinhey (1969c) in what is still the most thorough investigation of odonate tandem linkage. Despite the morphological richness, no family requires more taxonomic attention than this one.

COENAGRIONIDAE

This is a large and problematic family. The status of a host of small or monotypic genera require study. Two species assigned to the oriental genus *Argiocnemis*, one from Cameroon and the one from the Indian Ocean island Rodriguez, are only known from the holotypes (Pinhey 1966b, 1970b). The anomalous *Argiagrion leoninum* is known only from the type female from Sierra Leone. Perhaps this specimen represents a mislabelled specimen from another fauna? Two West African *Pseudagrion* species were described by Pinhey (1973) in the same paper, but neither fits the genus: Relegation was indirectly proposed in the description of *Aciagrion walteri* Carfi & D'Andrea, 1994, an apparent synonym of *Pseudagrion cyathiforme* Pinhey, 1973. Gambles regarded *P. malagasoides* Pinhey, 1973 to represent a species of *Teinobasis* (G.S. Vick pers. comm.). *Teinobasis* is otherwise restricted to the eastern Oriental Region and the Pacific, save a complex of taxa described from Kenya, Madagascar, Malaŵi and the Seychelles, setting an interesting biogeographic scenario (V. Clausnitzer pers. comm.). What is the relationship of *Mortonagrion stygium* (Fraser, 1954) only African representative of an otherwise purely oriental genus to the varied complex of African *Agriocnemis* species? Finally, the Madagascar endemic *Millotagrion* exhibits similarities to *Aciagrion* not known from that island. The larger coenagrionid genera all require reviews. This is especially required for *Ceriagrion*. Numerous new species of *Pseudagrion*, described since Pinhey (1964a), make a re-evaluation valuable. Smaller taxonomic problems remain in this genus, particularly in the very variable group B (e.g. Dumont 1978). Research has shown that the African *Enallagma* break up into at least four genera, all unrelated to true *Enallagma* (May 1999).

PLATYCNEMIDIDAE

The taxonomic disarray of *Platycnemis* is almost legendary, authors having echoed each other's appeals for revision. The genus has an Equatorial African and a Malagasy radiation, numbering eight and 11 species respectively. The taxonomy of the Equatorial African group is especially troublesome, and revision shall probably lead to a reduction in the number of recognised species. The entire family would benefit from a phylogenetic study. In the platycnemidines, this would elucidate the relations of the two African radiations with that in the palearctic and with the oriental genus *Copera* Kirby, 1890. In the calicnemiines, the position of *Mesocnemis* and *Metacnemis*, and the origins of the many small, highly localised genera (relicts?) may be revealed. The first two are sometimes likened to the New World coenagrionid genus *Argia* Rambur, 1842 (e.g. Ris 1921).

PROTONEURIDAE

The genus *Elattoneura* is well-represented in the literature (e.g. Kimmins 1938; Legrand 1980, 1985; Lindley 1976), and an overview of it in its entirety would be valuable. *Prodasineura* numbers far less species, but has been treated only fragmentarily. Pinhey (1962b, 1981a) questions the validity of *Prodasineura* as separate from *Elattoneura*, but answering this also requires consideration of the oriental representatives of both. Similarly, *Chlorocnemis* is well-covered (Pinhey 1969a; Schmidt 1951c), but should be reviewed relative to the smaller, poorly known and closely related genus *Isomecocnemis*. Cowley (1936) and Schmidt (1951c) regarded *Chlorocnemis* and *Isomecocnemis* not as protoneurids, but as platycnemidids. These two genera have much in common with the platycnemidid *Allocnemis*, and the three may form a monophyletic group.

AESHNIDAE

Despite the broad review by Fraser (1962), the necessity of revising African *Gynacantha* is stressed by Pinhey (1974b) and repeated here. This genus is common in collections, which makes the production of good keys, especially to females, urgent. Much scarcer in collections are members of *Heliaeschna*, for which reason their taxonomic status is even more desperate. The African members of *Aeshna* are also awaiting treatment (G. Peters pers. comm.).

GOMPHIDAE

This family is without doubt the most problematic, and all African genera are in need of revision. Exceptions are the monotypic genera, together with *Ceratogomphus*, *Crenigomphus* and *Ictinogomphus*. The relationship of the monotypic *Cinitogomphus* with *Ictinogomphus* and *Gomphidia* deserves attention (Lieftinck 1969; Pinhey 1970d). The most daunting perspective in African odonatology is perhaps the taxonomic state of *Paragomphus*. Numerous species have been described, some only from females, while more stand in collections awaiting treatment. The status of the other genera is similarly bad, but they have fewer species. Gomphids are notoriously difficult to collect, and available material is often in a deplorable condition (e.g. teneral individuals). Although Fraser's (1960b) revision of *Crenigomphus* still appears to suffice, Fraser's (1957) treatment of *Phyllogomphus* is now completely outdated. The genus *Onychogomphus* ranges widely in the Old World and has partly been relegated to other genera. In that respect the remark of Carle (1986) that African representatives "… *are very likely* Cornigomphus" is of importance. For a systematist taking on the problems of gomphid taxonomy, the works of Corbet (1977), Fraser (1949a) and Pinhey (1969c) may offer inspiration (Figure 2 & 3).

CORDULIIDAE

The status of *Phyllomacromia* as an endemic genus distinct from *Macromia* was clarified by May (1997). Recent descriptions of numerous, often quite similar species illustrates the need of revision, despite progress outlined by Gambles (1979). Unravelling the phylogenetic position of the isolated genera *Libellulosoma*, *Nesocordulia*, *Syncordulia*, *Idomacromia* and *Neophya* is of particular biogeographic interest (M. May pers. comm.).

LIBELLULIDAE

This family numbers more species and genera than any other in Africa (Figure 4). The problems in it are similar to those in the second-largest family, Coenagrionidae. Firstly, the true value of many (small) genera must be established. Genera such as *Anectothemis*, *Congothemis*, *Lokia* and *Porpacithemis* have been mentioned as links between other genera and (the weakly defined) subfamilies. The discussion of Pinhey (1966c) on *Aethiothemis*, *Orthetrum* and *Oxythemis* is an example. The lack of clarity has in part been created by an overemphasis of wing venation characters and an underappreciation of their variability by previous authors. The Tetrathemistinae are particularly diverse in Africa, with numerous small genera inhabiting forests. The subfamily is probably an ancient one, and study of the phylogeny appears a promising perspective for biogeography, but also for the clear demarcation of the genera (G.S. Vick pers. comm.). Secondly, many of the larger genera require revisions or reviews.

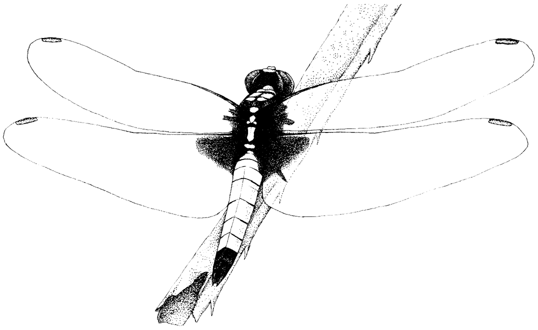

Figure **4**. Male of *Cyanothemis simpsoni* Ris. "*This is one of the most remarkable Libellulinae seen by me*" according to Ris (1915). As monographer of the libellulids, Ris was the best judge. After discussing its unique venation he continues: "*The colour-system is, perhaps, still more extraordinary: a very common pattern, sky-blue and black, is obtained, not as in all other known cases by pruinosity, but by pigmentation.*" The genus is monotypic, endemic to Africa and unmistakeable. Unfortunately such cases of taxonomic clarity are rare.

SUPPORTIVE ACTIVITIES

Besides pure systematic research, the following action is required to support and advocate the research on African Odonata.

Table 1. Regional reviews. Abbreviations: **Sub** = suborders covered (**Z** = Zygoptera; **A** = Anisoptera), **keys** = keys provided (**G** = to genera; **S** = to species).

Reference	Country or region	Sub	Keys
Pinhey 1962a	Africa	ZA	G
Pinhey 1961a	Africa, eastern	ZA	GS
Pinhey 1951	Africa, southern	ZA	GS
Brooks & Jackson 2001	Bioko	ZA	
Pinhey 1976	Botswana	ZA	GS
Vick 2000	Cameroon, southwest	ZA	
Pinhey 1966c	DR Congo, northeast	ZA	GS
Consiglio 1978	Ethiopia	Z	
Pinhey 1982	Ethiopia	A	
Gambles *et al.* 1998	The Gambia	ZA	
O'Neill & Paulson 2001	Ghana	ZA	
Lempert 1998	Liberia	ZA	
Schmidt 1951a	Madagascar	Z	GS
Fraser 1956	Madagascar	A	GS
Lieftinck 1965	Madagascar	ZA	
Pinhey 1966a	Malaŵi	ZA	GS
Barlow 1996	Malaŵi	ZA	
Pinhey 1981b	Mozambique	ZA	
Martens *et al.* 2002	Namibia	ZA	
D'Andrea & Carfi 1994	Sierra Leone	ZA	
Carfi 1974	Somalia	ZA	
Pinhey 1984b	South Africa	Z	
Pinhey 1985	South Africa	A	
Pinhey 1984a	Zambia	ZA	S
Pinhey 1967b	Zambia, northeast	Z	GS
Lieftinck 1969	Zambia, northeast	A	
Pinhey 1984a	Zimbabwe	ZA	S

REGIONAL REVIEWS & IDENTIFICATION MANUALS

For individuals to research (all aspects of) African Odonata they need means to identify species, as well as knowledge of regional faunas. Table 1 lists such sources, in which the paramount importance of Pinhey's work is again notable. Transferring taxonomic knowledge to a broader public in the form of keys and field guides has a high priority. Such initiatives are underway for the adult Odonata of East Africa (Viola Clausnitzer & Klaas-Douwe Dijkstra), Cameroon (Graham Vick), Namibia (Andreas Martens) and South Africa (Michael Samways). A key to larvae of all African genera would be another major step forward in African odonatology. Larval keys are in preparation for Cameroon (David Chelmick), Mascarenes (Andreas Martens & Ole Müller) and southern Africa (Michael Samways).

EXPEDITIONS & COLLECTIONS

Study of the taxonomy, identification and biogeography of African Odonata is impossible without good material being available for study. Acquiring and conserving it is, therefore, as important as systematic research itself. The most important collections of African Odonata are probably in museums in Berlin, Bulawayo, London, Paris and Tervuren. Only the fourth is presently in the hands of a specialised curator. Museums should be aided in the conservation, expansion and research of their collections. It is also necessary to create, expand and conserve collections in Africa itself, so the study of African Odonata can be taken from outside the continent, to within.

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Appendix List of genera of African Odonata. Classification follows Davies & Tobin (1984, 1985), except Gomphidae (Carle 1986). Abbreviations: **n** = number of valid species, in many cases a rough estimate; **e** = genus endemic (or near-endemic if between brackets) to a particular region (- = also found outside Africa; **A** = sub-Saharan Africa; **Ci** = Côte d'Ivoire; **Cm** = Cameroon Highlands; **Cp** = Cape Region; **Ec** = East Coast Forest from Kenya to Mozambique; **Md** = Madagascar and Comoros; **Ml** = Malaŵi; **Mr** = Mauritius; **Ms** = Mascarenes; **Sc** = Seychelles; **Sl** = Sierra Leone; **Tn** = Tanzania; **Wc** = forests of West and central Africa), **t** = taxonomic status (**?** = status of endemic genus or placement of species in non-endemic genus requires study; **+** = review of (parts of) genus required; **++** = revision of genus urgently required); **b** = interesting for study of African biogeography. The number of species discussed in each reference is given between brackets.

(Sub)family	Genus	n	e	t	b	Remark/ reference
Amphipterygidae: Rimanellinae	*Pentaphlebia* Förster, 1909	2	Cm		+	Asahina 1956 (1); Parr 1977 (2)
Calopterygidae: Calopteryginae	*Phaon* Sélys, 1853	2	A			
	Sapho Sélys, 1853	5	Wc	?		
	Umma Kirby, 1890	11	(Wc)	?	+	Pinhey 1969b (10); Vick 1996 (+1)
Chlorocyphidae	*Africocypha* Pinhey, 1961	1	Cm	?		Pinhey 1971c
	Chlorocypha Fraser, 1928	31	A	+	+	Pinhey 1967a (26)
	Platycypha Fraser, 1949	8	A	?	+	Pinhey 1967a (8)
Lestidae	*Lestes* Leach, 1815	14	-			Pinhey 1980b (14)
Perilestidae	*Nubiolestes* Fraser, 1945	1	Cm		+	Schmidt 1943
Synlestidae	*Chlorolestes* Sélys, 1862	7	(Cp)		+	(extends to Ml) Pinhey 1951 (5)
	Ecchlorolestes Barnard, 1973	2	Cp		+	Pinhey 1951 (2)
Megapodagrionidae: Argiolestinae	*Allolestes* Sélys, 1868	1	Sc	?	+	Blackman & Pinhey 1967
	Amanipodagrion Pinhey, 1962	1	Tn			Pinhey 1962b
	Nesolestes Sélys, 1891	17	(Md)	+	+	(one species in Cm) Fraser 1955a (11)
	Neurolestes Sélys, 1882	1	(Cm)	?	+	(Cm to Gabon) Fraser 1955b; Gambles 1970
	Protolestes Förster, 1899	8	Md	+	+	Aguesse 1967 (7)
Megapodagrionidae: Coryphagrioninae	*Coryphagrion* Morton, 1924	1	Ec		+	Kimmins 1931; Fraser 1955b
Megapodagrionidae: Megapodagrioninae	*Tatocnemis* Kirby, 1889	10	Md	+	+	Fraser 1960a (7)
Coenagrionidae: Agriocnemidinae	*Agriocnemis* Sélys, 1869	16	-			Pinhey 1974a (16)
	Argiocnemis Sélys, 1877	2	-	?		Pinhey 1966b (1); 1970b (1)
	Coenagriocnemis Fraser, 1949	4	Ms			
	Mortonagrion Fraser, 1920	1	-	?		Pinhey 1974a
Coenagrionidae: Ischnurainae	*Aciagrion* Sélys, 1891	14	-	+		Pinhey 1972 (10)
	Enallagma Charpentier, 1840	21	-	+		species to be relegated to endemic genera
	Ischnura Charpentier, 1840	5	-	+		
	Millotagrion Fraser, 1953	1	Md	?		Fraser 1953b; Lieftinck 1965
Coenagrionidae: Pseudagrioninae	*Argiagrion* Sélys, 1876	1	Sl	?		Pinhey 1966b
	Ceriagrion Sélys, 1876	22	-	+		Pinhey 1963 (13)
	Pseudagrion Sélys, 1876	96	-	+	+	Pinhey 1964a (72)
	Teinobasis Kirby, 1890	3	-	+		Schmidt 1951a (1); Pinhey 1966a (2)
Platycnemididae: Calicnemiinae	*Allocnemis* Sélys, 1863	2	(Cp)		+	(one species in Katanga)
	Leptocnemis Sélys, 1886	1	Sc		+	Blackman & Pinhey 1967
	Mesocnemis Karsch, 1891	4	A	+		Legrand 1982 (3); Lempert 1992 (+1)
	Metacnemis Sélys, 1863	3	(Cp)		+	(one species in Md) Pinhey 1980a
	Oreocnemis Pinhey, 1971	1	Ml		+	Pinhey 1971a
	Paracnemis Martin, 1902	1	Md		+	Schmidt 1951a
	Stenocnemis Sélys, 1886	1	(Cm)		+	Schmidt 1951b

Appendix cont. (*vide* Figure legend for abbreviations)

(Sub)family	Genus	n	e	t	b	Remark/ reference
Platycnemididae: Platycnemidinae	*Platycnemis* Burmeister, 1839	19	-	++	+	Schmidt 1951a (7)
Protoneuridae	*Chlorocnemis* Sélys, 1863	12	A		+	Pinhey 1969a (10)
	Elattoneura Cowley, 1935	15	-	+		Lindley 1976 (11); Legrand 1980 (3), 1985 (6)
	Isomecocnemis Cowley, 1936	3	(Wc)	+		
	Prodasineura Cowley, 1934	6	-	+		Pinhey 1981a
Aeshnidae: Aeshninae	*Aeshna* Fabricius, 1775	9	-	+		
	Anaciaeschna Sélys, 1878	1	-			
	Anax Leach, 1815	11	-			includes *Hemianax*
	Gynacantha Rambur, 1842	20	-	++		Fraser 1962 (20)
	Heliaeschna Sélys, 1882	9	-	++		Fraser 1939 (5)
Gomphidae: Austrogomphinae	*Lestinogomphus* Martin, 1911	5	A	++		Legrand & Lachaise 2002 (2)
Gomphidae: Epigomphinae	*Microgomphus* Sélys, 1857	7	-	+		includes *Africogomphus*, Pinhey 1961c
Gomphidae: Gomphinae	*Neurogomphus* Karsch, 1890	10	A	++		Pinhey 1967c (7)
	Notogomphus Hagen, 1857	19	A	++	+	
Gomphidae: Lindeniinae	*Cinitogomphus* Pinhey, 1964	1	A	?		Pinhey 1964b, 1970d
	Diastatomma Burmeister, 1839	7	Wc	++		
	Gomphidia Sélys, 1854	7	-	++		
	Ictinogomphus Cowley, 1934	3	-			Kimmins 1958 (3)
Gomphidae: Onychogomphinae	*Cornigomphus* Martin, 1907	1	Wc	?		
	Crenigomphus Sélys, 1892	6	A			Fraser 1960b (6)
	Nepogomphoides Fraser, 1952	1	(Tn)		+	(extends to Ml) Fraser 1952
	Onychogomphus Sélys, 1854		12	-	++	
	Paragomphus Cowley, 1934	31	-	++		
	Tragogomphus Sjöstedt, 1899	5	Wc	+		Pinhey 1961b (3)
Gomphidae: Phyllogomphinae	*Ceratogomphus* Sélys, 1854	2	(Cp)		+	(extends to Katanga)
	Isomma Sélys, 1892	1	Md		+	Fraser 1946
	Malgassogomphus Cammaerts,1987	1	Md		+	Cammaerts 1987
	Phyllogomphus Sélys, 1854	20	A	++	+	Fraser 1957 (9)
Corduliidae: Corduliinae	*Libellulosoma* Martin, 1907	1	Md	?	+	
	Hemicordulia Sélys, 1870	3	-			Fraser 1949b (3)
Corduliidae: Gomphomacromiinae	*Nesocordulia* McLachlan, 1882	6	Md		+	Fraser 1956 (5); Legrand 1984b (+1)
	Syncordulia Sélys, 1882	2	Cp		+	Barnard 1933 (2); Lieftinck 1961 (1)
Corduliidae: Idomacromiinae	*Idomacromia* Karsch, 1896	2	Wc		+	Legrand 1984a (2)
Corduliidae: Macromiinae	*Phyllomacromia* Sélys, 1878	41	A	++	+	Fraser 1954b (26); Gambles 1979 (12)
Corduliidae: Neophyinae	*Neophya* Sélys, 1881	1	Wc		+	
Libellulidae: Brachydiplacinae	*Anectothemis* Fraser, 1954	1	Wc	?		Fraser 1954a
	Chalcostephia Kirby, 1889	1	A			
	Congothemis Fraser, 1953	1	Wc	?		Fraser 1953a
	Eleuthemis Ris, 1910	2	(Wc)	+		
	Hemistigma Kirby, 1889	2	A			
	Porpacithemis Fraser, 1954	3	Wc	+		Fraser 1958 (2)
	Porpax Karsch, 1896	4	A			Pinhey 1966c (4)
	Thermochoria Kirby, 1889	2	A			

Appendix cont. (*vide* Figure legend for abbreviations)

(Sub)family	Genus	n	e	t	b	Remark/ reference
Libellulidae: Libellulinae	*Aethiothemis* Ris, 1908	9	A	++		
	Hadrothemis Karsch, 1891	7	A	+		
	Lokia Ris, 1919	7	A	+		Fraser 1953a (5); Lieftinck 1969 (+2)
	Nesciothemis Longfield, 1955	5	A	+		Gambles 1966 (4); Pinhey 1971b (5)
	Orthetrum Newman, 1833	29	-			Pinhey 1970a (28), 1979 (+1)
	Oxythemis Ris, 1909	1	(Wc)			
	Thermorthemis Kirby, 1889	2	Md			
	Viridithemis Fraser, 1961	1	Md	?		
Libellulidae: Palpopleurinae	*Palpopleura* Rambur, 1842	5	-			
Libellulidae: Sympetrinae	*Acisoma* Rambur, 1842	2	-			
	Brachythemis Brauer, 1868	4	-			
	Bradinopyga Kirby, 1893	2	-			
	Crocothemis Brauer, 1868	6	-			Lohmann 1980 (5)
	Cyanothemis Ris, 1915	1	Wc			Ris 1915
	Diplacodes Kirby, 1889	5	-	+		Pinhey 1976 (5)
	Philonomon Förster, 1906	1	A	?		
	Sympetrum Newman, 1833	4	-	?		
Libellulidae: Tetrathemistinae	*Allorrhizucha* Karsch, 1890	3	(Wc)	?	+	
	Archaeophlebia Ris, 1909	1	Md		+	
	Calophlebia Sélys, 1896	2	Md		+	
	Eothemis Ris, 1909	1	Wc	?	+	
	Malgassophlebia Fraser, 1956	6	(Wc)	+	+	(two species in Md) Legrand 1986 (3), 2002 (+2)
	Mesumbethemis Vick, 2000	1	Cm		+	Vick (2000): with key to genera subfamily
	Micromacromia Karsch, 1890	3	A		+	
	Monardithemis Longfield, 1947	1	A	?	+	Longfield 1947
	Neodythemis Karsch, 1889	8	A		+	
	Notiothemis Ris, 1919	2	A		+	Fraser 1944 (2)
	Sleuthemis Fraser, 1951	1	Wc	?	+	Fraser 1951; Aguesse 1968
	Tetrathemis Brauer, 1868	10	-	+	+	Fraser 44 (6); Legrand 77 (4)
Libellulidae: Trameinae	*Parazyxomma* Pinhey, 1961	1	A			
	Pantala Hagen, 1861	1	-			
	Tholymis Hagen, 1867	1	-			
	Tramea Hagen, 1861	2	-			
	Rhyothemis Hagen, 1867	6	-			
	Zyxomma Rambur, 1842	2	-			
Libellulidae: Trithemistinae	*Atoconeura* Karsch, 1899	2	A	+	+	Longfield 1953 (2)
	Thalassothemis Ris, 1912	1	Mr		+	Pinhey 1955
	Trithemis Brauer, 1868	37	-	+		Pinhey 1970c (35)
Libellulidae: Urothemistinae	*Aethriamanta* Kirby, 1889	1	-			
	Macrodiplax Brauer, 1868	1	-			
	Selysiothemis Ris, 1897	1	-			
	Urothemis Brauer, 1868	4	-			
Libellulidae: Zygonychinae	*Olpogastra* Karsch, 1895	4	A			
	Zygonychidium Lindley, 1970	1	Ci			Lindley 1970
	Zygonyx Hagen, 1867	17	-	+	+	Lieftinck 1963 (4); Pinhey 1964b (11)

chapter 2

Tropical African *Platycnemis* damselflies (Odonata: Platycnemididae) and the biogeographical significance of a new species from Pemba Island, Tanzania

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Tropical African *Platycnemis* damselflies (Odonata: Platycnemididae) and the biogeographical significance of a new species from Pemba Island, Tanzania

Abstract The damselfly, *Platycnemis pembipes* sp. nov., is described from Pemba Island (Ngezi Forest, Tanzania) and its affinities with Guineo-Congolian and Malagasy congeners are examined. For this purpose the identity and distribution of Afrotropical *Platycnemis* is reviewed, especially the taxonomically confused continental species. The Pemba species is nearly identical to some species of the Malagasy radiation of *Platycnemis*, but distant from the Guineo-Congolian species that have tropical Asian affinities. It is argued that the species is a long-distance wind-borne arrival from Madagascar, which survived due to favourable climatic conditions on Pemba. Habitats on the mainland, only 50 km further, are or have been drier and therefore seem unsuitable. The new species, living proof of a remarkable colonisation event, is under immediate threat, confined to a single stream in an imperilled forest, over 1000 km from its nearest relatives. The holotype of the enigmatic *P. mauriciana*, not recorded on Mauritius after its description, cannot originate from the island as it pertains to the European *P. latipes*. Five species recalling the Asian genus *Copera* are known in the male sex from central and western Africa; all were confused to some degree with *P. congolensis* and a key is given. The lectotype of *P. congolensis* is designated and its identity is clarified. *Platycnemis flavipes* and *P. xanthopus* are junior synonyms of *P. nyansana*. Discovery of the *P. rufipes* female showed that *P. escherichi*, known only from the female holotype, is a junior synonym of it. The generic classification of *Platycnemis* and *Copera* is not resolved, but data and hypotheses that should aid future analysis are provided.

Key words damselflies, Zygoptera, *Platycnemis*, Africa, Pemba, biogeography, taxonomy, synonyms

Introduction

A damselfly of the genus *Platycnemis* Burmeister, 1839 was recently discovered on Pemba Island, 50 km off the Tanzanian coast; separated by 1000 km of dry land and a similar distance of sea from its most proximal relatives in Uganda and the Comoros (Figs 1a, 2). Platycnemidine damselflies are represented by at least 35 species in Africa, Europe and Asia. Geographically four disjunct groups can be recognised: (1) six Western Palaearctic species, including the type species of *Platycnemis*; (2) at least five Guineo-Congolian species; (3) at least 10 species on Madagascar and associated islands, including the type species of *Proplatycnemis* Kennedy, 1920; (4) between 13 and 16 species in eastern Asia, including the type species of *Copera* Kirby, 1890 and *Pseudocopera* Fraser, 1922. Although highly distinctive as a group (Fig. 1), platycnemidine taxonomy is unresolved. Most species are classified as *Platycnemis*, while part of the Oriental species have been placed in *Copera*, but this generic classification is poorly supported (Ris, 1915; Schmidt, 1951b; Martens, 1996; Hämäläinen, 2003). To understand the Pemba species' affinities and biogeography, the taxonomy, range and ecology of the Afrotropical *Platycnemis* (groups 2 and 3) must be reviewed (Tables 1–2, Fig. 2). In particular the taxonomy of the continental species is notoriously confused (Martens, 1996; Dijkstra, 2003). That of the insular species is quite well resolved (Schmidt, 1951b; Lieftinck, 1965), although their ecology is poorly known. Better knowledge of the group can only be obtained once the study of Madagascar's Odonata is intensified (Dijkstra & Clausnitzer, 2004). Besides the continental species we examined the enigmatic *P. mauriciana* of Mauritius. It is of particular interest because, like the Pemba species, it is highly isolated from its nearest

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Figure 1 *Platycnemis* males. (a) *P. pembipes* sp. nov., Ngezi Forest, Pemba Island, 1 October 2001; (b) *P. nyansana*, Mpanga Forest, Uganda, 14 May 2003. Photographs by V. Clausnitzer (a) and K.-D.B. Dijkstra (b).

relatives. We do not attempt to resolve problems of the generic classification of *Platycnemis* and *Copera*, but provide data and hypotheses that should aid future analysis.

Materials and methods

We reviewed relevant Afrotropical *Platycnemis* (type) material in the Natural History Museum, London (BMNH), Institut Royal des Sciences Naturelles de Belgique, Brussels (ISNB), Museo Civico di Storia Naturale “Giacomo Doria”, Genova (MCSN), Muséum National d’Histoire Naturelle, Paris (MNHN), Musee Royal de l’Afrique Centrale, Tervuren (MRAC), Naturhistoriska Riksmuseet, Stockholm (NHRS), National Museums of Kenya, Nairobi (NMKE), Nationaal Natuurhistorisch Museum Naturalis, Leiden (RMNH), University of Michigan Museum of Zoology, Ann Arbor (UMMZ) and Museum für Naturkunde der Humboldt-Universität, Berlin (ZMHB). The Pemba species was compared with all continental African species and the insular *P. alatipes*, *P. hova*, *P. malgassicum*, *P. pseudalatipes* (all BMNH), *P. agrioides* and *P. aurantipes* (RMNH).

	Continental group	**Insular group**
Range (Fig. 2)	Uganda to The Gambia	Madagascar, Comoros and Pemba Island
Thorax	Often with distinct pale speckling, like spatter of bleach (Figs 3b–e)	Usually without pale speckling (Fig. 3a)
Dilations mid and hind tibiae	At most 2× as wide as shaft (Fig. 4b)	Up to 5× as wide as shaft (Fig. 4a)
Leg colour	Yellow to rufous, but never white and at most joints and tarsi darkened	Often white, but sometimes a reddish or bluish colour, can be extensively marked with black
Penis	Apex rounded; lateral branches absent (Fig. 6b)	Apex deeply incised; long lateral branches probably always present (Fig. 6a)
Cerci	Long, often with prominent internal branch (Figs 5b–f)	Short, with small (often poorly visible) branch (Fig. 5a)
/paraprocts	Two-thirds or more	Half or less
/segment 10	Equal or more	Equal or less

Table 1 Comparison of Afrotropical *Platycnemis* groups.

Insular	
agrioides Ris, 1915	Mayotte, Comoros
alatipes (McLachlan, 1872)	Madagascar
aurantipes Lieftinck, 1965	Madagascar
hova Martin, 1908	Madagascar
longiventris Schmidt, 1951	Madagascar
malgassica Schmidt, 1951	Madagascar
*melana** Aguesse, 1968	Nzwani, Comoros
pembipes sp. nov.	Pemba, Tanzania
protostictoides Fraser, 1953	Madagascar
pseudalatipes Schmidt, 1951	Madagascar
sanguinipes Schmidt, 1951	Madagascar
Continental	
congolensis Martin, 1908	Western Congo and Gabon
guttifera Fraser, 1950	Liberia to Nigeria, possibly Cameroon
nyansana Förster, 1916	Congo Basin to Uganda
rufipes (Selys, 1886)	Cameroon, possibly Gabon
sikassoensis (Martin, 1912)	Uganda to The Gambia

Table 2 Distribution of continental and insular Afrotropical *Platycnemis* species.

*corrected spelling

Systematics

Key to Afrotropical *Platycnemis* males

The differences between the continental and insular species are given in Table 1. The key below is only applicable for mature *Platycnemis* males west of the Mozambique Channel. The species are difficult to key as they demonstrate extreme colour change with age; the characters of colour and markings refer to fully mature specimens and are included with some caution. A key to the Malagasy species is provided by Schmidt (1951b), with additions by Lieftinck (1965).

1 Dilations of mid and hind tibiae more than 3× as wide as shaft (Fig. 4a). Legs white. Cerci less than half length of paraprocts (Fig. 5a). Pemba Island, Tanzania .... *pembipes* sp. nov.

Dilations of mid and hind tibiae at most 2× as wide as shaft (Fig. 4b). Legs yellow to rufous. Cerci at least two-thirds length of paraprocts (Figs 5b–f). Uganda to The Gambia 2

2 (1) Branches of cerci short, usually only visible in caudal view (Fig. 5f). Subapical pale ring of segments 3–7 reduced, abdomen appearing dark. Legs uniformly orange. Postclypeus with narrow pale border; synthorax usually with narrow complete antehumeral (pale) and humeral (black) stripes (Fig. 3e). Hindwing length 14–17 mm. Sunny rivers and streams .... *sikassoensis*

Branches of cerci long, usually well visible in lateral and dorsal view (Figs 5b–e). Segments 3–7 with pale basal and subapical rings (may be incomplete dorsally), giving abdomen annulated effect. Legs yellow to rufous, often darkened at joints ('ringed knees'). Postclypeus black at border; antehumeral stripe often broad and not bounded by humeral stripe, or mesepisternum largely dark (Figs 3b–d). Hindwing length 17–21 mm. Shaded forest pools, streams and rivers 3

3 (2) Cerci distinctly shorter than paraprocts; branches of cerci diverge from and usually fall (just) short of cerci tips (Figs 5b, d). Mid- and hind tibiae distinctly widened. Legs yellow and darkened at joints ('ringed knees'). Synthorax with pale speckles and complete antehumeral stripe (Fig. 3c). Uganda to Gabon 4

Cerci almost as long as paraprocts; branches of cerci lie close to and often surpass cerci tips (Figs 5c, e). Tibiae

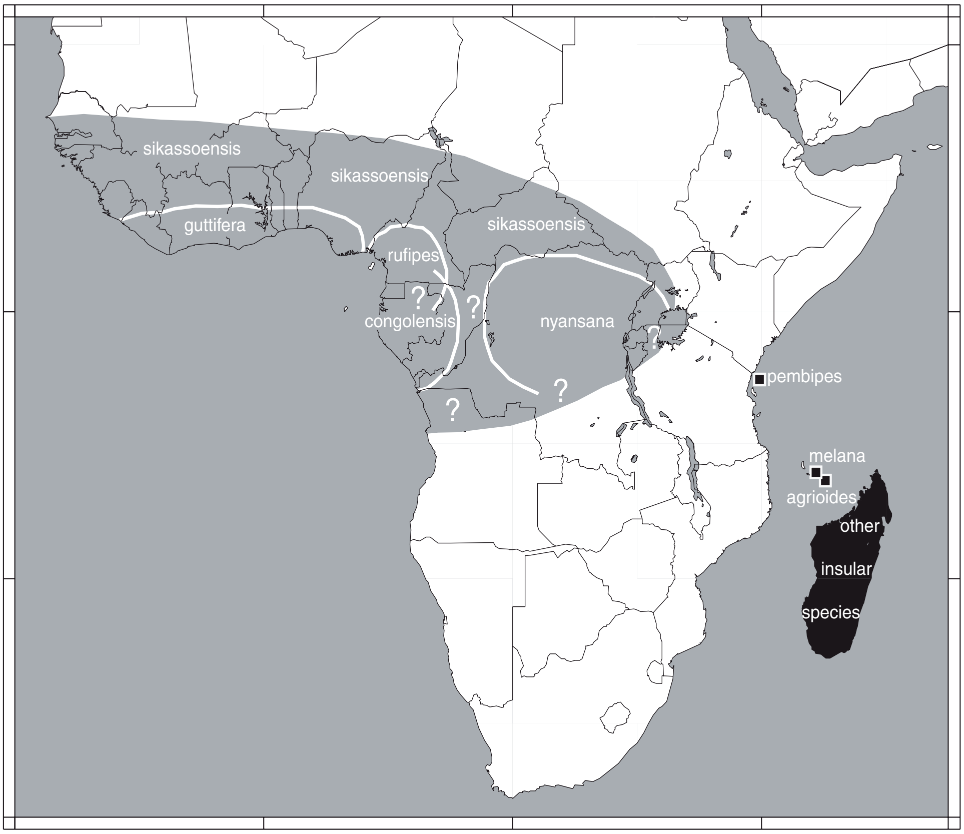

Figure 2 Approximate distributions of Afrotropical *Platycnemis* species; insular (black) and continental (grey). Especially the general southern limits and contact zones of continental species are unclear; range of *P. sikassoensis* (at least partly) incorporates ranges of other continental species. See Table 2 for further details.

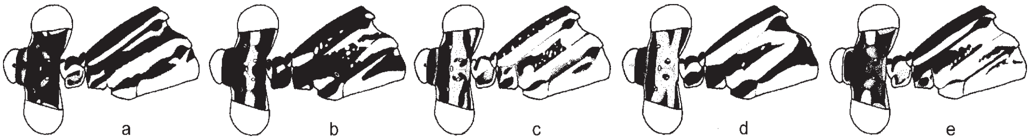

Figure 3 *Platycnemis* mature male head in dorsal and thorax in lateral view. (a) *P. pembipes* sp. nov.; (b) *P. guttifera*; (c) *P. nyansana*; (d) *P. rufipes*; (e) *P. sikassoensis*. Individual variation is great; dark markings are strongly reduced in younger specimens. *P. congolensis* is similar to *P. nyansana*.

not widened, or dilations are mere ridges. Legs uniformly rufous or yellow with darkened joints. Synthorax often either with only speckles or antehumeral stripe (Figs 3b, d). Liberia to Cameroon, possibly Gabon 5

4 (3) Posterior border of pronotum drawn out into two slender vertical processes. Branches of cerci reach almost to tips of cerci. Western Congo and Gabon . . . . *congolensis*

Pronotum without vertical processes. Branches of cerci fall well short of tips. Congo Basin to Uganda . . . . *nyansana*

5 (3) Branches of cerci with expanded tips (Fig. 5e). Legs rufous. Synthorax with smooth-edged black and pale stripes, including complete antehumeral stripe, at most speckled with a dot or two (Fig. 3d). Cameroon, possibly Gabon . . . . *rufipes*

Branches of cerci with slender pointed tips (Fig. 5c). Legs yellow with darkened joints. Synthorax with irregular speckled markings, antehumeral stripe often reduced to some pale speckles on an otherwise all black mesepisternum (Fig. 3b). Liberia to Nigeria . . . . *guttifera*

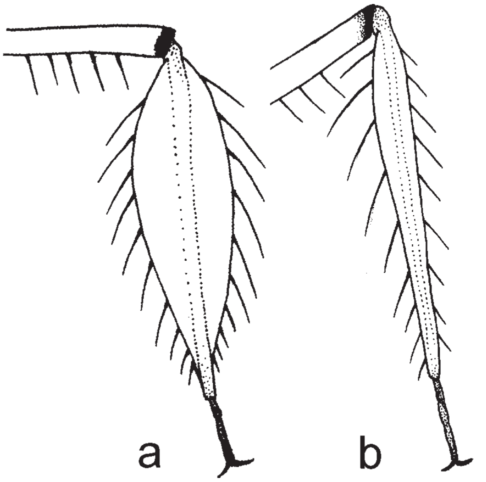

Figure 4 *Platycnemis* male hind leg in lateral view. (a) *P. pembipes* sp. nov.; (b) *P. nyansana*.

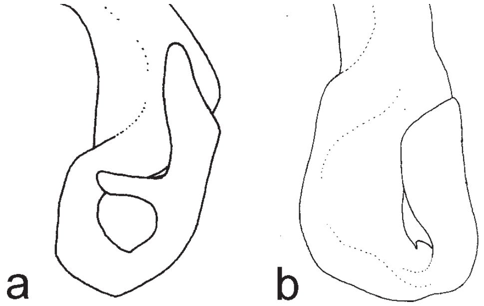

Figure 6 *Platycnemis* male penis (genital ligula) in lateral view. (a) *P. pembipes* sp. nov.; (b) *P. nyansana*.

Platycnemis pembipes sp. nov.

Figs 1a, 3a, 4a, 5a, 6a, 7

Material examined

Holotype ♂, paratypes (7 ♂, 2 ♀): Tanzania, Pemba Island, Ngezi Forest (04°56′16.6″S 39°42′38.6″E), 38 m a.s.l., 6–8 October 2001, leg. V. Clausnitzer. The holotype (RMNH INS 228162) and 7 paratypes (RMNH INS 228163 through 228169; 5♂, 2♀) are deposited in RMNH; 2 ♂ paratypes will be deposited in NMKE.

Description

Holotype male

Black-and-white *Platycnemis* with strongly dilated white tibiae (Fig. 1a). Labium and genae whitish; labrum cream with a small blackish central spot at base; postclypeus black, narrowly pale at base; antennae black with second segment pale distally; dorsum of head black with restricted pale markings (tiny indistinct spot beside each lateral ocellus, narrow dot and line on eye border, long postocular streaks); underside largely white (Fig. 3a). Prothorax brownish black dorsally, with pale sublateral band and narrow lower border. Synthorax black dorsally down to interpleural suture, with complete creamy white antehumeral stripe less than one-fifth as wide as mesepisternum and as wide as humeral black stripe below it (Fig. 3a). Humeral stripe separates it from an equally wide pale stripe posterior of humeral suture, this posthumeral stripe interrupted along anterior two-fifths of suture but continued by pale stripe on mesokatepisternum. Synthorax sides and venter uniformly cream with a broad brownish black stripe on metapleural suture. Legs creamy white except for dark brown tarsi, blackish joints (especially femoral apices) and outer face of fore femora and tibiae; bristles brown. Fore tibiae with whitish expansions barely differentiated; mid and hind tibiae strongly expanded (about 3.5× as long as wide), all white (Fig. 4a). Abdomen brownish black; tergites 1 and 2 whitish ventrally, 3 to 6 with narrow pale ventral borders reduced apically but extended basally into narrow incomplete rings, giving abdomen an annulated impression; 7 to 9 dark; 9 with small apical white spot on each side; 10 entirely creamy white with apical rim narrowly and partially black. Appendages creamy white, cerci darkened ventrally, paraprocts black dorso-basally. Cerci roundly triangular, with black internal subbasal tooth, which is almost invisible without dissection. Paraprocts over twice as long as cerci and tergite 10, strongly curved in and down, with small dorsal subbasal knob (Fig. 5a). Penis (genital ligula) with deeply incised apex, making it strongly bilobed, and long and slender lateral branches (Fig. 6a). Wings clear; pterostigma blackish and about 1 cell long; its anterior and posterior borders equal in length, about 1.5× as long as distal and

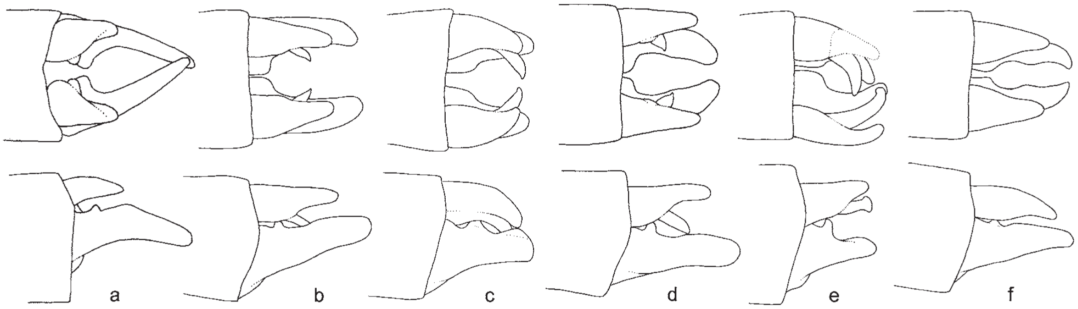

Figure 5 *Platycnemis* male appendages in dorsal (above) and lateral view (below). (a) *P. pembipes* sp. nov.; (b) *P. congolensis*; (c) *P. guttifera*; (d) *P. nyansana*; (e) *P. rufipes* (possible outline of damaged right cercus indicated); (f) *P. sikassoensis*.

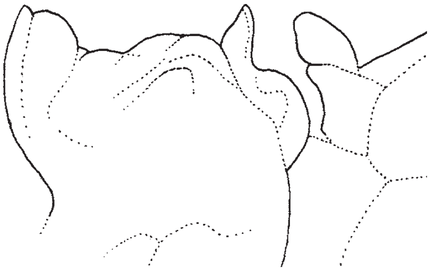

Figure 7 *Platycnemis pembipes* sp. nov. female pronotum in lateral view.

proximal borders. 15 postnodal veins in both fore wings. Measurements: abdomen (excluding appendages): 33.1 mm; hindwing: 18.5 mm; mid tibiae length × width: 3.35 × 0.95 mm; hind tibiae length × width: 3.80 × 1.12 mm.

Paratype female

Similar to holotype, but more faded, with dark markings reduced, indistinct and browner overall. Head pale brown overall with mere hints of darker markings, most clearly a dark line between eyes through bases of antennae. The hind lobe of the pronotum is slightly raised, forming a fairly low ridge that is shallowly incised at two points and therefore tripartite (Fig. 7). Pale brown synthorax with only dark brown dorsal half of mesepisterna and dark spot in humeral fossa distinct, latter extended into a very fine dark humeral stripe; a similar but weaker dark marking on metapleural suture. Legs evenly beige, very faintly darkened at femoral apices; tibiae not dilated. Tergites 1 and 2 pale brown, darker dorsally; 3 to 5 pale brown, apical sixth dark brown, slightly paler at base and basally of dark apical ring; 6 to 9 dark brown; apical border of 9 and entire tergite 10 dark cream. Ovipositor projects slightly beyond cerci. Pterostigma with pale brown centre, surrounded by a narrow cream border. 15 postnodal veins in fore wings. Measurements: abdomen: 32.0 mm; hindwing: 20.3 mm.

Variation

Paler, probably younger, males have all white cerci, facial markings more extensive and contrasting; dark thoracic markings reduced and slightly fragmented. 14–16 postnodal veins in fore wings.

Habitat, behaviour and accompanying species

Ngezi Forest is the only remaining large patch of tropical moist forest that once covered most of Pemba. It attained Forest Reserve status in 1959; today's gazetted area is about 1500 ha. The reserve is situated in the northwestern corner of the island and is bordered on most sides by the Indian Ocean, as well as by agricultural land. The climate is hot and humid with a mean annual rainfall of 1860 mm, with downpours almost every week of the year. Pemba has the highest rainfall in the coastal region, where the mean annual rainfall is below 1000 mm (Clarke, 2000). The monthly temperature variation of 3.8 °C is less than on the nearby mainland. The underlying bedrock is Pleistocene Azanian limestone. Most of the soils are alluvial sands; clayey soils are found in waterlogged areas by streams and ponds. Ngezi is coastal swamp forest; a rare forest type in the coastal forest belt that is very distinct from other vegetation types (Clarke & Robertson, 2000): the dominant trees are often monocots and some parts are at least seasonally flooded. The small sluggish stream that supported *P. pembipes* is the only permanent one. It runs through the forest's centre towards mangroves in the north, bordered by a 30–50 m wide belt of riverine swamp forest dominated by *Barringtonia racemosa* and *Raphia farinifera*. The surrounding forest is defined as moist forest; dominated by the tree *Odyendea zimmermannii* (Beentje, 1990). No sunshine penetrates the dense canopy and the stream has cut a 1 m deep gully. The amount of light reaching the forest floor of moist coastal closed-canopy forest is only 0.2% of the sunlight (Moreau, 1935) and the stream's entrenchment increases its shadiness further.

Both sexes, including freshly emerged specimens, were found close to the stream. Males settled on twigs and leaves closely above or along it, facing the water. They approached females carefully, taking them into tandem position. Oviposition (seen only once) took place in tandem into dead plant material lying in the stream. The slight annual climatic variation on Pemba suggests the absence of seasonality, but more observations are needed to confirm this.

Ngezi Forest's odonates represent a typical coastal forest assemblage: *Teinobasis alluaudi* (Martin, 1896), *Gynacantha usambarica* Sjöstedt, 1909 and *Thermochoria jeanneli* Martin, 1915 were found in the flooded swamp forest, where they most likely reproduce, while *Tetrathemis polleni* (Selys, 1869) oviposited in puddles along the stream. Reproductively inactive *Aciagrion* cf. *zambiense* Pinhey, 1972 were found in the dense forest understorey. The *Aciagrion* may be a distinct East Coast species (own observations); more on *T. alluaudi* is provided in the discussion.

Etymology

The name, meaning 'Pemban foot', is consistent with names with the suffix *pes* that are prevalent in the genus.

***Platycnemis congolensis* Martin, 1908**
Fig. 5b

Platycnemis congolensis Martin, 1908: 664 [lectotype ♂: Congo; MNHN (here designated)].

The identity of *P. congolensis* has long been unclear: records of that species appear to pertain to three to five species, although mostly the diagnosis by Schmidt (1951a) has been followed. MNHN possesses six and MCSN two specimens probably considered '*Platycnemis congolensis*' by Martin (1908, 1912), which are of diverse origin, specific identity, sex and completeness (Table 3). Three specimens have the indication 'type', although a primary type has not been designated. Only one of these is literally labelled 'Congo' and fortunately this is one of only four complete males. Because this is the only specimen with labels identifying it as a type of *P. congolensis* from the Congo, we designate it as the lectotype in order to end further confusion regarding the species' identity. It is not conspecific with Schmidt's species, differing in having the posterior border of the prothoracic hindlobe drawn

	Collection	Indicated locality	Labelled 'P. congolensis'	Labelled 'Type'	Damage	Identity
1♂	MNHN	'Congo'	yes	yes	none	*P. congolensis* LECTOTYPE
1♂	MNHN	'Congo'	yes	no	none	*P. congolensis*
2♀	MNHN	'Congo'	yes	no	none	unknown
1♂	MNHN	'Congo'	no	no	S8–10 absent	probably *P. nyansana*
1♂	MNHN	'Côte d'Ivoire'	yes	yes	S8–10 absent	probably *P. guttifera*
1♂	MNHN	'Sikasso' (Mali)	yes	yes	none	*P. sikassoensis*
1♂	MCSN	'F. Vaz'*	yes	no	none	*P. congolensis*
1♀	MCSN	'Guinée française'	yes	no	none	possibly *P. congolensis*

Table 3 Details of 'Congolese' *Platycnemis* specimens labelled by René Martin in MNHN and MCSN.

*Fernand-Vaz, present-day Omboué, on the Gabon coast south of Port-Gentil.

out into two slender vertical processes and the longer branch of the cerci. Schmidt's species is prevalent in Democratic Republic of Congo (DRC) and Uganda and should be called *P. nyansana* (see below). The distribution of *P. congolensis* is poorly known: The MCSN specimens are from coastal Gabon; NHRS possesses three of each sex from Mukimbungu in far western DRC on the Congo River just downstream of Luozi (Sjöstedt, 1917).

***Platycnemis guttifera* Fraser, 1950**
Figs 3b, 5c

Platycnemis guttifera Fraser, 1950: 615 [holotype ♂: Ziabli, Liberia; MNHN].

Described from Liberia and since reported from Côte d'Ivoire (Legrand, 1982; Legrand & Couturier, 1985), Ghana (O'Neill & Paulson, 2001), Liberia (Lempert, 1988) and Togo (T. Lieckweg, *pers. comm.*). BMNH possesses material from Nigeria, identified by R.M. Gambles as *P. rufipes*. Possibly ranges to Guinea and Cameroon, but no specified records have been published (Legrand & Couturier, 1985). Reported from deeply shaded calm and stagnant sections of larger streams and small rivers in rainforest (Legrand & Couturier, 1985; Lempert, 1988; Dijkstra & Lempert, 2003).

***Platycnemis latipes* Rambur, 1842**

Platycnemis latipes Rambur, 1842: 242 [type not designated: Montpellier, France; MNHN (not seen)].

Platycnemis mauriciana Selys, 1862: 34; nomen nudum (no description).

Platycnemis mauriciana Selys, 1863: 167 [holotype ♂: Ile Maurice; ISNB (seen)]; new synonymy.

Platycnemis mauritiana Selys, 1863 – Selys (1869: 24); misspelling.

The Odonata of Mauritius have been well studied, but *P. mauriciana* was not recorded after its description (Clausnitzer & Martens, 2004). A single male in Selys's collection labelled '(Ile de France)' and 'Platycn. mauriciana DS.' must represent the holotype, but lacks the terminal abdomen half, secondary genitalia, lower synthorax and three wings. Selys (1863, 1869) already doubted the specimen's origin, regarding it a possible variety of the Western Palaearctic *P. latipes*. Fraser (1949) suggested that it could be close to a Malagasy species, possibly *P. hova*. Nonetheless the markings and broad tibiae clearly show that the male represents a Western Palaearctic species, either *P. latipes* or *P. dealbata*, which can best be separated by the appendages (lost in holotype). It is remarkable that Selys interpreted 'Ile de France' as Mauritius, as the island only bore that name officially from 1715 to 1810, while the part of France around Paris has been known by it since the late 14th century. The Ile de France region lies at the extreme northern limit of the recent range of *P. latipes* (Martens, 1996), of which we consider *P. mauriciana* a synonym.

***Platycnemis nyansana* Förster, 1916**
Figs 1b, 3c, 4b, 5d, 6b

Platycnemis nyansana Förster, 1916: 25 [type ♂: Entebbe, Uganda; lost].

Platycnemis flavipes Navás, 1924: 12 [holotype ♂: Kibwezi, eastern Africa; MNHN (seen)]; new synonymy.

Platycnemis xanthopus Navás, 1924: 13 [holotype ♂: Kibwezi, eastern Africa; MNHN (seen)]; new synonymy.

Platycnemis congolensis nec Martin, 1908 – Schmidt (1951a: 223); Pinhey (1961: 19); Miller (1995: 4); Miller and Miller (2003: 121).

P. nyansana was described from Entebbe, but the type is not in UMMZ (where types from the same publication have been found) and thus appears to be lost (Garrison, von Ellenrieder & O'Brien, 2003). Two species occur in Uganda, including the Entebbe area. Fraser (1928) described *Copera subaequistyla*, a synonym of *P. sikassoensis* (see below), from Entebbe. Pinhey (1961) supposed that specimens from Kampala, Bwamba Forest (= Semliki NP) and nearby Congolese Mutwanga could pertain to *P. flavipes*, but listed them as *P. congolensis*. Indeed Navás's (1924) drawings of the *P. flavipes* appendages are similar to those by Schmidt (1951a) of so-called *P. congolensis* from Akula, Democratic Republic of Congo. Miller (1995) also reported *P. congolensis* from near Kampala. This second species differs from the *P. congolensis* lectotype in details of the male cerci and prothoracic hindlobe (see above) but matches the description of *P. nyansana*, being larger than *P. sikassoensis* with darkened leg joints, double-ringed tergites 3 to 5 and shorter cerci.

Navás (1924) described *P. flavipes* and *P. xanthopus* from 'Africa oriental inglesa: Kibwezi'. We only know of a place by that name halfway between Nairobi and Mombasa in the dry thornbush. This is an unlikely locality for the genus; moreover there are no other *Platycnemis* records from Kenya. The specimens could have come from Uganda and we do not regard *Platycnemis* as part of the Kenyan fauna. Contrary to Pinhey (1962), the holotypes of *P. flavipes* and *P. xanthopus* are not lost (Legrand & Lachaise, 1993). Their labels add no information about their origin, reading 'B.E. Africa, Kibwezi'. The two are alike; differences described may follow from the *P. xanthopus* appendages being partly covered with glue. Both agree with *P. nyansana*, which is the oldest and thus valid name. *P. nyansana* favours stagnant pools in the deep shade of rainforest (Miller, 1995; Miller & Miller, 2003; own observations). Its range encompasses Uganda and most of the Congo Basin (Schmidt, 1951a; MRAC; own observations).

***Platycnemis rufipes* (Selys, 1886)**

Figs 3d, 5e

Metacnemis rufipes Selys, 1886: 139 [holotype ♂: Cameroon; BMNH (seen)].
Allocnemis rufipes (Selys, 1886) – Kirby (1890: 131).
Platycnemis escherichi Schmidt, 1951a: 224 [holotype ♀: Ekododo, Cameroon; ZMHB (seen)]; new synonymy.
Platycnemis rufipes (Selys, 1886) – Pinhey (1962: 110); Kimmins (1970: 181).
Platycnemis congolensis nec Martin, 1908 – Vick (1999: 246).
Platycnemis camerunica Fraser, in litteris [holotype ♂: Cameroon; BMNH (seen)]; nomen nudum.

The identity and generic affiliation of this species has been uncertain. Pinhey (1962) stated that 'whilst this insect does not appear to be considered a true *Platycnemis* it does not seem to belong to *Allocnemis* nor perhaps to the related *Stenocnemis*. Gambles who has taken the species in Nigeria thinks it is a *Stenocnemis*.' Kimmins (1970) added 'currently placed (with doubt) in *Platycnemis*'. Neither author explained their doubts. The holotype perfectly matches *Platycnemis* by build, markings and appendages; moreover BMNH possesses conspecific material labelled as *Platycnemis camerunica* by Fraser (unpublished name).

Platycnemis escherichi is known only with certainty from the female holotype, which has two diagnostic spikes on the middle of the pronotum. Legrand (1975) reported males from NE Gabon, without diagnosing the male or explaining his identification. Considering the *P. escherichi* holotype's origin and Schmidt's (1951a) remark '*Allocnemis rufipes* Selys [. . .] hat uns nicht vorgelegen' it stands to reason that both are conspecific. The *P. rufipes* holotype perfectly matches the markings illustrated by Schmidt (1951a), including the dark wedges beside the eyes and the wide tapering antehumeral stripe that are not seen in other species (Fig. 3d). Material from SW Cameroon published as *P. congolensis* by Vick (1999) includes both sexes; the males agree with *P. rufipes* and the females with *P. escherichi*, although 'the size of the spikes is a little variable and mostly a bit smaller than Schmidt's drawing, but I do not think this significant' (Vick, in litt.). Both sexes agree in markings and were collected in the same general area and once at the same site, substantiating the synonymy.

***Platycnemis sikassoensis* (Martin, 1912)**

Figs 3e, 5f

Psilocnemis sikassoensis Martin, 1912: 98 [holotype ♂: Sikasso, Mali; MNHN (seen)].
Copera subaequistyla Fraser, 1928: 127 [lectotype ♂: Entebbe, Uganda; BMNH (seen; designated by Kimmins, 1966: 214)]; junior synonym – Legrand (1982: 9).
? *Copera congolensis* (Martin, 1908) – Nielsen (1934: 180).
Platycnemis subaequistyla (Fraser, 1928) – Pinhey (1961: 19).
Platycnemis sikassoensis (Martin, 1912) – Pinhey (1962: 110).

Unlike its continental Afrotropical congeners, *P. sikassoensis* favours exposed habitats and is wide-ranging, inhabiting rather open flowing waters like large rivers and sunny streams, both in forest and savanna (Legrand & Couturier, 1985; Dijkstra & Lempert, 2003). The distribution of this small species incorporates the combined ranges of the larger ones, which appear to be allopatric and restricted to forest shade (Fig. 2). It has been recorded from Benin (Tchibozo & Dijkstra, 2004), Central African Republic (Pinhey, 1971), Côte d'Ivoire (Lindley, 1974; Legrand, 1982; Legrand & Couturier, 1985), Gambia (Gambles *et al*., 1998), Ghana (Marshall & Gambles, 1977; O'Neill & Paulson, 2001), Guinea (Legrand & Girard, 1992; Legrand, 2003), Liberia (Lempert, 1988), Mali (Martin 1912; Dumont, 1977), Sierra Leone (Aguesse, 1968; Carfì & D'Andrea, 1994), Togo (T. Lieckweg, *pers. comm.*) and Uganda (Fraser, 1928; Pinhey, 1961). The species illustrated as *Copera congolensis* from Mobeka, Democratic Republic of Congo by Nielsen (1934) may also pertain to this species.

Discussion

Relationships

The two Afrotropical *Platycnemis* groups can be clearly separated by morphology and coloration (Table 1). The continental species are diagnosed and compared with *P. pembipes* in the key. The Pemba species perfectly fits the diagnosis of the insular group (Table 1) and is nearly identical to the Malagasy *P. aurantipes* and *P. hova*. The former is more colourful, with a more contrasting head pattern and orange-yellow legs. The male tibiae are shaped similarly, but are slightly narrower. Morphological differences are especially slight; the penises appear identical. The male cerci of *P. pembipes* are a bit more pointed; both species have a pale bulge on the inner border that lies more dorsal in *P. aurantipes*, making the internal profile more angular (dorsal view). The internal tooth of the cerci is well visible and pale with only a black tip in *P. aurantipes*, but entirely black and hard to see in *P. pembipes*. The female pronotal hindlobe of *P. aurantipes* is slightly broader and more deeply incised; the gap between the mesostigmal plate and mesepisternum is larger. *Platycnemis hova* also has more extensive and contrasting pale facial markings; the penis apex is less deeply incised, the tibiae narrower and the appendages entirely white. The internal cercal tooth is black, but more prominent than in *P. pembipes*. Width and colour of the *P. pembipes* legs recall the Malagasy *P. alatipes* and *P. pseudalatipes*, whose body markings differ. *Platycnemis agrioides* and *Platycnemis melana* from the Comoros, geographically between *P. pembipes* and the Malagasy species (Fig. 2), are relatively dissimilar with their narrow tibiae and dark coloration.

The insular species are very uniform in their contrasting coloration and penis and appendage morphology (Schmidt, 1951b; Lieftinck, 1965), and are probably monophyletic. Similar traits are seen in Eurasian species, but not elsewhere in the Afrotropics. Several authors noted the similarity between the southern Asian *Copera* s.s. – as defined by Selys (1863) under the homonym *Psilocnemis* with type species *C. marginipes* (Rambur, 1842) designated by Kirby (1890) – and the Guineo-Congolian (continental) platycnemidines: Nielsen (1934) transferred *P. congolensis* to *Copera* and Schmidt (1951a) placed *P. nyansana* close to that genus by penis characters; at least *P. guttifera* and *P. sikassoensis* are similar in this regard (own observations). Fraser (1928, 1950) described *Copera subaequistyla*, now a synonym of *P. sikassoensis*, and *P. guttifera* emphasising their similarity to *C. marginipes* and *C. vittata* (Selys, 1863). Recently Donnelly (2002) listed the species as *Copera sikassoensis* for that reason, despite the status quo to place all African platycnemidines in *Platycnemis*. Indeed the two most common species in their respective continents, *P. sikassoensis* and *C. vittata*, are virtually identical except for differences in the male appendages and female pronotum.

Although it can be concluded that the Pemba species' nearest relatives are found in Madagascar and those of the continental species in tropical Asia, only worldwide phylogenetic research of the group can elucidate the exact relationships. The platycnemidine damselflies are probably a monophyletic group, but the prevailing separation into two genera almost undoubtedly makes *Platycnemis* paraphyletic. Of the four geographically disjunct platycnemidine groups, three are morphologically uniform and probably monophyletic. Only the large eastern Asian group is heterogeneous; besides species with Guineo-Congolian affinities (*Copera* s.s.), it includes species ranging into the Eastern Palaearctic that are more similar to the Western Palaearctic and Madagascar groups. Interesting in this regard is that Fraser (1962) illustrated a *Platycnemis* larva from Madagascar with frilled caudal lamellae. This is like those described for *C. marginipes* and *C. vittata* by Lieftinck (1940), while Western Palaearctic and Japanese *Copera* and *Platycnemis* (including the latter's type species) have unfrilled lamellae (Kawai, 1985; Martens, 1996). Discovery of the larva of African *Platycnemis* will help enlighten their position; it is assumed to have frilled lamellae. Another overlooked but possibly informative feature is eye-coloration, which is lost in preservation. Examined species with (assumed) frilled lamellae have a darker dorsum of the eye plus a distinct horizontal band below it, while unfrilled species only have a dark dorsal half (Eastern Palaearctic) or very faint markings altogether (Western Palaearctic).

Biogeography

The forests of the eastern African coast and adjacent mountains are recognized as core areas of biodiversity and endemism in Africa (Kingdon, 1989; Fjeldså & Lovett, 1997; Burgess, 2000) and are listed as important conservation areas (Stuart *et al*., 1990). This richness, especially of relict species, has been explained by the area's relative climate and habitat stability (Fjeldså *et al*., 1997). Most island biota are similar to those on the mainland (Burgess, 2000). Pemba, however, is recognized for its great distinctiveness with a high degree of endemism despite its size (about 1000 km^2) and proximity to the mainland (50 km, similar to the distance between Zanzibar and Tanzania). The moist forest of Ngezi, for instance, is peculiar in its floristic composition, combining tree species restricted to coastal East African forests, Madagascan links, eastern Indian species and Afromontane elements (Beentje, 1990). Despite the nearness of its mainland relatives, the owl *Otus pembaensis* is one of the most distinctive *Otus* species in and around the western Indian Ocean (Rasmussen *et al*., 2001). The comparatively early separation from the mainland by faulting that produced the Pemba Channel, possibly 6–10 million years ago, may explain Pemba's unique position (Richmond, 1997; Clarke & Burgess, 2000). The Malagasy connection of *P. pembipes* has parallels in other Pemban taxa. The tree *Chrysaliduocarpus pembanus* and palm *Dypsis pembanus* are endemics belonging to otherwise Madagascan genera (Beentje, 1990; Krain *et al*., 1994). The tree genus *Typhonodorum* and the fruit bat *Pteropus voeltzkowi* also have their closest relatives in Madagascar (Beentje, 1990; Entwistle & Corp, 1997). Similarly, the latter's relative *Pteropus comorensis* inhabits Mafia off the Tanzanian coast and the Comoros, and is closely related to *Pteropus seychellensis* of the Seychelles. Other Pemban taxa show a stronger affinity to mainland Africa than to Madagascar: the milkweed genus *Secamone* has its greatest diversity in Madagascar (62 species) with only 16 species in continental Africa, but is represented on Pemba only by a mainland species (Goyder, 1991).

Keeping these affinities in mind, the questions arise (1) what the origin of *Platycnemis* on Pemba is and (2) why populations are absent from the mainland. The origin of *P. pembipes* is most likely from Madagascar by wind-aided dispersal across the Mozambique Channel. A strong monsoon follows the East African coast north(west-)wards from June to September (Richmond, 1997) and could carry damselflies over long distances. The American damselfly *Ischnura hastata* (Say, 1839) that has colonised the Azores and Galapagos Islands has been collected with nets fixed to aeroplanes at 300 m altitude (Cordero Rivera *et al*., 2005). It is unlikely that *P. pembipes* is an ancient relict: Madagascar separated from the African mainland many millions of years earlier than Pemba, although it '. . . apparently slid south along the east African coast for most of the Cretaceous rather freely interchanging plant and animal taxa with the mainland at least until 90 Ma and perhaps intermittently thereafter' (Gentry, 1993). Such an ancient split would predict a much greater character divergence between species on Madagascar and Pemba, moreover *Platycnemis* species on the volcanic and relatively young

Comoros (at most 8 million years old) could also only reach these islands airborne. The Comoran species pair and *P. pembipes* both have close relatives on Madagascar, but are rather dissimilar to each other, suggesting the Comoros did not act as a stepping-stone between Madagascar and Pemba, but were colonised in a separate event.

The second question is more difficult to answer. Undiscovered populations may be present in unsampled coastal forests in Mozambique, southern Tanzania and Mafia Island. Alternatively insular species may have never reached the mainland or become extinct there. Considering the proximity of Pemba and the suspected mode of dispersal it is unlikely that *Platycnemis* never arrived on continental shores (see below). Subsequent extinction, on the other hand, seems probable. Tropical Africa has undergone marked climatic changes, for instance with a relatively wet period 12–10 000 years ago and a dry one in the few thousand preceding years (Hamilton, 1981). The impoverishment of the forest flora and fauna of Africa is due to extinctions during dry spells, glacial advances and the lack of refugia during the Pleistocene. Extinctions would have mainly hit the moist and hot lowland forests, i.e. cooling below the tolerance of tropical stenothermic species and altering their habitats. A number of plant taxa shared by the lowland forests of Madagascar and South America, for instance, are known as fossils but absent in mainland Africa today (Gentry, 1988, 1993). Examples of such random extinctions in the African rain forests are discussed by Colinvaux (1993) and Clausnitzer & Lindeboom (2002). Although the coastal forests of eastern Africa are considered relicts of a former pan-African tropical forest and are believed to have been more stable during cooler and drier periods than other African forests (Fjeldså *et al*., 1997; Fjeldså & Lovett, 1997), small changes in temperature or humidity may have caused the extinction of forest species. The mainland coast is much drier than Pemba and is even drier now than in the past (Clarke, 2000): suitable habitats for *P. pembipes* or a related species may no longer be present.

The insular *Platycnemis* scenario has parallels in other Odonata, be it on a larger scale. The genera *Teinobasis* Kirby, 1890 and *Hemicordulia* Selys, 1870 have their greatest diversity in Australasia and the adjacent Pacific. They are poorly represented on the Asian mainland, but occur on several Indian Ocean islands, Madagascar and eastern Africa, with only a single species in each area occupied. This distribution and the restricted taxonomic differentiation of the scattered populations, suggest a recent wind-borne transoceanic colonisation. The damselfly *T. alluaudi* inhabits Madagascar, the Seychelles, coastal Kenya and Tanzania, Zanzibar and north Malawi, but populations are widely separated due to the scarcity of appropriate swamp forest habitat (Clausnitzer, 2003b). A complex of very similar *Hemicordulia* species inhabits Madagascar, the Seychelles and Mascarenes, and eastern Africa west to the Albertine Rift and south to KwaZulu-Natal, but records and habitat information are more fragmentary than in *Teinobasis* (K.-D.B. Dijkstra, unpublished). These cases show that the dispersal of Malagasy *Platycnemis* to the African coast is feasible, but restricted and probably reduced availability of habitat may have precluded their survival in large parts of this region; perhaps conditions were only favourable on Pemba.

Conservation

Owing to its distinctive fauna and flora, Pemba is recognised as a high priority site for conservation (Rodgers & Burgess, 2000): the Ngezi Forest is significant for biodiversity conservation on the regional and global level. Until recently Pemba was entirely covered with forest; clearing for cash crop plantations (cloves, cardamom) began in 1830 (Clarke & Karoma, 2000). Now just a few square kilometres of forest are left and endemic forest species are already thought to be extinct (Clarke *et al*., 2000). This fate definitely awaits *P. pembipes*, living proof of a unique colonisation event, if the remaining forest on Pemba is not conserved. The species is one of several odonates that are almost certainly confined to a single stream and thus under imminent threat (IUCN, 2005). Others are *Amanipodagrion gilliesi* Pinhey, 1962 from the Usambaras on the nearby Tanzanian mainland (Clausnitzer, 2003a, 2004) and *Risiocnemis seidenschwarzi* Hämäläinen, 2000 from Cebu in the Philippines (Hämäläinen, 2004). *Platycnemis pembipes* has been submitted for inclusion in the global Red List as Critically Endangered.

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chapter 3

The *Pseudagrion* split: molecular phylogeny confirms the morphological and ecological dichotomy of Africa's most diverse genus of Odonata (Coenagrionidae)

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The *Pseudagrion* split: molecular phylogeny confirms the morphological and ecological dichotomy of Africa's most diverse genus of Odonata (Coenagrionidae)

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Key words: Odonata, dragonfly, Zygoptera, *Pseudagrion* diversification, molecular phylogeny, ecology, morphology, Africa.

ABSTRACT

The continental African representatives of the genus *Pseudagrion* fall into two groups (A and B) based on their ecology and larval and adult morphology. While the B-group species are found in generally warmer habitats, which are more sunny, lentic or low-lying, the A-group representatives occur more in cooler habitats. We compared molecular genetic and ecological data of twelve species representing both groups. Mitochondrial DNA sequence analyses strongly support their segregation into two major clades and suggest the monophyly of each. High bootstrap support confirms the deep phylogenetic split. Overall, only a minority of species have been studied for each group. However, genetic distances of the species within each clade indicate that they are significantly more closely related to each other than to species of the opposite clade. We conclude that the observed ecological and morphological similarities are due to common ancestry, suggesting two independent radiations within the continental African *Pseudagrion* species. The biogeographic and palaeoecological history of the two clades remains unresolved.

INTRODUCTION

Pseudagrion Selys, 1876 is the largest genus of Odonata in Africa and one of the largest in the world: almost 100 species occur in Africa and Madagascar, another 40 range across southern Asia into Australia. The genus has occupied all freshwater habitats in tropical Africa, dominating zygopteran communities from pools in the Kalahari to alpine streams on the Kilimanjaro. Diverse assemblages inhabit equatorial rainforests, while relict populations survive in the Saharan mountains, Morocco and the Levant (Dijkstra & Clausnitzer 2006).

The most comprehensive revision of the Afrotropical species was made by Pinhey (1964a), who subsequently published numerous addenda (e.g. Pinhey 1971, 1973, 1978). However, over one-fifth of Afrotropical species was described since Pinhey's revision (e.g. Balinsky 1964, 1971; Aguesse 1968; Dumont 1978; Legrand 1987; Carletti & Terzani 1997; Terzani & Carletti 2001; Terzani & Marconi 2004). The ecological literature of the genus is comparatively extensive for its largely tropical distribution, e.g. for southern Africa information was published by Balinsky (1957), Chutter (1961), Meskin (1985, 1986, 1989) and Reinhardt (1999).

In continental Africa, the genus is subdivided into an A-group of 41 species and a B-group of 24, based on morphology as well as ecology (Table 1). Following more complex groupings of earlier authors, the morphological dichotomy was first observed in females by Balinsky (1957), confirmed in larvae by Chutter (1961) and firmly established in males by Pinhey (1964a) (Table 2). However, two western African species described by Pinhey (1973) cannot be assigned to any group and may not be congeneric (Dijkstra 2003). 31 species of forest streams in Madagascar and the Comoros probably form a third, separate group (K.-D.B. Dijkstra unpubl.).

The ecological segregation between the two continental groups is mostly clear-cut. For example, in Ethiopia Clausnitzer & Dijkstra (2005) found five B-group species restricted to swampy borders of the Rift Valley lakes, while five A-group species occupied streams and rivers flowing off the highlands. Dijkstra & Lempert (2003) found three A-group species confined to the upper courses of a stream-size gradient in Upper Guinean rainforest and five B-group species occurring only on exposed rivers.

The morphological and ecological traits lead to the hypothesis that the separation of two distinct groups is based on close genealogical relationships of the species within each group. To determine whether the morphological segregation of continental African *Pseudagrion* is based on common ancestry, twelve species (six of each group) were subjected to phylogenetic analysis using a mtDNA sequence comprising of three partial gene fragments.

Material and methods

Taxon survey and sampling

A total of 214 localities was surveyed in Ethiopia, Kenya, Tanzania and Uganda in different seasons from 1994 to 2005, resulting in over 2,500 field records, of which 284 were of the twelve studied species. Two habitat categories were scored for each locality; one pertaining to the type of water body (stream, river, pool, or lake) and the other to the prevailing vegetation cover (forest, gallery/secondary forest, bush, or open land). For each species the preferred habitat and the altitudinal and geographical range were determined (Table 3). For phylogenetic analyses 23 individuals belonging to twelve *Pseudagrion* species were collected during October 2001 through September 2002 in Namibia, Kenya and Tanzania (Table 4). Most specimens were sampled non-invasively (Fincke & Hadrys 2001), although voucher specimens were retained from most localities. Samples were stored in 70% or 98% ethanol prior to DNA-extraction.

Table 1. Morphological and ecological traits separating the continental African *Pseudagrion* species into two groups (A and B).

	A-group	**B-group**
Diversity		
	41 species; exclusively continental, with many small highland and rainforest ranges	24 species; mainly large open land ranges on the continent, two species in Madagascar, Comoros and Mascarenes
Apex S10 ♂		
	Without denticles	With distinct denticles
Cerci ♂		
	Generally with a strongly developed lower branch	With a weakly developed lower branch, or without one
Apex of penis		
	With two funnel-shaped lobes; shape rather uniform between species	Rounded to bilobed, these lobes rounded to pointed, but not funnel-shaped; diverse
Mesokatepisternum ♀		
	With epaulette and/or bristle pad	Without adornments
Mesostigmal lamina ♀		
	Simple	Well-developed
Mature coloration		
	Predominantly black with pale markings, some species with extensive pruinosity; limited variation within species	Predominantly pale with narrow black markings, rarely pruinose; extreme variation within species, may even be largely black
Habitat		
	Generally cooler; mostly running waters, often shaded and/or at high altitude	Generally warmer; running but also standing waters, often exposed, mostly at low altitudes

Table 2. Taxonomic history of continental African *Pseudagrion*.

	A-group	**B-group**
Selys (1876)	*angolense* *furcigerum* *melanicterum* *praetextatum* (= *kersteni*)	*glaucescens* *nubicum* *torridum*
Ris (1936)	*bicoerulans*-group *caffrum*-group *melanicterum*-group *spernatum*-group	*glaucescens*-group *punctum*-group *torridum*-group
Pinhey (1951)	Group a Group b Group d (part)	Group c Group d (part)
Balinsky (1957)	*salisburyense*-group *gigas* (by itself)	*massaicum*-group
Chutter (1961, 1962)	Group A	Group B
Pinhey (1964a, b)	Group A (*caffrum*-group)	Group B (*punctum*-*glaucescens*-group)

Table 3: Occurrence and habitat of studied *Pseudagrion* species — provided are the observed geographical and altitudinal range [m a.s.l.] and habitat parameters (percentage of recorded localities assigned to each category). These categories are exclusive for water body type (str[eam], riv[er], pool or lake) and prevailing vegetation (for[est], gall[ery/secondary forest], bush or open[land]). E: Ethiopia, K: Kenya, T: Tanzania, U: Uganda.

	Range		**Type of water body**				**Prevailing vegetation**			
	geogr.	altitude	str	riv	pool	lake	for	gall	bush	open
A-group										
P. bicoerulans	KTU	2,000-3,000	100	0	0	0	16.5	67	16.5	0
P. gamblesi	EKTU	561-1,000	50	50	0	0	0	33	50	17
P. hageni	EKTU	35-1,875	94	6	0	0	56	38	6	0
P. kersteni	EKTU	0-2,100	89	11	0	0	11	58	31	0
P. salisburyense	KT	1,500-1,850	86	14	0	0	0	29	57	14
P. spernatum	EKT	520-2,223	86	14	0	0	17	63	0	20
B-group										
P. acaciae	T	64-561	33	67	0	0	0	50	25	25
P. commoniae	KT	20-1,200	66.5	26.5	0	7	0	40	53	7
P. lindicum	KT	20-120	17	50	0	33	0	20	80	0
P. massaicum	EKTU	0-900 *	55	25	10	10	0	53	26	21
P. nubicum	EK	738-1,700	0	0	0	100	0	0	25	75
P. sjoestedti	K	720	100	0	0	0	0	100	0	0

* isolated record on Mt Marsabit at 1,350 m.

DNA extraction, amplification and sequencing

The tissue samples were freeze-dried using liquid nitrogen to allow for better homogenisation and DNA was extracted following a slightly modified standard protocol (Hadrys et al. 1992). An approximately 610bp long mitochondrial DNA sequence, containing a partial fragment of the 16S rRNA gene, the intervening $tRNA^{Leu}$ and the NADH dehydrogenase region 1 (ND1), was amplified using the primers 5'>TTC AAA CCG GTG TAA GCC AGG<3' and 5'>TAG AAT TAG AAG ATC AAC CAG C<3' (Weller et al. 1994; Abraham et al. 2001). Two individual sequences from each *Pseudagrion* species were generated, except for *P. nubicum* (Table 4). All reactions were carried out in a 25 µl reaction mix, containing 1x amplification buffer [20 mM tris-HCl, pH 8.4; 50 mM KCl; Invitrogen], 2.5 mM $MgCl_2$, 0.05 mM dNTPs, 0.5 pmol/µl each primer, and 0.03 U/µl taq DNA polymerase (Invitrogen). Amplification was accomplished on a Gene Amp PCR System 9700 (Applied Biosystems). PCR-profiles were as follows: 2 min initial denaturation at 95°C, followed by 30 cycles of 94°C 30 s, 48°C 30 s, 72°C 1 min and 6 min extension at 72°C. All PCR-products were purified with Microcon-PCR Centrifugal Filter Devices (Millipore) following manufacturer's instructions. The sequencing reaction was carried out using the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit and products were subsequently purified over Sephadex columns (Sigma). Sequencing was performed on an ABI PRISM 310 Genetic Analyzer (Applied Biosystems).

Table 4: Species identification — localities with geographical coordinates and GenBank accession numbers (GBAN) for sampled species.

Pseudagrion	**Locality**	**Coordinates**	**GBAN**
A-group			
P. bicoerulans Martin, 1907	Kilimanjaro, Tanzania	03°10′S, 37°14′E	EF221857
	Mt Elgon, Uganda	01°02′N, 34°46′E	EF221856
P. gamblesi Pinhey, 1978	Pangani River, Tanzania	04°37′S, 38°00′E	EF221858 EF221859
P. hageni Karsch, 1893	Kiboko River, Kenya	02°15′S, 37°32′E	EF221860 EF221861
P. kersteni (Gerstäcker, 1869)	Ongongo, Namibia	19°08′S, 13°49′E	EF221862
	Pemba River, Kenya	04°11′S, 39°24′E	EF221863
P. salisburyense Ris, 1921	Athi River, Kenya	01°24′S, 36°54′E	EF221864 EF221865
P. spernatum Selys, 1881	W Usambara Mts, Tanzania	04°50′S, 38°40′E	EF221866 EF221867
B-group			
P. acaciae Förster, 1906	Pangani River, Tanzania	04°37′ S, 38°00′E	EF221868 EF221869
P. commoniae (Förster, 1902)	Pemba River, Kenya	04°11′ S, 39°24′E	EF221870 EF221871
P. lindicum Grünberg, 1902	Rufiji, Ikwiriri, Tanzania	07°56′ S, 38°58′E	EF221872 EF221873
P. massaicum Sjöstedt, 1909	Kiboko River, Kenya	02°15′ S, 37°32′E	EF221875
	Kuiseb River, Namibia	22°40′ S, 16°37′E	EF221874
P. nubicum Selys, 1876	Lake Jipe, Kenya	03°36′ S, 37°46′E	EF221876
P. sjoestedti Förster, 1906	Mzima Springs, Kenya	02°58′ S, 38°01′E	EF221877 EF221878
Ceriagrion			
C. glabrum (Burmeister, 1839)	E Usambara Mts, Tanzania	01°08′ N, 23°36′E	EF221879

Genetic data analyses

Sequences were edited manually using SeqManII (DNASTAR) and aligned with SeaView (Galtier et al. 1996). Pair-wise genetic distances were calculated using the Simple Matching Coefficient (or uncorrected Hamming distance) as implemented in PAUP* 4.0 Beta 10 (Swofford 2002). Phylogenetic trees were estimated using PAUP* under the framework of Maximum Parsimony (MP), Maximum Likelihood (ML) and Neighbour Joining (NJ). Where appropriate, a model of evolution was assumed, as calculated by the hierarchical Likelihood Ratio Test in Modeltest 3.7 (Posada & Crandall 1998). Starting trees were obtained using random stepwise addition with 100 replicates. The branch-swapping algorithm employed was tree-bisection-reconnection (TBR). Characters were unordered and not weighted. The trees were rooted using *Ceriagrion glabrum* (Coenagrionidae). The results were tested for robustness by bootstrap analyses with 1,000 pseudo-replicates under the optimality criterion of parsimony (heuristic search).

Table 5. Genetic similarity of the twelve *Pseudagrion* species — figures represent percentages of the average interspecific genetic distance (uncorrected "*p*") based on the mtDNA fragment: lower values represent greater similarity. A-group species and distances between them are italic, B-group ones bold.

	ga	*ha*	*sa*	*sp*	*bi*	*ke*	**co**	**li**	**ac**	**nu**	**sj**
gamblesi											
hageni	*6.5*										
salisburyense	*5.4*	*8.0*									
spernatum	*4.9*	*7.8*	*7.3*								
bicoerulans	*8.9*	*11.0*	*10.1*	*9.3*							
kersteni	*3.9*	*6.7*	*5.2*	*3.8*	*9.6*						
commoniae	13.8	16.2	14.9	14.4	15.7	14.5					
lindicum	13.4	14.4	14.6	14.6	15.0	14.8	**11.2**				
acaciae	12.8	15.9	15.2	13.9	15.1	13.5	**10.3**	**12.0**			
nubicum	11.6	14.2	14.7	11.9	14.3	12.2	**10.3**	**8.0**	**10.4**		
sjoestedti	14.5	15.1	15.3	14.7	14.8	14.5	**11.9**	**8.5**	**11.1**	**9.2**	
massaicum	14.8	16.9	15.6	15.7	16.2	15.9	**4.6**	**11.4**	**10.8**	**10.3**	**12.4**

Results

The two groups showed clear differences in habitat requirements. Whereas A-group species were only found in running water, B-group representatives inhabited all types of water bodies. B-group species were never observed at truly forested sites, but four of the six A-group species were present in this category (Table 3).

The phylogenetic analyses based on the mtDNA sequence data and the genetic distance measures both supported the division of the genus *Pseudagrion* into two distinct clades (Fig. 1; Table 5). All three tree-building methods used (NJ, ML and MP) yielded trees with two clades, which coincide with the morphological classification. Of the 154 variable characters, 130 were parsimony-informative. A heuristic search under the framework of MP resulted in nine most parsimonious trees, whose topologies only differed in the species relationships within the A-group but showed no differences within the B-group. The ML tree ($-lnL = 2042.94304$) calculated under the TrN+I+G model (Tamura & Nei 1993) is shown (Fig. 1). Although only 15% and 25% of the known A- and B-group species were studied, the deep split into two clades was supported by MP bootstrap values of 80 and 100 respectively, suggesting the monophyly of the two clades.

Nucleotide diversity between the mtDNA sequences of the species showed a similarly clear pattern. The genetic distance values were significantly higher between species of the two groups than among species of the same group ($p = 0.00$; *t*-test; two-tailed). Ranging from 4% to 11% (mean 7.22 ± 2.28) within the A-group, from 5% to 12% within B (mean 10.16 ± 1.99) and from 12% to 17% between the groups (mean 14.6 ± 1.17) (Table 5).

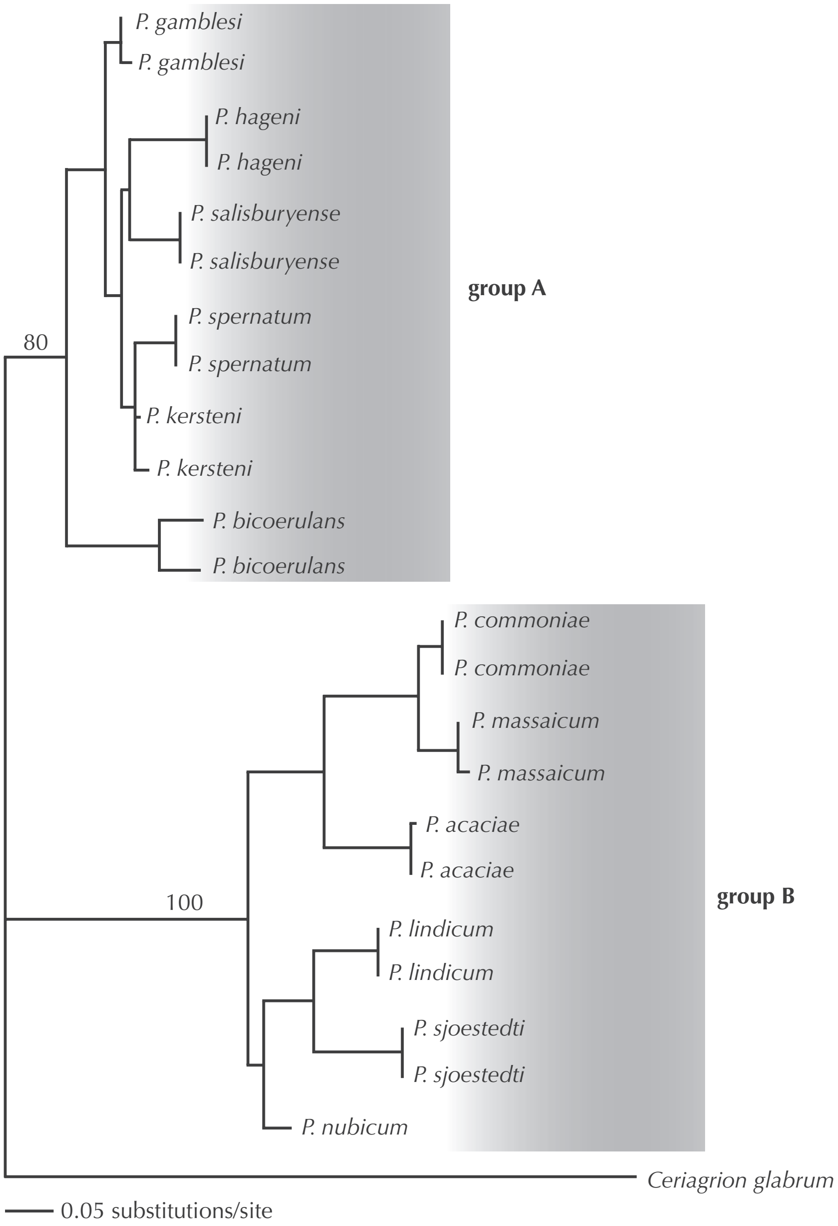

Figure 1: Maximum Likelihood phylogram of Afrotropical *Pseudagrion* spp. based on three partial mtDNA gene fragments (see text), with *Ceriagrion glabrum* as outgroup. The numbers above the branches indicate MP bootstrap support.

DISCUSSION

Although all of the selected A-group species are confined to running waters, they are rather 'atypical' in having adapted to some degree to open habitats. No true rainforest species were, for instance, included. The six studied species are mainly distributed across eastern Africa. One of the selected species, *Pseudagrion kersteni* is abundant throughout tropical Africa on most streams outside dense forests. In contrast, *P. bicoerulans* is endemic to high-altitude forest streams in Kenya and adjacent Uganda and Tanzania. Regardless of their more 'borderline' ecological position, the genetic patterns are clear-cut. The basal phylogenetic split separates all species into the A- and B-groups, in concordance with their morphological differences.

The deep phylogenetic split of the A- and B-groups is a strong indication of independent radiations. Considering the concordance of the split with ecological patterns, differences in radiation events may be related to different habitat adaptations of A- and B-group species. In a comparative population genetic study of two A-group (*P. bicoerulans* and *P. kersteni*) and one B-group species (*P. massaicum*), differences in habitat and distribution are strongly reflected in the genetic structure of the species (Hadrys et al. 2006). Analyses of the same mtDNA fragment used in this study showed that mean genetic diversity and genetic isolation increased with habitat specificity and restricted distribution of the species. The two widespread species (*P. kersteni* and *P. massaicum*) displayed similarly low genetic diversities (ranging from 0.0% to 1.9%). The localized *P. bicoerulans* (see above) showed a much higher intraspecific genetic diversity (6.7%) and complete genetic isolation between populations. Comparison with the genetic distances of species in Table 5 suggests that speciation is in progress within this species (compare the two mtDNA-haplotypes from Mt Elgon and Kilimanjaro in Fig. 1). This pattern of divergence is neither correlated with geographic distance nor with differences in morphology. Therefore the results provide a good example of how genetic data can provide information about cryptic speciation. Since the A-group includes many species with relatively small and fragmented ranges (e.g. in highland and rainforest), subsequently faster radiation within the group may be expected.

Although our study shows that the basal split into two clades is deep and well supported, their evolutionary history remains unknown. Dijkstra & Clausnitzer (2006) postulated that forest streams are the ancestral habitat of *Pseudagrion* and that the A- and B-groups diversified separately in non-forest habitats. Reflective pruinosity is considered an adaptation to increased insolation (Corbet 1999: 282). Perhaps A-group species with pruinosity evolved in cool but sunny highland habitats and were thus better suited to invade open lowland habitats. Such habitats presently dominate the African continent and *P. kersteni*, which is the most strongly pruinose A-group species, is also the most widespread one there. The B-group species share morphological similarities with Asian species and possibly arrived later, radiating into warmer habitats left unoccupied by A-group members.

The inclusion of more A- and B-group species and Malagasy and Asian species will shed more light into the evolution of the two clades. However, it was not the purpose of this study to analyse the history of the two clades, nor to verify or falsify Dijkstra & Clausnitzer's (2006) hypothesis of *Pseudagrion* radiation in continental

Africa. Further tests of the hypothesis demand additional biogeographical data and a more complex, fine-scale phylogenetic analysis. This may help identify the closest non-African relatives, thus determining the phylogeographic history of the genus. Ultimately a more fine-scale reconstruction of the ecological and distributional history of Afrotropical *Pseudagrion* could be mapped onto to the climatological and geological history of the continent. Such reconstruction may clarify evolutionary pathways within the clades, e.g. whether the pruinose A-group species of more open habitats evolved from forest species or vice versa, and whether this happened once or repeatedly, e.g. under influence of orogenesis or forest regression.

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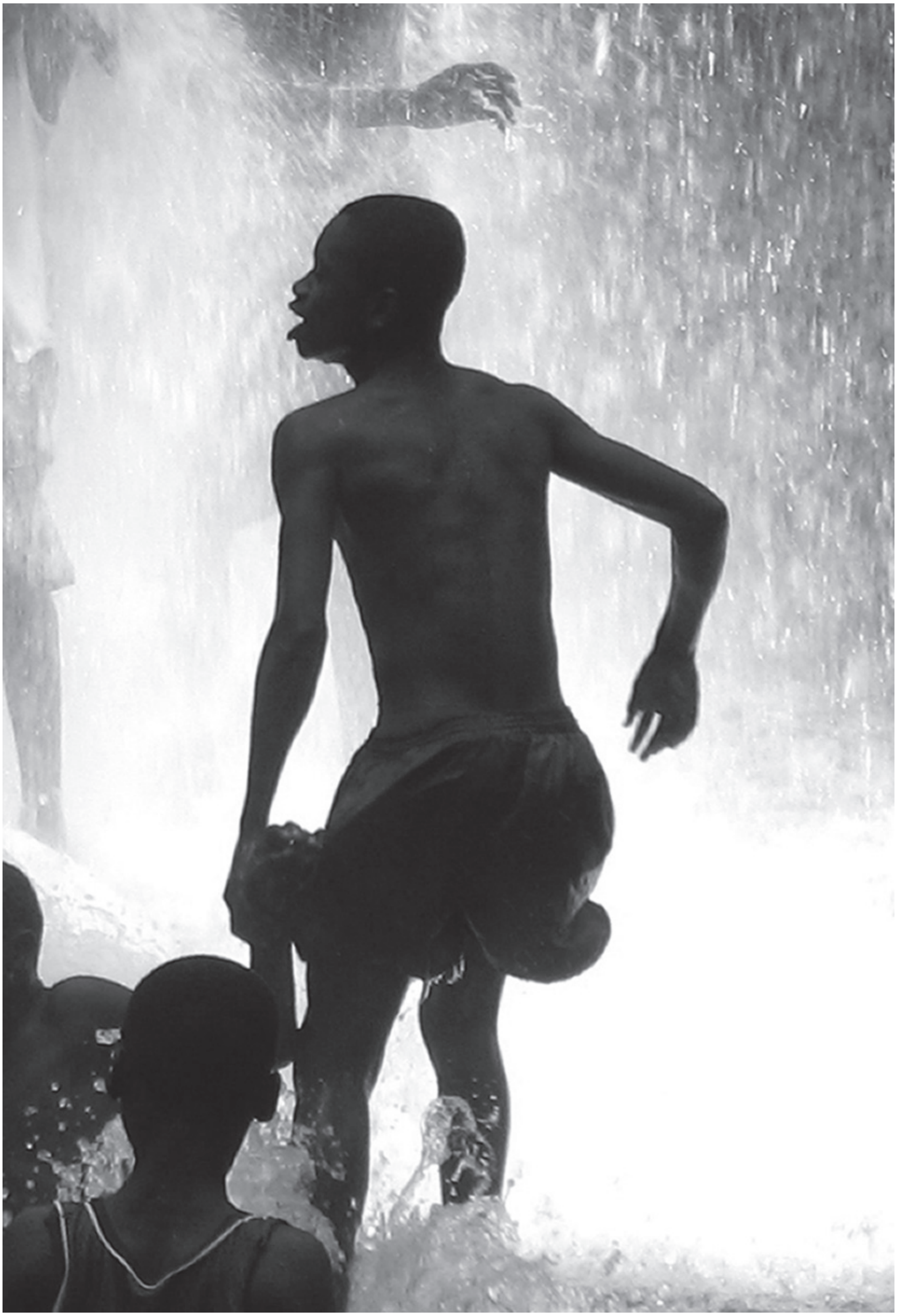

chapter 4

Gone with the wind: westward dispersal across the Indian Ocean and island speciation in *Hemicordulia* dragonflies (Odonata: Corduliidae)

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Gone with the wind: westward dispersal across the Indian Ocean and island speciation in *Hemicordulia* dragonflies (Odonata: Corduliidae)

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Abstract

The taxonomy and biogeography of the western representatives of the largely Papuan-Australian genus *Hemicordulia* are discussed and compared with other alate fauna including butterflies, birds, bats and other dragonflies. Specimens from Malawi, Mozambique, Réunion, South Africa, Tanzania and Uganda were compared with Indian specimens of *H. asiatica*, with which they were previously regarded conspecific. They are found to be distinct and are described as the continental *H. africana* **n. sp.** and those from Réunion as *H. atrovirens* **n. sp.** The three species were compared with *H. similis* of Madagascar and *H. virens* of Mauritius. Insufficient material of the Seychelles taxon *H. similis delicata* was available; it may represent another insular endemic species. The distribution of *Hemicordulia* is discussed in the light of the dispersal capacity of Odonata and the biogeography of taxa with similar distributions in the region, with an emphasis on the survival of 'oceanic' species on the continent. Recent (i.e. in the last few million years) trans-oceanic airborne dispersal aided by westward storms, is the most likely explanation for the distribution of the genus in Africa and the Indian Ocean islands, as well as for other winged animals of Asian affinities in the region. The world range of *Hemicordulia* is largely insular, broadly excluding continents, and *H. africana* **n. sp.** demonstrates 'inverted insularity': all continental sites are in proximity to large water bodies, such as the great African lakes. This pattern may be related to the climatological instability of these sites, which offer suitable cool habitat where competition is (temporarily) reduced. *Hemicordulia* prefer cool conditions, but may be vulnerable to overheating and competition with more warm-adapted species.

Key words: Anisoptera, *Hemicordulia*, Africa, India, Indian Ocean islands, taxonomy, biogeography, key

Introduction

"The […] possibility can immediately be ruled out on good reasons: both the behavioural characteristics and habitat preference of this non-migrating, forest-dwelling […] species are fully incompatible with long-range flight over open seas. Hypothetically, only natural disasters like volcanic eruptions or tidal waves could force survivors […] to suddenly leave their habitats, and this too, only soon to reach the nearest safe forest habitat […]. Neither are the prevailing systems of trade winds […] in the Indian Ocean […] in any way favourable to transport viable propagules […] from the nearest landmass in the indo-malayan region to Madagascar."

Farkas's (1985) emphatic dismissal of westwards trans-oceanic dispersal of an alate forest animal, the passerine genus *Copsychus* in his case (Fig. 21), neatly summarises the opposition against the notion that eastern elements of the terrestrial fauna in the western Indian Ocean may have arrived airborne. Nonetheless, avian examples alone suggest that such dispersal from Asia towards Africa may be frequent (Keith 1980). Louette (1987) hypothesised that several overseas colonisations of the passerine genus *Hypsipetes* from India to Madagascar and surrounding islands gave rise to five similar species (Fig. 22). Phylogenetic reconstructions place Indian Ocean *Hypsipetes* and *Copsychus* within Asian radiations of their families (Farkas 1985; Jønsson & Fjeldså 2006; Moyle & Marks 2006). Thomassen *et al*. (2005) found the nearest relatives of Seychelles and Mascarene endemic *Collocalia* swiftlets in the genus's centre of diversity in Sundaland, but did not sample species occurring in the Himalayas and southern India (Fig. 20). Groombridge *et al*. (2004) found molecular support for the trans-oceanic colonisation of Mauritius by a *Psittacula* parakeet from India, although samples of extinct species from the Seychelles and Rodrigues were unavailable. Of other alate fauna, about fifty *Pteropus* fruit bat species inhabit Australasia and the Pacific, while nine endemic taxa occupy all major Indian Ocean islands up to those on the Tanzanian coast (Bergmans 1990; Fig. 23). Preliminary phylogenetic results are compatible with long-range trans-oceanic dispersal from the east (Colgan & da Costa 2002; Giannini & Simmons 2003; Juste B. *et al*. 1999; O'Brien & Hayden 2004). Two endemic *Euploea* butterflies in the Seychelles and Mascarenes are western isolates of a large tropical Australasian genus, but their phylogeny is poorly resolved (Ackery & Vane-Wright 1984).

The distribution of the dragonfly genus *Hemicordulia* Selys (including the closely related *Procordulia* Martin) is similar to that of *Pteropus* (Fig. 18). The highest number of over fifty species and their greatest morphological and ecological variation is found in New Guinea and Australia (van Tol 1997; Tsuda 2000). Some species are strong migrants that are among the most abundant Papuan-Australian dragonflies, others are adapted to extreme habitats like isolated desert pools and high-altitude lakes or are endemic to remote oceanic islands (e.g. Asahina 1940; Lieftinck 1962). Outside Australia the group is local on continents, together accounting for less than one-tenth of known species. For instance, there are no records from mainland China, although *Hemicordulia* extends to Taiwan and the Ryukyus. The group ranges across the Pacific to New Zealand, French Polynesia and the Bonin Islands, and across the Indian Ocean to the Seychelles, Mascarenes and Madagascar. Pinhey (1961) first reported the Indian species *H. asiatica* (Selys) from eastern Africa, stating that "as Fraser has remarked to me, there seems to be no difference between Uganda and Indian examples". Couteyen & Papazian (2000) recorded the species from Réunion. However, similar populations found in-between, were treated as distinct species, with *H. virens* (Rambur) on Mauritius and *H. similis* (Rambur) on Madagascar and the Seychelles. The western distribution of *Hemicordulia* and the other groups, raises the question of their origin. Lieftinck (1942) described *Hemicordulia* as "one of the few 'modern' or ectogenic, Australian dragonflies that, having passed northward into the Papuan region, has spread far and wide beyond its Australian zoocentre. As is clearly shown by its distribution, the genus has most decided powers of dispersal but not generally a wide specific range." Fraser (1949) also wrote of "strong migratory tendencies", adding that "the genus is essentially a Papuan one, […] *H. asiatica* […] has extended into continental Asia […]. Two others, concerning which there is good evidence to show that they are lineal descendants of *H. asiatica*, are found in the Mascarene Islands and Madagascar [*H. virens*, *H. similis*]". On finding '*H. asiatica*' in South Africa, Pinhey (1985) indicated it was "possibly a migrant" but refrained from suggesting its origin. Van Tol (1997) found Fraser's remarks "in support of an Indo-Australian origin of the genus, with westward migration in a later phase" and Donnelly & Parr (2003) also stressed that *Hemicordulia* "seems to have wide powers of dispersal, and its occurrence in Madagascar (and in Africa, as well) suggests an origin from the east."

In Odonata, the distribution of *Hemicordulia* is mirrored by several groups (Fig. 26), especially the coenagrionid genus *Teinobasis* Kirby (Donnelly & Parr 2003; Fig. 19). Its less extensive range has a western Pacific centre of diversity, with a scattering of insular endemics (e.g. Paulson & Buden 2003). The genus is peripheral on continents, but *T. alluaudi* (Martin) occurs in the Seychelles, Madagascar and East Africa (Clausnitzer 2003). The south-eastern African aeshnid *Gynacantha immaculifrons* Fraser is related to endemics of the Seychelles, Madagascar and the Mascarenes, but their possible Oriental affinities are unresolved (Dijkstra 2005). Dijkstra *et al*. (2007) argued that the Comoros and Pemba (just off the Tanzanian coast) were colonised on two separate events by *Platycnemis* Burmeister damselflies from Madagascar, possibly crossing 1000 km of sea with the strong monsoon that follows the East African coast. Similar distributions in other freshwater insects, possibly established "with the aid of cyclones", are seen in *Aulonocnemis* beetles and *Setodes* and *Potamyia* caddisflies (Gibon 2003; Paulian & Viette 2003).

An emphasis on vicariance has led to the neglect of oceanic dispersal as a major factor in biogeography, in part because such dispersal is considered almost impossible to falsify: as dispersal can potentially explain any pattern, it could conclusively explain no pattern in particular (McGlone 2005). This has led to the arbitrary situation in which dispersal is generally accepted for oceanic islands, for lack of alternatives, but denied for continents and continental islands (de Queiroz 2005). Sanmartín & Ronquist (2004) found a general temporal and spatial mismatch between phylogenies of trans-oceanic groups and Gondwanan vicariance, although this was less pronounced for animals than plants, which were considered less vagile. However, winged fauna such as Odonata, may be equally mobile as these often wind-dispersed plants. Moreover, the direction of oceanic dispersal is not necessarily random. Muñoz *et al*. (2004) demonstrated that distribution patterns of cryptogams on sub-Antarctic islands were better explained by the direction of prevailing winds, than by their geographic proximities. Considering the dispersive heterogeneity of the studied taxa, they implied that wind transport in lower atmospheric layers should work for many other groups, including arthropods. Gillespie & Roderick (2002) considered that “butterflies and other large insects, such as dragonflies and sphinx moths, may have a wider range of dispersal than most insect groups” and found a good correlation between proportions of insect groups trapped in aerial nets over the ocean and those that make up oceanic island faunas. Zakharov *et al*. (2004) concluded that prevailing winds favour dispersal from Asia to the western Indian Ocean and from Madagascar to Africa, especially for vagile taxa such as large butterflies. This paper examines the anomalous distribution and taxonomy of western Indian Ocean *Hemicordulia* and discusses its origin in the light of the revived emphasis on long-distance dispersal in biogeography.

Method and material

The investigation of African ‘*H. asiatica*’ was prompted by a note in the BMNH: “Pinhey calls these [three Ugandan specimens] *asiatica* Selys, I think they are a new species. Anal app[endages] and pt[erostigma] different. (C. Longfield 1955.)”. Lieftinck (1962) wrote that *Hemicordulia* species “are much alike and extremely difficult to distinguish. Males can best be separated by slight differences in the genital organs, anal appendages, length of posterior femur and tibial keels; females, by the pubescence of the occiput, length and shape of the anal appendages, and wing color; both sexes in combination, by color, body size and (occasionally) venation.” The Indian Ocean species can best be distinguished by the shape of the vulvar scale (Fraser 1949). I examined material of both sexes (see lists under species) of African and Asian ‘*H. asiatica*’ for these and potential additional characters and, with this comparison as calibration, also the insular taxa *H. similis* and *H. virens*. Most western species are elusive and local; specimens are almost exclusively collected while hunting in open spaces in forest (e.g. Fraser 1936; Pinhey 1966; 1976). Therefore an effort was made to examine as many specimens as possible.

Abbreviations

Ax: antenodal cross-veins; Ax1: first antenodal (counted from base) etc.; Cux: cubital cross-vein; Fw: forewing(s); Hw: hindwing(s); Pt: pterostigma; Px: postnodal cross-veins; S1: first abdominal segment; S2–3: second and third abdominal segments etc.

Acronyms for collections

BMNH: Natural History Museum, London; ISNB: Institut Royal des Sciences Naturelles de Belgique, Brussels; MNHN: Muséum National d’Histoire Naturelle, Paris; NHRS: Naturhistoriska Riksmuseet, Stockholm; NMBZ: Natural History Museum of Zimbabwe, Bulawayo; NMKE: National Museums of Kenya, Nairobi; RMNH: Nationaal Natuurhistorisch Museum Naturalis, Leiden; SUEC: Stellenbosch University Entomology Collection, Stellenbosch; UMO: University Museum, Hope Entomological Collections, Oxford;

ZMMU: Zoological Museum of Makerere University, Kampala; ZMUH: Zoologisches Institut und Zoologisches Museum, Universität von Hamburg, Hamburg.

Results

Consistent differences were found between African and Asian '*H. asiatica*', especially in the shape of the male cerci and female vulvar scale, which were sufficient to regard them as distinct species (Table 1). No differences were found in the hamule, femora, tibiae and female cerci. The African '*H. asiatica*' was similar to Madagascan *H. similis* and Réunion '*H. asiatica*' to *H. virens* of nearby Mauritius, but the species in each pair were distinct by coloration (Table 2, Key). With all diagnosable entities confined to defined geographic areas, each is best treated as a species. Thus five species occur west of the Gulf of Bengal, which are discussed below ordered from east to west.

TABLE 1. Comparison of *Hemicordulia africana* **n. sp.** ('*H. asiatica*' from continental Africa) with typical *H. asiatica* from Asia (see Table 2 for measurements).

Character	Comparison
Size	Smaller, only 12.5% of *africana* and 17.6% of *asiatica* males had overlapping Hw lengths. Corresponding lower Px counts with mode of 5 (average 5.17) versus 6 (5.67).
Frons (♂)	Metallic green restricted to upper half of rough area on frons, leaving lower half yellow (best seen in dorsal view, where yellow is visible anteriorly). In *asiatica* green extends ventrally to cover entire rough area, leaving only smooth portion bordering postclypeus free.
Occiput (♀)	Paired rounded swellings bear a cluster of short thick brown bristles on each side, besides long pale hairs. These clusters are absent in *asiatica*.
Synthorax	Less intensely metallic green and pale markings more extensive. Markings of both species are extremely variable and their interpretation is complicated by age-related melanisation and often weak contrast between metallic (melanised) and pale (less melanised) parts. Teneral specimens are largely pale. Mature *asiatica* males tend to be more strongly melanised on synthorax. This results in more extensive areas of a deeper green, with a more brightly metallic lustre, which contrasts more sharply with less melanised parts.
Abdomen	Pale markings on abdomen less extensive, in contrast to state of synthorax. There is much variation and mature males may loose pale markings almost completely. *Asiatica* has prominent pale lateral markings on S2–7 or S2–8. In *africana* markings on S2–3 are much reduced, those on S4–5 are barely discernible (infused with melanin) or absent, and those on S6–8 tend to be clear. As darkening progresses, *asiatica* males loose marking on S8 before those on S5–6, the reverse in *africana*. A typical *asiatica* male thus has a string of pale marks from abdomen base to S7, whereas *africana* has an isolated string on S5–8 or S6–8. Females (in which pale markings are more extensive) differ in a similar way, the markings on S2–5 being relatively reduced in *africana*.
Pterostigma	Pt marginally shorter, an impression emphasised by small size. Fw Pt length was 13.2% (12.5–13.8) of the postnodal wing half in *africana* (n=10) and 14.2% (12.5–15.3) in *asiatica* (n=10).
Wing colour (♀)	Yellow in wing bases more extensive, up to arculus or even Ax2 in Fw and Hw in *africana*, whereas virtually indiscernible in Fw and at most a little past Hw Cux in *asiatica*.
Cerci (♂)	More slender and sinuous in dorsal view (Fig. 6). Rather thick halfway in *asiatica*, the outer border being less strongly curved inwards (Fig. 2). In lateral view ventral border is evenly concave in *asiatica* (Fig. 7), but has a distinctly convex bulge at midpoint in *africana* (Fig. 11).
Vulvar scale (♀)	Incision narrower, its sides nearly parallel: angle between them being 10–30° in *africana* (Fig. 17) versus 35–55° in *asiatica* (Fig. 12). Scale protrudes slightly further over sternite of S9, reaching 35–45% down sternite in *africana* versus 30–35% in *asiatica*.

Systematic part

Hemicordulia Selys

Cordulia nec Leach, 1815 – Rambur (1842: 146).
Cordulia (*Hemicordulia*) Selys, 1870: v [type species: *Cordulia australiae* Rambur, 1842; by original designation].
Hemicordulia Selys, 1870 – Kirby (1890: 46).

Diagnosis. The genus combines characters typical of Corduliidae with reductions shared with Libellulidae. 'Corduliid' features are: (1) posterior margin of eyes infracted; (2) male hind tibiae keeled; (3) S2–3 without transverse subbasal ridges; (4) body largely metallic green. 'Libellulid' features are: (1) anal triangle and angle of Hw reduced in males; (2) auricles on S2 reduced in males. Aside from aforementioned 'libellulid' features, a combination of venation characters in unique among Afrotropical 'corduliids': (1) only 6–9 Ax in Fw; (2) arculus lies between Ax1–2; (3) Hw arculus more or less aligned with proximal border of triangle; (4) only one bridge cross-vein in all wings; (5) supratriangles without cross-veins; (6) Hw with only one Cux; (7) subtriangle of 3 cells; (8) anal loop boot-shaped. The separation of the closely related Australasian genus *Procordulia*, which has an anal triangle, is not well resolved (van Tol 1997).

Key to Afrotropical *Hemicordulia* species

1 Fw usually with 8 Ax and 7 Px. Vulvar scale covering less than one third of sternite S9, not reaching paired processes on sternite (Figs 13–14). ♀ occiput only with long pale hairs. Distal third of ♂ cerci almost parallel-sided, tips abruptly rounded (Figs 3–4, 8–9). Hw 32–38 mm in ♂, 35–39 in ♀. Mascarene Islands 2

\- Fw usually with 7 Ax and 5 Px. Vulvar scale covering over one third of sternite S9, extending over bases of paired processes (Figs 16–17). ♀ occiput with cluster of short thick brown bristles on each side, in addition to long pale hairs. Distal third of ♂ cerci tapering to a blunt point (Figs 5–6, 10–11). Hw 27–32 mm in ♂, 28–33 in ♀. Africa, Madagascar and Seychelles 3

2 Yellow anterior to metallic area on frons not visible in dorsal view (perhaps marginally in ♀). Fore femora predominantly black. Synthorax predominantly metallic green. S6–8 entirely dark. Réunion.. *atrovirens* **n. sp.**

\- Yellow anterior to metallic area on frons visible in dorsal view. Fore femora predominantly yellow. Synthorax predominantly yellow. S6–8 dark with yellow lateral spots. Mauritius .... *virens*

3 Yellow anterior to metallic area on frons not visible in dorsal view (perhaps marginally in ♀). Labrum with two dark blotches at base. ♀ Hw at most yellow to Cux and Ax1, yellow almost absent in Fw. Madagascar and Seychelles .... similis

\- Yellow anterior to metallic area on frons visible in dorsal view. Labrum all yellow. ♀ Fw and Hw at least yellow to arculus. Continental Africa .... *africana* **n. sp.**

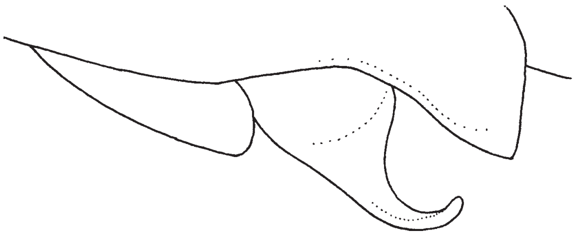
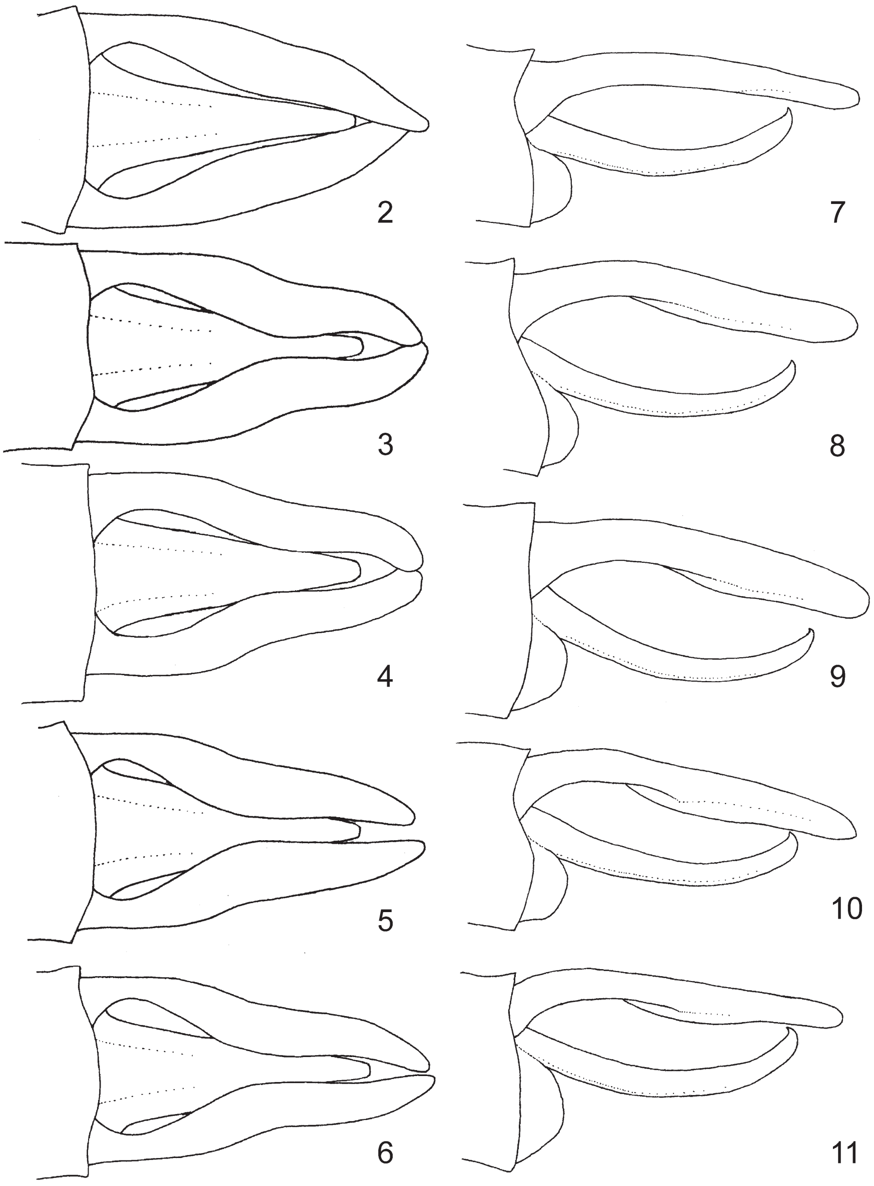


FIGURE 1. Secondary genitalia of *Hemicordulia africana* **n. sp.** in lateral view.

Hemicordulia asiatica (Selys)
Figs 2, 7, 12.

Cordulia (*Hemicordulia*) *asiatica* Selys, 1878: 186 (bulletin), 8 (reprint). Holotype ♂ with labels: handwritten “Khasiya Hills [India]”, yellow, printed “Atkinson”, handwritten by Selys “Hemicordulia asiatica S ♂”, printed and handwritten by Martin “Collection Selys, Hemicordulia asiatica Sel. Type, Révision Martin 1906 Hemicordulia asiatica Sel.”, printed red and handwritten by Martin “Type Hemicordulia asiatica Sel.” (ISNB) [examined].

Hemicordulia asiatica (Selys, 1878) – Kirby (1890: 47).



FIGURES 2–11. 2–6, Male appendages of *Hemicordulia* species in dorsal view. (2) *H. asiatica*; (3) *H. virens*; (4) *H. atrovirens* **n. sp.**; (5) *H. similis*; (6) *H. africana* **n. sp.; 7–11,** Male appendages of *Hemicordulia* species in lateral view. (7) *H. asiatica*; (8) *H. virens*; (9) *H. atrovirens* **n. sp.**; (10) *H. similis*; (11) *H. africana* **n. sp.**

Further material: INDIA (Karnataka): 1 ♂, Coorg, Fraserpet [= Kushalnagar]-Mercara Road, 3000 ft. (= 915 m), 25.v.1923, F.C. Fraser (BMNH). – INDIA (Kerala): 1 ♀, Mudis Hills, 14.v.1934, F.C. Fraser. – INDIA (Meghalaya): 1 ♂, Shillong, 1.ix.1919, Fletcher (BMNH); 1 ♂, Shillong, Assam, 10.viii.1928, J. Muller (ISNB). – INDIA (Tamil Nadu): 1 ♂, 1 ♀, Nilgiri Hills, Coonoor, Syms Park, 7–14.v.1921, F.C. Fraser; 5 ♂, 2 ♀, Nilgiri Hills, Ootacamund, 7250 ft (= 2210 m a.s.l.), 18.x.1921–18.xi.1922, F.C. Fraser & T.B. Fletcher; 1 ♂, Nilgiri Hills, Lovedale Lake, 7250 ft (= 2210 m a.s.l.), 8.x.1922, F.C. Fraser; 1 ♂, Nilgiri Hills, date & leg. unknown; 1 ♂, 1 ♀, Palni Hills [= Palani H.], Kodaikanal, Bear Stream, 2.vi.1923, Maj. Frere; 1 ♂, Bear Stream, date unknown, F.C. Fraser; 1 ♂, Annaimallai Hills [= Anaimalai H.], Varataparai, 7.v.1933, F.C. Fraser; 1 ♂, Annaimallai Hills, Varataparai, on hill-side road, iv–v.1934, F.C. Fraser; 1 ♂, Annaimallai Hills, date & leg. unknown (BMNH).

Diagnosis. Differs from all other species discussed in the shape of the male cerci (Figs 2, 7) and incision of the vulvar scale (Fig. 12). The greatly restricted yellow on the female wings is also distinctive.

Range and ecology. Known from two disjunct highland areas in the south-west and north-east of the Indian Subcontinent (Prasad & Varshney 1995), ranging into Myanmar (Asahina 1970). The status of *Hemicordulia* from northern Thailand and Vietnam is unclear relative to the Sundaic *H. tenera* Lieftinck, 1930 (Asahina 1987; Donnelly 1994; H. Karube pers. comm.). According to Fraser (1936) “the larva breeds in mountain lakes and, less often, in pools in montane streams”. The adult “rarely strays far from its watery habitat and is to be found patrolling the borders of lakes or flying rapidly along open roads and glades on the hillsides above the lakes. The females are rarely seen, and appear to keep to jungle, except for brief intervals when they come to oviposit and then depart again, pairing taking place during these short visits to water.” Fraser (1949) indicated an altitudinal range of 915 to 2300 m in southern India.

Hemicordulia virens (Rambur)
Figs 3, 8, 13.

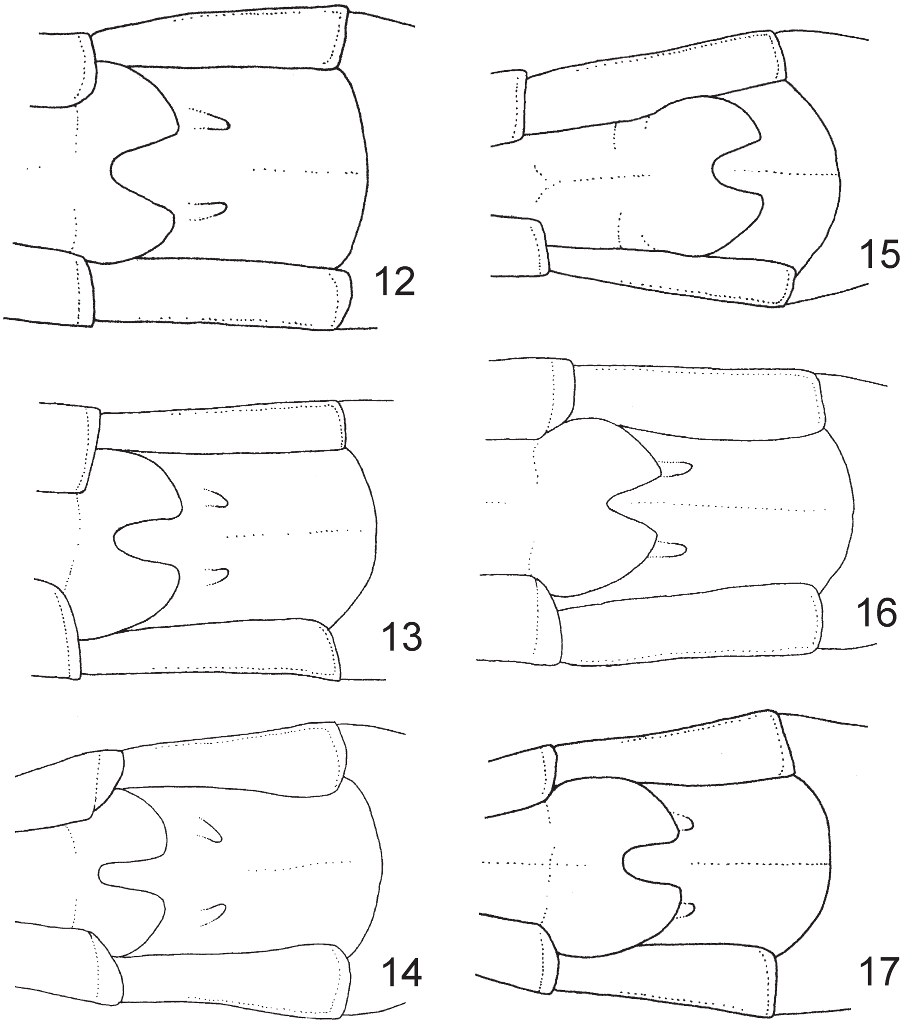
Cordulia virens Rambur, 1842: 147. Holotype ♀: Mauritius (UMO) [not examined].
Cordulia (*Hemicordulia*?) *virens* (Rambur, 1842) – Selys (1871: 253 (bulletin), 19 (reprint)).
Hemicordulia (?) *virens* (Rambur, 1842) – Kirby (1890: 47).

Further material: MAURITIUS: 4 ♂, 4 ♀, Moka, 30.vi.1945–30.xii.1948; J. M. Vinson (BMNH); 1 ♂, Macak’Rd, 11.v.1959, leg. unknown (MNHN); 1 ♀, F[ôre]t de Machabée, 19.iii.1981, L. Matilé (MNHN); 1 ♂, Cachette, Ruisseau Saint-Denis, 350 m a.s.l., 2.ii.1999, D. Grand (Coll. D. Grand); 1 ♂, Cachette, ruisselet forestier, 300 m a.s.l., 2.ii.1999, D. Grand (MNHN); 1 ♂, Rivière Tamarin, 1 m a.s.l., 2.ii.1999, D. Grand (MNHN); 1 ♀ (head missing), Black River, 120 m a.s.l., 7.iv.1999, A. Martens (Coll. A. Martens); 1 ♂, Rivière du Poste, W Grand Bassin, 645 m a.s.l., 12.iv.1999, A. Martens (Coll. A. Martens); 2 ♂, Black River, spring area, 680 m a.s.l., 16.iv.1999, A. Martens (Coll. A. Martens).

Diagnosis. Palest and one of the largest species. *H. atrovirens* from neighbouring Réunion, by contrast, is the darkest known. The two species agree in their large size, high Ax and Px counts, thick blunt-tipped cerci (Figs 3, 8) and the basal position of the vulvar scale (Fig. 13).

Remarks. The holotype was not seen, but is described as a large, pale specimen from Mauritius, conforming with the diagnosis. As morphological and geographic proximity suggest, *Hemicordulia* populations on Mauritius and Réunion are closely related. The extreme difference in coloration makes separation straightforward and warrants recognition at the species level. Similar differences separate Micronesian species (e.g. Buden & Paulson 2003). All specimens listed by Fraser (1949; 1950) were re-examined, and inconsistencies between my Fig. 13 and Fraser’s (1949) illustration of the vulvar scale and S9 (where the segment is very short) result from a degree of variability in this structure and Fraser’s inaccurate depiction thereof.

Range and ecology. Endemic to Mauritius, where restricted to the mountains in the south-west, which harbour the island's main forest remnants. It is notable that records are from an altitudinal range of 120 to 680 m (Mauritius is only up to 823 m high), lower than most sites of its sibling species *H. atrovirens*. Breeds in pools in rocky streams and rivers, which are mostly forested. Males have been observed patrolling such streams in search of females. Adults have been observed from December to June (D. Grand & A. Martens in litt.).



FIGURES 12–17. Vulvar scale and S9 of *Hemicordulia* species in ventral view. (12) *H. asiatica*; (13) *H. virens*; (14) *H. atrovirens* **n. sp.**; (15) aberrant *H. similis* (cf. Fraser 1949); (16) typical *H. similis*; (17) *H. africana* **n. sp.**

***Hemicordulia atrovirens* n. sp.**

Figs 4, 9, 14.

Hemicordulia asiatica nec (Selys, 1878) – Couteyen & Papazian (2000: 107).

Hemicordulia atrovirens **n. sp.** Holotype ♂ and paratype ♀: Réunion, Rivière de Sainte-Suzanne, 730 m a.s.l., 8–9.iv.1996, A. Martens (RMNH) [examined].

Further material: RÉUNION: 1 ♀ (Coll. Martin), “Réunion” (MNHN); 2 ♂, Bras Cabot, 1325 m a.s.l., 4.iv.1996, A. Martens (Coll. A. Martens); 2 ♂, Rivière des Marsouins, 1330 m a.s.l., 4.iv.1996, A. Martens (Coll. A. Martens); 3 ♂, ravine near Rivière Langevin, 350 m a.s.l.,14.iv.1996, A. Martens (Coll. A. Martens); 1 ♂, Chemin-de-Ceinture, forêt de ravenales, 12.ii.1999, J. & Cl. Pierre (MNHN); 1 ♀, commune de Saint-Philippe, Ravine Basse Vallée, altitude 280 m a.s.l., 22.v.1999, S. Couteyen (Coll. M. Papazian); 1 ♂, Saint-Paul, old watermill, 2 m a.s.l., 1.v.2000, A. Martens (Coll. A. Martens); 2 ♂, Saint-Benoit, Bras Cabot, 1100 m a.s.l., xii.2001, S. Couteyen (Coll. M. Papazian); 1 ♂, La Plaine des Palmistes, Forêt de Bébour, Rivière des Marsouins, 1330 m a.s.l., 14.ii.2003, D. Grand (Coll. D. Grand).

Diagnosis. Largest and darkest species, with the most extensive and deepest metallic green markings of all species under consideration (see *H. virens*).

Description. Holotype male. Measurements (mm): entire length: 51, abdomen length (without appendages): 34, Fw length: 35, Hw length: 34.5, Fw Pt: 2.0. Labium beige, darker anteriorly (discoloured?). Mandibles, genae, labrum, clypeus and narrow area on lower frons brownish yellow; darker on edges. Vertex and dorsum of frons deep metallic green-blue, merging via a deep brown band into yellow area on antefrons (latter is not visible in dorsal view). Antennae, occipital triangle, occiput and postgenae black; paired rounded swellings on occiput lower than in *H. africana*. Labrum, clypeus, frons, vertex and occipital triangle with long bristly black hairs. Labium, genae and occiput with finer whitish hairs. Prothorax dark brown. Synthorax deep metallic green with weakly contrasting brownish yellow areas on anterior half of mesepisternum and centres of mesepimeron, metepisternum and metepimeron: metallic areas are much wider than the pale areas between them making entire synthorax almost uniformly green. Mesokatepisternum, metakatepisternum and synthoracic venter brownish yellow with metallic green lustre; poststernum posteriorly dark. Synthorax covered with dense pale long hairs, especially long on mesepisternum; shorter, darker and denser hairs on antealar sinus. Legs black save for yellow coxae and a hint at base of fore femora. Keels present on anterior face of apical half of fore tibiae and almost whole length of hind tibiae (just falling short of their bases), but absent on middle tibiae. Venation blackish. Wing membrane evenly but very lightly tinted brown, tinged yellower at extreme bases. Membranule dark brown, slightly paler at extreme base. Pt dark brown. Venation as for genus. 8 Ax in both Fw, 6 in Hw. 7–8 Px in Fw, 9 in Hw. Fw and Hw triangles with single cross-veins. Discoidal field of 2 rows of cells at base. Anal loops of 18 cells. Abdomen black with green- and blue-purple gloss, tergites unmarked except for an indistinct brownish yellow lateral spot on S2, S2–3 intersegmental ring and narrow streaks on lateral carinae S3. Sternites black. Cerci and epiproct slender, black (Figs 4, 9). Cerci with thick, blunt tips. Secondary genitalia similar to *H. africana* (cf. Fig. 1), hamule blackish brown.

Paratype female. Measurements (mm): entire length: 55, abdomen length (without appendages): 39, Fw length: 39, Hw length: 38, Fw Pt: 2.5. Larger and slightly paler than holotype. Paired rounded swellings on occiput more strongly swollen than in male, only with long pale hairs. Pale areas on synthorax larger and brighter, appearing as distinct spots. Fore femora ventrally largely pale. Basal yellow in wings more extensive than in male, to Cux and almost to Ax1 in Fw, and just beyond Cux and to Ax1 in Hw. 8–9 Ax in Fw, 6 in Hw. 7 Px in Fw, 9 in Hw. Anal loops of 19–21 cells. Vulvar scale appressed, dark brown, extending over less than a third of sternite S9, semi-circular with deep cleft (Fig. 14). Cerci black, long and slender, 2.5x longer than S10.

Variation. Limited. Pale markings are slightly more extensive in females; teneral specimens were not examined.

Etymology. The Latin *atrovirens* (being dark green) emphasises both the close relationship and the main difference with its Mauritian neighbour.

Range and ecology. Endemic to Réunion. The larval habitat has been said to range from torrents to stagnant water under closed cover, but is probably principally pools and calm sections of shady fast-flowing streams (Couteyen & Papazian 2000; Grand 2004; A. Martens in litt.). *H. atrovirens* seldom cohabits with any of the ten other anisopterans found on Réunion (Couteyen 2006): overlap (number of sites where two species co-occur as percentage of sites where either or both occur) with each of the nine species shared with mainland Africa was at most 9%, while that with *Gynacantha bispina*, the only other Mascarene endemic on the island, was 12%. Moreover, within its usual altitudinal range of 300 to 1500 m (one record provided here is near sea level), below 750 m only forested habitats were occupied. Because all nine widespread species avoid forest and six are confined to lower altitudes, Couteyen (2006) suggested that both endemics are out-competed by the mainland species. However, the distribution may also be explained by different habitat preferences (A. Martens in litt.). Males fly along streams, both under forest cover and in full sun. In cloudy weather and towards dusk, adults appear in clearings and on the forest edge, making prolonged flights close to the vegetation (Couteyen & Papazian 2000; D. Grand in litt.). Adults have been observed from December to May.

Remarks. See *H. virens*. Paulson & Buden (2003) observed increasing size of *H. haluco* Asahina with increasing altitude on Pohnpei. The slight size difference seen between *H. atrovirens* and *H. virens*, and the darker colour of the latter, may be linked to the greater elevation of the Réunion habitats.

Hemicordulia similis **(Rambur)**

Figs 5, 10, 15–16.

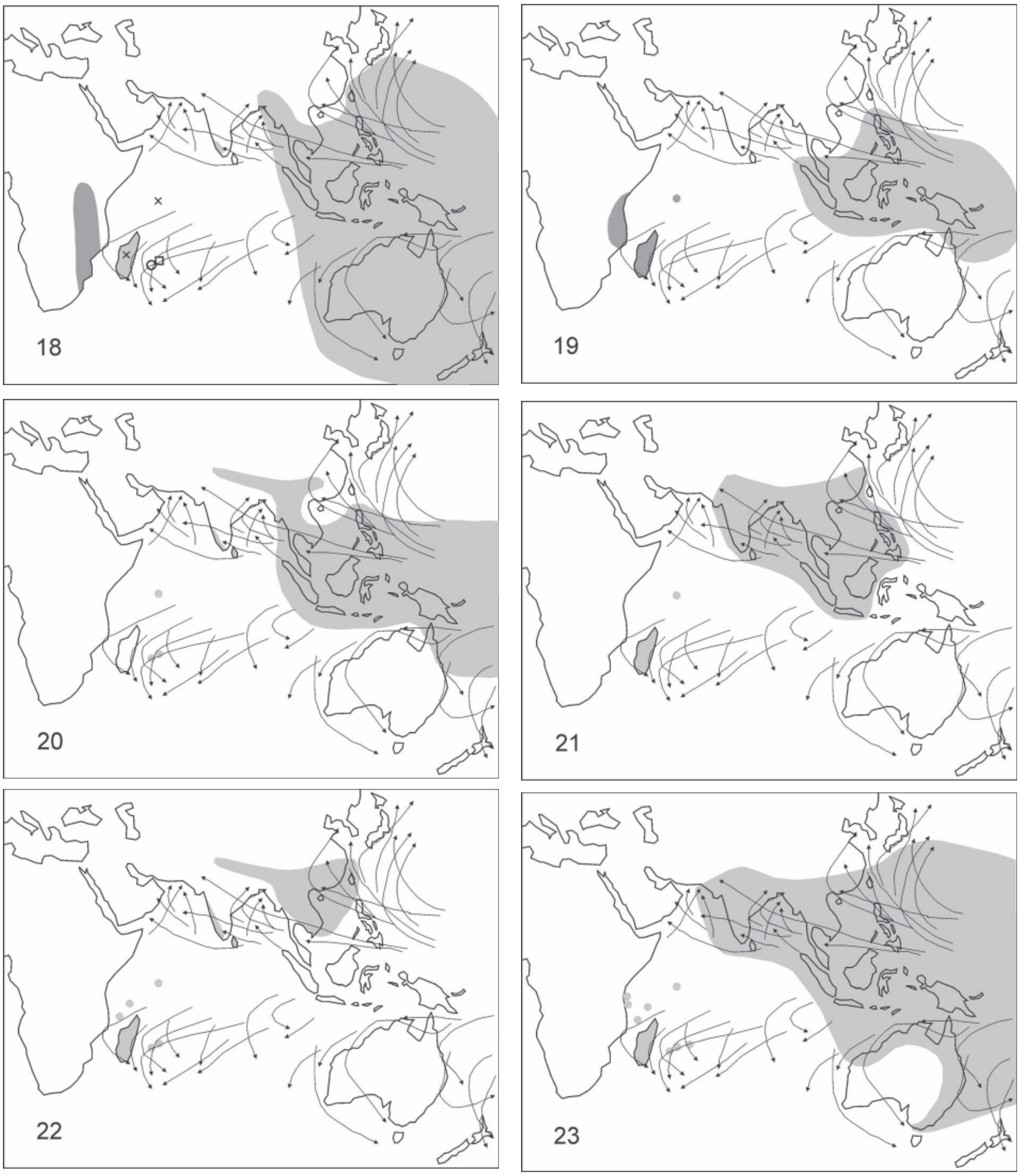
Cordulia similis Rambur, 1842: 147. Holotype ♀ with labels: handwritten “Madagascar”, handwritten “Ramb.”, handwritten “Cordulia similata Rb.”, handwritten by Selys “Hemicordulia similis, R. ♀”, printed and handwritten by Martin “Collection Selys, Hemicordulia similis Rb. Type, Révision Martin 1906 Hemicordulia similis Rb.”, printed red and handwritten by Martin “Type Cordulia similis Rb.” (ISNB) [examined].
Cordulia similata Rambur – probably Selys (in litt., see above), *nomen nudum*.
Cordulia (*Hemicordulia*?) *similis* (Rambur, 1842) – Selys (1871: 252 (bulletin), 18 (reprint)).
Hemicordulia (?) *similis* (Rambur, 1842) – Kirby (1890: 47).
Hemicordulia delicata Martin, 1896: 105. Holotype ♂ with labels: handwritten by Martin “Hemicordulia Séchelles.”, “Coll. R. Martin 1920 MUSEUM PARIS” (MNHN) [Martin (1896, 1907) did not specify the number of specimens from the Seychelles and presumably saw no females. Only this male was located in MNHN and it is assumed to be the holotype, although it bears no type labels.].
Hemicordulia similis delicata Martin, 1896 – Pinhey (1962: 208).

Further material: MADAGASCAR: 1 ♂, “Madag. Schauf[uss].” (BMNH); 2 ♂, blue handwritten by Selys “Madag. Schauf[uss].”, handwritten by Selys “Hemicordulia similis, R. ♂”, printed and handwritten by Martin “Collection Selys, Hemicordulia similis Rb., Révision Martin 1906 Hemicordulia similis Rb.” (ISNB); 4 ♂, 2 ♀, “Madagascar” (MNHN); 1 ♂, 1 ♀, Madagascar (NMBZ); 1 ♂, “E. Madagascar” (MNHN); 2 ♂, 1 ♀, Miarinarivo (MNHN); 1 ♂, “Tamatave”, “Madagask. Kaudern”, “Hemicordulia similis Yngve Sjöstedt det.” (NHRS); 3 ♂, 1 ♀, “Madagascar” (RMNH); 1 ♂, 1 ♀, Tananarive, 1919, G. Waterlot (MNHN); 1 ♀, Ambohimangana, 4.xii.1946, leg. unknown (BMNH); 1 ♂, Tananarive, Tsimbazaza, 24.xii.1947, leg. “A.R.” (BMNH); 3 ♂, 10 km N of Tôlanaro (24°56’S 46°59’E), 17–20.iii.2004, K. Schütte (ZMUH); 2 ♂, 1 ♀, 33 km NE of Tôlanaro (24°46’S 47°10’E), 1–3.iv.2004, K. Schütte. – SEYCHELLES: 1 ♂, Mahé, slopes of Morne, xii.1952, Vesey Fitzgerald (NMBZ).

Diagnosis. Similar to *H. africana*, but marginally larger on average and with darker face, perhaps slightly straighter ends of cerci (Fig. 5), more triangular cleft of the vulvar scale (Fig. 16) and reduced yellow at the female wing bases: almost none in Fw and at most to Cux and Ax1 in Hw.

Remarks. Martin (1907) discussed the taxon *delicata* under *H. similis* without indicating whether it is a synonym or subspecies of the latter, but because he later omitted *delicata* he probably considered it a synonym (Martin 1914). That is also how Fraser (1949) treated it, but Pinhey (1962) considered it a subspecies. Each distinct geographic area studied had its single endemic species and therefore *H. s. delicata* may be a separate species too. The current status is however retained because only two males were seen and no female with its potentially diagnostic vulvar scale. The unusually stalked vulvar scale, as illustrated by Fraser (1949) was only seen on the BMNH female and must be aberrant (Fig. 15). All other examined females, including the type, have an unstalked scale (Fig. 16).

Range and ecology. Widespread on Madagascar. Otherwise known only from Mahé, the largest of the granitic Seychelles (Blackman & Pinhey 1967; Martin 1896), where it was recently reported from a marsh at Police Bay (Gerlach 2003; A. Martens in litt.). Ecology unknown, but is probably similar to other species, as is the adult flight season.



FIGURES 18–23. Distribution of discussed genera. The courses of storms from May to November in the northern hemisphere and November to May in the southern hemisphere are indicated by arrows (after Times Books 1997). (18) *Hemicordulia* and *Procordulia* dragonflies, pale shading: main range in Australasia and Pacific; dark shading: *H. africana* **n. sp.**; crosses and pale shading: *H. similis*; square: *H. virens*; circle: *H. atrovirens* **n. sp.**; (19) *Teinobasis* damselflies, pale shading: main range in Australasia and Pacific; dark shading: *T. alluaudi*; (20) *Collocalia* swiftlets; (21) *Copsychus* magpie robins; (22) *Hypsipetes* bulbuls; (23) *Pteropus* flying foxes.

***Hemicordulia africana* n. sp.**

Figs 1, 6, 11, 17.

Hemicordulia similis nec (Rambur, 1842) – Martin (1906 in litt.).
Hemicordulia asiatica nec (Selys, 1878) – Pinhey (1961: 105).
Hemicordulia africana **n. sp.** Holotype ♂ and paratype ♀ with labels: printed "Van Someren, Katera Forest. Masaka Uganda, Oct.-Nov.1953" and printed "V.G.L. van Someren Collection. Brit. Mus. 1959-468." (BMNH) [examined].

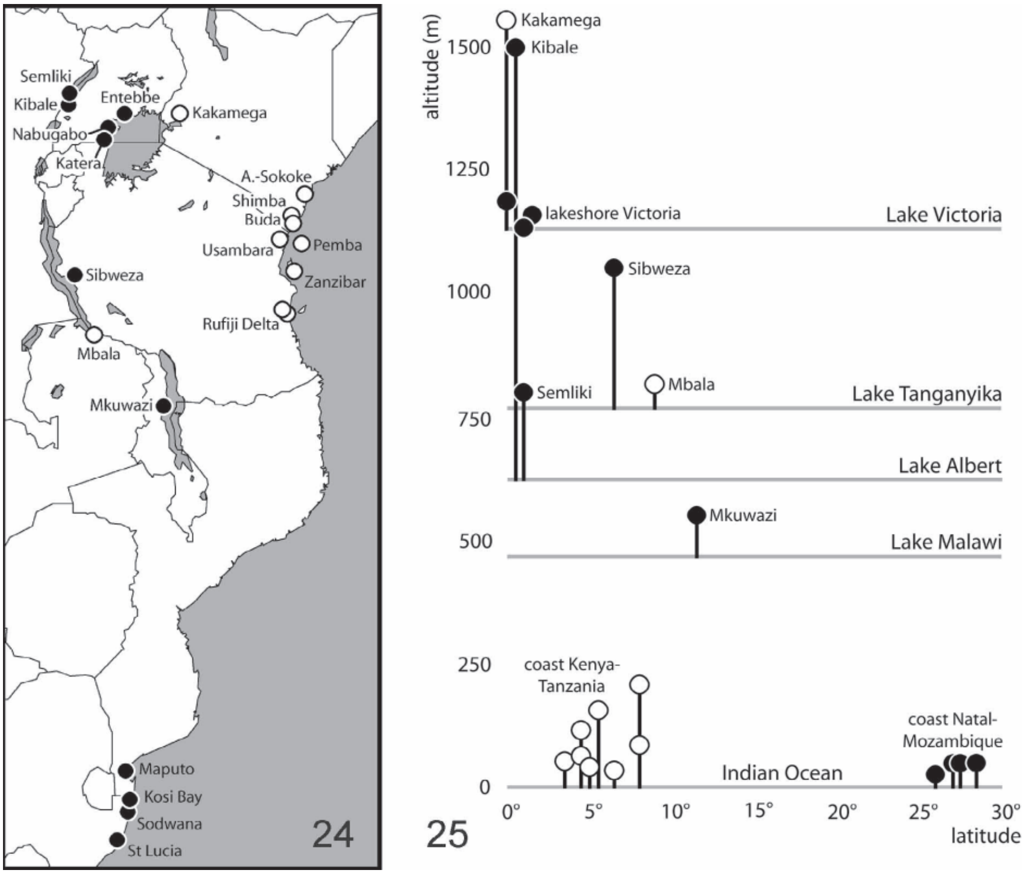
Further material: MALAWI: 1 ♂, Nkhata Bay, Mkuwazi Forest, 6.v.1966, E. Pinhey (NMBZ). – MOZAMBIQUE: 1 ♀, blue, handwritten "Delagoa B. [= Maputo]", printed and handwritten by Martin "Collection Selys, Hemicordulia similis Rb., Révision Martin 1906 Hemicordulia similis Rb. [but not listed by Martin (1907).]" (ISNB). – SOUTH AFRICA (KwaZulu-Natal): 1 ♂, Lake St Lucia, pools near small river, *Barringtonia* trees, 24.xi.1995, G. Carchini; 1 ♀, Sodwana, small forest stream, 20.x.1996, G. Whiteley & J. Bannatyne; 1 ♀, Sodwana, stream in *Barringtonia* forest, 21.xi.1996, G. Whiteley; 1 ♀ (perching high up on twig among trees, 100 m from water), Sodwana, near Lake Ngoboseleni, 9.ii.1997, M.J. Samways; 1 ♂ (hawking up and down roadside in forest), Cape Vidal, 10.ii.1997, M.J. Samways; 4 ♂ (hawking among trees and open bush next to forest), 1 ♀ (perching in shade, forest edge), Kosi Bay (26°57'S 32°49'E), among trees and bush, 45 m a.s.l., 16.xii.2000, M.J. Samways (SUEC). – TANZANIA: 1 ♂, Sibweza, 35 mi., Mpanda-Karema Rd., 1050 m a.s.l., 5.xi.1966, J. Kielland (RMNH). – UGANDA: 1 ♂ (label states: "Hemicordulia asiatica Selys F.C. Fraser det. 1953), Entebbe, 17.v.1952, E.C.G. Pinhey (BMNH); 1 ♂, Entebbe, v.1952, E.C.G. Pinhey (NMKE); 2 ♂ (label states: "Hemicordulia ?asiatica or sp.n. det. Miss C. Longfield"), Entebbe, x.1952, E.C.G. Pinhey (BMNH); 4 ♂, Entebbe, x.1952, E.C.G. Pinhey (NMKE); 6 ♂, 2 ♀, Katera Forest, Masaka, x–xi.1953, V.G.L. van Someren (BMNH); 7 ♂, 1 ♀, Katera, xi.1953, T.H.E. Jackson (NMKE); 1 ♂, Zika, 28.iii.1962, P.S. Corbet (BMNH); 1 ♀, Lake Nabugabo, 4.v.1999, V. Clausnitzer (Coll. V. Clausnitzer); 1 ♂, 1 ♀, Kibale National Park, Kanyawara, Makerere University Biological Field Station (0°35'N 30°20'E), open area, 1500 m a.s.l., 8–30.v.2001, R.H.A. van Grunsven (RMNH); 1 ♂, Semliki Game Reserve, 16.i.2002, C. Williams (ZMMU).

Diagnosis. Smallest species, with very extensively yellow wing bases in females (see *H. similis*).

Description. Holotype male. Measurements (mm): entire length: 44.5, abdomen length (without appendages): 29.5, Fw length: 29, Hw length: 28, Fw Pt: 1.7. Labium pale beige. Mandibles, genae, labrum, clypeus and broad area on lower frons pale brownish yellow. Dorsum of frons metallic green-blue, contrasting weakly with visible yellow on antefrons in dorsal view; vertex with weaker metallic lustre. Occipital triangle and occiput brown; occiput with paired rounded swellings. Postgenae and antennae black. Labrum, clypeus, frons, vertex and occipital triangle with long bristly black hairs. Labium, genae and occiput with finer whitish hairs. Prothorax dark brown. Synthorax metallic green with weakly contrasting large pale brownish yellow areas on anterior half of mesepisternum and centres of mesepimeron, metepisternum and metepimeron resulting in pattern of metallic bands posterior to humeral and metapleural sutures, both of which are narrower than pale areas between them. Mesokatepisternum, metakatepisternum and synthoracic venter pale brownish yellow, with dark transverse band on posterior poststernum. Synthorax covered with dense pale long hairs, especially long on mesepisternum; shorter, darker and denser hairs on antealar sinus. Legs black save for yellow coxae, trochanters, most of fore femora and a hint at base of mid femora. Keels present on anterior face of apical half of fore tibiae and almost whole length of hind tibiae (just falling short of their bases), but absent on middle tibiae. Venation blackish. Wing membrane clear, very narrowly and faintly yellow at extreme bases. Membranule dark brown, slightly paler at extreme base. Pt dark brown. Venation as for genus. 7 Ax in both Fw, 5 in Hw. 5 Px in Fw, 6–7 in Hw. Fw triangles with single cross-veins, Hw triangle uncrossed. Discoidal field of 2 rows of cells at base. Anal loops of 15 cells. Abdomen black with green-purple gloss, marked with weakly contrasting brownish yellow: tergites S1–3 largely pale but darker dorsally (S1–3) and laterally (S3), S4–8 pale laterally and ventrally, from base to apex on S4–6 sides and almost to apex on S7–8; S9–10 all black.

Sternites blackish brown. Cerci and epiproct slender, black (Fig. 6, 11). Cerci with fairly pointed but blunt tips. Secondary genitalia as in Fig. 1, hamule blackish brown.

Paratype female. Measurements (mm): entire length: 46, abdomen length (without appendages): 32.5, Fw length: 31, Hw length: 30, Fw Pt: 2.0. Larger and paler than holotype. Occiput bears a cluster of short thick brown bristles on each side, besides long pale hairs. Metallic green areas reduced, e.g. broken into two blocks on frons by pale median line, almost no gloss on vertex, and only intense on synthorax behind humeral and metapleural sutures. Fore and mid femora largely pale. All tergites except S9–10 laterally and ventrally yellow. Sternites blackish brown, except on S9–10 paler brown. Basal yellow in wings extensive, to arculus and halfway Ax1–2 in Fw, and arculus and Ax2 in Hw. 7 Ax in both Fw, 5 in Hw. 5 Px in Fw, 7 in Hw. Anal loops of 15–17 cells. Vulvar scale appressed, pale brown, extending over almost half of sternite S9, semi-circular with deep cleft (Fig. 17). Cerci black, long and slender, 2.5x longer than S10.



FIGURES 24–25. Geographic (24) and altitudinal (25) distribution of *H. africana* **n. sp.** relative to large water bodies. Filled circles are known records (present paper), open circles forested localities near large waterbodies that have recently been intensively surveyed by V. Clausnitzer (pers. comm.), except Mbala by Pinhey (1984). Many sites in the region away from large water bodies have also been researched. A line connects each site to the altitude of the nearest large water body.

Variation. Substantial. Pale markings are more extensive in females and younger specimens. Thorax and abdomen largely pale when teneral, but may loose pale markings almost completely when mature; typical mature males have restricted narrow lateral streaks on S5–8 or S6–8. The relative length of the vulvar scale and the shape of its cleft is variable, as in all species (Table 2).

TABLE 2. Comparison of the discussed *Hemicordulia* species. Figures represent averages for continuous measures and sums, and modi for counts (frequencies given), with ranges given in brackets. The extent of the vulvar scale along S9 is measured as the distance from the base of the scale to its tip, divided by the distance from its base to the tip of sternite S9. Relative characters are defined in comparison to *H. africana* **n. sp.** and *H. asiatica* (see Table 1 for details), e.g. the extent of yellow in female wing bases in *H. similis* is intermediate between the extensive state in *H. africana* **n. sp.** and the restricted state in *H. asiatica*.

	H. asiatica	*H. virens*	*H. atrovirens*	*H. similis*	*H. africana*
n (♂ : ♀)	17 : 5	11 : 6	13 : 3	24 : 9	33 : 10
Range	India to Myanmar	Mauritius	Réunion	Madagascar; Mahé	eastern Africa
Hw length (♂)	31.0 (30.0–32.5)	34.0 (32.0–36.0)	35.3 (32.5–37.5)	29.2 (27.5–31.5)	28.7 (27.0–30.0)
Hw length (♀)	33.2 (31.0–34.5)	36.4 (35.5–37.5)	38.5 (38.0–39.0)	31.3 (30.0–32.5)	29.8 (28.0–32.5)
Fw Ax	7 in 65% (7–8)	8 in 72% (7–9)	8 in 69% (7–9)	7 in 82% (6–8)	7 in 88% (7–9)
Fw Px	6 in 67% (5–6)	7 in 63% (6–8)	7 in 66% (6–9)	5 in 71% (5–6)	5 in 81% (5–6)
Paired dark blotches at base of labrum	absent or vague	absent	vague	distinct	absent
Green on frons	extensive	reduced	extensive	extensive	reduced
Extent of yellow in wing bases (♀)	restricted	intermediate	intermediate	restricted to intermediate	extensive
Angle of vulvar scale incision (♀)	35–55°	20–30°	0–15°	30–50°	10–30°
Extent of vulvar scale along S9 (♀)	30–35%	25–35%	25–35%	35–40%	35–45%

Etymology. The species is named for its native continent, after having been mistaken for a species named after Asia for about half a century.

Remarks. It is surprising that Fraser (in Pinhey 1961) did not recognise an African species, as the vulvar scale differs clearly from that of true *H. asiatica*. Pinhey (1985) indicated that his Natal material comprised of "all undersized males". The species is indeed small, although Pinhey did not explain the background of his remark. The continental taxon is very close to the Madagascan *H. similis*, but the slight differences appear stable and warrant specific distinction.

Range and ecology. Probably confined to eastern Africa (Fig. 24). The first records are from Entebbe, where also found recently (Pinhey 1961; Graves 1999). Later found in Malawi and KwaZulu-Natal (Pinhey 1966; 1985). Interestingly, the single Malawian site is also the only inland African locality for *Teinobasis alluaudi* and the only Malawian site for *Gynacantha immaculifrons*, two other suspected trans-oceanic arrivals (Fig. 26). The present records are the first for Mozambique and Tanzania, although Tsuda (2000) did list '*H. asiatica*' for Mozambique, probably because Pinhey (1981) predicted its presence. Lindley (1974) listed *H. asiatica* for the "high forest" of Côte d'Ivoire without providing details. This anomalous record may pertain to *Idomacromia* Karsch. *H. africana* "hawks up and down on the edges of forests or in forest glades, often high in the air" (Pinhey 1961), but its ecology is otherwise unknown. Adults have been observed from October up to February in South Africa and up to May elsewhere.

Discussion

Biogeographic hypothesis

The eastern Afrotropical distribution of *Hemicordulia* and its presence on all the major Indian Ocean islands match a biogeographic scenario with large, trans-oceanic distances covered in flight. Presently, the shortest distance between Indian and insular *Hemicordulia* populations is the 2750 km to the Seychelles. Thence to continental Africa, Madagascar and Mauritius is 1300, 1050 and 1700 km respectively. The distance directly from India to Mauritius is 3800 km; Sumatra is 5000 km away. Summer storms move from east to west, providing a medium for trans-oceanic transport (Fig. 18). Whereas *Hemicordulia* includes well-dispersing species, there is also a tendency to quick speciation of isolated populations, producing closely similar island species. Differences between the studied species are too small for a robust phylogenetic analysis of morphology. However, the morphological diversity of the Papuan-Australian species, and the geographic and morphological proximity of those around the western Indian Ocean suggest an eastern origin of the genus and expansion westwards. Because the four westernmost species form two distinct sister-species pairs they may represent two, rather than one, colonisation events.

Odonate dispersal

Flight is an effective means of dispersal in adult Odonata, and long-range dispersal is frequent and widespread. Numerous observations are consistent with the transportation of dragonflies by wind across water over distances of up to 4000 km (Corbet 1999). Within the genus *Hemicordulia*, Armstrong (1978) inferred that *H. australiae* (Rambur) only colonised New Zealand in the 1930s. The American damselfly *Ischnura hastata* (Say) colonised the volcanic Galapagos Islands (925 km from Ecuador) and the Azores (3100 km from Maine and Bermuda), and has been collected at 300 m altitude with nets fixed to aeroplanes (Cordero Rivera *et al.* 2005). *Ischnura ramburii* (Selys) is not closely related to other American species of the genus, but probably shares a recent ancestor with the abundant Paleotropic *I. senegalensis* (Rambur) (Chippindale *et al.* 1999; Donnelly & Parr 2003; H.J. Dumont pers. comm.). *Anax ephippiger* (Burmeister) has reached French Guiana, Iceland and Japan from Africa and India, and *Anax junius* (Drury) Great Britain, France and eastern Siberia from North America (Haritonov & Malikova 1998; Machet & Duquef 2004; Meurgey 2004; Pellow 1999; Tuxen 1976; Ugai 1996). Belle (1988) treated a Surinam specimen of the African migrant *Tramea basilaris* (Palisot de Beauvois) as an accidental introduction, but prevailing winds make north-eastern South America the most likely place for Afrotropical arrivals in the Neotropics (see *A. ephippiger* above). The scale and effect of long-range odonate dispersal has best been studied in the most cosmopolitan species, *Pantala flavescens* (Fabricius). The well-documented arrival in New Zealand, where it probably cannot breed, indicated that over 2000 km of ocean were crossed with speeds of 18–50 km/hr (Corbet 1979). Observations of migratory swarms across the Chinese Bohai Sea indicated similar speeds and a flight height of up to 1000 m, but usually 200–500 m (Feng *et al.* 2006). *P. flavescens* is the only odonate to reach Easter Island, 1900 km from the Pitcairn Islands and 3600 km from Chile. Individuals in this population are darker, robuster, more asymmetrical, shorter-winged and have a weaker flight than continental populations, probably under extreme ecological and genetic stress (Dumont & Verschuren 1991; Moore 1993; Samways & Osborn 1998). The (partial) loss of flight in oceanic insects, whose ancestors are typically highly dispersive representatives of their group, is a paradoxical but recurrent feature of their evolution (Gillespie & Roderick 2002).

Timing and means of dispersal

The age of western Indian Ocean colonisations by alate terrestrial fauna may be inferred from the history of the occupied islands and prevailing weather patterns, and by phylogenies of groups with similar distributions calibrated by such events. *Platycnemis* species could only reach the Comoros airborne after these were created by volcanism at most 8 million years (Ma) ago (Dijkstra *et al.* 2007). Mauritius is about 8 Ma old, Réunion 2 Ma and Rodrigues 1.5 Ma (Austin *et al.* 2004; Shapiro *et al.* 2002). Estimates that *Psittacula* arrived on Mauritius 0.7–2.0 Ma ago and *Pteropus* colonised the western Indian Ocean in the last 1.5 Ma conform with these ages (Groombridge *et al.* 2004; O'Brien & Hayden 2004). Thomassen (2005) estimated that Indian Ocean *Collocalia* separated from a Sundaic ancestor 1.43–1.50 Ma ago, with the split between the Seychelles and Mascarene species at 0.50–0.65 Ma. Indian Ocean sunbirds represent two separate colonisation events from Africa to Madagascar and the Comoros in the past 3.9 Ma, while the Seychelles were only reached 1–2 Ma and Aldabra 125 thousand years (ka) ago (Warren *et al*. 2003). In contrast, Shapiro *et al*. (2002) estimated that the flightless dodo of Mauritius and solitaire of Rodrigues separated 18–36 Ma ago, having diverged from an Australasian ancestor 32–56 Ma ago, supporting the suspected presence of dry land here in the late Oligocene. Present-day prevailing winds across the Indian Ocean blow westwards towards Madagascar. However, the island probably only moved into the belt of easterly trade winds in the Paleocene, becoming warmer and wetter, and lying fully in it by the early Oligocene, around 30 Ma ago. The current monsoon system, which seems especially suitable to transport airborne propagules across from Asia, only emerged in the last 8 Ma (Wells 2003). Flight speed estimates for *Pantala flavescens* imply that a windborne odonate can cover the distance between India and the Seychelles within two to six days, and with a suitable weather-system in place, dispersal may be ongoing. Considering this and the apparently limited morphological divergence between the species discussed, a long-term explanation for their distribution seems unnecessary (see de Queiroz 2005). The significant number of well-dispersing Oriental and Afrotropical species on the Seychelles, suggests frequent and contemporary long-range dispersal of Odonata across the Indian Ocean in two directions (Blackman & Pinhey 1967).

Alternative hypotheses

Hemicordulia could have been present in Africa, Madagascar, Seychelles and India before Gondwanaland fractured and later colonised the Mascarenes, or colonised Africa through south-western Asia, expanding later to Madagascar, the Seychelles and Mascarenes. The latter scenario incorporates Dumont's (1980) hypothesis of an overland route through the Middle East and along the Nile Valley before the present extent of aridity in the intervening regions. The additional evolutionary time (tens of millions of years) and space that these scenarios provide, predict a greater divergence of taxa, i.e. more different and more species. Within Odonata, for instance, morphologically distinct groups of *Zygonyx* occur in Africa, Madagascar, Seychelles and Asia, suggesting the first scenario, and Chlorocyphidae has great generic diversity in Asia and great species diversity in Africa but is absent on Madagascar and the Indian Ocean islands, conforming with the second. Neither scenario conforms with the emphasis of *Hemicordulia* occurrence on the Indian Ocean seaboard and both, especially the second, still require substantial trans-oceanic dispersal. Considering the morphological diversity of Indian Ocean *Pteropus*, Bergmans (1997) concluded that a trans-oceanic scenario implied multiple colonisations from various, sometimes very distant, sources. He preferred an overland scenario, relating the current absence on the mainland to extinction. This is difficult to accept for a predominantly insular genus (86% of species occurs on islands) with a possibly very recent western history (O'Brien & Hayden 2004). Bergmans accepted that trans-oceanic dispersal takes place, referring to records of vagrancy, but found the scale and frequency unacceptable. That argument is arbitrary and in reality dispersal is probably an extensive phenomenon.

Trans-oceanic species on the continent

The assumption that islands contribute little to continental biotas, including contributions to mainland Africa from Madagascar and the Indian Ocean islands, remains relatively untested (Gillespie & Roderick 2002; Zakharov *et al*. 2004). Island species may be at a competitive disadvantage on the continent, just as they are when islands are colonised by continental species. Competitive exclusion by already present *Zosterops* white-eyes may, for instance, explain the mysterious absence of *Nectarinia* sunbirds in the Mascarenes (Warren *et al*. 2003). However, the widespread Paleotropical lime swallowtails (*Papilio*) probably originated in Madagascar, possibly after the arrival of an ancestor from Asia (Zakharov *et al*. 2004). Some satyrine and acraeine butterflies may also have colonised Africa from Madagascar, as have chameleons and certain rodents (Jansa *et al*. 1999; Raxworthy *et al*. 2002; Torres *et al*. 2001).

Although many records of suspected trans-oceanic Odonata on the mainland are coastal, most species are also known well inland (Fig. 26). Their continental distribution cannot be attributed to research intensity, as large parts of Kenya, Malawi and Zambia (for instance) are well-studied, although some coastal regions remain unsampled. Especially surveys of Mozambique and southern Tanzania may improve the resolution of observed patterns. Because occupied island habitats are also seldom coastal in nature, the distribution of *Hemicordulia* and also *Teinobasis* (see Introduction) raises the question how they colonised islands but remained so localised on the mainland. *H. asiatica* and *H. atrovirens*, for instance, favour higher elevations and the apparent correlation between altitude and latitude in *H. africana* suggests that its absence on the equatorial coast is linked to higher ambient temperatures there (Fig. 25). All *H. africana* records are within 50 km of large water bodies, thus the inland localities are 'insular' in having 'sea' and 'habitat' in close proximity (Fig. 25). However, their elevation above some lakes excludes the possible importance of large water bodies as breeding habitats, which are more likely forest streams (Fig. 25).

FIGURE 26. Distribution of suspected trans-oceanic Afrotropical Odonata (see Introduction). Black bottom-left quarter of circle: *Hemicordulia africana* **n. sp.**; bottom-right: *Platycnemis* species of Madagascan radiation; top-left: *Gynacantha immaculifrons*; top-right: *Teinobasis alluaudi*; enlarged circles: presence of these species or close relatives on Madagascar and the islands just east of the map's border, the Mascarenes (M) and Seychelles (S).

Recent climatic fluctuations especially affected local convectional rainfall near the great lakes (Fjeldså & Lovett 1997; Lovett 1993). The levels of Lakes Malawi and Tanganyika were lowered by 250–500 and 600 m before 25 ka ago and were also lowered about 12 ka ago (Scholz & Rosendahl 1988). Lake Victoria is only between 30 and 400 ka old and was largely dry about 14–17 ka ago (Griffiths 1993; Lovett 1993). Lake-generated rainfall may have remained erratic throughout the Holocene (Stager 2001), with high lake levels in Africa 7–10 ka ago (Diamond & Hamilton 1980). There was little or no lowland forest in Uganda before 12 ka ago, and its spread since was not as an advancing front, but by the wide dissemination of efficient dispersers and gradual coalescence of forest patches (Hamilton *et al*. 2001). The persistence of a diversity gradient here (marked eastwards impoverishment) shows that there is a long lag-period in the adjustment of forest ecosystems to a new equilibrium after a major climatic event (Hamilton 1981). Diamond & Hamilton (1980) argued that "competitive exclusion often prevents establishment by long-distance wanderers" and that it "is likely to be least important in new, [...] vacant areas of a particular habitat type, such as might be created by the spread of a vegetation type as a result of climatic change" and also "species that are at present restricted to montane forest may formerly have occurred also at lower altitudes and been forced to higher elevations as the lowlands were gradually colonized by species better adapted to lowland conditions".

The confinement of *Hemicordulia* to relatively unstable habitats would explain its distribution, including its absence on the equatorial coast. This is one of the climatologically most stable areas on the continent, in contrast to the coast further south that lies in Madagascar's rainshadow (Lovett 1993). White (1981; 1993) noted that montane plants with isolated lowland populations are often readily-dispersing pioneers (e.g. by birds or wind) that occupy rather specialised habitats (spray zones, poor soils) where competition with lowland species is reduced. *Hemicordulia* may indeed be a good disperser, but a poor competitor, as suggested by Couteyen (2006) for *H. atrovirens*. This could explain both the genus's insular distribution, where competition is reduced in impoverished faunas, as its continental distribution in areas where suitable habitat is comparatively recent and therefore impoverished (lakeshores, highlands). The competitive position of *Hemicordulia* may be related to thermoregulation. Holarctic Corduliidae are generally relatively cold-tolerant, but sensitive to overheating (Wildermuth 2006; A. Martens in litt.). Although the physiological limitations of tropical corduliids are largely unknown, the studied *Hemicordulia* species do prefer shaded habitats, often at greater elevations, and are active at cooler times of the day. The presence of trans-oceanic species on the continent may generally be a 'peripheral' phenomenon. Dijkstra *et al*. (2007) argued that reduced habitat availability during recent dry spells could have largely exterminated *Platycnemis* and *Teinobasis* damselflies in eastern Africa, where both genera are respresented by a single species. However, the *Platycnemis* species is confined to an island (Pemba) and the *Teinobasis* species to two islands (Pemba, Zanzibar) and other sites near sea or lake level, which are susceptible to frequent disturbances like submersion. Perhaps their survival depends on the persistence of suitable habitat in areas with reduced competition.

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chapter 5

Two new relict *Syncordulia* species (Odonata: Corduliidae) found during museum and field studies of threatened dragonflies in the Cape Floristic Region

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Two new relict *Syncordulia* species found during museum and field studies of threatened dragonflies in the Cape Floristic Region (Odonata: Corduliidae)

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Abstract

Red List assessments often require the verification of records and taxonomy in museum collections and the field. Such research during an assessment of threatened dragonflies in the Cape Floristic Region (CFR) biodiversity hotspot, led to the discovery of two new narrow-range endemic *Syncordulia* species, bringing the known total to four in the genus. The new species, *Syncordulia legator* and *S. serendipator*, are described with emphasis on their identification, ecology and biogeography. Morphological diversity within the genus and the absence of obvious close relatives suggest an ancient and isolated presence in the CFR, emphasizing the uniqueness and conservation importance of the region's endemic odonate fauna.

Key words: Anisoptera, *Syncordulia*, South Africa, conservation, systematics, biogeography, key

Introduction

The Cape Floristic Region (CFR) in South Africa is a globally-significant biodiversity hotspot (Myers *et al*. 2000). It is home to a substantial number of localized, specialist and threatened dragonfly species (Samways 1999; 2006; Grant & Samways 2007; Samways & Grant 2007). Taxonomic verification is a first step towards their conservation. This study relates to the phylogenetically significant dragonfly genus *Syncordulia* (Corduliidae), which is almost entirely endemic to the CFR. Corduliids, as traditionally defined, but excluding macromiines, are much more poorly represented in Africa than in the Holarctic, Neotropics and Australasia. The family may be a paraphyletic assemblage of groups basal to Libellulidae (e.g. May 1995), which is the dominant anisopteran family in Africa today (Kalkman *et al*. 2007). Corduliids were first discovered in the Cape region by Barnard, who described the adults (1933) and larvae (1937) of the new genus *Presba* with the species *P. piscator* and *P. venator*. Lieftinck (1961) found that *P. piscator* was a synonym for *Syncordulia gracilis*, whose origin had remained unknown for over twelve decades. *Presba* thus fell into synonymy with the genus *Syncordulia*, which Selys-Longchamps (1882) had erected for the species described by Burmeister (1839). Because *Syncordulia* species are localized and scarce, collected specimens and even sight records are few. Recent investigations in collections and the field doubled the number of known species in the genus from two to four.

Method and material

Research on *Syncordulia* was intensified in early 2006 as part of a Red List assessment of South African Odonata (see Samways 2004; 2006). In February 2006, the first examinations of Elliot Pinhey's collections in NMBZ were conducted since his work on the fauna (1951; 1984; 1985). We also reviewed material in BMNH, CUMZ, RMNH, SAMC, SUEC and TMSA, and undertook intensive field assessments. We then collated species records in an MS Access (Kaufeld 2003) database and mapped the species using ArcGIS 3.2a (ESRI 1997).

Abbreviations

Ax: antenodal cross-veins, Ax1: first antenodal (counted from base) etc., Cux: cubital cross-veins, Fw: forewing(s), Hw: hindwing(s), Pt: pterostigma, Px: postnodal cross-veins, S1: first abdominal segment, S2–3: second and third abdominal segments etc.

Acronyms for collections

BMNH: Natural History Museum, London; CUMZ: Museum of Zoology of Cambridge University, Cambridge (UK); MCZ: Museum of Comparative Zoology of Harvard University, Cambridge (USA); NMBZ: Natural History Museum of Zimbabwe, Bulawayo; RMNH: Nationaal Natuurhistorisch Museum Naturalis, Leiden; SAMC: South African Museum, Cape Town; SUEC: Stellenbosch University Entomology Collection, Stellenbosch; TMSA: Transvaal Museum, Pretoria.

Results

Of ten NMBZ specimens studied in February 2006 labelled as *S. venator*, three were correctly identified, while six pertained to a new *Syncordulia* species. These six were collected by the lepidopterist Neville Duke in 1975 and 1977 during his attempt to rediscover another elusive Cape endemic, *Orthetrum rubens* Barnard, which has not been recorded since (Pinhey 1979; Samways 2006). The tenth, a female, could not be ascribed to any known species. Similar females and matching males, pertaining to a second new species, were discovered the following month during field assessments. Single overlooked specimens of the first new species were also found in SAMC and SUEC, as well as a pair in the RMNH, which had been presented as paratypes of *S. venator* by Barnard. This new species was rediscovered in the field in October 2006.

Systematic part

Syncordulia Selys — 'Presbas'

Gomphomacromia (*Syncordulia*) Selys, 1882: clxviii [type species: *Epophthalmia gracilis* Burmeister, 1839; by monotypy].
Syncordulia Selys, 1882 – Kirby (1890: 52).
Presba Barnard, 1933: 167 [type species: *Presba venator* Barnard, 1933; by original designation]; junior synonym – Lieftinck (1961: 410).

Etymology. The etymology of *Presba* was never specified, but probably derives from the Greek *presbys* (elder). Meaning honoured or august, it conveys the distinct and ancient character of the genus. Barnard (1933) honoured two friends, an angler and a hunter (of insects), with the names *piscator* and *venator*. In keeping with this, it seems appropriate to honour 'the gatherer'. We propose *legator* to highlight the legacy of collectors like Pinhey and Duke, who assembled most material of the species by that name. As was the case for the fourth species, most new species are chance discoveries: *serendipator* is derived from ‘The Three Princes of Serendip’. Horace Walpole coined the word serendipity to describe how the fairy-tale’s heroes “were always making discoveries, by accidents and sagacity, of things which they were not in quest of” (Winstanley 1984). The names acknowledge the importance of collections and renewed surveys and emphasize that voucher specimens play an important role in conservation biology. The form *presba* is feminine, and therefore does not match well with Barnard’s names, which are masculine nouns (H. Fliedner in litt.). However, because Barnard did not specify the etymology and gender of *Presba*, and because we regard the names as nouns in apposition, we do not amend them, placing nomenclatory stability and uniformity above a possible imbalance of gender.

Diagnosis. The only corduliid genus in the region, where its venation is unique: (1) Fw with 7–10 Ax and 5–8 Px; (2) sectors of arculus not fused; (3) Fw with one, Hw with two Cux; (4) triangles, subtriangles and supratriangles in all wings uncrossed (save occasional exceptions); (5) Fw discoidal field of single cell-row at base; (6) Hw arculus distinctly proximal of triangle; (7) anal loop bow-shaped, with 6–11 cells in males and 9–14 in females. A notable feature of all species is that the eyes are bluish grey, whereas they are typically bright green in Corduliidae (including Macromiinae).

Key to *Syncordulia* species

Unique characters of each morphological type in the genus are asterisked: *gracilis, serendipator* and *legator–venator*. These are potential autapomorphies of the groups (see Discussion).

1 Synthorax with dark-bordered cream stripes posterior to humeral and metapleural sutures*. Costa pale, contrasting with dark Pt*. Dorsal carina of S2–9 pale* (Fig. 1). ♂: Abdomen slender, thickest (indistinctly in dorsal view) at S4–6* (Fig. 1). Cerci only bent toward each other at tips*; epiproct almost as long as cerci, with a pair of small dorsal teeth at about midlength (sometimes lost) and an apical knob* (Fig. 5). ♀: Vulvar scale with inconspicuous appressed and incurved lateral lobes* (Fig. 13)...................... *gracilis*

\- Synthorax rather more uniform, at most darker on sutures. Costa dark, like Pt. Dorsal carina of S2–9 (largely) black (Figs 2–4). ♂: Abdomen club-shaped, thickest (in dorsal and lateral view) at S7–8 (Figs 2–4). Cerci bent toward each other at about midlength, obscuring epiproct in dorsal view; epiproct less than three-quarters as long as cerci, apex without knob but hooked (Figs 10–12). ♀: Vulvar scale with prominent, often finger- or petal-like, lateral lobes (Figs 14–16)... 2

2 Pale markings on S3–8 concentrated apically on segments (Fig. 4). ♂: Cerci stout, less than 3x as long as S10, robustly angled ventrally near base and laterally near apex*; epiproct bifurcate* (Fig. 12). S1 ventrally without spikes; hamules massive* (Fig. 8). ♀: Lobes of vulvar scale less than half as long as the distance between their bases (Fig. 16)..*serendipator* **n. sp.**

\- Pale markings on S3–8 concentrated basally on segments (Figs 2–3). ♂: Cerci slender, over 3x as long as S10, at most weakly angled ventrally near midlength and laterally near base*; epiproct triangular (Figs 10–11). S1 ventrally with pair of spikes*; hamules small (Figs 6–7). ♀: Lobes of vulvar scale over half as long as the distance between their bases* (Figs 14–15) 3

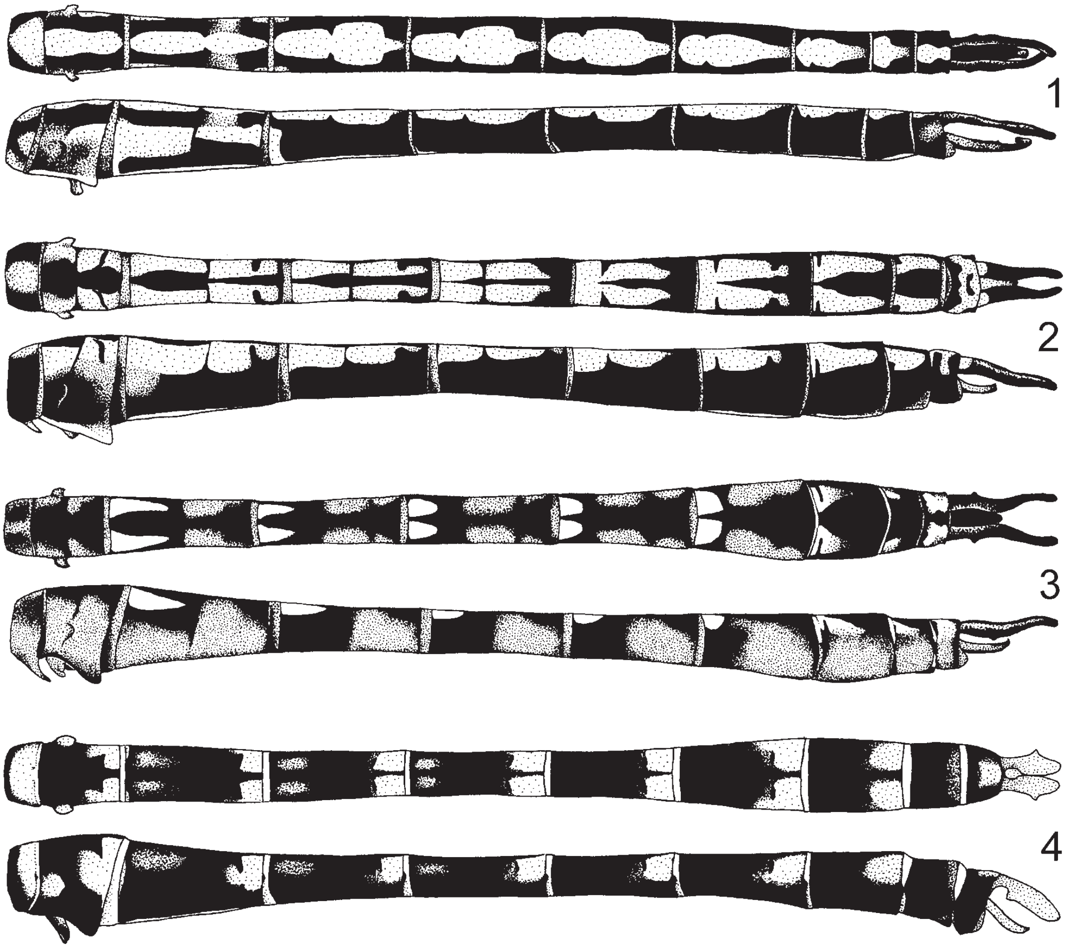
3 Small dorsal plate at base of each costa is pale, contrasting with dark surroundings. S3–10 brown-yellow, with contrasting narrow black line over dorsal carina and broadly black sides (Fig. 2). Sum of Fw Ax and Px equals 24–28. ♂: Cerci not angled laterally; epiproct just under half as long as cerci (Fig. 10). Ventral spikes on S1, border of genital fossa and genital lobe pale, contrasting with dark surroundings; spikes short (Fig. 6). ♀: Lobes of vulvar scale narrow and finger-like; cerci about 2x as long as S10 (Fig. 14) ....*legator* **n. sp.**

\- Costal plates dark, like surroundings. S3–10 deep red-brown grading into black at base and along dorsal carina; basal black enclosing pairs of contrasting whitish triangular spots (Fig. 3). Sum of Fw Ax and Px equals 28–35. ♂: Cerci angled laterally near base; epiproct half as long as cerci or slightly longer (Fig. 11). Ventral spikes on S1, border of genital fossa and genital lobe dark, like surroundings; spikes long (Fig. 7). ♀: Lobes of vulvar scale broad and petal-like; cerci about as long as S10 (Fig. 15) ....*venator*

Syncordulia gracilis (Burmeister) — 'Yellow Presba'

Figs 1, 5, 9, 13, 17–18.

Epophthalmia gracilis Burmeister, 1839: 847. Holotype ♂: origin unknown (MCZ) [not examined, but diagnosed in detail by Lieftinck (1961: 414)].
Oxygastra gracilis (Burmeister, 1839) – Selys-Longchamps (1871: 307 bulletin, 73 reprint).
Gomphomacromia (*Syncordulia*) *gracilis* (Burmeister, 1839) – Selys-Longchamps (1882: clxviii).
Syncordulia gracilis (Burmeister, 1839) – Kirby (1890: 52).
Presba piscator Barnard, 1933: 168. Lectotype ♂ (designated by Kimmins 1968: 299): Cape Province, Groot Drakenstein, xii.1931, A.C. Harrison (BMNH) [examined]; junior synonym – Lieftinck (1961: 410).
Chlorosoma gracilis (Burmeister, 1839) – Anonymous, in litt. in Lieftinck (1961: 414).



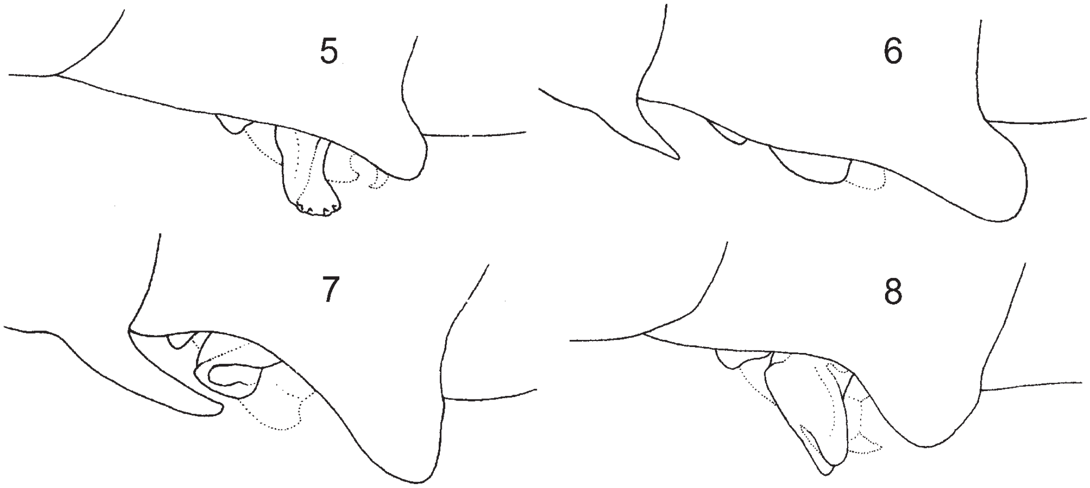
FIGURES 1–4. *Syncordulia* male abdomen in dorsal (above) and lateral (below) view. (1) *S. gracilis*; (2) *S. legator* **n. sp.**; (3) *S. venator*; (4) *S. serendipator* **n. sp.**

Further material: 1 ♂, Natal, Cat[h]kin Peak, 5.x.1948, Dr. H.A. Newton (NMBZ); 1 ♀, Cape Province, Ouderbosch [= Oubos], near Rivier Zonderend [= Riviersonderend], 15.xii.1968, C.G.C. Dickson (NMBZ); 1 ♀, Cape Province, Matroosberg, 16.xii.1975, Neville Duke (NMBZ); 5 ♂, 3 ♀, Bain's Kloof, N. of Stellenbosch, 1–6.xii.1987, D.A.L. Davies (CUMZ); 1 ♂, Du Toit's Kloof, N. of Stellenbosch, 1.xii.1987, D.A.L. Davies (RMNH); 1 ♂, Western Cape, Bontebok National Park, rest camp at Breede River, 9.xi.1997, D. Paulson (Coll. D. Paulson); 1 ♀, Eastern Cape, Prentjiesberg, Mooirivier, 10.xi.2000, M.J. Samways and R. Kinvig (SUEC); 7 ♂, Kogelberg Nature Reserve, Oudeboschrivier, 18.xi.2000, M.J. Samways (SUEC); 1 ♀, Kogelberg Nature Reserve, hawking over fynbos, date unknown, P.B.C. Grant (Coll. M. May).

Observations: 1 ♂, Kogelberg Nature Reserve, Palmiet River, 16.xi.2000, M.J. Samways; 1 ♀, Kogelberg Nature Reserve, Oudeboschrivier, 2.i.2002, M.J. Samways.

Unverified records: larval exuviae (cannot be identified to species), Ceres, iii.1922, K.H. Barnard (Barnard 1937; not found in SAMC); larval exuviae (cannot be identified to species), Bain's Kloof, Wellington Mts, Breede River side, v.1933, K.H. Barnard (Barnard 1937; SAMC).

Range and ecology. This species has a greater extent of occurrence than other *Syncordulia* (Fig. 17), but the area of occupancy is relatively small. In the Western Cape it is restricted to the south-western mountains, but is fairly widespread there (Fig. 18), while single locations in the Eastern Cape and KwaZulu-Natal are the only ones of the genus outside the Western Cape. This disjunct distribution suggests that the species's area of occupancy was once much greater. Details of adult activity in the Western Cape are given by Samways & Grant (2007), with the first individuals appearing in October, a peak in November and December, and rapid decline in January. At least in the Western Cape, *S. gracilis* is distinctly a fynbos species, associated with small, rapid, stony-bottomed streams and rivers. In the Eastern Cape, it is known from streams with solid rocky bottoms. Adults typically remain away from water, hawking over low bushes.



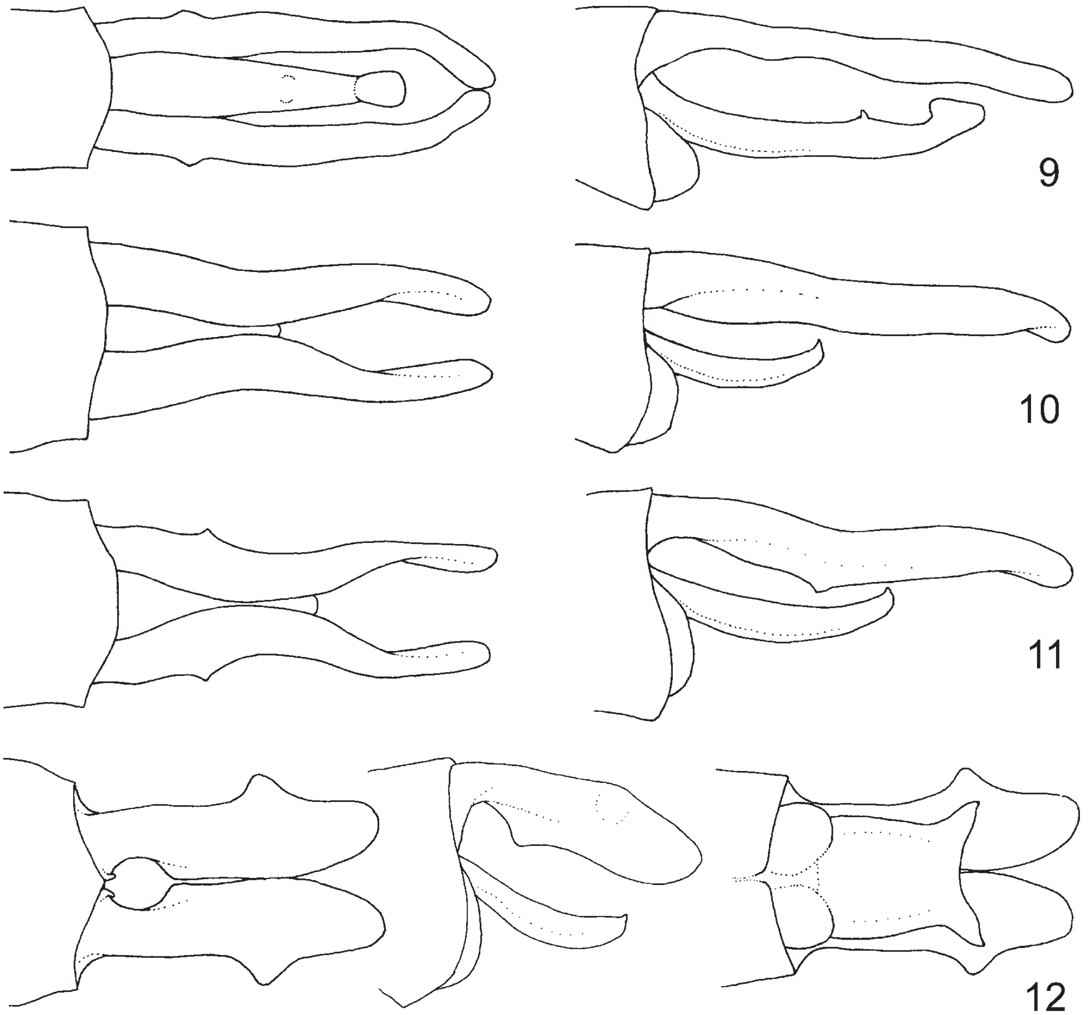
FIGURES 5–8. *Syncordulia* male secondary genitalia in lateral view. The penis is indicated by dotted lines, as its position is variable. (5) *S. gracilis*; (6) *S. legator* **n. sp.**; (7) *S. venator*; (8) *S. serendipator* **n. sp.**

Syncordulia legator n. sp. — 'Gilded Presba'

Figs 2, 6, 10, 14, 19.

Type material: Holotype ♂, paratype ♀, Cape Province, Fransc[h]hoek Pass, 20.xi.1975, Neville Duke (NMBZ).

Further material: 1 ♂, 1 ♀ (paratypes *venator*), Cape Province, French Hoek [= Franschhoek], 8.x.1933, K.H. Barnard (RMNH); 1 ♂ Hott[entots] Holl[and] Mts, Steenbras, xi.1932, K.H. Barnard (SAMC); 1 ♂, W. Cape Province, Clanwilliam, 17.ix.1977, Neville Duke (NMBZ); 2 ♂, 1 ♀, Cape Prov., Hawekwasberg [= Hawequas Mts], Du Toit's Kloof, 5.xi.1977, Neville Duke (NMBZ); 1 ♀, SW Cape, upper reaches of the Palmiet River (19°25'E 34°34'S), 20.xii.1992, leg. unknown (SUEC); 3 ♀ Western Cape Province, Franschhoek Pass, lower Du Toit's River, 18.x.2006, M.J. Samways and J.P. Simaika (SUEC).



FIGURES 9–12. *Syncordulia* male appendages in dorsal (left), lateral (right) and ventral (*S. serendipator* **n. sp.** only) view. (9) *S. gracilis*; (10) *S. legator* **n. sp.**; (11) *S. venator*; (12) *S. serendipator* **n. sp.**

Description. Holotype male. Measurements (mm): total length: 49.4, abdomen length (excluding appendages): 34.7, Fw length: 32.3, Hw length: 30.9, Fw Pt: 3.0. Head brownish yellow, darkened at base of labrum, centres of postclypeus and antefrons, dorsum of vertex and lateral corners of occipital triangle; postgenae with two smudged dark bars near excision of eye margin. Anterior and dorsal surfaces of head covered with dense black hairs, posterior surfaces with longer but equally dense pale hairs. Thorax glossy dark brown, broadly but indistinctly black on humeral, metapleural and ventral part of interpleural sutures; middorsal carina contrasting pale brown-yellow. Thorax densely covered with pale long hairs, especially long on mesepisternum. Legs black, pale keels present on anterior face of slightly more than apical half of fore and middle tibiae, and just over three-quarters of hind tibiae. Venation and Pt blackish, more basal Ax brown. In contrast, dorsal sclerites at base of costa of all four wings (the ‘intermediary’ or ‘distal costal’ plates) pale yellow. Wings clear, very faintly smoky towards tips. Membranule pale grey, slightly darker on outer-posterior border. Venation typical of genus. 8 Ax in both Fw, 5 in Hw; 6 Px in Fw, 7 in Hw; anal loops of 7 cells. Abdomen slightly clubbed, brown-yellow, marked with black as in Fig. 2, ventral border of tergites narrowly pale yellow (broadest on border of genital fossa), contrasting with black sides. Sternites black. Appendages black, save yellow spot at base of cerci, shaped as in Fig. 10; in lateral view, cerci straighter and epiproct shorter than in *S. venator* (epiproct 40–47% as long as cerci vs 50–56%). Secondary genitalia as in Fig. 6. Hamules deeply folded longitudinally, their borders concealed behind border of genital fossa. Anterior half of hamule black, posterior half pale yellow. Ventral borders of tergite of S1 posteriorly drawn out into elongate processes: this pair of ventral spikes reaching about 20% of distance from base of S2 to tip of genital lobe (about 40% in *S. venator*). Profile of genital fossa (lateral view) straighter than in *S. venator*.

Paratype female. Measurements (mm): total length: 48.9, abdomen length (excluding appendages): 35.5, Fw length: 33.5, Hw length: 32.0, Fw Pt: 3.0. Heavier than holotype with straight-sided abdomen, but coloration similar. All wings lightly but distinctly yellow in subcostal and cubital spaces, approximately to Ax2 and Cux1, and faintly smoky anteriorly from base to tip. 8 Ax in both Fw, 5 in Hw; 6 Px in Fw, 7–8 in Hw; anal loops of 11 cells. Vulvar scale appressed, black, as in Fig. 14 with distinct finger-like lateral extensions. Cerci black, slender with pointed tips, about twice as long as S10 and paraprocts (clearly longer than in *S. venator*).

Variation. Coloration rather consistent, but may be darker than in Fig. 2 and wings are tinged deeper in younger specimens. Size variation is considerable, as in *S. venator*. Males (n = 5): abdomen length (excluding appendages): 31.1–34.7 mm, Hw 27.4–32.5 mm, Fw 7–8 Ax and 5–7 Px, anal loop of 6–9 cells. Females (n = 5): abdomen length (excluding appendages): 32.0–35.7 mm, Hw 31.6–33.2 mm, Fw 7–8 Ax and 5–6 Px, anal loop of 10–11 cells.

Range and ecology. This species has been recorded from the Cederberg and the Hawequas and Hottentots-Holland Mountains (Fig. 19). It is associated with tree-lined streams with distinct deposition zone pools. It flies swiftly up and down streams, over boulders and pools, and over fynbos. It has been recorded from September, earlier than any other *Syncordulia*, to December.

Syncordulia venator (Barnard) — ‘Mahogany Presba’

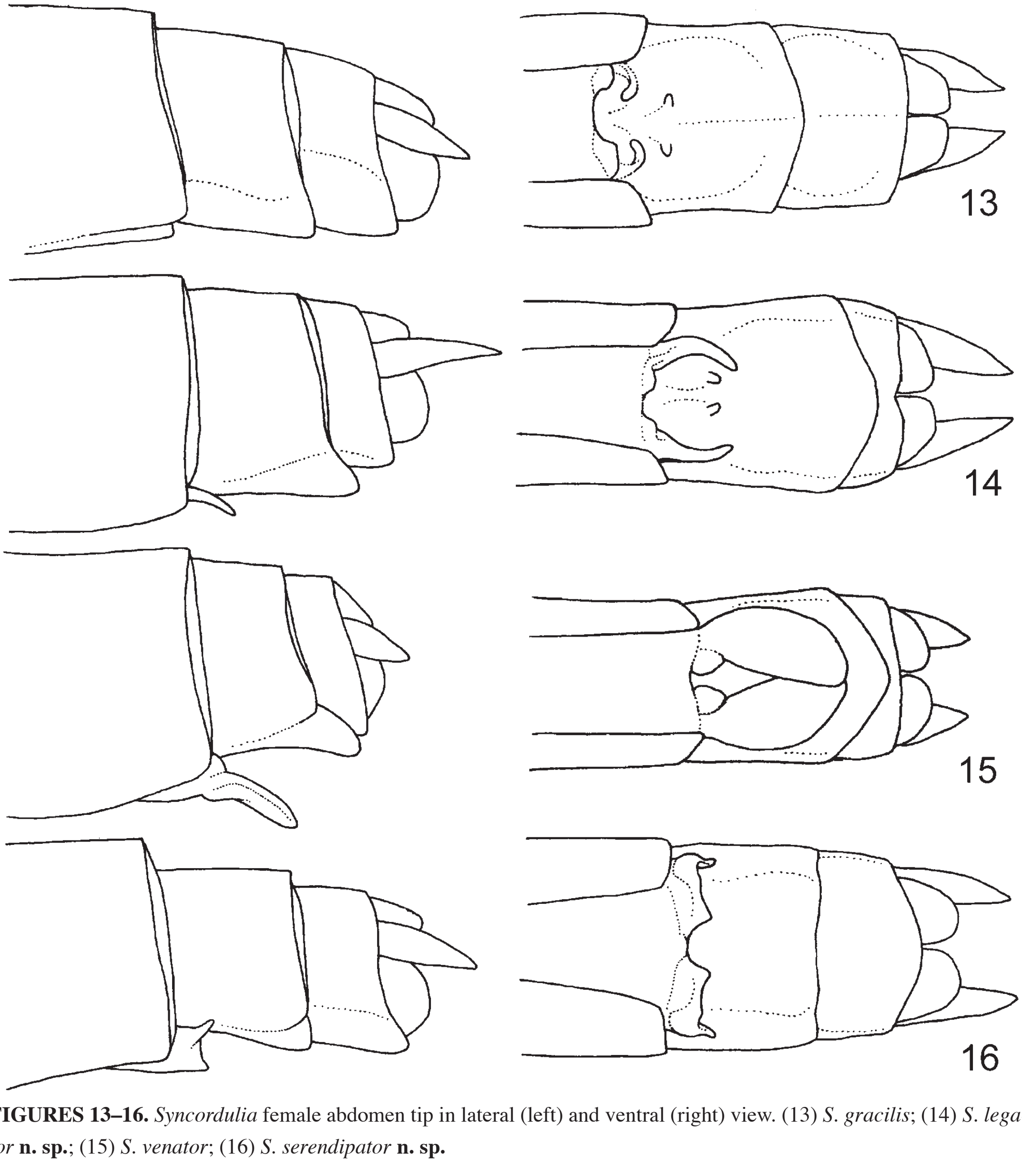
Figs 3, 7, 11, 15, 20.

Presba venator Barnard, 1933: 167. Lectotype ♂ (designated by Kimmins 1968: 301): Cape Province, French Hoek [= Franschhoek], xii.1932, K.H. Barnard (BMNH) [examined].
Syncordulia venator (Barnard, 1933) – Lieftinck (1961: 415).

Further type material: Paratype ♀ (‘allotype’), Cape Province, French Hoek, xii.1932, K.H. Barnard (BMNH); paratype ♂, Hott[entots] Holl[and] Mts, East side, 4000 ft, i.1933, K.H. Barnard (BMNH).

Further material: 1 ♂ Hott[entots] Holl[and] Mts, East side, 4000 ft, xi.1932, K.H. Barnard (SAMC); 1 ♀ Hott[entots] Holl[and] Mts, East side, 4000 ft, i.1933, K.H. Barnard (SAMC); 1♂, 2 ♀ Cape Province, French Hoek, xii.1932, K.H. Barnard; 3 ♂, 1 ♀ Cape, Table Mt, Orange Kloof, i.1933, H.G. Wood (SAMC); 1 ♂, Cape, Bain’s Kloof, Wellington Mts, Witte River, i.1934, H.G. Wood (SAMC); 1 ♂, Cape, Table Mt, Orange Kloof, 7.i.1934, K.H. Barnard (BMNH); 1 ♂, Cape, Table Mt, Orange Kloof, 7.i.1934, leg. unknown (NMBZ); 1 ♀, Cape Province, Ladismith, Garcia’s Pass Forestry, 15.xi.1940, G. van Son (TMSA); 1 ♂, George, Jonkersberg, 18.xi.1940, G. van Son (TMSA); 1 ♀, Cape, Bain’s Kloof, Wit River, xii.1949, Museum Staff (SAMC); 2 ♀, Cape Province, Knysna, Kruis Valley, N. of Buffelsnek Forest, 22.i.1971, Cottrell (NMBZ); 3 ♂, Robinson Pass, N. of Mosselbaai, 9–13.xii.1987, D.A.L. Davies (CUMZ); 1 ♂, ♀, Du Toit’s

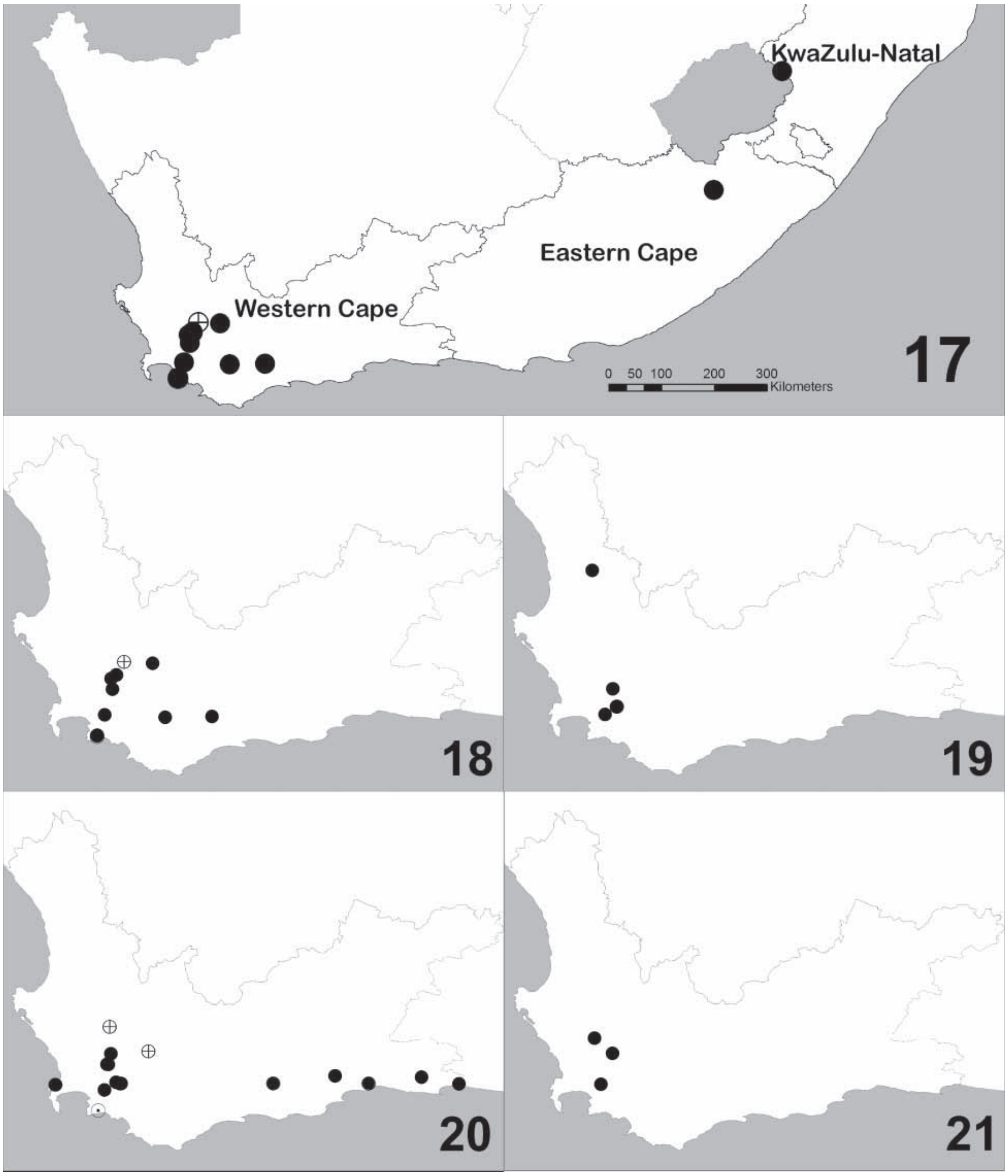
Kloof, 13.xii.1996, M.J. Samways (SUEC); 1 ♂, Villiersdorp, 15.xii.1996, M.J. Samways (SUEC); 1 ♀, Du Toit's Kloof, 9.xi.1999, M.J. Samways (SUEC); 1 ♀, Villiersdorp, 11.xi.1999, M.J. Samways (SUEC); 1 ♀ (teneral), Table Mountain, 22.xi.2005, J.P. Simaika, M.J. Samways & T.R. New (SUEC); 1 ♂, border of Western and Eastern Cape, Bloukrans River at crossing of R102, broad rocky river in forested gorge, 30.i.2006, K.-D.B. Dijkstra (RMNH); 1 ♂, Western Cape, Table Mountain, gorge above Hely Hutchinson Dam, rocky stream in fynbos, 22.ii.2006, K.-D.B. Dijkstra (RMNH); 1 ♀, Western Cape, Limietberg Nature Reserve, Du Toit's Kloof, Kromrivier, 12.xi.2006, M. Samways, M.J. Samways, J.P. Simaika & J. Ott (SUEC); 1 ♂, 1 ♀, Limietberg Nature Reserve, Bain's Kloof, Witte River, 14.xi.2006, J.P. Simaika & J. Ott (SUEC); 2 ♂, Western Cape, Villiersdorp Wild Flower Garden and Nature Reserve, 16.xi.2006, A.A. Johnson, J.P. Simaika & J. Ott (SUEC); 1 ♂, without data (SAMC).



FIGURES 13–16. *Syncordulia* female abdomen tip in lateral (left) and ventral (right) view. (13) *S. gracilis*; (14) *S. legator* **n. sp.**; (15) *S. venator*; (16) *S. serendipator* **n. sp.**

Observations: 1 ♂, Western Cape, Kogelberg Nature Reserve, 15.xii.2003, M.J. Samways.

Unverified records: larval exuviae (cannot be identified to species), Keerom[s]berg, Worcester, i.1930, K.H. Barnard (Barnard 1937; not found in SAMC); larval exuviae (cannot be identified to species), Great Winterhoek Mountains, Tulbagh, i.1934, K.H. Barnard and H.G. Wood (Barnard 1937; not found in SAMC).



FIGURES 17–21. Geographical distribution of *Syncordulia* species in South Africa (17) and the Western Cape (18–21). Legend: solid circles: verified records; dotted circles: observations; crossed circles: unverified records. (17–18) *S. gracilis*; (19) *S. legator* **n. sp.**; (20) *S. venator*; (21) *S. serendipator* **n. sp.**

Range and ecology. This species, although localized, is widely distributed throughout the mountains of the Western Cape (Fig. 20). It occurs with the three other species in the mountains of the south-western Western Cape, but it is the only *Syncordulia* known from Table Mt and in a string of sites along the Langeberg range, east to the Eastern Cape border. It is associated with fast-flowing streams with large boulders and deposition pools, bordered by bushes or trees. It is mainly a summer species, with records from early November to late February.

Syncordulia serendipator n. sp.—'Rustic Presba'

Figs 4, 8, 12, 16, 21.

Type material: Holotype ♂, paratype ♀ (in copula with holotype), paratype ♀ (ovipositing), Western Cape, Witrivier, Bain's Kloof, 17.iii.2006, J.P. Simaika and M.J. Samways (SUEC).

Further material: 1 ♀, Cape Province, Riebeeck Kasteel [= Riebeek-Kasteel] Mtn, 9.iii.1971, C.G.C. Dickson (NMBZ); 1 ♂, Jonkershoek Nature Reserve, Stellenbosch, 19.iii.2006, J.P. Simaika (SUEC); 1m#, Bain's Kloof, 18.ii.2007, M.J. Samways, M. Samways and J.P. Simaika (SUEC).

Description. Holotype male. Measurements (mm): total length: 51.6; abdomen length (excluding appendages): 34.8; Fw length: 34.0; Hw length: 31.4; Fw Pt: 2.9. Head, including postgenae, warm brown-yellow throughout, with two small dark spots on central postclypeus and black margins posteriorly along eyes. Labium cream, with brown smudges along inner borders of central and lateral lobes. Anterior surfaces (up to vertex) of head covered with dense black hairs, posterior (up to occipital triangle) surfaces with finer and longer pale hairs. Thorax glossy brownish black, with paler areas concentrated on central and dorsal portions of thoracic plates: middorsal carina and antealar sinuses are warm brown-yellow, as is a band across the mesepisterna adjacent to (and of similar width as) sinuses; most of the central mesepimeron, dorsal corner of metepisternum and posterior half of metepimeron. Thorax densely covered in long whitish hairs. Legs black, femora dorsally warm brown-yellow. Pale tibial keels present on anterior face of just under apical half of fore and middle tibiae, and just over three-quarters of hind tibiae. Venation and Pt black, except for pale brown subnode and basal antenodal cross-veins. Base of costa and adjacent plate dorsally pale brown, marked with black. Wings clear, very faintly yellow at base. Membranule grey. Venation typical of genus. 9 Ax in both Fw, 7 in Hw; 7–8 Px in Fw, 8 in Hw; anal loop of 9 cells. Abdomen club-shaped, black, S1–8 with warm brown-yellow paired dorso-apical markings as shown in Fig. 4, S9 unmarked and S10 with small dorso-subapical spot. Basal halves of S3–5 dorsally blackish brown with centres grading to paler brown. Sternites brown-black. Auricles and intersegmental rings brown-yellow. Tergites covered with fine whitish hairs, longest on undersides of S1–2 and S8. Appendages (Fig. 12) robust, epiproct two-thirds as long as cerci; cerci stout and dark brown, becoming paler grey-brown towards tips. Cercus bearing two blunt teeth: one ventral and subbasal, the other lateral and subapical. Epiproct broad, warm brown-yellow, shallowly and widely incised posteriorly, separating into two diverging tips that each bear a single black tooth at apex. Secondary genitalia as in Fig. 8. Hamules massive, leaf-shaped, folded longitudinally, with black-brown exterior and cream interior. Ventral borders of tergite of S1 not drawn out to form a pair of spikes.

Paratype female. Measurements (mm): total length: 50.0, abdomen length (excluding appendages): 35.5, Fw length: 34.2, Hw length: 33.3, Fw Pt: 2.7. More robust than holotype and pale areas more extensive but darker in tone (thus less distinct). Anterior face of frons darker and dark spots on postclypeus larger. Centres of most thoracic plates broadly pale, with black stripes along sutures and beside middorsal carina. Venation darker than in holotype; all wings lightly but distinctly yellow at base, approximately to arculus. 9–10 Ax in both Fw, 7 in Hw; 8 Px in Fw, 8–9 in Hw; anal loops of 9 cells. Abdomen thicker than in holotype, not clubbed, S9–10 relatively longer than in other *Syncordulia* females (Fig. 16). Abdominal pattern as in male, but pale markings more extensive (extending about to midpoint of each segment), also present on S9, and enclosing pairs of small black transverse hyphens near segment's apex and dorsal carina on S2–8 (connected to black dorsal carina on S2–4), approximately in middle of each pale area. These dashes are obscured by the greater extent of black in the holotype. Vulvar scale appressed, black with narrow brown-yellow border with wide medial incision and short (less than a third of lateral length of S9) lateral extensions (Fig. 16). Cerci black, pointed but with blunt tips, about 1.3x as long as S10 and paraprocts.

Variation. Females may have strongly reduced dark markings, e.g. no spots on postclypeus and abdomen dorsally largely pale brown, although broadly black laterally. The Riebeek-Kasteel female has the thorax pale with only dark lines over the sutures; its abdomen is only narrowly black along the dorsal carina and transverse subbasal sutures of S2–8; the dorsum of S9–10 and the cerci are pale. Males (n = 2): abdomen length (excluding appendages): 34.5–34.8mm, Hw length: 31.4–32.4mm, Fw 9 Ax and 7–8 Px, anal loops of 8–9 cells. Females (n = 2): abdomen length (excluding appendages): 35.5–36.7 mm, Hw length: 33.3–33.7 mm, Fw 8–10 Ax and 6–7 Px, anal loops of 9–10 cells.

Range and ecology. This species is only known from three separate localities, in different mountain ranges in the CFR (Fig. 21). Probably owing to habitat specialization, it has a very small area of occupancy. It is a powerful flier, patrolling deposition pools of streams strewn with large boulders, and virtually treeless. It oviposits in pools by swiftly flying over and dipping its abdomen. On overcast days and late in the afternoon, it may leave the water's edge and fly swiftly over mountain sides even near mountain peaks.

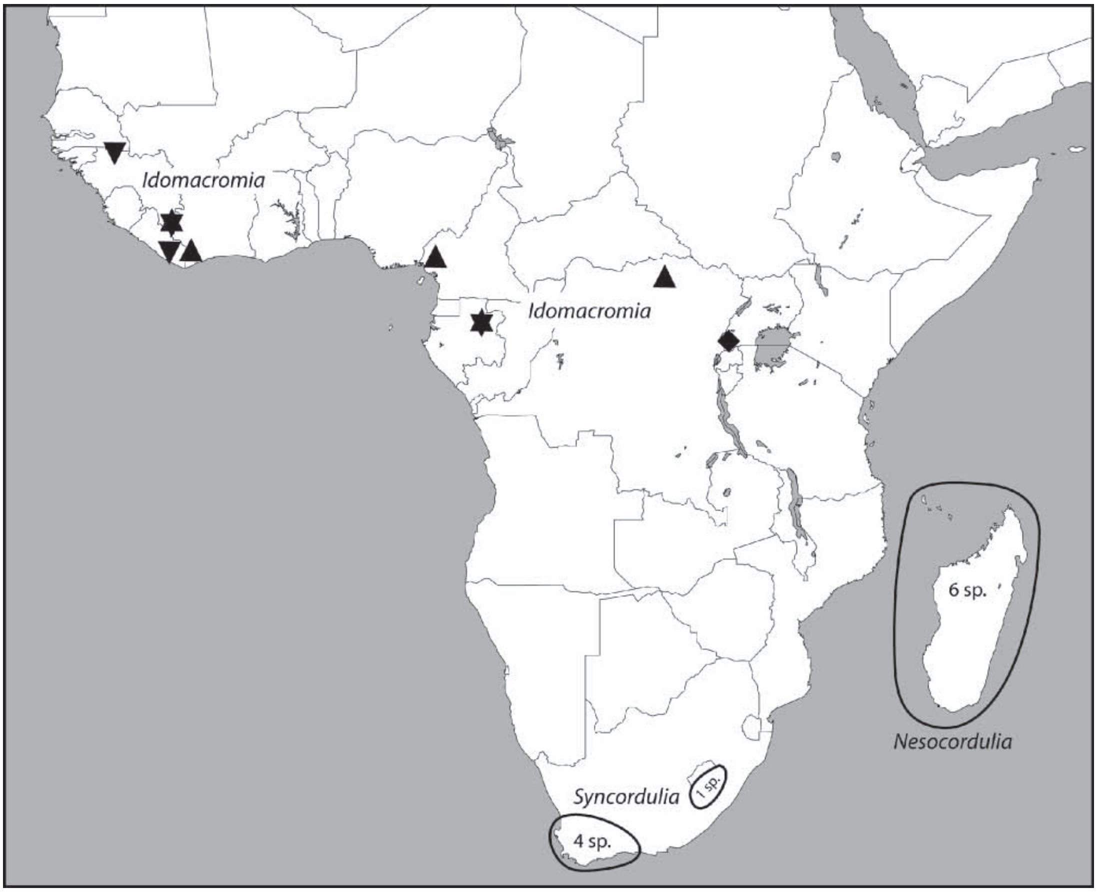


FIGURE 22. Distribution of 'gomphomacromiine' Afrotropical Corduliidae. *Nesocordulia* and *Syncordulia* species are not indicated separately, but the number of species in each region is provided. *Idomacromia* species are separated (diamond: *I. jillianae* Dijkstra & Kisakye; inverted triangle: *I. lieftincki* Legrand; standing triangle: *I. proavita* Karsch; star: both *I. lieftincki* and *I. proavita*).

Discussion

Relationships

Selys-Longchamps (1882) first described *Syncordulia* as a subgenus of *Gomphomacromia* and Fraser (1957) defined the Gomphomacromiinae to include it. The subfamily is largely founded on plesiomorphic characters of venation, and like the Corduliidae is probably para- or polyphyletic. However, other similarities suggest that the relatives of *Syncordulia* are within this assemblage of relict 'corduliids'. Three genera with 14 species are found in the Neotropics, as well as the monotypic genus *Oxygastra* in the western Mediterranean and six *Nesocordulia* species in Madagascar and the Comoros (Carvalho *et al*. 2004; Legrand 1984b; May 1992; von Ellenrieder & Garrison 2005). The group is richest in Australia (8 genera, 15 species) and it is not surprising that *S. gracilis* was first thought to be Australian (Carle 1995; Lieftinck 1961; Theischinger & Watson 1978; Watson 1980). Lieftinck (1961) believed the Mediterranean *Oxygastra* or alternatively an Australian genus (*Hesperocordulia*, *Lathrocordulia* or *Micromidia*) to be closest to *Syncordulia*.

Fleck & Legrand (2006) considered the Madagascan genus *Nesocordulia* nearest the equatorial African *Idomacromia*, but did not compare *Syncordulia* despite its geographic proximity (Fig. 22). Fraser (1957: 109) created the monogeneric Idomacromiinae, but because "the majority of the characters are Gomphomac[r]omi[i]ne and I am of opinion that it is a highly specialized off-shoot of this subfamily" effectively placed it within Gomphomacromiinae. These three Afrotropical genera share a similar penial structure (Legrand 1984a; own observations) with *Oxygastra* and the neotropical *Neocordulia*, two genera that are likely to be each other's sister group (cf. Fleck & Legrand 2006). The Australian *Micromidia* (and to some degree *Austrophya* and *Hesperocordulia*) shares the remarkable spikes of S1 with two *Syncordulia* species. Although the secondary genitalia may provide reliable clues on relationships, these similarities too may be plesiomorphic. As each 'corduliid' genus is defined by a confusing mix of apo- and plesiomorphies, molecular analysis may elucidate relationships. Unfortunately this has not yet clarified the position of *Syncordulia* (pers. comm. H. Karube and M. May). The nearest relatives of the other relict odonate group in South Africa, two genera of synlestid damselflies, are possibly also Australian (Brinck 1955; Dijkstra & Clausnitzer 2006), but this is wholly speculative.

Morphologically, *Syncordulia* falls into three distinct groups: (1) *S. gracilis* (*Syncordulia* s.s.); (2) *S. legator* and *S. venator* (*Presba*); and (3) *S. serendipator* (see key for autapomorphies). The remarkable morphological diversity might warrant the reinstatement of *Presba* and the creation of a third genus. Venation, by which odonate genera were traditionally defined, within *Syncordulia* is uniform. Such characters are often homoplasious and plesiomorphic and therefore of relatively little value (see Dijkstra & Vick 2006 for a discussion): the venation of *Syncordulia* is for instance similar to the Australian genera *Austrocordulia* and *Lathrocordulia*. Sexual characters may define 'gomphomacromiine' genera more soundly. All Australian genera, for instance, possess marked autapomorphies of the secondary genitalia, often supported by features of the vulvar scale and male appendages. While the three South African groups each possess clear autapomorphies, with morphological diversity within *Syncordulia* appearing almost as great as that between Australian genera, these are not obvious for the three combined. However, nomenclatoral stability favours the current classification, until the depth of difference between these probably ancient species is sufficiently examined.

Biogeography

It is tempting to link the history of *Syncordulia* to that of the fynbos biome which they predominantly inhabit, especially because their centre of occurrence overlaps with the area of greatest plant diversity in the CFR (e.g. Moline & Linder 2006). The Cape is the most remote corner of a continent with a prolonged history of isolation. Until about 30 million years (Ma) ago, South America and Australia were still in contact through Antarctica, from which Africa had completely separated over 100 Ma before (Sanmartín & Ronquist 2004).

Nonetheless the flora had an austral character (e.g. with *Casuarina*, *Araucaria*, Proteaceae) in the Paleocene, and although the present CFR was covered in warm temperate forest, fynbos elements were found in Namaqualand (Coetzee 1993; Morley 2000). Many plant groups typical of the CFR were present by the Eocene (Galley & Linder 2006), but the Cape vegetation remained rather tropical until the upwelling of cold water off the South African coast started to block off summer rainfall about 8–10 Ma ago, establishing the fynbos biome at its current position only 3–5 Ma ago (Coetzee 1993; Goldblatt 1997; Linder & Hardy 2004; Tolley *et al*. 2006). However, Axelrod & Raven (1978) mapped fynbos in Namibia and Botswana 25–30 Ma ago, although it was possibly restricted to mountains about 10–15 Ma ago (Linder & Hardy 2004).

Galley & Linder (2006) found that trans-Indian Ocean relationships, mostly with Australia, dominate the CFR plant radiations. However, the Cape groups were estimated to have diverged between 80 and 37 Ma ago, well after continental links were lost. The phylogeny of basal passerines suggest possibly direct dispersal from Australia to Africa about 45–50 Ma ago along continental fragments including Kerguelen, Crozet and Madagascar, where a temperate climate would have prevailed (Fuchs *et al*. 2006; Jønsson & Fjeldså 2006). The chironomid midges of the genera *Afrochlus* and *Archaeochlus* are considered a classic example of Gondwanan relicts among southern African arthropods (Saether & Ekrem 2003). However, the species may have diverged only in the past 10 Ma; their Australian relatives in *Austrochlus* are about 18 Ma old (Martin *et al*. 2003). While there is no estimate of the divergence of these genera, the data suggest a much less ancient history than assumed by Gondwanan vicariance (>120 Ma). Tolley *et al*. (2006) found the South African endemic radiation of *Bradypodion* chameleons to predate the emergence of fynbos in its present location and considered their dispersal from forest into fynbos as secondary, as some vegetation transitions may be as recent as 10,000 years ago.

Summarizing, existing studies suggest that the CFR biota, including Africa's assumed austral odonates (*Syncordulia* and possibly Synlestidae) may not be of 'Gondwanan' age and have even more recently attained their current habitat and range. *Syncordulia* inhabits cold and nutrient-poor streams, which are almost devoid of more widespread Afrotropical Odonata. The relict midges are similarly cold-stenotherm (Saether & Ekrem 2003). The montane character of their habitat and the absence of strongly competitive species there, suggest that the gomphomacromiines in South Africa are the last vestiges of an older Afro-montane odonate assemblage, surviving in a habitat to which they are better adapted than the more competitive and advancing modern Afrotropical species. The fynbos habitat created recently by the cold upwelling in the Cape Region may be their last refuge from extinction. There are indications that the fynbos flora did not evolve under the summer-dry conditions now prevalent in its centre of diversity (Axelrod & Raven 1978). This may also be true for the CFR odonates, and it would be worthwhile to investigate the role of summer-drought and winter-rain in their ecology.

Ecology and conservation

This study has shown that a detailed examination of threatened species in a biodiversity hotspot can unearth previously unknown species. The validation of historical records, for instance, stimulates a closer look at museum collections (Ponder *et al*. 2001). It was surprising that two new species, which are seemingly large and visible, should be found in what is considered a well-explored area. This is in part due to the superficial similarity of the species, as well as similarities of their biology. The four species are broadly sympatric (Figs 18–21) and could all occur within a single river system. Three species, for instance, were recorded both from Bain's Kloof (only *S. legator* missing) and Du Toit's Kloof (*S. serendipator* missing). In both cases the three were recorded within a 20-year period and the missing species is known from surrounding sites.

Indications of seasonal segregation and different habitat preferences are only preliminary. Our data suggest that *S. gracilis* and *S. legator* adults are mainly on the wing in spring, emerging in October and September respectively, and disappearing by January and December. The season of *S. venator* is concentrated in summer, from November to late February. The recorded earliest and latest dates indicate that simultaneous adult activity of the two most closely related species (*S. legator* and *S. venator*) is only for about a quarter of their combined flight season. Three records of *S. serendipator* are all in March, the only *Syncordulia* adults collected in that month, a fourth in late February. Little is known about their larval ecology (Barnard 1937), but the species may well differ in their preferred microhabitats, for instance in relation to the exposure, size, current and substrate of stream sections.

All species rely on cool, clear and rocky streams in fynbos or lightly wooded landscapes. The threat of invasive alien plants has been pervasive in such habitats in the CFR. As these aliens gradually extended and intensified their hold, they shaded out local populations of rare and sensitive odonate species, including those of the genus *Syncordulia*. However, their populations may now have stabilized through the large scale removal of aliens. The huge national effort to remove these was stimulated by the need to improve hydrology and create jobs, rather than for biodiversity conservation, but has led to the recovery of the odonate assemblage (Samways *et al*. 2005).

Acknowledgements

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chapter 6

The *Atoconeura* problem revisited: taxonomy, phylogeny and biogeography of a dragonfly census in the highlands of Africa (Odonata: Libellulidae)

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This work is not issued for purposes of zoological nomenclature and is not published within the meaning of the International Code of Zoological Nomenclature (1999) (see article 8.2).

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THE *ATOCONEURA* PROBLEM REVISITED: TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF A DRAGONFLY GENUS IN THE HIGHLANDS OF AFRICA (ODONATA, LIBELLULIDAE)

Dijkstra, K.-D. B., 2006. The *Atoconeura* problem revisited: taxonomy, phylogeny and biogeography of a dragonfly genus in the highlands of Africa (Odonata, Libellulidae). – Tijdschrift voor Entomologie 149: 121-144, figs. 1-48, tables 1-2. [ISSN 0040-7496]. Published 1 December 2006.

The genus *Atoconeura* previously comprised two species; one with five subspecies. Principal Component Analysis of 33 characters of 148 specimens and cladistic analysis of 28 characters revealed six discrete taxa, partly with narrowly overlapping ranges. Subspecies *aethiopica*, *kenya* and *pseudeudoxia* of *biordinata* are raised to specific rank; the synonymy of *chirinda* with *biordinata* is confirmed; *A. luxata* sp. n. is described from West Africa. A key to the species is provided and the poorly known behaviour, ecology and biogeography are discussed. The author has not witnessed oviposition; one report suggests that it may be perched, solitary and epiphytic, which is unusual within the family. The species are largely restricted to streams above 1000 m, except *A. luxata* sp. n. that is only known below that altitude, but always at the foot of highlands. Four species demonstrate a distribution pattern recalling a 'ring species' in highlands, circling Lake Victoria and the dry north of Tanzania. The phylogeny suggests an expansion of the genus from the western lowlands to the eastern highlands, or vice versa, followed by an expansion through the Albertine Rift and Eastern Arc Mts to the Kenyan and ultimately Ethiopian highlands. Especially in the case of a western origin there appears to have been a tendency of the species to occur at increasing altitudes in the course of their evolution.

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Key words. – Odonata; Anisoptera; *Atoconeura*; Afro-montane; systematics; keys.

In her paper 'The *Atoconeura* Problem' Longfield (1953) sketched the taxonomic disorder in the genus, caused by considerable variation in the sparse material available. Her solution was the recognition of two species based on epiproct morphology, *A. eudoxia* and *A. biordinata*, the latter with four subspecies differing mainly in markings: *A. b. biordinata* from highlands in Tanzania, Malawi and Katanga; *A. b. chirinda* in Zimbabwe; *A. b. kenya* in Kenya; and *A. b. pseudeudoxia* in W Uganda. Kimmins (1958) added *A. b. aethiopica* from Ethiopia, stating apologetically that 'one might question the wisdom of adding yet another subspecies'. Pinhey (1961a) remarked that 'Longfield has divided this [genus] into two species, but I think *kenya* may eventually prove to be a third species.' Later Pinhey (1982) suggested that 'it is possibly more correct to regard them [the subspecies] all as *biordinata*, with variable forms rather than subspecies'. Bridges (1991) listed *A. kenya* as a good species with the subspecies *A. k. aethiopica*, but made *chirinda* and *pseudeudoxia* synonyms of *A. biordinata.* The problem demands a more objective analysis of variation, as well as the study of new material and characters. This paper presents the outcome of that study, with a revised classification of the taxa and a reassessment of their biogeography.

Methods and material

To validate the views of Longfield (1953) and her contemporaries, the analysis was designed to test how well their characters applied to their classification. Most of Longfield's specimens (BMNH) were restudied, besides new material including West

African *Atoconeura*, which Longfield did not have. Previously used characters were translated to 33 ordered variables, of which 28 were applicable to males and 26 to females (see appendix 1). These were scored for 148 complete specimens (107 males; 41 females), and a portion of them for 15 incomplete specimens (12; 3), including most primary types and specimens from throughout the genus's range. Principal Component Analysis (PCA) of the complete specimens was performed using a correlation matrix (i.e. standardizing all data to a common mean and variance) in PC-ORD4 software (McCune & Mefford 1999). PCA performs excellently in the reduction of morphological data (e.g. Gardner & Mendelson 2004, Malhorta & Thorpe 2004, Tadauchi 1983). The resulting components were correlated with the character variables to establish which variation they describe. Data of incomplete specimens were only used to measure variability of characters within taxa (table 1).

After this analysis, further specimens (details are provided in separate material lists) were studied and additional characters investigated, including details of the penis with scanning electron microscopy (figs. 21-28). Characters used in the PCA were evaluated for use in cladistic analysis of the clusters identified by the PCA. Where necessary character states were simplified or fine-tuned, undiscriminating or uninformative characters (e.g. binary, with one state unique to a single species) were removed, and additional characters were incorporated. 22 'old' characters and six 'new' ones (all ordered and of equal weight) were adopted (see appendix 2 and table 2). Some characters were not scored for the outgroups, because of the absence of obvious putative homologies, especially in the penis. Analysis based on maximum parsimony was carried out using both an exhaustive search and parsimony bootstrap (1000 randomized runs). Both analyses were also performed with unordered characters. All analyses were run with PAUP* 4.0 Beta 10 (Swofford 2002) and three different outgroups: *Olpogastra lugubris* Karsch, 1895, *Malgassophlebia bispina* Fraser, 1958 and *Zygonyx flavicosta* (Sjöstedt, 1900).

Each recognised species was diagnosed and variation assessed. Full descriptions of known taxa were not prepared, those given by Longfield (1953) and Kimmins (1958) being sufficient. Order of species in the text and figures follows the cluster numbers from the PCA and also reflects the phylogenetic results, placing the more basal groups first (see Results).

Acronyms of collections

BMNH	Natural History Museum, formerly British Museum (Natural History) (London, UK)
CGVL	Collection Graham Vick (Little London, UK)
CVCH	Collection Viola Clausnitzer (Halle, Germany)
ISNB	Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)
MNHN	Muséum National d'Histoire Naturelle (Paris, France)
MRAC	Musee Royal de l'Afrique Centrale (Tervuren, Belgium)
MZUF	Museo Zoologico 'La Specola' (Firenze, Italy)
NHRS	Naturhistoriska Riksmuseet (Stockholm, Sweden)
NMBZ	Natural History Museum of Zimbabwe (Bulawayo, Zimbabwe)
RMNH	Nationaal Natuurhistorisch Museum Naturalis, formerly Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands)
UMMZ	University of Michigan Museum of Zoology (Ann Arbor, USA)
ZMHB	Museum für Naturkunde der Humboldt-Universität (Berlin, Germany)

Abbreviations. – Ax: antenodal cross-veins, Ax1: first antenodal (counted from base) etc., Cux: cubital cross-veins, Fw: forewing(s), Hw: hindwing(s), Pt: pterostigma, Px: postnodal cross-veins, S1: first abdominal segment, S2-3: second and third abdominal segments etc.

Results

PCA of complete males resulted in 10 axes accounting for 93.0% of variation. 70.0% of variation was explained by the first three axes: Axis 1 (36.9% of variation) was correlated with variables related to abdomen shape, Ax count, head and thorax markings, and pruinosity. Axis 2 (18.9%) correlated with Px counts, markings of S3-9 and cercus shape, and Axis 3 (14.2%) with markings of S2 and epiproct shape. Plotted against Axis 1 and 2, four clusters were apparent (fig. 1): (1) all West African males, except one from Cameroon; (2) all *eudoxia* and *pseudeudoxia* males including holotypes, plus some Katangan '*biordinata*'; (3) all males from Zimbabwe including the *chirinda* holotype, plus most '*biordinata*' and one male from Cameroon; (4) holotypes of *aethiopica* and *kenya* and all other Ethiopian and Kenyan males, plus singles from Uganda (Ruwenzori) and Tanzania (Mt Meru). Introduction of Axis 3 (fig. 2) divided two clusters further: (2a) all *eudoxia*; (2b) remainder of cluster 2; (4a) non-Ethiopian material in cluster 4; (4b) all Ethiopian material.

PCA of complete females resulted in 10 axes accounting for 91.6% of variation. 60.9% of variation was explained by the first three axes: Axis 1 (32.3% of variation) was correlated with variables related to abdomen shape, Ax and Px counts, head and thorax markings, and shape of vulvar scale. Axis 2 (15.3%) correlated with vertex colour, markings of S3-9, cercus shape and vulvar scale length, and Axis 3 (13.3%) with number of cells in Fw triangle and the colour of the antefrons. Plotting Axis 1 against 2 (fig. 3) and 3 (fig. 4) gave similar clusters as in males: (1) West African females; (2a) all females assigned to *eudoxia*; (2b) females from Uganda ('*pseudeudoxia*') and Katanga; (3) all females from Zimbabwe including the *chirinda* allotype, plus most '*biordinata*' and one from Kenya (Taita Hills); (4a) one Kenyan (*kenya* allotype) and four Tanzanian females (Mts Kilimanjaro and Meru); (4b) two Ethiopian females including the *aethiopica* allotype.

Males in cluster 2 (*eudoxia* and *pseudeudoxia*) shared distinctive setation of the hind femora and poststernum (figs. 14-15), while only 2a (*eudoxia*) had diagnostic abdominal setation. Compared with the third segment, all species have a notably short fourth segment of the penis when deflated (figs. 21-28): a short collar-like hood encloses a complex of smooth and scaly (i.e. covered with numerous, small and overlapping flattened spines) pleats, which are at least partly formed by the apical lobe (terminology follows Miller 1991). A pair of tusk-like cornua emerges from among the pleats in all examined penes, except of cluster 1, where clear sockets mark their position. Representatives of clusters 1, 2, 3 and 4 had differently shaped pleats and cornua, those of 4a (*kenya*) and 4b (*aethiopica*) were essentially similar, as were those of 2a (*eudoxia*) and 2b (*pseudeudoxia*), which are rather close to 3 ('*biordinata*'). These characters are discussed further in the species texts.

All cladistic analyses using ordered characters and *O. lugubris* and *Z. flavicosta* as outgroups produced the same topology (fig. 5), with bootstrap support of all nodes at 87% or higher. With *M. bispina* as outgroup the tree only differed in cluster 1 being the sister group to cluster 2, but bootstrap support of this node was only 49%. Analyses with unordered characters produced similar results, although some search combinations grouped either cluster 1 or 3 with cluster 2, but bootstrap support of these changes was 51% or lower. Fig. 5 reflects the PCA results, with cluster 1 being most basal, followed by clusters 2, 3 and 4; the apomorphies of the nodes are provided in appendix 3.

Discussion

The analysis testing Longfield's characters, specimens and taxa resulted in six discrete clusters of specimens, but some specimens were 'out of place' according to her views (figs. 1-4). Indeed Longfield (1953) observed that 'in the series I have examined, there have always been one or two specimens that did not exactly conform to either group and I prefer to give them only subspecific rank.' That discordance was not caused by imperfect separation of Longfield's subspecies by their characters, but by their geography: the distributions of her taxa *biordinata*, *kenya* and *pseudeudoxia* overlap. Pinhey (1961a) predicted the sympatry of *biordinata* and *kenya* on 'the northerly or westerly foothills of Mount Kilimanjaro or, perhaps, Mount Meru': both indeed occur on Kilimanjaro. *Biordinata* and *pseudeudoxia* overlap in Katanga (fig. 6).

The clusters corresponding with Longfield's taxa not only overlap geographically without intergrading in characters of size and markings, but are also discrete by characters of setation, appendages, penis and poststernum. Therefore I conclude that each cluster represents a good species. Pinhey (1960, 1984) found that the subspecies *chirinda* intergrades with nominotypic *biordinata*, which is confirmed by both PCAs. With all other former subspecies of *A. biordinata* raised to specific rank, I treat *A. aethiopica* equally, although it is close to *A. kenya* and perfectly allopatric. No name is available for cluster 1, which represents a sixth species of *Atoconeura* from western Africa.

Has 'the *Atoconeura* problem' now been solved? The genus comprises of six readily identifiable, broadly (but not entirely) allopatric species. More extensive overlap is suggested by single males of *A. biordinata* from Cameroon, *A. kenya* from W Uganda and the new species from Katanga, but see the discussion in each species account. Considerable geographic sampling gaps may harbour further overlap, but also possible areas of transition or undescribed species.

Taxonomic part

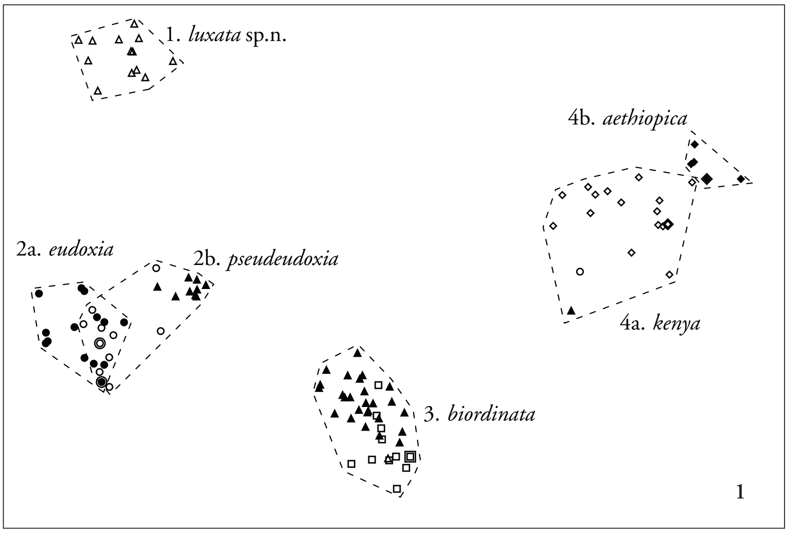
Atoconeura **Karsch**

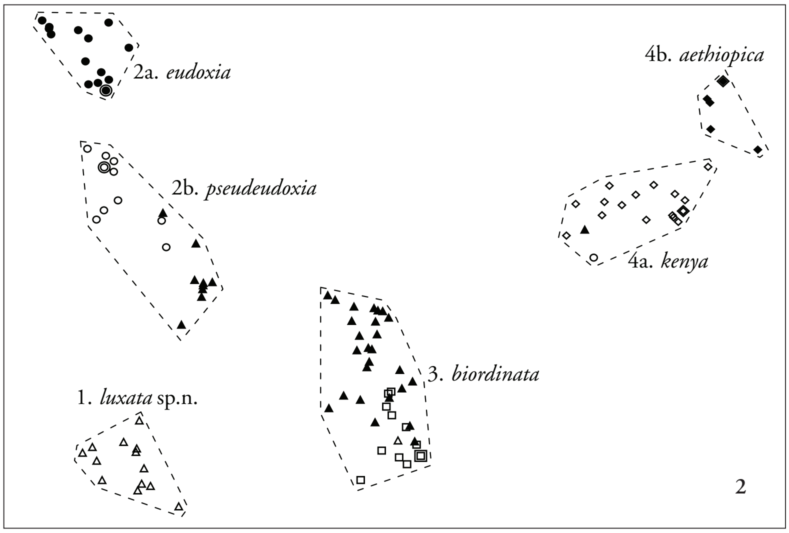
Atoconeura Karsch, 1899: 371. Type species: *Atoconeura biordinata* Karsch, 1899 (by monotypy).

Accaphila Kirby, 1909: 59. Type species: *Accaphila eudoxia* Kirby, 1909 (by monotypy); junior synonym (Ris 1919: 1195).

Diagnosis

Fairly large libellulids (Hw 28-39 mm), predominantly glossy black marked with yellow. When not pruinose, the dorsal yellow spot on S7 is conspicuous (figs. 43-48), a feature seldom seen in African libellulids of similar size and behaviour. The following combination of venation characters is diagnostic in most cases: (1) distal Ax complete; (2) arculus distal of Ax2; (3) Fw discoidal field partly of two rows of cells; (4) Hw with 2 Cux; (5) Rspl subtending single row of cells. The species are best separated





Figs. 1-4. Scatter plots of males (1-2) and females (3-4) along the PCA Axes 1 (horizontal axis; figs. 1-4), 2 (vertical axis; 1, 3) and 3 (vertical axis; 2, 4). The symbols represent the original identification of specimens sensu Longfield, based mainly on range, the indicated clusters represent the revised classification (see Results). Legend. – ♦: specimens assigned to *aethiopica* by range (Ethiopia); ▲: to *biordinata* by range (Tanzania to Malawi and Katanga); □: to *chirinda* by range (Zimbabwe); ●: to *eudoxia* by epiproct or vulvar scale; ◇: to *kenya* by range (Kenya); ○: to *pseudeudoxia* by range (Uganda); △: unassigned specimens from West Africa; framed symbols: holotype.

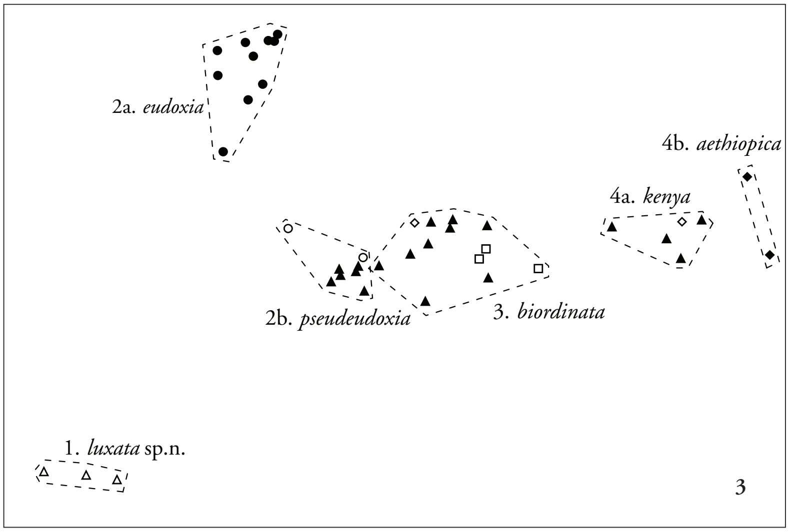
by markings (figs. 8-13, 17-19), male appendages and vulvar scales (figs. 29-42). The external secondary genitalia are remarkably uniform within the genus (fig. 20), but the species differ in the penis (figs. 21-28).

Affinities

Although *Atoconeura* is rather singular among African Libellulidae, Pinhey (1962) placed it close to *Trithemis* Brauer, 1868. The larva of *A. biordinata* shows a general similarity (own observations), but the adult differs by venation, pronotal hindlobe and penis. Preliminary molecular analysis placed the genus close to *Malgassophlebia* Fraser, 1956 and *Olpogastra* Karsch, 1895 (G. Fleck, M. Brenk & B. Misof pers. comm.). These genera are very distinct, but their combination of black-with-yellow coloration and claw-like hamule is shared only with *Atoconeura* in continental Africa. Ris (1912) considered his *Thalassothemis* of Mauritius close to *Atoconeura* and placed the two in the *Trithemis-Zygonyx* group of Libellulidae. The superficial resemblance between *A. luxata* sp. n. and *Z. flavicosta* is especially striking.

Ecology and biogeography

Longfield's (1953) summary still applies well: 'The genus *Atoconeura* inhabits forested regions and swift rivers from between about 4,000 and 9,000 feet



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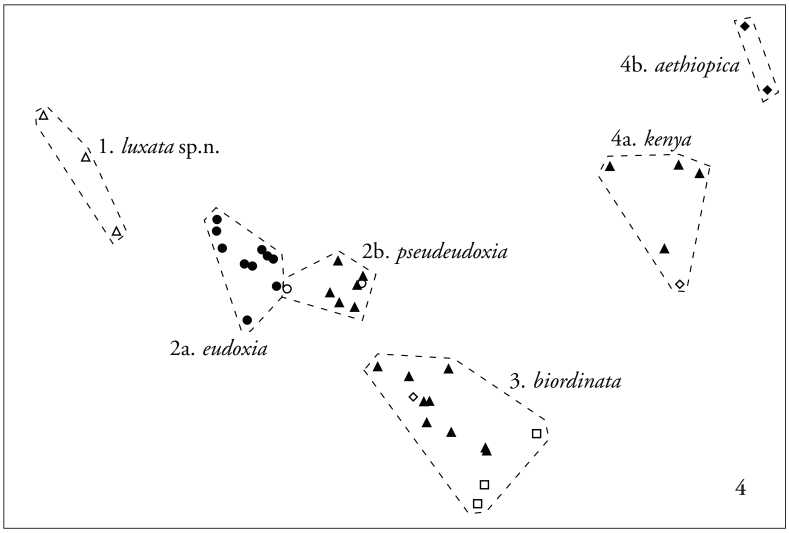

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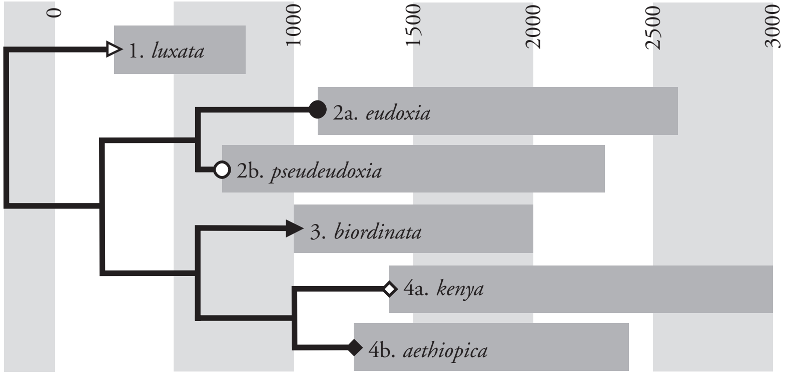


Fig. 5.
Phylogeny of *Atoconeura* species superimposed on their observed altitudinal range (m). PCA cluster numbers and plot/map symbols are provided for correspondence with figs 1-4 and 6. See appendix 3 for apomorphies of nodes.

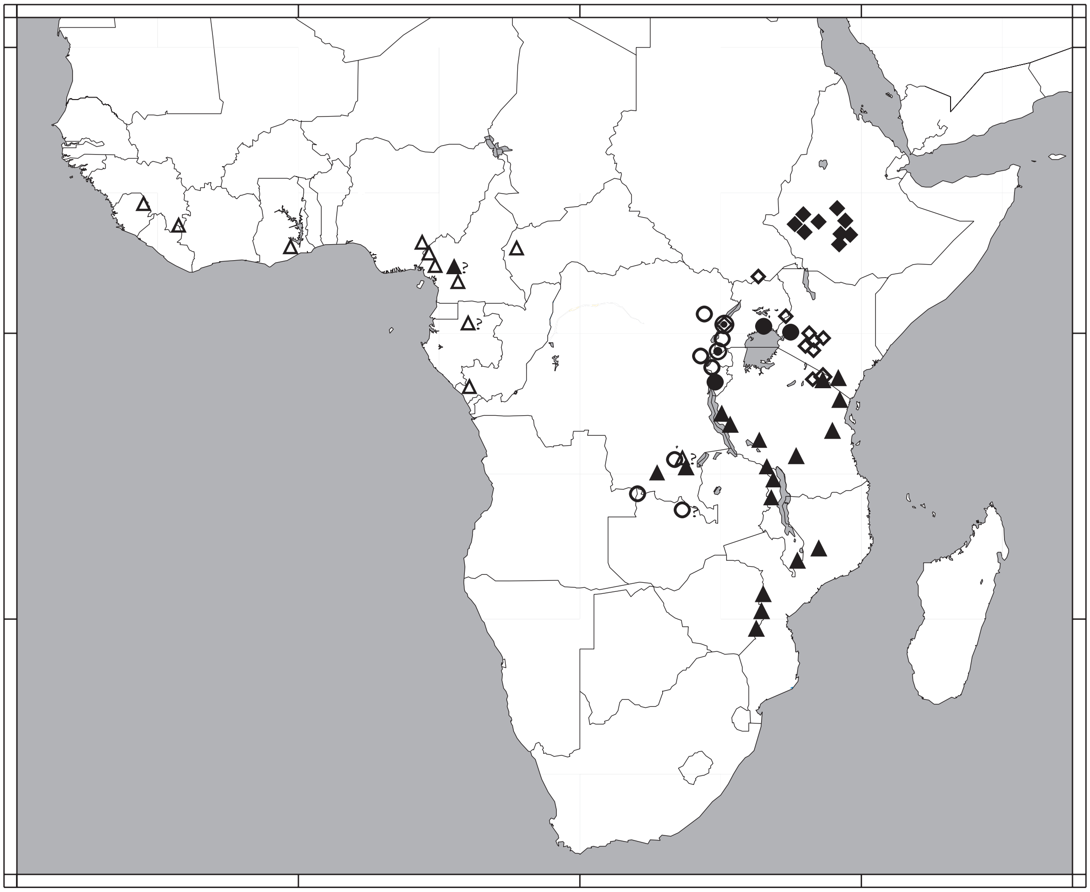


Fig 6 Distribution of *Atoconeura* species, based on records and sources provided in the species accounts. Legend – ♦: *A. aethiopica*; ▲: *A. biordinata*; ●: *A. eudoxia*; ◇: *A. kenya*; △: *A. luxata* sp. n; ○: *A. pseudeudoxia*. Composite symbols indicate overlap of species, records with question marks are discussed in the text of the relevant species.

[1220-2745 m] altitude, and it is obvious that the dragonfly has been isolated for many generations in certain mountain and highland areas.' Pinhey (1961a) added: 'Whereas *biordinata* generally prefers fast running streams, often stony or rocky ones, and is partial to patches of riverine bush as well as forest (except *pseudeudoxia*, a forest insect), *eudoxia* is a forest dweller, inhabiting muddy, rather sluggish streams. It settles on overhanging twigs or on floating debris. However I have found that the *chirinda* race of *biordinata* also favours this sort of life, at Mount Selinda (November 1955).'

Atoconeura species (own observations) mainly inhabit streams between 1000 and 2500 m, and can be dominant above 1500 m: *A. biordinata* is the most common anisopteran on streams on the Mulanje and Namuli plateaus (about 2000 m) of S Malawi and N Mozambique. *A. kenya* probably ventures highest; between 1400 and 3000 m. All records of *A. luxata* sp. n. lie below 1000 m, but are concentrated around highlands (some not higher than 800 m) such as Loma, Nimba and Atewa in the Upper Guinea and Adamawa and Mayumbe in the Lower Guinea. This 'piedmont effect' is also seen in *A. pseudeudoxia*, which occurs at 700 m in the Semliki Valley at the foot of the Ruwenzori Mts. The species may be segregated in elevation in areas of overlap, but data are scarce. In sympatry, *A. eudoxia* and *A. pseudeudoxia* are found at calm and fast-flowing sections of streams respectively. All species occur in forest, but *A. aethiopica*, *A. biordinata* and *A. eudoxia* often enter adjacent open areas.

The genus's association with highlands is reflected by its distribution (fig. 6). Five of the six species occur only in eastern Africa, where the continent's main highlands lie. Four species form an interlocking chain of ranges around the dry plains of NW Tanzania (fig. 6), a pattern mirrored by morphology (figs. 1-4):

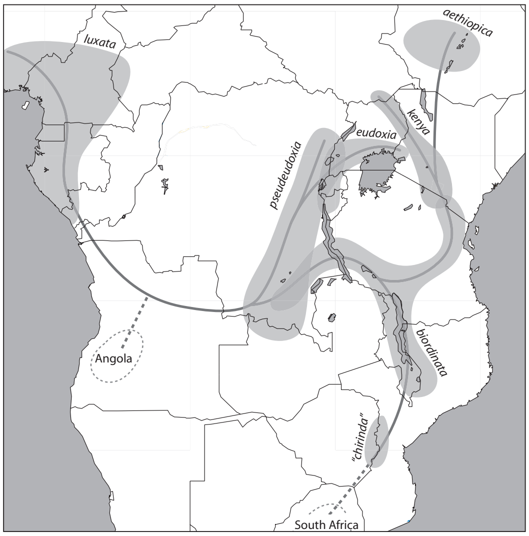


Fig. 7. A biogeographic hypothesis for *Atoconeura*. The phylogeny of the species is superimposed on their ranges, marking speculative expansion routes, but no direction along these routes is suggested. Species ranges are inferred by known records (questionable ones omitted) and the position of highlands, the clades follow these as much as possible. Note that the position of evolutionary splits within species ranges is an artefact of the presentation form and has no bearing on the hypothesis. Notable distributional gaps are indicated, marked by dashed area outlines and clades, as is the southern isolate of *A. biordinata* ('*chirinda*').

A. pseudeudoxia combines characters of *A. eudoxia* and *A. biordinata* and also lies in between geographically; *A. biordinata* shares further characters with its neighbour *A. kenya*. The morphologically most disparate taxa, *A. eudoxia* and *A. kenya* overlap north of Lake Victoria, closing the chain. This pattern recalls a 'ring species', suggesting expansion across montane stepping stones. The obtained phylogenetic hypothesis suggests an expansion of the genus from the western lowlands to the eastern highlands, or vice versa, followed by an expansion through the Albertine Rift and Eastern Arc Mts to the Kenyan and ultimately Ethiopian highlands (fig. 7). Especially in the case of a western origin there appears to have been a tendency of the species to occur at increasing altitudes in the course of their evolution (fig. 5). However, molecular analysis and more clarity of the genus's affinities are required to determine the relative age and direction of colonisations.

The absence of *Atoconeura* in two highland regions with high endemism and suitable habitat in southern Africa is notable: the South African highveld has been sufficiently surveyed, but would not have been colonised if cooler periods (when more stepping stones were available) coincided with harsher conditions, making it uninhabitable then and unreachable now. Angola has been poorly researched and *Atoconeura*, possibly a seventh species, could be found there.

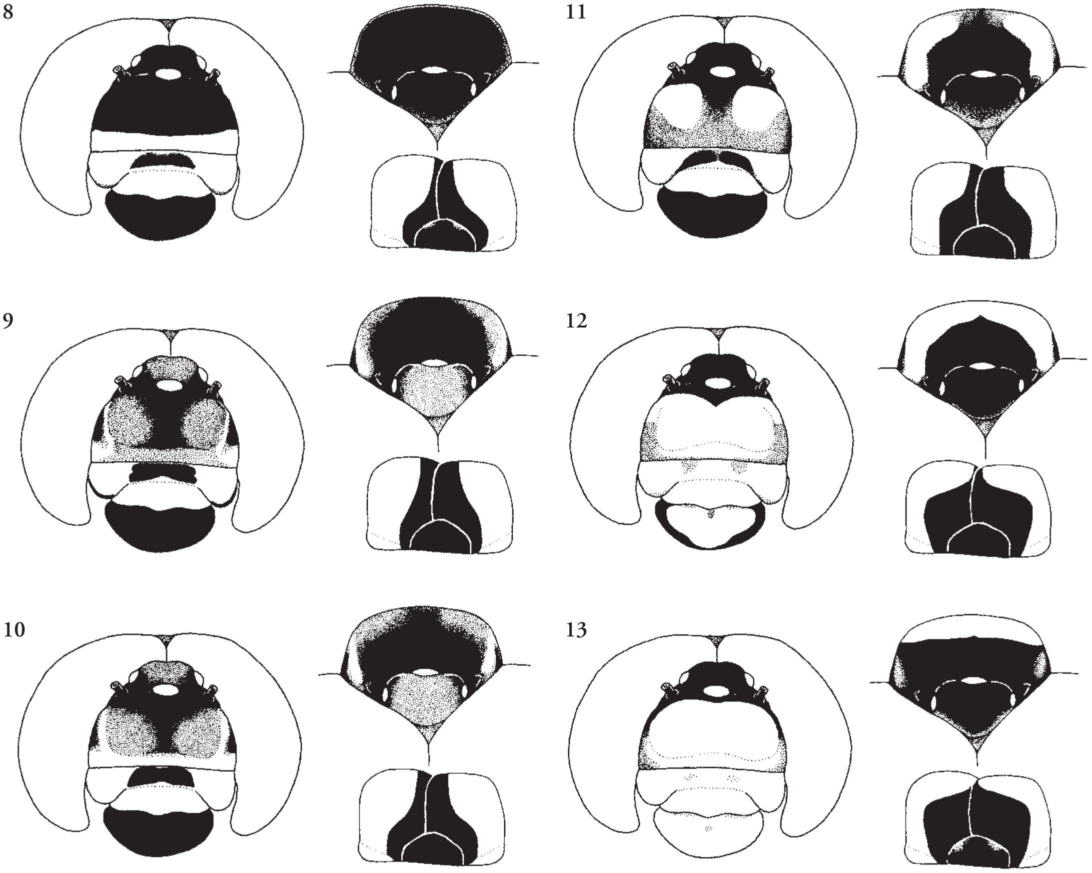
Behaviour

Males often perch prominently on rocks or twigs above streams, the abdomen held somewhat curved (figs. 43, 45-46). Males of *A. luxata* sp. n. in Ghana hovered persistently over rapid sections and near waterfalls in a manner recalling *Zygonyx* Hagen, 1867 and often perched only briefly (own observations). It is my impression that male behaviour at the waterside reflects the genus's phylogeny, with the proportion of time spent on the wing decreasing from the basal node upwards. This can only be confirmed by careful observations. Moreover, this effect may also be environmental, with lower ambient temperatures at greater elevations inhibiting sustained flight.

The reproductive behaviour is largely unknown. Despite being the commonest anisopteran on the Mulanje Plateau, I observed only three copulas of *A. biordinata* during 11 days of fieldwork there. They appeared to form at the streams and then go high up into the trees. S. Kyobe (pers. comm.) observed possible perched solitary epiphytic oviposition of *A. eudoxia* at Ruhija, Uganda: a female was reportedly laying on a twig floating on the stream surface and clad with bearded moss, while perched on twigs 1-3 cm above the substrate, repositioning herself once (by flight) before capture. Seated oviposition is uncommon and mainly facultative in Libellulidae: African *Tetrathemis* Brauer, 1868 females typically oviposit alone on substrates overhanging pools, while *Zygonyx natalensis* (Martin, 1900) tandems may use it to brave the torrential flow of waterfalls (Corbet 1999).

Key to males of *Atoconeura*

1. Labrum at least half pale (figs. 12-13). Mesepisternum with yellow hyphen bordering antealar sinus; abdomen often pruinose when mature (figs. 47-48). Cornua longer than half width of fourth segment of penis (fig. 28) 2
– Labrum all black or at most narrowly pale at base (figs. 8-11). Mesepisternum without hyphen; abdomen never pruinose (figs. 43-46). Cornua shorter than half width of fourth segment, or absent (figs. 25-27) 3
2. Dark area on frons rounded, sometimes with point down central groove (fig. 12; dorsal view) .... *kenya*
– Dark area on frons with straight anterior edge (fig. 13) .... *aethiopica*
3. Epiproct deeply bifid, its halves widely splayed,



Figs. 8-13. Details of male head of *Atoconeura* species: face in rostral view (left), frons and vertex in dorsal view (top right) and labium in ventral view (bottom right). – 8, *A. luxata* sp. n.; 9, *A. eudoxia*; 10, *A. pseudeudoxia*; 11, *A. biordinata*; 12, *A. kenya*; 13, *A. aethiopica*.

like fishtail (fig. 39). Underside S7-9 with many long dark hairs .... *eudoxia*

– Epiproct narrow and slender, with only slightly notched apex (fig. 38). Underside S7-9 at most with some fine hairs 4

4. S4-9 all black except for large dorsal spot on S7; basal spot S3 oval to triangular (fig. 17). Hw amber at base of subcostal and cubital spaces. Cerci rather straight and epiproct relatively long (figs. 29, 32). Cornua on fourth segment of penis absent (fig. 25) .... *luxata* sp. n.

– S4-9 with basal yellow spots, which are lateral on S4-6 and ventral on S7-9; basal spot S3 crescent-shaped (fig. 19). Hw base clear. Cerci more sinuous and epiproct shorter (figs. 31, 34-35). Cornua on fourth segment present (figs. 26-27) 5

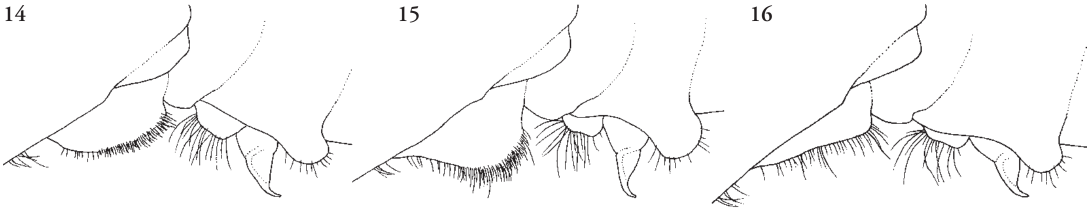
5. Hind femora anteriorly with dense long dark hairs. Poststernum strongly raised and with dense patch of short bristly hairs (fig. 15). Frons largely dark, lower border often paler; vertex brown (fig. 10). Hw 32-36.5 mm .... *pseudeudoxia*

– Hind femora with only some fine hairs. Poststernum barely raised and with only scattered fine long hairs (fig. 16). Frons with pale areas on shields, contrasting with dark lower border; vertex usually glossy black (fig. 11). Hw 28-33.5 mm .... *biordinata*

Key to females of *Atoconeura*

(couplets 4 and 5 are tentative)

1. Points of vulvar scale lie close to each other, normally well visible, space between them narrow, <60° (figs. 40-41). Postclypeus usually heavily marked with central black bar and darkened antero-lateral borders (figs. 8-9) 2



Figs. 14-16. Poststernum of *Atoconeura* species in lateral view (secondary genitalia included for reference). – 14, *A. eudoxia*; 15, *A. pseudeudoxia*; 16, *A. biordinata*.

– Points of vulvar scale wider apart, normally (partially) hidden under tergite, space between them wide, >60° (fig. 42). Postclypeus often not so heavily marked (figs. 10-13) 3

2. S4-9 with small yellow basal spots. Points of vulvar scale reach just beyond end of S8 (fig. 41). Cerci slightly longer than epiproct, blunt .... *eudoxia*

– S4-9 without basal spots. Points of vulvar scale reach as far as end of S8 (fig. 40). Cerci over twice as long as epiproct, with sharp point .... *luxata* sp. n.

3. Labrum at least half pale (figs. 12-13). Mesepisternum dark with pale markings including hyphen bordering antealar sinus, or uniformly brown 4

– Labrum all black or at most narrowly pale at base (figs. 10-11). Mesepisternum dark with pale markings, but without hyphen 5

4. Synthorax brownish black with yellow markings. Cerci about as long as epiproct .... *kenya*

– Synthorax uniformly brown. Cerci almost twice as long as epiproct .... *aethiopica*

5. Frons rather gradually darkening dorsally, palest along lower border (fig. 9). Hw 34-36.5 mm, 12-14 Fw Ax, seldom 11 .... *pseudeudoxia*

– Frons with pale areas on shields, contrasting with darkened areas along lower border (fig. 11). Hw 30-33.5 mm, seldom up to 35.5. 10-11 Fw Ax, seldom 12 .... *biordinata*

Atoconeura luxata sp. n.

(figs. 8, 17, 20-21, 25, 29, 32, 38, 40, 43-44)

Type material. – Holotype ♂: CAMEROON (SW): Meme, Atop, 1.5km from Ngusi, 250 m, 4.ix.1997, O. Mesumbe (CGVL). – Paratypes: CAMEROON (SW): 1♂, Tombel area, Lala, Lala and Ndibe streams, 18-22.iv.1995; 1♀, Meme, Atop, 1.5km from Ngusi, 250 m, 6.ix.1997, O. Mesumbe (CGVL); 1♂, Takamanda Camp, 568 m, 25.iv.2001, J. Groves (CGVL). [*A. b. pseudeudoxia* Karsch, 1899 [sic] in Vick (1999); *A. biordinata* in Vick (2002, 2003)].

Other material (included in PCA). – CONGO-BRAZZAVILLE: 1♀, Mts du Mayombe, Dimonika, 15.iv.1979, J. Legrand (MNHN). – GUINEA-CONAKRY: 8♂, 1♀, Mt Nimba, Bord du Zougué, galerie forestière, 12.xii.1983-15.i.1984, M. Lamotte & C. Girard (MNHN) [*A. biordinata* in Legrand (1985)]; 3♂, Mt Nimba, Zougué River, Plateau de Zougouepo station, env. Popote, ca. 750 m, 28.v-30.vi.1991, J. Legrand (MNHN) [*A. biordinata* in Legrand (2003)].

Other material (not included in PCA). – CAMEROON: 1♂, Mamfe, Gorilla Mt, 1700 ft (≈520 m), ii.1958; 1♂, Mamfe, ii.1958, E. Pinhey (NMBZ) [*A. b. pseudeudoxia* in Pinhey (1961c)]; 1♂, about 20 km W of Yaoundé, ca. 700 m, partly shady stream with sandy bottom in rainforest, 28.iv.1983, R. Niedringhaus (Coll. Niedringhaus, Oldenburg) [examined by T. Lieckweg]. – CENTRAL AFRICAN REPUBLIC: 1♂, Bouar, Artillery Range, 10.iv.1975, R.P. Lindley (NMBZ). – CONGO-KINSHASA: 1♂, 40 miles N of Quibo Falls, iii.1958, leg. unknown (NMBZ) [*A. b. biordinata* in Pinhey (1961c)]. – GHANA: 5♂, Eastern Region, Atewa Range Forest Reserve, Obeng-ne-obeng stream, 640 m, 17-21.vi.2006, K.-D.B. Dijkstra (RMNH). – NIGERIA (SE): 1♂, Ajassor-Ikom, ii.1958, E. Pinhey (NMBZ) [*A. b. pseudeudoxia* in Pinhey (1961c)]. – SIERRA LEONE: 1♀, Loma Mts, waterfall of Denkale river, ca. 800 m, 30.xi.1984, W. Rossi (MZUF) [*A. biordinata* in Carfì & d'Andrea (1994)].

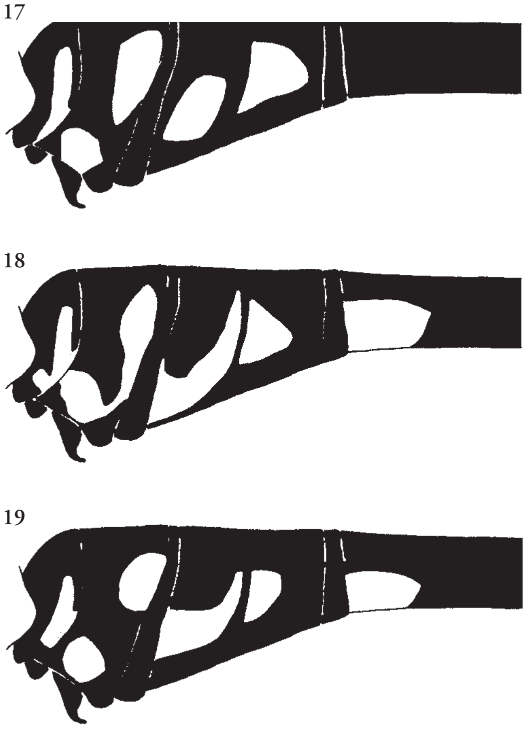
Diagnosis

Fairly large, dark and slender *Atoconeura* species, identified by the absence of basal spots on S4-9 in both sexes (fig. 17), the absence of penile cornua (figs. 21, 25), the slender male appendages (figs. 29, 32) and the vulvar scale (fig. 40). Males of other species usually have clear wing bases, but these are distinctly marked with amber in this species. Densely veined, the sum of Ax and Px in both Fw is on average 44.1 in males (range 39-48; n=18) against a range of 32-45 in other species (table 1).

Description

Holotype male. – Measurements (mm): entire length: 45, abdomen (without appendages): 33, Fw: 37, Hw: 35.5, Fw Pt: 3.5.

Prementum black, anteriorly with two small paired yellow blotches, and labial palps yellow with inner quarter black, this central black area of



Figs. 17-19.
Abdomen base of *Atoconeura* species in lateral view. – 17, *A. luxata* sp. n.; 18, *A. eudoxia*; 19, *A. biordinata*.

labium triangular, narrowing anteriorly and extending thinly along anterior border. Mandibles yellow, tipped black. Genae yellowish. Labrum glossy black. Ante- and postclypeus yellow, centre of postclypeus with blackish brown bar (above anteclypeus), antero-lateral border brownish. Frons entirely black with blue sheen, except anterior part, which is yellow, sharply demarcated from black along lower border of frontal shields. Vertex black with blue sheen, glossy brown above anterior ocellus. Occipital triangle dark brown, blacker laterally. Postgenae and back of occiput black, browner internally, with small circular yellow spot about halfway along eye margin and similar streak bordering ventral end of margin. Antennae and their bases black. Labrum, clypeus, frons, vertex and occipital triangle with black hairs. Postgenae with pale hairs, these longer than black facial hairs.

Prothorax brown, darker on posterior lobe, which has dense long pale hairs. Synthorax brownish black with bluish gloss, marked with yellow as follows: mid-dorsal carina yellow; antehumeral stripe complete but narrow, about as wide as one-sixth of mesepisternum; thin stripe on mesepimeron anterior to interpleural suture reaches dorsad about halfway metastigma and subalar ridge, and is aligned with isolated blotch on antero-dorsal corner of metepisternum; complete stripe (about as wide as antehumeral) on metepisternum anterior of metapleural suture, which is fused with mesepimeral stripe below metastigma, continuing onto largely yellow metakatepisternum; metepimeron with antero-dorsal spot and stripe along posterior carina, the latter about as wide as antehumeral. Mesokatepisternum yellow, anterior half darker. Synthoracic venter yellow, posterior stripe of metepimeron continuing onto venter, leaving it black anteriorly and posteriorly. Posterior border of poststernum black. Antealar sinus and sclerites brownish black. Synthorax entirely covered with long pale hairs, longest and densest on dorsal mesepisternum, darker latero-ventrally. Poststernum slightly raised posteriorly, with long, fairly dense pale hairs.

Legs black save largely yellow coxae, and yellow on interior sides of trochanters and basal three-quarters of interior side of fore femora. Trochanters and especially coxae with numerous pale and dark long hairs. Legs otherwise quite bare, save the usual black bristles and denticles, and patches of fine pale hairs on anterior face of hind femora, near base. These hairs quite dense and up to two-thirds as long as femur is wide.

Venation black. Wing membrane clear, amber at base of Hw and Fw, concentrated in subcostal and cubital spaces, most extensive in Hw cubital space where it reaches about halfway to Cux1. Membranule and Pt blackish brown. 14 Ax in both Fw, 10-11 in Hw. 10 Px in Fw, 10-11 in Hw. Arculus about halfway Ax2 and Ax3 in all wings. 1 Cux in both Fw, 2 in Hw. Fw triangles about 3x as long as wide, each with one cross-vein; Hw triangles uncrossed. Supratriangles without cross-veins, subtriangles of 3 cells. Discoidal field of 3 cells bordering triangle, then 2 rows for 6-8 cells, becoming 3 rows just proximal of nodus, Mspl scarcely defined. IR3 and Rspl enclosing single row of 9-10 cells in all wings. Anal field of 3 rows near rounded tornus. Anal loop of 21-23 cells, distinctly boot-shaped with pointed 'toe' and rectangular 'heel'. Bridge spaces with 1 cross-vein.

Abdomen slender, S7-9 slightly expanded, but not club-shaped. Abdomen black marked with yellow: S2-8 very thinly yellow along dorsal carina, most clearly on S2-4; S1 with long lateral mark; S2 with round spot above genital fossa and large wedge-shaped lateral spot posterior of transverse ridge; S3 with oval lateral spot anterior of transverse carina and large roundly triangular spot posterior of it, the former shifted somewhat ventrad relative to the latter; S4-6 and S8-10 unmarked; S7 with elongate dorsal spot, occupying about basal two-thirds of segment. Cerci and epiproct black. Cerci weakly sinuous in lateral view, straight in dorsal view; narrowed near base, swollen subapically, with slender pointed,

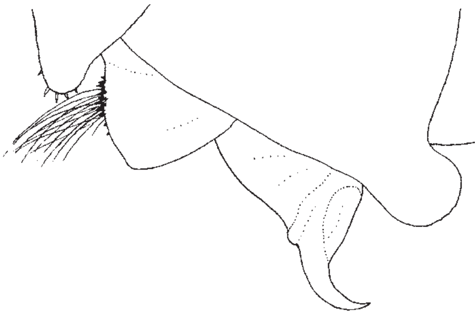


Fig. 20. Secondary genitalia of *Atoconeura luxata* sp. n. in lateral view.

somewhat up-curved tips; ventral ridge rather short with about 7 irregular, coarse teeth (figs. 29, 32). Epiproct long and rather narrow, almost reaching halfway ventral ridge and apex of cerci (figs. 32, 38). Cerci with bristly black hairs, abdomen otherwise rather bare, mainly with fine, short hairs along carinae. Venter of abdomen (sternites and ventral portions tergites) black, narrowly yellow along ventral carinae. Anterior lamina low and brown, with numerous long pale hairs and short black denticles. Hook of hamule blackish brown, strongly curved (fig. 20). Genital lobe black and short with many long pale hairs. Penis not extracted (see paratype).

Paratype males. – Similar to holotype but slightly smaller: Hw 34 (Tombel) and 34.5 mm (Takamanda). Tombel male has labium only narrowly black along inner border of palps, paired yellow blotches occupying most of prementum. Postclypeus slightly blacker laterally, vertex all black. Venation similar but 12 Ax in Fw, 9-10 in Hw. 8-9 Px in Fw, 9 in Hw. Discoidal field of 2 rows of cells from base to level of nodus. Anal loop of 21-24 cells. Takamanda male has labium as holotype but prementum all black. Postclypeus slightly darker laterally, vertex all black. Venation similar but 11-12 Hw Ax and 10 Hw Px. Anal loop of 20-23 cells. Penis of Takamanda male extracted: fourth segment relatively long with greatly developed pleats; ventral hump and cornua absent (figs. 21, 25).

Paratype female. – Measurements (mm): entire length: 49, abdomen (without appendages): 34, Fw: 38.5, Hw: 37, Fw Pt: 3.7. Similar to holotype but slightly more robust. Black on labial palps reduced to narrow band along inner borders. Antero-lateral borders of postclypeus blacker, frontal shields and vertex dorsum largely brown. Thorax alike, but spot and stripe on metepisternum are fused. Interior side of all femora yellow on basal half. Amber at wing bases deeper and more extensive, reaching Ax1 and Cux1. Venation similar but 12 Fw Ax, 10 Hw Ax and 11-12 Hw Px. Anal loop of 22-24 cells. The two lateral yellow markings of S2 fused. S4 with a yellow lateral streak on about middle third of segment. A similar, but almost indiscernible, streak on S5. Vulvar scale with two small points just reaching to end of S8, separated by U-shaped excavation that is about as wide as one point (fig. 40). Yellow along ventral carinae of tergites wider than in holotype. Cerci about 3x as long as epiproct and paraprocts, elongated with fine spiny point, with scattered black bristly hairs.

Variation

The males from Mt Nimba are slightly smaller (average Hw 33.6 mm, n=11) and paler than the type material (34.7, n=3). They often have paired pale spots at the labrum base and the postclypeus is normally all pale. The dark area on the frons dorsum is browner and less extensive, sometimes leaving the anterior half of the shields pale. The vertex is brown, rather than black. The basal spot on S3 may be larger and more crescentic (i.e. more like *A. biordinata*) and the dorsal spot of S7 is longer, about as long as 75% of the segment. Ghanaian males are intermediate in coloration, but even smaller (32.1, n=5).

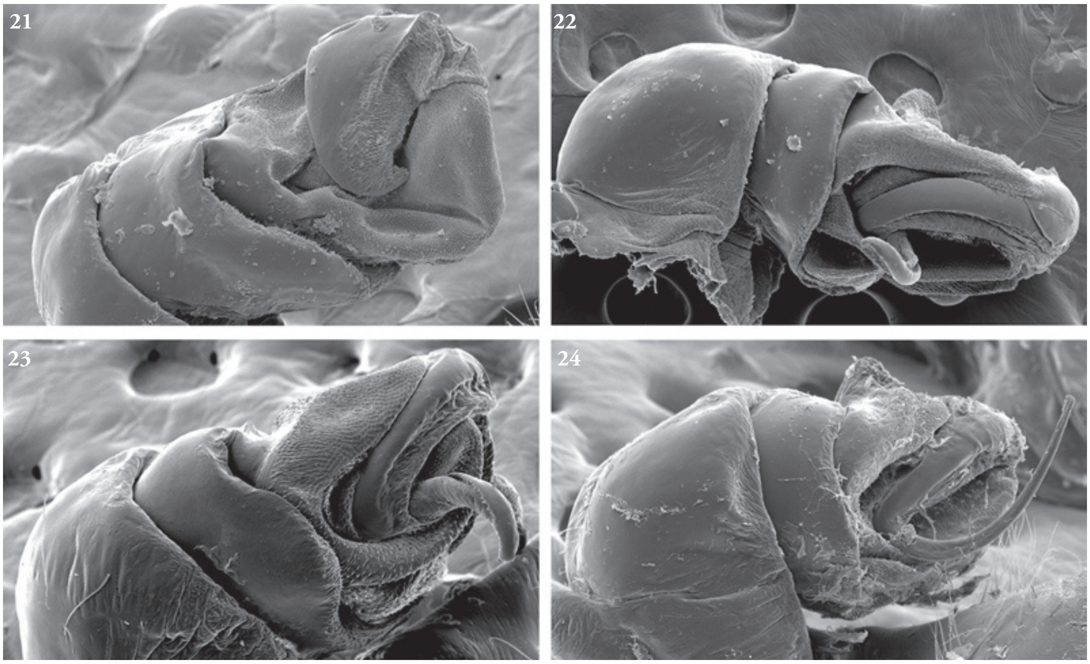
Etymology

The adjective *luxata* (dislocated) refers to the species's isolation by characters and geographic and altitudinal range.

Range

Known from Sierra Leone, Guinea-Conakry, Ghana, SE Nigeria, Cameroon, W Central African Republic and W Congo-Brazzaville (fig. 6) at 250-800 m, much lower and further west than other *Atoconeura*. The genus was collected in Gabon (J. Legrand pers. comm.), but no material was available for study. Pinhey (1961b, c) passed the Chutes de Kiubo in Katanga (9°31'S 27°02'E) on his way north in January 1958. However, the male from near 'Quibo Falls' is dated two months later and would originate from well outside the species's known geographic and altitudinal range (the site should lie south of Mitwaba above 1000 m). Pinhey collected *A. luxata* sp. n. in Cameroon a month later, but returned south by aeroplane. Perhaps the Quibo Falls specimen was mislabelled, although Pinhey's assistant returned overland and could have collected it then.

Males in Ghana preferred sunny spots on a shaded rainforest stream with rocks and gravel, hovering over the swiftest parts, for instance near a small waterfall (larvae were not found). This is corroborated by Legrand (1985) who found the species 'sur les petits cours d'eau forestiers, la larve, très rhéophile, se tient fixée sur les dalles rocheuses en plein courant' and the waterfall habitat in Sierra Leone.



Figs. 21-24. Electron microscope scans of penes of *Atoconeura* species in lateral view. – 21, *A. luxata* sp. n. (Takamanda, Cameroon); 22, *A. pseudeudoxia* (Kibale NP, Uganda); 23, *A. biordinata* (Mulanje, Malawi); 24, *A. kenya* (Mt Kenya, Kenya).

Atoconeura eudoxia (Kirby)
(figs. 9, 14, 18, 26, 30, 33, 39, 41, 45)

Accaphila eudoxia Kirby, 1909: 60. Holotype ♂: UGANDA: round label, white with red border 'Holotype', rectangular, blue '20 Jan 06 alt 6000 ft. [≈1830 m], Ruwenzori East', rectangular, white 'Accaphila eudoxia Kb. type.', leg. probably G. Legge & A.F.R. Wollaston (BMNH) [examined].

Atoconeura extraordinata Fraser, 1950: 56. Lectotype ♂ (designated by Kimmins 1966: 191): UGANDA: round label, white with purple border 'Lectotype', 'UGANDA Ruwenzori, Bwamba V., 6500-7500 ft. [≈2000-2300 m], 13-15.i.1926. G.D. Hale Carpenter.', rectangular, white 'Atoconeura extraordinata Fraser. ♂. TYPE. (Atoconeura eudoxia (Kirby) F.C. Fraser det., 1951', rectangular, white 'F.C. Fraser Bequest. Brit. Mus. 1963-234.' (BMNH) [examined]; junior synonym (Longfield 1953: 44).

Atoconeura eudoxia (Kirby, 1909) – (Longfield 1953: 44).

Diagnosis

Male is immediately identified by bifid epiproct (fig. 39) and the numerous long dark hairs on the underside of S7-9, female by vulvar scale (fig. 41). The male cerci are much more swollen medially than in other species: the dorsal profile is rather flat, the ventral ridge is shallow and drawn-out (fig. 33), and the apices diverge (fig. 30). Despite these unusal male characters, the female head morphology is similar to that of other species, although the vertex and occiput appear slightly flatter.

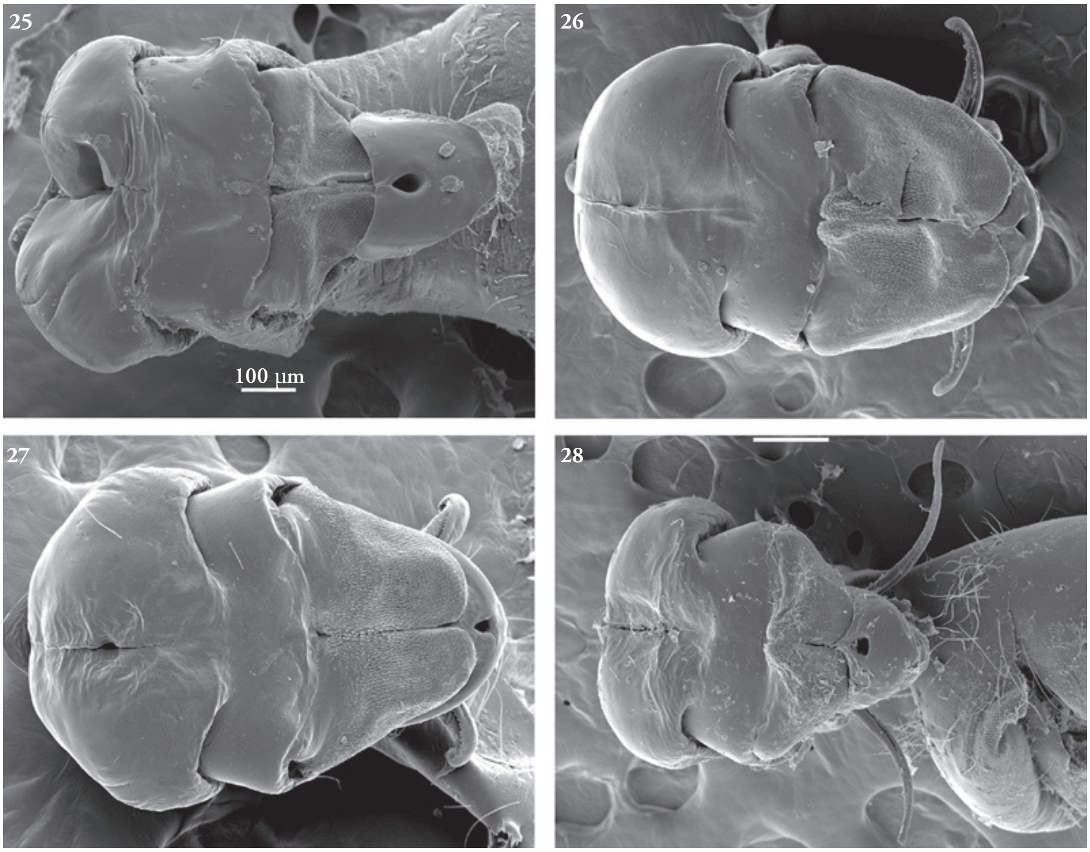
Although *A. eudoxia* differs from all other species by sexual characters, it is almost identical to the sympatric *A. pseudeudoxia* in five respects (see *A. pseudeudoxia* for a comparison): (1) Large size (table 1). (2) Cone-shaped labial marking, largely dark frons and brown vertex (figs. 9-10). Other species in eastern Africa have the labial marking on average wider at base but narrower at apex, the frons paler with more contrast and the vertex blacker (figs. 10-13). (3) Strongly swollen poststernum with medially a dense patch of short, bristly pale and dark hairs (figs. 14-15). This patch strengthens the 'pot-belly' and recalls a coconut fibre mat in lateral view. Female poststerna are similar, but with only sparse hairs. (4) Anteriorly densely, long and dark haired hind femora. The femoral surface appears rather rough where these hairs are present. (5) The fourth segment of the penis is relatively long and flat, with a clear ventral hump and distinct but short cornua (figs. 22, 26).

Variation

Not notable within small range.

Range

Most records are from S and W Uganda (fig. 6) at 1400-2600 m, e.g. Ruwenzori Mts and Bwindi Impenetrable NP. The Burundi record also lies within the Albertine Rift and suggests the species's presence



Figs. 25-28. Electron microscope scans of penes of *Atoconeura* species in ventral view. – 25, *A. luxata* sp. n. (Takamanda, Cameroon); 26, *A. eudoxia* (Bwindi Impenetrable NP, Uganda); 27, *A. biordinata* (Mulanje, Malawi); 28, *A. kenya* (Mt Kenya, Kenya).

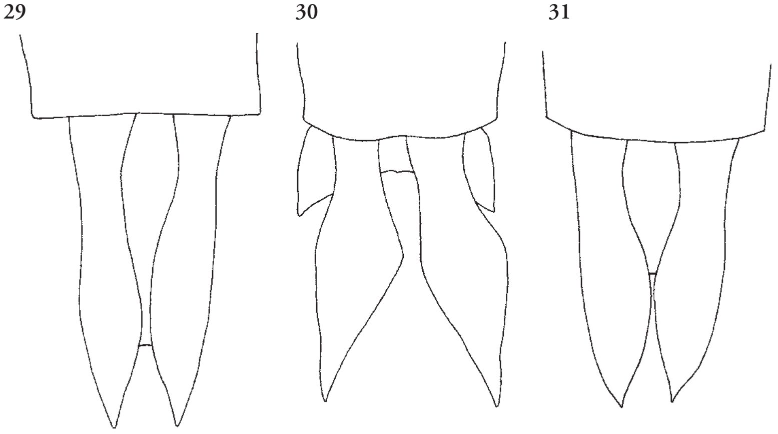
in Rwanda and E Congo-Kinshasa. Rather isolated populations occur in Mabira Forest near Kampala at 1100-1300 m (J.J. Kisakye pers. comm.) and Kakamega Forest, W Kenya.

Remarks

A. eudoxia is so similar to *A. pseudeudoxia* that Fraser (1950) found it to possess 'so strange an inferior anal appendage that I came to the conclusion [at first] that it must be a deformity'. Longfield (1953) did not 'consider it strange that, on comparing these [*A. pseudeudoxia*] specimens with the type of *A. eudoxia* from the same locality, and finding that the only apparent difference was the deeply bifid inferior appendage of the *eudoxia* type, I thought this was a structural anomaly.'

Further type material (included in PCA). – Paratype ♀ ('allotype') *eudoxia*: UGANDA: round label, white with red border 'Allotype', rectangular, white 'Nyamgasani Valley, 8-9,000ft. [≈2500-2700 m], D.R. Buxton', rectangular, white 'UGANDA: Ruwenzori Range, xii.1934-i.1935. B.M.E. Afr. Exp. B.M. 1935-203.', rectangular, white 'Atoconeura eudoxia Kirby allotype ♀ det. Miss C. Longfield.' (BMNH).

Other material (included in PCA). – BURUNDI: 1♂, Usumbura (=Bujumbura), 17.i.1934, Lefevre (MRAC). – KENYA: 4♂, Kaimosi Forest, Kakamega, i.1951-i.1953, E.C.G. Pinhey (BMNH); 1♀, Kakamega Forest, ca. 1600 m, i.1995, V. Clausnitzer (CGVL). – UGANDA: 1♀, Ruwenzori, Bwamba Pass, 6500-7000 ft. (≈2000-2100 m), 13-15.i.1925, G.D. Hale Carpenter (BMNH); 1♂, Ruwenzori Range, Nyamgasani Valley, 8-9,000 ft. (≈2500-2700 m), xii.1934-i.1935, D.R. Buxton (BMNH); 1♂, Ruwenzori Range, Namwamba Valley, 6,500 ft. (≈1980 m), xii.1934-i.1936; 1♀, Kigezi, Mafuga Rain Forest, vi.1951, T.H.E. Jackson (BMNH); 1♂, Kigezi, Mitano Rain Forest, vi.1951; 1♂, 2♀, Kigezi, Rutenga Forest, vi.1951-vi.1952; 1♂, 1♀, Kayonza Forest, Kigezi, iv.1951-xi.1953, V.G.L. van Someren (BMNH); 2♂, 1♀, Bwindi Impenetrable NP, Buhoma, Munyaga Valley, 1600 m, 17-18.v.2003; 1♂, 1♀, Bwindi Impenetrable NP, Rushamba, 1450 m, 21-23.v.2003; 1♀, Bwindi Impenetrable NP, Ruhija, 2100 m, 24.v.2003, K.-D.B. Dijkstra (RMNH).



Figs. 29-31.
Male appendages of *Atoconeura* species in dorsal view. – 29, *A. luxata* sp. n.; 30, *A. eudoxia*; 31, *A. aethiopica*.

Atoconeura pseudeudoxia Longfield stat. rev.
(figs. 10, 15, 22, 34)

Atoconeura biordinata pseudeudoxia Longfield, 1953: 46. Holotype ♂: UGANDA: round label, white with red border 'Holotype.', rectangular, white 'Uganda: Ruwenzori Range, Mobuku [=Mubuku] Valley, Bikoni Peak, 7000 ft. [≈2130 m] 30.XII.1937. C.E. Longfield', rectangular, white 'Atoconeura biordinata pseudeudoxia det. Miss C. Longfield. Type ♂ subsp.n.', rectangular, white 'Brit. Mus. 1952-581' (BMNH) [examined].

Diagnosis

Has a 'hybrid' appearance, being almost identical to *A. eudoxia* in many respects (see that species), but the vulvar scale and male appendages are close to *A. biordinata* (figs. 34, 42). However, the male cerci are more strongly sinuous than in other species: the tips are curved upwards more, while the extreme apices curve slightly down again, and the ventral ridge is so strongly sinuous that it appears as two separate short ridges in lateral view (fig. 34).

Although 'carbon-copy' *A. eudoxia* and *A. pseudeudoxia* probably exist, they tend to differ in details of markings (figs. 9-10). Both sexes of *A. eudoxia* always have black antero-lateral edges of the postclypeus, which are absent in most *A. pseudeudoxia*. The lower frons is more often pale in *A. pseudeudoxia*, in contrast with the shields. In *A. eudoxia* males the yellow lateral spots on S2 are often fused (fig. 18), but always separated by black in *A. pseudeudoxia* (cf. fig. 19). In *A. pseudeudoxia* the poststernum is most strongly raised posteriorly and slopes anteriad, giving a triangular profile in lateral view (fig. 15), but it is relatively high anteriorly and therefore plateau-like in *A. eudoxia* (fig. 14).

Variation

Specimens from Katanga are paler and smaller (average Hw 33.6 mm, n=10) than other specimens (34.6, n=12). Most notably the postclypeus is normally unmarked.

Range

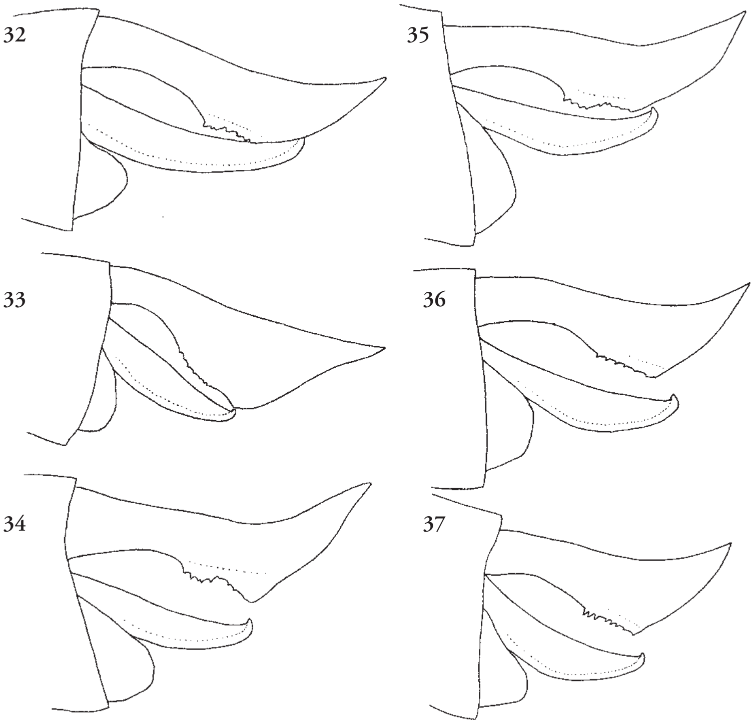
Described from S and W Uganda, from where it extends into E Congo-Kinshasa and through Katanga to N Zambia (fig. 6), occurring at 700-2300 m.

Remarks

Longfield (1953) remarked that 'when found, it [the female of *A. pseudeudoxia*] will be extremely difficult to determine'. None of the details of a female discussed by Pinhey (1961a) are diagnostic. Two kinds of females recalling *A. eudoxia* were studied. That treated as *A. eudoxia* by Longfield has a uniquely formed vulvar scale (fig. 41) and is known from W Kenya, where *A. pseudeudoxia* does not occur. The other is known from Uganda and Katanga, and has the scale similar to *A. biordinata*, and includes the presumed *A. pseudeudoxia* female found by Dijkstra & Dingemanse (2000).

Further type material (included in PCA). – Paratypes: UGANDA: 1♂, Bikoni, Mobuku valley, 7,500 ft. (≈2290 m), 31.xii.1934, leg. unknown (BMNH) [head belongs to another genus]; 1♂, Ruwenzori Range, Mpanga Forest, 25.i.1935, F.W. Edwards; 1♂, Ruwenzori, 6-8000 ft. (≈2130 m), xii.1895, Scott-Elliot (BMNH).

Other material (included in PCA). – CONGO-KINSHASA: 1♂, Région Lac Kivu, Kadjudju, 1930, G. Babault (MNHN); 9♂, 5♀, PN Upemba, River Mubale, 1480 m, 1-20.v.1947, G.F. de Witte (ISNB); 1♀, PN Upemba, River Mubale, 1480 m, 20.v.1947, G.F. de Witte (BMNH). – UGANDA: 1♂, Bwamba Valley, 2500 ft. (≈760 m), 8-12.i.1928, G.D. Hale Carpenter (BMNH); 1♂, Fort Portal, Bwamba Forest, 2400 ft. (≈730 m), iv.1951, E.C.G. Pinhey (BMNH); 1♂, Kigezi, Rutenga Forest, viii.1951, V.G.L. van Someren (BMNH); 1♂, Kalinzu Forest Reserve 4,700 ft. (≈1430 m), 25.vi.1994,



Figs. 32-37.
Male appendages of *Atoconeura* species in lateral view. – 32, *A. luxata* sp. n.; 33, *A. eudoxia*; 34, *A. pseudeudoxia*; 35, *A. biordinata*; 36, *A. kenya*; 37, *A. aethiopica*.

T. Graves (Coll. T. Graves); 1♂, Kibale NP, Kanyawara, 29.x.1995; 1♀, Kibale NP, Ngogo, 3.ii.1996; 3♂, Bwindi Impenetrable NP, Buhoma, Munyaga Valley, 1600 m, 17-18.v.2003; 1♂, Bwindi Impenetrable NP, Rushamba, 1400 m, 22.v.2003; 1♀, Semliki NP, Ntandi, Nkisi River, 700 m, 1.vi.2003, K.-D.B. Dijkstra (RMNH).

Other material (not included in PCA). – CONGO-KINSHASA: 1♂, Ituri Forest, ii.1958, E. Pinhey (NMBZ). – ZAMBIA: 1♂, Ikelenge, Sakeshi, v.1961; 1♂, Mwinilunga, v.1964, E. Pinhey (NMBZ); 1♂, Mwinilunga, Ikelenge, Lisombo River, 28.iv.1972, F.C. de Moor & E. Pinhey (NMBZ).

Atoconeura biordinata Karsch

(figs. 11, 16, 19, 23, 27, 35, 42, 46)

Atoconeura biordinata Karsch, 1899: 371. Holotype ♀: TANZANIA: Kitope [not found ZMHB, i.2004].

Atoconeura leopardina Förster, 1906: 38. Holotype ♂: TANZANIA: Nguelo (UMMZ) [not examined]; junior synonym (Ris 1912: 750).

Atoconeura biordinata chirinda Longfield, 1953: 46. Holotype ♂: ZIMBABWE: round label, white with red border 'Holotype', rectangular, white 'Chirinda For. Melsetter Dist. Dept. Agric. S. Rhodesia 27/12.1948', rectangular, white 'J.A. Whellan Collector', rectangular, white 'Atoconeura biordinata chirinda det. Miss C. Longfield. Type ♂ subsp.nov.' (BMNH) [examined]; junior synonym (Bridges 1991: VIII.9).

Oreoxenia leopardina Förster, label name – (Pinhey 1962: 266).

Atoconeura biordinata f. *chirinda* Longfield, 1953 – (Pinhey 1984: 47).

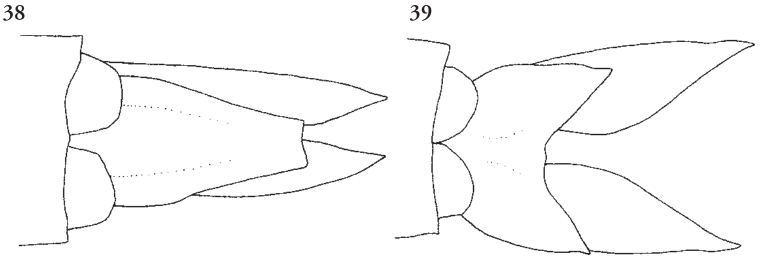
Oreocema leopardina Förster, label name – (Garrison et al. 2003: 58); possible misspelling.

Diagnosis

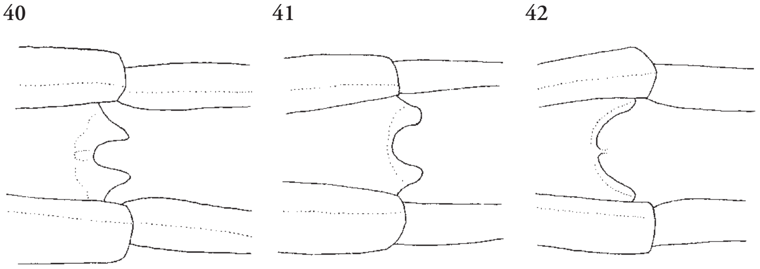
Smallest *Atoconeura* species, best separated from others with black labrum by frons: although this is variable, the pale shields always contrast with the dark area below them (fig. 11). It is otherwise rather intermediate between *A. pseudeudoxia* and *A. kenya* in markings (including labium), abdomen shape and cerci (fig. 35). The small size is reflected by venation: in males 79% of Fw have 10-11 Ax (range 9-13, n=86) while in *A. pseudeudoxia* 79% have 12-13 (10-14, n=43). 44% of *A. biordinata* males (n=43) have one or both Fw triangles uncrossed, whereas 100% of *A. pseudeudoxia* (n=22) have both crossed. The fourth segment of the penis is nearest that of *A. eudoxia*, with similar cornua, although the general shape is intermediate to *A. kenya*; the ventral hump is reduced (figs. 23, 27).

Variation

Specimens from Zimbabwe ('*chirinda*') are smaller with more open venation: most examined males (average Hw 28.9 mm, n=11) had Fw with 7 Px, 10 Ax and uncrossed triangles, while non-Zimbabwe



Figs. 38-39.
Male appendages of *Atoconeura* species in ventral view. – 38, *A. luxata* sp. n.; 39, *A. eudoxia.*



Figs. 40-42.
Vulvar scales of *Atoconeura* species in ventral view. – 40, *A. luxata* sp. n.; 41, *A. eudoxia*; 42, *A. biordinata.*

A. biordinata (31.2, n=32) more often had 8-9 Px, 11 Ax and crossed triangles in Fw.

Range

The first Kenyan record is from the Taita Hills, which (bio-) geographically are considered the northernmost outlier of the Eastern Arc Mts (Burgess et al. 1998). Ranges further from Mt Kilimanjaro and the Usambara Mts to Katanga, Malawi, Mozambique and Zimbabwe (fig. 6), occurring at 1000-2000 m and probably higher. Pinhey's (1984) Zambian records probably all pertain to *A. pseudeudoxia*. An old and poorly labelled male, already examined by Ris (1912), may indicate an isolated presence of *A. biordinata* in the Cameroon highlands. However, it is the only specimen seen from the region, and clusters with males from Zimbabwe (figs. 1-2).

Remarks

Longfield (1953) did not see the holotype of this species, a teneral female from central Tanzania, and I could not relocate it. By origin the present interpretation of its identity is probably correct. The description by Karsch (1899) contains little specific information, but the open Fw triangle in one wing and low measurements match the known female. Longfield's (1953) diagnosis of *A. biordinata* incorporated unpruinose specimens of *A. kenya* from N Tanzania: 'The Arusha [=Mt Meru] series [plural] vary considerably and in some, the colour-pattern resembles the subspecies from the Kenya Highlands [*A. kenya*], to a slight extent.' As a consequence, most of the characters in her key for *A. biordinata* refer to *A. kenya.*

Further type material (included in PCA). – Paratypes *chirinda*: ZIMBABWE: 1♀ ('allotype'), round label, white with red border 'Allotype'; rectangular, white 'Chibudzana R., Melsetter Dist. Dept. Agric. S. Rhodesia 26/2.1948', rectangular, white 'J.A. Whellan Collector', rectangular, white 'Atoconeura biordinata chirinda allotype ♀ subsp.n. det. Miss C. Longfield.' (BMNH); 1♂, Umtali District, 4.xii.1947; 3♂, Chirinda Forest, Melsetter District, 14.xi-27.xii.1948, J.A. Whellan (BMNH).

Other material (included in PCA). – 1♂, 'Cameroun', date and leg. unknown (MNHN) [origin doubted]. – CONGO-KINSHASA: 1♂, Katentania, v.1924, Ch. Seydel (MRAC); 1♂, PN Upemba, Kavizi (affl. Lusinga), 14.vii.1945, G.F. de Witte (MRAC). – KENYA: 1♀, Teita [=Taita] Hills, Wesu, vii.1947, V.G.L. van Someren (BMNH). – MALAWI (MISUKU HILLS): 1♀, Matipa Forest, 5.xii.1987; 1♂, Mughese Forest, 10.xii.1987, J.T. Wilson (CGVL). – MALAWI (MULANJE): 2♂, Lichenya Path, 1780 m, 8.xi.2001; 1♂, Lichenya Plateau, 2000 m, 8.xi.2001; 1♂, Muloza Stream, 1980 m, 10.xi.2001; 1♀, Nessa Path, 1860 m, 9.xi.2001; 4♂, Dzole Stream, 2000 m, 16.xi.2001; 2♀, Ruo Gorge, 1750 m, 17.xi.2001; 2♂, Ruo Gorge, 1090 m, 17-18.xi.2001; 1♀, Lichenya Path, 1200 m, 13.i.2002, K.-D.B. Dijkstra (RMNH). – MOZAMBIQUE (NAMULI): 3♂, Khurukani Stream, 1490 m, 4.xii.2001; 1♂, 1♀, Muretha Plateau, 1870 m, 6.xii.2001, K.-D.B. Dijkstra (RMNH). – TANZANIA: 2♂, W Kilimanjaro, Ngare-Nairobi, 4-5,000 ft. (≈1200-1500 m), i-ii.1937, B. Cooper (BMNH); 1♂, Kigoma, Mahale Mt. nr Ujamba, 2000 m, 28.viii.1966; 1♀, Sibweza, 35 mi, Mpanda-Karema Rd. (1050m), 26.xi.1968; 2♂, Sibweza,

Figs. 43-48. Males of *Atoconeura* species. Note characters of frons and mesepisternal 'hyphens'. – 43-44, *A. luxata* sp. n. in the Atewa Range, Ghana; 45, *A. eudoxia* near Ruhija, Uganda; 46, *A. biordinata* on Mulanje, Malawi; 47, *A. kenya* on Mt Elgon, Uganda; 48, *A. aethiopica* at Wushwush, Ethiopia. Photographs taken by author (43-46, 48) and V. Clausnitzer (47).

35 mi. Kampisa-Mpanda (1500m), 26.xi.1968; 2♂, 1♀, Kigoma, Ujamba at Mahale Ridge, 2000-2500 m, x.1969-4.ii.1972, J. Kielland (RMNH); 1♂, 1♀, Mts Uluguru, Chenzema, 1700 m, 21-22.vii.1971, L. Berger, N. Leleup & J. Debecker (MRAC); 2♂, Kigoma, Lukandamira, 1600-1700 m, viii.1971-ii.1972; 1♂, Mpanda District, Kampisa, 1500 m, ix.1971, J. Kielland (RMNH); 2♂, Mbizi Mts, Mkutwa, 1987-1988, leg. unknown (CGVL); 1♂, Kiwira River, Isongole, 1930 m, 23.ix.2001; 1♀, Kilimanjaro, Machame Gate, 1700 m, 19.iii.2002, V. Clausnitzer (CVCH). – ZIMBABWE: 1♂, Imbiza Valley, Umtali, 21.i.1948; 2♂, 1♀, Vumba Mt, Umtali S.R., x.1953; 1♀, Inyanga, i.1960, E.C.G. Pinhey (BMNH); 1♂, Inyanga, 2.i.1960, E.C.G. Pinhey (RMNH); 2♂, Inyanga NP, 1800 m, 17.x-6.xi.1964, G.F. Mees (RMNH).

Other material (not included in PCA). – TANZANIA: 1♂, Kilimanjaro, Kibonoto, 1300-1900 m, 15.v.1906, Y. Sjöstedt (NHRS).

Atoconeura kenya Longfield
(figs. 12, 24, 28, 36, 47)

Atoconeura biordinata kenya Longfield, 1953: 46. Holotype ♂: KENYA: round label, white with red border 'Holotype', rectangular, white 'B.E. Africa, Kenya, Meru. 29.I.1934. On swift stream. C.E. Longfield. 6,000 ft. [≈1830 m]', rectangular, white 'Atoconeura biordinata kenya det. Miss C. Longfield. Type ♂ subsp.n.', rectangular, white 'Brit. Mus. 1952-581' (BMNH) [examined].

Atoconeura kenya kenya Longfield, 1953 – (Bridges 1991: VIII.9).

Diagnosis

Medium-sized with relatively short, club-shaped abdomen (fig. 47). *A. kenya* and *A. aethiopica* (see latter for a comparison) differ from all other species by their pale labrum (figs. 12-13), mesepisternal 'hyphens', pruinose abdomen in mature males (figs. 47-48) and the distribution of black pigment. While the face is paler, the vertex is often black, and the labial black marking is large with its greatest extent shifted anteriad (fig. 12). The pale markings on the thorax and abdomen base are strongly broken up. Besides the characteristic 'hyphens', there is always a spot on the mesepimeron near the wing base just behind the humeral suture, unlike most individuals of other species. Altogether this gives the thorax a more spotted than striped appearance. The dorsal spot on S7 is relatively large (fig. 47) and the abdomen underside can be predominantly yellow. The cerci have an almost straight ventral ridge (fig. 36). In both species the fourth segment of the penis is very short, with a strong ventral hump and very long cornua (figs. 24, 28).

Variation

Pruinosity either develops slowly or is easily lost in preservation: of 20 examined males only 6 had an entirely pruinose abdomen, 10 were only pruinose at the base (fig. 47) and 4 lacked it completely. The width of the black labral border varies from fairly broad (fig. 12) to absent (cf. fig. 13; 2 of examined males).

Range

Most records are from Kenya's central highlands (e.g. Mt Kenya and Aberdare Mts), but also occurs on Mt Elgon (including Ugandan side), N Tanzania (Mts Meru and probably Kilimanjaro) and the Imatong Mts of S Sudan (fig. 6), at 1400-3000 m. Cooper collected *A. kenya* on Mt Meru in the same period that he obtained the only specimens known from Kilimanjaro, but his *A. biordinata* males from Kilimanjaro were collected earlier. Hale Carpenter collected three *Atoconeura* species in the Bwamba Valley in the W Ruwenzori, including the only *A. kenya* specimen known from the Albertine Rift. Both records require confirmation as mislabelling cannot be ruled out, although Hale Carpenter did concentrate his collecting in W Uganda.

Remarks

The larva is briefly described by Pinhey (1959), the karyotype by Wasscher (1985).

Further type material (included in PCA). – Paratypes: KENYA: 1♀ ('allotype'), round label, white with red border 'Allotype', rectangular, white 'Africa, Kenya, Thompson's Falls April 1950.R.W. Barney. B.M. 1952-582', rectangular, white 'Atoconeura biordinata kenya det. Miss C. Longfield. allotype ♀ subsp.n.' (BMNH); 1♂, Nairobi, xi.1926, leg. unknown (BMNH); 3♂, Nyeri, vi.1949, E. C. G. Pinhey (BMNH).

Other material (included in PCA). – KENYA: 1♂, Thiririka River, near Ruiro, date unknown, G.R.C. van Someren (BMNH); 1♂, Meru, viii.1937; 1♂, Katamayu, iii.1942, V. G.L. van Someren (BMNH); 1♂, Meru, Kasita River, 10,000 ft. (≈3050 m), iv.1947; 1♂, Meru, Kasita River, 6000 ft. (≈1830 m), iv.1947, G.R.C. van Someren (BMNH); 3♂, Nyeri, vi.1949, E.C.G. Pinhey (BMNH); 1♂, Naivasha, R. Gilgil (irrigation canal), North Lake Rd, 27.xii.1982, P.C. Barnard (BMNH); 1♂, Mt Kenya, Kentrout, iv.1983, V. Clausnitzer (CVCH); 1♂, Njoro, Ndaragu River, 12.x.1987, leg. 'AW' (BMNH). – TANZANIA: 2♂, 3♀, Mt Meru, 7500 ft. (≈2290 m), xii.1937-ii.1938; 3♀, W Kilimanjaro, 4500-5000 ft. (≈1400-1500 m), xii.1937-ii.1938, B. Cooper (BMNH). – UGANDA: 1♂ Bwamba Pass, Ruwenzori, ca 4500-5000 ft. (≈1400-1500 m), 13-15.i.1926, G.D. Hale Carpenter (BMNH); 1♂, Mt Elgon NP, 2.iv.1997, V. Clausnitzer (CVCH).

Other material (not included in PCA). – SUDAN: 1♂, Imatong Mts, south of Gilo, 2000 m, 12.ii.1981, M. Wasscher [*A. biordinata* in Wasscher (1985); specimen lost, photograph examined]. – TANZANIA: 2♀, Meru Niederung, 27.xii.1905, Y. Sjöstedt (NHRS).

Atoconeura aethiopica Kimmins
(figs. 13, 31, 37, 48)

Atoconeura biordinata aethiopica Kimmins, 1958: 357. Holotype ♂: ETHIOPIA: round label, white with red border 'Holotype', rectangular, white 'Ethiopia, Segheria, 25.iii.1948. K.M. Guichard. B.M. 1948-248.', rectangular, white 'Atoconeura biordinata ♂ aethiopica Kim D.E. Kimmins det. 1958 Type' (BMNH) [examined].

Atoconeura kenya aethiopica Kimmins, 1958 – (Bridges 1991: VIII.9).

Atoconeura aethiopica Kimmins, 1958 – (Clausnitzer & Dijkstra 2005: 126).

Diagnosis

Similar to *A. kenya* (see that species), but the epiproct was marginally shorter (fig. 37), the abdomen somewhat narrower and abdominal pruinosity complete in all examined males (fig. 48). The dark area on the frons has a straight anterior edge in *A. aethiopica* males, but is rounded in *A. kenya* (figs. 12-13). Facial markings tend to be even paler and the marking on the labium is more variable: it can be exactly as in *A. kenya*, but is sometimes strongly reduced. The dark colour of the thorax is more brown than black, making pale markings ill-defined. Unlike other species, females are so light that their thorax appears uniformly brown.

Variation

The pattern on the labium is very variable (Kimmins 1958, Pinhey 1982). The labrum may be all pale (fig. 13) or have a narrow black border.

Range

Endemic to Ethiopia and not uncommon along clear streams and rivers (often with forest) at 1250-2400 m south of Addis Abeba (Clausnitzer & Dijkstra 2005).

Remarks

Only two females could be examined. Their all-brown appearance may be a preservation artefact, although I believe my interpretation of their lack of markings is correct.

Further type material (included in PCA). – Paratypes: ETHIOPIA: 1♀ ('allotype'), round label, white with red border 'Allotype', rectangular, white 'Ethiopia, Segheria, 25.iii.1948. K.M. Guichard. B.M. 1948-248.', rectangular, white 'Segheria, 25.3.48', rectangular, white 'Atoconeura biordinata ♀ aethiopica Kim D.E. Kimmins det. 1958 Allotype' (BMNH); 1♂, Segheria, 25.iii.1948; 1♂, Dilla, iv.1948; 1♂, Wondo, iv.1948, K.M. Guichard (BMNH).

Other material (included in PCA). – ETHIOPIA: 1♂, Lac Zouay, 19.iii.1914, leg. unknown (MNHN); 1♀, Segheria, 25.iii.1948, K.M. Guichard (BMNH).

Other material (not included in PCA). – ETHIOPIA: 1♂, Gubali, 4.iii.1934, leg. unknown (NHRS); 2♂, Baro River between Gordomo and Masha (1630m), 30 km south of Gore, 17.iii.2004; 1♀, stream near Gecha, 40 km north of Tepi, 17.iii.2004; 1♂, Wushwush Tea Plantation (1900m), 13 km west of Bonga, 19.iii.2004; 1♂, Borkana River near Yayu (1290m), 35 km east of Matu (Metu), 21.iii.2004, V. Clausnitzer & K.-D.B. Dijkstra (RMNH).

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Table 1. Measurements of the species. Figures represent averages for continuous measures and sums, and modi for counts, with ranges given in brackets.

	A. luxata sp. n.	*A. eudoxia*	*A. pseudeudoxia*	*A. biordinata*	*A. kenya*	*A. aethiopica*
♂ : ♀	19 : 3	15 : 9	22 : 8	43 : 14	20 : 7	5 : 2
Hw ♂ (mm)	33.4 (30.5 - 36)	34.5 (33.5 - 36)	34.1 (32 - 36.5)	30.6 (28 - 33.5)	32.5 (31 - 35)	32.4 (31 - 34)
Hw ♀ (mm)	36.8 (36.5 - 37)	36.8 (35 - 38.5)	35.3 (34 - 36.5)	32.1 (30 - 35.5)	32.8 (32 - 34)	34.5 (34 - 35)
Fw Ax ♂♀	12 - 13 (11 - 14)	11 - 12 (10 - 14)	12 - 13 (10 - 14)	10 - 11 (9 - 13)	10 - 11 (9 - 12)	9 - 10 (- 11)
Fw Px ♂♀	9 - 10 (8 - 11)	8 - 9 (7 - 11)	8 - 9 (7 - 11)	7 - 9 (6 - 10)	8 - 9 (- 10)	8 (- 9)
Σ Fw Ax Px ♂♀	44.4 (39 - 50)	40.6 (36 - 45)	42.7 (39 - 47)	37.0 (32 - 44)	38.8 (36 - 43)	35.4 (34 - 37)
Abd ♂ (mm)	30.3 (28 - 33)	31.5 (30 - 34)	31.6 (29 - 35)	27.2 (25 - 31)	27.0 (26 - 28)	27.2 (27 - 28)
% Abd / Hw ♂	89.6	91.2	92.5	89.1	82.8	84.0

Table 2. Character matrix for cladistic analysis. Numbers correspond to those in appendix 2.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
A. luxata	2	2	3	2	1	2	1	0	1	1	1	0,1	1	1	0	2	1	1	0	2	2	0	0	0	2	0	0	0
A. eudoxia	2	2	1	2	0	2	1	0,1	1	1	1	0	1	1	0	0,1	0	0	1	0	1	1	1	1	2	2	1	1
A. pseudeudoxia	2	2	2	2	0	2	1	0	1	1	1	0	1	1	0	1,2	0	2	2	0	0	0	1	1	2	2	1	1
A. biordinata	0	1	0	1	0	1	1	1	0	1	0	0,1	1	1	0	2	0	1	1	1	0	0	0	0	1	1	0	1
A. kenya	1	0	1	0,1	0	0	0	0,1	0	0	0	1	0	0	1	2	0	1	0	1	0	0	0	0	0	0	1	2
A. aethiopica	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	2	0	1	0	1	0	0	0	0	0	0	1	2
M. bispina	0	1	1	0	0,1	2	1	0	1	1	?	1	1	1	0	0	0	0	0	2	2	1	0	0	2	?	?	?
O. lugubris	2	2	3	2	1	2	1	0	1	1	1	1	0	1	0	2	0	1	0	1	2	0	0	0	2	?	?	?
Z. flavicosta	2	1	2,3	2	0,1	2	1	0	1	1	1	1	1	1	0	2	1	1	0	2	2	0	0	0	2	?	?	?

Appendix 1: Characters used in Principal Component Analysis.

States (all ordered) are arranged from small to large and from pale to dark as much as possible.

Size

1. Hw length: in mm.
2. Relative abdomen length (♂ only): abdomen length / Hw length.

Wings

3. Px: sum of both Fw.
4. Ax: sum of both Fw.
5. Fw triangles crossed: (0) neither; (1) one; (2) both.
6. Membranule: (0) beige; (1) brown with beige basal lining; (2) brown.
7. Amber wing base: (0) absent; (1) present.

Head

8. Lengthwise extent of labial black: (0) not reaching apex along inner edges; (1) narrow along entire inner edge; (2) broad along entire inner edge.
9. Breadthwise extent of labial black: (0) restricted to prementum; (1) reaching up to a third of length and breadth of labium; (2) up to two-thirds; (3) more than two-thirds.
10. Labrum: (0) all pale; (1) pale with thin black edge; (2) pale with broad black edge; (3) all black.
11. Centre of postclypeus: (0) all pale; (1) with paired black spots; (2) with black bar.
12. Antero-lateral edges of postclypeus: (0) pale; (1) marked with black.
13. Anterior edge of frons (antefrons): (0) pale; (1) brown; (2) shiny black.
14. Medial part of frons (shields): (0) pale; (1) brown; (2) shiny black.
15. Lengthwise extent of dark mark on frons: (0) restricted to base; (1) extends slightly down central groove; (2) extends well down the groove.
16. Breadthwise extent of dark mark on frons: (0) restricted to central groove; (1) laterally bordered pale; (2) extending over lateral sides.
17. Vertex: (0) pale; (1) brown; (2) shiny black.

Thorax

18. Yellow 'hyphens' anterior to antealar sinus: (0) obliterated by paleness of dorsum; (1) present; (2) absent.
19. Sides: (0) evenly brown; (1) black and yellow with extra spot near Fw base; (2) black with yellow spots.

Abdomen

20. Pruinosity (♂ only): (0) absent; (1) present only basally; (2) present throughout.
21. Yellow markings on S2 (♂ only): (0) joined; (1) narrowly severed; (2) broadly severed.
22. Basal yellow marking on S3: (0) crescentic; (1) ovoid or triangular.
23. Basal yellow spots on S4-9: (0) present; (1) absent.
24. Relative width of S7: (0) broad; (1) intermediate; (2) narrow.

Sexual characters ♂

25. Dorsal profile of cerci: (0) rather flat; (1) weakly curved up; (2) strongly curved up.
26. Ventral ridge of cerci: (0) straight; (1) weakly sinuous; (2) strongly sinuous.
27. Length of epiproct: (0) falls short of ventral angle of cerci; (1) reaches to angle; (2) reaches beyond angle.
28. Shape of epiproct: (0) entire; (1) bifid.

Sexual characters ♀

29. Length of cerci: (0) as long as epiproct; (1) slightly longer; (2) much longer.
30. Tip of cerci: (0) blunt; (1) pointed.
31. Epiproct: (0) bare; (1) sparsely hairy; (2) densely hairy.
32. Cleft of vulvar scale: (0) wide; (1) intermediate; (2) narrow.
33. Reach of vulvar scale: (0) to end of S8; (1) beyond end of S8.

Appendix 2: Characters used in cladistic analysis.

Numbers of corresponding characters in PCA are given in brackets. All character states are ordered and were taken from males only, except for female sexual characters.

Size

1. (1). Size, based on Hw length: (0) small; (1) medium-sized; (2) large.
2. (2/24). Abdomen shape: (0) S7 broad, abdomen length is about 80-85% of Hw length; (1) S7 intermediate, abdomen is about 85-90% of Hw; (2) S7 narrow, abdomen is about 90-95% of Hw.

Wings

3. (3/4). Density of venation, based on sum of Ax and Px in both Fw: (0) very open; (1) fairly open; (2) fairly dense; (3) very dense.
4. (6). Membranule: (0) beige; (1) brown with beige basal lining; (2) brown.
5. (7). Amber wing base: (0) absent; (1) present.

Head

6. (8/9). Shape of labial black: (0) relatively narrow at apex and with greatest extent subapically; (1) intermediate; (2) relatively broad at apex and with greatest extent at base.
7. (10). Labrum: (0) largely pale; (1) largely black.
8. (13). Anterior edge of frons (antefrons): (0) pale; (1) dark.
9. (14). Medial part of frons (shields): (0) pale; (1) dark.
10. (15). Lengthwise extent of dark mark on frons: (0) at most extends slightly down central groove; (1) extends well down the groove.
11. (16). Breadthwise extent of dark mark on frons: (0) laterally bordered pale; (1) extending over lateral sides.
12. (17). Vertex: (0) tends to be brown; (1) tends to be shiny black.

Thorax

13. (18). Yellow 'hyphens' anterior to antealar sinus: (0) present; (1) absent.
14. (19): Sides: (0) black and yellow with extra spot near Fw base; (1) black with yellow spots.

Abdomen

15. (20). Pruinosity: (0) always absent; (1) present when mature.
16. (21): Yellow markings on S2: (0) joined; (1) narrowly severed; (2) broadly severed.
17. (23). Basal yellow spots on S4-9: (0) present; (1) absent.

Sexual characters ♂

18. (25). Dorsal profile of cerci: (0) rather flat; (1) weakly curved up; (2) strongly curved up.
19. (26). Ventral ridge of cerci: (0) straight; (1) weakly sinuous; (2) strongly sinuous.
20. (27). Length of epiproct: (0) falls short of ventral angle of cerci or just reaches it; (1) reaches slightly beyond angle; (2) reaches well beyond angle.

Sexual characters ♀

21. (32). Cleft of vulvar scale: (0) wide; (1) intermediate; (2) narrow.
22. (33). Reach of vulvar scale: (0) to end of S8; (1) beyond end of S8.

Characters not corresponding with any used for PCA

23. Poststernum: (0) flat and sparsely hairy; (1) raised and densely hairy.
24. Hind femora: (0) sparsely hairy; (1) densely hairy.
25. Length of fourth segment of penis: (0) short; (1) intermediate; (2) long.
26. Apex of fourth segment of penis: (0) narrow; (1) intermediate; (2) broad.
27. Ventral hump on fourth segment of penis: (0) absent; (1) present.
28. Cornua of penis: (0) absent; (1) short; (2) long.

Appendix 3: Apomorphies of nodes in fig. 5.

Numbers of characters are given before, of states after the point. All characters refer to males only, except for female sexual characters. Ambivalent (i.e. variable within species) and homoplasious (prone to reversal or parallelism) characters were omitted (except 27).

Clusters 2, 3 and 4 (all species except *A. luxata* sp. n.):
5.0: Amber at wing base absent.
17.0: Basal yellow spots on S4-9 present.
20.0,1: Epiproct does not reach well beyond ventral angle of cerci.
21.0,1: Cleft of vulvar scale (rather) wide.
27.1: Ventral hump on fourth segment of penis present [reversal to absence (0) in cluster 3].
28.1,2: Cornua of penis present.

Cluster 2 (*A. eudoxia* and *A. pseudeudoxia*):
20.0: Epiproct falls short of ventral angle of cerci or just reaches it.
23.1: Poststernum raised and densely hairy.
24.1: Hind femora densely hairy.
26.2: Apex of fourth segment of penis broad.

Clusters 3 and 4 (*A. aethiopica*, *A. biordinata* and *A. kenya*):
1.0,1: Small or medium-sized.
2.0,1: S7 (rather) broad, abdomen length is about 80-90% of Hw length.
4.0,1: Membranule at least with beige basal lining, not all brown.
6.0,1: Labial black not relatively broad at apex but narrow at base.
9.0: Medial part of frons (shields) pale.
20.1: Epiproct reaches slightly beyond ventral angle of cerci.
25.0,1 Fourth segment of penis (rather) short.

Cluster 3 (*A. biordinata*):
1.0: Small size.
2.1: S7 intermediate, abdomen is about 85-90% of Hw.
6.1: Shape of labial black intermediate.
25.1: Length of fourth segment of penis intermediate.
26.1: Breadth of apex of fourth segment of penis intermediate.

Cluster 4 (*A. aethiopica* and *A. kenya*):
1.1: Medium-sized.
2.0: S7 broad, abdomen length is about 80-85% of Hw length.
4.0: Membranule all beige, only occasionally brown with beige basal lining (4.1).
6.0: Labial black relatively narrow at apex and with greatest extent subapically.
7.0: Labrum largely pale.
10.0: Dark mark on frons at most extends slightly down central groove.
13.0: Yellow 'hyphens' anterior to antealar sinus present.
14.0: Sides of thorax black and yellow with extra spot near Fw base.
15.1: Pruinosity present when mature.
25.0: Fourth segment of penis short.
28.2: Cornua of penis long.

chapter 7

Taxonomy and biogeography of *Porpax*, a dragonfly genus centred in the Congo basin (Odonata, Libellulidae)

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Disclaimer

This work is not issued for purposes of zoological nomenclature and is not published within the meaning of the International Code of Zoological Nomen-clature (1999) (see article 8.2).

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TAXONOMY AND BIOGEOGRAPHY OF *PORPAX*, A DRAGONFLY GENUS CENTRED IN THE CONGO BASIN (ODONATA, LIBELLULIDAE)

Dijkstra, K.-D.B., 2006. Taxonomy and biogeography of *Porpax*, a dragonfly genus centred in the Congo Basin (Odonata, Libellulidae). – Tijdschrift voor Entomologie 149: 71-88, figs. 1-47, tables 1-2. [ISSN 0040-7496]. Published 1 June 2006.

The tropical African genus *Porpax* is revised, five species are recognised, including the new species *P. sentipes* from Congo-Kinshasa. All species are fully diagnosed for both sexes and new records are included. A key to the species and illustrations of important characters are provided. The peculiarities of the genus are discussed, but little is known of its ecology. *P. garambensis* and *P. sentipes* sp. n. are confined to the Congo Basin, while *P. asperipes* is also present in the adjacent Lower Guinean forest. *P. risi* is spread out across highlands in south-central Africa. *P. bipunctus* is known from four disjunct rainforest regions from Liberia to eastern Congo and has different markings in each region. This distribution coincides with Africa's main rainforest refugia and is the best example of such disjunction seen in Afrotropical Odonata so far. The species' isolation appears to be linked to an ephemeral habitat, confining it to areas with perennial and predictable rainfall.

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Key words. – Anisoptera; Libellulidae; *Porpax*; systematics; refugia; keys; Africa.

The genus *Porpax* is endemic to tropical Africa. Karsch (1896) based the genus on the single species *P. asperipes*, of which Pinhey (1958) described the subspecies *P. asperipes risi*. He raised *P. risi* to species level when it was found to co-occur with *P. asperipes* in NW Zambia (Pinhey 1964a, b). Pinhey (1966) revised the genus, adding *P. bipunctus* and *P. garambensis*, the latter known only from the holotype. Many specimens in the Musée Royal de l'Afrique Centrale, Tervuren (MRAC), all placed under *P. asperipes*, in fact belonged to four taxa: *P. asperipes*, *P. bipunctus*, *P. garambensis*, and a new species. Fraser (1954) indicated his 'hope to deal with *Porpax* [material in MRAC] later', but his wish never materialised. This paper aims to (re-)describe and compare the five species of this small and highly characteristic genus , and review their ecology and biogeography.

Methods and material

All available material was compared (table 1), with an emphasis on the extensive Congolese collections in MRAC and primary types in BMNH, MRAC, NMBZ and ZMHB.

Acronyms of collections

BMNH	Natural History Museum, formerly British Museum (Natural History), (London, UK)
CGVL	Collection Graham Vick (Little London, UK)
CJLH	Collection Jochen Lempert (Hamburg, Germany)
ISNB	Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)
MNHN	Muséum National d'Histoire Naturelle (Paris, France)
MNMS	Museo Naçional de Ciencias Naturales (Madrid, Spain)
MRAC	Musee Royal de l'Afrique Centrale (Tervuren, Belgium)
NHRS	Naturhistoriska Riksmuseet (Stockholm, Sweden)
NMBZ	Natural History Museum of Zimbabwe (Bulawayo, Zimbabwe)
RMNH	Nationaal Natuurhistorisch Museum Naturalis, formerly Rijksmuseum van Natuurlijke Historie (Leiden, Netherlands)
ZMHB	Museum für Naturkunde der Humboldt-Universität (Berlin, Germany)

Table 1: Comparison of *Porpax* species. Average measurements and vein counts are based on stated samples sizes (range between brackets).

species n ♂ : ♀ =	*risi* 22 : 2	*garambensis* 12 : 8	*asperipes* 21 : 19	*bipunctus* 17 : 3	*sentipes* sp. n. 20 : 12
Hw length ♂ (mm)	23.1 (22.0-24.5)	22.4 (21.5-23.0)	26.2 (24.5-28.5)	26.0 (24.5-27.5)	24.2 (22.5-25.5)
Hw length ♀ (mm)	23.8 (23.5-24.0)	23.8 (23.0-25.0)	26.7 (25.0-28.0)	28.0 (27.5-28.5)	25.4 (23.5-26.0)
Labrum (figs. 1-3)	pale, black border	black	black	black, sometimes 2 large pale spots	black, often 2 small pale spots
Pale band on frons (figs. 1-3)	complete	severed	often severed	at most thinly severed	severed
Occipital triangle	largely pale to largely black	largely pale	largely black	largely black	largely black
Postgenae (figs. 4-7)	black, 4 sharp spots	black, 2 sharp spots	black, 2-3 sharp spots	brown to black, 2-3 sharp to vague spots	black, 2 sharp spots
Prothorax above coxa	with spot	at most with small spot	all dark	all dark	with spot
Spiracular dorsum ♂ (figs. 8-9)	large central spot	all dark	large central spot	large central spot	all dark, some with central spot
Postdorsal stripes (figs. 8-9)	slightly oblique, narrow	oblique, wide	parallel, narrow	parallel, narrow	parallel, narrow
Mesokatepisternum (figs. 10-14)	two pale spots	one pale spot	one pale spot	one pale spot	one pale spot
Interpleural stripe (figs. 10-14)	narrow	wide, but enclosing small pale spot	wide	narrow to fairly wide	wide
Metepisternal stripe (figs. 10-14)	wide and broken	narrow, often broken	narrow, often broken	wide	narrow, sometimes broken
Synthoracic venter ♂	all black, or small pale blotches on metepimera	all black, at most small pale blotches on metepimera	black, poststernum and metepimera largely pale	brown to black, pale blotches on poststernum and metepimera	black, poststernum and metepimera largely pale
Costa and subcostal cross-veins	pale	dark	dark	dark	dark
Number of Fw Ax	9.8 (8½-10½)	9.8 (8½-10½)	11.2 (9½-13)	11.1 (9½-14)	10.4 (9½-11½)
% of Hw with >1 Cux	93.8	30.0	96.2	100.0	95.3
Anal loop (figs. 15-16)	closed	closed	closed	open	closed
Fore coxae	with spot	all dark	all dark	all dark	all dark
Hind femur ♂ (figs. 17-25)	thinly hairy, single strong spine row	densely hairy, single weak spine row	quite densely hairy, single spine row	bare, single strong spine row	bare, double spine row
Pruinosity ♂ (figs. 43-45)	on dorsum synthorax and abdomen	on s2-4	on dorsum synthorax and abdomen	none	none
Abdomen shape ♂ (figs. 26-31)	broad	waisted	waisted	waisted	waisted
Hook of hamule (figs. 36-39)	long	short	long	long	long
Lobe of hamule (figs. 36-39)	slightly pointed	pointed	rounded	rounded	rounded

Dorsum S2 basal pale marking ♂ (figs. 26-31)	spot	band	spot or band	spot or band	band
Dorsum S2 apical pale marking ♂ (figs. 26-31)	spot	none	none or spot	spot or band	none
S3 anterior marking ♂ (figs. 26-31)	dorsal and lateral spots	complete or thinly interrupted ring	thinly interrupted ring	complete or thinly interrupted ring	complete or thinly interrupted ring
S3 posterior marking ♂ (figs. 26-31)	dorsal and lateral spots	broadly interrupted ring	broadly interrupted ring	complete to broadly interrupted ring	broadly interrupted ring
S6 marking (figs. 32-35)	dorsal and lateral spots	narrow perpendicular band, seldom black on dorsal carina	narrow perpendicular band, black on dorsal carina	dorso-apically skewed band, not black on dorsal carina	narrow perpendicular band, not black on dorsal carina
Vulvar scale (figs. 41-42)	appressed, concave	projecting, convex	appressed, concave	appressed, concave	appressed, concave
Epiproct ♂	dark	pale	dark	pale to dark	pale

Scanning electron microscopy was used to examine details of leg armature (figs. 22-25) and secondary genitalia (figs. 36-39). Abbreviations. – Ax: antenodal cross-veins, Ax1: first antenodal (counted from base) etc., Cux: cubital cross-veins, Fw: forewing(s), Hw: hindwing(s), Pt: pterostigma, Px: postnodal cross-veins, S1: first abdominal segment, S2-3: second and third abdominal segments etc.

Taxonomic part

Porpax Karsch

Porpax Karsch, 1896: 17. Type species: *Porpax asperipes* Karsch, 1896 (by monotypy).

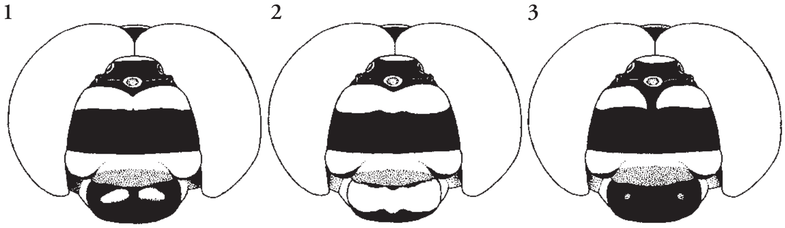
Diagnosis

In Africa the following combination of venation characters is found only in *Porpax*: (1) arculus placed between Ax2 and Ax3; (2) distal Fw Ax incomplete; (3) subtriangle normally of three cells (sometimes two); (4) Fw discoidal field of two rows of cells at base (sometimes three cells bordering triangle); (5) Fw with one Cux but Hw with two (occasionally three or four, usually one in *P. garambensis*); (6) all wings with one bridge cross-vein. The genus is further characterized by its small size (Hw 21.5-28.5 mm) and stocky build, black body marked boldly with greenish yellow, the barred face and often banded S6 being especially conspicuous (figs. 1-3, 32-35), and the short legs ornamented with stout spines and often with long bristly hairs (figs. 17-25).

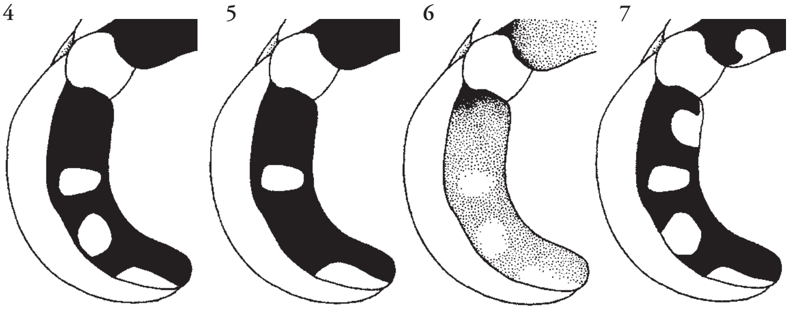
Characters

Males of the various species are similar in structural characters such as secondary genitalia and appendages (figs. 36-40), differing mainly in colour pattern (figs. 1-14, 26-35) and ornamentation of the legs (figs. 17-25). Especially the uniformity of the secondary genitalia (including anterior lamina, hamule and genital lobe) is atypical within the Libellulidae (figs. 36-39). Another feature unusual for the family, and the Anisoptera as a whole, is the position of the prominent pale marking on the abdomen. All species possess a broad pale ring on S6, with the exception of *P. risi* that lacks a striking subterminal marking altogether (figs. 32-35). Generally in Anisoptera such a 'signal spot' is situated on S7. African examples of a prominently marked S7 are found in most Gomphidae, *Phyllomacromia* Selys, 1878 (Corduliidae) and all *Atoconeura* Karsch, 1899 and some *Zygonyx* Hagen, 1867 species (Libellulidae).

Females appear more washed-out and variable than males, with less contrasting and sometimes more extensive pale markings, which reduces the usefulness of these characters. Pruinosity does not develop and all have thick spindle-shaped abdomens. Hind femur ornamentation is more uniform and although hairy-legged males have relatively hairy-legged females, these differences are hard to quantify and only useful in direct comparison. Mated pairs were unavailable for this study, and females had to be associated with males by locality and resemblance. For *P. risi* and *P. garambensis* this posed few problems, but females of the two most abundant species in the MRAC material, *P. asperipes* and *P. sentipes* sp. n., so different as males, proved quite similar. Nonetheless characters shared with the males, although more weakly expressed, make a correct association possible. The *P. bipunctus* female stands out by her open anal loop.



Figs. 1-3.
Head of *Porpax* species in rostral view. – 1, *P. bipunctus* Cameroon; 2, *P. risi*; 3, *P. sentipes*.



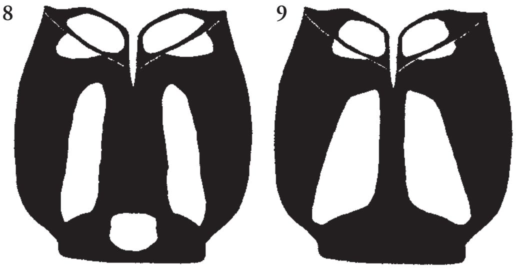
Figs. 4-7.
Head of *Porpax* species in caudal view. – 4, *P. bipunctus* Côte d'Ivoire; 5, *P. bipunctus* Cameroon; 6, *P. bipunctus* NE Congo-Kinshasa; 7, *P. risi*.

Ecology and biogeography

Porpax species are generally scarce in collections, possibly because they occur locally, and therefore their distributions and habitat preferences are imperfectly known. The scanty ecological data suggest that the species breed in shallow standing and slow-flowing water with bottom substrates of coarse detritus, such as temporary forest pools, muddy streams and grassy swamps. The species have large and widely overlapping ranges and the Congo Basin appears to be the genus' centre of distribution (fig. 46): at Bambesa (NE of basin) all species except *P. risi* have been collected and at Kabongo (SE) all but *P. bipunctus* (fig. 47). Of the three shared species *P. garambensis* and *P. sentipes* sp. n. are as yet unknown outside Congo-Kinshasa, while *P. asperipes* just extends into adjacent Zambia and across to SE Nigeria. *P. risi* is unusual in appearance, range and possibly ecology, occurring well south of the other species. It seems to be the only species that is not associated with forest, occurring in open swamps scattered across highlands from Angola to Katanga and Mozambique. *P. bipunctus* is exclusively associated with forest. It has been found in highly disjunct areas, which correspond with important rainforest refugia in the Upper Guinea (Liberia, Côte d'Ivoire), Lower Guinea (Cameroon, Gabon) and the eastern side of the Congo Basin (NE Congo-Kinshasa) (Clausnitzer 2003, Fjeldså & Lovett 1997, Kingdon 1989). This is the best example of refugial disjunction found in Afrotropical Odonata so far. The pattern is supported by the absence of records from regions in-between and the presence of marked regional forms (see *P. bipunctus* text). This is in contrast to the other *Porpax* species, which have been collected more widely and are geographically uniform. The isolation of *P. bipunctus* may be linked to the probably ephemeral nature of its reproductive habitat (see range and ecology op p. 82). In his discussion of a Papuan rainforest odonate community, Oppel (2005) remarked on the relative paucity of species inhabiting pools under closed canopy left by temporary streams in Africa. This may be linked to the more seasonal and unstable climatology of African tropical forest. Possibly *P. bipunctus* is confined to areas with perennial and predictable rainfall.

Key to males of *Porpax*

1. Anterior side of hind femur and trochanter bare, at most some scattered very short hairs (figs. 18, 21, 23, 25). Abdomen never pruinose 2
– Anterior side of hind femur and trochanter densely hairy, hairs about as long as femur is wide (figs. 17, 19-20, 22, 24). Abdomen (partly) pruinose when mature 3
2. Anal loop open on wing border (fig. 16). About 15-20 spines in outer anterior row of hind femur, entirely in single file (figs. 18, 23). Pale band across frons often complete (fig. 1). Prothorax usually without pale spot above coxa. Spiracular dorsum with large central pale spot (cf. fig. 8). Interpleural stripe narrower than anteriorly adjacent pale stripe and often narrower than



Figs. 8-9. Synthorax of *Porpax* species in dorsal view. – 8, *P. asperipes*; 9, *P. garambensis*.

posteriorly adjacent pale stripe (fig. 11). Pale ring on S6 skewed, dorsal part shifted apically (lateral view, fig. 33). Hw 24-27 mm .... *bipunctus*

– Anal loop closed before wing border (cf. fig. 15). About 30-40 spines in outer anterior row of hind femur, row doubled at base of femur (figs. 21, 25). Pale band across frons broken by black in median groove (fig. 3). Prothorax with large pale spot above coxa. Spiracular dorsum often all black (cf. fig. 9). Interpleural stripe at least as wide as adjacent pale stripes (fig. 14). Pale ring on S6 perpendicular (cf. fig. 34). Hw 22-26 mm .... *sentipes*

3. Labrum pale with black anterior border; pale band across frons complete (fig. 2). Mesokatepisternum with anterior and posterior pale spots; interpleural stripe narrower than adjacent pale stripes (fig. 13). Costa and subcostal cross-veins pale. S3-9 with pale dorsal spots, S6 without pale ring (figs. 30, 35; not visible when pruinose) .... *risi*

– Labrum all black; pale band across frons often broken by black in median groove (cf. fig. 3). Mesokatepisternum only with posterior pale spot; interpleural stripe at least as wide as adjacent pale stripes (figs. 10, 12). Costa and subcostal cross-veins black. S3-9 black dorsally, S6 with pale ring (figs. 26, 29, 32, 34; not visible when pruinose) 4

4. Postdorsal stripes converging dorsally, black area between them narrower than stripes; spiracular dorsum all black (fig. 9). Less than half of occipital triangle black (dorsal view). Venter of synthorax largely to entirely black. Abdomen only becomes pruinose on S2-4. Hamules with pointed lobe and short hook (fig. 37). Hw 21-23 mm. 8½-10½ Fw Ax. 1 Hw Cux (30% of wings have 2-3) .... *garambensis*

– Postdorsal stripes parallel, black between them at least as wide as stripes; spiracular dorsum with large central pale spot (fig. 8). More than half of occipital triangle black. Venter of synthorax with extensive pale areas enclosed by black. Entire abdomen pruinose when mature. Hamules with rounded lobe and long hook (fig. 36). Hw 23-29 mm. 10½-12½ Fw Ax. 2-3 Hw Cux (4% of wings have 1) .... *asperipes*

Key to females of *Porpax*

1. Labrum pale with black anterior border (fig. 2). Mesokatepisternum with anterior and posterior pale spots; pale metepisternal stripe wider than interpleural stripe and broken (fig. 13). Costa and subcostal cross-veins pale. S6 with dorsal and lateral pale streaks, rather like S5 and S7 (fig. 35) .... *risi*

– Labrum black, sometimes with two central pale dots (figs. 1, 3). Mesokatepisternum only with posterior pale spot; pale metepisternal stripe either entire or narrower than interpleural stripe (figs. 10-12, 14). Costa and subcostal cross-veins black. S6 with pale ring, unlike darker S5 and S7 (figs. 32-34) 2

2. Postdorsal stripes converging dorsally, black area between them narrower than stripes (fig. 9). Occipital triangle less than half black (dorsal view). 7-8 spines in outer anterior row of hind femur. Vulvar scale projecting (lateral view), its border bare and convex (ventral view, fig. 42). 1 Hw Cux (30% of wings have 2-3) .... *garambensis*

– Postdorsal stripes parallel, black between them at least as wide as stripes (fig. 8). Occipital triangle more than half black. 10-14 spines in outer anterior row of hind femur. Vulvar scale appressed, its border concave with two lateral hairy swellings (fig. 41). 2-3 Hw Cux (4% of wings have 1) 3

3. Anal loop open on wing border (fig. 16). Pale metepisternal stripe entire, often wider than interpleural stripe (fig. 11). Pale band across frons often complete (fig. 1). Pale ring on S6 skewed, dorsal part shifted apically (lateral view, fig. 33) .... *bipunctus*

– Anal loop closed before wing border (fig. 15). Pale metepisternal stripe often broken, narrower than interpleural stripe (figs. 10, 14). Pale band across frons normally interrupted by black in median groove (fig. 3). Pale ring on S6 perpendicular (figs. 32, 34) 4

4. Prothorax at most with slight pale spot above coxa. Pale ring on S6 interrupted by black along dorsal carina (fig. 32). Hind femur with some long hairs. Hw 25-28 mm .... *asperipes*

– Prothorax with large pale spot above coxa. Pale ring on S6 continuous across pale dorsal carina (cf. fig. 34). Hind femur rather bare. Hw 23-26 mm .... *sentipes*

Figs. 10-14. Synthorax of *Porpax* species in lateral view. – 10, *P. asperipes*; 11, *P. bipunctus* NE Congo-Kinshasa; 12, *P. garambensis*; 13, *P. risi*; 14, *P. sentipes*.

Porpax asperipes Karsch
(figs. 8, 10, 15, 17, 22, 26, 32, 36, 41, 43)

Porpax asperipes Karsch, 1896: 18. Syntype ♀: CAMEROON: ‘Kamerun, Hinterland. **Jaunde-Stat., Zenker S.**’ (ZMHB); syntype ♀; with identical labels and ‘16/3 [1895]’ (ZMHB) [examined].

Other material. – 1♂, ‘S. Leone’, undated, Rutherford (ISNB) [origin doubted]. – CAMEROON, 3♂, 2♀, undated, Rutherford (ISNB); 2♂, 1♀, South-west Province, Lake Edib (4°57.495’N 9°39.157’E), 23.vi.1998, G.S. Vick (CGVL). – CONGO-BRAZZAVILLE: 1♂, Kingoyi, undated, Laman (NHRS). – CONGO-KINSHASA: 1♂, Boma Sundi, undated, P. Rohn (ISNB); 1♂, Mayumbe, undated, R. Mayné (MRAC); 1♂, Bumbuli, 19.iv.1915, R. Mayné (MRAC); 1♂, Banana, viii.1920, H. Schouteden (MRAC); 1♂, Katompe, 9.ii.1929, Ch. Seydel (MRAC); 2♂, Lulua, Kapanga, i.1933, G.F. Overlaet (MRAC); 1♂, Dingila, 1.vii.1933, J.V. Leroy (MRAC); 9♂, Uele, Bambesa, iv.1933-1934, J.V. Leroy (MRAC); 2♂, 1♀, Uele, Bambesa, ix.1933-viii.1934, H.J. Brédo (MRAC); 1♂, Ubangi, Terr. **Giri, Bomboma,** Gulukulu, ii.1935, A. Bal (MRAC); 1♀, Kapanga, i-ii.1936, G.F. Overlaet (MRAC); 1♂, Elisabethville (= Lubumbashi), iii.1936, Ch. Seydel (MRAC); 1♂, 1♀, Likete, xi.1936, J. Ghesquière (MRAC); 49♂, 11♀, Uele, Bambesa, vi.1937-iii.1939, J.M. Vrijdagh (MRAC); 5♂, Uele, Bambesa, vii-x.1938, P. Henrard (MRAC); 11♂, 4♀, Lualaba, Kabongo, xi.1952-x.1953, Ch. **Seydel** (MRAC); 1♂, 1♀, Orientale, Territoire de Basoko, Lokutu, between Lukumete and Lunua (1°16-17’N 23°23-28’E), 375-400 m, forest with streams and clearings, 1-4.xi.2004, K.-D.B. Dijkstra (RMNH). – NIGERIA, 1♂, Old Calabar, undated, Rutherford (ISNB); 3♂, Old Calabar, undated, leg. unknown (ISNB).

Diagnosis

The largest of the pruinose, hairy-legged species. Males are most easily separated from *P. garambensis* and *P. risi* by the lack of their unique characters. Females are very close to *P. sentipes* sp. n. but both sexes (males when not pruinose) can usually be distinguished by the marking of S6: the pale ring is interrupted by black along the dorsal carina (figs. 32, 43).

Remarks

Karsch (1896) diagnosed the genus and species on the basis of two females from Cameroon. Ris (1911) described males from the Selys collection. The latter material largely originates from Cameroon and adjacent Nigeria. Because the variable *P. bipunctus* also occurs in this area and Karsch’s description is brief, it is conceivable that Karsch’s females and Ris’ males were not conspecific. However, now all the involved material has been re-examined it can be stated that it belongs to a single species.

Variation

Sometimes a third pale spot is present between the two usual spots on the postgenae (cf. figs. 4-5).

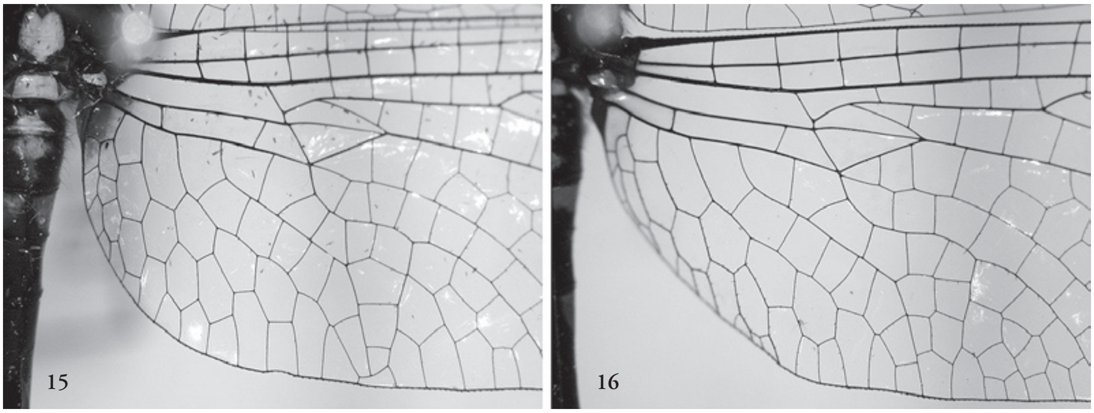
Range and ecology

Most material was from sites throughout Congo-Kinshasa, from where the species ranges west through Congo-Brazzaville (Aguesse 1966), Gabon (seen in MNHN), Rio Muni (in MNMS) and Cameroon to SE Nigeria, and south into the extreme NW Zambia (Pinhey 1984). The species’ presence in Sierra Leone is doubted: like a number of species not found recently in West Africa, the only record pertains to material in the Selys collection (own observations). This material probably originated in Cameroon or adjacent Nigeria and was mislabelled by Rutherford, an important supplier to Selys. The habitat is poorly known. Pinhey (1964a, 1984) mentioned ‘swamp’ and ‘swampy grassland’ for NW Zambia, I found it at a half-sunny muddy stream in rainforest in the central Congo Basin and G.S. Vick (pers. comm.) at a lake edge with floating vegetation, especially grass and mosses, in Cameroon.

Porpax bipunctus Pinhey
(figs. 1, 4-6, 11, 16, 18, 23, 27-28, 33, 44)

Porpax bipunctus Pinhey, 1966: 49. **Holotype** ♂: CAMEROON: ‘Porpax bipunctus Pinhey ♂’, ‘Holotype ♂ Porpax bipunctus Pinhey 1963’, ‘MAMFE BRITISH CAMEROONS II – 1958 Nat. Museum S. Rhodesia’ (NMBZ) [examined].

Porpax bipunctatus de Moor, 1976: 102. – Misspelling.



Figs. 15-16. Hw base of *Porpax* species. – 15, *P. asperipes*; 16, *P. bipunctus*.

Other material. – 1♂, no data, leg. unknown (MNHN). – CAMEROON: 1♀, 16.iv.1891, Y. Sjöstedt (NHRS); 2♂ (paratypes), Mamfe, ii.1958, E. Pinhey (NMBZ); 1♂ (paratype), Mamfe, Gorilla Mountains, ii.1958, E. Pinhey (NMBZ). – CAMEROON (SW): 1♂, Tombel, Ebonji, Sandwater Falls, 200m, 6.iv.1995, G.S. Vick (CGVL); 1♂, Meme Tombel, Lala, R. Ndibe, 400m, 29.vii.1995, O. Mesumbe (CGVL); 1♂, Matene Camp (6°11.029’N 9°20.596’E), 16.iv.2001, O. Mesumbe (CGVL); 1♂, Takamanda Camp (6°03.181’N 9°14.483’E), 25.iv.2001, O. Mesumbe (CGVL); 1♂, Kekpane Village (6°05.841’N 9°23.929’E), 26.vi.2001, O. Mesumbe (CGVL). – CONGO-KINSHASA (UELE): 6♂, 1♀, Bambesa, iv.1937-ii.1939, J.M. Vrijdagh (MRAC); 1♂, Bambesa, v.1937, P. Henrard (MRAC); 1♂, Bambesa, xii.1938, J.M. Vrijdagh (BMNH). – COTE D’IVOIRE: 2♂, Forêt de Taï, 8.v.-3.vi.1980, G. Couturier (MNHN). – GABON (MAKOKOU): 3♂, 1♀, Ipassa, 14.x.-17.xi.1976, J. Legrand (MNHN); 1♂, Ebieng, 11.i.1978, J. Legrand (MNHN); 1♂, Mezale, 3.ii.1978, J. Legrand (MNHN). – LIBERIA (SE): 1♂, Sinoe River, 19.i.1987, J. Lempert (CJLH); 1♂, Jalay Town, 24.ii.1987 (CJLH) [both examined by J. Lempert]. – NIGERIA (SE): 1♂, 1♀ (paratypes), Ajassor-Ikom, ii.1958, E. Pinhey (NMBZ).

Diagnosis

Large, bare-legged species with three unique structural features: the anal loop is poorly defined distally and therefore open on the posterior wing border (fig. 16); the hind femora are plump and bare with a saw-like single row of large denticles (figs. 18, 23); the cerci have 8-10 rather scattered ventral denticles (in others 8-12 denticles are placed on a slight, sinuous ridge). Maculation is variable, especially on the head, thorax and abdomen base, but with two distinctive features: the pale lateral synthoracic stripes are relatively broad and straight, with the black interpleural stripe narrower than the anteriorly adjacent pale stripe and often that posteriorly adjacent (fig. 11); the dorsal portion of the pale band on S6 is shifted apically (fig. 33).

Remarks

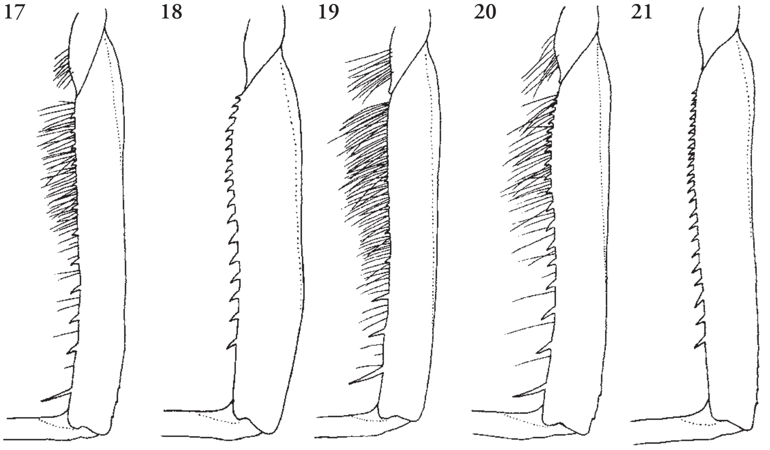
The open anal loop is a remarkable species character, because the loop’s shape is typically constant within libellulid genera. An open anal loop characterises some genera that are highly distinct from *Porpax*, like *Tholymis* Hagen, 1867 and *Zyxomma* Rambur, 1842. In all mentioned cases the feature is remarkably stable, although an open loop only requires a slight reconfiguration of cells (figs. 15-16).

Pinhey’s (1966) brief description of the holotype unfortunately does not cover the variable features of *P. bipunctus* in detail. It seems apt to provide a fuller description of the species, for which I chose the most disparate form, from NE Congo-Kinshasa.

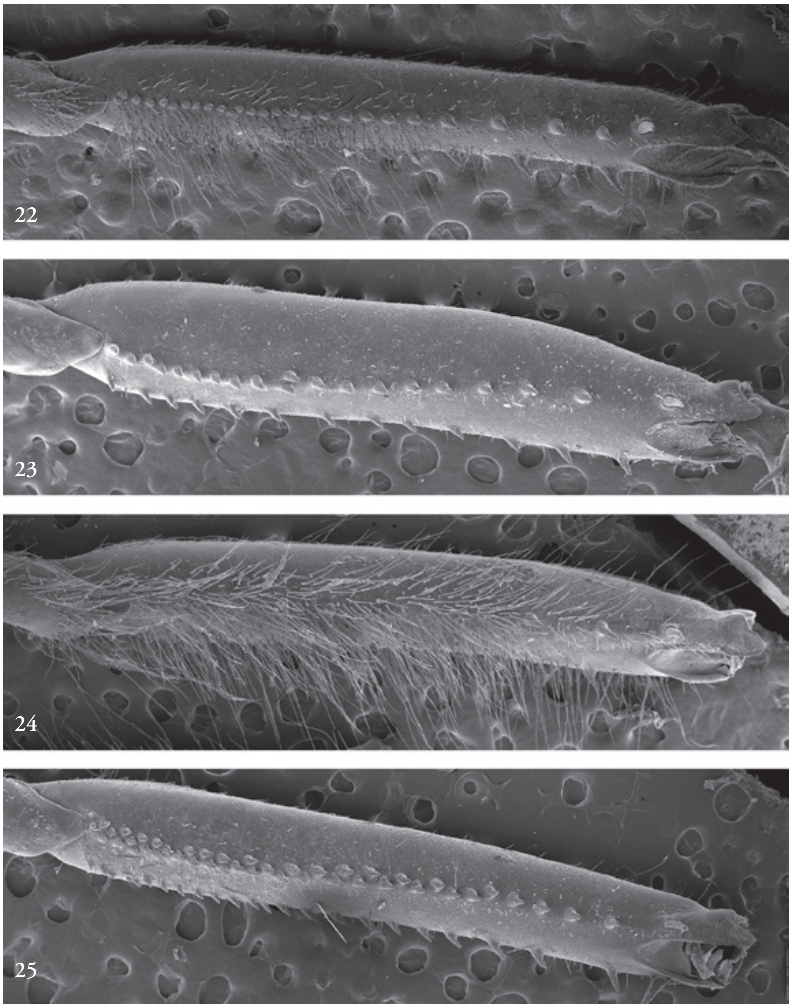
Redescription

Bambesa male. – Measurements (mm): entire length: 32, abdomen length (without appendages): 20, Fw length: 28, Hw length: 27, Fw Pt: 2.2.

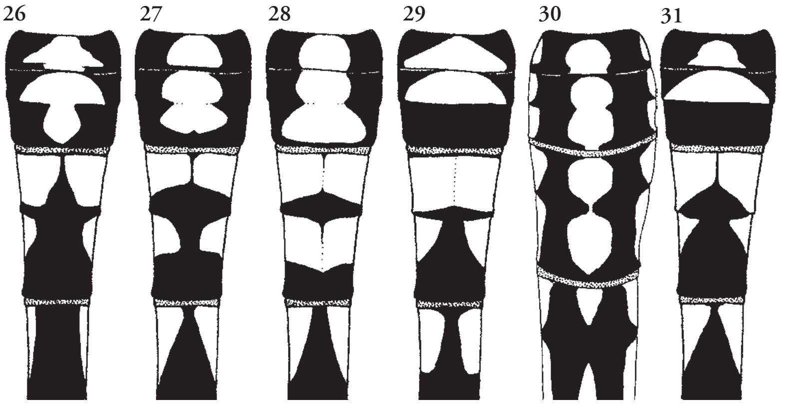
Prementum dark brown, labial palps including squames yellow with inner third black, this central black area widening anteriorly and extending broadly along anterior border. Mandibles yellow, genae brown. Labrum glossy black, becoming deep brown at centre of base. Anteclypeus dark brown, postclypeus greenish yellow with anterior border narrowly black laterally. Frons broadly glossy brown-black anteriorly, narrowly black bordering vertex, enclosing broad pale green band on dorsum. Vertex black, dorsally with large pale green spot. Anterior two-thirds of occipital triangle brown-black, posterior part and down occiput pale green. Postgenae deep brown (slightly rusty), blacker where bordering occiput, with vaguely outlined roundish greenish yellow spots subdorsally, a similar yellow streak along eye border at ventral end and a smaller yellow spot in-between (fig. 6). Antennae and their bases black. Labrum,



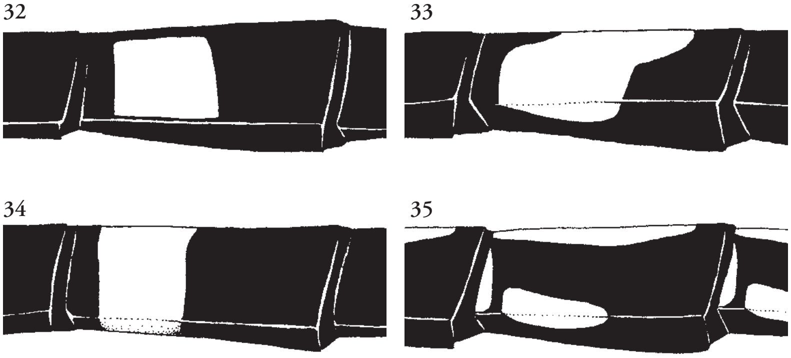
Figs. 17-21.
Male hind femur of *Porpax* species in lateral view. – 17, *P. asperipes*; 18, *P. bipunctus*; 19, *P. garambensis*; 20, *P. risi*; 21, *P. sentipes*.



Figs. 22-25. Male hind femur of *Porpax* species in ventrolateral view. – 22, *P. asperipes*; 23, *P. bipunctus*; 24, *P. garambensis*; 25, *P. sentipes*.



Figs. 26-31.
Male S1-4 of *Porpax* species in dorsal view. – 26, *P. asperipes*; 27, *P. bipunctus* Côte d'Ivoire; 28, *P. bipunctus* NE Congo-Kinshasa; 29, *P. garambensis*; 30, *P. risi*; 31, *P. sentipes*.



Figs. 32-35.
Male S6 of *Porpax* species in lateral view. – 32, *P. asperipes*; 33, *P. bipunctus*; 34, *P. garambensis*; 35, *P. risi*.

clypeus, frons, vertex, occiput and genae with long black hairs.

Prothorax dark brown with pale green hindlobe and anterior half forelobe. Hindlobe with fringe of long black hairs. Synthorax dark brown with yellowish green markings (fig. 11): postdorsal stripes linear, closer to middorsal carina than humeral suture, parallel to carina, dark area between the two postdorsal stripes about 1.5x as broad as one stripe. Antealar sinuses each with large oval spot, bordered anteriorly by similar-sized roughly triangular spots on mesepisternum, which are almost fused with postdorsal stripes. Mesepimeron and metepisternum both with broad, unbroken, rather straight pale stripe, both of similar width and slightly widened dorsally, latter enclosing brown-rimmed metastigma (and the thin brown sutural line connecting it to metapleural stripe). These stripes so broad that interpleural dark stripe is very thin, less than a quarter as wide as one of the pale stripes. Metepimeron largely pale, dark brown on borders, a dark smudge extending from ventral side towards centre of metepimeron. Metapleural dark stripe about as wide as interpleural stripe. Mesokatepisternum and metakatepisternum with pale spot on ventral corner. Synthoracic venter brown with large faint yellow blotches on metepimeron and small ones on sides of poststernum. Antealar sclerites blackish brown with greenish yellow central spots, interalar plates greenish yellow narrowly outlined with blackish brown.

Venation blackish. Wing membrane clear, narrowly and faintly yellow at base of subcostal and cubital spaces and along membranule in all wings. Membranule dark brown, pale at base. Pt brown. 11-11½ Ax in Fw (complete distal antenodal in left Fw is aberrant in genus), 9 in Hw. 10 Px in Fw, 9 in Hw. Arculus roughly midway Ax2-3 in all wings. 1 Cux in both Fw, 2-3 in Hw. Fw triangles just over 3x as long as wide, with single cross-vein, supratriangles without cross-veins, subtriangles of 3 cells. Discoidal field of 2 rows at base (for 6 cells), becoming 3 rows just proximal of nodus, Mspl scarcely defined. Hw triangle uncrossed. IR3 and Rspl enclosing single row of 7 cells in Fw, 6 in Hw. Anal field of 2 rows near rounded tornus. Anal loop of 18-20 cells, but veins enclosing them ill-defined and not confluent

Table 2. Comparison of regional variation in males of *P. bipunctus*, ordered from west to east.

	Côte d'Ivoire & Liberia	SW Cameroon	NE Gabon	NE Congo-Kinshasa
Squames of labial palps	black	black	black	pale
Labrum	unspotted	two large central pale spots (fig. 1)	unspotted	unspotted
Pale frontal band	at most thinly interrupted	at most thinly interrupted	at most very thinly interrupted	complete
Postgenae	black, 3 sharp spots (fig. 4)	black, 2 sharp spots (fig. 5)	brown, 3 vague spots (cf. fig. 6)	brown, 2-3 vague spots (fig. 6)
Interpleural stripe : metepisternal stripe	slightly broader	slightly narrower	equal	much narrower (fig. 11)
Dorsum S2	2 equal spots (fig. 27)	2 equal spots (cf. fig. 27)	2 equal spots (cf. fig. 27), 2nd wider in some specimens	spot preceding band (fig. 28)
Dorsum S3	1st (rather narrow) ring thinly interrupted, 2nd widely (fig. 27)	2 thinly interrupted rings	1st ring thinly interrupted, 2nd thinly or widely	2 complete or thinly inter-rupted rings (fig. 28)
Epiproct	pale (fig. 44)	dark	pale	often dark

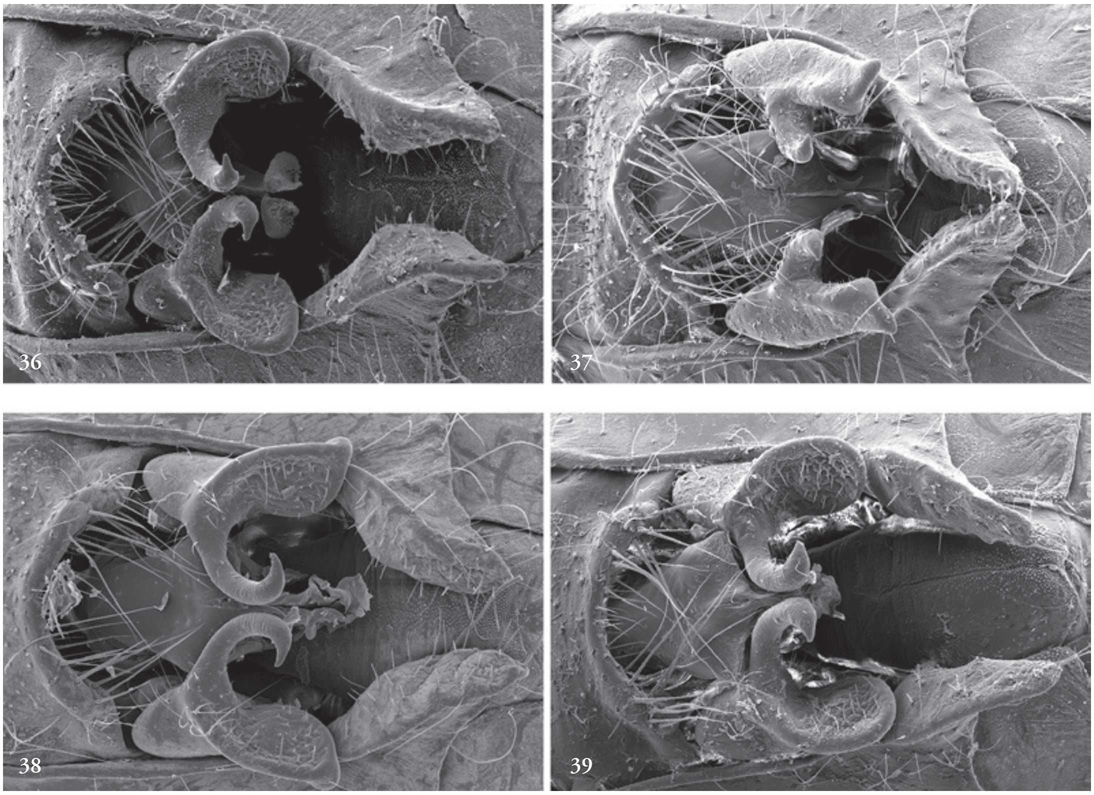
before posterior wing border, leaving anal loop open (cf. fig. 16). Bridge spaces with 1 cross-vein.

Legs black except posterior yellow spots on mid and hind coxae and greenish yellow interior side of fore femora and trochanter. Hind femora and trochanters with only scattered hairs. Hind femur thicker than in other species, with 16-19 spines in outer anterior row placed in single but somewhat irregular file (fig. 18, 23). These spines quite stout, closely and evenly spaced, diminishing in size only slightly towards base, in lateral view appearing like the serrations of a saw. The spine closest to apex is the longest, about as long as half-width of femur, remaining spines much shorter, third or less as long as apical spine, most basal spine only about a tenth of femoral width long.

Abdomen slender, S3 about 2x as long as wide with posteriorly slightly converging sides, S4 about 3x as long as wide and parallel-sided. Abdomen brown-black, marked with pale green (figs. 28, 33): S1 with largely latero-apical marking and roughly semicircular spot on dorsum. Ventral half S2 largely pale, black on genital lobe and ventral border, with dorsal spot anterior of subbasal transverse ridge, of similar size and shape as S1 spot, and posterior of ridge a dorsal bar that is about twice as broad as the two preceding spots. S3 largely pale, with dark apical ring and dark transverse bar lying anterior of transverse ridge (unlike the ring, the bar is laterally interrupted), resulting in a pattern of four bands in dorsal view: two basal and subapical pale ones and two slightly narrower subbasal and apical ones, the pale bands traversed by slight darkening on dorsal carina. S4 with large triangular latero-basal spots, which extend along two-thirds of lateral carina and are quite narrowly separated by black on dorsum. S5 with oval subbasal spot on lateral carina. S6 with yellow subbasal band occupying about three-fifths of segment. Basal dark area and subbasal band extend somewhat posteriorly along dorsal carina, thus the band appears skewed in lateral view. S7-10 all dark. Cerci dull greenish yellow, with about eight black denticles scattered on ventral side and black denticle on apex, epiproct dark brown but yellowish in centre and black at apex. Paler appendages hardly contrasting with S10. Venter of abdomen (sternites and ventral portions tergites) brownish black, tergites largely greenish or yellowish where pale lateral markings extend below lateral carinae. Secondary genitalia similar to *P. asperipes*, with round lobe and long curved hook of hamule (cf. fig. 36).

Bambesa female. – Measurements (mm): entire length not taken (too fragmented), abdomen length (without appendages): 16.5, Fw length: 30, Hw length: 28.5, Fw Pt: 2.5.

More robust and stouter than male, S3 as long as wide, S4 about 1.5x as long as wide, both almost parallel-sided. Marked similarly to male but dark areas much browner, there hardly being any black on body. Head especially pale, only blackish on inner third of labial palps, anterior third of labrum and on postgenae against occiput. Head markings thus very ill-defined, especially on postgenae where only



Figs. 36-39. Secondary genitalia of *Porpax* species in ventral view. – 36, *P. asperipes*; 37, *P. garambensis*; 38, *P. risi*; 39, *P. sentipes*.

ventral yellow streak is distinguishable. Thoracic pale markings on the other hand crisp, pale green on rusty brown background, less extensive than in male: postdorsal stripes well-separated from spots against antealar sinus, interpleural stripe as broad as posteriorly adjacent pale stripe on metepisternum. Unlike male, prothorax with small lateral spot above coxa. Abdomen marked like that of male, but contrast so weak that potential differences are hard to make out especially on S6 where the pale band can barely be distinguished. Wings similar to those of male, including open anal loop, differing as follows: Faint yellow at bases more extensive, about to Ax1 and Cux1. 11½ Ax in both Fw. 10-11 Px in Fw, 10 in both Hw. 2 Cux in both Hw. Discoidal field of 3 cells bordering triangle, then 2 rows for 3-4 cells. Anal field of 3 rows at tornus. Open anal loop of 23 or more cells (damaged in left wing). Legs black, save basal two-thirds mid and hind femur, interior side of fore and mid femur yellowish for their entire and half-length respectively. Hind femora and trochanters with only scattered hairs. 10-11 rather long spines in outer anterior row of hind femur widely spaced and in single file. Most apical spine almost as long as width of femur, most basal spine only about a tenth as long as apical one. Vulvar scale appressed, extending just beyond tergite S8, with two round lateral swellings densely set with short hairs, the swellings separated by a shallow round concavity that is slightly wider than one swelling (fig. cf. 41). Cerci and epiproct brown, not contrasting with S10, cerci with black denticle on apex.

Variation

This species is uniform in morphology, but the specimens studied from four disjunct areas showed slight but discrete differences in markings, mainly of the head (table 2). Although the eastern- and westernmost forms are the palest and darkest respectively, the variation is not perfectly clinal: at least the extent of pale marking on the labrum, postgenae, synthoracic sides, dorsum S3 and epiproct does not increase linearly eastwards. Because of the clear geographic pattern, it might seem appropriate to consider the forms as subspecies. Unfortunately that category

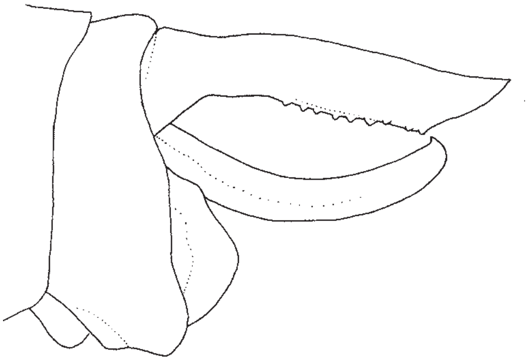
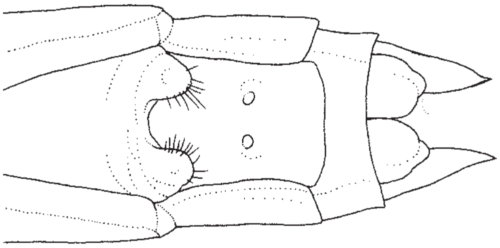


Fig. 40.
Male appendages of *Porpax sentipes* in lateral view.

41



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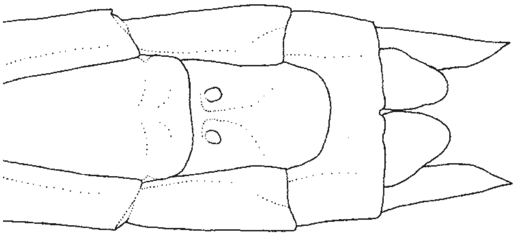

Figs. 41-42.
Female S8-10 with vulvar scale of *Porpax* species in ventral view. – 41, *P. asperipes*; 42, *P. garambensis*.

has lost most of its value, having been loosely and haphazardly applied in odonate taxonomy, generally without consideration of geography and intraspecific variation. With only small samples to study, I therefore prefer not to name the variation. The pale easternmost variety is most distinctive, dark areas being brown rather than black, which includes the postgenae marked with faint spots (fig. 6). The Gabonese variety shares the brown postgenae but is otherwise quite black and most similar to the Liberian-Ivorian variety. Both have conspicuous entirely pale appendages, but broad black markings on thorax and abdomen (fig. 44). The distinguishing feature of the westernmost variety is the black postgenae with three distinct pale spots (fig. 4). The Cameroonian variety has only two such spots (fig. 5) and – uniquely – also has two pale spots on the labrum (fig. 1), the feature for which the species is named. Some variation is also observed within regions. In the Bambesa specimens the upper postgenal spot may be reduced or missing and the middle one is then also small. The extent of dark markings varies, for instance on the posterior border of the labium, the dorsal carina of S3 and the synthorax.

Range and ecology

Studied material originates from four discrete areas: around the Liberia-Côte d'Ivoire border, SW Cameroon and adjacent Nigeria, NE Gabon, and Bambesa in NE Congo-Kinshasa, which lies on the northernmost edge of the Ituri Forest. Lempert (1988) stated 'Kongo' as part of this species' range. Although Pinhey (1966) described *P. bipunctus* as part of the treatment of a Congolese collection, his specimens were all from Cameroon and Nigeria. Legrand & Couturier (1985) found the species on standing water on the upper courses of rainforest streams in Taï Forest, Côte d'Ivoire. In Liberia, Lempert (1988) observed several males perching near a dry side-arm of such a stream; tenerals emerged from moist leaf litter on the stream bank at the beginning of the relatively dry season and adults were subsequently seen along forest roads. Labels of the Gabonese males read 'bord inondee' and 'ruisseau'. The larvae may live among leaf litter in rainforest pools when these are temporarily filled by small streams; adults surviving drier periods.

Porpax garambensis Pinhey
(figs. 9, 12, 19, 24, 29, 34, 37, 42)

Porpax garambensis Pinhey, 1966: 53. Holotype ♂: CONGO-KINSHASA: Parc National de la Garamba, 7.v.1952, H. De Saeger (MRAC) [examined].

Other material. – CONGO-KINSHASA: 1♀, Lulonga, Lukolenge, 18.vi.1927, J. Ghesquière (MRAC); 1♂, Lubonga, 24.iii.1929, R. Geldof (MRAC); 1♀, Nioka, ii.1934, J.V. Leroy (MRAC); 2♂, 2♀, Ubangi, Bomboma, ii.1934-x.1935, A. Bal (MRAC); 1♀, Ubangi, Terr. Giri, Banza, ii.1935, A. Bal (MRAC); 6♂, 1♀, Uele, Bambesa, i-xii.1938, J.M. Vrijdagh (MRAC); 2♂,♀, Uele, Bambesa, v.1939, P. Henrard (MRAC); 2♀, Lualaba, Kabongo, xi.1952, Ch. Seydel (MRAC).

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44

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Figs. 43-45.
Porpax species. – 43, female *P. asperipes* near Lokutu, Congo-Kinshasa; 44, male *P. bipunctus* near Jalay Town, Liberia; 45, male *P. risi* on the Nyika Plateau, Malawi. Photographs by K.-D.B Dijkstra (43, 45) and J. Lempert (44).

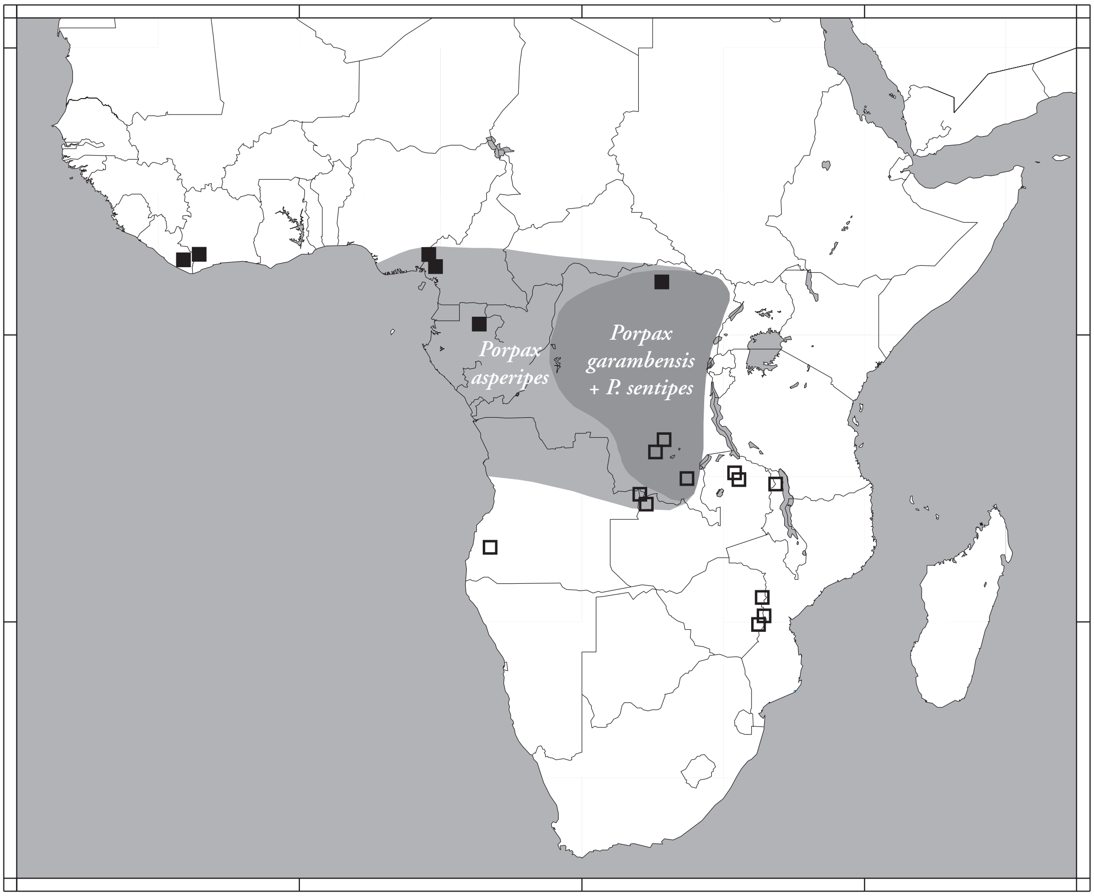

Fig. 46. Distribution of the genus *Porpax*. Legend. – dark grey: approximate range of *P. garambensis* and *P. sentipes* (see fig. 47); pale and dark grey: *P. asperipes*; filled squares: *P. bipunctus*; open squares: *P. risi*.

Diagnosis

The smallest species, easily identified by its dark synthoracic venter and spiracular dorsum, and the shape of the postdorsal stripes (fig. 9). The only species with distinctive hamule and vulvar scale morphology (figs. 37, 42), and usually single Hw Cux; the hair on the male's hind femora is especially long and dense (figs. 19, 24). Males appear to become pruinose only on S3 and sometimes on adjacent parts of S2 and S4.

Female

Not described by Pinhey (1966). Head similar to male but thorax and abdomen generally pale, and rather variable in this respect. Although the pale markings are identically configured, these may be so extensive and weakly contrasting with the darker surrounding that they become fused. There may also be large pale areas where these are not seen in males, e.g. often on synthoracic venter and spiracular dorsum. Hind femora and trochanters are distinctly hairy. The outer anterior row of hind femur has 7-8 rather long spines that are widely spaced and in a single file. The most apical spine is almost as long as the width of the femur. Wings are distinctly brown at bases, almost to Cux1 in Hw. The vulvar scale is bare, curved ventrad, its distal border at a 45° angle to abdominal axis, and extends along about a third of tergite S9, its distal border smooth and round. Cerci and epiproct are yellowish, contrasting with S10, cerci with black denticle on apex.

Range and ecology

Previously known only from the fragmented and rather teneral holotype, but widespread in Congo-Kinshasa (fig. 47). The habitat is unknown.

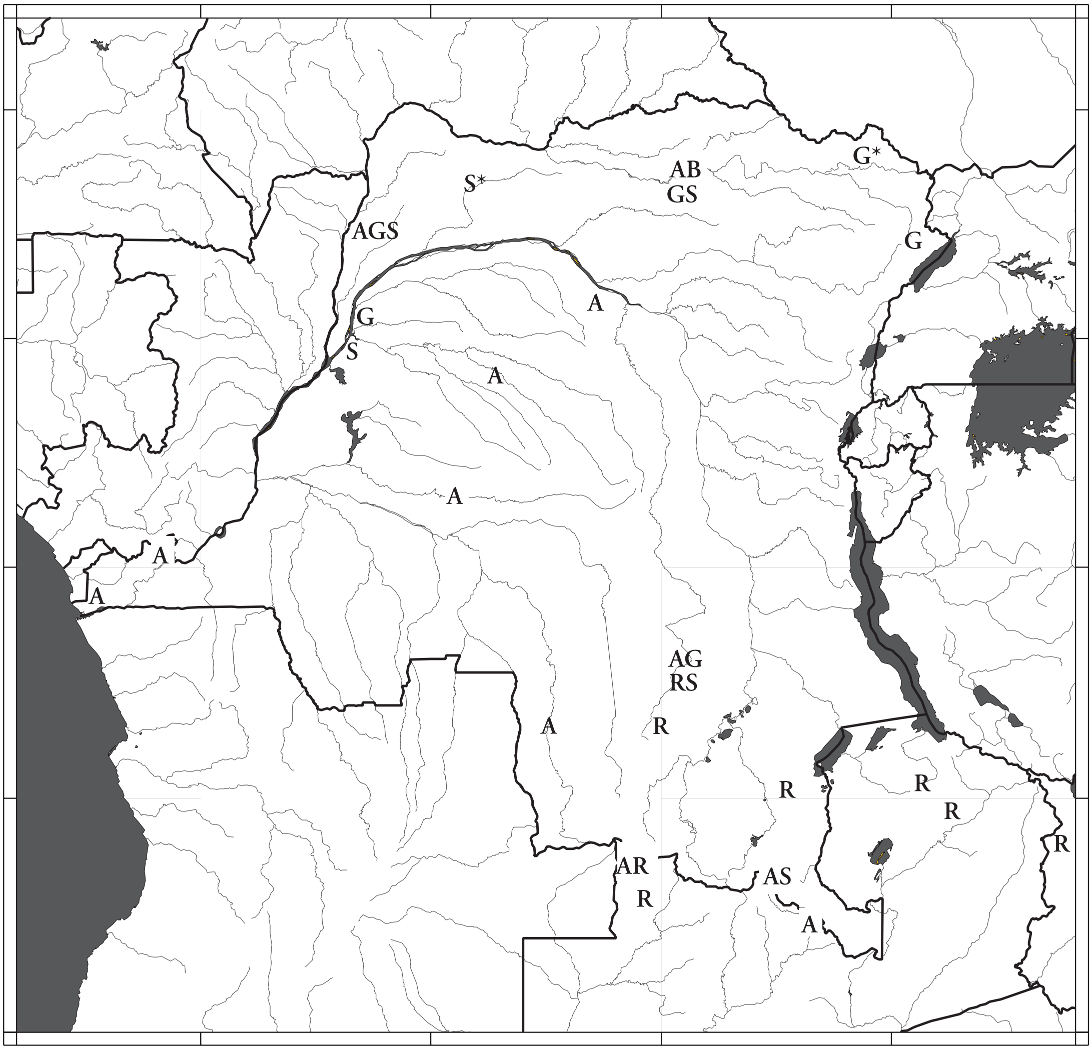

Figure 47. Distribution of *Porpax* species in Congo-Kinshasa, Zambia and Malawi. Legend. – A: *P. asperipes*; B: *P. bipunctus*; G: *P. garambensis*; R: *P. risi*; S: *P. sentipes*; *: type locality.

Porpax risi Pinhey
(figs. 2, 7, 13, 20, 30, 35, 38, 45)

Porpax asperipes nec Karsch, 1896 – Ris 1919: 1129.
Porpax asperipes risi Pinhey, 1958: 115. Holotype ♂: ZIMBABWE: 'Chibudzana R., Melsetter Dist. Dept. Agric. S. Rhodesia, 26/2.1948', 'J.A. Whellan, Collector', 'TYPE ♂ Porpax asperipes ssp. risi Pinhey 1956', 'BRIT.MUS. 1959-138' (BMNH) [examined].
Porpax risi Pinhey, 1958 – Pinhey (1964a: 117, 1964b: 334, 1966: 52).

Other material. – CONGO-KINSHASA, 1♂, Lualaba, Kabongo, xi.1953, Ch. Seydel (MRAC); 2♂, Lualaba, Kamina, xi.1953, Ch. Seydel (MRAC); 1♂, Katshupa, 1.xi.1962, J.J. Symoens (MRAC); 1♂, 2♀, 15 km SW of Msipashi, 2.xi.1962, J.J. Symoens (MRAC); 17♂, 10♀, 20 km SW of Msipashi, 2.xi.1962, J.J. Symoens (MRAC). – MALAWI: 2♂, 2♀, Northern Region, Rumphi District, Nyika National Park, Mwenyenyesi Valley below Chelinda Campsite (10°35.19'S 33°47.73'E), 2285 m, herbaceous marsh in montane grassland, 20.xii.2001, K.-D.B. Dijkstra (RMNH). – ZIMBABWE: 1♀ ('allotype'), Melsetter Dist., Chibudzana R., 14.xi.1948 (BMNH).

Diagnosis

This small, broad-bodied species is the most distinctive by markings, appearing pale and spotted rather than dark and banded, differing in both sexes by the largely pale labrum, pale veins and abdominal spotting (figs. 2, 30, 35). There are additional pale spots on the upper postgenae, sides of prothorax, fore coxae and anterior mesokatepisternum, which are not or only indistinctly seen in all other species (figs. 7, 13). Pt is relatively long and pale; 2.5-3.5 mm and pale brown rather than 2-2.5 mm and dark brown. Morphologically it is similar to *P. asperipes*, but the lobe of the hamule is somewhat pointed and its hooks are especially long and slender (fig. 38).

Remarks

First described by Ris (1919, 1921) as an aberrant *P. asperipes* and later described as a subspecies by Pinhey (1958). Pinhey (1964a, b, 1966) raised *P. risi* to species level in three separate papers; Lieftinck (1969) provided a full comparison of the two.

Variation

The holotype has a continuous pale mesepimeral stripe (fig. 13) and half-black labrum. Specimens from NW Zambia and Katanga may have the mesepimeral stripe broken and the labrum largely pale (fig. 2). Both entire and broken mesepimeral stripes occur in the Malawian material (fig. 45).

Range and ecology

The species was known from NW and NE Zambia, the Kundelungu Plateau in S Katanga, and the mountains on the Mozambique-Zimbabwe border and in SW Angola (Lieftinck 1969, Pinhey 1975, 1984). *P. risi* was found for the first time in Malawi at 2285 m altitude on the Nyika Plateau (fig. 45). The habitat was open, herbaceous montane marsh. Syntopic species on the Kundelungu Plateau (*Africallagma sinuatum* (Ris, 1921) and *Pseudagrion inconspicuum* Ris, 1931; Pinhey 1967) suggest that the habitat there was similar. The species can be expected in SW Tanzania, e.g. in the Ufipa and Kipengere highlands. Pinhey (1966, 1984) stated ‘open swamps’ and ‘swampy grasslands or reed-beds in or near forest or litus [= gallery streams]’ as the habitat.

Porpax sentipes sp. n.
(figs. 3, 14, 21, 25, 31, 40)

Type material. – Holotype ♂: CONGO-KINSHASA: Ubangi, Businga, 2-4.iii.1932, H. J. Brédo (MRAC). – Paratypes: CONGO-KINSHASA: 7♂, 1♀, Eala, xii.1934-xi.1936, J. Ghesquière (MRAC); 1♂, 1♀, Ubangi, Busu Bombenga, 15-25.viii.1935, A. Bal (MRAC); 1♂, Elisabethville (= Lubumbashi), iii.1936, Ch. Seydel (MRAC); 68♂, 7♀, Uele, Bambesa, iii.1937-v.1939, J.M. Vrijdagh (MRAC); 15♂, 4♀, Uele, Bambesa, x.1938-v.1939, P. Henrard (MRAC); 1♂, Lubumbashi, 13.vii.1951, Ch. Seydel (MRAC); 1♂, Lualaba, Kabongo, x.1953, Ch. Seydel (MRAC).

Diagnosis

A fairly small, bare-legged species with uniquely duplicated row of spines on the hind femora (figs. 21, 25). Rather average in other features, the markings are quite like *P. asperipes*, the combination of the lateral prothoracic spot, (usually) dark spiracular dorsum and the S6 ring uninterrupted by black dorsally being diagnostic.

Description

Holotype male. – Measurements (mm): entire length: 31, abdomen length (without appendages): 19, Fw length: 24.5, Hw length: 23.5, Fw Pt: 1.7.

Prementum black, labial palps yellow with inner three-fifths and squames black, this central black area widening anteriorly and extending thinly along anterior border. Mandibles greenish yellow, genae blackish. Labrum glossy black. Anteclypeus dark brown, postclypeus pale green, with anterior border narrowly black laterally and dark brown centrally (above anteclypeus). Frons broadly glossy black anteriorly, narrowly black bordering vertex and in median groove, enclosing two large pale green blotches on dorsum (fig. 3). Vertex black, dorsally with large pale green spot. Anterior half of occipital triangle black, posterior half and down occiput pale green. Postgenae black with isolated, contrasting, small, roundish yellow spot subdorsally and similar streak bordering eyes at ventral end (cf. fig. 5). Antennae and their bases black. Labrum, clypeus, frons, vertex, occiput and genae with long black hairs.

Prothorax black with pale green markings (fig. 14): anterior half forelobe and entire hindlobe, two vague and tiny spots on midlobe bordering hindlobe, prominent spots on pleura, occupying most of proepimeron. Hindlobe with fringe of long black hairs. Synthorax black with greenish yellow markings: Two small, closely apposed spots of unequal size on spiracular dorsum, just anterior of middorsal carina. Postdorsal stripes linear, closer to middorsal carina than humeral suture, parallel to carina, black area between the two postdorsal stripes just under twice as broad as one stripe. Antealar sinuses each with large oval spot, bordered anteriorly by smaller triangular spot on mesepisternum, these separated from postdorsal stripes by distance about equal to the width of the stripes. Mesepimeron and metepisternum both with pale stripe, former straight and unbroken, latter broken at metastigma and with dorsal section strongly sigmoid. Interpleural black area broader than two aforementioned stripes. Metepimeron largely pale, black on borders, this black extending from ventral side towards centre of metepimeron. Metapleural black area wider than pale stripe on metepisternum. Mesokatepisternum and metakatepisternum with pale spot on ventral corner. Synthoracic venter black with large contrasting yellow blotches on metepimeron and sides of poststernum. Antealar sclerites black with greenish yellow central spots, interalar plates greenish yellow narrowly outlined with black.

Venation blackish. Wing membrane clear, very narrowly brown at base of Hw cubital space and along membranule. Membranule dark brown, paler at base. Pt brown. 10½ Ax in both Fw, 8-9 in Hw. 9 Px in Fw, 9-10 in Hw. Arculus distal of Ax2 in all wings. 1 Cux in both Fw, 2 in Hw. Fw triangles just over 3x as long as wide, uncrossed, supratriangles without cross-veins, subtriangles of 2-3 cells. Discoidal field of 3 cells bordering triangle, then 2 rows for 4-6 cells, becoming 3 rows just proximal of nodus, Mspl scarcely defined. Hw triangle uncrossed. IR3 and Rspl enclosing single row of 5 cells in all wings. Anal field of 2 rows near rounded tornus, anal loop of 13 cells with blunt tip. Bridge spaces with 1 cross-vein.

Legs black save some yellow on outer ridge fore coxae, yellow posterior spots on mid and hind coxae and yellowish interior side of fore femora and trochanter. Hind femora and trochanters with only scattered long hairs. About 28 small spines, densely arranged in outer anterior row of hind femur: 16 spines in two files on basal third of femur, and irregular single file of about 12 spines in apical two-thirds (cf. figs. 21, 25). Most apical spine longest, about as long as half-width of femur, remaining spines much shorter, most apical spine about twice as long as most basal, but still only about a seventh of femoral width long. Right hind leg missing.

Abdomen slender, S3 about 2x as long as wide with posteriorly converging sides, S4 about 3x as long as wide and parallel-sided. Abdomen black, marked with greenish yellow (fig. 31): S1 with long lateral mark along apical border and roundly triangular apical spot on dorsum. S2 with round spot above genital fossa and dorsal band narrowing laterally anterior of subbasal transverse ridge. S3 broadly pale laterally and basally, forming a basal ring, which is almost complete (very thinly dark on dorsal carina), occupying half of distance between basal border and subbasal ridge. Pale lateral area S3 also extends slightly dorsally on posterior side of ridge. S4 with large triangular latero-basal spots, which extend along two-thirds of lateral carina and are only narrowly separated by black on dorsum. S5 with small latero-basal dots and streak on lateral carina. S6 with complete, rectangular subbasal band occupying less than half of segment (cf. fig. 34). S7-10 all black. Cerci and epiproct pale yellowish, contrasting with S10, cerci with 8-9 black denticles in a neat slightly sigmoid row (ventral view) on ventral side, and black denticle on apex, epiproct darkened at extreme tip. Venter of abdomen (sternites and ventral portions tergites) black, only narrowly yellowish below lateral carinae where there are pale lateral markings. Secondary genitalia similar to *P. asperipes*, with round lobe and long curved hook of hamule (fig. 39).

Female paratype Busu Bombenga. – Measurements (mm): entire length: 30, abdomen length (without appendages): 17.5, Fw length: 26.5, Hw length: 25.5, Fw Pt: 2.3.

Larger, more robust and stouter than holotype, S3 as long as wide, S4 about 1.5x as long as wide, both almost parallel-sided. Markings as in holotype but pale areas less green and more extensive, especially on abdomen and dark areas of thorax and abdomen browner. Greater extent of pale markings and fainter contrast especially obvious on S3, which on dorsum has complete basal and subapical pale brown rings, and narrower subbasal and apical dark brown rings. Wings similar to those of holotype, differing as follows: Hw base has slightly more brown. 10½ Ax in both Fw, 8 in Hw. 8-9 Px in Fw, 8-9 in Hw. One Fw triangle crossed, both subtriangles of 3 cells. Discoidal field of 2 cells bordering triangle in left wing. Anal loop of 14-15 cells. Hind femora and trochanters with only scattered long hairs. 10-11 rather long spines in outer anterior row of hind femur widely spaced and in single file. Most apical spine about two-thirds as long as width of femur, most basal spine about a fifth as long as apical one. Vulvar scale appressed, extending just beyond tergite S8, with two round lateral swellings densely set with short hairs, the swellings separated by a shallow round concavity that is about as wide as one swelling (cf. fig. 41). Cerci and epiproct pale yellowish, contrasting with S10, cerci with black denticle on apex.

Variation

The labrum and spiracular dorsum are typically all black, but both can have two small pale dots in their centre (fig. 3), which can be fused into one larger marking on the spiracular dorsum.

Etymology

The name (noun in apposition) is an analogy to *asperipes* (rough legs) and is derived from the Latin *sentus* (briary, thorny), referring to the diagnostic patch of thorns on the hind femora.

Range and ecology

Appears to range throughout the Congo Basin (fig. 47). Nothing is known about the ecology.

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chapter 8

Demise and rise: the biogeography and taxonomy of the Odonata of tropical Africa

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Demise and rise: the biogeography and taxonomy of the Odonata of tropical Africa

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Introduction

Dragonflies and damselflies (Odonata) have two lives, as rather immobile aquatic larvae and as mobile airborne adults. The African continent forms a large and continuous landmass, virtually uninterrupted by mountain chains or large waterbodies (Griffiths 1993). The most significant barriers are the sea between the continent and Madagascar, and the Sahara, separating the Afrotropics from the Palearctic. In contrast, the climate is characterised by extreme variability, also and most significantly in a recent past (Morley 2000). The synthesis of geography and climatology predicts a relatively low diversity, but the long and shifting gradients in both space and time also imply a broad array of evolutionary and ecological responses within the fauna.

This review describes patterns of diversity and diversification in Afrotropical Odonata, examines possible origins and addresses how odonate properties, such as their dispersal capacity and habitat preference, may interact with the vicissitudes of their environment. This will supplement knowledge from better-known taxonomic groups such as plants, birds and mammals, because of the order's distinct combination of characteristics. The main text follows a regional approach, describing the diversity of Afrotropical Odonata (*i.e.* occurring south of the Sahara, including Madagascar and the western Indian Ocean islands). Examples of observed patterns and suspected processes are provided in Boxes 1-15. These are more taxon-oriented and were mostly taken from the author's work. A discussion of how, when and where speciation took place concludes the review.

Box 1. Problems in taxonomic and biogeographic progress

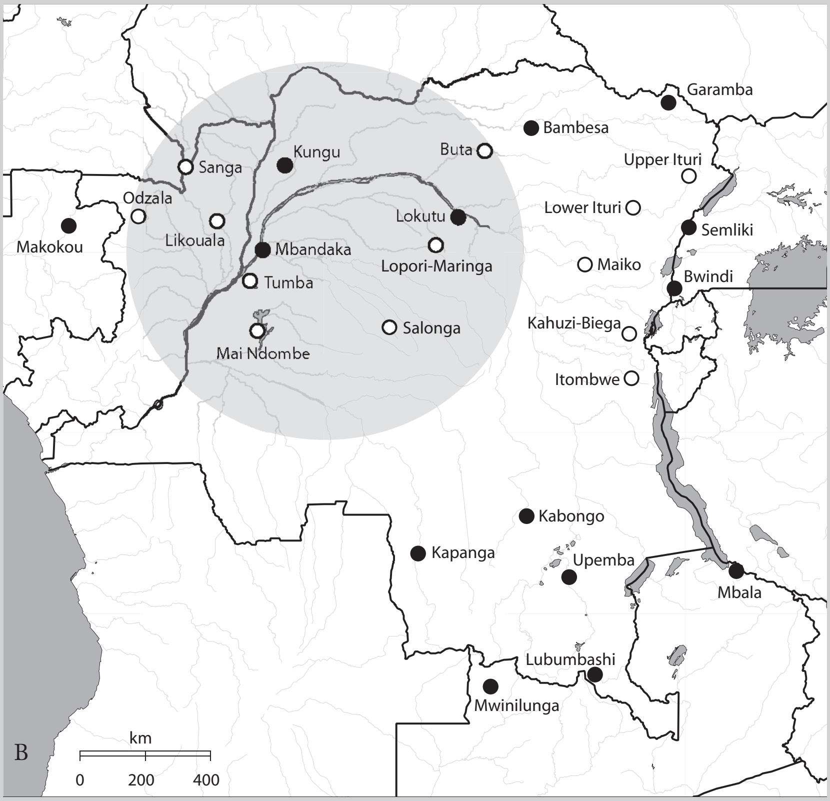
Platycnemidine damselflies constitute an important element of both Madagascan and continental African forest faunas (Fig. A), and although both groups are traditionally placed in the genus *Platycnemis*, they are not closely related (Dijkstra *et al.* 2007a). The continental group is remarkably similar to the Oriental genus *Copera*, while the relationships of the insular fauna are unclear. The close African-Asian relationship suggests recent contact, while the connection with the insular group may be much older (Boxes 3, 4). On the other hand, insular species expanded recently to the eastern African coast, probably crossing the ocean (Box 11).

The Congo Basin is a centre of odonate diversity as ever-shifting rivers, swamps, forests, woodlands and savannas create an enormous mosaic of prime habitat in time and space (Dijkstra in prep. c; Boxes 9, 12). The 'heart' of the continent has always been on a crossroads, between the forests to the west and east in wet periods, and between the savannas to the north and south in drier times, when sensitive species could survive in presumed forest refuges west and east of the basin and along its rivers. Kingdon (1989) postulated that the basin is an "evolutionary whirlpool" of species diversification, conservation and dispersal, leading to high endemism and diversity. This should be especially true for Odonata, because of their strong ties to freshwater and vegetation structure. Unfortunately our knowledge of the fauna is concentrated in a handful of peripheral sites, sampled mostly in the 1930s to 1960s (Fig. B). The most notable hiatuses lie in the eastern highlands and the central basin, both likely zones of refuges and faunal overlap. An impression of the remarkable diversity of the central basin – a seemingly monotonous forested plain crossed by countless rivers – was obtained by Dijkstra (2007c), who recorded 86 species within 13 days of sampling around Lokutu; over one-tenth of the Afrotropical fauna. Only 28% were widespread species; the local fauna was estimated to number over 125 species. The survey produced new species in the conspicuous genera *Mesocnemis* and *Platycypha* (Box 15), as well as range extensions over up to thousands of kilometres, indicating that the continent's odonatological heartland remains mysterious.

K.-D.B. Dijkstra. Demise and rise: the biogeography and taxonomy of the Odonata of tropical Africa.
PhD Thesis, 2007, Leiden University, pp. 143-187.

Fig. A Distribution of Afrotropical *Platycnemis*. Legend – black: insular group; grey: continental group; white lines: approximate limits of ranges of continental species (range of *P. sikassoensis* at least partly incorporates ranges of other continental species). From Dijkstra *et al*. (2007a).

Fig. B Odonatological coverage of the Congo Basin. Legend – open circles: selected sites within areas of highest and high conservation priority following the assessment of the Congo Basin Forest Partnership, none of which have been surveyed for Odonata; filled circles: sites with reasonable (historic) odonatological data, none of which lie within CBFP areas of conservation priority; grey: approximate extent of 'cuvette centrale', defined as part of basin below 500m. Adapted from Dijkstra (2007c).



Character of Odonata

Odonata have a strong relation with freshwater, with permanence and flow of water as principal habitat determinants. The larvae are critical in regard to aquatic habitat morphology, such as bottom substrate and water clarity. Adult habitat selection is strongly dependent on structural characteristics, especially related to vegetation, like degree of shading. Because of their sensitivity to physical habitat quality, odonates show strong responses to habitat change, such as forest loss and erosion. Different ecological requirements are linked to different dispersal capacities. Species with narrow niches disperse poorly, while pioneers of temporary habitats are excellent colonisers. Thus ubiquitous species prevail in disturbed waters, while habitats like pristine streams and swamp forests harbour more vulnerable and localised species. This range from extremely good to extremely poor dispersers contrasts with other aquatic groups, such as fish, and offers an insight into different degrees of vicariance and dispersal. Altogether, their sensitivity and amphibious habits make Odonata well suited for evaluating environmental change in the long term (biogeography) and in the short term (conservation biology), both above and below the water surface (Clausnitzer 2003; Corbet 1999; Dijkstra & Lempert 2003). Odonata are an ancient group, most extant families originated in the Jurassic, more than 150 Ma (million years ago) (Grimaldi & Engel 2005). Thus they potentially provide a much deeper grasp in time than well-studied groups such as butterflies. However, it remains to be seen if the present-day Odonata represents such an archaeic fauna.

Interest for Odonata

Odonata are receiving increasing attention from the public, conservationists and scientists on regional and global levels (Clausnitzer & Jödicke 2004). Due to their attractive appearance, they can function as guardians of the watershed, being the quintessence of freshwater health. They can be flagships for conservation, not only of water-rich habitats such as wetlands and rainforests, but also for habitats where water is scarce and, therefore, especially vital to the survival of life. Human disturbance of watersheds, with the consequent loss of soil and water-sources, is a problem world-wide, especially in the tropics and certainly in Africa. In order to use Odonata as monitors of degradation, conservation and restoration of watersheds, baseline knowledge of assemblages and habitat preferences of species is required. The need for a biogeographic overview of African Odonata has been voiced both within the odonatological community as within the entomological community at large (Dijkstra 2003c; Miller & Rogo 2001). Considering the ever-changing nature of the African landscape, be it under human, geological or climatic influence, the study of the geography, ecology and phylogeny of African Odonata will help us understand the past and future of a rapidly changing continent.

Knowledge of Odonata

Odonate taxonomy is well-resolved in comparison to other Afrotropical insects and their distributions are sufficiently known for biogeographic studies, although our understanding is still partly obscured by taxonomic problems or the lack of regional data (Box 1). Dijkstra (2003c) reviewed the state of taxonomic knowledge in Afrotropical Odonata. Extensive progress has been booked since and a new overview is provided in the appendix: the presence of many synonyms and relatively few undescribed species has reduced the known species number by about 4%. Two problems are central to the taxonomic disorder encountered. Firstly, an overvaluation of wing venation has lead to the recognition of more taxa than are supported by other characters, such as genitalia (Dijkstra & Vick 2006). Venation was favoured because it is quantifiable, but is much more plastic than previously believed. Characters that were traditionally treated as primitive may rather be apomorphic reconfigurations of veins induced by changes in wing shape as an ecological adaptation. This problem applies mainly at the genus level and is probably rife worldwide. Almost all synonymies of genera in the appendix refer to venation bias. Secondly, many supposed taxa represent variation in size and melanism, as they are not supported by morphological differences (Dijkstra 2003b; 2005a; d; Dijkstra *et al.* 2006a). Such variation is probably mostly environmentally induced, but can also be age-related. This problem applies mainly at the species level, but has also lead to the description of numerous superfluous forms and subspecies (*Gomphidia* is an example; Box 9). The problem may be greater in Africa than elsewhere, as many species can realise a broad geographic and environmental range across a huge continent with few natural barriers, and is exacerbated by fragmentary collecting.

Box 2. Poor Africa: comparison of the world's three tropical odonate faunas

The table provides an impression of the faunal differences between America, Africa and Asia, although higher classifications in the order and biogeographic divisions are contentious. The poverty of the Afrotropical fauna at the species, genus and family level is most notable. The known number of species represents less than one-sixth of the world fauna; both the Neotropical and Oriental regions have twice as many species. The Afrotropical fauna is classified into only 16 families, compared to 21 for both other regions. With both regions it shares all but two of its families: Perilestidae and Pseudostigmatidae are shared with the Neotropics, but are represented by only two species (0.2% of the fauna), while the Chlorocyphidae and Platycnemididae represent almost 11%. Moreover macromiids can hardly be considered Neotropical, occurring only in northern Mexico, and therefore the rich representation of this family in the Paleotropics is further evidence of the greater similarity between Africa and Asia. Only the Afrotropical diversity of Coenagrionidae and Libellulidae is on a par with the American and Asian tropics. Their dominance and the impoverishment of all other families mirrors the composition of the Holarctic fauna (Dijkstra & Clausnitzer 2006; Kalkman *et al.* 2007).

Comparison of tropical odonate diversity. Data from Kalkman *et al.* (2007) and the appendix.

	Neotropics		**Afrotropics**		**Oriental**	
family	**genera**	**species**	**genera**	**species**	**genera**	**species**
Zygoptera						
Amphipterygidae	2	3	1	2	1	5
Calopterygidae	3	61	3	17	10	60
Chlorocyphidae	–	–	3	43	14	80
Coenagrionidae	38	370	11	179	23	185
Dicteriadidae	2	2	–	–	–	–
Euphaeidae	–	–	–	–	12	65
Lestidae	2	38	1	14	5	39
Lestoideidae	–	–	–	–	1	4
Megapodagrionidae	14	130	5	38	10	298
Perilestidae	2	18	1	1	–	–
Platycnemididae	–	–	9	45	8	130
Platystictidae	1	42	–	–	5	119
Polythoridae	8	58	–	–	–	–
Protoneuridae	14	94	2	23	8	57
Pseudolestidae	–	–	–	–	3	15
Pseudostigmatidae	5	18	1	1	–	–
Synlestidae	1	1	2	9	2	17
Anisoptera						
Aeshnidae	15	127	5	39	18	138
Austropetaliidae	2	7	–	–	–	–
Chlorogomphidae	–	–	–	–	1	40
Cordulegastridae	1	1	–	–	5	27
Corduliidae	2	37	6	19	7	57
Epiophlebiidae	–	–	–	–	1	1
Gomphidae	26	273	15	134	43	358
Libellulidae	44	352	46	217	56	190
Macromiidae	2	2	1	36	2	50
Neopetaliidae	1	1	–	–	–	–
Petaluridae	1	1	–	–	–	–
total	**186**	**1636**	**112**	**816**	**235**	**1665**

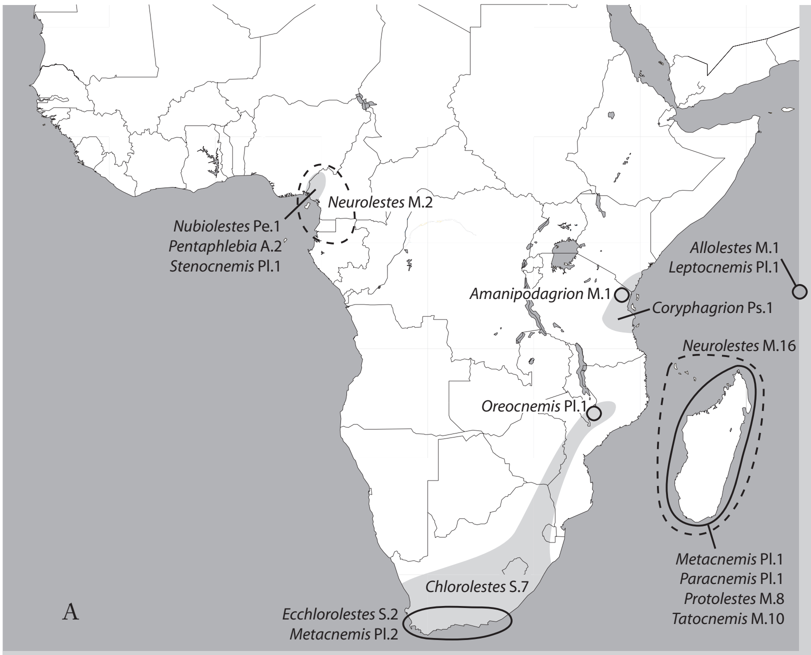


Fig. A Distribution of relict Afrotropical Zygoptera. The number of species and the family for each genus/area is indicated (A: Amphipterygidae; M: Megapodagrionidae; Pe: Perilestidae; Pl: Platycnemididae; Ps: Pseudostigmatidae; S: Synlestidae). *Nesolestes* is included in *Neurolestes* because of their close relationship (see appendix). Adapted from Dijkstra & Clausnitzer (2006).

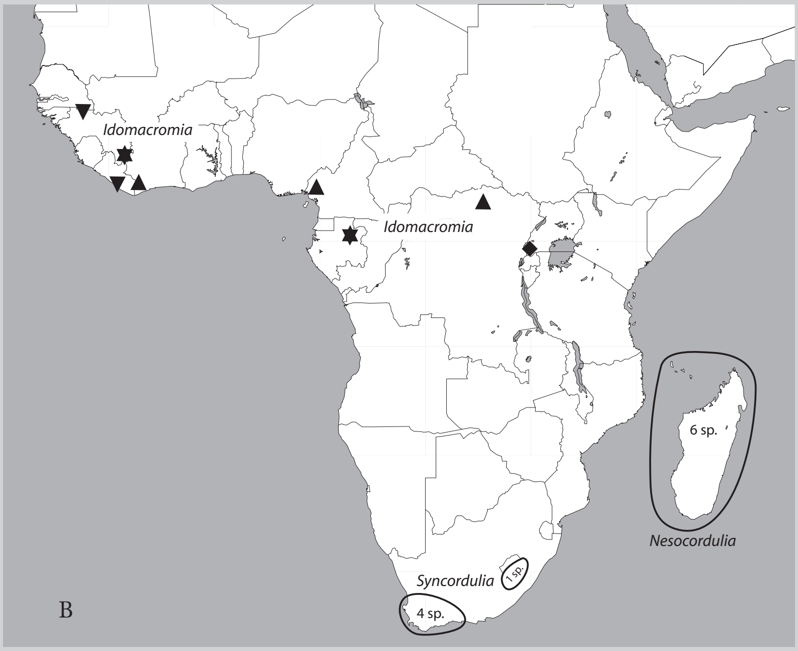


Fig. B Distribution of 'basal' Afrotropical Corduliidae. *Nesocordulia* and *Syncordulia* species overlap too widely to be indicated separately (species number provided); *Idomacromia* species are separated (diamond: *I. jillianae*; inverted triangle: *I. lieftincki*; standing triangle: *I. proavita*; star: both *I. lieftincki* and *I. proavita*). From Dijkstra *et al.* (2007c).

Afrotropical Odonata

General patterns and diversity

The Afrotropical odonate fauna is comparatively impoverished (Box 2). Dijkstra & Clausnitzer (2006) distinguished between 'old Africans', relict species that are now generally rare and localised (Box 3), and 'new Africans' that dominate the modern continental fauna (Box 4). The continent's 'continuous' nature allows extensive range overlap of species, making a biogeographic classification of both species and regions difficult. Box 5 provides a schematic synthesis of general diversity patterns in the Afrotropics, as a key to the review that follows below.

Guineo-Congolian fauna

Central and western Africa are naturally dominated by almost continuous Guineo-Congolian lowland rainforest, which has a gradual transition of riverine forests and woodland into peripheral areas. The highest diversity in the Afrotropics is found here: all African countries with well over 200 odonate species have a considerable portion of this forest within their borders (Dijkstra & Clausnitzer 2006). Although many species range throughout the forested region, it can be subdivided into four main areas of local endemism (Box 5), as demonstrated by groups of allopatric species in genera such as *Sapho*, *Chlorocypha* and *Platycnemis* (Box 1). The Lower Guinea, with the Cameroon highlands as its focus, is the richest area: it harbours six relict Zygoptera with Madagascan and Neotropical affinities (Box 3) and typical rainforest groups such as Calopterygidae, Chlorocyphidae and *Chlorocnemis* are about twice as speciose here as elsewhere in the region (Box 6). Furthermore, these highlands have the most distinct 'Afro-montane' character beyond eastern and southern Africa (Box 7). The Congo Basin has an especially interesting but insufficiently known fauna (Boxes 1, 9, 12).

Afro-montane fauna

Eastern and southern Africa harbour diverse but fragmented forests, restricted to areas of higher precipitation, especially at greater elevations but also on the coast. White (1981) characterised the upland forests as an "Afro-montane archipelago" because of their isolated and dispersed nature and Dowsett-Lemaire & Dowsett (2001) also identified an "eastern archipelago" of scattered lowland forests. The term Afro-montane is perhaps not apt for the entire

Box 3. Old Africans: rare relicts of an ancient fauna

A comparison of the continental African Odonata with the faunas of Madagascar and other tropical areas may identify the oldest Afrotropical fauna, and thus probable centres of climatic stability. The comparison should focus on ecologically sensitive taxa, which have relatively small or isolated ranges, and that (largely) lack close relatives within the continent. This includes all African members of the damselfly families Amphipterygidae, Megapodagrionidae, Perilestidae, Pseudostigmatidae and Synlestidae, as well as several small (mostly monotypic) restricted-range genera of undetermined relations now placed in Platycnemididae (Fig. A). Relationships within the Corduliidae are poorly understood, but three 'plesiomorphic' genera also show a relict distribution (Fig. B). Strong candidates to be qualified as 'old Africans' are taxa conserved both in Madagascar and locally on the continent, such as *Neurolestes* (including *Nesolestes*; see appendix) and *Metacnemis* (Fig. A). Others are the endemic gomphid subfamily Phyllogomphinae, represented by *Isomma* (including *Malgassogomphus*; see appendix) on Madagascar, *Phyllogomphus* in equatorial Africa and *Ceratogomphus* in southern Africa, and the libellulid genera *Malgassophlebia* and *Neodythemis*, confined to forest streams in central and western Africa and eastern Madagascar (compare Fig. B). A third genus with a Guineo-Congolian/Madagascan disjunction is *Platycnemis*, but see Box 1.

Five centres where these 'old' odonates survived can be identified within the Afrotropics (Figs. A-B and Box 5), in order of importance: (1) Madagascar, especially the eastern rainforests; (2) South Africa, especially towards the Cape; (3) the equatorial rainforest, particularly the Cameroon highlands and surrounding Lower Guinea; (4) the coastal and Eastern Arc forests of eastern Africa; (5) the granitic Seychelles. The affinities of most of the relict inhabitants are unclear, although *Nubiolestes* and *Pentaphlebia* of the Cameroon highlands only have surviving relatives in northern South America. The relationships of the Synlestidae and *Syncordulia* of South Africa are possibly Australian (Dijkstra *et al.* 2007c). Especially mysterious is the isolated presence of the otherwise exclusively Neotropical Pseudostigmatidae on the 'wrong' side of the African continent (Box 10).

fauna: Afro-montane forest descends to sea-level in South Africa, while localised inhabitants of equatorial coastal forests and swamps at moderate altitudes are also included here. Nonetheless, almost all of Africa above 1000m is included within the region where the discussed fauna occurs, and most of this region is also above that altitude.

Species numbers are lower here than in western and central Africa – national diversity generally lies between 100 and 200 species – but regional endemism is greater. Except for some ubiquitous highland species like *Pseudagrion spernatum* and *Proischnura subfurcata*, few taxa inhabit the total expanse of this geographically and climatologically diverse region. The genera *Proischnura*, *Aeshna*, *Notogomphus*, *Atoconeura* (Boxes 7, 14) and to some degree *Platycypha* (Box 15) most clearly demonstrate an Afro-montane distribution. *Africallagma* and the A-group of *Pseudagrion* also show marked Afro-montane diversity and endemism. All these groups have their greatest abundance above about 1000m altitude, but there is a 'piedmont effect' in which species occur at considerably lower altitudes in the proximity of highlands (Box 14). The transition to montane habitat on the equator is at 1500-1800m (Dowsett 1986) and the upper limit of forest at 2800-3300m (de Jong & Congdon 1993), but a truly montane fauna, with species occurring exclusively above 2000 or even 3000m is virtually absent (see below). Adding to the Afro-montane complexity is the strong Guineo-Congolian and even insular influence in the periphery, as is most apparent from Uganda to Zambia (Box 13) and on the coast (Box 11). The latter is one of several elements that make the fauna of the Eastern Arc Mountains among the most diverse (in terms of suspected age and origin, but to some degree also by species numbers) in Africa. Several endemics in the Tanzanian highlands, some of which extend to Malawi or even Zimbabwe, have Guineo-Congolian affinities, such as the endemic monotypic genus *Nepogomphoides* (Box 6). The monotypic genera *Amanipodagrion* and *Oreocnemis* have among the smallest ranges in African Odonata, and are completely isolated taxonomically, while the presence of the pseudostigmatid *Coryphagrion* in eastern Africa may be the greatest biogeographic anomaly discussed (Boxes 3, 10).

South Africa is one of the most significant centres of endemism on the continent, and certainly that harbouring most relict species. Almost one-fifth of the national fauna of about 160 species is endemic, a figure that almost stands at one-third if the peripheral presence of tropical species is excluded. The 30 or so endemics are split about equally between the 'relict' (near-)endemic genera *Chlorolestes*, *Ecchlorolestes*, *Metacnemis*, *Ceratogomphus* and *Syncordulia* (Box 3), and genera (or species groups) with an Afro-montane character: *Platycypha*, *Africallagma*, *Pseudagrion*, *Proischnura*, *Allocnemis*, *Elattoneura*, *Aeshna* and *Orthetrum* (Boxes 6, 7). Smaller centres of endemism (three to twelve species each) are found in the highlands of Ethiopia (Box 8), Kenya (extending just into eastern Uganda and northern Tanzania), Zimbabwe-Mozambique and Angola (Box 1). The few Angolan endemics known have Guineo-Congolian affinities (Box 6), but the apparent poverty of a typical upland fauna (Boxes 7, 14) may be due to insufficient research. On the other hand, restricted-range species of *Platycypha*, *Africallagma*, *Aeshna*, *Paragomphus*, *Atoconeura* and especially *Pseudagrion* and *Notogomphus* feature prominently in the other Afro-montane faunas. The most 'elevated' Afrotropical odonate fauna is found along the Eastern Rift Valley around Mts Elgon, Kenya, Meru, Kilimanjaro and the Aberdares, where permanent snow extends from about 5000m. Of the endemics, *Platycypha amboniensis* remains between 1500 and 2000m, *Notogomphus maathaiae* between 2200 and 2600m, and only *Pseudagrion bicoerulans* and *Atoconeura kenya* occur up to and occasionally slightly over 3000m. *P. bicoerulans* is the most 'alpine' African odonate, being characteristic of altitudes above 2500m and not found below 2000m (Clausnitzer & Dijkstra 2005b).

Insular fauna

Of the approximately 175 odonate species of Madagascar, 60% of Anisoptera and almost 95% of Zygoptera species are endemic. About 80% of endemics belong to endemic genera (*Protolestes*, *Tatocnemis*, *Paracnemis*, *Isomma*, *Libellulosoma*, *Nesocordulia*, *Archaeophlebia*, *Calophlebia*, *Thermorthemis*, *Viridithemis*) or to distinct radiations of *Nesolestes* (see appendix under *Neurolestes*), *Platycnemis*, *Pseudagrion*, *Malgassophlebia* and *Neodythemis*. These are largely forest species, while the remaining fifth inhabits mostly open habitats and has close relatives on the mainland (*i.e.* pan-African species). Endemism and diversity is greatest on the island's wet eastern coast (Dijkstra & Clausnitzer 2004). The Odonata of the Comoros are

Box 4. New Africans: dominant odonates in today's continent

None of the 'old Africans' are nowadays dominant in continental Africa and they are even absent from large areas of high species diversity, such as most of the Guineo-Congolian forest (Box 3). Especially the continental forest fauna is dominated by groups that are absent on Madagascar or represented only by one or a few adaptable species that probably colonised the island recently from the mainland (see table below). The examples alone represent 35% of Afrotropical species diversity, of which 97% is continental (by contrast, the 'old African' examples in Box 3 form 12% of diversity, with only 48% continental species). The distinction between continental and insular faunas is less clear for openland species, which are better dispersers, but most of those occurring on Madagascar are also considered recent arrivals (Dijkstra & Clausnitzer 2004). All mentioned continental groups are related to more diverse faunas in tropical Asia and are characterised by many relatively similar species (*i.e.* classified in few genera). This suggests comparatively recent, rapid diversification.

Examples of large (>10 species), morphologically homogeneous groups, which are widespread in tropical Africa and often Asia, but are (largely) absent on Madagascar.

	species African continent	**species Madagascar, Comoros and Mascarenes**	**relatives in southern Asia**
Calopterygidae	17	1 shared with continent	many, but no shared genera
Chlorocyphidae	43	-	many, but no shared genera
ischnurine Coenagrionidae*	35	5 endemics in shared genera	many, *Aciagrion* and *Ischnura* shared
Pseudagrion A-group	41	-	many in genus, probably not related
Pseudagrion B-group	22	2 endemic	many in genus, probably closely related
Allocnemis and *Chlorocnemis*	17	-	none known
Protoneuridae	23	-	many, *Elattoneura* and *Prodasineura* shared
lindeniine Gomphidae**	13	-	many, *Gomphidia* and *Ictinogomphus* shared
Neurogomphus	17	-	none known
Notogomphus	17	-	many, but genus not shared
Macromiidae	35	1 endemic in shared genus	many, but no shared genera

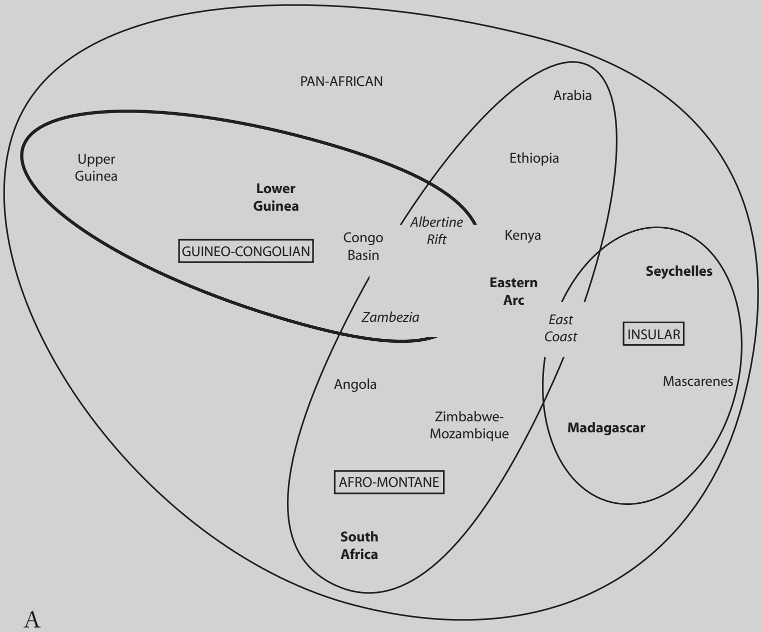
* *Aciagrion*, *Africallagma*, *Azuragrion*, *Ischnura*, *Pinheyagrion* and *Proischnura*

** *Diastatomma*, *Gomphidia* and *Ictinogomphus*

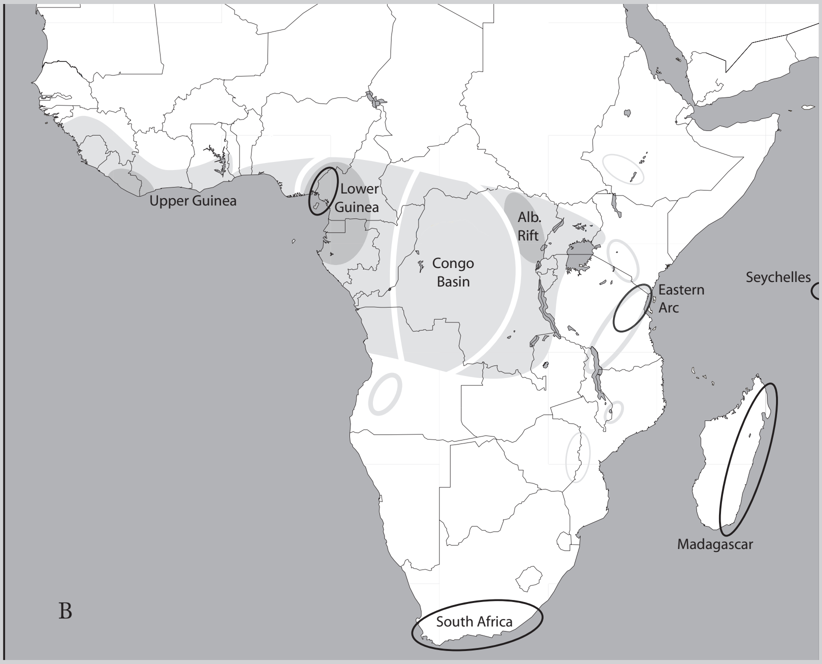
part of the same fauna, as shown by endemic species in the Madagascan complexes of *Nesolestes*, *Platycnemis*, *Pseudagrion*, *Nesocordulia* and *Thermorthemis* (Dijkstra 2004). The fauna of the Mascarenes and Seychelles are considered here principally for geographic reasons, as neither archipelago harbours any true Madagascan genera. Both island groups have two endemic genera, but while *Allolestes* and *Leptocnemis* of the Seychelles (ancient continental fragments) belong to the 'relict' families Megapodagrionidae and Platycnemididae (Box 3), *Coenagriocnemis* and *Thalassothemis* of the Mascarenes (recent volcanoes) belong to the 'modern' Coenagrionidae and Libellulidae (Box 2), although their nearest relatives are unknown. The islands do share the presence of species of *Teinobasis* (Seychelles only), the *bispina*-group of *Gynacantha* and *Hemicordulia* with Madagascar; an insular element that also extends to the adjacent mainland (Box 11).

Pan-African fauna

The dominance of Coenagrionidae and Libellulidae in the Afrotropical fauna (50% of species; Box 2) is even greater among the widespread fauna of open habitats (70%). Countries with a purely pan-African fauna are very impoverished, such as the Sahel nations with mostly fewer than 100 species each. The majority of pan-African genera and species occurs throughout the Afrotropics, with the possible exception of the wettest, driest and coldest areas, and may extend well into Eurasia or to oceanic islands. Examples are *Phaon iridipennis*, *Agriocnemis exilis*, *Ceriagrion glabrum*, *Ischnura senegalensis*, *Anax tristis*, *Acisoma panorpoides*, *Aethriamanta rezia*, *Brachythemis leucosticta*, *Chalcostephia flavifrons*, *Crocothemis erythraea*, *Diplacodes lefebvrii*, *Orthetrum trinacria*, *Palpopleura lucia*, *Pantala flavescens*, *Rhyothemis semihyalina*, *Tetrathemis polleni*, *Tholymis tillarga*, *Tramea*



A



B

Fig. A Schematic representation of Afrotropical odonate diversity. Each ellipse represents about one-fifth of species richness, the thick-bordered ellipse two-fifths. The name of the fauna represented by each ellipse is given in upper case; discussed regions are given in lower case. Regions in bold font harbour ancient relicts, often in regionally endemic genera (Box 3), those in italic font have a 'mixed' character where faunas intersect (Boxes 11, 13).

Fig. B Afrotropical forests and their presumed refuges. Legend – pale shading: approximate current distribution of Guineo-Congolian forest Odonata, divided into four main areas of regional endemism; dark shading: approximate position of main Pleistocene rainforest refuges, as traditionally identified; black-bordered ellipses: approximate position of centres of ancient relict Odonata (Box 3); grey-bordered ellipses: approximate position of Afro-montane centres of Guineo-Congolian odonate relicts, thickness of border indicates relative importance (Box 6).

Box 5. Composition of the Afrotropical odonate fauna

Odonate diversity is greatest in tropical forests, also in Africa (Kalkman *et al.* 2007). Dijkstra & Clausnitzer (2006) identified three Afrotropical regions of forest odonate richness. Almost two-fifths of species occur predominantly within the extensive Guineo-Congolian forests of the western and central continent (Fig. A). Just over a fifth is found in the eastern and southern part of the continent dominated by highlands, which is therefore referred to as Afro-montane. About another fifth of diversity is insular, centred in Madagascar and associated islands. The remaining fifth is not associated with forests or highlands, but with open and generally low habitats, such as savannas. Many of these species are very widespread and can be seen as the pan-African part of the fauna. The forest fauna can be further divided by discontinuities in species distributions, the presence of relict species (Box 3), and centres of diversity, which are often identified as rainforest refuges (Fig. B).

basilaris, *Trithemis arteriosa* and *Urothemis assignata*. Some mainland species are replaced in Madagascar by a close relative, such as *Diplacodes deminuta* by *D. exilis*, *Hemistigma albipunctum* by *H. affine*, and *Zygonyx natalensis* by *Z. elisabethae*. The northern and eastern savanna belt may also harbour two vicariants, *e.g. Bradinopyga strachani* and *B. cornuta*, *Nesciothemis pujoli* and *N. farinosa*, and *Trithemis dejouxi* and *T. donaldsoni*. Such pairs with also a Madagascan relative are *Azuragrion vansomereni* and *A. nigridorsum* with *A. kauderni*, and *Zygonoides fraseri* and *Z. fuelleborni* with *Z. lachesis*. Both latter examples also have isolated siblings within the forest matrix; *A. buchholzi* in the Cameroon highlands and *Z. occidentis* in the Congo Basin (Box 9).

Discussion

As their taxonomy has only recently become more settled (see appendix), distribution patterns are just emerging (Boxes 1, 3, 6, 7, 9, 11-15) and phylogenetic reconstruction is still in development (Box 15), the history of Afrotropical Odonata can as yet only be inferred from parallels in the biogeographic literature. This is attempted in the following discussion.

Old and new origins

The Gondwana problem

Many distribution patterns in the southern continents have been related to the fragmentation of Gondwanaland. The supercontinent began to break up 150-165 Ma (million years ago) and Africa's direct contacts with Antarctica and Australia were lost ±135 Ma. The southern Atlantic began to open 120-135 Ma and the final separation of Africa and South America, near the present Niger Delta, was between 110 Ma and 84 Ma. The rifting between Africa and Madagascar began 155-170 Ma, and the island came to occupy its present isolated position 120-121 Ma, separating from India 83-89 Ma. The Seychelles block split from India 65 Ma (Daniels *et al.* 2006; Masters *et al.* 2006; Sanmartín & Ronquist 2004). However, the significance of this scenario for comtemporary distributions is increasingly doubted (Sanmartín & Ronquist 2004). For instance in freshwater crabs, which occur in similar habitats as Odonata but have a much lesser dispersal capacity, Daniels *et al.* (2006) found that both the timing and sequence of evolutionary divergences were irreconcilable with continental fragmentation, the radiation of African, Malagasy and Seychelles species beginning at most 78 Ma. Such findings have lead to the revival of dispersal (de Queiroz 2005; McGlone 2005) and terrestrial corridors (*e.g.* Fuchs *et al.* 2006; Jønsson & Fjeldså 2006; McCall 1997) in biogeographic hypotheses, although continental vicariance continues to play a role (*e.g.* Sparks & Smith 2005), as outlined below for relict Afrotropical Odonata.

Ancient Americans and not-so-ancient Africans

The only relative of *Pentaphlebia* is the monotypic genus *Rimanella* of the Guianan Shield; besides *Nubiolestes*, Perilestidae is represented by two genera and eighteen species with a centre of diversity in northern South America (Box 3). Dumont *et al.* (2005) dated the divergence of *Pentaphlebia* and *Rimanella* at ±150 Ma. This and their distribution support Gondwanan vicariance for these Cameroon relicts, highlighting them as the possibly oldest surviving odonates in continental Africa. Their range coincides with the wettest (cumulatively and perennially) part of Africa (Maley 1989; Box 12). The distribution of pseudostigmatids demands a more complex

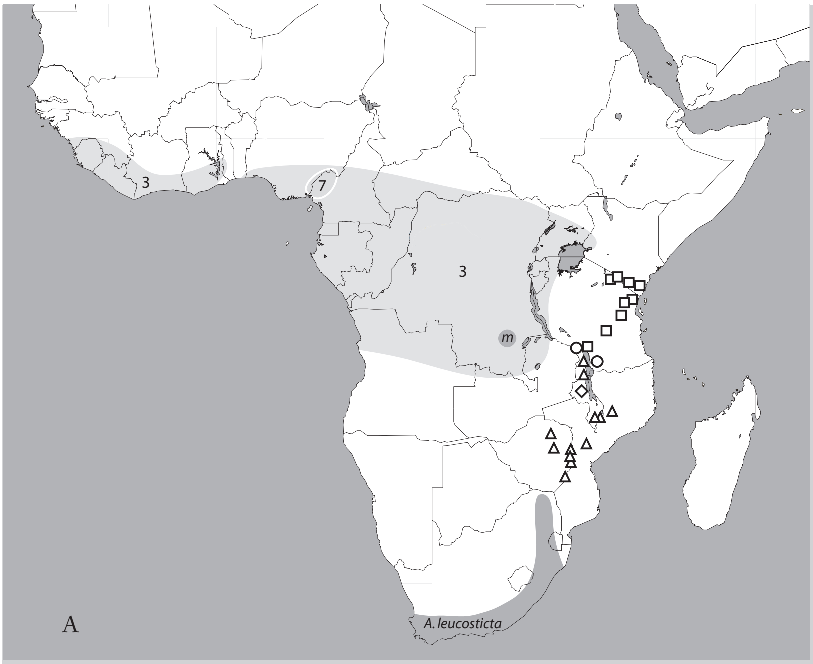


Fig. A Distribution of *Allocnemis* and *Chlorocnemis*. Legend – dark shading: range of *Allocnemis leucosticta* and *A. mitwabae* (m); pale shading: range of *Chlorocnemis* (regional maximal number of sympatric species indicated); squares: *C. abbotti*; circles: *C. montana*; diamond: *C. maccleeryi*; triangles: *C. marshalli*. Adapted from Dijkstra & Clausnitzer (2006).

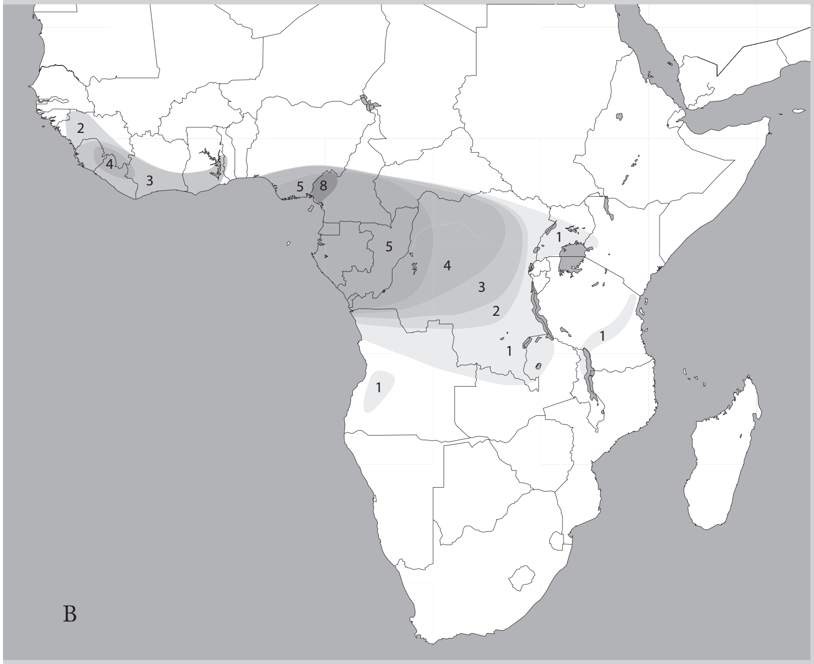


Fig. B Distribution of *Sapho* and *Umma* combined. Shading intensity and figures indicate the number of sympatric species.

biogeographic hypothesis (Box 10): eighteen species in five genera, occurring throughout the American tropics, are nowadays separated by 5500 km of Atlantic Ocean and 2500 km of African interior from the monotypic genus *Coryphagrion* (Box 3). A vicariance scenario implies its extinction in an area where two other Neotropical relicts survived (Groeneveld *et al.* 2007) and raises the question why these two did not survive in the east as well. Although pseudostigmatids differ by breeding in lowland forest phytotelmata, rather than submontane forest streams, contemporary Lower Guinean rainforests bear a greater resemblance to the perhumid habitats of Neotropical pseudostigmatids than the East Coast forests.

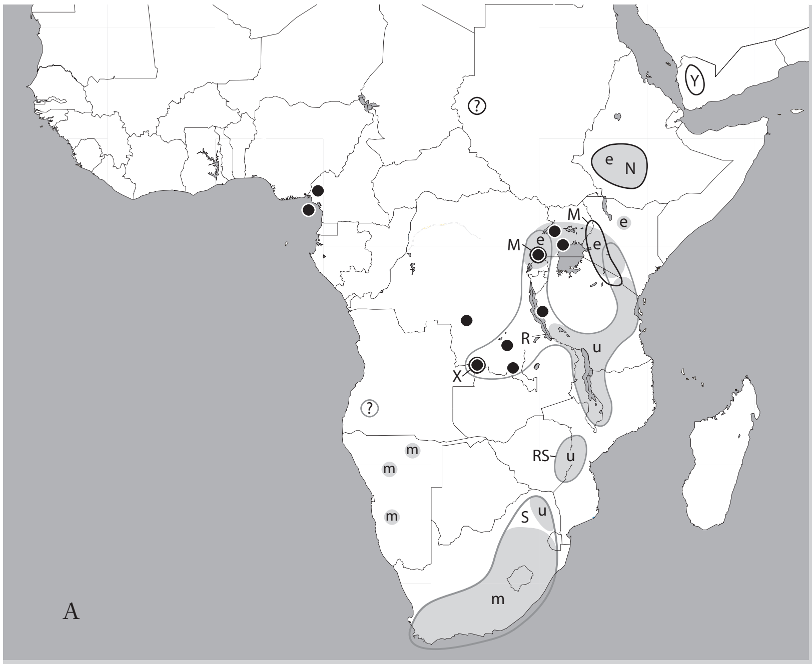
Madagascar's biota are often seen as relicts from before continental fragmentation (*e.g.* Dijkstra & Clausnitzer 2006). Davis *et al.* (2002) believed the island was "protected from the dramatic climate changes that influenced Africa beginning in the late Paleogene" and hence is home to "many representatives of the rainforest flora that are now extinct on the continent". Morley (2000) also ranked these rainforests among the most ancient in the world, considering them remnants of the southern rainforests (Box 10) that were lost temporarily on the mainland in the Oligocene and definitively in the late Miocene, but that survived dry periods since the Cretaceous because of moisture carried from the warm Indian Ocean by easterly trade winds. Despite its isolation from Africa by ±120 Ma, Madagascan fossil faunas prior to 65 Ma were cosmopolitan in nature, with ancestors of the characteristic present-day vertebrate radiations appearing later. The arrival of reed frogs estimated 19-30 Ma, tortoises 14-22 Ma, warblers 9-17 Ma, lemurs 55-60 Ma (mean of many estimates, range is 40-70), tenrecs 37-53 Ma (alternative estimate 25-42), carnivores 19-26 Ma and rodents 20-24 Ma (or 15-19) are all believed to be from Africa, while chameleons dispersed from Madagascar to Africa on at least three occasions 33-65 Ma (Caconne *et al.* 1999; Cibois *et al.* 2001; Masters *et al.* 2006; Poux *et al.* 2005; Raxworthy *et al.* 2002; Vences *et al.* 2003). McCall (1997) postulated the existence of a landbridge across the Mozambique Channel 26-45 Ma, and passerine dispersal along a sub-Antarctic route from Australia to Africa 45-50 Ma suggested by Fuchs *et al.* (2006) and Jønsson & Fjeldså (2006) might have passed through Madagascar too. Briggs (2003) suggested that as the Indian subcontinent separated from Madagascar and drifted northwards, it had a more westerly position and greater northern landmass than is generally assumed. This might have allowed more frequent and extensive exchanges to take place with Africa and Asia at least 83-121 Ma.

The above estimates and hypotheses suggest that colonisation may be more or less continuous, especially if the increasing emphasis on wind-dispersal for airborne biota (Box 11) and rafting for terrestrial biota is considered (de Queiroz 2005). As Poux *et al.* (2005) suggested, only considering McCall's land-

Box 6. The distribution and diversity of forest damselflies

The related genera *Chlorocnemis* (including *Isomecocnemis*; see appendix) and *Allocnemis* demonstrate the distribution of forest odonates in continental tropical Africa, as all species are obligate dwellers of shaded permanent streams (Fig. A). *Chlorocnemis* is widespread in the Guineo-Congolian forest, where up to three species co-exist and even up to seven in the Cameroon highlands. The Afro-montane archipelago is inhabited by four allopatric *Chlorocnemis* species, which are replaced in the southernmost extent of the archipelago by *A. leucosticta*. A second *Allocnemis* species is only known from the Mitwaba Escarpment in Katanga and stands between *Chlorocnemis* and *A. leucosticta* morphologically. The group is absent in the northernmost Afro-montane sites, despite the presence of suitable habitats (Boxes 7, 8).

A more detailed picture of forest odonate diversity is provided by the Saphoinae, a monophyletic Afrotropical radiation of fifteen calopterygid species restricted to forested streams and rivers (Fig. B). Diversity is centred on the highlands in the Lower and – to a lesser degree – Upper Guinea, with only single species in the Guineo-Congolian periphery, as well as the endemic *U. femina* in Angola and *U. declivium* in the Eastern Arc highlands. The latter is most similar to *U. purpurea*, one of the Cameroon endemics. An almost identical but simpler pattern is shown by *Micromacromia*, with a sympatric pair of similar species in western Africa, of which one extends to western Kenya, and the endemic *M. flava* in Angola and *M. miraculosa* in Tanzania (Dijkstra & Vick 2006). Other probable Guineo-Congolian relicts in the Eastern Arc, besides the *Chlorocnemis* species (see above), are *Platycypha auripes* (Box 15) and the endemic monotypic genus *Nepogomphoides*, which is probably related to *Tragogomphus*.



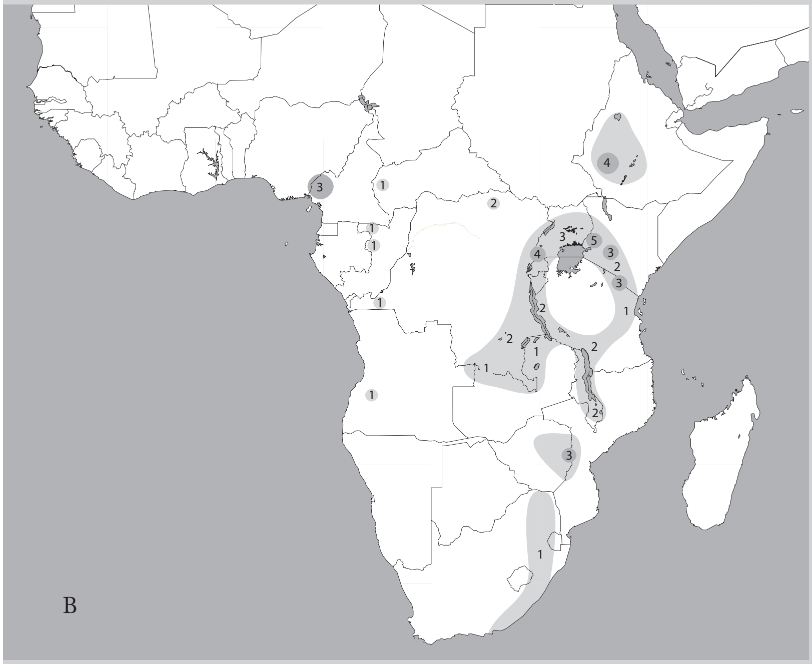


Fig. A Distribution of Afrotropical *Aeshna* species. Legend – filled circles: *A. scotias* (includes *A. wittei*); shading: *ellioti*-group (e: *A. e. ellioti*; u: *A. e. usambarica*; m: *A. minuscula*); outlines: *rileyi*-group with northern (black – M: *A. meruensis*; N: unnamed species; X: *A. moori*; Y: *A. yemenensis*; ?: Sudan record, species uncertain) and southern subgroup (grey – R: *A. rileyi*; S: *A. subpupillata*; ?: Angola record, species uncertain).

Fig. B Distribution of *Notogomphus*. Figures indicate the number of allopatric species; local peaks in diversity are shaded darker. Scattered Guineo-Congolian records are given as separate sites.

bridge, Madagascar's faunal similarity with Africa might then be expected to be much greater. Perhaps it is more important to consider the opportunities for groups to radiate in Madagascar, than the accessibility of these chances to potential ancestors. Because of their size and isolation, islands are more prone to catastrophic extinctions, which may subsequently allow immigrants more ecological space to radiate (de Queiroz 2005). Madagascar drifted through a subtropical high pressure zone 30-65 Ma, possibly "emptying the island for colonisation by chance immigrants and subsequent evolutionary radiations" (Wells 2003). The severity of this 'arid passage' is unknown, but according to Wells (2003) rainforests in the east may only have emerged with the advent of orographic rainfall in the Eo- or Oligocene (±25-55 Ma), those in the north-west with monsoons in the past 8 Ma. However, if dispersal was rather continuous, even across marine barriers, why are so many groups absent from smaller islands and did others fail later in Madagascar? A larger landmass will receive more chance arrivals and offer these more opportunities, but the latter may diminish as existing radiations become established. In summary, Madagascar's unique biota may result from a rather random history of opportune arrivals, in which events like Wells's arid passage may be more relevant than McCall's landbridge. In the specific case of Madagascan odonates (megapodagrionids, corduliids, *Platycnemis*) the problem remains that their relationships are largely unknown. For obligate rainforest stream dwellers found also on the mainland (*Nesolestes*, *Malgassophlebia*, *Neodythemis*), continental barriers may be more significant than oceanic ones, as limitations posed by habitat and competition outweigh opportunities of ecological vacancy and aided dispersal (Box 11). These links would date from times when forest was trans-continental (>10 Ma). In any case, Madagascan endemic Odonata may be characterised more by their isolation than by their age.

As with Madagascar's 'ancient' biota, it is tempting to link the histories of South Africa's relict odonates and the fynbos biome that they inhabit (Dijkstra *et al.* 2007c). They occur in the most remote corner of a continent with a prolonged history of isolation. Although the flora had an 'austral' character already in the Paleocene, the Cape was covered in warm temperate forest until the cold upwelling off the South African coast blocked off summer rainfall 8-10 Ma, establishing fynbos at its current position only 3-5 Ma. Moreover, local plant radiations (mostly with Australian relationships) diverged between 80 and 37 Ma, passerines possibly dispersed directly from Australia about 45-50 Ma, and midges thought to be archaeic only diverged in the past 10 Ma. These data suggest that the Cape biota are much less ancient than assumed by Gondwanan vicariance (>120 Ma) and that they attained their current habitat and range even more recently. *Syncordulia* species inhabit cold and nutrient-poor streams, which are almost devoid of more widespread Afrotropical Odonata (Box 3). The montane character of this habitat and the ab-

Box 7. The distribution and diversity of highland dragonflies

The occurrence of the Afrotropical *Aeshna* species offers the best example of an Afro-montane distribution (Fig. A). The species belong to three distinct groups, which probably represent separate genera (see appendix). The *rileyi*-group extends from the northernmost extent of the Afro-montane area (southern Arabia) to the southernmost, the Cape Peninsula. The species are largely allopatric, but those of the distinct northern and southern subgroups overlap narrowly; and the two very similar southern species may be sympatric in Zimbabwe. The assignment of *A. moori* – known only from the type pair – to the northern group is preliminary (Dijkstra 2007a). Females of the *rileyi*-group are known from isolated mountains in Sudan and Angola, but cannot be identified reliably. The three taxa of the *ellioti*-group occur locally within the range of the *rileyi*-group and are strictly allopatric. Records of *A. scotias* (including *A. wittei*) roughly follow the Albertine Rift, with a disjunct population in the Cameroon highlands, including Bioko.

Notogomphus further illustrates Afro-montane diversity (Fig. B). Of seventeen species, fifteen occur east of the Congo Basin and three to the west. Especially the northern highlands harbour several species with rather small and partly overlapping ranges, leading to the local sympatry of up to five species, such as around the central and western Kenyan highlands and Mt Kilimanjaro. Similar distributions are seen in *Proischnura* and *Atoconeura* (Box 14). In all above cases a small number of species of an Afro-montane character occur in the highlands or piedmont of western Africa.

sence of strongly competitive species there, suggest that they are the last vestiges of an older Afro-montane odonate assemblage, surviving in a habitat to which they are better adapted than modern Afrotropical species. Their 'young' and isolated habitat may be their last refuge from extinction (see Dijkstra *et al.* 2007c for references).

New Asians

While Madagascar's 'old African' odonate fauna (Box 3) was possibly assembled in the Eo-Oligocene and perhaps early Miocene, dispersal towards the island would have diminished with the loss of trans-continental rainforests (>10 Ma) and hypothetical trans-oceanic landbridges (>26 Ma). The 'new Africans' (Box 4), may mostly have arrived on the continent afterwards. Their modern relatives are tropical Asian, although they would have ranged widely across Eurasia in warmer, wetter times. Nonetheless odonate fossils from Europe generally show no distinct Afrotropical affinities, with the exception of 25-26 Ma old wings associated with *Sapho* and *Umma* (Nel & Paicheler 1993). Although Briggs's (2003) hypothesis of a more westerly and larger Indian subcontinent (see above) allows earlier and more extensive exchange with Eurasia (*e.g.* 65 Ma), Morley (2000) reported little evidence of plant dispersal before India approached Asia 36-54 Ma, which is contemporaneous with the arrival of *Chiromantis* frogs from Asia 33-51 Ma (Vences *et al.* 2003). Kappelman *et*

Box 8. Poor in species, rich in endemics: Odonata of the Ethiopian Highlands

Clausnitzer & Dijkstra (2005a) surveyed the Odonata of Ethiopia, with the following notable results: (1) low total number of species; (2) low average number of species per locality; (3) low average proportion of sites at which each species was found; (4) scarceness of species known to be common in similar habitats as far south as Malawi; (5) high proportion of endemics. Altitude may explain observations 1-4, as the majority of sites was above 1450 m. A comparison of Kenyan and Tanzanian records above this altitude revealed that openland species are generally shared but seemed comparatively scarce in upland Ethiopia, while Ethiopia has many fewer and no shared forest species. A high number of the openland species is non-seasonal in permanent water further south, but a more extreme cold and dry season could induce stronger seasonality in the Ethiopian highlands. Possibly many species have difficulty colonising the highlands for this reason. On the other hand the Ethiopian records for six species were East African altitude records. Ethiopia's impoverishment rests mainly on the paucity of forest species. Two *Gynacantha* species, that otherwise range from central Uganda to western Africa, are the only signs of a former Guineo-Congolian forest connection. Forest genera like *Chlorocypha*, *Umma*, *Chlorocnemis*, *Hadrothemis*, *Micromacromia* and *Notiothemis* are absent, despite the presence of suitable habitat (Boxes 6, 13).

Whereas diversity in Ethiopia is low, endemism is high at 12%, versus between 1 and 3% for Kenya, Tanzania and Uganda each. Among the fourteen most widespread high-altitude species in Ethiopia were four endemics. Almost all belong to genera (*Aeshna*, *Pseudagrion*, *Elattoneura*, *Notogomphus*, *Crenigomphus*, *Paragomphus*, *Atoconeura*, *Orthetrum* and *Trithemis*) that dominate further south in tropical Africa, both in species as individual numbers, and most appear closely related to species occurring in the highlands there (Boxes 7, 14). Only *Ischnura abyssinica* lacks obvious southern links and possibly has Palearctic affinities. Such a relationship is dominant in Ethiopia's endemic montane grassland butterflies (de Jong & Congdon 1993). The genus *Ischnura* is practically cosmopolitan, well represented in the Holarctic and most poorly in the Afrotropics, but molecular analysis has not revealed any close relatives of *I. abyssinica* (H.J. Dumont, in litt. 2 October 2006).

Ethiopia's history and isolation may explain its species-poor but endemic-rich character (see Clausnitzer & Dijkstra 2005a for an overview). Climatic fluctuations were probably relatively severe due to the Ethiopian highlands' large mass of land at great altitude. During cooler periods, species adapted to relatively warm and wet conditions (like Odonata) were literally crushed between the descending cold and arid piedmont. The Red Sea, (semi-)deserts of Kenya and Somalia, White Nile floodplains and the escarpments of Ethiopia itself are formidable barriers, even for openland species, hampering (re-)colonisation of the highlands. Nonetheless, in warmer or wetter periods tropical African species must have expanded into the Ethiopian highlands, with the possible exception of the predecessor of *I. abyssinica*. Especially those species best adapted to montane conditions survived the climatic vicissitudes following their colonisation. A handful of species requiring warmer conditions, such as the *Gynacantha* species, survived in the warmer and wetter south and west of the highlands.

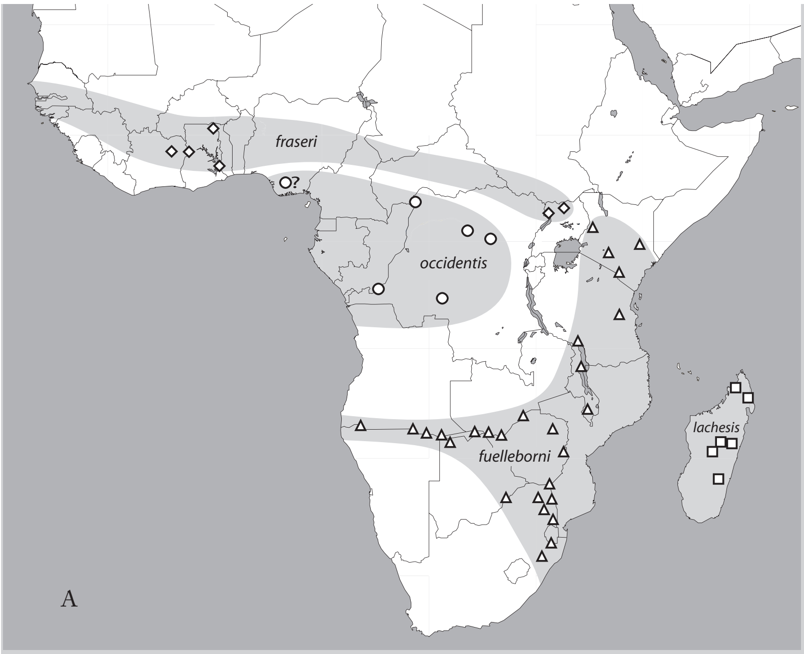
al. (2003) reported Oligocene mammal interchange between Africa and Eurasia 24-27 Ma and Barker *et al.* (2004) an African-Asian passerine disjunction 26-27 Ma, but otherwise most evidence of Asian links come from the Miocene. This is associated with the gradual closure of the Tethys Sea after 24 Ma and by 10-16 Ma, with a land connection through Arabia originating around 18 Ma. Major turnover in the African mammal fauna, which resulted from interchange with Eurasia and the extinction and radiation of local and immigrant groups, occurred 17-19, 14-15, 5-8 and 2.5 Ma (Vrba 1993). Major dispersal of plants began 10 Ma (Morley 2000). Based on molecular and fossil data, Agnese & Teugels (2005) reconstructed that clariid catfish, now dominant in African freshwaters, originated in Asia 40-50 Ma and arrived in Arabia 30 Ma, but did not enter Africa before 15 Ma, probably 12-13 Ma. Other immigrations through forested corridors in Arabia were proposed for viverrids, fruit bats (16-19 Ma) and *Rana* and *Hoplobatrachus* frogs (4-26 and 4-12 Ma respectively) (Gaubert & Cordeiro-Estrela 2006; Juste B. *et al.* 1999; Vences *et al.* 2003). Orogenesis and desertification in Africa and Arabia subsequently severed links with Eurasia, although savanna dragonflies like *Bradinopyga* and *Palpopleura*, like *Rousettus* bats (Juste B. *et al.* 1999) and *Pycnonotus* bulbuls (Moyle & Marks 2006), could easily have crossed recently when conditions were slightly wetter than now. In summary, Asian immigrants could arrive over a prolonged period, although they seem concentrated in the later Miocene, conforming to their virtual absence from Madagascar. Dumont *et al.* (2005) estimated that ancestors of *Sapho* and *Umma* separated from Asian stock 77-85 Ma and that these genera split 49-53 Ma, but had they been present in African rainforests this early, they might also have reached Madagascar. These authors believed that the separation of continental and Madagascan populations of *Phaon iridipennis* also took place in the Cretaceous, but that figure is questionable given the morphological uniformity of this ubiquitous species.

The paradox of Miocene dispersal into Africa is that it coincided with extensive aridification, especially after 16 Ma (see below): the closure of a marine barrier, the Tethys Sea, lead to the opening of a terrestrial hurdle, the Sahara. Even 17-20 Ma Arabia was probably comparatively arid (Kosuch *et al.* 2001). The marked interchange of mammals with Eurasia was not seen in tropical plants, probably because the latitudinal zonation of vegetation facilitated access for non-forest biota, but obstructed forest biota (Morley 2000). Perhaps true forest species arrived earlier, or evolved from ancestors of open habitats (de Jong & Congdon 1993). Afrotropical squirrels, which are absent from Madagascar, possibly derived from terrestrial species and are secondarily arboreal (Kingdon 1989). Molecular evidence suppors this hypothesis, but is not entirely conclusive (Steppan *et al.* 2004). The damselfly *Arabineura khalidi* is endemic to Arabian stream oases, but is closely related to diverse complexes of *Elattoneura* and *Prodasineura* species, which occur predominantly in African and Asian rainforests. *Arabicnemis caerulea* has a similar range and habitat, but more enigmatic affinities. Both species could be relicts of the ancestors of Africa's rainforest Odonata passing through an 'Arabian filter'. Like the suggested 'arid passage' of Madagascar, ecological changes induced by the Miocene aridification may be more important to the appearance of new arrivals in continental Africa, than the disappearance of marine barriers. Moreover, the dispersal of winged insects of wet habitats along a series of forested islands is perhaps more plausible than through broad swathes of hostile drylands. Morley (2000) described the Tethys Sea as an "ancient Malay Archipelago". Dijkstra (2007d) proposed overseas dispersal of Odonata over even greater distances and much more recently that implied by Tethyan stepping-stones (Box 11).

Rainfall, uplift, demise and rise

"Mountain ranges [...] were pushed up by volcanic activity, from their earlier peneplain [...]. Forests of [...] highlands would have been preserved during forest retreat in the arid interpluvials and speciation resulted from this isolation. Small forest patches have more chance for mutation than the huge, overcrowded rain forest belt. The reverse effect occurred during pluvial extensions which encouraged uniformity."

This concise but visionary description of odonate speciation by Pinhey (1978) hinted at three elements central to the contemporary understanding of Africa's biodiversity: the importance of mountains and the forest periphery in speciation, and the uniformity of the modern forest fauna. The discussion below focuses on the climatological and geological setting of speciation, as well as the debate on the character



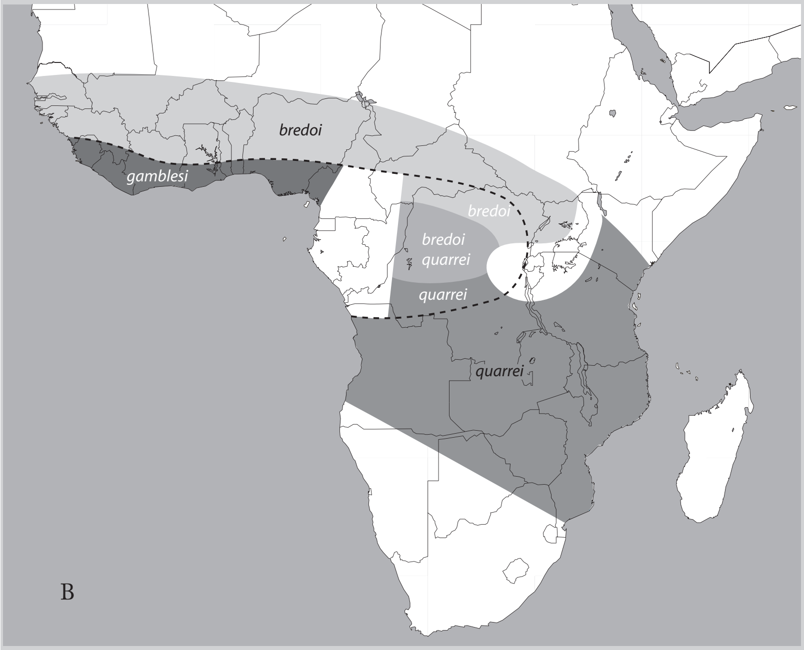


Fig. A Distribution of *Zygonoides* species. Legend – squares: *Z. lachesis*; triangles: *Z. fuelleborni*; diamonds: *Z. fraseri*; circles: *Z. occidentis*; shading: inferred ranges. From Dijkstra *et al.* (2006b).

Fig. B Inferred distribution of Afrotropical *Gomphidia* species. Legend – pale shading: *G. bredoi*; intermediate shading: *G. quarrei* (overlap with *G. bredoi* shown); dark shading: *G. gamblesi*; dashed line: approximate limit of dark forest forms; unshaded: areas with insufficient data to reasonably infer present species and form. From Dijkstra (in prep. d).

of forest refuges and if, how, when and where they functioned as centres of speciation or species preservation. Besides speciation, change will have lead to extinction, and causes of impoverishment are investigated too.

The Cenozoic Setting

During the Paleogene (23-65 Ma) the African flora diversified almost uninterrupted and by the end of the Eocene and the Oligocene the taxa that today characterise the Guineo-Congolian rainforest were at their most diverse. These forests stretched to northern Ethiopia, with galleries extending to Egypt (Jacobs 2004; Morley 2000). The Miocene (5-23 Ma) was "one of the most defining periods of Africa's geological and climatological history" (Plana 2004). Initially the continental divide was low and rainforest stretched between coasts, but uplift in eastern Africa (12, 10 and 7 Ma), global cooling and the closure of the Tethys Sea resulted in increasing aridification: savanna began expanding 16 Ma and became widespread 8 Ma (Jacobs 2004; Morley 2000; Sepulchre *et al.* 2006; Vrba 1993). Thus eastern and western rainforests began to separate by 17-18 Ma and finally by 10 Ma, although gallery forests may have allowed partial contact later on (Lovett 1993). By the end of the Miocene (5 Ma) rainforest was limited and much of Africa's Paleogene diversity was probably eliminated (Plana 2004). The start of the Pliocene (3.5-5 Ma) was again moist and tropical forest expanded as far north as the Tibesti Mts, but pronounced drying occurred 3.5, 3.2 and 3.0 Ma and especially 2.5-2.8 Ma with the onset of the first northern hemisphere glaciation (Morley 2000). At this time, montane *Podocarpus* extended to the far west of Africa; the first post-Cretaceous gymnosperm there. Further step-like increases in aridity took place 1.7-1.8 and 1.0 Ma (deMenocal 1995). During the Pliocene and early Pleistocene major uplift also created the Great Rift Valley and the Congo Basin (Plana 2004). The Sahara opened up 4-5 Ma and modern climatic zonation became established, with a true desert climate prevailing in the late Pliocene (1.6-3.5 Ma), and during glacial maxima rainforests occupied only about one-tenth of their present area (Morley 2000; White 2001).

The last 1 Ma remained changeable and generally dry, with relatively lush conditions prevailing now. There was a strong increase of climatic variability 800 ka (thousand years ago), with maximum rainforest reduction at the time of the last northern hemisphere glaciation (12-20 ka), although fragmentation must have reoccurred numerous times, with rainforest more restricted than now 80-90% of the time (Livingstone 2001; Maley 2001). Also at Lake Manyara only 20% of past 55 ka were wetter than now and 50% drier (Livingstone 1982). Despite overall trends, local conditions varied: pollen cores from southern Ghana show no forest there 15-19 ka, while it persisted in south-west Cameroon (Maley 2001). West

Box 9. Congo captives: openland species in a forested basin

Forest expansions and contractions may strand species on forest islands (Box 6), but can also trap openland dragonflies in enclaves within the forest matrix. Several widespread non-forest group are represented in the Congo Basin by larger and darker forms, although their morphology is similar. These populations were apparently sufficiently isolated from the periphery and interconnected with each other to diverge, although their ecology remains poorly known (Box 1). *Zygonoides fraseri* and *Z. fuelleborni* principally inhabit open rivers and large streams in the dry northern and eastern belts of continental Africa (Fig. A). In central Africa they are replaced by *Z. occidentis*, which appears to inhabit very large rivers such as the Congo and Ubangi. The only reliable record outside the Congo Basin is allegedly from Nigeria, where suitable habitat may be present on the lower Niger (Dijkstra *et al.* 2006b).

The situation in *Gomphidia* is similar, with *G. bredoi* and *G. quarrei* occupying a similar range and habitat as *Z. fraseri* and *Z. fuelleborni* (Fig. B). However, these morphologically distinct species overlap in the Congo Basin, where they are considerably – and similarly – darker; *G. bredoi* has been observed along large open rivers here. The two savanna and two forest forms were previously considered four species, but intermediates occur; the dark *G. gamblesi* from western Africa is well-separated by range and morphology (Dijkstra in prep. d). *Gynacantha manderica* and *Trithemis aconita* occupy half-shaded habitats in a huge part of tropical Africa, excluding only the driest parts and some densely forested areas. The former is represented in the Congo Basin by a distinct dark form, whose taxonomic status is unresolved (Dijkstra 2005d), and *T. aconita* is replaced by the larger and darker *T. congolica* (Dijkstra 2007a). Their ecology in the basin is unknown, but possibly the dynamics of large rivers provide suitably open habitats.

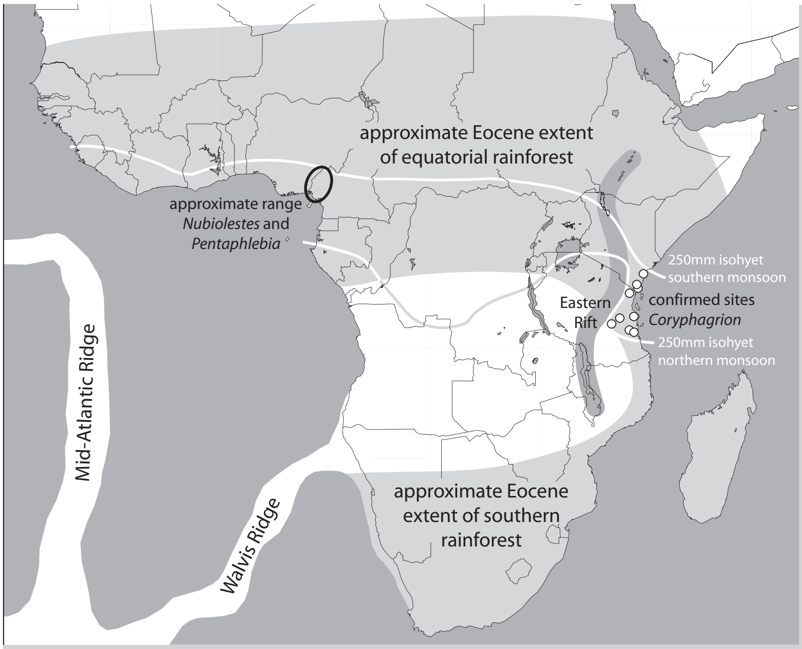
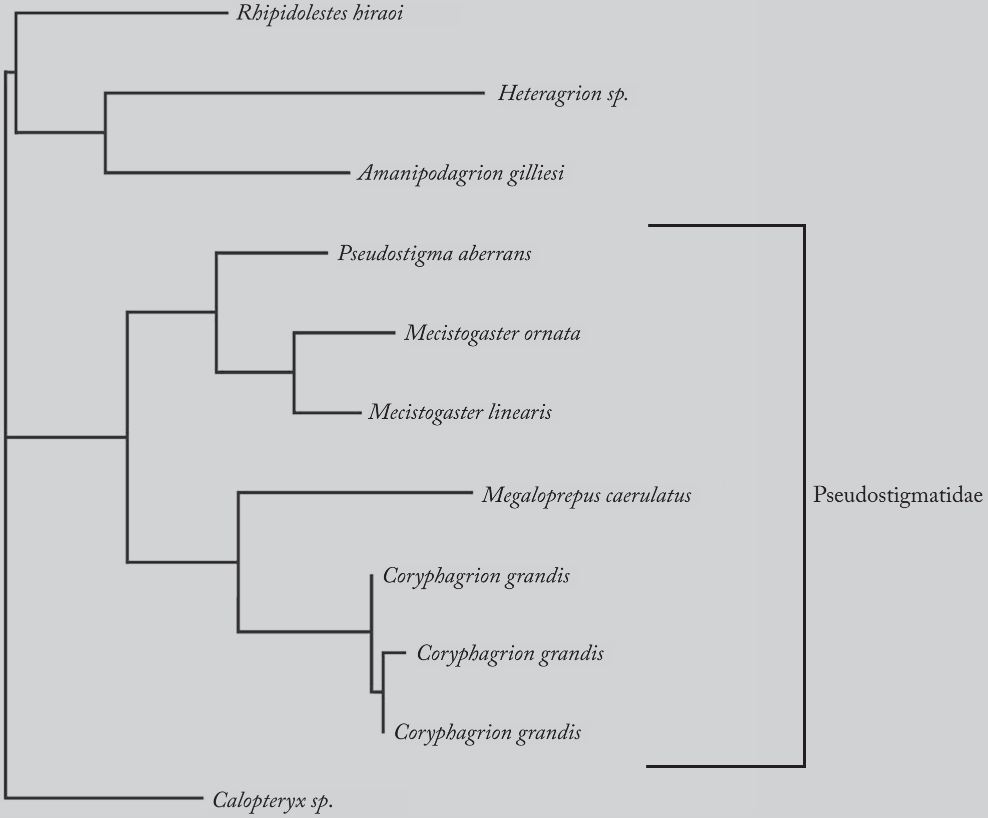


Fig. A Biogeographic hypothesis for *Coryphagrion*. The pale shading represents the approximate extent of rainforest during the Eocene, the dark shading the zones of uplift in the Eastern Rift Valley. The area between the two thin lines receives >250mm of rain during both halves of the year.

Fig. B Molecular phylogeny of Pseudostigmatidae. From Groeneveld *et al.* (2007).



African rainforests had roughly their contemporary extent in the last 12 ka, but were restricted to Upper and Lower Guinea refuges and several scattered remnants 12-74 ka. Their 'modern' extent is also inferred for 74-85 ka, 95-105 ka and 115-130 ka, but relatively montane conditions prevailed intermittently, with the last occurrence of *Podocarpus* in the Upper Guinea 74-85 ka (Dupont *et al.* 2000). Dune building in the northern and southern deserts was possibly a considerable threat to equatorial forests, with evidence of windblown sands from the Sahara almost in the Niger Delta 90-250 ka and from the Kalahari to Kinshasa 30-50 ka (Nichol 1999; Stokes *et al.* 1997). It must not be overlooked that cold and dry phases were interspersed with warm and wet ones: such an archetypical Afrotropical animal as the hippopotamus was still present in Britain only 125 ka (Vrba 1993).

Even in the last 10 ka, conditions were sometimes very different from now. The maximum recent extent of rainforest was 4-9 ka; before 6 ka in equatorial and northern Africa and after in the south and Madagascar (Livingstone 2001; Maley 2001). 8-9 ka the Sahara and Sahel were dotted with swamps and lakes, facilitating contact between the Niger, Chad and Nile basins, and 3-9 ka levels in the great lakes were very high (Coetzee 1993; Lovett 1993). This explains the 'peripheral' distribution of *Mesocnemis robusta* along the southern border of the Sahel as well as in northern Nile Valley, and the presence of *Chlorocypha curta* in the Jebel Marra, now enclosed by desert (Dumont 1988). African rainfall patterns remain unstable: the most recent arid phase culminated 2.0-2.5 ka in association with a change to a shorter, more concentrated wet season, although annual precipitation remained the same (Maley 2001).

The Demise: how species were lost

Tropical Africa has fewer families, genera and species of plants and animals than tropical America and Australasia, with many groups dominant elsewhere virtually absent (Box 2). Large parts of the African

Box 10. An alternative biogeographic hypothesis for Afrotropical Pseudostigmatidae

The last likely dispersal route between South America and Africa was probably along the Rio Grande Rise and Walvis Ridge, which connect southern Brazil, through the present-day hotspot at Tristan de Cunha, with 125 Ma flood basalts in northern Namibia (McDougall & Duncan 1988). The Ridge submerged by the end of the Eocene (±34 Ma); the Rise finally subsided in the late Oligocene (±25 Ma). Although an uninterrupted intercontinental connection may have been severed early in the Cretaceous, (diminishing) opportunities for island-hopping persisted well into the Paleogene (Parrish 1993). At this time, rainforests extended in three circumglobal bands, with two subtropical bands flanking the equatorial one (Morley 2000). Southern African forests, roughly opposite the Walvis Ridge, were separated from equatorial forests by more open landscapes. However, during a warmer phase ±55 Ma, the southern forests extended towards the equator along the humid Indian Ocean coast, allowing *Coryphagrion* to attain its present range before the southern forests disappeared around 36 Ma (Morley 2000). Uplift and associated aridification created a barrier to westward dispersal by 17-18 Ma (Lovett 1993). Given the small volume of larval habitats and the poor dispersal of adults, *Coryphagrion* is vulnerable to rainfall fluctuations both in the short (desiccation of phytotelmata; see Box 12) and longer term (forest fragmentation). The coastal climate of Tanzania was little influenced by Pleistocene changes, unlike the area further south in Madagascar's rainshadow (Fjeldså 1994; Fjeldså & Lovett 1997; Lovett 1993): while equatorial Atlantic surface temperatures dropped 4-5°C during the last glaciation (lowering implies less rainfall), the Indian Ocean did not cool off Tanzania, but temperatures did drop 3-4°C at the Zambezi mouth (Lovett 1993). The genus's range still coincides with an area of relatively perennial precipitation (Fig. A).

The above scenario falls within a timeframe of ±100 Ma. Only a robust estimate of the divergence of *Coryphagrion* provides some test of its credibility: the more recent the estimate, the more probable the scenario becomes. The only fossil pseudostigmatid known is the ±120 Ma old *Euarchistigma* from western Brazil (Carle & Wighton 1990), indicating the family's presence in the South American-African rift system, but a recent molecular phylogeny of the group was not dated (Fig. B). In this light, we may consider the New World monkeys, which as a biogeographic anomaly are the mirror image of *Coryphagrion*, having African affinities. Monkeys only arrived and began to radiate in South America 25-26 Ma (and caviomorph rodents 31.5 Ma), which forces acceptance of some kind of dispersal across the southern Atlantic at an even later stage, possibly during dramatic climatic and oceanographic change around the Eo-Oligocene boundary ±34 Ma (Flynn & Wyss 1998; Opazo *et al.* 2006).

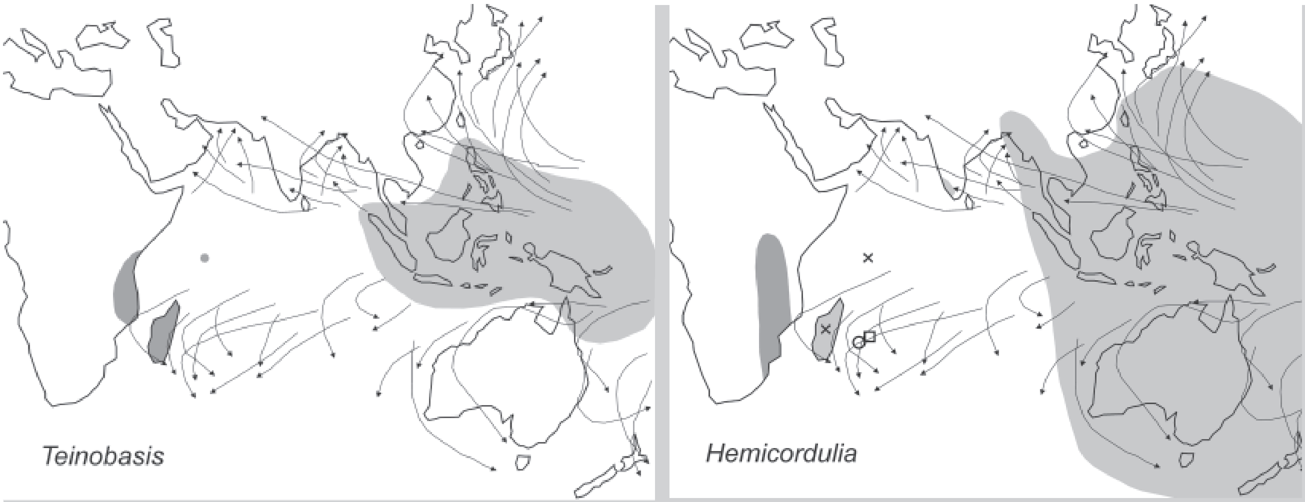


Fig. A Distribution of *Teinobasis* and *Hemicordulia* (including the closely related *Procordulia*). Arrows indicate the courses of summer storms. Legend *Teinobasis* – pale shading: main range in Australasia and Pacific; dark shading: *T. alluaudi*. Legend *Hemicordulia* – pale shading: main range in Australasia and Pacific; dark shading: *H. africana*; crosses and pale shading: *H. similis*; square: *H. virens*; circle: *H. atrovirens*. From Dijkstra (2007d).

Box 11. Arrivals from overseas: a trans-oceanic element among Afrotropical Odonata

Oceanic dispersal has been neglected as a major biogeographic factor, partly because it can potentially explain any pattern and thus conclusively no pattern in particular (McGlone 2005). Although dispersal is generally accepted for oceanic islands for lack of alternatives, it has been arbitrarily denied for continents and continental islands (de Queiroz 2005). Sanmartín & Ronquist (2004) found support of dispersal in trans-oceanic groups formerly thought to have separated by Gondwanan fragmentation, although this was less pronounced for animals than plants. However, winged fauna such as Odonata, may be equally mobile as these often wind-dispersed plants. Moreover, Muñoz *et al.* (2004) demonstrated that the direction of oceanic dispersal is not necessarily random: distribution patterns of cryptogams on sub-Antarctic islands were better explained by the direction of prevailing winds, than by their geographic proximities. They implied that wind transport should work for many other groups, including arthropods. Gillespie & Roderick (2002) considered that "butterflies and other large insects, such as dragonflies and sphinx moths, may have a wider range of dispersal than most insect groups". There is extensive proof of dispersal over thousands of kilometres in Odonata (Dijkstra 2007d). Zakharov *et al.* (2004) concluded that prevailing winds favour dispersal from Asia to the western Indian Ocean and from Madagascar to Africa. Dijkstra (2007d) examined the origin of western Indian Ocean *Teinobasis*, *Hemicordulia* (Fig. A) and other suspected trans-oceanic Afrotropical Odonata. Recent (*i.e.* in the last few million years) trans-oceanic airborne dispersal aided by westward storms, is the most likely explanation for their distribution in Africa and the Indian Ocean islands.

The contribution of islands to continental biotas (*e.g.* of Madagascar and the Indian Ocean islands to mainland Africa) is poorly studied, but is assumed to be small because island species are at a competitive disadvantage (Gillespie & Roderick 2002; Zakharov *et al.* 2004). Although many mainland records of sus-

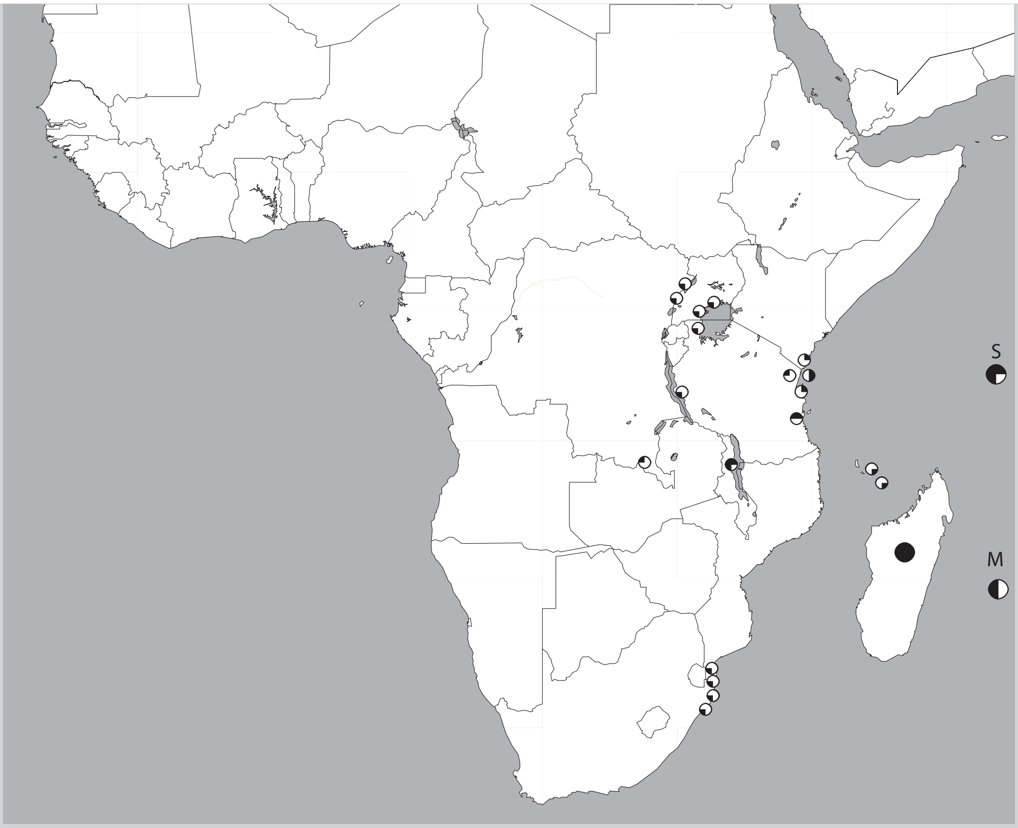


Fig. B Distribution of suspected trans-oceanic Afrotropical Odonata. Legend – black bottom-left quarter of circle: *Hemicordulia africana*; bottom-right: *Platycnemis* species of Madagascan radiation; top-left: *Gynacantha immaculifrons*; top-right: *Teinobasis alluaudi*; enlarged circles: presence of these species or close relatives on Madagascar and the islands just east of the map's border, the Mascarenes (M) and Seychelles (S). From Dijkstra (2007d).

pected trans-oceanic Odonata are coastal, most species locally occur well inland (Fig. B). Because also the island habitats are seldom coastal in nature (*e.g.* forested highland streams), the observed distributions (Figs. A-B) raise the question how trans-oceanic species colonised islands but remained so localised on the mainland. All *Hemicordulia* africana records are within 50 km of large waterbodies: even the inland localities are 'insular' in having 'sea' and 'habitat' in close proximity (Fig. B). Recent climatic fluctuations especially affected local convectional rainfall near the great lakes, resulting in lake level fluctuations of hundreds of metres in the last 25 ka (see Dijkstra 2007d for summary). Many of the forests inhabited by *H. africana* are therefore recent, *e.g.* <12 ka along Lake Victoria (Hamilton *et al.* 2001). Diamond & Hamilton (1980) argued that "competitive exclusion often prevents establishment by long-distance wanderers" and that it "is likely to be least important in new, [...] vacant areas of a particular habitat type, such as might be created by the spread of a vegetation type as a result of climatic change". *Hemicordulia* may indeed be a good disperser, but a poor competitor (Dijkstra 2007d). This explains both their insular distribution, where competition is reduced in impoverished faunas, and their continental confinement to relatively unstable areas where suitable habitat is comparatively recent and therefore impoverished (lakeshores, highlands); the equatorial coast, where *Hemicordulia* is absent despite suitable habitat, is one of the climatologically most stable areas (Lovett 1993). The preference of *Hemicordulia* species for shaded habitats, often at greater elevations, and their activity at cooler times of the day, suggest that their competitive position is related to thermoregulation. The 'continental' presence of trans-oceanic species may generally be a 'peripheral' phenomenon: the *Platycnemis* species is confined to an island (Pemba) and the *Teinobasis* species to two islands (Pemba, Zanzibar) and other sites near sea or lake level, which are susceptible to frequent disturbances like submersion.

savanna and lowland rainforest have local diversity comparable to non-African tropics, but are devoid of narrow endemism; African species have larger ranges on average (Fjeldså 2003; Plana 2004). A history of climatic vicissitudes and progressive aridification is the foremost explanation for this impoverishment, simply due to subsequently higher extinction rates. Africa has the most elevated tropical landmass and a relatively steep continental slope, limiting the retreat of lowland rainforest during phases of adverse climate or sea levels (Morley 2000). The coincidence of aridification and uplift exacerbated this effect. Palms symbolise the dramatic 'squeeze' of African biodiversity. Their diversity in the three tropics was about equal 65 Ma, but now the whole of continental Africa has fewer species than the island of Singapore (Morley 2000; White 2001). Similarly strong is the demise of Odonata of specialised rainforest habitats (Box 12).

Africa is still comparatively dry throughout (Livingstone 1982; Livingstone 1993; Plana 2004), receiving less and more seasonal rainfall than other tropics. Almost all of Africa, however high the rainfall, has a distinct dry season, *e.g.* most of Congo Basin has a few rainless months each year (Fjeldså & Lovett 1997; White 2001). Local climates varied widely and rapidly over the past 10 ka, and severe droughts and floods were frequent and widespread in the last ten centuries (Stager 2001). Considering the marked correlation between rainfall and species richness in Africa (Fjeldså & Lovett 1997; Linder 2001), its impoverishment is thus as much recent as historic. Africa has the largest tropical landmass, but possesses only one-fifth of global rainforest (Morley 2000). Considering that tropical rainforest harbours most of the world's odonate diversity, Africa's proportion is thus quite reasonable. Moreover, in response to (recurrent) aridity, Africa's biota may have greater dispersal capacities. This enables larger ranges and more widespread competition, leading to a geographically more uniform fauna and flora. Genetic studies of widespread species suggest considerable population movement and gene flow, their ranges being dynamic and responsive to change (Fjeldså 2003).

While Africa's 'shallow' poverty (lower species count) is related to historic and contemporary aridity, its 'deep' poverty (missing families) may also stem from its isolation. Africa has the most isolated history of the three tropics, being 'unconnected' from the break-up of Gondwanaland until the closure of the Tethys Sea. It was isolated 54-60 Ma when most other landmasses were tropical and in contact, and thus 'missed out' on much of the biota that radiated at the time (Morley 2000). This isolation made it difficult for Eurasian warm temperate taxa to retreat southwards and into Africa during colder periods. Finally, fewer species result from higher rates of extinction and lower rates of colonisation, but possibly also from less speciation. Compared to other landmasses, Africa has been geologically stable since the break-up of Gondwanaland and therefore has less varied relief (*e.g.* fewer mountain chains) and associated habitat complexity (Fjeldså & Lovett 1997; Morley 2000; Plana 2004; White 2001).

The Rise: how species were gained

Africa's Neogene desiccation had a profound impact on the landscape and its biota, especially for groups related as intricately to water and forest as Odonata. However, the precise character and importance of forest refuges is debated. Livingstone (2001) advised "to view with scepticism all published maps of forest refugia" as most were inferred from modern biogeographic and climatological data, while the resolution of paleontological data was negligible. White (1993) warned against "those who see things in black and white" as the reality suggested a complex history of Africa's modern biota, unlike the simple reinvasion of Europe's post-glacial wastelands. While early reconstructions proposed a limited number of discrete refuges, there is increasing proof of networks along rivers rather than patches (White 2001). Fjeldså & Lovett (1997) found little evidence of the proliferation of species by forest contraction, and postulated that gallery forests maintained gene flow between isolated fragments. Refuges may indeed be of minor importance in Afrotropical Odonata, as many Guineo-Congolian species inhabit galleries well beyond rainforest centres (Box 13).

Aside from doubts cast on the discreteness and form of refuges, doubts have been raised on their role in speciation (Connor 1986). The conclusion of Moritz *et al.* (2000) that "areas with high habitat heterogeneity and recent climatic or geological instability appear to harbor more species of recent origin" contradicts the popular concept of Pleistocene (*i.e.* most recent) refuges as centres of speciation. By mapping the distributions of phylogenetically relict and recent bird and plant species Fjeldså (1994) and Fjeldså & Lovett (1997) found that 'old' species were rather uniformly distributed, with peaks in lowland forest diversity centres and especially the traditional refuges, while 'young' species were generally found in savanna, and within forests in highlands. Furthermore, species richness was associated with high rainfall, river dynamics and habitat complexity. Because these are contemporary factors, no historical explanations (like refuges) are required for modern diversity patterns. They concluded that lowland forests were areas of species accumulation, while species proliferate in habitat mosaics at the periphery of forest blocks, often in areas of considerable topographic complexity.

Endler (1982) postulated that genetic isolation occurs along 'ecological escarpments', rather than in habitat refuges, and Fjeldså (1994) highlighted their importance in bird speciation, with the forest-savanna transition playing the foremost role. Smith *et al.* (1997) found that the contrasting selective environments across these ecotones lead to morphological differentiation within bird species (see also Schilthuizen 2000). The three models for speciation in tropical rainforest are by allopatry in refuges, by allopatry across river barriers, and by parapatry across ecological gradients (Moritz *et al.* 2000). Examples of forest vicariants in Afrotropical Odonata suggest some allopatric speciation (Box 5), but even very broad (>3 km) rivers like the Congo should not pose significant barriers for them. Thus the gradient model emerges as a potentially major force in the speciation of tropical Odonata. Considering the sensitivity of Odonata to micro-climate and water permanence, trans-gradient selection pressures may be comparatively intense in the order. Turgeon *et al.* (2005) found speciation of Holarctic *Enallagma* damselflies in the last 250 ka to occur at the periphery of each clade's range, while clades that were the furthest from the influences of recent glaciation included older species. Thus speciation theory is turned inside out, from the centres to the periphery: not forest cores but ecotones generate species. The traditional refuges (Box 5) are 'museums' or 'lifeboats' of species rather than 'pumps', receiving species from 'above' (highlands) and 'below' (lowlands) depending on contemporary climatic trends (Colyn *et al.* 1991) and functioning as genetic reservoirs for speciation processes on their periphery.

The Rise: when?

However species evolved, the question arises what effect habitat change had on speciation. When and where did radiations take place, and in which direction? Most extant species (*i.e.* conserved speciation events) in tropical rainforest predate the Pleistocene, suggesting that the most recent climatic oscillations played a minor role in their evolution (Fjeldså & Lovett 1997; Moritz *et al.* 2000; Nicolas *et al.* 2006). Radiations of mountain and savanna birds took place in the Plio-Pleistocene (Fjeldså 1994; Fjeldså & Lovett 1997; Roy 1997; Roy *et al.* 1998), but many groups in putative Guineo-Congolian refuges diverged in the Mio-Pliocene, well before Pleistocene vicissitudes (Beresford 2003; Beresford & Cracraft 1999; Bowie *et al.* 2004a; 2004b; Fjeldså 1994; Roy *et al.* 2001). Eight species of *Hylomyscus* woodmice diversified rapidly 2-6 Ma, mostly in the early Pliocene (Nicolas *et al.* 2006). The first *Cercopithecus* guenons appeared 10 Ma and the arboreal species radiated largely in the Pliocene (Tosi *et al.* 2005). *Xenopus* clawed frogs radiated 3-32 Ma, with Lower Guinea and Albertine refuges acting as 'lifeboats' for polyploid lineages (Evans *et al.* 2004). Despite these observations, the last glaciations must have offered ample opportunity for rapid speciation (Moritz *et al.* 2000). Why are there then not more young species? Perhaps Pleistocene change was so rapid that elimination out-balanced isolation. Alternatively, despite opportunity for speciation, too many competitors may have survived from previous climatological events. Such events would already have produced a suite of species adapted to changing conditions. However, as Avise & Walker (1998) noted, what is observed may actually be protracted speciation with (Mio-)Pliocene origins and Pleistocene completions. Vrba (1993) estimated that in the average life-span of a terrestrial mammalian species of 2 Ma, climatic changes "swept back and forth" twenty times.

The Rise: which way?

Did forest species 'descend' into savanna, or savanna species 'ascend' into forest? Kingdon (1989) considered most forest fauna as savanna-derived. Indeed the arboreal guenons, Africa's dominant forest monkeys, evolved only in the past 5 Ma from terrestrial ancestors (Tosi *et al.* 2005) and the same may apply to forest squirrels (Steppan *et al.* 2004). On the other hand, phylogenetic studies of *Streptocarpus* herbs in-

Fig. A Distribution of dendrolimnetic Afrotropical Odonata. Legend – open circles: *Coryphagrion grandis*; filled circles: *Hadrothemis scabrifrons*; halved circles: both species; shading: *H. camarensis*.

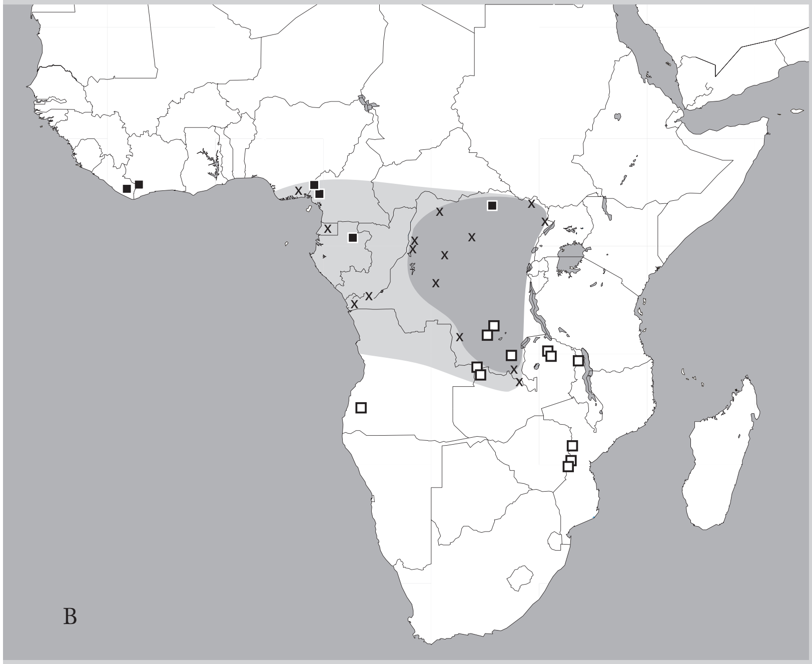


Fig. B Distribution of *Porpax* species. Legend – filled squares: *P. bipunctus*; open squares: *P. risi*; crosses: other species (only *P. asperipes* in pale shaded area, also *P. garambensis* and *P. sentipes* in dark shaded area). Adapted from Dijkstra (2006c).

Box 12. Specialised demise: Africa's lack of Odonata in vulnerable rainforest habitats

The Afrotropics are poor in odonate species that breed in specialised forest habitats vulnerable to desiccation, such as seepages, treeholes and temporary streams. This explains the absence or impoverishment of 'ancient' families such as Megapodagrionidae, Platystictidae, Pseudostigmatidae and Petaluridae (Box 2). Those specialists present are relicts, such as *Stenocnemis*, which is thought to inhabit rocks wetted by waterfall spray (Vick 1998; Box 3). Due to the presence of particular plant species, Madagascar has a relatively high potential for fauna of phytotelmata, such as leaf axils (Paulian & Viette 2003). Nonetheless, no dendrolimnetic odonates are known, which may be testimony of a drier past. Only three dendrolimnetic species are known from the mainland (Fig. A), while many more occur in the Neotropical and Oriental regions (Corbet 1999). Notably, two of the species occur in eastern Africa, rather than in the moister centre and west of the continent, where ecological comparisons with America and Asia would predict their presence. In the case of *Coryphagrion* this may be proof of survival in one of the continent's most stable environments (Box 10). However, the two dendrolimnetic *Hadrothemis* species could have evolved recently from species that breed in temporary forest pools. This is the habitat of four of the other five *Hadrothemis* species. Discovery of the habitat of *H. vrijdaghi*, the sister species of *H. camarensis* that is sympatric with it in the Congo Basin, would shed light on this evolution. Moreover, the morphology and coastal range of *H. scabrifrons* suggest that it might be nearer the genus *Thermorthemis* from Madagascar and the Comoros (Box 11) than to the six Guineo-Congolian *Hadrothemis* species.

Porpax species breed in temporary forest pools, muddy streams and grassy swamps. The Congo Basin appears to be the genus's heartland: all five species occur there (up to four in sympatry), two are endemic and a third extends only to the Lower Guinea (Fig. B). *Porpax risi* is unusual in appearance and is the only species not associated with forest, occurring in open swamps scattered across highlands mostly south of the other species' range. *Porpax bipunctus* is most strongly associated with forest and occurs in four disjunct populations, which coincide with the traditional rainforest refuges in the Upper Guinea, Lower Guinea and eastern side of the Congo Basin (Fjeldså & Lovett 1997; Kingdon 1989; Box 5). The pattern may be an artefact of under collecting (Box 1) but is supported by the absence of intervening records and distinctive coloration in each population, suggesting allopatric speciation in progress. Other *Porpax* species have been collected more widely and are geographically uniform. The species's isolation may be linked to the ephemeral nature of its probable reproductive habitat, flooded areas in stream beds. Species inhabiting pools under closed canopy left by temporary streams are comparatively rare in Africa (Oppel 2005). Possibly *P. bipunctus* is confined to areas with perennial and predictable rainfall.

The poverty of the Afrotropical montane fauna may also be related to climatological vicissitudes, but is further explained by the youth and isolation of the highlands. Moreover, highlands may be an ecologically less diverse environment with stronger constraints (de Jong & Congdon 1993). Certainly for Odonata cold temperatures are limiting, especially if species must derive locally from warm-adapted species.

dicated that forest species were basal, with more derived species being increasingly dry-adapted (Plana 2004). Similarly, African *Acridocarpus* trees diverged from Asian lineages ±50 Ma and dispersed to Madagascar ±35 Ma through more or less continuous rainforest. West African species diversified 23-27 Ma by adapting to increasingly drier habitat, and with the Miocene spread of savanna dispersed to East Africa 17-23 Ma, where increasingly drought-tolerant species developed (Davis *et al.* 2002). Genets diversified from a forest ancestor, with a small savanna radiation diverging 8.5 Ma, followed by a forest radiation in the wet ±5 Ma, followed by a large savanna radiation 3.5 Ma, with two species reverting to forest in the Pleistocene (Gaubert *et al.* 2004). *Hyperolius* reed frogs radiated from a lowland forest ancestor in response to savanna expansion, with most recent speciation taking place around the Rift Valley lakes (Wieczorek *et al.* 2000). The observations suggest that radiations are space-dependent, *i.e.* when there is much forest, many forest species evolve, and much savanna habitat promotes savanna species. This is opposite to what refuge theory predicts, where fragmentation leads to speciation. Two genera of killifishes, inhabiting small streams in rainforest understorey, radiated out of Cameroon east into the Congo

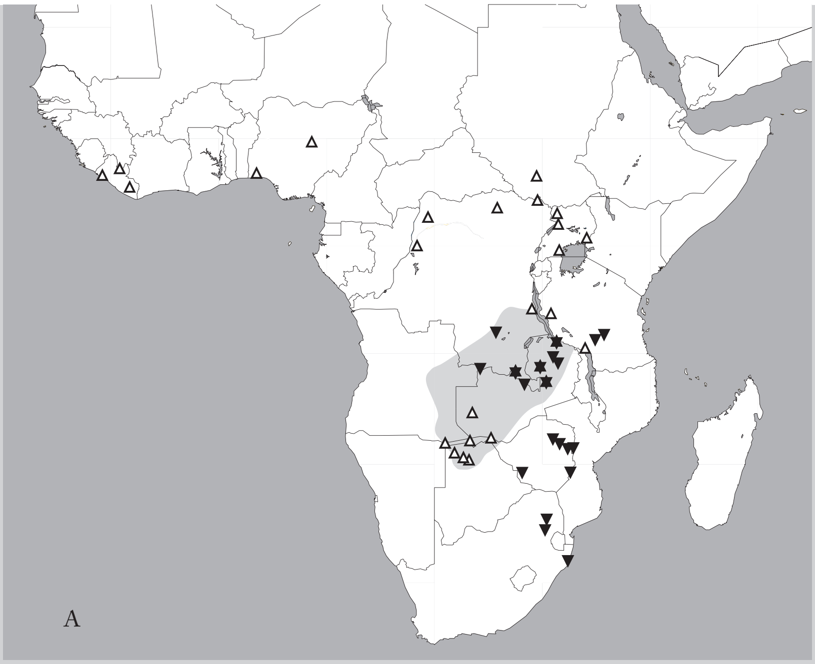
Box 13. Recent speciation hotspots

“The richest area [in southern Africa] in number of species and genera [of Odonata] […] is that of the tropical riparian forest swamp-streams and adjacent swamps, which also exhibit the greatest number of endemics. The total number of species known there is over 250, which is well over a quarter [near 30%] for the entire Ethiopian Region […]. Other zones rich in dragonflies are the middle Zambezi valley and the Okavango delta. There are similarities between Zambian/Angolan streams and swamps, and the swamps of Botswana’s Okavango delta which may lend support to the belief of the diverted course of the Zambezi River.”

Pinhey (1978), who studied this area intensively (Dijkstra 2007a; Pinhey 1961; 1976; 1984), described what may be the best contemporary example of a centre of odonate speciation in Africa. About 45 odonate species are endemic to the region, with 13 in three of the most succesful Afrotropical genera: *Aciagrion*, *Pseudagrion* and *Trithemis*. The area in the heart of the Zambezian biome is delimited by the Paleo-Chambeshi system, which drained into the Makgadikgadi Pan in the past, but is now split across the Congo, Okavango and Zambezi drainages. The present levels of species richness and endemism are equal to better-known centres in Africa, and with its complex history of tectonic activity since the Pliocene, climate change and watershed reconfigurations, is a probable centre of recent speciation in plants, amphibians, reptiles, birds and mammals (Broadley & Cotterill 2004; Brooks *et al.* 2001; Carcasson 1995; Cotterill 2005; 2006; Linder 2001). This may be especially true for aquatic fauna, as indicated by fish diversity (Cotterill 2005). Curiously, this diversity has been ignored by scientists and conservationists, perhaps because it is “not associated with high, spectacular mountains or […] impressive rainforests” (Linder 2001). It is the third richest area of plant endemism and diversity in Africa (Linder 2001) and was the most prominent centre of overlooked bird diversity in Fjeldså’s (2003) analysis.

The regional abundance of swampy habitats is especially important for Odonata (Fig. A). They range from the numerous wet depressions called *dambos*, which are often associated with gallery forest, to huge swamps such as the Bangweulu, Okavango and Upemba systems, and harbour the only restricted-range odonate fauna of open swamps in Africa. The vast majority of range-restricted African species is found in running waters, especially in forests and highlands, while most swamp-dwelling species are widespread. Endemics include *Ceriagrion katamborae*, *Pseudagrion deningi*, *Anax bangweuluensis*, *Ictinogomphus dundoensis*, *Nesciothemis fitzgeraldi*, two *Rhyothemis* species and *Trithemis aequalis*, as well as the monotypic *Pinheyagrion*, the region’s only unique genus. Pinhey (1978) emphasised this “palustrine” diversity and separated tropical (centred on northern Zambia) and subtropical (mostly Botswana) palustrines. The region’s rivers have a complex history of recombination; the Zambezi and even Limpopo once drained headwaters that now feed the Congo (Moore & Larkin 2001). Swamps may be a transient feature of river ‘piracy’ and alluvial deposits suggest these existed in basins now drier (Kafue, Lufira) or drowned (Lake Mweru). Cotterill (2005) described how alternate contractions, expansions, separations and connections in an archipelago of wetlands led to speciation in *Kobus* antelopes, most likely in the Plio-Pleistocene. Simultaneously, shifting river barriers induced vicariance in *Cryptomys* mole-rats (Van Daele *et al.* 2004). The link between the Zambezi and Okavango-Makgadikgadi was repeatedly breached and established in the past 50 ka. Thus the Okavango Delta was not as isolated as it seems today, but connected by a river corridor, as demonstrated by its distinctly ‘Zambezian’ Odonata. Therefore, Pinhey’s (1978) palustrine categories seem arbitrary. Ultimately the Zambezi will capture the Okavango again and drain this swamp refuge (Moore & Larkin 2001).

The region further is a patchwork of recently formed plains and plateaus varying 1500 m in altitude, with a corresponding diversity of vegetation including grassland, savanna, woodland, and montane, groundwater and gallery forests, which harbour all varieties of flowing water, from upland streams to large lowland rivers. Particularly characteristic are the so-called *litus* (or *muhulu*, *mushitu*) which, in the words of Pinhey (1978) are “streams, tending to swamp formation in parts, and more or less fringed with thick gallery forest [...] there are also some stagnant, partially forested swamps”, where “a great many endemics are known”. Among these are *Pseudagrion coeruleipunctum*, *Chlorocnemis wittei*, *Prodasineura flavifacies*, *Diastatomma soror*, *Phyllogomphus schoutedeni*, *Neodythemis fitzgeraldi* and *Zygonyx atritibiae*. These galleries also allow rainforest species to penetrate well beyond their main range in the Congo Basin. Endler (1982) envisaged that “populations living in tongues or peninsulae of forest receive gene flow from only one direction, and hence are even more isolated and likely to diverge even more dramatically from the main populations”. Marked genetic divergence must occur towards the end of these forest tendrils, functioning both as micro-refuges and ecotones. Aside from habitat diversity, the region’s position is strategic for speciation, lying in a transition zone between biomes. The adjoining Congolian and Albertine forests are huge genetic reservoirs (Box 5), while montane taxa dispersed along the region’s rather high relief (Boxes 7, 14). The latter is demonstrated by isolated populations of many upland plants and animals, which occupy specialised habitats and can thus readily become genetically isolated (White 1981). Possibly former dispersal



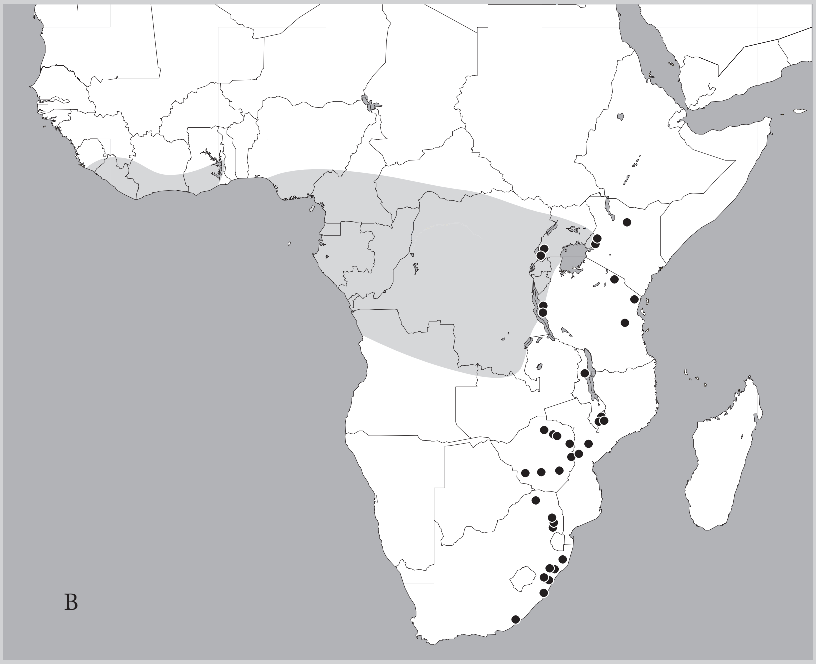


Fig. A Distribution of small continental African *Diplacodes* species and the Paleo-Chambeshi region. Note the concentration of *D. deminuta* in the large swamps in the north and south of the region and that of *D. pumila*, which generally inhabits smaller and more elevated swamps, in the north. Legend – open triangles: *D. deminuta*; closed triangles: *D. pumila*; stars: both species; shading: approximate extent of Paleo-Chambeshi region. Adapted from Dijkstra (2006a).
Fig. B Distribution of *Notiothemis* species. The overlap of these two shade-dwelling species approximately demarcates the Albertine Rift. Legend – shading: approximate range of the Guineo-Congolian *N. robertsi*; circles: known sites of the Afro-montane *N. jonesi*.

routes are more generally speciation centres.

The region may have been 'stable in diversity', its physiography allowing the landscape mosaic to shift gradually but persist through climatic vicissitudes. Fjeldså & Lovett (1997) attribute the remarkable regional proliferation of *Crotalaria* legumes to micro-geographic differentiation supported by habitat heterogeneity and eco-climatic stability. Nonetheless, possibly half the region was covered by Kalahari sands only 30-50 ka (Moore & Larkin 2001; Nichol 1999), while Hamilton (1981) showed it almost completely smothered 18 ka, although the extent of dune expansions is contested (White 1993). The absence of equivalent diversity north of the equatorial rainforest could be the debilitating result of recent Saharan perturbations (Linder 2001), also wiping out any potential evidence of the migration of montane elements along a northern track (White 1981). However, the highlands west (Lower Guinea) and east (Albertine Rift; Fig. B) of the Congo Basin are other ecologically complex regions with extensive faunal overlap. Local endemism of forest species suggests active speciation in typical Guineo-Congolian genera such as *Chlorocypha*, *Chlorocnemis*, *Neodythemis* and *Tetrathemis*, as well as in the more montane genera *Platycypha* (Box 15), *Notogomphus* (Box 7) and most notably *Atoconeura* (Box 14).

Basin and west into Nigeria and Ghana, another out of the Upper Guinea forest centre westwards (Murphy & Collier 1999; Murphy *et al.* 1999). This suggests that habitat was occupied as it became available, which was followed by speciation. By contrast, in two speciose rainforest plant genera, *Aframomum* and *Begonia*, speciation coincided with Miocene and Pleistocene aridification respectively, suggesting these evolved by vicariance in forest remnants (Plana 2004). The above observations, the predominance of 'young' species in savannas and 'old' species in forest (Fjeldså 1994; Fjeldså & Lovett 1997), and the tendency towards drier climates in Africa's recent history, suggests that the direction of speciation has predominantly from forest to savanna species. Dijkstra & Clausnitzer (2006) proposed such scenarios for *Platycypha* and *Pseudagrion* damselflies and *Trithemis* dragonflies (Box 15). Plana (2004) suggested that African groups with a larger proportion of savanna species tend to have radiated earlier. This seems paradoxical, but if predominant direction of speciation is from forest to savanna, these groups may simply have had more time to accumulate savanna species. However, the main conclusion is that African biota appear ecologically flexible, with speciation constantly straddling environmental barriers.

The Rise: where?

Moritz *et al.* (2000) concluded that speciation rates were highest in "heterogeneous landscapes within and adjacent to large rainforest areas". Fjeldså (1994) believed that "rainforests played no great role in recent diversification, which in stead happened in the forest/savanna transitions on its periphery, such as the mosaics of savanna and gallery forest in southern Zaire [= Katanga] and parts which were uplifted or influenced by recent rifting". Speciation-prone conditions are concentrated in consistently gradient-rich areas. Ecotones relevant to odonate ecology occur in areas with diverse vegetation, water types and altitudes, such as on the watershed of the Congo and Zambezi. This area probably presents the most concentrated diversity of odonate habitats in Africa today (Box 13). Roy *et al.* (1998) stated that "diversification in the Afrotropics involves intensive speciation in montane areas and a gradual adaptive redistribution and persistence of deep lineages in the lowland forests, leading to peaks of species richness in areas with a high carrying capacity in humid premontane areas". Such an important role of highlands must especially apply to water-dependent animals such as Odonata, because orographic rain ensures reliable and suitable habitat in a dry continent (Box 14).

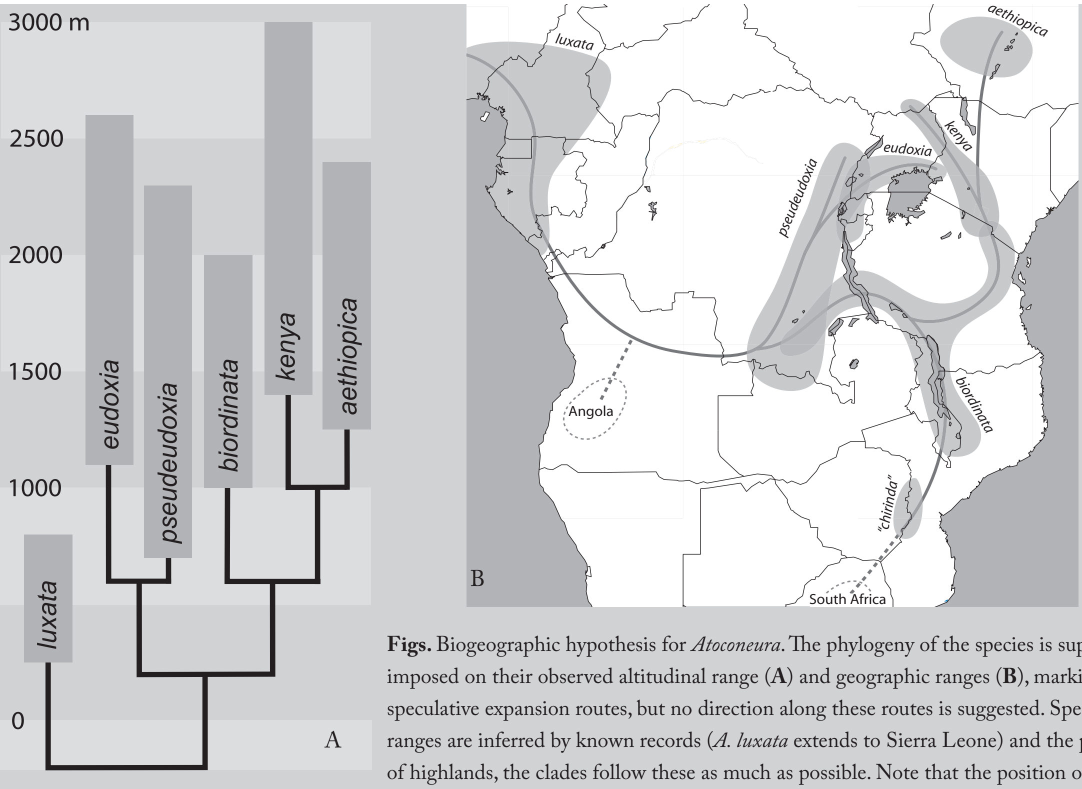
An implication of a changeable landscape is that speciation processes shift with their ecotones: the final separation of two species could take place far from initial genetic isolation. In any case, historic speciation centres may not be centres of diversity today. Zambezia (Box 13) is a modern model of earlier speciation centres, for instance in the Congo Basin during glacials and the eastern highlands in interglacials. Marked tectonic activity in the last 7 Ma combined with a heterogeneous environment in warm and wet periods 6.4-9.0 and 2.4-4.6 Ma would have created a congenial environment for odonate speciation in the topographically complex Rift Valley in the Mio-Pliocene, but this area is now relatively cold, dry and impoverished (Lovett 1993). Plant and vertebrate fossils from the Tugen Hills in Kenya, for example, indicate a mosaic of forest, open woodland and savanna 6.8-12.6 Ma (Jacobs 2004). Pinhey (1978) inferred that "during interpluvials [...] forests of the Zaïre [= Congo] basin became fragmented by rivers and swamps which may have been and still are very rich in Odonata, as evidenced by their riparian feelers, the 'litus' and 'mushitus' [...]." Conditions similar to modern Zambezia would indeed have moved north into the basin during arid phases, shifting the focus of speciation. The basin remained comparatively green because it was dissected by rivers with sources in a distant ring of highlands, creating a vast and stable network of ecotones, which is today 'drowned' in forest (Maley 2001). Kingdon (1989) described the Congo Basin as an "evolutionary whirlpool", mainly for mammals, which diverged on opposite banks of large rivers. On the other hand, the basin has a poor bird fauna for a forest area (Crowe & Crowe 1982; Diamond & Hamilton 1980) and Fjeldså (1994) concluded that the whirlpool "appears to have been quiet in the Pleistocene". This may apply to birds, but probably not Odonata.

Synthesis: the demise and rise

As their taxonomy and distribution become better known and hypotheses of dispersal, environmental change and speciation are fine-tuned, an impression of the history of Afrotropical Odonata slowly emerges.

Africa has a large and almost uninterrupted land surface, is isolated from surrounding continents, and has had a variable and increasingly dry climate, especially in the latter half of the Neogene (>10 Ma). As a result the Afrotropics have only half as many odonate species as tropical America or Asia. Although they belong to an ancient order, few Afrotropical odonate species probably date back to Mesozoic (>65 Ma) or even Paleogene (>34 Ma) times. 'Relict' families are scarce and concentrated in five isolated, climatically stable areas: (1) the Cameroon highlands, (2) locally in East Africa, (3) the Cape region, (4) the granitic Seychelles, and especially (5) Madagascar. Most African odonate species, about two-fifths, are restricted to the Central and West African forests. The remainder is found, in three fairly equal parts, in (1) the highlands stretching from Arabia to the Cape, (2) Madagascar and surrounding archipelagos, and (3) open habitats throughout the region. Most mainland species appear related to the relatively diverse fauna of tropical Asia, but have few relatives on Madagascar, suggesting that the modern continental fauna mostly diversified after the arrival of Eurasian ancestors in the Miocene. Being best adapted to change, Coenagrionidae and Libellulidae are the largest odonate families on Earth. Only in temperate regions, impacted strongly by the ice ages, is their dominance comparable to that in changeable Africa. The climatic influence is further seen in forest species 'stranded' in highlands by forest reduction, savanna species 'trapped' by forest expansion, and overseas colonisation of East Africa by island species.

Traditional theory is that speciation took place in habitat fragments created by climatic change, especially in forest refuges, but such refuges seem to conserve old species rather than generate new ones. Abrupt habitat gradients in heterogeneous landscapes (highlands, forest-savanna transitions) may be more important in speciation, especially close to areas where potential ancestors are conserved. The habitat mosaic on the Congo-Zambezi watershed is the best modern example of such an area. Possible historic equivalents in the Congo Basin are now 'drowned' in forest, or 'dried up' and 'cooled down' along the Rift Valley. Phylogenetic research of various African plants and animals indicate that environmental and dispersal barriers are easily straddled, with savanna species radiating from forest ancestors and vice versa. Climatic change eliminated species, but also constantly created new ecological space. Thus the demise of an ancient fauna coincided with a sequence of change and opportunity, which lead to the rise of Africa's rich contemporary fauna from versatile ancestors, also in Odonata. Now the offspring of those developments, species like *Crocothemis erythraea* and *Anax imperator* that are increasingly common in temperate Eurasia, are spreading out across a world that is, once more, in change. How the diversification of Afrotropical Odonata took place remains largely hypothetical, but opportunities to study the history of these flying amphibians in a continent of contrasts are many (Box 15).



Figs. Biogeographic hypothesis for *Atoconeura*. The phylogeny of the species is superimposed on their observed altitudinal range (**A**) and geographic ranges (**B**), marking speculative expansion routes, but no direction along these routes is suggested. Species ranges are inferred by known records (*A. luxata* extends to Sierra Leone) and the position of highlands, the clades follow these as much as possible. Note that the position of evolutionary splits within species ranges is an artefact of the presentation form and has no bearing on the hypothesis. Notable distributional gaps are indicated, marked by dashed area outlines and clades, as is the southern isolate of *A. biordinata*, the former subspecies *A. b. chirinda*. From Dijkstra (2006b).

Box 14. Highland speciation: the genus *Atoconeura*

The highlands of eastern Africa have a complex history of uplift (Griffiths 1993; Knox & Palmer 1998). Mt Elgon is ancient (15-23 Ma), but most volcanoes are much younger, like Mts Kenya (2.0-3.5), Kilimanjaro (230-1100 ka) and Meru (90-190 ka). The larger highlands have more diffuse and protracted histories, some dating back many tens of millions of years: Mt Mulanje is a 130 Ma extrusion of magma, now isolated with its surroundings weathered away (Eastwood 1979). Most highlands are more recent, such as Ethiopia (9-22, but possibly <37 Ma), Ruwenzori (1-12 Ma) and the Aberdares (5.0-6.5 Ma). The main crystalline blocks of the Eastern Arc probably formed simultaneously with the reactivation of faults in the East African Rift system, 7 Ma. Climatic changes further complicate the reconstruction of the history of montane habitats and their biota. "Much of the floristic diversity in African highland areas [is] the result of recent speciation" (Plana 2004): giant senecios originated high on Kilimanjaro, and radiated and spread to other highlands in the past 1 Ma, while giant lobelias colonised eastern Africa in the Miocene, diversified on ancient upland features, and subsequently colonised more recent mountains, with the most recent speciation being altitudinal and predominantly upward (Knox & Palmer 1998). Similarly, most montane grassland butterflies "originated on the spot from species with other habitat preferences", while "strictly montane forest species must have originated from a [forest] species [...] at lower elevations", indicating that "parapatric speciation […] has been of paramount importance" (de Jong & Congdon 1993). The montane *Andropadus* greenbuls derived from a Miocene lowland ancestor and diversified by a complex pattern of dispersal and isolation in the Plio-Pleistocene (Roy 1997; Roy *et al.* 1998). Montane *Nectarinia* sunbirds followed a similar scenario 1.5-4.8 Ma (Bowie *et al.* 2004b).

The phylogeny and distribution of *Atoconeura* dragonflies, which mainly inhabit streams between 1000 and 2500 m, also imply recent speciation determined by dispersal between highlands and subsequent isolation, with an altitudinal upward tendency (Figs. A-B). Four species form an interlocking chain of ranges around the dry north of Tanzania, a pattern mirrored by their morphology (Dijkstra 2006b). This pattern recalls a 'ring species', suggesting expansion across montane stepping stones. The phylogeny perfectly matches the minimum geographic distance model of (Knox & Palmer 1998), *i.e.* the most closely related taxa are also the most proximal geographically. Thus dispersal explains the observed pattern with maximum parsimony, while all alternative hypotheses (*e.g.* geological history) are more complex and therefore less parsimonious. How montane taxa reached certain highlands but not others, is debated. Most colder periods were also drier, but 220, 176 and 21.5 ka were maybe cool and wet, with montane vegetation lowering 1000-1500m, *i.e.* to about 500m a.s.l. (Lovett 1993). However, there is no biogeographic evidence of a dramatic expansion of montane habitats, enabling direct connections between currently isolated sites (Brühl 1997; Colyn *et al.* 1991; Diamond & Hamilton 1980), nor palynological evidence for an east-west connection (Livingstone 1982). Active dispersal explains observed distributional patterns better than habitat fragmentation (de Jong & Congdon 1993). Isolated populations of montane biota along the Congo-Zambezi watershed may be traces of a historical expansion of montane habitat (Dowsett-Lemaire & Dowsett 2001), but strictly only imply the dispersal of their inhabitants (Box 7, 13). Diamond & Hamilton (1980) suggested that when lowland forests were expanding after a dry climatic phase, competition in these novel habitats would be reduced, allowing highland species to disperse before arrival of more competitive lowland species.

Afro-montane species probably originated mostly in eastern Africa, with dispersal toward Cameroon and South Africa (*e.g.* de Jong & Congdon 1993). However, montane *Andropadus* greenbuls dispersed at least once from Cameroon to the Albertine (= Western) Rift, and hence to the Eastern Arc (Roy 1997; Roy *et al.* 1998). Such a scenario fits the phylogeny of *Atoconeura*. All records of the western species *A. luxata* lie below 1000 m at the base of highlands (Fig. A). The 'basal' position of this species, both phylogenetically and ecologically, suggests it is close to the ancestor of the eastern *Atoconeura* radiation. Lowland taxa tend to be 'older' (*e.g.* Fjeldså & Lovett 1997; Roy 1997; Roy *et al.* 1998) and if the genus had dispersed westwards rather than eastwards, it might be expected at much higher altitudes in the west too. Considering the ecology of extant *Atoconeura* species, eastward dispersal of the lowland representative is easier than that of a highland representative westwards, simply because more intervening habitat is low than high. Nonetheless, *A. luxata* has the character of a montane relict, with localities confined to the base of highlands such as Loma, Nimba, Atewa (all Upper Guinea), Adamawa and Mayumbe (Lower Guinea). Lowland relict populations of montane plants survive in specialised habitats, such as spray zones (White 1981). *Atoconeura luxata* occurs near waterfalls in its piedmont streams, and its sole Ghanaian locality lies in Ghana's only stand of *Cyathea* treeferns. *Cyathea* and *Podocarpus* trees are distinctive of Afro-montane forests (White 2001). Assisted by a colder climate and Mio-Pliocene uplift, the latter first appeared in western Africa 2.7 Ma (Morley 2000) and extended to the highlands of Upper Guinea, where it last occurred ±80 ka (Dupont *et al.* 2000). *Atoconeura luxata* may have a similar history, but survives where most Afro-montane vegetation has since disappeared.

The distributions of *Atoconeura* species in eastern Africa are similar to those of montane butterflies, spiders, birds and mammals (de Jong & Congdon 1993; Dowsett 1986; Scharff 1992), but the reasons for these recurrent patterns are unclear. The Albertine Rift is a logical 'root' for the eastern radiation of *Atoconeura*, especially with a lowland ancestor. Despite their modest age, these highlands have among the highest montane biodiversity, owing to the proximity of a vast species pool in the adjacent Congolian rainforest (de Jong & Congdon 1993; Dowsett 1986; Roy *et al.* 1998). *Atoconeura* is notably absent in two highland regions with high endemism and suitable habitat in southern Africa. *Atoconeura* could still be found in Angola, but the South African highveld is well-surveyed. The few montane species to reach South Africa probably had a relatively wide ecological tolerance (de Jong & Congdon 1993). For instance most montane birds here speciated in open habitats (Dowsett 1986), while forest is the preferred habitat of *Atoconeura*. The highveld may be uninhabitable in cooler periods, while it is unreachable when habitats are suitable. Major glaciation took place on the higher equatorial mountains 11-15 ka (Brühl 1997; Lovett 1993) and very dry conditions during colder times may have resulted in complete forest loss, for instance on Mt Kenya (Brühl 1997; Diamond & Hamilton 1980; Scharff 1992); as is reflected by low endemism of birds (Diamond & Hamilton 1980; Dowsett 1986). *Atoconeura kenya* probably developed from an ancestor (near *A. biordinata*) that expanded from the benign Eastern Arc when conditions in Kenya began to ameliorate. Ethiopian montane forest is of recent origin, and most of it species spread out from Kenya (Brühl 1997; Diamond & Hamilton 1980). This conforms with the phylogenetic position of *A. aethiopica*. Thus the history of speciation in *Atoconeura*, and that of Afro-montane biodiversity in general, may reflect phases of suitable habitat 'opening up', followed by rapid adaptation and dispersal within the new habitat.

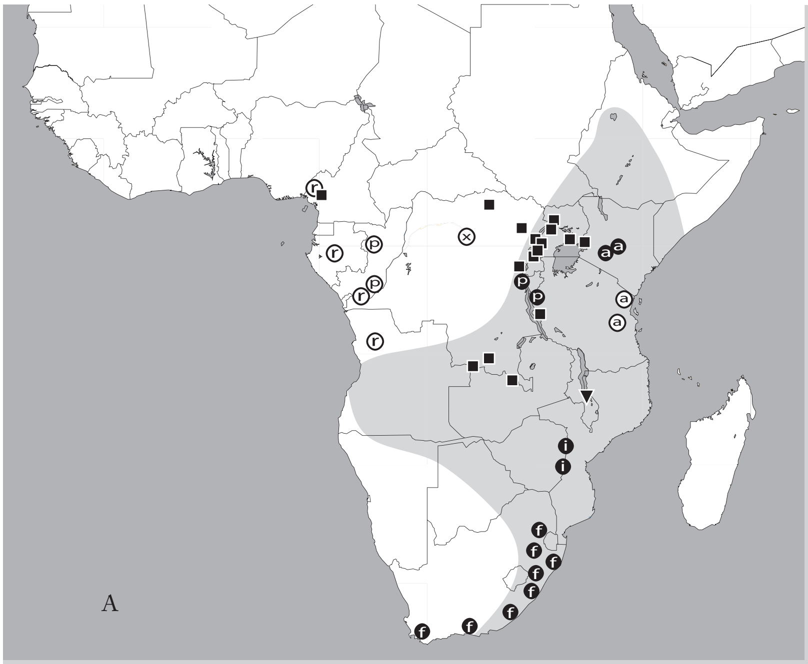
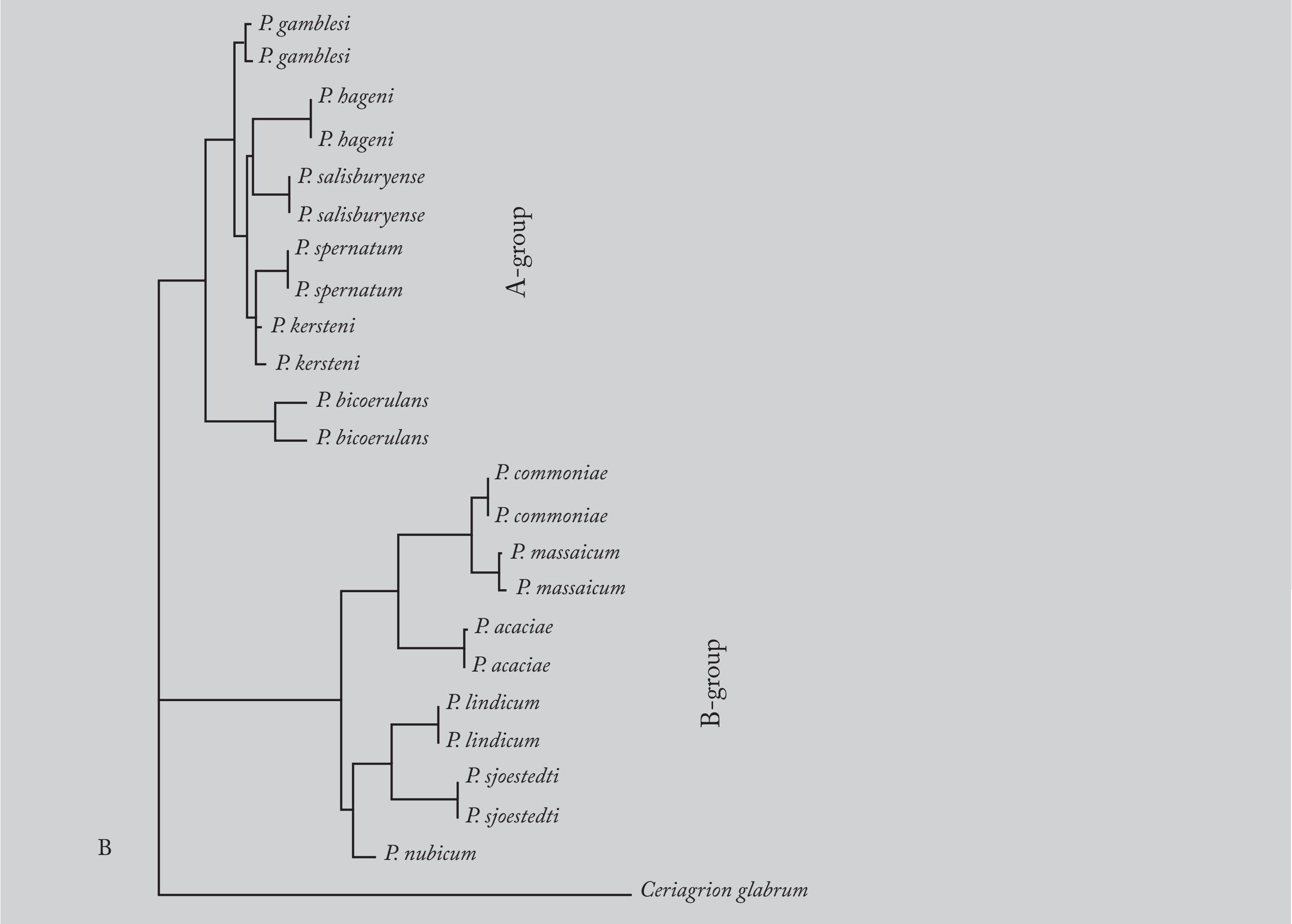


Fig. A Distribution of *Platycypha* species. Legend – open circles: lowland relict species (a: *P. auripes*; p: *P. picta*; r: *P. rufitibia*; x: undescribed species); filled circles: sub-montane relict species (a: *P. amboniensis*; f: *P. fitzsimonsi*; i: *P. inyangae*; p: *P. pinheyi*); squares: *P. lacustris*; shading: *P. caligata*; triangle: morphologically deviant lacustrine population of *P. caligata*. Adapted from Dijkstra (2007e).

Fig. B Molecular phylogeny of selection of *Pseudagrion* species. From Dijkstra *et al.* (2007b).



Box 15. Studying speciation in Afrotropical Odonata

Speciation stretches further into space and deeper back in time than suggested by the original hypotheses. Today's species did not just originate in the Pleistocene and not just in refuges: the majority could have evolved in peripheral habitats during the Neogene (<23 Ma). Moreover, the refuge and gradient models of speciation are not mutually exclusive (Maley 2001) and may often be geographically inseparable. Plana (2004) noted that the majority of postulated refuge areas coincided with mountain regions and that "this probably reflects both the role of these mountains in speciation by providing a wide range of new habitats, and these same peaks and valleys providing refugia for species during periods of climatic turmoil." Speciation by selection across ecological gradients, especially its preponderance, remains to be proven (Moritz *et al.* 2000; Schilthuizen 2000). These authors further emphasised the need to explore the role of sexual selection in promoting speciation and to focus more attention on species-rich lineages occupying regions with concentrations of young species (Moritz *et al.* 2000). Studies of Afrotropical Odonata would be suitable to achieve this, especially because good studies of speciation in invertebrates are lacking (Moritz *et al.* 2000). Dijkstra & Clausnitzer (2006) described how several forest groups appear to have expanded and diversified in highland and openland habitats. However, phylogenetic data supporting for their hypotheses is still insufficient.

While most of the over 40 species of Afrotropical Chlorocyphidae inhabit Guineo-Congolian lowland forest streams (compare Box 6), *Platycypha* is more eastern in occurrence (Fig. A). Three species inhabit sub-montane streams, and *P. caligata* exposed rivers and even lakeshores. Perhaps *Platycypha* extended east when lowland forest was extensive and became fragmented into several relict species when forest shrunk. Some members spread south in highland forests, becoming isolated as the climate became relatively dry or hot. Change along temporal, altitudinal and climatic gradients may have favoured selection for tolerance to non-forested habitats, of which the abundant *P. caligata* may be the epitome. It spread widely in a habitat virtually unoccupied by its relatives and is now bounded by unsuitable habitat on almost all sides of its range. Being adapted to rather extreme conditions, *P. caligata* was the only chlorocyphid to colonise lakeshores. On Lake Malawi individuals are smaller and the males' conspicuous colours blacken with age, unlike riverine males. Perhaps this constitutes a speciation event across a stream-lake ecotones, reinforced by sexual selection (Dijkstra 2005b; Dijkstra 2007b).

With almost 100 species, *Pseudagrion* has occupied all freshwater habitats in tropical Africa and Madagascar, dominating from pools in the Kalahari to alpine streams on the Kilimanjaro. The genus is subdivided on morphological and ecological grounds: 41 species of the dark-bodied A-group generally inhabit cooler mostly running water habitats. This includes many rainforest species with small ranges, confined to deeply shaded habitats, but other species occur in open habitats and their reflective pruinosity may be an adaptation to increased insolation. Among these are species with small high-altitude ranges, relicts in the Levant and Arabia, but also the most widespread and strongly pruinose species: *P. kersteni*. The 24 species of the pale-bodied B-group generally inhabit warmer habitats; sunny and often exposed, generally at low altitudes, and also standing waters. The two groups may have diversified separately in non-forest habitats, as these expanded during periods of forest regression. Perhaps the pruinose A-group species evolved in highlands and were pre-adapted to invade open lowland habitats, such as grassland streams. The B-group share morphological similarities with Asian species and possibly arrived later, radiating into warmer habitats left unoccupied by A-group members. Analysis of more species, also from Madagascar and Asia, may confirm this scenario, but preliminary data only indicate the monophyly of the A- and B-groups (Fig. B; Dijkstra *et al.* 2007b).

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Appendix: diversity and taxonomic status of Afrotropical Odonata; an update of the overview in Dijkstra (2003c)

family / genus, synonym / group – Genera listed by Dijkstra (2003c) but now considered synonymous (?: synonymy suspected) are listed in the second column. *Coryphagrion* was transferred from Megapodagrionidae to Pseudostigmatidae (Clausnitzer & Lindeboom 2002; Groeneveld *et al.* 2007); *Chlorocnemis* from Protoneuridae to Platycnemididae (Dijkstra & Clausnitzer in prep.). Species formerly placed in *Enallagma* Charpentier, 1840 were transferred to *Africallagma*, *Azuragrion*, *Pinheyagrion* and *Proischnura* (May 2002). Other *Enallagma* records and those of *Argiagrion* Selys, 1876 and *Argiocnemis* Selys, 1877 are considered as misidentifications or labelling errors. Information is given for separate groups in four heterogeneous genera (see table with taxonomic priorities): *Pseudagrion* (Dijkstra *et al.* 2007b); *Platycnemis* (Dijkstra *et al.* 2007a); *Aeshna* (Dijkstra 2007a); *Gynacantha* (Dijkstra 2005d).

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no. – Minimum estimate of number of valid species ($^{+}$: at least one undescribed species known to the author).

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dis. – Distribution of genus/group, those in square brackets are also found outside Africa. See Box 5. *: see remark field for details.

PI		pan-African, including both Madagascar and the Indian Ocean islands (Comoros, Mascarenes, Seychelles)
	PA	pan-African, excluding both Madagascar and the Indian Ocean islands
	Pm	pan-African, including Madagascar but excluding the Indian Ocean islands
	GA	Guineo-Congolian and Afro-montane
	Gm	Guineo-Congolian and Madagascar
GC		Guineo-Congolian
	ci	Côte d'Ivoire
	cm	Cameroon highlands (including adjacent Nigeria)
AM		Afro-montane (Ethiopia to South Africa)
	ec	East Coast
	ml	Malawi
	sa	South Africa
	tn	Tanzania
	zm	Zambezian
IN		insular (Madagascar and Indian Ocean islands)
	md	Madagascar and Comoros
	mr	Mauritius
	ms	Mascarenes
	sc	Seychelles

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references / [remarks] – Remarks refer to the **dis**. column. The number of species at least diagnosed or discussed in some detail (*e.g.* images, keys) in each reference is indicated: because the species discussed may overlap, only the additional species for later references are given. Species and larval descriptions without an additional taxonomic context are generally not listed. See Dijkstra (2003c) for significant references prior to 2001. Taxonomic priorities are listed in a separate table.

family / genus	synonym / group	no.	dis.	references / [remarks]
ZYGOPTERA				
Amphipterygidae				
Pentaphlebia Förster, 1909		2	cm	
Calopterygidae				
Phaon Selys, 1853		2	Pm	Dijkstra in prep. c (2)
Sapho Selys, 1853		6	GC	
Umma Kirby, 1890		9	GC*	[* 1 sp. in ml-tn; 1 Angola] Dijkstra in prep. c (1)

Chlorocyphidae				
Africocypha Pinhey, 1961		1	cm	Dijkstra 2007b (1)
Chlorocypha Fraser, 1928		32^{+}	GC*	[* 1 sp. to AM] Dijkstra 2003b (4); Dijkstra 2007b (+10); Dijkstra in prep. a (+8)
Platycypha Fraser, 1949		10	AM*	[* 4 sp. to cm] Dijkstra in prep. a (10)
Lestidae				
Lestes Leach, 1815		14	[Pm]	
Perilestidae				
Nubiolestes Fraser, 1945		1	cm	
Synlestidae				
Chlorolestes Selys, 1868		7	sa*	[* 1 sp. to ml]
Ecchlorolestes Barnard, 1937		2	sa	
Megapodagrionidae				
Allolestes Selys, 1868		1	sc	
Amanipodagrion Pinhey, 1962		1	tn	
Neurolestes Selys, 1882	? *Nesolestes* Selys, 1891	18^{+}	md*	[* 2^{+} sp. in cm]
Protolestes Förster, 1899		8	md	
Tatocnemis Kirby, 1889		10	md	
Pseudostigmatidae				
Coryphagrion Morton, 1924		1	ec	Clausnitzer & Lindeboom 2002; Groeneveld *et al.* 2007 (1)
Coenagrionidae				
Aciagrion Selys, 1891	? *Millotagrion* Fraser, 1953	14	[Pm]	Dijkstra 2007b (6)
Africallagma Kennedy, 1920		11	Pm	May & Dijkstra in prep. (11)
Agriocnemis Selys, 1869	*Mortonagrion* Fraser, 1920	17	[PI]	Dijkstra 2007b (3); Dijkstra in prep. c (+3)
Azuragrion May, 2002		6	Pm*	[* 1 sp. to Arabia] May & Dijkstra in prep. (6)
Ceriagrion Selys, 1876		19	[PI]	Dijkstra 2005c (15); Dijkstra 2007e (erratum)
Coenagriocnemis Fraser, 1949		4	ms	
Ischnura Charpentier, 1840		5	[PI]	Clausnitzer & Dijkstra 2005a (2)
Pinheyagrion May, 2002		1	zm	May & Dijkstra in prep. (1)
Proischnura Kennedy, 1920		3	AM*	[* 1 sp. to Nigeria] May & Dijkstra in prep. (3)
Pseudagrion Selys, 1876	A-group	41	[PA]*	[* to Levant and Arabia] Dijkstra 2002 (1); Dijkstra 2007b (+5); Dijkstra in prep. c (+2)
	B-group	24	[PI]*	[* to North Africa and Arabia] Dijkstra 2002 (1); Dijkstra 2007b (+1)
	M-group	31	md	
	W-group	2	GC	
Teinobasis Kirby, 1890		1	[IN]*	[* 1 sp. to ec] Dijkstra 2007b
Platycnemididae				
Allocnemis Selys, 1863		2	sa*	[* 1 sp. in Katanga] Dijkstra 2007b (1)
Chlorocnemis Selys, 1863	*Isomecocnemis* Cowley, 1936	15^{+}	GA	Dijkstra 2007b (5); Dijkstra in prep. c (+1)
Leptocnemis Selys, 1886		1	sc	
Mesocnemis Karsch, 1891		5	PA	Dijkstra in prep. c (3)
Metacnemis Selys, 1863		3	sa*	[* 1 sp. in md] Samways & Tarboton 2006 (1)
Oreocnemis Pinhey, 1971		1	ml	Dijkstra 2007b (1)
Paracnemis Martin, 1902		1	md	
Platycnemis Burmeister, 1839	continental group	5	GC	Dijkstra *et al.* 2007a (5)
	insular group	11^{+}	md*	[* 1 sp. on Pemba] Dijkstra *et al.* 2007a (1)
Stenocnemis Selys, 1886		1	cm	
Protoneuridae				
Elattoneura Cowley, 1935		18^{+}	[PA]	Dijkstra 2007b (2); Dijkstra in prep. c (+4)
Prodasineura Cowley, 1934		5	[GC]	Dijkstra 2007b (1)

ANISOPTERA				
Aeshnidae				
Aeshna Fabricius, 1775	*ellioti*-group	2	AM	
	rileyi-group	4^{+}	[AM]*	[* 1 sp. in Arabia] Clausnitzer & Peters 2003 (3); Dijkstra 2007a (+1)
	scotias-group	1	GC	
Anaciaeschna Selys, 1878		1	[Pm]	
Anax Leach, 1815		11	[PI]	

Gynacantha Rambur, 1842	*africana*-group	6	Pm	Dijkstra 2005d (6)
	bispina-group	4	IN*	[* 1 sp. in ec] Dijkstra 2005d (4)
	bullata-group	5	Pm	Dijkstra 2005d (5)
Heliaeschna Selys, 1882		5	[GC]*	[* 1 sp. to ml] Dijkstra 2005d (5)
Gomphidae				
Ceratogomphus Selys, 1854		2	sa*	[* 1 to Katanga]
Crenigomphus Selys, 1854		6	PA	
Diastatomma Burmeister, 1839		6	GC	Dijkstra in prep. d (6)
Gomphidia Selys, 1854		3	[PA]	Dijkstra in prep. d (3)
Ictinogomphus Cowley, 1934	*Cinitogomphus* Pinhey, 1964	4	[PA]	Dijkstra in prep. d (4)
Isomma Selys, 1892	? *Malgassogomphus* Cammaerts, 1987	3^{+}	md	Legrand 2003b (2)
Lestinogomphus Martin, 1911		7^{+}	PA	Legrand & Lachaise 2001 (2)
Microgomphus Selys, 1857		4	[GA]	Dijkstra 2007a (4)
Nepogomphoides Fraser, 1952		1	tn*	[* to ml]
Neurogomphus Karsch, 1890		17	PA	Cammaerts 2004 (17)
Notogomphus Hagen, 1857		17	AM*	[* 3 sp. to cm] Vick 2003 (3); Dijkstra in prep. b (+14)
Onychogomphus Selys, 1854		9	[Pm]	Dijkstra in prep. b (2; note on genus)
Paragomphus Cowley, 1934		27^{+}	[Pm]	Legrand 2003a (2); Clausnitzer & Dijkstra 2005a (+1); Dijkstra 2007a (+5); Dijkstra in prep. c (+5)
Phyllogomphus Selys, 1854		10	PA	Legrand 2003a (2); Dijkstra *et al.* 2006a (+4)
Tragogomphus Sjöstedt, 1899	? *Cornigomphus* Martin, 1907	8^{+}	GC	Legrand 2002 (1); Legrand 2003a (+1); Dijkstra 2007a (note on genus)
Corduliidae/Macromiidae				
Hemicordulia Selys, 1870		4	[IN]*	[* 1 sp. in AM] Dijkstra 2007d (4)
Idomacromia Karsch, 1896		3	GC	Dijkstra & Kisakye 2004 (3; ♀ only)
Libellulosoma Martin, 1907		1	md	
Neophya Selys, 1881		1	GC	Dijkstra in prep. c (1)
Nesocordulia McLachlan, 1882		6	md	
Phyllomacromia Selys, 1878		36	Pm	Dijkstra 2005a (14)
Syncordulia Selys, 1882		4	sa	Dijkstra *et al.* 2007c (4)
Libellulidae				
Acisoma Rambur, 1842		2	[Pm]	
Aethiothemis Ris, 1908	*Lokia* Ris, 1919; *Sleuthemis* Fraser, 1951	13	Pm	Dijkstra in prep. e (13)
Aethriamanta Kirby, 1889		1	[Pm]	
Archaeophlebia Ris, 1909		1	md	
Atoconeura Karsch, 1899		6	AM*	[* 1 sp. in GC] Dijkstra 2006b (6)
Brachythemis Brauer, 1868		3	[Pm]	
Bradinopyga Kirby, 1893		2	[PA]	
Calophlebia Selys, 1896		2	md	
Chalcostephia Kirby, 1889		1	Pm	
Congothemis Fraser, 1953	*Anectothemis* Fraser, 1954; *Porpacithemis* Fraser, 1954	4	GC	Dijkstra in prep. c (4)
Crocothemis Brauer, 1868		6	[Pm]	
Cyanothemis Ris, 1915		1	GC	
Diplacodes Kirby, 1889	*Philonomon* Förster, 1906	5	[PI]	Dijkstra 2006a (5)
Eleuthemis Ris, 1910		1^{+}	GC*	[* to tn] Dijkstra 2007a (1)
Hadrothemis Karsch, 1891		7	GC*	[* 1 sp. in ec] Dijkstra in prep. c (2)
Hemistigma Kirby, 1889		2	Pm	
Macrodiplax Brauer, 1868		1	[*]	[* vagrant from east]
Malgassophlebia Fraser, 1956		4	Gm	Legrand 2001 (2); Dijkstra 2007a (+1)
Micromacromia Karsch, 1890	*Eothemis* Ris, 1909; *Monardithemis* Longfield, 1947	4	GC*	[* 1 sp. in tn; 1 Angola] Dijkstra & Vick 2006 (4)
Neodythemis Karsch, 1889	*Allorrhizucha* Karsch, 1890; *Mesumbethemis* Vick, 2000	12	Gm	Dijkstra & Vick 2006 (8)
Nesciothemis Longfield, 1955		5	PA	Dijkstra 2007a (2)
Notiothemis Ris, 1919		2	GA	

Olpogastra Karsch, 1895	1	PA	Dijkstra *et al.* 2006b (1)
Orthetrum Newman, 1833	30	[PI]	Dumont & Verschuren 2004 (1); Dijkstra 2007a (+3); Dijkstra & Clausnitzer in prep. (+2)
Oxythemis Ris, 1909	1	GC	
Palpopleura Rambur, 1842	6	[Pm]	Mitchell & Samways 2005 (2); Dijkstra & Clausnitzer in prep. (+0)
Pantala Hagen, 1861	1	[PI]	
Parazyxomma Pinhey, 1961	1	PA	Dijkstra 2003a (1)
Porpax Karsch, 1896	5	GC*	[* 1 sp. in AM] Dijkstra 2006c (5)
Rhyothemis Hagen, 1867	6	[PI]	Dijkstra & Clausnitzer in prep. (2)
Selysiothemis Ris, 1897	1	[*]	[* vagrant from north]
Sympetrum Newman, 1833	2	[PI]	
Tetrathemis Brauer, 1868	8	[Pm]	Dijkstra 2007a (3)
Thalassothemis Ris, 1912	1	mr	
Thermochoria Kirby, 1889	2	GA	Dijkstra & Clausnitzer in prep. (2)
Thermorthemis Kirby, 1889	2	md	
Tholymis Hagen, 1867	1	[PI]	
Tramea Hagen, 1861	2	[PI]	
Trithemis Brauer, 1868	35	[PI]	Clausnitzer 2001 (2); Dijkstra 2007a (+8)
Trithetrum Dijkstra & Pilgrim, 2007	2	GC*	[* slightly exceeds GC] Dijkstra & Pilgrim 2007 (2)
Urothemis Brauer, 1868	4	[PI]	
Viridithemis Fraser, 1961	1	md	
Zygonoides Fraser, 1957	4	Pm	Dijkstra *et al.* 2006b (4)
Zygonychidium Lindley, 1970	1	ci	
Zygonyx Hagen, 1867	13	[PI]	Dijkstra in prep. c (1)
Zyxomma Rambur, 1842	2	[PI]	

Taxonomic priorities for Afrotropical odonatology per family.

Calopterygidae	Review relation between *Sapho* and *Umma* and assignment of species to these genera.
Chlorocyphidae	Review *Chlorocypha*, especially of red species.
Megapodagrionidae	Review *Nesolestes* species; assess relationship with *Neurolestes*.
	Review *Protolestes* and *Tatocnemis* species.
Coenagrionidae	Revise *Aciagrion*, especially *gracile*-group; assess status *Millotagrion* and relationship with genera formerly treated under *Enallagma*.
	Revise *suave*-group of *Ceriagrion*, including Madagascan species.
	Overview of entire genus *Pseudagrion* worthwhile (21% of species described since last complete revision), especially of Madagascan species (M-group); generic status *cyathiforme* and *malagasoides* (W-group).
Platycnemididae	Review Madagascan *Platycnemis* species; assess relationship with Asian genus *Copera*.
Protoneuridae	Review limits between *Elattoneura* and *Prodasineura* in relation also to Asian species; revision of some species, especially those now in *Prodasineura*.
Aeshnidae	Determine generic status of three distinct groups in *Aeshna*.
Gomphidae	Completely revise *Lestinogomphus*.
	Review *Microgomphus* species.
	Completely revise *Onychogomphus*, including generic status.
	Completely revise *Paragomphus*, especially cognatus-group; assess relationship with *Crenigomphus*.
	Revise western *Phyllogomphus* species.
	Completely revise *Tragogomphus*, including generic status.
Macromiidae	Review *Phyllomacromia* species; revise parts of genus, *e.g. paula*-group.
Libellulidae	Review of large genera (*Orthetrum*, *Trithemis*, *Zygonyx*) worthwhile.

samenvatting

Vergaan en verrijzen: de taxonomie en biogeografie van de Odonata van tropisch Afrika

Hoofdstuk 1. Een overzicht van de taxonomie van Afrikaanse Odonata: de weg naar betere herkenning en biogeografisch inzicht.

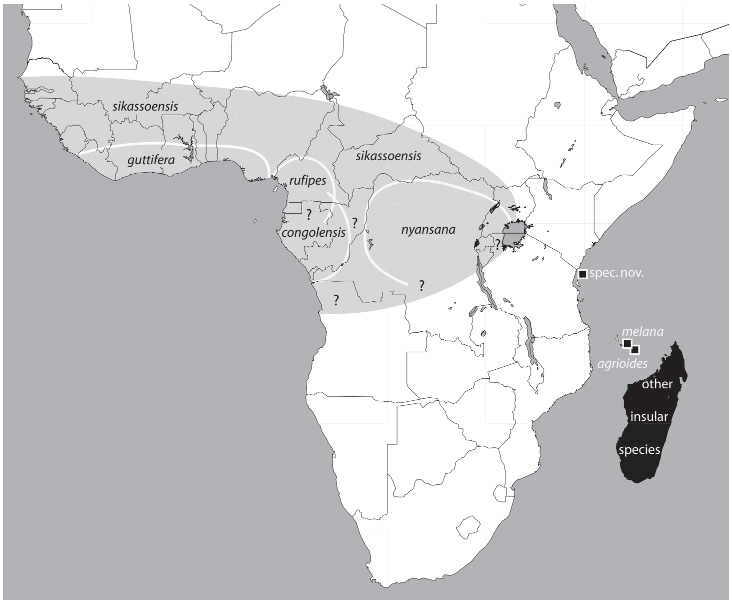
De sterke gebondenheid van libellen aan zoetwater en begroeiing maakt dat deze dieren gevoelig zijn voor de ingrijpende klimatologische schommelingen die Afrika in de afgelopen miljoenen jaren hebben gekenmerkt, waardoor warme en natte periodes werden afgewisseld met koudere en drogere. De soorten variëren van zeer mobiel, haast kosmopolitisch, tot zeer immobiel, wat inzicht kan geven in de mate van dispersie en versnippering. Bovendien zijn libellen een oude diergroep, waardoor ze potentieel informatie kunnen verschaffen over een ver verleden. De taxonomie van de ongeveer 850 libellensoorten die ten zuiden van de Sahara (inclusief Madagaskar) voorkomen, is goed bekend ten opzichte van tropisch Azië en Amerika, deels omdat de fauna hooguit een vijfde omvat van de diversiteit in de tropen. Toch weten we zeer weinig over de afstammings- en verspreidingsgeschiedenis van de diverse soorten (fylogenie en biogeografie). Door hun kenmerken en verwantschappen beter te beschrijven wordt het mogelijk ze beter te herkennen, hun verspreiding en ecologie vast te stellen, en daarmee hun geschiedenis te herleiden. Deze kennis, gecombineerd met geologische en klimatologische gegevens, vergroot ons begrip van de Afrikaanse biodiversiteit.

Een van de voornaamste problemen bij het indelen van soorten is hun vaak onderschatte variabiliteit. Individuen van dezelfde soort verschillen bijvoorbeeld van plaats tot plaats aanzienlijk (vooral in formaat en zwartkleuring) en kunnen daardoor voor verschillende soorten zijn aangezien. Neerslag en temperatuur kunnen het uiterlijk van een libel sterk beïnvloeden; als er alleen op enkele ver uiteen liggende locaties verzameld wordt, ontstaat een vals beeld van aparte soorten terwijl de soort in werkelijkheid geleidelijk verandert over een klimatologische gradiënt. Dit is vooral in Afrika een probleem omdat soorten vaak een groot en aaneengesloten verspreidingsgebied hebben met grote klimatologische verschillen daarbinnen. Daarnaast verschillen individuen met een verschillende sekse of leeftijd ook meer dan eerder is gedacht. Een tweede pro-bleem, in het bijzonder in de grote familie Libellulidae, is dat de indeling van soorten in geslachten vroeger grotendeels gebaseerd werd op onbetrouwbare kenmerken van de vleugeladering. Aderkenmerken zijn gemakkelijk te kwalificeren en kwantificeren, maar zijn relatief plastisch en zeggen mogelijk meer over bijvoorbeeld het vliegvermogen van een soort dan over zijn verwantschappen. Om bovenstaande redenen zijn veel soorten en geslachten van Afrikaanse libellen meer dan eens beschreven. Om inzicht te krijgen in de geschiedenis van de libellenfauna is het is daarom noodzakelijk om eerst de taxonomie op orde te brengen.

Hoofdstuk 2. Tropisch Afrikaanse breedscheenjuffers (*Platycnemis*) en de biogeografische betekenis van een nieuwe soort van het eiland Pemba, Tanzania (Odonata: Platycnemididae).

Breedscheenjuffers komen voor in Europa en aangrenzend Afrika en Azië, Oost-Azië, Centraal- en West-Afrika, en Madagaskar en de Komoren. In 2001 werd een soort ontdekt op het kleine eiland Pemba (ongeveer 1000 km^2), 50 km voor de Tanzaniaanse kust in Oost-Afrika. Deze soort is door 1000 km droge savanne gescheiden van zijn verwanten in het westen (Oeganda) en door een vergelijkbare afstand open zee van de verwanten in het oosten (de Komoren) (Figuur 1). Om de herkomst van deze geïsoleerde soort te bepalen, was het noodzakelijk om eerst de taxonomie van de tropisch Afrikaanse *Platycnemis*-soorten te herzien. Daaruit bleek dat slechts vijf van de acht van het vasteland bekende beschreven soorten biologische soorten waren. Bovendien ging het bij de sinds de beschrijving in 1863 uitgestorven gewaande *P. mauriciana* van het eiland Mauritius om een Europese soort. De locatiegegevens “Ile de France” waren verkeerd geïnterpreteerd, hoewel Mauritius die naam alleen van 1715 tot 1810 droeg, terwijl de Parijse omgeving al sinds de 14e eeuw zo wordt aangeduid.

De soort van Pemba lijkt sterk op enkele soorten van Madagaskar, terwijl de soorten van het vasteland vooral overeenkomen met soorten uit tropisch Azië. De meest waarschijnlijke verklaring voor de aanwezigheid van een breedscheenjuffer op Pemba is daarom dat deze is ‘overgewaaid’ vanuit Madagaskar, mogelijk door de moesson die in deze richting beweegt. Dit is ook de manier waarop verwante soorten de Komoren konden bevolken. Dat deze juffersoort zich niet elders aan de Afrikaanse kust gevestigd



Figuur 1. Verspreiding van tropisch Afrikaanse breedscheenjuffers (Platycnemis), *met in grijs de vastelandsgroep en in zwart die van Madagaskar, de Komoren en Pemba.*

heeft, hangt mogelijk samen met het relatief natte klimaat van Pemba, zowel nu als in het verleden. De nieuwe soort, levend bewijs van een opmerkelijke kolonisatie, is ernstig bedreigd: Het voornaamste bosreservaat van Pemba is 15 km^2 groot en herbergt maar één beek.

Hoofdstuk 3. *Pseudagrion* gesplitst: moleculaire fylogenie bevestigt de morfologische en ecologische tweedeling van Afrika's soortenrijkste libellengeslacht (Odonata: Coenagrionidae).

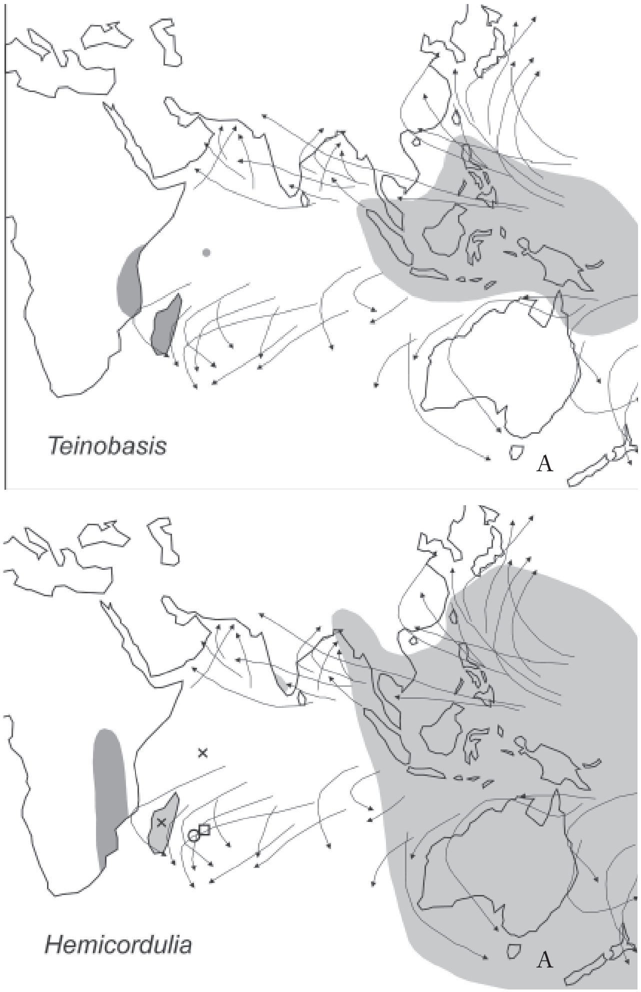
In Afrika komen bijna 70 *Pseudagrion*-soorten voor, op Madagaskar 30, en nog eens 40 van Azië tot in Australië. Deze juffers hebben alle zoetwaterbiotopen in tropisch Afrika bezet, van poelen in de Kalahari tot beken op de berg Kilimanjaro. Veel soorten leven in regenwoud, terwijl andere geïsoleerd voorkomen in de bergen van de Sahara en Marokko. Taxonomen die naar de morfologie van mannelijke imago's, vrouwtjes en larven keken, ontdekten al in de jaren 1950 en 1960 een duidelijke tweedeling binnen deze soortengroep. Eenenveertig soorten behoren tot de zogenaamde A-groep en bevolken koelere biotopen, zoals schaduwrijk of hooggelegen stromend water. Vierentwintig soorten behoren tot de B-groep en prefereren warmere biotopen, waaronder ook stilstaande wateren, die dikwijls zonnig zijn en in het laagland liggen. Zo vond de auteur in Ethiopië langs drassige oevers van meren in de Grote Slenk alleen vijf B-soorten en langs beken en rivieren die van het omliggende hoogland afstromen alleen vijf A-soorten. In Ghana en Liberia kwamen A-soorten alleen voor op de beschaduwde bovenlopen van regenwoudrivieren, terwijl B-soorten de zonnigere delen benedenstrooms bevolkten.

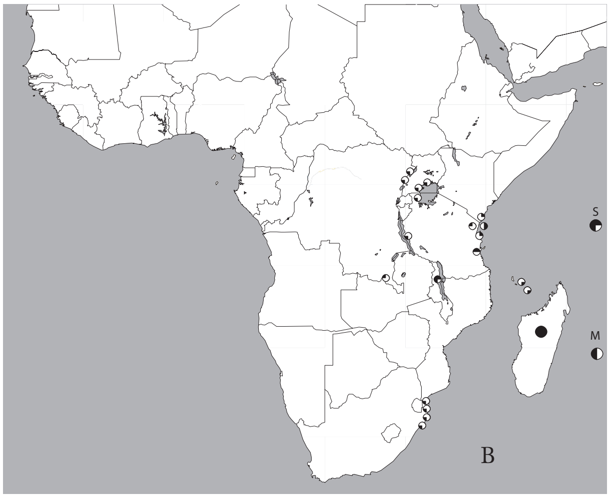
Om te onderzoeken of deze tweedeling een genetische basis heeft, werd van zes soorten van iedere groep een sequentie van 610 basenparen van het mitochondriaal DNA vergeleken. Deze steekproef toonde aan dat de genetische afstanden tussen soorten van verschillende groepen groter was dan de afstanden tussen soorten binnen een groep, wat het aannemelijk maakt dat de twee een onafhankelijke afstammingsgeschiedenis hebben. Het onderzoek is te beperkt om met zekerheid te kunnen zeggen hoe *Pseudagrion* zo dominant is geworden. Vermoedelijk zijn bosbeken de oorspronkelijke biotoop en zijn de A- en B-groepen apart geradiëerd in open biotopen. Weerkaatsende berijping beschermt tegen blootstelling aan zonlicht en komt voor bij A-soorten van open en hooggelegen biotopen. Mogelijk ontstond deze aanpassing aanvankelijk in koele maar zonnige berggebieden, waardoor soorten beter in staat waren onbeboste laaglanden te koloniseren. Zulke biotopen domineren nu in Afrika en *P. kersteni*, de meest berijpte A-soort, is daar ook de meest verbreide. De B-soorten lijken meer op Aziatische soorten en arriveerden mogelijk later op het continent, waarop zij zich uitbreidden in warmere biotopen die onbezet waren gebleven. Onderzoek van meer soorten, ook uit Madagaskar en Australazië, moet leiden tot een beter beeld van de geschiedenis van *Pseudagrion* en de relatie met de klimatologie en geologie van Afrika.

Hoofdstuk 4. Gejaagd door de wind: westwaartse verspreiding en soortvorming van glanslibellen (*Hemicordulia*) in de westelijke Indische Oceaan (Odonata: Corduliidae).

De meeste van de ongeveer 50 soorten van het geslacht *Hemicordulia* (inclusief het nauw verwante geslacht *Procordulia*) komen voor in Nieuw-Guinea en Australië, tot in de Stille en Indische Oceaan. De groep komt op continenten nauwelijks voor, maar is wel in Oost-Afrika aanwezig (Figuur 2A). Tot voor kort werden de *Hemicordulia* populaties van India, Réunion en Oost-Afrika tot dezelfde soort gerekend, met daartussen andere soorten. De populatie van Réunion is echter een aparte soort die lijkt op die van het nabijgelegen Mauritius, en ook Oost-Afrika heeft een eigen soort, die nauw verwant is aan die van Madagaskar en de Seychellen. Een verspreiding zoals die van *Hemicordulia* komt ook voor bij het juffergeslacht *Teinobasis* (Figuur 2A), enkele andere libellen (Figuur 2B) en diverse gevleugelde landdieren zoals vlinders, vogels en vleerhonden. Hoe is deze verspreiding ontstaan en waarom zijn de groepen schaars of afwezig op het vasteland?

In het gebied van de Indische Oceaan is de overheersende windrichting westelijk, wat ook geldt voor de zomerse cyclonen (Figuur 2A). Dit kan het transport van dieren door de lucht vanuit Azië verge-





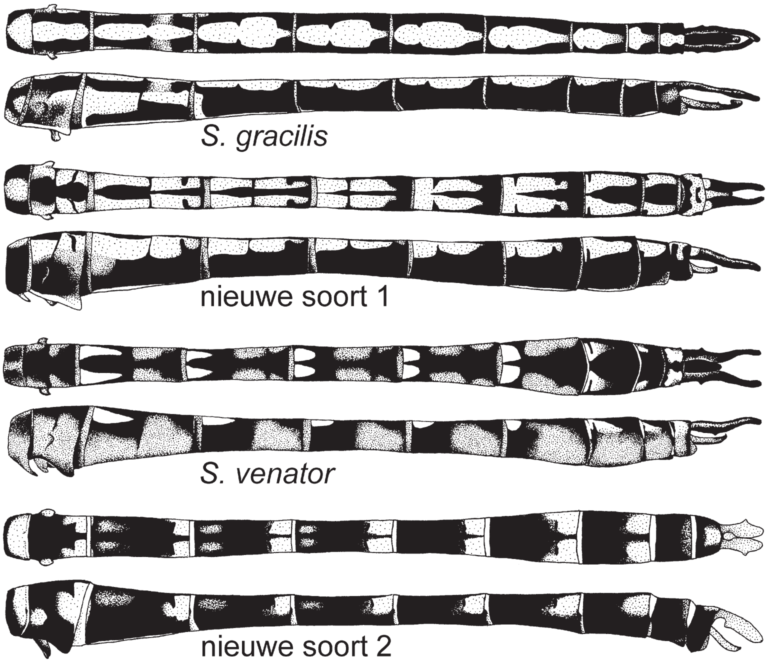
Figuur 2. (A) Verspreiding van Teinobasis *en* Hemicordulia *(inclusief het verwante* Procordulia*). Pijlen geven de loop van zomerstormen weer. In lichtgrijs is de hoofdverspreiding van elk geslacht in het oosten weergeven, in donkergrijs het voorkomen van verschillende soorten (symbolen) in het westen.*
(B) Verspreiding van vermoedelijk trans-oceanische libellen in tropisch Afrika. Elk zwarte kwart van een cirkel vertegenwoordigt een andere groep. Linksboven, bispina*-groep van* Gynacantha*; linksonder,* Hemicordulia*; rechtsboven,* Teinobasis*; rechtsonder, eilandgroep van* Platycnemis *(Hoofdstuk 2). De grotere cirkels geven het voorkomen aan in Madagaskar, de Maskarenen (M) en de Seychellen (S) (beide ten oosten van de marge).*

makkelijken. Gezien het voorkomen van een geschikte luchtcirculatie en de vaak geringe verschillen tussen de besproken soorten, is het aannemelijk dat dispersie die tot soortvorming leidt nog altijd plaatsvindt. Schattingen op basis van het moleculaire klok model geven aan dat salanganen, parkieten, honingzuigers en kalongs zich pas in de laatste twee miljoen jaar (m.j.) over de westelijke Indische Oceaan hebben verspreid. Met de snelheid die gemeten is bij de trekkende *Pantala flavescens* kan een libel zich in twee tot zes dagen van India naar de Seychellen verplaatsen. Alternatieve hypothesen, zoals geleidelijke uitbreiding over land vanuit Azië naar Afrika, voorspellen een andere geografische verdeling van de diversiteit van deze groepen. Bovendien blijft verspreiding over zee voor bepaalde eilandgroepen de enig mogelijke verklaring.

Vaak wordt gedacht dat eilanden weinig bijdragen aan continentale fauna's, omdat eilandsoorten onvoldoende zouden kunnen concurreren met soorten van het vasteland. Hoewel veel waarnemingen van trans-oceanische libellen op het vasteland uit het kustgebied komen, zijn de meeste soorten ook in het binnenland gevonden (Figuur 2B). Vooral de locaties van *Hemicordulia* zijn opvallend 'eilandachtig' omdat ze altijd nabij grote wateroppervlakten liggen. Recente klimaatswisselingen hadden grote gevolgen voor lokaal gegenereerde regenval bij de grote meren. Het niveau in het Malawi- en het Tanganyikameer was in de laatste tienduizenden jaren soms honderden meters lager dan nu, en het Victoriameer lag soms zelfs bijna droog. De bossen die *Hemicordulia* bewoont zijn daarom vaak jong, waardoor de concurrentie met plaatselijke soorten mogelijk (tijdelijk) is verminderd. *Hemicordulia* lijkt gebonden aan koelere biotopen, wat heeft geleid tot een perifeer continentaal bestaan.

Hoofdstuk 5. Twee nieuwe relictaire *Syncordulia* soorten gevonden tijdens museum- en veldonderzoek van bedreigde libellen in de Kaapregio (Odonata: Corduliidae).

De uiterste zuidpunt van Afrika wordt gekenmerkt door een afwijkende flora (fynbos) en fauna. Hiertoe behoren enkele zeer plaatselijk voorkomende libellen, waaronder de soorten van het geslacht *Syncordulia*, die elders in Afrika geen duidelijke verwanten hebben. Sinds hun ontdekking in de jaren 1930 waren maar twee *Syncordulia*-soorten bekend. In 2006 werd in verband met de herziening van de Rode Lijst van Zuid-Afrikaanse libellen het beperkte beschikbare materiaal opnieuw onderzocht. Hierbij kwamen



Figuur 3. Achterlijven van mannetjes van Syncordulia *in dorsaal (boven) en lateraal (onder) aanzicht. Zie de verschillen in de vorm, tekening, aanhangselen (rechts) en onderop de eerste twee segmenten (links).*

twee nieuwe soorten aan het licht, die vervolgens ook in het veld werden aangetroffen (Figuur 3). Dit toont het belang aan van collecties en taxonomisch onderzoek voor de bescherming van bedreigde libellensoorten en hun biotopen. Fynbosdalen zijn gevoelig voor overwoekering door exotische boomsoorten, vooral Australische acacia's. Het verwijderen hiervan voor waterbeheer is gunstig voor de inheemse libellenfauna. De vier soorten komen tezamen voor in fynbosbeken in de zuidwestelijke Kaapregio. Ecologische verschillen zijn nochtans onbekend, hoewel de soorten in vliegtijd lijken te verschillen.

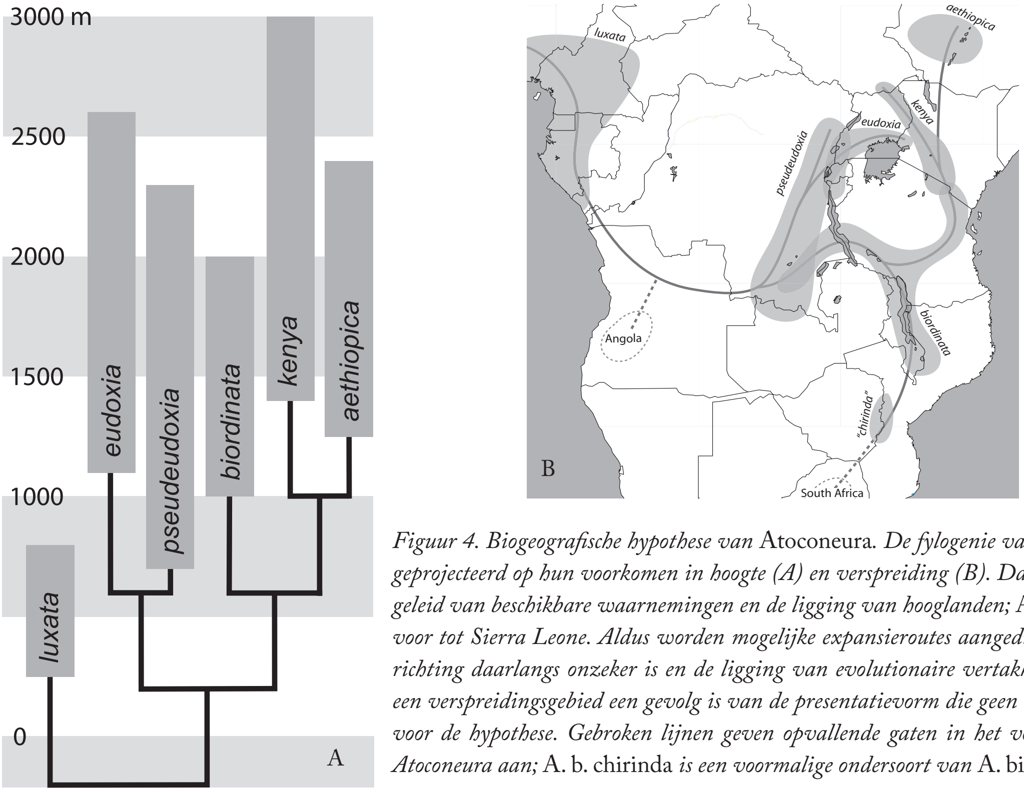
Het is onduidelijk welke de nauwste verwanten van *Syncordulia* zijn. Er op lijkende soorten komen voor in Madagaskar, equatoriaal Afrika, tropisch Amerika en het westelijke Middellandse-Zeegebied, maar de grootste diversiteit wordt in Australië aangetroffen. De morfologische verscheidenheid binnen *Syncordulia* is opvallend omdat tussen veel Australische geslachten minder verschil bestaat. Dit doet vermoeden dat de vier een overblijfsel zijn van een zeer oude radiatie. De huidige biotoop ontstond echter hooguit 5 m.j. geleden, nadat een koude opwelling voor de Zuid-Afrikaanse kust tot droge zomers ging leiden. De koude en voedselarme beken worden nauwelijks door wijdverspreide Afrikaanse libellensoorten bevolkt. Mogelijk vertegenwoordigt *Syncordulia* een oude Afrikaanse bergfauna en kreeg het geslacht met het ontstaan van biotoop waaraan het beter is aangepast dan de moderne fauna een nieuwe overlevingskans.

Hoofdstuk 6. Taxonomie, fylogenie and biogeografie van *Atoconeura*, een libellengeslacht in de hooglanden van Afrika (Odonata: Libellulidae).

Atoconeura-soorten leven vooral bij beboste bergbeken. In haar artikel 'The *Atoconeura* Problem' loste Cynthia Longfield in 1953 de taxonomische wanorde op door twee soorten te onderscheiden, waarvan een met vier ondersoorten in verschillende berggebieden. Later werd een vijfde ondersoort toegevoegd, waarbij de status van veel populaties onduidelijk bleef. Om te bepalen hoe goed de door Longfield gebruikte kenmerken haar classificatie ondersteunen, was een objectieve analyse van het oorspronkelijke materiaal noodzakelijk. Daaruit kwamen zes groepen naar voren die redelijk overeenkwamen met Longfield's indeling. Eén groep bleek echter twee ondersoorten te omvatten en een andere groep kwam niet overeen met een bekende (onder)soort. De groepen bleken bovendien plaatselijk te overlappen in verspreiding. Omdat ze ook verschilden in nieuwgevonden kenmerken, konden de groepen het beste als soorten beschouwd worden, waarvan er een nog onbeschreven was. Een fylogenetische analyse van de onderzochte kenmerken verschafte tevens een hypothese met betrekking tot hun afstamming (Figuur 4).

Zoals in hoofdstuk 8 wordt besproken, lijken de meeste Afrikaanse hooglandsoorten in de laatste 5 m.j. plaatselijk te zijn ontstaan uit laaglandsoorten, met vervolgens een verschuiving naar nog hogere gebieden en dispersie naar andere hooglanden. De fylogenie van *Atoconeura* toont aan dat de nauwste verwanten elkaars buren zijn (Figuur 4A). Dispersie is dus de eenvoudigste verklaring van het waargenomen beeld; alternatieve hypothesen (bijvoorbeeld geologische) zijn meer complex. Hoe heeft deze uitbreiding plaats gevonden, en in welke richting? Hoewel de bergvegetatie destijds soms uitgebreider was dan nu, is er geen bewijs dat de tegenwoordig geïsoleerde hooglanden ooit verbonden zijn geweest. Mogelijk konden gebergtesoorten zich gedurende landschappelijke veranderingen wel gemakkelijker door het laagland verspreiden. De westelijke *A. luxata* komt alleen aan de voet van hooglanden voor en vertegenwoordigt met een basale fylogenetische en ecologische positie mogelijk de voorloper van de oostelijke *Atoconeura*-radiatie. Als *Atoconeura* zich vanuit het oosten naar het westen had verspreid, zou het geslacht ook hoger in West-Afrika verwacht worden.

De hooglanden ten oosten van het Kongobekken danken hun hoge biodiversiteit aan het grote soortenreservoir in het aangrenzende laaglandregenwoud, van waaruit hooglandsoorten kunnen ontstaan. Ze zijn daarmee een logisch startpunt voor een oostelijke radiatie, vooral als de voorouder uit het westelijke laagland komt. Koude periodes (tot ongeveer elfduizend jaar geleden) waren droger, waardoor bergen zoals in Kenia vermoedelijk bosvrij waren. De voorouder van *A. kenya* kon zich vanuit gunstiger gebied in Tanzania uitbreiden toen de omstandigheden in Kenia verbeterden. Het Ethiopische bergwoud is ook recent en net als *A. aethiopica* hebben de meeste soorten er een Keniaanse oorsprong. De afstammingsgeschiedenis van de Afrikaanse hoogland-



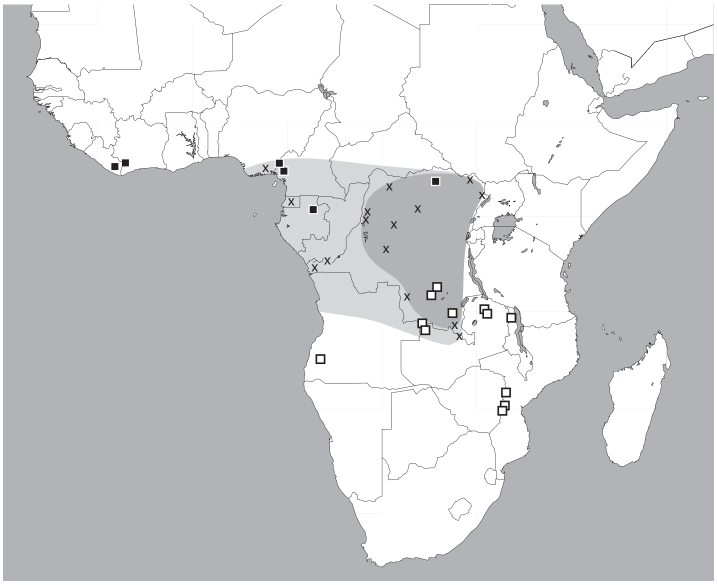
Figuur 4. Biogeografische hypothese van Atoconeura. *De fylogenie van de soorten is geprojecteerd op hun voorkomen in hoogte (A) en verspreiding (B). Dat laatste is afgeleid van beschikbare waarnemingen en de ligging van hooglanden;* A. luxata *komt voor tot Sierra Leone. Aldus worden mogelijke expansieroutes aangeduid, hoewel de richting daarlangs onzeker is en de ligging van evolutionaire vertakkingen binnen een verspreidingsgebied een gevolg is van de presentatievorm die geen betekenis heeft voor de hypothese. Gebroken lijnen geven opvallende gaten in het voorkomen van Atoconeura aan;* A. b. chirinda *is een voormalige ondersoort van* A. biordinata.

fauna en -flora, en van *Atoconeura* in het bijzonder, lijkt fasen te weerspiegelen waarin geschikte biotoop vrijkwam, gevolgd door snelle kolonisatie, adaptatie en verdere uitbreiding. *Atoconeura* is niet bekend in Angola, waar mogelijk onvoldoende is verzameld, en Zuid-Afrika, waar veel soorten meer gebonden zijn aan open landschappen dan aan bos. Het gebied was mogelijk onbewoonbaar voor *Atoconeura* in koudere periodes en onbereikbaar in periodes waarin de biotoop wel geschikt was.

Hoofdstuk 7. Taxonomie en biogeografie van *Porpax*, een libellengeslacht uit het Kongobekken (Odonata: Libellulidae).

Porpax-soorten planten zich voort in ondiep water, zoals tijdelijke bospoelen, modderige beekjes en grazige moerassen. Tot voor kort werd het merendeel van het schaarse materiaal toegeschreven aan één soort, terwijl drie andere beschreven soorten nauwelijks bekend waren. Het uitgebreide materiaal uit het Kongobekken (aanwezig in het Afrikamuseum in Tervuren) was echter nooit bewerkt. De vier soorten komen alle verspreid voor in het bekken, waar tevens een vijfde, eerder onopgemerkte, soort voorkomt. Hoewel in het Kongobekken plaatselijk tot vier soorten samenleven, is het geslacht daarbuiten zeer lokaal (Figuur 5). De uiterlijk afwijkende *P. risi* is de enige soort die niet in bos leeft, maar verspreid voorkomt in de open moerassen van de zuidelijke hooglanden (Hoofdstuk 6).

Van de sterk aan bos gebonden *P. bipunctus* zijn vier populaties bekend die ver uit elkaar liggen. Hun ligging komt overeen met de traditioneel onderscheiden bosrefugia aan weerszijden van het Kongobekken en in West-Afrika. Dit patroon zou een waarnemingseffect kunnen zijn, maar de verschillende lichaamstekening in elke populatie impliceert plaatselijke soortvorming. Andere *Porpax*-soorten zijn uiterlijk eenvormig en meer verspreid verzameld. Omdat Afrika in het verleden relatief droog was en nog altijd met onregelmatige onderbrekingen neerslag ontvangt, komen er nauwelijks soorten voor van biotopen die gevoelig zijn voor uitdroging. *P. bipunctus* plant zich voort in onderstroomde delen



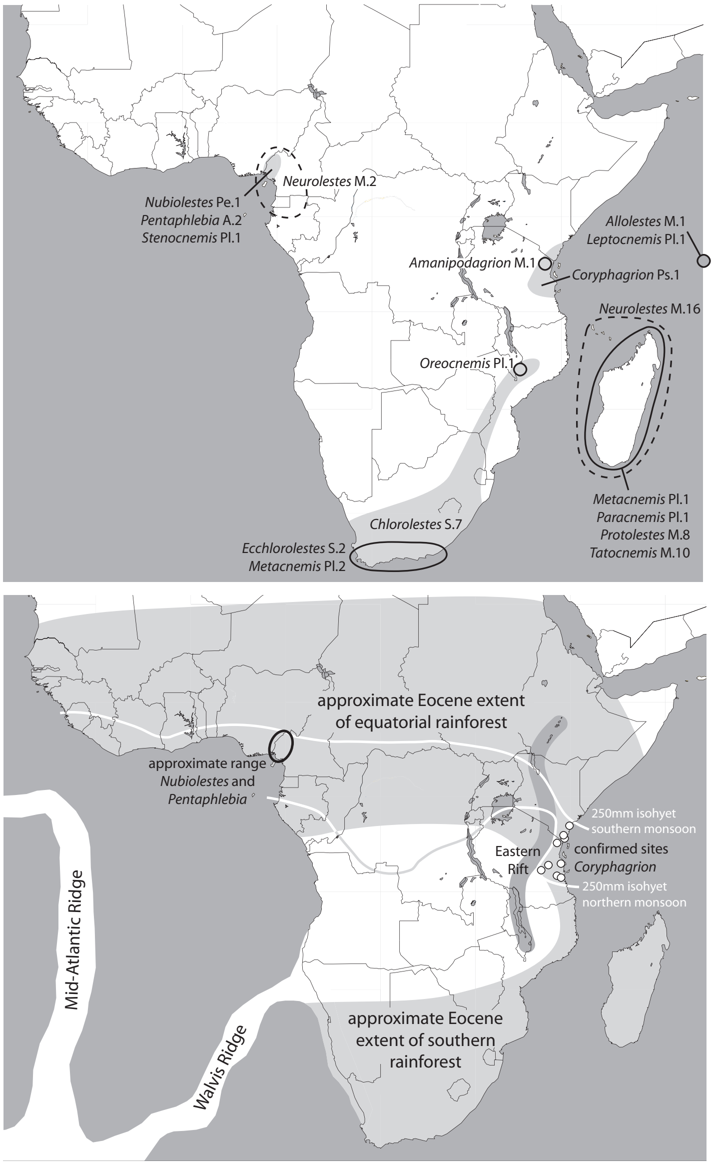
Figuur 5. Verspreiding van Porpax. *Zwarte vierkanten geven* P. bipunctus *aan, witte* P. risi. *Waarnemingen van andere soorten zijn met kruizen weergegeven; in het lichtgrijze gebied komt alleen* P. asperipes *voor, in het donkergrijze gebied ook* P. garambensis *en* P. sentipes.

in beekbeddingen en is daarom mogelijk beperkt tot gebieden met betrouwbare regenval, zowel binnen als tussen jaren. Dit zijn dezelfde plekken waar in droge periodes bos kan voortbestaan.

Hoofdstuk 8. Vergaan en verrijzen: de taxonomie en biogeografie van de Odonata van tropisch Afrika.

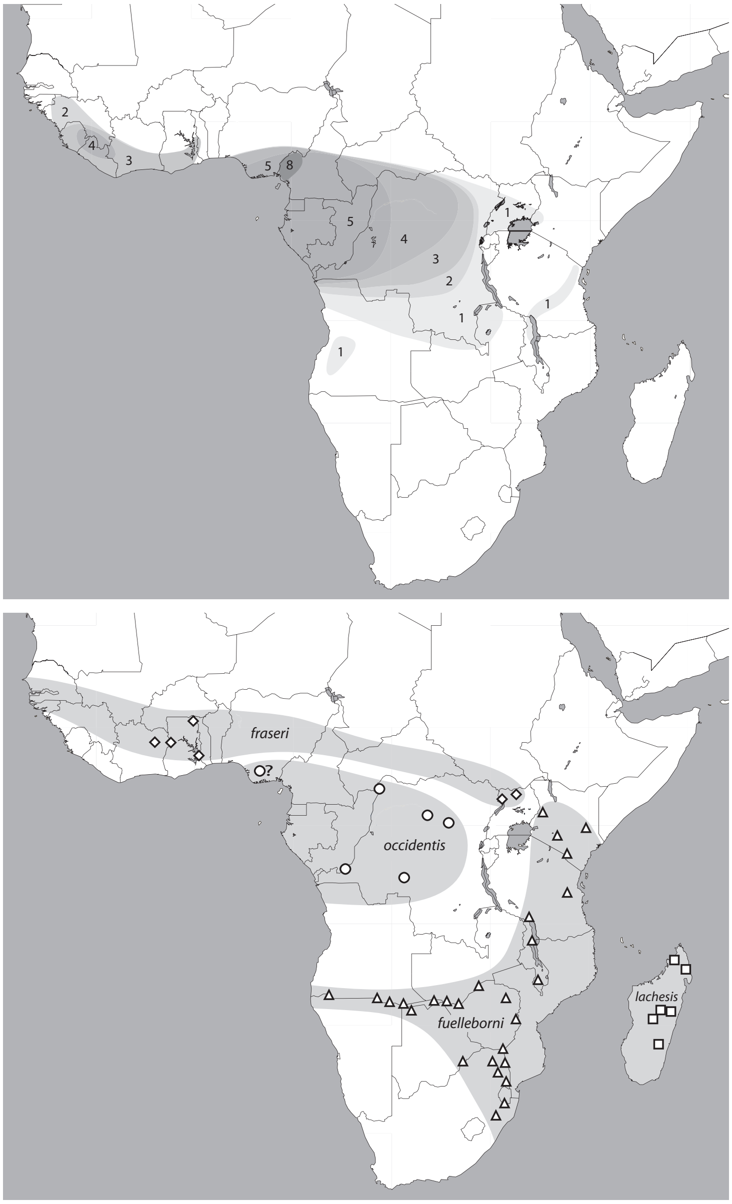
Afrika is een groot continent dat nauwelijks onderbroken wordt door gebergten of watermassa's, maar wel door zeeën en woestijnen van omliggende continenten is afgesneden. De laatste 20 m.j. was Afrika onderhevig aan sterke klimaatschommelingen, met almaar drogere omstandigheden. Deze veranderingen hebben een sterke weerslag gehad op het landschap: de laaglandregenwouden werden sterk teruggedrongen, vaak veel meer dan nu het geval is. Als gevolg van dit alles telt tropisch Afrika (inclusief Madagaskar) maar half zoveel libellensoorten als tropisch Amerika of Azië herbergen. Opvallend is de schaarste van 'oorspronkelijke' families. De weinige relicten zijn beperkt tot vijf kerngebieden: de hooglanden van Kameroen, plaatselijk in Oost-Afrika, de Kaapregio (Hoofdstuk 5), de continentale fragmenten van de Seychellen en vooral Madagaskar (Figuur 6A). Deze gebieden danken deze elementen aan een relatief stabiel klimaat en een geïsoleerde ligging. Het is aannemelijk dat twee relicten met Amerikaanse verwanten zich al in Kameroen bevonden toen Afrika ongeveer 100 m.j. geleden losraakte van Zuid-Amerika. Het voorkomen van de derde 'Amerikaan' aan de oostkust is echter minder makkelijk te verklaren (Figuur 6B).

De meeste Afrikaanse libellensoorten, ongeveer 40%, zijn gebonden aan het Centraal- en West-Afrikaanse bosgebied (Hoofdstukken 2 en 7). Het restant komt in drie vrij gelijke delen voor in het hooggelegen gebied van Jemen tot de Kaap (Hoofdstukken 5 en 6), in Madagaskar en de omliggende archipels (Hoofdstukken 2 en 4), en verspreid over open delen van het gehele gebied (Hoofdstuk 3). Het merendeel van de soorten van het vasteland heeft geen verwanten op Madagaskar, tenzij zij daar pas recent zijn aangekomen. De continentale fauna heeft meer gemeen met de meer diverse fauna van tropisch Azië. Deze relatie en hun ontbreken op Madagaskar suggereert dat de moderne Afrikaanse fauna vooral gediversifieerd is na aankomst van Aziatische voorouders. Coenagrionidae en Libellulidae zijn de grootste libellenfamilies op aarde en zijn het beste aangepast aan verandering. Alleen in de gematigde streken, die sterk zijn beïnvloed door de ijstijden, is hun overheersing even groot als in het veranderlijke Afrika. De klimaatsinvloed is verder zichtbaar bij bossoorten die door een gekrompen bosgebied geïsoleerd zijn geraakt in hooglanden (Figuur 7A), savannesoorten die nu juist zijn ingesloten door bosgebied (Figuur 7B) en de kolonisatie van Oost-Afrika door eilandsoorten (Hoofdstukken 2 en 4).



Figuur 6. (A) Verspreiding van relictaire tropisch Afrikaanse Zygoptera. Het aantal soorten alsmede de familie is voor elk geslacht/gebied gegeven (A: Amphipterygidae; M: Megapodagrionidae; Pe: Perilestidae; Pl: Platycnemididae; Ps: Pseudostigmatidae; S: Synlestidae). (B) Biogeografische hypothese voor de reuzenjuffer Coryphagrion. *Nadat Zuid-Amerika al van Afrika gescheiden was, kon een voorouder mogelijk via eilanden (de nu verzonken Walvis Ridge) het regenwoud (lichtgrijs) in zuidelijk Afrika bereiken, dat door een savannegordel van het equatoriale regenwoud was gescheiden. Langs de nattere oostkust was een smalle bosstrook, waardoor* Coryphagrion *zijn huidige verspreidingsgebied kon bereiken, maar verheffing en verdroging langs de Oostelijke Slenk (donkergrijs) voorkwam verdere uitbreiding. Nu overleeft het geslacht, dat gevoelig is voor uitdroging van de boomholtes waarin het zich voortplant, alleen in een smalle strook die in beide jaarhelften meer dan 250mm regen ontvangt (witte lijnen).*

Omdat er nauwelijks fylogenetisch onderzoek is gedaan naar Afrikaanse libellen (Hoofdstukken 3 en 6), kan er weinig gezegd worden over de herkomst van de fauna en de processen die tot soortvorming hebben geleid. Uit de literatuur blijkt dat Afrika's uitwisseling van fauna met Madagaskar en Eurazië vaak veel recenter en langduriger was dan de geologie voorspelt. Kolonisaties van het al 120 m.j. gescheiden Madagaskar vonden meestal eerder plaats (tussen 65 en 15 m.j. geleden) dan die vanuit Eurazië (vooral laatste 20 m.j.). De waargenomen patronen worden vaak verklaard door kansen op verspreiding en isolatie, maar mogelijk zijn de kansen voor vestiging en (snelle) soortsvorming belangrijkere factoren. Landschappelijke veranderingen kunnen bijvoorbeeld de beschikbaarheid van biotopen en de competitie met al gevestigde soorten beïnvloeden. Madagaskar verplaatste zich tussen 65 en 30 m.j. geleden door een subtropische, droge zone. Toen het geleidelijk de tropen in dreef, creëerde toenemende bosontwikkeling ruimte voor nieuwe soorten. Gelijktijdig met het toegenomen contact tussen Afrika en Eurazië, tussen 20 en 5 m.j. geleden, werd Afrika droger en ontstonden de huidige savanne en de Sahara.



Figuur 7. (A) Gecombineerde verspreiding van Sapho- *en* Umma-*beekjuffers. Grijswaardes en cijfers geven het aantal soorten dat samen voorkomt weer. Hun voorkomen is een goede weergave van de verspreiding en diversiteit van de bosfauna van Centraal- en West-Afrika, omdat ze stromend water in bos bewonen. Twee soorten zijn geïsoleerd in Angolese en Oost-Afrikaanse hooglanden.*
(B) Verspreiding van Zygonoides. *Drie soorten bewonen bewegend water in open landschappen op Madagaskar en het vasteland, een vierde komt alleen op zeer grote rivieren in het bosgebied voor.*

De heersende opvatting was dat bosfragmentatie gedurende droge periodes in het Pleistoceen en daarvoor leidde tot de versnippering van populaties van plant- en diersoorten, die zich in isolatie tot een groter aantal soorten konden ontwikkelen. Savannes werden tijdens nattere periodes opgedeeld. Er is weinig direct bewijs voor zulke biotooparchipels; bosfragmenten konden bijvoorbeeld langs rivieren verbonden blijven. Bovendien zijn de zogenaamde bosrefugia vooral plaatsen waar oudere soorten overleven, niet waar nieuwe ontstaan. Dat laatste gebeurt in afwisselende landschappen, zoals gebergtes en overgangen van bos naar savanne, vooral waar aan de rand van refugia een breed aanbod is van vooroudersoorten. Dit komt tegenwoordig voor in het grensgebied van Kongo en Zambia. Hier is een hoog endemisme van in Afrika dominerende geslachten. Vergelijkbare situaties waren in drogere periodes aanwezig in het nu geheel beboste Kongobekken en in nattere periodes in nu dorre delen van de oostelijke hooglanden. Fylogenetisch onderzoek geeft aan dat soorten niet alleen in Pleistocene refugia ontstonden, maar dat ze een veel oudere en meer complexe geschiedenis hebben. Radiaties van bossoorten kwamen voort uit savannesoorten (bijvoorbeeld meerkatten, eekhoorns), en andersom (boomkikkers, genetkatten, mensen). Door klimaatsverandering ontstond telkens ecologische ruimte, die werd ingevuld door een flexibel reagerende fauna. Met de Afrikaanse uitdroging verging ook veel oude libellendiversiteit, maar een rijke nieuwe fauna kwam op in het huidige landschap van bos, savannes en gebergten.

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After obtaining an MSc in evolutionary biology, biogeography and systematics at Leiden University in 1998 (*cum laude*) I worked on African and European Odonata on a freelance basis, as research associate of the National Museum of Natural History in Leiden, The Netherlands. Since February 2007 I am curator of invertebrates at the National Zoological Collection of Suriname, where I work on the taxonomy and ecology of Neotropical Odonata.

I published almost forty peer-reviewed papers on the taxonomy and biogeography of tropical African Odonata. Research was undertaken in the museums of Berlin, Bulawayo, Brussels, London, Madrid, Nairobi, Paris, Stockholm and Tervuren and in the field in Ethiopia, Ghana, Kenya, Malawi, Mozambique, South Africa, Tanzania, Uganda and Zambia, as well as during Conservation International's RAP biodiversity assessments in Liberia, Ghana and the Democratic Republic of Congo. I shared the first Worldwide Dragonfly Association (WDA) outstanding achievement award for this work in 2005 and am completing an identification manual for eastern Africa's 470 species. As a member of the IUCN Odonata Specialist Group since 2003, I coordinated Odonata for their Freshwater Biodiversity Assessment of West Africa in 2006.

I published an English fieldguide to European Odonata (with Richard Lewington) in July 2006; French and Dutch editions will appear in 2007 and 2008. I was a member of the editorial board and co-author of the handbook of Dutch Odonata (1998-2002) and co-founded the Dutch society for odonatology (NVL) in 1997, being editor-in-chief of its journal (*Brachytron*) until 2001.

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Employment and official functions

2007-present: Curator of invertebrates of the National Zoological Collection of Suriname.
2005-2006: Invited speaker at international odonatological meetings in Freising (Germany), Pontevedra (Spain) and Hong Kong (China).
2004-2006: Editor and co-author of fieldguide to European Odonata for British Wildlife Publishing.
2004-2006: Participant of Conservation International's RAPs (biodiversity assessments) in the Democratic Republic of Congo (2004), Liberia (2005) and Ghana (2006).
2003-present: Member of the IUCN Odonata Specialist Group and coordinator of Odonata for IUCN's Freshwater Biodiversity Assessment of West Africa.
2001-present: Co-author and illustrator of eastern African Odonata identification manual, as part of German Government funded BIOTA project Biogeography, Diversity and Ecology of East African

	Odonata. The manual will be published by the Royal Museum for Central Africa, Belgium.
1998-present:	Research associate of the National Museum of Natural History in The Netherlands, where I set up a large reference collection of Afrotropical Odonata.
1998-2002:	Co-editor and co-author of the handbook of Dutch Odonata; a joint effort of the Dutch society for odonatology NVL, the youth organisation for natural history research NJN and the European Invertebrate Survey (EIS-Nederland).
1997-2001:	Member of the founding committee of NVL and first editor-in-chief of journal Brachytron and newsletter of NVL.

Publications Klaas-Douwe B. Dijkstra

Newsletters, presentations and posters are excluded. Titles between square brackets were published in Dutch, those marked with an asterisk were reproduced in this thesis. An identification manual for the Odonata of Eastern Africa is in preparation for Studies in Afrotropical Zoology, based on a revised checklist for that region (Sudan to Zimbab-we, east of 22°E, with special focus on Ethiopia, Kenya, Malawi, Tanzania and Uganda). Both publications are with V. Clausnitzer and are scheduled for 2007. Revisions and reviews are in preparation for the following Afrotropical Odonata: some Chlorocyphidae, Coenagrionidae formerly placed in *Enallagma* (with M.L. May), lindeniine Gomphidae, *Notogomphus* and *Aethiothemis* (including *Lokia*). Faunal overviews are planned for the Congo Basin and several West African nations.

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NVL (Editors: **Dijkstra, K.-D.B.**, V.J. Kalkman, R. Ketelaar & M.J.T. van der Weide), 2002. [The Dutch dragonflies (Odonata)]. Nederlandse Fauna 4. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey-Nederland. 1-440. Chapters:
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- Bos, F., **K.-D.B. Dijkstra**, J.T. Hermans & D. Groenendijk. [Ecology and behaviour]. 27-42.
- **Dijkstra, K.-D.B.** [Diversity and nomenclature]. 43-60.
- **Dijkstra, K.-D.B.** & W.-J. Hoeffnagel. *Aeshna grandis*. 236-238.
- Delft, J. van & **K.-D.B. Dijkstra.** *Sympetrum flaveolum*. 361-364.
- **Dijkstra, K.-D.B.** *Sympetrum fonscolombii*. 365-368.
- Delft, J. van & **K.-D.B. Dijkstra.** *Sympetrum sanguineum*. 374-376.
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- **Dijkstra, K.-D.B.** *Sympetrum vulgatum*. 380-382.

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