

chapter 8

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

Platynemidine damselflies constitute an important element of both Madagascar and continental African forest faunas (Fig. A), and although both groups are traditionally placed in the genus *Platynemis*, 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).

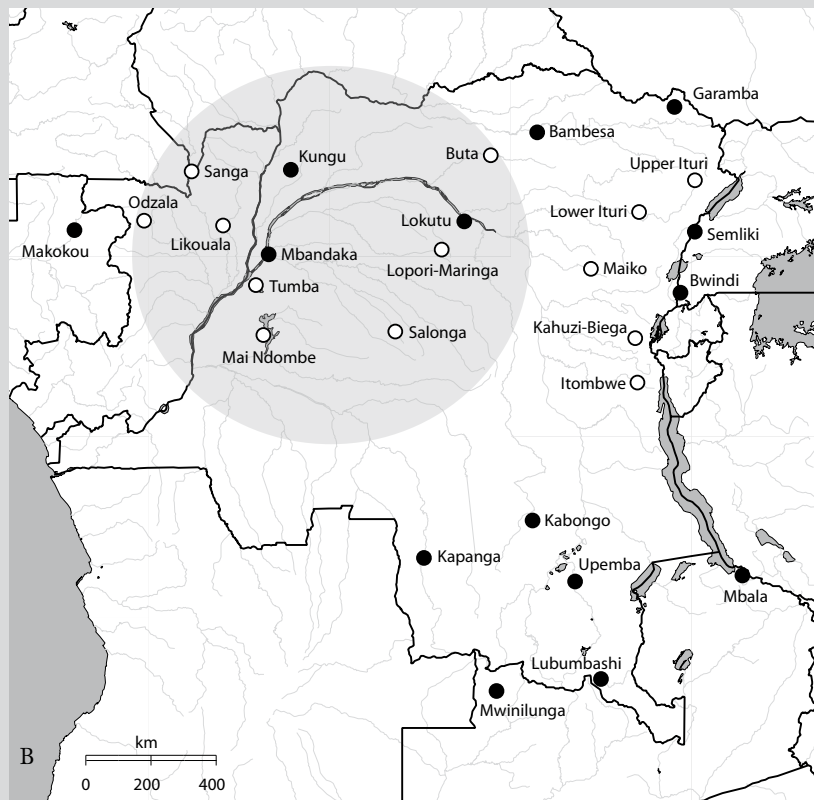
The Congo Basin is a centre of odonate diversity as ever-shifting rivers, swamps, forests, woodlands and savannas create an enormous mosaic of prime

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 high-

lands 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.

Fig. A Distribution of Afrotropical *Platynemis*. 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 archaic 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 led 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 led 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 Afro-

tropical 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 Palearctic 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).

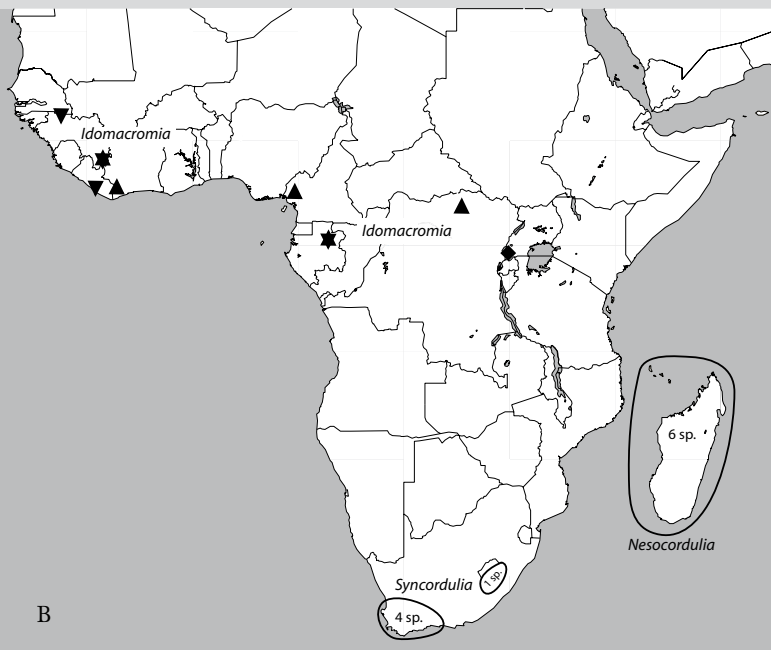
Comparison of tropical odonate diversity. Data from Kalkman *et al.* (2007) and the appendix.

family	Neotropics		Afrotropics		Oriental	
	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: Platynemididae; 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).



B

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 *Pentaplebia* 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 *Platygypha* (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: *Platygypha*, *Africallagma*, *Pseudagrion*, *Proischnura*, *Allocnemis*, *Elattonneura*, *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 *Platygypha*, *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, *Platygypha amboniensis* remains between 1500 and 2000m, *Notogomphus maathaia* between 2200 and 2600m, and only *Pseudagrion bicocerulans* and *Atoconeura kenya* occur up to and occasionally slightly over 3000m. *P. bicocerulans* 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*, *Thermothemis*, *Viridithemis*) or to distinct radiations of *Nesolestes* (see appendix under *Neurolestes*), *Platycnemis*, *Pseudagrion*, *Malgasophlebia* 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, <i>Aciagrion</i> and <i>Ischnura</i> shared
<i>Pseudagrion</i> A-group	41	-	many in genus, probably not related
<i>Pseudagrion</i> B-group	22	2 endemic	many in genus, probably closely related
<i>Allocnemis</i> and <i>Chlorocnemis</i>	17	-	none known
Protoneuridae	23	-	many, <i>Elatoneura</i> and <i>Prodasineura</i> shared
lindeniine Gomphidae**	13	-	many, <i>Gomphidia</i> and <i>Ictinogomphus</i> shared
<i>Neurogomphus</i>	17	-	none known
<i>Notogomphus</i>	17	-	many, but genus not shared
Macromiidae	35	1 endemic in shared genus	many, but no shared genera

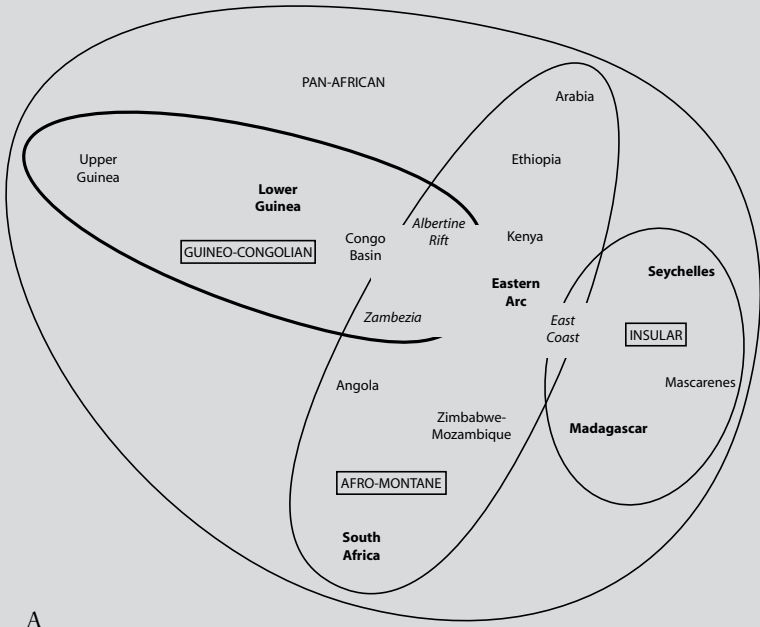
* *Aciagrion*, *Africallagma*, *Azuragrion*, *Ischnura*, *Pinheyagrion* and *Proischnura*

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

part of the same fauna, as shown by endemic species in the Madagascan complexes of *Nesolestes*, *Platycnemis*, *Pseudagrion*, *Nesocordulia* and *Thermothemis* (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 lefebvreii*, *Orthetrum trinacria*, *Palpopleura lucia*, *Pantala flavescens*, *Rhyothemis semihyalina*, *Tetrathemis polleni*, *Tholymis tillarga*, *Tramea*

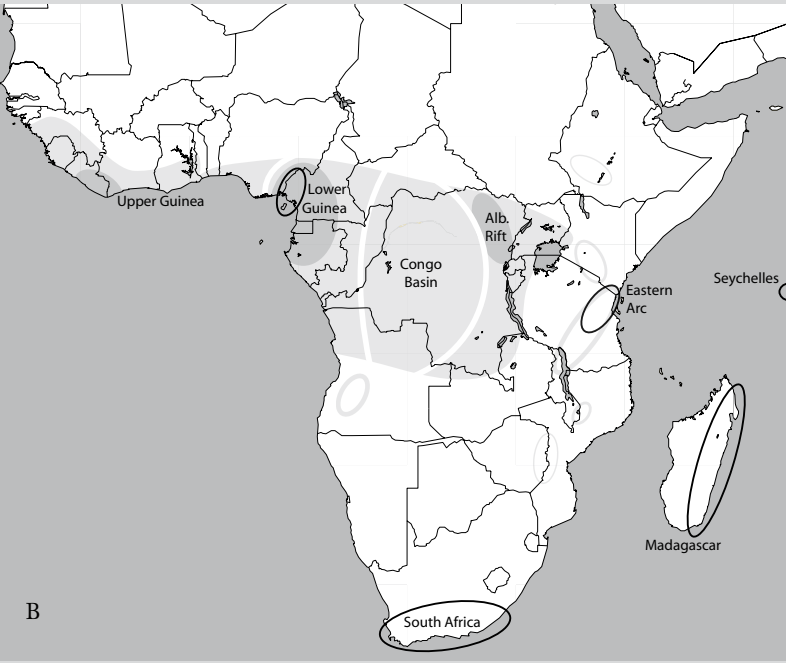


A

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).



B

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

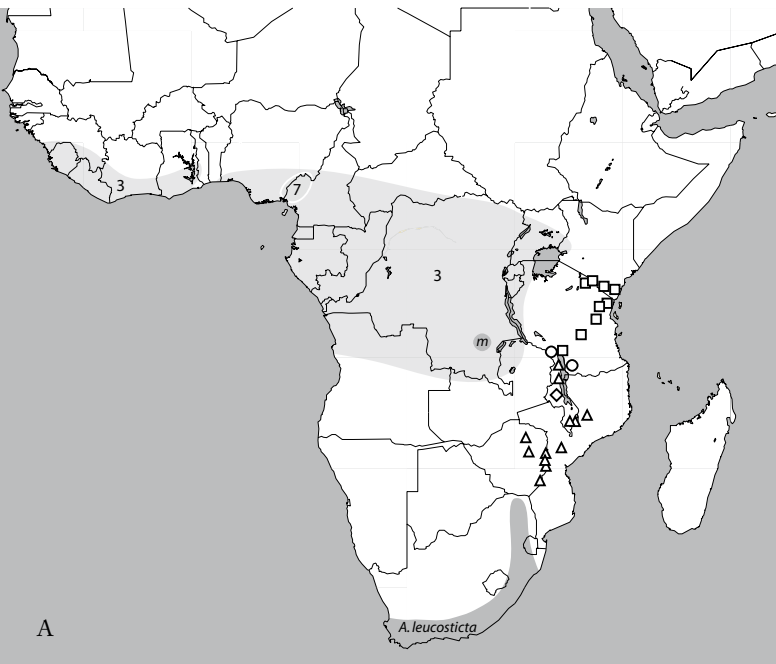
The Gondwana problem

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

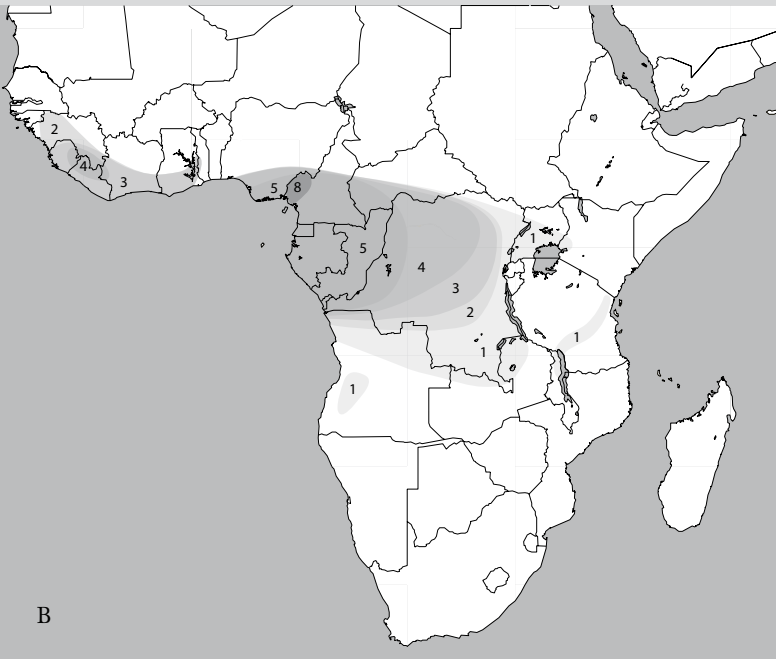
Africa and Madagascar began 155-170 Ma, and the island came to occupy its present isolated position 120-121 Ma, separating from India 83-89 Ma. The Seychelles block split from India 65 Ma (Daniels *et al.* 2006; Masters *et al.* 2006; Sanmartín & Ronquist 2004). However, the significance of this scenario for contemporary 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 led to the revival of dispersal (de Queiroz 2005; McGlone 2005) and terrestrial corridors (*e.g.* Fuchs *et al.* 2006; Jönsson & 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 *Pentaplebia* 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 *Pentaplebia* 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



A



B

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 Jönsson & 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 Afro-tropical 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 *Tragomphus*.

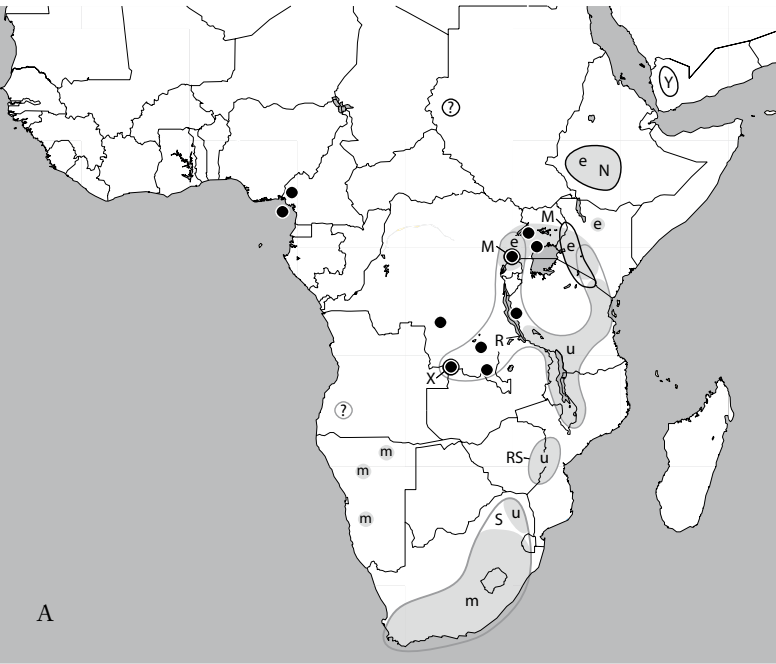
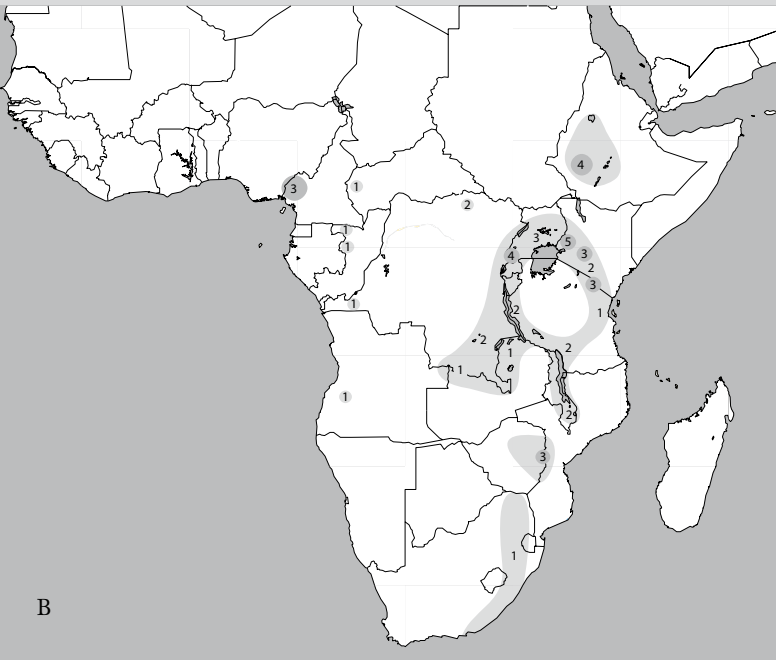


Fig. A Distribution of Afrotropical *Aeshna* species. Legend – filled circles: *A. scotias* (includes *A. wittei*); shading: *elliotti*-group (e: *A. e. elliotti*; u: *A. e. usambarica*; m: *A. minuscula*); outlines: *rileyi*-group with northern (black – M: *A. meruensis*; N: unnamed species; X: *A.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



A

B

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 archaic 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 *elliotti*-group occur locally within the range of the *rileyi*-group and are strictly allopatric. Records of *A. scotias* (including *A. witteii*) 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 *Ataconeura* (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 Afro-tropical 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 Afro-tropical affinities, with the exception of 25–26 Ma old wings associated with *Sapfo* 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*, *Elatoneura*, *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 supports 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 *Elatoneura* and *Prodasineura* species, which occur predominantly in African and Asian rainforests. *Arabincnemis 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. fueleborni*; 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).



A

B

of forest refuges and if, how, when and where they functioned as centres of speciation or species preservation. Besides speciation, change will have led 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 groups 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. oc-*

cidentis, 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 inter-

mediates 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.

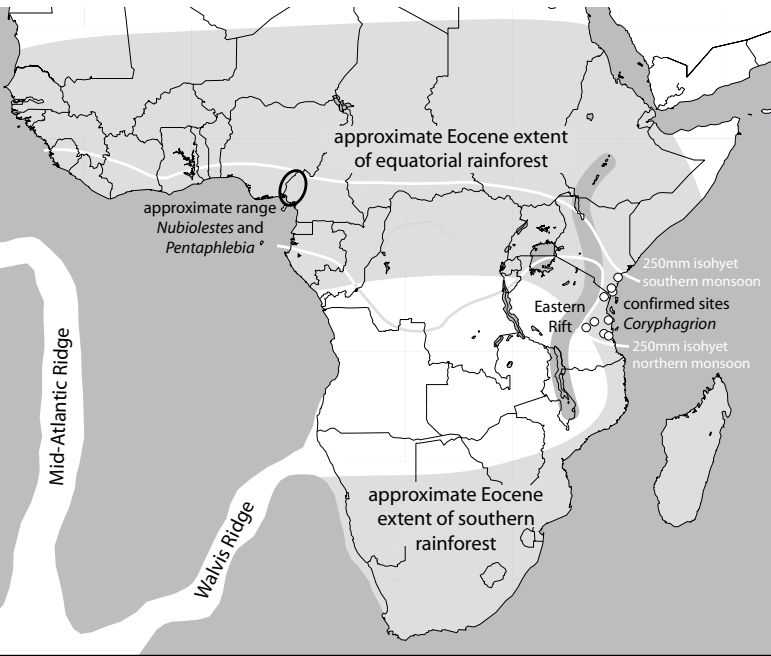
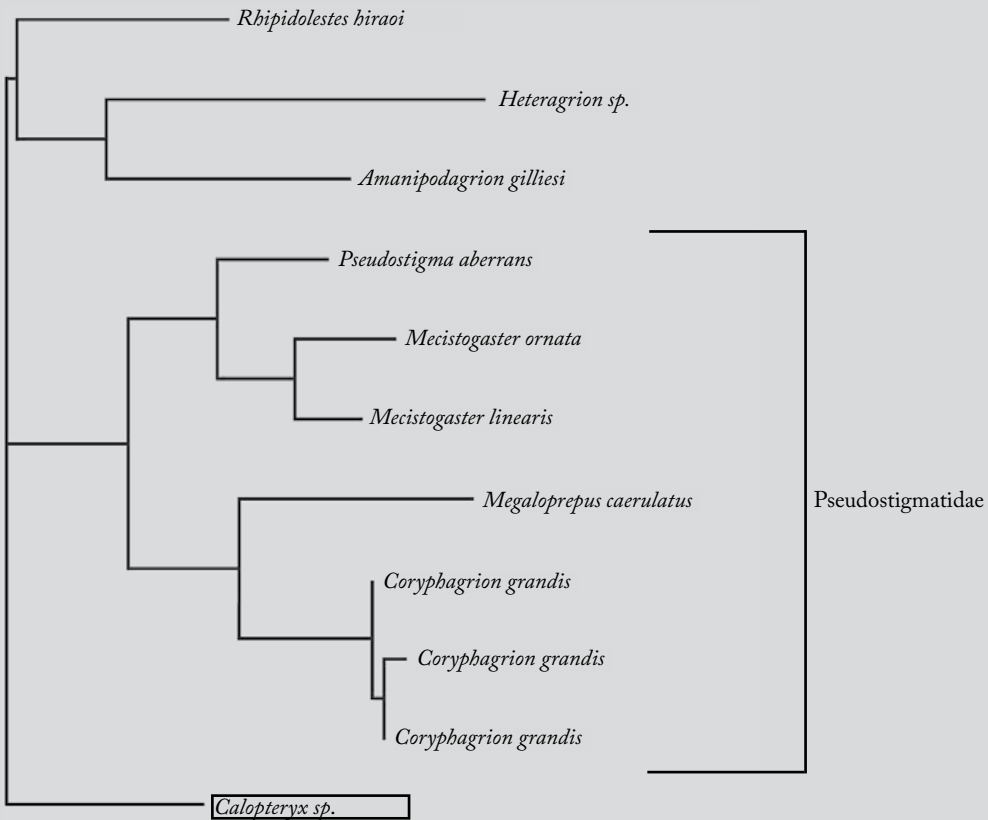


Fig. A Biogeographic hypothesis for *Coryphagrion*. The pale shading represents the approximate extent of rainforest during the Eocene, the dark shading the zones of uplift in the Eastern Rift Valley. The area between the two thin lines receives >250mm of rain during both halves of the year.

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 equa-

torial 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 (Fjelds  & 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 time-frame 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).

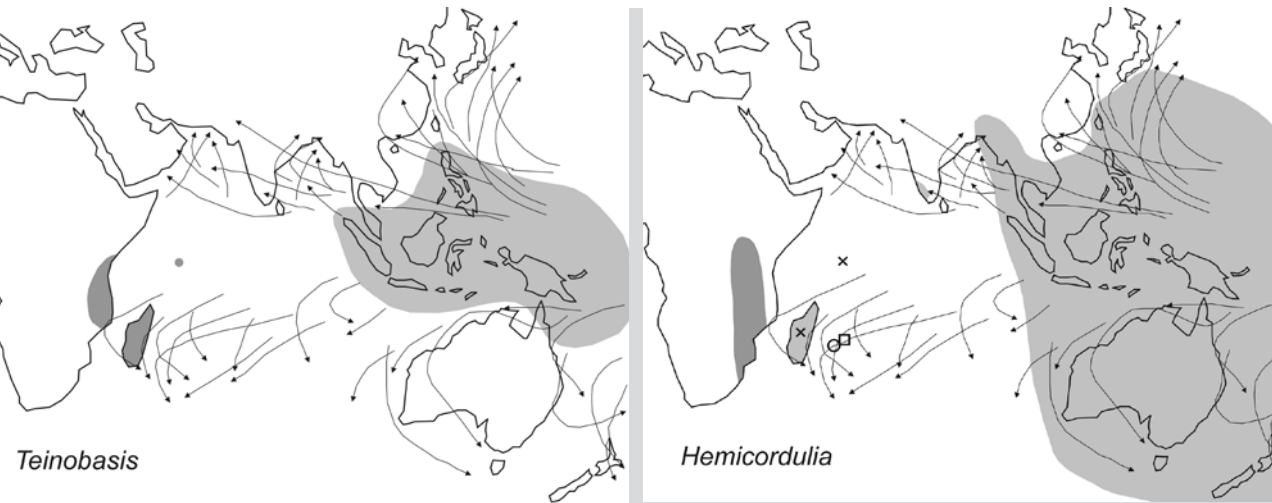


Fig. A Distribution of *Teinobasis* and *Hemicordulia* (including the closely related *Procordulia*). Arrows indicate the courses of summer storms. Legend *Teinobasis* – pale shading: main range in Australasia and Pacific; dark shading: *T. alluaudi*. Legend *Hemicordulia* – pale shading: main range 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: *Platynemesis* 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 (lake-

shores, 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 *Platynemesis* 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 Fjelds  (1994) and Fjelds  & 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 Fjelds  (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 Schilthuisen 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 (Fjelds  & Lovett 1997; Moritz *et al.* 2000; Nicolas *et al.* 2006). Radiations of mountain and savanna birds took place in the Plio-Pleistocene (Fjelds  1994; Fjelds  & 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; Fjelds  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-

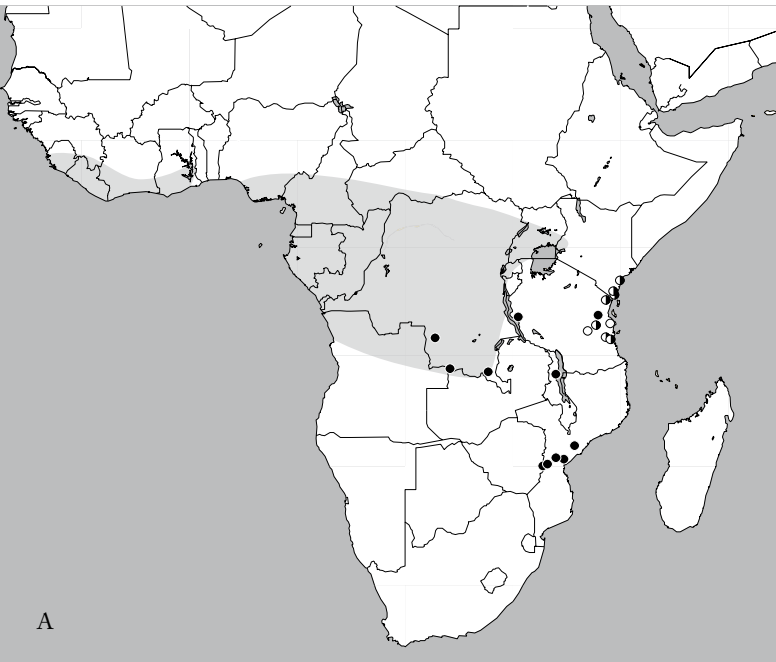
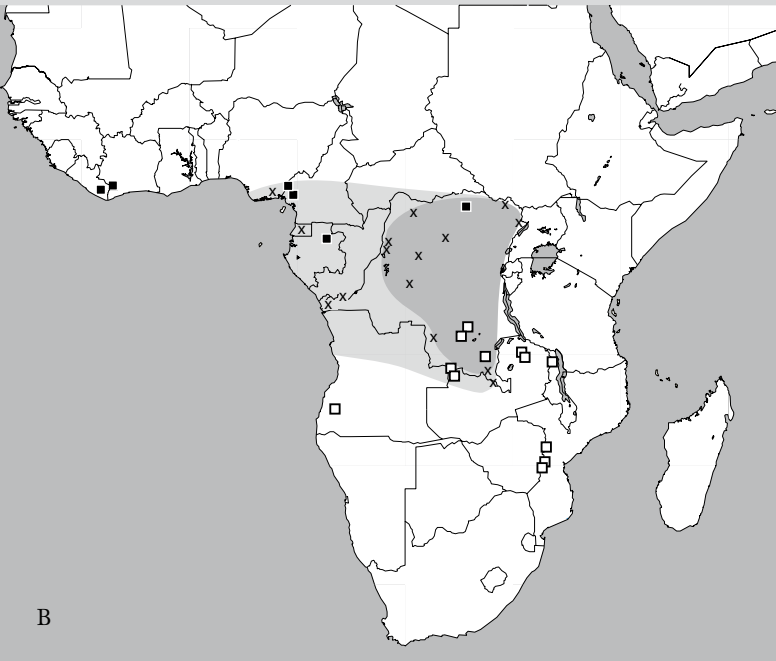


Fig. A Distribution of dendrolimnetic Afrotropical Odonata. Legend – open circles: *Coryphagrion grandis*; filled circles: *Hadrothemis scabrifrons*; halved circles: both species; shading: *H. camarensis*.

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).



A

B

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 *Thermothemis* 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 (Opell 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.

dedicated 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 ra-

diation 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 swamps 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 successful 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 promi-

nent centre of overlooked bird diversity in Fjelds s’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 *Pinbeyagrion*, 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) palus-

trine 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 atritribiae*. 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

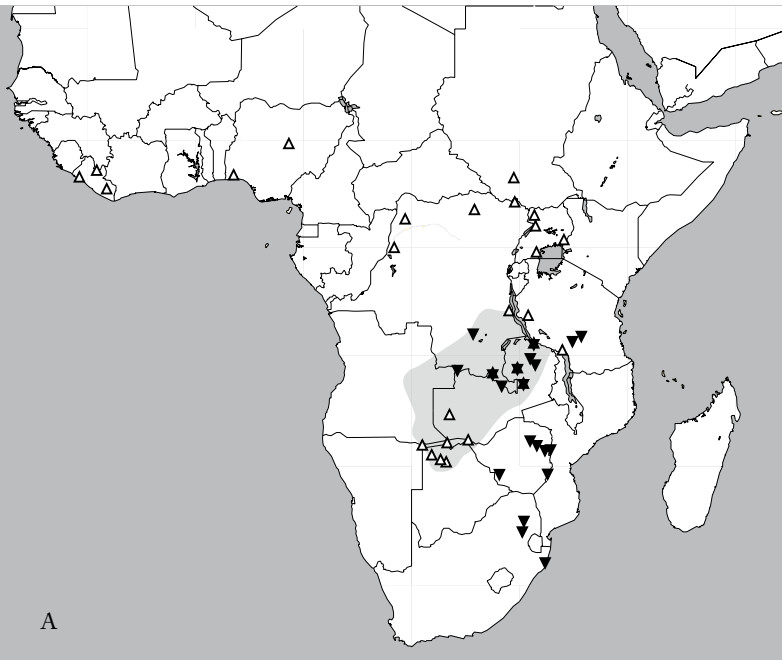
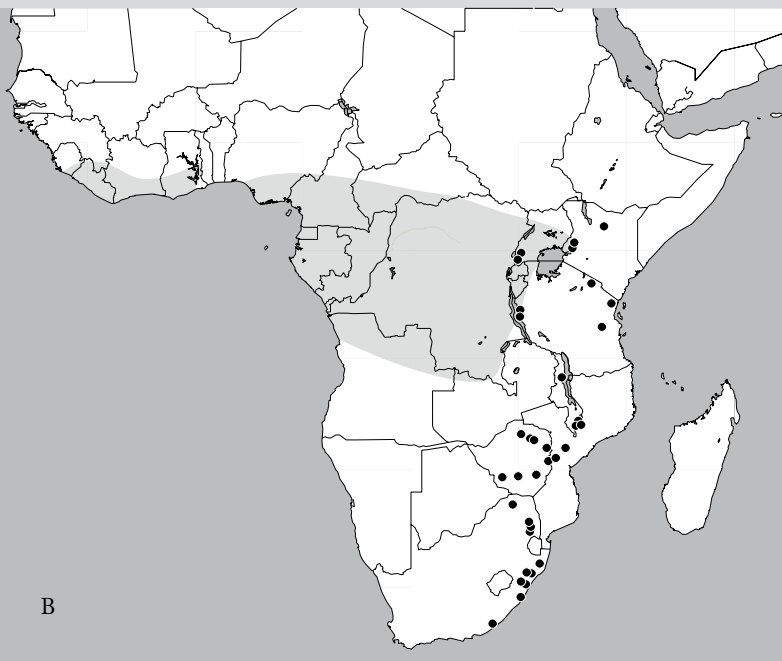


Fig. A Distribution of small continental African *Diplacodes* species and the Paleo-Chambeshi region. Note the concentration of *D. diminuta* in the large swamps in the north and south of the region and that of *D. pumila*, which generally inhabits smaller and more elevated swamps, in the north. Legend – open triangles: *D. diminuta*; 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*.



(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).

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



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 (Fjelds  1994; Fjelds  & 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". Fjelds  (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 pre-

montane 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 Zaire [= 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 Fjelds  (1994) concluded that the whirlpool "appears to have been quiet in the Pleistocene". This may apply to birds, but probably not Odonata.

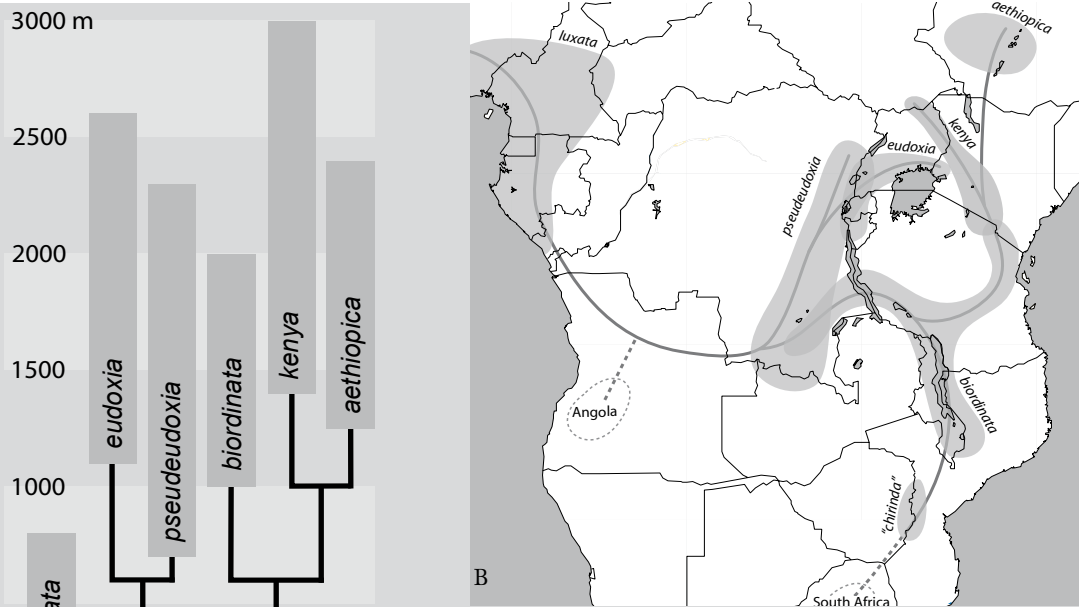
Synthesis: the demise and rise

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 con-

stantly 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 reacti-

vation 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 habi-

tat 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 sub-

sequent 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 rea-

sons 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 its 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.

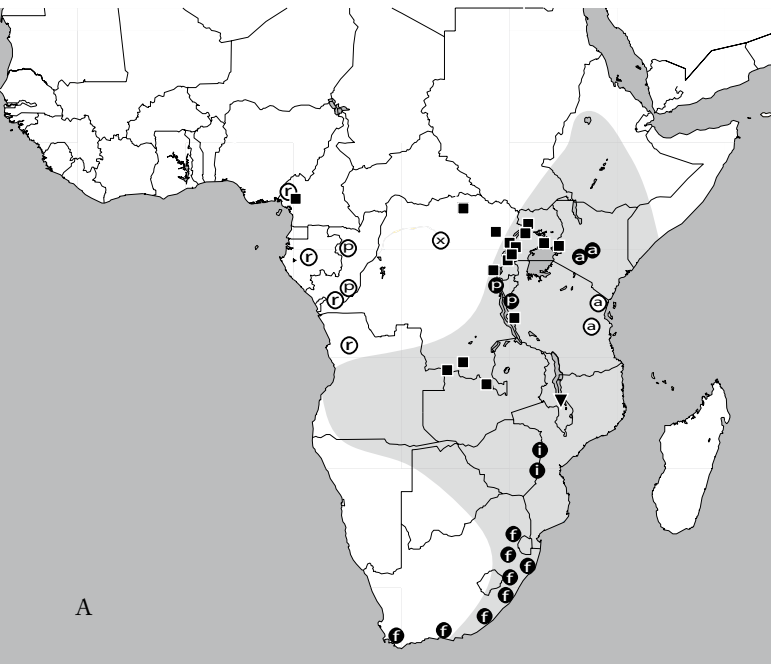
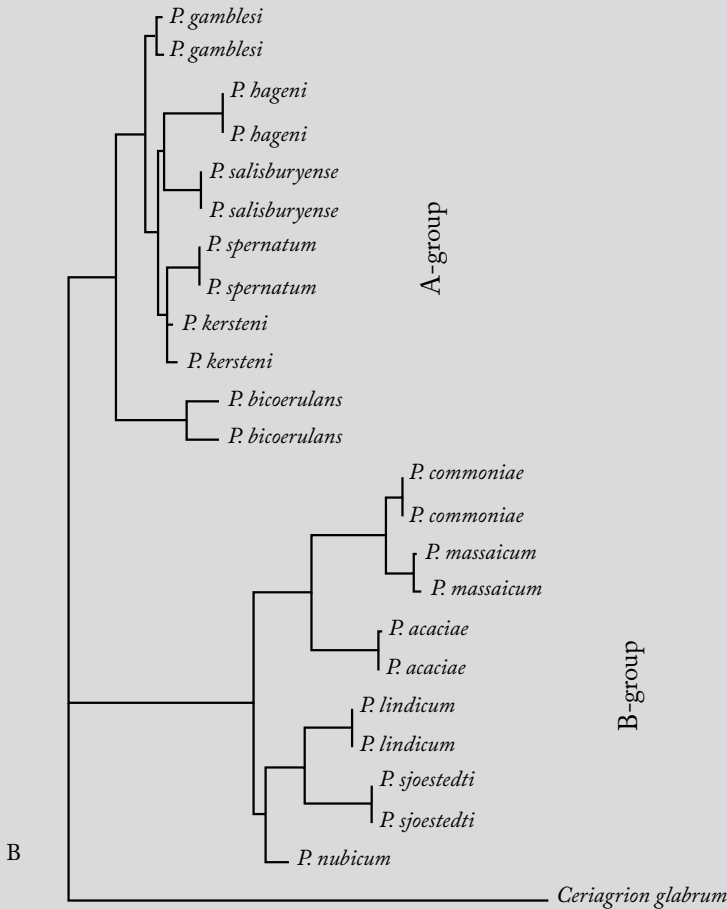


Fig. A Distribution of *Platycypha* species. Legend – open circles: lowland relict species (a: *P. auripes*; p: *P. picta*; r: *P. rufitibia*; x: undescribed species); filled circles: sub-montane relict species (a: *P. amboniensis*; f: *P. fitzsimonsi*; i: *P. inyangae*; p: *P. pinheyi*); squares: *P. 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).

A



B

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; Schilthuisen 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 ecotone, 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*, *Pinbeyagrion* 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).

no. – Minimum estimate of number of valid species (*: at least one undescribed species known to the author).

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

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				
<i>Pentaplebia</i>	Förster, 1909	2	cm	
Calopterygidae				
<i>Phaon</i>	Selys, 1853	2	Pm	Dijkstra in prep. c (2)
<i>Sapbo</i>	Selys, 1853	6	GC	
<i>Umma</i>	Kirby, 1890	9	GC*	[* 1 sp. in ml-tn; 1 Angola] Dijkstra in prep. c (1)

Chlorocyphidae

<i>Africocypha</i> Pinhey, 1961	1	cm	Dijkstra 2007b (1)
<i>Chlorocypha</i> Fraser, 1928	32'	GC*	[* 1 sp. to AM] Dijkstra 2003b (4); Dijkstra 2007b (+10); Dijkstra in prep. a (+8)
<i>Platycypha</i> Fraser, 1949	10	AM*	[* 4 sp. to cm] Dijkstra in prep. a (10)

Lestidae

<i>Lestes</i> Leach, 1815	14	[Pm]	
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Perilestidae

<i>Nubiolestes</i> Fraser, 1945	1	cm	
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Synlestidae

<i>Chlorolestes</i> Selys, 1868	7	sa*	[* 1 sp. to ml]
<i>Ecchlorolestes</i> Barnard, 1937	2	sa	

Megapodagrionidae

<i>Allolestes</i> Selys, 1868	1	sc	
<i>Amanipodagrion</i> Pinhey, 1962	1	tn	
<i>Neurolestes</i> Selys, 1882	18'	md*	[* 2 ⁺ sp. in cm]
<i>Protolestes</i> Förster, 1899	8	md	
<i>Tatocnemis</i> Kirby, 1889	10	md	

Pseudostigmatidae

<i>Coryphagrion</i> Morton, 1924	1	ec	Clausnitzer & Lindeboom 2002; Groeneveld <i>et al.</i> 2007 (1)
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Coenagrionidae

<i>Aciagrion</i> Selys, 1891	14	[Pm]	Dijkstra 2007b (6)
<i>Africallagma</i> Kennedy, 1920	11	Pm	May & Dijkstra in prep. (11)
<i>Agriocnemis</i> Selys, 1869	17	[PI]	Dijkstra 2007b (3); Dijkstra in prep. c (+3)
<i>Azuragrion</i> May, 2002	6	Pm*	[* 1 sp. to Arabia] May & Dijkstra in prep. (6)
<i>Ceriagrion</i> Selys, 1876	19	[PI]	Dijkstra 2005c (15); Dijkstra 2007e (erratum)
<i>Coenagriocnemis</i> Fraser, 1949	4	ms	
<i>Ischnura</i> Charpentier, 1840	5	[PI]	Clausnitzer & Dijkstra 2005a (2)
<i>Pinheyagrion</i> May, 2002	1	zm	May & Dijkstra in prep. (1)
<i>Proischnura</i> Kennedy, 1920	3	AM*	[* 1 sp. to Nigeria] May & Dijkstra in prep. (3)
<i>Pseudagrion</i> Selys, 1876	41	[PA]*	[* to Levant and Arabia] Dijkstra 2002 (1); Dijkstra 2007b (+5); Dijkstra in prep. c (+2)
	24	[PI]*	[* to North Africa and Arabia] Dijkstra 2002 (1); Dijkstra 2007b (+1)
	31	md	
	2	GC	
<i>Teinobasis</i> Kirby, 1890	1	[IN]*	[* 1 sp. to ec] Dijkstra 2007b

Platycnemididae

<i>Allocnemis</i> Selys, 1863	2	sa*	[* 1 sp. in Katanga] Dijkstra 2007b (1)
<i>Chlorocnemis</i> Selys, 1863	15*	GA	Dijkstra 2007b (5); Dijkstra in prep. c (+1)
<i>Leptocnemis</i> Selys, 1886	1	sc	
<i>Mesocnemis</i> Karsch, 1891	5	PA	Dijkstra in prep. c (3)
<i>Metacnemis</i> Selys, 1863	3	sa*	[* 1 sp. in md] Samways & Tarboton 2006 (1)
<i>Oreocnemis</i> Pinhey, 1971	1	ml	Dijkstra 2007b (1)
<i>Paracnemis</i> Martin, 1902	1	md	
<i>Platycnemis</i> Burmeister, 1839	5	GC	Dijkstra <i>et al.</i> 2007a (5)
	11*	md*	[* 1 sp. on Pemba] Dijkstra <i>et al.</i> 2007a (1)
<i>Stenocnemis</i> Selys, 1886	1	cm	

Protoneuridae

<i>Elatoneura</i> Cowley, 1935	18'	[PA]	Dijkstra 2007b (2); Dijkstra in prep. c (+4)
<i>Prodasineura</i> Cowley, 1934	5	[GC]	Dijkstra 2007b (1)

ANISOPTERA**Aeshnidae**

<i>Aeshna</i> Fabricius, 1775	2	AM	
<i>elliotti</i> -group	4*	[AM]*	[* 1 sp. in Arabia] Clausnitzer & Peters 2003 (3); Dijkstra 2007a (+1)
<i>rileyi</i> -group	1	GC	
<i>scotias</i> -group	1	[Pm]	
<i>Anaciaeschna</i> Selys, 1878	1	[PI]	
<i>Anax</i> Leach, 1815	11	[PI]	



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

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

Taxonomic priorities for Afrotropical odonatology per family.

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

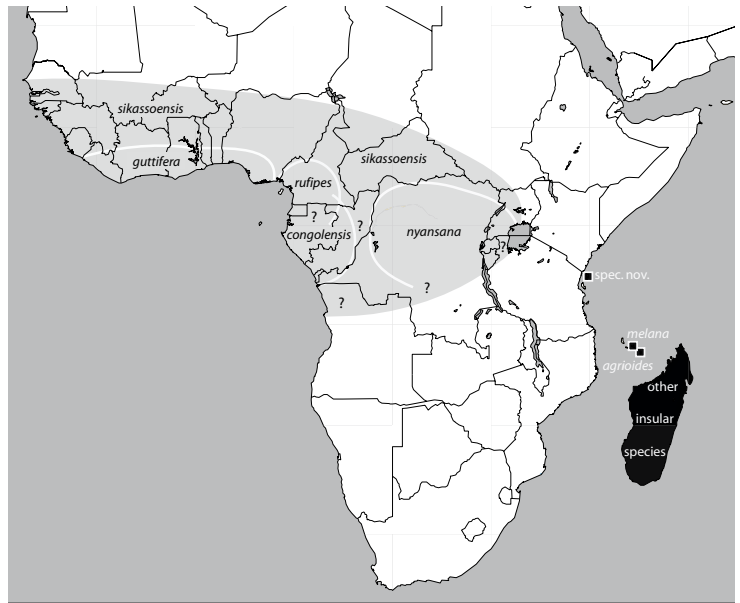
merken van de vleugeladering. Aderkenmerken zijn gemakkelijk te kwalificeren en kwantificeren, maar zijn relatief plastisch en zeggen mogelijk meer over bijvoorbeeld het vliegvermogen van een soort dan over zijn verwantschappen. Om bovenstaande redenen zijn veel soorten en geslachten van Afrikaanse libellen 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 km²), 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 14^e 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 km² groot en herbergt maar één beek.

Hoofdstuk 3. *Pseudagrion* gesplitst: moleculaire fylogenie bevestigt de morfologische en ecologische tweedeling van Afrika's soortenrijkste libelengeslacht (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. Eenenvertig 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 gradiëerd 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



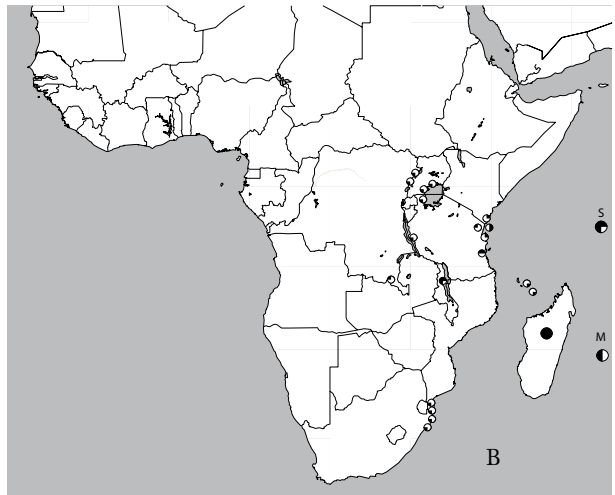
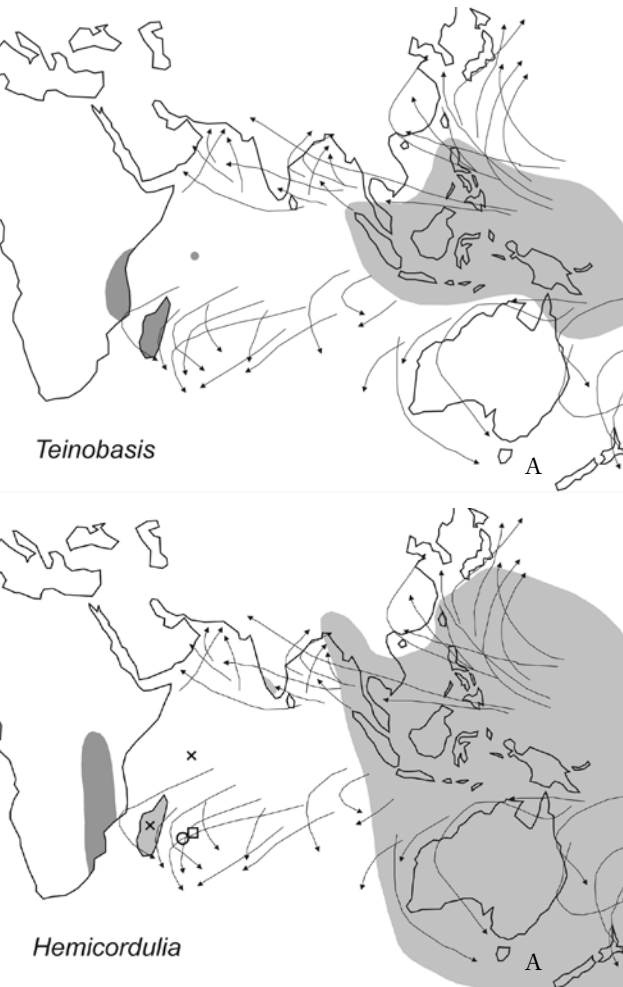
zich uitbreiden in warmere biotopen die onbezeten waren gebleven. Onderzoek van meer soorten, ook uit Madagaskar en Australazië, moet leiden tot een beter beeld van de geschiedenis van *Pseudagrion* en de relatie met de klimatologie en geologie van Afrika.

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 vlerhonden. 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 weergegeven, 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 *Platygnemis* (Hoofdstuk 2). De grotere cirkels geven het voorkomen aan in Madagaskar, de Maskarenen (M) en de Seychellen (S) (beide ten oosten van de marge).

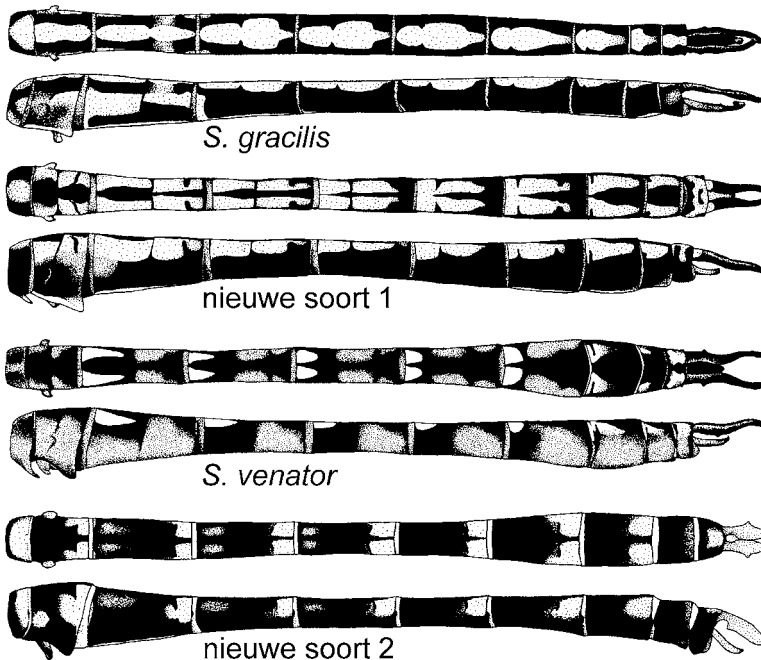
makkelijken. Gezien het voorkomen van een geschikte luchtcirculatie en de vaak geringe verschillen tussen de besproken soorten, is het aannemelijk dat dispersie die tot soortvorming leidt nog altijd plaatsvindt. Schattingen op basis van het moleculaire klok model geven aan dat salanganen, parkieten, 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 eilandsorten 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 relicttaire *Syncordulia* soorten gevonden tijdens museum- en veldonderzoek van bedreigde libellen in de Kaapregio (Odontata: 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.

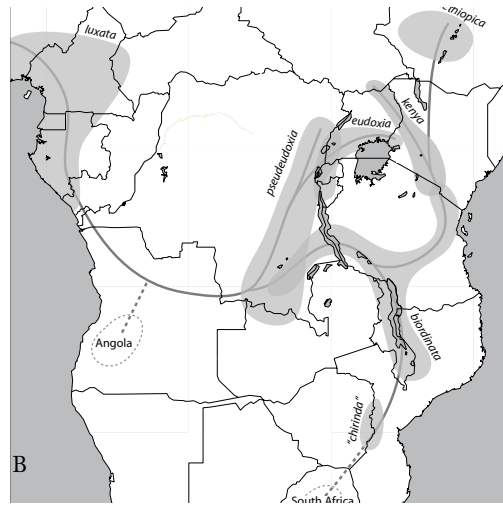
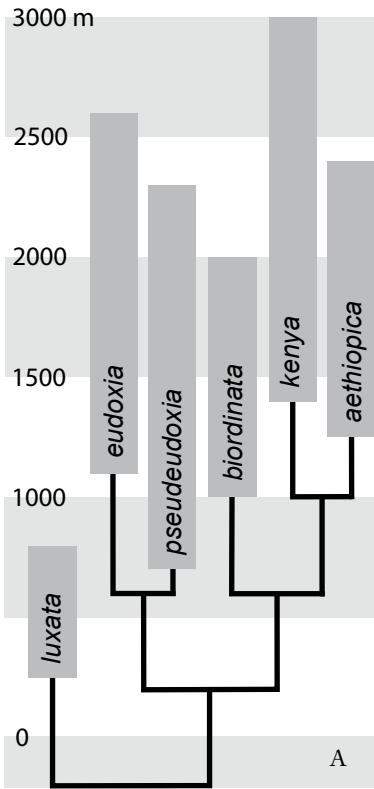
Hoofdstuk 6. Taxonomie, fylogenie and biogeografie van *Atoconeura*, een libellengeslacht in de hooglanden van Afrika (Odonata: Libellulidae).

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 verschaftte 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 burens 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 Kongo-bekken 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 regenwoud 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*.

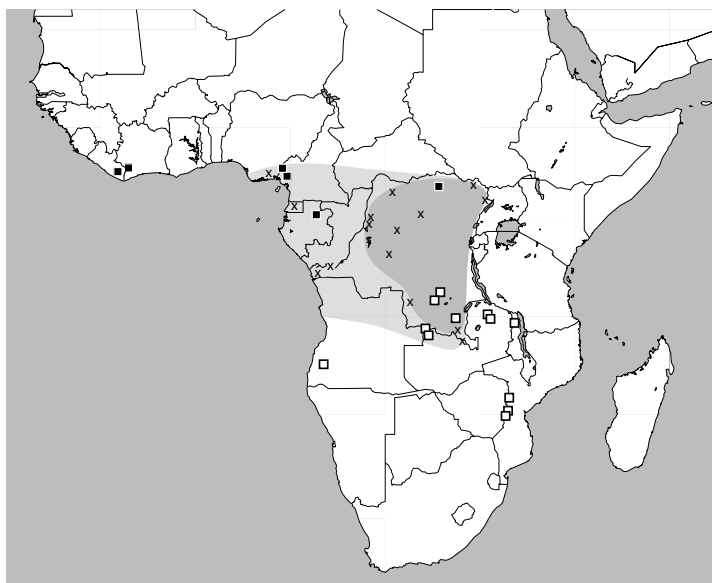
fauna en -flora, en van *Atoconeura* in het bijzonder, lijkt fasen te weerspiegelen waarin geschikte biotoop vrijkwam, gevolgd door snelle kolonisatie, adaptatie en verdere uitbreiding. *Atoconeura* is niet bekend in Angola, waar mogelijk onvoldoende is verzameld, en Zuid-Afrika, waar veel soorten meer 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 Afrikamu-

seum 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.

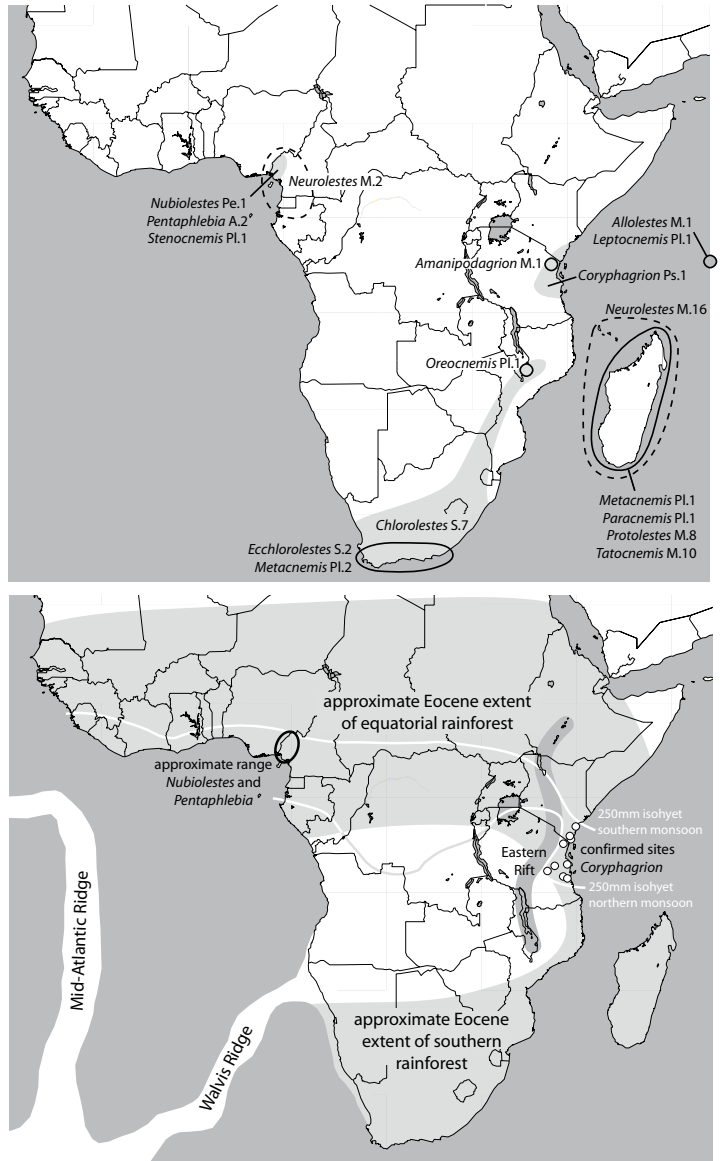
Hoofdstuk 8. Vergaan en verrijzen: de taxonomie en biogeografie van de Odonata van tropisch Afrika.

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 relictten 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 relictten met Amerikaanse verwanten zich al in Kameroen bevonden toen Afri-

ka 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).

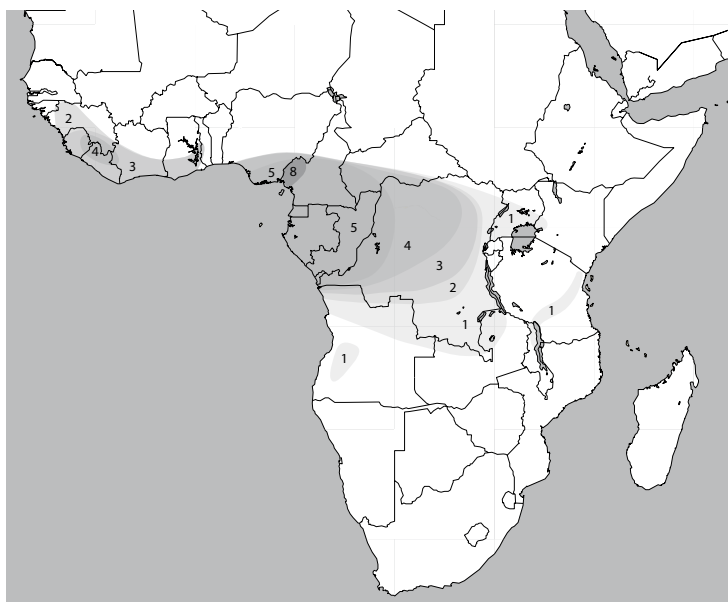
De meeste Afrikaanse libellensoorten, ongeveer 40%, zijn gebonden aan het Centraal- en West-Afrikaanse bosgebied (Hoofdstukken 2 en 7). Het restant komt in drie vrij gelijke delen voor in het hooggelegen gebied van Jemen tot de Kaap (Hoofdstukken 5 en 6), in Madagaskar en de omliggende archipels (Hoofdstukken 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 Zygotera. 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 voorplant, alleen in een smalle strook die in beide jaarhalften meer dan 250mm regen ontvangt (witte lijnen).



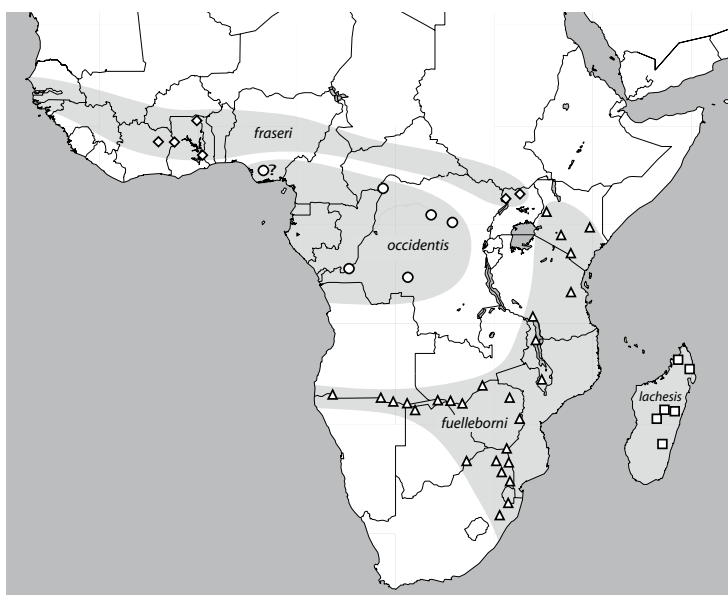
Omdat er nauwelijks fylogenetisch onderzoek is gedaan naar Afrikaanse libellen (Hoofdstukken 3 en 6), kan er weinig gezegd worden over de herkomst van de fauna en de processen die tot soortvorming hebben geleid. Uit de literatuur blijkt dat Afrika's uitwisseling van fauna met Madagaskar en Eurazië vaak 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 isola-

tie, 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.



beurt 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

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 ge-

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, genetskatten, mensen). Door klimaatsverandering ontstond telkens ecologische ruimte, die werd ingevuld door een flexibel reagerende fauna. Met de Afrikaanse uitdrijving verging ook veel oude libellendiversiteit, maar een rijke nieuwe fauna kwam op in het huidige landschap van bos, savannes en gebergten.