

Thoughts from Africa: how can forest influence species composition, diversity and speciation in tropical Odonata?

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ABSTRACT

We introduce tropical African forests and their Odonata, and speculate how climatic oscillations and associated large-scale habitat shifts may have governed speciation across the forest-savanna ecotone, presenting several hypothetical scenarios. Ecological traits of forest species and possible reasons for their disappearance when forest is opened up are discussed. We believe that low insolation in forest habitats and interspecific competition are key factors segregating forest and non-forest species. While openland species cannot cope with low insolation inside the forest, forest species have evolved a slow lifestyle to cope with the forest environment, but are out-competed by more aggressive non-forest species beyond forest borders. Casual field observations support this hypothesis, although the reality is likely to be more complex. Phylogenetic reconstruction of groups that straddle the habitat divide, linked to ecological observations, may elucidate evolutionary reactions to landscape change. The reaction of odonate assemblages to forest loss is studied easily in Africa's imperilled forests. Because many of these forests are believed to be relatively young and highly forest-adapted species may have very low dispersal capacities, comparative ecological research of 'forest-dependent' odonate assemblages inside and outside ancient forest refugia is recommended.

Key words: Afrotropical, dragonflies, forest, competition, speciation, biodiversity, biogeography

INTRODUCTION

The mechanisms which keep odonate species inside or outside forests are essential for understanding present-day distribution patterns and speciation in relation to historical landscape change. Knowledge of these mechanisms in tropical dragonflies is limited. We aim to discuss characteristics of Odonata and their habitats which may influence their distribution in the landscape (species assemblages, distribution patterns) and their development in time (speciation). Our basis is largely anecdotal, relying on our experience in tropical continental Africa, rather than on quantitative data. This paper must therefore be read as an essay of ideas, rather than an in-depth analysis of the available literature and data. Observations which we believe are supportive of our ideas are presented in text boxes. We investigate four related issues:

1. What is the geographic and historical setting of Africa's forest odonate diversity?
2. Which characteristics of forest odonates do we observe at a larger scale of time and space? Their diversity and distribution is governed by geography and history. How might patterns be explained and where did the present diversity originate?
3. Which patterns do we observe at a smaller scale? Deforestation and the replacement of indigenous vegetation by exotic species offer a means to test the role of habitat structure. Differential dispersal capacities or environmental tolerances of species further affect assemblages, providing additional 'natural experiments' which help assess interspecific effects of assemblages. Which factors determine the composition of these assemblages?
4. How can formulated hypotheses be implemented in research?

The importance of forest conservation is not addressed explicitly, but becomes obvious in the context. An overview on conservation issues of African forests is given by Clausnitzer (2003b, 2004a).

African forests

The term 'forest' is often used indiscriminately to describe dense stands of trees. White (1983, p. 44-55) defines forest, as opposed to woodland, as closed-canopy stands with a more or less complete shading of the ground, hindering the development of a grass layer (see also Clarke 2000). In considering forests of continental tropical Africa, two major categories can be distinguished, which are also represented by the distribution of forest odonates (Fig. 1). Central and

western Africa are dominated by Guineo-Congolian lowland rainforest, which is almost continuous from Uganda to Sierra Leone (Figs. 2, 3), and which has a broad transition (mainly of riverine forests) into peripheral areas. Eastern and southern Africa harbour diverse but fragmented forests, restricted to areas of higher precipitation, especially at greater elevations but also on the coast. The former is often referred to as the Afromontane archipelago (Fig. 4).

The history of tropical Africa is governed by strong climatic oscillations with associated habitat shifts across a relatively continuous land surface. "Climate is always changing, but fluctuations have been particularly marked in tropical Africa [...] during the 2.43 million years which have passed since the first major glaciation in the northern hemisphere" (Hamilton 1992). The Quarternary has seen a general trend towards increasing aridity and more pronounced oscillations. The severest recent forest contraction was 21-14,000 BP, at the height of the last major world glaciation, restricting tropical forest in Africa to a few relatively small refugia, the latest maximum extent of forest was 8-7,000 BP (Hamilton 1992).

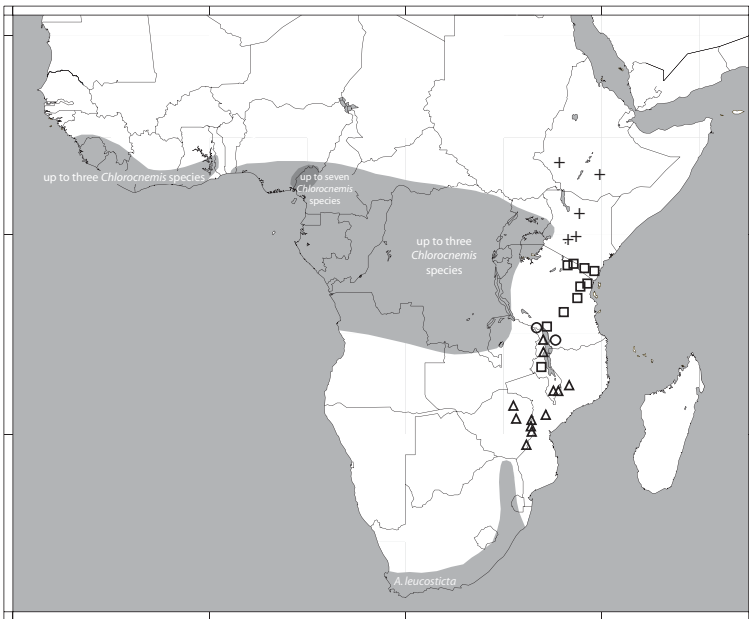


Fig. 1. Distribution of *Chlorocnemis* and *Allocnemis leucosticta*, an Afro-endemic group restricted to shaded forest habitat. *Chlorocnemis* (including *Isomecocnemis*) is widespread in the continuous forests of central and western Africa, with up to three species occurring together, although up to seven species co-exist in the Cameroon highlands. *C. abbotti* (squares), *C. montana* (circles) and *C. marshalli* (triangles) represent the genus in the Afromontane archipelago, the related *A. leucosticta* replaces it in the southernmost extent of the archipelago. Afromontane sites where representatives are apparently absent are marked with crosses.



Fig. 2. Swampy rainforest with natural glade, Budongo Forest, Viola Clausnitzer, April 1999.



Fig. 3. Rainforest of the Congo Basin, Klaas-Douwe B. Dijkstra, November 2004.



Fig. 4. Afromontane forest, Mt. Kenya, 2200 m, Viola Clausnitzer, March 1993.

African forest Odonata

As elsewhere in the tropics, the greatest diversity of Odonata in Africa is in its forests (Boxes 1-2). Most publications on Afrotropical dragonflies have a taxonomic or regional focus, giving at most only a little general habitat information (e.g. Pinhey 1970; Consiglio 1978; O'Neill & Paulson 2001). Few authors have provided more specific habitat requirements (e.g. Neville 1960; Pinhey 1984; Legrand & Couturier 1985; Lempert 1988; Miller 1993, 1995; Clausnitzer 1999; Vick 1999) and even fewer have attempted to quantify the available

information (Clausnitzer 2003a; Dijkstra & Lempert 2003). The latter task is difficult because the data are heterogeneous and often apply only to fractions of species' ranges. There are barely any studies on Afrotropical odonate larval assemblages and none comparing forest and non-forest habitats.

Box 1. Diversity of Odonata in subsaharan African

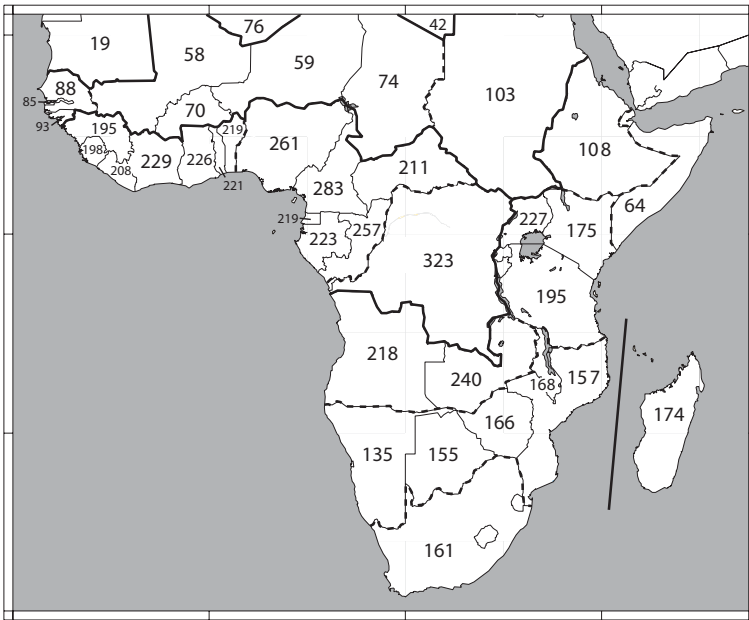


Fig. 5. Figures indicate the estimated number of species in each country, based on literature and our own data; doubtful literature records were omitted. Data are of varying quality and therefore records were interpolated: 'gaps' between countries where species occurred were filled, e.g. a species recorded from Ghana, Benin and Cameroon was also added to Nigeria and Togo. This may 'over-correct' species with truly disjunct distributions, but we believe this effect is minimal. Some smaller states were omitted for lack of data. Similarity of country faunas was established with a cluster analysis (distance measure: Sorensen; linkage method: group average). The most dissimilar groups of countries are separated by solid lines, less dissimilar groups by dashed lines, revealing three main regions of diversity: *Madagascar* and the *southern and eastern countries* are both regions where national diversity generally lies between 100 and 200 species. The greatest diversity (generally over 200 species per country) is found in the *western and central countries* (compare Fig. 1). The Sahel countries have impoverished faunas, mostly with fewer than 100 species per nation. In northern Africa (largely not on map) Afrotropical influence decreases further and Palearctic species predominate.

Box 2. Correlations between distribution and habitat preference in eastern African dragonflies

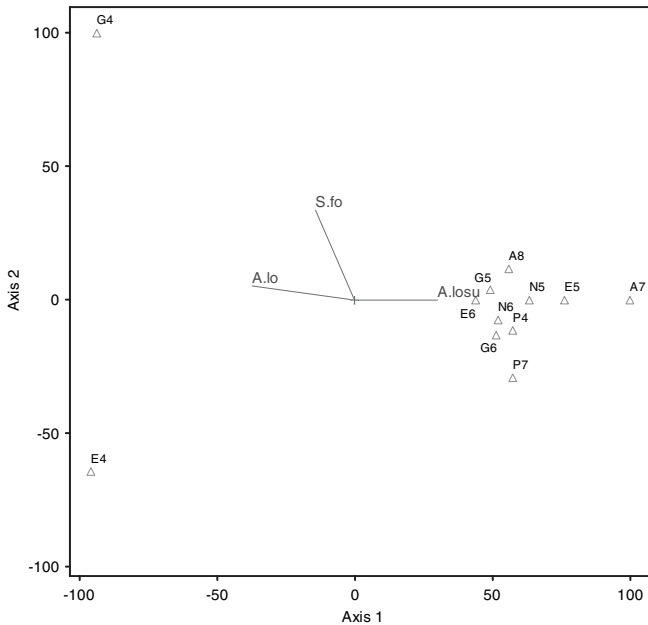


Fig. 6. The distributions and habitat requirements of 467 species of eastern African dragonflies (the area from Sudan to Zimbabwe, east of 22°E) were analysed to assess general correlations of biogeography and ecology. The information on habitat requirements is based on literature surveys (mainly Pinhey 1984; Lempert 1988; Vick 1999) and personal experience. Since this is unsatisfactory for many species, we have used a coarse classification of habitats and ranges. Habitat parameters used were current (running; standing; 2), insolation (shady; sunny; 3), size (small; large; 1), aquatic vegetation (present; absent; 1), landscape (forest; open; 3) and altitude (lowland; montane; 4), extreme values and the number of intermediate value recognised are indicated in brackets. Distribution parameters used to categorise the ranges of eastern African dragonflies are provided in the figure legend. Only one value can be assigned to each species for each parameter. A Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) was performed with distribution as main matrix and habitat parameters as secondary matrix. The species distributions were mainly explained by the habitat parameters forest cover and altitude, although even these vectors were not strong (Axis 1 describes 26% and Axis 2 11% of the variance). Most range types grouped together along the lowland and submontane vector. This is not surprising, as few African dragonfly species are montane. The only disparate range types were G4, characterised by numerous western

and central Africa forest species confined to the Congo basin in eastern Africa, and E4, which contains endemics of the highlands and coastal forest of eastern Africa. A Mantel Test was performed to test for the similarity of the distribution and habitat parameter matrices. The result (randomisation, Monte Carlo Test) shows a significant positive association ($p=0.001$) between the two matrices (observed z slightly greater than average z from randomised runs), but still the similarity is quite low ($r=0.08026$).

Legend. – S.fo: forest cover; A.lo: lowland (0-1000 m a.s.l.); A.losu: lowland and submontane (0-2000 m a.s.l.); A: widespread in Afrotropics (A7: endemic; A8: not endemic); peripheral, predominantly with Asian affinities (P4: Sahara and Arabia; P7: widespread in Asia, just reaching Africa); E: eastern and southern Africa (E4: Angola, NE South Africa to SE Kenya; E5: as previous and to Uganda and E DRC; E6: as previous and to Ethiopia and Sudan); G: centred on Guineo-Congolian biome (G4: western Africa to Congo Basin; G5: as previous and to C Uganda and W Kenya; G6: as previous and to W Ethiopia and N Malawi); N: northern and western Africa (N5: W Africa to NE Congo; N6: as previous and to N Uganda, NW Kenya and W Ethiopia). Values. – $r^2 = 0.05$, vector scaling = 500%, total variance ('inertia') in the species data: 11.00%.

BIOGEOGRAPHY OF AFROTROPICAL FOREST ODONATE DIVERSITY

Although extinctions may have resulted from fluctuations in forest cover and forest types related to climatic change, climatic fluctuations must also have created opportunities for rapid evolution for some forest organisms. Climatic change will have resulted in repeated isolation and connection of populations of some species. Speculation on patterns of speciation related to forest history suggests that some groups [...] have had complicated histories and it can be difficult to describe evolutionary connections of modern taxa from their present distribution and morphological similarities alone. This is a field in which considerable progress will soon be made with the application of [...] DNA analyses.

These words by Hamilton (1992) neatly summarize the scenarios and research opportunities for Afrotropical forest biogeography. Although the greatest diversity of African Odonata is in forests (see Box 1, Fig. 5), the fauna is impoverished in comparison to tropical America and Asia. The small and isolated African highlands functioned poorly as forest refugia during drier periods, unlike the long mountain chains of South America and southern

Asia, while the proximity of many forests to the sea moderated aridity in tropical Asia. Thus climate-induced habitat shifts posed a greater threat to African forest biota, demanding a greater tolerance to change. Scenarios of the origin and diversification of African Odonata are still wholly speculative. Nonetheless several patterns are apparent that offer some clues to the history of today's diversity and an incentive for future investigation.

History of diversity: old and new Africans

Statements on the origin and age of the Afrotropical forest Odonata can only be made by comparing the continental and Madagascan faunas with each other and with tropical faunas elsewhere. Especially Madagascar can be considered as a 'time capsule' that provides an impression of Africa's ancient forest odonates, because it was separated from the mainland long ago and has harboured rainforest ever since. The best examples are endemic Afrotropical taxa conserved both here and in climatically relatively stable areas on the continent. Such probably 'old Africans' are *Nesolestes* (also found in the Cameroon highlands together with the closely related *Neurolestes*), *Metacnemis* (also in Cape region), phyllogomphine Gomphidae (*Isomma* on Madagascar, *Phyllogomphus* in equatorial Africa and *Ceratogomphus* in southern Africa) and libellulid genera like *Malgassophlebia* and *Neodythemis* (both also equatorial Africa). Notable is the impoverishment of 'ancestral' families, such as Megapodagrionidae (Fig. 7). Synlestidae are largely confined to South Africa (*Chlorolestes*, *Ecchlorolestes*), and Corduliidae (excluding macromiines and *Hemicordulia*) are represented only by *Idomacromia* and *Neophya* in equatorial Africa, *Libellulosoma* and *Nesocordulia* in Madagascar and *Syncordulia* in South Africa. The isolated presence of *Nubiolestes* and *Pentaphlebia* in the Cameroon highlands and *Coryphagrion* on the East Coast, suggest that the otherwise exclusively neotropical Perilestidae, rimanelline Amphipterygidae and Pseudostigmatidae were once more widespread in Africa (Figs 7, 8). Of mysterious relations are several monotypic genera now placed in Megapodagrionidae and Platycnemididae with small, probably relict ranges: *Amanipodagrion* (Usambara Mts), *Leptocnemis* (Seychelles), *Oreocnemis* (Mt Mulanje in Malawi), *Paracnemis* (Madagascar) and *Stenocnemis* (Cameroon highlands). One can only speculate if obligate rainforest dwelling families like Platystictidae ever inhabited Africa.

None of the 'old Africans' are nowadays dominant in the forests of continental Africa. The 'new Africans' are in families that are absent on Madagascar, or only represented by one adaptable species that probably colonised the island recently from the mainland. Examples are Calopterygidae (e.g. *Umma*), Chlorocyphidae (*Chlorocypha*), Protoneuridae (*Elattonaura*), lindeniiine Gomphidae (*Diastatomma*) and macromiine Corduliidae (*Phyllomacromia*). The genera *Platycnemis* and *Pseudagrion* are important elements in

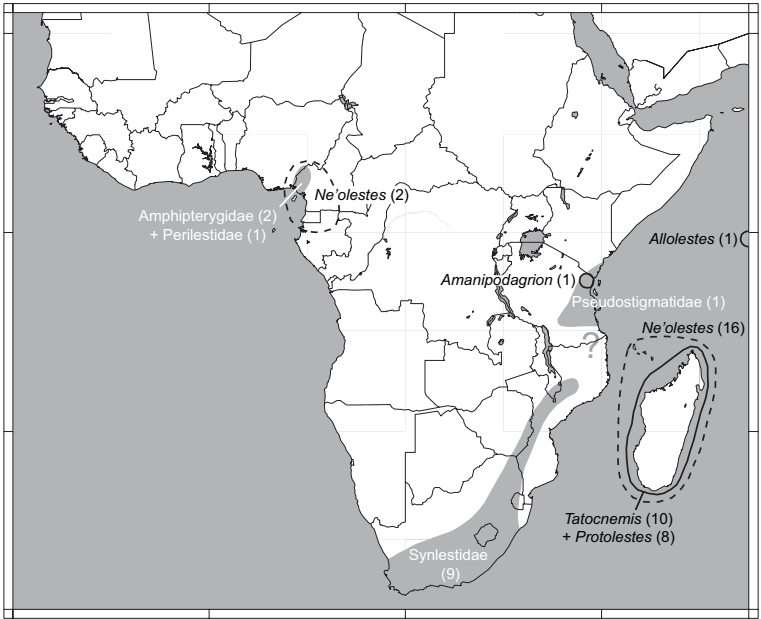


Fig. 7. Approximate distribution of relict damselfly families in tropical Africa, indicating probable centres of climatic stability. The number of species in each group/area is indicated. Genera classified in Megapodagrionidae are marked with a black line, other families with grey shading. *Nesolestes* and *Neurolestes* (= *Ne'olestes*; indicated with broken line) are combined because they are closely related.

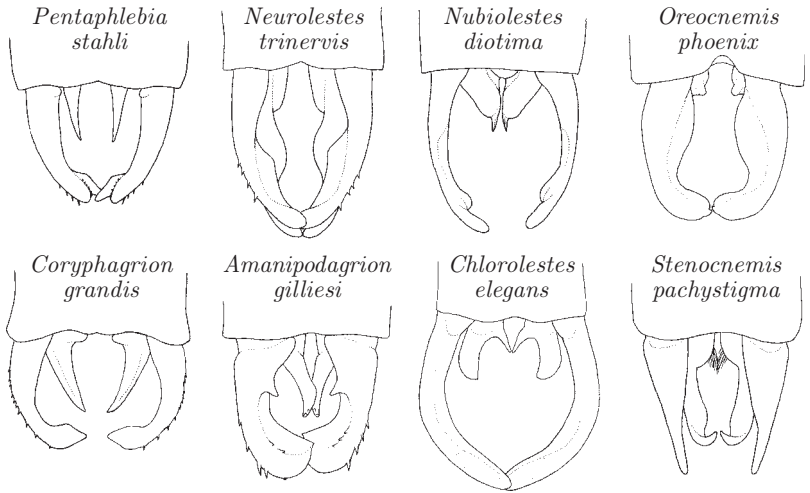


Fig. 8. Male appendages of eight relict Afrotropical damselflies in dorsal view. Classified in six different families (see text), all share the plesiomorphic fociate cerci.

both the forests of Madagascar and continental Africa, but each group is highly distinctive and does not appear closely related (Fig. 9). All mentioned continental groups are related to more diverse faunas in tropical Asia and are characterised by many relatively similar species. This and their absence on Madagascar suggest rapid radiations after a comparatively recent arrival from the east. A few of these arrivals were probably trans-oceanic. *Hemicordulia* and *Teinobasis* are dominant groups in (parts of) Indonesia, New Guinea and Australia, which hardly occur on the Asian mainland, but range across to eastern Africa through the Seychelles, Mascarenes and Madagascar (e.g. Clausnitzer 2003c; see also Fig. 9). A similar scenario may apply to the *bispina*-group of *Gynacantha* (Dijkstra 2005).

What is the age of these faunas? The oldest fossils of typical Anisoptera and Zygoptera date from around the Triassic-Jurassic boundary, 210 million years ago (Mya). Neotropic affinities may date back to the Cretaceous, before Africa and South America separated 100 Mya (Goldblatt 1993). Madagascar “apparently slid south along the east African coast for most of the Cretaceous

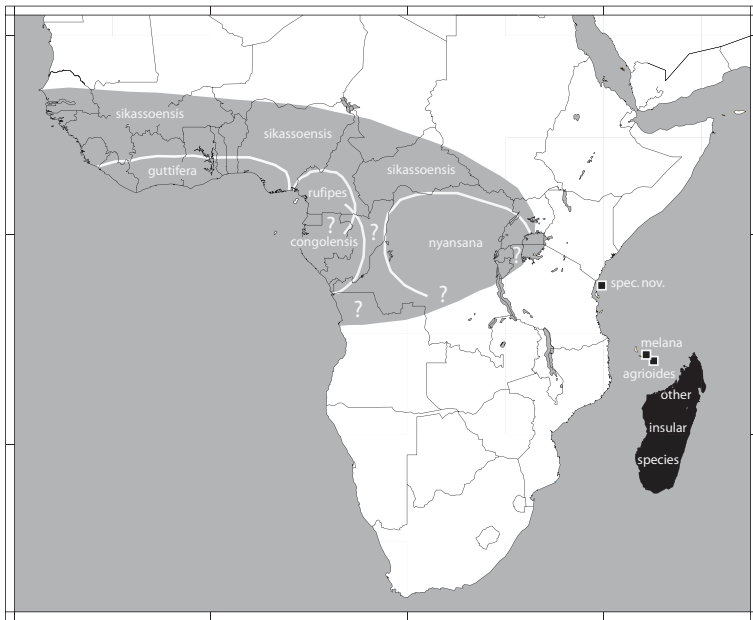


Fig. 9. Approximate distributions of Afrotropical *Platycnemis* species; insular (black) and continental (grey) groups. Especially the general southern limits and contact zones of continental species are unclear; range *P. sikassoensis* (at least partly) incorporates ranges of other continental species. The continental group is remarkably similar to the Oriental *Copera*, but the relationship with the insular fauna appears more distant. Trans-oceanic dispersal over hundreds of kilometres is the only plausible scenario for the presence of insular species on the Comores and Pemba. From: Dijkstra *et al.* (in press).

rather freely interchanging plant and animal taxa with the mainland at least until 90 Mya and perhaps intermittently thereafter” (Gentry 1993). The temperate faunas of Patagonia and Australia were still linked through Antarctica during the Paleocene and Eocene (65–35 Mya), but Africa probably separated much earlier. In conclusion, the ‘old Africans’ are probably of mesozoic age. The ‘new Africans’ must be largely cenozoic, expanding between the separation of Madagascar and the end of the trans-African rainforest belt and the tropical connection with Asia. The latter was probably in the Oligocene or Miocene, 25–5 Mya. The current fauna was probably largely shaped by strong climatic fluctuations of the Quaternary, roughly in the last two million years. Trans-oceanic colonisations probably also took place so recently.

In conclusion, although Odonata are an ancient group of insects, the Afrotropical fauna is relatively young with a ‘broad but shallow’ diversity, being rich in species but poor at higher taxonomic levels (especially families). Instability favours adaptable taxa, but eliminates those which adapt slowly. Extinctions may have created ecological ‘vacuums’ into which adaptable taxa radiated during the more favourable (i.e. hot and wet) periods that followed. This may explain notably speciose genera like *Chlorocypha*, *Pseudagrion*, *Elatoneura*, *Phyllomacromia*, *Orthetrum* and *Trithemis*, and the dominance of Coenagrionidae and Libellulidae. The two families are considered as the largest and evolutionary most advanced in Odonata, and are adapted better to temporary conditions than any other.

Geography of speciation

The image of forest species as ‘habitat hermits’ —poorly dispersing specialists that are confined by the limits of their ancestral habitat (see below)—implies that their distribution and evolution is governed by the geography and history of their forest home. Present-day diversity suggests that habitat change not only leads to extinctions, but also to adaptation and ultimately speciation. How did these species evolve and where? Did savanna species evolve from forest species, or vice versa?

How may a climatic cycle drive speciation? A rainfall decrease will result in the gradual contraction of wet habitat (e.g. forest streams) and the corresponding intensification of selection on adaptations for a drier habitat (e.g. faster larval development), especially at the periphery. Peripheral habitats become fragmented, with genetic isolation of dry-adapted populations and the possible rise of new species. While at the height of an arid period wet-adapted species are restricted to wet refugia, where they speciate in allopatry (see Fig. 11), dry-adapted species can expand. A rainfall increase will induce the expansion of wet habitat and fragmentation of dry habitat, and further speciation of the dry-adapted species may then take place. Moreover it may induce a ‘reverse scenario’, in which non-forest populations adapt to increas-

ingly wet circumstances, becoming isolated in open enclaves in a forested world. A succession of wet and dry periods may function as a ‘species pump’.

What sort of distributional patterns does this scenario predict? For instance, might broader or more structured gradients between forest and open habitats generate and conserve more species? That could explain the greater odonatological richness south of the rainforest belt than north of it. The wet, large, central and connected Congo Basin is an obvious focus for odonate diversity (Figs 5, 10). Ever-shifting rivers, swamps, forests, woodlands and savannas, created a mosaic of habitats in time and space. With its position in the heart of the continent, the basin has always been on a cross-roads, between the forests to the west and east in wet periods, and between the savannas to the north and south in drier times. Moreover, sensitive species could survive in forest refugia west and east of the basin and along its rivers. Kingdon (1989) postulated that the basin is an “evolutionary whirlpool” of species

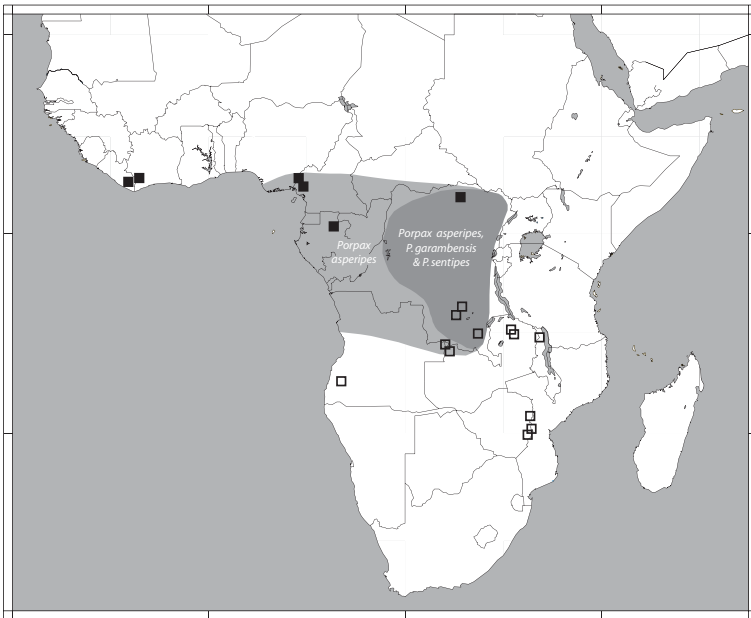


Fig. 10. Distribution of *Porpax* species. Two species are endemic to the Congo Basin, a third extends to the Lower Guinea. *P. bipunctus* (black squares) occurs in four disjunct populations, which coincide with important rainforest refugia. This is the clearest example of refugial disjunction found in Afrotropical Odonata so far. The pattern is supported by distinctive coloration in each region (suggesting allopatric speciation in progress) and the absence of intermittent records. Other *Porpax* species have been collected more widely and are geographically uniform. The species’ isolation may be linked to the ephemeral nature (probably flooded areas in stream beds) of its reproductive habitat, confining it to areas with perennial and predictable rainfall. *P. risi* (open squares) inhabits highland swamps, as is shown by its archipelago-like distribution. From: Dijkstra (2006).

evolution, 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.

Endemic species in the eastern African highlands with affinities to the Guineo-Congolian rainforests (*Umma declivium*, *Chlorocnemis abbotti*, *Nepogomphoides stuhlmanni*, *Micromacromia miraculosa*) are testimony of former links between these areas. While the ‘oscillating landscape’ has stranded these species on forest islands, the reverse may apply to open-land dragonflies ‘trapped’ in forest. Several widespread non-forest species are represented in the Congo Basin by larger and darker forms or sister species: the dark forms of *Gomphidia bredoi*, *G. quarrei* (Müller *et al.* 2005) and *Gynacantha manderica* (Dijkstra 2005), *Trithemis congolica* (sister species of *T. aconita*; see Box 3, Fig. 11) and *Zygonoides occidentis* (sister species of *Z. fraseri* and *Z. fuelleborni*). These populations were apparently sufficiently isolated from the periphery and interconnected with each other to develop, but their ecology remains unknown.

Many of the dominant African genera have species exclusively in either forest, savanna or intermediate woodland habitats. Box 3 presents two possible scenarios of how a (group of) non-forest species may have radiated out of an ancestral rainforest stream habitat, but perhaps most intriguing is the

Box 3. Hypotheses of speciation

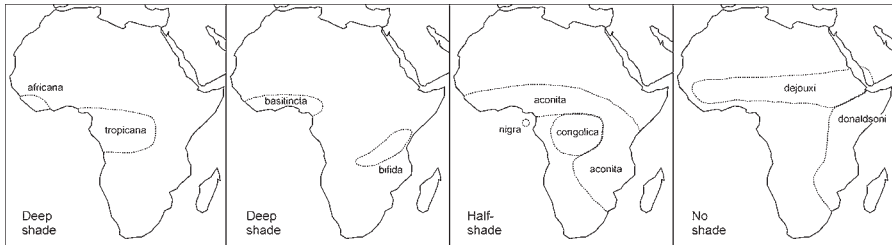


Fig. 11. Each map shows the distribution of a morphologically uniform subgroup of the *basitincta*-group of *Trithemis*, which appear as concentric layers focused on a forest core. All species inhabit running waters, but their shadiness differs between subgroups. Adaptation and range expansion during two or more phases of forest regression may have given rise to the two outer layers, while allopatric speciation in forest fragments could have split the pairs in the first two subgroups. Forest expansion may have separated the fourth pair and isolated *T. congolica* from *T. aconita* in open pockets in the Congo Basin. Endemic to Príncipe, *T. nigra* represents the dispersal of (something near) *T. aconita* to this volcanic island. Its smaller size, wing shape (less suitable for sustained flight) and bold yellow and black coloration (replacing pruinosity) are adaptations to its insular rainforest environment.

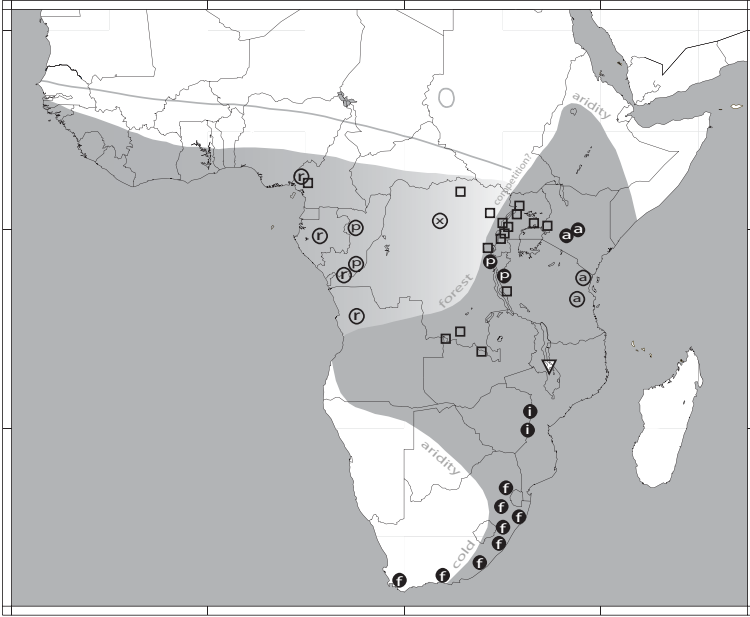


Fig. 12. Compared with their Oriental relatives, the over 40 species of Afrotropical Chlorocyphidae are uniform in their venation, morphology and the lack of coloured wings. This and their absence on Madagascar suggests that they diversified rapidly quite recently from Asian stock. While lowland forest streams appear to be the ancestral habitat of Chlorocyphidae, *Platycypha* species are more extreme: *P. fitzsimonsi* and *P. amboniensis* inhabit submontane streams, *P. caligata* exposed rivers and even lakeshores. The genus also possesses an especially elaborate set of colour signals, most notably their expanded legs and strong colour contrasts (Figs 13-14). Perhaps *Platycypha* developed from *Chlorocypha*-like stock that extended east when tropical forest



Fig. 13. *Platycypha* undescribed species, K.-D.B. Dijkstra.



Fig. 14. *Platycypha caligata*, K.-D.B. Dijkstra.

was continuous, but when forest shrunk became fragmented into several relict species in eastern African lowland forest. Some members spread south to the Cape, possibly becoming isolated in highland forests 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. The currently most abundant eastern African chlorocyphid, *P. caligata*, may be the epitome of that development, which spread more than any other in a 'vacuum' of potential habitat. It has expanded almost as far as its ecology allows, bounded by unsuitable habitat on all sides of its range. It barely overlaps with other chlorocyphids and these are confined to more sheltered habitats where they co-occur (e.g. *C. consueta*). The only 'escape' is the savanna corridor to the west, but perhaps there competition with *C. curta* is limiting. The relict population of *C. curta* in Sudan's Jebel Marra (Dumont 1988) shows that this species is equally adapted to non-forest habitats and that the 'front' against *P. caligata* was once broader. Being adapted to rather extreme conditions, *P. caligata* was the first and only chlorocyphid to colonise lakeshores. This scenario demonstrates a remarkable parallel with mankind: in geologically recent times, an 'enhanced' savanna species developed from a forest group and conquered an unprecedented habitat array. Interestingly, here too evolution is paired with a strong development of sexual characters.

Legend. – Open circles: relict species of lowland occurrence (A: *P. auripes*; P: *P. picta*; R: *P. rufitibia*; X: undescribed species); black circles: relict species of sub-montane occurrence (A: *P. amboniensis*; F: *P. fitzsimonsi*; P: *P. pinheyi*); squares: *P. lacustris*; dark shading: *P. caligata* (possible factors limiting its spread westwards indicated); triangle: morphologically deviant lacustrine population of *P. caligata*; paler shading: main range of other Chlorocyphidae (areas with 2 or more species), mostly *Chlorocypha*, outside that of *Platycypha*; grey line: probable extreme northern limit of *Chlorocypha* (including isolate of *C. curta* in W Sudan).

evolution of *Pseudagrion*, the largest odonate genus in Africa and one of the largest in the world. Some 140 species are known, two-thirds occur in Africa and Madagascar, the remainder ranges across southern Asia into Australia. The genus has occupied all freshwater habitats in tropical Africa, dominating damselfly communities from pools in the Kalahari to alpine streams on the Kilimanjaro. Diverse assemblages inhabit equatorial rainforests, while relict populations survive in the Saharan mountains, Morocco and the Levant. In Africa, the genus is subdivided on morphological and ecological grounds: the A- and B-group dominate on the continent, while Madagascar hosts a third group (Pinhey 1964). The dark-bodied A-group generally inhabits cooler habitats: mostly running waters, often shaded or montane. It includes many rainforest species with small ranges, confined to deeply shaded habitats. Some

species develop extensive pruinosity on the body, and occur in more open habitats. The reflective pruinosity may be an adaptation to increased insolation. The latter category includes species with restricted ranges at considerable altitude, but also *P. kersteni*, the most widespread and strongly pruinose species. The pale-bodied B-group generally inhabits rather hot habitats: running and standing waters, sunny and often exposed, generally at low altitudes. Possibly forest streams are the ancestral habitat of *Pseudagrion* and the A- and B-groups diversified separately in non-forest habitats, as these expanded during periods of forest regression. Judging from similarities with the Madagascar group, the presence of the A-group in tropical Africa is relatively ancient. Perhaps the pruinose species evolved in highlands and were pre-adapted to invade open lowland habitats, such as grassland streams. The B-group possibly arrived later (from Asia?) and radiated into warmer habitats left unoccupied by A-group members.

FOREST AND THE ECOLOGY OF SPECIES ASSEMBLAGES

Habitat selection is strongly dependent on structural characteristics, like shading and vegetation structure. [...] Numerous interrelated variables determine the characteristics of [river] habitats from the source to the mouth [...] and therefore a strong turnover of odonate species and assemblages is expected as one goes downstream. Similar change may also be expected as human disturbance increases. Deforestation and damming, for instance, will result in a more open character of running water sites. Associated changes may be a decrease of flow velocity and permanence of water, and an increase of silt load. This may result in a habitat shift and the accompanying change of the odonate assemblage. A dammed forest stream, for instance, could result in a sunny, slow-flowing stretch of water with species typical of a small river. A river that has been cleared of forest, resulting in increased erosion and an irregular discharge of water, may lead to a fauna of temporary pools.

This prediction by Dijkstra & Lempert (2003) for West African rainforest, characterizes how the relation of forest dragonflies and their habitat may be perceived. Many forest species appear to be stenotopic and sensitive to disturbance. As discussed, this may have a profound influence on their speciation and diversity. But why are some Odonata restricted to forest? The decrease of shading is an obvious change for odonate assemblages as forest is opened up, but other factors must also have an impact. Interactions between species, by predation and competition, further complicate assemblage composition (Suhling & Lepkojus 2001). All factors must interact, but only shadiness is discussed further here, as it seems to determine odonate assemblages most strongly.

Forest structure and species assemblages

Clausnitzer (2003a) demonstrated that as coastal forests in Kenya deteriorated, habitats were colonized by widespread and generalistic dragonflies. Although this resulted in a species increase per site, the localized specialists disappeared. This agrees with studies on amphibian communities in pristine and disturbed forests in Madagascar. Although the diversity and abundance were not significantly affected by selective logging, Vallan et al. (2004, p. 416) concluded that “species typical of pristine rainforests (specialists) are [...] replaced by species adapted to secondary habitats (often generalists).” To the human observer, the balance of shade and sunlight (degree of shadiness) is an obvious habitat characteristic, that coincides with a marked faunal break between streams and rivers (Dijkstra & Lempert 2003), and forested and deforested sites (Clausnitzer 2003a). The importance of this balance is illustrated by the ‘shade paradox’: in South Africa *Phaon iridipennis*, *Pseudagrion sjoestedti* and *Trithemis aconita* are characteristic of heavily shaded parts of the Sabie River, while they favour open sites in West Africa (Clark & Samways 1996, Dijkstra & Lempert 2003). This can be explained by the environmental context. In the highly exposed South African savanna these species can perhaps only cope under the most forest-like conditions, the reverse applies in the West African rainforest.

“The structure and appearance (the “architecture”) of the plants or plant communities rather than individual plant species are likely to serve as cues for biotope and habitat recognition” (Corbet 1999, p. 13). The degree of shadiness seems to be the principal cue for dragonflies to select a forest habitat, but the forest type (species composition) and “the age of the forest bordering running water sites is of little influence for the odonate assemblage there, as long as the required cover is present” (Dijkstra & Lempert 2003, p. 409). The importance of structure can be seen in the response of assemblages to the replacement of indigenous vegetation by exotic species. Kinvig & Samways (2000) concluded that for Odonata in South African *Pinus* groves “it does not matter whether the trees are exotic or indigenous, [...] but whether the architecture permits the right combination of sunlight and shade. This right combination is necessary for thermal balance and for encouraging low bushes under the tree canopy, which are necessary for perching and ovipositing.” This was highlighted by the response of two endemic *Chlorolestes* species to exotic wattles *Acacia mearnsii* overgrowing streams. The shade-seeking *C. fasciatus* is abundant at such sites, while the sun-loving *C. apricans* disappears. Observations in East Africa supplement the hypothesis that if general habitat structure remains unaltered, dragonflies tolerate a degree of exotic vegetation, but if these severely alter habitat architecture, this can have a detrimental effect on dragonfly populations (Box 4).

Box 4. Habitat structure change and specialized species.

Teinobasis alluaudi is known from the Seychelles, Madagascar, Zanzibar, Pemba and three localities in mainland Africa, where it inhabits seasonal swamp forest with a dense pinnatifolious understorey. The habitat on Zanzibar has been largely transformed into exotic plantations, mainly of Teak (*Tectona grandis*), but *T. alluaudi* was found in huge numbers in the dense fern thickets in the undergrowth (Clausnitzer 2003c).

The treehole-breeder *Hadrothemis camarensis* (Fig. 15) oviposits into introduced bamboo in Uganda (Corbet 1983). *Coryphagrion grandis* larvae were found in nearly every water-filled stump of exotic bamboo in the Amani Botanical Garden in Tanzania. The species inhabits pristine coastal forests of Kenya and Tanzania, but also coastal thickets and forests where all large overstorey trees have been logged: dense, shady vegetation with phytotelmata (even half coconut husks lying on the ground) are the most important habitat attributes for *C. grandis* (obs. & Clausnitzer 2004b).

Oreocnemis phoenix (Fig. 16) is endemic to the isolated Mulanje plateau in S Malawi, having been found both in forest and open habitats at 82% of the 51 sites investigated, with an average density of 5.8 individuals per 100 m stream. Of six sites surveyed in pine plantations only two males were present at a single 100 m stretch. Unlike natural streams, plantation streams sometimes contained algae and silt, or were clogged up with wood and pine needles (obs. K.-D.B. Dijkstra).



Fig. 15. *Hadrothemis camarensis*, D. Motshagen.



Fig. 16. *Oreocnemis phoenix*, K.-D.B. Dijkstra.

Insolation and competition as key factors for distribution

Two energy components in forest habitats are limited: insolation and nutrients. For dragonflies these components are interrelated, because they need a sufficient body temperature to fly and forage. Corbet (1999, p. 382) concluded that “foraging incurs a high opportunity cost, and its energy cost may constitute a large proportion of total somatic effort”. Reproductive be-

haviour costs additional energy. We see a major factor segregating forest and non-forest species in this conflict between energy demand and supply. Despite high ambient temperatures in the tropics, most forest dragonflies need direct sunlight to maintain a sufficiently high body temperature. Species with a shaded rendezvous on the forest floor frequently return to sunny clearings or the canopy to bask, and even leave the rendezvous when it becomes overcast (e.g. Lempert 1988; Miller 1993; Clausnitzer 1998; Clausnitzer & Dijkstra 2005b). In some rainforest species (e.g. Corduliidae, Gomphidae), only females appear to venture into the cool understorey to oviposit, suggesting that they mate and forage elsewhere, probably in the forest canopy.

The forest dragonfly *Notiothemis robertsi* holds small territories in a shade-sun mosaic near an oviposition site. These territories are defended against all intruders, including males of other species (Clausnitzer 1998). Intruding males never took over an occupied territory, but the chance for them to establish a territory later without energy-costly fights was high (Clausnitzer 1996, 1998). This strategy is suitable for dragonflies of small water bodies on the forest floor. Once the forest opens up, whether by human impact or the natural widening of water bodies, more aggressive and opportunistic non-forest species can invade the habitat, diminishing the chances for *N. robertsi* males to obtain and hold a territory long enough for successful reproduction. The defensive territoriality of rainforest dragonflies is considered to be an adaptation to save energy in the shady environment (Shelly 1982), but it becomes a disadvantage when an increase of sunlight allows intrusion of more competitive species. A long adult lifetime and/or a long-term territoriality has been observed in many rainforest dragonflies, e.g. in Polythoridae (Fraser & Herman 1993), Pseudostigmatidae (Fincke 1992; Clausnitzer 2004b), Protoneuridae (Lempert 1988) and 'tetrathemistine' Libellulidae (Clausnitzer & Lempert 1998).

We postulate that many forest dragonflies have developed a 'slow' lifestyle to cope with the low insolation and low nutrient levels of their environment, not investing in territorial clashes or fast mating success. This low-energy lifestyle is compensated by longevity, ensuring reproductive success in the long run, enabling a 'first come, best served' strategy: forest species can wait to become first, but in direct competition with the more aggressive non-forest species their chance to gain and maintain a territory is negligible. Competition may be the most important factor that keeps forest dragonflies inside the forest, while the low levels of nutrients and insolation inside the forest prevents the non-forest species from living their high-energy lifestyles there. Examples of microclimatic differences in tropical areas between forest, forest edge and non-forest are provided by Turton & Freiburger (1997) and, in relation to stream temperature, by Benstead & Pringle (2004). Interspecific competition is frequently asymmetrical, where one species is (almost) completely unaffected (Begon et al. 1996).

Of course the competition hypothesis is only applicable within a certain range of habitat parameters. Even without competition many open habitats will be unsuitable for forest dragonflies, but their fundamental niche is considered to be much larger than the realized niche.

The credibility of our hypothesis can be tested in areas where numbers of strong competitors are constrained, e.g. by elevation (Box 5). These may, however, be the ‘wrong’ examples. Highland species like most in Box 5 must have evolved under naturally fluctuating circumstances. This predicts a certain tolerance to ecological vicissitudes (drought, temperature), disturbance and probably competition. ‘Real’ forest species that evolved and remained within stable rainforest, like Madagascan *Nesolestes* or Cameroonian *Pentaplebia*, may respond to deforestation and competition much more strongly. A ‘reverse scenario’ in which one forest species pushes another into an open habitat would contradict our hypothesis. This may be the case with *Chlorocypha tenuis*, which occurs on rainforest streams at many sites in Uganda, but is replaced in that habitat in Bwindi Impenetrable Forest by the closely related *C. molindica* (hybrids have been found on two occasions). Here *C. tenuis* occurs on streams outside the forest, a habitat not occupied elsewhere (obs. K.-D.B. Dijkstra). Our hypothesis and observations also have implications for conservation. Locally reduced degrees of competition may leave species like Ethiopia’s endemics less vulnerable to forest destruction, but this may be only temporary as other species gradually invade the altered landscape.

Box 5. Habitat and competition

Chlorocnemis abbotti occurs at small forest streams in Tanzania and S Kenya, but was found on Mt Kasigau along a tiny stream in largely waterless thornbush. Almost no non-forest species are found in this part of S Kenya due to the unreliable presence of water (obs. V. Clausnitzer).

Pseudagrion bicoerulans is endemic to Kenya and adjacent Tanzania and Uganda. It inhabits forest streams, mainly between 2000 and 3000 m a.s.l. (Fig. 4), but also ventures into open moorlands higher up. Similar habitats at the low end of its elevational range are occupied by the more competitive *P. spernatum*. Below 2000 m *P. bicoerulans* is only found rarely, but always in dense forest, where *P. spernatum* is scarce. Competition might explain the observations, but maybe *P. bicoerulans* is just restricted to a certain low temperature regime found only in deep shade low down (obs. V. Clausnitzer). The Mulanje plateau (see Box 4) is at most 24 km wide, and was probably once completely covered by Afromontane forest. Frequent fires now maintain large areas of grassland and bracken. *Oreocnemis phoenix* was found at 82% of the 51 stream sites investigated, although only a quarter of all sites was

(partially) forested. Average densities at (partially) forested stream sites (8.9 individuals per 100 m, $n = 13$) were higher than at open sites (4.6, $n = 29$). Only five additional zygopteran species have been recorded on the plateau (only two commonly), but thirteen occur in the surrounding lowlands, including three families that are absent on the plateau (obs. & Dijkstra 2004).

The endemic species of the Ethiopian highlands occur in completely deforested habitats (*Pseudagrion kaffinum*, *Elattonneura pasquini* (Fig. 17)) or seem tolerant of forest disturbance (*Pseudagrion guichardi* (Fig. 18), *Notogomphus ruppeli*). Nonetheless the original vegetation of the highlands and the species' taxonomic affinities suggest they originally all inhabited forest. Densities of many ubiquitous Afrotropical species in the highlands appear comparatively low (Clausnitzer & Dijkstra 2005a).

Streams near the Sempaya hot springs in W Uganda are well shaded by rainforest, but were inhabited by *Platycypha caligata* and *Pseudagrion sublacteum*, rather than by typical forest species. Similar streams away from the springs were inhabited by the usual forest species. The two species are always found in largely exposed streams elsewhere. Possibly a higher water temperature allows them to displace the forest species (obs. K.-D.B. Dijkstra).



Fig. 17. *Elattonneura pasquini*, K.-D.B. Dijkstra.



Fig. 18. *Pseudagrion guichardi*, K.-D.B. Dijkstra.

RECOMMENDATIONS

Our African hypotheses suggest several directions of research that will shed light on the question why forests have such rich and special dragonfly faunas. We see three main components in which we can deepen our knowledge:

1. The ecosystem component. What are the ecological, behavioural and physiological aspects that determine survival inside or outside the forest environment? Are competition and insolation the main factors explaining the loss of forest species by deforestation, or are other factors equally detrimental,

such as the loss of prey (types) or the change of substrate in the larval habitat (due to erosion, loss or increase of detritivore organisms)? How do these factors interact?

2. The geographic component. Comparison of the composition and change-tolerance of odonate assemblages in areas with distinct climatological histories, may clarify how absolute is the relationship of the present dragonfly fauna with the forest. The assemblages in stable rainforest cores (refugia), such as in SW Cameroon and E Madagascar, may prove to be much more sensitive than those in areas where forest is relatively young.

3. The evolutionary component. Phylogenetic reconstructions for groups that have radiated on both sides of the 'sunlight-shade divide' (see Box 3) may clarify the effect and direction of landscape structure and change in speciation.

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